Physical Processes, Ecological Dynamics, & Management Implications:

Louisiana Sea Grant
College Program

Results of Research in the Atchafalaya Bay Delta

Editors: John W. Day, Jr. and William H. Conner

PHYSICAL PROCESSES, ECOLOGICAL DYNAMICS, AND MANAGEMENT IMPLICATIONS:

RESULTS OF RESEARCH IN THE ATCHAFALAYA DELTA REGION

edited by

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LOUISIANA SEA GRANT COLLEGE PROGRAM

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PREFACE

The development of the new Atchafalaya delta and the effects of river water on the surrounding region have created a unique opportunity for coastal scientists to study the evolution of a new coastal system. From a geological standpoint, this is the first opportunity to study a delta lobe in the growth stage. Past studies have all focused on declining systems. From an ecological point of view, the understanding of the development of a coastal ecosystem in a high-discharge area provides important new knowledge about the evolution of coastal ecosystems in general. This information has great applied value also. Because of the high loss rate of coastal wetlands, there is active planning for major freshwater diversions from the Mississippi River. Information gained from the Atchafalaya region will be important in planning and managing these diversions.

For a decade, the Louisiana Sea Grant College Program, as well as a number of other agencies, has supported research on the Atchafalaya delta and surrounding waters and wetlands in recognition of the great importance of this area's resources. It is particularly significant that the Atchafalaya delta is one of the few areas where active land building is taking place. The focus of the studies has been to (1) describe and understand the dominant physical, chemical, and ecological processes taking place in the delta, and (2) apply these scientific findings to management issues of the region.

The papers presented here represent a synthesis of the work carried out in the Atchafalaya delta region. Several of these papers have appeared in the scientific literature as journal articles and conference proceedings, but some have not been published before. We have chosen works that bring together information on various aspects of the area in order to provide an in depth view of the program and area. In order that current work be represented, summaries of ongoing projects are also included.

PART 1

INTRODUCTION

The emergence of the new Atchafalaya delta is a coastal geological event that is unprecedented in modern times. It provides scientists with the opportunity to study a major coastal system in its developmental stages, allowing them to formulate and test hypotheses about the evolution of deltas and the development of coastal ecosystems.

Before the initiation of research in the Atchafalaya delta region, much of the knowledge concerning the evolution of Louisiana's coastal systems was based on studies of systems that were undergoing deterioration. Concepts of deltaic growth were largely derived from interpretations of previously deposited and preserved sedimentary sequences as there were no major, actively prograding, subaerial shallow water deltas until the emergence of the delta in Atchafalaya Bay in 1973. Wetlands developing in the Atchafalaya delta are evolving under conditions similar to those that initially created most of the coastal wetlands in the state. Thus, examination of the Atchafalaya delta and the adjacent waters and wetlands is providing important insights about the evolution of wetland and coastal ecosystems and associated hydrologic and sediment transport processes. The research being carried out is making important contributions to the understanding of coastal ecosystems in general.

The research program in the region is not motivated, however, only by scientific inquiry. New land is being built in the area, in marked contrast to the widespread coastal deterioration occurring in most other parts of the coast. There is the opportunity to observe the colonization of new habitat sites by plants, benthic organisms, fishes, and wildlife, to study carbon and nutrient cycles that account for the remarkable biological productivity of juvenile deltas, and to learn about the interplay between riverine and oceanic processes.

Ambitious schemes are being planned and implemented by state and federal agencies for rejuvenating rapidly deteriorating wetlands in other parts of Louisiana through river diversion projects into shallow coastal waters. In the Atchafalaya delta, we have the opportunity to test and observe the effects of river diversions on a variety of coastal habitats including shallow bays, existing wetlands, and the nearshore coastal zone.

The focus of the Atchafalaya subprogram of the Louisiana Sea Grant College program is comprehensive. From initial studies of geological and ecological processes of the emerging delta, the subprogram has grown to be an integrated program of study of the Atchafalaya delta region. This is because the ecological changes in the Atchafalaya basin from the Old River control structure to the continental shelf off the emergent delta represent one of the most exciting opportunities in America today for research applied to management needs. This area has been termed the Atchafalaya Corridor. By increasing research activities along the entire corridor, the work in the delta region will contribute to a more powerful understanding of the continuum from the river to nearshore coastal waters.

The Atchafalaya Corridor context is drawn from a central tenent in estuarine ecology, that freshwater inputs greatly affect coastal systems (Cross and Williams 1981, Nixon 1981a, b, 1982, Boynton et al. 1982, Kemp and Boynton 1984, Deegan et al. 1985, Malone et al. 1986). Figure 1 is a conceptual diagram of the river-to-marine continuum. Inputs of water, nutrients, and suspended materials flow into and affect both wetlands and shallow bays, and there are direct interactions between wetlands and bays as well. Explicit in the diagram is the impact of human activities, which shunt more and more of the river flow directly offshore. Elucidating the interactions among river, wetlands, and tidal waters in a setting affected by natural and human changes is the central objective of the LSU Atchafalaya research program. No other river-delta system in the U.S. affords such an excellent opportunity for productive inquiry.

The papers presented in this volume illustrate the breadth of coverage of the research program. We have distinguished a number of different habitats, including freshwater forested wetlands to the north of Atchafalaya Bay, the emerging delta, adjacent wetlands and shallow water bays, and the nearshore coastal zone. In studying these habitats, we have attempted to understand the important processes taking place. Sediment transport, deposition, and resuspension have been measured. In the emerging delta this has provided new geological insights about the process of delta formation (van Heerden et al. 1980a, b). Sediment flux has been measured through open bay entrances (Madden 1986) and small bayous (Baumann and Adams 1981, Madden 1986, Stern et al. 1986), and off and on the marsh (Childers 1988). Sediment deposition on the marsh has also been measured (Baumann et al. 1984). Sediment transport offshore is contributing to new land formation along the chenier plain to the west (Wells 1983, Wells and Kemp 1981). From an ecological point of view, research has focused on the structure and development of emergent wetland communities in the Atchafalaya delta and adjacent wetlands (Johnson et al. 1985, Rejmanek et al. 1987, Fuller et al. 1985), nutrient dynamics (Teague et al. 1988, Stern et al. 1986, Caffrey and Day 1986, Madden 1986, Twilley 1988), aquatic primary productivity (Ran-

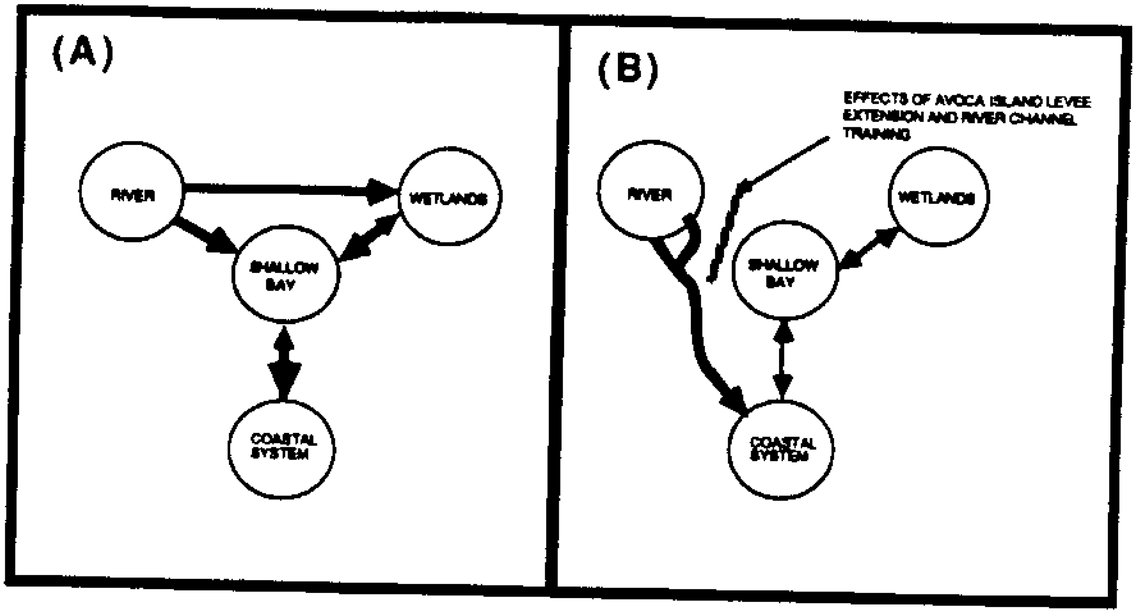

Figure 1. (A) Linkages of riverine inputs to inshore and coastal systems under natural conditions, and (B) linkages of riverine inputs to inshore and coastal systems after freshwater flow to the shallow system is blocked by a protection levee.

dall and Day 1987, Madden 1988), and the dynamics of consumer populations (Deegan and Thompson 1985, Dagg 1988).

Modeling has played an important role in integration of research information. Wells et al. (1984) and Wang (1985) produced models of delta development which explained the growth of new deltas. Wang et al. (1982) developed a model of wetland hydrology to determine the effect of human impacts on regional hydrology. The development of wetland communities in the deltaic cycle was modeled by Rejmanek et al. (1987). Finally, a spatial simulation model was developed to predict long-term habitat succession in the Atchafalaya delta region (Costanza et al. 1986, 1987, Sklar et al. 1985, Sklar and Costanza 1986).

Finally, there has been a conscious effort to design studies whose findings can be applied to management of the area. The two major management issues that have been considered are coastal wetland loss and maintaining the productivity of natural resources such as fish and wildlife. One important issue is the effect of canals and levees, especially the Avoca Island levee extension. Wang et al. (1982) conducted studies of water movement in the area and estimated the effects of alterations on natural hydrology and sediment distribution. The spatial simulation model has been used to determine the effects of human activities on habitat succession over periods of up to 50 years. The ecological studies of the area allow an understanding of the factors supporting natural resource productivity and of the potential impacts of human activities.

The management implications of research in the Atchafalaya delta region were recently summarized in a paper by Day et al. (1987), which drew the following conclusions. (1) Studies of sediment dynamics and vegetation succession in the new Atchafalaya delta have suggested ways in which delta growth can be increased. (2) Older marshes have responded dramatically to increased freshwater, sediment, and nutrient influxes, suggesting that deteriorating marshes can be rejuvenated. (3) Riverine input to shallow inshore lakes and bays stimulates the productivity of these areas in ways that have not been described before. This information can be used to direct fresh water in the coastal zone to stimulate productivity. (4) Westward sediment transport along the coast is leading to accretion along the chenier plain shore. (5) A spatial landscape simulation model has been effective in integrating information and predicting future conditions under various management alternatives.

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PART 2

GEOLOGICAL PROCESSES

THE ATCHAFALAYA DELTA — LOUISIANA'S NEW PROGRADING COAST*

I.L. van Heerden and H.H. Roberts

INTRODUCTION

Delta switching is the major mechanism responsible for building the Louisiana deltaic plain. Upstream diversions occur every 1000 to 2000 years, resulting in changes in the loci of sedimentation and subsequent growth of new delta lobes (Kolb and Van Lopik 1958, Frazier 1967). The Atchafalaya River is the most recent diversion in the delta switching process (Fig. 1).

The Atchafalaya Delta, forming at the mouth of the Lower Atchafalaya River, represents one of the most dynamic geological events in historical times within the Mississippi Delta complex. The Atchafalaya diversion and subsequent delta growth represents the first opportunity to document, from its inception, the evolution of a new delta lobe.

From its junction with the Old River segment of the Mississippi River, the Atchafalaya flows 226 km before entering the sea. In contrast, the Mississippi winds 482 km to Head of Passes and an additional 51 km to the mouth of Southwest Pass. Because of this inherent difference in gradient, a condition favoring abandonment of the modern channel exists. Full flow of the Mississippi River through the Atchafalaya distributary, excluding man's intervention, was predicted by the year 1975 (Fisk 1952). Today the Atchafalaya River is regulated by a U.S. Army Corps of Engineers control structure, completed in 1963 to carry 30% of the combined flow of the Mississippi and Red Rivers.

The subaqueous phase of delta development has been discussed by Cratsley (1975) and Shlemon (1972, 1975). Rouse et al. (1978) monitored the rapid subaerial growth of the Atchafalaya Delta through analysis and interpretation of LANDSAT imagery. Most recently, Roberts et al. (1980) reported on the early evolution of the sand-dominant subaerial phase of the delta. In May

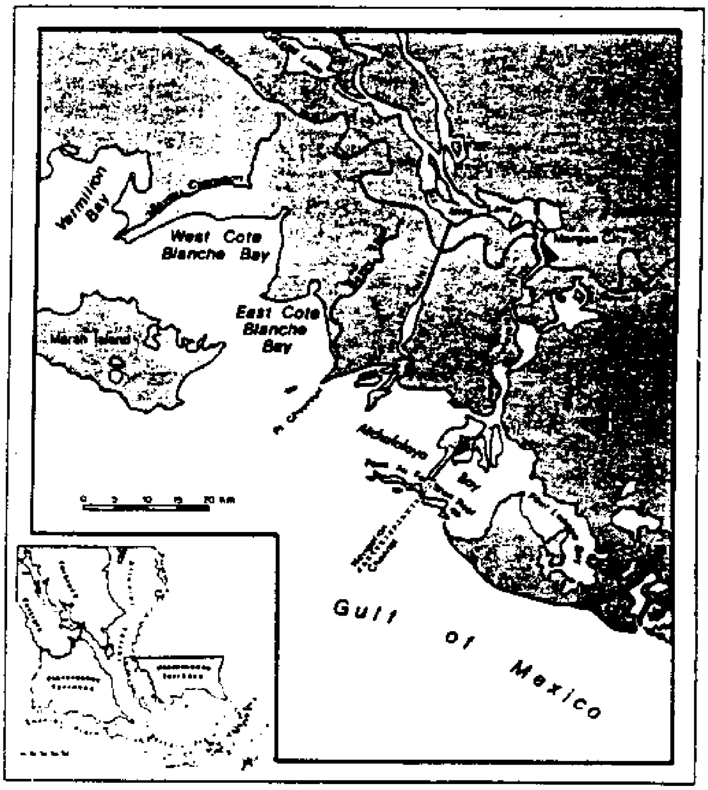

Figure 1. Location of the Atchafalaya Delta.

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*van Heerden, I.L. and H.H. Roberts. 1980. The Atchafalaya delta - Louisiana's new prograding coast. Trans. Gulf Coast Assoc. Geol. Soc. 30:497-506. Used with permission.

1977, a project was initiated by the Center for Wetland Resources, Louisiana State University, with support from NODCOE, to extend previous investigations of the Atchafalaya Delta. The project involved extensive time-series field data collection and was aimed at studying the processes of sedimentation and geomorphic development during the early evolutionary stages of this delta.

This paper presents the results of studies undertaken to determine process-response relationships in sedimentation and channel-lobe morphology, under flood and non-flood conditions. Field work was concentrated in the natural (dredge spill-free) eastern half of the Atchafalaya Delta. This study was structured specifically to provide (1) quantitative assessment of subaerial delta accretion from inception to present, and (2) determination of net gain or loss of sediment and the sedimentological characteristics of channels and interdistributary lobes during flood and non-flood events.

Figure 2. Photomosaic of Atchafalaya Delta, 21 October 1976. Water level M.S.L. -0.75 ft (-0.22 m).

GEOLOGICAL SETTING

The Atchafalaya Delta (Fig. 2) is inherently different from the modern Mississippi Balize delta lobe. Unlike the modern "birdfoot" delta which is spreading sediment on the continental shelf, the Atchafalaya River is building its delta into a shallow bay with an oyster reef barrier forming the seaward margin. The average salinity of the waters in Atchafalaya Bay is 0.37 ppt (U.S. Fisheries and Wildlife Service 1976). These essentially fresh bay waters are well-mixed and unstratified. In contrast, the modern birdfoot distributaries are depositing their sediments in stratified waters, resulting in buoyant spreading of sediment-laden freshwater plumes over saline Gulf water (Wright and Coleman 1974). This phenomenon constitutes and important part of the birdfoot sediment dispersal process. Salt wedge intrusion does not affect the Atchafalaya system.

Tectonic influence on the depositional site strongly distinguishes the modern Mississippi Delta from the Atchafalaya example. Atchafalaya Bay lies on the western boundary of a major subsiding area associated with the Gulf Coast geosyncline (Fisk and McFarlan 1955, Bernard and LeBlanc 1965, Gould 1970). The Pleistocene Prairie Formation here has been downwarped about 30 m in Quaternary time, compared to more than 160 m near the mouth of the present birdfoot delta (Fisk and McFarlan 1955). The relative stability of the Atchafalaya site is also suggested by the presence of numerous shell reefs within the bay, which flourished until recently when they died as a result of fresh-water encroachment and increasing sedimentation.

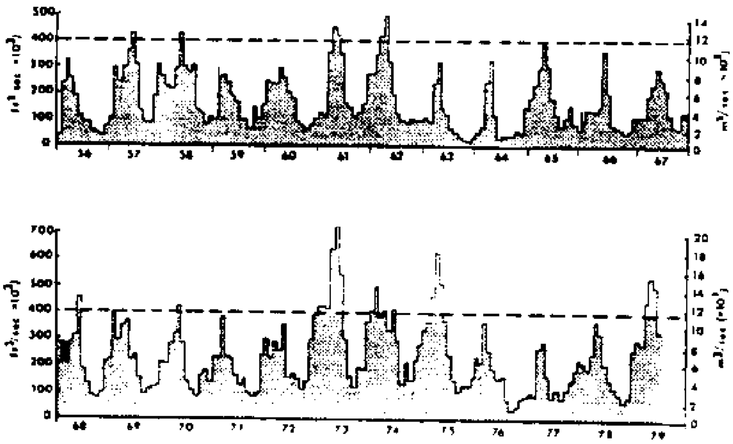

Figure 3. Average monthly discharge of the Atchafalaya River. Modified from Roberts *et al.*, (1980).

HYDROLOGIC REGIME

The annual Atchafalaya River flow, averaged from 1938 to 1972 at Simmesport, near the diversion point in the upper Atchafalaya Basin, is 5,126 cms (USACOE 1974). High flows generally occur between January and June. The average annual peak flow is 11,326 cms. Approximately 70% of the flow at Simmesport now passes through the Lower Atchafalaya River to eastern Atchafalaya Bay, and the remainder passes through the 21-km shortcut to the western part of the bay created by Wax Lake Outlet (Fig. 1).

A comparison of the relative magnitudes of yearly Atchafalaya River floods for the past 24 years, modified from Roberts et al. (1980), is given in Figure 3. During 1956-1972 the Atchafalaya River average monthly discharge exceeded 11,326 cms during only 3 years. During this period the annual peak flow was never exceeded for more than two months out of a year. However, during the flood of 1973, the average annual peak flow was exceeded for 6 months. This pattern was repeated during the following two years, 1974 and 1975 (Fig. 3). the period between 1976 through 1978 an be characterized as average in terms of Atchafalaya River flood discharges. Another major flood occurred in 1979.

Figure 4. Extent of subaerial depositional environments in the fall of each year from 1973 to 1977. Stenciled in are net areas of annual accretion. For simplicity, portions of Delta not shown.

MORPHOLOGICAL CHANGES IN THE EASTERN HALF OF THE ATCHAFALAYA DELTA, 1973-1979

Atchafalaya basin deposition (lacustrine delta fill) and initial delta growth have been summarized by Roberts et al. (1980) and van Heerden and Roberts (1980). As a generalization, the development of the Atchafalaya Delta can be divided into four phases. The first phase (from the late 1500s) was the accretion of clays on the continental shelf and the slow accumulation of fine-grained sediments (bay clays) in Atchafalaya Bay. The period 1952-1962 can be identified as the initial phase of delta-front sedimentation, when significant thicknesses of prodelta-clays began to be deposited in Atchafalaya Bay. From 1962 to 1972 slightly coarser material (silts and some fine sands) began to be introduced and a phase of distal bar and subaqueous bar growth was initiated. In 1973, the subaerial phase of delta development started with the appearance of several small island near the lower Atchafalaya River mouth.

AREA CHANGES

The limits of land exposed in a section of the eastern half of the delta, above the -0.6 m contour in the fall of each year from 1973 to 1979 (excluding 1977), were determined by the combined use and comparison of aerial photography and LAND-SAT (band 7) imagery (Fig. 4). Overall subaerial change from 1976 to 1977 in the Atchafalaya Delta was too minor to be displayed. Total area of subaerial land in this section of the eastern

Table 1. Area of new land in the fall of each year, 1973-1979 (obtained from electronically digitizing the area shown in Figure 4).

Year	Area mi^2	Area km^2
1973	0.2	0.57
1974	0.69	1.79
1975	3.06	7.83
1976	3.23	8.28
1977	—	—
1978	3.44	8.81
1979	4.56	11.68

half of the delta was determined for the fall of each year from 1973 to 1979 be electronically digitizing the area shown in Figure 4 (Table 1).

In the fall of 1973, 0.57 km^2 of former bay bottom was exposed (Fig. 4) at low tide in the eastern half of the delta (Table 1). Growth of new land rapidly continued during the 1974 and 1975 floods (Fig. 4 and Table 1). This dramatic growth rate declined during the minor flood years of 1976, 1977, and 1978. Net increase in new land from fall of 1975 to fall of 1978 was 0.98 km^2, an average of 0.33 km^2 per year. As a result of the major flood that occurred in 1979, 2.87 km^2 of new land appeared (Table 1). This rapid increase in emergent area after the 1979 flood dramatically emphasizes the delta growth response to major floods. These data suggest that subaerial accretion, which has occurred under the impetus of major floods, might not have been so rapid if average-sized floods have occurred since 1972.

Deposition is sporadic when the entire hydrological year is considered. Wave action and levee overwash are effective in reworking lobes between floods. Erosion is most significant in late fall and winter when cold air frontal incursions dominate weather patterns (Rouse et al. 1978, van Heerden and Roberts 1980, and van Heerden 1980).

The emergence of new land appears to follow a bifurcating pattern. Prior to the 1973 flood, the river was divided into two forks by a mid-channel bar, the Poullideux Islands (Fig. 2). The easterly fork, East Pass, underwent a series of bifurcations, beginning in the 1973 flood (Fig. 4). During the 1974 flood, the major channels themselves were bifurcated. In addition, some minor channels branching off East Pass were closed as midchannel bars increased in size and in some cases coalesced. The same processes were repeated in the 1975 flood, extending the bifurcation patterns baywards, while coalescing bars reached farther upstream. During the minor flood years of 1976 through 1978, former small channels and back-bar algal flats tended to emerge (Fig. 4). Heads of bars, situated where large (secondary) channels leave major (primary) channels, increases in size. As a result of the 1979 flood, some subaerial bars coalesced while others prograded bayward. These changes show that progradation of subaerial depositional environments prograde extensively during major floods and development of new subaerial lobes is related to the process of channel bifurcation.

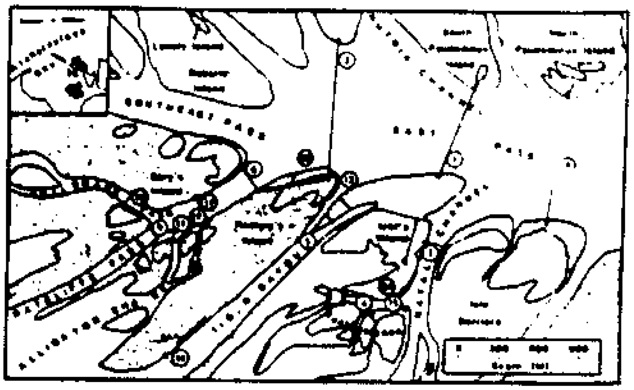

Figure 5. Subaerial lobes and channels of the eastern delta and positions of channel cross sections and subaerial profiles. Numbers indicate location of cross sections.

CHANNEL CHANGES

Channel cross sections reflect changes that the "arteries of sedimentation" undergo during both non-flood and flood periods. Seventeen channel cross sections (Fig. 5) were monitored form 4 to a maximum of 10 times each. Thus, a time sequence of channel profiles was collected from May 1977 to February 1980. In the following discussion, an arbitrary channel classification is used — primary, secondary, and tertiary channels. Size and shape of river channels is generally considered to be a function of the volume and character of the flow, sediment load, type of materials making us the bed and banks of the channel, and character and density of the vegetation (Axelsson 1967).

Primary Channels

Large-scale bifurcations at the river mouth give rise to primary channels. Primary channels in the Atchafalaya Delta are usually greater than 915 m wide, "U" shaped, and continuously experiencing a reduction in cross sectional area (Fig. 6). During major floods, this reduction proceeds as the confining channel levees aggrade. Loss of area due to the 1979 flood might have been larger, but for the fact that as the irregular nature of the channel bottom indicated, a shell dredger was active in East Pass during the spring of 1979.

Primary channels are sites of dynamic mid-channel bar formation (Fig. 7). Subdivision of primary channels creates secondary channels. During the 3-year study

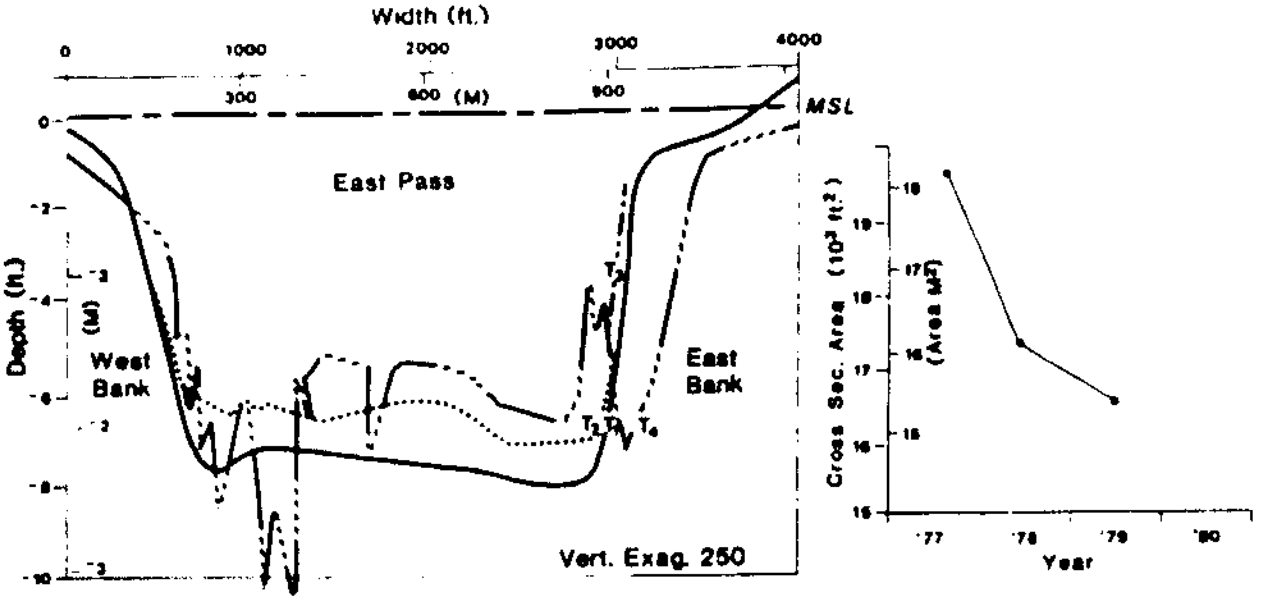

Figure 6. Profiles of channel cross section 1 and cross sectional areas, a primary channel.

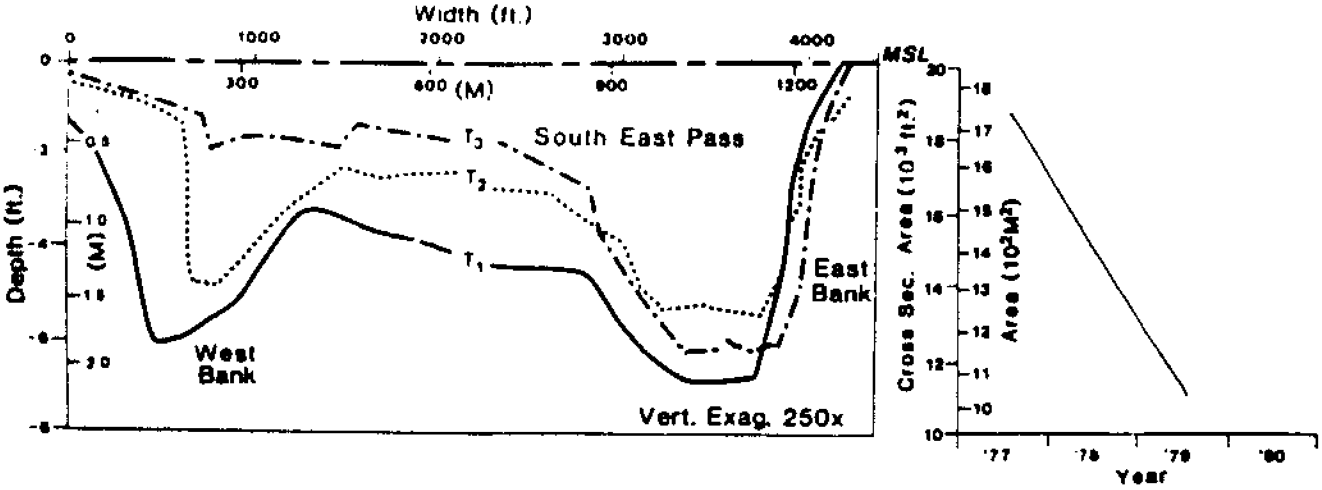

Figure 7. Profiles of channel cross section 2 and cross sectional areas, a primary channel.

period, almost 1 m of sediments was deposited on the mid-channel bar in East Pass. The smallest channel formed in the bifurcations process sealed during this same time period.

Natural channel forks in the Atchafalaya Delta are most often asymmetrical, with the less efficient branch being smaller and diverging at a greater angle from the mother stream. Similar results were reported by Axelsson (1967) from the Laitaure Delta, a lacustrine example Welder (1959) concluded that this mechanism of abandonment of the least efficient channel occurs where discharge is concentrated in one channel in order to attain maximum efficiency of flow. Primary and secondary channels in the Atchafalaya Delta are generally straight, possibly due to the cohesive sediments forming their banks (Axelsson 1967).

Secondary Channels

The heads of established secondary channels in the Atchafalaya Delta are relatively stable features as the cross sectional area did not alter during the minor flood years of 1977 and 1978 (Fig. 8). During the 1979 flood secondary channels deepened, while the levees bordering the channels aggraded a maximum of 0.6 m, leading to a loss of cross sectional area. However, by February 1980, scour of the channel bottom had occurred, which tended to maintain the original cross-sectional area.

Hjulstrom (1935) showed that the relationship between particle size and critical erosion velocity for uniform material revealed an erosion velocity minimum within the particle size interval 0.1-0.5 mm. The critical velocity for erosion normally increases towards both coarser non-cohesive and finer cohesive sediments. For this reason Atchafalaya deltaic channels with fine-grained cohesive banks and minor bed loads are deeper and have steeper banks and better fixed positions and shape than deltaic channels with banks of sand and high bed loads (Axelsson 1967). While heads of secondary channels are seemingly stable, bifurcation occurs in their shallower lower reaches. In order to maintain flow efficiency, one of the minor channels, formed originally from a bifurcation, may become inactive and create a tertiary channel.

Tertiary Channels

Tertiary channels, such as South Natal Channel (Fig. 9), show steady decreases in cross-sectional area through the study period. Generally, tertiary channels shallow downstream as the width and levee height decrease. These essentially closed systems make excellent sediment traps for fine suspended sediment. The "V" shape of tertiary channels appears to result from periods of low water, when the flanks of these channels are exposed and flow occurs only in their deeper parts where tidal scour is important.

Eventually, the channel cross section will be reduced until the channel is no longer hydrodynamically efficient. At this point, the mouth of the channel will start to close due to subaqueous levee construction associated with the mother channel. Sealing due to reverse eddies, as discussed by Welder (1959) for the Cubits Gap area, has not observed in the Atchafalaya Delta. Sealed channels slowly fill with extremely fine sediment introduced from the downstream end by tidal pumping. This entire sequence is displayed be Ivor's Island (Fig. 10). Along the eastern half of the island are 4 channels, each in a different stage of degradation. Channel A is South Natal Channel (Fig. 9), which is undergoing a reduction in cross-sectional area and hydraulic efficiency. Channel B is a former channel which, in places, is still deep but has a closed mouth. After closure, channels fill with fine sediment and marsh vegetation takes root (channel C) until there is almost no trace of the former channel (channel D). Channel-fill sequences act to fuse small subaerial lobes to create a larger lobe.

BIFURCATION PROCESS

The complex network of sand lobes, separated by branching distributaries, characterizes deltas whose river mouths are frictionally dominated and are generally building into unstratified, low-energy, shallow-water environments (Welder 1959, Wright and Coleman 1974). Many theories have been proposed for the appearance of these features (Axelsson 1967, Bates 1953, Welder 1959, and Wright 1977). In Atchafalaya Bay, initiation of mid-channel bar appears to be a consequence of a reduction in suspended-sediment carrying capacity coupled with the formation of subaqueous levees. Suspended sediment concentration, seemingly, is related to current velocity (Allen 1974, Axelsson 1967, Muller and Forstner 1968, Postma 1967, and Ward 1978). Maximum current velocity and, this, maximum suspended load occur in the central portions of rivers. Atchafalaya River, upon entering Atchafalaya Bay, goes from a confined to an unconfined state. A dramatic reduction in depth accompanies this process (Fig. 11). Current velocities at the river mouth undergo a marked decrease from the confined to the unconfined stream state. At the mouths of distributary channels, the reduction in depth is not as dramatic but stream velocity still decreases upon entering the unconfined state. Under these conditions

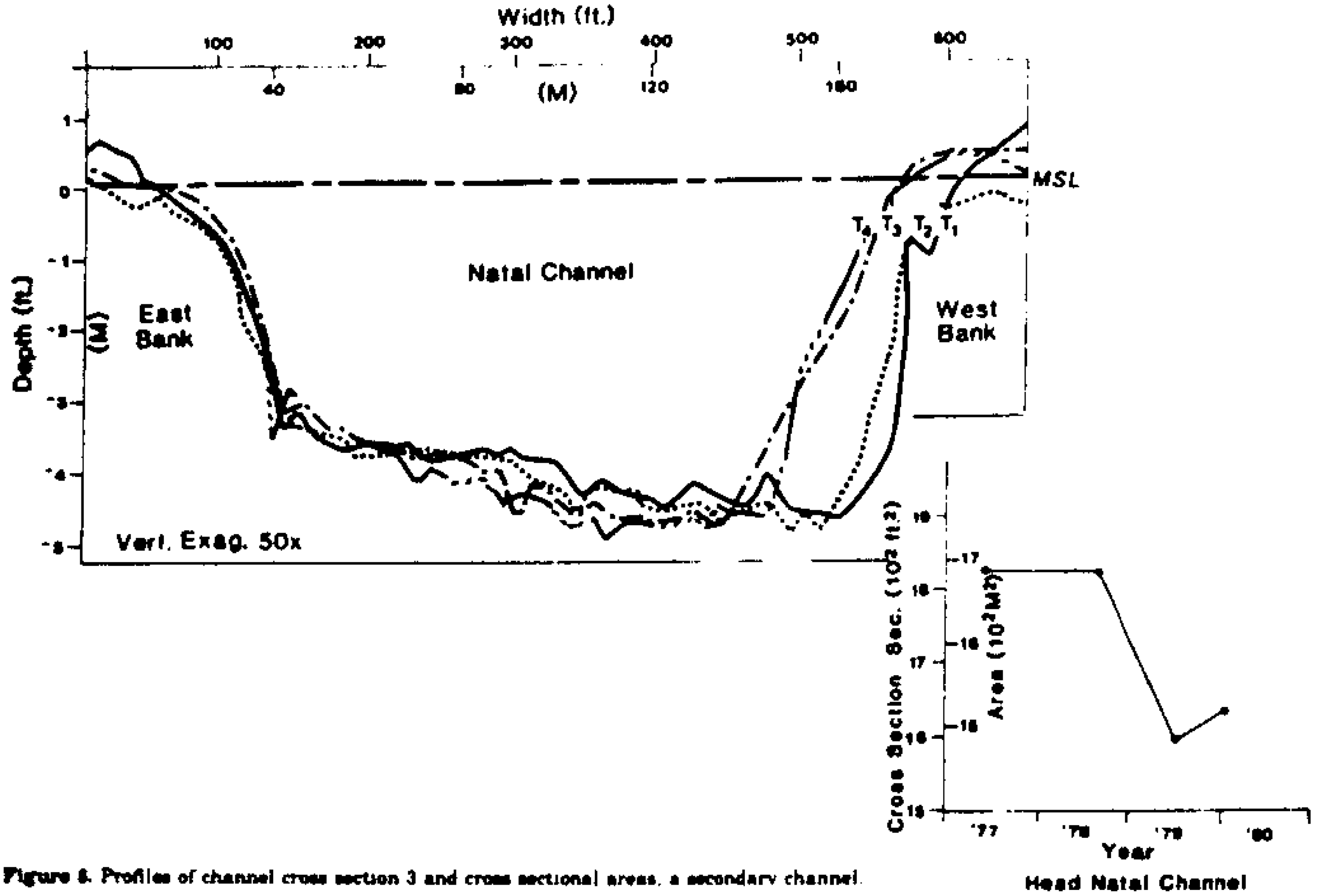

Figure 8. Profiles of channel cross section 3 and cross sectional areas, a secondary channel.

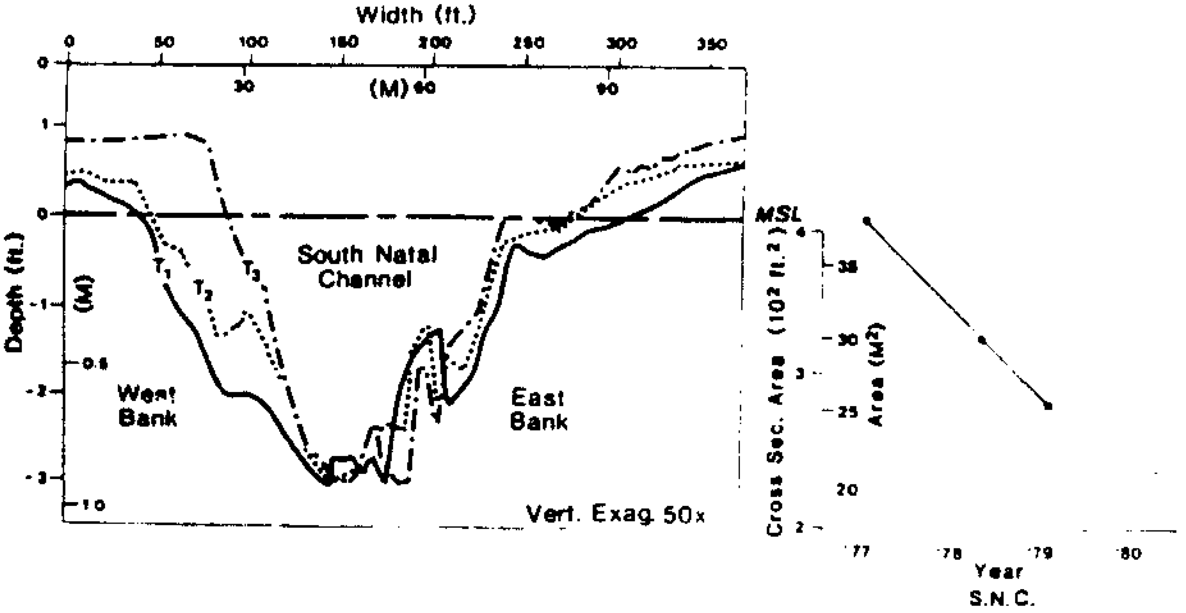

Figure 9. Profiles of channel cross section 6 and cross sectional areas, a tertiary channel.

Figure 10. 1:10,000 aerial photograph of Ivor's Island taken 21 October 1976 showing locations of tertiary channels and position of cross section depicted in Figure 26. A) South Natal Channel. B) Channel with sealed mouth. C) Former channel course. D) Marsh vegetation growing in former channel.

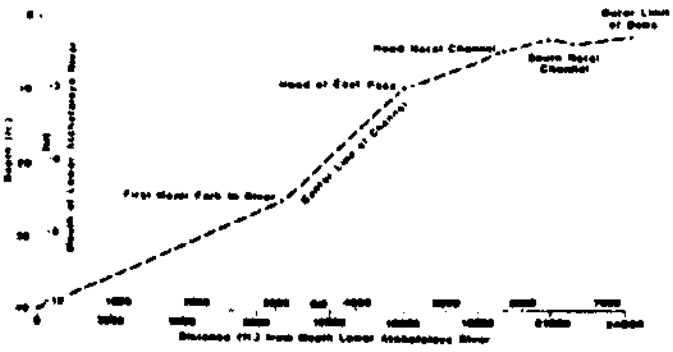

Figure 11. Longitudinal channel profile from mouth Lower Atchafalaya River mouth to mouth of South Natal Channel.

the deep central portions of the stream can no longer support their original high suspended-sediment load. The coarser fraction is thus deposited (Fig. 12a). Due to a larger sediment pool, greater amounts of suspended sediment are deposited in the center of the channel mouth than on the edges. Once initiated, shoaling seaward of the mouth causes an increase in the friction-induced deceleration and effluent spreading, which in turn increases the shoaling rate (Bates 1953, Wright 1977).

The overall effect of the differential sedimentation is a branching of the channel into two distributaries (Fig. 12b). Because frictional resistance per unit volume of flow increases with decreasing channel size, other factors being equal, the channel appears to lose efficiency upon bifurcation (Axelsson 1967, and Welder 1959). This phenomenon is interesting as it would appear that the channel bifurcates not to improve efficiency but because river-mouth dynamics are controlled by bathymetry.

Velocities also decrease away from the center line of the diverging current field. Deposition of coarser sediment takes place, to a large extent, on each side of the center line, giving rise to subaqueous natural levee ridges that eventually accrete into subaerial forms (Fig. 12b). The levee ridges flare away from the mouth, reflecting the diverging current field that results from the abrupt transition to unconfined flow.

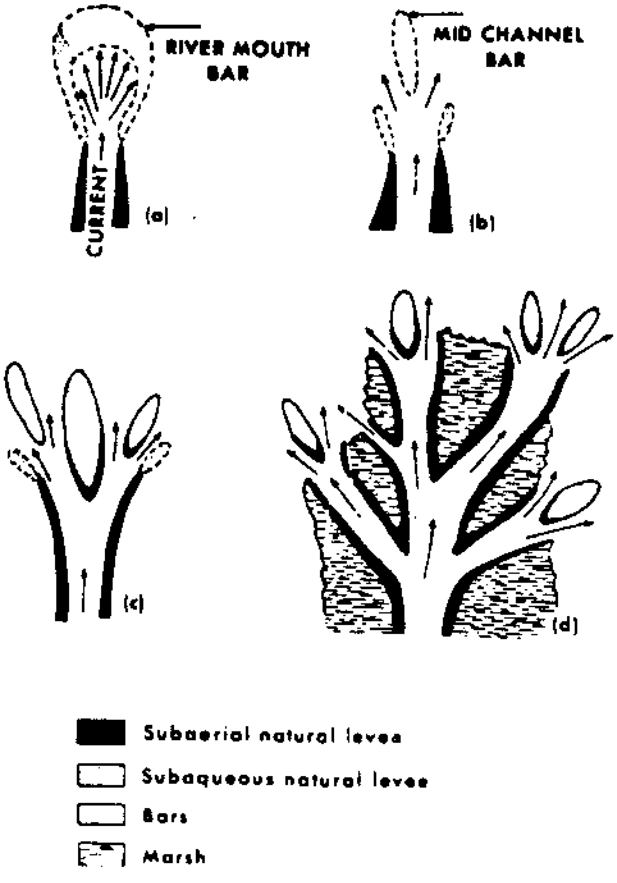

Figure 12. Schematic diagram of delta development.

The same process may then be repeated on the two newly formed channels (Fig. 12c). In the above manner, the subaerial components of the emergent delta have evolved into a complex network of sand lobes separated by branching distributaries (Fig. 12d).

LOBE FUSION

The process of lobe fusion is related to reductions in discharge in distributary channels. Distributary channels in the eastern half of the delta have undergone large reductions in width and, consequently, in cross-sectional area since 1973 (Fig. 4). Measurements from aerial photographs show that by 1979 East Pass had halved its 1973 flow width and, thus, reduced its potential discharge. Lack of flow efficiency in tertiary channels has been shown to be a mechanism of lobe fusion. Continued reduction of discharge in the eastern half of the delta will increase the rate of channel abandonment. This process will in turn lead to further coalescence of minor lobes into larger subaerial features. It is feasible that eventually none of the channels will be able to maintain flow efficiency and the whole eastern half of the delta will be abandoned. Welder (1959) revealed that a reduction in the number of distributaries in the modern Mississippi Delta was accompanied by a reduction in crevasse width. Channel abandonment and subsequent lobe fusion may be the mechanism that leads to the abandonment of Mississippi subdeltas and crevasse splays. However, the reduction in discharge in the Atchafalaya may not be totally a natural phenomenon. The Western fork of the Lower Atchafalaya River (the navigation channel) is maintained by dredging to a minimum depth of 6.1 m and thus carries a greater proportion of the river discharge than if left in a natural site.

In the long term, the eastern half of Atchafalaya Delta will cease to prograde. However, short-term future growth is still possible (Fig. 13). Once the easterly secondary channels have been sealed, the levees along East Pass and South East Pass will aggrade, while areas farther east of these channels will resemble modern Mississippi Delta interdistributary bays. Sediment passing down the navigation channel will be deposited outside the confines of Atchafalaya Bay. A marine delta will eventually develop south of Point au Fer Shell Reef. When the new delta starts building on the inner continental-shelf, buoyant spreading and exposure to waves will be important factors in sediment distribution and delta morphology.

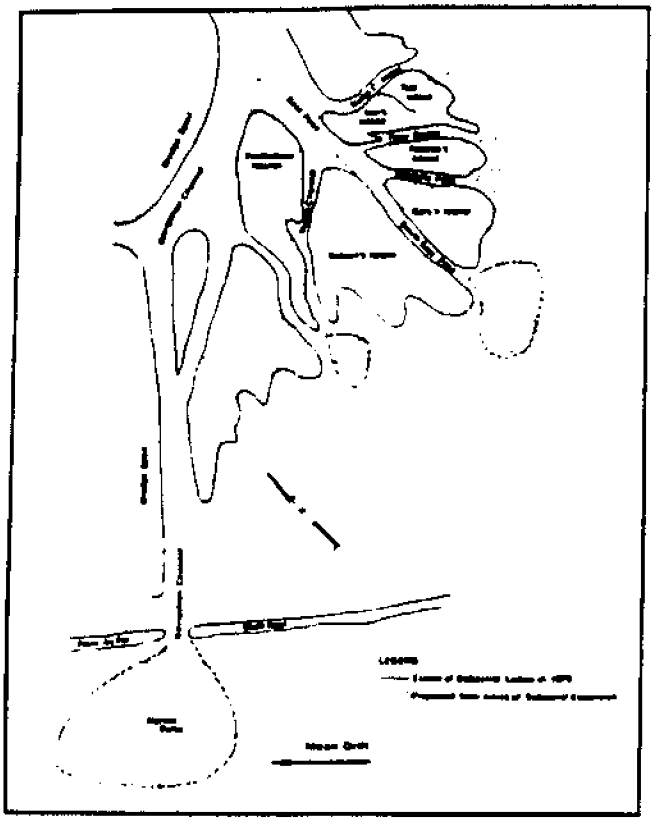

Figure 13. Predicted areas of future delta growth.

SUMMARY AND CONCLUSIONS

Delta switching is the major mechanism responsible for building the Louisiana deltaic plain. Upstream diversions occur every 1000 to 2000 years, the results of which are changes in the loci of sedimentation and subsequent growth of new delta lobes. The Atchafalaya River is the most recent of these diversions. This study, involving extensive field data collection, was designed to investigate the processes of sedimentation and evolution of the initial stage of this important new phase of delta building in the Mississippi River delta complex, through analysis and interpretation of aerial photography and LANDSAT imagery, channel cross-sections, and subaerial profiles, the following conclusions have resulted.

(1) Large increases in the area of subaerial depositional environments occur during major floods. In the section of the eastern half of the delta studied, maximum increases of 2.87 km^2, 1.18 km^2, 6.08 km^2 and 2.87 km^2

occurred in the abnormal floods of 1973, 1974, 1975, and 1979, respectively.

(2) During minor floods, fine-grained sediments are deposited in hydrodynamically inefficient areas. Increases in subaerial exposure are minimal (average 0.33 km^2/yr). Thus, subaerial growth occurs on two activity levels — a high level during major floods and a low level in normal floods.

(3) The processes of Atchafalaya Delta growth are dominated by river mouth dynamics. Different deposition of the suspended load appears to initiate channel bifurcation. Shoaling seaward of the mouth causes an increase in the bed friction-induced deceleration and effluent spreading which, in turn, increases the shoaling rate. The bifurcation process continues as the delta progrades seaward. Natural channel forks in the Atchafalaya Delta are generally asymmetrical. Eventually the smaller channel seals as the discharge is concentrated in one channel in order to maintain flow efficiency.

(4) The mechanisms by which subaerial lobes fuse may be an indication of how crevasse splays are terminated. Distributary channels in the eastern half of the delta are generally undergoing reduction in cross-section due to progradation of subaerial environments. Eventually, cross-sectional area will become so small that flow efficiency will be lost and the eastern half of the delta may be abandoned. At his point, migration of both subaqueous and subaerial levees associated with the main channel will seal East Pass. This process is developing a sizable new sand body along the Louisiana coast. In contrast to the Modern Mississippi River delta, the Atchafalaya should prograde more rapidly, form thinner sand bodies, and eventually cover a wider area much like the Lafourche, St. Bernard, or Teche delta lobes. The ultimate rate of growth and geometry depends on the degree on man's intervention in the delta-building process.

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ATCHAFALAYA MUD STREAM AND RECENT MUDFLAT PROGRADATION: LOUISIANA CHENIER PLAIN*

John T. Wells and G. Paul Kemp

INTRODUCTION

According to the early work of Russell and Howe (1935), the Louisiana chenier plain evolved during the Holocene as a sequence of prograding mudflats that were intermittently partially reworked into sand/shell chenier ridges. More recently, Gould and McFarlan (1959) reconstructed the development of the chenier plain and adjacent shelf from cores using radio carbon dating techniques. Their interpretation indicates that, as sea level rose from -5 m to its present level, a transgressive sequence of marine sediments was deposited over the dissected Pleistocene Prairie Formation, first filling estuaries, then later spreading across shallow-bay and marsh environments.

During the final asymptotic stage of post-glacial rise in sea level some 3000 years ago, the chenier plain began to prograde rapidly, and eventually a wedge of recent sediments 6-8 m thick was deposited to a width of 24 km, thus placing the shoreline roughly where we see it today (Fig. 1). Pulsations of sediment from the Mississippi River, transported by coast-parallel currents, were responsible for the various stages of progradation. At times when the Mississippi River introduced sediment in the vicinity of the present chenier plain, the shoreline shifted seaward; during periods when its course took the discharge farther east, sediment influx to the chenier plain was low and wave attack was able to slow or halt the advance (Gould and McFarlan 1959). Cheniers formed during these latter periods and now stand as "islands" in the marsh.

A new pulse of sediment, the first in some 1000 years, began adding soft muds to the eastern margin of the chenier plain in the late 1940s, coincident with the subaqueous development of a new delta in Atchafalaya Bay (Morgan et al. 1953). Although the delivery of sediment from the Mississippi River down the Atchafalaya River had been in progress since the mid-1500s (Fisk 1952), it was not until the mid-1900s that sedimentation the bay and areas offshore became noticeable. This large-scale introduction of silts and clays to the coast occurred when the inland Atchafalaya basin to the north became essentially sediment filled and sediment began bypassing these basin-lakes for areas tot he south. In the early 1950s Morgan et al. (1953) documented the occurrence of mud deposition along

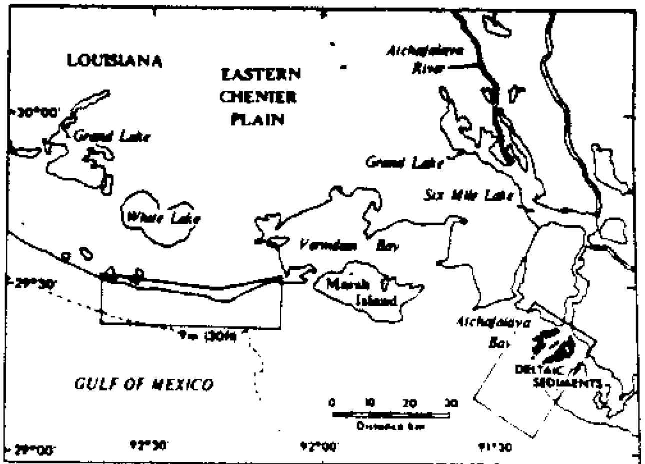

Figure 1. Index map to coast of central and western Louisiana. Enclosed region of Atchafalaya Bay shows source of fine-grained sediments; enclosed segment of chenier plain is present-day downdrift recipient of these sediments.

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*Wells, J.T. and G.P. Kemp. 1981. Atchafalaya mud stream and recent mudflat progradation: Louisiana Chenier Plain. Trans. Gulf Coast Assoc. Geol. Soc. 31:409-416. Used with permission.

approximately 50 km of coast from Marsh Island to Rollover Bayou which, in places, formed broad mudflats up to 2 m thick.

Nearly 30 years have passed since Morgan et al. (1953) first described these coastal mudflats and tied their origin to the Atchafalaya River, to the east. Whereas our understanding of the basic processes for delivering sediments to the eastern margin of the chenier plain (Fig. 1) has remained the same, our ability to monitor these processes has improved significantly. Ready access to satellite imagery, color infrared photography, and digital current-meter data now allows us to monitor remotely shoreline changes and the processes that govern their behavior. In the following paragraphs we report initial observations using these tools in the mud stream-mudflat system of the central and western Louisiana coast.

ATCHAFALAYA MUD STREAM

Turbid water that enters the Gulf of Mexico from the Atchafalaya River and flows along shore as a muddy plume is herein described as the Atchafalaya mud stream. This sediment-laden water is visible from aircraft and shows up well in LANDSAT imagery as partially saturated returns in band 5. Mud stream dimensions vary and are controlled by river discharge, tide stage, wind speed and direction, and residual currents. However, the plume persists throughout the year and trails off to the west in approximately 75 percent of the images (unpublished data compiled by R.H.W. Cunningham, USACOE, New Orleans).

Figure 2A shows the well-defined seaward extent of the sediment plume on February 9, 1979, during rising river stage. This image is typical of many in that turbid water is found not only in Atchafalaya Bay and offshore, but also in the bays to the west. Figure 2B shows suspended sediment concentrations taken on the day of the satellite overpass along a transect that runs down the navigation channel and ends at the seaward edge of the sediment plume. Suspensate concentrations, determined by Millipore filtration, are reported for surface waters only, and thus represent a conservative estimate of sediment throughout the water column.

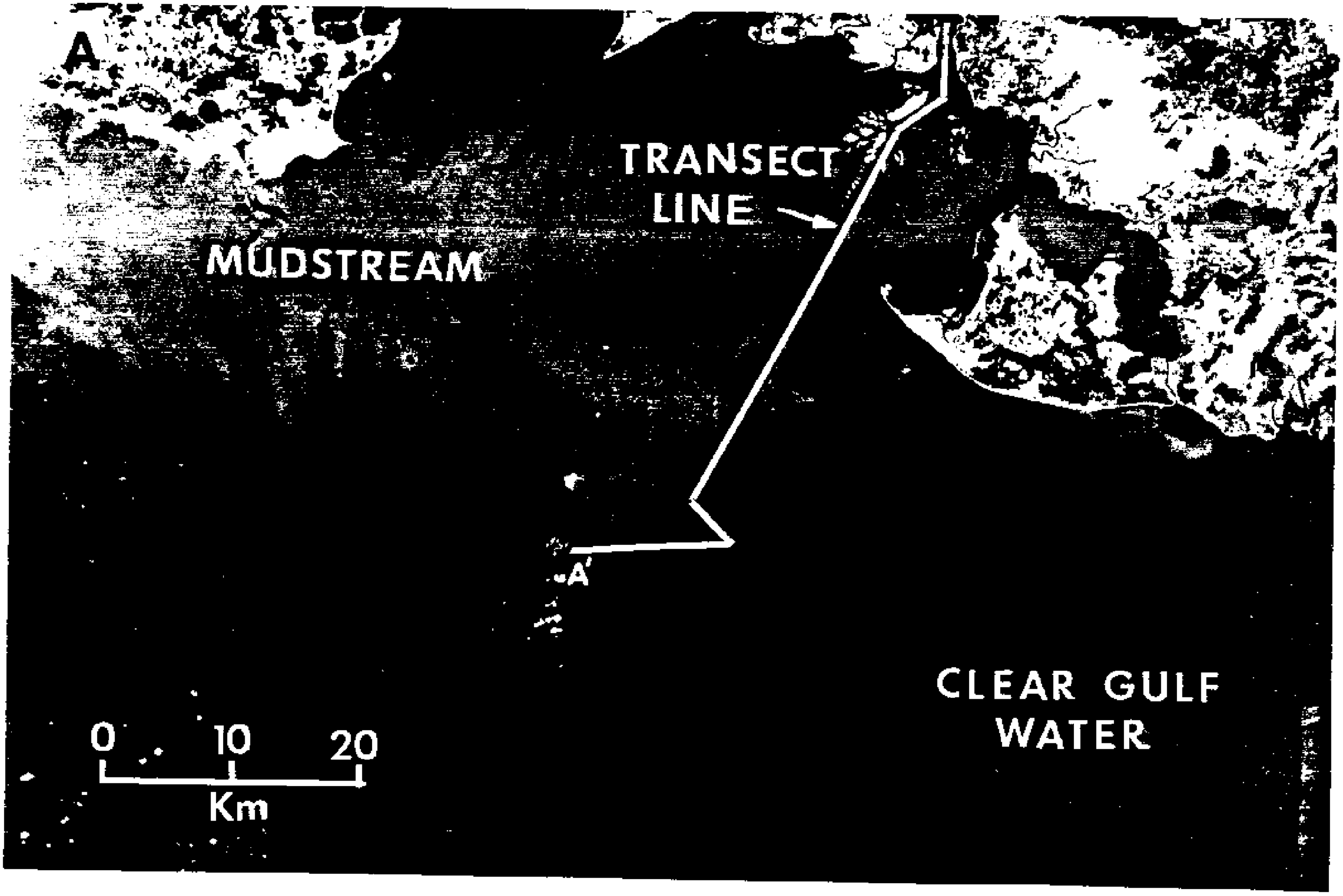

Figure 2a. LANDSAT band 5 image of central Louisiana coast taken on 9 February 1979. Light tones indicate high turbidity.

Within Atchafalaya Bay concentrations range from 250 to 400 mg/l (0 to 20 km, Fig. 2B), but increase to more than 800 mg/l seaward of the shell reef barrier (25 to 35 km). The sudden increase in concentration is perhaps a result of wave resuspension of soft sediments that are deposited rapidly as prodelta clays seaward of the bay mouth. Beyond this extremely turbid zone, concentrations decrease across the shelf to the plume edge (50 to 63 km). Outside the sediment plume, concentrations are 1 mg/l or less.

Composition of sediment in the mud stream is the same as that in the lower Atchafalaya River, primarily silt- and clay-sized particles with median diameters of 2 to 6 microns. Clay mineralogy is montmorillonite, illite, and kaolinite in the ratio 3:1:1. Data reported by Roberts et al. (1980) indicate that 63 percent of the sediment that enters Atchafalaya Bay is silt-and clay-sized. Using a mass to volume conversion of 425 kg/m^3, Wells and Roberts (in press) determined that this silt and clay load is 146 x 10^6 m^3 per year.

Evidence that sediments which enter the Gulf of Mexico from Atchafalaya Bay are transported to the west, as indicated by satellite imagery, is also provided by current meter moorings. Beginning in the spring of 190, current meter data were taken at numerous stations in and seaward of Atchafalaya Bay. Typical records of speed and direction at three of these stations are shown in Figure 3. Data are from mid-depth current meter moorings made with Endeco 174 ducted-impeller, magnetic recording current meters at the locations given in Figure 4. Thirty-five days of data were obtained at station 1, five days at station 2, and over a year of continuous readings have been obtained at station 3.

Current speeds on the inner shelf at station 1 are typically 10-30 cm/sec; direction of flow, although setting to the northwest, is influenced strongly in this February data set by the passage of cold fronts every 5 to 7 days, which sequentially produce winds first from the southwest, then from the northwest. Current speeds at station 2, just outside the bay, are 10 to 50 cm/sec and occur as well-defined pulses related to stage of the tide. Direction, however, does not fully reverse as a result of tidal effects, but instead is dominated by river flow to the south from Atchafalaya Bay and flow to the west from the westerly drift component of coastal waters. In Atchafalaya Bay current speeds are substantially higher, reaching values of 40 to 80 cm/sec. Rise and fall in current speed is coincident with tidal period in the bay. Direction of flow is oriented down the navigation channel and does not change with stage of the tide.

Residual currents computed from these records are shown in Figure 4. The overall pattern is that of strong flow down the axis of the navigation channel, spreading

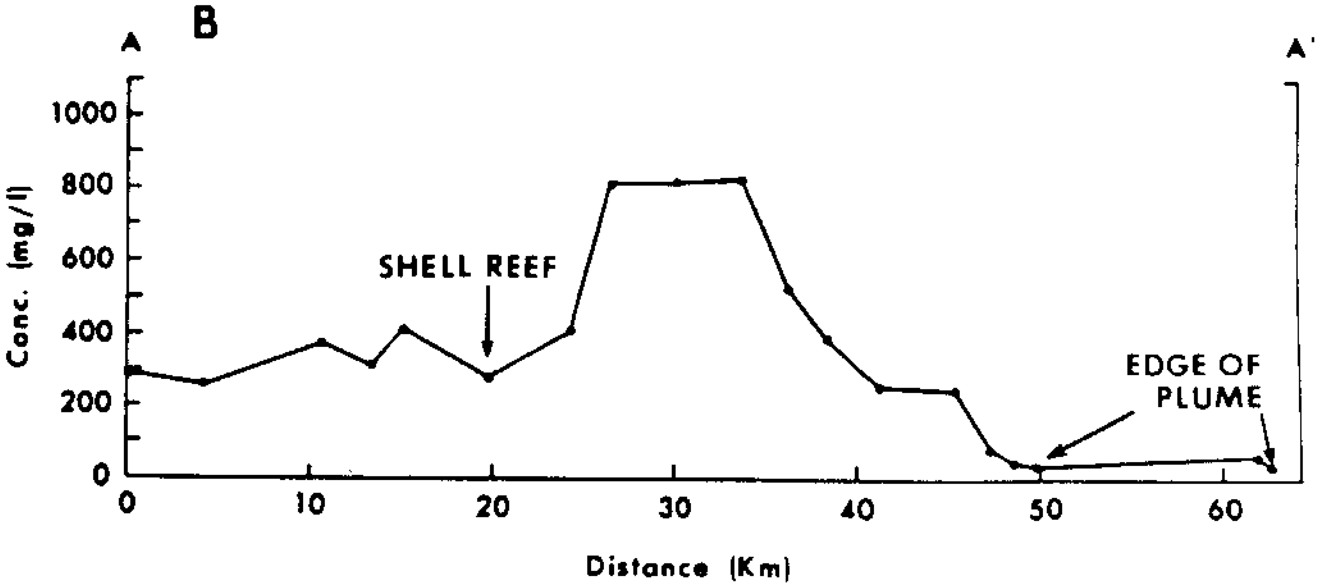

Figure 2b. Suspensate concentrations along transect line A-A' from lower Atchafalaya River outlet to seaward edge of sediment plume (data courtesy R. H. W. Cunningham, USACOE, New Orleans)

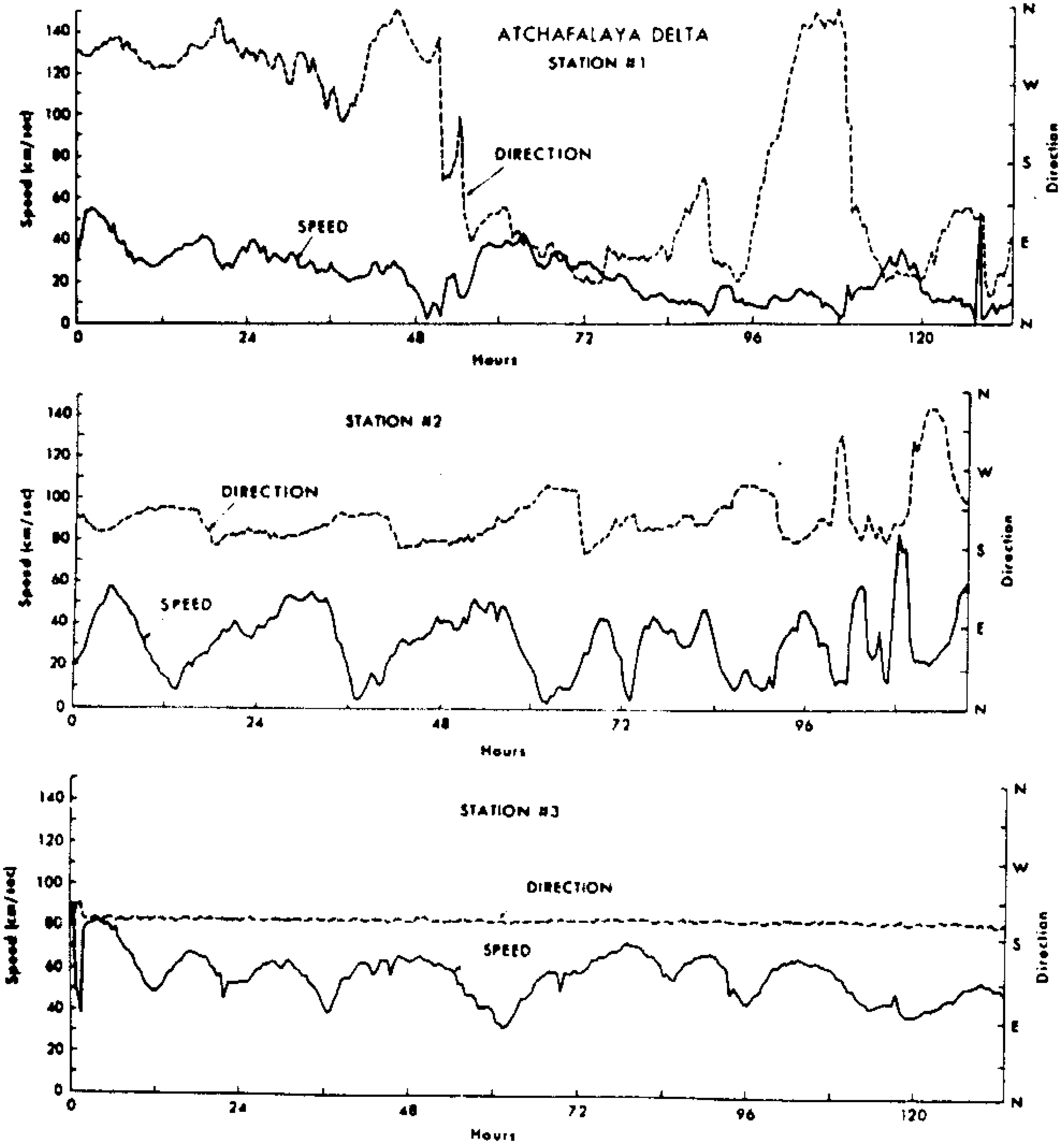

Figure 3. Time series of current speed and direction taken in and seaward of Atchafalaya Bay in spring 1980. Station locations given in Figure 4.

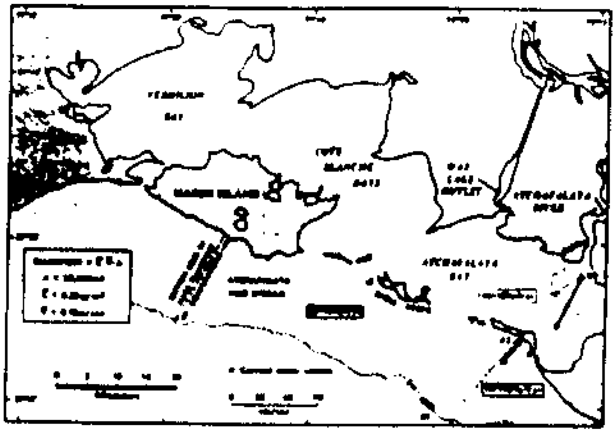

Figure 4. Central Louisiana coast showing Atchafalaya mud stream and volume flux of sediment into and through the Atchafalaya system. Greater than 50×10^6 m^3/yr of silt and clay is transported to the eastern margin of the chenier plain. Current meter stations and residual current vectors are numbered.

and reduction in speed on reaching the Gulf of Mexico, then deflection to the west on the inner shelf. Analysis of current data taken on the shelf farther to the west (longitude 93° 30') also indicated residual flows to the west (Crout and Hamiter 1981).

First-order approximations of sediment mass transported in the Atchafalaya mud stream have been made by taking the product of average suspensate concentration, cross-sectional area of the mud stream, and average drift speed of currents (Fig. 4). Conversion of volume transport is made using a density of 375 kg/m^3 (Wells and Roberts, in press). When converted to transport per year, the volume of sediment moving in the Atchafalaya mud stream is 53×10^6 m^3, almost half of the volume of sediment that leaves Atchafalaya Bay.

RECENT MUDFLAT PROGRADATION

Deposition of fine-grained sediments from the Atchafalaya mud stream can be noted by the transitory mudflats that have formed along the eastern margin of the chenier plain. Areas of mudflat accumulation were determined from color infrared photographs taken in October 1974 and October 1978 (NASA Missions 74-293 and 78-148, respectively), from 1974 orthophotoquads, and from aerial and ground reconnaissance in 1974, 1979, and 1981. Results of these photo and ground comparisons, together with Adams et al. (1978) for the period 1954-1969, are shown in Figure 5.

Three patterns have been recognized during the 12-yr period from 1969 to 1981: 1) simultaneous erosion and accretion at the shoreline, 2) increasing length of shoreline fronted by mudflats, and 3) shift in the locus of sedimentation to the west. No attempt has been made to plot previous shorelines, and our contention is simply that the presence of mudflats indicates an instantaneously prograding shoreline (Fig. 6A). The segments of coast between mudflats are typically those that are eroding most rapidly (Fig. 6B). The processes of erosion and accretion are cyclical in both time and space, as becomes evident from close examination of Figure 5.

Because of low tide range (0.5 m), intertidal exposure of mudflats are only 100-300 m wide. However continuity of a single mudflat along shore may exceed 5 km (Fig. 5). The upper 1 to 2 m are often a gel-like fluid mud that thins both landward and seaward. Although the subtidal extent of mudflats is known, patches of fluid mud have been found 5 km offshore.

The major effect of subtidal muds is to attenuate incoming wave energy, thus creating conditions favorable for further sedimentation (Wells and Coleman, in press; Wells and Roberts, in press). Formation of mudflats, then, is the first stage in the feedback loop between coastal energy and shoreline response, which eventually leads to stabilization and progradation.

Newly deposited muds are easily eroded and are often ephemeral features because of their low bulk density (1.25-1.35 g/cm^3) and high water content (60 to 80 percent). Longshore currents generated by incoming waves redistributed these fine-grained sediments in such a way that mudflats appear to move along the coast in a westerly direction, leaving a trail of unconsolidated material in their wake. Although localized hurricane mudbank deposits have become permanent shoreline features in the rcent past (Morgan et al. 1958), there is little evidence that large-scale mudflats stabilization by marsh vegetation presently occurs under normal conditions.

Volume calculations show that more sediment reaches the chenier plain via the Atchafalaya mud stream than appears as new mudflats. For example, if a typical mudflat has a volume of 1 to 2×10^6 m^3, then 25 to 50 such mudflats could form each year. Since new mudflats have not been observed to form at this rate, much of the sediment be spread across the inner shelf as a thin veneer over a longshore distance of perhaps 100 km or more. Shelf studies are currently underway to examine sedimentation rates and to refine our understanding of the sediment dispersal system.

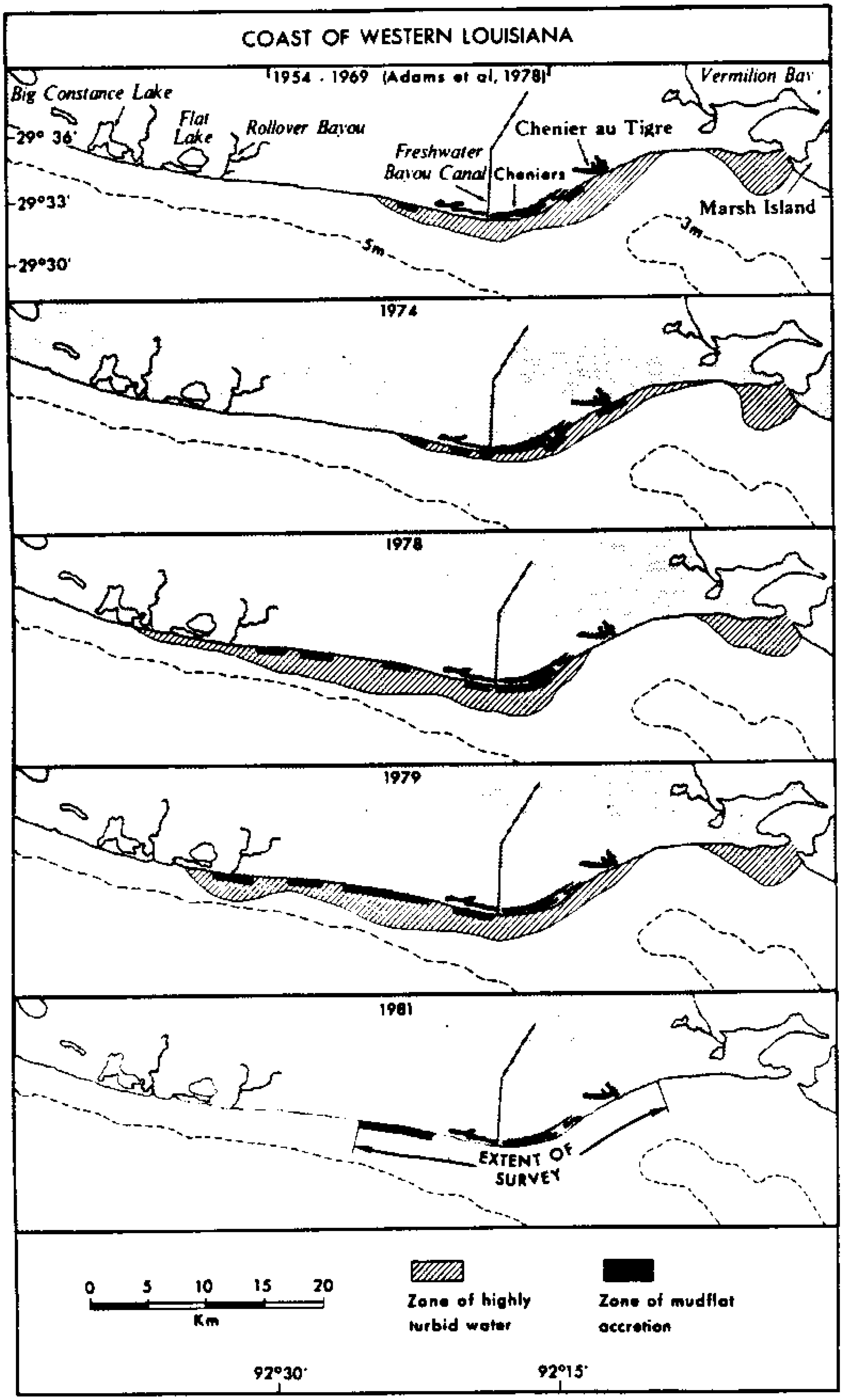

Figure 5. Areas of mudflat accretion from 1969 to 1981. Segments of coast between mudflats are generally eroding. Note shift in sedimentation to west.

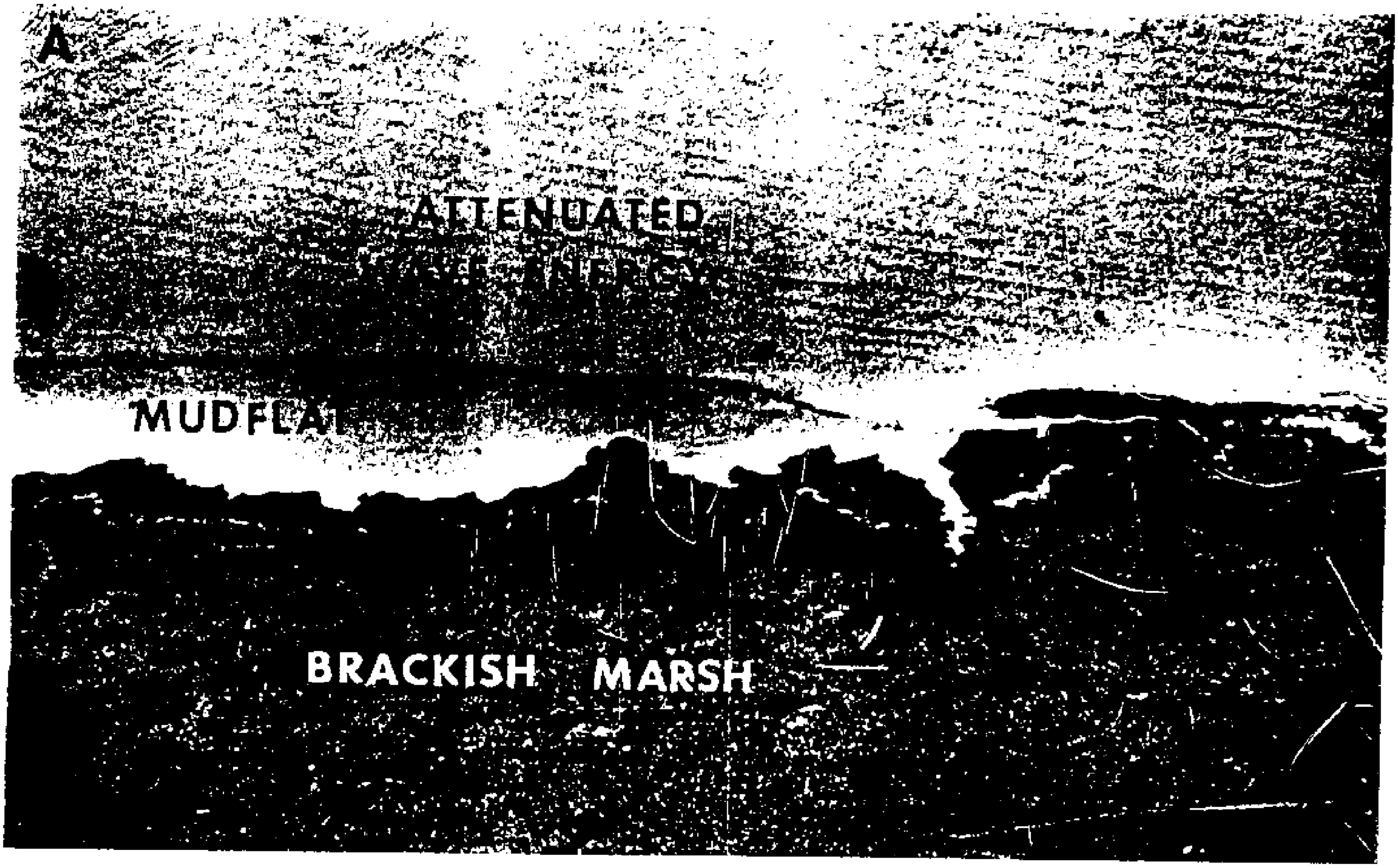

Figure 6a. Coastal mudflat, vicinity of Chenier Au Tigre. Width of intertidal zone is approximately 150 m.

CONCLUSIONS AND IMPLICATIONS TO FUTURE DEVELOPMENT

1) The chenier plain of southwestern Louisiana is presently receiving a major new influx of fine-grained sediment from the Atchafalaya River to the east, the first such sediment pulse in recorded history.

2) Sediment is delivered by the Atchafalaya mud stream, a westerly flowing band of turbid water that may extend 20 km offshore.

3) Growth of the chenier plain appears initially to be by a series of transitory mudflats, a few of which become welded at the shoreline.

4) The pattern of mudflat sedimentation is increasing and shifting to the west, consistent with the direction of coastal and wave-induced currents.

5) The Atchafalaya mud stream transports more sediment, by an order of magnitude, to the chenier plain than can be accounted for in yearly mudflat accretion.

Future development of the chenier plain will be tied intimately to the fate of Atchafalaya Bay. The good time correlation between subaqueous deltaic sedimentation in the bay and the first appearance of mudflats near Chenier au Tigre (both in the 1950s) established the relationship. Further evidence was provided when abnormally high river discharge in 1973-75 correlated well with a renewal of mudflat development after a period of erosion in the 1960s. Accelerated growth of the chenier plain is expected when Atchafalaya Bay becomes sediment filled, thus allowing an even greater volume of sediments to enter the dynamic shelf region seaward of the bay.

The ephemeral nature of these mudflats suggests that the process of shoreline progradation has just begun to accelerate. As a result, we hypothesize that the initial stage of coastal progradation from a new sediment pulse is one of transitory mudflats only. As sedimentation continues, new mudflats will appear and merge with existing mudflats. At its peak of development, the shoreline will become "choked" with fine-grained sediment, mudflats will stabilize and grow seaward, and new marsh vegetation will become established. The time scale for widespread reversal in present coastal erosion is perhaps 50 to 100 yr.

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Figure 6b. Eroding marsh between mudflats, vicinity of Freshwater Bayou.

PART 3

CHEMICAL STUDIES

SEDIMENT-WATER OXYGEN AND NUTRIENT FLUXES IN A RIVER-DOMINATED ESTUARY*

K.G. Teague, C.J. Madden, and J.W. Day, Jr.

INTRODUCTION

Rivers can contribute to the availability and long-term accumulation of inorganic nutrients and organic matter in estuaries through high nutrient loading (Ho and Barrett 1977, Nixon 1981a, Nixon 1981b, Stanley and Hobbie 1981). Several studies have shown sediment-water fluxes of nutrients to be important nutrient sources to estuaries as well (Nixon et al. 1976, Boynton et al. 1980, Nixon et al. 1980, Callender and Hammond 1982, Fisher et al. 1982, Boynton and Kemp 1985). Alternatively, sediments may be a sink for nutrients in the water column (Boynton et al. 1980, Callender and Hammond 1982) in which case riverine inputs may be removed from the estuary through sediment processes. Riverine sediment loading may affect sediment-water nutrient fluxes directly by the addition of organic matter and adsorbed inorganic nutrients, by affecting redox equilibria, or indirectly by the formation of estuarine wetlands which may influence the nutrient and organic matter mass balances of estuaries (Nixon 1980). Water depth can determine the significance of sediment-water nutrient fluxes to the water column by controlling the size of the nutrient pool and the degree of coupling of near-surface and bottom processes (Nixon et al. 1976).

Relatively few sediment-water flux studies have been done in estuaries. All of the published studies of estuarine sediment-water fluxes been from estuaries with low riverine input, low sedimentation rates, moderate water depth, and low proportion of wetland to open water area (Table 1), providing a narrow range of estuarine types on which to base new hypotheses, or to assess existing ones. Here we report *in situ* measurements of sediment-water oxygen and nutrient fluxes from coastal Louisiana, in an estuary with exceptionally high rates of riverine input and very shallow depth.

AREA DESCRIPTION

Fourleague Bay is a 9300 ha estuary located in south-central Louisiana, USA (Fig. 1). It is shallow (mean = 1.5 m), receives high river input, and is characterized by low tidal amplitude, fine-grained sediments, high suspended sediment loads and nutrient concentrations, and a high wetland/water ratio (0.73). The Atchafalaya River carries approximately 30% of the combined flow of the Mississippi and Red Rivers and empties directly into Atchafalaya Bay and Fourleague Bay. Peak annual discharge averages 11,300 $m^3\ s^{-1}$ (Roberts et al. 1980) and normally follows a temperate seasonal pattern with a spring peak and a fall-winter minimum.

Fourleague Bay is surrounded by expanses of fresh, brackish and saline marshes (Chabreck 1972), and an extensive, rapidly emerging delta is forming at the mouth of the river (Roberts et al. 1980). The hydrodynamics of Fourleague Bay are complex, influenced by river discharge, tides (0.3 m), and meteorological events (Wax et al. 1978, Denes 1983). During spring, a large volume of fresh water enters Fourleague Bay from Atchafalaya Bay and flows southeast through Oyster Bayou to the Gulf of Mexico. During summer and fall, high salinity Gulf water enters the estuary through Oyster Bayou. Vertical strati-

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*Teague, K.G., C.J. Madden, and J.W. Day, Jr. In press. Sediment-water oxygen and nutrient fluxes in a river-dominated estuary. Estuaries.

Table 1. Selected physical characteristics and sediment-water fluxes of various estuaries with published sediment flux estimates.

Characteristic	Atchafalaya-Fourleague	Patuxent	Narragansett Bay	Potomac	Neuse	San Francisco Bay
Mean river discharge ($m^3 s^{-1}$)	5700[1]	14[5]	52[9]	306[10]	55[11]	600[13]
Inorganic nitrogen loading ($gN m^{-2} s^{-1}$)	57[2]	11[6]	5[9]	20[6]	12[12]	92[6]
Mean depth (m)	1.5[1]	3[5]	8.8[9]	7.3[10]	3[11]	6.1[13]
Wetland/water ratio*	0.73[3]	0.20[7]	0.02[9]	—	–	0.12[14]
Salinity range (ppt)	0-24[2]	6-13[5]	20-30[9]	—	–	0-35[15]
Temperature range (°C)	7-35[3]	0-30[5]	0-24[9]	—	–	7-25[15]
Sedimentation rate ($cm\ y^{-1}$)	1.1-2.1[4]	0.5-3.7[5]	0.03-0.04[9]	—	–	0.01-0.1[16]
O_2 flux ($mg\ m^{-2} hr^{-1}$)	0 to -143[17]	21 to -171[5]	-10 to -150[9]	-30 to -104[10]	-5 to -69[11]	——
NH_4^+ flux ($\mu mol\ m^{-2} hr^{-1}$)	-157 to +758[17]	-50 to +1577[5]	0 to +400[9]	+2 to +875[10]	+71 to +454[11]	+167[19]
NO_3^- flux ($\mu mol\ m^{-2} hr^{-1}$)	-1839 to +908[17]	-674 to +700[5]	-30 to +110[9]	—	0 to +8[11]	——
PO_4^{3-} flux ($\mu mol\ m^{-2} hr^{-1}$)	-231 to +46[17]	+1 to +295[5]	0 to +60[18]	+4.1 to +82[10]	–	——
DON flux ($\mu mol\ m^{-2} hr^{-1}$)	-4851 to +4484[17]	-428 to +216[5]	+100 to +400[9]	—	–	——
DOP flux ($\mu mol\ m^{-2} hr^{-1}$)	-414 to +978[17]	-11 to +34[5]	-5 to +15[18]	—	–	——

[1] Denes 1983
[2] Madden 1986
[3] Bahr et al. 1983
[4] Smith et al. 1985
[5] Boynton et al. 1980
[6] Jaworski 1981
[7] Cassell 1985
[8] Oviatt and Nixon 1975
[9] Nixon et al. 1976
[10] Callender and Hammond 1982
[11] Fisher et al. 1982
[12] Matson et al. 1983
[13] Peterson 1979
[14] Josselyn 1983
[15] Conomos et al. 1979
[16] Graham 1974
[17] This study
[18] Nixon et al. 1980
[19] Hammond and Fuller 1979
* Dimensionless ratio (not % wetland)

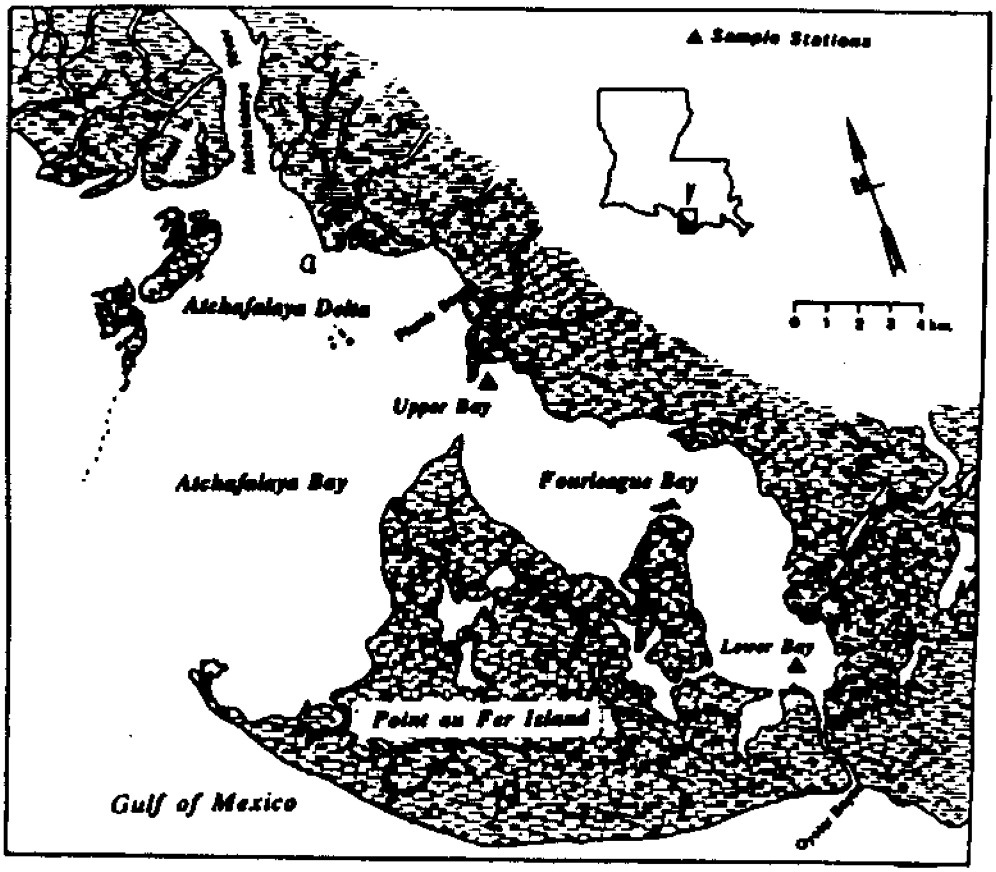

Figure 1. Atchafalaya and Fourleague Bay in Louisiana. Locations of upper and lower bay study sites are marked by triangles.

fication of the water column has only been observed in deeper channels draining into and out of the bay, while horizontal stratification is common throughout the bay (Madden 1986).

