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THE ECOLOGY OF OPEN-BAY BOTTOMS OF TEXAS:

A COMMUNITY PROFILE

Fish and Wildlife Service
U.S. Department of the Interior

The cover photo is an aerial view of Galveston Bay, Texas (courtesy of National Aeronautics and Space Administration).

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THE ECOLOGY OF OPEN-BAY BOTTOMS OF TEXAS: A COMMUNITY PROFILE

by

Neal E. Armstrong
Department of Civil Engineering
The University of Texas at Austin
Austin, TX 78712

Project Officers

Michael Brody
U.S. Fish and Wildlife Service
National Wetlands Research Center
1010 Gause Boulevard
Slidell, LA 70458

and

Nicholas Funicelli
U.S. Fish and Wildlife Service
National Fishery Research Laboratory-Gainesville
7920 N.W. 71st Street
Gainesville, FL 23606

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PREFACE

This community profile, like others developed in this series, is intended to provide an introduction to the ecology of subtidal bay bottoms, a biotope which dominates the estuaries of the northwestern Gulf of Mexico region and specifically the estuaries of Texas. It is in these estuaries that the majority of the in-bay commercial finfish and shellfish harvest is taken, and it is from these estuaries that most of the northwestern gulf commercial harvest migrates to become available offshore. While this community profile is specific to the bays of Texas, the physical, chemical, and biological processes described are similar to those in other open-bay systems such as San Francisco Bay on the west coast, Chesapeake Bay, Delaware Bay, and others on the east coast. What makes Texas estuaries unique and distinct is the tremendous gradient in precipitation from the upper to lower coast and indeed across the drainage basins to these estuaries producing brackish water estuaries with very low residence times like Sabine Lake and hypersaline systems with very long residence times like the Laguna Madre. Following the wetland classification system of Cowardin et al. (1979), these open bay bottom systems could be classified as follows: SYSTEM Estuarine, SUBSYSTEM Subtidal, CLASS Unconsolidated Bottom, SUBCLASSES Sand and Mud, WATER REGIME Subtidal, WATER CHEMISTRY Mixosaline to Hypersaline.

The text of this report is organized in the following way. The physiographic characteristics of the bays in which the open-bay bottom systems are found are described in Chapter 1 followed by a physical-chemical characterization in Chapter 2. In Chapter 3, the general ecology of these open-bay bottom systems is described followed by detailed descriptions of the structure of the benthic communities (Chapter 4) and their function (Chapter 5). Finally, the factors one must consider in managing open-bay bottom systems are discussed in Chapter 6. R. Warren Flint, previously with the University of Texas Marine Science Institute at Port Aransas and now with the Research Center at State University of New York at Oswego, supplied the early drafts for Chapters 3, 4, and 5 and parts of Chapter 6.

As other community profiles have shown, no one part of an estuarine ecosystem exists in isolation but in fact interfaces with other parts. This is probably no truer than with the open-bay bottom system which exchanges strongly with the intertidal areas on the estuary periphery, with the ocean through the tidal inlet, and with the riverine systems bringing fresh water to them. This fact becomes especially evident in the discussions of nutrient budgets for estuaries in which the external and internal nutrient sources are discussed in Chapters 2 and 5. The dominant role of phytoplankton in providing organic material to the open-bay bottom systems is discussed along with the emerging realization of the importance of the benthos in recycling nutrients further; the role that saltwater marsh systems play in the nutrient budget is recognized. Yet, the sensitivity of the estuary to nutrients brought into these systems with freshwater inflows helps one realize that the ultimate source of nutrients to an estuary is external to it, but that nutrient cycling within the estuary involves a substantially greater mass of nutrients than that in the external sources. The role of the biota in this cycling and the effects of nutrient cycling on the biota are discussed at

length. It is in this context that the ties between open-bay bottom systems and other parts of this estuary become quite clear, and it is hoped that this picture of the physical, chemical, and biological structure and function of these systems is described clearly herein.

Any questions or comments about or requests for this publication should be directed to:

Information Transfer Specialist
National Wetlands Research Center
U.S. Fish and Wildlife Service
NASA-Slidell Computer Complex
1010 Gause Blvd.
Slidell, LA 70458
(504)646-7564; FTS 680-7564.

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	283.5	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556(°F - 32)	Celsius degrees

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CHAPTER 1.
THE PHYSICAL ENVIRONMENT

1.1 DEFINITION OF OPEN-BAY BOTTOMS

Open-bay bottoms represent one of the most extensive habitats in any estuarine system, and while other habitats such as salt marshes and seagrass beds are important and are discussed relative to the open-bay bottoms systems, most of the attention is given to the benthic communities that exist in the unvegetated subtidal bottoms. Like the intertidal flats described by Peterson and Peterson (1979), the open-bay bottoms are also open systems and interact strongly with ocean waters through the tidal inlet, with marshes and intertidal flats on the periphery of the estuary, and with riverine systems where they enter the estuary. Thus, these systems are included and discussed herein to the extent they are needed to explain processes occurring within the open bay.

Open-bay bottom systems may be defined as the subtidal portion of the estuary lying below the extreme low spring tide. Bottom types are typically sand or mud, varying considerably from area to area depending on proximity to high-energy inlets where sandy bottoms dominate, to delta areas associated with river inflows in which consolidated sediments are prevalent, to the open-bay areas where muddy bottoms are found.

The living things in these systems are predominantly animals although in the very shallow areas with good transparency, seagrasses may flourish over large areas. Usually, they are limited to the shallow peripheral areas where light transmission is great enough to support them. The most important biological components of the open-bay bottoms are the benthic (bottom-dwelling) animals consisting of the epifauna and the very complex infaunal community.

The Texas estuaries are used to exemplify the open-bay bottom system in this report, and a description of these systems will be helpful in understanding their nature, as well as providing background for the discussion on their general ecology and the ecology of the benthic community.

1.2 BAY DESCRIPTIONS

Seven estuarine systems with open-bay bottoms lie on the Texas coast: Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Copano-Aransas Bays, Corpus Christi Bay, and the Laguna Madre (see Figure 1). Three minor riverine estuaries also located in the area are the Brazos, San Barnard, and Rio Grande Estuaries, but their open-bay bottoms have been filled by sedimentary deposition, and the rivers that feed these estuaries now empty directly into the gulf. These three riverine estuaries contain minimal amounts of open-bay bottom system compared to the other seven estuaries and are not discussed in detail in this report. The other seven estuaries have a total water surface area of about 623,756 ha. A more detailed discussion of each of these seven systems follows. Much of the information is taken from the excellent reports for these systems prepared by the Texas Department of Water Resources (1980a, 1980b, 1981a, 1981b, 1981c, 1983). Some of the physiographic data are summarized in Table 1.

1.2.1 Sabine Lake Estuary

The Sabine-Neches Estuary lies along the Texas-Louisiana border, has a surface area of 17,798 ha, and receives the Sabine and Neches Rivers. The Sabine Lake Estuary includes Sabine Lake, the Sabine-

Neches Canal, the Port Arthur Canal, and Sabine Pass (see Figure 2). Water depths at mean low water vary from about 3 m or less in Sabine Lake to greater than 12 m in dredged areas; the average depth is about 1.8 m and the total volume is 0.326 km^3. Much of the area around Sabine Lake is in urban and industrial land use in the Golden Triangle area of Beaumont, Orange, and Port Arthur. It lies in the coastal prairie and coastal marsh land-resource area, and marsh land constitutes a sizeable percentage of the lands near the estuary, with vegetation of saltgrass, cordgrass, and weeds. This marsh area totals 13,760 ha; most of it lies to the

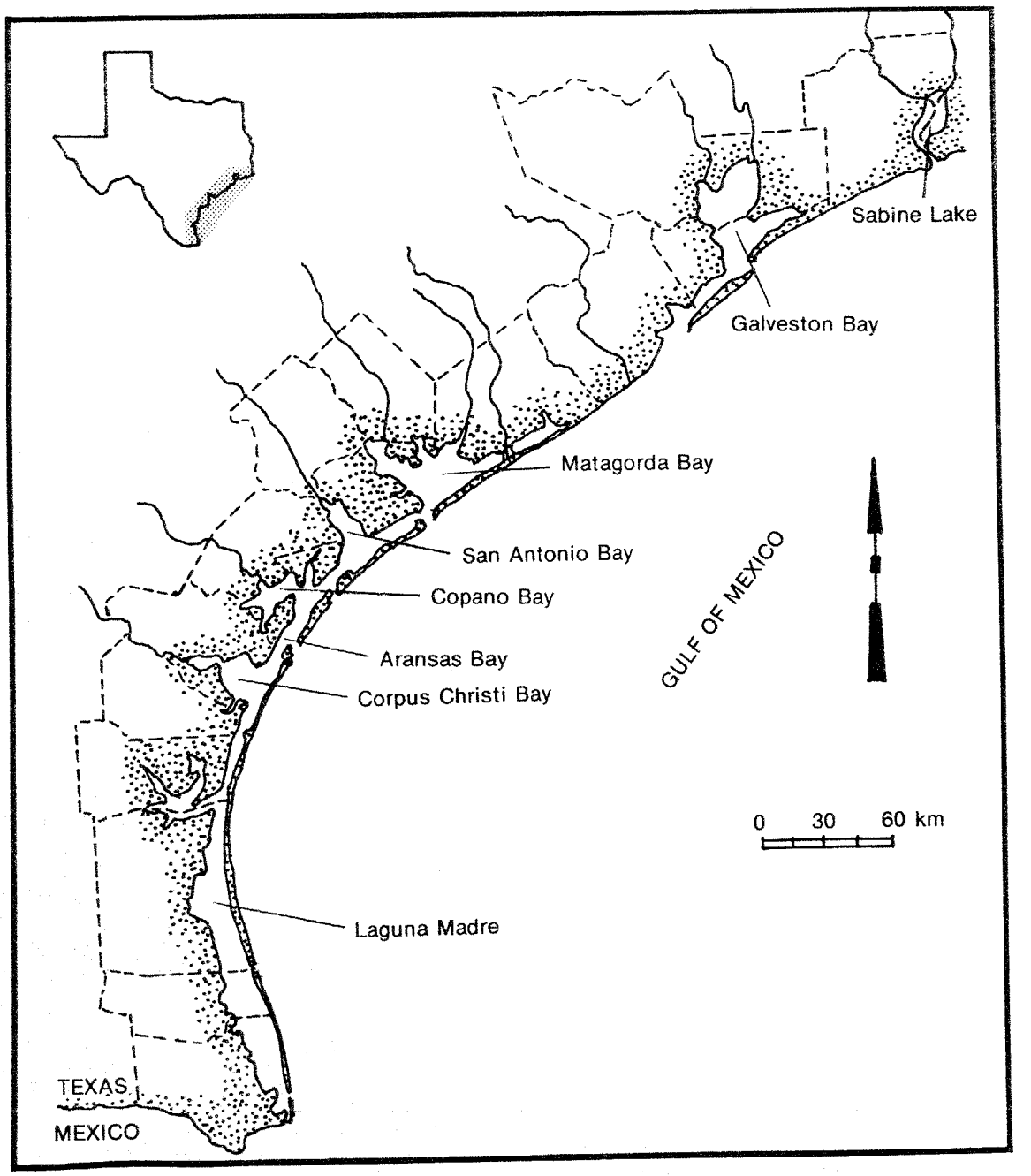

Figure 1. Locations of Texas estuaries (Armstrong 1982).

Table 1. Physiographic data for Texas estuaries (Texas Department of Water Resources 1980a, 1980b, 1981a, 1981b, 1981c, 1983).

Estuary	Surface area (ha)	Surface area (%)	Volume (km^3)	Average depth (m)	Marsh (ha)
Sabine Lake	17,798	2.9	0.326	1.8	13,760
Galveston Bay	143,153	23.0	2.911	2.1	5,420
Matagorda Bay	101,368	16.2	2.134	2.3	11,430
San Antonio Bay	56,162	9.0	0.754	1.4	4,833
Copano-Aransas Bays	46,279	7.4	0.925	2.0	
Corpus Christi Bay	44,451	7.1	1.147	2.4	5,350
Laguna Madre	214,545	34.4	2.574	1.2	
Total	623,756	100.0	10.771		

south and west of Sabine Lake, while the balance parallels the Sabine and Neches Rivers at the head of the estuary. The urban areas lie primarily to the west and north of Sabine Lake and have a population of 329,300 people (1980 census).

1.2.2 Galveston Bay Estuary

To the west of Sabine Lake lies Galveston Bay, which is greatly influenced by the urbanization on its west, south, and north boundaries. The Houston-Texas City-Galveston metropolitan and associated industrial areas make up the urban complex; and the 1980 population is approximately 2,994,500. This estuary (shown in Figure 3) is the second largest on the Texas coast with a surface area of 143,153 ha or about 23% of the total estuarine surface area of Texas. It has an average depth of 2.1 m, although it is traversed by a major navigation channel, the Houston Ship Channel, which extends from the mouth of the estuary (Boliver Roads) through the bay and into the San Jacinto River Channel. A short distance into this channel it turns west into Buffalo Bayou and finally ends on the east side of Houston. Most of the industrial complex in the Houston area borders this navigation channel, from Morgan City, Louisiana, where the channel enters the San Jacinto River Channel, to Houston.

The total wetland area around this estuary is some 20,200 ha, although only about 5,420 ha can be considered to be contributing marsh or marsh affected by tidal action. Like Sabine Lake, the Galveston Bay Estuary lies in the coastal prairie and coastal marsh land-resource areas, but this area is probably changing more rapidly due to man's activities than any other area on the Texas coast.

The major freshwater inflows to Galveston Bay come from the Trinity River and the San Jacinto River. Sedimentary deltas are forming at the mouths of both of these rivers, and it is on these deltas, especially that of the Trinity River, where extensive marsh lands may be found.

1.2.3 Matagorda Bay Estuary

Matagorda Bay is the third largest estuary on the Texas coast (see Figure 4) with a surface area of 101,368 ha. Its average depth is 2.3 m and its volume is 2.134 km^3. Like the Galveston Bay Estuary, Matagorda Bay is traversed by a

navigation channel that extends from a cut through the barrier island up to Lavaca Bay in the northwest corner of the estuary. Major freshwater sources to Matagorda Bay include the Lavaca River, flowing into Lavaca Bay, and the Colorado River, which flows into the northeast arm of Matagorda Bay. Because of the configuration of the Colorado River delta, the proportion of the river flow that actually reaches the estuary is largely unknown. A channel dredged through this river delta permits the river to discharge directly into the Gulf of Mexico, but there are points of access between the river channel and the bay which do permit some water to flow into the estuary as long as a hydraulic gradient exists. On occasion, bay water flows into the river channel and out to the gulf through these same access points. Most of the marshes are found in the Lavaca Bay area and the Colorado River delta area, and they total some 11,430 ha.

Despite its size and location, Matagorda Bay has relatively little urban development around its periphery. Small cities are scattered along its western and northern boundaries, and some major industry is located on the shores of Lavaca Bay. Despite the industrialization taking place, it should be some time before the amount begins to approach that of Corpus Christi Bay or Galveston Bay. The population in urban areas surrounding the Bay totals 123,700 people. More detailed information about this estuary is contained in the Texas Department of Water Resources (1980b) report.

1.2.4 San Antonio Bay Estuary

The San Antonio Bay Estuary lies immediately west of Matagorda Bay and has a total surface area of 56,162 ha or 9% of the total surface area of Texas bays (see

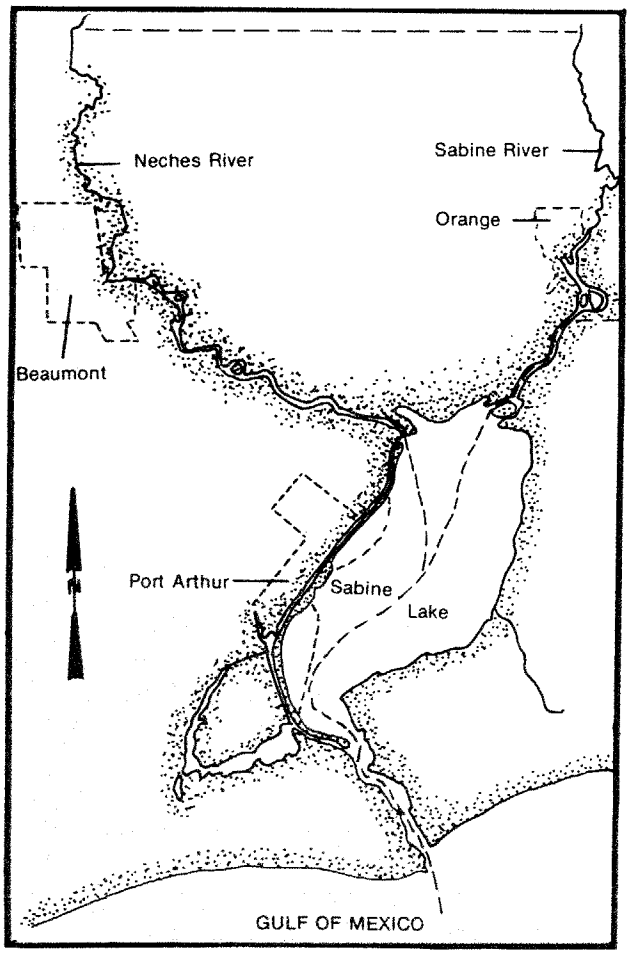

Figure 2. Sabine Lake system.

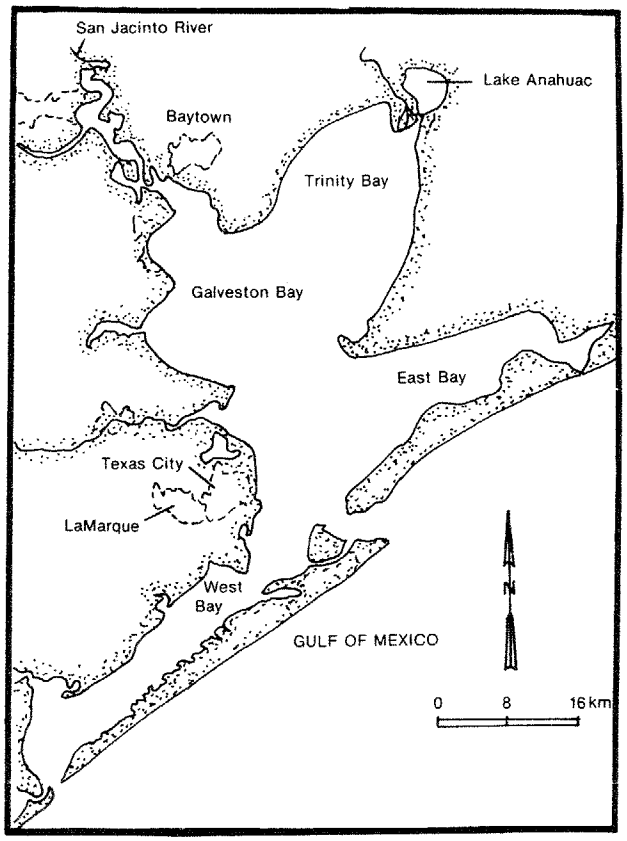

Figure 3. Galveston Bay system.

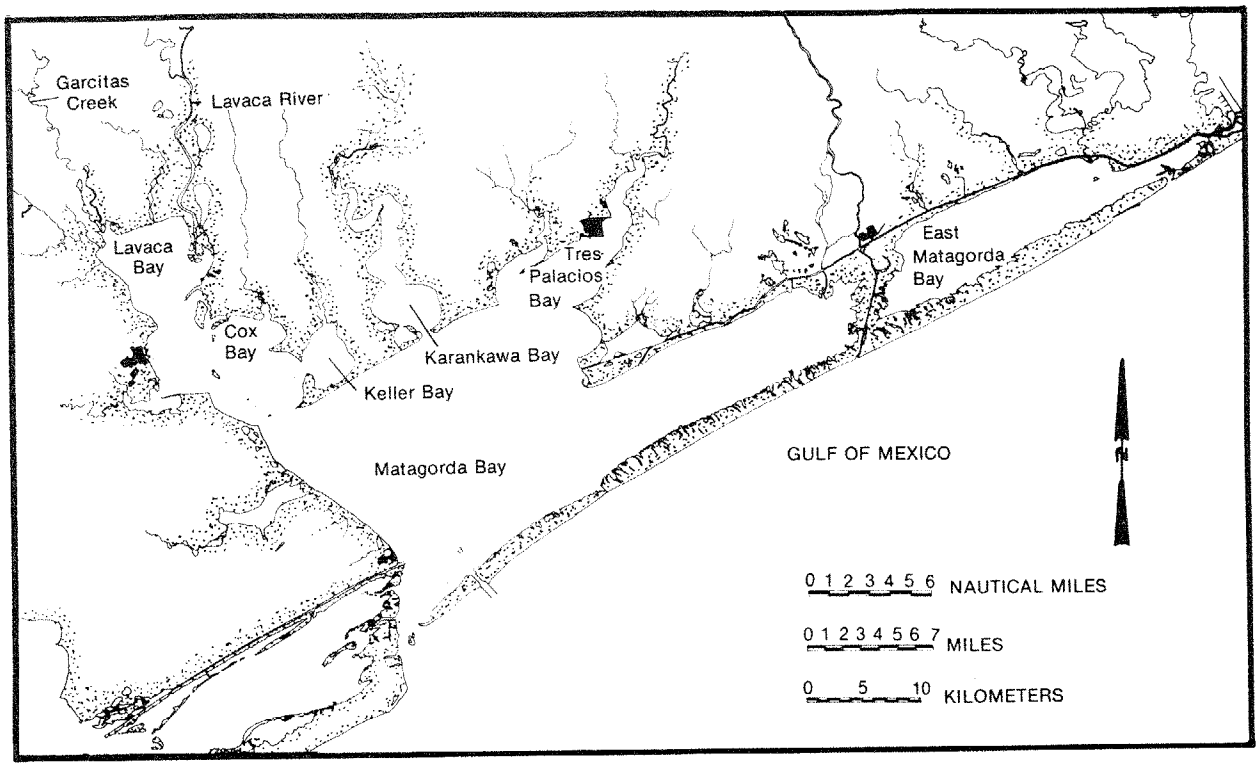

Figure 4. Matagorda Bay system.

Figure 5). It is fed by the Guadalupe River, which has built a large delta at the head of the estuary. This estuary exchanges waters with Matagorda Bay to the east and the Copano-Aransas Bays estuarine system to the west; it has no direct opening to the Gulf of Mexico. The average depth in this estuary is only 1.4 m and the volume is 0.754 km^3. Land use around the bay is primarily agricultural and ranching activities. Rice is the principal irrigated crop, but other crops such as grain sorghum, corn, and cotton are dry-land crops produced in the area. Some forested areas, primarily oak, are found. On the southwest shore of this estuary lies the Aransas Wildlife Refuge, an important area where the endangered whooping crane overwinters.

Wetlands are found primarily on the delta at the head of the estuary but also on the northeast and southwest edges of the primary bay and on the lee side of the barrier island. Although there is some urban development on the northeast shore of this estuary, it is quite small, the population around the estuary totaling only 102,600 people. Industrial activities around the estuary include manufacturing, agriculture-forestry-fisheries, and mining. Manufacturing activity involves primary metals (mainly aluminum), chemicals, and allied products. Crude oil and natural gas production comprise the mining activities.

1.2.5 Copano-Aransas Bays Estuary

The Copano-Aransas Bays Estuary is made up primarily of Copano Bay and Aransas Bays as shown in Figure 6. Mission Bay is a very small area immediately northwest of Copano Bay. Major freshwater flows into these estuaries come from the Mission and Aransas Rivers although, as shown later, these inputs are relatively small. This estuarine system has a total surface area of 46,279 ha, an average depth of 2 m, and a volume of 0.925 km^3.

The Copano-Aransas Bays Estuary is found in the coastal prairie land-resource area. Land use is dominated by agricultural and ranching activities with only

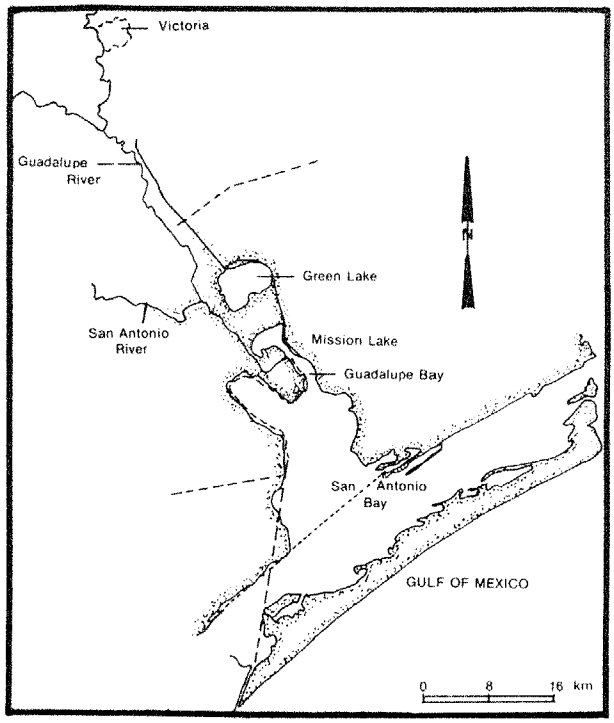

Figure 5. San Antonio Bay system.

minor areas of irrigated crops. The large amount of agricultural area around this estuary and the lack of urbanization are reflected in the small population of about 21,300 people in the counties adjoining this estuary.

1.2.6 Corpus Christi Bay Estuary

The Corpus Christi Bay estuarine system, shown in Figure 7, is made up of Nueces Bay, Oso Bay, and Corpus Christi Bay, with a total surface area of 44,451 ha or 7.13% of the total bay area in Texas. The average depth is about 2.4 m and the volume is 1.147 km^3. Like other Texas bays, Corpus Christi Bay is also traversed by a major navigation channel that begins in Aransas Pass where it cuts through the barrier island traversing Corpus Christi Bay and ends in the port of Corpus Christi. The Nueces Estuary also lies in the coastal prairie area, and land use around it is also dominated by agriculture and ranching. The city of Corpus Christi, with its associated port and industrial complex, however, is located on the west side of the estuary and dominates land use in that area. There is an additional industrial complex on the north shore of Corpus Christi Bay in the Ingleside region. The industrial activity is mainly aluminum production and chemicals and petroleum refining. The port of Corpus Christ is ranked thirteenth in cargo handled in the United States (in 1970) and the second largest in Texas, and it is linked via the Intracoastal Waterway to other major ports in Texas. Crude oil and natural gas production constitute the principal mining activities in the area; agriculture, forestry, and fisheries contribute significantly to the economy of the area. The population in the counties joining the Nueces estuarine system totals 314,400 people.

1.2.7 Laguna Madre Estuary

The Laguna Madre Estuary consists of Upper and Lower Laguna Madre, Baffin Bay, and part of Arroyo Colorado (Figure 8). The surface area is 214,545 ha which makes it the largest estuary in the State based on surface area at mean sea level. Because of its shallowness (average depth 1.2 m), however, its water surface area at mean low water is less than that of Galveston Bay Estuary. This estuary extends 150 miles south from Corpus Christi Bay to the lower tip of Texas. With its shallow water and large surface area, its volume is 2.574 km^3.

The Laguna Madre Estuary lies in the west gulf coast land resource area, an undulating to rolling, moderately dissected, brush-covered plain. Land use around the estuary is primarily agriculture and ranching with cotton, grain sorghum, fruits, and vegetables as the principal irrigated crops. Major urban and industrial areas lie at the southern tip of this estuary in the Brownsville area. The population there plus the very small population bordering the rest of the estuary total 252,000 people.

1.3 GEOLOGIC HISTORY

Sedimentary materials in Texas bays were deposited by formerly and presently active geologic processes in delta, fan,

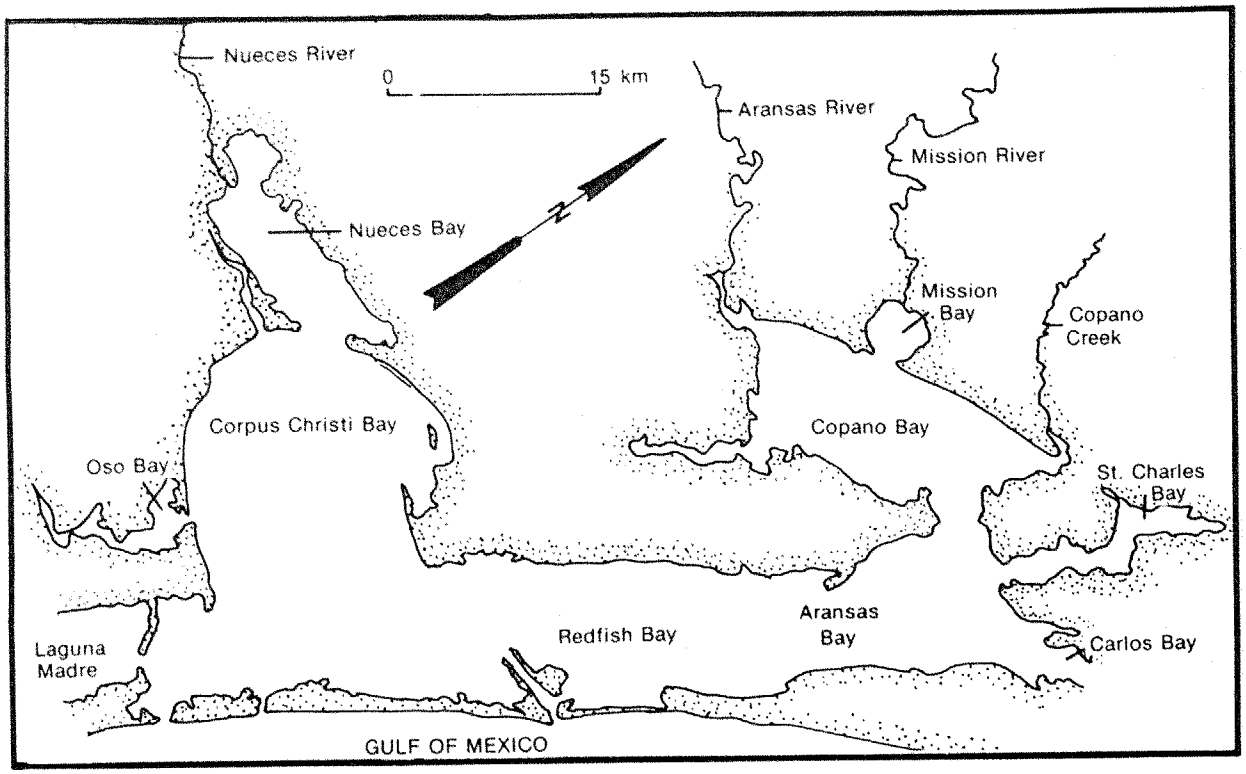

Figure 6. Corpus Christi, Redfish, and Copano Bay systems.

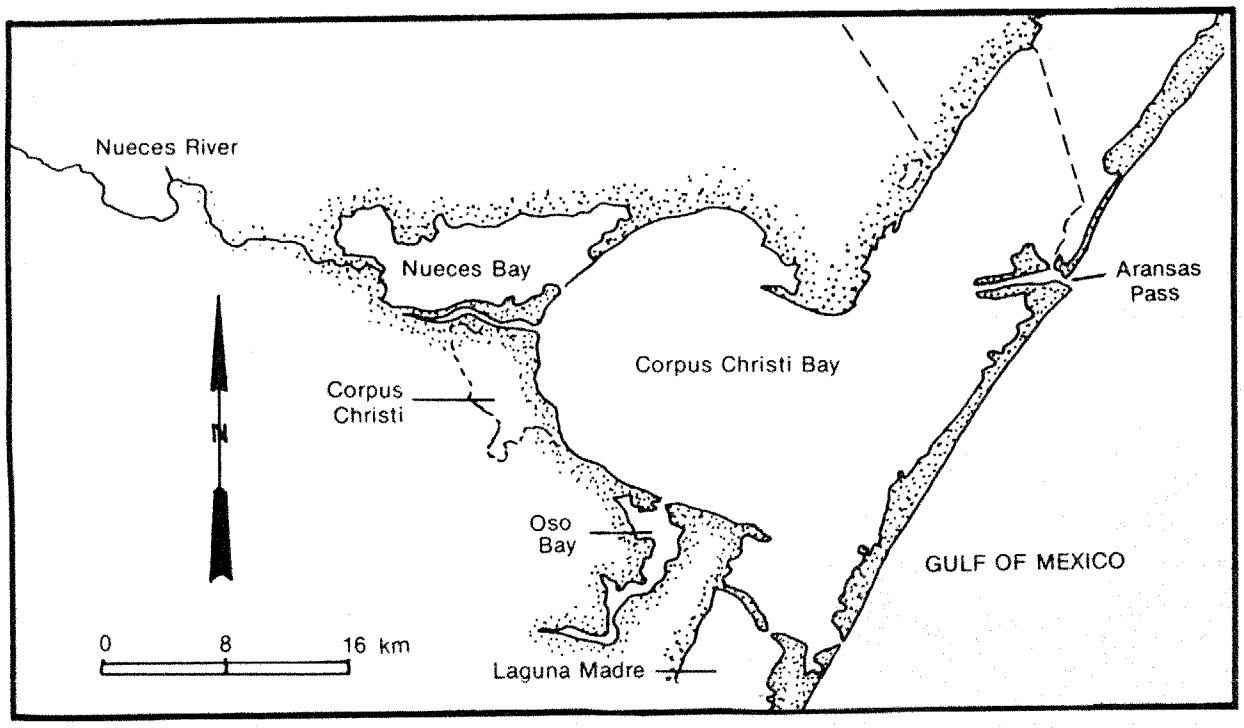

Figure 7. Corpus Christi Bay system.

river, bay-estuarine, and barrier-island-shoreline systems (Kier and White 1978). The oldest substrate in the coastal zone was deposited as a fan approximately 3 million yr ago; younger Pleistocene Age deposits (3 million to approximately 18,000 yr old) compose most of the coast plain (Figure 9). These deposits accumulated in river, delta, and delta-margin environments during one of the interglacial intervals.

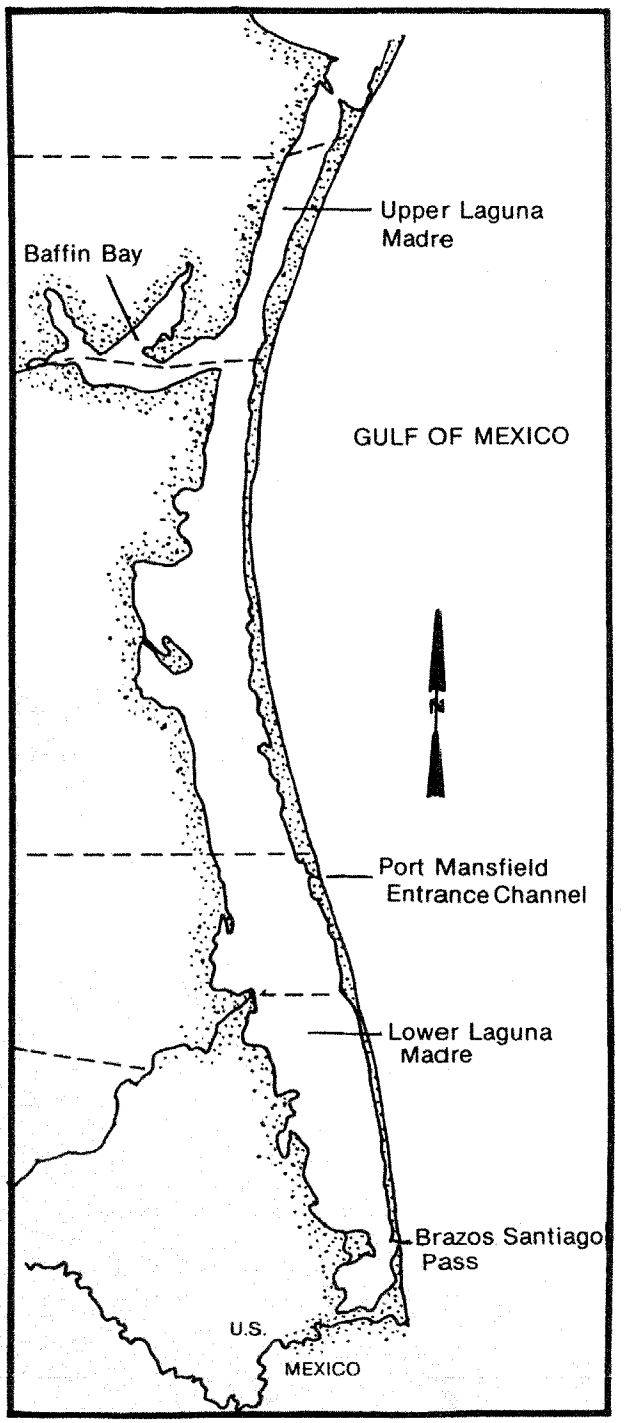

Figure 8. Laguna Madre estuarine system.

