COMMUNITY STRUCTURE AND CARBON BUDGET OF A SALT MARSH AND SHALLOW BAY ESTUARINE SYSTEM IN LOUISIANA

CENTER for WETLAND RESOURCES
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ABSTRACT

The coastal zone of Louisiana comprises more than 7 million acres of marshes and estuaries, representing about 40% of the total coastal marsh area of the 48 contiguous United States. Partly as a result of this large estuarine zone, total fisheries are in excess of one billion pounds annually and rank first in the United States. This paper is a description of Barataria Bay, one of the estuaries in the coastal zone. The salt marsh, water column and benthic communities are each divided into several subunits. Each of these components is treated in terms of seasonal and spatial variations of abundance, feeding habits, life histories, trophic position and commercial importance. A carbon budget is presented for each of the components and for the whole marsh-estuarine community.

The marsh is dominated by the cord grass, *Spartina alterniflora*. Net production of the grass is 2,960 g dry wt/m²/yr streamside and 1484 g/m²/yr 50 meters inland. The highest rates of production of the grass occur in late spring with the highest standing crop of live grass in September. The grass flowers in early fall, after which most of it dies. Extremely low water levels in the winter allow a high biomass of dead grass to accumulate. There is a peak of detritus loss from the marsh in the spring which coincides with rising temperatures and water levels. In the water column, phytoplankton dominate primary production during the warmer months and benthic producers dominate during the colder months. The most numerous and important member of the water primary producers are diatoms. Macrophytes and other phytoplankton species are of lesser importance. Total production in the water is highest during the summer. Typically, phytoplankton productivity is highest during midsummer and the characteristic spring phytoplankton peak of higher latitudes is not found. Net production of the water column (phytoplankton plus benthic production) is 906 g dry wt/m²/yr.

The fauna of the marsh community is composed mainly of detrital feeders, including most of the meiobenthos, crabs, snails, mussels, and many of the insects. Populations of these organisms were much higher near shore and decreased with increasing distance into the marsh. Peak populations near shore of greater than 45 g dry wt/m² were measured. Populations are higher in late summer and lowest during late winter.

The fauna of the submerged sediments is composed mainly of small deposit feeders with very few filter feeders. Sediments near marsh shores are characterized by high organic levels and larger particle size than sediments distant from the shore. Meiofaunal populations are highest near shore, corresponding to the higher organic levels. Seasonally, peak meiobenthic populations occur during the spring corresponding to the high loss rate of detrital material from the marsh. Peak biomass was greater than 3.0 g dry wt/m². Amphipods, copepods and nematodes are the most important members of this group.

Zooplankton populations are dominated by copepods, especially *Acartia tonsa,* which represents from 60 to 90% of the total zooplankton. There is a characteristic spring peak of zooplankton which occurs at the same time as the peak of detritus washout from the marsh. Zooplankton biomass during the spring peak reaches 7.5 g dry wt/m².

Several species are treated in some detail because of their commercial importance. These include blue crabs, brown and white shrimp, and oysters. Shrimp spawn in offshore water and move into the estuary as postlarvae. After several months in the estuary, they leave as post-adults. Brown shrimp migrate into the estuary in early spring and leave in the summer while white shrimp move in during the summer and leave in late fall or early winter. Both species of shrimp are omnivorous, consuming detritus and small benthic organisms. Peak shrimp biomass is 0.2-0.4 g dry wt/m². Blue crabs spawn in the estuary and larvae are released offshore. Juvenile stages are spent in the estuary. Peak populations 0.1-0.2 g dry wt/m²) are in late summer. Crabs feed mainly on crustaceans, mollusks, and fish.

Early extensive natural oyster reefs in Louisiana have largely disappeared due to overfishing, salinity encroachment, and pollution. Most oysters taken today are from artificially planted beds. Young oysters are allowed to grow for about 15 months in low salinity water, then moved into higher salinity water for overwintering and harvest. Oysters are herbivorous, taking detrital particles and phytoplankton.

Fish taken during this study were divided into four trophic groupings: herbivores, primary canivores, mid carnivores, and top carnivores. The fish represented a diverse group. There were 113 species collected with 44 of them being taken more than 100 times. The bay anchovy, Gulf menhaden, spot, croaker, and a

group of cyprinodonts were the most abundant fishes. There were two distinct biomass peaks. A spring peak represented recruitment of juvenile fishes into the estuary and a fall peak represented adults moving offshore with the onset of cold weather. Biomass ranged from 0.4 to 3.0 g dry wt/m^2 over the entire study area.

Birds were divided into five trophic groupings. These included wading birds, water fowl, fishing birds, and birds of the marsh proper. These birds represent a wide range of feeding habits—from herbivores to top carnivores. There were no extremes seasonal variations because of the large influx of water fowl into the estuarine area during winter. Biomass of birds ranged from 0.03 to 0.06 g dry wt/m^2.

Bacteria were studied from several different areas within the estuary including water, submerged sediments, marsh soil and *Spartina* plants. Organisms from the water were characteristically slow growing and were mainly proteolytic and alginolytic. Species of the genera *Vibrio*, *Pseudomonas* and *Achromobacterium* were most abundant. All were aerobic. Bacteria of the submerged sediments were also slow growing. Both aerobic and anaerobic bacteria were present. The aerobes were mainly proteolytic and the most abundant were *Bacillus* species. The anaerobes were dominated by sulfate reducers. The marsh soil (including the bottom, regularly wet portion of the *Spartina* stalk) was characterized by more active bacteria which attacked carbohydrates (especially cellulose). There were many facultative aerobes and *Pseudomonas* species and *Vibrio* species were the most abundant organisms. The top portions of the *Spartina* was characterized by aerobes, many of which were pigmented. The most abundant organisms were of the genera *Micrococcus, Sarcina,* and *Bacillus.* Bacterial populations ranged from 30 x 10^9/gram on the bottom *Spartina* to 9 x 10^4/gram in the water. Peak populations seem to have correlated with high water levels and high standing crops of dead organic matter. Respiration of bacterial populations in the marsh, sediments, and water were calculated to be 777, 507, and 170 g dry wt/m^2/yr respectively.

From the studies of the different components of the estuary a budget of the entire estuary was constructed. Net production over the entire marsh was 1,518 g dry wt/m^2/yr. Consumer respiration on the marsh was 754 g/m^2/yr, leaving a net community production of 764 (about 50%) available for export to the water. Net production by primary producers of the water was 906. Consumer respiration was 864, leaving a net community production in the water column of 48. Because of the detritus exported from the marsh, the total dry matter available to the water column was 1500 g/yr. After consumer use 636 g/m^2 water/yr were available for export offshore. This amounted to 42% of the total organic matter available to the water column or 30% of the total net production of the estuary.

ACKNOWLEDGMENTS

Even a partial listing of persons contributing directly and indirectly to this study would be far too long. A project of this kind has enormous data collection needs and could not be accomplished without the assistance of a large number of people, not all of whom are specifically thanked below.

A major part of our debt is owed to participants in the Systems Ecology Program of Louisiana State University's Sea Grant Program (NOAA Grant No. 2-35231) in which all of the authors are also participants. Louisiana State University's Sea Grant Program is a part of the National Sea Grant Program which is maintained by the National Oceanic and atmospheric Administration of the U.S. Department of Commerce. Dr. James Gosselink is especially thanked for his overall guidance of the program and for his studies on primary production, along with his students, Dr. Conrad Kirby, Dr. Wilmer Stowe and Sharon Brkich. Dr. Harold Loesch, Joseph Jacob, Paul Wagner and Arthur Crowe provided much of the information on standing crops of fish and crustaceans. Dr. Ted Ford was very helpful in writing the chapter on oysters. Meiobenthos of the submerged sediments and zooplanktonic data were made available to by Dr. Harry Bennett, Robert Rogers, James Blackmon and Martha Hiegel. Merobenthos in the marsh was studied by Alice Simmons. Microbiological information was provided by Dr. Arthur Colmer, Mary Hood, Dr. Samuel Meyers, and Sidney Crow. Respiratory studies of the marsh floor and sediments were conducted by Charles Hopkinson and Tim Gayle. Field logistical support was arranged and maintained by Rodney Adams, Edwin Bishop, Jack Blackmon, Kerry Blackmon, and Dennuis Selig. Richard Day and Will Pozzi gave valuable field assistance.

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INTRODUCTION

Stretching along the Atlantic and Gulf coasts of North America is a band of saline coastal marshes. These marshes reach maximum development along the Louisiana coast in the deltaic plain of the Mississippi River. There are about 7.5 million acres of marshes and estuaries in the coastal zone in Louisiana, of which 3.5 million acres are coastal marshes (Fig. 1). This represents about 40% of the total coastal marsh area of the 48 contiguous states. The productivity of marshes and estuaries has been well documented (E. P. Odum, 1961; Darnell, 1967b, and others) and they constitute a valuable resource. Partially as a result of the extensive estuarine area, Louisiana normally ranks first in total volume of fish harvested. In order to understand and better utilize this resource, personnel of the Center for Wetland Resources and others at Louisiana State University have been conducting extensive studies in the estuarine area under the Sea Grant Program. This paper is a partial report of the ecological studies conducted under this program.

Others have reported on studies of this type: Teal (1962) reported on the energy flow in a salt marsh system in Georgia; Golley, Odum, and Wilson (1962) studied a mangrove swamp system in Puerto Rico; and William Odum (1971) and Heald (1971) reported on the structure and function of the mixed mangrove and marsh communities of South Florida. We have attempted to extend our report to cover the whole marsh-estuarine community as one unit and to quantify as much of the food web and environmental parameters as possible.

MORPHOLOGY OF THE AREA

In order that the discussion in this paper will be better understood we are including a brief discussion of the geology and form processes in the deltaic plain of the river. This is an area of rapid land building, erosion and subsidence. The deltaic plain extends, in places, as much as 100 miles inland before reaching the Pleistocene Uplands (Fig. 1). The level of the Gulf of Mexico is rising relative to the land (Fig. 2), probably as a result of the generalized subsidence in the whole area. As a result of land-building by the river, extensive areas of near sea-level marshes and swamps have developed.

The width of the deltaic plain results from the frequent channel changes by the Mississippi River. Over the past 5000 years there have been seven major channel alterations and numerous minor ones (Frazier, 1967). Erosion is constantly taking place along the coast. In an active delta complex, deposition exceeds erosion and there is a net land gain. In abandoned deltas, erosion will normally exceed deposition. During the past several thousand years, there has been a net land gain along the Louisiana coast.

The major estuaries in Louisiana are interdistributary bays located between river channels. The major part of the studies discussed in this paper were conducted in the Barataria Bay estuarine complex (Fig. 3). This system is located between the present Mississippi channel and Bayou Lafourche, an abandoned distributary. (For more detailed discussions of these processes see Russell, 1936, 1967; Saucier, 1963; Morgan, 1967; Gagliano and van Beek, 1970, and AAAS Pub. No. 83, *ESTUARIES*.)

The Barataria Bay system is bordered by the Mississippi River and Bayou Lafourche (Fig. 3). The estuary is triangular with the base formed by several barrier islands with tidal inlets between them. It contains 919,000 acres of marsh and open water areas and more than 50,000 acres of fresh water swamp.

The Barataria Bay complex is made up of two major bays, Barataria and Caminada, and many other smaller bays and lakes. These bays are shallow with average depths of 1.0 to 1.5 meters; the water is characteristically turbid. The marsh area contains many lakes and ponds. It is cut extensively by both natural and man-made canals and bayous (Fig. 3). Because of the low tidal range, there is very little relief. The distance from low water to the top of the streamside levee is less than 0.5 m. As a comparison, this distance is greater than 2.0 meters for the Georgia salt marsh (Teal, 1958).

ENVIRONMENTAL PARAMETERS

Louisiana coastal waters are very productive for commercial and sport fishing. There are large fisheries for shrimp, oysters, crabs, and several species of fish. The area on either side of the Mississippi River has been called the "fertile fisheries crescent" (Gunter, 1967). Lindall, et al. (1972) reported that Barataria Bay was the most biologically productive estuary along the Louisiana coast.

The marshes of the bay system range from saline marshes dominated by *Spartina alterniflora* to fresh marshes dominated by *Panicum hemitomon*. The

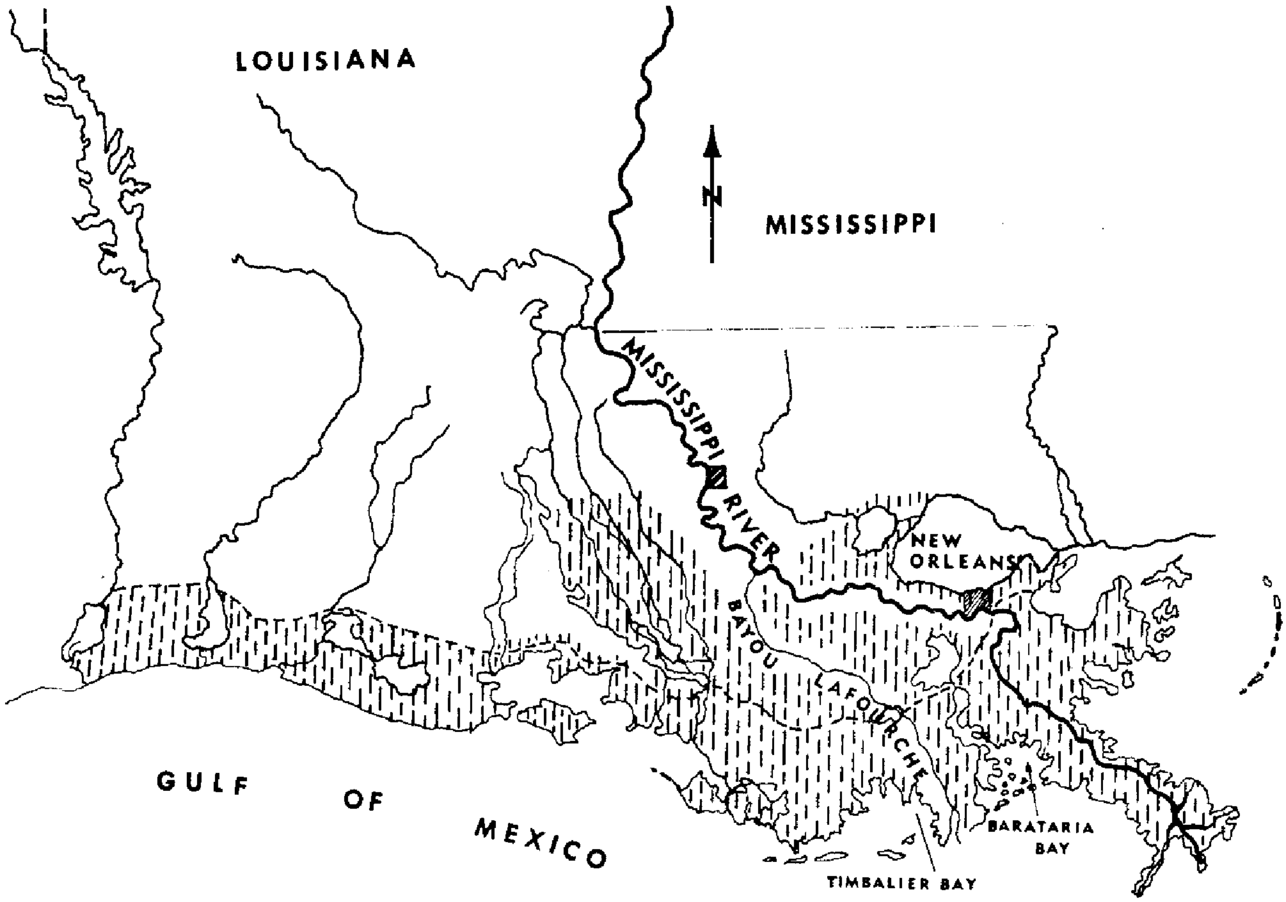


Figure 1. Map of Louisiana showing the coastal wetlands (shaded) and location of Barataria Bay where the most intensive studies took place. Dashed line is Gulf Intracoastal waterway.

major species of grasses in the different marsh types are shown in Table 1.

Table 1. Major species of grasses in different marsh types in the Barataria Bay hydrologic unit (form Chabreck, 1970).

Marsh type/species	% of total	Number of species comprising greater than 1% of total
Saline Marsh		6
Distichlis spicata	10.0	
Juncus roemerianus	14.9	
Spartina alterniflora	62.8	
Spartina patens	7.8	
Brackish Marsh		7
Distichlis spicata	29.0	
Spartina alterniflora	9.0	
Spartina patens	45.8	
Intermediate Marsh		8
Bocopa monnieri	24.0	
Pluchea camphorata	16.8	
Spartina patens	42.0	
Fresh Marsh		14
Eleocharis sp.	12.3	
Panicum hemitomon	41.4	
Sagittaria falcata	17.4	

There are several factors which contribute to the high productivity of the estuary and determine the environmental setting of the area. One of the most important is the Mississippi River. The river provides fresh water, nutrients, and sediment material to the estuarine areas. As stated earlier, the major estuaries are interdistributary bays. Before the coming of the white man there was annual overbank flooding during spring high water, introducing fresh water and materials into the upper ends of the bays. Because of this overbank flooding, heavier material settled close to the stream channel, resulting in the land next to the stream channels being the highest. This area is termed the natural levee. The Mississippi is now leveed most of the way to the Gulf and no overbank flooding occurs. Fresh water input to the upper ends of the bays comes mainly from rain. Introduction of river water and nutrients is realized mainly through the tidal passes. Water flowing out the river mouth turns to the west, flowing past the tidal inlets of Barataria Bay where mixed river and Gulf waters can move into the bay on high tide. The volume of

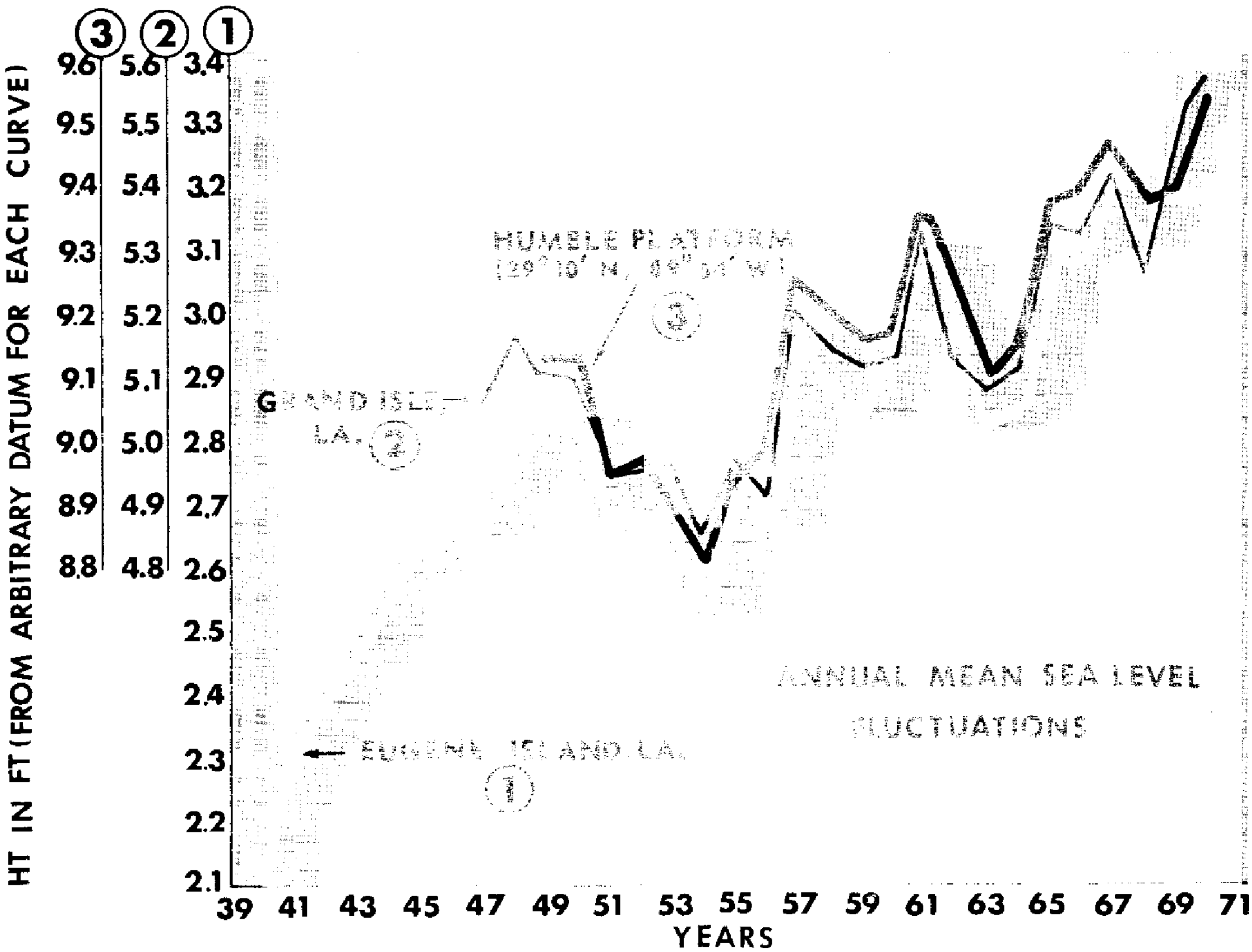


Figure 2. Record of rise in mean sea level from three stations along the Louisiana coast.

river flow and rainfall as well as the average salinity of the Barataria Bay region are shown in Figure 5. The salinities in Airplane Lake, the major study site, are normally betwen 15 and 25 ppt. In general, salinities in the bay are controlled by the river rather than rainfall.

A second important environmental parameter is the near-subtropical climate of the coastal area. Insolation and water temperature data are presented in Figure 4. The average water temperature is above 20°C and there is abundant solar insolation. This, along with the abundant rainfall, creates conditions for a long growing season. Infrequent killing freezes (average of one every 7 years) and mild winter weather allow growth of such tropical plants as the black mangrove.

Another important parameter is the low coastal energy regime (Wright and Coleman, 1972a,b; Becker, 1972a). This low wave activity allows the coastal area to be dominated by riverine processes and minimizes land loss due to erosion.

The tidal cycle characteristic of the area is a diurnal tide, varying from only a few inches to about two feet in amplitude. Tidal range varies with lunar declination with maximum range tides (tropic tides) recurring every 13 2/3 days, alternating with minimum range (equatorial) tides. At times of equatorial tides a semidiurnal component usually can be seen.

There is considerable annual variation in mean Gulf level. The highest mean water level normally occurs during September and October and the lowest levels occur from December to the first part of March (Fig. 4). These patterns are generally true for the Gulf of Mexico region (Marmer, 1954). Winter north winds push water out of the estuary and lower water levels even more. As a result the marshes are rarely covered with water during this period. Water begins to cover the marsh regularly during the latter part of March. This seasonal pattern of low water levels greatly affects such things as population levels in the marsh and washout of detritus.

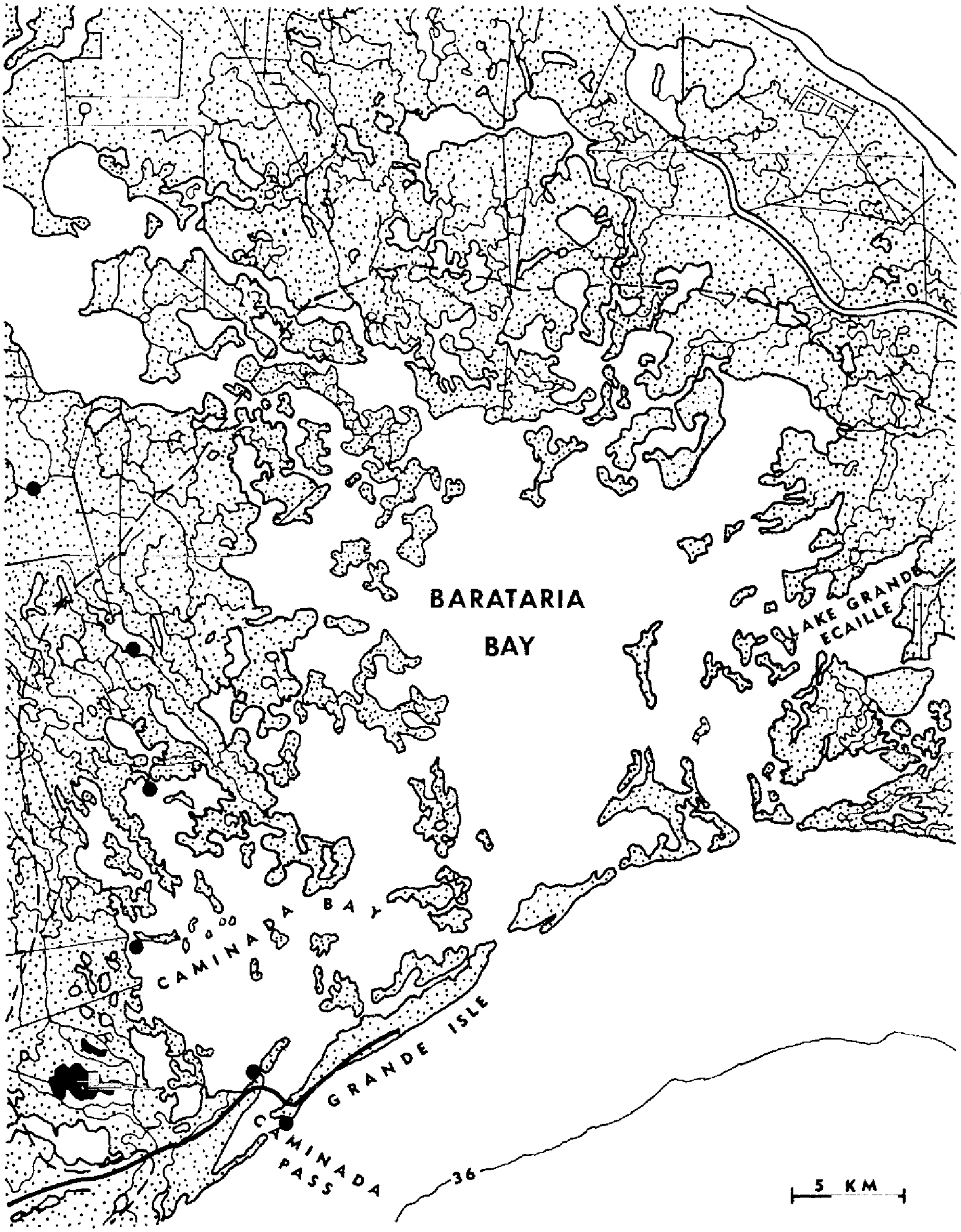


Figure 3. Map of the Barataria Bay region showing the main study sites for the sea grant project. The two lakes shaded black in the lower left are where the most intensive studies were carried out. The smaller one is Airplane Lake and the larger is Lake Palourde. Straight lines are man-made canals. Dark circles are fish collection sites. Dashed line is approximately boundary between saline and brackish marshes.

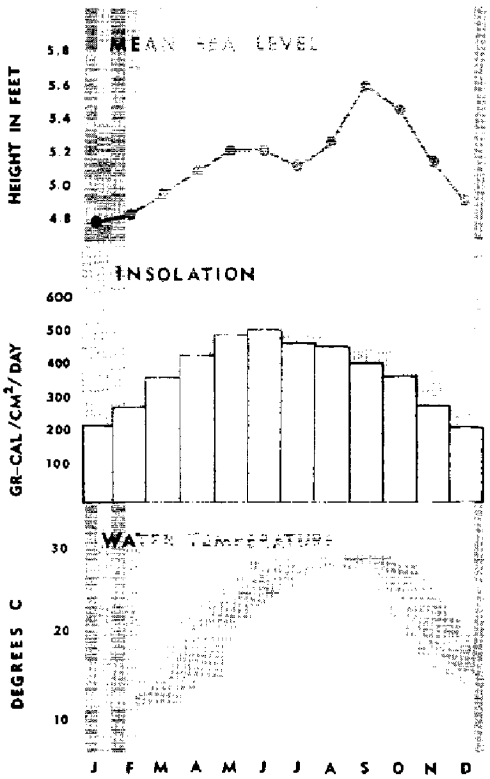


Figure 4. Annual variation in median temperature, insolation, and mean sea level from stations along the Louisiana coast.

Besides the periodic components of the tides there is an important aperiodic control on water level in the estuaries by winds. During periods of low mean tide level it may be that the only tides which can flood the marsh are those due to wind. At such times the frequency and duration of winds from various directions can be of critical importance to maintenance of marsh biota found in differing hydrographic circumstances.

By way of summary, the most important environmental parameters are:

1. Near subtropical climatic regime and abundant rainfall.
2. The broad near-sea level plain that has resulted from land building by the Mississippi River.
3. The large input of fresh water and nutrients by the river.
4. The low coastal wave activity which allows the river to dominate the form proceses.
5. Daily tidal flushing which is so important in all coastal marshes. For a more detailed discusion of mechanisms maintaining marsh productivity see Schelke and Odum (1961).

ORGANIZATION OF THE PAPER

This work follows upon the ideas presented by Teal, Golley, et al., W. E. Odum, and Heald, and attempts to enlarge these concepts by extending the community considered to more nearly encompass the whole of the marsh-estuarine system. The system is treated in what we believe to be logical compartments (Table 1). An attempt has been made to be as complete as possible but it was inevitable that some parts of the system were not considered.

For each component we have attempted to establish seasonal trends in biomass as well as average biomass for the year. Also, for each component we calculated respiration, feces production, organic tissue production, and harvest by man. For the most part respiration data was obtained from values reported in the literature. Feces production was assumed to be 50% of total food intake unless other information was available. The types of food consumed by the different components was determined by gut analysis and/or data available in the literature. In the final chapter, we have synthesized the data on the individual components into a diagram of the whole system, emphasizing the most important flows.

Throughout the paper and in the summary diagrams we have used energy symbols of H. T. Odum (1971). The three main symbols used are shown in Figure 6. They include primary producers, consumers, and passive storage compartments. The diagrams show the meaning of each of the inputs and exports to be used in the text.

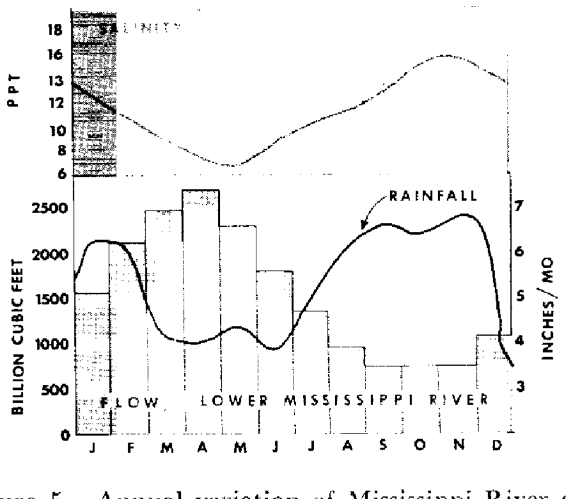


Figure 5. Annual variation of Mississippi River discharge, rainfall along the Louisiana coast, and average salinity in Barataria Bay. Salinities in the study area were normally higher (15-25 ppt). Rainfall data from U.S. Department of Commerce (1968). Salinity and discharge data from Gagliano and van Beek (1970).

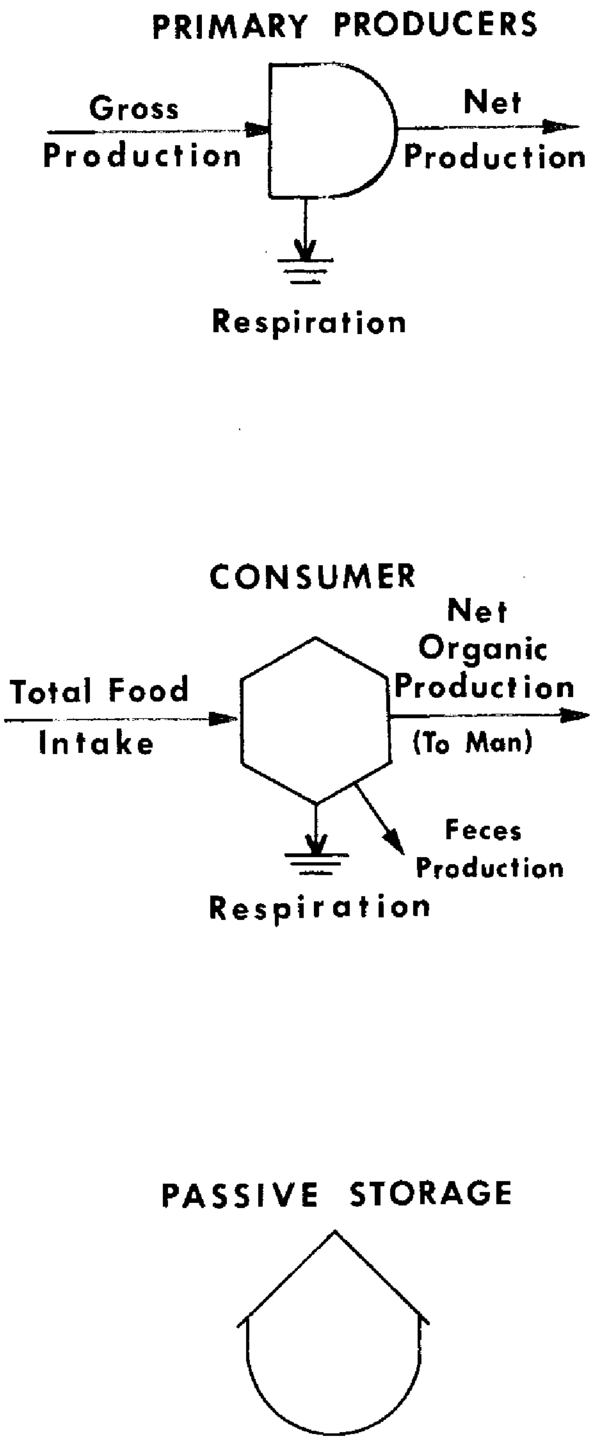


Figure 6. Energy symbols of H. T. Odum (1971) used in describing the marsh-estuarine system. All flows are grams dry weight/m²/yr, and storages are grams dry wt/m².

Table 2. Components considered in the Marsh-Estuarine system.

PRODUCERS		
		Angiosperms
		Epiphytic diatoms
		Benthic macrophytes
		Benthic diatoms
		Phytoplankton
CONSUMERS		
	Marsh	
		Bacteria, Fungi
		Meiofauna
		Snails
		Crabs
		Polychaetes
		Modiolus
		Insects
		Birds and mammals
	Submerged Sediments	
		Microbiota
		Meiobenthos
	Water	
		Bacteria
		Zooplankton
		Blue crabs
		Brown and white shrimp
		Oysters
		Fish
		Birds

PRIMARY PRODUCTION

Primary production in the Barataria Bay Area of Louisiana has been divided into three sub-units--production by the marsh grasses, production by the epiphytic algae on the marsh grasses, and production by the phytoplankton and benthic organisms. Production by the mudflat algae and algae under the *Spartina* canopy has not been considered. A partial listing of the major primary producers is given in tables 2 and 7.

HIGHER PLANTS

The dominant angiosperm is the oyster grass, *Spartina alterniflora*. It comprises about 93-95% of the biomass of higher plants in the Airplane Lake area of Barataria Bay and about 65% of the total salt marsh. In addition to these plants the salt worts, *Batis maritima* and *Salicornia virginica*, and the black mangrove,*Avicennia germinans*, are significant members of the saline marsh community.