Stations for flux measurements were located in upper and lower Fourleague Bay to bracket the extremes of riverine and marine characteristics in the estuary (Fig. 1). At the upper station, salinity is consistently low, averaging <1 ppt. At the lower station salinity is highly variable, often reaching 25 ppt NH_4^+ in the water column exhibits spatial and temporal heterogeneity, with an average annual concentration of 2.9 µM throughout the bay. NO_3^- concentrations average 60 µM in the upper bay and 19 µM in the lower bay (Madden 1986). However, NO_3^- concentrations in the lower bay are highly variable, ranging from 0.1 to 60 µM. NO_3^- concentrations in the Atchafalaya River have reached 180 µM (Madden 1986). Inorganic nitrogen loading from the river has been estimated from three intensive time series studies of water flux and NH_4^+ and NO_3^- concentrations, and averages 57 gN $m^{-2}s^{-1}$ (Madden 1986). In addition, there is preliminary evidence of net input of nutrients and organic matter to the bay from surrounding wetlands (Stern et al. 1986). Sediments in the bay consist primarily of silt and clay (Barrett 1971) but consistencies vary. In the upper bay, sediments are firm and highly cohesive, while at the lower bay they are nearly fluid in consistency. Net sedimentation rates in the bay range from 1.1 to 2.1 cm yr^{-1} (Smith et al. 1985) and organic matter content of the sediments averages about 3.75 % by weight (Teague 1983).

METHODS

Sediment-water oxygen and nutrient fluxes were measured in situ seven times between August, 1981 and May, 1982, using four opaque, 25 L plexiglass domes covering 0.16 m^2 of sediment surface. A horizontal flange and vertical edge enabled easy penetration of the chamber into the sediment, yet prevented over-insertion and insured consistent chamber volume. Nutrient concentrations were measured in four chambers, while dissolved oxygen was measured in two (YSI polarographic oxygen electrodes). Chambers were equipped with submersible pumps to maintain water motion. Water samples were pumped to the surface through tygon® tubing (25 cc volume) which was purged before sampling. Withdrawals from the chambers during entire incubations resulted in replacement of less than 1% of chamber volume with outside water. A small vent (1.0 mm) at the top of the chamber insured that samples withdrawn from the chambers were replaced by the water column, not by sediment interstitial water.

Before beginning each incubation, water column dissolved oxygen, temperature, and salinity were measured and samples were collected for determination of water column NH_4^+, NO_3^-, PO_4^{3-}, dissolved organic nitrogen (DON), and dissolved organic phosphorus (DOP). Dissolved oxygen was monitored at 0.5 hr intervals during 3-5 hr incubations. Dissolved oxygen meters were calibrated against Winkler titrations in the laboratory and using standard calibration tables in the field.

All water samples collected before and during the incubations were filtered through pre-rinsed Millipore type AP glass fiber prefilters (mean pore size 0.65 µm) and frozen immediately on dry ice for later laboratory analysis. Water samples were drawn from chambers hourly, filtered, and preserved as described. All nutrient analyses were performed using the Technicon autoanalyzer, according to U.S. Environmental Protection Agency methods (1979). Salinity was determined in situ with a Beckman RS-5 induction salinometer.

Sediment-water oxygen and nutrient fluxes were calculated from changes in concentrations in the chambers over time. Dark bottles (1L) were incubated with bottom water to estimate water column contribution to oxygen uptake and nutrient fluxes. Estimates of water column oxygen and nutrient fluxes were subtracted from sediment chamber measures of oxygen and nutrient fluxes to evaluate oxygen uptake and net nutrient fluxes attributable to sediment processes alone.

Net sediment-water fluxes were calculated using the following formulas:

$$\Delta N/\Delta T_{(dome)} = (N_j - N_i)/T$$

$$\Delta N/\Delta T_{(bottle)} = (N_j - N_i)/T$$

$$\Delta N/\Delta T_{(net)} = ((\Delta N/\Delta T_{(dome)} - \Delta N/\Delta T_{(bottle)}) \times 25\ l)/0.16\ m^2$$

Where:

$\Delta N/\Delta T$ = Rate of change of O_2 or nutrient

N_j = Ending O_2 or nutrient concentration

N_i = Beginning O_2 or nutrient concentration

T = Duration of experiment

Annual fluxes were computed by calculating the arithmetic means of all replicate chamber measurements for each measurement period and station and then calculating the arithmetic means of these by station. Positive fluxes indicate net release from the sediments to the water column, while negative fluxes indicate net uptake by the sediments.

Sediment pore water profiles of NO_3^- were obtained in October, 1981 using pore water "peepers" (Hesslein 1976). Each of 50 cups along the length of the 1 m long peeper was filled with about 10 ml of distilled water under a pure nitrogen atmosphere. The peeper cups were covered with dialysis membrane which was held firmly in place by a frame. In the field the apparatus was gently driven vertically into the sediment so that the water in the peeper cups was in contact, through the dialysis membrane, with the sediment interstitial water to a depth of about 75 cm. After a 1 week equilibration, the peeper was withdrawn, water samples were collected from the cups with a hypodermic syringe, injected into plastic vials, frozen on dry ice, and analyzed for dissolved nutrients in the laboratory.

NO_3^- vs salinity plots were generated using data from transects from the Atchafalaya River through Fourleague Bay. Details of interpreting mixing diagrams such as these may be found in Liss (1976). Water samples were collected, preserved, and analyzed, and salinity measured, as previously described.

Atomic ratios of O/N of the sediment-water fluxes were calculated using only positive inorganic nitrogen fluxes. Means of the ratios were calculated by each measurement period and station, and then for the duration of the study. Only positive fluxes were used in this analysis since negative fluxes do not reflect nutrient regeneration processes. Similarly, N/P ratios are not presented because of the numerous negative ratios measured.

RESULTS

Ambient Conditions

River discharge varied from 2000 to 10,000 m^3s^{-1} during the study and peaked in spring. Water temperature ranged from 7.5-29.9°C. Salinity was usually low, ranging from 0-19.0 ppt, and was higher in the lower bay than in the upper bay. As river flow increased, average salinity in the bay decreased and nutrient concentrations increased. Dissolved oxygen in the water column was always above 3 ppm, and was often near saturation even at the sediment interface. Water column concentrations at the two study sites ranged as follows: NH_4^+: 0.6-16.8 µM; NO_3^- : 0.1- 84.5 µM; PO_4^{3-}: 0.1-1.6 µM; DON: 6.2-113.1 µM; and DOP: 0.0-17.6 µM, during flux measurements. NO_3^- and DON were significantly higher at the upper bay, and displayed a strong seasonality related to river discharge (Figs. 2a,c). Nitrate vs salinity plots indicate that the river was the main source of NO_3^-, and the bay was a strong sink for NO_3^- (Fig. 2b). A profile of NO_3^- from the overlying water into the sediment at the upper bay station showed values decreasing from 36 µM in the bottom water to 10 µM in the surface sediments and further decreasing with depth. At the lower bay, low NO_3^-

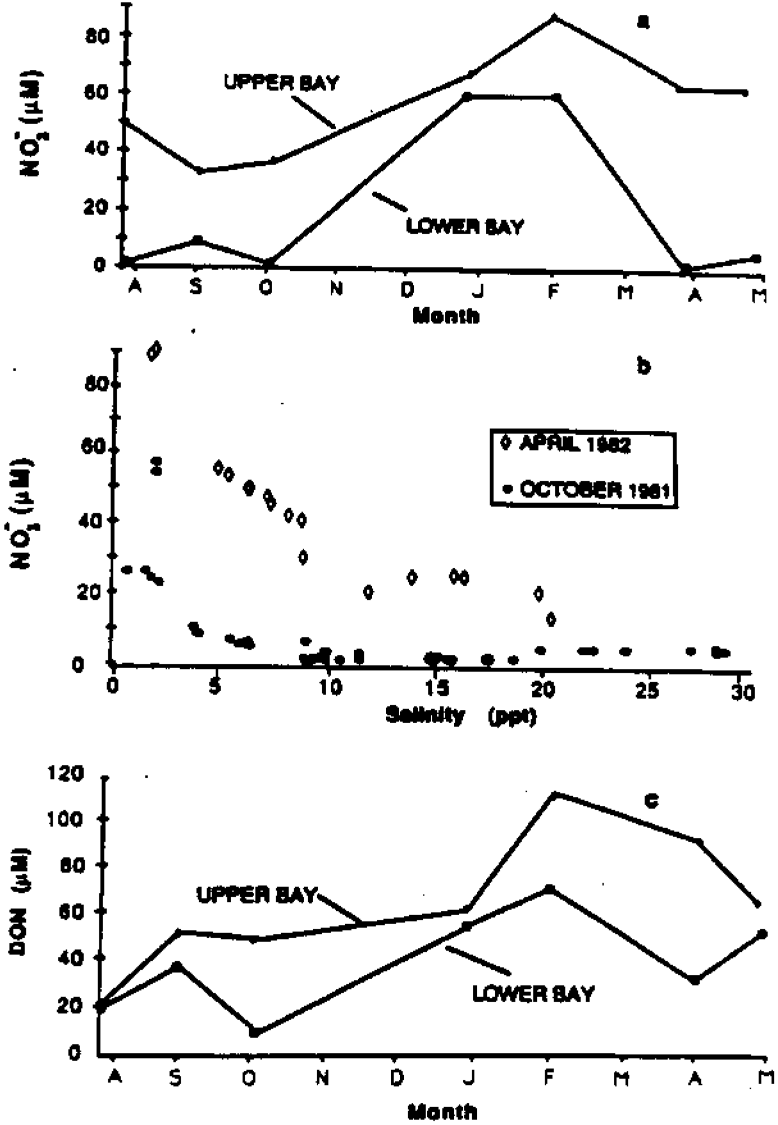

Figure 2. Dissolved nitrogen in upper and lower Fourleague Bay. (a) NO_3^- concentrations at the study sites during sediment flux measurements showing a spring peak and upper-lower bay differences. (b) NO_3^- vs. salinity mixing diagram for October, 1981 and April, 1982 showing seasonal differences in the degree of non-conservative mixing of NO_3^-. (c) DON concentrations at the study sites during sediment flux measurements.

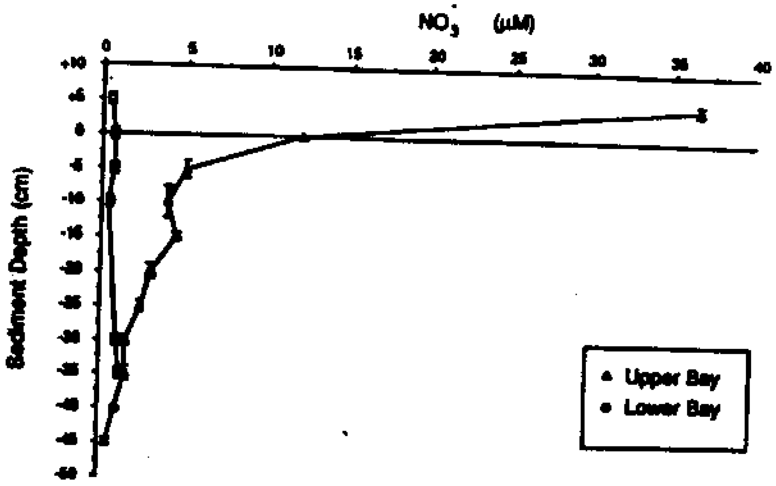

Figure 3. Sediment NO_3^- vertical profile from the upper and lower Fourleague Bay in October 1981.

concentration (<1 μM) in the bottom water did not vary with depth into the sediments (Fig. 3).

Oxygen Uptake

Mean sediment oxygen uptake was 49 mg m^{-2} hr^{-1}, ranging from near 0 in January and February to 140 mg m^{-2} hr^{-1} in August (Fig. 4). There was no significant difference in mean annual oxygen uptake rates at the two sites. Sediment-water oxygen uptake was positively correlated with water temperature at the upper bay site (r^2=0.40, p<0.01), but not at the lower bay.

Nutrient Fluxes

NH_4^+ was nearly always released from the sediments to the overlying water. Mean annual NH_4^+ fluxes

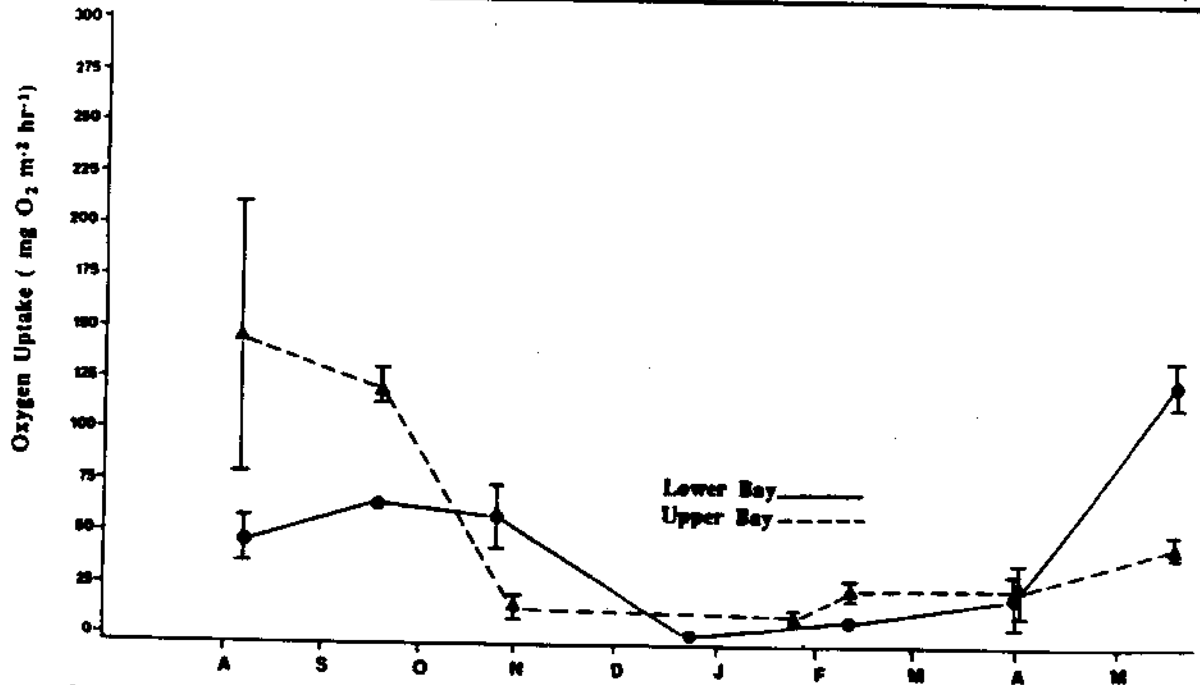

Figure 4. Sediment oxygen uptake rates at upper and lower Fourleague Bay. Error bars are ±1 standard error of the mean.

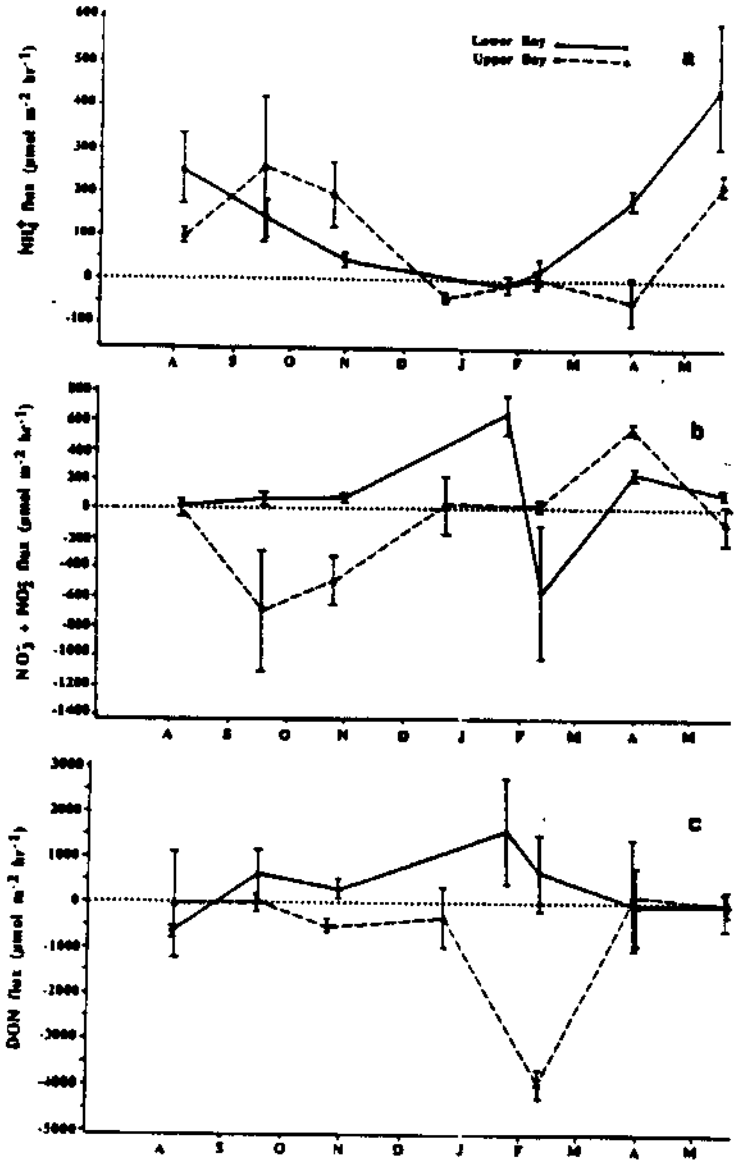

Figure 5. Sediment-water nitrogen fluxes in upper and lower Fourleague Bay. Error bars are ± 1 standard error of the mean. (a) NH_4^+ flux, (b) NO_3^- flux, (c) DON flux. Positive fluxes denote sediment release, negative fluxes denote uptake.

were 153 μmol m^{-2} hr^{-1} at the lower bay and 103 μmol m^{-2} hr^{-1} at the upper bay, ranging from -50 to 450 μmol m^{-2} hr^{-1} (Fig. 5a). Net NH_4^+ flux was positively correlated with water temperature (r^2=0.42, $p<0.05$) at both sites, and with oxygen uptake (r^2=0.23, $p<0.01$) only in the upper bay. There was a negative correlation between NH_4^+ flux and NH_4^+ concentration in the overlying water at the lower bay (r^2=0.51, $p<0.05$).

Mean annual NO_3^- fluxes were large and showed net uptake (mean flux=-112 μmol m^{-2}hr^{-1}) at the upper bay, and release (+79 μmol m^{-2} hr^{-1}) at the lower bay (Fig. 5b). In the lower bay, small positive NO_3^- fluxes were usually observed, except during spring flood when a large negative flux was measured (Fig. 5b). At the upper bay, large negative fluxes were measured during late summer-early fall (-625 μmol m^{-2} hr^{-1}) and a significant positive flux was measured in mid-spring (Fig. 5b).

Mean annual DON fluxes were +305 μmol m^{-2} hr^{-1} at the lower bay site and -710 μmol m^{-2} hr^{-1} at the upper bay site. The highest flux rates at both stations occurred

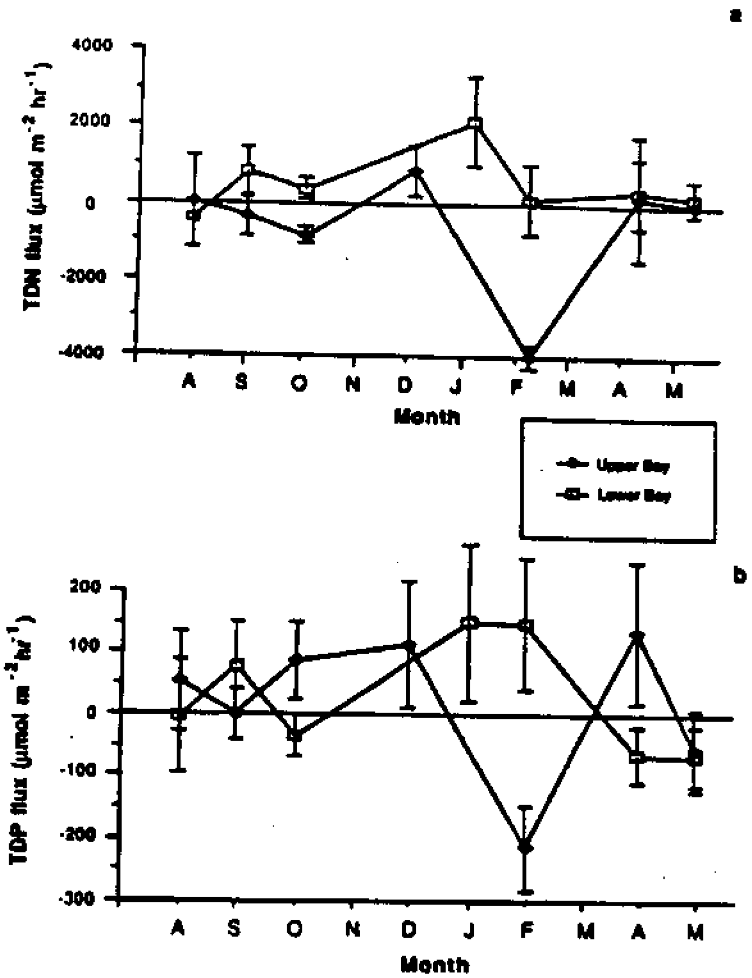

Figure 6. Sediment-water phosphorus fluxes in upper and lower Fourleague Bay. Error bars are ± 1 standard error of the mean. (a) PO_4^{3-} flux, (b) DOP flux. Positive fluxes denote sediment release, negative fluxes denote uptake.

during February, but flux in the upper bay was into the sediments and flux in the lower bay was into the water column (Fig. 5c). Mean annual total dissolved nitrogen fluxes were +543 μmol m^{-2} hr^{-1} at the lower bay and -553 μmol m^{-2} hr^{-1} at the upper bay, dominated by DON and NO_3^- fluxes, displaying considerable monthly variation (Fig. 6a).

At the upper bay site, mean annual PO_4^{3-} flux was only -1 μmol m^{-2} hr^{-1}, while it was -16 μmol m^{-2} hr^{-1} at the lower bay. These mean fluxes were not significantly different from 0 ($p<0.05$). PO_4^{3-} fluxes were somewhat variable over the year, but displayed no obvious seasonal pattern (Fig. 7a). DOP fluxes were high and also exhibited no clear seasonal pattern (Fig. 7b). Mean DOP fluxes were +161 μmol m^{-2} hr^{-1} at the lower bay and +89 μmol m^{-2} hr^{-1} at the upper bay site. Mean annual total dissolved phosphorus fluxes were 30 μmolm^{-2} hr^{-1} at the lower bay and 17 μmol m^{-2} hr^{-1} at the upper bay, varied significantly from month to month (Fig. 7b), and were dominated by DOP fluxes.

The ratio of O_2 uptake to positive inorganic nitrogen release averaged 18:1 in the lower bay and 27:1 in the upper bay. O/N ratios varied significantly between months at both stations.

DISCUSSION

The Atchafalaya/Fourleague Bay estuarine system differs from other estuaries where sediment-water nutrient fluxes have been described. High river discharge and nutrient loading, low salinity, shallow

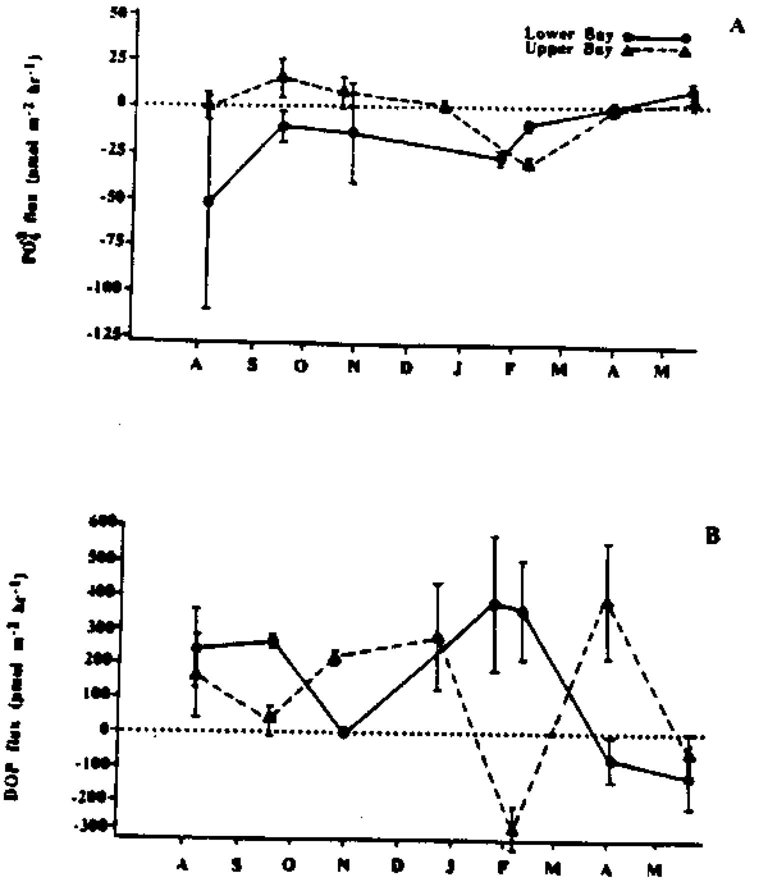

Figure 7. Fluxes of (a) total dissolved nitrogen (TDN), and (b) total dissolved phosphorus (TDP) in upper and lower Fourleague Bay. Error bars are ± 1 standard error of the mean. Positive fluxes denote sediment release, negative fluxes denote uptake.

depth, and high proportion of wetland to water area make Fourleague Bay different from the sites of most significant published studies of estuarine sediment-water nutrient fluxes such as Narragansett Bay, RI, Chesapeake Bay and its tributaries, and Neuse River, NC (Table 1).

Oxygen uptake in Fourleague Bay followed a seasonal pattern, high in summer and fall and low in the colder months, comparing closely with oxygen uptake in other estuarine sediments (Nixon et al. 1976, Hopkinson et al. 1978, Boynton et al. 1980, Boynton and Kemp 1985). NH_4^+ flux rates fit a temperate seasonal pattern and are among the highest in the literature (Table 1). Recent ^{15}N measurements of NH_4^+ dynamics in estuarine sediments in Louisiana (Smith and DeLaune 1985) suggested that little net regeneration may be occurring here, but that technique may ignore the importance of rapid regeneration in the top few mm of sediment, which this net flux chamber technique is designed to measure (Kemp et al. 1982). Although sediment-water NH_4^+ fluxes were similar at both sites, they were related to O_2 uptake in the upper bay, but not the lower bay, suggesting a difference in the degree of dependence of NH_4^+ flux on aerobic metabolism at the two sites. The negative relationship of NH_4^+ flux to water column NH_4^+ concentration indicates that fluxes buffer water column NH_4^+ concentrations.

Both NO_3^- uptake and release occur in Fourleague Bay sediments, and the uptake rates are the highest reported to date (Table 1). NO_3^- uptake dominated at the nitrate-rich riverine upper bay location during high temperatures, while release dominated at the marine-influenced, lower bay site. The sediment pore water profile from the upper bay showed rapidly decreasing NO_3^- concentrations with depth, indicating that the concentration gradient is directed from the water column (higher concentration) to the sediments (lower concentration), suggesting NO_3^- consumption in the sediments and replacement of pore water NO_3^- by diffusion from the water column. NO_3^- vs salinity plots for a transect along the long axis of the bay showed the sharp decrease in NO_3^- with increasing down-bay salinities (Madden 1986), providing additional evidence for rapid NO_3^- uptake by sediment and water column processes, and indicating that sediment fluxes may be more important to the nutrient budget here than in deeper estuaries. Net releases of NO_3^- from upper and lower bay sediments indicate that nitrification is probably occurring in these sediments during at least part of the year. Furthermore, despite average O/N ratios close to the Redfield ratio in the lower bay, a ratio of 48:1 in August indicates a large loss of nitrogen from the system, possibly by a coupling of mineralization, nitrification and denitrification processes, where mineralized NH_4^+ is nitrified to NO_3^-, then subsequently denitrified, as described by Jenkins and Kemp (1984) for the Patuxent River. Such a coupling of processes would generate a high metabolic demand for oxygen while removing a portion of the remineralized nitrogen from the sediment pool. While we have no direct measurements of nitrification in the upper bay, we suspect an even stronger coupling of these processes, as suggested by O/N ratios that were always above the Redfield ratio, and averaged 27:1.

Denitrification rates of 17 µmol m^{-2} hr^{-1} measured by Smith et al. (1985) nearly equal the high net NO_3^- uptake we calculated for these sediments (19 µmol m^{-2} hr^{-1}), when both measurements are averaged over all stations and all sampling periods. However, when the denitrification data are segregated between upper and lower bay, they do not agree with differences in NO_3^- fluxes we observed between stations (-112 µmol m^{-2} hr^{-1} at the upper bay and +79 µmol m^{-2} hr^{-1} at the lower bay). More significantly, the rate of denitrification accounts for only 15% of our observed net NO_3^- flux at the upper bay. Assimilatory NO_3^- reduction and dissimilatory reduction to NH_4^+ may be responsible for a significant portion of the NO_3^- uptake by the upper bay sediments, as has been hypothesized for other coastal waters (Koike and Hattori 1978, Sorensen 1978). The failure of our net flux measurements to agree with Smith et al.'s (1985) laboratory denitrification measurements might also be explained by their requirement to mix different sediments in the laboratory to obtain integrated measurements, or by the possibility of disruption or outright loss of the top flocculent sediment layer during sediment collection and transport to the laboratory. The net flux technique is performed in situ and disturbance of the sediments is minimized.

The spatial trend of DON fluxes was similar to NO_3^- fluxes, with a shift from uptake in the upper bay to release in the lower bay on an annual basis. Great amounts of NO_3^- and DON are removed from the water column with a significant amount of uptake in the upper bay sediments. Highest DON uptake occurred during periods of peak water column DON concentrations and low temperatures; highest NO_3^- uptake occurred during periods of moderate NO_3^- concentrations and high temperatures. TDN fluxes followed the trends in NO_3^- and DON fluxes and, on an annual basis, there was net uptake by the upper bay sediments. Annual mean TDN fluxes in the lower bay were out of the sediments, indicating the site's importance as a nutrient source. The high rate of nitrogen uptake in the upper bay contributes to the water quality of the estuary and may contribute to the productivity of the ecosystem via the benthic food web.

We expected a release of PO_4^{3-} from sediments as reported in other studies (Table 1), and especially given the sometimes large nitrogen fluxes we found, but only very low PO_4^{3-} releases or negative fluxes were measured. Callender and Hammond (1982) measured similar negative fluxes in the Potomac estuary and attributed them to sorption of PO_4^{3-} by sedimentary oxyhydroxides. Fourleague Bay sediments consist of silt and clay (Barrett 1971) which have a high capacity for PO_4^{3-} sorption (Khalid et al. 1977), theoretically increasing the affinity of sediments for water column and sediment interstitial PO_4^{3-}. Throughout our study, bottom water was found to be well-oxygenated, which would facilitate the precipitation of PO_4^{3-} and insure that soluble PO_4^{3-} in anaerobic sediment interstitial water would not diffuse across the aerobic sediment-water interface. However, DOP fluxes were almost always from the sediments and were the highest yet reported in the literature. As reflected by their large contribution to TDP fluxes, these high, positive DOP fluxes may offset the effects of the PO_4^{3-} uptake on the water column.

We conclude that Fourleague Bay sediments have a moderately active metabolism, release NH_4^+ and DOP to the overlying water, and take up NO_3^-, DON, and PO_4^{3-}. The lower bay sediments are a source of total dissolved nutrients to overlying water for much of the time, but over an annual cycle the entire bay is a powerful nutrient sink. High O/N ratios of the fluxes in the upper bay sediments indicate the nitrification of regenerated NH_4^+, followed by denitrification. Nutrient fluxes had broader ranges than in other reports, and in some cases were the highest reported for any estuary. High riverine loading of NO_3^- and DON resulted in high water column concentrations at the riverine site, which may have supported high sediment uptake. Sediment nutrient uptake in the upper bay is at least partially responsible for the reduced nutrient concentrations in water transported to the lower site, where nutrients are released by the sediments. The influence of sediment fluxes on the overlying water is greater in Fourleague Bay than most estuaries, probably owing to the shallow depth. The rapidity of NO_3^- depletion in the water column with distance from the river is likely due to the shallow depth, and the relatively small nutrient pool in the overlying water. The high sedimentation rate in Fourleague Bay may affect fluxes through direct introduction of organic matter, by the addition of adsorbed inorganic nutrients, and by causing shifts in redox equilibria. Although the independent effects of nutrient loading, sedimentation rates, and water depth on sediment-water fluxes have not been directly and individually determined by our study, our work provides an insight into the result of these interacting factors and the net effect on sediment-water fluxes.

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BENTHIC NUTRIENT REGENERATION AND RESPIRATION IN FOURLEAGUE BAY, LOUISIANA

Robert R. Twilley

INTRODUCTION

In shallow coastal systems, in situ regeneration of nutrients may be several orders of magnitude greater than allochthonous inputs and thus be the dominant source of nutrients to primary producers. Fisher et al. (1982) concluded that sediments supply on an annual average from 28-35% of the nitrogen (N) and phosphorus (P) required for the primary productivity of shallow marine systems in North Carolina. Sediment fluxes of ammonium averaged from 15 to 27% of calculated N demand for photosynthesis during the summer in upper Chesapeake Bay (Boynton and Kemp 1985), 65% in the Patuxent River estuary (Boynton et al. 1980), and 35% in the Potomac River estuary (Callender and Hammond 1982). Nixon (1981) calculated that benthic fluxes of ammonium and phosphate contributed about 25 and 50% of the quantity of these nutrients needed for net primary productivity in Narragansett Bay. In the North Sea, 75% of the nitrogen requirements are meet by benthic regeneration (Billen 1978) and in the Kiel Bight this flux may provide 100% of the phytoplankton demand for nutrients (Zeitzschel 1980). Thus, benthic regeneration may represent a significant source of N and P in various types of coastal ecosystems.

Kemp and Boynton (1984) described a conceptual model of how benthic and pelagic processes may be coupled to account for this importance of sediment processes to primary productivity. They suggested that the pulse of nutrients entering a system during high river flow are largely deposited to sediments in association with the fate of suspended particulate material. Deposition of materials from the water column is enhanced at density fronts where the coagulation and precipitation of materials occur (Sholkovitch 1976). These deposited materials may travel from the upper to mid and lower areas of the estuary, but are trapped within the system by a two-layer flow of water in a stratified estuary (Kemp and Boynton 1984). Later in the summer, these nutrients are regenerated to the water column which fuels primary productivity. The transport of nutrients from a river to the water column is generally a spring pulse, and without the temporary storage of nutrients in the sediments they would be very poorly utilized (Fisher et al. 1982).

Besides influencing the seasonal and spatial scale of nutrient availability in estuaries, sediment regeneration may also be a selective process on the relative availability of N vs P to primary producers. These shifts in the N:P ratio have been attributed to controlling the metabolism of estuarine ecosystems. The theoretical ratio of particulate material in the water column according to Redfield (1958) is 106C:16N:1P. Stoichiometric signals of elements buried in the sediment that vary from this theoretical ratio are used to model processes that have dominated the system. Models based on the stoichiometric ratios of elements in sediments developed by Grundmanis and Murray (1977) demonstrate the presence of selective processes operating on N relative to P in pore waters of marine sediments. Nixon and Pilson (1983) using stoichiometric models of Narragansett Bay concluded that the low N:P ratios often observed in estuarine systems occur because benthic remineralization of organic matter yields inorganic N and P fluxes back to the water column which are low in N relative to P and low in N relative to sedimenting organic matter. The amount of P recycled in Narragansett Bay was 125% of the input to the sediment, whereas N recycling rates were only 70% of the inputs (Nixon 1981). Material deposited to sediments had N:P ratios of 13.3, yet the ratio of sediment remineralization was 3.8 to 7.5 (Nixon 1981). This pattern was also observed by Boynton et al. (1980) in the Patuxent River estuary where N flux back to the water column was only 19% that expected based on N:P in the water column. The ratio of remineralized N and P in Patuxent River estuary was only 3.0, less than half the ratio of material in the water column.

Nixon (1981) and Seitzinger et al. (1980) have argued that the low N:P ratio in benthic nutrient fluxes back to the water column are primarily the result of N losses via denitrification. In sediments, the oxygen (O):nitrogen ratio of fluxes across the sediment-water interface should be 17 if oxidation goes to NO_3 and 13 if NH_4 is the end product. If ratios are high, then ammonium regeneration is low and N loss may be occurring via denitrification. Ratios of O:N were greater than 100 in spring compared to ratios near the theoretical model of 13 in summer tributaries of Chesapeake Bay (Boynton and Kemp 1984). Coupled nitrification/denitrification rates could account for increase in O relative to N flux ratios in spring because of the transformation of NH_4 to N_2. In summer, anoxia prevented nitrification and lowered the loss of fixed N, whereas P flux from sediments increased resulting in a low N:P ratio of nutrient exchange. Balzer (1984) also measured different relative fluxes of N and P under oxic and anoxic conditions in the Kiel Bight. As O disappeared from the water column and sediments became more reduced, the N:P ratio of nutrient exchange across the sediment-water interface decreased to values less than 3.9 (Balzer 1984). Along with these changes in the seasonal nature of N metabolism in sediments, these shifts in relative rates of N and P benthic regeneration are also due to the preferential storage of P in sediments due to chemical adsorption processes (Boynton and Kemp 1985, Balzer 1984). In order for these processes to influence the metabolism of estuarine ecosystems they must be significant relative to N and P budgets, and evidence from several studies indicates that this may be the case for denitrification (Jenkins and Kemp 1984, Twilley and Kemp 1986, Smith et al. 1985).

Benthic remineralization of nutrients may also be very important to primary productivity in shallow land margin ecosystems in the northern Gulf of Mexico, such as Fourleague Bay. Here the majority of nutrients are transported by the river in spring, but high levels of primary productivity occur in summer, when clearer but comparatively low nutrient waters move into shallow bays. Primary productivity appears to be partially supported by nutrients from the sediments in this system thus enhancing the utilization of nutrients delivered to this shallow system in the spring (see Kemp and Boynton 1984 for temperate estuaries). However, features of this coastal ecosystem such as organic matter input and production, depth of water column and stratification change from upper to lower regions of Fourleague Bay and these changes may influence the relative rates of benthic nutrient regeneration.

METHODS

Intact sediment cores from four stations (Fig. 1) were incubated aboard ship under near ambient conditions to determine the exchange of ammonium, nitrate plus nitrite, phosphate and dissolved oxygen across the sediment-water interface. Undisturbed sediment cores were taken with 9 cm diameter, 20 cm long acrylic tubes. The end of the core with sediments was sealed with a rubber stopper, and the end with overlying water is sealed with gaskets and plexiglass plates (6 mm thick). The ambient overlying water is removed via siphon and replaced with filtered (0.45 µm pore size) ambient estuarine water to represent ambient nutrient flux. Problems associated with substrate and dissolved oxygen depletion in batch core experiments are remedied by a flow-through design in which an autoanalyzer pump (Cole Palmer) delivers the experimental solutions from reservoirs at controlled flow rates (4 ml/min) through influent and effluent lines connected to the cores (Koike and Hattori 1978). Miniature immersible water pumps (0.47 l/min capacity at 0.3 m head, Edmund Scientific) with variable transformer control are used to stir the overlying water within the cores. Reservoirs of the respective filtered waters and sediment cores are incubated at ambient seawater temperatures aboard ship. The influent and effluent solutions are sampled at 1.5 h intervals for 8 h for analyses of dissolved oxygen and inorganic nutrients.

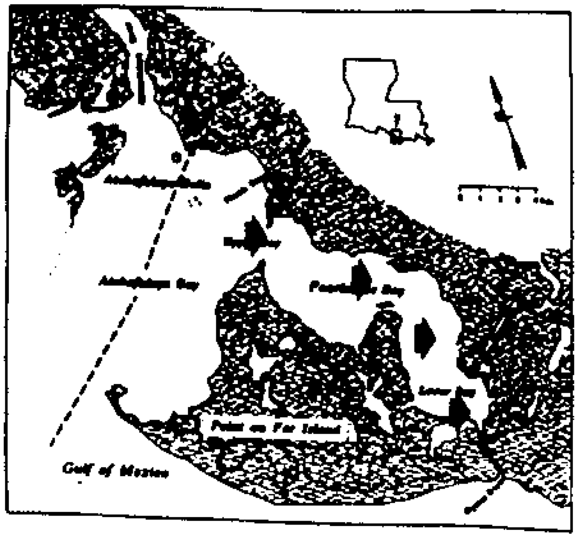

Figure 1. Fourleague Bay and Atchafalaya Bay, Louisiana. Dashed lines represent proposed levee extensions.

Rates of nutrient flux are calculated by comparing influent (I) and effluent (E) concentrations of the respective nutrient by the following equation:

$$(I-E)V/A = \text{Flux } (\mu\text{mol m}^{-2}\text{ h}^{-1})$$

where V is the flow rate (l/h) and A is the surface area of the core (0.0062 m^2).

Sediments collected at each station in acrylic tubes were sectioned at 2 cm intervals and two 40 cm^3 subsamples from each interval were mixed and placed in 50 ml centrifuge tubes. The remainder was placed in plastic-pak bags and frozen. The tubes were centrifuged at 2000 rpm for 20 min and the supernatant (pore waters) filtered (GFF glass fiber) and assayed for dissolved inorganic nitrogen and phosphorus using standard colorimetric techniques (Strickland and Parsons 1972). Sample preparation and reagent additions were make in anaerobic environments to prevent precipitation of inorganic P in pore waters. Subsamples of 3 cm^3 fresh sediment were dried at 85°C to constant weight for determination of bulk density and percent water. These dried samples were ground with mortar and pestle, and one set of subsamples ashed at 550°C for 3 h. Another subsample was assayed for total carbon and nitrogen with a Perkin Elmer Elemental Analyzer. Total phosphorus was determined by dissolving the ashed samples with HCl and measuring ortho-phosphate on the digestate. Redox was measured on 1 cm intervals to a depth of 15 cm using platinum wire and standard calomel electrode standardized with quinhydrone (Whitfield 1969). Surface sediment chlorophyll was extracted from 1 cm^3 samples with DMSO for 1 h and assayed on a Turner fluorometer. A survey of macrofauna was made by sieving core samples from each station through 500 um sieves.

RESULTS AND DISCUSSIONS

The results presented are very preliminary, but suggest some very interesting patterns for sediment nutrient regeneration in this shallow coastal ecosystem. Respiration rates generally increased from station 1 at Oyster Bayou in the lower bay to station 4 in the upper bay (Fig. 2). At each station, highest rates occurred during September and August, while lowest rates occurred in November, 1987. The range in respiration rates was from a high of 8.01 µmols m^{-2} h^{-1} at station 3 during September, 1986, to a low of 1.73 µmols m^{-2} h^{-1} at station 1 during November 1987.

During the fall and spring, inorganic phosphorus uptake occurred at all four stations with particularly high rates at stations 1, 2 and 3 during November 1987 (Fig. 2). Highest rate of inorganic phosphorus uptake was -33 µmols m^{-2} h^{-1} at station 2 during November 1987. Phosphorus regeneration was seldom observed and all rates of phosphorus release were less than 10 µmols m^{-2} h^{-1}. As observed in other estuarine systems, phosphorus regeneration occurred during the summer in Fourleague Bay, but only at stations 1, 2, and 3.

There was regeneration of nitrate (plus nitrite) at station 1 during all the surveys except for April when nitrate concentrations were high (Fig. 2). Nitrate (plus nitrite) was removed from the water column at stations 2, 3, and 4 during all the surveys. At station 2 during November 1987 uptake rates were greater than -150 µmols m^{-2} h^{-1}. This pattern suggest that the upper and mid bay stations are utilizing nitrate from the water column, possibly representing denitrification. Yet Smith et al. (1985) concluded that denitrification rates in the sediments in Fourleague Bay did not account for all the nitrogen in nitrate uptake. The results from station 1 suggest that the sediments in this region of Fourleague Bay are sites of active nitrification resulting in the production of nitrate from the sediments to the water column. Nitrate (plus nitrite) regeneration at this station was particularly high during August 1987 at about 65 µmols m^{-2} h^{-1}.

Ammonium regeneration rates exhibited a very inconsistent pattern among the stations and surveys (Fig. 2). During September 1986, regeneration rates increased from station 1 and 2 at about 100 µmols m^{-2} h^{-1} to nearly 200 µmols m^{-2} h^{-1} at station 3. However during August 1987, regeneration rates decreased from station 1 to station 4, with an uptake of ammonium from the water column at stations 3 and 4. This contrasting pattern between these two summer months may be related to the much higher concentrations of ammonium in the water column during the August cruise. The highest ammonium regeneration rate occurred at station 4 during April 1988 at greater than 400 µmols m^{-2} h^{-1}.

This preliminary survey of sediment nutrient dynamics shows little relation between respiration and nutrient flux across the sediment water interface. Thus, chemical reactions, particularly for inorganic phosphorus, may be important mechanisms in the patterns of nutrient exchange observed. Further studies will look at the fate of nitrate taken up by sediments in the mid bay stations.

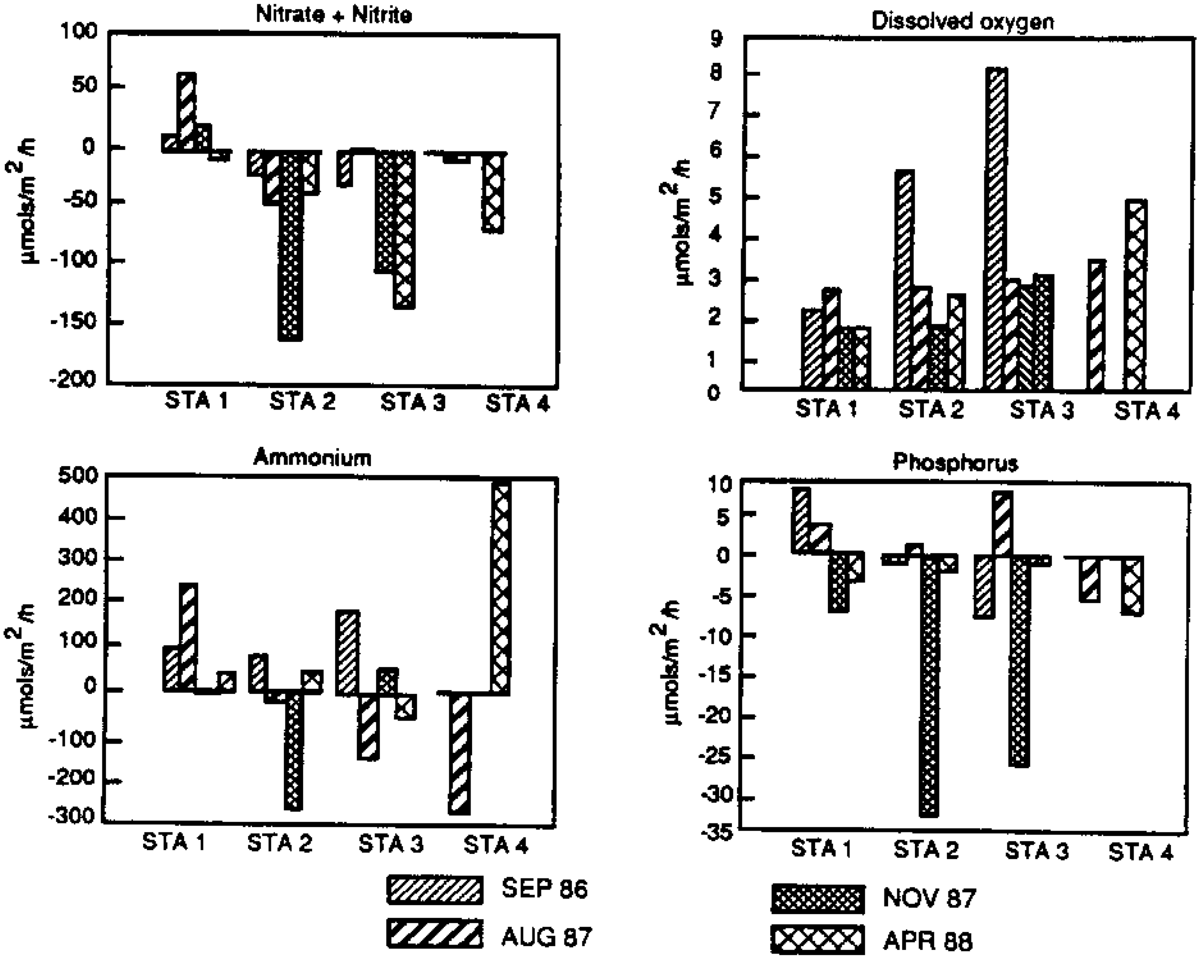

Figure 2. Fluxes of nitrate+nitrate, ammonium, dissolved oxygen (respiration), and phosphorus in Fourleague Bay.

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SEASONALITY OF MATERIALS TRANSPORT THROUGH A COASTAL FRESHWATER MARSH: RIVERINE VERSUS TIDAL FORCING*

M.K. Stern, J.W. Day, Jr., and K.G. Teague

INTRODUCTION

Many studies have recently investigated nutrient and sediment transports through salt (Nixon 1980, Chrzanowski et al. 1982, Valiela et al. 1978, Woodwell et al. 1979, Wolaver et al. 1983) and brackish marshes (Jordan et al. 1983, Stevenson et al. 1976, Heinle and Flemer 1976). However, there have been few similar studies of tidal freshwater marshes. Of these most have focused on changes in nutrient concentrations over a tidal cycle (Stevenson et al. 1976, Simpson et al. 1978, Grant and Patrick 1970). Flows have not been quantified as precisely as in salt marshes and there has been little discussion of riverine versus tidal forcing. Furthermore, studies of seasonal changes over the course of one year or longer are lacking (Simpson et al. 1983). Most studies have been from the Atlantic coast of the United States, since tidal freshwater marshes are extensively developed there (Odum et al. 1984). However, Louisiana also has large areas of freshwater marsh (U.S. Army Corps of Engineers 1983), many of which are tidally influences. Tidal freshwater marshes support a high standing biomass and high rates of primary productivity (Odum et al. 1984, Simpson et al. 1983) so they could be important in the nutrient and sediment budgets of estuaries.

In salt marshes, tides drive transport (Nixon 1980), whereas in freshwater tidal marshes, tide and river discharge may alternate as the major hydrologic forcing. Salt marsh transport studies rely on precise measurements of net water transport (Kjerfve et al. 1981, Kjerfve and McKellar 1980, Boon 1978). Thus accurate determination of the net transport is often difficult. Since tidal freshwater marshes can have a riverine hydrologic component, this problem of nearly balanced ebb- and flood-directed transports may not always be important.

This study was conducted in a freshwater tidal channel, Willow Bayou, located in the marshes at the terminus of the Atchafalaya River floodplain in Louisiana. The hydrologic regime of marshes in this area is influenced by Atchafalaya River discharge, tides, and coastal weather patterns. Dominance by one of these factors depends on the magnitudes of the others at any given time (Wang et al. 1985).

The Atchafalaya River has a large influence on the waters and wetlands of the central Louisiana coast. During high flow in late winter and spring, backwater flooding raises water levels, causing water to flow into wetlands surrounding Atchafalaya and Fourleague Bays where considerable sedimentation takes place (Baumann et al. 1984). During low flow in summer and fall, the freshwater hydraulic head diminishes and the tide becomes the most important factor in moving water.

The purpose of this report is to describe a study of the seasonal influence of Atchafalaya River discharge on water, nitrate plus nitrite (nitrate) and suspended solids (SSL) transports in Willow Bayou. We also compare SSL and nitrate concentrations in the river and bayou to show how transport through the marsh system influence concentrations. These materials were chosen because their primary source is presumably the Atchafalaya River (Caffrey 1983), and they can be used to illustrate riverine influence on materials transport through the bayou and

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*Stern, M.K., J.W. Day, Jr., and K.G. Teague. 1986. Seasonality of materials transport through a coastal freshwater marsh: riverine versus tidal forcing. Estuaries 9(4A):301-308. Used with permission.

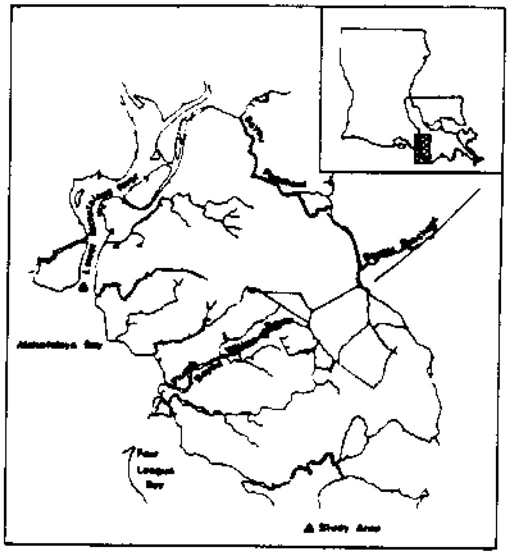

Fig. 1. The study area, showing lower Atchafalaya River, western Terrebonne Parish marshes, Bayou Penchant and Willow Bayou. The Willow Bayou study site and lower Atchafalaya station are indicated by triangles.

the influence of the marsh/aquatic system on water passing through it.

Site Description

Willow Bayou (approximately 6 km long), is a tributary of Plumb Bayou, which flows through the western Terrebonne Parish marshes and discharges into Atchafalaya Bay about 10 km from the mouth of the Atchafalaya River (Fig. 1). Sampling was conducted on a relatively straight reach of the channel (Fig. 1), where the cross section is about 27 m wide, 3 m deep and has a relatively symmetrical bathymetry.

The marshes surrounding Willow Bayou are vegetated primarily by fresh marsh species. Emergent vegetation along the channel bank is dominated by *Zizaniopsis* sp. (giant cutgrass), while the levee ridges are dominated by *Myrica cerifera* (waxmyrtle) and *Salix nigra* (black willow) or *Phragmites hemitomon* (maidencane), *Sagittaria lancifolia* (bulltongue), and *Leersia hexandra*. Some brackish and intermediate species occupy this zone also, including *Spartina cynosuroides* (hogcane), *S. patens* (marshhay cordgrass), *Juncus roemerianus* (needlegrass), and *Eleocharis fallax* (spikerush).

Willow Bayou is connected via a series of dredged canals with Bayou Penchant, a major artery of Atchafalaya River water transport through the western Terrebonne Parish marshes (Baumann and Adams 1981). The Atchafalaya River carries about 30% of the flow of the Mississippi River and the entire flow of the Red River (U.S. Army Corps of Engineers 1983). River discharge is lowest in September or October and highest in May (Fig. 2).

Marshes in this region exhibit almost no topographic relief, and because of the connection to Bayou Penchant, Willow Bayou is dominated by flows from outside its own drainage area. Thus local drainage is overwhelmed by flows from the canal system to the north and east much of the time.

Mean sea level (MSL) of the northern Gulf of Mexico, which influences propagation of the tidal wave into coastal marshes, has two peaks, one in spring and another in fall. In September high salinity Gulf water moves inshore (U.S. Army Corps of Engineers 1983), presumably due to interaction of low river discharge and high MSL. Tides in the northern Gulf are primarily diurnal with a 0.3 m range.

Winds are important in moving Louisiana coastal waters due to the small tidal range, shallow depths, and low elevation of coastal marshes. Winds are mostly southerly during summer and northerly in late fall and winter (Muller and Willis 1983). Southerly and easterly winds tend to raise water levels in the estuaries and marshes and north winds tend to lower water levels (Wax et al. 1978).

MATERIALS AND METHODS

We sampled during January, March, May, August, and October 1984 and January 1985 to assess changes in transport coinciding with seasonal variations in river discharge, MSL, and weather types. For this report, the March and August data are not discussed in detail because they represent transitional periods in the river discharge and MSL cycles. During each trip, water level, current velocity, nitrate, and SSL were measured for 48-50 h (2 tidal cycles). For all months sampled except January 1984, samples were taken hourly at the center of the cross section. Current velocity was measured using either a Bendix S-19 current meter or a Montedoro-Whitney Model PVM-2a flow meter. Water level was measured at 0.5-h intervals during the sampling periods using a fixed reference point.

In January 1984, current velocity and nitrate were sampled at 9 points vertically and horizontally in the cross section, at 2-h intervals to determine spatial variability (Boon 1978, Kjerfve et al. 1981). Samples were pumped

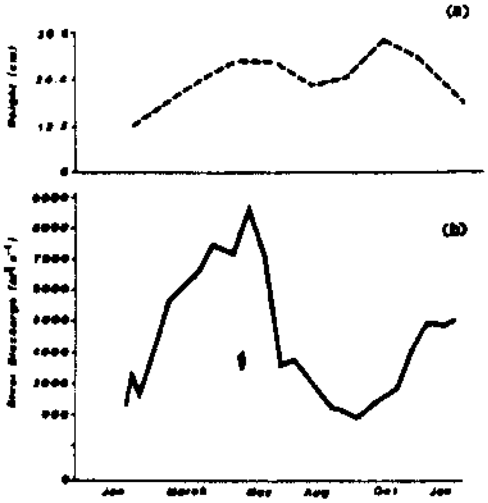

Fig. 2. Mean Gulf of Mexico water levels (a) (Hicks et al. 1983) and lower Atchafalaya River discharge at Morgan City, LA. (b) (U.S. Geological Survey 1985).

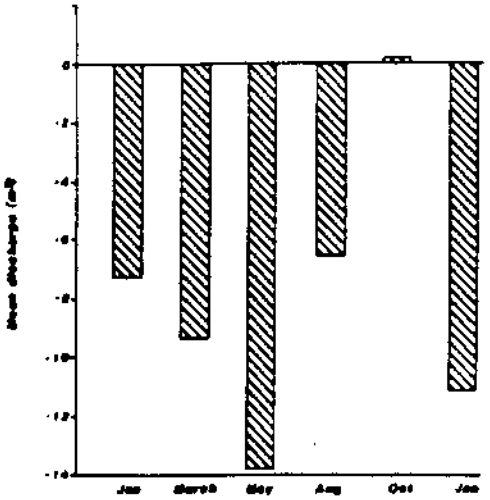

Fig. 3. Seasonal net water fluxes through Willow Bayou. Negative fluxes indicate net ebb directed transport (to the bay), while positive fluxes indicate net flood directed transport (upstream).

from mid-depth and a subsample was filtered immediately (Millipore Type AP glass fiber) and then frozen on dry ice in plastic vials for nitrate analysis in the laboratory. Nitrate was determined using a Technicon Autoanalyzer (U.S. Environmental Protection Agency 1979). Suspended solids were sampled only from the center, every 2 hours. Samples (250 ml) for suspended solids were collected in polyethylene bottles and returned to the laboratory for gravimetric analysis (Strickland and Parsons 1972) using Gelman Type A/E glass fiber filters (0.3 mm). Samples were split into two 100 ml duplicates, and the means were used in all calculations.

Transports were calculated hourly from each velocity, water level and concentration value. Changing cross sectional area due to changing water level was calculated hourly. Cross sectional area was calculated from a dense array of depth profiles measured in the beginning of the study and water level measurements taken during the individual tidal cycle studies. The transports reported are the means of all instantaneous fluxes for each sampling period. The term "ebb-directed" refers to transport toward the estuary, while "flood-directed" refers to upstream transport.

RESULTS AND DISCUSSION

The velocity and nitrate data from the January 1984 trip were analyzed statistically to determine if the center point provided a good representation of the entire cross section. Nitrate flux was calculated for each station and time, and an analysis of variance (ANOVA) was performed on the nine stations, blocking on time to remove exogenous error. In addition, a linear contrast was performed comparing the center station with the other eight stations (SAS Institute Inc. 1985). The two analyses showed that sampling at the center of the cross section was sufficient to characterize nitrate flux, probably because the cross section was small, relatively symmetric, and contained flows that were unidirectional at all times. For the analysis of variance blocking on time, the overall F test comparing all nine means was not significant ($F_{8,200} = 0.50, p < 0.858$). The linear contrast comparing the center station with the others was not significant (producing $F_{1,200} = 0.66, p < 0.48$), indicating that the center station adequately represented the flux through the entire cross section.

Atchafalaya River discharge followed a typical seasonal pattern (Fig. 2) similar to, but with maximum discharge somewhat lower than, the 40-year average (Denes 1983). Minimum discharges during the study period occurred in January 1984 and September 1985. Peak river discharge was in May. MSL is typically highest during spring and fall and lowest in winter (Fig. 2). In January 1984 Atchafalaya River discharge was very low and coincided with low MSL (Fig. 2), but moderately low water levels and high current velocities (Fig. 4a) resulted. Peak river discharge in May, during high MSL, resulted in high water levels and high current velocities (Fig. 4b).

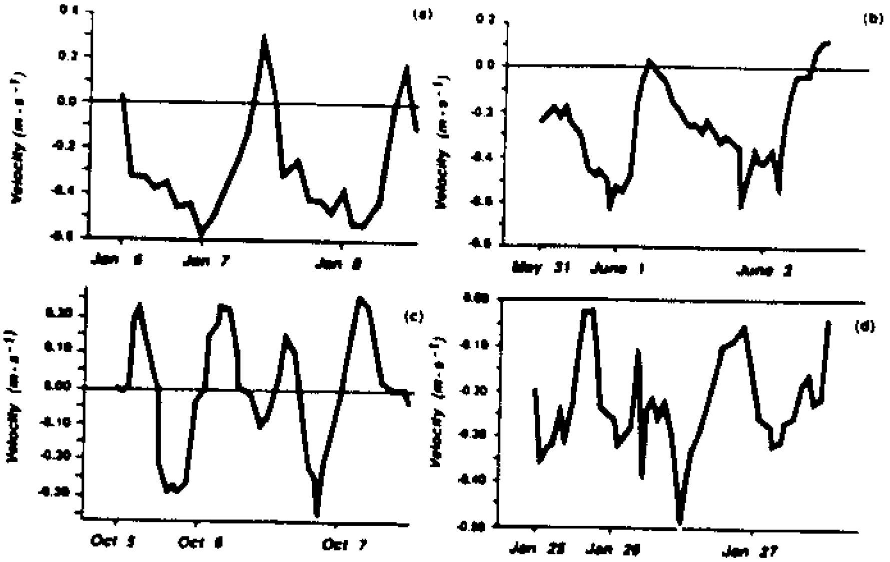

Fig. 4. Hourly instantaneous current velocities in Willow Bayou for January (a), May (b) and October 1984 (c) and January 1985 (d).

Low river discharge coincided with high MSL in October, leading to moderate water levels and low current velocities. In January 1985, moderately high river discharge coincided with low MSL. These conditions, combined with a cold front passage, resulted in very low water levels and relatively high current velocities (Fig. 4c), very different from January 1984.

Current velocities from January, May and October 1984 and January 1985 show the transition from river-dominated to tidally dominated hydrologic regimes (Fig. 4). Current velocities in all months except October were ebb-dominant, because of high river discharge. In October, current velocities were relatively symmetric, indicating tidal forcing when discharge was low and MSL high. In January 1985 strong north winds influenced discharge, resulting in negative current velocities and an irregular tidal signal.

Discharge from Willow Bayou was consistently ebb-directed except for the month of October (Fig. 3). Discharge increased from January through May then decrease to August. Net flow reversed in October when there was small flood-directed transport (import). In January 1985 there was a large net export again which corresponded with strong north winds.

Nitrate and water transports were consistently ebb-directed, increasing from January to May. Nitrate transport decreased from May through October, then increased in January 1985. Nitrate transport in August was low (Fig. 5) compared to the amount of water transported out of the bayou (Fig. 4), due to low nitrate concentrations (Fig. 6). In October both nitrate and water transport were very low, a result of nearly balanced ebb and flood tidal flows and low concentrations of nitrate. Therefore, nitrate transports in January, March, and May were primarily related to water transports, whereas nitrate transports in August and October were affected by concentration variations.

There were large exports of SSL in January, March, and May, a moderate export in August, and a very small export in October (Fig. 7). The decrease from May to August was correlated more with changes in net water transport than with changes in sediment concentration. The concentration difference between May and August was 0.003 g l^{-1} but the difference in net SSL transport was almost no net SSL and nitrate, means of all samples from Willow Bayou, for each trip, were compared to single samples from a station in the lower Atchafalaya River (Figs. 6 and 8). Concentrations of nitrate were consistently higher in the river than in Willow Bayou (Fig. 6). Both sites had increasing concentrations of nitrate through winter and early spring. Bayou concentrations began decreasing in May probably as a result of increasing temperature (Simpson et al. 1978), but river concentrations continued to increase. Net removal could be due to plant uptake (U.S. Army Corps of Engineers 1983) and to microbial transformations, including denitrification and

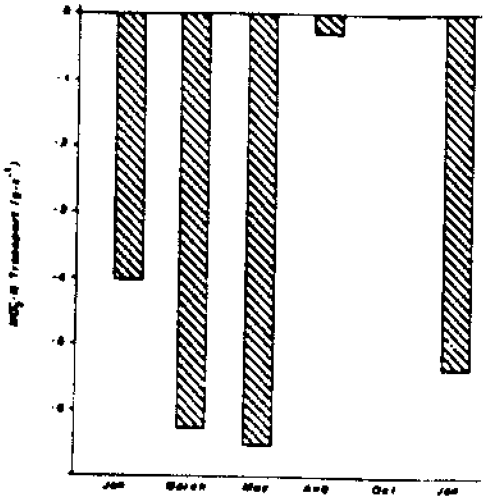

Fig. 5. Seasonal net nitrate fluxes through Willow Bayou. Negative fluxes indicate net ebb directed transport.

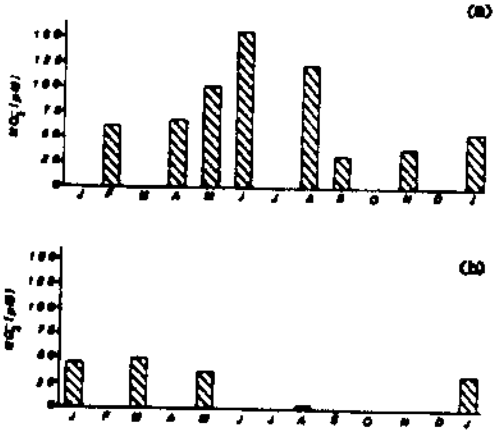

Fig. 6. Comparison of nitrate concentrations at lower Atchafalaya River (a) and Willow Bayou (b).

other forms of nitrate reduction (Buresh and Patrick 1978; Smith and DeLaune 1983). The large decrease in nitrate concentration in the bayou from May to August undoubtedly reflects these processes.

SSL concentrations in the river were high during water, spring, and early summer and low in early fall (Fig. 8). During November, concentrations in the river increased and then decreased in January 1985. Bayou concentrations decreased gradually from January 1984 to October and increased in January 1985. River concentrations were higher than bayou concentrations in all months except January 1985, when the concentrations in the bayou were slightly higher than in the river. This could have been the result of resuspension of bottom sediments during the cold front passage. Despite reduction in sediment concentration of water flowing through the marsh system, sediments are transported the marsh system, sediments are transported through the marsh to the estuary.

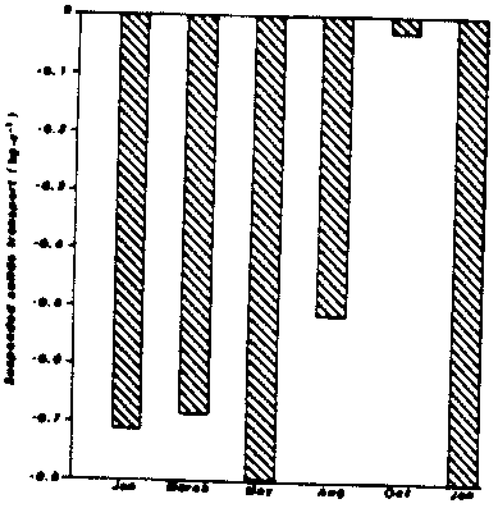

Fig. 7. Seasonal net suspended solids fluxes through Willow Bayou. Negative fluxes indicate net ebb directed transport.

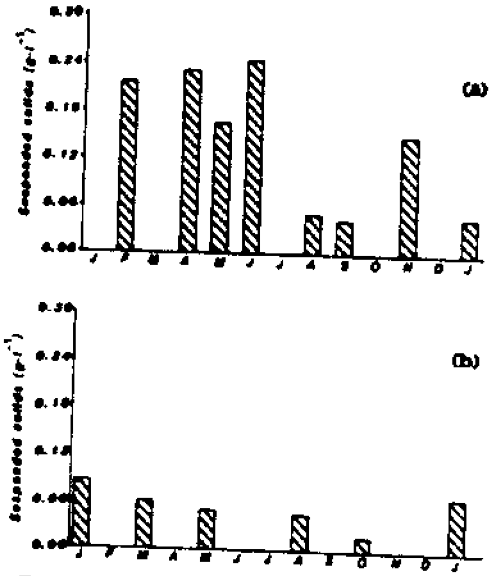

Fig. 8. Comparison of suspended solids concentrations at lower Atchafalaya River (a) and Willow Bayou (b).

Highest sediment rates in the western Terrebonne Parish marshes occur during peak river discharge, then decrease through summer and fall (Baumann et al. 1984). Our data qualitatively support this. Suspended solids concentrations and transports are high during peak river discharge (Fig. 8). In the neighboring Barataria Basin, Louisiana, marshes are deteriorating, and they rely on deposition of sediment resuspended from open water areas to maintain elevation (Baumann et al. 1984). The western Terrebonne Parish marshes are located far inland of estuarine open water, are no rapidly deteriorating, and are presumably regularly inundated with river water (Baumann et al. 1984).

The results indicated that for most of the year there was a strong net transport of water, nitrate, and SSL from Willow Bayou to Atchafalaya Bay. This resulted from a hydraulic slope created by water flowing from the Atchafalaya River into marshes north and east of Willow Bayou. Net ebb transports characterize river dominated estuarine systems, whereas very small net transports in either direction characterize tidally driven systems, due to equality of ebb and flood currents. Water, nitrate, and suspended solids transports in Willow Bayou displayed both river-dominated and tidally-dominated characteristics, depending on river stage, MSL, and coastal weather patterns. Decreases in concentrations of SSL and nitrate between the river and Willow Bayou indicated that physical and biological processes acted to remove these from the water column.

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NUTRIENT AND MATERIALS EXCHANGES BETWEEN FOURLEAGUE BAY AND ITS SURROUNDING MARSHES

D.L. Childers

INTRODUCTION

A detailed understanding of marsh:water column interactions is critical to any study of estuarine ecosystem dynamics. In his review of 20 years of estuarine ecological research, Nixon (1980) concluded that highly variable data from exchange studies make generalizations about marsh:water column interactions difficult. Work published in the 1960's and 1970's appear to implicate coastal marshes as sources of organic carbon, but with fluxes occurring over a wide range of values. Based on his summary, Nixon (1980) noted that marshes seem to transform nitrogen—by importing oxidized inorganic species and exporting dissolved and particulate reduced forms—as well as phosphorus—by taking up total phosphorus and releasing remobilizing phosphate. Odum (1984) has proposed a dual-gradient concept for estuarine detrital [organic carbon] processing and transport which enhances Nixon's review of nitrogen and phosphorus dynamics. His gradient concept has implications to analysis of marsh:water column exchange data. Concentrations of POC and DOC generally decline with increasing salinity due to 1) supply of each by terrestrial freshwater and wetland sources, and 2) dilution down-estuary by coastal oceanic water low in DOC and POC concentrations (Odum 1984). As part of an ongoing Seagrant Project, nutrient and materials exchanges across the wetland:open water marginal interface in brackish marshes of lower Fourleague Bay are being quantified.

In the 1980's, studies quantified exchanges between marshes and adjacent water bodies. Most of these, however, indirectly measured fluxes through narrow, shallow channels which connect small wetland embayments to larger basins. Exchange studies conducted in tidal channels are difficult to interpret in terms of actual marsh:open water marginal interactions because the intertidal and subtidal systems are not separable. This method is logistically impractical in Fourleague Bay because coastal marshes here lack well-defined marsh embayments. An excellent way to examine interactions between an intertidal marsh and an inundating water body is to measure the process directly. Recently, some investigators have quantified marsh:water column fluxes using flumes built on the wetland surface. Using a marsh flume on Carter's Creek, VA, Wolaver et al. (1980, 1983) reported marsh uptake of ammonium, nitrate, phosphate, total N and P, and DON. Only nitrite was exported. Sapelo Island, GA, marshes appear to release POC but show no significant net DOC flux (Chalmers et al. 1985). Freshwater marshes along the North River, MA, imported all forms of dissolved inorganic nitrogen (Bowden 1986). At North Inlet, SC, a marsh flume study indicated net uptake of ammonium, nitrate, and nitrite by the marsh while DON was released (Whiting et al., in press). A modified flume technique is being used here to quantify exchanges of carbon, nitrogen, phosphorus, and suspended sediments between Fourleague Bay and its associated marshes (Childers and Day, in press).

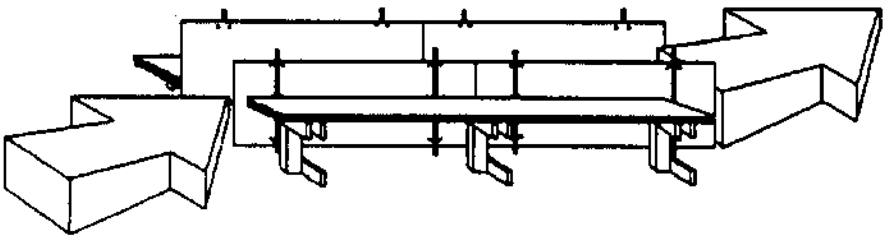
MATERIALS AND METHODS

The Fourleague Bay marsh flume is located in the brackish marshes of Old Oyster Bayou. The flume consists of clear, corrugated fiberglass panels (each 0.66 m high and 2.7 m long) which form vertical walls 2 m apart. Boardwalks on either side prevent disturbance of the marsh surface. The 30 m long flume prevents lateral water movement, without altering normal flow, as the flooding tide inundates the marsh. The panels are removed after each sampling to prevent long-term panel effects, such as shading, edge scouring, and wrack accumulation. Water levels are continuously monitored in a nearby estuary at a coastal marsh site, about the same distance from the coast as the Fourleague Bay flume, using a Richards-type water level recorder (Weathertronics Inc. Model 6510).

A throughflow design is used in these flumes; a modification necesssary for use in expansive, microtidal, low energy estuarine marshes. Replicate water samples are drawn simultaneously from both ends of the flume every 30-45 minutes over a full tidal cycle. Fluxes of constituents are determined by comparing instantaneous flux into the flume with that out of the flume. This method follows the convention that negative fluxes are exports from the marsh surface to the inundating water column and positive fluxes are imports. Details of the flume design, sample treatments, flux computations, and data interpretation are presented in Childers and Day (in press). Figure 1 conceptualizes the flume design and briefly details the flux calculation procedures.

Water samples are simultaneously taken from both ends of the flume every 30-45 minutes over the tidal cycle sampled. From each, replicated subsamples for NH_4^+, $NO_3^- + NO_2^-$, and DOC are immediately filtered through pre-ashed, pre-weighed 0.45 µm glass fiber filters. Unfiltered samples for TN are also taken. Subsamples and filter papers, for POC, PON, and TSS analysis, are frozen in the field. Fluxes of TSS, POC, and PON (calculated as mg X/m^2 marsh inundated/hr of inunda-

Figure 1: Conceptual diagram of the throughflow flume and equations used in the flux calculation model.



$$\underset{(\text{mgX/sec})}{\text{Instanteneous Flux In}} = \left[[x]_t * \left(\begin{matrix} \text{Inst. } H_2O \\ \text{flux} \end{matrix} \right)_t \right]_{\text{mouth}} \qquad (2.1) \qquad \underset{(\text{mgX/sec})}{\text{Instanteneous Flux Out}} = \left[[x]_t * \left(\begin{matrix} \text{Inst. } H_2O \\ \text{flux} \end{matrix} \right)_t \right]_{\text{inland}}$$

$$(2.2) \quad \underset{(\text{mgX})}{\text{Total Flux}} = \sum_{t=1}^{n} \left[\frac{\left(\begin{matrix} \text{Inst} \\ \text{flux} \end{matrix} \right)_t + \left(\begin{matrix} \text{Inst} \\ \text{flux} \end{matrix} \right)_{t+1}}{2} * \left(\begin{matrix} \text{time} \\ \text{int.} \end{matrix} \right)_{t,t+1} \right]$$

for n= number
of samples in
flooding or
ebbing tide

$$(2.3) \quad \underset{(\text{mgX/sec})}{\text{Net Flux}} = \frac{[\text{Total Flux}]_{\text{mouth}} - [\text{Total Flux}]_{\text{inland}}}{\text{Total Time}_{(t=1 \text{ to } n)}}$$

$$\underset{(\text{mgX/m}^2\text{/hr})}{\text{Net Areal Flux}} = \left[\frac{[\text{Total Flux}]_{\text{mouth}} - [\text{Total Flux}]_{\text{inland}}}{\left[\sum_{t=1}^{n} \frac{[\text{Mean Flume length}]_t * [\text{time interval}]_t}{\text{Total Time}_{(t=1 \text{ to } n)}} \right] * \frac{\text{Total Time}}{3600}} \right] \qquad (2.4)$$

tion) are based on these concentrations multiplied by the associated water flux (Figure 1). Water levels within the flume are monitored continuously. At each sampling, aboveground macrophyte biomass samples (0.25 m^2) are taken at randomly chosen sites near the creekside, central, and inland areas of the flume.

Samples have been taken at the Old Oyster Bayou marsh flume three times—September 28, 1986, March 7, 1987, and June 10, 1987. Water levels on the August, 1987, November, 1987, and April, 1988 cruises were low, and the marsh did not flood. Data from the September, March, and June samplings are discussed in this paper.

RESULTS AND DISCUSSION

The most critical physical force moderating exchanges between marshes and their associated estuary is hydrology, specifically the local flooding regime. As noted above, water levels were high enough to inundate the marsh on only half of the sampling cruises to date. Climatological wind forcing is an important control on water level fluctuations in Louisiana's microtidal estuaries (Baumann 1980). The Fourleague Bay estuary is oriented on a northwest-southeast axis; winds from the northwest (characteristic of post-frontal weather) depress water levels while southerly winds (characteristic of pre-frontal weather) tend to elevate water levels. This effect can be dramatic—a strong frontal passage occurred during the November, 1987, cruise lowered water levels 30-50 cm below normal basal levels (Figure 2). An anomalously low flooding regime has characterized the last year, with the marsh inundated less than 25% of the time in 8 of the last 9 months (August, 1987 through April, 1988; Figure 3). This lowered flooding frequency represents a decreased interaction between the marshes and the Fourleague Bay estuary (this is demonstrated by three successive cruises where the marsh failed to flood, shown in Figure 3 as "NO").

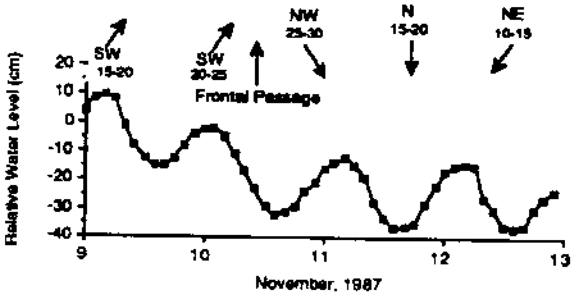


Figure 2. Climatological and water level data, November cruise.

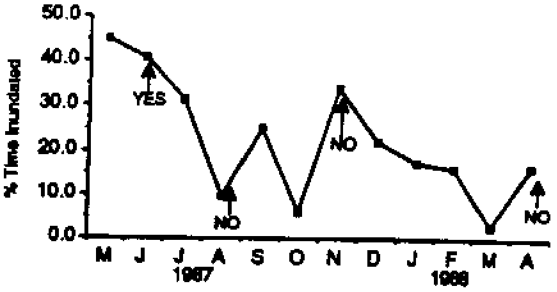


Figure 3. Coastal marsh flooding regime.

Net areal fluxes from the September, 1986, March, 1987, and June, 1987 samplings are shown in Figures 4-6 (fluxes are per m^2 marsh inundated per hour of flooding). The exchange patterns for ammonia (Figure 4a) show a trend of marsh uptake in the spring (380 µg NH_4^+-N/m^2/hr) to release in the fall (740 µg NH_4^+-N/m^2/hr). When we compare these fluxes with ammonia concentration data from Fourleague Bay, an interesting pattern emerges: During spring, high river flow delivers a large amount of dissolved inorganic nitrogen (DIN) to the bay and its marshes. This corresponds with spring uptake by the marshes. As the summer progresses, riverine nitrogen inputs drop off, and bay N concentrations decrease. At this time, the marshes release DIN to the water column. The marginal marshes of the Fourleague Bay estuary appear to be acting as nutrient buffers for the water column by taking up DIN during the spring—when riverine supply is high and water column productivity is relatively low—and releasing DIN during the fall—when riverine supply is low and aquatic productivity is maximal. Interestingly, the March DIN flux results show a net marsh import, but a release of 240 µg NO_3^--N/m^2/hr of nitrate-nitrite (Figure 4a). This is the only sampling in which the marsh appears to transform DIN from reduced to oxidixed forms during tidal inundation.

Phosphorus, as both orthophosphate and total phosphorus, was released by the Old Oyster Bayou marsh during all samplings (Figure 4b). In all three cases, the magnitude of this release is proportional to the concentrations of phosphorus in the overlying waters—March concentrations of 20-60 mg PO_4-P/m^3 correspond to an export of only 140 µg PO_4-P/m^2/hr while June phosphate

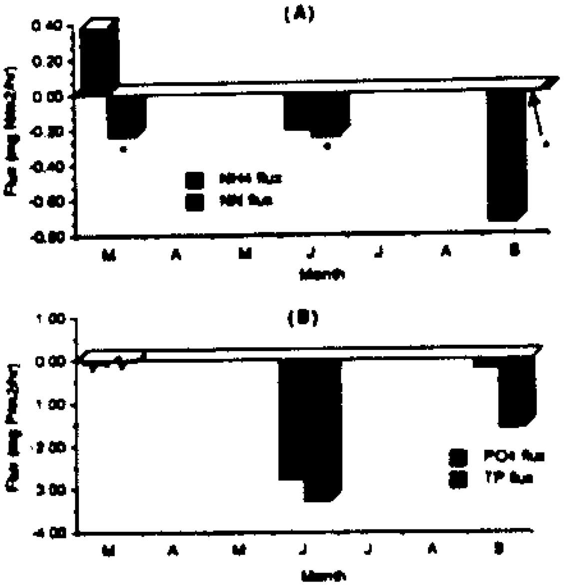


Figure 4. Old Oyster Bayou NH_4 and NO_3+NO_2 (A) and phosphorus (B) exchanges.

contents of 200-300 mg PO_4-P/m^3 correspond to a 2770 µg PO_4 P/m^2/hr release. It is difficult to conclude cause and effect based on only three samplings. The marsh does appear to be a major supplier of phosphorus to the Fourleague bay water column, however. Whether the high concentrations are caused by large marsh exports remains to be seen.

Odum (1984) proposed that POC and DOC concentrations will be [roughly] inversely related to estuarine salinity levels. In Fourleague Bay, the salinity gradient is likely to be temporal rather than spatial—during spring, high river discharge decreases baywide salinities to nearly 0, while fall and winter are characterized by oceanic influence and much higher salinities. The Old Oyster Bayou marsh exported particulate organics (as POC and PON; Figure 5a) and imported DOC (Figure 6a) during all samplings, but the largest release and uptake rates occurred during spring and early summer. If Odum's hypothesis applies to the Fourleague Bay estuary, then marsh POC export may be partly responsible for the inverse relationship between open water salinities and POC concentrations. The marsh appears to be [merely] a passive sink for DOC, however, taking up more when open water concentrations are higher (during lower salinities).

Exports of total nitrogen (TN; Figure 6b) were significant during all samplings, and highly significant in March and June samplings. Interestingly, these three samplings show a definite seasonal trend in N:P ratios of TN and TP exports (both totals showed exports during all samplings). In March, the N:P ratio of the totals export was 41.6. By June, the ratio had fallen to 5.4 and in September the totals flux N:P ratio was only 3.1. This relationship between nitrogen and phosphorus supply by the marsh across the land margin interface may have implications to N:P ratios in Fourleague Bay and thus to phytoplankton productivity there.

SUMMARY

It is difficult to draw conclusions using a data set with only three samplings. Nonetheless, these results from Fourleague Bay do indicate a seasonal pattern in inorganic nitrogen dynamics, with the fringing marshes acting as important seasonal nutrient buffers to the Bay water column. This buffering action has implications to pelagic productivity in the nearshore coastal ocean as well. The marshes are sinks for inorganic nitrogen in the spring, when it is in greatest supply, [perhaps] reducing the chances of coastal eutrophication and bottom water anoxia caused by high productivity.

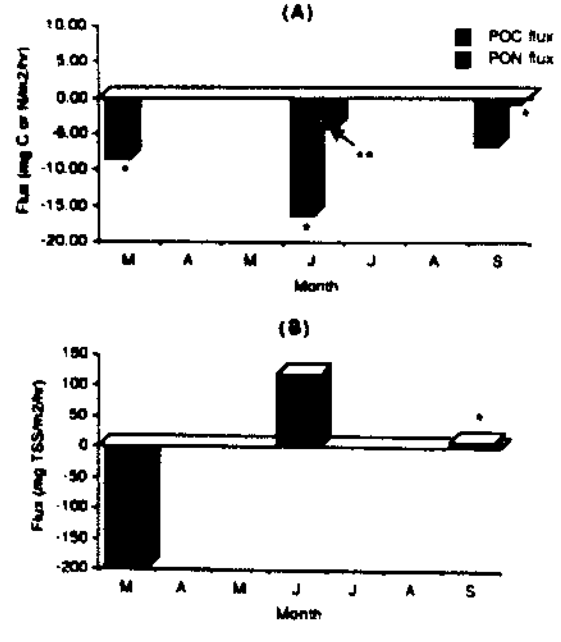


Figure 5. Old Oyster Bayou particulate organics (A) and suspended sediment (B) exchanges.

