CHAPTER THREE

An Ecosystem Conceptual Model

Ecosystems are open systems, that is, things are constantly entering and leaving, even though the general appearance and basic functions may remain constant for long periods of time.

–E. P. Odum, *Ecology and Our Endangered Life-Support Systems,* 1989

The First Law of Ecology, "We can never do merely one thing," warns us that any human intervention in the order of things will likely have unforeseen consequences; and that many, perhaps most—perhaps all—will be contrary to our expectations and desires.

–Garrett Hardin, *Filters Against Folly,* 1985.

Estuaries such as Galveston Bay are complex and constantly changing ecosystems. To best manage human activities which affect the ecosystem, and to be able to predict the potential impact of specific proposed human actions, it is necessary to understand how the system is constructed and how it interacts with its environs. Knowledge of the structure of the ecosystem or the diverse plants and animals which build and inhabit its distinct habitats does not automatically lead to an understanding of ecosystem function. The function of an estuary–that is, how it acquires its materials and energy, processes its waste products, and interacts with adjacent waters and the surrounding landscape–is a much more subtle and challenging problem.

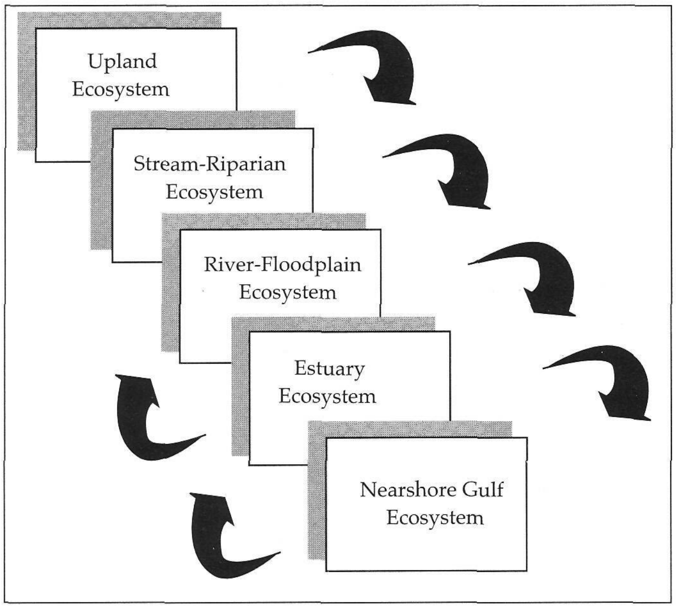
Conceptual models of complex systems can be useful management tools if they identify the critical components of the ecosystem and if they demonstrate important (or reveal hidden) linkages between these components. Over the past decade scientists have come to recognize a hierarchy of structure in ecosystems, with each successively higher level of organization operating at a slower speed than, and constraining activity within, the next lower level (O'Neill et al., 1986). The model described in this chapter is a set of habitat-based, problem-oriented, nested, hierarchical, box-and-arrow conceptual models (McFarlane, 1994).

OVERVIEW OF THE ECOSYSTEM

A human observer standing on the shore of Galveston Bay typically perceives two extreme ends of the ecological spectrum–individual organisms that inhabit the environment and the entire landscape that provides the overall setting. The individual organisms could be fish reeled in from the waters below, the crab scurrying across the beach, or the bird flying overhead. The landscape is the sum total of surrounding environs–the water, the beach, the nearby marsh and uplands. Unseen (and much more difficult to elucidate) are the intervening levels in the hierarchy, for example **populations**. However, it is in the intermediate levels where the bulk of ecological activities defining an ecosystem occur.

Populations are reproducing aggregations of individuals of a given species. Individuals have life histories–they are born in particular places, grow up in certain habitats, and reproduce to ensure continuity of the species. The aggregation of individuals composing a population may migrate to and from the bay, or perhaps go extinct. 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.

When populations of different plants and animals intermingle they compete for scarce resources, establish a food web as they eat one another, and thus exhibit **competition** and **predation** as community characteristics. When the non-living components of the environment are added to these interacting communities, an ecosystem is created. At this level of complexity, new functions like energy flow and the cycling of matter arise and can be mea-



Source: McFarlane, 1994

FIGURE 3.1. Diverse ecosystems from the upper watershed to the open sea all affect estuaries. Each link in the system is affected by all of the upstream links, but the effect of the nearshore Gulf of Mexico and estuary ecosystems only extends upstream to the lower reaches of the river-floodplain.

sured. From the perspective of bacteria and parasites, individual humans are wonderful ecosystems. On a larger scale, Galveston Bay can be conveniently considered as a single ecosystem.

Ecosystems are difficult to define because they have "fuzzy" edges, come in all sizes, and overlap and interact with one another. Galveston Bay is influenced significantly by two-way interchange with both the river-floodplain and nearshore Gulf of Mexico ecosystems. The nearshore gulf ecosystem is a major contributor of organisms, as larvae and juveniles of many marine species enter the estuary seeking food and sheltering habitat. A few marine or estuarine species even reach the lower reaches of the river-floodplain ecosystem. Thus the distribution of organisms highly varies in time and space. The aggregate of species seen on the inland shore of Galveston Island will differ somewhat from species frequenting the shoreline at Kemah or the Trinity River delta. Species commonly observed at a single site during the summer may be replaced with other species in winter.

The entire Galveston Bay watershed could be considered the next higher level of the hierarchy. The 26,000 sq mi of watershed dwarf the 600 sq mi of bay (which is matched by 580 sq mi of urban-industrial development within the city limits of Houston alone). Within this larger system, streams and rivers are important features affecting the bay. 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 to the stream-**riparian** ecosystems, often filtered by greenbelts of riparian corridor vegetation (National Research Council, 1992). Portions of stream-riparian ecosystems have flowing waters transparent enough to permit the growth of aquatic plants and algae and establish self-sustaining food webs. Headwater streams and larger streams with murky waters have food webs dependent on the input of plant products and animals from the surrounding upland ecosystems. In the downstream reaches, river-floodplain ecosystems contribute water, nutrients and sediments to floodplain forests, which return organic material of terrestrial origin to the river system.

The aquatic ecosystems of the watershed (FIGURE 3.1) provide both "goods" and "services" to society (Odum, 1989). Ecosystem "goods" include food, such as fresh water 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, and absorbing and detoxifying pollutants. In human terms, services also include providing sites for recreation, tourism, research and inspiration. When human activities disrupt the essential functions of an ecosystem, the **assimilative capacity** of the natural system is exceeded and the normal flow of "goods" and "services" provided by healthy ecosystems is impaired. Highly managed ecosystems, such as agro-ecosystems and urban-industrial ecosystems, are embedded within, and highly dependent upon, unmanaged natural ecosystems which ultimately provide human life-support.

