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.

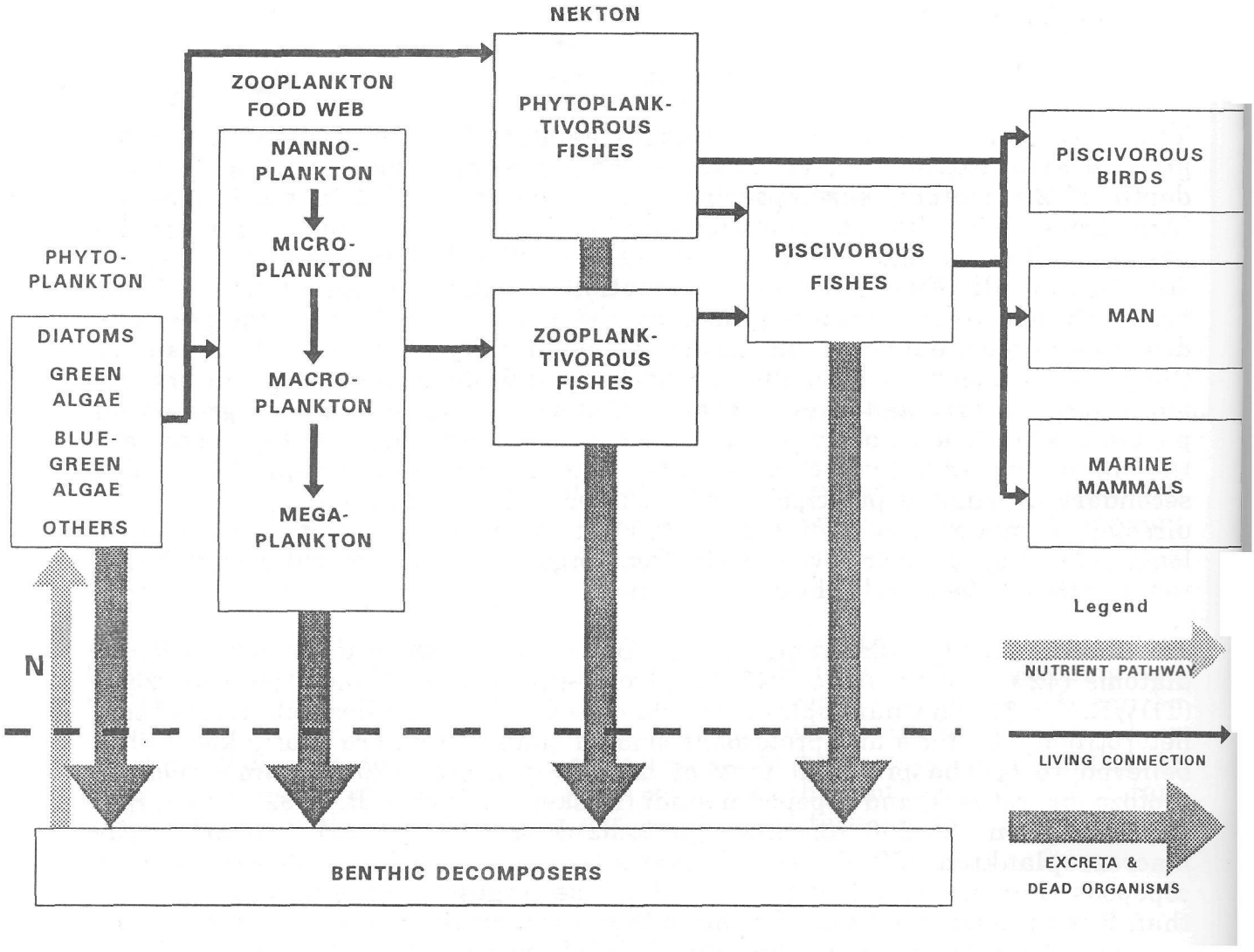


Figure 8. Connectivity of the open-bay water habitat.

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.