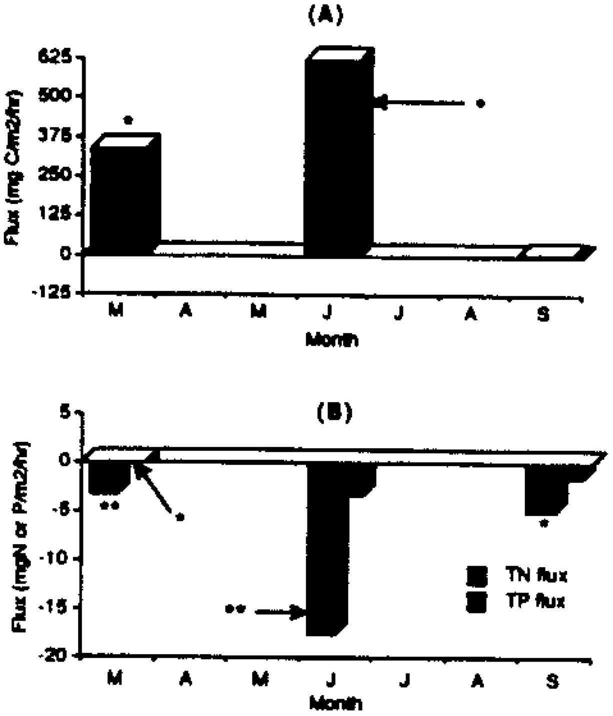


Figure 6. Old Oyster Bayou DOC (A) and total nitrogen and phosphorus (B) exchanges.

Fourleague Bay marshes appear to continuously supply phosphorus, as orthophosphate and total phosphorus, as well as particulate organics (detritus) to the estuary. These fluxes may be important to estuarine trophic dynamics in two ways: 1) the inorganic phosphate release maintains high rates of aquatic primary productivity, driving phytoplankton-based energetics, and 2) the particulate organics provide a detrital source to the aquatic detrital food chain. Clearly, more work is needed to clarify this interaction.

Estuarine water levels are the ultimate controller of these marsh:water column dynamic interactions. If the marsh rarely floods, its importance to the ecosystem is intrinsically reduced. This preliminary data set indicates that, beginning in July, 1987, a major reduction in coastal water levels has occurred. Research into the reasons for this anomaly, and how often such deviations occur, will be critical to all future analyses.

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CONTROL OF THE VARIABILITY OF NUTRIENTS AND SUSPENDED SEDIMENTS IN A GULF COAST ESTUARY BY CLIMATIC FORCING AND SPRING DISCHARGE OF THE ATCHAFALAYA RIVER*

J.M. Caffrey and J.W. Day, Jr.

INTRODUCTION

Rivers can be important sources of nutrients and suspended sediments for estuaries. In temperate areas, high spring river discharge is responsible for increased concentrations of dissolved inorganic nutrients and suspended sediments in such estuaries as Chesapeake Bay (Carpenter et al. 1969), Patuxent River (Kemp et al. 1982), Columbia River (Geffenbaum 1963), Gironde Estuary (Allen et al. 1977), Barataria and Caminada Bays (Ho and Barrett 1977). In estuaries as well as the nearshore zone, these "new" nutrients, primarily dissolved inorganic nitrogen compounds, support considerable primary production (Boynton et al. 1982, Kemp et al. 1982, Wafar et al. 1983). The timing and duration of these inputs undoubtedly exerts a controlling influence on estuarine production.

The delivery of nutrients to estuaries by rivers is modified by circulation. Circulation patterns partially determine the distribution and variability of suspended and dissolved materials within estuaries. Subtidal circulation in many Gulf Coast estuaries is wind driven (Kjerfve 1975, Smith 1977). Synoptic weather types which are useful in classifying different climatic conditions (Muller 1977), have been related to changes in water elevation, salinity (Wax et al. 1978), and circulation (Denes 1983). Climatic effects, such as frontal passages, occur on the order of days to weeks, and intermediate period between tidal cycles and seasonal cycles. Variability in estuarine circulation patterns should affect spatial and temporal distributions of nutrients and suspended sediments, particularly when different water masses move into the estuary. In the present paper, we examine variations in nutrient and suspended sediment concentrations over time scales of hours to days relative to changes in water mass transport, which is inferred from physical and chemical measures. Specifically, we consider the question of whether nutrient and suspended sediment concentrations in Fourleague Bay are controlled by river input during a period when discharge is at a maximum, or by processes and events that occur over shorter time scales (tides and frontal passages).

STUDY AREA

Fourleague Bay is a shallow (1 m average depth) coastal bay located in south central Louisiana and part of the Mississippi River distributary delta. The bay is 93 km^2 and is surrounded by fresh, brackish and salt marshes. Salinity ranges from 0 to 26 in the lower bay and from 0 to 8 in the upper bay over a tical cycle. The only direct outlet to the Gulf of Mexico is through Oyster Bayou (Fig. 1). The mouth of the Atchafalaya River opens into Atchafalaya Bay about 11 km northwest of the upper entrance to Fourleague Bay. The Atchafalaya River carries 30 to 40% of the discharge of the lower Mississippi River and averages 10,000 m^3 s^{-1} during peak spring discharge in March (U.S. Geological Survey 1940-1982).

MATERIALS AND METHODS

Water samples were collected at two stations in Fourleague Bay by an ISCO automatic sampler over

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*Caffrey, J.M. and J.W. Day, Jr. 1986. Control of the variability of nutrients and suspended sediments in a Gulf coast estuary by climatic forcing and spring discharge of the Atchafalaya River. Estuaries 9(4A):295-300. Used with permission.

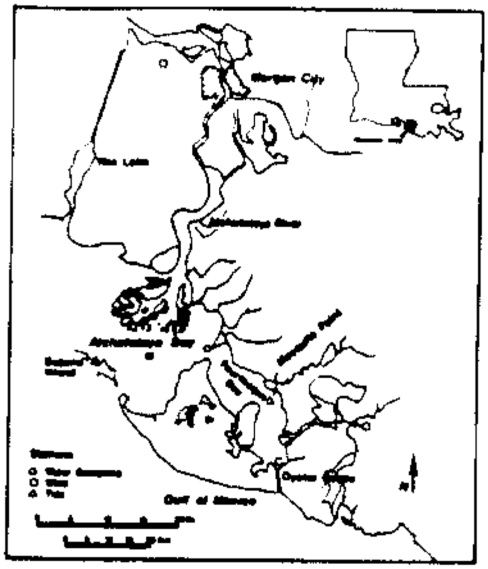

Fig. 1. Fourleague Bay, Louisiana showing location of sampling stations and wind and tide gauges.

several tidal periods in March, 1982. Samples were collected at the lower bay station (Fig. 1) at 2-h intervals over one tidal cycle during March 5-6, 1982, and at 4-h intervals over two tidal cycles during March 19-21, 1982. On March 31-April 1, 1982, water samples were collected at the upper bay station over one tidal cycle. Water samples were preserved with chloroform (Ho et al. 1970), filtered through glass-fiber filters (0.45 mm), frozen, and analyzed for nitrate plus nitrite (NO_3^-), ammonium (NH_4^+), soluble reactive phosphate (SRP), total Kjeldahl nitrogen (TKN), and total phosphorus (TP) using the automated methods of the U.S. Environmental Protection Agency (1979). Suspended sediment samples (SS) were measured gravimetrically (Banse et al. 1963).

Records of wind speed and direction in Atchafalaya Bay (Fig. 1) were obtained from the U.S. Army Corps of Engineers Waterway Experimental Station (ACE-WES) for the sample periods and two days prior to sampling. Tide height records from Mosquito Point light in Fourleague Bay were available for the third sampling period from C. Coleman (ACE-WES). On the other dates, records were obtained for the Eugene Island tide gauge form R. Cunningham (personal communication, ACE New Orleans district office). Dr. Robert Muller (personal communication, Dept. of Geography and Anthropology, Louisiana State University, Baton Rouge) provided synoptic weather types for the sampling periods.

A running average over 25 h was calculated for time series records of water elevation for the sampling periods to remove the frequencies associated with the astronomical tide. The residual tide components indicate changes in water level attributable to factors other than astronomical tides, primarily meteorological forcing. Correlation analysis was used to test for relationships between variations in physical factors and variations in nutrients and suspended sediments ($a \leq 0.10$).

RESULTS AND DISCUSSION

Annual mean values in the upper and lower bay (Caffrey 1983) and means for each sampling period in March are shown in Table 1 for nutrients and suspended sediments. Three weather types occurred during the sampling periods: frontal overrunning (FOR), frontal gulf return (FGR), and gulf return (GR). FOR and FGR are both stormy weather types associated with frontal passages either from the north (FOR) or from the south (FGR), while gulf return is typical of fair conditions (Muller 1977).

The first sampling period was characterized by frontal overrunning conditions and declining water elevations (Fig. 2) because of strong northerly winds. The highest salinity (16) and lowest NO_3^- concentrations (Fig. 3) occurred at the beginning of the study period at 1000 h when southeast winds prevailed. NO_3^- concentrations during the rest of the 28-h period were between 20-52 µM, much higher than the average concentration of 14 µM for the lower bay. NO_3^- concentrations were negatively correlated with salinity ($r = -0.64$) as were total phosphorus ($r = -0.90$). During periods of high river discharge and frontal passage, southwesterly winds raise water elevation and bring in high-salinity, low-nitrate waters. The switch to northerly and northwesterly winds lowers water elevations and salinity, thus increasing NO_3^-, TKN, TP and SS concentrations. Overall, the concentrations of SS and TP were lower than average, while TKN concentrations were similar to lower bay annual averages (Table 1). NH_4^+ concentrations were not significantly correlated with winds, tide, or salinity, so other processes such as pore water exchange, water high in NH_4^+ coming out of the marshes, benthic regeneration (Teague 1983), or phytoplankton uptake could be responsible for the variability.

Two weeks after the first sampling period (March 19-21), weather conditions were very different, with moderate southeasterly winds prevailing, with moderate southeasterly winds prevailing, typical of gulf return. At that time, river discharge had a minimal effect on the lower bay. Salinity varied from 14 to 26 during this 4h sampling

TABLE 1 Annual, March 5–6, March 19–21, and March 31–April 1, 1982, means (±1 standard error) for upper (UB) and lower (LB) bay stations for nitrate + nitrite (NO_3^-), ammonium (NH_4^+), soluble reactive phosphate (SRP), total Kjeldahl nitrogen (TKN), total phosphorus (TP) and suspended sediments (SS).

	NO_3^-	NH_4^+	SRP µM	TKN	TP	SS mg l^{-1}
Annual*						
UB	51.3 (4.0)	2.59 (0.34)	1.12 (0.10)	67.3 (3.5)	8.0 (0.6)	97.7 (9.7)
LB	14.1 (2.0)	7.69 (0.90)	1.27 (0.09)	97.5 (4.2)	8.7 (0.7)	187.6 (27.2)
March 5–6						
LB	24.3 (3.8)	3.7 (0.35)	1.1 (0.06)	98.0 (9.1)	5.3 (1.5)	87.7 (20.3)
March 19–21						
LB	1.2 (0.28)	4.4 (1.10)	1.2 (0.17)	76.7 (14.6)	5.8 (2.4)	175.4 (2.4)
March 31–April 1						
UB	66.9 (8.3)	2.0 (0.54)	0.94 (0.18)	74.0 (4.3)	3.3 (0.9)	81.0 (26.3)

* From Caffrey (1983).

period (Fig. 4) and there was little net change in residual water elevation (Fig. 2). Nitrate concentrations were very low, averaging 1-3 µM (Table 1), and were significantly related to salinity (r = 0.20) and SRP levels (r=0.63). Ammonia concentrations were high on falling tides (Fig. 4), although the maximum concentration of 12.5 µM occurred on the rising tide. This pattern occurred in the lower bay because of NH_4^+-rich water flowing out of the marshes on falling tides and NH_4^+-rich water coming out of Oyster Bayou on the flood tides (Caffrey 1983). In general, the nutrient concentrations for this sampling period were lower than the average concentrations found in the lower bay (Table 1).

Gulf return conditions with moderate easterly winds prevailed prior to the beginning of the third sampling period. This changed to frontal gulf return conditions with light winds during the first hours of sampling and finally changed to gulf return conditions for the remainder of the study. Salinity was less than 1. Nitrate concentrations (Fig. 5) for the first 24 h of the study averaged about 50 µM, similar to the annual average NO_3^- concentration for the upper bay. Nitrate levels more than doubled (120 µM) at 900 h and 1300 h, as did suspended sediments, which increased from 50 mg l^{-1} to 350 mg l^{-1}. Nitrate concentrations were significantly correlated with tide (r = 0.58), with TP (r = 0.57), and SS (r = 0.68). TKN was correlated with wind stress (r = 0.58). Ammonia concentrations were highest on the falling tide and correlated with SRP (r = 0.76).

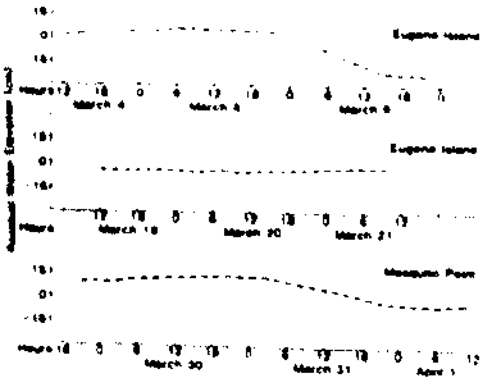

Fig. 2. Residual water elevation for March 4–6 and March 19–21, 1982, at Eugene Island and for March 30–April 1, 1982, at Mosquito Point.

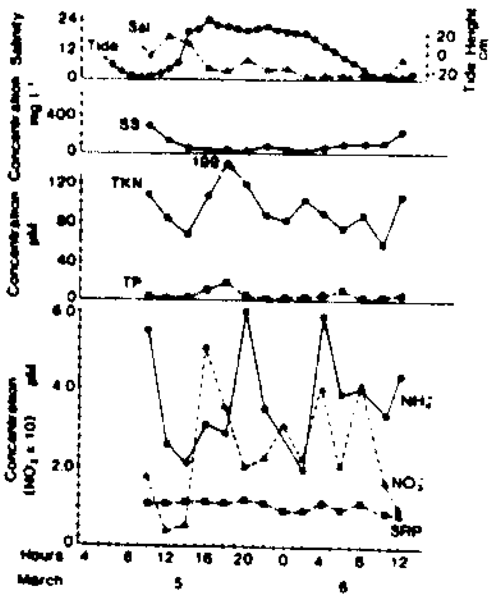

Fig. 3. Tide height, salinity, suspended sediments (SS), total Kjeldahl nitrogen (TKN), total phosphorus (TP), ammonium (NH_4^+), nitrate and nitrite (NO_3^-), and soluble reactive phosphate (SRP) during March 5–6, 1982, in lower Fourleague Bay.

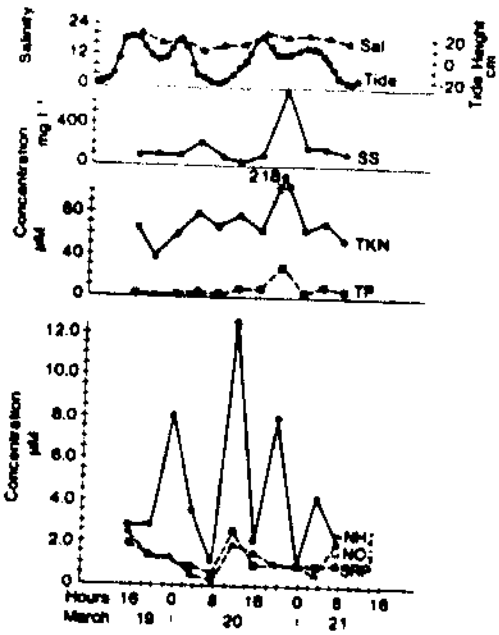

Fig. 4. Tide height, salinity, suspended sediments (SS), total Kjeldahl nitrogen (TKN), total phosphorus (TP), ammonium (NH_4^+), nitrate and nitrite (NO_3^-), and soluble reactive phosphate (SRP) during March 19–21, 1982, in lower Fourleague Bay.

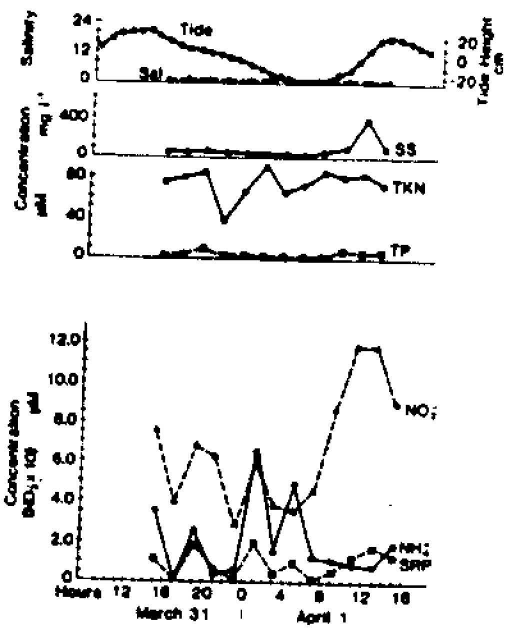

Fig. 5. Tide height, salinity, suspended sediments (SS), total Kjeldahl nitrogen (TKN), total phosphorus (TP), ammonium (NH_4^+), nitrate and nitrite (NO_3^-), and soluble reactive phosphate (SRP) during March 31–April 1, 1982, in upper Fourleague Bay.

These results illustrate how the physical factors of tide, winds, and river discharge interact to control nutrient concentrations. In March, 1982, the Atchafalaya River was at peak discharge of 9,330 m^3s^{-1} (U.S. Geological Survey 1982). Because of Fourleague Bay's proximity to the mouth of the Atchafalaya, one would expect the bay to be inundated with fresh water high in NO_3^-, TKN, TP as observed during the first study. However, the results from the second and third sampling periods indicate how factors, other than river discharge, also affect nutrient concentrations. During periods of gulf return with steady southeasterly winds, river water is directed away from the bay and water is set up along the coast (Denes 1983). This was the case on March 31 when winds diminished after several days of gulf return conditions and strong southeasterly winds. The rising tide brought river water into the upper bay, causing dramatic increases in some nutrient concentrations. During the second study, winds were consistently southeasterly and residual water elevations did not change. Consequently, water from the Atchafalaya River did not reach the lower bay as it did in the first sampling period.

These results emphasize the time scales of variability within Fourleague Bay during March. Riverine discharge, frontal passages, and tides act over seasonal, 3-d to 5-3, and 12-h to 24-h cycles, respectively. Even during periods when one would expect the river discharge to dominate, climatic conditions can have a significant effect. Part of the reason for this is the configuration of the bay and the location of the Atchafalaya River inflow relative to Fourleague Bay. The river plume is directed southeast, south, or southwest, depending on the wind stress, and could have reduced flow into the Gulf of Mexico because of increased water elevations along the coast (Denes 1983). Because of this, Fourleague Bay does not receive a steady input of river water. Instead, pulses of river water enter the bay on rising tides and during frontal overrunning conditions.

The effect of the Atchafalaya River on nutrient concentrations in Fourleague Bay appears highly variable, much more so than in typical river-dominated estuaries such as Chesapeake Bay (Carpenter et al. 1969), Hudson River (Malone 1984), Patuxent River (Kemp et al. 1982), and other East Coast estuaries (Nixon and Pilson 1983). The pattern of high spring NO_3^- concentrations observed in Fourleague Bay is characteristic of many river-dominated estuaries. A similar seasonal pattern for suspended sediments occurs in the Gironde estuary (Allen et al. 1977). Variability in nutrient and suspended sediment concentrations over time scales of hours to days is also significant in Fourleague Bay and has been observed in other estuarine systems such as the Columbia River (Gelfenbaum 1983) and tidal Creeks (Heinle and Flemer 1976, Wolaver et al. 1984).

These studies and our observations suggest that variability on time scales of hours to days may be as important as seasonal variability of nutrient concentrations. This is particularly true where physical forces such as tides and frontal passages operate to transport water with different nutrient and suspended sediment compositions through an estuary, as in Fourleague Bay.

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SEASONAL VARIATIONS IN ADVECTIVE NUTRIENT FLUXES IN FOURLEAGUE BAY, LOUISIANA*

C.J. Madden

INTRODUCTION

Water and nutrient flows in Fourleague Bay were measured in February, April and September, 1982 at the upper bay passage which receives freshwater input, the mouth of the estuary at Oyster Bayou, and several bayous which drain into the estuary. The studies were made in spring and fall under conditions representative of the major hydrological conditions (flood and low water) and climatic regimes (frontal passage, calm) which occur in the area, permitting accurate nutrient flow "snapshots" under the annual environmental extremes of the system.

The trend of research in estuaries has been toward intensive process measurement of the system and away from annual budgeting. Fourleague Bay, Louisiana, which undergoes a major transformation from river-dominated estuary in spring to near-coastal lagoon in fall, is subjected to a wide range of hydrologic and meteorological changes over the course of the year. This paper investigates how physical forcings influence advective nutrient fluxes across the boundaries of the shallow, river-dominated estuary.

In each tidal cycle study, five entrances to Fourleague Bay were sampled continuously for water flow and water quality at hourly intervals over fifty hours or two tidal cycles. Stations were located as follows: three to five stations across the main entrance to the bay, one in Oyster Bayou, the narrow mouth of the estuary, and one each in Creole Pass, Carencro Bayou, and Blue Hammock Bayou, three major bayous around the perimeter of the bay which drain fresh, brackish and salt marshes (Fig. 1).

Spring flood studies in February and April were carried out under high river flow conditions. During February, winds were predominantly from the north-northwest, encouraging riverine flow into the bay; during April, winds shifted to the south-southeast creating an obstructing head and preventing water from flowing out of the lower estuary to the gulf. In September tidal fluxes were measured during the lowest river flow of the year and winds were light and variable.

AREA DESCRIPTION

Fourleague Bay is a large (100 km^2), shallow bay located to the east of the mouth of the Atchafalaya River on the central Louisiana coast. Due to the proximity of Fourleague Bay to one of the largest rivers on the continent, it at times receives substantial sediment and freshwater inputs from adjacent Atchafalaya Bay. Fourleague Bay (Fig. 1) connects with Atchafalaya Bay via a 2.5 km wide passage, and communicates with the Gulf of Mexico at its south end through a 0.3 km wide tidal inlet called Oyster Bayou. Salt water from the Gulf of Mexico enters directly into the lower end of the bay through this bayou, where tidal currents often exceed 1 m/s. The mean depth of the entire bay is 1.5 m, which contributes to a well-mixed water column. There are no appreciable vertical salinity or nutrient gradients, except in a large scour hole at the entrance to the bay, which has a depth of 7 m, and in Oyster Bayou at the bay mouth, which at its deepest attains a depth of 8 m.

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*This chapter is part of a thesis submitted in 1986 to the graduate faculty of Louisiana State University in partial fulfillment of the requirements for a M.S. in the Department of Marine Sciences.

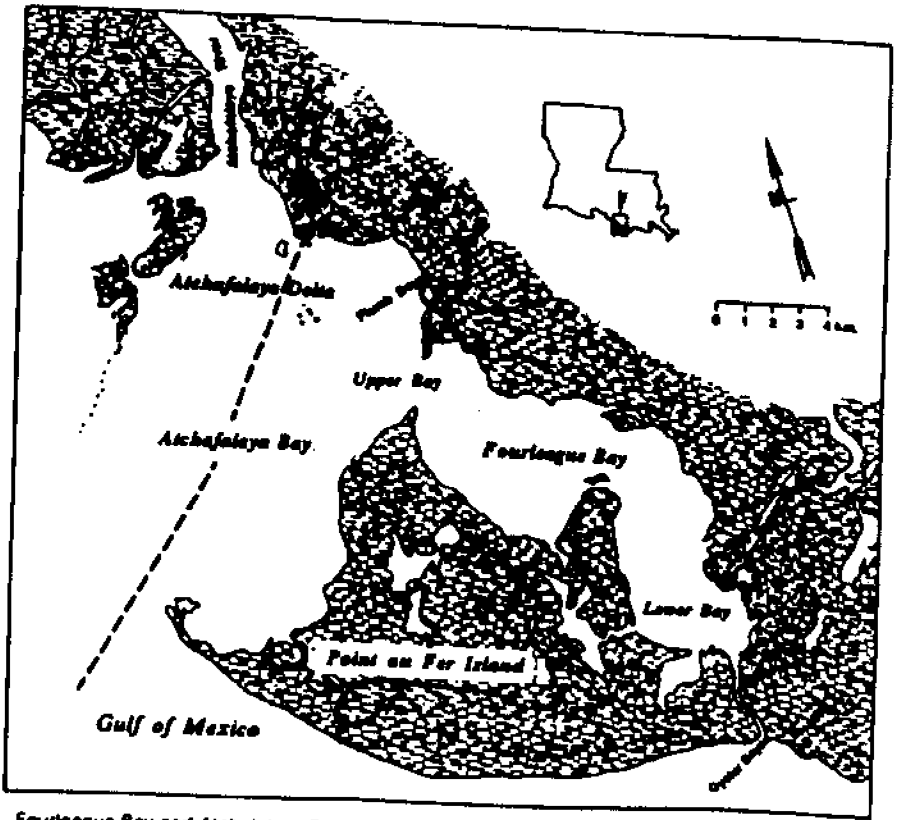


Figure 1. Fourleague Bay and Atchafalaya Bay, Louisiana. Dashed lines represent proposed levee extensions.

The bay is oriented roughly NW-SE in its upper, fresher half and N-S in its saltier lower half; the orientation is important because prevailing northwesterly winds enhance the flow of riverine water into the bay. The bay is surrounded by fresh, brackish and saline marshes.

The Atchafalaya River carries between 30% and 50% of the flow of the lower Mississippi River and debouches into Atchafalaya Bay where in 1973 a new delta attained sub-aerial expression, the easternmost lobes of which approach to within 3 km of the entrance to Fourleague Bay. Atchafalaya River water entering Fourleague Bay is highly turbid and carries high concentrations of silt and clay sediments which are responsible for active and ongoing land-building in the Terrebonne marshes that surround Fourleague Bay (Baumann and Adams 1981, Miller 1983). The lower Atchafalaya region represents the only area of active land-building in coastal Louisiana. The build-up of the marshes is facilitated by the many bayous and tidal creeks around the perimeter of Fourleague Bay which permit tidal exchange between the bay and surrounding marsh (Baumann et al. 1984).

METHODS

On the intensive tidal cycle studies, carried out in February, April and September, 1982, each over two consecutive tidal cycles (~50 h), the three major bayous (Creole Pass, Big Carencro Bayou, and Blue Hammock Bayou) and two entrances to Fourleague Bay (Upper Bay entrance and Oyster Bayou) were sampled simultaneously. Nutrient samples and current and tide measurements were taken at one station in each bayou, and at three to five stations across the main entrance to the bay hourly or more frequently for the duration of each study. Water fluxes through each cross-section were calculated by Denes (1983) using the following equation:

$$Q = V w (z + r_0)$$

where Q = transport (m^3/s), V = average velocity through the passage (m^3/s), w = average width of passage (m), z = average water depth (m), and r_0 = the change in water depth (m).

Instantaneous nutrient fluxes were calculated by multiplying mean laterally averaged nutrient concentrations by mean hourly water flux. Net fluxes (E) of parameters were calculated by summing instantaneous flows as in Platt and Conover (1971) using the following equation:

$$E = \sum_{j=1}^{n} Q_j(t)\ P_j(t)$$

where Q (t) is mean water flux and P (t) is nutrient concentration in µg-at/l during interval j.

Flow data were modified from published U. S. Army Corps of Engineers documents which report daily river discharge data measured at Simmesport, Louisiana. Simmesport is upriver of all tidal effects which bias stage-discharge measurements. Tidal effects reach about fifty river miles inland from the mouth in the Atchafalaya River (CWR 1978).)

Chlorophyll *a*, nitrate-nitrite, ammonium, and ortho-phosphate concentrations, conductivity, temperature, water depth, secchi depth, salinity and suspended sediment concentration were measured for this study. For each of the direct measurements of water properties and nutrient and chlorophyll analyses, water samples were taken from a depth of 30 to 50 cm for surface readings. When depth series were taken, Van Dorn samplers were used to recover water samples from approximately 50 cm off the bottom and, where depth permitted, at intervals between surface and bottom samples. Because most of the station depths were 1.5 m or less, generally bottom samples were taken only at the deeper stations, such as in bayou mouths.

Inorganic nutrient samples were filtered immediately through Swinny™ filtration devices using 0.6 µ glass fiber filters. Tortuous pore glass fiber were used because clogging from the high suspended solid load rendered capillary pore filters unusable. The filtrate was collected in pre-rinsed 5 ml plastic Auto-Analyzer vials (AAVs) and placed immediately on dry ice. We found this method of sample storage very convenient as such small sample volumes would freeze within 5 min and remain frozen for several days if necessary and large numbers of samples could be collected without space becoming a problem.

Water samples for chlorophyll *a* were collected in 300 ml Nalgene bottles and stored in the dark on ice until they could be filtered. Filtration of chlorophyll samples was almost always completed within six hours of sampling and always within 12 hours. Due to the turbidity of the water, usually only 50 to 100 ml was filtered for chlorophyll analysis. Tortuous pore nitrocellulose membrane filter pads, with a pore size of 0.45 µ were frozen immediately after filtration of water samples, and were transferred to the laboratory for storage at -20° C.

In the laboratory water samples for inorganic nutrients were thawed and analyzed for nitrate-nitrite, ammonium and ortho-phosphate on a Technicon Auto-Analyzer II as described in Methods for Chemical Analysis of Water and Wastes (USEPA 1983). Chlorophyll *a* was determined by dissolving the filter pads containing the sample in 25 ml acetone and measuring per cent absorbance of the solution on a Varian Techtron Model 635 Spectrophotometer at wavelengths of 665, 645, 630, 580 nm. Chlorophyll *a* concentrations were calculated using the equations developed by Parsons and Strickland (1972).

Suspended sediment concentrations were determined gravimetrically by filtering 100 to 200 ml of water through pre-weighed Gelman GFC glass fiber filters of pore size 0.6 µ. Filterpads were dried at 65° C for 24 h and weighed to determine sediment load by difference. Suspended solid concentrations were calculated as described in Madden (1986).

Salinity was measured in the field using a Beckman RS-5 salinometer and an American Optical temperature-compensating refractometer, and in the laboratory using a AutoSal 9000 against which the field instruments were intercalibrated. Dissolved oxygen concentrations were measured in the field using an Orbisphere Model 2714 oxygen meter modified for field use, and YSI Model 57 oxygen meters, which are temperature and salinity compensated.

RESULTS

Time Series Studies of Advective Nutrient Fluxes

Atchafalaya discharge averaged 7788 m^3/s in February, and 8779 m^3/s during the April study. Water flux through the upper bay entrance into Fourleague Bay averaged approximately +150 m^3/s during each study (Denes 1983). This equals a turnover period of about 10 days for the bay volume. During September, Atchafalaya discharge averaged 4366 m^3/s and net water transport at the upper bay entrance averaged +15 m^3/s into the bay, corresponding to a water renewal rate of 107 days for the estuary.

Nutrient Concentrations in Riverine Inputs

Import-export dynamics of nutrients in Fourleague Bay varied greatly over the year in response to differences in riverflow, tide and weather conditions. The rate of advective import of nutrients to Fourleague Bay was dependent on net water flux and on the concentration of nutrients in the inflowing water, both of which varied seasonally. Nitrate concentration in water entering the upper bay varied from 30 to nearly 200 µg-at/l during the three studies and from 0 to 25 µg-at/l for ammonium. The intensive time series studies at the bay entrance gives an opportunity to determine the magnitude of short-term variations in nutrient concentrations.

During each tidal cycle trip, nutrient concentrations in the upper and lower bay differed significantly (Table 1). Upper and lower bay stations showed strong inter-trip concentration differences as well, indicating that the overall nutrient regime of the bay was significantly different during each tidal cycle study (Table 2). In February, water and nutrient fluxes through the upper bay entrance were measured at five stations across the width of the upper bay inlet. Two stations were dropped from the upper bay cross-section for the subsequent tidal cycle studies without significantly reducing the precision of the nutrient profiles.

Upper Bay Nutrient Concentrations

The mean nitrate concentration at the upper bay entrance was 65.45 ± 6.56 µg-at/l during the February study, increased to 84.38 ± 19.69 µg-at/l in April, and declined to 33.33 ± 14.99 µg-at/l in September (Fig. 2). Ammonium concentrations in February averaged 8.2 ± 1.72 µg-at/l at the upper bay entrance; in April ammonium fell to 2.49 ± 1.55 µg-at/l, and in September, was highly variable throughout the course of the 50-hour sampling period, averaging 5.15 ± 5.22 µg-at/l. Phosphate concentrations in February varied little around an average of 0.97 ± 0.29 µg-at/l in the upper bay, in April increased to 1.37 ± 0.44 µg-at/l and in September, averaged 1.51 ± 0.56 µg-at/l.

Oyster Bayou Nutrient Concentrations

Concentrations in the lower bay at Oyster Bayou were far more variable than those in the upper bay owing to the influence of the tidal import of seawater. In February with the high riverine flow of nitrate and freshwater into the bay, high concentrations of nitrate and relatively low salinities were measured in Oyster Bayou, where the mean concentration was 44.23 ± 17.98 µg-at/l, ranging from 8.9 to 63.9 µg-at/l. This was significantly lower than at the upper bay (65.45 µg-at/l) for the same period (p = 0.0001, t-test; see Table 1).

NITRATE

UPPER BAY

LOWER BAY	FEB	APR	SEP
FEB	65/44 p<.0005	▨	▨
APR	▨	84/16 p<.0005	▨
SEP	▨	▨	33/1.3 p<.0005

AMMONIUM

UPPER BAY

LOWER BAY	FEB	APR	SEP
FEB	5.6/8.2 p<.0005	▨	▨
APR	▨	2.4/5.5 p<.0005	▨
SEP	▨	▨	5.1/5.1 .01<p<.025

PHOSPHATE

UPPER BAY

LOWER BAY	FEB	APR	SEP
FEB	.97/1.4 p<.005	▨	▨
APR	▨	1.4/.43 p<.0005	▨
SEP	▨	▨	1.5/1.2 .005<p<.01

Table 1. Probability matrices showing that nutrient concentrations at upper and lower bay stations are significantly different for each tidal cycle study. Values are displayed as lower bay/upper bay and concentrations are µg-at/l.

In April, despite higher nitrate levels in the upper bay (84.38 µg-at/l), Oyster Bayou concentrations were much lower than those measured in the February study, averaging 16.55 ± 11.98 µg-at/l and ranging from 1.5 to 39.7 µg-at/l. In September, nitrate in the lower bay was low, averaging only 1.33 ± 0.7 µg-at/l and ranging from 0.60 to 3.8 µg-at/l, significantly lower than in the upper bay (33.34 µg-at/l) at the p = 0.0001 level, (t-test).

Ammonium concentrations in Oyster Bayou during February ranged from "trace" to 11.25 µg-at/l and averaged 5.63 ± 1.8 µg-at/l, (upper bay concentration,

UPPER BAY

	FEB	APR	SEP	
FEB		65.7/84.4 p<.0005	65.7/33.3 p<.0005	NITRATE
APR	2.5/8.2 p<.0005		84.4/33.3 p<.0005	
SEP	5.1/8.2 .0005<p<.005	5.1/2.5 .0005<p<.005		
	AMMONIUM			

	FEB	APR	SEP	
FEB		.97/1.36 p<.0005	.97/1.5 p<.0005	PHOSPHATE
APR			1.36/1.5 .05<p NS	

LOWER BAY

	FEB	APR	SEP	
FEB		44/16.6 p<.0005	44/1.5 p<.0005	NITRATE
APR	5.5/6.0 .1<p NS		16.6/1.5 p<.0005	
SEP	6.2/6.0 .01<p<.025	6.2/5.5 .0005<p<.005		
	AMMONIUM			

	FEB	APR	SEP	
FEB		1.5/.43 p<.0005	1.5/1.23 .05<p NS	PHOSPHATE
APR			.43/1.23 p<.0005	

Table 2. Trip-to-trip comparison of nutrient concentrations at upper and lower bay during tidal cycle studies. Left hand numbers are row months and right hand numbers are column months concentration in µg-at/l.

8.2 µg-at/l, p = 0.0001). In April ammonium at Oyster Bayou averaging 5.54 ± 2.99 µg-at/l was about twice as high as the upper bay (2.49 µg-at/l, p = 0.0001). During the September study, ammonium concentrations averaged 7.11 ± 5.4 µg-at/l, highest of the three studies, ranging from 0.7 to 21.7 µg-at/l. These values were higher, although not significantly, than the upper bay concentration of 5.15 µg-at/l.

An ortho-phosphate concentration of 1.49 ± 1.01 µg-at/l in Oyster Bayou in February was the highest level recorded at that station during the tidal cycle studies, and was higher than upper bay concentration of 0.97 (p = 0.003), suggesting phosphate enrichment within the bay or in nearshore gulf waters. In April the mean phosphate concentration of 0.43 ± 0.12 µg-at/l Oyster Bayou was the lowest for the year and only a third that in the upper bay (1.37 µg-at/), a significant difference at the p = 0.0001 level. September phosphate values averaged 1.16 ± 0.42 µg-at/l in the lower bay, slightly, but significantly, lower than in the upper bay (1.51~± .56, p = .002).

In summary, nitrate concentrations were high in spring and low in fall, bay-wide. Spatially, nitrate declined predictably from the upper to lower bay in all seasons. Ammonium was high in the upper bay in February, low in April, and high again in September. This pattern corresponds to the annual major and minor peaks observed on independent synoptic transects for this study. There was a tendency for ammonium to increase in the down bay direction during the warmer months. Ortho-phosphate increased from spring to fall in the upper bay; spatially, it declined toward the lower bay in the warmer months.

Tidal Fluxes of Nutrients

Upper Fourleague Bay is influenced by Gulf of Mexico tides via Atchafalaya Bay, and flow through the inlet was therefore not uni-directional into the bay from the Atchafalaya River during these studies; flow was directed out of Fourleague Bay toward the river on ebb tides. During most tidal cycles, water entering the upper bay on flood tides was significantly different in nutrient composition than the water leaving on ebb tides (Figs. 3-5). This was also true in the lower bay at Oyster Bayou. The effect was probably due to nutrient transformations and to the mixing of water masses inside the bay. In the average concentrations reported above, all values at each sampling station for the 50-hour study were used to obtain an average daily concentration. It is worthwhile to further investigate the sub-tidal scale components of the mean nutrient values.

For this analysis, nutrient profiles, which usually showed clear bimodal peaks in nutrient concentration during each of two tidal cycles in each study for each two-day period, were split into quarter-cycle segments (eg. Fig. 6). During the course of a tidal cycle, fluctuations in nutrient concentration often followed but lagged fluctuations in current direction by intervals of one or more hours. This was likely due to a time-dependent component of nutrient transformation within a water parcel after entering the bay. When current direction changed from flood to ebb-directed in the upper bay, the nutrient composition of the first water samples taken on the ebb tide would resemble that of the riverine water that had last flowed into the upper bay. As ebb flow continued, water from progressively farther inside the bay began to pass the sampling point. Changes in nutrient concentrations which had occurred in the upper bay were manifested as progressive shifts in concentration over time. The reverse of this processes occurred during flood tide.

The relationship between current direction and nutrient concentration was investigated by simple and multivariate regressions and phase-lagging of the nutrient

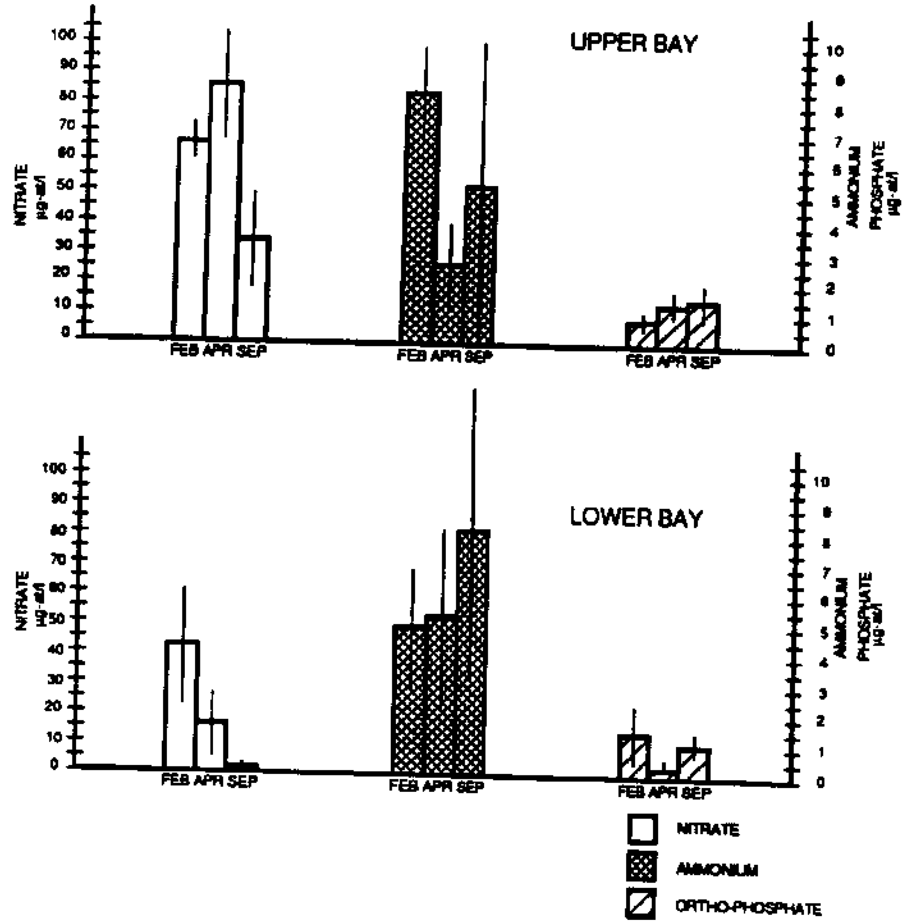


Figure 2. Mean nutrient concentrations at upper and lower bay stations during three tidal cycle studies.

time series. Nutrient concentrations were used as the dependent variable and tide flux was broken into two components with the absolute flow rate and the flow direction as independent variables. Regressions were iteratively run with the nutrient concentration profile progressively phase-shifted backward by one-hour intervals. The total hours of time shift which produced the highest correlation was assumed to depend on both the flow and rate processes involved in nutrient transformations in the bay.

I assume that the lag time represents an index of the transforming power of the biological processes within the bay. For example, if the greatest disparity between flood and ebb concentrations occurred at a three hour lag of the data with respect to flow, the bay interior could be considered less biogeochemically active than a series which showed a significant disparity after a one hour lag. Obviously this is a grand simplification because processes other than biological transformation can induce differences in concentrations. These include mixing of different water masses and dilution by gulf water within the bay. Monitoring of salinity can control for the latter variable. During both spring studies, no salinity was detected in water flowing in or out of the upper bay. As for other sources of water differing in nutrient concentrations, bayous could provide a source of such variation, but as explained later in this report, bayou flows, although significant, were small compared to the volume of the bay. Thus, with a few simplifying assumptions, we consider the extent of time lag to contain some information concerning the biological activity of the bay water column and sediment-water column processes.

Simple regressions of concentration versus the water flow rate, with plus or minus indicating flow direc-

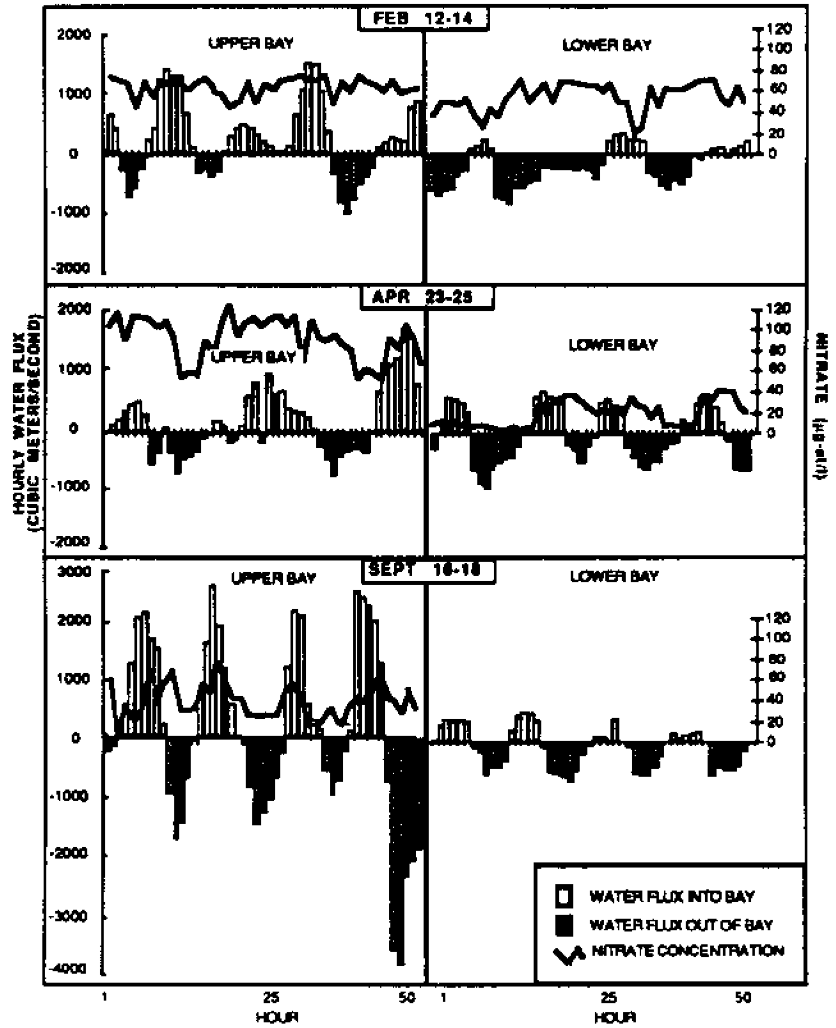


Figure 3. Nitrate concentrations and water flux rates in upper and lower Fourleague Bay during tidal cycle studies in February, April, and September, 1982.

tion, gave the highest correlations, so the separate multivariate component of direction was dropped. Thus, nitrate for example would theoretically show its lowest concentration during the highest ebb flow from the bay and its highest concentration during its highest flood into the bay with a smooth linear progression between these two extremes. This is not an entirely perfect model because in reality during slack high tide after a strong flood flow, nitrate concentration would remain high, but flow would be zero and vice versa after ebb flow. However, because the samples were taken approximately hourly, and slack tides comprised a relatively small part of the total sampling period, these errors were minimized and the flow-concentration relationship proved surprisingly strong.

The time-series profile of nitrate concentration at the lower bay station in April provides an excellent example of the effect of phase-lagging on nutrient concentration and tidal flux correlation (Fig. 6). Nitrate concentrations varied regularly throughout each tidal cycle, with four peaks and four troughs approximately corresponding to changes in the tide direction, peaks occurring on ebb tides (water flowing out of the bay). However, the nutrient profile in this example is clearly offset from the tidal signature by several hours. By shifting the offset concentration backwards in time, the r^2 of the relationship was increased from 0.03 to 0.68 (Fig. 7).

Upper Bay Concentration Profile

Upper bay nitrate, ammonium and phosphate concentration variations in the February study tracked water

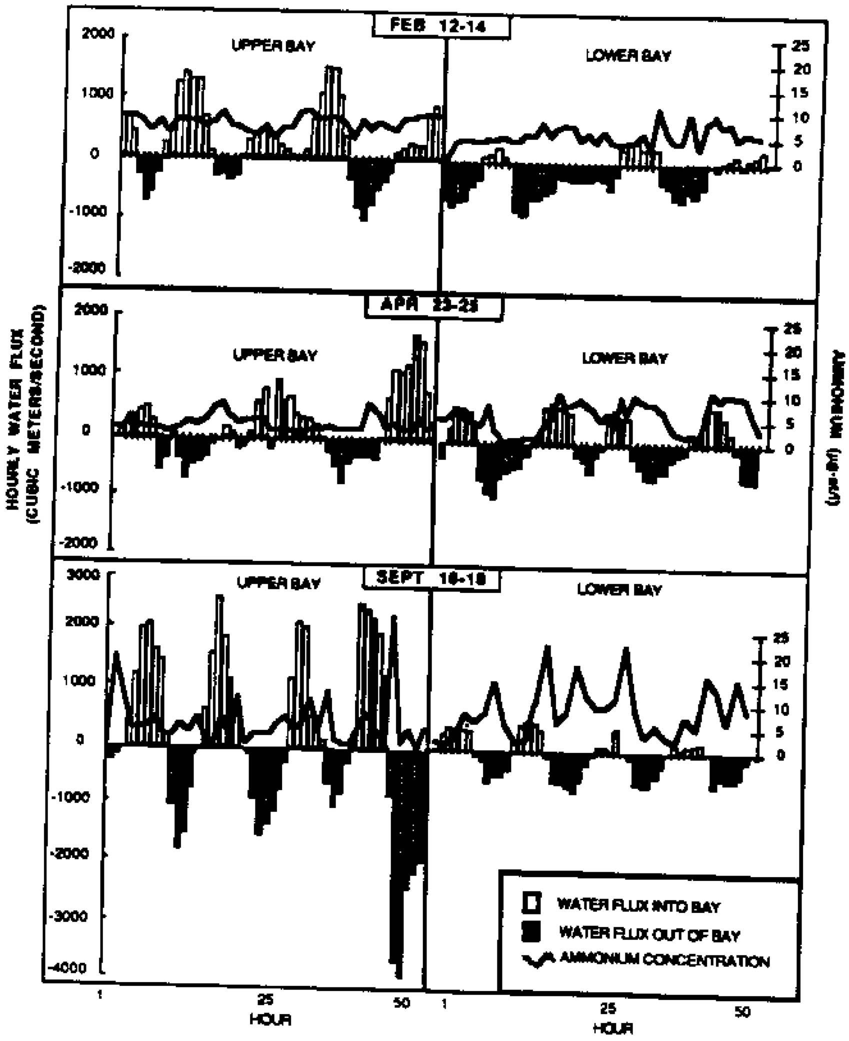


Figure 4. Ammonium concentrations and water flux rates in upper and lower Fourleague Bay during tidal cycle studies in February, April, and September, 1982.

flow closely. Correlations of nitrate and phosphate versus water flow were significant. Nitrate versus flow had an r^2 of 0.16 (p=.01) after a two hour lag and ammonium showed a significant correlation with water flow (r^2 = 0.14, p=.025) with no lag time (Fig. 8). Phosphate versus flow had an r^2 of 0.25 (p=.002) after lagging the data series for two hours (Fig. 9). All other lag intervals, including 0, were much less significant.

Correlations of nutrient concentrations with each other were highly significant, evidence that nutrients varied together in regular ways which were not entirely explained by water flux. R^2 for ammonium versus nitrate was 0.29 (p=.001), for ammonium versus phosphate was 0.30 (p=.0006), and for nitrate versus phosphate was 0.56 (p=.0001) (Fig. 10).

In April in the upper bay, nitrate was strongly correlated with water flow (r^2= 0.28, p=.001) after lagging for four hours (Fig. 11). Ammonium was well correlated after lagging five hours (r^2= 0.36, p=.002), but the relationship was the reverse of that in February: ammonium concentrations were significantly higher on the ebb than on the flood tides indicating export from the bay. Phosphate showed no relationship with water flow, but a significant one with nitrate (r^2 = 0.21, p=.002) (Fig. 12); ammonium showed some correlation with nitrate (r^2 = 0.17, p=.008) but none with phosphate.

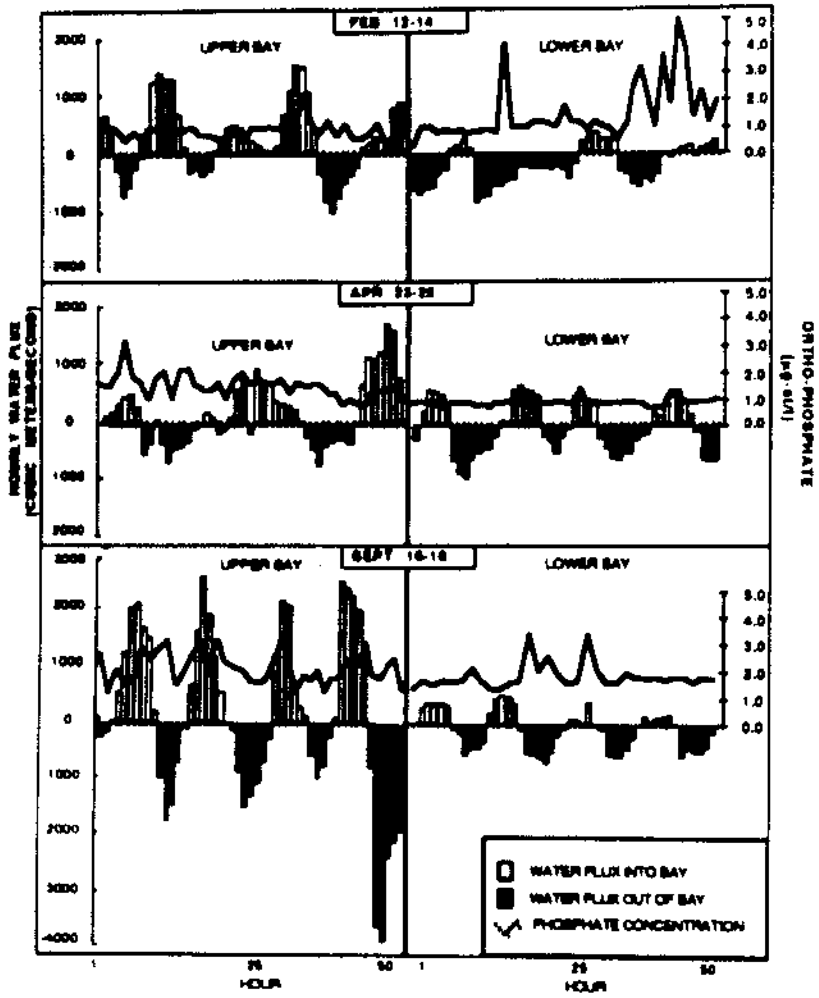


Figure 5. Phosphate concentrations and water flux rates in upper and lower Fourleague Bay during tidal cycle studies in February, April, and September, 1982.

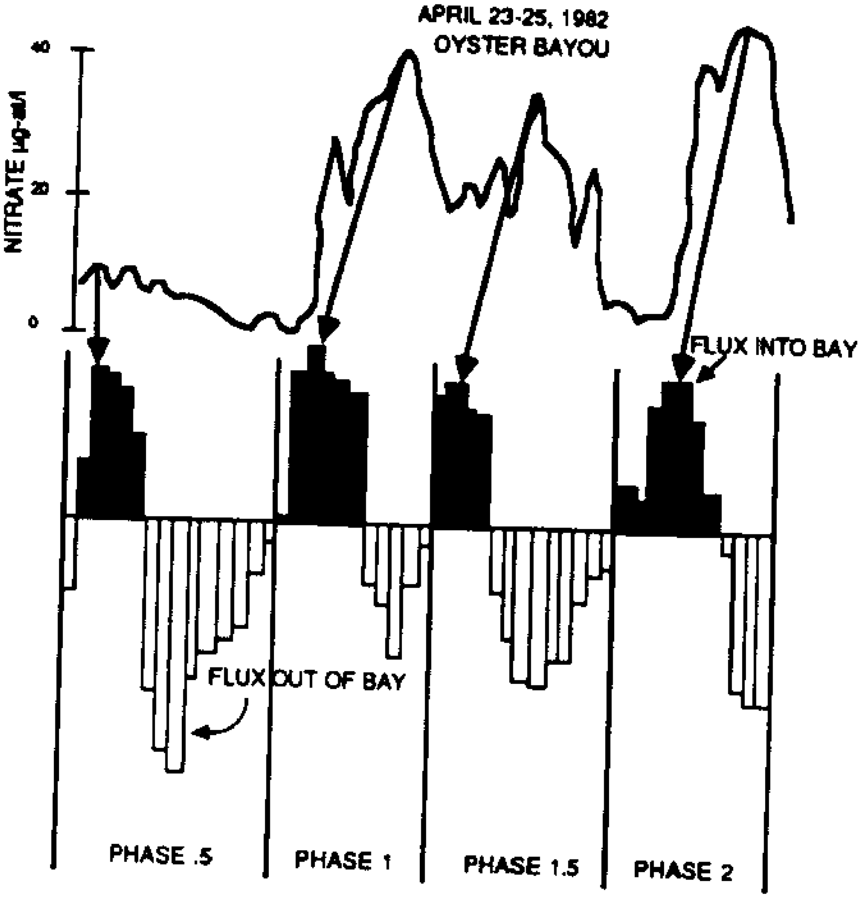
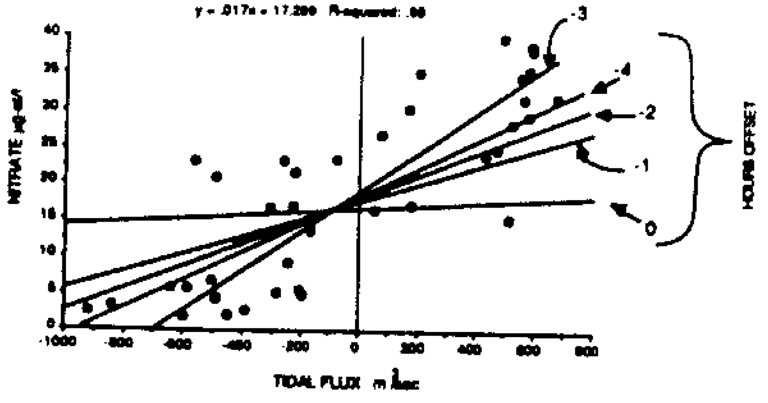


Figure 6. Example of a tidal cycle profile of nitrate concentration and water flux recorded over two tidal cycles showing division of data into half-cycle phases and showing offset of nutrient and water flux trends.



HOURS LAGGED	R-SQUARED	SIGNIFICANCE
0	03	.25<p
-1	.17	.005<p<.01
-2	.30	0001<p<.005
-3	.68	p<.0001
-4	.39	p<.0001

Figure 7. Phase lag analysis for nitrate, April 23-25, 1982, at Oyster Bayou. Graph illustrates results of progressively offsetting the nitrate concentration and regressing against water flux. Significance and correlation coefficient maximize when nitrate concentrations are lagged three hours.

In September nitrate (r^2 = 0.25, p= .001) and phosphate (r^2 = 0.31, p=.0002) showed a strong relationship with water flow, higher on the floods than on the ebbs, after lagging two hours (Fig. 12). There is some indication that ammonium was higher on the outgoing flows than on the inflows, although the relationship is weak. Nitrate and phosphate tracked each other closely (r^2 = 0.73, p= .0001) while ammonium was not correlated with either nitrate or phosphate.

Oyster Bayou Concentration Profile

In the lower bay at Oyster Bayou during the February study, nitrate correlated with water flow (r^2 = 0.23), due principally to two sharp drops in concentration during flood tides (Fig. 13). Otherwise the concentration of nitrate varied erratically from 40-60 µg-at/l. But the concentration drop on flood tides was so significant that the relationship was significant (p = .001) and a strong inference can be made that Fourleague Bay was importing water low in nitrate from the Gulf of Mexico at these times, and exporting water high in nitrate from the bay. Ammonium and phosphate showed strong spikes during ebb flows but no significant relationship with water flow due to variability in the data.

In April, very strong correlations were found between nitrate and water flux and ammonium and water flux after lagging for 2-3 hours (Fig. 14). High concentrations of nitrate (r^2 = 0.68, p = .0001) entered the bay on flood tides from the Gulf of Mexico, opposite the pattern observed in February. Ammonium also increased on flood tides and declined on ebb flows (r^2 = 0.60, p = .0001). Phosphate showed no correlation with water flow but high correlations between each nutrient were observed (N vs. A 0.54, A vs. P 0.17).

In September, nitrate levels were low in the bay and concentrations flowing out of Oyster Bayou on ebb tides dropped sharply (Fig. 15); on flood tides, nitrate levels rose (r^2 = 0.32, p = .0001). Ammonium, although erratic, was also significant with an r^2 of .25 (p = .05). Nitrate and ammonium (r^2 = 0.54, p = .0001) and ammonium and phosphate (r^2 = 0.41, p = .0001) were well correlated showing some relationship between them that was not related to water flux .

Tide-Specific Nutrient Concentrations-Upper Bay Entrance

To determine average nutrient concentrations as a function of tide direction, separate mean concentrations

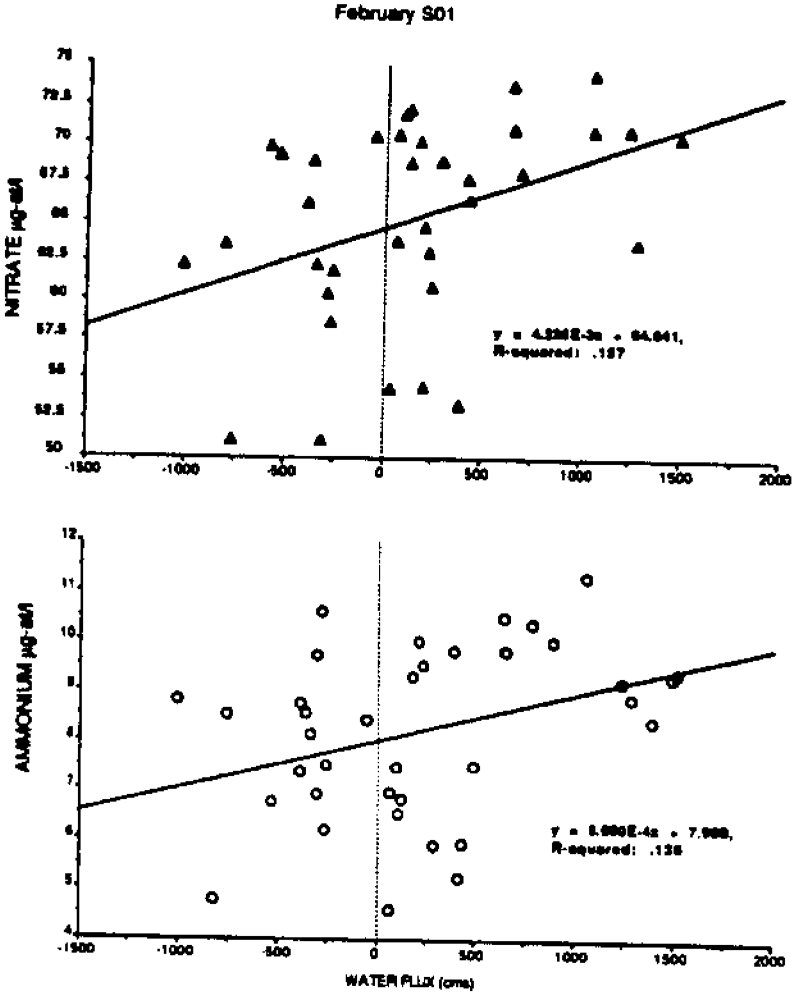


Figure 8. Nitrate and ammonium versus water flux through the upper bay at station SO1 in February, 1982, after lagging 2 hours for nitrate and zero hours for ammonium. Positive water flow is into the bay. See text for explanation.

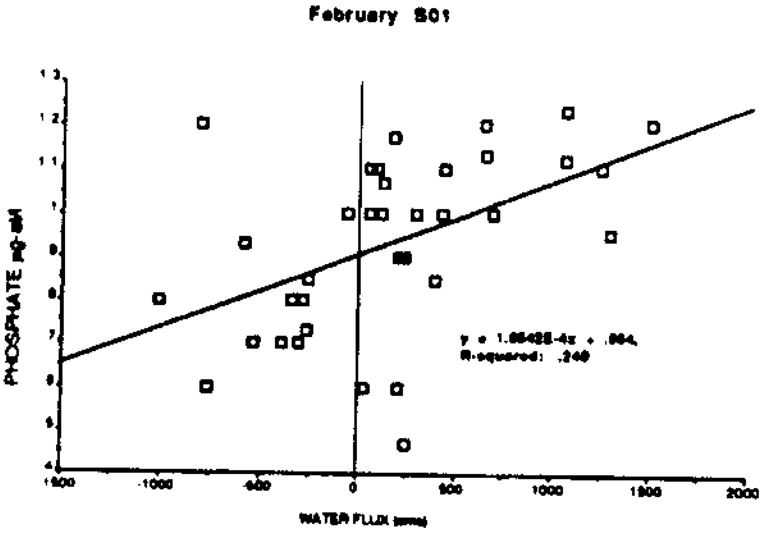


Figure 9. Phosphate versus water flux through the upper bay at station SO1 in February, 1982, after lagging 2 hours. Positive water flow is into bay. See text for explanantion.

were determined for the period during inflowing tides and for ebbing tides for each tidal cycle study. Then, based on the above analysis of lag time, the means were recalculated for several lagged configurations of the time series. The configuration which produced the best correlation coefficient determined the optimum differential between ebb and flood concentrations.

Nitrate. In February, nitrate concentrations in the upper bay varied between 51.1 and 74.37 µg-at/l over the fifty hour study period. Mean nitrate concentration in both the inflowing and outflowing water was 66 µg-at/l (Fig. 16). After lagging the data for 2 hours, flood concentrations remained at 66.68 µg-at/l, and ebb concentrations fell to 63.51 µg-at/l, which was not significantly different (p = .08, t-test). In April, without lagging, flood and ebb flows had mean nitrate levels of 88.3 and 77.8 µg-at/l. After lagging 4 hours the average nitrate concentration on flood tides was 90.0 µg-at/l and 74.7 µg-at/l on ebb tides; these concentrations were statistically different from each other (p = .005). Nitrate concentrations in September fluctuated within a range of 1.7 to 65.3 µg-at/l. Without lagging, both flood and ebb concentrations were about 33 µg-at/l. After lagging 2 hours, average concentration on the flood tide was 38.1 µg-at/l and on the ebb tide was significantly lower at 25.2 µg-at/l, (p = .006).

Ammonium. Ammonium concentrations in ebb and flood flows displayed a much larger variance over each tidal cycle than did nitrate (Fig.17). In February, ammonium concentrations in the upper bay averaged 8.55 µg-at/l on flood tides and 7.61 µg-at/l on ebbs and were neither significantly correlated with water direction nor significantly different from each other.

In April, ammonium concentrations without lagging averaged 2.5 and 2.7 µg-at/l on ebb and flood flows. After a 5 hour lag, on ebb flows concentrations averaged 3.3 µg-at/l, significantly higher than the 1.85 µg-at/l mean on flood flows (p = .008, t-test). In September, there was no relationship between ammonium and water flow, making interpretation of the tidal changes in concentration difficult. After lagging 1 hour, ebb concentrations increased, but lagging 2 more hours produced an decrease in ebb concentrations to 2.65 µg-at/l, while flood concentrations increased to 5.89 µg-at/l.

Phosphate. In February, phosphate concentrations were well correlated with flow direction, and mean concentrations on the flood (1.03 µg-at/l), and ebb (0.86 µg-at/l) tides differed significantly after 3 hours of lagging (p = .03, t-test), whereas concentrations were .95 µg-at/l in both directions with no lag (Fig. 18). In April, phosphate was higher on flood than ebb tides as well, averaging 1.4 µg-at/l and 1.1 µg-at/l, respectively, after 5 hours of lag (p = .02). In September, flood concentrations of phosphate averaged 1.70 µg-at/l and concentrations on the ebb tide averaged 1.20 µg-at/l, significantly different from each other (p = .004) after 2 hours of lag.

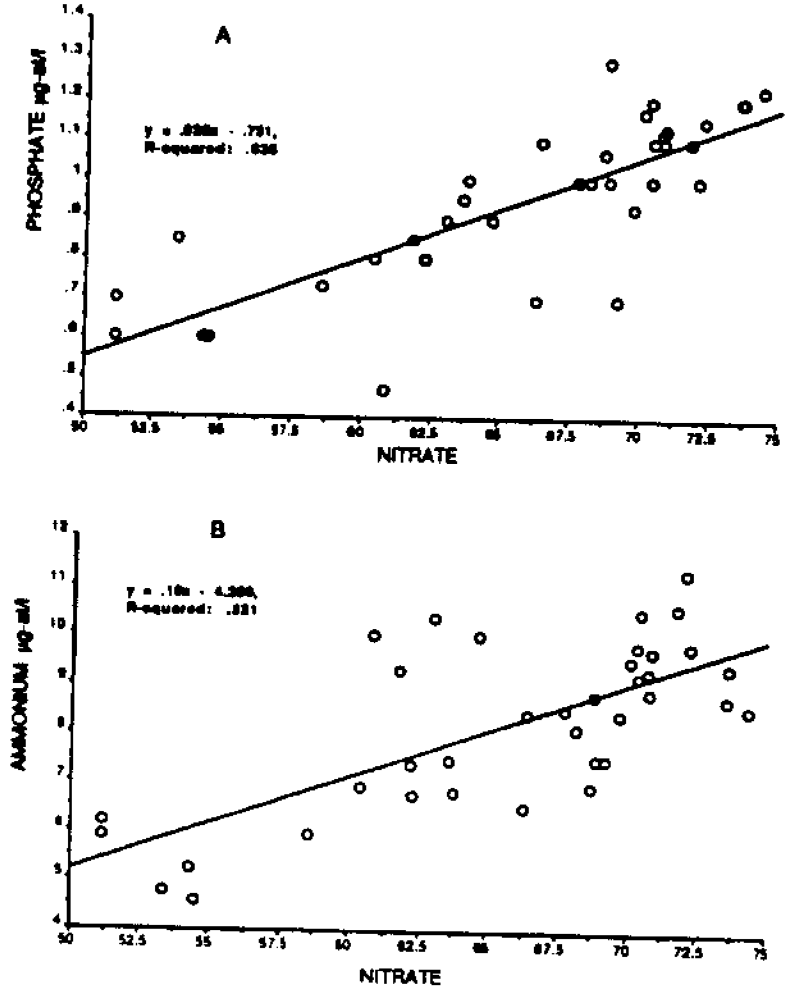


Figure 10. Relationships between nutrients over two tidal cycles through the entrance to Fourleague Bay (Station SO1) in February, 1982.

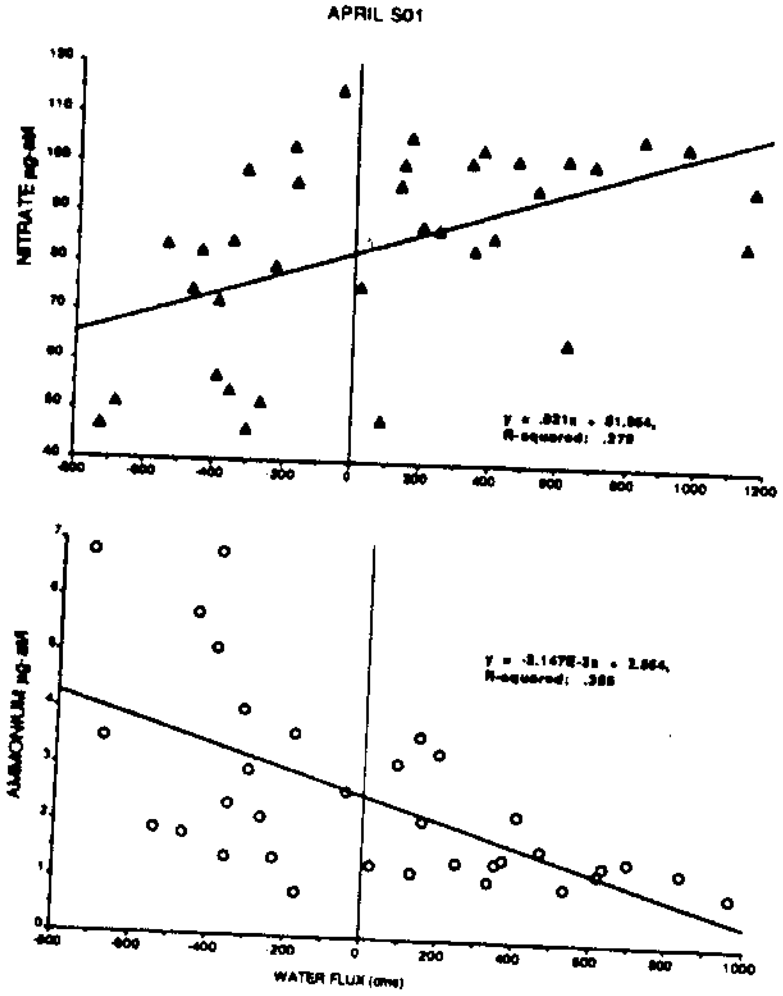


Figure 11. Nitrate and ammonium versus water flux through the upper bay at station SO1 in April, 1982, after lagging 4 hours for nitrate and 4 hours for ammonium. Positive water flow is into the bay. See text for explanantion.

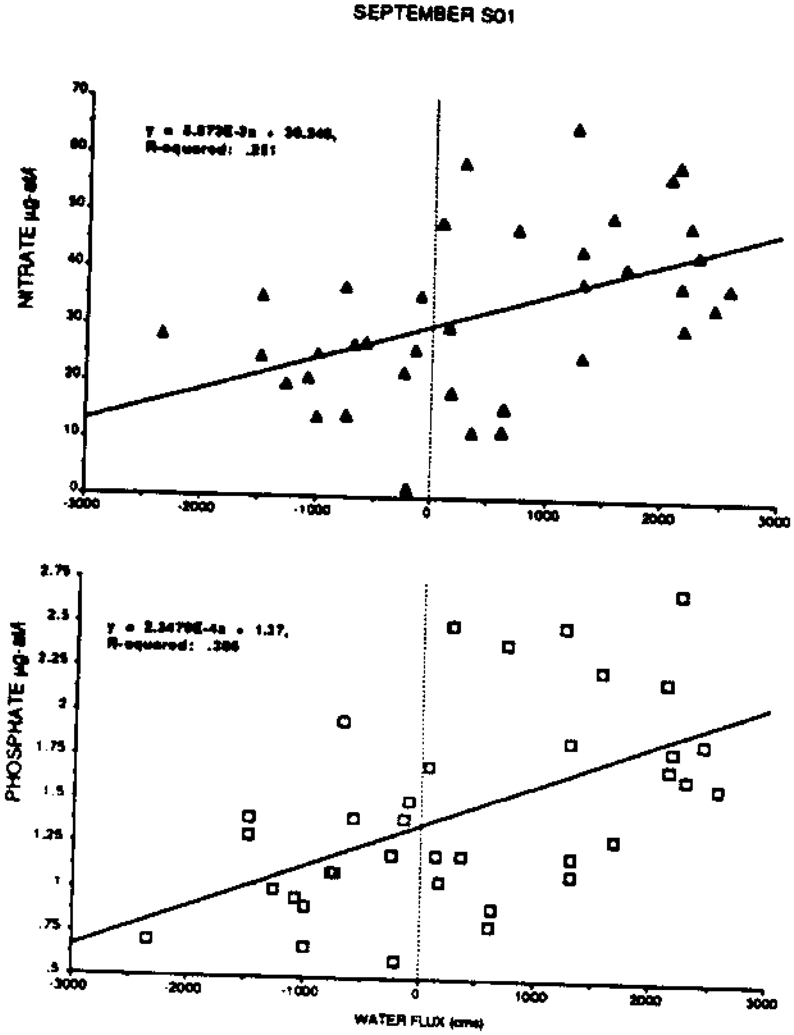


Figure 12. Nitrate and phosphate versus water flux through the upper bay at station SO1 in September, 1982, after lagging 2 hours for nitrate and 2 hours for phosphate. Positive water flow is into the bay. See text for explanantion.

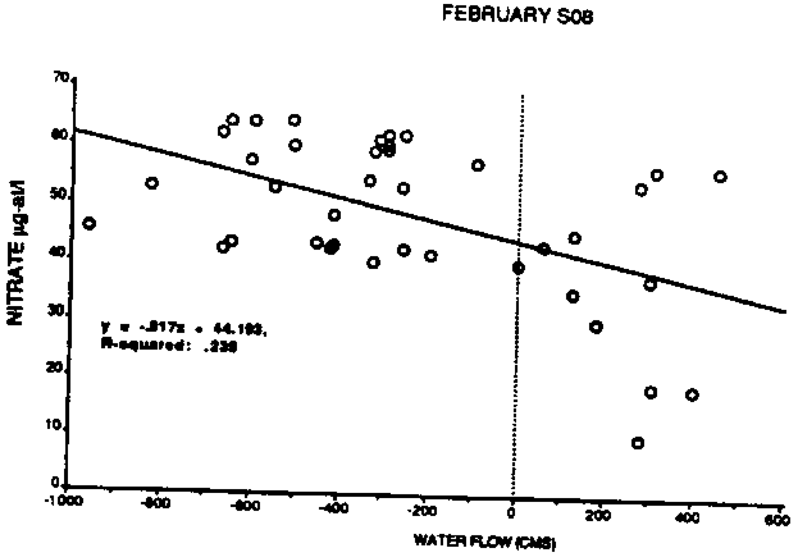


Figure 13. Nitrate versus water flux through the estuary mouth at station SO8 in February, 1982, after lagging zero hours. Positive water flow is into the bay. See text for explananation.

Tide-Specific Nutrient Concentrations-Oyster Bayou

Nitrate. The same analysis was performed for Oyster Bayou. In February, nitrate concentrations in water flowing from Fourleague Bay to the Gulf were higher than in water entering the bay (Fig. 16). Mean levels in ebbing water were 51.2 µg-at/l, and in flooding water were 37.1. Highest significance (p = .002, t-test) occurred with no lagging. In April water entering from the gulf averaged 24.8 µg-at/l after 3 hours lag, significantly higher than the 10.1 µg-at/l in water flowing out of the bay (p=.0001). In September nitrate concentrations were strongly correlated with tide flux. Nitrate on flood flows was 1.6 µg-at/l, about 50 % higher than the 1.1 µg-at/l on ebb flows, a significant difference after lagging 2 hours (p=.003).

Ammonium. In February in the lower bay, ammonium averaged 5.24 µg-at/l and was not significantly different in ebb and flood tidal flows (Fig. 17). In the April study, there was a strong positive correlation between ammonium concentrations and flow direction. Ammonium levels on flood tides averaged 7.5 µg-at/l, and on ebb tides averaged 3.5 µg-at/l after lagging 2 hours (p=.0001, t-test). In September, the ebb-flood concentration differential increased with 4 hours lagging from about 7 µg-at/l in both directions to 9.37 µg-at/l in the flooding tides and 5.85 µg-at/l in the ebb flows (p=.04).

Phosphate. Ortho-phosphate in the lower bay showed no correlation with tide direction in February, April or September.

Differences in Water Chemistry of Two Sources to the Upper Bay: River Input and Fresh Marsh Drainage

During the three tidal cycle studies, nutrient and current data were taken at a second location in the upper bay in addition to the main entrance. Nearby Creole Pass draining fresh marshes is a tidal channel 40 m wide located about 1.5 km from the main entrance (Fig.18). The water flowing through Creole Pass probably combined Atchafalaya Bay water and drainage from the fresh marshes north of Fourleague Bay. The pass acts as a natural flume and affords an opportunity to study the diurnal changes in nutrient concentrations in water flowing from the fresh marsh area of the upper bay.

Nutrient concentrations in water flowing through Creole Pass were significantly different from nutrient concentrations at the main inlet. More importantly, in February, at a station the middle bay about 10 km from the upper bay entrance, nutrient concentrations were similar to those in the upper bay, while nutrient concentrations in Creole Pass were quite different from concentrations in the upper bay (Table 3). This pattern of significant differences in Creole Pass waters was also observed frequently on synoptic transects.

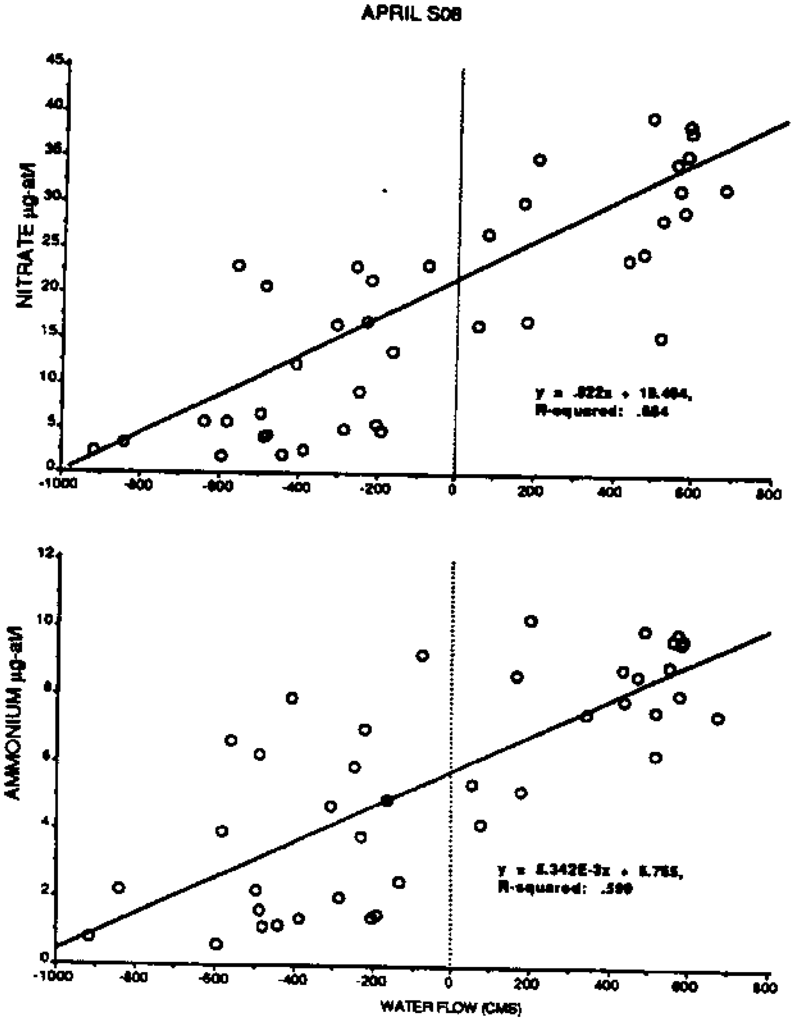


Figure 14. Nitrate and ammonium versus water flux through the estuary mouth at station SO8 in April, 1982, after lagging 3 hours for nitrate and 2 hours for ammonium. Positive water flow is into the bay. See text for explanantion.

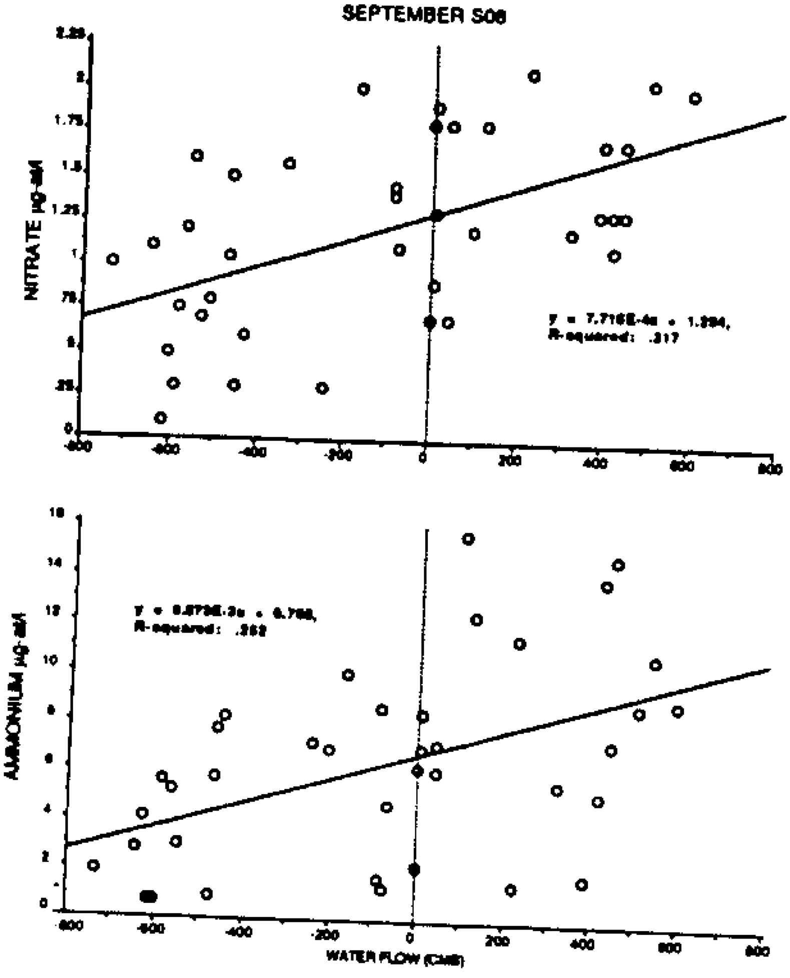


Figure 15. Nitrate and ammonium versus water flux through the estuary mouth at station SO8 in September, 1982, after lagging 3 hours for nitrate and 4 hours for ammonium. Positive water flow is into the bay. See text for explanantion.

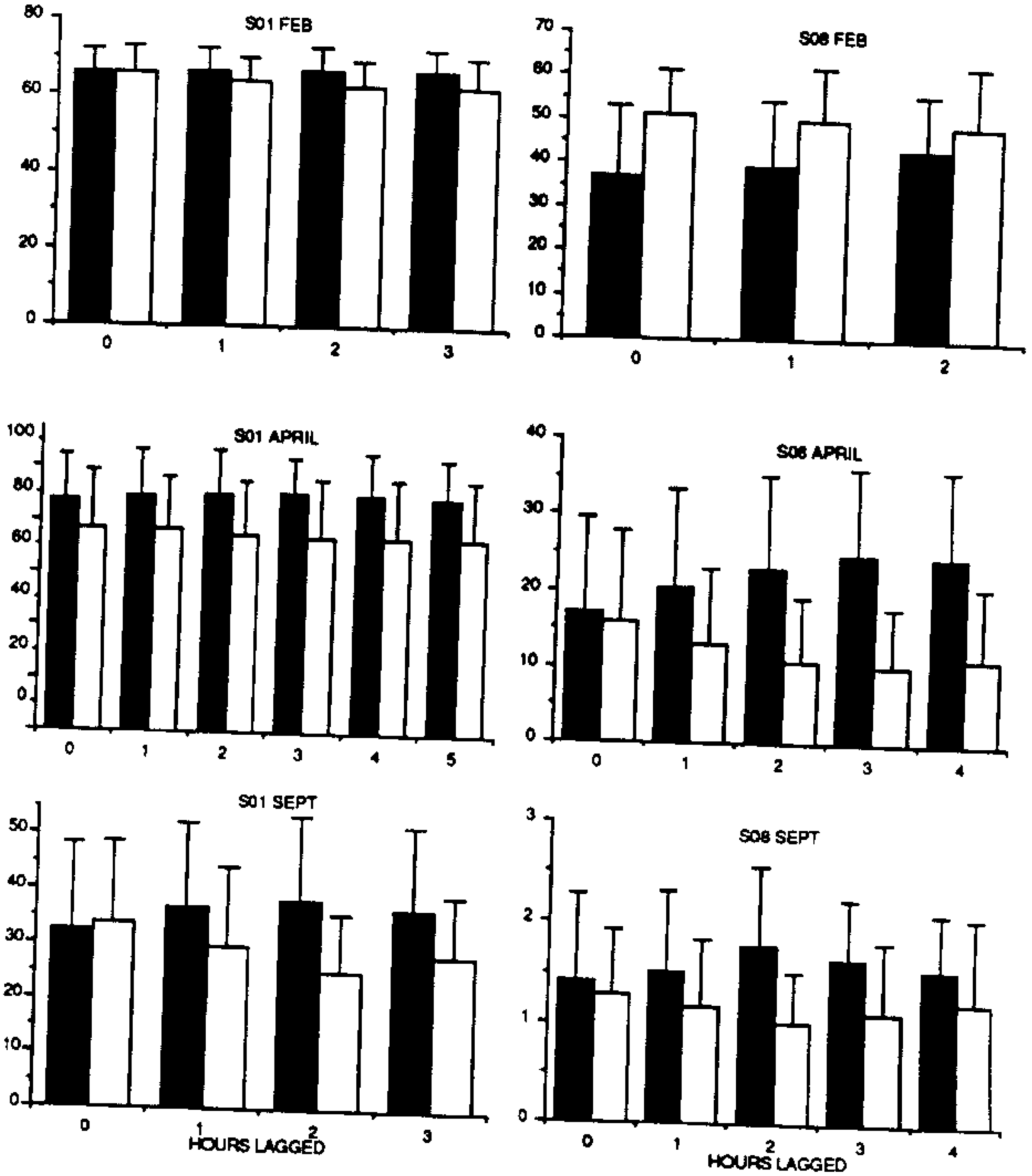


Figure 16. Nitrate concentrations in flood and ebb flows through the upper bay (Station SO1) and estuary mouth (Station SO8) during 50 hour tidal cycle studies in 1982. Each graph shows the increase in flood/ebb difference as nutrient data are shifted back relative to water flow data. Concentrations in µg-at/l; black bars represent inputs to the bay, white bars are exports.