The Estuary as an Ecosystem

An estuary is a semi-enclosed body of water with variable salinity intermediate between salt and fresh water. Estuaries are among the most naturally fertile waters in the world (Odum, 1989). Their high productivity results from their unique juxtaposition at the edge of the continent. Nutrients from four sources contribute to the productivity of estuaries: 1) fresh water flowing off the land; 2) tidal exchange with the ocean; 3) the atmosphere; and 4) the recycling of material from the estuarine bottom sediments. The most important nutrient is nitrogen–a component of all protein. Phosphorus, silica, and other compounds in lesser amounts also serve as nutrients to living things in the estuary.

The estuary functions as an efficient nutrient trap that is partly physical and partly biological. Three major life forms of photosynthesizing organisms play key roles in maintaining high productivity by exploiting nutrient sources: 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 habitats which create **nursery habitat** for most coastal shellfish and finfish. Physical processes contribute to the acquisition and transformation of nutrients by living things. For example, the importation of nutrients and exportation of waste products to and from the estuary are subsidized by gravitational energy in the form of streamflow and tidal exchange. As a result, the estuary becomes a productive seafood factory.

Events occurring in the estuary's watershed (even hundreds of miles away) greatly influence processes in the estuary itself. Some watershed processes are vital. Without fresh water inflow and the nutrients and sediments transported by rivers and streams, the estuary would not exist; it would be a lagoon, a salty extension of the gulf. But the rivers do not discriminate. Any material reaching a river–including pollutants–will be transported, perhaps undergoing chemical transformation enroute.

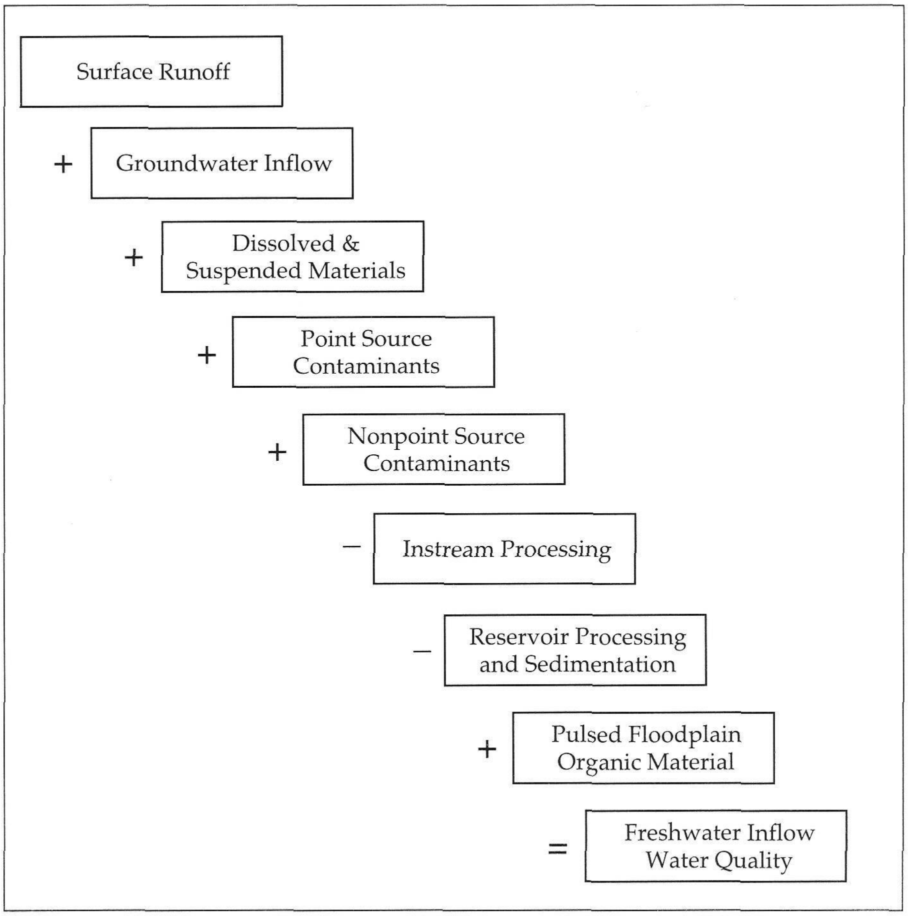
Water quality in the estuary is a key attribute affected by watershed events. FIGURE 3.2 illustrates the determinants of water quality in sequential order as they occur from watershed to estuary. Dissolved and suspended materials are incorporated wherever water moves, even by raindrops moving through the atmosphere. Precipitation results in surface runoff and groundwater inflow to streams. Point and nonpoint source discharges add various contaminants, particularly from urban-industrial areas and intensely cultivated sub-watersheds. Stream microorganisms and in-stream chemical events typically alter or reduce contaminant levels. Further processing and settling out occur in each reservoir upstream from the estuary. Flooding of the lower river floodplain periodically introduces pulses of organic material from the surrounding landscapes. Water quality may both degenerate and regenerate during passage through various river segments before entering the bay.

COMPONENTS OF THE ESTUARINE ECOSYSTEM

The bay itself shows marked variability. Even the apparently homogeneous open water is composed of subtly varying water masses. Recreational fishermen search for patches of clear "green water" where artificial lures can be seen by visual-feeding fishes, and "slicks", said to exude a "watermelon" odor associated with feeding predaceous fish (a phenomenon yet undescribed by scientists). These areas contrast with the turbid, river-influenced regions sought by commercial crabbers. Of course, bay habitats themselves are more readily distinguished. Patches of differing habitat are prominent along the shoreline and across the bottom of the estuary; corridors of forest or brush stretch as greenbelts along the shoreline and line small tidal streams. Edges, created where two habitats meet, are particularly significant in the estuary, sought by **planktonic** larvae and stalked by predators.

Habitats emerge as a compelling way to ecologically classify an estuary. The major habitats are quite distinctive and easily recognized (see FIGURE 2.4 on page 20). The largest habitat is the three-dimensional open-bay water itself, to which all other habitats are linked. Equally large in areal extent but virtually two-dimensional, is the underlying open-bay bottom. The bottom functions as a matrix upon which two different 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 emergent intertidal vegetation, the peripheral marshes, line the shore. Some low-sloping shore zones do not support emergent vegetation, remaining as intertidal mud flats. Patches of very soft, unconsolidated subtidal bottom are scattered within various shoreline wetlands to create the peripheral marsh embayments.