Production of the marsh grass, *Spartina alterniflora*, was measured by obtaining the dry weight of live and dead grass at monthly intervals from clipped plots (Kirby, 1972). Two sampling areas were studied--a 125 x 5 meter area along the stream in the tall *Spartina* and a second area 25 x 25 meters in the short *Spartina* approximately 50 meters from the stream. Ten randomly selected 0.25 m^2 plots were clipped monthly at each location for 14 months. This method only considers production by the above ground portion of the plants, the part most available to higher trophic levels.

Net production was measured by summing the monthly changes in living and dead standing crops from successive months (Smalley, 1958 and Teal, 1962). An instantaneous loss rate was calculated to determine the loss of dead standing crop each month. These measurements were done by placing 30 grams dry weight *Spartina* in a nylon mesh bag and placing these bags in the stream at the streamside and at the inland area. Duplicate bags were collected from each area at monthly intervals. The bags were rinsed to remove sediment, dried at 65°C for 24 hours and weighed. The loss in weight was expressed as a percentage of the weight at the beginning of the month. This percentage is assumed to represent the percent loss from the dead standing crop from the respective areas. Loss rate was calculated from a curve fit of dead standing crop. This was necessary since clipping and litter bag experiments did not occur at the same time.

Annual variations in live and dead standing *Spartina* is shown in figures 7a and 7b. Data are presented from streamside and 50 meters inland. The live streamside grass attained maximum biomass of 925 g dry/wt/m^2 while the inland area reached a maximum of 600 g dry wt/m^2; both reached their maximum in September. The dead standing crop (Fig. 6b) has the highest biomass in February and March with almost 1,500 g dry wt/m^2 streamside and 1,200 g/m^2 for the inland area. Minimum levels of approximately 925 g/m^2 streamside and 750 g/m^2 inland occurred in August. The rapid decline in live standing crop following the August-September high is attributed to the death of the grass following flowering. Loss of the dead grass is due to decomposition by microbes and the physical flushing of the grass from the marsh by tides. One measurement of root biomass in early October indicated about 3,000 g dry wt/m^2 of root material to a depth of one foot. Winter tides very rarely cover the marsh, resulting in large dead standing crops and low loss rates. During the remainder of the year the marsh is regularly flooded, removing the dead material as seen by low dead standing crops and high loss rates (Kirby, 1971).

The total net production of Spartina is presented in Figure 7c. The highest rates of production were measured in April and May when production was almost 300 grams dry wt/m^2/month. Table 3 compares the annual net production of *Spartina alterniflora* from several locations. The data for Louisiana show much higher production than the other areas. However, if the other data had been corrected for loss between clippings, they would be much higher. (Using Smalley's technique, our production is 1,409.6 and 1,005.5 g/m^2/year at the streamside and inland locations respectively.)

While all of the above studies except one were limited to the Atlantic coast, a geographic gradation of *Spartina* production does appear. Production in the Louisiana salt mash is higher, probably due to the extended growing season.

The loss rate curves show two peaks of detrital loss from the marsh. The first occurs during late spring in April and May and the second occurs in September and October. The high loss rate during the spring results from higher spring tides and rising temperatures which increase decomposition. During

Table 3. Annual net production of *Spartina alterniflora* marshes g dry wt/m²/year.

	Inland	Streamside	Combined	Reference
Louisiana	1484	2960	—	Kirby, 1971
New York	508.3	827.2	—	Udel, et al., 1969
Delaware	—	—	445	Morgan, 1961
North Carolina	—	—	650	Williams, Murdock, 1969
North Carolina	329.0	1296.0	—	Stroud, Cooper, 1968
North Carolina	610	1300	—	Marshall, 1970
Georgia	643.2	1098.0	—	Smalley, 1959

the winter months water levels are very low due to the low sea level (Figure 4) and water rarely covers the marsh. Thus, there is a buildup of dead grass material in the marsh and when water levels and temperature rise there is a rapid breakup and washout of the dead grass material.

As will be shown in succeeding chapters, many groups of organisms in the estuary use this pulse of organic material as a food source. Thus, in contrast to many areas where the spring pulse is phytoplankton based, it seems to be mainly detrital based in Barataria Bay.

Respiration of *Spartina alterniflora* in the Georgia marsh was measured by Teal and Kanwisher (1961). From their laboratory and field studies an annual respiration rate may be projected on temperature change. They found a range of 40 mm³ O_2/g wet weight/hour at 5°C and approximately 400 mm³ O_2/g wet weight/hour at 25°C.

Using these respiration rates and assuming that light and dark respiration are equal and an average annual temperature of 20°C, annual gross production was estimated at 14,000 grams/m² for the streamside and 9,750 for the inland area.

PHYTOPLANKTON AND BENTHIC PRODUCTION AND FLORA

Phytoplanton and benthic production was studied by Sharon Brkich as a part of her doctoral work. Productivity and chlorophyll *a* of phytoplankton were measured. Some of the unicellular algae described as planktonic are normally classified as benthic or neritic (Patrick, 1967) but because of the shallow water in the study area they often are found suspended in the water column.

Primary production in the open water was determined by a combination of light-dark bottle and diurnal oxygen curve methods. The light-dark bottle

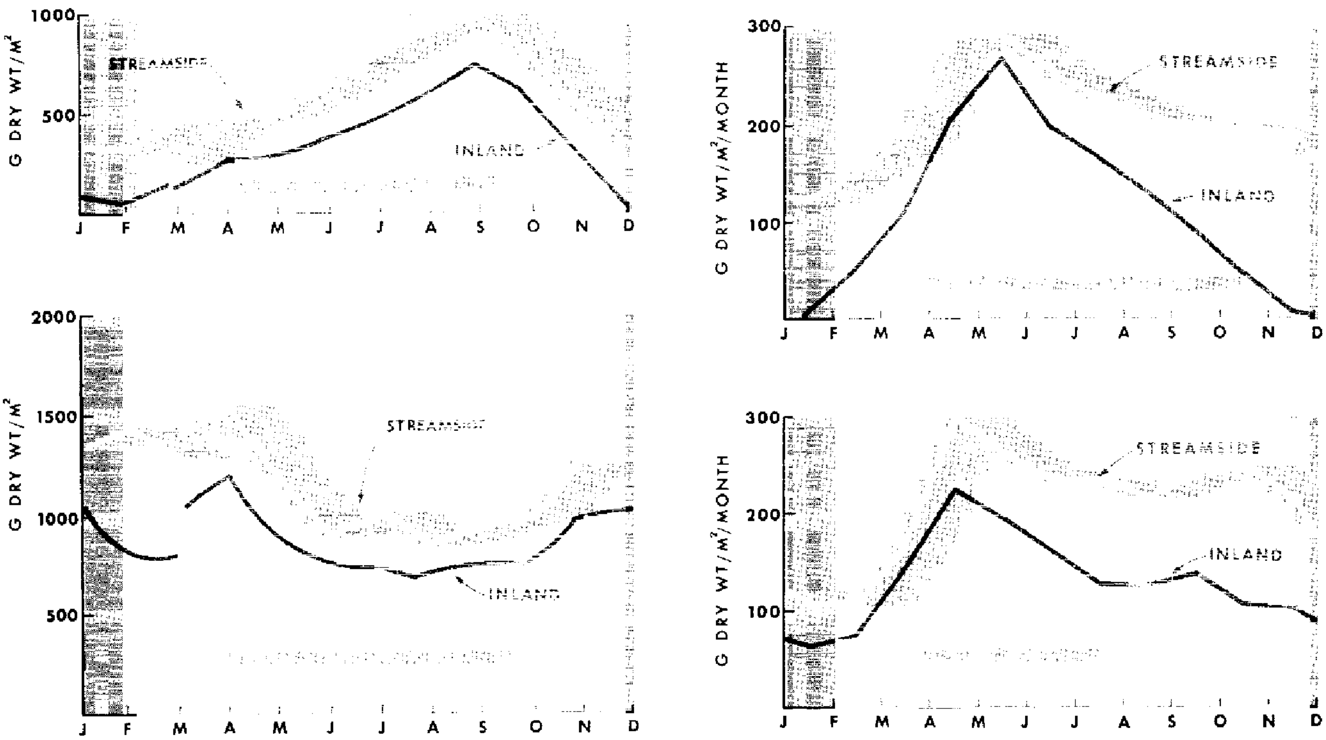


Figure 7. Standing crop of live (a) and dead (b) *Spartina alterniflora* in the vicinity of Airplane Lake. Also shown are total net production (c) and loss rate (d).

method follows the method outlined by Strickland and Parsons (1968). The diurnal oxygen method follows the procedure of H. T. Odum (1956). Oxygen determination was done by Winkler titration or oxygen probe. Estimations of phytoplankton density were accomplished by measurements of active chlorophyll *a* using the method outlined in Strickland and Parsons (1968). Samples were collected at biweekly intervals. Results of production studies are presented in Figure 8 and Table 6.

Chlorophyll *a* levels (Fig. 8a) corresponded to phytoplankton production. The common spring bloom of phytoplankton as described by Raymont (1963) and others has not been found to occur in the shallow waters of Barataria Bay. Rather, both chlorophyll *a* and phytoplankton production were highest in midsummer. As shown earlier, the spring peak of organic material in the estuary is due to washout of detritus from the marshes. The marsh-estuarine system seems to be synchronized with the major organic production during spring and fall resulting from detritus washout from the marsh and during the summer from phytoplankton production.

Gross photosynthesis and total respiration in the open water areas are shown in Figure 8b. Gross photosynthesis exceeded total respiration from March to August, with the greatest excess of photosynthesis ever occurring during July and August. For the remainder of the year respiration is greater than gross photosynthesis in the water column. Over the year there was a slight net community production of 48 g dry wt/m² (Table 6). This is much lower than the net community production of the marsh of 764 g dry wt/m²/yr. During the year respiration and production in the open water areas occur primarily in the water column during the warmer months and in the sediment during the colder months (Fig. 8c, Fig. 8d, and Table 6).

Production data are presented in Table 6 as gross and net photosynthesis. In calculating net photosynthesis, the respiration of the plants was assumed to be 30% of gross photosynthesis. This is somewhat lower than others have reported, but because of the characteristic turbidity of the water, we believe this to be a reasonable estimate. Some of the common species of phytoplankton are given in Table 7. The net productivity of phytoplankton and benthic plants in Barataria seems to be higher than measured in other areas (Table 4).

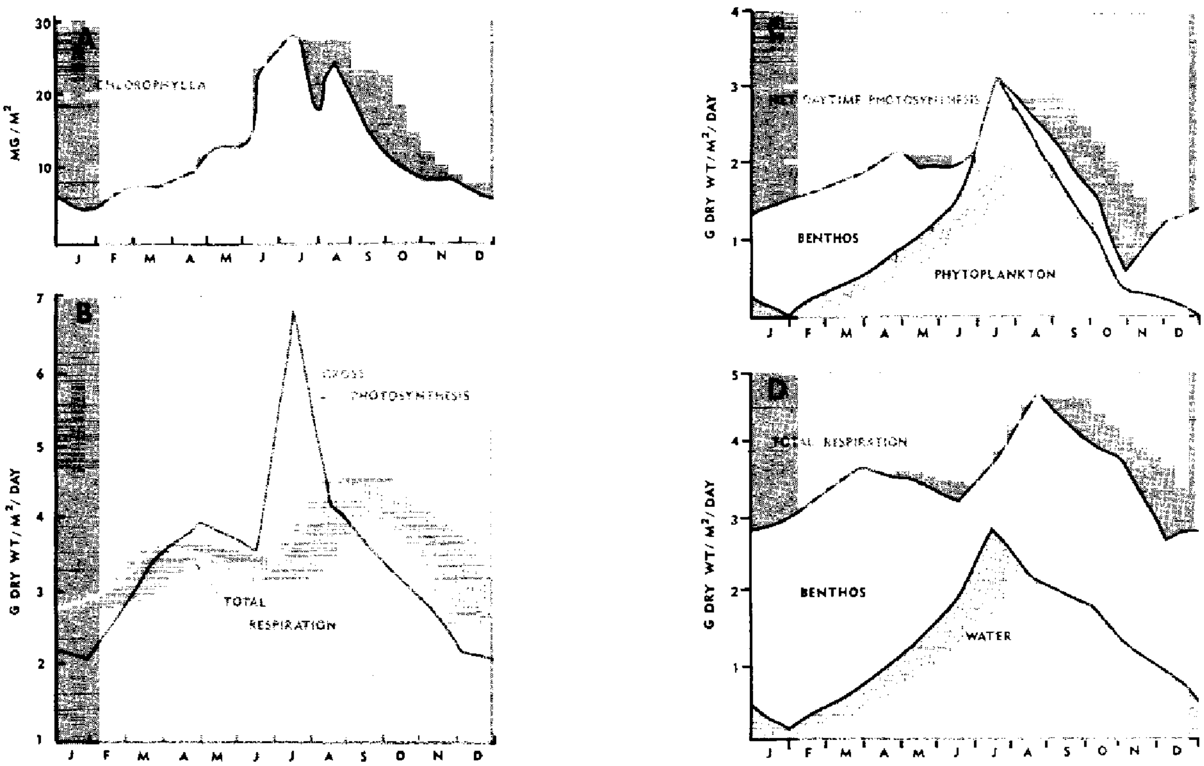


Figure 8. Annual metabolic patterns in Airplane Lake. (a) Chlorophyll *a* concentration. (b) Rates of gross photosynthesis and total respiration. (c) Net daytime photosynthesis of phytoplankton and benthic plants. (d) Respiration of water column (phytoplankton, zooplankton and bacteria) and benthose (including nekton).

Table 4. Annual production of selected areas (gC/m^2)

	Method	Gross	Net	C_{14}	References
La. phytoplankton	0_2	300	210	—	Brkich, 1972
La. benthos	0_2	362	244	—	Brkich, 1972
Estuary, N.C.	0_2	99.6	52.5	—	Williams, 1966
Long Island Sound	0_2	380	170	—	Riley, 1956
Sargasso Sea	C_{14}	—	—	72	Menzel, Ryther, 1960

Winter benthic macrophytes are almost exclusively composed of two genera, *Ectocarpus* and *Enteromopha*. A list of some common benthic macrophytes is shown in Table 7. No accurate assessment of their biomass has been made yet, but during the winter, bands of Ectocarpus 2 to 3 meters wide and 40+ meters long are commonly seen at low tide.

The importance of each of the three major primary producers is shown in Figure 10. Detritus from the marsh grasses represents from 50 to 70% of the total organic production available to the water areas of the estuary.

BENTHIC ALGAE

The north coast of the Gulf of Mexico has been described as being a barren region for benthic marine algae (Taylor, 1960). The chief reasons cited for this are the unstable bottoms backed by vast marshes and the inflow of fresh water from the Mississippi. While this observation is basically correct, the Barataria Bay Area does have a small macroscopic algal flora. In the marsh proper, away from the coast, larger filamentous algae are found mainly during the winter months. The most common genera are *Enteromorpha* and *Ectocarpus*. These two forms are most abundant on the banks of the streams and lakes and in quiet pools. They are found from early November to mid-April and early May with their peak occurring in January.

Gracilaria follifera has been found in only one location on the Louisiana coast west of the Mississippi River (Kapraun, personal communication). That location is a small bayou near the Gulf. It has been observed in late spring to mid-summer. During this period it grows in very dense masses lining either bank of the bayou 4 to 6 meters wide ond in strips 1,000 to 2,000 meters long. Samples of 0.25 m² weighed about 350 grams dry weight.

Table 5. Comparison of Epiphytic Production from different areas.

Environment	Gross Production grams/C m²/yr.	Reference
Submerged substrate—Fresh water	660	Allen (1971)
Emergent substrate—Fresh water	71	Allen (1971)
Periphyton—Borax Lake	267	Wetzel (1964)
Epiphytes of *Equisetum*	279*	Hickman (1971)
Spartina Marine—La.	103.9	Stowe (1972)
Inland	27.3	Stowe (1972)
Epiphytes of *Thalssia*	315	Jones (1968)

* Production 0_2 converted to g/C.

Table 6. Primary Production in the Barataria Bay Area of Louisiana in g dry wt/m²/year.

		Production Gross	Net*
Marsh			
Grass:	Streamside	14000	2960
	Inland (50 m)	9750	1484
	Average over marsh	8418**	1518**
Epiphytes:	Streamside	103.9	60†
	Inland (2 m)	27.3	−18.4†
	Average (to 2 m)	32.2	25.8
Water			
	Phytoplankton	598	418
	Benthos	698	488

* Net production is less respiration of plants
**Takes into consideration bare areas on marsh
† Community net production for epiphytes

Benthic diatoms have not been studied frequently enough to establish seasonal trends. Table 7 shows a list of some of the more common species.

A number of less numerous filamentous algae have been found in the benthos and mud flats. Kapraun (personal communication) has found *Ulvella* sp., *Ulothrix* sp., *Cladophora* and *Rhizoclonium*. These algae, for the most part, were found in the tidal pools located away from the main tidal streams, bayous, and lakes. *Rhizoclonium* has often been found in thick mats growing in tidal pools less than 10 cm in depth. *Vaucheria* has been found infrequently growing on the banks of the smaller tidal streams. *Ulva lactuca*, another winter form, has been found rarely growing on oyster shells and on abandoned boats.

Brkich (unpublished data) conducted a brief survey of the blue-green algae in the Barataria Bay Area. Three genera of the Oscillatoriaceae were common: *Lyngbya*, *Oscillatoria*, and *Spirulina*, growing on mudflats and on grass stems. The benthic blue-green mats were dominated by *Oscillatoria princeps*, with

Table 7. Partial list of the major primary producers in the Barataria Bay area.

Angiosperms	Epiphytic diatoms	Benthic diatoms	Phytoplankton
Spartina alterniflora	Amphiprora	Amphora	Merismopedia
S. patens	Amphora	Denticula	Actinoptychus
Avicennia germina	A. angusta	Diploneis	Biddulphia
Distichlis spicata	Camphylodiscus	D. interrupta	Chaetoceros
Juncus roemerianus	Cocconeis	Gyrosigma	Coscinodiscus
Batis maritima	C. disculoides	Navicula directa	Ceratium fusus
Salicornia	C. disculus	Nitzschia	C. hircus
	C. placentula	Opephora	C. trichoceros
Benthic macrophytes	Cylindrotheca fusiforma	Paralia	C. tripos
Enteromorpha flexuosa	Denticula	Amphiprora	C. vultur
E. intestinalis	Diploneis bombus	Caloneis	Dinophysis caudata
Ectocarpus	Gyrosigma terryanum	Mastogloia	Gonyaulax monilata
Bostrychia rivularis	Hantzschia	Pleurosigma	Peridinium
Polysiphonia havanensis	Navicula	Surirella	Prorocentrum gracile
Ulva lactuca	Nitzschia	Cylindrotheca closterium	Prorocentrum maximum
Gracilaria foliifera	N. paradoxa		Skeletonema
Cladophora repens	Pleurosigma		Ditylum brightwellii
Cladophora gracilis	Rhopalodia gibberula		Thalassionema
	Surirella americana		Cylindrotheca closterium
Benthic cyanophyta	Grammatophora marina		Nitzschia pungens
Oscillatoria	Melosira distans		Rhizosolenia
Lyngbya	Isthmia nervosa		
Spirulina	Cylindrotheca closterium		
Chroorococcus			
Merismopedia			
Anacystis			

Lyngbya and *Spirulina* making up the most notable secondary members of the algal mat. The Chroorocceas were represented in the mats by *Chroocroccus, Merismopedia,* and *Anacystis.*

EPIPHYTES

Epiphytic algae on the two plants that occupy the bulk of the stream side flora, *Spartina alterniflora* and *Avicennia germinans,* were studied by Stowe (1972).

The epiphytic community was divided into the filamentous and non-filamentous algae. The major filamentous forms are *Bostrychia, Polysiphonia, Enteromorpha,* and *Ectocarpus.* The non-filamentous algal community is composed almost exclusively of diatoms. Blue-green algae are conspicuous by their absence. Only when the stems become heavily sedimented do they become important components of the epiphytic community.

The seasonal distribution for the filamentous algae is shown in Fig. 8a. These algae exist in two distinct seasonal forms, *Bostrychia* and *Polysiphonia* in the summer, and *Enteromorpha* and *Ectocarpus* in the winter. The summer algae in 1971 demonstrated a bimodal curve with peaks near the end of April and mid-July through October. During the May-June decline, *Chaetomorpha* became a conspicuous member of the community and remained so until mid-July. The winter forms reached a peak in early January. They were more common on the banks of the streams than on the stems.

Temperature is the major factor controlling the epipthytic population but there seems to be a distinct correlation between levels and species composition of filamentous algae. When tide levels are high (Fig. 4), *Bostrychia* and *Polysiphonia* are dominant. The drop in the biomass of these two species in May and June corresponds to the lower water level at that time. During the winter when water levels are low, *Enteromorpha* and *Ectocarpus* are dominant.

Diatom density was estimated by counts of permanently mounted, millipore-filtered aliquotes of suspended material from the stems collected at the waters' edge and five feet inland. There was considerable variation between samples and sampling periods. This variation is attributed to the variation in the level of the marsh floor, the lack of homogeneity of the epiphytic population and the collection of whole stems which made it impossible to sample the same location twice. If the individual stations were compared, variations of the magnitude found by Hickman (1971) would be seen. The density of epiphytic diatoms on the *Spartina* stems was greater at the waters edge than five feet inland (Fig. 9b).

The epiphytic diatoms show a continual rise in density from January to September with a bloom occurring from October to November. After this the population does not decline to the low found during the previous January and February. *Amphora, Cocconeis,* and *Melosira* are limited primarily to the water edge stems and compose from 40 to 60% of the popu-

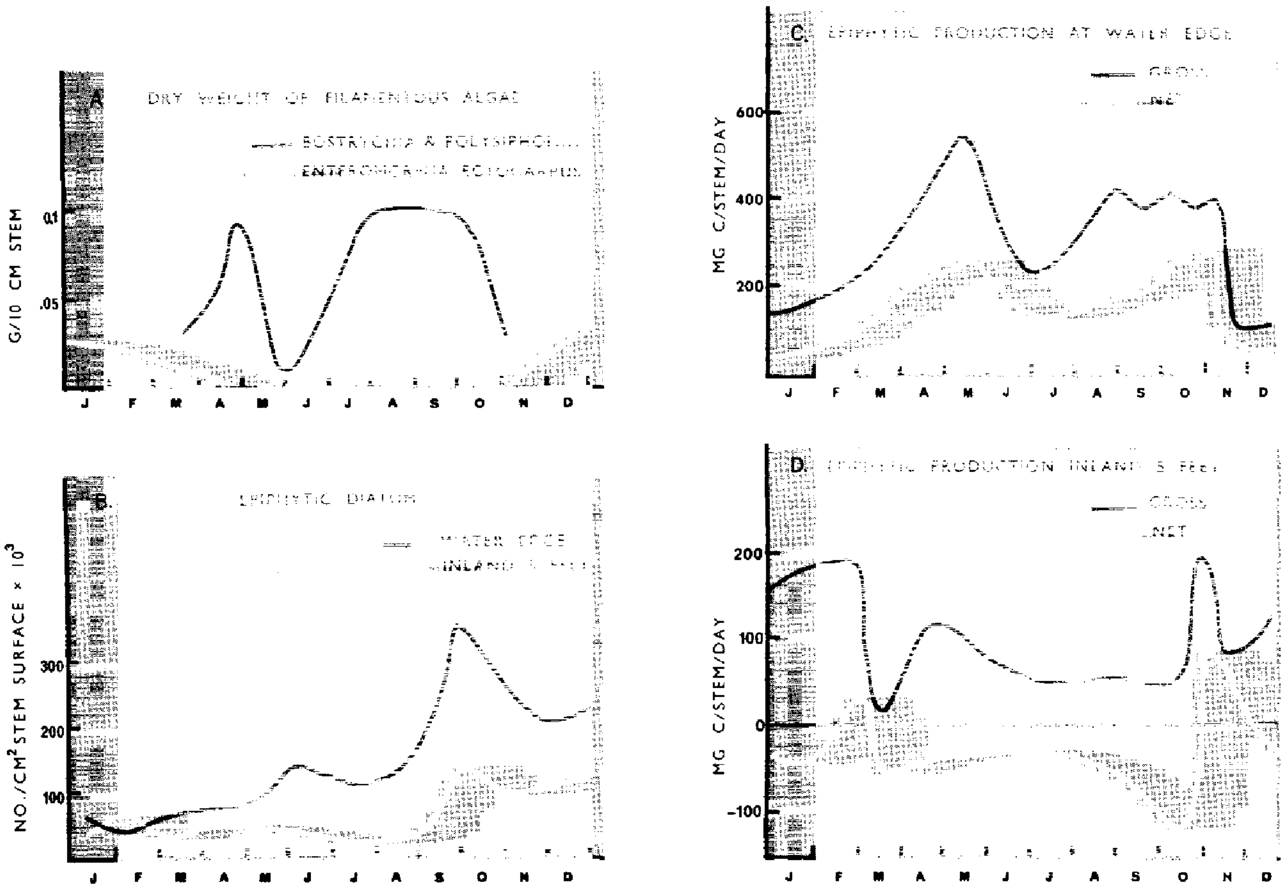


Figure 9. Productivity of the epiphytic community and standing crop of filamentous algae and epiphytic diatoms in the vicinity of Airplane Lake (Stowe, 1972).

lation. *Nitzschia* is the most common genus on the inland stems and comprises 10 to 20% of the population.

The seasonality of three of the more abundant genera of diatoms is discussed below. *Cocconeis* has a major peak during the early summer with a minor peak in mid-October. It is often found as an epiphyte on the filamentous red algae. *Amphora* has a major peak of 30% of the population in mid-May. During the rest of the year, it varies from zero to 10% of the population. *Denticula* is found in great abundance during most of the year and ranges as high as 30% of the population. During periods of sustained high water the population drops. An inverse relationship of population to degree and length of submergence has been seen. Examination of the stems shows an increasing dominance with increasing heights on the stem. On higher portions of the stems this genus may comprise as much as 60% of the population.

Production of epiphytic algae was measured by the light-dark bottle method. Two 10 cm stem sections were incubated in BOD bottles in aged bay water under conditions similar to those found in their natural habitat. Changes in dissolved oxygen were measured either by Winkler titration or by polarographic methods using a Martek oxygen probe.

Gross and net production for the water's edge community is presented in Figure 9c. Summer production ranges from 220 to 460 mg C/m²/day gross and 100 to 197 mg C/m²/day net. The winter low was a gross of 125 mg C/m²/day, and a net of 75 mg C/m²/day. These production curves follow very closely the density of the summer filamentous forms. These water-edge figures are found to be limited to a band around most lakes and streams in an active zone 30 to 40 cm wide.

The large discrepancy between gross and net production is understood if it is realized that these are community figures. This is a highly organic environment containing a large number of meiofaunal species, bacteria, yeast, and other fungi. Net production reflects that which escapes from this environment and is available to the water column.

Productivity figures for the inland community indicate a negative net production (Fig. 9d). This means there must be additional inputs of organic materials,

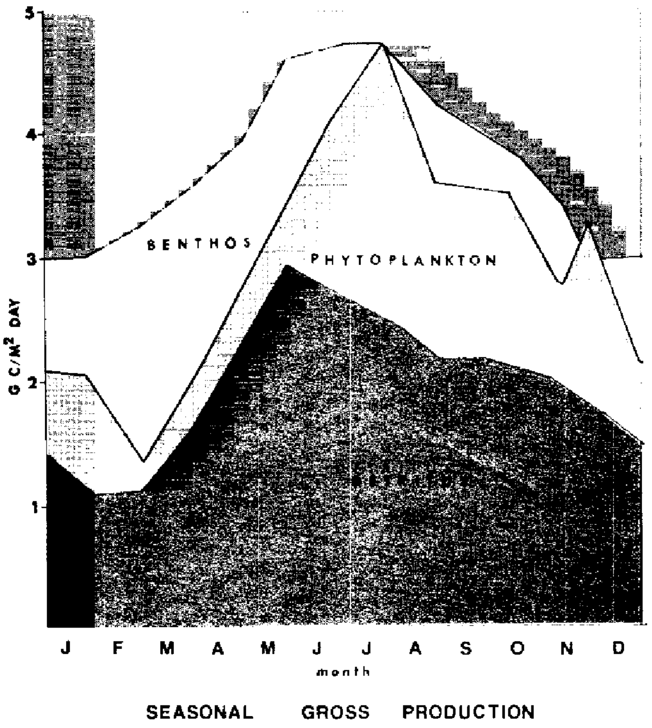


Figure 10. Comparison of production of benthic plants, phytoplankton, and detritus (Kirby and Gosselink, 1972).

most likely from *Spartina*. Only during November and February does the inland community become productive. During this time of year, low temperatures suppress microbial respiration. Also, the thinning of *Spartina* stands allows light to penetrate to the lower portions of the stems, thus allowing this community to become more productive. The inland community is composed of diatoms, a few blue-green algae and a large number of bacteria and fungi. Except for mid to late spring, the lower portions of the *Spartina* sheaths are in a state of decay.

Taking community respiration as the difference between gross and net production and calculating production on a 12-hour day and respiration on a 24 hour day, then annual respiratory rates of 87.0 and 90.0 g C/m^2 were observed for the water's edge and inland communities respectively.

The difference between the gross production and community respiration for the water's edge community is 16 g C/m^2 released to the water column. The inland community has such a high respiratory rate that it requires the addition of 64 g C/m^2 in order to maintain itself.

Due to the variety of epiphytic environments studied, general comparisons are difficult. The production rates of an emergent fresh water substrate (Allen, 1971) and brackish stream side vegetation (Stowe, 1972) are surprisingly similar. A general comparison of epiphytic production from several areas is shown in Table 5.

During most of the year the epiphytic community of *Spartina alterniflora* can be divided into producing and consuming communities based on their relation to the edge of the water. Production by the water-edge community is dependent on heavy growth of filamentous algae, primarily *Bostrychia* and *Polysiphonia*, during the warmer months of the year.

MARSH FAUNA

The diversity of animals which live mainly in and on the marsh is lower than that of adjacent open water areas, but the biomass is higher, especially in marsh areas close to the water. The food chain in the marsh is based, in large part, on detritus from the marsh grasses. As indicated earlier, very little of the marsh grass is consumed alive; most of it dies and is broken down by a combination of microbes and physical factors.

In discussing the marsh fauna, we have divided the marsh into two zones: a marsh edge habitat and an interior marsh habitat. The marsh edge is characterized by more tidal flushing, thicker growths of grasses, higher animal biomass and greater diversity. We established transects with sampling sites at the shore and 3, 10, 20, 50 and 300 meters into the marsh. We consider the first four stations, out to 20 meters, as marsh edge. The interior marsh is characterized by sparser growth of grasses with some bare areas, and lower biomass and diversity of animal populations. The 300 meter station is representative of this habitat. The 50 meter station is a transition zone. Some populations in the marsh such as crabs, snails, and sparrows have been studied more intensively and will be discussed in light of the zonation. Others, such as insects, have been sampled irregularly or not at all and must be discussed in a more general nature.

The principle factor which seems to determine density of organisms in the marsh is frequency of tidal inundation or proximity to tidally affected water bodies.

It was shown earlier that the highest mean gulf level occurs in September-October, with a smaller peak in late spring. (Figure 4) This means the marsh will be covered more often and for longer periods at these times. On the other hand, during the winter the marsh may not be covered at all for several months because of low water levels. During times of frequent tidal inundation, animals move further into the marsh, and the marsh edge is wider. When water levels are low, biomass levels drop and the marsh edge habitat is narrower.

SMALL INFAUNA

Feeding directly on the detrital-bacteria-algae base are groups of small infaunal animals including protozoa and the meiobenthos. Included in this group are ciliates, foraminifera, nematodes, oligochaetes, polychaetes, and small crustaceans.

Protozoa

Ciliates have been observed in cores taken from both the marsh soil and the submerged sediments. No quantitative counts have been made, but the ciliates seem to be more abundant in the marsh soil. W. E. Odum (1971) reported moderately large numbers of ciliates in association with benthic deposits of vascular plant detritus and sediments. He listed 16 species identified from mangrove detritus. The food of these organisms included ciliates, flagellates, diatoms, bacteria, and dead metazoa. Johannes (1965) studied the influence of marine protozoa on nutrient regeneration. He identified three species of ciliates—*Euplotes crassus, E. vannus,* and *E. trisulcatus*—from mud flats, tidal creeks, and beaches of Sapelo Island, Ga. Regeneration of dissolved phosphate proceeded faster and more completely in the presence of ciliates or colorless flagellates than in the presence of bacteria alone. He suggested that bacteria are not responsible for the bulk of nutrient regeneration in these areas and that a significant fraction of benthic regeneration of phosphorus from organic detritus may be attributable to protozoa. This may be a general statement in that not only ciliates but other small infaunal organisms also may be responsible for a great part of the regeneration of all nutrients (NO_3 as well as PO_4). Therefore, the meiobenthic organisms may have a dual role of nutrient regeneration in conjunction with the bacteria and "packaging" of small particles (detritus, bacteria, algae, etc.) so that they are more available to organisms higher in the food chain. The importance of ciliates associated with detritus also has been noted by Burkholder (1959), Mare (1942), and Lackey (1936).

Another group of protozoans which is important in the marsh environment is the foraminifera. Cruz (1970) identified several genera of foraminifera from the salt marsh adjacent to Airplane Lake. Among the genera listed were *Ammoastuta, Arenoparella, Trochammina, Ammobaculites, Miliammina, Ammotium,* and *Ammonia*. *Miliammina* is siliceous, *Ammonia* is calcareous and the other species are agglutinated forms. Warren (1956) studied the foraminifera from the Burns-Scofield Bayou area, a salt marsh area east of Barataria Bay. The marsh areas were characterized by *Ammotium, Arenoparella, Miliammina,* and *Trochammina*. Lake sediments were characterized by *Am-*

mobaculities, Cribroelphidium, and *Eponidella.* Jaspers (unpublished data) sampling in the same general area as Cruz, counted an average of 210,000 foramimifera tests per m^2. She made no attempt to differentiate living from dead.

Phleger (1965) studied populations of living foraminifera from six areas of marine marsh in Galveston Bay, Texas. The general marsh assemblage is an *Ammotium salsum-Miliammina fusca* one, with *Ammonia beccarii, Arenoparrella mexicana,* and *Trochammina inflata* common, and in somewhat smaller frequencies *Ammoastuta inepta, Elphidium* spp., *Tiphotrocha comprimata* and *Trochammina macrescens.* Phleger reported that several marsh environments had distinctive assemblages of foraminifera. These included channel or bay bordering a marsh, fringing *Spartina alterniflora* zone, *Salicornia* zone, lagoon barrier marsh, and more and less saline marsh. The inner *Spartina* zone was composed mainly of *S. patens.* Total living populations ranged from less than 10^4 to greater than 16^6 per m^2. The percent of the total population which was living ranged from zero to 84% and averaged about 30%.

