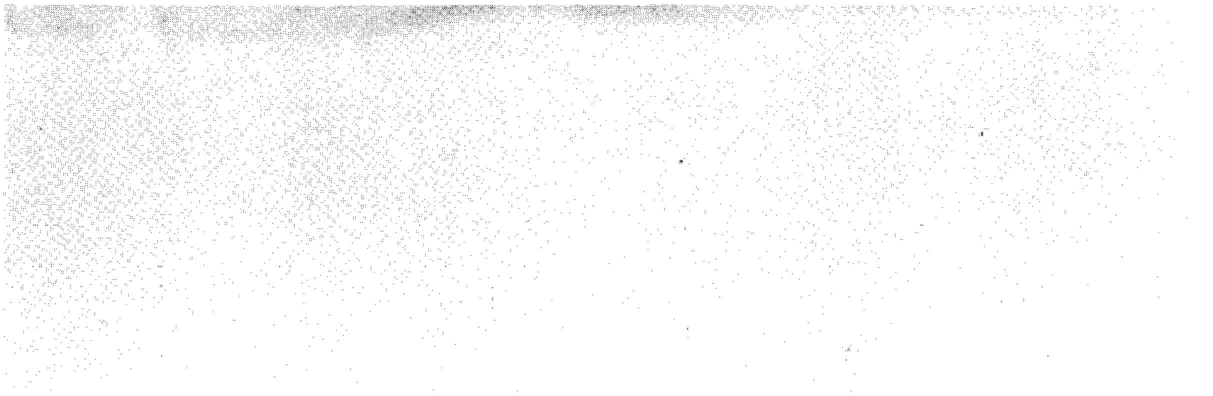
FWS/OBS – 84109
May 1984

THE ECOLOGY OF DELTA MARSHES OF COASTAL LOUISIANA: A Community Profile

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

Corps of Engineers
U.S. Department of the Army



Salt marshes along the Mississippi deltaic coast characterized by extensive tidal channels (Photograph by Charles Sasser).

FWS/OBS-84/09
May 1984

THE ECOLOGY OF DELTA MARSHES OF COASTAL LOUISIANA: A COMMUNITY PROFILE

by

James G. Gosselink
Center for Wetland Resources
Louisiana State University
Baton Rouge, LA 70803

Project Officer
Edward C. Pendleton
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

Performed for
National Coastal Ecosystems Team
Division of Biological Services
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

Library of Congress Card Number 84-601047.

This report should be cited:

Gosselink, J.G. 1984. The ecology of delta marshes of coastal Louisiana: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-84/09. 134 pp.

PREFACE

This report is one of a series of U.S. Fish and Wildlife Service Community Profiles synthesizing the available literature for selected critical ecosystems into comprehensive and definitive reference sources. The objective of this particular account is to review the information available on the marshes of the Mississippi River Deltaic Plain. The river system is the largest in North America. It drains an area of 3,344,560 km^2. Over the past 6,000 years the river has built a delta onto the continental shelf of the Gulf of Mexico covering about 23,900 km^2. This low land is primarily marshes and represents about 22 percent of the total coastal wetland area of the 48 conterminous United States. The delta is notable for its high primary productivity, its valuable fishery and fur industry, and the recreational fishing and hunting it supports.

At the same time, the Mississippi River Deltaic Plain marshes are subject to the unique problem of extremely rapid marsh degradation due to a complex mixture of natural processes and human activities that include worldwide sea-level rise; subsidence; navigation and extractive industry canal dredging; flood control measures that channel the river; and pollution from domestic sewage, exotic organic chemicals, and heavy metals.

The future of the marshes in this region is in jeopardy, and if they are to be saved, it is important to know how they function and what measures can be taken to arrest the present trends.

Any questions or comments about this publication or requests for the report should be directed to the following address.

Information Transfer Specialist
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
NASA/Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

CONVERSION TABLE

Metric to U.S. Custanary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (1)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (k)	2.205	pounds
metric tons 4t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

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

CONTENTS

	Page
PREFACF	iii
CONVERSION TABLE	iv
FIGURES	vii
TABLES	xii
ACKNOWLEDGMENTS	xiv
INTRODUCTION	1
MAN IN THE MISSISSIPPI RIVER DELTA	1
HISTORY OF DELTA RESEARCH	4
WETLAND DEFINITIONS, TYPES, LOCATION, AND EXTENT	5
CHAPTER ONE. THE REGIONAL SETTING	g
THE CLIMATE, THE OCEAN, AND THE RIVER	g
Insolation	9
Temperature	10
Water Balance	10
GEOLOGICAL PROCESSES	14
Pleistocene sea levels	14
Modern Mississippi Delta	18
CHAPTER TWO. TEMPORAL AND SPATIAL GRADIENTS IN DELTA MARSHES	28
TEMPORAL GRADIENTS	28
SPATIAL GRADIENTS	32
Flooding	33
Soils	34
Salt	35
Soil Nutrients	36
Vegetation	37
CHAPTER THREE. ECOLOGICAL PROCESSES IN DELTA MARSHES	43
PRIMARY PRODUCTION	43
Emergent Vascular Plants	44
Epiphytic Algae	54
Benthic Microflora in Marsh Ponds	55
Submerged Grasses in Marsh Ponds	55
DECOMPOSITION	55
CONSUMERS	60
Benthos	60
Nekton	61
Wildlife	63
Carbon Budget	71
NUTRIENT CYCLES	74
Nitrogen	74
Phosphorus	76
Sulfur	77
STORMS	77

CHAPTER FOUR. THE MARSH IN THE COASTAL BASIN 79
COUPLINGS AMONG ECOSYSTEMS 79
Intra-Basin Couplings 79
Extra-Basin Couplinqs 80
Intercontinental Couplings 81
TEMPORAL USE OF MARSHES 81

CHAPTER FIVE. WETLAND VALUES, HUMAN IMPACTS, 4ND MANAGEMENT 84
WETLAND VALUES 84
Wetland Harvest 84
Environmental Quality 85
Esthetics 86
Conflicting Values 86
WETLAND EVALUATION 87
WETLAND MANAGEMENT 89
Marsh Loss and Salt Intrusion 89
Habitat Quality 93
Water Quality 96

REFERENCES 100

APPENDICES 116
1. Plant species composition of salinity zones in the Louisiana coastal marshes..................... 116
2. Marsh plant decomposition rates, Mississippi River delta marshes................................... 118
3. Fishes of the Mississippi River Deltaic Plain that are found in marshes and associated water bodies.. 120
4. Representative vertebrate species of marsh habitats in the Mississippi River Deltaic Plain....... 128

FIGURES

Number		Page
Frontispiece.	Salt marshes along the Mississippi deltaic coast characterized by extensive tidal channels	INSIDE COVER
1	The groves of trees in the middle of this broad expanse of marsh identify the site of old Indian villages	2
2	The oil storage facility for the nations's only superport is constructed in a salt dome in the middle of a Mississippi delta brackish marsh. The maze of pipes is the primary aboveground expression. An old oilfield also sits atop this submerged salt dome as shown by the network of tree-lined oilwell access canals	3
3	Across this expanse of marsh and swamp looms the New Orleans skyline through the haze, a reminder of the proximity of heavy industries and concentrated populations	4
4	Louisiana oil and gas production	5
5	Map of the Mississippi River Deltaic Plain showing the hydrologic units	7
6	The seasonal variation of insolation at various latitudes. The computation assumes a transmission coefficient of 0.7 throughout	9
7	Mean monthly air temperature at New Orleans, Louisiana	10
8	Generalized water budget for the Mississippi delta marshes	10
9	Average water budget for the upper Barataria basin, 1914-1978. P=precipitation, PE=potential evapotranspiration, AE=actual evapotranspiration	11
10	Freshwater inflows to the Mississippi Delta. Discharges are in cumecs. All discharges are for water year 1978 except Mississippi River, which is a long-term mean representing the combined average annual discharge above the confluence of the lower Mississippi (10400 cumecs) and the Atchafalaya (5000 cumecs) Rivers	12
11	Water level trends in delta marshes:. a) long term; b) seasonal; c) daily	13
12	Tide levels at Shell Beach, in the Pontchartrain-Lake Borgne basin, associated with nine major storms	14

Nurnbe r Page

13 The relationship of glacial advance and retreat to continental shelf exposure and sedimentation during the Late Quarternary.................. 15

14 Location of major buried river channels formed durinq the Wisconsin glacial period...... 16

15 The position of major delta lobes on the gulf coast during the previous 25,000 years. (A) Late Wisconsin, 25,000 - 20,000 yr B. P. (B) Late Wisconsin, 15,000 yr B. P. (C) Early Holocene, 12,000 - 10,000 yr B. P. (D) Present, 5,000 - 1,000 yr B. P. 17

16 Oeltaic lobes of Mississippi River deltas............................... 18

17 Satellite image of the Mississippi Delta Region showing delta lobes of different ages 19

18 Six subdeltas of the modern Mississippi Balize Delta recognized from maps and sediment analysis. Dates indicate year of crevasse opening...... 20

19 Plan view and cross sections through A-A' and B-B' of environments of deposition in a crevasse... 21

20 Sequential development of Cubits Gap subdelta.......................... 22

21 Linear, areal, and volume qrowth curves for the Cubits Gap subdelta...... 23

22 Composite subaerial growth curve, Mississippi River subdeltas. Total subaerial land determined from averages at 10-yr intervals.............. 24

23 The accelerating wetland loss rate in the Mississippi Delta............. 24

24 Computerized re-creation of the west side of Barataria Bay showing the change in wetlands between 1945 (a) and 1980 (b). Black is open water; marshes are shown as varying shades of grey...................... 25

25 Environmental succession of an idealized delta cycle.................... 29

26 Mineral content of marsh soils in Mississippi delta hydrologic units, arranged in order of increasing age.................................... 30

27 Marsh soil salinity and percent fresh marsh in Mississippi delta marshes by hydrologic unit, arranged in order of increasing age. Soil salinity is a mean for the whole basin weighted by area of each marsh zone. The fresh marsh is percent of total marsh area.................. 30

28 Marsh edge length:area ratio and total marsh edge length for delta hydrologic units. The units are arranged in order of increasing age...... 31

29 Net primary production and fishery yield of Mississippi River Deltaic Plain hydrologic units. Production calculated from average production of each habitat type and its area in the hydrologic unit. Shrimp data from Barrett and Gillespie (1975). Basins are, in order of increasing age: I - Pontchartrain-Lake Borgne, II- Balize, III- Barataria, IV - Terrebonne, V- Atchafalaya, VI-Vermilion. 31

Number		Page
30	Seasonal salt marsh inundation patterns	34
31	Variation in soil density and soil carbon content with distance inland from the stream edge in a salt marsh in the Barataria basin	34
32	Sedimentation rates on the Barataria saline marsh. (A) Mean seasonal sedimentation 1975 - 78. (B) Mean seasonal sedimentation 1975 - 79. Sedimentation rates were highest during the winters of 1975 - 78. Hurricane Bob and tropical storm Claudette passed through the area during the summer of 1979, resulting in very high deposition rates	34
33	The decrease in free soil water salinity (mg/g) of chenier plain marshes with distance (km) from the gulf	36
34	Concentrations of available Na, Ca, K, Mg, P, and N in different marsh zones	37
35	Vegetation zones in the Mississippi River delta marshes	39
36	A deltaic plain brackish marsh. Note the "hummocky" appearance which is typical of Spartina patens stands. The birds with black-tipped wings are white pelicans, the smaller ones ducks, mostly teal	40
37	A diverse deltaic plain fresh marsh scene. Species are: Sagittaria falcata (foreground), Typha sp. (right edge), mixed grasses and vines, Myrica shrubs in r	41
38	Vegetation zonation in an intermediate marsh transition zone in the Barataria basin. Factors arise from statistical clustering techniques and are identified by the dominant species	41
39	Effects of substrate drainage conditions on the dry weight accumulation by (A) Spartina alterniflora and (B) S. cynosuroides	42
40	A conceptual model of a typical wetland ecosystem, showing major components and processes	44
41	Monthly growth rates of Panicum hemitomon and Spartina alterniflora	46
42	Seasonal changes in live and dead biomass of Phragmites australis and Spartina patens during 1973 - 1975	47
43	Production of intertidal S. alterniflora vs. mean tide range for various Atlantic coastal marshes. Different symbols represent different data sources	49
44	Variation in total aboveground biomass and he'ight of Spartina alterniflora with distance inland from the marsh edge in a Barataria basin salt marsh	50
45	Gulf-inland variations in live and total biomass in Spartina alterniflora marshes	50
46	Effects of NaCl concentration in the root medium on the rate of Rb	

Number		Page
	absorption by excised root tissue of S. alterniflora and D. spicata	51
47	Metabolic conversions of pyruvic acid. This "key" intermediate in metabolism can be converted to a variety of end products, depending on the organism and the electron acceptors available	52
48	Marsh soil transformations that result from tidal flooding	53
49	Seasonal changes in various physical, chemical, and biotic factors in a Barataria basin salt marsh	54
50	Net epiphytic production on stems of Spartina alterniflora collected at the water's edge and inland 1.5 m with the averages, extremes, and fitted curve for the water's edge production superimposed	55
51	Number of shore-line epiphytic diatoms/cm culm surface area of Spartina alterniflora. Results are pooled averages for four stations and height classes.~~	55
52	Disappearance of S. patens litter from litter bags in the Pontchartrain-Borgne basin	58
53	Decomposition rates (mg/g/day) of S. alterniflora litter incubated in 2-mm mesh bags in different locations	59
54	Major pathways of organic energy flow in a Mississippi River deltaic salt marsh and associated water bodies	61
55	Length class frequency of qulf menhaden captured in and near Lake Pontchartrain	62
56	Density of vegetation, detritus,and consumers at the edge of the salt marsh	63
57	Pelt production from marsh zones in coastal Louisiana	65
58	Annual muskrat harvest from a 52,200-ha brackish Scirpus olneyi marsh in the Mississippi Delta	66
59	Ground plan of a typical muskrat house with underground runways and surface trails	66
60	A muskrat "eat-out." in the brackish marsh in the Barataria basin. Note the high density of muskrat houses	67
61	Carbon dioxide flux measurements in a deltaic salt marsh community	72
62	Carbon budget of a Mississippi River deltaic salt marsh (see Table 29 for sources). Rates (g $C/m^2/yr$) are from CO_2 flux measurements, except numbers in parentheses, which are from other sources.	72
63	A schematic outline of the redox zones in a submerged soil showinq some of the N transformations. The aerobic layer has been drawn thick for clarity. In reality it is seldom over 1-2 mm in flooded marshes.	75

Number		Page
64	Nitrogen and phosphorus budgets for a Mississippi deltaic salt marsh	76
65	Conceptual diagram illustrating the coupling of delta marshes to other ecosystems	79
66	Patterns of estuarine use by nektonic organisms and waterfowl in the Barataria basin. LA	80
67	The life cycle of the brown shrimp	81
63	Major duck migration corridors to gulf coast marshes	82
69	Seasonal use of wetlands by migratory birds, shellfish, and fish	83
70	The increase in open water in natural and impounded wetlands. The pattern of greater wetland loss in impoundments is consistent in both fall, when water levels are low, and winter when impoundments are flooded	92
71	Wildlife management areas in the Mississippi Delta	94
72	A weir in the deltaic plain marshes. The strong flow of water across the weir is an indication of the effectiveness of the barrier. These structures are favorite sport fishing spots	95
73	Cumulative number of days per year that ponds in the study area will equal or exceed certain percentages of bottom exposure. Rased on depth contours of 43 ponds and 20 years of tide data on the central Louisiana coast	96
74	The percentage of different types of vegetation in impoundments in the Rockefeller State Wildlife Refuge	97
75	Habitat type, vegetative cover, and fish and wildlife values achieved with water management programs operating on the Rockefeller Refuge	98