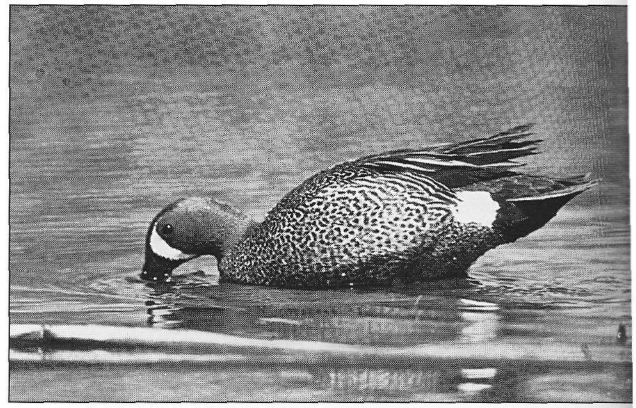
The conceptual model presented in this chapter is based upon the varying relationships of bay habitats to the surrounding upstream and marine systems, and to one another. Each habitat is connected (directly or indirectly) to the upstream fresh water riverine-floodplain ecosystem and downstream to the marine waters of the nearshore-gulf ecosystem, and via migratory birds, to the interior of the continent. Seven key habitats are singled out for the sake of the model (FIGURES 3.3–3.9) The structure and connectedness



Source: McFarlane, 1994

FIGURE 3.2. *The quality of fresh water feeding an estuary is greatly influenced by events in the watershed. Human and natural influences on runoff reaching streams–and alterations of the streams themselves–help shape water chemistry and physical processes in the downstream bay.*

of an eighth habitat type, the peripheral marsh **embayments**, are so poorly known that a model would be conjectural at this time. For each habitat, the living components have been aggregated into functional groups based upon their distribution within the habitat and their primary feeding or energy/nutrient gathering technique. These functional groups have been arranged to reflect the general flow of nutrients and energy through the food web, although they do not represent schematics of energy flow or nutrient cycling in the strictest sense. In some instances unique subsystems of the habitat emerge from the models and have been identified.

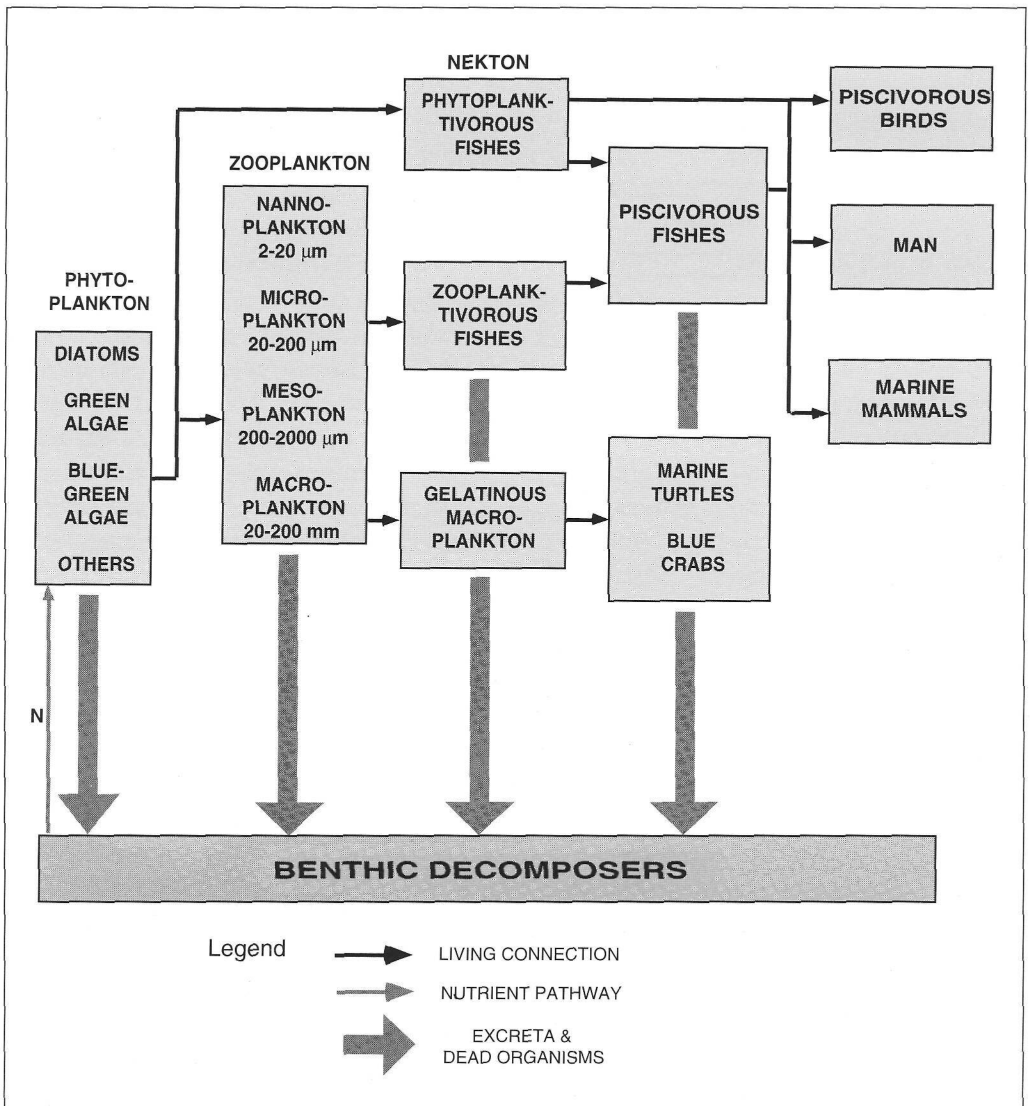


Source: Frank S. Ship

The bay can be clasified by its habitats, areas that sustain the needs of particular living species. This blue-winged teal utilizes shallow, fresher marsh areas in the upper bay system.

Open-Bay Water

The open-bay water is the largest and most conspicuous habitat of the ecosystem (FIGURE 3.3). It has the greatest areal extent, 354,000 ac, and is three-dimensional, with an average depth of seven feet. 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 the habitats considered, and is essentially featureless except for an invisible horizontal and vertical salinity gradient, and at times, gradients of temperature and dissolved oxygen.