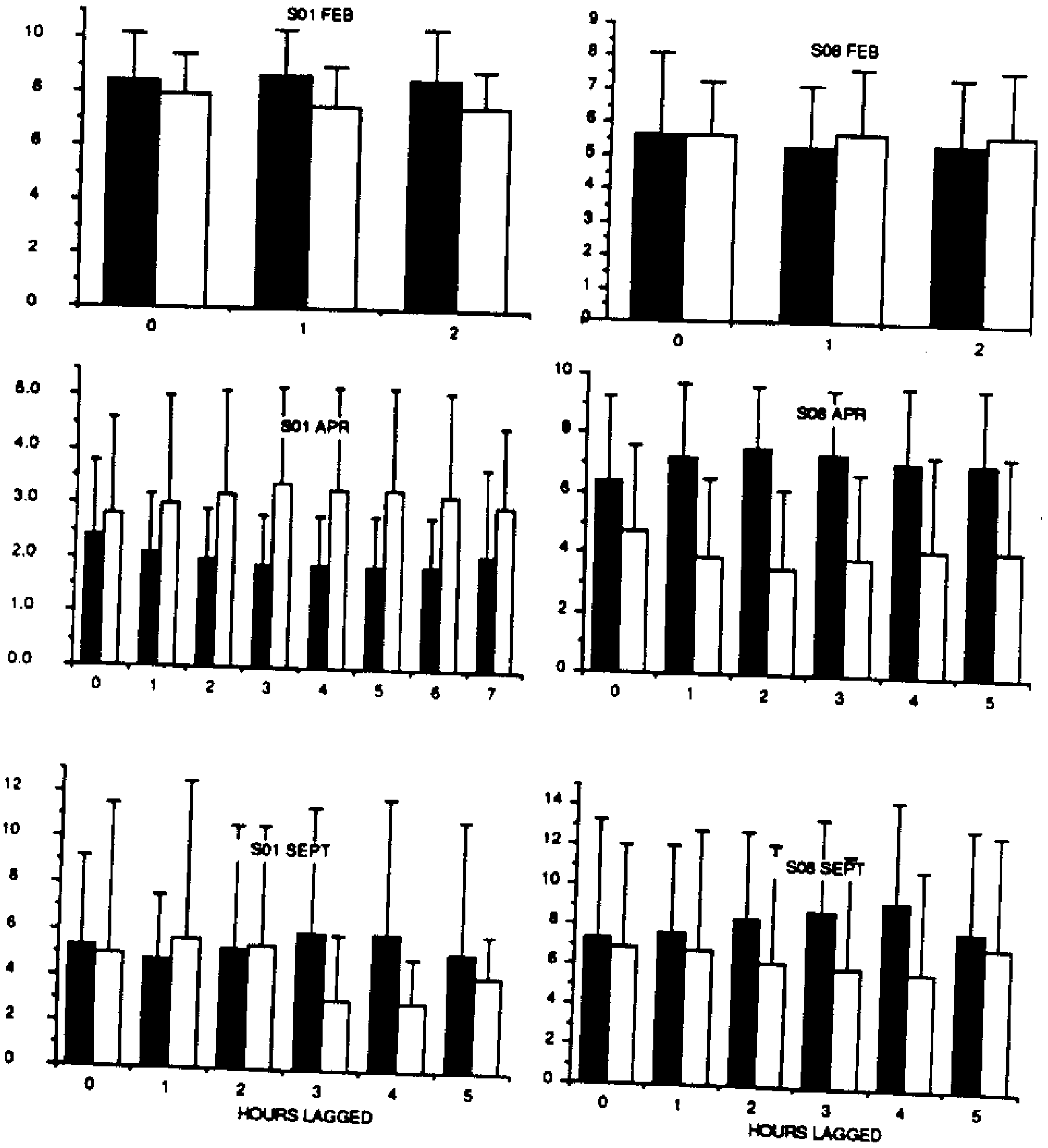


Figure 17. Ammonium concentrations in flood and ebb flows through the upper bay (Station SO1) and estuary mouth (Station SO8) during 50 hour tidal cycle studies in 1982. Each graph shows the increase in flood/ebb difference as nutrient data are shifted back relative to water flow data. Concentrations in µg-at/l; black bars represent inputs to the bay, white bars are exports.

FEBRUARY 12-14

	BAY	CREOLE
MEAN NITRATE:	65.40	40.58
MAX:	74.37	62.20
MIN:	51.10	12.90

significantly different according to unpaired t-test p<.0001

APRIL 23-25

	BAY	CREOLE
MEAN NITRATE:	84.38	52.80
MAX:	114.90	88.00
MIN:	46.30	11.20

significantly different according to unpaired t-test p<.0001

SEPTEMBER 16-18

	BAY	CREOLE
MEAN NITRATE:	34.33	11.58
MAX:	65.30	26.20
MIN:	1.70	2.50

significantly different according to unpaired t-test p<.0001

Table 3. Average nitrate concentrations at main upper bay entrance and Creole Pass which drains fresh marshes. Data are averaged from three 48-50 hour tidal cycle studies.

In all three tidal cycle studies, nitrate levels in the water flowing through Creole Pass were consistently lower than in the main entrance to the bay (Fig. 19). In February at Creole Pass the mean nitrate concentration averaged 42.21 µg-at/l (12.90 to 62.2) and at the bay entrance, nitrate averaged 65.45 µg-at/l (51.1 to 74.37), different at the p = .0001 level (t-test). In April Creole Pass nitrate averaged 51.5 µg-at/l (11.2 to 88.9), while the upper bay station averaged 84.38 µg-at/l (46.3 to 114.9), (p = .0001). In September mean nitrate at Creole Pass was 11.47 µg-at/l (2.50 to 26.2) and was again significantly lower than the 33.33 µg-at/l (1.7 to 65.3) measured at upper bay (p = .0001).

Upper bay and Creole Pass ammonium concentrations were also distinctly different. In February, the mean Creole Pass ammonium concentration of 4.7 µg-at/l, was about half the concentration at the upper bay station (8.2 µg-at/l) (p = .0001, t-test). Conversely, in April the mean ammonium concentration in Creole Pass was 7.50 µg-at/l, significantly higher than those in the upper bay entrance (2.49 µg-at/l, p = .0001). In September ammonium was slightly lower at Creole Pass (4.11 µg-at/l) than at the bay entrance (5.15 µg-at/l) but not significantly different.

Phosphate averaged .57 µg-at/l in Creole Pass and .95 µg-at/l at the bay entrance in February (p = .0001, t-test). In April, phosphate averaged .93 µg-at/l in the pass while it was 1.37 µg-at/l at the entrance (p = .0018). The September phosphate mean was 0.72 µg-at/l in Creole Pass and 1.5 µg-at/l in the bay entrance (p = .0001).

The relationship between tide direction and nutrient concentration in Creole Pass is not as meaningful as at the bay entrance. The flow through the pass involves complex hydrology, with several water sources and tidal waves influencing both the mouth and the head of the pass. Although there is a relationship between tide in Creole Pass and in the entrance, it is not very predictable. In February and April, ebbing tide in the main entrance usually appeared as only a slowing of the flood tide in the pass. In September, the Creole Pass tides were better-correlated to the main entrance tides.

Because there was not a directional change in many tides in Creole Pass, the functionality of water flow as an indicator of nutrient source breaks down. On the other hand, strong relationships between nutrient species were evident. In February ammonium fluctuations in Creole Pass closely paralleled nitrate ($r^2 = 0.60$, $p = .0001$, t-test) (Fig. 20A). In April ammonium and nitrate concentrations at Creole Pass fluctuated inversely ($r^2 = 0.51$, $p = .0001$) (Fig. 20B). In September, ammonium and nitrate were not closely related but ammonium and phosphate paralleled each other closely ($r^2 = 0.75$, $p = .0001$) and declined over the fifty-hour period (Fig. 21). Phosphate and nitrate were related as well ($r^2 = 0.34$, $p = .002$).

In February, although nutrients and water flow in the pass were not closely related, changes in Creole Pass nitrate were well-correlated with water flow through the main inlet after lagging 3 hours ($r^2 = 0.51$, $p = .001$, t-test). During flood flows, nitrate-rich water entering Fourleague Bay through the main entrance was reaching Creole Pass and elevating concentrations there. During ebb flows at the entrance, water continued to flood at Creole Pass, as nitrate concentrations declined. At these times, water was apparently being drawn off the marsh and pulled into the main stem of Fourleague Bay through Creole Pass.

In April, an inverse relationship between nitrate concentrations in Creole Pass and water flow at the main entrance was observed after lagging for 3 hours. During

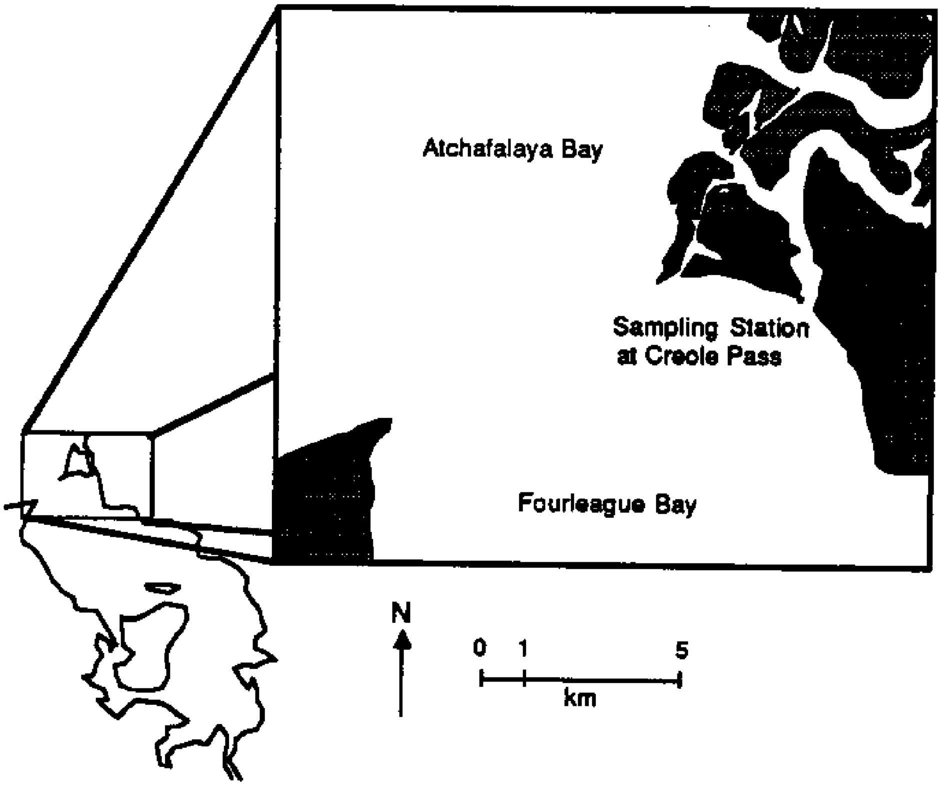


Figure 18. Creole Pass station showing proximity of both Atchafalaya Bay and Fourleague Bay and extensive marshes.

flood tides, nitrate declined, while during ebbs, nitrate increased ($r^2 = 0.20$, $p = .01$, t-test).

In September, the only trip with well-defined bidirectional tidal flows in Creole Pass, fluctuations in nitrate concentrations correlated with the direction of water flow in the pass ($r^2 = .23$, $p = .01$, t-test). Nitrate concentration increased in Creole Pass when water flowed from Fourleague Bay into the pass (ebb flows) and decreased on flood flows from the pass toward Fourleague Bay.

Nutrient Concentrations in Other Bayous

Tidal cycle profiles were taken at two other large bayous which drain into Fourleague Bay (see Fig. 1). Carencro Bayou, about mid-way down the bay drains brackish marshes and Blue Hammock Bayou, farther toward the mouth of the bay, drains brackish and salt marshes. There were large differences in nutrient composition of the water in the bayous over the three studies (Fig. 22 A, B). Nutrient changes relating to tidal features will be examined in another study. Here, I will report the average nutrient concentrations at these bayou mouths and their relation to time of year and the composition of the water input to the main entrances of the bay.

The nutrient gradient in the three bayous along the bay indicates a strong trend of decreasing nitrate concentrations, and generally increasing ammonium concentrations at all times of year. Phosphate increased down the bay in February and September and decreased significantly in April (Figs. 23-25).

For the following results, nutrient concentrations will be reported by station in order of distance down bay: Main entrance, Creole Pass, Carencro Bayou, Blue Hammock Bayou. During the February study when the bay was inundated by fresh water, nitrate concentrations in bayou stations were similar to concentrations in the main entrance: 65.45, 42.21, no data, 61.45 ± 5.17 µg-at/l. In April, bayou stations showed a nitrate decrease with distance from the river. Concentrations averaged 84.38, 51.5, 57.53 ± 19.0 µg-at/l, and 5.43 ± 2.4 µg-at/l. In September, nitrate concentrations dropped sharply down the bay: 33.33, 11.47, 2.94 ± 1.9 µg-at/l and 1.16 ± 1.39 µg-at/l.

Ammonium concentrations in February, like nitrate,

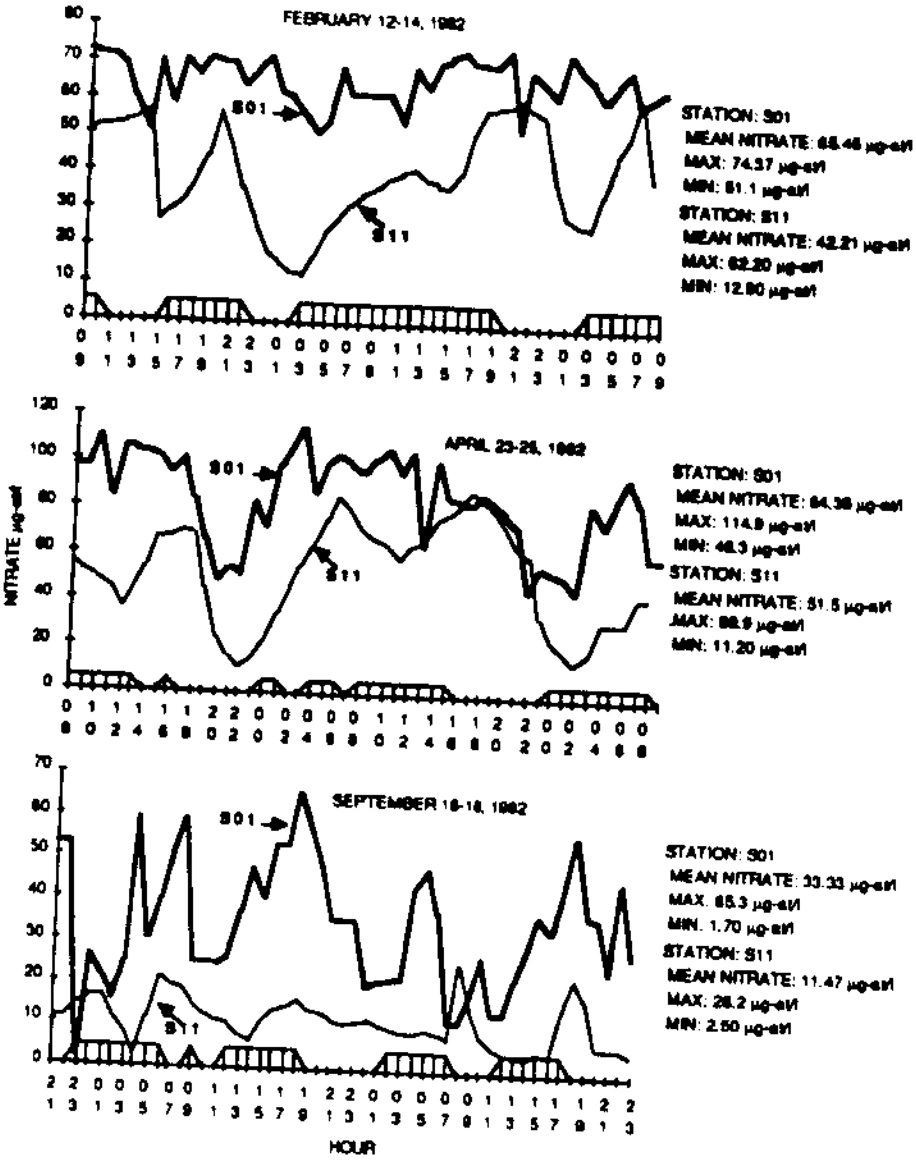


Figure 19. Hourly nitrate concentrations at upper bay entrance (SO1) and Creole Pass (S11), a tidal channel draining marshes about 1.5 km from SO1. Drop lines indicate flood tide at SO1.

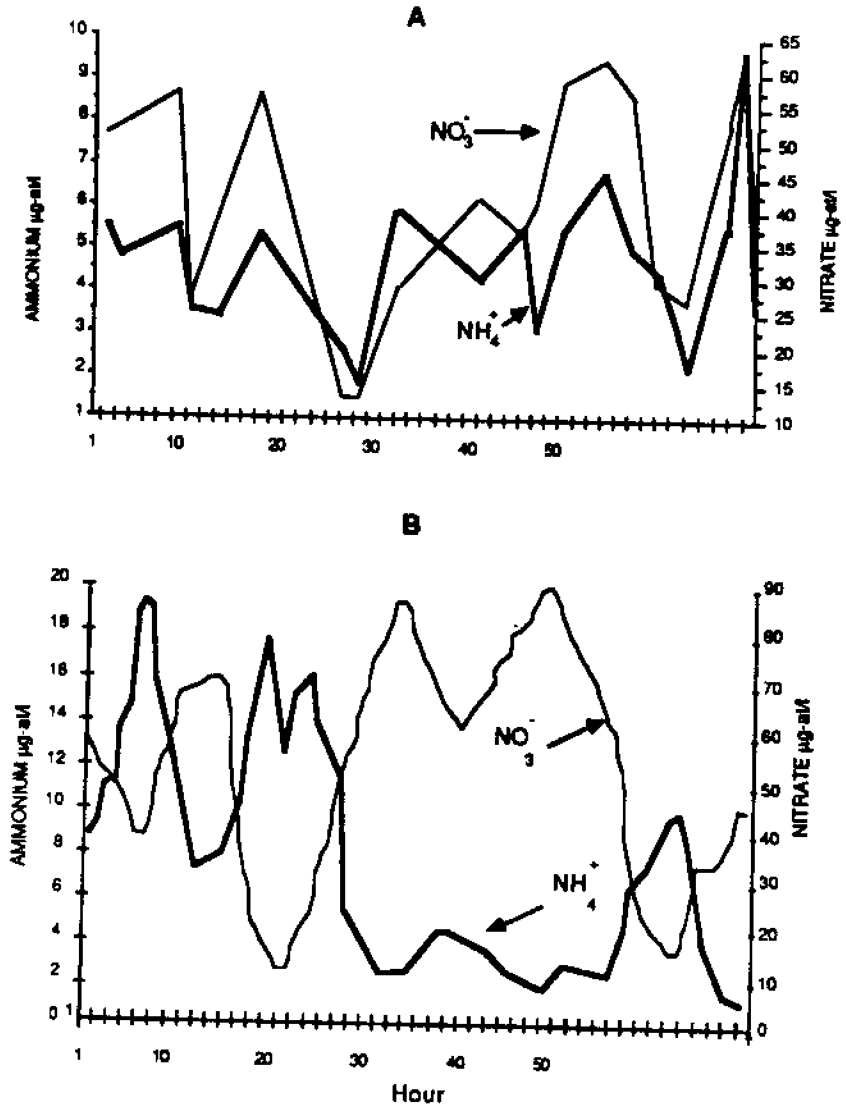


Figure 20. Nutrient profile for Creole Pass for A: February 12-14, and B: April 23-25, 1982, showing close relationship between nitrate and ammonium concentrations in February and inverse relationship in April.

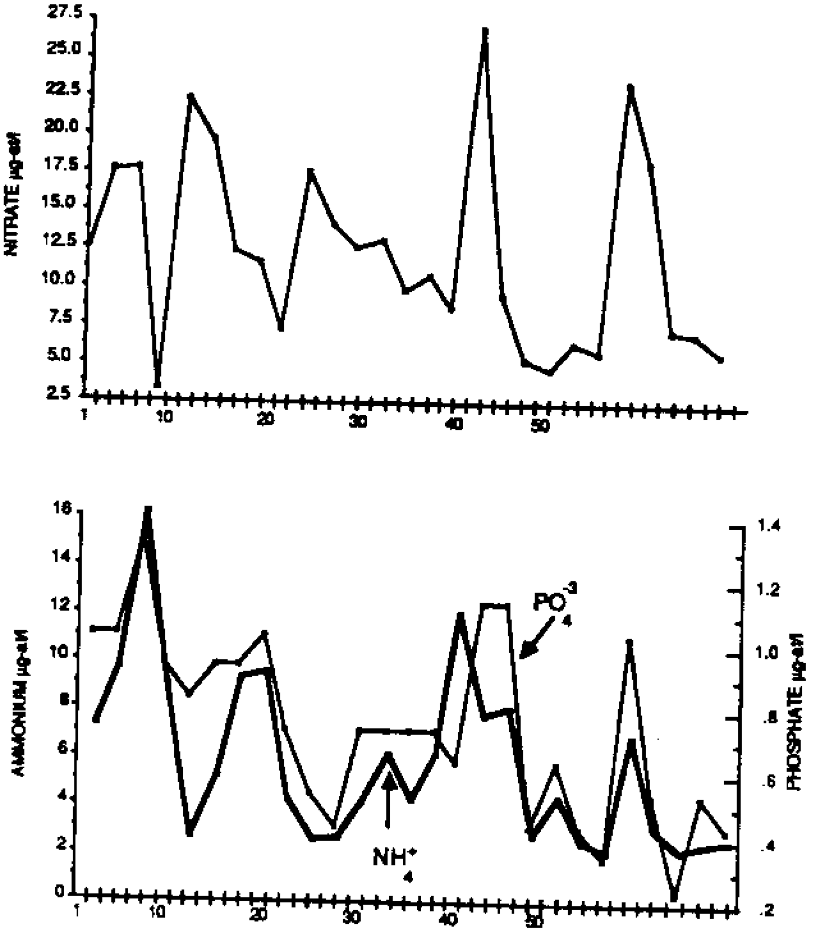


Figure 21. Nutrient profile for Creole Pass, September 16-18, 1982, showing the close relationship between nitrate (A), ammonium and phosphate concentrations (B).

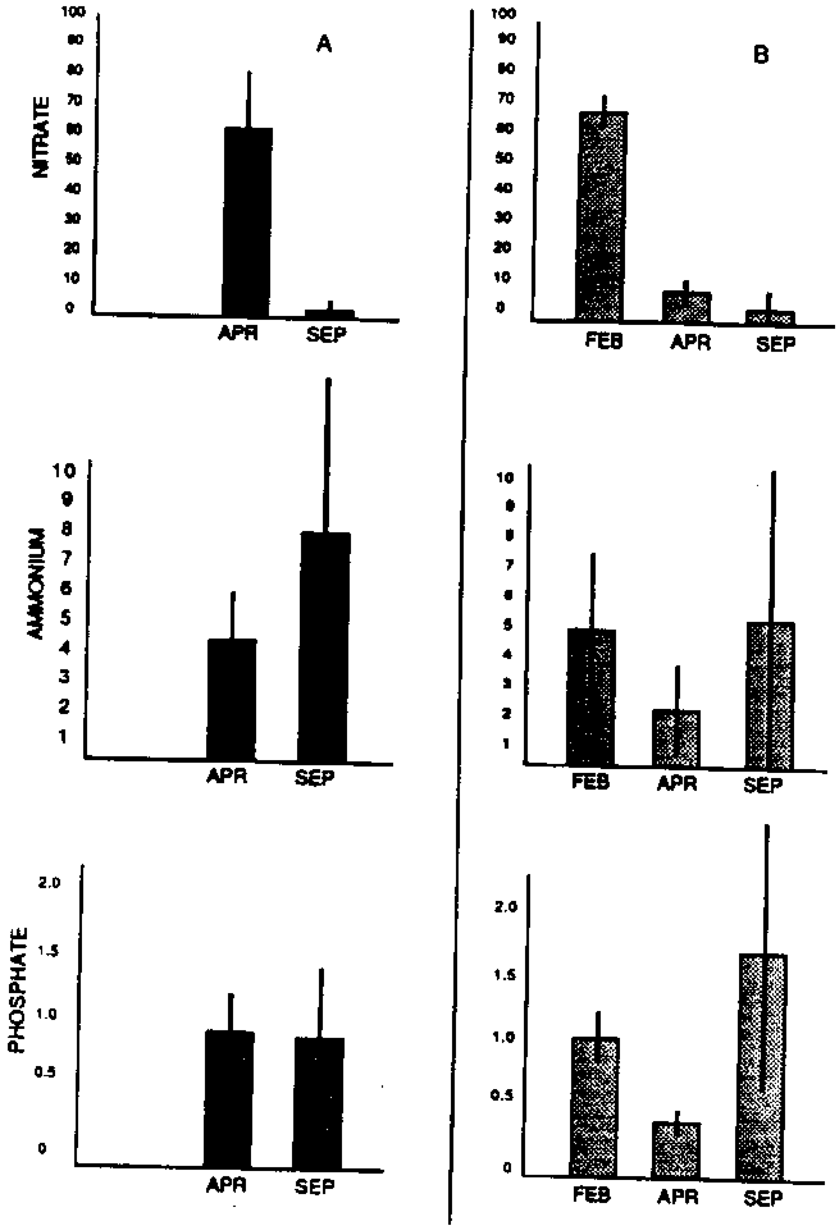


Figure 22. Mean nutrient concentrations in A: Carencro Bayou and B: Blue Hammock Bayou on tidal cycle studies in 1982. No data were taken in Carencro in February. Concentrations in μg-at/l.

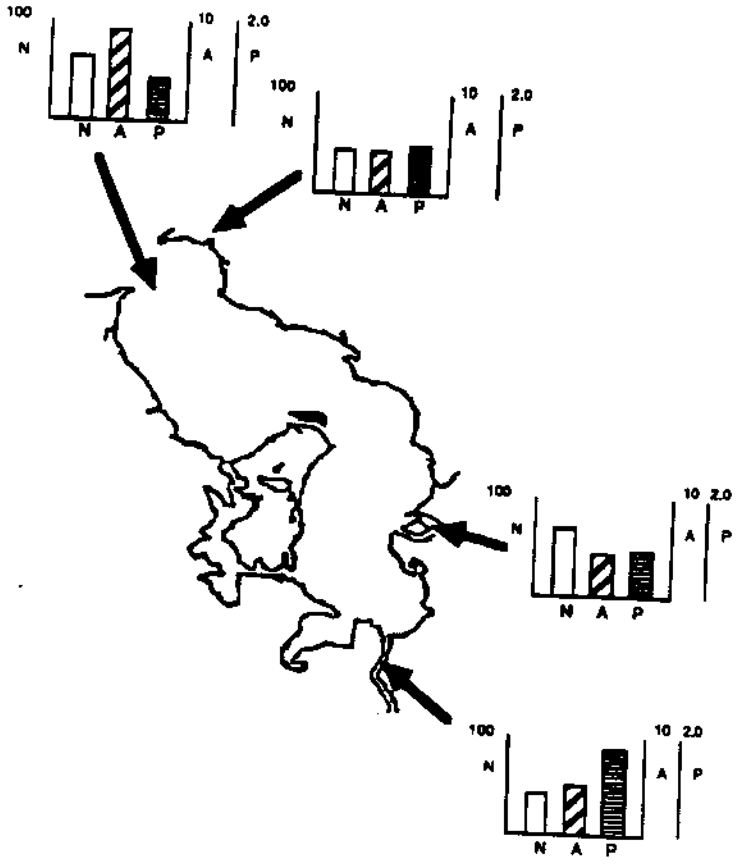


Figure 23. Summary of nitrate (N), ammonium (A), and phosphate (P) concentrations in µg-at/l at Fourleague Bay boundaries on February 12-14, 1982.

decreased down the bay: 8.2, 4.7, no data, and 5.04 ± 2.45 µg-at/l. In April, ammonium was higher in the bayous in the middle bay than in the main entrance, averaging 2.49, 7.5, 4.43 ±1.43 µg-at/l, 2.49 ± 1.55 µg-at/l. For September, ammonium again was highest in the middle bay, 5.15, 4.11, 8.19 ± 6.92 µg-at/l, and 5.73 ± 7.96 µg-at/l.

Phosphate in February averaged .95, .57, no data, and .9 ± 26 µg-at/l. In April, phosphate declined toward the lower bay averaging 1.37, .93, .96 ± .36 µg-at/l, .37 ±.16 µg-at/l. In September concentrations were highest in the lower bayou 1.5, 0.72, .99 ±.66 µg-at/l, and 1.73 ± 1.53 µg-at/l.

Summary

In February and April, two months typically dominated by high river discharge, Fourleague Bay received a high loading of inorganic nutrients from the river. The ultimate fates of these nutrients differed in response to water flow, wind influence and possibly temperature. In February, the bay was a "flow-through system" with large export of inorganic nutrients to the nearshore gulf out of Oyster Bayou. In April, southerly winds pushed gulf water into the lower bay preventing export and forcing nutrient-rich waters to flow over the marsh. Increasing temperatures and higher insolation probably stimulated

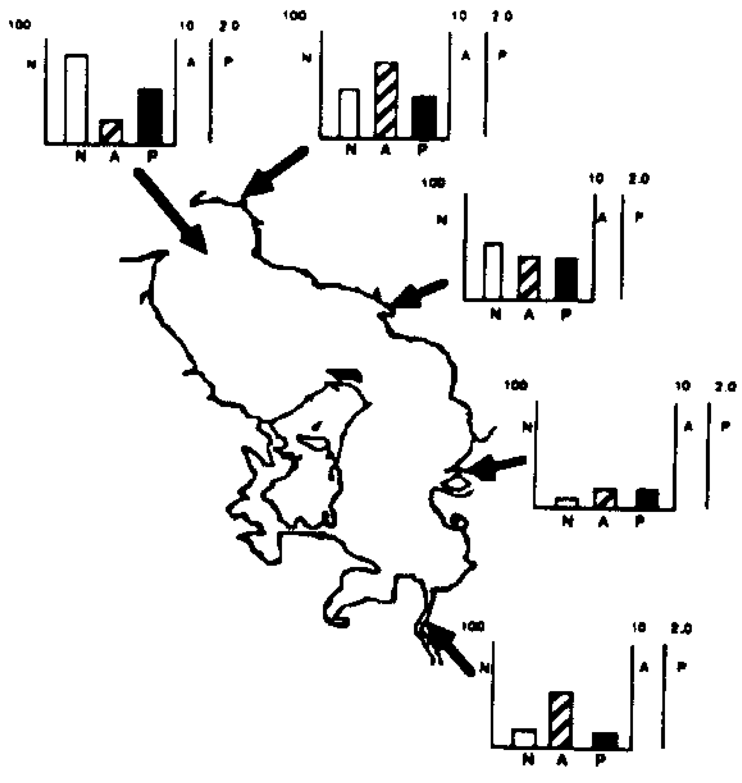


Figure 24 Summary of nitrate (N), ammonium (A), and phosphate (P) concentrations in µg-at/l at Fourleague Bay boundaries on April 23-25, 1982

nutrient uptake by autotrophs, further reducing the nutrient concentrations. In September river water had lower nutrient concentrations but the flows out of Oyster Bayou were much lower in nitrate and phosphate than river water. Water flowing from Oyster Bayou was enriched in ammonium.

DISCUSSION

Tidal Cycle Studies

Measurement of nutrient flows through major bay passages over a tidal cycle demonstrates strong patterns in the processing of nutrients in Fourleague Bay. This study offers the opportunity to compare the relative contributions of advected or "new" nutrient inputs and "recycled" nutrients at certain times of the year, and enables comparison of riverine, fresh marsh, brackish marsh and salt marsh contributions simultaneously.

Few large scale intensive studies can be found in the literature, owing to the difficulty of conducting field studies of this magnitude. Most tidal exchange studies have been conducted in small, well-defined drainages with one or two inlets (Nixon and Lee 1980, Wolaver et al. 1980, Kjerfve and McKellar 1981, Jordan et al. 1983) or in larger areas during only one part of the year (Farfan and Alvarez-Borrego 1983). Jordan et al. (1983) measured fluxes from a large drainage in the Rhode River at eleven points in the year but concentrated on flux from a brackish marsh, and McPherson and Sonntag (1984) monitored loadings from several tributaries of the Loxahatchee River, Florida, intensively, over a two month period.

Hydrologic and nutrient flows to upper Fourleague Bay from Atchafalaya Bay were remarkably similar in the two tidal cycle studies conducted during the flood months of February and April, 1982. However, there were significant differences in the import-export dynamics

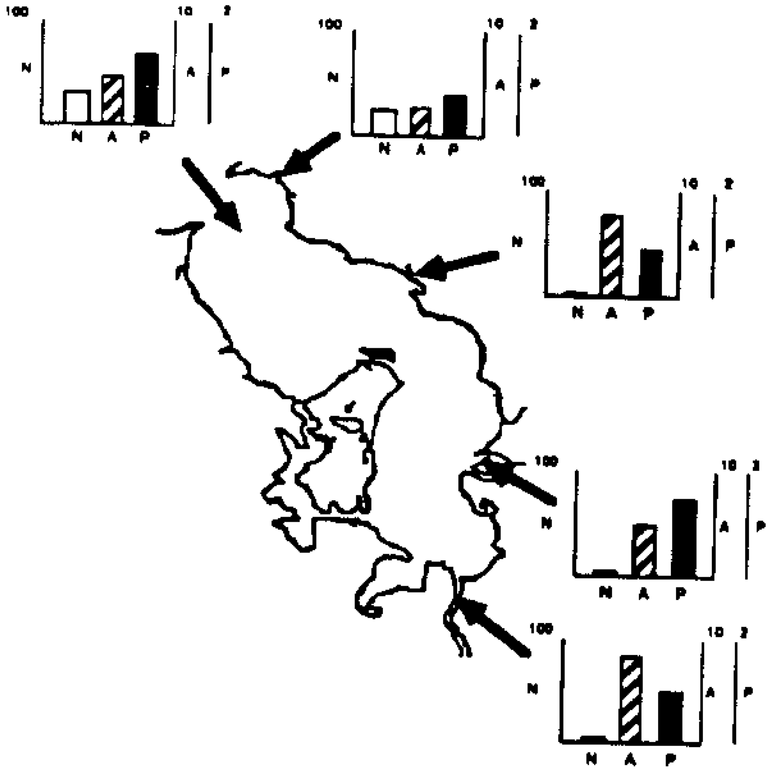


Figure 25. Summary of nitrate (N), ammonium (A), and phosphate (P) concentrations in µg-at/l at Fourleague Bay boundaries on September 16-18, 1982.

between the flood period in spring and the low-water period in September. Export dynamics at the lower bay at Oyster Bayou varied more broadly, and were strongly influenced by wind regime, and less influenced by river flow than the upper bay.

Tidal Cycle Profiles

The hydrology of Fourleague bay was river-dominated during the February study, with a positive net inflow to the bay over each tidal cycle, and net outflow from the lower bay. Moreover, nutrient concentrations were similar in the water entering the upper bay and leaving the lower bay. In April, although conditions of Atchafalaya River discharge and net water flux into the upper bay were similar to those in February, the nutrient profile at the upper and lower bay stations differed substantially. Southerly winds contributed to this by pushing gulf water into the lower bay and increased temperature in April probably increased the biological uptake of inorganic nutrients within the bay as well.

Hydrologic flux and nutrient profiles in September were significantly different from the river-dominated regimes observed during February and April. Flood and ebb water transports through the upper bay entrance were nearly symmetrical indicating dominance by tidal forces over river forces. In both the February and April studies, no salinity was measured at the upper bay stations suggesting that reductions in nutrient concentrations in the upper bay were completely attributable to non-conservative processes rather than to dilution. Interpretation of the nutrient fluxes in the September study is complicated by the encroachment of salt water as far as the upper bay entrance during ebb flows indicating that mixing and dilution of riverine input had occurred.

In the upper bay in February, the relationship between tide direction and nitrate concentrations was weak. Furthermore, nitrate concentration on ebb flows was the same as on flood flows showing that there was probably little biological uptake in the bay during this period. In April, nitrate concentrations in ebb flows were much lower then flood concentrations in the upper bay indicating strong uptake within the bay. Increased temperature and insolation in April probably provided the energy to "switch on" the system. The September nitrate profile showed even larger differences in ebb and flood concentrations, indicating active uptake in the bay. The lack of a strong hydrological component in September also promoted long residence times in the bay giving biological reactions more time to occur.

Ammonium dynamics in the upper bay in February were also fairly static: ebb and flood concentrations were similar and there was no correlation with tide direction. Ammonium was quite high in riverine inflow in February, and was clearly imported by the bay. Ebb flow from the upper bay was slightly reduced in ammonium indicating uptake within the bay. This contrasts sharply with the higher ammonium concentrations observed on ebb flows in April which indicate a source in the bay and export to coastal waters on ebb tides through the upper bay. Nevertheless in April ebb flows were uncommon due to the force of the river, and daily net flux of ammonium was into the upper bay. Ammonium concentrations increased within the estuary, doubling between the upper and lower bay, supporting the hypothesis that ammonium was actively produced within the bay.

Phosphate concentrations through the upper bay entrance in February, April and September, were significantly lower in ebb flows than flood flows indicating that the river was a source, and the upper bay a sink for phosphate. Significant decreases occurred within the span of a quarter tidal cycle or 5 hours. September showed the largest proportionate reduction in concentrations between flood and ebb flows in the upper bay, indicating that the phosphate sink processes within the upper bay were probably strongest at that time of year. Due to colder temperatures the rate of biological remineralization of phosphate within the bay may also have been declining and no longer compensating uptake. Because the lower bay concentrations were higher than ebb concentrations from the upper bay, the decline in the upper bay cannot be attributed to dilution by gulf water. If anything, the saline water reaching the upper bay increased the phosphate concentration, so declines were most likely due to uptake within the bay.

Daily variations in the nitrate concentration in the lower bay were strongly correlated with the direction of water flow. In February when nitrate concentrations were elevated throughout the bay, nitrate-rich water was exported to the gulf on ebb tides. In April, nitrate levels in the lower bay were greatly reduced and nearshore gulf waters actually supplied lower Fourleague Bay with nitrate. Potential sources of this nitrate in the gulf nearshore water may have been enrichment by recent heavy Atchafalaya flows through Oyster Bayou such as observed in February, or enrichment by the Mississippi River plume from the east. Ho and Barrett (1977) measured average nitrate concentrations above 20 µg-at/l in the Mississippi River plume during January, 1973 extending west of Caminada Bay in the nearshore zone of the gulf.

The February flows of ammonium in the lower bay indicate no gradient. The lower bay and nearshore areas were pervaded by a uniform ammonium level of about 5 µg-at/l. In April concentrations of ammonium in the lower bay were double those in the upper bay and lower bay concentrations on flood tides were double those on the ebb tides, indicating that the gulf inflow was significantly raising the inorganic nitrogen levels. In the September study this pattern was diminished and ammonium concentrations on flood tides averaged only slightly higher than those in ebb flows. The April profiles indicate a large degree of ammonium activity at all bay boundaries. Upper and lower bay passes showed large differences in ebb and flood concentrations and Creole Pass ammonium showed a strong link to tide. All evidence indicates a low riverine input of ammonium and increasing concentrations within the bay. Ammonium is exported from the upper bay on ebb tides and is higher in Oyster Bayou than in the upper bay indicating significant remineralization within the bay and possibly the surrounding marshes. The Creole Pass data support the latter possibility. Ammonium is imported on flood tides in Oyster Bayou indicating that significant remineralization processes extend into the nearshore zone.

Ortho-phosphate concentrations in the lower bay showed no correlation with tide direction in February, April or September. This pattern is understandable during the spring period of freshwater discharge due to inundation and homogenization of the nearshore gulf zone by terrestrial runoff. The presence of phosphate in the lower bay and into the gulf in September, when discharge was low and nitrate concentrations were so rapidly depleted, suggests that phosphate concentrations were buffered: regenerative processes in the bay and nearshore gulf may have been maintaining concentrations or liberation from the bay sediments may have occurred due to reductions in redox potential.

Variations in nutrients can be caused by a number of factors which have been well documented. Loder and Glibert (1982) noted that natural riverine variability can cause significant end-member variability. Gael and Hopkinson (1979), Kemp (1978) and Day et al. (1977) reported significant short-term changes in stream nutrient concentrations were due to episodic storm events in Barataria Basin, due to increased runoff. McPherson and Sonntag (1984) measured increased inorganic nutrient concentrations in the Loxahatchee River, Florida following Tropical Storm Dennis. Mixing of the water column can also bring up bottom water nutrients. This tide direction analysis for Fourleague Bay is susceptible to such variation, but the high resolution time series serves to demonstrate variation caused by flow reversals, segregating nutrient changes due to processing within the estuary.

Nutrient Loading

The seasonal shifting of hydrology from a river-dominated flow to a tidally-dominated flow in controlling the loading of new nutrients to the bay far outweighs the importance of the seasonal changes in nutrient concentration. During three days in February, 1982 an average of 21,967 kg/day, and in April an average import rate of 21,150 kg/day inorganic nitrogen was advected into the upper bay. In September inorganic N import dropped to 6,812 kg/day N despite the fact that the average import on flood fluxes was approximately equal to the import during both spring studies. The lower import in September was due to losses on the ebb flows back though the entrance which were 2-3 times greater than in February and April. Thus spring flood in addition to higher nutrient levels provides a strong hydrologic pressure which keeps water high in nutrients inside the bay by opposing tidal forces.

The net influx of phosphate in Fourleague Bay was low compared to other estuaries and concentration changes were more significant than hydrologic flow rate in controlling the rate of advective input. Due to high concentrations of phosphate in September, the input of 1,024 kg/day was nearly twice as high as the input in either February (660 kg/day) or April (652 kg/day). Nevertheless, low phosphorus inputs relative to nitrogen results in a nitrogen-rich advective input that is much higher than usually found in other systems.

The importance of riverine nutrient inputs becomes clearer when converted to loading on an areal basis. Averaged over the surface area of the bay (9,300 ha), 703 μg-at/m^2/hr-N were added in February, 676 μg-at/m^2/hr-N in April and 219 μg-at/m^2/hr-N in September (Fig. 26). The measurements of loading rates for Fourleague Bay cannot be discussed in annual terms, but the three intensive measurements in February, April, and September 1982 probably represent the extreme maximum and minimum rates of inorganic nitrogen loading during that year.

Net Bay Nutrient Balance

Net nutrient fluxes for the whole bay generally reflected the dominant water flux direction: into the upper bay and out of the lower bay. However, important deviations from this pattern were evident. In February, the rate of import of nitrate through the upper bay was 617 μg-at/m^2/hr. Nitrate was lost from the lower bay through Oyster Bayou at a rate of 402 μg-at/m^2/hr for a net retention in the bay of 215 μg-at/m^2/hr (Fig. 27). Ammonium showed a net import of 85 μg-at/m^2/hr into the upper bay, a loss of 42 μg-at/m^2/hr from the lower bay and a net retention of 44 μg-at/m^2/hr in the bay. Phosphate was also supplied in surplus to the upper bay at a rate of 9.54 μg-at/m^2/hr but was lost from the lower bay at a rate of 12.23 μg-at/m^2/hr, resulting in a total net loss from the system of 2.69 μg-at/m^2/hr (Fig. 28). The source of the excess phosphate leaving the lower bay may have been a combination of remineralization products from within the bay and runoff from the surrounding marshes.

In April nitrate was imported into the upper bay at a rate of 661 μg-at/m^2/hr. There was a small import of nitrate through Oyster Bayou as well, resulting in a net gain of 677 μg-at/m^2/hr nitrate to the bay. Ammonium was imported through both the upper entrance and Oyster Bayou as well, at rates of 16 μg-at/m^2/hr and 2 μg-at/m^2/hr respectively resulting in a net gain for the estuary of 18 μg-at/m^2/hr. Phosphate import with riverine water was nearly identical to that of the February study, 9.43 μg-at/m^2/hr. However, due to extremely low transport out of the lower bay, the bay retained 9.32 μg-at/m^2/hr of this input. Although a large part of this accumulation was due to the build-up of water in the bay over the two day study, the decline in the nitrate concentration in the down-bay direction was greater than the decline in phosphate. This indicates that the bay is a stronger sink for nitrate than for phosphate. During the April study, the mean concentration of phosphate at the lower bay site was 32 % of that at the upper station, while nitrate concentrations declined to only 20 % of upper bay concentrations.

A net September inflow of nitrate to the upper bay of 232 μg-at/m^2/hr and loss of only 5 μg-at/m^2/hr at Oyster Bayou indicated that the bay was assimilating 227 μg-at/m^2/hr of nitrate in September. Ammonium was net

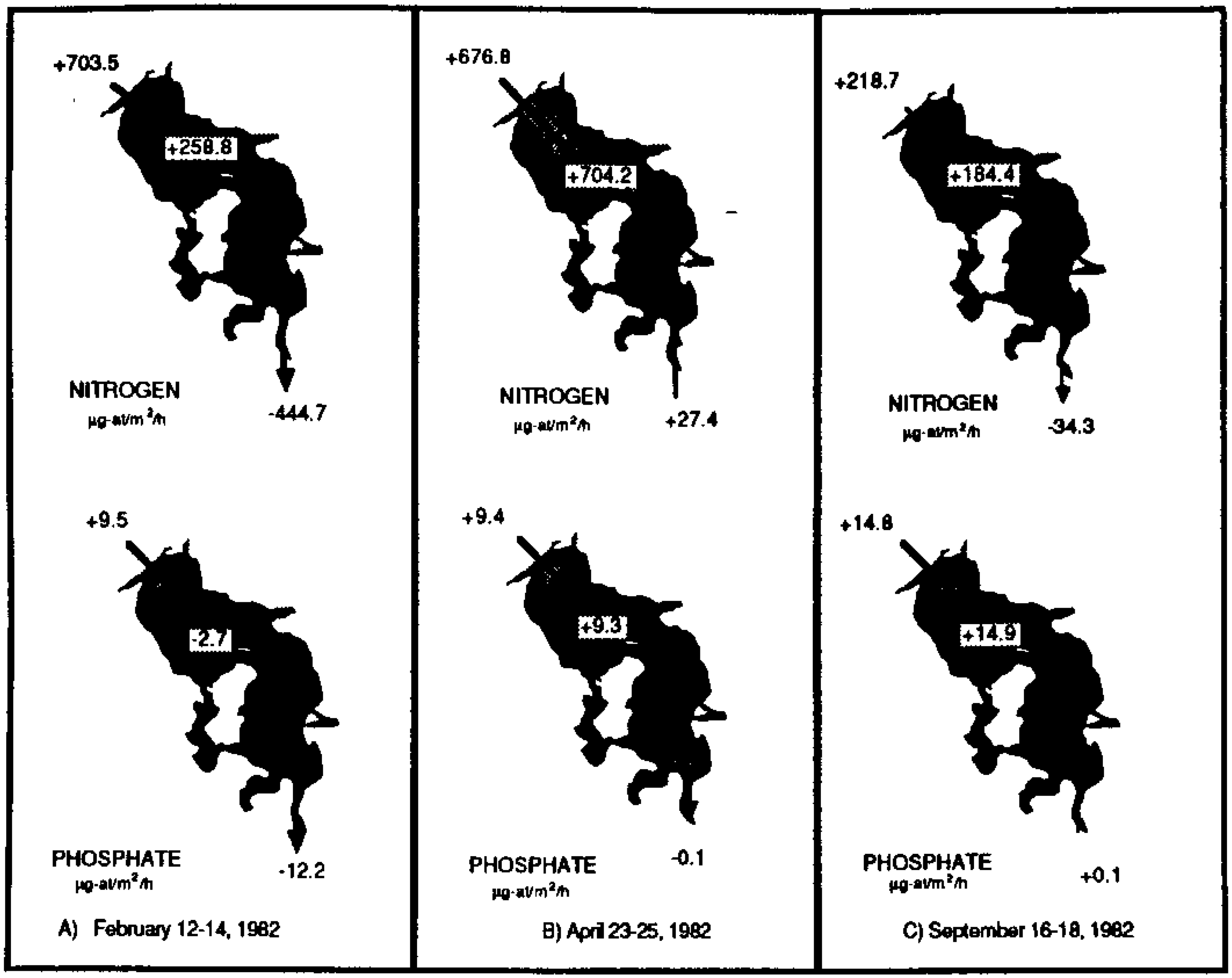


Figure 26. Summary of average net nutrient fluxes in µg-at/m^2/h through the boundaries of Fourleague Bay during tidal cycle studies in A: February, B: April, and C: September, 1982. Numbers inside bay maps represent average hourly net loss or gain to the whole bay of N or P.

exported from the upper bay at a rate of 24 μg-at/m^2/hr and from Oyster Bayou at a rate of 29 μg-at/m^2/hr resulting in a total net loss of 53 μg-at/m^2/hr from the estuary indicating that the bay was acting as a strong source of ammonium to the nearshore zone. Despite the near-balance of water inflows and outflows at the upper bay entrance, there was a positive influx of phosphate in September at a rate of 14.8 μg-at/m^2/hr due to high riverine concentrations. Flux through the lower bay mouth was also positive into the bay (0.12 μg-at/m^2/hr) resulting in an overall accumulation of 14.9 μg-at/m^2/hr of phosphate.

The September increase of phosphorus and ammonium concentrations between the upper and lower Fourleague Bay may indicates that there are sources of both nutrients within the bay, most likely the benthic remineralization observed by Teague (1983). The concomitant disappearance of nitrate indicates that year-round, the bay is a sink for nitrate and lends support to the hypothesis that nitrate was being denitrified in the sediments of the bay.

The net flux of nitrate and phosphate into the upper bay entrance in all three months was not balanced by the fluxes out of Oyster Bayou. Both nutrients showed net accumulations in the estuary for all the tidal cycle periods studied. Rather than simple flow-through mechanics, this suggests an active uptake mechanism within the bay. Ammonium export from the bay in September suggests that Fourleague Bay may be an important supplier of inorganic ammonium to the nearshore zone.

Marsh-Bay Nutrient Exchanges

The total hydrological flow of the three largest bayous, Creole, Carencro and Blue Hammock, was on the order of 10-20 % of the fluxes through the upper bay entrance but maximum flows through these bayous were much higher (Denes, 1983). The marsh flows are important because collectively, they represent a large fraction of the water that drains into Fourleague Bay at certain times of the year, both from bayous and non-point

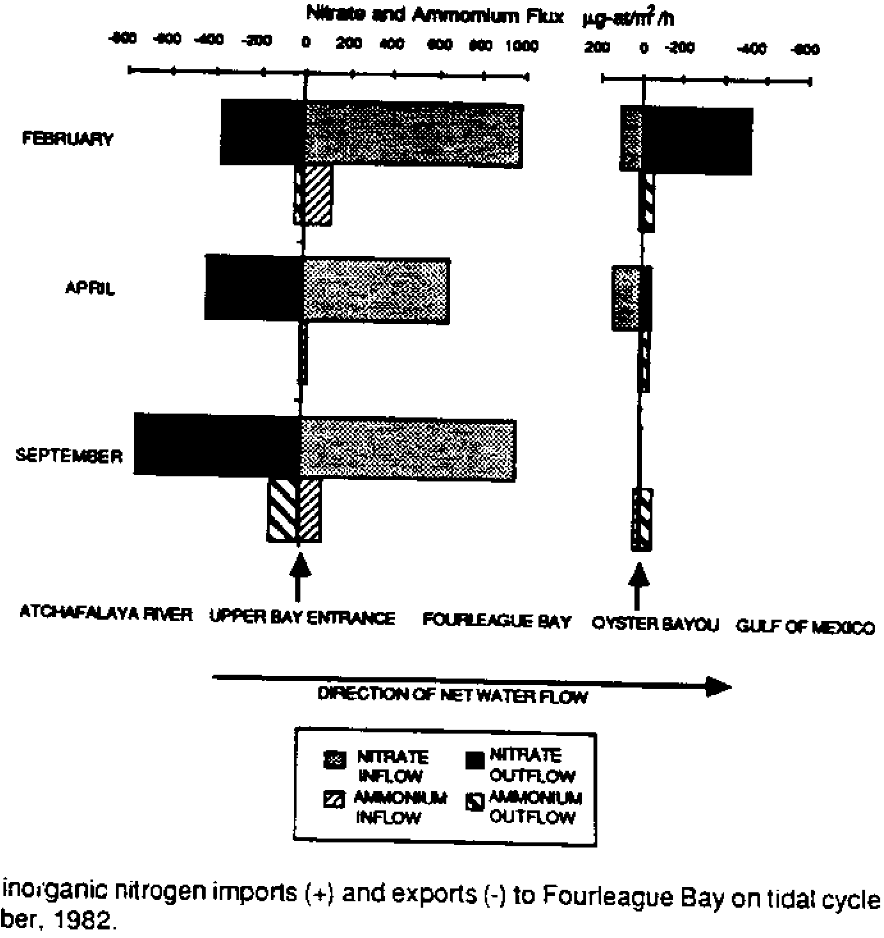


Figure 27. Hourly inorganic nitrogen imports (+) and exports (-) to Fourleague Bay on tidal cycle studies in February, April, and September, 1982.

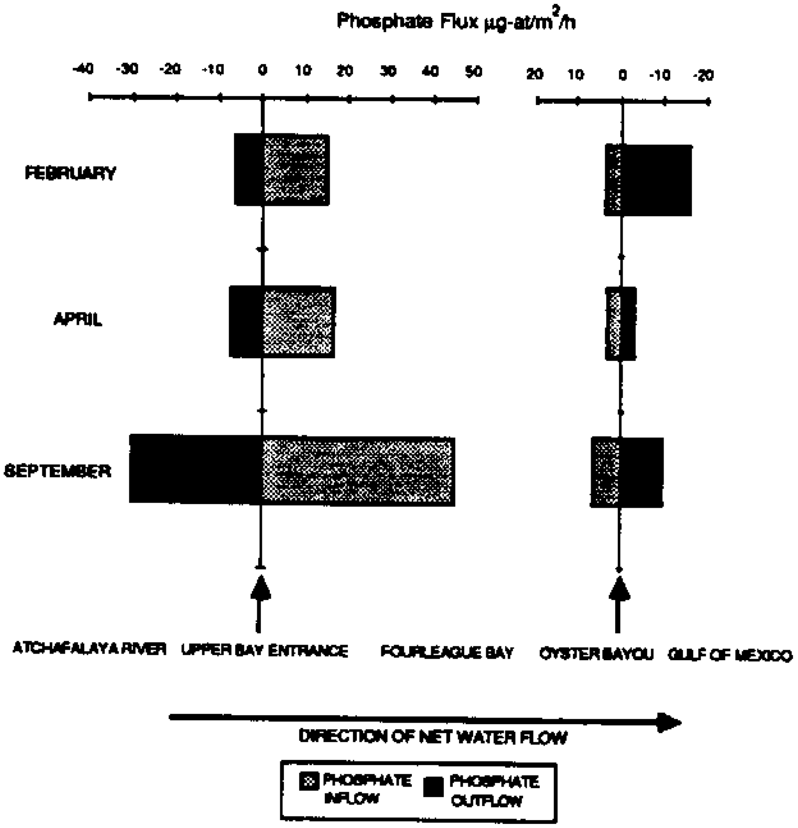


Figure 28. Hourly inorganic phosphorus imports (+) and exports (-) to Fourleague Bay on tidal cycle studies in February, April, and September, 1982.

sources. Bayou exchanges may at times be important as a source of marsh-generated ammonium, and as a sink for nitrate.

During the two spring flood studies water flow was nearly constant into Fourleague Bay from Creole Pass in the upper bay. This may be attributed to the hydrologic head built up by water accumulating on the flooded marsh which experience backwater flooding all along the Atchafalaya Basin during spring (Wang et al. 1985); the general direction of flow throughout the flood period is toward the Gulf. Thus, the contribution of marsh water to the bay and nearshore zone in general may be significant during spring flood. In September, river discharge and backwater flooding are reduced and there is little or no hydrologic gradient to force flow through the marshes into Fourleague Bay.

During the February and April tidal cycle studies in Creole Pass, despite consistent flow in one direction, into the bay, the nutrient profile showed regular variability. I propose a scenario which explains the regular variations as due to the influence of the tide on the proportions of marsh drainage and riverine water mixing and entering the north end of the pass. When flows in the main stem of the bay were ebb directed, water was drawn off the marshes and through Creole Pass into the bay. At these times, the Creole Pass water had a nutrient composition typical of marsh drainage. During flood tides, Creole Pass received river water pushed through its open north end which continued into the bay. At these times, Creole Pass water chemistry was typical of river water.

In April ammonium concentrations in Creole Pass were 50 to 90 % higher than riverine concentrations entering the upper bay or in the bay itself. During flood flows, ammonium concentrations were low and similar to those in river water. During ebb flows, when water was apparently being drawn off the marsh, ammonium concentrations rose significantly. This is consistent with the findings of Stevenson et al. (1976) at Horn Point where ebb concentrations of ammonium were nearly twice as high as flood concentrations throughout much of the year.

There is evidence that marsh processes contributed to declines in nitrate concentrations within the bay as well. In all three tidal cycle studies water draining off the marshes into the bay was significantly lower in nitrate than the estuarine water. This nitrate loss has been observed in other estuaries. Jordan et al., (1983) observed a net import of nitrate to low marshes near the Rhode River. Stevenson et al. (1976) observed diurnal changes in nitrate concentrations in the Horn Point Marsh suggesting uptake during daylight hours and regeneration at night. In all three tidal cycle studies, the three marsh types in Fourleague Bay were exporting water lower in nitrate than the adjacent estuarine waters. At times, nitrate also showed a general decrease in concentrations over the entire two-tidal cycle period which is part of a longer-term pattern. This phenomenon requires further study.

The flux of nitrate into the marsh and ammonium from the marsh observed during the two spring studies at Creole Pass probably reflects the general dynamics of the large volume of water moving in sheetflow across the coastal marsh surface during spring flood. In September during low river flow, marshes were not inundated, and ammonium concentrations in Creole Pass were not significantly different from river water. During this month of high temperatures and presumably high rates of remineralization, there may be a significant accumulation of ammonium on the marsh but there is no tidal energy to flush them to the bay. This may partly explain the large pulse of ammonium observed in the bay early in each spring flood, as accumulated ammonium is flushed from the marsh by the first high water. Stern (1986) reported a similar pattern in nearby Willow Bayou. They observed high rates of ammonium export from January through May when tidal flow was ebb directed due to backwater flooding by the Atchafalaya, driving water across the marshes.

Fourleague Bay marshes display nutrient flux dynamics similar to the Fourleague Bay bottom sediments where Teague (1983) measured uptake of nitrate and regeneration of ammonium. These processes at both the bay-marsh boundary and the sediment-water interface manifest themselves in the rapid decline in water column nitrate concentrations and increases in ammonium concentrations down the bay.

Intensely reducing marsh soils and anaerobic bay bottom sediments are well-known as sites of denitrification by facultative anaerobes (Payne 1973). Nitrate is also involved in a dissimilatory fermentation reaction (Fenchel and Blackburn 1979, Focht and Verstraete 1977) where, instead of acting as a terminal electron acceptor in respiration, it acts as an "electron sink" (Hattori 1983), is converted to ammonium in an energy-producing reaction, and exuded from the cell. This "fermentative nitrate reduction" is an obligately anaerobic reaction. Sorensen (1978) proposed that this process may be "equally as significant as denitrification in the turnover of NO_3^- in marine sediments." Thus, nitrate in sediments is exploited over a range of Eh regimes from temporary to long-term anaeroby. Additionally, bacterial reduction of organic matter results in the release of remineralized ammonium to the water column. This process occurs in both the sediments (Boynton and Kemp 1985) and the water column (Harrison 1978).

In the Louisiana coastal zone, it is clear that marsh and bay sediments are sites of denitrification. In Fourleague Bay marshes (Smith et al. 1985) and in Barataria Bay (DeLaune and Patrick 1980), moderate rates of denitrification were measured begging the question "Where goes the remainder of the disappearing nitrate?". Clearly part of the loss is due to phytoplankton uptake, however, Teague (1983) measured nitrate loss to bay sediments five times that accounted for by Smith et al.'s denitrification measurements. A probable pathway is for the nitrate to be reduced directly to ammonium and exuded from the cells creating an additional source of ammonium to the bay sediments.

SUMMARY

In a system-wide study such as this, water and nutrient flows among components of the ecosystem are not always well-defined, but the evidence from synoptic transects and three tidal cycle studies suggests the following scenario: Upper Fourleague Bay is influenced through three boundaries- Atchafalaya Bay, which is an extension of the Atchafalaya River and its high nutrient loads, the fresh marsh, and the upper bay bottom sediments. The Atchafalaya is clearly the dominant source of inorganic nitrogen in the form of nitrate to the bay. In the upper bay a large fraction of the nitrate load is removed from the water column, supporting algal photosynthesis and energy-producing reactions in the bay sediments. The result of the reduction of nitrate and uptake of organic material is the liberation of ammonium to the water column. The marsh performs the same role in the nitrogen cycle, perhaps to an even greater extent, but its contribution to the bay is requires water movement across the marsh surface. Thus, the marsh contribution is switched on and off depending on wind driven or tidal energy inputs as well as the river's hydrologic cycle.

The April flows through Creole Pass clearly showed the interplay of the three different water masses during what may be the period of greatest interaction: high ammonium was exported from the marshes to the bay on falling tides, nitrate was injected to the bay from the river during rising tides, and nitrate was scavenged from the water overlying the marsh and apparently in the bay sediments. In September, salinity encroachment on ebb flows added the influence of a fourth zone: saline water from the lower bay and the Gulf of Mexico. Low water levels during the summer period may reduce the role of the marsh in the nutrient cycling in the bay during that time.

The lower half of Fourleague Bay is different and distinct from the upper bay in nutrient sources and the processing of nutrients. It is characterized by reduced nutrient loading, clearer water and a high degree of tidal influence. The export from the mouth of the estuary at Oyster Bayou contains reduced nutrient loads, illustrating the role of Fourleague Bay as a filter. Much of the nutrients removed in the bay go to support phytoplankton and secondary production which may be exported to thtough Oyster Bayou to the nearshore zone. This remains to be studied.

High ammonium levels from regeneration processes may be more important than nitrate as a nitrogen source to phytoplankton, especially during summer and fall. Phosphorus levels are generally maintained near 1 µg-at/l throughout the bay, through remineralization, desorption or liberation from the sediments. N/P ratios are lower in the lower bay than in the upper bay, indicating the phosphate is in greater supply relative to inorganic nitrogen and at times P is in excess of N requirements for photosynthesis.

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PART 4

AQUATIC PRIMARY PRODUCTIVITY

EFFECTS OF RIVER DISCHARGE AND VERTICAL CIRCULATION ON AQUATIC PRIMARY PRODUCTION IN A TURBID LOUISIANA (USA) ESTUARY*

J.M. Randall and J.W. Day, Jr.

INTRODUCTION

Rivers influence primary production in estuaries and coastal areas in a number of ways (Goldberg 1969, Parsons et al. 1977, Cadee 1978, Mann 1982). Rivers contribute nutrients directly and can stimulate benthic remineralization, all of which can promote production (Nixon 1981a, Boynton et al. 1982, Kemp et al. 1982). At the same time suspended sediments and colored substances are introduced which diminish the available irradiance in the water and may thereby reduce production. Parsons et al. (1977) noted that maximum production is often found at some distance from the mouth of a river, although nutrient levels may be lower there, and suggested that this was due to increased light availability.

Phytoplankton in turbid water with a sharp vertical light gradient are exposed to significant changes in light levels when they are vertically displaced by turbulence or sinking. These temporal variations in irradiance may have important effects on production that would be ignored by measurement techniques in which samples are held at a constant depth or light intensity. For this reason a number of studies have been conducted in which estimates of production from samples of phytoplankton moved through the water column or a light gradient were compared with those from samples held at certain depths or light levels (Kowalczewski and Lack 1971, Jewson and Wood 1975, Marra 1978, Platt and Gallegos 1980, Gallegos and Platt 1982, Falkowski and Wirik 1981, Joiris and Bertels 1985). The results of these experiments have been variable, some indicating that under certain circumstances incubations in which samples were moved yielded higher production rates and others finding no significant differences.

The objectives of this study were to determine: 1) temporal and spatial patterns of aquatic primary productivity in Fourleague Bay, 2) the factors controlling these patterns with special attention given to river discharge, and 3) the effect of circulation through the sharp light gradient in the water column on phytoplankton production. Fourleague Bay is an excellent site to study riverine influences on estuarine production because it receives large inputs from the Atchafalaya River. The shallow, well-mixed water column and turbid water also provided an opportunity to study the effects of circulation through a light gradient on production.

STUDY SITE DESCRIPTION

Fourleague Bay is a 9300 hectare estuary in the central coastal zone of Louisiana (Fig. 1). Its upper end opens to the eastern side of Atchafalaya Bay 10 km from the mouth of the Atchafalaya River. The river carries approximately 30% of the combined flow of the Mississippi and Red Rivers and is at present building an extensive delta at its mouth (Roberts et al. 1980). The delta first achieved subaerial expression in 1973 and its easternmost lobe is now approximately 3 km from the entrance to Fourleague Bay. The bay is uniformly shallow with an average depth of about 1.5 meters and is bounded by fresh and salt marshes. Two sites were chosen for this study: one located at the entrance to the

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*Randall, J.M. and J.W. Day, Jr. 1987. Effects of river discharge and vertical circulation on aquatic primary production in a turbid Louisiana (USA) estuary. Netherlands Journal of Sea Research 21(3):231-242. Used with permission.

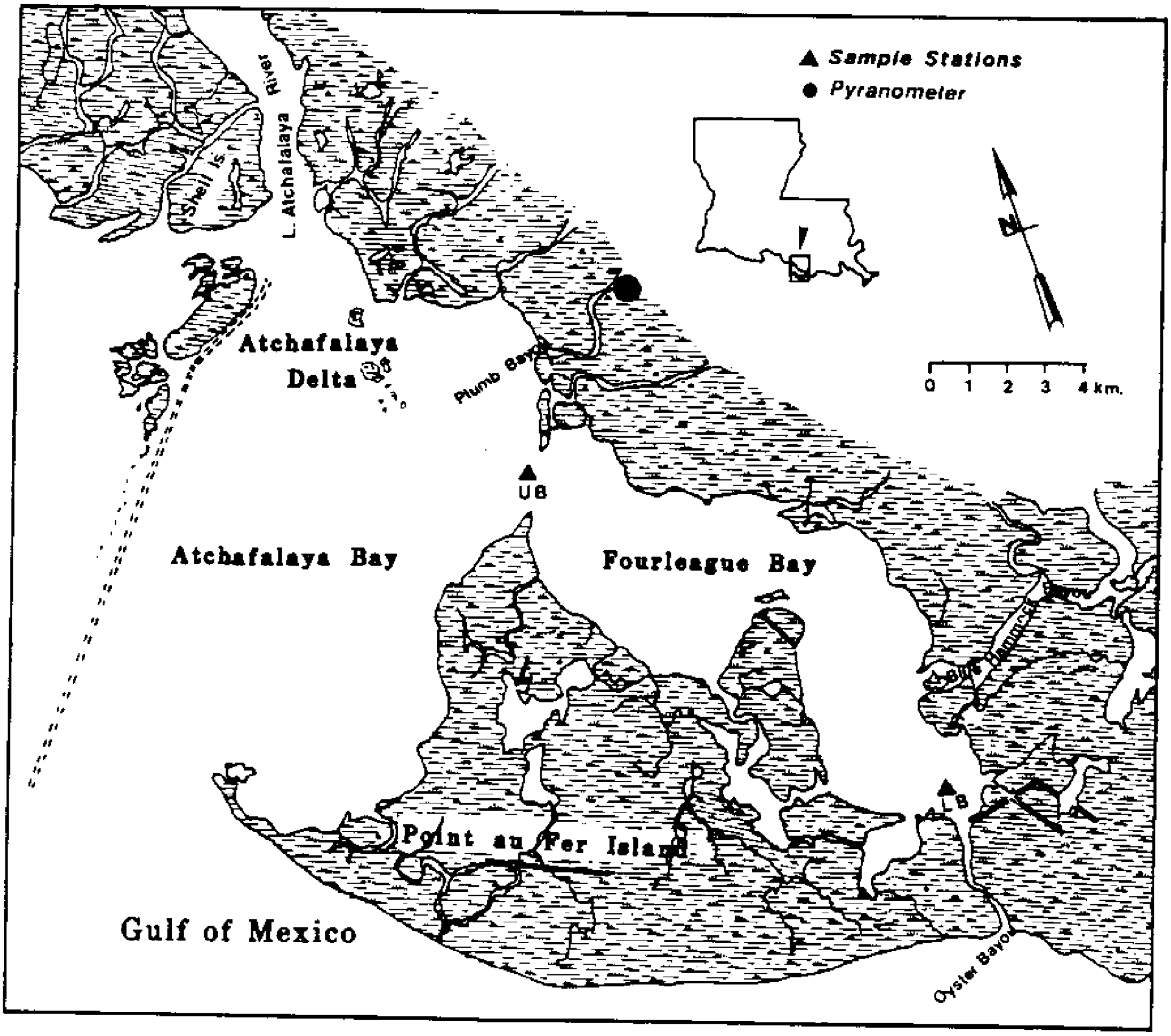

Fig. 1. Map of the study site showing locations of the sampling stations and the pyranometer.

upper bay, and the other in the lower bay approximately 1 km north of the entrance to Oyster Bayou. The upper bay is dominated by turbid, nutrient-rich river water, especially during periods of high flow. Salinity ranges from fresh in the spring to about 10 ppt during periods of low river flow in the early fall and averages 1.5 ppt. Secchi disk depths in the upper bay range from 5 to 35 cm (Madden 1986). The lower end of the bay is directly connected to the Gulf of Mexico by Oyster Bayou. Gulf water is characterized by higher salinity, and relatively low turbidity and nutrient concentrations. Mean salinity in the lower bay is 13.4 ppt but it and secchi disk depth vary greatly with time due to changes in river flow, tides and winds, ranging from 0 to 26 ppt and 5 to 60 cm, respectively (Madden 1986). Astronomical tides in the bay have a range of 30 to 50 cm (Cunningham 1980). Wind driven tides often mask astronomical tides, especially during frontal passages.

MATERIALS AND METHODS

Measurement of Phytoplankton Production and Respiration

Aquatic primary production and respiration were measured at both sites every 4 to 8 weeks from mid-June 1984 to mid-May 1985 using the "light/dark bottle" oxygen technique (Strickland and Parsons 1972). Bottles were incubated for approximately 4 hours around local noon and initial and final oxygen concentrations were measured with an Orbisphere Model 2714 Dissolved Oxygen Detector. The water column was always well mixed and water for incubations was taken from the upper half meter.

Stationary and moving incubations were used. For a stationary incubation, 4 light bottles were suspended

TABLE 1

Definition of symbols used in the text (and their units). Yearly rates are from standard incubations and hourly rates are from standard incubations unless otherwise stated.
*These values are also given in $\mathrm{mg\ C \cdot m^{-2} \cdot y^{-1}}$ in Table 3.

symbol	*definition*	*units*
NDP_h	hourly water column net daytime production	$\mathrm{mg\ O_2 \cdot m^{-2} \cdot h^{-1}}$
NDP_y	annual water column net daytime production	$\mathrm{mg\ O_2 \cdot m^{-2} \cdot y^{-1}}$*
GP_h	hourly water column gross production	$\mathrm{mg\ O_2 \cdot m^{-2} \cdot h^{-1}}$
GP_y	annual water column gross production	$\mathrm{mg\ O_2 \cdot m^{-2} \cdot y^{-1}}$*
DR_h	hourly daytime water column respiration	$\mathrm{mg\ O_2 \cdot m^{-2} \cdot h^{-1}}$
DR_y	annual daytime water column respiration	$\mathrm{mg\ O_2 \cdot m^{-2} \cdot y^{-1}}$*
NR_y	annual night-time water column respiration	$\mathrm{mg\ O_2 \cdot m^{-2} \cdot y^{-1}}$*
NO_3	concentration of NO_3 plus NO_2	$\mathrm{\mu gat \cdot dm^{-3}}$
SRP	concentration of soluble reactive phosphorus	$\mathrm{\mu gat \cdot dm^{-3}}$
PI	production versus irradiance	N.A.

from a floating rack at each of the following depths: the surface; 1 secchi depth ; 2 secchi depths; and near the bottom. Four dark bottles were also incubated. Hourly water column net daytime production, NDP_h (all symbols and units are defined in Table 1), was calculated as the integral of production in the light bottles over all depths while hourly daytime respiration, DR_h ,was the average of the dark bottles and was regarded as constant for the water column. Hourly gross production, GP_h, equaled NDP_h plus DR_h.

Moving incubations were used less frequently and only concurrently with stationary incubations so that results could be compared. During moving incubations 2 sets of 6 light and 4 dark bottles were manually moved through the water column so that a complete cycle took either 0.5 or 1 hour in an attempt to mimic vertical water movement. Hourly net production and respiration in these bottles were calculated as the averages of all light and dark bottles, respectively.

Four estimates of water column net production were generated for each stationary incubation by integrating the areas under curves defined by values from randomly chosen replicates from each sample depth. Results of moving and stationary incubations were analyzed for significant differences ($p < .05$) using linear contrasts (SAS 1985).

Secchi disk depths were determined and whole water samples taken at the start and finish of each incubation. Two 100 ml replicates from each sample were analyzed for suspended solids gravimetrically (Strickland and Parsons 1972) using Gelman Type A/E glass fiber filters. The euphotic zone was assumed to extend to the depth at which light was diminished to 1% of its surface value as calculated from secchi depth (Poole and Atkins 1929).

Incident solar radiation was measured with an Eppley pyranometer located approximately five km north of the upper bay site (Fig. 1) and used to construct photosynthesis versus irradiance (PI) curves using Secchi depth data. Incident radiation was also estimated from climate data. Weather conditions in southeastern Louisiana are classed according to 8 synoptic weather types defined by Muller (1977) based on data taken at 06:00 and 15:00 hours each day by the National Weather Service office at New Orleans. These data were taken for days of incubations and assigned radiation values based on the work of Muller and McLaughlin (1985) which gives levels of mean daily solar radiation by month for each of the 8 weather types. We assumed that the weather type at New Orleans was the same as that at Fourleague Bay on any given date (R. Muller, Dept. of Geography, LSU, personal communication) and field observations confirmed this.

Estimates of Annual Production and Respiration

To estimate annual rates of Net Daytime Production, NDP_y, the hourly rates determined during stationary incubations were first converted to daily rates. The most common way of doing this is to multiply the hourly rate by the number of hours of daylight on the day in question (method A). However, this may overestimate production because it assumes rates measured around noon are supported by the lower levels of irradiance earlier and later in the day (Shaffer and Onuf 1985). Therefore, production rates were also calculated from hourly rates with the following method (method B). The daylight hours of an incubation day were separated into periods before, during and after incubations. The average hourly irradiance for each of these periods was calculated from the pyranometer data. These percentages were used to calculate average irradiance values for the morning and afternoon periods for each depth at which samples had been incubated. Production rates for these irradiance levels were taken from the PI curve for the incubation and plotted with depth. The production rates were then integrated with depth to yield areal rates. Hourly rates for each period were then multiplied by the number of hours in that period and production from the 3 periods summed to yield a daily net production estimate (see Randall 1986 for further detail).

The daily rate of daytime respiration was calculated by multiplying DR_h by the hours of daylight on the day in question and the daily rate of night-time respiration equaled DR_h times the hours of darkness. The daily rate of gross production equaled the daily rate of net daytime production plus the daily rate of daytime respiration.

Annual rates of net daytime production, NDP_y, gross production, GP_y, daytime respiration, DR_y, and night-time respiration, NR_y, were calculated by plotting the respective daily rates with date and integrating the areas under the curves. Measurements made on consecutive days at the same site were averaged. A photosynthetic quotient (PQ) of 1.2 and a respiratory quotient (RQ) of 1.0 were used to convert values from g O_2 to g C (Strickland and Parsons 1972).

Chlorophyll *a*

Whole water samples were collected immediately prior to incubations and placed on ice for later analysis. Within 5 hours two 50 ml replicates from each sample were filtered through Millipore 0.45µ membrane filters which were immediately frozen on dry ice. They were later thawed, dissolved in 90% acetone, and the percent absorbance of the solutions measured on a Varian Techtron Model 635 Spectrophotometer according to methods outlined in Strickland and Parsons (1972). Chlorophyll *a* concentrations were calculated using the equations of Lorenzon (1967). Production per unit biomass was estimated by dividing NDP_h by chlorophyll *a* concentration.

Nutrients and Other Physical Parameters

Water samples were taken prior to incubations, immediately filtered through Millipore Type AP glass fiber prefilters into Technichon autoanalyzer vials and frozen on dry ice. They were later analyzed with a Technichon autoanalyzer for nitrate plus nitrite (NO_3), ammonium (NH_4^+), and soluble reactive phosphorus (SRP) (U.S. Environmental Protection Agency 1979). Discharge of the Atchafalaya River at Simmesport, Louisiana, was obtained from the U.S. Army Corps of Engineers (1984,1985). Average flow for the 7 days preceding incubations were used in the data analysis. Water temperature and salinity were recorded with a Beckman RS5-3 salinometer. An analysis of variance (SAS, 1985) was performed on the data to determine relationships among the different variables.

RESULTS

Seasonal and Spatial Patterns

Production and Respiration (stationary incubations). Aquatic primary production exhibited similar seasonal patterns in lower and upper Fourleague Bay with peaks in the late summer and early fall respectively, and smaller secondary peaks at both sites in late winter (Fig. 2). Generally, production was significantly greater at the lower bay. The difference was especially pronounced in June and July during the lag between the start of the period of peak production there and at the upper bay. However, the range of rates at the 2 sites were not significantly different (Table 2). At the upper bay, over 80% of the annual net production and nearly 60 % of the annual gross production occurred during the period from late July to mid-November. At the lower bay, with higher rates of production for more of the year, figures for the comparable mid-June to early October period are 55% and 50%, respectively.

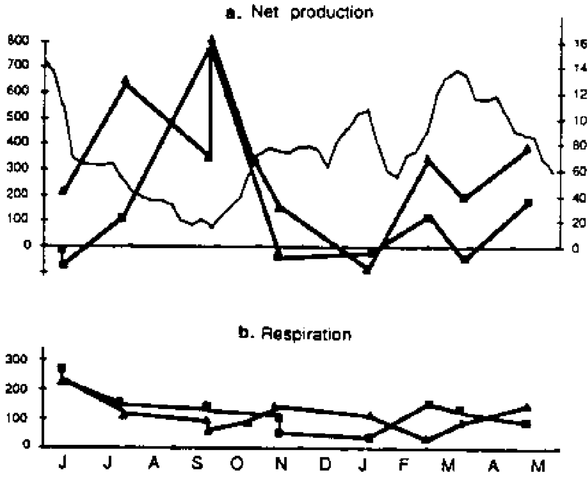

Fig. 2. Seasonal production and respiration patterns at both sites. Production and respiration in mg $O_2 m^{-2} h^{-1}$; scale on left. River discharge at Simmesport, Louisiana, in $m^3 s^{-1}$; scale on right. ■ upper bay, ▲ lower bay, — river discharge.

TABLE 2

Means and ranges of hourly rates of net daytime production, NDP_h, gross production, GP_h, and daytime respiration, DR_h, measured during incubations. Units = mg $O_2 \cdot m^{-2} \cdot h^{-1}$.

measurement	*site*	*mean*	*range*
NDP_h	upper bay	147.0	−76.6 to 775.8
	lower bay	325.7	−88.0 to 798.7
GP_h	upper bay	273.8	2.6 to 899.8
	lower bay	430.6	19.8 to 858.3
DR_h	upper bay	126.8	31.0 to 255.0
	lower bay	104.8	26.2 to 230.4

NDP_h and GP_h were near zero in mid winter at the lower bay and from mid-fall to mid-winter at the upper bay. NDP_h was near zero at the upper bay again in late March and mid-June but there was substantial GP_h at these times. Seasonal patterns of DR_h did not track production, neither site consistently exhibited higher rates than the other, and seasonal variations were small relative to those for production (Fig. 2b, Table 2).

Chlorophyll *a*. Chlorophyll *a* concentration at the upper bay ranged from 3.2 mg m^{-3} in January to 19.8 in both November and early March with a mean of 13.4 mg m^{-3}. At the lower bay it ranged from 4.0 in May to 26.7 mg m^{-3} in July with a mean of 14.5. Chlorophyll a concentration was correlated with secchi depth at the upper bay but it was not correlated with net production or any other factor at either site or in the bay as a whole. Production per unit biomass (NDP_h / chlorophyll a concentration) varied considerably both spatially and temporally. At the upper bay, the ratio ranged from -8.9 g O_2 $m^{-2}hr^{-1}$ mg Chl a^{-1} in January to 50.1 in September with a mean of 6.7. At the lower bay production per unit chlorophyll a ranged from -8.2 g O_2 $m^{-2}hr^{-1}$ mg Chl a^{-1} in January to 96.6 in May and averaged 30.9. In the bay as a whole the P/B ratio was positively correlated with surface irradiance (r^2=0.335 $p<.01$) and water temperature (r^2=0.321 $p<.025$) and negatively correlated with riverflow (r^2=0.209 $p<.05$). At the upper bay it was negatively correlated with riverflow (r^2=.523 $p<.025$) and at the lower bay it was positively correlated with surface irradiance (r^2=.358 $p<.025$).

Riverflow. Seasonal variations in the flow of the Atchafalaya River have marked effects on physical and chemical characteristics of the water in Fourleague Bay (Madden, 1986; Caffrey, 1983). The variations were more pronounced than usual during the period of this study. The spring flood peaks were above average in 1984 and 1985 while the 1984 annual low was slightly below average. The highest flow during the period, 13,800 m^3 sec^{-1}, occurred on March 21, 1985 and the lowest flow, 1,400, occurred on September 21 1984. The peak was unusually late in 1984 and was still a factor in June when the study began. Flow was also exceptionally high in late 1984 and early 1985 and the mean flow in January, 9,200 m^3 sec^{-1}, was one of the highest recorded at that time of year. Production was negatively correlated with riverflow at both sites and in the bay as a whole (Fig. 2a). The relationship was much stronger at the upper bay where secchi depth was negatively correlated with riverflow (r^2=0.51 $p<.025$).

Light. Secchi disk depth at the upper bay ranged from 15 to 30 cm with a mean of 20.5 cm. At the lower bay it ranged from 20 to 60 cm with a mean of 36.5 cm. At the upper bay the depth of the euphotic zone averaged 53.9 cm and ranged from 41 to 81 cm. At the lower bay it averaged 98.5 cm and ranged from 54 to 160 cm (coincident with the bottom). Turbidity varied widely and without a recognizable seasonal pattern at the lower bay and, unlike the upper bay, secchi depth was not significantly correlated with riverflow there. Flocculent sediments in the area are often mixed into the water column by winds and currents (Teague 1983) and the estuarine turbidity maximum is located in the lower bay for much of the year (Madden 1986). Secchi depth was not correlated with suspended sediment load at either site, indicating that colloidal and dissolved compounds may be responsible for much of the light attenuation in the bay. Suspended sediment load ranged from 0.05 to 0.175 g l^{-1} at the upper bay and from 0.013 to 0.202 g l^{-1} at the lower bay with means of 0.087 and 0.116 g l^{-1}, respectively.

Incident radiation on days of incubations ranged from 9.3 in November to 24.7 in June. NDP_h was correlated with incident radiation at the lower bay (r^2=0.486 $p<.025$) and GP_h was correlated with incident radiation at the lower bay (r^2=0.515 $p<.025$) and in the bay as a whole (r^2=0.215 $p<.025$).

Nutrients and other physical factors. Nutrient concentrations varied seasonally and spatially in the bay. The river is a source of NO_3 and the bay acts as a net sink so that concentrations decrease non-conservatively with increases in salinity (Teague 1983, Madden 1986). Concentrations ranged from 0.4 to 87.5 µg at l^{-1} with a mean of 41.7 µg at l^{-1} at the upper bay and from undetectable to 45.3 µg at l^{-1} with a mean of 6.0 µg at l^{-1} at the lower bay. Production was negatively correlated with NO_3 at both sites and in the bay as a whole reflecting the high NO_3 levels in turbid river water. Thus, NO_3 did not negatively affect production but its negative correlation with secchi depth for the entire bay (r^2=.305 p<.025) indicates that it served as a tracer for turbidity. During the fall NO_3 concentrations were low at the lower bay and production may have been N limited.

At the upper bay SRP ranged from 0.3 to 2.3 µg at l^{-1} with a mean of 1.2 µg at l^{-1} and at the lower bay it ranged from 0.1 to 1.4 µg at l^{-1} with a mean of 0.6 µg at l^{-1}. At the upper bay NH_4^+ ranged from 0.4 to 12.2 µg at l^{-1} with a mean of 2.7 µg at l^{-1} and at the lower bay it ranged from 0.3 to 5.5 µg at l^{-1} with a mean of 2.4 µg at l^{-1}. N:P ratios (total inorganic nitrogen/SRP) ranged from 2.7 in September to 63.6 in March and averaged 34.4 at the upper bay, and from 0.6 in September to 45.0 in July and average 14.7 at the lower bay.

Salinity in the bay also varied seasonally due to riverflow variations although tides and winds may cause short term changes, especially at the lower bay (Caffrey 1983, Madden 1986). The upper bay was fresh or nearly fresh (<2 ppt) most of the year with a mean salinity of 1.5 ppt. Only during the fall low flow period did brackish water penetrate into the upper bay. The highest value, 13.6 ppt, occurred in September. Salinity was more variable at the lower bay, ranging from 1.6 ppt in January to 23.9 ppt in September with a mean of 11.6 ppt. NDP_h was correlated with salinity in the upper bay (r^2=0.875 p<.005) and in the bay as a whole (r^2=0.383 p<.005), apparently because salinity was correlated with secchi depth at the upper bay (r^2=0.546 p<.025) and in the bay as a whole (r^2=0.592 p<.0001) and served as an indicator of water clarity. Salinity tracked riverflow at the upper bay and was negatively correlated with it (r^2=0.516 p<.025) .

Water temperature ranged from 8.5° C at the upper bay and 9.7° C at the lower bay in January to 28.8° C at the upper bay in July and 29.7° C at the lower bay in June. NDP_h and GP_h were correlated with water temperature (r^2= =0.412 p<.05; r^2=0.566 p<.025) in the lower bay while at the upper bay respiration was correlated with water temperature (r^2=0.459 p<.05).

Within and Between Depth Differences

Coefficients of variation for hourly rates of net production in sets of light bottles incubated at one depth averaged 15.8% (n=4). For all incubations differences between means of samples held at the surface and those held near the bottom were greater than the greatest within group variation so differences in production with depth were considered significant. Light diminished rapidly in the turbid water and net production was rarely positive near the bottom. Surface net production was less than that at 1 secchi depth (indicating photoinhibition) in more than half of the incubations with no seasonal pattern at both sites.

Annual Production and Respiration Estimates

NDP_y at the lower bay was more than double that at the upper bay, and GP_y at the lower bay was over 60% greater than that at the upper bay (Table 3). DR_y was similar at both sites (Table 3). Short-lived blooms and major storms may have been missed by our sampling schedule resulting in over- or under- estimation of actual annual production.