TABLES

Number		Page
1	Salinity values (ppt) recorded by various investigators for delta lnarshes	6
2	Classification of coastal marshes of the Mississippi River Delta, and area of different marsh zones in 1978	6
3	Averdge coastal sub.nergence on the U.S. east and gulf coasts	13
4	Land-use changes along the northwest edge of the Barataria basin, on the Bayou Lafourche natural levee.	26
5	Land use changes, in hectares, in the Mississippi Delta, 1955-78	27
6	Regression analyses relating net primary production (NPP) and inshore shrimp production (1955-74) in hydrologic units to various physical parameters	32
7	The annual duration and frequency of inundation of marshes in the Barataria basin, Louisiana	33
a	Marsh accretion rates (mm/yr) in Louisiana delta marshes, based on the 1963 ^{137}Cs fallout peak	35
9	Concentration (C) and accumulation rates (A) of organic carbon, nitrogen, phosphorus, iron, and manganese in Louisiana delta marsh soils	35
10	Multiple linear regression models of soil ions showing what factors control their distribution	36
11	The ratio of the major cations to the chloride ion in normal seawater and in the saline, brackish, intermediate, and fresh marshes of Louisiana	37
12	Percent cover of the dominant plant species in major marsh zones of the Louisiana coast	38
13	Production of marsh vascular plant species in the Mississippi Delta	45
14	Belowground biomass of Mississippi delta marsh plant species	48
15	Production estimates for a <u>Spartina alterniflora</u> stand based on different techniques	48

Number		Page
16	Year-to-year variations in peak live biomass of Spartina alterniflora at a single site in the Barataria basin	49
17	Spartina alterniflora root alcohol dehydrogenase (ADH) activity, adenosine triphosphate (ATP) and ethanol concentrations, and soil Eh in a Louisiana salt marsh	52
18	Percentage of marsh community metabolism by Spartina alterniflora	54
19	Submerged aquatic plant species composition of ponds and lakes by marsh zone along the Louisiana coast	56
20	Range and mean loss rates (mg/g/day) of litter from different marsh plant species (summarized from Appendix 2)	59
21	Monthly occurrence and abundance of the fish species collected in small salt marsh ponds	62
22	Wildlife species richness (number of species) in the chenier plain marshes	64
23	Muskrat house-building activity in 10-ha brackish and salt marsh areas in Barataria basin	66
24	Density of waterfowl (number/100 ha) by marsh zone in the Barataria basin in 1980-81	68
25	Density of ponds and lakes of various size classes in marsh zones along the Louisiana coast, August, 1968	69
26	The percent of the area of ponds and lakes covered with submerged vegetation in August, 1968 by size and marsh zone	70
27	Density of wading birds and pelicans (number/100 ha) by marsh zone, in the Barataria basin, 1980-81	70
28	Birds of the Mississippi Deltaic Plain on the Audubon Society "Blue List," indicating that their populations are declining	71
29	Estimates of different components of the carbon budget of a Mississippi deltaic salt marsh community	73
30	Influence of Spartina alterniflora plants on recovery of ^{15}N-ammonium added over 18 weeks to soil cores	76
31	The estimated economic value of harvests from the Barataria basin, Louisiana	a5
32	Estimates of the economic value of Louisiana's coastal wetlands comparing willingness-to-pay approaches with energy analysis approaches	a9
33	Major wetland issues and human impacts in Mississippi delta wetlands	89
34	Impacts of canals in Louisiana coastal marshes leading to habitat loss, and mechanisms and management practices to minimize these impacts	90

ACKNOWLEDGMENTS

This profile is dedicated to the graduate students in Marine Sciences and Fisheries at Louisiana State University (LSU), Baton Rouge, who carried out much of the original field research upon which this profile is based. I have been privileged to work closely with thirteen of them. Fifty-six literature citations in the profile are authored or coauthored by students. They have made a major contribution toward unravelling the ecology of our coastal ecosystems.

I have been fortunate to enjoy a group of coworkers for the last 15 years who introduced me to the marshes and participated with me in the intellectual stimulation of wetland research. Their contributions are cited throughout this work. They are Len Bahr, John Day, Charles Hopkinson, Roland Parrondo, Jim Stone, Gene Turner, and more recently Bob Costanza, Flora Wang, Bob Baumann, Deborah Fuller, Gary Paterson, and Charles Sasser.

Special thanks are extended to Jim Coleman, who drafted the geology section of this report,and to Linda Deegan and Jean and Walt Sikora for information and advice on the benthos and nekton sections, respectively. John Day and Irv Mendelssohn (LSU), Gerry Bodin [U.S. Fish and Wildlife Service (FWS), Lafayette, La.], Ed Pendleton (FWS National Coastal Ecosystems Team), and Steve Matheis, Suzanne Hawes, and John Weber (U.S. Army Corps of Engineers, New Orleans District) reviewed an early draft and provided many helpful suggestions for improving it. Thanks to Kathryn Lyster and Susan Lauritzen (FWS National Coastal Ecosystems Team); they edited and did the layout for the profile, respectively. Dawnlyn M. Harris provided word processing assistance. Diane Baker, as usual, did a superb job drafting the figures. She created the cover. My wife, Jean, showed great forbearance and understanding while I labored long hours over the word processor.

Much of the research cited in this manuscript was supported by the National Sea Grant Program and the U.S. Army Engineers District, New Orleans. The preparation of this profile has been sponsored by the Office of the Chief of Engineers in association with the Waterways Experiment Station, the Lower Mississippi Valley Division, and the New Orleans District, Army Corps of Engineers, and the Fish and Wildlife Service.

INTRODUCTION

The history of the marshes of the Mississippi River Delta is inextricably intertwined with the history of the river itself. Like some ancient god, it broods over the coastal plain, implacable in its power, its purpose inscrutable. With its sediment it spawns the flat, verdant marshes of the delta, nourishes them with its nutrients, and finally abandons them to senesce slowly under the influence of time and subsidence, while it renews the cycle elsewhere along the coast.

This community profile deals with the facts and the quantitative analysis of this cycle. But the cold numbers often defy our comprehension. How much is 15,400 cubic meters per second (cunecs), the average discharge of the Mississippi River? How large is 0.2 μ, the size of a bacterium? And what does it mean to say that there are one thousand million of them in a cubic centimeter of marsh soil? These scales are almost unimaginably different, yet understanding a natural ecosystem demands the ability to deal with both.

As one examines the technical details of a system like a coastal marsh, the complexity becomes increasingly apparent, and the cold, technical analysis breaks down more and more often into a sense of wonder at the system's sophistication and the delicate interplay of parts that make up the whole. Migratory waterfowl's ability to respond to subtle environmental cues and navigate thousands of miles from Alaskan prairie potholes to the Louisiana coastal marshes rivals our most sophisticated inertial guidance systems. After years of study we still have little understanding of how passively floating shrimp larvae in the Gulf of Mexico find their way through estuarine passes into the coastal marshes. The idea of energy flow in ecological systems is still only a guiding principle; the complex details of molecular biochemistry in the marsh substrate and the complexity of the meiofaunal food chain are still largely unexplored.

This monograph details the human struggle to understand, and through understanding to manage the Mississippi delta marshes. I will emphasize what we know - and that is considerable - but I hope that the presentation of technical detail does not obscure the large areas of uncertainty about how to manage the system. Above all I hope that it does not reduce the delta marshes to cold statistics; for understanding, I believe, is heightened by emotional involvement.

MAN IN THE MISSISSIPPI RIVER DELTA

When de Soto found and named the Rio del Esperitu Santo, now the Mississippi River, in 1543, the Indians had been living on the coast for 12,000 years. They preferred the easy living of the marshes to the uplands because food was abundant and easy to harvest. Oysters and the *Rangia* clam were in nearly endless supply. Fish, turtles, and edible plants were plentiful. The tribes now known as Tchefuncte, Marksville, Troyville, Coles Creek, Caddoan, Mississippian, and Plaquemine settled on the slightly elevated banks of river distributaries where they literally ate themselves up out of the water. As they ate oysters and clams, the shells accumulated beneath them. The evidence of these prehistoric villages now dots the marshes as small groves of trees on slightly elevated shell mounds in an otherwise treeless vista (Figure 1).

De Soto approached the river from the Florida Peninsula. It was 140 years before the next European, LaSalle, explored the coast in 1682, having approached from upriver. He claimed the great basin drained by the river for France and in 1684 led an expedition to establish a colony at the mouth of the river. Although he failed in this attempt, and lost his life, he was followed by Iberville, who explored and mapped the river and by Bienville, who established New Orleans in 1718.

Thus began a settlement phase that resulted in the development of the distributary (a diversion near the mouth of a river that distributes water out of the main channel) levees for agriculture. Rice, indigo, tobacco, corn, cotton, and later sugarcane were the large plantation crops, but many other crops brought in from Europe and elsewhere were also grown. During this period Germans settled part of the coast, beginning in about 1720. In 1760 an influx of French refugees from Eastern Canada began. These poor farmers, trappers, and fishennen brought with them a strong culture still characteristic of the coastal villages (Kane 1943).

One hundred years ago Louisiana had only about 900,000 inhabitants (Kniffen 1968). Many developments led to the present industrialized state. The construction of levees along the

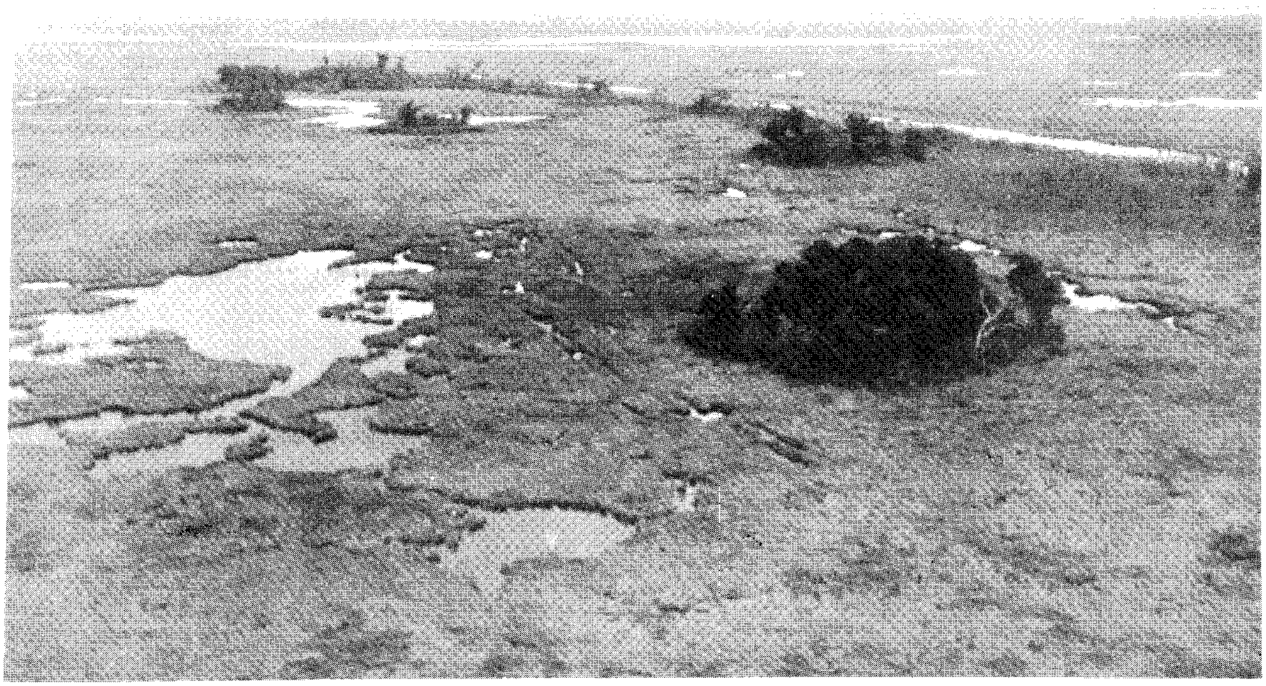


Figure 1. The groves of trees in the middle of this broad expanse of marsh identify the site of old Indian villages (Photograph courtesy of Louisiana State University Museum of Geosciences, Robert Newman, curator).

Mississippi River did much to develop a sense of permanence and encourage industrial expansion. The levees also promoted waterborne transportation by channelling the Mississippi 'River and its distributaries. Dredging to deepen channels and create new ones became commonplace. These fostered more transportation and stimulated further commercial expansion.

New industries developed based on Louisiana's coastal resources. The late 1800's and early 1900's were a time of widespread harvesting of the extensive cypress forests of the coast. The fishing and fur-trapping industries expanded. But the most significant event in the state's life was the discovery of oil in Jennings in 1901.

Oil reserves in Louisiana are concentrated around salt domes that occur across the coastal wetlands and on the continental shelf. The inland fields were developed first. An enormous expansion of petroleun demand began in the war years of 1941-45. This resulted in dredging thousands of miles of canals through the coastal wetlands for access to drilling sites and for pipelines, constructing enormous refineries and petrochemical processing facilities, and secondarily stimulating many other industries (Figures 2 and 3). As oil and gas reserves were depleted in the inland marshes, production moved offshore. This shift increased pressure for more and deeper navigation canals to link the offshore rigs with land-based facilities. Production of oil and gas reached its peak in 1971 and has since been declining (Figure 4). However, the search for new oil continues, and wetland modification has by no means stopped. Louisiana's wetland management problems continue to be related to its

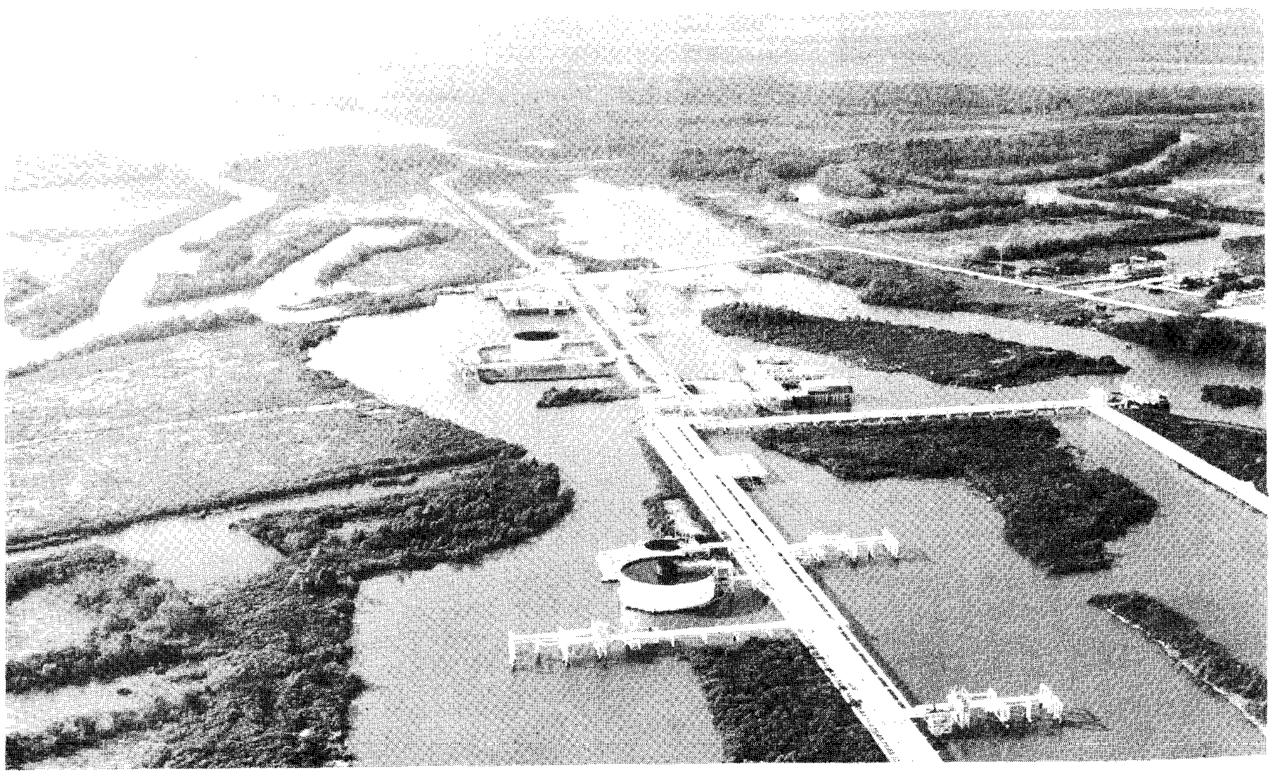


Figure 2. The oil storage facility for the nation's only superport is constructed in a salt dome in the middle of a Mississippi delta brackish marsh. The maze of pipes is the primary aboveground expression. An old oil field also sits atop this submerged salt dome as shown by the network of tree-lined oilwell access canals (Photograph by Robert Abernathy).

major coastal industries - transportation and fossil fuel extraction.