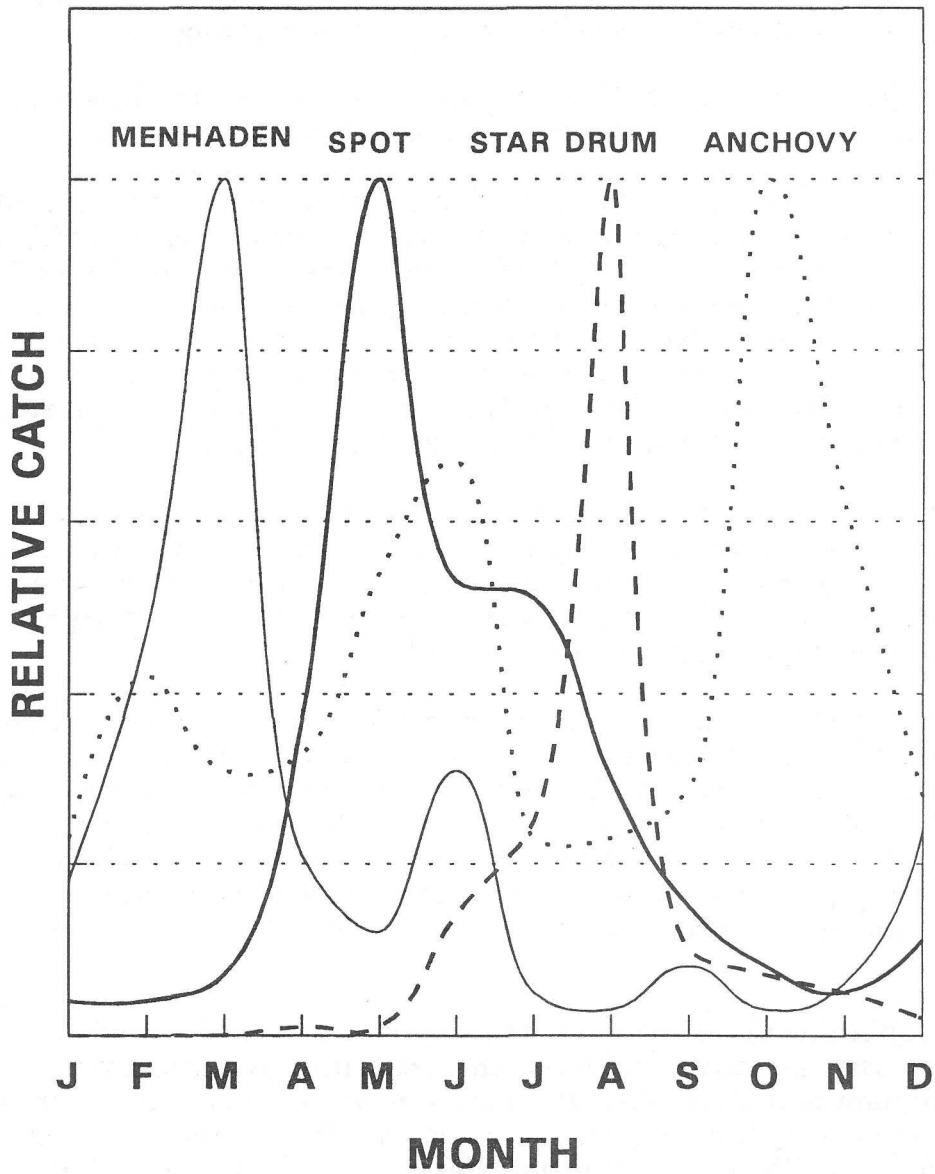
Zooplankton- Optimal conditions for growth and survival occur at different times of the year for different species. In Trinity Bay, immature barnacles were prominent in late winter and early spring, their period of greatest spawning activity. Copepod nauplii and protozoans were dominant in April. The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

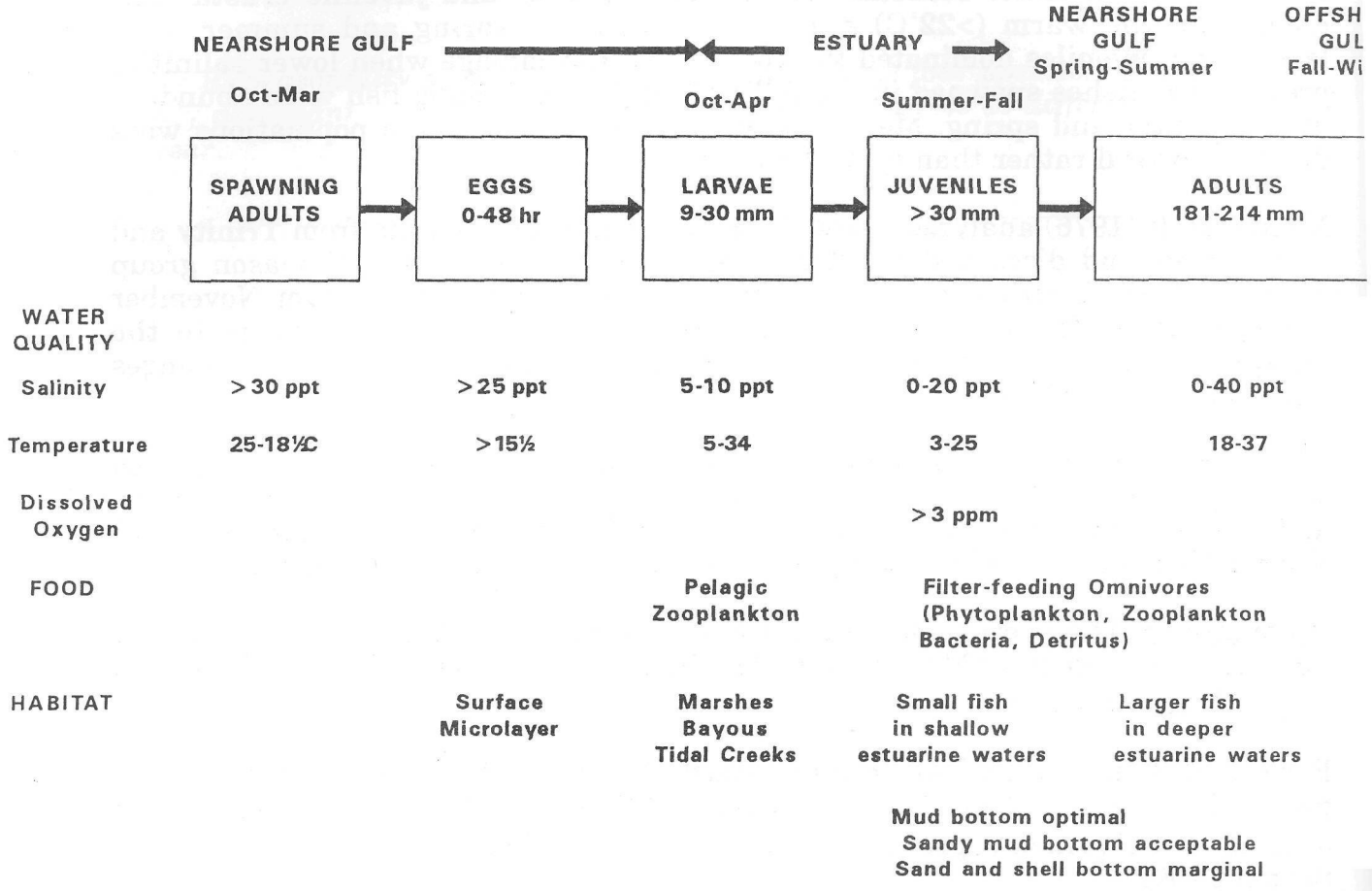
Habitat Subsystems: The surface microlayer of open-bay water habitat frequently supports a distinct community at the air-water interface, a region of high light intensity and oxygen concentration. This aggregate of minute organisms - phytoplankters, zooplankters, and the eggs and larvae of fishes - is 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.