TABLE 3

Estimates of NDP_y, GP_y, R_y and NR_y at both sites. Estimates were converted to g C m^{-2} with a photosynthetic quotient (PQ) of 1.2 and a respiratory quotient (RQ) of 1.0 (Strickland & Parsons, 1972). The two methods of calculation are described in the text.

estimate	*method*	*site*			
		upper bay		*lower bay*	
		g O_2 m^{-2}	*g C m^{-2}*	*g O_2 m^{-2}*	*g C m^{-2}*
NDP_y	A	627	196	1404	439
	B	383	120	1016	317
GP_y	A	1167	399	1927	635
	B	923	322	1539	514
DR_y		541	203	523	196
NR_y		489	183	484	182

TABLE 4

Comparison of NDP_h ($mg\ O_2 \cdot m^{-2} \cdot h^{-1}$) estimates from stationary and moving incubations and the difference between them as a percentage of the stationary incubation estimate. Negative differences indicate lower moving estimates and positive differences indicate higher moving estimates. Differences greater than errors (percentage greater than 16 or less than − 16) are indicated with a *. U.B. = upper bay, L.B. = lower bay.

date	*site*	*type of incubation*				
		stationary	*1 hour moving*		*0.5 hour moving*	
		NDP_h	*NDP_h*	*% difference*	*NDP_h*	*% difference*
11/18/84	U.B.	− 46.9	− 43.2	8	− 86.4	− 84*
03/03/85	U.B.	121.0	29.4	− 76*	62.0	− 49*
03/28/85	U.B.	− 37.7	− 54.0	− 43*	− 48.0	− 27*
05/14/85	U.B.	188.1	85.9	− 54*	87.5	− 53*
10/27/84	L.B.	353.3	283.5	− 20*	309.0	− 12
11/17/84	L.B.	150.0	212.6	42*	200.2	34*
01/19/85	L.B.	− 86.0	− 87.5	1	− 88.8	− 1
03/02/85	L.B.	332.2	351.0	6	391.3	18*
03/27/85	L.B.	187.5	214.2	14	189.0	1
05/13/85	L.B.	387.6	351.4	− 9	305.4	− 21*

Comparison of Incubation Methods

Significant differences were found between estimates of NDP_h from stationary incubations and moving incubations when only experiments conducted at the upper bay were considered. Table 4 compares NDP_h mates from stationary and moving incubations for each date and presents the differences between them as percentages of the stationary estimates. Differences less than 16% (positive or negative) were considered smaller than errors because coefficients of variation for sets of light bottles held at one depth in stationary incubations averaged 15.8% (coefficients of variation between replicates in moving incubations averaged 15.1%). The differences ranged from -84 to 42%.

At the lower bay only two 1-hour and three 0.5-hour moving incubations out of a total of 12 conducted varied from stationary incubations by more than 16% and of those, 3 were greater than and 2 less than the stationary incubation estimates. At the upper bay three of four 1-hour and four of four 0.5-hour incubations were more than 16% lower than the stationary estimates.

When comparisons from both sites were considered, the difference between 0.5 hour moving and stationary estimates as a percentage of stationary incubation estimates was significantly correlated with secchi depth (r^2=0.402 $p<.05$) and with the depth of the water divided by the depth of the euphotic zone (r^2=0.496 $p<.025$; Fig. 3). Secchi depths were less than 25 cm during the 7 comparisons in which differences were greater than errors at the upper bay while they were 38 and 60 cm on the 2 occasions when moving estimates were higher at the lower bay. However, on October 27 when the moving estimates at the lower bay were lower, the secchi depth was 60 cm.

DISCUSSION

Spatial and Temporal Patterns of Aquatic Primary Production

The spatial and temporal patterns of production in Fourleague Bay were strongly influenced by the dis-

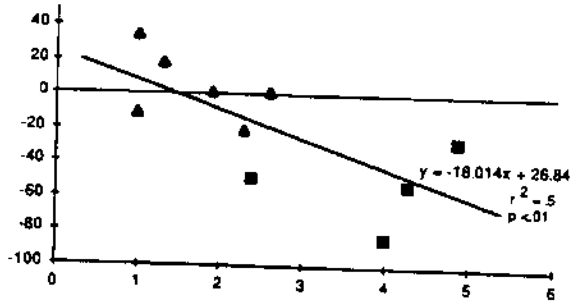

Fig. 3. Relative production estimates from 0.5-h moving and stationary incubations (difference as a percentage of stationary estimate) as a function of relative light penetration (depth of water column: depth of euphotic zone). ■ upper bay; ▲ lower bay. Regression was fit with the least squares method.

charge of the Atchafalaya River. Spatially, NDP_y at the upper bay site was less than half that at the more distant lower bay site. Temporally, NDP_h and GP_h were negatively correlated with riverflow at both sites and in the bay as a whole, undoubtedly caused by light limitation due to the extreme turbidity of the river water. In general, light penetration increased with distance from the river due to the settling of particles and mixing with clearer Gulf water, and turbidity decreased as riverflow decreased.

At the upper bay the negative correlations of NDP_h, GP_h, production per unit biomass and secchi depth with riverflow and positive correlations of NDP_h and GP_h with secchi depth indicate that for most of the year, production was limited by the extreme turbidity of river water. Light was so strongly attenuated in the water column that production rates decreased rapidly below one secchi depth and net production was always negative at the bottom. NDP_h was negative during 6 of the 11 incubations conducted at the upper bay, indicating that the critical depth was less than the water depth. At the lower bay production also appeared to be limited by turbidity for part of the year, especially during periods of high river flow when fresh turbid water inundated the entire bay. However, relationships of NDP_h and GP_h with secchi depth were not consistent at the lower bay and although the greatest secchi depths were encountered during low river flow, at times resuspension of flocculent sediments increased turbidity independent of riverflow there. Production declined rapidly below one secchi depth at the lower bay except in October when positive net production was measured at the bottom. Negative NDP_h was encountered at the lower bay only in January when secchi depth, water temperature and salinity were minimum and net production was negative at all depths. The higher NDP_h and GP_h generally encountered at the lower bay were apparently due to the deeper euphotic zone. In addition, a euphotic zone of the same depth occupied a greater proportion of the water column at the lower bay because it was 30 to 50 cm shallower than the upper bay. Horizontal gradients of increasing production from areas of high turbidity to areas with clearer water have also been found in San Francisco Bay (Cole and Cloern 1984), the upper Chesapeake (Flemer 1970), the Wadden Sea (Cadee and Hegeman 1974), Corpus Christi Bay estuary (Flint 1984), Bristol Channel, U.K. (Joint and Pomeroy 1981) and the Mississippi Delta (Thomas and Simmons 1960).

The Atchafalaya also contributed nutrients, notably inorganic N, which apparently stimulated production when light was not limiting. NDP_h and GP_h were generally highest in a zone intermediate in water clarity and nutrient concentrations where relatively clear, nutrient-poor water from the Gulf mixed with the turbid, nutrient-rich riverwater (Fig. 4a). This zone of low-salinity water (the mixing zone) advanced toward the Gulf and retreated seasonally as riverflow varied. Thomas (1966) found a similar mobile zone of relatively high production off the mouth of the Altamaha River, Georgia.

The mixing zone was usually in the lower bay during the mid to late summer and retreated up-bay as flow decreased moving as far as the upper bay site during the early fall. Because the mixing zone retreated no farther, NDP_h and GP_h there were positively correlated with salinity which acted as a tracer for water clarity. However, at the lower bay production rates decreased at salinities above about 15 ppt despite increasing water clarity (Fig. 4a). Data taken by Sklar (1976) at a site in the nearshore zone influenced by the discharge of the Mississippi River, also showed decreases in hourly net production with salinity from about 10 to 30 ppt (Fig. 4b). In addition, Sklar and Turner (1981) found maximum rates of production in this area during peak riverflow in May indicating that the mixing zone indeed moves into the nearshore region when flows are high. They suggested that the decrease in production with increasing salinity was due to deficiencies of some nutrient(s) and

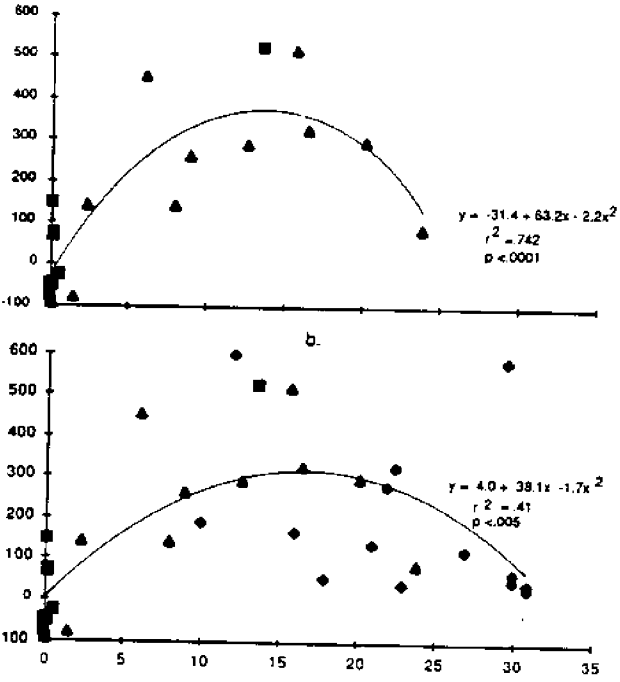

Fig. 4. Net production versus salinity. (a) In upper and lower Fourleague Bay. (b) In Fourleague Bay and nearshore Louisiana (from SKLAR, 1976). ■ upper bay; ▲ lower bay; ◆ nearshore Louisiana. The curves were plotted with the least squares method.

suspected that N was the primary limiting nutrient. Inorganic N concentrations and N:P ratios were low when salinity was high in Fourleague bay and it is likely that N was limiting at these times. Cadee (1978) reported a similar production-versus-salinity relationship when he plotted data from the Amazon River plume.

Surface irradiance, water temperature, chlorophyll *a*, and interactions of these factors were also related to production rates, especially at the lower bay. A multiple of surface irradiance and chlorophyll *a* was the best single predictor of NDP_h at the lower bay, explaining 49% of its variability. Falkowski (1981) related integral production to chlorophyll *a* and surface irradiance in the New York Bight, and Gieskes and Kraay (1977) concluded that the production of surface samples from the southern North Sea could be estimated from chlorophyll *a* and surface irradiance. Cole and Cloern (1984) noted that water clarity was an important factor in turbid estuaries and found that a composite parameter of chlorophyll *a*, surface irradiance and extinction coefficient explained 82% of the spatial-temporal variability in production in San Francisco Bay. However, NDP_h in Fourleague Bay was better correlated with the multiple of surface irradiance and secchi depth, which explained 39% of its variability, than it was with factors including chlorophyll *a*. Secchi depth alone explained 64% of the variation in production at the upper bay.

Production Estimates from Moving Incubations

This is the first study we know of in which production estimates from samples moved through the water column were, on numerous occasions, significantly lower than estimates derived from samples held at fixed depths. Jewson and Wood (1975) obtained estimates from samples circulated in glass tubing that ranged from 10% higher to 18% lower than those derived from samples held at fixed depths in bottles but concluded that the differences were less than errors. Other comparisons carried out in the field and laboratory or with simulation models indicated that production in samples moved through the water column or a light gradient was either always higher (Kowalczewski and Lack 1971), higher when there was photoinhibition in surface samples of stationary incubations (Marra 1978, Platt and Gallegos 1980), or not significantly different (Gallegos and Platt 1982, Falkowski and Wirik 1981).

The relationship of relative production estimate (moving incubation : stationary incubation) to relative light penetration (depth : euphotic depth) for 0.5 hour moving incubations shown in Fig. 3 suggests that at least 2 distinct time-dependent light-versus-irradiance phenomena affected production rates. When phytoplankton are exposed to light after a period in the dark they do not immediately fix carbon and evolve oxygen at the maximum rate for the new light intensity but instead require an induction period on the order of minutes to reach full photosynthetic rate (Walker 1973, Walker 1976, Harris 1978). At high light intensities, photoinhibition, a decay from the maximum rate, will occur after periods ranging from 10 minutes to several hours depending on the species and the light intensities involved (Harris and Piccinin 1977, Belay 1981, Kirk 1983).

The relative importance of these two phenomena apparently varied with relative light penetration and thus circulation affected rates of production differently at different times. When relative light penetration was low samples from moving incubations were exposed to irradiance levels adequate to support photosynthesis only for the brief periods when they were near the surface; when the water was most turbid photosynthesis was probably possible only for the 4 or 8 minutes when the samples were actually at the surface. On these occasions phytoplankton may have been in the induction period and evolving oxygen at suboptimal rates for a substantial portion of the time that they were exposed to light during each rotation, leading to lower total production (lower right Fig. 3). The induction period is often appreciably shorter after a brief period of darkness (e.g. 10 minutes) than it is following longer periods of darkness (Walker et al. 1973). Thus, the relative importance of the induction period would have decreased in moving incubations as relative light penetration increased and the amount of time samples spent in the dark decreased. When samples were exposed to irradiance during most or all of a rotation photosynthetic reactions may not have ceased entirely and there may have been no induction period when they were returned to the surface.

On the other hand, samples in stationary incubations held at a depth with high levels of irradiance were sometimes photoinhibited while samples moved through the water column were not exposed long enough to be photoinhibited (upper left Fig. 3). Several workers have suggested that this was in part responsible for the higher production rates they found in samples that were moved through the water column or exposed to varying light levels (Marra 1978, Jewson and Wood 1975, Platt and Gallegos 1980). On the days when moving incubations yielded higher production estimates, surface samples were photoinhibited; however, if production in surface samples had equaled the maximum rates, stationary incubations still would not have yielded estimates as high as moving incubations. Marra (1978) also noted that photoinhibition alone was not sufficient to explain the differences between methods of incubation in his study. He showed that the maximum (light-saturated) rate of production was time-dependent and decreased with the length of incubation from 12.5 minutes to 4 hours. Thus, he suggested, bottles circulated through the light gradient were able to photosynthesize at greater rates for a given light intensity than were samples held at 1 depth and so yielded greater and more realistic estimates of integral production.

The difference between 1-hour moving incubations and stationary incubations showed the same trend with relative light penetration but the relationship was not significant. This difference between 0.5-hour and 1-hour incubations and the time-dependent nature of the production-versus-irradiance phenomena suggest that the rate of movement through the light gradient is an important factor to consider. The rate is probably rapid in turbid areas like Fourleague Bay where light is often attenuated by 50% or more in 10 cm, and this may be why a decrease in production because of circulation was noted on numerous occasions for the first time in this study. All of this points to the need for more accurate determinations of rates of vertical motion experienced by phytoplankton in order to assess how production is affected by circulation in nature.

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AQUATIC PRIMARY PRODUCTION AND CHLOROPHYLL MAXIMA AT FRONTAL ZONES IN FOURLEAGUE BAY AND THE COASTAL WATERS OF LOUISIANA

Christopher J. Madden and J. W. Day, Jr.

INTRODUCTION

Phytoplankton production in estuarine systems is generally high, averaging on the order of 250 g C/m^2/yr and ranging from 70 to 600 g C/m^2/yr (Boynton et al. 1982). Production varies seasonally, and in temperate estuaries peak production tends to occur in summer. Most marine phytoplankton production is by nanoplankton, but netplankton tend to be more important in coastal areas because high netplankton production is often associated with mixing events (Malone 1980). The spring bloom in coastal estuarine plumes has been associated with netplankton (Malone et al. 1983, Malone 1980, Hallegraeff 1981). There is also some indication that netplankton are more important in low salinity areas of estuaries (McCarthy et al. 1974). Nanoplankton primary production is generally based on remineralized nitrogen while that of netplankton is based on new nitrogen (Malone 1987).

There has been some controversy over the relative importance of new versus remineralized nutrients to estuarine production (Nixon 1981, Kemp et al. 1982). Because peak aquatic primary productivity (APP) often lags peak riverine nutrient input (Kemp and Boynton 1984, Nixon 1981) and remineralization rates are often coincident with and more than sufficient to meet peak APP requirements (Nixon 1981), it has been suggested that recycled nutrients are more important that new inputs. However, riverine inputs of nutrients have been significantly correlated with APP and ambient nutrient levels (Boynton et al. 1982, Cadée 1986) and it has been suggested that new riverine inputs are taken up and subsequently recycled (Kemp and Boynton 1984, Malone et al. 1986).

Primary productivity of estuarine systems is dependent on the combined interactions of light and nutrients such that maximum rates of production occur when neither of these is limiting (e.g. Riley 1967, Pratt 1965, Hitchcock and Smayda 1977). Both horizontal and vertical water movements can alter light and nutrient regimes. During periods of high river flow, water column light levels increase away from the river mouth while nutrient levels decrease. These changes are due to several factors including dilution with clearer, low nutrient marine water, flocculation, and nutrient uptake. In many partially mixed and well mixed shallow estuaries, the highest chlorophyll levels and rates of phytoplankton production tend to occur seaward of the turbidity maximum. This zone is an interface between turbid nutrient-rich fresher water and clearer high salinity water with lower nutrient levels (Kemp et al. 1982, Fisher et al. 1986, Randall and Day 1987). This high production zone varies from year to year as well as on a shorter term (Malone et al. 1980, Cloern et al. 1983, Filardo and Dunstan 1985, Pennock and Sharp 1986, Litaker et al. 1987). The pattern of increasing production from areas of high nutrients and turbidity to clearer waters have been reported for a number of estuaries including San Francisco Bay (Cole and Cloern 1984), the upper Chesapeake (Flemer 1970), the Wadden Sea (Cadée and Hegeman 1974), Corpus Christi Bay estuary (Flint 1984), Bristol Channel, UK (Joint and Pomroy 1981), the Mississippi Delta (Thomas and Simmons 1960), and Fourleague Bay (Randall and Day 1987).

Vertical mixing also affects APP. Such processes as vertical mixing, coastal upwelling and frontal shears are often associated with high phytoplankton productivity because they make nutrients available for exploitation by phytoplankton. The formation and destruction of the summer thermocline control the nutrient regimes and thus APP in several types of systems (Pingree et al. 1976, Blasco 1977, Seliger et al. 1981, Incze and Yentsch 1981, Tyler 1984, Morin et al. 1985). In well mixed systems, nutrients from benthic remineralization can be mixed into the surface waters and stimulate APP, while if stratification occurs, nutrients can be trapped beneath the pycnocline. As pointed out by Malone et al. (1986), summer in most estuaries is the period of maximum vertical stability and minimum mixing of the regenerated nutrient flux through the water column. Summer stratification often results in trapping of nutrients below the pycnocline which mix to the surface only infrequently (Kemp and Boynton 1984, Malone et al. 1986). Sometimes the mixing of different waters produce sharp, distinct density fronts and high plankton productivity and biomass levels are associated with these fronts (Blasco 1977, Parsons et al. 1981, Seliger et al. 1981).

Other water movements can lead to complex spatial patterns of APP. Malone et al. (1986) reported that lateral sloshing in Chesapeake Bay led to injections of nutrient rich bottom water onto the shallow flanks of the bay and resulted in higher production there. In the St. Lawrence Estuary, internal tides in combination with semidiurnal tides lead to periodic upwellings and subsequent phytoplankton blooms in surface waters which were then advected downstream (Therriault and Lacroix 1976). The initial nutrient concentrations in the upwelled waters was the factor which determined which nutrient first became limiting (Levasseur and Therriault 1987).

High river flow can result in low APP and chlorophyll levels if phytoplankton growth rates are less than the flushing rate. Welsh et al. (1972) reported that reduced phytoplankton levels during high flow years in the Duwamish River estuary, Oregon, was due to washout of phytoplankton cells. Malone and Chervin (1979) reported that this also happened in the spring in the Hudson River estuary. This process does not simply transfer the productivity related processes to a region further offshore because sinking material may not be recycled offshore whereas it would have been in shallow inshore regions.

Phytoplankton production in the Fourleague Bay system is as high as 2.5 g C/m^2/day (Madden 1986, Randall and Day 1987). Randall and Day reported that production was greater in the lower bay (317 g C/m^2/yr) than in the upper bay (120 g C/m^2/yr) over an annual cycle. Peak production at both sites occurred in September during low river flow. Production began to increase in the lower bay in June, two months earlier than in the upper bay, due to higher light levels. Within the bay there was a strong relationship between productivity and salinity with highest productivity at intermediate salinity. Randall and Day (1987) concluded that this was likely due to light limitation at low salinities and nutrient limitation at high salinities.

This paper investigates the spatial distribution of phytoplankton production and water column chlorophyll in Fourleague Bay and the nearshore zone. Expanding the earlier study at two sites by Randall and Day (1987), we present chlorophyll and productivity maps of the bay during different hydrological and weather regimes. The data presented here are preliminary.

METHODS

Data from three cruises in Fourleague Bay are presented here. Each three day cruise aboard the RV ACADIANA was for a duration of four days during which chlorophyll a and nutrient concentrations, salinity, and phytoplankton productivity were measured at several sites along an axial NW-SE transect of the bay. Fluorometry transects were used to map the chlorophyll distribution in Fourleague Bay and to identify sites of chlorophyll maxima and shipboard incubations were used to determine the productivity of plankton in these fronts. A Turner Designs fluorometer outfitted for continuous flow-through sampling (Lorenzen 1966) carried on a small boat on transects though areas of the bay continuously measured chlorophyll concentrations by fluorescence. Periodic samples were taken for immediate acetone extraction and measurement of chlorophyll on board ship to calibrate the in vivo transects (Strickland and Parsons 1972).

Frontal zones were identified as areas of rapid horizontal change in water column parameters such as temperature, salinity, and chlorophyll concentration. Water samples were collected from within the frontal zone(s) and other areas in the bay for aquatic productivity measurements.

Aquatic primary productivity was measured in a shipboard phytoplankton incubator under ambient light. The incubator worked as follows: 300 ml BOD bottles are placed on their sides in a three-point framework of thin stainless steel rods. The steel frames formed long cylinders, each accommodating eight bottles. Eight cylinders allowed 64 bottles to be incubated at a time. Frames rotated at 12 rpm so as to maintain water movement, and sediment and plankton suspension in even distribution. Ambient bay water was drawn by pumps from the bay and circulated through the incubator to maintain the samples at ambient bay temperatures. Oxygen concentration in the bottles was measured before and after the incubations with an Orbisphere Model 2714 oxygen meter and carbon fixation rate was calculated from the change in oxygen concentration. Photosynthesis-insolation (P-I) curves were calculated for each site based on continuous insolation measurements by a Li-Cor 1700 data logging radiometer, and underwater light profiles measured with a Li-Cor 1200 radiometer outfitted with an underwater sensor. Spatial patterns of aquatic productivity over the bay were estimated based on rates of photosynthesis in incubated samples and the algal distribution determined from the mapping studies.

RESULTS

There was a strong seasonality in total APP, the spatial patterns of APP, chlorophyll concentrations, nutrient concentrations, and physical factors affecting production. In a spring chlorophyll transect in June, 1987, there was a strong frontal zone with chlorophyll increasing from about 5 µg/l in the upper bay to over 13 µg/l in the mid-bay (Figure 1a). This increase occurred abruptly about 9 km from the upper bay entrance at a salinity of 10-12 ‰. Although the chlorophyll maximum occurred where salinity was increasing, it was not associated with a sharp salinity change and probably is related to a decrease in turbidity with distance from the river. At 13 km from the bay entrance, chlorophyll declined, returning to a level of about 7 µg/l.

In August, 1987, when river flow was much reduced, the chlorophyll profile was inverted, with highest levels (3-5 µg/l) at the end members, and a minimum (1.5 µg/l) in the central bay (Figure 1b). In three successive transects over two days, the pattern was replicated closely.

Spring production was higher than fall production and highest rates were associated with fronts (Figure 2a). Data from April, 1986 show highest production in mid-bay, where riverine turbidity had decreased but riverine nutrients remained in the water column. Rates ranged from 193 mg $O_2/m^2/hr$ in the lower bay at Oyster Bayou to 633 mg $O_2/m^2/hr$ in the middle bay. Measurements on consecutive days showed good consistency of data.

Measurements in a fall, 1987 transect showed much lower production rates ranging from 5 to 488 mg $O_2/m^2/hr$. Lowest rates occurred in mid-bay, increasing toward either end of the bay. This pattern parallels the chlorophyll pattern measured contemporaneously (Figure 2b). Overall productivity was lower in fall than in spring, although the Oyster Bayou station was more than twice as productive as in spring.

DISCUSSION

Preliminary results (Robert Twilley, unpub. data) indicate that the link between nutrient supply and phytoplankton demand may be nutrient regeneration processes. Nutrient retention within the estuary occurs by flocculation, adsorption onto soil particles, and incorporation by plankton which settle to the estuary bottom. As temperatures increase, regeneration processes in the estuarine sediments accelerate and liberate remineralized nutrients to the overlying water column. As pointed out by Kemp and Boynton (1984) for the Chesapeake, summer is the period in temperate estuaries of maximum vertical stability and minimum mixing of the regenerated nutrient flux through the water column. Summer stratification often results in trapping of nutrients below the pycnocline which mix to the surface only infrequently (Kemp and Boynton 1984, Malone et al. 1986). Fourleague Bay does not stratify and thus nutrients regenerated from the sediments are continuously available for uptake by phytoplankton.

In the spring during high river flow, APP is low in most of Fourleague Bay due to light limitation and flushing of cells. High APP occurs in the lower bay associated mainly with fronts. These fronts are highly mobile, lasting on a time scale of hours to a few days, responding to wind events and tides. In the coastal boundary layer, APP is also high due to lower turbidity and abundant nutrients from the river. Phytoplankton stocks in both the lower bay and the coastal boundary layer are isolated from inner shelf water by fronts and therefore can build up to high levels. In both the bay and the coastal boundary layer, the river is the primary source of nutrients. Nutrient inputs from the coastal boundary layer to the surface waters of the inner shelf are greatly restricted by the coastal boundary layer front, resulting in lower primary productivity.

During the summer and early fall low flow period, there is high levels of APP on a volumetric basis in both Fourleague Bay and the coastal boundary layer. We expect this to be due to high levels of recycled nutrients from sediments, the water column and possibly the marshes. Areal productivity will be higher in the coastal boundary layer because of lower turbidity coupled with

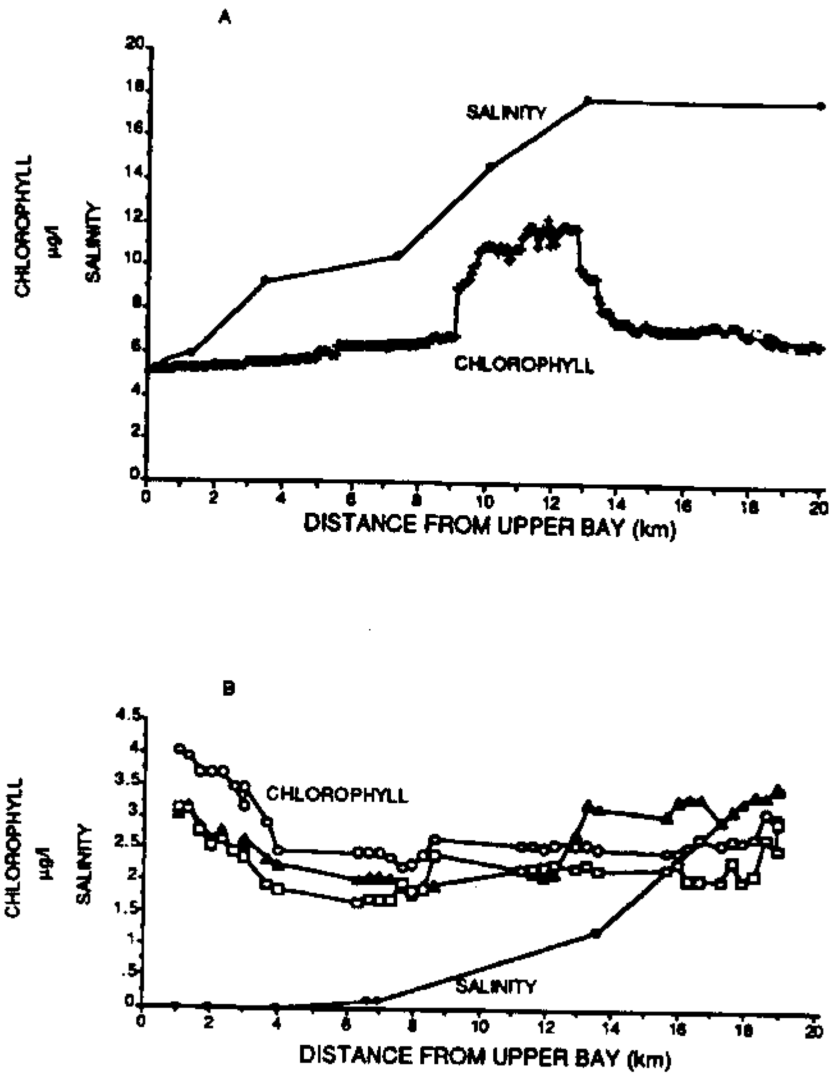

Figure 1. Chlorophyll and salinity transects in A: June, and B: August, 1987. June transect was during a weak spring flood, but frontal maximum is apparent. Three August transects were during low flow and exhibit inner bay minimum.

the deeper water column. APP is low in inner shelf surface waters because the only nutrient source is water column remineralization. Because Fourleague Bay and the coastal boundary layer are well mixed, sinking cells are not permanently lost and nutrients from benthic remineralization are available for surface productivity. This is not the case in the stratified inner shelf.

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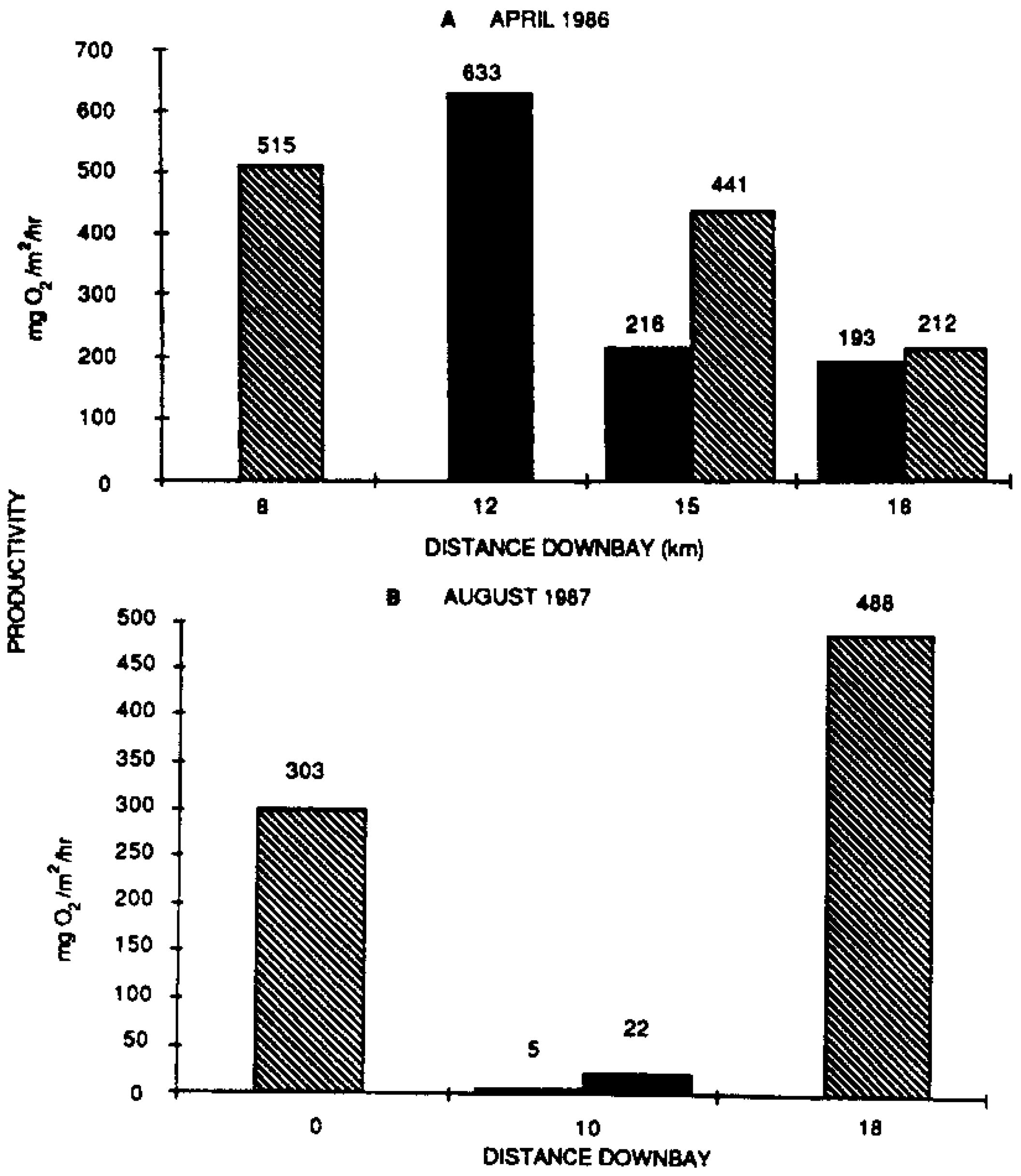

Figure 2. Phytoplankton productivity during A: spring flood and B: low flow. Spring measurements show mid bay peak while fall measurements show generally lower rates and a mid-bay minimum. Measurements were taken on two consecutive days, each day represented by differently shaded bars.

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PART 5

EMERGENT WETLANDS

SUCCESSION OF VEGETATION IN AN EVOLVING RIVER DELTA, ATCHAFALAYA BAY, LOUISIANA*

W.B. Johnson, C.E. Sasser, and J.G. Gosselink

INTRODUCTION

The geomorphology of Louisiana's coast is largely a product of the Mississippi River. Repeated upstream diversions of the river have resulted in the formation of overlapping delta lobes, associated with the successive dominance during the last 8000 years of several different distributaries (Kolb and Van Lopik 1958, Frazier 1967, Shlemon 1972). The Mississippi River's present major distributary is the Atchafalaya River, which discharges into the Gulf of Mexico through Atchafalaya Bay. Diverging at Simmesport, Louisiana, about 87 km upriver from Baton Rouge, the Atchafalaya River follows a much shorter (by 307 km), and thus hydrologically more efficient, route to the Gulf of Mexico than the present Mississippi River channel.

Throughout this century, the flow of the Mississippi River has been shifting gradually to the Atchafalaya River. At present, the flow of the Atchafalaya River is stabilized, at approximately 30% of the combined flow of the Mississippi and Red rivers, by control structures located at Simmesport, Louisiana. Since the 1930s, sediments carried by the Atchafalaya River have been filling Atchafalaya Bay (van Heerden and Roberts 1980). After the severe spring flood of 1973, the first land above mean low tide was observed in the bay at the mouth of the Atchafalaya River (29° 61' N, 91° 18' W). Emergent plants began to colonize these islands immediately after sediments accreted to intertidal elevations. By 1979, after several high-flood years added large quantities of sediment, newly formed islands totalled 38 km^2 of new land (van Heerden 1980), of which over 16 km^2 was vegetated.

The purpose of this study was to describe the dominant plant associations that have become established on these islands and the environmental factors that are important in determining the distribution of these associations.

METHODS

We have mapped annually the extent of vegetation on islands in the delta since the first emergent vegetation was observed in 1973 (C.E. Sasser, unpublished). Vegetation patterns were mapped using color infrared aerial photography in October 1979. These maps were verified in the field, and the area of each vegetation group determined. Subsequently a field survey provided detailed data describing the vegetation associations and related environmental variables. Stations were established on twelve of the delta islands (Fig. 1) within each vegetation association, using a technique similar to that of Noy-Meir (1971). Sixty stations were sampled between 27 and 30 May and fifty-seven between 8 and 12 September 1980. At each station duplicate samples were taken. Stations and samples were located randomly in May within each mapped association; September sample locations were established 3 m to the north of May sampling locations.

A sample consisted of the live and dead aerial biomass in a rectangular plot (1.0 x 0.5 m) and one

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*Johnson, W.B., C.E. Sasser, and J.G. Gosselink. 1985. Succession of vegetation in an evolving river delta, Atchafalaya Bay, Louisiana. Journal of Ecology 73:973-986. Used with permission.

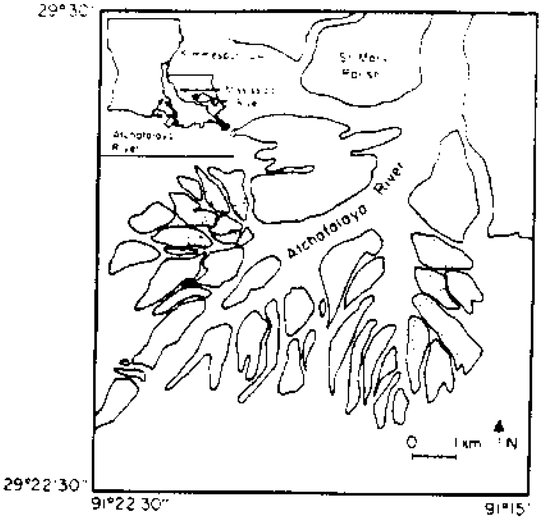

Figure 1. Sample stations (dots) on the Atchafalaya Delta, Atchafalaya Bay, Louisiana.

sediment core 7.6 cm in diameter by 25 cm deep. Live and dead vegetation were separated, and live vegetation was sorted into species. Both live and dead vegetation were dried at 65°C to constant weight and weighed to the nearest 0.1 g. Species were identified using Correll and Correll (1975) and Godfrey and Wooten (1979) and nomenclature follows these. In *Salix nigra* stands, when the diameter at breast height (1.50 m above the soil surface) exceeded 0.85 cm, dry weight standing crop was calculated from:

$$\text{Standing crop (g)} = -122.1 + 187.9\ (\text{dbh (cm)})$$
$$(r^2 = 0.93)$$

This relationship was determined from a least-squares regression of data from twenty-four *S. nigra* trees sampled in the Atchafalaya delta.

The sediment core was dried to constant weight at 65°C. All sediment analyses were on sub-samples from the homogenized core. Sand (>50 µm) and silt (> 2 to < 50 µm) fractions were determined using a hydrometer (Patrick 1958). Sediments were analyzed for organic carbon after 24 h treatment with 6N HCL to remove inorganic carbon, using a gasometric CO_2 evolution method (LECO 1974). Total Kjeldahl nitrogen (TKN) was determined by the macro-Kjeldahl U.S. Environmental Protection Agency method 351.2 (Darrell and Sommers 1980, U.S. Environmental Protection Agency 1979). The Louisiana State University Soil Testing Laboratory determined extractable P, K, Mg, and Ca, as described in Brupbacher, Bonner and Sedberry (1968). Phosphorus was determined colorimetrically by the molybdenum blue-stannous chloride method after extraction from the soil with a solution of 0.1M HCL containing 0.03M NH_4F. A soil-to-solution ratio of 1:30 and an extraction period of 15 min were used. Potassium, Mg, and Ca were determined by atomic absorption spectrophotometry after leaching of the soil sample for 15 min in 1M NH_4OAc (pH 7.0) at a soil-to-solution ratio of 1:10.

Using a self-leveling Lietz level and stadia rod, elevations of each station were determined between July 1980 and January 1981 in relation to the nearest benchmark of a network established in the delta and maintained by the U.S. Army Corps of Engineers.

Three recording tide gauges, levelled to the benchmarks, are maintained in Atchafalaya Bay—at the mouth of the Atchafalaya River and at 7.4 km and 15.9 km south of the mouth (Fig. 1). Readings at 0800 hr Central Standard Time during 1980, excluding the flood period from 15 March to 15 May, were used to estimate mean water levels at each tide gauge. From these data, the water level slope from the mouth of the Atchafalaya River to the Gulf of Mexico was determined by least-squares regression. This regression equation and the distance of each sample station from the mouth of the river were used to estimate the mean water level at each station. This established elevations at each station relative to the water level.

Several indices were used to describe the plant community. Percent constancy was estimated using Mueller-Dombois and Ellenberg (1974). Diversity (H') and a component of diversity, evenness (J'), were calculated following Pielou (1975).

A non-centered principal components analysis (PCA) was used to classify the delta's vegetation into species associations, to verify objectively the manually mapped patterns. Principal components analysis is a technique used to summarize community data. It allows a large matrix of standing crop estimates by species at each station to be reduced to a few principal components. Each principal component represents a species association and consists of a vector or linear combination of species loadings, one for each station. The analysis gives an index of the degree of relationship between any two stations, based on the degree of similarity of the species spectra. The use and interpretation of PCA results have been described by Isebrands and Crow

(1975) and Nichols (1977). The specific PCA methodology used was nodal component analysis and has been described by Carleton and Maycock (1980), Feoli (1977), Noy-Meir (1971, 1973), and Orloci (1966, 1967).

A sums of squares/cross products (SS/CP) matrix was estimated from the community matrix for May and September. Then the SS/CP matrices were used to derive the principal component vectors for May and September. In each period eleven principal components were used and rotated following Kaiser (1958). Only unipolar components (having only high positive values and near zero values) were used. Also, only those components which included three or more stations were considered (stations were included in a component if the loading was greater than or equal to 0.25).

Components identify species groups or vegetation associations within the overall plant community. Stations become associated with a component by having high positive values, in contrast to near zero values for stations not associated with that component. Within a component the group of stations with high values have a similar species assemblage, based on biomass, at each of the stations in the component. Components are not entirely distinct because some stations are included in more than one component. This allows an index of resemblance to be estimated between all pairs of components or species associations. Plant association similarities were determined by estimating the conjunction coefficients (described by Noy-Meir (1971)) between all pairwise principal components.

Environmental factors were analyzed using linear models, which allowed sources of variation to be separately examined. The models that were used included two sources of nested error-terms. One was the error due to variation among replicate samples that were taken at each station. (This source of variation could not be estimated for elevation because only one value was available at each station.) The other source of error variation was the variation among stations that were classified by the PCA within the same vegetation type. The main effect components of the linear model were in a factorial arrangement and included the variation due to differences between the May and September samplings, the variation due to differences among PCA plant associations, and the interaction of the seasonal effect with the plant association effect. The variation due to the main effects was pooled and represented as a single source of variation. Because grain size and elevation were only measured once, a seasonal effect is not included in pooled main effect variation for these factors. Using the 0.25 loading criterion, stations appeared in more than one component, but, for the purposes of these linear models, stations were classified into one of four associations using the maximum loading across the eleven components from the results of the September PCA analysis.

RESULTS

Vegetation

The vegetation that has established on the islands within Atchafalaya Bay includes wetland species commonly found in freshwater marshes along the Louisiana coast (Chabreck 1972). Forty-five plant species were found during our study. Since our sample sites were restricted to the naturally formed deltaic islands, excluding islands influenced by dredged spoil, our species list is not as extensive as that of Montz (1978), who sampled transects across disturbed and elevated spoil islands. Of the forty-five plant species, three are the most common and occur in fairly homogeneous stands: Sagittaria latifolia, Typha latifolia, and Salix nigra. In the PCA for May, five unipolar components were identified, accounting for 55% of the total variation within the community matrix; while in September, six components were identified, accounting for 53% of the variation. The identification of more than a single unipolar principal component indicates that several of the vegetation associations were segregated spatially within the delta's vegetation (Feoli 1977, Noy-Meir 1971). Table 1 shows the percentage constancy of plants in the Atchafalaya River delta by species and the number of stations each species occurs at within each component (association). Percentage constancy is the ratio of the number of sampling stations at which a given species occurs to the total number of stations at the study site during each sampling period, times 100. Table 2 summarizes the biomass of each of the most abundant species in the unipolar components in May and September.

The first three principal components in the May and September analyses identify the three most pervasive associations on the delta islands. Although these associations were named from the genera of the dominant species — Sagittaria, Typha, and Salix — each association includes a group of species. The results of our mapping confirmed that, in 1979, these three associations were areally the most extensive and occupied 93% of the vegetated area in the delta. The Sagittaria association covered 64%, Salix 19%, and Typha 10% of the vegetated area.

The mapping and ground verification reported by C. E. Sasser (unpublished) have suggested that these three

TABLE 1. Frequency of occurrence (%) of the most common vascular plant species at sites in the Atchafalya River Delta, Louisiana, in May and September. Only species with a percentage constancy (PC) greater than 10 during at least one sampling are shown. Abbreviations: SAG, *Sagittaria* association; SAL, *Salix* association; TYP, *Typha* association; NAJ, *Najas* association; SEA, *Eleocharis parvula–Cyperus difformis* association; SEA1, seasonal association 1; SEA2, seasonal association 2; SEA3, seasonal association 3.

	PC	May associations					PC	September associations					
		SAG	SAL	TYP	NAJ	SEA		SAG	SAL	TYP	SEA1	SEA2	SEA3
Cyperus difformis	28	15	4	5	1	4	60	19	6	7	8	3	3
Sagittaria latifolia	80	45	6	7	7	5	93	34	8	9	8	3	3
Salix nigra	27	15	11	1	0	1	30	5	11	2	5	1	1
Typha latifolia	15	8	0	9	0	0	17	0	1	9	1	0	0
Najas guadalupensis	30	18	0	1	9	1	28	16	0	0	0	1	1
Eleocharis parvula	20	9	3	2	1	5	8	3	0	2	1	0	0
Bacopa monnieri	15	9	2	3	1	2	10	1	3	2	0	0	0
Ammania coccinea	3	2	1	0	1	0	38	11	3	6	8	2	3
Hydrocotyl sp.	7	3	4	0	0	0	10	0	5	1	0	0	0
Polygonum punctatum	10	6	4	2	0	0	10	0	4	2	0	0	0
Scirpus validus	0	0	0	0	0	0	13	3	3	0	4	1	0
Rotala ramosior	0	0	0	0	0	0	10	3	0	1	3	1	0
Cyperus odorata	0	0	0	0	0	0	10	3	2	0	4	0	0
Sagittaria platyphylla	0	0	0	0	0	0	48	23	1	3	2	1	1
Sphenoclea zeylanica	0	0	0	0	0	0	27	10	1	2	7	2	3
Other species		36	28	5	3	2		10	40	11	11	3	2
Percentage of total variation explained (variance explained by each principal component)		29	10	9	4	3		31	10	8	2	1	1
Total number of stations		34	11	9	9	5		35	11	9	8	3	3
Total number of species		28	24	12	8	8		21	31	20	19	11	9
Average number of species per sample		2·9	5·7	3·9	2·6	4·0		4·0	8·1	6·3	7·8	6·0	6·0

TABLE 2. Aerial standing crop biomass (g dry weight m^{-2}) estimates of the most common ($\geq$ 10% constancy) species in each of the major vegetation associations of the Atchafalaya Delta, Louisiana, in May and September. Abbreviations: SAG, *Sagittaria* association; SAL, *Salix* association; TYP, *Typha* association; NAJ, *Najas* association; SEA, *Eleocharis parvula–Cyperus difformis*; SEA1, seasonal association 1; SEA2, seasonal association 2; SEA3, seasonal association 3.

	May associations						September associations				
	SAG	SAL	TYP	NAJ	SEA	SAG	SAL	TYP	SEA1	SEA2	SEA3
Cyperus difformis	0·2	0·9	0·5	0·4	0·5	3·5	0·3	3·9	18·2	23·6	14·8
Sagittaria latifolia	7·6	0·5	2·4	2·1	1·6	171	3·8	43·0	54·8	5·7	91·7
Salix nigra	1·2	1860	<0·1	<0·1	0·3	1·1	5170	0·2	4·6	<0·1	12·5
Typha latifolia	0	0	209	0	0	0	1·2	336	8·6	0	0
Najas guadalupensis	0·6	0	<0·1	2·3	<0·1	0·7	0	0	<0·1	<0·1	<0·1
Eleocharis parvula	0·1	0·1	<0·1	0·0	0·6	<0·1	0	<0·1	0·2	0	0
Bacopa monnieri	0·2	0·2	0·8	<0·1	<0·1	<0·1	0·2	0·1	0	0	0
Ammania coccinea	<0·1	0	0	<0·1	0	10·9	0·5	12·5	68·9	12·0	37·1
Hydrocotyle sp.	<0·1	19·7	0	0	0	0	0·4	0·1	0	0	0
Polygonum punctatum	0	2·7	0·6	0	0	0	7·5	4·4	0	0	0
Scirpus validus	0	0	0	0	0	0·2	10·6	0	7·1	7·7	0
Rotala ramosior	0	0	0	0	0	0·5	0	1·1	0·1	<0·1	0
Cyperus odorata	0	0	0	0	0	0·4	0·7	0	0·6	0	0
Sagittaria platyphylla	0	0	0	0	0	15·7	4·8	0·2	3·3	9·5	9·5
Sphenoclea zeylanica	0	0	0	0	0	2·5	0	1·0	15·0	17·2	39·4
Dead weight	7·4	134	94·3	1·1	1·5	124	184	238	182	111	133
Total weight	10·4	1920	215	4·7	3·6	239	5250	437	216	82·1	218

primary associations were discrete, with abrupt transitions between them (Fig. 2, Table 3). The degree of similarity between all pairwise comparisons of the three most extensive plant associations in May and September was low, never exceeding 0.12 (where 1.0 represents identity).

The analysis of the community diversity characteristics also supports the PCA similarity and mapping results. The overall diversity (H') in the three major associations is low (Fig. 3). The reason for this is that one component of diversity, evenness (J'), is low. Evenness is a measure of the similarity of the biomass of all species in an association. The low value of J' in these associations reflects the presence of a dominant species. Table 2 shows that the standing crop biomass is dominated by the type species on each association.

Several minor plant groups were also identified in the PCA. In contrast to the major associations, these are less constant both spatially and temporally, and have higher diversity. They can be placed into two categories. One category, referred to as seasonal associations, includes those that undergo a marked seasonal shift in the species that are dominant. In May the single seasonal association accounted for 3% of the variation in the analysis. It was characterized by an even mixture of *Sagittaria latifolia*, *Eleocharis parvula*, and *Cyperus difformis* and was located close to the *Sagittaria* association at the rear of the island. By September the aerial standing crop at most of the stations in this seasonal association had become dominated by the annual species *Ammania coccinea* and *Sphenoclea zeylandica* (Table 2). In the September PCA these stations fell into three distinct associations, characterized by similar species, but in different proportions (Tables 1 and 2, Fig. 4).

The second category of minor associations was dominated by *Najas guadalupensis*, a submerged plant, in May. In September most of the stations of this association were included in the *Sagittaria* association. *N. guadalupensis* is seldom found as the dominant species except early in the spring before *Sagittaria* growth overwhelms it.

Environmental Factors

There was little spatial variation or change over time of soil nutrients. The variation in organic carbon, TKN, P, K, Ca, and Mg was primarily due to the variation between replicate samples and the variation among stations within a vegetation association and sampling time. The percentage variation in soil nutrients among the associations and between May and September (main effects) was small (Table 4).

In contrast, grain size (percentage sand) and elevation above mean water level have larger percentage variations that can be related to variation among vegetation associations (variation due to different sampling times for water level and grain size cannot be estimated because these variables were measured only once). Table 5 shows that the seasonal and *Salix* associations which exist on the island levees (Fig. 2) occupy substrata which have a relatively high percentage of sand. Also, *Salix* associations are found on the island head levees and therefore have a higher elevation than the seasonal associations. The *Typha* and *Sagittaria* associations are in areas having intermediate percentages of sand and intermediate water levels, while the *Najas* association is found at the downstream ends of the island which have the lowest elevations and the lowest percentages of sand.

DISCUSSION

The distribution and species composition of wetland plant communities can be influenced by hydrology (Segal 1971, van der Valk 1981). This has been demonstrated repeatedly in a variety of situations, but is particularly true of riverine freshwater marshes (Junk 1970, Tansley 1953, Klopatek 1978). The results of our study indicate that this is also true of the wetland community on the Atchafalaya delta. The environmental factors which vary the most consistently as plant associations change are physical factors that depend directly on hydrology, in contrast to sediment chemical factors which are indirectly determined by the flooding regime. Although sediment chemical variables in wetland ecosystems (such as redox potential, salinity, and limiting nutrients) have potential for influencing the distribution of species, this does not appear to be true in the Atchafalaya delta. The chemical variables we measured varied little throughout the delta, probably because they are largely determined by the tremendous volume of river water that flows across the islands during spring floods.

In contrast to the chemical environment, the physical environment is made heterogeneous by river sedimentation. Riverine delta formation and evolution are controlled largely by physical processes (Wright, Coleman, and Erickson 1974) which create physical heterogeneity both within and among the delta islands. The general pattern of delta formation in Atchafalaya Bay involves repeated mouth-bar development from deposition of suspended sediments at the end of the delta distributaries (van Heerden and Roberts 1980). This results in a

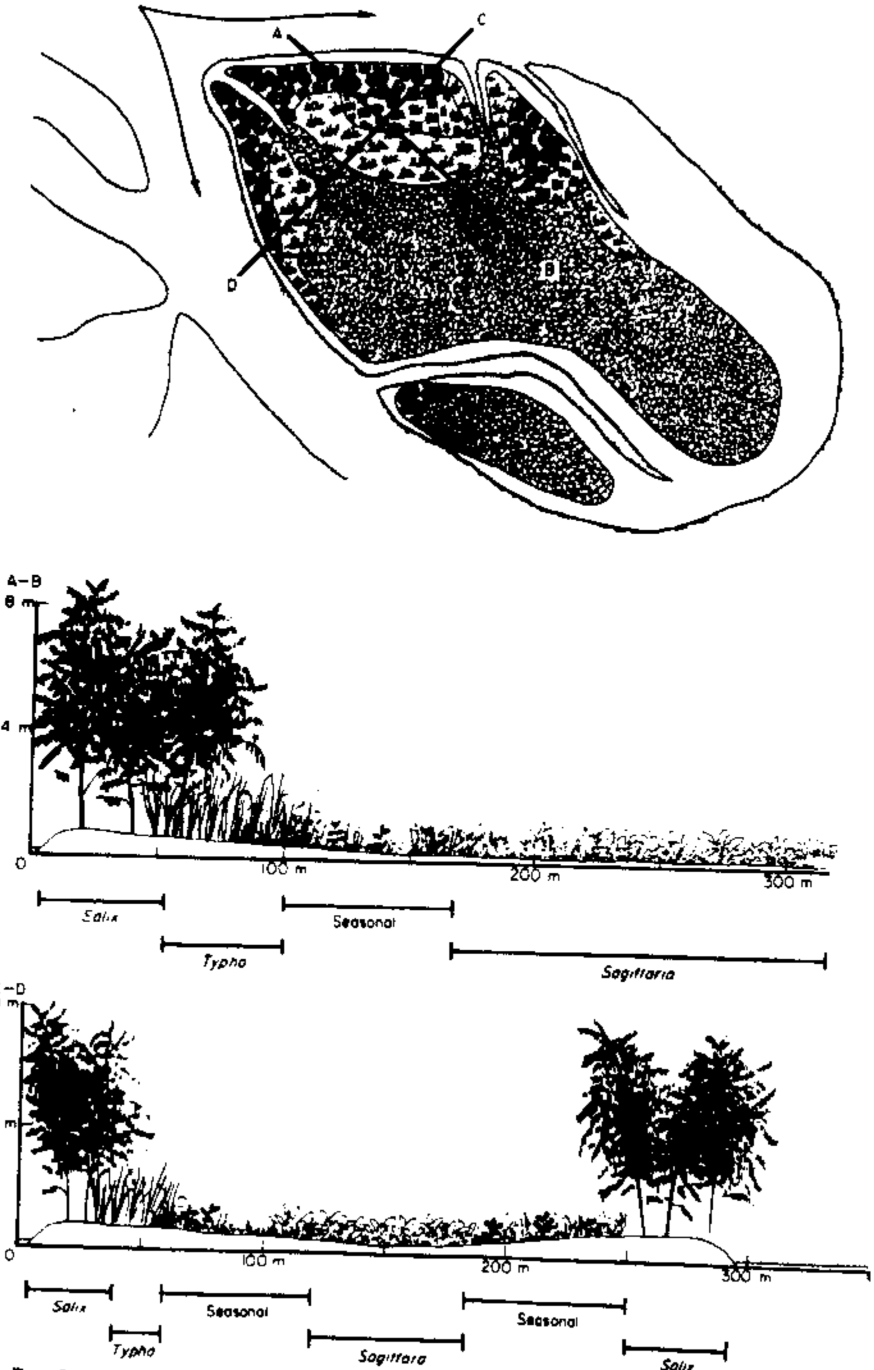

FIG. 2. Illustration of a typical mouth-bar island in the Atchafalya River Delta, Louisiana, showing both aerial and cross-sectional views. Arrows represent direction of predominant water flows.

May

SAG				
0·022	SAL			
−0·013	−0·030	TYP		
0·318	−0·030	−0·032	NAJ	
0·281	−0·022	−0·033	0·134	SEA

September

SAG					
−0·018	SAL				
0·121	0·032	TYP			
0·327	−0·010	0·097	SEA1		
0·136	−0·033	0·002	0·281	SEA2	
0·214	−0·007	0·017	0·385	0·418	SEA3

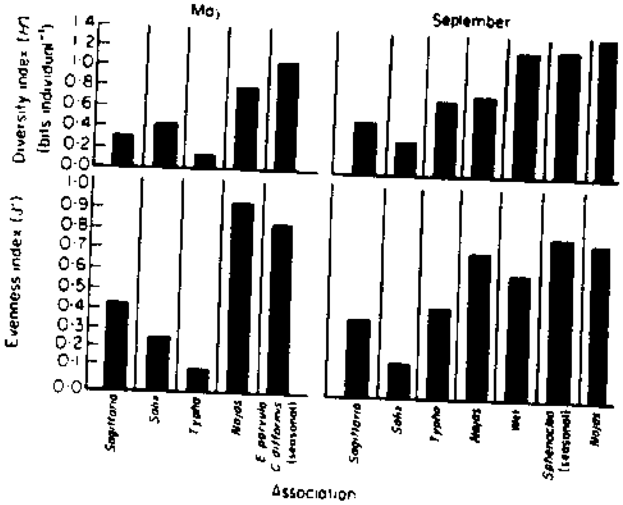

FIG. 3. Diversity characteristics of the important floral associations (noda) of islands in the Atchafalaya River Delta, Louisiana, in May and September. H' is the Shannon–Wiener diversity index ($H' = -\sum p_i \ln p_i$) and J' is Pielou's evenness ($J' = H'/H'_{max}$) (Pielou 1975).

series of islands forming at the point of channel bifurcations (Figs. 1 and 2). Because of the deposition patterns, each island has its highest elevation at the upstream end and along the leading edge, with elevation decreasing inland and towards a flat at the back of the islands. There is also a range in age of the delta islands from young islands at the downstream deltaic periphery to older islands higher upstream.

This physical heterogeneity and island age influence the distribution of plant associations on the delta islands. The distribution of Salix is one example of this. The heads of the mature delta islands are exposed directly to riverflow. During the spring floods when fast flowing river water passes over these islands, flow velocity decreases, and suspended sediments are deposited. As a result, the mature island heads have the highest elevations and the greatest sand content in the natural delta. The only species that can withstand the physical stress of the high sedimentation rates and grow vigorously is S. nigra, a woody, fast-growing plant with large fibrous roots. On the youngest islands that develop at the extreme downstream end of the delta, S. nigra has not developed. The elevations are lower on these islands. Only when elevations increase through repeated overflooding can S. nigra invade.

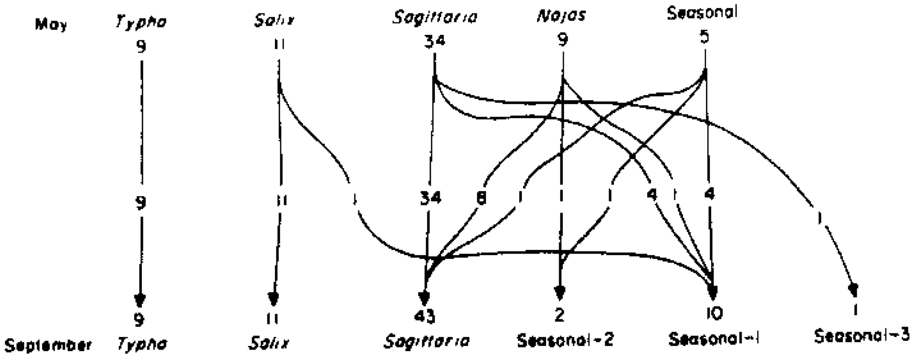

FIG. 4. Change in the Atchafalaya Delta, Louisiana, vegetation associations from May to September. Numbers at the top and bottom refer to the number of stations that were classified (principal component loading >0·25) as being in each association at each sampling time. Arrows illustrate the pattern of change and the numbers that accompany each arrow indicate the number of stations that follow each pattern. Number of stations does not equal the number sampled and is not conserved between times because a station may be classified into more than one plant association.

TABLE 4. Percentage variation in soil variables in soils from islands in the Atchafalaya River Delta attributable to different sources. (The percentages were estimated assuming a mixed linear model with a nested error structure.)

	Variation sources		
	Main effects	Error	
	Vegetation association and sampling times	Station within vegetation association	Replicates within stations
Altitude	34·9	65·1	
TKN	9·9	36·2	53·9
P	12·6	29·0	58·5
K	17·5	53·9	28·6
Ca	9·4	65·6	25·0
Mg	15·4	68·8	15·8
Organic carbon	11·5	49·2	39·3
Percentage sand	24·1	56·3	19·6

Gleason et al. (1979), Kellerhals and Murray (1969), and Pezzetta (1973) showed the importance of vegetation in stabilizing and trapping sediments in river deltas and on beach swales. In the Atchafalaya delta sediment deposition is strictly physically controlled until elevations are reached that can sustain *S. nigra*. Biotic modification of sedimentation, as described by these scientists, can occur only after this species is established.

In contrast to *S. nigra*, *Typha latifolia* is the dominant plant in another primary association which appears to be distributed in response to both the physical environment and the presence of the *Salix* association. It does not occur on the young islands, but only at intermediate elevations on the most mature islands immediately behind the *Salix* associations. *T. latifolia*, like *S. nigra*, has an extensive fibrous root system (Fiala 1971, 1973). It is capable of withstanding flood waters near the island heads, but apparently only when protected by *S. nigra* stands from the direct effect of upstream spring flood waters.

Sagittaria latifolia is the dominant member of the *Sagittaria* association, which has the largest areal extent in the delta. It is the first emergent species that invades channel mouth-bar islands. *S. latifolia*, a succulent herbaceous marsh species, has a perennial root system but the top dies to the sediment surface each winter, re-emerging from rhizomes and tubers in the early summer after spring floods recede. The species becomes established at elevations immediately above mean low water and can colonize all areas of the delta. Other species—for example, *Salix nigra*—appear in the *Sagittaria* stands when sediment deposition raises the island elevation,

TABLE 5. Means and 1 S.E. (in parentheses) of percentage organic carbon, percentage sand, and altitudes in each vegetation association on islands in the Atchafalaya River Delta. Abbreviations: SAG, *Sagittaria* association; SAL, *Salix* association; TYP, *Typha* association; NAJ, *Najas* association; SEA, *Eleocharis parvula–Cyperus difformis* association; SEA1, seasonal association 1; SEA2, seasonal association 2; SEA3, seasonal association 3; *n* = the number of observations.

May	SAG	SAL	TYP	NAJ	SEA
Organic carbon	0·56	0·60	0·65	0·63	0·27
(%)	(0·03)	(0·06)	(0·09)	(0·14)	(0·03)
n	56	11	9	9	5
Sand (>50 μm)	47	55	45	42	70
(%)	(2)	(4)	(5)	(5)	(6)
n	55	11	9	9	5

September	SAG	SAL	TYP	SEA1	SEA2	SEA3
Organic carbon	0·55	0·64	0·73	0·30	0·51	0·33
(%)	(0·04)	(0·06)	(0·11)	(0·03)	(0·09)	(0·10)
n	35	11	9	8	3	3
Elevation above mean	9·6	21·9	17·4	9·7	−2·1	−5.0
water level (cm)	(2·3)	(2·8)	(4·3)	(2·8)	(1·2)	(8·7)
n	35	11	9	8	3	3

but *S. latifolia* continues to grow in these stands and is found in all of the plant associations.

The *Najas* association is influenced by the river's annual flood cycle of high spring water levels and lower summer and autumn water levels. In late spring, before flood waters recede, *N. guadalupensis*, a submerged plant, dominates in areas too deeply flooded, and perhaps too cold, for emergence of *S. latifolia* plants from underground parts. As spring flood waters recede, *S. latifolia* develops in association with *N. guadalupensis* and becomes the dominant plant. Later in the season it is only in the extremely low elevation areas on the downstream flats of the islands that *N. guadalupensis* exists independently.

Thus, although *S. latifolia* is the first emergent species to invade the delta islands, the *Salix* association first introduces a degree of biotic control into the successional sequence. The *Salix* association provides a degree of protection from direct river flows that enables the *Typha* association to become established. As the *Salix* association on the island levees develops and overall elevations increase with island age (decreasing the depth and duration of tidal flooding) an increasing barrier to the movement of flood water is created and more diverse and seasonally dynamic freshwater wetland plant associations develop. These "seasonal" associations usually invade *Sagittaria* stands in the protected zone immediately behind the *Salix* and *Typha* associations and are above the deeply flooded flats at the back of the islands. The higher diversity and evenness of these seasonal communities are characteristic of mature freshwater marshes (Doumlelle 1981, Whigham and Simpson 1976), whereas the floristic simplicity of the pioneering associations is typical of early successional communities (Odum 1969).

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MODELING OF VEGETATION DYNAMICS IN THE MISSISSIPPI RIVER DELTAIC PLAIN*

M. Rejmanek, C.E. Sasser, and J.G. Gosselink

INTRODUCTION

Deltaic plains of big rivers belong to the most variable and least predictable environments on earth (Bird 1985, Wright 1985). The complicated development of vegetation in river deltas reflects the unstable character of these landscapes. Realistic modeling of vegetation dynamics in river deltas is therefore necessarily limited to stochastic simulations. However, only long-term field studies can provide data for the estimation of those parameters needed for stochastic models. Available data from the Atchafalaya delta, Louisiana, give an opportunity for the first estimation of transition probability between different river flow regimes.

The Atchafalaya delta represents one of the most dynamic geological events in historical times. Throughout this century, the flow of the Mississippi River has been shifting gradually to the Atchafalaya River. Since 1963, the flow of the Atchafalaya River has been stabilized at approximately 30% of the combined flow of the Mississippi and Red rivers by control structures at Simmesport, Louisiana. Sediments carried by the Atchafalaya River have been filling Atchafalaya Bay. Between 1965 and 1972, the average annual flood discharge was 7500 m^3/s, which carried an average sediment load of 42.6 X 10^6 metric tons (Roberts et al. 1980). New islands which first emerged in 1973 are the first stages in the formation of a new Mississippi delta in the center of Louisiana's coastal zone. This delta lobe has not been increasing monotonically (Fig. 1). In general, the growth of the delta only occurs during floods with mean monthly discharge greater than 14,000 m^3/s. Erosion or no growth takes place in intervening years with normal or sub-normal regimes. Islands situated adjacent to the navigation channel are influenced by dredged spoil. Their vegetated are is not shown in Fig. 1. The vegetated area of natural islands is still relatively small and follows, with a one year delay, changes in the total area of land above mean water level. In addition, heavy grazing by nutria (coypu, Myocastor coypus (Molina) Rodentia), has affected vegetation dynamics recently. Vegetation development from 1973 to 1982 was described by Montz (1978) and Johnson et al. (1985).

The active delta building is in sharp contrast to prevailing subsidence and erosion of Louisiana coastal marshes which occupy the area of ancient Mississippi deltas successively formed and abandoned during the last 8000 years (Kolb and Van Lopik 1966, Van Heerden, 1983, Baumann et al. 1984). The Atchafalaya River is building a delta lobe in an area where Maringouin and Teche deltas were built and abandoned 7000 to 4000 years ago. While wetland loss is part of the natural geomorphic scene, historically it has been balanced by land extension elsewhere, so that since the last ice age the Mississippi River deltaic plain has grown enormously. In this century this trend has been reversed and net loss of coastal wetlands is the rule. The present coastal land erosion rates are estimated to be 102 km^2/yr, or 0.8% annually (Gagliano et al. 1981).

DATA AND METHODS

A total of 110 permanent plots, each 1 x 1 m, placed at intervals 20 - 40 m along two perpendicular transects on each of four natural islands, have been maintained

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*Rejmanek, M., C.E. Sasser, and J.G. Gosselink. 1987. Modeling of vegetation dynamics in the Mississippi River deltaic plain. Vegetatio 69:133-140. Used with permission.

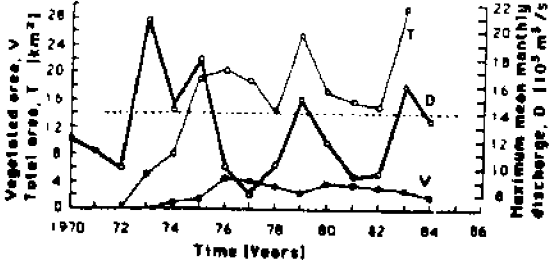

Fig. 1. Total exposed area of the Atchafalaya delta (T, area above mean sea level), vegetated area of natural islands (V) and maximum mean monthly discharge for the Atchafalaya River at Simmesport, Louisiana (D). The dotted line represents the approximate critical D value for positive growth of exposed area. The values of vegetated area of natural islands are based on LANDSAT and low level aerial imagery for the years 1973 – 1980 and estimated from relative changes of vegetated area covered by permanent plots during 1979 to 1984.

since 1979. Two of the islands, Hawk and Log islands, are on the west side of the delta; the other two, Rodney and Teal islands, are located on the east side of the delta. Cover estimates of vascular plant species and elevation changes in relation to the nearest benchmark were monitored in all plots during the period 1979-1984.

For the estimation of transition probabilities between particular vegetation stages, four main vegetative types were distinguished on the basis of multivariate analysis. They were characterized by dominance of Cyperus difformis, Sagittaria (S. latifolia and S. platyphylla), Typha domingensis, or Salix nigra. Remaining plant communities dominated by Justicia ovata, Scirpus americanus, S. tabernaemontanii, or Leersia oryzoides were considered as a fifth category ('Other'). Aquatic vegetation was therefore classified in a sixth category 'Non-vegetated', together with mud flats and open water. The proportion of quadrats remaining in the same category, or changing to another was determined for the five year-to-year changes during 1979-1984. The set of transformation probabilities for six vegetation categories constitutes a transition matrix. By multiplying a vector of abundances of these categories by a transition matrix, vegetation dynamics could be simulated. Because the matrices were very different, depending on flood (erosion or sedimentation) conditions, they were combined in a stochastic sequence derived from the analysis of long-term discharge data for the Atchafalaya River. Further details on the use of transition matrices can be found in Kemeny and Snell (1976), Austin (1980), Usher (1981), and Hobbs (1983).

A similar matrix was completed for transitions from solid marsh to open water in abandoned Lafourche Mississippi delta, southwestern Barataria Basin. Air photographs from 1945 and 1956 were used (Dozier et al. 1983). Marsh vegetation in photographs was classified according to digitized water area in 10,000 quadrats (50 x 50 m).

RESULTS

Simulation of vegetation succession based on four different transition matrices (Table 1) is shown in

Table 1. Transitions between the six states included in the model. C: *Cyperus*, S: *Sagittaria*, T: *Typha*, X: *Salix*, O: Other vegetation types, N: Non-vegetated.

Transition	Probability			
	'80 – '81 '81 – '82	82' – '83	'79 – '80	'83 – '84
C – C	0	0.500	0	0.170
C – S	0.570	0.500	0.375	0
C – T	0	0	0.500	0
C – X	0	0	0	0
C – O	0	0	0.125	0.510
C – N	0.430	0	0	0.320
S – S	0.794	0.840	0.857	0.428
S – C	0	0.072	0.024	0
S – T	0.029	0.028	0.024	0.042
S – X	0	0	0.024	0
S – O	0.029	0	0	0.042
S – N	0.148	0.060	0.071	0.488
T – T	0.850	0.625	0.900	0.499
T – C	0	0.125	0	0.167
T – S	0	0	0	0
T – X	0	0	0	0
T – O	0.150	0.250	0.100	0
T – N	0	0	0	0.334
X – X	0.660	0.920	1	0.860
X – C	0	0	0	0
X – S	0	0	0	0.140
X – T	0	0	0	0
X – O	0	0	0	0
X – N	0.340	0.080	0	0
O – O	0.500	0.500	0.500	0.383
O – C	0	0	0	0
O – S	0	0.160	0.500	0.083
O – T	0.100	0.180	0	0.167
O – X	0.400	0.160	0	0
O – N	0	0	0	0.367
N – N	0.600	0.900	0.229	0.700
N – C	0.100	0	0.183	0
N – S	0.300	0.100	0.500	0.250
N – T	0	0	0	0
N – X	0	0	0.088	0
N – O	0	0	0	0.050

Figs. 2 and 3. Matrices 1980-1981 and 1981-1982 represent times of rather low river discharge, with erosion prevailing over sedimentation, on the average. These two matrices were very similar, and resulting simulations were practically indistinguishable. The average matrix was therefore used for all simulations. Matrix 1982-1983 represents high river discharge (maximum mean monthly discharge over 14 x 10^3 m^3/s). Under such conditions, the whole subaerial area of delta is growing, but the vegetated area is slightly decreasing. During years of high floods, the prolonged submersion and reduced light penetration, combined with low river water temperatures, shorten the growing season and apparently inhibit germination and growth. The most remarkable difference between low and high river discharge is in contraction and expansion of stands dominated by *Cyperus difformis*. The first year after high river discharge (matrix 1979-1980) is characterized by a rapid increase of vegetated area.

Vegetation responses are different under different discharge-sedimentation conditions. It would be completely misleading if only one year-to-year transition were used for prediction of succession in a deltaic environment. Moreover, the transition 1983-1984, which was predicted to be similar to that of 1979-1980 was completely different (Fig. 3). We believe that the heavy grazing by nutria is mainly responsible for this discrepancy. Exclosures established by Fuller et al. (1985) in dense stands of *Sagittaria latifolia* were the only spots where *Sagittaria* was present in 1984. Surrounding, unprotected marsh was converted to non-vegetated area. There were no differences in elevation (sedimentation/erosion) between exclosures and surrounding mud flats in 1984. Because a high number of nutria has been observed in the delta in the last years, we assume that an increase of their abundance in 1984 is the reason for decrease of vegetated area. This opportunistic feeder consumes a variety of marsh plants, but tubers of *Sagittaria* species are preferred over other vegetation (Chabreck et al. in press, Wentz 1971). Nutria grazing may also be responsible for the lack of recovery of *Salix nigra* in 1984.

A more realistic simulation of vegetation dynamics should reflect patterns of river floods and subsequent sedimentation, erosion, and vegetation change. The final model (Figs. 4 and 5) combines three transition matrices corresponding to three discussed river discharge situations. The probability of switching between

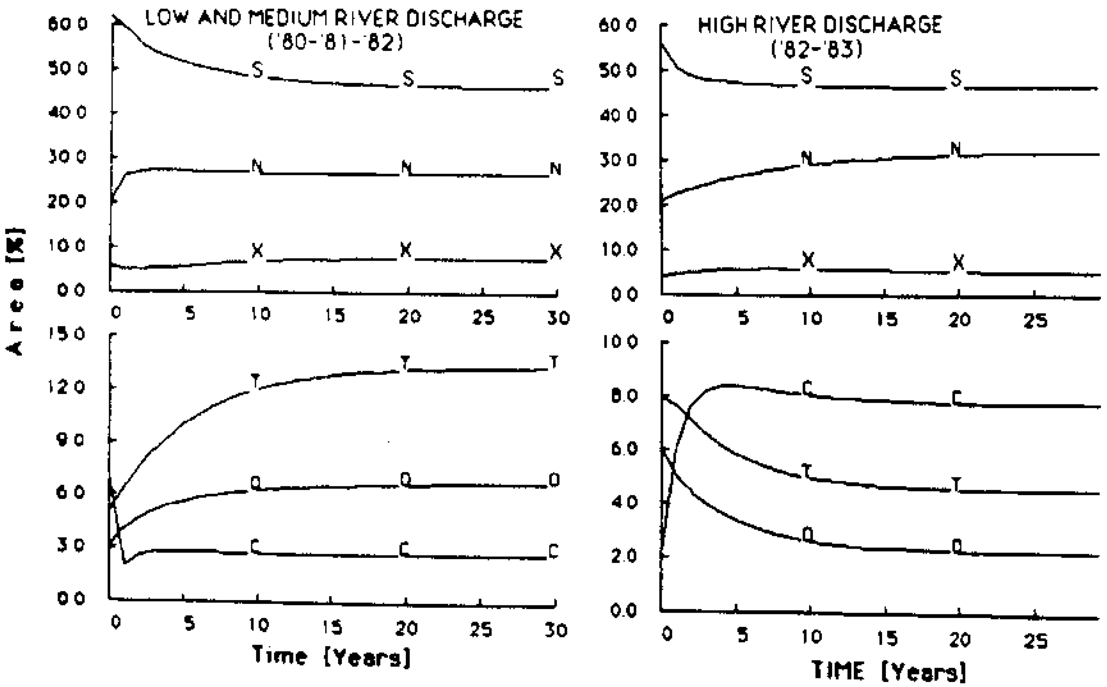

Fig. 2. Vegetation development on the Atchafalaya delta islands as predicted by the transition matrices for low/medium river discharge and for high river discharge. Vegetation categories are abbreviated as follows: S – *Sagittaria* spp., X – *Salix nigra*, T – *Typha domingensis*, C – *Cyperus difformis*, O – other types, N – nonvegetated area.

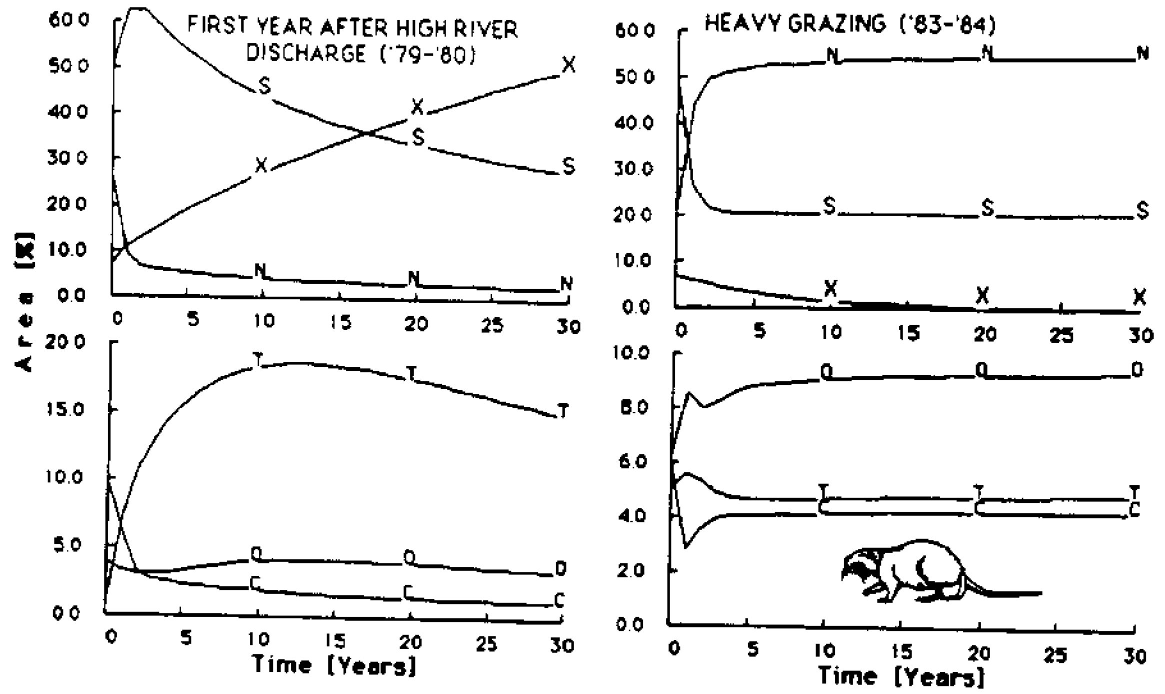

Fig. 3. Vegetation development on the Atchafalaya delta islands as predicted by the transition matrices for the first year after high river discharge and for heavy grazing by nutria. Abbreviations for vegetation categories are the same as in Fig. 2.

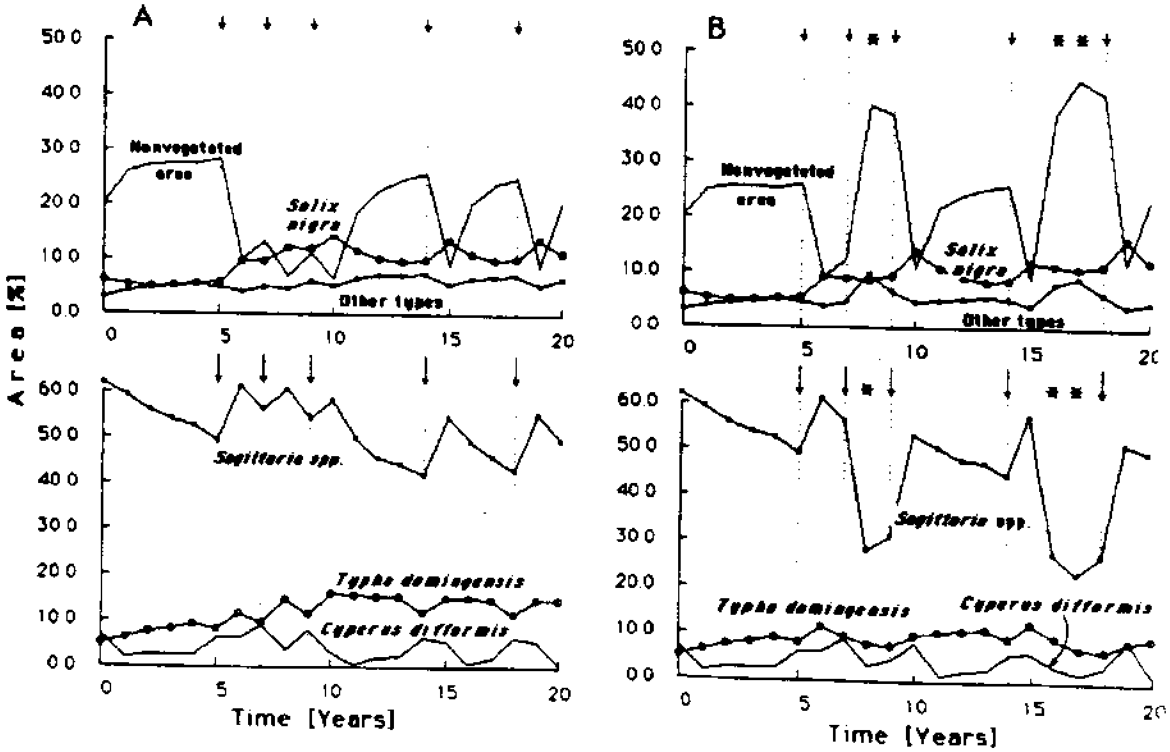

Fig. 4. An example of simulated vegetation development on the Atchafalaya delta islands by the model combining three transition matrices for different river discharge situations (A) and by a model combining the same three matrices with matrix for heavy grazing (B). Years with a high annual peak river flow are indicated by arrows; years with heavy grazing are indicated by asterisks.

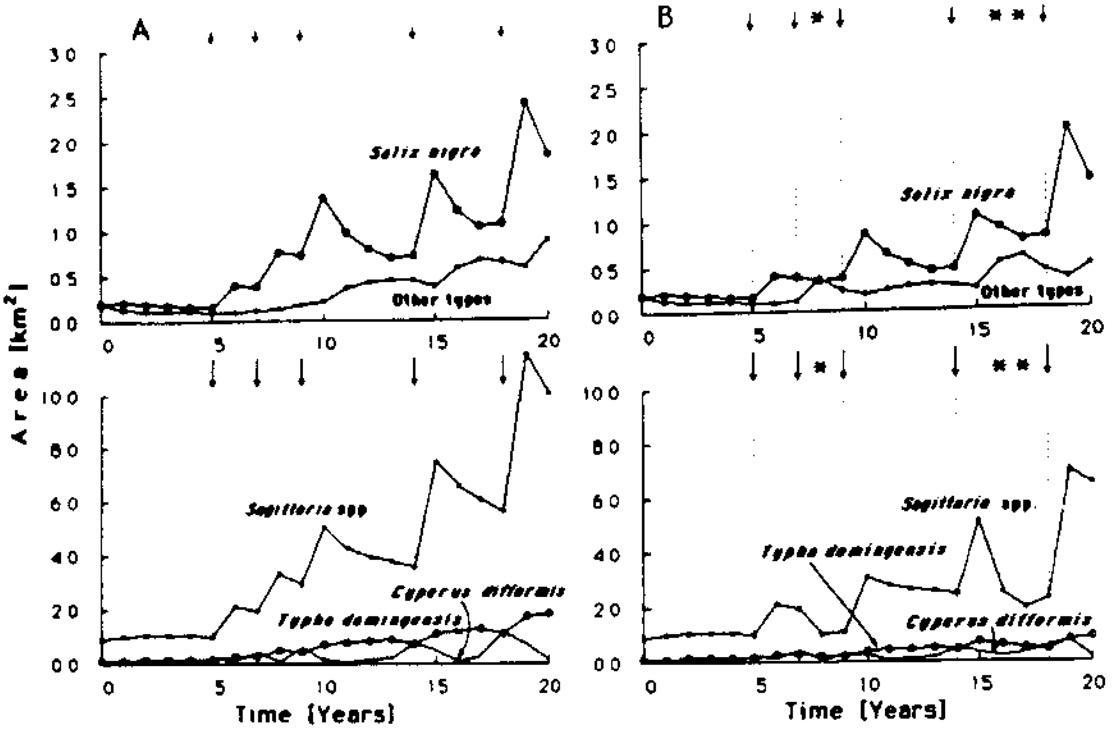

Fig. 5. An example of simulated vegetation development in the whole Atchafalaya delta by the model combining three transition matrices (A) and by the same model combined with the transition matrix for heavy grazing (B). Additional assumptions about discharge dependent vegetated area growth (See text) were applied in this model. Years with a high annual peak river flow are indicated by arrows; years with heavy grazing are indicated by asterisks.

them is based on the analysis of long-term hydrological data. In particular, probability of high flood is 0.23. The simulation example in Fig. 4A shows the possible relative areal changes of six vegetation categories on islands existing in 1980. There was a more or less consistent increase of area occupied by Salix nigra and Typha domingensis vegetation types in all simulations during the next 20 years. The area dominated by Sagittaria spp. slightly decreased. The Cyperus difformis vegetation type (C. difformis and Eleocharis pauciflora) exhibited maximum relative fluctuations which reveal an L-strategy of component species (see Whittaker 1975, p. 51). The Typha domingensis type exhibited the highest constancy. Heavy grazing (Fig. 4B) can change some proportions dramatically, namely non-vegetated and Sagittaria dominated areas.

Changes of the actual area occupied by different vegetation categories are simulated assuming that a high discharge year (>14 x 10^3 m^3/s) causes the extension of the Cyperus difformis type area by 70%, and the first year after a high discharge year causes extension of existing area of all other vegetation types by 60%. Available data do not allow better estimates of vegetated area extensions. Resulting simulations of vegetated area changes (Fig. 5) are in agreement with analytical (Wang 1984) and regressional (Wells et al. 1982) model predictions of the Atchafalaya delta growth. Heavy herbivory (Fig. 5B) can change the vegetated area substantially: the difference in the potential area of Sagittaria spp. is most remarkable. Regarding data from the modern Mississippi subdeltas, it is very unlikely that some vegetation types not considered here could play and important role in the next 20 years of Atchafalaya delta development. A possible exception might be a new type dominated by Phragmites australis.

A similar Markov model was completed for simulation of temporal changes in coastal marshes in southwestern Barataria Basin (Table 2). This area, covered by a mixture of saline, brackish, intermediate, and fresh marshes, represents the Lafourche Mississippi delta formed about 2000 years ago and completely abandoned only 60 years ago. The simulation based on transition matrix 1945-1956 is shown in Fig. 6. Although simulation predicts dramatic land losses, the prediction is

Table 2. Matrix of the probabilities for transition between marshes differing in the proportion of water area. M1: solid marsh, M2: marsh with 5% – 10% water, M3: 10% – 25% water, M4: 25 – 80% water, OW: 80% – 100% water. Transitions between marshes, levees, beaches and developments are not shown.

		From				
		M1	M2	M3	M4	OW
To	M1	0.323	0.117	0	0	0
	M2	0.505	0.575	0.440	0.396	0.048
	M3	0.052	0.151	0.460	0.124	0.013
	M4	0.016	0.053	0.020	0.369	0.016
	OW	0.070	0.079	0.080	0.111	0.923

optimistic compared with reality. Since the 1960's, intrusions of salt water, erosion, and subsidence have been dramatically accelerated by the construction of many navigation and pipeline channels in Louisiana coastal marshes (Deegan et al. 1984). Even the 1945-1956 period was not without human impact, and because we have no undisturbed reference area, we will never know how much our simulation of the natural marsh disintegration is exaggerated.

DISCUSSION AND CONCLUSIONS

Since the last glaciation, the Mississippi River has shifted its course several times, and sediments have been transported to different portions of the Gulf of Mexico coast (Kolb and Van Lopik 1966, Frazier 1967). New deltas have been built and old deltas have been abandoned. We tried to model vegetation dynamics in two short periods of this gigantic geomorphic scene. Cyclic patterns of landform changes do not provide enough opportunities for autogenic and/or unidirectional succession. Evidence from the Mississippi deltaic plain and cyclic vegetation changes described from other deltas and floodplains (Drury 1956, Waldemarson-Jensen 1979) led us to the conception of cyclic vegetation succession in the Mississippi deltaic plain (Fig. 7) and to refusal of the earlier unidirectional and convergent succession scheme for the same area (Penfound and Hathaway 1938).