HISTORY OF DELTA RESEARCH

Investigations of geological and biological aspects of the Mississippi Delta both followed the same historic trend from descriptive accounts to greater emphasis on functional processes. In geology early studies are typified by that of Lerch et al. (1892), who carried out a fairly inclusive preliminary survey of Louisiana that included geology, soils, and groundwater. Davis' (1899) physiographic interpretation ushered in the "golden age" of coastal qeomorphology (Fisk 1939, 1944; Fisk and McFarlan 1955; Russell 1936, 1967; Kolb and Van Lopik 1958; and many others). This was a period of deciphering the geomorpholoqy of the delta on a regional scale and qualitatively documenting the major formative processes. In the last 20 years the emphasis has shifted to intensive investigation, usually at specific locations, of process-response relationships.

In the biological arena early comments on delta biota were common, at first emphasizing economically important animals such as furbearers. De Montigny (1753, as quoted in Gowanloch 1933), who spent 25 years in Louisiana, and Le Page du Pratz (1758) observed fish and terrestrial animals in the coastal zone. In the early 1800's Rafinesque, a professor at Transylvania University, Lexington, Kentucky, described many fish species of the South (Gowanloch 1933). John J. Audubon and Alexander Wilson described Louisiana birds in the early 1800's. George E. Reyer published "The

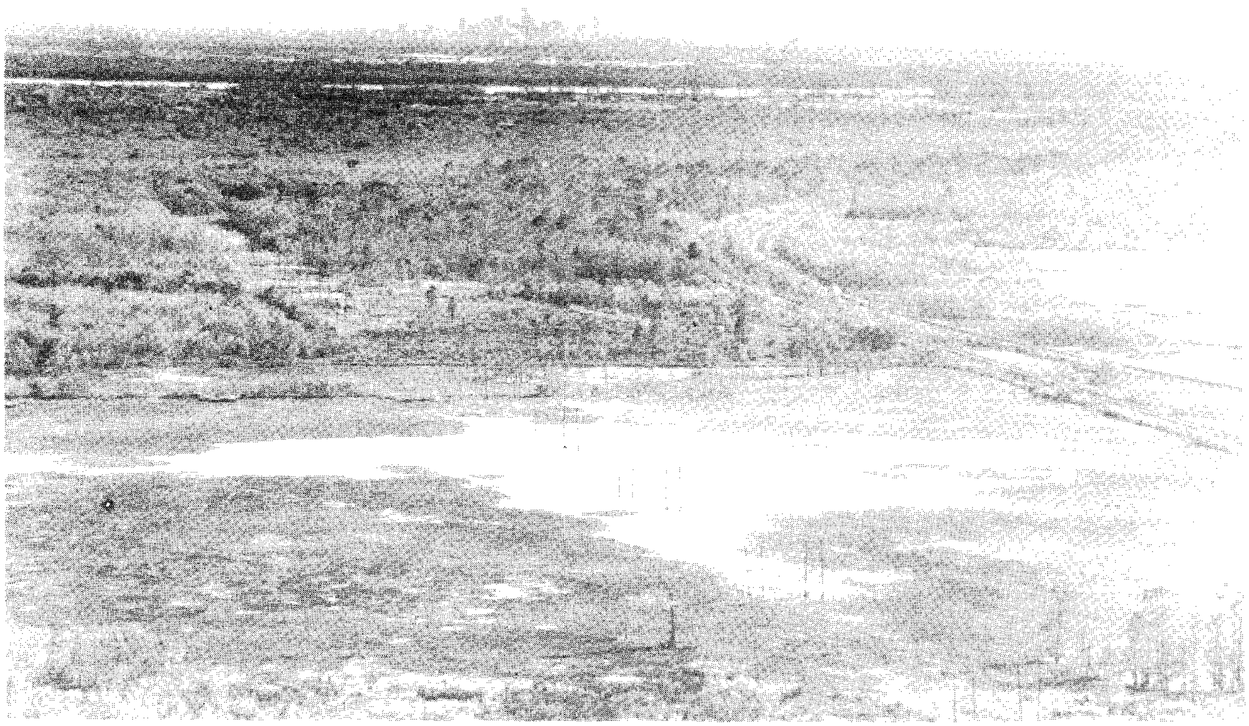


Figure 3. Across this expanse of marsh and swamp looms the New Orleans skyline through the haze, a reminder of the proximity of heavy industries and concentrated populations (Photograph by Charles Sasser).

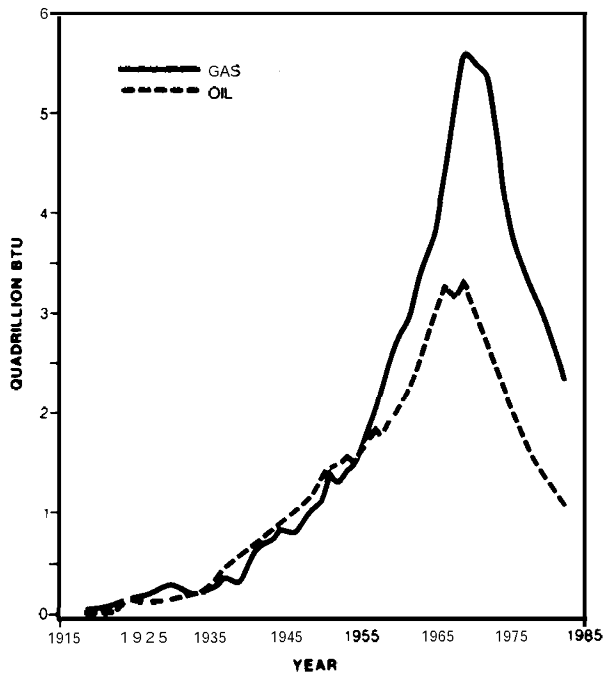


Figure 4. Louisiana oil and gas production (Costanza and Cleveland 1984).

Avifauna of Louisiana" in 1900, a classic description. A.B. Langlois collected 1,200 plants near Plaquemine in the late 1800's; Riddill, Hale, and Carpenter collaborated between 1839 and 1859 to publish a list of 1,800 names of Louisiana plants, excluding grasses and sedges. Cocks (1907) stated that Langlois' collection was shipped to St. Louis University and that most of the Riddell et al. collection was lost. Cocks incorporated their lists into his own list of the flora of the Gulf Biologic Station at Cameron, Louisiana. This station also published pioneering studies on oysters (Kellogg 1905; Cary 1907) and shrimp (Spaulding 1908) during this period.

The 1930's brought a sudden wealth of publications. Noteworthy are a series of bulletins published by the Louisiana Department of Conservation on birds, fur animals and fishes (La. Dept. of Conservation 1931; Gowanloch 1933) that sumnarized the available knowledge on these topics. By the late 1930's the general life history pattern of the commercially valuable estuarine organisms of the delta had been described, and the beneficial effect of the Mississippi River water and nutrients on aquatic productivity was generally understood (Gunter 1938; Viosca 1927; Riley 1937). Also during this decade articles devoted specifically to marsh plants were published (Brown 1936; Penfound and Hathaway 1936). These were soon followed by articles that focused on the relation of environmental factors, particularly salinity and inundation, to plant occurrence (Hathaway and Penfound 1936; Penfound and Hathaway 1938; Brown 1944; Walker 1940).

Since that time the focus of biotic research has shifted to the processes that control the distribution and abundance of organisms and to analyses of whole communities and ecosystems. While this was a national trend, on the Louisiana coast it was seen in a series of studies funded by the Louisiana Sea Grant program in the early 1970's.

WETLAND DEFINITIONS, TYPES, LOCATION, AND EXTENT

The marshes considered in this monograph are classified by Cowardin et al. (1979) as persistent or nonpersistent emergent wetlands. Most of them lie within the estuarine intertidal or palustrine systems of this classification scheme, al though some could be construed to be riverine, particularly where the Mississippi and Atchafalaya river flows are not confined by levees. In Louisiana these marshes are further subdivided as freshwater, intermediate, brackish, or salt, based on vegetation associations established by Penfound and Hathaway (1938) and Chabreck (1972), rather than on salinity per se. However, the salinity ranges for these associations have been determined by various investigators (Table 1). They correspond fairly closely with the salinity modifiers - fresh, oligohaline, mesosaline and polysaline - of Cowardin et al. (1979) as shown in Table 2. This table also shows the area of each marsh type in the Mississippi Delta region.

In both Figure 5, a map of the delta marshes, and in Table 2 the region is divided into drainage basins, the natural ecosystem units of the delta (Costanza et

Table 1. Salinity values (ppt) recorded by various investigators for delta marshes (from Wicker et al. 1982).

Investigator	Delta marshes			
	Fresh	Intermediate	Brackish	Saline
Penfound & Hathaway 1938	5	N.A.*	5 -20	20+
O'Neil 1949	5	N.A.	0.7-18	18+
Allan 1950	0 -10	8 -35	4 %	30 -50
Lemaire 1960	1 - 2	2 -10	.6	9.6-26
Wright et al. 1960[a]	1 N.A.	2 4- 7	10 -20	20+
Giles 1966[b]		[illegible]	7 -12	11.6-17
Chabreck 1972	1.1- 6.7	2.7- 2.8	4.7-18.4	0.6-30
USDI/FWS unpubl.[c]	0 - 1	0.6- 5.9	0.9-19	1.5-26
Palmisano 1971[d]	1.1- 3.2	2.7- 2.8	4.7-18	17.3-29
USACE 1974	0 - 5	5 -10	10 -20	20+
Montz 1976	0 - 1	1 -8	8 -18	18+
USDA/SCS no date	- 5	0.4- 9.8	0.4-28	0.6-52

*Data not available.
[a]Salinity contours established by Dept. of Oceanography and Meteorology, Texas A.& M. College, 1959.
[b]Average minimum and maximum annual range of soil water salinity.
[c]Fruge (1980) pers. comm.; extremes of recorded salinity range from 1968 sampling.
[d]Water salinity range of vegetative types in hydrologic unit I.

Table 2. Classification of coastal marshes of the Mississippi Delta, and area of marsh in 1978 within each major hydrologic basin (Cowardin et al. 1979; Wicker 1980; Wicker et al. 1980a, 1980b).

Level of classification	Classification			
System/subsystem	Estuarine intertidal---------------------Palustrine			
Class	--------------------Emergent wetland			
Subclass	Persistent-------------Persistent or nonpersistent			
Modifiers				
Tide	Tidal---------------------------------------Nontidal			
	Irregularly exposed to regularly or irregularly flooded		Intermittently flooded to intermittently exposed	
Salinity (ppt)	Polyhaline 18 - 30	Mesohaline 5 - 18	Oligohaline 0.5 - 5	Fresh 0.5

Marsh designation Basin	Salt	Brackish and intermediate	Fresh	Total
	hectares			
I Pontchartrain	45,793	129,487	14,519	189,799
II Balize	0	10,386	16,397	26,783
III Barataria	19,388	79,483	65,358	164,229
IV Terrebonne	57,866	92,010	69,423	219,299
V Atchafalaya	0	0	23,855	23,855
VI Vermilion	2,541	77,902	20,233	100,676
Total	125,588	389,268	209,785	724,641

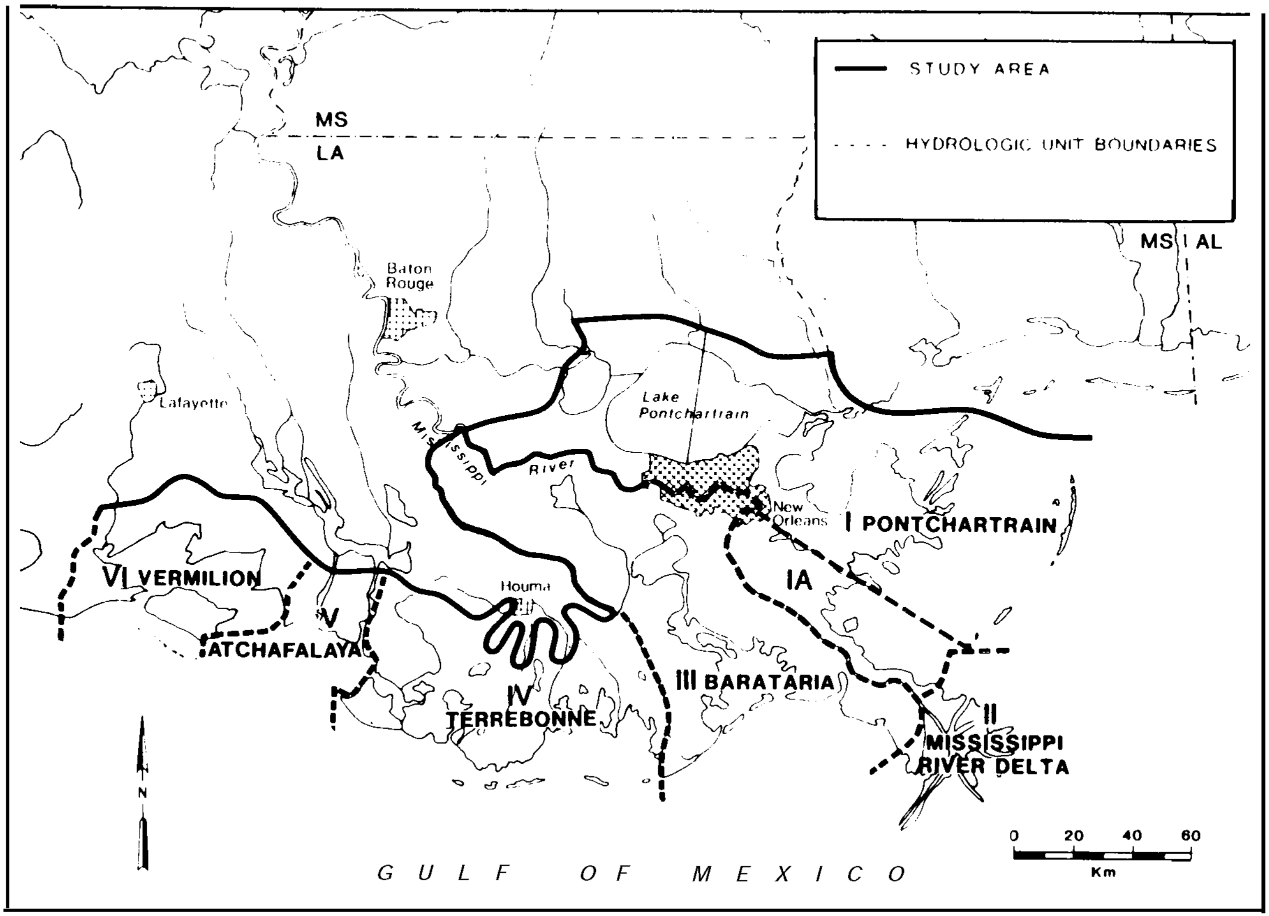


Figure 5. Map of the Mississippi River Deltaic Plain showing the hydrologic units.

al. 1983). These data and maps are from a recent Fish and Wildlife, Service study of the Mississippi Delta Plain Region (Wicker 1980; Wicker et al. 1980a, 1980b). The drainage basins are interdistributary basins formed by shifts in the major distributary of the river. Thus they form a time series of delta lobes of different ages and allow one to see in space the time sequence of the development and decay of the marshes of a delta lobe.