Phleger stated that knowledge of the environment was inadequate to explain the distributions within the marsh. While this is true, several general patterns were evident. In most cases the highest populations were located at the marsh-water interface where *Spartina alterniflora* dominated or in shallow near-shore areas with turtle grass or emergent *Spartina.* Mud seemed to have general higher populations than sand. Lowest populations were generally in the backmarsh areas where *Salicornia* or *S. patens* was dominant.

Lee, et al. (1969) measured the standing crop of foraminifera in sublittoral epiphytic communities of a Long Island salt marsh. Foraminifera were most abundant in epiphytic communities of *Enteromorpha* in early summer and later spread to *Zostera, Zanichellia, Ulva, Polysiphonia,* and *Ceramium.* By summers end *Enteromorpha* rarely had a standing crop of foraminifera per gram of substrate (plant plus epiphyte) but there was no correlation between epiphytic community weight and total number of foraminifera recovered. *Ammonia* was one of the most common genera encountered and exhibited little substrate preference. Less abundant genera from Long Island which were common in Louisiana marshes were *Trochammina, Ammobaculities,* and *Miliammina.*

Foods taken by foraminifera include algae, bacteria, and yeasts (Muller and Lee, 1969). They probably also take detrital particles. Muller and Lee also reported that bacteria were required for the sustained reproduction of four species of foraminifera in gnotobiotic culture. This indicates—with the other bacteria-infaunal relationships mentioned above— that the relationships among the meiofauna, protozoa, microbes, detritus, and primary producers are very complex. Food links, reproduction, and nutrient regeneration are not as straight-forward as was once thought.

Meiobenthos

Meiobenthos is a practical term first used by Mare (1942) relating to small benthic organisms. This group includes such things as nematodes, ostracods, small polychaetes and oligochaetes, amphipods, and harpacticoid copepods, but does not normally include the protozoa.

The meiobenthos of the marsh soil was studied during the summer of 1972 by Alice Simmons (unpublished data). She counted total populations in the first three meters of the marsh at 50 and 300 meters inland. Results of the sampling are presented in Tables 8 and 9. Meiobenthic populations declined over the summer (Table 8). This is similar to findings by Bennett (see next chapter) who reported that meiobenthic populations of the submerged sediments also declined during the summer months.

Table 8. Total meiobenthic populations in the salt marsh during the summer of 1972 (from Simmons, unpublished data).

Distance	Month		
from shore	June	July	August
0–3 m	1,196,587	626,780	555,962
50 m	930,000	183,150	109,076

In general, populations and diversity of meiobenthic organisms are higher in the first three meters of marsh adjacent to the shore. Only one sample was collected at 300 meters. The population at that point was 700,000 organisms/m^2. These were mostly nematodes so that even though the total population is higher than some of the stations nearer shore, the biomass is lower because of the lower individual weight of nematodes. Nematodes, copepods, amphipods, polychaetes, and oligochaetes comprised greater than 90% of the total meiobenthic populations. Population levels of individual groups are presented in Table 9.

Meyer (1971) collected a new species of nematode from the marsh soil near Airplane Lake which has been described by Hopper (1971) as *Diplolaimelloides bruciei.* This nematode was an abundant bacterial feeder type. This is the only nematode which was specifically identified from the Louisiana salt marshes. It is likely that most meiobenthic organisms in the salt marsh feed on bacteria and detritus.

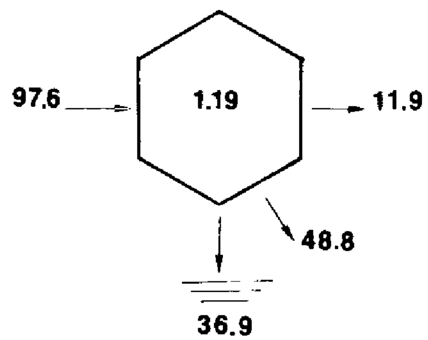
Table 9. Presence of meiobenthic organisms at various locations in the salt marsh (from Simmons, unpublished data).

Organism Group	Population (number/m²)x 10³	0-3 meters	Present at 50 meters	300 meters
Nematodes	(70-900)	yes	yes	yes
Harpacticoid copepods	(30-400)	yes	yes	yes
Amphipods	(5-45)	yes	no	no
Polychaetes	(16-50)	yes	yes	yes
Oligochaetes	(8-45)	yes	yes	yes
Ostracods	(3-18)	yes	yes	no
Tanaidaceans	(11-14)	yes	no	no
Mites	(3-24)	yes	yes	no
Small snails	(2-5)	yes	yes	no
Other annelids	(10)	yes	no	no
Insect larvae	(5-8)	yes	yes	yes
Total groups present		11	8	5

Meiobenthic populations have been studied from salt marshes along the Atlantic coast. Teal and Wieser (1966) reported populations of nematodes of 0.46–16.3 x 10^6/m² in a Georgia salt marsh. The biomass ranged from 0.2–7.6 g wet wt/m². Wieser and Kanwisher (1961) reported lower populations but higher biomass of nematodes from Penzance Point salt marsh near Woods Hole, Mass. They found 1.4–2.1 x 10^6/m² and an average biomass of 18.4 g wet/m² in November and 8.7 g wet/m² in June. The average weight of one nematode in the Massachusetts study (.00265 mg) was about 10 times higher than that reported in the Georgia study (.000256). The average wet weight of single nematodes collected by Rogers (1970) from soft bottom sediments in Barataria Bay was calculated to be .000269 mg (Loesch, 1971). The weight of the nematodes was calculated by Loesch by using twice the volume of a cone ½ the length of the nematode and multiplying by a specific gravity of 1.13 (Wieser, 1960). Using the same method, the average weight of single *D. bruciei* is approximately .00018 mg. Average polychaete densities in the Georgia salt marsh were 6700/m² in summer and 12380/m² in winter, excluding *Neanthes,* (Teal, 1962). For oligochaetes, the densities were 5000/m² and 5630/m² in summer and winter, respectively. Insect larvae levels were 370/m² and 25/m² in winter and summer, respectively. These data are from Table VIII of Teal's work (1962). Site 21 was excluded from the average because it is a mud flat and there is very little comparable area in Louisiana marshes.

Biomass was calculated by multiplying average populations by average weights of single individuals. For nematodes, a weight of 0.00018 mg wet weight was used. Bennett (unpublished data) provided individual weights for amphipods and copepods of 200 and 10 mg dry wt/individual, respectively. For Polychaetes and Oligochaetes, a weight of 50 mg wet/individual was used. Tietjen (1969) reported an average weight for polychaete from two New England estuaries as 33 mg wet wt. The above five groups comprised about 90% of the total population and the total meiobenthic biomass was corrected to reflect this. All wet wts. were converted to dry weight assuming 80% water. Calculated thus, the total meiobenthic biomass was 7.6 g dry wt/m² at the shore and 1.99 g dry wt/m² when averaged over the entire marsh. The high value at the marsh edge is due mainly to the presence of amphipods. The large individual size (200 mg dry) makes them a large part of the total biomass.

We calculated respiration using a rate of 0.085 g dry wt respired/g dry body weight/day. We have made no measurements of respiration on the Louisiana salt marshes and a rate of 0.085/day is our best estimate calculated from Teal (1962), Teal and Wieser (1966), and Wieser and Kanwisher (1961). Using the rate of 0.085/day, respiration was calculated to be 0.101 g dry wt/m²/day or 36.9 g/m²/year. We used 10 turnovers per year in calculating the production of the meiobenthos. Gerlach (1971) gave a figure of 9 turnovers/year and McIntyre (1969) used a figure of 10/year. We will assume an assimilation efficiency of 50%, giving a fecal production of 48.8 g dry wt/m²/year. Thus the total intake for the meiobenthos is 97.6 g dry wt/m²/year. Two amphipods are



MEIOBENTHOS

commonly found associated with Spartina roots near the water's edge. These are *Corophium* sp. and *Ampilesca* sp., however no quantitative counts have been made. Heald (1971) reported that two species of amphipods, *Melita nitida* and *Corophium lacustre,* and the crab, *Rithropanopeus harrisii,* were important in the breakdown of larger detrital fragments derived from red mangrove leaves. Fenchel (1970) found that the amphipod, *Parhyalella whelpleyi,* was important in decreasing the particle size of detritus dervied from Turtle grass. It is likely that amphipods and probably most of the meiobenthos in the Louisiana marshes play similar roles.

MARSH MACROFAUNA

The larger organisms of the marsh community were collected from 0.25 m^2 quadrants at the shore and 3, 10, 20, 50, and 300 meters into the marsh at Airplane Lake in August, October, and December, 1971, and at Lake Palourde in August, 1971. Data collected at Lake Palourde in August gives an idea of the spatial variation in species composition that can occur in the marsh. At each sampling location an area was selected by walking the appropriate distance from shore and throwing a wooden frame of 0.25 m^2 in one direction or another. Two persons then walked around the spot where the frame landed, stomping the grass and making noise. The purpose of this action was to drive any crabs in the area into their burrows. The frame was then pushed down to the surface of the marsh. All organisms readily visible were collected and placed in formalin as the grass was slowly removed from the plot. These organisms included mainly the snails, *Littorina, Neritina,* and *Melampus.* After removal of all animals and grass from the plot, the marsh soil was removed a little at a time and sifted by hand to remove polychaetes, crabs, and *Modiolus.* All organisms were removed to the lab where they were washed, counted, and dried at 105°C for 3 days, then weighed, fired at 450°C for 24 hours and reweighed. This procedure was followed for each species at each station. The results are reported in ashfree dry weight (organic matter) /m^2. Biomass distribution is presented in figures 11 and 12.

The effect of tide level can be seen in the distribution of organisms in the marsh at Airplane Lake on the three sampling dates (Fig. 11, Table 10). The high-

Table 10. Distribution of numbers and biomass of macrofauna in the marsh at Airport Lake. Number before slash is biomass in number/m^2.

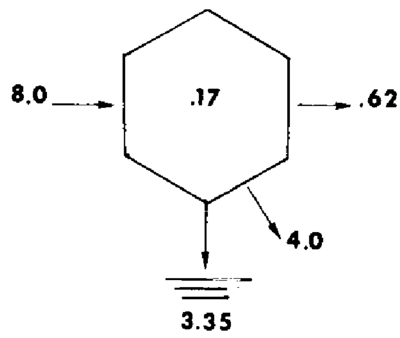
Organism	Distance into Marsh from Water Edge						average biomass
	shore	3m	10m	20m	50m	300m	to 50m
Polychaetes							
Aug.	0	0	.1/22	.2/8	.4/36	.3/16	.14
Oct.	.2/8	.22/20	0	.29/10	.36/20	0	.18
Dec.	.69/40	.47/12	.07/4	0	0	0	.20
							$\bar{x}$ = .17
Neritina							
Aug.	0	0	1.2/36	1.3/200	.8/20	0	1.16
Oct.	.07/4	0	1.4/28	1.6/52	.25/4	0	1.15
Dec.	0	.08/4	0	6.9/136	.4/8	0	3.18
							$\bar{x}$ = 1.83
Sesarma							
Aug.	7.9/4	5.8/8	0	0	0	0	.88
Oct.	0	3.6/8	4.2/8	.03/4	0	0	1.03
Dec.	1.1/4	5.5/8	0	0	0	0	.67
							$\bar{x}$ = .86
Fiddler							
Aug.	3.0/8	14.8/20	4.7/8	1.8/4	0	0	2.50
Oct.	0	1.7/4	6.7/8	2.1/2	7.5/12	0	4.68
Dec.	0	4.7/8	0	0	0	0	.45
							$\bar{x}$ = 2.54
Blue Crab							
Aug.	0	0	0	0	0	0	0
Oct.	0	2.75/8	.02/2	.02/2	.016/4	0	.61
Dec.	.0188/4	0	0	0	0	0	.005
							$\bar{x}$ = .20
Littorina							
Aug.	2.8/28	6.3/52	4.9/36	16.9/112	0	0	8.16
Oct.	3.6/32	7.6/76	6.3/52	10.0/76	0	0	5.81
Dec.	0	1.1/8	8.9/56	6.7/40	0	0	3.95
							$\bar{x}$ = 5.98
Melampus							
Aug.	1.2/316	3.6/688	4.1/444	1.3/208	6.1/1088	4.3/680	3.64
Oct.	1.1/112	2.4/497	1.6/216	0.4/108	1.4/284	.7/52	1.30
Dec.	6.2/68	3.3/600	1.6/176	.14/16	.07/28	0	1.05
							$\bar{x}$ = 1.99
Modiolus							
Aug.	0	3.6/64	6.6/148	0.6/24	2.0/80	0	2.43
Oct.	.5/4	4.8/44	.9/12	6.3/64	3.4/72	0	4.21
Dec.	1.4/36	9.5/40	3.3/16	3.0/20	0	0	2.94
							$\bar{x}$ = 3.19

est total biomass at the 50 m station occurred in October; the December biomass was less than 1/10 of the level occurring during October. The level in August was 77% of that in October. The highest mean sea level occurs in September and October. Intermediate levels occurred through the summer with very low levels in the winter (Fig. 4). In the following paragraphs, each group of animals will be considered separately.

Polychaetes collected in the quadrat samples are much larger than those of the meiobenthos. These are between 5 and 10 cm in length and have been identified as *Neanthes succinea*. In August they were collected at all but the shore and 3 m stations. In October, they were absent at 300 m; in December they were present at only the shore, 3 m, and 10 m stations. The highest polychaete biomass occurred at 50 m in August and October, and at the shore in December. The highest number and biomass of polychaetes for all trips was at the shore station in December. Teal (1962) reported that the highest numbers of *Neanthes succinea* were collected during the winter in a Georgia salt marsh. When placed in jars of mud in the lab, some specimens constructed U-shaped tubes and pumped water through them. Others burrowed through the mud. Teal reported that an examination of the gut of *Neanthes succinea* revealed only diatoms, detritus, mud, and sand. W. E. Odum (1971) identified two nereid worms, *Nereis pelagica* and *Neanthes succinea*, from the sediments in the North River estuary in the Everglades National Park. *N. succinea* was present at all times and was more abundant. He reported that both worms were omnivorous feeders, consuming fine detritus, algae, and even small crustaceans such as harpacticoid copepods and amphipods.

The average standing crop of polychaetes was 0.17 g org/m². This was obtained by integrating the area on the three curves representing polychaetes for each month and then averaging the three months. Only Airplane Lake data was used. This same procedure was used in determining average weight of the other members of the macrofauna. The budget data shown for Polychaetes is an average over the whole marsh, while that for the other groups is for the first 50 meters of marsh.

Respiration of Polychaetes was calculated using a rate of 3% body wt/day (Prosser and Brown, 1961). Assimilation efficiency of total food intake was assumed to be 50%. Production was taken at twice the average standing crop (Gerlach, 1971). Using this data the total intake is 8 g org/m²/year; respiration is 3.35, fecal production is 4, and production is 0.62.



POLYCHAETES

Crabs collected in the marsh sampling include the fiddler crab, *Uca pugnax;* the square-backed crab, *Sesarma reticulatum*, and small (less than 25 mm) blue crabs, *Callinectes sapidus*. Crabs are confined to marsh edge type habitat with fiddlers and blue crabs extending in as far as 50 m in October. In October there were no crabs collected from the shore station and the peak of crab biomass measured in August and December at 3 m was considerably reduced. This may represent increased predation by fishes during times of the high tidal levels. No small blue crabs were collected in August because spawning does not take place until late summer and crabs of this small size would not appear until late September or October. The highest biomass of fiddler crabs was at 3 m, except during October when it was at 50 m. The peak biomass was 34.9 g/m² at 3 m at Lake Palourde. Highest biomass for *Sesarma* was at the shore in August, at 10 m in October, and at 3 m in December. The only significant blue crab biomass was found at 3 m during October. Biomass at other stations was all less than 0.1 g/m². Again, the higher biomass at the interior stations is correlated with high tide levels. Teal (1958) reported that *U. pugnax* occurred throughout the Georgia salt marsh and that *Sesarma* sp. was confined to the water's edge. He also reported that *U. pugnax* burrows were found only where there was vegetative cover. Similar observations were made in this study. Teal reported biomass of *U. pugnax* of 5.7 to 54.3 g/m² on the levee and 3.1 to 12.2 g/m² in the short *Spartina* and biomass of *Sesarama* of 4.8 to 7.4 g/m² streamside and 0.8 to 22.1 g/m² on the levee.

The average biomass of the crabs in the Louisiana marsh (Fiddlers, *Sesarama*, and blue crab) was 3.60 g org/m². A respiratory rate for crabs of 4.8% body wt/day was used (Waterman, 1961). This gives a total respiration of 65.23 g org oxidized/m²/year in the

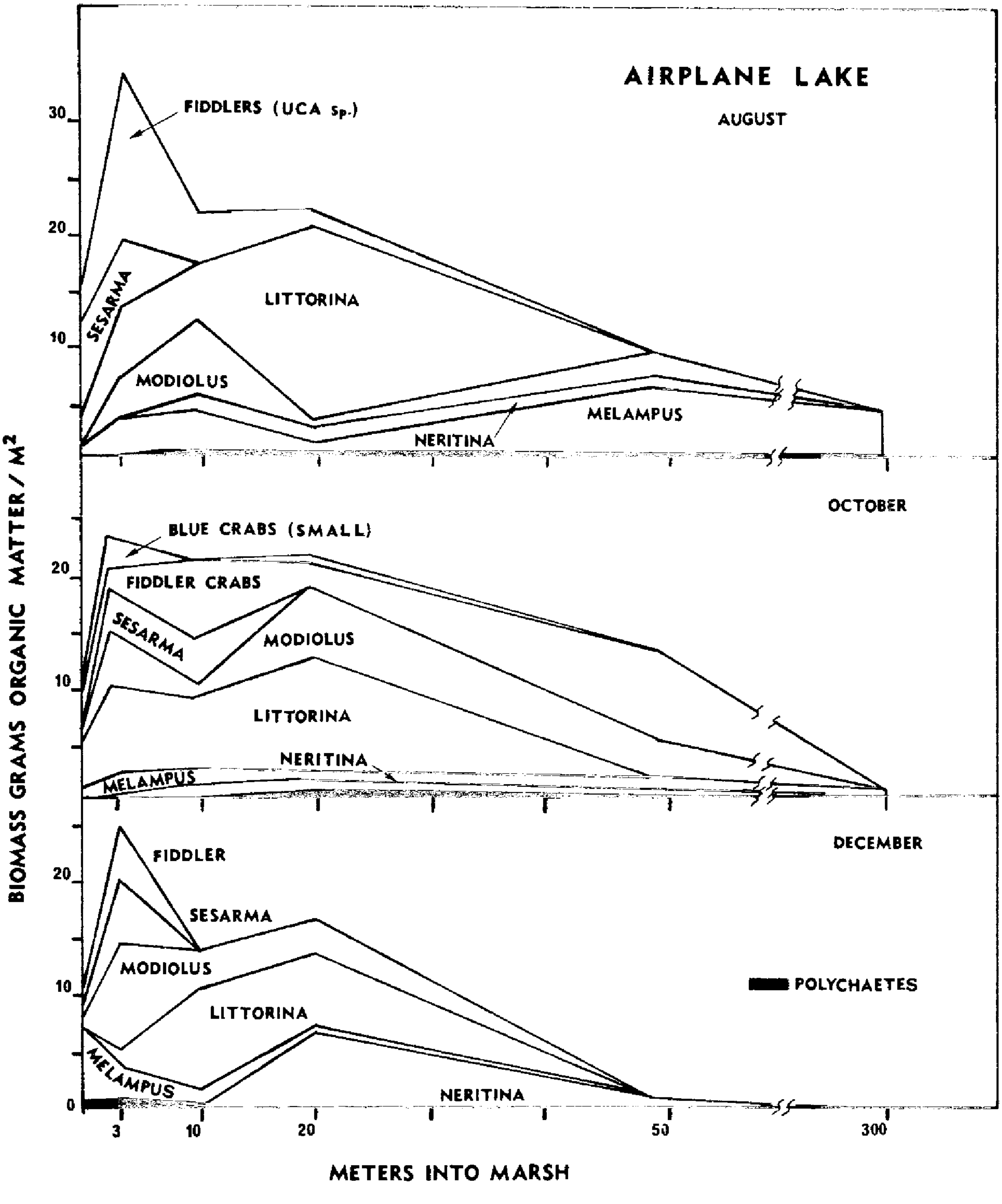


Figure 11. Distribution of macrofauna in *Spartina alterniflora* marsh at Airplane Lake.

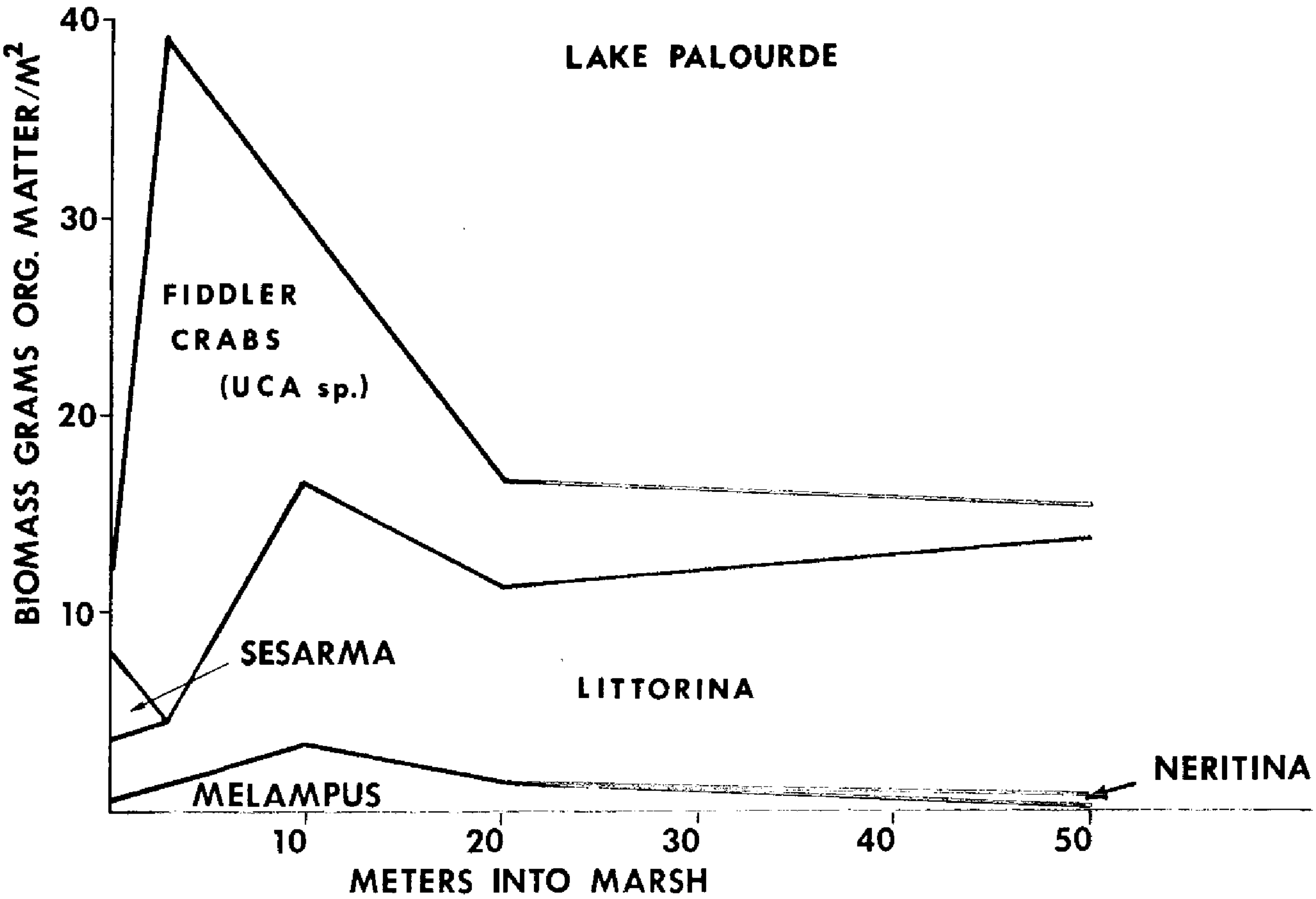
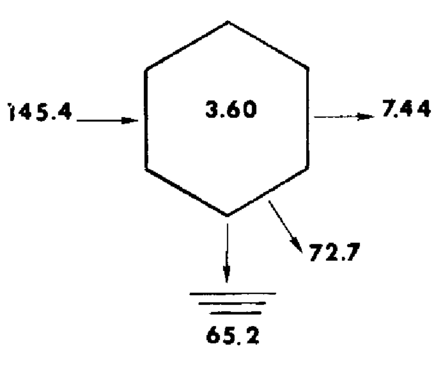


Figure 12. Distribution of macrofauna in *Spartina alterniflora* marsh at Lake Palourde.

marsh edge habitat. An assimilation efficiency of 50% was assumed and annual production of twice the average standing crop (Gerlach, 1971). Thus calculated, the total intake for crabs is 145.4 g org/m²/year, feces production is 72.7, and production is 7.44. These data are average for the streamside marsh.



Fiddler crabs feed by picking up clawfuls of mud and sorting it with their mouth parts, taking out nematodes, bacteria, and detritus (Teal, 1958, 1962). Teal found that *U. pugnax* was able to live on a mixture of bacteria, detritus, and sand in the lab.

Mud crabs were not collected in any of the transects, but they have been taken occasionally from the same area. Wagner (1970) reported *Panopeus herbstii, Rithropanopeus harrisii,* and *Menippe mercenaria* from the marsh edge and along the shore in the vicinity of Airplane Lake. The hermit crab, *Clibanarius sp.* was also observed along the shore. Teal (1962) reported the biomass of the mud crab, *Eurytium limosum,* in the streamside and levee marsh, ranged from 2.6 to 15.6 g/m². He classified this species as a secondary consumer. W. E. Odum (1971) found *R. harrisii* at all stations in the North River system. Examination of the buccal cavity revealed plant detritus (52%), animal matter including mostly copepods and amphipods (21%) and diatoms and filamentous algae (9%).

At distances greater than 10 meters into the marsh, molluscs were the predominant larger organisms. These included three species of snails and one species of mussel. Snails included the marsh periwinkle, *Littorina irrorata;* the smooth periwinkle, *Neritina reclivata;* and the snail *Melampus bidentata.* The snails have been observed both on the grass stalks and on the marsh floor but they commonly climb the grass stalks as the tide rises. They feed on the epiphytic algal film on the plants and on the marsh floor. Thus, the diet probably consists of diatoms, filamentous algae, detritus, and small animals living in the epiphytic film. Smalley (1958) reported that *Littorina* consumes *Spartina* detritus, film algae, planktonic larvae, and microscopic consumers on the mud surface and *Spartina* aufwuchs.

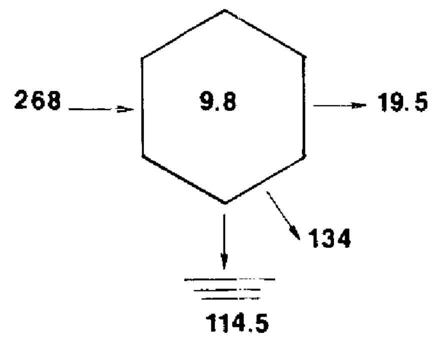
In terms of biomass, *Littorina* was the most important of the snails. The range of biomass was from 1.1 to 16.9 g/m² at stations where it was collected. Smalley reported an average of about 10 g/m². lackmon (1970) studied *Littorina* in the marsh around Airplane Lake. On a 17 meter transect, he found the highest biomass (27 g dry wt/m² between 8 and 10 meters into the marsh. The highest number was 196 individuals/m². The highest number encountered along our transect in this study was 148/m², but we have observed *Littorina* populations as high as 520/m².

With the exception of the shore station in December, *Littorina* was present out to the 20 m station for all sampling dates at Airplane Lake. In addition, it was present at 50 meters at Lake Palourde. The highest biomass at Airplane Lake was at 20 meters for August and October but at 10 meters during December. This biomass decrease seems to be due to a withdrawal from landward areas because of lowered water levels as well as a general decrease in the population.

The small snail, *Melampus,* was the most numerous species collected in the quadrat samples, but because of its small size (1-5 mm) it was less important in terms of biomass. It was collected at all stations with the exception of the 300 m station in December. None of the other macrofaunal organisms was found at the deep station in December. The highest biomass was found in August at 50 m and at the shore station in December. *Melampus* and polychaetes were the only organisms which inhabited both the marsh edge habitat and the interior marsh habitat.

The smooth periwinkle, *Neritina,* was most abundant at the 10 and 20 meter stations. The highest *Neritina* biomass at Airplane Lake was at the 20 m station for all three sampling dates.

The average biomass of snails (*Neritina, Melampus,* and *Littorina*) was 9.80 g dry/m². Using a respiratory rate of 3.2% body wt/day (Prosser and Brown, 1961) total respiration in the marsh edge habitat was figured to be 114.5 g org oxidized/m²/year. As with crabs, the production is assumed to be twice the standing crop, and assimilation efficiency is assumed to be 50%. The total intake for snails is then 268 g org/m²/year of which 134 is lost as feces and 19.5 is production. These data are for the marsh edge habitat.

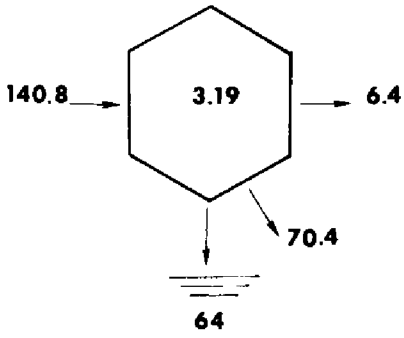


SNAILS

The ribbed mussel, *Modiolus demissus,* is also an important representative of the marsh fauna. *Modiolus* lives buried in the mud with the anterior end protruding slightly above the surface and occurs in a clumped distribution. Groups live associated with clumps of *Spartina,* attached to the roots with their byssal threads. The largest clumps encountered were 0.2 to 0.3 m in diameter. Kuenzler (1961) reported clumps as large as one meter in diameter in a Georgia salt marsh. *Modiolus* is a filter feeder. Because of its location in the marsh, it probably feeds on suspended detritus, algae, zooplankton, and other material which becomes suspended or flushed in by the tides.

It was found only at Airplane Lake, and only in the marsh edge habitat. Highest biomass levels occurred between 3 and 20 meters. The highest was 9.5 g dry/m² at 3 m in December. When high numbers of mussels were found (148 in August) they were mostly small.

Kuenzler found that the average biomass in a Georgia salt marsh was 4.55 g/m² with the highest measured being 31.6 g/m². The highest populations were in tall *Spartina* at creek heads. In the Louisiana marsh the highest populations were found at 10 meters from the water. By integrating the area on the curve to 50 m the average biomass of *Modiolus* was 3.19 g org/m². Respiration was calculated using a rate of 5.5% while production was assumed to be twice the average standing crop (Gerlach, 1971). Using the above data, total intake was determined to be 140.8 g dry wt/ m²/year, with 64 g/m²/year going to respiration, 70.4 for feces, and 6.4 for production. These data are for streamside marsh to 50 meters.

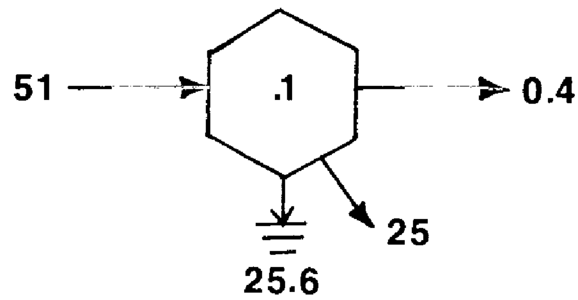


MUSSELS

MARSH INSECTS

There has been no detailed study of insects in the Louisiana marshes. We will use data from other works and general observations in our study area to estimate insect populations. McMahn et al. (1971) studied micro-arthropods during the summer in a North Carolina salt marsh in the vicinity of Morehead City. They counted and weighed all arthropods (exclusive of crabs) captured in a box placed over the marsh. Biomass ranged from 0.12 to 0.14 g dry wt/m². Insects, spiders, mites, pseudoscorpions, and amphipods were collected. Of the insects, the orders homoptera, heteroptera, diptera, and collembola were the most important. They calculated a diversity index (no. species/sq. root no. specimens) of 2.6. This is much higher than that reported by E. P. Odum (1963) for insect diversity in a Georgia salt marsh. Smalley (1958) studied the grasshopper, *Orchelimum*, in a Georgia salt marsh. He measured average population densities for adults and nymphs at 3.4 and 3.15 individuals per square meter, respectively. The average dry weights per individual were 0.37 g and 0.2 g for adults and nymphs respectively. This gives biomass for adults as 1.25 g dry wt/m² and for nymphs as 0.63 g dry wt/m². These values are much higher than those measured in North Carolina. Golley et al. (1962) estimated insect biomass in a Puerto Rican mangrove swamp at 0.103 g dry wt/m². This is close to that measured by McMahn et al., but again much lower than that reported by Smalley. Most of the insects feed on the marsh grass or on the detritus. The spiders are mostly carnivores.

We will assume an insect biomass of 0.1 g dry wt/m² and average respiratory rate of 0.7 g organic matter respired/g dry wt/m²/day or 25.6 g/m²/year. For a similar biomass level, McMahn et al. (1971) estimated insect productivity in the North Carolina marshes at 0.4 g/m²/year. We will use the same figure. Assuming an assimilation efficiency of 50%, feces production is 25 g/m²/year and total food intake is 51 g/m²/year.

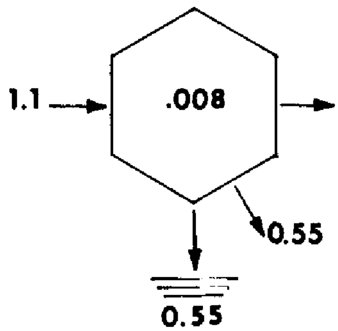


INSECTS

MAMMALS

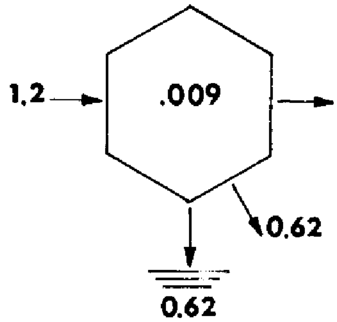
Mammals which are important in the marsh are the raccoon, *Procyon lotor*, and the muskrat, *Ondatra zibethicus*. Raccoons are true omnivores which seem to show a preference for animal matter. There are no specific studies of raccoon feeding habits in the Louisiana marsh. Studies in other areas indicate that they will take whatever is available (Stains, 1956; Stuewer, 1943; Whitney and Underwood, 1952; and Martin et al., 1939). Raccoons will feed on more plant material at certain times than at others. In summer and fall their diet probably has a higher plant material content. Fruits are the principal plant foods. Raccoon fecal pellets have been collected from the marsh around Airplane Lake. The pellets are composed of 60 to 80% fragments of mollusk and crab shells. Another source of information as to their feeding habits is examination of rejected material at sites where they have been feeding. This includes mainly *Modiolus* and crab shells. Bateman (1966) noted that raccoons fed on rail eggs. Therefore, the diet of raccoons in the marsh probably includes plant material, crabs, snails, fish, bird eggs, and mussels. Crabs and mussels seem to be the most important. The population density of raccoons is estimated at 0.025/acre (Palmisano, 1971). Weights of individual raccoons range from 8 to 15 pounds. An average wet weight of about 12 pounds or 4,500 grams was used. The biomass calculated was about .028 grams wet wt/m². In our lab we found the average dry weight content of mice to be about

30% of total weight. We use this value for marsh mammals. Thus, the average dry weight of raccoons is 0.0084 g/m^2. An average respiratory rate of 19% body wt/day was calculated from Altman, et al. (1958). This gives an average respiration of 0.0015 g/m^2/day or 0.55 g/m^2/year. Assimilation efficiency was assumed to be 50%. Production is probably less than one turnover per year since these animals live longer than one year. Thus, it is less than .008 g/m^2/year.