Our studies and other available data (Gosselink 1984, Neill and Deegan in press) show that only about 65% of the area of an open bay is converted to fresh marsh (Sagittaria spp., Typha spp., Phragmites australis, Panicum hemitomon, etc.) when a new delta is formed and input of sediments if high. Apparently no more than 25% of the total area of a delta can be converted to

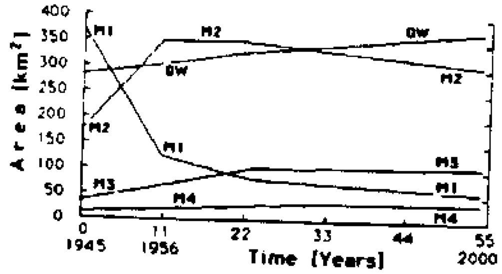

Fig. 6. Simulation of the Barataria Basin marsh development based on the transition matrix 1945–1956. Marsh categories are abbreviated as follows: M1 – solid marsh, M2 – marsh with 5%–10% water, M3 – 10%–25% water, M4 – 25%–80% water, OW – 80%–100% water.

swamp forests (Salix nigra, Taxodium distichum, Nyssa aquatica, Acer rubrum var. drummondii, etc.) and only about 1% reaches temporarily the 'climax' stage of hardwoods on natural levees (Quercus virginiana, Q. nigra, Celtis laevigata, Ulmus americana, etc.). Remaining woody vegetation (shrub communities dominated by Myrica cerifera or Baccharis halimifolia and Iva frutescens) can cover about 2% of the area in some periods of delta development. Later, when the river shifts its course and sedimentation is restricted, the whole area starts to sink because compression of sediments is not compensated by the external sediment supply. Salt water intrusions are more and more frequent. Fresh marshes and swamps are converted into brackish and salt marshes (Spartina patens, Distichlis spicata, Juncus roemerianus, Spartina alterniflora, etc.). Subsidence

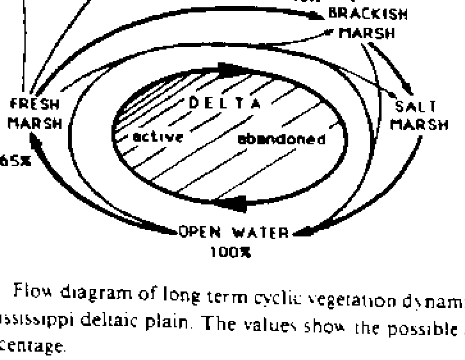

Fig. 7. Flow diagram of long term cyclic vegetation dynamics in the Mississippi deltaic plain. The values show the possible areas in percentage.

continues and erosion takes place until deltaic wetlands are converted into open water again. The complete cycle lasts several hundred to several thousand years.

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THE IMPACT OF RISING WATER LEVELS ON TREE GROWTH IN LOUISIANA*

W. H. Conner and J.W. Day, Jr.

INTRODUCTION

Numerous reports and papers (e.g. Barth and Titus 1984, Gornitz et al. 1982, Hoffman et al. 1983) have recently emphasized the potential impact of global warming trends on future sea level rise in coastal areas. Predictions are that many coastal wetlands of the United States will be flooded as sea levels rise as much as 2 m by the year 2100 (Hoffman et al. 1983). The impact of this increase in water levels on wetland forests is generally not considered. In southern Louisiana, the Lake Verret basin presents a unique opportunity to study water level changes and tree growth patterns. The basin is located in the Mississippi Deltaic Plain and ranges in elevation from less than 1 m above mean sea level (MSL) at the southern end of the basin to 6 m above MSL at the northern end of the basin. Previous work in the basin (Conner and Day 1984) has shown that subsidence exceeds sedimentation and apparent water level rise is approximately 1 m per century. The majority of the forests in the area are either bottomland hardwood or baldcypress-tupelo. It was the purpose of this study to look at the growth rates of the major bottomland species across an elevation/flood gradient to determine differences in growth patterns.

METHODS

Three 0.1 ha plots (called WCl, WC2, and WC3 hereafter) were established along an elevation gradient on a bottomland hardwood ridge in the upper Lake Verret basin. The logging history of the area is not known precisely, but we do know that the entire area was logged around the turn of the century. WC1 was located on the top of the ridge and was the driest plot. WC2 was on the ridge slope, while WC3 was at the lowest end of the ridge and in an area flooded nearly year-round. Within each plot, aluminum vernier dendrometer bands (Liming 1957) were installed on all trees greater than 10 cm diameter at breast height in December 1983. Monthly readings were begun in November 1984 after the bands had experienced one growing season. This wait was to allow the trees to grow into the bands in order to ensure a tight fit. There were a total of 49, 41, and 50 bands in plots WC1, WC2, and WC3, respectively. All measurements were converted to basal area (BA) increments and plotted as the average cumulative basal area change per species per plot. Shrub and seedling numbers by species were also inventoried to get an idea of what was coming up in the plots.

Water level measurements were taken on each field trip. Water depths were taken approximately 1 m from each tree and then all measurements were averaged to arrive at the depth of water over the plot for each trip. Two water wells were installed in each plot to monitor the depth of the water table when water levels dropped below the surface during the summer.

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*Conner, W.H. and J.W. Day, Jr. 1988. The impact of rising water levels on tree growth in Louisiana. Pages 219-224 in D.D. Hook et al., eds. The Ecology and Management of Wetlands, Vol. 2. Timber Press, Portland OR. Used with permission.

RESULTS AND DISCUSSION

Total elevation differences between the highest and lowest point in the forest study area was approximately 30 cm. Water levels in WC2 were approximately 6 cm greater than in WC1, and water levels in WC3 were 20 cm greater than WC1. Flooding of the study plots is typical of alluvival floodplain forests of the Mississippi River. Flooding occurred in the winter and early spring and floodwaters covered the plots until the spring or summer. The forest floor, with the exception of WC3, remained dry or nearly dry until late autumn. WC1 was flooded about 50% of the year but only 1-2 months of the growing season. WC2 was flooded for 75% of the year and 2-3 months of the growing season. WC3 was flooded for all except 3-4 weeks during the summer. WC3 is generally flooded year-round, but the period from April to August 1985 was exceptionally dry (Louisiana Office of State Climatology 1985). During the summer of 1985, the water table dropped to 75, 60, and 30 cm below the forest floor in WC1, WC2, and WC3, respectively. Peaks in flooding were caused by heavy rains (October-November 1984) and hurricanes (August and October 1985).

Growth started for almost all species between the middle of March and the middle of April and was completed by the end of September (growth patterns of the 6 major species are illustrated in Fig. 24.1). Nuttall oak (Quercus nuttallii) started rapid growth between mid-February and mid-March which is common for the ring-porous oaks. Eggler (1955) observed that live oak (Quercus virginiana) started growth by late February in New Orleans and Day (1985) found that laurel oak (Quercus laurifolia) started growth one month earlier than other species in the Dismal swamp. Baldcypress (Taxodium distichum) and water hickory (Carya aquatica) were the last trees to start growth (between April 19 and May 23).

Across the elevation/flood gradient there were differences in growth rates among species (Table 24.1) similar to what was observed by Briscoe (1955) in Mississippi

Figure 24.1: Growth patterns for six of the major bottomland hardwood species in the Lake Verret watershed. ● = WC1 plots, ○ = WC2 plots, ■ = WC3 plots.

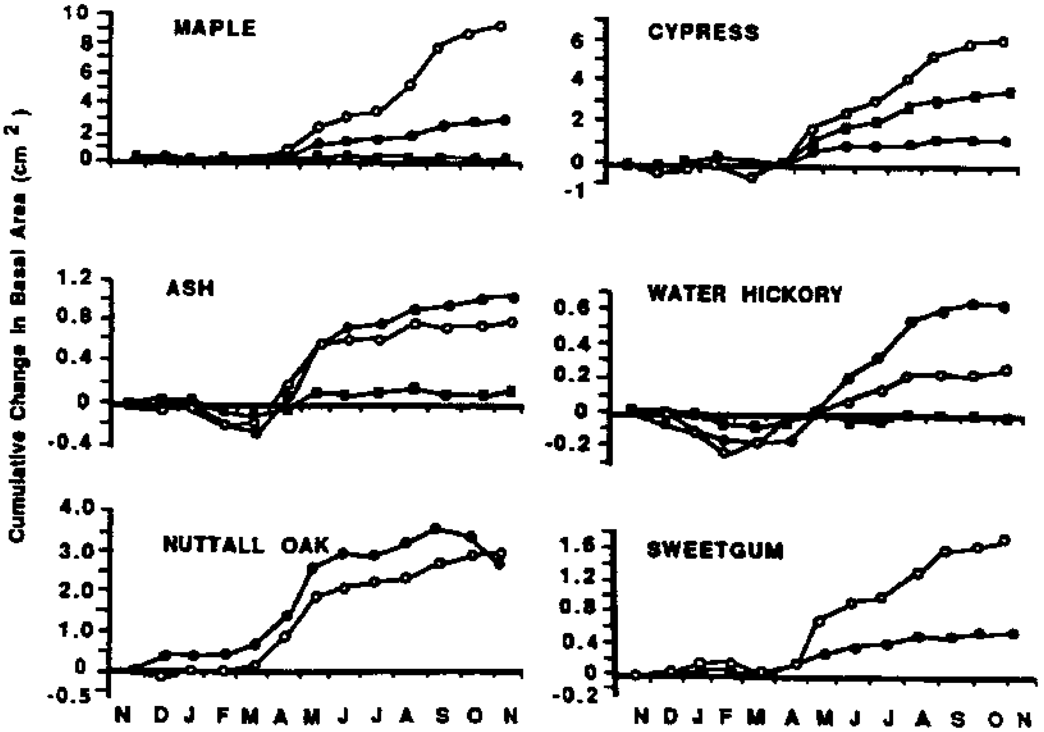

Table 24.1. Mean annual basal area (BA) increases for tree species on the three study plots in Louisiana.

PLOT	SPECIES	BA INCREASE (cm^2)	SD	N
WC1	green ash	1.04	0.73	9
	water hickory	0.67	0.40	5
	sugarberry	0.99	0.74	10
	sweetgum	0.52	0.40	7
	Nuttall oak	2.73	1.15	7
	baldcypress	1.27	0.71	5
	swamp red maple	2.79	—	1
	American elm	0.65	0.57	5
WC2	green ash	0.82	0.45	13
	water hickory	0.29	0.18	5
	sugarberry	0.45	0.32	4
	sweetgum	1.70	0.90	5
	Nuttall oak	2.91	3.35	2
	baldcypress	6.23	10.29	3
	swamp red maple	9.17	9.44	2
	water elm	0.62	0.44	5
	hawthorn	0.11	0.15	2
WC3	green ash	0.13	0.13	14
	water hickory	0.00	0.00	5
	baldcypress	3.45	1.86	8
	swamp red maple	0.24	0.32	16
	water elm	0.92	0.11	3
	persimmon	0.02	0.06	2
	water tupelo	1.82	0.84	2

River bottoms near Baton Rouge. Sugarberry (Celtis laevigata), American elm (Ulmus americana), green ash (Fraxinus pennsylvanica), and water hickory grew best in the driest area. Nuttall oak, baldcypress, swamp red maple (Acer rubrum var. drummondii), and sweetgum (Liquidambar styraciflua) grew best in the intermediately flooded site. With all species except baldcypress, poorest growth occurred in the permanently flooded site. Baldcypress grew the least on the ridge where intense competition with other bottomland hardwood species probably limits its growth.

Water hickory, water elm (Planera aquatica), persimmon (Diospyros virginiana), green ash, and swamp red maple growth rates were significantly lower in WC3 than in other plots. All of these species are moderately to highly tolerant of some flooding (Hook 1984). However, as water levels continue to rise in the Lake Verret forests, the trees will eventually die as they cannot stand permanent flooding (Broadfoot and Williston 1973, Eggler and Moore 1961, Green 1947, Hall and Smith 1955). The largest increases in BA occurred in plot WC2. Baldcypress, swamp red maple, and sweetgum growth in WC2 were significantly higher than in the other plots.

The stress that many of the bottomland trees are undergoing is visually evident in the number of dead tops and branches. As one goes from WC1 to WC3 the number of visibly stressed trees increases from 8 to 53% of the total number of trees in each plot. If present trends of increasing water level continue as the coastal area subsides, all but the most flood tolerant trees (baldcypress and water tupelo) will die in the near future as a result of permanent flooding. Even though baldcypress and water tupelo do well under flooded conditions, there is a limit to the depth and length of flooding they can endure (Brown and Lugo 1982, Eggler and Moore 1961, Harms et al. 1980), and eventually they also will die.

The shrub and sapling and seedling data give us an idea of what is coming into the areas as floodwaters increase. In WC1 and WC2, the understory is composed mainly of deciduous holly (Ilex decidua), water elm, and swamp red maple. The total number of stems/ha in each plot was 1,050 and 1,630, respectively. In the flooded area, there were 3,570 stems/ha with 90% of them being swamp red maple. With the seedlings, the differences between the plots is striking. WC1 being the driest area contained a variety of hardwood seedlings such as oak, persimmon, water hickory, and sweetgum. Over 50% of the total number/ha, however, were swamp privet (Forestria acuminata). The greatest number of seedlings occurred in WC2 (1,230/ha). Oak and persimmon were still common in this plot, but baldcypress also becomes a dominant member. In WC3, very few seedlings were found (270/ha), and 95% of those came in during the short dry period during the summer of 1985.

Overall, what we see occurring in the Lake Verret basin is a general decline in the growth of the major timber species and the establishment of more water tolerant shrubby species in many hardwood areas as water levels rise. For the future management of these areas for timber and wildlife, this increase in water level must be considered.

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PART 6

ZOOPLANKTON

PATTERNS OF EGG PRODUCTION IN THE COPEPOD ACARTIA TONSA IN A SHALLOW LOUISIANA ESTUARY

M.J. Dagg and W.E. Walser, Jr.

INTRODUCTION

Biological production rates in copepods of the genus Acartia can be high. For example, in Narragansett Bay during the warm summer months, Acartia tonsa is capable of doubling its biomass through growth and reproductive processes in less than a day (Durbin and Durbin 1981). Egg production in A. tonsa is dependent on several factors including temperature and salinity (Walser 1985), food concentration (Durbin et al. 1983), and food quality (Parrish and Wilson 1978). Egg production by A. tonsa responds quickly to environmental changes; for example, changes occurred within several hours after a change in available food (Kiorboe et al. 1985, Dagg 1987). Given the sensitivity of egg production in A. tonsa to the physical and biological environment, it is not surprising that reported egg production rates range widely. At 17.5°C, egg production averaged 31-44 eggs/female/day, with peak values between 60-70 (Wilson and Parrish 1971, Parrish and Wilson 1978); at 21°C rates averaged 30.5 eggs/female/day (Johnson and Miller 1973); at 10.5 and 20.2°C, rates averaged 15.6 and 18.4 eggs/female/day (Corkett and Zillioux 1975); at 15°C rates averaged about 40 eggs/female/day (Dagg 1977); at about 25°C, maximum rates observed in Narragansett Bay were about 60 eggs/female/day (Durbin et al. 1983); and over a 1 year study in a subtropical Texas lagoon, egg production varied between 23 and 105 eggs/female/day (Ambler 1986).

Fourleague Bay is a shallow (mean depth 1.5 m) 93 km^2 estuary in the central coastal zone of Louisiana. The upper Bay is oriented in a northwest-southeast direction allowing significant fresh water influence from adjacent Atchafalaya Bay. The lower Bay is oriented in a north-south direction, and is influenced by the Gulf of Mexico through a deep (18 m) tidal channel called Oyster Bayou. The upper Bay is dominated by turbid nutrient-rich river water, especially during periods of high flow. Salinity in the upper Bay ranges from 0 to approximately 10 ppt., and secchi disk depth ranges from 5 to 35 cm (Madden 1986). The lower end of the Bay is connected to the open Gulf of Mexico by Oyster Bayou. Gulf water is characterized by higher salinity and relatively lower turbidity and nutrient concentrations. Salinity, turbidity, nutrient concentrations and chlorophyll concentrations in the lower Bay vary widely, depending primarily on river flow, tide, and wind speed and direction.

Aquatic primary production is high in the Bay despite its shallowness and high turbidity. Annual net production was 119.5 gC/m^2/yr in the upper Bay, and increased to 317.4 gC/m^2/y at a lower Bay site. Production was highest at intermediate salinities. At low salinities, production was apparently light limited because of the extreme turbidity in the river water. At high salinities production declined because of nitrogen limitation (Randall and Day 1987). Chlorophyll concentrations ranged between 3.2 and 19.8 µg/l in the upper Bay, and between 4.0 and 26.7 µg/l in the lower Bay during the study by Randall and Day (1987). These may be underestimates because values are derived from frozen samples.

Laboratory studies with A. tonsa were completed as a part of this project. The relationships between egg production under conditions of saturating food availability and temperature and salinity were examined in the laboratory as a part of this project (Walser 1985), and the relationships between egg production and suspended particulate material in the phytoplankton diet of A. tonsa were examined in the laboratory (White 1986). In this paper we examine the egg production of A. tonsa in the field, Fourleague Bay, and compare rates predicted from the laboratory studies with those observed in the natural system.

METHODS

Cruises to Fourleague Bay were in April and September 1986 and March and August 1987. The 57 ft RV Acadiana was anchored in Oyster Bayou and used as a laboratory during each 3 day cruise. Sampling was accomplished from a small boat which could operate in most places within the shallow Bay.

The rate of egg production by A. tonsa females was measured every 6 h over a 48 h period on each cruise. Copepods were collected from 2 salinity regimes at each sampling interval; in a typical small boat trip, salinity was periodically measured with a refractometer until the target salinity was found. A more accurate salinity measurement and a temperature measurement were then made with a Beckman RS5-3 salinometer. A water sample was collected by bucket, and covered until it was returned to the shipboard laboratory, 5-30 min later. Zooplankton were collected with a 0.5 m ring net, with 256 µm mesh, towed slowly behind the boat for 2-3 min. Cod end contents were diluted into a second bucket of surface water, and returned to the ship.

Aboard ship, an aliquot of water was analyzed for chlorophyll and pheopigment (as chlorophyll equivalents) content. Aliquots were filtered through 25mm GF/F glass fiber filters, and homogenized by grinding in several ml of 90% aqueous acetone. The supernatent was analysed before and after acidification with 2 drops of 10% HCl, using a Turner Designs Model 10 fluorometer. Calculations were made according to equations modified slightly from Strickland and Parsons (1968):

$$\text{chlorophyll } (\mu g/l) = \frac{K(f_o - f_a)}{v}$$

$$\text{pheopigment (as } \mu g/l \text{ chlorophyll equivalent)} = \frac{K(Rf_a - f_o)}{v}$$

where F_o and F_a are fluorescence readings before and after acidification, R is the acid factor, k is the calibration constant, and v is the volume of filtered in ml.

Triplicate water samples were filtered through preweighed glass fiber filters and placed in a drying oven for later determination of suspended matter concentration.

Two A. tonsa females were added to each of 10 125-ml glass bottles containing water from the copepod sample sight that had been screened through a 63 µm mesh sieve to remove eggs and nauplii. Bottles were sealed with plastic lids, and placed on a rotating wheel in a dark incubator. Temperature was maintained by pumping seawater continuously through the incubator. Control bottles, containing only screened water, were run on several occasions to assure that no eggs or nauplii were passing the 63µm mesh sieve. Incubations were for approximately 6 h, and samples were then preserved by the addition of several ml of full strength formalin, resealed and stored. At the Marine Center, the nauplii and eggs were entirely counted from each sample by filtering the sample onto a gridded glass fiber filter, and counting the eggs and nauplii under a dissecting microscope.

RESULTS

Diel Patterns

In 4 of the 8 time series, there was a pattern of diel periodicity in egg production (Figure 1). In these cases, the maximum was always during the midnight to early morning period. Sometimes diel cycling occurred when egg production rates were high, such as during the April 1986 cruise, but nighttime maxima were also apparent when rates were low, such as during the August 1987 cruise. On the other occasions, there were no apparent short term temporal patterns in egg production.

Between and Within Cruise Patterns

Except for cruise 2, egg production rates were similar within a cruise at both of the salinity regimes examined (Table 1); i.e. cruise 1, 3.0 and 3.0 eggs/female/hour at 16 and 6 ppt; cruise 3, 2.0 and 1.8 egg/female/hour at 18 and 7 ppt.; and cruise 4, 0.6 and 0.5 eggs/female/hour at 21 and 6 ppt. Thus within cruises 1, 3, and 4 egg production was not correlated with salinity. Cruise 2 however, was different. During this cruise, copepods from the high salinity water had a low egg production rate (0.6 eggs/female/hour) with no indications of any diel periodicity whereas copepods from the low salinity water showed a significantly higher egg production rate (1.7 eggs/female/hour) and strong diel periodicity. Cruise 2 indicates that conditions within the Bay can sometimes be significantly different in terms of Acartia egg production rate and patterns. More typically however, in 3 of 4 cruises, egg production rates and patterns were similar

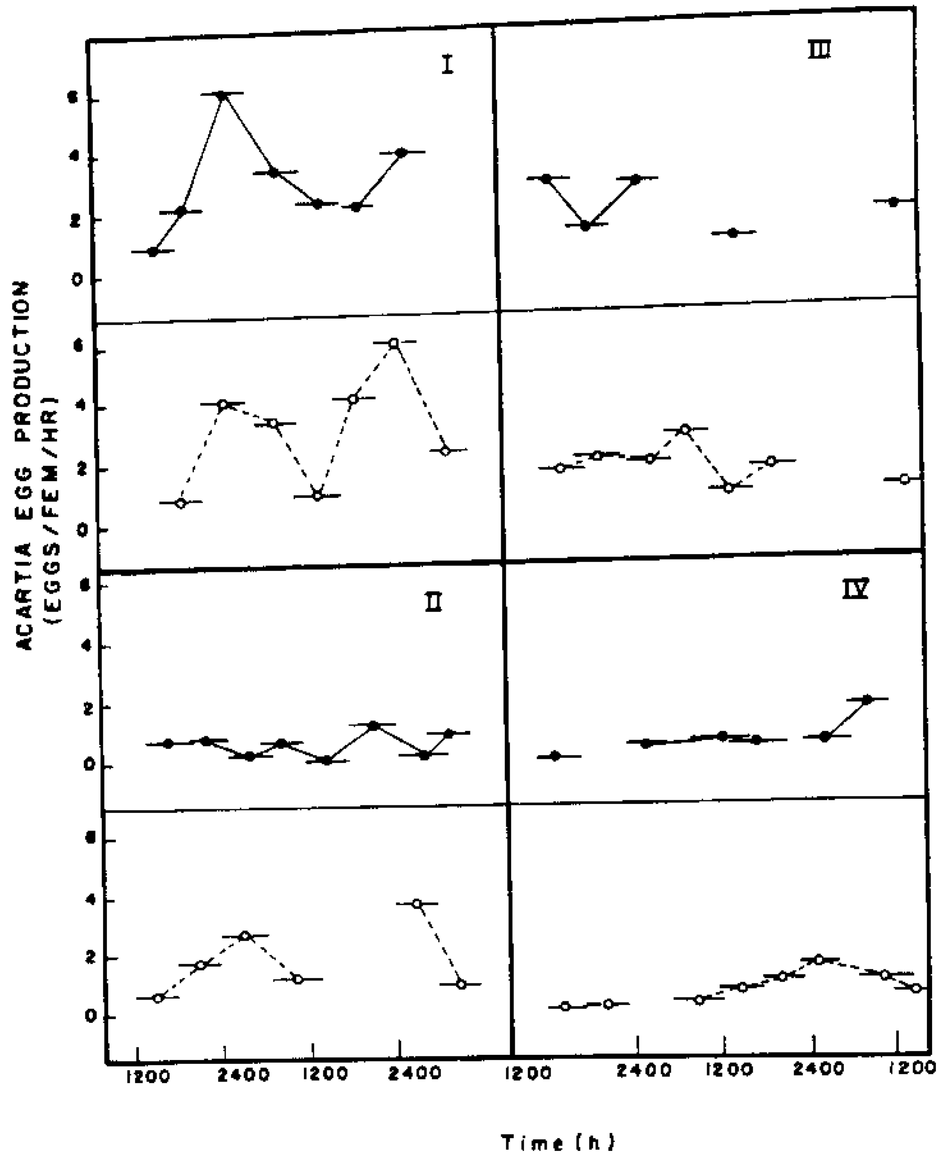

Figure 1. *Acartia tonsa* egg production in Fourleague Bay during April 1986 (I), September 1986 (II), March 1987 (III), and August 1987 (IV).

throughout the Bay on a given cruise. Most of the variability in *Acartia* egg production apart from diel variation, was between cruises.

Environmental Variation

Temperature varied little within a cruise but widely, between 13.9 and 31.1°C, between cruises. Average temperatures for each cruise are shown in Table 1.

Salinity, of course, typically varies widely within the Bay during a single cruise. Within a cruise, the same salinity regimes were repeatedly sampled if possible, every 6 h. On some occasions however, conditions within the Bay changed during the study and water of the desired experimental salinity could not be found over the entire 48 h period. For example, for several h during the second day of cruise 3, water throughout the entire Bay

Cruise	Date	Temperature (°C)	Salinity ($^o/_{oo}$)	Chlorophyll (mg/l)	SPM (mg/l)	Egg production (eggs/female/day)
I	Apr/86	23.0+0.7	16.1+2.0	33.5	47.7	69.6
			6.4+0.5	53.5	78.6	71.9
II	Sept/86	29.4+0.7	28.5+0.4	17.1	45.8	14.7
			20.3+2.0	35.9	38.7	41.8
III	Mar/87	13.9+0.5	15.7+4.1	24.7	193.4	42.7
			5.4+1.0	27.6	113.2	47.2
IV	Aug/87	31.1+1.1	21.0+2.4	11.8	43.9	5.5,17.1
			6.3+1.3	25.6	32.2	3.5,24.7

Table 1. Fourleague Bay water characteristics and *Acartia tonsa* egg production.

was completely fresh (0.0 ppt). Salinity also varied considerably between cruises so that the same salinity regimes could not be utilized throughout the study. In particular, low salinity water, in the 5-6 ppt range, was not encountered during cruise 2. Average salinities for each 48 h period over which egg production measurements were made are shown in Table 1.

Laboratory Rates

Laboratory experiments with A. tonsa were conducted by Walser (1986). These experiments were designed to measure egg production rates under saturating food concentrations over temperature and salinity regimes spanning those found in Fourleague Bay. At 14°C, Walser observed egg production rates of about 24 eggs/female/day at 16 ppt and about 19 eggs/female/day at 5 ppt. These rates are considerably less than those observed in situ in Fourleague Bay under similar temperature and salinity conditions (43 and 47 eggs/female/day respectively, see Table 1).

At 23°C, Walser measured egg production of about 45 eggs/female/day at 16 ppt and about 35 eggs/female/day at 6 ppt. These rates are also lower than those observed in the Bay under similar temperature and salinity conditions (70 and 72 eggs/female/day respectively, see Table 1).

At 29°C, Walser measured egg production rates of about 46 eggs/female/day at 28.5 ppt and about 58 eggs/female/day at 20 ppt. These rates are higher than those observed in the Bay under similar temperature and salinity conditions, (15 and 42 eggs/female/day respectively, see Table 1).

The highest experimental temperature used by Walser was 30°C. However, if his data are extrapolated to 31°C, then egg production rate at 21 ppt would be about 58 eggs/female/day, and at 6 ppt about 38 eggs/female/day. These rates are higher than those observed in the Bay under similar conditions of temperature and salinity (6 and 17 eggs/female/day at 21 ppt, and 4 and 25 eggs/female/day at 6 ppt, see Table 1).

In summary, during the 2 spring cruises, egg production in the Bay was higher than predicted by the Walser empirical model, and during the 2 late-summer cruises egg production in the Bay was lower than predicted by the empirical model.

Food limitation is a possible explanation for the low egg production rates observed in situ in Fourleague Bay during the late summer cruises (cruises 2 and 4). Feeding rates were not measured so there is no direct information on food limitation. However, chlorophyll concentrations were measured at each collection and can be used as an approximate index of phytoplankton concentration.

During cruise 2, phytoplankton concentration in the 20 ppt water was uniformly high over the 48 h study period, averaging 35.9 µg/l. Observed egg production in this water was only slightly lower than predicted (42 vs 58 eggs/female/day) indicating that the field copepods were feeding at least near their maximal rates. In contrast, chlorophyll concentration in the high salinity waters was lower and varied considerably over the 48 h study, averaging 17.1 μg/l with a standard deviation of 9.8 μg/l. Observed egg production rates were significantly lower than predicted (15 vs 46 eggs/female/day), significantly lower than observed in the 20 ppt water, and were significantly correlated with chlorophyll concentration, suggesting food limitation in this high salinity water at this time.

During cruise 4, the average chlorophyll concentration in the low salinity water was significantly higher than that of the high salinity water (25.6 vs 11.8 μg/l), but egg production rates were about the same in both water types. Either chlorophyll concentration was a poor indicator of food availability or food concentration was not limiting during this cruise; if food was limiting, egg production should have been higher in the water containing higher chlorophyll content.

In addition, it does not seem that egg production is affected by chlorophyll concentration within cruises 1 and 3. During cruise 1, egg production patterns were essentially identical in both parts of the Bay but phytoplankton concentrations were considerably higher in the low salinity waters (53.5 vs 33.5 μg/l). On cruise 3, phytoplankton concentrations were approximately the same in both regimes, and egg production rates were about the same also; possible variations with food concentration cannot be discerned because food concentration was essentially constant. On both of these cruises, observed egg production rates in the Bay were higher than predicted. Reasons for this are not clear.

Suspended Particulate Matter

Suspended particulate material (Table 1) can interfere with feeding processes of copepods or, if ingested along with food particles, can lower the average nutritional value of the ingested material (White 1985). During cruise 1, SPM in the low salinity waters increased substantially during the second day, but egg production rate was not diminished. This indicates that egg production was not inhibited by SPM in the diet during this cruise. During cruise 2, SPM concentrations were low and similar at both sampling salinities, whereas egg production rates were higher in the low salinity water, indicating that SPM was not related to egg production. During cruise 3, river flow was the highest observed during our study; on several sampling occasions the entire Bay was fresh. SPM concentrations ranged widely and the highest concentrations in the study were observed. Even so, only the highest value observed was in the range that has been shown to cause a reduction in egg production in laboratory studies, greater than 500 mg/l (White 1986). Egg production rates were about the same in both water types during cruise 3, and so there is insufficient data to determine if SPM affected egg production, but there are no indications of food limitation during this cruise and we therefore conclude that SPM in the diet did not reduce egg production seriously. During cruise 4, SPM concentrations were low at both salinity regimes. There were no significant differences between SPM concentrations during day 1 and 2, whereas egg production rates increased substantially on day 2, implying that egg production rate was independent of SPM concentration during this cruise. This would be anticipated from the lab experiments of White (1986).

DISCUSSION

In this study, egg production rate by <u>A. tonsa</u> in Fourleague Bay varied in several ways: dielly in 4 of 8 data series, daily in 2 of 8 series, between stations within the Bay on 1 of 4 comparisons, and between cruises.

Diel patterns in egg production or egg release have been observed in copepods previously (Marcus 1985, Runge 1985, Checkley et al. in prep). Diel periodicity in several aspects of copepod physiology and behavior including vertical migration, feeding rate, and excretion rate, are commonly observed and are thought to be associated primarily with predator avoidance. Other important components of the copepod's environment have also been implicated as determinants of diel behavior patterns in copepods however, including light, food availability, and temperature. Even in shallow systems such as the 1.5 m Fourleague Bay, <u>A. tonsa</u> apparently migrates vertically on some occasions. In this study, the factors determining the diel pattern in egg release on 4 of the 8 occasions could not be identified.

During each of the first 3 cruises, egg production rates were essentially the same on day 1 and 2. However, at both study sites during cruise 4, egg production rates during the second day were substantially higher than during day 1. This change was not correlated with changes in salinity, temperature, chlorophyll or suspended particulate material, and it is not clear what caused this pattern.

In 3 of the 4 cruises, egg production rate by <u>A. tonsa</u> was essentially the same at both stations within the Bay; egg production was unaffected by wide ranges in salinity, chlorophyll concentration, and suspended particulate material in these cases. Only on 1 of the 4 cruises did egg production significantly vary between the 2 stations within the Bay. We suggest that, at this time, egg production was food limited in the high salinity water of the lower Bay, which contained comparatively small amounts of phytoplankton.

Between cruises, egg production varied widely from an average of 12.7 eggs/female/day during cruise 4 to 70.8 eggs/female/day during cruise 1. Some variation is due to temperature, which ranged during our cruises from average of 13.8°C to 31.2°C. Egg production was actually higher during the 2 cruises with the lowest temperatures so the role of temperature is not clear cut. Inhibition of egg production at high temperatures is commonly observed in copepods but laboratory studies with A. tonsa failed to show any such inhibition as temperature increased from 10-30°C (Walser 1986), although the rate of egg production increase as temperature increased had begun to decline at 30°C.

Within a cruise, temperature did not vary sufficiently to contribute much to variations in egg production within the Bay system.

In laboratory studies, suspended sediment only interfered with egg production at very high (> 500 mg/l) concentrations unless phytoplankton concentrations are low, or by inference, unless the copepods were stressed by some other factor. These sediment concentrations were not observed during our studies in Fourleague Bay except on a single occasion, and we conclude that suspended sediment in Fourleague Bay is unlikely to be a factor that affects egg production in A. tonsa.

Temperature and food are typically thought to be the dominant determinants of egg production in copepods. In a study done with 2 species of Acartia, Uye (1981) showed a strong relationship between temperature and egg production. Significantly, Uye also showed that summer and winter adapted copepods behaved differently in their response to temperature, although the shape of the curves was the same. The pattern shown in Uye's study is typical; egg production rate increased with temperature up to an optimal temperature and then declined dramatically as temperature increased further.

Also shown by Uye (1981), was the effect of food availability on egg production in the same 2 Acartia species. Egg production was closely related to food concentration, increasing initially as food concentration increased and saturating at higher food concentrations. Combining the effects of temperature and food availability into a predictive model, Uye was able to closely predict the the observed seasonal pattern in egg production. Marked seasonal variation in reproductive rate was observed (primarily related to phytoplankton food availability and temperature, although other food sources are not quantified).

The saturating food concentration for egg production is difficult to identify; for example, Uye (1981) showed 2 Acartia species saturating at about 1 µg chlor/l in laboratory studies whereas Durbin and Durbin (1983) showed that saturation had still not occurred at 10 µg/l of natural chlorophyll in Narragansett Bay. The quality of the food particles is undoubtedly a factor in this comparison, but it is clear that, even though estuarine environments are highly productive and frequently contain high stocks of phytoplankton, detritus, and microzooplankton, food limitation of physiological processes in Acartia can exist.

Salinity also has an effect on egg production rate in Acartia spp. For example, between 5 and 35 ppt, egg production in A. tonsa was maximum at 20 ppt and declined at higher and at lower salinities, regardless of the temperature, although the salinity effects were more dramatic at higher temperatures (Walser 1985).

Our laboratory studies indicated that egg production rates of A. tonsa should be high under the conditions of temperature, salinity, suspended sediment and chlorophyll that are found in Fourleague Bay. Field measured rates under a wide range of environmental conditions supported these laboratory findings indicating that the environment of Fourleague Bay is highly productive year round for A. tonsa. However, during the 2 spring cruises rates were higher than predicted, and during the 2 late summer cruises rates were lower than predicted, indicating that some factor other than the ones we measured has a significant impact on the egg production of A. tonsa in this system.

The estuarine copepod A. tonsa actively produces eggs under a diversity of physical and biological environments. In this study, reproduction took place at salinities ranging from completely fresh to near 30 ppt, at temperatures ranging from 13-32°C, and under conditions of phytoplankton availability ranging from less than 8 to greater than 55 µg/l of chlorophyll. The productivity of Acartia in Fourleague Bay appears to be quite high at all times during our study, but varies widely seasonally. Usually, it is constant within the Bay system at any one time, although physical and biological conditions within the Bay vary widely. The food limitation effect observed in the high salinity water of cruise 2 suggest that Acartia flushed from the Bay into the continental shelf waters will quickly become food limited as the chlorophyll is diluted by the oceanic water.

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PART 7

NEKTON

THE ECOLOGY OF FISH COMMUNITIES IN THE MISSISSIPPI RIVER DELTAIC PLAIN*

Linda A. Deegan and Bruce A. Thompson

INTRODUCTION

The estuaries of southern Louisiana are vast and support large numbers of many different fish species. Gunter (1967) referred to this area as the 'fertile fisheries crescent' because the area supports one of the world's largest commercial fish catches. These huge commercial fish catches are, for the most part, dependent on species that during their juvenile stages use estuaries formed during the successive delta complexes of the Mississippi River. In this chapter we consider how these fish populations contribute to the structure, metabolism, and regulation of energy and nutrient fluxes in the deltaic plain estuaries, and examine how differences in the ecosystem affect fish communities. To do this we first present an overview of the estuarine environment of Louisiana's deltaic plain, then examine general characteristics of fish community structure and energy flow in these estuaries, and finally compare differences in productivity and community structure among systems and relate these differences to changes in attributes of the estuaries.

DESCRIPTION OF THE STUDY AREA

The coast of Louisiana is fringed by a band of marshland 16-128 km in width which is naturally divided into two zones. The eastern part is the deltaic plain of the Mississippi River and the western part is the chenier plain formed by down drift sediments from the river. In this paper we consider only the fish communities of the deltaic plain spans almost 320 km of coastal Louisiana (Fig 1), and forms a distinct physiographic unit which encompasses the active and abandoned deltas of the Mississippi River. Several major deltaic complexes, reflecting significant changes in the course of the Mississippi River, have been formed during the last 7000 years (Fig. 2). The Mississippi River deltaic plain maintains itself by the cyclic nature of delta building depositional events (Frazier 1967). New delta complexes develop over older deltaic lobes in other areas. As time progresses each delta complex goes through a cycle beginning with subaqueous (below water) growth, subaerial (above water) growth, through abandonment of the delta by the river, and subsequently a period of deterioration due to sediment compaction and sea level rise (Gagliano and Van Beek 1975). Figure 3 illustrates the sequence of physiographic changes for a given delta complex and indicates the relative position of the four existing complexes we will consider in this chapter. The product of these cyclic events is a diverse assemblage of habitats which change as deltas advance through the cycle. Progression through the cycle is indicated by changes in subaerial extent, length of the land water interface, and salinity. Gagliano and Van Beek (1975) suggest that habitat diversity increases as the delta complex enters the subaerial growth phase (Fig. 3) and is maximal in the early stages of deterioration. Maximum length of land water interface and an increase in salinity to moderate levels are also characteristics of the early stage of deterioration. The physical processes which form the delta complexes are believed to control the distribution and productivity of the plants and animals of the area (Penfound and Hathaway 1938, O'Neil 1949, Gagliano

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*Deegan, L.A. and B.A. Thompson. 1985. The ecology of fish communities in the Mississippi River deltaic plain. Pages35-56 in A. Yanez, ed. Fish Community Ecology in Estuaries and Lagoons: Towards an Ecosystem Integration, Universidad de Nacional Autonoma de Mexico Ciudad Universitaria. Used with permission.

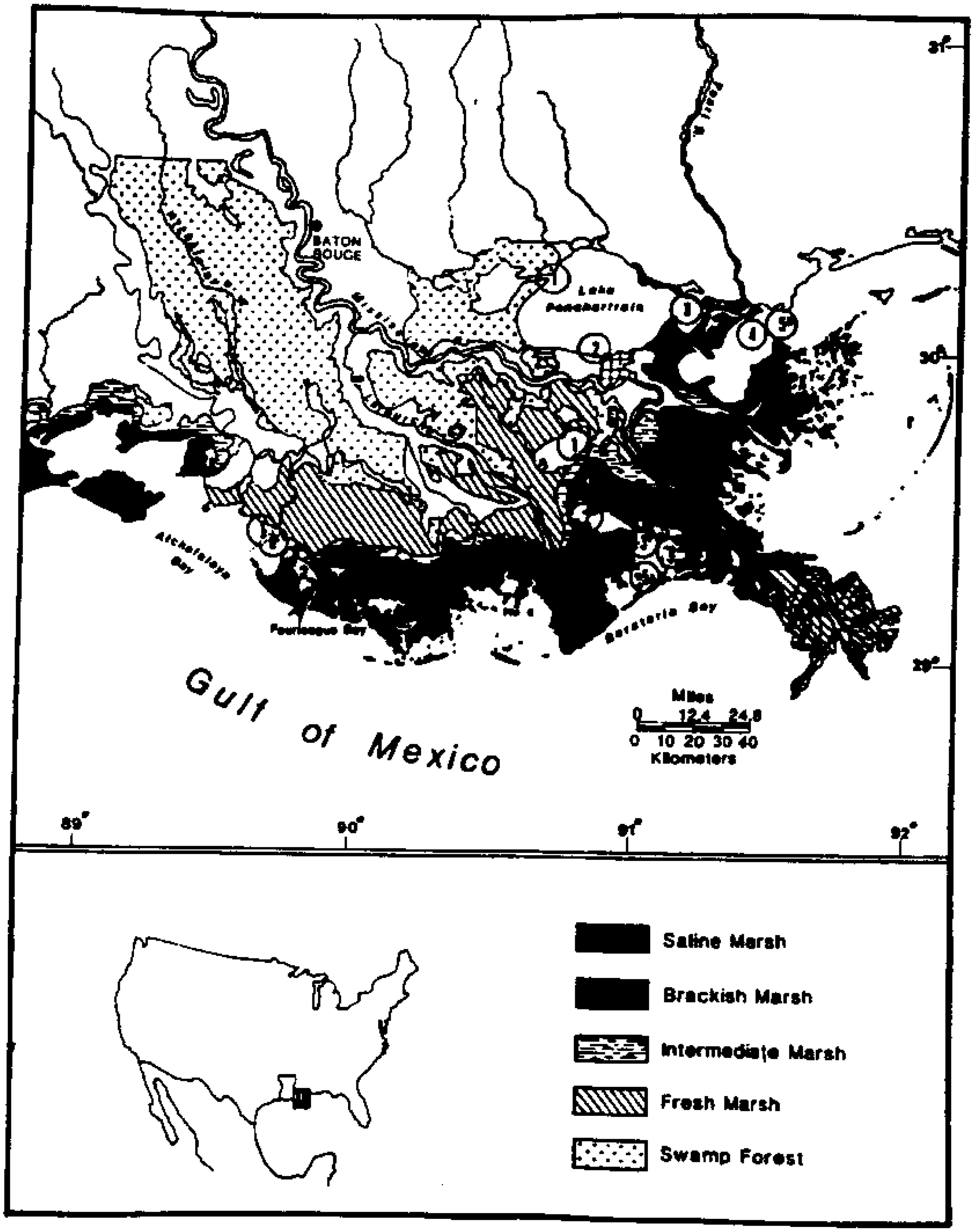


Fig. 1. Map of the Mississippi River deltaic plain region. Station locations withinin the four estuaries are noted by numbers 1-5.

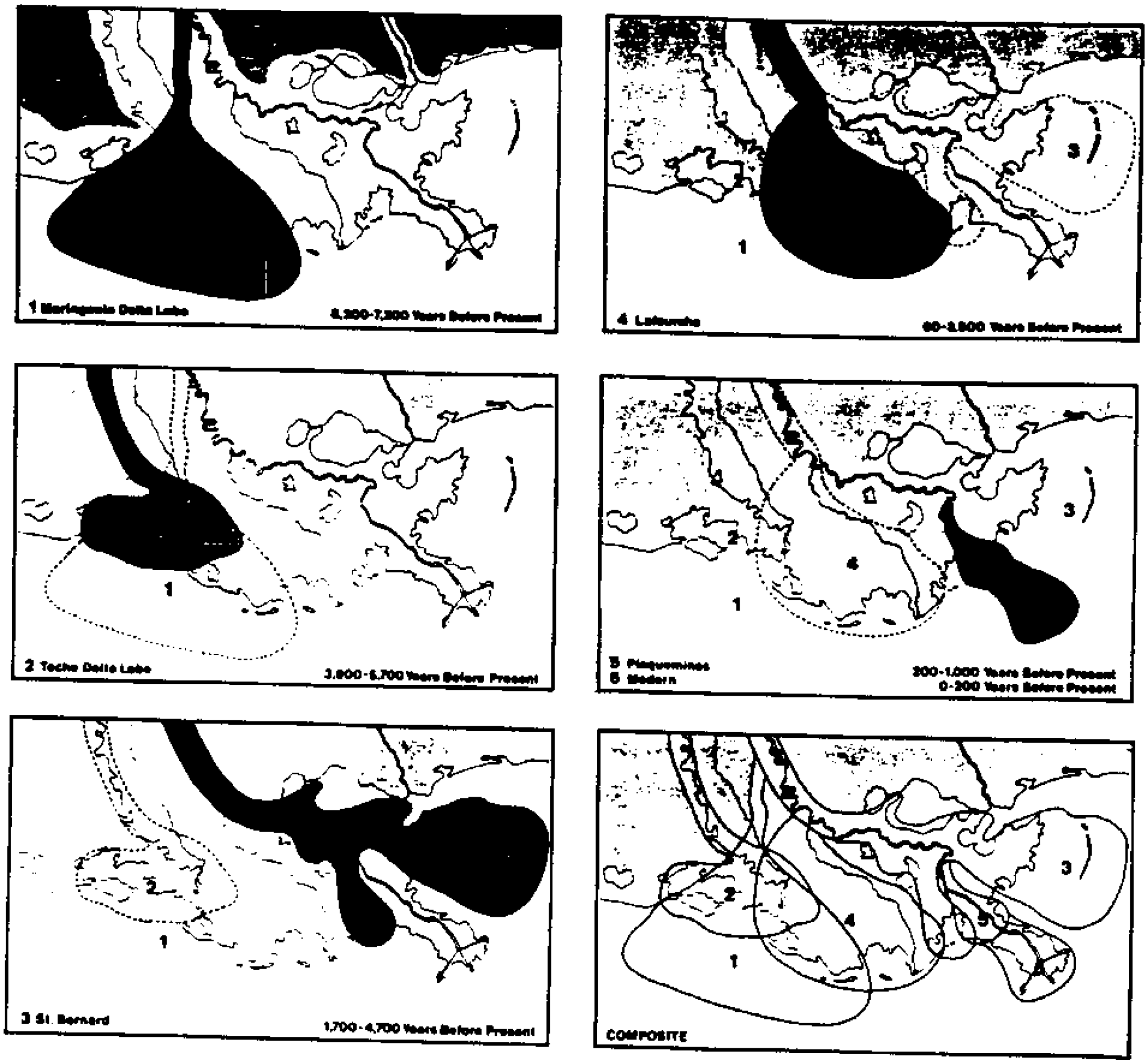
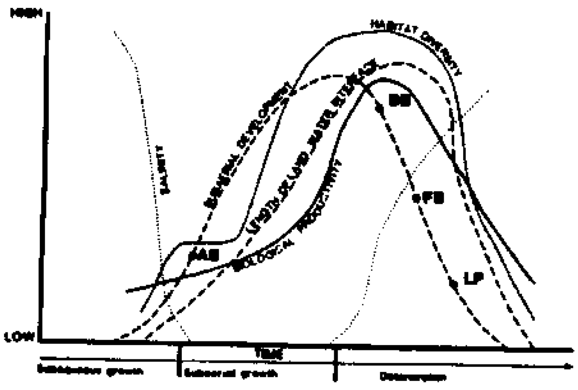


Fig. 2. Mississippi River's previous delta lobes and their influence on the evolution of Louisiana's coastline.

and Van Beek 1975). Biological productivity and diversity are believed to be directly related to the physiographic changes. Gagliano and Van Beek (1975) suggested highest biotic productivity and diversity are associated with the earliest stage of deterioration.

Sufficient information exists for four of the estuaries within Mississippi River deltaic plain to describe spatial and temporal occurrence, food chain relationships and ecosystem roles of nekton. We will also discuss the effects of changes in ecosystem structure, which are related to their relative position within the delta cycle, on fish productivity and diversity.. The bay systems examined in this chapter are (Fig. 1): The Atchafalaya Bay delta, Fourleague Bay, Barataria Bay, and Lake Pontchartrain.

There are several differences among these four systems which are pertinent to the analysis in this chapter (Table 1). One of the most important differences among the estuaries is the source and amount of freshwater influx because this controls the salinity regime. The differences in salinity regime are reflected in the timing (Fig. 4) and range of salinities observed (Table 1)



Mod. from Gagliano & VanBeek (1970)

Fig. 3. Diagramatic representation of the cycle of delta growth and decay, with proposed cycles in biological productivity and diversity. The relative positions in this cycle of the four estuaries of this study are indicated on the sub-areal development line: Atchafalaya Bay (AB), Barataria Bay (BB), Fourleague Bay (FB) and Lake Pontchartrain (LP). Modified from Gagliano and VanBeek (1975).

TABLE I

COMPARISON OF THE PHYSICAL CHARACTERISTICS OF THE ATCHAFALAYA BAY DELTA (AB), FOURLEAGUE BAY (FB), BARATARIA BAY (BB), AND LAKE PONTCHARTRAIN (LP)

	AB	FB	BB	LP
Wetland area (ha)[a]	1,200	50,000	400,000	750,000
Approximate water:wetland ratio[a]	12	0.5	2.0	5.0
Source of freshwater	river	river	rainfall	river
Average freshwater input[b]				
cms	7,000	425		370
cm/yr			146	
Salinity				
Average	0	6	15	5
Range	0-1.5	0-22	0-32	0-27
Temperature				
Average (°C)	18	23	21	21
Range (°C)	7-31	10-31	5-31	5-30
Secchi disk depth				
Average	8	20	76	30
Range	5-30	5-50	9-150	5-150
Average depth (m)	1.2	1.5	1.5	3.0

[a] based on Chabreck (1972) and map measurements by authors.
[b] value is cms for river discharge and cm/yr for rainfall.

and the areal extent of the different marsh types in each estuary (Fig. 1). The major source of freshwater to the Atchafalaya Bay delta, Fourleague Bay, and Lake Pontchartrain is from river discharge and as a consequence these systems have lower yearly averages for salinity and remain fresh longer in the spring than Barataria Bay (Fig. 4). The salinity regime of Fourleague Bay was more like Barataria Bay than the Atchafalaya Bay delta or Lake Pontchartrain because of low river discharge during 1981. Lake Pontchartrain and the Atchafalaya Bay delta have the largest relative extent of fresh wetland systems, followed by Fourleague Bay and then Barataria. Turbidity values are also related to freshwater discharge with high turbidity (low secchi disk values) in the Atchafalaya Bay delta and Fourleague Bay (Table 1). Despite differences in freshwater input water temperature differences among the systems are slight (Fig. 4), probably because all of these systems are shallow and easily heated by solar inputs. Each of these systems is also in a different stage of the delta cycle (Fig. 3) which affects the physiography of the estuary. The Atchafalaya Bay delta represents an area which is currently building a delta, while the other three are abandoned deltas in the process of deterioration. One consequence of their stage in the delta cycle is the difference in wetland to open water ratio (Table 1). The Atchafalaya Bay delta has very little wetland relative to open water because it is in the initial stages of development while Lake Pontchartrain has a large ratio because it is the most advanced (hence deteriorated) system in the delta cycle. Fourleague Bay and Barataria Bay have lower water to wetland ratio's because they are in the intermediate stage of the delta cycle. The ratio for Fourleague Bay is not as large as anticipated on the basis of its position in the cycle relative to the other systems. Baumann and Adams (1981) have shown that the marshes in this system are no longer deteriorating and attribute this to the influx of sediment laden water from the Atchafalaya River.

METHODS AND DEFINITIONS

Data Collection

The data reported on in this chapter are from a variety of studies in the individual systems (Suttkus et al. 1954, Davis et al. 1970, Fontenot and Rogillio 1970, Perret 1971, Wagner 1973, Juneau 1975, Rogillio 1975, Hoese 1976, Tarver and Savoie 1976, Barrett et al. 1978, Chambers 1980, Thompson and Verret 1980, Guillory 1982, Thompson unpubl.). For comparison of community structure and abundance stations of similar habitat in each system were selected along a salinity transition

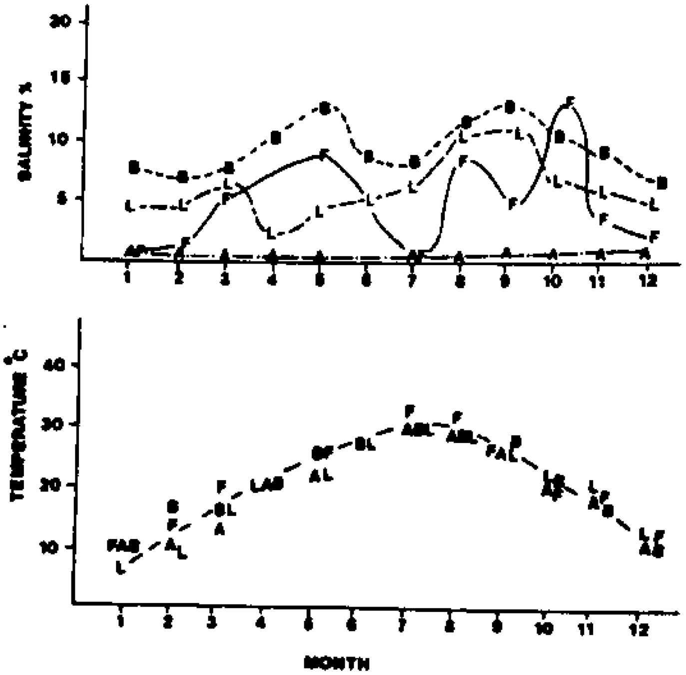


Fig. 4. Yearly cycle of salinity and temperature averaged over all stations by month. A = Atchafalaya delta. F = Fourleague Bay. B = Barataria Bay. L = Lake Pontchartrain.

from fresh to saline (Fig. 1). Data from trawling studies were used because they are quantitative and could be adjusted to eliminate differences in effort between studies. All data were adjusted to a per square meter basis. Data for the Atchafalaya Bay delta and Fourleague Bay systems are part of a current investigation on use of these areas by fish populations. The Atchafalaya Bay delta has two stations because there is essentially no salinity gradient within the delta region. Fourleague Bay has three stations. For the Barataria Bay system, stations 1, 2, and 3 are from Chambers (1980) and correspond to his stations 4, 12, and 15; Stations 4 and 5 are from Barrett et al. (1978) and correspond to stations 1 and 2 of his study. Stations 1, 2, and 3 in Lake Pontchartrain are from Thompson and Verret (1980) and correspond to stations 1,9, and 6; stations 4 and 5 are from Barrett et al. (1978) and correspond to stations 2 and 4. The most recent study is the Atchafalaya study (1981-1982). Data in the other studies were taken either 1976 or 1978.

Measures of Community Structure

Simple measures of community structure are the total number of species which have been recorded for the ecosystem and the species which dominate the community. The relative number of individuals per unit area and the average number of species per sample are also an useful measure of community structure. To aid in understanding species occurrence patterns each species was classified into one of four ecological affinity groups (after McHugh 1967):

Freshwater (FW) - affinities primarily with freshwater. Spawn in freshwater (below 0.5 ppt); have slight to moderate salinity tolerances.

Estuarine (ES) - spends most of life cycle within the estuary. Generally has greatest spawning in the estuary. Wide salinity tolerances.

Estuarine-Marine (ESM) - time spent in estuary is primarily as young of the year. Spawn in either nearshore or offshore marine habitat. Very wide salinity tolerances; species often referred to as 'estuarine dependent.

Marine (MA) - spend most of life in nearshore or offshore marine habitat; generally intolerant of low salinity conditions; spawns in marine habitat.

The use of the estuarine area by these four groups is summarized in Figure 5. The Shannon-Weiner (H) index was used as a measure of ichthyofaunal diversity (Pielou 1975). The Shannon-Weiner index increases as the number of species increases and the equitability of species distribution increases and has a theoretical maximum of around 4 (Margalef 1968). Species richness (D), which relates the total number of species to the total abundance, was estimated using Margalef's index (Margalef 1968). Evenness was estimated by Pielou's index (J), which is the ratio of the Shannon-Weiner index for the total number species and is equal to one when all species are found in equal abundance (Pielou 1975). All

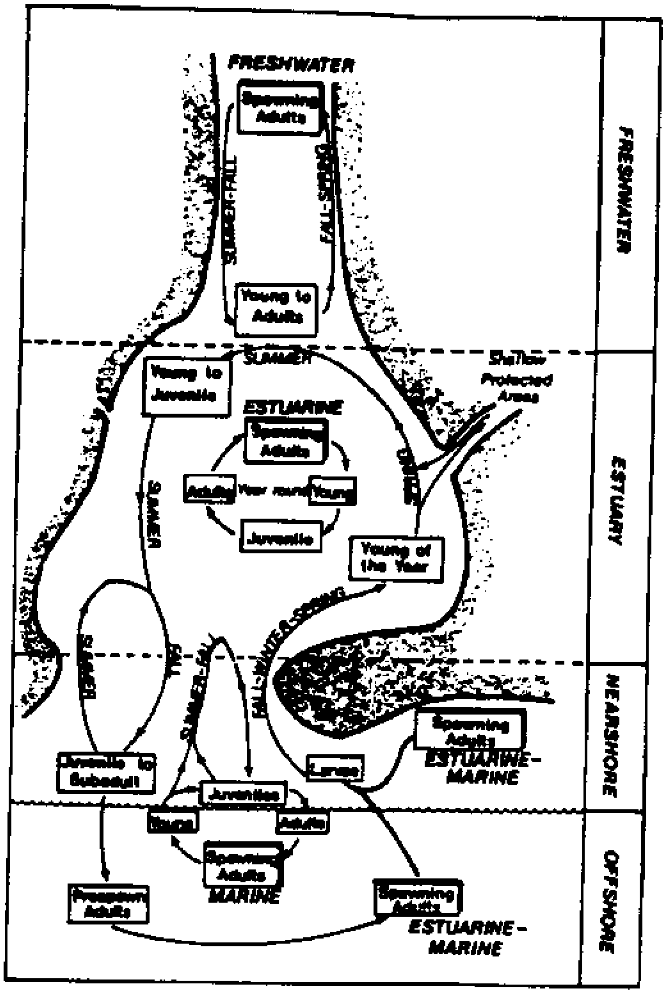


Fig. 5. Schematic representation of the four major types of fish migrations in Louisiana's estuaries. See text for description of ecological affinity groups.

indices were calculated for each station every month, then averaged over months to look at spatial trends or averaged over stations to look at seasonal trends. Because these indices are based on trawl samples and do not represent the entire estuarine fish community values are low. Studies of trawl caught fish in other areas report values in the same range as this study (0-3). (See Thompson and Verret 1980 for a discussion). We believe these samples represent the basic aspects of the demersal fish community structure in these estuaries.

RESULTS AND DISCUSSION

Species that use Louisiana Estuaries

A total of 208 species in 69 families have been recorded from these estuaries (Table 2), but 7-10 spe-

TABLE 2

COMPARISON OF SPECIES OCCURRENCE AND ECOLOGICAL AFFINITIES IN ATCHAFALAYA BAY DELTA (AB), FOURLEAGUE BAY (FB), BARATARIA BAY (BB), AND LAKE PONTCHARTRAIN (LP).

FISH SPECIES	LP[1]	BB[2]	AB[3]	FB[3]	ECOL. AFFIN.
Carcharhinus leucas	X	X	X	X	MA
Rhizoprionodon terraenovae		X			MA
Pristis pectinata	X	X			MA
Dasyatis americana	X	X			MA
D. sabina	X	X	X	X	MA
D. sayi	X				MA
Rhinoptera bonasus	X				MA
Acipenser oxyrhynchus	X	X			FV
Scaphirhynchus platorhynchus	X				FV
Polyodon spathula	X				FV
Lepisosteus oculatus	X	X	X	X	FV
L. osseus	X	X	X		FV
L. spatula	X	X	X	X	FV
Amia calva	X	X			FV
Elops saurus	X	X	X	X	ESM
Megalops atlanticus	X	X			ESM
Albula vulpes				X	MA
Anguilla rostrata	X	X	X	X	MA
Congrina flava		X			MA
Paraconger caudilimbatus		X			MA
Gordiichthys irretitus		X			MA
Myrophis punctatus	X	X	X	X	MA
Ophichthus gomesi		X		X	MA
O. ocellatus		X			MA
Alosa alabamae	X	X			FV
A. chrysochloris	X	X	X	X	FV
Brevoortia patronus	X	X	X	X	ESM
Dorosoma cepedianum	X	X	X	X	FV
D. petenense	X	X	X	X	FV
Harengula jaguana	X	X		X	MA
Opisthonema oglinum	X	X			MA
Anchoa cubana		X			MA
A. hepsetus	X	X		X	MA
A. lyolepis	X	X			MA
A. mitchilli	X	X	X	X	ESM
Esox niger	X	X			FV
Synodus foetens	X	X		X	MA
Cyprinus carpio	X		X		FV
Hybopsis meeki			X		FV
Notemigonus crysoleucas	X	X	X		FV
Notropis blennius			X		FV
N. emiliae	X		X		FV
N. venustus	X				FV
Carpiodes carpio	X				FV
Ictiobus bubalus	X		X		FV
I. niger	X				FV
Arius felis	X	X	X	X	ESM
Bagre marinus	X	X	X	X	ESM
Ictalurus furcatus	X	X	X	X	FV
I. melas	X				FV
I. natalis	X		X		FV
I. punctatus	X	X	X	X	FV
Noturus funebris			X		FV
N. gyrinus			X		FV
Pylodictis olivaris	X	X	X		FV
Aphredoderus sayanus	X	X	X		FV
Opsanus beta	X	X		X	MA
O. pardus		X			MA
Porichthys plectrodon	X	X	X	X	MA
Gobiesox strumosus	X	X		X	ESM
Antennarius radiosus		X			MA
Histrio histrio		X			MA
Ogcocephalus radiatus		X			MA
Urophycis cirrata		X			MA
U. floridana	X	X			MA
U. regia		X			MA
Gunterichthys longipenis		X			MA
Lepophidium graellsi		X			MA
Ophidion welshi		X			MA
Cypselurus heterurus		X			MA
Hirundichthys affinis		X			MA
H. rondeletii		X			MA

Table 2. (continued)

FISH SPECIES	LP[1]	BB[2]	AB[3]	FB[3]	ECOL. AFFIN
Hyporhamphus unifasciatus	X	X			MA
Prognichthys gibbifrons		X			MA
Strongylura marina	X	X	X	X	ESM
Adinia xenica	X	X			ES
Cyprinodon variegatus	X	X	X	X	ES
Fundulus chrysotus	X		X		FW
F. grandis	X	X	X	X	ES
F. jenkinsi	X	X	X	X	ES
F. pulvereus	X	X	X		ES
F. similis	X	X		X	ES
Lucania parva	X	X	X	X	ES
Gambusia affinis	X	X	X	X	FW
Heterandria formosa	X	X	X	X	FW
Poecilia latipinna	X	X	X	X	FW
Labidesthes sicculus	X				FW
Membras martinica	X	X	X	X	ES
Menidia beryllina	X	X	X	X	ES
Hippocampus erectus		X			MA
H. zosterae		X			MA
Syngnathus floridae	X	X			ESM
S. louisianae	X	X		X	ESM
S. scovelli	X	X	X	X	ES
Morone chrysops	X		X		FW
M. mississippiensis	X	X	X		FW
M. saxatilis	X	X	X		FW
Centropristis philadelphica	X	X		X	MA
Centrarchus macropterus	X				FW
Elassoma zonatum	X	X			FW
Lepomis cyanellus	X				FW
L. gulosus	X	X			FW
L. humilis	X	X			FW
L. macrochirus	X	X	X		FW
L. marginatus		X			FW
L. megalotis	X				FW
L. microlophus	X	X	X		FW
L. punctatus	X	X	X	X	FW
L. symmetricus	X				FW
Micropterus salmoides	X	X	X		FW
Pomoxis annularis		X			FW
P. nigromaculatus	X	X			FW
Stizostedion canadense	X				FW
Pomatomus saltatrix		X		X	MA
Rachycentron canadum		X			MA
Echeneis naucrates	X				MA
Remora remora		X			MA
Alectis ciliaris		X			MA
Caranx crysos		X			MA
C. hippos	X	X	X	X	MA
C. latus		X			MA
Chloroscombrus chrysurus	X	X		X	MA
Hemicaranx amblyrhynchus	X			X	MA
Oligoplites saurus	X	X		X	ESM
Selene setapinnis	X	X		X	MA
S. vomer	X	X		X	MA
Trachinotus carolinus	X	X		X	MA
T. falcatus		X			MA
Trachurus lathami		X			MA
Coryphaena hippurus		X		X	MA
Lutjanus apodus		X			MA
L. griseus	X	X			MA
L. synagris		X			MA
Lobotes surinamensis	X	X			MA
Diapterus plumieri		X			MA
Eucinostomus argenteus	X	X	X	X	ESM
E. gula		X			MA
Haemulon sp.	X				MA
Orthopristis chrysoptera	X	X			MA
Archosargus probatocephalus	X	X	X	X	ESM
Lagodon rhomboides	X	X	X	X	ES
Aplodinotus grunniens	X	X	X		FW
Bairdiella chrysoura	X	X	X	X	ESM
Cynoscion arenarius	X	X	X	X	ESM
C. nebulosus	X	X	X	X	ESM
C. nothus	X	X			MA
Larimus fasciatus	X	X			MA
Leiostomus xanthurus	X	X	X	X	ESM
Menticirrhus americanus	X	X		X	MA
M. littoralis	X	X			MA
M. saxatilis		X			MA
Micropogonias undulatus	X	X	X	X	ESM
Pogonias cromis	X	X	X	X	ESM
Sciaenops ocellatus	X	X	X	X	ESM
Stellifer lanceolatus	X	X	X	X	ESM
Chaetodipterus faber	X	X		X	ESM
Lachnolaimus maximus	X				MA
Mugil cephalus	X	X	X	X	ESM
M. curema		X			MA
Sphyraena barracuda		X			MA
S. borealis		X			MA
S. guachancho	X	X			MA
Polydactylus octonemus	X	X		X	MA
Astroscopus y-graecum	X	X		X	MA
Chasmodes bosquianus	X				MA
Hypleurochilus geminatus		X			MA
Hypsoblennius hentzi	X				MA
H. ionthas	X	X		X	MA
Dormitator maculatus	X	X	X	X	ES
Eleotris pisonis	X	X	X		ES
Erotelis smaragdus		X			MA
Bathygobius soporator		X			MA
Evorthodus lyricus	X	X	X		ES
Gobioides broussoneti	X	X		X	ES
Gobionellus boleosoma	X	X	X	X	ES
G. hastatus	X	X	X	X	ES
G. shufeldti	X	X	X		ES
Gobiosoma bosci	X	X	X	X	ES
G. robustum		X			ES
Microgobius gulosus	X	X		X	ES
M. thalassinus	X	X		X	ES
Microdesmus longipinnis	X	X			MA
Trichiurus lepturus	X	X		X	MA
Scomberomorus cavalla		X			MA
S. maculatus	X	X		X	MA
Peprilus alepidotus	X	X	X	X	MA
P. burti	X	X		X	MA
Prionotus roseus		X			MA
P. rubio	X	X			MA
P. scitulus	X	X			MA
P. tribulus	X	X	X	X	MA
Ancylopsetta dilecta		X			MA
A. quadrocellata		X			MA
Citharichthys spilopterus	X	X	X	X	ESM
Etropus crossotus	X	X		X	MA
Paralichthys albigutta	X	X			MA
P. lethostigma	X	X	X	X	ESM
Achirus lineatus	X	X	X	X	ESM
Trinectes maculatus	X	X	X	X	ES
Symphurus plagiusa	X	X	X	X	MA
Aluterus schoepfi		X			MA
A. scriptus		X			MA
Canthidermis sufflamen		X			MA
Monacanthus hispidus	X	X			MA
Lagocephalus laevigatus		X			MA
Sphoeroides parvus	X	X		X	MA
Chilomycterus schoepfi	X	X			MA
Mola mola		X			MA
Number of Species	149	97	174	77	84

[1] Based on Suttkus et al. (1954), Davis et al. (1970), Fontenot and Rogillio (1970), Perret (1971), Rogillio (1975), Tarver and Savoie (1976), Barrett et al. (1978), Thompson and Verret (1980).

[2] Based on Perret (1971), Wagner (1973), Barrett et al. (1978), Guillory (1982), Chambers (1980).

[3] Based on Juneau (1975), Reese (1976), Thompson (unpubl.).

cies dominate the community and constitute between 90-98% of the total catch (Table 3). This dominance by a few groups is also shown in that of the 69 families 9 (13%) contribute 84 species (40.4%). The dominant families in these estuaries and the number of species they contribute are: Scianidae (14 species), Centrarchidae (14), Carangidae (12), Gobiidae (10), Cyprinodontidae (8), Clupeidae (7), Ictaluridae (7), Cyprinidae (6), Bothidae (6). Absolute ranking as first or second varies from year to year, but the top four or five species (Anchoa mitchilli, Micropogonias undulatus, Cynoscion arenarius, Brevoortia patronus, and Arius felis) are estuarine-marine forms common to most Louisiana estuaries. Differences in salinity regime are usually reflected in the species ranked 5-10. The freshwater nature of the

TABLE 5

TOP TEN SPECIES IN THE ATCHAFALAYA BAY DELTA (AB), FOURLEAGUE BAY (FB), BARATARIA BAY (BB) AND LAKE PONTCHARTRAIN (LP) BASED ON TOTAL NUMBER OF INDIVIDUALS CAUGHT

	AB		FB		BB		LP	
	No.	Rank	No.	Rank	No.	Rank	No.	Rank
Anchoa mitchilli	1563	2	154405	1	154417	1	48485	1
Micropogonias undulatus	1287	3	11483	2	10056	2	4923	2
Cynoscion arenarius	757	5	3405	5	729	7	195	7
Brevoortia patronus			5544	3	1901	4	1044	5
Arius felis			1436	7	1020	6	1235	4
Chloroscombrus chrysurus			381	10	9977	3	1307	3
Leiostomus xanthurus					1491	5	467	6
Ictalurus furcatus	11735	1	1763	6				
Bagre marinus			554	8	489	10		
Trinectes maculatus	893	4	399	9				
Ictalurus punctatus	599	6						
Stellifer lanceolatus	260	7						
Citharichthys spilopterus	130	8						
Aplodinotus grunniens	124	9						
Paralichthys lethostigma	18	10						
Dorosoma petenense			4708	4				
Polydactylus octonemus					725	8		
Anchoa hepsetus					694	9		
Sphoeroides parvus							150	8
Symphurus plagiusa							137	9
Peprilus burti							91	10
TOP TEN TOTAL NUMBER	17366		184078		191306		58309	
TOTAL NUMBER CAPTURED	17507		186269		193791		58876	

Atchafalaya Bay delta is reflected by the presence of Ictalurus furcatus in the top ten, while the more saline nature of Barataria Bay system is shown by the presence of Polydactylus octonemus and Anchoa hepsetus in the top ten. The ecological affinity distribution based on the total number of species that occur in the estuary reflects this same pattern (Table 1). Barataria Bay, which is the most saline system, has 46 unique marine species. Lake Pontchartrain is intermediate in salinity regime and has fewer marine species than Barataria Bay, and the Atchafalaya Bay delta has the highest number of freshwater forms (Table 1).

The estuaries of the Mississippi River deltaic plain have been influenced by the presence of large amounts of freshwater throughout their development, and have vast expanses of brackish and fresh marsh, as well as saltmarsh. It should not be surprising, given their evolutionary history, that many species are successful in a wide salinity range. The deltaic plain probably has local stocks or populations of fish species that are specially adapted to exist in these low salinity regimes. The result of this adaptation is a fish fauna with some unusual characteristics. One aspect of the deltaic plain fish fauna that differs from many of the more classical estuaries is the component of almost resident freshwater forms. Three of the major families (Centrarchidae, Ictaluridae and the Cyprinidae) are generally considered to be freshwater families. For example in Lake Pontchartrain, bass and sunfishes (family Centrarchidae) are commonly found in the shallow protected areas of the entire system. In Lake Pontchartrain and the Atchafalaya Bay delta some even spawn. Another important difference is the presence of many estuarine-marine forms in completely freshwater. Larvae of Brevoortia patronus, gulf menhaden, are commonly found in fresh marshes; our studies have found this species in the Atchafalaya Bay delta and upstream in the river. The occurrence of freshwater forms in saline regions and estuarine-marine forms in freshwater regions has resulted in some interesting and unusual species combinations in our samples. For example, Notropis blennius, a freshwater minnow, was taken along with a huge school of Brevoortia patronus, the gulf menhaden. The freshwater drum, Aplodinotus grunniens, is a common member of the family Sciaenidae, and often occurs with other estuarine-marine drums such as Sciaenops ocellatus, Micropogonias undulatus, Stellifer lanceolatus, and Cynoscion arenarius. Numerous other examples could be given.

Spatial and Temporal Patterns of Community Structure

Species diversity varies with space and time and very few species are found during the entire year or throughout the entire estuary at any one time. The nekton community of these estuaries shows complex ecological properties with recognizable patterns of species composition and abundance and resource partitioning. In this section we will first discuss locations of particular importance and then temporal sequences of use.

Spatial Patterns of Community Structure. The fish community structure of Louisiana estuaries is dominated by estuarine marine species that use these areas as nursery grounds. The percentage of estuarine-marine species captured in an average sample is high, ranging from a low of 35% in the Atchafalaya Bay delta region to a high of 72% in Lake Pontchartrain (Fig. 6). Resident species, the estuarine forms, are a very small part of the total number of species (Table 1). Of the 208 species recorded from these estuaries only 23 (11%0 are estuarine forms, predominantly of the Cyprinodontidae and Gobiidae families. Joseph (1973) characterized nursery areas as places that 1) are physiologically suitable in terms of physical and chemical features, 2) provide some degree of protection from predators and 3) provide an abundant food supply. Marsh tidal creeks have higher biomass catches (Day et al. 1982). Smaller average size, and higher species richness (Wagner

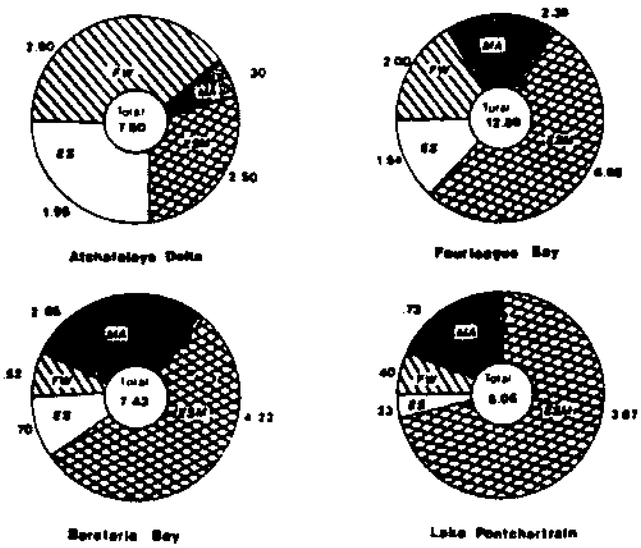
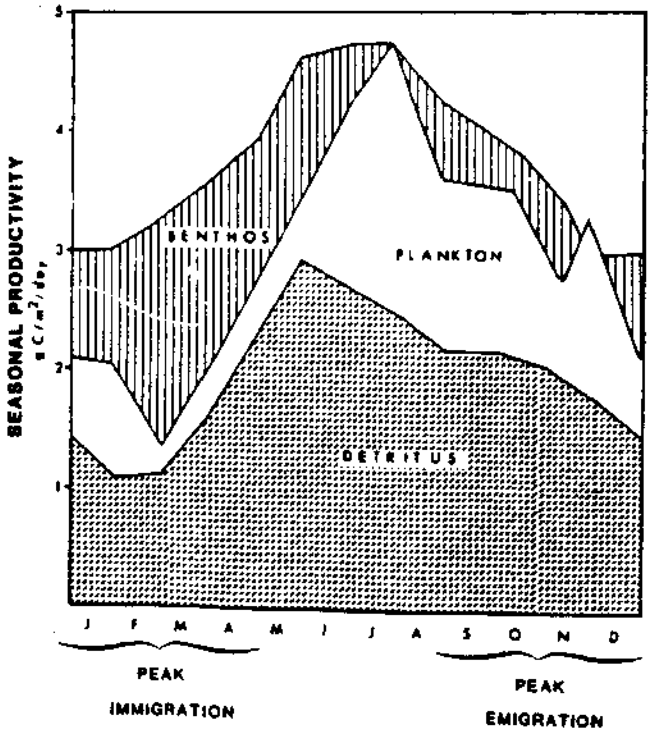


Fig 6. Comparision of the average occurrence of the four ecological affinity groups among estuaries. Number in small circle in middle is the average number of species per trawl. Numbers on outside of large larger circle are the average number of species the corresponding ecological affinity group.

1973, Chambers 1980, Thompson and Verret 1980, Miller and Guillory 1981) than adjacent open water areas indicating the importance of these areas as nursery grounds. Migration to these nursery areas is energetically demanding. However, these areas apparently provide enough predator protection and food to compensate for the expense. Tidal creeks are characterized by high turbidity levels which may provide protection from predators because predation on fish is essentially dependent on sight for capture success (Nikolsky 1963, Hyatt 1979). Our studies have shown few large piscivorous fish in these areas relative to abundance of larval and juvenile fish. Rapid exploitation of a temporarily abundant food supply has been hypothesized as a major determinant in the evolution of migratory pattern (Nikolsky 1963, Cushing 1975, Northcoate 1978). Food items, such as nematodes, amphipods and other meiofauna, often have their highest densities in these areas (Sikora and Sikora 1982b, Philomena 1983) and, in general, the migration of larval or post-larval forms of estuarine-marine species into the estuarine system is timed to occur just before peak abundance of food supplies (Fig. 7). Many Louisiana estuarine-marine species enter estuarine areas in late winter or early spring just prior to the peak standing crop of food items. For example B. patronus reach their shallow marsh feeding areas in early spring at the beginning of the growing season when water temperatures and plankton populations are increasing and other conditions for rapid growth and survival are better. Even though food availability is high, because of the unpredictability of food resource composition, it would not be advantageous for estuarine species to reduce competition by becoming specialized in food type. Competition has adjusted the migration timing of closely related species within these areas and the immigration and peak occurrence sequence seems to make exploitation of food sources optimal by reducing direct competition. Peak occurrence time varies among estuaries, but in general, within the major groups (i.e., drums, flatfishes) where feeding habits are most similar, peak occurrence of species do not greatly overlap (Fig. 8). Using the occurrence of species in the Atchafalaya deltas as an example, L. xanthurus and M. undulatus both use shallow areas as nursery areas and have similar diets (Levine 1980), but the peak abundance of L. xanthurus is in early spring, while M. undulatus has two peaks; a much larger fall-early winter peak and a second smaller peak in the spring. Migration out of these areas is usually size related, with the larger individuals leaving first (Herke 1977). Exhaustion of food supplies would occur if they did not disperse and emigration of the larger individuals, which are less susceptible to predation, leaves the marsh areas as a nursery for the smaller juveniles.



Modified from Day et al. (1973)

Fig. 7. Typical seasonal productivity profile of a Louisiana estuary and the relationship to migration of estuarine-marine forms. Adapted from Day *et al.* 1973.

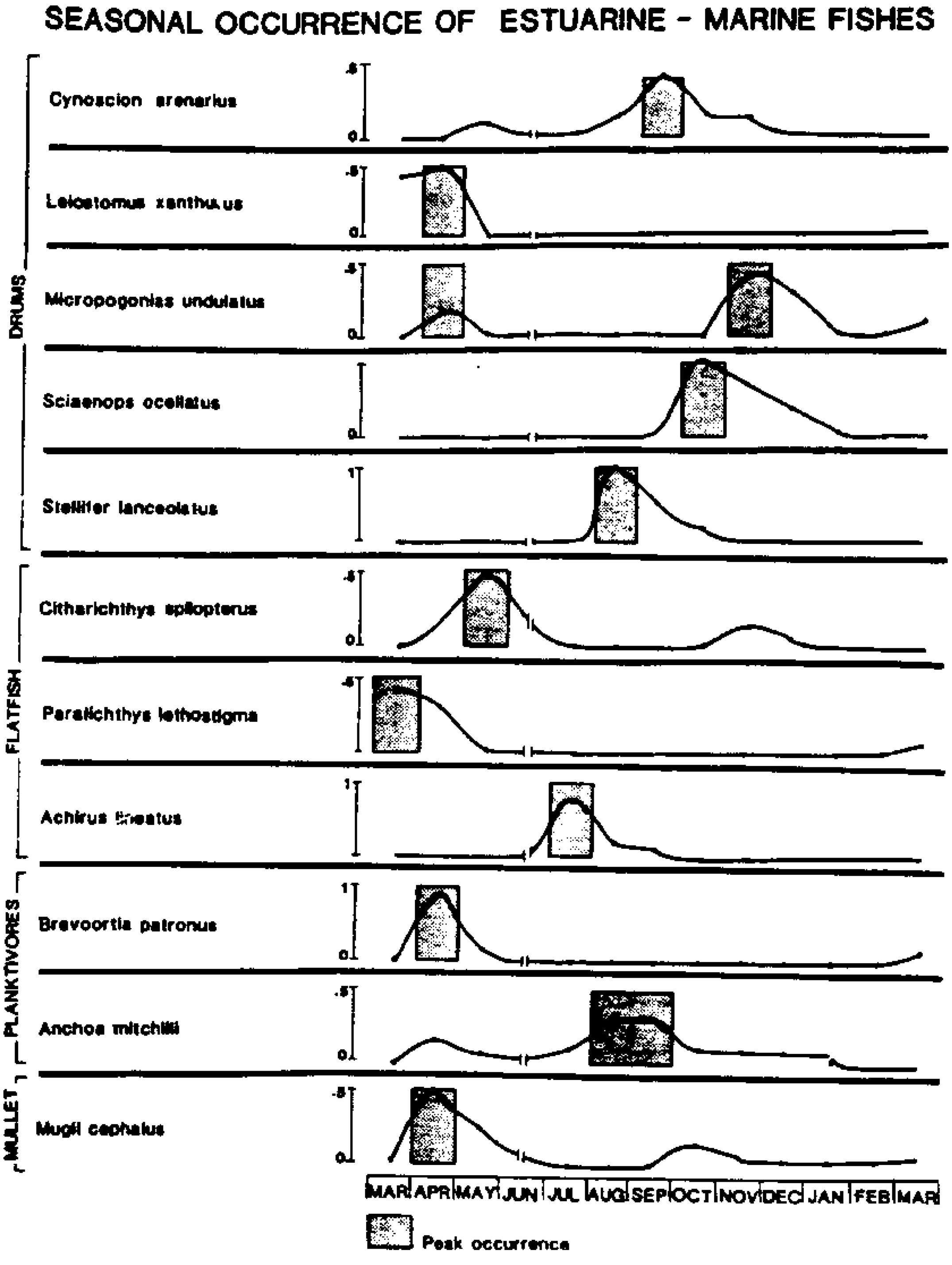


Fig. 8. Seasonal occurrence of some major estuarine-marine forms. Vertical scale is the fraction of yearly total caught during that month. Data includes seines and trawls from the Atchafalaya estuary.

Another region of particular importance to fish community structure is the mid-salinity zone of the estuary. Averaged over the year the number of species in a sample (T), and species richness (D) and species diversity (H) generally have a peak in the mid-salinity zone (Fig. 9). The annual average mid-salinity zone represents an 'interface zone' where all four ecological affinity groups occur at different times of the year. The occurrence of freshwater forms is negatively correlated ($r^2 = -.46$, $p < 0.001$) with salinity, and these forms occur in the 'interface zone' during the low salinity period of the year (Jan.-April). The occurrence of marine forms in positively correlated ($r^2 = .66$, $p < 0.001$) with salinity and they are present in this area during the summer and early fall during high salinity incursions. The use of these areas by estuarine-marine forms is not significantly correlated with salinity, but is related to individual species life history patterns. During their stay in the estuary estuarine-marine forms are broadly distributed within the estuaries occupying different areas at different times of the year. The location within the estuary of this 'interface zone' varies between estuaries and is dependent on the factors which control the salinity. The high inflow of river waters pushes the 'interface zone' for the Fourleague Bay system near the opening to the Gulf. The equivalent zone in Barataria Bay, which has rainfall as its only freshwater input, is further inland at about the geographic middle of the estuary. Lake Pontchartrain, which is intermediate in freshwater inflow, has the equivalent 'interface zone' closer to the opening to the gulf, about a third of the way into the estuary. Salinity in the Atchafalaya delta is maintained at near zero levels by river discharge resulting in a basically freshwater estuary. The Atchafalaya and Lake Pontchartrain systems, which remain fresh for longer in the spring, also have high values for total number of species and species richness in low salinity areas. This high value in the low salinity zone is attributed to the co-occurrence of freshwater and estuarine-marine forms for a longer period of time in these systems because of the extended freshwater period.

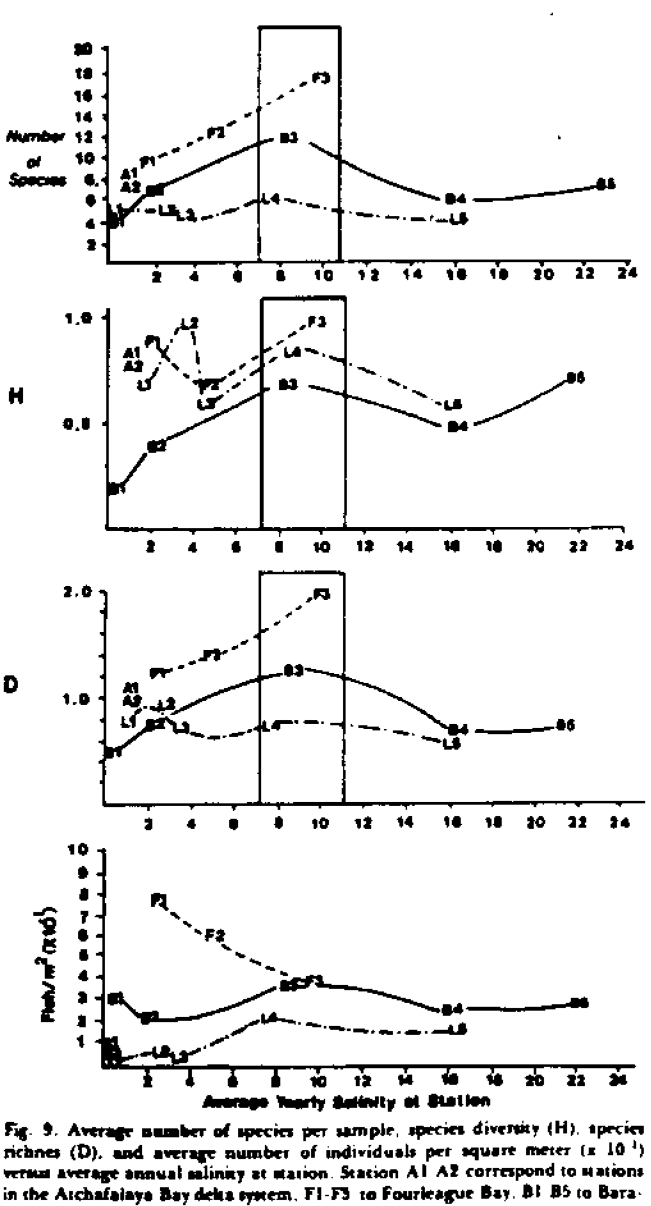


Fig. 9. Average number of species per sample, species diversity (H), species richness (D), and average number of individuals per square meter (x 10^{3}) versus average annual salinity at station. Station A1 A2 correspond to stations in the Atchafalaya Bay delta system, F1-F5 to Fourleague Bay, B1 B5 to Barataria Bay, and L1-L5 to Lake Pontchartrain (see Fig. 1)

The distribution of the number of individuals per square meter (N) showed no trend with salinity. This was attributed to the admixture of adults and juveniles at different times of the year in the different salinity zones which results in a fairly even distribution of number of individuals.