During the early Wisconsin glaciation, which was the last major period of glaciation, sea level was as much as 450 ft lower than it is today. The ancestral rivers reaching the coast cut deeply into the coastal plain and discharged sediment far out on the Continental Shelf, which was as much as 50 mi offshore from the present shoreline. Between the early and late Wisconsin glacial periods, sea level apparently returned to today's level, and old delta deposits were reworked by waves and marine currents. Lakes and lagoons developed landward of these deposits. Then some 30,000 yr ago, after the continental glaciers had once again begun advancing and sea level was about 400 ft below today's level, rivers crossing the coastal plain again cut downward. About 18,000 yr ago, sea level began to rise gradually as the last glaciation period diminished. River valleys began to fill with sediment, but sea level rise exceeded sedimentation and the lower portions of the valleys were drowned. Shorelines of the modern bays and estuaries often reflect the position of old river and stream meanders (Kier and White 1978).

About 4,500 yr ago when sea level was approximately 15 ft lower than at present, modern geologic processes became active. Upon reaching present sea level approximately 2,500 yr ago, several natural changes began to occur: (1) the estuaries began to fill with sediment from rivers and streams, from bay margins and oyster reefs, and from the Gulf of Mexico; (2) small streams extended their courses headward; (3) offshore shoals coalesced into barrier islands, gradually restricting the bays and estuaries behind them; (4) marshes became established; and (5) wind action modified several sandy areas that were deposited earlier (Kier and White 1978). The shoreline within the Texas estuarine systems and the beaches facing the Gulf of Mexico continue to experience erosion and sedimentation. Extensive studies by the University of Texas at

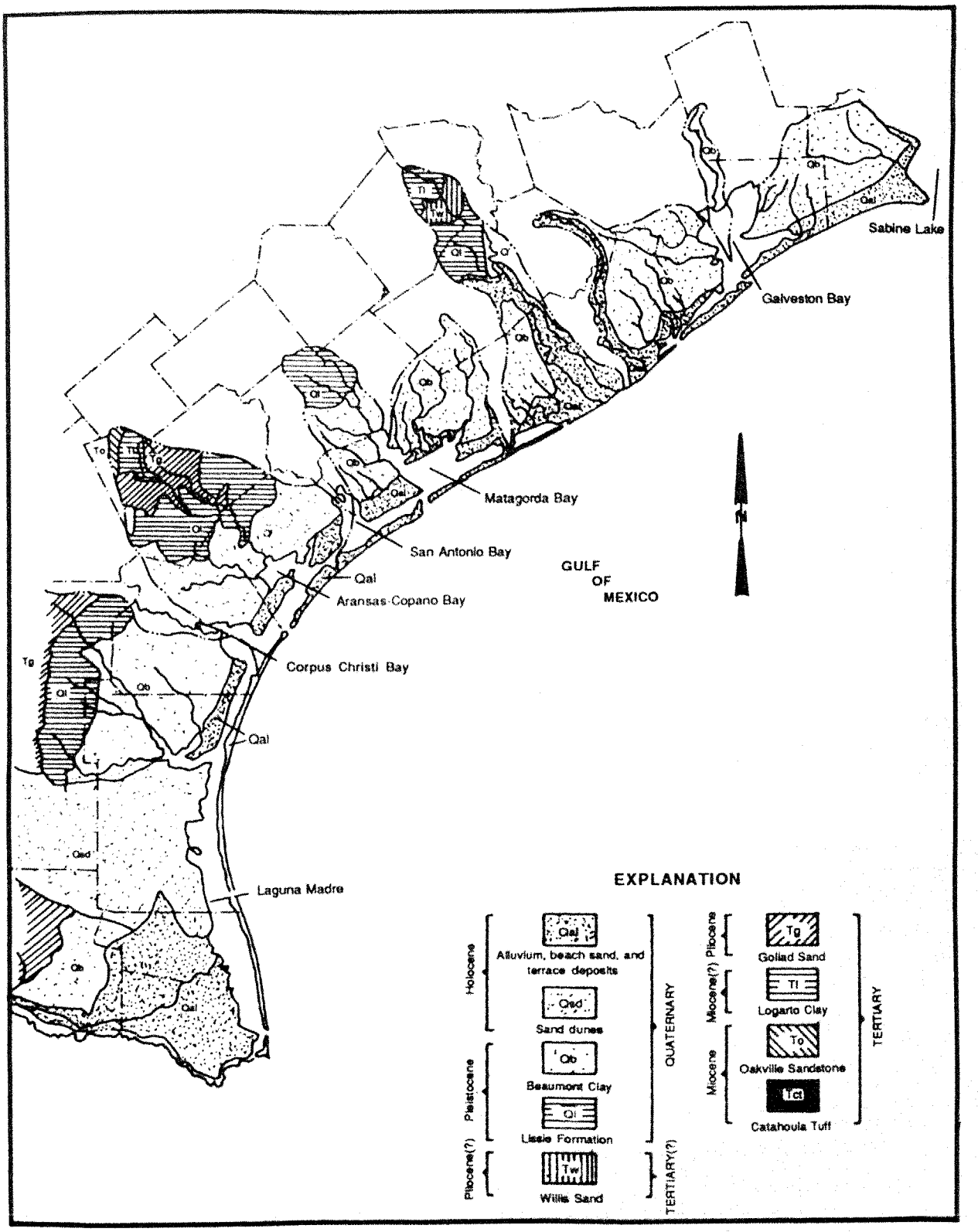

Figure 9. Sedimentary deposits in Texas bays.

Austin Bureau of Economic Geology have determined these areas of erosion and accretion, and these areas have been reported by the Texas Department of Water Resources (1980a, 1980b, 1981a, 1981b, 1981c, 1983). Naturally, the substrate within estuarine systems reflects to some extent these geologic processes within the estuaries.

1.4 CLIMATE

The Texas coast may be divided into two major climatic regions, the upper coast climatological region extending from the San Antonio Bay Estuary north and the south central climatological division lying south of the San Antonio Bay Estuary. The upper coast climatological region lies in the warm temperate zone. Its climatic type is classified as subtropical (humid and warm summers), but it is also predominantly marine because of the proximity of the Gulf of Mexico. Prevailing winds are southeasterly to south-southeasterly throughout the year, and day-to-day weather during the summer varies little except for occasional thunderstorms. Summer daytime temperatures are moderated because of the sea breeze, and winters are mild because the moderate polar air masses which push rapidly southward into the gulf bring cool, cloudy, and rainy weather for brief periods.

The south central climatological division is classified as subtropical (humid and hot summers with mild, dry winters). Again the climate is predominantly marine because of the proximity of the Gulf of Mexico, and prevailing winds are southeasterly to south-southeasterly throughout the year. Some of the heavier rainfalls occur during late summer and early fall in conjunction with tropical disturbances. Mild winter temperatures and hot, humid summer weather are due to the warm, tropical air from the Gulf of Mexico.

Precipitation changes drastically from north to south along the Texas coast, ranging from 151.7 cm/yr in Sabine Lake down to 74.4 cm/yr in the Laguna Madre area. Values in between are given in Table 2. On the other hand, evaporation rates are opposite to those of precipitation with evaporation amounting to 112.4 cm/yr in the Sabine Lake area and increasing to 158.3 cm/yr in the Laguna Madre. As a consequence, there is a net water gain from precipitation-evaporation in the Sabine Lake Estuary of 39.3 cm/yr, while in the Laguna Madre there is a net loss of 83.9 cm/yr. This tremendous loss in the Laguna Madre coupled with very small freshwater inflows produces the hypersaline conditions found in that system.

Table 2. Climatological data for Texas estuaries (Texas Department of Water Resources 1980a, 1980b, 1981a, 1981b, 1981c, 1983).

Estuary	Precipitation		Evaporation		Net
	(km^3/yr)	(cm/yr)	(km^3/yr)	(cm/yr)	(cm/yr)
Sabine Lake	0.263	151.7	0.196	112.4	+39.3
Galveston Bay	1.926	134.8	1.696	118.8	+16.0
Matagorda Bay	1.058	105.6	1.490	143.0	-37.4
San Antonio Bay	0.543	97.6	0.794	142.4	-44.8
Copano-Aransas Bays	0.405	88.6	0.690	151.3	-62.7
Corpus Christi Bay	0.326	74.2	0.661	150.7	-76.5
Laguna Madre	1.596	74.4	3.396	158.3	-83.9

1.5 HYDROGRAPHIC CONDITIONS

With precipitation and evaporation varying so widely along the coastline as well as across the drainage basins to the various estuaries, it is not surprising that there is a large variation of freshwater inflows to each estuary. Coupling the freshwater inflows with bay geomorphology and tidal mixing, it is again not surprising that large changes in salinity exist from estuary to estuary. Of course, as in other estuarine systems, these freshwater inflows interact with waters brought into the estuary from the ocean through tidal inlets to produce spatial and temporal variations in salinity. Because the freshwater inflow and tidal regimes are very different from other regions of the U.S. coastline, it is appropriate here to discuss these two important hydrologic and hydrographic factors in more detail.

1.5.1 Tidal Exchange

Tidal exchange in Texas estuaries is due to astronomical tides (i.e., true tides), meteorological phenomena (winds and barometric pressure), and density stratification. Of these influences, winds are the most important and produce "windtides" which over long periods can account for substantial exchange of water between the gulf and the estuaries (Ward et al. 1982). Other influences can be important locally at certain times.

Astronomical tides in the Gulf of Mexico are dominantly diurnal; consequently, it is the declination of the moon that primarily governs the tidal range. At minimum declination, the diurnal component becomes small enough so that the tide is effectively semidiurnal. The tidal range at maximum declination (diurnal) is about 0.8 m, and at minimum declination (semidiurnal) about 0.2 m. Thus, tides in the northwestern Gulf of Mexico are quite feeble in comparison to those of the Atlantic and Pacific coasts and exert a relatively small influence on mixing in these estuarine systems as compared to those elsewhere (Ward et al. 1982).

As a general rule, the Texas estuaries are meteorologically dominated primarily as a consequence of their large surface-area-to-volume ratios and the predominantly south to southeasterly winds from the Gulf of Mexico during the spring, summer, and fall seasons. During the winter, significant northerly winds occur as cold fronts pass through the gulf coast region. This meteorological dominance has two consequences. First, the wind-driven waves that are generated over the long overwater fetches develop into rather intense surface waves under even light to moderate winds. Again, because of the shallowness, the mixing action of the waves results in water that is usually vertically homogeneous and rather turbid. The second effect is the rise in water surface in the direction of the winds, or denivillation. The "setup" and "setdown" are common, and the resulting "windtides" frequently overshadow the weaker astronomical tides. During periods of strong northerly winds, for example, it is common for large areas of the shallower portions of the estuaries to become exposed as water is literally blown out of the estuary. Under such condition, the total change in water level in the bay system can be in excess of a meter within a relatively short period of time. It has been observed that the amount of water moved out of the bay system during a moderate frontal passage is on the order of the great-declination tidal prism (i.e., the volume of water between mean low water and mean high water at maximum tidal range) and may even be larger than this for an intense meteorological system (Ward et al. 1982).

Of great importance to the exchange of water that occurs during tidal excursion are salinity stratification and the density currents developed because of this stratification. These currents arise from the pressure-gradient acceleration associated with the horizontal variation in density. This density current is the mean current from the mouth of the estuary to its head. It is forced by the seaward gradient in salinity. While this density current is generally an order of magnitude smaller in intensity than the tidal current, under conditions of weak tidal currents, such as small lunar declination or around slack water, density currents can be measured directly. Ward (1980) summarizes the physics of the density current by four principles: (1) the intensity of the

density current increases with the horizontal gradient of salinity; (2) all other factors being equal, the intensity of the density current increases approximately as the cube of water depth; (3) in an equilibrium configuration, the density current must force a return flow from the head of the estuary to the mouth; and (4) vertical stratification is no index to the existence of a density current, for a pronounced density current can, and frequently does, exist in a vertically homogeneous estuary. Because of principle number 2 (the dramatic increase in current intensity with water depth), the dredged navigation channels transecting the bays have significantly greater depths than surrounding water, making them effective conveyences for density currents (Ward et al. 1982). Ward (1983) states that a dredged channel twice the natural depth of an estuary will carry a density current whose intensity is eight times as great as the current at the natural depth, and in some gulf coast estuaries these navigation channels are three to four times the natural depth. Two types of density-current circulations can be distinguished corresponding to the confined and the unconfined channel. In the confined channel configuration, the channel is bounded on either side by shore so that lateral currents are very small relative to those along the longitudinal dimension. In such channels, the return flow is in the surface layer so that net circulation is two-layered, i.e., flow up the estuary in the lower layer and down the estuary in the upper layer. In the unconfined channel which is so common to Texas estuaries, a unidirectional landward current in the channel occurs and, with vertical mixing and free access to the open water either side of the channel, the return flow is found in the shallower open-bay waters.

The net increase in salinity in an estuary because of enhanced ocean water intrusion via a navigation channel can be significant. In a recent study of Matagorda Bay (Ward et al. 1982), the changes in base salinity due to the dredging of a navigation channel was 5 ppt, a substantial increase in an estuary which receives only moderate freshwater inflows as described below.

1.5.2 Freshwater Inflows

Using the extensive analyses summarized in the Texas Department of Water Resources reports on each Texas estuary (Texas Department of Water Resources 1980a, 1980b, 1981a, 1981b, 1981c), Armstrong (1982) summarized these data while relating the responses of Texas estuaries in terms of finfish and shellfish harvest to the freshwater inflows. These data are presented in Table 3 along with more recent data from the Laguna Madre taken from Texas Department of Water Resources

Table 3. Hydrologic data for Texas estuaries (Texas Department of Water Resources 1980a, 1980b, 1981a, 1981b, 1981c, 1983).

Estuary	Gaged inflows (km^3/yr)	Ungaged inflows (km^3/yr)	Combined inflows (km^3/yr)[a]	Precipitation (km^3/yr)	Evaporation (km^3/yr)	Net inflows (km^3/yr)[b]	Drainage area (km^2)	Yield (m^3/ha)
Sabine Lake	13.18	2.41	16.05	0.26	0.20	16.11	53,421	3,004.4
Galveston Bay	8.48	3.13	12.06	1.93	1.70	12.29	62,015	2,256.0
Matagorda Bay	2.34	1.19	3.62	1.06	1.44	3.24	114,600	315.9
San Antonio Bay	2.23	0.57	2.80	0.54	0.79	2.54	28,614	978.5
Copano-Aransas Bays	0.13	0.34	0.48	0.40	0.69	0.22	6,800	705.9
Corpus Christi Bay	0.71	0.10	0.84	0.33	0.66	0.51	44,963	186.8
Laguna Madre	0.40	0.41	0.83	1.60	3.40	-0.97	10,499	790.6
Totals	27.47	8.15	36.68	6.12	8.88	33.94		

[a]Includes diversions.
[b]Combined inflow plus precipitation minus evaporation.

(1983). The combined inflow of freshwater from overland runoff, return flows, and diversions ranges from 16.05 km^3/yr into the Sabine Lake Estuary down to 0.48 km^3/yr into the Copano-Aransas Bays Estuary. When one takes into account precipitation onto the water surface and evaporation from the estuaries, the net inflows that result range from 16.14 km^3/yr in the Sabine Lake Estuary down to 0.19 km^3/yr in the Copano-Aransas Bays Estuary. The halving of precipitation from the Sabine Lake Estuary down to the Laguna Madre, the 34% increase in evaporation in the same direction, the location and size of the drainage basin areas, and in particular the dramatic decrease in precipitation and land runoff from the eastern portions of the state to the west (annual rainfall amounts diminish 10 mm for every 9.5 km as one moves east to west) produce these tremendous changes in net freshwater inflow. These large differences in freshwater inflows coupled with the tidal regime described above help produce the large differences in salinities and nutrient budgets described in the next chapter.

CHAPTER 2.
PHYSICAL-CHEMICAL DESCRIPTION

2.1 TEMPERATURE

Temperature variations in Texas estuaries are primarily temporal and specifically seasonal. There is very little variation spatially within an estuary either horizontally or vertically. Vertical variations are essentially damped because of the intense vertical mixing of the water column due to wind-wave action. Horizontal gradients, if they exist at all, are found in the tidal inlet, between very shallow and deep areas, and near thermal discharges. For the most part, water temperatures follow air temperatures, and it has been shown in Corpus Christi Bay that a regression between air temperature and water temperature had a correlation coefficient of 0.91 (Henningson, Durham, and Richardson 1978).

Matagorda Bay, which lies in the middle of the Texas coast, has typical temporal and spatial variations in temperature. Annual average bay temperature is approximately 23°C with minimum temperatures averaging 12 °C in January and maximum temperatures in July and August with an average of 29 °C (Ward and Armstrong 1980). Geographic variation of annual average temperatures in the bay are demonstrated by the range from 21.6 °C near Pass Cavallo to 24.6 °C in East Matagorda Bay, a confined, shallow region of the estuary.

2.2 SALINITY

Large variations in annual average salinities in Texas estuaries have been noted by Armstrong (1982). He found values ranging from 2.3 ppt in the Sabine Lake Estuary to 36.2 ppt in the Laguna Madre. Average salinities for other estuaries are given in Table 4.

Table 4. Annual average water quality in Texas estuaries (after Armstrong 1982; Texas Department of Water Resources 1980a, 1980b, 1981a, 1981b, 1981c, 1983).

Estuary	TOC (mg/l)	Total N (mg/l)	Total P (mg/l)	Salinity (ppt)
Sabine Lake	9	0.3	0.07	2.3
Galveston Bay	8	0.12	0.27	17.6
Matagorda Bay	5	0.04	0.05	23
San Antonio Bay	ND	0.20	0.18	11
Copano-Aransas Bays	ND	0.06	0.07	13
Corpus Christi Bay	ND	0.06	0.06	27
Laguna Madre	12.2	0.38	0.11	36.2

Seasonal variations in salinity, of course, reflect freshwater inflows and vary considerably from estuary to estuary as well as within each estuary.

2.3 NUTRIENTS

Nutrients in estuaries have received much attention over the years, but particular interest in nutrient cycling has emerged in recent years. An excellent summary of current thought on nutrients in estuaries is contained in Neilson and Cronin (1981), and the paper by Nixon (1981) presents the historical change in thought about these processes. Within the last 10 years, some views on the importance of emergent marshes in providing nutrients to open bay bottom systems have changed markedly. Even more recently, the realization of the importance of the benthos in open bay bottom systems to nutrient recycling has become evident. The calculation of nutrient budgets has revealed the major external sources of nutrients to estuarine systems, and that information coupled with nutrient cycling process data has provided a clearer picture of nutrient dynamics in estuaries than ever before.

2.3.1 Nutrient Loading Budgets

Nutrient loading budgets were prepared for the Texas estuaries by Armstrong (1982) for carbon, nitrogen, and phosphorus. The carbon budget includes particulate and dissolved organic carbon, the nitrogen budget includes the particulate and dissolved forms of organic and inorganic (ammonia, nitrite, and nitrate) nitrogen, and the phosphorus budget includes particulate and dissolved total phosphorus. These chemical nutrient forms are available either immediately or eventually to primary producers in the estuarine systems. The budgets accounted for the flux of nutrients to the estuaries with freshwater inflows and wet flux with precipitation to the bay water surface directly. They also included nutrients released to the estuary from peripheral marshes either with tidal exchange or during flood events in which flood waters inundate the brackish marshes at the head of the estuary and flush out nutrients. They do not include the movement of nutrients in biomass larger than plankton. Finally, to compare one estuary to another, the nutrient flux data were normalized by calculating an areal loading rate which was simply the nutrient flux to the estuary divided by its water surface area. The units for the areal loading were expressed as grams of carbon, nitrogen, or phosphorus reaching the estuary per square meter of water surface per year. These budgets are updated here to include the Laguna Madre.

From this nutrient loading information presented in Table 5, several interesting comparisons may be made. First, because of its large freshwater inflows, the Sabine Lake Estuary receives the highest areal loading of any of the estuaries considered. This pattern held true for nitrogen and phosphorus also, and there was a general decrease in areal loading rates as one moved from the Sabine Lake Estuary down to the Laguna Madre. The second observation was that nutrients derived from freshwater inflows dominated the nutrient budgets of all estuaries. In fact, freshwater inflows accounted for over 80% of the nutrients reaching each system. Marshes contributed only a small fraction of the nutrients reaching the estuaries either through tidal exchange or through flood inundation and dewatering. Precipitation also accounted for a very small amount of nutrients, although in some cases it contributed as much or more nitrogen and phosphorus as marshes. The third observation was that the amount of nutrients derived from inundation and dewatering of delta marshes was less than those obtained from tidal exchange. While the nutrients flushed from these marshes during flooding events was substantial, the events occurred only rarely during the year and tidal inundation, because of its regularity, eventually dominated. In summary then, freshwater inflow is the dominant external source of nutrients to estuarine systems (Armstrong 1982).

When one considers internal sources of nutrients, it becomes very clear that the cycling of nutrients within the estuarine system accounts for a substantially greater mass of nutrients than those coming in with external sources. For example, Armstrong and Hinson (1972)

Table 5. Carbon, nitrogen, and phosphorus loading budgets for Texas estuaries (Armstrong 1982).

Nutrient	Estuary	Freshwater inflows (10^6kg/yr)	Marshes Tidal (10^6kg/yr)	Marshes Flood (10^6kg/yr)	Precipitation (10^6kg/yr)	Total (10^6kg/yr)	Areal loading (g/m^2/yr)
Carbon	Sabine Lake	115.70	2.50	1.44		119.64	672.20
	Galveston Bay	103.44	4.02	0.14		107.60	75.20
	Matagorda Bay	75.75	5.35	0.14		81.62	80.50
	San Antonio Bay	17.95	0.88	0.30		19.13	34.10
	Copano-Aransas Bays	5.98				5.98	12.90
	Corpus Christi Bay	8.21	9.11	0.42		17.74	39.90
	Laguna Madre	6.00				6.00	2.90
Nitrogen	Sabine Lake	9.32	0.02	0.36	0.04	9.75	54.80
	Galveston Bay	11.58	0.12	0.04	0.34	12.08	8.40
	Matagorda Bay	3.58	0.05	0.04	0.51	4.33	4.30
	San Antonio Bay	5.80	0.01	0.08	0.14	6.02	10.70
	Copano-Aransas Bays	0.44			0.11	0.55	2.00
	Corpus Christi Bay	0.55	0.02	0.01	0.11	0.68	1.52
	Laguna Madre	0.61				0.61	.28
Phosphorus	Sabine Lake	0.74	0.50	0.41	0.01	1.21	6.82
	Galveston Bay	3.63	0.09	0.04	0.04	3.81	2.66
	Matagorda Bay	1.31	0.11	0.04	0.04	1.54	1.52
	San Antonio Bay	1.00	0.02	0.09	0.02	1.12	2.00
	Copano-Aransas Bays	0.07			0.01	0.08	0.18
	Corpus Christi Bay	0.22	0.18	0.12	0.01	0.53	1.20
	Laguna Madre	0.72				0.72	0.34

showed that phytoplankton contributed over 98% of the organic carbon coming to or produced in Galveston Bay despite the large amount of organic carbon coming from waste discharges and river flows. Similarly, Ward and Armstrong (1980) showed that phytoplankton produced over 95% of the organic carbon in Matagorda Bay, and Flint (1984) has shown that phytoplankton contributed 52% of the total estimated production for Corpus Christi Bay. With this tremendous production of organic carbon via the phytoplankton, there must be a comparable recycling of inorganic nutrients to support this production. And it is the nutrient cycling processes which become of primary interest at this point.

2.3.2 Nutrient Cycling

Nutrient cycling per se has received little detailed attention in Texas estuaries. A description of the work to date and the magnitude of nutrient cycling processes are discussed later in Section 5.3.

2.4 CONTAMINANTS

Little information is available on contaminants such as heavy metals, pesticides, and complex organics in Texas estuaries. Galveston Bay, which receives the effluents of very large industrial complexes, has been examined for heavy metal contamination. Lavaca Bay, which has a large aluminum plant on its shores, has also received attention because of high mercury concentrations there. Armstrong (1980) summarized the available heavy metal data for Galveston Bay and showed that in many sections of that estuarine system U.S. Environmental Protection Agency criteria for heavy metals in sediments were being exceeded by such metals as mercury, lead, and others. Data from the Texas Department of Health have shown

the high mercury concentrations in Lavaca Bay and the high levels in biota found in the region (Texas Department of Water Resources 1977).

In the lower Laguna Madre, specifically the Arroyo Colorado, excessive concentrations of pesticides have been noted and their impact on finfish and shellfish discussed. Other scattered data add to the data base, but little is known about the toxic contaminants in Texas estuaries and whether they pose a problem to fish and wildlife in these systems.

CHAPTER 3.
GENERAL BAY ECOLOGY

3.1 ESTUARINE HABITATS

As defined by Pritchard (1967), an estuary is a semienclosed body of water along the coast of a land-mass, with a permanent connection to the open ocean and within which the oceanic waters are diluted with freshwater derived from the land-mass drainage. The estuarine ecosystem is not just a simple overlapping of environmental factors extending from the sea and land, however, but is a unique set of factors which integrate to form several biotopes (habitat types, that is, areas homogeneous in both physical conditions and inhabitants) within the ecosystem. All of these biotopes interact to provide an important environment for the evolution of true estuarine organisms as well as the habitation by euryhaline and oligohaline plants and animals. Included in the various biotopes are river mouths, saltwater marshes, mud and sand flats, seagrass beds, oyster reefs, and open-bay bottoms, often referred to as bay planktonic systems. Within the open-bay bottoms are habitats that have been created by man's activities in estuaries, including dredged channels, jetties and bulkheads, and dredge-spoil disposal banks.

Northwestern Gulf of Mexico estuaries and associated saltwater marshes cover a total surface area of 10,820 km^2 (Diener 1975). Of this total, 4,619 km^2 is emergent saltwater marsh vegetation; open-bay bottoms comprise 4,322 km^2 (67.7%) and thus characterize the majority of the Texas estuarine subtidal environment. Seagrass beds make up another 16.3% (1,009 km^2) of the total estuarine surface area, while sand/mud flats contribute 14.0% (870 km^2). A large proportion of the seagrass and sand/mud-flat surface area is found in the Laguna Madre; these two biotopes represent approximately 80% of the total estuarine surface area of the Laguna Madre, which is the largest of Texas estuaries.

Although open-bay bottoms are the dominant habitat type in Texas estuaries, all of the others listed above contribute to the dynamics of life within the habitat. Thus, a summary of these other biotopes is given here as background for a description of the biota that are found in the open-bay bottoms. This will help in understanding the discussion of open bay bottom community function with respect to the total estuarine ecosystem in a later chapter.

The river mouth is a low-salinity area ranging from 0 to 10 ppt where freshwater is discharged into the estuary. Bottom sediments associated with this fluctuating salinity regime are predominantely muds and sandy muds; the water is usually turbid. Heavy surges of freshwater and particulate matter (usually resuspended sediment) during periods of heavy rain followed by surges of saltwater intrusion during exceptional tides and low river discharge periods, make this biotope unfavorable for supporting a diverse community of organisms. This area is also usually characterized by high humic acid concentrations from upstream runoff. Plant species in these areas may include the freshwater grasses Najas sp. and Potamogeton sp. and the widgeon grass Ruppia maritima. Dinoflagellates usually dominate the phytoplankton assemblages. Commonly found animal species include the clams Rangia cuneata, Polymesoda sp., Macoma sp., and Mya sp., and several genera of ostracods. Young crabs (Callinectes) and shrimp (Penaeus and Macrobrachium) will often seek out the protective

cover of submerged grasses in this habitat while feeding.

Salt marshes surrounding Texas estuaries are normally dominated by the cordgrass Spartina, although in some areas the black mangrove Avicennia germinans predominates. These marshes are subject to intermittent inundation due to tidal action and high levels of freshwater inflow. Fluctuations in temperature, salinity, water depth, and sediment composition exert a strong selective effect, limiting the number of species found. Other plants found include Salicornia bigelovii (woody glasswort), Distichlis spicata (saltgrass), Batis maritima (saltwort), and Croton punctatus (beach tea). The substrate supports numerous annelids and nematodes; the scavengers are dominated by the fiddler crabs (Uca sp.) and hermit crab, Pagurus sp. Littorina irrorata, the common periwinkle, grazes on the sediment surface and on grass blades. Numerous birds nest and feed in the salt marshes including Ajaia ajaja (roseate spoonbill), Ardea herodias (great blue heron), Butorides striatus (green heron), Casmerodium albus (great egret), Rallus longirostris (clapper rail), and Cistothorus palustris (terry billed marsh wren). Although the salt marsh biota is not very diverse, these habitats are thought to be some of the most productive in the entire aquatic environment with respect to the primary production of carbon. Mann (1972) estimated that the annual rate of primary production for salt marsh biotopes ranged between 200 and 800 g $C/m^2/yr$. Oppenheimer et al. (1975) calculated that salt marsh carbon production in several Texas estuaries ranged between 0.3 and 7.4 g $C/m^2/day$ with an average annual production estimate of 1,350 g $C/m^2/yr$.

While the most dominant feature of estuarine systems is salinity variation, other parameters are important in determining which parts of the open-bay will develop as sand/mud flats, seagrass beds, oyster reefs, or open-bay bottoms. These other parameters include water depth, current velocity, water clarity, and amount of wind-related wave activity.

Sand/mud flats are characterized as flat areas exposed at low tide and inundated by excessive high tides or wind-induced wave action, with a bottom consisting of unstable sand or mobile fine silt. Larger species do not stabilize the substrate, and consequently most of the organisms are subsurface sediment dwellers. These sediment dwellers are quite productive and can include tube-dwelling annelids, nematodes, copepods, amphipods, razor clams, aerobic and anaerobic bacteria and benthic diatoms. Occasionally, animals from the open-bay bottom such as crabs and shrimp will be found on inundated flats, retreating to deeper waters when the tide recedes. Many birds are common visitors, including Calidris mauri, Limnodromus scolopaceus, Arenaria interpres, Calidris alba, Haematopus palliatus, and Tringa melanoleuca.

When water regularly inundates the sand/mud flats to a depth of perhaps 10 cm or less, blue-green algal mats often dominate on the surface sediments, and dissolved oxygen levels of these periodic shallow waters fluctuate widely between supersaturation during the day and anaerobic conditions at night. When the algal mats on these flats are covered with water, the algae can produce gas bubbles through photosynthesis in the mats, causing them to break away from the sediment surface and to be washed by tidal action into adjacent areas of the estuary. These algal mats act as nutrient concentrators, drawing up nutrient byproducts from the deeper sediments of the flat by the capillary action inherent in the algal composition. Excessive nutrient concentrations develop at the mat surface, and during periods of inundation these nutrients are washed into adjacent waters. Blue-green algal mats covering the flats consist of numerous species of blue-green algae, including Nodulania spp. and Holopedia irregularis, as well as several benthic diatom species. Many of the same species of animals that inhabit the bare sand/mud flats also live in the sediments of blue-green algal flats. The birds include the herons, egrets, and many other wading species.

In deeper waters (up to a meter or two) where light may still penetrate to the bottom and salinity is not excessive, extensive submerged meadows of seagrasses may develop and serve as a shelter and breeding ground for fish and various invertebrates. Such grass areas usually

persist only where the morphology of the estuary is such that the fetch of prevailing winds remains relatively small, and turbid conditions do not usually result from resuspension of shallow bottom sediments by wind-generated waves. In Texas estuaries, the typical grass flat is characterized by turtle grass (Thalassia testudinum), shoal grass (Halodule wrightii), and widgeon grass (Ruppia maritima). Combined with the heavy growths of attached plants (epiphytes) and animals, the biomass represented by grass flats is large, and when autumn die-off occurs this biomass contributes large amounts of detritus to the open-bay bottom of the estuary. Estimates of carbon production for the seagrass beds in Texas estuaries (including associated epiphytes) range from 2.86 g $C/m^2/day$ (Mark Morgan, pers. comm.) to 3.83 g $C/m^2/day$ (Oppenheimer et al. 1975). Because of the quieting action of the grass beds and resultant accumulation of organic matter, the sediments upon which they grow are often anaerobic. This habitat tends to serve the larger, more mobile migratory species of the estuary as a temporary habitat; thus, very few large organisms are observed in these beds on a permanent basis. Species included in this group are the grass shrimp (Palaemonetes vulgaris), the penaeid shrimp (Penaeus sp.), the blue crab (Callinectes sapidus), the hermit crab (Clibanarius vittatus), and the gastropod Melampus sp. Fishes observed on occasions in the grass beds include Brevoortia patronus (gulf menhaden), Cynoscion nebulosus (spotted seatrout), Micropogonias undulatus (Atlantic croaker), Sciaenops ocellatus (red drum), and Mugil cephalus (stiped mullet). The pinfish, Lagodon rhomboides, the longnose killifish (Fundulus similis), the sheepshead minnow, Cyprinodon variegatus, and the bay anchovy, Anchoa mitchilli, are more permanent members of the fish fauna in the grass beds. Numerous annelids and nematodes inhabit the sediments of seagrass beds as do several burrowing molluscs, including Chione cancellata, Ensis minor, Phacoides pectinatus, and Tellina sp.

Wherever currents strong enough to carry suspended material are found in combination with solid substrates, sedentary filter-feeding animals tend to cluster. This is true for biotopes created in the open-bay waters by such human-made features as jetties and bulkheads. Oyster reefs, numerous throughout Texas estuaries except in the Laguna Madre, also occur under these conditions. Generally, the reef will become a shoal, rising as much as a meter from the bottom, with live oysters covering the surface. Typical associated reef plants are Cladophora sp., Ulva lactuca and Hypnea musiformis, all macroalgae. Other sessile species in the reef habitat include barnacles (Balanus sp.), anemones, hydroids, mussels (Modiolus americana), and annelids (e.g., Polydora sp. and Hydroides sp.). Predominant grazers in oyster reefs include Busycon contrarium (whelk), Palaemonetes sp. (grass shrimp), Ischnochitin papillosus (chiton), and Ophiotrix sp. (brittle star). Fish normally associated with these reefs include the Pogonias cromis (black drum), the Opsanus beta (gulf toadfish), the Hypleurochilus geminatus (crested blenny), and the Gobiesox strumosus (skilletfish). When these reefs are exposed at extreme low tides, various birds such as herons, egrets, laughing gulls, and white pelicans use them as a resting place. For a recent account of locations of these oyster reefs in Texas estuaries, see Diener (1975).

As water depth and turbidity increase, a shift to a planktonic-based habitat occurs. The absence of benthic plants or other stabilizing structures such as oyster reefs result in a different sediment composition in the open-bay bottom than in the sand/mud flats, the seagrass beds, or the oyster reefs, along with changes in the abundance and species compositions of the characteristic communities. The open-bay bottoms, which dominate Texas estuaries, may vary from very uniform chemical and biotic compositions to mosaics of distinctive patches. The open bays, comprising most of the estuarine surface area along the Texas coast, are examined in the following pages, which present a comparison of the biota inhabiting the various estuaries of the Texas coast.

3.2 OPEN-BAY BOTTOM PRIMARY PRODUCERS

Phytoplankton are the major primary producers in the open-bay bottoms biotope,

and certain plankton associations are its most constant biological feature. These flora fix carbon by photosynthesis and pass it through the food chain, either directly to pelagic consumers or indirectly as detritus to benthic consumers. In most Texas estuaries, diatoms dominate the winter flora of this biotope and share or yield dominance to the dinoflagellates during the summer. Green algae are usually present throughout the year and may exhibit spring or fall blooms.

In a study from September 1974 to August 1975, Espey, Huston and Associates (1976) found Sabine Lake phytoplankton communities composed of a mixture of freshwater and marine populations with diatoms (45%) and green algae (36.4%) dominating. The diatom Cyclotella meneghinjana was observed throughout the study, while Skeletonema costatum and Melosira crenulata dominated in the spring and early summer. Green algae (Chlamydomonas sp. and Chlorococcum sp.) maintained high winter populations, while Kirchneriella sp. was dominant in the spring. Maximum total abundances for the Sabine Lake phytoplankton community ranged from 180 cells/ml in the fall to 200 cells/ml in the early summer. Minimum abundances of 70 cells/ml were observed in early winter.

From a 12-mo study of Trinity Bay, a component of the Galveston Bay Estuary (Texas Department of Water Resources 1981b) the following seasonal succession of phytoplankton populations was observed. The diatom component peaked in the early spring and was dominated by Skeletonema costatum, Thalassionema nitzschoides, and Navicula abunda. Over the entire study, diatoms comprised 41.6% of all phytoplankton populations. The green algae (24.2%) peaked in the fall as the Ankistrodesmus sp. population reached peak abundances. Blue-green algae (23.0%) represented primarily by Oscillatoria sp. reached maximum abundances during the summer. The freshwater diatom Cyclotella meneghiniana was dominant in January during peak freshwater inflows. Total abundances for the Trinity Bay phytoplankton community exhibited a peak mean abundance of approximately 480 cells/ml in late summer and a second peak mean abundance of 400 cells/ml in late winter-early spring. Minimum mean abundances of approximately 50 cells/ml were observed in the late fall.