The youngest basin is the Atchafalaya, which is actively prograding out through the shallow Atchafalaya Bay. It receives one-third of the flow of the combined Mississippi and Red river systems, whose freshwater flows into the shallow bay keep the whole basin fresh or nearly fresh all year. All the marshes in this basin are fresh.

The active Mississippi River delta, the Balize Delta, is next youngest. It receives two-thirds of the flow of the Mississippi River, but it is debouching into deep water at the edge of the continental shelf. Most of this basin is fresh also, but there has been marine invasion of abandoned subdelta lobes around the edges of the main distributaries, and the marshes here are brackish.

In succession Barataria, Terrebonne, Vermilion-Cote Blanche, and the Pontchartrain-Lake Borgne basins are of increasing age. They all have extensive marshes with well-developed salt and brackish zones. These six basins together form the Mississippi Delta Plain Region, one of the best-developed deltas in the world. The Mississippi Delta Plain Region is also the largest continuous wetland system in the United States with 725,000 ha of marshes, not including the forested wetlands at the inland extremes of the basins. The delta supports the nation's largest fishery, produces more furs than any other area in the United States, and is an important wintering ground for migratory waterfowl. In addition to these renewable resources the delta is also the scene of intensive mineral extraction; the Mississippi River ports between New Orleans and Baton Rouge handle greater tonnage than any other port in the United States; and dense urban, industrial, and agricultural activity crowds the distributary levees.

CHAPTER ONE
THE REGIONAL SETTING

The unique characteristics of the region and its marshes result from the interaction of three forces - the subtropical climate, the oceanic regime, and the river - all acting on the physiographic template of the northern gulf coast. The forces control the geomorphic processes that have formed the delta and also the biological characteristics of the delta marshes.

For individual plants on the coastal marsh these forces resolve into insolation, temperature, and water. Insolation and temperature determine the potential and the rate, respectively, of biotic productivity. Within the constraints set up by these two parameters water is the major controlling function which makes a wetland wet and determines, directly or indirectly, its characteristics. It is also the most complex of the three parameters. Insolation and temperature are determined primarily by latitude, with only minor modification by local circumstances. But, the water available to marshes, the depth and duration of flooding, current velocity, and water quality are complex functions of marine energy, fluvial processes, rainfall, and evaporation, operating over an irregular surface.

THE CLIMATE, THE OCEAN, AND THE RIVER

Insolation

There is apparently no weather station in the Mississippi Delta region that routinely records insolation. Existing records of this important parameter are scattered and fragmentary. However, the insolation reaching the top of the atmosphere is a constant that varies seasonally at a particular point on the earth's surface, depending on latitude. Assuming an atmospheric transmission coefficient of 0.7, Crowe (1971) showed how insolation varied seasonally with latitude (Figure 6). In the Mississippi Delta region, at about 30" north latitude, solar energy reaching the earth's surface varies from about 200 cal/cm^2/day during the winter to a peak of nearly 600 cal/cm^2/day in June and July. During the summer insolation at this latitude is higher than anywhere else on the globe; it falls off both north toward the Arctic and south toward the Equator. Therefore, midsummer growth potential in terms of solar energy is as high in the Mississippi Delta as it is anywhere on earth.

Cloud cover diminishes the potential irradiance, and on the coast where daytime seabreezes move moisture-laden gulf waters inshore, there are clouds almost every day during the hot summer. Consequently the

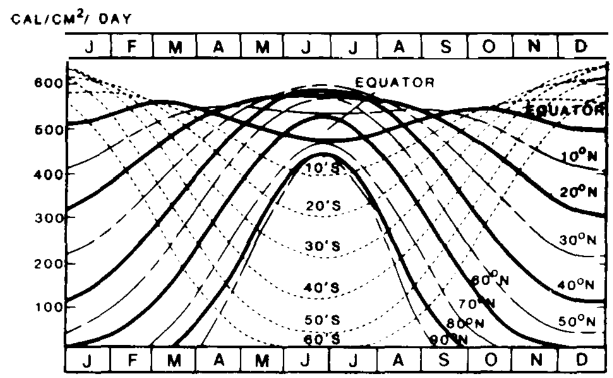


Figure 6. The seasonal variation of insolation at various latitudes. The computation assumes a transmission coefficient of 0.7 throughout (Copyright. Reprinted from "Concepts of Climatology," 1971, by P.R. Crowe with permission of Longman Group Ltd., England).

seasonal insolation curve for the delta coast is probably skewed to the left with peak insolation in May, falling off somewhat in June and July because of clouds.

Temperature

As one might expect, seasonal air tenperatures follow insolation closely. Mean monthly temperatures range from a December/January low of about 14°C to a midsummer high of about 30°C. Temperature at the U. S. Weather Bureau station in New Orleans (Figure 7) is fairly representative of the coast because New Orleans is surrounded by marshes and water. Because of the moderating effect of the water bodies and the high humidities, midday temperatures seldom exceed the low 30's (Celsius) despite the high insolation. During winter in the coastal marshes, freezes are infrequent, and the average number of frost-free days is about 300. In fact, the barrier island, Grand Isle, was chosen for the site of a sugar cane breeding laboratory by the Louisiana State University (LSU) Agricultural Experiment Station because the lack of frost allowed sugar cane fruit to ripen there. Since most of the inshore waters are less than 1 m deep, water temperature follows air temperature closely, with a lag time of a few hours at most.

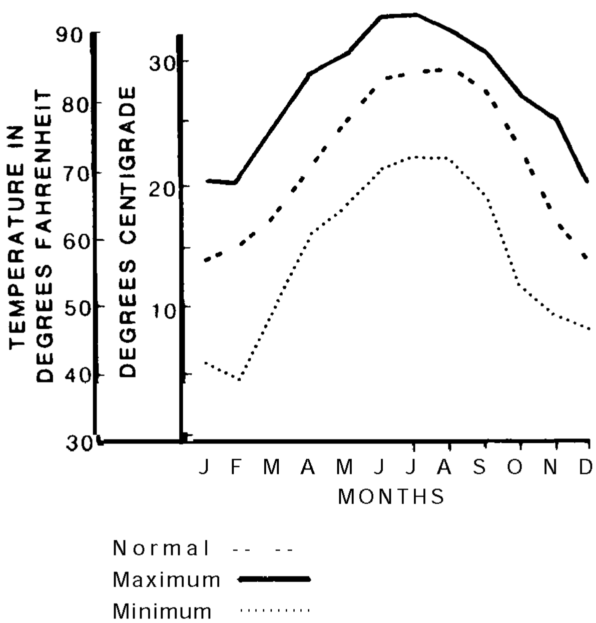


Figure 7. Mean monthly air temperature at New Orleans, Louisiana (NOAA 1979).

Water Balance

The water budget includes rain, evapotranspiration, local runoff from adjacent uplands, upstream discharge into wetlands by rivers entering the region, and marine water pumped in and out by tidal and meteorologic forces (Figure 8). Each of these varies in both time and place; the resultant flooding frequency, volume, and water quality on the marsh are at present predictable only as average trends. No present models capture the details adequately.

Precipitation. Annual precipitation averages about 160 cm spread fairly evenly over the year (Figure 9). October tends to be the driest month and July the wettest, but torrential rains are common so that any month can be either dry or experience precipitation of up to 60 cm. Muller (Wax et al. 1978) analyzed the atmospheric circulation of the Louisiana coast. Typically high pressure systems moving in from the north and west bring cool, dry air. They are easily recognized during the winter as "cold fronts" but occur throughout the year. They are typically followed by atmospheric conditions that bring warm gulf air in from the coast, usually with heavy cloud cover and rain. About two-thirds of the coastal rainfall is associated with frontal activity of this kind. During 1971-74 about 13 percent of the rainfall was from infrequent, severe tropical stonns and hurricanes.

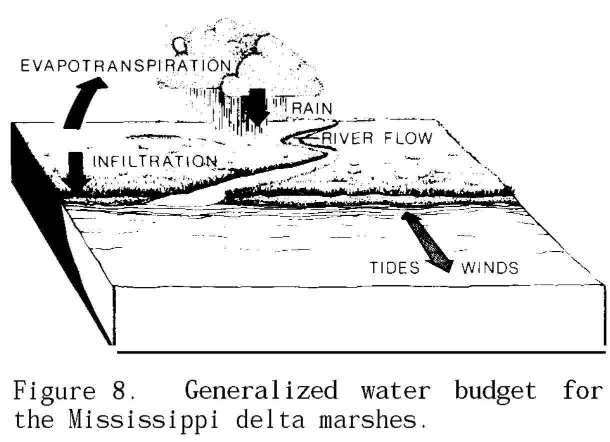


Figure 8. Generalized water budget for the Mississippi delta marshes.

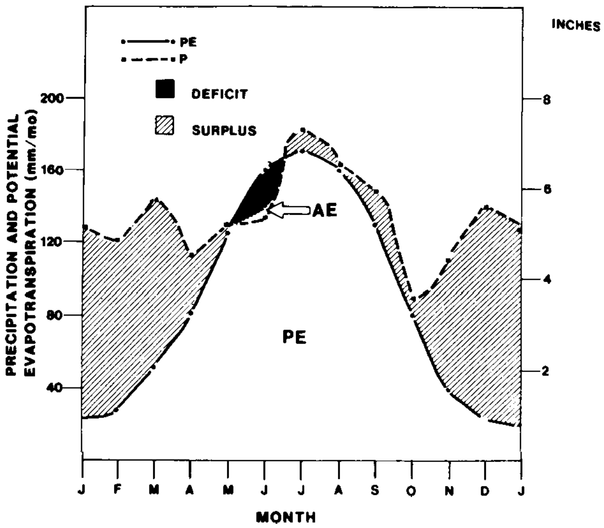


Figure 9. Average water budget for the upper Barataria basin, 1914-1978 (Sklar 1983). P=precipitation, PE=potential evapotranspiration, AE=actual evapotranspiration.

Evapotranspiration and rainfall surplus. The effect of precipitation depends not so much on the absolute amount but on the relationship between rainfall and evaporation from water and plant surfaces. Although apparently no one has recorded evapotranspiration directly in the delta marshes, water balances have been calculated from equations developed by Thornthwaite and Mather (1955). These show that water surpluses occur during the winter months, but during the summer precipitation and evaporation tend to be fairly closely balanced, with occasional deficits in May through August (Figure 9). Annual rainfall surplus is about 60 cm along the northern edge of the delta marshes (Gagliano et al. 1973), decreasing to about 40 cm on the coast. This surplus is important in the total water balance of the marshes that includes riverine inputs and gulf marine water, as will be discussed in the following sections.

Upstream freshwater inflows. The largest source of freshwater to delta marshes is the Mississippi River and its major distributary, the Atchafalaya River. The combined annual flow of these two rivers averages about 15,400 cumecs. The flow is strongly seasonal, peaking in late spring, fed by melting snow and spring rains in the upper Mississippi watershed (Figure 10). River flow can be nearly independent of local rainfall because of the size of the Mississippi River watershed, but often spring rains along the coast reinforce the river flow.

The older basins of the delta are isolated from direct riverine input by natural and manmade levees. Therefore the rivers debouch through the Balize and Atchafalaya hydrologic units and in extreme floods through the Bonnet Carre control structure into Lake Pontchartrain. Their waters flow on out into the gulf and are carried westward along the coast, freshening the tidal water that moves in and out of the Barataria, Terrebonne, and Vermilion basins. Thus, while these three basins have almost no direct freshwater inflow except from local runoff, the salt marshes are never strongly saline because of the moderated salinities offshore.

In addition to the Mississippi and Atchafalaya Rivers, smaller rivers also feed freshwater into the coastal marshes (Figure 10). The Pearl River delivers its water to the mouth of the Pontchartrain basin, freshening the Lake Borgne marshes and through tidal action the lower Lake Pontchartrain marshes. Other small rivers flow into the northern edge of Lake Pontchartrain. The other basins receive negligible stream flow; however, the interior marshes are maintained as fresh marshes by the precipitation surplus.

Marine processes. Water fluxes in delta marshes are driven by the water level differences across the estuary. These change in three time scales: long term, seasonal, and daily. Since the ocean reached its approximate present level about 7,000 years ago, it has been rising relative to the land at a rate measured in centimeters per century, The term "coastal submergence" is used to identify this long-term process, which is due not only to true sea-level rise but also to land subsidence as discussed in the following section on geomorphology.

