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B. Living Resources - Habitats

Detailed community profiles of estuarine habitats within the CCBNEP study area are not available. Therefore, in the following sections, the organisms, community structure, and ecosystem processes and functions of the major estuarine habitats (Open Bay, Oyster Reef, Hard Substrate, Seagrass Meadow, Coastal Marsh, Tidal Flat, Barrier Island, and Gulf Beach) within the CCBNEP study area are presented. The following major subjects will be addressed for each habitat: (1) Physical setting and processes; (2) Producers and Decomposers; (3) Consumers; (4) Community structure and zonation; and (5) Ecosystem processes.

HABITAT 1: OPEN BAY

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HABITAT 1: OPEN BAY

1.1 Physical Setting and Processes

1.1.1 Distribution within Project Area

The open bay community is defined as the unvegetated and soft-bottomed portion of the subtidal estuarine environment. This community is the dominant subtidal community in Texas estuaries comprising 68% of the total subtidal area (Armstrong, 1987). Extent of the open bay community is determined primarily by factors limiting success of submerged plants and oysters such as depth, turbidity, exposure to wave action, and salinity.

Most of Corpus Christi Bay, Nueces Bay, Oso Bay, Mission Bay, and Aransas Bay, except for a few scattered areas of oyster reefs and seagrass meadows, can be characterized as open bay. Extensive reefs of *Crassostrea virginica* (eastern oyster) limit the open bay community to inter-reef areas in Copano and Nueces Bays. Extensive grass beds limit the open bay community in the shallower Redfish Bay and Laguna Madre. Seagrass meadows have greatly expanded in Oso Bay since the Barney Davis Power Plant began introducing Laguna Madre water into this system.

1.1.2 Historical Development

In geologic terms the open bay community is an intermediate stage along a successional continuum that will end in the ultimate filling of the estuary and creation of flat coastal plains. Rivers continue to deposit sediment, as estuaries become shallower and smaller in areal extent. Sediment accumulation is slow, perhaps a few centimeters per 100 years, but the ultimate fate of these estuaries is illustrated by coastal plain farmlands that were once the Brazos and Rio Grande estuaries. The Mission/Aransas and Nueces estuaries and Baffin Bay formed from the combination of two processes: drowning of river valleys and formation of barrier islands. Present geomorphology of estuarine systems of the study area depict the geologic past. Morphology of bays that are oriented perpendicular to the coastline (e.g., Corpus Christi, Nueces, and Baffin bays) may be the result of drowning of ancestral river valleys, whereas general morphology of those bays oriented parallel to the coastline (e.g., Aransas Bay and Laguna Madre) may be explained with reference to formation of barrier islands.

1.1.3 Physiography

Estuarine systems of the CCBNEP study area, classified as predominately open bay, include the Nueces and Mission/Aransas estuaries and encompass 14.5% of estuarine areas of Texas.

The Nueces Estuary, comprised of Nueces, Oso and Corpus Christi bays with a total surface area of 44,451 ha, represents 7.13% of total estuarine area in Texas. Average depth for the entire system is 2.4 m., yielding a volume of 1.147 km^3 (Armstrong, 1987). Corpus Christi Bay (deepest bay in the study area) is 4.2-4.8 m deep over most of the bay area; bay margins are generally steeply sloped (White et al., 1983). Oso and Nueces bays are shallower, ranging from

0.6 to 1.2 m respectively. Nueces Estuary has access to Gulf waters through Aransas Pass which traverses the barrier island to the northeast, and to freshwater from Nueces River which flows into Nueces Bay.

The Mission/Aransas Estuary is made up of Aransas, Copano, and Mission bays, and has a total surface area of 46,279 ha; an average depth of 2.0 m yields a volume of 0.925 km^3 for the entire estuary (Armstrong, 1987). The Aransas Bay center is about three meters, and bay margins are generally steep. Depths (2.4-3.0 m) and margin slopes are more variable in Copano Bay due to extensive oyster reefs (White et al., 1983). Mission Bay is a small shallow bay to the northwest of Copano Bay. The Mission/Aransas Estuary receives Gulf waters through Aransas Pass and Cedar Bayou and freshwater from the Mission and Aransas Rivers.

1.1.4 Geology and Soils

Sediments of the open bay community in the study area are derived from suspended and bed-load material from streams and rivers eroded from bay-shores, sediments from the Gulf transported through passes and washover channels, wind-born sediments blown across barrier islands, biogenic materials such as oyster shells, and dredge spoil deposited along channels (White et al., 1983). Mud (silt and clay) is the most abundant sediment type found in the estuaries; of this fraction, silt is generally more abundant than clay. White et al. (1983) found silt to be distributed over most of Corpus Christi and Aransas bays, as well as the northern and northwestern parts of Copano Bay, and the west-central part of Nueces Bay. Clay was found more abundant than silt in southeastern areas of Copano Bay, in a few scattered areas of Corpus Christi and Aransas bays, in Oso Bay, and near the mouth of the Aransas River. Mud occurs most frequently in deeper central-bay areas and in shallow protected areas, especially near river mouths such as in Nueces, Mission, and Oso bays, where relatively calm waters allow fine suspended sediments to settle.

Distribution of sands followed a pattern in the largest bays (Corpus Christi, Aransas, and Copano) in which bay margins containing high sand percentages graded rather abruptly into areas of less than 20% sand (White et al., 1983). A transitional zone of muddy sand (50-75% sand) and sandy mud (50-70% mud) was generally found between sandy bay margins and predominantly mud bay-center areas in these bays. Sandy mud was also found in the eastern half of Nueces Bay, along the southern shore of Corpus Christi Bay, in southwest Aransas Bay, throughout much of Mission Bay, and along flanks of oyster reefs in the western part of Corpus Christi Bay and in northwestern Copano Bay. Although muddy sand and sandy mud are natural transitional units, they can also be artificially produced by dredging activity, which apparently accounts for the presence of this sediment type in local areas around channels in Corpus Christi, Redfish, and Aransas bay (White et al., 1983).

The third sediment type was composed of gravel-sized shell and shell fragments (White et al., 1983). Areas in which sediment was composed of 75% shell were rare, occurring mostly in Copano Bay, where oyster reefs are abundant. Mixtures of shell with mud or sand were more widely distributed than pure shell. Shelly sand was abundant only in Redfish and Aransas bays, whereas mixtures of shelly sand and mud were significant sediment components in Redfish, Aransas, and Corpus Christi bays.

1.1.5 Hydrology and Chemistry

1.1.5.1 Tides

Tidal exchange in Texas estuaries occurs due to astronomical tides, meteorological phenomenon (e.g., winds and barometric pressure), and salinity stratification. Astronomical tides are largely diurnal with a semidiurnal component, and range from 0.8 m (diurnal) to 0.2 m (semidiurnal) (Armstrong, 1987). All tidal amplitudes are reduced in the Nueces Estuary due to damping effects of Aransas Pass. The diurnal component is reduced by 66% and semidiurnal component by more than 85% (Smith, 1974), thus increasing the importance of longer period exchanges brought about by wind-stress (Smith, 1977) and variations in atmospheric pressure (Smith, 1979) to exchange dynamics in this estuary. Small tidal amplitudes exhibited in estuaries contribute to low flushing rates (Smith, 1982; 1985) and long residence times for waters entering the Mission/Aransas (3.02 yrs.) and Nueces (0.46 yrs.) estuaries (Armstrong, 1982).

1.1.5.2 Freshwater Inflow

Freshwater inflows are vital to estuaries providing freshwater, nutrients, and sediment, and affecting conditions such as salinity gradients, circulation patterns, nutrient levels, and erosion. Inflows occur as drainage from coastal areas and inputs from streams and rivers as well as direct precipitation on water surfaces.

Inflow rates vary widely among Texas estuaries. In an extensive survey of effects of freshwater inflow on estuarine processes, Longley (1994), using hydrological data from previous TWDB reports (1980a; 1980b; 1981a; 1981b; 1981c) and extending this data set through 1987, provided analysis of hydrological patterns from 1941-1987. Mean freshwater inflow rates for the Nueces and Mission/Aransas estuaries were lowest of all estuaries considered (52,800 ac ft/mo and 35,800 ac ft/mo respectively); these rates generally followed precipitation patterns which decrease from north to south along the coast. Inflow rates for Nueces and Mission/Aransas estuaries represent less than one estuary volume of inflow each year.

Longley (1994) found inflow rates varying from year to year and annual variation for Mission/Aransas and Nueces estuaries was much greater than for systems to the north, as these two estuaries experienced extensive periods of very low inflow. Monthly inflow variation was apparent for all estuaries with lowest inflows occurring in August. Monthly inflow peaks for Nueces and Mission/Aransas estuaries occurred in early autumn, reflecting significance of late summer-early fall storms in the region.

In an analysis of long-term inflow patterns, the only statistically significant trend over the 47-year inflow record was a 2.1%/yr increase in inflow to the Mission/Aransas Estuary ($P = 0.05$) (Longley, 1994). Nueces Estuary inflow records revealed a large decrease (-4.33%/yr) in inflows during 1966-1987, a trend which was not statistically significant due to large variations in the inflow record (*P*= 0.20).

1.1.5.3 Salinity

Climatic variation and associated differences in freshwater inflow produce large differences in annual mean salinities among estuaries. Armstrong (1982) found mean salinities ranging from 13 . in the Mission/Aransas Estuary to 36.2 in the Laguna Madre. Salinity levels are not only result of freshwater inflow, but may also be influenced by access to Gulf waters of oceanic salinities, a factor which has been used to classify Texas estuaries. Texas estuaries have been classified as open or closed based on their connection to oceanic waters of the Gulf of Mexico. Open bays are those with direct access to the Gulf (e.g., Nueces/Corpus Christi), which are more readily influenced by marine waters, and closed bays are those without such access (e.g., San Antonio Bay) (Kalke and Montagna, 1989). Complex and estuary-specific nature of salinity patterns have been illustrated in salinity levels of open bays of the study area. Although freshwater inflow rates are similarly low for both Nueces and Mission/Aransas estuaries, average salinities of the two systems are quite different (27 and 13 , respectively). This difference may be explained by greater influence of Gulf waters within the Nueces Estuary.

Salinities not only vary among estuaries but significant variation may also be found within bay systems. This variation has been used to classify constituent segments of larger estuarine systems based on proximity to freshwater sources or Gulf inlets (TDWR, 1982). Tertiary bays are lakes associated with headwaters of the estuary and are typically low salinity areas due to their proximity to freshwater inflows. Secondary bays are semi-enclosed bays of low to moderate salinities which are connected to primary bays, the central part of the estuary with moderate to high salinities. This intra-estuarine salinity gradient varies seasonally and this seasonal variation can be extreme within the Nueces Estuary. The gradient between Nueces Bay and all other parts of the estuarine system from December through May is about 5 . However, beginning in June, differences between the lower-salinity Nueces Bay and higher-salinity Corpus Christi Bay increases to about 15 and remains at this level through August. These variations in salinity levels may occur between the Nueces Estuary and other estuarine locations within the CCBNEP study area (Longley, 1994).

A trend analysis of salinity regimes of Texas estuaries revealed a statistically significant 2.1% per year increase of salinity levels in Nueces Bay from 1968-1987 (Longley, 1994). Although no statistically significant trends in freshwater inflow rates for Nueces Estuary were determined, decreasing freshwater inflow should not be entirely discounted as an explanation for this trend. No other significant trends in salinity within the study area were found.

Although Texas estuaries differ with regard to general climate and freshwater inflow, all areas experience both seasonal and year-to-year variation in rainfall. This variation can be extreme in the northwestern Gulf. Drought conditions which occurred from 1948-1956 caused salinities in Texas bays to increase to record highs with little variation among years. The drought was broken in the spring of 1957, during which floods dropped salinities in Mesquite and Aransas Bays from

40 ppt to 2-4 ppt in less than three weeks (Parker, 1959). These dramatic climatic events can change the entire salinity pattern of an estuary in a very short time. Although timing of a particular event is unpredictable, they are predictable over the long term and are an important part of the estuarine budget.

1.1.5.4 Nutrient Loading

Nutrients are a vital element in the estuarine ecosystem and are largely a function of freshwater inflow. Carbon, nitrogen, and phosphorus in various chemical forms are essential to autotrophic and heterotrophic processes which form the base of productivity of estuaries.

Relative importance of different components of nutrient loading vary among estuaries. Direct precipitation to the bay surface is an important component to nitrogen loading budgets of the Nueces and Mission/Aransas estuaries accounting for 16% and 28%, respectively, of nitrogen reaching these estuaries. The Nueces River contributes 34% of nitrogen loading to its estuary whereas the Mission and Aransas rivers supply 24% of nitrogen available to their estuarine system. Additionally, municipal and industrial outputs account for 40% of terrestrial nitrogen reaching the Nueces Estuary.

Despite large differences among nutrient loading rates of Texas estuaries, the range of average nutrient concentrations is similar for all bays and suggest nutrient concentrations are determined more by processes within the estuary than by inputs to the system. These processes include geochemical trapping of nutrients in the sediment and regeneration or remineralization by biological communities, a process termed benthic pelagic coupling. A similar pattern of decreasing nutrient concentrations from the headwaters to the Gulf occurs in all Texas estuaries. A gradient existing under both high and low inflow conditions suggests similar processes are at work in all estuaries (Longley, 1994).

1.1.5.5 Nutrient Distributions

Dissolved inorganic nitrogen. - Nitrogen is generally considered to be the nutrient in shortest supply in coastal waters, and, thus, the most likely potential limiting nutrient requirement of estuarine primary producers (Ryther and Dunstan, 1971). Inorganic nitrogen, required for photosynthesis by estuarine autotrophs, is found in three chemical forms (ammonia, nitrite, and nitrate) in estuarine waters collectively referred to as dissolved inorganic nitrogen (DIN). Ammonia may come from benthic metabolism, remineralization in the water column or from municipal or industrial outflows. Nitrate is the nitrogen form primarily found in river water whereas nitrite is generally a product of the chemical oxidation of ammonia which occurs in estuarine sediments. DIN concentrations > 0.028 mg/l are generally considered optimum for phytoplankton growth (Whitledge, 1989). All Texas estuaries maintain a zone of high nitrogen concentrations near their headwaters particularly during dry periods. During periods of high inflow, nitrogen concentrations may increase by a factor of two or more in the upper estuarine zone. A general decline in nitrogen levels from the headwaters to near the Gulf is also exhibited.

Nitrogen brought into an estuary with freshwater inflow is not uniformly distributed throughout the estuary. Patterns of nitrogen distribution within Corpus Christi Bay are most likely the result of differences in nutrient processing by benthic and planktonic organisms rather than by advection and circulation patterns within the bay (Whitledge, 1989). The main nitrogen source for phytoplankton productivity was ammonia rather than nitrate in Corpus Christi Bay. Any direct influence on nitrogen distributions by inflows from the Nueces River were largely confined to Nueces Bay and effects of inflow on the lower bay are largely indirect through the production and transport of organisms or the advection of regenerated nutrients from Nueces Bay sediments. Concentrations of nitrogen were generally high enough to support maximum phytoplankton growth.

Phosphorus. - Phosphorus enters the estuary primarily with freshwater inflows and municipal discharges. Phosphorus concentrations within the estuary may be largely controlled by geochemical processes involving adsorption and release of phosphorus from clay particles and large organic molecules within the sediment. This process is reversible, the direction of the process dependent upon ambient concentrations of phosphorus within the water column (Pomeroy et al., 1965). Resuspension of surface sediments increases the exchange of phosphorus from the bound phase to the dissolved phase, thus illustrating the importance of wind and fine resuspendable sediments to estuarine phosphorus budgets (Montagna et al., 1989).

Total organic carbon (TOC). - Dissolved and particulate organic carbon within the estuary is derived from organic material delivered by river inflow, from primary production within the estuary and from partial breakdown of organic material in the process of regeneration. Generally, higher concentrations of TOC are found in the upper estuary near river mouths and in bay centers where high TOC levels are associated with finer sediments (White et al., 1983). Distribution of TOC in Corpus Christi Bay suggests the relatively greater importance of phytoplankton responding to inorganic nutrients, rather than terrestrial carbon entering the bay with inflow events, in the carbon cycle (Longley, 1994).

1.2 Producers and Decomposers

1.2.1 Primary Producers

Open bay bottoms are defined as the unvegetated subtidal portion of the estuary, thus primary production is dominated by phytoplankton. Phytoplankton are organisms which are unable to swim against currents and are photosynthetic (create energy from sunlight). Phytoplankton are the base of the food chain, providing carbon directly to higher trophic level pelagic consumers and indirectly as detritus to benthic consumers. Phytoplankton is also remineralized by benthic decomposers, providing nutrients needed for further photosynthesis.

Phytoplankton of the open bay community are commonly grouped into four major taxonomic divisions: diatoms, dinoflagellates, greens, and blue-greens (Armstrong, 1987). Relative abundance of these groups varies with changing environmental conditions, and this variation in relative composition of the phytoplankton may indicate accessibility of primary production to consumers based on consumer trophic preferences. For example, diatoms are generally a more readily available food source for zooplankton than blue-green or green algae (Ryther and Officer, 1981). Further, freshwater phytoplankton, which mixes with marine species during periods of high freshwater inflow, may not be the preferred food of zooplankton, and may enter the estuarine food chain through benthic filter feeders (bivalve molluscs) rather than through pelagic food chains.

Diatoms dominate the phytoplankton assemblages of Aransas Bay, with a peak abundance in the winter primarily composed of *Coscinodiscus* spp. (Freese, 1952). Another peak, comprised of the diatom *Rhizosolenia alata*, have been observed in July. Other dominant species include *Thalassiothrix frauenfeldii* and *Skeletonema costatum.* Blue-green and green algae dominate upper estuary locations in the Mission/Aransas estuary whereas diatoms dominate lower estuarine sites (Holland et al., 1975).

In a three-year study of the Nueces, diatoms comprised over 70% of the phytoplankton community in Corpus Christi Bay (Holland et al., 1975). The diatoms *Thalassionema nitzschioides*, *Thalassiothrix frauenfeldii* and *Chaetoceros* spp. dominated this assemblage. Blue-green algae *Anabaena* spp. and *Oscillatoria* spp. dominated upper estuarine sites in Nueces Bay during periods of high nitrogen concentrations. In a separate study of Nueces Bay, diatoms comprised the majority of the phytoplankton assemblage (Murry and Jinnette, 1974). A six-year study of Oso Bay and the upper Laguna Madre, reported maximum abundances of phytoplankton including the diatoms *Chaetoceros affinis*, *Thalassionema nitzschioides*, *Thalassiothrix frauenfeldii* and *Nitzschia* spp. normally occurring from December through March. The only abundant dinoflagellate observed was *Ceratium furca* (Hildebrand and King, 1978).

In a recent study of the Nueces Estuary, the importance of nanophytoplankton (< 0.02 mm), the smallest size class of phytoplankton, was noted in the overall trophic structure of this estuary (Stockwell, 1989). Eighty-five percent of the phytoplankton photosynthesis and standing crop in the Nueces Estuary were within nanoplankton size range. This size class is known to be grazed by microzooplankton (smallest zooplankton size class), thus, nanoplankton-to-microzooplankton energy transfer may represent a major pathway from photosynthesis to higher trophic levels.

1.2.2 Decomposers

Decomposers are one of the most important components of open bay benthos. Decomposers are thought to serve as major links between primary producers and higher trophic level consumers (Odum and de la Cruz, 1967), as little plant material is consumed directly (Whitlach, 1982). Decomposers are also important by remineralizing organic material and replenishing available nutrients into the water column for phytoplankton.

Decomposers are single-celled animals and include bacteria, yeasts, fungi, microalgae (diatoms and flagellates) and protozoans (including ciliates and foraminiferans). Generally termed microbenthos, these organisms are the smallest size class of benthic organisms (< 0.063 mm, the mesh opening size of a US Standard No. 230 sieve). Due to their small size and morphological plasticity, microbenthos are generally not identified to lower taxonomic levels.

Large amounts of resuspended sediment in shallow and windy Texas estuaries and large inputs of detritus, provide many substrates for colonization and remineralization by bacteria, fungi, and protozoans. These colonized surfaces provide additional nutritional value to detrital feeders. Larger organisms, such as crabs, shrimp, and polychaete worms mechanically and chemically break down detrital material providing larger surface areas for colonization.

Feeding habits of microbenthos are diverse. Some species are autotrophic, whereas others are saprozoic, obtaining nourishment by absorbing dissolved organics from detritus. Holozoic microfauna ingest or engulf organic particles or other microbes. Additionally, many microbenthos make use of several of these modes of nutrition, depending on environmental conditions.

1.3 Consumers

1.3.1 Invertebrates

1.3.1.1 Zooplankton

Zooplankton are microscopic animals that are weak swimmers and are largely transported by water currents within the estuary. Zooplankton has been divided into two size classes: microzooplankton (0.02-0.2 mm) and macrozooplankton (0.2-2.0 mm), based on mesh size of collecting nets. Some zooplankton, termed holoplankton, spend their entire life cycle in the plankton remaining within the size range mentioned previously. Examples of holoplankton are the calanoid copepods. Meroplankton are temporary members of the plankton, spending only part of their life cycles as eggs and larvae in the plankton, then leaving to settle as benthic organisms or to develop into larger fish or shellfish.

Zooplankton are generally principal consumers of carbon fixed by phytoplankton. They also feed upon other zooplankton and on organic matter imported into the estuary. Zooplankton are an essential link in the transfer of energy from autotrophs to higher consumers such as larval fish, shellfish, and other invertebrates (Steele, 1974; Govoni et al., 1983; Minello et al., 1987).

The calanoid copepod *Acartia tonsa* has been reported as the dominant zooplankter in the Nueces and Mission/Aransas estuaries (Holland et al., 1975). Subdominant zooplankters included a cyclopoid copepod (*Oithona* sp.) found during warmer months in the Mission/Aransas Estuary and barnacle nauplii (meroplankton) in the Nueces Estuary. The dinoflagellate *Noctiluca scintillans*, known to feed on phytoplankton (Sverdrup et al., 1964), was often the most abundant “zooplankter” during late winter and early fall in the Nueces Estuary. Freshwater zooplankters including *Cyclops* sp. and *Daphnia* sp. were found mixed with marine species, such as the copepods *Centropages hamatus* and *Labidocera aestive* and the dinoflagellate *Noctiluca scintillans* in the upper reaches of the Nueces Estuary.

Acartia tonsa was reported as the dominant holoplankton of Oso Bay and upper Laguna Madre (Holland and King, 1978). Subdominant calanoid copepods included *Pseudodiaptomus* spp. and

Centropages spp. Meroplankton, including trochophore larvae, bivalve larvae, gastropod veligers, and barnacle nauplii were significant components of the zooplankton during the spring.

Only one study has measured size fractions of plankton in Texas estuaries and indicated the possible importance of microzooplankton to the trophic dynamics in the Nueces Estuary (Buskey, 1993). Microzooplankton abundance was much greater (10-100 times) in Texas estuaries than in other coastal environments studied. Tintinnids, which are ciliated protozoans, were the dominant microzooplankters during periods of peak abundance.

1.3.1.2 Meiobenthos

Meiobenthos are metazoans (multi-celled animals) ranging in size from 0.063 mm to 0.59 mm (mesh opening size of the US Standard No. 30 sieve). Meiobenthos are further divided into permanent meiobenthos, those organisms never > 0.59 mm that include nematodes, harpacticoid copepods, gastrotrichs, and kinorhynchs; and, temporary meiobenthos that grow large enough to be classified as macrobenthos and include juvenile stages of clams, snails, polychaete worms, and amphipods.

Composition of meiobenthos of Texas estuaries are similar to those found in shallow marine sediments world-wide. In general, nematodes were the most abundant organisms, representing 83% of meiofaunal counts in sediments of San Antonio Bay (Rogers, 1976). Harpacticoid copepods represented an additional 5%. Other important constituents of the meiofauna include juvenile stages of molluscs, polychaete worms, and amphipods. Due to their short life spans and large turnover rates, meiofauna can maintain large populations throughout the year (Rogers, 1976). Meiofauna may comprise 12-30% of the living biomass of aquatic sediments (Gerlach, 1978).

Most meiobenthic organisms are grazers selecting single-celled microbenthos for food (Montagna and Yoon, 1991); some, such as nematodes, are deposit feeders. Although nematodes are numerically dominant, they probably do not dominate trophic dynamics as they process <5% of food consumed by the meiofaunal community, at least in high-inflow conditions of San Antonio Bay (Montagna and Yoon, 1991). Grazing rates by meiobenthos on microalgae was four times as great as on bacteria in the Guadalupe Estuary. Juvenile molluscs consumed 39% of the microalgae and 68% of the bacteria whereas other meiofauna consumed 33% of the microalgae. Grazing rates on microalgae found in their study were several times higher than those found from other areas, but grazing rates on bacteria were lower. It is not known whether these findings apply to other Texas estuaries.

1.3.1.3 Macrobenthos

The largest size class are the macrobenthos, those animals larger than 0.59 mm, and include adult stages of clams, polychaete worms, snails and crabs. Macrofauna of Texas estuaries have been studied more frequently than either of the other two size classes. Polychaetes and molluscs dominated assemblages in most estuarine systems.

Macrobenthos employ various feeding strategies. Most infaunal molluscs and some polychaetes are suspension feeders, obtaining food from the water column. Many polychaetes are deposit feeders obtaining nutrition from organic material and associated with sediments they ingest. Mobile gastropods and polychaetes may be scavengers of predators. In general, most infauna of the open bay bottom derive most of their nutrition from organic material in sediments or from each other through both active predation and/or deposit feeding which often entails ingestion of small living organisms (Armstrong, 1987). Suspension feeding may be somewhat limited in areas of the estuary due to turbidities associated with easily resuspended sediment.

The polychaetes *Mediomastus californiensis* and *Streblospio benedicti* were the most abundant and ubiquitous benthic organisms in the Mission/Aransas Estuary (800-2,500 organisms/m^2) (Holland et al., 1975). In a survey of the Mission/Aransas Estuary, *Paraprionospio pinnata* was the dominant polychaete of Aransas Bay (Calnan et al., 1983). Dominant polychaetes of Copano Bay were *Glycinde solitaria* and *P. pinnata* (Calnan et al., 1983). Dominant molluscs were *Macoma mitchelli* and *Mulinia lateralis*, and the dominant crustacean was *Lepidactylus* sp.

Polychaetes and bivalve molluscs were the most abundant macrobenthic groups in the Nueces Estuary (Holland et al., 1975). *Mediomastus californiensis*, *S. benedicti*, *P. pinnata*, *Cossura delta*, and *G. solitaria* were the dominant polychaetes, whereas *M. lateralis*, *Lyonsia hyalina floridana*, and *M. mitchelli* dominated the molluscs. Although *M. californiensis* and *S. benedicti* consistently dominated faunal collections from Corpus Christi Bay, the bivalve mollusc *M. lateralis* dominated early collections from Nueces Bay. The amphipod *Corophium acherusicum* also dominated samples from one collection in Nueces Bay. In marked contrast to most studies of Texas estuaries, Jinnette (1976) reported molluscs comprising 78% of the total macrobenthic abundance collected from Nueces Bay. *Mulinia lateralis* was the dominant mollusc and *M. californiensis*, *P. pinnata*, and *G. solitaria* were dominant polychaetes. In an intensive study of the macrobenthos of Corpus Christi Bay, Flint and Younk (1983) found polychaetes comprised 60% of the total macrofaunal abundance. *Mediomastus californiensis* (1,443/m^2) and *S. benedicti* (238/m^2) usually dominated benthic samples. Bivalve molluscs which were seasonally abundant included *M. lateralis* (417/m^2), *L. hyalina floridana* (607/m^2), and *Abra aequalis* (2,210/m^2). Castiglione (1983), in a one year study of the molluscs of Corpus Christi Bay, found open bay molluscan communities dominated by the bivalves *M. lateralis*, *L. hyalina floridana*, *N. acuta*, and *Pandora trilineata* which were abundant seasonally during recruitment periods in late winter and early spring. In a nine-month study of the Nueces Estuary, Montagna and Kalke (1992) reported the polychaetes *M. californiensis* and *S. benedicti* as dominant in all but the most marine station in Corpus Christi Bay which was dominated by polychaetes *Polydora caulleryi* and *Tharyx setigera*. *Mulinia lateralis* and *M. mitchelli* were the most abundant molluscs and were especially important constituents of benthic assemblages in freshwater influenced sites in Nueces Bay.

Polychaetes were the most abundant macrobenthic fauna of Oso Bay (Hildebrand and King, 1978). *Streblospio benedicti* was most abundant, followed by *Arenicola cristata*, *Capitella capitata*, *M. californiensis*, and *Heteromastus filiformis*. The amphipod *Ampelisca abdita* was the most abundant crustacean and *M. lateralis* was the dominant mollusc.

1.3.1.4 Epibenthos

Invertebrates which live on the surface of sediments are termed epibenthos; they include crabs, shrimp, and snails. Although many epibenthos prefer more protected areas such as seagrass beds and salt marshes, they are also found in the open bay biotope. This component of the benthos probably exerts the greatest trophic pressure on macrobenthic infauna as many epifauna (e.g., shrimp and crabs) are active predators seeking surface dwelling or shallow burrowing infauna. Other epibenthos, such as gastropod molluscs, are probably important scavengers within the open bay community. Further, burrowing activities of shrimp, crabs, and gastropods probably cause mortality to surface dwelling infauna due to sediment disturbances.

Trachypenaeus similis (roughback shrimp), *Penaeus aztecus*, *Callinectes similis*, and *C. sapidus* (blue crab) were the most abundant epifauna in Corpus Christi Bay in a study by S. Ray in Armstrong (1987). *Penaeus setiferus* and *Squilla empusa* were ubiquitous during the study period. *Penaeus setiferus*, exhibiting population peaks in the summer and fall, was the dominant epibenthic organisms collected in Nueces Bay (Murray and Jinnette, 1976). *Callinectes sapidus* and the penaeid shrimps *P. aztecus* and *P. setiferus* were the dominant epifauna from Oso Bay and the upper Laguna Madre (Hildebrand and King, 1978).

Other epifaunal crustaceans reported from open bay areas include the amphipod *Gammarus mucronatus*, xanthid crabs including *Neopanope texana*, the *Pagurus annulipes* (hermit crab), *S. empusa* (mantis shrimp), and *Palaemonetes pugio* (grass shrimp) which moves from grassbeds to open bay areas (Armstrong 1987). Many of these animals are considered detritus feeders which ingest surface sediments. *Squilla empusa* is a predator surprising prey from its burrow. Epifaunal gastropods have been noted in open bay areas including the predators *Busycon contrarium* and *Polinices duplicatus* (moon snail), and the detritivore *Olivella dealbata* (dwarf olive shell).

Important nektonwhich frequent the open bay biotope include: cnidarians such as *Aurelia aurita* (moon jellyfish); *Chrysaora quinquecirrha* (sea nettle), *Cyanea capillata* (lion's mane jellyfish), *Stomolophus meleagris* (cabbage head), *Mnemiopsis leidyi* (ctenophore), and *Lolliguncula brevis* (bay squid) (Britton and Morton, 1989). Jellyfish (esp. *S. meleagris*) and ctenophores can be seasonally abundant in open bay areas and may be important predators regulating zooplankton abundance (Jones et al., 1986).

1.3.2 Fish

Fish are dominant constituents of the nekton of the open bay community. Because of their mobility, many fish are not permanent residents of the open bay, but spend only part of their life cycles within the estuary. Thus, a knowledge of life history patterns of these organisms is needed to assess trends in the abundance and distribution of fish within the estuary.

Fish are dominant secondary consumers within the open bay community deriving nutrition from benthic organisms such as polychaetes, bivalve molluscs, crustaceans, and detritus and its associated decomposer populations or from pelagic organisms such as zooplankton and other smaller fish (including juveniles and larval forms). Fish serve as a primary link between the open bay community and man, as most commercial and recreational fisheries are considered estuarine dependent.

Moore (1978) reported on a seven-year study (1966-1973) of nekton from Aransas Bay in which 3,000-4,000 fish per hour representing 24-28 species/yr were collected. The dominant species collected were *Micropogonias undulatus*, *Leiostomus xanthurus*, *Anchoa mitchilli*, *Arius felis*, *Lagodon rhomboides*, and *Cynoscion arenarius.* Armstrong (1987) cited a 53-month study of the nekton within Corpus Christi Bay (A. Ray, Texas A&M Univ., pers. comm.) in which *Stellifer lanceolatus*, *A. mitchilli*, *M. undulatus*, *L. xanthurus*, and *C. arenarius* were the dominant fish. A creel census of Nueces Estuary (Bowman et al., 1976) revealed the following abundant game fish from the open bay which had not been collected in large numbers by trawl surveys: *Cynoscion nebulosus*, *Sciaenops ocellatus*, *Pogonias cromis*, *Paralichthys lethostigma*, *Bagre marinus*, and *L. rhomboides*. Murray and Jinette (1974) found the dominant fish during a study of Nueces Bay were *Brevoortia patronus*, *A. mitchilli*, *L. xanthurus,* and *M. undulatus*. Hildebrand and King (1978) reported *A. mitchilli*, *Mugil cephalus*, *M. undulatus*, *Menidia beryllina*, *B. patronus,* and *L. xanthurus* as the dominant fish during a six-year study in Oso Bay.

1.3.3 Reptiles and Amphibians

No amphibians are found in the open bays of the CCBNEP study area. There is little information concerning reptile use. *Alligator mississippiensis* (American alligator) has been reported by fishermen to cross enclosed bays (D. McKee, pers. comm.). There is no information concerning the use of open bays in the CCBNEP study area by *Macroclemys littoralis* (diamondback terrapin) and sea turtles.

1.3.4 Birds

Birds are high trophic level consumers within the open bay community. Birds which frequent open bay areas may be divided into four groups, based primarily upon feeding strategies (Peterson and Peterson, 1979): waders, aerial searchers, floaters and divers, and birds of prey.

Waders frequent peripheral open bay areas feeding primarily upon small fish and crustaceans. Herons and egrets are the dominant birds of this group, including the ubiquitous Great Blue Heron (*Ardea herodias*). Other birds of this group include Reddish Egret (*Egretta rufescens*), Great Egret (*Casmerodius albus*), and Tricolor Heron (*Egretta tricolor*). Of all bird groups, floating and diving birds probably exert the most feeding pressure on the benthic organisms of the open bay community, as they dive to feed on pelagic fish in the water column, or, all the way to the bottom, to feed on benthic invertebrates such as the bivalve mollusc *M. lateralis*. Cormorants, loons, and grebes normally feed upon fish, whereas, ducks, such as the Lesser Scaup (*Aythya affinis*), Redhead (*A. americana*) and Ruddy Duck (*Oxyura jamaicensis*), feed on benthic invertebrates and submerged vegetation. Gulls and terns belong to the group of aerial searchers which dive from flight into the water seeking fish; size of fish sought generally corresponds to size of the bird. Many terns and gulls are seasonal residents within Texas estuaries. Other birds of this group include the resident Brown Pelican (*Pelecanus occidentalis*) and Black Skimmer (*Rynchops niger*). Osprey (*Pandion haliaetus*) winters along the shoreline and feeds on large fish from open bay areas (Armstrong, 1987).

Although it might at first glance appear unlikely given the depth of water associated with open bay areas, birds are important consumers within the open bay community. Bowman et al. (1976) estimated the average fish-eating bird consumed 450 g of fish/day. As high level consumers, birds are especially susceptible to the biological concentration of toxic substances, through bioaccumulation and biomagnification, as evidenced by the recent plight of the Brown Pelican, and other birds within Nueces Estuary (White et al., 1979; 1980).

1.3.5 Mammals

The only resident mammal of open bay areas of Texas estuaries is *Tursiops truncatus* (Atlantic bottlenose dolphin). Armstrong (1987) estimated the population of bottlenose dolphins within the Nueces Estuary at about 300 (Oppenheimer, pers. comm.). He further estimated that an adult dolphin will consume up to 18 kg fish/day. Thus, this population would appear to be an important high level consumer within the open bay community. Additional information on marine mammal use of the bay systems of the CCBNEP study area is presented in Section IV.C.1.11, Marine Mammals.

1.4 Community Structure and Zonation

1.4.1 Planktonic Communities

1.4.1.1 Phytoplankton

Phytoplankton productivity is a major source of fixed carbon within estuaries. Flint (1984) estimated phytoplankton photosynthesis accounting for approximately 52% of the total annual carbon input to the Nueces Estuary. Phytoplankton are not uniformly distributed in the estuary both spatially and temporally. Variation in phytoplankton distributions are measured as differences in abundance (concentrations of algal cells) or biomass (concentrations of chlorophyll extracted from algal cells). Productivity is a function both of abundance and photosynthetic efficiency (chlorophyll content and light availability).

Phytoplankton abundance. - Factors which have been found to affect phytoplankton abundance include temperature, salinity, nutrient levels, grazing, and flushing rates. Average chlorophyll levels in Texas estuaries range from 12.9 µg/l in the Trinity/San Jacinto Estuary to 3.1 µg/l in the Mission/Aransas Estuary (Armstrong 1987). These levels fall in the mid-to--high range of averages listed by Boynton et al. (1982) for US river dominated estuaries. Chlorophyll concentrations are generally higher in the upper estuary (following nutrient distribution), except in the Mission/Aransas Estuary where higher chlorophyll concentrations are found near regions of Gulf exchange, perhaps a response to nutrient additions from adjacent estuaries (Longley, 1994).

Phytoplankton populations are temporally quite dynamic varying both daily and seasonally. When a particular algal species occurs in favorable physical conditions within an estuary, their populations grow rapidly at the expense of other species. Occasionally, high densities are reached such that a characteristic water color is produced (e.g., brown tide in Texas). In general, peak abundance of phytoplankton within estuaries of the study area occur with peaks in diatom abundance in winter and early spring (Table IV.B.1.1). Freese (1952) and Holland et al. (1975) both noted peaks in diatom abundance during winter in studies of the Mission/Aransas Estuary. Holland et al. (1975) also found peak phytoplankton abundance corresponding with peak diatom abundance occurred in winter (Feb 1973 - 1,100 cells/ml; Dec 1973 - 1,041 cells/ml; Dec 1974 - 468 cells/ml) in Corpus Christi Bay. In Nueces Bay, Holland et al. (1975) found peak phytoplankton abundances occurred in February and April 1973 (418 cells/ml), February 1974 (139 cells/ml) and September 1974 (513 cells/ml). Holland et al. (1975) noted an exception to diatom dominance in phytoplankton assemblages in Nueces Bay in the Fall 1973 and 1974 when two blue-green algal species dominated phytoplankton samples. These periods correspond with higher nitrogen levels. Minimum phytoplankton abundances appear more variable than maximum abundances and usually correspond with peaks in dinoflagellates or green algae (Armstrong, 1987). Minimum phytoplankton abundances were found in fall (Freese 1952, Aransas Bay); mid-late summer (Holland et al., 1975, Aransas Bay - 2-10 cells/ml); summer (Holland et al., 1975, Corpus Christi Bay - 77 cell/ml); February (Holland et al., 1975, Corpus Christi Bay - 20 cells/ml); October (Holland et al., 1975, Corpus Christi Bay - 60 cells/ml); summer (Holland et al., 1975, Nueces Bay - 6 cells/ml); March (Holland et al., 1975, Nueces Bay - 7 cells/ml); and November (Holland et al., 1975, Nueces Bay - 7 cells/ml). Variation in phytoplankton abundance occurs not only seasonally, but large variations may also occur daily. Stockwell (1989) documented three- to four-fold day-to-day changes in surface chlorophyll levels in Nueces Bay.

Table IV.B.1.1 Seasonal abundance and characteristic groups of phytoplankton from open bay biotopes of the study area (after Armstrong, 1987).

	Seasonal abundance (cells/ml)		Dominant
Bay System	Minimum	Maximum	Group
Aransas Bay	6 (summer)	381 (winter)	diatoms
Corpus Christi Bay	50 (summer-fall)	900 (winter-spring)	diatoms blue-green algae
Nueces Bay	7 (summer-fall)	300 (winter-spring)	diatoms blue-green algae

The close coupling of phytoplankton and zooplankton consumers makes it difficult to explain variations in phytoplankton abundance and productivity on physical factors alone. Holland et al. (1975) reported (as others have in other estuaries; e.g., Matthews et al., 1975) tremendous depletion of phytoplankton in Corpus Christi and Aransas bays occurring in the spring that was correlated with peak abundances of zooplankton. Thus, although phytoplankton production may be increased with increased nutrient loading, the effects of this increased production cannot be shown from phytoplankton abundance alone, as the increased productivity may be masked by increased zooplankton consumption.

1.4.1.2 Zooplankton

Zooplankton are essential links in the transfer of energy from autotrophic phytoplankton to higher trophic level organisms such as fish and shellfish. Dead zooplankton are also important to the detrital inventory which is vital to the regeneration processes of the estuary. Zooplankton abundance is generally reported as standing crop: number of zooplankters/m^3. Biomass, the dry weight of zooplankton/m^3, may also be useful, as dry weight can be converted to carbon units to evaluate energy flow through estuarine food webs.

Abundance of zooplankton. - In an analysis of zooplankton studies in several Texas estuaries [Nueces Estuary (Holland et al., 1975; Buskey, 1993); Guadalupe Estuary (Matthews et al., 1975; Buskey, 1993); Lavaca Bay system (Gilmore et al., 1976; Jones et al., 1986)], Longley (1994) reported zooplankton standing crops in most of these systems greater in lower bay sites than in sites near their deltas. The Nueces Estuary was the only estuary which did not fit this pattern. Zooplankton abundance was not statistically related to station location for the Holland et al. (1975) data set ($P < 0.001$). The Buskey (1993) data set, representing low inflow conditions, produced the opposite trend in which zooplankton abundances increased from mid Corpus Christi Bay-to-mid Nueces Bay-to-Nueces delta stations ($P < 0.05$). Buskey also found diurnal differences in zooplankton abundance and biomass in the Nueces Estuary. Zooplankton abundance was higher in night samples and zooplankton biomass was nearly three times greater at night than during the day.

Several studies of south Texas estuaries report zooplankton abundance to be indirectly related to water temperature and directly related to salinity (Armstrong, 1987). Holland et al. (1975) stated temperature and salinity as the most important factors regulating species composition, seasonal occurrence and distribution of zooplankton. Low salinities resulted in low abundances of more species (primarily freshwater species) and high salinity in higher abundances. Several species could be classified as estuarine as they occurred throughout the year in most all parts of the estuarine systems including: *Acartia tonsa*, *Paracalanus crassirostris*, *Oithona* spp., *Pseudodiaptomus corontus*, and barnacle nauplii. *P. crassirostris* populations were restricted in upper estuary sites, apparently a reaction to lower salinities in these sites. Other species were classified as neritic, appearing mainly in the lower estuary on a seasonal basis; their occurrences apparently determined by temperature preferences. The two copepods *Centropages velificatus* and *C. hamatus*, both classified as neritic, were separated on the basis of temperature preference: *C. velificatus* occurred in warmer water temperatures and *C. hamatus* preferred colder water. Regression analysis on the Buskey (1993) data set revealed a statistically significant inverse relationship between abundance and temperature ($P < 0.05$), but no relationship between abundance and salinity, however, the salinity range during this study was very limited (Longley, 1994).

Seasonal abundance patterns reported by Holland et al. (1975) correspond with those reported by Armstrong (1987) for central and southern Texas estuaries, namely maximum zooplankton abundance in the winter and minimum abundances in the summer and fall. Buskey (1993) found maximum zooplankton abundances in the Nueces Estuary occurred in the winter and fall, while spring and summer abundances were generally lower.

Longley (1994) compared the results of the Holland et al. (1975) study of Nueces Estuary, during a period of high inflow (September 1973 - August 1974), in which inflows exceeded 76% of all other annual inflows over the 47-year inflow record, with those of Buskey (1993), during a low inflow period (September 1987 - August 1988), in which inflows exceeded only 5% of annual inflows from the 47-year inflow record, to compare the effect of freshwater inflow on zooplankton abundance. Analysis of the two data sets revealed a statistically significant positive relationship between zooplankton abundance and inflow ($P < 0.01$). The seasonal pattern of abundance was found to differ between high and low inflow years. In the high inflow year, abundance followed the pattern noted in many other Texas estuaries, in which abundance is high during winter, a little lower during spring, and much lower in summer and fall. During the low inflow year, average abundance did not vary much, but was highest during winter and fall and slightly lower in spring and summer. Summer and fall abundances were very similar between the high and low inflow years, so the effect of low inflow was seen mainly in the spring and winter (the periods of maximum abundance in the high inflow year). Average zooplankton abundance under high inflow was 7,868/m^3 and 3,994/m^3 under low inflows.

The Holland et al. (1975) data set was long enough duration to explore the timing of inflow peaks and peaks in zooplankton abundance. Longley (1994) found zooplankton abundance peaks 4-6 months after inflow peaks, although a longer record of zooplankton abundance would be needed to adequately test this hypothesis.

Importance of microzooplankton in south Texas estuaries. - Buskey (1993) reported microzooplankton (tintinnids, non-loricate ciliates, rotifers, and nauplii) abundance in Texas estuaries (30-60 million/m^3) was at least an order of magnitude greater than in other temperate bays and estuaries studied. In Texas estuaries, the biomass of microzooplankton exceeded that of macroplankton in the Nueces and Guadalupe estuaries. Microzooplankton, with very rapid generation times (days vs. weeks or months for macrozooplankton), can respond quickly to favorable environmental conditions and must have a significant impact on nanophytoplankton standing crops through grazing. Buskey sampled microzooplankton in the Nueces Estuary about every two weeks and observed abundance peaks in the range of 80-400 million organisms/m^3. The abundance of microzooplankton vs. macrozooplankton is consistent with the distribution of phytoplankton size-classes found by Stockwell (1989) in the Nueces Estuary, in which nanophytoplankton provided the majority of the phytoplankton photosynthesis (85%) and standing crop in this estuary. These findings suggested that the nanophytoplankton-to-microzooplankton energy transfer must be an important link between autotrophs and higher level consumers in these estuaries.

Abundance patterns of the dominant zooplankter Acartia tonsa .- The copepod *Acartia tonsa* usually dominates the zooplankton of Texas estuaries. *Acartia tonsa* comprised 40- 60% of the individual macroplankton during studies in the Nueces and Mission/Aransas estuaries (Holland et al., 1975; Buskey, 1993). Lee et al. (1987) performed an analysis of *Acartia* abundance related to temperature and salinity from data obtained from studies in six Texas bay systems (Holland et al., 1975; Matthews et al., 1975; Gilmore et al., 1976; Wiersma et al., 1976; Espey, Huston and Associates, in TDWR, 1981d). Combining data from all six bay systems, they found the abundance of *Acartia tonsa* was more highly correlated with salinity than temperature. However, when the bay systems were evaluated separately, *Acartia* abundance was more dependent upon temperature than salinity in Corpus Christi Bay. *Acartia* abundance in Nueces Bay followed the statewide pattern in which salinity was more important than temperature in explaining *Acartia* abundance. There was significant seasonal variation in *Acartia* for Corpus Christi Bay.

The positive relationship between *Acartia tonsa* abundance and freshwater inflow may be explained by changes in the quality and quantity of food and/or by changes in the density of predators, such as ctenophores, accompanying inflow events (Buskey, 1993). Several other studies suggested that *A. tonsa* may be food limited at certain times in some Texas bays. *Acartia tonsa* cease feeding at chlorophyll concentrations below 1 µg/l (Reeve and Walter, 1977); concentrations of large (> 2 µ) phytoplankton chlorophyll were often found below 1 µg/l in the Nueces Estuary (Stockwell, 1989). Furthermore, egg production of *A. tonsa* has been found to be food limited under normal environmental conditions (Ambler, 1985; Durbin et al., 1983). Other studies reported temporal variation in the fecundity of copepods did not follow changes in total chlorophyll biomass, but in changes of larger chlorophyll size fractions (> 10 µ and > 20 µ) (Peterson and Bellantoni, 1987). Buskey (1993) hypothesized increases in *A. tonsa* abundances followed inflow events possibly due to increases in large size classes of phytoplankton; however, corroboration of this hypothesis is not possible as size-fractionated chlorophyll samples have not been taken in plankton studies of Texas estuaries. Alternatively, *A. tonsa* abundance may increase following inflow events may be explained by a release from predation by ctenophores. Jones et al. (1986) identified *Mnemiopsis mccradyi* (ctenophore or comb jelly) as a probable predator controlling *A. tonsa* abundance. *Acartia tonsa* may be less susceptible to flushing from the estuary or may be faster in re-establishing populations following inflow events.

1.4.1.3 Summary

Plankton are important constituents of estuarine food webs; the phytoplankton-to-zooplankton energy transfer is a major pathway between autotrophic processes and high level consumers within the estuarine system. The close coupling of phytoplankton and zooplankton consumers results in a dynamic relationship which can respond quickly to favorable conditions within the estuary promoting rapid transfer from nutrients to organic biomass. Planktonic abundance has been correlated with salinity and temperature. Seasonal patterns have been found for both phytoplankton and zooplankton. Changes in zooplankton abundances have most often been explained by variations in freshwater inflow to the estuaries. The effect of inflows is generally a tradeoff between increased nutrient loading and the flushing of plankton out of the estuary or the limitation of estuarine and marine species due to decreased salinities. Longley (1994) reported freshwater inflows having a more dramatic positive effect on zooplankton abundances in estuaries receiving little inflow in terms of bay volumes (the Nueces and Mission/Aransas estuaries both receive less than one bay volume of inflow per year). In estuaries normally receiving inflows of five to six bay volumes per year, the flushing effect of inflows above this level generally counterbalance increases in nutrient loading.

1.4.2 Benthic Communities

The open bay bottom community is not homogeneous among Texas estuaries or within a particular estuary. Patterns of distribution exist both horizontally across the estuary and vertically within the sediment along several environmental gradients. Furthermore, these patterns are not static, but vary with time and climate, both in the short-term with changing seasons and in the long-term with interannual fluctuations caused by stochastic effects such as storms and droughts. Any discussion of Texas estuaries must take into account this dynamic multi-dimensional variation.

Seasonal variables are thought to effect the benthic community structure of Texas estuaries including: salinity, temperature, sediment type, waves and currents, radiant energy, and sediment chemistry. Salinity and sediment type are the two variables used most often to explain the spatial distribution of species, abundance, and biomass of benthic fauna.

1.4.2.1 Salinity Effects on Horizontal Distributions of Benthos

Salinity has most often been used to organize Texas estuaries into zoogeographic zones (Ladd, 1951; Parker, 1959; Mackin, 1971; Blanton et al., 1971; Matthews et al., 1975; Gilmore et al., 1976; Calnan et al., 1983; Jones et al., 1986; White et al., 1985; Montagna and Kalke, 1989;1992). Although various authors have used different terms to categorize these zones, by examining only at those zones applying to the open bay bottom definition, a general model can be formulated. Kalke and Montagna (1989) recognize three generic zones relating benthic faunal communities to the gradient in salinity: a freshwater zone, an estuarine zone, and a marine zone. The freshwater zone is the upper portion of the estuary which is influenced most strongly by the freshwater source. The estuarine zone occurs where fresh and saltwater are mixed and salinities are intermediate. The boundaries of the estuarine zone are most subject to varying climatic conditions. The marine zone is that area of the estuary in which salinities approach those of the open ocean; the extent of this zone is influenced by a bay's proximity to Gulf passes.

Meiobenthos. - Montagna and Kalke (1992) studied the meiobenthos of the Guadalupe and Nueces estuaries. The average density of meiobenthos in the Guadalupe estuary was four times greater at lower bay stations than at the upper bay sites. Lower bay stations within the Nueces Estuary also had higher meiobenthic densities than upper bay sites, averaging 2.5-7 times higher than those at upper bay stations.

Taxonomic groups of organisms comprising the meiobenthic community also varied among upper and lower bay sites. Nematodes constituted 60% of the individuals of the lower bay stations but only 35% of the individuals of upper bay sites. In the Nueces Estuary nematodes comprised 50% of upper bay individuals, but more than 80% of the meiobenthic community occurred at the most marine station. Montagna and Kalke concluded that the meiobenthos was typically a marine community.

Macrobenthos. - Each of the three estuarine salinity zones have a characteristic benthic macrofauna composed of several ubiquitous and sub-ubiquitous species which tolerate very broad salinity ranges and others which are more limited to a particular range of salinity. Kalke and Montagna (1989) compiled lists of characteristic fauna for these three zones in several Texas estuaries (Table IV.B.1.2). Two species are found in all zones of each estuary except the marine zone of San Antonio Bay. These species, *Mediomastus californiensis*, a euryhaline deposit-feeding polychaete and *Mulinia lateralis*, a mactrid bivalve known for its hardiness (salinity range 5-80), are thought to have low competitive fitness but thrive under adverse conditions (Parker, 1975; Shaffer, 1983). *Mulinia lateralis* has been considered an opportunist and due to its short generation time it has been known to rapidly colonize disturbed areas (Flint and Younk, 1983). Another species of polychaete, *Streblospio benedicti*, a tube-building, surface deposit-feeder, has been found in all but the marine zones of two of the considered estuaries, and was found by Harper (1973) to prefer salinities between 10-12 .

Several species of molluscs are limited to the freshwater zone of these estuaries. Populations of *Littoridina sphinctostoma*, a gastropod mollusc, increase following peaks of freshwater inflow, apparently a breeding response related to salinity decline (Harper 1973). *Littoridina sphinctostoma* is commonly reported as a dominant gastropod of the river-influenced upper bays of the Texas coast (Parker, 1955; Harper, 1973; Calnan et al., 1983). *Rangia cuneata* is a brackish water clam in the family Mactridae which is an excellent indicator of salinity changes in coastal waters and has been studied extensively by Hopkins et al. (1973). It is commonly the dominant species from 0-15 , but apparently cannot maintain a population beyond this range as embryos and early larvae survive only between 2 and 15 (Hopkins and Andrews, 1970).

The breadth of species found in the marine zone of the three estuaries reflects the openness of the estuary to marine influence via passes to the Gulf. San Antonio Bay has been classified as a closed bay system (Kalke and Montagna, 1989) due to its lack of access to the Gulf which is reflected in the paucity of species found in its marine zone compared to the marine zones of the more open Nueces/Corpus Christi bays. Common species from this zone include *Paraprionspio pinnata*, a tube-building, surface, deposit/suspension feeding polychaete, and *Glycinde solitaria*, a polychaete also known from shallow shelf areas in the Gulf.

Diversity. - Diversity is positively correlated with salinity up to typical oceanic levels and with the openness of the bay system to colonization by marine species. As waters approach marine salinities, there are increased opportunities for colonization by numerous marine species. In contrast, the possible pool of freshwater species to colonize portions of the bay which are periodically fresh is more limited. Figure IV.B.1.2 represents diversity measurements for each benthic sample collected by a number of studies (Copeland and Fruh, 1970; Holland et al., 1975; Matthews et al., 1975; Gilmore et al., 1976; Wiersma et al., 1976) and long-term average salinities for collection sites spanning the Texas coast from Sabine Lake to Corpus Christi Bay (Longley, 1994). This plot illustrates the positive relationship between salinity and benthic

Table IV.B.1.2. Community characteristics of the macrobenthos from three salinity zones of the Nueces Estuary and San Antonio Bay (after Kalke and Montagna 1989).

Zone	Species	Bay system
Freshwater[1]	chironomid larvae	Nueces, San Antonio
	Rangia flexuosa	Nueces, San Antonio
	Mulinia lateralis	Nueces, San Antonio
	Macoma mitchelli	Nueces
	Streblospio benedicti	Nueces, San Antonio
	Mediomastus californiensis	Nueces, San Antonio
	Paraprionospio pinnata	Nueces
	Hobsonia florida	San Antonio
	Rangia cuneata	San Antonio
	Littoridina sphinctostoma	San Antonio
Estuarine[2]	*Mediomastus californiensis*	Nueces, San Antonio
	Streblospio benedicti	Nueces, San Antonio
	Cossura delta	Nueces
	Glycinde solitaria	Nueces
	Mulinia lateralis	Nueces, San Antonio
	Macoma mitchelli	Nueces
	Littoridina sphinctostoma	San Antonio
Marine[3]	*Mediomastus californiensis*	Nueces
	Streblospio benedicti	Nueces
	Mulinia maculata	Nueces
	Paraprionospio pinnata	Nueces, San Antonio
	Gyptis vittata	Nueces
	Tharyx setigera	Nueces
	Glycinde solitaria	Nueces, San Antonio
	Polydora caulleryi	Nueces
	Clymenella torquata calida	Nueces
	Phoronis architecta	Nueces
	Nuculana acuta	Nueces
	Aligena texasiana	Nueces
	Leucon sp.	Nueces
	Periploma cf. *oriculare*	Nueces
	rhynchocoels (nemerteans)	Nueces
	Schizocardium	Nueces
	Haploscoloplos foliosus	San Antonio
	Cossura delta	San Antonio
	Diopatra cuprea	San Antonio

[1] Nueces 0-34 ; San Antonio 0-10
[2] Nueces 25-30 ; San Antonio 10-12
[3] Nueces 30-45 ; San Antonio 12-32

diversity noted by many authors (Springer and Woodburn, 1960; Gunter, 1961). Montagna and Kalke (1992), in a study of the macrofaunal and meiofaunal populations of Guadalupe and Nueces estuaries, found three communities based on diversity curves: a freshwater, low diversity community; an estuarine, medium diversity community; and a high diversity marine-influenced community (Fig. IV.B.1.1).

Abundance. The relationship between benthic abundance and salinity is not as simple as that of diversity and salinity, as shown by Figure IV.B.1.2, which represents benthic faunal abundances and average salinities from the same studies mentioned in the previous discussion of benthic diversity (Longley, 1994). The relationship between benthic macrofaunal abundance and salinity seems to be more estuary specific. In some estuaries abundances are higher at low salinity sites, whereas in other estuaries abundances are higher at high salinity sites.

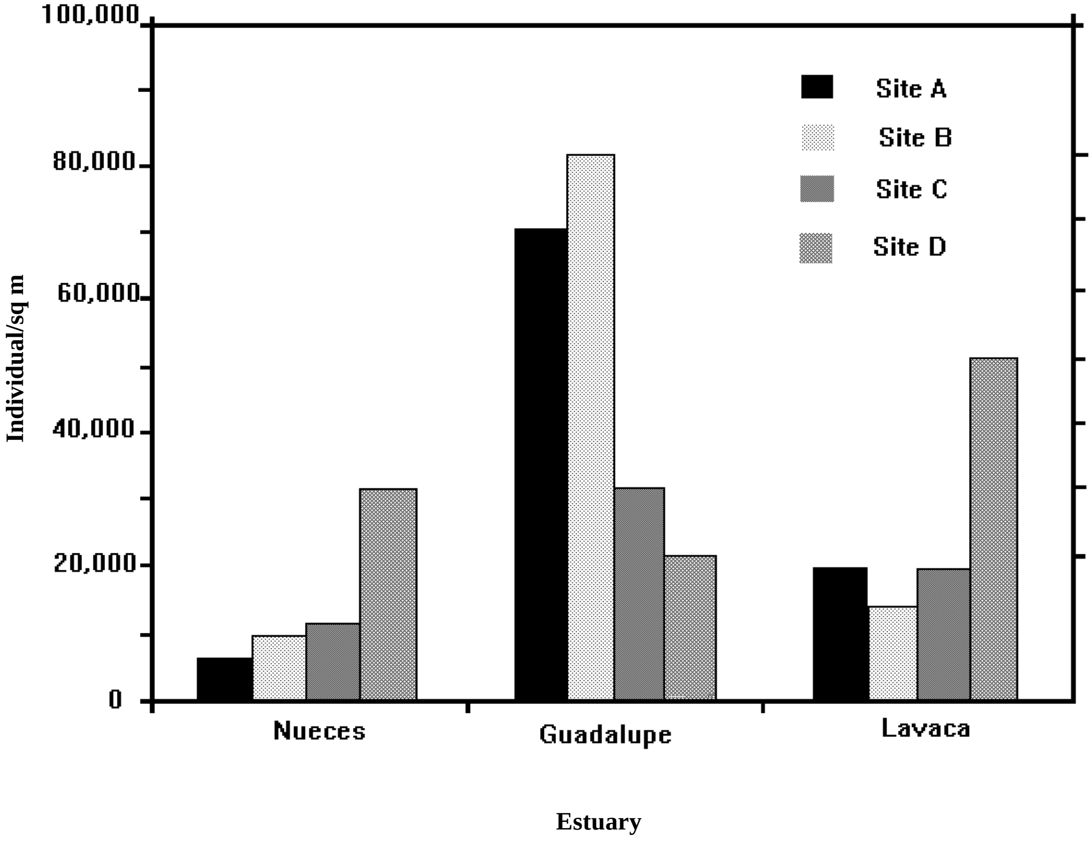
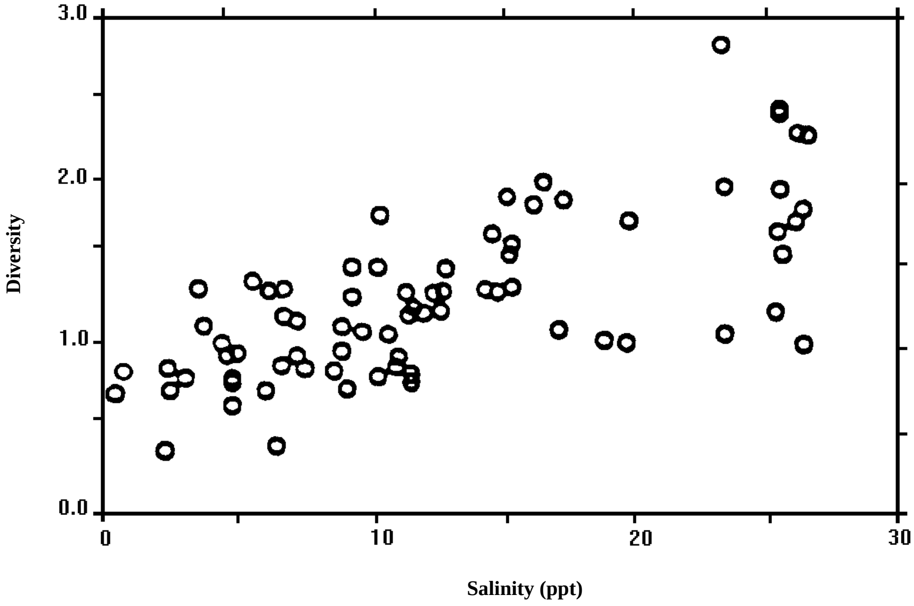


Fig. IV.B.1.1. Density of macrofauna in the Nueces Estuary representing three community types: a freshwater, low-diversity community (station A); estuarine, medium-diversity community (stations B and D); and, an estuarine high-diversity community (station C). Percent dominance vs species rank for all samples combined (modified from Montagna and Kalke, 1992).

A



B

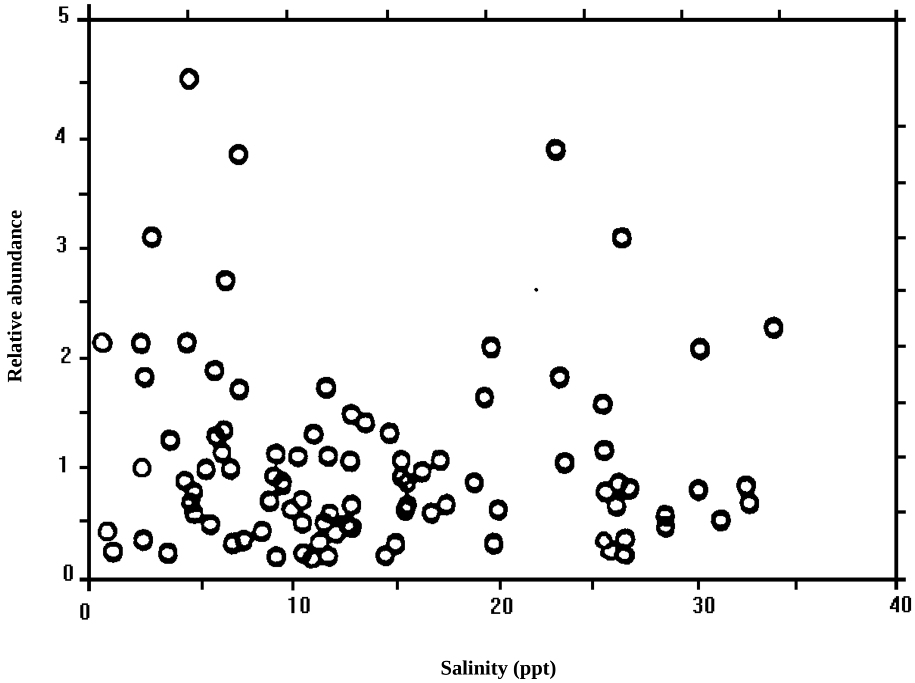


Fig. IV.B.1.2. Relationships between salinity and abundance and diversity in Texas estuaries: (A) Average benthic species diversity (H') vs average salinity; (B) Relative average abundance of benthos vs average salinity (from Longley, 1994)

Comparisons of benthic populations were made among Nueces, Guadalupe, and Lavaca/Colorado estuaries by Montagna and Kalke (1989). Similarities were found between the Nueces and Lavaca/Colorado estuaries in trends of increasing macrobenthic biomass and abundance toward Gulf-influenced portions of the estuaries. Conversely, Guadalupe Estuary stations produced an opposite trend with abundance increasing toward the freshwater-influenced stations. Further, considering all stations within the estuaries, benthic abundance was greatest in the Guadalupe Estuary followed by the Lavaca/Colorado and Nueces estuaries. Two factors were cited by Montagna and Kalke to explain this difference. First, the Guadalupe Estuary has high inflows in proportion to its volume which might result in a higher delivery of nutrients to this system. Because the Guadalupe Estuary lacks a direct connection with the Gulf, higher salinities during periods of low inflow can not be ameliorated and brackish fauna of the bay may be impacted.

1.4.2.2 The Effects of Variation in Freshwater Inflow on Horizontal Benthic Distributions

Salinity is not a stable factor in the estuarine ecosystem, but varies with seasonal rainfall patterns and also among years with interannual rainfall fluctuations brought on by storms and droughts. This variation makes the boundaries among the different estuarine zones (freshwater, estuarine, and marine) fluid. Freshwater is delivered to the estuary by streams and rivers; this inflow has two primary effects on the benthos of the open bay bottom community. First, freshwater inflow is a controlling factor of estuarine salinities. During periods of high inflow, the freshwater zone of the estuary may be expanded and the estuarine zone may even replace the marine zone. During periods of low inflow, the freshwater zone may diminish and the marine zone expand. The second effect of freshwater inflow is the delivery of nutrients to the bay which may stimulate primary productivity and benthic abundance and biomass, assuming freshwater and low salinity do not have a negative impact on benthic organisms. Salinity stress on physiology and hypoxia caused by algal bloom could reduce benthic populations. The net effect of freshwater inflow is a function of the interaction between physical processes (e.g., sedimentation, resuspension, and advection), chemical processes (nutrient enrichment), and biological processes (e.g., enhanced productivity, recruitment gains and losses via salinity tolerances) (Montagna and Kalke 1992).

Microbenthos. - There is relatively little information on the abundance and distribution of microbenthos in Texas bays. However, a comparison of the results of bacterial cell counts from two studies done in the Guadalupe Estuary during a relatively wet year in 1987 (Montagna and Yoon, 1991), and a relatively dry year in 1988 (Montagna and Kalke, 1989), suggested that high average bacterial densities may be associated with high inflows, as the average bacterial density measured in 1988 was less than half of 1987. This comparison of one component of the microbenthos was based upon limited data and did not provide confirmation of this suspected pattern.

Meiobenthos. - Montagna and Kalke (1992) studied meiofaunal populations among two estuaries with vastly different long-term inflow patterns. Over a 46-year period, between 1941 and 1987, freshwater inflow was on average 6.5 times greater in the Guadalupe Estuary than in the Nueces Estuary. Samples were also taken from three zones in the two estuaries: freshwater, estuarine, and marine. Meiofaunal density was found to decrease from the low-inflow Nueces Estuary to the high-inflow Guadalupe Estuary and within each estuary from the marine zone to the river-influenced freshwater zone. The lower densities in the freshwater-influenced zone were due predominately to decreased numbers of nematodes. An increase in the recruitment of juvenile molluscs (temporary meiofauna) was also noted at upper bay stations associated with inflow pulses. Negative response of meiobenthos to freshwater inflow may be either the result of low salinity intolerance or macrofaunal competition and/or predation.

Longley (1994) combined results from a 1972 Guadalupe Estuary study (Rogers, 1976) and a 1988 Nueces Estuary study (Montagna and Kalke, 1992) and found increases in meiobenthic density 5-8 months after large inflows. By integrating observations from these studies, an overall cycle for meiobenthos was proposed. Very high inflows or long periods of moderately high inflow may produce low salinity conditions for several months and reduce the density of meiobenthos by eliminating individuals not adapted to prolonged periods of low salinity. As salinity increases, meiofaunal density also increases and remains high for several months. At some point, perhaps after nutrients associated with the inflow event have been reduced, meiobenthic density declines and remains low until after the next major inflow.

Macrobenthos. - Montagna and Kalke (1992) compared macrofaunal standing crops from the low-inflow Nueces Estuary with those of the high-inflow Guadalupe Estuary to test the hypothesis that benthic standing crops are enhanced by freshwater inflow. The Guadalupe Estuary had 79 times more freshwater inflow over the course of the study and overall average macrofaunal densities were 41% higher in the Guadalupe Estuary. Biomasses were also slightly higher in the high-inflow Guadalupe Estuary (4.7 g/m^2) compared to the low-inflow Nueces (4.2 g/m^2).

A review of past studies in both estuaries found corroboration for the hypothesis that macrofauna production is stimulated by freshwater inflow. Harper (1973) and Matthews et al. (1975) both sampled San Antonio Bay following periods of relatively low inflow and both found macrofaunal densities lower than those found by Montagna and Kalke (1992) after a period of high inflow which occurred in 1987. Similar trends were reported for the Nueces Estuary. Parker and Blanton (1970) sampled the Nueces Estuary during a period of extreme drought in the 1950's and, although they used a smaller mesh (0.25 mm) sieve, they reported average densities of only 3000 m^{-2} in Nueces Bay and 500 m^{-2} in Corpus Christi Bay. Flint et al. (1983) sampled the Nueces Estuary using 0.5 mm sieves between July 1981 and July 1983, which covered a wet year with high inflow followed by a dry year with low inflow. Average densities were 13,800 m^{-2} in Nueces Bay and 21,070 m^{-2} lower and central Corpus Christi Bay. Since macrofaunal diversity has been shown to decrease with lowered salinities, Montagna and Kalke (1992) concluded that the higher productivity of macrofauna in zones of high inflow was associated with those few species tolerant of low salinities.

Kalke and Montagna (1991), in a study of the effects of freshwater inflow on the macrobenthos of the Lavaca River Delta and upper Lavaca Bay, reported changes of inflow effecting spatial distribution of macrofauna. Within a month following high freshwater inflow, the low salinity species chironomid larvae and the polychaete *Hobsonia florida* increased their spatial distribution in the upper bay replacing estuarine and marine species. During a period of decreased freshwater inflow, the estuarine polychaetes *M. californiensis, S. benedicti*, and *Laeonereis culveri* and *M. lateralis* and *Macoma mitchelli,* estuarine molluscs, all increased in abundance at the expense of low salinity species. This study highlights the fluidity of salinity zones within the estuary.

Kalke and Montagna (1989) present a conceptual model of the interactions between nutrient richness and habitat stability involved with freshwater inflow for estuarine benthos (Fig. IV.B.1.3). Typically, the hydrology of Texas estuaries consists of pulses of inflows followed by periods of low inflow. During or immediately after high inflows, a large quantity of nutrients is delivered to the sediments. Benthic abundances increase as low salinity species multiply and grow. At the same time, other species (generally marine or estuarine species) suffer declines from low salinity stress, and diversity decreases. As inflows decrease and salinity increases, more species take advantage of the added nutrients and diversity increases. As the benthos uses up the available nutrients, numbers decline to sizes supported by input from plankton and other sources.

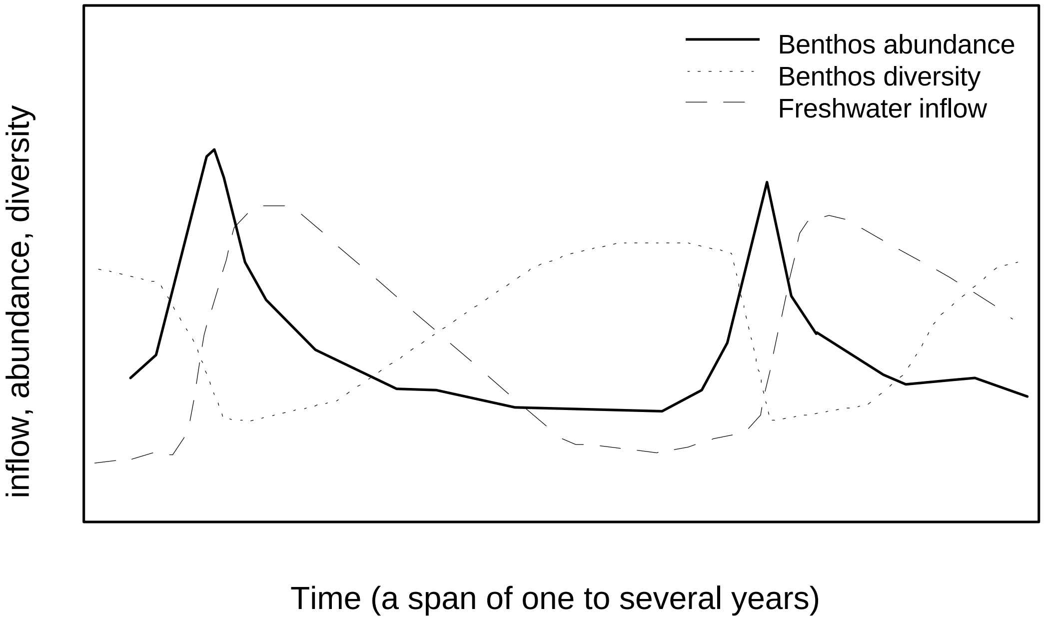


Fig. IV.B.1.3. The Kalke-Montagna conceptual model of macrobenthic dynamics in Texas estuaries (from Longley, 1994).

1.4.2.3 Seasonal Variation in Macrobenthos

Armstrong (1987) combined data from several studies of benthic macrofauna in Corpus Christi Bay (Flint and Younk, 1983; R. W. Flint, State Univ. of New York, Oswego, pers. comm.; Holland et al., 1975) to provide nine years of data exhibiting long-term seasonal variation (Fig.

IV.B.1.4). Macroinfaunal abundance exhibited a consistent trend of maximum numbers during the winter and spring period of each year. These increases were always correlated with the appearance of several bivalve molluscs in the study area (e.g., *Abra aequalis*).

Data on macroinfaunal biomass from these studies exhibited similar patterns reported for total abundance (Fig. IV.B.1.4). Standing stocks were greatest in the winter and early spring. Benthic infauna which exhibited the greatest increases in biomass were the molluscs *A. aequalis, Lyonsia hyalina floridana, Lucina multilineata,* and *Mulinia lateralis*; the enteropneust *Balanoglossus* sp. and rhynchocoels. Organisms which exhibited consistent seasonal patterns include the polychaetes *S. benedicti, Tharyx setiger,* and *G. solitaria,* and the molluscs *M. lateralis* and *L. hyalina floridana*, all of which were usually present and dominated during winter and spring. The mollusc *A. aequalis* and the enteropneust *Balanoglossus* sp. were extremely seasonal, occurring only in the winter and spring and often dominating the infaunal assemblages.

1.4.2.4 The Effects of Sediment Type on Horizontal Distributions of Benthos

Although most studies have found salinity to be the major physical factor controlling horizontal spatial distributions of benthic fauna in Texas estuaries, sediment features may also be an important factor in determining such distributions within the salinity zones. Sediment features affecting horizontal distributions include sediment particle size, sediment stability, and food concentrations within the sediment.

Microbenthos. - Although no study of Texas estuaries has attempted to correlate microbenthos with sediment type, sediments of smaller particle size such as silts and clays generally contain larger populations of bacteria and fungi than do sands, because their greater surface-area-to-volume ratios provide a larger area for colonization (Newell, 1970). In addition, larger amounts of organic matter in the sediment should also correspond with higher microbenthic density. Therefore, higher microbenthic densities might be found in estuaries with greater freshwater influence if microbenthos are not adversely affected by low salinity.

Meiobenthos. - In the only study relating meiobenthos of Texas estuaries to sediment type, Rogers (1976) found higher meiobenthic densities in silty compared to sandy sediments in San Antonio Bay. Armstrong (1987) reported that extremely flocculent silty clay surface sediments are easily resuspended and may limit small-sized meiofauna.

Macrobenthos. - Sediment type has been cited in many studies as an important factor determining macrobenthic horizontal distributions. Parker (1959) reported that soft bottom bay centers usually contained a low diversity deposit feeding community. Larger clams (e.g., *Mercenaria* and *Cyrtopleura*) were limited to the sandy sediments associated with the bay margins of large open bays because the fine silty clays of the bay centers will not support the weight of these large clams. White et al. (1983), in an extensive survey of the bay bottom communities of Texas estuaries, reported diversity generally increasing with an increase in sand content and decreasing with higher percentages of silt and/or clay. Two sites in Corpus Christi Bay which had similar salinity patterns but differed in sediment type were followed for two years by Flint (reported in Armstrong, 1987). From one site, characterized by a sediment containing

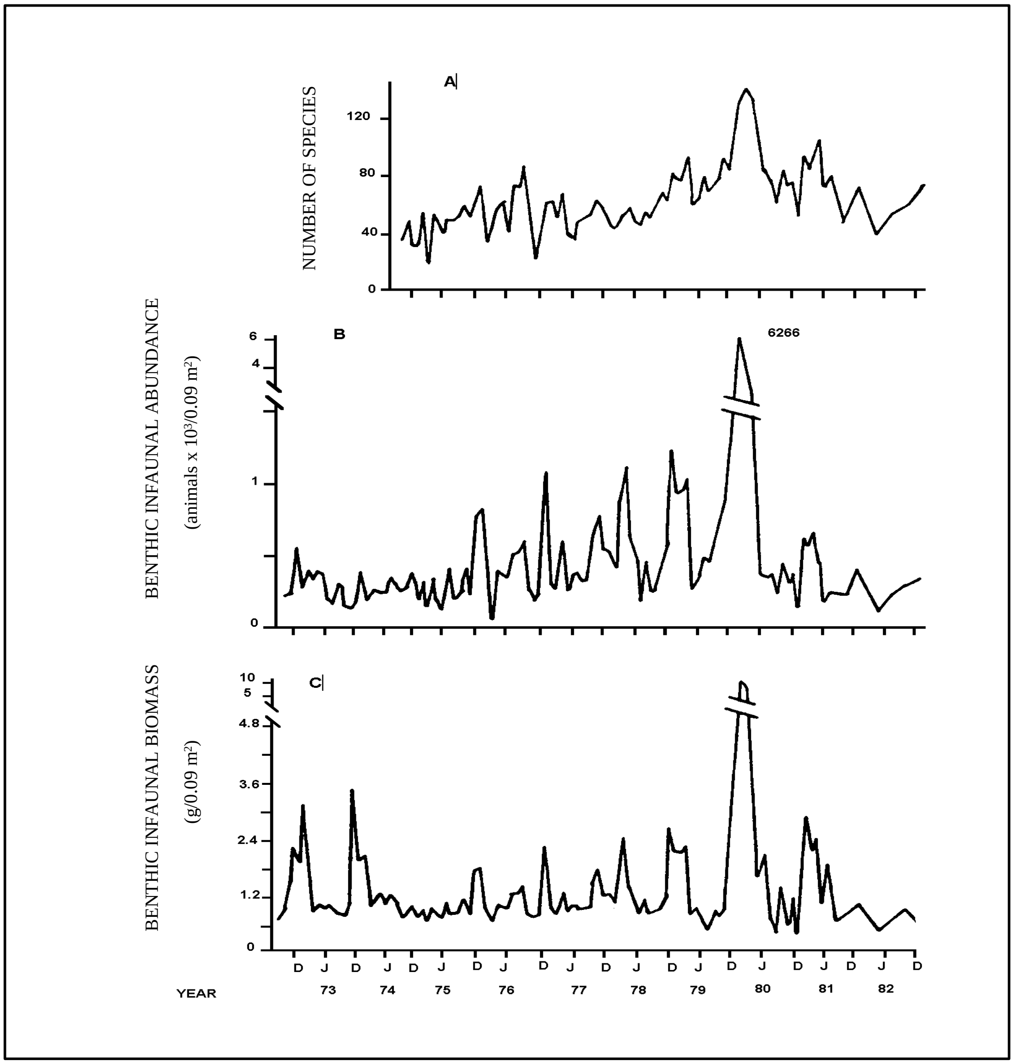


Fig IV.B.1.4. Plots of macroinfaunal species number (A); total abundance (B); and total biomass (C) over nine years for a study site in Corpus Christi Bay (from Armstrong, 1987).

90% sand, 82 species of macrofauna were collected, with a mean total abundance of 1924.5 organisms/m^2 and a total biomass of 26.7 g/m^2. In contrast, the other site with a clay content of more than 70% , 22 species were observed with a mean total abundance of 2,237.6 organisms/m^2 and a total mean biomass of 62.8g/m^2.

Flint and Kalke (1986) attempted to characterize physical gradients infauna, which were considered members of the same community assemblage, might use to partition a common habitat. Of the variables chosen to discriminate among species on the basis of habitat utilization, sediment type, measured as increasing clay content (which was correlated with increased carbon content), was the most important, accounting for 45.3% of community variation. Their results allowed them to categorize 13 dominant taxa of Corpus Christi Bay as to preference for sediment type. The polychaetes *P. caulleryi*, *Gyptis vittata* and *Paraprionospio pinnata* along with the enteropneust *Schizocardium sp.*, occurred in more clay-like, organically-rich sediments. In contrast, the polychaetes *Magelona phyllisae, Onuphis eremita oculata, Owenia fusiformis,* and *Nassarius acutus* inhabited very sandy sediments. An intermediate group including the polychaetes *Glycera americana, Mediomastus californiensis, S. benedicti,* and *Heteromastus filiformis* and the bivalve mollusc *M. lateralis* were also segregated, occurring in a bottom habitat characterized by a moderate amount of sand and clay.

These studies suggested that, within zoogeographic zones based on salinity tolerances, sediment type is an important factor influencing horizontal distributions of macrobenthos. In Corpus Christi Bay, and probably other open bay bottoms along the Texas coast, benthic faunal communities of muddier sediments are generally less diverse but exhibit greater abundance and productivity than comparable communities of sandier sediments (Whitlach, 1982).

1.4.2.5 The Effects of Biological Interactions on Benthic Horizontal Distributions

Although few studies have been done on the effects of biological interactions on horizontal distributions of benthos in Texas estuaries, several authors have mentioned effects of such interactions. Rhoads and Young (1970), in a process they termed "trophic group amensalism", proposed that subsurface deposit feeders of the open bay bottom may limit the distribution of suspension feeders in these sediments by increasing the water content of surface sediments, through burrowing activities, making them more easily resuspended. This results in increased quantities of suspended material in the water overlying the sediments, which tends to clog the filtering apparatus of suspension feeders.

Another form of indirect interaction among macroinfauna was found to be beneficial rather than inhibiting. Tubes of *Diopatra cuprea*, a polychaete prevalent in Texas open bay bottoms, may provide refuge from predation for other macroinfauna (Woodin, 1982). Tubes at the sediment surface tend to vary the local hydrodynamic environment and create a more stable microhabitat for other macroinfauna (Eckman et al., 1981).

In addition to this indirect effect, macroinfauna can act directly to limit the distributions of other fauna by preying on the larval stages of potential colonizers. Suspension feeders have been observed capturing larvae of many infaunal species when they are still in the water column (Woodin, 1976). Deposit feeders consume newly settled infaunal larvae and also disrupt settlement processes by their reworking of the sediments; therefore, direct interactions by the infauna may be strong enough and frequent enough to determine which species can coexist. Large populations of the surface deposit feeding spionid polychaete *Paraprionospio pinnata* may limit the colonization of sites within Corpus Christi Bay due to their predation on larvae and disruption of settlement processes (Flint and Kalke, 1986). Reliance on different food sources may allow high densities of infauna occupying the same physical habitat to reduce competitive pressures.

1.4.2.6 Vertical Distributions of Benthic Fauna

The spatial extent of the open bay bottom community extends in two dimensions, not only horizontally across the bottom, but vertically within the sediment. Differences in vertical space utilization is apparently an effective mechanism for reducing interspecific competition in soft-bottom communities (Peterson, 1979; Whitlatch, 1980; Wilson, 1981). The vertical distributions of fauna are affected by such physical variables as the depth of available food and oxygen.

Meiobenthos. - Montagna and Kalke (1992) sampled the meiofauna from Nueces Estuary along a salinity gradient from freshwater to marine influenced sites. More animals were found in the surface sections at 0-1 cm (0.931 $10^6/m^2$), of all but the most marine station, than in the subsurface section of 1-3 cm (0.477 10^6/m2). At the most marine site, densities were lower in the surface section (2.68 $10^6/m^2$) than in the subsurface section (3.055 $10^6/m^2$), due almost entirely to higher densities of nematodes.

Macrobenthos. - Montagna and Kalke (1992) measured the vertical distribution of macrofauna from 0-3 cm and 3-10 cm along a salinity gradient within the Guadalupe and Nueces estuaries. Within the high-inflow Guadalupe Estuary macrofaunal density, biomass and overall community structure varied temporally and among stations. Higher biomasses in the deeper sections (3-10 cm) usually occurred during June (except in the freshwater station) and were generally more prevalent at marine-influenced stations. There were high densities in the surface section (0-3 cm) during April and June in the freshwater stations. The biomass and density of the surface section was dominated by molluscs and the deep section by polychaetes at freshwater sites. Molluscs dominated the biomass in both sections (0-10 cm), but polychaetes dominated the density of marine-influenced stations. The overall mean biomass in the surface section was 2.82 g/m^2, and the density was 15,800 individuals/m^2. Overall mean biomass in the bottom section (3-10 cm) was 1.85 g/m^2 and the mean density was 3,450 organisms/m^2.

In the low-inflow Nueces Estuary there was generally less biomass in the surface 3 cm (1.58 g/m^2) than in the subsurface (3-10 cm) sediments (2.78 g/m^2). In all but the most marine-influenced station, abundance was almost twice as high in the surface sediments ($5.56x10^3/m^2$) as in the subsurface sections ($2.47x10^3/m^2$). At the most marine station, which generally had higher densities of deeper dwelling organisms, a large recruitment of the polychaete *P. caulleryi* (total density reached $68.2x10^3/m^2$) caused the average densities to be similar in the surface ($6.92x10^3/m^3$) and subsurface ($6.75x10^3/m^2$) sections. Molluscs dominated density and biomass of surface sections, but polychaetes dominated the density of subsurface sections at freshwater stations. Polychaetes dominated both density and biomass of both surface and subsurface sections of marine-influenced stations (Montagna and Kalke, 1992).

Presence of species at different sediment depths was a useful variable to distinguish the niche space of species occupying the same physical habitat. For example, the polychaetes *Paraprionospio pinnata* and *P. caulleryi* were both found in organically-rich sediments with high clay content and with similar preferences for other physical parameters measured. These species were separable by the fact that *P. caulleryi* was found much deeper in the sediment than was *P. pinnata* (Flint and Kalke, 1986).

Flint and Kalke (1986) offered an extensive review of the effects of bioturbation by large infauna on the vertical distribution of polychaetes in Corpus Christi Bay. Prior to colonization by the large funnel-feeding enteropneust *Schizocardium* sp., a mid-estuary station in Corpus Christi Bay had been dominated by tube-dwelling, surface deposit-feeding spionids, such as *Paraprionospio pinnata* and *S. benedicti,* which confined their populations to the upper 3 cm, and by *M. californiensis,* a burrowing deposit feeder, which occurred to depths of 10 cm. Following establishment of enteropneust biomass concentrations in deeper sediments, the burrowing, subsurface, deposit-feeding polychaete *G. vittata* and the tubiculous polychaete *P. caulleryi* colonized the site to a depth of 20 cm. Species richness increased from an average of four prior to *Schizocardium* colonization to an average of 15 after colonization. Macrofaunal density increased from 2974/m^2 to 19,039/m^2. Macrofaunal biomass increased in the deeper section (10-20 cm) from 58.9 g/m^2 to 146.0 g/m^2. A similar situation involving stimulatory effects of bioturbation by a large burrowing ophiuroid are also reported for a site in Corpus Christi Bay.

A general trend of high densities of small organisms with short turnover rates are found in the surface sediments of Texas bays. In the long run, this provides more biomass for consumption by higher trophic levels. Deeper dwelling animals which are larger and less abundant are not as easily incorporated into the food chain because of their deep burrowing activities (Kalke and Montagna, 1991).

1.4.3 Nektonic Communities

Nekton is a collective term for those organisms which can swim through the water column in any direction regardless of water currents. Nektonic organisms include epibenthos such as shrimp and crabs which live on the sediments, large jellyfish and the numerous fish species occupying the water column. Due to their mobility, nektonic organisms are generally less affected by small scale changes within the estuary than are benthic and planktonic organisms. Most nekton, such as fish, also have longer life spans than benthic or planktonic fauna. Because of their longer life spans, nektonic organisms may be viewed as integrators of environmental fluctuations over extended periods of time. Nektonic production, especially fish production, can thus be considered a measure of an aquatic ecosystem’s overall health and long-term trends (Price, 1979). Many nektonic species are also of commercial (e.g., shrimp) or recreational (e.g., red drum and spotted seatrout) value. Because of the commercial and recreational value of nektonic animals, long term data sets are most available for this class of organisms in Texas estuaries; due to the longer life spans of nekton, these data sets are especially useful in assessing overall conditions and trends within the estuary.

1.4.3.1 Data Sets

Extensive data sets are available for estuarine nekton of the Texas coast. The Texas Parks and Wildlife Department, Coastal Fisheries Division (TPWD-CF) independent monitoring program is an extensive ongoing sampling project in Texas estuaries. Random monthly trawl sampling from salinity zones within each Texas estuary was begun in 1983. Gill net sampling, which selectively samples large fish, was begun in 1977. The gill net program was changed in 1981 to randomly sample one-mile grids. Sampling procedures for these data are standardized and well-documented, providing more reliable density estimates than harvest data which are influenced by market activity and unreliable self-reporting (Green and Thompson, 1981). Long-term harvest data for commercial fish and shellfish from Texas estuaries are available from several sources. Annual catch data from 1962-1976 commercial harvests of coastal fish and shellfish are reported in Texas Landings, a cooperative publication of the US Department of Interior and TPWD (Farley, 1963-1969), and the US Department of Commerce and TPWD (Farley, 1970- 1978). Commercial landings data from 1977 are available from TPWD (e.g., Quast et al., 1988). Similarly, the 1959- 1976 annual catch and effort data from the Texas shrimp fishery are available in Gulf Coast Shrimp Data, a publication of the US Department of the Interior (1960-1969) and the US Department of Commerce (1970- 1978), which was prepared in cooperation with Gulf state fishery agencies. Commercial shrimp data from 1978 is available from the US Department of Commerce, National Marine Fisheries Service. The TPWD independent monitoring program data set will be worked up as a year two project for the CCBNEP.

1.4.3.2 Habitat Partitioning

Common nekton of the open bay areas of the Nueces and Mission/Aransas estuaries are presented in Table IV.B.1.3. Although these species share a common habitat, each species has a unique combination of biological adaptations with which it may partition the habitat lessening competitive pressures. Factors often cited for such partitioning within open bay areas of Texas estuaries include: life history patterns, feeding strategies and salinity preferences. An examination of Table IV.B.1.3 reveals the differential attributes of common open bay nektonic species which might be used for niche partitioning.

Feeding strategies. - Nektonic organisms are the chief consumers of biomass produced by planktonic and benthic fauna of the open bay. Feeding strategies of these organisms include planktonivores, detritivores, and predators. The importance of benthic fauna to these nekton can be seen in the large number of organisms whose food preferences include constituents of the benthos (Table IV.B.1.3).

Some of the most abundant species of the open bay are planktonivores, feeding primarily upon zooplankton and phytoplankton. Included in this group are *Anchoa mitchilli*, *Brevoortia patronus*, and *Menidia beryllina*. Because these fishes feed low in the food chain, they stay relatively abundant in the estuary (Darnell, 1958). *Mugil cephalus* is the prime detritivore of the open bay which takes mouthfuls of surface sediment and digests what is nutritionally valuable. Other nekton which are not solely detritivores, but which include detritus in their diet, include penaeid shrimp, *A. mitchilli*, *Arius felis*, *Micropogonias undulatus*, *Lagodon rhomboides*, and *Bagre marinus*. Most of the nekton of the open bay are considered predators of benthic fauna.

Table IV.B.1.3 Dominant nekton of the open bay communities of the Nueces and Mission-Aransas estuaries including seasonal abundance patterns and preferences for food and salinity which might be used for habitat partitioning. (adapted from Armstrong 1987).

Species	Peak abundance &/or bay presence	Food Preference	Estuarine salinity preference
Penaeus aztecus (brown shrimp)	Spring	Detritus, polychaetes, larval fish, molluscs (Farfante, 1969)	15.0-19.9[1] 15.0-25.0[2]
Penaeus setiferus (white shrimp)	Summer	Detritus, molluscs, larval fish, polychaetes (Farfante, 1969)	10.0-14.9[1] density < as salinity > from 15.0-39.0[2]
Callinectes sapidus (blue crab)	Winter-Spring	Molluscs, polychaetes, small crustaceans (Darnell, 1958; Farfante, 1969; Lindner & Cook, 1970)	10.0-20.0[1] no statistically significant relationship[2]
Callinectes similis		Barnacles, molluscs, detritus, polychaetes, small crustaceans (Darnell, 1958)	
Lolliguncula brevis (bay squid)	Summer-Fall		
Squilla empusa (mantis shrimp)		Small shrimp, crabs (Peterson & Peterson, 1979)	
Trachypenaeus similis (roughback shrimp)			
Neopanope texana (mud crab)			
Palaemonetes spp. (grass shrimp)		Epiphytes, polychaetes, small crustaceans (Peterson & Peterson, 1979)	
Paralichthys lethostigma (southern flounder)		Small fish, crabs, mysids, shrimp, amphipods, squid (Darnell, 1958; Adams, 1976; Day, 1960)	20.0[2]
Anchoa mitchilli (bay anchovy)	Late Spring-Fall	Mysids, detritus, zooplankton (Darnell, 1958; Thomas et al., 1971; Rogers, 1977; Dineen & Darnell, 1976)	
Sciaenops ocellatus (red drum)		Crustaceans, molluscs, small fish, polychaetes (Darnell, 1958; Hildebrand & Schroeder, 1927; Day, 1960)	< 15.0[1]
Cynoscion nebulosus (spotted seatrout)		Fish, crustaceans (Darnell, 1958; Rogers, 1977; Hildebrand & Schroeder, 1927; Day, 1960)	5.0-20.0[1]
Cynoscion arenarius (sand trout)	Spring-Summer	Fish, mysids, crabs, polychaetes, molluscs (Rogers, 1977; Hildebrand & Schroeder, 1927)	
Leiostomus xanthurus (spot)	Spring	Polychaetes, molluscs, small crust., young fish (Darnell, 1958; Thomas et al., 1971; Hildebrand & Schroeder, 1927; Dineen & Darnell, 1976)	
Brevoortia patronus (Gulf menhaden)	Spring	Phytoplankton & zooplankton (Darnell, 1958; Hildebrand & Schroeder, 1927; Dineen & Darnell, 1976)	density < as salinity > from 15.0-39.0[2]
Arius felis (sea catfish)	Summer	Detritus, benthic invert. (Dineen & Darnell, 1976)	
Micropogonias undulatus (Atlantic croaker)	Winter-Spring	Polychaetes, molluscs, detritus, shrimp (Darnell, 1958; Hildebrand & Schroeder, 1927; Dineen & Darnell, 1976)	20.0-30.0[2]

Table IV.B.1.3. Continued.

Species	Peak abundance &/or bay presence	Food Preference	Estuarine salinity preference
Archosargus probatocephalus (sheepshead)			
Lagodon rhomboides (pinfish)		Vegetation, detritus, small crust., polychaetes (Darnell, 1958; Adams, 1976)	30.0-35.0[2]
Bagre marinus (gafftop catfish)		Detritus, benthic invert. (Dineen & Darnell, 1976)	
Pogonias cromis (black drum)		Molluscs, esp. Mulinia (Andrews, 1971; Morris, 1973; Hildebrand & King, 1978)	
Symphurus plagiusa (blackcheek tonguefish)	Late Spring-Summer		
Stellifer lanceolatus (star drum)	Late Spring-Summer		
Opsanus beta (Gulf toadfish)		Polychaetes, amphipods, anemones, small fish, molluscs (Thomas et al., 1971; Hildebrand & Schroeder, 1927)	
Menidia beryllina (inland silverside)		Small crust., plankton, juvenile shrimp (Darnell, 1958; Hildebrand & Schroeder, 1927)	
Mugil cephalus (striped mullet)		Detritus, benthic diatoms (Darnell, 1958)	26.0[3]

[1] Gunter, 1950
[2] Longley, 1994
[3] Ward & Armstrong, 1980

The crustaceans *Callinectes* spp. and *Squilla empusa* seek out bivalve molluscs, smaller crustaceans and polychaete worms. *M. undulatus* and *Leiostomus xanthurus* are two of the most abundant fishes of Texas estuaries and both predate primarily on benthic invertebrates. *Pogonias cromis* is known to feed heavily on *Mulinia lateralis*.

Life history. - In addition to feeding strategies, estuarine nekton have different life cycle patterns which further partition the open bay nektonic community. Two groups of open bay nekton can be defined based on differences in spawning migration patterns. One group is composed of nekton which spend their entire life cycles within the estuary seldom moving to the Gulf and are thus entirely dependent on estuarine conditions for feeding and spawning (e.g., *Cynoscion nebulosus*). The other group consists of nekton which spawn in near coastal waters or Gulf passes (e.g., shrimp, *Callinectes sapidus,* and *Sciaenops ocellatus*) or offshore (*Micropogonias undulatus*), and then migrate to estuaries as they mature into post-larvae and juveniles. In general, abundance and biomass of nekton are reportedly lowest in the fall when adult Gulf spanners are absent from estuarine open bay areas (Armstrong, 1987). The newly spawned fish and shellfish begin migrating into the estuary through the winter and early spring, and the abundance of these populations increase to a maximum in the spring. Although mortality is usually high for juveniles, growth is so rapid that for most species maximum biomasses occur in the summer. Differences in the timing of spawning and migration cycles allow similar species to be temporally separated; this factor is illustrated in Table IV.B.1.3 by the column peak abundance and/or bay presence. Because estuaries are important nursery grounds for many nekton species, estuarine nektonic communities are often dominated by juveniles. This fact must be kept in mind when assessing the possible effects of varying physical conditions within the estuary on nektonic populations, as juveniles may have different physiological tolerances and requirements than adults.

Salinity preference. - The environmental gradient most often used to explain the distribution of nekton within the estuary is salinity. Several studies with various sampling methods and durations have attempted to estimate salinity preferences of nekton within Texas estuaries (e.g., Hoese, 1960; Hedgpeth, 1967; Simmons and Breuer, 1962). In addition, various laboratory studies have also attempted to determine salinity preferences of nekton (e.g., Zein-Eldin, 1963; Zein-Eldin and Griffith, 1969; Keiser and Aldrich, 1976; Holt and Banks, 1989; Wohlschlag, 1977; Wohlschlag and Wakeman, 1978). Within the study area, Gunter (1945; 1950) used differential catch rates of nekton within the Mission/Aransas Estuary to estimate salinity preferences of nekton (see Table IV.B.1.3). Longley (1994) used data from the TPWD-CF independent monitoring program, mentioned previously, to compare the catch rates (densities) among major estuarine systems of the Texas coast each with a different salinity regime. Analysis was done to determine statistically significant differences among mean catch rates for each estuary for both trawl and gill net data. Regression analysis was then done relating the mean catch rate groups to mean salinities found within these groups. Statistically significant ($P < 0.05$) or near significant ($P < 0.15$) were found for all trawl data sets except that for blue crabs, enabling an estimate of optimum salinity levels for those nekton studied to be made (see Table IV.B.1.3). No statistically significant regressions were found for the gill net data set, suggesting that the larger fish caught by gill nets may be less sensitive to salinity regimes than the smaller fish caught in trawls. Besides estimating salinity preferences, this analysis also reveals the high production of nekton within the study area as trawler and gill net catch rates from the Nueces and Mission/Aransas estuaries were either among the highest catch rate group or among the next highest catch rate group for every nektonic species considered. Powell and Green concluded, from their results and the results of other field studies and laboratory experiments, that increases in mean salinities above 25 . within an estuary could reduce the densities of *Penaeus setiferus* and *B. patronus*. Decreases in salinities below 15 or above 30 could reduce densities of *P. aztecus*, small *M. undulatus*, and small *Paralichthys lethostigma*. *Lagodon rhomboides* densities were highest at estuarine salinities of around 30 . No relationship between salinity and gill net catches of larger *P. cromis*, *P. lethostigma*, *B. patronus*, *M. cephalus*, *S. ocellatus*, or *C. nebulosus* was found, therefore, a reduction in freshwater inflow would not immediately affect these species. Such reductions may have longer term effects on species dependent upon these habitat types if substantial vegetation or sediment changes accompany the inflow reductions.

The case of penaeid shrimp: a possible example of niche partitioning. - Penaeid shrimp have similar feeding strategies and food preferences. *Penaeus aztecus* spawns offshore year-round with a peak spawn in the fall. Recruitment of juvenile shrimps on estuarine nursery grounds peaks during spring (Copeland and Truitt, 1966). *Penaeus aztecus* generally prefer salinities of between 15-25 within the estuary (see Table IV.B.1.3). As the juvenile shrimp grow they migrate to progressively deeper water within the estuary eventually leaving for offshore spawning grounds. *P. setiferus* spawns at least once between March and September, and possibly twice, spring and fall. Migration into the estuarine nursery grounds occurs during the summer, usually following the peak migration of juvenile *P. aztecus*. Juvenile *P. setiferus* seek shallower, lower salinity portions of the estuary (preferred salinities below 15). As they increase in size, *P. setiferus* also move to deeper estuarine waters, and eventually to offshore spawning grounds (Britton and Morton, 1989). Thus, two species with similar feeding strategies which might potentially compete for the same resources are segregated by differences in spawning migration cycles and salinity preferences.

1.4.3.3 Freshwater Inflow and Fisheries Harvests

The commercial fisheries harvest data, mentioned earlier in this section, represents the longest data base of estuarine faunal abundance available for Texas estuaries. These data span three decades, during which time coastal fisheries experienced a wide range of environmental conditions. Although these data are extensive, potential sources of error may occur from incomplete and inconsistent data reporting, concerns about the measures of fishing effort, and questions of whether landings from one estuary include catch from adjacent estuaries (Longley, 1994). In addition, this harvest data does not include recreational catch. While these are serious problems, to date no other data set has been found long enough to establish significant statistical relationships among environmental conditions and estuarine faunal abundances.

Up to 97.5% of the fishery species harvested from the Gulf coast are considered estuarine dependent, as they depend upon the estuary for food and/or protection for part or all of their life cycles (Boesch and Turner, 1984). Not all Texas estuaries are equal producers of fishery harvests. From 1980-1987, 35% of shellfish (bay shrimp, crabs, and oysters) harvested in major Texas estuaries were taken in the Trinity-San Jacinto Estuary. However, on the basis of harvest rate (lbs harvested/acre of water surface/yr) the Mission/Aransas Estuary was the highest producer, producing 49.9 lbs ac^{-1} yr^{-1} compared to 29.1 lbs ac^{-1} yr^{-1} for the Trinity-San Jacinto Estuary. The Nueces Estuary produced an average of 15.7 lbs ac^{-1} yr^{-1} over this period. Commercial finfish harvests were likewise greatest in the Trinity-San Jacinto Estuary, but again areal production rates were higher in the Nueces and Mission/Aransas estuaries (2.5 lbs ac^{-1} yr^{-1} and 1.5, lbs ac^{-1} yr^{-1} respectively) than in the Trinity-San Jacinto Estuary (1 lbs ac^{-1} yr^{-1}.).