RACCOONS

The muskrat population was estimated from a count of the number of muskrat houses in the marsh. Newsom (1971) counted .025 houses per acre in the salt marsh in the vicinity of Airplane Lake during August 1969. O'Neil (1949) gives an average of 5 muskrats per house and an average weight of 1000 grams wet wt. per individual. Using these figures, there are .125 muskrats/acre or .031 g wet wt/m^2. Assuming 30% as the dry weight fraction, the biomass is 0.0092 g dry wt/m^2. Using the same respiratory rate as for raccoons, the respiration is 0.0017 g/m^2/day or 0.6205 g/m^2/year. Nutria, *Myocastor coypus,* are generally 1/5 as abundant as muskrat in the salt marshes (Chabreck, personal comm.). Mink is found in the salt marsh and its biomass was calculated to 0.0056 g wet wt/m^2. Otters are probably about as abundant as mink. Marine animals such as porpoises have a trophic position which is similiar to top carnivorous fishes and are considered in the section of fishes.



MUSKRAT AND NUTRIA

The muskrat is principally a herbivore, but it will occasionally take animal matter. Martin et al. (1939) report that bulrush and cattail make up the major portion of the diet with *Spartina* accounting for only 2 to 5%. The first two plants are fresh and brackish water plants; thus, salt marsh grasses must make up most of the diet in the area of study. Our observations indicate they eat mainly the roots rather than the above-ground portion of the plants. Nutria generally have similar food habits to the muskrat, but feed largely on the basal portion of the stems of plants.

The data above are for saline marshes. Muskrats, raccoons, and nutria are much more abundant in the brackish and fresh water marshes.

Birds which feed principally on the marsh include sparrows, wrens, rails, blackbirds, and grackles. Many wading birds and shore birds feed on the animals in the marsh as well as those of ponds, lakes, and bays. The trophic relationships of the birds will be considered in detail in a later section.

Table 11. Distribution of Marsh Fauna in Lake Palourde in August

Organism	Distance into Marsh from Water Edge: shore	3m	10m	20m	50m	average biomass to 50 m
Neritina	0	0	0	0	0.2/16	.04
Sesarma	3.2/4	0	0	0	0	.64
Fiddler	3.2/20	34.9/80	11.7/20	5.6/16	1.3/4	11.34
Littorina	3.6/40	2.9/40	13.3/148	9.8/80	13.5/88	8.62
Melampus	.2/28	1.4/392	3.1/672	1.3/260	0.2/20	1.24

FAUNA OF SUBMERGED SEDIMENTS

The submerged sediments of Barataria Bay consist mainly of soft peaty or muddy materials. Because of the soft nature of the sediments there is a scarcity of large sessile forms. Large flats of molluscs such as clams or scallops are absent from most of Barataria Bay. The only larger sessile benthic organisms which have developed large populations are oysters which are reef building organisms and *Rangia* clams which inhabit the oligohaline portions of the bay. Oysters are considered in a separate chapter. *Rangia* clams are not discussed because they fall out of the saline zone which is the subject of this paper. The greatest amount of the biomass of the submerged sediments is represented by meiofaunal organisms. This chapter will be concerned mainly with these organisms. A number of extensive studies and reviews concerning the meiobenthos have been reported in the literature. Among these are works of McIntyre (1969), Gerlach (1971), Wieser (1960), Tietjen (1969), and Fenchel (1968, 1969, 1970).

FORAMINIFERA

Waldron (1963) studied foraminifera in Timbalier Bay which is west of Barataria Bay (Fig. 1). Bottom samples were collected at 17 stations throughout the bay with a 2¾-inch core tube. Very few specimens were less than 0.149 mm in diameter. The following species represented the greatest part of the foraminifera collected: *Ammotium dilatatum, A. fragile, A. salsum, Elphidium gunteri, E. limosam, E. matagordanum, Streblus parkinsoniana, S. tepida,* and *Miliammina fusca.* Warren (1956) studied foraminifera of saline marshes in the Mississippi Delta just east of Barataria Bay. The most important genera characterizing lake sediments were *Ammobaculities, Cribroelphidium,* and *Eponidella.* Waldron found that individual stations showed peak populations at different times of the year. He suggested that organic materials in the water were responsible for higher numbers of foraminifera in the sediment. Mean monthly populations of foraminifera were calculated by averaging the populations at the 17 stations for each month. Although peak populations at individual stations occurred at different times, the highest mean peak occurred during April corresponding to the time of high loss of detrital material from the marshes (Fig. 13d and Table 12). Watkins (1961) found there were higher populations of foraminifera near sewage outfalls on the California coast.

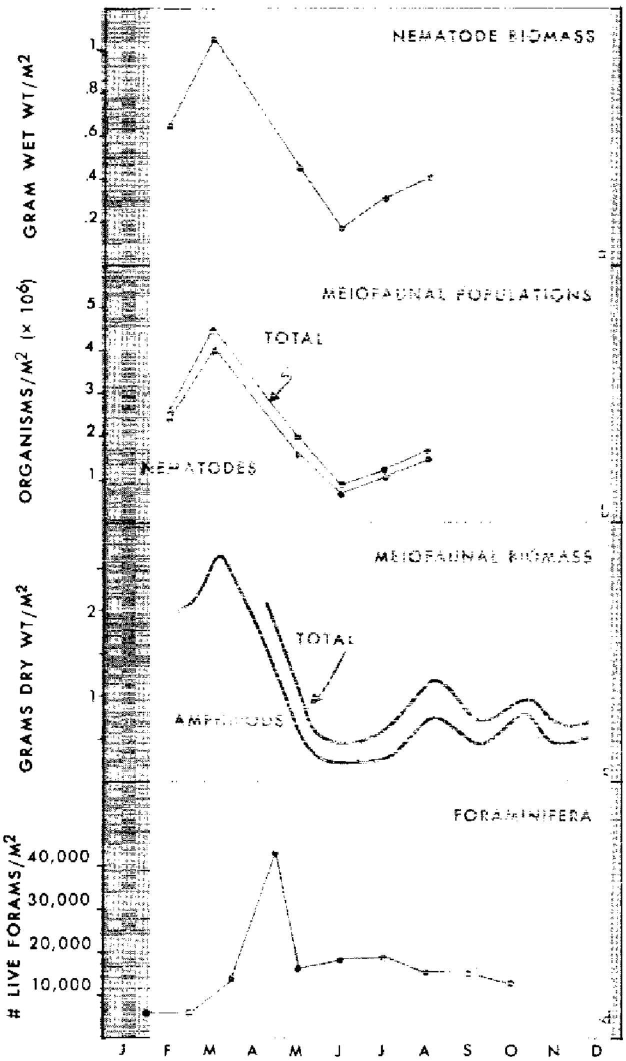


Figure 13. Annual variations of biomass and population levels of meiobenthic organisms of the submerged sediments in Airplane Lake (Bennett, 1972).

Table 12. Population levels of foraminifera in Timbalier Bay, La. (Recalculated from Waldron, 1963).

Month	Number live forams/m²
January	5557
February	5609
March	13945
April	43188
May	15894
June	18308
July	19451
August	15685
September	15322
October	13764

The average size of a single foraminiferan calculated from Waldron's data was between 0.2 and 0.3 mm, a sphere 0.25 mm in diameter in a specific gravity of 1.2 weighs approximately 10^{-5}g. The average population of living foraminifera during the year was 16,600/m^2. Assuming that these are all spheres with specific gravity = 1, this represents an average biomass of 0.16 g wet wt/m^2. Gerlach (1971) reported a foraminifera biomass range of 0.43 g–4.91 g wet/m^2 in 3 sublittoral zones off Goteborg. The average was 2.22 g/m^2. The organic content of foraminifera is about 4% of fresh weight (Gerlach, 1971). This gives a biomass of .0064 g org/m^2 for the calculation from Waldron and .089 g/m^2 for Gerlach.

Very few ciliates have been observed in submerged sediment samples from Barataria Bay. Gerlach states that in soft bottom sediments, nematodes and crestacea dominate and the numbers of Turbellaria, Gastrotricha and Ciliata are relatively small. This is true for the sediments of Barataria Bay. Fenchel (1968, 1969, 1970) has reported extensively on marine ciliates.

MEIOFAUNA

Rogers (1970) studied meiofaunal populations in several areas in the Barataria Bay system. In the Airplane Lake area, populations of nematodes ranged from 685,000 to 4,165,000/m^2. Biomass of nematodes was calculated using 0.000269 mg as the average weight of a single nematode. The determination of this weight was discussed in the section on the meiofauna of the marsh soil. Graphs of nematode biomass and numbers are present in Figures 13a and 13b, respectively. Both numbers and biomass were higher in March and lowest in the summer months. Nematodes represented about 90% of the total numbers of meiobenthic organisms. Wieser (1960) reported nematode populations of 1.69 to 1.86 x 10^6/m^2 in Buzzards Bay, Mass. The average weight of a single nematode was higher than that of the Louisiana nematodes (0.0012 to 0.0041 mg) thus the total biomass was higher (0.1 to 0.6 g dry wt/m^2). Nematodes and kinorhynchs comprised between 89 and 99% of numbers of meiofauna in Buzzards Bay.

Tietjen (1969) studied the meiofauna of two New England estuaries. Nematodes were the dominant group, averaging 83% of the total numbers and 64% of the total biomass. Nematode populations ranged from 0.82 to 4.8 x 10^6/m^2 and biomass ranged from 3.3 to 32 grams wet wt/m^2. Epigrowth and deposit feeding nematodes were most abundant. Epigrowth-feeding species reached maximum numbers in spring and summer; deposit and omnivorous-feeding species in fall and winter. The maximum in epigrowth-feeders coincided with increases in benthic microflora production and the maximum of deposit and omnivorous feeder coincided with increases in organic detritus levels. The high level of nematodes in March in Louisiana coincides with high levels of detrital washout from the marsh.

Bennett (unpublished data) and his co-workers have studied the larger meiobenthic population in Airplane Lake. The most common organisms (excluding nematodes) were harpacticoid copepods and the second most common were amphipods. These two groups represent about 80% of the total number of organisms counted. The next most common groups were ostracods, chironomid larvae, and polychaetes. The above five groups made up greater than 95% of the total. Tanaidaceans and cumaceans were numerous at times. The most common amphipods were *Corophium lacustre* and *Ampilesca sp. C. lacustre* was most common in *Spartina* roots near the shore. *Ampilesca* was most common in the submerged sediments adjacent to the shore.

Bennett provided population densities of copepods and amphipods. The average annual population level of amphipods was 3080/m^2 and that for copepods was 6832/m^2. The average length of amphipods was 2-3 mm and the average weight was about 200 μg dry wt/individual. The harpacticoid copepods were much smaller, weighing about 10 μg dry wt. each. The weights for these organisms is much higher than the 25 μg wet weight for amphipods, but close to the 7.5 μg for harpacticoids reported by Tietjen (1969). Bennett estimated that amphipods and harpacticoid copepods make up, on the average, about 80% of the total meiofaunal population and 90% of the biomass in the submerged sediments (excluding nematodes). The rest consists mainly of ostracods, chironomid larvae, and polychaetes. We estimated the biomass of meiobenthic organisms other than copepods and amphipods as twice that of harpacticoid copepods.

These data are presented in figure 13c. The highest biomass levels occurred during February and March; the lowest levels were in May, June, July, and September. The low populations during the summer months could be the result of higher predation or perhaps lower oxygen levels in the sediments because of higher temperatures. Amphipods dominate the meiofaunal biomass because of their large individual size as compared with other meiobenthic organisms. It should be remembered that these data are for Airplane Lake only, and are not necessarily representative of the entire Barataria Bay region.

Hiegel (1971) conducted detailed studies of the harpacticoid copepods in the sediments of Airplane Lake. The majority of benthic copepods were harpacticoids, but several species were ones commonly found in the plankton. There was a consistently greater population density in parts of the lake with the greatest current (highest current = 3 feet/sec). After a rain copepod numbers increased near shore. This is probably because the rain washed detritus into the near shore areas and copepods moved from deeper water to feed on it. Controlled lab experiments have shown that harpacticoids will actively seek out areas of favorable feeding conditions (Gray, 1968). Although there are no sharp ecological zonations in this shallow lake, each copepod species showed a definite preference for a certain portion of it. The most numerous species was *Canuella elongata*. It was found over the whole lake but preferred the deeper central portions where higher currents have been measured. *Pseudozosime* sp. were most numerous in the middle ground between the deep and shallow water about 70 feet from shore. *Nitocra spinipes* and *Paralaophonte lacerdai* were both found in the shallow water around the edge of the lake and absent from the deeper portion. *N. spinipes* was found in areas with higher currents (1-2 ft/sec) and *P. lacerdai* inhabited shallow areas of sluggish currents (less than 0.5 ft/sec). *Tachidius littoralis* was restricted to the deepest portion of the lake and completely absent from near-shore stations.

SPATIAL VARIATIONS

Spatial variation of meiobenthic biomass is presented in figure 14. The figure represents a typical transect across Airplane Lake. The transect is about 400 meters in length and stations 1 and 9 are each about 20 m from the two respective shores. The biomass of meiobenthic organisms is higher nearer the shore. As in the seasonal picture, amphipods dominate the biomass of the meiobenthic organisms because of their large size. One must examine the nature of the bottom sediments to understand this distribution of animals. The sediments near the shore are typically brown, highly organic and of a larger particle size as a result of detrital material being washed in from the surrounding marsh. However, sediments in the center of the lake contain a much higher portion of silt and clay, are typically grey colored, and have small particle size (Bennett, personal communication). Since many of the meiobenthic organisms are detrital feeders, there would be higher populations in areas of higher organic levels.

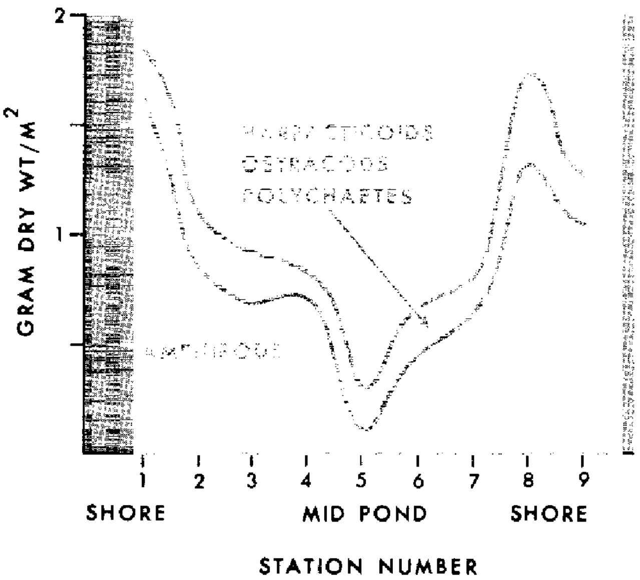


Figure 14. Variation of biomass of meiobenthic organisms on a transect across Airplane Lake. Note that biomass is higher near shore (Bennett, 1972).

FEEDING HABITS

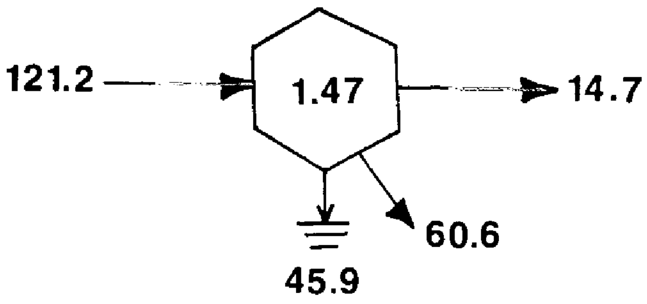
Weiser (1960) reported that most of the meiofauna feed on the substrate itself (i.e., they are deposit feeders). Perkins (1958) found the gut content of 16 specimens of nematodes with strong buccal armatures to consist chiefly of diatoms, bacteria, and possible minute flagellates.

The only nematodes identified from the Louisiana marshes had a small unarmed buccal cavity. "Nematodes with small unarmed buccal cavities have been classified by Wieser (1959) as selective deposit feeders and are thought to feed on small pieces of detritus and bacteria which they ingest by the sucking power of the esophagus" (Tietjen, 1967).

BIOMASS, RESPIRATION AND PRODUCTIVITY

The average annual total biomass (nematodes, foraminifera, and other meiobenthic organisms) was 1.47 g dry wt/m². We used the same respiratory rate that was used for the marsh soil meiofauna to calculate respiration of submerged sediment meiofauna. Thus, for an average biomass of 1.47 g org/m², the total respiration is 45.9 g/m²/year.

Gerlach (1971) gives 10 as the average number of turnovers per year for the meiobenthos. Production for an average biomass of 1.47 g org/m² is 14.7 g org/m²/year. Assuming an assimilation efficiency of 50%, feces production is 60.6 and total intake is 121.2 g org/m²/year.



MEIOBENTHOS

Forman (unpublished data) has qualitatively investigated the larger infauna in Lake Grande Ecaille (Fig. 3) in the eastern part of Barataria Bay. He collected samples with a Peterson Dredge. The most abundant organisms were two species of polychaetes similar to those collected in the marsh. Also fairly abundant were several species of small mollusks. Forman also collected epibenthic invertebrates in trawl hauls in Lake Grande Ecaille. The minor invertebrate components during 1970 consisted of *Thais haemostoma* (oyster drill), *Clibanarius vittatus* (hermit crab), *Squilla empusa* (mantis shrimp), *Alpheus heterochaelis* (snapping shrimp), *Callinectes similis* (a swimming crab), two species of non-commercial penaeid shrimp—*Trachypeneus similis* and *Xiphopeneus kroyeri*—and several species of xanthid crabs. The biomass for these minor components is shown in Table 13.

Table 13. Biomass of minor components in trawl samples from Lake Grand Ecaille, 1970 (Forman, unpublished data).

Season	g wet/m²
Winter	0.0009
Spring	0.0077
Summer	0.0024
Fall	0.0063

ZOOPLANKTON

This discussion of zooplankton is based mainly on the works of Cuzon du Rest (1963) and Gillespie (1971). Cuzon du Rest studied zooplankton in salt and brackish water areas north of Brenton and Chandeleur Sounds on the eastern side of the Mississippi River. Gillespie's samples were collected along the entire coast including nearshore areas and passes of the Barataria Bay complex. No extensive studies of zooplankton have been undertaken as part of the LSU sea grant program because the above works have given a fairly detailed and extensive description in Louisiana estuarine areas.

POPULATION COMPOSITION

Both Gillespie and Cuzon du Rest reported similar patterns of composition and seasonal abundance of the zooplankton, although significantly higher numbers were reported by Cuzon du Rest. Maximum zooplankton populations occurred in April. The most important zooplankter is the copepod *Acartia tonsa.* This single species accounted for an average of 60% of the total number of organisms counted by Gillespie and 83% for those counted by Cuzon du Rest. At times it represented more than 95%of the organisms caught (Fig. 15). *A. tonsa* has been reported to be the major component of the zooplanton in many estuarine areas including Biscayne Bay (Woodmansee, 1958); St. Andrew Bay, Florida (Hopkins, 1966); the Laguna Madre of Texas (Simmons, 1957); Long Island Sound (Conover, 1956); the surface waters of the Delaware Bay region (Deevey, 1952 a, b); Great Pond, Falmouth, Mass. (Barlow, 1952), and Lake Pontchartrain, La. (Darnell, 1961). Darnell found the greatest abundance of copepods in surface waters of areas "characterized by mixing of water masses, bottom roiling, and proximity to eroding marshes." *A. tonsa* is a euryhaline and eurythermal organism. It was found throughout all the temperature (5-35°C) and salinity (0.3 to greater than 30 ppt) ranges studied by Gillespie.

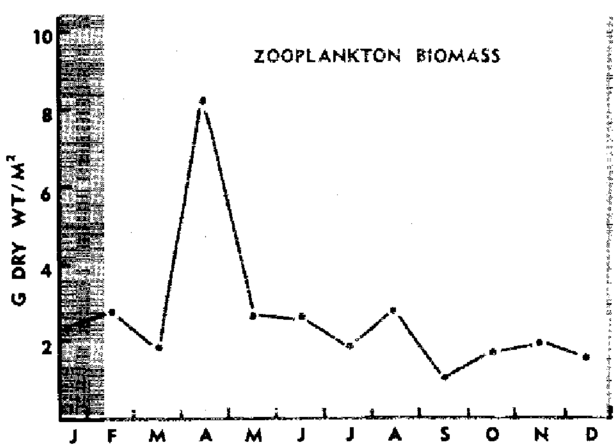


Figure 15. Annual cycle of zooplankton from salt marshes east of the Mississippi River (from Cuzon du Rest, 1963).

Other copepods of importance were *Labidocera aestiva, Centropages hamatus, Temora turbinata, Tortanus* sp., *Undinula vulgaris, Halicyclops fosteri,* and *Eurytemora hirundoides.* Gillespie noted that, as the number of other copepods increased (particularly *Labidocera aestiva*), *Acartia tonsa* decreased. *L. aestiva* is considered a predatory copepod and this may account for the diminishing numbers of *A. tonsa* with an increase in the *L. aestiva* population.

Decapod larval forms were present throughout the year but were most abundant during the spring months. Zoea and megalops of the blue crab were often abundant. The peak period for these larval forms was during the spring months but they were encountered throughout the year. Two decapods, *Acetes americanus carolinae* and *Lucifer faxoni,* and the caridean, *Leander tenuicornis,* were often abundant. *L. faxoni* is considered a carnivore.

Ctenophores were taken throughout the year but were particularly abundant during the summer months. When high concentrations of ctenophores were present, the rest of the zooplanton was low. The ctenophores seem to be important predators on the zooplankton. The most common species were *Beroe ovata* and *Mnemiopsis mccradyi.* Phillips, et al. (1969) studied jellyfishes and ctenophores in the Mississippi Sound. They reported that ctenophores and hydromedusae constituted the most important group of predators affecting zooplankton populations due to: (1) the extreme local abundance and (2) their voracious feeding habits. They presented a trophic diagram which indicated that jellyfishes and ctenophores feed mainly on zooplanton and, to a lesser extent, on small fishes. They are fed upon by several fishes, crabs, and shore birds.

Small bivalve larvae were common from July to November. Annelid larvae and post-larvae, mainly of the species *Neanthes succinea,* were most numerous around October. The chaetognath, *Sagitta hispida,* was abundant in September and October. The tunicate, *Oikopleura* sp., occurred throughout the year and was most abundant during the spring.

Gillespie states that "salinity appears to be the chief controlling factor in the number of species present, while temperature, competition, and predation control the number of individuals present."

FOOD HABITS

Both Gillespie and Cuzon du Rest commented that detrital material accounted for most of the volume of material collected on most tows. Gillespie found this especially true of waters of the Barataria Bay region. This information, along with Darnell's observation that copepods are numerous near eroding marshes, indicates that detritus is probably an important component of the diet of most zooplankters. Most zooplankters are considered to be herbivorous filter-feeders (with the exception of the carnivores mentioned above) and will probably take any small particulate material. Detritus is the most abundant suspended particulate material in the waters of Barataria Bay, thus it is probably taken more often by the filter-feeders.

Cuzon de Rest showed a major peak during April. This peak occurs at the same time the majority of fish larvae appear in the estuary and they probably serve as food for the fish. He showed no other well defined peaks and only slightly less zooplankton biomass during the colder months. Gillespie, however, showed a smaller, but well defined zooplankton peak during September and October and definite winter minimum.

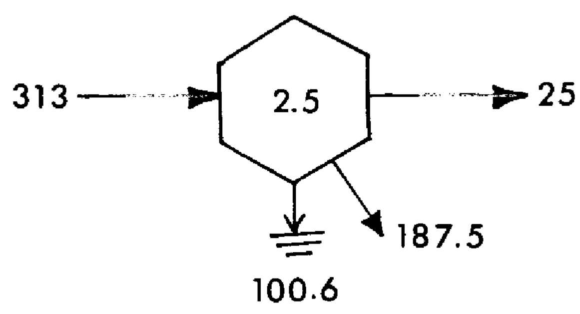
BIOMASS

Biomass and respiration of zooplankton were calculated based on Cuzon de Rest's data for *Acartia tonsa,* then corrected for the whole zooplankton population assuming that *A. tonsa* represented 80% of the population. Cuzon du Rest collected plankton from three areas in the estuary—a brackish marsh, an intermediate marsh type, and a saline marsh type. The data presented below are the average of all collections made in all types of marshes. *A. tonsa* represented about 83% of all organisms collected. There was a large biomass peak in April and perhaps a smaller one in August. This compares with peaks in June and October measured by Gillespie. Cuzon de Rest's numbers are about 10 times higher than those reported by Gillespie. Cuzon du Rest measured the highest populations of *Acartia* in the brackish marsh. The intermediate marsh population was 76% and the saline area population was 44% of that in the brackish marsh. Gillespie's low numbers in the pass areas may be indicative of the same trend. She also found that *A. tonsa* represented 60% of the total population as compared to 83% for Cuzon de Rest. This may be representative of higher diversity with increasing salinity.

The biomass figures were calculated as follows: Cuzon du Rest reported results as numbers per 5 minute drag of a 0.5 m plankton net hauled at the surface at approximately 2 knots. He suspected that much of the water did not filter because detritus clogged the net. Assuming half of the water filtered through the net, a column of water 152 m x 0.196 m^2 = 30 m^3 was filtered. Assuming water 2 meters in depth and that *Acartia* was equally distributed in the water column, the number of copepods per unit area can be calculated. Loesch (1971) gave the average wet weight of one *Acartia* as 0.09 mg. This figure was used to convert to biomass. Dry weight biomass for *Acartia* was calculated assuming 80% water. Biomass for total zooplankton was then calculated assuming *Acartia* represented 80% of the total.

RESPIRATION

Respiration was calculated using a rate of 10% body weight oxidized per day. Qasim (1970) reported a figure of 12%. Using these methods, respiration was calculated to be 0.22 g org material oxidized/m^2/day



ZOOPLANKTON

or 80.5 g/m^2/year for *Acartia tonsa*. Assuming *Acartia* represented 80% of total respiration, the zooplankton population respired 0.28 g org/m^2/day or 100.6 g/m^2/year. Woodmansee (1958) estimated that *Acartia tonsa* passed through about 11 generations per year in Biscayne Bay, Florida. The temperature is somewhat cooler in Louisiana estuaries so we will assume 10 generations per year. Using 2.0 g org/m^2 as the average biomass then the production of organic material by *Acartia* is 20 g org/m^2/year or 25 g/m^2/year for the total population. Mullin and Brooks (1970) gave gross growth efficiency of about 40% for copepods. Assuming that this means that 60% of total organic intake goes to feces, then feces production is 150 g/m^2/yr for Acartia or 187.5 g/m^2/yr for the total zooplankton population. Engleman (1961) found that the percentage feces production for Daphnia was 75%.

BLUE CRABS

In the next several sections we will consider separately several populations of animals which are of commercial importance. These include blue crabs, shrimp, and oysters.

LIFE HISTORY

Blue crabs, *Callinectes sapidus,* are fished heavily along the Louisiana coast, especially in Barataria Bay. The blue crab fishery in Barataria Bay has been considered in detail by Jaworski (1970). There are five periods of migration which have been recognized in Barataria Bay.

a. Spring up-estuary migration of large juvenile and adult males.
b. Recruitment of small juveniles to the upper estuary (late spring).
c. Return of the spawned females to the lower estuary and offshore in summer. The females spawn in the lower estuary during the early summer months. They then migrate offshore where they release the larvae (usually in August). The larvae pass through the zoea stages offshore and migrate into the estuary as megalops in late August or September.
d. Migration of gravid females to the lower estuary in autumn (the fall run of the females).
e. Out migration of large juveniles and adult males from the upper estuary in November and December.

The life span is 2 to 4 years, but they are fished as soon as they reach commercial size at 12 to 18 months after hatching. (See also Costlow, Rees, and Bookhout, 1959; Darnell, 1959; Tagatz, 1968, and Ven Engel, 1958).

FOOD HABITS

Food habits of the blue crab have been discussed by Darnell (1958), W. E. Odum (1971), and Tagatz (1968). Darnell found that the adult diet consisted of (% by volume) crabs and crustacea—10.4%; molluscs —63%; fish remains—5.4%, and organic detritus—8%. Crabs and crustaceans were most important for younger crabs, while molluscs and fish were less important. Darnell's study was done in a brackish lake which has a lower salinity than the Airplane Lake area. The oligohaline clam, *Rangia cuneata,* represented 46% of the total diet. Since these organisms are not found in the higher salinity areas, it may be that molluscs are not as important in the diet of blue crabs in the higher salinity areas. Tagatz reported the diet of blue crabs as molluscs—39%; fish—19%, and crustaceans—15%. His work was done in the St. Johns River, Florida. W. E. Odum reported the diet in the North R. estuary in the Everglades in order of abundance as mussels, crabs, fish, and a small volume of organic detritus. Crabs are preyed upon mainly by top carnivorous fish including gar, catfish, yellow bass, croaker, and several species of drum (Darnell, 1958).

BIOMASS

Examples of the annual patterns of blue crab biomass in Louisiana estuaries are presented in Figure 16. The data of Perret (1967) have been recalculated and are the average of three stations in Vermillion Bay, Louisiana, which is west of Barataria Bay. The data of Forman (unpublished data) are an average of three trawl stations in Lake Grande Ecaille in Eastern Barataria Bay during 1969 and 1970. Perret's data were presented as numbers, length, and frequency distribution of crabs caught in a 10-minute tow with a 16-foot otter trawl. Observations on otter trawls in the course of research at LSU indicate that a 16-foot otter trawl will open about 2.5 meters when in use. Using this figure and an average trawling speed of 2 knots, the appropriate area covered during the trawl can be calculated. This area is then divided into the total number of crabs caught for a particular trawl to obtain the number of crabs per square meter. The average carapace width for each was estimated from the length-frequency diagram.

Figure 16. Annual variation of blue crab biomass from Vermillion Bay, Louisiana for 1964-65 (solid line; from Perret, 1967) and from Lake Grande Ecaille in eastern Barataria Bay for 1969-70 (dashed line; from Forman, unpublished data).

Larger crabs are present in the summer. The crab biomass/m² was computed as follows: The weight of an average crab for each trawl was determined from a graph of carapace width versus weight presented by Truesdale (1970). The weight for an average crab was then multiplied by the number of crabs for that trawl to obtain the total biomass. Forman weighed the crabs he caught so that biomass on a g/m² basis had only to be divided by the total area covered by the trawl. We are assuming that the trawl is 50% efficient in capturing crabs; therefore biomass data from Forman and Perret has been multiplied by a factor of two. Wet weight biomass was converted to dry weight assuming 80% water.

For both workers, the highest biomass peak was during the summer. There is fairly close agreement except for measurements of Perret during April and May. Records of crab fishery catch indicate that there may be considerable variation in the quantity of fishery yield for different years which may account for the differences. The biomass ranged from 0.23 g dry wt/m² during the summer to a low of 0.02 g dry wt/m² during the winter.

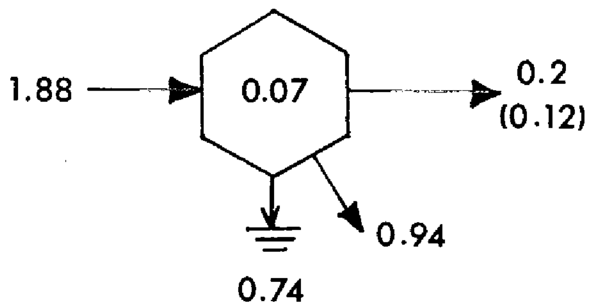
Biomass of several species of less abundant crabs was also obtained from Forman for collections in Lake Grande Ecaille. Included among these species of crabs caught during 1970 were *Callinectes similis, Menippe mercenaria, Rhithropanopeus harrisii,* and *Eurypanopeus* sp. The biomass of these organisms averaged about .012 g wet wt/m².

RESPIRATION

Respiration was calculated using data from Waterman (1960). An average respiratory rate of 0.03 respired/g C body weight/day was recalculated from Waterman. This figure was multiplied by the average biomass to obtain respiration. The average respiration for the entire year is 0.002 g dry wt respired/m²/day or 0.74 g/m²/year when calculated either from Perret's or Forman's data.

It takes about 12 to 18 months for total maturation of blue crabs. We will assume that all of the population must be replaced each year. This gives a figure of about 0.2 g dry wt/m²/year for production if we use 0.2 g/m² as the peak summer population. It must be remembered that these data are calculated from trawl tows. We do not know how efficient trawls are in sampling the crab population and are assuming 50% efficiency. Fischler (1965) estimated the blue crab population in the Neuse River in North Carolina using catch-effort, catch-sampling, and tagging methods. From maps of the region, we estimated the total area sampled and obtained a biomass figure of 0.15 g org/m². This is a rough figure, but it is relatively close to the one presented here.

Jaworski's (1970) report of the total crab catch for both commercial and sports fishing claimed 2,200,000 pounds for 1970. If we assume that dry organic matter (less water and ash) is about 10% of the fresh weight, then the total crab fishery in Barataria Bay is approximately 10^8 g org/year. Using a figure of 1.6×10^9 m² for the area of the Barataria Bay system, the take of crabs by man is approximately 0.06 g dry wt/m²/year. The bay system is about 50% water, thus the total catch on a water area basis would be about twice this or 0.12 g dry wt/m² water/year. Thus the total intake of organic matter by the blue crab population must be 1.88 g/m²/year to account for 0.2 g of production, 0.74 g for respiration, and 0.94 for feces production (assuming 50% assimilation efficiency).



BLUE CRABS

SHRIMP

Shrimp are among the most important commercial species in Louisiana coastal and estuarine waters. They rank first in dollar value and second to menhaden in total poundage. The average annual shrimp harvest from inshore Louisiana waters from 1963 to 1967 was 30.6 million pounds (live weight) valued at more than $10 million to the fisherman. These data were obtained from an IBM listing provided by the National Marine Fisheries Service (NMFS) Statistical Office in New Orleans, La. During the 1963-67 period, the Barataria Bay complex accounted for about 27% of the total shrimp production in Louisiana (Lindall et al., 1972). Brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, are commercially important in Louisiana. Other shrimp present but not nearly so abundant are pink shrimp, *P. duorarum;* seabob, *Xiphopeneus kroyeri;* rock shrimp, *Sicyonia brevirostris;* mantis shrimp, *Squilla empusa*, and snapping shrimp, *Alpheus* sp.

LIFE HISTORY

"The normal shrimp cycle is now well established and involves the movement of postlarvae into inland waters, thence deep into the shallow nursery areas where they metamorphose into rapidly growing juveniles. These juveniles, as they increase in size, begin a movement into the deeper, larger bays and out the passes to osffhore waters" (St. Amant et al., 1965). Generally, both brown and white shrimp spawn offshore. Brown shrimp spawn in water of 10 to 60 fathoms and white shrimp spawn in 7½ to 15 fathoms.