In the last 20 years the rate of submergence has accelerated. Presently in delta marshes it averages about a

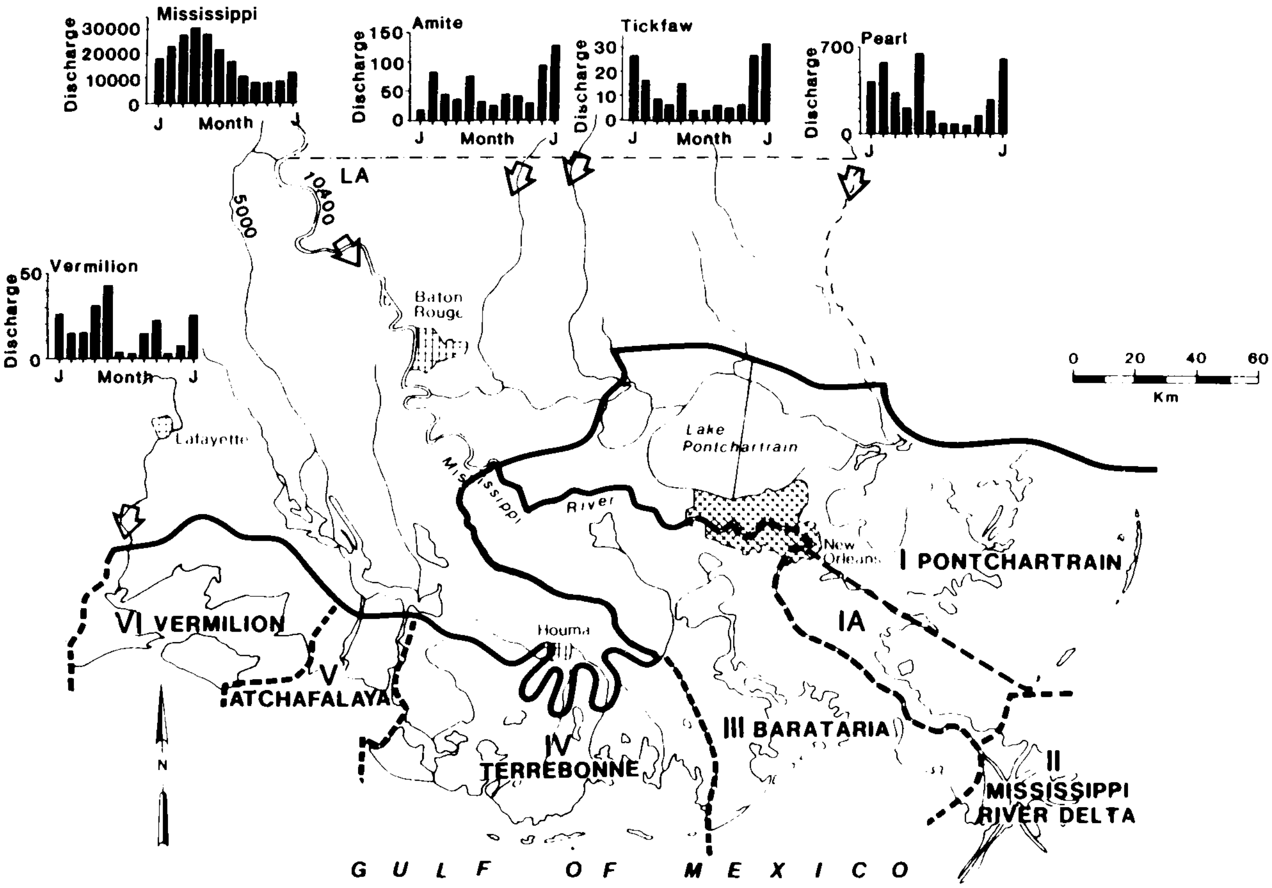


Figure 10. Freshwater inflows to the Mississippi Delta. (Data from USGS 1978). Discharges are in cumecs. All discharges are for water year 1978 except Mississippi River, which is a long-term mean representing the combined average annual discharge above the confluence of the lower Mississippi (10400 cumecs) and the Atchafalaya (5000 cumecs) Rivers.

centimeter per year (Figure 11a). This is double the rate anywhere else along the eastern United States coast (Table 3). Superimposed on this long-term trend is a seasonal variation in mean water level that itself has an excursion of 20 - 25 cm. This bimodal variation (Figure 11b) occurs consistently throughout the different salinity zones of the delta, with peaks in the spring and late summer. In the Barataria basin the spring maximum increases in an inland direction, that is from salt toward fresh marshes, possibly because of the considerable volume of surplus precipitation during this time of the year (Baumann 1980).

The seasonal changes in water level are attributed to several interacting factors. Water level varies inversely with barometric pressure which averages 1,021 millibars (mb) during December and January and 1,015 mb during early summer and fall. Several investigations have shown that water level decreases nearly 1 cm for each mb increase in barometric pressure (e.g. Lisitzin and Pattullo 1961). Thus the expected mean seasonal range in water level as a response to barometric pressure is approximately 6 cm or 25 percent of the total observed range. In addition, the seasonal warming (expansion) and cooling (contraction) of nearshore waters contribute to a seasonal high in the late summer and a low in January and February.

These astronomical events can be modeled and compared to the actual water levels. When this is done (Byrne et al. 1976) there is always a significant residual which is presumably due to other forces and changes dramatically from year to year. Dominant among these other forces and responsible for the secondary maximum in spring and the following secondary minimum in mid-summer is the seasonally changing, dominant wind regime over the Gulf of Mexico (Chew 1962). Maximum east and southeast winds in spring and fall result in an onshore transport of water. During winter and summer westerly winds (southwest in summer, northwest in winter) strengthen the Mexican Current and draw a return flow of water from the estuaries (Baumann 1980).

Superimposed on the seasonal water level change is a diurnal tide averaging

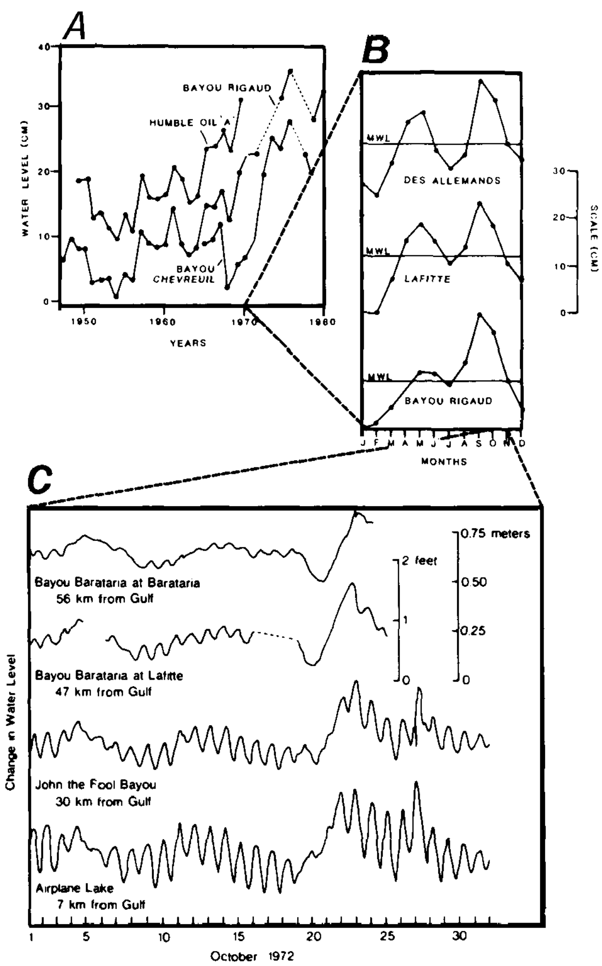


Figure 11. Water level trends in delta marshes: a) long term; b) seasonal; c) daily.

about 30 cm at the coast. Because of the broad, shallow expanse of the coastal estuaries,the tides attenuate in an inland direction. Figure llc shows how the normal tide range decreases from salt to freshwater marshes. In this example tides are still perceptible 50 km inland from the tidal passes because of the extremely slight slope of the land.

It would be misleading to infer that water levels slavishly follow predictable daily and seasonal cycles. In reality they are modified strongly by stochastic meteorologic events which set up or set down water in the bays and marshes. The effect is clearly shown in Figure llc, where gradually decreasing water levels associated with a "cold front" began on 12 October. Then the water levels suddenly rose on 19-22 October when the wind came around to the south. Typically, "cold fronts" moving across the coast lower water levels dramatically. "Warm fronts" with winds from the southern quadrant set up water in the estuaries. The magnitude of these wind effects is often 40-50 cm, which when combined with astronomic tides can result in water level shifts of over a meter within 12 hours.

Table 3. Average coastal submergence on the U.S. east and gulf coasts (Bruun 1973 compiled by Hicks).

Location	Record *yr*	Rate cm/yr
Eastport, Maine	1930-1969	0.338
Portsmouth, N.H.	1927-1970	0.165
Woods Hole, Mass.	1933-1970	0.268
Newport, R.I.	1931-1970	0.210
New London, Conn.	1939-1970	0.229
New York, N.Y.	1893-1970	0.287
Sandy Hook, N.J.	1933-1970	0.457
Baltimore, Md.	1903-1970	0.259
Washington, D.C.	1932-1970	0.244
Portsmouth, Va.	1936-1970	0.341
Charleston, S.C.	1922-1970	0.180
Fort Pulaski, Ga.	1936-1970	0.198
Mayport, Fla.	1929-1970	0.155
Miami Beach, Fla.	1932-1970	0.192
Pensacola, Fla.	1924-1970	0.040
Eugene Island, La.	1040-1970	0.905
Galveston, Tex.	1909-1970	0.430

These meteorologically driven water level changes are common events. Tropical storms are much more unusual. When they occur water levels can be dramatically elevated. The water level height/frequency curve for Shell Beach, southeast of New Orleans (Figure 12), shows that wind tides as high as 3.5 m have been recorded, and 1.5-m tides occur about once every eight years. On a coast with a slope of about 0.2 mm/km (Byrne et al. 1976) a 1.5-m tide can cause flooding hundreds of kilometers inland. The ecological effects of such flooding can be dramatic.

GEOLOGICAL PROCESSES

The Mississippi River, the largest river system in North America, drains an area of 3,344,560 km^2 (Coleman 1976). The average discharge of the river at the delta apex is approximately 15,360 cunecs with a maximum and minimum of 57,900 and 2,830 cumecs, respectively. Sediment discharge is generally about 2.4×10^{11} kg annually. The sediments brought down by the river to the delta consist primarily of clay, silt, and sand. The sediments are 70 percent clay.

The river has had a pronounced influence on the development of the northern Gulf of Mexico throughout a long period of geologic time. In the Tertiary Period (70 - 1 million years before the present) the large volumes of sediment

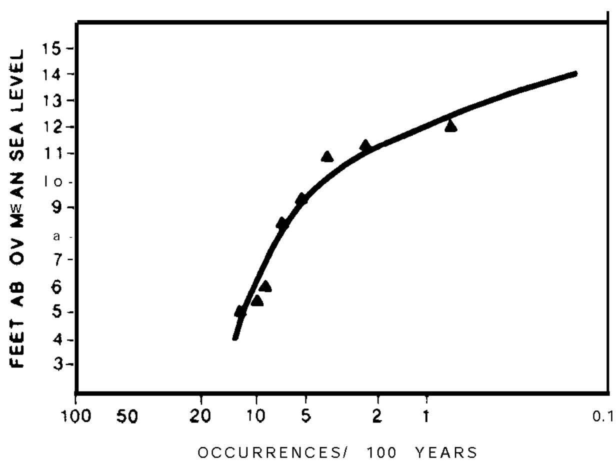


Figure 12. Tide levels at Shell Beach, in the Pontchartrain-Lake Borgne basin, associated with nine major storms (Wicker et al. 1982).

brought down by the Mississippi River created a major sedimentary basin, and many of the subsurface deposits, especially those that formed in localized centers of deposition, have been prolific hydrocarbon-producing reservoirs.

In more recent geologic times, changing sea levels associated with the advance and retreat of inland glaciers during the Pleistocene Ice Ages have strongly influenced the sedimentary patterns off the coast. In order to understand the development of the present-day coastal wetlands it is necessary to view the progradation of the delta and its adjacent coastal plains in relationship to several time scales. These scales range from the long periods of geologic time associated with changing sea levels to the changes in the last 100 years in the patterns of minor subdeltas that formed the most recent deltaic lobe, the Balize Delta. In addition, the heavy sediment load deposited by the river during the last several million years has caused excessive subsidence. This factor has to a large degree controlled the construction rate and the rate of coastal wetland loss throughout much of the recent geologic history.

Pleistocene Sea Levels

During the Pleistocene Epoch, some 1.8 - 2.5 million years long, sea level fluctuated several times. Most authorities agree on at least four major low sea-level stands and four or five high level stands. In addition to these major changes in sea level, numerous more rapid fluctuations took place. The minor changes in level undoubtedly affected the development of the delta marshes, but in the younger Pleistocene deposits it is extremely difficult to document the precise changes. At the lower sea-level stands, the ocean surface was 150 - 200 m below its present level. During the higher stands water surfaces were slightly above or near present sea level. These fluctuations resulted in periodic valley cutting during the low stands and valley filling or terrace formation during the high sea-level stands. This concept is diagrammed in Figure 13. Fisk's 1944 paper should be consulted for details of

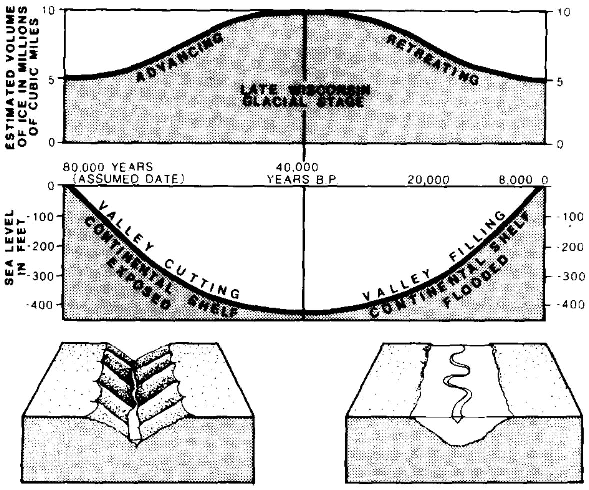


Figure 13. The relationship of glacial advance and retreat to continental shelf exposure and sedimentation during the Late Quaternary (after Fisk 1956).

the relationship of sea level changes to delta and river valley response.

In addition to causing cutting and valley filling, changes in sea level resulted in migration of the site of sediment deposition. During falling sea level, deposition shifted seaward, depositing deltaic sediments at or near the edge of the continental shelf. The progradation of the deltas seaward over thick sequences of shelf clays resulted in major sedimentary loading of the underlying clays, causing rapid downbowing and subsidence. As sea level began to rise, the delta site shifted landward.

The most recent cycle of sea-level lowering and subsequent rise to its present level began about 50,000 years ago (Fisk and McFarlan 1955). This Late Quaternary cycle began in response to cooling Pleistocene climates. Sea level was lowered approximately 150 - 170 m below its present level by withdrawal of water into the expanding Wisconsin-stage glaciers. Streams along the gulf coast and Mississippi River eroded extensive valleys across the shelf and dumped their sediment at or near the present-day shelf edge. The generalized locations of these river channels, now buried beneath the younger deltaic sediments, are shown in Figure 14. During this period large expanses of coastal wetlands, some 50 - 60 percent larger than present-day wetlands, existed along the Louisiana coast. Borings along the present-day coastline and offshore often hit these buried freshwater marsh and swamp deposits.

Warming of the Late Pleistocene climate returned polar meltwaters to the ocean basins, raised sea level, and progressively decreased the stream gradients and carrying capacities of the rivers. As a result, the channels filled and large expanses of coastal wetlands were buried beneath the present continental shelf. Sedimentation could not keep pace with the rising sea level and the rapid subsidence, and a series of deltas were left stranded on the present continental shelf.

Seismic data and offshore foundation borings have been used to reconstruct the major deltaic lobes at various times during the last major rise of sea level. The positions of these lobes, shown in Figure 15 a through d, illustrate that at different times in the past the area of the coastal wetlands was governed by the locus of deposition of the major deltaic lobe. The presence of numerous delta lobes, now buried beneath the continental shelf deposits, points out the role that submergence plays in controlling the total area of coastal marshes. If submergence did not occur along the Louisiana coast, many of these older deltaic lobes would still be present, and the present-day coastal marshes would be much more extensive.

The latest phase of the Quaternary cycle, characterized by relative stability of climates and relatively small changes in sea level, began approximately 5,000 - 6,000 years ago. This sequence involves the modern delta cycles described by Fisk and McFarlan (1955) and Frazier (1967). Figure 16 illustrates the major Mississippi River delta lobes that have developed during this period. Although numerous, slightly differing terminologies have evolved to describe the individual delta systems and their ages, most authorities agree on at least seven delta lobes. The result of the building and subsequent abandonment of the Late Recent delta lobes was construction of a modern deltaic coastal plain which has a total area of 28.568 km^2 of which 23,900 km^2 is exposed above the sea surface (subaerial) (Coleman 1976).