Fishery harvests not only vary among estuaries, but also inter-annually within an estuary. In Texas, Hildebrand and Gunter (1953) were the first to demonstrate a significant relationship between rainfall and the harvest of *Penaeus setiferus*. Other studies on relationships between freshwater inflow and fisheries harvests from Texas estuaries included Gunter and Hildebrand (1954), Gunter and Edwards (1969), Hackney (1978), Powell (1979), Texas Department of

Water Resources (1980a, 1980b, 1981a, 1981b, 1981c, 1982d, 1983), Armstrong (1982), and Mueller and Matthews (1987). Relationships between biological communities and changes in their physical environment brought about by climatic changes are complex and far-reaching. Biologists often find connections between environmental parameters and fisheries, without knowing the causative mechanism behind such connections (Knauss, 1979). Even without such knowledge, significant correlations among empirical data may lead to better understandings of causative factors, as well as provide a tool for forecasting fisheries production, when a lack of knowledge prevents the development of a deterministic model (Ulanowicz et al., 1982).

Such relationships have been developed explaining variation in fisheries harvests in Texas estuaries by regression equations relating harvest to freshwater inflows. These equations were first developed by the Texas Department of Water Resources (TDWR) for a series of reports on the influence of freshwater inflows on Texas estuaries. The report produced for the estuaries within the study area provided 52 statistically significant regression equations providing insight into variation in *P. setiferus*, *P. aztecus*, *C. sapidus*, *C. nebulosus*, *S. ocellatus*, and *P. cromis* harvests in the Nueces and Mission/Aransas estuaries (TDWR, 1981a). Virtually all harvest responses to spring (April-June) and late fall (November-December) inflows are estimated to be positive for increased inflow in these seasons. In addition, most estimated harvest responses to increased summer (July-August) inflow are also positive. Although several shellfish organisms (e.g., *P. setiferus* and *C. sapidus*) are described to relate positively to winter (Jan.-March) inflow, all fisheries components containing fish species (e.g., *C. nebulosus*, *S. ocellatus*, and *P. cromis*) may relate negatively to winter inflow. Harvest responses to autumn (Sept.-Oct.) inflow are more variable. In general, most shellfish relate positively to autumn inflow, whereas fish relate negatively. Exceptions occur with the positive relationships of *C. nebulosus* and *S. ocellatus* harvests to Mission/Aransas estuary inflow during autumn.

The regression equations relating inflow to fisheries harvests show similarities and unique differences among estuaries in their responses to freshwater inflow, and competitive responses within an estuary among fisheries nekton with differing requirements for inflow. Although the equations do not represent a causal relationship between inflow and fisheries harvests, they do illustrate the best empirical correlation between freshwater inflow and faunal abundance currently available for Texas estuaries, and are a useful tool to better understand possible causative mechanisms inherent in the response of the open bay community to variations in freshwater inflow. Furthermore, these regression equations form the backbone of all comprehensive management plans for Texas estuaries.

1.5 Ecosystem Processes

1.5.1 Energy Flow

In order to address the relative importance of different components of estuarine food webs, it is useful to view the food webs on the basis of carbon production and flow between trophic components. A hypothesized food chain with estimated carbon production and transfer rates for trophic components of Nueces Estuary, is illustrated in Figure IV.B.1.5.

1.5.1.1 Primary Production

Phytoplankton potentially contributes 62.1 % of the total carbon within the system, whereas seagrass beds and *Spartina* marshes potentially contributes another 30.5% (Fig. IV.B.1.5). Although the estimates of primary production carbon (other than for phytoplankton) available to consumers within the estuary allows a comparison of the relative importance of these sources, the actual values represent maximum potentials and should not be taken as representative of conditions within the open bay community, as these values assume all primary production is exported.

Phytoplankton productivity. - Primary productivity rates have been measured for several Texas estuaries, including the Nueces Estuary, using the diurnal curve or carbon-14 methods. These rates, standardized by procedures in Flint (1984) as reported by Longley (1994), ranged from 0.048 to 1.76 g C/m^2/day for the Nueces Estuary (Odum and Wilson, 1962; Flint, 1984; Stockwell, 1989). A comparison of these rates with those presented by Boynton et al. (1982) revealed that Texas estuaries are among the more productive river dominated estuaries known.

Productivity rates are affected by turbidity, seasonal temperature variation, flushing rate and nutrient concentrations. In a trend analysis of phytoplankton chlorophyll concentrations and DIN inputs, Boynton et al. (1982) reported chlorophyll concentrations in central portions of estuaries as positively correlated with DIN inputs. Flint et al. (1983) developed a prediction equation for daily phytoplankton productivity in Nueces Estuary from salinity, water temperature, ammonia concentration, average total daily sunlight for the sample month, secchi disc depth, station water depth, and average water surface sunlight for the sampling day. Stockwell (1989) found salinity, temperature and total nitrogen/m^2 were significant in explaining primary productivity. The most useful variables in explaining primary productivity were chlorophyll concentrations and light availability. Whitledge (1989) presented evidence that nitrogen is the chief potential nutritional limit to phytoplankton productivity in the Nueces Estuary. Increases in freshwater inflow may increase primary productivity. Freshwater inflow volumes were correlated with higher chlorophyll concentrations in San Antonio Bay, but the regression explained only 39% of chlorophyll variation (Stockwell, 1989). Longley (1994) reported an apparent positive correlation between chlorophyll concentrations and low to moderate inflow for 30 days prior to sampling, but a slow decrease in concentrations as inflow increases for an eight-year data set from San Antonio Bay. This relationship was explained as phytoplankton responding to increased nutrients accompanying inflow events up to the point when the physical removal of phytoplankton due to flushing surpasses the increased production due to nutrient increases. No increases in chlorophyll levels were found following a 36% increase in freshwater inflow during a study of the Nueces Estuary, which may reflect the small direct effect of inflow on estuarine processes within this estuary (Whitledge, 1989).

A majority (93-96%) of the carbon productivity within the Nueces Estuary occurred in the nanophytoplankton size class (< 20 µm), as a result of the importance of ammonia as a nitrogen source in this estuary (Stockwell, 1989). As much as 85% of the ammonia uptake was found to

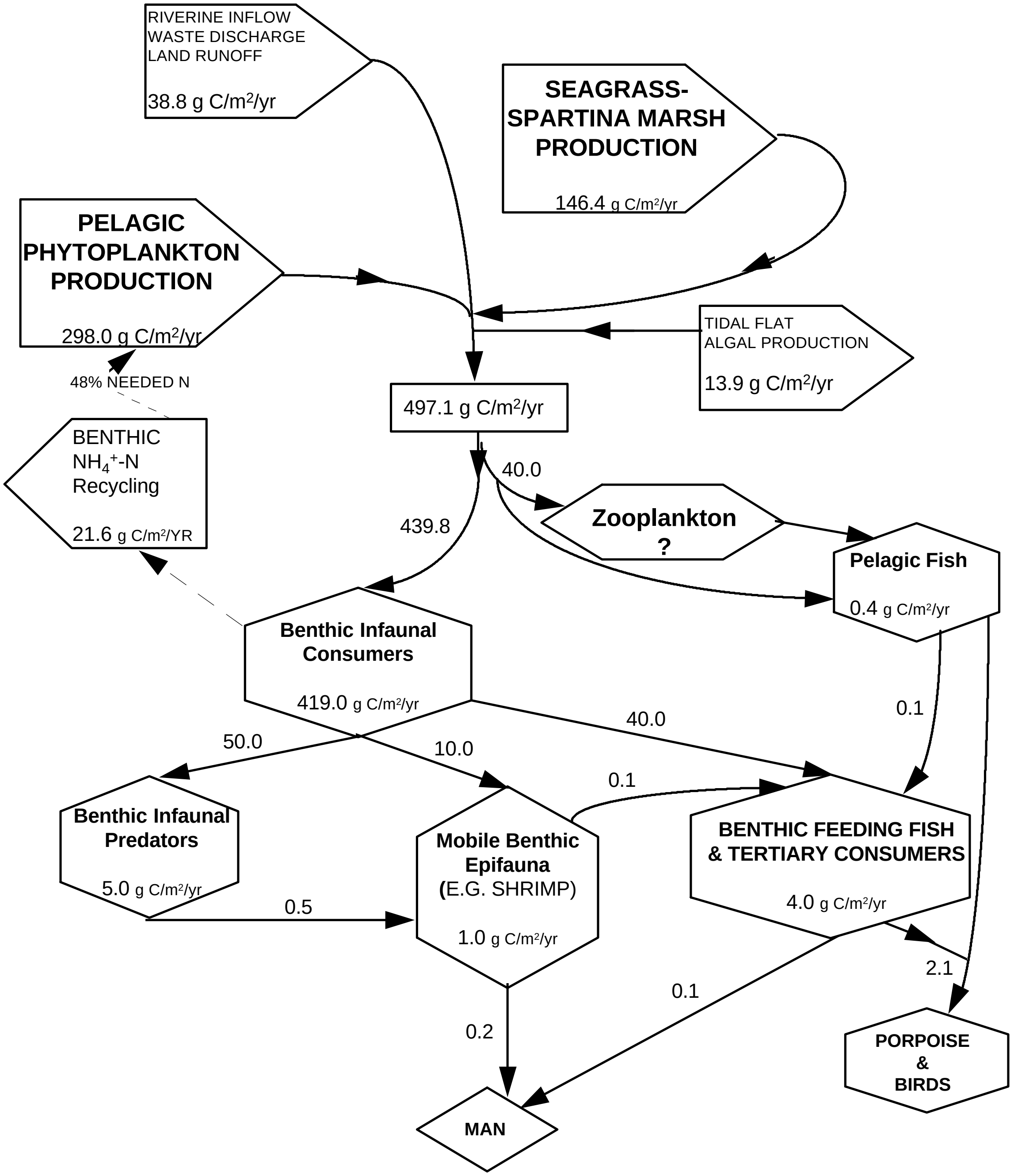


Fig. IV.B.1.5. Hypothesized food chain for Corpus Christi Bay showing flow of carbon between trophic levels (from Armstrong, 1987).

be driven by this size class. Unfortunately, distribution patterns and seasonal variation for nanophytoplankton are unknown.

1.5.1.2 Secondary Production

In addition to the mechanisms that bring carbon into the estuary, other components transfer it through and remove it from the system. Benthic infaunal consumers are the most important secondary producers of carbon within the estuary, packaging 87.3% of the total autotrophic carbon for higher level consumption (see Fig. IV.B.1.5). The pelagic component of the system requires just 8.3% of the carbon entering the system (since zooplankton production is mostly unknown in Texas estuaries, the pelagic carbon requirement was estimated from the production rate of the major estuarine planktonivore, *Anchoa mitchilli*). Even after subtracting the portion of carbon utilized by pelagic consumers, almost all of the carbon remaining is transferred into benthic biomass (95 %), an extremely high transfer efficiency. If the usual 10% transfer efficiency (Odum, 1971) was assumed, 10 times the primary producer detrital carbon would be necessary to support the observed benthic production. Thus, the benthos of the open bay community of the Nueces Estuary must be very efficient in the utilization of detrital carbon. Not only is the benthos a highly efficient energy trap, utilizing carbon from phytoplankton, terrestrial organic detritus and estuarine detritus, it is also a pivotal transfer point between this detrital carbon and other consumers within the estuary.

Benthic production can be estimated from the uptake of oxygen by estuarine sediments (Rowe and Smith, 1977). Armstrong (1987) reported on data from Flint et al. (1982) that benthic production rates varied within the Nueces Estuary. Upper estuary sediments produced an average of 0.96 ± 0.37 g C m^{-2} day^{-1} More active mid-bay sites exhibited a mean benthic carbon production of 1.30 ± 0.54 g C m^{-2} day^{-1}, whereas more Gulf-influenced lower bay sites produced a mean production rate of 1.23 ± 0.46 g C m^{-2} day^{-1}. Armstrong emphasized the importance of turnover ratio (production rate/average biomass) vs. comparing only biomass standing stocks, in assessing the food quality or potential for production of benthic biomass, according to which fast-growing, shorter-lived organisms may achieve food production levels of over five times their standing stock biomass. The three Nueces Estuary sites mentioned above exhibited turnover rates as follows: 0.019 - upper bay; 0.021b - mid-bay; 0.046 - lower bay. Although the lower bay site generally had the lowest benthic standing stock biomass, this site had the highest turnover rate as it was generally dominated by smaller sized polychaetes such as *Mediomastus californiensis.*

Within benthic infaunal species assemblages there are several predatory polychaetes such as *Diopatra cuprea* and *Glycera americana*. Where they occur, these polychaetes have been found to comprise 1.2% of the infaunal biomass (Flint et al., 1981). Assuming a 10% transfer efficiency among trophic levels Armstrong (1987) estimates a total of 50 g C m^{-2} day^{-1} are needed to support the 1.2% of total benthic infaunal production of these predatory polychaetes, leaving 368 g C m^{-2} day^{-1} of benthic infaunal production to support the production of epifauna and fish, 10 and 40 g C m^{-2} day^{-1} respectively.

In summary, benthic infauna perform a pivotal role in the trophic dynamics of the open bay community. The benthos is an efficient trap of autotrophic carbon, packaging carbon derived from phytoplankton, terrestrial organic detritus, and detrital material from seagrass beds, marshes, and tidal flats for consumption by higher trophic level consumers. Thus the benthos is the chief link between autotrophic carbon and the nutrition of other estuarine fauna.

1.5.2 Trophic Levels and Food Web Relationships

Two types of food chains are recognized in estuaries: one based on the grazing of carbon fixed by photosynthetic organisms (e.g., phytoplankton); the other based upon the consumption of carbon from autochthonous and allochthonous detrital material and associated microbial populations (Armstrong, 1987). Because detrital material is conspicuous in the guts of many open bay consumers (Tenore, 1977; Alexander, 1983), most food chains within this biotope are thought to be based on detritus.

The primary producer-based food chain is relatively simple and straightforward, as carbon fixed by phytoplankton goes primarily to zooplankton feeders, and, then, to pelagic predators such as redfish, birds, and man (Fig. IV.B.1.6). Very few fish are solely planktonivorous. However, planktonivores such as *A. mitchilli*, are some of the most abundant estuarine fish attesting to the minority of organisms involved in this food chain, as the few species dependent on this feeding strategy are able to dominate due to a lack of competitive species.

Conversely, the detritus-based food chain (Fig. IV.B.1.7) is thought to be more complex with many more links among consumers. This food chain is also much more difficult to detect as it is very difficult to follow the transfer of carbon through different trophic levels within the sediment, especially at lower trophic levels. This task is complicated by the heterotrophic nature of lower trophic benthic fauna. With increased study of meiofauna, the relationships among these lower trophic rungs has been complicated by the observed heterotrophic tendencies of these organisms. It has long been suspected that bacteria and diatoms are the principal microbial foods of meiofauna (Coull, 1973; Brown and Sibert, 1977). Consumers within the detritus-based food chain may go through several trophic level changes during their life cycles (Peterson and Peterson, 1979).

The detrital food chain starts with organic input to the estuary from both outside the estuarine system (allochthonous) and from within the system itself (autochthonous), generally material from the water column. Microbial populations colonize this material and in addition to their role in remineralization, some ecologists feel this living portion of the detritus provides the primary nutrition to consumers (Newell, 1970; Tenore, 1977). The majority of detritus in the benthos is consumed by benthic infauna, primarily deposit-feeding polychaetes, amphipods, and bivalves. Some of the detrital material may also be consumed by mobile epifauna (e.g., shrimps and crabs) as well as some fish such as *Mugil cephalus*. Other fauna within the sediments serve as secondary consumers (e.g., predatory polychaetes and small burrowing crabs) as well as the invertebrates living on the sediments such as shrimp. Numerous species of fish also feed upon

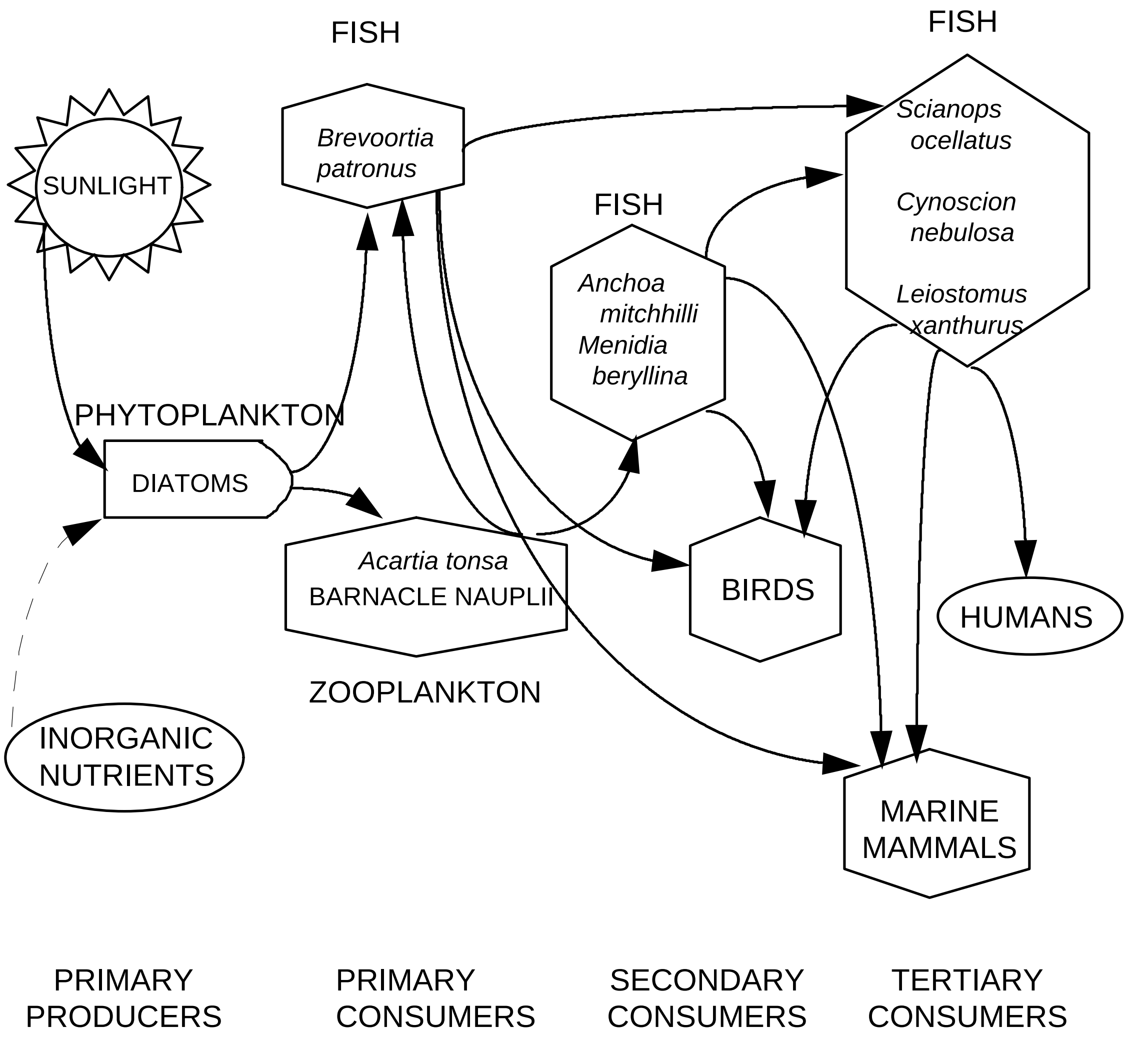


Fig. IV.B.1.6. Hypothesized primary-producer based food chain for Texas open-bay communities (from Armstrong, 1987).

the invertebrate sediment dwellers; and the tertiary consumers, predaceous fish, feed on these smaller bottom-feeding fish.

The detritus-based food chain is much more complex than the primary producer-based food chain; thus, it is probably of greater significance to the overall trophic dynamics of the open bay community. The preceding discussion highlights the importance of benthic food webs within the estuarine system. However, this importance extends well beyond trophic interactions. Recent studies have emphasized the connection between benthic and water column processes, and the importance of the regeneration of nutrients which occurs in estuarine sediments.

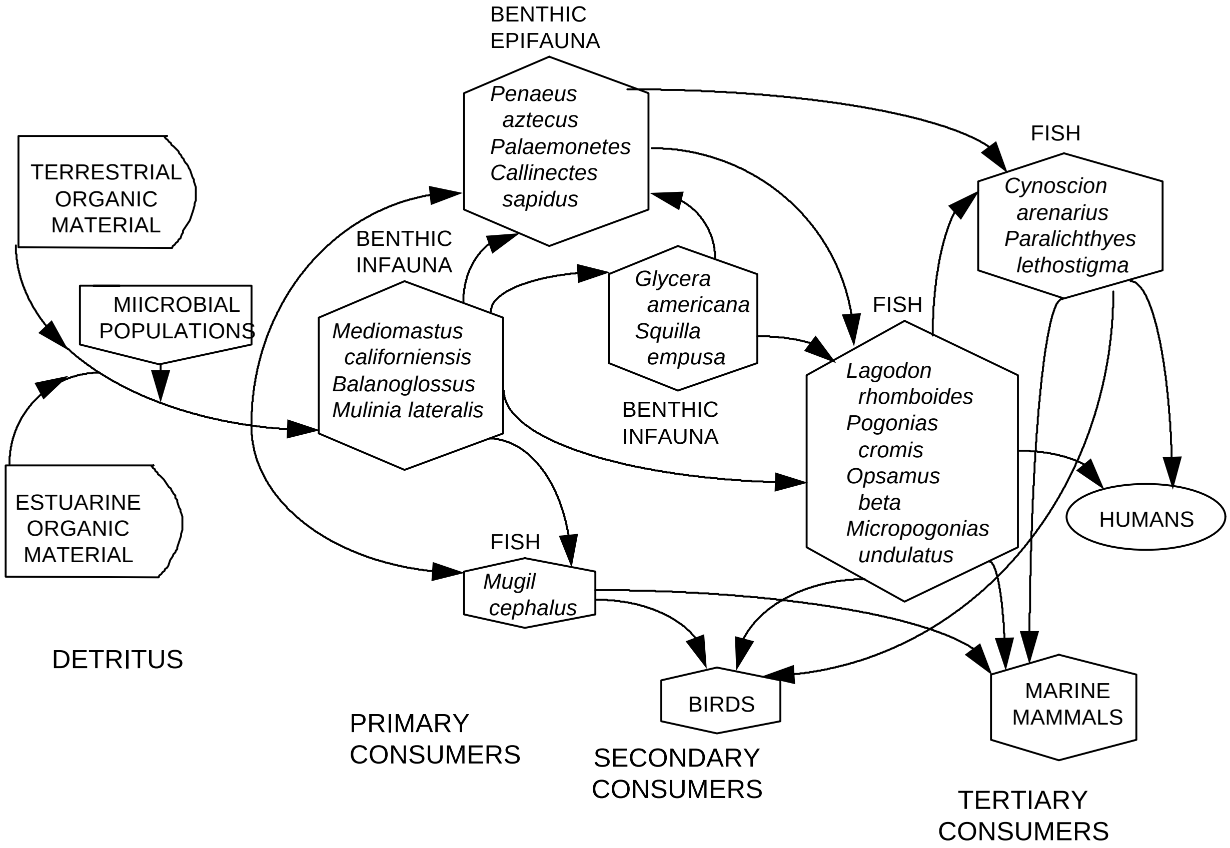


Fig. IV.B.1.7. Hypothesized benthic food chain for Texas open bay communities (from Armstrong, 1987).

1.5.3 Nutrient Cycling

The importance of regeneration to estuarine processes has been increasingly emphasized by recent authors as a defining characteristic of the estuary (Nixon, 1981a; 1981b; Nixon et al., 1986; Fisher et al., 1982; Kemp et al., 1982; Teague et al., 1988). Nixon (1981a) has pointed out the relative shortage of nitrogen in coastal waters, illustrated by low N:P ratios, compared with offshore waters, and attributed this shortage to the greater importance of benthic regeneration in nutrient cycles of shallow coastal areas and the associated process of denitrification occurring in anaerobic benthic sediments. Nixon (1981b) noted that productivity levels are very similar for estuaries (ranging by a factor of 2 or 3), whereas nutrient loading varies by orders of magnitude among estuaries. These figures suggest that processes within the estuary are actually controlling the productivity of the system. High productivity of estuarine waters was brought about and maintained by the almost complete and rapid coupling of heterotrophic and autotrophic processes; the upper limit of this production was set by the slower process of benthic regeneration. These interpretations did not imply that freshwater inflow was unimportant, but rather has an important role in the long-term productivity of the estuary by replacing nutrients lost from the system by extended reliance upon recycling (Nixon, 1981b; Flint et al., 1986).

1.5.3.1 The Process of Regeneration

Benthic regeneration begins with particulate organic matter (POM) settling to the bottom of the bay mixing with the fine surface sediments. POM includes: dead estuarine organisms; organic matter imported from rivers, adjacent bays, or the Gulf; material excreted by living estuarine organisms; waste materials from human activities; and, organic aggregates produced by physical or bacterial action on dissolved organic matter. As the POM settles to the bottom, bacteria, fungi, and protozoans inhabit the surface of the decaying matter, slowly digesting it. Larger scavengers, such as crabs, and deposit feeders, including polychaete worms, mechanically and chemically break the particles into smaller pieces, digesting some of the organic material, and providing the reprocessed material as feces or pseudofeces for further microbenthic processing.

Regeneration involves the splitting of large organic macromolecules by hydrolysis into small organic molecules, and the remineralization of some of this organic material into inorganic compounds. The regenerated materials include phosphate, sulfate, silicate, carbon dioxide, ammonium, nitrate, nitrite, free amino acids, and other dissolved organic forms. Regenerated inorganic materials such as ammonium, nitrate, and phosphate are used as nutrients by estuarine autotrophs to support their growth. Some microorganisms directly take up amino acids, carbohydrates, and inorganic nutrients for growth; a few chemotrophic bacteria use regenerated ammonium as an energy source and oxidize it to nitrite or nitrate.

Phosphate and nitrogen compounds are usually of greatest interest since their availability is known to limit plant and bacterial productivity in aquatic environments. The regeneration of phosphorus is relatively straightforward; phosphate is taken up by microorganisms and autotrophs, incorporated into their tissues, and regenerated as phosphate and organic phosphorus compounds when they die. In general, the oxidation state of phosphorus does not change throughout this process.

Nitrogen is considered to be the nutrient in shortest supply in coastal waters (Ryther and Dunstan, 1971); consequently it has received the most study. Hydrolysis of proteins into amino acids and nitrogenous bases, and their deamination (release of ammonium) under aerobic conditions produces much of the regenerated nitrogen, but other biochemical reactions involving microorganisms in the aerobic and anaerobic layers of the sediments complicate nitrogen recycling. Nitrogen may occur in at least seven different oxidation states in estuarine water and sediments, ranging from its most reduced form, ammonium, to its most oxidized form, nitrate. Regenerated ammonium may be oxidized to nitrite or nitrate used by phytoplankton and bacteria. Regenerated ammonium and free amino acids may be adsorbed onto sediment particles and released to interstitial waters at a later time, or remain fixed and buried with the sediment. A portion of the regenerated nitrate may be reduced by bacteria back to ammonium and taken up by other microorganisms to support their growth; some of the nitrate and nitrite may be denitrified by bacteria to form nitrogen gas or nitrous oxide which eventually escapes to the atmosphere. Factors such as temperature, salinity, reduction-oxidation potential of the sediment, water depth, rate of sediment and organic material deposition, nutrient loading of inflowing water, and benthic community composition all influence the many different pathways of oxidation and reduction of nitrogen compounds, and complicate attempts to understand observed rates of regeneration (Longley, 1994).

The relative masses and magnitudes of rates of transfer of nitrogen among different estuarine components are illustrated in Figure IV.B.1.8. The standing stock of phytoplankton and zooplankton at any one time is small compared with the other components of the system. However, rates of growth, nutrient utilization and predation are high, and turnover is rapid in this segment of the system. Nitrogen is transferred through other components, including the benthos and the planktonic primary producers.

Regeneration occurs in the water column as well as in bay sediments. Nixon (1981a) pointed out that a defining characteristic of coastal marine systems is the relatively greater importance of benthic recycling in these systems compared with oceanic systems. Benner and Yoon (1989) measured water column and benthic regeneration at several stations in Nueces and Guadalupe estuaries. The contributions of each of these processes to regeneration within the estuaries was about equal. Their measurements were consistent with Nixon's (1981a) observation that one-quarter to one-half of all organic production and loading in shallow coastal marine systems is mineralized by the benthos.

The relative importance of benthic regeneration may also be determined by comparing the demand for nitrogen by phytoplankton, which is obtained by multiplying net phytoplankton productivity by the C:N ratio of healthy populations of phytoplankton with that regenerated by the sediments (Redfield et al., 1963). Regeneration could potentially satisfy about 40% of the phytoplankton nitrogen demand in 13 coastal systems reported by Nixon (1981a). Benner and Yoon (1989) estimated that the benthos of Nueces and Guadalupe estuaries could supply an average of 38% and 44% respectively of the phytoplankton demand.

Whitledge et al. (1989) emphasized the importance of regeneration to the nutrient dynamics of south Texas estuaries and found these rates to be quite high compared to other coastal systems studied. Characteristics of south Texas estuaries cited as contributing to this high level of regeneration included shallow depth, salinity, wind mixing, and temperature. Small tidal ranges and relatively small freshwater inflows do not flush organic material from the estuaries and allow the recycling of nutrient material to occur more frequently than in deeper estuarine ecosystems. This high level of regeneration allows south Texas estuaries with relatively low levels of freshwater inflow (e.g., Nueces Estuary) to remain highly productive.

1.5.3.2 Nitrogen Losses

Nitrogen is lost from the system through burial in the sediments, export and advection out of the estuary, harvest, and loss to the atmosphere through denitrification. These losses have been estimated to amount to about 10% of annual primary production and recycling processes within an estuary (Whitledge et al., 1989). Increased importance of benthic regeneration in coastal waters and associated losses through denitrification may be responsible for maintaining low N:P

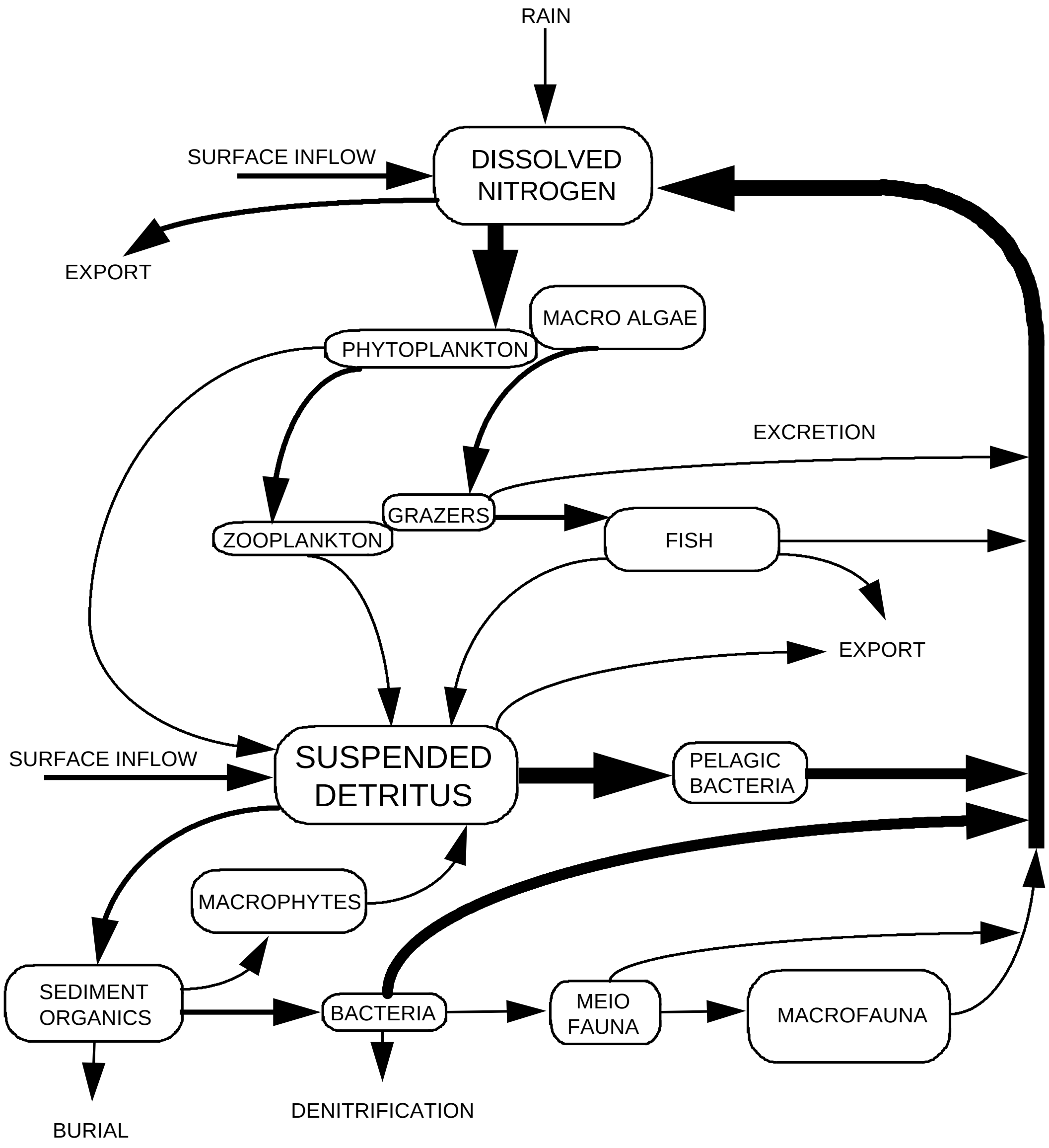


Fig. IV.B.1.8. General diagram of compartments and flows of the nitrogen cycle in an estuary. Sizes of boxes and arrows reflects typical relative magnitudes of rates and masses ([based on Nixon (1981) from Powell and Green, (1991)]).

ratios compared with oceanic waters (Nixon, 1981a). Denitrification is the biochemical reduction of available nitrate and nitrite to the biologically unavailable nitrogen gas by sediment bacteria which use the oxidized nitrogen compounds as electron receptors in their respiration. Denitrification occurs in anoxic sediments that contain nitrate or nitrite in the sediment porewater (Seitzinger, 1988). Nitrate and nitrite are present in the porewater as the result of sediment nitrification in which ammonium (derived from the breakdown of detritus) is oxidized to form nitrate and nitrite. Significance of denitrification to estuarine nitrogen cycles can be illustrated by estimates of 50% of all riverine nitrogen entering Four League Bay, La. being lost to the denitrification process (Smith et al., 1985).

Benner and Yoon (1989) found the strongest determinant of denitrification rates to be temperature as rates were highest during the summer. They reported no correlation between denitrification rates and salinity within estuaries, and found rates for Guadalupe and Nueces estuaries very similar. Since these estuaries represent very different inflow regimes, denitrification rates in Texas bays may not be influenced by salinity.

1.5.3.3 Factors Affecting Regeneration

Powell and Green (1992), referencing three studies of regeneration rates [Jones et al. (1986) Lavaca Bay; Flint and Kalke (1985) Nueces Estuary; Montagna and Yoon (1991) Nueces and Guadalupe estuaries] proposed a provisional model investigating the effect of freshwater inflow on regeneration rates in Texas estuaries. In this model, periods of three or more months with low inflows resulted in low regeneration rates, sometimes even uptake of ammonium by the sediments. If a period of low inflow and low regeneration was followed by a moderately large freshwater inflow pulse, regeneration increase substantially. If the inflow pulse was very large or followed by other large pulses in succeeding months, regeneration declined. Although Powell and Green emphasized the provisional nature of this model, they suggested that freshwater inflow pulses may turn on or off higher levels of regeneration depending on the timing and quantity of inflows. The duration of these studies and frequency of sampling did not provide confirmation for this proposal. Furthermore, regeneration was not well correlated with abundance and biomass patterns of macrofauna, and meio- and microbenthic population data was inadequate to provide a causative agent for this pattern.

Recent studies of the nitrogen cycle in Guadalupe and Nueces estuaries allow comparisons of nutrient cycles between two bays with very different inflow patterns (Whitledge, 1989). The Guadalupe Estuary during the 1986-1987 study period received almost ten times the nitrogen input as did the Nueces Estuary (1987-1988) due to much larger inflows. Figure IV.B.1.9 shows the nitrogen masses and exchange rates during average inflow conditions normalized to the rate of surface water input for these two estuaries (Longley, 1994). A comparison of these two figures revealed that, with the exception of macrophytes, the normalized nitrogen masses in the biological components of each estuary were quite similar. In contrast, the flux rates were much greater in the Nueces Estuary than in the Guadalupe Estuary, even though the absolute mass of nitrogenous material processed is greater in the Guadalupe Estuary. Longley (1994) provided two possible explanations for this pattern: in the Guadalupe Estuary biological processes may be overwhelmed by physical flushing and sedimentation rates; or, in the Nueces Estuary, conditions may be more stable, allowing the development of an efficient chain of nutrient processes. The results of these studies may not represent average long-term differences among these estuaries, as the Guadalupe Estuary was studied during a period of higher than normal flow (1987), and the Nueces Estuary during low inflow conditions (1988).

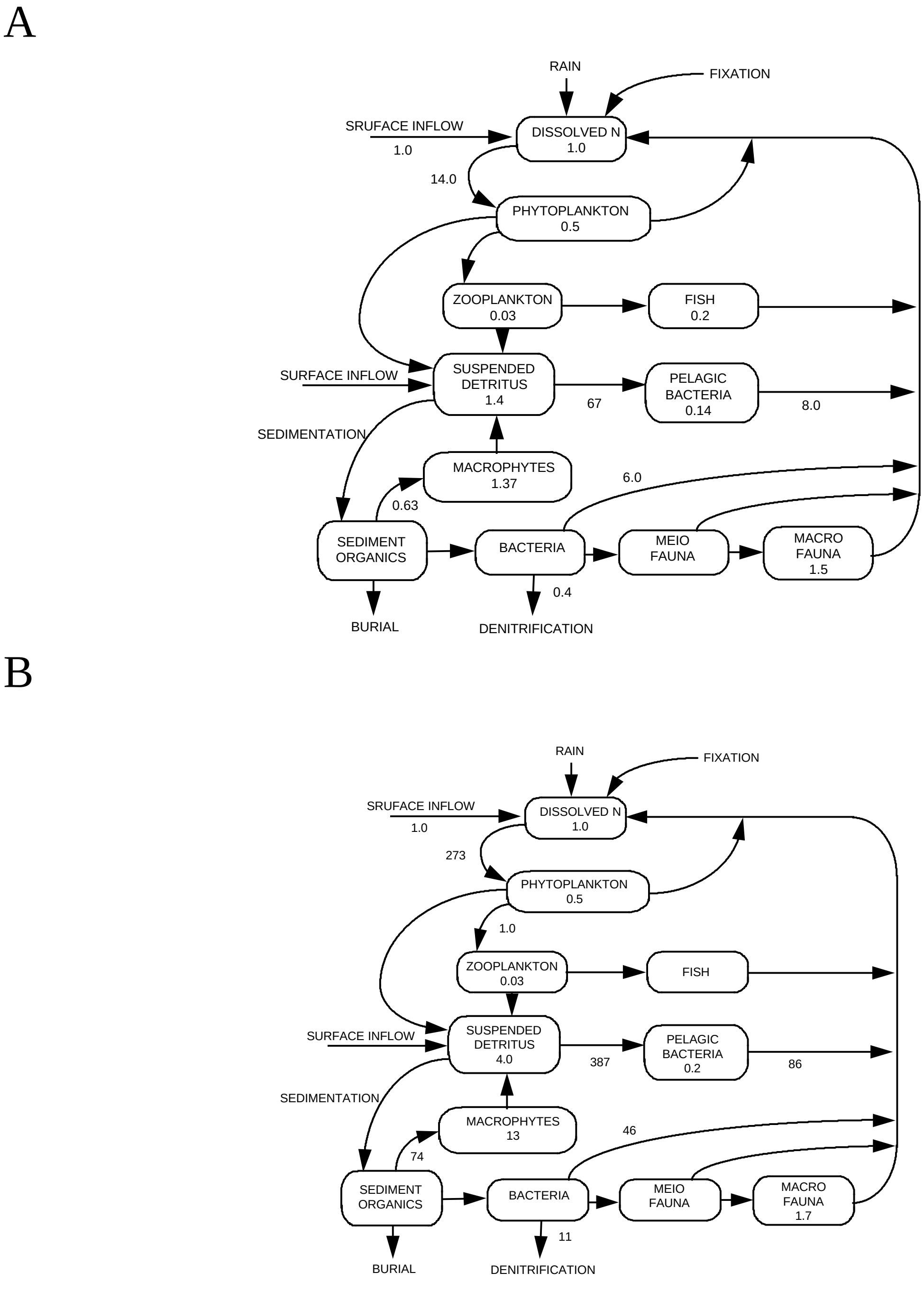


Fig. IV.B.1.9. Nitrogen cycles, average conditions, with flows normalized to the rate of N input from terrestrial sources and masses normalized to the mass of N dissolved in the water column for the Guadalupe Estuary (A) and the Nueces Estuary (B) (from Longley, 1994).

Regeneration rates within an estuary may be an indication of long-term effects of freshwater inflow on estuarine nutrient cycles. High levels of nutrients brought into the system during periods of increased freshwater inflow are not flushed from the system due to the small tidal ranges of Texas estuaries. Larger organisms biomass and sediments of the open bay bottoms are the only storage capacity for such increases in the estuary. The nutrient processes associated with larger organismic biomass and/or enhanced sediment organic matter would be higher regeneration rates. Whitledge et al. (1989) suggested that large peaks in nitrate and ammonium concentrations found during mid-summer in Corpus Christi Bay may be a possible example of how organic matter could be accumulated in the sediment and then quickly metabolized when conditions are optimum. Not all of the stored nitrogen would be available for regeneration as other processes, such as denitrification, would be competing for the increased nutrients.

1.5.3.4 Nutrient Process Zones

Longley (1994) provide a model of the major zones of estuarine nutrient processing based upon the conceptual organization of Delaware Bay presented by Sharp et al. (1984), on figures presented in Blanton et al. (1971), and from ideas in Fisher et al. (1988), to explain the observed patterns of nutrient distributions in Texas estuaries. These zones are illustrated in Figure IV.B.1.10, and parallel the structural zonation along the salinity gradient. The following discussion of these zones is after Longley (1994).

Upper estuary zone. - At the head of the estuary, geochemical mechanisms cause nutrient-laden material to deposit on the sediment surface, lowering the concentrations in the influent plume. Deltaic marsh vegetation may augment this process. In the upper bay, organisms use dissolved nutrients to fuel the breakdown of particulate organics such as bits of leaves and twigs. Wind provides energy to periodically mix and redistribute materials, promoting heterotrophic activity. Regeneration of dissolved nutrients from the sediments occurs, but turbidity suppresses phytoplankton growth and so prevents phytoplankton from taking up all available nutrients. Therefore, during high inflow periods, nutrients accumulate in the sediments, or pass through the zone. During low inflow periods, regeneration of nutrients from sediment storage exceeds uptake and nutrients are passed down to the next zone.

Mid-estuary zone. - The mid-bay region, with typically greater volume and water depths, has less turbid waters. This allows phytoplankton to use the dissolved nutrients and reduce nutrient concentrations. Benthic metabolism of river-borne materials is also important, with processing rates as high as rates in the upper bay (Montagna et al., 1989). In the mid-bay, however, more of the regenerated nutrients are incorporated into planktonic cells. Zooplankton find salinity levels in the mid-bay region accommodating, and add an important link in the food chain. With the development of a planktonic food chain comes regeneration of dissolved nutrients in the water column, supplementing benthic recycling processes. Oyster reefs in this part of the estuary also regenerate nutrients from the particulates they consume.

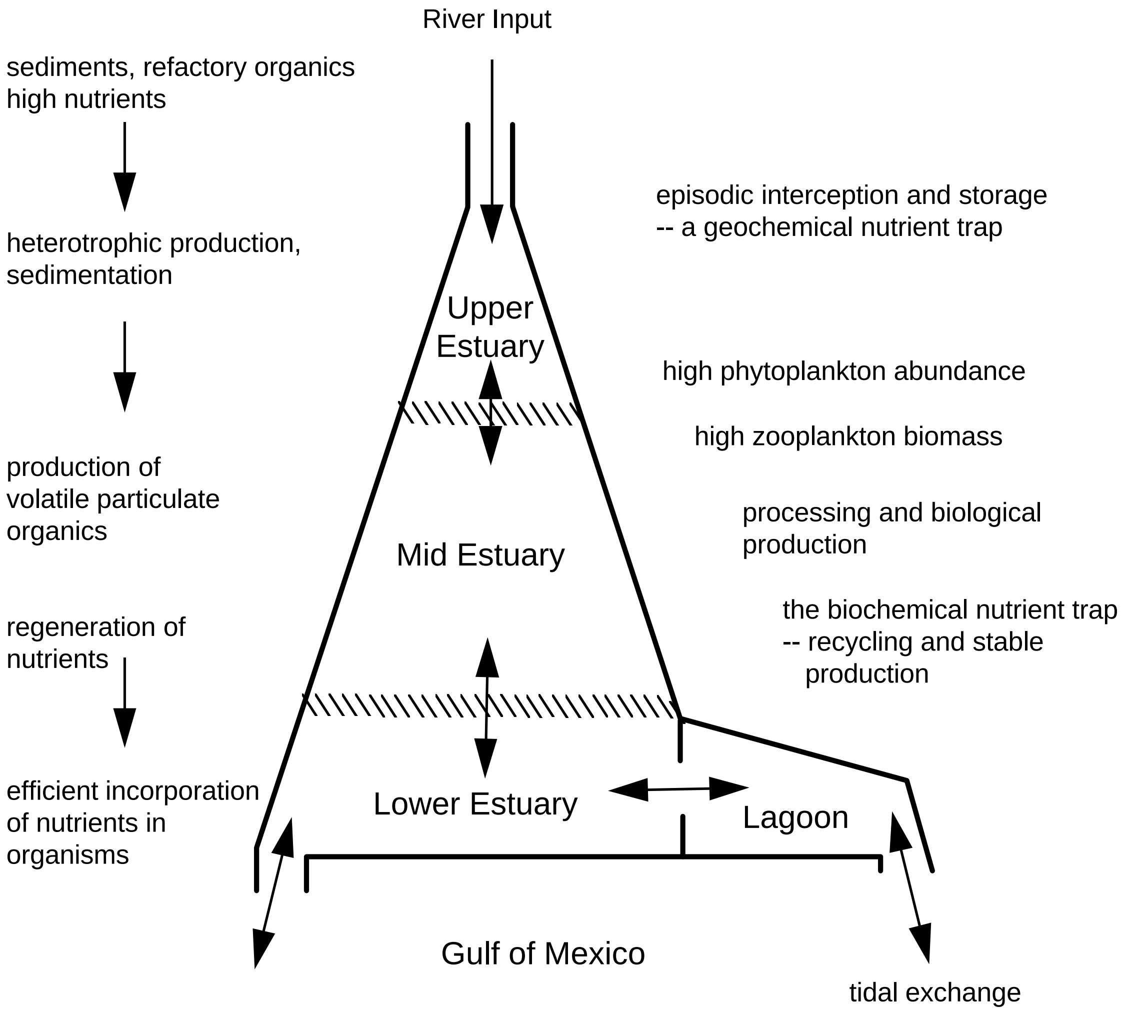


Fig. IV.B.1.10. Conceptual zonation in an estuary with respect to nutrient processing (from Longley, 1994).

Lower estuary zone. - The lower bay provides a more consistent habitat for marine and estuarine organisms. Favorable habitat promotes higher species diversity, more complete food chains, and more efficient use of resources. Increased efficiency leads to a concomitant decrease in the concentrations of available nutrients. Fixed materials go through longer cycles within biological compartments before becoming available as dissolved nutrients. Light penetration is typically greatest in the lower bay of the estuary, so there is a greater volume of phytoplankton capable of growing (and using nutrients) at a high rate. Recycling is important in this section of the estuary. The uptake of dissolved products of nutrient regeneration is rapid, subsequently, the concentrations in the water remain low.

Inter-estuarine comparisons. - The above generalization of estuary organization may help classify Texas bays by dominant functions. Most of Sabine Lake may function as an upper estuary. Lower estuary functions may occur only in a limited zone of the Trinity-San Jacinto

Estuary. Conversely, at times of low inflow in the Nueces Estuary, the functions and nutrient processing of the upper estuary may be compressed into the tidal stretch of the Nueces River. Each estuarine zone has prevalent geochemical or biochemical mechanisms to trap nutrients. Therefore, estimating the relative importance of the conceptual zones in an estuary may help explain general features of the nutrient distributions.

1.5.4 Linkages with Other Systems

The estuary is an intermediate environment linking oceanic and upland communities. The primary link with upland communities occurs through freshwater inflow from streams and rivers. Freshwater inflow is a major factor in almost every biological component investigated and was documented as a vital factor in determining the salinity gradient within the estuary which, in turn, determines community structure and zonation of planktonic, benthic and nektonic organisms of the open bay. Freshwater inflow was also an important factor in nutrient cycles within the estuary which controls the productivity of the system through trophic interactions and regeneration processes. Although freshwater inflow in the study area is low compared with other Texas estuaries and its influence may thus be episodic and indirect (i.e., excess nutrients entering the bay during storms or floods and the resultant increases in organismic biomass may be stored in the sediments to be regenerated when conditions are optimal), such inflow is vital to replenish nutrient store which could be depleted with continued reliance on regeneration (Flint et al., 1986; Whitledge et al., 1989).

The open bay community is a part of the larger estuarine system and relationships with other community types within the estuary are important in determining conditions within the open bay biotope. As was shown in Figure IV.B.1.5, energy flow within the open bay may be directly linked to sources of detrital carbon from outside the open bay system, such as seagrass beds, marshes, and algal flats. Although these potential sources are highly productive, their actual contributions to open bay nutrient dynamics is problematic as transfer rates among community systems are either unknown or inconclusive.

Armstrong (1987) estimated the productivity of potential allochthonous carbon sources to the open bay community as follows: Spartina marsh - 52.2 g C m^{-2} yr^{-1}.; seagrass and epiphytes - 1,043.9 g C m^{-2} yr^{-1}.; blue-green algal flats - 388.9 g C m^{-2} yr^{-1}.; benthic mudflat diatoms - 133.1 g C m^{-2} yr^{-1}. All of these estimates are quite high compared to estimates from other estuaries. Although these sources of fixed carbon would appear quite significant, the actual contributions from these sources are unknown. For example, in several laboratory and field studies in Texas estuaries (Armstrong et al., 1977; Wiersma et al.. 1977) no consistent pattern of movement of materials between marsh and bay waters was found. Some materials were imported into various marshes but exported from others; some materials were imported during one or more seasons of the year but exported during other seasons. In a review of 20 years of research on the role of marshes in estuarine productivity and water chemistry, Nixon (1980) noted no consistent evidence that marshes were strong sources or sinks for nutrients in coastal nutrient cycles. Although most material movement is episodic and occurs during major storms and floods, no direct measurements are available to substantiate this possibility (Longley, 1994). Evidence from stable isotope studies suggested that phytoplankton, seagrass and benthic algae are the primary carbon sources within the Nueces Estuary (Parker et al., 1989).

Oyster reefs are another estuarine community which affects the open bay biotope. Oyster feces and pseudofeces contribute to the organic silts which fuel benthic regeneration processes within the open bay community. Oyster shell fragments can also become an important constituent of bay bottom sediments affecting benthic community structure in areas of extensive reef systems, such as those found in Copano Bay, (Holland et al., 1975). Oysters also participate in the process of regeneration remineralizing nutrients from particulate organic matter, making nutrients available to primary producers of the open bay. In turn, primary production rates of planktonic organisms of the open bay system control the nutrients available for oyster production.

Besides linkages with other estuarine community types, the open bay biotope may be influenced by interactions with other estuarine systems and with Gulf waters. Tidal inflows of Gulf waters, tidal exchange, and advective transport of materials among adjoining estuaries make significant contributions to nutrient budgets in a three-bay simulation model encompassing the Mission/Aransas, Guadalupe, and Lavaca-Colorado estuaries (Longley, 1994). The mixing rate between Gulf and bay waters during flood tide may determine how much new Gulf water is actually incorporated in the estuary with each tidal cycle (Longley, 1994), and is probably dependent on the morphology of each major pass (Smith 1985). Conversely, Whitledge (1989) found that nutrient concentrations in the Nueces Estuary were not affected by physical circulation patterns, and found no evidence of Gulf water in Corpus Christi Bay. Net flow of water Gulfward from Corpus Christi and/or Aransas bays and net flow of water out of Corpus Christi Bay into the Laguna Madre, suggested an influence of the open bay community within these estuaries on coastal and seagrass communities. The openness of the Nueces Estuary to Gulf influence has also been cited as a determinant of benthic community structure of open bay bottoms in Corpus Christi Bay (Kalke and Montagna, 1989).

Perhaps the greatest linkage, and one which summarizes relationships between the open bay community and other communities within and without the estuary are those nektonic species which traverse the open bay biotope in their migrations to and from protected nursery areas and Gulf spawning grounds. Although many of these organisms prefer the structure of seagrass beds, oyster reefs or salt marshes, most also frequent open bay areas. Estuarine production of these organisms is dependent upon productivity of open bay communities (productivity dependent upon other estuarine and upland communities) and health and extent of structural habitats (e.g., salt marshes, seagrass beds, and oyster reefs) and salinity gradients (result of freshwater inflow) which serve as protection for juvenile nektonic organisms in the estuarine nursery role (Browder and Moore, 1981).

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HABITAT 2: HARD SUBSTRATE

2.1. Physical Setting & Processes

2.1.1 Distribution within Project Area

2.1.1.1 **Introduction**

The hard substrate habitat within the Corpus Christi Bay National Estuary Program (CCBNEP) study area is comprised primarily of artificial, man-made structures such as jetties, groins, breakwaters, and bulkheads. These artificial substrates came into existence within the past 100 years with the development of concrete. Introduction of these structures created a stable, hard substrate habitat within a region of predominantly unstable, soft sediments. This development provided a new ecological environment suitable for the establishment of hard-bottom communities that otherwise did not previously exist in nearshore coastal waters (Hedgpeth, 1954; Britton and Morton, 1989).

Natural hard substrates discussed in this section include serpulid reefs at Baffin Bay and the coquina outcrop at Penascal Point located at the southern mouth of Baffin Bay. Oyster reefs are the most extensive natural, hard substrate found throughout the central and northern part of the CCBNEP area; however, due to its complexity this habitat will be addressed in the following chapter (Habitat 3: Oyster Reefs). Other artificial substrates in the CCBNEP study area which provide a hard substrate suitable for organismal colonization include petroleum platforms, rip rap, pier pilings, navigation buoys, floating debris, causeway bridges, and channel markers, however, they have not been extensively studied.

Literature specifically pertaining to ecology of artificial hard substrates, other than the Aransas Pass jetties, in the CCBNEP area is scarce. The remainder of this chapter, with the exception of this section (3.1 Physical Setting & Processes), therefore, will be specifically addressing those organisms that inhabit the Aransas Pass jetties. Ecology of these structures has been studied since the late 1940's (Whitten and Rosene, 1946; Whitten et al., 1950; Hedgpeth, 1954; Hoese, et al., 1968; Edwards and Kapraun, 1973; Kapraun, 1980; Rabalais, 1982; Britton and Morton, 1989) and continues to undergo investigations to the present (Whorff, 1992; Hicks and Tunnell, 1994).

2.1.1.2 Artificial Hard Substrates

Jetties, groins, bulkheads, and breakwaters. - These structures have contributed significantly to shoreline alteration (Brown et al., 1976). About one-half of the shores of Corpus Christi, Nueces, and Oso Bays have been altered by coastal projects since the early twentieth century and continues today (Morton and Paine, 1984). These substrates provide a suitable environment for a hard-substrate community to establish, and influence nektonic fauna.

Jetties are two parallel walls built perpendicular to the shoreline usually traversing barrier islands; they serve to protect navigation channels among coastal bays and the Gulf of Mexico by impeding longshore sedimentation (Morton, et al., 1983; Britton and Morton, 1989). Groins are much smaller walls built on straight stretches of beach away from channels and inlets, and are intended to trap sand flowing in the longshore current (Morton, et al., 1983). Bulkheads can be described as barriers built along shallow bays and marinas intended to stabilize or reinforce the soft shoreline by preventing erosion that results from waves, storm surges, or the wake of navigation traffic. Breakwaters are structures constructed from the mainland that extend out into the open water lying more or less parallel to the mainland where they function in creating areas of reduced water movement.

One major and one minor jettied inlet exists within the CCBNEP area: Aransas Pass jetties and Fish Pass (or Corpus Christi Water Exchange Pass) jetties, respectively. The Aransas Pass jetties are located at the north end of Mustang Island in Port Aransas, Texas, and at the south end of St. Joseph Island at approximately 27^{o} 50’ N, 97^{o} 09’ W bordering the navigable Aransas Pass tidal inlet (Fig. IV.B.2.1). Mustang Island separates Corpus Christi Bay from the Gulf of Mexico, is oriented in a south-southwest direction, and is approximately 26 km (16 mi) long and 2-5 km (1-3 mi) wide (Mason and Folk, 1958). St. Joseph Island lies between Aransas Bay and the Gulf of Mexico and is located north of the tidal inlet. The Aransas Pass tidal inlet is the primary link between Redfish and Aransas Bays and the Gulf of Mexico serving as the major pass between about 200,000 ha of bays and wetlands and the Gulf of Mexico (Whorff, 1992). The Fish Pass jetties are located on Mustang Island within Mustang Island State Park at approximately 27^{o} 41’ N, 97^{o} 09’ W (Fig. IV.B.2.1). Although this pass has filled in with sand and vegetation, the rock jetties remain projecting east into the Gulf of Mexico.

Groins, breakwaters, and bulkheads are found along the periphery of the bay systems within the study area wherever there are ports, marinas, docks, finger canals, piers, pilings, or residential or commercial development. Concentrations of piers and jetties are found along the bay shores west of White Point, at Corpus Christi, North Beach, Portland, Rockport, Fulton, Bayside, and the Salt Lake area of Copano Bay (Brown et al., 1976). Other areas include Loyola Beach on the west shore of Cayo del Grullo, adjacent to Baffin Bay, where privately owned piers, jetties, and groins have been constructed (Brown et al., 1977). Along the margins of Corpus Christi Bay, for example, is a system of groins at McGee Beach along Shoreline Drive in Corpus Christi. Other breakwaters and bulkheads extend continuously from Corpus Christi Naval Air Station westward and northward to the Port of Corpus Christi. An extensive framework of seawalls and bulkheads reaching heights of 3 m (10 ft) or more above mean sea level (Morton and Paine, 1984) border the highly developed area near downtown. Extensive breakwaters and bulkheads can also be found in the vicinity of the Aransas Pass tidal inlet at Port Aransas and along the bay shore of Mustang Island surrounding residential, commercial, and oil-field developments (Morton and Paine, 1984). An east and west breakwater is present along the entrance to the Port Aransas Channel and the basin that serves surrounding commercial and private boat owners within the vicinity of Port Aransas. A 3.6 m (12 ft) high seawall exists along the Gulf shoreline in the Packery Channel area to protect privately owned recreational and community developments on the barrier island (Brown et al., 1976).

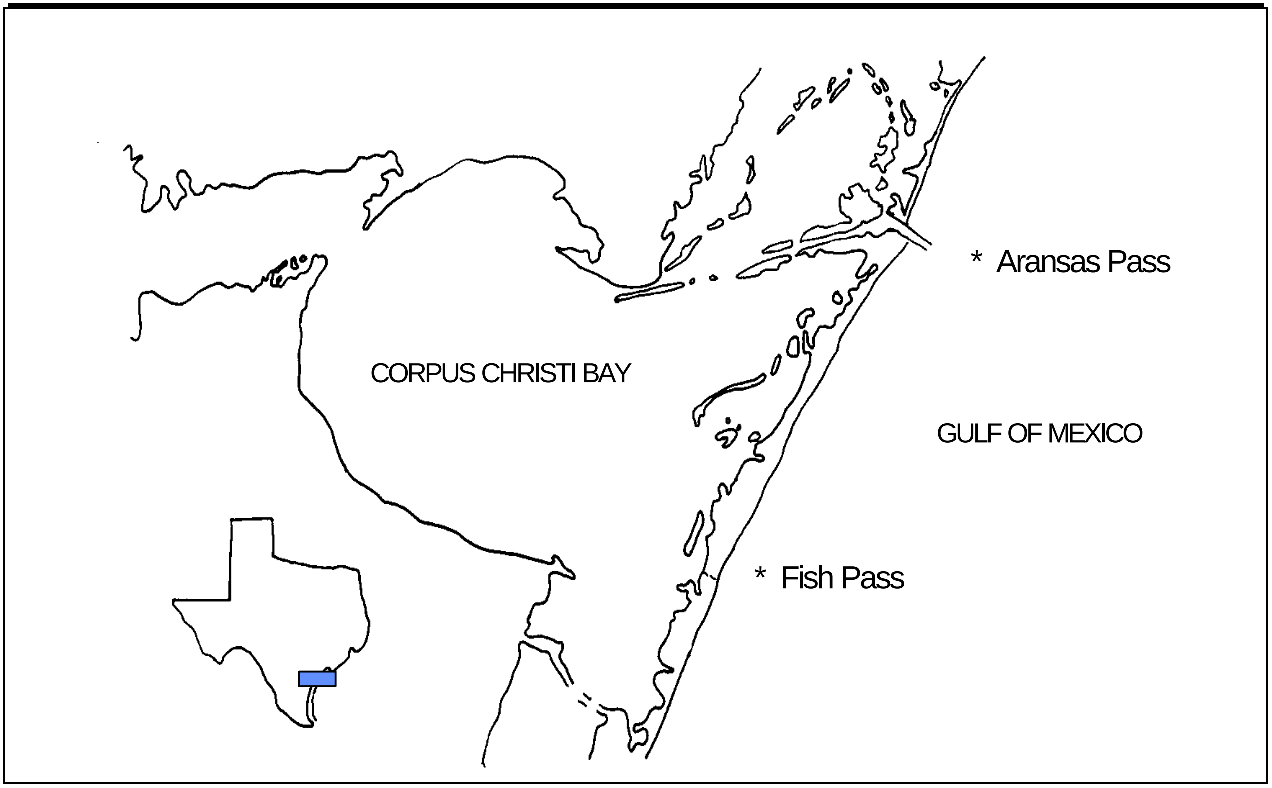

Fig. IV.B.2.1 Locations of Aransas Pass and Fish Pass along Mustang Island, Texas (modified from Behrens et al., 1977).

2.1.1.3 Natural Hard Substrates

Serpulid reef. - The serpulid reefs of the Baffin Bay complex represent one of the few naturally occurring hard substrates in Texas coastal waters (Cole, 1981). These reefs have been documented since the early 1950's (Hedgpeth, 1954; Andrews, 1964; Behrens, 1968; Behrens and Land, 1972; Behrens, 1974; Cole, 1981; ten Hove and van den Hurk, 1993). Baffin Bay and adjoining portions of Laguna Madre have been described as unique among Texas bays because these reefs composed of calcareous tubes of serpulid polychaete worms are widely distributed along the bay margins and across the mouth of Baffin Bay at Point of Rocks and Alazan Bay near Starvation Point (Fig. IV.B.2.2) (Andrews, 1964; Behrens, 1974; Cole, 1981). Thick densities, with an areal coverage of approximately 16 km^2, have been recorded (Brown et al., 1977) making navigation outside marked channels hazardous (Andrews, 1964).

Distribution and morphology of the reef structure has been described by Andrews (1964) and Cole (1981). A summarization of differences and similarities between serpulid polychaete and vermetid (Gastropoda) tubes from other parts of the world, as well as those of Baffin Bay, has been compiled by ten Hove and van den Hurk (1993).

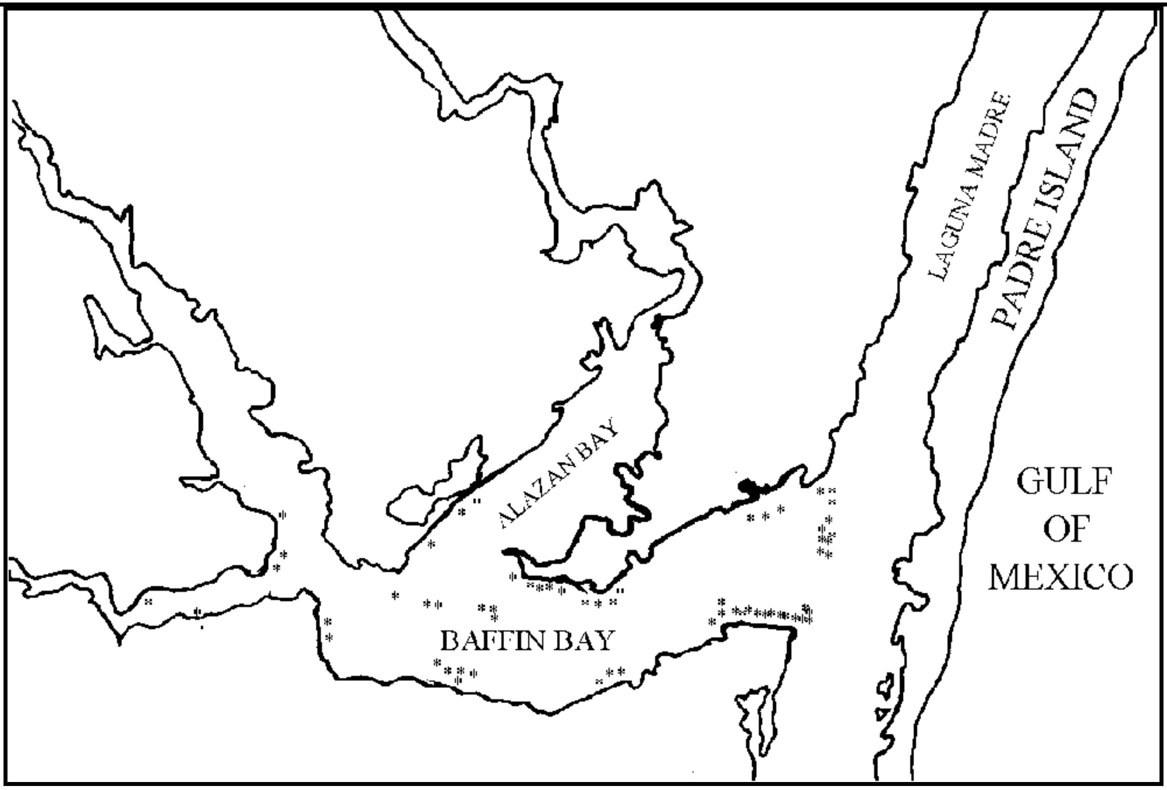

Fig. IV.B.2.2 Serpulid reef distribution in Baffin Bay, Texas (modified from Andrews, 1964).

Currently, Beau Hardegree, a graduate student at Texas A&M University-Corpus Christi, is conducting a study to determine productivity of flora and fauna associated with the reefs, and the role these structures play as food sources and habitat for associated fauna.

Coquina outcrop. - A natural, rocky coquina outcrop, referred to as the Penascal Point outcrop, is located South of Baffin Bay along the mainland shore of the Laguna Madre (Fig. IV.B.2.3) (Prouty, 1993). The areal extent of this outcrop ranges from Penascal Point southward for 10 km and inland for 150 m. The coquina also extends into the shallow waters of the Laguna Madre, where barnacles and calcareous tubes of serpulid worms encrust the rock. The exact thickness of the coquina is unknown, but is thought to be at least 2 m thick (Prouty, 1994). These exposed outcrops are inaccessible to the general public because they lie on private Kenedy Ranch land.

2.1.2 Historical Development, Physiography, and Geology

2.1.2.1 Artificial Hard Substrates

Origins of the development of the Aransas Pass inlet began as early as 1853 (Kuehne, 1973). In 1861, the *Texas Almanac* reported that the Corpus Christi Ship Channel Company had begun work on a project to deepen and widen the channel between Aransas and Corpus Christi Bay on

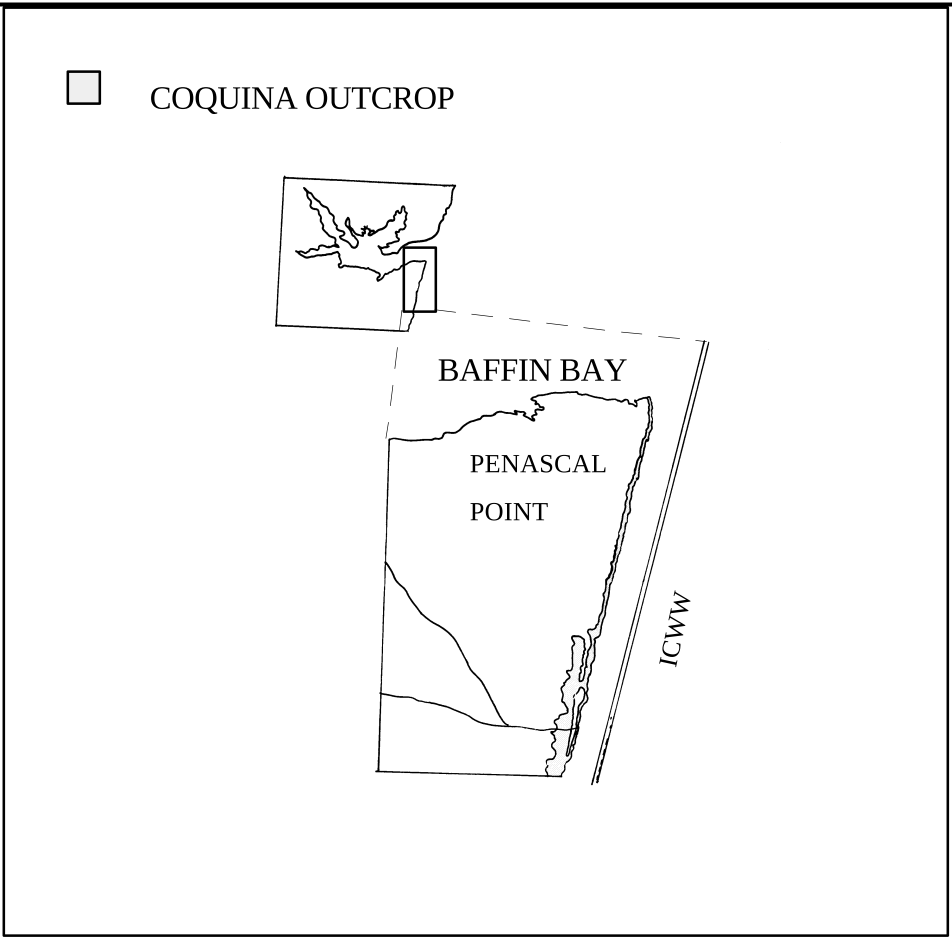

Fig. IV.B.2.3 Location of Penascal Point outcrop south of Baffin Bay, Texas (modified from Prouty, 1994).

3 March 1879; the first project for improvement of the pass was adopted by the US Congress. This project provided for construction of two jetties, several groins and revetment work along the north shore of Mustang Island. Construction of the jetties continued in 1906 when Congress appropriated one-half million dollars for further development. In addition, a stone dike approximately 5 km (3 mi) long was built along the bay shore of St. Joseph Island to prevent high tides from cutting in behind the north jetty. The original pass was approximately 3 m (7 ft) deep, but through the years has been dredged to a depth of 14.1 m (47 ft) and a width of 240 m (800 ft) (US Army Corps of Engineers, 1993).

Physical characteristics of a jetty structure are important components that determine the longevity of its existence and effectiveness. Paine and Morton (1989) describe the Aransas Pass jetties as an effective barrier to longshore sand. These jetties reach lengths of 2.55 km (8,500 ft) and 1.89 km (6,300 ft), for each of the north and south jetties, respectively (D. Gallindo, pers. comm.). However, of these lengths, only 1.2 km (4,000 ft) and 1 km (3300 ft) on each side extend out into the Gulf of Mexico from the shoreline, the remainder lines the tidal inlet along the inner margins of both islands. The north jetty is slightly concave, whereas the south jetty is straight and perpendicular to shore.

In 1971, plans were made by the State of Texas to construct the Fish and Water Exchange Pass (also known as Fish Pass) about 19 km (12 mi) south of Port Aransas (Kuehne, 1973). The dimensions of the Pass would be approximately 3.6 m (12 ft) deep, 30.0 m (98 ft) wide, and 283 m (10,000 ft) long traversing Padre Island and connecting the Gulf of Mexico to Corpus Christi Bay with jetties projecting into the Gulf to prevent littoral transport from shoaling the Pass. By the end of July 1972, granite jetties were in place and the channel was dredged. The Fish Pass jetties are approximately 30 m (98 ft) wide and 261 m (870 ft) long that extend into the Gulf (Behrens et al., 1977). The portion of jetties extending into the Gulf, however, is only 150 m long (Hicks and Tunnell, 1994). The primary function of the Fish Pass is to allow for migration of fish to and from the nursery and spawning grounds of the upper Laguna Madre, and to aid in salinity control in Corpus Christi Bay and adjacent bay systems (Schmeltz and Sorensen, 1973). However, due to low current velocities in the long, narrow channel and short jetties, when compared to the Aransas Pass jetties, this pass began shoaling immediately after it was opened; it has been closed since the late 1970's (Brown et al., 1976; Paine and Morton, 1989).

Most Texas jetties possess a common morphological profile (Whitten et al., 1950; Britton and Morton, 1989) described as triangular in shape, with a base width of about 50 m, and a crest width of about 4 m (Fig. IV.B.2.4). Four types of materials were used in the construction of the jetty: 1) blanket stones composed of granite and weighing 7-90 km (15-200 lbs.) 2) core stones weighing 90-180 km (200-400 lbs.) 3) cover stones - of granite, comprise the crest of the jetty structure and weigh 4-18 tons; and, 4) secondary fill or blocks of limestone and/or sandstone used to fill empty spaces. Periodic maintenance of the jetty is under the direction of the US Army Corps of Engineers, Galveston District, and includes replacing secondary fill where necessary and resetting displaced stones. This procedure takes place about every 10 years and is expensive (D. Gallindo, pers. comm.). The most recent renovation project on the Aransas Pass jetties was completed in 1994 at a cost of over $4 million dollars (D. Gallindo, pers. comm.).

Dredged channels associated with Aransas Pass are maintained at various depths by the US Army Corps of Engineers and constitute approximately 282 km (175 linear mi) of transportation canals within bays, estuaries, and tidal passes in the Corpus Christi area (Brown et al., 1976). For example, the Lydia Ann Channel and Aransas Pass Channel (Shrimp Channel) to Conn Brown Harbor are both maintained at 3.6 m (12 ft), the Corpus Christi Ship Channel to 13.5 m (45 ft), and the Gulf Intracoastal Waterway (GIWW) is maintained at 4.5 m (15 ft). Both deep- and shallow-water channels allow access to ports at Harbor Island, Aransas Pass, and Corpus Christi.

Tidal inlets along barrier islands are the most geologically active area along a coast (Schmeltz and Sorensen, 1973). Areas of shoreline accretion in the CCBNEP study area include those areas south of Aransas Pass and Fish Pass jetties which result from trapped sediment transported by prevailing longshore currents (Paine and Morton, 1989). Erosion occurs north of the jetties because the structures interrupt natural erosion/deposition processes (Morton and Pieper, 1977).

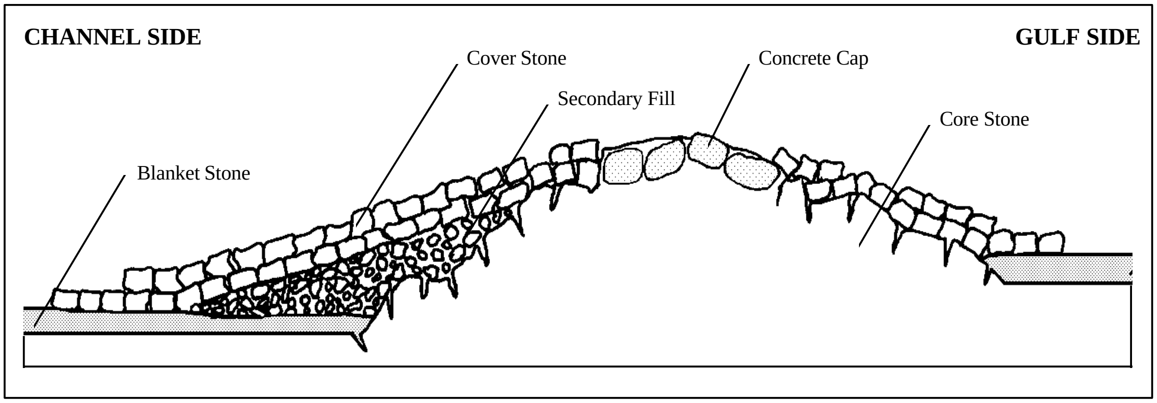

Fig. IV.B.2.4 Profile of Aransas Pass jetty, Texas, showing the different types of stones used in the construction of the structure (adapted from USACOE map).

2.1.2.2 Natural Hard Substrates

Serpulid reef. - Serpulid polychaetes are benthic, suspension-feeding worms that secrete calcareous tubes and are attached to submerged surfaces in marine or estuarine waters (ten Hove and van den Hurk, 1993). Prior to the early 1980's no live colonies of the serpulid polychaetes had been observed (Andrews, 1964; Breuer, 1957; and Hedgpeth, 1953). However, Cole (1981) reported live specimens of *Hydroides dianthus* had been found. Beau Hardegree (pers. comm.) also has observed live specimens on patch reefs near the mouth of Baffin Bay. Radiocarbon data indicate growth of these structures took place in the past 300 years and at 3,000 YBP., but these data did not preclude formation at other times (Behrens, 1974). Currently, no significant growth is taking place (B. Hardegree, pers. comm.), probably due to hypersaline conditions of Baffin Bay which are not conducive to serpulid worm reef growth (Behrens, 1974). Behrens (1974) traced the historical development of Baffin Bay and noted that a diverse molluscan fauna representing near normal marine salinities was present until about 5,300 YBP. This, coupled with the occurrence of serpulid worm reefs and oyster reefs in Baffin Bay in the past, suggests that salinity levels were once much lower than the present. Optimum salinities for serpulid worm reef growth are between 32 and 55 ‰ (Vuillemin, 1969). Oyster reefs, however, are indicative of lower salinities; they existed in Baffin Bay in the past but are not now present (Behrens, 1966).

Two distinct types of serpulid reefs are recognized from shallow waters of Baffin Bay: patch reefs and reef fields (Andrews, 1964). These shallow water reefs are predominantly found along bay margins, but have been found across mouths of Baffin and Alazan Bays. Patch reefs are small, isolated, ellipsoidal or circular reefs; reef fields are comparatively large, irregularly-shaped expanses of reef rock (Andrews, 1964). Patch reefs consist of alternating layers of random tube growth and oriented tube growth, whereas, reef fields consist of rock composed solely of random growth form. The two forms, random and oriented, have been perceived to indicate optimum and adverse ecological conditions, respectively (Andrews, 1964). Andrews (1964) suggests that optimum ecological conditions once existed when bays were filled with normal salinity waters at a time when the bays were connected to the Gulf, perhaps by way of a natural tidal pass across Padre Island.

Coquina outcrop. - The only lithified bedrock exposures along the South Texas coast are those at Penascal Point bordering southern Baffin Bay (Prouty and Lovejoy, 1992). This structure is thought to correlate with the Ingleside complex of the Pleistocene Beaumont Formation and occurs as a low bluff, approximately 1 m high in the surf zone. Prouty and Lovejoy (1992) identify it as having paleoenvironmental significance and well-displayed erosional features.

The outcrop is described as a variable sandy coquina, white to tan on fresh surfaces, and weathering to shades of gray and brown (Prouty and Lovejoy, 1992). Shell fragments, whole shells, quartz grains, and clay, cemented together with calcium carbonate are the major components of this structure. Coquina primarily occurs as a sandy, bioclastic, coarse limestone, but also occurs as a shelly sandstone. Composition of this outcrop includes medium- to fine-grained, angular to subangular, quartzose sand with minor amounts of chert and feldspar dominating the detrital fraction; minor pebbles of a yellow-brown, limonitic, quartzose sandstone are also present. The biogenous component consists of intact mollusc shells and fragments. Coquina has planar bedding, and individual laminae generally dipping steeply seaward.

Fossil shells identified from sections of this outcrop are nearly identical to those found in localized shell beaches immediately seaward on central Padre Island, suggesting that the coquina represents a lithified Gulf-beach shell deposit that predates the barrier island. Another indication to support the predating of the barrier island is the presence of intense karstification, which presumably formed when the sea level was much lower than the present (Prouty and Lovejoy, 1992). Although no studies have been undertaken to identify biological activity occurring on the outcrop, this substrate may be suitable for colonization of plants and animals adapted to living on hard substrates.

2.1.3 Hydrology & Chemistry

2.1.3.1 Artificial Hard Substrate

Tidal inlets serve as links between Gulf waters and estuarine bay waters, and provide for exchange of excess water caused by astronomical tides, wind-driven currents, river discharge, and storm-surge flooding (Morton and McGowen, 1980). The Aransas Pass tidal inlet is the only major dependable source of Gulf tidal exchange in the Corpus Christi Bay system (Harrington, 1973). The tidal inlet is also influenced by fresh water and suspended sediment load by discharges from Mission, Aransas, Nueces, San Antonio, and Guadalupe Rivers to the west (Brown et al., 1976). Generally, ebb velocities are slightly greater than flood velocities through major inlets such as Aransas Pass (White et al., 1978). Maximum diurnal current velocities influencing Aransas Pass were measured at approximately 0.7 m (2.37 ft) per second for flood velocities and 0.8 m (2.51 ft) per second for ebb velocities (White et al., 1978). Ebb current velocities are significantly altered under conditions that increase the volume of water transported out of the bay such as floods and strong north winds.

Hydrodynamics of the Aransas Pass tidal inlet plays a major role in transporting nutrients between the adjacent bays and the Gulf. Copeland (1965) estimated an average of 318,960 kg/day of biomass passed through the Port Aransas inlet from highly productive bays and wetlands into the Gulf. Factors such as river discharges, tides, wave energy, and current energy determine survival of certain plants and animals that inhabit the jetty structures. For example, river discharges and tides transport nutrients from surrounding coastal marshes that are necessary for primary producing algae attached to jetties. Wave and current energy are vital to sessile organisms associated with this habitat because water movement brings food particles within the range of filter feeding organisms. Water salinity is also influenced by the hydrology of tidal inlets. Constant mixing of freshwater discharged from influencing rivers and saltwater from adjacent hypersaline bay systems and the Gulf of Mexico help maintain a constant salinity near that of average seawater (approximately 35‰).

Many natural tidal inlets form after unusual high storm tides and runoff from bays. After a particular event, the quantity of flow necessary to maintain the hydraulic efficiency of inlets is no longer available; therefore, many natural tidal inlets fill with sediment from longshore transport (Schmeltz and Sorensen, 1973). Artificial passes are believed to alter natural circulation patterns, subject protected bays to greater effects of storm surges (Brown et al., 1976), and may accelerate shoaling and closure of tidal inlets.

2.1.3.2 Natural Hard Substrate

Serpulid reef. Salinities in Baffin Bay play a major role in the faunal composition of this system. Salinities ranging from 40 to 70 (Behrens, 1966) are the result of a complex interaction of hydrological factors. Limited tidal activity, limited water circulation, lack of fresh water inflow, strong predominant southeast winds, and the arid south Texas climate are all contributing factors to hypersalinity. Circulation with Gulf waters is limited to the Port Mansfield channel, approximately 73 km (45 mi) south of the mouth of Baffin Bay, and Aransas Pass, approximately 65 km (40 mi) to the north. Evaporation exceeds precipitation as a result of the arid south Texas climate. Runoff into the Baffin Bay complex via the Olmos, San Fernando, Santa Gertrudis, and Petronila Creeks is minimal. Serpulid reefs in Baffin Bay are of interest in view of these conditions which occur in the region (Hedgpeth 1954). Behrens (1974) suggests conditions in Baffin Bay are not favorable for serpulid reefs because they would be killed by the dilution process of rare fresh water floods resulting from tropical storms and extremely high salinities produced by frequent droughts, however, current studies indicate that live specimens of serpulid worms have been found but no extensive growth is currently taking place (Hardegree, per. comm.).

Coquina outcrop. Hydrological parameters affecting formation of the Penascal Point Coquina extended over many years as sea level rose and fell. Behrens and Land (1972) concluded dolomites of Baffin Bay are the result of precipitation of some carbonate phase from bay water having a Mg/Ca ratio near that of normal sea water. Watson (1971) stated that Penascal Point coquinas are lithified equivalents of modern central Padre Island shell beaches which became cemented due to sea level rise and fall.

2.2 Producers & Decomposers

2.2.1 Primary Producers

Primary producers on the Aransas Pass jetty consist primarily of sessile (attached) macroalgae. Many studies have been undertaken on the macroalgae component of the jetties (Hedgpeth, 1953, 1954; Edwards and Kapraun, 1973; Kapraun, 1980; Britton and Morton, 1989; and Whorff, 1992). Other primary producing components include microscopic phytoplankton. Several studies have accounted for the phytoplankton within the major bay systems in the CCBNEP area (Armstrong, 1987; Holland et al., 1975; Freese, 1952), however, no studies have focused on phytoplankton utilizing the Aransas Pass inlet. Freese (1952) surveyed phytoplankton of Aransas Bay and found diatoms were the dominant component of that assemblage.

The role of primary producers is to convert light or chemical energy into tissue. The algal community takes up light and other nutrients that flow through the tidal inlet and converts them to plant material. Plant materials, along with phytoplankton that reach the jetties via the tidal inlet, are then utilized by higher trophic levels such as secondary producers which possess feeding strategies that facilitate consumption of raw plant material, detritus, or phytoplankton. Four divisions of algae are found on the jetties, Cyanophyta, Chlorophyta, Phaeophyta, and Rhodophyta (Fig. IV.B.2.5). Rhodophytes make up the greatest proportion of the macroalgae, followed by the chlorophytes, phaeophytes, and cyanophytes, respectively. Abundant species within each division, seasonal occurrence, and zonation are discussed in Section 3.4.1 Plant Communities.

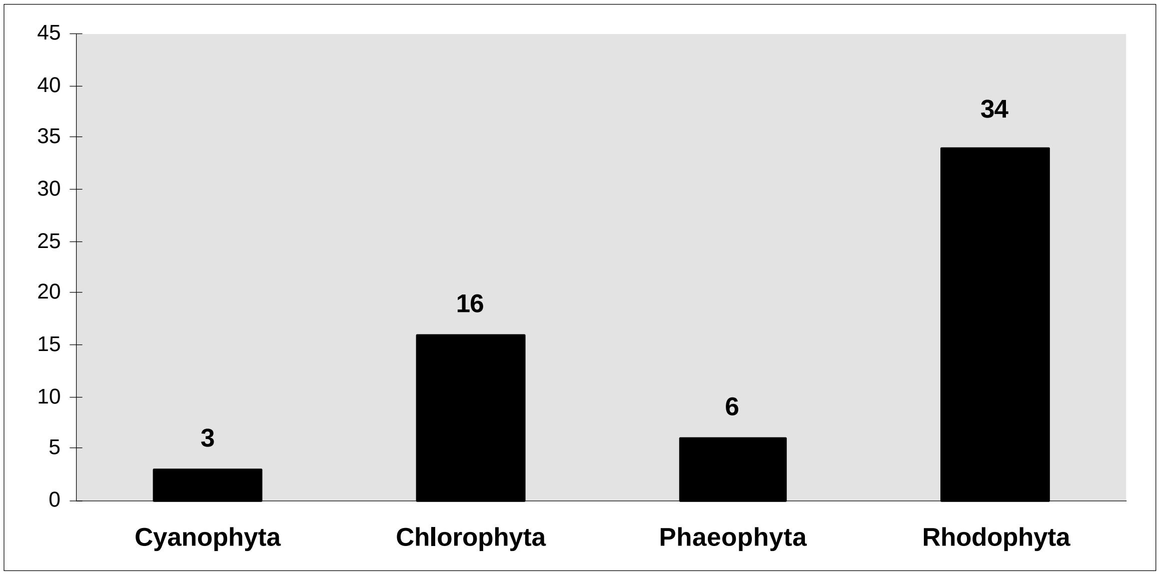

Fig. IV.B.2.5. Major primary producing algal divisions showing relative number of species found on the Aransas Pass jetties at Port Aransas, Texas (compiled from Humm and Hildebrand, 1962; Edwards and Kapraun, 1973; Edwards, 1976; Britton and Morton, 1989; and Whorff, 1992).

2.2.2 Secondary Producers

Secondary production is productivity by heterotrophic components of an ecosystem. This includes net energy left over from maintenance and respiration that goes into production of new tissue, energy storage, growth, and reproduction. Secondary producers feed directly on primary producers and are the link between primary producers and higher order consumers. Secondary producers, also referred to as basal species, primarily consist of herbivorous gastropods, bivalves, and barnacles (Paine, 1966; Whorff, 1992).

Herbivorous gastropods commonly found on south Texas jetties include *Siphonaria pectinata* (False Limpet), *Nodilittorina lineolata* (Lined Periwinkle), and *Littorina nebulosa* (Cloudy Periwinkle). *Siphonaria pectinata* has been found in high concentrations on intertidal hard substrates where thick layers of microscopic algae exist, however, the species also showed an increase in size in areas where mats of the chlorophytes *Ulva* sp. and *Enteromorpha* sp. were found (Voss, 1959). The characteristic littorine gastropods, *N. lineolata*, often seen supratidally are grazing snails that utilize a file-like radula to scrape microscopic algae from rocks. Britton and Morton (1989) reported that several hundred individuals per m^2 of *N. lineolata* have been observed on Texas jetties in cracks and crevices where they seek refuge. Andrews (1977) stated that *L. nebulosa*, reported from the Aransas Pass jetties (Whitten et al., 1950), prefers wooden substrates such as pier pilings and wooden wreckage, rather than high energy rock jetties. However, this species is often seen supratidally on the protected side of the jetty. Other epifaunal molluscan herbivores include *Anachis semiplicata* (Semiplicate Dove Shell), *Diastoma varium* (Variable Bittium), and *Haminoea succinea* (Paper-bubble). A pelagic opisthobranch sea hare, *Aplysia brasiliana*, has been described as a voracious herbivore, relatively fast growing and short lived, grazing heavily upon macroalgae on the jetties (Carefoot, 1980; Britton and Morton, 1989). The seahare is called an “ink-fish” (Whitten et al., 1950) or a “sea cow” (Strenth and Blankenship, 1977) because it forages extensively on the algal component of a community.

Filter-feeding bivalves contributing to secondary production include *Perna perna* (Edible Brown Mussel), *Crassostrea virginica* (Eastern Oyster), *Isognomon bicolor* (Tree Oyster) and *Brachidontes exustus* (Scorched Mussel). While all four bivalve species are filter feeders, *C. virginica* is a permanently sessile filter feeder and the remaining three species are attached by byssal threads. Filter feeding barnacles include *Chthamalus fragilis* (fragile barnacle), *Balanus eburneus* (ivory barnacle), and *Balanus amphitrite amphitrite* (striped barnacle). Sessile cirripedian barnacles obtain food by filtering water with cirri creating a current much the same way oysters do.

Herbivores are comprised primarily of molluscs, however, some amphipods and echinoderms also forage on the algal component of the jetty. Two herbivorous echinoderms, *Arbacia punctulata* and *Echinometra lucunter*, have been reported from the Aransas Pass jetties. *Arbacia punctulata* is the more common temperate species on Texas jetties, whereas *E. lucunter* is more tropical and not as common. Both species contribute significantly to biologic factors involved in distribution of algae on Texas jetties (Lawrence, 1975).

The omnivorous amphipod, *Hyale frequens*, was not recognized as playing an important role in the grazing of algae, until a recent finding by Brawley and Adey (1981). A correlation between numbers of amphipods and biomass of filamentous algae on a coral reef was reported and results indicated that increasing numbers of amphipods resulted in decreasing algal biomass. *Hyale frequens* has been recorded as one of the most common herbivorous amphipods on the Aransas Pass jetties (McKinney, 1977; Whorff, 1992). Other tube dwelling organisms found attached to algae or within trapped sediment included a *Corophium* sp. amphipod and a *Tanais* sp. tanaid.

2.2.3 Decomposers

Decomposers function in releasing nutrients contained in plant and animal biomass back into nutrient cycles, the opposite of primary production. Decomposition takes place primarily by bacteria and fungi, none of which have been documented from the Aransas Pass jetty. Since decomposition makes up a portion of the food web used to characterize the jetty community (see Fig. IV.B.2.8), the lack of information in this area has been identified as a data gap.

2.3 Consumers

2.3.1 Invertebrates

Poriferans, cnidarians, molluscs, crustaceans, and echinoderms make up the greatest portion of consumers that inhabit the Aransas Pass jetties. Feeding mechanisms of invertebrates include carnivores, predators, scavengers/detritivores, deposit feeders, filter feeders, and omnivores.

Invertebrate carnivores consist of cnidarians, molluscs, crustaceans, and echinoderms. Whorff (1992), stated that neogastropods and large crabs are dominant consumers of large prey in the intertidal zone. Relative importance of neogastropod predation on the intertidal community was examined and results indicated two neogastropods, *Stramonita haemostoma* (Oyster Drill) and *Pisania tincta* (Tinted Cantharus), reached densities of 6.0/m^2 and 5.7/m^2 respectively (Whorff, 1992). Neogastropods accounted for approximately 87% of the predation on “large prey” in late fall and winter, consisting primarily of *Crassostrea virginica* (Eastern Oyster). Menzel (1955) revealed that *S. haemostoma* was the primary predator of oysters. Three other neogastropods not addressed by Whorff (1992) but found on the jetties include *Pleuroploca gigantea* (Florida Horse Conch), *Murex fulvescens* (Giant Eastern Murex) and *Cantharus cancellarius* (Cancellate Cantharus) (Andrews, 1977). These species are also carnivores and have been reported to prey on *C. virginica* (Hofstetter, 1959; Menzel, 1955). Other molluscan carnivores include the cephalopods *Lolliguncula brevis* (Bay Squid) and *Octopus vulgaris* (Common Octopus) which have been caught in the tidal inlet (Gunter, 1950). The former is the most common bay squid in the CCBNEP area, however, like in Florida this species is commonly used by local fishermen as bait with only minimal human consumption (Dragovich and Kelly, 1967). *Octopus vulgaris* is the common octopus often seen by divers taking refuge in the jetty cracks and crevices.

Whorff (1992) revealed from his predator exclusion plots that small xanthid crabs (i.e. *Panopeus herbstii*) were dominant consumers of small prey (<10 mm), primarily bivalves such as *Isogonomon bicolor* (Two-toned Tree Oyster) and *Brachidontes exustus* (Scorched Mussel). Other small prey included the barnacle *Chthamalus fragilis* (fragile barnacle) and herbivorous gastropod *Nodilittorina lineolata* (Lined Periwinkle). *Menippe adina* (stone crab) preys upon both neogastropods and bivalves, however the majority of its prey consists of *C. virginica* (Menzel, 1955). *Callinectes sapidus* (blue crab) feeds on *C. virginica*, but also is considered a scavenger and omnivore, feeding on fishes, benthic invertebrates and plant material (Williams, 1984).

Predators inhabiting the jetty structure include *Caprella equilibra* (skeleton shrimp) which has been described as an amphipod version of a praying mantis that preys upon copepods and amphipods (Britton and Morton, 1989). Other predatory organisms include the echinoderms *Ophiactis savignyi* and *Ophiothrix angulata* and the common ectoparasite of the Eastern oyster, *Odostomia impressa* (Impressed Odostome). The latter species has been proven to reduce growth rate of parasitized oysters and, therefore, exerts a significant influence on the population structure and health of oyster reefs (White et al., 1984). Another predator includes the carnivorous cnidarian *Bunodosoma cavernata*, a constituent of the midlittoral algal mat fauna (Whorff, 1992).

Consumers categorized as scavengers/detritivores are dominated by decapod crustaceans, with the exception of the semiterrestrial isopod, *Ligia exotica*, and two echinoderms (*O. savignyi* and *O. angulata*) previously mentioned as predators, and also considered scavengers. *Ligia exotica*, the common sea roach, inhabits the supratidal zone within the jetty complex and has been recorded to feed on epiphytic algae and a variety of other foods including carrion (Britton and Morton, 1989). This species is nocturnal and prefers to stay out of the water except when endangered (Whitten et al., 1950). Decapod crustaceans include *Clibinarius vittatus* (striped hermit crab), *Pachygrapsus transversus* (mottled shore crab), *Petrolisthes armatus* (porcelain crab), and *Menippe adina* (stone crab). *Clibinarius vittatus* is one of the most common and conspicuous hermit crabs on the jetty rocks in Texas (Whitten et al., 1950; Williams, 1984). This euryhaline crustacean is commonly found inhabiting the intertidal zone where it scavenges for food just below the water line, however, it has been found to migrate to the subtidal zone during winter to seek refuge from decreasing temperatures (Williams, 1984). This species is commonly seen occupying a variety of gastropod shells, especially those of *S. haemastoma* (Oyster Drill) and *Polinices duplicatus* (Moon Snail). *Pachygrapsus transversus* is found intertidally and less abundant than other decapods. *Petrolisthes armatus,* predominantly a filter feeder, and *M. adina* also feed on detritus and carrion to supplement the diet (Britton and Morton, 1989).

Until recently, one annelid had been reported from the jetties (Whitten et al., 1950). Apparently, with added accumulation of sediment on the jetty rocks and algal mat, a new niche has been created conducive to deposit-feeding annelids. Whorff (1992) accounted for the amount of sediment trapped by algal mats on vertical and horizontal rock surfaces, and revealed that horizontal rock surfaces had the greatest accumulations of fine and very fine sand. Whitten et al. (1950) identified one annelid species, *Platynereis dumerilii*, from the Aransas Pass jetty; however, Whorff (1992) identified a total of seven polychaetes representing five families from the intertidal zone forty-two years later (Table IV.B.2.1). Although most annelids represented within the five families are predominantly deposit feeders, some species within these families are also carnivores and/or predators. None of the species reported, however, were distinctly

Table IV.B.2.1. Polychaetes recorded from the north Aransas Pass jetty, Texas (Whitten et al., 1950; Whorff, 1992).

Species	Species
SYLLIDAE	**CAPITELLIDAE**
Syllis prolifera	*Pseudoleiocapitella* sp.
Exogone dispar	**EUNICIDAE**
Brania clavata	*Lysidice nenetta*
NEREIDAE	**SPIONIDAE**
Nereis falsa	*Polydora aggregata*
Platynereis dumerilii	

identified as predators in the literature and only generalizations about the entire families were made.

Biota on hard substrates are considered net consumers of organic matter, much like oyster reefs, because of the organisms' ability to consume both detritus and phytoplankton by filter-feeding (Longley et al., 1989). Hiscock (1986) described organisms inhabiting the intertidal zone as primarily passive suspension-feeders relying on food carried by water movements. The flow regime of water influences growth rates and population structure of species that depend on water flow for suspension feeding by providing sufficient food for consumption (Sebens, 1986). Dominant suspension/filter feeders on the Aransas Pass jetties include barnacles *Chthamalus fragilis* (fragile barnacle), *Balanus eburneus* ivory barnacle), and *Balanus anphitrite anphitrite* (striped barnacle), and molluscs *Crassostrea virginica* (Eastern Oyster), *Isognomon bicolor* (Two-toned Tree Oyster), and *Brachidontes exustus* (Scorched Mussel) (Whorff, 1992). Other filter feeding molluscs include *Anadara transversa* (Transverse Ark), *Ischadium recurvum* (Hooked Mussel), *Isognomon radiatus* (Lister's Tree Oyster), *Ostrea equestris* (Crested Oyster), *Anomia simplex* (Common Jingle Shell) and the exotic *Perna perna* (Brown Edible Mussel). Filter feeding barnacles and molluscs were reportedly more common at the more wave exposed stations, but no significant differences in abundance were found when compared to rock angle.

Other filter feeding organisms include poriferans and cnidarians. Poriferans consist of an unidentified Demospongiae, *Haliclona* sp. and *Microciona* sp. Abundant filter feeding cnidarians include the hydroids *Tubularia crocea*, *Hydractinia echinata*, *Bougainvillia inaequalis*, *Zanclea costata*, *Clytia cylindrica*, *Sertularia inflata*, *Gonothyraea gracilis*, *Obelia dichotoma*, and *Plumularia diaphana*. Of these hydroids, the more common species include *B. inaequalis* and *O. dichotoma* (Britton and Morton, 1989). *Leptogorgia setacea* and *L. virgulata* (sea whips) are two species of gorgonian octocorals found occasionally on the jetty. *Anthopleura krebsi* and *Bunodactis texaensis* are two common filter-feeding anemones usually found under jetty rocks. The only common, shallow water stony corals on the Texas coast are *Astrangia astreiformis* and *Oculina diffusa*. These solitary corals, which are found on the Aransas Pass jetties, are capable of withstanding a wide range of salinity and temperatures, and low light conditions resulting from high levels of suspended particulate matter and turbid waters in the bay inlet

2.3.2 Fish

Most fish are not permanent residents of the Aransas Pass jetties as a result of their mobility, but, are transient, inshore, or jetty-associated species that utilize the adjacent bays, tidal inlet, jetties, and/or shallow sandy beaches (Table IV.B.2.2). Some fish species are intimately associated with the jetty and seek protection among the rocks or feed on the flora and fauna associated with its structure (Britton and Morton, 1989).

Jetty-associated species include the herbivores *Labrisomus nuchipinnis* (hairy blenny), *Blennius cristatus* (blenny), *Hypleurochilus geminatus* (crested blenny), *Abudefduf saxatilis* (damselfish or sergeant-major), and *Chaetodipterus faber* (Atlantic spadefish), and the carnivores *Epinephalus itajara* (spotted jewfish), *Strongylura marina* (Atlantic needlefish), *Hyporhampus unifasciatus* (halfbeak), and *Opsanus beta* (toad fish). Inshore species can be found in a variety of habitats in the shallow waters of the Gulf of Mexico, and are commonly seen in the vicinity of the jetties. Those species include *Lagodon rhomboides* (pinfish), *Archosargus probatocephalus* (sheepshead), *Lutjanus griseus* (gray snapper), *Trachinotus carolinus* (Florida pompano), and *Caranx hippos* (crevalle jack). Whorff (1992), stated that *Lagodon rhomboides*, *Abudefduf saxatilis*, *Blennius cristatus*, *Opsanus beta*, and *Archosargus probatocephalus* were all observed feeding on the substrate of the jetty. These species of fish are thought to feed on small crabs (i.e. *Panopeus herbstii*), amphipods, and isopods that seek refuge within the algal turf. Transient species include those species that inhabit shallow waters both in the Gulf and adjacent bays and use the tidal inlet as a route for spawning migration. Transient species include *Caranx latus* (horse-eye jack), *Arius felis* (hardhead catfish), *Lobotes surinamensis* (tripletail), *Cynoscion nebulosus* (spotted seatrout) and *Sciaenops ocellatus* (red drum). The latter two are probably the most characteristic fish species known to most sport fishermen in and around the Aransas Pass jetty. Red drum migrate to the Gulf via tidal inlets in the fall from the adjacent bays and estuaries. Most red drum spawn in shallow Gulf waters where larvae enter the bays and spend their first years in bay water (Hoese and Moore, 1977).