Several studies in Lavaca Bay, a component of the Matagorda Bay estuarine system, exhibited contrasting results concerning the distribution of phytoplankton. According to a 1970 study (Blanton et al. 1971) phytoplankton concentration maxima were characteristic of winter months and to a lesser extent in the early fall, while minimum concentrations were observed in the summer. The diatoms were observed in peak abundances in late winter, while the dinoflagellates reached maximum concentrations in the summer. In a study reported by Davis et al. (1973), standing crops of phytoplankton peaked in January (3,400 cells/ml) and declined to lowest concentrations in July (150 cells/ml). Gilmore et al. (1974), in a 12-mo study during 1973-74, reported that peak abundances of phytoplankton occurred during late spring-early summer, with minimum abundances in the winter. Their peak concentrations were around 9,000 cells/ml and their minimum concentrations averaged 2,000 cells/ml. Dinoflagellates comprised the majority of species observed by Gilmore, et al. while diatoms were the second most abundant. During a study in Cox Bay, an embayment off Lavaca Bay, Moseley and Copeland (1974) also reported the dominance of diatoms in the phytoplankton throughout most of the year. Skeletonema costatum, Chaetoceros affinis, and Thalassiothrix frauenfeldii were the dominant forms and were responsible for the winter maxima during the study. The dinoflagellates Ceratium fuses and Ceratium furca were the dominant populations observed in summer. Chlorophyll a maxima for the Lavaca Bay studies appeared to lag the peak cell concentrations by several months. Davis et al. (1973) reported peak chlorophyll a concentrations in the spring several months after their observed January peak cell concentrations. Gilmore et al. (1974) reported higher chlorophyll a concentrations in late spring and early summer, well after the maximum cell concentrations observed.

In an 11-mo study of the San Antonio Bay phytoplankton distributions, Matthews et al. (1974) observed that the green algae dominated the community in the fall while the dinoflagellates, rather than

diatoms, dominated the community in the late winter and spring. Overall, the dinoflagelattes dominated during the entire study period. Minimum mean cell concentrations of 549 cells/ml were observed in the fall during the green algal dominance. Maximum concentrations were observed in winter when 19,000 cells/ml were recorded. In contrast, minimum chlorophyll a concentrations (8.1 μg/l) were measured in January while maximum concentrations (37.2 μg/l) were measured just a month later, in February, at the start of observed peak cell densities for the system. The dominant dinoflagellates were Chroomonas sp. and Eutreptia sp., while abundant green algae included Ankistrodesmus falcatus, A. convoluta and Chlorella sp.

A study by Freese (1952) in Aransas Bay indicated that diatoms were the dominant flora of the phytoplankton assemblages. He noted that the winter peak in phytoplankton abundance was comprised mostly of Coscinodiscus sp. A second peak of diatoms was observed in July when Rhizosolenia alata was the dominant species. Other dominant diatom species included Thalassiothrix frauenfeldii and Skeletonema costatum. The fall appeared to be a period of minimum abundances for diatoms in the phytoplankton community. Holland et al. (1975) in a 3-yr study of Aransas Bay phytoplankton, observed highest mean concentrations of 214 and 584 cells/ml for the months of January during two sampling years. During the other year of study the peak occurred earlier (October) and exhibited a mean of 179 cells/ml. Minimum abundances observed by Holland et al. (1975) occurred in the mid and late summer of each year and ranged from a mean of 2 cells/ml to 10 cells/ml. Again, diatoms were the dominant group comprising the phytoplankton assemblages during this study.

A 3-yr study by Holland et al. (1975) indicated that in the phytoplankton assemblages of Nueces and Corpus Christi Bay, the dominant flora was diatoms. Thalassionema nitzschioides, Thalassiothrix frauenfeldii, and Chaetoceros sp. were dominant, while the diatoms in general comprised more than 70% of the total community over the study period. Exceptions to this trend were the dominance of the blue-green algae Anabaena sp. and Oscillatoria sp. in the fall of 1973 and 1974 in Nueces Bay. Oscillatoria sp. were also observed to dominate in Corpus Christi Bay in the spring and summer of 1974. According to Holland et al. (1975), these periods of blue-green algal domination corresponded with greater nitrogen contents in these bay waters. In another study of Nueces Bay (Murry and Jinnette 1974), diatoms were found to comprise the majority of phytoplankton in Nueces Bay during 1972 and 1973. Dinoflagellates were the only other algal group observed in any number. For Corpus Christi Bay, Holland et al. (1975) observed mean maximum phytoplankton abundances in February and April 1973 (1,100 cells/ml), in December 1973 (1,041 cells/ml), and in December 1974 (468 cells/ml). Minimum mean abundances occurred in the summer of 1973 (77 cells/ml), February 1974 (20 cells/ml), and October 1974 (60 cells/ml). In Nueces Bay this same study indicated that peak mean abundances of phytoplankton occurred again in February and April 1973 (418 cells/ml), February 1974 (139 cells/ml), and September 1974 (513 cells/ml). Minimum mean abundances occurred in the summer of 1973 (6 cells/ml), March 1974 (7 cells/ml), and November 1974 (7 cells/ml).

Hildebrand and King (1978) observed that diatoms were the dominant flora during a 6-yr study of Oso Bay and the upper Laguna Madre Estuary. Maximum abundances were normally observed in December through March of each year with minimum counts recorded during the summer. The dominant diatoms were Chaetoceros affinis, Thalassionema nitzschioides, Thalassiothrix frauenfeldii and Nitzschia sp. The only dominant dinoflagellate observed was Ceratium furca. The maximum abundance recorded for the total phytoplankton assemblage was 1,600 cells/ml in January 1976 in Oso Bay. Hildebrand and King (1978) indicated that salinity was the apparent controlling factor of phytoplankton dynamics in these areas. They observed that blooms generally occurred following salinity changes, but never in salinities exceeding 40 ppt. Similarly, Simmons (1957) observed that in the higher saline areas (equal to or greater than 60 ppt) of the upper Laguna Madre, phytoplankton were usually nonexistent.

As in the previous study, Espey, Huston and Associates (1977) found that diatoms were the dominant flora in a study they conducted in the lower Laguna Madre Estuary. Unfortunately, this study covered only the summer month of July for one year and did not include winter-spring maxima that occur in other Texas estuaries. Observed phytoplankton abundances during this short study ranged from 23 cells/ml to 181 cells/ml.

Other than the blue-green algal mats that often occur on flats within the Texas estuaries, the only benthic microalgae that were ever observed were diatoms in the surface sediments by Oppenheimer and Wood (1965). It is questionable whether these were actually healthy and capable of photosynthesis or whether they were simply individuals that had settled out of the water column. It was observed during this study, however, that the largest cell counts occurred in sediments from water depths of less than a meter while the smallest counts were observed in sediments from 2-m water depth.

Several observations have been made in Texas estuaries concerning drift algal communities that contribute to the diversity of the open-bay bottom areas. Unattached algae on an open coast would soon be washed out to sea or stranded on the upper shore. In the quieter waters of many Texas bays, however, extensive communities of unattached or loosely attached seaweeds often develop. Edwards and Kapraum (1973) observed floating macroalgal communities in Redfish Bay made up of species such as Gracilaria verrucosa, Digenia simplex, and Chondria cnicophylla. They noted that these alga mats were often attached to small shells, but since the substratum had a low specific gravity, they were easily moved. Hildebrand and King (1978) recorded a drift macroalgal community in the upper Laguna Madre made up chiefly of the red algae Gracilaria blodgetti, Gracilaria foliifera, and Laurencia poitei. Another drift community that often enters Texas estuaries from the Gulf of Mexico is associated with floating Sargassum sp. These Sargassum communities are most often observed in the summer near the oceanic inlets to the estuaries.

The phytoplankton are an important source of carbon in the estuarine ecosystem and are the major primary producers of the open-bays. Despite the apparent abundance of nutrients in estuaries, however, these primary producer communities do not have such a dominant role as, for example, phytoplankton in oceanic environments or freshwater lakes, because other factors besides nutrients (e.g., light penetration) may limit the production of estuarine phytoplankton. The carbon production of open-bay phytoplankton provide one means of comparing the dynamics between various estuarine systems. Oppenheimer et al. (1975) summarized the information on primary production for Galveston, San Antonio, and Corpus Christi Bay Estuaries, measured by the oxygen method, and found values of 5.87, 1.0, and 2.52 g C/m^2 for gross phytoplankton production in these three estuaries. Odum et al. (1974) measured gross phytoplankton production by the oxygen method in the upper, middle, and lower Laguna Madre. His values, converted to carbon production (Oppenheimer et al. 1975), indicated that the upper Laguna was characterized by production of 2.75 g C/m^2/day, the middle Laguna by 0.37 g C/m^2/day, and the lower Laguna by 1.79 g C/m^2/day. In general, these studies overestimated carbon production by phytoplankton because of their use of the oxygen method for measurement.

A more recent 2-yr investigation of primary production rates in Nueces and Corpus Christi Bays, using the carbon-14 method of measurement (Flint, 1984) and converting the mean estimates to gross production (Riley and Chester 1971: p. 235) in order to compare to other study results yielded the following carbon production rates. From 17 measurements over the 2-yr study, it was estimated that gross primary production in Nueces Bay was 0.52 g C/m^2/day. In Corpus Christi Bay, where a total of 45 measurements were made over the same period, a mean gross production rate of 0.91 g C/m^2/day was estimated.

Table 6 summarizes the major characteristics of phytoplankton in the open-bay bottoms of Texas estuaries. With the exception of San Antonio Bay, diatoms dominate the community assemblages throughout the year. In most systems the

peak diatom abundances occur in the winter and early spring, which corresponds with the overall peak abundances for total phytoplankton in those systems for which we have data (Table 6). Minimum abundances in these estuaries appear to be much more varied, but occur primarily in the summer and fall. The minimum in total phytoplankton counts usually corresponded with peaks in dinoflagellate or green algal populations in the estuaries studied. As far as the diatom populations are concerned in Texas estuaries, Cyclotella appeared to be frequent in the eastern estuaries that normally receive more freshwater, while Thalassionema, Chaetoceros, and Thalassiothrix were more common in the southern, more saline estuaries. Blue-green algae appeared to dominate only the assemblages in the upper reaches of the Galveston Bay Estuary (Trinity Bay) and in Nueces Bay, again associated with less saline waters.

According to Table 6, plankton primary production of carbon is highest in Galveston Bay, decreases along the Texas coast, and increases again in the upper Laguna Madre. Another means of assessing plankton production potential is to examine chlorophyll a concentrations. For open-bay bottoms, Zein-Eldin (1961) indicated that Texas estuaries generally yield between 43 and 200 mg chlorophyll a/m^2,

Table 6. Summary of the major characteristics of phytoplankton assemblages in the open-bay bottom biotopes of Texas estuaries.

Estuary	Seasonal phytoplankton abundance (cells/ml)[a] Minimum	Maximum	Dominant groups (by % of)	Primary production estimate (g C/m^2/day)[b]
Sabine Lake	70 (W)	200 (S)	Diatoms (45%) Green algae (36%)	ND
Galveston Bay (Trinity Bay)	50 (F)	400 (W-Sp)	Diatoms (41%) Green algae (25%) Blue-green algae (23%)	5.87
Lavaca Bay	150 (S)	4,500 (W)	Diatoms	
San Antonio Bay	549 (F)	19,000 (W)	Dinoflagellates	1.0
Aransas Bay	6 (S)	381 (W)	Diatoms	
Corpus Christi Bay	50 (S-F)	900 (W-Sp)	Diatoms Blue-green algae	2.52 (0.91)[c]
Nueces Bay	7 (S-F)	300 (W-Sp)	Diatoms Blue-green algae	0.52
Oso Bay and Upper Laguna Madre	ND (S)	1,600 (W)	Diatoms	2.75
Lower Laguna Madre	ND	ND	Diatoms	1.79

[a]Seasons are: S = summer, F = fall, W = winter, Sp = spring.
[b]Carbon fixation based on oxygen method of measurement.
[c]Carbon fixation based upon ^{14}C method of measurement and converted to gross production.

while in one study Galveston Bay waters yielded 370 mg chlorophyll a/m^2. This certainly fits the pattern suggested by Table 6 for higher carbon production by phytoplankton in the more eastern of the Texas estuaries.

3.3 OPEN-BAY BOTTOM ZOOPLANKTON

In general, the zooplankton of estuaries are limited by two features. The first is turbidity, which can limit phytoplankton production and thus limit the food available for zooplankton; and the second is currents, which can carry zooplankton both out to sea and away from concentrated food masses that otherwise were within close swimming distance. Within the zooplankton one can recognize two groups: the holoplankton, which are true permanent zooplankton (e.g., copepods, cladocerans, chaetognaths), and the meroplankton, which are animals whose earliest life stages are planktonic and thus are temporary members of the zooplankton community (e.g., larval stages of fish, crabs, shrimp, etc.).

Zooplankton communities in estuaries can serve as valuable indicators of processes going on in the estuarine complex. They appear to be quite sensitive to changes in the estuary, especially changes in salinity. Freshwater inflow influences zooplankton in several ways. It can carry in freshwater species and transport food into the estuary (thus enhancing the production of estuarine assemblages). On the other hand, sudden increases in inflow rates can flush resident populations out of the estuary, decreasing standing stocks. Perkins (1974) reports that the primary factor affecting the composition and abundance of estuarine zooplankton communities is development rate versus flushing time.

Peak abundances in zooplankton species assemblages in Sabine Lake during 1974 and 1975 (Espey, Huston and Associates 1976) occurred in the summer and early fall (15-20 x 10^3 organisms/m^3), when salinities were observed to be at their highest. Acartia tonsa was recorded as the dominant zooplankton species (85% of total) in this estuary and, along with several other marine copepods, was found in greatest numbers at the lowest reaches of the estuary. In contrast, rotifers and cladocerans characterized as "freshwater forms" were found closer to the mouth of the river. Minimum mean abundances for zooplankton in this estuary were 0.4 x 10^3 organisms/m^3 recorded in the winter and spring.

The dominant organisms found during a study in Trinity Bay in 1975-76 (Texas Department of Water Resources 1981) were the barnacle nauplii and calanoid copepod Acartia tonsa. These organisms contributed more than 70% to the total observed standing crop of zooplankton. Freshwater zooplankton assemblages included such organisms as the cyclopoid copepods (Cyclops sp.) and rotifers (Asplancha and Brachionus sp.). Besides Acartia tonsa estuarine and marine forms included the copepods Oithona sp., Labidocera aestiva, and the protozoan dinoflagellate Noctiluca scintillans. Peaks in standing crop abundances occurred in April and late summer with mean densities of 190 x 10^3 organisms/m^3 and 16 x 10^3 organisms/m^3, respectively. The April peak was almost exclusively composed of Noctiluca, while the August peak was composed of species similar to those observed in the Sabine Lake summer-fall peaks. Minimum mean abundances of 1.2 x 10^3 organisms/m^3 were observed in the winter. According to Holt and Strawn (1983), two major seasons were distinguishable for the zooplankton assemblages of Trinity Bay. A warm season dominated by crustacean larvae and copepods when temperatures were above 22 °C was identified using numerical classification, while a cool season was found dominated by larval fish. Besides the holoplankton, these investigators found that larval and juvenile crustaceans such as Palaemonetes zoeae, brachyuran zoeae, Callinectes megalops, Penaeus setiferus zoeae, and Petrolisthes armatus zoeae dominated the warm-season catch. Larvae of fishes such as Brevoortia patronus, Leiostomus xanthurus, Micropogonias undulatus, and Myrophis punctatus dominated the cool-season catch. Kalke (1972) concluded from studies in Trinity Bay that low salinities and temperatures of late fall and winter produce a favorable environment for fish larvae, while the higher

salinities and temperatures through the late spring and summer are ideal conditions for larval crustaceans.

In direct contrast to the two estuaries discussed above, Gilmore et al. (1974) found that minimum mean abundance for zooplankton communities in the Lavaca Bay Estuary (1.9 x 10^3 organisms/m^3) in the fall and maximum mean abundances occurred in the spring (28 x 10^3 organisms/m^3). Barnacle nauplii and Acartia tonsa were the two dominant forms of zooplankton, comprising over 75% of the community during the entire study. The barnacles, presumed to be larvae from Balanus eburneus, predominated in samples from late winter and spring, while Acartia tonsa was dominant in late summer and early fall. Standing crops in the bay were always greater than river-influenced stations. The rotifer Brachionus quadridentata and the copepod Diaptomus sp. were often found associated with these river-influenced stations. According to Moseley et al. (1975) in a study of Cox Bay, a component of the Lavaca Bay system, Acartia tonsa was the dominant zooplankter, but its peak abundances occurred in the spring rather than the fall as in Lavaca Bay proper.

The copepod Acartia tonsa was also the dominant zooplankter of San Antonio Bay (Matthews et al. 1974). Many of the zooplankton found in this estuary, however, were freshwater forms. Matthews et al. (1974) concluded that the relatively large amount of freshwater inflow coupled with restricted access to the Gulf of Mexico had substantially influenced the zooplankton assemblages. Besides Acartia tonsa, Balanus eburneus larvae were also quite abundant during the 12-mo study. The results of all collections indicated that peaks in standing crop (46 x 10^3 organisms/m^3) occurred in January, associated with higher salinities, while minimum mean abundances (0.8 x 10^3 organisms/m^3) were observed in June when salinities were low.

Over a 3-yr study of Copano and Aransas Bays, Holland et al. (1975) found that minimum mean zooplankton abundances generally occurred in the fall, while maximum mean abundances were observed in the winter and spring. Acartia tonsa was determined to be the dominant species. Cyclopoid copepod (Oithona sp.) appeared to peak during the warmer months of in these estuaries.

The dominant zooplankton in the Corpus Christi Bay and Nueces Bay Estuaries over a 3-yr study period was Acartia tonsa and barnacle nauplii (Holland et al. (1975). These organisms dominated in every season except late winter and early spring where the dinoflagellate Noctiluca scintillans was most abundant. Holland speculated that this organism was brought into the estuaries by inclusions of cool Gulf of Mexico water during this period. Peaks in mean abundance for each bay were observed in late winter and early spring of each year; an average of 2,139 x 10^3 organisms/m^3 were recorded for Nueces Bay and an average of 11,705 x 10^3 organisms/m^3 were observed in Corpus Christi Bay. Minimum abundances usually occurred in the fall. Average abundance estimates for Nueces Bay during this period were 3.3 x 10^3 organisms/m^3, and for Corpus Christi Bay estimates were 5.2 x 10^3 organisms/m^3. Freshwater zooplankton observed in the upper reaches of the estuary during this study included Cyclops sp. and Daphnia sp. More typically marine species observed were Centropages hamatus, Labidocera aestive and Noctiluca scintillans. Holland et al. (1975) concluded that temperature and salinity were the two most important factors regulating species composition, seasonal occurrence, and geographic distribution of zooplankton populations in the Corpus Christi Bay and Nueces Bay open-bay bottoms.

In Oso Bay and the upper Laguna Madre, a 6-yr study (Hildebrand and King, 1978) revealed that the calanoid copepods, especially Acartia tonsa, were the dominant holoplankton. Other major genera of calanoid copepods included Pseudodiaptomus and Centropages. In general, peak abundances for these as well as the entire zooplankton assemblage occurred in the spring of each study year. The meroplankton, dominated by trocophor larvae, bivalve larvae, gastropod veligers, and barnacle nauplii, contributed heavily to the spring peaks each year. The polychaetous annelids were also counted as meroplankton and made a major contribution to one species diversity of the collections.

Although salinities are often much higher in the lower Laguna Madre, Hedgpeth (1967) noted that Acartia tonsa was still the dominant species in these waters. Another copepod, Metis japonica, was also observed in the lower Laguna Madre, but not in as great numbers as Acartia tonsa. Hedgpeth observed that the occurrence of Acartia tonsa in salinities exceeding 80 ppt was interesting in light of its distribution as a bay and coastal water species as far north as Cape Cod. He concluded that this zooplankton species has a wider salinity range than most other fauna and certainly a wider range than reported previously.

The ecological niches for zooplankton in the open-bay bottoms of estuaries are such that optimal conditions for growth and survival occur at different times of the year for different species. Optimal conditions for a given species result in high abundances for that species as long as favorable conditions persist. If conditions are favorable for more than one species at the same time, usually the more competitive species will be found in greatest abundance. Because the zooplankton can vary in abundance and species composition both seasonally and from year to year, reliable conclusions concerning these open-bay bottoms assemblages can be drawn only on the basis of long-term investigations. Studies on open-bay bottom habitats in Texas have yet provided the long-term data needed to adequately assess zooplankton dynamics.

Enough information has been collected on the open-bay bottoms of Texas estuaries, to detect some interesting patterns in the zooplankton communities. In several of the Texas estuaries it has been observed that the zooplankton standing crops are inversely related to water temperature and directly related to salinity. Gilmore et al. (1974) noted this for Lavaca Bay, Matthews et al. (1974) observed the pattern for San Antonio Bay, and as already mentioned above, Holland et al. (1975) found the same trend for Corpus Christi and Nueces Bays. In contrast, however, the more eastern estuaries, Galveston Bay and Sabine Lake, exhibited opposite trends.

Another common trend among many of the studies reported for Texas estuaries has been the relationship observed between large abundances for the zooplankton communities occurring simultaneously with decreases in phytoplankton counts. Matthews et al. (1974) observed that peak zooplankton abundances occurred in the spring when phytoplankton densities were depressed. The tremendous depletion of phytoplankton in Corpus Christi Bay and Aransas Bay each spring observed by Holland et al. (1975) was correlated with peak abundances in zooplankton species, especially the protozoan dinoflagellate Noctiluca scintillans. Extending this pattern one more trophic level, Gilmore et al. (1974) in Lavaca Bay observed that peak abundances of copepods and barnacle larvae in the zooplankton occurred in the spring at approximately the same time as larval and juvenile fish, potential predators of these smaller forms.

A number of the studies of Texas estuarine zooplankton assemblages, besides identifying Acartia tonsa as the dominant species, indicated that in the spring the protozoan dinoflagellate Noctiluca scintillans is often the dominant zooplankton species. This species taxonomically belongs to a borderline group of biota that contains both plants and animals. It is often identified and associated with phytoplankton communities rather than zooplankton. Noctiluca are voracious feeders, however, engulfing particulate food such as diatoms and other small material (Sverdrup et al. 1964) and should be classified as a member of zooplankton community. This species reproduces by binary fission, which enables it to produce masses of individuals when conditions are favorable. This is the primary reason why this organism becomes dominant in the estuarine zooplankton during the spring, taking advantage of and drastically depressing phytoplankton densities.

Table 7 summarizes the major trends for zooplankton in the open-bay bottoms of Texas estuaries for which information exists. In general, the southern estuaries appear to support larger numbers of organisms than the more eastern water bodies. With the exception of these eastern estuaries, the most abundant periods for zooplankton appear to be in the winter

and spring, while the minima usually occur in the summer and early fall. The reverse is true for Sabine Lake and Galveston Bay, which may be related to the greater freshwater influence on these estuaries. This is evidenced in study results showing greater abundances of freshwater species.

3.4 OPEN-BAY BOTTOM BENTHOS

The bottom sediments of estuaries develop communities of invertebrate animals that live on and in these sediments. Included in these fauna, referred to as the benthos, are annelid worms, clams and other mollusks, and many kinds of crabs and smaller crustaceans. The majority of these animals obtain their foods from the waters above and from each other. The flat expanse of submerged mud and sand, with their associated biota, are some of the most important components of the open-bay communities because of the large amounts of food resources and nutrients they contribute. In addition, since many benthic organisms are of limited mobility or even completely sedentary, standing stock and diversity fluctuations have often been investigated in order to demonstrate habitat changes that may upset ecological balances. Benthic biota provide a good record of recently past happenings in an estuarine system.

The proportion of polychaete annelids appears greatest at the Gulf of Mexico-influenced study sites in Sabine Lake

Table 7. Summary of the major patterns for zooplankton assemblages in the open-bay bottom biotopes of Texas estuaries.

Estuary	Mean seasonal zooplankton abundance (10^3 animals/m^3) Minimum	Maximum	Dominant fauna
Sabine Lake	0.4 (W-Sp)[a]	17.2 (S-F)	ND
Galveston Bay (Trinity Bay)	1.2 (W)	16.0 (F) 190.0 (Sp)[b]	Barnacle nauplii *Acartia tonsa* *Noctiluca scintillans*
Lavaca Bay	1.9 (F)	27.9 (Sp)	Barnacle nauplii *Acartia tonsa*
San Antonio Bay	0.8 (S)	46.0 (W)	*Acartia tonsa*
Copano Bay	1.3 (F)	53.6 (W)	*Acartia tonsa*
Aransas Bay	2.5 (F)	653.5 (W)	*Acartia tonsa*
Corpus Christi Bay	5.2 (F)	11,705.0 (W-Sp)	*Acartia tonsa* Barnacle nauplii *Noctiluca scintillans*
Nueces Bay	3.3 (F)	2,139.0 (W)	*Acartia tonsa* Barnacle nauplii
Upper Laguna Madre	ND	ND (Sp)	*Acartia tonsa*

[a]Seasons are: S = summer, F = fall, W = winter, Sp = spring.
[b]Peak abundance for spring was comprised almost entirely of *Noctiluca scintillans* bloom. Otherwise peak abundances follow those for Sabine Lake, in the fall.

(Espey, Huston and Associates, 1976). Closer to the Sabine River and more freshwater influence, the polychaetes dominated only during the fall, while the mollusks were most abundant during the remainder of the year. The bivalve mollusk Rangia cuneata along with an unidentified capitellid polychaete were the most abundant fauna observed over the 12-mo study. Armstrong (1982) calculated that the mean observed abundance for Sabine Lake benthos was 310 organisms/m^2.

A general survey of lower Galveston Bay by Holland et al. (1973) indicated that four benthic species were ubiquitous at all sites studied. These included the polychaetes Nereis succinea, Streblospio benedicti, and Mediomastus californiensis, and the barnacle Balanus eburneus. Another set of species observed at most study sites included the polychaete Diopatra cuprea and the mollusk Mulinia lateralis. Williams' (1972) list of dominant benthic fauna for Trinity Bay included Mediomastus and Streblospio, but also indicated that Rangia cuneata and the oligochaete Peloscolos abriellae were abundant in these less saline waters of the estuary. According to a report from the Texas Department of Water Resources (1981b), polychaetes dominated benthic collections from Trinity Bay, comprising 74% of all fauna observed. Mollusks accounted for another 15% of the organisms collected from this estuary. An unidentified capitellid polychaete and Mediomastus californiensis were the dominant biota observed throughout the bay during the study period. Amnicola sp. of freshwater gastropods were dominant at river-influenced stations during the spring. Although there was considerable variation in total benthos abundance at all collection sites over the study duration, in general, the benthos appeared to peak in the late winter and spring around an average of 1,200 organisms/m^2. Minimum abundances occurred in the early summer and fall around 400 organisms/m^2.

Mackin (1971) studied the effect of oil-field brine effluents on benthic organisms in Lavaca Bay. During these studies, Streblospio benedicti, Mulinia lateralis, the amphipod Corophium acherusicum, and the oligochaetes Limnodrilus sp. were dominant in the river-influenced area. In the bay, Mulinia lateralis, Mediomastus californiensis, the cumacean Retusa canaliculata and the polychaete Glycinde solitaria dominated collections. Gilmore et al. (1974) observed that benthic species diversity generally decreased from the lower reaches of the Lavaca Bay Estuary to the higher, more river-influenced areas. They noted that diversities were greatest in the spring when freshwater inflows were low. The mollusks Rangia cuneata and Littoridina sphinctostoma and chironomid larvae dominated at river-influenced collection sites, while Mediomastus californiensis and Mulinia lateralis were most abundant at the middle bay sites. Maximum abundances of benthos were observed in the spring at a mean of 300 organisms/m^2, while minimum abundances were recorded in the fall at approximately 100 organisms/m^2. In Cox Bay, a component of the Lavaca Bay Estuary, Moseley et al. (1975) noted that mollusks and polychaetes comprised 95% of the benthic biota. The species found in Lavaca Bay were also abundant here, along with the polychaete Paraprionospio pinnata and the bivalve mollusk Macoma mitchelli.

The only reported study of benthic meiofauna (those small biota of the benthos that will pass through a 0.62-mm mesh screen) for Texas estuaries was conducted in San Antonio Bay (Rogers 1976). The meiofauna component of the benthos in this estuary consisted of nematodes, ostracods, copepods, kinorhynchs, polychaetes, gastropods, pelecypods, and pycnogonids. The nematodes were consistently the most dominant, representing 83% of the total. Ostracods and copepods each accounted for another 5%. Total meiofaunal abundance was observed to be low in the spring (Rogers 1976) and to increase through the summer and fall to winter maximums. Rogers concluded that this trend was due to predatory pressure from the macrofaunal benthos since dominant meiofaunal populations normally spawn throughout the year. He also noted that sediment structure appeared to be the primary factor influencing geographical distribution of meiofauna, with higher silt fractions usually supporting greater abundances.

Peak abundances of benthic macrofauna in San Antonio Bay were observed by Matthews et al. (1974) to begin in the spring

(mean of 450 organisms/m^2) and continue into early summer. Minimum mean benthic abundances were recorded at approximately 60 organisms/m^2 in the fall months. Molluscan gastropods and bivalves dominated faunal assemblages in the river-influenced upper bay area while the polychaetes again were most abundant in the more saline middle bay area. Littoridina sphinctostoma and Rangia cuneata were again the dominant bivalves of the less saline areas while Mediomastus californiensis, Streblospio benedicti and Mulinia lateralis dominated at higher salinity collection sites. Matthews et al. (1974) observed that although the smallest number of species were taken from the river-influenced regions of the bay, this area usually supported the largest benthic abundances. Harper and Hopkins (1976) also noted that peak abundances occurred in areas of lower salinity and recorded the same dominant species as observed by Matthews et al. (1974). They further observed that Mulinia lateralis normally exhibited peak population abundances in the winter and early spring. Harper and Hopkins (1976) attributed the increased benthic abundances in the river-influenced areas to the increased inflow of freshwater-associated nutrients, since according to the investigators, benthic organisms like Rangia cuneata and Littoridina sphinctostoma are known to spawn in response to increased nutrients and rapid decreases in salinity.

Holland et al. (1975) recorded peak benthic faunal abundance for Aransas Bay in late winter and spring of each year during a 3-yr study. Mean peak abundances for this period were approximately 2,500 organisms/m^2. Minimum mean abundances of approximately 800 organisms/m^2 occurred in the fall of each study year. Mediomastus californiensis and Streblospio benedicti were the most abundant and also the most ubiquitous biota observed. Calnan et al. (1983) indicated that the dominant polychaete in this bay was Paraprionospio pinnata, and the dominant crustacean was the amphipod Ampelisca verrilli. This study was of extremely limited duration. These investigators further observed that the open-bay bottom supported the lowest abundance of biota of all habitats investigated in Aransas Bay.

Calnan et al. (1983) found characteristic benthic species of Copano Bay to be the polychaetes Glycinde solitaria and Paraprionospio pinnata, the mollusks Macoma mitchelli and Mulinia lateralis, and crustacean Lepidactylus sp. Holland et al. (1975) observed peak benthic abundances to occur in Copano Bay during late winter to spring over a 3-yr study with mean abundance equalling 500 organisms/m^2. Minimum benthic mean abundances consistently occurred in the fall at 180 organisms/m^2. Those polychaetes that dominated in Holland's Aransas Bay samples were most abundant here also.

The Corpus Christi Bay system, including Nueces Bay, has probably been the most heavily studied of Texas estuaries with respect to benthic populations of the open-bay bottom. Holland et al. (1975) took monthly bottom samples at a total of 20 collection sites within these two bays between the fall of 1972 and spring of 1975. Of the 331 species collected during the study, polychaetes were the most abundant group. Dominant in this group were Mediomastus californiensis, Streblospio benedicti, Paraprionospio pinnata, Cossura delta, and Glycinde solitaria. Dominant mollusks, the second most abundant group observed in these estuaries, included Mulinia lateralis, Lyonsia hyalina flordidana, and Macoma mitchelli. Benthic faunal abundances peaked in the winter of each study year in Corpus Christi Bay, exhibiting mean abundances of 5,000 organisms/m^2. Minimum abundances usually occurred in late summer and fall around 1,750 organisms/m^2. In Nueces Bay these trends were similar, except that during some study years there appeared to be a secondary peak in benthic abundance in midsummer. The spring peak mean abundances in Nueces Bay were much greater than in Corpus Christi Bay, averaging approximately 15,000 organisms/m^2, while minimum abundances occurring in the fall averaged 1,200 organisms/m^2. While Mediomastus californiensis and Streblospio benedicti were consistently the dominant fauna in Corpus Christi Bay, Holland et al. (1975) observed that Mulinia lateralis, a bivalve mollusk, dominated earlier collections of the study in Nueces Bay. The amphipod Corophium acherusicum also dominated samples during one collection in Nueces Bay. Species diversity in these

two bays was observed to peak in the spring of each year; Corpus Christi Bay was consistently higher in species diversity than Nueces Bay. In contrast to most other Texas estuaries, Jinnette (1976) reported that mollusks rather than polychaetes were the dominant fauna for Nueces Bay. He indicated that 78% of the total benthic abundance over his study was comprised of mollusks, while only 19% were polychaetes. Mulinia lateralis was the dominant mollusk, while Mediomastus californiensis, Paraprionospio pinnata, and Glycinde solitaria were some of the dominant polychaetes. Jinnette (1976) and Murray and Jinnette (1976) indicated that peak Nueces Bay benthic abundances occurred in the winter and early spring and were usually influenced by large populations of Mulinia lateralis. In contrast, they noted that Mulinia lateralis was absent from collections in the fall, which often exhibited maximum abundances of Nemerteans.

The most intensive study of benthic invertebrate populations along the Texas coast was that reported by Flint and Younk (1983) for a single area of Corpus Christi Bay that included a shoal habitat and a channel habitat of the open-bay bottom. This study, plus continued sampling to the present, covered the period of 1974-1983 and included monthly collections at the sampling sites from 1974-1979. A total of 313 taxa representing 13 phyla was collected during this study of benthic macroinvertebrates in Corpus Christi Bay. The polychaetes were the most abundant group (60% of total); Mediomastus californiensis, with a mean abundance of 1,443/m^2, and Streblospio benedicti, with a mean abundance of 238/m^2, often predominated over all other species in the grab samples. Several pelecypod mollusks also occasionally predominated in grab samples, especially on a seasonal basis. These included Mulinia lateralis (417/m^2), Lyonsia hyalina floridana (607/m^2), and Abra aequalis (2,210/m^2).

Total benthic abundance was generally quite variable over the study period. Peak abundances averaged 1,700 organisms/m^2 while minimums went almost down to 350 organisms/m^2. Significant differences were observed between the shoal and channel sites, with the shoal sites showing higher abundances. Obvious peaks, especially for the shoal sites, occurred in the winters of 1975, 1977, and 1979. These winter peaks were always associated with increased abundances of mollusks, such as Mulinia lateralis and Abra aequalis that regularly occurred in winter.

Although this study focused on a relatively small area of the Corpus Christi open-bay bottom, the habitat studied (shoal and channel) showed results comparable to a previous study of similar habitats (Holland et al. 1975). In the earlier study, a central Bay station where environmental conditions were similar to the shoal stations of the 1974-1983 study exhibited faunal abundances between 1,767 and 8,600 organisms/m^2 with an annual mean species diversity of 3.61. In contrast, shoal stations sampled by Flint and Younk (1983) exhibited mean abundances between 2,000 and 18,900 organisms/m^2 with a mean species diversity of 3.76. Another station from the earlier study (1972-1975) was similar in depth and ship traffic activity to the 1974-1983 channel stations. This station exhibited benthic community abundances between 867 and 8,580 organisms/m^2 with an annual mean species diversity of 1.84. In the Flint and Younk (1983) study, the channel stations exhibited abundances between 390 and 6,450 organisms/m^2 and a mean diversity of 2.96.

Hildebrand and King (1978) studied the Oso Bay benthos for a 6-yr period and as with other studies noted that the polychaetes were the most abundant fauna. They observed that Streblospio benedicti was the most abundant polychaete, followed by Arenicola cristata, Capitella capitata, Mediomastus californiensis, and Heteromastus filliformis. Polychaetes appeared to reach maximum abundances in the winter and minimums during the summer. The most abundant crustacean observed in Oso Bay was the amphipod Ampelisca abdita; Mulinia lateralis was the dominant mollusk.