In one of its earlier channels the river built the Sale-Cypremont Delta along the western flanks of the present Mississippi River Delta Plain, In approximately 1,200 years an extensive coastal marshland emerged before the river switched its course to another locus of deposition, the Cocodrie system. A similar sequence of events continued, and with time this site of deposition was abandoned and a new delta lobe began a period of active buildout. This process has continued, each delta completing a cycle of progradation that requires approximately 1,000 - 1,500 years.

Over approximately the last 500 years, the most recent delta cycle has formed the modern birdfoot or Balize Delta (Figure 16). The modern delta has nearly completed its progradation cycle, and in the recent past a new distributary, the Atchafalaya River, began tapping off a portion of the Mississippi River's water and sediment discharge. A new delta is beginning its progradational phase (Van Heerden and Roberts 1980; Wells et al. 1982).

In each progradational phase of the delta cycle, broad coastal marshes are constructed. Scruton (1960) referred to this as the constructional phase. However, once the river begins to abandon its major deposition site, the unconsoli-dated mass of deltaic sediments is immedi-ately subjected to marine reworking pro-cesses and subsidence. Waves and coastal currents, and subsidence result in pro-gressive inundation of the marshes, and within a few thousand years the delta lobe

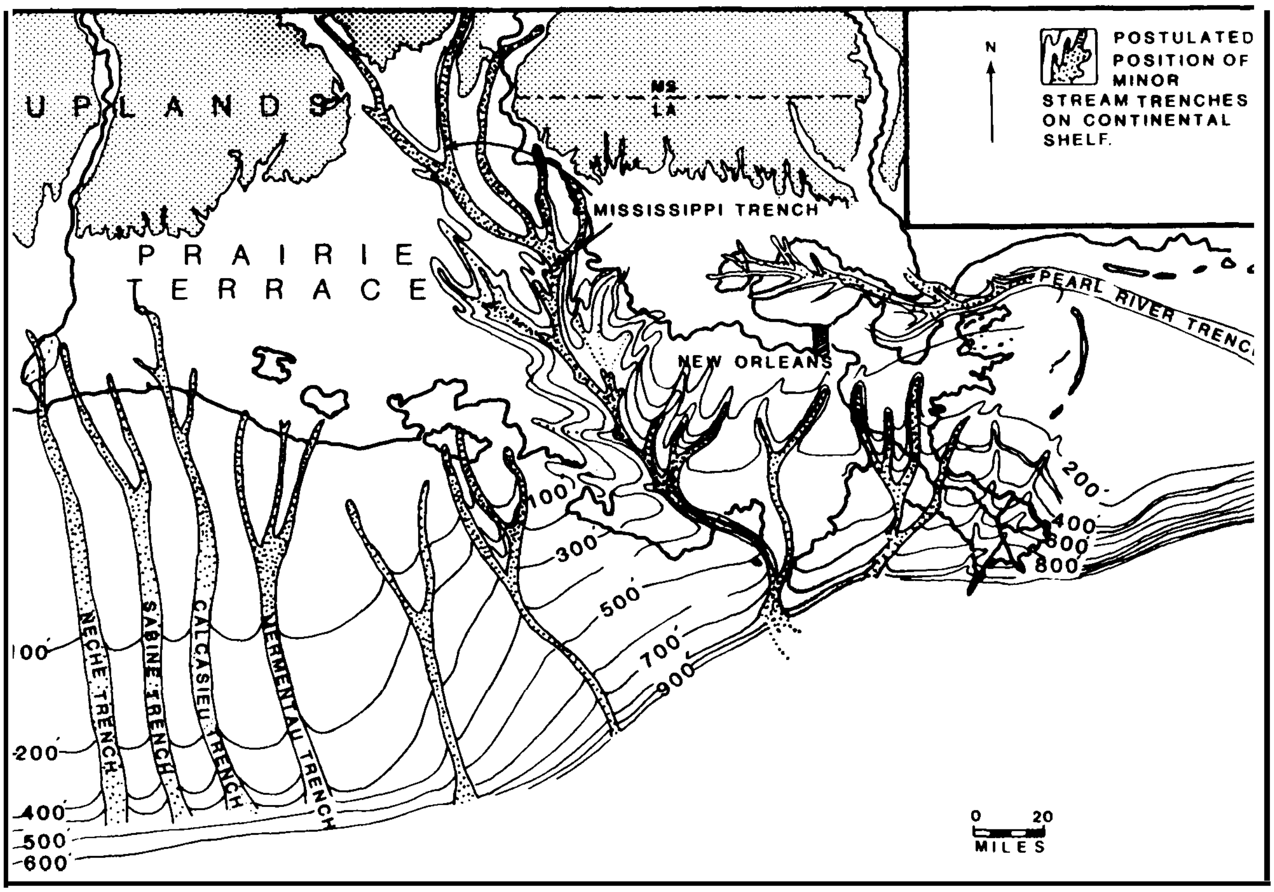


Figure 14. Location of major buried river channels formed during the Wisconsin glacial period (after Fisk 1954).

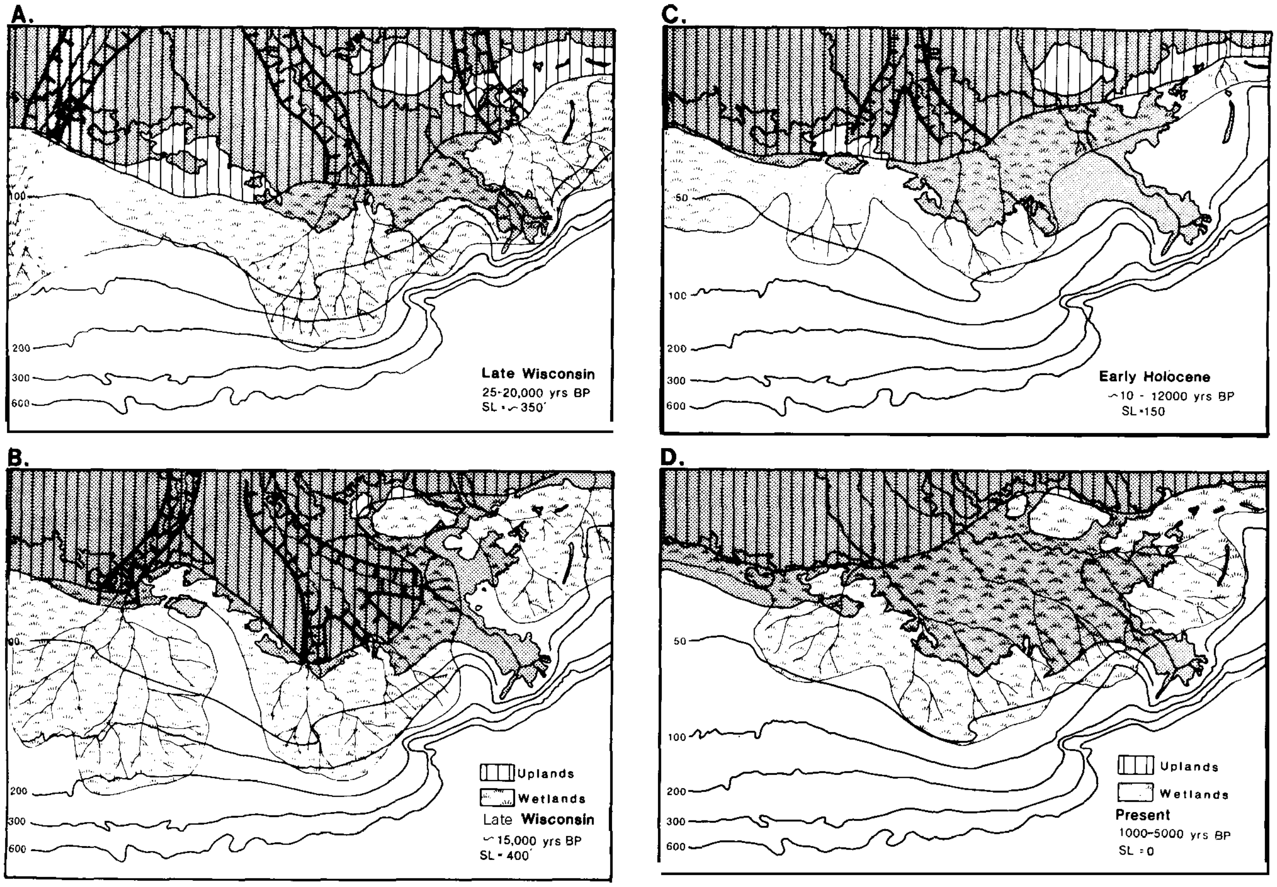


Figure 15. The position of major delta lobes on the gulf coast during the previous 25,000 years. (A) Late Wisconsin, 25,000 - 20,000 yr B. P. (B) Late Wisconsin, 15,000 yr B. P. (C) Early Holocene, 12,000 - 10,000 yr B. P. (D) Present, 5,000 - 1,000 yr B. P. SL = relative sea level.

has sunk beneath the marine waters. Scruton (1960) referred to this stage of the delta cycle as the destructional phase. Thus, in a relatively short period of geologic time both land gain and land loss occur, a function of the stage of the normal delta cycle. The initial phase of delta progradation is characterized by formation of coastal marshes associated with the advancing delta. Coastal marshes deteriorate when a delta lobe is abandoned, and a new delta cycle begins elsewhere.

Figure 17, a satellite image of the eastern portion of the Mississippi Delta Plain, shows several delta lobes in different stages of construction and destruction. The oldest shown on this image is the St. Bernard Delta, a delta lobe that was actively prograding some 3,000 years before present. This delta lobe remained active for approximately 1,200 years, forming a broad, coastal marshland along the eastern deltaic plain.

Approximately 1,800 years ago, the Lafourche channel began its progradation. In the St. Bernard Delta, deprived of its sediment load, marine processes and subsidence (primarily compaction) became dominant. The Lafourche distributary gradually increased its sediment yield and within 1,000 years built out a major delta lobe west of the modern or Balize Delta. During this time the St. Bernard Delta continued to be dominated by marine processes and subsidence. Marine waters began to intrude into the formerly freshwater marshes, and marshland deterioration

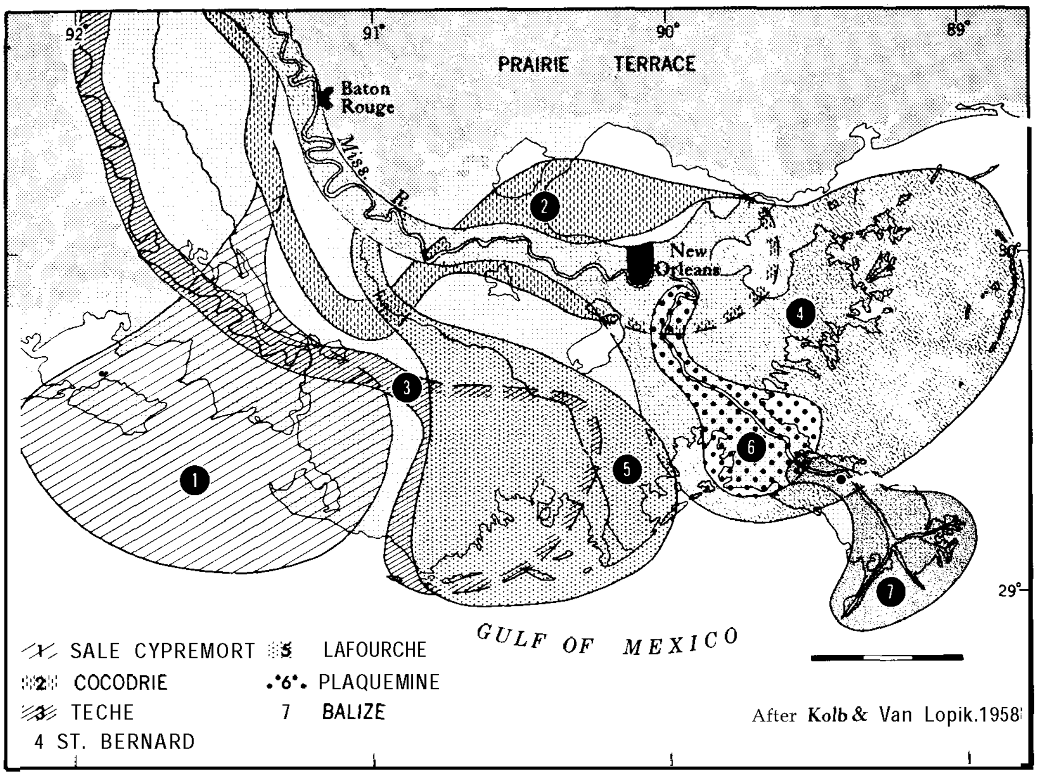


Figure 16. Deltaic lobes of Mississippi River deltas (modified from Kolb and Van Lopik 1958).

increased rapidly. Initially the interior marshes deteriorated, and the coastal barrier islands were attached to the ends of the former distributaries. Eventually the Lafourche Delta system reached its maximum development and the modern delta lobes (Plaquernine and Balize) began their progradation. The Lafourche Delta was then subjected to marine reworking and compaction.

During the past 800 or so years subsidence in the St. Bernard Delta has reached a stage in which little or no freshwater marshes exist, and the reworked barrier islands have been separated from the mainland. During this same period the Lafourche Delta has lost land, mainly by saltwater intrusion and opening of the marshland behind a coastal barrier still attached to the former distributaries.

Meanwhile, in the modern Balize Delta the river has constructed a major delta lobe. The river would abandon this lobe in favor of the Atchafalaya River course if manmade river control structures at Simmesport did not limit diversion to about one-third of the Mississippi River's discharge. Even with this limited flow the modern Atchafalaya River will continue to build its delta onto the continental shelf for the next several hundred years.

Modern Mississippi Delta

The modern Balize Delta has been constructed during the past 500 years. Because it is relatively young, it offers an opportunity to evaluate the short-term processes responsible for delta building and deterioration. When a break (or crevasse) occurs in the levee of one of the river distributaries, water rushing through the break deposits sediment in the adjacent bay. These bay fill deposits form the major coastal marshes of the subaerial delta. Figure 18 illustrates the bay fill sequences within the modern delta during the past few hundred years. Of the six crevasses shown, four have been dated historically, and much of their development can be traced by historic maps.

After an initial break in the levee of a major distributary during flood stage, flow through the crevasse gradually increases through successive floods, reaches a peak of maximum deposition, wanes, and is cut off (Coleman 1976). As a result of compaction, the crevasse system is inundated by marine waters and reverts to a bay environment, thus completing its sedimentary cycle. These crevasse systems are similar to the larger delta lobes but develop faster so that the details of the processes responsible for their formation can be adequately evaluated.