2.3.3 Reptiles

The western Gulf of Mexico is an important habitat for many sea turtle species (Owens et al., 1983). Of the five species that inhabit the Gulf, two species, *Lepidochelys kempi* (Kemp's Ridley) and *Eretmochelys imbricata* (Hawksbill), are listed as endangered and two, *Caretta caretta* (Loggerhead) and *Chelonia mydas* (Green), as threatened (US Fish and Wildlife Service, 1994). *Chelonia mydas* has been observed by the author on two occasions from the Aransas Pass jetty. Seagrass beds in South Texas bays were an important feeding ground for *C. mydas* (Owens et al., 1983) utilizing the tidal inlet as a migration route to and from the adjacent bays. It is contended that young green turtles enter the bays in late summer. Seagrass beds in adjacent bays once supported vast numbers of *Chelonia mydas*, but commercial overharvest lead to their decline. In the late 1800's 247,500 kg (550,000 lbs) of green turtles were harvested from Texas shores contributing to the decline of the species (Hildebrand, 1983).

Table IV.B.2.2. List of ichthyofauna associated with the jetty community at Aransas Pass, Texas, including trophic level and habitat preference. JA = jetty associate, IS = inshore species, TS = transient species (Compiled from Britton and Morton, 1989; Whorff, 1992).

Species	Trophic Level	Habitat Preference
Abudefduf saxatilis	Herbivore	JA
Epinephalus itajara	Carnivore	JA
Strongylura marina	Carnivore	JA
Hyporhampus unifasciatus	Carnivore	JA
Labrisomus nuchipinnis	Herbivore	JA
Hypleurochilus geminatus	Herbivore	JA
Blennius cristatus	Omnivore	JA
Lagodon rhomboides	Omnivore	IS
Opsanus beta	Carnivore	JA
Archosargus probatocephalus	Carnivore	IS
Chaetodipterus faber	Herbivore	JA
Lutjanus griseus	Carnivore	IS
Trachinotus carolinus	Predatory	IS
Caranx latus	Predatory	TS
Caranx hippos	Predatory	IS
Arius felis	Scavenger	TS
Lobotes surinamensis	Carnivore	TS
Sciaenops ocellatus	Omnivore	TS

2.3.4 Birds

Bird species on the jetties have not been studied extensively, however, gulls and terns (Laridae) have been documented as the most common birds frequenting barrier island beaches (Shew et al., 1981), the habitat adjacent to the Aransas Pass jetties. Some species of gulls and terns found in the adjacent sandy beach habitat are listed in Table IV.B.2.3. Other bird species seen on the jetties feeding on *Perna perna*, the introduced edible brown mussel, include the Willet (*Catoptrophorus semipalmatus*), Ruddy Turnstone (*Arenaria interpres*), and American Oystercatcher (*Haematopus palliatus*) (D. W. Hicks, pers. comm.). Bird species seen resting on the jetty include the Brown Pelican (*Pelecanus occidentalis*), Snowy Egret (*Leucophoyx thula*), Great Blue Heron (*Ardea herodias*), and Double-crested Cormorant (*Phalacrocorax auritus*) (pers. observ.).

2.3.5 Mammals

Tursiops truncatus (Atlantic bottle-nose dolphin) is the most common cetacean in the inshore waters of Texas (Schmidly and Shane, 1978). Its range extends from shallow waters of the Gulf

Table IV.B.2.3. Gulls and terns commonly seen on the sandy beaches adjacent to the Aransas Pass jetties (compiled from Bird checklist in Vol. 3 of the current study).

Species	Common Name	Season
Larus atricilla	Laughing Gull	Permanent resident, breeding
Larus argentatus	Herring Gull	Winter resident, Fall transient, Spring transient
Larus delawarensis	Ring-billed Gull	Winter resident, Fall transient, Spring transient
Larus pipixcan	Franklin's Gull	Fall transient, Spring transient
Sterna nilotica	Gull-billed Tern	Spring and Summer resident, Fall transient, Spring transient
Sterna forsteri	Forster's Tern	Permanent resident, breeding
Sterna maxima	Royal Tern	Spring and Summer resident, Fall transient, Spring transient
Sterna sandvicensis	Sandwich Tern	Spring and Summer resident, Fall transient, Spring transient
Sterna caspia	Caspian Tern	Permanent resident, breeding
Sterna antillarum	Least Tern	Spring and Summer resident, Fall transient, Spring transient
Chlidonias niger	Black Tern	Spring and Summer resident, Fall transient, Spring transient
Rynchops niger	Black Skimmer	Spring and Summer resident, Fall transient, Spring transient

of Mexico to bays, estuaries, waterways, and freshwater rivers. This species is common in the Aransas Pass tidal inlet and is often seen riding bow waves of boats.

2.4 Community Structure & Zonation

2.4.1 Plant Communities

Rocky shores support some of the most productive and extensive algal populations in the marine environment (Dawes, 1981). Of 200 species of multicellular algae described from Texas shores and adjacent Gulf states of Louisiana, Mississippi, and Alabama, about 52 species occur regularly on Texas shores and about 90 species occur during different seasons at the Port Aransas jetties (Britton and Morton, 1989). Results from the compilation of the species checklist in the current study (Vol. 3 of this report), however, indicate that a total of 106 species of algae have been documented from the Aransas Pass Jetties. The discrepancy in total numbers of species found on the jetties is attributed to additional studies on the jetties since the publication of Britton and Morton (1989) and synonymies within species.

The vertical distribution of algae into three major zones is evident on the southwest Aransas Pass jetty despite the narrow tidal range (Edwards and Kapraun, 1973). Algal zonation and seasonal succession has been well documented on the Port Aransas jetties (Hedgpeth, 1953, 1954; Conover, 1964; Edwards, 1969, 1976; Edwards and Kapraun, 1973; Kapraun, 1970, 1979, 1980; Britton and Morton, 1989; Whorff, 1992). While most studies refer to zonation in the same general manner, some researchers elaborate more on specific zones (Fig. IV.B.2.4). Whorff (1992), for example, divided the midlittoral zone into two specific subzones which he referred to as the upper yellow zone and the lower algal zone. Stephenson and Stephenson (1972) and Britton and Morton (1989) included a supralittoral fringe and an infralittoral fringe above and below the midlittoral zone, respectively. Because of narrow zonation patterns resulting from limited tidal range on the Aransas Pass jetties, and for the sake of simplicity, zonation will be referred to as supratidal, intertidal, and subtidal in the following discussion.

Table IV.B.2.4 Comparison of vertical zonation schemes of a typical rocky shore.

ZONATION	Stephenson & Stephenson, 1949	Hedgpeth, 1953; 1954	Kapraun, 1980	Britton & Morton, 1989	Whorff 1992	
SUPRATIDAL	SUPRALITTORAL ZONE	SPLASH ZONE	UPPER LITTORAL	SUPRALITTORAL ZONE		
		Ulva sp. ZONE				
MHWST	SUPRALITTORAL FRINGE			SUPRALITTORAL FRINGE	MIDLITTORAL	UPPER YELLOW ZONE
INTERTIDAL	MIDLITTORAL ZONE	RED ALGAE ZONE	MID LITTORAL	MIDLITTORAL ZONE		LOWER ALGAL ZONE
MLWST	INFRALITTORAL FRINGE	*Padina* sp. ZONE	SUB LITTORAL	SUBLITTORAL FRINGE		
SUBTIDAL	INFRALITTORAL ZONE			SUBLITTORAL ZONE		

The supratidal zone is that region above mean high water spring tides (MHWST). Marine plants and animals inhabiting this zone are subjected to greater dehydration and greater salinity extremes than those in lower zones (Russell, 1991); relatively few species inhabit this zone due to the harsh physiological conditions. This zone is influenced by the ocean via salt spray resulting from wave action and/or wind, exposure to air, wide temperature fluctuations, intense solar radiation and desiccation. Four cyanophytes, four chlorophytes and two rhodophytes occupy this zone, *Entophysalis deusta*, *E. conferta*, *Oscillatoria corallinae*, *Calothrix crustacea*, *Enteromorpha clathrata*, *E. flexuosa*, *E. prolifera*, *Chaetomorpha linum*, *Bangia atropurpurea*, and *Gelidium latifolium*, respectively (Table IV.B.2.5). Doty (1957) and Russell (1991) stated that the supratidal zone in many areas consists of blue-green algae of the genus *Calothrix*.

Consequently, Humm and Hildebrand (1962) include one species of that same genera, *C. crustacea*, as well as *E. deusta*, *E. conferta* and *O. corallinae*.

The intertidal zone is the region regularly covered and uncovered by tides and ranges from MHWST to mean low water spring tide (MLWST). This zone is also influenced by waves, tides, exposure, desiccation, and temperature, but for shorter durations than the supratidal zone. A wide variety of algal species are encountered within this zone (Table IV.B.2.5) and include: the chlorophytes *Entocladia* sp., *Ulva* sp., *Enteromorpha* sp., *Cladophora* sp., and *Acetabularia* sp.; phaeophytes *Bachelotia* sp., *Ectocarpus* sp., *Hincksia* sp., *Padina* sp., and *Petalonia* sp.; twenty-five rhodophytes; and over twenty epiphytes.

The subtidal zone is defined as the region below MLWST that remains inundated most, if not all, of the time. This zone is the most stable of the three zones because of its constant inundation and usually only undergoes temperature variations with changes in seasons. The algal species found in this zone include the chlorophytes of the genera *Ulvella* sp., *Cladophora* sp., *Bryopsis* sp. and *Derbesia* sp., the characteristic phaeophytes include *Feldmannia* sp., *Padina* sp., *Hummia* sp. and *Dictyota* sp., and twenty rhodophytes (Table IV.B.2.5).

Comparisons between the algal composition of the exposed (Gulf) side and protected (channel) side of the jetties at Aransas Pass have been made (Edwards and Kapraun, 1973; Kapraun, 1980; Britton and Morton, 1989; Whorff, 1992). Most studies found that species limited to protected sites are often delicately filamentous or articulated corallines, whereas species most abundant in exposed sites are typically coarsely filamentous or cartilaginous with thick fronds (Kapraun, 1980). Kapraun discovered eighteen species with distributions limited to either the exposed or protected side of the south jetty. *Haliptilon subulatum*, *Polysiphonia denudata*, and *Callithamnion cordatum* were essentially restricted to the protected side, while *Cladophora dalmatica*, *Pterocladia capillacea*, and *Gracilaria tikvahiae* were most abundant on the exposed side. Whorff (1992), in his study of the north jetty, found that all of the *Haliptilon cubense* encountered was recovered from exposed stations; *Ceramium deslongchampii*, *Spyridia hypnoides*, and *Padina gymnospora*, however, were recovered from protected stations. The aforementioned studies noted broader zonation bands and an upward deflection of vertical ranges with increasing wave action in a seaward direction along the length of the jetty.

A striking seasonal succession of jetty flora occurs on the northern Gulf of Mexico jetties, with temperate forms dominating in winter and tropical species prevalent in summer (Hedgpeth, 1953,1954; Edwards and Kapraun, 1973; Britton and Morton, 1989; Whorff, 1992) (Table IV.B.2.5). This seasonal fluctuation is attributed to varying physical factors including salinity, turbidity, light intensity, day length, tidal fluctuation, wave exposure, temperature, and tolerance to desiccation. During winter months, diversity and vertical range of jetty flora diminishes significantly. Britton and Morton (1989) noted three species that emerge as cold weather upper- and mid- shore dominants, *Bangia fuscopurpurea*, *Petalonia fascia*, and *Porphyra leucosticta*. Green algae tended to become more prominent during winter and early spring forming a bright green belt at mid-tide level, gradually changing into a mixture of reds, browns and greens as

Table IV.B.2.5 Vertical zonation and seasonal occurrence of algal species recorded from the Aransas Pass jetties at Port Aransas, Texas. W=Winter, S=Summer, T=Throughout, A=Autumn (compiled from Humm and Hildebrand, 1962; Edwards and Kapraun, 1973; Edwards, 1976; Kapraun, 1980; Britton and Morton, 1989; and Whorff, 1992).

DIVISION	**SPECIES**	**ZONATION****	**SEASONAL OCCURRENCE**
CYANOPHYTA	*Entophysalis deusta*	Supratidal/epiphyte	*
	Entophysalis conferta	Supratidal	*
	Oscillatoria corallinae	Supratidal/epiphyte	*
	Calothrix crustacea	Supratidal/epiphyte	*
CHLOROPHYTA	*Ulothrix flacca*	Epiphyte	W
	Entocladia viridis	Intertidal/epiphyte	T
	Ulvella lens	Subtidal/epiphyte	*
	Enteromorpha clathrata	Intertidal	W
	Enteromorpha flexuosa	Intertidal	W
	Enteromorpha lingulata	Subtidal	S
	Enteromorpha prolifera	Intertidal	W
	Enteromorpha ramulosa	Intertidal/subtidal	W
	Ulva fasciata	Intertidal/subtidal	S
	Ulva lactuca	Intertidal	W
	Chaetomorpha linum	Supratidal/intertidal	S
	Cladophora albida	Intertidal	W
	Cladophora dalmatica	Intertidal	T
	Cladophora montagneana	Intertidal/epiphyte	S
	Cladophora prolifera	Subtidal	*
	Cladophora ruchingeri	Subtidal	*
	Cladophora vagabunda	Intertidal/subtidal	T
	Bryopsis pennata	Subtidal	*
	Bryopsis hypnoides	Subtidal	S
	Bryopsis plumosa	Subtidal	S
	Derbesia vaucheriaeformis	Subtidal	*
	Acetabularia crenulata	Intertidal/epiphyte	S
PHAEOPHYTA	*Bachelotia antillarum*	Intertidal/epiphyte	*
	Ectocarpus siliculosus	Intertidal/epiphyte	S
	Feldmannia indica	Subtidal/epiphyte	T
	Hincksia mitchelliae	Intertidal/epiphyte	T
	Hincksia irregularis	Intertidal/epiphyte	T
	Streblonema oligosporum	Epiphyte	W
	Dictyota menstrualis	Subtidal	S
	Padina gymnospora	Intertidal/subtidal	S
	Hummia onusta	Subtidal/epiphyte	W
	Petalonia fascia	Intertidal/subtidal	W
RHODOPHYTA	*Stylonema alsidii*	Intertidal/epiphyte	S
	Erythrotrichia carnea	Intertidal/epiphyte	S
	Sahlingia subintegra	Intertidal/epiphyte	S
	Bangia atropurpurea	Supratidal/epiphyte	W
	Porphyra leucosticta	Intertidal/subtidal	W
	Audouinella microscopica	Epiphyte	*
	Audouinella flexuosa	Subtidal/epiphyte	T
	Audouinella hoytii	Epiphyte	*

Table IV.2.5. Continued.

DIVISION	**SPECIES**	**ZONATION****	**SEASONAL OCCURRENCE**
	Audouinella hypneae	Subtidal/epiphyte	*
	Audouinella secundata	Subtidal/epiphyte	S
	Gelidium latifolium	Supratidal	*
	Gelidium crinale	Intertidal/subtidal	A
	Pterocladia bartlettii	Intertidal	A
	Pterocladia capillacea	*	*
	Titanoderma pustulatum	*	*
	Dermatolithon pustulatum	Intertidal/epiphyte	T
	Haliptilon cubense	Intertidal	S
	Haliptilon subulatum	Subtidal	T
	Halymenia floridana	Intertidal	*
	Jania capillacea	Subtidal	*
	Grateloupia filicina	Intertidal	T
	Prionitis pterocladina	Intertidal/subtidal	T
	Agardhiella subulata	Intertidal/subtidal	W/S
	Solieria filiformis	Intertidal	S
	Hypnea valentiae	Intertidal	S
	Hypnea musciformis	Intertidal	T
	Gracilaria cornea	Subtidal	S
	Gracilaria tikvahiae	Subtidal	T
	Gracilaria verrucosa	Subtidal	S
	Rhodymenia pseudopalmata	Subtidal	S
	Lomentaria baileyana	Subtidal	S
	Lomentaria uncinata	Subtidal	*
	Aglaothamnion westbrookiae	Intertidal	S
	Callithamnion cordatum	Intertidal	*
	Centeroceras clavulatum	Intertidal	S
	Ceramium flaccidum	Subtidal	S
	Ceramium cimbricum	Intertidal	S
	Ceramium deslongchampii	Intertidal	S
	Spermothamnion sp. A	Subtidal	S
	Spermothamnion sp. B	*	*
	Spyridia hypnoides	Intertidal	S
	Spyridia filamentosa	Subtidal	S
	Bryocladia cuspidata	Intertidal	S
	Bryocladia thyrsigera	Intertidal	S
	Chondria dasyphylla	Subtidal	*
	Chondria littoralis	*	T
	Chondria capillaris	*	*
	Herposiphonia secunda	Subtidal	S
	Herposiphonia secunda f. tenella	Subtidal	S
	Laurencia obtusa	*	*
	Polysiphonia boldii	Intertidal	T
	Polysiphonia echinata	*	*
	Polysiphonia denudata	Intertidal/subtidal	T/S
	Polysiphonia gorgoniae	Subtidal	S
	Polysiphonia havanensis	*	W
	Polysiphonia subtilissima	*	T
	Polysiphonia tepida	Intertidal	S

Table IV.2.5. Continued.

DIVISION	SPECIES	ZONATION**	SEASONAL OCCURRENCE
	Polysiphonia atlantica	Subtidal	*
	Digenia simplex	Subtidal	S

* Information not available ** Zonation and/or mode of attachment are listed in this column, i.e. epiphytes.

summer approaches. Edwards and Kapraun (1973) determined in their two year study that seasonal fluctuation of vegetation was brought about by an annual temperature range of 17º C, extensive rainfall (during their study) that altered salinity values, and the occurrence of Hurricane Celia in September, 1973. They concluded that because of the environmental artifacts that took place during the duration of their study the algal distribution could not be correlated directly to tide levels.

2.4.2 Invertebrate Communities

The invertebrate community, like the plant community, also exhibits vertical zonation. The same zonation scheme used for plants (Table IV.B.2.4) is used for invertebrates. Dayton (1971) stated that community structure should be explained using evidence that growth and regulation of component populations in the community are affected in a predictable manner by either natural physical disturbances and/or interactions with other species. Therefore, factors affecting the invertebrate community structure within each prospective zone will be described where evidence exists.

Many factors are attributed to zonation patterns, but no specific factor can solely be responsible for this phenomena. Parameters such as tidal range, desiccation, inundation, wave action, currents, sand scour, solar radiation, salinity fluctuations, predation, and competition have been attributed to zonation patterns (Connell, 1961, 1970; Dayton, 1971; Lubchenco and Menge, 1978; Menge, 1991; Whorff, 1992). Britton and Morton (1989) described the hard substrate community on Texas jetties as one of the simplest in the world. A list of invertebrates inhabiting the Aransas Pass jetties is included in Table IV.B.2.6, however, the more common species will be described in detail within their respective zones.

2.4.2.1 Supratidal

The supratidal zone is dominated by the herbivorous littorinid molluscs *Nodilittorina lineolata* (Lined Periwinkle) and *Littorina nebulosa* (Cloudy Periwinkle), and the semiterrestrial isopod, *Ligia exotica* (rock louse). *Nodilittorina lineolata* was thought to be the sole littorine characterizing Texas supratidal hard shores (Britton and Morton, 1989), however, *L. nebulosa* has also been documented from this zone (Whitten et al., 1950). *Ligia exotica*, a nocturnal

Table IV.B.2.6. Invertebrate species reported from the Aransas Pass jetties, Texas, including higher taxonomic classification, zonation, and trophic level (compiled from Whitten et al., 1950; Andrews, 1977; McKinney, 1977; Fotheringham, 1980; Williams, 1984; Britton and Morton, 1989; Whorff, 1992).

Zonation	Species	Taxonomic Classification	Trophic Level
Supratidal	*Littorina nebulosa*	Mollusca	Herbivore/sub. scraper
	Nodolittorina lineolata	Mollusca	Herbivore/sub. scraper
	Ligia exotica	Crustacea	Scavenger
	Ocypode quadrata	Crustacea	Scavenger
Intertidal	*Demospongiae (unid.)*	Porifera	Filter-feeder
	Clytia cylindrica	Cnidaria	Filter-feeder
	Syllis prolifera	Annelida	Deposit feeder
	Brania clavata	Annelida	Deposit feeder
	Exogone dispar	Annelida	Deposit feeder
	Nereis falsa	Annelida	Deposit feeder
	Lysidice nenetta	Annelida	Deposit feeder
	Polydora aggregata	Annelida	Deposit feeder
	Pseudoleiocapitella sp.	Annelida	Deposit feeder
	Ischnochiton papillosus	Mollusca	Herbivore
	Nerita fulgurans	Mollusca	Carnivore
	Siphonaria pectinata	Mollusca	Herbivore/sub. scraper
	Bulla striata	Mollusca	Carnivore
	Diodora cayensis	Mollusca	Herbivore
	Diastoma varium	Mollusca	Herbivore
	Anachis avara	Mollusca	Herbivore
	Stramonita haemastoma	Mollusca	Carnivore
	Pisania tincta	Mollusca	Carnivore/Predatory
	Cantharus cancellarius	Mollusca	Carnivore/Predatory
	Odostomia impressa	Mollusca	Ectoparasite
	Anachis semiplicata	Mollusca	Herbivore/Detritivore
	Heliacus bisulcata	Mollusca	Carnivore
	Haminoea succinea	Mollusca	Herbivore
	Anadara transversa	Mollusca	Filter feeder
	Ischadium recurvum	Mollusca	Filter feeder
	Isognomon bicolor	Mollusca	Filter feeder
	I. radiatus	Mollusca	Filter feeder
	Brachidontes exustus	Mollusca	Filter feeder
	Perna perna	Mollusca	Filter feeder
	Aplysia brasiliana	Mollusca	Herbivore
	Lolliguncula brevis	Mollusca	Carnivore
	Octopus vulgaris	Mollusca	Carnivore
	Alpheus heterochaelis	Crustacea	Omnivore, detritivore
	Tozeuma carolinense	Crustacea	Herbivore
	Petrochirus diogenes	Crustacea	Predator, herbivore, scavenger
	Pagurus longicarpus	Crustacea	Omnivore, detritivore
	Lepas anatifera	Crustacea	Suspension feeder
	Chthamalus fragilis	Crustacea	Suspension Feeder
	Balanus eburneus	Crustacea	Suspension feeder
	B. amphitrite amphitrite	Crustacea	Suspension feeder

Table IV.2.6. Continued.

Zonation	Species	Taxonomic Classification	Trophic Level
Subtidal	*B. improvisus*	Crustacea	Suspension feeder
	Megabalanus antillensis	Crustacea	Suspension feeder
	Clibinarius vittatus	Crustacea	Scavenger/detritivore
	Panopeus herbstii	Crustacea	Omnivore
	Pachygrapsus transversus	Crustacea	Scavenger/omnivore
	Petrolisthes armatus	Crustacea	Herbivore/suspension feeder/scavenger
	Menippe adina	Crustacea	Carnivore/Predatory/scavenger
	Pilumnus pannosus	Crustacea	Omnivore
	Callinectes sapidus	Crustacea	Carnivore
	Tanais sp.	Crustacea	*
	Hyale frequens	Crustacea	Herbivore/omnivore
	Parhyale hawaiensis	Crustacea	*
	Corophium spp.	Crustacea	Detritivore
	Gamaropsis spp.	Crustacea	*
	Microdeuptous brasiliensis	Crustacea	*
	Caprella equilibra	Crustacea	Predator
	Haliclona sp.	Porifera	Filter-feeder
	Microciona sp.	Porifera	Filter-feeder
	Scypha barbadensis	Porifera	Filter-feeder
	Haliclona loosanoffi	Porifera	Filter-feeder
	Haliclona permollis	Porifera	Filter-feeder
	Haliclona rubens	Porifera	Filter-feeder
	Haliclona viridis	Porifera	Filter-feeder
	Halichondria bowerbanki	Porifera	Filter-feeder
	Syncoryne eximia	Porifera	Filter-feeder
	Chrysaora quinquecirrha	Porifera	Filter-feeder
	Cyanea capillata	Porifera	Filter-feeder
	Tubularia crocea	Cnidaria	Filter-feeder
	Bunodosoma cavernata	Cnidaria	Carnivore
	Hydractinia echinata	Cnidaria	Filter-feeder
	Bougainvillia inaequalis	Cnidaria	Filter-feeder
	Zanclea costata	Cnidaria	Filter-feeder
	Clytia cylindrica	Cnidaria	Filter-feeder
	Sertularia inflata	Cnidaria	Filter-feeder
	Gonothyraea gracilis	Cnidaria	Filter-feeder
	Obelia dichotoma	Cnidaria	Filter-feeder
	Plumularia diaphana	Cnidaria	Filter-feeder
	Leptogorgia setacea	Cnidaria	Filter-feeder
	Leptogorgia virgulata	Cnidaria	Filter-feeder
	Renilla mulleri	Cnidaria	Filter-feeder
	Anthopleura krebsi	Cnidaria	Filter-feeder
	Bunodactis texaensis	Cnidaria	Filter-feeder
	Aiptasiomorpha texaensis	Cnidaria	Filter-feeder
	Astrangia astreiformis	Cnidaria	Filter-feeder
	Pagurus pollicaris	Crustacea	Detritivore, scavenger
	Oculina diffusa	Cnidaria	Filter-feeder
	Lucapinella limatula	Mollusca	Herbivore

Table IV.2.6. Continued.

Zonation	**Species**	**Taxonomic Classification**	**Trophic Level**
	Tricolia affinis	Mollusca	Herbivore
	Mitrella lunata	Mollusca	Herbivore
	Pleuroploca gigantea	Mollusca	Carnivore
	Murex fulvescens	Mollusca	Carnivore
	Crassostrea virginica	Mollusca	Filter feeder
	Ostrea equestris	Mollusca	Filter feeder
	Anomia simplex	Mollusca	Filter feeder
	Ophiactis savignyi	Echinodermata	Scavenger/predator
	Ophiothrix angulata	Echinodermata	Scavenger/predator
	Hemipholis elongata	Echinodermata	*
	Echinometra lucunter	Echinodermata	Herbivore
	Arbacia punctulata	Echinodermata	Herbivore

* information not available

isopod often found under rocks, is considered to be a primitive species. This isopod primarily respires by way of gill-like abdominal pleopods which must be kept moist by periodic immersions in the sea; it is also capable of limited gaseous exchange directly with the atmosphere across thin membranes located on the abdomen. Organisms inhabiting the supratidal zone display morphological adaptations conducive to withstanding environmental conditions intermediate between terrestrial and marine habitats.

2.4.2.2 Intertidal

The intertidal zone of the Aransas Pass jetties has the greatest species richness of the three primary zones. Poriferans, cnidarians, annelids, molluscs, crustaceans, and echinoderms all live within the limits of this zone. Until recently only two annelids had been documented from the Aransas Pass jetties (Whitten et al., 1950), however, Whorff (1992) documented seven annelids (Table IV.B.2.1). In addition, Whorff includes a poriferan of the family Demospongiae.

The molluscan community within the intertidal zone consists primarily of herbivores, carnivores, and filter-feeders, respectively. *Siphonaria pectinata* (False Striped Limpet) is considered a characteristic herbivore of this zone. This limpet is referred to as a primitive pulmonate because of its ability to breathe air via a mantle lung and true accessory gill. Voss (1959) found a positive correlation between the occurrence of *S. pectinata* and the macroalgae *Ulva* sp. and *Enteromorpha* sp. and Craig et al. (1969) determined that *S. pectinata* plays a role in the destruction of beach rock by rasping the thin layer of algae and rock material from beach-rock outcrops. Characteristic carnivorous gastropods within this zone include *Stramonita haemastoma* (Oyster Drill), *Cantharus cancellarius* (Cancellate Cantharus), and *Pisania tincta* (Tinted Cantharus). These predatory gastropods feed on barnacles and other bivalve molluscs including *Crassostrea virginica* (Eastern Oyster). Hedgpeth (1954) described the middle zone of the hard substrates at Port Aransas as inhabited by the filter feeding oysters but absent of mussels. Since the discovery of *Perna perna* (Edible Brown Mussel) on the Aransas Pass jetties in February 1990 this is no longer true (Hicks and Tunnell, 1993). In only four years since its discovery, *P. perna* has colonized many different types of hard substrates, primarily the high energy intertidal zone of jetties and other natural and artificial shores from Matagorda Peninsula, Texas, to southern Veracruz, Mexico (Hicks and Tunnell, 1994). Other filter feeding bivalves found intertidally include *Isognomon bicolor* (Two-toned Tree Oyster), *I. radiatus* (Lister's Tree Oyster), *Brachidontes exustus* (Scorched Mussel), and *Ischadium recurvum* (Hooked Mussel). The pelagic sea hare, *Aplysia brasiliana*, is largely restricted to subtidal habitats; however, it is often seen intertidally where its preferred food, green algae (*Enteromorpha* sp., *Ulva* sp., and *Cladophora* sp.), is abundant (Carefoot, 1981).

Cephalopod molluscs sometimes seen by divers in jetty cracks and crevices include *Lolliguncula brevis* (Bay Squid) and *Octopus vulgaris* (Common Octopus). *Lolliguncula brevis* is common in shallow marine waters. Gunter (1950) collected more squid in the Gulf than in Aransas Bay, even though more trawls were made in the bay. Squid typically enter the bay in late winter/early spring and leave for the Gulf with the onset of cooler weather in fall. *Octopus vulgaris* is not as common in this area as *L. brevis*. Gunter (1950) stated that this cephalopod is occasionally caught by fishermen in Aransas and Corpus Christi Bays, however, he attributed its paucity to the lack of rocks and protective crevices for them to inhabit.

Five species of sessile crustaceans characterize the intertidal zone: *Chthamalus fragilis* (Fragile Barnacle), *Balanus eburneus* (Ivory Barnacle), *B. amphitrite amphitrite* (Striped Barnacle), *B. improvisus* (Acorn Barnacle) and *Megabalanus antillensis* (Giant Barnacle)(Whorff, 1992). *Cthamalus fragilis* is the dominant intertidal barnacle on all Texas jetties and always zoned the highest (Whorff, 1992). *B. eburneus*, *B. amphitrite amphitrite* and *B. improvisus* have all been recorded from the intertidal and are usually located below *C. fragilis* ranging into the subtidal zone (Stephenson and Stephenson, 1949).

Common decapod crustaceans inhabiting the intertidal zone include *Clibinarius vittatus* (Striped Hermit Crab), *Panopeus herbstii* (Common Mud Crab), *Pachygrapsus transversus* (Mottled Shore Crab), *Petrolisthes armatus* (Porcelain Crab), *Callinectes sapidus* (Blue Crab), and *Menippe adina* (Stone Crab) (Whorff, 1992). Although these crustaceans are predominantly found intertidally, they are not restricted to this zone because of their mobility. Other crustaceans inhabiting this zone include both amphipod and isopod species. These small organisms live among filamentous algae; some common species include the herbivore *Hyale frequens* and *Caprella equilibra* (Skeleton Shrimp).

2.4.2.3 Subtidal

The subtidal community consists of poriferans, cnidarians, molluscs, and echinoderms. Eleven sponges have been recorded from the hard substrate community within the CCBNEP study area. Cnidarians have predominantly been zoned subtidally and include both hydrozoans and anthozoans. Common hydrozoans include *Tubularia corcea*, *Syncoryne eximia*, *Zanclea costata*, *Hydractinia echinata*, *Bougainvillia inaequalis*, *Clytia cylindrica*, *Gonothyraea gracilis*, *Obelia dichotoma*, *Sertularia inflata*, and *Plumularia diaphana*. The most common anthozoan is

Bunodosoma cavernata (Warty Anemone) found on the sheltered side of the jetty. Two gorgonian octocorals (sea whips) found on the jetties are *Leptogorgia setacea* and *L. virgulata.* These species are well adapted to the tidal inlet by their ability to bend with currents. Other anthozoans include *Renilla mulleri*, *Anthopleura krebsi*, *Bunodactis texaensis*, and *Aiptasiomorpha texaensi*. Two shallow water, colonial, stony corals, *Astrangia astreiformis* and *Oculina diffusa*, found in Texas are common on the jetty at Port Aransas (Whitten, et al., 1950).

Subtidal Molluscan species found on the jetty include the carnivorous *Murex fulvescens* (Giant Eastern Murex) and the filter feeding oysters *Anomia simplex* (Common Jingle Shell), *Crassostrea virginica* (American Oyster), and *Ostrea equestris* (Crested Oyster). Oysters, in general, do not successfully colonize the Port Aransas jetties, as they may be inferior to more competitive species of plants and animals. Although a suitable substrate for attachment is available, other factors including salinity fluctuations and thermal stress may prevent oysters from establishing long term populations.

Two species of spiny sea urchins have been recorded from the Aransas Pass jetties, *Arbacia punctulata* and *Echinometra lucunter*. *Arbacia punctulata* is more common while *E. lucunter* is more abundant on the southern-most Texas jetties in areas of maximum exposure. *Arbacia punctulata* prefers the sheltered side of the jetty, is found in association with *Padina* (Hedgpeth, 1954), and is primarily a herbivore believed to play an important role in the distribution of algae on Texas jetties (Lawrence, 1975). Other echinoderms reported from these jetties include the brittle stars *Ophiactis savignyi*, *Ophiothrix angulata*, and *Hemipholis elongata*. *Ophiactis savignyi* is more tropical, often found associated with sponges (Britton and Morton, 1989). The other two species are commonly found in offshore sands, however, they have been reported at the jetties.

2.4.3 Vertebrate Communities

2.4.3.1 Ichthyofauna

Although no studies have been conducted delineating zonation patterns for fish species, some general statements can be made. Because of their mobility, fish are not limited to one zone. Some fish are, however, classified as bottom dwellers or floaters (Britton and Morton, 1989). For example, a bottom dweller *Epinephalus itajara* (Spotted Jewfish) inhabits deeper waters surrounding rocks and crevices of the jetties. The floater *Lobotes surinamensis* (Tripletail) is commonly associated with flotsam in open water, but can be found around pilings and bulkheads in enclosed areas and is occasionally seen floating on its side near the surface of the water in and around the jetties.

2.4.3.2 Aves

Two dominant shore bird species, gulls and terns, inhabit the adjacent sandy beaches (Table IV.B.2.3). As previously mentioned, birds have not been specifically documented from the jetties, however, gulls have been seen in the supratidal zone of the jetties scavenging for dead crabs or discarded bait from local fishermen.

2.5 Ecosystem Processes

2.5.1 Productivity

Many studies of the artificial hard substrate community at the Aransas Pass jetties have been undertaken, specifically concerning plant community structure. Other studies focused on biological interactions and species accounts. Many gaps, however, exist in the overall role this habitat plays in its contribution of productivity to the marine ecosystem. This habitat is unique because it provides a substrate suitable for many plants and animals that otherwise would not exist. With increasing shoreline alterations by way of rip rap, bulkheads, seawalls, pier pilings, etc. (Morton and Paine, 1984), this community could become a significant contributor to the productivity of surrounding bays. Therefore, studies focusing on the productivity of hard shore communities should be considered.

Approximately 318,960 kg/day of biomass is transported by way of the Aransas Pass tidal inlet from adjacent highly productive bays and wetlands into the Gulf of Mexico (Copeland, 1965). Although this biomass is not directly representative of the productivity on the jetties, it does influence jetty flora and fauna by providing nutrients necessary for their survival.

2.5.2 Nutrient Cycling

Nutrients including phosphorus, silica, and nitrogen are used by primary producers to synthesize organic material (Schramm, 1991). Phosphorous, an element in seawater, is added to marine ecosystems through runoff, removed through plant uptake and animal consumption, and is later returned to the marine ecosystem when organisms die and decay. Silica is the element critical to cell wall formation in diatoms (Dawes, 1981), which were found to be the dominant component of the phytoplankton assemblage in Aransas Bay (Freese, 1952).

Nitrogen fixing-cyanophytes transform nitrates into a useable form that is utilized by plants. The role of marine bacteria in the oceanic nitrogen cycle is important (Dawes, 1981). Although no studies have been undertaken on the rate of the nitrogen fixing abilities of blue-green algae found on the Aransas Pass jetties, other cyanophytes of the same genera have been known to show high rates in other localities. For example, in the Baltic Sea, nitrogen fixation by the benthic blue-green alga *Calothrix scopulorum* ranged from 2 to 87 mg N m^{-2} d^{-1} (Schramm, 1991).

2.5.3 Energy Flow

Major energy inputs to artificial structures in general include sunlight, wave energy, and current energy (Longley, et al., 1989). Sunlight is necessary for photosynthesizing primary producers such as algae which primarily inhabit hard substrates; wave and current energy bring nutrients and particulate matter to sessile plants and animals. In addition, wave and current energy also affect distribution of organisms and niche segregation.

2.5.4 Trophic Levels and Food Web Relationships

Trophic levels are defined as a functional classification of organisms in an ecosystem according to feeding relationships, from first-level autotrophs through succeeding levels of herbivores and carnivores (Smith, 1990). A food web is the interconnecting web that results when organisms within a community are classified by trophic levels.

Three types of food webs characterizing hard substrate communities were encountered during the research phase of this study: (1) a subweb (Paine, 1966), (2) an interaction web (Whorff, 1992), and (3) a simplified food web (Britton and Morton, 1989). The former is when groups of organisms are capped by a terminal carnivore and trophically interrelated in such a way that at higher levels there is little transfer of energy to co-occurring subwebs (Fig. IV.B.2.6). This subweb is the basis for Paine's (1980) "keystone species concept" which states that as long as a keystone predator exists within a compartmentalized subweb the remaining superior resource competitors will maintain a balance which allows them to coexist. Once this association between the keystone predator and the superior prey is broken, i.e. the keystone predator is removed, the compartment, or lower trophic levels within this subweb, begin to outcompete each other and the foodweb no longer exists as a subweb. An interaction web is a food web where only strong links between dominant species are shown (Fig. IV.B.2.7). Although this interaction web is specific for the Aransas Pass jetties, it is limited to the intertidal component of the jetties and does not include any external sources of energy and nutrients, perhaps due to a lack of information in this area. A simplified food web shows all sources of energy, both biotic and abiotic, involved in the transfer of energy within a community (Fig. IV.B.2.8). This simplified food web seems to best represent the entire community structure on the Aransas Pass jetty and, therefore, will be used to diagramatically show the interactions between the biotic and abiotic components of this community.

The jetty fauna represents a composite of colonization from various habitats, including oyster reefs, sand and mud bottoms of adjacent areas, salt marshes, and possibly pelagic sargassum (Whitten et al., 1950). The centralized location of the jetties and diverse origin of the organisms that inhabit them have created a unique food web similar in some respects to other communities, yet, different in other ways. For example, most other foodwebs from other habitats are primarily detritus-based food webs. The food web used in this chapter, however, is primarily an attached macroalgae-based food web, where the major primary producing component is benthic macroalgae. Although detritus is a component in this foodweb, little is known about the origins and decomposition of this material; only speculations can be made that this material originates in and around adjacent communities. Little is known about decomposers in this habitat as well. Studies on other rocky shores (Paine, 1966), however, reveal decomposers to be important in decomposition of dead plant and animal matter utilized by higher trophic levels.

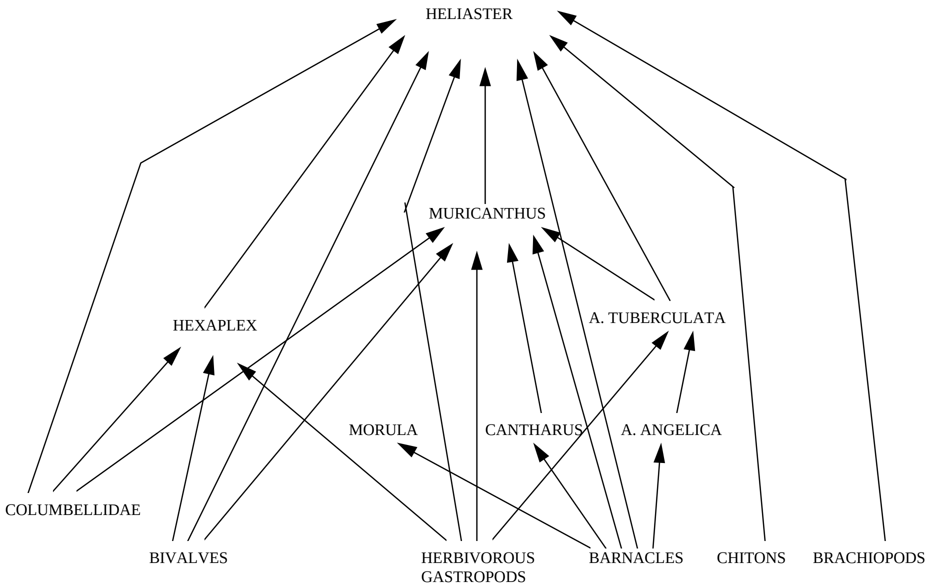

Figure IV.B.2.6. Subweb showing feeding relationships from a northern Gulf of California rocky shore (adapted from Paine, 1966).

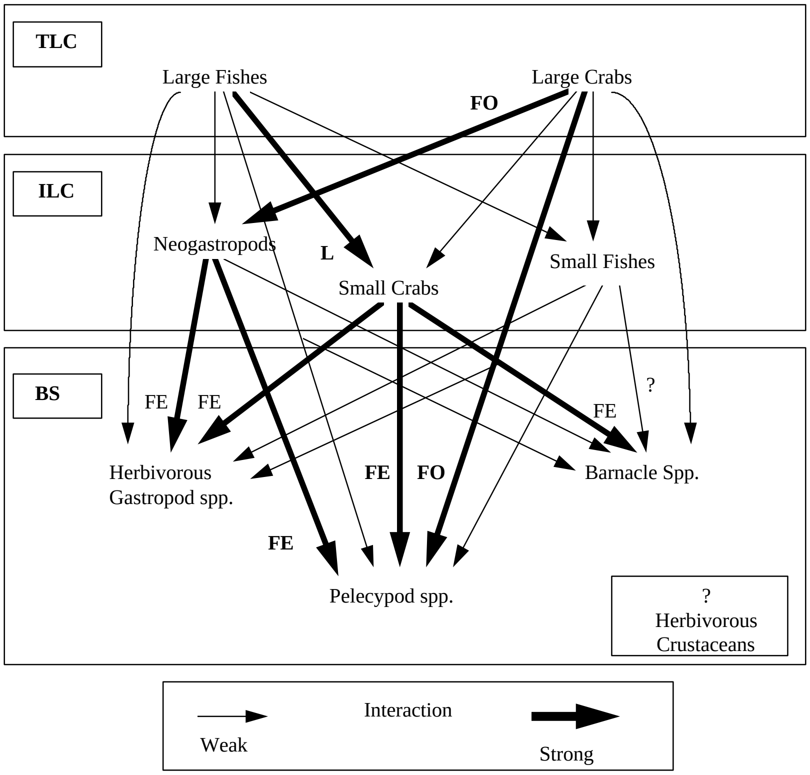

Figure IV.B.2.7. Intertidal interaction web of the Aransas Pass jetties, Texas (modified from Whorff, 1992). Strong interactions were supported by direct field observations (FO), field experiments (FE), and previous literature (L). TLC = Top level consumer, ILC = Intermediate level consumer, BS = Basal species.

Abiotic components included in the food web necessary for the survival of plants and animals include sunlight, nutrients, and detritus (Fig. IV.B.2.8). Biotic constituents of the food web include primary producers, secondary producers, consumers, and decomposers. Primary producers consist primarily of benthic macroalgae. Phytoplankton, predominantly diatoms, contribute to primary productivity, but their direct influence on the jetty community is unknown. Secondary producers, or basal species, are composed of organisms that feed directly on primary producers. This trophic level consists primarily of herbivorous gastropods, bivalves, and barnacles such as *Siphonaria pectinata*, *Nodolittorina lineolata*, *Crassostrea virginica*, *Isognomon bicolor*, *Brachidontes exustus*, *Perna perna*, *Chthamalus fragilis*, *Balanus amphitrite*, and *B. eburneus*. Although no studies have been undertaken pertaining to the role, if any, that the jetty community plays in zooplankton, Britton and Morton (1989) include this group in their food web. Consumers consist primarily of filter feeders, carnivores, and/or scavengers. A major portion of this trophic level includes the carnivorous crustaceans, *Menippe adina*, *Callinectes sapidus*, and xanthid crabs. In addition, some carnivorous gastropods that are also important predators include *Stramonita haemostoma*, *Pisania tincta*, and *Murex fulvescens*. Decomposers primarily consist of bacteria and fungi, however, none have been documented from the Aransas Pass jetty.

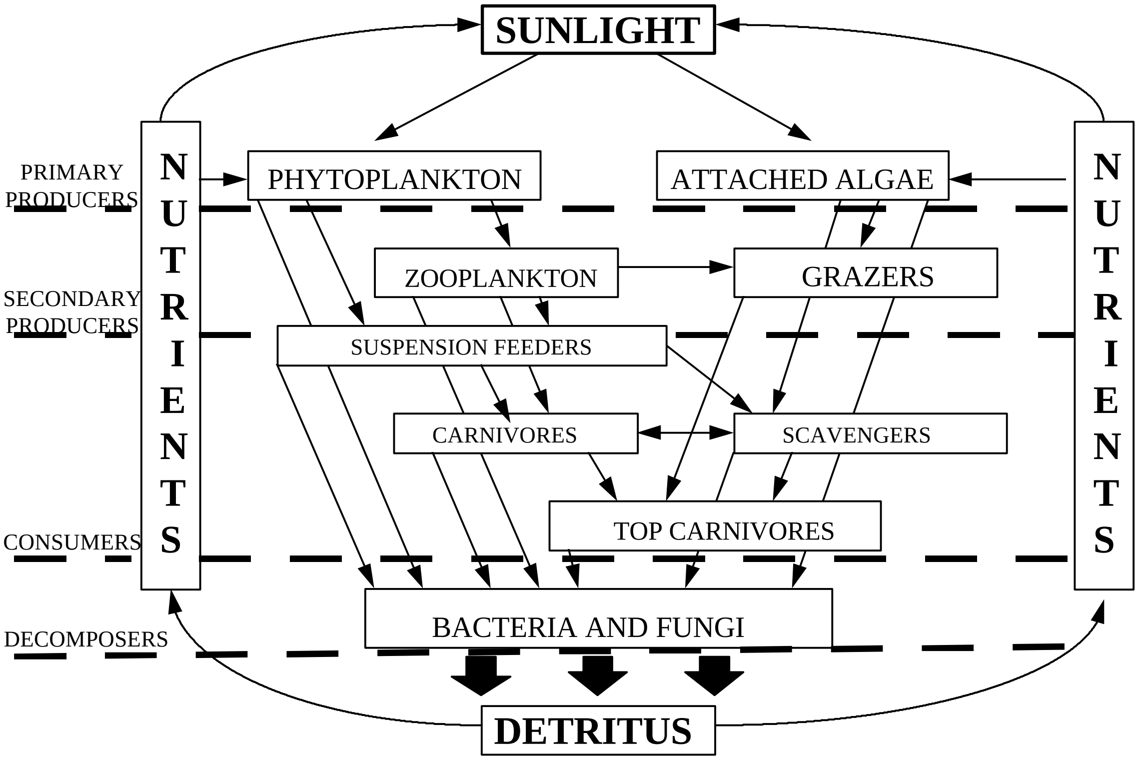

Fig. IV.B.2.8. Simple food web adapted to characterize the Aransas Pass jetties, Texas (modified from Britton and Morton, 1989).

2.5.5 Linkages with Other Systems

Intertidal and littoral ecosystems, as defined by Schramm (1991), are areas of transition between terrestrial and oceanic environments and recipients of terrigenous materials. The location of Aransas Pass jetties allows for mixing of Gulf waters with runoff and discharge from adjacent uplands and rivers, directly affecting the jetty community. For example, high energy waves which arise from prevailing southwest winds often aid in mixing of these waters, resulting in an increase in nutrient levels and enhanced primary production (Schramm, 1991). Other factors affecting the mixing processes include turbidity resulting from navigation traffic in the Pass and dredging effects resulting from maintenance dredging of channels in and around the Pass. Intertidal ecosystems are also impacted through the discharge of industrial, agricultural or domestic wastes into rivers or directly into the sea, thereby altering the chemical characteristics of coastal waters.

Aransas Pass serves as a primary link between the Gulf of Mexico and approximately 200,000 ha of wetlands (Hedgepeth, 1953). In addition, this Pass is influenced by discharges from Mission, Aransas, Nueces, San Antonio, and Guadalupe Rivers. These rivers flow into adjacent bays and estuaries including Mission/Aransas Estuary, Nueces Estuary, and Baffin Bay-upper Laguna Madre System. Many of the nutrients utilized by the jetty community probably originate from these vast expanses of wetlands, therefore Aransas Pass serves as a means of transportation for these nutrients to reach the jetty community.

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HABITAT 3: OYSTER REEF

3.1 Physical Setting & Processes

3.1.1 Definition and Distribution within Study Area

Oyster reef, as defined by Norris (1953), refers to natural accumulation of shells, primarily Eastern oyster, *Crassostrea virginica*, which results from successive growth of generations of oysters in the same place. Oyster shell and living oysters provide a hard substrate for settlement of a variety of sessile organisms as well as a protective habitat for many mobile organisms.

Maps presented in the Texas Oyster Fishery Management Plan (Quast et al., 1988) and data on oyster harvest in Texas reveal oyster reefs are most numerous and best developed within the CCBNEP area in Mesquite, Aransas and Copano bays (Fig. IV.B.3.1). Reefs in Redfish Bay consist primarily of dead shell material (Copeland and Hoese, 1966). Small patch reefs are widely scattered in the Nueces-Corpus Christi Bay system (Fig. IV.B.3.2). Most live oyster reefs within this system occur in Nueces Bay; reefs occurring throughout Corpus Christi Bay are mostly dead (Galtsoff, 1931). No oyster reefs have been reported within upper Laguna Madre; no live oysters were found in dredge samples taken throughout upper Laguna Madre (Hofstetter, 1959; Martin et al., 1990).

3.1.2 Historical Development

Buried oyster reefs have been found from a few centimeters to as much as 4 m below the bottom of San Antonio, Mesquite, Aransas, and Copano bays (Norris, 1953). Price and Gunter (1942) found vast submerged reefs 18 m below the bottom of Baffin Bay. The following sequence of events leading up to present conditions has been suggested based on occurrence of buried reefs: (1) lowering of late Pleistocene sea-level accompanied by down-cutting of river valleys through Pleistocene-deposited marine sediments (ca 18,000-23,000 YBP). As an example, the San Antonio River valley was 15-23 m or more below present sea level; (2) early Holocene rise in sea-level flooded the lower river valleys forming estuaries (ca 12,000-10,000 YBP). Drowned river valleys acted as traps for sediment carried in by rivers. Oyster reefs probably started to grow in San Antonio and Copano bays first, because freshwater inflows would be expected to reduce salinities enough to be suitable for oyster growth, and (3) Barrier island system development (ca. 3,000 YBP), which coincided with sea-level reaching its approximate current position, closed Aransas and Mesquite bays from the Gulf of Mexico, allowing oyster reefs to form. Presence of buried reefs up to 4 m suggests that bays were somewhat deeper at the end of the Pleistocene and have since filled with sediment, although as much as 0.3 m of sediment has been deposited in certain places within these bays during the last 100 years (Norris, 1953). Oysters shells have been excavated from aboriginal shell middens in numerous places along the shores of the entire CCBNEP area. Accounts by early explorers during the mid-sixteenth century indicate oysters were a primary food source for Karankawa Indians. Oyster reefs have been reported as spanning the entrance to Nueces Bay during the 1500's; it served as a bridge across the bay (Briscoe, 1972). Galtsoff (1931) also reported a large reef in the same area.

Fig. IV.B.3.1. Locations of natural oyster reefs in the Aransas-Copano Bay system (from Quast et al., 1988).

3.1.3 Physiography

Oyster reefs along the Texas coast are described by Price (1954) as being long and narrow with their long axis perpendicular to prevailing water currents or parallel to channels, with a tendency to grow out into the bay at right angles to shore (Norris, 1953). Many reefs identified on maps (Diener, 1975) within Copano, Aransas, and Mesquite bays demonstrate this arrangement. Reefs within the Nueces-Corpus Christi Bay system are predominantly small scattered patch reefs. All reefs within the CCBNEP area are typically an accumulation of shell material in mound form. The highest point of intertidal reefs, frequently exposed by low tides and subject to sediment accumulation, is mostly composed of dead shell with a few live oysters. The upper surface of

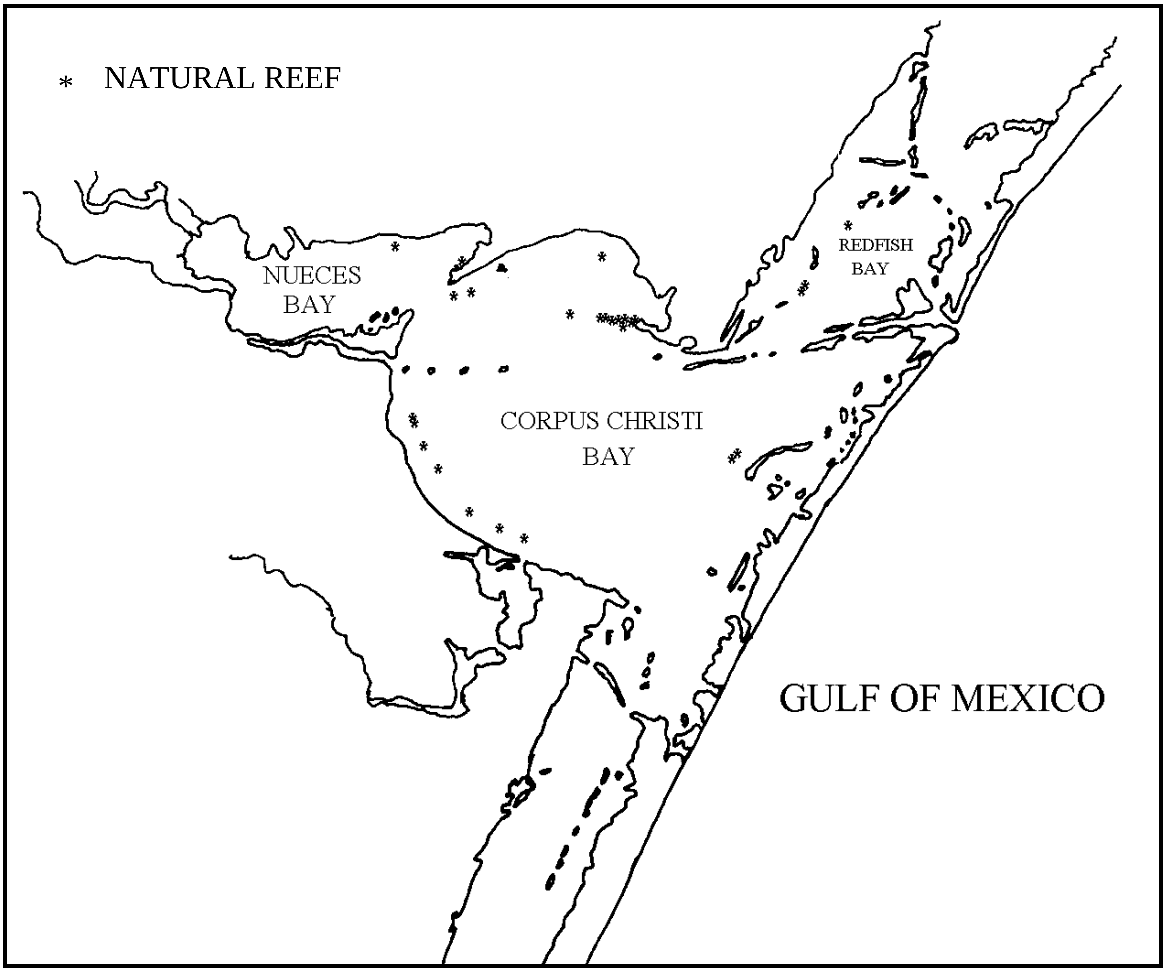

Fig. IV.B.3.2. Locations of natural oyster reefs in the Corpus Christi-Laguna Madre estuarine complex (from Quast et al., 1988).

this type of reef is usually flat with steep slopes along the edges. Density of live oysters is greatest along the edges (Bahr and Lanier, 1981). The structure of developing subtidal reefs that occur within deeper waters are rarely described. Vertical upbuilding is characteristic of reefs undergoing subsidence; younger oysters are typically found in upper layers of such a developing reef.

Valves of mature oysters are elongate with growing edges oriented in an upward position. Micro-orientation of valves to dominant currents for maximum feeding and waste removal has been observed (Lawrence, 1971). Oysters in waters with multi-directional currents do not demonstrate definite micro-orientation (Bahr and Lanier, 1981). No information is available on micro-orientation of oyster valves within the study area.

Maximum vertical growth or thickness for some modern reefs occurring in the Aransas Bay system ranges from about 3.7 to 6 m (Norris, 1953). Richards (1939) reported a thickness of up to 30 m for some reefs in Copano Bay. Flat, "pancake" reefs form patch reefs in shallow areas of Nueces Bay (Scott, 1968). Oysters occur intertidally on surfaces of pilings and other submerged, solid substrates within, and along the perimeter of the CCBNEP area. Scattered live oysters are found throughout Redfish Bay in shallow waters along margins of the islands (L. McEachron, pers. obs.)

3.1.4 Geology and Soils

Sediments transported by low energy inlets entering upper reaches of bay systems are composed primarily of clay and silt and are deposited onto the middle bay bottoms. Muds mixed with sand and shell fragments are found along bay margins and the lower reaches of bays. The only natural hard bottom substrate to occur within most Texas bays is provided by oyster reefs (Britton and Morton, 1989). Oyster reef development usually occurs within firm muddy environments, and developing reefs tend to form small isolated islands of solid substrate within surrounding mud deposits (Bahr and Lanier, 1981). A sediment profile associated with development of a typical reef in Aransas Bay indicates initial development of reefs begins on the surface of mud deposits. Layers which accumulate along outer edges of a developing reef include mud and loose shells (Norris, 1953). Successful settlement of oyster spat most frequently occurs on clean, stable shell surfaces associated with the surface or periphery of developing reefs. Loose, shifting sands and soft muds provide less stable surfaces for oyster spat settlement (Bahr and Lanier, 1981, Quast et al., 1988). Long reefs which develop within bay systems tend to interfere with sediment transport (Britton and Morton, 1989).

3.1.5 Hydrology and Chemistry

Texas bays are categorized according to location relative to barrier islands and tidal inlets. Mesquite Bay, Aransas Bay, Redfish Bay, Corpus Christi Bay and upper Laguna Madre are considered primary bays due to their proximity to Gulf waters. Copano Bay, Nueces Bay and Baffin Bay are considered secondary bays due to their more isolated positions (Britton and Morton, 1989).

Oyster reef development is dependent upon several hydrological and water quality factors, including current flow, salinity, water temperature, dissolved oxygen and sedimentation. Current flow is required by oysters for feeding, waste removal, sediment removal and dispersal of larvae (Grave, 1905; Grinnell, 1971). Long narrow reefs in Copano, Mesquite and Aransas bays demonstrate macro-orientation with respect to current flow. These reefs have developed perpendicular to dominant currents to maximize feeding and waste removal. This growth pattern is thought to disturb normal current flow and influence a partial retention of water within upper reaches of Copano Bay (Collier and Hedgpeth, 1950). Water circulation is primarily wind driven within the CCBNEP area (Smith, 1974), although tidal flow contributes some water movement within the bays (Collier and Hedgpeth, 1950). Heavy discharge by the San Antonio and Guadalupe rivers into San Antonio Bay may influence circulation within Mesquite and Aransas Bays.

Crassostrea virginica is broadly euryhaline, but is most common in Texas bays with a salinity range of 10 - 30‰. Salinities outside this range tend to stress physiological and reproductive processes by limiting growth (Quast et al., 1988) and impacting spatfall (Hopkins, 1931; Gunter, 1955). Survival of oyster populations during salinity fluctuations is dependent upon the range of fluctuation as well as the rate and duration of change (Quast et al., 1988). Salinity changes may also alter the biotic profile of an oyster reef (Hoese, 1960). Salinities within Copano and Nueces Bays are generally lower than adjoining primary bays during periods of high precipitation and river discharge. During periods of low rainfall and high evaporation, secondary bays may become hypersaline. Although both the Aransas and Mission rivers discharge into Copano Bay, their influence on salinities is minimal compared to that of the San Antonio and Guadalupe rivers to the north of the study area (Collier and Hedgpeth, 1950). Mean salinities in Aransas Bay commonly range between 10 and 20‰, whereas those in Copano Bay range from 10 - 15‰ (White et al., 1989). Mean salinities for Nueces and Corpus Christi bays range between 15 - 30‰ (Holland et al., 1975). Salinities within Baffin Bay are usually equal to or higher than the adjoining Laguna Madre due to more arid conditions and limited freshwater discharge (Britton and Morton, 1989). Behrens (1966) reported salinities within upper Laguna Madre ranged from 30 - 40‰ during normal seasons, whereas in Baffin Bay they ranged from 40 - 50‰. Behrens also noted salinities had not exceeded 85‰ even during drought conditions since construction of the Gulf Intracoastal Waterway. Fluctuating salinities are common within the bay systems of the study area, but seem to be most pronounced within Nueces Bay (Holland et al., 1975; Drumright, 1989).

High and low temperatures are limiting factors that mainly affect shallow water and intertidal oysters. Temperatures have a greater range and change more rapidly in more isolated bays such as Nueces and Copano bays (Holland et al., 1975). Both prolonged freezing temperatures and prolonged exposure to high water temperatures caused by intense solar heating during summer may cause death of intertidal oysters (Galtsoff, 1964; Copeland and Hoese, 1966). Concurrent high temperatures and salinity changes stress physiological functioning in oysters (Andrews, 1982). Water temperature also influences timing of spawning. Maximum spawning in Galveston Bay occurred after water temperatures had reached 25º C (Hopkins, 1931).

Oysters were described by Quast et al. (1988) as facultative anaerobes. They were able to tolerate dissolved oxygen (DO) concentrations of <1 ppm for up to five days (Sparks et al., 1958). Dissolved oxygen concentrations generally increase from upper secondary bay reaches to lower primary bays (Bahr and Lanier, 1981). Low DO within upper reaches of secondary bays is probably due to oxidation of organic detritus (Bahr and Lanier, 1981). Sediment disturbance is also reported to deplete dissolved oxygen levels (Frankenberg and Westerfield, 1968). Dissolved oxygen concentrations in bays within the study area varied with temperature; from May 1974 to May 1975 DO ranged from 6.5 to 11.2 mg/l in Aransas Bay, 5.0 to 12.8 mg/l in Copano Bay, 5.8 to 9.6 mg/l in Redfish Bay, 6.1 to 9.3 mg/l in Corpus Christi Bay and 5.6 to 10.0 mg/l in Nueces Bay (Holland et al., 1975).

Sedimentation processes contribute to turbidity levels within estuarine systems. Turbidity is greater within secondary bays, especially during periods of heavy runoff or high winds. Siltation limits oyster survival within subtidal and lower intertidal zones (Bahr and Lanier, 1981). During periods of excessively high turbidity caused by storms or floods, oysters close their valves tightly for a week or more depending on water temperature (Cake, 1983). Sediments are removed from the water column by oysters and discharged as pseudofeces. Large oysters are reported to be more tolerant of normal estuarine sedimentation rates than small spat, however, continued accumulation of sediments without current removal may lead to burial and eventual death of large oysters (Galtsoff, 1964). In addition, sediment accumulation may impair spatfall (Crisp, 1967).

3.2 Producers and Decomposers

3.2.1 Primary Producers

Holland et al. (1975) found 247 phytoplankton taxa belonging to seven classes within the Aransas-Copano Bay and Corpus Christi-Nueces Bay estuarine systems but not necessarily specifically associated with oyster reefs. Diatoms accounted for 63% of the total number of phytoplankton species found during the three-year study. Dinoflagellates, green algae, and euglenoids comprised the remaining groups. Blooms of various species were noted to occur with changes in salinity and temperature. Standing crop values were highest in Corpus Christi Bay followed by Nueces, Aransas and Copano bays. No data were given on benthic microalgae species. Phytoplankton species provide a nutrient source for many of the suspension-feeding organisms inhabiting oyster reefs.

A thin algal film often occurs on surfaces of intertidal reef oyster shells (Bahr and Lanier, 1981). Algal films were noted on the surfaces of oyster shells within Nueces and Redfish bays (A. Drumright, pers. obs.). Several species of epiphytic and drift macro-algae forms occur throughout the bay systems of the study area. Some species were found attached to oyster shell or drifting among oyster shells within Nueces and Redfish bays (Table IV.B.3.1) (Drumright, 1989). Algal films and macroalgae on surfaces of oysters provide a source of nutrients for the many algae-grazing and algae-scraping herbivorous and omnivorous organisms associated with oyster reefs.

3.2.2 Decomposers

Bahr and Lanier (1981) described the decomposer community within a typical estuarine ecosystem as being comprised of two major groups: (1) aerobic heterotrophs, including bacteria and fungi that utilize inorganic matter in standing dead plant material, the water column and aerobic sediments; and, (2) anaerobic bacteria within anoxic sediments including sulfate- reducing bacteria and photolithotrophic bacteria. Decomposers play a vital role in providing for the continuous availability of carbon, nitrogen and phosphorous so that these substances may be assimilated by primary producers.

Table IV.B.3.1. Species list of macroalgae collected from oyster reef samples in Nueces and Redfish Bays from January 1987 to December 1987 (Drumright, 1989). X = presence of species.

Species	Nueces Bay	Redfish Bay
Division Chlorophyta		
Enteromorpha lingulata	X	X
Cladophora albida	X	
Division Rhodophyta		
Corallina cubensis		X
Jania capillacea		X
Gracilaria debilis		X
Gracilaria verrucosa		X
Bryocladia cuspidata		X
Digenia simplex		X
Chondria littoralis		X
Laurencia poitei		X

3.3 Consumers

3.3.1 Invertebrates

Most consumers associated with oyster reefs are invertebrates. Heffernan (1959) lists thirty two species of invertebrates collected among oyster reefs in Nueces and Corpus Christi Bays. Twenty three species of invertebrates were also reported by Heffernan (1960) to occur on reefs within Copano and Aransas Bays. A total of 116 invertebrate species representing eight phyla, 31 orders and 78 families was collected from intertidal oyster reefs from Nueces and Redfish Bays (Table IV.B.3.2) (Drumright, 1989).

Invertebrates that occur on or frequent oyster reefs utilize a variety of feeding methods and can be grouped accordingly. Invertebrate consumer groups associated with oyster reefs include suspension feeders (comprised of both filter feeders and suspension-feeding carnivores) deposit feeders, algal grazers, oyster parasites, predators, and a variety of omnivorous, scavenging arthropods. Suspension feeders remove food from the water column by utilizing siphoning with internal filtering mechanisms or specialized external structures such as radioles, cirri, setae, or tentacles. Food utilized by suspension feeders varies among species. Range of food items taken from the water column includes detrital material, bacteria, phytoplankton and various forms of zooplankton. Bivalves were the dominant suspension-feeding group.

Common bivalve suspension feeders include *Crassostrea virginica, Brachidontes exustus, Sphenia antillensis, Anadara transversa, Gemma purpurea* and *Mulinia lateralis* (Drumright,

Table IV.B.3.2. Species list of invertebrates collected from oyster reef samples within CCBNEP study area. Nueces Bay - Drumright, 1989; Redfish Bay - Drumright, 1989; Aransas Bay - Ladd, 1951; Puffer and Emerson, 1953; Copano Bay - Ladd, 1951; Puffer and Emerson; St. Charles Bay - Ladd, 1951. Most studies (excluding Drumright, 1989) focused on molluscan assemblages, hence the lack of entries for most other taxa.

Species	Nueces Bay	Redfish Bay	Aransas Bay	Copano Bay	St. Charles Bay
Phylum Porifera					
Cliona celata	X	X			
Microciona prolifera		X			
Phylum Coelenterata					
Aptasiomorpha texaensis		X			
Phylum Platyhelminthes					
Euplana gracilis	X	X			
Stylochus ellipticus	X	X			
Stylochus frontalis		X			
Phylum Rhynchocoela					
Zygonemertes virescens	X	X			
Phylum Annelida					
Class Oligochaeta					
Paranais littoralis	X				
Peloscolex cf.. *sabriella*	X	X			
Class Polychaeta					
Armandia agilis	X				
Brania clavata	X	X			
Capitella capitata	X	X			
Chaetozone sp.	X	X			
Dexiospira spirillum		X			
Eteone heteropoda	X	X			
Eumida sanguinea	X	X			
Eupomatus dianthus	X	X			
Gyptis brevipalpa	X	X			
Hypsicomus phaeotaenia		X			
Marphysa sanguinea	X	X			
Mediomastus californiensis	X	X			
Megaloma bioculatum		X			
Naineris cf. *dendritica*		X			
Neanthes succinea	X	X			
Nereiphylla fragilis	X	X			
Paraprionospio pinnata	X	X			
Pectinaria gouldii	X				
Polydora cf. *ligni*	X	X			
Polydora websteri		X			
Pomatoleios caerulescens	X	X			
Prionospio steenstrupi	X	X			

Table IV.B.3.2. Continued.

Species	Nueces Bay	Redfish Bay	Aransas Bay	Copano Bay	St. Charles Bay
Sabella microphthalma	X	X			
Streblosoma hartmanae	X	X			
Syllis gracilis	X				
Trypanosyllis parvidentata	X	X			
Phylum Mollusca					
Class Polyplacophora					
Ischnochiton papillosus		X			
Class Gastropoda					
Acteocina canaliculata	X	X	X		X
Acteon punctostriatus		X			
Anachis avara	X	X	X		X
Anachis obesa	X	X	X		X
Anomia simplex			X	X	X
Berghia coerulescens	X	X	X		
Bulla striata		X			
Caecum pulchellum		X			
Caecum sp.			X		X
Cerithiopsis greeni		X			
Cerithium lutosum	X	X			
Cerithium variabile					X
Crepidula convexa	X	X			
Crepidula plana	X	X	X	X	X
Diastoma varium	X	X		X	X
Diodora cayenensis		X			
Diodora sp.					X
?Doridella obscura	X	X			
Epitonium angulatum		X			
Epitonium sp.					X
Littordina sphinctostoma					X
Mitrella lunata	X	X	X		X
Nassarius acutus					X
Nassarius vibex	X				X
Odostomia (Evalea) cf. emeryi		X			
Odostomia cf. dianthophila	X	X			
Odostomia impressa	X	X	X		
Odostomia sp.			X	X	X
?Okenia impexa	X	X			
Pyrgocythara plicosa	X	X			
Rissoina sp.			X		X
Sayella livida		X			
Seila adamsi			X		

Table IV.B.3.2. Continued.

Species	Nueces Bay	Redfish Bay	Aransas Bay	Copano Bay	St. Charles Bay
Thais haemastoma floridana		X			
Triphora perversa nigrocinta	X	X			
Triphora sp.					X
Turbonilla sp.		X			X
Vitrinella cf. *helicoidea*					X
Vitrinella floridana					
Class Bivalvia					
Amygdalum papyria		X			
Anadara brasiliana (=*Arca incongrua*)					X
Anadara transversa		X	X		X
Argopecten irradians		X			
Brachidontes exustus	X	X	X	X	
Chione cancellata		X			
Corbula cf. swiftiana	X	X			
Corbula sp.					X
Crassinella sp.			X		
Crassostrea virginica	X	X	X	X	X
Diplothyra smithii		X	X	X	X
Gemma purpurea		X			
Ischadium recurvum		X	X	X	X
Laevicardium mortoni	X	X			X
juv. ?*Lucina sp.*		X			
Lyonsia hyalina floridana		X			
juv. ?*Macoma* sp.		X			
Mercenaria campechiensis		X			
Mulinia lateralis	X		X		X
Nuculana acuta	X	X			X
Nuculana concentrica			X		X
Pandora trilineata			X		
Rangia cuneata					X
Semele sp.					X
Sphenia antillensis	X	X			
Tellina texana	X				
Tellina versicolor		X			
Trachycardium muricatum		X			
Phylum Arthropoda					
Alpheus heterochaelis	X	X			
Ampelisca verrilli	X	X			
Amphiporeia virginica	X				
Ampithoe valida	X	X			

Table IV.B.3.2. Continued.

Species	Nueces Bay	Redfish Bay	Aransas Bay	Copano Bay	St. Charles Bay
?Anoplodactylus lentus		X			
Balanus improvisus	X	X			
Batea catharinensis		X			
Callinectes sapidus	X	X			
Cassidiniea lunifrons		X			
Cerapus tubularis	X	X			
Clibanarius vittatus		X			
Corophium acherusicum	X	X			
Cymadusa compta	X	X			
Cymodoce faxoni	X	X			
Elasmopus levis	X	X			
Erichsonella attenuata	X	X			
Erichsonella filiformis isabelensis		X			
Erichthonias brasiliensis	X	X			
Eurypanopeus depressus	X				
Gammarus mucronatus	X	X			
Hargeria rapax	X	X			
Hippolyte zostericola	X	X			
Libinia dubia		X			
Melita nitida	X	X			
Menippe adina	X	X			
Micropanope nuttingi					
Mysidopsis almyra	X	X			
Neopanope texana sayi	X	X			
Ostracods				X	X
Oxyurostylis smithi	X	X			
Palaemonetes intermedius	X	X			
Palaemonetes pugio	X				
Palaemonetes vulgaris		X			
Penaeus setiferus	X				
Panopeus herbstii	X	X			
Panopeus turgidus	X	X			
Penaeus aztecus	X	X			
Petrolisthes armatus	X	X			
Podocerus brasiliensis					
Rithropanopeus harrisii	X				
Stenothoe minuta		X			
Unciola irrorata	X	X			

Table IV.B.3.2. Continued.

Species	Nueces Bay	Redfish Bay	Aransas Bay	Copano Bay	St. Charles Bay
Phylum Bryozoa					
Bugula neritina	X	X			
Membranipora tenuis	X	X			
Membranipora sp.				X	X
Phylum Protozoa					
Order Foraminifera					
Ammobaculites sp.			X		X
Elphidium sp.			X		X
Nonion sp.			X		X
Rotalia sp.			X		X
Quinqueloculina sp.			X		
Bolivina sp.			X		
Buliminella sp.			X		
Cibicides sp.			X	X	X

1989). *Ischadium recurvum* is a common bivalve suspension feeder found inhabiting oyster reefs within Aransas and Copano Bays (White et al., 1983, 1989). Other common suspension feeders collected from oyster reefs within Nueces and Redfish bays included poriferans (e.g., *Cliona celata*, *Microciona prolifera*), the small anemone *Aiptasiomorpha texaensis*, gastropods such as *Crepidula* spp*.*, the bryozoans *Bugula neritina* and *Membranipora tenuis,* the ascidians *Molgula* cf. *complanata* and *M. manhattensis*, and polychaetes (e.g., *Polydora* spp., *Eupomatus dianthus*). Suspension-feeding arthropods included *Balanus improvisus*, *Corophium acherusicum*, and *Petrolisthes armatus*.

Most deposit feeders on oyster reefs in Nueces and Redfish bays were polychaetes. Dominant species included *Paraprionospio pinnata*, *Capitella capitata* and *Mediomastus californiensis. Stylochus ellipticus* (flatworm), *Thais haemastoma* (oyster drill), *Bulla striata* (bubble shell), and *Mennippe adina* (stone crab) were common predators collected from Redfish Bay oyster samples (Drumright, 1989).

Gastropods such as *Cerithium lutosum, Diastoma varium, Cerithiopsis greeni, Anachis avara,* and *Mitrella lunata* were common bottom-feeding, algal film grazers collected from oyster reefs in Nueces and Redfish bays. Other algal grazers included a minute nudibranch, (cf. *Berghia coerulescens*), and *Ischnochiton papillosus.* Common parasitic gastropods found among oysters included *Odostomia cf. dianthophila* and *O. impressa* (Drumright, 1989).

Decapods associated with oyster reefs exhibit a wide variety of feeding habits (Barnes, 1987). *Callinectes sapidus* (blue crab), collected from reefs in Nueces and Redfish bays, couples predacious feeding with scavenging. *Neopanope texana*, and *Panopeus turgidus*, were common in reefs of Nueces and Redfish bays (Drumright, 1989), whereas *Micropanope nuttingii* was the most common crab species on Copano Bay reefs (White et al., 1983). Xanthids couple detrital-feeding and algal film scraping with scavenging (Barnes, 1987). Xanthid crabs *Eurypanopeus depressus* and *Panopeus herbstii*, which both occur on reefs in Nueces and Redfish bays, are omnivorous (Bahr and Lanier, 1981). *Eurypanopeus depressus* was observed feeding on amphipods and *P. herbstii* was noted to feed on small oysters on Sapelo Island, Georgia reefs. Both species were reported to occur within the detrital zone during low tide and migrated to higher, submerged intertidal zones to scrape algal film from shells during rising tides. Shrimp, such as *Penaeus aztecus*, *P. setiferus*, *Palaemonetes* spp., and *Alpheus heterochaelis*, were common omnivorous detrital feeders found frequenting oyster reefs in Nueces and Redfish bays (Drumright, 1989). Most amphipods are detritus feeders or scavengers (Barnes, 1987).

3.3.2 Fish

Species collected from oyster reef samples taken from Nueces and Redfish Bays from January 1987 to December 1987 (Table IV.B.3.3) belonged primarily to juvenile and small adult age classes (Drumright, 1989). However, feeding activity by larger fish in and around the reefs was commonly observed (A. Drumright, pers. obs.). Juvenile species included *Lagodon rhomboides* (pinfish), *Archosargus probatocephalus* (sheepshead), and *Leiostomus xanthurus* (spot). Decreases in densities of amphipods and polychaetes collected from oyster reef samples were noted to coincide with an increase in number of fish and shrimp collected, possibly indicating predation (Drumright, 1989). Observations of heavy feeding activity by larger fish coincided with high juvenile xanthid crab abundance in oyster samples (A. Drumright, pers. obs.).

Studies on food preferences for various growth stages of *Cynoscion nebulosus* and *Sciaenops ocellatus* indicated that organisms commonly found among oyster reefs such as polychaetes, amphipods, penaeid shrimp, caridean shrimp and xanthid crabs are a preferred food source (Miles, 1950; Moody, 1950; Tabb, 1961). Miles (1950) listed oyster reefs as one of the substrates frequented by adult *Sciaenops ocellatus*. *Pogonias cromis* (black drum) feed on oysters. (Pearson, 1929; Cave and Cake, 1980). Fish known to feed on oyster spat include *Micropogonias undulatus*, *Leiostomus xanthurus*, and *Rhinoptera bonasus* (cownose ray) (Haven et al., 1978; Krantz and Chamberlin, 1978). Common adult inhabitants collected from oyster reefs within Nueces and Redfish Bays include the benthic species *Opsanus beta* (Gulf toadfish), *Gobiosoma robustum* (code goby), and *G. bosci* (naked goby) (Drumright, 1989).

3.3.3 Reptiles and Amphibians

No information was found concerning reptile and amphibian occurrence on oyster reefs in the study area.

3.3.4 Birds

Birds frequenting oyster reefs are primarily predators that feed on oysters and associated fauna. A variety of birds were noted to be feeding on and around intertidal oyster reefs within Nueces and Redfish bays from January 1987 to December 1987 (Table IV.B.3.4) (A. Drumright, unpubl.

Table IV.B.3.3 Fish species collected from oyster reef samples within Nueces and Redfish Bays from January 1987 to December 1987 (Drumright, 1989).

Species	Nueces Bay	Redfish Bay
Anchoa mitchelli	X	
Opsanus beta	X	X
Lagodon rhomboides	X	X
Archosargus probatocephalus	X	X
Leiostomus xanthurus	X	X
Bairdiella chrysura		X
Chasmodes bosquianus	X	
Hypleurochilus germinatus		X
Bathygobius soporator		X
Gobionellus boleosoma		X
Gobiosoma robustum		X
Gobiosoma bosci	X	
Sygnathus scovelli	X	X
Stephanolepis hispidus	X	

data). The American Oystercatcher (*Haematopus palliatus*) was commonly seen at both sites feeding along fringes of oyster reefs. The diet of the oystercatcher includes oysters and other bivalves as well as small crabs (Britton and Morton, 1989). Other species seen feeding on or near oyster reefs included Laughing Gull (*Larus atricilla*), Willet (*Catoptrophorus semipalmatus*), Least Tern (*Sterna antillarum*), Black Skimmer (*Rynchops niger*), Boat-tailed Grackle (*Quiscalus major*), and a variety of migratory duck species. Great Blue Heron (*Ardea herodias*), Brown Pelican (*Pelecanus occidentalis*), White Pelican (*Pelecanus erythrorhynchos*), Dowitchers (*Limnodromus* spp.) Long-billed Curlew (*Numenius americanus*), Black-necked Stilt (*Himantopus mexicanus*), Reddish Egret (*Egretta rufescens*), Common Egret (*Casmerodius albus*), Snowy Egret (*Egretta thula*), Double-crested Cormorant (*Phalacrocorax auritus*), Least Tern (*Sterna albifrons*), Black Skimmer (*Rhynchops niger*), Boat-tailed Grackle (*Quiscalus major*) and a variety of migratory duck species were also observed.

3.3.5 Mammals

Feral hogs have been reported using oyster reefs to cross the bay at low tide on Matagorda Island, and appear to forage for whatever they can capture as they cross (McAlister and McAlister, 1993).

Table IV.B.3.4 Birds observed on or near intertidal oyster reefs within Nueces and Redfish Bays from January 1987 to December 1987 (A. Drumright, unpubl. data.).

Species	Nueces Bay	Redfish Bay
White Pelican	X	X
Brown Pelican		X
Double-crested Cormorant		X
Anhinga	X	
Northern Shoveler		X
Redhead	X	X
Lesser Scaup	X	X
Bufflehead		X
Great Egret	X	X
Snowy Egret	X	X
Great Blue Heron	X	X
Reddish Egret		X
Tricolored Heron	X	X
American Oystercatcher	X	X
Black-necked Stilt	X	X
Black-bellied Plover		X
Killdeer	X	
Long-billed Curlew	X	X
Willet	X	X
Dowitcher	X	X
Ruddy Turnstone	X	X
Sanderling		X
Ring-billed Gull		X
Laughing Gull	X	X
Least Tern	X	X
Common Tern	X	X
Black Skimmer		X
Boat-tailed Grackle	X	

3.4 Community Structure and Zonation

3.4.1 Plant Communities

Little information is available on plant community structure associated with subtidal or intertidal oyster reefs. Three horizons based on presence/absence of algae and color have been described for reefs around Sapelo Island, Georgia (Fig IV.B.3.3) (Bahr and Lanier, 1981). Algal films were found only in the upper pale greenish-gray horizon (5-10 cm) of the reef that is exposed at

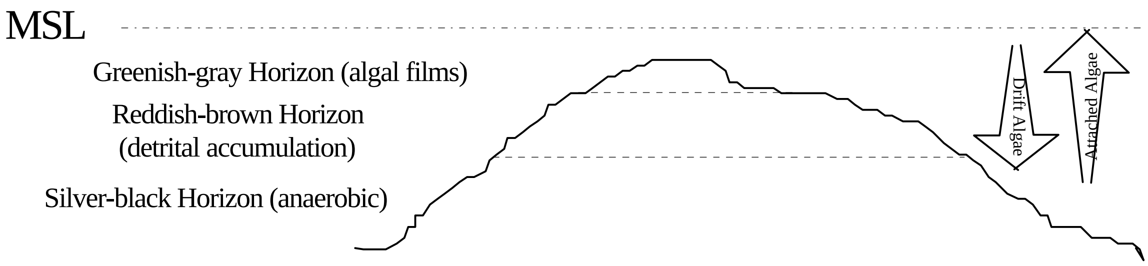

Fig. IV.B.3.3. Zonation of algal communities on oyster reefs in the CCBNEP study area. Arrows indicate direction of increasing abundance.

low tides. The reddish-brown mid-horizon and silver-black low horizon appear to lack algae. Algae also appear to be limited to the living areas of the reef. Algal films were noted on reefs in Nueces and Redfish Bays as well as attached and drift macroalgae. Growth of attached macroalgae occurred primarily at subtidal levels on oyster shells within both bays. The chlorophytes, *Cladophora albida* and *Enteromorpha lingulata,* grew on oyster shells within Nueces Bay with heaviest growth occurring during winter; light growth occurred during spring and fall. During May, June, and July, high turbidity may have contributed to reduced growth of these species. Attached macroalgal communities were more diverse in Redfish Bay, but were generally light throughout the year. *Digenia simplex* occurred throughout the year on shells within deeper portions of the reef, whereas *Bryocladia cuspidata* grew at all depths. *Jania capillacea* and *Corallina cubensis* were not abundant; *Enteromorpha lingulata* was a common chlorophyte species found growing on shell material. No drift algae accumulated on the Nueces Bay reef. In Redfish Bay, heaviest accumulations of drift algae occurred between October and December. Drift algae were collected at all depths; density increased with depth (Drumright, 1989).

3.4.2 Invertebrate Communities

Arthropods, dominated the invertebrate assemblage on shallow, intertidal oyster reefs in Nueces and Redfish bays (Fig IV.B.3.4) (Drumright, 1989). Amphipods were most numerous, followed by brachyuran crabs and caridean shrimp. Amphipods were more numerous on sublittoral reefs than intertidal reefs along the coast of Georgia (Bahr, 1981), but, only three species were reported (Bahr, 1974). Dame (1979) reported a single species with low densities occurring on reefs along the South Carolina coast. In contrast, eleven species of amphipods accounted for about 63 % of the total number of organisms collected from intertidal reefs in both Nueces and Redfish Bays between January and December 1987 (Drumright, 1989). The most abundant species in Nueces bay were *Unciola irrorata, Corophium acherusicum,* and *Amphithoe valida*. *Elasmopus levis, Ampithoe valida* and *Stenothoe minuta* were most abundant in Redfish Bay. In Nueces Bay, densities of most common amphipods peaked once during the year, generally between February and April. The exceptions were densities of *Melita nitida* which peaked during June, and remained high from September through December, and *Unciola irrorata* which

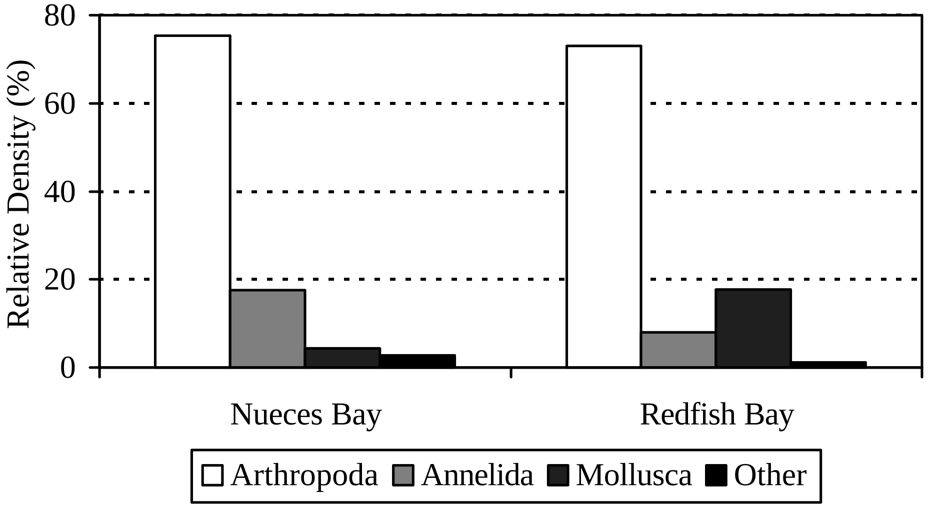

Fig. IV.B.3.4. Relative density of major taxa collected from shallow intertidal oyster reefs in Nueces and Redfish bays (after Drumright, 1989).

peaked in November. Amphipod densities in Redfish Bay were more variable. Densities of *Stenothoe minuta*, *Corophium acherusicum* and *Ampithoe valida* peaked between March and April and again between September and December.

Elasmopus levis peaked in January, April, and June, and maintained fairly high densities between September and December. *Melita nitida* densities peaked in February, May, September, and December. *Neopanope texana* was the most abundant crab and *Petrolisthes armatus* was common from both Nueces and Redfish Bays (Drumright, 1989). Caridean shrimp collectively comprised the next most abundant group of arthropods (Drumright, 1989). *Palaemonetes intermedius* and *P. pugio* were dominant species in Nueces Bay, whereas *Hippolyte zostericola, Palaemonetes intermedius* and *Alpheus heterochaelis* occurred most frequently in Redfish Bay samples. Other important arthropods which occurred on intertidal oyster reefs within Nueces and Redfish Bays included *Mysidopsis almyra*, *P. aztecus*, and *P. setiferus.*

Polychaete worms comprised the next most abundant group of invertebrates found on oyster reefs within Nueces Bay, whereas molluscs were the next most abundant group in Redfish Bay (Drumright, 1989). Twenty-three species of polychaetes were collected from Nueces Bay and 28 from Redfish Bay. *Paraprionospio pinnata*, *Brania clavata* and *Eupomatus dianthus* dominated the assemblage in Nueces Bay; *Brania clavata, Eupomatus dianthus* and *Polydora* cf. *ligni* were dominant in Redfish Bay.

Molluscs were more numerous on the Redfish Bay reef (Drumright, 1989); 27 gastropod and 18 bivalve species were collected. *Diastoma varium*, *Cerithium lutosum* and *Odostomia impressa* were the dominant gastropods and *Brachidontes exustus, Anadara transversa, Gemma purpurea* and *Sphenia antillensis* were the most common bivalves. Eighteen gastropods and eight bivalves were collected from the Nueces Bay reef. *Odostomia impressa*, *Mitrella lunata* and *Odostomia* cf. *dianthophila* were the most common gastropods; *Mulinia lateralis, Brachidontes exustus* and *Nuculana acuta* were the dominant bivalves. *Ischnochiton papillosus,* a chiton, was found only on Redfish bay reef.

Zonation of macrofaunal invertebrates on oyster reefs is the result of interspecific tolerances to desiccation rather than feeding limitation resulting from reduced inundation time (Fig IV.B.3.5) (Bahr and Lanier, 1981). Thickness or width of each zone is dependent upon tidal amplitude with decreased thicknesses in areas of lower tidal amplitude. At Sapelo Island, Georgia, oysters are limited to an elevation (1.5 m above MLW) which corresponds to maximum elevation of reefs. The upper intertidal zone is the maximum elevation of oyster growth and is characterized by the barnacle *Chthamalus fragilis,* which is tolerant of exposure. Maximum oyster growth and the less tolerant barnacle (*Balanus eburneus*) as well as other associated fauna, occur within the mid- to lower-intertidal zones.

Number of invertebrate species as well as invertebrate densities increased with depth on the Nueces and Redfish bay reefs (Drumright, 1989). Fewer species and individuals were collected from the shallowest areas that were exposed during low tides. Arthropods were the dominant group at both sites. Greater densities of organisms were collected during the day on both reefs. No specific information concerning invertebrate zonation on reefs in the study area was found.

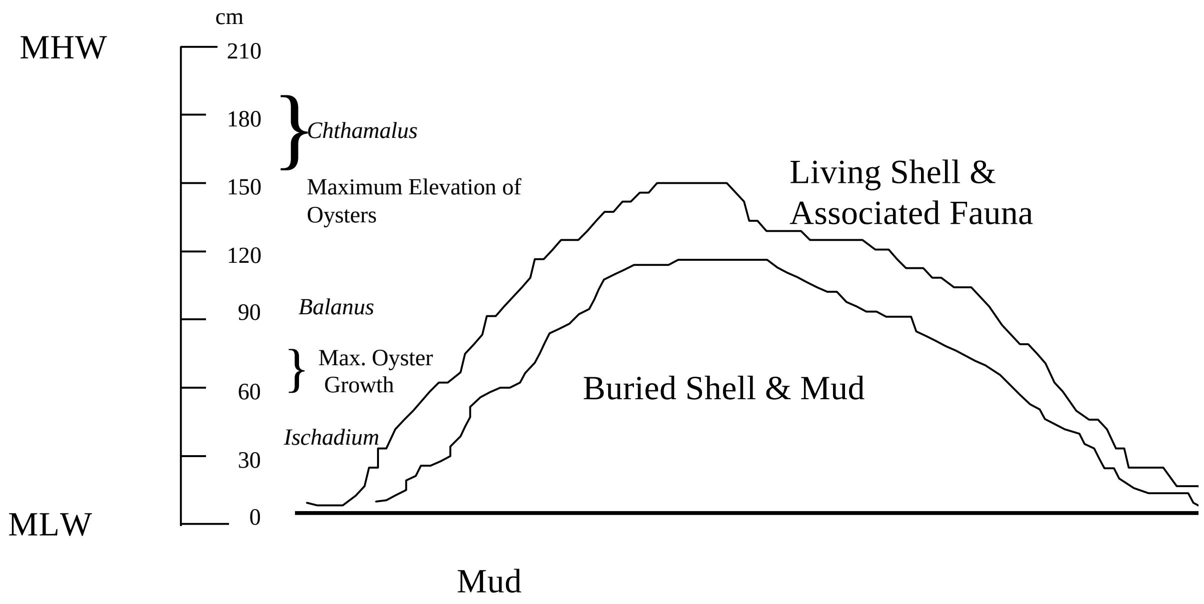

Fig. IV.B.3.5. Diagrammatic section through an oyster reef illustrating relative elevation with respect to mean tidal levels and corresponding fouling pattern on pilings (modified and redrawn from Bahr and Lanier, 1981).

3.4.3 Vertebrate Communities

The only vertebrates associated with intertidal reefs in the study area were fish and birds (A. Drumright, unpubl. data). Fourteen fish species were collected from oyster reefs within Nueces and Redfish bays. *Opsanus beta*, *Lagodon rhomboides*, *Archosargus probatocephalus*, *Leiostomus xanthurus*, *Gobiosoma* spp., *and Sygnathus scovelli* were collected at both sites. *Gobiosoma* spp. were the most numerous and occurred in about the same abundance at each site. Collecting techniques for this study only allowed for collection of juvenile and smaller adult fish however, feeding activity by larger fish in and around reefs was commonly observed (A. Drumright, pers. obs.)

Observations on oyster reef sites within Nueces and Redfish Bays included birds on and within a 20-m radius of the reefs. A total of 28 species were observed (A. Drumright, unpubl. data). Most species were feeding on or around reefs whereas others used the upper exposed reef surface as a roosting or resting site. Species which were commonly seen at both sites included Laughing Gull, Willet, Great Blue Heron, Brown Pelican, and American Oystercatcher. Species numbers, as well as population densities for some species, increased during winter. Ducks were most numerous during winter as well.

3.5 Ecosystem Processes

3.5.1 Energy Flow

Oyster reefs are heterotrophic "hot spots" within typical marsh-estuarine systems (Bahr and Lanier, 1981). Metabolic rate of an oyster reef community is high compared to other benthic communities. On reefs around Sapelo Island, Georgia, Bahr (1974), used the enclosed reef sample method, to calculate oxygen consumption for a typical intertidal reef. He found oxygen consumption ranged from 6 to 50 $g/m^2/day$ over a temperature range of 9° to $30^\circ C$. Respiration by oysters accounted for about 50% of total reef community respiration, whereas associated macrofauna only accounted for about 10%. Microbial and meiofaunal organisms associated with extensive reef surface area account for about 22% of total reef metabolism. The remaining 20% of oxygen consumption was utilized for the oxidation of reduced compounds from the anaerobic decomposition of reef-derived organic matter.

Primary energy inputs into oyster reefs include sunlight, water current energy, organic matter, microbes, and nutrients (Longley et al., 1989). Factors which may influence energy input, therefore altering reef development, include alteration in current flow, tidal-exposure frequency, toxins, salinity changes, suspended sediments and sedimentation rate, and availability of hard substrate for spat settlement. No information was found on energy flow associated with oyster reefs within the CCBNEP study area.

3.5.2 Trophic Levels and Food Web Relationships

Most organisms associated with intertidal oyster reefs are suspension-and deposit feeders (Bahr and Lanier, 1981; Drumright, 1989). This suggests the primary trophic role of the oyster reef macrofaunal community is assimilation of carbon from phytoplankton and detrital sources. Assimilated carbon is then made available to higher consumers such as predatory gastropods, fish, and birds. Figure IV.B.3.6 illustrates a typical food web associated with oyster reefs and identifies representative species within the various trophic levels. No studies on oyster reef trophic levels and food web relationships within the CCBNEP area were found.

3.5.3 Nutrient Cycling

A variety of complex pathways exist within estuarine systems which continually replenish inorganic materials needed by photosynthesizing organisms such as phosphate, nitrate, ammonia, carbon dioxide and trace elements. Oyster reefs and most associated organisms are most dependent upon the import of organic matter. Filtering activity of oysters and other associated filter feeders provide a high rate of organic input into surrounding sediments. Increased organic deposit provides a rich source of energy for deposit feeders and microorganisms (Longley et al.,

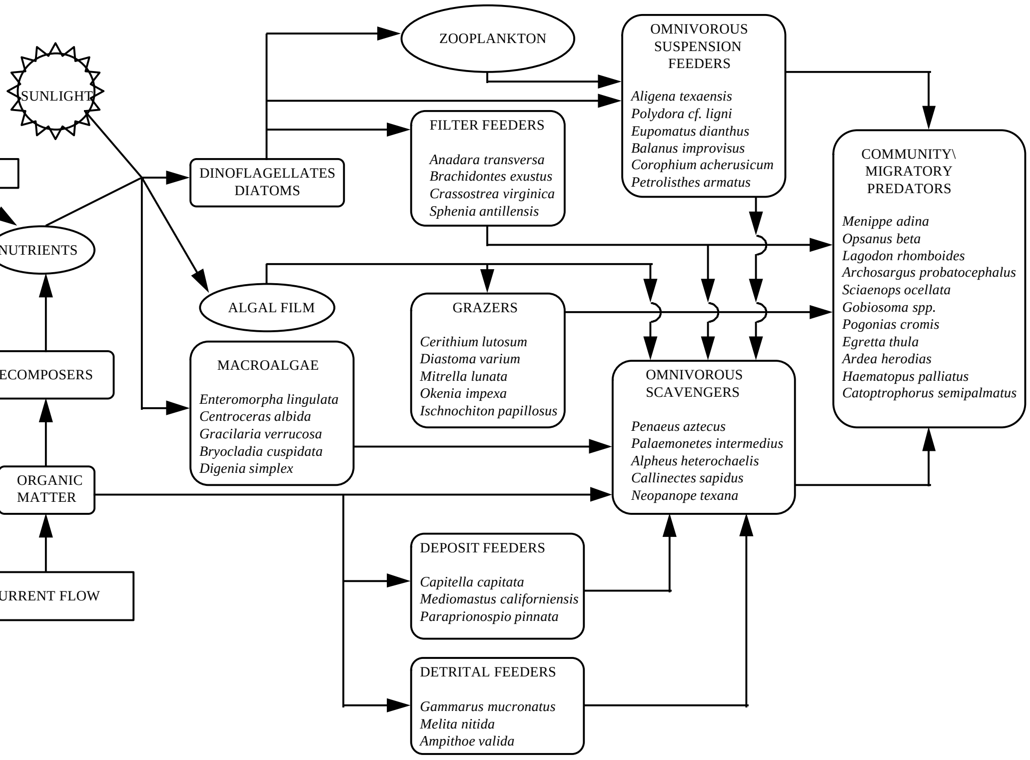

Fig. IV.B.3.6. Food web of a typical oyster reef within the CCBNEP study area (modified from Longley, et al., 1989).

1989). Carbon assimilated by the many deposit- and suspension-feeding organisms associated with oyster reefs is made available to higher consumers. The reef community also continually provides usable nitrogen and phosphorus for primary producers. Oysters also provide a high quality protein for other estuarine organisms with the release of gametes and development of larvae (Bahr and Lanier, 1981).

3.5.4 Linkages with Other Systems

Oyster reefs are most common in areas that receive continuous flow of fresh water. Fresh water inflow, provided by rivers and runoff, transports nutrients for phytoplankton and algal growth as well as detritus for associated fauna. Differences in number of species as well as relative density of organisms collected from oyster reef samples within Nueces and Redfish Bays were attributed in part to occurrence of adjacent communities (Drumright, 1989). The oyster reef site within Redfish Bay was close to a variety of adjacent communities including mud and sand bottom, seagrass meadows, fringing salt marsh, and mats of drift algae. Many organisms associated with these outlying communities were collected in reef samples indicating high recruitment of transient species. The reef in Nueces Bay was more isolated, with only soft muddy bottom nearby; this was reflected in the somewhat depauperate character of the community.

Oyster reefs contribute to the overall estuarine production of nutrients and organic matter required for maintenance of high level photosynthesis in the nearshore Gulf. Phytoplankton and penaeid shrimp, which spend part of their life cycle in a suitable estuarine environment, are critical links in the nearshore food chain (Longley et al., 1989). Threats to oyster reef habitats in the CCBNEP study area include reduced freshwater inflow, turbidity or smothering from dredging operations, oil or other chemical spills, and uptake of point source or non-point source pollution.

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HABITAT 4: SEAGRASS MEADOWS

4.1 Physical Setting & Processes

4.1.1 Definition and Distribution within Project Area

Seagrasses are submergent, flowering plants (angiosperms) that grow in marine environments; they are not true grasses. Seagrass meadows (subaqueous grassflats) are found primarily in shallow water (<2 m) in estuaries, hypersaline lagoons and brackish water areas (den Hartog, 1967). They are among the most productive ecosystems in shallow waters and constitute one of the most conspicuous and common coastal ecosystem types (Thayer et al., 1975).

Seagrasses occur in two principal settings within the study area, subaqueous bay-margins and subaqueous bay- or lagoon-flat environments. Bay-margin environments are generally relatively narrow areas, usually only a few centimeters to 1 m deep, and are occupied principally by seagrasses or bare sediments (Brown et al., 1977). Grassflats in these areas occur as narrow bands along the entire perimeters of virtually all bays in the CCBNEP study area (Adair et al., 1990). Marginal grassflats often grade shoreward into wind-tidal flats or saltmarsh and are also transitional with bay-margin shoal environments (Brown et al., 1977).

Seagrasses are sparse and local along high-energy shoal environments that characterize the mainland shoreline of the Laguna Madre near the entrance to Baffin Bay and most of the Corpus Christi and Nueces bay shorelines (Brown et al., 1976; Brown et al., 1977). Most seagrasses in Corpus Christi Bay are found in the Shamrock Cove-East Flats area, with a narrow band from Indian Point eastward, disappearing before reaching La Quinta Channel. In Nueces Bay, seagrasses are distributed in a narrow band along the northern shoreline only, from White Point eastward (Adair et al., 1990).

“Seagrass meadow” generally refers to the broad grassflats that are found in bay or lagoon-flat environments which are characterized as low-energy, moving water areas <1 m deep (Brown et al., 1976; Brown et al., 1977). Extensive seagrass meadows are found in the upper Laguna Madre, Redfish Bay, and in some tertiary bays such as Little Bay (Aransas Bay system) and Salt Lake (Copano Bay system) (Adair et al., 1990).

Density of seagrasses in the upper Laguna Madre diminishes south of the mouth of Baffin Bay. Seagrasses occur locally near Middle Ground and within The Hole, but meadows are poorly developed (Brown et al., 1977). Baffin Bay and its secondary bays were essentially devoid of seagrasses until 1970 when they appeared in Laguna Salada. Dense, marginal grassflats continue to grow on the narrow, shallow shelf along the north shore of Baffin Bay, along the southeast shore of Alazan Bay, in Cayo del Grullo, and in Cayo del Infiernillo (Kreuz, 1973; Cornelius, 1984).

Sparse grassflats, created when storm-generated waves and currents erode dredge material burying all or part of large seagrass meadows, are found in the Redfish Bay-Harbor Island area and the upper Laguna Madre. Distribution of this environment is spatially and temporally variable because seagrasses may eventually recolonize these areas (Brown et al., 1976).