In the Upper Laguna Madre, Hildebrand and King (1978) observed the greatest number of benthic species and total macroinfaunal abundances in the winter and early spring. The polychaetes were the most varied and abundant group, followed

by the mollusks. Mediomastus californiensis and Streblospio benedicti were the dominant polychaetes while Mulinia lateralis was the dominant mollusk in the open-bay bottom. Parker (1959) found that a distinct physiographic and biologic environment existed in the Laguna Madre due to the high salinities, high summer water temperatures, and minimal water exchange with either Corpus Christi Bay or the Gulf of Mexico. Consequently, he and others (e.g., Hedgpeth 1967) have reported that invertebrate populations of the benthic sediments differ from the brackish-water organism-dominated assemblages found in less saline estuaries. Simmons (1957) observed that Penaeus aztecus was the only penaed shrimp able to withstand salinities above 45 ppt. He further observed that amphipods were extremely numerous in higher salinities but that only four bivalve mollusks occurred, with Anomalocardia cuneimeris most abundant. Although observations on polychaetes in the Lower Laguna Madre have not been reported, the dominant mollusks of this hypersaline environment appear to be Mulinia lateralis and Tellina tampaensis.

A summary of benthic faunal data for the open-bay bottoms along the Texas coast is presented in Table 8. Two trends are evident from this summary. First, the observed abundances generally seem to increase as one moves along the coast from the more freshwater-influenced eastern estuaries to the more saline southern estuaries. Second, in all the estuaries where there are data available, peak benthic abundances occur in the winter and spring with minimum abundances usually occurring in the late sumer and fall. An examination of the dominant species observed for each estuary (Table 8) indicates that the more freshwater-influenced systems support fauna that are often characteristic of less saline waters, such as Rangia cuneata and Littoridina sphinctostoma, as well as many oligochaetes. These species disappear from the dominant lists in the more saline southern estuaries along the coast. For the majority of Texas estuaries where benthic data exist, the polychaetes usually dominate the species assemblages, while Mediomastus californiensis and Streblospio benedicti are normally the most abundant populations found. Paraprionospio pinnata, one of the most dominant polychaetes of Corpus Christi Bay, is indicative of the higher salinity in this estuary, since this species is normally observed as a member of coastal-shelf benthic communities.

3.5 OPEN-BAY BOTTOM NEKTON

Nekton is a collective term for all organisms which swim in the water column and which can move in any direction, rather than a direction governed by the currents. The nekton of the open-bay bottoms include the epibenthic crustaceans that live on the sediments and in the water overlying the sediments, large jellyfish, and the numerous fish species that live throughout the water column. The nekton encompass the majority of secondary-consumer biomass that inhabits estuaries. These organisms derive most of their nutrition either from the biotic components of the open-bay bottom already discussed or from juveniles and smaller fauna of the nekton themselves. The nekton serve as the primary link between man and the open-bay bottom since many of the species comprising this component are of commercial or recreational importance. One characteristic of the estuarine nekton is that many of the species included in the group are not permanent residents, but rather spend only part of their life cycles in the estuary. Because migrations and spawning cycles can affect the diversity of the nekton at any time during the year, knowledge of the life-history patterns of these fauna is important in assessing the overall trends of the nekton in estuaries.

In a summary of trawl surveys of East Bay, a part of Galveston Bay, Reid (1957) found that Micropogonias undulatus and Anchoa mitchilli (bay anchovy) were the dominant nekton (33.7% and 31.0%) of the total fishes, respectively, during summer. Chambers and Sparks (1959) recorded Dorosoma cepedianum, Micropogonias undulatus, Penaeus setiferus, Brevoortia patronus, and Leiostomus xanthurus as the five dominant nekton species during an ecological survey of the Houston Ship Channel in Galveston Bay over a 10-mo period. Parker (1965), in a general survey of all Galveston Bay, found that eight estuarine-dependent species comprised over 80% of the total nekton collected. These, in order of

Table 8. Summary of the major characteristics of benthic invertebrate assemblages in the open-bay bottom biotopes of Texas estuaries.

Estuary	Mean seasonal benthic abundance (10^2 organisms/m^2) Minimum	Maximum	Dominant fauna
Sabine Lake	3.1[a]		*Rangia cuneata*
Galveston Bay (Trinity Bay)	4.0 (S)[b]	12.0 (W-Sp)	*Streblospio benedicti* *Mediomastus californiensis* *Balanus eburneus* *Mulinia lateralis* *Rangia cuneata*
Lavaca Bay	1.0 (F)	3.0 (Sp)	*Rangia cuneata* *Littoridina sphinctostoma* *Mediomastus californiensis* *Mulinia lateralis*
San Antonio Bay	0.6 (F)	4.5 (Sp)	*Littoridina sphinctostoma* *Rangia cuneata* *Mediomastus californiensis* *Streblospio benedicti* *Mulinia lateralis*
Aransas Bay	8.0 (F)	25.0 (W-Sp)	*Mediomastus californiensis* *Streblospio benedicti*
Copano Bay	1.8 (F)	50.0 (W-Sp)	*Mediomastus californiensis* *Streblospio benedicti*
Corpus Christi Bay	17.5 (F) 3.5 (S)	50.0 (W)[c] 170.0 (W-Sp)[d]	*Mediomastus californiensis* *Streblospio benedicti* *Paraprionospio pinnata* *Glycinde solitaria* *Mulinia lateralis* *Lyonsia hyalina floridana*
Nueces Bay	12.0 (F)	150.0 (Sp)	*Mulinia lateralis* *Corophium acherusicum* *Mediomastus californiensis* *Streblospio benedicti*

[a]Single value.

[b]Seasons are: S - summer, F - fall, W - winter, Sp - spring.

[c]Estimates from Holland et al. (1975) for the entire bay.

[d]Estimates from Flint and Younk (1983) for a small component of the entire bay.

their abundance, are Micropogonias undulatus, Anchoa mitchilli, Penaeus aztecus, Penaeus setiferus, Leiostomus xanthurus, Cynoscion arenarius (sand seatrout), Callinectes sapidus, and Arius felis (hardhead catfish). Of the eight species, only the bay anchovy, Anchoa mitchilli, a forage species, was not of direct commercial importance. Micropogonais undulatus were most abundant in the spring of each sampling year. Peaks in this species' abundance were followed by maximum abundances for Penaeus aztecus (May) and lesser peak abundances for Leiostomus xanthurus (May-July) and Cynoscion arenarius (May-September). Penaeus setiferus exhibited peak abundances in Galveston Bay in summer and fall (July-November) as did Arius felis (July-September). Anchoa mitchilli exhibited two peak abundance periods: May-June and October-November. Callinectes sapidus was most abundant in the winter of each year. Bechtel and Copeland (1970), in a quarterly survey of nekton in Galveston Bay, observed that Micropogonias undulatus and Anchoa mitchilli were again the most dominant species throughout most of the year. The one exception was that Arius felis was observed to be dominant in the fall within many areas of Galveston Bay. Johnson (1973), besides recording the dominance of Micropogonias undulatus and Anchoa mitchilli, noted that Brevoortia patronus was extremely abundant in Trinity Bay, a part of the Galveston Bay system. He also observed that three permanent residents of the estuary, Cyprinodon variegatus, Mugil cephalus, and Menidia beryllina (tidewater silverside) were collected in large numbers. Galloway and Strawn (1974), in a 2-yr study of upper Galveston Bay, recorded Micropogonias undulatus as the dominant nekton species which, together with Anchoa mitchilli and Arius felis, comprised over 75% of the total nekton catch. Odum et al. (1974) reported that in a study of Clear Lake, an extension of Galveston Bay, Micropogonias undulatus was again the dominant nekton species, followed by the shrimp species Penaeus aztecus and Penaeus setiferus. According to Chapman (1964), Clear Lake was the prime habitat area of the Galveston Bay system for these shrimp, which comprised 44% of the total nekton catch compared to only 22% in Trinity Bay. In contrast, the five dominant fish from the nekton, Anchoa mitchilli, Micropogonias undulatus, Cynoscion arenarius, Brevoortia patronus, and Leiostomus xanthurus contributed 70% to total nekton abundance in Trinity Bay and only 50% in Clear Lake. Besides the shrimp and blue crab, Schmidt (1972) observed that three other species comprised the epibenthic crustacean contribution to nekton total abundance in Trinity Bay. These species included the grass shrimp Palaemonetes pugio and Palaemonetes vulgaris, and the mud crab Rhithropanopeus harrisii.

The most extensive survey of Galveston Bay fish species was reported by Sheridan (in preparation). He observed 96 species of fish among 364,815 individuals over a 24-mo study period. Six species that accounted for 91.3% of the total fish abundance were Micropogonias undulatus (51.2%), Anchoa mitchilli (22.3%), Stellifer lanceolatus (8.0%), Leiostomus xanthurus (4.1%), Cynoscion arenarius (3.3%), and Arius felis (2.4%). Micropogonias undulatus was the dominant species during 14 winter through summer months. Anchoa mitchilli was the dominant fish during eight fall and early winter months, and Stellifer lanceolatus (star drum) predominated in two late summer months during the total study period. Fish total abundance showed peaks in the spring (April and May) and minimums in the fall. Seven fishes, including the six most abundant species, comprised 73.8% of the total fish biomass observed in Galveston Bay during the 2-yr study period. Micropogonias undulatus was the dominant biomass contributor, comprising 36.5% of total biomass. Besides the other most abundant fish listed above, the stripped mullet, Mugil cephalus, was a dominant biomass contributor with 7.6% of total biomass of population. In general, during this study, Sheridan observed that fishes were most abundant in the upper reaches of the estuary and that most species were recorded in waters close to the oceanic influence of the Gulf of Mexico. Stellifer lanceolatus was the most abundant fish in the channel areas of the open-bay bottom, while in most other areas of this estuary, Micropogonias undulatus and Anchoa mitchilli usually dominated collections.

Moseley et al. (1975) conducted a multiyear study of the nekton in Cox Bay,

a part of Lavaca Bay. They observed that the highest mean biomass catch of nekton occurred during the late winter and spring months and concluded that this was probably a reflection of an influx of the young of such species as Micropogonias undulatus and Leiostomus xanthurus. They recorded a midsummer biomass peak, comprised primarily of Penaeus sp. Anchoa mitchilli, Arius felis, and Micropogonias undulatus were collected in most trawls during the study and did not appear to show a preference for salinity. These investigators observed, however, that the other dominant nekton, including Brevoortia patronus, Penaeus aztecus, Cynoscion arenarius, Penaeus setiferus, and Callinectes sapidus preferred lower-salinity waters. The bay squid, Lolliguncula brevis, was recorded in high numbers during the summer and fall in the open-bay bottom biotope of Cox Bay.

Harper and Hopkins (1976) noted that unlike other studies, nekton in San Antonio Bay reached maximum abundances in the fall with a winter decline and spring increase. Anchoa mitchilli, Micropogonias undulatus, Brevoortia patronus, and the sergestid shrimp Acetes americanus comprised 90% of the total nekton abundance for this estuary. Anchoa mitchilli, which was abundant during the entire study, accounted for 74% of this total. Micropogonias undulatus reached peak abundances in the spring, and Brevoortia patronus was most abundant in the winter. The shrimp, Acetes americanus, exhibited peak abundances in fall and early winter.

In a study of Aransas Bay from 1966-1973, Moore (1978) reported that 3,000-4,000 individuals of fish per hour were collected and between 24 and 28 species were observed each year. The six most dominant species observed were Micropogonias undulatus, Leiostomus xanthurus, Anchoa mitchilli, Arius felis, Lagodon rhomboides (pinfish), and Cynoscion arenarius. Moore (1978) calculated that the Shannon-Wiener species diversity index for fish of the open-bay areas of Aransas Bay ranged between 1.38 and 2.13 with an overall study mean of 1.80. He concluded from the patterns observed that climatological changes, especially temperature, exerted a major influence over the dynamics of the fish populations in Aransas Bay.

A study of nekton over a 53-mo period in Corpus Christi Bay (S. Ray, Texas A&M University, pers. comm.) indicated that most of the dominant species were those observed in other open-bay bottom areas of Texas. The 10 most abundant species collected during this study were Trachypenaeus similis (roughback shrimp), Stellifer lanceolatus, Anchoa mitchilli, Micropogonias undulatus, Leiostomus xanthurus, Penaeus aztecus, Callinectes similis, Cynoscion arenarius, Symphurus plagiusa (blackcheek tonguefish), and Callinectes sapidus. These species, along with Penaeus setiferus and Squilla empusa, were also the most frequently caught nekton during the study period. During the study, differences were noted between the nekton assemblages in the shallower shoal waters of the open-bay bottom and the channel areas. In general, the shoal areas exhibited much lower total abundances and smaller species diversity measures than the channel waters. Anchoa mitchilli was the most abundant species in the shoal collections. A creel census of the Corpus Christi Bay Estuary (Bowman et al. 1976) identified high abundances of several game fish in the open-bay bottoms that for one reason or another had not been collected in large numbers by trawl surveys. Included in this list were Cynoscion nebulosus, Sciaenops ocellatus, Pogonias cromis, Paralichthys lethostigma (southern flounder), Bagre marinus (gafftopsail catfish), and Lagodon rhomboides.

Murray and Jinnette (1974) conducted a nekton survey in the Nueces Bay Estuary and recorded five dominant species in their collections. These included Penaeus setiferus, whose populations peaked in summer and fall; Brevoortia patronus, with peak abundances in spring; Anchoa mitchilli, occurring all year round; Leiostomus xanthurus, with peak abundances in spring and winter; and Micropogonias undulatus, whose populations exhibited a late winter and spring peak.

Hildebrand and King (1978) reported on the nekton observed in a 6-yr study of Oso Bay and the upper Laguna Madre. In Oso Bay, either according to abundance or biomass contribution to total catch, they noted the following species as important: Anchoa mitchilli, Callinectes sapidus, Penaeus aztecus, Mugil cephalus, Micropo-

gonias undulatus, Penaeus setiferus, Menidia beryllina, Brevoortia patronus, and Leiostomus xanthurus. In the Laguna Madre, their collections revealed that according to the same criteria the following were the most important nekton species: Lagodon rhomboides, Anchoa mitchilli, Callinectes sapidus, Penaeus aztecus, Opsanus beta, Leiostomus xanthurus, Mugil cephalus, Neopanope texana, Menidia beryllina, and Micropogonias undulatus. Hedgpeth (1967) indicated that the above species were generally found throughout the Laguna Madre along with the important commercial and recreational species Sciaenops ocellatus, Pogonias cromis, and Cynoscion nebulosus.

From the above comparisons of dominant species recorded from various nekton studies in estuaries along the Texas coast, it appears that there is great similarity among the nekton assemblages that inhabit these Texas open-bay bottoms, irrespective of the differences in salinity regimes. The dominant species of Texas estuaries appear to be able to tolerate quite a wide range of salinity. One species, however, which was not reported as dominant from any of the studies summarized above, was the sheepshead, Archosargus probatocephalus. From numerous underwater observations in the Corpus Christi Bay Estuary (W. Flint, unpublished data), this species is known to exist in large numbers in the open-bay bottom. Because of its large size, the sheepshead probably makes a considerable contribution to total nekton biomass in estuaries it inhabits.

In general, the reports summarized above indicate that the seasonal pattern of variation of nekton populations in Texas estuaries is such that fall populations are usually the smallest in both number and biomass. For the nonpermanent species that spawn in the Gulf of Mexico, this is the period when most adults are absent from the open-bay bottom area. The newly spawned fish and shellfish begin migrating into the estuaries through the winter and early spring, and the numbers and biomasses of these populations correspondingly increase to a maximum in the spring. Although mortality is usually high for the juveniles, growth is so rapid that for the majority of nekton species maximum biomasses are observed during summer months.

The similarity of dominant nekton species that inhabit the open-bay bottoms of Texas estuaries is evident from the information presented in Table 9. This information is a summary of preliminary data collected from a 12-mo trawling survey of all Texas estuaries by the Texas Parks and Wildlife Department (R.L. Benefield, Texas Parks and Wildlife Department, Austin; pers. comm.). A total of 161 taxa were collected during this survey from all estuaries along the Texas coast in 1982. For comparison, Parker (1965) reported 151 taxa collected in a trawling survey of Galveston Bay alone. Table 9 lists the dominant nekton organisms, as suggested by all the reports summarized above, and shows the Texas estuaries where these fauna were collected in the 1982 survey. It is obvious that most of the dominant fauna that probably play a major role in the general dynamics of the open-bay bottoms of Texas estuaries are fairly ubiquitous. Furthermore, from existing information concerning their peak periods of abundance in the estuarine ecosystem, it appears that many of the populations are temporally separated, thus eliminating or decreasing competition for food resources.

As indicated earlier, nekton species are the major consumers of biomass produced by other inhabitants of the open-bay bottoms. The dominant nekton that generally inhabit Texas estuaries represent many different feeding stategies and include planktivores, detritivores, and producers. Examples of some of the food items that these dominant nekton feed upon are listed in Table 9. Some of the most abundant species of the open-bay bottom are planktivores, feeding primarily on phytoplankton and zooplankton. Included in this group are Anchoa mitchilli and Brevoortia patronus. Anchoa mitchilli is also known to eat detritus and small shrimp that are found in the water column. Menidia beryllina is another abundant fish of Texas estuaries that is considered a planktivore. Because these fishes feed so low in the food chain, they stay relatively abundant in the open-bay bottoms (Darnell 1958). The striped mullet, Mugil cephalus, is a prime example of a detritivore

Table 9. Dominant nekton (invertebrates and fish) species in the open-bay bottoms of Texas estuaries. Recorded occurrences from L. Benefield (Texas Department Parks and Wildlife, Austin, Texas; pers. comm.).

Scientific name (Common name)	Peak abundance period and/or bay presence	Occurrence							Food preferences	References
		Galveston Bay	Matagorda Bay	San Antonio Bay	Aransas Bay	Corpus Christi Bay	Upper Laguna Madre	Lower Laguna Madre		
Penaeus aztecus (brown shrimp)	Spring	X	X	X	X	X	X	X	Detritus (e.g. seagrass), polychaetes, larval fish, mollusks	Farfante (1969)
Penaeus setiferus (white shrimp)	Summer	X	X	X	X	X	X	X	Detritus (e.g. seagrass), mollusks, larval fish, polychaetes	Farfante (1969)
Callinectes sapidus (blue crab)	Winter-Spring	X	X	X	X	X	X	X	Mollusks, polychaetes, small crustaceans	Darnell (1958) Farfante (1969) Lindner & Cook (1970)
Callinectes similis		X	X	X	X	X	X	X	Barnacles, mollusks, detritus, polychaetes, small crustaceans	Darnell (1959)
Lolliguncula brevis (bay squid)	Summer-Fall	X	X	X	X	X	X			
Squilla empusa (mantis shrimp)		X	X		X	X	X	X	Small shrimp, crabs	Peterson & Peterson (1979)
Trachypenaeus similis (roughback shrimp)		X	X		X	X				
Neopanope texana (mud crab)		X		X	X	X	X			

(continued)

Table 9. (Continued).

Scientific name (Common name)	Peak abundance period and/or bay presence	Occurrence: Galveston Bay	Matagorda Bay	San Antonio Bay	Aransas Bay	Corpus Christi Bay	Upper Laguna Madre	Lower Laguna Madre	Food preferences	References
Palaemonetes spp. (grass shrimp)				X	X	X	X		Epiphytes, polychaetes, small crustaceans	Peterson & Peterson (1979)
Paralichthys lethostigma (southern flounder)		X	X	X	X	X	X	X	Small fish, crabs, mysids, penaeid shrimp, amphipods and squid	Darnell (1958), Adams (1976), Day (1960)
Anchoa mitchilli (bay anchovy)	Late Spring-Fall	X	X	X	X	X	X	X	Mysids, detritus, zooplankton	Darnell (1958), Thomas et al. (1971), Rogers (1977), Dineen & Darnell (1976)
Sciaenops ocellatus (red drum)		X	X	X	X	X	X		Crustaceans, mollusks, small fish, polychaetes	Darnell (1958), Hildebrand & Schroeder (1927), Day (1960)
Cynoscion nebulosus (spotted seatrout)		X	X	X	X	X	X	X	Fish, crustaceans, including penaeid shrimp	Darnell (1958), Rogers (1977), Hildebrand & Schroeder (1927), Day (1960)

(continued)

Table 9. (Continued).

Scientific name (Common name)	Peak abundance period and/or bay presence	Occurrence: Galveston Bay	Matagorda Bay	San Antonio Bay	Aransas Bay	Corpus Christi Bay	Upper Laguna Madre	Lower Laguna Madre	Food preferences	References
Cynoscion arenarius (sand trout)	Spring-Summer	X	X	X	X	X	X	X	Fish, mysids, crabs, polychaetes, mollusks	Rogers (1977), Hildebrand & Schroeder (1927)
Leiostomus xanthurus (spot)	Spring	X	X	X	X	X	X	X	Polychaetes, mollusks, small crustaceans, and young fish	Darnell (1958), Thomas et al. (1971) Hildebrand & Schroeder (1927) Dineen & Darnell (1976)
Brevoortia patronus (gulf menhaden)	Spring	X	X	X	X	X	X	X	Phytoplankton and zooplankton	Darnell (1958), Hildebrand & Schroeder Dineen & Darnell (1976)
Arius felis (sea catfish)	Summer	X	X	X	X	X	X	X	Organic detritus and large benthic invertebrates	Dineen & Darnell (1976)
Micropogonias undulatus (Atlantic croaker)	Winter-Spring	X	X	X	X	X	X	X	Polychaetes, mollusks, *Balanoglossus*, detritus and penaeid shrimp	Darnell (1958), Hildebrand & Schroeder (1927), Dineen & Darnell (1976)

(continued)

Table 9. (Concluded).

Scientific name (Common name)	Peak abundance period and/or bay presence	Occurrence: Galveston Bay	Matagorda Bay	San Antonio Bay	Aransas Bay	Corpus Christi Bay	Upper Laguna Madre	Lower Laguna Madre	Food preferences	References
Archosargus probatocephalus (sheepshead)		X		X	X	X	X	X		
Lagodon rhomboides (pinfish)		X		X	X	X	X	X	Vegetation, detritus, small crustaceans, and polychaetes	Darnell (1958), Adams (1976)
Bagre marinus (gafftopsail catfish)		X	X	X	X	X	X		Organic detritus and large benthic invertebrates	Dineen & Darnell (1976)
Pogonias cromis (black drum)		X		X	X	X	X		Mollusks, especially Mulinia	Andrews (1971), Morris (1973), Hildebrand & King (1978)
Symphurus plagiusa (blackcheek tonguefish)	Late Spring-Summer	X	X	X	X	X	X	X		
Stellifer lanceolatus (star drum)	Late Spring-Summer	X	X		X	X		X		
Opsanus beta (gulf toadfish)		X	X	X	X	X	X	X	Polychaetes, amphipods, anemones, small fish, and mollusks	Thomas et al. (1971), Hildebrand & Schroeder (1927)
Menidia beryllina (inland silverside)		X		X	X			X	Small crustaceans, plankton and juvenile shrimp	Darnell (1958), Hildebrand & Schroeder (1927)
Mugil cephalus (striped mullet)		X	X	X	X	X	X	X	Organic detritus and benthic diatoms	Darnell (1958)

among Texas estuarine fish. This species feeds by taking mouthfuls of surface sediments in the open-bay bottoms and digesting what it can. Although Lagodon rhomboides is considered a resident of grass-flat communities, this fish is also found on the open-bay bottom feeding off the surface sediments in the fashion of a detritivore. Although the penaeid shrimps are often considered predators, they can also be classed as detritivores because they will often take portions of sediment and silt with their mouth parts, removing and ingesting what items may be of food value.

The majority of species listed in Table 9 are considered predators of the open-bay bottoms. The crustaceans, Callinectes sp. and Squilla empusa, actually seek out bivalve mollusks, smaller crustaceans, and polychaete worms. Micropogonias undulatus, a voracious bottom-feeding predator, and Leiostomus xanthurus are two of the most abundant fishes in Texas estuaries; both are predators primarily on the invertebrates in the sediment. Other common predators include Paralichthys lethostigma, Pogonias cromis, and Cynoscion arenarius. Pogonias cromis is known to feed heavily on the dominant bivalve in many Texas estuaries, Mulinia lateralis.

3.6 OPEN-BAY BOTTOM MARINE BIRDS AND MAMMALS

Although probably not obvious to the casual observer, birds and marine mammals, which act as higher order consumers, play an important role in the trophic dynamics of the open-bay bottoms in Texas estuaries. One of the primary reasons why birds may not be thought of as important to the open-bay bottoms is that the water is often more than 1 or 2 meters deep. Many floating and diving birds, such as ducks, cormorants, and geese, however, are known to live here. In addition, aerial-searching birds, such as the terns, gulls, pelicans, and skimmers, routinely visit this area of the estuary for food. Even such birds of prey as the osprey and marsh hawk often dive below the surface of open-bay waters to capture good-sized large fish. Bowman et al. (1976) estimated that the average fish-eating bird consumed 450 g fish/day. As described by Peterson and Peterson (1979), the birds that regularly live in the open-bay bottom areas can be classed into four groups primarily related to their feeding strategies. These four groups are the waders, aerial searchers, floaters and divers, and birds of prey; the bird species in Texas estuaries that may be so classified are listed in Table 10.

The least obvious of these groups are the waders, which are often seen standing in water more than half a meter deep or perched on pilings and oyster reefs associated with the open-bay bottom. The wading birds around the periphery of the open-bay bottom can exert as much trophic pressure on this habitat as any animal found in deeper waters. Many of the same fish and benthic invertebrate populations live both at the periphery and in deeper waters; these birds feed primarily on small fish and larger crustaceans such as penaeid and grass shrimp. Probably the most noticeable member of this group is the great blue heron, Ardea herodias.

The floating and diving birds probably exert the most feeding pressure upon the benthic habitat of the open-bay bottom. These birds usually float on the surface of the water and either dive below the surface to feed on pelagic fish or dive all the way to the bottom to retrieve large numbers of benthic mollusks. The cormorants, loons, and grebes normally feed on pelagic and demersal fish. The scaup, redhead, and ruddy duck feed on benthic invertebrates and submerged vegetation. The majority of these benthic feeders occur in Texas estuaries in the winter; the period of peak abundance for one of their preferred food items, the bivalve mollusks, Mulinia lateralis.

All the gulls and terns associated with the open-bay bottoms belong to the group called aerial searching birds. The terns dive from flight to pick up their food at the water surface or beneath. Gulls dive from flight as well as dive beneath the water surface from a floating position. Also included in this group are such Texas residents as the brown pelican, the black skimmer, and the belted kingfisher. All of these birds seek fish as their primary diet, and the size of fish

Table 10. Birds known to inhabit the open-bay bottoms of Texas estuaries. Information for diet from Peterson and Peterson (1979) and Terres (1980).

Scientific name (Common name)	Most abundant occurrence	Diet
Waders		
Ardea herodias (great blue heron)	Year round	Small fish
Butorides striatus (green heron)	Spring-Fall	Small fish
Casmerodius albus (great egret)	Year round	Small fish
Egretta rufescens (reddish egret)	Year round	Small fish and crustaceans
Egretta tricolor (tricolored heron)	Year round	Small fish and shrimp
Nycticorax nycticorax (black-crowned night-heron)	Year round	Small fish
Plegadis chihi (white-faced ibis)	Year round	Crustaceans and small fish
Ajaia ajaja (roseate spoonbill)	Spring-Summer	
Floating and diving birds		
Gavia immer (common loon)	Winter	Fish
Podiceps nigricollis (eared grebe)	Winter	Small fish
Podilymbus podiceps (pied-billed grebe)	Winter	Small fish
Pelecanus erythrorhynchos (white pelican)	Winter	Fish
Phalacrocorax auritus (double-crested cormorant)	Winter	Fish
Aythya affinis (lesser scaup)	Winter	Fish
Aythya marila (greater scaup)	Winter	Mollusks

(continued)

Table 10. (Concluded).

Scientific name (Common name)	Most abundant occurrence	Diet
Aythya americana (redhead)	Winter	Seagrasses, mollusks, crustaceans
Chen caerulescens (snow goose)	Spring-Fall	Submerged grasses, crustaceans and fish
Oxyura jamaicensis (ruddy duck)	Winter	Benthic invertebrates
Aerial-searching birds		
Pelecanus occidentalis (brown pelican)	Year round	Fish
Sterna nilotica (gull-billed tern)	Year round	Small fish, pelagic invertebrates
Sterna antillarum (least tern)	Summer	Small fish
Sterna hirundo (common tern)	Spring-Fall	Small fish
Sterna maxima (royal tern)	Spring-Fall	Small fish
Sterna sandvicensis (sandwich tern)	Summer	Small fish
Larus atricilla (laughing gull)	Winter	Fish, mollusks, and carion
Larus delawarensis (ring-billed gull)	Winter	Fish
Rynchops niger (black skimmer)	Spring-Summer	Small fish
Ceryle alcyon (belted kingfisher)	Winter	Small fish
Birds of prey		
Circus cyaneus (northern harrier)	Winter	Fish and small birds
Pandion haliaetus (osprey)	Year round	Large fish

taken as food is usually closely correlated to the size of the bird. Many of these birds are seasonal residents in Texas estuaries; several use dredge-spoil islands associated with the open-bay bottoms for colonial nesting. The gulls are the only members of this group that are not selective in their feeding on live prey. They will scavenge whatever they find floating on the water surface.

The last group of birds frequenting the open-bay bottoms of Texas estuaries is that of birds of prey. These include the osprey and the marsh hawk. The osprey nests along the shoreline and feeds on large pelagic fish taken from surface waters or on demersal fish that can be captured when they enter the shallower waters of the bay periphery. The marsh hawk, although feeding primarily upon smaller terrestrial birds and occasionally those that frequent the open-bay bottom waters, will sometimes take fish.

Another group not often associated with the open-bay bottoms of Texas estuaries is the marine mammals, for three reasons: (1) these animals are not fished for, (2) they do not occur in large numbers, and (3) they are usually associated with oceanic waters. In fact the only marine mammal regularly living in Texas estuaries is the bottlenose dolphin, *Tursiops truncatus*. Oppenheimer (pers. comm.) has estimated that in the Corpus Christi Bay Estuary, the bottlenose dolphin population is about 300. He also speculated that the adult dolphin will consume up to 18 kg fish/day, which exerts a sizeable pressure on fish populations of the estuary. Thus, this population acts as an extremely important secondary consumer of the open-bay bottom biotope.

3.7 GENERAL COMMENTS

In the preceding description of different biotopes affecting the open-bay bottoms of Texas estuaries, as well as the analysis of all biotic components comprising the open-bay bottom biotope, and the contrast of these between various estuaries along the coastal Northwestern Gulf of Mexico (Texas), an attempt has been made to familiarize the reader with the biotic environment upon which this monograph is focused. Hopefully from this background sketch, one will be able to more clearly envision the complete picture of how the open-bay bottom biotope functions in nature. Although the following two chapters will focus upon the benthic habitat, it is extemely important for the reader to keep in mind how the community structure and function of this habitat depends upon and influences all biotic components that integrate to make up the open-bay bottom environment. On numerous occasions in the next two chapters, reference will be made to information concerning the description of biotic assemblages contained in this present chapter.

CHAPTER 4.
BENTHIC COMMUNITY STRUCTURE

4.1 INTRODUCTION

Estuaries with their extensive open-bay bottoms are highly productive aquatic environments; throughout the world they sustain important shellfish cultures and fisheries. A major contribution to this high production of biomass, which supports extensive estuarine food chains, comes from secondary production of the benthos in the open-bay bottom (Wolff 1977). High benthic production greatly enhances the role that estuaries play as nursery grounds for juvenile nekton, which often derive their nutrition from the benthos.

Benthic organisms are in an intermediate position in estuarine food chains, functioning as a "trap" for all sources of food from primary trophic levels (i.e., phytoplankton, macrophytes, and land-derived detritus) and providing a mechanism of energy transfer to higher consumers such as shrimp and fish. Benthic organisms are the most important primary consumers of the open-bay bottom because strong tidal currents and/or riverine flushing plus high turbidity of the water column diminish the role of zooplankton in the estuarine ecosystem. Because of the relatively small primary consumer populations in the water column, much of the plant carbon production and detrital material of the estuary reaches the bottom, where it is available for benthic processing and cycling to higher trophic levels.

Invertebrates that live in the estuarine sediments of the open-bay bottom form an integral part of the biotope because of their role in benthic-pelagic coupling. Although riverine input often serves as a substantial supply of nutrients to the estuary, there is now good evidence that bottom sediments play an important role in the supply of nutrients to euphotic (upper water layer) primary production (Zeitzschel 1980). Rowe et al. (1975), Rowe and Smith (1977), and Hargrave and Connolly (1978) have calculated that the release of nutrients from shallow-water sediments may make up between 30% and 100% of phytoplankton nutrient requirements in coastal ecosystem euphotic zones. Evidence is accumulating that suggests the activities of the sediment inhabitants of these shallow habitats regulate the flow of nutrients from the sediments to the overlying waters(e.g., Rhoads 1974; Aller 1978). Such activities as sediment mixing by the benthos have the potential of greatly modifying the biological, physical, and chemical attributes of the sands and muds. Besides altering the abundance patterns of other sediment inhabitants, these activities also change sediment stability, vertical profiles of chemical materials, and the movement of these across the mud-water boundary.

Green (1968) illustrated that the biomass of benthic fauna increases as the general productivity of the estuarine ecosystem increases. Since many benthic organisms are of limited mobility or even completely sedentary, biomass, abundance, and diversity fluctuations are often monitored for these fauna in order to detect changes which may upset the fine ecological balance of the biotope. Thus, the animals that live in the sediments of the open-bay bottom serve not only as an important link in estuarine food webs and act as an integral part of estuarine benthic-pelagic coupling through their regulatory role in sediment nutrient regeneration, but they also provide an ideal barometer of the conditions that exist in the habitat.

For these reasons, detailed knowledge of the dwellers in the benthic habitat of the open-bay bottom is important to obtaining a good understanding of the dynamics of this community and to build a basis upon which to develop a realistic community profile. The details include information on community structure of the benthos, information on factors that affect this structure, and specific information on the functions of the benthos that place its role in perspective with respect to the total ecosystem picture.

From the time of early classical studies in benthic ecology, the creatures that live in close association with the substrata have been divided into generalized groups based upon mode of life. Animals that live on the sediment surface are termed epifauna and include both invertebrates and vertebrates. Most of these organisms are mobile and many occasionally swim in the water column. The other general group of sediment-associated biota is the infauna, organisms that live in the sediment. Included in this group are the microfauna, those animals that pass through a 0.062-mm mesh; meiofauna, organisms that pass through a 0.50-mm mesh but are retained on a 0.062-mm mesh; and macrofauna, those retained on a 0.50-mm mesh. The infaunal animals that inhabit open-bay bottom sediments can be trophically divided into several groups based upon how they derive their food. These groups include the suspension feeders that usually obtain food from the water column; deposit feeders that ingest sediment and obtain their nutrition from any organic matter (living or dead) associated with the sediment ingested; predators which actively seek out live prey in the benthos for food; and scavengers, which include most mobile gastropods that move around on the sediment surface ingesting dying or dead animal tissue. Distinctions among these various trophic groups is often complicated by the diversity of ways individual benthic organisms go about obtaining their food. In general, however, most infaunal animals in the open-bay bottom derive the majority of their nutrition from organic material in the sediments or from each other through both active predation and/or deposit-feeding, which often includes the ingestion of small live organisms. Suspension feeding in the estuarine benthic habitat is somewhat limited because of the high degree of sediment resuspension and turbid waters, especially in Texas estuaries.

4.2 BENTHIC PRODUCERS, DECOMPOSERS, AND MICRO/MEIOFAUNA

In general, the waters of the open-bay bottoms of Texas estuaries are too turbid to pass sufficient light to the sediments to support viable primary producers. The euphotic zone of most of these waters is less than 2 m deep. For example, from numerous periods of photosynthesis measurements of phytoplankton in Corpus Christi Bay, Flint (1984) has observed that primary productivity rates are often decreased by 50%, and often up to 80% in the shallower and more turbid waters of Nueces Bay in measurements made between 0.5 and 1.0 m depth. Since most of the open-bay bottom areas include deeper waters with a high occurrence of turbid conditions, benthic algae, including phytoplankton, are probably not an important component of the community. However, Oppenheimer and Wood (1965) did report the presence of diatom populations on surface sediments of several Texas bays. Because of the absence of a consistent deep euphotic zone, these occurrences of sediment diatom populations probably reflect the accumulation of detritus from the overlying water column.

Probably one of the most important components of the open-bay benthos is the decomposer population, most notably the fungi and bacteria. These organisms will use any available organic-matter substrate. Because of the large amounts of resuspended sediments in estuaries and the large inputs of allochthonous (external) detrital material from surrounding watersheds, many substrates are available for decomposers to attach to, multiply on, and mineralize. These organisms serve as the major link between primary carbon production (plants) and the consumption of the carbon by animal populations (Odum and de la Cruz 1967), since very little living plant material is consumed directly within the benthic habitat (Whitlatch 1982).