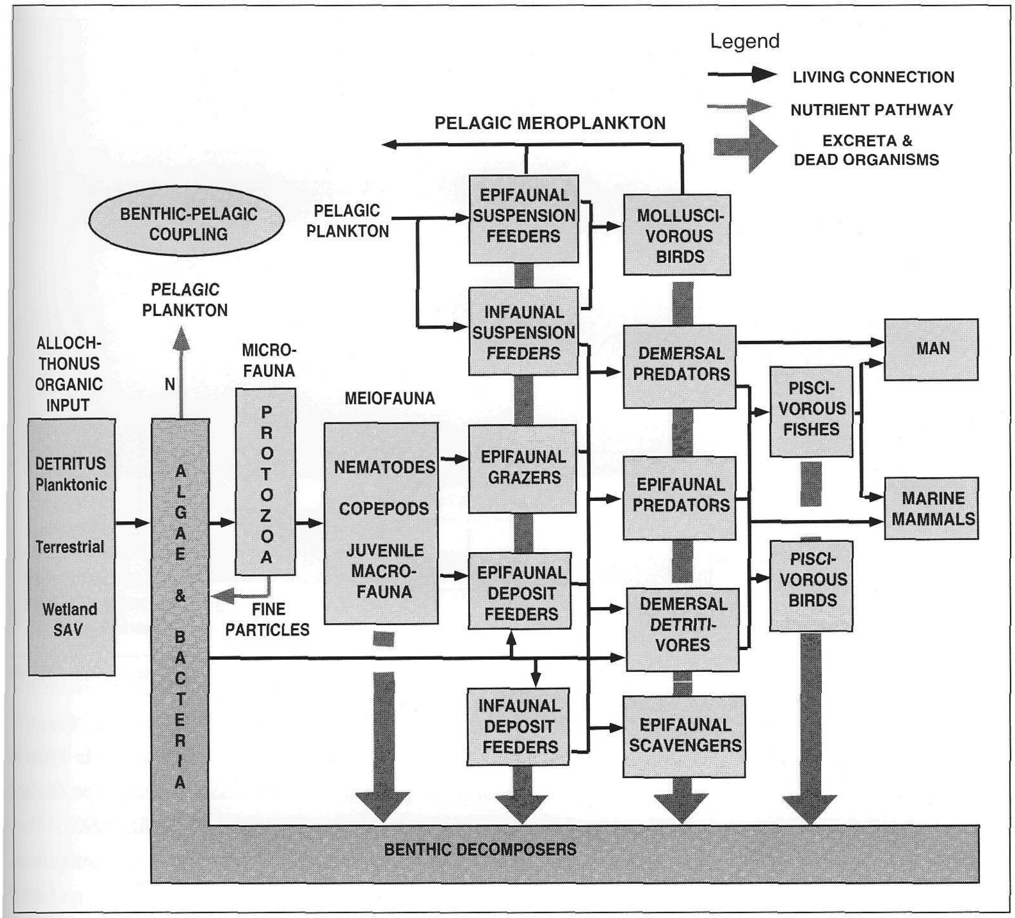
Source: McFarlane, 1994

***FIGURE 3.3.** Schematic model of open bay water habitat in Galveston Bay.*

The **primary producers** of the open-bay water are composed of various groups of phytoplankton which capture the physical energy of sunlight and package and store this energy in organic molecules constructed from carbon dioxide gas (Buskey and Schmidt, in Green et al., 1992). The **primary consumers** which feed upon these phytoplankton are the numerous and diverse **zooplankton** and phytoplanktivorous fishes. The **secondary consumers** are principally **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** inhabiting the open-bay bottom.

Open-Bay Bottom

The open-bay bottom (FIGURE 3.4) is the second largest habitat of the ecosystem, being equivalent to the open-bay water habitat minus those areas of the bay bottom covered with oyster reef or seagrass meadow. This habitat is essentially two-dimensional; while its length and breadth are measured



Source: McFarlane, 1994

FIGURE 3.4. Schematic model of open bay bottom habitat in Galveston Bay.

in miles, its depth is measured in inches. For the most part, the surface seems featureless except for sculpted waveforms, trawl marks, and evidence of burrowing animals. To a burrowing benthic organism, however the features of this benthic environment can be patchy, caused by the specific distribution of sediments of different particle size and the clumped distribution of life forms themselves.

The food web of the bottom habitat is based upon biological decomposition of **detritus**. Except for shallow shoreline areas where light penetrates the turbid water to reach the bottom, photosynthetic algae and primary productivity are limited or nonexistent. Organic matter reaches this zone in the form of "planktonic rain" as dead organisms or egested material sink to the bottom, or 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 (Day et al., 1989).

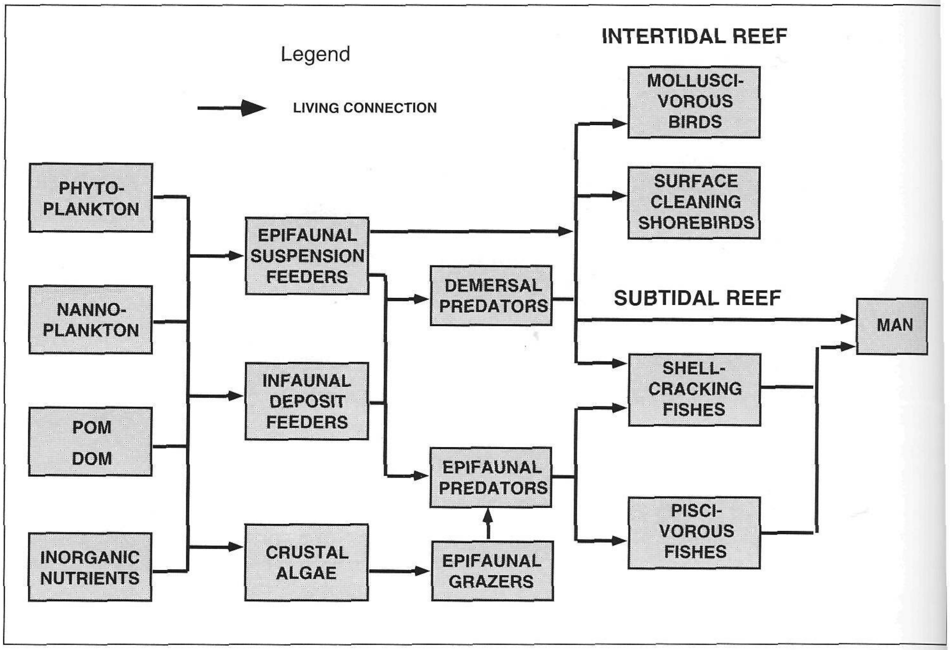
The most striking feature of the benthic food web is the key role of fungi, bacteria, and **protozoans** which comprise the benthic decomposer organisms at both the beginning and the end of the food chains. Vascular plant material has limited usefulness to most estuarine organisms in its raw state. It must first undergo "conditioning" or partial digestion by certain types of the fungi and bacteria. Few animals manufacture the digestive enzymes necessary to break down cellulose, the structural component of higher plants. 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 penetrate 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 this manner organic molecules (originally bound in plant tissue) become bundled into bite-sized packages; first as fungi and bacteria, then as larger protozoans. The protein content of the food "packages" also increases with each successive step, creating higher quality food.

Dependent upon the microfauna for food is a 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 **macrobenthos** 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 to macrobenthos (> 2/100ths of an inch) they also begin to subdivide the habitat into two components (Harper, in Green et al, 1992; LaSalle et al., 1991; Ray et al., 1993). One diverse assemblage of organisms, the **epifauna**, 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 **infauna**.

Epifaunal and infaunal organisms overlap in feeding strategies. Some feed by straining suspended particles from the water column (the **suspension feeders**, e.g. most **bivalve** mollusks). Others feed by ingesting sediment and extracting nutrients in the digestive tract (these are known as **deposit feeders** 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.

The open-bay bottom habitat 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. At the larger end of the scale, numerous fishes (e.g. croakers, spot, mullet and drum) and shrimp forage on benthic organisms. These are considered as **demersal** predators and **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.



Source: McFarlane, 1994

FIGURE 3.5. Schematic model of oyster reef habitat in Galveston Bay.

Oyster Reef

Clusters of oyster shell, live oysters, and other **commensal** organisms form a distinct oyster reef habitat (FIGURE 3.5). Oyster reefs tend to form wherever a hard bottom and sufficient current exist to transport planktonic food to the filter-feeding oysters and carry away sediment, feces, and **pseudofeces**. The reefs form in the open bay, along the periphery of marshes, and near passes and cuts, and can be either subtidal or intertidal (Powell, 1993). They are particularly abundant along the side slopes of navigation channels where tidal exchange currents are dependable. The reef itself is three-dimensional to the extent that the shells cemented together create an irregular surface that establishes a myriad of microhabitats for smaller species.