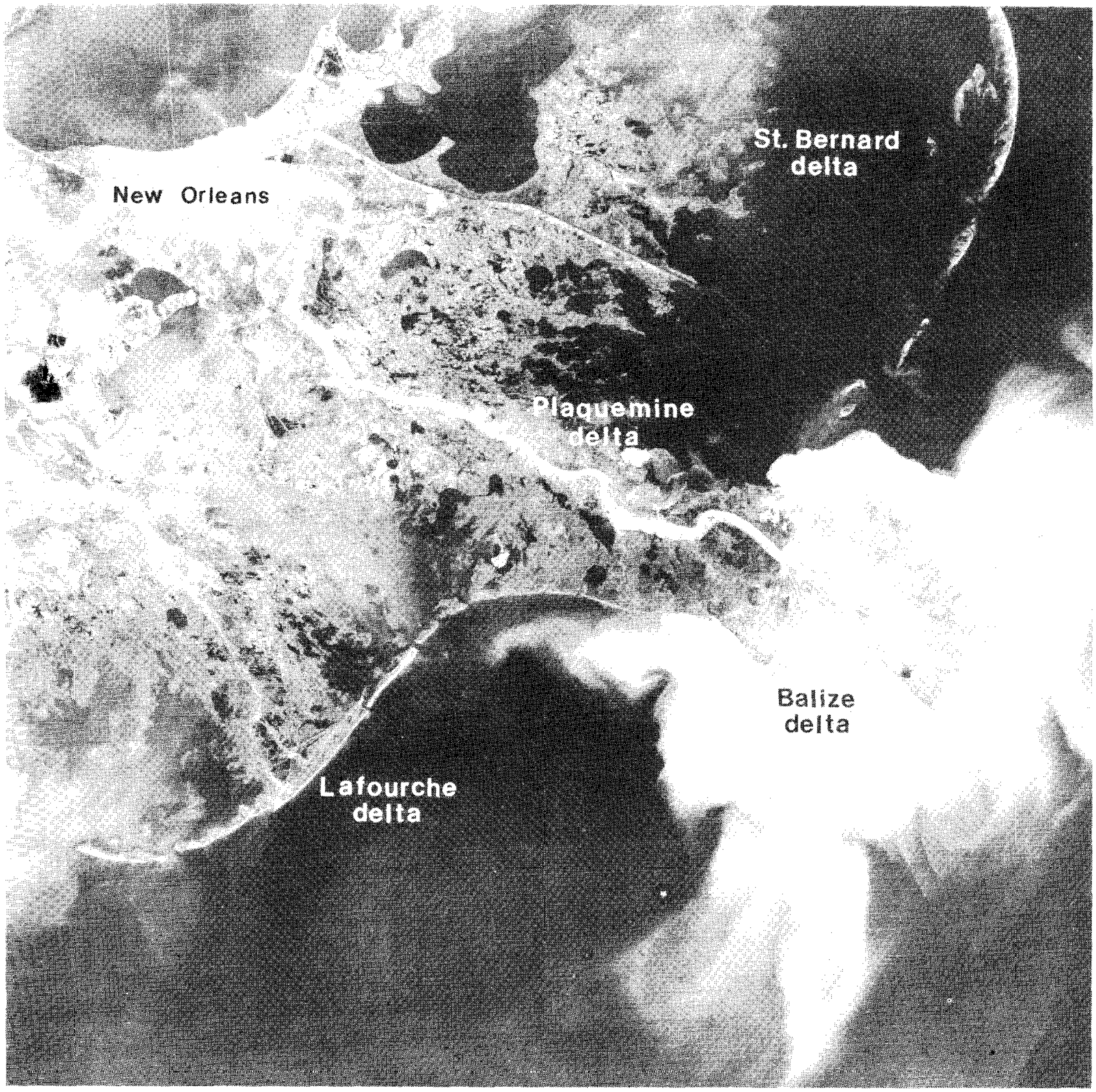


Figure 17. Satellite image of the Mississippi Delta Region showing delta lobes of different ages (NASA photograph 1973).

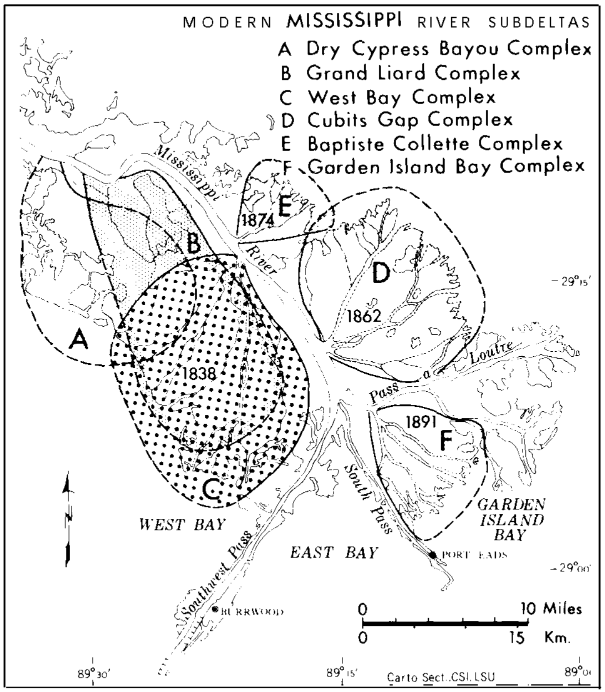


Figure 18. Six subdeltas of the modern Mississippi Balize Delta recognized from maps and sediment analysis. Dates indicate year of crevasse opening (Wells et al. 1982).

The idealized sequence is shown in the plan view in Figure 19. The crevasse initiates as a break in the major distributary levee in the vicinity of point A. During the early formative years coarse-grained sediments are deposited in the immediate vicinity of the break. With time new channels form, bifurcate and reunite, forming an intricate pattern of distributaries. Later, some distributaries are abandoned and become inactive. When a systematic channel pattern develops, the bay fill front advances rapidly into the bay, resulting in the deposition of a sheet of relatively coarse sediment thickening locally near the channels. Seaward of the active channel mouths, fine-grained sediments settle out in deposits commonly referred to as prodelta clays. Other parts of the crevasse system which have been abandoned or are deprived of a continuing sediment supply compact rapidly, and many areas tend to open up and revert to shallow marine bays.

In cross section, the prodelta clays constitute the base of the sequence (Figure 19b). The lowermost clay marks the first introduction of sediment into the bay. Above the prodelta clays are the coarser-grained silts and sands that form the delta front environment. These sandy deposits are laid down immediately in front of the advancing river mouth. Once active sedimentation ceases in the crevasse system, compaction and retreat dominate. For a time marsh growth can keep pace with compaction, but eventually large bays tend to develop, and the shoreline retreats rapidly. Small beaches accumulate near the major distributaries where coarser-grained sediment is available for reworking. Oyster reefs may find a foothold along the old channel margins of the submerged levee ridges.

Historic maps of one of these crevasses, Cubits Gap, can be used to illustrate a cycle of delta building and abandonment. Figure 20 shows the sequential development of the Cubits Gap crevasse. The 1838 map was surveyed prior to the break and shows a narrow, natural levee separating the Mississippi River from the shallow Bay Rondo.

In 1862 a ditch excavated by the daughters of an oyster fisherman named Cubit to allow passage by shallow draft boats caused the crevasse break. The original ditch was about 120 m wide; the flood of 1862 enlarged the opening, and by 1868 the the break was 740 m wide.

By 1884 the map shows the initial buildout of a complex series of distributary channels that had deposited relatively coarse sediment near the break. Note also the shoaling in the bay caused by subaqueous deposition of the finer-grained deposits. The map of 1905 shows that many of the major distributaries had developed and that rapid progradation had taken place in the 11-year period since 1884.

A major portion of the crevasse had been constructed by 1922; some small bays were already beginning to open up, indicating that some parts of the crevasse system were being deprived of sediments. The 1946 map shows that sedimentation was

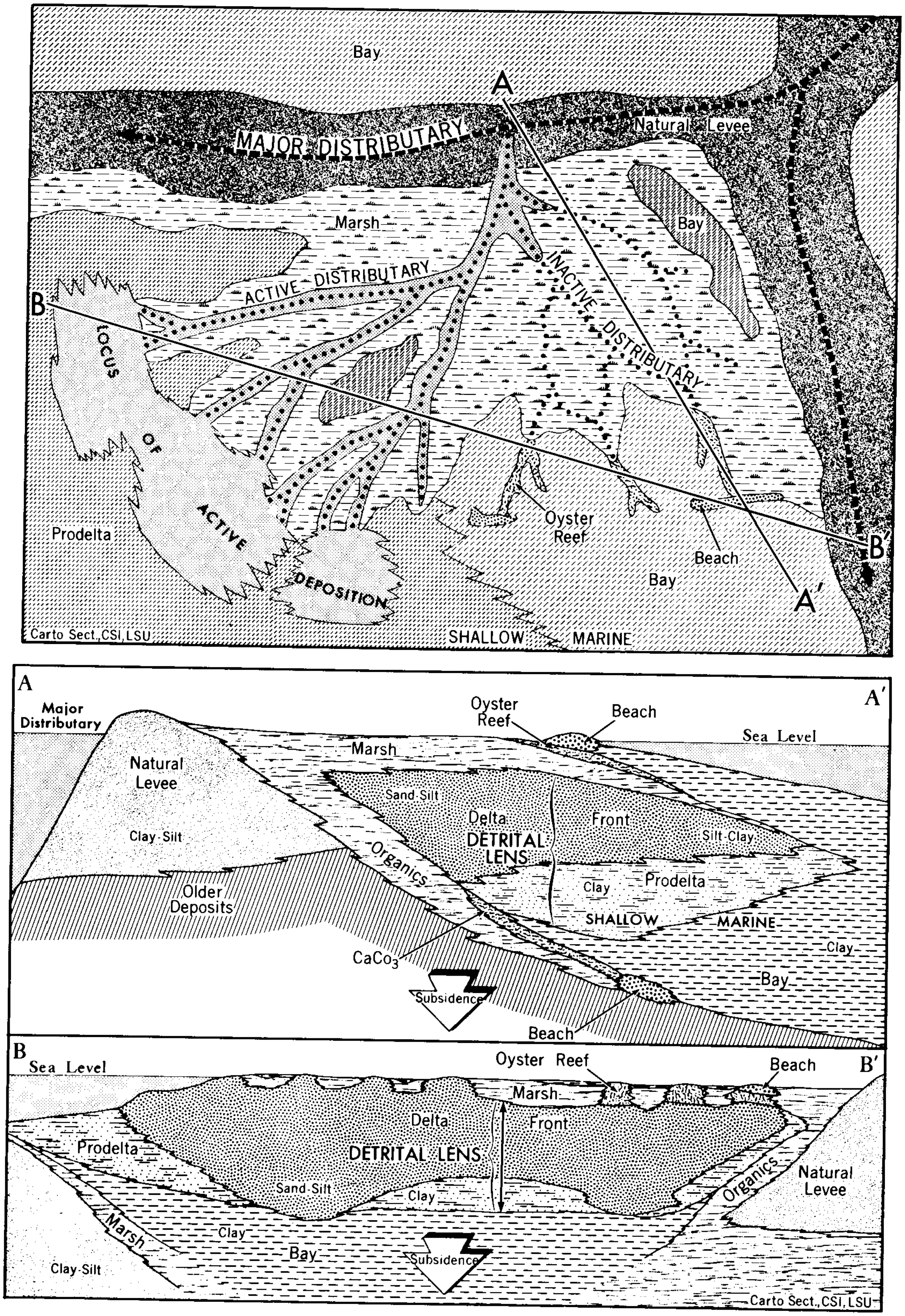


Figure 19. Plan view and cross sections through A-A' and B-B' of environments of deposition in a crevasse (after Coleman and Gagliano 1964).

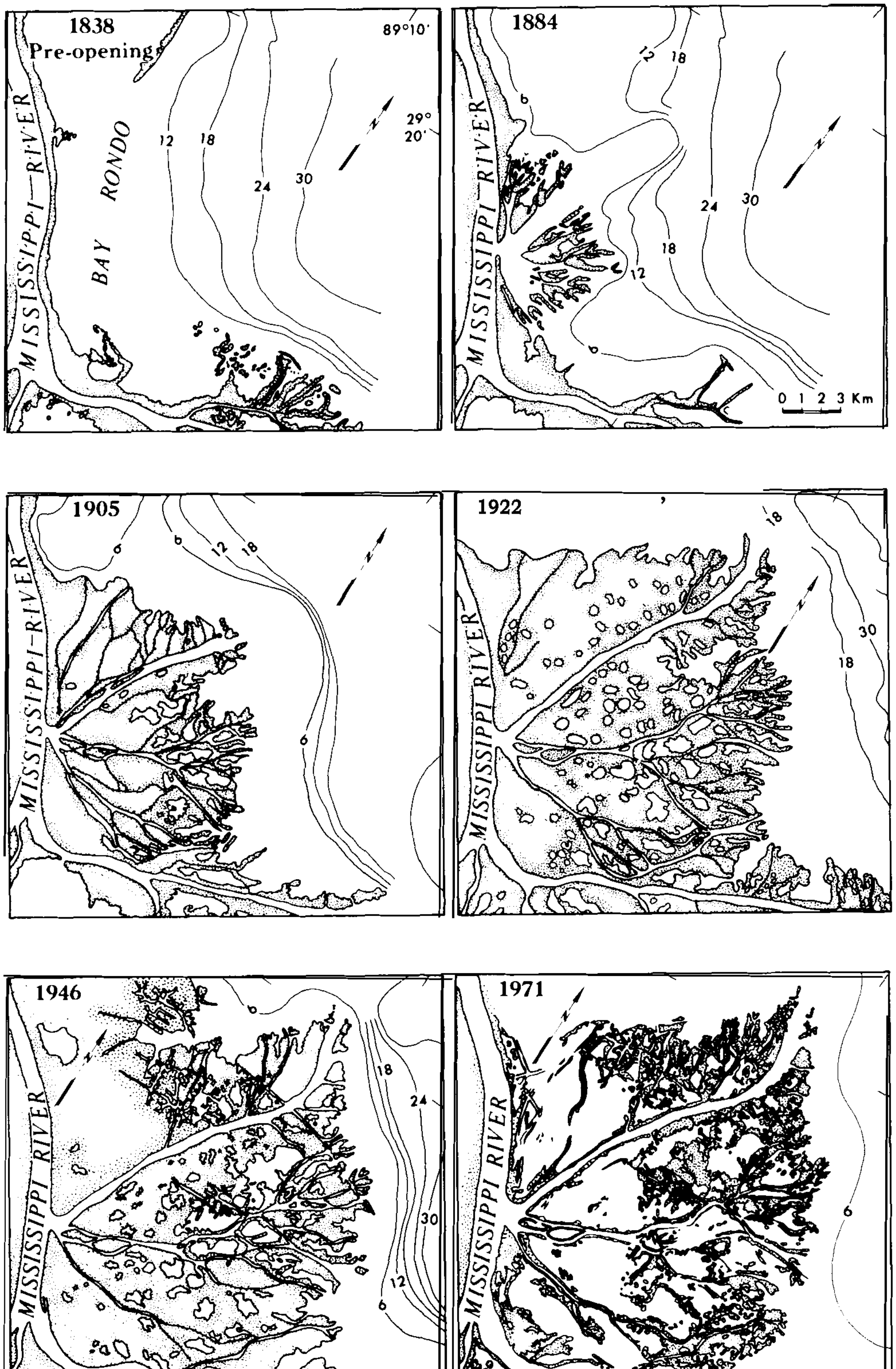


Figure 20. Sequential development of Cubits Gap **subdelta** (Wells et al. 1982).

primarily taking place at the seaward ends of selected distributaries and that marshland loss was beginning to take place.

By 1971 a large part of the crevasse system was being inundated by marine waters, and marsh loss was becoming significant. The only deposition was at the seaward ends of some of the distributaries and subaqueously in the bay fill front. Yote that land loss begins first near the crevasse break. Here sedimentation is extremely slow, depending only on overbank flooding, whereas higher sedimentation rates are still prevailing near the distal parts of the crevasse system. Figure 21 illustrates the crevasse growth and deterioration.

Figure 22 shows on a single plot the cyclic nature of four of the Mississippi River crevasses; each cycle consisted of growth followed by deterioration. Projection of the present-day trends indicates a life cycle for a crevasse system that lasts 115 - 175 years.