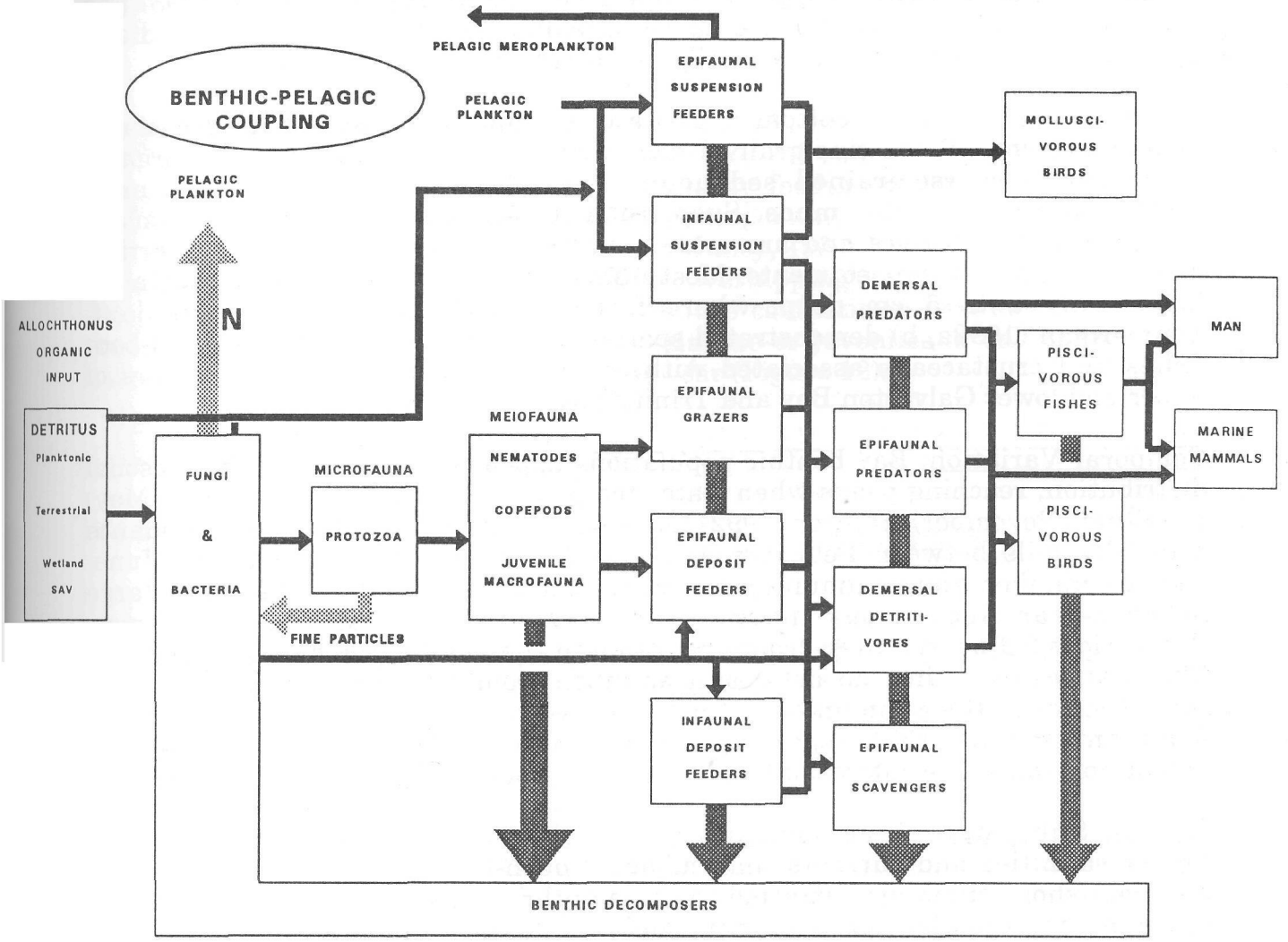
The next component is the diverse meiofauna comprised of organisms between 2/1000ths and 2/100ths of an inch (0.062-0.5 mm) in size. Nematodes are most numerous but copepods and juvenile stages of the larger macrofauna are also abundant. These organisms find protozoans and bacteria to be conveniently-sized 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 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 share feeding habits. Some feed by straining suspended particles from the water column, the suspension feeders (e.g. bivalve mollusks). Others feed by ingesting the sediments and extracting nutrients as it passes through 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. Numerous fishes (e.g. croakers, spot, mullet and drum) and shrimp forage on benthic organisms. These are considered as demersal predators 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.

Spatial Variation: 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 open bay center 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 open bay margin 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 river-influenced 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).