The oyster reef community is very diverse. While oysters contribute the dominant **biomass**, other bivalve mollusks, gastropods, barnacles, crabs, amphipods, **isopods**, and **polychaete** worms are normally abundant. In West Bay, for example, oyster reef communities were shown to be comprised of 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. **Nanoplankton** 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;

Source: Texas Parks and Wildlife Department

Oysters, an economically important seafood species in Galveston Bay, create reef habitat utlilized by many other species. Encrusting organisms such as ribbed mussels, bryozoans, and barnacles take advantage of the hard substrate created by the oysters as they secrete calcium shell. These species in turn attract predators like oyster drills (a snail) and fish species adopted to crush shellfish with specialized teeth as they forage.

Source: Galveston Bay National Estuary Program

Underwater seagrass meadows, as shown here in Christmas Bay, support a diverse and productive community, including such organisms as pipefish and seahorses, as well as recreational species such as spotted seatrout. Of the 2,500 acres of seagrass habitat present during the 1950s, only about 700 acres remain today.

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, supporting a small grazing food chain.

Secondary consumers of the reef include predators, parasites and pathogens, some of 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 three-dimensional microhabitat provided by the aggregated oyster shells.

Oysters have a valuable ecological role as filter-feeders in the estuary. The volume of water filtered per hour is about 1500 times the volume of their body (but see Powell, et al., in press). A large, healthy oyster population is able to filter large volumes of bay water, and may therefore influence conditions such as water clarity bay-wide. At the same time, their propensity to **bioaccumulate** some pollutants, combined with their lack of mobility, make them important indicator organisms for determining the health of the estuary.

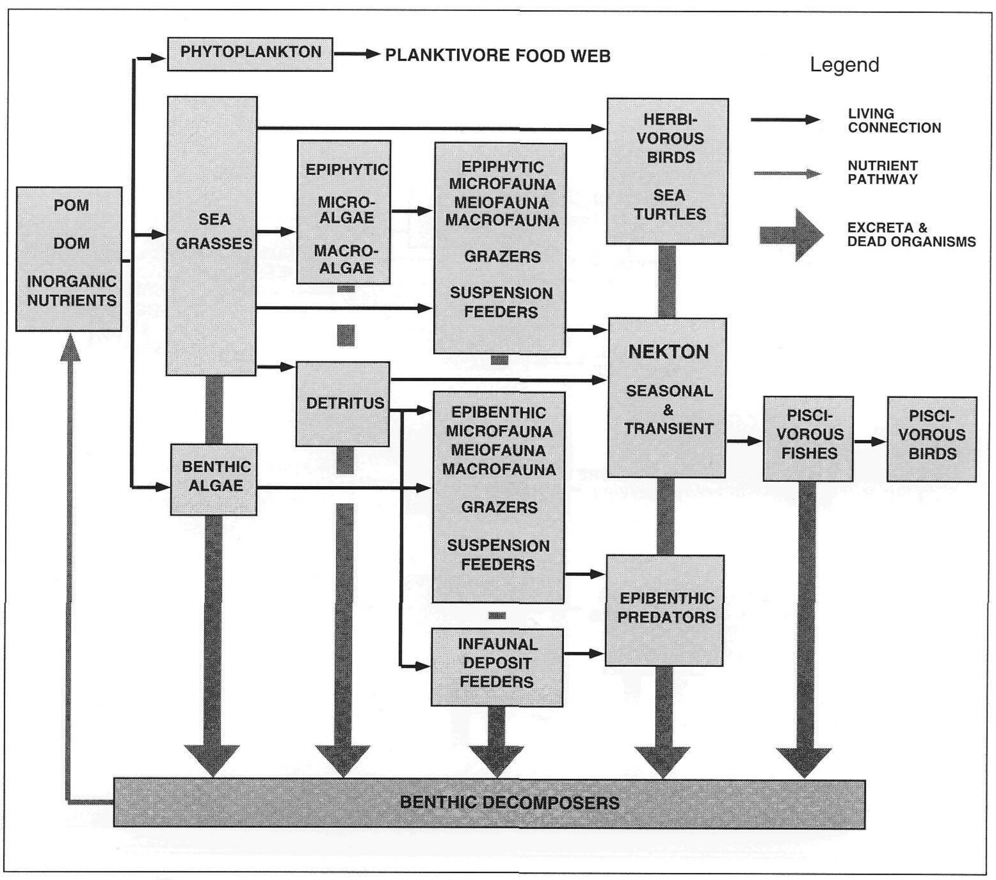
Seagrass Meadow

Patches of **submerged aquatic vegetation** (SAV), composed of fresh water and marine plants and their attached **epiphytic** algae, form the three-dimensional seagrass meadow habitat in soft sediments along the shorelines (FIGURE 3.6). Only 700 ac of this habitat remain in Galveston Bay, half within Christmas Bay alone (White et al., 1993; Pulich and White, 1989; Pulich et al., 1991). This habitat provides food resources and protective cover for a number of associated species and contributes substantial quantities of detritus to the food web. The fauna associated with these patches of SAV is quite diverse (e.g. 20 fish and 15 crustacean species; Zimmerman et al., 1989; Czapla, 1991).

Marsh

Approximately 61 percent (142 mi) of the Galveston Bay shoreline is vegetated by intertidal emergent plant communities (Paine and Morton, 1991), totaling 108,200 ac (White et al., 1993). These marshes (FIGURE 3.7) are subjected to periodic subsidies of tidal energy (highly modified by winds) as they are inundated by the ebb and flood of tides once or twice each day. Flow from the adjacent upland watershed is unidirectional, but subject to extreme pulses corresponding to rainfall episodes. Flow onto and off the marsh from both the watershed and the tides determines the nature of flow through the interstitial pore space of the marsh sediment (Wiegert and Freeman, 1990).