Brown shrimp postlarvae migrate into the estuaries in greatest numbers during the months of February, March, and April. The postlarvae appear to come through the passes as waves on the incoming tides. There is very little growth of postlarvae at temperatures under 20°C and salinities less than 15 ppt. "The appearance of postlarvae at the passes seems to have little relationship to water temperature on the nursery ground, but survival and growth of the postlarvae is apparently strongly affected by temperature and possibly salinity" (St. Amant et al., 1965). Brown shrimp move offshore during early to mid summer. Crowding and high summer temperatures seem to be the most important factors influencing this offshore movement.

Postlarval white shrimp move into the estuaries in greatest numbers in July and August. Most of the shrimp leave the estuary during November and December. The first movement appears to be due to size and later, as the temperature drops, there is general exodus.

HABITAT

Both brown and white shrimp prefer soft muddy or peaty substrata, while pink shrimp tend towards more firm bottoms (Hildebrand, 1954; Williams, 1958; Kutkuhn, 1962). The scarcity of pink shrimp in Louisiana waters probably results primarily from the fact that most of the water bottoms are soft mud or peat. Loesch (1962 and 1965) studied shrimp populations in Mobile Bay, Alabama. He found that white shrimp were concentrated in water less than 2 feet deep in areas with large amounts of organic detritus. Brown shrimp were more abundant in water 2 to3 feet deep among attached vegetation.

FOOD

Shrimp are generally omnivorous, eating plants, animals, and inorganic and organic detritus (Farfante, 1969). Shrimps in Lake Pontchartrain, Louisiana consumed detritus and ground organic matter (58%), small molluscs (12%), and microcrustacea (4%) (Darnell, 1958). Flint 1956) reported that small shrimp (less than 10mm) consumed mostly blue-green filamentous algae and diatoms while adults fed on bryozoans, algae, coral, roots, and stems. Williams (1955) reported shrimp food, in order of abundance, as unrecognizable detritus, chitin, fragments (crustaceans), setae and worm jaws (annelids), and plant fragments. Lindall et al. (1972) reported that there are some indications that algae provide an important part of the diet of white shrimp in Louisiana waters. W. E. Odum (1971) studied pink shrimp in the North River estuary in the Everglades. Gut analyses indicated 15% plant detritus, and 69% inorganic and unidentified fine particles. Also observed were harpacticoid copepods, small molluscs, ostracods, benthic diatoms, and filamentous green and blue-green algae.

BIOMASS

It is much easier to estimate the population of brown shrimp than it is for white shrimp. Brown shrimp tend to distribute themselves uniformly while white shrimp tend to "school." Trawls for brown shrimp tend to be fairly close on both spatial and time basis. For white shrimp, however, trawling in an area can give almost no shrimp one week and very high populations the next. Thus, it is much more difficult to obtain good population and biomass data on white shrimp.

Brown shrimp. Brown shrimp biomass was calculated from data from collections in Airplane Lake in 1969 and 1970 (Jacob and Loesch, 1971) (Fig. 17). Loesch (personal communication) estimated that the trawl was about 50% efficient in capturing shrimp: thus, trawl data has been multiplied by a factor of 2 to obtain figures we believe to be closer to the actual biomass. Shrimp were dried and ashed to determine the percentage of organic matter. Average figures determined were 80.1% water, 16.0% organic matter (ash-free dry weight), and 4.1% ash (Loesch, personal communication). The area under each of the brown shrimp curves was integrated to obtain an average biomass for the entire year. These were 0.06 g dry wt/m² for 1969 and 0.09 dry wt/m² for 1970, or an average of 0.075 g dry wt/m² for the two years.

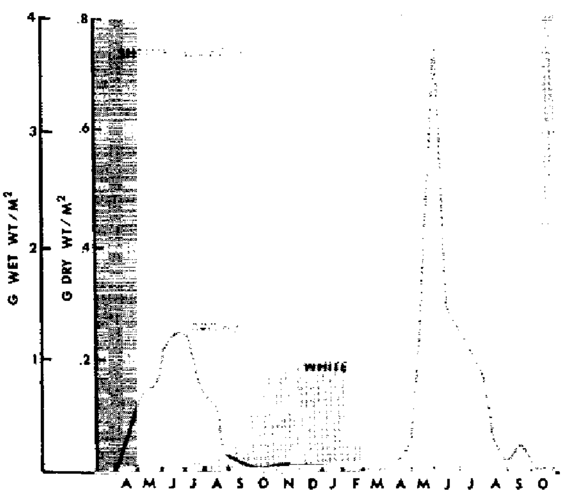


Figure 17. Annual biomass variation for brown shrimp (Jacob and Loesch, 1971) in Airplane Lake and white shrimp (Crowe, unpublished data) in parts of Barataria Bay. The two years of data for brown shrimp are 1969 and 1970. The data for white shrimp is for 1971-72.

There was a much higher brown shrimp population in 1970. As stated earlier, if temperature and salinity conditions are not optimal when the postlarvae arrive on the nursery grounds, then growth will be slow and mortality will be high. For the first year the peak biomass was reached in mid-June while, for the second year, the peak was in early May. Winter temperatures in early 1970 were much milder than in 1969. This resulted in a longer growing season and probably resulted in the higher biomass levels in 1970. The decline during both years is the result of commercial shrimping, natural mortality and migration out of the estuary.

White shrimp. Annual biomass patterns for white shrimp are shown in Figure 16. The postlarvae migrate into the estuary during the summer. Maximum biomass normally occurs in late fall with emigration soon after. There was a smaller biomass peak in late February. The white shrimp taken in late February were adults which had overwintered in the estuary. The 1971-72 winter was very mild. It is not uncommon to have fairly high numbers of shrimp stay in the estuary during mild winters, but almost all leave during colder winters. An average annual biomass of 0.03 g dry wt/m² was calculated by integrating the area under the curve for white shrimp. The peak biomass was 0.16 g dry wt/m² (0.98 g wet wt/m²). Data on white shrimp are from an M. S. thesis in progress by Arthur Crowe.

Biomass levels of some of the less important shrimp species have been provided by Forman (unpublished data) from Lake Grand Ecaille in the eastern part of the Barataria Bay system. The grass shrimps, *Palaemonetes vulgaris* and *P. pugio,* were taken with a 25-foot seine in areas close to shore. They were not collected in open water. The biomass of *Palaemonetes* in 1969 was 0.22 g wet wt/m² for spring collection, 0.40 g/m² for the summer, and 0.21 g/m² in the fall. No collections were made during the winter because of low water. Trawl collections of less important shrimps gave biomass levels of 0.0, 0.001, 0.006, and 0.0009 g wet/m² during the winter, spring, summer, and fall of 1970, respectively. These shrimps included *Penaeus duorarum* (pink shrimp), *Trachypeneus similis* (penaeid shrimp), *Xiphopeneus kroyeri* (seabob), *Alpheus heterochaelis* (snapping shrimp), and *Squilla empusa* (mantis shrimp).

RESPIRATION AND PRODUCTION

Brown shrimp. A respiratory rate of 5.7% body wt/day was used in calculating shrimp respiration (Waterman, 1960). Using an average annual biomass of 0.075 g org/m², the total brown shrimp respiration is 0.0042 g org/m²/day or 1.53 g org/m²/year. Respiration at the time of peak biomass of 0.37 g/m² (average for the two peaks) was 0.021 g org/m²/day. Loesch and Jacob estimate that shrimp production is roughly twice the maximum standing crop. Thus, for a peak crop of 0.37 g/m², the yearly production would be 0.74 g org/m²/year.

Loesch and Cobo (1966) reported that commercial landings of shrimp were 1.5 to 1.8 times maximum standing crop in Ecuador and Loesch (1962) estimated that commercial landings were twice the maximum standing crop in Mobile Bay, Alabama.

The average annual commercial catch of shrimp in Barataria Bay from 1963 to 1967 was 4,544,000 pounds of 2.065 x 10^9 g fresh weight (Lindall et al., 1972). The Barataria Bay marsh-estuarine area is approximately 1.6 x $10^9 m^2$, thus the average catch for the 5 years is 0.26 g dry wt/m^2/year. The area is about 50% water, thus the total catch on the basis of water is 0.52 g dry wt/m^2 of water surface/year. Roughly 57% of the total shrimp catch is brown (Lindall et al, 1972), thus the take of brown shrimp is 0.30 g org/m^2/year, or 41% of production by brown shrimp is harvested by man.

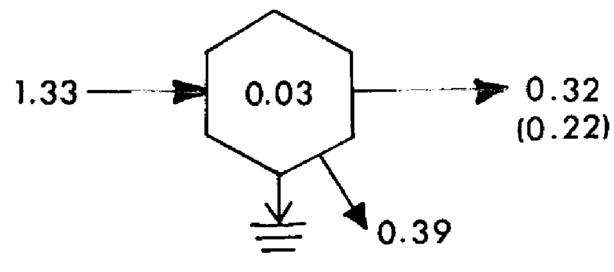
Condrey et al. (1971) estimated the assimilation efficiency of organic matter by brown shrimp to be about 75%, giving a feces production of 0.77 g org/m^2/year.

White shrimp. Data for respiration and production were calculated using the same rates as were used for brown shrimp. Using 0.057/day for the respiratory rate and an average annual biomass of 0.03 org/m^2, the total white shrimp respiration is 0.0017 g org respired/m^2/day or 0.62 g/m^2/yr.

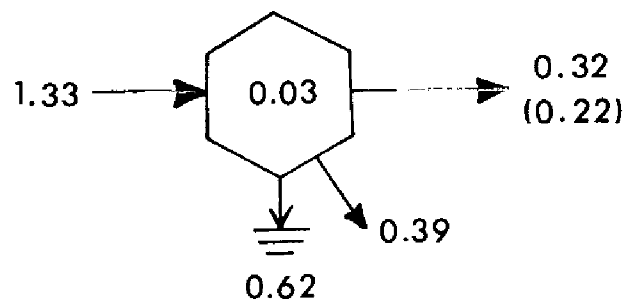
Using Loesch and Jacob's estimate that production is twice the maximum standing crop, the yearly production for white shrimp is 0.32 g org/m^2/yr.

As stated earlier, the total shrimp catch in Barataria Bay is 0.52 g dry wt/m^2 of water surface/yr. About 43% of this is white shrimp, giving a commercial catch of 0.22 g org/m^2/yr or 69% of white shrimp production.

Using 75% as the assimilation efficiency (Condrey et al., 1971), the production of feces is 0.39 g/m^2/yr and the total intake is 1.33 g/m^2/yr.



BROWN SHRIMP



WHITE SHRIMP

OYSTERS

The fishery for the American oyster, *Crassostrea virginica*, is estimated to be from 8 to 12 million dollars per year in Louisiana. Barataria Bay is second only to areas on the east side of the Mississippi River in oyster production. One volume of the Publications of the Institute of Marine Science of the University of Texas (Vol. 7, 1962) has been devoted to the Louisiana oyster industry and its relationship to the oil industry. This volume contains detailed reports of various studies of oysters and oyster diseases.

LIFE HISTORY

Oysters have a planktonic larval stage and are sessile as adults. Female oysters may produce 70 million eggs in a single spawning. There are two larval stages—a trochophore and then a veliger. The larvae feed on smaller planktonic organisms and detritus. After about 18 days the young oysters settle and begin the sessile adult life. The larvae seem to be able to choose a place for settling and prefer firmer substrates. In Louisiana, oysters are usually harvested when they are between 18 and 30 months old. They have been found to live as long as 30 to 40 years. For more detailed discussions, see Lindall et al (1972), Galtsoff (1964), Loosanoff (1965), and St. Amant (1964).

Oysters are filter feeders, taking in detritus, phytoplankton, bacteria, and any other small particulate material in the walter column. Through the feeding process a large amount of suspended material is sedimented as feces and pseudofeces. Kuenzler (1961) reported that mussels in a Georgia salt marsh were very important in removing phosphorus from the water and depositing it on the bottom in fecal material where it could be used by rooted vegetation and benthic algae. Oysters may play a similar ecological role in cycling of minerals and organic material.

Under natural conditions oysters will often build extensive reefs. These reefs formed the basis for the early oyster fishery in Louisiana. However, because of over-fishing, salinity encroachment, and pollution, there is very little fishing done on natural reefs today. The higher salinity water allowed the oyster drill to devastate many of the old reefs. Because of these conditions most of the oyster fishery is artifically planted. Young oysters are allowed to grow to about 15 months on seed grounds in waters of 1 to 15 ppt. The low salinity waters protect the young oysters from drills, *Thais haemostoma*, a major predator. Since the latter part of the time on the seed grounds is usually in the summer, the low salinity water makes the oysters less susceptible to the fungus, Dermocyctidium. Above 12 to 15 ppt oysters are much more susceptible to these and other parasites, predators and diseases such as boring sponges, *Cliona;* polychaete worms, *Polydora;* boring clams, *Martesia;* and stone crabs, *Menippe* (Gunter, 1952).

Oysters are moved to "fattening" beds in Barataria Bay in waters of 10 to 25 ppt. The oysters are planted on these beds chiefly from September through November. Oysters are harvested from February to May. The average time on the "fattening" beds is about 6 months.

An average planting of seed oysters on the fattening beds consists of about 900 sacks of 500 seed oysters/acre (Ted Ford and H. J. Bennett, personal communication). This is 450,000 seed oysters/acre or 110 oysters/m^2. Seed oysters are 1½ to 2 inches in diameter and weigh about 3 grams, not including the shell. Thus the biomass at the time of planting is about 330 grams of fresh oyster meat/m^2 of oyster bed. Assuming oysters are 90% water and ash, this is 33 g org/m^2. We will assume a mortality of 30% over the 6 months on the fattening beds (St. Amant et al., 1957). Thus, of the 110 oysters/m^2 planted, 77 will be alive at the time of harvest.

Conversations with oyster men indicate that an average harvests consists of some 900 sacks of about 160 oysters (Ted Ford, personal communication). Thus, for each sack planted, there is one sack harvested, Mackin and Hopkins (1962), reported yields of 0.89-1.52 sacks harvested per sack planted in Louisiana waters. The above mentioned harvest yields 144,000 oysters/acre or 35.5 oysters/m^2. If 77 oysters/m^2 are present at harvest time, then 45% of available oysters are harvested. These oysters are 3½ to 4 inches long when harvested. Measurements in our lab indicate that an oyster this size weighs about 20 g wet wt. for the meat alone. Thus the harvest is 711 g wt/m^2 or 71 g org/m^2. Lindall, (et al 1972) estimated that an average of 10,650 acres annually were in oyster production in Barataria Bay from 1963-67. The average production of cannery oysters was 357 lbs/acre. They estimated that, because of the large fishery for raw oysters, total production was about 5 times the production of cannery oysters. This is 1,715 lbs/acre or

200 grams wet wt/m²/year. This figure is less than 1/3 of the figure of 711 g/m² mentioned above. Our observations indicate the latter figure is probably more nearly correct.

RESPIRATION

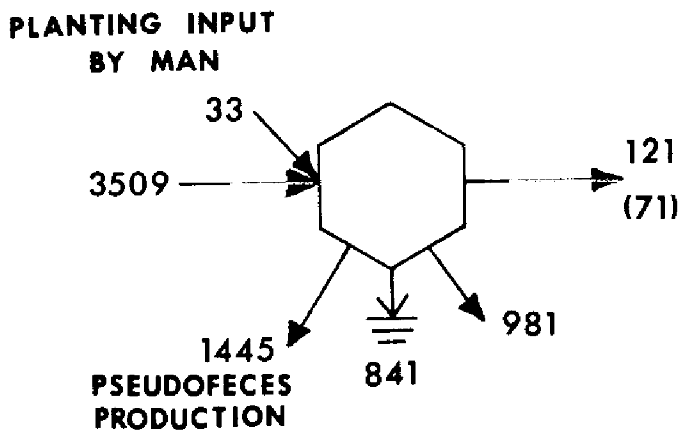
Calculations from Galtsoff (1964) indicate that oysters respire about 5% of their dry body wt per day. The initial seed oyster biomass was 33 g org/m². At harvest time there were 77 oysters weighing 2 g org/m², or 154 grams org/m². This is the highest biomass attained because almost half of the oysters are harvested and the remainder suffer heavy mortality during the summer months (St. Amant, et al, 1957). The average of the initial and highest biomass, 93.5 g org/m², will be used to calculate respiration. Using this biomass and the 5% respiratory rate, the average oyster respiration over the six months on the fattening beds is 4.5 g org/m²/yr.

Mackin (1962) measured rates of production of fecal and pseudofecal material from adult oysters from Louisiana waters at 1.11 cc of fecal material and 1.71 cc pseudofecal material per oyster per day. Assuming that the average weight of each oyster was 20 grams and that the specific gravity of the material was 1.0, then an oyster produces 5.6% of its weight in feces and 8.6% of in pseudofeces per day. For a 3 gram oyster, there are 0.17 g of fecal material and 0.26 g of pseudofecal material produced per oyster/day. For a 20 gram oyster, the rates are 1.12 and 1.72 grams/oyster/day. Since there were 110 seed oysters/m² at the beginning of the season, the production by small oysters was 18.7 g/m²/day of fecal material and 28.6 g/m²/day of pseudofecal material. There were 77 adult oysters (20 grams) at harvest time. The production by these large oysters was 86.24 g feces and 132 g of pseudofecal material per m²/day. The average production of fecal and pseudofecal material of the small and adult oysters was 54.47 g/m²/day and 80.3 g/m²/day, respectively. Over a six month season (180 days) this production is 9,810 g wet wt/m² of fecas and 14,450 g wet wt/m² of pseudofeces. We will assume an organic content of 10%. Thus, the fecal production is 981 g org/m²/yr and the pseudofecal production is 1,445 g org/m² of oysterbed/yr.

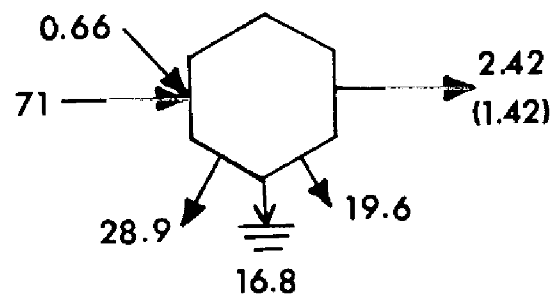
PRODUCTION

The initial biomass on the beds was 33 g org/m² and the biomass at harvest time was 154 g org/m². Thus the increase in oyster biomass over the 6 month growing season is 121 g org/m². The initial input of 33 g org/m²/yr. is all at once when the planting is done. The intake of food by the oysters during the time can be obtained by summing the amount of organic matter used for feces, pseudo-feces, respiration and production while on the fattening beds. This gives a total of 3,502 g org/matter/year. All of the above data are based on the area of actual oyster production which represents about 2.3% of the total water area of the bay. Since the oysters are dependent of currents bringing food to them from other parts of the bay, a better idea of the significance of the oysters is obtained when they are considered over the whole bay. Thus data is presented below on the basis of the oyster beds and also over the whole water area.

ON OYSTER BEDS



OVER WHOLE WATER AREA



FISHES

In order to study the trophic significance of fishes, trawl collections were made at seven stations in Caminada Bay (Fig. 3.) The results of this sampling were used to study biomass, seasonal abundance, food habits, and growth rates of the fishes in the area.

Ten major species of fish and one combined group of species with similar habitat requirements were selected for stomach analysis. These fishes make up 88.7 percent of the total number and 71.6 percent of the biomass of fish taken in the Caminada Bay area.

The species selected were *Anchoa mitchilli,* bay anchovy; *Brevoortia patronus,* Gulf menhaden; *Leiostomus xanthurus,* spot; *Cynoscion arenarius,* sand seatrout; *Cynoscion nebulosus,* speckled seatrout; *Arius felis,* sea catfish; *Mugil cephalus,* striped mullet; *Citharichthys spilopterus,* bay whiff; and *Menidia beryllina,* tidewater silverside. Five species of the family Cyprinodontidae were selected: *Cyprinodon variegatus,* sheepshead minnow; *Adenia xenica,* diamond killfish; *Fundulus grandis,* Gulf killifish; *Fundulus confluentus,* marsh killifish; *Lucania parva,* rainwater killifish; and *Poecilia latipinna,* saillin molly (poeciliidae). A more complete listing of fishes is presented in Table 2.

Food studies of fish have proved useful in revealing ecological relationships among the various organisms in the estuarine food web. Earlier workers, notably Darnell (1958, 1961) and W. E. Odum (1971), have used this technique to determine trophic structure and pathways of energy flow. Food studies may also reveal changes in food habits due to aging, sex, or seasonal variation in food availability. On the basis of this analysis, fish may be classified into several trophic levels (W. E. Odum, 1971): herbivores; omnivores, and primary, middle, and top carnivores.

Fish were obtained with a 16' otter trawl. They were placed in plastic bags on ice immediately after collection, then in 10 percent formalin after weight and total length had been recorded. In the laboratory, the anterior stomachs (esophagus and stomach to pyloric sphincter) were dissected out, placed in small vials of 40 percent isopropyl alcohol, and labeled. Food items removed from the stomachs were counted, identified, and their relative frequency determined. Observations made on morphometric and meristic characteristics associated with feeding included shape and position of mouth, presence or absence of teeth, length of intestine, and numbers and shape of gill rakers.

SEASONAL DISTRIBUTION AND ABUNDANCE

The majority of fishes found in the Caminada Bay System are of two general categories: truly estuarine species indigenous to the area that spend their entire lives in the estuaries, and marine species that use the estuary as a nursery area, usually spawning in the Gulf, moving into the bays as post-larvae, and returning to the Gulf as subadults. In the first category are *Anchoa mitchilli, Menidia beryllina,* and the killifishes. Seasonal migrants include the remainder of the fishes selected for analysis—*Micropogon undulatus, Leiostomus xanthurus, Cynoscion arenarius, Arius felis, Brevoortia patronus, Mugil cephalus,* and *Citharichthys spilopterus.* It might be mentioned that *Arius felis* is known to spawn both in the bay and the Gulf, usually from July to September. The remainder of the seasonal migrants spawn in the Gulf from October to March and move into the bay through late summer. The general exodus from the bays coincides with the first pronounced temperature drop in the fall, but may start for some species in early or mid-summer. According to Gunter (1938), the temperature cycle is chiefly responsible for seasonal movements and variations in abundance of fish in the estuaries. The general pattern of fish movements is correlated closely with seasonal temperature changes. As the temperature rises from a winter minimum there is a general inshore movement of fish, building up to a spring maximum. As the temperature begins to drop in the fall, maturing subadult fish leave the estuary and the fish fauna of the area decrease rapidly in number and species. The lowest temperatures of the year correspond with the lowest number of fish in the estuary.

A few general comments on species diversity and size distribution as related to salinity and temperature may be appropriate here. Some authors, notably Gunter (1956, 1961), have observed a gradual decrease in species numbers as one proceeds up an estuary from saline to fresh water. This study has shown some correlation between species diversity and salinity but superimposed on this relationship is the influence of different habitats. Each of 7 sampling stations which range from almost full strength Gulf water to nearly fresh water, represent a different habitat type. Habitats in lower salinity water may be more attractive to a greater number of species than habitats in more saline water. In the spring and summer, greater numbers and biomass of fish are found near the shore-lines of the bays rather than in the deeper areas. The opposite is true in the fall and winter. Sampling stations represent a sand beach, a deep pass, a small shallow marsh lake, a deeper marsh bay, a channel between two bays, an intermediate size marsh bay, and a dead end oil canal. The greatest number of species occur in late summer to early fall and the lowest in late winter. Species diversity is therefore directly correlated with temperature.

A direct correlation also exists between size distribution and salinity and temperature. Smaller juvenile fishes are able to tolerate lower salinities and lower temperatures than adults of the same species. Post-larval fishes of many species move into upper fresher sections of the estuary and gradually move Gulfward as they mature. What results is a distribution of small fishes in upper estuaries in the spring after spawning and larger fishes in the lower bay in the summer and fall as the fishes near adult size. With a rise of temperature through the spring and summer months, growth rates accelerate and fish reach subadult size in late summer before moving offshore to spawn. Another offshore movement occurs when the first pronounced temperature drop occurs in the fall. A mass migration of many species is triggered by this change in temperature. Three migrations are therefore noticeable in fishes in this area: an inshore feeding migration of post-larval fish, an offshore spawning migration, and an offshore overwintering migration.

Individual species seasonality has been studied in Barataria Bay which is just east of Caminada Bay by Gunter (1938) and Fox and Mock (1968). Gunter used an otter trawl exclusively and Fox and Mock a beach seine. This tends to bias results severely because certain species are susceptible to only certain kinds of gear. These authors found different species to be the most aboundant fish. This is due largely to the utilization of different types of collecting gear. Gunter found the Atlantic croaker most abundant while Fox and Mock found the bay anchovy most abundant. During the present study three types of collecting gear were used—a 16-foot otter trawl, a 75-foot bag seine, and a 300-foot trammel net. Fintrol, a fish poison, was used for sampling the small ponds in the marsh interior.

Results from March 1971 to June 1972 of this sampling are presented in Table 14. A total of 97,223 fish of 100 species from 82 genera representing 46 families were collected. The 16 species of fish mentioned earlier make up 88.7 percent of the total number. The remaining 84 species make up approximately 11 percent of the total. It should be mentioned that the data on the last three species (or group of species) is thought to underestimate their true abundance. The striped mullet easily escapes the trawl and often jumps over the seine and trammel net. They are visibly, however, a very important component in the fish fauna, especially in marsh creeks and ponds, yet are not being adequately sampled. They do become more vulnerable in the colder winter months when forced to leave the shallow littoral areas for the deeper channels where they may be collected with the otter trawl. The speckled trout, because of its swiftness, is adept at avoiding the trawl and is more abundant than indicated. The cyprinodonts are an extremely important element of the fish fauna in the interior marsh or "prairie" as it is called in South Louisiana. They typically inhabit shallow marsh ponds and tidal creeks with a bottom composed of mud, clay, and organic detritus. They have not been sampled adequately because the three nets used could not be fished in the small ponds which they inhabit. Foreman (1968) made a detailed study of cyprinodonts in Barataria Bay. The tidewater silverside is also more abundant than indicated and probably ranks higher in the order of abundance. It has only been taken with the 75-foot seine because of its nearshore shallow water habitat. The seine was used at five stations on an alternating schedule while the trawl was used at every station on every collecting trip. Thus, bottom and slow-moving fishes more susceptible to trawl capture are more frequently taken.

Table 14. Numbers, order of abundance, and percent of total catch for 16 species collected at 7 stations in the Caminada Bay area. (March 1971-June 1972)

Species	Number	Order of Abundance	Percent of Total Catch
Anchoa mitchilli	52633	1	55.1
Brevoortia patronus	14782	2	15.4
Leiostomus xanthurus	5786	3	6.1
Micropogon undulatus	5300	4	5.6
Cyprinodonts (collectively)	2301	5	2.4
Arius felis	2166	6	2.2
Menidia beryllina	831	7	0.9
Cynoscion arenarius	493	8	0.5
Citharichthys spilopterus	214	9	0.2
Mugil cephalus	177	10	0.2
Cynoscion nebulosus	76	11	0.1
Total	84759		
Total all species	97233		
% above species of total species		88.7	

SMALL POND STUDIES

Two ponds were sampled in October, 1971, with Fintrol-5, a fish toxicant with 1 percent Antimycin A as the active ingredient. It was used at a concentration of 1.5 ppm in both ponds. Two types of ponds were sampled. One was a blind or isolated pond of

224 m^2 size with a depth of 8 to 30 cm and a soft silty bottom of *Spartina* detritus. The other was slightly smaller (193 m^2), but somewhat deeper (30 to 50 cm). The bottom was of a firmer silty-clay texture. The latter pond had a small tidal creek connecting it to a larger bayou and was therefore not isolated or land-locked.

Some significant differences were noted in species composition, numbers, and biomass in the two ponds. Nine species were collected in the blind pond, the majority of which were fishes of the family Cyprinodontidae and Mugilidae. The fish fauna were representative of the typical shallow water and shoreline assemblage of fishes. A total of 1,649 fish, weighing 10,314.9 grams, were taken. Ten species were taken in the connected pond but were representative of fishes occurring in deeper bays and marsh lakes. It is significant that no cyprinodonts were taken in the connected pond. The predominant species were *Anchoa mitchilli, Cynoscion nebulosus, Cynoscion arenarius, Menidia beryllina, Paralichthys lethostigma,* and *Strongylura marina*. A total of 105 fishes weighing 2,665.8 grams were collected.

The isolated pond had a much higher standing crop biomass than the connected pond: 46.1 grams wet/m^2 as opposed to 13.8 grams/m^2. Nevertheless, these biomass figures are much higher than those obtained with the 16-foot otter trawl. We feel this is a reflection of gear selectivity since the otter trawl captures primarily small or slow-moving bottom fishes while the fish toxin is effective on a wide variety of species. These small marsh ponds may, however, be naturally more productive than the deeper bay areas. They have a greater productivity zone, ie. fringing surface area of marsh vegetation. This peripheral zone produces most of the organic detritus found in estuarine waters and is the link between primary and secondary productivity. The blind pond had a much greater volume of detritus on the bottom than the connected pond, and the dominant fishes found here were herbivores and detritus feeders. The connected pond is subject to daily tidal flushing, undoubtedly removing much of the detritus. There may be two reasons for the difference in the standing crop biomass of the two ponds. The blind pond may be naturally more productive than the connected pond, but sampling procedures and existing conditions of turbidity may have had an effect. The blind pond was clear to the bottom while the connected pond was more turbid and the bottom not visible. These figures are minimum estimates of biomass in these ponds because not all fishes were recovered. They were visited 7 hours after initial treatment and many dead fishes were observable on the bottom. Many others were lost to diving birds and blue crabs which eat the fishes before they could be netted. From the number observed subsequent to collection and those lost to birds and crabs, probably only about one quarter of the fishes present were collected.

STANDING CROP BIOMASS

Biomass data is presented in Figure 18. The data is based on fish biomass available to a 16-foot otter trawl collected in a five-minute drag at each of six stations per collecting trip. A 5-minute drag samples approximately 333 meters of bottom. This figure was arrived at by repeated measurement of the distance covered at a trawling speed of 2,200 rpm. The 16-foot otter trawl has an opening of 2.5 meters when being fished. This figure multiplied by the distance covered in a 5-minute drag gives in m^2 the area fished. Since six stations per trip are sampled, the area fished multiplied by six gives the area sampled per trip—approximately 5,000 m^2.

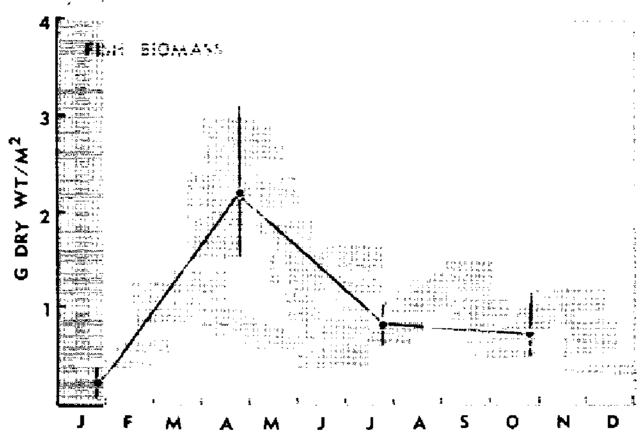


Figure 18. Annual patterns of trawl biomass of fishes. White line is average of seven sites in western Barataria Bay (see Fig. 3) for 1971-72. Black line is average of 3 years (1968-71) at 3 stations in Lake Grand Ecaille and vertical lines are the range over this period (from Forman, unpublished data).

It should be re-emphasized that this data is essentially for only seven species of fish collected with one type of sampling gear. These seven species are among the most abundant, however, and it is thought that the biomass figures, although underestimated, begin to approach what is actually present. The period of peak abundance for these species is presented in Table 15. It is readily evident that peak populations occur from early to late summer. The seasonal marine visitors start to leave the estuary for their offshore spawning grounds around June with the greatest period of offshore movement occurring in the fall.

Table 15. Period of peak abundance of selected species in Barataria and Caminada bays. Dashes incidate no reference.

	Reference		
	Gunter, 1938	Fox & Mock, 1968	Wagner, 1972
Anchoa mitchilli	——	Sept - Oct	July - Aug
Brevoortia patronus	May	Sept - Nov	May - June
Arius felis	Aug - Sept	June - Oct	Aug
Micropogon undulatus	May - Sept	May - June	Mar - May
Leiostomus xanthurus	Aug	Sept - Oct	Feb - April
Cynoscion arenarius	June - Oct	June - July	May - July
Menidia beryllina	——	July - Aug	May - July
Citharichthyes spilopterus	Sept	July	June
Mugil cephalus	——	Aug - Sept	May - July
Cynoscion nebulosus	Jan - Feb	April	April
Cyprinodonts	——	June	May

In general the biomass is highest in the spring and late summer periods; lower during the fall and lowest during the winter. Similar patterns were found by Forman (unpublished data) during 1969-1971 in Lake Grand Ecaille on the eastern side of Barataria Bay. Forman's data are an average of three trawl stations in Lake Grande Ecaille that have been adjusted for unusually large weights of individual fishes. The spring peak in fish biomass is associated with migration into the estuary of juvenile fishes. The late summer and fall peaks are larger fish. Thus, for equal biomass levels in spring and fall, the numbers of fish will be more numerous in the spring. The peak biomass reported here is 3.0 g dry weight/m^2 in March-April. It must be remembered that these data are fish biomass available to the trawl. Fish biomass from methods which capture all fish indicate that actual biomass may be much higher. Hellier (1962) reported a winter minimum of 2.0 g wet/m^2 and a summer maximum of 37.8 g wet/m^2 for fish biomass in the upper Laguna Madre of Texas. He used a drop net frame for collecting fish. Jones et al. (1963) used a helicopter borne purse net for sampling fish populations in Corpus Christi Bay, Texas. They reported biomass levels of 5.07-18.7 g wet wt/m^2. If the data for the shallow Texas bay are representative of shallow Louisiana bays, then it seems that the trawl may be about 20 percent efficient in sampling fish biomass. The data in figure 18 assumes that wet weight is 20% dry wt. and that the trawl is 20% effective in capturing the fish. By taking the area under the curve, an average annual standing crop biomass of 1.17 g dry wt/m^2 was obtained.

The squid, *Lolliguncula brevis,* was collected by Forman (unpublished data) from trawl samples in Lake Grand Ecaille. The biomass of squid available to the trawl was .0009 g wet wt/m^2 in the summer and .055 g wet wt/m^2 in the fall. No squid were taken in winter or spring. These data are the average of three stations in Lake Grande Ecaille during 1970.