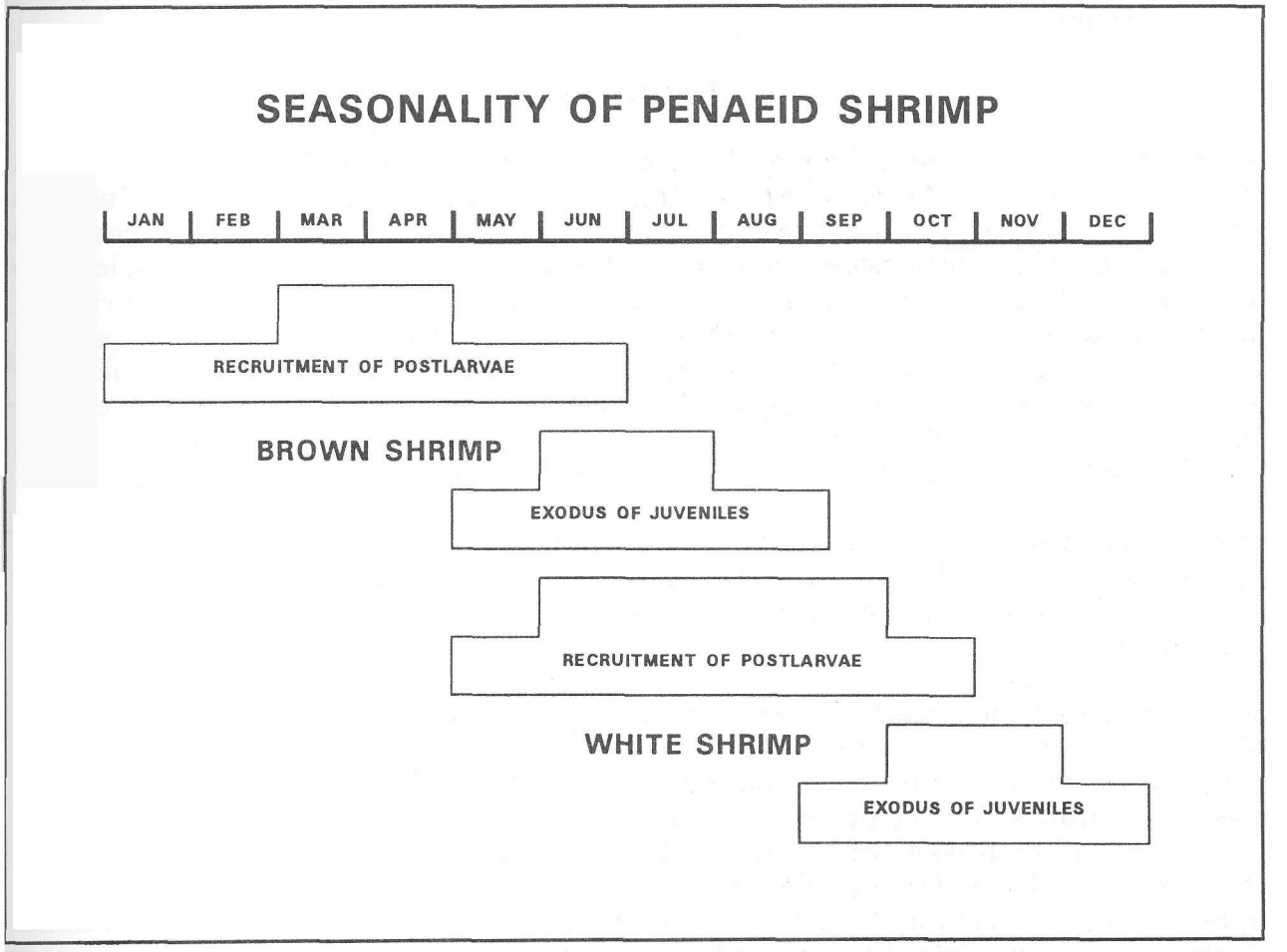


Figure 12. Seasonality of penaeid shrimp, which share bay-bottom habitat by temporal displacement.

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.