The decomposers of the open-bay bottoms are important to the entire community

because: (1) they mineralize organic matter, releasing important nutrients to be reused by primary producers; (2) they act as trophic links between primary producers and primary consumers; and (3) they can also aggregate dissolved organics within estuarine waters, thus providing another source of particulate material for consumers (Peterson and Peterson 1979). In general, the decomposition of detrital material within the sediments, and indirectly, the abundance of decomposer populations that perform those tasks, is related to the particle size of the sediments or resuspended material. Smaller particles such as silts and clays usually contain larger populations of bacteria and fungi than sands because their smaller size and greater surface-to-volume ratio (Newell 1970) provide a larger overall surface area for colonization. In addition to the size of particles, the kind of organic material available dictates the success of decomposers in providing the above functions in the community. Terrestrial material entering open-bay bottom waters is usually more resistant to decomposition than indigenous organic material because of a higher content of structural polymers (Whitlatch 1982). Fungi, because they extend their hyphae into the detrital material, are often more successful at decomposing terrestrial material and larger particles than bacteria, which usually colonize only the surface of particles. Animal populations feeding on the detritus tend to aid the bacterial decomposition of this material by breaking the detritus into smaller particles in their grazing processes (Lopez et al. 1977).

The presence of fungi and bacteria in the open-bay bottoms of Texas estuaries helps to stabilize this biotope. The decomposer populations are always breaking down the ever-present organic matter of the estuary and providing a food source to primary consumers of the community. Thus, these consumers are less dependent on either the seasonal primary production or the periodic and unpredictable riverine input of terrestrially originated materials. In short, they assure a constant source of energy to the animal populations.

The combination of small size with difficulty in sampling has severely limited our knowledge of the microfauna and meiofauna of Texas estuaries. What information is available is presented here, because the micro and meiofauna are most closely linked to the decomposers of the sediment habitat because of their small size, feeding strategies, and stimulation of decomposition by bacteria through particle breakup (Barsdate et al. 1974).

Microfauna include the protozoans such as the ciliates and foraminiferans. These groups can be extremely abundant, especially in finer sands (Whitlatch 1982) close to the sediment surface. Although little is known of their ecological significance in open-bay bottoms it is speculated that they feed on bacteria and in turn may provide a food source for meiofauna and macrofauna of sediment habitats (Fenchel and Jorgensen 1977).

As is typical of shallow marine sediments world-wide, nematodes are the most abundant populations characterizing the meiofauna in Texas estuaries. Harpacticoid copepods are usually second in abundance. Other important meiofauna of open-bay bottom sediments in Texas estuaries are usually characterized as temporary because they are juveniles of what are normally reported as macrofaunal populations.

Rogers (1976) observed that nematodes were the most abundant group of meiofauna in the San Antonio Bay sediments, comprising more than 83% of total meiofaunal counts. The harpacticoid copepods represented an additional 5%. Rogers (1976) speculated that predation pressure by larger fauna of the benthic habitat was responsible for the annual abundance patterns of the total meiofauna community. Minimum abundances were observed in the spring when peak populations of many other benthic consumers were common. Rogers (1976) indicated that meiofaunal populations can be large throughout the year because they are constantly reproducing and have short life cycles with large turnover rates. Because of these large turnover rates, Gerlach (1978) estimated that the meiofauna may comprise from 12% to 30% of the living biomass in many aquatic sediments. Meiofaunal group abundances in the community are usually regulated

by the sediment particle size and depth of the oxygenated surface layers. For example, Rogers (1976) observed that nematodes were more abundant in sediments with high silt contents.

Meiofaunal samples collected in Corpus Christi Bay in January 1982 showed that these benthic fauna prefer sandier sediments to areas that contain more silt and clay (R. Kalke, University of Texas at Austin; pers. comm.). At two sites where the sediment sand content was greater than 50%, total meiofaunal abundances for January in the surface sediments (0-2 cm) were 1.73 x $10^6/m^2$ and 2.01 x $10^6/m^2$, with nematodes comprising greater than 72% of these totals. In contrast, a third site that contained sediments with more than 70% clay exhibited total surface meiofaunal counts of 0.51 x $10^6/m^2$. Again, nematodes comprised more than 72% of the total. The samples taken at these sites were sectioned each 2 cm of sediment depth. Surprisingly, counts of meiofaunal organisms in the second (2-4 cm) and third (4-6 cm) sediment sections at each station were similar. Second-section abundances were 0.55 x $10^6/m^2$, 0.54 x $10^6/m^2$, and 0.71 x $10^6/m^2$; where the last count was for the station with greater clay content. Similarly, the third section counts were 0.21 x $10^6/m^2$ and 0.15 x $10^6/m^2$ for the two sandier stations and 0.26 x $10^6/m^2$ for the station with a higher clay content. In both the second and third sections, the nematodes were again the dominant taxa, representing more than 90% of total abundance. With respect to vertical distribution of meiofaunal populations in Corpus Christi Bay, seventy percent of the total abundance at the stations containing more sand occurred in the first 2 cm. In contrast, at the station with a high clay content a fairly even distribution of total abundance from the surface down to 4 cm sediment depth was observed, with a slight increase in the deeper sediments.

4.3 BENTHIC MACROINFAUNA

The benthic macroinfauna of the open-bay bottoms of Texas estuaries contribute a much higher proportion of total community production and are larger and more easily studied than micro and meiofauna. Thus, a great deal more information on composition, distribution, and abundance of these species assemblages is known for Texas estuaries. General taxonomic distribution data for these estuaries has already been presented (Chapter 3) and a complete listing of those taxa found in all Texas estuaries is presented in the Appendix. To develop a fuller understanding of the dynamics of these populations, however, in-depth investigations covering several years are required. Texas estuaries lack such coverage, with the exception of Corpus Christi Bay. Thus, most of what follows concerning macroinfauna community structure comes from extensive long-term studies in Corpus Christi Bay.

Understanding the dynamics of the macroinfaunal populations in open-bay bottom requires knowledge of both their temporal and their spatial variations. (In addition, vertical distribution of these fauna may differ under various sedimentary characteristics.) Therefore, the following description of benthic community structure is given in terms of temporal and spatial (horizontal and vertical) variations observed for the Corpus Christ Bay Estuary, which includes Nueces Bay. Although this description will focus on only one of the seven major Texas estuarine systems, the patterns of benthic distribution appear to be comparable across all these estuaries with the same dominant organisms usually occurring and all estuaries showing similar peak abundance periods during the year.

4.3.1 Temporal Variation

A study of benthic macroinfauna was conducted in one 0.25-km^2 area of Corpus Christi Bay between 1974 and 1979 (Flint and Younk 1983) to identify variations in species assemblage dynamics from monthly sample collections over a long-term investigation. This study covered both a shoal (1.6 m deep) and a channel (15 m deep) habitat site in the open-bay bottom. Cluster analysis procedures distinguished distinct species assemblages of macroinfauna for the shoal and the channel habitats. Channel stations generally exhibited smaller species numbers, lower total abundances, and lower species diversity measures. The channel habitat, however, exhibited a more even distribution

of species abundances than the shoal habitat, whose macroinfaunal assemblages were usually dominated by a few species. Because the channel habitat was affected by disturbances such as dredging and ship traffic, a more realistic picture of long-term patterns of the benthic macroinfauna can be obtained from information on the shoal habitat.

Cluster analysis performed on data at this site covering 5 years (Flint and Younk 1983) as well as data from later studies after this period (Flint 1983) indicated that there was a great deal of temporal variability in the benthos over 7 years (Figure 10). The greatest dissimilarity was between the earlier years of study (1974-1978) and more recent years (1979-1981), which was related to differences in rainfall patterns for this estuary (Flint et al. 1981). In general, within small clusters of Figure 10 that covered similar years, the winter and spring month groupings usually separated from the summer. This indicated that there were differences in species assemblages of macroinfauna not only over years but also within a year.

Twenty-four groups of benthic macroinfauna were associated with the patterns observed in Figure 10. The most ubiquitous over the entire study were the polychaete Mediomastus californiensis and a Paraonid group of polychaetes. Another group, including the polychaetes Streblospio benedicti, Tharyx setiger, and Glycinde solitaria and the mollusks Mulinia lateralis and Lyonsia hyalina floridana, were almost always present and dominated during winter and spring. More oceanic species such as the polychaetes Magelona pettiboneae, Sigambra tentaculata, and Paraprionospio pinnata were abundant during the earlier, higher salinity years in the estuary. The mollusk Abra aequalis and the enteropneust Balanoglossus sp. were extremely seasonal, occurring only in the winter and spring and often dominating the infaunal assemblages. Species such as the polychaete Glycera capitata, the amphipod Corophium acherusicum, and the bivalve mollusk Pandora trilineata appeared in variable abundances only after 1979.

The number of species of macroinfauna in Corpus Christi Bay varied considerably

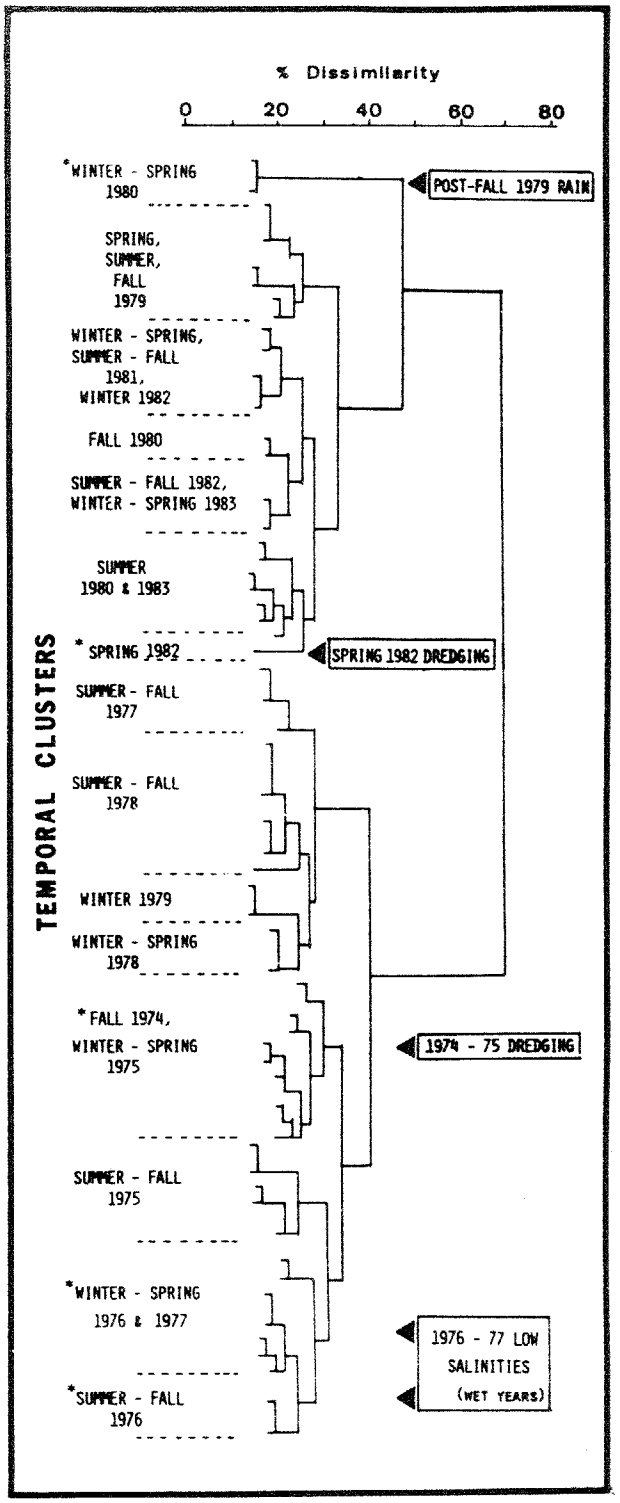

Figure 10. Cluster analysis of benthic macroinfaunal species assemblages from the Corpus Christi Bay Estuary over a period from September 1974 to July 1983. Major clusters are divided into seasons, and periods of environmental change to the estuary, such as high freshwater inflow or dredging, are indicated and the seasonal groups marked (*).

over the 7 years of sample collection (A, Figure 11). The only repeatable pattern to this variation appeared to be a fairly consistent increase during the late winter-early spring of most years (January to March). Some years, however, exhibited species number increases in the summer (e.g., 1976). The winter-spring species number increases were always correlated with the appearance of several bivalve mollusks in the study area (e.g., Abra aequalis), and these fauna usually dominated the species assemblages. Species number also increased later in the 7-yr period, with higher numbers of infaunal species observed from 1979-1981.

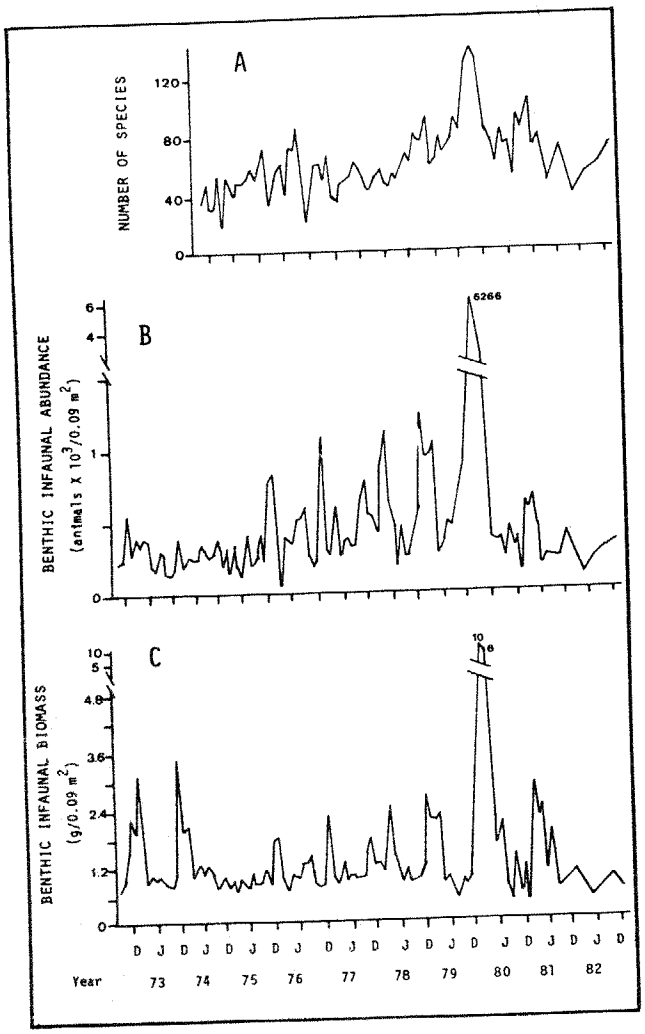

Figure 11. Plots of benthic macroinfaunal species number (A), total abundance (B), and total biomass (C) for a study s.. in the Corpus Christi Bay Estuary.

Data from Flint and Younk (1983) as well as information on macroinfauna abundance after 1979 (R.W. Flint, State University of New York, Oswego; pers. comm.) and from 1972-1975 (Holland et al. 1975) were combined to give 9 years of data on long-term variation (B, Figure 11). Macroinfaunal abundance exhibited a consistent trend of maximum numbers during the winter and spring period of each year. These peak abundance periods showed increases from 1976 to 1980 and then the maximum abundance decreased again in 1981. These periods of maximum macroinfaunal abundance were always associated with the appearance of several dominant mollusks during this period (e.g., Abra aequalis).

Data on macroinfaunal total biomass from these studies exhibited patterns (C Figure 11) that were similar to species number and total abundance. Standing stocks were greatest in the winter and early spring of each year. The benthic infauna which exhibited the greatest increases in biomass were the mollusks Abra aequalis, Lyonsia hyalina floridana, Lucina multilineata, and Mulinia lateralis; the enteropneust Balanoglossus sp. and Rhynchocoels.

As indicated above, for the period that information is available on the benthic macroinfaunal populations of Corpus Christi Bay at one site (1972-1981), changes in rare species occurred, usually related to changes in environmental characteristics. The overriding pattern of the infaunal species assemblages associated with changes over time, however, did not arise from species changes for the rarer species in the community, but rather from changes in abundance patterns of the dominant fauna that regularly occurred over the entire period.

4.3.2 Spatial Variation

4.3.2.1 Horizontal variation. Although a number of benthic studies in open-bay bottoms of Texas estuaries have been conducted, most have not covered a large enough bottom area to obtain a

good picture of spatial variability in benthic community structure or the data from these studies have not been adequately analyzed. Holland et al. (1975) performed cluster analyses on 104 selected benthic macroinfauna species from Copano, Aransas, Corpus Christi, and Nueces Bays, covering stations which had been sampled for 3 years. They found that Corpus Christi and Nueces Bay benthos were distinctly different from Copano and Aransas Bay benthos. In Corpus Christi and Nueces Bays the dominant and ubiquitous benthic infauna included the polychaetes Mediomastus californiensis, Streblospio benedicti, Cossura delta, Paraprionospio pinnata, Gyptis vittata, and Glycinde solitaria. The dominant mollusks were Mulinia lateralis and Lyonsia hyalina floridana. In Copano and Aransas Bays the benthos was observed to be less consistent in general patterns. Mediomastus californiensis and Streblospio benedicti were again observed to be the dominant and ubiquitous polychaetes. Other polychaete species occurring in high numbers which differed from Corpus Christi and Nueces Bays included Capitella capitata, Driloneris magna, Lumbrineris parvapedata, Neanthes succinea, and Pectinaria gouldii. In addition to the species assemblage trends being less consistent in Aransas and Copano Bays, Holland et al. (1975) also observed lower total infaunal abundances for these estuaries than for Corpus Christi and Nueces Bays.

The most intensive study of spatial variation in benthic infaunal species assemblages has been conducted in the Corpus Christi Bay estuarine system, which includes part of Nueces Bay (Flint and Kalke 1985). In this investigation three stations characteristic of different sedimentary and salinity environments within the estuary are being monitored for benthic macroinfaunal species abundance and biomass. The lower-bay collection site is characterized by sediments containing in excess of 90% sand, usually exhibiting a water content of 20% total weight, and this site is strongly influenced by gulf waters. The midbay collection site contains sediments that are predominantly clay (greater than 70%), exhibit a water content of 50%-70% total weight and are extremely flocculent. This collection site is usually characterized by salinities from 24-31 ppt. The upper-bay collection site is characterized by sediments containing 50% sand, 20% clay, and 20%-30% shell, with water content averaging around 35% total weight. Salinity at this site varies the most and can range from 5-32 ppt, depending upon rainfall and Nueces River flow.

With respect to benthic infaunal species assemblages at these sites, they are all dominated by the deposit-feeding polychaete Mediomastus californiensis. The similarity between sites, however, ends with this species. The upper bay site exhibits abundances of Streblospio benedicti during July, October, and January. The bivalve mollusks Tagelus divisus, Mulinia lateralis, and Mysella planulata dominate collections in the winter and spring at the upper bay site. The capitellid polychaete Heteromastus filiformis is abundant in the winter and is usually deeper in the sediments. When salinities go up at this site, Diopatra cuprea is often observed. Standing stock biomass of benthic infauna at this site ranges from lows around 0.4 g/m^2 in lower saline summer periods to highs of 151.8 g/m^2 during the winter and spring.

The midbay station, besides exhibiting Mediomastus californiensis as the dominant polychaete, also supports populations of Paraprionospio pinnata in the spring and summer and the bivalve mollusk Mysella planulata in the winter. During the monitoring period at this site salinities increased to and stayed around 30 ppt. With the occurrence of higher salinities, the enteropneust Schizocardium sp. colonized at the midbay collection site, and while this species became more abundant in the sediment, others such as the polychaetes Gyptis vittata and Polydora sp. also began to appear in abundance. Nemerteans also became more abundant in the surface sediments after the development of large Schizocardium populations. Total infaunal standing stock biomass at this site ranged from a low of 0.05 g/m^2 in the absence of Schizocardium to a high of 157.0 g/m^2 during summer peak abundances of Schizocardium.

The lower bay station generally exhibited a much more diverse group of benthic infaunal species than either of the other

two collection sites. Although Mediomastus californiensis again dominated the total collections from this site, a group of Paraonid polychaetes were often as abundant as M. californiensis, especially in winter and spring. Other abundant polychaetes at the lower bay site included Apoprionospio pygmaea, Clymenella torquata, Streblospio benedicti and Magelona phyllisae. Abundant mollusks were Lucina multilineata, and on occasion Abra aequalis. Total infaunal standing stock biomass at this collection site ranged from a low of 15.4 g/m^2 in October 1981 to a high of 47.1 g/m^2 in January 1982.

The results of this ongoing study indicate that the Corpus Christi Bay Estuary is an extremely dynamic environment with a great deal of variation spatially within the open-bay bottom in the benthic species assemblages. Much of the temporal variation in dominant populations discussed earlier is again apparent here. Within the same system the faunal assemblages differ greatly and much of the difference can be linked to sediment property differences. In addition, as illustrated by results of the midbay station monitoring, a large part of the temporal variation in species assemblages can be linked to changes in salinity patterns as well as changes in dominant fauna in the sediment.

4.3.2.2 Vertical variation. Most benthic macroinfauna live in the upper layers of the sediment, probably reflecting the greater quantities of food and oxygen available in this zone. McIntyre and Eleftherion (1968) observed that macrofauna in subtidal sands and muds were most abundant in the first 4 cm of sediment. Johnson (1967) noted that the largest numbers of macroinfauna in a sandflat community lived in the top 10 cm. Whitlatch (1982) indicated that in temperate estuarine mudflats, most of the polychaetes are in the first 3 cm of sediment, amphipods are even closer to the surface in the first 2 cm, and bivalves spread out more into the first 4 cm of sediment.

Although most studies of estuarine benthos do not consider vertical distribution of the fauna within the sediments, there is usually considerable knowledge to be gained from examining vertical structuring of the species assemblages, which can be related not only to their own ecology but also to the overall dynamics of the biotope. For example, Peterson (1977) investigated the pattern of depth stratification for dominant infauna in soft-bottom benthic communities of California lagoons. He found very little overlap in abundance of these dominant species and concluded that their distributions were such that competitive interactions would be minimized since competition is usually a predominant community structuring mechanism (Woodin 1976; Whitlach 1982).

In studies of vertical distribution of benthic macroinfauna in Corpus Christi Bay sediment (R.W. Flint, in prep.), observations have been made concerning the enhancement of deep-burrowing species abundances by the presence of one dominant species living deep in the sediments. The funnel-feeding enteropneust Schizocardium sp., a major sediment bioturbator in estuarine muds, colonized a study site in Corpus Christi Bay in April 1982. Prior to this species' appearance, no macrofauna were observed below 3 cm sediment depth and biomass of the total macrobenthos ranged from 0.05 g/m^2 to 4.01 g/m^2. After colonization by Schizocardium and movement of this species into the deeper sediment (10-20 cm), other organisms were observed in sediment depths as great as 20 cm, including the polychaetes Gyptis vittita, Mediomastus californiensis, and Polydora sp. in abundances up to 1,320 individuals/m^2. Macroinfaunal biomasses in these sediments also exhibited large increases throughout the sediment column, but in particular in the deeper strata (58.9 g/m^2 to 146.0 g/m^2) where species were extremely abundant on account of the sediment reworking abilities of Schizocardium.

In contrast to the results observed at this study site in Corpus Christi Bay, other open-bay bottom sites investigated (Flint and Kalke 1985) within the same estuary showed more of the normal pattern of benthic infaunal vertical distribution, with the majority of species abundances occurring in the top 3-5 cm of sediment. For example, at an upper bay collection site total macroinfaunal

abundance averaged 2,037 individuals/m^2 in sediment depths of 0-3 cm, 1,245 individuals/m^2 in depths of 4-10 cm, and 283 individuals/m^2 from 10-20 sediment depth over 2 years of sample collection. Correspondingly, total infaunal average biomass for the same three sediment sections was 51.5 g/m^2 for 0-3 cm, 14.8 g/m^2 for 4-10 cm, and 3.3 g/m^2 for 10-20 cm. Thus, as illustrated by these examples as well as the little information in the literature, it appears that the extent of faunal vertical distribution in the open-bay bottom sediments is related to the kinds of fauna present in these sediments and the kinds of functions that they perform in the community (e.g., bioturbation). This kind of information serves to pinpoint the types of ecological relationships that exist among sediment dwellers and emphasizes the importance of different kinds of fauna to the open-bay bottom community.

4.4 MOBILE BENTHIC EPIFAUNA

This component of the benthic community probably exerts the most trophic pressure upon the macroinfaunal populations described above. A number of the organisms included in the epifauna of Texas estuaries are active predators, feeding on the live biomass of sediment dwellers. These active predators usually include the shrimps and crabs, as well as other dominant crustaceans within this habitat. The epifauna also include a group of gastropods that represent the largest group of fauna in the scavenger class in the open-bay bottom. Many of the gastropod mollusks found inhabiting the surface sediments seek out dead and dying animal tissue for food. Indirectly, these animals also affect the infauna of these same surface sediments because of the disturbance to these sediments these mobile gastropods cause in their food-searching movements. During dives to the bottom sediment surface of estuaries, one can observe deep furrows and other types of tracks left on these surface sediments by searching gastropods.

Several of the dominant epifauna of Texas open-bay bottom estuaries are of commercial importance because of their fishery value. These species include the penaeid shrimp such as Penaeus aztecus and Penaeus setiferus, and the blue crab Callinectes sapidus. These fauna usually cause substantial mortality among the benthic infauna, especially among the shallow burrowers and surface dwellers that can be easily excavated and consumed by shrimp and crabs. The shrimp burrow into the sediment as means of protection against demersal fish predators. This excavation and disturbance of surface sediments can also cause mortality to smaller subsurface-dwelling fauna.

Other epifaunal crustaceans that have at least been observed on the open-bay bottom sediments of the Corpus Christi Bay Estuary (R. Kalke, University of Texas Marine Science Institute, Port Aransas; unpubl. data) include the amphipod Gammarus mucronatus, the mud crab Neopanope texana, the hermit crab Pagurus annulipes, the mantis shrimp Squilla empusa, several other xanthurid crabs, and on many occasions the grass shrimp Palaemonetes pugio which moves off adjacent grassbeds to the open-bay bottom. Many of these fauna are detritus feeders, ingesting surface sediments and obtaining food from whatever animal material and other organic matter accompanies the sediment. Squilla empusa, however, is a very active predator, usually sitting in the entrance of its sediment burrow and preying upon whatever comes close.

The other group of common epifaunal organisms in the open-bay bottom are the gastropod mollusks. Most obvious among these fauna are the whelk Busycon contrarium and the moon snail Polinices duplicatus. Both of these epifaunal populations are predators. The whelk feeds on clams such as Chione cancellata and Mercenaria campechiensis. The moon snail has a much broader diet, feeding on clams as well as other gastropod species by using its rasping radula to drill through the shell of the mollusk prey.

Other mollusk gastropods common in Texas estuaries include the dwarf olive shells Olivella dealbata and on occasion Thais sp. The olive shells are thought to be detritivores, ingesting the surface sediments and any associated organic matter.

A few other epifaunal species are occasionally observed on the sediment surface or taken in benthic trawls. For instance, taxa belonging to the Echinoidea such as the sand dollars and urchins are often present on the sediment surface of the open-bay bottoms. Sand dollars will forage at the sediment surface or just below the surface by plowing along at a fairly rapid pace. They normally feed on organic deposits, but like so many of the larger epifauna, their feeding activities in the surface sediments must also have a large impact upon many smaller infauna that live there.

4.5 ENVIRONMENTAL EFFECTS ON COMMUNITY STRUCTURE

The close association of benthic organisms with sediment features is a result of limited mobility. Benthic fauna not only rely on sediments for shelter, protection, and areas to reproduce, but also for food. One feature of macroinfaunal species assemblages is the long-recognized association of particular groups of species with particular sediment types. Particle size is usually considered the most important influential factor of sediments upon species distributions. Other properties of sediments, however, that either directly or indirectly influence the distribution patterns of macroinfauna, on both horizontal and vertical scales, include sedimentation rates, sediment stability, food availability and depth of oxygenated sediments. The depth of oxygenated sediments is usually delineated by the redox potential discontinuity (RPD) where the sediment Eh mv reading equals zero (Rhoads 1974).

Rogers (1976) noted that there was a distinct difference in benthic meiofauna of the open-bay bottom in San Antonio Bay, which he concluded was related to differences in sediment structure. Meiofauna were more abundant in the silty sediments of this estuary, rather than the sandy sediments. Meiofaunal surveys in Corpus Christi Bay (R. Kalke, pers. comm.) indicated that abundances in the sandier sediments were higher than in sediments containing a higher clay fraction. This difference, rather than being related to the actual sediment grain size, may have been related more to the instability of the silty clay surface sediments, which were extremely flocculent and often contained more than 60% water. These sediments could be much more easily resuspended than sandier sediments, resulting in an extremely unpredictable environment for small-sized meiofauna. As the sediment depth increased at this site containing large amounts of clay, abundances of meiofauna were much closer in number to the deeper sediments of the sandier collection sites.

Study sites in the Corpus Christi Bay Estuary which have been investigated over the last few years (Flint 1982) show some interesting comparisons concerning fauna and sediment characteristics. Two of these sites have exhibited similar salinity patterns, but contain widely different sediments: a lower bay site characterized by more than 90% sand and a midbay site with sediments consisting of more than 70% clay. Over 2 years of monitoring, 82 species of macroinfauna have been observed from the sandier site with a total mean abundance of 1,924.5 organisms/m^2 and total mean biomass of 26.7 g/m^2. In contrast, at the site with a high clay content, 22 species have been observed with a total mean abundance of 2,237.6 organisms/m^2 and a total mean biomass of 62.8 g/m^2. The sandier site supported a more diverse group of macroinfauna with lower abundances and much lower biomass than the site containing more clay. Therefore, the long-recognized notions (1) that different species assemblages exist in different sediment types and (2) that fewer species normally occur in muddier sediments but are usually more abundant and are more productive than sandier sediment populations (Whitlatch 1982) appear to apply to the Corpus Christi Bay Estuary and probably other open-bay bottoms along the Texas coast.

The depth of oxygenated sediments is another factor important in influencing the distribution of benthic taxa, especially those that do not maintain consistent connections (i.e., burrows and tubes) with the sediment surface. As Rhoads (1974) has shown, this characteristic of sediment vertical structure can often be determined by making Eh (redox) profile measurements through the sediments to

determine the redox potential discontinuity (RPD) layer. When the voltage reaches zero, this usually defines the depth of the RPD layer and the beginning of anoxic sediments. Kalke et al. (1982) observed that as laboratory experimental benthic species assemblages were subjected to the disturbance of oil layered over surface sediments (thus decreasing the depth of oxygenated sediments by causing a shallower sediment RPD layer to occur), macroinfaunal populations decreased in abundance. The investigators concluded that the migration of the RPD layer closer to the sediment surface decreased the habitat space for many of the abundant subsurface fauna such as Mediomastus californiensis which did not maintain permanent connections with the sediment surface, thus forcing their population numbers to decline.

Numerous observations have been made in the Corpus Christi Bay Estuary (R.W. Flint, pers. comm.) where the depth of the RPD is directly related to the abundance and biomass of macroinfauna. Figure 12 illustrates how the benthic macroinfauna changed over time at a midbay site as the depth of the RPD changed. As the habitat space deepened, the number of species increased and the standing-stock biomass also increased. Since there generally appeared to be a lag between the deepening of the RPD and the macroinfaunal response, especially for biomass, one can speculate that the increase in oxygenated sediment space was influencing the response the fauna exhibited.

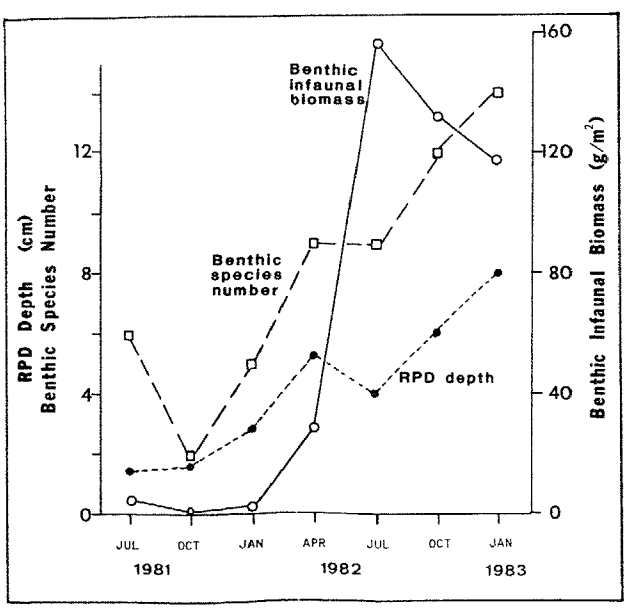

Figure 12. Seasonal measures of sediment redox potential discontinuity (RPD) depth, total benthic macroinfaunal species number, and total benthic macroinfaunal biomass at a midbay study site in the Corpus Christi Bay Estuary.

In addition to the conditions in the sediment, other physical factors limit the distribution of benthic fauna. Primary among these would be salinity. Numbers of benthic species were observed to decline in Lavaca Bay as salinities declined in the upper reaches (Gilmore et al. 1974). Not only were the numbers of benthic species low for areas of the Bay that consistently exhibited lower salinities, but when high river discharge lowered salinities throughout the estuary Gilmore et al. (1974) noted decreases in benthic species.

In contrast, Harper and Hopkins (1976) observed increases in San Antonio Bay benthic populations in response to lowered salinities. They concluded that these responses were directly related to the inflow of more nutrients from the same river discharge that decreased salinities. Consistent with the observations on San Antonio Bay benthos were long-term data collected by Flint et al. (1981) on benthic macroinfaunal populations at a sandy shoal sampling site in Corpus Christi Bay. Species number and total abundance both exhibited increases during the winter periods of 1974-1975 and 1976-1977 (Figure 11, A and B) which corresponded to two of the lowest salinity periods during the entire study duration. These periods corresponded to extremely wet winters, as illustrated by increased flow rates for the Nueces River (Texas Department of Water Resources, Austin; unpubl.). The corresponding lower salinities were assumed to be correlated with increased riverine inputs of nutrients, causing higher production in the system as reflected by the benthos during these periods.

Also during this same study Flint et al. (1981) sampled the benthos during and after a major storm (September 1979) in Corpus Christi Bay which was accompanied by high-intensity rains (33 cm in 24 hr).

This rainfall resulted in freshwater inflows to the Corpus Christi Bay Estuary which surpassed all previously recorded inputs to this system and dramatically lowered the salinity of the estuary below normal for more than a month. Four months after the September 1979 storm, the total abundance and biomass of benthic macroinfaunal populations increased dramatically (Figure 11B and 11C). The increased production was in existing dominant populations, rather than a complete shift in benthic species assemblages as had been observed for other estuaries receiving major freshwaer inflows and accompanying salinity shifts (e.g., Thomas and White 1969; Boesch et al. 1976). These increases in benthic abundance and biomass correlated with the storm suggested that production of the open-bay bottom macrofauna had been stimulated by the rainfall with its associated input of nutrients and detrital material to the Corpus Christi Bay Estuary (Flint 1983).

A more subtle effect of salinity on open-bay bottom fauna was observed from investigations on benthic macroinfaunal species assemblages at a midbay collection site in the Corpus Christi Bay Estuary (Flint and Kalke 1985). For all of 1981, salinities in this estuary were consistently low, usually ranging between 22 and 26 ppt during quarterly sampling cruises. The lower salinities were caused by above-normal rainfall and were much lower than the average range for this portion of the Corpus Christi Bay Estuary (Holland et al. 1975). During the 1981 period of lower salinities, the midbay sediments supported a depauperate macroinfaunal assemblage with total abundances of 1,500 organisms/m^2 in July and 37 organisms/m^2 in October, and the species assemblages were dominated by Streblospio benedicti, a polychaete associated with the less saline upper reaches of Texas estuaries.

In 1982 the salinities at this midbay collection site increased 27-32 ppt, caused by normal and slightly below normal rainfall. These trends continued into 1983. Associated with these salinity changes were substantial changes in the open-bay bottom macroinfaunal species assemblage. In April 1982 the deep-burrowing enteropneust Schizocardium sp. appeared in collections. Not only did the species represented at the midbay site increase in association with Schizocardium (Figure 12), but biomass and total abundance of the macroinfauna also increased and several polychaete species became codominant with Schizocardium, including Mediomastus californiensis and the higher saline species Paraprionospio pinnata. The Streblospio benedicti population decreased to very small numbers during dominance by these other fauna and the continued presence of Schizocardium, the major biomass contributor to the benthos. These patterns have continued at this site through the period of elevated salinities.