Temporal Patterns of Community Structure. The average values of species per sample (T), number of individuals per square meter (N), species diversity (H), and species richness (D) are different among the estuaries, but in all cases did not change significantly over the coarse of the year (Fig. 10) because the migration patterns of the fish result in 'species compensation' or sequential replacement of one species by another. Seasonally four major migrations (Fig. 5) occur among the fishes of Louisiana's estuaries:

1) an early spring inshore feeding migration of post larval estuarine-marine species using the area as a nursery ground. These species tend to enter the estuary as larvae in winter and early spring (Jan.-Mar.), spend the summer months in shallow marsh areas and move

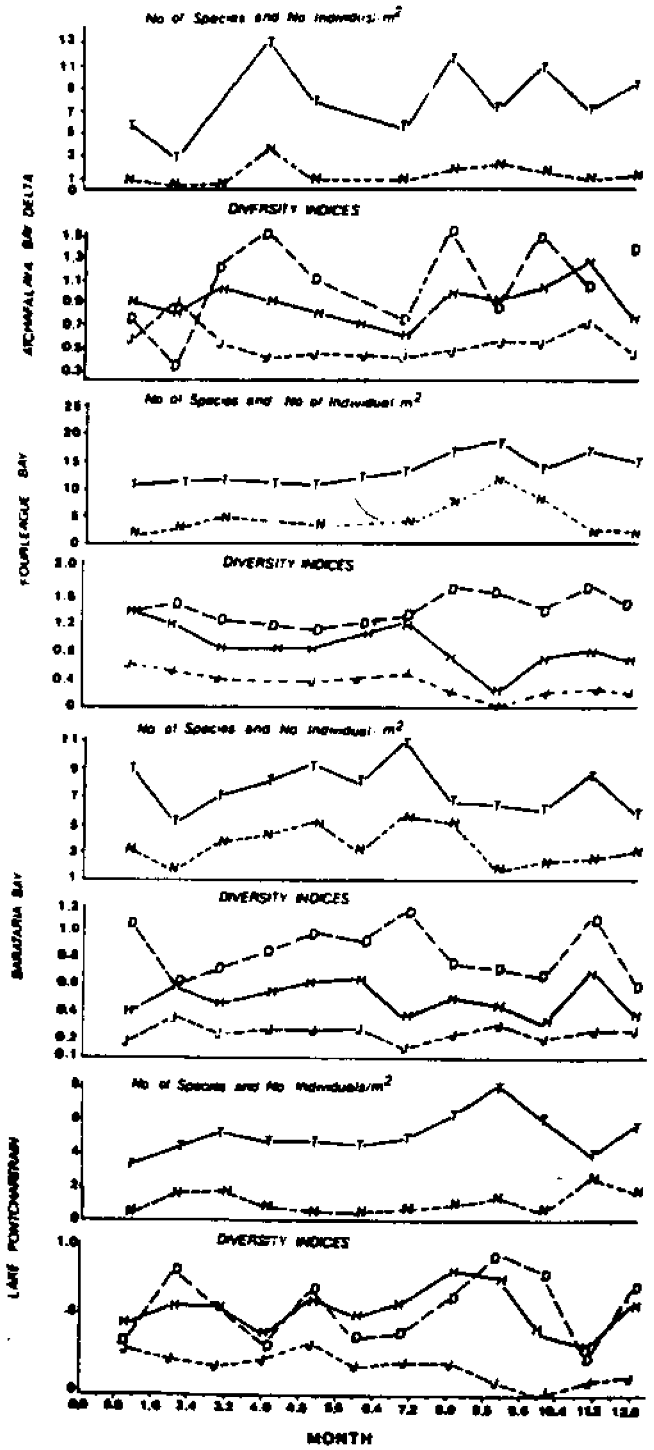


Fig. 10. Average number of species per sample (T), average number of individuals per square meter (x 10^{1}) (N), species diversity (H), species richness (D), and species evenness (J) averaged over all station by month.

back into the open bay on their way to the Gulf in the fall (Sept.-Nov.).

2) a mid summer to early fall inshore migration by juveniles and sub-adults of marine species and sub-adults of some estuarine-marine species.

3) a late fall offshore overwintering migration by juveniles of estuarine-marine species. A combination of physiological readiness and changes in day length and temperature is probably important in initiating the offshore migration of fish in the estuary.

4) a late fall early spring downstream migration of freshwater forms into the upper reaches of the estuary.

Seasonal extension of the freshwater community into low salinity areas often coincides with the offshore emigration of juvenile estuarine-marine forms in the fall. The reverse upriver movement of certain freshwater forms and inshore movement of estuarine-marine forms occurs in the spring.

The migration pattern is similar in all of the estuaries but the timing and the extent of mixing of the different forms differs among estuaries because of salinity regime (Fig. 11). The fish population of Atchafalaya Bay delta system is dominated by the estuarine-marine forms which move into the shallow areas of this system for nursery grounds, and by freshwater adults and juvenile which use this area as a feeding and nursery ground. Because this system is fresh year round these forms co-occur for a long time, with maximum overlap occurring in the late spring after peak river discharge. Marine forms which usually cannot tolerate freshwater, only occasionally wander into the delta in late summer with low salinity waters. The fish population of Fourleague Bay is also dominated by estuarine-marine forms, but has strong representation by both marine and freshwater forms. These forms are well represented in this estuary because of the large variation in salinity gradient caused by seasonal changes in river discharge. Freshwater forms use the upper end of the estuary during peak discharge. Marine forms enter the lower portion of the estuary during high salinity periods in late summer and fall. Barataria Bay, which is a more saline system, has predominantly estuarine-marine and marine forms, with a regular but small number of freshwater forms which occur in the winter. Lake Pontchartrain is almost completely estuarine-marine species, but has a freshwater component which is small in number of species, but often represents a large number of individuals.

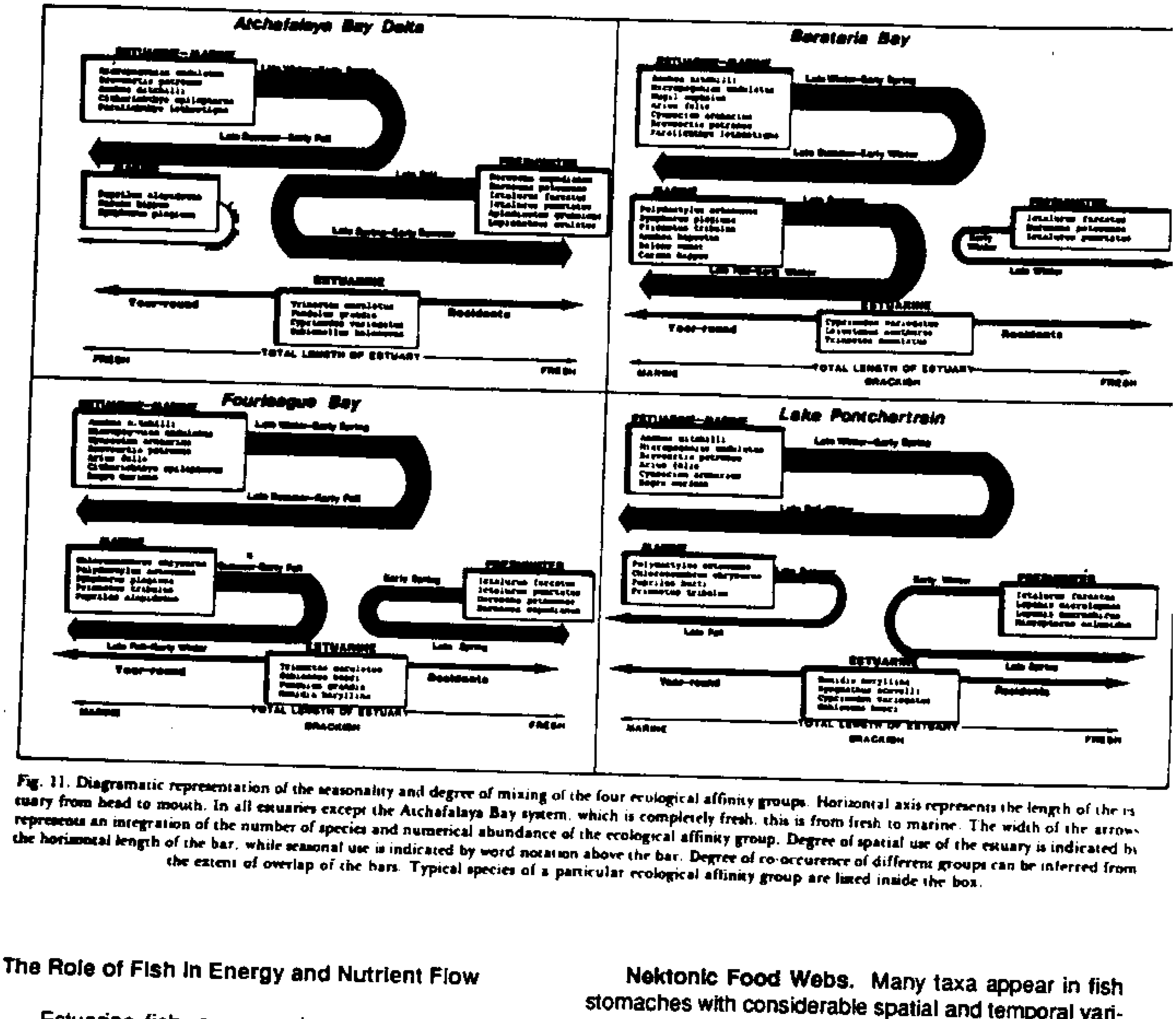


Fig. 11. Diagramatic representation of the seasonality and degree of mixing of the four ecological affinity groups. Horizontal axis represents the length of the estuary from head to mouth. In all estuaries except the Atchafalaya Bay system, which is completely fresh, this is from fresh to marine. The width of the arrows represents an integration of the number of species and numerical abundance of the ecological affinity group. Degree of spatial use of the estuary is indicated by the horizontal length of the bar, while seasonal use is indicated by word notation above the bar. Degree of co-occurence of different groups can be inferred from the extent of overlap of the bars. Typical species of a particular ecological affinity group are listed inside the box.

The Role of Fish in Energy and Nutrient Flow

Estuarine fish, as secondary consumers, can be important in energy and nutrient flow in several ways. Secondary consumers can be stores of nutrients and energy; they can control rates and magnitudes of energy flow through grazing of food sources, and they can, because of their migratory nature, move energy and nutrients across ecosystem boundaries (Yanez-Arancibia and Nugent 1977, Kitchell et al. 1979). One of the first steps in determining the importance of an organism's role in the ecosystem is the study of food habits because diet selection determines the actual paths of energy flow and nutrient cycling (Ellis et al. 1976). This section first presents an overview of the relationship of fish to the food web of a Louisiana estuary, discusses the energy costs of production and metabolism and then considers evidence for functional roles in energy and nutrient flux.

Nektonic Food Webs. Many taxa appear in fish stomaches with considerable spatial and temporal variation (Darnell 1958, 1961, Fontenot and Rogillio 1970, Rogillio 1975, Levine 1980). Levine (1980) has shown most species exhibit spatial variation in prey items selected. For example, he analyzed the prey items of similar sized M. undulatus from three habitat types within Lake Pontchartrain (Fig. 12) and found variations in prey selection that were correlated with available prey. In the open lake stations where bivalves and mysids were dominant members of the benthic community these were an important component of the food. These two food items were fed upon by about 50% of all croakers examined and constituted 58% of the total food items. In the river mouth stations bivalves were a small portion of the diet (5.5%) and were fed upon by less than 10% of the croaker analyzed. In these areas bivalves were replaced as an important food source by insect larvae; chi-

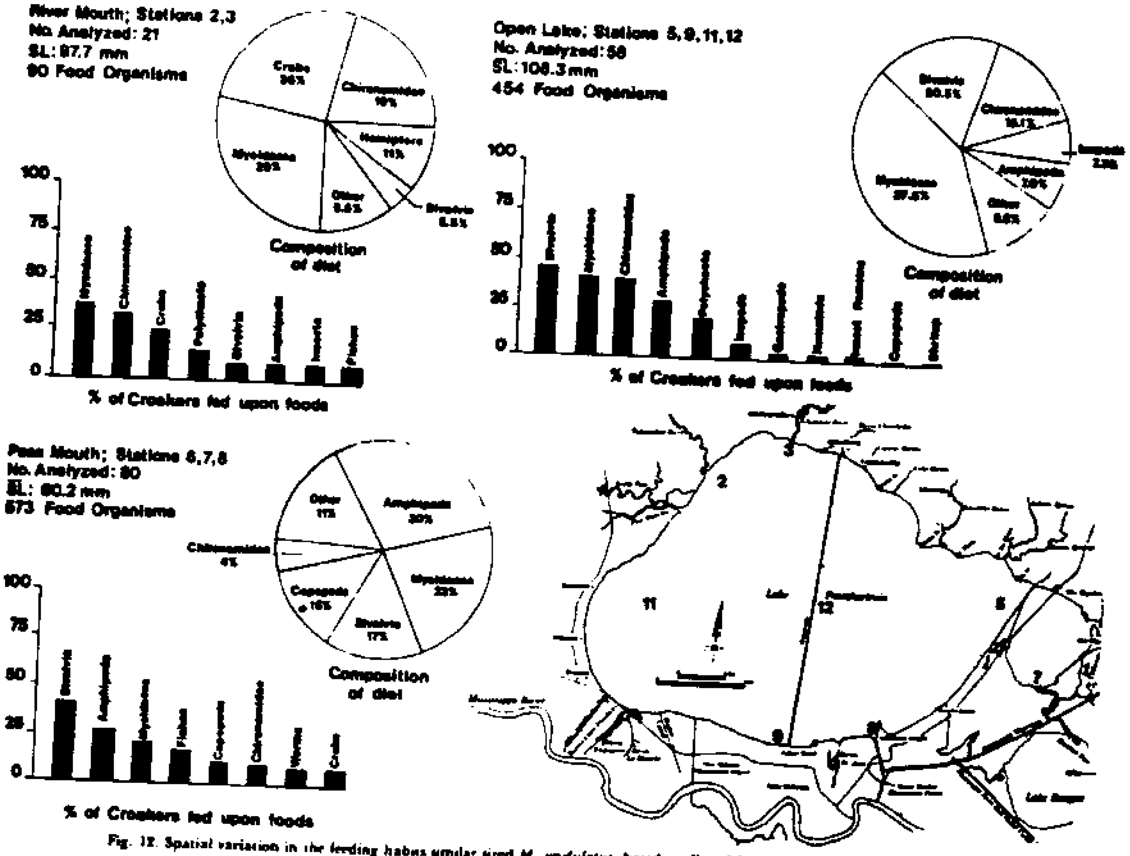


Fig. 12. Spatial variation in the feeding habits similar sized *M. undulatus*, based studies of Lake Pontchartrain. From Levine (1980).

ronomids and hemiptera together were 80% of the total food. In the pass stations mysids and amphipods were the two most frequently taken prey, 30 and 23% while bivalvia represented the third most frequently taken prey (17%). In most fish, feeding selection often also shows progressive changes with growth (ontogenetic changes) which often involves successive specialization upon widely different food taxa, often changing from an omnivorous mid-level feeder to a more specialized higher level carnivore (Levine 1980, Darnell 1961). This is exemplified by M. undulatus (Fig. 13). At small sizes (<56-75 mm) croaker feed primarily on amphipods and copepods. As the croaker grow they increasingly feed on more motile organisms such as crabs and fishes. However even the largest size studied (>151 mm) was not dependent on these food items alone. The use of a wide variety of taxa as food and shifts in feeding selection with growth are characteristics of many species in Louisiana estuaries, especially the forms which dominate the community (Fig. 14). Anchoa mitchilli and B. patronus, the dominant planktivores in these estuaries, both use four of the seven major food types outlined by Darnell (1961). B. patronus in particular shows a distinct change in feeding between larvae-postlarvae and juvenile-adult, changing from predominantly a zooplankton feeder to a detritus feeder, but still feeds on the same four food types. Arius felis, the dominant catfish, feeds predominantly on benthic organisms, and takes a greater proportion of larger prey in the adult form. The fish present in greatest abundance in these systems are omnivorous opportunistic feeders suggesting diet breadth is a critical factor controlling the abundance of a species and that delineation of distinct trophic levels in these fish is not possible (Darnell 1961, Levine 1980). This supports Margalef's (1968) view of feeding behavior in relation to resource availability and fits the expected feeding behavior of organisms in unpredictable environments characterized by high abiotic stress. Feeding behavior is a species characteristic which is formulated during its evolution (Margalef 1968, Ellis et al. 1976). Margalef (1968) predicts the more variable the feeding conditions of the species during its evolution the greater the variety of foods eaten and that selection for a particular feeding habit should be strong during critical periods in the fishes life history. Healy (1982) has suggested that the range of feeding specificity in salmon is inversely related to the

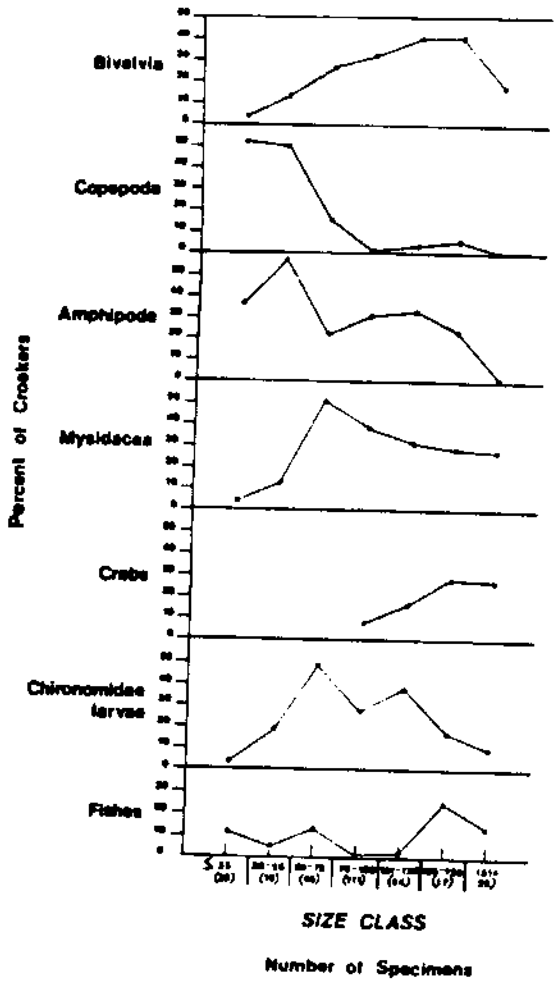


Fig. 15 Ontogenetic changes in feeding habits of M. undulatus, based studies of Lake Pontchartrain. From Levine (1980)

degree of estuarine dependance. The selection for omnivorous feeding in fishes dependent on the estuary for a nursery ground is a result of the unpredictability of food resources which vary considerably both temporally (year to year) as well as spatially (with salinity) within the estuary (Sikora and Sikora 1982b, Barrett et al. 1978). Wide variations in salinity and food supplies during the development of different delta complexes may have been a contribution factor to the evaluation of omnivory in deltaic plain fishes. Although many fish use a variety of food sources, most of the energy is transferred through relatively few pathways. Studies on the major food sources (Darnell 1961, Levine 1980) of some of the dominant species, based primarily on Lake Pontchartrain, reveal a basic dependance on detritus and phytoplankton as food sources through two major pathways (Fig. 15): (1) through small benthic meiofauna (copepods, polychaetes, crustacea, nematodes and others), to small bottom dwelling fish (catfish, young drums and flatfish) to large predators and (2) through pelagic copepods, decapods, and mysids, to small fishes (*Anchoa*, *Brevoortia*, young drums) to large predators. These two trophic pathways are not mutually exclusive. Many fish species, such as *A. mitchilli*, *M. undulatus*, and *I. furcatus* eat prey items from both pathways and *A. mitchilli* is also a major food source in the pelagic pathway. The importance of the benthic pathway in linking fishes to productivity is thought to have been previously underestimated partially because of the difficulties associated with estimating food items (Sikora and Sikora 1982a), but also because some fishes classically considered to be planktivores are now known to consume benthic animals. Levine (1980) reported that many of the copepods consumed by pelagic estuarine fish were harpacticods, indicating a previously unsuspected link between the pelagic and benthic systems. Research in the Maniamo estuary on the relationship between primary production and juvenile salmon production led to a similar conclusion (Sibert et al. 1978, Naiman and Sibert 1979).

Energy Costs of Production and Metabolism. There are not many studies of fish production in Louisiana's estuaries but they (Wagner 1973, Hinchee 1977) indicate fish productivity is high. Average values for annual productivity (sum of average daily biomass x growth rate) for two of the dominant species, *B. patronus* and *M. undulatus*, were estimated at 13 and 23 g wet weight/m^2/year respectively (Table 4). Because these estimates are based on averages for all estuaries and fish are not evenly distributed within the estuary production in preferred habitats may be higher. Hinchee (1977) reported an annual production for *B. patronus* in shallow marsh creeks of 14 g wet weight/m^2/year during their 3.5 month stay in this area. These estimates for annual productivity are higher than estimates for other fish in other ecosystems (Gerking 1978, Jorgenson 1979), but on the same order as has been estimated for other species in estuaries (Meredith and Lotrich 1979, Valiela et al. 1977, Warburton 1979). Because of the life history patterns of these fish and the nature of the estuarine system high fish productivity should not be surprising. Several worker (Allen 1951, Mathews 1971, Meredith and Lotrich 1979) have shown the young-of-the-year to be the most productive year class for a given fish species, accounting for up to 78% of the total production. This is due primarily to the high growth rate characteristic of younger year classes. Robertson (1979) has shown that production/biomass ratios are negatively related to the total life expectancy of the organism. Warburton (1979) also found the highest production/biomass ratios in fish

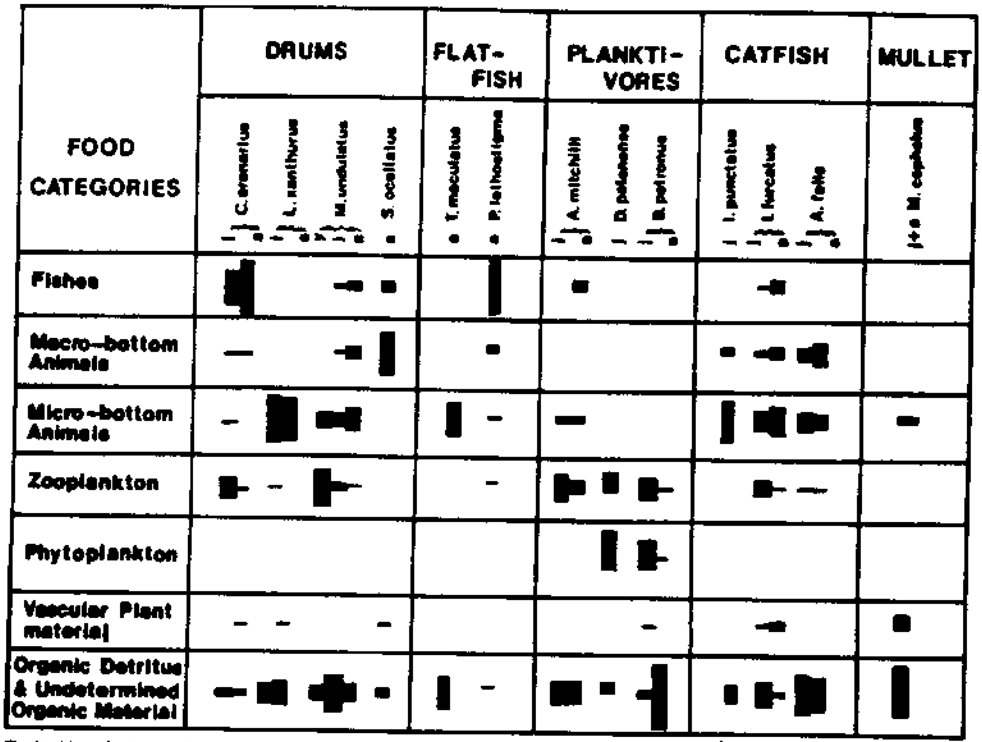


Fig. 14. Major food types of juvenile and adults of the dominant fishes in Louisiana's estuaries. Species are grouped according to ecological type. Adapted from Darnell (1961).

TABLE 4

ESTIMATED AVERAGE ANNUAL PRODUCTION AND FOOD REQUIREMENTS FOR *BREVOORTIA PATRONUS* AND *MICROPOGONIAS UNDULATUS*

	Brevoortia patronus	Micropogonias undulatus
Standing stock (No./m²)[a]	0.02	0.03
Standing crop (g wet wt/m²)[a]	0.11	0.26
Average size of individual (mm)[a]	60	65
Average wet wt of individual (g)[a]	6.4	8.7
Instantaneous growth rate (%/day)[a]	0.39	0.33
Annual production[b] g wet wt/m²/yr	13.47	23.40
Annual metabolism[b] g wet wt/m²/yr	27.13	81.17
Ration[b]		
g wet wt/m²/yr	50.75	130.71
g C/m²/yr	7.84	19.60
Peak ration[b]		
g wet wt/m²/week	17.13	13.68
g C/m²/week	2.14	1.46

[a] Based on information from Hinchee (1977), Wagner (1973), and unpublished data of the authors.

[b] Annual productivity is the sum of average daily biomass x growth rate. Annual metabolism is the sum of estimates of daily metabolism from an equation relating metabolism to weight. Ration was estimated at 1.25 (production and metabolism). Peak ration was based on highest density of fish.

with early maturation and short life cycles. This intuitively makes sense as an organism that completes its lifespan in one year has to complete more physiological functions in a shorter time span than an organism that lives 10 years or more (Mann 1982). The life expectancy of some of the most dominant species in Louisiana's estuaries are fairly short. M. undulatus has a typical life expectancy of 2 years (White and Chittenden 1981) as does Cynoscion arenarius (Schlossman and Chittenden 1981) and B. patronus (Nicholson and Schaaf 1978). Based on size class information (Verret 1980), A. mitchilli may live only one year. Obviously total life expectancy is not the only determinant of production/biomass ratios. Nekton productivity is also dependent on such factors as food availability, predation and competition all of which we have shown previously to favor high fish productivity particularly in nursery areas. These factors combined with the life history characteristics of estuarine fish result in high fish productivity.

Food requirements for metabolism were 2 to 4 times greater than the food requirements for production (Table 4). Annual metabolism (M) per day was estimated from average weight (w) using the relationship M=a*w (exp(0.8)) (Paloheimo and Dickie 1966, Warren and Davis 1966, Gerking 1978, Brett and Groves 1979) and summed over the average length of stay (days) in the

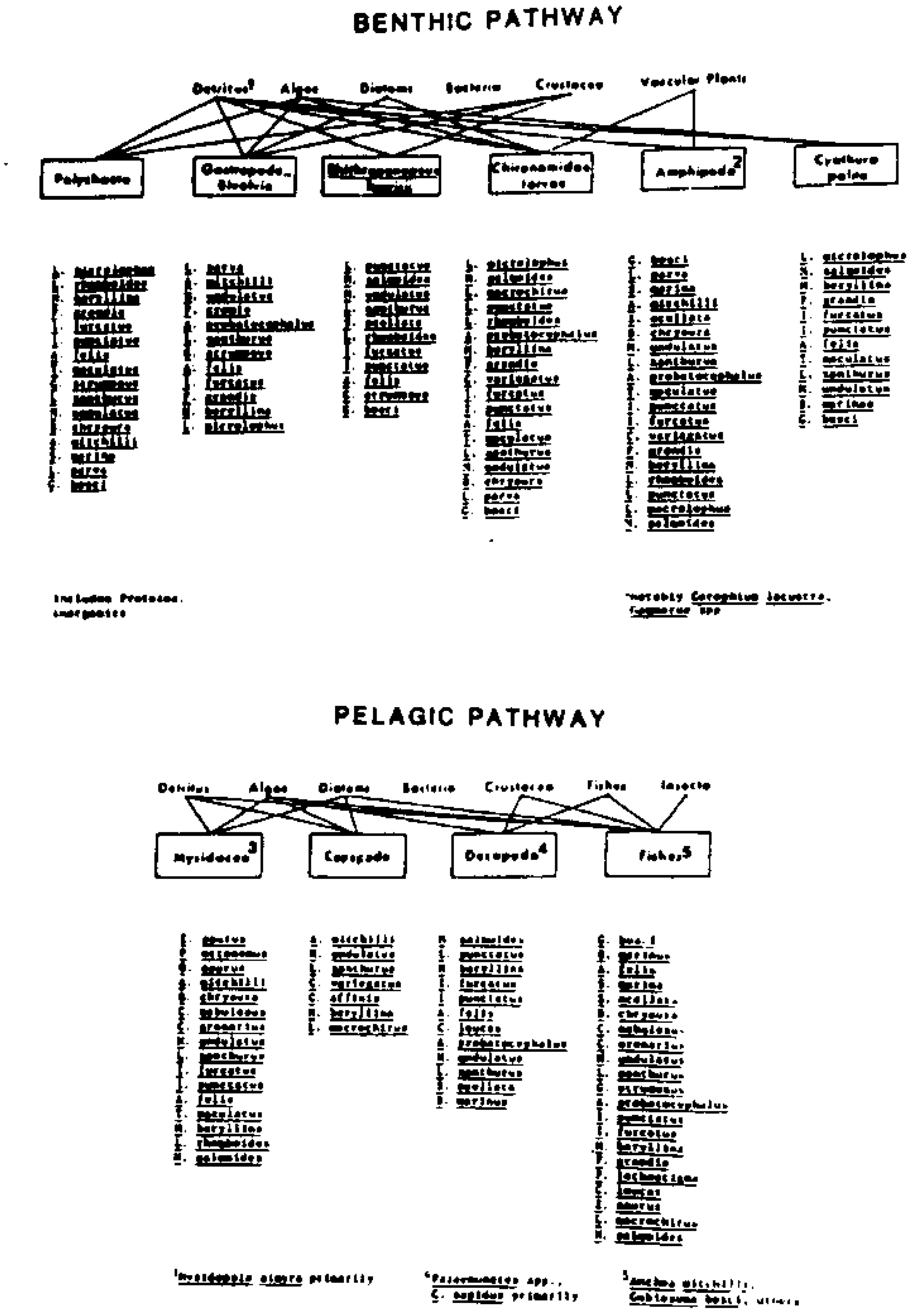


Fig. 15. Planktonic and benthic food pathways in Louisiana's estuaries, based on studies of Lake Pontchartrain. From Levine (1980).

estuary. Annual metabolism for B. patronus and M. undulatus was estimated at 27 and 81 g wet wt./sq meter/year (Table 4). Because of their small size and numerical abundance energy flow through these populations is high. This support Margalef's (1968) prediction that the rate of energy flow through secondary consumers in unpredictable and physically stressed ecosystems should be high.

Total ration, or food requirement, can be estimated from the following equation: Ration=1.25(Productivity + Total metabolism) (Gerking 1978). The average food requirements of B. patronus and M. undulatus were estimated at 51 and 131 g wet weight/m^2/year respectively or about 8 and 20 g C/m^2/year (Table 4). Because fish abundance varies greatly over the course of the year, an estimate of peak ration was calculated as outlined above based on peak densities and average weight of individual fish at that time. Peak ration was estimated at 17 and 12 g wet weight/m^2/week (2 and 1 g C/m^2/week) for B. patronus and M. undulatus respectively.

Functional Roles in Energy and Nutrient Flux. The next section presents evidence for three functional roles of fish: 1) regulation of prey species by predation, 2) transport of nutrients across ecosystem boundaries, and 3) energy and nutrient storage.

Comparison of the average food requirements of B. patronus and M. undulatus to production rates of food sources indicates they could be cropping a substantial portion of the benthic and pelagic secondary production, and at peak fish abundance standing crop of prey organism may limit production. Benthic macrofauna productivity has been estimated at between 0 to 240 g C/m^2/year, depending on location within the estuary, with an average of about 100 g C/m^2/year for the mid-salinity range (Philomena 1983). This represents an average production rate of between 0-5 g C/m^2/week. The combined food requirement of M. undulatus and B. patronus was estimated at 28 g C/m^2/week which represents about 28% of the average benthic production. At peak fish densities food requirements (3 g C/m^2/week) exceed the average benthic production rate (2 g C/m^2/week) and are about 60% of the maximum average production rate (5 g C/m^2/week). While these estimates of weekly benthic production rates are conservative this comparison indicates fish are probably cropping a substantial portion of the benthic production, especially during periods of peak abundance. Zooplankton production has been estimated at between 16 and 104 g wet weight/m^2/year or approximately 2-13 g C/m^2/year (Day et al. 1973, Stone and Deegan 1980). Based on these estimates pelagic zooplankton apparently provide only a small proportion of the food requirements of fish. Darnell (1964) suggested that fish utilize detritus directly but current evidence suggests the microbial populations which colonize the detrital particles may be the actual food. Unfortunately a definitive answer to this question does not exist but it seems likely that fish are using either the detritus or the bacteria because at peak fish consumption rates the standing crop benthic and planktonic organisms probably limits fish production. During periods of peak fish abundance the standing crop, not the annual productivity, of food organisms may limit fish production because the fish can eat the organisms faster than they can reproduce leading to depletion of the local food supply. This has been suggested as an explanation for some of the spatial variation in food habits of some fish in Lake Pontchartrain (Levine 1980).

There is also experimental and field evidence which indicates fish are influencing the structure of prey communities in these estuaries. Experiments excluding predators from benthic areas in other systems have shown large increases in the numbers and biomass of benthos supporting the concept that fish cropping is important in determining benthic community structure and biomass in estuaries (Virnstein 1977, 1978, Peterson 1979). In similar exclusion/inclusion experiments in a Louisiana marsh Fitzhugh (1982) observed decreases in harpacticod copepods in inclusion cages, and an increase in polychaete numerical abundance and species present in the exclusion cages, indicating that gobies were important in regulating benthic populations. Indirect evidence indicates fish are controlling benthic populations in the open waters of Louisiana's estuaries as well. The 'peaks and valleys' of meiofauna and macrofauna abundances in open water areas closely correlate with the migrations of certain predatory nekton species (Sikora and Sikora 1982b). Evidence for grazing control in the pelagic system is less obvious. Both of the dominant forms of pelagic feeders, Anchoa mitchilli and B. patronus, are either active or passive selective plankton feeders (Levine 1980, Durbin and Durbin 1975) and could affect the size spectra of zooplankton by selectively cropping the larger size classes. Selective feeding has been shown to alter the size spectrum of zooplankton populations in some freshwater lake systems (Brooks and Dodson 1965, Sprules 1972). This could have important implications for nutrient regeneration rates because these rates generally increase as size decreases (Kitchell et al. 1979). Other effects of fish on the structure of prey communities remains a little studied aspect of the ecology of Louisiana's estuarine fish.

The feeding of young fish on detritus dependent fauna forms a transport mechanism for the movement of energy produced in the marsh to offshore (Yanez-Arancibia and Nugent 1977, Weinstein et al. 1980, Sikora and Sikora 1982a, Hughes and Sherr 1983). Several workers (Richey et al. 1975, Durbin and Durbin 1975) have shown that fish transport significant quantities of nutrients in other systems and there is indirect evidence to indicate this may occur in Louisiana estuaries. Estuarine-marine forms increase their individual biomass up to 2000 times during their stay in the estuary (Wagner 1973, Hinchee 1977). The predominance of estuarine-marine forms in the top ten species based on numerical abundance (Table 3), combined with phenomenal growth rates during the estuarine portion of their lives (Table 4), indicate fish could be transporting energy and nutrients to the offshore area. Other indirect evidence which supports this concept is the work of Moore et al. (1970) who found the highest catch of estuarine-marine forms in the gulf directly offshore from the deltaic plain region indicating that large numbers of estuarine-marine forms cross the ecosystem boundary to the offshore gulf region. This area has been called the 'fertile fisheries crescent', (Gunter 1967) because B. patronus, a pelagic estuarine-marine form, supports the largest commercial catch (in numbers and weight) in the United States (NMFS 1981). These commercial landings are derived primarily from age classes of estuarine-marine species which have recently left the estuary (Nicholson and Schaaf 1978).

Recently investigators have hypothesized that fish may influence phosphorus dynamics of freshwater systems by storing phosphorus in their bones and releasing phosphorus after death (Durbin et al. 1979). Storage of phosphorus in the bones of fish may be important in freshwater systems which are usually deficient in the nutrient, but comparison of nitrogen and phosphorus stored in fish biomass to other nutrient pools (Table 5) in estuaries suggest that nutrient storage is not an important function of estuarine fish. The dominant nutrient storage pool in Louisiana estuaries is the soil which has been formed by deposition of peat by saltmarsh plants (Table 5). However, most of the nutrients and energy in peat are unavailable to the ecosystem because peat forms the structural base of the marsh. It is possible fish may be an important storage of available energy and nutrients and may serve a short term storage function. However, nitrogen and phosphorus in fish tissue is about the same as zooplankton and an order of magnitude lower than nutrients available in the water column, suggesting that fish are not important as short term storage pools.

TABLE 5

COMPARISON OF NITROGEN AND PHOSPHORUS POOLS IN LOUISIANA ESTUARIES

Component	g N/m²	g P/m²
Fish[a]	0.09	0.003
Zooplankton[b]	0.09	0.003
Water column[c]	0.50	0.08
Marsh soil[d]	450.00	20.00
Marsh grass[d]	25.00	1.30

[a] Based on average biomass and N:P ratios (Jorgensen 1979).

[b] Based on average biomass (Day et al. 1973) and C:N and N:P ratios (Nixon 1981).

[c] Based on average values from Costanza et al. (1982) and Happ et al. (1977) and average values for C:N and N:P ratios (Nixon 1981). Includes inorganic and organic forms.

[d] From DeLaune and Patrick (1980). Soil estimate is to a depth of 50 cm. Marsh grass includes both above and belowground storage.

Differences in Fish Communities among Delta Systems

The cycles of delta growth and decay have been proposed to control the diversity and production of plants and animals within the systems (Fig. 3). It has been suggested that biological productivity and diversity follow the same pattern as the physiography of the delta lobes, with peaks occurring immediately after abandonment during the initial stages of deterioration (Gagliano and Van Beek 1975). According to this hypothesis both the Atchafalaya Bay delta and the Lake Pontchartrain systems should have low productivity and diversity (Fig. 3), but for different reasons: the Atchafalaya delta because it is a new emerging system, and Lake Pontchartrain because it is the oldest, most deteriorated system. Barataria Bay and Fourleague Bay should have higher values, with Barataria Bay higher than Fourleague Bay because of their respective positions within the delta cycle (Fig. 3). We will first discuss differences in productivity and then diversity.

Differences in standing stock (number of individuals per m^2, Table 6) are significant ($F = 11.59$, $p < .0001$) and suggest fish productivity is related to characteristics of the ecosystem which change with position in the delta cycle. The lowest values are in the Atchafalaya Bay delta area and Lake Pontchartrain and the highest values are in Barataria Bay, followed by Fourleague Bay. It is suggested that peak fish production occurs later in the delta cycle because of the role of detritus in supporting the food web of these systems. It is characteristic of estuarine ecosystems to build detritus as an alternative to direct consumption of primary production (Odum 1972). This results in a modulated transfer of energy to the upper trophic levels and damps oscillations caused by variation in primary production (Reichle 1975). Because primary production is not directly linked to the food web but passes through a detrital storage phase there is a time lag between primary and secondary production peaks. Areas in the early stages of the delta cycle will not have built up a sufficient detrital base to support the aquatic system. The fish production potential of these estuaries is probably related to not only the detritus producing capacity of the estuary but also the detritus availability of these areas. Systems in the initial stages of deterioration still have vast areas of uninterrupted marsh to produce detritus, but this detritus is essentially unavailable to aquatic organisms. As deterioration proceeds small water bodies and sinuous streams are developed which trap and hold detritus and make this organic carbon source available to the aquatic system. Fish access detrital production through the use of these shallow water areas as a nursery and feeding habitat. Detrital availability probably decreases rapidly at the end of the delta cycle because, as the system deteriorates, the primary production base to replenish the detritus is gone and the system is more open and exposed to the flushing actions of storms and wind. Thus, fish production should be highest in systems which have an appropriate mix of marsh area to produce detritus and streams and bayous to trap detritus and provide fish access to the stored organic base. Average standing crop does seem to be related to the ratio of open water to wetland, with peak standing crop at intermediate values of water to wetland rations (Fig. 16). Cavit (1981) also found that catches of menhaden off a particular hydrologic unit increased with the product of total marsh acreage to intermediate marsh area and with the proportion of total marsh to total water surface area. However different species adapt to different portions of the estuarine system and Turner (1977), in a similar study, found commercial penaeid shrimp yields are directly related to the area of intertidal vegetation, not to the ratio of water to wetlands. We are still far from understanding the complete mix of physiographic factors which combine to make these systems so productive for fish, but the importance of the wetlands seems clear.

While there is some evidence to indicate that habitat diversity is correlated with age of the delta lobe (Gagliano and Van Beek 1975) ichthyofaunal diversity apparently does not follow the simple curve suggested by Gagliano and Van Beek (1975). Analysis of variance indicated significant differences in average number of species per sample (F = 33.36, $p < 0.001$, H (F = 5.89, $p < 0.009$), D (F = 29.96, $p < 0.001$) and J (F = 9.79, $p < 0.001$) among the estuaries, however nekton diversity is highest in the Atchafalaya Bay delta and Fourleague Bay systems, lowest in Barataria Bay, and has an intermediate value in Lake Pontchartrain (Table 5). Fish species diversity is influenced not only by the factors which control the growth and decay of the delta systems, but also responds to the immediate environment created by physical factors. Differences in diversity among these estuaries is

TABLE 6

COMPARISON OF FISH COMMUNITY STRUCTURE AND STANDING STOCK AMONG THE ATCHAFALAYA BAY DELTA, FOURLEAGUE BAY, BARATARIA BAY, AND LAKE PONTCHARTRAIN.

	ATCHAFALAYA BAY	FOURLEAGUE BAY	BARATARIA BAY	LAKE PONTCHARTRAIN
NUMBER OF SPECIES PER SAMPLE	7.60[a] (0.73)[b]	12.09 (0.53)	7.63 (0.32)	5.05 (0.26)
DIVERSITY INDICES				
H'	0.86 (0.05)	0.88 (0.10)	0.52 (0.06)	0.75 (0.05)
D'	1.23 (0.11)	1.76 (0.11)	0.86 (0.07)	0.76 (0.05)
J'	0.48 (0.04)	0.36 (0.04)	0.28 (0.03)	0.49 (0.03)
STANDING CROP (No./m²)	0.029 (0.006)	0.219 (0.056)	0.323 (0.038)	0.098 (0.026)

[a] Mean yearly value per sample.

[b] Standard error of mean.

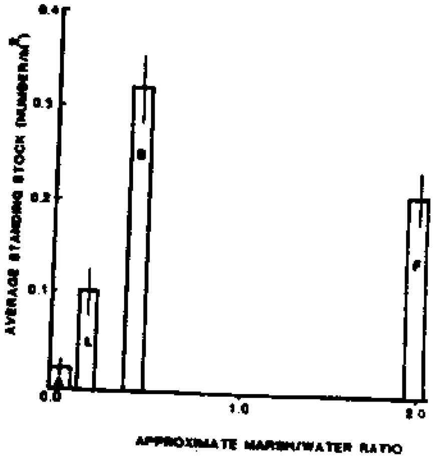


Fig. 16. Average standing stock (number of individuals per square meter) versus approximate open water to wetland area ratio. Vertical bars are standard error.

related to the relative ability of the ecological affinity groups to use these areas. Diversity is highest in the two areas (Atchafalaya Bay delta and Fourleague Bay) which have the highest average number of species per sample (7.6 and 12.89 respectively) and the most even distribution of species among the ecological affinity types (Fig. 6). Barataria Bay has a low diversity because of the overwhelming numerical abundance of the estuarine-marine forms in the samples as indicated by the low value for species evenness (J). The interplay of low numerical abundance and number of species per sample gives Lake Pontchartrain a fish community of intermediate diversity compared to the other estuaries in the deltaic plain.

CONCLUSIONS

Estuaries are ecosystems generally considered to be characterized by high stress caused by fluctuations in the abiotic environment (primarily temperature and salinity). Predictions about ecosystem function suggest areas such as these should be dominated by fish species with high potential rates of increase, high turnovers and short life spans. Energy flow through these species should be high and they should be flexible in their basic requirements to survive fluctuations. Evidence presented in this chapter indicates these are attributes of Louisiana estuarine fish populations. Fish in Louisiana's estuaries have three characteristics, short life expectancies, predominance of the young of the year, and high growth rates, which combine to make production and energy flow through the population high. Generalized characteristics of feeding relationships are: 1) flexibility of feeding habits in space and time; 2) omnivory; 3) sharing a common pool of food resources among species; 4) ontogenetic change in diet with rapid growth; and 5) short food chains based on detritus-algal feeders. Evidence is also presented to show that Louisiana's estuarine fishes control the structure of some prey communities through grazing, and could possibly be important in transporting nutrients across the ecosystem boundary, but they are most probably not significant nutrient storage pools.

Fish production and community structure respond to the cyclic changes in the environment caused by delta formation and decay. The most diverse and productive system is the marsh region where the ratio of water to wetland area is intermediate in value. These areas are characterized by high fish production because the large marsh areas are highly dissected by creeks and bayous which allow fish access to detrital production and serve as nursery habits.

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ESTUARINE FRONTS AS EPHEMERAL NURSERY ZONES FOR ICHTHYOPLANKTON: A PILOT STUDY

R.F. Shaw and R.C. Raynie

INTRODUCTION

It is generally recognized that density fronts or discontinuities and riverine/estuarine discharge plumes are important sites for energy transfer and intense biological activity with potentially large phytoplankton and zooplankton standing stocks (Simpson and Hunter 1974, Bowman and Esaias 1978, PROBES 1980, Holligan 1981, Incze and Yentsch 1981, Parson et al. 1983). The timing and spatial occurrence of fish spawning tends to take advantage of periods and areas of high productivity (Crisp 1954, Cushing 1967); special predator-prey relationships (Frank and Leggett 1982); and oceanographic features and conditions, which not only affect the distribution and concentration of fish eggs, larvae and their food, but also their transport, survivorship and ultimate yearclass success (see Norcross and Shaw 1984 for review). Recruitment may be enhanced by "safe sites" (Frank and Leggett 1982) in which physical processes usually insure that biological conditions are stable and favorable for survival (Lasker 1975, 1981). Reproductive success for some species depends upon a "match or mismatch" (Cushing 1972) of the most influential physical and biological factors (Townsend 1983).

Fish with pelagic eggs often reproduce in gyres and fronts (Loeb 1980, Frank and Leggett 1983) thus making areas of upwellings, fronts, and boundary currents among the most productive for fisheries (Garrod and Knights 1979, Mills and Fournier 1979, Bakum and Parrish 1982, Atkinson and Targett 1983). Larval fish aggregations are common in areas of concentrated nutrients and chlorophyll found in oceanic fronts (Hamann et al. 1981) and plumes, i.e., Columbia River (Richardson 1981) and Mississippi Delta (Govoni et al. 1983, Ortner and Hoss 1983). Therefore, any processes or mechanisms responsible for small-scale elevated gradients or patches of microcopepod forage relevant to larval fish searching behavior are crucial for survival.

The significance of physical stratification and boundaries caused by the large riverine/estuarine inputs of fresh water are greatest in the Atchafalaya Delta/Fourleague Bay system during late winter to early summer when river discharge is maximum. Conversely, the significance of nutrient inputs to the estuarine/coastal system is probably greatest when the coastal/oceanic waters for inner shelf-estuarine exchange are typically stratified and surface layers are oligotrophic. It is important to note that these exchange processes are multidirectional. The original source or direction of new nutrients entering the Atchafalaya Delta/Fourleague Bay area is from the river (Madden 1986), although in such a dynamic, shallow-water system (van Heerden 1983) settled nutrients/materials are frequently moved, resettled, resuspended or remineralized (Teague 1983). The extreme shallowness of the system increases the efficiency of the sediment charging-liberation cycle and tightens the coupling between sediments and surface waters. The resulting nutrient recycling illustrates the importance of exchanges in the vertical or benthos-to-water column direction in shallow-water systems. A third axis of exchange is the route of biotic immigration, whereby this rich estuarine environment is inoculated with the planktonic early life history stages of inner shelf or coastal spawners, whose offspring use the estuary as a nursery ground. It is the larval fish component of this group that is the focus of this research. Of specific interest is (1) their flux through Oyster Bayou as they are transported and successfully recruited into Fourleague Bay, (2) once recruited into the bay, how their survivorship and growth is affected by the elevated estuarine productivity and the presence of ephemeral estuarine fronts, and (3) if estuarine fronts are encountered, how do they respond to the dynamics of the frontal interface/ boundary.

METHODS

Our sampling design consists of ichthyoplankton collections from three environments along the continuum of the continental shelf-to-estuarine recruitment corridor: (1) an offshore transect consisting of seven stations starting at the mid-shelf and extending landward to the mouth of Oyster Bayou; (2) within Oyster Bayou, the major tidal exchange or transport/immigration route into Fourleague Bay; and, (3) with the Bay itself.

To date all larval fish collections have been taken at the surface. The sampling year consists of a 60-cm, bongo-type, plankton sampler fitted with 500 micron mesh netting and a General Oceanics flowmeter (model no. 2030). Tow duration is 3 minutes. Towing speed is approximately 1m/sec, except for the Oyster Bayou collections which are made passively by fishing the nets in the tidal stream from the side of the boat while it is anchored in the channel. Tidal velocity and mixing is very intense in Oyster Bayou and current velocities quite often exceed 1m/sec. During the November 1987 and April 1988 cruises the mean current velocity from the 12 readings taken during sampling was 0.63 and 0.96 m/sec, respectively. Starting on the next cruise, August 1988, we will also take near-bottom collections in Oyster Bayou as well. Also starting in August 1988, we will discontinue towing in Fourleague Bay and convert to sampling with a bow-mounted pushnet (60-cm, 500 micron mesh) because of the extreme shallowness of the Bay. Pushnets have been used effectively for sampling larval as well as juvenile fish, especially in shallow waters

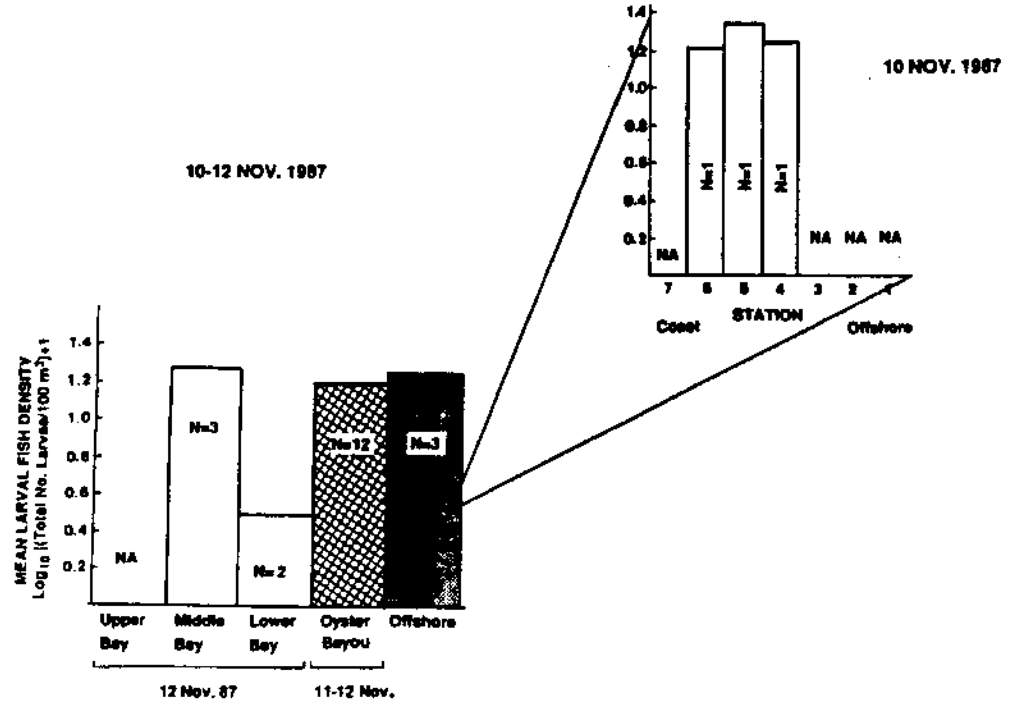

Figure 1. Mean larval fish density, $\log_{10}$[(total number of larvae /100m^3) + 1], from ichthyoplankton collections taken 10-12 November 1987 from Fourleague Bay (upper, middle and lower bay), Oyster Bayou, and from a transect from the mouth of the bayou to the mid-continental shelf (Offshore). N = number of replicate collections; NA = sample not available

(Dovel 1964, Miller 1973, Kriete and Loesch 1980, Rogers 1985, Hillman-Kitalong and Birkeland 1987, Meador and Bulak 1987, Bryan et al., MS).

Temperative and salinity are measured during each station collection with a Beckman Portable Electronic Salinometer (model no. RS5-3). A continuously recording CSTD (Sea Bird) is suspended from the boat wile anchored in Oyster Bayou. Weather and hydrographic observations (e.g., wind velocity and direction, occurrences of cold front passages, Atchafalaya River discharge, etc.) are also recorded. One replicate (or one-half of our net collections) are field fixed in 10% buffered formalin and latter changed to 4% in the lab. The other half of the collections are field preserved in 95% ethanol, stored in ice (to further ensure against spoilage), and later changed over again in the lab before processing for otolith analyses.

The offshore sampling along the seven station transect consists of a single, surface tow at each station. As mentioned previously the ichthyoplankton sampling in Oyster Bayou is passive and conducted over a complete tidal and diel cycle. Three replicate surface tows (and bottom tows starting August 1988) are taken during each tidal-diel combination (i.e. 6 collections for PM flood, 6 collections AM ebb, etc.). Tidal current velocity measurements are taken with a Montedoro-Whitney flow meter (Model No. PVM2) during each of the twelve bayou collections.

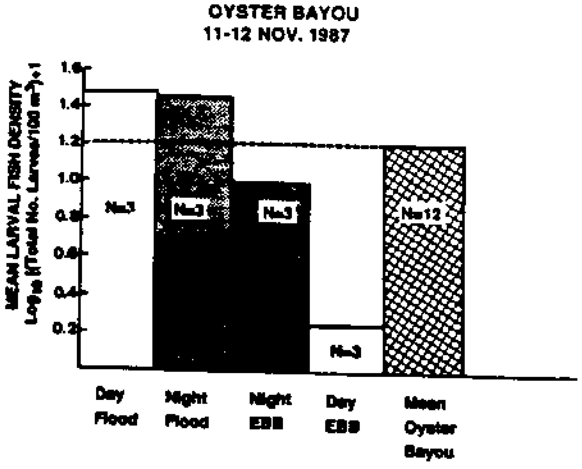

Figure 2. Mean larval fish density, $\log_{10}$ [(total number of larvae/100m^3) + 1], from ichthyoplankton collections taken during 11-12 November 1987 from Oyster Bayou Samples were taken over a complete tidal and diel cycle N = number of replicate samples.

There are two sampling options/protocols in Fourleague Bay with implementation dependent upon whether there is an estuarine front present or not. If a convergent zone is encountered, we will determine the fine-scale horizontal ichthyoplankton distribution and abundance on a transect along the axis of the Bay and through (i.e., perpendicular to) the observed front. The transect will consist of five plankton stations. One station will be in the front (just along its seaward edge) and 2 stations will be located in the upstream and downstream (seaward) directions with the distance between stations determined by the salinity gradient. The transect will be replicated at least twice if the front is long-lived. In the absence of an estuarine front, we sample 3 stations (the upper, middle and lower Bay) and each station is replicated 3 times.

RESULTS

To date we have had two cruises: 10-13 November 1987 and 6-9 April 1988 with the next cruise scheduled for early August 1988 (Table 1). Presented are results from the November cruise (Figs. 1 and 2). Preliminary analyses suggest a density maxima in mid bay (Figure 1) which may be associated with the observed chlorophyll maxima. In Oyster Bayou observed densities closely reflect those encountered offshore. Also there appeared to be a slight elevation in offshore densities at station 5, where similar elevations in chlorophyll have been observed in the coastal boundary layer. Sampling within Oyster Bay over the tidal-diel cycle (the tidal pass component of this study) revealed elevated flood densities (regardless of day vs night) over ebb collections suggesting net transport/recruitment of ichthyoplankton into (and retention within) Fourleague Bay.

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Table 1. Numbers of larval fish collections taken with a 60-cm (500 micron mesh) plankton net. NT= sample not taken.

DATE	Fourleague Bay			Oyster Bayou				Offshore Station							Total No. of samples	Samples Picked/Identified
	Upper	Middle	Lower	Flood	Ebb	Flood	Ebb	7	6	5	4	3	2	1		
10-12 Nov. 1987	NT (Low water)	3 (one day only)	2	3	3	3	3	NT	1	1	1	NT	NT (Too rough)	NT	20	20/20
6-9 Apr 1988	NT (Fresh)	3+3 (Two days)	3+3	3	3	3	3	1	1	1	NT	NT (Too rough)	NT	NT	27	10/0

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PART 8

SYNTHESIS STUDIES

A DYNAMIC SPATIAL SIMULATION MODEL OF LAND LOSS AND MARSH SUCCESSION IN COASTAL LOUISIANA*

R. Costanza, F.H. Sklar, M.L. White, and J.W. Day, Jr.

THE LAND LOSS PROBLEM IN COASTAL LOUISIANA

Wetland loss in coastal Louisiana is a cumulative impact, the consequence of many impacts both natural and artificial. Natural losses are caused by subsidence, decay of abandoned river deltas, waves, and storms. Artificial losses result from flood control practices, impoundment, dredging, and subsequent erosion of artificial channels. Wetland losses also occur because of spoil disposal upon wetlands and land reclamation projects (Craig et al. 1979). Land loss has been defined "as the substantial removal of land from its ecologic role under natural conditions" (Craig et al. 1979).

Losses occur in three basic ways: (1) wetlands become open water due to natural or artificial processes (loss of this type may be caused by erosion, subsidence, or dredging to form canals, harbors, etc.); (2) wetlands are covered by fill material and altered to terrestrial habitat; and (3) wetlands can be wholly or partly isolated by spoil banks (Craig et al. 1979). Wetland loss in abandoned river deltas was once compensated for by land building in the region of the active delta. Today, due to human intervention, there is a net loss of wetlands of 102 km^2 (39.4 mi^2) annually in coastal Louisiana (Gagliano et al. 1981).

NATURAL WETLAND LOSS

The deltaic plain is an area of dynamic geomorphic change. For the past several thousand years, the Mississippi River has followed a pattern of extending a delta seaward into the gulf in one area, and, after a few hundred years, abandoning it gradually in favor of a shorter adjacent route of steeper gradient (Morgan and Larimore 1957). When a delta lobe is abandoned, active land building via sedimentation ceases and net loss of land occurs because of erosion and subsidence. Because of levee construction, the Mississippi River has been effectively "walled in", and presently most of the sediments and nutrients of the river are deposited in the deep Gulf of Mexico and are unable to contribute to the buildup or maintenance of the coastal wetlands (Craig et al. 1979).

The most important processes affected by lack of sediment input are the rates of sedimentation and net marsh accretion of both streamside and inland marsh types (Cleveland et al. 1981). DeLaune et al. (1978) found that marsh sites closer to natural streams were accreting at a higher rate than inland marsh sites (1.35 cm/yr vs 0.75 cm/yr), and only streamside marsh areas were accreting fast enough to offset the effects of subsidence. Similar patterns of accretion were noted by Baumann (1980), who observed a mean aggradation deficit of 0.18 cm/yr for 80 percent of the marsh in Barataria basin. He proposed that this mechanism was responsible for a large portion of the marsh currently being lost in the Barataria basin. Most of the sediments which allow streamside marsh to maintain its elevation comes from resuspended bay bottom sediments (Baumann et al. 1984).

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*Costanza, R., F.H. Sklar, M.L. White, and J.W. Day, Jr. 1988. A dynamic spatial simulation model of land loss and marsh succession in coastal Louisiana. Pages 99-114 in W.J. Mitsch, M. Straskraba, and S.E. Jorgensen, eds. Wetland Modelling. Developments in Environmental Modelling, 12. Elsevier, Amsterdam. Used with permission.

Barrier islands along the coast are a strong defense against marine processes and hurricanes. The tidal passes between the islands act as the control valves of the estuaries by regulating the amount of high salinity water, storm energy, etc., that enter the estuaries (Gagliano 1973). The barrier islands of the Barataria basin are currently eroding; Grand Isle and Grand Terre are listed as areas of "critical erosion" by state and federal agencies. Limited coastal sand supply in Louisiana has caused one of the most serious barrier island problems in the country. Barrier island retreat rates are as high as 50 m/yr and loss rates of 65 ha (160 acres) per year have been reported (Mendelssohn 1982).

HUMAN-INDUCED WETLAND LOSS

Primary human activities that contribute to wetland loss are flood control, canals, spoil banks, land reclamation, and highway construction. There is increasing evidence that canals and levees are a leading factor in wetland loss (Craig et al. 1979, Scaife et al. 1983, Cleveland et al. 1981, Deegan et al. 1984). For example, in the 14-year period between 1962-1974, 18,138 ha of wetland in Barataria basin were drained or converted to water, with agricultural impoundments and oil access canals accounting for the largest acreages (Adams et al. 1976).

Mississippi River Levees

The leveeing of the Mississippi and Atchafalaya Rivers, along with the damming of distributaries, has virtually eliminated riverine sediment input to most coastal marshes. This has broken the deltaic cycle and greatly accelerated land loss. Only in the area of the Atchafalaya delta are sediment-laden waters flowing into wetland areas and land gain occurring (Baumann and Adams 1981).

Canals

Canals interlace the wetlands of the Louisiana coastal zone. Natural channels are generally not deep enough for the needs of oil recovery, navigation, pipelines, and drainage, so a vast network of canals has been built to accommodate these needs. The construction of canals leads to direct loss of marsh by dredging and spoil deposition and indirect loss by changing hydrology, sedimentation, and productivity. Canals lead to more rapid salinity intrusion, causing the death of freshwater vegetation (Van Sickle et al. 1976). Canal spoil banks severely limit water exchange with wetlands, thereby decreasing deposition of suspended sediments. The ratio of canal to spoil area has been estimated to be 1 to 2.5 (Craig et al. 1979), indicating the magnitude of spoil deposition to wetland loss.

It has been estimated that between 40-90% of the total land loss in coastal Louisiana can be attributed to canal construction, including canal/spoil area and cumulative losses (Craig et al. 1979, Scaife et al. 1983). In the Deltaic Plain of Louisiana, canals and spoil banks are currently 8% of the marsh area compared to 2% in 1955; there was an increase of 14,552 ha of canals between 1955 and 1978 (Scaife et al. 1983). Barataria basin had a 0.93%/year direct loss of marsh due to canals for the period of 1955-1978 (Scaife et al. 1983). Canals indirectly influence land loss rates by changing the hydrologic pattern of a marsh, such as by blockage of sheet flow, which in turn lessens marsh productivity, quality, and the rate of accretion. Spoil banks specifically block the import of resuspended sediments which are important in maintaining marsh elevation in wetlands distant from sediment sources. In time, canals widen because of wave action and altered hydrologic patterns, and apparently the larger the canal, the faster it widens. Annual increases in canal width of 2 to 14% in Barataria basin have been documented, indicating doubling rates of 5 to 60 years (Craig et al. 1979).

Generally, where canal density is high, land losses are high, and where land losses are low, canal densities are low. The direct impacts of canals are readily measurable. For example, from 1955 to 1978, canal surface area accounted for 10% of direct land loss. The indirect influence of canals extends far beyond this direct loss. Craig et al. (1979) estimated the total direct plus indirect loss of wetland due to canals in 3-4 times the initial canal area alone. Although total canal surface area alone may not be a dominant factor in wetland loss, direct and indirect impacts of canals may account for some 65% or more of the total wetlands loss between 1975 and 1978 (Scaife et al. 1983).

Cumulative Impact of Canals

The canals, when viewed on a regional basin level, become a network ultimately resulting in higher rates of wetland loss (Craig et al. 1979), increased saltwater intrusion (Van Sickle et al. 1976), changes in the hydrology of the wetland system (Hopkinson and Day 1979, 1980a, 1980b), a reduction in capacity for wetlands to buffer impacts of large additions of nutrients resulting in eutrophication (Hopkinson and Day 1979, 1980a, 1980b, Kemp and Day 1981, Craig and Day 1977), a loss in storm buffering capacity, and a loss of important fishery nursery grounds (Turner 1977, Chambers 1980).

Since canals are an important factor affecting land loss, one measure of the impact of canals is potential fisheries loss. An estimated $8-$17 million of fisheries products and services are annually lost in Louisiana due to wetland destruction (Craig et al. 1979). Commercial fish yields are related to the area of coastal wetlands; higher shrimp yields are associated with larger areas of wetlands and only incidentally with water surface area or volume (Turner 1977). Therefore any wetland loss caused by canals is detrimental to fisheries.

Suggested Solutions

1. Canal Regulation. Canals are an important agent in wetland alteration, affecting not only marsh loss, but salinity intrusion and eutrophication as well. It has been suggested that canaling be permitted only where there is absolutely no other alternative and then with a mitigation clause of "no net wetland loss." There are other management techniques that have been suggested to reduce the direct impact of the canals. The least damaging construction technology available could be employed in all cases. Several alternatives are available, including directional drilling, that would reduce the number of canals needed for oil and gas exploration, and hydro-air cushion vehicles that would eliminate the need for canals entirely. Mitigation schemes to compensate for the unavoidable adverse impacts associated with human activities have also been suggested. Mitigation options which seek to achieve zero habitat loss while maintaining the functional characteristics and processes of wetlands such as natural biological productivity, wildlife habitats, species diversity, water quality, and other unique features have been suggested (Coenen and Cortright 1979).

2. Creative Use of Spoil. Approximately 80% to 90% of the dredging that takes place within the continental U.S. occurs in Louisiana (Lindall and Saloman 1977). An enormous amount of spoil is generated every year, and spoil disposal on wetlands is the general rule. It has been reported that for every mile of pipeline installed by flotation canal, 30-36 acres of marsh are altered as a result of spoil deposition (McGinnis et al. 1972).

In order to reverse this trend in wetland alteration, spoil could be viewed as a reusable resource rather than as waste. It is possible to use these sediments productively to create and aid in the management of habitat. A 5-year (1973-1978) Dredged Material Research Program (DMRP) was conducted by the Corps of Engineers at the Waterways Experiment Station in Vicksburg, Mississippi, based on this idea. Several uses of spoil are: a substrate for wildlife habitat such as islands for nesting birds, marsh habitat, beach renewal, restoration of bare ground, construction material, and sanitary landfill. Wetland substrates which are subject to subsidence or erosion can benefit from a deposit of dredged material to replenish what has been lost (National Marine Fisheries 1979, Hunt 1979). Major field experiments have tested vegetation establishment techniques and principles for spoil. As a result of these studies, the ability to dispose of dredged material in a biologically productive manner was demonstrated, and the engineering characteristics and behavior of dredged and disposed sediments can be predicted and determined.

3. Barrier Island Stabilization. Barrier island stabilization has been used to retard land loss of both islands and the wetlands they protect from storm wave activity. Structural and biological approaches have been considered. The structural approach involves construction of groins and riprap, which may stabilize one area at the expense of another. Beach nourishment (pumping sand onto the beach from offshore) is another technique that has been used, especially along the south Atlantic coast. The biological approach generally involves planting grass to stabilize dunes. This method appears to be successful, at least in the short-term (Mendelssohn 1982).

4. Controlled Water Diversions. Flood control measures such as leveeing along the Mississippi River have interrupted the balance between riverine and marine processes which result in sediment transport, deposition, and introduction of valuable freshwater and nutrients. These processes, which built and stabilized the marsh and swamp areas via overbank flooding, are now virtually eliminated in most of coastal Louisiana.

Schemes for controlled diversions of the Mississippi River have been developed as a means of introducing river water and sediment into wetlands for offsetting wetland loss. "Basically, this approach would reestablish the overbank flow regime of the Deltaic plain, presently disrupted by flood protection levees, and restore more favorable water quality conditions to the highly productive deltaic estuaries" (Gagliano et al.1981). The feasibility of controlled diversion is indicated by the relatively small input of energy and materials needed to build a major subdelta (Gagliano et al. 1971). The U. S. Army Corps of Engineers (1980) has suggested a number of potential sites for controlled diversions into the Barataria basin. In addition, several diversion schemes for the western Terrebonne basin have been proposed.

THE NEED FOR AN INTEGRATED SPATIAL SIMULATION MODELLING APPROACH

The various suggested solutions to the land loss problem all have far-reaching implications. They depend on which combination of solutions are undertaken and when and where they are undertaken. Outside forces (such as rates of sea level rise) also influence the effectiveness of any proposed solution. In the past, suggested solutions have been evaluated independently of each other and in a "seat of the pants" manner. In order to more objectively evaluate the many interdependent implications of the various management strategies and specific projects that have been suggested to remedy the coastal erosion problem, an integrated spatial simulation modeling approach is needed (Sklar et al. 1985, Costanza et al. 1986). This approach can simulate the past behavior and predict future conditions in coastal areas as a function of various management alternatives, both individually and in any combination. It simulates both the dynamic and spatial behavior of the system, and will keep track of the important variables in the system, such as habitat type, water level and flow, sediment levels and sedimentation, subsidence, salinity, primary production, nutrient levels, and elevation.

Models of this type are large and expensive to implement, but once implemented can be used to quickly and inexpensively evaluate various management alternatives. We envision an ongoing modeling capability for the state's coastal areas, constructed in stages. We have already spent considerable effort designing and implementing this type of model for the western Terrebonne basin and it has been used to evaluate several current management alternatives for this area.

THE COASTAL ECOLOGICAL LANDSCAPE SPATIAL SIMULATION (CELSS) MODEL

The model consists of 2,479 interconnected cells, each representing 1 square kilometer. Each cell contains a dynamic simulation model, and each cell is connected to each adjacent cell by the exchange of water and suspended materials. The volume of water crossing from cell to cell is controlled by habitat type, drainage density, waterway orientation, and levee heights. The buildup of land or the development of open water in a cell depends on the balance between net inputs of sediments and organic peats and outputs due to erosion and subsidence. The balance of inputs and outputs is critical, and is important for predicting how marsh succession and productivity is affected by natural and human activities.

Forcing functions (inputs) are specified in the form of time series over the simulation period. Weekly values of Atchafalaya and Mississippi River discharges, Gulf of Mexico salinity, river sediments and nutrients, rainfall, sea level, runoff, temperature, and winds are supplied to the simulation with each iteration. The location and characteristics of the major waterways and levees are also supplied as input to the simulation. Water can exchange with adjacent cells via canals, natural bayous and overland flow or it may be prevented from exchanging with adjacent cells by the presence of levees. The overall water flow connectivity parameter (K2) is adjusted during the model run to reflect the presence and size of waterways or levees at the cell boundaries. If a waterway is present at a cell boundary a large K2 value is used, increasing with the size of the waterway. If a levee is present a K2 value of 0. is used until water level exceeds the height of the levee. The model's canal and levee network is updated each year during a simulation run, i.e. dredged canals and levees are added to the model's hydrologic structure at the beginning of the year they were built.

Each cell in the model is potentially connected to each adjacent cell by the exchange of water and suspended materials. Before this exchange takes place however, the ecological and physical dynamics within a cell is calculated. For example, Fig. 6-1 shows diagramatically how the water (the large "tank"), suspended sediments (top, small "tank"), and bottom sediments (elevation: bottom, small "tank") components are interconnected within a typical cell. The volume of water crossing from one cell to another carries a specified sediment load. This sediment is deposited, resuspended, lost due to subsidence, and carried to the next cell. The amount of sediment in each "tank" is a function of the habitat type. Not shown in Figure 1 but included in the model is the fact that plants and nutrients within each cell will also influence these exchanges and flows.

Habitat succession occurs in the model (after a time lag) when the state variables within a cell become more like another habitat type due to the changing conditions. The biotic components in a cell (primary production) respond to the abiotic changes according to the functions illustrated in Figure 6-2. In this figure the model's relationship between weekly productivity and salinity for three of the habitat types is shown, indicating that productivity and thus succession change with changing salinity. This same type of function is used to simulate the dependence of primary production upon the cumulative impacts of changing flooding regimes, nutrient levels, turbidity, and elevation.

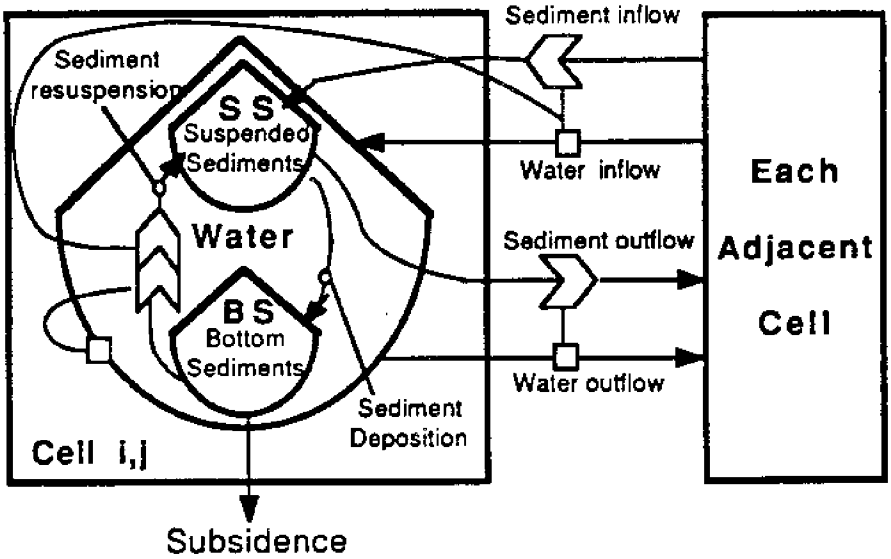

Figure 6-1. Storages (tank symbols) and flows (lines) of water, suspended sediments (SS), and botom sediments (BS) for a typical cell. Fluxes of suspended sediments are a function to water flows and sediment concentrations.

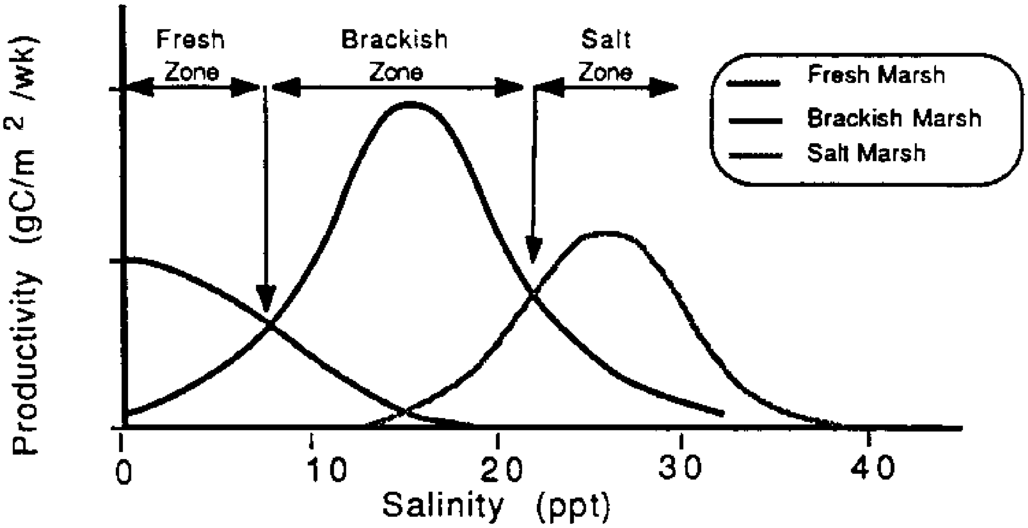

Figure 6-2. Plant primary production as a function of salinity showing points of habitat succession in the model for three of the habitat types.

Model Output

The model can produce a huge amount of output, most useful of which is a contour map for each state variable as well as habitat maps for each week of the simulation. To produce these maps the model must solve over 17,000 simultaneous difference equations and generate over one million simulated data points for each year of simulation. With present day computers models with such large numbers of computations are feasible, and as computers continue to improve in speed and convenience, this type of modeling should become more practical.

The results of the model are best comprehended by viewing a video tape of the model's time series mapped output for each state variable and habitat type. Since we can't run the video in this chapter, we present a few "snap shots" of habitat change (Figure 6-3) and discuss some of the findings.

The model predicts the gradual intrusion of salt into the system from the southeastern part of the study area with the concurrent freshening in the northwestern sector. It also illustrates a loss of elevation in the north and an increase in elevation in the south. Both of these trends are indicative of river water and sediments moving further south in recent times plus a lack of connectivity with the more northern fresh marsh areas. Predicted water volume and suspended sediments behaved in a similar way and are generally consistent with what is known about the historical behavior of the system. These physical changes, in turn, have an impact upon the biology of the area. The relationship between plants and elevation of the marsh results in a feedback loop that enhances the rate of land loss as suspended sediments are diverted from an area of marsh.

The model accurately predicted changes in salinity zones and generalized water flow patterns. Overall, the present model does a fairly good job of predicting landscape succession.

To quantitatively assess the validity of the CELSS model the 1978 habitat map generated by the model is compared to the actual 1978 habitat map. The most straightforward method to compare the maps is to calculate the percent of corresponding cells in the two maps which have the same habitat type. In our current runs, a cell-by-cell comparison has resulted in a fit of 86% correct.

Another method has been proposed (Costanza, in prep) to compare the degree of fit between two maps of categorical data. This method looks at the way the fit changes as the resolution of the maps is degraded by using a sampling window of gradually increasing size. The sampling window is moved through the scene one cell at a time until the entire image is covered.

The formula for the fit at a particular sampling window size (F_w) is:

$$F_w = \frac{\sum\limits_{s=1} \left[1 - \frac{\sum\limits_{i=1}^{p} \left| a_{1i} - a_{2i} \right|}{2w^2} \right]_s}{t_w} \qquad (1)$$

where:

F_w = the fit for sampling window size w

w = the dimension of one side of the (square) sampling window

a_{ki} = the number of cells of category i in scene k in the sampling window

p = the number of different categories (e.g., habitat types) in the sampling windows

s = the sampling window of dimension w by w which slides through the scene one cell at a time

t_w = the total number of sampling windows in the scene for window size w

n = the maximum window size

One can then plot the fit between the scenes (F_w) vs. the size of the sampling window (w) as in Figure 6-4. Figure 6-4 contains plots of goodness of fit, F_w, as a function of window size (w) for various model runs compared with the data. If the plot behaves as it does for the 1978 real vs. simulated maps (i.e., increasing rapidly at small window sizes) the pattern between the two scenes is well matched despite the low fit at window size 1. This would be the case if the patterns between the scenes were similar, but the precise boundaries in the maximum resolution scenes were off. Conversely, if the plot were flat the spatial pattern would not be well matched even though the initial fit might be higher.

A weighted average of the fits at different window sizes seems to be the most appropriate single measure

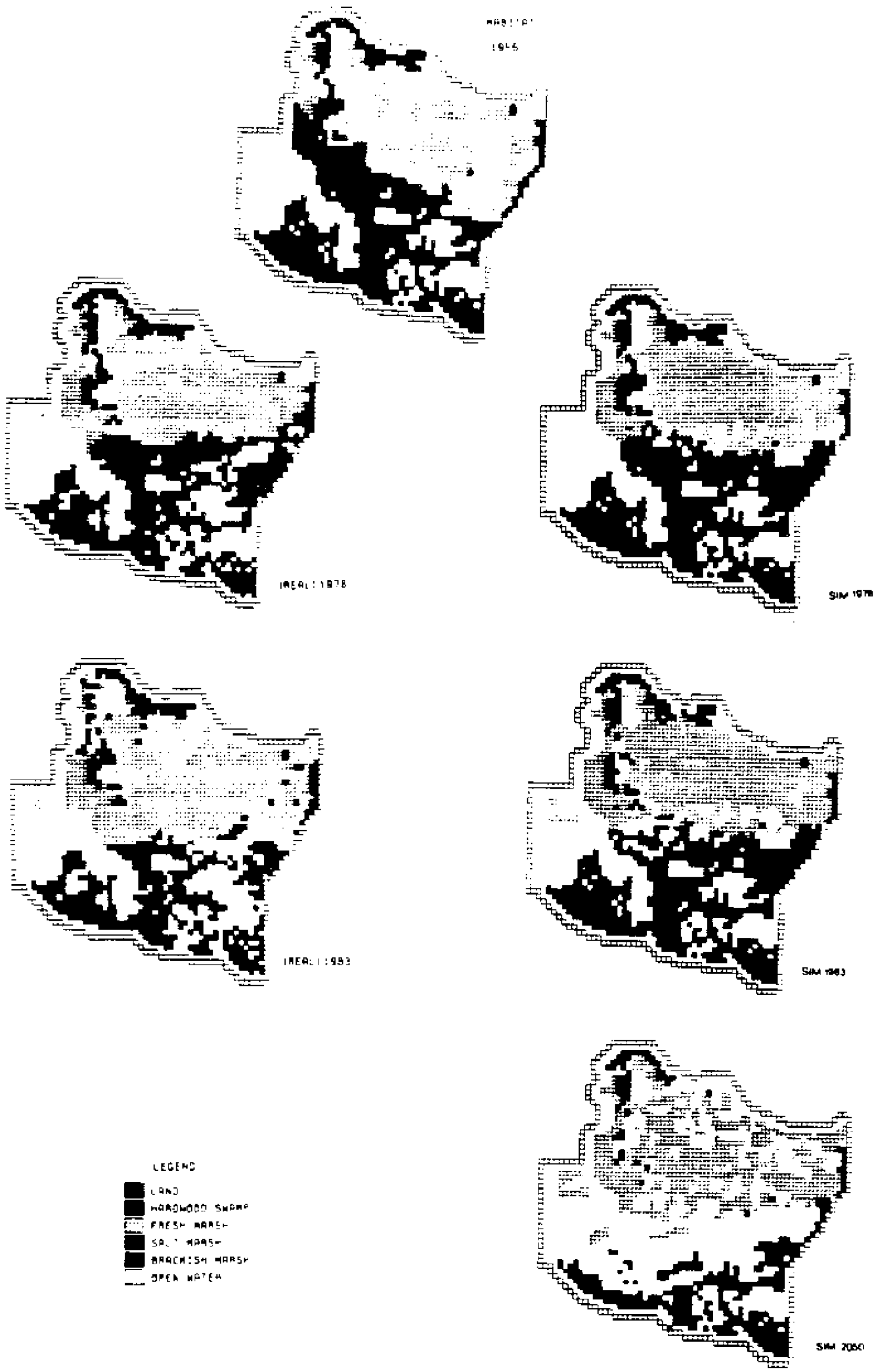

Figure 6- 3. Sample habitat map output from the base case model run (right column) compared with real data (left column).

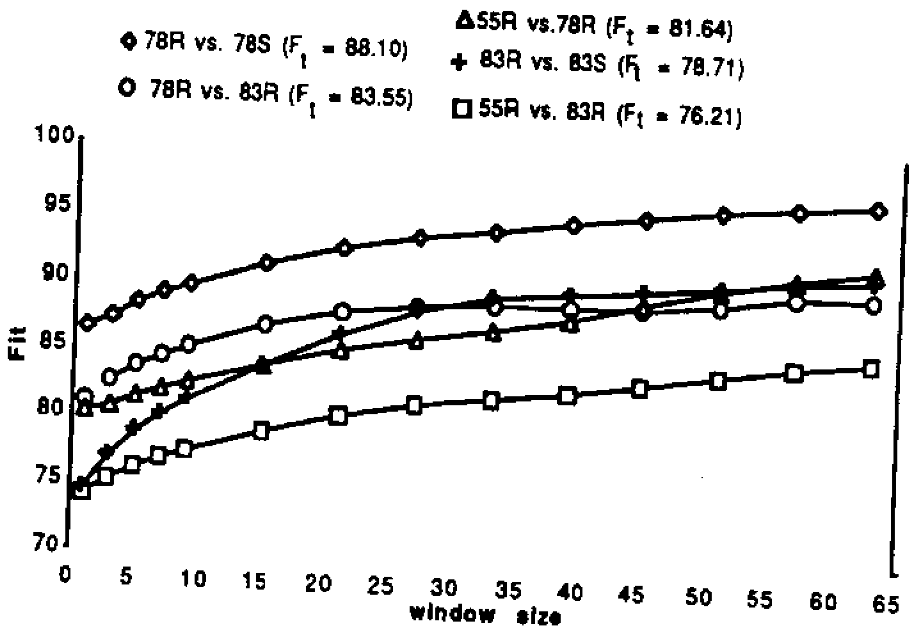

Figure 6-4. Plots of window size (w) vs. fit (F_w) for various runs of the model compared with real data. R refers to real data and S refers to simulated model output. F_t is the total weighted fit over all window sizes.

of fit. For this purpose we use the following formula:

$$F_t = \frac{\sum_{w=1}^{n} F_w e^{-k(w-1)}}{\sum_{w=1}^{n} e^{-k(w-1)}} \qquad (2)$$

This formula gives exponentially less weight to the fit at lower resolution. The value of k determines how much weight is to be given to small vs. large sampling windows. If k is 0 all window sizes are given the same weight. At k = 1 only the first few window sizes will be important. The relative importance of matching the patterns precisely vs. crudely must be answered in the context of the model's objectives and the quality of the data.

Sensitivity analysis is presently being conducted to determine the effects of combinations of over one hundred parameters on the goodness of fit (F_t) of the model. The analysis consists of a factor screen design in which each factor has two levels (high - low). This will provide information on all two factor interactions in the test as well as imply which three factor interactions produce the greatest effect in the simulated landscape. Preliminary results indicate that waterflow parameters associated with waterways and habitat type are most sensitive in tuning the model. Further parameter adjustments are expected to achieve an overall spatial goodness-of-fit (F_t) of better than 90%.

THE MANAGEMENT POTENTIAL OF THE CELSS MODEL

The simulation of long-term habitat changes in the coastal marshes of the Atchafalaya River demonstrates that ecological and physical processes can be realistically and relatively accurately modeled. The results of the CELSS Model indicate that the current trend of habitat succession will continue to result in wetland degradation unless something is done. Each oil access canal, levee, and dredge and fill activity that is permitted may seem small and unimportant on a case-by-case basis, appearing only as an insignificant localized impact. However, we have shown that when spatial processes and cumulative impacts are considered, the effects are greatly magnified. In addition, the effects of some management options are contingent upon which other options are simultaneously employed. The long-term implications of canal dredging, for example, may be dependent on the sediment environment, an environment which may be drastically affected by marsh management plans or other options.

We are currently in the process of running the model to the year 2050 for several different scenarios. These include the effects of the proposed Avoca Island levee extension, various canal dredging and backfilling options, controlled water diversions, and semi-impoundments. These options will also be investigated in various combinations. This will give government agency personnel, landowners, oil industry representatives, and the general public better predictions of the complex implications of human activities in the Louisiana coastal zone, and should lead to better management of the resource.

In addition, we can do "hindcasts" with the model to study the impacts of past activities. For example, we have run the model without any of the canals dredged between 1956 and 1978 to look at the impacts of past canal dredging. Preliminary results are shown in Figure 6-5. We could also pick out types of canals or even individual canals to eliminate in a simulation and thus estimate historical impacts.

At present models of this size and complexity are fairly new and expensive. But as we gain experience, and as supercomputers and array processors become more readily available, models of this type will become practical tools for understanding and managing natural coastal systems.

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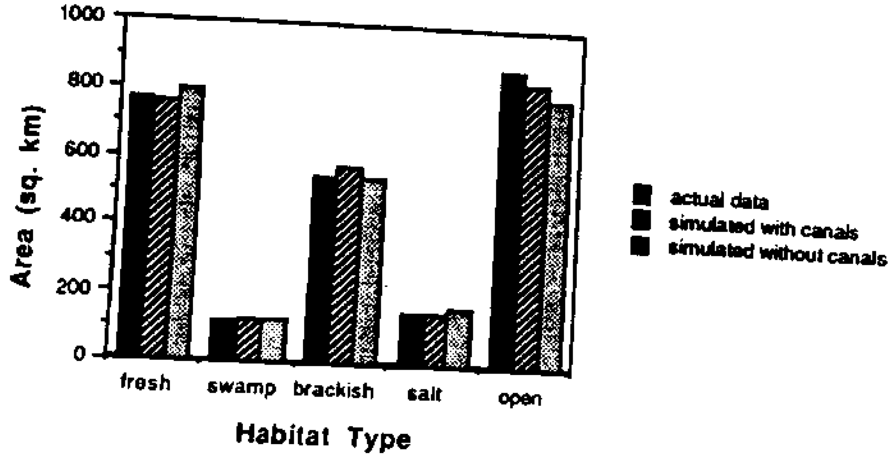

Figure 6-5. Preliminary results of running the model with and without artificial canals and levees. Chart shows the area of each of the habitat types in 1978 for the data and model runs including and excluding canals. Eliminating canals decreases the open water habitat and increases the marsh habitats (except brackish).