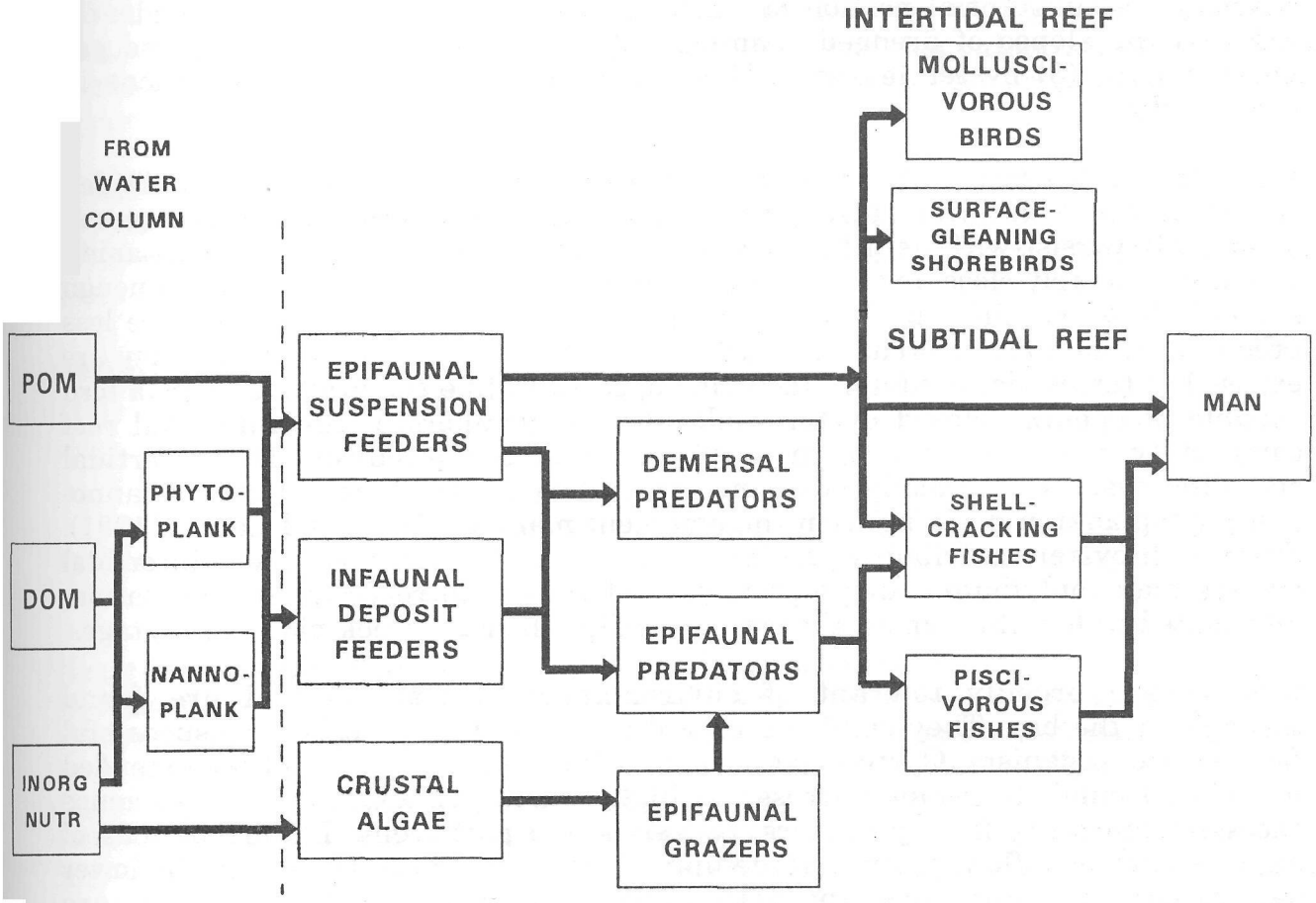


Figure 13. Connectivity of oyster reef habitat. Nutrients, organic material and plankton are imported from the open-bay water habitat.

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.

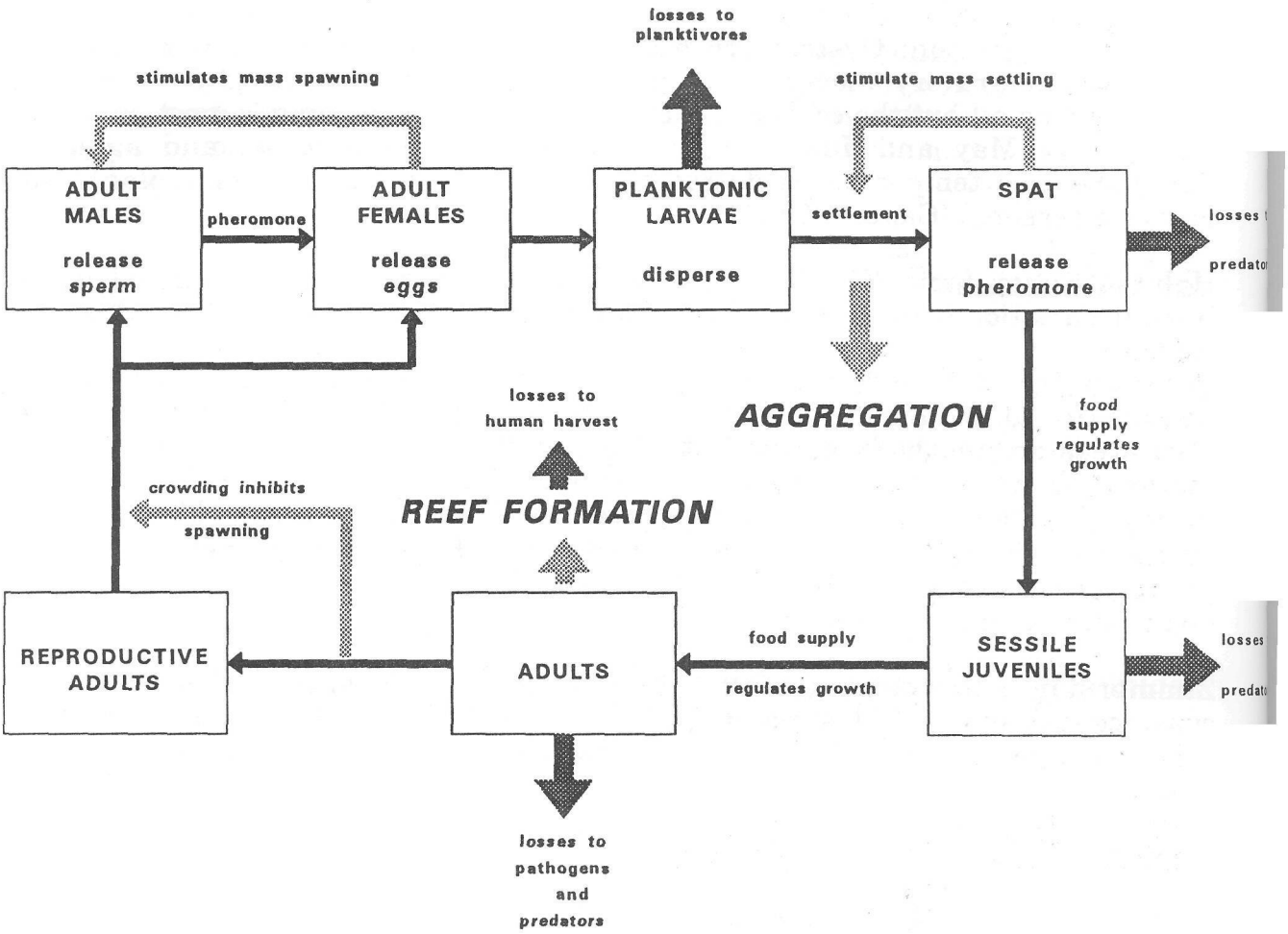
Productivity: Although the commercial harvest of oysters is reasonably well documented, it is difficult to extend this data to a per unit area productivity value. Reef areas are inexactly known but a minimum of 9883 acres (1613 ac closed to harvest; Quast et al., 1988) are regulated by the TPWD, with 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.