FISH PRODUCTION

In energetic studies an estimate of fish production is a more valuable and meaningful measurement than is the standing crop biomass. There has been much confusion over the terms, "production" and "standing crop." Standing crop biomass is the weight in grams of fish found in a unit area at one point in time. Change in seasonal standing crop is a useful indication of growth, distribution and abundance of fish, but reveals little about the rate of production in a certain area. Some workers have called fishery yield the production of an area. We will define fish production as the rate of increase in biomass through growth or recruitment while the fish are in a defined area in a given period of time. It will be a minimal estimate because no correction has been made for natural or fishing mortality. Natural mortality includes predation and emigration from the study area. Fishing mortality is that part of total production which is harvested by man as fishery yield. Production estimates were calculated from 0 age class Atlantic Croakers at three-week intervals from July 1971 to June 1972. This tends to minimize the fluctuation in production caused by motality. Hopefully, gear selectivity and bias has been partially eliminated by combining data on croakers collected with three gear types–trawl, trammel net, and seine.

Two computaion methods were utilized in estimating fish production. The first was based on the Allen (1950) graphical method (Table 16) and the second on the Ricker (1946) numerical method (Table 17). In Allen's graphical method, the number of fish (N) in the study area at successive time intervals is plotted versus the mean weight ($\bar{w}$) of an individual in the same interval of time. The production in a small interval of time would be equal to $N\Delta\bar{w}$ where $\Delta\bar{w}$ is the growth in mean weight of the fish in the time interval. Summation of the production in each time interval would give the total production during the year. Mean weight was determined by first obtaining an estimate of growth by change in length as revealed from length frequency analysis and converting this length to weight by using the following length-weight relationship derived from fish in the study area:

$$\log w = -5.5082 + 3.2454 \log L$$

Where w = weight in grams

L = length in mm

Ricker (1946) formulated production during Δt as:

$$P = G\bar{B}$$

Where G, the instantaneous growth rate, equals $\frac{\ln \overline{w}_2 - \ln \overline{w}_1}{\Delta t}$ and $\overline{B}$, the mean biomass, is $\frac{B_1 + B_2}{2}$. Instaneous growth rates and mean biomass were calculated for each time interval from July 1971 to June 1972 and summed to get total production for the year. Dividing the number of grams of fish weight produced by the sampling area gives the production estimate in terms of grams/meter²/year. Both estimates of production were then compared for reliability. Data is presented in Tables 16 and 17. Negative values are apparent in December and February. Although it is obvious that true growth is not negative, it is possible to get negative figures in calculation of production due to apparent mean weight loss caused by recruitment of post larval croakers into the study area. This recruitment extends from November to April. The negative values of production were summed together with the new production of biomass in both calculations. The highest production occurred in April when the croakers averaged about 90 mm total length. Peak populations of croakers were present at this time because emigration from the study area had not yet started. The water temperature was also near optimal conditions, averaging between 21 and 22°C. Emigration occurred from May to October, causing a decrease in the number of croakers present. The instanteous growth rates and mean biomass also decreased through this period, causing lower production.

Table 16. Atlantic croaker production (0 age class) in the Caminada Bay area derived from Allen's graphical method.

Date	Mean Length (mm) $\overline{L}$	Mean Weight (g) $\overline{w}$	Change in w $\overline{w}$	Number N	Production $N\overline{w}$
Nov. 4-5	25	0.25	0.25	45	11.25
Nov. 23	28	0.64	0.39	164	63.96
Dec. 16	27	0.40	–0.24	673	–161.52
Jan. 12-13	34	0.98	0.58	255	147.90
Feb. 2	38	0.95	–0.03	210	– 6.30
Feb. 24	35	1.00	0.05	540	27.00
Mar. 14-15	38	1.90	.90	476	428.40
April 4	63	3.40	1.50	593	889.50
April 29-30	89	8.00	4.60	704	3238.40
May 17-18	96	11.80	3.80	400	1520.00
June 7-8	106	13.90	2.10	103	216.30
June 28-29	111	18.50	4.60	22	101.20
July 28-29	122	30.00	11.50	22	253.00
Sept. 21-22	142	30.65	0.65	7	4.55
				Sum =	6746.24

6746.24 g/7842 m² = .86 g/m²/year

If the estimates from the two methods of calculation are averaged, the production for Age Class 0 croakers in the Caminada Bay area would be 0.93 g/m²/year. This is a very high production rate because the highest standing crop biomass of croakers in April 1972 is only 71% of the yearly production of croakers, it is possible to get a crude estimate of total fish production. We must assume all species are equally susceptible to capture with the gear used and that 0.93 g/m²/year is an average rate of growth. Croakers are about 1.2% of the total yearly fish biomass, therefore 1.2% /100% = (0.93 g/m²/year)/(x g/m²/year) x = 72.8 g/m²/year wet weight total fish production. Assuming 30% dry wt this is 21.8 g dry wt/m²/year.

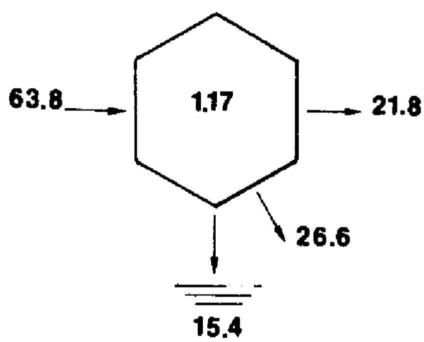
Table 17. Atlantic croaker production (0 age class) in the Caminada Bay area derived from Ricker's method.

Date	Mean Weight (g) $\overline{w}$	Biomass (g) B	Instantaneous Growth Rate G	Mean Biomass $\overline{B}$	Production
Nov. 4-5	0.25	11.25	.95	58.11	55.20
Nov. 23	0.64	104.96	–.48	187.08	–89.80
Dec. 16	0.40	269.30	.90	259.55	233.60
Jan. 12-13	0.98	249.90	–.03	224.70	–6.74
Feb. 2	0.95	199.50	.06	369.75	22.19
Feb. 24	1.00	540.00	.64	722.20	462.21
Mar. 14-15	1.90	904.40	.58	1460.30	846.97
April 4	3.40	2016.20	.85	3824.10	3250.49
April 29-30	8.00	5632.0	.39	5176.0	2018.64
May 17-18	11.80	4720.0	.17	3075.85	522.89
June 7-8	13.90	1431.7	.28	919.35	257.42
June 28-29	18.50	407.0	.48	533.50	256.08
July 28-29	30.00	660.0	.02	437.28	8.75
Sept. 21-22	30.65	214.55			
				Sum =	7837.90

7837.90 g/7842 m² = .99 g/m²/year

RESPIRATION

Total fish respiration was computed using an average respiratory rate of 3.6% body wt/day (Prosser and Brown, 1961). No consideration of age of fish (i.e., juvenile or adult) or temperature was made. The total respiration/m² was computed from the trawl biomass data by multiplying the rate constant times the fish biomass (1.17 g dry ft/m²). In this manner respiration levels were 0.042 g dry wt respired/m²/day or 15.4 g org/m²/year. Using the above figures, the annual car-



FISHES

bon budget of the fish is as follows, assuming an assimilation efficiency of 50%:

The data on fishery take by man were calculated using the area of the Barataria Bay system as 1.6 x 10^9 m^2 and the average fishery for Barataria Bay for the years 1963-1967 (NMFS personnel). Commercial fishing for finfish, as opposed to oysters, crabs, or shrimp, is not very important in inshore waters in Louisiana. The largest finfish fishery is that for Menhaden, which are taken offshore. However, the estuary serves as a nursery for most of the fish which are caught offshore. The total catch for Louisiana in 1970 was 1.1 billion pounds. Most of this poundage is menhaden, which represented about 84% of the total catch for the years 1963-1967 (see Tables 20 and 21). Practically all Louisiana fisheries are dependent on the inshore estuarine areas for nursery grounds. Taking this inshore area for Louisiana to be 25,200 km^2, the total annual catch (assuming dry weight equal to 20% wet weight) for Louisiana is 2.704 g dry wt. of fisheries/m^2 of inshore estuarine area/yr. or 0.0074 g/m^2/day. This gives a much better idea of the fishery importance of the estuary than looking at fishing only within Barataria Bay.

Data on the sport finfish fishery were obtained from a phone survey conducted by personnel of the Bureau of Sport Fisheries and Wildlife, Fish and Wildlife Service in Vicksburg, Mississippi. They estimated that the total sport finfish fishery for the Barataria Bay complex in 1968 was 6,378,000 pounds. This is more than 10 times the inshore commercial finfish fishery for Barataria Bay. Assuming 20% dry weight, this is 5.78 x 10^8 g dry wt/yr. Assuming an area for the Barataria Bay System of 1.6 x 10^9 m^2, this is 0.36 g dry/m^2/yr. or 0.01 g dry/m^2/day. This includes both sports fishing in the bays and sports fishing offshore in both private and commercial boats. We assumed that about 50% of the total sport fishery was inshore. Thus the take by man from sports fishing within the bay system is 0.18 g/m^2/yr or 0.005 g/m^2/day.

Figures presented above are for the total fish population. To gain a better understanding of the trophic relationships, it is desirable to break the total figures into the different trophic components shown in Table 19 (herbivores, and primary, mid, and top carnivores). We accomplished this through a knowledge of numerical abundance of different fishes (Table 14) and biomass distribution among the species studied. The figures were adjusted for species of fish which are not readily caught by the trawl. These include trout and mullet because of their fast swimming, and cyprinodonts because they are normally found in areas which are not easily trawled. From this analysis the herbivores constitute 4.7% of the total fish biomass, primary carnivores constitute 3.5%, mid carnivores constitute 48.6% and top carnivores constitute 42.8%. The data for the different trophic levels using these percentages are presented in Table 18.

Table 18. Organic budgets for the different trophic levels of fish. Units are grams dry weight/m^2/year.

	Total Intake	Respiration	Feces	Production
Herbivores	3.00	0.72	1.25	1.03
Primary carnivores	2.23	0.54	0.93	0.76
Mid carnivores	31.00	7.48	17.93	10.95
Top carnivores	27.30	6.59	11.38	9.33

As stated earlier the total commercial fisheries in Barataria Bay was 0.016 g org/m^2/year. From an IBM listing of the NMFS statistical office in New Orleans, it was calculated that 22% of this was top carnivores, 73% was mid carnivores, and 0.7% was herbivores. The top carnivores were trout and flounder, the mid carnivores included drum, catfish, croaker, and sheepshead. The herbivores included the striped mullet. Using the above figures, the take of commercial fisheries is 0.0036 g org/m^2/year for top carnivores, 0.012 for mid carnivores and 0.0001 for herbivores. The most important species of fish for sports fishing are trout, redfish, flounder, black drum, and sheepshead. The trout is the most important fish and is a top carnivore. The other species are mid carnivores. We will assume that 40% of the total sports fishery is for top carnivores and 60% is for mid carnivores. The total sports fishery is 0.18 g/m^2/year. Thus the amount of biomass for sports fisheries is 0.11 for mid carnivores and 0.07 g/m^2/year for top carnivores.

FOOD HABITS

Anchoa mitchilli — W E. Odum (1971), in a study on the fishes and major invertebrates in the North River System of South Florida, found the major food items in bay anchovy stomachs were copepods, amphipods, mysids, plant detritus, ostracods, small mollusks and chironomid larvae. Darnell (1958) in a study of the food habits of fishes and larger invertebrates in Lake Pontchartrain, Louisiana, listed zooplankton (largely the copepod *Acartia tonsa*), organic detritus, small fishes, and microbenthic animals as the major items. We found crab megalops and zooplankton most important in anchovies taken from Caminada Bay.

Brevoortia patronus — Darnell (1958) found the major items in Gulf menhaden stomachs to be largely organic detritus, with lesser quantities of phytoplankton and zooplankton. June and Carlson (1971) reported that larval Atlantic menhaden, *B. tyrannus*, ate zooplankton (mainly copepods), while prejuveniles and juveniles fed chiefly on phytoplankton.

Arius felis — Darnell (1958) found organic detritus, microbenthos, macrobenthos, and zooplankton, while W. E. Odum (1971) found small crabs, amphipods, mysids, and fishes in sea catfish stomachs. Harris and Rose (1968) found these fish to be significant predators on the commercial penaeid shrimp in Texas. We found crab megalops, fish remains, and organic detritus in sea catfish stomachs.

Micropogon undulatus — Extensive food studies have been done on the Atlantic croaker in varying geographical areas. Pearson (1928) found croakers to subsist largely on shrimp, annelids, fish, crabs, and mollusks on the Texas coast. Roelofs (1954) listed annelids, copepods, pelecypods, mysids, amphipods, diatoms, fish, and decapods in North Carolina. In Louisiana, Darnell (1958) found microbenthos, organic detritus, fishes, macrobenthos, and zooplankton. Hansen (1969), near Pensacola, Florida, established annelids, crustaceans, fish, and mollusks as the major items while Parker (1971) found that juvenile croakers fed on copepods, mysids, amphipods, and organic detritus with larger individuals additionally consuming mollusks and insects. We found amphipods, annelids, copepods, organic detritus, fish, and insect larvae in croakers from the Caminada Bay area.

Leiostomus xanthurus — The spot has also received considerable attention concerning its feeding and food habits. Pearson (1928) found crustaceans, annelids, small molluscs, fish, and organic detritus while Roelofs (1954) had copepods, nematodes, diatoms, and forams as the primary items. Townsend (1956) listed copepods, annelids, and fish in spot stomachs from Alligator Harbor, Florida. Darnell (1958) listed microbenthos (largely ostracods and harpacticoid copepods), organic detritus, and vascular plants. Dawson (1958), in South Carolina, determined small planktonic and demersal crustaceans and annelids to be most important. Parker (1971) studied spots in two areas—the Lake Borgne region of Louisiana and Galveston Bay, Texas. In Louisiana spots utilized pelecypods, detritus, and copepods while in Texas, they ate copepods, vascular plants, and ostracods. Thomas, Wagner, and Loesch (1971) listed amphipods, calanoid copepods, and organic detritus.

Cynoscion arenarius — In sand seatrout stomachs Darnell (1958) found fishes almost exclusively with minor occurrences of macrobenthos, organic detritus, zooplankton, and vascular plants. We recovered amphipods, fish remains, and other small microbenthos.

Menidia beryllina — According to Darnell (1958), tidewater silversides feed on amphipods, isopods, and chironomid larvae with lesser quantities of organic detritus, zooplankton, and vascular plants. W. E. Odum (1971) removed copepods, mysids, amphipods, terrestrial insects (those falling into the water near shore), and chironomid larvae from silverside stomachs. We found primarily zooplankton, insect larvae, and fish remains.

Citharichthys spilopterus — Little information was available on the food habits of the bay whiff. Thomas, Wagner, and Loesch (1971) found polychaetes, mysidaceans, amphipods, copepods, nematodes, fishes, and insect larvae in bay whiff stomachs from the Caminada Bay area.

Mugil cephalus — Darnell (1958) reports the striped mullet's main diet as consisting of largely organic detritus with small amounts of vascular plants, microbenthic animals, and blue-green algae. W. E. Odum (1971) lists benthic diatoms, filamentous algae, vascular plant detritus, and inorganic sediment particles. We found primarily organic detritus and green algae and rarely an annelid in mullet stomachs.

Cynoscion nebulossu — Speckled seatrout are predaceous on fishes, macrobenthic animals, microbenthos, and vascular plants according to Darnell (1958). W. E. Odum (1971) reports juveniles to consume mysidaceans, amphipods, chironomid larvae, caridean shrimp, and small fishes with adults feeding on larger fish and caridean shrimp. Moody (1950) reported Florida speckled seatrout as passing through four feeding stages: less than 50 mm — copepods and other plankters; 50-150 mm — caridean shrimp; 150-275 mm — penaeid shrimp, and 275 mm — other fishes. In large speckled trout, we found exclusively fishes.

Cyprinodon variegatus — Hildebrand and Schroeder (1928) report sheepshead minnows as feeding on algae, plant detritus, and sand particles. Odum (1971) lists them as predominantly detritus — algal feeders. Forman (1968) lists detritus, plant fibers and algae as the main food items.

Adinia xenica — W. E. Odum (1971) classifies the diamond killifish as a herbivore feeding on vascular plant detritus and benthic diatoms with occasional small amphipods, copepods, and small insects. Foreman lists detritus, diatoms and small crustaceans and insects.

Fundulus grandis — W. E. Odum (1971) found gulf killifish consuming amphipods, isopods, small xanthid crabs, chironomid larvae, terrestrial insects, small gastropods, and filamentous algae. Foreman gives the main foods as polychaetes, insects, and small fishes. We found fish remains, amphipods, crab megalops, and nematodes in gulf killifish stomachs from the Caminada Bay area.

Fundulus confluentus — W. E. Odum (1971) lists *Palaemonetes,* small fishes, amphipods, isopods, adult and larval insects, copepods, mysids, ostracods, and algae filaments as the main diet of marsh killifish.

Lucania parva — W. E. Odum (1971) records amphipods, chironomid larvae, mysids, ostracods, copepods, and plant detritus as the food items found in rainwater killifish.

Poecilia latipinna —Sailfin mollies, according to W. E. Odum (1971), are primarily herbivores, feeding on vascular plant detritus, algae, and diatoms.

Table 19. Trophic Spectrum of the Most Common Fishes in the Caminada Bay Area (Design after R. M. Darnell

Fishes	Macrobenthic animals	Microbenthic animals	Zooplankton	Phytoplankton	Algae	Vascular plants	Organic detritus	Species	
		—			—	—	**	*Mugil cephalus*	Herbivores
					*		*	*Poecilia latipinna*	Herbivores
		—	—				*	*Adenix xenica*	Herbivores
					—	*	*	*Cyprinodon variegatus*	Herbivores
			—	*			**	*Brevoortia patronus*	Herbivores
—		—	**				*	*Anchoa mitchilli*	Primary Carnivores
—		*	—		—			*Fundulus confluentus*	Mid Carnivores
—		*			—			*Fundulus grandis*	Mid Carnivores
		*	—				—	*Lucania parva*	Mid Carnivores
—		*	—					*Citharichthyes spilopterus*	Mid Carnivores
—		*	—			—	—	*Menidia beryllina*	Mid Carnivores
		**	—			—	—	*Leiostomus xanthurus*	Mid Carnivores
—	—	*	—				—	*Micropogon undulatus*	Mid Carnivores
—	*	*	—				—	*Arius felis*	Mid Carnivores
**	—	—	—			—	—	*Cynoscion arenarius*	Top Carnivores
**	*	—						*Cynoscian nebulosus*	Top Carnivores

Key: — Trace
* Frequent
** Dominant

Table 20. Commercial fisheries in Barataria Bay, Louisiana from 1963 to 1967. Fish yield data from NMFS personnel in New Orleans (Allen, 1971). These data calculated from total Louisiana catch and total Louisiana estuarine area. Total commercial catch/year in pounds.

Year	Fish	Shrimp White	Shrimp Brown	Crabs	Oysters*
1963	292,400	2,889,000	3,875,000	720,000	3,664,500
1964	376,200	3,821,000		683,800	5,383,000
1965	158,700	5,781,000		655,400	3,467,500
1966	238,800	6,405,000		1,288,500	1,100,400
1967	390,500	6,717,100		1,371,200	2,457,800
5 yr av.					
lbs/yr	291,320	4,544,800		812,700	3,210,640
g/yr	132,259 x 10^3	2,063,339 x 10^3		368,965 x 10^3	1,457,612 x 10^3
g wet/				0.2306	0.91
m^2/yr	0.0826	1.2895			
Barataria Bay					
g dry/m^2/yr					
(20% = dry/wet)	0.0165	0.2579		0.0461	0.182
Total Louisiana					
g dry/m^2/yr	2.704	0.2648		0.0029	0.0035

*Private lease only

TROPHIC SPECTRUM ANALYSIS

After determination of the food habits of these fishes, it becomes possible to arrange them in a sequence based on the food items they ingest (Table 19). This technique enables analysis of the food web and of the interdependence of one trophic level on another. Divisions may be made into several feeding categories as defined below:

Herbivores—fishes feeding primarily on vegetable matter, phytoplankton, or oganic detritus; only occasionally taking small animal forms.

Omnivores—fishes showing no particular perference for plant or animal material, the one or the other predominantly, depending on availability in the particular habitat.

Primary carnivores—fishes feeding mostly on zooplankton and microbenthic animals but occasionally on plant matter and organic detritus.

Mid carnivores—fishes feeding on both microbenthic and macrobenthic animals such as mollusks, amphipods, penaeid shrimp, small crabs; small fishes of lower trophic levels, and organic detritus. The latter is probably taken incidentally in feeding on animals.

Top carnivores—highly predaceous fishes feeding mostly on smaller fishes such as the largescale menhaden, bay anchovy, tidewater silverside, and larval Atlantic croakers and the larger invertebrates such as penaeid shrimp and blue crabs. The larval and juvenile stages of these fishes may function as mid carnivores as pointed out by W. E. Odum (1971).

The following is a compilation of studies done on the food habits of the most common fishes in the Caminada Bay area. Data is drawn from previous studies as well as stomach analysis done by the authors. Food items are listed in decreasing frequency of occurrence.

Some general conclusions can be drawn from this analysis. It appears that organic detritus is the major component of the herbivorous fishes. Fishes of the higher trophic levels may utilize detritus somewhat, particularly the bay anchovy, but ingestion may be accidental. The bay anchovy, a primary carnivore, feeds primarily on zooplankton. Little utilization of phytoplankton was observed, lending further evidence that nutrition in this system is based on allochthonous organic detritus such as *Spartina* and other marginal marsh macrophytes.

Table 21. Average annual harvest (1963-67) of the major commercial fish and shellfish produced in Louisiana waters (Lindall et al., 1972).

Species	Pounds* (Million)	Percentage of Total	Value† (Millions) of dollars	Percentage of Total
Menhaden	713.06	84.6	10.12	23.3
Shrimp	73.51	8.7	26.68	61.4
Croaker	23.71††	2.8	0.42	0.9
Oyster	9.97	1.2	4.39	10.1
Blue Crab	8.27	1.0	0.73	1.7
Catfish and Bullheads	4.59	0.5	0.78	1.8
Spot	4.62††	0.6	0.08	0.2
Seatrout (Spotted and White)	4.11††	0.5	0.19	0.4
Red Drum	0.53	0.1	0.09	0.2
Total	842.37	100.0	43.48	100.0

*Live weight
†1967 exvessel prices ($)
††Includes industrial bottomfish

The microbenthic animals are utilized by the majority of these fishes. The microbenthos (or meiobenthos according to some authors) includes small animal crustaceans and insects. These organisms are the main diet of the mid carnivores.

The top carnivores, represented by sand seatrout and speckled seatrout, feed largely on the fishes of lower trophic levels and macrobenthic forms such as blue crabs and penaeid and caridean shrimp.

Table 22. Checklist of fishes taken more than 10 times in the Caminada Bay sampling during 1971-72. The fishes are grouped into trophic levels according to their feeding habits. The groupings are discussed in the text.

HERBIVORES	
Skipjack herring (Alosa chrysochloris)	Sheepshead minnow (Cyprinodon variegatus)
Gulf menhaden (Brevoortia patronus)*	Sailfin molly (Poecilia latipinna)
Diamond killfish (Adenia xenica)	Striped mullet (Mugil cephalus)*
PRIMARY CARNIVORES	
Striped anchovy (Anchoa hepsetus)	Bay anchovy (Anchoa mitchilli)
MID CARNIVORES	
Atlantic bumper (Chloroscombrus chrysurus)	Green goby (Microgobius thalassinus)
Florida pompano (Tracinotus carolinus)†	Fringed flounder (Etropus crossotus)*
Spotfin mojarra (Eucinostomus argenteus)	Least puffer (Sphoeroides parvus)
Sheepshead (Archosargus probatocephalus)†	Spot (Leiostomus xanthurus)*
Gafftop catfish (Barge marinus)*	Bay whiff (Citharichthys spilopterus)*
Gulf killifish (Fundulus grandis)	Darter goby (Gobinellus bolesoma)
Longnose killifish (Fundulus similis)	Ladyfish (Elops saurus)
Rough silverside (Membras martinica)	Sea catfish (Arius felis)
Tidewater silverside (Menidia beryllina)	Crevalle jack (Caranx hippos)†
Silver perch (Bairdiella chrysura)*	Sharptail goby (Gobinellus hastatus)
Banded drum (Larimus fasciatus)	Naked goby (Gobisoma bosci)
Southern kingfish (Menticirrhus americanus)†	Lined sole (Achirus lineatus)
Atlantic croaker (Micropogon undulatus)*†	Pinfish (Lagodon rhomboides)
Atlantic spadefish (Chaetodipterus faber)*†	
Blackneck tongue fish (Symphurus plagiusa)*	
Bighead searobin (Pronotus tribulus)	
TOP CARNIVORES	
Atlantic cutlass fish (Trichiurus lepturus)*	Sand seatrout (Cynoscion arenarius)*†
Southern flounder (Paralichthys lethostigma)†	Shrimp eel (Ophichthus gomesi)
Spotted seatrout (Cynoscion nebulosus)*†	Inshore lizard fish (Synodus foetens)*
Atlantic needlefish (Strongylura marina)	

*Important to commercial fisheries
†Sport-fisheries importance

BIRDS

Birds, along with certain mammals and fish, represent the top of the food chain in the estuarine ecosystem. For this paper we have separated the birds into several different trophic groups (Table 25). The listing in Table 25 is not exhaustive, but includes those birds deemed to be most important. The groups include wading birds, waterfowl, shore birds, fishing birds and birds of the marsh proper. The wading birds include the herons, egrets, and ibis. Waterfowl includes ducks and coots. Sandpipers, willets, and plovers comprise the shore birds while gulls, terns, pelicans, and skimmers make up the fishing birds. Formerly, the brown pelican was an important fishing bird, but populations have declined and it is now very rare along the Louisiana coast. Birds which live almost entirely within the marsh include sparrows, wrens, rails, grackles, and redwing blackbirds.

SEASONAL ABUNDANCE

The seasonal abundance of the various birds is indicated in figure 19. Much of this information was taken from Lowery (1960). Shore birds are more abundant in the salt marsh during the colder months. These birds feed pirmarily on exposed mud flats which are extensive during the the colder months when the water levels are low. Terns are more abundant during the summer while most gulls are winter residents. White pelicans migrate into the coastal marshes during the colder months. Many wading birds migrate southward into Mexico during the colder months. Sparrows decrease during the winter months, primarily because of natural mortality. Rails follow a similar pattern. The Clapper rail is a year-round resident, while Virginia and Sora rails migrate into the area during the winter. Ducks migrate into the coastal marshes in great numbers during the fall season and most leave by late spring. Only mottled ducks are permanent residents. The data for ducks represent the net effect of constant movement into and out of the salt marshes. Some ducks stop in Louisiana on their way further south while others spend the entire winter in the area. There is also considerable internal movement by all waterfowl within the marsh areas as habitat conditions are changed by rain, tides, and other factors. For example, local weather conditions and food availability constantly influence the number of lesser scaup found in the salt marshes along Louisiana's coast. Louisiana'a coastal scaup population often remains in offshore, Gulf waters for the entire winter, but in some years reduced food availability, weather, or other factors require many of these diving ducks to move into shallow bays and salt marsh ponds.

During December, Louisiana's coastal duck population estimates usually decline. This results from both the dispersal of ducks from Louisiana's coastal marshes which have been inundated with winter rains and a loss of transient puddle ducks that continue their southward migration at this time. (H. Bateman, personal communication)

FOOD HABITS

The food habits of the various birds are presented in Table 25. Wading birds take mostly small fishes, crustaceans, molluscs, and insects. They commonly feed in small marsh ponds and channels and within the marsh itself. Gulls and terns feed in the small marsh ponds as well as larger lakes and bays. Stomach examination of several terns and gulls showed only fish and shrimp. Gulls and terns will also feed on carrion (Lowery, personal communication). Plovers and sandpipers feed mainly on bare mud flats, taking small worms, crustaceans, etc. During the winter, flocks of White Pelicans gather around small ponds in the marsh, apparently feeding on the small cyprinodont fishes which inhabit these areas. Palmer (1962) reported that the diet of White Pelicans consisted almost solely of small fish of no commercial value. The majority of the food of ducks consists of plant material. Martin and Uhler (1939) examined 200 gizzards of 17 species of ducks and found that 75.2% of the content was plant material and 24.8% was animal. Of the animal matter snails were 11%, insects were 4%, and fish were 2%. Stieglitz (1966) studied the food consumed by several species of diving ducks and found that plant material made up 68.5% and animal material made up 31.5%. Of the animal matter, molluscs made up 29% and crabs made up 3%. In general, diving ducks tend to take a larger proportion of animal material than do puddle ducks. In Louisiana, molluscs, shell fish, and small fish are important food sources for divers in coastal waters.

Clapper Rails, *Rallus longirostris,* are one of the more important top consumers in the marsh. They have been studied in Louisiana by Bateman (1965) and in Georgia by Oney (1954). Oney gave the food of rails (% by volume) as snails--14%, crabs--74% (*Sesarma*--54%, *Uca*--14%, mud crabs--14%), insects--

9%, and traces of spiders, fishes, and plants. Bateman reported essentially the same diet including crabs (*Uca* and *Sesarma*), snails (*Littorina*), and insects. Analysis of stomach contents of seaside sparrows indicates that insects account for about 60 to 80% of the food consumed. Other items include small crustaceans (10 to 20%) small snails (5%) and plant material (5%). Wrens have similar feeding habits, while blackbirds and grackles take a greater proportion of plant material.

BIOMASS AND RESPIRATION

The annual distribution of bird biomass is shown in Figure 19. Points marked with circles are measured data points. We have counted seaside sparrows on a 300-meter transect in the marsh surrounding Airplane Lake. Annual population and biomass variations are shown in Table 23. The average weight of all birds

Table 23. Population and biomass of Seaside Sparrows, along a 300-meter transect in *Spartina alterniflora* marsh adjacent to Airplane Lake.

Date	Birds/m²	g dry wt/m²
Sept. 1	.0065	.046
Sept. 20	.0036	.026
Oct. 27	.0015	.011
Nov. 20	.0012	.008
Dec. 12	.0013	.009
Jan. 28	.0009	.007
Feb. 25	.0021	.016
Apr. 5	.0029	.022
May 6	.0043	.032
June 9	.0039	.029
July 24	.0043	.032
Aug. 23	.0039	.029

captured was 22.7 g. This was used to convert birds/m² to g wet wt/m² and dry weight was taken as 33.7% of wet weight. This figure is the average of five Wilson's Plovers, *Charadrius wilsonia*, which were dried and weighed in our lab. During the warmer months, sparrows were abundant throughout the marsh surrounding Airplane Lake. During the fall and winter months most were within 100 meters of the shore. Oney (1954) estimaetd the rail population in Georgia at 1.3 to 1.5 per acre. Louisiana Wild Life and Fisheries Commission personnel (Bateman, personal communication) estimated 5/acre. We estimated 2.1/acre in the Airplane Lake area. This is an average of 2.8 birds/acre or 0.0007/m². Bateman reported an average weight for males and females of 290 grams, giving a biomass of 0.29 g wet wt/m² or 0.098 g dry wt/m² using 33% as the fraction of dry weight. The biomass figures in Table 23 are for the marsh area only, and for rail, only for the marsh edge habitat where they are abundant. Gagliano (unpublished data) reported that 43% of the area of Barataria Bay is marsh, the remainder being open water (53%) or high land (5%). Sparrow biomass was determined by multiplying the data for the marsh alone by .43 to obtain an average area based biomass for the whole bay system. For rails it was assumed that marsh edge is approximately 37% of the marsh and thus the biomass for rails was multiplied by 15.9%. Rails winter population were assumed to be ½ of the summer levels.

Wading birds were counted by Newsom (unpublished data) during August 1968. He supplied figures in terms of number of birds/acre. This was divided by 4,050 m²/acre and multiplied by the average weight per bird (640 g) to obtain the biomass in g wet wt/m². This mean weight was obtained by averaging weights of nine different wading birds as listed by Palmer (1962). Winter levels of wading birds were assumed to be ¼ of the summer levels.

Ducks are counted monthly by Louisiana Wild Life and Fisheries Commission personnel. These data were supplied to us by H. A. Bateman, a waterfowl biologist for the commission. Diving ducks, mainly lesser scaup, are the most abundant waterfowl found in Louisiana's salt marshes. Their use of these marshes is unpredictable and erratic from year to year. The scaup is not as accessable or highly sought after by waterfowl hunters in Louisiana as are puddle ducks. Consequently, hunting pressure is low in salt marshes and much higher in the fresher marshes. It should be noted that the

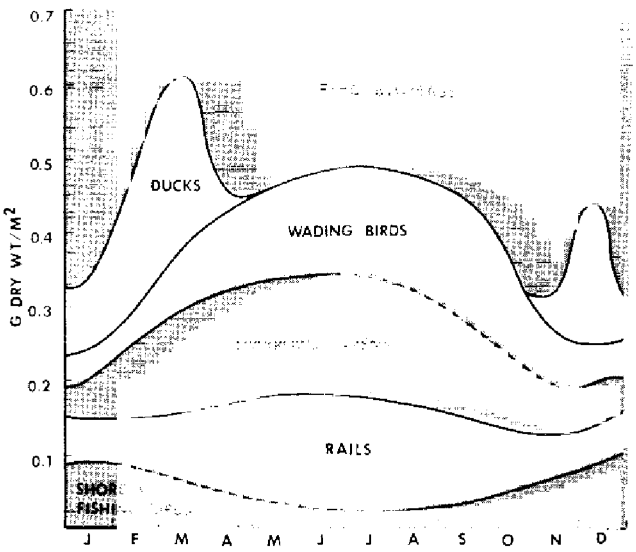


Figure 19. Pattern of population composition and biomass of birds in the salt marsh. Data on ducks from Bateman (1971), wading birds from Bateman (1971), Newsom (1971), and Lowery (1960, 1971).

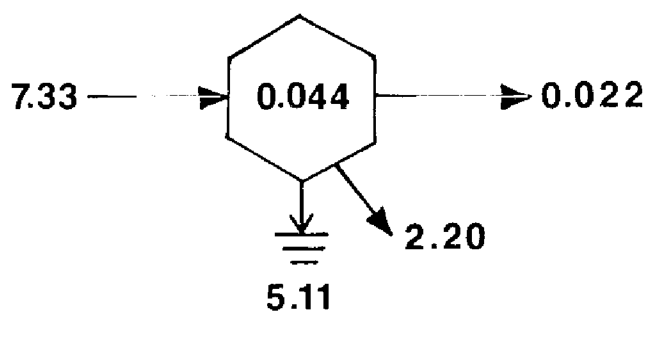
salt marsh is not the prime habitat for all ducks in Louisiana. Puddle ducks are perhaps ten times as abundant in the brackish and fresh marshes.

An average weight of 789 g wet wt for ducks was obtained from Smith (1961). This figure was used to convert the population numbers to biomass on a g/m² basis as was done for the wading birds. The biomass of shore birds and fishing birds was assumed to be 25% of that of the wading birds and to be twice as high in the winter. The average bird biomass for the entire year was 0.044 g dry wt/m² (assuming 33.7% organic matter). This is divided among the various groups as shown in Table 24. The respiration was

Table 24. Average annual biomass of different groups of birds in the saline area of Barataria Bay.