Intertidal marshes are structurally resilient. Where they have

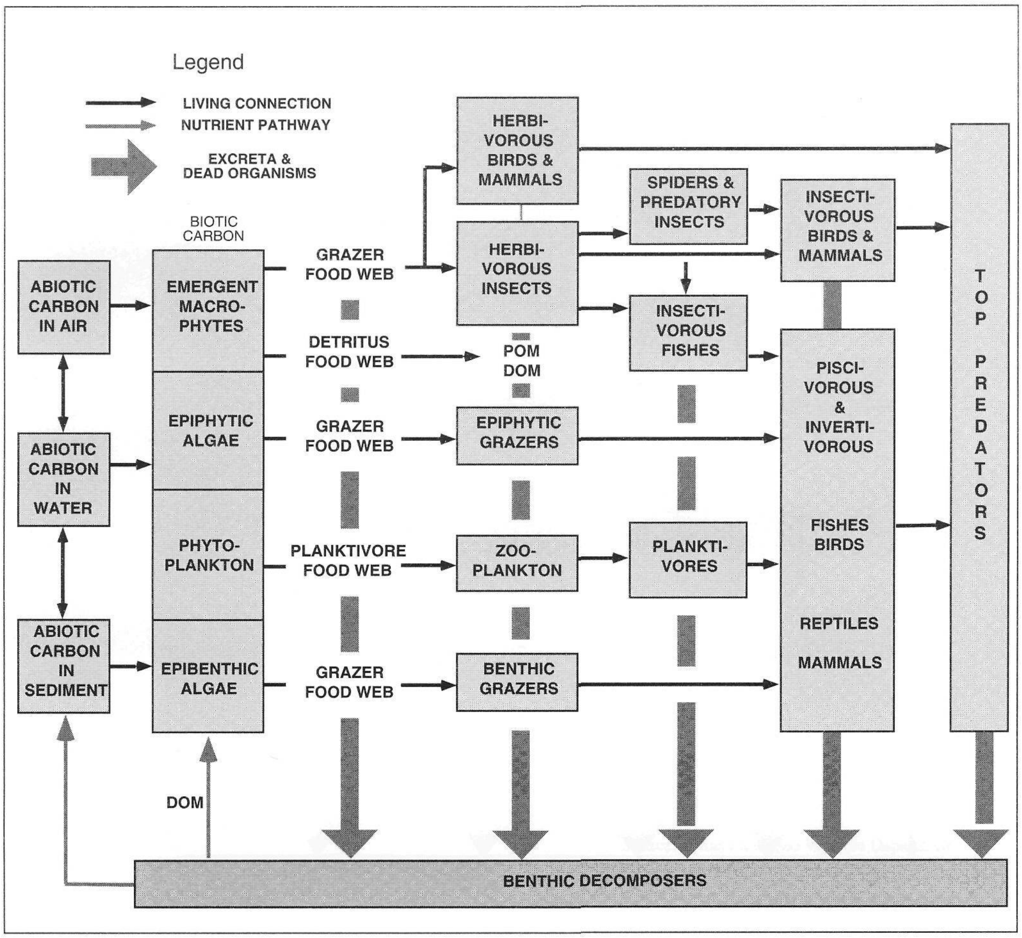


Source: McFarlane, 1994

FIGURE 3.6. *Schematic model of seagrass meadow habitat in Galveston Bay.*

Source: Galveston Bay National Estuary Program

Intertidal salt marshes dominated by smooth cordgrass (Spartina alterniflora) *form productive nursery areas for many invertebrate and fish species. More than 90 percent of the commercial and recreational harvest from the Gulf of Mexico is composed of species dependent on wetlands like this for some part of their life cycle.*



Source: McFarlane, 1994

FIGURE 3.7. *Schematic model of intertidal marsh habitat in Galveston Bay.*

not been disturbed by subsidence, construction, transportation, or energy-extraction activities, marshes appear little 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. The grasses evolved in high-salinity marshes are particularly tough, being mineralized and therefore resistant to herbivory. Unlike the continental grass, desert or forest ecosystems, the extinction of large herbivores did not alter the vegetational composition and productivity of intertidal marshes. In addition, the osmotically-stressed intertidal system is not an easy target for the invasion of exotic plants and animals.

Marshes, however, can be converted by extensive and expensive modification to uplands, and 35,600 ac of marshes surrounding Galveston Bay have been so converted since the 1950s (White et al., 1993; see Chapter Seven). Fresh marshes appear to be the most vulnerable, being composed of species with softer tissue, and sometimes occurring in smaller patches. Only in fresh water tidal lands have introduced species, such as water hyacinth, nutria, and grass carp caused physical obstruction and destruction. Thus the less-modified brackish and saltwater marshes represent a relict of the most nearly pristine wetland types, surrounded by greatly modified ecosystems (Wiegert and Freeman, 1990).

Marsh function is influenced by three distinct environmental conditions, with which each plant must cope. Their culms and leaves are continually exposed to direct sunlight, neither filtered nor attenuated, the basal stem is periodically bathed in water, while their roots are anchored in **anaerobic** sediments (see the left portion of FIGURE 3.7). From all three layers, emergent plants are able to extract or interchange **abiotic** carbon; in addition the plants promote the production of biotic carbon in four different compartments shown in the model.

As photosynthesizers, the emergent **macrophytes** produce carbon molecules that support a grazing, herbivorous, terrestrial food chain. Typically, only about ten percent of this primary production is incorporated into the grazing food chain. The remainder is diverted to the estuarine detrital food web. The enormous productivity of marshes and the significance of their detrital pathways to the estuary at large 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 known (Wiegert and Freeman, 1990).

One of the most significant ecological roles of tidal wetlands is their function as habitat for key estuarine species, particularly for those requiring food and cover as juveniles. The closely ranked stems of the emergent plants create an environment that supports epiphytic algae and shelters phytoplankton and **epibenthic** algal assemblages (Zimmerman, in Green et al., 1992). These, in turn, support additional grazer and **planktivore** food webs which include 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.

Intertidal Mud Flat

The intertidal mud flat habitat is an exceptionally open ecosystem (FIGURE 3.8) 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" only by **microalgae**, **macroalgae** and phytoplankton. Import 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.

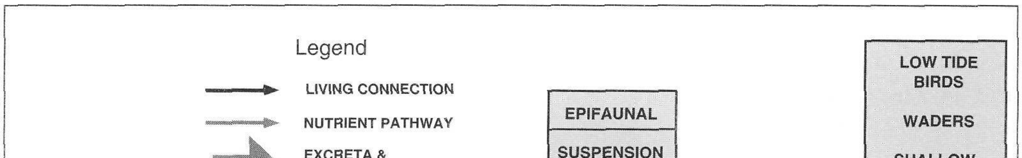
On mud flats, members of the higher trophic levels appear as transients with the tides. At high tide, planktivorous, detritivorous, and demersal fishes move onto the flats to feed, followed by **piscivorous** predators, both birds and fishes. At low tide, gleaning and probing shorebirds feed on and in the exposed surface while waders seek prey stranded in tidal pools. Overall, nutrients, organic particles and living organisms readily move in and out of the habitat.

Bacteria and fungi play an important ecological role in mineralization of 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 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 mud flats serve as a nutrient sink. Nutrients and other compounds adsorb to sediment particles. In this shallow zone, the sediments are subject to **resuspension** by wave action and **bioturbation** from the many infaunal animals. Biodepositon by suspension feeders in the form of feces and pseudofeces adds to the nutrient bank. When nutrient concentrations in the water column decline, the sediments give up their adsorbed nutrients to establish chemical equilibrium.

Secondary and Tertiary "Lakes"

A conspicuous feature of bay topography is a number of shallow, soft-bottomed, "lakes" (actually small embayments) which



Source: McFarlane, 1994

FIGURE 3.8. Schematic model of intertidal mud flat habitat in Galveston Bay.

Source: Galveston Bay National Estuary Program

Mudflats offer rich foraging grounds for many species of birds. Here, laughing gulls loaf at low tide (above) and a stilt sandpiper forages for such sediment-dwelling organisms as polycheate worms, clams, and burrowing crabs (right).