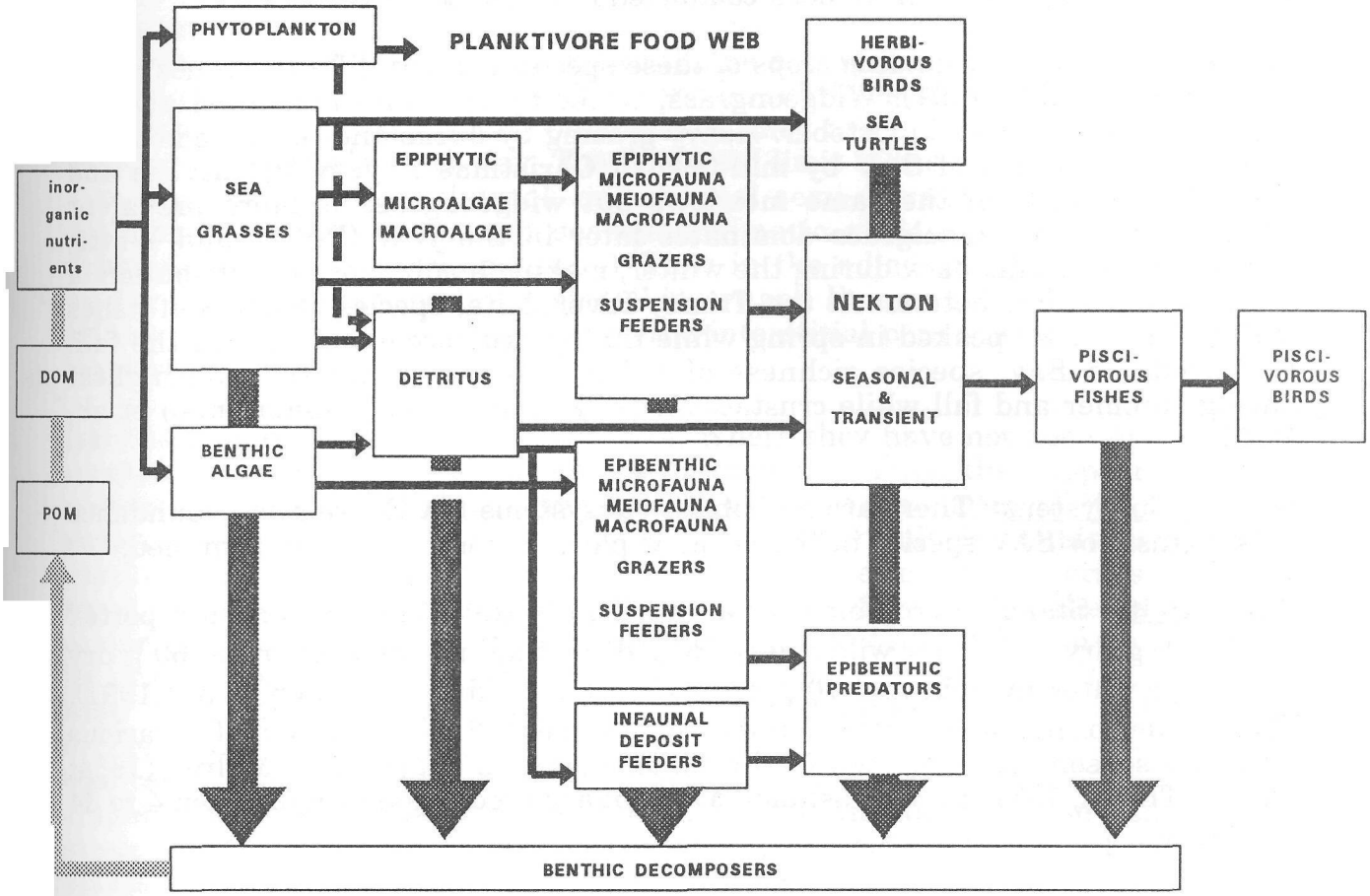


to the prevailing currents, resulting in the maximum number of individuals gaining access to planktonic food particles. As they rise above the bottom, the reefs alter bottom current patterns, leading to silt deposition on the reef flanks and smothering of oysters at those points. If too many adults result 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.