Trophic group	Biomass (g dry wt/m²)
Ducks	0.0063
Wading birds	0.0106
Sparrows, wrens, etc.	0.0118
Rails	0.0099
Shore birds and fishing birds	0.0054
Total =	0.044

calculated using a respiratory rate of 31.8% body wt/day. This figure is an average rate calculated from Altman et al. (1958), and Prosser and Brown (1961). Using this figure the total bird respiration is 0.014 g organic matter oxidized/m²/day or 5.11 g/m²/year. Stieglitz (1966) reports that an average food intake for ducks (food as dry weight) is 10% of the wet body weight. This is equivalent to 0.0089 g dry wt intake/m²/day or 3.27 g/m²/year for the entire bird population, which is lower than the computed respiration. It must be remembered that the 10% figure is for ducks, and the intake rate for small birds like sparrows should be higher. Production is taken to be half the average standing crop: that is 0.022 g dry wt/m²/year. This was determined by assuming that birds replace themselves each year and most spend about half of the year in the marsh. Feces production was calculated to be 2.20 g/m²/year, assuming an assimilation efficiency of 70%. Using these figures the total intake of the birds is 7.33 g dry wt/m²/year.



BIRDS

Table 25. Food Habits of principal estuarine birds

Species	Food Habits
Wading Birds	
Great Blue Heron	minnows—67%, shrimp & crabs—10%, small mammal—5%
Little Blue Heron	
Louisiana Heron	
American Egret	
Snowy Egret	small fishes, crustaceans, snails, insects
Cattle Egret	mostly insects
White Ibis	crustaceans—60%, fish—13%, snails—13%, insects—13%
Wood Ibis	crustaceans, insects
White-faced Ibis	(Palmer, 1962)
Water Fowl	
Puddle Ducks	Stieglitz, 1968- 68% plant
Shoveler	31.5% animal—mollusc29%
Gadwall	crabs 3%
Pintail	
Widgeons	
Mallard	Martin and Uhler, 1939
Mottled Duck	75.2% plant
Blue-winged Teal	24.8% animal—snails 11%
Green-winged Teal	insects 4%
Diving Ducks	fish 2%
Lesser Scaup	
American Merganser	
Hooded Merganser	
Coots	
Redheads	
Fishing Birds	
Herring Gull	
Laughing Gull	
Ring-billed Gull	minnows and open water fish
Forster's Tern	Shrimp
Royal Tern	
Least Tern	
White Pelican	fish (Palmer, 1962)
Skimmers	
Shore Birds	
Plovers, willets	snails, crustaceans and other animals of
Sandpipers	mud flats and bare areas
Marsh Proper	
Rails	crabs, snails, insects (Bateman, 1965; Oney, 1954)
Sea Side Sparrow	Insects and plant material
Wrens	
Blackbirds and Grackles	

MICROBIOLOGY

The importance of bacteria and fungi in the breakdown of the marsh grasses in the formation of detritus has been recognized for some time. The nutritive value of detritus to higher consumers is increased because the percentage of protein (due to bacterial biomass) is increased in the detritus-bacteria mixture (Burkholder and Bornside, 1957; Burkholder and Burkholder, 1956; Udell et al., 1969; Odum and de la Cruz, 1967; and others). Studies by Newell (1965) and Fenchel (1969) have indicated that the most important food source to detritus consumers is the microorganisms living in association with the detritus. Heald (1971) and Fenchel (1970) have shown the importance of higher organisms such as amphipods in the formation of detritus. Heald showed that the amphipods do not attack mangrove detritus until it has been in the water and subjected to bacterial action for several months. Fenchel found that the detritus-consuming amphipods increase the total metabolic rate of the microbes by decreasing the particle size of the detritus. Meyers (1971) presented a general discussion of the microbiological studies conducted in Barataria Bay under the LSU Sea Grant Program.

BACTERIA

Hood (1970) studied bacterial types and population densities in the vicinity of Airplane Lake.

Submerged Sediments

Bacteria of the top few centimeters are typically inactive and slow growing .The predominant bacteria in both aerobic and anaerobic sediments are *Bacillus* (10 to 15 important species). These *Bacillus* species make up about 50 to 60% of the total number of bacteria. Less important in the aerobic zone are the *Pseudomonas* species. In the lower anaerobic zone *Clostridium* is important.

The most important nutritional types in the aerobic zone are proteolytic species, making up 50 to 60% of the total. The other 40% includes lipolytic and alginolytic types. Cellulolytic activity is low in the submerged sediments. In the anaerobic zone, the most important activity is that of sulfate reducers.

Marsh Soil

This includes the bottom 1 or 2 inches of the Spartina stalk as well as the soil itself. The most important species are *Pseudomonas* and *Vibrio* with the first being more numerous. There are a few Bacillus but they are different from the Bacillus found in the submerged sediment. The marsh species are more biologically active than the species in the submerged sediments as the marsh soil bacteria exhibit a considerably shorter generation time and utilize a larger variety of carbon sources. They produce very active enzymes which readily attack carbohydrates such as starches, free sugars, and cellulose. Most are facultative aerobes.

Celluloylytic bacteria are found in high concentrations within the marsh soil but the highest biomass of cellulose utilizers is found on the bottom of the *Spartina* stalk. These data suggest that greatest cellulose activity occurs on the plant itself. The genus *Pseudomonas* is found to be the predominant type of cellulolytic bacteria.

On Spartina

Bacteria on the *Spartina* grass are aerobic. They are least abundant on the top portion of the grass which is very rarely wet by the salt water. The organisms on the top of the live *Spartina* are mostly pigmented. They are similar to air contaminants one would get on an open petri dish in a lab. They are different in that they require sodium, thus they are "true marine" organisms. They probably represent bacteria indigenous to the sea water dispersed in the form of aerosols. The most common are genera of *Micrococcus, Sarcina,* and *Bacillus.*

The next higher numbers are found in the mid portion or splash zone of the *Spartina.* This is the zone which is wet by the high tides and by waves. The types of organisms found in this zone are intermediate between those found on the top and on the bottom. There are a few pigmented forms and a few are like those found on the bottom part.

Bacteria on the bottom of the *Spartina* were discussed earlier. These are on dead *Spartina* sheaths, which normally cover the live culms. In general, the numbers of bacteria increase from top to bottom.

Water

The most important organisms in the water are species of *Vibrio, Pseudomonas,* and *Achromobacterium* in that order. These are fairly slow growing and are mostly proteolytic. There are very few *Bacillus.* There are also large populations of organisms which decompose agar (alginolytic) but not as large as the proteolytic types. The water organisms seem to constitute a different population than those which grow in the submerged sediments. Hood (1970) measured bacterial populations in various parts of the Barataria Bay system using standard dilution and plate techniques (Hood and Colmer, 1970, 1971). These data are presented in Table 26 and Figure 20. Because of the plate technique, it must be assumed that these are minimum estimates since plate counts give low values. Zobell and Feltman (1942) stated that plate count procedures detect a maximum of only 10% of total living bacteria.

Table 26. Bacterial populations in various habitats of the marsh-estuarine system in Barataria Bay. Numbers are average over the year (1969-1970). Numbers are estimates by Hood (1970) and Hood and Colmer (971) from standard dilution and plate techniques.

	% Moisture	# Cells/g dry wt or ml H_2O
Spartina — top	35	15.7 x 10^8
Spartina — mid portion	66	30.0 x 10^8
Spartina — bottom portion	91	30.0 x 19^9
Marshland soil	66	6.6 x 10^8
Submerged sediment	73	4.8 x 10^6
Water	—	9.5 x 10^4

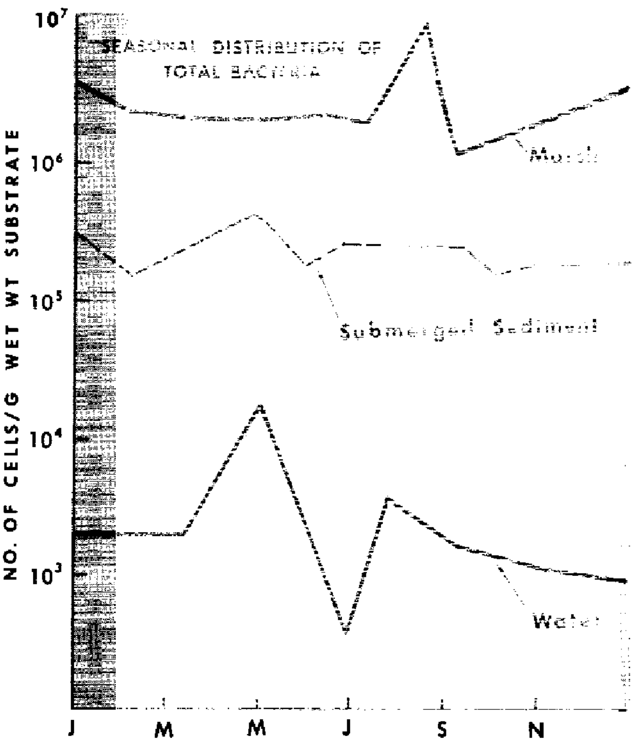


Figure 20. Seasonal distribution of total bacterial populations in three estuarine environments (Hood, unpublished data).

Total bacterial populations in three different estuarine environments are presented in Figure 20. Highest populations in three different estuarine environments are presented in Figure 20. Highest populations in the water and submerged sediments occurred during April and May. These high populations coincide with rising spring temperatures and the time of greatest detrital export from the marsh as shown by Kirby (1972), (Fig. 10). Volkmann and Oppenheimer (1962) also measured increases in bacterial numbers in spring in Redfish Bay, Texas, but numbers continued to rise throughout the summer. Hood (unpublished data) stated that average bacterial populations in Barataria Bay were closely correlated to organic matter present. Volkmann and Oppenheimer (1962) and Oppenheimer (1960) also reported that bacterial activity in shallow Texas bays was proportional to the amount of organic matter present. Bacterial populations in the marsh soils were higher towards the end of the summer (late August and early September). It is also during this time that the live *Spartina* begins to die off. It may be that bacteria are responsible for the initial degradation of *Spartina.*

Oppenheimer and Jannasch (1962) reported bacterial populations of 9 x 10^5 to 5.2 x 10^7/cc in water and sediment of shallow Texas bays. Using 2 x 10^{-13} g as the weight of one bacterium (Kriss, 1959) they calculated biomass ranges of (0.2 to 6 g/m²). Zobell and Feltman (1942) used an average weight of 0.5 x 10^{-12} g and estimated dry weight of 2 g/m² for bacterial biomass.

Respiration

There have been no direct measurements of bacterial metabolism made in the Barataria Bay area. Therefore, we will try to infer the magnitude of the bacterial metabolism from other studies. Teal and Kanwisher (1961) studied gas exchange in a Georgia salt marsh. They estimated that bacterial respiration consumed 1.608 g dry wt/m²/day or 586.9 g/m²/year. Total animal respiration was 0.62 g dry wt/m²/day or 262.9 g/m²/year. These figures were calculated from the 0_2 consumption data of Teal and Kanwisher using a conversion of one liter 0_2 consumed = 1.34 g carbohydrates (Wieser and Kanwisher, 1961), and assuming carbohydrate is identical tc organic matter.

The respiratory demand of detritus consumers on the marsh, excluding microorganisms, has been calculated elsewhere in this paper. Summarized here, they are:

	Respiratory consumption, g dry wt/m²/year
Meiobenthos	77.3
Polychaetes	1.86
Crabs	65.2
Snails	115
Modiolus	64
Insects	25.6
	348

These figures are for streamside or marsh-edge habitat. This habitat encompassed approximately the first 50m of marsh adjacent to the water. To obtain respiration of the meiofauna in the marsh edge we assumed that the average biomass to 50m was 2.49 g dry wt/m². This gives a respiration of 77.3 g dry wt/m²/year.

We will assume that the ratio of the respiration of detritus consumers to bacterial respiration reported by Teal and Kanwisher (i.e., 262.9:586.9) holds for our marsh. The bacterial respiration, estimated in this way, would be 777 g dry wt/m²/year. Thus, total consumption on the marsh is 777 g/m²/year (bacteria) plus 348 g/m²/year (consumers) or 1,125 g/m²/year. Net production of plant material has been given by Kirby (1972). Production at the edge of the streams was 2,960 g dry wt/m²/year and the production at 50m inland was 1,480 g/m²/year. Our observations of the marsh edge indicate that the average production in this edge habitat is about 2,366 g dry wt/m²/year (assuming that 60% is like streamside and 40% is like the 50m measurement). Thus, with a consumption on the marsh of 1,125 /m²/year, 1,241 g/m²/year or 52.4% of the net production is available for export to the adjacent water.

Total respiration of the marsh floor was measured during the summer of 1972. During June total respiration was equivalent to 1,054 g dry wt/m²/year. For July and August, rates were 834 and 545 g dry wt/m²/year, respectively. Thus, the trend was for the respiration to fall during the summer. The highest respiration levels probably occur during the spring when there is a large loss of detrital material from the marsh. Thus, even though the respiration rates calculated in the preceeding paragraph are determined from the literature, we believe that they represent a good estimate of bacterial respiration in the Louisiana marshes.

We estimated bacterial respiration in the water and sediments from total respiration less the sum of plant and animal respiration. Total benthic respiration was calculated to be 798 g dry wt/m²/year. This was determined from the difference between total respiration calculated from the diurnal oxygen curve method and water respiration calculated from the light-dark bottle method. Thus, the figure for benthic respiration includes that of larger nekton such as fish, crabs, and shrimp and the water respiration includes those organisms which would be captured in a BOD bottle. This would be phytoplankton, bacteria and zooplankton. For calculating plant respiration, we assumed that plant respiration was 30% of gross production. Respiration data for the water and submerged sediments are presented in Table 27.

Table 27. Respiration for various components of the water and submerged sediments. Plant respiration assumed to be 30% of gross production. All figures are g dry wt/m²/year.

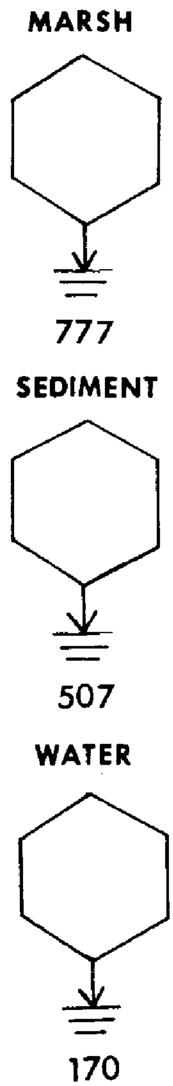
Total Benthic Respiration		798	Total Water Respiration		450
Benthic Plants	209		Phytoplankton	179	
Meiofauna	45.9		Zooplankton	101	
Blue Crabs	.94				280
Shrimp	3.15				
Oysters	16.8				
Fish	15.4				
		291			
Total Bacterial Respiration (Benthic)		507	Total Bacterial Respiration (water)		170

Measurements of benthic respiration were conducted during the summer of 1972 by Tim Gayle and Charles Hopkinson (unpublished data). They found a total benthic respiration of 635 g dry wt/m²/year near the shore and 332 g/m²/year in the center of Airplane Lake. Becker (1972b) reported the total shoreline length in Barataria Bay was 2,739 miles. This indicates that about 25% of the total water area is within 50 meters of the shore. To obtain an average value of 391 g/m²/year for benthic respiration, we assumed that the nearshore value represened 25% of the total area and the mid-lake value represented 75% of the area. This figure is corrected for respiration in the water so that it represents bacteria, benthic plants, and meiofauna. Both meiofauna and benthic plants are low during the summer months so that the respiration is mainly bacterial. A benthic respiration rate of 391 g/m²/year is 116 less than the 507 /m²/year given in Table 27. Benthic respiration is greater during the colder months (Fig. 8). Therefore, if measurements were conducted year-round, a higher value would likely be obtained. We used 507 as the bacterial respiration for the sediments. This indicates that about 65% of total benthic respiration is bacterial. Hargrave (1969) estimated that 35% of total benthic respiration was bacterial in a freshwater lake in Canada.

Total respiration in the water was 450 g dry wt/m²/year. Since this was estimated from light-dark bottle experiments, it includes phytoplankton, zooplankton, and bacteria. Zooplankton respiration was 100.6 g/m²/year. Phytoplankton, estimated at 30% of gross production, is 179 g/m²/year. The sum of phytoplankton and zooplankton respiration is 280 g/m²/year leaving 170 g/m²/year which we will consider as bacterial respiration in the water column.

It is interesting to note that Teal and Kanwisher (1961) found that bacterial respiration was lower at

25° C than at 20° (8.1 mm^3 $0_2/cm^2/hr$ as compared to 9.20). As stated earlier, Hood found lower populations of bacteria during the warmest months of the year. Bacterial populations were closely correlated to the amount of organic matter present. Our measurements show that respiration of the marsh and sediments were lowest at the end of the summer. This seems to indicate that maximum bacterial populations and metabolism do not coincide with the highest temperatures, but are more substrate controlled.



BACTERIA

In calculating utilization of detritus by bacteria we have only considered respiratory loss. Some detritus is, of course, converted to bacterial biomass. Since it is very hard to separate bacteria from the detritus, and since larger organisms feeding on the detritus take the bacteria, we are considering the bacteria to be part of the detritus insofar as standing crop is considered.

YEAST AND FUNGI

Yeast and fungal populations in the marsh study area have been studied by S. P. Meyers and his coworkers of the Department of Food Science at Louisiana State University (Meyers et al., 1970, 1971, and Miles, 1971). There is a high predominance of sexual species of yeast, the most abundant being those of the genera *Pichia* and *Kluveromyces*. There is a comparatively sparse asexual population.

The abundance of yeasts compares to the richest terrestrial habitats. Numbers of yeasts in the water and submerged sediments tend to be highest in summer and lowest in winter, while the yeast numbers in the marsh soil are generally higher in the winter. The average population in the water column was 470 cells/ml with the maximum measured being 1,400 cell/ml. Higher numbers were found in the submerged sediments with an average concentration of 7,950 cells/cc sediment and a maximum population of 1.8 x 10^4 cells/cc. Yeast were most abundant in the marsh soil. The highest populations occurred during the summer months with a secondary peak in midwinter. Very low numbers were present during the fall. The average population was about 1.6 x 10^4 cells/cc and a maximum of 9 x 10^4 cells/cc. Meyers et al. (1970) suggested that the high winter populations in the marsh soil were due to the *Spartina* "die back" during the colder months which provides a variable and rich source of carbohydrates for the yeast population present. Since tides do not normally cover the marsh during the winter, the dead *Spartina* material would not be available to yeasts of the water and submerged sediments until the higher spring tides.

It was found that several species of yeasts could utilize amines (Nicholson, 1970). This suggests a role for yeasts in nitrogen regeneration in the marsh system.

A number of species of molds (filamentous fungae) have been found in association with *Spartina* stems. Fungal growth is prevalent throughout the plant stem, both on the outside and inside. The predominant organisms are deuteromycetous forms. The most abundant species are representatives of the genera *Fuscarium, Phoma*, and *Nigrospora*.

No specific measurements have been made of the yeasts and fungi. The calculations for bacterial respiration presented earlier probably represent total microbial respiration rather than just bacterial. We do not have any data on the portion of the total microbial respiration which is due to the fungi, but because of their smaller numbers and larger size, they have been estimated to represent less than 25% of the total respiration (Crow, personal communication).

DETRITUS

That detritus plays an extremely important role in estrarine ecosystems is a point that has been made clear by several, perhaps most emphatically by Darnell (1961, 1967a, 1967b). Despite the recognition of its importance, there remains a great degree of ignorance as to the nature, quantity, and quality of detrital matter, so much so that these problems can be readily identified as the least understood aspects of the estuarine ecosystem.

Darnell (1967a) defined detritus as all types of biogenic material in various stages of microbial decomposition which represents potential energy sources for consumer species. This definition excludes the microbiota, which use detritus particules as a substrate, from being considered a part of the detritus itself. Many reports of measured standing crops of detritus probably included the microbiota as well, but in most instances this lead to a small overestimate in terms of total organic carbon, but not in terms of organic nitrogen. Ideally, measurements would be made that would allow separation of the detrital substrate and the associated microbiota. This is of increased importance with the realization that a number of detrital feeders assimilate primarily the microbiotic elements with the detrital substrates passing out virtually unaltered in the feces (Newell, 1964; Fenchel, 1969); W. E. Odum, 1971).

The standing crop of detritus in the estuary at any given time is a complex product of events in different sections of the marsh-estuarine ecosystem. The live standing crop of *Spartina* is transformed to dead standing crop at a fluctuating rate and this is, in turn, transformed to mulch or debris on the marsh surface. About half of this material is consumed on the marsh and about half enters the water (Teal, 1962; Golley, et al., 1962). The detritus in the estuary can be partitioned into suspended detritus and detritus settled on the bottom, but this partition constantly fluctuates, depending on water turbulence.

Kirby (1972) has shown that the live standing crop of *Spartina alterniflora* is maximal in the July-September period and minimal in the January-March period. He also shows (Fig. 7) that the seasonal distribution of dead standing crop is very nearly the reverse of this with a maximum in January-March and a minimum in June-September. The fall and early winter months then are the period in which transfer from the live standing crop component to the dead standing crop component is most rapid. The spring months are the period in which the dead standing crop is removed from the marsh most rapidly as is corroborated by the rapid decrease in dead standing crop in early spring and by the litter bag loss studies made by Kirby (1972) (Fig. 7). The high rate of loss of detritus from the marsh corresponds to peaks in biomass of zooplankton, larval, shrimp and fishes, *Foraminifera,* and others.

Mulkana (1968, 1969) has reported data on suspended matter in seven stations in Barataria Bay. He termined material retained by a plankton net (76 micron mesh size) as plankton and material passing through the net as nannoplankton. This terminology is confusing; a better usage would be to divide the two size fractions into seston and nannoseston since the material he sampled included detritus and mineral constituents as well as planktonic organisms. The quantities of mineral matter are roughly suggested by ash values exceeding 50% in all samples of seston and nannoseston. On an ash-free dry weight basis (estimated from Mulkana's data), the seston varies from .09 g/m^2 to 0.52 g/m^2. Golley, et al. (1962), measured export over a tidal cycle in a Puerto Rico mangrove swamp to be 1.37 g C/m^2 day which in this case was a quantity in excess of net production indicating more data were needed to get a longer term average figure. E. P. Odum and de la Cruz (1967) made measurements of detritus flux in and out of a small tidal stream in Georgia over a five-month period from June to November. Their figures indicate a net export not as great as Teal estimated, but this is probably because the rapid spring export was not observed. The nannoseston is much more abundant, ranging from about 10 g/m^2 to 30 g/m^2. Mulkana gives as an overall average figure that nannoseston standing crop is 113 times more abundant than seston standing crop. This relative size distribution compares favorably with that reported from Georgia by Odum and de la Cruz (1967) who stated that nanno-detritus (in this case less than 64 micron sized material) was 95% of the total standing crop of detritus.

Cruz-Orozco (1970) measured suspended solids in smaller water bodies connected to Barataria Bay on its western side and found values of 35 to 42 g/m^3, slightly lower than Mulkana reported when allowance is made for water depth. The results also differ in that Cruz-Orozco found proportions of organic matter (measured by loss on ignition) that were just under 50% of total suspended solids. These discrepancies are slight, probably less than the errors of the comparison since different methods were used and the hydrographic conditions of sampling stations differed.

Cruz-Orozco (1970) also reports organic content (as loss on ignition at 500° C) of the uppermost bottom sediments (0-1 cm) to vary from 3.8 - 14.8%. Ho (1971) reported that organic carbon in the uppermost sediments ranged from 3.6 to 6.4 percent which is in reasonable agreement with the above if the organic matter is assumed to be about half carbon. She has also measured dissolved organic levels in the water of 4 g/m^3 (personal communication). For water bodies that are 1m deep, this is 4 g/m^2.

Elsewhere, estimates have been made of detritus production. Teal (1962), after accounting for all consumption of net production in a Georgia marsh, reckoned that there was an export of 45% of net production which escaped from the marsh into the estuary as detritus.

ECOSYSTEM BUDGET

The structure and budget for the marsh-estuarine system calculated in the preceeding sections is shown in figures 21-24. The data are presented using energy language symbols (H. T. Odum, 1971).

The data for primary production can be considered in several ways. As stated earlier, Kirby (1972) measured gross production of 14,000 g/m²/year streamside and 9,750 at a distance of 50 meters from the water. Net production was 2,960 and 1,480 from streamside and inland areas, respectively. As shown in the section on marsh fauna, most of the animal biomass occurs within 50 meters of the shore. The average net production of grasses in this 50-meter zone (calculated in the section on bacteria) is 2,366 g/m²/yr. Kirby found that 18% of the marsh area in the vicinity of Airplane Lake was streamside habitat, 52% was inland habitat (i.e. similar to the 50 m station), and 30% was bare areas and small ponds. Using these percentages the average production over the entire marsh was calculated to be 8,418 g/m²/yr for gross production, 1518 g/m²/yr for net production and 6,900 for respiration. These figures are based on the marsh in the vicinity of Airplane Lake, but we believe that Airplane Lake is a good representative of the saline *Spartina alterniflora* marsh in Barataria Bay. It should be emphasized that this data is only for saline marsh. The following data of Chaubreck (1970) gives the amounts of the different types of marsh in the Barataria Bay hydrologic unit.

Marsh Type	*Acreage*	*% of Total*
Saline	144,214	30.7
Brackish	125,296	26.7
Intermediate	20,084	4.3
Fresh	179,717	38.2
TOTAL	469,311	

In addition, the open water area of the hydrologic unit is 449,891 acres of which 186,974 acres (41.6%) are in the saline area. Thus, in the saline zone, 43.6% of the total area is marsh and 56.4% is open water.

Respiratory data for the marsh fauna was summarized in the section on bacteria. In the first 50 m the respiration of the marsh fauna was 348 g/m²/yr and that of the bacteria was 777 g/m²/yr. Again, these data are for the 50 meters adjacent to the water. The only larger organisms found at the 300 meter station were snails (*Melampus*) and polychaetes. The calculated respiration for these two at 300 m is 18.4 g/m²/yr. Average meiobenthic respiration over the marsh is 36.9 g/m²/yr. For bacterial respiration, we will assume that the spatial variations follow that of the *Spartina*. Inland *Spartina* biomass is 60% of streamside. A similar reduction for bacteria gives respiration of 539 g/m²/yr. Thus, the total respiration for the deep marsh is 575 g/m²/yr (539 for bacterial and 18.4 for polychaetes and snails and 18 for meiofauna). Becker (1972b) measured the total shoreline length in Barataria Bay. From his data it can be estimated that about 27% of the marsh lies within 50 meters from the shore. We will use 30% as an average for the size of the 50-meter zone. The following summarizes the respiration of the marsh fauna.

	Marsh edge (30%)	*Inland ((70%)*	*Average*
Bacteria	782	539	611
Fauna	350	55.3	143
Total	1132	594	754

units are g dry wt/m²/yr

Thus, the total consumption for an average m² of saline marsh is 754.4 g/m²/yr. The average net primary production is 1,518 g/m²/yr. Thus, 764 g/m²/yr or 50.3% of the net production is exported as detritus from the marsh into the surrounding waters each year. This compares to an export of 1,125 g/m²/yr for the rich marsh edge habitat. Chabreck's data show that in the saline area 56.4% of the area is water and 43.6% is marsh. Because there is more water than marsh, an export of 764 grams dry wt/m² marsh surface/yr is equivalent to 594 g/m² of water surface/yr.

The question arises whether all of this net production is exported to the water. The subsidence curve of Figure 2 is direct evidence that some contribution from net primary production goes to sedimentation on the floor of the marsh and estuary. The overall rate of subsidence appears to be about 0.81 cm per year. If sedimentation is keeping pace with this rate of subsidence then the same thickness of sediment must accumulate each year. Since sediment supply from the Mississippi River has for the most part been interrupted by levee construction it is likely that most such compensatory sedimentation is from organic matter. Wet organic sediments typical of the marsh floor have a bulk density on the order of 1.1, a dry weight organic matter content of about 60%, and a water content of 80%. This means that a cubic centimeter of surface sediment contains about .88 g of water, 0.13 g of organic matter, and .09 g of mineral matter. In keeping with the subsidence rate of .81 cm per year it follows that about 1,053 g/m² of organic matter could be lost to sedimentation each year.

For the most part this loss to sedimentation must come from root production since this is emplaced in the sediment during the growth of the plant. Consequently, we feel this has little effect on our judgment concerning the fate of above-ground net production which, for the most part, is utilized by marsh consumers or finds its way to the adjacent estuarine water bodies. It is also apparent that the marsh is losing out in the battle against subsidence since there is a net loss of land in the Barataria Bay hydrologic unit (Gagliano and van Beek, 1970). This implies that, for the most part, the production of organic matter cannot keep pace with the rising sea level or is something less than the 1,053 g/m² mentioned above.

The production of the epiphytes was discussed in the section on primary production. This data was for the epiphytic community which includes bacteria, protozoa, and meiobenthic organisms as well as the algae. A negative value was obtained for net production because the total community respiration was included. We estimated the respiration of the epiphytic algae alone by assuming that the respiration was 20% of gross production. This is the average of phytoplankton and benthic flora respiration.

The budget data for the marsh macrofauna present in the marsh fauna section are for the marsh edge habitat. As shown earlier the respiration for the marsh fauna averaged over the entire marsh is 37.3% of the respiration in the marsh edge (130.4 g/m²/yr as compared to 350 g/m²/yr. We will assume that the budget data for the different populations is 37.3% of that for the marsh edge. These data are presented in Table 28.

Table 28. Data on carbon budget of major detrital consumers of salt marsh. Units are g dry wt/m²/yr. Of each pair of numbers, the first is the value for the marsh edge (50 meters adjacent to the water) and the second is the average for the entire marsh. Data for polychaetes and meiobenthos are over the entire marsh.

	Meio-benthos	Poly-chaete	Snails	Crabs	Modiolus
Total intake	97.6	4.4	268/100	145.4/54.2	140.8/52.5
Respiration	36.9	1.86	114.5/42.7	65.2/24.3	64/23.9
Feces	48.8	2.2	134/50	72.7/27.1	70.4/26.3
Production	11.9	0.34	19.6/7.3	7.44/2.8	6.4/2.4

From Table 28 it can be seen that the amount of organic matter available to the higher consumer on the marsh can be calculated by summing the production for snails, crabs, *Modiolus*, and polychaetes. This is 12.84 g/m²/yr.

Higher consumers in the marsh which feed on the detrital group include raccoons, rails, wading birds, and crabs. Raccoons take 1.1 g/m²/yr and rails take 1.64 g/m²/yr. Our calculations show wading birds consume about 1.76 g/m²/yr. Data in Table 20 indicate that about half of their food (about 0.88 g/m²/yr) consists of marsh organisms. We calculate that shore birds take about 0.45 g/m²/yr. We have not obtained any data for mud crabs. We will use the data of Teal (1962) for mud crabs. He reported that they consume 5.4 g/m²/yr. Thus, the total intake by secondary consumers on the marsh is 9.47 g/m²/yr leaving 3.37 g/m²/yr unaccounted for.

As stated earlier, 594 g/m²/yr of marsh grass detritus is introduced into the water. The net benthic production (gross photo-synthesis-plant respiration) is 488 g/m²/yr and the net phytoplankton production is 418 g/m²/yr. the total production of organic matter in the open water zone is 1500 g/m²/yr.

If the consumption in the water is summed for all trophic levels (less feces production), the total organic use is 864 g/m²/yr. Of the 1500 dry wt/m²/yr available to the estuary, 636 g/m²/yr are left after consumption. Most of this material is probably flushed from the estuary by the tides. Dr. Frank Truesdale (Per. Comm.) encounters large amounts of detrital material flowing out along the bottom of Caminada Pass on the ebbing tide. Phytoplankton and zoolplankton are also flushed out by the tide. The organic material can be utilized on the shelf by many organisms. There is large fishery for white shrimp and menhaden in these shell waters. This data on flows of carbon and community structure are presented in figures 21-24. The structure of the entire marsh-estuarine community is shown in Figure 21. We have included this figure to allow the reader to visualize the entire system as a unit. The details of the three subsystems (marsh, submerged sediments, and water) are presented in figures 22-24. We have used values for detritus in the submerged sediments and in the marsh soil of 500 and 1000 g organic matter/m², respectively. These values are for the first cm of sediment material. The average organic content of the submerged sediment is about 5%. We have assumed the level in the marsh soil to be twice this. All numbers used in figures 22-24 are the average over the whole water or marsh surface.

The production and flow of organic material in Barataria Bay is summarized in Fig. 25. In order to calculate export from the estuary, net production on the marsh was recalculated on the basis of water area. Therefore, 1,518 g dry wt/m² marsh/yr becomes 1,208 g/m² water yr. The export from the marsh is 50.4% of net production, and the export from the estuary is 42.4% of net production available to the water or 30% of the total net production in the estuary.

The production and utilization of organic matter is also presented in Table 29. There is a pronounced difference between the net community production on the marsh and in the water. In the marsh there is a net community production of 764 g dry wt/m² marsh/year, while the net community production of the water column is 48 g dry wt/m² water/year. This indicates the importance of the marsh in producing the characteristic net production of this estuarine system.

Table 29. Production and use of organic matter in the Barataria Bay Area of Louisiana. Data for marsh are g dry wt/m² marsh/year and data for water are g dry wt/m² water/year.

MARSH		Production Gross	Production Net*	Consumer Respiration	Community Net Production
Grass:	Streamside	14000	2960	—	—
	Inland (50 m)	9750	1484	—	—
	Average over marsh	8418**	1518**	754**	764**
Epiphytes:	Streamside	103.9	—	—	60
	Inland (2 m)	27.3	—	—	-18.4
	Average (to 2 m)	32.2	25.8	—	
Total:					764
WATER		**Production Gross**	**Production Net***	**Total Respiration**	**Community Net Production**
	Phytoplankton	598	418	—	—
	Benthic Plants	698	488	—	—
	Water Column†	—	—	450	—
	Benthis and Nekton	—	—	798	—
Total:		1296	906	1248	48

* Net production is less respiration of plants
**Takes into consideration bare areas of marsh
† Phytoplankton, zooplankton, and bacteria

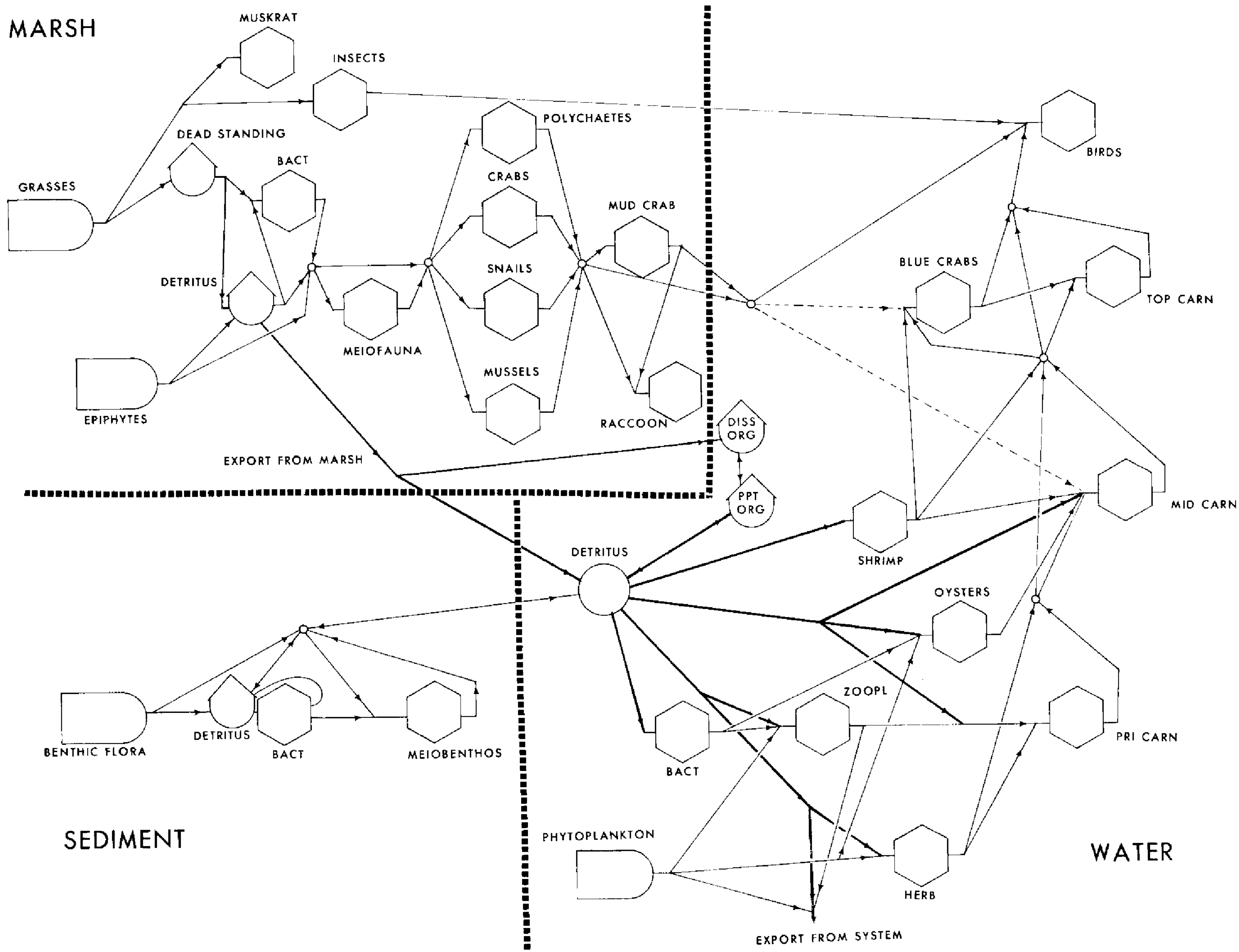


Figure 21. Diagram of marsh-estuary system showing components and pathways considered in this paper. Heavy lines indicate flow of detritus. Details of the three susbsystems are shown in the following three figures. A legend explaining the symbols is presented in the introduction.