Thus, for the Corpus Christi Bay Estuary, two examples of how changes in estuarine salinity will affect the open-bay bottom benthos have been documented. In one instance the salinity change was sudden and dramatic, associated with record rainfalls. The benthos responded by taking advantage of increased resource inputs to the estuary and exhibited record production rates. In the second case, the salinity changes to the estuary were more subtle and prolonged. The benthos responded to this set of circumstances by going through a complete change in species assemblages, which over the long term also appeared to stimulate benthic production.

Individual species of the benthos often interact strongly enough with one another to affect distributions and abundance patterns of all the population. These interactions can represent both direct and indirect effects, and the effects can be in terms of inhibition or stimulation of other fauna.

The major form of indirect interaction among benthic macroinfauna of the open-bay bottom is what Rhoads and Young (1970) termed "trophic group amensalism." According to this phenomenon, the subsurface deposit feeders of open-bay bottom sediments increase the water content of surface sediments, thus creating a flocculent, easily resuspended surface. Large quantities of material suspended in the water overlying the sediments tend to clog the filtering apparatus of suspension feeders in the benthos. Therefore, the action of the deposit feeders upon the

sediments limits the distribution of suspension feeders and often reduces their abundance in the open-bay bottom.

In addition to interacting indirectly through effects on the sediments, macroinfauna can act directly to inhibit one another. Woodin (1976) observed that adult infauna in a benthic species assemblage feed on the larvae of potential colonizers to the assemblage. Suspension feeders capture larvae of many infaunal species while they are still in the water column. Deposit feeders affect the survival of newly settled infaunal larvae by consuming these as part of their diet, disrupting settlement processes or causing mortality by their sediment reworking during feeding. Woodin (1976) concluded that direct interactions by the infauna are strong enough and frequent enough to determine which species can coexist in the benthos, thus limiting the membership of any dense infaunal assemblage.

Another form of indirect interaction among macroinfauna is stimulatory rather than inhibitory. Woodin (1982) demonstrated that the tubes of Diopatra cuprea, an onuphid polychaete abundant in Texas open-bay bottoms, provide refuges for other macroinfauna of the sediments against predation from such species as Callinectes, the blue crab. Eckman et al. (1981) has also shown that tubes at the surface of sediments tend to vary the local hydrodynamic environments of these sediments, thus creating a more stable sediment habitat for other infaunal species around certain areas of the tubes.

The burrowing and reworking of deeper sediment in the open-bay by large macroinfauna have been observed to stimulate the presence of a more diverse species assemblage in sediments where this bioturbation occurs. For example, replicate cores taken at a sandy site in Corpus Christi Bay for meiofaunal analysis revealed interesting differences in vertical distribution of fauna (R. Kalke, pers. comm.). Two of the three cores taken side-by-side from the sediment by scuba divers exhibited mean peak abundances of 4.9×10^5 organisms/m^2 for infauna in the top 2 cm of sediment. In sediments 2-4 cm deep in these cores, mean infaunal abundance decreased to 0.4×10^5 organisms/m^2, and in sediments 4-6 cm deep no infauna were observed. The third core of the three taken side-by-side exhibited similar abundances of infauna for the first 2 cm of surface sediments. In contrast to the other two cores, however, this core contained a large burrowing ophuroid (brittle star) at a depth of 5 cm in the sediments. The second core section (2-5 cm depth) contained 5 different infaunal species, exhibiting a total abundance of 4.5×10^5 organisms/m^2, and the third sediment section (4-6 cm depth) where the ophuroid was present, contained 9 different infaunal species and a total abundance of 3.0×10^5 organisms/m^2. The third core, in contrast to the first two, contained brown-colored sediments throughout, indicative of oxygenated sediments, due primarily to the sediment reworking abilities of the ophuroid.

For a further example of sediment infaunal bioturbation and its positive effect upon the benthic species assemblages of the open-bay bottom, the effects of the burrowing enteropneust Schizocardium sp. can be examined further. Flint (in prep.) observed that the colonization and ultimate habitation of Corpus Christi Bay sediments by Schizocardium deepened the RPD and increased the amount of oxygenated sediment available for colonization by other fauna (Figure 12). The result of these activities was a diversification of species assemblages observed deeper in the sediment and a tremendous increase in macroinfaunal abundance and biomass in deeper sediment than at other bay sites having a shallow RPD layer. Thus, as these two examples illustrate, reworking of sediments by larger infauna, besides interfering with the life cycles of other fauna, can also have a positive effect upon the abundance distribution of many populations by increasing their oxygenated habitat space. Effect is most apparent on populations of infauna that do not maintain a consistent connection with the sediment surface through tubes and open burrows.

CHAPTER 5.
BENTHIC COMMUNITY FUNCTION

5.1 INTRODUCTION

In the past 20 years, important advances have been made in studying benthic community structure in marine and estuarine environments. The great strides in describing the benthic communities of a particular environment, however, have often obscured the fact that the benthos is a changing, dynamic subsystem of this environment, whose functioning is extremely important to the total estuarine system. For example, difficulties that have arisen in attempting to model marine ecosystems indicate a need to better understand the effect on benthic production of changing energy transfer between trophic levels and the resultant impact that these changes might represent to fishery yields. In addition, the benthos is now being considered as an integral part of marine ecosystems because of interest in benthic-pelagic coupling and the potential role of the benthos in regulating sediment processes that contribute to pelagic production.

Recently, the importance of the benthos to marine ecosystems, and especially those systems supporting major commercial fisheries, has been emphasized (Mills 1975). Data collected from several studies suggest a fine balance between the benthos as a food source for fisheries (McIntyre and Murison 1973; Wolff 1977; Arntz 1980) and the benthos as a regulator of dynamics within the ecosystem as a whole via benthic-pelagic coupling processes, emphasizing nutrient regeneration (Davis et al. 1975; Rowe and Smith 1977; Hargrave and Connolly 1978; Zeitzschel 1980). Evidence has also accumulated implicating northwestern Gulf of Mexico marine benthos in foodweb dynamics of the shrimp fishery (Flint and Rabalais 1981) and the flux of nutrients from subtidal sediments that are important to pelagic producers (Flint and Kamykowski 1984). Thus, the indication is that benthic communities potentially contribute to ecosystem production through both the transfer of energy and the regulation of processes such as mud-water interface nutrient fluxes, which help to maintain and stabilize the base of foodwebs.

The benthic communities of Texas open-bay bottoms have a number of functions that are now considered important to the general dynamics of the entire estuary. Most obvious of these functions, from what is known about life on and in the sediments of marine environments, include the production of biomass as food resources for higher trophic levels and the bioturbating of estuarine sands and muds. The first is self-explanatory. The second, bioturbating of sediments, as will be presented in detail later, is an activity of the benthos that directly affects the rate of production by the community and is thought to enhance nutrient regeneration by the estuarine sediments. Since very little information exists concerning benthic secondary production and nutrient regeneration (including regulating factors) for Texas estuaries, much of the following discussion is based on research results of Flint et al. (1982) covering investigations in the Corpus Christi Bay Estuary, as well as more recent, as yet unpublished, research results from the continuation of these investigations.

5.2 BIOMASS PRODUCTION

The most important component of biomass production in all biotopes of the estuary, including the open-bay bottom, is that produced by the primary consumers. These organisms, which include the benthos, are the essential link between the

photosynthetic carbon production in plants and the transfer of this energy to higher trophic levels such as important fisheries. The benthos serve as a "trap" in the open-bay bottom, taking the energy from all the different materials provided it (i.e., phytoplankton, terrestrial organic detritus, and estuarine detritus) and concentrating this energy into biomass packages ready for consumption (and energy transfer) by secondary consumers in the complicated estuarine food chains.

From 1981 to 1983, three distinctly different sampling sites were monitored for benthic community processes in the Corpus Christi Bay Estuary. These sites are characterized as follows:

a. Station 2 - Upper bay, with sediment more than 50% sand; average RPD depth 2.9 cm
b. Station 7 - Midbay; sediment more than 70% clay; RPD depth 4.5 cm
c. Station 10- Lower bay; sediment more than 90% sand; RPD depth 3.3 cm; water more saline than other two

A summary of the findings at the three stations is shown in Figure 13.

Standing stock biomass of benthic macroinfauna was greatest at the midbay site and lowest at the more oceanic lower bay site over the 2 years of observation (Figure 13). At the midbay site, however, there was a great deal of variation in these larger standing stocks. During the first year of observation, this station supported an average of less than 4 g/m^2 of benthic biomass. During the second year, these same sediments harbored macroinfaunal biomasses exceeding 100 g/m^2. The upper bay collection site consistently showed minimum standing stocks of benthic macroinfauna in the summer and fall (0.4 - 20.1 g/m^2) and maximum biomasses in the winter and spring (49.4 - 151.8 g/m^2). The standing stock biomass of benthic macroinfauna at the lower bay site was much less variable than biomass at the other two sampling stations, probably because of the environmentally stabilizing influences of oceanic waters from the gulf. The maximum biomass, of 47.1 g/m^2 was observed in the winter of 1982 and the minimum, 16.1 g/m^2, in the winter of 1983, indicating that consistent seasonal cycles in standing stock of the benthos did not

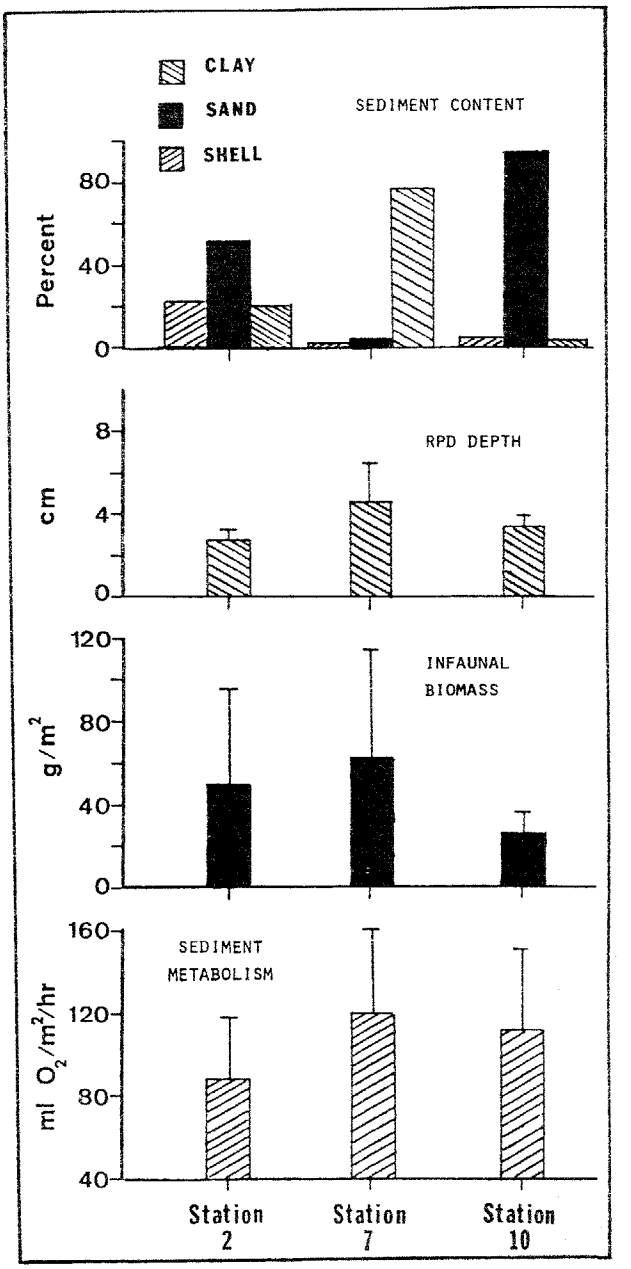

Figure 13. Total study period (1981-83) average measures for sediment structure characteristics, redox potential discontinuity (RPD) depth, benthic macroinfaunal biomass, and sediment metabolism at three stations in the Corpus Christi Bay Estuary. Bars represent 95% confidence intervals around the means.

occur here as they did at the other Corpus Christi Bay locations.

Measurement of benthic sediment metabolism in the open-bay bottom provides information about faunal respiration, feeding, reproduction, bioturbation and overall mineralization of organic material (decomposition). Data on sediment oxygen uptake permit comparison of the amount of benthic activity in various kinds of sediments in an estuary or between estuaries, and also estimates of the amount of primary consumer carbon production by the benthos (Rowe and Smith 1977).

The upper bay sampling site in Corpus Christi Bay showed the lowest mean sediment metabolism over the 2-year study period (Figure 13). The maximum average sediment oxygen uptake rate at this site was 144.8 ml $O_2/m^2/hr$ in July 1981; the minimum was 44.5 ml $O_2/m^2/hr$ in January 1982. The midbay site, as it did with standing stock biomass, exhibited the highest average rate of sediment metabolism. These higher rates were characterized by a low of 54.1 ml $O_2/m^2/hr$ in October 1981 and a maximum 181.2 ml $O_2/m^2/hr$ in July 1982. The lower bay collection site exhibited no seasonal trends for sediment metabolism with a low of 66.8 ml $O_2/m^2/hr$ measured in both October 1981 and April 1982 and a maximum recorded in January 1982 (171.7 ml $O_2/m^2/hr$).

Estimates of benthic production from the sediment metabolism measures indicated that the upper bay sediments were capable of producing an average of 0.96 ± 0.37 g $C/m^2/day$. In contrast, the more active sediments of the midbay area exhibited a mean benthic carbon production of 1.30 ± 0.54 g $C/m^2/day$. The more ocean-influenced lower bay site of Corpus Christi Bay exhibited a mean benthic production rate of 1.23 ± 0.46 g $C/m^2/day$.

In assessing the quality of food from primary consumers of the benthos for the secondary consumers that rely upon them, the standing stock biomass is not always a good measure. Many slow-growing larger animals such as bivalve mollusks have large biomasses, but even when the heavy shells are discarded, the remaining tissue may have a low potential for production as expressed by the turnover ratio (Production Rate/Average Biomass or P/B) of the organism. Other organisms such as polychaete worms and amphipod crustaceans are faster growing and shorter lived and may often achieve food production levels for the next trophic level which are over five times their standing stock biomasses.

The three sites investigated in Corpus Christi Bay revealed some very interesting trends with respect to turnover ratios of various benthic species assemblages. The lowest turnover ratio was calculated for the upper bay site, at 0.019. Similar calculations produced a turnover ratio of 0.021 at the midbay site and 0.046 at the lower bay site. The lower bay site supported the lowest average standing stock over the study (Figure 13), yet the benthic populations in these sandy sediments were the most productive as judged by calculation of turnover ratios. These trends are consistent with the kinds of benthic macroinfauna observed at these three collection sites in Corpus Christi Bay. The upper bay site often supported dominant populations of larger mollusks such as Mulinia lateralis (Holland et al. 1975). The midbay site was dominated by populations of the larger enteropneust Schizocardium sp. (Flint and Kalke 1985), especially after the winter of 1982. In contrast, the more productive lower bay site was usually dominated by smaller sized polychaetes such as Mediomastus californiensis (Flint and Younk 1983). Thus, as illustrated here, the only way to truly understand the dynamics of the benthos in assessing the production of biomass in an open-bay bottom is to have information not only on species composition but also on standing stocks and productivities. Only then can one really determine the importance of benthic species assemblages between open-bay bottom habitats with respect to the provision of biomass to secondary consumers.

Another major biomass production component of the open-bay bottoms of Texas estuaries includes those fauna, both shellfish and finfish, which are fished commercially. Commercial catches of shrimps, crabs, oysters, and finfish are recorded by various governmental agencies;

these annual tabulations can be used to make a comparison of secondary consumer biomass production by these species across all the Texas estuarine open-bay bottoms. Since typical fishery statistics report the total catch weight for a particular water body, however, in comparing water bodies this total may be misleading because the effort expended (i.e., number of trips) to obtain the poundage differ between estuaries. Therefore, in order to arrive at a more realistic comparison of shrimp fishery yields between Texas estuaries and to attempt to remove fishing biases, adjustments were made to catch statistics for 1970-1982, reported by National Oceanic and Atmospheric Agency (G. Kinkle, National Marine Fisheries Service, NOAA, Miami, Florida; pers. comm.). These adjustments included making corrections to the annual shrimp fishery yields for each Texas estuary based upon the assumption that the overall mean catch/effort value of 69.1 kg/trip) for the 13-year data base gave a good representation of the general open-bay bottom density of shrimp (g/m^2) for the Texas estuaries, while also taking into account the biases of shrimp statistics for different efforts both between estuaries and between years. Thus, if an annual mean catch/effort value for a particular estuary fell below this grand mean, which meant that the ratio of the two was below 1, then the total yielded shrimp poundage for this estuary was decreased by this proportion (multiplied by the ratio). This adjustment assumed that catch/effort was less because the density of shrimp may have been less in this estuary than the density assumed present to yield the overall grand mean catch/effort. Correspondingly, estuaries exhibiting catch/effort ratios above 1 had their yields increased assuming that the fishery was catching more because their overall estuarine density was greater. These adjustments were made to all Texas estuary shrimp yields between 1970-1982 and produced the results illustrated in Table 11.

The highest annual yield of shrimp biomass for open-bay bottoms of Texas estuaries came from the Galveston Bay Estuary. This estuary's yield was almost double any other along the coast. Next in total yield was the Matagorda Bay Estuary. The lowest yields came from either end of the Texas coast with Sabine Lake and the Upper Laguna Madre each yielding less than 10^5 kg/yr. Production of shrimp biomass caught by man on an areal basis for Texas estuaries showed a slightly different pattern (Table 11). Again, the most productive estuarine open-bay bottom was Galveston Bay. In contrast to total estuary yields, however, the second most productive Texas estuary on a per unit area basis was the Copano-Aransas estuarine system. Sabine Lake and the Upper Laguna Madre again exhibited extremely low production values and the Corpus Christi Bay Estuary also showed a shrimp population value below 1 $g/m^2/yr$.

It should be noted that shrimp fishery yield statistics present biomass production estimates for only a portion of shrimp populations in Texas estuaries. An additional quantity of shrimp biomass production serves as food for higher trophic levels of the estuary besides man, such as finfish and birds. In addition, an unknown proportion of shrimp biomass produced in the estuaries is subject to natural mortality from disease each year as well as maintenance costs in shrimp growth, survival, and reproduction. For example, Flint and Rabalais (1981) estimated that 22% of the offshore shrimp stocks served as brood stock for the next year's spawn and egg supply. Finally, a large portion of the shrimp populations in the estuaries contribute biomass to offshore shrimp production. For the majority of the above losses for biomass produced by shrimp in Texas estuaries, there is not enough information to make even an educated guess as to the values of these losses.

5.3 NUTRIENT REGENERATION

The basic requirements for maintaining a healthy estuarine environment, resulting in maximum production of fisheries, include high rates of primary production and sufficient supplies of nutrients. Although riverine input and land runoff often result in an adequate supply of nutrients to drive estuarine primary production of the open-bay bottom, there is now good evidence that the sediments at the bottom of these shallow habitats play

Table 11. Mean annual shrimp yields (head-on weight) for all Texas estuaries between 1970 and 1982.

Estuary	Open-bay bottom surface area (10^6 km^2)	Total converted yield[a] (10^6 kg/yr)	Annual production[b] ($g/m^2/yr$)	Contribution to total estuarine production (%)
Sabine Lake	183.41	0.028	0.156	0.5
Galveston Bay	1,416.89	2.414	1.705	43.7
Matagorda Bay	1,157.19	1.369	1.182	24.8
San Antonio Bay	551.36	0.640	1.160	11.6
Copano-Aransas Bays	452.77	0.670	1.481	12.1
Corpus Christi-Nueces Bays	432.98	0.345	0.798	6.3
Upper Laguna Madre	276.65	0.061	0.221	1.1
Total shrimp production for all estuaries		5.527		

[a] Total shrimp yield converted to account for effort-biases between estuaries (see text for explanation).
[b] Annual production only based upon fishery yields, and does not include shrimp biomass taken by other predators or migration from the estuarine systems.

an important role in the nutrient supply to euphotic primary production (Zestzschel 1980).

While a total picture of nutrient patterns and strategies for estuarine nutrient cycling is still lacking, quantitative data on major pathways of nutrient flux are now being collected. As Nixon (1981) has pointed out, our perspective on the importance of various components and mechanisms of nutrient cycling has changed markedly over the past decade. One of the most striking of these changes has been the widespread documentation of benthic remineralization as a source of recycled nutrients available for primary producers in several different types of aquatic systems (e.g., Davis 1975; Hale 1975; Rowe et al. 1977). This is in direct contrast to the thought that water-column processes dominate estuarine remineralization (McCarthy et al. 1974). It has recently been suggested that benthic remineralization and nutrient regeneration from the sediments in estuaries may be the primary factor controlling the relative availability of nitrogen and phosphorus for photosynthesis (Nixon et al. 1976, 1980).

The significance of the bottom sediments' supplying nutrients to Texas estuaries becomes apparent when one considers the semiarid climate that many of these estuaries are subject to and the variable riverine flow into these systems. Although riverine inputs, and to a lesser extent, exchanges with the open gulf oceanic waters, result in periodic nutrient inputs to the estuarine habitat, the recycling of nutrients regenerated in the bottom sediments may be most important to the open-bay bottoms over the long term. The continuous input of organic material to the sediments from the water column and

mineralization of this material with ultimate regeneration of nutrients at the mud-water interface, referred to as benthic-pelagic coupling, may actually buffer nutrient availability to the estuary, thereby dampening the effect on primary production of periodic external nutrient supplies such as river flow.

Release of ammonium nitrogen from the sediment surface usually dominates nitrogen fluxes at the mud-water interface in at least one Texas estuary (Flint et al. 1982). Unfortunately, very little information for the regeneration of nitrogen from sediments exists for Texas estuaries other than Corpus Christi Bay. Comparative benthic fluxes of ammonium-nitrogen from other selected estuaries and coastal ecosystems are presented in Table 12, along with available general information for the Gulf of Mexico. The values for the Patuxent Estuary were among the highest regeneration rates recorded. The North Carolina Estuary, Buzzards Bay, and Narrangansett Bay were all much lower in ammonium nitrogen regeneration rates, while the annual mean of all stations investigated for the Corpus Christi Bay Estuary was above these, but much lower than rates observed for the Patuxent Estuary. The Texas estuarine rate was also greater than regeneration rates for coastal sediments of the northwestern Gulf of Mexico.

At three sites in Corpus Christi Bay, described earlier in this chapter (Figure 13), rates of sediment ammonium nitrogen regeneration were measured seasonally over 2 years. At the upper bay collection site (Station 2), the highest mean rate for all sites for the 2 years of measurement was observed. This mean rate was 144.4 µg-at NH_4-N/m^2/hr with minimum rates of regeneration from the sediment observed in the

Table 12. Mean annual benthic fluxes of ammonium-nitrogen from selected estuarine and coastal systems.

Water body	Benthic ammonium flux (µg-at NH_4^+-N/m^2/hr)	Source
Patuxent Estuary	295	Boynton et al. (1980)
Cap Blanc	250	Rowe et al. (1975)
New York Bight	150	Rowe et al. (1975)
Corpus Christi Bay Estuary (Texas)	127	Flint in prep.
North Carolina Estuary	120	Fisher and Carlson (1979)
Narragansett Bay	100	Nixon et al. (1976)
Northwestern Gulf of Mexico (coastal)	90	Flint in prep.
Buzzards Bay	68	Rowe et al. (1975)
La Jolla, California	30	Hartwig (1976)
Loch Thurnaig, Scotland	25	Davies (1975)
Sea of Japan	< 5	Propp et al. (1980)

fall of each year and maximum rates in the summer at 413.8 and 384.4 μg-at NH_4-N/m^2/hr for July 1981 and July 1982, respectively.

The midbay site of the Corpus Christi Bay Estuary (Station 7) exhibited the second highest mean rate of nutrient regeneration over the study period at 137.2 μg-at NH_4-N/m^2/hr. Variation at this collection site was less than at the upper bay site. With the exception of lowest rates observed in January (83.6 μg-at NH_4-N/m^2/hr) of each study year, however, seasonal patterns at the midbay site were not apparent. Maximum regeneration rates at this site occurred in April 1982 at 223.5 μg-at NH_4-N/m^2/hr.

The lower bay site of this estuary, which was influenced by oceanic waters from the Gulf of Mexico, exhibited an annual mean regeneration rate of 99.7 μg-at NH_4-N/m^2/hr. This rate was very close to that observed for the sandy sediments in the coastal Gulf of Mexico (Table 12). Minimum regneration rates were consistently observed in October of each year (21.8 μg-at NH_4-N/m^2/hr in 1982) and the maximum rate of 236.2 μg-at NH_4-N/m^2/hr was measured in April 1982.

In general, nutrient regeneration rates from the sediments of the Corpus Christi Bay Estuary were greater and also much more variable in the upper reaches of this system. As oceanic influences increased in the lower reaches of the estuary, nutrient regeneration rates declined. There seemed to be no consistent seasonal pattern in nutrient regeneration at all three sites in the open-bay bottom and no defineable correlation between sediment type of the sampling site and nutrient regeneration rate. Although the midbay site, characterized by a high clay content (Figure 13), exhibited higher rates of nutrient regeneration than the lower bay site with more than 90% sand in the sediments, the upper bay site with more than 50% sand (Figure 13), exhibited the highest mean rate of nutrient regeneration.

Another source of nitrogen for phytoplankton production in the Corpus Christi Bay Estuary comes from Nueces River flow. An interesting comparison can be made between this flow as one source of nutrients and the estuary sediments as another source, to emphasize the importance of open-bay bottom sediments to estuarine production. Table 13 illustrates the difference in total nitrogen supplied from the Nueces River during four periods of a high flow year and nitrogen in the form of ammonium nitrogen recycled from the bottom sediments of this estuary. During all periods the bottom sediments contributed more nitrogen to the system. Only in October, when riverine nitrogen represented 30.5% of the nitrogen from both sources, did the Nueces River appear to have nearly as much impact on the estuary as the sediments with respect to nutrient supply.

As illustrated above, benthic nutrient regeneration in the shallow waters of many estuaries is now recognized as a potentially important process to these ecosystems in terms of maintaining high rates of primary production. According to numerous measurements made in different estuaries, a sizeable portion of nitrogen needed for phytoplankton photosynthesis is supplied by the benthos. Boynton et al. (1980) estimated that fluxes of nitrogen from Patuxent Estuary sediments could satisfy up to 190% of the nitrogen required by primary producers in the open-bay bottom of this estuary. Since it is becoming more widely accepted that the open-bay bottom sediments of estuaries play a significant role in nutrient supply to these systems, the role of benthic fauna as potential regulators of this process must be evaluated.

Evidence from a variety of investigations demonstrates why benthic fauna are important in the process of sediment nutrient regeneration. Sediments inhabited by high densities of deposit-feeding benthic invertebrates undergo considerable particle transport in as much as the upper 30 cm of the seafloor (Rhoads 1974; Aller and Cochran 1976; Aller 1978). The vertical movement of materials and burrow irrigation by these creatures expose nutrient reservoirs to overlying waters that would not otherwise be available (see Figure 14), as illustrated by the previously described effects of the deep-burrowing enteropneust Schizocardium sp. on the sediment structure in Corpus Christi Bay.

Table 13. Comparison of Nueces River inorganic nitrogen inputs to the Corpus Christi Bay Estuary with sediment ammonium-nitrogen regeneration during the months of January, April, July, and October. Nutrient regeneration is based upon mean flux from three sampling sites and then expanded over the total day for the entire open-bay bottom surface area (432.98 km^2) of this estuary. Riverine inorganic nitrogen input is represented by the maximum mean value for each month over 5 years of study (1972-1976) according to data from the Texas Department of Water Resources (1981a).

	January	April	July	October
Nueces River total inorganic nitrogen input (10^4 kg/day)	0.090	0.069	0.139	0.436
Estuarine sediment ammonium-nitrogen regeneration (10^4 kg/day)	1.119	3.852	4.280	0.994
River contribution as percent of total	7.4	1.7	3.2	30.5

To obtain further information on the potential role of benthic fauna in regulating sediment nutrient regeneration rates, laboratory experiments were conducted on experimental estuarine benthic communities (Flint and Kalke 1983). If fauna were removed from the sediments and nutrient regeneration rates changed, one could conclude that the fauna played a role in this process. Eighty days after treatment of benthic faunal-colonized sediments with methyl parathion, an insecticide to kill fauna and eliminate the effect of their activity on sediment processes, there were significant differences observed between control and treated sediments for nutrient regeneration rates. The nutrient fluxes from the sediments decreased by half the control rate in the treated replicates. This treatment changed the benthic communities dramatically, reducing biomass to near zero, and eliminating many species, resulting in decreases in metabolism of the sediments. These experiments indicated that a decrease in the faunal activity within marine sediments was directly related to a decrease in the flux of ammonia from these sediments, implicating the fauna in the regulation of nutrient regeneration. In conjunction with the change in benthic species assemblage and biomass after treatment in these experiments, there were also significant changes in the sediment RPD depth, where the RPD of treated sediments was much shallower than in untreated sediments. This again was related to the activities of the control versus treated fauna with respect to bioturbation of the deeper sediments.

The significance of the open-bay bottom sediments of Texas estuaries becomes apparent when one considers the information presented above. The contribution of nutrients by these sediments to the requirements for phytoplankton production can be sizeable. The role that benthic fauna inhabiting these sediments play also appear to be important in the mechanisms which regulate benthic nutrient regeneration in the open-bay bottom. The functions of these fauna in the benthos can thus be related to the overall functioning of the ecological system of the entire coastal region.

5.4. FOOD CHAIN RELATIONSHIPS

Nutrition by organisms inhabiting estuaries is gained through two types of food chains: one based on grazing, which starts with the use of carbon produced by photosynthesis; and the other based upon the consumption of carbon from both autochthonous and allochthonous detrital

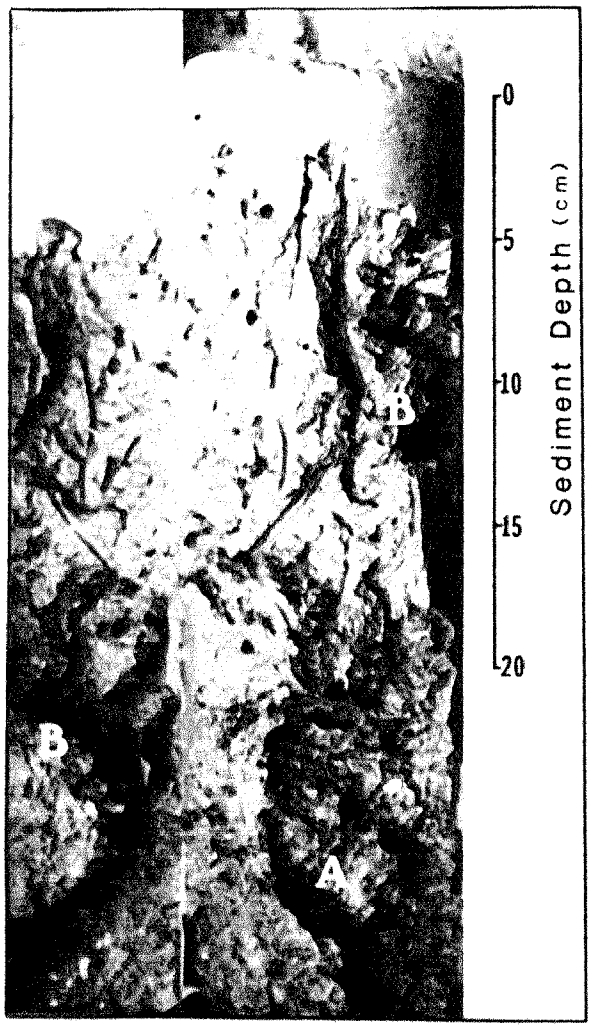

Figure 14. Photograph of a sediment core (split) taken in Corpus Christi Bay at a mid-estuary sampling site after colonization by *Schizocardium* sp. Burrows of this enteropneust are indicated (A) as are its feeding pockets (B) in the sediments.

material and associated microbial populations. Both kinds of food chains are present in Texas estuarine open-bay bottom biotopes, although they are not well defined. Because detrital material is so conspicuous in the guts of many open-bay bottom consumers (e.g., Tenore 1977; Alexander 1983), the majority of food chains in this biotope are thought to be detritally driven.

For Texas estuaries, hypothesized simple food chains for both types of carbon channeling, primary producer-based and detrital-based, are illustrated in Figures 15 and 16. For example, the primary producer-based food chain (Figure 15) starts with carbon-fixers (phytoplankton) in the estuary. This trophic level provides nutrition to both invertebrates and fish as primary consumers. Carbon transfer from phytoplankton goes primarily to zooplankton feeders and from here to the predators of the water column such as redfish, birds, and man. As a rule, this food chain is relatively simple and straightforward. Very few fish within the estuary are solely planktivores, and thus, this type of food chain is usually limited in its occurrence in the open-bay bottom. The planktivores of the estuary, however, such as Anchoa mitchilli, are some of the most abundant fish species present. This further attests to the minority of organisms that are involved in the primary producer-based food chain, since the few species using this feeding strategy are able to dominate for lack of competition by other species.

The detritus-based food chain, on the other hand, can be extremely complicated and have many more links between consumers than the primary producer-based food chain. This food chain is also much more difficult to detect and follow in nature. As illustrated in Figure 16, the detritus food chain starts with organic input to the estuary from outside (allochthonous material) as well as input to the sediments of the estuary from its own organic carbon production (autochthonous material), usually within the water column. Microbial populations colonize this detrital material and in addition to their role in mineralization, many ecologists feel that this living portion of the detritus provides the primary nutrition to consumers (e.g., Newell 1970; Tenore 1972). The majority of detritus in the benthos is consumed by benthic invertebrates, primarily the deposit-feeding polychaetes, amphipods, and bivalves. Some of the detrital material of the sediments, however, may also be consumed by mobile epifauna (e.g., shrimps and crabs) as well as some fish (e.g., striped mullet). There are fauna within the sediments that serve as secondary consumers (e.g., predaeous polychaetes, small burrowing crabs) as well as the invertebrates living on the

sediments such as the shrimp. Numerous species of fish also feed upon the invertebrate sediment dwellers; then there are the tertiary consumers, predaceous fish that feed on the smaller bottom-feeding fish. As Figure 16 suggests, the detritus-based food chain is extremely complex, compared to the primary producer-based food chain (Figure 15) of the open-bay bottom.

5.4.1 Organic Carbon Source

Few studies have attempted to determine the organic carbon sources and to estimate input or utilization rates of organic carbon in the open-bay bottoms of Texas estuaries. Several different potential sources of carbon, both allochthonous and autochthonous, have been estimated as input to the open-bay bottom area of Corpus Christi Bay Estuary (Table 14). Oppenheimer et al. (1975) calculated that waste discharge from sewage treatment plants and industrial complexes around the estuary accounted for 1.1 x 10^6 kg C/yr of input to estuarine waters. Armstrong (1982), using data from the Texas Department of Water Resources (1981a), estimated that a total of 8.2 x 10^6 kg C/yr was supplied to Corpus Christi Bay from local land runoff plus the flow of the Nueces River. For the organic carbon produced by

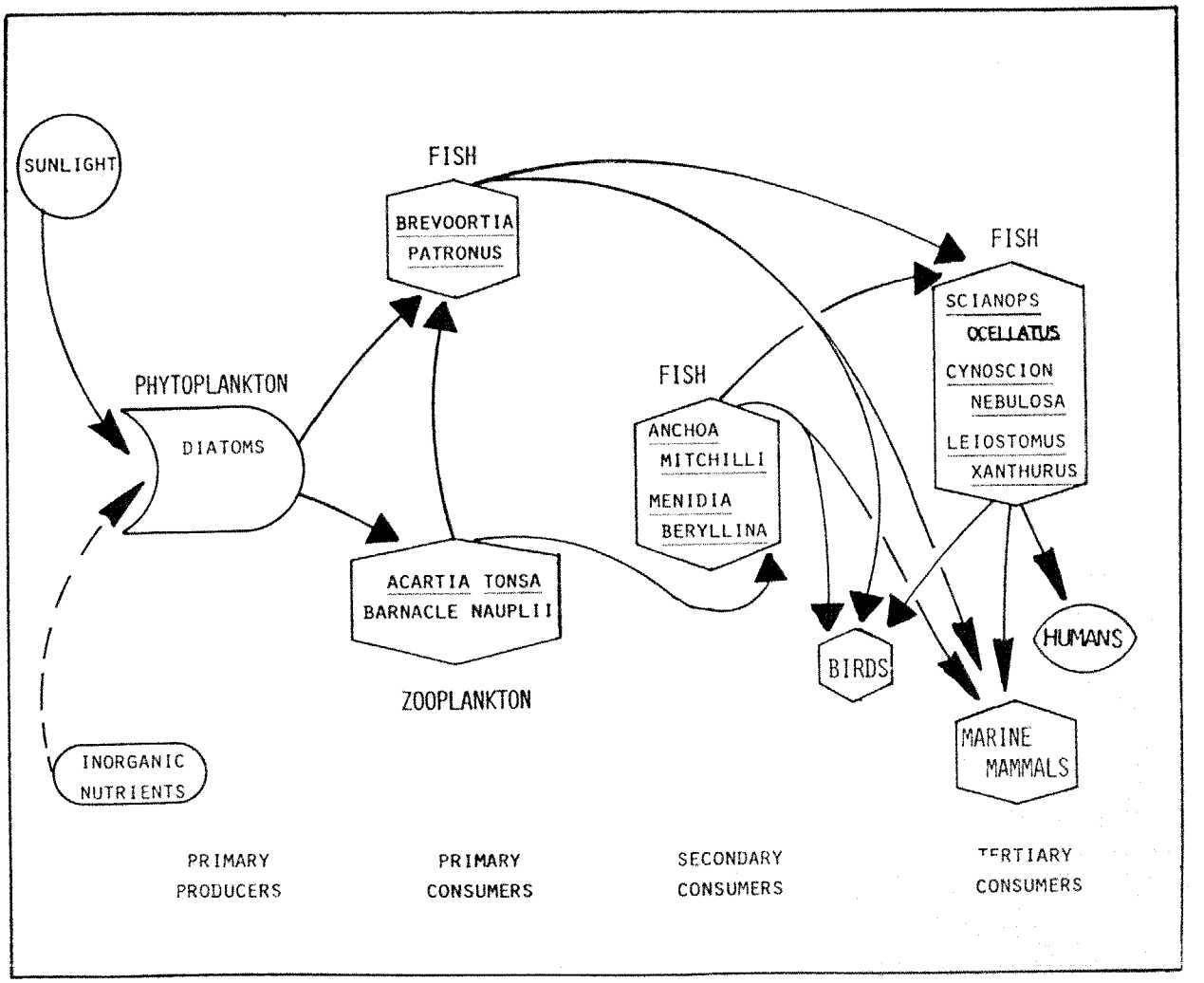

Figure 15. Hypothesized primary-producer-based food chain for Texas open-bay bottom biotopes.