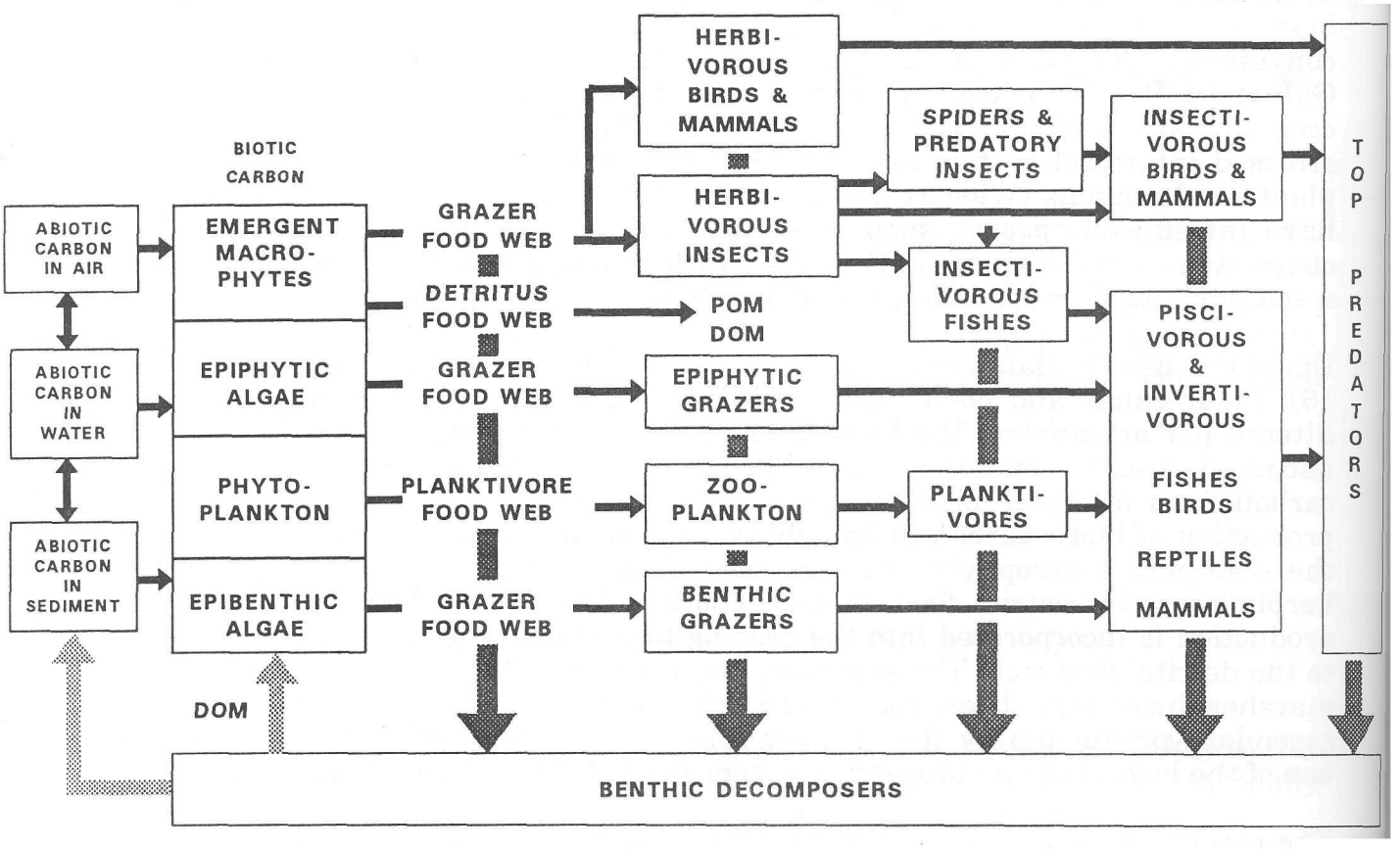


Figure 16. The connectivity of marsh habitat.

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 edge effects in both *Spartina* and *Juncus* marshes. White and Paine (1992) provide species lists for dominant plants of various marshes and localities around Galveston Bay.

Temporal Variation: 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.

Habitat Subsystems: 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^2using several methods.

Limiting Factors: Nutrients
Tidal exchange
Soil and water salinity

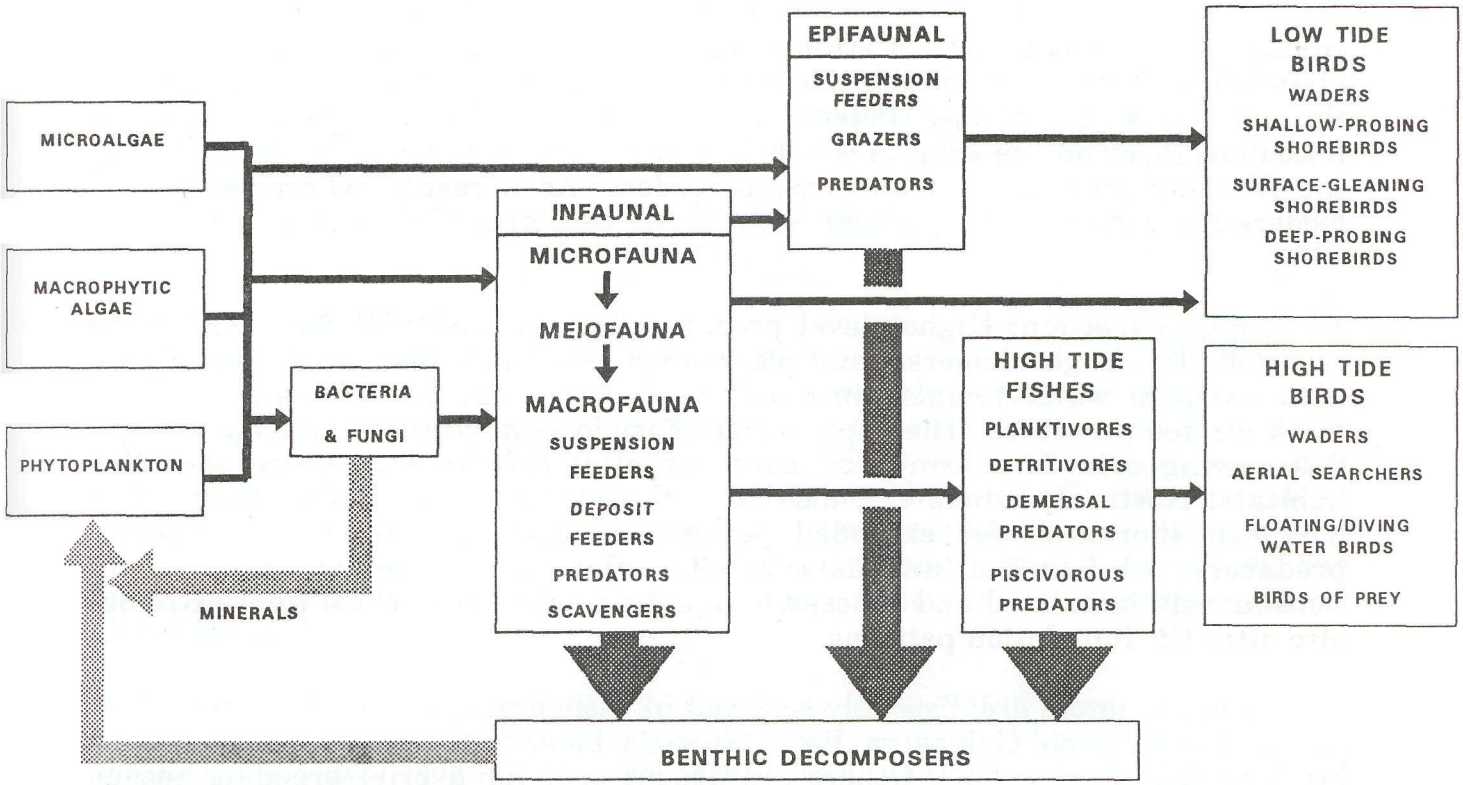
Key Species: There appear to be sufficient salt-tolerant plants so that no one species dominates to the extent that a given category of marsh would be nonexistent in the absence of that species. Smooth cordgrass, at the upper salinity limit and deepest edge of the marsh, is the closest approximation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