Approximately 26,283 ha of seagrass meadows occur within the study area (Table IV.B.4.1). Nearly 87% of the seagrass meadows in the study area are found in the upper Laguna Madre and Redfish Bay. Detailed mapping of all seagrass habitats within the CCBNEP study area is planned as a CCBNEP Year-2 project. The recent, prolonged brown tide in the Laguna Madre has caused the loss of at least 10 km^2 of seagrass cover (Onuf, in press).

Table IV.B.4.1. Areal extent and dimensions of seagrass meadows in the Corpus Christi Bay National Estuary Program study area by bay (from Adair et al., 1990). Values for the Laguna Madre are from Merkord (1978).

Bay System Bay	Areal extent of seagrasses (ha)	Mean width (m)	Mean length (km)
San Antonio			
Mesquite Bay	100	250	4
Copano			
Copano Bay	237	53	9.8
Mission Bay	100	250	4
Swan Lake	175	n/a	n/a
Port Bay	668	557	6
Salt Lake	120	100%	
Aransas			
Aransas Bay	472	142	17
Little Bay	34	100%	
St. Joseph Lake	188	100%	
Redfish			
Redfish Bay	3,906	1547	14
Harbor Island Flats	924	n/a	n/a
Corpus Christi Bay	310	151	9
Nueces Bay	109	217	5
Laguna Madre	18,940	n/a	n/a
Total	26,283		

4.1.2 Historical Development

Seagrass meadows can only develop in shallow, low-energy waters with sufficient light penetration. Seagrass communities probably began developing in the study area after 2,800 YBP, when sea level reached its approximate current position. The extensive network of shallow-water bays in the study area was formed when sea level rose after the last glacial period, flooding older river valleys (Brown et al., 1976). Bays gradually filled with a mixture of riverine, estuarine, marine, and eroded bay shoreline sediments (Shew et al., 1981). Water depths range from a few centimeters to 2 m, but are generally less than 1 m (Brown et al., 1976, 1977).

The bay and lagoon-margin zone which may be occupied by marginal grassflats is composed of sediments that have been winnowed to some extent by waves and currents. Bay and lagoon-margin sands are derived principally from eroded Pleistocene deposits along the mainland shore. Longshore transport along shorelines continually redistributes winnowed sediment. Towards the mouths of bays and into lagoons this high to moderate-energy environment grades into low-energy environments where broad grassflats have developed (Brown et al., 1976, 1977).

4.1.3 Physiography

Seagrasses cannot carry out their life cycle unless they are completely submerged in seawater (Zieman, 1982) but some (e.g., *Halodule*) can tolerate brief periods of exposure (Fonseca, 1994). They are found only in the eulittoral to sublittoral areas of the shore zone, no higher in elevation than spring mean high-water (MHWS), and primarily below spring mean low-water (MLWS) (den Hartog, 1977). Figure IV.B.4.1 shows their position relative to mainland (bay) and island environments.

4.1.4 Geology & Soils

The most significant role of sediment texture may be in determining density of seagrass growth, since most are able to grow on a variety of substrates (Burrell and Schubel, 1977). Seagrasses grow best on muddy-sand substrates (Phillips and Meñez, 1988). Depth of the substrate is the single most important characteristic determining seagrass colonization although it is dependent on the morphology of the root system and varies somewhat from species to species (Burrell and Schubel, 1977). *Thalassia* standing crop in Florida Bay was positively correlated with sediment depth ($r = 0.64$). Regression analysis revealed sediment depth accounted for 49% of variation in *Thalassia* standing crop ($F = 94.4$, $P < 0.001$). Areas with shallow water and deep sediments supported more grass than deepwater areas with shallow sediments (Zieman et al., 1989).

Substrates in bay- and lagoon-margin and flat areas inhabited by seagrasses in the study area are typically muddy sand and shell (Table IV.B.4.2) (Brown et al., 1976). Sand is usually found only in bay-margin environments and is not as widely distributed as mud except in the Laguna Madre and Redfish Bay. In the upper Laguna Madre, sand increased with depth (3-10 cm) in sites PI1G and PI2G (Padre Isles) to about 90%, while at channel marker 189 (mouth of The

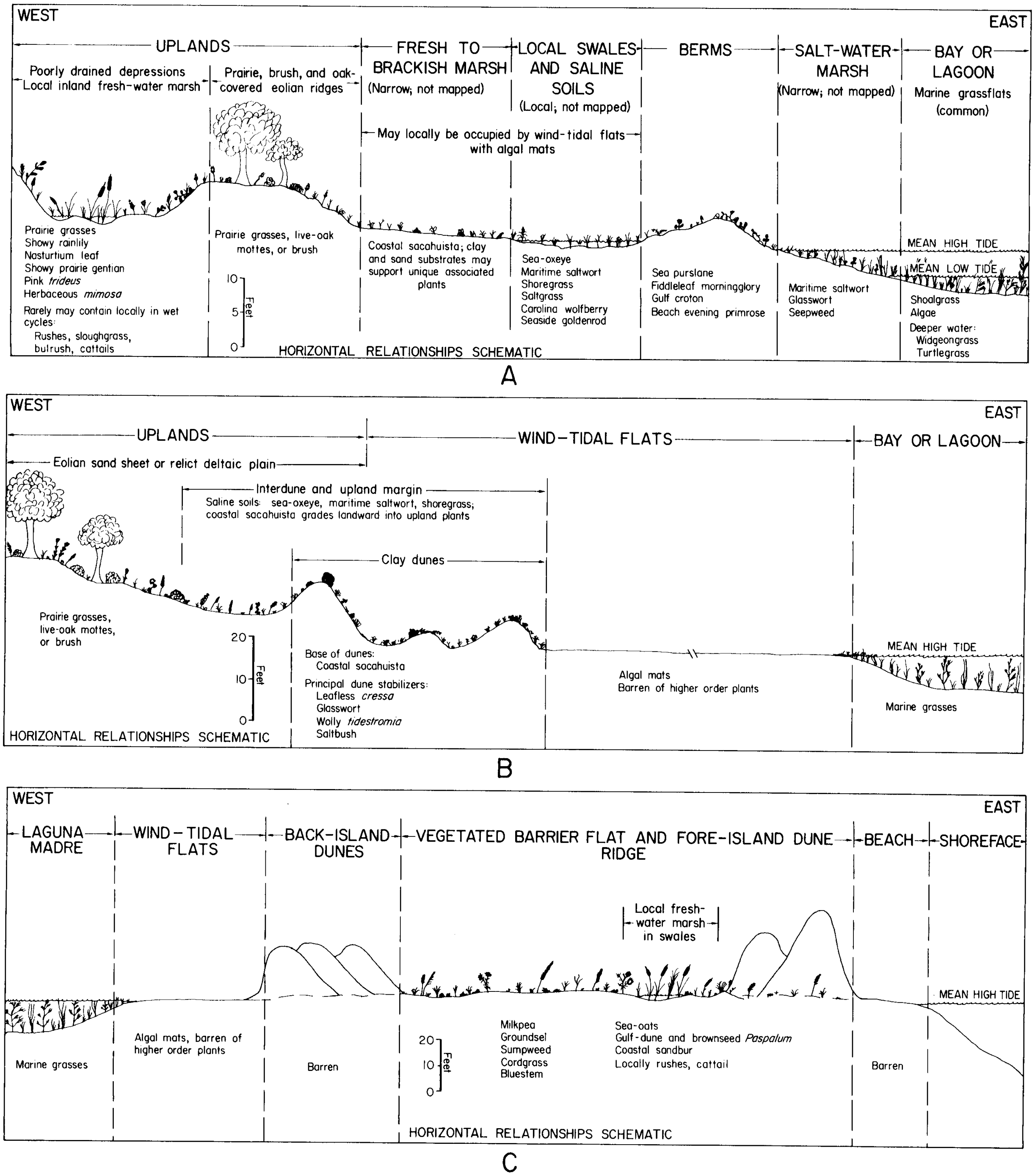

Fig. IV.B.4.1. Relationship of seagrass meadows to mainland and island environments. (A) and (B) show the position of seagrass meadows in relation to mainland environments; (C) showS the position of seagrass meadows in relation to barrier island environments (from Brown et al., 1977).

Table IV.B.4. 2. Sediment composition of selected areas with seagrass meadows in the CCBNEP study area.

Bay, Site	% Rubble (Shell)	% Sand	% Silt	% Clay
Laguna Madre				
PI1G[1] (Padre Isles)	10	55	10	25
PI2G[1] (Padre Isles)	14	74	25	10
189[1] (GIWW channel marker)	21	50	4	19
47[2] (GIWW channel marker)	5	80	7.5	7.5
49[2] (GIWW channel marker)	5	90	2	3
77[3] (GIWW channel marker)	2	71	11	15
4[4] (near Corpus Christi Pass)	0	90	8	2
Port Bay				
81[4] (Italian Bend)	1	91	5	3
Redfish Bay				
12[4] (GIWW between Ransom & Dagger islands)	14	61	17	8
13[4] (GIWW between Ransom & Dagger islands)	30	59	9	2
23[4] (Hog Island)	4	48	36	12
27[4] (Estes Flats)	24	37	26	13
28[4] (Estes Flats)	5	72	18	5

[1] Montagna, 1993
[2] Center for Coastal Studies, unpubl. data
[3] Williamson, 1980
[4] White et al., 1983

Hole) clay increased with depth to 35% (Montagna, 1993). Bay-margin sands generally grade bayward into muddy sand (50-75% sand) and sandy mud (50-75% clay) (White et al., 1983). Seagrass meadows in bay- and lagoon-flat environments in the CCBNEP study area are underlain by muds and muddy sands (Brown et al., 1976, 1977).

Several geological factors affect colonization and distribution of seagrasses: (1) morphology and character of bottom; (2) sources, routes, and rates of sediment transport; and (3) rates of sediment accumulation. Once seagrasses become established, they may significantly alter sedimentary processes, depending on species composition and shoot density. These alterations may lead to increased or decreased rates of seagrass colonization and changes in species composition of the meadow (Burrell and Schubel, 1977).

Major effects that seagrasses have on local sedimentological processes are to increase sedimentation rates, to preferentially concentrate finer particle sizes, and stabilize deposited sediments. Mechanisms responsible for these effects are: (1) extraction and entrapment of fine particles by leaves; (2) formation and retention of particles produced locally within meadows; and (3) binding and stabilization of substrate by their rhizome and root systems. The effects of (2) are probably not pronounced in the study area since epiphytic, coralline algae are not common or abundant. Although these effects are localized, they may result in notable changes in sedimentological characteristics over large areas in geologic time (Burrell and Schubel, 1977).

Seagrasses extract and trap sediments both directly and indirectly. Fine-grained, waterborne particles adhere to sticky coatings of epiphytic organisms frequently found on seagrass leaves. When plants die or coatings are degraded, particles are added to sediments. By acting as baffles to slow current flow and produce quiet waters, seagrass meadows indirectly extract fine-grained sediments from the water column by promoting deposition. Seagrasses also affect the sorting, skewness, roundness, and shape of particles. Increased fine sediments, poorer sorting, and decreased angularity of sand-sized particles have been reported in seagrass meadows (Burrell and Schubel, 1977).

Efficiency of seagrass meadows at baffling flow and removing suspended particles depends on leaf structure and shoot density (Burrell and Schubel, 1977). For example, *Thalassia*, a broad-leaved species, was more effective than *Syringodium*, a thin-leaved species, at baffling flow and directly and indirectly trapping particles because of its greater surface area (Wood et al., 1969). Shoot density is also important. The density of *Thalassia* shoots had a marked effect on the meadow's ability to trap and retain fine sediments in Bimini Lagoon, although no distinction was made between imported sediments and fine-grained carbonate material produced within the meadow by epiphytic, coralline algae (Scoffin, 1970).

Binding and stabilization of sediments by seagrass meadows also depends on species composition and plant density (Burrell and Schubel, 1977). *Thalassia* generally has a dense rhizomal/root system which extends 10-15 cm into the substrate and overlies a thick accumulation of peat produced by previous stands of *Thalassia* (Britton and Morton, 1989). This rhizome and peat network binds the sediment 1.2-1.8 m below the surface.

Syringodium has rhizome and root systems which only penetrate a few centimeters below the surface. *Halodule* roots and rhizomes are able to penetrate sandy substrates to at least 50 cm, but are unable to penetrate other substrates deeply (C. Onuf, pers. comm.) The genus *Halophila* has extremely light rhizomal and root structures in comparison to the other three. The binding capacity of *Thalassia* is approximately 50% greater than either *Halodule* or *Syringodium* and approximately 90% greater than *Halophila*. The binding capacity of either *Syringodium* or *Halodule* is approximately 40% greater than *Halophila*. There is little difference between *Syringodium* and *Halodule* (Thorhaug, 1981).

Trapping and stabilization of sediments generally results in a buildup of substrate in seagrass-covered areas when compared with surrounding seagrass-free areas. These effects are generally local, often small circular or irregular patches of a few square meters, but may result in banks that are hundreds or thousands of square meters. Buildup ranges from several centimeters for a small bed to several meters for relatively large, seagrass-covered mud banks (Burrell and Schubel, 1977). In South Biscayne Bay, Florida, small seagrass meadows were approximately 3 cm higher than adjacent unvegetated areas (Zieman, 1972).

4.1.5 Hydrology and Chemistry

Strong currents and high-energy waters preclude planting of most seagrasses for mitigation. Only deep-rooted species such as *Thalassia* are able to withstand high energy regimes, and then only with the help of heavy anchors (Thorhaug, 1981; 1986). Natural seagrass colonization is restricted by the same factors. In most parts of the world, seagrasses naturally colonize shallow-water areas with restricted circulation. Meterological or seasonal mixing processes may predominate over astronomical tidal action in these types of areas (Burrell and Schubel, 1977), as is the case within the CCBNEP study area. Astronomical tides have some affect on water levels in bay systems which have direct connections with the Gulf of Mexico such as Redfish and Corpus Christi bays, but winds and seasonal effects are the predominant agents by which water is moved (White et al., 1983). The astronomical tide range along bay shorelines in the CCBNEP study area is approximately 15 cm, which is approximately 0.3 m lower than the mean diurnal range in the Gulf of Mexico (Watson and Behrens, 1976). In Baffin Bay and the Laguna Madre, effects of astronomical tides are virtually nonexistent. Mean annual tide range is about 10 cm with the maximum range of water levels produced by wind-driven tides about 1.0 m (Fisk, 1959).

Water temperature, salinity, and turbidity are variable within seagrass meadows in the CCBNEP study area (Table IV.B.4.3). Only two studies, both conducted in the upper Laguna Madre, have measured dissolved oxygen and pH in the waters over seagrass meadows in the study area. In a study of natural and created meadows of *Halodule* that encompassed the area between Markers 49 and 189, dissolved oxygen ranged from 5.72-12.63 mg/l (mean 8.11 mg/l,) and pH ranged from 8.37-9.44 (mean 7.47) (Montagna, 1993). The other study was of a seagrass meadow dominated by *Halodule* in the vicinity of Marker 155. Dissolved oxygen ranged from 4.15-11.36 mg/l (mean 7.82 mg/l) and pH ranged from 7.9-8.64 (mean 7.98) (Montagna, 1992).

Seagrass meadows provide large amounts of detritus and reduce wave action which results in a thin oxic layer overlying a deep anoxic zone (Fenchel, 1977; Fenchel and Riedl, 1970). Decaying plants create a reducing environment at depth (Brown et al., 1976); seagrass metabolism is well-adapted to this environment. Some seagrasses (i.e., *Zostera marina*) are capable of releasing reducing complexes which may regulate the redox potential of the sediments (Burrell and Schubel, 1977), while *Thalassia* may meet its nitrogen requirement using gaseous nitrogen fixed by anaerobic bacteria in the sediments (Patriquin, 1972). During hours of darkness, anoxic conditions may extend into the water column (Burrell and Schubel, 1977).

In a study of the geochemistry of natural and created seagrass meadows, and adjacent bare areas in the upper Laguna Madre, Montagna (1993) found that redox potential decreased with depth at all sites. Vegetated sediments were always more negative than bare areas. Created sites had virtually no vertical differences in redox potential indicating a lack of reducing power. Sediment

Table IV.B.4.3. Water temperature, salinity, and turbidity in seagrass meadows in the CCBNEP study area. H=*Halodule*; R=*Ruppia*; T=*Thalassia*.

Bay Study	Temperature (°C)	Salinity ( )	Turbidity	Dominant Seagrass Species
Laguna Madre				
McMahan, 1968	n/a	31-52	n/a	H
Koenig, 1969	16-33	14-54	turbid	H, R
Circé, 1979	11-32	18-34	9-50%[1]	H
Rickner, 1979	12-36	13-37	n/a	H
Williamson, 1980	14-33	26-39	n/a	H
Chaney, 1988	9-32.5	25-45	n/a	H
Jewett-Smith, 1991	n/a	39.5 (30-46)	72.5%[2]	H
Montagna, 1992	23.4 (10.6-30.8)	40.1 (28.2-54.0)	n/a	H
Hicks, 1993	n/a	30-43	n/a	H
Montagna, 1993	23.9 (10.5-29.8)	26 (24-38)	n/a	H
Dunton and Tomasko, 1994	12-30	32-50	n/a	H
Baffin Bay				
Kreuz, 1973	21-36	12-70	48-82%	H, R
Redfish Bay				
Zimmerman, 1969; Zimmerman and Chaney, 1969	9-33.5	9-40	<50%[3]	T
Kreuz, 1973	18-31.5	18-41	75-90%	H, T
Rickner, 1975	17-35.5	13-36	300-1300mm[4]	H, T
Gourley, 1989	9-29	18-40	n/a	T, H
Jewett-Smith, 1991	n/a	30.9	50-80%[2]	H
Nueces Bay				
Dunton, 1990	14-30	30-35	200.1[5]	H, R
Jewett-Smith, 1991	n/a	31.4	49.6%[2]	H
Corpus Christi Bay				
Jewett-Smith, 1991	n/a	35.1	58-75%[2]	H
Dunton, 1990	10-32	27-32	150-377.1[5]	H

[1] % light transmittance at the bottom
[2] % light transmittance at 30 cm depth
[3] Hach colorimeter, Jackson turbidity units converted to % light transmittance; no depth given
[4] Secchi depth
[5] Photosynthetically active radiation (PAR); photon flux fluence rate (PFFR), µmol/m^2 at 40-60 cm depth

organic matter was greatest in vegetated sediments although all sites had considerable amounts of seagrass-derived organic matter. Oxygen consumption by the sediments was high in seagrass meadows (mean -8.0 mmol $O_2/m^2/h$) and low in unvegetated sediments (mean -1.1 mmol $O_2\ m^{-2}\ h^{-1}$).

4.2 Producers and Decomposers

4.2.1 Primary Producers

4.2.1.1 Seagrasses

Seagrasses are one of the major primary producers found in seagrass meadows. Seagrass taxonomy follows den Hartog (1970) and Fonseca (1994). Of the approximately 50 species of seagrasses, five species in two families are found in the CCBNEP study area: *Halodule wrightii* den Hartog (shoal grass) [=*H. beaudettii*] [=*Diplanthera wrightii*]; and *Syringodium filiforme* Kützing (manatee grass) [=*Cymodoceae filiforme*] in the family Potamogetonaceae; and *Thalassia testudinum* König (turtle grass); *Halophila engelmannii* Ascherson (clover grass); and *Ruppia maritima* Linnaeus (widgeon grass) in the family Hydrocharitaceae.

In a study of distribution of seagrasses in the bay systems of the middle Texas coast excluding the Laguna Madre, *Halodule* (78.1% occurrence) and *Ruppia* (49.1% occurrence) were the most common species. *Thalassia* was locally common, particularly in Aransas Bay (13.0% occurrence), Corpus Christi Bay (13.9% occurrence) and around Harbor Island (29.2% occurrence). All five seagrass species were found in Redfish Bay with *Halodule* (70.8% occurrence), *Ruppia* (47.9% occurrence), and *Thalassia* (63.5% occurrence) dominating (Adair et al., 1990).

Three distinct species associations are found in the upper Laguna Madre: (1) 10, 582 ha of sparse regions of *Halodule*; (2) 8,044 ha of dense meadows of *Halodule* with *Halophila* present as a subdominant vegetation; and (3) 314 ha of *Halophila* as a dominant seagrass in association with dense *Halodule* as a subdominant vegetation (Merkord, 1978). *Thalassia* (Phillips, 1974; McMillan, 1979), *Syringodium* (Merkord, 1978; McMillan, 1979), and *Ruppia* (Phillips, 1974; Merkord, 1978; Williamson, 1980) occur locally in the upper Laguna Madre. *Ruppia* can be very abundant locally and seasonally (C. Onuf, pers. comm.), and has been found in channels paralleling the John F. Kennedy Causeway, east of Marker 21, close to Pita Island, and at the northern end of The Hole (Merkord, 1978). Seeds of *Ruppia* were found in 44% of sediment samples from both the upper and lower Laguna Madre indicating it may be more common than documented (McMillan, 1985). *Thalassia* was found in deeper water (>0.5 m) where salinity was not excessive (Brown et al., 1977). Merkord (1978) mapped no *Thalassia* in the upper Laguna Madre, however one fairly large meadow existed near an old oil well blowout near Humble Channel in 1989 (K. Withers, pers. obs.)

The distinctive appearance of Texas seagrasses along with few of species makes use of a standard dichotomous key unnecessary. General systematic approaches with detailed descriptions (den Hartog, 1970; Edwards, 1976; Tomlinson, 1980) may be consulted when necessary. Identification of seagrasses is limited to morphological and anatomical criteria because flowers of most species are difficult to find (McMillan, 1976). In some cases, seagrasses do not produce flowers or an appreciable abundance of flowers (Johnson and Williams, 1982). The following genera key is based on vegetative and morphological characters, nearly all of which can be recognized with the aid of a simple hand lens.

1. Leaves terete .... *Syringodium*
1. Leaves flat 2

2. Leaves without a basal sheath; in whorls or pseudo-whorls;
   differentiated into a petiole and a blade .... *Halophila*
2. Leaves without a ligula; 0.5-1 cm wide; 2 pericentral veins...... *Thalassia*
2. Leaves with a basal sheath; not arranged in whorls................. 3

3. Leaf tip forms 3 point crown; two roots per node................... *Halodule*
3. Leaf tip tapers to a sharp point; one root per node .... *Ruppia*

Halodule wrightii is a pioneer species that is extremely important as an early colonizer of disturbed areas and in locations where *Thalassia* and *Syringodium* are abiotically excluded. *Halodule* is able to establish itself quickly and achieves maximum coverage faster than competing species (Fonseca, 1994). *Halodule* has narrow, flat leaves 1.5-2 mm wide which are distinctly truncate with two or three teeth at the apex. The herbaceous, short, erect stems which bear 1-4 leaves arises from a creeping rhizome which has one or more unbranched roots. Although flowering has been rarely observed, the flowers are solitary, terminal and enclosed in a leaf similar to the vegetative leaves (Edwards, 1976; den Hartog, 1970); the primary means of reproduction is vegetative. In low salinity areas, it is often confused with *Ruppia.*

Syringodium filiforme is commonly mixed with other seagrasses or in small, monospecific patches, rarely forming extensive meadows (Zieman, 1982). A dense understory of unattached macroalgae is often found in association with the patches (Fonseca, 1994). *Syringodium* is easily recognized by its long (10-30 cm), terete leaves with blunt apices which arise in clusters of two or three. Blades are cylindrical in cross section (McMahan 1968). Scale leaves are present on rhizomes and the short shoots. Rhizomes are cylindrical, and vegetative growth occurs when the existing meristem is damaged or through development of short shoots. Roots occur at nodes and generally three roots are produced within the terminal (tip) meristem of the rhizome. *Syringodium* flowers occur in cymose clusters (Phillips, 1960). Pistillate flowers have a short style and two stigmas, and are subtended by hyaline bracts. The fruit is 3 mm long and is beaked by a persistent style (den Hartog, 1970; Edwards, 1976).

Thalassia testudinum is commonly called turtle grass because it is a favorite food of the endangered *Chelonia mydas* (green sea turtle). This seagrass is noted for its longevity (often > 10 years for an individual shoot) and the production of dense, extensive stands (Fonseca, 1994). The plant has erect shoots that produce a cluster of 3-7 broad (up to 2 cm wide) leaves which develop from a basal meristem. Leaves have sheaths that enclose the upper portion of the short shoots and arise from a rhizome that is usually buried from 3 to 15 cm in the substratum. The rhizome has an apical meristem first branching left, then right during vegetative growth. Roots develop on the rhizome close to the short shoots. The plant is dioecious, with staminate flowers having a long base (pedicel), while pistillate flowers are almost sessile. Flowering is common (Loraamm, 1980) and occurs throughout the year but not at the same time in all plants. In Florida, fruits were evident in January and flowers occurred as early as February (Moffler and Durako, 1980). The fruit is beaked and contains four to five seeds.

Halophila engelmannii is dioecious with thin, fragile, creeping rhizomes that have one root at each node. Leaves are attached to erect lateral shoots, and are pseudo-whorled or distichously arranged pairs. Leaf blades are oblong or linear-oblong with an obtuse apex and cuneate base and finely serrated margins. Female flowers consist of a small perianth with a sessile or subsessile, ovoid ovary 3-4 mm long (den Hartog, 1970). Male flowers are born singly on a pedicel 4-10 mm long. Sepals are broadly elliptic and reflexed when mature. Anthers are 4 mm long and bilocular, producing yellow pollen grains in fine filaments (Short and Cambridge, 1984).

McMillan (1986) studied fruits of *Halophila engelmannii* found in Redfish and Corpus Christi bays, and the Laguna Madre. He found fruits, which are borne on short stalks, resemble spherical air-filled vesicles of *Sargassum* in size, shape, and ability to float. Fruits collected from beach drift during May and June were globose to subglobose with diameters between 3.0-5.5 mm. They usually had two subtending bracts still attached at the base, but most were missing leaves from the whorls. Fruits had a stylar beak with mean lengths between 4.4-5.2 mm; the pericarp was membranous and the endocarp fleshy. The green fruit capsule ruptures and the wall splits roughly along three lines. Seeds are expelled as the wall folds back toward the stylar beak, and the fruit wall drops out of the water column, while the seeds remain afloat. There are 1-20 seeds per fruit which are subspherical, apiculate at both ends and approximately 1 mm in diameter.

Ruppia maritima, not a true seagrass, is a freshwater angiosperm with a pronounced salinity tolerance. It is both eurythermal and euryhaline (Zieman, 1982) and can grow and reproduce within many hypersaline bays and estuaries in Texas (Dunton, 1990). *Ruppia* has no stalk, differing from the other local seagrass species. Leaves arise directly from a thin, partially upright rhizome located above the substratum and are narrow (1-1.5 mm wide) and pointed. Flowering is common, and sexual reproduction is important in propagation. Fruits are asymmetrical and attached to stalks which may be several centimeters long (Fassett, 1957). Vegetative reproduction is common (Edwards, 1976).

It is often difficult to distinguish between *Halodule* and *Ruppia*. *Ruppia* is often found adjacent to *Halodule* beds in areas of reduced salinity. Five visual clues that separate *Ruppia* from *Halodule* include: (1) *Ruppia* produces copious flowering pedicles with numerous seed clusters which may reach one meter in length; (2) *Ruppia* blades taper to a single sharp point; (3) rhizomes of *Ruppia* are often zigzagged when viewed from above and may be either green or white in color; (4) *Ruppia* has one root per node at the rhizome; and (5) *Ruppia* has extensive above ground branches and plant material (Fonseca, 1994).

4.2.1.2 Attached Macroalgae

Attached, benthic macrophytic algae are not common in seagrass meadows in the CCBNEP study area (Cowper, 1978). In northern *Zostera* meadows, *Caulerpa* spp. is common. Amount of algae is dictated by sediment type. Poorly sorted sediments with large numbers of stones provide the best attachment sites for larger macroalgae (McRoy and McMillan (1977). The only marine and estuarine algae which are able to use soft sediments like those in the CCBNEP study area are members of the order Caulerpales (division Chlorophyta). These algae possess creeping rhizoids that provide an anchor in the sediment (Zieman and Zieman, 1989).

Pencillus capitatus and *Caulerpa crassifolia* have been reported from the soft bottoms of seagrass meadows in the study area. Other algae such as *Acetabularia* spp. and *Gracilaria* spp. may be found occasionally attached to shell or other solid substrates within seagrass meadows. Kreuz (1973) found *A. crenulata*, *Digenia simplex*, *Dictyota dichoma*, *Chondria littoralis*, *G. debilis* and *G. foliifera* in a *Thalassia* meadow in Redfish Bay, attached primarily to oyster clumps. Several species of *Gracilaria* have been reported from *Halodule* meadows in the upper Laguna Madre, and *D. simplex* has been reported from *Halodule* meadows in Aransas Bay. These algae often host populations of epiphytic algae (Humm and Hildebrand, 1962; Conover, 1964).

4.2.1.3 Epiphytic Algae

Leaves of seagrasses provide substrate for a community of epiphytic organisms which includes many species of macro- and microalgae. Epiphytic algae are highly productive, and because of their palatability, have a more important trophic role than their seagrass hosts (Kitting et al., 1984). Several studies addressed epiphytic flora of seagrass beds in or near the study area (Table IV.B.4.4). Blue-green algae such as *Calothrix*, *Lyngbya*, *Oscillatoria*, and *Phormidium* also occur as epiphytes, but little information concerning their distribution is available (Conover, 1964; Morgan and Kitting, 1984).

4.2.1.4 Unattached Drift Algae

Large quantities of unattached drift algae have been noted in seagrass meadows in Redfish Bay and the Laguna Madre. Attached macroalgae is not common in seagrass meadows, suggesting that drift algae originates outside of the meadows, although epiphytes may break off and become drift algae. Intense grazing pressure from reef fish and sea urchins (e.g., *Diadema*) and constant directional currents probably prevent accumulation of drift algae in subtropical and tropical seagrass systems (Cowper, 1978).

Drift communities composed largely of red algae (*Laurencia* and *Gracilaria*) were common in *Halodule* meadows of the Laguna Madre (Merkord, 1978). The algae collected in depressions, in the taller leaves of *Syringodium* associated with *Halodule*, and wherever their movement was hindered. Accumulations of algae occupying the entire water column were not unusual. Williamson (1980) noted *Jania capillacea* formed dense balls and was very abundant in the drift

Table IV.B.4.4. Epiphytic algae on found on seagrasses and algae in the middle and lower Texas Gulf Coast. ULM=upper Laguna Madre (Humm and Hildebrand, 1962; Conover, 1964); LLM=lower Laguna Madre (Humm and Hildebrand, 1962; Conover, 1964; Pressley, unpubl.); RB=Redfish Bay (Conover, 1964; Edwards, 1976; Morgan and Kitting, 1985); AB=Aransas Bay (Humm and Hildebrand, 1962; Conover, 1964; Edwards, 1976); CB=Copano Bay (Conover, 1964; Edwards, 1976). SG=seagrasses; H=*Halodule*; S=*Syringodium*; T=*Thalassia*; A=algae. Taxonomy follows Schneider and Searles (1991) except Bacillarophyta (Round et al., 1990) and Cyanophyta (Humm and Wicks, 1980).

	Laguna Madre		Redfish	Aransas	Copano	Plant
Epiphytic Algae	Lower	Upper	Bay	Bay	Bay	Host
D. Rhodophyta						
F. Goniotrichaceae						
Goniotrichum alsidii	X		X	X		H,S,A
F. Ceramiaceae						
Ceramium byssoideum	X		X			H,S,A
Spyridia filamentosa	X					H
F. Acrochaetiaceae						
Audouinella flexuosum	X					H,S,A
A. hypneae				X		H, A
F. Corallinaceae						
Heteroderma lejolisii	X		X	X		H, T, A
Amphiroa beauvoisii	X		X			SG, A
Titanoderma pustulatum			X	X		SG, A
Fosliella farinosa				X		T
F. Rhodomelaceae						
Laurencia poitei				X		T
Chondria curvilineata	X					T
Herposiphonia tenella	X		X			H,S,A
P. gorgoniae			X			H
P. havanensis			X	X		H
P. ferulaceae	X	X	X	X	X	SG, A
P. echinata			X		X	SG, A
P. macrocarpa	X			X		H, S
F. Porphyyridiaceae						
Astercytis ramosa	X		X			H,S,A
F. Erythropeltidaceae						
Erythrotrichia carnea	X		X	X		SG, A
F. Hypneaceae						
Hypnea musciformis	X			X		SG, A
F. Champiaceae						
Champia parvula				X		T

Table IV.B.4.4. Continued.

Epiphytic Algae	Laguna Madre Lower	Laguna Madre Upper	Redfish Bay	Aransas Bay	Copano Bay	Plant Host
D. Chlorophyta						
F. Ulvellaceae						
Uvella lens				X		T
Phaeophila dendroides				X		T
F. Ulvaceae						
Enteromorpha plumosa	X	X	X			H,S
E. flexuosa	X					H,S
F. Cladophoraceae						
Chaetomorpha linum (*aerea*)	X		X	X		H, S, A
C. gracilis				X		T
Cladophora albida		X	X	X		H, A
C. vagabunda	X					H,S
C. luteola		X	X			SG
F. Ulotrichaceae						
Ulothrix flacca			X	X		SG, A
F. Dasycladaceae						
Acetabularia crenulata	X		X			SB, A
D. Bacillariophyta						
F. Thalassionemataceae						
Thalassiothrix frauenfeldii	X					H,S
F. Fragilariales						
Fragillaria pectinalis	X					H,S
F. Striatellaceae						
Grammatophora angulosa	X					H,S
F. Naviculaceae						
Navicula spp.	X	X	X	X	X	SG
F. Cocconeidaceae						
Cocconeis spp.			X			H
D. Phaeophyta						
F. Myrionemataceae						
Hecatonema floridana				X		H
F. Striariaceae						
Hummia onusta				X		H
F. Ectocarpaceae						
Ectocarpus siliculosus	X		X	X		SG, A
Hincksia mitchelliae	X		X	X	X	T, A
F. Chordariaceae						
Cladosiphon occidentalis	X			X		SG, A

Table IV.B.4.4. Continued.

Epiphytic Algae	Laguna Madre Lower	Laguna Madre Upper	Redfish Bay	Aransas Bay	Copano Bay	Plant Host
F. Dictyotaceae						
Dictyota ciliolata	X			X		SG,A
F. Sphacelariaceae						
Sphacelaria furcigera	X	X	X	X		H, S, A
D. Cyanophyta						
F. Chroccaccaceae						
Agmenellum thermale				X		H
Anacystic aerruginosa				X		H
A. dimidiata				X		H
F. Oscillatoriaceae						
Spirulina subsala		X				H
Oscillatoria corallinae				X		T
Microcoleus chthonoplastes				X		T

algae community in seagrass meadows around a dredge material island in the upper Laguna Madre. *Laurencia poitei*, *L.* cf. *gemmifera*, *Chodiria littoralis*, *Champia parvula*, *Polysiphonia subtilissima*, and *Acetabularia crenulata* were also common. Macroalgae occurred at 72% of vegetated stations in the upper Laguna Madre and was the second largest contributor (after *Halodule*) to bay-wide biomass (Onuf, in press). Drift algae were also common in Redfish Bay *Thalassia* meadows (Cowper, 1978). Oyster reefs were considered the most likely source for the algae. *Hypnea* spp. was the most common species and overall composition remained fairly constant throughout the six-week study (Table IV.B.4.5).

4.2.1.5 Benthic Microalgae

No studies of species composition of benthic microflora of seagrass meadows in the CCBNEP study area or elsewhere could be found. Moncreiff et al. (1992) noted sand microflora sometimes formed a thick crust within seagrass beds in Mississippi Sound. It is likely that many blue-green algae and diatoms, found as epiphytes on seagrasses and algae, could be found in sediments as well.

4.2.1.6 Phytoplankton

No comprehensive studies of the species composition of phytoplankton associated with seagrass meadows in the CCBNEP study area were found. In an early survey of the upper Laguna Madre, Simmons (1957) collected 22 species of plankton (Table IV.B.4.6). Nine of the 13 stations sampled were in *Halodule* meadows, but no distinction was made as to which species were found

Table IV.B.4.5. Major species of drift algae from seagrass meadows in Redfish Bay (from Cowper, 1978).

Division Chlorophyta
Chaetomorpha linum
Division Phaeophyta
Dictyota dichotoma
Padina vickersiae
Division Rhodophyta
Digenia simplex
Gracilaria debilis
G. foliifera
G. verrucosa
Grateloupia filicina
Hypnea cornuta
H. musciformis
Jania capillacea
Laurencia poitei
Soliera tenera

in non-vegetated areas. Pennate diatoms (*Pleurosigma angulatum*, *Gyrosigma balticum* and *Navicula* spp.) were the most common species collected. Hildebrand and King (1978) collected phytoplankton from only one station in the upper Laguna Madre (L-10) which was vegetated with *Halodule* during a six-year study. Diatoms always constituted at least 93% of that assemblage. Overall, they found *Thalassionema nitzchioides* to be the most abundant phytoplankter, and the genera *Chaetoceros*, *Nitzschia*, *Thalassionema*, *Thalassiothrix* occurred most frequently. Dinoflagellates were found several times at the Laguna Madre station. The most freqently occuring genera were *Ceratium* and *Noctiluca*. In *Halodule* meadows near Bird Island Basin, unidentified diatoms dominated. Dinoflagellates, primarily *Ceratium*, *Noctiluca*, and *Peridinium*, were also found in fairly high numbers (Chaney, 1988).

4.2.2 Decomposers

Fresh seagrass material is not available to most detritivores (e.g., deposit-feeding polychaetes and molluscs) due to its fibrous content (up to 59% of dry weight) that requires specific enzymes for digestion (Zieman, 1982) and presence of phenolic compounds (Valiela et al., 1979). Bacteria, fungi, and other microorganisms with the enzymatic capacity to degrade seagrasses are necessary trophic intermediaries between seagrasses and detritivores. No information concerning the composition of seagrass decomposer communities in the CCBNEP study area was found.

Table IV.B.4.6. Phytoplankton species and relative abundances in the upper Laguna Madre collected in association with *Halodule* meadows (from Simmons, 1957). VC= very common; C=common; U=uncommon; R=rare.

Species	Relative Abundance
O. Centrales	
F. Coscinodisaceae	
Coscinodiscus asteromphalus	R
C. radiatus	R
Thalassiosira sp.	U
Skeletonema sp.	U
Stephanopyxis palmeriana	R
Melosira sulcata	U
M. moniliformis	U
F. Soleniaceae	
Rhizosolenia acuminata	U
R. alata	U
R. imbricata	U
R. setigera	C
F. Chaetoceraceae	
Chaetoceros sp.	U
F. Biddulphiaceae	
Biddulphia mobiliensis	R
O. Pennales	
F. Nitzchiaceae	
Nitzschia seriata	U
N. longissima	C
N. closterium	C
F. Naviculaceae	
Pleurosigma angulatum	VC
Gyrosigma balticum	VC
Navicula sp.	VC
F. Fragillariaceae	
Thalassiothrix sp.	U
Thalassionema nitzschioides	U
Synedra superba	C

The microbial component of seagrass detritus is highly complex and contains organisms from many phyla. Bacteria have been considered dominant decomposers in seagrass systems and are important in both aerobic and anaerobic decomposition. They are particularly important for fine-particle (<2 mm) processing since those particles are too small for fungal colonization. Dominant heterotrophic bacterial groups and genera mentioned as being associated with seagrasses (particularly *Zostera*) are *Cytophaga*, other myxobacteria, *Achromobacter*, *Alcaligenes*, and *Pseudomonas* and other nonfluorescent pseudomonads (Fenchel, 1977; Klug, 1980). Many observations suggest that most seagrass detritus is decomposed under anaerobic conditions. White sulfur bacteria such as *Beggiatoa* and *Thiovolum* have been found in the anaerobic zone of Danish *Zostera* beds where light intensity is low. Where light reaches the anaerobic zone, green and purple sulfur bacteria predominate (Fenchel, 1977).

Fungi are more invasive than bacteria due to the elaboration of a variety of exoenzymes. They have been shown to be of considerable significance in the early processing of deciduous leaves in lotic environments (Bärlocher and Kendrick, 1974; Suberkropp and Klug, 1976). The fungi *Labyrinthula*, the cause of *Zostera* wasting disease (Muehlstein, et al., 1988), was commonly observed with decaying marine plant material (Johnson and Sparrow, 1961); it has been observed on decaying *Thalassia* (Myers and Hopper, 1967). Chytrid fungi have been cultured from suspensions of decomposing *Zostera* (Fenchel, 1977). It is not known if fungi are as significant in seagrass systems as they are in other ecosystems (Klug, 1980).

There are two possible successional sequences of microbiota on decaying seagrass leaves. Fenchel (1970) suggested that bacteria and fungi colonize dead leaves and decompose the plant tissues, followed by heterotrophic protozoa (flagellates and ciliates) which consume the microflora. Larger protozoans, primarily ciliates, and small metazoans follow. The other sequence is dead plant tissue-fungi-nematodes-higher metazoans (Meyers and Hopper, 1967). *Lindra thalassiae* and other fungi (ascomycetes, deuteromycetes, and myxomycetes) colonized decaying leaves of *Thalassia*, that were fed upon by nematodes; the nematode population increased with increased fungal growth. Nematodes are then fed upon by higher metazoans.

4.3 Consumers

4.3.1 Invertebrates

4.3.1.1 Macroinfauna and Epifauna

A diverse epibenthic, benthic, and epiphytic invertebrate macrofauna is associated with seagrass meadows in the study area (Table IV.B.4.7). Most studies of seagrass invertebrates in the study area concentrated on molluscs; there is little information concerning distribution or abundance of annelids and crustaceans (e.g., crabs, amphipods).

Upper Laguna Madre. - Twenty-five polychaete species in 13 families and 12 mollusc species (6 gastropod families; 3 bivalve families) were collected from a *Halodule* meadow near Bird Island Basin (Montagna, 1992). Polychaetes were the most abundant members of the assemblage except during October. Total numbers of organisms declined from spring to fall (Fig IV.B.4.2).

Montagna (1993) compared the macrofaunal communities of natural and created *Halodule* meadows in the upper Laguna Madre. Thirty-six species of polychaetes (14 families) and 14 species of molluscs (6 gastropod families; 4 bivalve families) were recovered. Polychaetes were

Table IV.B.4.7. Macroinvertebrates found in seagrass meadows and/or associated microhabitats (e.g., oyster clumps within seagrass meadow) in the CCBNEP study area. Baffin Bay (Laguna Salada) - Kreuz, 1973; Upper Laguna Madre - Simmons, 1957; Parker, 1959; Koenig, 1969; Hildebrand and King, 1973; Circé, 1979; Rickner, 1979; Williamson, 1980; Montagna, 1992; 1993; Corpus Christi-Nueces bays - Castiglione, 1983; Redfish Bay - Parker, 1959; Zimmerman and Chaney, 1969; Kreuz, 1973; Rickner, 1975; Aransas-Copano bays - Parker, 1959; Calnan, 1980. Most studies outside the Laguna Madre have concentrated exclusively on molluscs, hence the lack of entries for most other taxa in other bay systems.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
P. Bryozoa					
C. Gymnolaemata					
F. Bugulidae					
Bugula neritina				X	X
P. Platyhelminthes					
C. Turbellaria		X			
P. Rhynchocoela		X		X	
P. Annelida					
C. Oligochaeta		X			
C. Polychaeta					
F. Syllidae					
Sphaerosyllis cf. *sublaevis*		X			
Brania furcelligera		X			
Opisthosyllis sp.		X			
Exogone dispar		X		X	
F. Goniadidae					
Glycinde solitaria		X			
F. Lumbrineridae				X	
F. Nereidae					
Laeonereis culveri				X	
Nereis succinea	X	X		X	
Nereis pelagica occidentalis		X			
Platynereis dumerilii		X		X	
Nereiphylla fragilis					
F. Sigalionidae					
Sthenelais boa				X	
F. Spionidae					
Polydora socialis				X	
P. websteri				X	
P. ligni		X			
Scolelepsis texana		X			

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
Spiophanes bombyx					
Streblospio benedicti	X	X			
Spio setosa		X			
Prionospio heterobranchia		X			
Pseudomalacoceros (=*Nerinides*) cf. *bidentata*		X			
F. Chaetopteridae					
Spiochaetopterus costarum		X			
F. Capitellidae					
Capitella capitata		X		X	
Dasybranchus lumbricoides		X			
Heteromastus filiformis		X		X	
Mediomastus californiensis		X		X	
M. ambiseta		X			
F. Cirratulidae					
Tharyx setigera				X	
F. Orbiniidae					
Scoloplos robustus		X			
S. fragilis		X			
S. rubra		X		X	
Haploscoloplos foliosus		X			
Naineris laevigata		X			
F. Arenicolidae					
Arenicola cristata		X			
F. Onuphidae					
Diopatra cuprea		X			
F. Hesionidae					
Parahesione luteola		X			
F. Phyllodocidae					
Glycera americana		X			
Anaitides erythrophyllus		X			
Eteone heteropoda	X	X		X	
F. Maldanidae					
Branchioasychis americana		X			
Clymenella torquata		X			
Clymenella mucosa		X		X	
Maldane sarsi		X			

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
F. Pilargidae		X			
F. Spirorbidae					
Spirorbis sp.		X			
F. Ampharetidae					
Melinna maculata		X		X	
F. Dorvilleidae					
Schistomeringos rudolphi		X			
Dorvillea sociabilis		X			
F. Magelonidae					
Magelona pettiboneae		X			
F. Terebellidae					
Thelepus setosus		X			
Loimia medusa		X			
F. Serpulidae					
Dexospira spirillum				X	
Mercierella enigmatica				X	
Hydroides sp.				X	
F. Sabellidae					
Sabella micropthalma		X		X	
Fabricia sp.		X			
Chone duneri		X			
F. Pectinariidae					
Pectinaria (=*Cistenides*) *gouldii*		X		X	
P. Mollusca					
C. Polyplacophora					
F. Ishnochitonidae					
Ischnochiton papillosus				X	
C. Gastropoda					
F. Ellobiidae					
Melampus bidentatus				X	X
F. Buccinidae					
Cantharus cancellarius				X	X
F. Trochidae					
Tegula fasciata		X		X	
F. Cerithidae					
Cerithium variabile		X		X	
C. lutosum		X	X		
Diastoma varium		X	X	X	X

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
F. Nassariidae					
Nassarius vibex		X		X	X
F. Pyramidellidae					
Turbonilla sp.		X			
T. cf. *aequalis*					X
T. cf. *portoricana*		X	X		
Sayella crosseana		X			
S. livida			X		
Pyramidella candida				X	
P. crenulata			X		
Eulimastoma cf. *harbisonae*			X		
Odostomia impressa		X		X	X
O. bisuturalis		X			
O. cf. *livida*		X			
O. laevigata					X
F. Scaphandridae					
Acteocina (=*Retusa*) *canaliculata*		X		X	
F. Acteonidae					
Acteon (=*Rictaxis*) *punctostriatus*		X			
F. Neritidae					
Neritina virginea		X	X	X	X
Smaragdia viridis				X	
F. Naticidae					
Polinices (=*Nevrita*) *duplicatus*				X	
F. Littorinidae					
Littorina irrorata				X	X
F. Melongenidae					
Buscyon contratrium				X	
F. Hydrobiidae					
Texadina sphinctostoma					X
F. Vitrinellidae					
Solariorbis infracarinata		X			
Vitrinella helicoidea		X			
Teinostoma lerema					X
F. Columbellidae					
Anachis avara		X	X	X	
A. semiplicatus		X			
A. obesa		X		X	
A. translirata				X	

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
Mitrella lunata		X	X	X	X
F. Truncatellidae					
Truncatella pulchella				X	
F. Caecidae					
Caecum nitidum		X		X	X
C. pulchellum		X		X	X
C. glabrum		X			
F. Modulidae					
Modulus modulus				X	X
F. Triphoridae					
Triphora nigrocinta		X		X	
F. Turridae					
Pyrogocythara plicosa		X	X	X	
Pyrogocythara (=*Mangelia*) *sp.*				X	
F. Cerithiopsidae					
Cerithiopsis greeni		X		X	
Seila adamsi				X	
F. Potamididae					
Cerithidea pliculosa		X		X	X
F. Epitoniidae					
Epitonium rupicola		X			
F. Bullidae					
Bulla striata		X	X	X	
F. Crepidulidae					
Crepidula fornicata				X	
C. maculosa		X			
C. plana				X	
C. convexa		X		X	X
F. Muricidae					
Stramonita (=*Thais*) *haemastoma*				X	X
F. Hamineidae					
Haminoea antillarium		X	X	X	
H. succinea		X			
C. Bivalvia					
F. Mactridae					
Mulinia lateralis		X		X	X
Mactra fragilis		X		X	
Spisula solidissima				X	

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
F. Anomidae					
Anomia simplex		X		X	
F. Tellinidae					
Macoma constricta				X	
M.mitchelli					X
M. tenta		X			
M. brevifrons		X			
Tellina tampaensis		X	X		
T. lineata		X			
T. texana		X	X		
F. Veneridae					
Anomalocardia auberiana (= *cuneimeris*)		X	X	X	X
Chione cancellata		X	X	X	
Gemma purpurea				X	
Mercenaria mercenaria				X	
M. campechiensis					
F. Pectinidae					
Argopectin irradians aplicostatus		X	X	X	X
F. Mytilidae					
Amygdalum papyria		X	X	X	X
Ischadium recurvum					X
Brachiodontes exustus		X		X	X
B. modiolus (=*citrinus*)		X		X	X
F. Pinnidae					
Atrina serrata				X	
A. seminuda				X	
F. Isognomonidae					
Isognomen alatus				X	
F. Ostreidae					
Ostrea equestris				X	X
Crassostrea virginica				X	
F. Arcidae					
Anadara transversa		X	X	X	
A. ovalis			X	X	
Noetia ponderosa		X			

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
F. Lucinidae					
Anodonta alba				X	X
Lucina pectinata			X	X	X
Phacoides pectinatus				X	X
F. Ungulinidae					
Diplodonta semiaspera		X		X	
F. Periplomidae					
Periploma margaritaceum				X	
F. Solenidae					
Ensis minor		X		X	
F. Corbiculidae					
Pseudocyrena floridana		X			
F. Cardiidae					
Laevicardium mortoni		X		X	X
Trachycardium muricatum				X	
F. Lyonsiidae					
Lyonsia hyalina		X		X	
F. Psammobiidae					
Tagelus plebius		X	X	X	
T. divisus		X			
F. Montacutidae					
Mysella planulata		X	X		
F. Semelidae					
Cumingia tellinoides		X			
Abra aequalis			X		
F. Kellidae					
Aligena texasiana		X			
SP. Crustacea					
C. Malacostraca					
O. Ostracoda		X			
O. Cumaceae					
F. Diastylidae					
Oxyurostylis smithi		X			
O. salinoi		X			
O. Decapoda					
F. Xanthidae					
Menippe adina				X	
Europanopeus depressus				X	

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
Panopeus herbstii				X	
P. turgidus				X	
P. bermudensis				X	
Neopanope texana				X	
Hexopanopeus augustifrons				X	
F. Diogenidae					
Petrochirus diogenes				X	
Clibanarius vittatus				X	
F. Paguridae					
Pagurus longicarpus				X	
P. pollicaris				X	
P. annulipes				X	
F. Porcellanidae					
Petrolisthes armatus				X	
F. Majidae					
Libinia dubia				X	
F. Upogebiidae					
Upogebia affinis				X	
F. Pinnotheridae					
Pinnotheres maculatus				X	
Pinnixa retinens				X	
O. Amphipoda					
F. Atylidae					
Atylus (=*Nototropis*) sp.		X			
F. Ampeliscidae					
Ampelisca abdita		X			
F. Corophiidae					
Cerapus tubularis		X			
Corophium louisianum		X			
Grandidierella bonnieroides		X			
F. Caprellidae		X			
F. Podoceridae					
Podocerus sp.					
F. Amphilochidae					
Amphilochus sp.		X			
F. Amphithoidae					
Cymadusa compta		X			
F. Gammaridae					
Gammarus mucronatus		X			

Table IV.B.4.7. Continued.

Species	Baffin Bay	Upper Laguna Madre	Corpus Christi-Nueces	Redfish Bay	Aransas-Copano
F. Melitidae					
Melita sp.		X			
Elasmopus sp.		X			
O. Isopoda					
F. Anthuridae					
Xenanthura brevitelson		X			
F. Idoteidae					
Edotea montosa		X			
Erichsonella attenuata		X			
F. Sphaeromatidae					
Cymodoce faxoni		X			
O. Tanaidaceae					
F. Tanaidae					
Hargeria rapax		X			
C. Cirripedia					
F. Balanidae					
Balanus balanus				X	
SP. Chelicerata					
C. Pycnogonida		X			
P. Echinodermata					
C. Brittle star				X	
C. Echiuroid				X	
C. Holothuridea					
O. Dendrochirotida					
F. Phyllophoridae					
Thyone sp.		X			
P. Chordata					
C. Ascidiacea					
O. Stolidobranchia					
F. Molgulidae				X	
Molgula manhattensis				X	

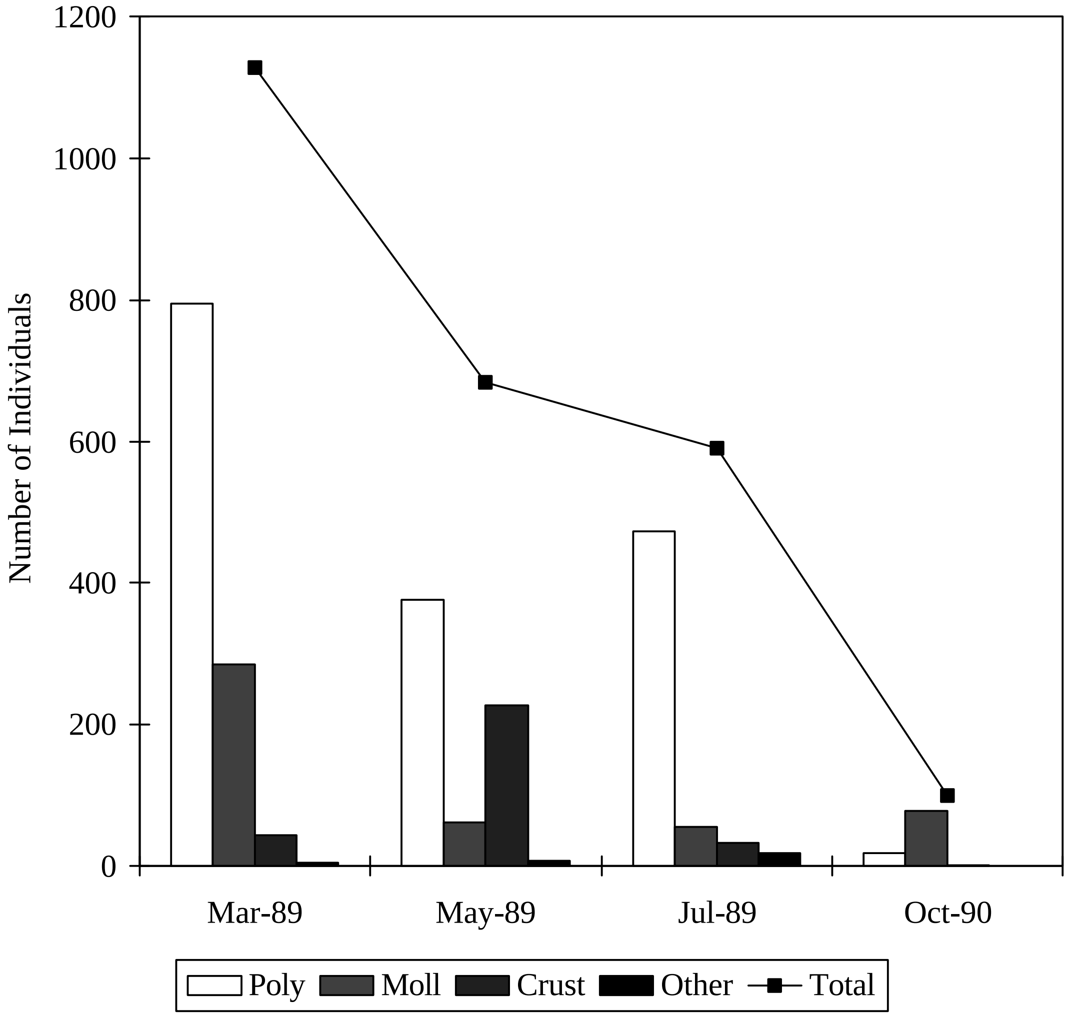

Fig. IV.B.4.2. Total numbers of organisms found in three replicate 6.7 cm diameter core samples taken from a *Halodule* meadow near Bird Island Basin. Cores were taken to a depth of 10 cm (from Montagna, 1992).

the most abundant organisms collected at all sites (Fig. IV.B.4.3) in both the top (0-3 cm) and bottom (3-10cm) sections; total numbers were always greatest in the top section.

Several studies examined seagrass meadow macrofauna in connection with dredge material disposal sites/islands in the upper Laguna Madre. Forty-five species of molluscs (16 gastropod families; 16 bivalve families) were recovered *Halodule* meadows around a dredge material island (Marker 83) (Williamson, 1980). Mean densities were highest in summer (440 m^{-2}) and lowest in fall (175 m $^{-2}$). Mean monthly populations ranged from approximately 2,100 m^{-2} (November) to 10,729m $^{-2}$ (July). Species richness was constant (38) in all seasons, although not all species were found in all seasons. The most abundant species were *Crepidula maculosa* in winter and spring, *Mysella planulata* in summer, and *Cerithium lutosum* in fall.

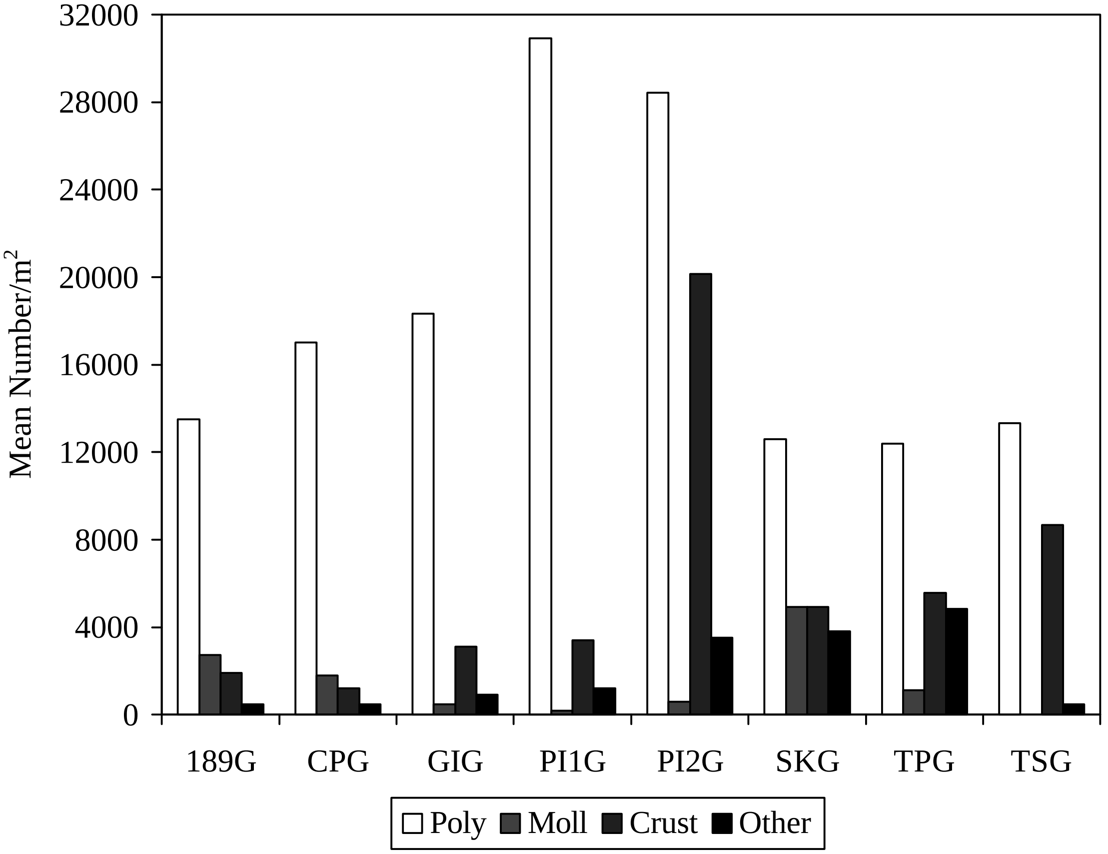

Fig. IV.B.4.3. Mean densities (#/m^2) of macrofaunal organisms recovered from natural (189G, PI1G, PI2G) and created (CPG, GIG, SKG, TPG, TSG) *Halodule* meadows in the upper Laguna Madre (from Montagna, 1993).

Circé (1979) studied dynamics of natural colonization of dredge material by *Halodule*. A total of 50,522 macrofaunal organisms were collected. The polychaete, *Brachyioasychis americana*, was the most abundant infaunal organism and comprised 72.5% of the total number of organisms collected. The bivalve, *Mulinia lateralis*, comprised 13.7% of the total. The "original" (undisturbed), deep water (1.0-1.5 m) seagrass meadows had the lowest numbers of both species and individuals, followed by the high energy "pioneer" station. The "complete" (*Halodule* colonization complete) station had the highest macrofaunal densities and species richness.

Rickner (1979) studied effects of dredge material on seagrasses and macrofauna in the upper Laguna Madre. He considered only polychaetes and bivalves since few gastropod species were large enough to be retained in the sieve (2 mm). Twenty-one species of polychaetes were collected; *Melinna maculata* (29%), *Heteromastus filiformis* and *Mediomastus californiensis* (21%) and family Maldanidae (21%) were most abundant. An average of 475±45 individuals m^{-2} (± SD) were collected in summer and 1,163±114 were collected in winter. Of 18 bivalve species collected, *Tellina texana*, *T. tampaensis*, *Ensis minor*, *Amygdalum papyria*, and *Mulinia* *lateralis* comprised 65% of the total. He did not separate bivalves by season, but compared samples taken randomly from natural seagrass meadows (mean 334 m^{-2}) to those around dredge material islands that were >20 years old (mean 242 m^{-2}). Analysis of variance revealed no statistically significant differences ($P > 0.05$) in bivalve numbers between meadows. *Diastoma varium* was listed as the most abundant gastropod.

In a study of winter food habits of waterfowl, Koenig (1969) collected macrofaunal samples from several *Halodule* meadows. Density of "worms" was 153/m^2, and density of molluscs was 117/m^2. *Anomalocardia auberiana* and *Tellina lineata* were the only molluscs collected from the sediments. The polychaete *Nereis pelagica occidentalis*, the bivalve *Anomalcardia aurberiana*, and gastropods *Neritina virginea* and *Cerithium variabile* were found in duck stomach contents.

Parker (1959) considered *Amygdalum papyria* and *Laevicardium mortoni* as characteristic species of the "open, shallow, hypersaline lagoon" in which abundant seagrass meadows are found. Overall, 33 mollusc species were collected from this environment in the Laguna Madre, although only 13 were alive.

Baffin Bay. - Although seagrass meadows are not widespread in Baffin Bay, the polychaete fauna of the *Halodule*/*Ruppia* grassflats found in the Laguna Salada, smallest and westernmost tertiary bay in the Baffin Bay system, was studied (Kreuz, 1973). The fauna was depauperate, consisting of only two species in two families. Only three individuals, (two *Nereis succinea*; one *Eteone heteropoda*), were collected during the year-long study. Lack of circulation between the upper Laguna Madre and Baffin Bay which impedes recruitment, coupled with lack of suitable substrates probably prevents establishment of an abundant and/or diverse macroinfaunal community.

Corpus Christi-Nueces Bay. - Only one study examined seagrass meadow macrofauna in Corpus Christi Bay. Three *Halodule* meadows, located on the backside of Mustang Island, at Shamrock Cove, and adjacent to La Quinta Channel, were included in a year-long study of the molluscan fauna of Corpus Christi Bay (Castiglione, 1983). Forty-seven live molluscan species (21 gastropods; 26 bivalves) were collected from the meadows with seven species found nowhere but in the meadows: *Lucina pectinata*, *Anomalocardia auberiana*, *Abra aequalis*, *Argopecten irradians amplicostatus*, *Anadara ovalis*, *Bulla striata*, and *Haminoea antillarum.* Shamrock Cove had highest species richness followed by Mustang Island and La Quinta Channel. Large populations of a few species were found in Mustang Island and La Quinta Channel meadows while individual species densities and species richness was fairly constant in Shamrock Cove (Table IV.B.4.8).

Gastropods, particularly *Diastoma varium*, dominated assemblages at all three stations. *Anachis avara*, *Neritina virginea*, *Pyrgocythara plicosa*, *Mitrella lunata*, and *Sayella livida* were also found at all three stations but average numbers varied considerably between stations (Fig. IV.B.4.4). Peak densities of *D. varium* occurred in March and November, *A. avara* in June and January, and *M. lunata* in July and September (Castiglione, 1983).

Table IV.B.4.8. Overall mollusc density (#/m^2), number of species, diversity, and eveness in *Halodule* meadows in Corpus Christi Bay (from Castiglione, 1983).

Station	Density (#/m^2) mean (range)	Number of Species	Diversity (H')	Eveness (J')
Shamrock Cove	1,081 (440-1,947)	36	2.65	0.51
Mustang Island	706 (7-2,296)	31	2.11	0.42
La Quinta Channel	1,062 (42-5,292)	28	1.16	0.24

Only three species of bivalve were collected regularly in large numbers. *Chione cancellata* was collected in all but one month. Densities ranged from 22/m^2 to 132/m^2 with peaks in July and January. *Amygdalum papyria* was collected from all three stations, usually attached to the base of a seagrass stem. Densities were fairly stable with a peak (110/m^2) in March. *Lucina pectinata* was not found at the La Quinta Channel station, but densities peaked in May, September, and February at the other two stations. Highest densities (66/m^2) were recorded in February (Castiglione, 1983).

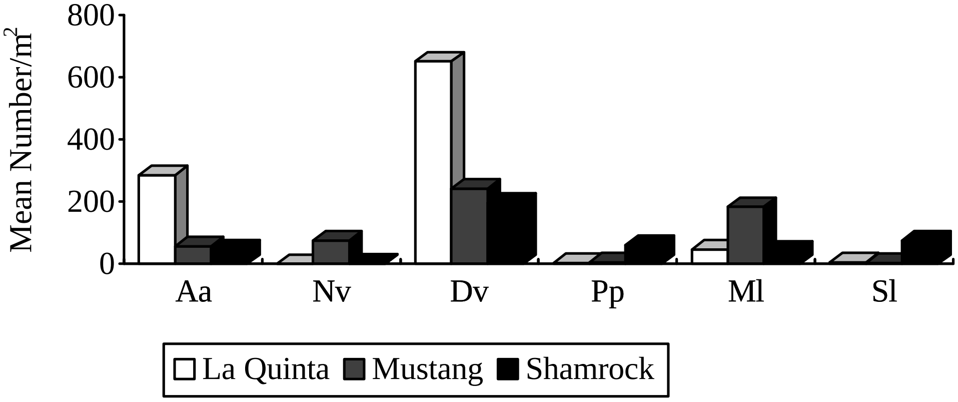

Fig. IV.B.4.4. Mean densities (#/m^2) of the dominant gastropod species collected from *Halodule* meadows in Corpus Christi Bay. Aa=*Anachis avara*; Nv=*Neritina virginea*; Dv=*Diastoma varium*; Pp=*Pyrgocythara plicosa*; Ml=*Mitrella lunata*; Sl=*Sayella livida* (modified from Castiglione, 1983).

Redfish Bay. - Polychaetes were listed as one of the most abundant animals in *Thalassia* meadows near Ransom Island, but no details were given (Zimmerman, 1969). Molluscan densities before and after Hurricane Beulah (September 1967), which decreased salinities for much of 1968, were also studied. *Chione cancellata* and *Phacoides pectinatus* were both conspicuous members of the community prior to the hurricane, after which *P. pectinatus* dominated. *Anomalocardia auberiana*, *Amygdalum papyria* and *Ensis minor* were also conspicuous members of the community. They occurred in low numbers until March 1968 after which numbers rose, peaking in August. *Diastoma varium*, *Anachis avara*, *Nassarius vibex*, *Cerithium variabile* and *Polinices duplicatus* were the most abundant gastropods in the assemblage (Zimmerman and Chaney, 1969).

Zimmerman (1969) also collected epibenthic crabs. *Menippe adina* was common in all areas. Several other species were collected, but they were not common or abundant. Densities of other xanthids (mud crabs) could not be determined accurately due to their benthic lifestyle but he considered them the most abundant crustaceans in *Thalassia* meadows. Hermit crabs were usually found in the shallowest areas of the meadows; they were most abundant between April and August. *Petrolisthes armatus* densities were also difficult to determine accurately, but they were common, usually in association with oyster clumps. *Libinia dubia* distributions and densities were related to grass densities, with 60% of the total number taken from the densest meadow.

Two studies addressed macrofauna of seagrass meadows around Stedman Island. Kreuz (1973) focused on the polychaete fauna of a meadow dominated by *Halodule* with *Ruppia* and *Halophila*, and a meadow dominated by *Thalassia* with *Halophila*, as well as several unvegetated areas between July 1971-June 1972. Fourteen species (11 eleven families) were collected. Fifty-four percent of the total number of individuals were collected from the *Thalassia* meadow, 10% were collected from the *Halodule* meadow. The serpulid, *Dexospira spirullum*, was found only in the *Thalassia* meadow during July (107 individuals), August (247 individuals) and September (9 individuals), and was the most abundant species collected. Most *Melinna maculata* and *Heteromastus filiformis* were collected in the seagrass meadows. No molluscs were common to both meadows. *Ensis minor* was found between January and April in the *Halodule* meadow, and *Phacoides pectinatus* in July, August, January, April and May in the *Thalassia* meadow.

Rickner (1975) studied molluscan assemblages of the same seagrass meadows near Stedman Island, including organisms associated with oyster clumps within meadows. The *Halodule* meadow was dominated by *Ensis minor* and *Amygdalum papyria*, while the *Thalassia* meadow was dominated by *Lucina pectinatus* (37.9%) and *Chione cancellata* (16.2%). Nearly 64% of individuals collected from seagrass meadows and an adjoining unvegetated area came from the *Thalassia* meadow. Five species were associated exclusively with *Thalassia*: *Anadara ovalis*, *Chione cancellata*, *Diplodonta semiaspera*, *Mactra fragilis* and *Periploma margaritaceum*. Five different species were associated exclusively with *Halodule*: *Amygdalum papyria*, *Lyonsia hyalina*, *Laevicardium mortoni*, *Ensis minor*, and *Tagelus plebius*; they comprised 32.8% of the total individuals. Apparently no gastropods were collected.

Oyster clumps were most numerous in the *Thalassia* meadow; a diverse assemblage of associated organisms was found. Nine gastropods, three bivalves, a chiton, seven polychaetes, and ten crab species were collected (Rickner, 1975). The most numerous species were *Brachiodontes exustus*, and *Crepidula convexa*; serpulid polychaete tubes were conspicuous as well. Several hundred xanthid crabs were collected from the meadows in or near oyster clumps along with porcellanid and hermit crabs. No additional information concerning abundance or temporal distribution was presented.

Summary: Bay System Review. - Overall, when polychaetes were collected and analyzed, they appeared to be the most abundant invertebrate in seagrass meadows. Ten species were common to the Laguna Madre and Redfish Bay: *Exogone dispar*, *Nereis succinea*, *Capitella capitata*, *Heteromastus filiformis*, *Mediomastus californiensis*, *Scoloplos rubra*, *Eteone heteropoda*, *Clymenella mucosa*, *Melinna maculata*, and *Sabella micropthalma*. This group deserves further study, since they probably numerically dominate the invertebrate assemblage in most seagrass meadow communities in the study area. Epibenthic crabs have received little attention; amphipods and other small crustaceans have been virtually ignored.

Parker (1959) observed that *Amygdalum papyria* and *Laevicardium mortoni* were indicator bivalves of *Halodule* meadows in the Laguna Madre and this appears to hold true for other bay systems. *Lucina pectinata* appears to be limited to *Thalassia* meadows. *Diastoma varium*, *Neritina virginea*, *Mitrella lunata*, *Anomalocardia auberiana*, *Argopectin irradians amplicostatus*, and *Amygdalum papyria* were found in all bay systems.

Consumer Roles of Macroinfauna and Epifauna. - Invertebrates discussed previously represent all trophic levels from secondary producers (deposit feeders) to top-level consumers (predaceous gastropods) (Table IV.B.4.9). A few graze on epiphytic algae or directly on seagrasses or seagrass detritus. *Capitella capitata* and *Arenicola cristata* were listed by McRoy and Helferrich (1980) as feeding directly on seagrass detritus. *Diopatra cuprea* and two species which are not found in the study area but which are in families with representatives in the study area, *Haminoea zelandiae* (gastropod family Hamineidae) and *Amphithoe vaillanti* (amphipod family Amphithoidae), were listed as grazing directly on *Zostera* and/or *Ruppia*.

4.3.1.2 Meiofauna

No studies were found concerning meiofauna inhabiting seagrass meadows in the study area.

4.3.1.3 Zooplankton and Microfauna

One study addressed zooplankton and microfauna associated with seagrass meadows in the CCBNEP study area. Chaney (1988) conducted weekly plankton tows (#20 net) in a *Halodule* meadow in the upper Laguna Madre (November 1986-October 1987). A total of 21,355,323 microfaunal organisms were collected. Crustaceans (39.7%), primarily eggs, nauplii, and copepods, Platyhelminthes (34.9%), primarily flatworm eggs, and molluscs (16.8%), primarily juvenile gastropods, were most abundant. Zooplankton, protozoa, polychaete larvae, cnidarians, ctenophores, rotifers, phoronids, nemerteans, nematodes, trochophore larvae, chaetognaths, and urochordates were also collected.

Table IV.B.4.9. Consumer-types of major epibenthic, benthic, and epiphytic invertebrate taxa found in seagrass meadows in the CCBNEP project area. Categories and/or food types are after McRoy and Helfferich (1980); Rehder (1981); Uebelaker and Johnson (1986); Barnes (1987); and Ruppert and Fox (1988). SD=selective deposit feeder; DD=direct detritivore; NsD=non-selective deposit feeder; DF=deposit feeder; P=predator; C=carnivore; O=omnivore; SF=suspension feeder; FF=filter feeder; Sc=scavenger; H=herbivore; SfD=surface deposit feeder; AS=algal scraper; A=algae; D=detritus; BS=blood-sucking parasites; S=sponges; C=commensal food stealer.

Taxon	Consumer-Type
P. Bryozoa	FF
P. Platyhelminthes	
C. Turbellaria	P,C
P. Rhynchocoela	DF, P
P. Annelida	
C. Oligochaeta	DF
C. Polychaeta	
F. Syllidae	P, SD
F. Goniadidae	P, C
F. Nereidae	C, H, O, Sc, DF
F. Lumbrineridae	P
F. Sigalionidae	C
F. Spionidae	SF, DF
F. Chaetodipteridae	FF
F. Capitellidae	NsD
Capitella capitata	DD
F. Cirratulidae	SD, SfD
F. Orbiniidae	NsD
F. Arendicolidae	DF
Arenicola cristata	DD
F. Onuphidae	O, Sc
Diapatra cuprea	H (*Zostera*)
F. Hesionidae	DF
F. Phyllodocidae	P, C, Sc
F. Pectinariidae	NsD
F. Maldanidae	SD
F. Pilargidae	C, O
F. Spiorbidae	FF
F. Ampharetidae	SfD
F. Dorvilleidae	C, H
F. Magelonidae	SfD
F. Terebellidae	SfD
F. Serpulidae	FF

Table IV.B.4.9. Continued.

Taxon	Consumer-Type
F. Sabellidae	FF
P. Mollusca	
C. Polyplacophora	AS
C. Gastropoda	
F. Ellobiidae	H, AS
F. Buccinidae	P, Sc
F. Trochidae	A, D
F. Cerithidae	DF, A, D
F. Nassariidae	Sc
F. Pyramidellidae	BS
F. Scaphandridae	C
F. Acteonidae	C
F. Neritidae	AS
F. Naticidae	C
F. Littorinidae	H
F. Melongenidae	C
F. Hydrobiidae	DF
F. Vitrinellidae	SD, A
F. Columbellidae	C, Sc
F. Truncatellidae	D, A
F. Caecidae	?
F. Modulidae	D, A
F. Triphoridae	S, D, A
F. Turridae	P
F. Cerithiopsidae	S, D, A
F. Potamididae	DF
F. Epitoniidae	C
F. Bullidae	C, A
F. Crepidulidae	SF, FF
F. Muricidae	C
F. Hamineidae	H
C. Bivalvia	FF
SP. Crustacea	
O. Ostracoda	H, FF
O. Cumaceae	FF
O. Decapoda	
F. Xanthidae	P
F. Diogenidae	O, D
F. Paguridae	O, D
F. Porcellanidae	FF
F. Majidae	?

Table IV.B.4.9. Continued.

Taxon	Consumer-Type
F. Upogebiidae	FF
F. Pinnotheridae	C (capitellids)
O. Cirripedia	FF
O. Amphipoda	D, Sc
F. Amphithoidae	H (*Zostera*)
O. Isopoda	DF, D, O
O. Tanaidaceae	A
SP. Chelicerata	
C. Pycnodonida	C, H, D
SP. Echinodermata	
C. Holothuridea	DF
C. Echinoidea	AS
C. Stellaroidea	
SC. Ophiuroidea	Sc, C, DF, FF
P. Chordata	
C. Ascidiacea	FF

4.3.1.4 Nekton

Invertebrate nekton have only been collected from seagrass meadows in the upper Laguna Madre and Redfish Bay in the CCBNEP study area (Table IV.B.4.10). In the Laguna Madre, *Palaemonetes intermedius* was the most abundant nektonic invertebrate in the *Halodule* meadow studied (Chaney, 1988). Grooved shrimp (*Penaeus aztecus* and *P. duorarum*) (Zimmerman, 1969; Gourley, 1989) and *Hippolyte pleuracantha* (Rickner, 1975) were most abundant in Redfish Bay. Gourley (1989) did not collect any *Palaemonetes* spp. during his study, however, this genus was fairly abundant in Redfish Bay 20 years earlier (Zimmerman, 1969); they were the second most abundant species found by Rickner (1975). This is likely an artifact of different sampling methods. Zimmerman (1969) used 13 mm (1/2 in) and 3 mm (1/8 in) square mesh seines, and Rickner (1975) used a push-net seine, while Gourley (1989) used a “benthic sled” with 1.8 mm mesh. Benthic sleds have a tendency to push water rather than straining, especially in dense vegetation.

It is possible to compare relative abundances of invertebrate nekton in meadows dominated by *Thalassia* or *Halodule* in Redfish Bay. Gourley (1989) found grooved penaeid shrimp were most abundant in *Halodule*, while Zimmerman (1969) found the opposite. Rickner (1975) found found about the same numbers of *Penaeus aztecus* in both *Halodule* and *Thalassia* meadows. He also found more *Callinectes sapidus* in *Thalassia*, while it was most abundant in *Halodule* in the

Table IV.B.4.10. Invertebrate nekton ranked by total abundance (1=most abundant, etc.) collected from seagrass meadows in the upper Laguna Madre (Chaney, 1988) and Redfish Bay (I - Zimmerman, 1969; II - Rickner, 1975; III - Gourley, 1989). X = occurred but abundance data unavailable.

Species	Laguna Madre	Redfish Bay I	II	III
P. Cnidaria				
Aurelia sp.	9			
Dactylometra quinqeucirrha		X		
Stomolophus meleagris		X		
P. Ctenophora				
Beroe ovata		X		
Beroe sp.	5			
Mnemiopsis sp.	6			
unidentified ctenophore	8			
SP. Crustacea				
O. Decapoda				
F. Penaeidae				
Penaeus aztecus	3		4	1
P. duorarum		1		1
P. setiferus		9		
juvenile penaeids				2
F. Palaemonidae				
Palaemonetes intermedius	1	8		
P. pugio		4		
P. vulgaris		5		
Palaemonetes spp.			2	
Periclimenes longicaudatus		11		
F. Hippolytidae				
Hippolyte pleuracantha	2	2	1	
Leander tenuicornis		12		
Tozeuma carolinensis	7	6	3	
F. Alpheidae				
Alpheus heterochaelis		7	6	
Alpheus sp.		10		
F. Portunidae				
Callinectes sapidus	4	3	5	3
O. Mysidacea	10			
O. Stomatopoda	10			
P. Mollusca				
C. Cephalopoda				
Lolliguncula brevis	10			

other studies. *Hippolyte pleuracantha*, *Palaemonetes pugio*, *P. intermedius*, *Alpheus heterchaelis*, and *Penaeus setiferus* were most abundant in *Halodule* in Zimmerman's study, while *H. pleuracantha*, *Palaemonetes* spp., and *A. heterchaelis* were most abundant in *Thalassia* in Rickner's study.

Consumer roles of invertebrate nekton are not diverse. Most crustaceans are omnivorous, eating everything from invertebrate infauna to detritus and carrion. Cnidarians, ctenophores, and *Lolliguncula brevis* (squid) are carnivorous predators.

4.3.2 Fish

Fish have been collected only from seagrass meadows in the upper Laguna Madre and Redfish Bay in the CCBNEP study area (Table IV.B.4.11). Twenty-six species (16 families) were collected with a 6 mm mesh bag seine in a *Halodule* meadow in the upper Laguna Madre near Bird Island Basin (Chaney, 1988). A total of 81 species (44 families) were collected in *Thalassia* and *Halodule* meadows in Redfish Bay, using a benthic sled (1.8 mm mesh) (Gourley, 1989), and bag seines (both 13 mm and 3 mm mesh) and trammel nets (Zimmerman, 1969; Rickner, 1975). Most were collected by Zimmerman (1969) during his year-long study.

Menidia peninsulae (tidewater silversides) and *Lucania parva* (rainwater killifish) were the most abundant species found in the upper Laguna Madre (Chaney, 1988). *Menidia peninsulae* were taken in every seine haul, with greatest numbers coinciding with low water. Larvae were present in plankton samples in every month except August. No larval *Lucania parva* were caught, but small individuals appeared in collections made during June-September.

Only two game fish were caught during the Laguna Madre study. *Cynoscion nebulosus* (spotted seatrout) juveniles were collected only during November-December 1986 and July-October 1987 (Chaney, 1988). Spawning by this species peaks between late April and July (Lassuy, 1983). Post-larvae and juveniles prefer seagrass meadows, remaining there through the warmer months. Thirty-six early stage juvenile *Scianops ocellatus* (red drum) were collected between December and March (Chaney, 1988). This species spawns offshore from August to December, and the eggs and/or larvae are swept into estuaries. Young *Scianops ocellatus* remain in estuaries for no less than six months before moving into deeper water for the winter (Reagan, 1985), and many remain in the bays for up to five years before moving into the Gulf of Mexico (L. McEachron, pers. comm.).

Zimmerman (1969) provides the most comprehensive data concerning fish communities in the seagrass meadows of Redfish Bay. He collected bag seine (3 mm and 13 mm mesh) and trammel net data monthly for one year (1967-1968), capturing 14,392 individuals in 70 species, including four shark and ray species. Fifty-seven percent of the fish caught were under 100 mm total length. *Lagodon rhomboides* (35.3%),and *Anchoa mitchilli* (17.6%) were the most abundant species overall and in the <100 mm size class (70.6% both species). *Arius felis* (12.5%) was also and comprised 29.1% of the >100 mm size class. Twenty-seven species were collected only as individuals >100 mm long [e.g., sharks and rays; *Lipisosteus spatula* (alligator

Table IV.B.4.11. Fish collected from seagrass meadows in the Corpus Christi Bay National Estuary Program study area. Upper Laguna Madre - Chaney, 1988; Redfish Bay - Zimmerman, 1969; Rickner, 1975; Gourley, 1989. Size classes: S = <100 mm total length; L = >100 mm total length (from Zimmerman, 1969). X =occurred, but no size class information available.

Species	Laguna Madre	Redfish Bay
C. Osteichthys		
F. Engraulidae		
Anchoa hepsetus	X	S
A. mitchilli	X	S
F. Clupeidae		
Brevoortia patronus	X	L
Brevoortia spp.		S, L
Dorosoma cepedianum		L
Alsoa chrysochloris		L
Opisthonema oglinium		L
Harengula pensacolae		S
F. Sciaenidae		
Cynoscion nebulosus	S, L	S, L
C. arenarius		L
Sciaenops ocellatus	S	S, L
Leiostomus xanthurus	S, L	S, L
Larimus fasciatus		L
Bairdiella chrysura	S	S, L
Menticirrhus americanus		L
Micropogon undulatus		S, L
Pogonias cromis		L
F. Cyprinodontidae		
Cyprinodon variegatus	S	S
Fundulus grandis	X	S
F. similis	X	
Lucania parva	S	S
F. Gerreidae		
Gerres cineareus	X	
Eucinstomus gula		S
Eucinostomus sp.		S
F. Gobiidae		
Gobiosoma robustum	S	S
G. bosci		S
Gobionellus boleosoma		S
Microgobius thalassinus	X	S

Table IV.B.4.11. Continued.

Species	Laguna Madre	Redfish Bay
F. Syngnathidae		
Syngnathus floridae	X	S, L
S. louisianae		S, L
S. scovelli	S, L	S
Hippocampus zosterae	X	S
F. Exocoetidae		
Hyporhamphus unifasciatus	X	S, L
F. Sparidae		
Archosargus probatocephalus		S, L
Lagodon rhomboides	S, L	S, L
F. Atherinidae		
Membras martinica		S
Menidia peninsulae	S	
M. beryllina		S
Menidia sp.		S
F. Mugilidae		
Mugil cephalus	S	S, L
F. Ophidiidae		
Ophidion holbrooki		S
O. welshi	L	S
F. Batrachoididae		
Porichthys porosissimus		L
Opsanus beta	S, L	S, L
F. Pomadasyidae		
Orthopristis chrysoptera	L	S, L
Haemulon sciurus		L
F. Belonidae		
Strongylura marina	X	
F. Ophichthidae		
Myrophis punctatus	X	S, L
F. Bothidae		
Paralichthys lethostigma		S, L
Achirus lineatus		S
Citharichthys sp.		S
F. Cynoglossidae		
Symphurus plagiusa		S
F. Elopidae		
Elops saurus		S, L
F. Triglidae		
Prionotus tribulus		S, L

Table IV.B.4.11. Continued.

Species	Laguna Madre	Redfish Bay
F. Synodontidae		
Synodus foetens		S
F. Gadidae		
Urophycis floridanus		S
F. Arridae		
Arius felis		L
Bagre marinus		L
F. Diodontidae		
Chilomycteris schoepfi		S, L
F. Tetraodontidae		
Sphaeroides nephelus		S
Lagocephalus laevigatus		L
F. Trichiuridae		
Trichiurus lepturus		S, L
F. Chaetodontidae		
Chaetodipterus faber		L
F. Scombridae		
Scomberomorus maculatus		L
F. Stromateidae		
Peprilus paru		L
F. Balistidae		
Monocathus hispidus		S
F. Uranoscopidae		
Astroscopus y-graecum		L
F. Anguillidae		
Anguilla rostrata		L
F. Lobotidae		
Lobotes surinamensis		S
F. Carangidae		
Selene vomer		L
Oligoplites saurus		L
Caranx hippos		S
F. Pomatomidae		
Pomatomus saltatrix		L
F. Lepisosteidae		
Leipisosteus spatula		L
F. Polynemidae		
Polydactylus octomenus		L

Table IV.B.4.11. Continued.

Species	Laguna Madre	Redfish Bay
F. Blenniidae		
Chasmodes bosquianus		S
Hypleurochilus geminatus		S
Hysoblennium hentzi		S
F. Rachycentridae		
Rachycentrum canadum		L
F. Scorpeanidae		
Scorpeana plumieri		S
F. Ostraciidae		
Acanthostracion (=Lactophrys) quadricornis		S
C. Chondrichthys		
F. Dasyatidae		
Dasyatis sabina		L
F. Carcharhinidae		
Carcharhinus leucas		L
F. Gymnuridae		
Rhinopteras bononasus		L
F. Sphyrnidae		
Sphyrna tiburo		L

gar)]; 23 species were collected only as individuals < 100 mm long (e.g., *Anchoa mitchilli*). Individuals of nearly all species of game fish (e.g., *Cynoscion nebulosus*, *Scianops ocellatus*) were collected in both size classes, although generally more large individuals were captured.

Rickner (1975) collected bag seine (3 mm mesh) and trammel net data only during June 1974 and 1975 in Redfish Bay seagrass meadows. Thirty-three species were collected, but only *Lagodon rhomboides*, *Mugil cephalus*, *Cynoscion nebulosus*, *Paralichthys lethostigma*, and *Brevoortia* spp. were found in both nets. A total of 1,440 individuals were caught with the trammel net; eight species (12.6%) were game fish. *Arius felis* (38%), *Leistomus xanthurus* (12.2%), and *Lagodon rhomboides* (11.3%) were the most abundant species captured in trammel nets. A total of 1,209 individuals were caught in the bag seine; only 3 species (5.6%) were game fish. *Lagodon rhomboides* (31.2%) and *Bairdiella chrysura* (28.8%) were the most abundant species caught in the bag seine.

Gourley (1989) collected a total of 8,246 small fish (< 150 mm) during his study of Redfish Bay seagrass meadow nekton. *Leiostomus xanthurus* (22.5%) and *Lagodon rhomboides* (21.4%) were the most abundant species. Only two species were collected that exceeded 100 mm, *Syngnathus floridae*, and *Myrophis punctatus*. *Leiostomus xanthurus* was more abundant and significantly larger in *Halodule*, while *Lagodon rhomboides* was most abundant in *Thalassia*. There were no significant differences in sizes of *Lagodon rhomboides* between meadows. Overall, slightly more fish were found in the *Halodule* meadow (53%) than the *Thalassia* meadow.

Nearly all the fish species collected in the Laguna Madre were also found in Redfish Bay, although many more species were collected in Redfish Bay because trammel nets were used. However, there were differences in the dominant small (<100 mm) species. All studies in Redfish Bay list *Lagodon rhomboides* as the first or second most abundant small fish, even in *Halodule* meadows, often with *Leistomus xanthurus* (except Zimmerman (1969), *Anchoa mitchelli*). *Menidia peninsulae* and *Lucania parva* were the most abundant species found in the Laguna Madre, most likely a result of the direct connection between Redfish Bay and the Gulf of Mexico (Aransas Pass).

4.3.2.1 Consumer Roles

At some point in their life history, fish consume nearly every type of food. Adult foods of some of the more common fish species in the study area, all of which occur in seagrass meadows, are given in Section IV.C, Table IV.C.2.1 (this volume). Several species found in seagrass meadows include seagrasses in their diet. *Archosargus probatocephalus*, *Hyporhampus* spp. and *Pogonias chromis* eat *Halodule* leaves, and *Rhinoptera quadriloba* eats *Halodule* and *Thalassia* (Carangelo et al., 1974). *Lagodon rhomboides* eats the leaves of both *Ruppia* and *Halodule* (Darnell, 1958; Carr and Adams, 1973), and *Strongylura marina* (Darnell, 1958) and *Mugil cephalus* (Pullen, 1960) eat *Ruppia*. Two to three percent of the diets of *Acanthostracion quadricornis*, *Chaetodipterus faber* and *Harengula humeralis* in the West Indies was *Thalassia* leaves (Randall, 1967).

4.3.3 Reptiles and Amphibians

Leaves of seagrasses (*Thalassia*, *Halodule*, *Enhalus*, *Posidonia*) comprise up to 100% of the diet of sea turtles, *Chelonia mydas* (green turtle) in the Indo-Pacific and Red Sea (Bustard,1972; Hirth et al., 1973) and *Eretmochelys imbricata* (hawksbill turtle) juveniles in the Caribbean (Rebel, 1974). One small individual *Chelonia mydas* (carapace 275 x 220 mm) was taken from a *Thalassia* meadow near Ransom Island (Redfish Bay) in June 1967 (Zimmerman, 1969). No other information is available concerning sea turtle use of seagrass meadows in the study area. Information concerning the status of sea turtles in the study area is presented in Section IV.C.1.6-C1.10 (this volume).

4.3.4 Birds

Seagrass meadows are used by a variety of birds as feeding and resting areas, including many members of the families Ardeidae (waders) Scolopacidae (sandpipers), Charadriidae (plovers and allies), Laridae (gulls and terns), Pelecanidae (pelicans), Phalacrocoracidae (cormorants), Podicipedidae (grebes), Gaviidae (loons), Rallidae (rails and allies), Accipitridae (eagles and ospreys), and Anatidae (waterfowl). Waders such as the Great Blue Heron (*Ardea herodias*) and Reddish Egret (*Egretta rufescens*) feed in shallow seagrass meadows at low tide. Swimmers such as waterfowl and White Pelican (*Pelecanus erythrorhynchos*) and plungers such as Osprey (*Pandion haliaetus*) and Brown Pelican (*Pelecanus occidentalis*) feed in the meadows at high tide (Zieman and Zieman, 1989).

Only waterfowl use of seagrass meadows has been studied in the CCBNEP study area. *Halodule* meadows in the upper Laguna Madre are used extensively as feeding areas by wintering Redheads (*Aythya americana*). Approximately 78% of the North American population of Redheads winters in the Laguna Madre (Weller, 1964); they are most abundant December through March (Adair et al., 1990). Detailed trends analysis on bay waterfowl counts are presented in Volume II, “Current Status and Historical Trends of Avian Resources in the Corpus Christi Bay National Estuary Program Study Area”.

Redheads spend the greatest amount time feeding and moving while in estuarine habitats (Adair et al., 1990); they are most often found in shallow *Halodule* meadows along the perimeter of the Laguna Madre (McMahan, 1970; Cornelius, 1975; Adair et al., 1990). Typically, the diet of Redheads is composed of about 89% plant matter and 11% animal matter (Cottam, 1939). Plants made up 91.5% of foods found in stomachs of Redheads collected by Koenig (1969) in the Laguna Madre or nearby coastal ponds. *Halodule wrightii* rhizomes were the most common plant material found in stomachs of wintering Redheads, American Widgeon (*Anas americana*), and Pintail (*A. acuta*). In experimental studies using captive birds, only rhizomes were eaten.

4.3.5 Mammals

No information was found about mammal use of seagrass meadows in the CCBNEP study area. *Tursiops truncatus* (bottlenose dolphin), which is common in bay systems of the study area, has been reported feeding over seagrass meadows in Florida, even in water <1 m deep (Zieman and Zieman, 1989).

4.4 Community Structure and Zonation

4.4.1 Plant Communities

Spatial structure of seagrass meadows, which are generally dominated by one plant species, is more complex than it appears. Phenology (temporal pattern) of seagrass growth depends mainly on climatic factors such as temperature, precipitation, and wind strength. The annual cycle of the dominant seagrass species in turn regulates the floral composition of the epiphytic algae (Phillips and Meñez, 1988). Presence/absence of species, as well as community zonation, is largely a function of substrate composition, water energy, water depth (related to light penetration and exposure tolerance), salinity tolerance, and successional stage.

4.4.1.1 Phenology

Seagrasses tend to be perennial although populations of *Halodule* and *Halophila* can appear and disappear quickly (Phillips and Meñez, 1988). Seagrass phenology in the study area was studied in 1956-1957 (Conover, 1964). All species were dormant between December and March and began growing in April. Luxurious growth was noted between May and August. Flowers were observed on *Halodule* between June and August and on *Ruppia* between May and July; no flowers were observed on other species. The period of dormancy coincided with low temperature and solar illumination values, which were lowest in January. The period of maximum growth and sexual reproduction appeared to be correlated with the illumination maximum rather than the temperature maximum. The temperature maximum that occurred in August coincided with diminishing plant biomass in late July and early August (Fig. IV.B.4.5). Both precipitation and wind strength affect turbidity. Despite the fact that high winds and increased precipitation during late spring and summer increase turbidity compared with fall and winter values, maximum illumination and accumulation of solar radiation was higher during the period of maximum growth than during the period of dormancy.

Total above-ground biomass of *Halodule* was bimodal. It was lowest from November-January, reached a peak in April, declined through summer, and peaked again in early fall. Biomass generally peaked during months with midday temperature readings between 25-30º C and was lower during periods with either higher or lower temperatures (Morgan and Kitting, 1984) Maximum shoot density (10,000/m^2) occurs during summer. Peak growth (=leaf elongation) occurs between early May and mid-June, usually followed by a second interval of elevated growth in late summer. Leaf elongation rates drop rapidly from the summer maximum of 5-8 mm d^{-1} through fall reaching a minimum of <1 mm d^{-1} by January (Dunton, 1990; 1994).

4.4.1.2 Species Composition and Zonation

Species composition and zonation of seagrass meadows is largely determined by water depth and transparency, substrate composition, and salinity. Figure IV.B.4.6 shows the typical depth and salinity distributions of seagrasses in the study area.

Water Depth and Sediment Composition. - Most seagrasses must be covered even at the lowest tides. Even short-term exposure may alter populations and species distributions. In addition they require a minimum of 15-25% of the light present at the surface to photosynthesize (Fonseca, 1994). *Halophila* and *Halodule* have the widest range of depth tolerances, extending from mean high-water neap (MHWN) to considerable depths (Fig IV.B.4.7). *Thalassia* is restricted from mean low-water neap (MLWN) to about 10-12 m. *Syringodium* is further restricted because its stiff, subulate leaves are not well-adapted to temporary dessication (den Hartog, 1977). In very turbid waters, nearly all seagrasses are restricted to areas <1 m deep (Thayer et al., 1975).

In the Laguna Madre, density of *Halodule* appeared to be strongly correlated with water depth and sediment composition. Sparse *Halodule* was found at depths <0.7 m in firm, sandy

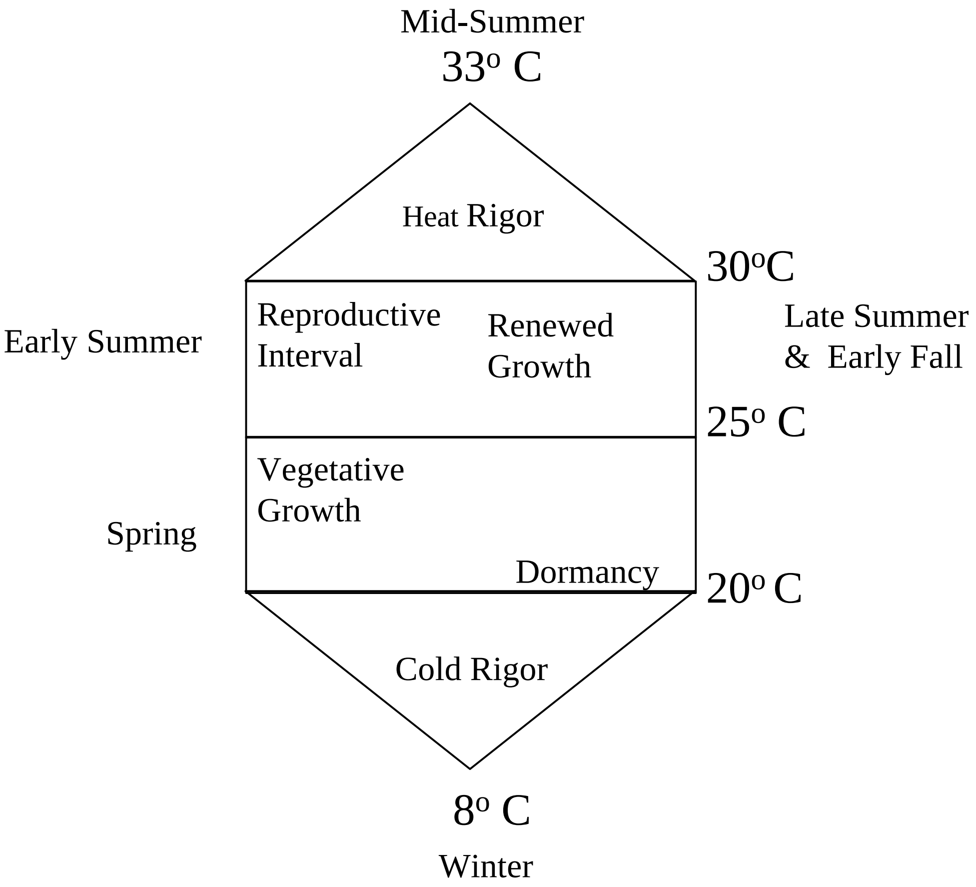

Fig. IV.B.4.5. Vegetative and reproductive patterns of seagrasses in the CCBNEP study area. Temperatures are based on the average summer maximum (August) and average winter minimum (January) for Corpus Christi (adapted from Setchell, 1929 in Phillips and Meñez, 1988).

substrates, while dense *Halodule* was found at depths >0.7 m in soft sediments with low sand content. *Halophila* (occuring as an understory) was usually present wherever dense *Halodule* was found. As water depth increased and dense *Halodule* graded into unvegetated bottom, *Halophila* often became the dominate species, sometimes in monospecific stands (Merkord, 1978). *Halophila* is generally dominant only in areas unsuitable for *Halodule*, and can occur from the low water mark in the understory of other seagrasses or in areas that are shaded to very great depths in undisturbed reefs. Other members of the genus are found in extreme habitats ranging from practically liquid eulittoral mud to bottoms of harbors polluted with organic pollutants (den Hartog, 1977).

Thalassia has a depth range of from 0.5-1.5 m in Redfish Bay, with *Halodule* found inshore, and separated from *Thalassia* meadows by a nonvegetated “sandy littoral zone” (Zimmerman and Chaney, 1969). In Bermuda, *Thalassia* grew in continuous meadows only in muddy sediments, and was patchy in coarse, sandy sediments (Bernatowicz, 1952). Because *Syringodium* is restricted to deeper water, this species is likely found in muddy substrates as well. Merkord

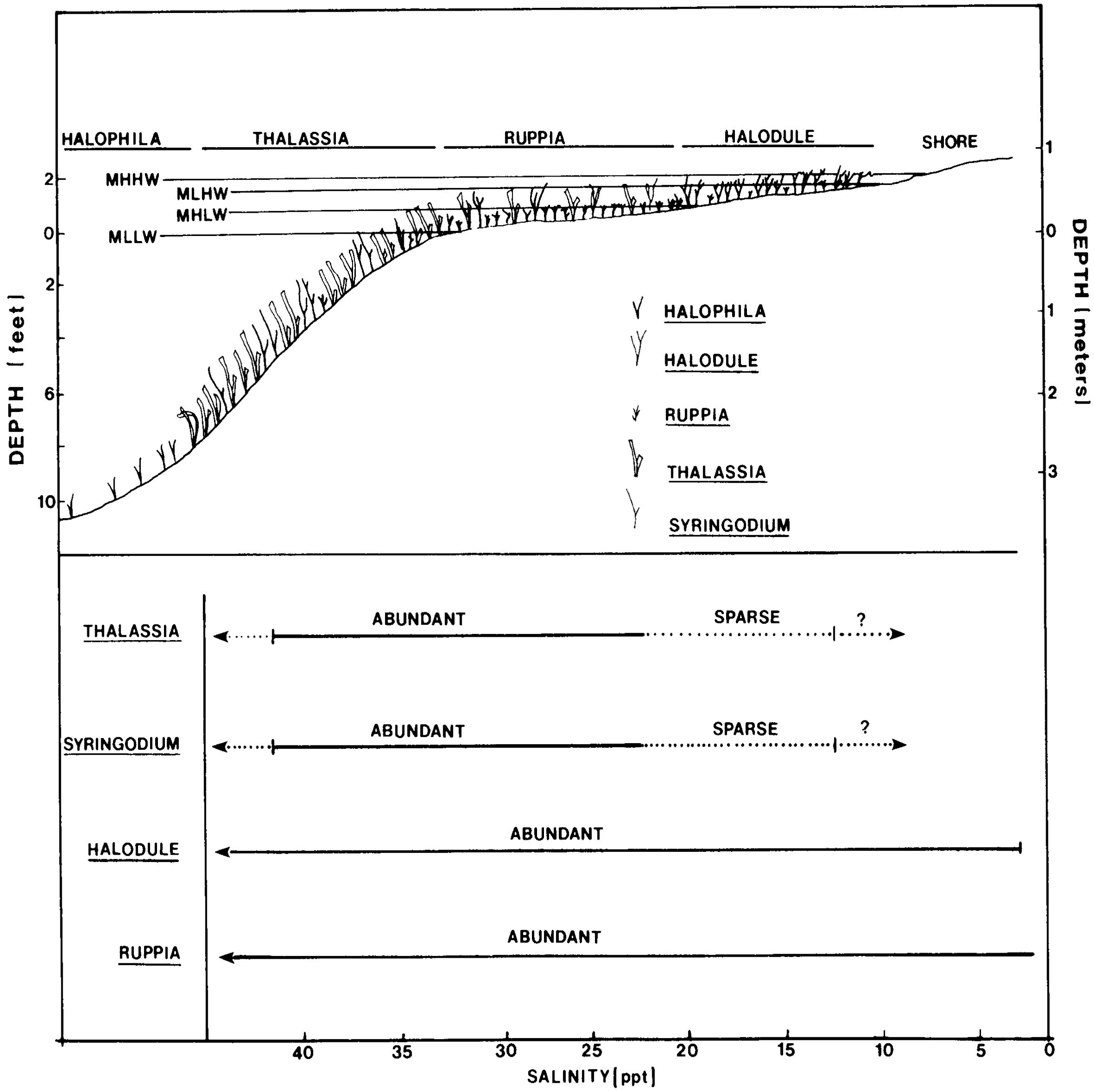

Fig. IV.B.4.6. Diagram showing typical depth and salinity distibutions of the seagrass species found in the CCBNEP study area (from Wolfe et al., 1988 after McNulty et al., 1972). MHHW = mean higher high water; MLHW = mean lower high water; MHLW = mean higher low water; and MLLW = mean lower low water.