MARSH

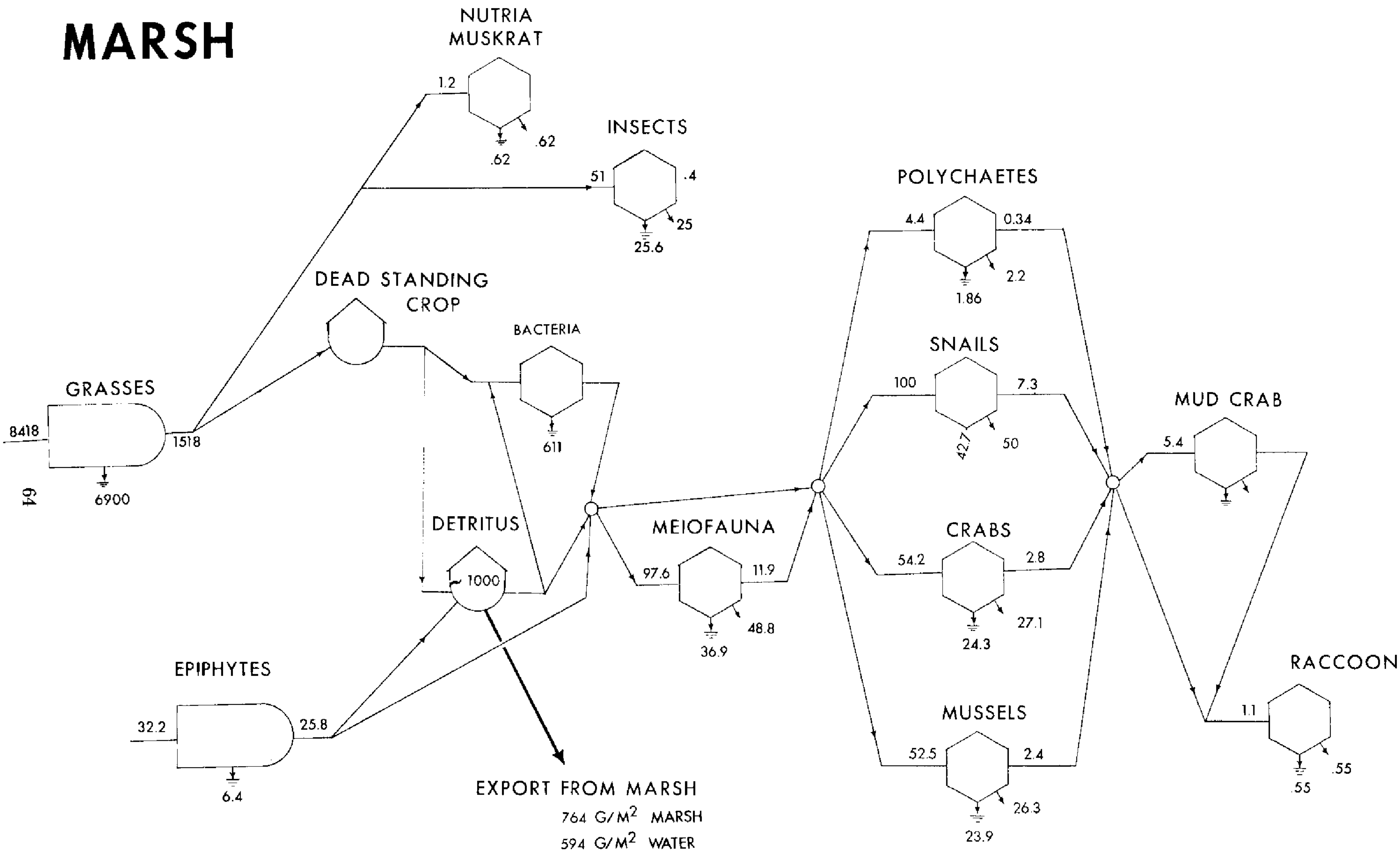


Figure 22. Summary diagram of the various flows of organic carbon in the salt marsh. Units are g organic matter/m²/yr.

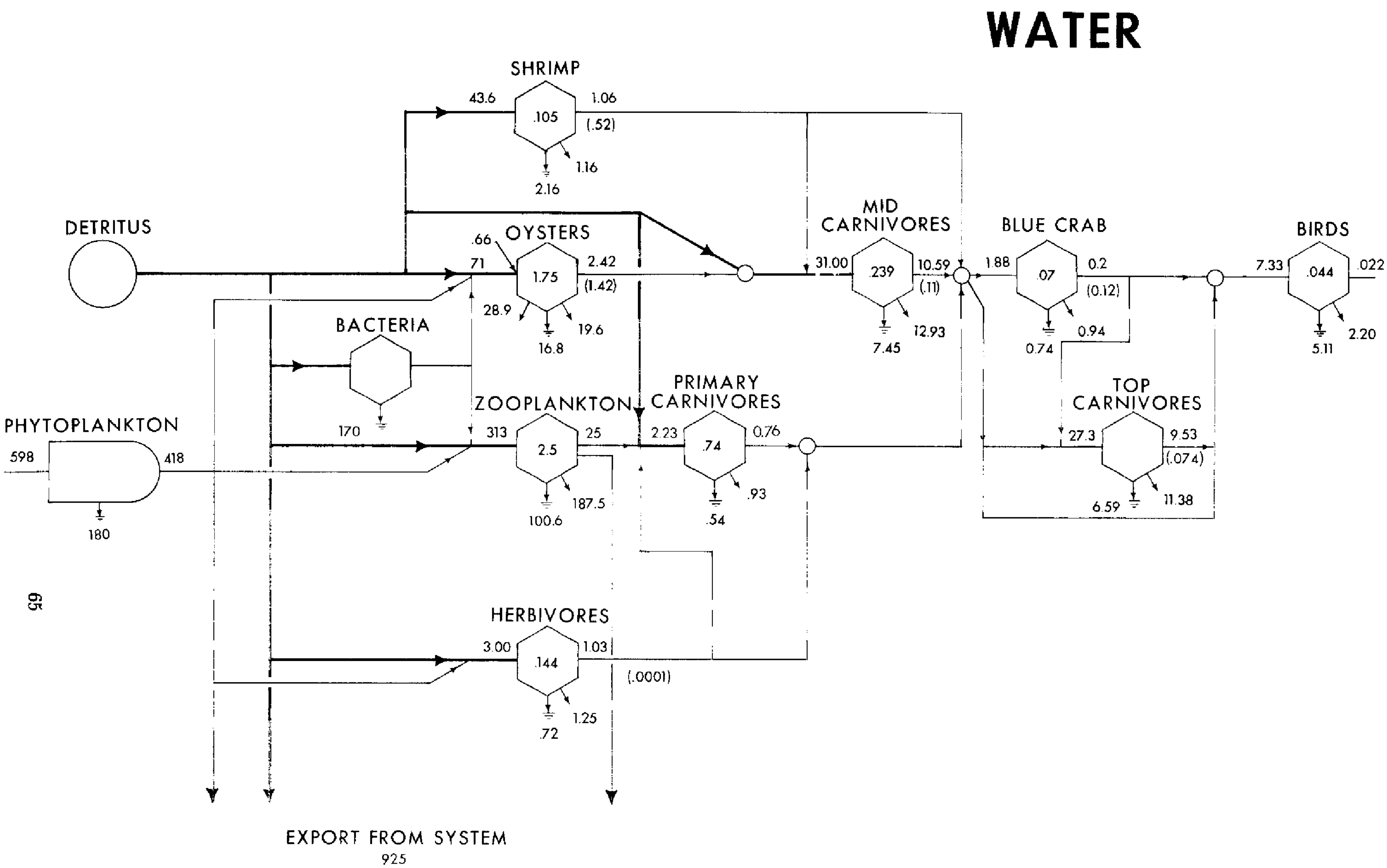


Figure 23. Summary of carbon flow in the water column. Units are g organic matter/m²/yr.

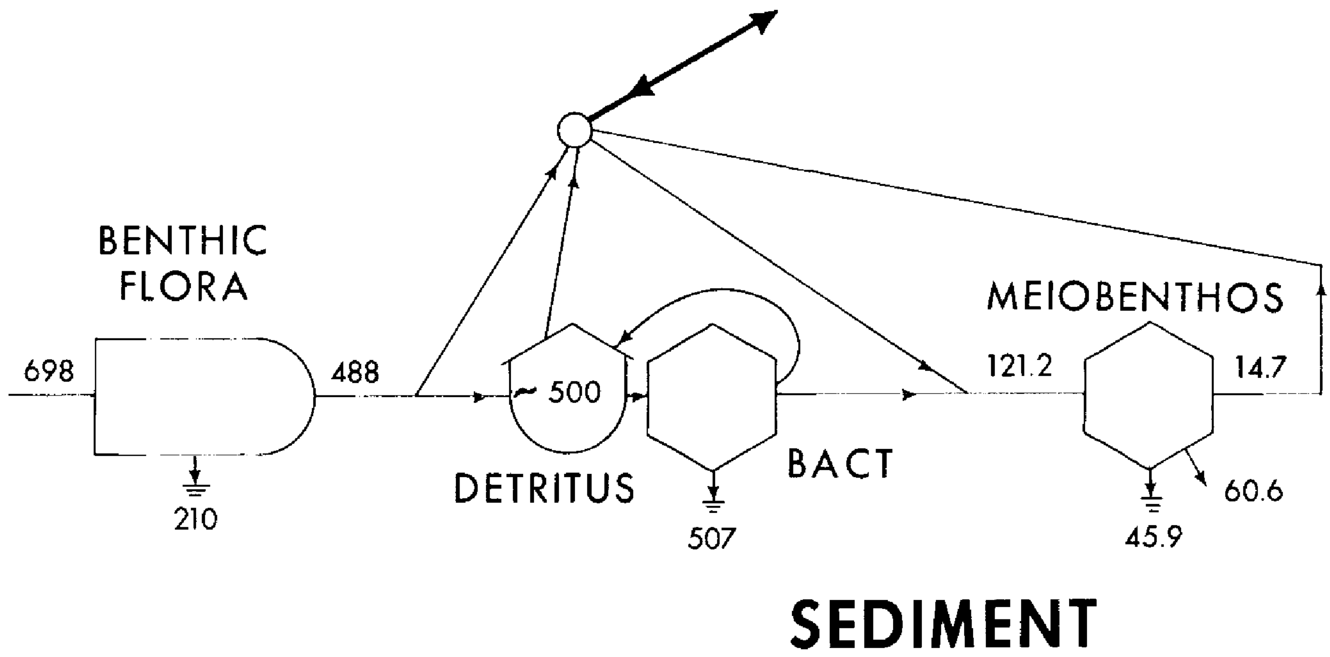


Figure 24. Summary diagram of the flows of organic carbon in the submerged sediments. Units are g organic matter/m²/yr.

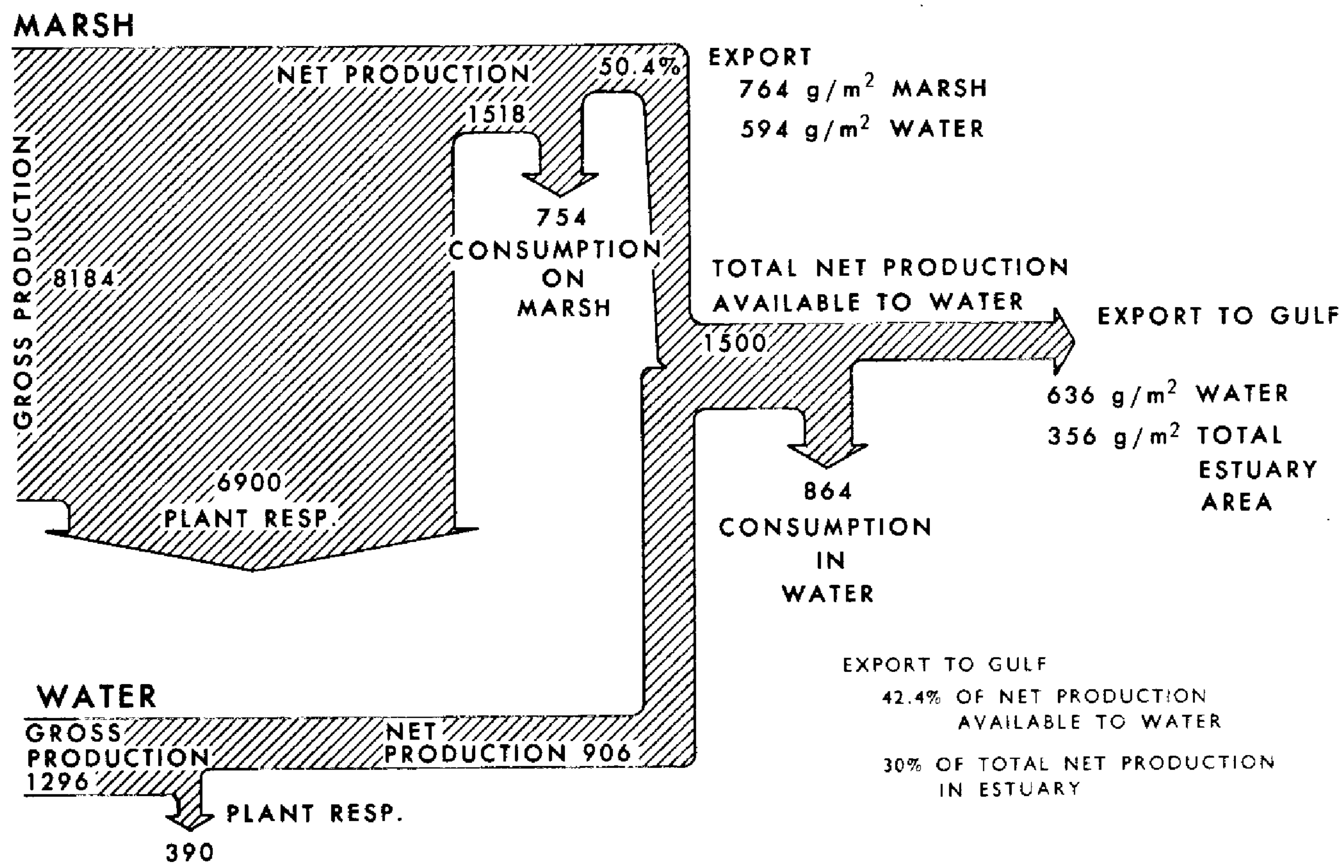


Figure 25. Production and flow of organic matter in Barataria Bay. Number for marsh are g dry wt/m² marsh/yr and g dry wt/m² water/yr for water areas.

DISCUSSION

In the previous chapters we have discussed the organic budgets, food habitats, and composition of the various populations in the estuary, but have ignored many of the interactions among the different populations and with the abiotic system. In this chapter we will investigate in some detail the interactions and processes which we consider most important. A diagram of the estuarine system showing some of these interactions is presented in Figure 26. In order that the diagram can be easily undersood, we have shown detail only for the processes which we are discussing. In several instances we have shown an interaction for one compartment when it should be shown for all such as the effect of temperature on detritus production. Temperature affects many other processes in the estuary, but we show it affecting only this one. All simplifications are pointed out in the text.

Forcing functions affecting estuarine processes are shown as circles. These include tides, insolation, temperature, water level variations, rainfall, inputs from the Gulf and Mississippi River and nitrogen gas in the atmosphere. The tide is very important in regulating many processes. It creates a "subsidized fluctuating water-level ecosystem" (E. P. Odum, 1971). It flushes water, nutrients, and salt into the estuary from both the Gulf and the River. Tidal action is also important in the movement of detritus from the marsh to the water and from the estuary to the Gulf. Many migrating organisms, especially larval and juvenile forms, ride tidal currents in moving in and out of the bays. The movement of post-larval shrimp into the estuary is a good example.

Salinity changes are one of the stresses with which estuarine organisms must be able to cope. The salt water balance in the estuary is determined by inputs of water from rainfall and water and salt from the Gulf and the River. Generalized salinity effects are indicated but no detail is shown.

The biotic communities in the marsh and water have been divided into three components: the primary producers, the detritus-microbe assemblage, and the fauna. Photosynthesis is an interaction between light energy and nutrients. Respiration of all components is shown by an arrow to a heat sink. The formation of detritus from marsh grass is one of the most important processes in the estuarine food web and it is shown in some detail. Very little of the grass is grazed alive (Smalley, 1958); most of it is converted to detritus. This conversion is dependent on a number of things. In the spring, rising water levels and temperatures, combined with the over-winter accumulation of dead grass, make conditions for microbial activity very good. The biological breakdown of the grass material results from an interaction of microbes with larger fauna, particularly the meiofauna. This type of interaction has been reported by Fenchel (1970) and Heald (1971). There is also an uptake of nutrients by the microbes during the breakdown of the grass (Fig. 4-11, E. P. Odum, 1971). Nutrient regeneration is also shown resulting from an interaction between the microbes and fauna (Johannes, 1965). Temperature affects the metabolic rates of all the biota and there is nutrient regeneration from all components, but we have shown these effects only for selected components.

Most evidence indicates that nitrogen is the primary limiting nutrient in estuarine systems. In a recent review article, Williams (1972) cites numerous examples of estuarine systems where nitrogen is the limiting nutrient. These include estuaries on the south shore of Long Island, the Potomac River estuary, parts of Chesapeake Bay, the York River, the James River, a series of North Carolina estuaries, and the Naccasassa estuary in Florida. Preliminary work indicates that nitrogen is limiting in the Barataria estuary. One of the most important new sources of nitrogen for the estuary is probably fixation by bacteria and blue-green algae. This is shown as bacteria and primary producers on the marsh pumping nitrogen gas in the atmosphere into the nutrient pool.

In the water zone, there is significant grazing on the primary producers as well as input into the detrital pool. The component labeled water fauna includes all top carnivores as well as herbivores and omnivores. Birds which feed in the marsh are in this category. Thus, there are flows from most of the other compartments. All migrating organisms are in the water fauna. These include shrimp, crabs, many fish, and birds. Migration is depedent on a seasonal program of the migrating organisms and, in many cases, the tide.

The presence of man is felt in several places. Fishing affects only the water fauna—shrimp, crabs, oysters, fish and birds. For simplicity, pollution stress is shown only on the water fauna, but it would affect all of the biota. Oil, pesticides, heavy metals, sewage, and turbidity represent the different types of pollution caused by man. The effects of dreging activity in the marshes are shown separately. When marsh is converted to water by dredging there is a lower productivity because primary production in the water is less than in the marsh.

There are some processes which are not shown in the diagram. Diffusion of oxygen and carbon dioxide across the air-water boundary is not considered a significant limiting factor. Studies in Texas bays (Park, et al, 1958; Odum and Wilson, 1962) and shallow estuarine ponds in North Carolina (Day, 1971) have shown that diffusion of these gases is not significant when compared with biologically caused changes. The wind is important in shallow sytems in determining circulation and temperature patterns. The effects of wind in the diagram are realized through the tide, water level, and temperature functions.

In the previous paragraphs we have discussed the processes and interactions which we consider most important and we now wish to consider some of these in more detail.

Estuarine areas exhibit very high net primary and secondary production. Indeed, the production of the marsh grasses in the Louisiana marshes is the highest yet reported. Other primary production units such as phytoplankton, and epiphytic and benthic plants contribute to the primary production but the marsh grasses are the largest contributor. This high net primary and secondary production is undoubtedly reflected in the yield of fishery products. The Louisiana coastal area has the largest fishery in the United States, yielding in excess of one billion pounds annually.

Factors responsible for the high primary production in estuaries have been discussed by Schelcke and Odum (1961). In general these include high year round production, the importance of detritus in the food web, the flushing action of the tides and abundant supplies of nutrients. Estuarine production in the Louisiana marshes is enhanced by its location in the deltaic plain of the Mississippi River. The wide continental shelf has allowed the development of extensive marsh and estuarine areas. The near subtropical position assures high solar insolation combined with the distinct climatic pulse common to higher latitudes. This makes for warm water temperatures in the shallow estuaries. As a result, conditions are ideal for maximum growth and low mortality.

The description of the estuary can be considered in terms of different types of structure. For convenience, we will consider three types of structure—temporal, spatial and community. Temporal structure refers to sequencing of events. Spatial structure refers to position and community structure refers to the interactions among the various components.

TEMPORAL STRUCTURE

The annual sequence of events in the estuary is determined by physical parameters. Of primary importance is the annual variation of solar insolation which gave rise to warm water temperatures—generally in the range of 10 to 30°C and averaging above 20°C. The Mississippi River has its highest discharge during the spring with rainfall being most abundant in the late summer, fall and winter. Thus, there is significant fresh water input year round. The marshes are normally flooded by the tides from March through November. Highest water levels occur in September and October.

As has been shown, the major unit of primary production is the marsh grasses. The highest net production is during April and May with high levels of production into November. The grass flowers in September and October, after which much of it dies. It is significant to note that there is a year lag in the utilization of the marsh grass by most of the consumers in the estuary.

The dead standing crop of marsh grass reaches maximum levels in late winter. There is an apparent sequence in the breakdown of the marsh grass. Highest bacterial populations in the marsh are present in late summer and this seems to indicate that the initial breakdown of the grasses is primarily bacterial. The winter die back of the grass combined with the low water levels result in a buildup of dead grass on the marsh. During this time of high dead grass biomass, a population peak of yeast and fungi occurs (Meyers, et al, 1970), probably causing a further breakdown of the grass. During the spring, water once again begins to cover the marsh regularly and there is a pulse of material loss from the marsh. This coincides with the highest meiofaunal populations of the year. The meiofauna with the associated bacterial flora are probably responsible for further breakup of the marsh grasses. The importance of detritus in detrital production has been noted elsewhere (Fenchel, 1970; Heald, 1971). Thus the production of detritus from the grass seems to be a sequential process with bacteria being most important, then yeast and fungi, followed by the meiofauna. Of course, all three groups are involved at all times, but it seems that they play the primary role at different times.

In summary, the main pulse of detritus loss from the marsh occurs in the spring. The loss is lower in the summer with a smaller pulse in the fall corresponding to the high water levels at that time. The highest

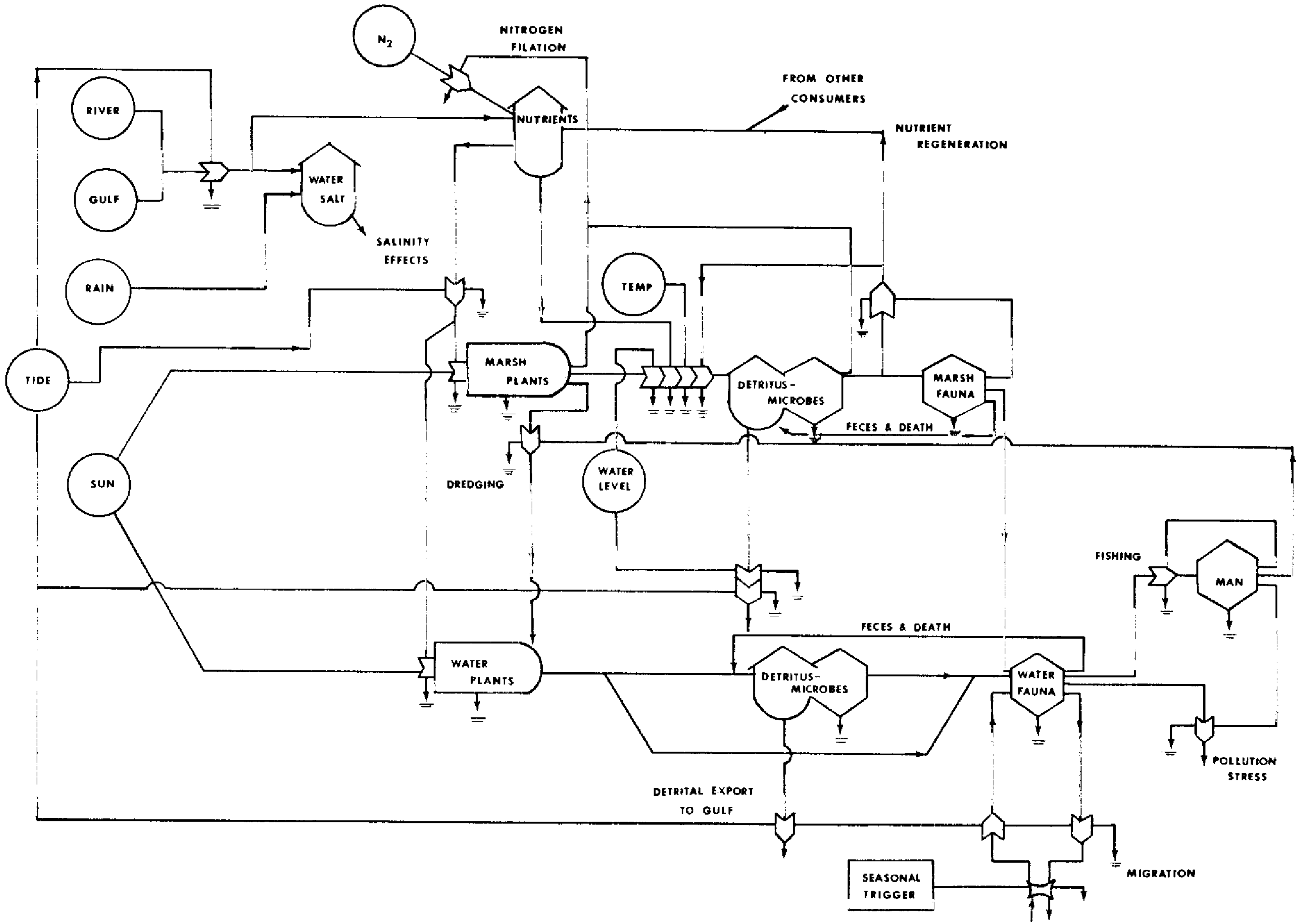


Figure 26. Energy flow diagram of the marsh-estuary system in Barataria Bay showing the most important processes and interactions. See text for discussion.

phytoplankton production is during mid-summer, coinciding with the lessened detrital production during that period. Production by benthic plants in the water and epiphytes in the marsh is highest in the winter. Thus, organic production available to the water comes mainly from detritus in the summer and fall, from phytoplankton and detritus in the summer and from benthic plants and epiphytes in the winter. The point is that primary production is high year round as a result of the different units of primary production.

An important factor to consider in the temporal structure is the large number of seasonal migrants. A seasonal pulse of food availability is more effectively used by a population which is largely migratory because they can move into the estuary when conditions are optimal. The larvae and juveniles of many species move into the estuary at the time of spring detrital pulse. This is true for brown shrimp, blue crabs and many pieces of fish. In general, non-migratory species are small and have fast growth rates which allow them to respond quickly to increased food availability.

In addition, the feeding habits of some species change as they grow and the change appears to be coupled with the changes of primary and secondary production in the esutary. An example is the Gulf Menhaden. Larval menhaden move into the estuary in greatest numbers in December. June and Carlson (1971) reported that pre-juvenile Atlantic menhaden consume mainly zooplankton. As the young menhaden metamorphose into juveniles they become herbivorous, consuming mainly phytoplankton. Our data indicate that many of the young menhaden are still in the pre-juvenile stage at the time of the zooplankton bloom in the spring. By May, most of the menhaden are juveniles and are consuming phytoplankton and probably detritus. As noted above, phytoplankton production has become significant by this time.

During the winter, many of the fishery species and birds migrate from the estuary and populations of many endemic species decline and there are low standing crops. Some species are more abundant, however, because of habitat changes. For example, populations of shore birds such as sandpipers, which feed on bare mud areas, increase during the winter. This results because many of the areas which are small ponds during times of high water are bare mud areas during the winter, thus creating greater habitat for the shore birds.

SPATIAL STRUCTURE

The spatial structure of the estuary includes such things as the geometry of the marsh and the structure of the water column and the bottom.

The most productive area of the estuary is the marsh-water interface. Production of marsh grasses is more than twice as high near the shore than in the interior marsh. Similar observations have been made in Georgia salt marshes (Teal, 1962). In the same general area the highest standing crops of marsh macrofauna and meiofauna occur. In addition, respiration rates of the surface sediments is about twice as high near the shore as in the middle of the water bodies. Standing crops of organic matter and meiobenthos in the submerged sediments are higher near shore. In contrast to the shore zone, bottom sediments away from shore are composed mainly of soft, fine-grained clay minerals and the benthic populations in these areas are sparse.

These factors suggest that overall marsh production will increase as the amount of marsh edge habitat is increased. The familiar picture of salt marshes with many twisting and dentritic channels probably reflect a tendency of the estuarine system to develop maximum production. Man-made channels which are usually straight are a striking contrast to the natural channels. From measurements of shoreline in Barataria Bay (Becker, 1972b) we estimate that nearly 30% of the marsh grass lines within 50 meters of a shore.

The water areas of Barataria Bay are non-stratified because of the shallow nature of the bay. As a result there is often not a distinct differentiation between the benthic system and the water column because benthic elements are mixed into the water.

COMMUNITY STRUCTURE

Much of this report has been concerned with an analysis of the marsh-estuarine community. Biomass variations, food habits, life cycles, and dominant species have been discussed for the various components of the system. The food web of the entire system has been summarized in Figures 21-24. We now wish to discuss the ecological roles played by the various species.

Role is a concept by which the many different organisms in a complex ecosystem may be grouped into general categories based on function and process. Basic roles are packaging, regulation and regeneration. All organisms act in all three roles but one role usually dominates. The roles may change during the life of the organism. In the marsh system described in this report some examples of these roles are indicated in Table 30.

Packagers organize organic material into forms available for convenient transfer to higher trophic levels. There is a progression from diffuse material form to concentrated bacterial form in packaging.

Table 30. Ecological roles of some estuarine species. See text for discussion.

Packagers	Regulators	Regenerators
Spartina	Mature fish	Bacteria
Benthic algae	Porpoises	Yeasts
Periphyton	Pelicans	Molds
Phytoplankton	Herons	Meiofauna
Killifish	Egrets	Protozoa
Shrimp	Gulls	
Fiddler Crabs	Comb-jellies	
Juvenile fish	Raccoon	
Marsh snails	Man	
Modiolus		
Oysters		

Packagers may be autotrophs or heterotrophs. The autotrophs include the grasses, phytoplankton, benthic plants, and epiphytes. Heterotrophic packagers include meiofauna, snails, fiddler crabs, shrimp, most zooplankton, and many small fishes. These organisms are principally herbivores. They typically have a high biomass, small size, rapid growth rates and short life spans. Microbes could be placed in this group because of their role in degradation of detritus, but because of their important role in nutrient regeneration we have placed them in a separate group. This group includes the organisms which are most important in nutrient regeneration, including protozoa and meiofauna as well as microbes. All organisms excrete waste products and are regenerators to an extent, but the organisms mentioned above play particularly critical roles in this respect. Regeneration is the opposite of packaging in the sense that it proceeds from concentrated material forms to diffuse material forms.

Regulators include organisms with generalized feeding habits. They can regulate populations by feeding on the most abundant food sources. In general, regulators have long life spans and larger individual sizes. In spite of slow growth rates, regulators can rapidly increase their biomass in an area because of high mobility as in migration.

Regulators can be subdivided into whole-system regulators and subsystem regulators. The subsystem regulators usually feed on specific types of organisms such as meiobenthos, macrobenthos, small fish or zooplankton. Included among the subsystem regulators are catfish, blue crabs, shore birds, drum, croakers and many others. These are generally analogous to mid level carnivores. Whole system regulators feed on subsystem regulators as well as many of the food items that the subsystem regulators feed on. The regulatory role of the whole system regulators is thus more comprehensive. Included in this group are top carnivorous fish (trout), mammals (raccoons and porpoises), most birds (wading birds, bulls, terns and pelicans), and man. There is very little predation on these top regulators except by man who has become a regulator of the whole system. Human effect on the system has accelerated spectacularly from the simple hunting, trapping, and fishing for survival roles of earlier populations to the immense commercial fishing, mineral extraction, transportation, recreational fishing, and residential development activities of the coastal zone at present. The rate of increase in activity has been so great that there can be little doubt that we are dealing with a system that is out of equilibrium in the Louisiana salt marsh. The most dramatic effect is the extensive channelization for transportation and mineral extraction.

It is worth noting that some of the principal packagers can have an effective regulation role of another kind. The copepod *Acartia tonsa* and the amphipod *Ampilesca* are cases in point for the Louisiana marsh-estuarine zone. These are very abundant packagers which are preyed upon by a wide variety of juvenile and adult fish. Supporting a large number of feeders as it does, each of these species will exert a regulatory role in some way on those species dependent on it The basic generation time in the life cycle of such species is an important regulating factor. The effect of physical-chemical factors in the rate of growth of these critical species gives us a clear conception of how regulation is imposed by non-biological factors. A given range of physical and chemical factors and a given set of community elements will lead to selection of certain organisms as major nodes in the web of relatiships through which energy and material flow rapidly. Such organisms are analogous to major valves in a chemical refinery process, just as are some of the top carnivores and the N_2-fixers. As such they are elements to be wary of with regard to man-imposed stresses on the system.

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