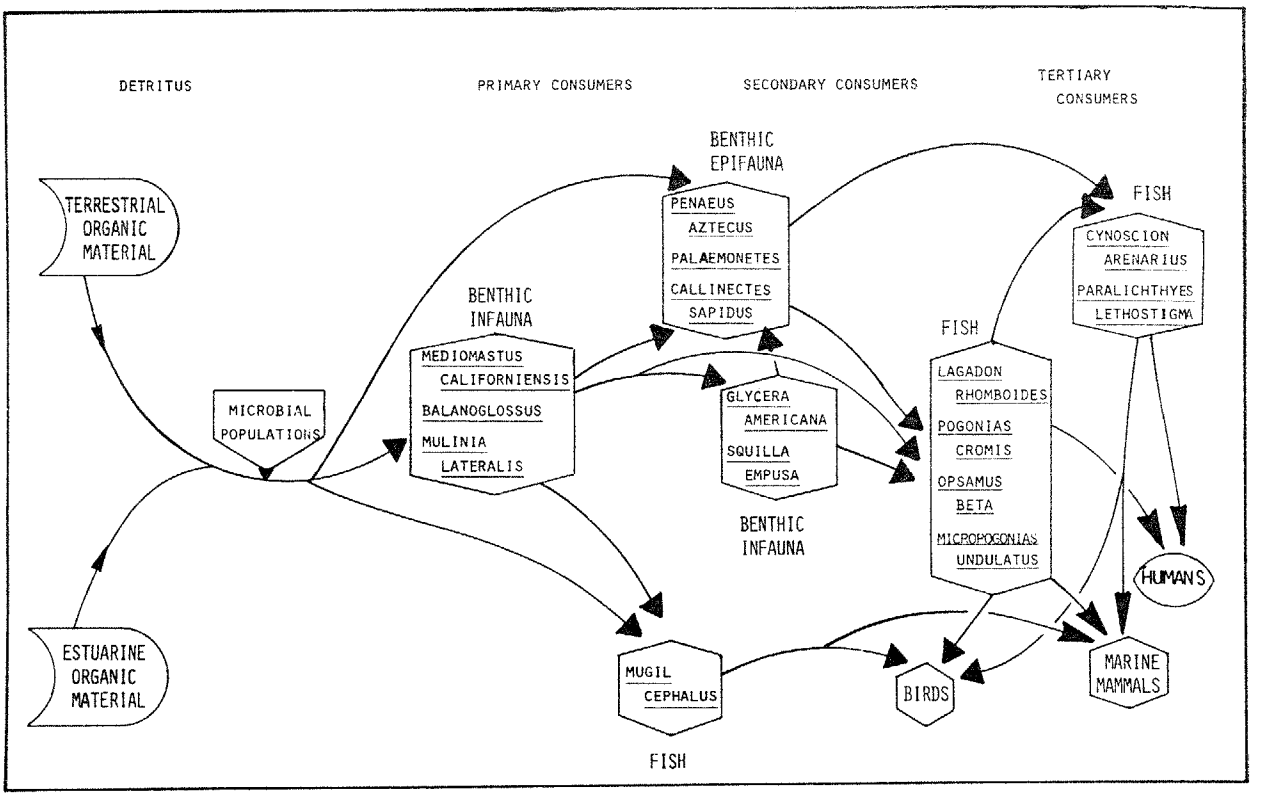

Figure 16. Hypothesized detritus-based food chain for Texas open-bay bottom biotopes.

Table 14. Organic carbon sources to the Corpus Christi Bay Estuary, with comparison to other estuaries.

Source	Contribution (10^8 kg C/yr)	Contribution (g C/m^2/yr)	Reference	Newport River[a] Estuary (g C/m^2/yr)	New England[b] Coastal Estuary (g C/m^2/yr)
Waste water discharge	0.011		Oppenheimer et al. (1975)		
Land runoff (other than riverine)	0.144		Oppenheimer et al. (1975)		0-10
Riverine inflow	0.013		Oppenheimer et al. (1975)		
Spartina marsh	0.660	52.2	Oppenheimer et al. (1975)	470	
Seagrass and epiphytes	0.539	1,043.9	J. Morgan, pers. comm.	403	125
Blue-green algal flats	0.045	388.9	W. Pulich, pers. comm.	34	90
Benthic diatoms of mud flats	0.015	133.1	W. Pulich, pers. comm.		
Pelagic phytoplankton	1.290	298.0	R.W. Flint, unpubl.	110	50

[a]Data from Peterson and Peterson (1979).

[b]Data from Marshall (1970).

182.11 km^2 of spartina marshes surrounding the Corpus Christi Bay Estuary, Armstrong (1982) further calculated that approximately 9.5 x 10^6 kg C was contributed annually to the open-bay bottoms of the Corpus Christi Bay Estuary (Table 9).

Primary productivity measurements on seagrass beds in Corpus Christi Bay (M. Morgan, Rutgers University, pers. comm.) including their associated epiphytes, indicated this component to be quite productive. Based on monthly measurements over a 7-month period from July to December, mean daily primary production was estimated to be 2.86 g C/m^2. This represented an annual production estimate of 1,043.9 g $C/m^2/yr$ for the seagrass beds in the Corpus Christi Bay Estuary as a potential source of organic detritus to the open-bay biotope for the estuary, not even including peak spring growth periods. In contrast, Marshall (1970) measured 125 g $C/m^2/yr$ primary production for seagrass beds (Zostera) in a New England estuary, and Peterson and Peterson (1979) indicated that the Newport River Estuary contained seagrass (Zostera) beds that produced 403 g $C/m^2/yr$ (Table 14).

As pointed out in Chapter 3, another potential source of organic matter to the open-bay bottoms is the benthic microalgae (diatoms) and blue-green algae that grow on some periodically submerged mudflats. From 36 daily measurements of blue-green algal mat primary productivity in the Upper Laguna Madre (W. Pulich, University of Texas Marine Science Institute, Austin; in prep.), it was estimated that annual production of these mats was 388 g $C/m^2/yr$. During peak spring growth periods, measurements were made for primary productivity rates of benthic microalgae inhabiting a mudflat in Corpus Christi Bay (W. Pulich, pers. comm.). These measurements revealed that the mudflat diatom assemblage could produce 1.1 g $C/m^2/day$. Since this measurement was made during peak bloom periods and these flats are probably only inundated (allowing diatom photosynthesis to occur) for one-third of the year, it was assumed that the annual production of mudflat diatom assemblages was 133.1 g $C/m^2/yr$. Therefore, these two biotopes together represented an annual production rate of 521 g $C/m^2/yr$ to the Corpus Christi Bay Estuary. In contrast, Marshall (1970) measured 90 g $C/m^2/yr$ of primary production for benthic microalgae in a New England Estuary, and Peterson and Peterson (1979) indicated that Newport River Estuary benthic microalgae produced 33.7 g $C/m^2/yr$ (Table 14). The total tidal flat surface area of the Corpus Christi Bay Estuary equals 22.71 km^2. Because there is no information concerning the amount of this area that is periodically inundated mudflat and the amount that represents blue-green algal mat, it was assumed that each biotope was represented by half the total surface area of Corpus Christi Bay Estuary tidal flats. On this basis, the benthic microalgae of the mudflats potentially contributed 1.53 x 10^6 kg C/yr to the estuary while the blue-green algal flats potentially contributed 4.46 x 10^6 kg C/yr (Table 14). These values are, of course, upper limits because it has been assumed that all primary production is exported, when in fact only a small portion is exchanged to the adjacent open-bay bottom area.

The surface area of Corpus Christi Bay Estuary is dominated by open-bay bottom (432.98 km^2). Thus, one would expect that the major source of organic matter to the estuary would come from pelagic phytoplankton production. From a total of 62 measurements of phytoplankton primary production, taken every three months at eight stations around the estuary from June 1981 to January 1983, it was estimated that the mean daily primary productivity rate (as measured by ^{14}C) was 0.816 g $C/m^2/day$ (Flint, 1984). Corpus Christi Bay phytoplankton produced 298.0 g $C/m^2/yr$, compared to 110 g $C/m^2/yr$, for the Newport River Estuary (Peterson and Peterson 1979), 50 g $C/m^2/yr$ for a New England Estuary (Marshall 1970), 90 $C/m^2/yr$ for St. Margaret's Bay, Nova Scotia (Platt 1971), and 380 g $C/m^2/yr$ (estimated by the oxygen method) for Long Island Sound (Riley 1956). On an annual basis for the entire open- bay bottom surface area, organic carbon contributed to the estuary from phytoplankton photosynthesis equalled 1.290 x 10^8 kg C/yr (Table 14).

Although it is currently impossible to state unequivocally which of the above sources of organic carbon production are

the most significant suppliers of nutrition to the primary consumers of the open-bay bottoms in Texas estuaries, it is possible to make certain generalizations. The detritus-based food chains are much more complex than the primary producer-based food chains. In addition, the consumers in the detritus-based food chain may go through a couple of trophic level changes during their development into adults. A progression of trophic changes through development as a function of increasing body size is common among marine animals (Peterson and Peterson 1979). This tends to further complicate the links of the detritus-based food chain. Most of the organic carbon sources for the Corpus Christi Bay Estuary (Table 14) appear to be more productive suppliers of nutrition to the estuary than they are in other comparable estuaries that have been studied. Although many of these sources are extremely productive, the dominating supplier of carbon to the system appears to be phytoplankton. These results are similar to those for Galveston Bay in which over 95% of the annual carbon flux to the Bay came from phytoplankton (Armstrong and Hinson 1973) and for Matagorda Bay in which almost 99% was from phytoplankton (Ward and Armstrong 1979).

5.4.2 Secondary Carbon Production

In addition to the mechanisms that bring carbon into the estuary, there are those components of the system that transfer it through and remove it from the estuary. As described previously, the group of consumers that is most pivotal in the transfer of carbon through the estuary, and probably also the group for which most information exists, is the estuarine benthic invertebrates, primarily the macroinfauna.

For the Corpus Christi Bay Estuary, data for 2 recent years have been collected to estimate benthic macroinfaunal production using *in situ* sediment incubation chambers and measuring sediment metabolism (Flint and Kamykowski 1984). To estimate benthic carbon production from sediment oxygen uptake, Rowe and Smith (1977) equated the sedimentary oxygen uptake with energy consumption of the sediment inhabitants. The amount of organic carbon converted to carbon dioxide can be estimated by means of a Respiratory Quotient table, according to their methods. The assumption used to convert oxygen uptake to benthic carbon production is RQ = 0.85, or 1 ml O_2 = 0.456 mg carbon produced.

From a total of 24 sediment metabolism measurements made over 2 years at three sampling sites in Corpus Christi Bay, it was calculated that a mean rate of carbon production for the benthos of this open-bay bottom biotope was 1.16 g $C/m^2/day$. This represented a rate of 424 g $C/m^2/yr$ for the Corpus Christi Bay Estuarine benthos of the open-bay bottom and a total carbon production by these primary consumers of 1.837×10^8 kg C/yr. Boynton et al. (1980) estimated that benthic annual production in the Patuxent Estuary amounted to only about 300 g $C/m^2/yr$.

Fishery catch statistics can be used to estimate finfish production, also (Table 15). Armstrong (1982) calculated that the mean annual finfish yield for the Corpus Christi Bay Estuary was 0.169×10^5 kg/yr; converting to carbon according to assumptions of Oppenheimer et al. (1975), at a factor of 10%, this yield is 1.169×10^4 kg C/yr. Bowman et al. (1976) calculated that for Corpus Christi Bay, the recreational yield of finfish was 2.6 times the commercial yield, or 3.039×10^4 kg C/yr. These investigators also assumed a 50-to-1 ratio of finfish to shrimp biomass in shrimp trawls, which amounted to 1.725×10^5 kg C/yr. Porpoise that live in the Corpus Christi Bay Estuary represent a population of approximately 300 and eat an average of 18.2 kg fish/day (Oppenheimer, pers. comm.). Based on these estimates the resident porpoise population would consume 1.99×10^5 kg C/yr of finfish production. If one assumes that, similarly to shrimp biomass production estimates, the various data on finfish production do not reflect losses for mortality from disease, predation by other fish, migration from the estuary, or natural metabolism maintenance, then the total of all losses of carbon for finfish discussed above can be increased. For the sake of argument, it is assumed here that all losses for finfish that have been quantified above represent only 50% of the carbon production of finfish in the Corpus

Table 15. Estimates of finfish carbon production for the Corpus Christi Bay Estuary.

Source	Production (10^6 kg C/yr)	Reference
Commercial fish catch	0.012	Armstrong (1982)
Recreational fish catch	0.031	Bowman et al. (1976)
Finfish yield from shrimp trawls	0.173	Bowman et al. (1976)
Bird catch of fish	0.714	Bowman et al. (1976)
Porpoise catch of fish	0.199	C. Oppenheimer, pers. comm.
Additional 50% to cover natural mortality, migration, metabolism maintenance, etc.	1.129	See text for assumptions
Total annual production	2.258	
Areal production	5.218 g C/m^2/yr	

Christi Bay Estuary and do not include losses to migration, metabolism maintenance, etc. Thus, the estimated production of finfish for the estuary, including assumptions (Table 15), is 2.259 x 10^6 kg C/yr or 5.218 g C/m^2/yr.

5.5 BENTHIC ROLE IN ECOSYSTEM FUNCTION

To adequately address the importance of the benthos of the open-bay bottom in the overall functioning of this biotope, it is best to view the estuary from the perspective of material flow (i.e., carbon), where the fauna of the benthos are directly involved. A hypothetical food chain for the Corpus Christi Estuary open-bay bottom is presented in Figure 17, showing the flow of carbon to various trophic levels. All the production rates for the various compartments of this food chain have been discussed above.

The riverine inflow, waste discharge, and land runoff carbon contribution comes from the sum of these in Table 14, expressed in an open-bay bottom areal basis (432.98 km^2) for the Corpus Christi Bay Estuary. Likewise, the seagrass and spartina marsh production estimates are a sum of these from Table 14 expressed on an areal basis. With respect to the several estimated carbon sources to this estuary's open-bay bottom habitat, pelagic phytoplankton contribute 62.1% of the total carbon, while seagrass beds and spartina marshes contribute another 30.5%. The transfer of carbon from the primary producer/detrital sources to the pelagic part of the food chain was estimated as follows. Zooplankton secondary production is unknown for the Corpus Christi Bay Estuary as well as all other Texas estuaries. The major planktivorous fish species of all Texas estuaries, however, is the bay anchovy, Anchoa mitchilli. Sheridan (in prep.) observed that this species comprised approximately 7% of the total fish biomass standing stock in Galveston Bay. If one assumes that a similar proportion exists for this species with regard to total finfish production (from Table 15),

then it can be estimated that this dominant planktivore exhibits a production rate of 0.4 g $C/m^2/yr$. Irrespective of zooplankton production in this estuary, if it is further assumed that two trophic levels must be passed through to support the populations of Anchoa mitchilli (phytoplankton-zooplankton, zooplankton-fish) and there is a 10% transfer efficiency at each level (Odum 1971), then approximately 40 g $C/m^2/yr$ from primary producer and detrital pathways are required to support this pelagic aspect of the open-bay bottom food chain.

After the carbon utilization for the pelagic levels of the Corpus Christi Bay Estuary food chain, 587.6 g $C/m^2/yr$ remains for other estuarine consumption (Figure 17). The majority of this carbon is diverted to the benthos of the estuary as has been shown for other coastal marine environments (Flint and Rabalais 1981). As Figure 17 suggests, most of this detrital carbon is required to support the 419.0 g $C/m^2/yr$ of benthic infaunal production in this estuary, but the absurdly high transfer efficiency (95% between trophic levels) has to be assumed. If the usual 10% transfer efficiency (Odum 1971) were assumed, approximately 10 times the amount of primary producer detrital carbon would be required to support the observed benthic carbon production. Thus, as discussed previously, the benthos of the open-bay bottom biotope of Texas estuaries receive the majority of primary-producer carbon and must be quite efficient in the utilization of this carbon. As further illustrated in Figure 17, the benthic component also serves as the major link between this primary-producer carbon and all other consumers of the estuary, with the exception of the small pelagic component discussed above.

Within the benthic infaunal species assemblages there are several predatory polychaetes such as Diopatra cuprea and Glycera americana. Where these polychaetes have been observed (Flint et al. 1981), they comprise approximately 1.2% of the total infaunal biomass. Using the same assumption used for calculating the production of Anchoa mitchilli populations, these benthic infaunal predators were assumed to make up 1.2% of total benthic production. This production of benthic infaunal predators is supported by 50 g $C/m^2/yr$ of benthic infaunal primary consumers (Figure 17), and leaves 368 g $C/m^2/yr$ of benthic infaunal production for other consumers.

Besides providing the open-bay bottom biotope with a large source of carbon for secondary consumers, the benthos has another role in this biotope, its contribution to nutrient regeneration. Using the ratio 6.6 for the C:N content of phytoplankton (Redfield et al. 1963), nitrogen requirements to support the observed annual phytoplankton production of the Corpus Christi Bay Estuary were calculated to be 45.2 g $N/m^2/yr$. Thus, approximately 48% of the nitrogen in this system can come from the benthos (Figure 17). There is, as previously mentioned, growing evidence suggesting that the benthic fauna of marine sediments play a large role in regulating this flux of nutrients from the sediment. Ward et al. (1982) present similar evidence for extensive nutrient cycling in Matagorda Bay and for a major role in this cycling by open-bay bottoms. It was estimated that about 20% of the nitrogen and 15% of the phosphorus used by phytoplankton to support primary production were recycled from the benthos.

Figure 17 indicates that there appears to be more than adequate production of carbon by the benthos of the Corpus Christi Bay Estuary to support the secondary consumer levels. Based upon the production estimates for shrimp (epifauna) and finfish, 10 and 40 g $C/m^2/yr$, respectively, go to support these secondary consumer levels from the benthos. The transfer of carbon from the finfish and the shrimp production to man, birds, and porpoise is simply the estimated yields of these secondary consumers from Table 11 and Table 15.

In summary, Figure 18 illustrates the pivotal role of the benthos in the open-bay bottoms of Texas estuaries. The benthos of this biotope truly serves as the major link between the primary production of carbon and detrital input of carbon for the estuary and the nutrition of other fauna. The benthos is an efficient trap of carbon and major transfer point for this carbon to higher consumer levels.

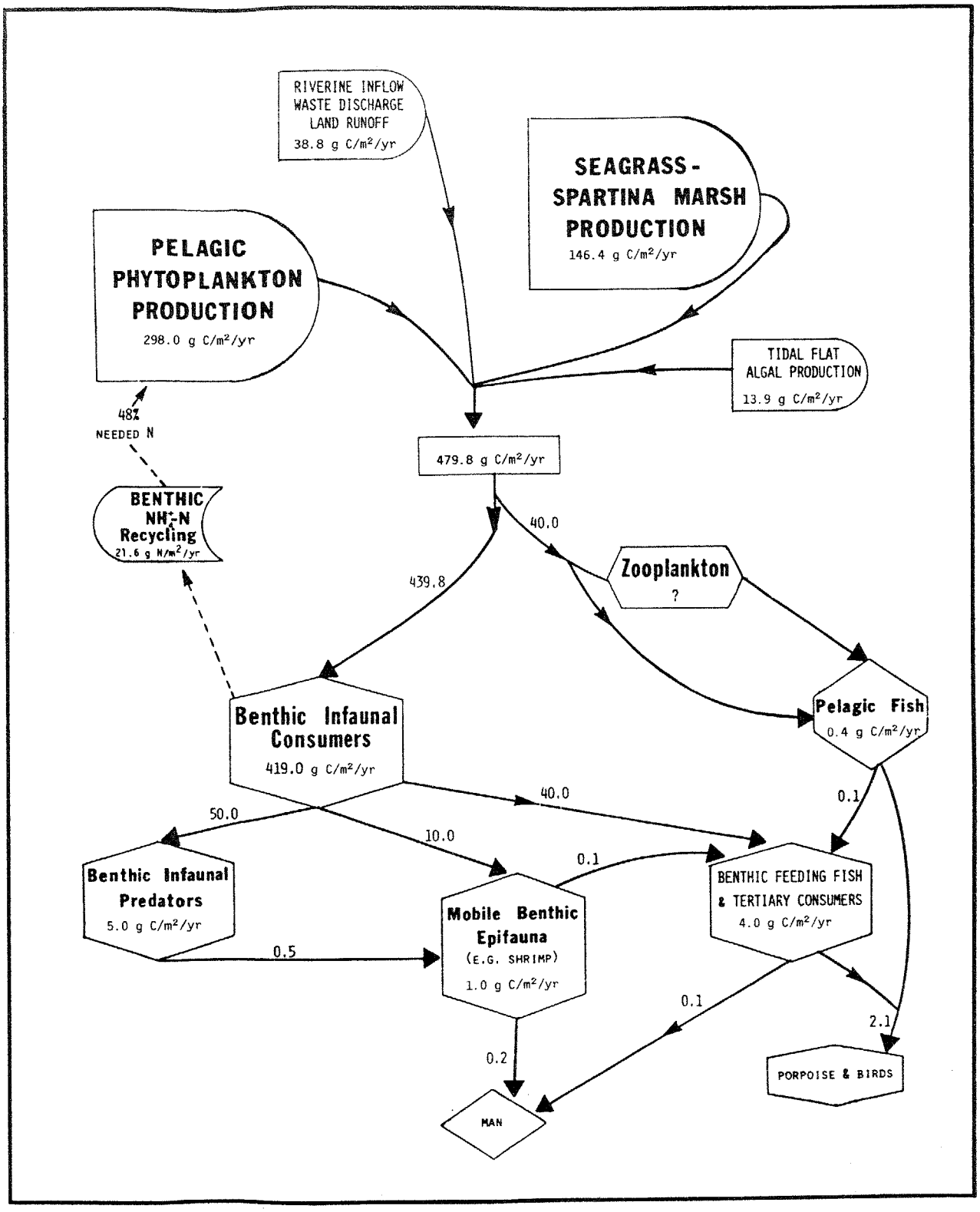

Figure 17. Hypothesized food chain for the Corpus Christi Bay Estuary showing flow of carbon between trophic levels. The flow rates are expressed in g C/m²/yr, similar to the production rates for each compartment. Production rates and flow rates are explained in the text.

The conceptual model in Figure 18 further illustrates the role the benthos plays in the cycling of nutrients in the estuarine open-bay bottom. The heavier lines show the flow of organic matter to the sediments and resultant return of nutrients, the mineralization products of this organic matter, to the water column to be cycled again by phytoplankton. This is the primary flow of organic matter and nutrients in the estuary contrasted to the lesser influence of riverine nutrients and oceanic inwelling. This primary flow of nutrients is mediated by activities of open-bay bottom benthos as discussed previously. Thus, the dynamic of the open-bay bottom biotope, resulting in the production of important fisheries, is the integrated product of trophic transfer processes and nutrient cycling processes, both of which rely heavily upon the functioning of the estuarine benthos.

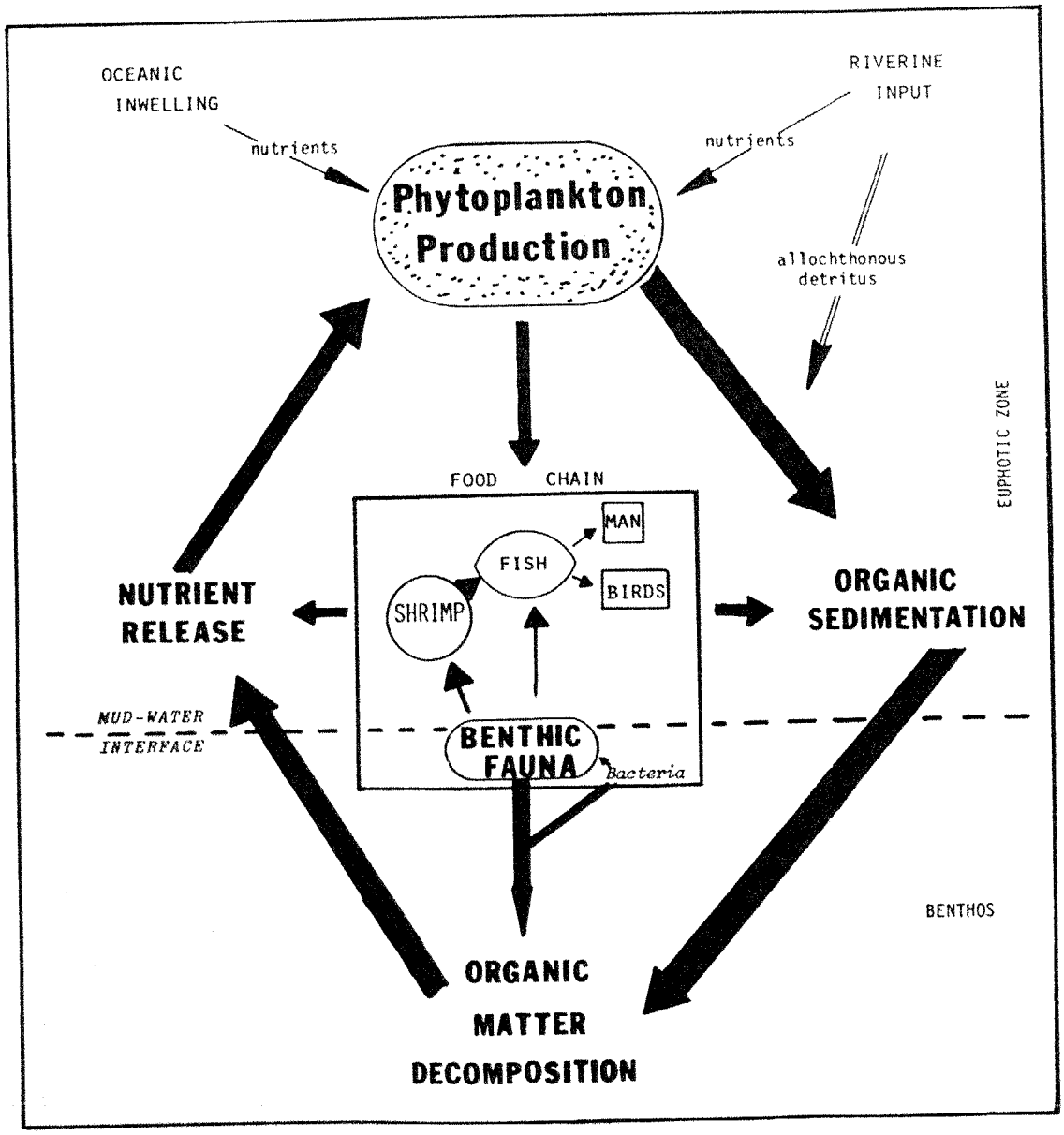

Figure 18. Conceptual model illustrating the role of the estuarine benthos in food chain dynamics and nutrient recycling, both important aspects of total ecosystem function.

CHAPTER 6.
MANAGEMENT CONSIDERATIONS

In preceding chapters, the bays of the northwest Gulf of Mexico have been described in terms of their physiographic and physical and chemical characteristics. The structure and function of the open-bay bottom benthic community have been discussed in detail, and the relations between this benthic community and adjacent and interacting communities have been described. With this background, it is possible to concern ourselves with management considerations for the open-bay bottom biotope and to include natural and human impacts in these considerations.

It is well known that estuaries are among the most productive ecosystems in the world (Odum 1971). Estuaries are also among the most stressed systems in the world due to the safe harbor they provide for ports and navigation, the food they provide for commercially and recreationally important finfish and shellfish, and the associated land infrastructure that supports all of these commercial activities. These uses of the estuary and the surrounding area are often incompatible with maintenance of estuaries as natural, productive systems. Not only must the immediate area around the estuary be considered, but activities upstream in the drainage basin must also be considered. There, increasing consumption threatens the supply of freshwater to the estuary, which is needed to mix with ocean water to make an estuary function as an estuary. The general scarcity of water in much of Texas and the small flows of water to Texas estuaries have prompted the State to consider freshwater inflow requirements.

In this chapter, consideration will be given to natural and human impacts that disturb the open-bay bottoms and how the system responds to both. In addition, specific recommendations for management of open-bay bottom systems will be presented.

6.1 NATURAL IMPACTS

Of all the natural impacts that may bear on estuarine systems the most important are geologic. That is, estuarine systems are ephemeral and their life spans can be measured in relatively short geologic time. Present Texas estuaries are around 10,000 years old, and their total life span can last only until the next glaciation period, when water will be lost to them once again and they will revert to dry land. Probably before that time, however, most estuaries will experience the end result of sedimentation, namely filling. Two Texas estuaries have experienced that fate, namely the Brazos River and the Rio Grande. While these estuaries are long and narrow, they no longer provide the broad, shallow type system which is characteristic of the rest.

Besides these two natural impacts, two others that have historically affected Texas estuaries perhaps more than human impacts are hurricanes and droughts. Droughts, whose impact may be more or less severe than hurricanes, are certainly of longer duration than hurricanes. Historically, droughts have occurred quite often in Texas. While there is no set return frequency of droughts, several have occurred during the last 30 years, of which one was quite severe. From 1950 to 1957, Texas experienced substantial decreases in normal rainfall and river flows were much below normal. Flows in some major channels were essentially zero. As a result, estuaries became so much more saline, that marine life forms were found in river mouths at the heads of the estuaries. Substantial changes occurred in some flora and fauna, and organisms requiring fresh

to brackish waters were forced far up into the river channels. In the benthic community, such organisms simply perished because of the unavailability of low-salinity water. When the 1950's drought broke in 1957, the rainfall pattern change was dramatic and extensive flooding occurred, changing what were near-marine salinity conditions in estuaries to essentially freshwater. Only the most euryhaline organisms or those that could quickly migrate into more saline waters were able to survive. Other drought periods have been less severe and the ends of the droughts have not usually been accompanied by floods of the magnitude of that in 1957. Changes in open-bay bottom populations and communities, however, are certainly effected by the changes in salinity and overlying water column as influenced by these meteorological events.

The other natural impact that may drastically affect the estuary is the hurricane. Three effects are immediately evident during a hurricane. First is the storm surge that usually impacts the estuary before the arrival of the hurricane. The storm surge drives saline ocean water into the estuary, raising salinities. Second is the high wind accompanying the hurricane and the waves generated by that wind. In the shallow Texas estuaries, these waves are large enough to greatly disturb the bottom sediment, to cause scour and resuspension, and undoubtedly disturb a substantial portion of the benthic community. The third effect is the heavy rainfall accompanying landfall of the hurricane. Often a normal year's worth of rainfall will be produced in a matter of a few days by a hurricane; the amount of runoff resulting will often change an estuary from brackish to freshwater conditions. Again, the major impact is the large salinity change produced by such inflows following the high salinities produced by the the storm surge. The mixing and high turbidity produced by wave action reduce primary production in the estuary for some period of time and certainly may limit food sources within the estuary during that time. It has been suggested, however, that hurricanes do provide some benefit to the estuarine system by causing nutrients to be recycled from the sediments to the overlying water column at a rate higher than normal. Such a pulse of nutrients stimulates primary production in the overlying water column unless turbidity is so great as to inhibit production; the nutrients eventually permeate the rest of the trophic levels.

Management of such natural impacts has been proposed in the following ways. First, the impacts of droughts may be offset to varying degrees by releases of water from upstream reservoirs so that some minimum supply of freshwater reaches the estuary. The major objection to such a proposition is that people in the drainage area receiving their water supply from this freshwater source will need the water more than the estuary and priority will be given to supplying people. While such a decision may be needed in severe droughts, a release policy to supply freshwater inflows during less critical dry periods might offset some of the deleterious impacts of low freshwater inflows. For several years, the state of Texas Department of Water Resources has studied the freshwater requirements of each of the major estuaries and measured freshwater inflow requirements to maintain present day productivity, to enhance it, and to allow a decrease. These flows turned out to be close to average freshwater inflows. Whether such flows could be assured on a consistent basis, and during drought periods in particular, would depend on upstream water development and release policies for reservoirs. Hurricanes are not as amenable to management as freshwater inflows, but proposals have been made for hurricane barriers across bays to limit the intrusion of storm surges.

6.2 HUMAN IMPACTS

While urbanization produces marked changes on the periphery of an estuary via shoreline modifications, salt marsh filling, waste discharges, and so forth, the open-bay bottom community is relatively unaffected by such activities. The major human impact in this community is through dredging for navigation channels and for shell. Peterson and Peterson (1979) reviewed the impacts of dredging in estuaries in their community profile on intertidal flats. In particular, they reviewed the impact of dredging on the benthic

community and the recovery of that community following dredging purterbation. They cite the work of McCall (1977) on recolonization of defaunated mud in Long Island Sound. He found that these sediments were rapidly recolonized by opportunistic benthic species such as polycheates and arthropods. Such species are characterized by certain life history features, namely rapid development, frequent reproduction, fast growth, high recruitment rates, and high mortality rates. Peterson and Peterson (1979) also suggest that opportunistic species are preyed upon heavily in soft sediments and may be responsible for much of the energy flow from the benthic invertebrates to fishes, crabs, and shore birds. The work by Flint and Younk (1983) in Corpus Christi Bay and the carbon budgets presented in earlier chapters bear out this suggestion for Texas estuaries. To minimize the impacts of dredging on the benthic community, Rhoads et al. (1978) have suggested careful seasonal timing of dredging activities in shallow waters to minimize the impact on natural estuarine systems. For example, dredging during winter months would have the least impact on the entire system, in part at least because the opportunistic species that would recolonize the area would not appear until springtime. Peterson and Peterson (1979) conclude that the intertidal community is capable of withstanding carefully controlled periodic dredging without substantial long-term ecological impact, although they caution that this pattern may apply more in temperate-zone estuaries than in tropical systems where natural environmental variability is reduced.

Another human impact worthy of note here is the impact of waste discharges on the open-bay bottom benthic community. In confined areas, the discharge of organic materials may produce localized areas of low oxygen concentration, especially near the bottom, which will impact the benthic community. Sludge deposits produced by solids settling from these discharges exacerbate the problem and change the sediment composition for the benthic community. Such problems are being alleviated with the levels of treatment now required of discharges, and the water quality problems that remain are those of toxic materials. Synthetic organics and heavy metals discharged with municipal and industrial waste waters find their way into the open-bay bottoms primarily because of the tendency of these toxics to associate with the particulate phase. This tendency, measured as the partition coefficient between water and particulates, varies widely for different materials, but while concentrations of these toxics in the water column may be quite low, it is typical to find high concentrations in the sediments. Whether these concentrations are producing deleterious effects on the organisms in the benthic community is not known, although it was pointed out that some of the concentrations measured were above EPA water quality criteria for sediment and thus did present a hazard to organisms in those sediments. Control of these toxic materials in the effluents of discharges is the primary mechanism for management of this situation.