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THE DEVELOPMENT OF AN ESTUARINE ECOSYSTEM IN A COASTAL FRESHWATER DELTAIC ENVIRONMENT

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L.A. Deegan, W.B. Sikora, and J.P. Sikora

INTRODUCTION

This paper describes some preliminary results of a research program undertaken to describe and understand the ecology of the Atchafalaya Bay region in coastal Louisiana. This area is unique among coastal systems of North America because of the tremendous influx of water, sediments, and other riverine constituents from the Atchafalaya River, a distributary of the Mississippi River (Fig. 1). Although the Atchafalaya River is only about 160 km in length and is part of the lower Mississippi River system, in terms of discharge it can be considered the second largest river in North America (mean discharge is about 7000 m^3/sec or 30% of the total lower Mississippi flow). The purpose of this paper is to describe the evolution of a coastal ecosystem in a freshwater deltaic environment. In doing so we want to raise several questions about the definition and nature of estuaries and estuarine ecosystems. Before discussing the ecology of the Atchafalaya Bay area, we will present a brief introduction to the geologic processes operating in the Mississippi deltaic plain.

Since the holocene sea level stabilization about 7000 years ago, sediments from the Mississippi River have formed a broad deltaic plain of almost 5 x 10^6 ha of wetlands, waterbodies, and low relief uplands. The growth of the deltaic plain did not take place uniformly in time and space. Rather, the plain was formed by a series of overlapping delta lobes that formed land in specific parts of the coast. At least six major lobes have been identified (Fig. 2).

A new phase of delta building has now been initiated in Atchafalaya Bay. Beginning in 1973, subaerial (above water) exposures first appeared and the new delta has grown rapidly since (Fig. 3). This subaerial growth was preceded by a long period of infilling of lakes in the Atchafalaya Basin to the north and subaqueous (below water) delta growth in the bay. More detailed descriptions of these processes can be found elsewhere (Kolb and Van Lopik 1966, Shlemon 1975, Roberts et al. 1980, Adams and Baumann 1980).

Accompanying the new deltaic growth have been rather profound changes in the Atchafalaya Bay region in general. The most obvious of these is the tremendous loading of water, sediments, and nutrients to waterbodies, wetlands, and the nearshore Gulf of Mexico. Marshes which were saline twenty years ago are now fresh. Wetlands which were deteriorating and disappearing are now growing. The river has assumed a much

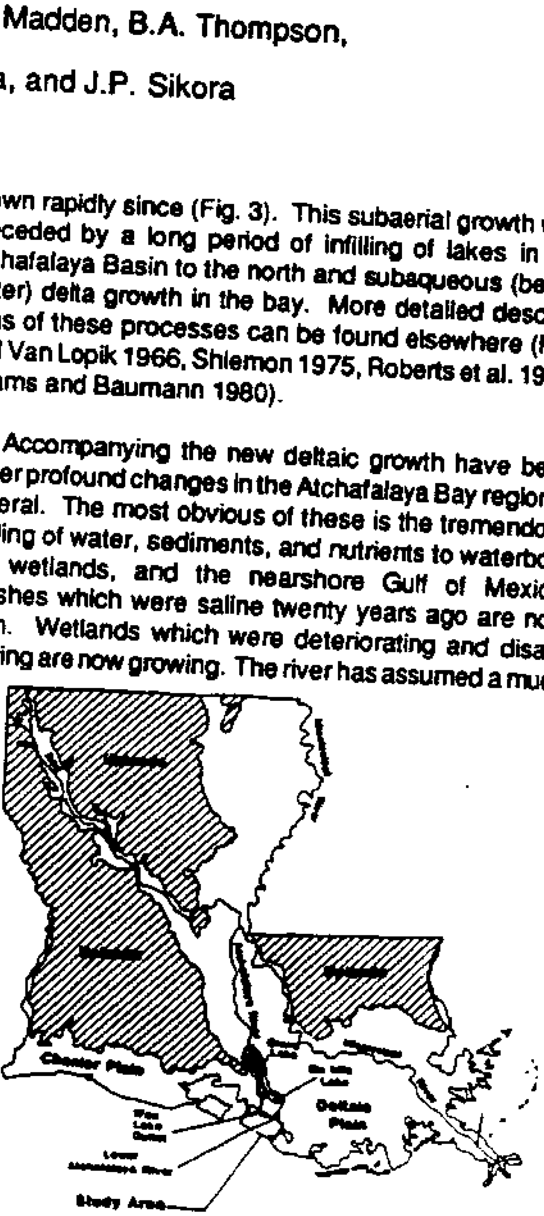

Figure 1. Map of the study area showing uplands and coastal plain areas in Louisiana The Lower Atchafalaya River empties into Atchafalaya Bay and Fourleague Bay

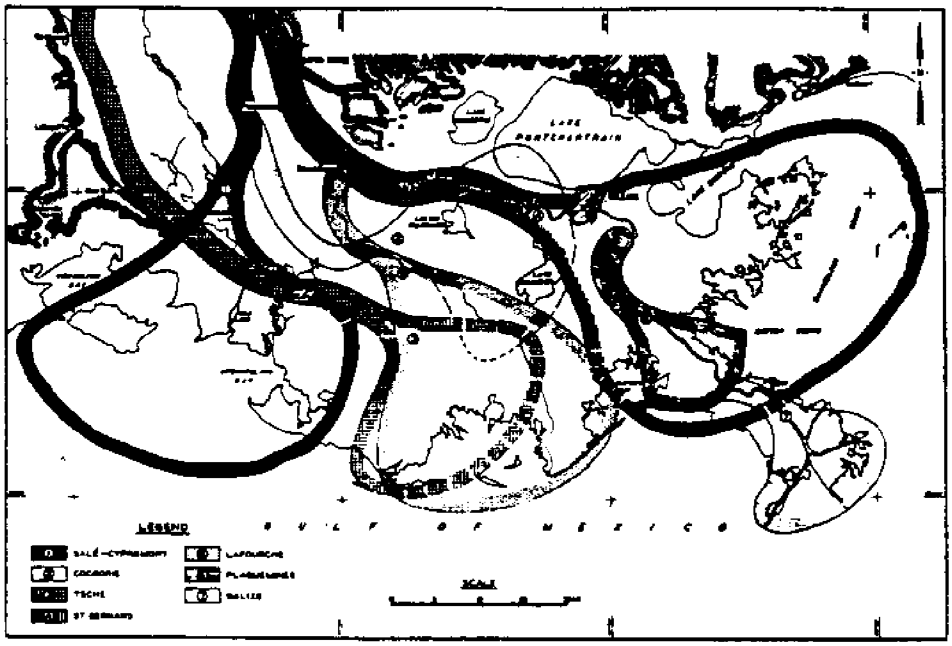

Figure 2. Location and relative size of the seven major delta complexes that have been active in southeast Louisiana during the last 6000-8000 years (from Kolb and van Lopik 1958).

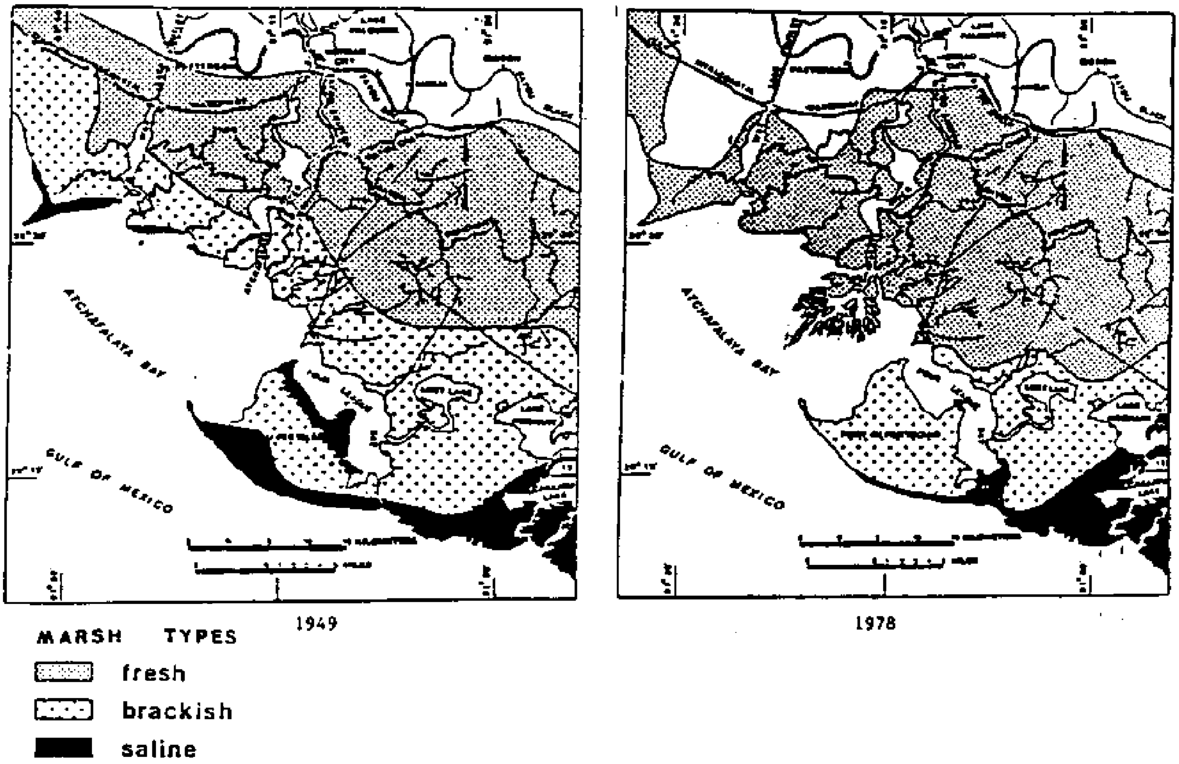

Figure 3. Comparison of vegetation in Lower Atchafalaya Basin and Terrebonne marshes in 1949 and 1978. Extent of saline marshes has diminished and fresh marsh has expanded to the coast. Brackish marsh zone has narrowed and in some cases disappeared. Note the delta at the river mouth in 1978 (from O'Neil 1949 and Chabreck and Linscombe 1978).

more dominant role as a source of nutrients and organic matter. In the following sections of this paper we will discuss these changes in more detail.

The area of intensive study includes not only the Atchafalaya Bay/delta complex but also Fourleague Bay and surrounding wetlands to the east. A major focus of the studies is the response of the estuarine ecosystem to the changing salinity regime. Atchafalaya Bay is almost continually fresh. In Fourleague Bay there is a strong gradient from fresh water to saline water from the Gulf of Mexico. There is a broad salinity range from 0-10 ‰ in the upper bay inlet to 0-30‰ at Oyster Bayou, the Gulf inlet. Fourleague Bay is almost completely landlocked; hydrologic boundaries are distinct and water flow through the boundaries can be measured with relative ease. The Atchafalaya River supplies large amounts of fresh water, nutrients and sediment while Gulf water entering Oyster Bayou has low concentrations of nutrients and sediments.

NUTRIENT DYNAMICS IN FOURLEAGUE BAY

This phase of the study consisted of five parts aimed at quantifying the nutrient dynamics within and through the bay system. Advective nutrient inputs and losses from the water column were measured by determining nutrient concentrations and water flow through the major bay inlets over two tidal cycles. Nutrients in the water column were measured in monthly synoptic surveys of sites throughout the bay; these surveys were used to characterize the salinity and nutrient distribution in a series of "snapshots". Benthic respiration, remineralization, and losses to the sediments were measured in domes placed on the bay bottom. Nutrient inputs to the marsh were measured via sediment accretion, precipitation, and nitrogen fixation.

Forcing Functions

The forces that control the advective nutrient inputs and exports in Fourleague Bay are river discharge, weather type and tide. Atchafalaya River discharge ranges from an average maximum of 11000 m^3/s in May to a low in September averaging 3000 m^3/s. During the spring flood the Atchafalaya River pumps fresh water, carrying sediments and nutrients, into Fourleague Bay. Wind or tide induced increases in salinity are generally damped by the large freshwater flow during spring. As the flood subsides in summer, weather events and tide play a larger role in determining the amounts of fresh and salt water entering the bay. Salinity and nutrient profiles are prone to short-term fluctuations during the period of low river discharge. Synoptic weather types in south Louisiana (Muller 1977) have been classified based on their influence on water movement in Atchafalaya and Fourleague bays (Cunningham 1981). Strong northwest or west winds drive fresh water into Fourleague Bay while east or south winds move fresh water out of the bay encouraging the inflow of saline Gulf water through Oyster Bayou.

A comparison of bay nutrient profiles from the February and April tidal cycle surveys show the importance of wind direction in determining bay nutrient levels (Figs. 4a, b). In February, Atchafalaya River discharge was increasing and nitrate levels were high throughout the bay, averaging 60-70 µg-at/l. Wind direction before and during the February tidal cycle study was from the northwest, directing the Atchafalaya plume into Fourleague Bay. Salinities were low throughout the bay except in Oyster Bayou (range 1 to 21 ‰). Discharge was about 12% higher in April, however winds were from the northeast, east, and southeast. Nitrate declined from 85 µg-at/l in the upper bay to 15 in the lower bay. Although there was a large net inflow through the upper bay inlet,

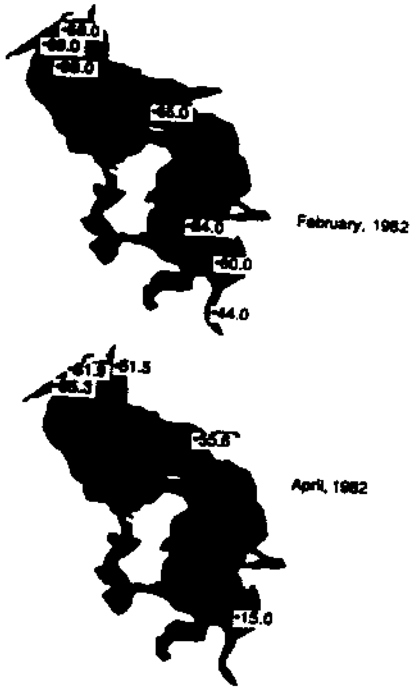

Figure 4. Distribution of nitrate in µg-at/l in Fourleague Bay in February and April, 1982, showing the variability in the lower bay versus the upper bay. During spring flood, the upper bay is always high in nitrate while the lower bay can be similar in character depending on tides and wind direction.

easterly winds prevented significant flow through the lower bay and deflected freshwater over surrounding wetlands.

Nutrient Distribution and Flux

Synoptic data were used to establish the concentration and distribution of nutrients and salinity. The Atchafalaya River is a source of high nitrate and phosphate while ammonium levels in the river are usually low. Nitrate in Atchafalaya Bay ranges from 45-174 µg-at/l, phosphorus from 1.1 - 3.9. After riverine water enters Fourleague Bay there is a trend of decreasing nitrate and phosphorus levels from the upper to lower bay. While th pattern of phosphorus disappearance is not consistent through the year, the disappearance of nitrate from the water column is dramatic, often complete, and occurs throughout the year. During non-flood months, the mean nitrate concentration in the upper bay and lower bay are 43.2 and 12.5 µg-at/l, respectively. This decrease in concentration is due to dilution of nitrate-rich river water by nitrate-poor salt water and to biological and chemical processes that remove nitrate from the water column. These processes may include uptake by primary producers, denitrification or dissimilatory nitrate reduction. Plots of nitrate and salinity versus distance were used to determine how much of the nitrate disappearance is biological and how much is due to saltwater dilution (Figs. 5a, b). The decrease in nitrate concentration far exceeds the decline anticipated from saltwater dilution alone, indicating that during non-flood months the bay is a sink for nitrate. The maximum decline was in the summer months (June-September) when NO_3^- dropped from 60 µg-at/l to 0 between the upper and lower estuary. During the spring flood, high-nitrate riverine water is pumped through the bay with an initial concentration of about 80 µg-at/l. Within the fresh upper estuary, nitrate levels decline rapidly to about 45 µg-at/l. In the saline lower bay the decline continues but is linear with respect to salinity, indicating simple dilution.

We measured nitrate fluxes into and out of the bay sediments. Losses of nitrate to the sediments averaged 19.4 µg-at/m^2/hr with loss rates as high as 1839. The strong flux into the bay bottom suggests that sediment denitrification is a major pathway of nitrate loss from the water column. The water column loss rates and sediment flux rates were highest in the upper estuary where the concentration of nitrate is also high. The lower estuary generally shows a small net flux of nitrate out of the sediments except during spring flood when lower bay nitrate is also high. Water column loss due to phytoplankton uptake may also be important and is under study.

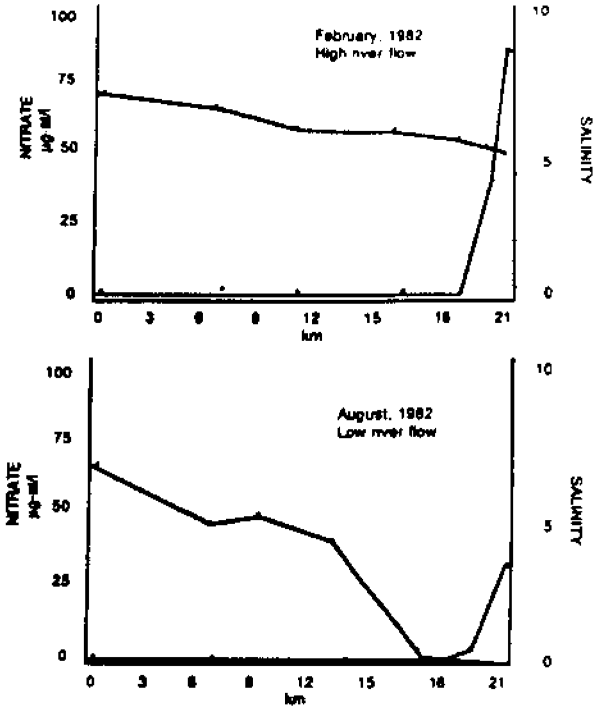

Figure 5. Nitrate and salinity profiles along the long axis of Fourleague Bay during spring flood and low water periods. X-axis is distance from the head of the bay in km. Lower graph shows that even during low water flow, the lower bay can be fresher than during spring flood. Netherless, nitrate is characteristically much higher throughout the bay during spring flood than during low water.

Inorganic phosphorus concentrations in the water column generally decreased toward the lower bay. Upper bay concentrations averaged 1.3 µg-at/l annually; the lower bay, 0.7. There was no significant net flux of phosphorus into or out of the sediments suggesting that water column loss may be due to phytoplankton uptake. Ammonium concentrations entering the upper bay vary between 0-20 µg-at/l and exhibit no seasonal pattern. Water column ammonia is lost through votilization and phytoplankton assimilation. Major inputs of ammonium to the water column are benthic, water column regeneration, and advective input from the river and surrounding marshes. Regenerative flux of ammonium into the water column from the sediments averaged 128 µg-at/m^2/hr.

Bay water flowing over the marsh seems to undergo processes which increase the concentration of ammonia. In April 1982 ammonium concentrations in marsh drainage reached 19.4 µg-at/l and averaged 7.5; bay ammonium concentrations averaged 2.5. Thus, marsh drainage may represent a significant ammonium input to bay waters. Nitrate concentrations in the marsh drainage averaged 51 µg-at/l while the water entering the marshes had an average concentration of 81. High rates of denitrification are apparently occurring in the marsh.

Bay water floods the marshes and deposits sediments and nutrients on the marsh surface. Accreting at the rate of 1.2 cm/yr the marsh receives 1.4-24.9 g/m^2/yr in total P and 1.3-120.0 g/m^2/yr in total Kjeldahl N imported in the sediments. In streamside marsh sedimentation rates are higher than inland and account for 99% of N imported. Ten per cent of N inputs are supplied by nitrogen fixation. Inland marsh receives less sediment gaining only 50% of annual N inputs through this process. In inland marsh nitrogen fixation provides the equivalent of 8 g N/m^2/yr or 50% of the total N input. Precipitation inputs are negligible.

N:P Ratios

In the first six months of the year, phosphate concentrations are relatively high throughout the bay. February concentrations range from 2 µg-at/l in the upper bay to 1 in the lower bay. In April concentrations everywhere vary slightly around 1 µg-at/l. During the high flow period extremely high concentrations of nitrate are supplied to the bay creating conditions of phosphate limitation with N:P ratios of 70:1 in the upper bay dropping to 40:1 in the lower bay. During summer Atchafalaya discharge is lowest, and less nitrate enters the bay. While N:P ratios of 50:1 are common in the upper bay, the rapid loss of nitrate from the water column results in an N:P ratio of 1.5:1 in the lower estuary, a condition of extreme nitrogen limitation(Figs. 6).

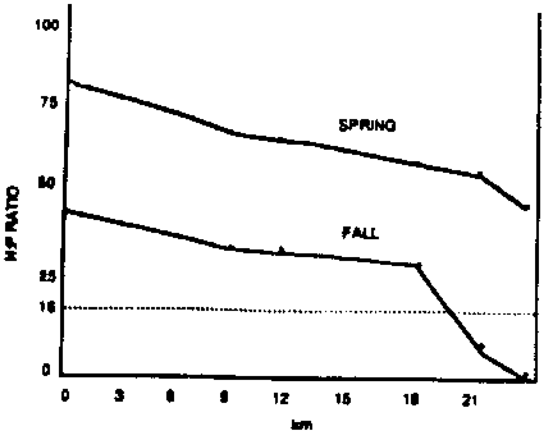

Figure 6. Ratio of inorganic nitrogen to inorganic phosphorus in Fourleague Bay in March, 1982 during spring flood and during October, 1982 during lowest riverflow. Transect in km is from upper Fourleague Bay near the river, toward lower near the Gulf of Mexico. Redfield's ratio of 16:1 is indicated.

THE VEGETATION COMMUNITY

Vegetation in the lower Atchafalaya River system (Fig. 3) begins as swamp forest (*Taxodium distichum*, *Nyssa aquatica*) near Morgan City, Louisiana. To the south is a large area of diverse freshwater marsh, which extends from west of the river to the northern end of Fourleague Bay. This area has the most diverse assemblages including emergent flotant marsh maidencane (*Panicum hemitomon*), wax myrtle floats (*Myrica cerifera*), submergent benthic lagoon plants (e.g., *Myriophyllum* spp., *Ceratophyllum* spp.), reed stands of cattail and roseau cane (*Typha* spp., *Phragmites* communis), choked canals of water hyacinth (*Eichhornia crassipes*), and arrowhead marshes (*Sagittaria* spp.). On the northwestern side of Fourleague Bay fresh marsh has developed on Point au Fer Island. The Atchafalaya delta is also a freshwater area, but the communities are structured by elevation and tidal influences into several discrete associations. Surrounding the south part of Fourleague Bay is a brackish marsh with a uniform assemblage of wire grass (*Spartina patens*) and three corner grass (*Scirpus olneyi*). These areas are burned in the late fall and early winter about every other year. The saltmarsh occupies a narrow band parallel to the coast. It is less than a km wide on Point au Fer Island and gets wider to the east. This area is predominantly smooth cordgrass (e.g., *Salicornia alterniflora*) and halophytic succulents (e.g., *Salicornia virginica*).

Surrounding Wetlands

The vegetation zones described above have changed drastically since the first accurate survey in 1948 (O'Neil 1949). The general trend is that increased freshwater input shifted the halophytes closer to the coast (Fig. 3). In 1948, brackish marsh of wire grass (*Spartina patens*) extended about 7.5 km in from the northern margin of Atchafalaya Bay. By 1968 (Chabreck et al. 1968), this marsh was fresh. To the east of the Atchafalaya River the brackish marsh extended 13 km north of the northern shore of Fourleague Bay in 1949. By 1968 the marshes north of Fourleague Bay were fresh and intermediate. In 1949, salt marsh occupied the southern border of Fourleague Bay. By 1968 this area had become a brackish marsh and salt marsh was limited to a narrow fringe along the Gulf of Mexico

The changes between 1968 and 1978 (Chabreck and Linscombe 1978) are less profound because the interval of time is smaller and the increased river flow had already exerted its impact on the area. The delta emerged during this time creating new freshwater marsh. Observations from recent work (1981-1982) in the area indicate that fresh marshes have replaced brackish marshes at the northern end of Fourleague Bay.

Atchafalaya Delta

The wetlands on the Atchafalaya delta are young; the first naturally vegetated subaerial land emerged in 1973. The vegetation communities that developed are controlled by the interaction of two hydrologic influences: river floods and tides. The spring floods of the river determine the height to which sediment is deposited on different parts of the emerging delta. Daily water level fluctuations (influenced by tides and weather events) determine the degree that different elevations of the delta are flooded. The daily flooding regime in turn also helps to determine the vegetative type.

It can be generally state that the vegetation associations which develop in a particular area are related to the hydrology of that area. At the lowest elevations in area most frequently and deeply inundated are beds of submerged aquatics (e.g., *Najas guadalupensis*, *Heteranthera dubia*). Arrowhead (*Sagittaria latifolia*) marshes comprise about 60 percent of the vegetated area in the delta and are found at an elevation so that they are tidally flushed. Black willow stands (*Salix nigra*) are at the highest elevations, infrequently flooded and well above the mean water level. This aboreal association remains standing after dieback and during the spring floods. Willows act to slow flood water, thus enhancing suspended sediment deposition and levee growth. At intermediate elevations between the arrowhead and willow association, the cattail (*Typha latifolia*) association is found. On islands whose levees are not sufficiently elevated, cattails may be found on the island heads, but when willows are present cattail stands are in intermediate zones above the arrowhead and below the willows. Finally, diverse assemblages with the greatest evenness and relative to the aforementioned assemblages are also found behind the protective stands of willow and cattail and mixed with arrowhead in intermediate elevations. These are composed primarily of annual plants and the dominant species are seasonally dynamic.

The structure and function of vegetation associations in the Atchafalaya delta are well integrated despite their youth. Woody vegetation which remains standing during the floods, help trap sediments and thus increase elevation. The resulting elevation gradient behind the island barrier produces an inundation regime and provides hydrologic protection so that highly productive and diverse wetland assemblages can develop including cattail, arrowhead, annual assemblages, and submerged aquatics.

The vegetation communities on the delta combine elements of an estuarine plant community structured by hydrologic fluctuation and a freshwater plant community characterized by spatially rapid and frequent changes in species composition.

THE BENTHIC COMMUNITY

The benthic community of the Atchafalaya delta is a highly dynamic, productive system. Initial survey collections made in 1981 ranged in abundance from a high of 94,462/m^2 macrofauna in the mudflats bordering delta islands to a low of 1,617/m^2 in a main channel. Mean abundance of 17,639/m^2 macrofauna was not significantly different from the mean abundance in another Louisiana low salinity estuary, Lake Pontchartrain, which had 23,458/m^2. Although these two estuarine areas exhibited similar mean macrofaunal abundance, the community structure at the two sites was quite different. In Lake Pontchartrain 94% of the abundance is contributed by the Mollusca, principally by 2 small hydrobid gastropods. Hydrobids have a productivity to biomass (P/B) ratio of from 1.9 to 2.6 (Siegismund 1982). In the Atchafalaya Delta the macrofauna is dominated by worms, chiefly Polychaeta and Oligochaeta. Most of these worms have high P/B ratios ranging from 5.5 to 9.3 (Waters 1977). This high turnover rate is characteristic of opportunistic species which are the pioneer, colonizing fauna in new habitats. The resultant high productivity of the benthos has created a rich nursery habitat for blue crabs, shrimp, and many estuarine dependent species of fish.

Diversity of the Atchafalaya Delta benthic community has increased from 1.08 (Dugas 1978) in 1974 to 1.82 measured at present. As predicted for new habitats (Sanders 1968) the diversity is low compared to older, more established, brackish areas of estuaries which have diversities of 2.2 to 2.8 (Rosenberg and Moller 1979). The diversity is, however, significantly higher than the 1.13 found in the heavily polluted, disturbed Lake Pontchartrain (Sikora and Sikora 1982a).

Meiofauna numbers ranged from an abundance of $11.26 \times 10^6/m^2$ in mudflats to $0.61 \times 10^6/m^2$ in main channel habitats. The mean of $3.91 \times 10^6/m^2$ is five times higher than the mean for meiofauna abundance in Lake Pontchartrain. The meiofauna are frequently resuspended in this early depositional environment, and provide a food source for young fishes in a system too turbid to provide enough phytoplankton for a significant zooplankton community.

Many of the species of the Atchafalaya delta are marine in origin, although the area is almost continually fresh. The abundance of these organisms suggests that a fairly typical estuarine benthic community is doing well in this freshwater environment.

THE NEKTON COMMUNITY

The dynamics of the coastal Louisiana fish fauna has been greatly influenced by the cycle of growth and decay of river deltas and the change in salinity regimes that accompany these cycles as described in the geology section.

Gunter (1945, 1950), Turner and Johnson (1973), Peterson and Peterson (1979), Thompson et al. (1980), Dovel (1981) and others have discussed the importance of bays and estuarine waters as nurseries for fishes. The concept of "estuarine dependent" species has developed from the widespread pattern of many fish species spending at least their first year of life in the estuaries. Despite a growing data base supporting the concept of an estuarine nursery, Walford (1966) and Schubel and Hirschberg (1978) have challenged the essential nature of estuaries. We used a classification scheme, based on ecological affinities, to evaluate the importance of the Atchafalaya Delta as a nursery ground.

Species, collected by trawls in channels and seines in bays, lagoons and beaches, were place into one of four "ecological affinity" categories based on a literature survey of the major salinity and coastal location patterns of their life history. The four ecological affinity types are:

(1) Freshwater - (FW) affinities primarily with freshwater (below 0.5 ppt); will enter estuaries; have slight salinity tolerance.

(2) Estuarine - (ES) affinities within estuary; spends much or most of life cycle there; spawns in estuary.

(3) Estuarine/Marine - (ES/M) affinities with estuary are primarily as young-of-the-year; spawns in marine (or rarely freshwater) habitat.

(4) Marine - (M) affinities primarily with open inshore/offshore marine habitat for all stages of life cycle; will enter estuary from time to time; spawns offshore.

Table 1 shows the monthly variation in the Atchafalaya fish community classified by "ecological affinity." Over the study period the percentage (based on number) of freshwater, estuarine, and estuarine/marine components were approximately equal, 30.2%, 25.4% and 31.7% respectively. The monthly figures for the fish assemblages show some variation, with April and October having more estuarine/marine than freshwater species. Marine species were rare (8 of 63 species). The yearly cycle of estuarine/marine species is related more to temperature than salinity. The salinity in the Atchafalaya delta varies from freshwater to a maximum of 1.6 ppt, with the higher salinity entering the delta between August and November (Table 1). This coincides with the lowest river flows and strongest south winds off the Gulf of Mexico.

Average water temperatures were similar to that found in many Louisiana estuaries, however the fluctuations were larger (Perret et al. 1971, Thompson et al. 1980). Several of the semi-enclosed, shallow island lagoons and flats reached temperatures higher than normally found in Louisiana estuaries. Temperatures varied between 6.5° and 37°C (Table 1), with the lowest temperatures associated with periods of high river discharge.

Earlier reports (Hoese 1976, 1981) hypothesized that with increasing amounts of fresh water being introduced into the Atchafalaya Bay, the nursery capacity of the area would be lost. Hoese (1981) suggested that in addition to salinity alterations, cold temperature effects from winter and spring floods may play a significant role in depressing the productivity of the system.

Data from our ongoing study, started in March 1981, suggests that with the emergence of the delta islands, the region has regained its nursery capacity, but that the large amounts of cold river water directly entering the system effectively "shuts down" most of the fish activity. The delta islands provide areas of "temperature refugia" and there is great potential to reduce the negative effects of cold river water if delta building continues.

The two numerically most abundant species were (1) the bay anchovy, Anchoa mitchilli, and (2) the gulf

Table 1 . Ecological affinities of fish community and temperature, salinity characteristics of the Atchafalaya Delta, March-December 1981.

Month		M	A	M*	J	A	S	O	N	D	Total
	Species	23	37	38	33	33	29	39	31	28	63
Freshwater	No.	7	7	10	10	9	8	10	10	8	19
	%	30.4	18.9	26.3	30.3	27.3	27.6	25.6	32.2	28.6	30.2
Estuarine	No.	9	13	13	13	12	12	11	12	12	16
	%	39.1	35.1	34.2	39.4	36.4	41.4	28.2	38.7	42.9	25.4
Est/Marine	No.	6	15	12	9	11	9	15	9	7	20
	%	26.1	40.5	31.6	27.3	33.3	31.0	38.5	29.0	25.0	31.7
Marine	No.	1	2	3	1	1	0	3	0	1	8
	%	4.3	5.4	7.9	3.0	3.0	0.0	7.7	0.0	3.6	12.7
Salinity		FW	FW	FW	FW	0.8	0.2	0.6	0.4	FW	
Temperature		14.3	22.2	22.6	28.9	26.6	25.8	19.4	18.0	13.8	

*no samples made in June 1981.

menhaden, Brevoortia patronus, each making up roughly a fourth of the community (Table 2). The blue catfish, Ictalurus furcatus, contributed most to standing stock. The contrast between the species which dominated based on number versus weight illustrates that estuarine/marine species, which are mostly young-of-the-year, are the most numerous, while the freshwater species, largely adults, dominated the biomass.

Hoese (1981) has questioned whether a change in fish community structure will take place as Atchafalaya Bay becomes more fresh. A shift to a freshwater community would eliminate the area as a nursery for estuarine and marine nekton. The delta area currently supports a diverse fish fauna that has major contributions from estuarine and estuarine/marine members. It is virtually identical to many other Louisiana estuarine fish communities. The novelty is that it exists in a freshwater environment. Because Louisiana's estuarine fish fauna has always been confronted with adapting to the cycles of delta growth and decay, we believe they will continue to use the delta area as a nursery.

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Table 2. Fifteen most abundant fish species, Atchafalaya Delta, March-December 1981.

SPECIES	ECOL. AFFINITIES	NUMBER	% TOTAL
1. *Anchoa mitchilli*- Bay Anchovy	ES/M	32,242	24.8
2. *Brevoortia patronus*- Gulf Menhaden	ES/M	31,456	24.2
3. *Cyprinodon variegatus*- Sheepshead Minnow	ES	17,378	13.3
4. *Fundulus grandis*- Gulf Killifish	ES	11,823	9.1
5. *Mugil cephalus*- Striped Mullet	ES/M	9,715	7.5
6. *Micropogonias undulatus*- Atlantic Croaker	ES/M	7,621	5.9
7. *Ictalurus furcatus*- Blue Catfish	FW	4,043	3.1
8. *Menidia beryllina*- Tidewater Silversides	ES	2,756	2.1
9. *Citharichthys spilopterus*- Bay Whiff	ES/M	2,252	1.7
10. *Gobionellus boleosoma*- Darter Goby	ES	1,788	1.4
11. *Gobionellus shufeldti*- Freshwater Goby	ES	1,484	1.2
12. *Gambusia affinis*- Mosquitofish	FW	1,438	1.1
13. *Cynoscion arenarius*- Sand Seatrout	ES/M	1,232	0.9
14. *Membras martinica*- Rough Silversides	ES	940	0.7
15. *Leiostomus xanthurus*- Spot	ES/M	616	0.5
			97.5

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MANAGEMENT IMPLICATIONS OF RESEARCH IN THE ATCHAFALAYA DELTA REGION*

J.W. Day, Jr., C.J. Madden, W.H. Conner, and R. Costanza

INTRODUCTION

One of the most exciting and encouraging processes taking place along the Louisiana coast is the emergence of the new Atchafalaya Delta (Fig. 1). Within the general context of a deteriorating coast, the Atchafalaya Delta region offers the possibility of creating new wetlands on a broad scale. Since the delta first emerged in 1973, over 50 km^2 of new land have formed in Atchafalaya Bay. In addition, there have been profound changes in adjacent waters and wetlands and along the coast of the Chenier Plain.

Since the delta first emerged, there has been an active research program designed to develop an understanding of the processes taking place. These studies have included research on physical, geological, chemical and biological processes. Along with the evolving delta there is also an evolving new ecosystem. An understanding of these processes allows a capability for prediction of what the system will be like in the future, what impacts different human activities will have, and what will be the effects of different management activities.

In this paper we will briefly review studies of the area and outline management implications of these studies. These include: 1) The new Atchafalaya delta. Studies of sediment dynamics and vegetation succession suggest ways in which delta growth can be increased. 2) Older marshes have responded dramatically to increased freshwater, sediment, and nutrient influxes suggesting that deteriorating marshes can be rejuvenated. 3) Riverine input to shallow inshore lakes and bays seems to stimulate productivity of these areas. 4) Westward sediment transport along the coast is leading to accretion along the Chenier Plain shore. 5) A spatial landscape simulation model has been effective in integrating information and predicting future conditions under various management alternatives.

EMERGENCE OF THE ATCHAFALAYA DELTA

The Atchafalaya River has been a distributary of the Mississippi at least since the mid-1500's (Fisk 1952). The Atchafalaya is about 300 km shorter than the Mississippi from the point where the two channels intersect to the gulf, making the Atchafalaya hydrologic gradient much steeper. In the course of time, the Mississippi River will divert into the Atchafalaya (Roberts et al. 1980). Because of this, the Corps of Engineers constructed a control structure at Old River to limit the flow in the Atchafalaya to approximately 30% of the combined flow of the Red and Mississippi Rivers. During the first half of this century, the Atchafalaya River deposited sediments in the Atchafalaya Basin, filling much of it. After about 1950 the locus of deposition shifted to Atchafalaya Bay which also began to fill in. The bathymetry of the bay had changed very little between the 1850's and the early 1950's (Cratsley 1975). Between 1952 and 1962, sedimentation in the bay accelerated (Shlemon 1975), and by 1972, almost two meters of fill had been deposited in the Wax Lake and Atchafalaya delta lobes.

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Figure 1. Regional setting, Atchafalaya Bay and surrounding areas.

The first significant subaerial exposure of the delta occurred in 1973, during the high water of that year. Floodwaters not only carried sediment from the Mississippi River but eroded channel banks along the Atchafalaya River and, for the first time, sand was deposited in Atchafalaya Bay (Roberts et al. 1980). Since then a complex network of sand lobes has formed, separated by branching distributaries (van Heerden and Roberts 1980a and 1980b, Fig. 2). This is characteristic of a delta building into unstratified, low-energy, shallow water environments (Welder 1959; Wright and Coleman 1974). Van Heerden and Roberts (1980a and 1980b) presented a schematic model of such delta development (Fig. 3) where many of the channels eventually close off by the process of lobe fusion. Distributary channels in the eastern half of the delta underwent reductions in cross-section between 1973 and 1979 (van Heerden and Roberts 1980a and 1980b). Van Heerden and Roberts (1980a and 1980b) concluded that the eastern half of the delta would cease to prograde in the long term. In the short term, growth is still possible as the main channels of the eastern delta consolidate. Areas between these channels will come to resemble interdistributary bays of the modern Mississippi Delta (van Heerden and Roberts 1980a and 1980b).

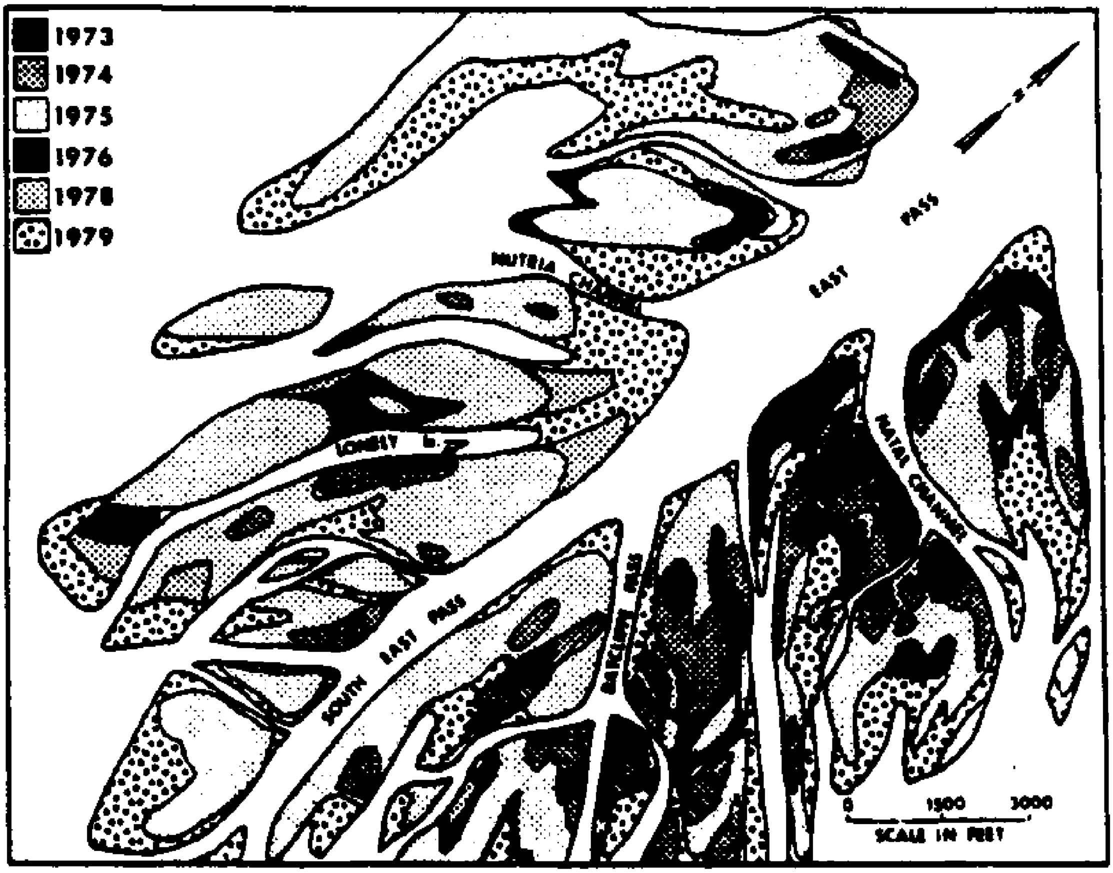

Figure 2. Extent of subaerial depositional environments, 1977-1979. For simplicity, portions of the delta are not shown (van Heerden and Roberts 1980a).

The dynamics of the process of deltaic evolution suggests a number of ways that management could lead to a greater area of wetland formation. Many channels which form during the development of bifurcating channels subsequently close. In some instances, it might be possible to reopen certain channels so that sediment accretion continues in certain areas. Spoil from the navigation channel could also possibly be used to create shallow areas which would then vegetate. Spoil placement might also be used to direct delta growth in desired directions.

Several studies have shown that westward sediment transport in the nearshore Gulf is leading shoreline accretion along the Chenier Plain (Wells and Roberts 1980; Wells 1983; Wells and Kemp 1981, 1982). An interesting and exciting possibility for stabilizing and enhancing vegetation establishment on these mud flats is the construction of brush fencing as in the Netherlands (Wagret 1968). This technique involves construction of fencing which enhances sedimentation and retards erosion. In the Netherlands, over 100 km^2 of wetland have been created over the past several decades using this approach.

VEGETATION DEVELOPMENT IN THE DELTA

The first subaerial land appeared in the Atchafalaya delta in 1973, and appreciable vegetation cover appeared in 1974 (Fig. 4). At the end of the 1974 growing season, there were about 394 ha of vegetation. Vegetated area generally increased over time, reaching 463 ha in 1975, and 1142 ha in 1976 (Baumann and Adams 1980). The increase in vegetated area was small in 1977, and there was a slight decrease in area during 1978. This decline in area was probably due to a combination of low river discharge and erosion (Adams and Baumann 1980). The 1979 flood was sufficient to cause an increase in vegetative area once again. Vegetation increase was less on the eastern half of the delta, probably as a result of lower rates of sedimentation and island formation discussed above.

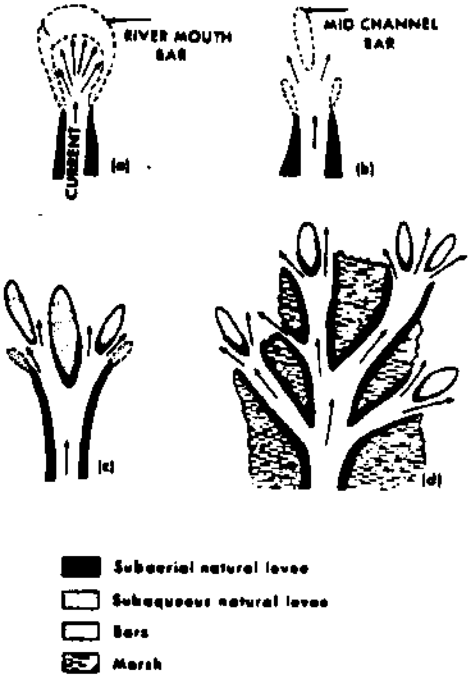

Figure 3. Schematic diagram of delta development (van Heerden and Roberts 1980a).

Adams and Baumann (1980) made several generalizations about vegetation establishment and growth. During high water years, the combination of prolonged submergence and low water temperatures seems to inhibit vegetation and growth. Prolonged spring floods shorten the growing season by reducing light penetration and lowering soil temperatures. Maximum increases in vegetated area occur when a high flood year supplying the sediment and seed is followed by a low-flood year, with warmer soil temperatures and greater light penetration.

There is a characteristic pattern of vegetation development in the delta (Johnson et al. 1985). Initially, extensive algal mats seasonally colonize shallow intertidal mud flats. As elevations of the delta islands increase, emergent vegetation becomes established. The characteristic zonation pattern on a typical delta island is shown in Figure 5. Johnson et al. (1985) described three vegetation associations characterized by a single species (*Sagittaria latifolia*, *Salix nigra*, and *Typha latifolia*) and a mixed community of *S. latifolia*, *Scirpus* spp., *Cyperus* spp. and others. *Salix* occurs on the heads of islands where the effects of river flow are greatest. During spring floods, current velocity decreases as water passes over the head of an island and sediments are deposited. Thus, these areas have the highest elevation and sand content. *Salix* can withstand the high physical stress and sedimentation rates. It does not occur on young islands which develop on the downstream end of the delta. *Typha* becomes established on intermediate and mature islands where *Salix* is present, in effect growing in the "protected shadow" of *Salix*. *Sagittaria* is the first emergent species to invade mouth bar islands. The top of the plant dies back in winter, but re-emerges in early summer after the spring flood. *Sagittaria* can grow on all areas of the islands. Other species, such as *Salix*, become established in the *Sagittaria* stands as elevation increases.

Although *Sagittaria* is the first species to become established, *Salix* is the first species to introduce strong biological control on the succession. *Salix* provides protection from the river and allows *Typha* to become established. As the *Salix* growth continues, it becomes an increasing barrier to the movement of floodwater, and a diverse and seasonally dynamic freshwater wetland plant association develops (Johnson et al. 1985).

Based on these studies of zonation and succession, Rejmanek et al. (1987) modeled vegetation dynamics on the delta islands. They concluded that succession during active delta building is heavily dependent on the sequence of flood conditions and on the intensity of grazing. From their analysis, they developed a generalized model of long-term vegetation dynamics in the Mississippi deltaic plain (Fig. 6). The importance of grazing is demonstrated in an ongoing study in the Atchafalaya delta. Preliminary results from large exclosures which exclude nutria show dramatic increases in emergent plant biomass (G. Peterson, Center for Wetland Resources, LSU, Baton Rouge, LA, pers. comm.)

These studies suggest several potential management strategies. As indicated in the preceding section, physical alteration of the delta (such as keeping a channel open or creating a new one) may prolong delta growth in a certain area. Likewise, this type of activity would serve to enhance vegetation development. The exclosure studies indicate that vegetation biomass production could be enhanced by controlling the nutria population in the delta. The effects and methods for doing this are fruitful areas for future research. In addition, researchers have noted that the Point au Fer reef reduces wave energy and allows more rapid delta growth and vegetation establishment (van Heerden and Roberts 1980a and 1980b; Adams and Baumann 1980). Thus, an important management implication is that these reefs should not be disturbed.

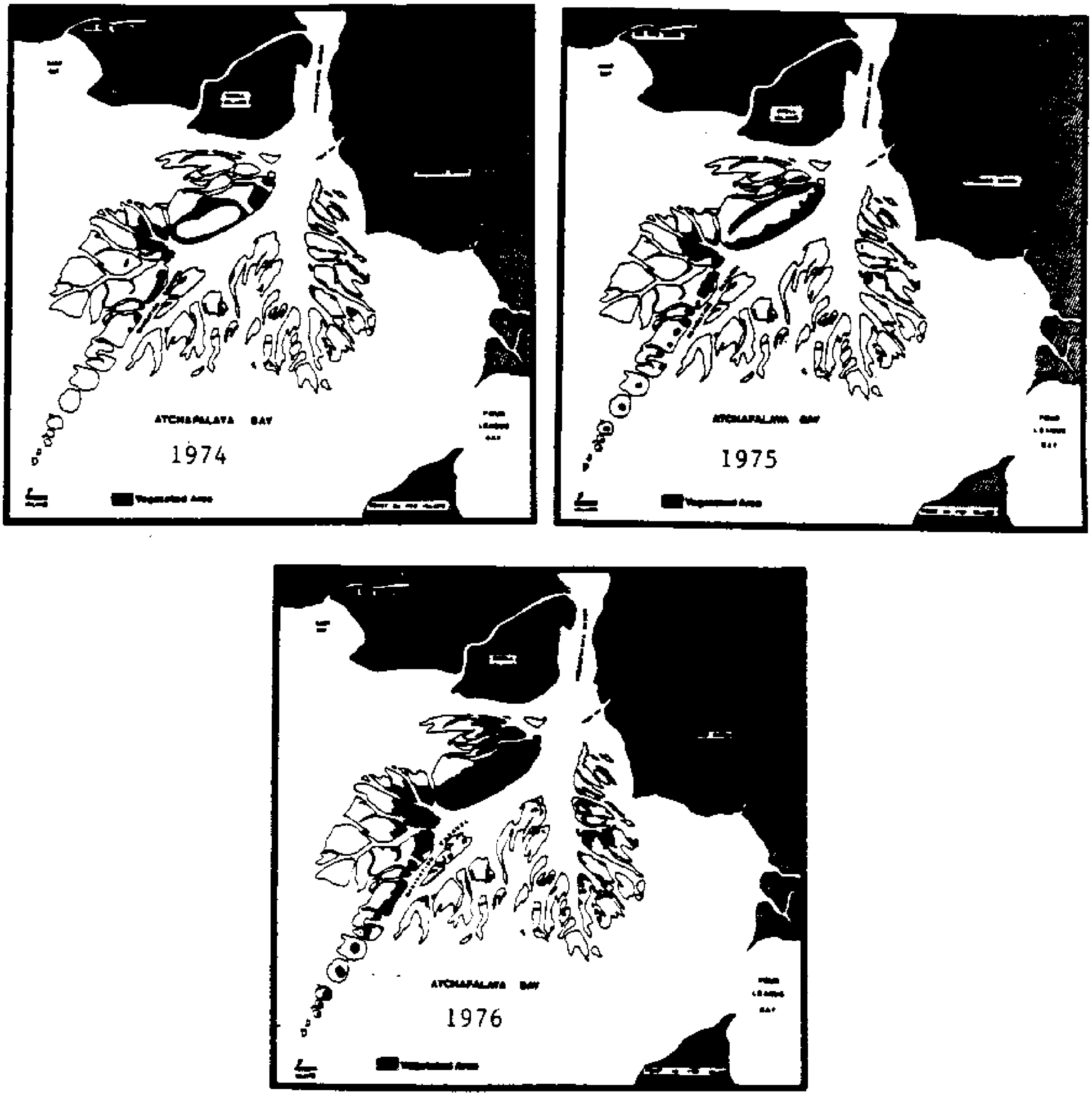

Figure 4. Atchafalaya delta vegetation maps, 1974-1976 (Adams and Baumann 1980).

CHANGES IN OLDER, PRE-EXISTING WETLANDS

The studies cited above show that sedimentation is important in delta development, but the role of sedimentation in maintaining or building adjacent, pre-existing wetlands has not been so well understood. Baumann and Adams (1981) measured wetland area from maps and aerial imagery. They found that the wetlands adjacent to the lower Atchafalaya River and in the western Terrebonne region were deteriorating rapidly before the emergence of the Atchafalaya delta and the floods of the early 1970's (Fig. 7). There was a total net wetland loss of 7,805 ha between 1955 and 1972. In contrast, there was a much reduced rate of land loss and, in some cases, a net wetland gain from 1972 to 1978. Generally, the areas closest to the source of sediment experienced the greatest wetland gains. Those sites farther away from the river experienced wetland loss, but the trend was highly variable and generally reduced. The area of greatest land loss (-346 in Fig. 7) occurred in an area of flotant, or floating marsh, that may have been damaged during the abnormally high and long-term flooding that occurred during 1973-1975. This loss appears to be

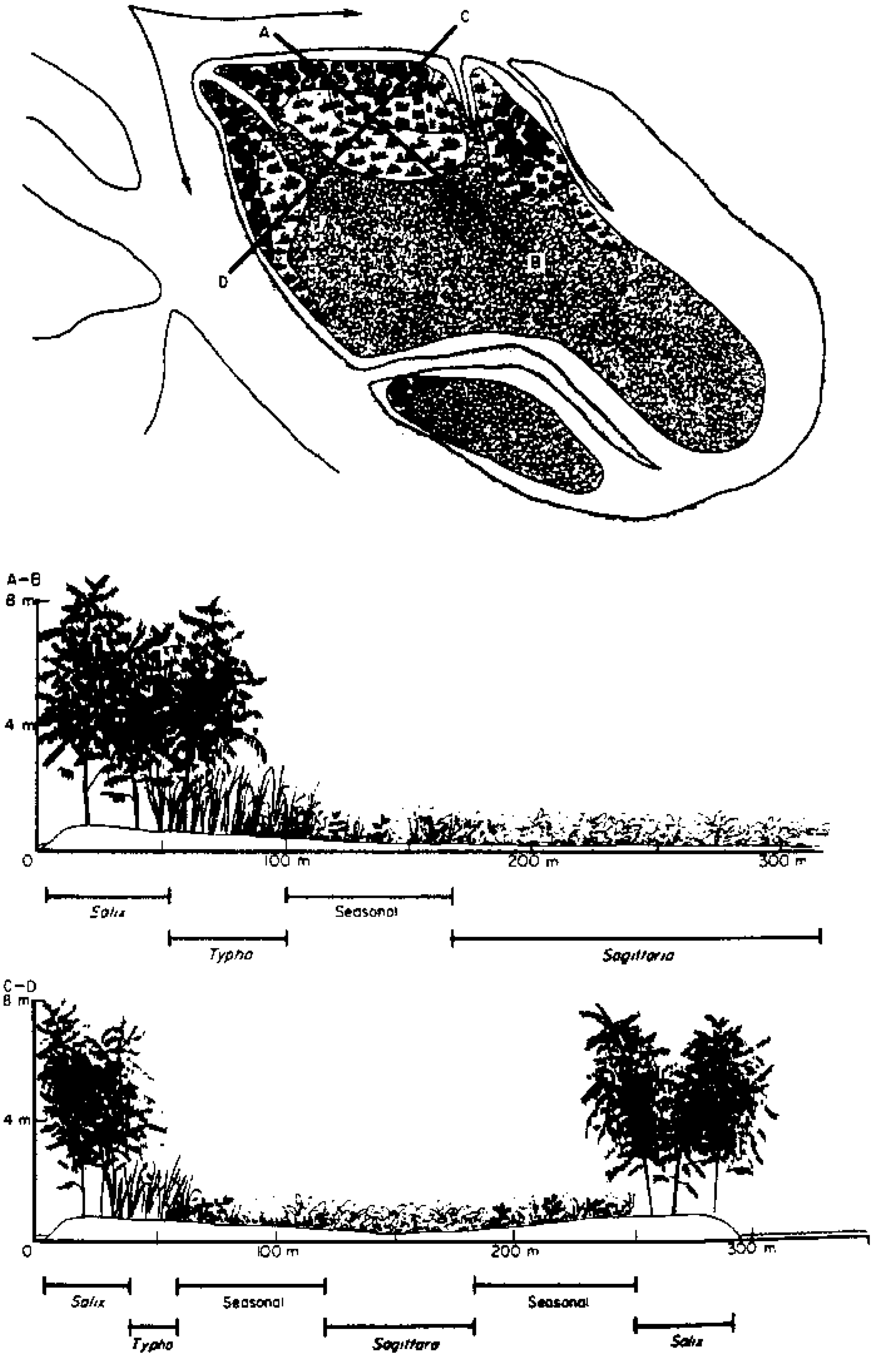

Figure 5. Illustration of a typical mouth-bar island in the Atchafalaya River delta, Louisiana, showing both aerial and cross-sectional views. Arrows represent direction of predominant water flows (Johnson et al. 1985).

temporary as the area is presently recovering (Kinler et al. 1980). Overall, the marshes peripheral to the new Atchafalaya delta experienced a reversal from 421 ha/yr lost to 66 ha/yr gained. Clearly then, influx of Atchafalaya river water into these marshes is having a dramatic effect. There have been a number of studies which provide insight as to how this impact is taking place.

Adams and Baumann (1980) estimated that for every 10 tons of sediment coming into the Atchafalaya system, 2 tons were deposited into the basin proper, and eight tons were dispersed into the bay, neighboring

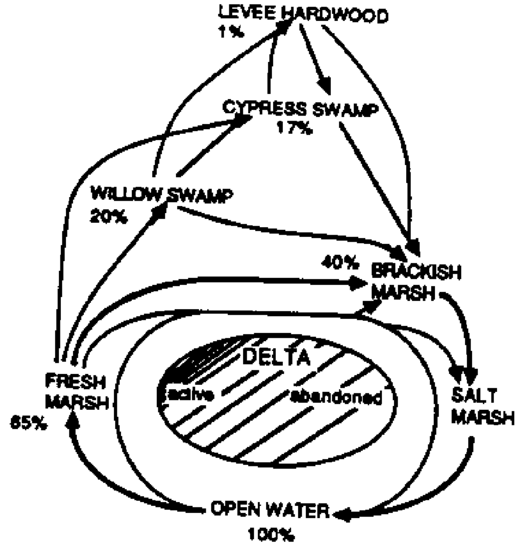

Figure 6. Flow diagram of long-term cyclic vegetation dynamics in the Mississippi River deltaic plain. The values show the possible areas in percentage (Rejmanek et al. 1987).

wetlands, and the Gulf of Mexico. The ratio is highly variable and depends upon the magnitude of the discharge during flood periods as well as prevailing winds. For predictive purposes, Adams and Baumann assumed 60% of the sediments in suspension in the lower Atchafalaya River and Wax Outlet will be dispersed in the peripheral marshes and offshore regions (based on sediment input and shoaling rates of Atchafalaya Bay during 1967-1977). Wells and Kemp (1981) working in the Chenier Plain region west of Atchafalaya Bay estimated that 50 x10^6 m^3 of sediment per year are carried westward from the Atchafalaya Bay resulting in increasing mudflat sedimentation.

For much of the year, there is a strong net transport of water and sediments from the Atchafalaya River into the western Terrebonne marshes (Stern 1986, Stern et al. 1986). A major avenue of transport is the Bayou Chene-Bayou Penchant system, although many smaller streams also carry sediment-laden water. Stern et al. (1986) reported that bayous which are tidally dominated during low discharge are riverine dominated during high discharge. Net transport of water, sediments, and nutrients are two orders of magnitude higher during high river flow. Comparison of suspended sediment and nutrient concentrations in the river and a bayou indicated that these materials are retained in the wetland system.

Actual rates of sedimentation have been measured at streamside and inland sites of the Atchafalaya system by Baumann et al. (1984, Table 1). The input of sediments to the streamside marshes (1.3 cm/yr) is greater in the spring and summer during spring flood events. Sedimentation in inland marshes (0.6 cm/yr) is significantly lower than streamside sedimentation and occurs mainly during the summer and fall/winter. Tidal flooding and winter storms tend to be largely responsible for introducing sediment to the inland marshes (Miller 1983). These studies reveal the magnitude and mechanism of sediment input to the marshes and show the importance of the river in maintaining and building wetlands.

The introduction of sediments has a direct influence on accretion rates in the surrounding area (Table 2). Future growth of the Atchafalaya delta is expected to take place at the rate 11.9 km^2/yr and infilling of older marshes is occurring at 4.9 km ^{2}/yr (Baumann and Adams 1981). A reversal of the Chenier Plain beach retreat is occurring ar a rate of 1.1 km ^{2}/yr (Wells and Kemp 1981).

Table 1. Seasonal sediment inputs (percent of net accumulation) at streamside and inland marshes, 1981-82 (after Baumann et al. 1984).

Season	Streamside	Inland
Spring	42.4	15.9
Summer	48.7	51.9
Fall/Winter	8.9	31.2

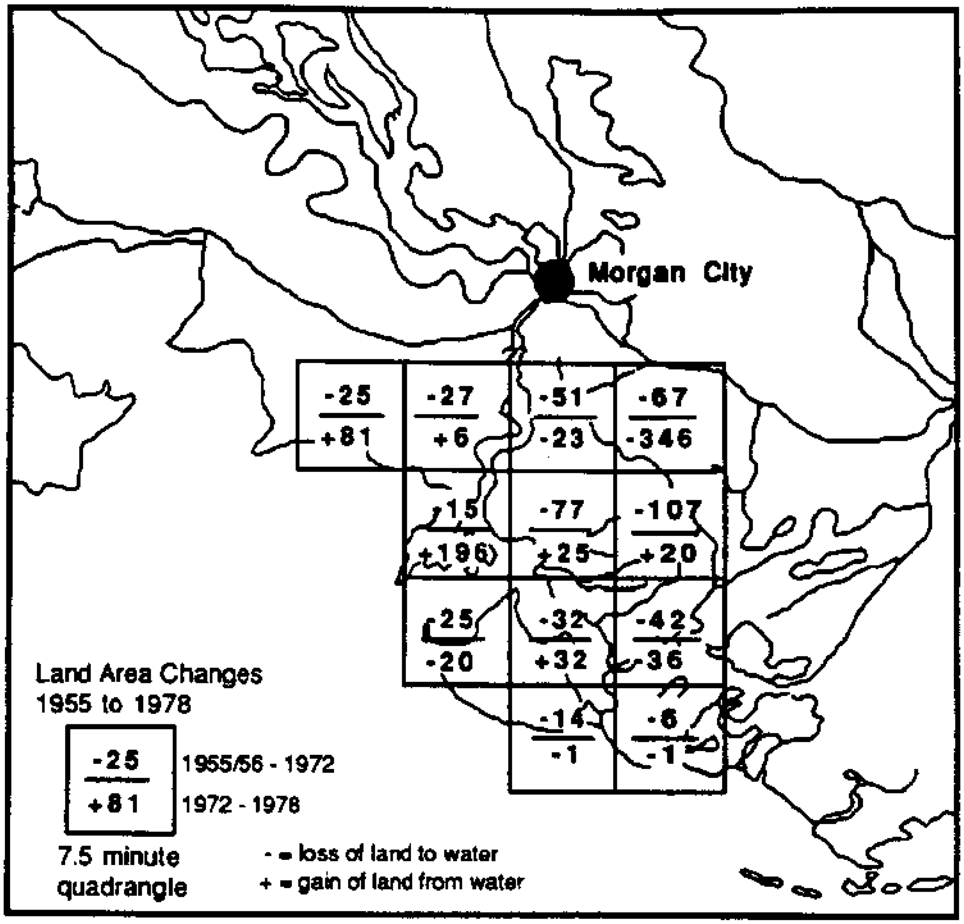

Figure 7. Land area changes for the marshes surrounding Fourleague Bay, 1955-1978. All values are expressed as hectares per year (after Baumann and Adams 1981).

Table 2. Land gain as the result of sedimentation by the Atchafalaya River (after Day and Craig 1982).

Activity	Land gain(km^2/yr)
New delta growth	11.9
Chenier plain beach buildup	1.1
Infilling of marsh area	4.9
Total	17.9

Unfortunately, the hydrology of the Atchafalaya Bay marshes has been extensively altered by the dredging of numerous waterways and access canals (Wang et al. 1983). The construction of levees along the Atchafalaya River and in the marshlands surrounding the Atchafalaya Bay area has the potential to cause sediment needed for wetland creation and maintenance to be lost to offshore waters just as has happened in the present Mississippi River delta (Baumann and Adams 1981). Modeling work by Wang (1987) has shown that levees decrease water stages, lessening water circulation, thus shifting sediment loads and decreasing the sedimentation potential of some marsh areas. The only feasible means of combating subsidence in wetlands is through the addition of sediment to the marsh surface (Baumann and Adams 1981).

Work is now being done on developing a spatial model of the marshes surrounding the Atchafalaya Bay area (Sklar and Costanza 1986; Sklar et al. 1985; Costanza et al. 1986). Spatial modeling has potential for use in coastal management because it can be used to project the impacts of natural and man-made stresses on the structure and function of large landscapes (Sklar and Costanza 1986).

All of these studies indicate that the influx of river water into older marshes of the Atchafalaya delta region leads to maintenance of the wetlands. One clear management implication is that freshwater and sediment input should be maximized. Thus, projects such as the Avoca Island levee (Fig. 1) should not be constructed. The purpose of this levee is to reduce backwater flooding, but Baumann and Adams (1981) showed that flooding would become increasingly worse in the area because of subsidence. The understanding gained from work in the western Terrebonne marshes also bears on the issue of marsh management plans using semi-impoundment and water control structures. Since this area is one of major freshwater and sediment input, careful consideration should be given to any plan which limits either channelized or overland sheet flow of freshwater and sediments. The abundance of freshwater and sediments offers an exciting opportunity to address the problems of salt water intrusion and land loss.

ENHANCEMENT OF PRODUCTIVITY OF SHALLOW INSHORE WATERS AS A RESULT OF RIVERINE INPUT

Shallow bays may be important sites of high coastal productivity because of the conjunction of riverine input, wetland habitat and marine waters. These bays receive high sediment and freshwater input. Fourleague Bay has been well studied, and it is the site of high planktonic primary production as well as an important nursery zone for fishes.

Fourleague Bay lies 10 km to the east of the Atchafalaya River mouth, and its chemistry is strongly influenced by both the river and the Gulf of Mexico. Measurements of water fluxes through the upper bay entrance during periods of high river flow in the months of spring flood in 1982 averaged 150 m^3/s (Denes 1983), equivalent to a flushing period of 6 days (Madden 1986). During fall low river discharge conditions, the average water input to the upper bay was 17 m^3/s, consistent with a bay flushing period of 61 days.

Upper Fourleague Bay is fresh throughout most of the year except during the August-December period of low river flow when salinity averages 1.5 ppt in the upper bay. The saline waters of the Gulf of Mexico influence lower Fourleague Bay in all seasons except during the strongest spring freshets. During spring flood, the bay is almost completely fresh and only in the lowest section of the estuary at Oyster Bayou does salinity abruptly increase to near gulf levels (Madden 1986). When fresh water input is at its lowest in October and November, salinity gradually increases with distance from the river, from an average of 10 ppt in the upper bay to about 32 ppt in the lower bay. The entire bay averages 1.5 m in depth which promotes a well-mixed, well-oxygenated water column with very little vertical stratification.

A proposed extension of the Avoca Island flood protection levee would border the Atchafalaya River along its eastern bank (Fig. 1) continuing through the eastern half of Atchafalaya Bay. The intent is to prevent backwater flooding of lowland urban areas north of the estuary. However, the levee would also cut off Fourleague Bay and the surrounding marshes from the Atchafalaya River and direct the flow straight offshore.

Turbid, nutrient-rich river water flows into shallow Atchafalaya and Fourleague Bays and the fresh plume of river water moves up and down the bay depending on river discharge, tides and wind conditions. During the spring, fresh water fills the bays for long periods of time. From August to November (low flow), the bay is more often dominated by saline Gulf waters, but there is still significant fresh water input.

The nutrient regime in Fourleague Bay is controlled by internal regenerative processes in addition to external inputs. An important focus in coastal ecology today is the relative contributions of new and remineralized nutrients in sustaining estuarine productivity (Nixon 1981b, Boynton et al. 1982). Pulses of "new" nutrients enter Fourleague Bay from the Atchafalaya River during spring flood (Madden 1986). Although inorganic nutrient concentrations peak during the annual high flood, aquatic primary productivity is highest in late summer and early fall, when temperatures peak and river discharge is low. The bay system is productive because of a high degree of recycling. Material and energy are constantly being recycled between water column and bottom and between organic and inorganic forms. Because this material is kept within the bay for longer periods of time by sediment-water column cycling and by frontal entrainment, inflowing energy (both organic and inorganic) can be used more efficiently in the shallow estuary.

The Atchafalaya River is the major source of advected nutrients to the bay (gulf waters are low in nutrients) and we hypothesize that the river is also the ultimate source of most remineralized nutrients in Fourleague Bay, via the sediment cycle. When nutrient-rich river water flows over an area of bottom, there is a strong uptake of inorganic nutrients, especially nitrate and organic matter (Teague 1983). When higher salinity water flows over the same area (on the rising tide or in fall during low river flow) ammonium is released into the water column. New inorganic nutrients can be thought of as "charging" the sediment nutrient supply via direct uptake by benthic processes such as dissimilatory nitrate reduction to ammonium, and incorporation by phytoplankton which are then grazed or die and sink to the sediments. As bacterial decomposition occurs or redox conditions change, these sediment nutrients can be liberated from the sediments and released to the overlying water column. This uptake and release cycle takes place on time scales from a few days to seasonally. With each tide change, any specific location in the bay will either be taking up or releasing nutrients depending on the diffusion gradient between the sediments and overlying water.

On a seasonal scale, during high river flow, the bay is inundated for long periods by nutrient-rich fresh water and the sediments become progressively more saturated with nutrients. The sediments that are charged during spring flood release nutrients to the water column during the summer when riverine input of "new" nutrients is at its lowest. These nutrients stimulate primary production in the clearer, higher salinity water. The sediment charging-release cycle seems to stabilize the nutrient supply and fertilize the overlying water column, thus extending the growing period and enhancing overall primary production in Fourleague Bay.

With distance from the shore into the Gulf of Mexico, as depth increases, bottom sediments become progressively decoupled from the whole of the water column. At depths of 5 to 8 meters, normal levels of turbulence are not adequate to mix the water column to the bottom and periods of stratification may occur (Fig. 8). Regenerated nutrients may be retained in bottom waters, especially during the warm season, and not reach the upper layer of the water column where they can be used in phytoplankton production. We believe that such water column-

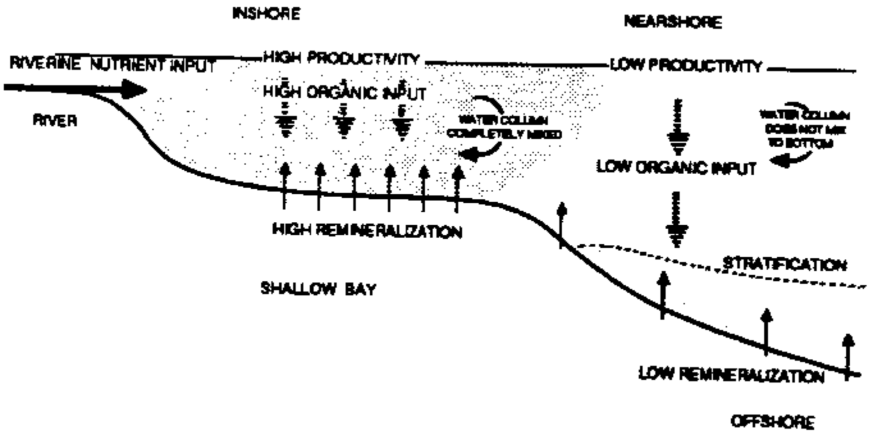

Figure 8. Feedback loops involved in maintaining high nutrient, high primary production regime in shallow bays. High riverine and regenerated nutrient inputs stimulate high primary production. The organic material which settles out of the water column stimulates higher benthic remineralization. In shallow bays, wind mixes regenerated nutrients throughout the water column. In deeper offshore waters, wind mixing is less effective in distributing nutrients. Lower productivity results in lower sediment regeneration rates and periodic stratification may create low oxygen "dead zones."

bottom decoupling has two major effects: Surface productivity is reduced, and stratification of the water column and metabolism of organic matter below the pycnocline results in low oxygen conditions.

We hypothesize that the uptake and release of nutrients by bottom sediments significantly controls aquatic primary production in Fourleague Bay and is probably significant in many shallow systems. The shallow depth of Fourleague Bay is important in maintaining the high productivity levels because the euphotic zone is close to the bay bottom where sediments are releasing mineralized nutrients. We postulate that the density fronts and their movements up and down the bay play an important role in controlling the chemistry, aquatic primary production, plankton dynamics and fisheries productivity of the system. As these fronts move, material including plankton cells, particulate organic material, and larval and juvenile nekton is trapped or concentrated at the frontal interface.

We expect that maximum aquatic primary productivity in Fourleague Bay occurs along the fronts and that zooplankton which feed there represent a particularly important link between primary productivity and fishery production. High zooplankton concentrations in the frontal zones may encourage juvenile fish to feed more efficiently and grow faster. Thus, the fronts serve as mobile, ephemeral nursery zones.

Upstream changes can have a great effect on the hydrology, ecological structure and productivity of Fourleague Bay. Because the inflow of river water is so important as a source of nutrients and in the formation of fronts, factors which would change river flow patterns could affect the entire system. Human impacts, such as training of the main Atchafalaya channel to carry a greater flow or the extension of the Avoca Island protection levee would reduce the amount of fresh water entering adjacent Fourleague Bay and adjacent marshes. This would result in lower productivity in the whole region because river water would be shunted directly offshore and nutrient input and frontal formation in Fourleague Bay would be reduced. However, aquatic primary productivity in the nearshore Gulf of Mexico would not increase proportionally with the increased river input. Decoupling of the sediment-water column system may reduce the efficiency of the system in reworking and retaining nutrients. Furthermore, the occurrence of low oxygen "dead zones" in bottom waters along the Louisiana coast may be aggravated by channelizing river flow (R. E. Turner, Center for Wetland Resources, pers. comm.) and by forcing organic material into regions which do not have tight sediment-water column coupling.

A common feature observed during much of the year is the formation of density fronts at the area of mixing of fresh and salt water. These discontinuities are ephemeral and seem to move up and down the bay in response to wind and tides. Zooplankton productivity is high along these fronts, probably because of intense grazing on live and dead organic material. The copepod *Acartia tonsa* is the dominant macrozooplanktonic organism in regions of Fourleague Bay with salinities greater than 5 ppt. This copepod plays a dominant role in the transfer of energy and materials within the bay. It is a major component of the community grazing on phytoplankton and, perhaps, microzooplankton and is a major component of the diet of organisms of higher trophic levels, particularly larval and juvenile fish and ctenophores such as *Mnemiopsis mccradyi* and larval and juvenile anchovies, particularly *Anchoa mitchilli*. Thus, *Acartia* plays a dominant role in the transfer of energy and materials from phytoplankton to the higher trophic levels in Fourleague Bay. Elucidation and quantification of these connections and the processes involved is an important component of the Atchafalaya Program.

Recent work has shown that a number of commercially important migratory fish species, which move into tidal creeks and marsh areas around Fourleague Bay, spend several weeks in the open bay and undergo a series of characteristic changes there (such as shifting from plankton to detritus consumption, Deegan 1985). It is generally recognized that density fronts or discontinuities at riverine discharge plumes are important sites for energy transfer and intense biological activity which potentially can support large phytoplankton blooms and zooplankton stocks. The timing and spatial occurrence of fish spawning tend to take advantage of such periods and areas of high productivity.

Hydrographic conditions not only affect the food supply, but also the transport and ultimate recruitment success of larval fish populations (see Norcross and Shaw 1984 for a review). Recruitment may be enhanced by "safe sites" (Frank and Leggett 1982) in which physical processes insure that biological conditions are stable and favorable for survival. Reproductive success or failure for some species depends upon a "match or mismatch" (Cushing 1967) of the most important physical and biological factors. Preliminary data from plankton tows in Fourleague Bay show ichthyoplankton concentrated at the fronts, and we postulate that juvenile fish actively seek these zones in response to the high food availability of phytoplankton, zooplankton, and organic detritus.

In summary, we believe that flow of river water into shallow bays increases coastal productivity due to high nutrient input, tight coupling between sediments and surface waters, and formation of fronts. The river is the major source of "new" and, via sediment remineralization, of regenerated nutrients. Frontal zones are sites of high phytoplankton and zooplankton productivity, and serve as ephemeral nursery zones for ichthyoplankton. Channelizing more of the flow of the Atchafalaya River offshore would lead to lower overall aquatic productivity and possibly exacerbate low oxygen problems.

We believe that these findings have a number of important management implications. As indicated above, "training" of the river into a single channel could lessen the input of river water into shallow systems such as Fourleague Bay. The completion of the Avoca Island levee would have the same affect. In either case, freshwater and nutrient input would be lowered. This would lead to reduced primary and secondary productivity due to the lack of fertilization as well as lowered incidence of frontal formation. The results of the studies also suggest implications for shell dredging in the area. Because the dynamics of the bays are so closely coupled to sediment nutrient dynamics, significant sediment disruption could have far reaching effects on nutrient uptake and release. In addition, because much of the area is light-limited in terms of aquatic primary productivity, increases in turbidity due to sediment resuspension would probably reduce primary production. These effects will probably be more than transient because dredging often renders sediments more easily resuspendable for long periods of time.

SPATIAL LANDSCAPE SIMULATION MODELING FOR ECOSYSTEM MANAGEMENT

The various management suggestions discussed in the previous sections all have far-reaching implications. They depend on which combination of solutions are undertaken and when and where they are undertaken. Outside forces (such as rates of sea level rise) also influence the effectiveness of any proposed management activity. In the past, suggested solutions have been evaluated independently of each other and in a "seat of the pants" manner. In order to more objectively evaluate the many interdependent implications of the various management strategies and specific projects that have been suggested to remedy the coastal erosion problem, an integrated spatial simulation modeling approach was developed (Sklar et al. 1985; Costanza et al. 1986). This approach can simulate the past behavior and predict future conditions in coastal areas as a function of various management alternatives, both individually and in any combination. It simulates both the dynamic and spatial behavior of the system, and will keep track of the important variables in the system, such as habitat type, water level and flow, sediment levels and sedimentation, subsidence, salinity, primary production, nutrient levels, and elevation.

Models of this type are large and expensive to implement, but once implemented can be used to quickly and inexpensively evaluate various management alternatives. We envision an ongoing modeling capability for the state's coastal areas, constructed in stages. We have already spent considerable effort designing and implementing this type of model for the western Terrebonne basin, and it has been used to evaluate several current management alternatives for this area.

The model consists of 2,479 interconnected cells, each representing 1 square kilometer. Each cell contains a dynamic simulation model, and each cell is connected to each adjacent cell by the exchange of water and suspended materials. The volume of water crossing from cell to cell is controlled by habitat type, drainage density, waterway orientation, and levee heights. The buildup of land or the development of open water in a cell depends on the balance between net inputs of sediments and organic peats and outputs due to erosion and subsidence. The balance of inputs and outputs is critical, and is important for predicting how marsh succession and productivity is affected by natural and human activities.

Forcing functions (inputs) are specified in the form of time series over the simulation period. Weekly values of Atchafalaya and Mississippi River discharges, Gulf of Mexico salinity, river sediments and nutrients, rainfall, sea level, runoff, temperature, and winds are supplied to the simulation with each iteration. The location and characteristics of the major waterways and levees are also supplied as input to the simulation. Water can exchange with adjacent cells via canals, natural bayous and overland flow or it may be prevented from exchanging with adjacent cells by the presence of levees. The overall water flow connectivity parameter (K2) is adjusted during the model run to reflect the presence and size of waterways or levees at the cell boundaries. If a waterway is present at a cell boundary a large K2 value is used, increasing with the size of the waterway. If a levee is present, a K2 value of 0 is used until water level exceeds the height of the levee. The model's canal and levee network is updated each year during a simulation run. For example, dredged canals and levees are added to the model's hydrologic structure at the beginning of the year they were built.

Each cell in the model is potentially connected to each adjacent cell by the exchange of water and suspended materials. Before this exchange takes place however, the ecological and physical dynamics within a cell is calculated. The volume of water crossing from one cell to another carries a specified sediment load. This sediment is deposited, resuspended, lost due to subsidence, or carried to the next cell. The amount of sediment in each "tank" is a function of the habitat type. Plants and nutrients within each cell will also influence these exchanges and flows.

Habitat succession occurs in the model (after a time lag) when the state variables within a cell become more like another habitat type due to the changing conditions. The biotic components in a cell (primary production) respond to the abiotic changes. Productivity (and succession) change with changing salinity, flooding regimes, nutrient levels, turbidity, and elevation.

The model can produce a huge amount of output, most useful of which is a contour map for each state variable as well as habitat maps for each week of the simulation. To produce these maps the model must solve over 17,000 simultaneous difference equations and generate over one million simulated data points for each year of simulation. With present day computers, models with such large numbers of computations are feasible, and as computers continue to improve in speed and convenience, this type of modeling should become more practical.

The results of the model are best comprehended by viewing a video tape of the model's time series mapped output for each state variable and habitat type. Since we can't run the video in this chapter, we present a few "snap shots" of habitat change (Fig. 9) and discuss some of the findings.

The model predicts the gradual intrusion of salt into the system from the southeastern part of the study area with the concurrent freshening in the northwestern sector. It also illustrates a loss of elevation in the north and an increase in elevation in the south. Both of these trends are indicative of river water and sediments moving further south in recent times plus a lack of connectivity with the more northern fresh marsh areas. Predicted water volume and suspended sediments behaved in a similar way and are generally consistent with what is known about the historical behavior of the system. These physical changes, in turn, have an impact upon the biology of the area. The relationship between plants and elevation of the marsh results in a feedback loop that enhances the rate of land loss as suspended sediments are diverted from an area of marsh.

The model accurately predicted changes in salinity zones and generalized water flow patterns. Overall, the present model does a fairly good job of predicting landscape succession.

To quantitatively assess the validity of the CELSS model, the 1978 habitat map generated by the model is compared to the actual 1978 habitat map. The most straightforward method to compare the maps is to calculate the percent of corresponding cells in the two maps which have the same habitat type. In our current runs, a cell-by-cell comparison has resulted in a fit of 86% correct.

The simulation of long-term habitat changes in the coastal marshes of the Atchafalaya River demonstrates that ecological and physical processes can be realistically and relatively accurately modeled. The results of the CELSS Model indicate that the current trend of habitat succession will continue to result in wetland degradation unless something is done. Each oil access canal, levee, and dredge and fill activity that is permitted may seem small and unimportant on a case-by-case basis, appearing only as an insignificant localized impact. However, we have shown that when spatial processes and cumulative impacts are considered, the effects are greatly magnified. In addition, the effects of some management options are contingent upon which other options are simultaneously employed. The long-term implications of canal dredging, for example, may be dependent on the sediment environment, an environment which may be drastically affected by marsh management plans or other options.

We are currently in the process of running the model to the year 2050 for several different scenarios. These include the effects of the proposed Avoca Island levee extension, various canal dredging and backfilling options, controlled water diversions, and semi-impoundments. These options will also be investigated in various combinations. This will give government agency personnel, landowners, oil industry representatives, and the general public better predictions of the complex implications of human activities in the Louisiana coastal zone, and should lead to better management of the resource.

In addition, we can do "hindcasts" with the model to

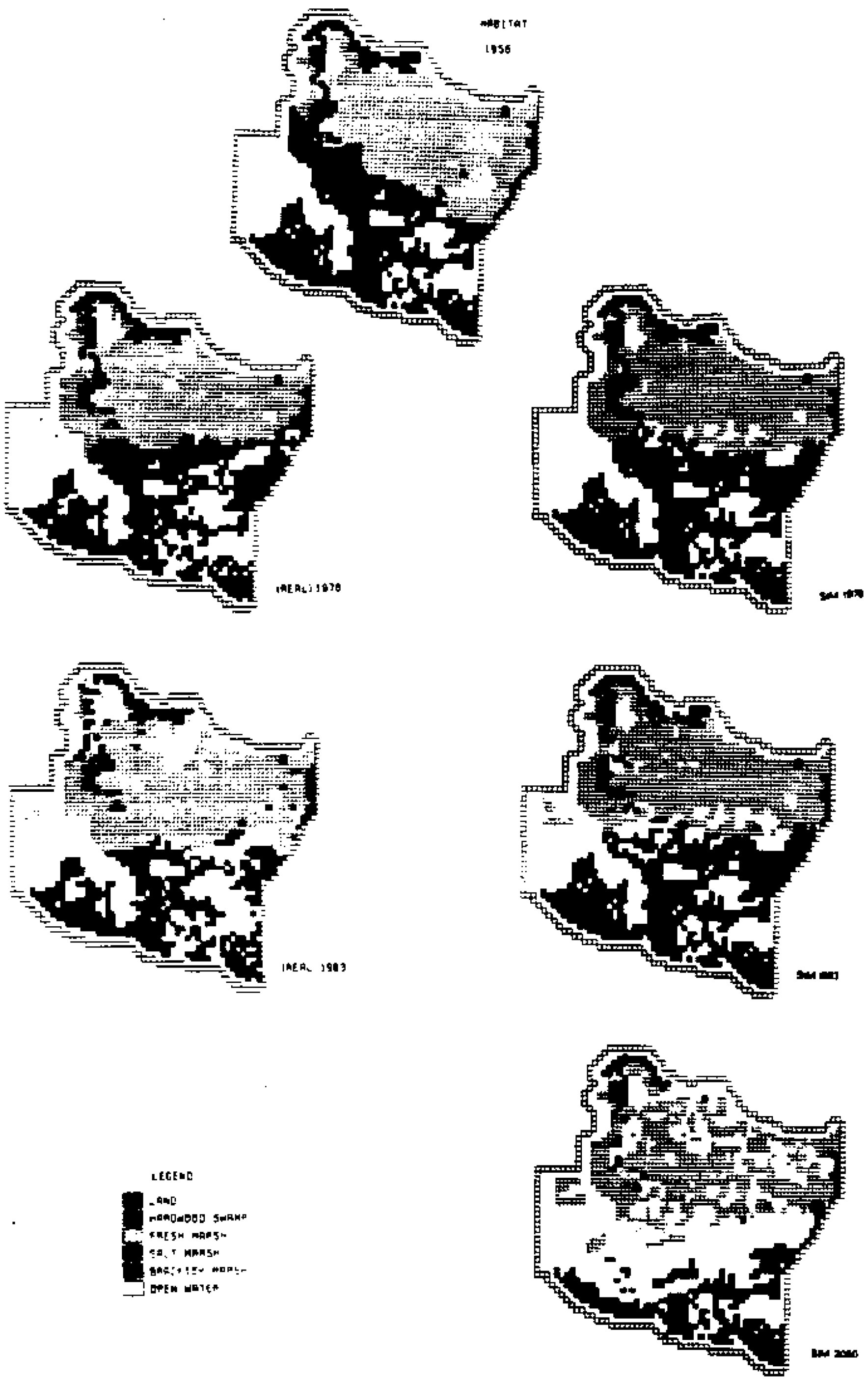

Figure 9. Western Terrebonne Parish marshes sample habitat map output from the base case model run (right column) compared with real data (let column).

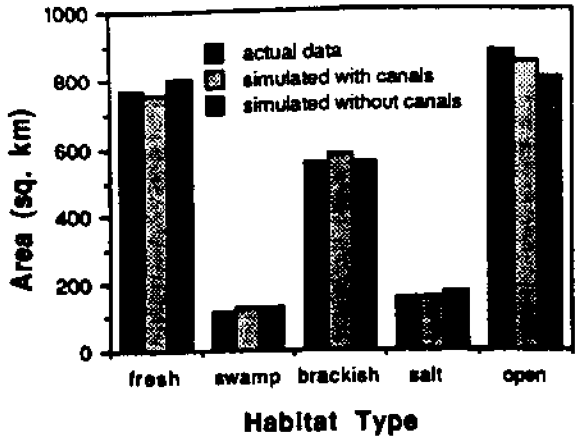

Figure 10. Preliminary results of running the model with and without artificial canals and levees. Chart shows the area of each of the habitat types in 1978 for the data and model runs including and excluding canals (Costanza et al. 1988).

study the impacts of past activities. For example, we have run the model without any of the canals dredged between 1956 and 1978 to look at the impacts of past canal dredging. Preliminary results are shown in Figure 10. We could also pick out types of canals or even individual canals to eliminate in a simulation and thus estimate historical impacts.

At present, models of this size and complexity are fairly new and expensive. However, as we gain experience, and as supercomputers and array processors become more readily available, models of this type will become practical tools for understanding and managing natural coastal systems.

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