(1978) found that *Syringodium* was dominant over fairly large areas in the lower Laguna Madre and suggested that it was distributed throughout dense *Halodule* meadows as well. It was uncommon near the Landcut and may be uncommon in the upper Laguna Madre. He mapped no *Syringodium* in the upper Laguna Madre, however, Quammen and Onuf (1993) recently reported *Syringodium* was expanding its range in the upper Laguna Madre. They did not find it during the systematic planned station sampling, but after seeing one patch in transit between stations, conducted visual searches specifically for *Syringodium* and found several additional patches.

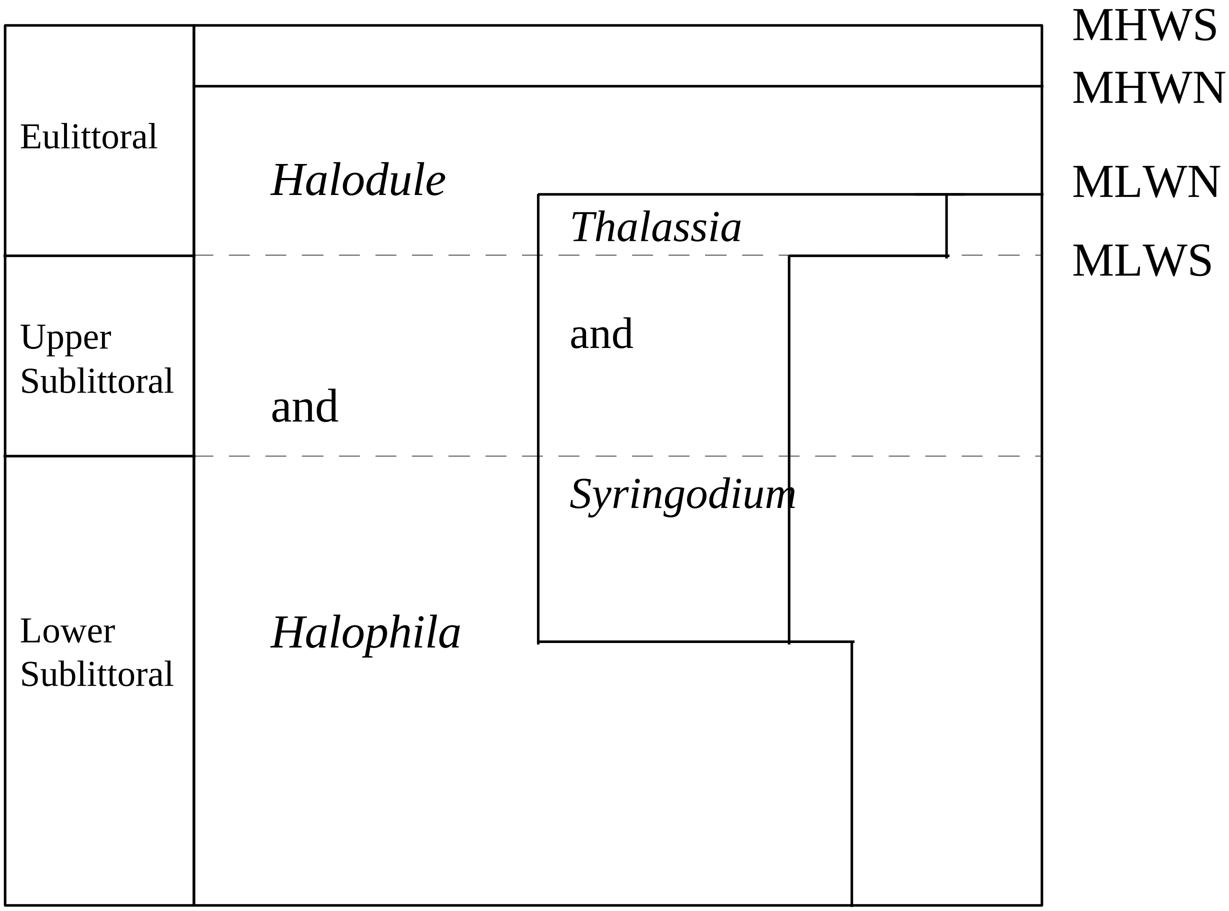

Fig. IV.B.4.7. Ideal water depth zonation for seagrass species in the CCBNEP study area (after den Hartog, 1977).

Salinity Tolerance. - Differing salinity tolerances can change species composition of a seagrass meadow, as well as affecting growth. *Halodule* has the widest range of salinity tolerance (0-70ppt, optimal ≈44ppt), followed by *Thalassia* (0-60ppt, optimal 20-36ppt) and *Syringodium* (3.5-50ppt, optimal ≈35ppt). *Ruppia* is a freshwater species with marked salinity tolerance (at least 30ppt), and has been found in an old oilfield channel in the Landcut growing in 54ppt (J.W. Tunnell, unpubl. data). Of the true seagrasses, *Halophila* has the narrowest range (13-50ppt) and is limited to brackish and saltwater areas (McMillan and Moseley, 1967; McMahan, 1968). Dwarfing of *Halodule* begins around 60ppt (Simmons, 1957). Rates of photosynthesis decline in *Thalassia* and *Syringodium* when salinities decrease below 35ppt (Zieman, 1975).

4.4.1.3 Succession

There is an ecological hierarchy within various seagrass species. *Thalassia* and *Syringodium* are medium-sized species with a fairly high tolerance to environmental variations and high competitive ability. *Halodule* and *Halophila* are small, eurybiontic species with low competition capacity, so they generally occur in habitats unsuitable for other species. These differences in ecological capacities suggest that succession will follow a similar pattern. *Halodule* and *Halophila* would be succeeded by *Thalassia* and *Syringodium* in areas with suitable environmental conditions, with *Thalassia* as the climax (Fig. IV.B.4.8) (den Hartog, 1977; Zieman, 1982).

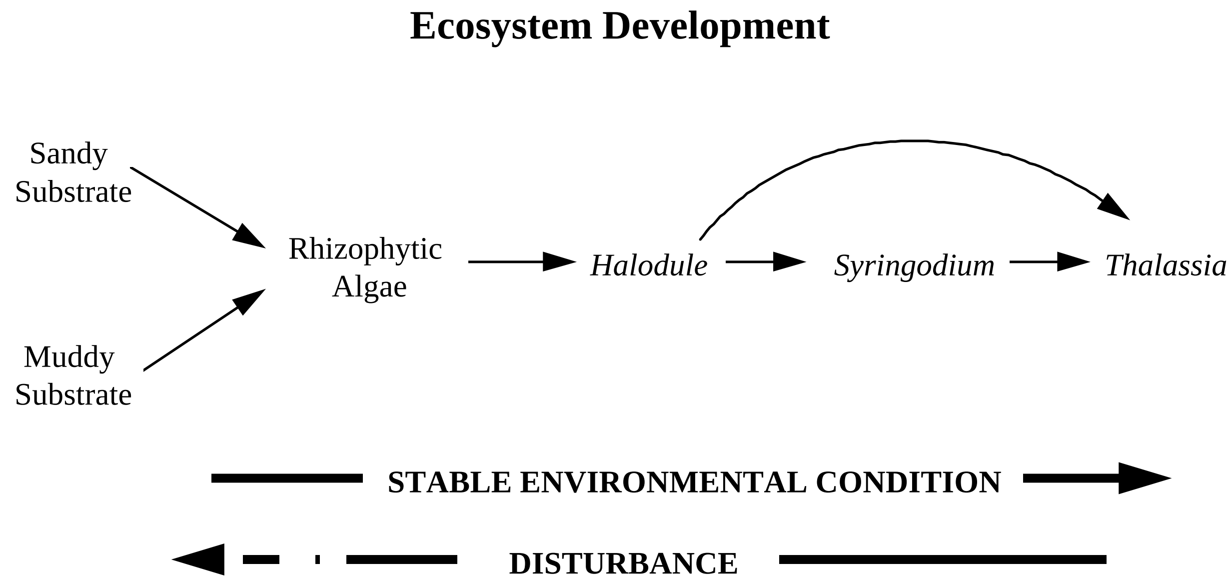

Fig. IV.B.4.8. Succession in seagrass meadows. In the absence of disturbance a *Thalassia* climax is reached (modified from Zieman, 1982).

Succession in seagrass meadows is commonly illustrated by the following recolonization scenario after a “blowout” (Fig IV.B.4.9). These localized disturbances occur following a major storm or other event (i.e.,. anchor dragging) that causes a “hole” in the meadow. If the area has sufficient current flowing in a dominant direction, the hole is enlarged by erosion on the down-current side resulting in a crescentic shape. The area at the base of the erosion scarp is highly agitated. Turbulence decreases away from the scarp and some deposition occurs. Calcareous green algae often colonize the turbulent area and help to stabilize the sediments. *Halodule* is the pioneer seagrass species and colonizes open areas readily and rapidly by either seed or vegetative branching. It further stabilizes the sediment and the leaves help buffer effects of the current to protect the integrity of the sediment surface. Although frequently absent, in some sequences *Syringodium* appears next, intermixed on either end of its distribution with *Halodule* and *Thalassia*. As sediments become stabilized, *Thalassia* begins to colonize the region. Its leaves

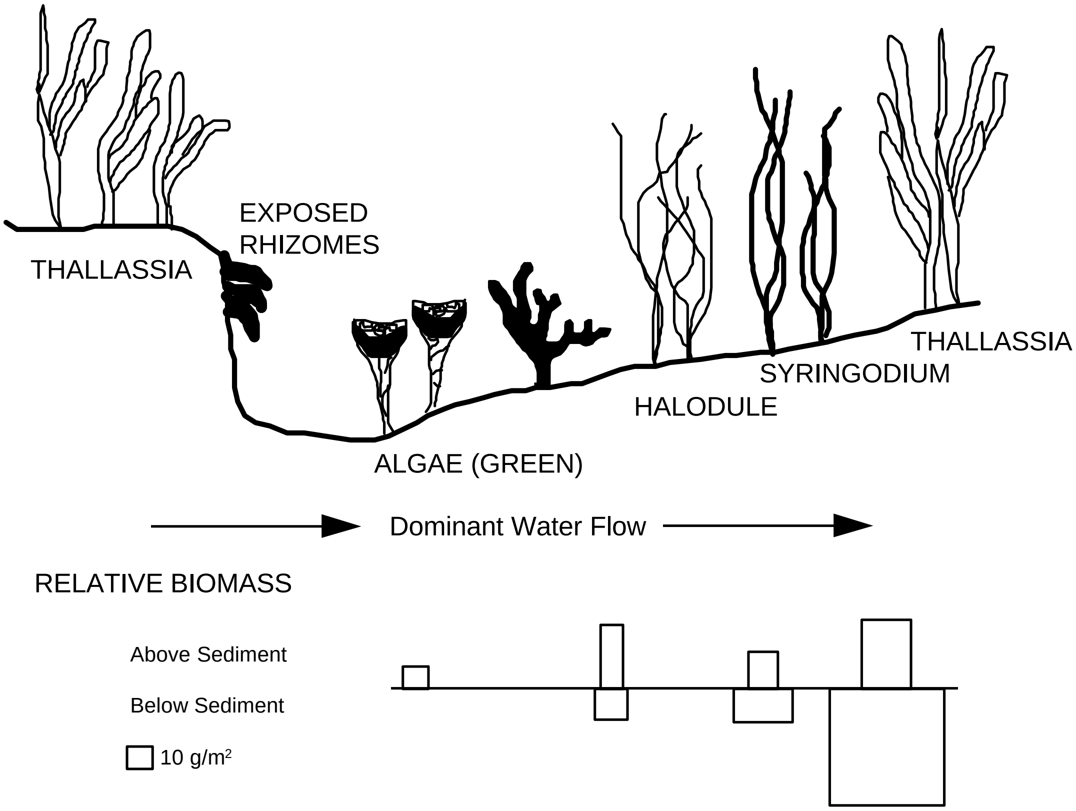

Fig. IV.B.4.9. Idealized recolonization and growth sequence following a blowout in a *Thalassia* meadow (from Zieman, 1982).

and massive root and rhizome system trap particles with greater efficiency than either *Halodule* or *Syringodium*, consequently both sediment height and organic content increase. Sediment height rises until rates of deposition and erosion are in equilibrium (Zieman, 1982).

Circé (1979) studied dynamics of seagrass colonization on recently deposited dredge disposal material in the upper Laguna Madre. He described four zones: (1) Original - deep (1-1.5 m) area with sparse *Halodule* and very fine sediments; (2) Transition - shallow (0.8 cm) area with coarser sediments and increased *Halodule* density; (3) Complete - shallow (0.7 m) area with dense *Halodule*, low water energy, and fine sediments; and, (4) Pioneer - high energy trough area which was unvegetated when the study began. In his sequence, dredge material was deposited on *Halodule* meadows establishing the Original zone. These meadows provided the material for initial colonization of what became the Transition zone. The Complete zone represents an area where *Halodule* growth has resulted in firmer substrate and calmer water. The Pioneer zone is an area of rapid colonization and sediment stabilization (Fig IV.B.4.10). Limited dispersal abilities of *Thalassia* apparently have not allowed the successional sequence to continue to a *Thalassia* climax in the upper Laguna Madre to date. The relatively recent establishment of *Syringodium* in the upper Laguna Madre suggest that succession is proceeding, albeit slowly, to the *Thalassia* climax (C. P. Onuf, pers. comm.).

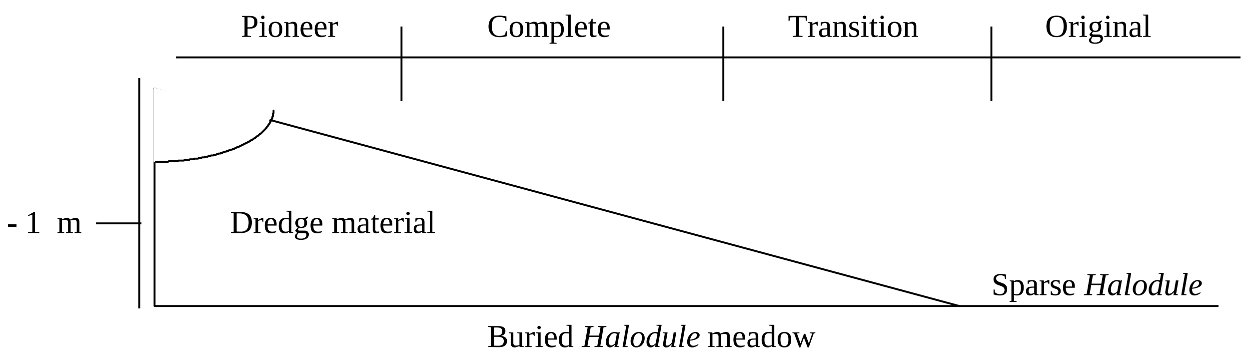

Fig. IV.B.4.10. Position of successional zones on dredge material in the upper Laguna Madre.

As succession or colonization occurs in seagrass meadows, the most obvious structural change is increase in leaf area that allows colonization by epiphytes (Zieman, 1982). No information is available concerning the structure of epiphytic, benthic, or drift algae communities in the CCBNEP study area. Communities characterized by *Halodule* and/or *Halophila* are generally a simple mosaic of the species. These communities develop rapidly in disturbed places (e.g., dredge material) and in areas where they do not constitute the final sere; epiphytic flora is composed mainly of diatoms. Epiphytic communities in *Thalassia* and *Syringodium* may contain hundreds of algae, which are usually confined to leaves. Leaf-sheaths and rhizomes of *Thalassia* are rarely populated with epiphytic algae (den Hartog, 1977). There is evidence that grazing controls epiphytic community composition. Species dominance by tightly adhering diatoms such as *Cocconeis* spp. and red algal crusts are, in part, the result of selective grazing (van Montfrans et al., 1984).

4.4.2 Invertebrate Communities

There is little information in the literature concerning structure or zonation of benthic invertebrate infauna and epifauna in seagrass meadows. This subject has not been addressed in detail in previous research in the CCBNEP study area. Voss and Voss (1960) distinguished three zones of faunal assemblages in Bimini seagrass beds of *Thalassia* mixed with *Halodule* and *Syringodium*: (1) on leaves with epiphytic flora and some fauna; (2) on and in shallow water sediments with bivalves (e.g., *Modiolus tulipus*), gastropods (e.g., *Cantharus*), and a holothurian (*Thyone* sp.); and, (3) on the sediment surface in deeper water (0.5-2.0 m) a rich fauna of large gastropods (e.g., *Murex brevifrons*), and some echinoderms. In the CCBNEP study area, *Bittium varium*, *Anachis avara*, and *Cymadusa compta* spent the majority of their time feeding at night in the upper or mid-blade regions of live *Halodule* (Morgan and Kitting, 1984). The same animals in *Thalassia* were found most often in upper live blades or *Thalassia* detritus (Kitting et al., 1984).

Stoner (1980) found that the abundance of macrobenthic animals and species richness increased with macrophytic density. He was also able to determine that sediment composition in the meadows had no effect. It has been hypothesized that species richness is a function of habitat heterogeneity, food availability, increased living space, and protection from predators which are all related to seagrass leaf density (Heck and Wetstone, 1977). Virnstein et al. (1983) also found differences in macrofaunal communities of seagrass meadows and nonvegetated areas, but emphasized they were primarily differences in abundance rather than species composition. Results from a caging experiment indicated predation by decapods and fishes was an important factor regulating densities of macrobenthos, especially epifauna. Within seagrass meadows, the epifauna are more heavily preyed upon than the infauna (Nelson, 1979). In studies from the CCBNEP study area which included both vegetated and unvegetated or sparsely vegetated sampling areas (e.g., Kreuz, 1973; Rickner, 1975), more macrofaunal species and greater numbers of organisms were usually found in densely vegetated areas.

There is also little information concerning the structure of invertebrate nekton communities in seagrass meadows within the CCBNEP study area. Hyppolitid and palaemonid shrimps have been classified as permanent residents, while penaeid shrimps and portunid crabs are seasonal residents, and use the meadows as nursery or spawning areas (Kikuchi, 1980). The diurnal structure of the communities also varies. Overall capture numbers of both shrimp and crabs were greater at night (61%) than during the day (Chaney, 1988). Gourley (1989) also collected fewer shrimp and crabs during the day (32.6%) in Redfish Bay meadows; those animals were significantly ($P<0.05$) larger than those collected at night. Zimmerman (1969) found greater numbers of *Palaemonetes pugio*, *P. intermedias*, and *Alpheus heterochaelis* in Redfish Bay during the day but all other nektonic invertebrates were more abundant at night; these species were not collected by Gourley (1989). Penaeid shrimp and palaemonids spent most of their time in upper blades of live *Thalassia* or among macroalgae in *Thalassia* meadows in Redfish Bay (Kitting et al., 1984).

4.4.3 Vertebrate Communities

Kikuchi (1980) classified fish and other nekton in *Zostera* meadows into three categories based on temporal use of the meadows: (1) permanent residents; (2) seasonal residents; and (3) transients. Permanent residents are generally small, cryptic, less mobile species which spend their entire life in the meadow. Members of the families Syngnathidae (pipefishes), Gobiidae (gobies), Blenniidae (blennies), and Ophichthidae (eels) are in this group. Seasonal residents spend their juvenile or subadult stages or spawning season in seagrass meadows. This group includes many important commercial or sport species such as Scianeidae (drum), Gerreidae (mojarras), Pomadasyidae (grunt), and Sparidae (porgy). Transients are present only infrequently and unpredictably. Representatives include large carnivores of offshore or oceanic origin such as the Carangidae (jackfish) and Scombridae (mackerel) (Zieman, 1982).

The diurnal structure of fish communities also varies. In a study of small (<150 mm) fish use of *Halodule* meadows in the upper Laguna Madre, more fish were captured during day (57.2%) than night. Of the five most abundant species, only *Cyprinodon variegatus* and *Syngnathus scovelli* were more abundant during the day (Chaney, 1988). In Redfish Bay, species composition and size class structure of both day and night fish communities were determined (Zimmerman, 1969). The nocturnal community was comprised of 14 species of large, primarily predaceous, fish, (e.g., *Cynoscion nebulosus*, *C. arenarius*, *Elops saurus*) and eight species of small "bait" fish such as *Lagodon rhomboides*, and *Anchoa* spp. The daytime community had fewer species, eight large fish, some of which were found in the nocturnal community as subadults (e.g., *L. rhomboides*, *Paralichthys lethostigma*) and six small species, some which were found as adults in the nocturnal community (e.g., *C. nebulosus*). Six species were found equally often day or night in one or the other size class (Table IV.B.4.12).

Gourley (1989) examined the structure of the small (<150 mm) fish communities of *Thalassia* and *Halodule* dominated meadows in Redfish Bay using classification analysis. Distinctive temporal and faunal groups were identified for each meadow (Fig. IV.B.4.11). The community structure of midday communities was different in each type of meadow for most of the year. Habitat differentiation broke down during the coldest months when the temporal aspect dominated. This could be related to the specific habitat requirements of winter spawning fish or to decreases in *Halodule* biomass and shoot density associated with winter cold stress. Local changes in shoot height and leaf density may operate at the species level only and not on communities (Bell and Westoby, 1986). The warm season *Halodule* fish community was characterized by *Cyprinodon variegatus*, *Sciaenops ocellatus*, juvenile syngnathids, and *Lucania parva*, while the *Thalassia* community was dominated by *Syngnathus floridae* and *Hippocampus zosterae*. The distinctive winter component of the faunal community was comprised of juvenile, non-bay spawning fish (*Lagodon rhomboides*, *Leiostomus xanthurus*). Recruiting *L. xanthurus* were ubiquitous while *L. rhomboides* were usually found in *Thalassia*.

To further complicate the situation, different taxa dominated the assemblage during day and night throughout most of the year. In most instances, species which characterized a particular time period were juveniles of species which use the seagrass meadows as nursery areas. However, during summer and fall resident nekton such as *Syngnathus scovelli*, *Gobiosoma robustum*, and *Hippocampus zosterae* dominated (Gourley, 1989).

Possible differences in utilization of structurally varied *Halodule* meadows in Redfish Bay by larval and juvenile *Sciaenops ocellatus* were investigated near Lydia Ann Island (Holt et al., 1983). Observed differences in habitat complexity, measured as water depth, plant length, and total aboveground biomass among adjacent *Halodule* meadows did not affect *S. ocellatus* density. Edge habitats in seagrass meadows containing patchy, unvegetated areas supported greatest numbers of *S. ocellatus*, reflecting a need for both open feeding areas and protection. Holt et al. (1983) concluded that patchiness was the most important element of habitat variability affecting the density of *S. ocellatus* in and around *Halodule* meadows.

4.5 Ecosystem Processes

4.5.1 Energy Flow

Seagrass meadows are among the most productive coastal ecosystems and are central to the viability of the fisheries in the CCBNEP study area. However, little of the productivity of the

Table IV.B.4.12. Alphabetized listing of diurnal species and size class structure of seagrass meadow fish communities in Redfish Bay (compiled from Zimmerman, 1969). D-day; N-night; = - equal use; ? - size class occurred by no diurnal distribution data available.

Species	Size classes	
	< 100 mm	> 100 mm
Anchoa hepsetus	N	
A. mitchilli	N	
Archosargus probatocephalus	=	N
Arius felis		N
Bagre marinus		N
Bairdiella chrysura	D	N
Brevoortia patronus	D	N
Chaetodipterus faber		D
Chilomycteris schoepfi		D
Cynoscion nebulosus	D	N
C. arenarius		N
Elops saurus		N
Eucinostomus gula	D	
Gobionellus boleosoma	=	
Gobiosoma robustum	D	
Harengula pensacolae	N	
Hippocampus zosterae	N	
Lagodon rhomboides	N	D
Leiostomus xanthurus	N	D
Lucania parva	D	
Membras martinica	N	
Menticirrhus americanus		N
Micropogon undulatus	?	=
Mugil cephalus		N
Opsanus beta		D
Orthopristis chrysoptera	=	N
Paralichthys lethostigma	N	D
Peprilus paru		D
Pogonias cromis		D
Porichthys porosissimus		N
Sciaenops ocellatus	?	=
Scomberomorus maculatus		=
Symphurus plagiusa	N	
Syngnathus floridae		D
S. scovelli	N	
Trichiurus lepturus		N

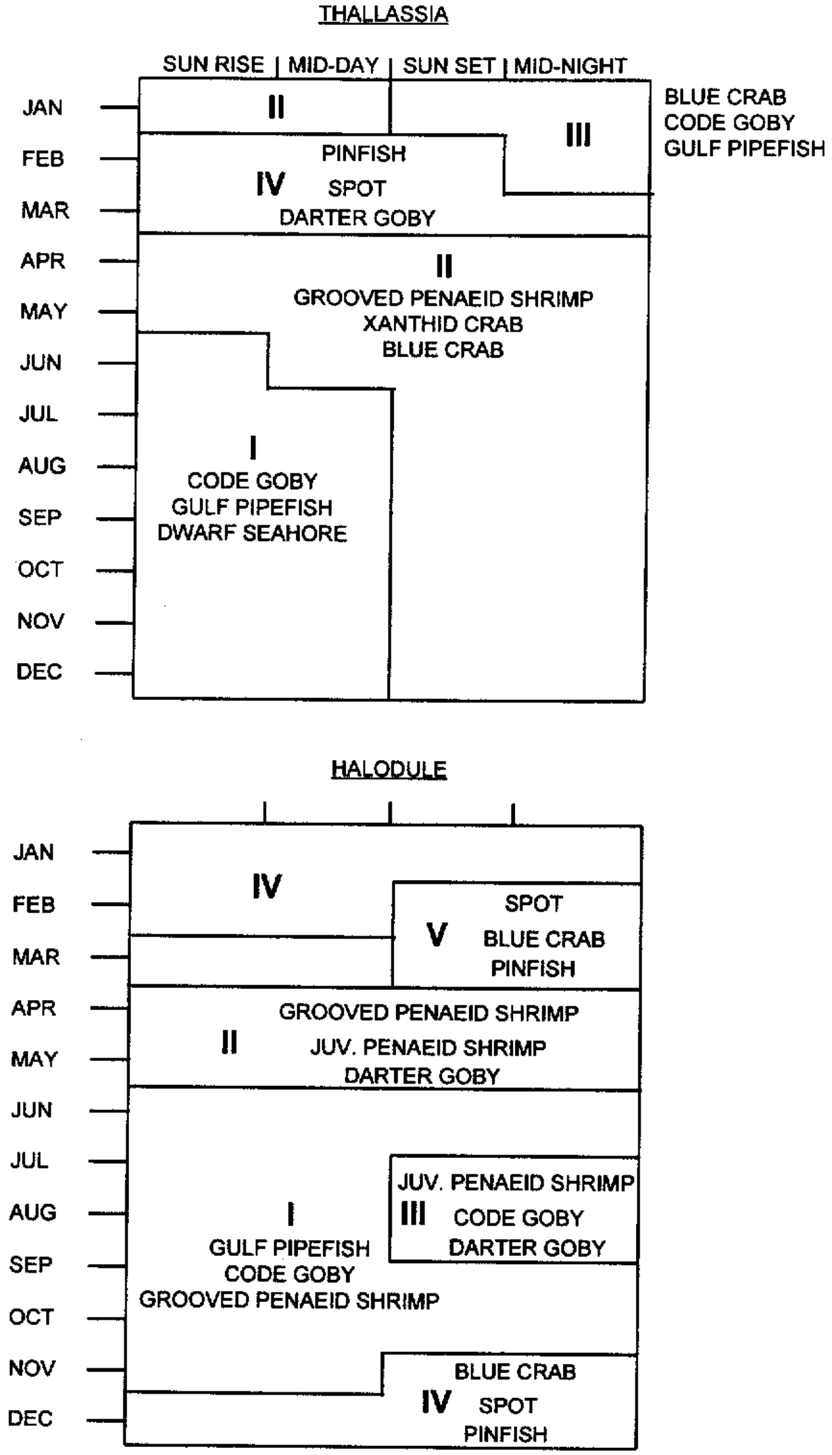

Fig. IV.B.4.11. Diagrammatic representation of the seasonal and diel distribution of dominant taxa in the *Thalassia* and *Halodule* seagrass meadow (from Gourley, 1989).

seagrasses themselves (either alive or as detritus) is used directly by consumers. Seagrass productivity has been measured using a variety of methods, making it difficult to compare results. In addition, few early researchers separated seagrass productivity from epiphyte productivity. Table IV.B.4.13 summarizes the results of previous research on productivity of seagrass species occurring in the study area.. The highest reported values (e.g., Odum 1963) represent community metabolism and reflect the production of seagrass, epiphytic algae, and benthic algae. Contribution of the seagrass component to community productivity has been estimated at only 50% in well-structured communities (den Hartog, 1979). Net above-ground production is commonly 1-4 g C m^{-2} day^{-1}, although maximum rates can be several times higher (Zieman and Wetzel, 1980).

Primary productivity of seagrasses is largely regulated by variations of light attenuation within the water column. Natural light attenuation occurs seasonally, and man-induced light attentuation occurs as a result of dredging and eutrophication. *Halodule* exhibited high rates of spring/summer leaf elongation (≥6 mm d^{-1}) and a high root:shoot ratio (≥4.0) when water clarity allowed 41-46% of surface irradiance to penetrate to the canopy, but showed signs of light stress (low elongation rates, low root:shoot ratios, biomass decrease) when surface irradiance dropped to 17-19% (Dunton, 1994). *Thalassia* shows signs of light stress at surface when surface irradiance drops to 15% but is able to survive longer than *Halodule* because of greater belowground reserves(Czerny and Dutton, 1995).

Epiphytic production often contributes most to overall productivity of seagrass meadows (Table IV.B.4.14). Productivity of *Halodule* and its epiphytes was determined in meadows in Redfish and Corpus Christi bays to test whether epiphytes contribute significant amounts of carbon to consumer diets (Morgan and Kitting, 1984). Epiphytes were 8 to 96% more productive than *Halodule* throughout the year. Absolute rates of productivity ranged from 0.53-4.12 mg C g^{-1}dry wt $h^{-1}$for epiphytes and 0.27-4.00 mg C g^{-1}dry wt h^{-1} for *Halodule*. Primary productivity for both compartments peaked in fall. Altogether, between June and December 1980, epiphytes accounted for 48-56% of total productivity per unit area.

In Mississippi Sound, sand microflora accounted for 17.5% and phytoplankton accounted for 23% of total primary productivity in *Halodule* meadows (Moncreiff et al., 1992). In the Bahamas, sand microflora accounted for 21% of the primary productivity excluding the contribution of phytoplankton (Jensen and Gibson, 1986). Overall, contribution of benthic microalgae (sand microflora, macroalgae, and epiphytes) represented the greatest portion of primary productivity in seagrass meadows. No information was found concerning contribution of sand microflora, attached or drift macroalgae, or phytoplankton to overall primary productivity of seagrass meadows in the CCBNEP study area. Increased epiphytism in shallow, nutrient-rich estuaries has been implicated in decreased seagrass productivity and increased turnover rate of seagrass blades (Fong and Harwell, 1994). Model simulation experiments using *Zostera* marina as the epiphytic substrate and the amphipod *Idotea baltica* as the epiphytic grazer indicate that grazing pressure is necessary to maintain seagrass productivity. A 50% reduction in

Table IV.B.4.13. Primary productivity values for seagrass species found in the CCBNEP study area.

Species	Location	Productivity		Source
		g C/m^2/d	mg C/g dry wt/h	
Halodule wrightii	North Carolina	0.48-2.0		Dillon, 1971
	Florida	1.1		Virnstein, 1982
			1.81	Brylinsky, 1971
	Texas		0.27-4.0	Morgan & Kitting, 1984
Syringodium filiforme	Florida	0.8-3.0		Zieman, 1982
	Virgin Islands	0.32		Zieman et al., 1979
Thalassia testudinum	Texas	0.9-9.0		Odum & Hoskin, 1958
	Florida	3.13		Odum, 1956
		10.2		Odum, 1957
		5.7-16.0	2.3-6.3	Odum, 1963
		0.35-1.14	0.36-1.3	Pomeroy, 1960
		0.9-2.5	0.13-0.25	Jones, 1968
		1.7-2.3		Zieman, 1968
			1-3	Brylinsky, 1971
	Virgin Islands	2.7		Zieman et al., 1979
	Cuba	9.3-12.5	1.7-2.3	Buesa 1972, 1974
		2.4-4.5		Odum et al., 1959
	Puerto Rico	2.5-4.5		Odum et al., 1959
	Jamaica	1.9-3.0		Greenway, 1974
	Bermuda	5.6 (leaves); 7.2 (total plant)		Patriquin, 1973
	Barbados	0.5-3.0		Patriquin, 1972: 1973

Table IV.B.4.14. Percent contribution of epiphytic algae to combined seagrass blade epiphytic production (modified from Moncreiff et al., 1992).

Location	Seagrass Species	Percentage of Total Production	Source
North Carolina	*Zostera marina*	18	Penhale, 1977
Massachusetts	*Zostera marina*	27-50	Mazella and Alberte, 1986
Florida	*Halodule wrightii,* *Syringodium filiforme,* *Thalassia testudinum*	6	Heffernan and Gibson, 1983
Florida, Bahamas	*Halodule wrightii,* *Syringodium filiforme,* *Thalassia testudinum*	56	Jensen and Gibson, 1986
Mississippi Sound	*Halodule wrightii*	78	Moncreiff et al., 1992
Texas	*Halodule wrightii*	48-56	Morgan and Kitting, 1983
Indonesia	*Halodule uninervis,* *Thalassia hemprichii*	36	Lindeboom and Sandee, 1989

grazing pressure resulted in a 40% decrease in seagrass productivity even though plant biomass dynamics (i.e.,. annual cycles) remained stable during the 10 year iteration of the model. However, a 75% reduction in grazing pressure resulted in a gradual loss of the vascular plant compartment over a 4-5 year period. When grazers were eliminated, loss of seagrasses accelerated, occurring in less than 4 years (van Montfrans et al., 1984).

Most carbon fixed by seagrasses is decomposed within the grassbed, but some is transported out of meadows by currents and storms. Export of seagrass material is a common phenomenon, with seagrass material observed in the deep sea and at great distances from the source of production. Because of the scarcity of food in deeper waters, quantitatively it could be an important food source. In the Virgin Islands, most detached blades of *Thalassia* remained on the bottom and were only transported as bedload. Export from *Thalassia* was estimated at only about 1% of production. Conversely, *Syringodium* was transported near the surface and 60-100% of its production was transported out of the system (Zieman et al., 1979).

4.5.2 Trophic Levels and Food Web

Although seagrass meadow food webs have traditionally been considered detritus-based, relative roles of the detrial and microalgae-epiphytic grazing pathways is under scrutiny. In a meadow, importance of one or the other pathways is dependent on local conditions and consumer community composition. In general, seagrasses and associated epiphytes transfer energy to higher trophic levels by: (1) direct grazing, (2) detrital food webs, or (3) export of material to other systems (Zieman and Zieman, 1989). Because many consumers in seagrass meadows are opportunistic (omnivorous), structure of the trophic network changes dynamically in reponse to seasonal variability in abundance and species composition of both predator and prey compartments. Predation pressure on a particular prey species may change because of relative abundance of other potential prey species. Diets of many fish change as they grow and may change greatly from night to day. This is probably due to changes in availability of prey species resulting from circadian rhythms of the invertebrates, which in turn, affects behavior of the predators (Kikuchi and Pérès, 1977). A generalized food chain for seagrass meadows in the study area is presented in Figure IV.B.4.12.

4.5.3 Nutrient Cycling

Although highly productive, seagrass meadows are often found in low-nutrient environments. It is conceivable that a high degree of nutrient conservation and recycling occurs in seagrass communities (Capone and Taylor, 1980). Because they occupy both sediments and water column, there has been controversy about whether nutrients were taken in by the leaves or by the roots (Zieman and Zieman, 1989); it appears the actual source is dependent on uptake kinetics and and nutrient concentration gradients (McRoy and McMillan, 1977). *Zostera* is capable of taking in nutrients through both leaves and roots and translocates ammonium and phosphate from the sediments to the leaves where they are excreted into surrounding waters (McRoy and Barsdate, 1970). Sediment interstitial water from rhizospheres of dense *Ruppia*-sparse *Halodule* and monotypic dense *Halodule* meadows in Redfish Bay and monotypic *Ruppia* in the Laguna Madre were analyzed (Pulich, 1985). During the period of rapid growth, the mixed meadow contained up to 10 µM of nitrate while the *Halodule* meadow contained only a trace (<1 µM). By fall, NH_4^+ and PO_4^{3-} were significantly ($P<0.05$) lower in the *Halodule* meadow while in the mixed meadow, NO_3 was generally undetectable, NH_4^+ was somewhat lower, and PO_4^3 was unchanged. Nitrate levels in the monotypic *Ruppia* meadow declined from 15 µM to 5 µM between May and September. Fertilizer addition experiments indicated that *Halodule* requires organic-rich sediments to obtain its nutrients, while *Ruppia* is adapted to low nutrient sediments, suggesting that the relative importance of sediment uptake of nutrients in *Halodule* is greater than water column uptake. While *Ruppia* obviously uses sediment nutrients, it would be outcompeted by *Halodule* in organic-rich sediments. Growth of *Thalassia* has been correlated with concentration of NH_4^+ in the sediments (Patriquin, 1972). No information concerning the relative importance of sediment vs water column uptake for the other species of seagrasses in the study area.

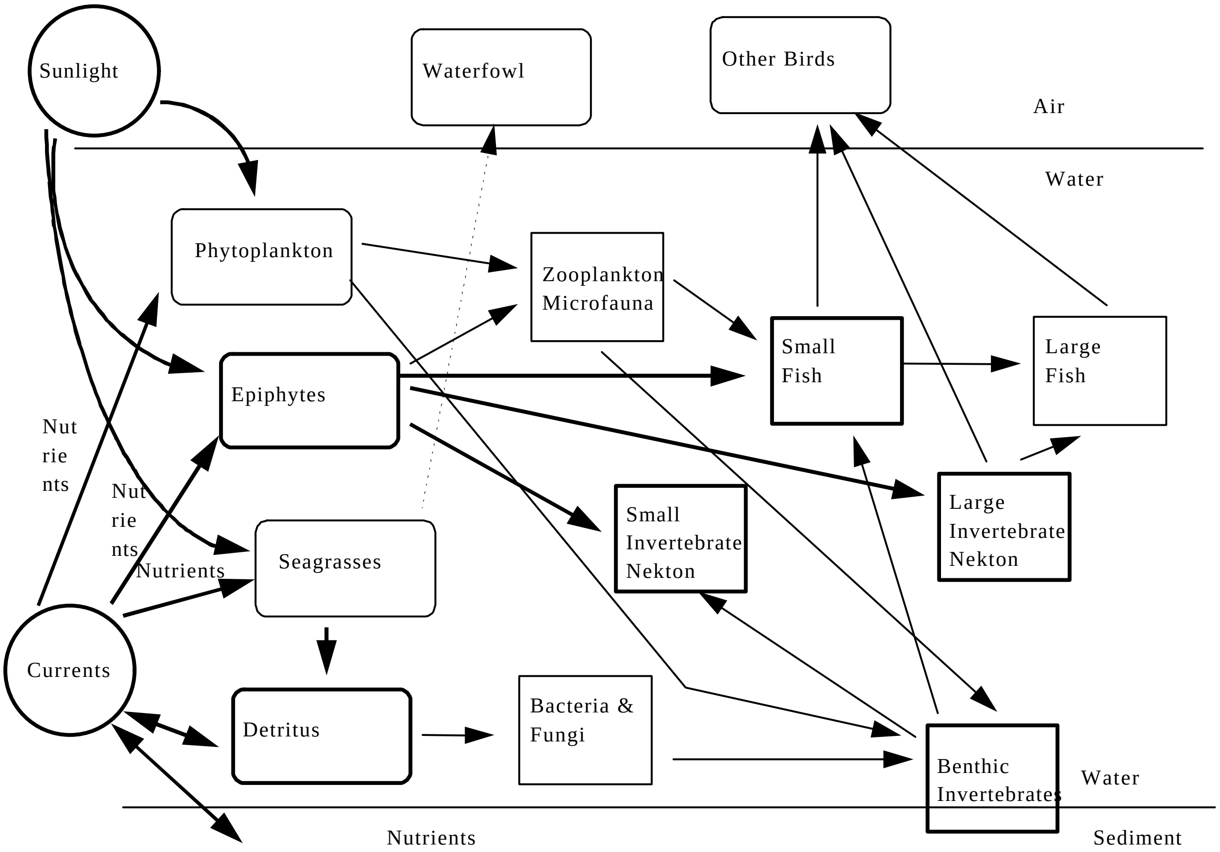

Fig. IV.B.4.12. Generalized food web for seagrass meadows in CCBNEP study area. The weight of the arrows and boxes reflect the relative importance of each compartment and pathway. Dotted lines indicated seasonal components.

Studies on nutrient cycling in seagrasses concentrated on nitrogen and phosphorus since they are primary constituents of plant material along with carbon. Three sources of nitrogen are available: (1) microbially recycled nitrogen from organic matter in the sediments; (2) dissolved ammonium and nitrate in the water column; and, (3) microbial or blue-green algal fixation of dissoved N_2. Organic material (detritus) is converted to ammonia by bacteria in the anoxic zone that begins a few millimeters below the sediment surface. Ammonia which is not bound by biologic uptake or chemical adsorption diffuses up to the aerobic zone where it either enters the water column or is converted to nitrate by nitrifying bacteria. Nitrate is either rapidly assimilated or denitrifyed to N_2 by bacteria (Zieman and Zieman, 1989). In *Thalassia*, recycled organic matter has been identified as the primary source of nitrogen for leaf growth, however, nitrogen fixed in the sediment could meet 20-50% of the plants requirements (Capone and Taylor, 1980). However, in another study, microbial fixation contributed most to epiphyte growth in *Thalassia* (Capone et al., 1979). *Halodule* dominated beds in Redfish bay showed consistently higher H_2S, indicating that reducing conditions necessary for microbial nitrogen recycling were nearly continuous; low H_2S and a significant steady-state pool of nitrate in *Ruppia* sediments indicated microbial recycling of organic matter was much more significant in *Halodule* meadows than in *Ruppia* meadows (Pulich, 1985).

The source of inorganic phosphorus is dissolved orthophosphate (PO_4), derived either from organic matter or from weathering of minerals, some of which are biologically precipitated (Zieman and Zieman, 1989). Phosphorus is relatively unavailable to plants under anaerobic conditions because it is precipitated into insoluble phosphates of iron, calcium, and aluminum (Mitsch and Gosselink, 1986). Water column concentrations in tropical areas are normally low, while sediment concentrations are often high. However, since much of the phosphate in sediments is undissolved and unavailable to plants, the water column is probably the primary source of phosphate to seagrasses (Patriquin, 1972). The prevalence of anoxic sediments in *Halodule* meadows in Redfish Bay and relatively steady concentrations of phosphate (Pulich, 1985) suggest that sediment phosphate is relatively unavailable to seagrasses in the study area.

Nutrient exchange experiments on *Thalassia*, *Ruppia*, and *Halodule* collected from Redfish Bay indicated that exchange rates for carbon, nitrogen, and phosphorus were larger in magnitude than those of emergent systems; this underscores the importance of seagrass meadows as sources of nutrients to other estuarine systems (Armstrong and Gordon, 1979). All experiments were conducted under conditions mimicking the seasons (water temperature, light intensity) and when seagrasses were dying and decomposing. Decomposition occurred under aerobic conditions only. Exchange rates for *Thalassia* indicated that both soluble and particulate organic compounds were exported during all seasons except winter. Total organic carbon was taken up in the *Thalassia* and *Ruppia* system, but exported from the *Halodule* system in all seasons but winter. Soluble nitrogen compounds were exported from all systems as ammonia during summer when conditions favored rapid decomposition. During all seasons, nitrite and nitrate nitrogen and all forms of phosphorus were exchanged at very low rates. The exception was particulate total phosphorus in *Thalassia* under summer decomposition conditions. Epiphytic algae consumed most of the oxidized forms of nitrogen and the available forms of phosphorus. During winter when growth is slow, soluble organic carbon only was exported while organic forms of nitrogen were not.

5.5.4 Linkages With Other Systems

Because seagrass meadows are aquatic habitats, they interact primarily with other aquatic habitats but also with some semi-terrestrial habitats as well. They are often found in the subtidal areas below tidal flats, and interface with salt marsh habitats as well. Little is known about the interactions of the faunas of the two habitats. Coastal marshes provide nursery shelter for larval nekton in much the same way that seagrasses do, so in areas where these habitats are in close proximity, a variety of faunal interactions are possible. In the upper Laguna Madre, polychaete diversity and relative abundance was greater on a tidal flat near a seagrass meadow than on a tidal flat without a nearby seagrass meadow (Withers, 1994). It seems likely that seagrass meadows can provide a source of benthic invertebrates which may colonize both tidal flat and saltmarsh sediments as well as nektonic consumers. Seagrass meadows are linked with upland pothole wetlands in the Rio Grande Valley providing feeding areas for a variety of waterfowl (e.g., Redhead Ducks) which use the potholes as resting and drinking habitats. They are also linked to a variety of other upland habitats (e.g., barrier island grasslands, rivers, freshwater marshes) by wading and other birds which use them as feeding habitats. Seagrasses are important to a variety of fish and other nekton (i.e.,. shrimp) which spawn in open bay or offshore waters. Many of the larvae and juveniles of these organisms depend on seagrass meadows for protection and food while they grow to maturity. Many fish and nekton which spend either day or night in non-seagrass habitats are found feeding in seagrass meadows.

Nutrient and detritus export link seagrass beds to tidal flat, coastal marsh, open bay, offshore,and even deep ocean habitats. Large rafts of decaying seagrasses can be found against virtually every shoreline during the late fall and winter, and particularly after strong storms. This detritus is probably the most important source of organic carbon in tidal flat systems and bay margin environments. Floating detritus eventually sinks, nourishing the nutrient-poor bay bottom, offshore bottom, and eventually deep ocean troughs. Blades of *Syringodium* and *Thalassia* were found in nearly all of the 5,000 bottom photographs taken in the Virgin Islands basins at depths averaging 3,500 m (Roper and Brundage, 1972; cited in Zieman and Zieman, 1989). Terrestrial runoff may eventually find its way into seagrass meadows, providing nutrients and sediments.

The greatest threats to seagrass meadows in the CCBNEP study area are dramatically illustrated by loss of seagrasses in the upper Laguna Madre caused by the brown tide. Light attenuation, whether from turbidity caused by maintanence dredging and boat traffic, or from long-standing algal blooms, can destroy many square kilometers of seagrass meadows in a relatively short period of time (3-5 years). Other threats include destruction caused by shallow-water boat traffic and propwash, dredging and dredge material deposition, coastal development, particularly marinas and canal housing developments, nutrient enrichment via point and non-point source pollution, chemical and industrial contaminants, and oil spills.

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HABITAT 5 : COASTAL MARSHES

5.1 Physical Settings & Processes

5.1.1 Distribution within Project Area

Coastal marshes are intertidal areas between upland and estuarine/marine systems. Species composition often contains organisms from upland and estuarine systems and species adapted to dynamic hydrologic regimes (Wiegert et al., 1981). Extensive coastal marshes occur in the northern part of the CCBNEP study area where freshwater inflow and precipitation are higher than in the southern portion. Coastal marshes are replaced by extensive wind tidal flats from Mustang Island southward, due to lower precipitation and higher evaporation rates (Brown et al., 1976).

Two types of coastal marshes have been characterized within the study area based on geologic formation of their sediment and hydrologic sources: deltaic marshes dependent upon riverine freshwater and sediment flow at the mouths of rivers; and, tidal marshes located on flood-tidal deltas near natural passes to the Gulf of Mexico and along bay shorelines. Deltaic marshes are located within the Nueces, Aransas, and Mission delta plains. Wetland plant composition and abundance vary based on salinity; the relative coverage of salt, brackish, and freshwater marsh communities are different among deltas, depending on salinities and freshwater inflow. Tidal marshes typically exhibit narrow bands of vegetation zonation along bay shorelines and tidal creeks, depending on shoreline slope and degree of tidal influence. Tidal marshes occur along parts of the lee sides of Matagorda, St. Joseph, and Mustang Islands, and are extensive along Blackjack Peninsula and Harbor Island (Brown et al., 1976; McGowen et al., 1976). Some marshes exhibit characteristics of both types; small tidal deltas have developed between bay-estuary-lagoon systems at passes between Oso and Corpus Christi Bays, upper Laguna Madre and Corpus Christi Bay, Redfish and Aransas Bays, and Mission and Copano Bays (Brown et al., 1976).

Coastal marshes occur on Fluvial-Deltaic System or Barrier-Strandplain System deposits of either Modern-Holocene or Pleistocene systems (Brown et al., 1976; McGowen et al., 1976). In Modern-Holocene, Fluvial-Deltaic Systems coastal marshes have developed on bayhead deltas of the Nueces, Aransas-Chiltipin, and Mission tributaries (Brown et al., 1976). These coastal marshes are similar in composition, history and general characteristics to the Guadalupe bayhead delta north of the CCBNEP study area (Donaldson et al., 1970). Depending on the freshwater inflow potential of the associated rivers, salt and brackish marshes may prograde into freshwater marshes further inland (Nueces Delta) or barren wind-tidal flats at elevations above 0.3-0.6 m above MSL (mean sea level) (Oso and Baffin Bays); however, freshwater marshes are poorly developed in this area (Brown et al., 1976). Small fan deltas have prograded into bay systems along the northern Nueces Bay shoreline (Gum Hollow Delta) and Oso Bay, but there are no extensive marshes.

Wetlands associated within the Modern-Holocene, Barrier-Strandplain System are principally salt marshes or wind tidal flats within the CCBNEP study area (Brown et al., 1976; McGowen et al., 1976). Salt marshes are typically monotypic stands of smooth cordgrass (*Spartina alterniflora*) in the intertidal zone and a variety of salt-tolerant grasses and forbs interspersed with barren tidal flats in the higher marshes. Thin, discontinuous, fringe marshes occur along Allyns Bight, Mud, and Lydia Ann islands, and Shamrock Cove. Extensive marshes historically covered Harbor Island tidal-flood delta prior to commercial development (Brown et al., 1976; McGowen et al., 1976). Grass-covered, mud-filled tidal creeks which cut into Pleistocene deposits occur on the northwest shore of St. Charles Bay and Port Bay. Tidal creeks eroded through sheet sands from recent and relict barrier island formations may connect to depressional wetlands within the mainland (Brown et al., 1976).

5.1.2 Historical Development

Coastal marshes commonly develop in the presence of several factors: (1) gradual slope, (2) low relief, (3) periodic flooding from tidal and/or freshwater inflow, and (4) protection from high-energy processes. Once coastal marshes become established, their features may change periodically from the constant interaction between water and sediment fluxes and vegetation dynamics (Weigert et al., 1981). Brown et al. (1976) described a variety of landforms on which marshes developed along the Texas coast: deltaic marshes formed on flood-tidal deltas, floodplains of principal rivers, and bayhead deltas; tidal marshes formed along barrier island shorelines, washover-channel margin, mainland shorelines, and abandoned tidal creeks.

Most present coastal marshes began forming about 2,800-2,500 YBP as sea levels reached their approximate present level. Brackish and freshwater marshes developed on delta plains, river valleys and fan deltas whereas salt marshes and wind-tidal flats developed along bay and barrier island margins (Brown et al., 1976, McGowen et al., 1976). Delta formation and expansion varied for each river system and was regulated by the amount of sediment discharge and depth of nearshore bay waters. The Nueces Delta has prograded almost 16 km (10 mi) while the Aransas and Mission River deltas extended 4.8 and 8.0 km (3 and 5 miles) respectively. Historically, Gum Hollow fan delta sediment discharge was minor; however, progradation recently increased due to human activities upstream. Other small fan deltas occur in the CCBNEP study area at the terminus of headward-eroding streams.

5.1.3 Physiography

Coastal marshes are shaped by complex interactions of sediment and shoreline structure, tidal and freshwater dynamics, climate, and vegetation structure. Plant zonation is often used as the primary feature that exhibits changes of elevation, salinity, and nutrient availability across these gradients (Fig. IV.B.5.1).

Physiographic features may change gradually due to accretion and erosional processes or abruptly due to storm surges or flooding events. Coastal marshes are systems where change is an integral part of function and structure. Long-term processes, such as sediment accretion and coastal submergence (a combination of sea level rise and regional subsidence), often balance each other in a natural coastal marsh system. Local changes in vegetation composition, tidal

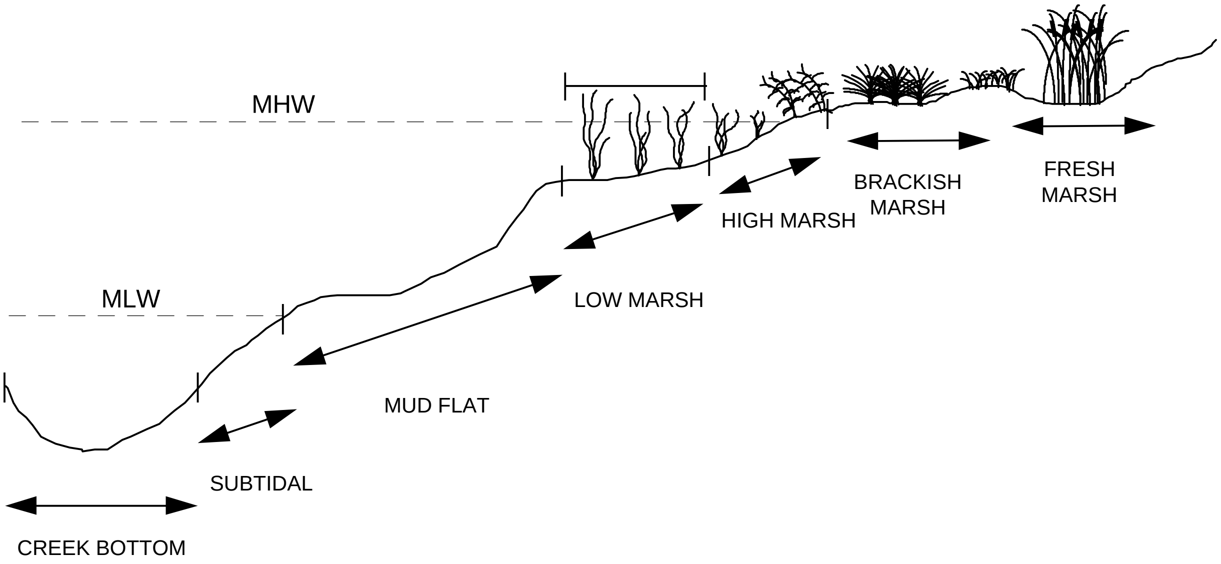


Fig. IV.B.5.1. Plant zonation in coastal marshes indicating elevations of various zones.

creek abandonment or development may be occurring within the coastal marsh (Mitsch and Gosselink, 1993) .

5.1.4 Geology & Soils

Two types of coastal marshes, deltaic and tidal, have been delineated in the CCBNEP study area by geologic formation of substrates. Sediment composition deposited in deltaic environments depends upon types of soils eroded by rivers. Bedload sands are typically deposited at river mouths and subsequently form delta-front sand deposits. Finer sediments are carried further into estuaries and deposited on bay bottoms as river flow decreases, and produces prodelta mud deposits. Progradation of deltas occurs as this process is repeated and levees are formed along discharge channels. These levees direct water flow across the delta under normal river discharge and are either built up or eroded during periods of river flooding. Sediments are deposited in interdistributary environments adjacent to levees, increase elevation, and aid deltaic marsh formation. Sediment composition changes from low to high marsh; low marsh sediments are generally dark gray mud or muddy-sand, whereas sand content increases in higher marshes (Brown et al., 1976).

Tidal marsh sediments are chiefly marine in origin and are deposited by tidal action through natural passes in barrier islands. Sediment composition varies according to distance from the pass, primarily shell and sand near mouths of channels grading to finer-grained sediments at distal, bayward parts of tidal deltas. Harbor Island is the largest tidal-deltaic marsh in the CCBNEP study area and Cedar Bayou is second largest; both sites support emergent and submergent wetlands. Several relict tidal deltas occur behind the southern part of Mustang Island and upper Laguna Madre; washover channels and fans extend through the island, wind-tidal flats behind the island, and seagrass meadows and sandy bottom in the Laguna Madre (Brown et al., 1976).

5.1.5 Hydrology & Chemistry

Coastal marshes are hydrologically driven systems; pulses of marine tidal cycles and riverine and upland flooding determine salinity regimes of coastal marsh systems (Mitsch and Gosselink, 1993). Low tidal ranges and minor freshwater inflows along the central Texas result in a unique complement of driving factors coast in relation to other coastal marsh systems of eastern United States (Brown et al., 1976; McGowen et al., 1976; Mitsch and Gosselink, 1993). Whereas tidal energy transports marine water and rivers deposit freshwater into the estuary, water levels may be more affected by wind forces in coastal marshes. Therefore, wind direction and intensity often play a more dominant role in water movement and exchange in the CCBNEP study area (White, et al., 1983). Section II.E (this volume) discusses overall hydrology and chemistry of the CCBNEP study area at the regional level. Currently, principal tidal exchange between Gulf waters and the estuaries occur at Aransas Pass between St. Joseph and Mustang Island with much less exchange at Cedar Bayou between Matagorda and St. Joseph Islands (Brown et al., 1976; McGowen et al., 1976). Due to historic tidal exchange at other passes, coastal marsh development and establishment occurred at several locations behind these barrier islands.

Natural freshwater inflows occur at the mouths of the Nueces, Aransas, and Mission Rivers within the CCBNEP study area (Brown et al., 1976), and the San Antonio-Guadalupe Rivers to the north (McGowen et al., 1976). Smaller inflows occur via several creeks emptying into bays and larger rivers; they add significant freshwater during periods of high rainfall. Southeasterly winds predominate during most of the year and affect water levels daily and seasonally. During the day, wind may move bay waters out of southeasterly portions of the bay to northwesterly shores; at night, water levels may change due to lighter wind velocity. Seasonally, water levels may remain higher in northwestern coastal marshes of a bay system during prevailing southeasterly wind conditions, whereas levels fall dramatically following winter storms with continuous north and northwesterly winds. In protected areas, this localized effect has direct influence on degree of inundation and salinity ranges in coastal marshes, and indirectly affects vegetation and animals utilizing marshes (Brown et al., 1976; McGowen et al., 1976).

In a five-year study in the Nueces River Delta marsh, hydrologic dynamics exhibited large variation in level of submergence over time (Fig. IV.B.5.2). The marsh was partially or totally submerged 84% of all days sampled. Totally emergence occurred only 6 times in 4 years; during winter low tides, and once in late spring and late summer. Mean water chemistry parameters were: dissolved oxygen - 7.1 mg l^{-1} (5.1-14.4 mg l^{-1}); pH - 8.4 (7.0-10.4); water temperature - 22.9° C (6.4 - 34.7° C); and, salinity - 22.0 ppt (0-50 ppt).

On a broad scale, salinities in coastal marshes are dictated by the relationship of marsh location to tidal passes and river discharge. Salinities also differ within a marsh and are dependent upon slope, drainage, and vegetative cover. Salinities in a given coastal marsh vary both spatially across elevational gradients and temporally, within a year and among years. Seasonal differences in salinity generally dictate plant species composition and relative abundance; but, more

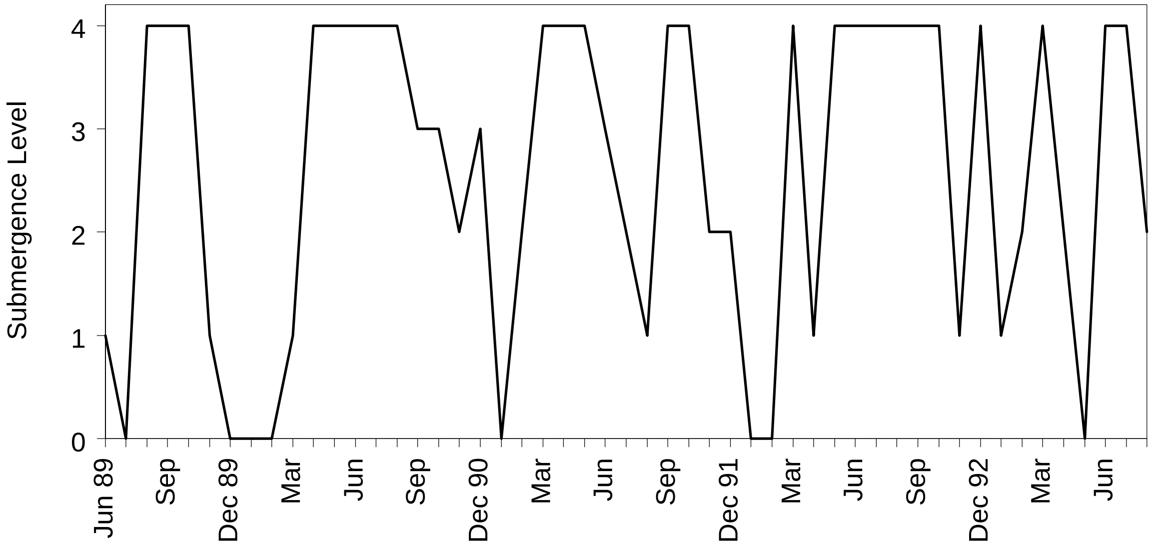


Fig. IV.B.5.2. Submergence levels of a marsh in the Nueces River delta. 0 = totally emergent; 1 = up to 25% submerged; 2 = up to 50% submerged; 3 = up to 75% submerged; 4 = totally submerged (Nicolau, 1995).

importantly, timing and duration of extreme salinities most likely determines a species' presence or absence (Mitsch and Gosselink, 1993). Because of the variability of precipitation within and among years in the CCBNEP study area, most intertidal areas exhibit low species richness; one or two plant species predominate at a given elevation range (Brown, et al., 1976). Low topographic relief in coastal marshes results in slow drainage with water becoming trapped in shallow depressions and behind natural levees. High insolation rates in south Texas throughout most of the year increases evaporation rates, resulting in increased salinities. Although evapotranspiration rates are higher in densely vegetated marshes, the indirect effect of vegetation shading the water may actually reduce evaporation and ameliorate water and soil salinities within the marsh (Bertness, et al., 1992).

Water and soil salinities can be quite different in coastal marsh systems and are primarily related to timing and duration of inundation and exposure cycles (Mitsch and Gosselink, 1993). Estuarine water saturating the marsh soil during inundation may not significantly increase soil salinity at low water levels during cool, winter months; however, soil salinity can increase dramatically during exposure of the marsh surface, due to high evaporation rates in summer. Prolonged exposure to heat and drying by wind will evaporate available soil porewater increasing soil salinities to lethal levels (> 70ppt for most organisms) in exposed coastal marsh sediments. Higher salinity levels predominate during summer and drought periods in intertidal sediments in the lower part of the CCBNEP study area; they are the primary reason for very low vegetative cover and high areal expanse of wind tidal flats.

5.2 Producers And Decomposers

5.2.1 Primary Producers

Whereas phytoplankton and benthic algae are major primary producers in the water column and seagrasses, and macroalgae predominate in the estuarine subtidal wetlands, vascular emergent plants predominate (Fig. IV.B.5.3) as major producers in coastal marshes (Wiegert et al., 1981). *Spartina alterniflora* (smooth cordgrass) is typically the key vascular plant species in intertidal, low marshes, often occurring in monotypic stands. This species is able to tolerate moderate to high salinities (20ppt to 35ppt) and frequent tidal inundation. Production rates vary for *S. alterniflora* in relation to these factors. Three growth forms (tall, medium, and short) have been described with productivity rates; above-ground biomass varies from high (1450 g dry wt/m^2) to low (280 g dry wt/m^2) values, respectively (Table IV.B.5.1). The tall growth form is typically found at lower elevations with frequent tidal inundation. Tidal flushing removes excess or toxic levels of salts and prevents the buildup of detritus and dead *S. alterniflora* stems and leaves. Medium growth forms are located further from the tidal creeks or upslope. The short growth form is generally found in areas that are either infrequently inundated, or must tolerate standing water for extended periods. Changes in flushing frequency affect nutrient availability and soil salinities. The short growth form, which exhibits lower productivity and biomass generally occurs in most Texas coastal marshes and in the CCBNEP study area, although higher production and biomass may occur under optimum conditions.

Spartina patens (marshhay cordgrass) typically predominates at higher elevations in coastal marshes of the eastern US and northern Gulf States. However, few areas in the CCBNEP study area support pure stands of *S. patens*. *Spartina patens* withstands frequent inundation, however, moderate to high salinities reduce the normally high production of above-ground biomass. *Distichlis spicata* (saltgrass) predominates the high marsh in the CCBNEP study area, in part because it tolerates periodic inundation and high soil salinities. In coastal marshes in North America, *D. spicata* often colonizes areas where some type of disturbance has removed or destroyed *S. patens*, *Juncus roemerianus* (black needlerush) or the short growth form of *S. alterniflora* (Bertness, 1991a, 1991b). Tolerance to higher salinities allows *D. spicata* to rapidly establish in these higher salinity bare areas. An example of re-establishment has been documented within the CCBNEP area at Chiltipin Creek (Tunnell et al., 1994). *Distichlis spicata* increased, with a concomitant decrease in bare areas for two years following an oil spill on a high marsh. If the original species are still available for recolonization, replacement of *D. spicata* usually occurs in two to four years by more competitive species. Both woody perennials (e.g., *Borrichia frutescens*) and other climax vegetation increased in cover, whereas *D. spicata* decreased. High soil salinities in summer and drought years combined with low tidal ranges may explain why *D. spicata* prevails in the high marsh in the CCBNEP study area.

Other vascular plant species may predominate locally in the high coastal marsh with *D. spicata*; they often comprise the ecotone species assemblage between high marsh and uplands in the CCBNEP study area. *Monanthochloe littoralis* (shoregrass) may form monotypic stands in infrequently flooded high marshes, and pure stands of *S. spartinae* occur on still higher, poor soil areas. Both *Salicornia bigelovii* and *S. virginica* (annual and perennial saltwort) can tolerate

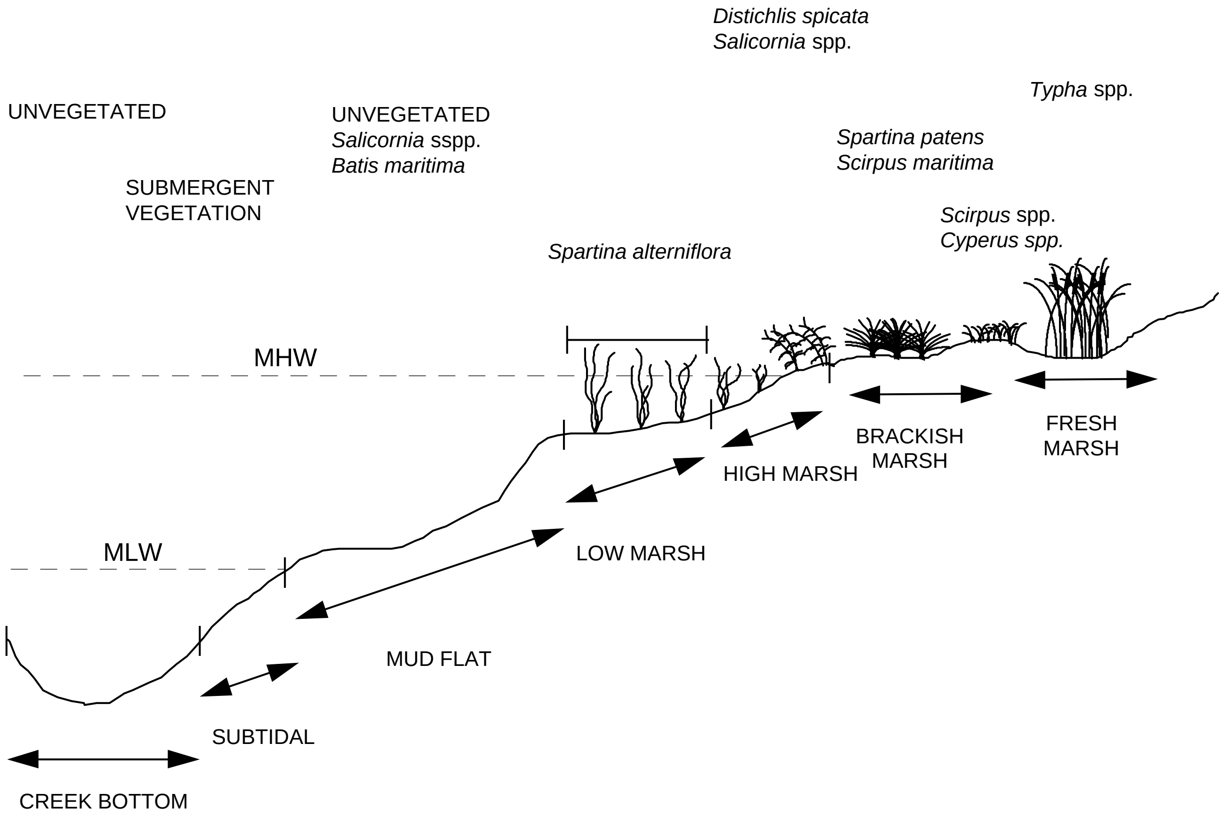


Fig. IV.B.5.3. Typical zonation pattern of coastal marshes for Gulf coast of Texas (adapted from Brown et al., 1976).

high soil salinities but are negatively affected by prolonged inundation. *Batis maritima* (glasswort) and several species of sedges (e.g., *Carex* spp., *Cyperus* spp., *Scirpus* spp.) occur in varying amounts, depending upon species specific inundation and salinity tolerances. Prominent forbs in the high marsh and ecotone include: *Borrichia frutescens* (sea-oxeye daisy), *Haplopappus phyllocephalus* (camphor daisy), *Limonium nashii* (sea lavender), *Iva* spp. (marsh elder), *Suaeda linearis* (sea-blite), and *Lycium carolinianum* (wolfberry). Many of these species are tolerant of poor soils and are found along bayshore ridges, barrier islands and dredge material islands.

Non-vascular primary producers include phytoplankton, benthic microflora, epibenthic and epiphytic algae, and microalgae. Although no comprehensive studies have investigated the proportion of primary production attributable to these groups in the CCBNEP study area, research results from other coastal marshes indicate they may play a significant role in seasonal primary production. The microalgae assemblage in a Georgia salt marsh was comprised of several hundred species of pennate diatoms contributing 75 to 93% of total algal biomass

Table IV.B.5.1. Peak biomass and annual production data for *Spartina alterniflora*, *S. patens*, and *Distichlis spicata* from published information.

Species	Height Category	Peak Biomass (g dry wt/m^2)	Annual Production (g dry wt/m^2)	Location	Source
S. alterniflora			6,250	GA	Weigert & Evans, 1975
	Tall	1,450		NC	Marshall, 1970
	Medium	680			
	Short	450			
	Tall		2,650	LA	Day et al., 1973
	Short		1,484		
	Tall		1,964	MS	De la Cruz, 1974
	Short		1,090		
	Tall	420	720	MA	Valiela et al., 1975
	Short	280	360		
			1,176	LA	Kirby & Gosselink, 1976
	Tall	1,300			Stroud, 1976
	Short	330			
		2,100	6,260	LA	Hopkinson et al., 1978
		754-1,080		LA	White et al., 1978
	Tall		3,683	LA	Pezeshki et al., 1991
	Short		2,008		
S. patens			840	New England	Nixon & Oviatt, 1973
			1,922	MS	De la Cruz, 1974
		1,376	6,043	LA	Hopkinson et al., 1978
			110	LA	DeLaune & Smith, 1984
			2,466	LA	Cramer & Day, 1980
			3,677	LA	Pezeski & DeLaune, 1991
D. spicata			360	VI	Wass & Wright, 1969
			1,484	MS	De la Cruz, 1974
		991	3,237	LA	Hopkinson et al., 1978

(Williams, 1962). Four genera, *Cylindrotheca*, *Gyrosigma*, *Navicula*, and *Nitzchia* made up about 90% of the diatom assemblage. Diatom cell counts and total cell volume were highest in tall *S. alterniflora*, and decreased in creek bottom and high marsh areas. The stem of *S. alterniflora* may serve as a structure for attachment of other macroalgal species; two species of red algae, *Caloglossa leprieurii* and *Bostrychia radicans* covered dead standing *S. alterniflora* culms during the summer (Chapman, 1971); *Ectocarpus confervoides* bordered the stems in mid-winter (Pomeroy et al., 1972). Low species richness of macroalgae in Georgia salt marshes was attributed to high turbidity, sedimentation processes, and extremes of temperature and desiccation due to the tidal cycle (Williams, 1962). Planktonic diatoms for other estuarine habitats listed four species of *Gyrosigma*, 34 species of *Navicula*, and 24 species of *Nitzchia*.

5.2.2 Decomposers

Decomposers play a prominent role by degrading complex plant and animal tissues into substances utilized by both producers and consumers. Fungi, bacteria, and protozoans are the primary decomposers in coastal marshes and are also utilized as food by other organisms (Daiber, 1982). Teal (1986) estimated almost three-quarters of the detritus produced in salt marshes was broken down by bacteria and fungi. Protein content of the substrate was increased via fungi, bacteria and protozoan colonization (Mitsch and Gosselink, 1993). Nutritive content of the detritus consumed by detritivores has been postulated to increase due to presence of bacteria (Odum and de al Cruz, 1967), although other interpretations indicated that increase in nutrition was due to consumption of nematodes and other microscopic benthic organisms that were feeding on detritus (see Mitsch and Gosselink, 1993). No known studies have been published on decomposer identification or function in coastal marshes within the CCBNEP study area.

5.3 Consumers

5.3.1 Invertebrates

Several major groups of invertebrates may be present as consumers at various levels, although most have not been studied comprehensively within the CCBNEP study area. With some exceptions, most species are not restricted to coastal marshes, but occur in estuarine, marine and some upland systems. General accounts from the literature will be used to introduce the importance and diversity of this consumer group. Although various categories have been designated to categorize food preferences, few species fit into one category exclusively; more often, they switch seasonally or during different developmental stages.

5.3.1.1 Filter and Deposit Feeders

Many molluscan filter feeders ingest both plant and animal matter and detritus during inundation periods. *Geukensia demissa* (ribbed mussel) ingests phytoplankton, small zooplankton, detritus, and associated microbial populations (Daiber, 1982). Other filter-feeding molluscs include *Polymesoda caroliniana* (Carolina marsh clam), *Mercenaria mercenaria* (edible clam), and *Crassostrea virginica* (eastern oyster). Montague et al. (1981) listed potential food items for deposit feeders: microalgae, decomposer microbes, microfauna, and meiofauna. Daiber (1982) listed several deposit feeder groups with associated citations and included: oligochaetes and polychaetes (Giere, 1975), nematodes (Teal and Wieser, 1966; Tietjen, 1967), snails (*Ilyanassa obseleta*, *Littorina irrorata*) (Odum and Smalley, 1959), fiddler crabs (*Uca* spp.) (Teal, 1958; Miller, 1961), mud crabs (*Rhithropanopeus* spp.) (Odum and Heald, 1975), grass shrimp (*Palaemonetes pugio*) (Welsh, 1975), amphipods (*Orchestia* spp.) (Averill, 1976), and dolichopodid and ephydrid flies (Davis and Gray, 1966). Grass shrimp (*Palaemonetes* spp.) may be categorized as both deposit and suspension feeders (Johannes and Satomi, 1966; Welsh, 1975) feeding opportunistically on detritus, meiofauna, algae, and dead animals (Welsh, 1975).

5.3.1.2 Grazers

Daiber (1982) defines grazers as “herbivores consuming a portion or the whole of an intact plant without any filtering from a volume of water”. Even within this definition, several snail grazers also ingest other food while feeding on the epidermis of grasses and epiphytes. *Neritina usnea* (olive nerite) has been observed grazing on encrusted algae and other microflora of *S. alterniflora* stems in Mississippi salt marshes (Heard, 1982). *Littoridinops monroensis*, found within brackish ponds of Galveston Island and *Cerithidea scalariformis* listed as a salt marsh inhabitant in Texas apparently feed on microflora (e.g., diatoms, filamentous algae, bacteria) and other epibenthic organic matter (Heard, 1982). *Littorina irrorata* (saltmarsh periwinkle), common in eastern US and Gulf salt marshes, and *Melampus bidentatus* (eastern melampus or coffee bean snail), common along the northern Gulf of Mexico marshes, feed on the marsh surface during low tides and on *S. alterniflora* stems when the marsh is inundated (Heard, 1972). True insect grazers, such as grasshoppers, will either feed selectively on plant parts, whereas homopterans, hemipterans, and dipterans feed on plant sap (Daiber, 1982).

5.3.1.3 Secondary Consumers

Several bacteria-eating protozoans have been isolated from mudflats and tidal creeks in Georgia including the ciliates *Euplotes crassus*, *E. vannus*, and *E. trisculatus* (Johannes, 1965). Other studies have discussed the requirement of bacteria for reproduction in some foraminiferans (Muller and Lee, 1969). Gut content analysis of two annelids, *Capitella capitata* and *Streblospio benedicti*, revealed diatoms, detritus, and sand. The oligochaetes, *Marionina subterranea* and *M. spicula*, are two species that occur in tidal marsh as well as other estuarine habitats gleaning microorganisms from detrital particles but not directly feeding on detritus (Giere, 1975). Both Giere (1975) and Gerlach (1978) believed many oligochaetes, polychaetes, nematodes, and foraminiferans have special food requirements and need certain bacteria and algae.

5.3.1.4 Predators

Some strictly predaceous organisms are also some of the smallest organisms found in the marsh; they include most crustacean larvae and a few adult copepods (Marshall and Orr, 1960). Davis and Gray (1966) distinguished between two types of predaceous arthropods: solid-tissue feeders and body-fluid feeders. Solid-tissue feeders in a North Carolina salt marsh included dragon flies (*Erythrodiplax berenice* and *Erythemis simplicicollis*), malachiid beetle (*Collops nigriceps*), and clerid beetles (*Isohydnocera tabida* from *S. alterniflora*, *I. aegra* from *S. patens*). *Tabanus* *nigrovittatus* (greenhead fly) larvae were observed feeding on most soft-bodied animals including *Chrysops fuliginosus* (dolichopodid fly) larvae, hydrophilid beetle larvae, and (*Orchestia grillus*) amphipods in Massachusetts tidal marsh sod (Meany et al., 1976). Body-fluid feeders (i.e., suckers) such as asilid flies, preyed upon grasshoppers, midges, mosquitoes, reduviids (e.g., *Doldina interjungens*, *Sinea diadema*, *Zelus cerviclis*) and nabids (e.g., *Nabis capsilformis*) in a North Carolina salt marsh (Davis and Gray, 1966).

Callinectes sapidus (blue crabs) have been described as predominantly carnivorous, although they are often categorized as scavengers. As opportunistic feeders, this species has been reported to eat motile prey such as other crabs, grass shrimp, fish, and snails and to search the sediments for infauna, bivalves, and plant parts (Darnell, 1961; Virnstein, 1977). Depending upon the abundance of prey items, *C. sapidus* feeds predominantly on *Uca* spp. and *L. irrorata* in Mississippi salt marshes (Heard, 1982).

Spiders constitute an important part of the predator trophic level, although little work has been conducted in coastal marshes. In an investigation of the ecology of spiders in a North Carolina *S. alterniflora* drift line, Barnes and Barnes (1954) identified *Lycosa modesta* as the most abundant species with *Clubiona nicholsi* as the second most abundant. Smalley (1960) also identified the genera *Clubiona* and *Grammamota* as the predominant spider predators in a Georgia salt marsh, living in leaf axils and hollow stems of dead *S. alterniflora* culms.

5.3.1.5 Omnivores

Neanthes succinea, a common nereid polychaete of coastal marshes, consumes a variety of items including detritus, algae, and small crustaceans (Heard, 1982). *Uca* spp. are excellent examples of an omnivorous crab genus, utilizing a variety of food resources including algae, detritus, foraminiferans, nematodes, inorganic particles, and carrion (Teal, 1958, 1962; Shanholtzer, 1973).

5.3.2 Fishes

5.3.2.1 Filter and Deposit Feeders

Brevoortia spp. (menhaden) and *Anchoa mitchilli* (anchovy) both inhabit the tidal marsh although they are not restricted to this habitat. *Brevoortia* spp. feed on both phyto- and zooplankton, whereas the *A. mitchilli* may feed primarily on brackish water copepods and zooplankton (Daiber, 1982). *Mugil cephalus* is often categorized as a deposit-suspension feeder, but may also ingests phytoplankton while grazing on biota in bottom sediments (Odum, 1968a; Odum, 1970).

5.3.2.2 Predators

Juvenile *Megalops atlantica* (tarpon) utilize pools and creeks of Sapelo Island, Georgia marshes, feeding on *Gambusia affinis*, *Poecilia latipinna*, or *Palaemonetes* spp. depending on size of the juvenile predator (Rickards, 1968). Historically, *M. atlantica* were abundant in the CCBNEP study area and most likely utilized coastal marshes in their development. *Fundulus heteroclitus* (mummichog) fed on *Melampus bidentatus* (coffee bean snail) and the amphipod (*Orchestia grillus*) in a Massachusetts salt marsh; this fish can affect the abundance and size distribution of both species (Vince et al., 1976). Other studies list *F. heteroclitus* as consuming *Palaemonetes* spp., or filtering detrital material from the water column and consuming carrion (Jefferies, 1972; Valiela et al., 1977). Vegetation density has significant impacts on predation success by *F. heteroclitus*. All three fish predators occur within the CCBNEP study area coastal marshes and presumably the same feeding relationship exists.

5.3.3 Reptiles and Amphibians

Few species of reptiles and no amphibians are permanent inhabitants of coastal marshes, mainly due to salinity stress. *Malaclemys terrapin littoralis* (diamondback terrapin) is a notable exception, inhabiting brackish marshes along the eastern US and Gulf coasts (Carr, 1952; Conant, 1975; Garrett and Barker, 1987). *Malaclemys terrapin littoralis* are generally carnivores, feeding on fish, crustaceans, molluscs, and insects (Conant, 1975). Many bird and mammal species prey on terrapin eggs and young, including *Urocyon* spp., *Procyon lotor* (raccoon), Laughing gull (*Larus atricilla*), crows (*Corvus* spp.), and night herons (*Nycticorax* spp.) (Burger, 1977a). *Nerodia fasciata clarki* (Gulf salt marsh snake) also inhabits coastal marshes along the Gulf Coast from west central Florida to south Texas (Conant, 1975); they feed on a variety of small prey items. *Alligator mississippiensis* (American alligator) utilizes coastal marshes as both feeding and nesting areas, although they are generally associated with lower salinities along the Gulf Coast (Garrett and Barker, 1987). This predator consumes a large variety of prey items and the adult has no natural predators. Alligators have been reported to reduce the population of *Ondatra zibethicus* (muskrat) and *Coypus coypu* (nutria) within these species' ranges. Populations of *A. mississippiensis* are typically associated with brackish marshes of the Aransas, Mission and tributary creeks flowing into the bay systems; alligators crossing shallow bays have been reported by local fisherman (McAlister and McAlister, 1993).

5.3.4 Birds

5.3.4.1 Grazers

Many species of waterfowl feed on submergent plants in ponds and tidal creeks of coastal marshes. *Ruppia maritima* (widgeongrass) occurs extensively in coastal marshes when areas are inundated for prolonged periods and is of primary importance to waterfowl in Chesapeake Bay (Stewart, 1962). Of the species of geese that winter along the Texas coast, the Lesser Snow Goose (*Chen caerulescens*) is the predominant species in upper and central coastal marshes and feeds on roots and rhizomes of all the predominant coastal marsh grasses. Certain plant species associated with brackish to intermediate marshes support a large diversity of grazing waterfowl; however, since these marshes comprise a small proportion of marshes within the CCBNEP study area, details are not available.

5.3.4.2 Predators

Although many waterfowl species are primarily grazers, invertebrates do comprise varying proportions of their diet and are based upon availability (Belrose, 1976). Mottled Ducks (*Anas* *fulvigula*) are one of the few waterfowl species that use Texas coastal marshes year-round (Stutzenbaker, 1988). Animal matter, including a large proportion of insects, and some fish, snails, and crayfish are primary prey items, although plant material is also ingested. Wading birds feed on both invertebrates, fish, amphibians, and young rails and moorhens in coastal marshes. Willets (*Cataptrophorus semipalmatus*) and Clapper Rails (*Rallus longirostris*) feed on virtually any small animal prey, including aquatic insects, marine worms, small crabs and molluscs, larval and juvenile fish (Daiber, 1972 as cited from Bent 1929, 1963). Several fish- and shellfish-feeding herons and egrets used a natural marsh site in the Nueces River delta from June 1989 to June 1990 including the Great Blue Heron (*Ardea herodias*), Tricolored Heron (*Egretta tricolor*), Black-Crowned Night Heron (*Nycticorax nycticorax*), Great Egret (*Casmerodius albus*), and Snowy Egret (*Egretta caerulea*) (Ruth, 1990). Several species of wading and aquatic shorebirds fed on benthic organisms in shallow intertidal areas. Other species capitalized on migration of prey in and out of marshes via tidal creeks including Lesser Scaup (*Aythya affinis*), Bufflehead (*Bucephala albeola*), White Pelican (*Pelecanus erythrorhynchos*) and the cormorants (*Phalacrocorax* spp.). Sixty-six species of birds were observed feeding and roosting in the same natural marsh in the Nueces River delta from September 1992 to August 1993 (Nicolau, 1993). The only natural, wild population of Whooping Cranes (*Grus americana*) in the world winters in coastal marshes of the Aransas National Wildlife Refuge (ANWR), feeding on a variety of prey items associated with brackish and saline areas. Whooping Cranes are largely opportunistic feeders, preying on *C. sapidus* when abundant, but also on clams, snails, grasshoppers, and wolfberry fruits (Blankinship, 1976). Their current status and historical trends are discussed in Section IV.C.1.1 (this volume).

5.3.5 Mammals

5.3.5.1 Grazers

Mammalian herbivores, when present, can significantly impact coastal marsh dynamics. Cyclic population densities are correlated to availability of vegetation. A decrease in vegetation due to over-exploitation is often followed by a decrease in herbivore populations. A natural mammalian herbivore is not typically part of the vegetation dynamics and resultant structure in south Texas coastal marshes. The range of an exotic herbivore, *Coypus coypu* (nutria), is expanding into the CCBNEP study area (T. Stehn, ANWR, and J. Holt, UTMSI pers. comm.) and may significantly alter coastal marshes. However, no information is available concerning degree of impact this exotic may have on the vegetation dynamics and species composition. *Odocoileus virginiana* (white-tailed deer) are reported to utilize salt marshes of the Aransas National Wildlife Refuge feeding on new grass and forb shoots (White, 1973).

5.3.5.2 Carnivores

Few carnivorous rodents actually reside within the coastal marsh; however, *Oryzomys palustris* (rice rat) is categorized as a wetland species (Martin et al., 1991) feeding on small crabs and snails (Hamilton, 1946; Shard, 1967), invertebrates, and plant material (Negus et al., 1961). Other small rodents that occasionally feed on invertebrates occur in the high marsh/upland interface and include *Sigmodon hispidus* (cotton rat), *Reithrodonomys fulvescens* (fulvous harvest mouse), and *Mus musculus* (house mouse) (Martin, et al. 1991). *Procyon lotor* is an opportunistic feeder in coastal marshes preying on fish, crabs, and bird eggs (Linscombe and Kinler, 1985). *Tursiops truncatus* (Atlantic bottlenose dolphin), a large, obligate carnivore in estuarine systems consumes live fish and squid. Although this species rarely enters the coastal marsh proper, they have been observed feeding adjacent to tidal creeks (E. H. Smith, pers. obs.).

5.4 Community Structure & Zonation

5.4.1 Plant Communities

Plant species' responses to stresses of inundation and salinity generally determine their location across an elevational and salinity gradient (Penfound and Hathaway, 1938; Adams, 1963; Chapman, 1974; Nixon and Oviatt, 1973). Marshes situated along gently-sloping coastlines typically exhibit zonation patterns parallel to the shoreline. Coastal marsh zones have been delineated according to elevation and tidal inundation. The lower or intertidal marsh generally is flooded daily, whereas the upper or high marsh is infrequently flooded (Mitsch and Gosselink, 1993). Chabreck (1976) divided Gulf coastal plant communities into four zones: saline, brackish, intermediate, and fresh. The saline zone is characterized by daily tidal inundation with salinities of 20-35 . The brackish zone has a salinity range of 5-19 and is affected by seasonality of tides, especially in spring and fall, and by storm surges due to tropical storms or hurricanes. Tides affect the intermediate zone only during extreme storm surge events, which may not change salinity (0-0.5) but may increase water depth by impeding normal runoff.

Tidal cycles are a primary component of hydrologic dynamics in coastal marsh systems. Varying degrees of inundation in relation to marsh elevation differentially affect vegetation dynamics. Effect of tides can be stressful to plants (e.g., submergence, anaerobic soil conditions, deposition of salts in the soil), but also have beneficial effects of periodic flushing of salts out of the marsh and moving nutrients into the marsh (Mitsch and Gosselink, 1986). Seasonal cycles superimposed on diurnal tide patterns have a significant impact on plant zonation patterns (Bleakney, 1972; Armstrong et al., 1985; Wood, 1986).

In Gulf coastal marshes *S. alterniflora* is found in the lower saline zone and *S. patens* predominates in the middle brackish zone (Fig. IV.B.5.2). *Distichlis spicata* generally occurs between *S. alterniflora* and *S. patens* and is present in varying amounts in Gulf coastal marshes. Other species are present, albeit in lesser abundance, throughout coastal marshes; their zonation patterns are presumably a response to environmental influences and physiological requirements (Chabreck, 1972; Gosselink, 1984). Species composition of plant zones in coastal marshes within the CCBNEP study area varies from north to south in relation to rainfall/evapotranspiration ratios. *Spartina alterniflora* meadows in the northern part are largely replaced by saltgrass and shoregrass in the middle coastal marshes. Thin bands of *S. alterniflora* may occur in areas of the low tidal range, interspersed with *Avicennia germinans* (black mangrove), although the latter species is not extensive in the study area and is negatively impacted by freezing temperatures (White et al., 1983). High marsh species, such as *Salicornia* spp., dominate in the higher salinity soils and forb species increase in importance at the high marsh and upland interface (Brown et al., 1976; White et al., 1983). Predominately

Salicornia/Batis associations are exhibited at Indian Point (adjacent to Nueces/Corpus Christi Bay juncture) and around Stedman Island in Redfish Bay.

Approximately 5,850 ha of high and middle salt marsh exists in the Nueces River delta with 35 ha of *Spartina alterniflora* randomly distributed along tidal channel fringes (Espey, Huston and Associates 1981; Ruth 1990). Salinity and elevation are the primary factors influencing salt marsh vegetation composition and zonation. Plants typical of the upper marsh are: *Borrichia frutescens*, *Limonium nashii*, *Lycium carolinianum*, *Haplopappus phyllocephala*, *Opuntia lindheimeri*, *Prosopis reptans*, and *Spartina spartinae*. Plants of the lower marsh within the mitigation site include: *Batis maritima*, *Distichlis spicata*, *Monanthochloe littoralis*, *Salicornia bigelovii*, *S. virginica*, *Scirpus maritimus*, and *Spartina alterniflora*.

5.4.2 Invertebrate Communities

No comprehensive studies have been undertaken within the CCBNEP study area on zonation of invertebrate communities. Other studies have described zonation patterns of animals as directly and indirectly related to vegetation, marsh elevation, frequency of tidal flooding, and drainage. In a study of coastal marshes of the northwest Gulf of Mexico, foraminiferans had different patterns of species preference and/or abundance for open bay, tidal flats, *Spartina* zone and *Salicornia* zone (Table IV.B.5.2) (Phleger and Bradshaw, 1966). Even the diversity of microhabitats within a zone had a pronounced effect on distribution of foraminiferans in Galveston Bay (Table IV.B.5.3) (Phleger, 1965). Spatial and vertical zonation patterns have been reported for several benthic meiofaunal groups, including nematodes, harpacticoid copepods, amphipods, polychaetes, oligochaetes, kinorhynch, turbellarians, and ostracods (Daiber, 1982). Availability of food resources is cited as a predominant factor in the distribution and abundance of these organisms, although presence of other species may have an effect on zonation patterns. Indirect effects of sediment mixing by bioturbators (e.g., fiddler crabs) may change availability of food items and abundance of predators. Copepod distributions in a South Carolina salt marsh varied in relation to sediment type and degree of exposure indicating each species' tolerance limits to environmental conditions (Fig. IV.B.5.4) (Coull et al., 1979).

A long-term comparison of a natural marsh and a marsh mitigation site in the Nueces River delta is the only study which has quantified benthic and epibenthic invertebrate abundance in the CCBNEP study area (Ruth, 1990; Ruth et al., 1990; Adams 1993; Nicolau and Adams, 1993; Nicolau, 1994; 1995). Since 1989, 49 species (5 phyla) of benthic invertebrates were collected including 18 species of polychaetes, 16 species of crustaceans, 7 species of bivalves, and 2 species of gastropods. Overall, mean monthly densities were 1,980 individuals m^{-2} (Fig. IV.B.5.5). Peak abundances occurred winter and spring during all four years. Five species were dominant (Fig. IV.B.5.6): polychaetes *Streblospio benedicti* (32.7%), *Mediomastus ambiseta* (18.8%), *Laeonereis culveri* (14.8%), and *Capitella capitata* (7.1%); and the *Corophium louisianum* (11.0%). These species accounted for 84.4% of all organisms collected.

Table IV.B.5.2 General distributions of foraminiferans in the northwest Gulf of Mexico (adapted from Phleger and Bradshaw, 1966).

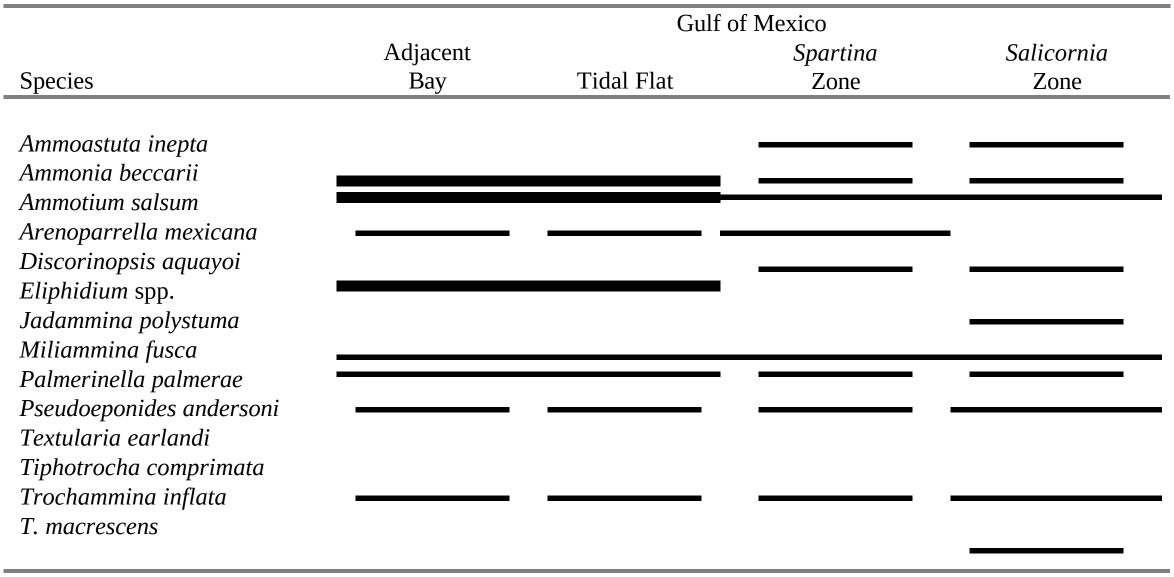
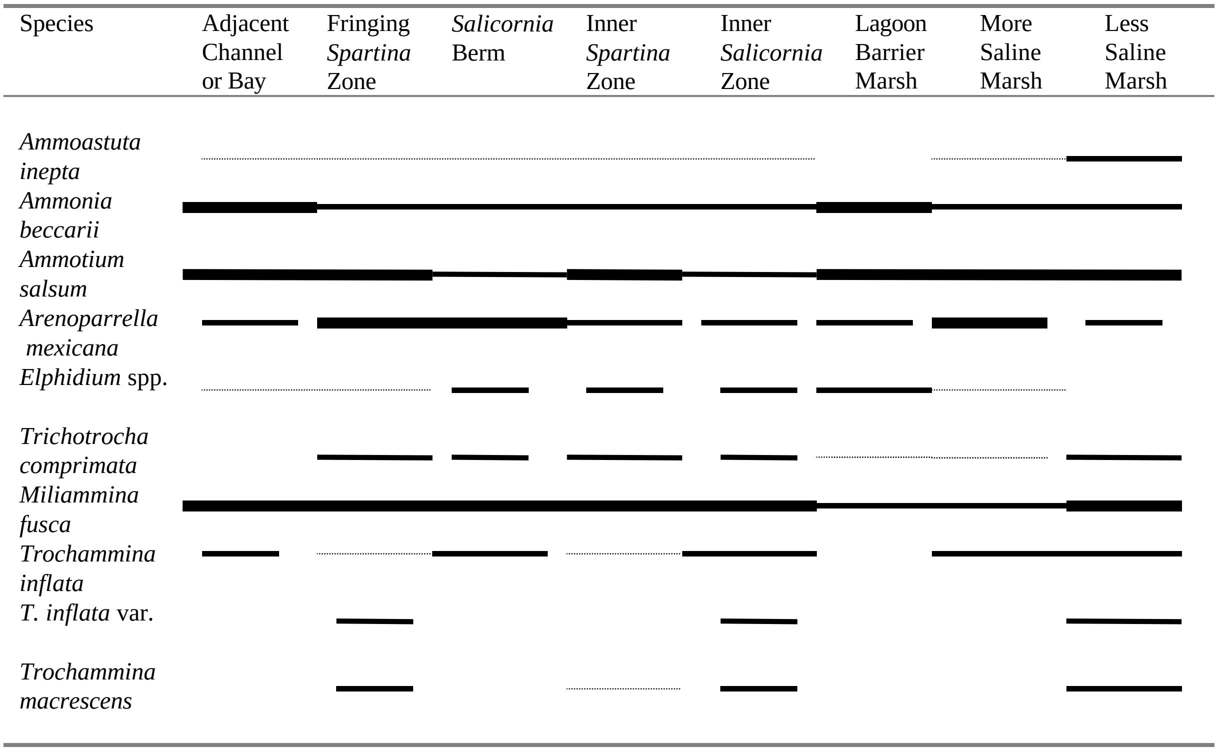


Table IV.B.5.3 General distribution of foraminiferans in relation to marsh environments (adapted from Phleger, 1965).



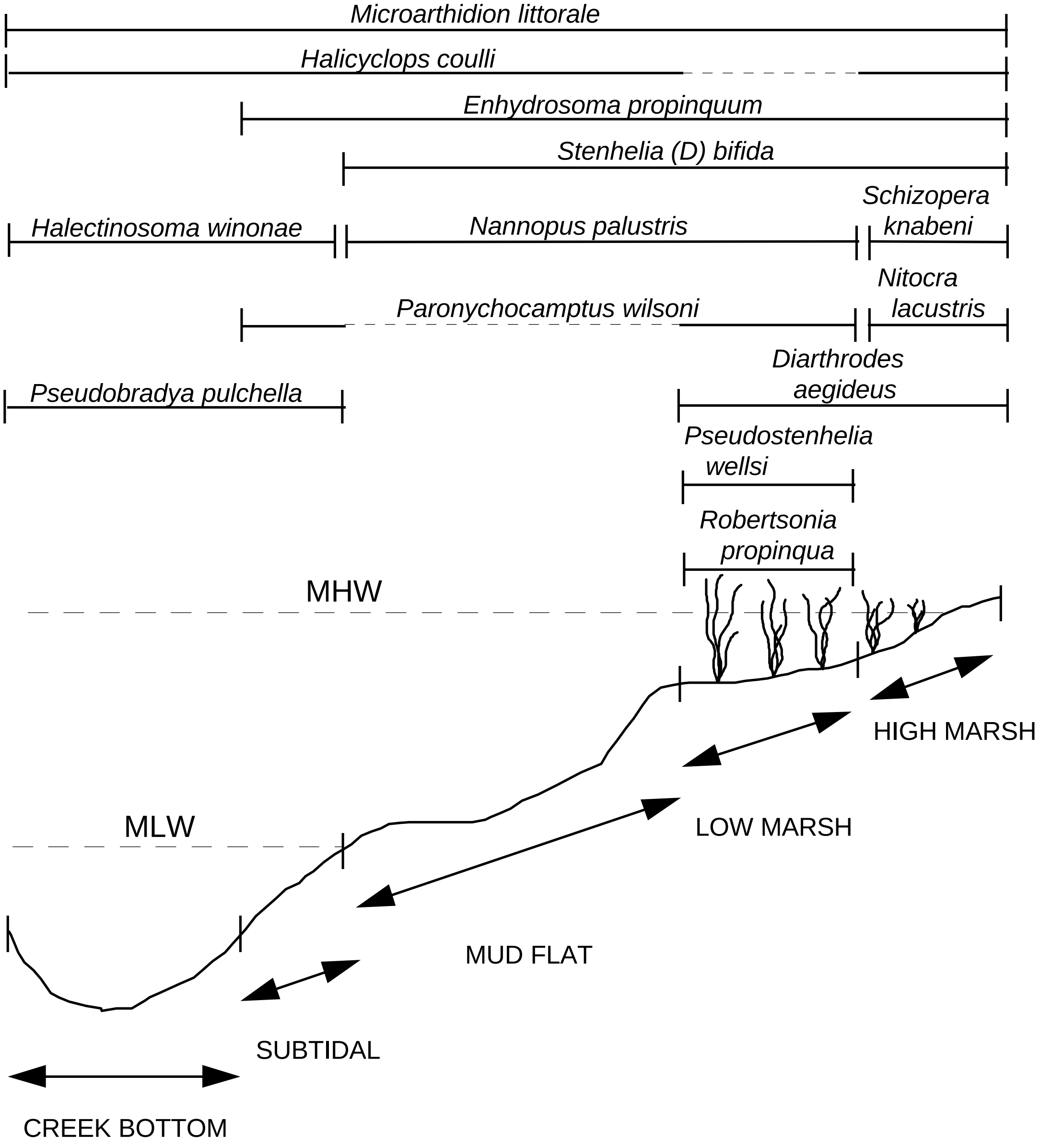


Fig. IV.B.5.4 Zonation patterns of meiobenthic copepods (>15% of total copepod fauna in at least one season) across a depth gradient in southeastern US salt marshes (adapted from Coull et al., 1979).