6.3 RECOMMENDATIONS FOR MANAGEMENT

The Texas coast is undergoing extensive development, and with this development come increased pressures of urbanization on and waste discharges to the estuaries. With a population increasing faster than other parts of the United States, these problems will become more acute in the future (Thayer and Ustach 1981). While many studies have been directed toward understanding the effects of pollutants in the estuarine environment, few provide solid cause-effect relationships, which are necessary to developing management recommendations for control of the pollutants. It is becoming increasingly apparent that long-term subtle impacts are producing significant ecosystem degradation beyond the population level (Van Lopik 1980). Some available methodologies for measuring the environmental effects of pollutants no longer meet the demands of scientific inquiry or the legal mandates imposed upon environmental managers, and consequently there is a definite need for the development of realistic monitoring strategies that are integrative, sensitive, and recognize subtle warning signs.

6.3.1 Impact Assessment

It is not economically feasible to study an entire ecosystem and derive sufficient information toward understanding and managing that ecosystem to justify the expenditure. Therefore, in assessing the state and change of the ecosystem, either during natural functioning or during stress and disturbance, numerous design factors should be incorporated into a monitoring effort that focus upon components lower than the ecosystem level (i.e., communities, populations, chemical cycling, etc.). These design factors must provide as much information concerning the entire system as possible, emphasize system components that represent a "barometer" of environmental events, contribute towards an integrated understanding of ecosystem functioning, and minimize expenditure. One approach to monitoring and developing an understanding of the open-bay bottoms of Texas estuaries would be to focus upon the benthic habitat. The reasons for concentrating on the benthos have already been discussed and are summarized in the theoretical model presented in Figure 19. This model illustrates hypotheses as to how the benthos functions under both natural environmental conditions and during periods of disturbance.

Recently, laboratory and field experiments have been conducted on entire benthic species assemblages of the estuary to collect data for either proving or disproving the hypotheses presented in Figure

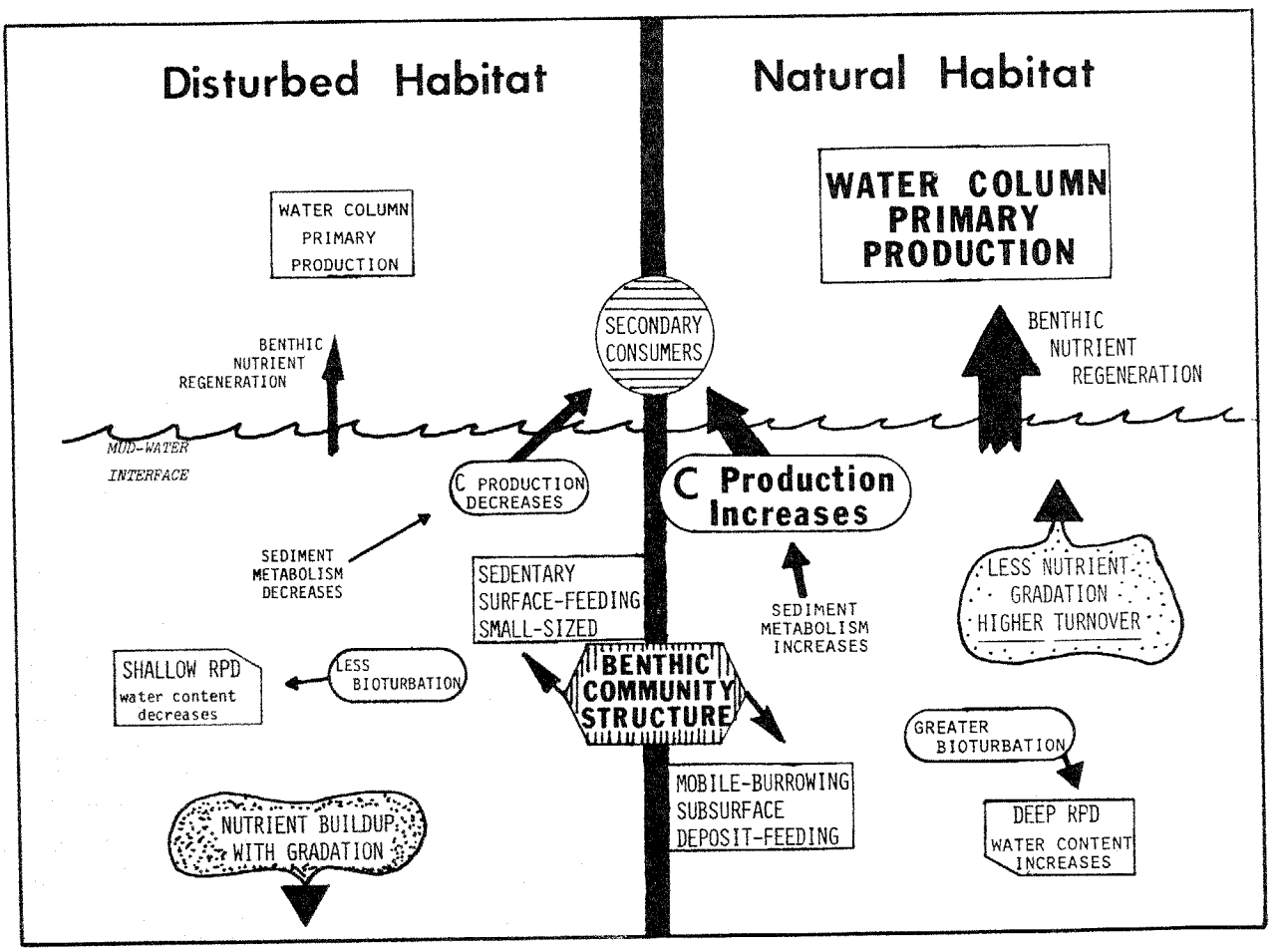

Figure 19. Conceptual model illustrating the potential processes that go on in the benthos, how community structure can affect these, how the benthic processes are linked to dynamics in the overlying waters, and the effect on all these processes from an environmental disturbance. Size of arrows and compartments imply the relative size of concentrations or biomass.

19 (e.g., Flint and Kalke 1983). The results of these experiments indicate that the natural benthos and the processes that these fauna play a role in regulating are sensitive to disturbance and show significant changes after a perturbation to the sediment surface. In all cases studied so far, however, after the initial impact, both the faunal abundance and biomass readily recover and the process rates, such as sediment nutrient regeneration and benthic metabolism, return to control levels after a short time (e.g., 60 days).

A monitoring strategy focusing on the points covered above enable us to assess integrated impacts to entire ecosystems while minimizing the costs, by concentrating on key processes within the ecosystem. Using the estuarine benthos ecological change may be assessed by evaluating community characteristics and relating the impact of this change to the ecosystem by measuring important processes that these benthic communities regulate. By concentrating on selected processes like nutrient regeneration, benthic metabolism, and secondary production, the long-term fate of an ecosystem can be predicted, since these processes are all important to the integrated health of that ecosystem.

For years the benthos has been studied by identifying, counting, and weighing organisms, often to meet the goal of assessing the change a disturbance has caused in an environment. These data by themselves do not contribute much to our knowledge concerning processes of the benthos. Other than obvious direct impacts to the organisms examined, conclusions cannot be drawn from these kinds of environmental assessments concerning integrated effects of purturbation on the estuarine ecosystem. Thus, the need now exists to establish methodologies that provide data directly related to the integrated ecosystem picture, so that we can determine the effects of impacts that are real and not simply assumed or implied by historical dogma and public emotion. A disturbance to an estuarine environment may change the actors in the community, but does it change the function of the community?

6.3.2 Decision Making

Estuaries and their surrounding tidal habitats are one of the most productive and most stressed systems on our planet, and possibly also one of the most complicated. Their value has been extensively documented. In recent years ecologists have expended considerable effort to understand the individual as well as the holistic processes at work in estuaries. To sort out and synthesize the complexities of biological, chemical, and physical interactions in these ecosystems, ecologists are turning to simplified models that integrate the information into an overall view of ecosystem functioning. These models afford a certain degree of predictive ability, but more importantly, they provide feedback indicating what kind of new data are needed for understanding and managing the ecosystem more soundly.

The benthos of the open-bay bottoms of Texas estuaries has been the primary emphasis of this monograph because they are numerous, regulate (potentially) sediment nutrient regeneration, cycle energy from all sources of primary production to higher level consumers, and produce large quantities of biomass in the estuary. All of these activities of the benthos are links to the overall dynamics of ecosystem functioning and emphasize the importance of this open-bay bottom component.

The benthos of the open-bay bottom is also one of the estuarine components that will be most readily impacted by an environmental disturbance to the estuary. The sedentary nature of many of the species that inhabit the benthic environment of the open-bay bottom make these animals more susceptible to environmental changes from a disturbance than, for example, zooplankton or fish, which are more mobile organisms. This sedentary nature, plus the important features of the benthos summarized above, make the benthic habitat of estuarine ecosystems an ideal estuarine component on which environmental decision-makers charged with managing these environments can concentrate.

Figure 20 provides an example of how the various dynamics of the estuarine benthos can be integrated into a simple schematic which can aid in making managerial decisions. It summarizes annual production patterns and temporal standing stock (biomass) distribution of the benthos for the Corpus Christi Bay Estuary.

Also illustrated are the seasonal rates of benthic nutrient regeneration for this estuary, along with the annual pattern of primary productivity rates and the trends for riverine input of nutrients and annual rainfall patterns. In addition annual fishery species abundance patterns, as derived from catch statistics, are shown. Superimposed upon all this information are the recruitment periods for the dominant members of the benthic species assemblages over the year and the period of peak estuarine abundance for one of the important commercial species, brown shrimp.

This schematic provides an overall view of how the various dynamics of the estuarine ecosystem, and in particular those of the benthos, relate to one another. Thus, if an environmental manager

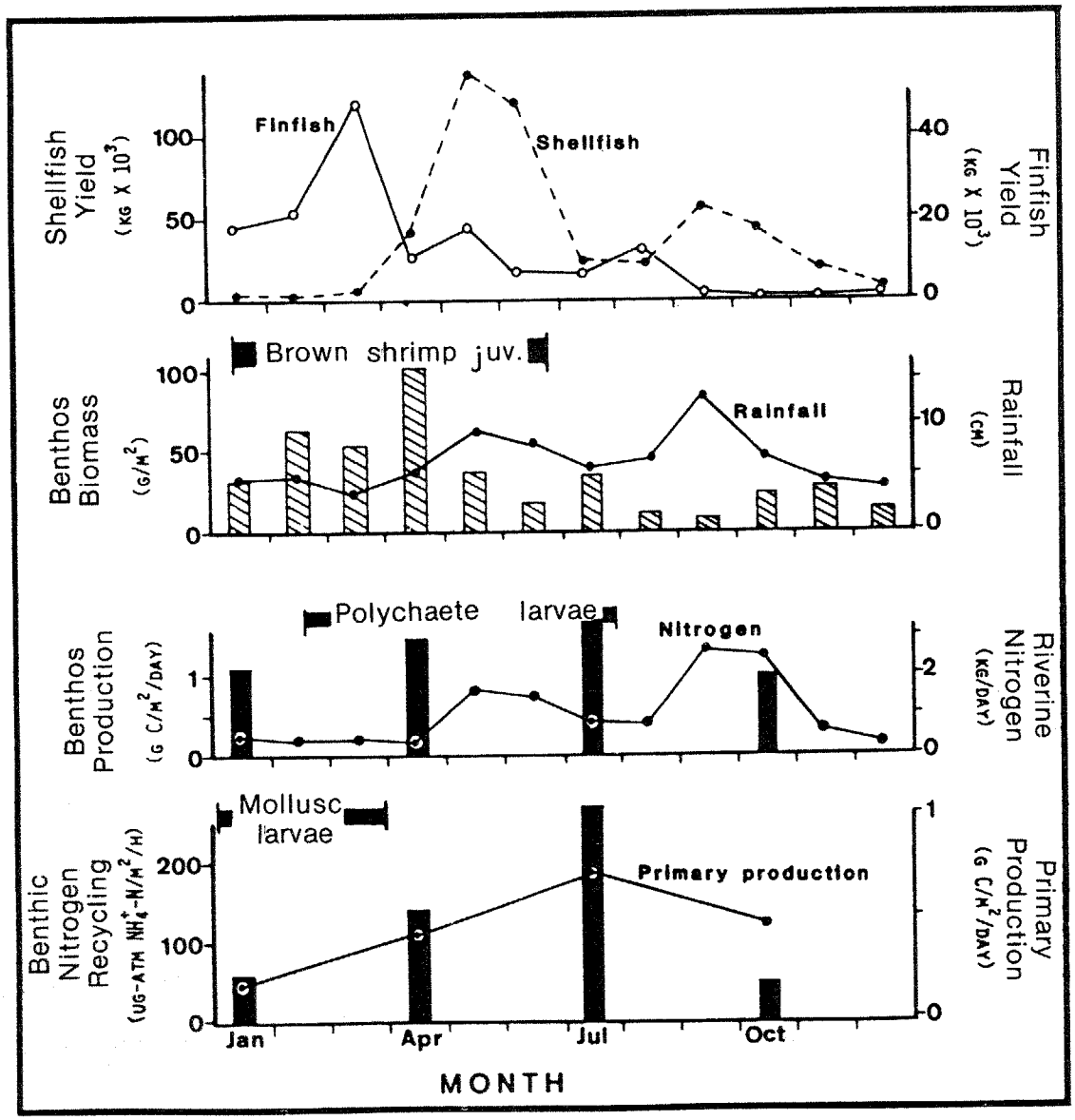

Figure 20. Multiyear data from the Corpus Christi Bay Estuary on fishery yields, benthic biomass, rainfall, benthic production, riverine nitrogen input, benthic nutrient regeneration, and phytoplankton production. Also shown are periods of peak brown shrimp (juvenile) abundance and benthic larvae colonization. These plots illustrate the development of an integrated picture showing how an estuarine ecosystem functions.

has to make a decision concerning the conduct of an essential activity that may disturb the environment in this estuary, he can use the integrated information of Figure 20 as a guide for whether to carry out the activity and when. For example, if the decision was when to do needed dredging in Corpus Christi Bay, he could consult Figure 20 and choose a time which would result in minimal disturbance to the estuary. Standing stocks of the benthic fauna are much lower during the fall than other periods of the year. Benthic secondary production and sediment nutrient regeneration rates are also lowest in the fall, as are phytoplankton primary production rates. In contrast, riverine input of nutrients is larger during the fall, supplementing decreased sediment cycling. Most larval recruitment for the benthos occurs in the winter, spring, and summer, and the period of peak brown shrimp abundance is from winter to early summer. Therefore, the environmental manager using this picture of ecosystem function as a guide would probably decide to conduct dredging activities in the fall, when the benthic dynamics, that aspect of the biotope most directly impacted by dredging of the bottom, would be the least inhibited with respect to overall contribution to ecosystem functioning. Of course, there are other considerations with respect to dredging that influence this decision, sucn as the economics of various dredging times. This example, however, illustrates how integrated information on environmental function can be used to aid in the decision-making process.

Another property of the environment to be impacted, which should be considered, is its resiliency after disturbance. Knowledge of this characteristic can also be incorporated into the decision-making process using the conceptual model described above. If one takes the example of dredging and, after utilizing the information of Figure 20, concludes that the fall would be the period of least impact, then he must consider the resiliency of the benthos so that processes will not be hindered long enough to affect more important periods of contribution by the benthos to ecosystem functioning during the year.

Table 16 presents data that indicate how resilient the benthic species assemblages of Corpus Christi Bay were after a

Table 16. Benthic community data obtained from a channel station in the Corpus Christi Bay Estuary prior to (1974-81) and after (1982-83) channel dredging occurred in April 1982, to illustrate resiliency of the benthic species assemblages. Data from Flint and Younk (1983) and Flint (in prep.).

Sampling date	Infaunal abundance (animals/m^2)	Infaunal species number	Infaunal biomass (g/m^2)
January 1982	5,055.6	26	4.59
April 1982[a]	214.8	9	1.39
July 1982	2,833.3	28	14.81
Average January	6,305.2 ± 2,031.2	29.7 ± 12.5	10.56 ± 4.83
Average April	5,873.3 ± 1,900.1	36.0 ± 17.4	16.86 ± 6.26
Average July	2,022.5 ± 1,242.3	38.9 ± 15.5	17.29 ± 6.04

[a]Sampling conducted 2 weeks after dredging completed.

period of dredging in March and April 1982 at one channel sampling site in this estuary. The January 1982 benthic characteristics of abundance, species number and total biomass were normal for this time of the year (Flint and Younk 1983). The April 1982 measures for these same characteristics, immediately after the dredging event, were far below the average values for April of other years (Table 16). By July 1982, however, the benthic species assemblages exhibited measures for abundance, species number, and biomass similar to average observations for this month during other years. Thus, within a period of 3 months after the dredging disturbance, the estuarine benthos of Corpus Christi Bay had regained community characteristics normal for these fauna. Incorporating this knowledge on resiliency into the integrated framework of Figure 20 would provide more predictive power to the environmental manager and help make his decision-making process sounder in its approach.

In the past, environmental managers concerned with maintaining the quality of an ecosystem and also allowing for reasonable development have focused on specific and "obvious" problems related to a particular aspect of the development, such as specific populations (e.g., fisheries) directly impacted. In many cases, the consideration of these specific and "obvious" problems, taken out of the context of total ecosystem function, has only confused issues and led to decisions that were not ecologically sound. The above example is intended to illustrate (1) how useful it can be to integrate as much information as possible on a habitat in order to obtain a holistic view of the environment and (2) what kinds of information one should consider in this holistic approach.

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APPENDIX

Common macro-invertebrates associated with the open-bay bottom biotopes of Texas estuaries. Compiled from Flint and Younk (1983), Calnan et al. (1983), Gilmore et al. (1974), and Holland et al. (1973).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
COELENTERATA			
Hydrozoa	Hydroids		
	Anemone, surface-dwelling		
	Anemone, burrowing		
	Paranthus rapiformis		
PLATYHELMINTHES			
Turbellaria	*Stylochus ellipticus*		
NEMATODA			
	Nematodes		
RHYNCHOCOELA			
	Rhynchocoel		C
	Cerebratulus lacteus		C
ANNELIDA			
Oligochaeta	Oligochaete		
	Peloscolex gabriella	B	DF
Polychaeta			
Polynoidae	*Lepidonotus sublevis*	S	C/SC
	Lepidonotus sp.	S	C/SC
	Lepidasthenia sp.		
	Grubeulepis cf. *mexicana*		
	Lepidametria commensalis		
	Eunoe cf. *nodulosa*		
Polyodontidae	*Eupanthalis kinbergi*	T-S	C
	Polyodontes lupina	T-S	C
Sigalonidae	*Sthenelais boa*	B	C
	Sthenelais limicola	B	C
	Ehlersileanira incisa		
Palmyridae	*Paleanotus heteroseta*		
Amphinomidae	*Pseudeorythoe ambigua*	S	C
	Chloeia viridis	S	C

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Phyllodocidae	Eteone lactea	B	DF/C
	Eteone cf. lactea	B	DF/C
	Eteone heteropoda	B	DF/C
	Eumida sanguinea	B	C
	Paranaitis speciosa	B	DF
	Paranaitis polynoides	B	DF
	Nereiphylla fragilis		
	Anaitides erythrophyllus	B	C
	Anaitides mucosa	B	C
	Mystides rarica		
Pilargidae	Ancistrosyllis jonesi		
	Ancistrosyllis papillosa		
	Ancistrosyllis groenlandica		
	Parandalia fauveli		
	Pilargis berkeleyae		
	Sigambra bassi	B	O?
	Cabira cf. incerta		
	Sigambra tentaculata	B	O?
	Litocorsa stremma	B	SC/C
Hesionidae	Gyptis vittata	B	DF
	Parahesione luteola		
	Podarke obscura	B	DF/G
Syllidae	Syllis gracilis	B	O
	Syllis cornuta	B	O
	Sphaerosyllis sublaevis	B	DF
	Sphaerosyllis sp.	B	DF
	Pionosyllis sp.		
	Typosyllis corallicoloides		
	Exogone dispar	B	DF/C
	Brania clavata	B	O/C
	Autolytus prolifer		
	Autolytus sp.		
Nereidae	Ceratonereis mirabilis	T-S	DF/C
	Ceratonereis irritabilis	T-S	DF/C
	Neanthes succinea	T-S	DF
	Nereis pelagica	T-S	DF/C
	Laeonereis culveri	T-S	O
Nephtyidae	Aglaophamus verrilli		
	Nephtys picta	B	C
	Nephtys bucera	B	C
	Nephtys magellanica	B	C
	Nephtys incisa	B	C
	Micronephtys sp.		

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Glyceridae	Glycera americana	B	C/DF
	Glycera capitata	B	C/DF
Goniadidae	Glycinde solitaria	B	C
	Goniada maculata	B	C
Eunicidae	Lysidice ninetta	B	O
	Marphysa sanguinea	B	DF/O
	Stauronereis rudolphi		
Onuphidae	Diopatra cuprea	T-S	C
	Onuphis eremita oculata	T-S	DF/SC
	Onuphis sp.	T-S	DF/SC
	Nothria cf. geophiliformis	T-S	O
Lumbrineridae	Lumbrineris parvipedata	B	DF/C
	Lumbrineris tetraura	B	DF/C
	Lumbrineris latreilli	B	DF/C
	Lumbrineris tenuis	B	DF/C
Arenicolidae	Arenicola cristata	UB	DF
Arabellidae	Drilonereis magna	B	DF
Dorvilleidae	Dorvillea rubra	B	C
	Dorvillea sp.	B	C
	Schistomeringos rudolphi	B	O/C
	Schistomeringos sp.	B	O/C
Magelonidae	Magelona pettiboneae	B-S	DF
	Magelona phyllisae	B-S	DF
	Magelona rosea	B-S	DF
Chaetopteridae	Spiochaetopterus costarum	T-S	DF/SF
	Mesochaetopterus taylori		
Cossuridae	Cossura delta		DF
Spionidae	Polydora websteri	T-S	DF/SF
	Polydora socialis	T-S	DF/SF
	Polydora ligni	T-S	DF/SF
	Polydora caulleryi	T-S	DF/SF
	Polydora sp.	T-S	DF/SF
	Prionospio cristata	T-S	DF
	Spiophanes bombyx	T-S	DF/SF
	Malacoceros indicus		
	Dispio uncinata		
	Spio pettiboneae		
	Spio setosa	T-S	DF

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
	Spio sp.		
	Streblospio benedicti	T-S	DF
	Paraprionospio pinnata	T-S	DF/SF
	Scolelepis texana	T-S	DF
	Apoprionospio pygmaea	T-S	DF
	Minuspio cirrifera		
	Prionospio heterobranchia	T-S	DF
	Prionospio steenstrupi	T-S	DF
Cirratulidae	Tharyx annulosus	B	DF
	Tharyx setigera	B	DF
	Chaetozone setosa	B	DF
	Caulleriella sp.	S	DF
Orbiniidae	Scoloplos rubra	B	DF
	Haploscoloplos foliosus	B	DF
	Haploscoloplos fragilis	B	DF
	Haploscoloplos robustus	B	DF
	Scoloplos sp.		
Paraonidae	Aricidea cf. fragilis	B	DF
	Aricidea brevicornis	B	DF
	Aricidea jeffreysii	B	DF
	Aricidea taylori	B	DF
	Aricidea wassi	B	DF
	Aedicira belgicae		
	Paraonis gracilis	B	DF
	Paraonis fulgens	B	DF
	Paraonis sp.	B	DF
	Paraonides lyra		
Opheliidae	Armandia agilis	B	DF
	Armandia maculata	B	DF
	Armandia sp.	B	DF
	Polyopthalmus pictus	B	DF
Capitellidae	Capitella capitata	T-S	DF
	Capitellides jonesi		
	Mediomastus californiensis	B	DF
	Heteromastus filiformis	T-SS	DF
	Heteromastus elongata	T-SS	DF
	Notomastus hemipodus	B	DF
	Notomastus latericeus	B	DF
	Notomastus lobatus	B	DF
Maldanidae	Branchioasychis americana	T-SS	DF
	Clymenella mucosa	T-SS	DF
	Clymenella torquata	T-SS	DF

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
	Maldane sarsi	T-SS	DF
	Asychis elongata		
	Asychis sp.		
	Macroclymene sp.	T-SS	DF
Oweniidae	Owenia fusiformis	T-S	DF/SF
	Myriowenia californiensis	T-S	DF
Flabelligeridae	Piromis arenosus	S	DF
	Brada sp.	S	DF
Pectinariidae	Pectinaria gouldii	T-SS	DF
Ampharetidae	Melinna maculata	T-S	DF
	Isolda pulchella	T-S	DF
	Amphicteis gunneri floridus	T-S	DF
	Ampharete americana	T-S	DF
	Samythella eliasoni		
Terebellidae	Pista palmata	T-S	DF
	Eupolymnia crassicornis	T-S	DF
	Streblosoma sp.		
Sabellidae	Potamilla cf. spathiferus	T-S	SF
	Chone duneri	T-S	SF
	Megalomma lobiferum		
	Megalomma bioculatum		
	Sabella melanostigma	T-S	SF
	Sabella microphthalma	T-S	SF
Serpulidae	Serpula vermicularis	T-S	SF
	Hydroides dianthus	T-S	SF
	Pomatoleios kraussi	T-S	SF
	Sphaeropomatus miamiensis	T-S	SF
	Eupomatus dianthus	T-S	SF
Hirudinea	Hirudinea		
MOLLUSCA			
Amphineura			
Ischnochitonidae	Ischnochiton papillosus		
Gastropoda			
Vitrinellidae	Cyclostremiscus suppressus		DF/G
	Vitrinella floridana		DF
	Teinostoma biscaynense		DF

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a]	and/or feeding type[b,c]
Caecidae	Caecum pulchellum		DF
	Caecum glabrum		DF
Epitoniidae	Epitonium angulatum		
	Epitonium rupicola		C
Calptraeidae	Crepidula fornicata	S	SF
	Crepidula plana	S	SF
Naticidae	Polinices duplicatus	S	C
	Natica pusila		
	Sinum perspectivum		
Columbellidae	Mitrella lunata		SC
Buccinidae	Cantharus cancellarius		
Melongenidae	Busycon contrarium		
	Busycon sp.		
Nassariidae	Nassarius vibex		DF/SC
	Nassarius acutus		DF/SC
	Nassarius sp.		DF/SC
Olividae	Olivella dealbata		SD/C
Cerithiidae	Bittium varium		SC
Pyramidellidae	Odostomia impressa		E
	Pyramidella crenulata		
	Eulimostoma sp.		
	Turbonilla sp.		E
Atyidae	Haminoea succinea		C
Retusidae	Acteocina canaliculata		C
	Acteon punctostriatus	S	DF/C
Corambidae	Doridella obscura		
Columbellidae	Anachis obesa	S	SC/C
	Anachis semiplicata	S	SC/C
Hydrobiidae	Littoridina sphinctostoma		
Muricidae	Thais haemostoma		
Turridae	Mangelia sp.		

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Cerithiopsidae	Seila adamsi		G
Neritidae	Smaragdia viridis viridemaris		
Truncatellidae	Truncatella caribacensis		G/DF
Scaphopoda			
Dentaliidae	Dentalium texasianum		
	Dentalium sp.		
Pelecypoda			
Nuculanidae	Nuculana acuta		DF
	Nuculana concentrica		DF
Arcidae	Anadara transversa		
	Anadara ovalis		
	Anadara sp.		
Mytilidae	Amygdalum papyria		SF
	Lioberis castaneus		
	Musculus lateralis		
	Brachidontes exustus		SF
	Modiolus demissus		O
Ostreidae	Crassostrea virginica	S	SF
	Ostrea equestris	S	SF
Pinnidae	Atrina serrata		
Ungulinidae	Diplodonta semiaspera		SF
	Diplodonta cf. soror		SF
Lucinidae	Lucina amiantus		SF
	Lucina multilineata		SF
	Phacoides pectinatus		
Killiidae	Mysella planulata	S	SF
Leptonidae	Lepton sp.		
Sportellidae	Aligena texasiana		SF
Cardiidae	Trachycardium muricatum		SF
	Laevicardium mortoni		SF
Mactridae	Rangia cuneata		SF
	Rangia flexuosa		SF
	Mulinia lateralis	B	SF/DF

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Solenidae	Ensis minor	S	SF
	Solen viridis		
Tellinidae	Macoma brevifrons	S	DF/SF
	Macoma tenta	S	DF/SF
	Macoma constricta	S	DF/SF
	Macoma mitchelli	S	DF/SF
	Tellina alternata	S	DF/SF
	Tellina aequistriata	S	DF/SF
	Tellina texana	S	DF/SF
	Tellina cristata	S	DF/SF
	Tellina sp.	S	DF/SF
Solecurtidae	Tagelus plebeius		SF/DF
	Tagelus divisus		SF/DF
Semelidae	Abra aequalis	B	DF/SF
	Cumingia tellinoides	B	DF/SF
Dreissenidae	Congeria leucophaeta		
Veneridae	Anomalocardia auberiana		SF
	Dosina elegans		
	Dosina sp.		
	Mercenaria texana	S	SF
	Mercenaria campechiensis	S	SF
	Cyclinella tenuis		
	Chione cancellata		SF
	Chione sp.		
Petricolidae	Petricola pholadiformis	S	SF
Corbulidae	Corbula contracta		
	Corbula dietziana		
	Corbula sp.		
Pholadidae	Cyrtopleura costata		
	Martesia striata		
	Diplothyra smythi		
	Barnea truncata		
Pandoridae	Pandora trilineata		
Periplomatidae	Periploma inequale		
Lyonsiidae	Lyonsia hyalina floridana	S	SF
Thraciidae	Asthenothaerus cf. hemphilli		
Hiatellidae	Hiatella arctica		

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
ECHIURA			
Echiuroidea	Echiuroideans		
ANTHROPODA			
Crustacea			
Podocopa	Ostracods		
Myodocopa			
Cylindroleberididae	Asteropella maclaughlinae		
	Asteropella sp.		
	Asteropteron oculitristis		
	Parasterope sp.		
Sarsiellidae	Sarsiella disparalis		
	Sarsiella texana		
	Sarsiella zostericola		
	Sarsiella sp.		
Calanoida	Labidocera aestiva		
	Pseudodiaptomus coronatus		
Harpacticoida	Alteutha depressa		
Cyclopoida	Cyclopoid copepod (commensal)		
	Hemicyclops sp.		
Thoracica	Balanus eburneus		
Mysidacea	Mysidopsis bahia		
	Mysidopsis bigelowi		
	Mysidopsis almyra		
	Bowmaniella brasiliensis		
	Bowmaniella dissimilis		
	Bowmaniella sp.		
Cumacea			
Bodotriidae	Cyclaspis varians		
	Cyclaspis sp.		
	Leptocuma sp.		
Leuconidae	Eudorella monodon	B	DF
	Leucon sp.		

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Diastylidae	Diastylis sculpta	B	DF
	Oxyurostylis salinoi	B	DF
	Oxyurostylis smithi	B	DF
Tanaidacea	Leptochelia rapax	T	DF
Isopoda			
Idoteidae	Edotea triloba	B	DF
	Erichsonella filiformis		
	Erichsonella attenuata		
Munnidae	Munna hayesi		
Sphaeromatidae	Cymodoce faxoni		
	Sphaeroma walkeri		
	Sphaeroma quadridentatum		
	Cassidinisca lunifrons		
Anthuridae	Xenanthura brevitelson		
Stomatopoda	Squilla empusa	B	C
Amphipoda			
Ampeliscidae	Ampelisca abdita	T-S	SF/DF
	Ampelisca verrilli	T-S	SF/DF
Caprellidae	Caprellid		
Bateidae	Batea catharinensis		
Corophiidae	Corophium louisianum	T-S	SF/DF
	Corophium acherusicum	T-S	SF/DF
	Photis macromanus		
	Photis sp.		
	Podocerus brasiliensis		
	Grandidierella bonnieroides		
	Lembos sp.		
	Microprotopus spp.		
Oedicerotidae	Monoculoides nyei	B	DF
	Synchelidium americanum		
Liljborgiidae	Listriella barnardi		
	Listriella bahia		
	Listriella clymenellae		

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Gammaridae	Gammarus mucronatus	B	DF/G
	Elasmopus levis		
Melitidae	Melita nitida		
Haustoriidae	Parahaustoris sp.	B	DF
	Platyischnopus sp.		
Amphilochidae	Amphilochus sp.		
Isachyroceridae	Jassa falcata		
	Erichthonias brasiliensis		SF
	Cerapus tubularis		
Amphithoidae	Amphithoe sp.	T-S	G
	Cymadusa compta		
Stenothoidae	Stenothoe sp.		
	Parametopella sp.		
Decapoda			
Alpheidae	Alpheus heterochelis		
Palaemonidae	Palaemonetes pugio		G/SC
	Leander tenuicornis		
Ogyrididae	Ogyrides limicola		
Callianassidae	Upogebia affinis	B-SS	SF
	Callianassa biformis	B-SS	DF
	Callianassa jamaicense	B-SS	DF
	Callianassa latispina	B-SS	DF
Hippolytidae	Latreutes parvulus		
	Hippolyte zostericola		
Porcellanidae	Euceramus praelongus		
	Petrolisthes armatus		
Paguridae	Clibanarius vittatus		SC
	Pagurus annulipes		SC
	Pagurus longicarpus		SC
	Pagurus pollicaris		SC
Hippidae	Emerita sp.		

(continued)

Appendix (Continued).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Calappidae	Hepatus pudibundus		
Leucosiidae	Persephona punctata		
Xanthidae	Rhithropanopeus harrisii		
	Hexapanopeus angustifrons		
	Eurypanopeus depressus		
	Panopeus herbstii		
	Panopeus tergidus		
	Panopeus bermudensis		
	Panopeus sp.		
	Neopanope texana		
Portunidae	Callinectes sapidus		SC/C
	Callinectes similis		SC/C
Parthenopidae	Heterocrypta granulata		
Majidae	Libinia dubia		SC/C
Penaeidae	Penaeus aztecus		SC/C
	Penaeus setiferus		SC/C
	Penaeus duorarum		SC/C
	Sicyonia brevirostris		
	Trachypenaeus constrictus		
Sergestidae	Acetes americanus		
Pasipheidae	Leptochela serratorbita		
Pinnotheridae	Pinnixa cristata		SC/C
	Pinnixa retinens		SC/C
	Pinnixa sayana		SC/C
	Pinnixa sp.		SC/C
	Pinnotheres sp.		
Processidae	Processa hemphilli		
SIPUNCULIDA	Phascolion strombi	B	DF
	Golfinigia sp.	B	DF
PHORONIDA	Phoronis architecta		
ECHINODERMATA			
Ophiuroidea	Hemipholis elongata	B	DF
	Micropholis atra	B	DF

(continued)

Appendix (Concluded).

Taxonomic group	Species	Living mode[a] and/or feeding type[b,c]	
Holothuroidea	*Pentamera pulcherrima*		
	Leptosynapta sp.	S	DF
Echinoidea	Echinoid		
HEMICHORDATA			
Enteropneusta	*Balanoglossus* sp.	UB	DF
CHORDATA	*Brachiostoma caribaeum*		SF
	Molgula manhattensis		

[a]Living modes include the following: B = burrower; T = tubiculous; S = surface; SS = subsurface; UB = U-shaped burrow.

[b]Feeding types include the following: C = carnivore; SF = suspension feeder; DF = deposit feeder; O = omnivore; SC = scavenger; G = grazer; E = ecotoparasite.

[c]Information on feeding types and living modes was obtained from the following: Winston and Anderson (1971); Bloom et al. (1972); Botton (1979); Fauchald and Jumars (1979); Virnstein (1979); Subramanyam and Kruczynski (1979); Calnan (1980); and Whitlatch (1982).

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15. Supplementary Notes

16. Abstract (Limit: 200 words)

Open-bay bottoms represent one of the most extensive habitats in any estuarine system, especially in the northwestern Gulf of Mexico estuaries of Texas. Seven major estuarine systems are found here (Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Copano-Aransas Bays, Corpus Christi Bay, and the Laguna Madre), along with three minor riverine estuaries (Brazos, San Bernard, and Rio Grande) which long ago filled. These bays are typically broad and shallow with average depths of 1.2 to 2.4 m and a total surface area of 624,000 ha. Salt marshes and seagrass beds are small.

The structure and function of the benthic communities in these Texas estuaries are examined by reviewing and integrating data from a number of past and ongoing studies. While studies in these systems have not been as numerous as in other estuaries, the patterns of structure and function are beginning to emerge. The key functions of the benthic system are production of biomass as food resources for higher trophic levels; bioturbation, which enhances nutrient regeneration; and nutrient regeneration itself. Benthic nutrient regeneration in the shallow waters of Texas estuaries may play a key role in regulating primary production in the estuaries.

Managers of these estuaries must consider the open-bay bottom systems as a critical part of the overall function of these estuaries.

17. Document Analysis a. Descriptors

Open-bay bottom
Benthic structure and function
Benthic system

b. Identifiers/Open-Ended Terms

Conceptual models
Estuarine processes
Estuarine hydrology
Benthic invertebrates

c. COSATI Field/Group

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