Spatial Variation: 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.

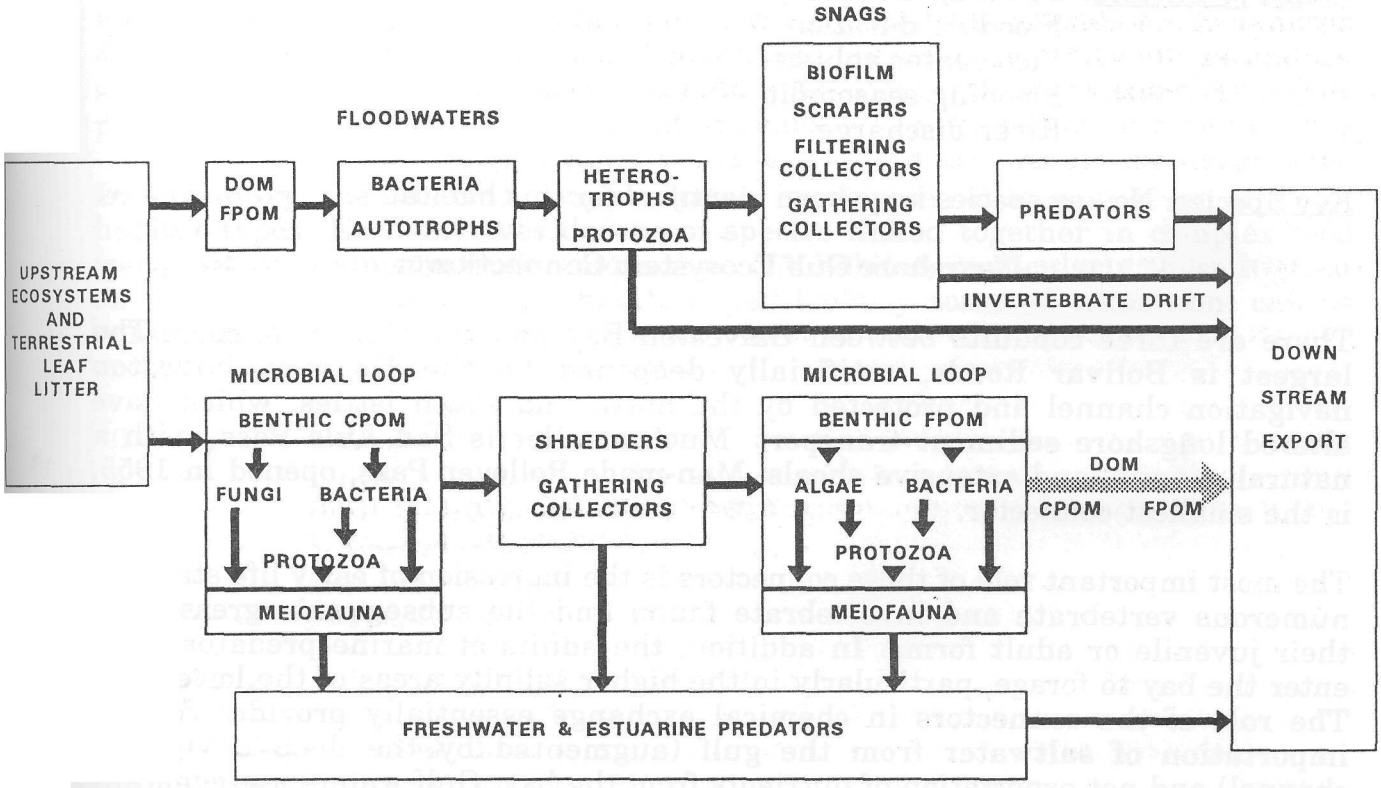


Figure 18. Connectivity of the riverine/floodplain habitat.

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.

=== Abundant --- Common

Source: Dauphin et al. 1989