Source: Frank S. Shipley

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 and Clear Lake on Galveston Bay; Robinson Lake on East Bay; and Cotton Lake, Lost Lake, and Old River in the Trinity River delta. Their deep, unconsolidated mud bottoms, (which poorly support the weight of humans) have inhibited scientific study of the systems. As a result, our incomplete knowledge of these systems precludes creation of a schematic model. Each of these water bodies is directly connected to the bay system, edged with emergent marsh habitat, and is subject to highly variable salinity depending upon recent precipitation and location in the estuary. High **turbidity**, perhaps wind-driven, hinders the growth of submerged aquatic vegetation.

These marsh embayments appear to be highly productive nursery areas (Conte, 1971; 1972a; 1972b). Alligator Lake and Oyster Lake harbor brown and white **penaeid shrimp**, grass shrimp, **sergistid shrimp**, and five species of mysid shrimp. Brown shrimp, grass shrimp, blue crabs, pinfish and bay anchovies have been collected in Hall's Lake (Minello et al., 1991). 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, 1994). Shallow, turbid, soft-bottomed lakes and blind bayous of interior marshes of the Trinity River delta are the target habitats of many migratory marine animals seeking food and protective cover. Atlantic croaker, gulf menhaden, sand seatrout, bay anchovy, hogchoker, pinfish, ladyfish, bay whiff, southern flounder, brown shrimp, and white shrimp are particularly abundant in these habitats.

With a high ratio of surrounding marsh to open water area, these marsh embayments appear ideal to support a detrital-based food web. The benthos of the exceptionally soft, nearly flocculant, bottom sediment is unknown. Microbial decomposers undoubtedly fill a critical **ecological niche** in this benthic habitat. In the water, Phytoplankton and zooplankton are also yet to be described, but the abundance and **diversity** of secondary consumers attests to the efficacy and productivity of the primary consumers and green plant producers. The vertical structure of the surrounding marshes provides protective cover for the smallest species and life stages while the shallowness of these systems may limit large predators.

INTERCONNECTEDNESS OF THE ECOSYSTEM

Food webs in Galveston Bay are essentially of two types (Armstrong, 1987). One web is based on production of live plant tissue–carbon produced by photosynthetic plankton and which can be grazed upon by consumers as described for the open-bay water habitat. This web is relatively simple and involves few species. The second web is based on detritus produced both within and out-

Source: Texas Parks and Wildlife Department

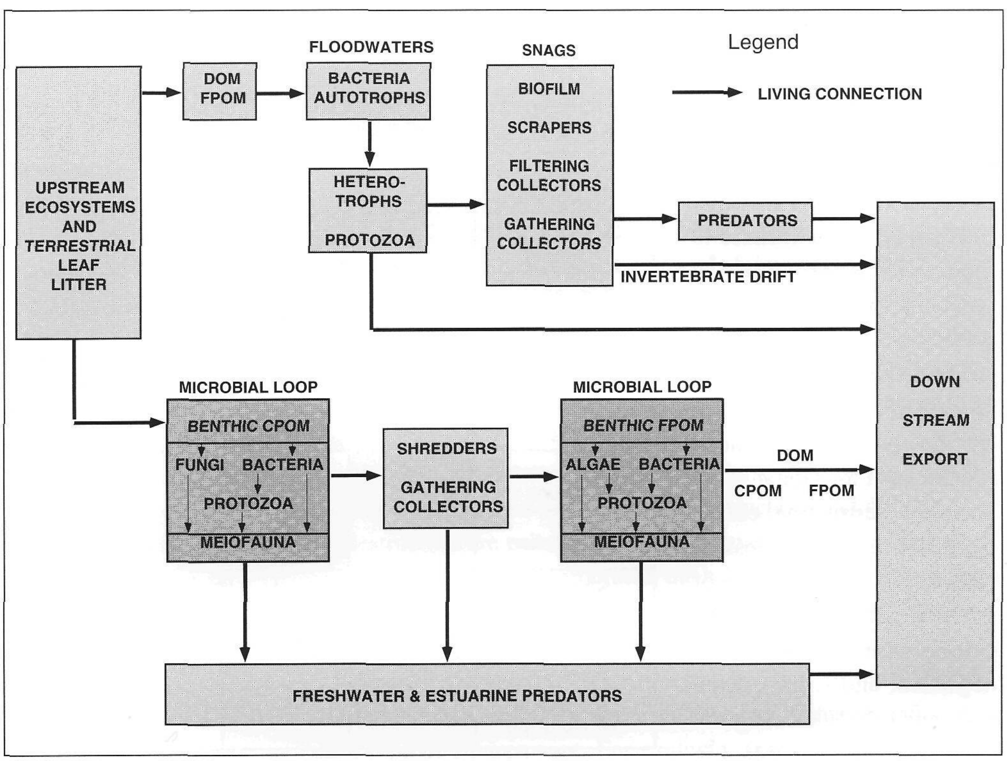
Tidal ponds ranging in size from small marsh openings to secondary and tertiary "lakes" covering many acres form an important but poorly understood habitat type within the bay. The salt marsh ponds shown occur along the north shore of West Bay.

side the bay system. From outside the bay itself, detritus is received from the watershed (transported to the bay with river and stream inflow) and from the fringing marshes (transported tidally). Within the bay, detritus arises from seagrass meadows and as planktonic "rain" as outlined above. Detritus-based food chains are more complex and poorly understood, with more links between consumers, and major roles for microbial populations.

Riverine/Floodplain Dynamics

Streams, rivers, and their floodplains are dynamic systems of great importance to estuarine trophic function (FIGURE 3.9). Stream and rivers are longitudinally linked systems: processes which take place upstream have impacts on downstream components. The in-stream biological community changes in a predictable manner in progressing downstream, responding to changes in channel geomorphology and available resources. Much of the degradation of organic matter occurs prior to reaching the estuary in moderate sized channels, and lateral linkages to the riparian zone (the source of much organic matter) are as vital as the longitudinal links of the river continuum itself (National Research Council, 1992). Floodplains play a critical role as sediment and nutrient filters, as contributors of pulses of nutrients and organic matter during floods, and as habitat for fishes at certain life stages (Wharton et al., 1982).

In the riverine/floodplain system (as in the bay itself), microbes are critical components in the sequential decomposition of leaf litter to coarse, then fine, particulate organic matter. Nutrient export from riverine floodplains is pulsed–leaves from terrestrial plants and trees are seasonally dropped to the forest floor where leaching and disintegrative processing begins. Periodic overbank flooding and drainage of the floodplain redistributes 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 (Meyer, 1990). One process is fueled by dissolved and particulate detritus that is consumed by bacteria, which then becomes food for protozoa and other organisms. Another process begins when shredding insect larvae in the unstable stream and river sediments participate in reducing detrital particle size and har-



Source: McFarlane, 1994

FIGURE 3.9. *Schematic model of riverine/floodplain habitat in Galveston Bay.*

vesting attached microbes. Grazers and filtering or gathering collectors inhabit stable substrates, such as snags and logs. Dissolved organic matter (DOM), coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), and invertebrate drift organisms are exported to downstream habitats, including the estuary.