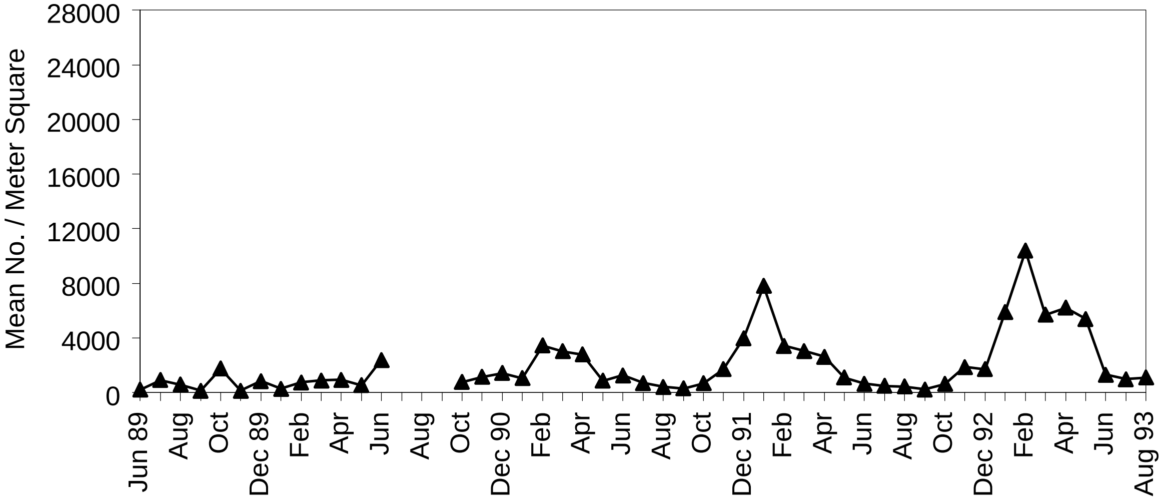


Fig. IV.B.5.5. Mean densities of benthic organisms collected 1989-1993 in a marsh in the Nueces River delta (Ruth, 1990; Ruth et al., 1990; Adams 1993; Nicolau and Adams, 1993).

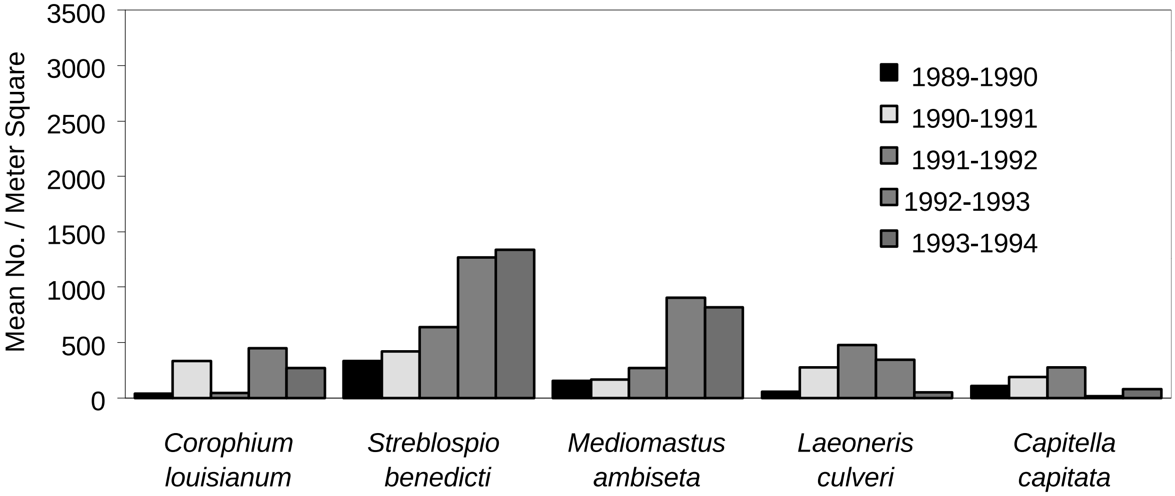


Fig. IV.B.5.6. Annual mean densities of dominant benthic organisms collected from a marsh in the Nueces River delta (Ruth, 1990; Ruth et al., 1990; Adams 1993; Nicolau and Adams, 1993; Nicolau, 1994).

Several molluscan species utilize coastal marshes of Texas, although little is known of the seasonal abundance within the CCBNEP study area. *Geukensia demissa* (ribbed mussel) is a pelecypod mollusc inhabiting coastal marshes, and is usually located along the intertidal zone above mean low water levels (Kuenzler, 1961a). Reported salinity tolerance values for the *Geukensia demissa* range from 5ppt (Wells, 1961) to 43ppt (Lent, 1969). *Melampus bidentatus* tolerates salinities of 9.38-14.72ppt; densities tend to decrease at lower salinities (Kerwin, 1972). This species generally occurs above the high marsh (Hauseman, 1932), or climbs up vegetation during high tide events to avoid submersion (Holle, 1957). This dependence on vegetation structure was observed in several marshes, with low densities occurring in areas with little or no vegetation (Daiber, 1982). *Littorina irrorata* (salt-marsh periwinkle) may be found on the marsh substrate during winter and spring, but was commonly located on the culms of *Spartina alterniflora* during the summer months in a Georgia salt marsh (Smalley, 1959a). Castiglione (1983) listed this species as abundant in a salt marsh in a Nueces-Corpus Christi Bay study.

Some of the common amphipods of coastal marshes display varying tolerance to salinities and thus exhibit distributional differences. For example, *Gammarus palustris* occurs in a wide range of salinities (5-20ppt) and is even capable of surviving fresh water inundation for short periods of time (Rees, 1975). Several fiddler crab species are found within the CCBNEP study area, although little is known of their distribution in Texas coastal marshes. Teal (1959) delineated the habitat preferences of *U. pugnax*, *U. pugilator*, and *U. minax* in a Georgia salt marsh and determined that individual species' salinity tolerance and substrate type separated the species' distribution across the marsh surface. *Uca pugnax* was tolerant of the highest salinities (21-29ppt) and narrowly overlapped in distribution with *U. minax* whose tolerance limits to salinity were lower (0-12ppt optimum). Shifts in species abundance were observed between 15 and 18ppt, and was interpreted as a less preferred habitat for both species (Miller and Maurer, 1973). Distribution cannot be explained by salinity patterns alone, however, as high abundances of both species were found at 4-5ppt in a marsh in Delaware (Daiber, 1982). Teal (1958) investigated the zonation of *Uca* spp. in relation to substrate type and determined that *U. pugnax* was located in substrate with low sand content, *U. minax* preferred a sand content of at least 30%, while *U. pugilator* was found in substrates with the highest sand content.

A total of 22 epifaunal and nektonic species (4 phyla) were collected including 7 crustacean and 13 fish species during the four year Nueces River delta marsh study (Ruth, 1990; Ruth et al., 1990; Adams 1993; Nicolau and Adams, 1993; Nicolau, 1994; 1995). Mean monthly densities natural marsh stations were 4.7 individuals m^{-2}, and ranged from $0/m^2$ (no water periods) to $38/m^2$ (Fig. IV.B.5.7). Peak abundances occurred winter and summer. Over the length of the study, *Americamysis* (=*Mysidopsis*) *almyra* was the dominant epifauna organism collected (1,726,502 individuals for the period 1990 through 1993). Although not quantified by Ruth (1990), A. *almyra* was present in overwhelming numbers and occurred in most samples (B. Ruth pers. comm.).

Due to the transient nature of many of the organisms collected in estuarine habitats a species that is dominant at one location one year may not be dominant the following sampling season. The

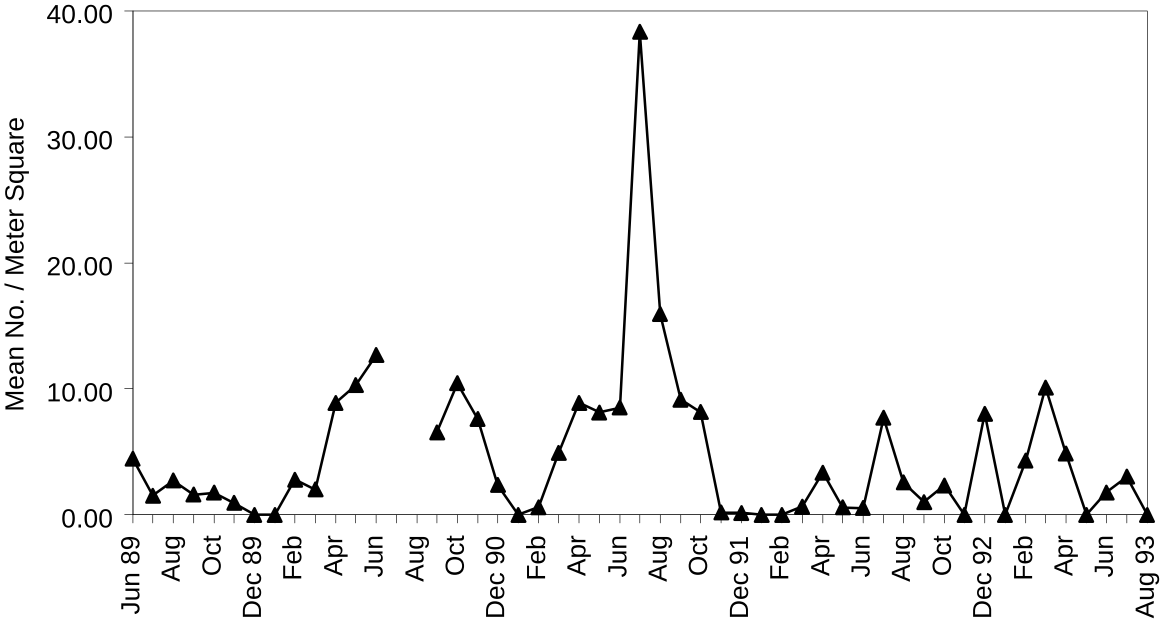


Fig. IV.B.5.7. Mean densities of epifaunal and nektonic organisms (excluding *Americamysis almyra*) collected 1989-1993 from a marsh in the Nueces River delta (Ruth, 1990; Ruth et al., 1990; Adams 1993; Nicolau and Adams, 1993).

overall dominant species (excepting *Americamysis almyra*) were: shrimps *Palaemonetes pugio* (58.2%), *Penaeus aztecus* (15.5%), and *P. setiferus* (4.4%); crabs *Callinectes sapidus* (2.6%); and the goby *Gobiosoma bosci* (3.8%) (Fig. IV.B.5.8).Annelids, crustaceans, and molluscs were the most abundant members of the benthic community, comprising 95.8% (Fig IV.B.5.9). The epifaunal and nektonic community was dominated by crustaceans (72%) and fish (28.0%). Dominant species (*Palaeomonetes pugio*, *Penaeus aztecus*, *P. setiferus*, *Callinectes sapidus*, *Gobiosoma bosci*) accounted for 84.4% of all epifauna and nektonic species collected (Ruth, 1990; Ruth et al., 1990; Adams 1993; Nicolau and Adams, 1993; Nicolau, 1994; 1995).

Insects are documented as displaying general zonation patterns in relation to tidal flooding and vegetation composition. Davis and Gray (1966) described the zonation patterns of homopterans (cicadas, hoppers, whiteflies, aphids, and scale insects) in North Carolina marshes as very pronounced, with the exception of *Prokelisia marginata*, (salt-marsh planthopper) and *Delphacodes detecta* which were found in varying numbers across most marsh zones (Fig. IV.B.5.10). McAlister and McAlister (1993) listed *Prokelisia marginata* as being present in coastal marshes on the leeward-side of Matagorda Island. Overall, Davis and Gray (1966) found insect species richness higher in the *Distichlis spicata* zone than the *Spartina patens* zone, and variation higher in the low marsh *S. alterniflora* zones.

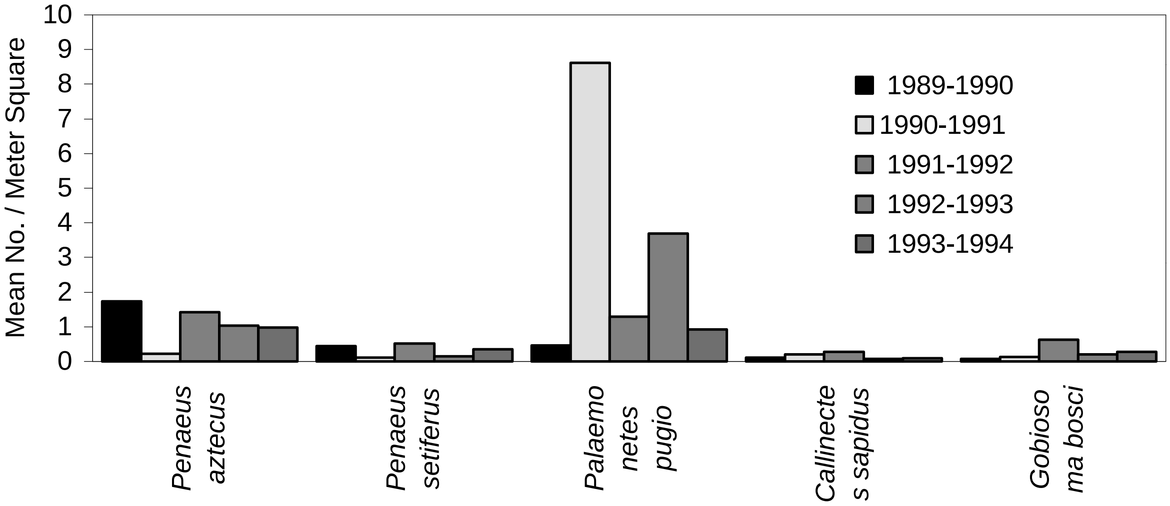


Fig. IV.B.5.8. Annual mean densities of dominant epibenthic and nektonic organisms (excluding *Americamysis almyra*) collected from a marsh in the Nueces River delta (Ruth, 1990; Ruth et al., 1990; Adams 1993; Nicolau and Adams, 1993; Nicolau, 1994).

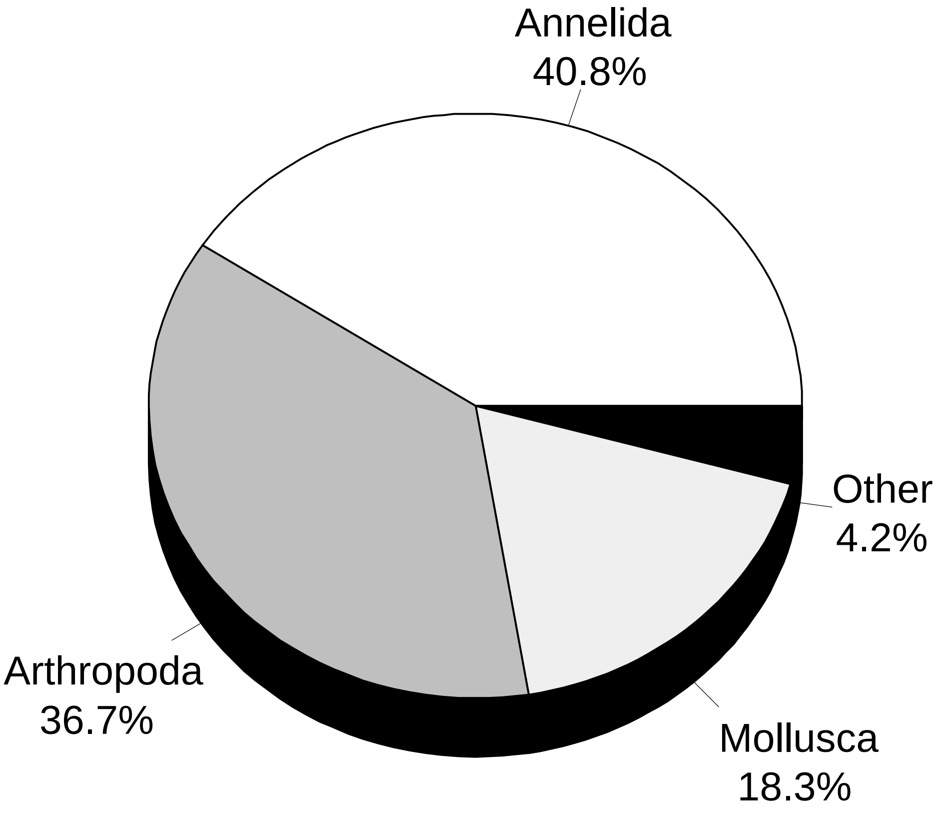


Fig. IV.B.5.9. Community composition of benthic invertebrates in a Nueces River delta marsh (data compiled from Ruth, 1990, Nicolau and Adams, 1993; Nicolau, 1994; 1995).

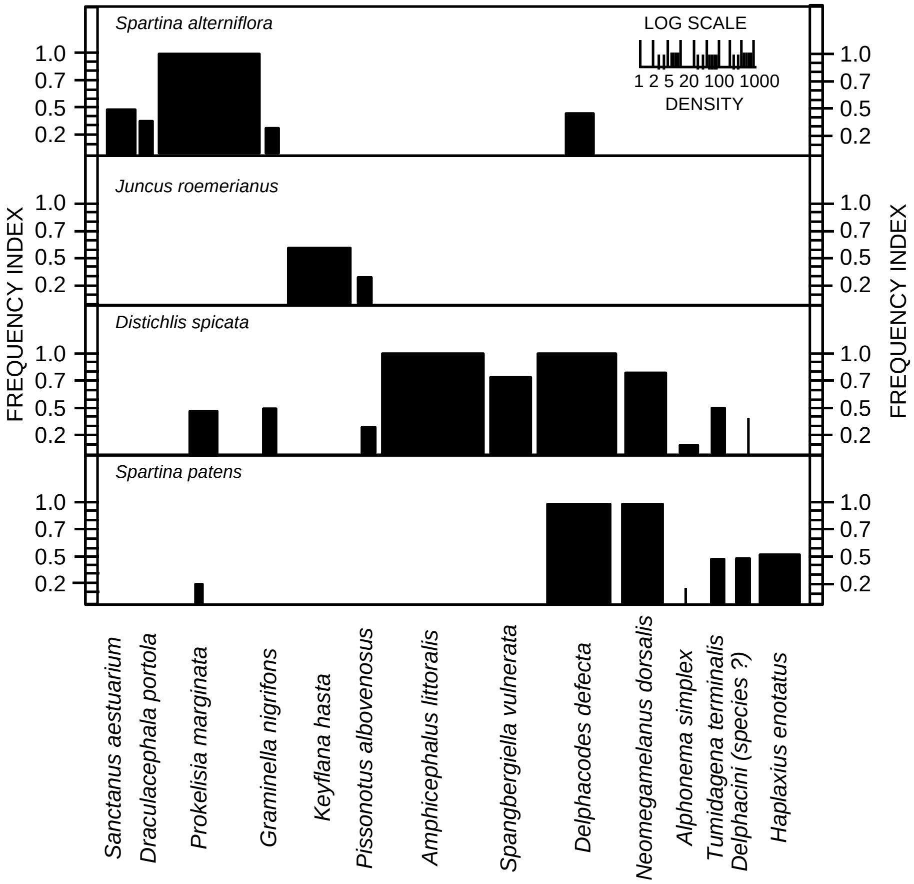


Fig. IV.B.5.10. Frequency-density diagram of the principal species of Homoptera from the herbaceous strata of four zones of salt-marsh vegetation (adapted from Davis and Gray, 1966).

Dipterans accounted for most of the species found in a North Carolina coastal marsh, being most frequent group encountered in the *S. patens* zone (Fig. IV.B.5.11) (Davis and Gray, 1966). *Oscinella infesta* occurred in all zones and was the most common species overall. Six species of hemipterans accounted most of the species assemblage. *Tyttus vagus*, *Trigonotylus americanus*, *Ischnodemus badius*, and *Rhytidolomia saucia*, were all abundant, but each species was restricted to a single marsh type (Fig. IV.B.5.12). *Cymus breviceps* occurred throughout the marsh, although they were more abundant in *S. patens* and *Panicum virgatum* in the high marsh.

Spiders had similar distributions within different plant zones, but exhibit large variations in densities in a North Carolina marsh (Barnes, 1953). Densities may have been related to vegetation structure, as *S. alterniflora* exhibits long-standing, stout culms, whereas the structure of *Spartina patens-Distichlis spicata-Salicornia* association was shorter and tended to dry out faster. Little is known about ecology of marsh-inhabiting spiders, although they are both predominant predators and important prey items.

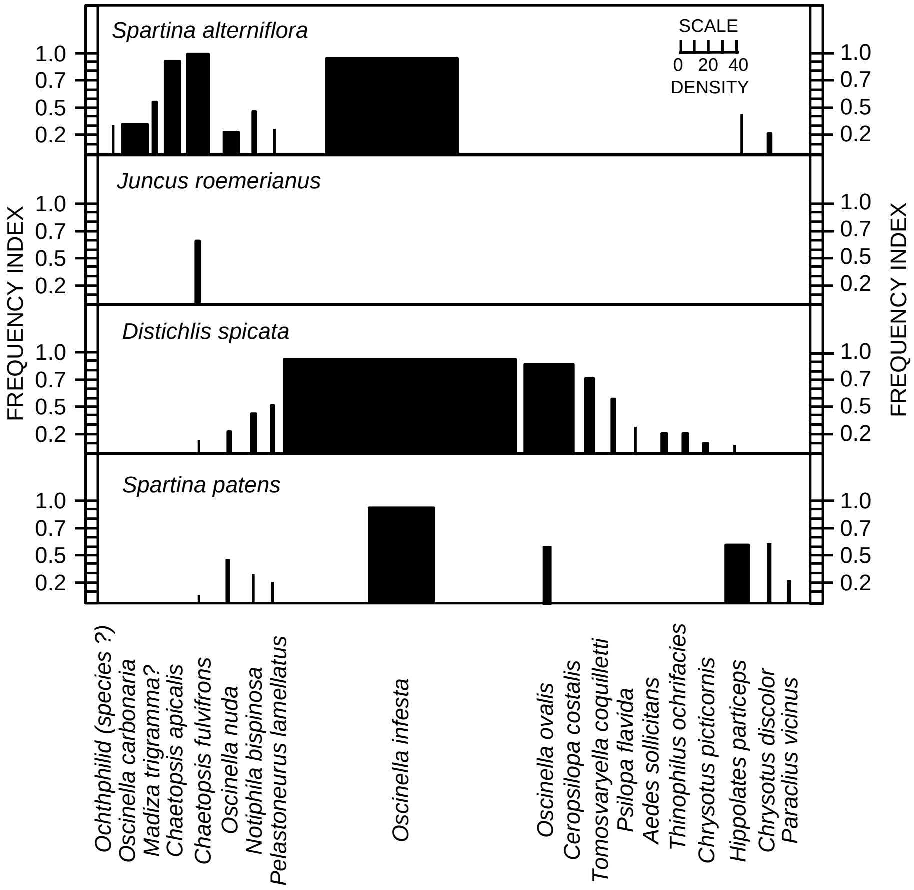


Fig. IV.B.5.11. Frequency-density diagram of the principal species of Diptera from the herbaceous strata of four zones of salt-marsh vegetation (adapted from Davis and Gray, 1966).

Zonation of mosquitoes has been related to both salinity tolerance of eggs and larvae and timing and duration of flood events in a coastal marsh (Table IV.B.5.4). Both *Aedes detritus* and *A. taeniorhynchus* larvae are able to physiologically tolerate a wide salinity range (Ramsey, 1958; Bradley and Phillips, 1975). *Anopheles bradleyi* is typically found in brackish pools associated with *Chara* sp. (muskgrass) or *D. spicata*. The abundance of mosquito larvae was correlated with continuous degree of inundation across a coastal marsh gradient, with no larvae in areas that are flooded 25 days during a lunar month (Ferrigno, 1958). Successful hatching of *Aedes* eggs are largely determined by presence of water, as the substrate-deposited eggs do not float. Single eggs of *Anopheles* spp. are deposited on the water surface, and are subject to desiccation and temperature stress. *Culex* eggs are deposited in rafts and are collectively buoyant. These strategies are important in both the ecological distinctions and distributions of mosquito species and in the management strategies employed for their control.

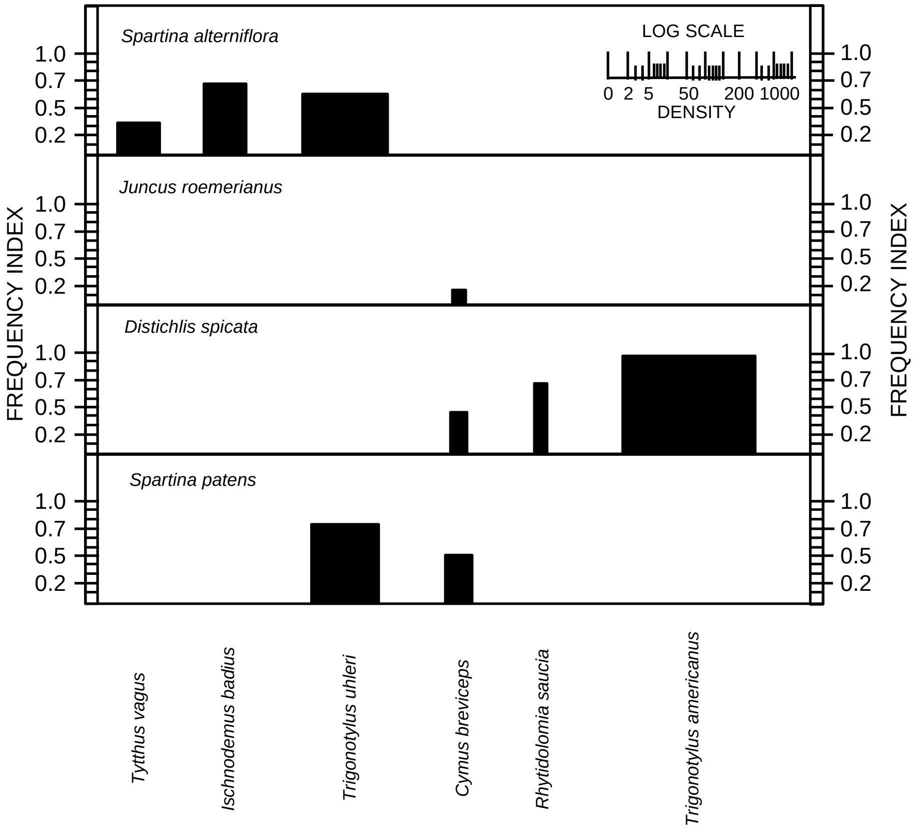


Fig. IV.B.5.12. Frequency-density diagram of the principal species of Hemiptera from the herbaceous strata of four zones of salt-marsh vegetation (adapted from Davis and Gray, 1966).

Table IV.B.5.4 . Average number of *Aedes* larvae and pupae per dip from salt marshes of Egg Island, New Jersey (adapted from Ferrigno, 1958).

	Average number of *Aedes* Larvae and Pupae per Dip		
Species	*A. cantator*	*A. sollicitans*	Total
Spartina patens	0.31	6.95	7.26
S. alterniflora	0.01	0.37	0.38
Mixed	0.29	2.42	2.71

5.4.3 Vertebrate Communities

Motility of fish and importance of water depth and flow may explain absence of distinct zonation patterns and structure in coastal marshes. Salinity tolerances and feeding preferences limit the presence of some species (Harrington and Harrington, 1961). The marsh is utilized by juvenile fishes as protection from predators. Temporal use of the coastal marsh is related to water movement and depth across the marsh surface. In addition, seasonal use of the marsh by juvenile fishes has been linked to life history cycles and physical factors, such as dissolved oxygen levels.

Birds display distinct zonation patterns in relation to vegetation composition, salinity, and water depth. Three species of rails, Virginia Rail (*Rallus limicola*), King Rail (*Rallus elegans*), and Clapper Rail, occur in coastal marshes; and each species is typically associated with different salinity zones. Virginia and King rails typically occur in fresh and brackish areas, where as the Clapper Rail inhabits more saline, low marshes (Stewart, 1951). Abundance of Clapper Rails has been related to plant density and height, which in turn is related to food availability and nesting locations. Resource partitioning between Seaside Sparrows (*Ammodramus maritimus*) and Long-billed Marsh Wrens (*Cistothorus palustris*) has been observed in a Georgia salt marsh (Wiegert and Freeman, 1990). Seaside Sparrows forage along the marsh surface, whereas Long-billed Marsh Wrens feed upon invertebrates on the culms and leaves of the vegetation (Kale, 1965).

No comprehensive studies have been conducted that investigate bird species' affinity to plant composition across elevation and salinity gradients of coastal marshes in the CCBNEP study area. However, surveys were conducted in a coastal marsh near the San Bernard River during summers 1985, 1986, and 1991 (Weller, 1994). Observations of bird use were made in several different plant-dominated areas associated with salinity and water-depth gradients representative of Texas coastal marshes. Both spatial and temporal patterns of bird use were detected and were related to either plant structure or water depth. Species richness was lowest in the high marsh zone dominated by *Spartina spartinae* (gulf cordgrass), and highest in *Scirpus olneyi* (Olney's three-square bulrush). *S. spartinae* zone was low in habitat diversity, whereas *S. olneyi* had several open ponds that were utilized by waders and ducks. Deeper water levels in 1991 in *Spartina patens* zone may have been influenced lower species richness and use in comparison with other years with lower water levels. Greatest bird species diversity in 1986 and 1991 occurred in the saline mud flat zone, under both low and high water conditions. Red-winged Blackbirds (*Aeglaius phoeniceus*) and Boat-tailed Grackles (*Quiscalus major*) utilized all habitats, but the latter did appear to prefer wet over dry vegetation. Eastern Meadowlarks (*Sturnella magna*) were most common in the upland gulf cordgrass zone. Seaside sparrows were observed in *S. patens* > 50% of the time; Greater and Lesser Yellowlegs (*Tringa melanoleuca* and *T. flavipes*) predominantly used the mudflat zone.

A total of 50 species in 18 families were observed in the Nueces River Delta study (Table IV.B.5.5). Great Blue Heron (*Ardea herodias*) were the most frequently seen. Gulls and terns (Laridae) and shorebirds (Charadriidae, Scolopacidae), and waders (Ciconiiformes) were the most abundant groups (Fig. IV.B.5.13).

Table I.V.B.5.5. Total numbers and frequencies of occurrence of birds in a marsh in the Nueces River delta September 1993 - August 1994 (compiled from Nicolau, 1995).

Common Name	Total	Frequency
Sandpipers	162	47.9
Swallows	140	35.4
Forster’s Tern	139	72.9
Laughing Gull	116	68.8
Least Tern	116	35.4
Ducks	76	20.8
Roseate Spoonbill	71	33.3
Great Blue Heron	67	83.3
Snowy Egret	61	50.0
Red-Winged Blackbird	56	27.1
Wood Stork	53	4.2
American White Pelican	40	12.5
Bronzed Cowbird	39	6.3
Cormorants	36	25.0
Black-necked Stilt	35	22.9
Willet	34	39.6
Dowitcher	29	4.2
Common Egret	28	31.3
Black Skimmer	21	18.8
Caspian Tern	17	29.2
Black-bellied Whistling Duck	16	10.4
Greater Yellowlegs	13	12.5
Northern Harrier	9	18.8
Northern Pintail	8	4.2
Meadowlark	8	8.3
Tricolored Heron	7	10.4
Mourning Dove	7	8.3
Turkey Vulture	7	8.3
Killdeer	6	6.3
Gull-billed Tern	5	6.3
American Avocet	5	6.3
Long-billed Curlew	5	10.4
White Ibis	4	8.3
Mallard	3	2.1
Brown Pelican	3	6.3
Royal Tern	3	6.3
Clapper Rail	3	6.3
Black-bellied Plover	2	2.1
Reddish Egret	2	4.2
Least Sandpiper	2	2.1
Common Nighthawk	2	4.2

Table IV.B.5.5. Continued.

Common Name	Total	Frequency
Black-crowned Night Heron	2	2.1
Least Bittern	2	4.2
Western Sandpiper	1	2.1
Herring Gull	1	2.1
Black Tern	1	2.1
American Coot	1	2.1
Marsh Wren	1	2.1
Spotted Sandpiper	1	2.1
Little Blue Heron	1	2.1
Total	1447	

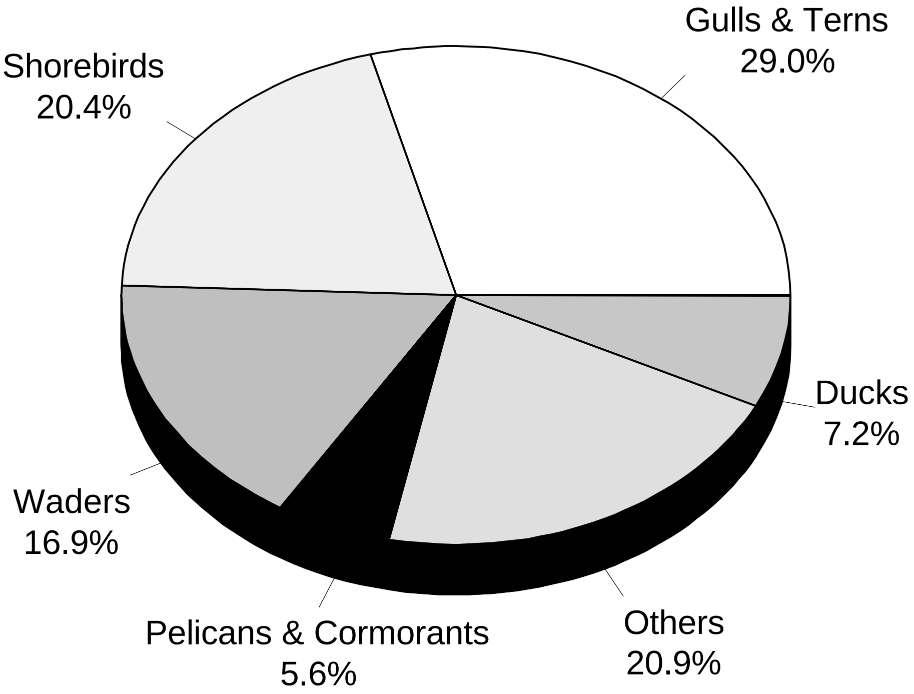


Fig. IV.B.5.13. Community composition of birds observed in a marsh in the Nueces River delta September 1993-August 1994 (data from Nicolau, 1995).

Although several species of rodents inhabit the interface between high marsh and uplands, *Oryzomys palustris* (rice rat) lives in and nests among vegetation of coastal marshes (Sharp, 1967; Davis and Schmidly, 1994). Larger mammals, such as *Procyon lotor* (raccoon), are widely distributed across the coastal marsh in search of prey items, but are found more often in salt, brackish, and intermediate marshes than in fresh marshes in Louisiana (Linscombe and Kinler, 1985).

5.5 Ecosystem Processes

5.5.1 Energy Flow

No comprehensive information was found concerning energy flow and nutrient cycling processes within the CCBNEP study area. A synthesis of related information is presented to describe the function of coastal marshes in general. Organisms within the coastal marsh habitat transfer and transform energy and matter through various ecological processes. Magnitude of flow is controlled by physiological rates of organisms, their ecological interactions with other organisms, and their environment that includes both resource availability and environmental factors (e.g., light, temperature, tidal regime, and salinity) (Wiegert et al., 1981). Primary production using solar energy is performed by phytoplankton in the water column, benthic algae in the substrate, and vascular plants in the aerial environment and substrate (Table IV.B.5.6). A minor amount of biomass produced is directly grazed by herbivores; therefore, much of the flow of energy is accomplished by the detritivores and decomposers via a detrital pathway. In addition, belowground roots and rhizomes of the wetland plants store energy for extensive periods of time and are unavailable to energy pathways. Transformation of vascular plant parts to organic and inorganic compounds is a continual process, although peaks of production and decomposition occur seasonally (Wiegert et al., 1981).

Carbon has commonly been used to follow flow of materials through coastal marsh systems. Carbon is imported into and exported out of the marsh via tidal forces, flooding, and migration of organisms between coastal marshes and adjacent systems (Wiegert et al., 1981). Most organic carbon enters the pathway as particulate organic carbon (POC), and smaller amounts of dissolved organic carbon (DOC) are secreted by living plant material and microorganisms on dead standing culms (Gallagher et al., 1976; Gallagher and Pfeiffer, 1977). Since a large amount of plant material is produced in coastal marsh systems, the potential of transformation of carbon in cellulose by cellulytic bacteria could be significant. However, activities of the cellulytic bacteria can be limited by availability of nitrogen in the form of ammonia which may increase degradation time of detritus (Tenore et al., 1977). Therefore, ammonifying bacteria control the flow of carbon and detrital degradation by controlling cellulytic bacterial activities.

Teal (1962) reviewed pathways of other systems and constructed a classic energy flow model for a Georgia salt marsh incorporating energy values (Fig. IV.B.5.14). Producers were the most important in assimilating energy from the sun, bacteria degraded about 1/7 of the energy of producers, and animal consumers degraded 1/7 of total bacterial degradation (Table IV.B.7). Respiration values are higher in coastal marshes than that of other systems and may be related to the osmotic stress on organisms in coastal marshes. In addition, a large proportion of the high

Table IV.B.5.6. Production values for the Duplin River marsh and estuary prorated on the basis of 21% subtidal and 79% intertidal area (adapted from Pomeroy et al., 1981).

Producer Population	g C^{-2} yr^{-1}	% Aboveground	% Total
Spartina whole plant	1,216		84
Spartina roots	608		42
Spartina shoots	608	73	42
Benthic algae	150	18	10
Phytoplankton	79	9	6
Total	1,445		
Total Aboveground	758		

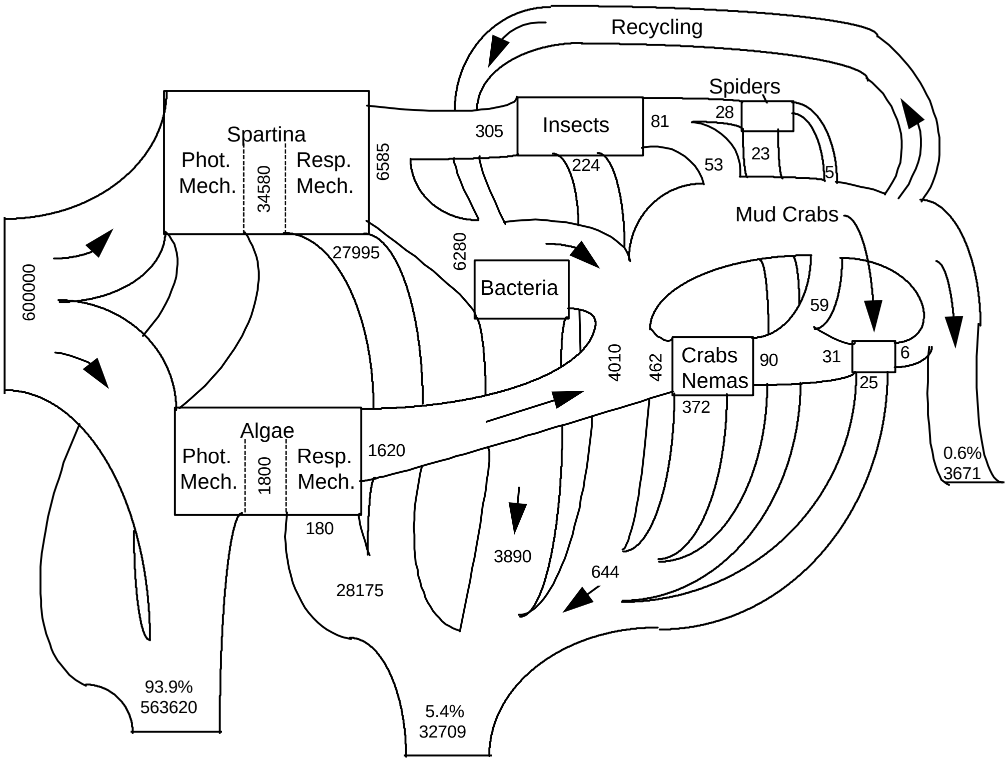


Fig. IV.B.5.14. Energy flow model from a Georgia salt marsh (adapted from Teal, 1962).

Table IV.B.5.7. Summarization of salt marsh energetics for a coastal marsh in Georgia (adapted from Teal, 1962).

Input as light	600,000 kcal/m^2/yr
Loss in photosynthesis	563,620 or 93.9%
Gross production	36,380 or 6.1% of light
Producer Respiration	28,175 or 77% of gross production
Net Production	8,205 kcal/m^2/yr
Bacterial respiration	3,890 or 47% of net production
Primary consumer respiration	596 or 7% of net production
Secondary consumer respiration	48 or 0.6% of net production
Total energy dissipation by consumers	4,534 or 55% of net production
Export	3,671 or 45% of net production

net production of coastal marsh is not utilized by grazers, but is assimilated into the detritus food web (up to 90%) and transported into adjacent bay systems (Wiegert et al., 1981).

5.5.2 Trophic Levels and Food Webs

Marsh structure is generally characterized by plant species assemblages in relation to elevational and salinity gradients in the vegetated areas, tidal creeks, and unvegetated tidal flats. Energy pathways follow transfer and transformation of energy from sunlight through autotrophic plants and heterotrophic organisms, and are best understood by construction of a food web. Each taxonomic group of organisms is an integral part of energy transfer in the coastal marsh system and can be generally grouped as producers and consumers. Producers are typically categorized as vascular plants, algae and phytoplankton. Delineation of consumers can be divided between herbivores and carnivores. Teal (1962) diagrammed the food web for a Georgia marsh using these categories and illustrated the feeding organization in important marsh organisms. These key organisms illustrated diversity of terrestrial, estuarine, aquatic, and benthic biota but did not include detritus-algae feeding group: fiddler crabs, oligochaetes, *Littorina*, and nematodes as deposit feeders, and *Modiolus* and *Manayunkia* as suspension feeders.

5.5.3 Nutrient Cycling

Availability of inorganic nutrients controls the productivity of organic matter in coastal marsh systems (Teal, 1962; Whitney et al., 1981; Mitsch and Gosselink, 1993). Toxic amounts of some nutrients can further limit growth production thus playing a key role in growth rates of marsh organisms. Although several inorganic nutrients are essential for growth and maintenance, availability of nitrogen, phosphorus, iron, manganese, and sulfur has been examined in detail. Periodic aerobic and anaerobic status of marsh sediments affects availability of these key nutrients. Nitrogen cycling in coastal marshes typifies the complex interrelationship of aerobic and anaerobic layers of marsh soils. Oxidation of ammonium into nitrate occurs in the aerobic layers, whereas nitrate is reduced to nitrous oxide and nitrogen gas in anaerobic layers (Fig. IV.B.5.15). Nitrates and ammonium can be utilized by wetland plants, although ammonium is typically the nitrogen form used. Most nitrogen is held in reserve in the sediment and new nitrogen sources are introduced via tidal waters (DeLaune, 1981). Phosphorus enters the coastal marsh via surface water flow, and is stored primarily in sediments (Pomeroy and Wiegert, 1981). Phosphorus is only available to plants under anaerobic conditions, because the nutrient is bound with iron, calcium and aluminum in aerobic sediments. Enough phosphorus is available for emergent plant uptake, so this nutrient does not limit growth or export to adjacent estuarine systems (Fig. IV.B.5.16).

Iron and manganese are available in high levels during flooded conditions and may reach toxic concentrations. Both elements are utilized by wetland plants in reduced forms (ferrous and manganous). Excess ferrous iron around roots of emergent plants is oxidized by oxygen diffusion from root cells, where it immobilizes phosphorus and forms an impenetrable coating on the root surface, thus effectively limiting nutrient uptake (Gambrell and Patrick, 1978). Very low levels of iron and manganese are needed by plants and, because of availability under anaerobic conditions, are taken up and stored in high concentrations in plant tissue (Ernst, 1990).

Carbon transformations can occur under aerobic and anaerobic conditions (Fig. IV.B.5.17), although the anaerobic process is of major interest in wetland science. Fermentation of organic matter is carried out by facultative and obligate anaerobes whereas bacteria play an important role in methanogenesis. Under extremely reduced conditions, methane is produced and released to the atmosphere when sediments are disturbed. Sulfides are also released during sediment disturbance, resulting in a “rotten egg” odor (Fig IV.B.5.18). Sulfur is reduced via two pathways: assimilatory reduction reduces sulfur that is incorporated into S-amino acids, and dissimilatory sulfate reduction as a result of anaerobic respiration of bacteria in the substrate.

5.5.4 Linkages with Other Systems

Physical positioning of coastal marshes between upland, riverine, and estuarine systems has a significant effect on structure and functioning of this habitat. Upland and riverine drainage transport freshwater, nutrients, sediments, organic material, toxins, and pollutants into coastal marshes. Freshwater inflow lowers salinity levels, thus causing a significant influence on species composition and productivity of plants and animals. Marshes also act as a sink for nutrients brought in by riverine and upland waters and, in return, function as a source for adjacent estuarine systems. Sediments carried into coastal marsh systems replenish that amount lost by tidal energy, thus maintaining coastal marsh elevation. Sediment types in coastal marshes are dependent upon sediment sources and influence the presence/absence and abundance of coastal marsh biota. Organic material from riverine systems is an important component in the food web and energy flow and is utilized by numerous plants and animals in the coastal marsh. Organic materials from the coastal marshes are also sources of organic carbon and reduced ammonia to adjacent estuarine systems. Toxins and pollutants may also accumulate in marsh sediments and plants because of the ability of marshes to absorb and assimilate many materials.

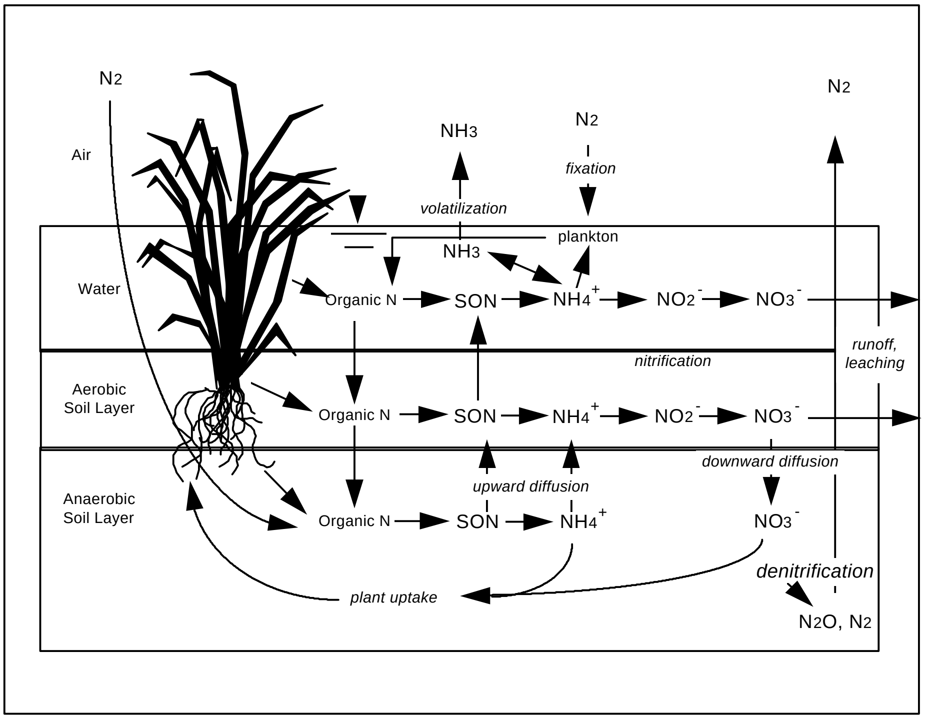


Fig. IV.B.5.15. Nitrogen transformations in wetlands (adapted from Mitsch and Gosselink, 1993; used by permission).

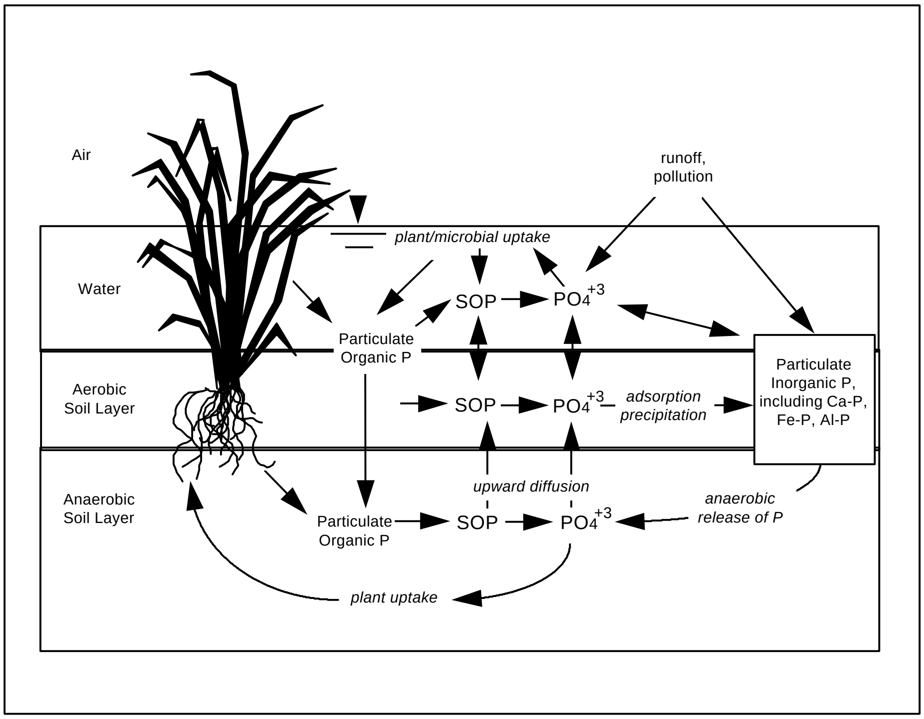


Fig. IV.B.5.16. Phosphorus transformations in wetlands (adapted from Mitsch and Gosselink, 1993; used by permission).

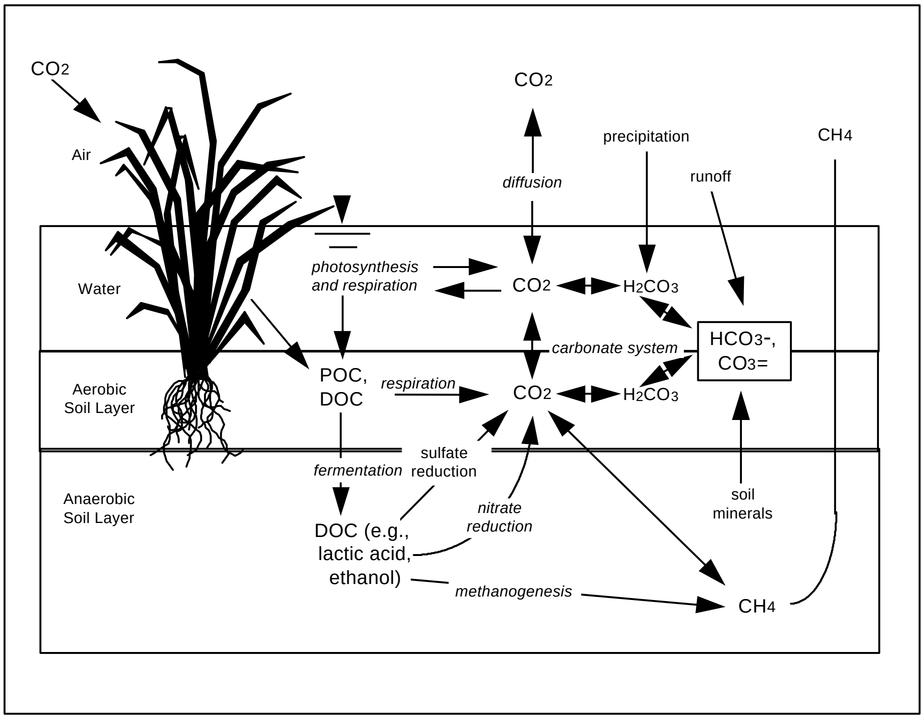


Fig. IV.B.5.17. Carbon transformations in wetlands (adapted from Mitsch and Gosselink, 1993; used by permission).

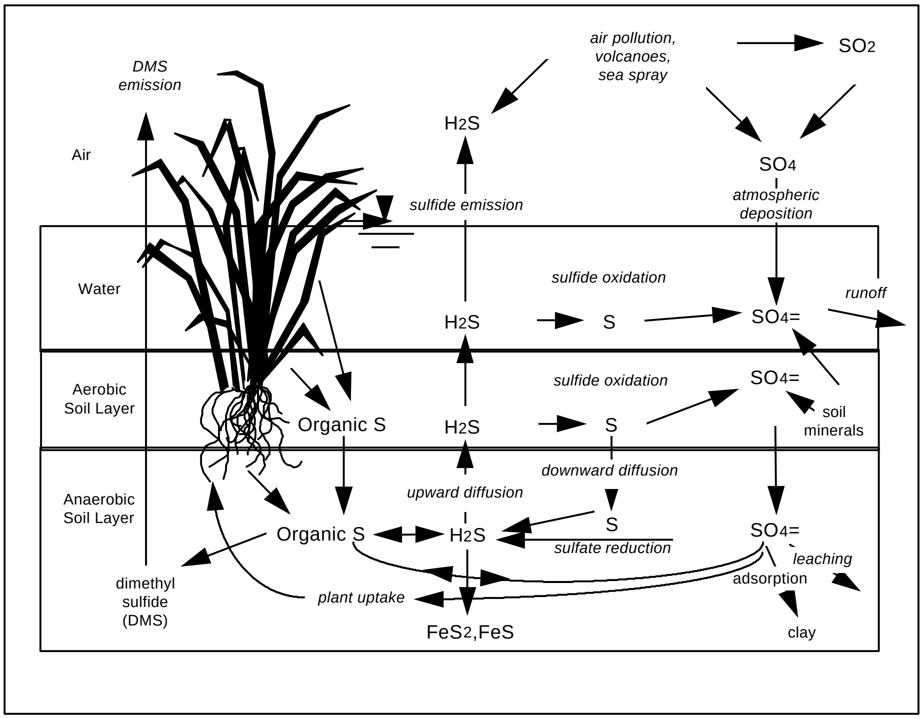


Fig. IV.B.5.18. Sulfur transformations in wetlands (adapted from Mitsch and Gosselink, 1993; used by permission).

Dredge and fill operations constitute threats to coastal marsh systems, as do oil and chemical spills, changes in freshwater inflows, coastal development, and coastal subsidence. Mitigation projects often involve attempts at to create coastal marsh systems, sometimes at the expense of other coastal ecosystems such as tidal flats. While we are often able to create a marsh that looks like a natural marsh, our ability to replace function is questionable. Too few studies have addressed what constitutes failure and success for us to feel comfortable in our ability to create a working marsh. Destruction of marshes and other coastal systems must be avoided; we must not be lulled into a false sense of security because we can “create more”. Avoidance of disturbance and destruction (thus mitigation) is our first best defense; restoration and enhancement projects should be chosen over creation whenever possible.

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HABITAT 6: TIDAL FLATS

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HABITAT 6: TIDAL FLATS

6.1 Physical Setting and Processes

6.1.1 Definition and Distribution within Study area

Tidal flats ("sabkhas") are seemingly barren, relatively featureless sand and/or mud environments bordering lagoons and bays. Within the study area, most tidal flats are "wind-tidal flats". These flats may be inundated by seasonal and astronomical tides, but are generally inundated and exposed only at irregular intervals by wind and stormtides, and/or by ponded rainwater. Inundation or exposure may occur rapidly (within a few hours) depending on the speed and direction of the wind (Fisk, 1959; Hayes and Scott, 1964; Hayes, 1965; Brown et al., 1977; White and Galloway, 1977; Weise and White, 1980). Because tidal inundation is irregular and extreme temperatures occur when thin sheets of water are heated by the sun, macrophytic plant communities cannot develop and biologic activity is often restricted to felts or mats of blue-green algae which form over the surface of and bind the sand and/or mud substrate (Pulich et al., 1982).

Tidal flats occur primarily along the bay sides of the barrier islands, and to a lesser extent, along bay margins, around river deltas, and the mouths of creeks. Moving southward, wind-tidal flats replace salt marsh vegetation, particularly on the barrier islands. The shift from salt marsh to wind-tidal flat coincides with the increased eolian erosion which accompanies decreasing barrier island vegetation (Brown et al., 1976). Wind-tidal flats reach their greatest development from Yarborough Pass (Padre Island) southward.

Approximately 160 square kilometers of wind-tidal flats occur within the study area (Table IV.B.6.1). Nearly 79% of the tidal flats in the study area are found on the bay sides of St. Joseph Island (Aransas County), Mustang Island (Nueces County) and Padre Island (Nueces and Kleberg counties), and at the bay margins of Baffin Bay and its secondary bays (Kleberg County). The remaining wind-tidal flats are found in the deltas of the Mission, Aransas, and Nueces rivers, scattered along the bay margins of Nueces, Copano, and Redfish bays, and in the valleys along the lower reaches of Oso, Petronila, San Fernando, and Olmos creeks where the gradient decreases and the streams flow onto the wind-tidal flats of Oso Bay, Alazan Bay, Cayo del Grullo, and Laguna Salada, respectively (Brown et al., 1976, 1977; McGowen et al, 1976).

6.1.2 Historical Development

Tidal flats in the study area began developing after sea level reached its approximate present level 2,800 to 2,500 YBP. During that time, the significant processes which contributed to the formation of tidal flats were: (1) headward-eroding streams eroding the coastal plain; and (2) development of flood tidal deltas and washover fans associated with bay and lagoon margin environments (Brown et al., 1976).

Table IV.B.6.1. Areal extent of wind-tidal flats in the CCBNEP study area by county (Brown et al., 1976; McGowen et al., 1976; Brown et al., 1977). All values are in square kilometers.

	County (north to south)				
Type of Tidal Flat	Refugio	Aransas	San Patricio	Nueces	Kleberg
Fluvial-deltaic System					
Wind-tidal flat, sand and mud, firm, occurs locally in lower stream valley, transitional between bay and stream	7.0	11.4	9.6	0.0	3.1
Bay-Estuary-Lagoon System					
Wind-tidal flat, sand and mud, firm	0.0	0.0	0.0	37.0	69.9
Wind-tidal flat, sand and mud, extensive algal mats, alternatively emergent-submergent	0.0	0.0	0.0	0.0	2.6
Wind-tidal flat, mud and sand, algal-bound mud, gypsiferous, firm	0.0	2.6	0.0	3.1	0.0
Wind-tidal flat, sand and mud, barren to sparsely vegetated, subaerial, burrowed	0.1	13.7	0.0	0.0	0.0
Transitional zone, wind-tidal flat to eolian sand sheet, wind deflation, concentrated clay dunes, sand	0.1	0.0	0.0	0.0	0.0
Total wind-tidal flat by county	7.2	27.7	9.6	40.1	75.6
Percent of total	4.5	17.3	6.0	25.0	47.2

In estuarine deltaic environments, tidal flats develop upon crevasse splays, abandoned levees, relict meanderbelt sands, and slopewash-alluvial fans along valley walls (Fig. IV.B.6.1). Wind-tidal flats in lower reaches of streams such as Oso and Petronila Creeks, develop on fluvial fan-delta sand deposits where the gradient decreases and erosional character of the stream diminishes (Fig. IV.B.6.1B). In Baffin Bay, these tidal flats develop on sandy valley-fill that was deposited in late Holocene and Modern times during brief periods of high discharge, usually associated with tropical storms or hurricanes. Between floods, long periods of eolian or wind-tidal modification and/or destruction of the fluvial deposits occurs (Brown et al., 1977). Since sea level reached its present level, the bayhead fan or lacustrine deltas at the mouths of rivers and ephemeral streams upon which tidal flats develop have been slowly filling the upper ends of the estuaries (Brown et al., 1976; Brown et al., 1977).

Wind-tidal flat development reaches its peak in bay and lagoon margin environments, particularly on Mustang and Padre islands (Fig. IV.B.6.2). Tidal flats form on the surface of sediments transported into the Laguna Madre from the islands by wind and storm-surge tides. During hurricanes when storm surges breach the islands, storm-generated currents carry sand to the bayside of the island where it is deposited as a washover fan behind the ridge. These low, unvegetated, sandy lobes are deposited at the point where the constricted hurricane channel opens onto submerged wind-tidal flats. Subsequent eolian modification of the fans has provided most sediment that has produced the extensive wind-tidal flats in the Laguna Madre (Fisk, 1959; Brown et al., 1977). A very large washover fan with wind-tidal flats occupies the northern end of St. Joseph Island in Aransas Bay (McGowen et al., 1976). Parts of the flood-tidal delta of Harbor Island (Redfish Bay) are also occupied by wind-tidal flats.

Tidal flats that occur on the mainland bay margin develop where southeasterly winds deflated older eolian deposits, Pleistocene barrier-strandplain deposits, and deltaic deposits. Mainland tidal-flats are generally small and are scattered throughout the study area. Their greatest development occurs around Baffin Bay (Brown et al., 1976; McGowen et al., 1976; Brown et al., 1977).

The most extensive tidal flats on the entire Texas coast are located immediately south of the CCBNEP study area. This area, known as the Landcut, consists of an area of the Laguna Madre that has been filled with barrier island sand linking Padre Island with the mainland. The mainland in the Landcut is distinctly indented and deflated to form extensive wind-tidal flats as well (Fisk,1959).

6.1.3 Physiography

Regardless of formation or location, tidal flats in the study area are found at elevations between mean sea level (MSL) and 1 m (2-3 ft) above MSL. They slope gently lagoonward (≈ 10 cm/km) (Herber, 1981) and may occasionally be sparsely vegetated with *Salicornia biglowii* or other halophytic vegetation, particularly after extended rainy periods. Tidal flats in the study area range from high, sandy flats to low, depressed, muddy flats.

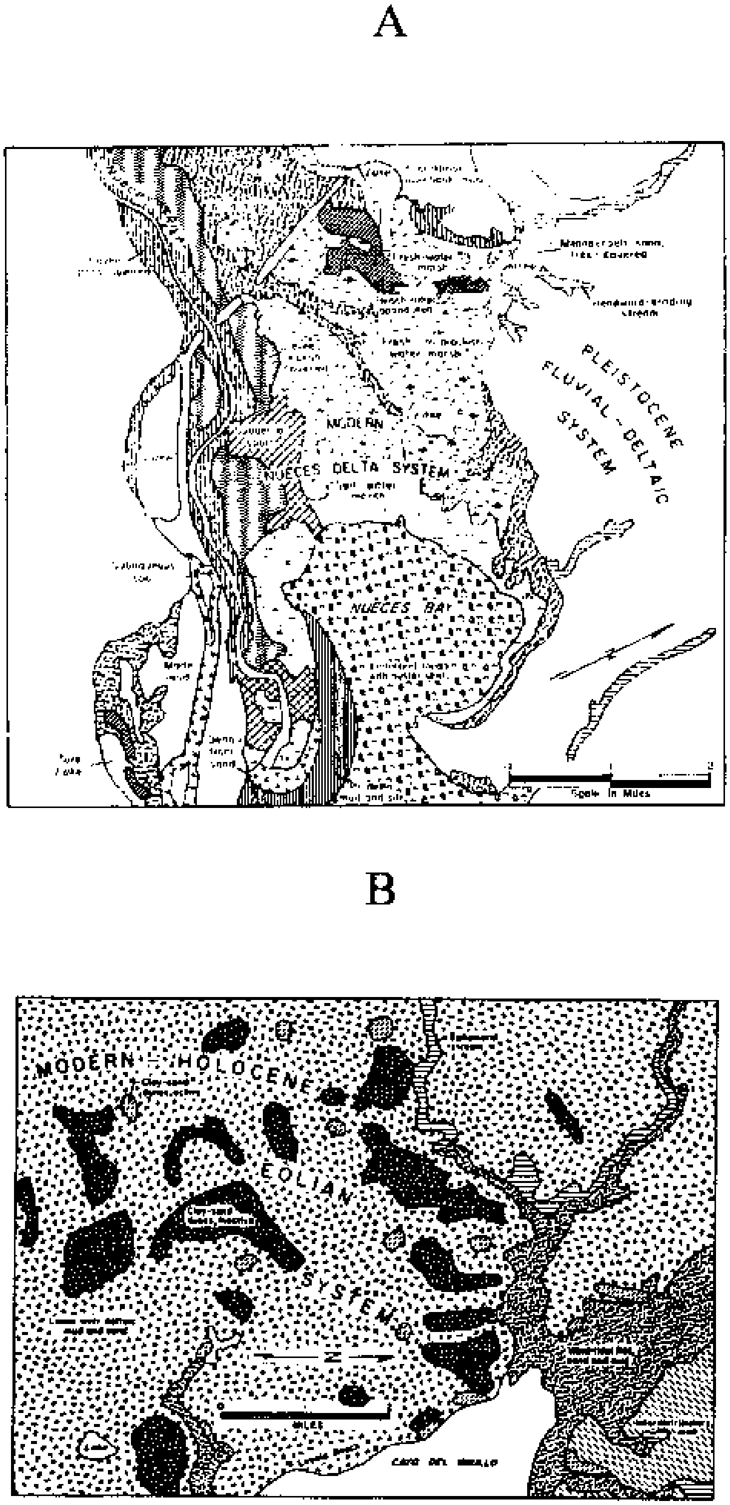


Fig. IV.B.6.1. Development of tidal flats in deltaic environments: (A) tidal flat development and extent in the Nueces River delta (from Brown et al., 1976); (B) tidal flat development in the stream courses of ephemeral streams flowing into Baffin Bay (from Brown et al., 1977).

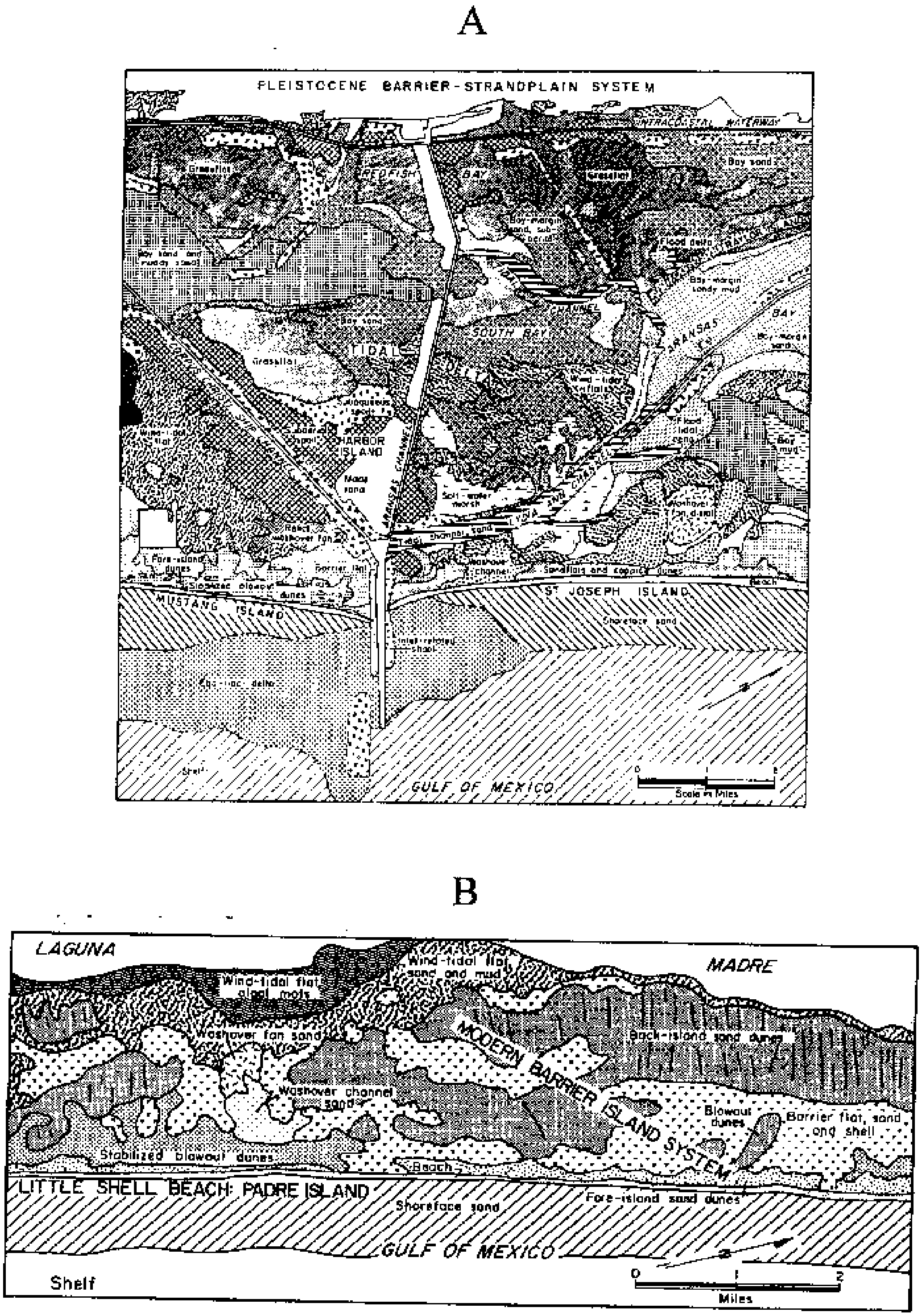


Fig. IV.B.6.2. Development of tidal flats in barrier island and tidal-delta environments. (A) Tidal flat development on Mustang and St. Joseph islands near Aransas Pass, including Harbor Island (from Brown et al., 1976); (B) Tidal flat development on Padre Island (from Brown et al., 1977).

Herber (1981) stated the entire wind-tidal flat should be classified as intertidal, however, this may be inappropriate since only a small portion of the flat is affected by astronomical tides. He divided Padre Island wind-tidal flats into upper, middle, and lower intertidal flats. The lower intertidal flat was flooded nearly daily and was completely dry only during extreme low tide during summer. The upper intertidal flat was totally covered with water about 20 days annually (≈5%) during very strong winter storms or extreme high tides. The middle flat was flooded for some intermediate number of days, usually during winter storms and extreme high tides.

Although Herber's observations concerning timing and length of inundation are correct, Withers (1994) recognized that because the effect of astronomical tides on wind-tidal flats is negligible, a mosaic of microhabitats occurs rather than zoned habitats similar to sandy beaches. Three microhabitats were defined based on water depth and saturation of substrate: (1) Intertidal - areas at the edge of the water covered with 2-5 cm of water; (2) Wet - usually saturated but always wet areas, often covered with a film of water up to 2 cm deep; and (3) Damp - areas that may appear dry on the surface but are damp to wet below the surface, occasionally with standing water (up to 2 cm deep) in depressions. Areal coverage of microhabitats differs with water levels, and occasionally microhabitats are nonexistent. A typical back island flat is generally dry and sandy at the highest elevations near back island dunes, where inundation is rare. As elevations decrease, bare sand and/or mud grade into sand and/or mud covered with a blue-green algal mat, particularly at and just above MSL where inundation and exposure normally occur, if somewhat irregularly. There is a sharp textural boundary between the rarely exposed sandy or muddy areas below MSL and the blue-green algal flat, with a "step up" onto the algal bound areas (Herber, 1981, K. Withers, pers. obs.) (Fig. IV.B.6.3). Flats on Padre Island are unique because they are not crossed by tidal channels (Herber, 1981).

In deltaic environments (Fig. IV.B.6.4A), tidal flats replace salt and brackish water marsh vegetation locally. In lower reaches of ephemeral streams and along bay margins, wind-tidal flats may be backed by clay dunes such as along Oso Bay and Baffin Bay lower tributary drainages (Fig. IV.B.6.4B). St. Joseph's Island is a unique case in which wind-tidal flats are interspersed with active washover fan components (Fig. IV.B.6.5).

6.1.4 Geology and Soils

Sedimentary processes are summarized in Table IV.B.6.2. Winds are the primary force which shape topographic and sedimentological features of tidal flats. Eolian transport of sands from barrier islands is the principal means by which flats increase in size. Previously estimated vertical accretion rates for Padre Island of approximately 6 mm/yr (1 ft/50 years) (Fisk 1959, Lohse 1958) have been discredited as too rapid. More recent work by Miller (1975) using ^{14}C dating of algal mat material revealed that vertical accretion of sediments in the Landcut area has been gradually decreasing during the past 2,500 years from 0.5 mm/yr to 0.25 mm/yr or less. The area became subaerial and deposition was complete about 200 years ago (Long and Gudramovics 1983).

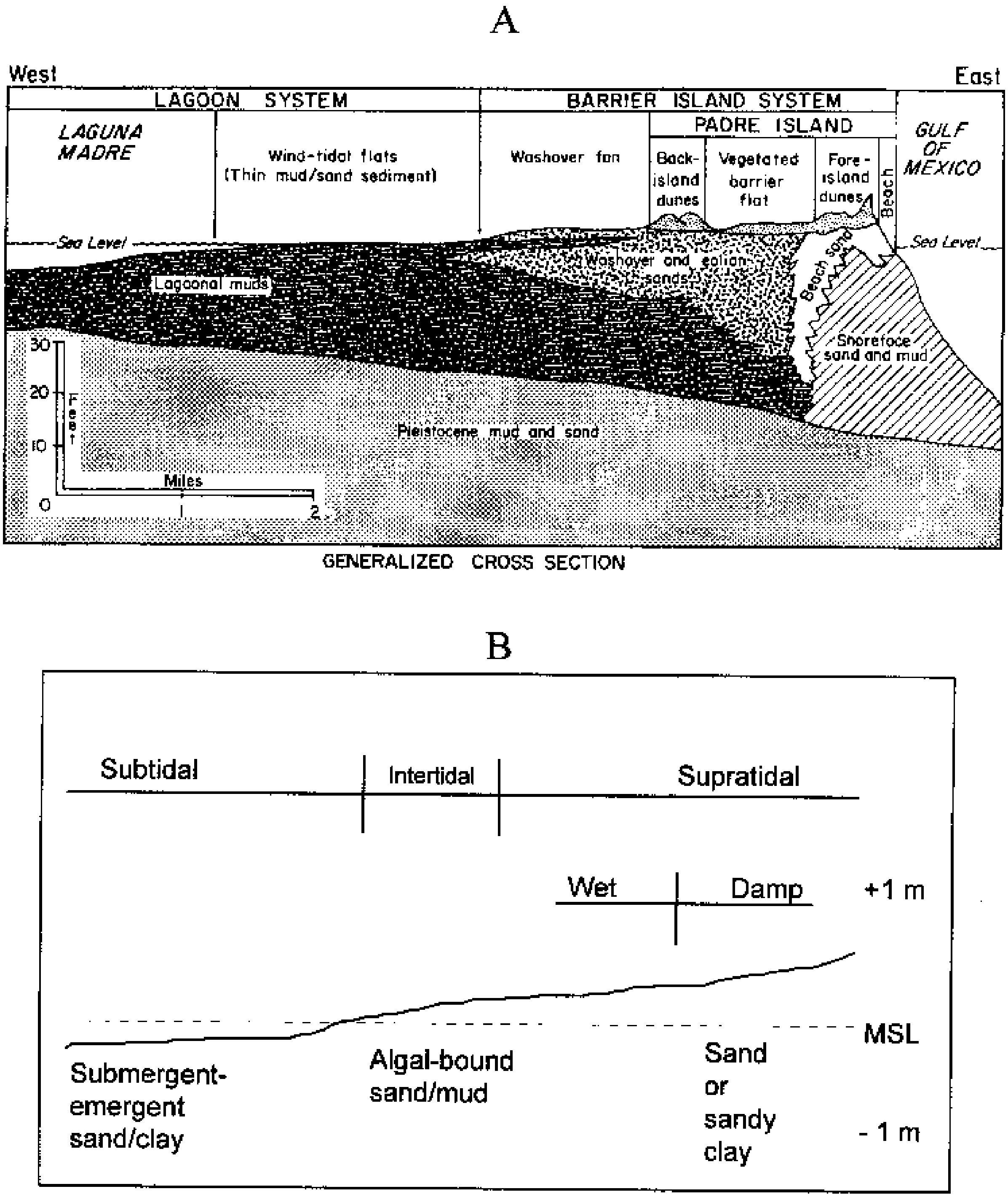


Fig. IV.B.6.3. (A) Profile of barrier island tidal flats showing relationships between flats and other topographic features (from Brown et al., 1977); (B) Schematic of tidal flat showing physiographic zonation.

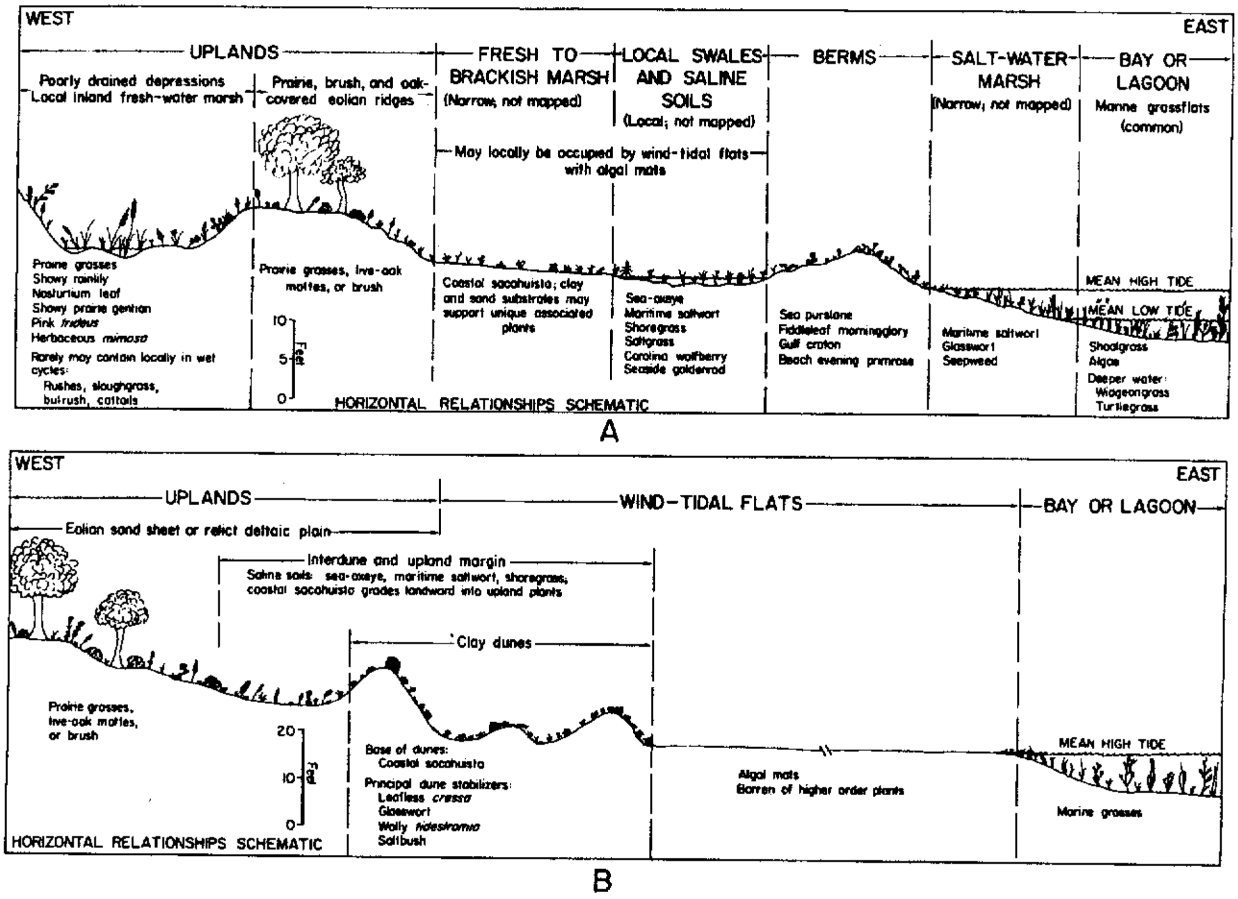


Fig. IV.B.6.4. Profiles of mainland tidal flats showing relationships between flats and other topographic features (from Brown et al., 1977). (A) Positioning of deltaic flats; (B) Positioning of bay margin or lower stream course tidal flats.

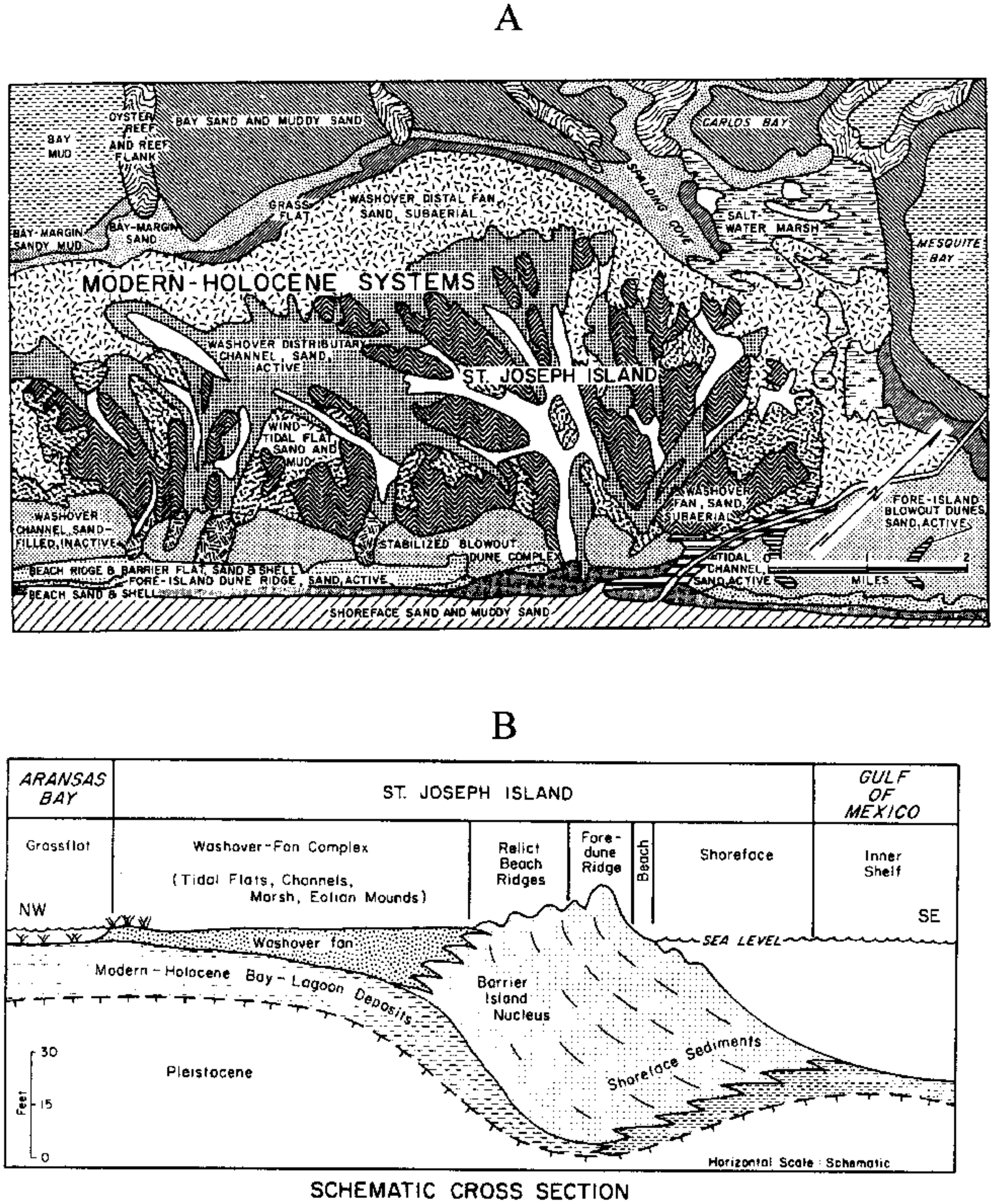


Fig. IV.B.6.5. Tidal flats on St. Joseph Island. (A) Relationships of tidal flats to other washover fan components (from McGowen et al., 1976); (B) Profile of flat showing relationships to other topographic features (from Brown et al., 1976).

Table IV.B.6.2. Summary of sedimentary processes affecting wind tidal flats (Herber 1981).

Type of Process	Process Description	Effect
Biologic	Disruption by plants	Minor
	Trapping or binding by blue-green algae	Major
	Addition of detritus by shell	Minor
	Addition of detritus by plants (seagrasses)	Major
Physical	Currents - wind tides	Major
	Currents - storms	Minor
	Eolian transport - sand	Minor
	Desiccation	Major
Chemical	Precipitation of carbonates	Major

In addition to direct transport, winds shift lagoonal waters which carry suspended materials, create currents capable of transporting sand, and generate waves that locally erode mainland margins. The upper Laguna Madre is aligned northeast across the prevailing wind direction. Southeasterly winds force sediment-laden waters away from Padre Island into Baffin and Corpus Christi bays. Fisk (1959) stated that floodwaters over mainland flats were usually murky with suspended particles while island floodwaters were generally "crystal clear". "Northers", winter storms with strong northerly winds of long duration, or other storms push sediment-laden waters back onto the island flats and some mainland flats (e.g., Oso Bay). Advancing sheets of water carry clays to the western sections of the flats and nourish the blue-green algal mats. Sedimentary events of this type are infrequent and seasonal on barrier island flats (Fisk, 1959; Herber, 1981).

Blue-green algal mats directly affect various sedimentation processes. When the mat is wet or wind velocity is too low to move sand, the mat acts a membrane keeping most transient sand separate until conditions are favorable for further transportation (Herber, 1981). When floodwaters lay over the mat for any length of time, the filamentous algae which compose it extend a few millimeters into the water. Clays settling from the water are intermixed with the algal carpet. When the mat is exposed for extended periods, a system of polygonal cracks forms and dry pieces of the mat are pulled up by the wind and blown across the flat. Curled laminae within the alternating laminated and massive gray clays attest to a long history of alternating wet and dry periods with concomitant algal growth and decay, resulting in diagenesis through bacterial action. Bacteria thrive in a reducing zone found directly beneath the mat surface and form massive gray clays by destroying organic portions of the algal mat (Fisk, 1959).

Although deflation is not a prominent process, when the algal mat becomes thoroughly desiccated, the resulting leathery crust cracks and peels away from the substrate. Clays exposed in cracks, 2-5 cm below the surface, aggregate into sand-sized granules which are blown across the flats (Fisk, 1959). These clay pellets provide the principal source of sediments for wind-accretion deposits such as clay dunes which fringe the landward edge of mainland wind-tidal flats (Brown et al., 1977). When the mat is flooded, bottom-feeding fish such as *Pogonias cromis* (black drum), *Sciaenops ocellata* (red drum), and *Mugil cephalus* (striped mullet) break the algal crust leaving small, circular pits that are readily scoured by wind when the mat is exposed (Fisk, 1959).

Wind-tidal flat sediments are composed of alternating layers of sand and mud. Flat sediments on barrier islands are texturally uniform and composed primarily of medium or fine sands (63-250 µm) (Withers, 1994). Bioturbation is virtually nonexistent as shown by distinctive alteration of sand and mud layers. Island flats are dominated by sand while mainland flats are dominated by mud. On all flats, thickness of sand layers decreases with depth while thickness of mud layers increase. Sand dominates on the eastward edge of a flat and decreases to the west, where mud becomes massive at the top and laminated at depth. Laminations are composed of organic rich layers alternating with authigenic mineral and mud. Shell is rare, limited to a few small shell berms on the islands and along the eastern margin of the mainland, and decreases westward (Herber, 1981).

Tidal flats in Baffin Bay and adjoining areas of the upper Laguna Madre contain abundant clay and sand lamina. Thick lamina composed of blue-green algae are also common. In areas where wind-tidal flow is restricted, algal-bound, gypsiferous clay and sand comprise the deposits. In locally depressed basins which retain water, thick clay lamina may be deposited interbedded with abundant algal mats (Brown et al., 1977). Clays in the northern lagoon area are probably transported by currents in Corpus Christi Bay, introducing material derived from both marine water entering Aransas Pass, and freshwater from the Nueces River. Smaller quantities of clay are derived from runoff from small streams which enter Baffin Bay and local runoff along the mainland margin (Fisk, 1959). Evaporite minerals (gypsum, halite, dolomite) are precipitated from thin sheets of water that advance across the flats. Shallow water is subject to high evaporation and salinity is greatly increased. Halite crystals which form on the tidal flat surface go into solution the next time the flat is inundated (Fisk, 1959; Brown et al., 1977).

6.1.5 Hydrology and Chemistry

Wind-tides are the primary cause of tidal flat flooding although astronomical tides may be important, particularly from Corpus Christi Bay northward. In deltaic and bay margin areas in the northern portion of the study area, astronomical tides may flood lower flats (approximately 0.25 m above MSL). Flats at elevations higher than 0.25 m above MSL are inundated mainly when winds are aligned to blow directly along the axis of the estuary. Bay waters are pumped through delta-plain marsh environments to flats via tidal creeks and small tidal passes during severe storms or long periods of persistent easterly or southeasterly winds (Brown et al., 1976).

In the Laguna Madre and Baffin Bay, affects of astronomical tides are virtually nonexistent although once or twice a year, they may temporarily meet or exceed wind tides (Brown et al., 1977). Mean annual tide range is about 10 cm but the maximum range of water levels produced by wind tides is about 1.0 m (Fisk, 1959). Flooding of flats in the Laguna Madre and upper Baffin Bay occurs at rates directly related to strength and persistence of winds. Southeasterly winds of 13-17 km/hr forced water over flats in the Landcut 0.5 to 1.0 km/day. When wind speeds increased to 30-50 km/hr, the wind-tidal surge moved 4.2 to 6.1 km/day. Strong northerly winds pushed water completely across the Landcut in 36 hours at rates of 12 km/day (Fisk, 1959). During a 24 hr period with north winds of 8-20 km/hr, Amdurer (1978) noted a 6 cm rise in water level on a site on the Laguna Madre Flats (Kenedy County). When the wind direction changed, floodwater receded rapidly, with a drop of 3 cm in four hours. Complete inundation and exposure of a flat approximately 1 km wide in only a few hours has been observed on north Padre Island (K. Withers, pers. obs.).

Hydrology of tidal flats in arid areas ("sabkhas") has been the subject of debate for many years. Four models have been proposed: seepage reflux (Adams and Rhodes, 1960), capillary fringe (Friedman and Sanders, 1967), evaporative pumping (Hsü and Siengenthaler, 1969), and flood-recharge (Butler, 1969; Masson, 1955). The reflux model proposes that because surface inflows of seawater are restricted, hypersaline brines formed in evaporating ponds on the surface of the sabkha percolate down through the sediment because it is denser than the underlying flood waters, and flows seaward at depth. This is a subaqueous process because reflux and evaporation takes place only while flood waters are present. The capillary fringe model is an extension of the normal flow regime for groundwater in coastal plains in which groundwater flows seaward through the sabkha. Interstitial water moves upward by capillary action where it evaporates, producing a caliche-like evaporite layer above the water table. In this model, dissolved solids and evaporite precipitates are derived from continental sources rather than seawater. The evaporative pumping model postulates that water moves upward in the sabkha to replace water lost near the surface by evaporation. With seawater recharge, the water table is level and slightly below high tide level. With continental recharge, the water table dips seaward and is located above the level of high tide (Amdurer, 1978; Long and Gudramovics, 1983). Flood-recharge is a subaerial process in which flood waters covering the sabkha are concentrated by evaporation and seep down into the sediment. Continued evaporation further concentrates subsurface water. Subsequent flooding by wind, tides, or rain results in more dilute waters near the surface. Movement of water in this model is caused by lowering the water table (Long and Gudramovics, 1983).

Amdurer (1978) stated the salient characteristic of hydrology in the Laguna Madre Flats was the extreme and rapid variability of surface conditions caused by sporadic and flashy distribution of precipitation combined with frequent episodes of wind-tidal flooding. In contrast, geochemistry of the interstitial waters was relatively constant throughout the year. He found the dominant direction of water movement in the Sand Bulge was westward across the flats, away from the freshwater lens on Padre Island (Fig. IV.B.6.6). Infiltration of standing water, as proposed by the reflux hypothesis, was the most important source of interstitial water recharge. It did not occur at a uniform rate and each flooding episode did not necessarily lead to a substantial recharge. Laminated clays and sands and the impermeable algal mat isolate interstitial waters from surface conditions. Infiltration occurs in small areas where the algal mat has been eroded by wind during dry periods, but most recharge occurs through small brine ponds found after wind-tidal flooding. The reflux moves more concentrated surface brines to greater depths. The brine leaves

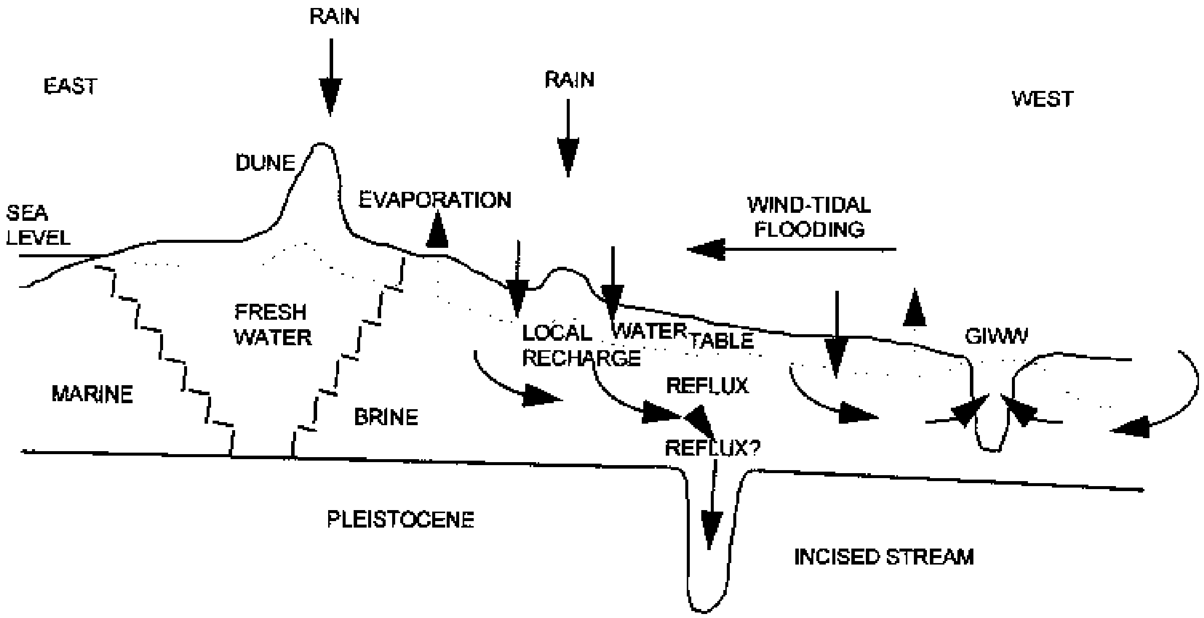


Fig. IV.B.6.6. Model of tidal flat hydrology in the Sand Bulge area of the Laguna Madre Flats (from Amdurer 1978).

the system either by reflux under Padre Island through entrenched Pleistocene stream valleys, mixing with the deeper, fresher regional groundwater, or by seepage into the Laguna Madre through the Gulf of Mexico.

Long and Gudromovics (1983) used bromide as a conservative indicator and found increased bromide concentrations at depth. Recharged waters moved down as salt fingers rather than a continuous salt sheet. They differentiated two water masses, one apparently derived from nonmarine parent water, possibly of continental origin, the other derived from the Laguna Madre. They interpret their data as supporting the flood recharge model proposed by Fisk (1959) and Masson (1959) with reflux and evaporitic pumping of only minor importance.

Freshwater inflows to tidal flats in deltaic areas are greater than those along bay margins and inflows are greatest in areas with sources of permanent water such as the rivers and streams from the Nueces River north. Freshwater inputs to tidal flats in ephemeral stream valleys and along bay margins are unpredictable, and limited to rainfall. Prevalence of hypersaline conditions may account for the greater development of blue-green algal mats in these areas.

Salinities of bay and lagoon waters range from 10-15‰ in Copano Bay, 20-25‰ in Nueces Bay, to 30-40‰ or higher in the Laguna Madre and Baffin Bay (White et al., 1983; White et al., 1989). Salinities of water overlying tidal flats in the northern Laguna Madre ranged from 0-55‰. Pore water (10 cm deep) salinities in wet and damp microhabitats of blue-green algal flats in the upper Laguna Madre ranged from 0 - >160‰. Salinities were lowest following intense rainstorms, or protracted periods of rainfall (Withers, 1994).

South of the study area, geochemistry of tidal flat interstitial (pore) water in the part of the Laguna Madre Flats known as the Sand Bulge was determined (Amdurer, 1978). Chlorinity increased from east to west and with depth. Greatest change was at the fresh water - brine mixing zone where chlorinity increased from 5-8‰ to 79-94‰ at a depth of 1.5 m. The Na/Cl ratio and, to a lesser extent, the K/Cl ratio were generally slightly higher in interstitial waters than in seawater. Interstitial brines reached salinities up to 6.7 times (>200‰) that of the Gulf of Mexico. Surprisingly, they were always undersaturated with respect to gypsum. Ca/Cl and HCO_3/Cl ratios in the brines dropped steadily with increasing salinities but sulfate concentrations were relatively conservative, increasing at about the same rate as chlorinity.

Chlorinity and Na/Cl and K/Cl ratios are generally considered to be conservative, that is, concentrations of ions are controlled by evaporation and/or dilution of source waters. Concentrations in the Sand Bulge area were consistent with the hydrologic model. However, behavior of Ca^{++} and SO_4^{--} was unexpected, with some reaction causing removal of calcium from interstitial brines or their source waters as they concentrate so that gypsum saturation does not occur in this area (Amdurer, 1978).

Several authors have suggested blue-green algae may be indirectly involved in precipitation of carbonates (Dalyrymple, 1965; Davies, 1970; Friedman et al., 1973; Logan, 1974; Monty, 1967). Algal micrites (crytocrystalline aragonite intermeshed with mucilaginous organic material), have been found in close association with blue-green algal mats in Baffin Bay (Rusnak, 1960; Dalrymple, 1965), Middle Ground (Zupan, 1972), and the Sand Bulge (Amdurer, 1978). Grains of algal micrite occurred within the algal mats, between algal laminations, and in the sediment just below mats.

Several hypotheses have been advanced to explain formation of algal micrite grains, directly or indirectly involving organic activity associated with the mat. Removal of CO_2 from surface brine ponds by algal photosynthesis substantially alters carbonate equilibrium in ponds (Oppenheimer and Master, 1965). Monty (1967), Friedman et al. (1973), and Logan (1974) concluded this process promoted precipitation of either cryptocrystalline aragonite or magnesium calcite in a lagoon on Andros Island (Bahamas), an algal pool adjacent to the Gulf of Aqaba (Red Sea), and the supratidal facies at Shark Bay (Australia), respectively. Dalrymple (1965) found no evidence for this process in Baffin Bay, but both Masson (1955) and Fisk (1959) found carbonates on the surface of the Laguna Madre Flats. Carbonate was also found on the surface of the Sand Bulge, as well as in the frothy, white scum found on the surface of brine ponds in the same area (Amdurer, 1978) which indicated reduction of CO_2 by algal photosynthesis could not be ruled out. The second process for precipitation of algal micrite involves decomposition of organic matter in algal mats by sulfate-reducing or ammonifying bacteria (Purdy, 1963; Berner 1971). The bacteria which cause these reactions are abundant in reducing environments found just below the algal mat (Fisk, 1959; Sorenson and Conover, 1962). Dalrymple (1965) found evidence for this process in algal mats around Baffin Bay.

6.2 Producers and Decomposers

6.2.1 Primary Producers

Tidal flats are halophilic, semi-terrestrial ecosystems due to variability in flooding frequency and the duration of exposure between flooding resulting in dry, hypersaline conditions which prevent establishment of macrophytic vegetation (Pulich et al., 1982). Benthic microalgae, which may form felt-like or leathery mats on sediment surfaces, are major primary producers found on tidal flats in the study area. In low-energy, hypersaline areas, mats consisting mostly of filamentous blue-green algae are found. These mats range in thickness from 1-2 mm to nearly 3 cm (Withers, 1994). Classification of blue-green algae is problematical, and taxonomy follows Dr. Francis Drouet as summarized by Humm and Wicks (1980), except where noted. *Lyngbya confervoides* (classification of Bold and Wynne (1978); Drouet classification *Microcoleus lyngbyaceus*), constitutes a minimum of 70% of the living community. *Microcoleus* spp., *Anabaina* spp., *Oscillatoria* spp., *Anacystis* spp., *Schizothrix arenaria*, *S. tenerrimus*, *S. salcicola*, *Spirulina subsala*, and *Johannesbaptistia pellucida* are found in small amounts (maximum 25% cover) (Fisk, 1959; Armstrong and Odum, 1964; Dykstra, 1966; Zupan, 1971; Herber, 1981; Pulich et al., 1982; Pulich and Rabalais, 1986). Pennate diatoms such as *Nitzschia*, *Navicula*, and *Pleurosigma* (<10% total algal biomass) may also be found interspersed among blue-green algae, particularly at moderate salinities (<60‰) (Simmons, 1957; Sorenson and Conover, 1962; Pulich et al., 1982; Pulich and Rabalais, 1986). Blue-green algal mats in the Laguna Madre do not usually contain green algae, unlike those in California and Mississippi (Pulich and Rabalais, 1986).

There has been no research on the benthic microflora of non-algal tidal flats in the study area. In other areas, several groups of microalgae have been found to be important on intertidal flats: benthic diatoms, benthic dinoflagellates, filamentous green algae, and euglenoids. Benthic diatoms may form films which color sediment surfaces brown, and green microalgae may tint sediments bright green. The most numerous diatoms are usually pennate forms such as *Nitzschia*, and *Navicula* (Peterson and Peterson, 1979; Whitlach, 1982). Benthic diatoms may form dense, multilayered sheets on intertidal flats (Pamatmat, 1968).

Photosynthetic and chemosynthetic bacteria may contribute significantly to primary productivity in intertidal flats (Lyons and Gaudette, 1979; Howarth and Teal, 1980). Photosynthetic purple sulfur bacteria such as *Chromatium* spp., *Desulfovibrio* spp. and *Beggiatoa* spp. (Sorenson and Conover, 1962; Armstrong and Odum, 1964; Pulich et al., 1982) and photosynthetic green and purple, nonsulfur bacteria (Horodyski, 1977) have been found with blue-green algal mats in the study area. They are undoubtedly found in sediments of non-algal flats as well, but their occurrence in the study area has not been documented.

When intertidal flats are flooded, phytoplankton are found in waters overlying flats. Little information is available concerning species composition of phytoplankton in these flood waters in the study area. On one occasion, water overlying a tidal flat in Oso Bay contained the diatoms *Nitschizia* (55.6%), *Navicula* (33.3%) and *Pleurosigma* (11.1%) (Hildebrand and King, 1974). Phytoplankton abundances were lowest during summer when temperatures and salinities rise in shallow waters, and highest during winter and early spring (Henley and Rauschuber, 1978). Phytoplankton abundance in tidal flat waters is influenced by nutrient concentrations, water temperature and circulation patterns, and grazing (Whitlach, 1982). In North Carolina tidal flats, various diatoms, especially *Skeletonema*, dominated the phytoplankton assemblage (Peterson and Peterson, 1979). In New England, diatoms were most abundant in cooler waters, while dinoflagellates predominated in warmer waters (Whitlach, 1982). The phytoplankton community in shallow estuaries was not diverse, usually consisting of large concentrations of only one or two species. This pattern was likely the result of physically unstable inshore conditions that favored motile species which do not sink to the bottom in shallow water (Hurlburt, 1956; 1963).

Fleshy, benthic macroalgae are not found on tidal flats in the study area and vascular plants are rare to nonexistent. Scattered salt marsh vegetation may be found, particularly along tidal channels that drain and fill flats, or after extended rainfall. Common species are *Salicornia virginica, S. bigelowii*, and *Batis maritima.* Some tidal channels are fringed by *Spartina alterniflora. Avicennia germinans* may be found fringing tidal channels in the Aransas Pass area (Herber, 1981; White et al., 1983; K. Withers, pers. obs.).

6.2.2 Secondary Producers

Invertebrates which live in the blue-green algal mat, or sediments (benthos) provide the link between primary producers and higher consumers such as birds and fish. On flats which stay wet or damp throughout most of the year (e.g., back sides of barrier islands), an abundant and diverse macroinvertebrate fauna consisting of deposit- or suspension-feeders or grazers develops (Withers, 1994). On drier flats, (e.g., Laguna Madre Flats and other flats south of the study area), invertebrates are limited to saltwater-adapted insects which live on the surface (Pulich et al., 1982). Information concerning taxonomic composition of tidal flat invertebrate communities in the study area is limited to three blue-green algal flats: two in the upper Laguna Madre, underlain by sand and one in Oso Bay, underlain by clay. No information is available on other sediment types or non-algal flats.

Fifty-one invertebrate taxa were identified from a blue-green algal flat on northern Padre Island and 65 taxa were identified from a similar flat on Mustang Island (Table IV.B.6.3). *Hargeria rapax*, a tanaid, was the most common and abundant organism found on both flats. Polychaetes and insect larvae, primarily dipterans were also common. Sixteen polychaete species (9 families) were found on Padre Island, 28 species (16 families) were recorded on Mustang Island. The dominant polychaete families on Padre Island were, in order of abundance: Capitellidae, Orbiniidae, Sabellidae, Spionidae, and Syllidae. The dominant polychaete families on Mustang Island were, in order of abundance: Spionidae, Orbiniidae, Capitellidae, Maldanidae, and Phyllodocidae. Dominant insects on both sites were dipteran families Canaceidae and Dolichopodidae. Benthic organisms were generally most abundant during winter and spring (Fig.IV.B.6.7) (Withers, 1994).

Twenty-seven species (five phyla) were found in the area known as the Blind Oso in Oso Bay (Table IV.B.6.3). There was a diverse assemblage of arthropods (17 species in 11 families). Amphipods, primarily *Corophium louisianum*, were the most abundant organisms on the flat.

Table IV.B.6.3. Macroinvertebrate species found on the blue-green algal flats on Padre and Mustang Islands (Withers, 1994) and on the mudflat in Oso Bay (T. Barrera, unpubl. data). X = presence.

Taxa	Padre Island	Mustang Island	Oso Bay
P. Rhynchocoela	X		X
P. Nematoda			X
P. Platyhelminthes			
C. Turbellaria		X	
P. Annelida			
C. Oligochaeta			X
C. Polychaeta			
F. Phyllodocidae			
Eteone heteropoda	X	X	X
F. Glyceridae			
Glycera americana			X
F. Spionidae			
Dispio uncinata			X
Paraprionospio pinnata			X
Polydora ligni	X	X	X
Prionospio heterobranchia	X	X	
Prionospio cirrifera	X		
Prionospio (Minuspio) sp.			X
Spio setosa		X	
Streblospio benedicti		X	X
Scolelepsis squamata		X	
F. Capitellidae			
Capitella capitata	X	X	X
Capitomastus aciculatus	X	X	
Mediomastus californiensis			X
Notomastus hemipodus		X	
F. Maldanidae			
Asychis elongatus		X	
Clymenella mucosa	X	X	
Clymenella torquata	X		
F. Arenicolidae			
Arenicola cristata	X	X	X
F. Syllidae			
Exogone atlantica			X
Exogone dispar	X	X	
Syllis cornuta	X	X	

Table IV.B.6.3. Continued.

Taxa	Padre Island	Mustang Island	Oso Bay
F. Sabellidae			
Sabella micropthalma	X	X	
Sabella sp. A	X	X	
Chone duneri	X	X	
Sabellastarte sp.		X	
F. Ampharetidae			
Melinna maculata		X	
F. Lumbrineridae			
Lumbrineris tenuis		X	
F. Eunicidae			
Marphysa sanguinea		X	
F. Orbiniidae			
Haploscoloplos foliosus	X	X	
Naineris laevigata	X	X	
F. Dorvilleidae			
Dorvillea rubra	X	X	
F. Terebellidae			
Neoleprea sp. A		X	
F. Paranoidae			
Aricidea taylori		X	
Aricidea fragilis		X	
F. Nereidae			
Laeonereis culveri		X	X
Neanthes succinea			X
Platynereis dumerilii			X
P. Mollusca			
C. Gastropoda			
F. Bullidae			
Bulla striata	X	X	
F. Acteocinidae			
Acteon punctostriatus	X		
F. Cerithidae			
Cerithium lutosum		X	
C. Bivalvia			
F. Solenidae			
Ensis minor		X	X
F. Solecurtidae			
Tagelus plebius			X
F. Mactridae			
Mulinia lateralis	X	X	X

Table IV.B.6.3. Continued.

Taxa	Padre Island	Mustang Island	Oso Bay
F. Tellinidae			
Tellina tampaensis	X	X	
F. Veneridae			
Chione cancellata			X
Anomalocardia auberiana	X	X	
F. Mytilidae			
Amygdalum papyria	X	X	
F. Lyonsiidae			
Lyonsia hyalina			
F. Corbiculidae			
Polymesoda maritima	X	X	
F. Cardiidae			
Laevicardium mortoni		X	
SP. Crustacea			
C. Malacostraca			
O. Ostracoda			X
O. Copepoda			X
O. Cumacea			
F. Diastylidae			
Oxyurostylis smithi	X	X	
O. Isopoda			
F. Cymothoidae			
Aegothoa oculata			X
F. Idoteidae			
Edotea montosa			X
F. Sphaeromatidae			
Ancinus depressus			X
Dynamenella perforata			X
Sphaeroma quadridentatum	X		
Sphaeroma walkeri			X
O. Amphipoda			
F. Aoridae			
Grandidierella bonnieroides			X
F. Ampeliscidae			
Ampelisca sp.			X
F. Atylidae			
Atylus sp.			X

Table IV.B.6.3. Continued.

Taxa	Padre Island	Mustang Island	Oso Bay
F. Corophiidae			
Corophium acherusicum	X	X	X
Corophium louisianum	X	X	X
Corophium tubularis			X
F. Hyalellidae			
Hyale frequens			X
Hyalella azteca			X
F. Melittidae			
Melita sp.	X		X
Melita dentata			X
F. Pleustidae			
Stenopleustes gracilis			X
F. Gammaridae			
Gammarus sp.	X		
Gammarus mucronatus			X
F. Taltridae			
Orchestia grillus			X
Orchestia platensis		X	
O. Tanaidacea			
F. Paratanaidae			
Hargeria rapax	X	X	
SP. Insecta			
O. Diptera			
F. Canaceidae	X	X	
F. Ceratopogonidae	X	X	
F. Chironomidae		X	X
F. Dixidae			X
F. Simulidae		X	
F. Empididae	X		
F. Ephydridae			X
F. Dolichopodidae	X	X	X
O. Coleoptera			
F. Carabidae		X	
F. Curculionidae	X		
F. Dysticidae			
Laccophilus sp.	X		
F. Hydrophilidae		X	
Hydrocharus sp.	X		
F. Melyridae	X		
F. Salpingidae	X	X	

Table IV.B.6.3. Continued.

Taxa	Padre Island	Mustang Island	Oso Bay
F. Staphylinidae			X
Bledius sp.	X	X	
Bryothinusa sp.	X	X	
Stenus sp.	X	X	
O. Collembola			
F. Entomybryidae			
Seira sp.	X	X	
F. Cyphoderidae			
Cyphoderus sp.	X		
O. Hemiptera			
F. Corixidae			
Hesperocorixa sp.			X
F. Saldidae			
Pentacora sp.	X	X	
F. Nabidae	X		
F. Hebridae			
Lipogomphus sp.		X	
O. Hymenoptera			
F. Eulophidae		X	
F. Scelionidae	X		
F. Pteromalidae	X	X	
O. Odonata			
F. Aeshnidae			
Gomphaeschna sp.		X	
O. Plecoptera			
F. Leuctridae			
Leuctra sp.	X		
SP. Chelicerata	X	X	

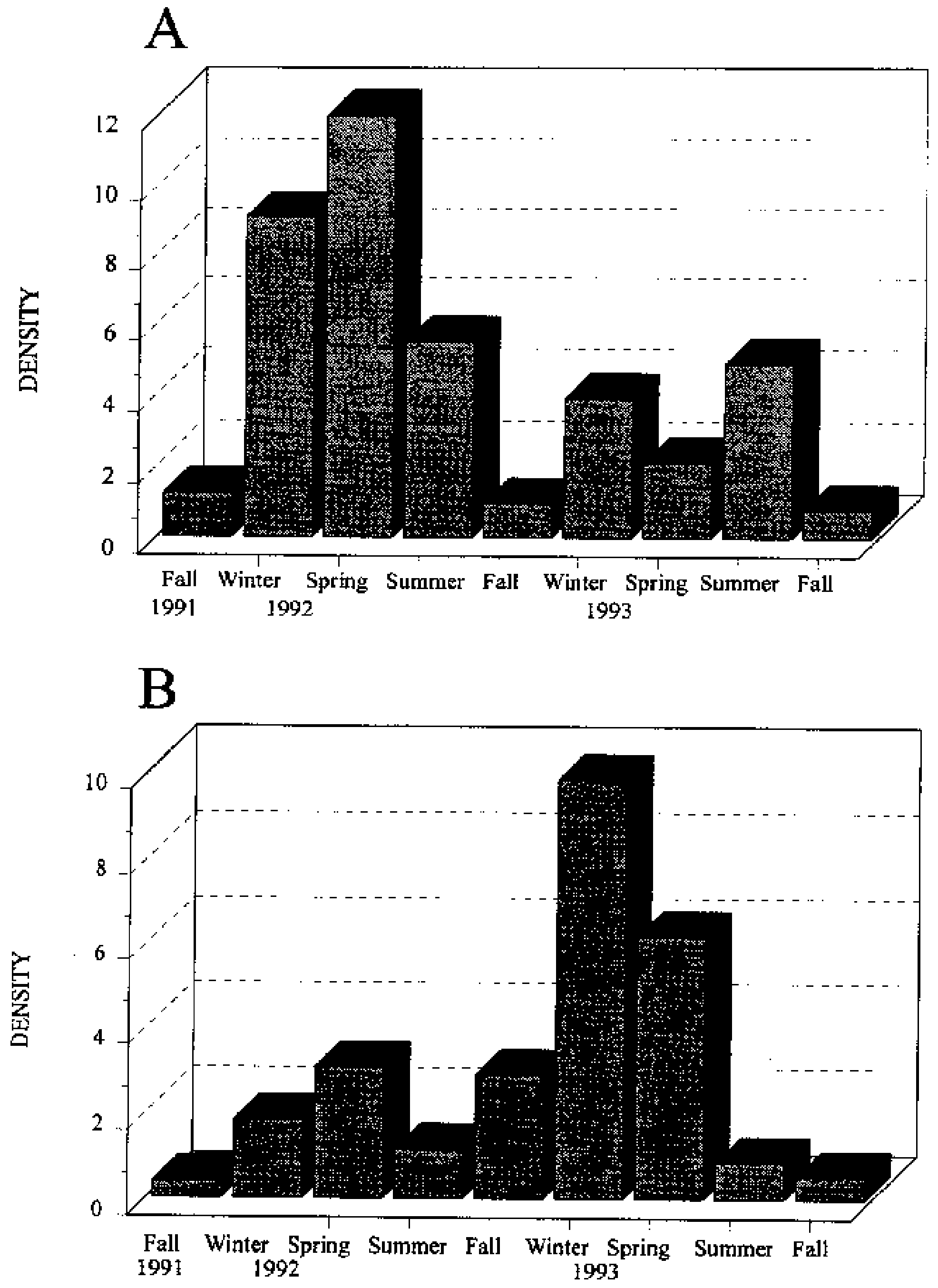


Fig. IV.B.6.7. Mean densities of organisms (10^3 m^{-2}) in the top 10 cm of sediment by season from algal flats on northern Padre Island (A) and Mustang Island (B) (Withers, 1994).

Polychaetes were also common; eight polychaete species (five families) were recovered. Spionids, primarily *Polydora ligni*, dominated. Benthic organisms were most abundant during November and December, followed by January, February, March, and June (T. Barrera unpubl. data).

Some obvious differences exist between benthic faunas of the two upper Laguna Madre algal flats, as well as between those flats and the Oso Bay flat. The polychaete fauna of the Mustang Island flat was more diverse than the Padre Island flat, probably due to its proximity to seagrass beds and Corpus Christi Bay (Withers, 1994). The Oso Bay flat had fewer polychaete and insect species than either upper Laguna Madre flats, but had a more diverse crustacean fauna, especially for amphipod species. Differences between the Oso Bay flat and upper Laguna Madre flats are likely due to differences in sediment type (i.e., sand vs clay) and hydrology, which attests to the importance of these factors in determining species composition. Species common to all three sites were those which are widely distributed with generalized habitat requirements such as *Capitella capitata* and *Polydora ligni*.

Composition of the meiofaunal community of tidal flats in the study area is not known. Some meiofaunal species (i.e., turbellarians, nematodes) were recovered incidentally when sampling for benthic macrofauna (Withers, 1994; T. Barrera, unpubl. data), but no systematic sampling for meiofauna has been attempted. Composition of meiofaunal communities in sandflats differs considerably from that of mudflats, primarily due to differences in interstitial spaces in sediments. Meiofauna inhabiting sandflats are generally interstitial organisms such as gastrotrichs and turbellarians, while those inhabiting mudflats are restricted to surface sediments. Mud meiofauna generally have large, stocky bodies, whereas sand meiofauna are smaller, vermiform animals (McIntyre, 1969). Meiofaunal communities in intertidal flats in North Carolina were dominated by nematodes, a pattern of abundance apparently typical of shallow marine sediments worldwide. Harpacticoid copepods were the second most abundant taxon. Others of importance were gastrotrichs, turbellarians, and gnathostomulids (Peterson and Peterson, 1979). Seasonal progressions of harpaticoids occurred regularly on mud flats in North Carolina, but in sandy habitats there was no predictable pattern of variation in abundance (Coull and Fleeger, 1977).

No information was found concerning microfauna of tidal flats in the study area; information is sparse in the literature as well. Microfauna includes all protozoans. Ciliates and foraminiferans can be extremely abundant on some intertidal flats. Their ecological role is poorly understood (Peterson and Peterson, 1979).

Like microfauna, information concerning the temporary zooplankton communities of flooded tidal flats is lacking in both the study area and the literature. Zooplankton, particularly larval polychaetes, were most abundant in the Laguna Madre during September and October (Hildebrand and King, 1978). Increased numbers of polychaetes inside predator exclosures during November 1992 on north Padre Island, compared with initial densities when exclosures were erected during September 1992, indicated recruitment of benthic organisms to the flat had occurred. It is likely that most recruitment was due to settling of larval polychaetes from the water column during seasonal high tides in September and October (Withers, 1994).

6.2.3 Decomposers

Microbial decomposition of organic material is the primary link between primary and secondary production (Odum and de la Cruz, 1967). A variety of fungi and bacteria are predominantly responsible for decomposition of detrital material on tidal flats (Peterson and Peterson, 1979; Whitlach, 1982). Dead plant matter often cannot be used directly by detritivores, but some polychaetes have the enzyme cellulase which aids in detrital breakdown (P. Montagna, UTMSI, pers. comm.). Both bacteria and fungi tend to be more abundant in sediments of mud flats because small-sized clay particles have greater surface areas than larger-sized, coarser sediments such as sands (Peterson and Peterson, 1979). Bacteria are also associated with interstitial water (Whitlach, 1982). Most detritus produced in estuaries ultimately reaches intertidal flats because it floats on the water's surface, and is deposited by winds and tides in the intertidal zone. After deposition, detritus is fragmented and processed by organisms, and is gradually worked into sediments. Detrital content of intertidal flats can be substantial (Odum, 1970), especially on mud flats, providing abundant food for detritivores (Peterson and Peterson, 1979).

Decomposer communities of tidal flats in the study area have not been studied. On the Laguna Madre Flats to the south, anaerobic, non-photosynthetic bacteria thrived in the reducing zone found just below the algal mat (Fisk, 1959; Herber, 1981). Bacterial counts of samples from an area where the reducing zone was 40 cm thick indicated densities decreased with depth. At the top of the zone, there were >40,000,000 bacteria/g, while at the base there were <6,000 bacteria/g (Fisk, 1959). Bacterial counts of sediments from an intertidal marsh also showed that bacterial abundance declined significantly with depth, suggesting resources for detritivores are most abundant in surface sediments (Peterson and Peterson, 1979).

6.3 Consumers

6.3.1 Invertebrates

The benthic invertebrates discussed in the section on secondary producers (6.2.2) are primary consumers on flats as well, feeding on bacteria and/or meiofauna, detritus, each other, or grazing on blue-green algae (Table IV.B.6.4). Most polychaetes on upper Laguna Madre flats are deposit feeders, feeding on particulate organic matter (detritus) or gleaning protozoans, bacteria, and diatoms from sediment grains. Only one filter-feeding family (Sabellidae), was collected. Predatory families such as Phyllodocidae were not abundant. Molluscs were never abundant. Gastropods recovered were grazing herbivores, bivalves were deposit feeders, and most crustaceans were grazers or scavengers. Larval and adult insects were dominant predators among benthic invertebrates (Withers, 1994). Predatory beetles and hemipterans were the most common and abundant invertebrate consumers on the Laguna Madre Flats to the south. Spiders (Lycosidae [wolf spiders] and Clubionidae [sac spiders]), feed in cracks in algal mats, preying on small insects and other invertebrates (Pulich et al., 1982).

Crabs are the other invertebrate consumers frequently found on flats. *Callinectes sapidus* (blue crab) are common when flats are flooded, and are generally scavengers. *Uca* spp., primarily

Table IV.B.6.4. Consumer-types of major secondary producer taxa found on blue-green algal flats in the upper Laguna Madre. Categories after Merritt and Cummins (1982) and Uebelacker and Johnson (1986). S=shredders; DF=deposit feeder; FF=filter feeder; Sc=scraper; P=predator; Ps=parasitoid; Sv=scavenger. Shredders and deposit feeders are generally detritivores, scrapers are grazing herbivores.

Taxon	Consumer-Type
P. Annelida	
C. Polychaeta	
F. Phyllodocidae	P
F. Spionidae	DF, P
F. Capitellidae	DF
F. Maldanidae	DF
F. Arenicolidae	DF
F. Syllidae	P, DF
F. Sabellidae	FF
F. Ampharetidae	DF
F. Lumbrineridae	P, Sv
F. Eunicidae	Sc, DF
F. Orbiniidae	DF
F. Dorvilleidae	P
F. Terebellidae	DF
F. Paranoidae	DF
F. Nereidae	P, DF, Sv, Sc
P. Mollusca	
C. Gastropoda	
F. Bullidae	Sc
F. Acteocinidae	Sc
F. Cerithidae	Sc
C. Bivalvia	
F. Solenidae	FF
F. Mactridae	FF
F. Tellinidae	FF
F. Veneridae	FF
F. Mytilidae	FF
F. Corbiculidae	FF
SP. Crustacea	
C. Malacostraca	
O. Cumacea	
F. Diastylidae	FF, DF
O. Isopoda	
F. Sphaeromatidae	S

Table IV.B.6.4. Continued.

Taxon	Consumer-Type
O. Amphipoda	S, DF, Sv
O. Tanaidacea	Sc
SP. Insecta	
O. Diptera	
F. Canaceidae	Sc
F. Ceratopogonidae	P, DF
F. Simulidae	FF
F. Empididae	DF, S
F. Dolichopodidae	P
O. Coleoptera	
F. Carabidae	P
F. Curculionidae	S
F. Dysticidae	P
F. Hydrophilidae	Larvae=P, Adults=DF
F. Melyridae	P
F. Salpingidae	P, S
F. Staphylinidae	P
O. Collembola	
F. Entomybryidae	DF, Sv
O. Hemiptera	
F. Saldidae	P
F. Nabidae	P
F. Hebridae	P
O. Hymenoptera	
F. Eulophidae	Ps
F. Scelionidae	Ps
F. Pteromalidae	Ps
O. Odonata	
F. Aeshnidae	P
O. Plecoptera	
F. Leuctridae	S
SP. Chelicerata	P

Uca subcylindrica (fiddler crab), are common in drier areas of flats and during the summer; they feed on a variety of foods including meiofauna and polychaetes.

6.3.2 Nekton

When flats are flooded, nektonic organisms may be present on the flats. The Blind Oso study (T. Barrera unpubl. data) is the only study which has addressed nekton using the flats. *Penaeus aztecus* (brown shrimp) and amphipods, primarily *Corophium louisianum*, were the most abundant invertebrate nekton recovered (Table IV.B.6.5). Other common species encountered were *Palaemonetes* spp. (grass shrimp), *Mysidopsis almyra*, and *Callinectes sapidus*. *Cyprinodon variegatus* (sheepshead minnow) was the most abundant fish found in the Blind Oso along with *Fundulus grandis* (Gulf killifish) and *Membras martinica* (rough silverside) (T. Barrera unpubl. data) (Table IV.B.6.5). Ten species of primarily juvenile individuals were recovered from the Blind Oso. *C. variegatus* were also the most abundant fish on the Laguna Madre Flats along with *Fundulus similis*, and *Menidia* spp. (silversides). Larval *Synodus foetens* (inshore lizard fish) were plentiful on one occasion during spring (Pulich et al., 1982). *C. variegatus* was the only fish caught on upper Laguna Madre flats. Adult *Paralichthys lethostigma* (southern flounder) were occasionally flushed from the sediments in shallow water just off the flats, with schools of small ("finger") *Mugil cephalus* in ankle-deep water (K. Withers, unpubl. data). Both *C. variegatus* and *Fundulus* spp. eat algae and detritus as juveniles. When they exceed 30 mm total length, they feed on crustaceans, small fish, and insects (Harrington and Harrington, 1972; Pfeiffer and Wiegert, 1981). As water recedes, they move into deeper water where they are prey for larger fish such as *Sciaenops ocellata* and *Cynoscion nebulosus* (spotted sea trout) (Pulich et al., 1982).

6.3.3 Reptiles and Amphibians

No information is available concerning reptile and amphibian occurrence on tidal flats. Because of the biologically harsh conditions which prevail, it is doubtful that either group would occur on tidal flats except accidentally.

6.3.4 Birds

Shorebirds (Charadriiformes) are the most conspicuous vertebrate consumers on flats. They feed on benthic invertebrate infauna and epifauna, and feed opportunistically on fiddler crabs, small fish and shrimp. Seasonal abundance of and habitat use by shorebirds was studied on blue-green algal flats in the upper Laguna Madre (Withers, 1994) and on a mudflat in Oso Bay (Withers and Chapman, 1993). Wading birds such as Great Blue Heron (*Ardea herodias*) and Reddish Egret (*Egretta rufescens*) are common in shallow waters adjacent to flats. Bay ducks such as scaup (*Aythya* spp.) and Redheads (*Aythya americana*) often feed in seagrass beds near flats.

Gulls and terns (Laridae) are often abundant, and use flats as "loafing" areas. Tidal flats are important foraging habitat for wintering Peregrine Falcon (*Falco peregrinus*), particularly south of the study area. Other birds such as Horned Lark (*Eremophila alpestris*), Barn Swallow (*Hirundo rustica*), Boat-tailed Grackle (*Quiscalus major*), Sandhill Crane (*Grus canadensis*),

Table IV.B.6.5. Nektonic species recovered from the Blind Oso wind tidal flat. Flat was sampled when flooded with a marsh seine (T. Barrera unpubl. data). D=demersal; C=carnivore; H=herbivore; Dt=detritivore; O=omnivore; Sc=scavenger; Df=deposit feeder.

Taxon	Consumer-Type
P. Arthropoda	
SP. Crustacea	
C. Ostracoda	H, Sc, C, Dt
C. Malacostraca	
O. Mysidacea	
F. Mysidea	
Mysidopsis almyra	Dt
O. Tanaidacea	
F. Paratanaidae	
Hargeria rapax	H
O. Amphipoda	
F. Gammarida	C, Sc
Gammarus mucronatus	
F. Melitidae	Dt, Sc?
Melita dentata	
F. Hyalellidae	Dt, Sc?
Hyale frequens	
F. Corophiidae	Df
Corophium volutor	
Corophium louisianum	
Corophium asherusicum	
O. Decapoda	
F. Penaeidae	O
Penaeus aztecus	
P. setiferus	
P. duorarum	
F. Palaemonidae	H, Dt
Palaemonetes pugio	
P. intermedius	
P. vulgaris	
F. Portunidae	Sc
Callinectes sapidus	
SP. Insecta	
O. Hemiptera	
F. Corixidae	
Hesperocorixa	H
O. Diptera	
F. Ephydridae	DF, S, Sc

Table IV.B.6.5. Continued.

Taxon	Consumer-Type
P. Chordata	
SP. Vertebrata	
C. Osteichthys	
O. Elopiformes	
F. Elopidae	P
Elops saurus	
O. Clupeiformes	
F. Clupeidae	H
Brevoortia patronus	
O. Cyprinodontiformes	
F. Cyprinidontidae	
Cyprinodon variegatus	Juveniles=H; Adults=C
Fundulus grandis	Juveniles=H; Adults=C
O. Antheriformes	
F. Antherinidae	H
Membras martinica	
Menidia beryllina	
F. Sciaenidae	P
Leiostomus xanthurus	
F. Mugilidae	H
Mugil cephalus	
F. Gobiidae	H
Gobionellus boleosoma	
O. Pleuronectiformes	
F. Bothidae	D, C
Paralichthys lethostigma	

White Pelican (*Pelecanus erythrorhynchos*), Black Skimmer (*Rhynchops niger*), and Canada Goose (*Branta canadensis*) turn up occasionally on flats or in shallow adjacent waters (K. Withers, pers. obs.).

Twenty-six species of shorebirds used the Oso Bay mudflat (Table IV.B.6.6); 34,822 individuals were observed between January 1985-January 1986 (Withers and Chapman, 1993). Peeps (primarily Western Sandpiper [*Calidris mauri*] and Semipalmated Sandpiper [*C. semipalmatus*]) were the most common and abundant species, followed by dowitchers (*Limnodromous* spp.), Dunlin (*Calidris alpina*), and American Avocet (*Recurvirostra americana*). Densities were

Table IV.B.6.6. Shorebird species observed on the blue-green algal flats on Padre and Mustang islands (Withers, 1994), on the mudflat in Oso Bay (Withers and Chapman, 1993) ranked by total abundance during the study. Blank = none observed.

Species	Padre Island	Mustang Island	Oso Bay
Peeps (*Calidris mauri, C. semipalmatus*)	1	1	1
Dunlin (*Calidris alpina*)	2	2	3
Least Sandpiper (*Calidris minutilla*)	3	3	
Dowitchers (*Limnodromous* spp.)	4	12	2
Piping Plover (*Charadrius melodus*)	5	4	21
Snowy Plover (*Charadrius alexandrinus*)	6	6	15
Willet (*Cataptrophorus semipalmatus*)	7	8	7
Sanderling (*Calidris alba*)	8	5	9
Black-bellied Plover (*Pluvialis squatorola*)	9	7	5
Long-billed Curlew (*Numenius americanus*)	10	14	12
Ruddy Turnstone (*Arenaria interpres*)	11	15	17
Red Knot (*Calidris canutus*)	12	19	
Semipalmated Plover (*Charadrius semipalmatus*)	13	18	11
Marbled Godwit (*Limosa fedoa*)	14	11	6
American Avocet (*Recurvirostra americana*)	15		4
Lesser Yellowlegs (*Tringa flavipes*)	16	22	14
Black-necked Stilt (*Himantopus mexicanus*)	17	21	8
Greater Yellowlegs (*Tringa melanoleucus*)	18	16	19
Wilson's Plover (*Charadrus wilsonia*)	19	10	10
Baird's Sandpiper (*Calidris bairdii*)	20	15	22
Wilson's Phalarope (*Phalaropus tricolor*)	21	20	18
American Oystercatcher (*Haematopus palliatus*)	22	13	
Spotted Sandpiper (*Actitis macularia*)		17	23
Stilt Sandpiper (*Calidris himantopus*)			13
Killdeer (*Charadrius vociferus*)			16
Whimbrel (*Numenius phaeopus*)			20
Pectoral Sandpiper (*Calidris melanotus*)			24

greatest during spring migration (February-April) and winter (November-January). The area did not appear to be an important stopover for large numbers of birds during fall (Fig. IV.B.6.8).

Twenty-four species of shorebirds were observed on the algal flats on Padre and Mustang islands (Table IV.B.6.6) between October 1991-October 1993 (Withers, 1994). Peeps, Dunlin, and Least Sandpipers (*Calidris minutilla*) were the most common and abundant species on both flats, followed by dowitchers and Piping Plovers (*Charadrius melodus*) on Padre Island and Piping Plovers and Snowy Plovers (*C. alexandrinus*) on Mustang Island. A total of 19,045 shorebirds were observed on Padre Island, with 4,197 on Mustang Island. Shorebirds were most abundant on both flats between October and March or April (Fig. IV.B.6.9). Like the Oso Bay mudflat, these areas were not used by many birds during the fall.

Although wading birds use flats when flooded, and are common in surrounding shallow waters, there is little information concerning their use of flats in the study area. Five species were observed on algal flats on Padre and Mustang Island, six were observed in the Blind Oso (Table IV.B.6.7) (Pulich et al., 1982; K. Withers, unpubl. data; T. Barrera, unpubl. data). Tricolor Heron (*Egretta tricolor*) were often abundant on upper Laguna Madre flats (K. Withers, unpubl. data). Pulich et al. (1982) listed the Reddish Egret as most common on flats of south Padre Island. Twenty to 30 of these birds were occasionally observed actively foraging on their study sites using characteristic "canopy feeding" behavior. This behavior appeared to be particularly well-suited for use on algal flats because of the dark background. Great Egret (*Casmerodius albus*) and Roseate Spoonbill (*Ajaia ajaja*) were most common in the Blind Oso, particularly after flooding when many egrets would "appear" (T. Barrera, unpubl. data).

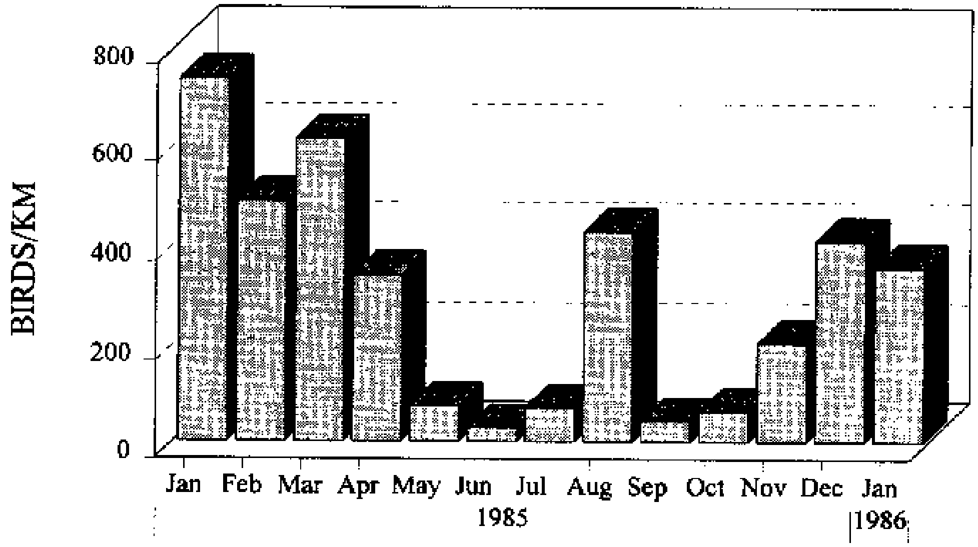


Fig. IV.B.6.8. Mean densities (#/km) of shorebirds on an Oso Bay mudflat. A large flock of migrating peeps stopped over briefly during August 1985 (after Withers and Chapman, 1993).

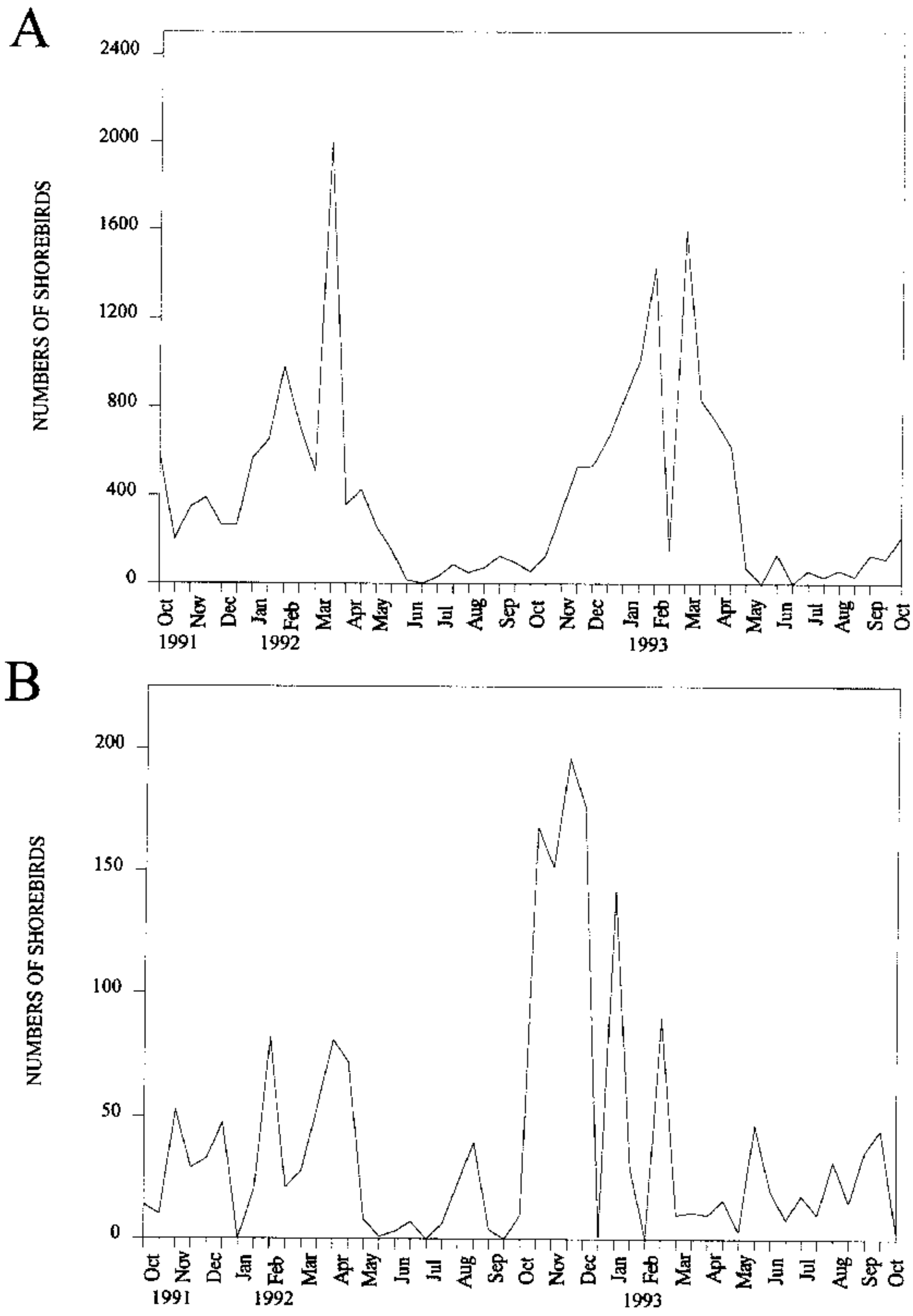


Fig. IV.B.6.9. Total abundance and seasonal distribution of shorebirds on north Padre Island (A) and Mustang Island (B) (Withers, 1994).

Table IV.B.6.7. Wading bird species observed on the dry or flooded blue-green algal flats on Padre Island (Pulich et al., 1982; K. Withers, unpubl. data), Mustang Island (K. Withers, unpubl. data), and the Blind Oso (T. Barrera, unpubl. data), or in the adjacent shallow waters.

Species	Padre Island	Mustang Island	Oso Bay
Great Egret (*Casmerodius albus*)	X	X	X
Snowy Egret (*Egretta thula*)	X		X
Great Blue Heron (*Ardea herodias*)	X	X	X
Reddish Egret (*Egretta rufescens*)	X	X	X
Louisiana Heron (*Egretta tricolor*)	X	X	X
Little Blue Heron (*Egretta caerulea*)	X	X	
Roseate Spoonbill (*Phoenicopterus ruber*)			X

Total numbers of wading birds were nearly always higher on Padre Island compared to Mustang Island (Fig IV.B.6.10A). Abundances were greatest in the late spring and summer on both sites, peaking during July and August (K. Withers, unpubl. data). In the Blind Oso, numbers of wading birds were counted in fixed, 100 m^2 plots (Fig. IV.B.6.10B). A total of 213 wading birds were counted in that area during the 13-month study. Numbers were highest in late spring and late fall within the plot, but when flats were flooded, three to four as many birds were found over the entire flat as were counted in the plot. Most common species were Great Egret (22%), Roseate Spoonbill (21.5%), and Great Blue Heron (19.2%) (T. Barrera, unpubl. data).

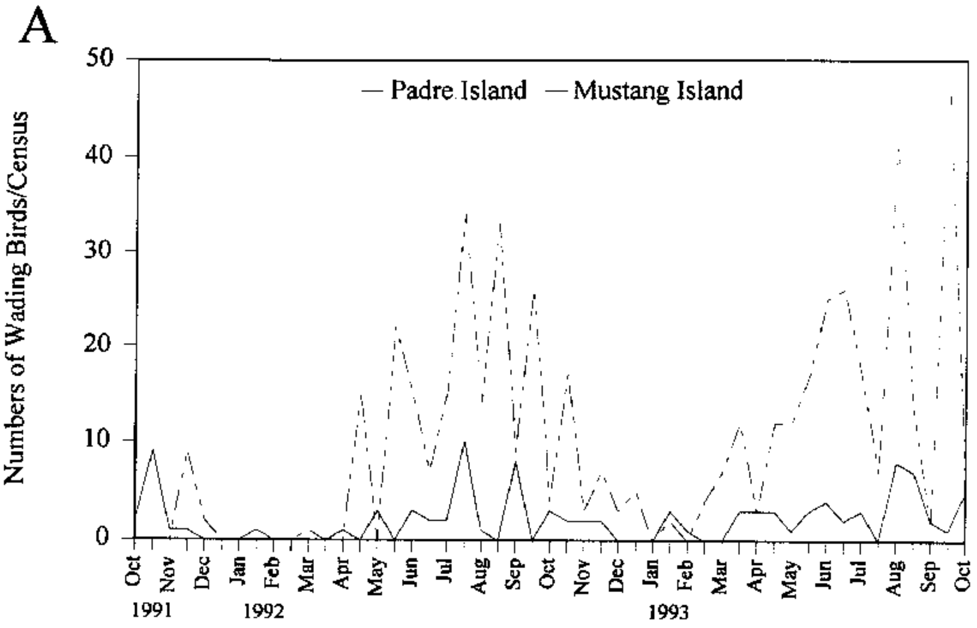
6.3.5 Mammals

Information concerning mammal use of tidal flats in the study area is anecdotal. *Urocyon cineroargentatus* (gray fox), *Procyon lotor* (raccoon), and *Canis latrans* (coyote) have been observed on flats. *Canis latrans* apparently forage for and eat fiddler crabs on the Padre Island algal flat during hot summer months, as evidenced by abundant crab parts found in their droppings. *C. latrans* have been observed cavorting on the flats, and running across the flats and throwing themselves into the water, possibly to cool off or remove fleas. *Odocoileus virginianus* (whitetail deer) and *Sylvilagus floridanus* (eastern cottontail rabbit) tracks have been observed on the flats; they probably use the flats as a "salt lick" (K. Withers, pers. obs.).

6.4 Community Structure

6.4.1 Plant Communities

Blue-green algal mats are zoned vertically by color, reflecting community interrelationships. Sorenson and Conover (1962) described five algal mat zones near Port Aransas: (1) darkly stained surface layer, (2) transitional zone which grades to, (3) lustrous blue-green, (4) yellow



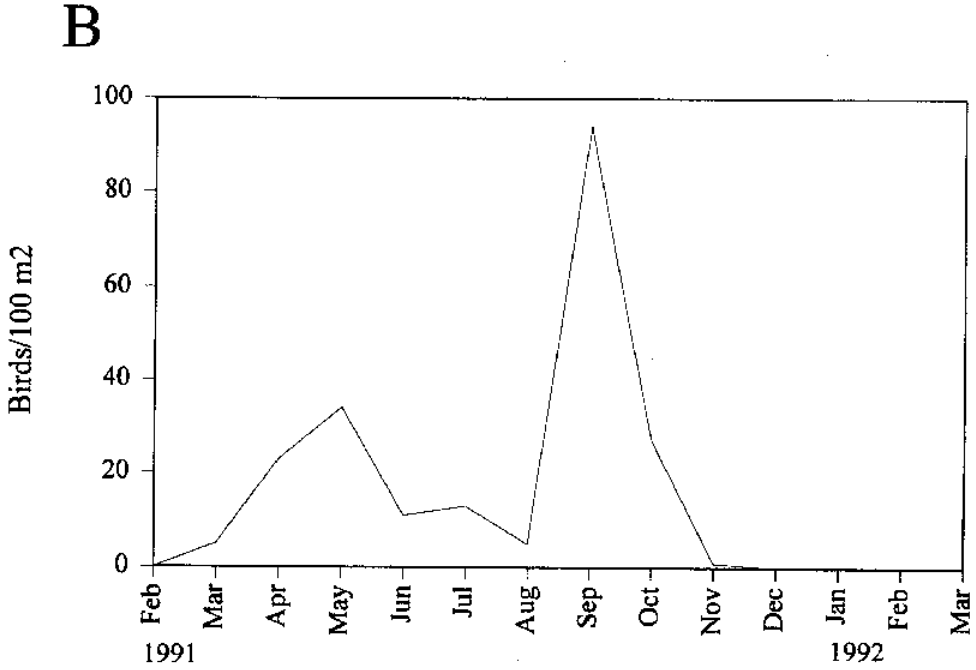


Fig. IV.B.6.10. Total densities of wading birds on or in the adjacent shallow waters of the blue-green algal flats on Padre and Mustang islands (A) (K. Withers, unpubl. data) and the Blind Oso (B) (T. Barrera, unpubl. data).

and pinkish-yellow, and (5) dirty yellow to black. Herber (1981) described four algal mat zones in the Laguna Madre Flats: (1) blackish to dark brown, (2) green, (3) salmon, and (4) black. Both designations are essentially the same except for differentiation of a transitional zone between the dark surface layer and the green layer. Color of surface zones range from light brown (diatoms) to grayish-tan (coccoid forms) depending on dominant biota (Herber, 1981).

The darkly stained surface layer may shield living sublayers from light and temperature extremes. Sheaths of *Lyngbya confervoides* contain a pigment, possibly a hydroxide of iron, that apparently darkens due to a photochemical reaction (Kylin, 1927, cited in Sorenson and Conover, 1962). The amount of pigment in mats increases as summer approaches and becomes an effective light shield, reducing penetration of incident light below the first millimeter by 95% (Sorenson and Conover, 1962). No additive growth of the mat community is contributed by the surface layer; there is actually a net loss of biomass (Fig. IV.B.6.11) due to shrinking and sloughing caused by alternating wet and dry periods. The transitional zone beneath the surface layer probably contributes some additive growth to the community, but growth is greatest in the blue-green mid-layer. Most light is attenuated at this depth, but it is enough to sustain photosynthesis. Chemosynthesis may provide some energy necessary to sustain plant life and provide storage products (Sorenson and Conover, 1962).

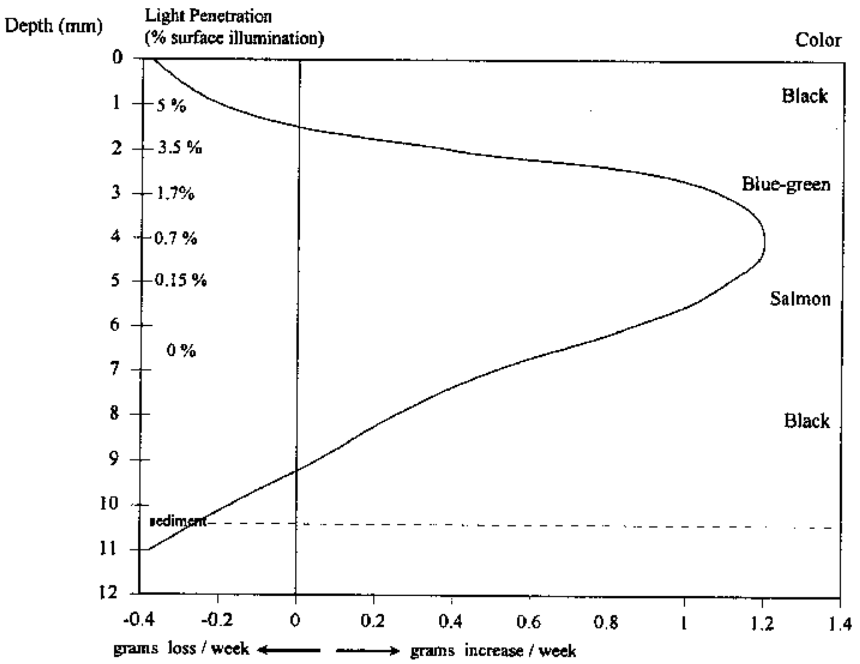


Fig. IV.B.6.11. Vertical zonation and estimated growth of blue-green algae within an algal mat near Port Aransas, Texas for May based on laboratory experiments (modified from Sorenson and Conover, 1962).

Bacteria begin to increase in importance from the blue-green mid-layer downward. Some additive growth occurs in the salmon or yellowish-pink layer, but this is marginal habitat for algae and is primarily populated by autotrophic purple bacteria (Sorenson and Conover, 1962; Pulich and Rabalais, 1986). These bacteria modify or decompose primary organics, diatoms, and blue-green algae. The black zone is a decomposition zone, populated by non-photosynthetic, anaerobic bacteria (Herber, 1981). The algal mat is also horizontally zoned according to flooding frequency (Fig. IV.B.6.12). Because each blue-green algal species differs in its ability to survive desiccation, elevation (=flooding frequency) determines composition of the mat community (Herber, 1981).

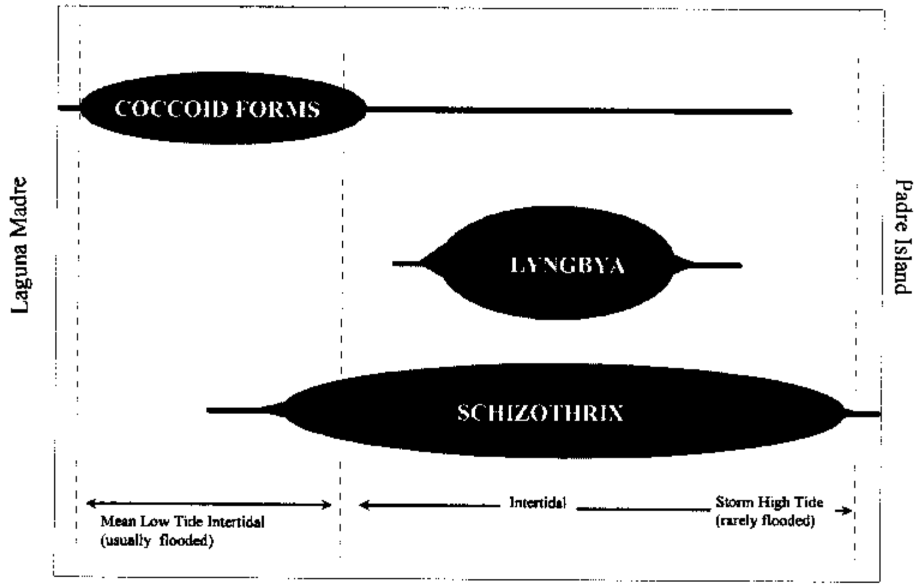


Fig. IV.B.6.12. Distribution of blue-green algae relative to the elevation of the tidal flat. Thickness of the bar roughly reflects abundance (after Herber 1981).

6.4.2 Invertebrate Community

Community composition of both blue-green algal flats in the upper Laguna Madre was similar (Fig. IV.B.6.13). Crustaceans, primarily tanaids, dominated assemblages at both sites. Relative abundance of both insects and polychaetes was greater on the Mustang Island flat than on the Padre Island flat. The influence of Corpus Christi Bay and nearby seagrass beds may explain the greater dominance of polychaetes. It is possible the more irregular inundation/exposure regime of the Mustang Island flat explains the greater dominance of insects. Other taxa such as molluscs, oligochaetes, and turbellarians were uncommon at both sites (Withers, 1994). Information concerning community structure of the algal flat in the Blind Oso is not presently available.

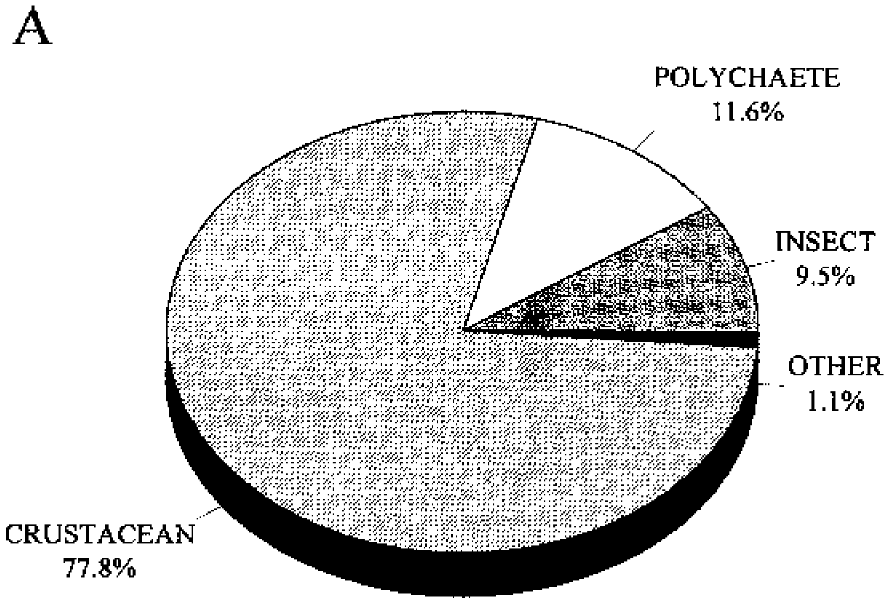
Elevational zonation of invertebrates is a prominent feature on rocky seashores and although it is not readily noticeable, it is also a common feature of tidal flat systems. Physical stress (e.g., osmotic imbalance, desiccation) and biological stress (e.g., inability to feed, aerobic respiration) associated with exposure at low tide sets upper limits of distribution for many rocky shore organisms and some soft sediment organisms (Peterson, 1991). Elevational zonation of organisms was seen in two blue-green algal flats studied by Withers (1994). Most organisms were concentrated in intertidal and wet microhabitats (Fig. IV.B.6.14). Analyses of variance revealed total density and biomass, polychaete density and biomass, and mollusc density increased from the damp microhabitat to the low intertidal. Community similarity indices revealed damp microhabitats were less similar to both wet and intertidal microhabitats than wet and intertidal microhabitats were to each other. There appears to be at least two or three horizontal zones, characterized by increasing numbers of primarily aquatic-adapted organisms such as polychaetes, crustaceans, and molluscs in the wet areas nearest water (wet and intertidal microhabitats), and increased dominance, if not abundance, of semi-terrestrial organisms such as insects in areas farther from the waters' edge (damp microhabitat) (Fig. IV.B.6.15).

Algal flats in the upper Laguna Madre also exhibited vertical zonation within sediments. Low-oxygen, deep (> 5 cm) sediments contained few organisms, with most concentrated in upper, oxygenated layers, either within the algal mat or at the algal mat-sediment interface (Fig. IV.B.6.16). The deep section was dominated by a few, large individuals, primarily *Arenicola cristata* and *Tellina tampaensis*, while the surface section was characterized by abundant polychaetes, crustaceans, and insects (Withers, 1994).

6.4.3 Vertebrate Communities

Little information is available concerning structure of vertebrate communities other than shorebirds on tidal flats. Sandpipers (*Calidris* spp.) dominated shorebird communities of both blue-green algal flats in the upper Laguna Madre as well as the mudflat in Oso Bay (Fig. IV.B.6.17) (Withers, 1994; Withers and Chapman, 1993). Relative abundance of plovers (Black-bellied Plover, *Pluvialis squatorola*, and banded plovers, *Charadrius* spp.) was greatest on the Mustang Island flat. Black-bellied Plovers accounted for most of the plovers in Oso Bay, while banded plovers dominated in the upper Laguna Madre. Dowitchers (*Limnodromous* spp.) were rarely observed on Mustang Island, but were an important part of the community in Oso Bay. These differences are probably due to species' abilities to forage in the presence of an algal mat. Plovers, which are visual foragers, feed on organisms on or just below the surface of the substrate. Sandpipers are largely visual foragers as well, but many, such as the Western Sandpiper (*Calidris mauri*), include a tactile element in their foraging strategy (Pienkowski 1981) allowing them to use a variety of habitats. Dowitchers and other long-billed, probing, tactile-foraging shorebirds, are inhibited by the presence of algal mats on the surface of the substrate.

Most shorebirds exhibit preferences for certain microhabitats (Tables IV.B.6.8 and IV.B.6.9); this results in partitioning of the tidal flat by the birds. In the upper Laguna Madre, most birds were found in wet microhabitats, while in Oso Bay, most were found in the shoreface (=intertidal) microhabitat (Fig. IV.B.6.18) (Withers, 1994; Withers and Chapman, 1993).



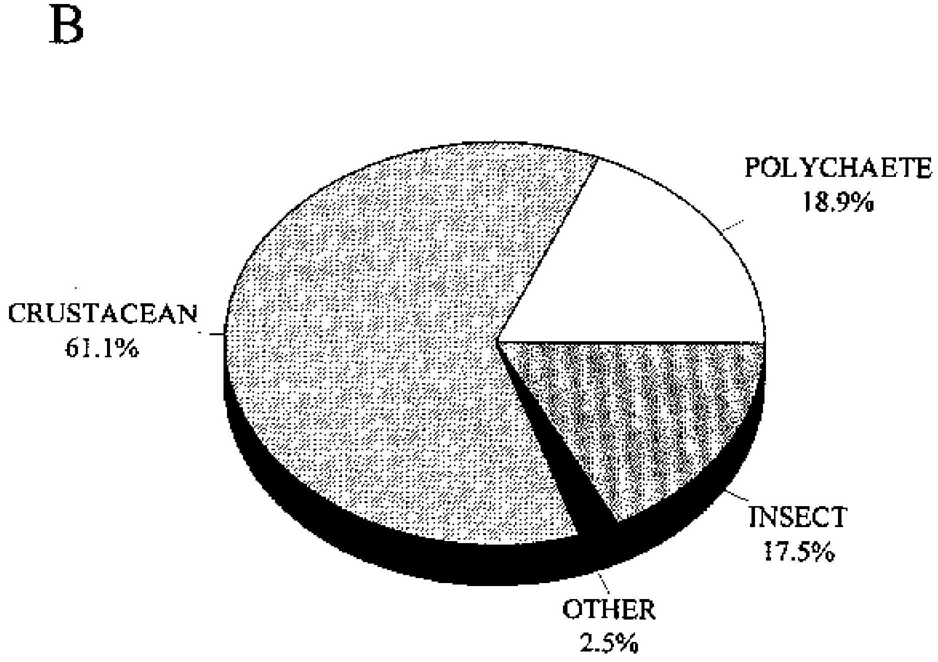


Fig. IV.B.6.13. Benthic invertebrate community composition on blue-green algal flats on north Padre Island (A) and Mustang Island (B) (after Withers, 1994).

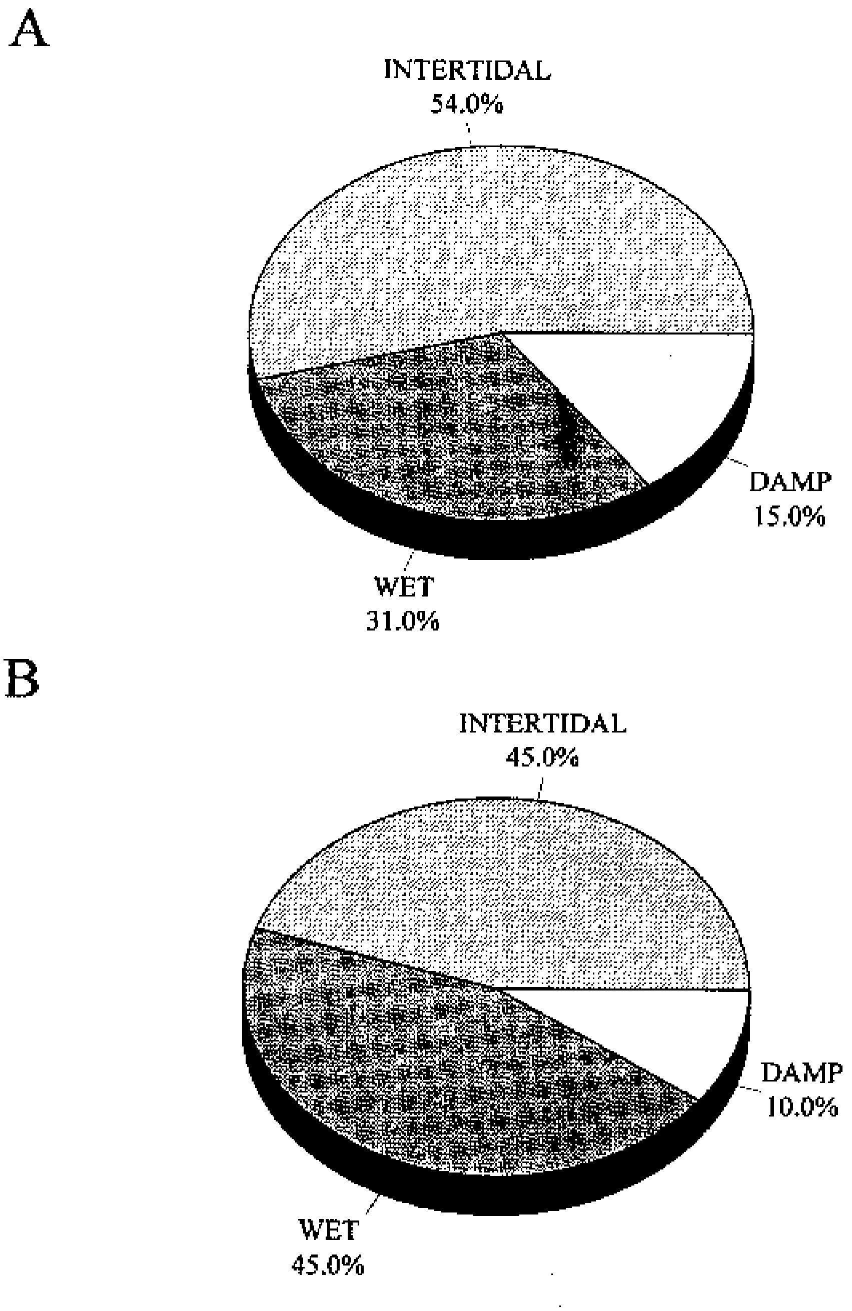


Fig. IV.B.6.14. Distribution of benthic organisms (density) recovered from blue-green algal flats on north Padre Island (A) and Mustang Island (B) by microhabitat (after Withers, 1994).

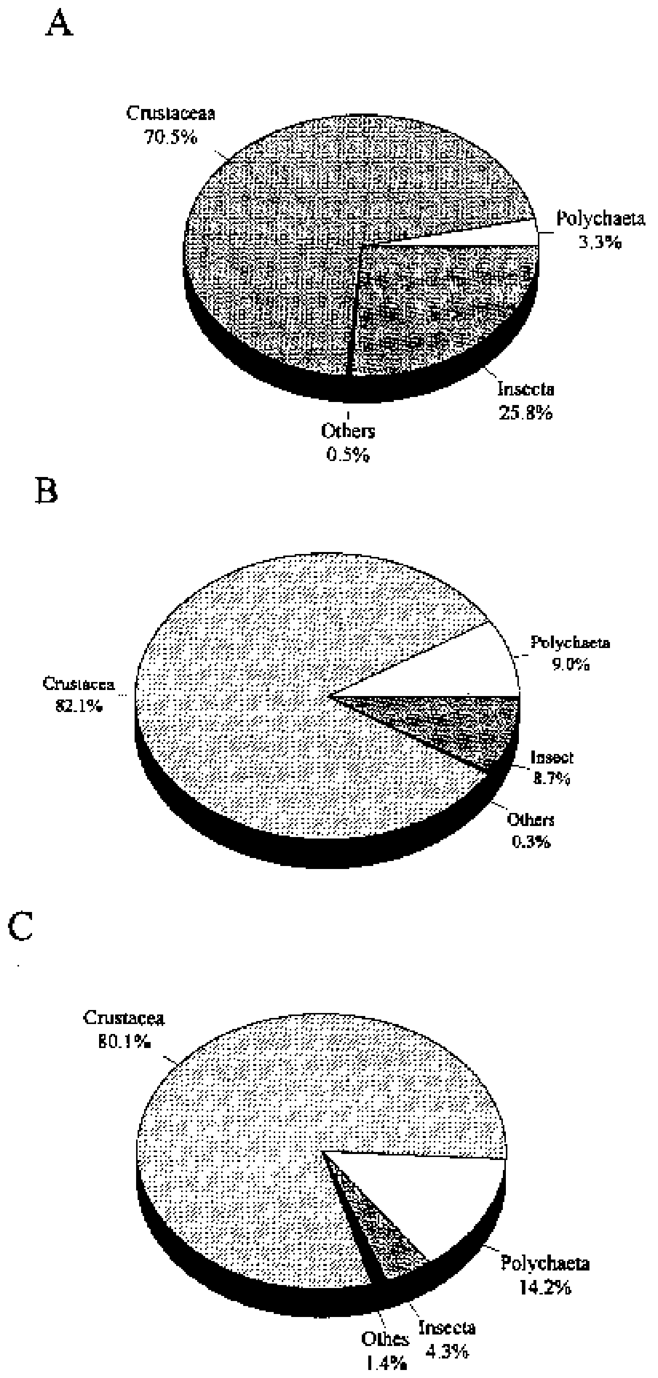


Fig. IV.B.6.15. Distribution of taxa in damp (A), wet (B) and intertidal (C) microhabitats of blue-green algal flats in the upper Laguna Madre (after Withers, 1994).

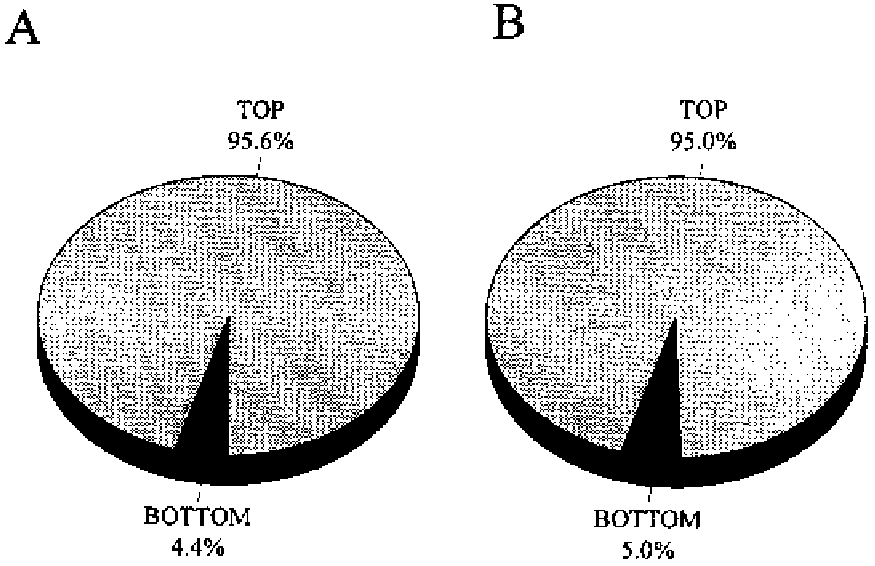


Fig. IV.B.6.16. Vertical distribution (density) of benthic organisms recovered in top five centimeters and bottom five centimeters of blue-green algal flat substrate from north Padre Island (A) and Mustang Island (B) (after Withers, 1994).

Because species exhibit preferences, the shorebird community within each microhabitat or zone is dominated by different species groups. On the Oso Bay mudflat, shallow water areas were dominated by long-legged, long-billed shorebirds such as American Avocets (*Recurvirostra americana*) and Willets (*Cataptrophorus semipalmatus*) (Fig IV.B.6.19A). The assemblage in the shoreface microhabitat was dominated by sandpipers and plovers, while that of the flat microhabitat (= wet+damp) was dominated by plovers (Fig. IV.B.6.19B, C) (Withers and Chapman, 1993). The pattern was somewhat different on blue-green algal flats in the upper Laguna Madre (Fig. IV.B.6.20). Long-legged shorebirds were not abundant on either site, as indicated by dominance of the open water area by sandpipers, primarily Dunlin (*Calidris alpina*). Western Sandpipers were the primary sandpiper in the intertidal microhabitat, with Least Sandpipers (*Calidris minutilla*) increasing in abundance in wet microhabitats. Plovers, primarily Piping and Snowy plovers (*Charadrius melodus*, *C. alexandrinus*), increased in importance in the community and dominated the assemblage found in the damp microhabitat (Withers, 1994).

The community of fish present on flooded tidal flats appears to be determined by water depth and salinity. No large fish (>30 mm) are usually found (Pulich et al., 1982; T. Barrera, unpubl. data). *Cyprinodon variegatus* is tolerant of salinities of up to 138 ‰, and larval *Synodus foetens* were found at a salinity of 110 ‰ (Pulich et al., 1982). *C. variegatus* was considered to be the most stress-tolerant of all Laguna Madre fishes (Gunter, 1967). The greater diversity of fish species seen in the Blind Oso was likely due to lower salinities and increased recruitment caused by water exchange with Corpus Christi Bay.

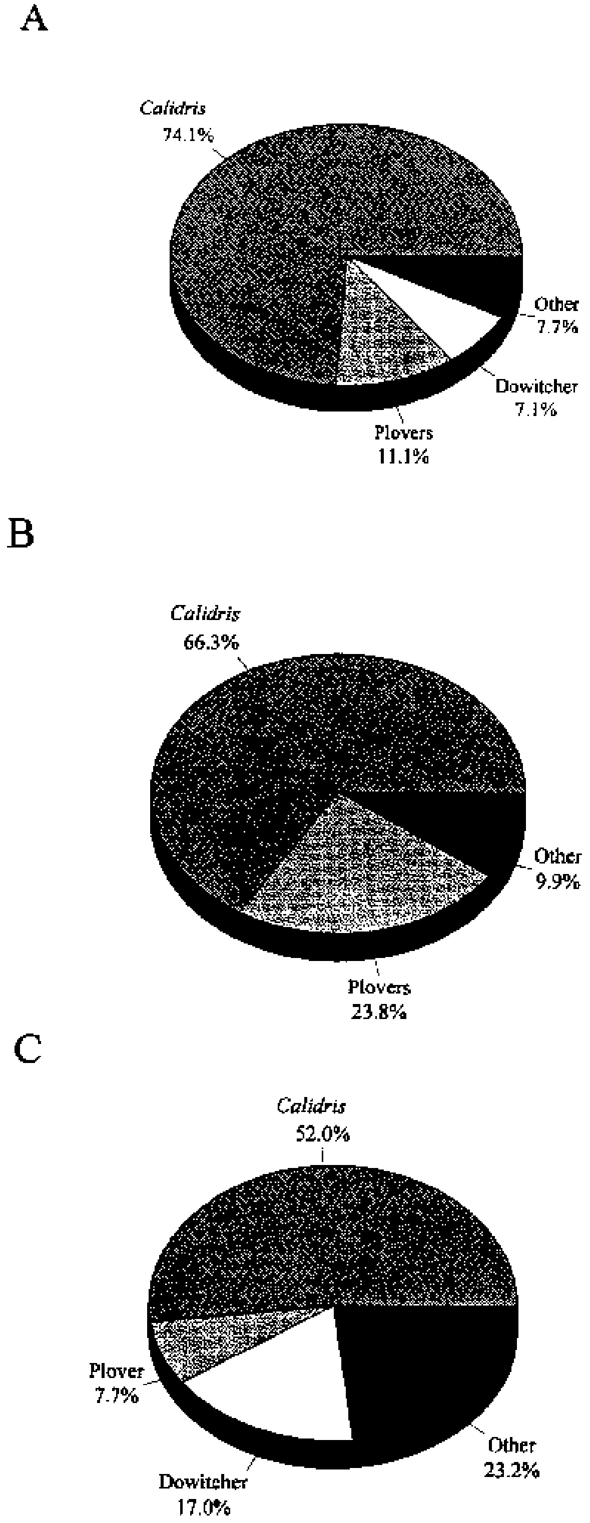


Fig. IV.B.6.17. Shorebird community composition on blue-green algal flats of Padre Island (A), Mustang Island (B) (Withers, 1994), and the mudflat in Oso Bay (C) (Withers and Chapman, 1993).

Table IV.B.6.8. Overall microhabitat preferences (frequency %) for all shorebird species observed on the Oso Bay mudflat (modified from Withers and Chapman, 1993).

Species	Open Water	Shoreface	Flat
American Avocet	74	20	6
Baird's Sandpiper	50	50	0
Black-bellied Plover	25	48	27
Black-necked Stilt	75	19	3
Dowitchers	60	37	4
Dunlin	51	37	12
Greater Yellowlegs	53	34	13
Killdeer	5	29	66
Lesser Yellowlegs	76	18	6
Long-billed Curlew	25	20	55
Marbled Godwit	69	22	9
Pectoral Sandpiper	0	100	0
Peeps	29	54	17
Piping Plover	0	64	36
Ruddy Turnstone	25	42	33
Sanderling	28	57	18
Semipalmated Plover	13	63	25
Snowy Plover	4	50	46
Spotted Sandpiper	0	50	50
Stilt Sandpiper	71	29	0
Whimbrel	6	31	63
Willet	44	22	34
Wilson's Phalarope	25	75	0
Wilson's Plover	10	34	56

Table IV.B.6.9. Pooled totals and proportions ± 95% confidence intervals of shorebird species in each microhabitat on blue-green algal flats in the upper Laguna Madre (modified from Withers, 1994). Microhabitats were significantly (*P* <0.05) preferred (*) if the confidence interval on the observed proportion(s) was greater than the expected proportion of 0.25 (Haney and Solow, 1993).

Species	Open Water	Intertidal	Wet	Damp
American Avocet n = 84	68 0.81±0.08 *	16 0.19±0.08	0	0
American Oystercatcher n = 29	6 0.21±0.15	16 0.55±0.18 *	5 0.17±0.14	2
Black-bellied Plover n = 766	181 0.24±0.03	219 0.29±0.03	272 0.36±0.03 *	94 0.12±0.02
Black-necked Stilt n = 47	47 1.00	0	0	0
Dowitchers n = 1,054	806 0.77±0.03 *	175 0.17±0.02	71 0.07±0.02	2
Dunlin n = 4,971	2,631 0.53±0.01*	1,145 0.23±0.01	1,181 0.24±0.01	14 <0.01
Greater Yellowlegs n = 33	25 0.76±0.15 *	6 0.18±0.13	1	1
Least Sandpiper n = 2,184	10 <0.01	352 0.16±0.02	1,567 0.69±0.02 *	255 0.11±0.01
Lesser Yellowlegs n = 80	69 0.86±0.08 *	9 0.11±0.07	2	0
Long-billed Curlew n = 54	17 0.32±0.10	19 0.35±0.13	5 0.09±0.08	13 0.24±0.11

Table IV.B.6.9. Continued.

Species	Open Water	Intertidal	Wet	Damp
Marbled Godwit	75	9	7	0
n = 91	0.82±0.08 *	0.10±0.07	0.08±0.04	
Peep	381	579	2274	100
n = 3,334	0.11±0.01	0.17±0.01	0.68±0.02 *	0.03±0.01
Piping Plover	0	29	531	582
n = 1,142		0.03±0.01	0.47±0.03 *	0.51±0.03 *
Red Knot	69	38	40	0
n = 147	0.47±0.08 *	0.26±0.07	0.27±0.07	
Ruddy Turnstone	10	30	261	83
n = 384	0.03±0.02	0.08±0.03	0.68±0.05 *	0.22±0.04
Sanderling	111	290	370	223
n = 994	0.11±0.02	0.29±0.03	0.37±0.03 *	0.22±0.03
Semipalmated Plover	0	2	57	61
n = 120			0.48±0.09 *	0.51±0.09 *
Snowy Plover	2	96	495	422
n = 1,015		0.10±0.19	0.49±0.03 *	0.42±0.03 *
Western Sandpiper	195	1778	2923	239
n = 5,139	0.04±0.01	0.35±0.01 *	0.57±0.01 *	0.05±0.01
Willet	550	335	308	68
n = 78	0.44±0.03 *	0.27±0.02	0.24±0.02	0.05±0.01
Wilson's Plover	2	11	16	49
n = 78		0.16±0.09	0.24±0.10	0.72±0.11 *

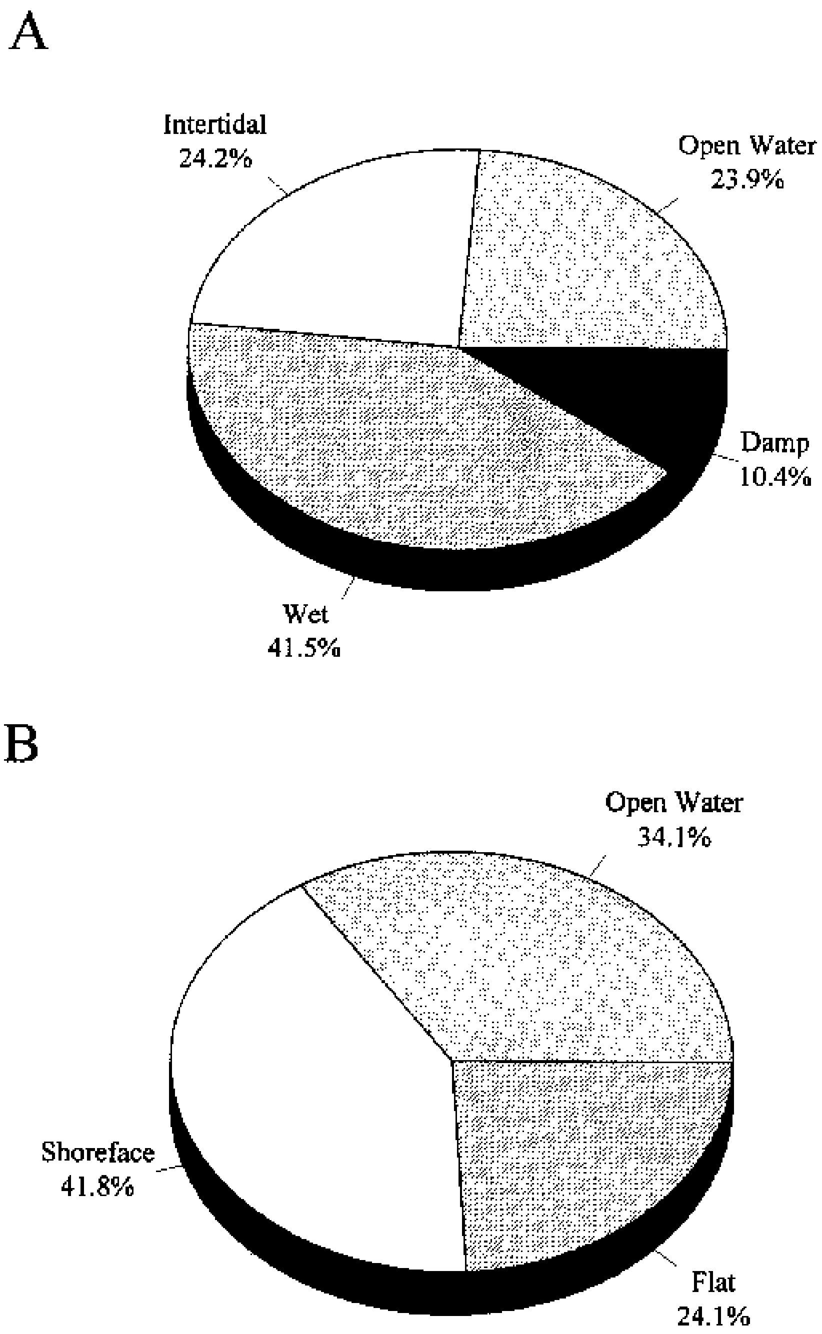


Fig. IV.B.6.18. Relative abundance of shorebirds in tidal flat microhabitats in the upper Laguna Madre (A) (Withers, 1994) and Oso Bay (B) (Withers and Chapman, 1993).

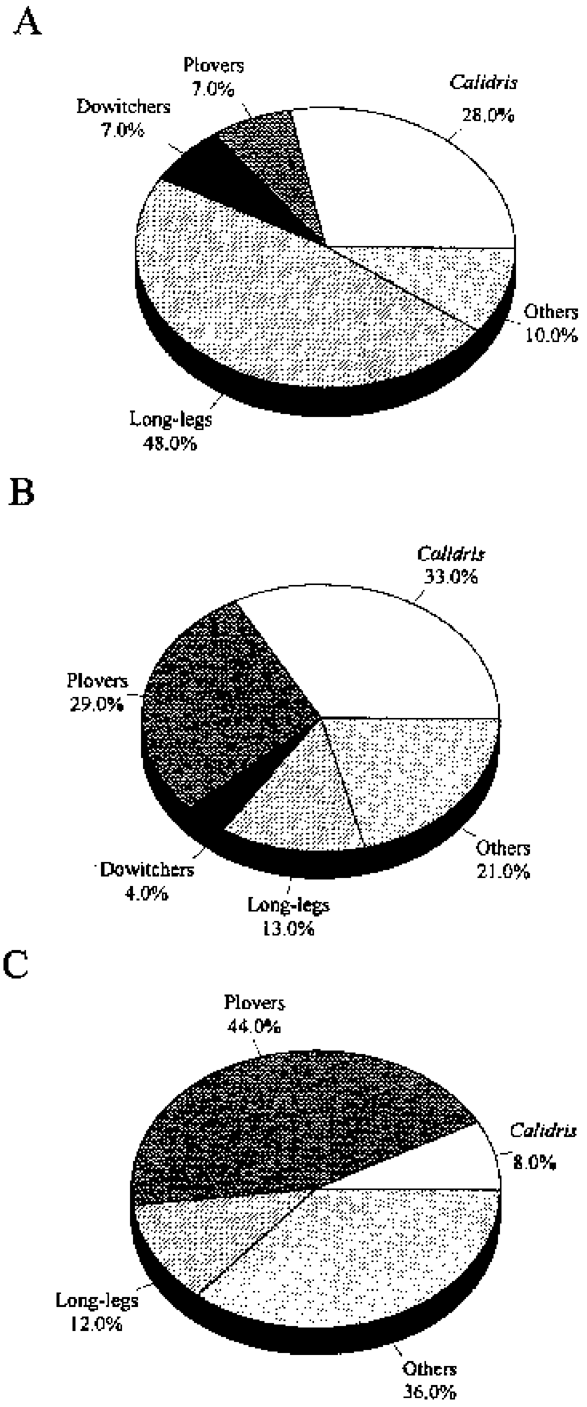


Fig. IV.B.6.19. Relative abundance of shorebirds by species on the Oso Bay mudflat: open water adjacent to the flat (A), shoreface microhabitat (B), and flat microhabitat (C) (from Withers and Chapman, 1993).

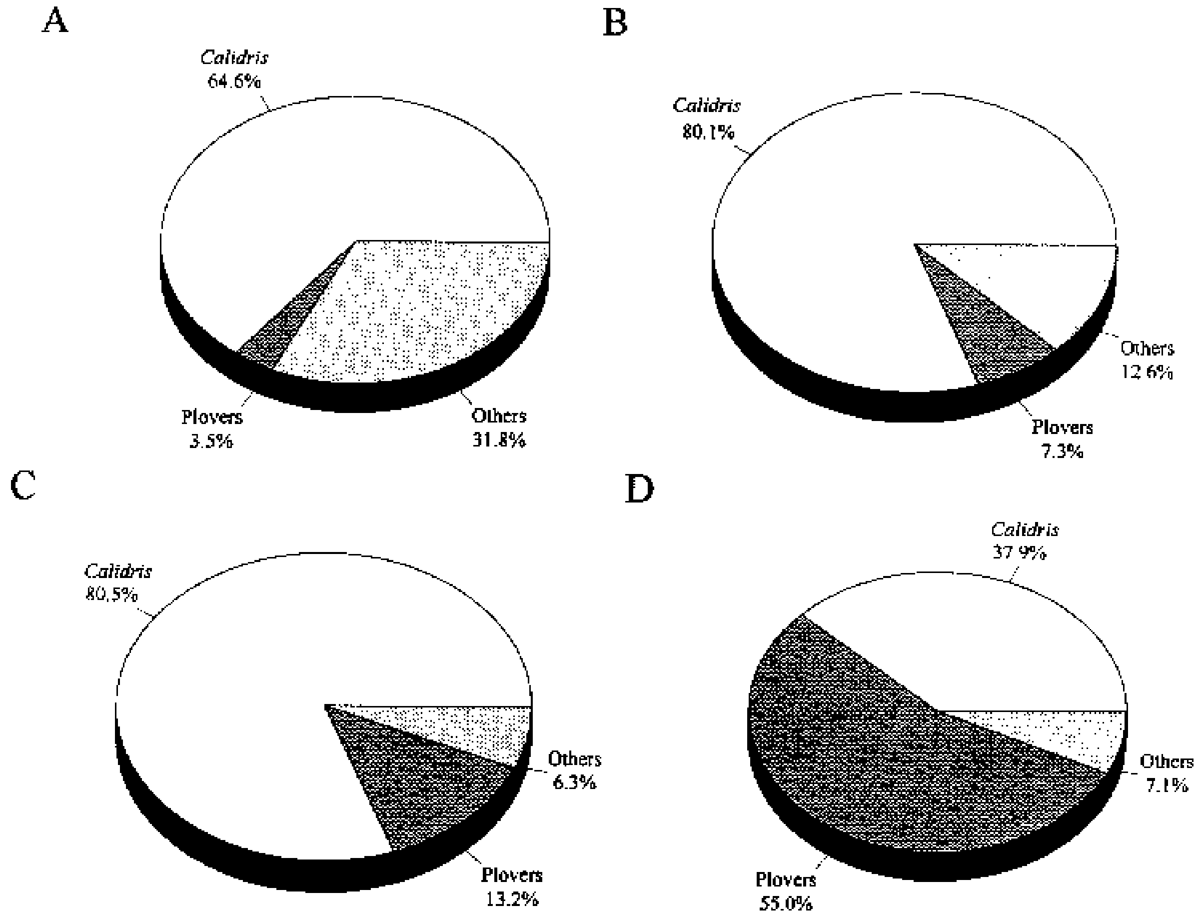


Fig. IV.B.6.20. Relative abundance of shorebirds by species on blue-green algal flats in the upper Laguna Madre: open water adjacent to flat (A), intertidal microhabitat (B), wet microhabitat (C), and damp microhabitat (D) (after Withers, 1994).

6.5 Ecosystem Processes

6.5.1 Productivity and Energy Flow

Productivity on tidal flats is often assumed to be insignificant due to lack of macrophytic vegetation, particularly by the public at large. However, large numbers of shorebirds use flats, and there are often well-developed benthic communities in wetter flats. Rather than being barren and unproductive, they are important biomass conversion sites, or areas where primary production is converted to animal biomass for use by higher-level consumers.

Very high productivity (388 g C/m^2/yr) and an algal turnover rate of 10.8 times/yr was estimated for the Yarborough Pass tidal flat on Padre Island (Pulich and Rabalais, 1982; 1986). Productivity on this flat was higher than in most other similar habitats (Table IV.B.6.10) and conforms to the latitudinal gradient in productivity (higher latitudes = lower productivity) in salt

Table IV.B.6.10. Primary productivity by benthic microalgae in the study area and in other temperate intertidal and shallow subtidal areas.

Area	Production ($g\ C/m^2/yr$)	Reference
North Padre Island algal mat	388[a]	Pulich and Rabalais 1982, 1986
Brownsville Ship Channel algal mat	222[a]	Pulich and Rabalais 1982, 1986
Texas algal mat	562[bc]	Odum and Wilson 1962
Texas sand flat	300[d]	Brogden et al. 1977
Georgia	200	Pomeroy 1959
Southern California	200	Onuf et al. 1980
North Carolina (Newport River Estuary)	40[e]	Bigelow 1977
Dutch Wadden Sea	35-435	Cadée and Hegeman 1974
False Bay, Washington	143-226[b]	Pamatmat 1968
Ythan Estuary, Scotland	31	Leach 1970
Long Island Sound	84	Burkholder 1965
Southern New England Shoals	81	Marshall et al. 1971
Laboratory (North Carolina)	75[bc]	Sollins 1969

[a] Extrapolated from 3 hr rates and 300 day of effective productivity/yr.
[b] Estimated using the oxygen method.
[c] Converted from g $O_2/m^2/d$ using 1g O_2 = 0.375 g C (Lind 1974) x 300 days.
[d] Values for inundated flat, estimated at 300 days of effective productivity/year.
[e] Probably not representative (Peterson and Peterson 1979).

marsh vegetation and mudflat microalgae suggested by other workers (Peterson, 1981; Whitlach, 1982). Odum and Wilson (1962) measured very high rates of productivity, but found net production of carbon was negligible because respiration rates were nearly equal to photosynthetic rates. These rates may not be typical; Pamatmat (1968) measured respiration at about 23% of production.

Tidal flat productivity in the study area is comparable to seagrass beds, and about 20-40% of a typical *Spartina* spp. (cordgrass) marsh (Pulich et al., 1982). Although less than half the productivity of a salt marsh, the value is substantial and cannot be ignored where tidal flats occupy a significant proportion of the total acreage in an estuary (Peterson, 1981). Benthic algae contributed as much as one third of total estuarine primary productivity in Georgia (Pomeroy, 1959). Benthic microalgae do not accumulate biomass *in situ* like marsh plants and many seagrasses, but some groups, like diatoms, are nutritious and highly edible, and consequently are of immediate use to consumers. Blue-green algae are also nutritious, but vary widely in their edibility. The often direct transfer of primary productivity to higher trophic levels on tidal flats results in energy flow which may be more efficient than the classical 10% efficiency of other food chains, possibly as high as 40%, which is similar to efficiency of decomposer food chains in marshes. A substantial amount of energy contained in marsh and seagrass detritus never appears in bacterial biomass, the edible form of that energy. It may take about 2.5 kg of marsh grass production to provide the same amount of food to consumers as only 1 kg of benthic microalgae (Fig. IV.B.6.21). This makes productivity of benthic microalgae appear to be even more significant (Peterson, 1981).

The question of energy transfer efficiency is complicated by dissolved (DOC) and particulate organic matter (POC) which is found in the water column and sediments. This organic matter is used by both bacteria and deposit-feeding organisms. DOC values of 5-11 mg C/l were recorded by Maurer (1971) for Laguna Madre waters. There may be high concentrations of organic matter in water over algal flats due to algal productivity (Longley et al., 1989) and the characteristic "leakiness" of algae. Organic matter enters tidal flat sediments as a result of alternation of sediment and old algal layers beneath the active mat and from the breakdown of marsh and seagrass detritus carried to the mat by wind tides and currents (Peterson, 1979). Organic content of content of tidal flat sediments is highly variable (Volkman and Oppenheimer, 1962). Few data are available on origin or amount of organic matter present in tidal flat sediments. Sollins (1969) found 270-640 g/m^2 organic matter in the top layers, and 970-1350 g/m^2 for the entire core. The living mat may contain 1.5-32.0% organic carbon (Parker and Leo, 1965; Volkman and Oppenheimer, 1962). Haines (1977) found the detrital pool of particles available for breakdown in a Georgia estuary was largely derived from algal sources. Significant export of productivity from tidal flats caused by winter breakup of the mat and wind may result in significant output to the estuary's detrital pool (Brock, 1983; Brogden et al., 1977).

No estimates were found concerning the contribution of phytoplankton to primary productivity of the CCBNEP tidal flat system when it is flooded. Although the prevailing view is that phytoplankton contribute an insignificant fraction of carbon to estuaries, Sellner and Zingmark (1976) found phytoplankton production as high as 350 g C/m^2/yr in shallow tidal creeks and estuaries of South Carolina. Peterson and Peterson (1979) suggest that because summer turbidity in shallow water of North Carolina sounds and estuaries is low, phytoplankton production could often be significant. Phytoplankton productivity above tidal flats in New England is generally low because they are only flooded part of the day and the water is turbid (Whitlach, 1982). The current brown tide event in the Laguna Madre is contributing a substantial amount of carbon to the system, since the organism is not grazed.

6.5.2 Trophic Levels and Food Web Relationships

Estuarine food webs are commonly viewed as detritus-based. Whitlach (1982) asserts that detrital material is conspicuous in guts of tidal flat organisms and the grazing food web contributes less than the detrital food web to tidal flat energy. However, Peterson and Peterson (1979) note that gut contents are not especially useful for determining diets of detritivores and other low-level consumers. Gut contents of these organisms are nearly always in an advanced stage of decomposition; the basic distinction of marsh plant and diatom or seagrass detritus is

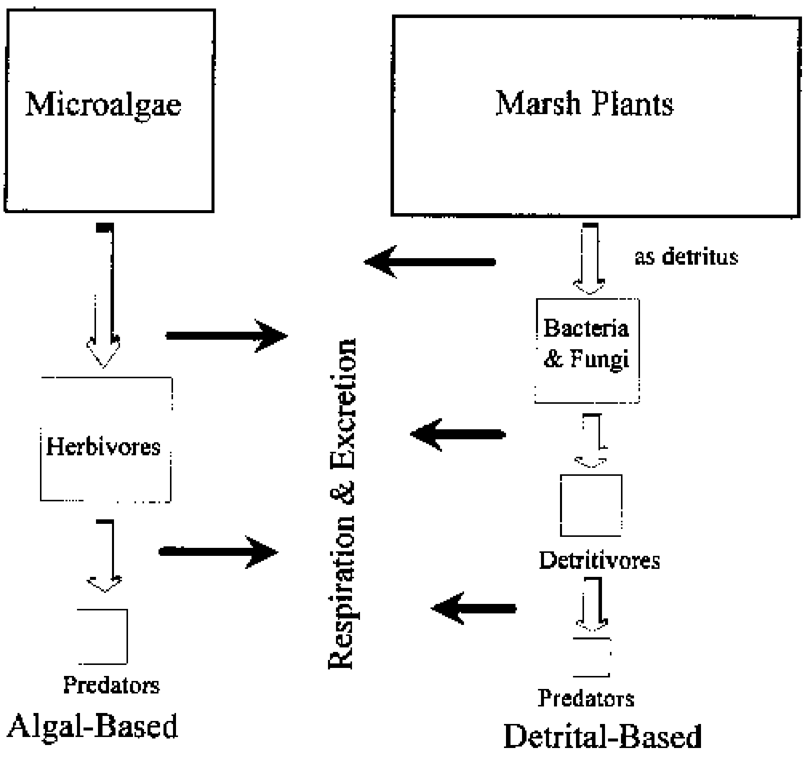


Fig. IV.B.6.21. The fate of primary productivity in algal-based (tidal flat) and detrital-based (salt marsh) food chains (redrawn from Peterson 1981). Boxes are sized to convey relative amounts of primary productivity at each level.

usually impossible. In addition, gut contents do not necessarily reflect what is being digested and assimilated since many detritivores use bacteria and fungi that colonize the detritus rather than the detritus itself. Results of $\delta^{13}C$ analyses of detritivores in a Georgia salt marsh tend to contradict previous assumptions of the importance of vascular plant detritus in the food webs of estuarine systems (Haines and Montague, 1979). These data indicate algae are far more important than expected in nutrition of primary consumers in estuarine systems. Benthic microalgae are highly nutritious and often palatable (Peterson, 1981); it is likely the grazing food chain is much more important than previously thought, particularly on tidal flats.

From their work on southerly Laguna Madre algal flats, Pulich and Rabalais (1982) suggest an abbreviated food chain based on microalgae and mature saltwater-adapted insects. Benthic invertebrates such as polychaetes and crustaceans, as well as larval insects are also important in the food chains of wetter algal flats in the study area (Withers, 1994; T. Barrera, unpubl. data). A generalized food chain for tidal flats is depicted in Figure IV.B.6.22. Presence of higher level consumers such as shorebirds and fish are dependent on inundation and exposure of the flat. Because of shallow water, large fish such as *Sciaenops ocellata* only rarely use the flats. The

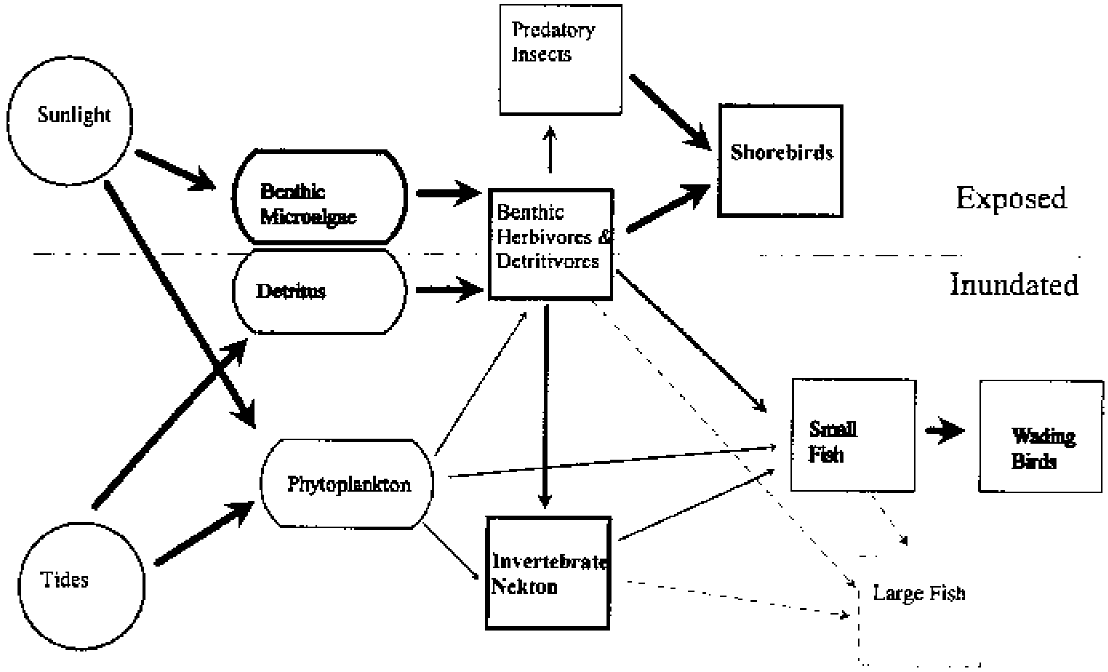


Fig. IV.B.6.22. Generalized food web for tidal flats. The weight of the arrows and boxes reflect the relative importance of each compartment and pathway.

grazing food chain may be more important on algal flats than non-algal flats, although most benthic organisms recovered from flats in the upper Laguna Madre were either deposit-feeders or predators (refer to Table IV.B.6.4). Detritus may be more important during some times of the year than others. Large amounts of seagrass detritus are often found along the high tide line after high tides, particularly in fall and winter, and after storms (K. Withers, pers. obs.). Regardless of the basis of tidal flat food chains, these are major sites for the conversion of plant biomass into animal biomass for use by larger estuarine predators.

6.5.3 Nutrient Cycling

Tidal flats appear to be nutrient sinks. Mudflat sediments in western Connecticut adsorbed nutrients derived from an adjacent saltmarsh and tidal creek. They were so effective in trapping nutrients that very little was transported into the open estuary (Welsh, 1980). Other significant sources of nutrients include local runoff during periods of high rainfall and sediment nutrients are brought to the surface by capillary action during dry periods and later redissolved (Oppenheimer and Ward, 1963). Nitrogen and phosphorus are major nutrients associated with primary production on tidal flats in the study area.

Nitrogen is often considered a limiting nutrient, however, most nitrogen used by blue-green algal flats in the study area is fixed by the mat or anaerobic bacteria in sediments beneath the mat. Gotto et al. (1981) estimated an average annual input of nitrogen in an algal mat in the Port Aransas area at 40.6 kg N/ha. This conservative estimate represents a considerable contribution to the nitrogen economy of the shallow coastal environment. Pulich and Rabalais (1982; 1986) measured nitrogen fixation in algal mats near Yarborough Pass on Padre Island and the Brownsville Ship Channel. They estimated average nitrogen inputs between 4-16 kg N/ha/yr and 19-89 kg N/ha/yr, respectively. Moisture content of the mat was correlated to nitrogen fixation activity; darkness and dim light supported better activity than full sunlight.

Substantial amounts of dissolved ammonia were always detected leaching out of algal mats at Yarborough Pass and the Brownsville Ship Channel. There was little pattern in the process, and the ammonia pools probably reflected local variation in decomposition occurring within or beneath the mat. The same measurements revealed a fairly consistent pattern of phosphate flux. Accumulated phosphate was readily washed out of a non-growing, desiccated mat when it was reflooded. Phosphate also appears to be lost by downward percolation. When the mat was wet or flooded, net uptake phosphate by the mat was observed. High nitrogen fixation combined with high ammonia leaching results suggest fixed nitrogen is generally available, if not abundant, for algal production. Conversely, the phosphate leaching pattern demonstrates potential for phosphate as a limiting nutrient (Pulich and Rabalais, 1982).

6.5.4 Linkages with Other Systems

Because tidal flats can be considered semi-terrestrial, they interact with both aquatic and terrestrial environments. Runoff from upland areas contributes freshwater, detritus, nutrients and sediment and may be a source for pollutants such as agricultural chemicals, industrial wastes, and chemical spills, particularly on the mainland. In urban areas, direct discharges of domestic and industrial wastes can constitute significant nutrient inputs into tidal flat systems. Approximately 15 million gal/day of treated municipal wastewater are discharged into Oso Bay adjacent to the wind-tidal flats. Some nutrients brought to wind-tidal flat systems via streams actually originate as waste discharges and agricultural runoff. Oso Creek receives municipal wastewater from Corpus Christi's westside and Robstown, and over 500 million gal/day of hypersaline water pumped out of the Laguna Madre from the Central Power and Light Barney Davis Power Plant. The power plant discharges significantly affects hydrology of lower Oso Creek and Oso Bay. In addition, Petronila Creek and many other ephemeral or intermittent flowing into Baffin Bay receive much agricultural runoff from intensively cultivated areas along their banks.

Deflation of barrier island dunes contributes most of the sediment to island flats. Coastal marshes contribute nutrients and detritus to tidal flats in deltaic and bay margin environments, particularly from Corpus Christi Bay northward. Benthic invertebrates may be recruited from coastal marshes onto tidal flats, and they also provide a source for consumers such as fish, shrimp, and crabs. Seagrass meadows also provide detritus and a source of invertebrates and nektonic consumers. Tidal flats interact with the open bay primarily as a water, nutrient, and invertebrate source and transport system.

Presence of tidal flats in the mosaic of the coastal environment is particularly important for shorebirds and wading birds. The flats provide an abundant source of food, and are near upland and transitional habitats for roosting and nesting. Alternate feeding sites on the beach are also nearby for wading birds when flats are exposed or for shorebirds when flats are completely flooded. Health of the bay ecosystem is one of the most critical aspects in survival of the tidal flat system because the bay supplies most of the water which nourishes the flats. The next most critical component in long-term maintenance of tidal flats is runoff from adjacent upland areas (Longley et al., 1989). The primary threat to tidal flat systems is public perception that they are barren wastelands. Tidal flats are often targeted for coastal development and frequently overlay oil and gas deposits. In the past, tidal flats were often chosen as sites for dredge material disposal and mitigation projects in which they were scraped down in order to attempt creation of coastal marsh or seagrass systems.

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HABITAT 7: BARRIER ISLANDS

7.1 Physical Setting And Processes

7.1.1 Distribution within Project Area

Barrier islands are elongate landforms that lie parallel to the mainland shoreline and are typically isolated from the mainland by bays and lagoons. Longshore currents, low tidal range and wave energy work together to form and maintain barrier island systems (Britton and Morton, 1989). Barrier islands extend along the easternmost boundary of the CCBNEP area and include southern Matagorda, St. Joseph, Mustang and northern Padre Islands. These islands function as protective barriers to the adjacent Texas mainland and shallow bays and lagoons. In addition, unique flora and fauna inhabit the islands and increase the biologic diversity of the CCBNEP study area.

7.1.2 Historical Development

Geologic formation of all barrier islands within the CCBNEP study area are similar (see Section I - Introduction, this volume); however, slight differences in topography, vegetation, and animal composition are evident on each island, due to the influence of physical factors and degree of isolation from the mainland and adjacent barrier islands. Barrier islands were formed by deposition of sands via Gulf longshore currents flowing parallel to the mainland. Constant redistribution of sands, driven primarily by prevailing southeasterly winds, contributes to formation of distinct topographic features across the island. These dynamic, eolian forces continue to erode some areas and build up others, as can be observed with active dune migration across the islands. Abrupt changes in topography occur during and after hurricanes and storm surges; these events may reopen passes through an island, denude and/or flatten active dune areas, and erode beach fronts (Price, 1933; Weise and White, 1980).

7.1.3 Physiography

Both natural and human-made passes separate the barrier island chain; a series of bays and lagoons separate islands from the mainland. The southern portion of Matagorda Island is separated from St. Joseph Island by Cedar Bayou and is separated from the mainland by Mesquite Bay within the CCBNEP area. Historically, Cedar Bayou existed as a narrow washover channel west of the storm-tide delta at Ayers Point. Channel migration occurred after the main pass between Matagorda and St. Joseph Island closed about 450 years ago (McGowen, et al. 1979). The area of recent fill between the relict and present pass has a distinctive topography of crescent-shaped dune fields. Cedar Bayou has been opened by hurricanes and storm surges but often closes between these events; the pass is currently migrating southward. Artificial opening of the pass by dredging has occurred several times during the past fifty years. The pass was purposely closed to prevent oil contamination from the *Ixtoc I* oil spill in 1979. The latest dredge operation to open the pass occurred in 1987 and the pass has remained open.