Our current understanding indicates that fresh water inflows transport 96 percent of the imported carbon and nitrogen, and 95 percent of the phosphorus, with the remainder contributed by peripheral marshes (Armstrong, 1982; Borey et al., 1983). Yet a large proportion of the annual **carbon flux** within the bay (that is carbon acquisition and transformation) is believed to come from phytoplankton within the estuary (Armstrong, 1987). The relative importance of plankton versus detritus as the base of secondary productivity in the bay deserves further study. Does the abundant seafood production in Galveston Bay ultimately depend more upon green plant tissue, or upon dead organic matter? Certainly detritivores are both prominent and dominant components of the ecosystem.

The Influence of Human Activities

Upon this complex and dynamic mosaic of natural functions are imposed the sometimes-disruptive activities of human society. Growth of the human population and increasing per capita use of resources mean human influences on the ecosystem are increasing, rather than decreasing. If not addressed, these activities will increasingly threaten the life-support system of the estuary. Agriculture, forestry, fisheries, water diversion, mineral extraction, fuel consumption, industrialization, urbanization and recreation, are intended to improve the quality of life by providing food and fiber production, shelter, water supply, consumer goods, and economic growth. These activities can also produce unintended results, such as habitat alteration and destruction, **eutrophication**, pollution, loss of biodiversity and extinction of species. Each of the seven estuary habitat types can be degraded, and some can be lost entirely. Ecological knowledge can be applied in the management of these activities to reduce the incidence of negative, unintended results.

A summary of human activities which potentially degrade or destroy habitats is provided in FIGURE 3.10. The vulnerability of the habitats varies. Open-bay waters, open-bay bottom, and intertidal mud flats are the least susceptible to degradation. The open-bay water habitat can be altered or degraded, but not destroyed, by changes in its physical gradients (depth, temperature, transparency, currents) or chemical constituents (salinity, dissolved oxygen, contaminants). Floating oil or chemicals can affect organisms inhabiting the **surface microlayer**. Likewise, the open-bay bottom habitat is very resilient. It can be temporarily destroyed by burial under dredged material or excess sedimentation, and degraded by brine discharge or **anoxia**. Subsidence can convert the intertidal mud flat habitat to subtidal bottom, shoreline development can displace the habitat, disposal of dredged material can bury it, and oil or chemical spills can coat the surface with toxic or smothering substances.

Three habitats are created and maintained by living organisms, and are therefore more vulnerable to degradation or destruction. Oyster reefs originate when oyster **spat** settle upon hard bottoms but, once the initial layer of oysters covers the bottom, subsequent reef growth occurs on existing oyster shell. This provides considerable resiliency to reefs because all of the oysters may be

	Open-Bay Water	Open-Bay Bottom	Oyster Reef	Seagrass Meadow	Marsh	Marsh Embayment	Mudflat
FW Inflow Modification	✓		✓		✓		
Subsidence			✓	✓	✓	✓	✓
Shoreline Development			✓	✓	✓	✓	✓
Dredge & Fill		✓	✓	✓	✓		✓
Point Source	✓			✓			
Nonpoint Source	✓			✓			
Commercial Fishing		✓	✓				
Recreational Fishing				✓			
Boating & Marinas		✓		✓			
Petroleum Activity		✓					
Oil/Chemical Spills	✓				✓		✓
Circulation		✓	✓				
Shoreline Erosion					✓		
Exotic Species					✓		
Storms & Hurricanes				✓			

Source: McFarlane, 1994

FIGURE 3.10. *Perturbation of Galveston Bay estuarine habitats. The seven habitats described in this chapter (across the top) are influenced by a variety of perturbations (in the left column), many of which result from human activities.*

killed during unfavorable conditions, only to be recolonized by spat from elsewhere when a favorable environment returns. The greatest vulnerability of this habitat is to changes that prevent long-term survival of oysters at that location in the bay. These include permanent changes in salinity and circulation (e.g. from navigation projects), alterations of currents over the reef, increased sedimentation that physically buries the reef, and overfishing that depletes the supply of oyster shell faster than it is replaced by oyster growth.

Seagrass meadows are known to be adversely affected by many kinds of environmental changes (Pulich and White, 1989). Subsidence can increase water depth, placing plants below the **photic zone** (rendering them incapable of **photosynthesis**). Point and nonpoint source discharge of excessive nutrients can overstimulate the growth of epiphytic algae. This reduces light penetration to the leaf surface and creates drag in water currents that can uproot the grasses during storms. Boat traffic can create propeller swaths through beds of seagrass, and wading fisherman trample the grass underfoot. Dredge and fill activity can bury the grasses beneath sediment. Shoreline development, particularly canal-access residential use, may result in all of the above.

Peripheral marshes are damaged or eliminated by subsidence and shoreline development, particularly dredge-and-fill projects (see Chapter Seven). Drainage and conversion to upland habitat is particularly destructive (White et al., 1993). Reduction of fresh water inflow can result in inadequate sediment transport and lead to erosion of delta marshes. Exotic species, particularly nutria and grass carp, can produce excessive cropping (eat-outs) of marsh plants and change the vegetative composition of these wetlands. Peripheral marsh embayments are poorly known but seemingly would be affected by subsidence and shoreline development.

The perturbations shown in FIGURE 3.10 could be improved by ranking the relative impact of each perturbation-habitat interaction. In reality, the severity of an impact will vary greatly by the type, site, and season of the impact. Each instance is unique.

Source: United States Fish and Wildlife Service

This sandwich tern forages in open-water habitats for such species as the bay anchovy. It nests in colonies, sometimes located on islands or banks created by disposal of dredged material.

SUMMARY

The Galveston Bay ecosystem is composed of a complex set of overlapping habitats that function with a myriad of natural and inter-linking energy and materials processes. This chapter has described seven distinct habitats which help define the larger estuary, and which link it to riverine and gulf ecosystems and more distant portions of the continent. The integrity of these highly connected, distinct but interacting habitats is vital to the continued natural function and life-support capability of the estuary.

The use of conceptual models of the various habitats has shown that the well-being of these habitats is partially dependent on distant events, such as the spawning of shrimp and finfish in the gulf or precipitation runoff from a remote watershed. Therefore, these habitats, and hence the estuary as a whole, can be greatly influenced by actions occurring far from the bay. This implies the need for an ecosystem-level approach to future management of the system.

Other, more immediate perturbations have more obvious outcomes. Water and sediment quality reductions and direct habitat destruction are examples. Having developed in a physically variable and stressful environment, the habitats which comprise the estuary ecosystem can withstand considerable abuse and survive. Some habitats are clearly more vulnerable than others; however, constant chronic abuse or frequent episodic abuse at intervals too short to permit recovery between episodes can ultimately influence each type of environment. For example, seagrass meadows and marshes have suffered well-documented losses over the last several decades.

FOR MORE INFORMATION

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