St. Joseph Island is about 27.3 km (17 mi) in length and is disconnected from Mustang Island by the human-made and actively dredged Aransas Pass channel and from the mainland by the

Aransas Bay system. Mustang Island is about 21.7 km (13.5 mi) in length and is separated from Padre Island by an intermittently-open washover pass, Packery Channel (historically known as Corpus Christi Pass), and from the mainland by the Corpus Christi Bay. Other washover passes occur in this area (Newport and Corpus Christi passes), however, they are only connected to the Gulf during and after tropical storms/hurricanes (Brown et al., 1976). Padre Island extends south to Brazos Santiago Pass (181 km, or 113 mi), is mostly isolated from the mainland by the Laguna Madre and is connected to the Gulf via Port Mansfield pass. Only the northern part of Padre Island is included within the CCBNEP study area as the southernmost boundary of the study area lies within the northern Land Cut area at the southern tip of The Hole. The Land Cut, expansive wind tidal flats that connect Padre Island to the mainland, bisects the Laguna Madre system into northern and southern sections connected only by the Gulf Intracoastal Waterway (Brown et al., 1977). Northern Padre Island is quite wide and has extensive fresh- to brackish marshes within the vegetated barrier flats in the central part of the island. Expansive wind tidal flats occur along the western shore of Padre Island and eastern Laguna Madre (Brown et al., 1976; Brown et al., 1977).

All barrier islands along the central Texas coast are elongate in shape and typically wider at the northern ends. Several habitat types occur across the islands and are related to elevation, physical forces, and geomorphology of the adjacent Gulf of Mexico, back bays, and lagoons. Physiographic zones extend the length of an island and include: foreshore (swash zone), backshore (from high tide line to dunes), foredunes, vegetated flats, ponds and marshes, back-island dunes, wind-tidal flats, and coastal marshes (Fig. IV.B.7.1). Foreshore habitat, wind-tidal flats, and coastal marshes are driven more by hydrologic and eolian forces, than the predominantly terrestrial dunes and vegetated flats, and are therefore specifically addressed in Chapters IV.B.5.8, IV.B.5.6, and IV.B.5.5 (this volume), respectively. Ponds and marshes within the vegetated flats are described here as they form an integral part of ecological relationships of barrier island systems.

7.1.3.1 Foredunes

Highest elevation points on barrier islands occur along foredune ridges landward from the Gulf beaches. Padre Island has the tallest dunes along the Texas coast, some as high as 15.24 m (50 ft) above sea level (Weise and White, 1980), although average dune heights range from 6.1-7.6 m (20-25 ft) on Mustang and northern Padre Island (Brown et al., 1976). Dune heights are lower on St. Joseph and Matagorda Islands, where beach ridges average 1.5-3.0 m (5-10 ft) (McGowen et al., 1976). Foredunes are also less vegetated from north to south due to lower average precipitation rates (Weise and White, 1980).

In many areas immediately seaward of the foredunes, smaller dunes termed coppice dunes may occur. These dunes typically have low, spreading vegetation that collect sand migrating up the beach face. In addition, wind-shadow dunes may form behind coppice dunes due to accumulation of sand in wind-protected areas (Weise and White, 1980).

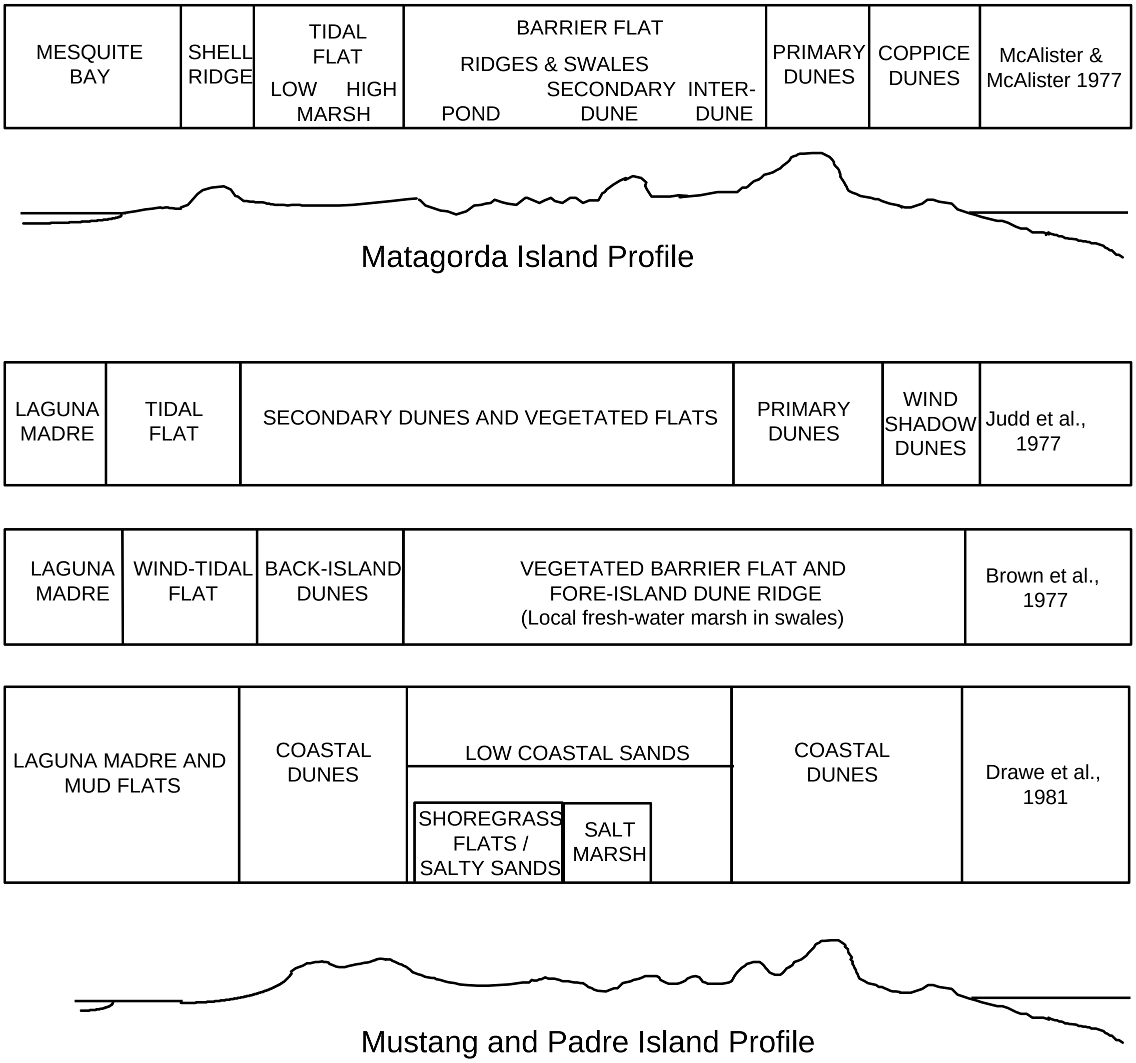

Fig. IV.B.7.1. Cross-section profiles of barrier island vegetation zonation for Matagorda, Mustang, and Padre Island.

Elevation of coppice and wind-shadow dunes typically average 1 m (3 ft) tall; however, taller dunes have been noted due to accumulation of sand in vegetation over extended periods. If these dunes are not eroded by storm surges or high tides, they may coalesce with the foredune ridge or form a new ridge.

7.1.3.2 Vegetated flats

Elevations within the central part of the barrier islands are not uniform due to formation of ridges and swales as a result of dunes migrating across the island from east to west (Prouty and Prouty, 1989). Ridge and swale topography forms during alternating wet and dry climates. During wet periods, vegetation growth stabilizes the active dune; however, during droughts, the active dune migrates ahead of the stabilized ridge and produces a long, linear depression or deflation trough

(Hunter et al., 1972). These troughs typically have standing water during years of high precipitation and support a diversity of wetland flora and fauna (Prouty and Prouty, 1989). Increases in vegetative cover will stabilize the deflation flat area, but migrating dune fields may locally cover areas of the flats, increase elevation, and bury vegetation (Longley et al., 1989).

7.1.3.3 Ponds and Marshes

In low areas, where wind scoured the surface down to the water table, moisture in the sediments eliminates further erosion. Average depth of the water table depends on precipitation, so amount of erosion varies from year to year. During wet years, these troughs will hold water and are very important to the ecology of barrier islands (Weise and White, 1980). The number and size of ponds and marshes vary from island to island; due to variability in rainfall from north to south and from year to year, areal extent of these habitats is difficult to quantify. Ridge and swale topography of vegetated flats are oriented longitudinally along northern Padre Island; therefore, ponds and marshes often exhibit a linear configuration (Weise and White, 1980). Ponds and marshes located immediately leeward of foredune ridges exhibit more elliptic shapes. These low areas were formed by erosion of fore-island dunes.

7.1.3.4 Back-island Dunes

Whereas orientation of foredune ridges is parallel to the Gulf beach and dune migration occurs in a southeast to northwest direction, back-island dunes on Padre Island are aligned east to west (Hunter, et al. 1972). These dunes typically are not as tall as foredunes and are generally <3 m (10 ft) high, but may reach about 7.5 m (25 ft) in protected areas on northern Padre Island (Weise and White, 1980). Vegetated density tends to increase with increased rainfall; dune stabilization typically occurs under these conditions. During droughts, devegetated dunes migrate across the island in a net west-northwest direction (Prouty and Prouty, 1989).

7.1.4 Geology & Soil

Geologic development and formation of barrier islands is discussed in Section I, Introduction. A series of models have been constructed to follow development of barrier islands throughout their formation and to show interrelationships of sea level changes, along with Gulf and river sediment deposition (Weise and White, 1980). Both erosional and accretionary dynamic processes formed the barrier island chain and continue to affect barrier island configuration.

Sediment composition on all barrier islands is predominantly sand with high to very high permeability and low water-holding capacity (McGowen et al., 1976). Shell fragments are intermixed with sand during periods of high wave and wind energy (Weise and White, 1980). Sediment composition changes from north to south, due to various sources of river sediment, and from east to west as a result of Gulf and bay processes. Offshore bars and older submerged sand bodies deposited by ancient river systems serve as sediment reserves. Longshore currents and waves resuspend and deposit the sediments on the beaches. As sediments dry, finer particles are transported by wind to backshore and dune ridges. Short-term sediment transfer from the beach to foredune ridges occurs by southeasterly wind transport during most of the year. Larger amounts of sediment are transported during hurricanes, tropical storms, and spring tides (Weise and White, 1980).

Matagorda Island, located near the Guadalupe-San Antonio River delta, is an excellent example of the influence of Gulf and riverine processes. Sediments composed of materials eroded from upland areas are first transported downstream into the San Antonio Bay system and later into the Gulf of Mexico. Finer sediments are deposited in bays and are resuspended during flooding events and by bay currents. The main island sands on the Gulf side have been suspended from the Gulf bottom by longshore currents and carried onshore by waves where they are dried, sorted, and transported by southeasterly winds to form the foredunes and low ridges and flats across the island interior. Back island sediments are transported and deposited by predominantly northerly winds, waves, and tides. Organic content on the Gulf side is typically low, whereas on the bay side, organic content may be quite high (McAlister and McAlister, 1993).

Foredune ridges are typically composed of fine, well-sorted sands transported up the beach face. Migrating dunes in the vegetated flats leeward of the foredune ridge and back-island dunes are of similar composition (Weise and White, 1980), although some finer sediments may be transported from deflation-flat areas that have lost vegetation (Longley, et al. 1989). Sand and shell deposits make up sediments in the vegetated flats, whereas some finer sediments and organic matter may accumulate and overlay sand and shell in ponds and marshes (Weise and White, 1980).

Soil analyses were conducted on northern Padre Island in four habitats, two of which included foredunes and low vegetated dunes in vegetated flats (Drawe et al. 1981). Overall, soil organic matter and nitrogen levels were low; phosphate levels were considered adequate in the foredunes, but not in the vegetated-flat dunes (Table IV.B.7.1). Both dune complexes were deficient in potassium, but were not deficient or toxic in sulfates, sodium, calcium or magnesium.

7.1.5 Hydrology & Chemistry

Average annual rainfall decreases and average temperature and evaporation increases from north to south. Permanent sources of freshwater may be lacking during droughts, although some freshwater will collect temporarily in low depressions following rainfall. These water sources usually become brackish or evaporate completely. The shallow, perched aquifer below the surface provides some water and is commonly the only source of freshwater from rain that has percolated through sands before it evaporates. This freshwater lens is situated above the saltwater table due to lower density and is located about 2.4-3.0 m (8-10 ft) below the surface of the island interior. High levels of relative humidity provide an additional source of water as dew collects on plants during the night. Relative humidity is a very important aspect of the barrier island climate regime and is typically high throughout the year as a result of moist Gulf air mediating air temperatures.

Table.IV.B.7.1. Chemical properties of soils from two habitat types on Padre Island National Seashore. Prefixes for soil fertility ratings are: - indicates a deficiency, + indicates an excess or toxic level, and ± indicates neither deficiency nor excess. Empirical ranges for soil fertility are: 0 - no problem for most plants, 1 - possible fertility problem but more work must be done to substantiate the problem, 4 - severe fertility problem, growth of many plants restricted (from Drawe, et al. 1981).

Soil Property	Primary Dune (Coastal Dune)	Soil Fertility Rating[a]	Low vegetated dunes in Vegetated Flats Habitat (Low Coastal Dune)	Soil Fertility Rating[a]
pH	7.7	0	7.8	0
Organic Matter (%)	0.12	-4	0.20	-4
Salinity (mmho/cm^2)	0.2	0	0.5	0
Chlorine (ppm)	27	0	85	0
Sulfate (ppm)	39	0	66	0
Boron (ppm)	0.5	0	0.4	0
Phosphorus (ppm)	16	0	11	0
Calcium (ppm)	1626	0	1277	0
Ca/Na h 100	1183		264	
Ca/K X 100	111366		8115	
Magnesium (ppm)	83	0	650	0
K/Mg ratio	0.17		0.02	
Potassium (ppm)	14	-1	16	-1
Sodium (ppm)	139	0	484	+1
Pseudo-ESP (%)[b]	11.8		26.1	
Iron (ppm)	1.8	±1	2.6	±1
Copper (ppm)	Trace	-1	Trace	-1
Manganese (ppm)	5.5	±1	2.6	±1
Zinc (ppm)	13.0	0	10.3	0

[a] (Mg + K) (Lunt, 1966)

[b] Pseudo exchangeable sodium (Na) percentage = 100 X extractable Na / extractable (Na + Ca)

In a recent survey of three ponds on the Padre Island National Seashore, Sissom (1990) reported water levels were lowest during September 1989 from the summer dry-down. The peak, full-water level was determined on changes of wetland to upland vegetation composition. Pond level fluctuated during the study, increasing in depth to about 0.6 m (2 ft), as a result of heavy rains in March 1990 that increased volumes and surface areas. Water levels eventually returned to preflood conditions as excess water percolated through surrounding sands.

7.2 Producers & Decomposers

7.2.1 Primary Producers

Vascular plants are the predominant primary producers of the barrier island habitat. Vascular plant species richness is quite high and is comparable to grassland-dominated mainland systems. Species diversity changes within habitats across the barrier island and among barrier islands (Drawe et al., 1981). Primary production is influenced by availability of fresh water and nutrients. Prevailing southeasterly winds transport sand, silt, and salts up the beach face (Whelan, 1975) and may also affect productivity of coppice and foredune vegetation (Britton and Morton, 1989). Due to high porosity of the soil, available nutrients are quickly leached out, particularly in the dunes (Drawe et al., 1981). Standing biomass may be negatively affected by fires, both natural and human-induced, but often productivity often increases the following growing season (Drawe and Kattner, 1978).

Dune plants are specially adapted to tolerate high salinities, low water availability, and sediment accretion. Conditions (e.g., lower salinities, higher water availability, more available nutrients) are less stressful in the barrier flat zone, so plant species richness often increases. Plants adapted to periodic flooding and drying are primary producers in ponds and marshes located within barrier vegetated flats (Britton and Morton, 1989).

7.2.2 Decomposers

Little is known about the decomposition processes in south Texas barrier islands; however, litter decomposition has been described as a gradual process (Longley and Brogden, 1989), accelerated only by fire (Kattner, 1973; Drawe and Kattner, 1978). No information is available on roles of bacteria and fungi in barrier island vegetation dynamics.

7.3 Consumers

7.3.1 Invertebrates

Invertebrates perform every type of consumer role in a barrier island system, from herbivores, to primary and secondary carnivores, scavengers, and detritivores. The importance of invertebrates as part of the food web has not been quantified for the central Texas barrier island chain; however, extensive species lists and habitat preferences have been compiled for Padre Island (Ortiz, 1976) and Matagorda Island (McAlister and McAlister, 1993) and are included in Appendix 1 in Volume 4.

7.3.1.1 Dunes

Invertebrate herbivores on Matagorda Island include *Trimerotropis citrina* (dunes grasshopper), *Tibicen* sp. (dunes cicada) and various species of katydids, planthoppers, and butterfly and moth caterpillars. *Anthrax analis* (bee flies), *Bombus* sp. (ground bumble bee), *Polistes exclamans* (yellow jacket), *P. rubiginosus* (red paper wasp) all feed on nectar of various plants; some species are typically found on one species, such as *Augochlora* sp. (halictid bee) on *Erigeron procumbens* (Corpus Christi fleabane) blossoms. Several species of butterflies are found on Matagorda Island, although larger winged species are less abundant due to winds above the vegetation. Several species breed on the island including *Junonia coenia* (buckeye), *Zerene cesonia* (dog-faced sulphur), *Phoebis sennae* (cloudless sulphur), *Euptoieta claudia* (variegated fritillary), *Agraulis vanillae* (Gulf fritillary), and *Strymon melinus* (gray hairstreak). Other mainland species may be absent from the island because of the absence of a larval host plant. *Battus philenor* (pipevine swallowtail) and *Danaus lexippus* (monarch butterfly) have been observed migrating throughout all of the island habitats. *Atta texana* (leaf-cutting ants) occur in secondary dunes (McAlister and McAlister, 1993).

Carnivorous insects of Matagorda Island include *Bembix* sp. (sand wasps) that prey on flies feeding on flower nectar. *Sphephius speciosus* (cicada killers) are the principal predators of *Tibicens* spp. (dunes cicadas). The following insects all feed on aphids and soft-bodied insects: *Apionerus* sp. (assassin bugs), *Efferia pogonias* (robber flies), Odonates (dragonflies), *Stagmomantis limbata* (praying mantis), *Dasymutilla gloriosa* (thistledown velvet ants), *Myrmeleon* sp. (ant lions), *Crematogaster laeviuscula* (valentine ants). *Solenopsis geminata* (tropical fire ants), *S. xyloni* (southern fire ants), and *Solenopsis globularia* (miniscule fire ants) prey on small, soft-bodied invertebrates. *Conomyrma flava* (pyramid ants) have been described as the most efficient ant predator and scavenger on Matagorda Island. Common detritivores include *Eleodes* sp. (sunflower seed beetles) and *Arenivaga bolliana* (sand roach) that forage for plant detritus in the sand (McAlister and McAlister, 1993).

7.3.1.2 Vegetated Flats

Common herbivorous insects on Matagorda Island include *Isoptera* spp.(termites) and grubworm larva of *Phyllophaga* spp. (June beetle). The arachnid group is an obvious invertebrate carnivore. Spiders must contend with the wind, so their webs are usually small, low, and constructed and used at night while the breezes are light. *Agelenopsis* spp. (grass spider) webs are close to the ground and snare low-flying, crawling or hopping prey. Other species use vegetation as structure at varying heights and include *Lycosa* spp. (burrowing wolf spider), *Eustala anastera* (humpbacked orb weaver), *Neoscona pratensis* (arabesque orb weaver), and *Acanthepeira stellata* (starbellied spiders). *Lycosa* spp. use vertical ground burrows to wait for passing prey. *Misumenops asperatus* (flower spiders) are camouflaged against the plant background and prey on various pollinating insects. *Phidippus audax* (emerald-jawed jumping spiders) are one of the most powerful spider predators on Matagorda Island and able to subdue prey their own size. *Latrodectus mactans* (black widow spiders) are common on the island. *Lithobius* sp. (brown centipedes) and *Centruroides vittatus* (scorpion) are less common and inhabit decaying vegetation and wood (McAlister and McAlister, 1993).

7.3.1.3 Ponds and Marshes

Sissom (1990) investigated several biotic parameters of barrier island ponds on Padre Island National Seashore, but listed no invertebrates.

7.3.2 Fishes

7.3.2.1 Ponds and Marshes.

In 1983, the TPWD sampled inland ponds on Matagorda Island and collected 20 different species of fish (Table IV.B.7.2) (McAlister and McAlister, 1993). The most abundant species was *Leiostomus xanthurus* (spot). An ecological study of the fish communities in three earthen ponds within Padre Island National Seashore reported only three species that occurred in varying abundances (Caudle, 1992). *Cyprinodon variegatus* (sheepshead killifish) was the most abundant fish species in two of the ponds examined. *Gambusia affinis* (mosquitofish) was predominant species in the third pond, whereas *Fundulus grandis* (Gulf killifish) abundance values were low in all ponds.

7.3.3 Reptiles & Amphibians

7.3.3.1 Dunes

No herbivorous reptiles and amphibians were listed for this zone. Carnivorous reptiles include *Cnemidophorus sexlineatus viridis* (prairie-lined racerunner) that occurs on Matagorda Island and feeds on termites, ants, grasshoppers, and other insects and arachnids (McAlister and McAlister, 1993). *Holbrookia p. propinqua* (keeled earless lizard) is very common on Mustang Island and Padre Island (PINS, 1984), but are not found on Matagorda Island (McAlister and McAlister, 1993).

7.3.3.2 Vegetated Flats

One herbivorous tortoise is listed for this habitat, although undoubtedly other turtles and terrapins cross while migrating from pond to pond on the island interior. *Gopherus berlandieri* (Texas tortoise), listed as rare on Padre Island National Seashore (PINS, 1984), is herbivorous and feeds on grass and the pads, flowers, and fruits of *Opuntia lindheimeri* (prickly pear) as well as other vegetation (Conant, 1975). Several carnivorous reptiles have been documented on barrier islands (Table IV.B.7.3).

7.3.3.3 Ponds and Marshes

Trachemys scripta elegans (red-eared turtles), *Kinosternon* spp. (mud turtles) feed on wetland vegetation in the ponds and marshes on Matagorda Island. During their aquatic life stages, tadpoles of various frog and toad species feed on algae and detritus within the pond habitats. Carnivorous turtles on Matagorda Island include the *Trachemys scripta elegans*, *Kinosternon*

Table IV.B.7.2. Fish species seined from a Matagorda Island pond (adapted from McAlister & McAlister, 1993 from TPWD data) (trophic level sources from Table IV.C.2.1).

Common Name	Scientific Name	Trophic Level
Atlantic croaker*	*Micropogonias undulatus*	piscivore, macrobenthos
bayou killifish*	*Fundulus pulvereus*	?
blackcheek tonguefish	*Symphurus plagiusa*	?
darters goby	*Gobionellus boleosoma*	?
fringed flounder	*Etropus crossotus*	?
gulf killifish*	*Fundulus grandis*	larvivore, omnivore
gulf menhaden	*Brevoortia patronus*	detritivore, planktivore
inland silverside*	*Menidia beryllina*	zooplanktivore, detritivore
mosquitofish	*Gambusia affinis*	larvivore, omnivore
pinfish*	*Lagodon rhomboides*	macrobenthos, crustaceans, fish
rainwater killifish*	*Lucania parva*	plankton, larvivore, omnivore
red drum*	*Sciaenops ocellata*	crabs, shrimp, fish
sailfin molly	*Poecilia latipinna*	?
sheepshead killifish*	*Cyprinodon variegatus*	herbivore
skipjack*	*Elops saurus*	piscivore
southern flounder*	*Paralichthys lethostigma*	fish, shrimp
spot*	*Leiostomus xanthurus*	detritivore, macrobenthos
white mullet*	*Mugil curema*	herbivore, plankton

* Marine fish that regularly invade northern Gulf coastal fresh water (Hoese and Moore, 1977).

spp., *Malaclemys terrapin littoralis* (Texas diamondback terrapin), and *Chelydra serpentina* (snapping turtle). About 30 *Alligator mississippiensis* (American alligator) occur on Matagorda Island, typically leading a solitary existence in the island ponds as opportunistic carnivores. Some species of tadpoles feed on insect larva whereas adults are carnivorous. Amphibian species listed for Matagorda Island include *Rana utricularia* (southern leopard frog), *Rana berlandieri* (Rio Grande leopard frog), *Hyla cinerea* (green treefrog), *Bufo valliceps* (Gulf coast toad), *Gastrophryne carolinensis* (eastern narrow-mouthed toad), and *Scaphiopus h. holbrooki* (eastern spadefoot toad) (McAlister and McAlister, 1993). *Hyla cinerea*, *S. holbrooki hurteri* (Hurter's spadefoot toad), and *R. berlandieri* were listed as uncommon in the Padre Island National Seashore during an inventory in early 1980's (PINS, 1984), although *H. cinerea* has increased in relative abundance in recent years (A. H. Chaney, pers. comm.). Moore (1976) studied the breeding season and life history stages of two species of toads (*B. valliceps* and *B. speciosus*) in a pond on northern Mustang Island, and correlated reproduction to high rainfall, a typical strategy of this genus in other areas.

Table IV.B.7.3. Carnivorous reptiles documented from vegetated flat habitats of barrier islands within the CCBNEP study area (PINS, 1984; McAlister and McAlister, 1993).

Scientific Name	Common Name	Padre Island	Matagorda Island
Western box turtle	*Terrepene carolina*		X
Mediterranean gecko	*Hemidactylus turcicus*	X	
keeled earless lizard	*Holbrookia propinqua*	X	
Texas horned lizard	*Phrynosoma cornutum*		X
six-lined racerunner	*Cnemidophorus sexlineatus viridus*	X	X
Great Plains skink	*Eumeces obsoletus*	X	
ground skink	*Scincella lateralis*	X	X
slender glass lizard	*Ophisaurus attenuatus*	X	X
Gulf salt marsh snake	*Nerodia clarki*		X
diamondback water snake	*Nerodia rhombifera*	X	
Texas brown snake	*Storeria dekayi texana*	X	X
Eastern checkered garter snake	*Thamnophis m. marcianus*	X	
Gulf Coast ribbon snake	*Thamnophis proximus orarius*	X	X
Eastern hognose snake	*Heterodon platyrhinos*	X	X
Eastern yellowbelly racer	*Coluber constrictor flaventris*	X	X
bullsnake	*Pituophis melanoeucus sayi*	X	
speckled kingsnake	*Lampropeltis getulus holbrooki*		X
Mexican milk snake	*Lampropeltis triangulum annulata*	X	X
Western massasauga	*Sistrurus catenatus tergeminus*	X	X
Western diamondback	*Crotalus atrox*	X	X

7.3.4 Birds

7.3.4.1 Dunes

Seed-eating birds most likely utilize the seasonal abundance of several plant species within this zone, as well as those within the vegetated barrier flat. However, no study has been conducted that identifies and quantifies the importance of dunes to resident and migrant herbivorous birds. McAlister and McAlister (1993) listed American Kestrels (*Falco sparverius*), Northern Harriers (*Circus cyaneus*), Short-eared Owls (*Asio flammeus*), and Barn Owls (*Tyto alba*) as occasional carnivores on dune ridges, preying on vertebrates that inhabit this zone, particularly on the leeward side.

7.3.4.2 Vegetated Flats

No information was found for herbivorous bird use in this zone. Two common insectivores that are seasonally herbivorous) are reported to inhabit this zone on Matagorda Island: Eastern Meadowlark (*Sturnella magna*) and Northern Bobwhite (*Colinus virginianus*) (McAlister and McAlister, 1993). Eastern Meadowlark females utilize *Andropogon* spp. (bluestem grasses) to construct and conceal the nest. Northern Bobwhites actually avoid dense grass areas, utilizing edges between grassland and sparsely vegetated dunes. About 50 species of plant parts (i.e., green shoots and seeds) are consumed. Predominate species include: *Ambrosia* spp. (ragweed), *Chamaecrista fasciculata* (partridge pea), *Croton punctatus* (Gulf croton), and *Helianthus argophyllus* (silverleaf sunflower). Carnivorous species include those that also inhabit the dune zone: Loggerhead Shrikes (*Lanius ludovicianus*), Peregrine Falcons (*Falco peregrinus*), and a variety of insectivorous passerines. Northern Harriers and American Kestrels use the vegetated flats during winter, the former covering large areas of terrain and feeding on *Sigmodon hispidus* (cotton rats) and various small birds. American Kestrels typically hover over a single area or hunt from a perch and feed primarily on grasshoppers. The Barn Owl is the most common nocturnal raptor on Matagorda Island. Owl pellet analysis disclosed the following prey species composition: skulls of 293 *S. hispidus*, 71 *Reithrodontomys fulvescens* (harvest mouse), 28 *Oryzomys palustris* (rice rats), one *Mus musculus* (house mouse), one meadowlark spp., one Boat-tailed Grackle (*Quiscalus major*), and five unidentified perching birds (McAlister and McAlister, 1993).

Loggerhead Shrikes on Matagorda Island commonly use a variety of habitats including: upland flats, coastal grasslands dominated by *Spartina patens* (marshhay cordgrass), *Paspalum monostachyum* (gulfdune paspalum), and *Schizachyrium scoparium littorale* (seacoast bluestem); woody vegetation, primarily *Prosopis glandulosa* (mesquite) and *Salix nigra* (black willow). Fifty-seven percent used non-woody perches [*Helianthus* spp. (sunflower) 33%, *C. fasciculata*, and *Sesbania drummondi* 14%, grasses 10%] and 22% perched on woody vegetation (*P. glandulosa* 16% and *S. nigra* 6%), 10 were observed on posts, and 11% on other structures (wood piles, signs, concrete structures) (Chavez-Ramirez et al., 1994).

All barrier islands within the CCBNEP study area are important stopovers for migrating Peregrine Falcons (Hunt and Ward, 1988); the islands support large concentrations of fall and spring migrating Peregrine Falcons (Hunt et al., 1975). Migrating Peregrine Falcons use Padre Island for hunting and foraging (Hunt et al., 1975). During spring migration, four falcons were monitored on Padre Island; they moved up to 70 km/day on the island, but usually returned to a roosting site near that of the previous night. During fall migration, three falcons were located in the same general area moving less than 10 km (6.2 mi) from the point of capture.

Three species of diurnal raptors nest on Matagorda Island: White-tailed Kite (*Elanus leucurus*), White-tailed Hawk (*Buteo albicaudatus*), and Red-tailed Hawk (*Buteo jamaicensis*) (McAlister and McAlister, 1993). Most raptors nest in woody vegetation on the southern part of the island, and feed primarily on vegetated flats. The Crested Caracara (*Caracara plancus*) feeds on both living and dead prey and nests in woody vegetation and *Rosa bracteata* (McCartney rose) thickets in the central part of the island. Although normally considered a wetland species, the

Great Blue Heron (*Ardea herodia*) has been recorded feeding on *Sigmodon hispidus* (cotton rats), grasshoppers, nestling meadowlarks and quail, and snakes in vegetated flats of Matagorda Island (McAlister and McAlister, 1993).

7.3.4.3 Ponds and Marshes

Although most duck species feed on both plant and animal matter, important vegetative forage in ponds and marshes on Matagorda Islands include: *Potamogeton pectinatus* (sago pondweed), *Polygonum* spp. (smartweed), *Naja guadalupensis* (naiad), *Zannichellia palustris* (common poolmat), *Chara* spp. (muskgrass), algae, sedge and bulrush seeds, *Salicornia* spp. (glasswort), *Hydrocotyle* spp. (coast pennywort), *Bacopa* spp. (water hyssop), and salt-tolerant marsh grasses such as *Distichlis spicata* (saltgrass), *Spartina patens* (marshhay cordgrass) (McAlister and McAlister, 1993). Two species of grebes, Eared Grebe (*Podiceps nigracollis*) and Pied-billed Grebe (*Podilymbus podiceps*), occur along the Texas coast. Pied-billed Grebes use vegetated, freshwater ponds on Matagorda Island and feed on aquatic insect larvae, tadpoles, and small crustaceans (McAlister and McAlister, 1993). Great Blue Herons and night herons use freshwater ponds on Matagorda island feeding upon a variety of vertebrates (e.g., frogs, tadpoles, watersnakes, aquatic insects, fledging birds, and young rice rats). American Bitterns (*Botaurus lentiginosus*) use vegetated freshwater ponds and marshes during spring and fall migration, but do not overwinter.

White-faced Ibises (*Plegadis chihi*) prefer freshwater ponds and marshes, but do not nest on Matagorda Island (McAlister and McAlister, 1993). Many dabbling duck species feed on both vegetation and aquatic insects in inland wetlands on the island, including Gadwall (*Anas strepera*), American Wigeon (*A. americana*), Green-Winged Teal (*A. crecca*) and Blue-Winged Teal (*A. discors*), Northern Shoveler (*A. clypeata*), Northern Pintail (*A. acuta*), and Mottled Duck (*A. fulvigula*). Shore fly and water beetle larvae, a few species of small fish, molluscs, and crustaceans are representative aquatic fauna inhabiting the vegetation or the sediments. Turkey vultures (*Cathartes aura*) forage on anything dead and decaying in all habitats on the islands; they have been recorded feeding on fish and frogs in drying ephemeral ponds on Matagorda Island (McAlister and McAlister, 1993).

7.3.5 Mammals

7.3.5.1 Dunes

Dipodomys c. compactus (Gulf Coast kangaroo rats) are predominant rodents in the sparsely vegetated dunes on Padre and Mustang Island (Smith, 1986), but are absent on St. Joseph and Matagorda Islands (McAlister and McAlister, 1993). This species is primarily herbivorous, but occasionally feeds on insects. *Spermophilus spilosoma* (spotted ground squirrel) inhabits Mustang and Padre Island and is an opportunistic feeder. Most forage analyses list tender forage, seeds, and roots as a primary food source, insects and even an occasional vertebrate (*Holbrookia p. propinqua*) have been found in the burrows. *Spermophilus spilosoma* utilize two main zones on Padre Island, active dunes and vegetated flats (Segers and Chapman, 1984). In the dunes, *S. spilosoma* forages in barren areas, where identification and escape from terrestrial predators (e.g., snakes) increases. However, aerial predators, such as raptors, are able to spot them in these open areas. Therefore, this animal constructs several refuge burrows throughout his home range for rapid escape in both the dune and vegetated areas. Home burrows are typically located high in the dunes and are constructed with varying complexity containing both a nest chamber and food cache chambers. *Spermophilus spilosoma* also forages in vegetated flats traveling via runways between and underneath vegetation. This species is opportunistic in a harsh environment, and the extensive foraging efforts and food cache reserves are important for survival.

7.3.5.2 Vegetated Flats

Lepus californicus (blacktail jackrabbits), *Canis latrans* (coyotes), *Odocoileus virginianus* (whitetail deer), *Sus scrofa* (feral hogs), and *Taxidea taxus* (badgers) utilize dunes to some extent, but primarily inhabit vegetated flats. *Lepus californicus* and *Odocoileus virginianus* are herbivorous, *T. taxus* carnivorous, and *C. latrans* and *S. scrofa* are opportunistic omnivores. Matagorda Island supports a considerable population of *S. scrofa* that feed on virtually anything; their impact on the island ecology is not known. *Oryzomys palustris*, *Reithrodontomys fulvescens*, and *Sigmodon hispidus* occur on all of the islands, are primarily herbivorous, and are an important prey item in the food web. Several omnivores including *Didelphis virginiana* (Virginia possum), *Dasypus novemcinctus* (nine-banded armadillo), and *Procyon lotor* (raccoon), have been seen on Padre Island (Baker and Rabalais, 1975). *Baiomys taylori* (pygmy mouse), *Perognathus flavus merriami* (silky pocket mouse), *Peromyscus leucopus* (white-footed mouse) and *Sylvilagus floridanus* (eastern cottontail) are additional herbivores that have been listed as inhabiting Padre Island (Baker and Rabalais, 1975). Insectivores [*Cryptotis parva* (least shrew) and *Scalopus aquaticus* (eastern mole)] have been documented on Matagorda Island (Baker, 1991) and Padre Island, respectively (Thomas, 1972; Baker and Rabalais, 1975; Yates and Schmidly, 1977; Harris, 1988). Insectivorous bat species, *Tadarida brasiliensis* (Mexican free-tailed bat) (Harris, 1988; Chapman and Chapman, 1990) and *Pipistrellus subflavus* (Georgia bat) (Zehner, 1985) have been located on Padre Island. Two species of carnivorous skunks, *Mephitis mephitis* (striped skunk) and *Conepatus leuconotus* (Gulf Coast hog-nosed skunk) have been reported on Padre Island (Bailey, 1905 in Blair, 1952; Baker and Rabalais, 1975; Harris, 1988).

7.3.5.3 Ponds and Marshes

Oryzomys palustris (rice rat) typically nests over water in its natural range, although no studies have been conducted on the island ponds. Most mammals probably utilize freshwater sources on the islands. Sissom (1990) identified the following species by track around ponds within PINS: *Lynx rufus* (bobcat), *Canis latrans*, *Taxidea taxus*, *Procyon lotor*, and *Odocoileus virginiana*. In addition, several *Lepus californicus* were observed adjacent to pond margins.

7.4 Community Structure & Zonation

7.4.1 Plant Communities

Carl, et al. (1990) reviewed literature regarding designation of Padre Island plant communities and listed the following: Gulf Prairies and Marshes of Texas (Thomas, 1975), Gulf Coastal Plain grassland ecosystem (NPS, 1972), Marsh/Barrier Island vegetation type (McMahan, et al. 1984), and Dune/Barrier Island subregion of the Gulf Coast Prairies and Marshes natural region (Diamond et al., 1987). The following zonation descriptions are a composite of several habitat designations and associated vegetation.

7.4.1.1 Backshore

The backshore zone is to the west of the berm crest in the Gulf Beach community to the seaward base of the primary dunes (Judd, et al., 1977). Two species may predominate within the backshore, *Sesuvium portulacastrum* (sea purslane) and *Uniola paniculata* (sea oats), although they occur in sparse patches. Infrequent inundation of this area by seasonal spring and storm tides precludes establishment of many species. Isolated patches of *Sporobolus virginicus* (seashore dropseed) may also occur in the backshore zone. Physical structure of the vegetation impedes movement of sand across the beach face, subsequently small coppice dunes are formed.

7.4.1.2 Dunes

Primary dunes are located upslope from the backshore zone and cover about 20% of Mustang Island (Gillespie, 1976). This zone is rarely inundated by tides (Judd, et al., 1981), however, high seasonal tides, and winter storm surges may inundate the bases of primary dunes and uproot vegetation and remove sand (Gillespie 1976) Effects of prevailing winds and salt content of the air influences the type of vegetation on the primary dune zone. The windward, or east side of the primary dunes on Matagorda Island are typically vegetated with the following plants: *S. portulacastrum*, *Spartina patens*, *Paspalum monostachyum* (gulfdune paspalum), *Panicum amarum* (bitter panicum), *Ipomoea pes-capre* (goats-foot morning glory), *I. imperati* (fiddleleaf morning glory) and *U. paniculata*. Leeward, or west sides of primary dunes are often densely vegetated with many of the windward grass species and various forbs, such as: *Heterotheca subaxillaris* (camphorweed), *Physalis c. cinerascens* (beach ground-cherry), *Chamaecrista fasciculata*, *Croton punctatus*, *Oenothera drummondii* (beach evening primrose), *I. pes-capre* and *I. imperati* (McAlister and McAlister, 1993). Drawe et al. (1981) described the same zone (classified as Coastal Dunes) for northern Padre Island and listed predominant grass species as *U. paniculata*, *P. monostachyum*, and *P. setaceum* (thin paspalum), and predominant forbs as *C. punctatus, O. drummondii, I. pes-capre, I. imperati*, and *C. fasciculata.*

7.4.1.3 Vegetated Flats

This zone is typically grass dominated with sandy soils and low relief interspersed with low vegetated dunes, ponds and marshes, and active dune fields. Topography of this zone is a result of various environmental and geologic factors and can be quite diverse in vegetation. Protection of primary dunes ameliorates prevailing winds most of the year; therefore, density of vegetation and areal vegetative coverage increases. An occasional group of stunted oak trees occurs in higher elevations of vegetated flats, but their occurrence decreases north to south along the barrier islands. Judd et al. (1977) noted that, although several woody species inhabit the adjacent mainland and have the potential to disperse seeds, low colonization and establishment rate is due to harsh environmental conditions.

Low vegetated dunes described within the vegetated flats by Judd et al. (1977) were analyzed separately by Drawe et al. (1981) on northern Padre Island and classified as low coastal sands. Plant diversity and vegetative cover increased in these areas and grass and forb compositions were slightly different than primary dunes. *Paspalum monostachyum*, *Eragrostis secundiflora* (lovegrass), *S. virginicus* (seashore dropseed), *U. paniculata*, *P. setaceum*, and *Fimbristylis castanea* (fimbry) were predominant grasses; dominant forbs included *Stemodia tomentosa* (woolly stemodia), *Heliotropium curassavicum* var. *curassavicum* (seaside heliotrope), *Phyla nodiflora* (frogfruit), *Hydrocotyle bonariensis* (largeleaf water-pennywort), and *Erigeron procumbens* (Corpus Christi fleabane). Additionally, the amount of plant litter and mulch increased in low dunes areas and was effective enough to limit some photosynthetic activity in some areas.

The final sere or climax vegetation on barrier islands has been described as a mid-grass prairie; however, because of the dynamic nature of barrier islands, potential climax communities may not be exhibited (Drawe et al., 1981). Inhibiting factors include continual migration of coastal dunes, variable soil salinities in relation to storm surge, limited nutrient availability and high evapotranspiration rates in the region. Extensive vegetation studies in the 1970’s and 1980’s were valuable in determining successional aspects of the vegetation. Climax vegetation has been postulated as slowly progressing toward a mid-grass, or even a tallgrass, prairie climax dominated by *Schizachyrium scoparium* var. *littorale* (seacoast bluestem), *Andropogon glomeratus* (bushy bluestem), and *Panicum amarum*.

7.4.2 Invertebrate Communities

No quantitative studies were found on community structure of invertebrates on barrier islands within the CCBNEP study area, although these species form a very important part of the grassland structure and function. Many insects, grass- and planthoppers, beetles, flies, and wasps form an integral part of the invertebrate communities, although *Ocypode quadrata* (ghost crabs) often inhabit the dunes. Vertical zonation within this area is typically related to wind speed and direction as most species are found within, or beneath the plant canopy, and in the soil on the leeward and windward sides of the dune ridges (Ortiz, 1976; McAlister and McAlister, 1993). Ortiz (1976) investigated insect fauna on Padre Island through four seasons and counted 245 species (nine orders) in the backshore, primary dunes (coppice dunes), foredunes, and vegetated flats. Distribution was primarily affected by offshore winds, blowing sand, and vegetation density for both food and shelter. More species were found on the leeward side of the dunes than the windward side due to these factors.

7.4.3 Vertebrate Communities

Spatial zonation of the vertebrate community is related predominately to distribution and abundance of prey items, and degree of feeding specializations. Barrier islands are very dynamic systems and are highly influenced by physical factors and processes; therefore, a generalist strategy would be an advantage over a selective feeding mode. Most resident vertebrates are either generally herbivorous or omnivorous; home ranges typically correspond to body size. Small rodents, such as cricetids, typically inhabit vegetated areas of islands and feed on seeds, leaves, and stems characteristic of a particular zone. Mode of locomotion through vegetation and ability to burrow in the sand further defines each groups' range. Cricetids [e.g., *Sigmodon hispidus* (hispid cotton rat), *Peromyscus leucopus* (white-footed mouse), *Reithrodontomys fulvescens* (fulvous harvest mouse)] use runways underneath vegetation for foraging and protection from predators; they feed on herbaceous plants, seeds, and small invertebrates. Primary food items of *D. c. compactus* include seeds and some herbaceous vegetation, and small invertebrates as available in the dune zone and along the edge of dune-vegetated flats (Davis and Schmidly, 1994). Larger mammals use most, if not all, the vegetated zones to search for prey items; most common species will feed opportunistically on both vegetation and animals (e.g., *Canis latrans*). Strict carnivores (e.g., *Taxidea taxus*, *Mephitis mephitis*) are uncommon on barrier islands, as prey populations fluctuate greatly due to adverse environmental conditions (McAlister and McAlister, 1993).

Utilization of island resources varies seasonally, as with Peregrine Falcons and neotropical passerine fallouts in spring and fall, or in spring and summer as invertebrate populations increase. Migrating Peregrine Falcons use sparsely vegetated dune fields and adjacent tidal flats to ambush low-flying avian prey. Neotropical passerines are found in all zones during migration, using islands for food and protection. Some resident bird species may nest in vegetated flats, yet feed in more open dune areas, particularly on the leeward, less windy sides (Rappole and Blacklock, 1985).

The ephemeral nature of inland ponds within vegetated flats of barrier islands may limit the complexity of community structure. Most amphibian species are opportunistic breeders, taking advantage of increases in habitat and food following heavy rains (Moore, 1976). Increases in numbers of adult frogs and toads surrounding ponds during breeding and subsequent population boom of tadpoles is capitalized upon by several other vertebrate predators including other adult frogs, snakes, birds, and mammals. Fish population dynamics and community structure have not been investigated in natural island ponds; however, studies of three earthen ponds with the PINS reported that environmental conditions of the pond (i.e., salinity, water temperature and dissolved oxygen vs. depth of pond) have an important impact on species diversity and complexity of this habitat. All physical parameters varied widely between ponds and within ponds during the study, and may have been the cause of low species richness and dominance of one fish species in each pond (Caudle, 1992).

7.5 Ecosystem Processes

No detailed information was available to quantify many of the ecosystem processes of barrier islands within the CCBNEP study area. Most information either addresses geologic history and formation, or descriptive vegetation dynamics. The following sections have been compiled from general information about barrier island and grassland systems.

7.5.1 Energy Flow

Energy input into the barrier island system is produced by sunlight to the vascular plants and is limited by water and nutrient availability. Plant diversity across various zones of the barrier island reflects the adaptive nature of these species to varying soil salinities, low soil moisture, and soil deposition and erosion. Biomass is probably quite high in grass-dominated vegetated flats, although no quantitative studies have addressed energy relationships from the producers to consumers. Rates of litter decomposition are not known, but the semi-arid climate most likely retards decomposition within the CCBNEP study area.

7.5.2 Trophic Levels and Food Webs

The barrier island food web is very similar to a grassland-dominated system, and probably follows a grazing pathway (Fig. IV.B.7.2). Most resident and migratory species are dependent upon production of roots, rhizomes, plant parts, nectar, and seeds of vegetation for survival. Herbivorous invertebrate and vertebrate species are numerous and are utilized as prey items for primary and secondary consumers, that range in size from spiders, lizards, and toads to snakes, raptors, and larger mammals (Fig. IV.B.7.3). Productivity of the barrier island system is highly influenced by physical factors including variable rainfall, high evaporation and temperatures, and tropical storm surge events. Therefore, population dynamics of most species cycles are closely correlated with environmental variability. Omnivory may give a consumer the advantage to survive in this stressful habitat.

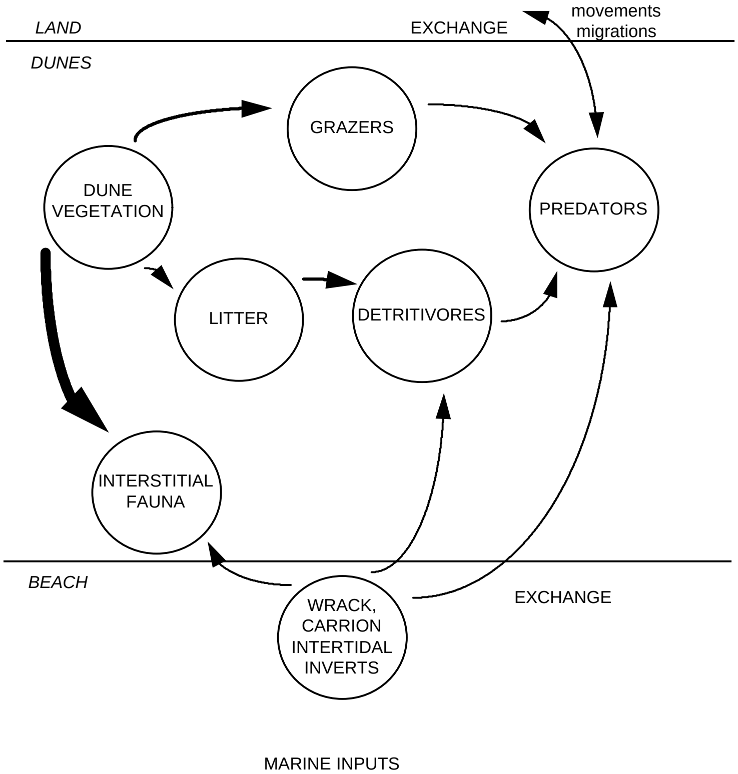

Fig. IV.B.7.2. Generalized food web and energy pathway for barrier island dune habitats (adapted from McLachlan & McLachlan, 1990).

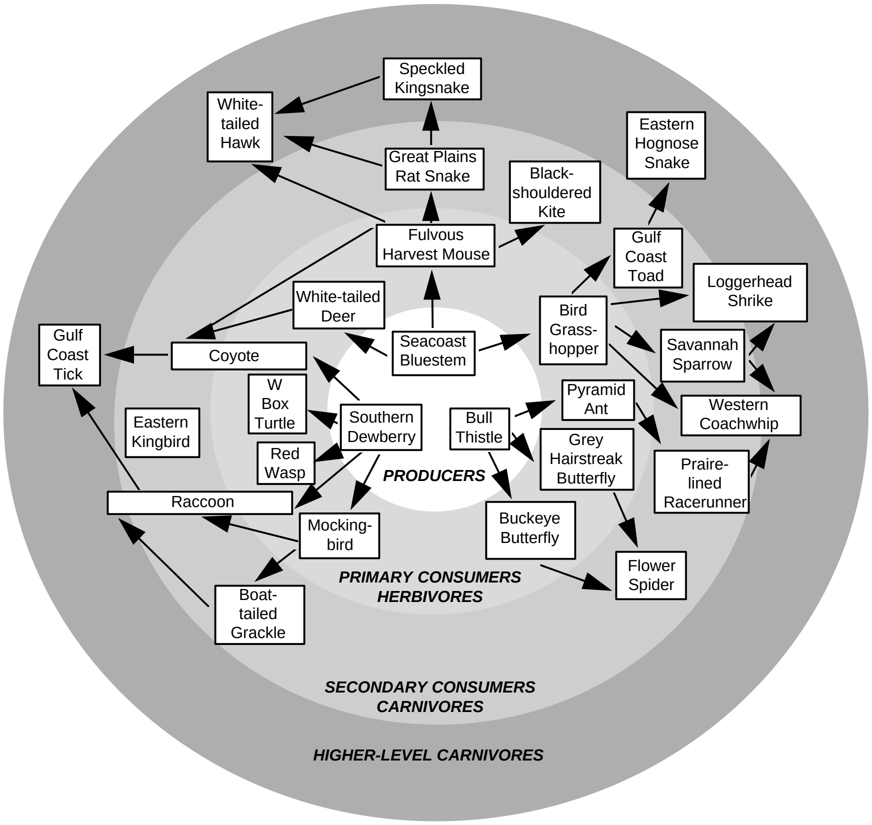

Fig. IV.B.7.3. Conceptual food web for organisms in the barrier flat habitat of Matagorda Island (adapted from McAlister and McAlister, 1993).

7.5.3 Nutrient Cycling

No nutrient cycling studies have been conducted on the barrier islands within the CCBNEP study area or elsewhere along the Texas coast.

7.5.4 Linkages with Other Systems

The geographic position of barrier islands between the open Gulf of Mexico and adjacent estuarine habitats delineates the importance of these systems to the integrity and dynamics of the barrier island chain. Sediments and nutrients discharged into the Gulf of Mexico function as a sediment source for barrier islands. Sand and shell deposited on Gulf beaches is the sediment sources for coppice dunes and foredune ridges. Vegetation composition on the dunes is influenced largely by deposition of salt spray from the Gulf of Mexico, thus affecting soil salinity and availability of nutrients. Extreme high tides from storm surges can flood vegetated flats; plant and animal community dynamics can be influenced by these events for several years afterward.

Barrier islands influence adjacent tidal flats, coastal marshes, seagrass meadows, and open bay habitats. Sand deposition on tidal flats is increased during droughts when areal coverage of unvegetated, active dunes increases. Coastal marshes form on the leeward side of barrier islands due to low topographic relief and protection from southeasterly wind fetch. Seagrass meadows also benefit from physical protection of barrier islands, but may also become shallower due to sediment deposition from adjacent island dune fields. Open bay habitats are indirectly affected by barrier islands as a protection from the Gulf of Mexico, and directly affected by transport of marine waters and organisms through island passes. The primary threat to barrier island systems is coastal development.

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HABITAT 8: GULF BEACHES

8.1 Physical Setting and Processes

8.1.1 Distribution within Project Area

The Gulf beach habitat encompasses the easternmost sandy shoreline and associated shallow, nearshore waters of the barrier island chain that fringes the Texas coast. Matagorda, St. Joseph, Mustang, and Padre islands serve as protective barriers to the three principal estuarine systems, Mission-Aransas, Nueces, and Baffin Bay-upper Laguna Madre, contained within the CCBNEP study area.

The northern limit of the Gulf beach component of the CCBNEP study area begins at the extreme southern tip of Matagorda Island, adjacent to Mesquite Bay. Most of Matagorda Island is under the jurisdiction of the US Fish and Wildlife Service (USFWS); a portion is maintained as a state park by Texas Parks and Wildlife Department (TPWD). The island is only accessible by boat. Cedar Bayou, a shallow, natural tidal pass separates Matagorda Island from St. Joseph Island.

St. Joseph Island, most of which is privately owned, stretches south about 24 km (15 mi.) to Aransas Pass. Originally a natural Gulf pass, Aransas Pass is maintained by the Army Corp of Engineers (COE) as a deep water channel by dredging and an extensive rock jetty system in order to provide access to the Port of Corpus Christi for heavy commercial shipping. Like Matagorda Island, the island is only accessible by boat.

Mustang Island stretches south from Aransas Pass about 19 km (12 mi) to Packery Channel (originally Corpus Christi Pass). Mustang Island was separate from Padre Island until 1930, when they were connected by gradual siltation which filled Packery Channel (Shepard and Wanless, 1971). Within the past several decades, the island has experienced rapid commercial development, primarily beachfront condominiums and hotels. Commercial development is currently concentrated along the northern half and extreme southern portion of the island.

Padre Island is the southernmost barrier island within the CCBNEP study area, and is the longest barrier island in the world, extending from Packery Channel to Brazos Santiago Pass north of the Rio Grande River. Like Mustang Island, north Padre Island (Nueces County) has experienced beachfront commercial development. Much of Padre Island south of Nueces County is within the jurisdiction boundary of Padre Island National Seashore (PINS). The southern boundary of the CCBNEP study area falls within PINS at Big Shell Beach.

8.1.2 Historical Development

Texas barrier islands originated as offshore shoals about 4,500 YBP (LeBlanc and Hodgson, 1959; Otvos, 1970a, 1970b; Brown et al., 1976; 1977). When sea level reached its present level about 2,800 to 2,500 YBP, these offshore shoals coalesced into a chain of barrier islands fronting the mainland estuaries that now occupy drowned Pleistocene river valleys (Morton and McGowen, 1980). After the islands became emergent, development continued by spit accretion resulting from longshore littoral sediment transport and eolian deposition (Weise and White, 1980; Britton and Morton, 1989). A continual supply of sediment from major rivers along with longshore transport permitted gulfward accretion of shoreface deposits and formation of ridge and swale topography. Evidence of accretionary ridge topography remains visible on northern St. Joseph Island (Brown et al., 1977). Historical shoreline monitoring indicates that, with the exception of a few sites, total net erosion has resulted on both Mustang and Padre Islands within the past 115 years, primarily as a consequence of diminished sediment supply from rivers and natural and human-induced alterations (Brown et al., 1974; Morton and Pieper, 1976; 1977). Episodic events (i.e., hurricanes, storm surges) are responsible for sudden, large scale depositional and erosional changes, creation of washover passes cutting through barrier islands, and temporarily creating additional connections between Gulf and bay/lagoon systems.

8.1.3 Physiography

8.1.3.1 Emergent Beach

Typical emergent barrier island beach environment in Texas consists of the intertidal and backshore zone, both of which extend from the shoreface, or surf line, to the foredune ridge. These two regions are best delineated by an abrupt change in substrate slope known as a berm (Fig. IV.B.8.1).

The intertidal zone is a continually wetted zone characterized by a gently sloping surface (between 2-5°) lying between the upper limit of high tide and the lower limit of low tide (Hill and Hunter, 1976). Intertidal sediments are composed of well-sorted sand and shell fragments and undergoes continual deposition and/or erosion due to swash/backwash flow of the surf (Shideler, 1981). Foreshore beach slope is inversely proportional to sediment grain size with beaches composed of finer sands being relatively flat compared to those of coarser composition (Morton and Pieper, 1977).

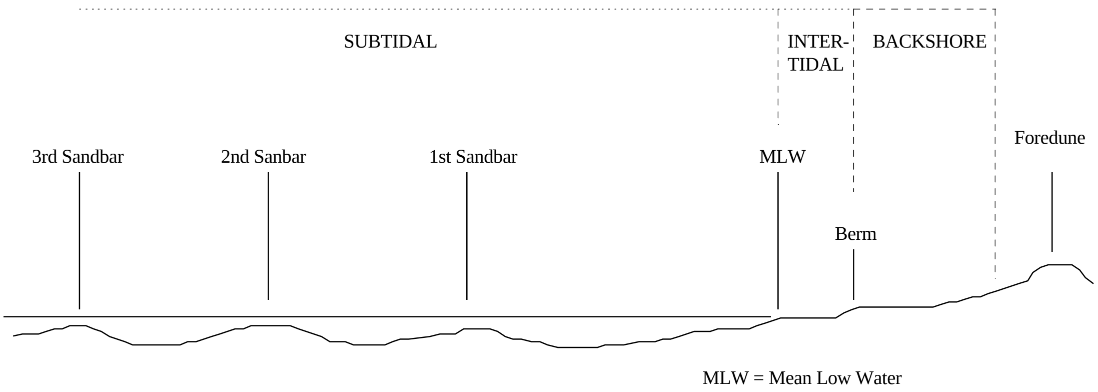

Figure IV.B.8.1. Typical profile of a Texas Gulf sandy beach.

A small berm delineates the upper intertidal slope and marks the landward transition to backshore environments. The backshore is relatively flat and broad and width varies between 50-100 m (Britton and Morton, 1989). It is not as physically active as the adjacent intertidal zone; most physical influences in the backshore are eolian. Occasional high tides and winter or tropical storms are the only influences that may change beach profile in this area (Hill and Hunter, 1976).

Coppice or embryo dunes, which are small, vegetated mounds of sand, typically mark the landward end of the backshore and the beginning of the foredune ridge complex. Coppice dunes precede larger foredune ridges and exhibit varying stages of development. In the absence of human activity, particularly vehicle traffic, the coppice dune ridge is usually pronounced and dense with vegetation.

Onshore winds create the high (5-15 m), steep foredune ridge complex that follows the coppice dune ridge. Well-sorted, fine-grain sands are trapped and stabilized by deep-rooted vegetation. Foredunes along the Mustang and northern Padre Island regions are often less vegetated compared to those along the northern coast, due to lower rainfall (Shepard and Wanless, 1971). On these two islands, dune topography is very dynamic and frequently changes appearance through eolian forces, especially within stretches of active dune fields (dunes devoid of vegetation). Foredunes are the islands main defense against energy generated by storms and waves since they store and trap sediment lost by erosion (Shideler, 1981).

Beach width changes seasonally (Hill and Hunter, 1976). Typically, the beach is eroded (narrower) in winter because high-energy surf (destructive waves) removes foreshore sediments. In summer, the beach is typically broader because low-energy surf (constructive waves) releases suspended sediments on to the shoreface.

8.1.3.2 Submergent Beach

A submerged system of three relatively stable, parallel bar-trough sediment structures have been created and are maintained by constructive waves and currents extending gulfward from the beach face (Hunter et al., 1972; White and Galloway, 1977). This subtidal environment is part of a gently sloping sand bottom referred to as the nearshore, inner shelf (Britton and Morton, 1989). The first and second longshore bars and troughs are positioned relatively close to shore in shallow waters (< 2m). The third bar is considerably farther offshore and located in water 4-5 m deep (Hedgpeth, 1953). Sandbar position varies, often migrating seasonally. In summer, sandbars are typically continuous and parallel to the shoreline; in winter, they often become discontinuous or broken, and are sometimes oblique to the shoreline (Hill and Hunter, 1976) (Fig. IV.B.8.1).

8.1.4 Geology and Soils

Texas Gulf beaches differ in mineral composition and grain size along the Texas coast, yet are primarily terrigenous in origin (Britton and Morton, 1989), with a foraminiferan component (Shepard and Moore, 1955). Beach sediment sources local major river drainage’s and longshore sediment transport by wave action (Van Andel and Poole, 1960; Shepard, 1960). McGowen et al. (1972) suggested some sediment contributed by Pleistocene and early Holocene sources on the inner continental shelf. Sediments along central coast beaches are mostly contributed by Colorado and Brazos Rivers, producing beaches of a well-sorted, slightly larger grain size.

Beaches between Matagorda Island and northern Padre Island (Malaquite Beach) are very similar in both composition and texture. They are generally composed of well-sorted fine to very-fine sands of primarily quartz, mixed with some feldspar and heavy minerals. The heavy mineral fraction consists primarily of zircon, black opaques, leucoxene, and hornblende, with minor quantities of garnet, staurolite, and epidote (Morton and Pieper, 1977). Mean grain size of shell-free sand on northern Padre Island ranges from 2.5- 3.0 phi (Hill and Hunter, 1976).

There is a gradual transition to coarser grains sizes south of Malaquite Beach. Beginning about 8 km (5 mi) south of Malaquite Beach to just south of Yarborough Pass is a region of Padre Island known as Little Shell, characterized by a higher percentage (1%-50%) of bivalve fragments of *Donax variabilis* (coquina clam) that compose the intertidal substrate (Watson, 1971). At about 27 km (17 mi) south of Malaquite, composition is characterized by very coarse, heavy mineral deposits (Hunter et al., 1972) mixed with large abraded shells of various bivalve molluscs including *Noetia ponderosa* (ponderous ark), *Mercenaria campechiensis* (southern quahog), and *Echinocama arcinella* (spiny jewel box) (Weise and White, 1980). In this province, known as Big Shell, the beaches are punctuated by high berms formed by high energy surf that deposits sediment upon the backbeach. The foreshore often dips steeply gulfward from the berm exhibiting a slope that is directly proportional to sediment size (Weise and White, 1980). Higher wave energy, increased sediment size, and steep beach profiles in this province are due to convergence north and south longshore Gulf currents and narrowing of the continental shelf.

8.1.5 Hydrology and Chemistry

8.1.5.1 Hydrology

The tidal regime on Gulf beaches is microtidal with an average diurnal range of 51.8 cm at Port Aransas. Tidal frequencies vary and may be: (1) diurnal - one high and one low tide per day; (2) semi-diurnal - two high and two low tides per day; or (3) mixed - an asymmetrical combination of high and low tides. Oncoming waves usually approach the beachface from the direction of prevailing winds, southeast during summer and northeast during winter. Height of surf breakers normally ranges from 0.3 to 1.0 m (visual observations), becoming larger during storm activity (Hill and Hunter, 1976).

Converging longshore currents occur along the central Texas coast around 27° latitude because of the curvature of the Gulf shoreline in the northwestern quadrant and movement of opposing oceanic gyres emanating from the Yucatan straits (Watson, 1971). The converging north and south longshore currents cause distinct changes in beach substrate composition, slope, and texture along the lower Texas coast. Currents also play an important role in maintenance and/or formation of tidal inlets and passes. Temporary passes form during storms at sites of low topography (washovers). Normal current velocities through existing passes averages 0.5 knots, however, they have been measured at up to two knots during periods high winds (Shepard and Moore, 1955).

8.1.5.2 Chemistry

Water chemistry in Gulf beach ecosystems is classified as marine with oceanic characteristics. Salinity remains relatively constant throughout the year because of the influence of neritic waters. Salinities range from 29.5-36.6‰ with an annual mean of 32.0‰ along northern Padre Island (Hill and Hunter, 1976).

8.2 Producers and Decomposers

8.2.1 Primary Producers

Pelagic phytoplankton and interstitial microalgae are the only primary producers on Gulf beaches as attached macrophytes are absent. On sandy beaches, epipsammic diatoms are often the resident primary producers. Surf phytoplankton are important foods for benthic and planktonic suspension feeders and may also be grazed by common surf zone fish such as *Mugil* spp. (mullet) (Romer and McLachlan, 1986). No information was found concerning species composition or community structure of phytoplankton on beaches in the CCBNEP study area. Pelagic algae, primarily *Sargassum* spp. (Phaeophyta), is often found stranded on beaches in the CCBNEP study area and form a drift line in the upper intertidal zone. It is not know whether *Sargassum* continues to photosynthesize after stranding like *Laurencia natalensis*, which forms similar wrack lines on sandy beaches in South Africa (van der Merwe and McLachlan, 1987).

8.2.2 Decomposers

No information concerning decomposer species composition on Gulf beaches in the CCBNEP study area was found. Fungi has been found associated with sea foam on north Padre Island beaches (Koehn, 1982). Heterotrophic bacteria, fungi, and protozoans are found in large numbers in sandy beaches, and are the primary processors of dissolved and particulate organic matter (Brown and McLachlan, 1990)

8.3 Consumers

8.3.1 Invertebrates

The widely fluctuating, dynamic, and often harsh physical conditions result in faunal communities with low species diversity and high densities of a few dominant organisms (Loesch, 1957; Parker, 1960; Hill and Hunter, 1976; Shelton and Robertson, 1981; Kindinger, 1981; Tunnell et al., 1981; Rabalais and Flint, 1983; Vega and Tunnell, 1987; Wicksten et al., 1987; Vega, 1988). *Ocypode quadrata* (ghost crab) dominates the backshore. In intertidal areas polychaetes *Scolelepsis squamata* and *Lumbrineris impatiens* dominate along with *Donax* spp. (coquina clam), *Emerita* spp. (mole crab), and haustoriid amphipods (e.g., *Haustorius* spp., *Parahaustorius* spp.). *Lumbrineris impatiens*, predatory gastropods such as *Hastula* spp., and

Mellita quinquiesperforata (sand dollar) dominate in the subtidal bar and trough system. Densities of these organisms are highly variable, however, peaks in overall abundance occurred in most studies between March and October; recruitment usually occurs in fall and spring. Because the benthic invertebrate community on a Gulf beach habitat constitutes the greatest animal biomass, it functions as a major primary consumer group as well as secondary producers (Table IV.B.8.1). Most of these invertebrates are either suspension, deposit or filter feeders.

8.3.2 Fish

The fish community of the Gulf beach includes many species found in estuarine habitats as well as some species typically associated with offshore oceanic waters. The Gulf passes connecting the Gulf with bays/lagoons provide means of travel for anadromous species such as *Sciaenops ocellatus* (red drum) and *Cynoscion nebulosus* (spotted seatrout) migrating between lower-salinity estuarine nursery grounds and higher-salinity offshore spawning grounds. Gulf passes link these important habitats, and the Gulf beach provides habitat for transitory deeper water species foraging within shallow nearshore zones in search of smaller vertebrate or invertebrate prey.

The only study that quantified seasonal abundance of surf-zone fish fauna within the CCBNEP study area was performed by Shaver (1984). Relative fish abundance was correlated with various environmental parameters and plankton abundance. Larvae and small juveniles of a few species comprised almost 90% of all species sampled. Fish sampled in the surf zone in order of abundance were: *Harengula jaguana* (sardine), *Micropogonias undulatus* (Atlantic croaker), *Anchoa nasuta* (anchovy), *Opisthonema oglinum* (Atlantic thread herring), *Mugil cephalus* (striped mullet), *Anchoa hepsetus* (striped anchovy), *Polydactylus octonemus* (Atlantic threadfin), *Trachinotus carolinus* (Florida pompano), *Mugil curema* (white mullet), and *Brevoortia patronus* (Gulf menhaden). Most species in Gulf nearshore waters are temperate in biogeographic distribution with a few tropical species. Those species in highest abundance in the surf zone tend to be plankton feeders, with their abundance influenced by abundance of available plankton. The surf zone serves as a nursery ground and refuge area for many small-size species due to high abundance of small juveniles sampled in her study. The families that numerically dominate the Gulf beach fish fauna are Clupeidae (menhaden), Engraulidae (anchovy), Sciaenidae (drum), Mugilidae (mullet), Carangidae (jacks and pompano), and Polynemidae (threadfin).

8.3.3 Reptiles and Amphibians

Terrestrial reptiles are generally absent within foreshore and backshore habitats. Few species of lizards and snakes are found in lower foredunes between the dune base and coppice dunes. Reptiles observed in this area include *Holbrookia propinqua propinqua* (keeled earless lizard), *Cnemidophorus gularis* (whip-tailed lizard) (Selander et al., 1962), *Crotalus atrox* (western diamondback rattlesnake), and *Sistrurus catenatus* (massasauga) (D. Rocha, pers. obs.). Community studies of terrestrial reptiles present in sandy beach habitats within the study area are lacking.

Table V.B.8.1. Benthic (bottom-dwelling) invertebrates associated with typical Gulf beach habitat along the Texas coast. Feeding strategies include: SF-Suspension Feeder, DF-Deposit Feeder, Omn-Omnivore/Scavenger, and Pred-Predator/Carnivore. Trophic levels include: 2^0 Prod-Secondary Producer, 1^0 Cons-Primary Consumer, and Dec-Decomposer. Compiled from species accounts obtained from sandy beach infaunal studies conducted within the CCBNEP study area (Hill and Hunter, 1976; Kindinger, 1981; Shelton and Robertson, 1981; Tunnell et al., 1981; Rabalais and Flint, 1983; Wicksten, 1987; Vega, 1988).

Taxon	Feeding Strategy	Trophic Level
Nemertea	Pred	2^0Prod, 1^0Cons
Nematoda	Pred	2^0Prod, 1^0Cons
Polychaeta		
Paraonis fulgens	DF	2^0Prod, 1^0Cons
Dispio unicinata	SF, DF	2^0Prod, 1^0Cons
Polydora ligni	SF, DF	2^0Prod, 1^0Cons
Spiophanes sp.	SF, DF	2^0Prod, 1^0Cons
Scolelepis squamata	SF, DF	2^0Prod, 1^0Cons
Magelona riojai	DF	2^0Prod, 1^0Cons
Spiochaetopterus sp.	SF	2^0Prod, 1^0Cons
Armandia sp.	DF	2^0Prod, 1^0Cons
Bhawenia goodei	Pred	2^0Prod, 1^0Cons
Pisionidens indica	Pred	2^0Prod, 1^0Cons
Glycera papillosa	Pred	2^0Prod, 1^0Cons
Nephtys picta	Pred, Omn	2^0Prod, 1^0Cons
Onuphis eremita	Pred, Omn	2^0Prod, 1^0Cons
O. nebulosa	Pred, Omn	2^0Prod, 1^0Cons
Lumbrineris impatiens	Pred, Omn	2^0Prod, 1^0Cons
Oligochaetes		
Pontodrilus gracilus	Omn	2^0Prod, 1^0Cons
Mollusca		
Gastropods		
Polinices duplicatus	Pred	2^0Prod, Dec
Hastula salleana	Pred	2^0Prod, Dec
Solariorbis infracarinata	Omn	2^0Prod, Dec
Litiopa melanostoma	Omn	2^0Prod, Dec
Epitonium sp.	Pred	2^0Prod, Dec
Crepidula convexa	SF	2^0Prod, Dec
Bivalves		
Anadara transversa	SF	2^0Prod, Dec
Lepton lepidum	SF	2^0Prod, Dec
Tellina spp.	SF	2^0Prod, Dec
Sphenia antillensis	SF	2^0Prod, Dec

Table IV.B.8.1 Continued.

Taxon	Feeding Strategy	Trophic Level
Donax variabilis	SF	2^{0}Prod, Dec
D. texasianus	SF	2^{0}Prod, Dec
Petricola pholadiformis	SF	2^{0}Prod, Dec
Insects		
Bledius sp.	Omn	2^{0}Prod
Crustaceans		
Amphipods		
Acanthohaustorius sp.	SF	2^{0}Prod, 1^{0}Cons
Parahaustorius obliquus	SF	2^{0}Prod, 1^{0}Cons
Protohaustorius bousfieldi	SF	2^{0}Prod, 1^{0}Cons
Haustorius sp.	SF	2^{0}Prod, 1^{0}Cons
Lepidactylus triarticulatus	SF	2^{0}Prod, 1^{0}Cons
Synchelidium americanum	Omn	2^{0}Prod, 1^{0}Cons
Talorchestia sp.	Omn	2^{0}Prod, 1^{0}Cons
Corophium sp.	Omn	2^{0}Prod, 1^{0}Cons
Pontogeneia sp.	Omn	2^{0}Prod, 1^{0}Cons
Isopods		
Ancinus depressus	Omn	2^{0}Prod, 1^{0}Cons
Chiridotea sp.	Omn	2^{0}Prod, 1^{0}Cons
Copepods		
Clausidium tenax	SF	2^{0}Prod, 1^{0}Cons
Cumaceans		
Oxyurostylus smithii	SF	2^{0}Prod, 1^{0}Cons
Spilocuma sp.	SF	2^{0}Prod, 1^{0}Cons
Mysids		
Bowmaniella brasiliensis	Omn	2^{0}Prod, 1^{0}Cons
Metamysidopsis swifti	Omn	2^{0}Prod, 1^{0}Cons
Decapods		
Callianassa islagrande	SF	2^{0}Prod, 1^{0}Cons
Isocheles wurdemanni	Omn	2^{0}Prod, 1^{0}Cons
Pagurus sp.	Omn	2^{0}Prod, 1^{0}Cons
Lepidopa websteri	SF	2^{0}Prod, 1^{0}Cons
Emerita benedicti	SF	2^{0}Prod, 1^{0}Cons
E. portoricensis	SF	2^{0}Prod, 1^{0}Cons
Dissodactylis mellitae	Omn	2^{0}Prod, Dec
Pinnixa chacei	Omn	2^{0}Prod, Dec
Arenaeus cribrarius	Omn	Dec
Calinectes sapidus	Omn	Dec
Petrolisthes armatus	Omn	Dec
Ocypode quadrata	Omn	Dec

Table IV.B.8.1. Continued.

Taxon	Feeding Strategy	Trophic Level
Echinoderms		
Astropecten duplicatus	Pred	Dec
Ophiophragmus moorei	Pred, DF	Dec
Mellita quinquiesperforata	DF	Dec

Five species of turtles are reported to inhabit nearshore waters adjacent to Gulf beaches (Table IV.B.8.2). All five species are federally protected as either endangered or threatened with varying degrees of abundance in our local waters. *Caretta caretta* (loggerhead turtle) is the most common species observed both swimming and nesting within the study area (Renaud and Carpenter, 1994). *Lepidochelys kempi* (Kemp's ridley turtle) has been reported to nest sporadically on Padre Island beaches (Ogren, 1977 cited in Shew et al., 1981). Padre Island National Seashore maintains a continuos monitoring of sea turtle tagging and nesting activity on its beaches. Refer to Section IV.C.1.6-IV.C.1.10 (this volume) for additional information.

Amphibians are generally absent in the Gulf Beach habitat due to harsh, salty conditions. Species typical to the barrier islands are usually restricted to freshwater ponds and marshes. Any occurrence of amphibians gulfward of the primary dunes would be considered accidental.

Table IV.B.8.2. Sea turtles documented within the western Gulf of Mexico. Abbreviated federal protections: E = Endangered, T = Threatened. Abbreviated abundance: C = Common, U = Uncommon, R = Rare. (Data compiled from Owens et al., 1983; Renaud and Carpenter, 1994).

Species	Common Name	Federal Protection	Abundance
Caretta caretta	loggerhead	T	C
Chelonia mydas	green	T	U
Lepidochelys kempi	Kemp’s ridley	E	R
Erethrochelys imbricata	hawksbill	E	R
Dermochelys coriacea	leatherback	T	R

8.3.4 Birds

Gulf beaches provide habitat for a wide variety of birds, primarily shorebirds (Charadriiformes). Some species are year-round users and are highly conspicuous (e.g., gulls, terns), some are migrants which stop to rest and feed, and others are winter residents. Gulf beaches serve as a landmark or staging area for migratory movements north and south (Chaney et al., 1993).

Benthic invertebrates (i.e., polychaetes, amphipods, and molluscs) living within the substrate provide an abundant food source for these predators. Gulls and terns (Family Laridae) are the largest taxonomic group of birds found foraging and loafing on sandy beaches in the CCBNEP study area, followed by sandpipers and sanderlings (Family Scolopacidae) and plovers (Family Charadriidae) (Chapman, 1984; Chaney et al., 1993)

Chaney (1993) documented seasonal abundance and distribution of bird activity emphasizing 14 targeted species (Fig. IV.B.8.2). Sanderlings (*Calidris alba*), which are year-round residents, were the most abundant bird on the beach (42.5%) and were found mainly in the foreshore. Least Terns (*Sterna antillarum*), a summer-resident, were second in abundance (12%), followed by Black Terns (*Chilodonias niger*), an abundant fall migrant, and Willets (*Catoptrophorus semipalmatus*), which occur year-round. The intertidal foreshore appeared to be preferred habitat for all birds. About 18% of all individuals, one of seven, are federally listed endangered or threatened species (Fig. IV.B.8.3)

Chapman (1984) studied seasonal abundance of shorebirds and their habitat-use patterns on both Mustang Island and northern Padre Island. Peak abundances coincided with spring and fall migrations; abundances declined in late spring and early summer as flocks departed for northern breeding grounds (Fig. IV.B.8.4). The most abundant species (except gulls and terns) were Sanderlings, Red Knots (*Calidris canutus*), Willets, Piping Plovers (*Charadrius melodus*), and the Black-bellied Plovers (*Pluvialis squatarola*).

8.3.5 Mammals

Few terrestrial mammals inhabit the Gulf beach habitat. Those species that have been recorded are transients which traverse briefly through the habitat in search of food. They are usually scavengers whose preferred habitat is the back island vegetated flats Species recorded are transients that traverse the habitat in search of food and include *Canis latrans* (coyote), *Procyon lotor* (raccoon), *Dipodomys compactus* (Gulf Coast kangaroo rat), and *Spermophilus spilosoma* (spotted ground squirrel). Some mammals that have been recorded in foredune habitats Tamaulipan barrier islands in northern Mexico include *Lepus californicus* (jackrabbit), *S. spilosoma*, *Geomys personatus* (Texas pocket gopher) and *D. compactus* (Selander et. al, 1962). No quantitative information was found concerning terrestrial mammals on Gulf beaches of the CCBNEP study area. Atlantic bottlenose dolphins (*Tursiops truncatus*) are occasionally sighted in nearshore waters of Gulf beaches in the study area, although it is not their primary habitat. Additional information on marine mammals is in Section IV.C.1.11 (this volume).

8.4 Community Structure and Zonation

8.4.1 Plant Communities

Few macroscopic plants survive on a sandy Gulf beach except temporarily as either epiphytes on a hard substratum or as stranded marine algae. Interstitial microflora comprised of unicellular algae live between the sand grains and contribute to primary production. The most conspicuous plant biota, however, of the Gulf beach habitat exists within the foredune/coppice dune ridge

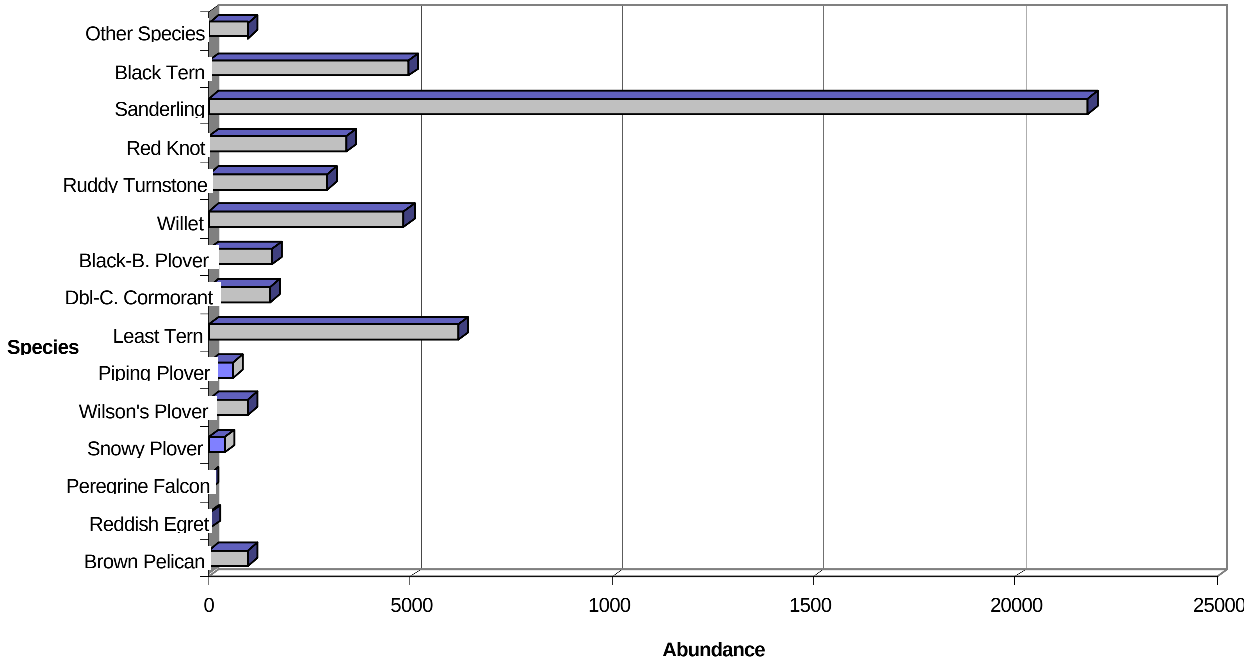

Figure IV.B.8.2. Relative abundance of bird use on Padre Island National Seashore sandy beach and nearshore waters from September 1992 to August 1993. (Compiled data from Chaney et al., 1993).

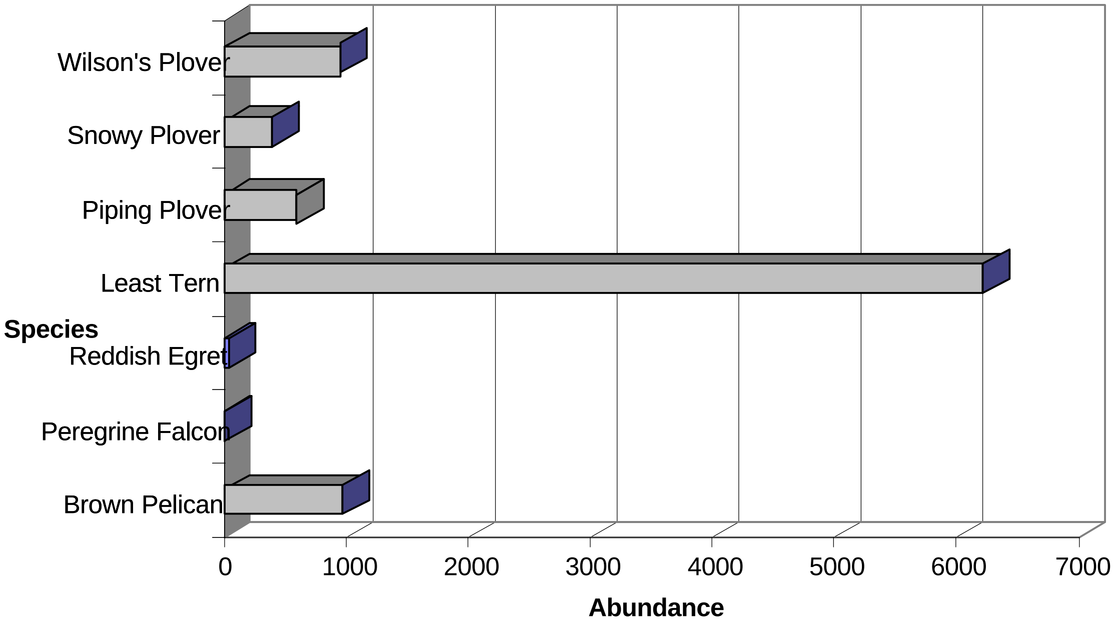

Figure IV.B.8.3. Relative abundance of federally protected bird species known to inhabit Padre Island National Seashore (compiled data from Chaney et al., 1993).

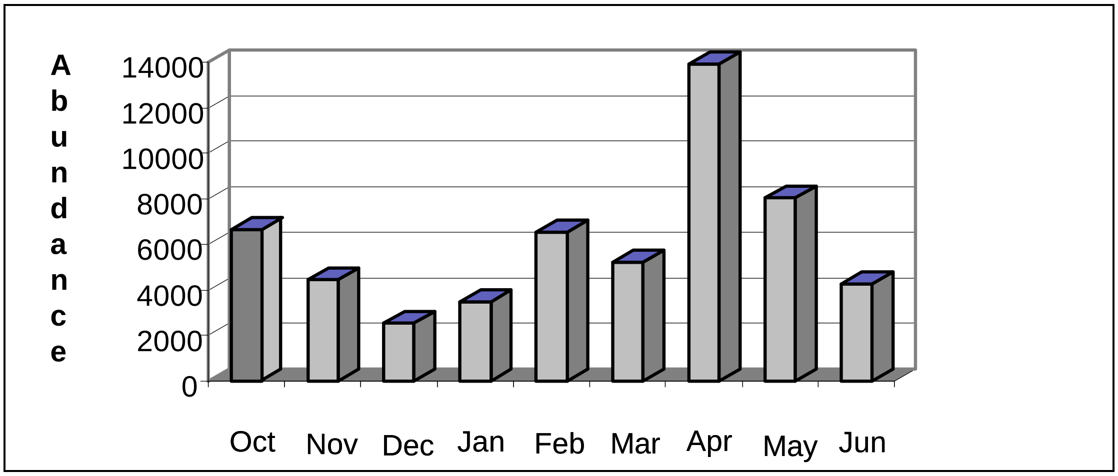

Figure IV.B.8.4. Monthly average abundance of coastal birds observed on Padre and Mustang Islands, October 1979-June 1981 (compiled data from Chapman, 1984).

complex. Macroscopic vegetation does not survive within the backshore nearest the surf due to harsh physical conditions. Rooted plant communities originate along the coppice dune ridge, then prograde up the foredune face to the foredune ridge. Plants in these habitats are typically hardy, deep-rooted or vine-like, perennial halophytes capable of withstanding the salt-laden air and nutrient-poor sediment of the sandy environment. Zonation and distribution of the barrier island plant community is discussed in detail in Section IV.B.7, Barrier Islands.

8.4.2 Invertebrate Communities

Generally, the permanent inhabitants of a sandy beach are burrowing invertebrates that occur in zones defined by physical processes. Beaches are generally low in species diversity compared to other aquatic habitats. High abundance of individuals representing “indicator” species occupy distinct zones delineated by the physical environment. Zones of distribution are often marked by changes in some environmental gradient, such as sediment composition or surf action.

Zonation of the benthic invertebrate community along sandy beaches has been widely documented and presented in the scientific literature. The bulk of community ecology studies on beach infauna are reported from the Atlantic coast regions of Georgia and the Carolinas (Dahl, 1952; Brett, 1963; Dexter, 1969; Croker, 1970;1977; Croker et al., 1975; Holland and Polgar, 1976; Dörges, 1977; Holland and Dean, 1977; Leber, 1982). Studies describing zonation patterns in the benthic communities on the Gulf barrier islands of Texas and associated nearshore waters include Parker (1960), Hill and Hunter (1976), Shelton and Robertson (1981), Kindinger (1981), Tunnell et al. (1981), Wicksten et al., (1987), and Vega (1988).

Three major zones of distribution occur on a sandy beach shore: backshore, intertidal foreshore, and subtidal bar-trough system. Each zone is characterized by a unique assemblage of dominant organisms (Fig. IV.B.8.5).

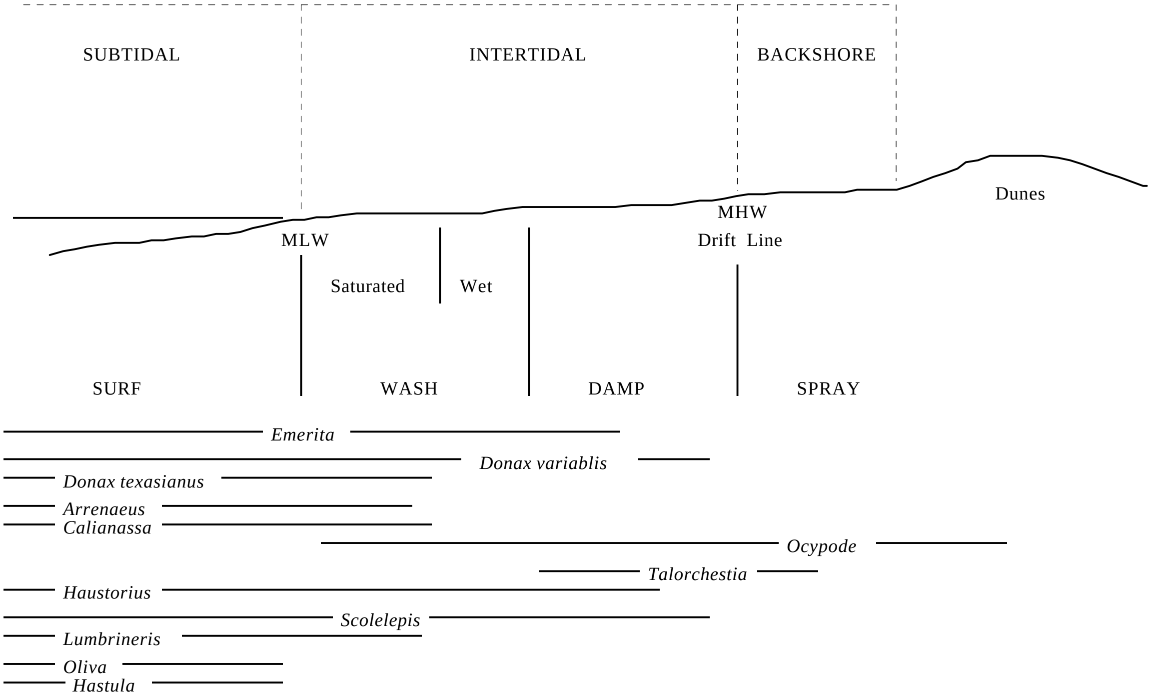

Figure IV.B.8.5. Invertebrate community profile within the emergent and nearshore submergent zones of the Gulf beach habitat (modified from Orth et al., 1991).

8.4.2.1 Backshore

This region is dominated by the burrowing ghost crab community of *Ocypode quadrata*. Effects of human disturbance on this community has been studied by Teerling (1970). *Ocypode quadrata*, a burrowing scavenger, digs holes to the water table to wet its gills, and often traverses the backshore in search of detritus as food. Most feeding activity occurs nocturnally. In general, maturity and size of the crab increases from the intertidal swash zone towards the foredunes with the more mature community occupying the region highest up the beach. Burrow orientations have been shown to be controlled by the direction of prevailing winds, a relationship that is useful in determining conditions of ancient shoreline environments (Hill, 1981).

8.4.2.2 Intertidal Foreshore

Filter-feeding molluscs, crustaceans, and polychaetes dominate intertidal foreshore. The community is dominated by an assemblage of the bivalve mollusc *Donax variabilis*, mole crabs *Emerita* spp., the haustoriid family of amphipods, and a spionid polychaete, *Scolelepis squamata*. Haustoriid amphipods often dominate in numerical abundance and density per surface area of substrate (Kingdinger, 1981; Shelton and Robertson, 1981; Vega, 1988). Seasonally, this group shows extreme highs and lows in population density due to sudden recruitment of juvenile individuals during fall and spring months. Depending on both seasonal and diurnal tidal fluxes, populations of these organisms shift up and down within the range of high intertidal areas to lower intertidal areas, exhibiting a patchy distribution within the swash zone. Amphipods have been known to migrate to deeper subtidal waters, during colder climates of winter (Sameoto, 1969). *Donax variabilis* is restricted in habitat to sandy beaches and is often an indicator of clean swept, high energy beaches. The ecology and migratory habits of this indicator species has been documented within the CCBNEP study area by Loesch (1957) and Vega and Tunnell (1987).

8.4.2.3 Subtidal Bar-Trough System

Species diversity is generally higher within this region. The subtidal environment, with lower physical energy, supports a broader assemblage of burrowing and epibenthic fauna with feeding modes ranging from filter feeding to predation. Two species of swimming crabs are common, *Calinectes sapidus* (blue crab) and *Arenaeus cribrarius* (speckled crab). Predatory gastropod found offshore to about the first sandbar include *Hastula salleana* (Auger Snail), *Oliva sayana* (Lettered Olive), and *Polinices duplicatus* (Moon Snail). The intertidal polychaete *Scolelepis squamata*, is replaced in abundance by the carnivorous species *Lumbrineris impatiens* along with other burrowing species, *Nephtys picta*, *Onuphis eremeita*, and *Magelona riojai*. At outer sandbars, various echinoderms are present including *Ophiophragmus moorei* (brittle star) and *Mellita quienquiesperforata* (sand dollar).

8.4.3 Vertebrate Communities

Shorebirds are the most conspicuous vertebrates, and are found foraging in the intertidal foreshore, and resting and/or roosting in the berm and backshore (Chapman, 1984). There has been little work describing the structure of bird communities on sandy beach habitats in the CCBNEP study area.

Fish communities exhibit seasonal and diel structure, as well as correlation with a variety of environmental parameters (Shaver, 1984). Highest abundances were recorded in summer and fall; abundances were higher during day compared to night. Mature individuals were most abundant during outgoing and high tides, while juveniles were most abundant during incoming tides, and at lower temperatures and salinities. Small schooling fish such as *Anchoa* spp. (anchovy) and *Brevoortia* spp. (menhaden) are often concentrated in the longshore bar-trough systems.

8.5 Ecosystem Processes

8.5.1 Energy Flow

Depending upon degree of wave energy, production by diatoms may be measurable, but is often not very high. Amounts of carbon fixed may range from 0-50 g C/m^2/yr, in beaches experiencing slight or no wave action, to values ranging from 500-2000 g C/m^3/yr in a high energy surf- zone (Brown and McLachlan, 1990). Net photosynthesis by surf phytoplankton on Mustang Island during summer averaged 0.99 g O_2/m^3/day, nearly three times the average winter rate (McFarland, 1963). Diatomaceous phytoplankton is the most consistent primary food source, that is available continuously, although it varies daily. McFarland (1963) correlated maximum plankton metabolism with abundance of organism at higher trophic levels illustrating synchronicity of plankton availability with seasonal energy requirements of beach animal communities.

Accumulations of *Sargassum* spp. in a drift line at the upper reaches of the intertidal zone is an important food source for colonies of talorid amphipods, insects, and foraging birds. On South African beaches, stranded *Laurencia natalensis* continues active photosynthesis, thus breaking down very slowly (van der Merwe and McLachlan, 1987). Amphipods and dipteran larvae consumed 60-80% of the stranded kelp on sandy beaches on the west coast of Africa (Griffiths and Stenton-Dozey, 1981). Shorebirds, particularly Ruddy Turnstones (*Arenaria interpres*) and plovers, often forage along the wrack line of south Texas beaches (K. Withers, pers. obs.). There are no studies of the contribution of wrack to energy flow on beaches in the CCBNEP study area.

8.5.2 Trophic Levels and Food Web Relationships

Sandy beaches are viewed as having two distinct communities in which there is no direct trophic linkage. The larger part of the food web is composed of the macrofauna which includes the zooplankton, fishes, and birds (Fig. IV.B.8.6). The other, less conspicuous community is the interstitial community of burrowing filter feeders, deposit feeders, and scavengers. In beaches composed of finer sediments, the smaller pore spaces and lower oxygen tensions result in larger burrowing meiofauna which concentrate near the surface and are more available as a food source to macrofauna. In this case, trophic links are more observable. In beaches with well-drained sands, meiofauna are confined to deeper depths and trophic links to macrofauna are not distinct (Brown and McLachlan, 1990). Both faunal communities, though, use a common food source derived from the sea. The main group of macroscopic animals in the food chain of a sandy beach are benthos including filter feeders, deposit feeders, herbivore scavengers, and carnivores/omnivores. Flow of energy in the system begins with the zooplankton, due to their great abundance and high level of activity. Deposit- and filter-feeding organisms such as burrowing polychaetes, and epibenthic amphipods, crustaceans, and crabs contribute most to overall biomass of the system. On Gulf beaches of the CCBNEP, the bivalve clam *Donax*, occurs frequently in dense patches, and is an important in moving suspended organic material to higher trophic levels. The trophic gradient continues toward the nektonic and terrestrial predators, fishes and birds respectively, which feed upon the benthic community. Fishes are the main predators of the intertidal and subtidal benthos.

The interstitial food chain consists of protozoans, bacteria, and meiofauna redundant receiving organic food sources from wave flushing into beach substrate. Activity in this food chain is controlled largely by the amount of water filtered into the sand, amount of organic material present, and temperatures controlling the metabolic rate of microbial organisms.

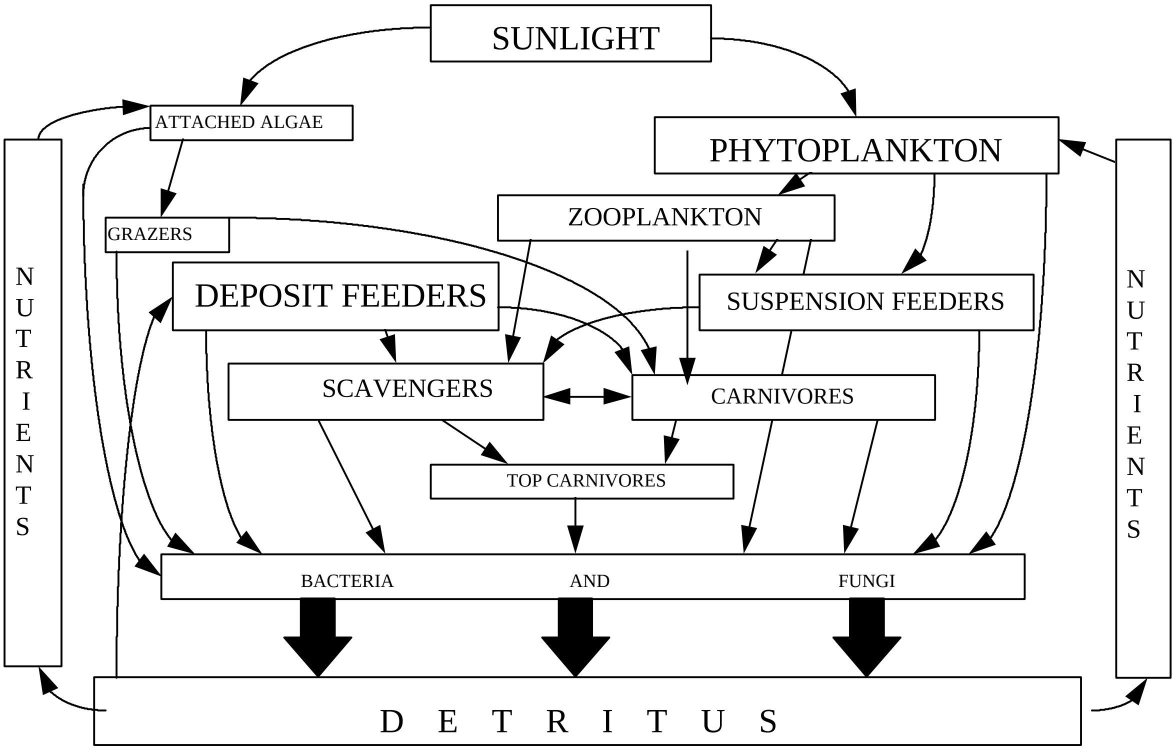

Fig. IV.B.8.6. Generalized food web of a typical sandy beach habitat on the Texas Gulf coast (modified from Britton and Morton, 1989).

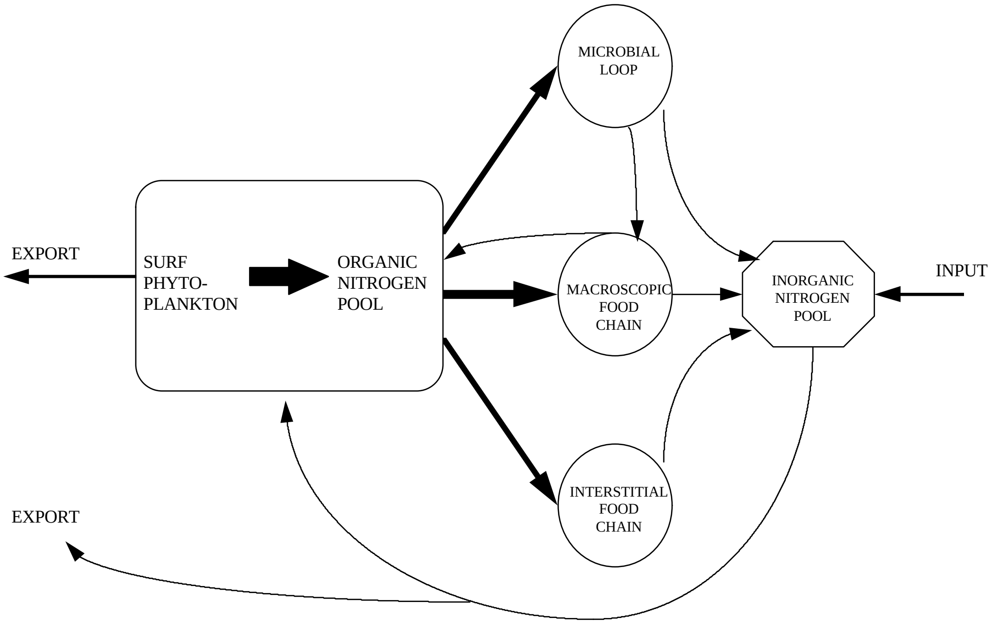

Figure IV.B.8.7. Nutrient cycling in the beach/surf zone of a typical sandy beach system (Modified from Brown and McLachlan, 1990).

8.5.3 Nutrient Cycling

No studies of nutrient cycling in sandy beach habitats have been conducted in the CCBNEP study area. Nitrogen and phosphorus are the limiting nutrients in most sandy beach systems. Nitrogen is commonly the most limiting, main sources of NO_3 include groundwater discharge and drainage. Interstitial meiofauna recycles nutrients from urine and feces via nitrification. Bacteria recycle nutrients from available organic pool of both dissolved organic carbon (DOC) and particulate organic carbon (POC). Organic materials occurring in seawater originate from various sources including phytoplankton discharges, faunal excretion, and leachates from dead animal and plant material (Fig. IV.B.8.7) (Brown and McLachlan, 1990).

Because of the dynamic movement of water through sandy beach habitats, it is thought that terrestrial decomposition contributes relatively little to nutrient cycling. However, wrack provides the major organic input on many beaches (McGwynne et al., 1988). On African beaches which received stranded algae, a portion of the high concentrations of organic leachates found beneath the decomposing algae was available for direct absorption by meiofauna (Koop et al., 1982), and groundwater nutrient analysis showed high levels of NH_4 (McGwynne et al., 1988). There have been no studies of the contribution of wrack to nutrient cycling on sandy beaches in the CCBNEP study area.

8.5.4 Linkages with Other Systems

The Gulf Beach environment is an open marine system which interacts with adjacent coastal systems (Brown and McLachlan, 1990). Gulf beaches are true marine systems with food chains that begin and end in the sea. The sea is both source and sink for nutrients and other materials. Exchange of materials with other coastal systems across landward boundaries occurs primarily as a result of tropical storm surges which breach barrier islands allowing importation of both biotic and geologic materials. Primary threats to the habitat include oil spills and tourist-related activities such as seawall construction, beach development and cleaning, and traffic.

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