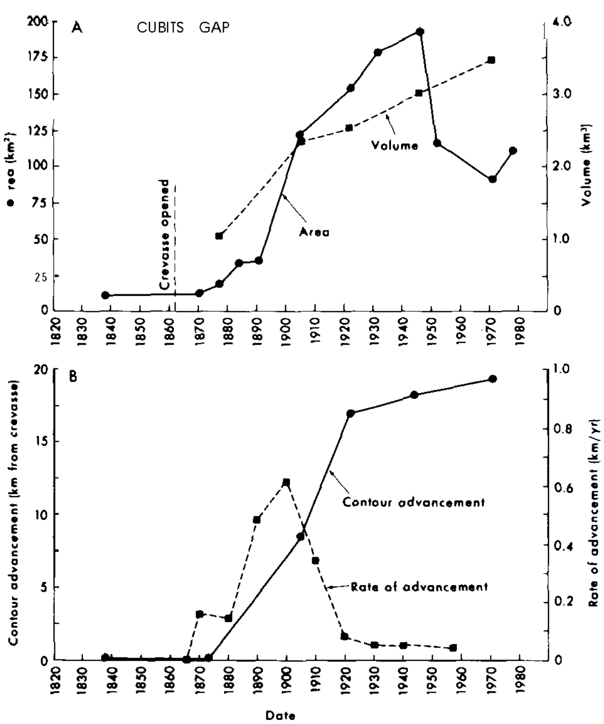


Figure 21. Linear, areal, and volume growth curves for the Cubits Gap subdelta (Wells et al. 1982).

Growth rates during progradation ranged from 0.8 km^2/yr to 2.7 km^2/yr. Degradation rates averaged from 1.0 to 4.1 km /yr.

This growth and deterioration cycle of bay fills, although representing a relatively short time period, is similar to the cycle of major delta lobes described earlier. The delta cycle is on a much longer time scale - a growth period that approaches 800 - 1,000 years and a deterioration period that can be as long as 2,000 years. These bay fills provide an excellent model for evaluation of the future growth of the newly formed Atchafalaya Delta (Wells et al. 1982) and for the deterioration of the former Mississippi River delta lobes.

The composite curve in Figure 22 shows a peak in the early 1940's, followed by a rapid loss of marshes that continues, with a temporary reversal during the flood years of the 1970's, to the present. The rapid degradation of this delta lobe, even though river flow has been maintained, is not well understood. In the Mississippi River Deltaic Plain as a whole the same rapid marsh loss is found. This is more understandable since, with the exception of the Atchafalaya Delta, the other hydrologic units are all abandoned, degrading lobes. Across the delta the marsh loss rates have been accelerating rapidly during this century to the present rate of 1.5 percent per year or about 100 $km^2/year$ (Gagliano et al. 1981; Figure 23, 24).

This rapid degradation rate is cause for considerable alarm. Strong evidence supports the contention by many that superimposed on the natural geomorphic processes described in this section are newer changes, both natural and human, that are strongly affecting the coastal marshes today. These changes range from local to global.

At the global scale the rate of sea-level rise has accelerated in recent years, as has been discussed (Figure 11). The acceleration has been imputed to the increase in the atmosphere's carbon dioxide resulting from burning fossil fuels and clearing forests. Increased carbon dioxide in turn creates a

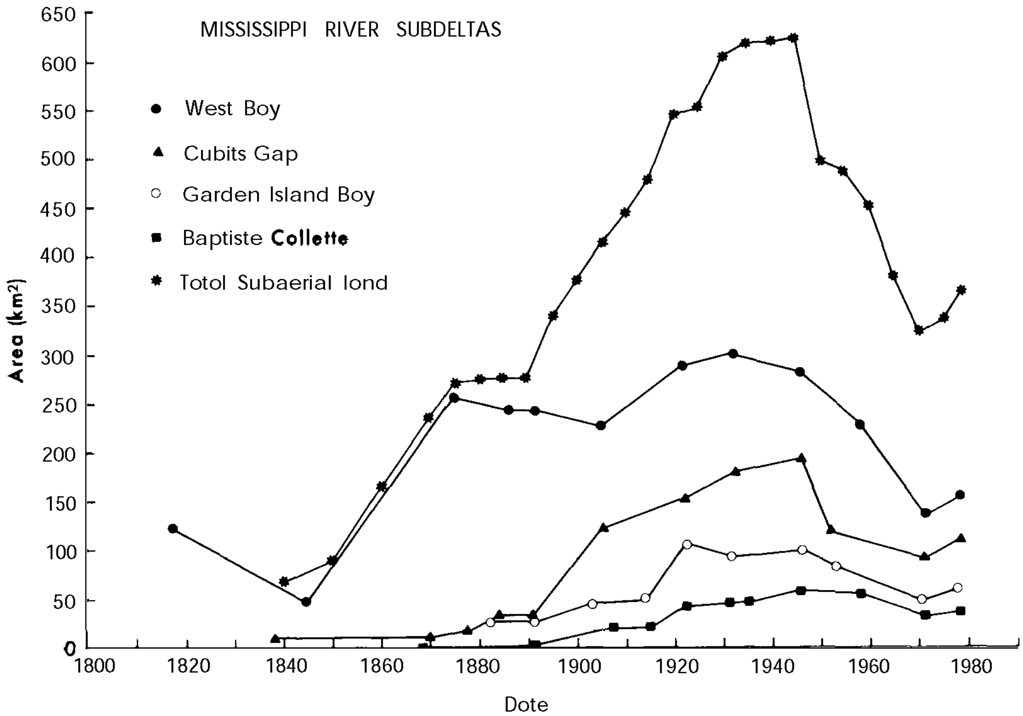


Figure 22. Composite subaerial growth curve, Mississippi River subdeltas. Total subaerial land determined from averages at 10-yr intervals (Wells et al. 1982).

"greenhouse" effect that is warming the earth's surface and melting the polar ice caps. The net affect of both true sea-level rise and coastal subsidence has been a change in the coastal submergence rate from about 0.27 cm/yr during 1948 to 1959, to nearly 1.3 cm/yr between 1959 and 1971. Although these data are for a gauge at Bayou Rigaud in the Barataria basin, the trend is similar along the whole Louisiana coast (Gosselink et al. 1979).

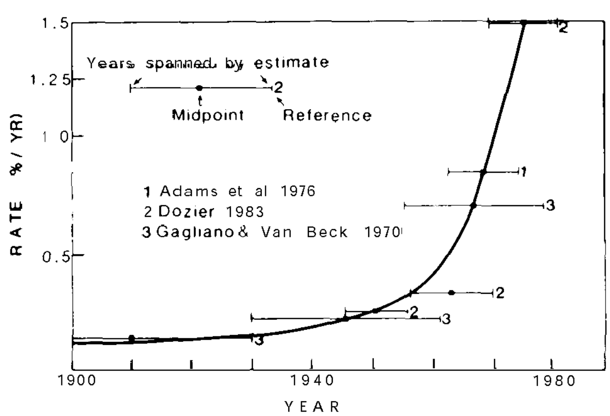


Figure 23. The accelerating wetland loss rate in the Mississippi Delta (based on data from Dozier 1983).

In order to remain at intertidal elevations marshes must accrete vertically as rapidly as they are sinking. The rapid rate of marsh degradation indicates that they are not doing so, an observation supported by recent research (Delaune et al. 1983). One reason is that the Mississippi River no longer supplies as much sediment to the coast as it has historically. Keown et al. (1980) reported that sediment supplies are only about 60 percent of what they used to be, despite the presumed increase in erosion that accompanies forest clearing on the upper watershed. The reduction is presumably due to the construction of dams on the upper reaches of the river and its tributaries. The dams also remove the coarser sediments selectively, so that the sediments reaching the coast are depleted of the sand that is the main foundation material for delta growth. This means that the river can no longer support as

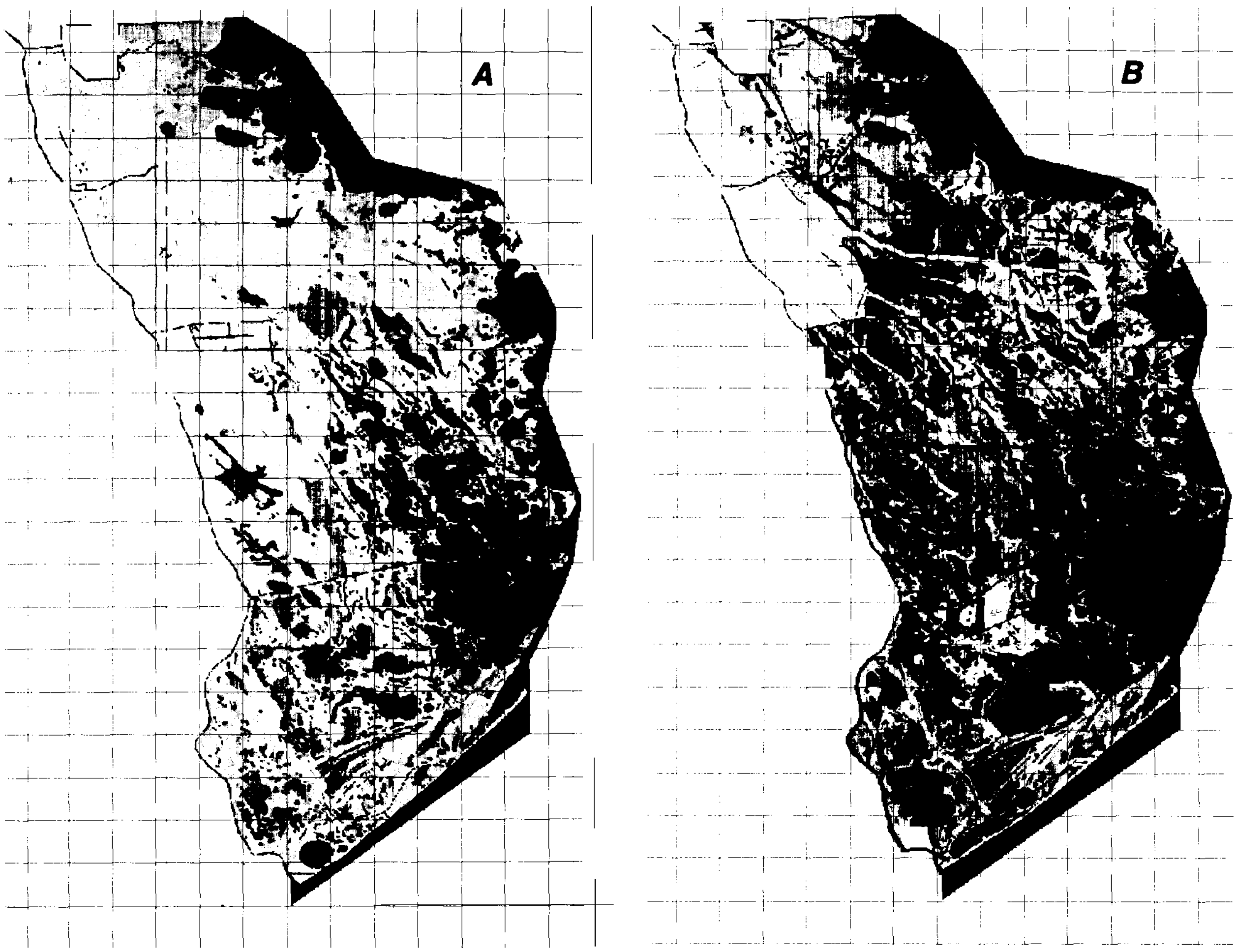


Figure 24. Computerized re-creation of the west side of Barataria Bay showing the change in wetlands between 1945 (a) and 1980 (b). Black is open water; marshes are shown as varying shades of grey (Dozier 1983).

large a delta as it has historically. In addition,channeling and leveeing the river entrains much of the sediment, preventing spring overbank flooding that nourishes the interdistributary marshes.

There is now strong evidence that the rate of marsh loss is beina accelerated bv local human activities in-addition to the reduction in the river's sediment load. Canals are the major culprit in this scenario. Formerly, rain runoff from adjacent uplands flowed across wetlands, dropping its load of sediment and nourishing the marshes. Now a network of drainage canals along the marsh-upland interfaces of the delta estuaries carries this runoff directly into estuarine lakes and bays, bypassing the swamps and marshes (Conner and Day 1982). If runoff flowed across the wetlands, the trapped sediment would help minimize wetland subsidence and the quality of the runoff water would be improved before it entered the lakes and bays. Instead, the portions of the estuaries near urban areas are becoming increasingly turbid and eutrophic (Craig et al. 1977).

At the other end of the estuary, navigation canals, especially those that cross the barrier islands, cause major disruption of circulation. The canals are straight and deep in estuaries that have an average depth of only 1 or 2 m. Therefore they capture flow from smaller channels and allow the intrusion of salt water deep into the estuary. Saltwater accelerates the conversion of fresh and intermediate marshes to saline marshes. When increases are sudden, salt-intolerant vegetation can be killed, and the marsh may erode before other vegetation can be established. There is also some suggestion that the biochemistry of marsh sediments changes with salinity, making the marsh more vulnerable to erosion (Dozier 1983).

A network of medium-sized canals that are dredged for access to oil and gas well sites is linking the navigation canals to the inner marsh and to the flood drainage canals. These canals are extensive; their impacts are multiple. The canals themselves act like the navigation canals and, in combination with them, change circulation patterns extensively. For example, in the Leeville oilfield (Terrebonne basin) the density of natural channels declined as dredged channels captured the flow of water (R. E. Turner, LSU Center for Wetland Resources; pers. comm.). These canals also allow salt intrusion. Their spoil banks block the flow of water across marshes, depriving them of sediments and nutrients. This is especially noticeable where canals intersect and their spoil banks interlock to impound or partially impound an area. The effect has not been rigorously quantified, but aerial photographs showing the loss of marsh in these semi-impounded areas are too striking to ignore.

Analysis of marsh loss rates between 1955 and 1978 (mapped by Wicker 1980) shows a direct linear relationship between canal density and the marsh loss rate (Turner et al. 1982). The rate of loss per unit of canal is higher in recently formed deltas where the sediments are less consolidated than in older deltas (Deegan et al. 1983). It seems to be maximum where fresh marshes are experiencing salt intrusion (Dozier 1983). Turner et al. (1982) found that the intercept of the regression of marsh loss on canal density (that is where canal density is zero) was always less than 10 percent of the total loss and usually nearly zero. This indicates that nearly all the loss can be attributed to canals. The direct impact of canals (the area they occupy) is less than 10 percent of the total loss. If the spoil area is taken to be three to five times the canal area (Johnson and Gosselink 1982), the direct loss of marsh due to canals is less than 50 percent of the total loss. The rest is attributed to indirect effects of circulation disruption by the canal and its spoil.

Table 4. Land-use changes along the northwest edge of the Barataria basin, on the Bayou Lafourche natural levee (Dozier 1983).

a. Change in developed land

Year	Developed land area (km)	Rate of increase (km /yr)
1945	19.27	
1956	20.80	0.13
1969	39.41	1.43
1980	71.69	2.93

b. Loss of marsh to indicated category, 1945-80

	Area (km)	Marsh loss (percent)
To canal	39	6
To development	52.4	8.2
To open water	127.6	20
Total to nonmarsh	218	34

An independent, lesser source of marsh loss is direct impoundment and drainage for agriculture or other development. Several large reclamation projects were initiated early in the century. Most of these were destroyed by floods like the one in 1927 and now appear as large, square lakes in the coastal zone. However, reclamation along the natural levees is proceeding apace, as is shown for the Bayou Lafourche levee on the northwestern side of Barataria basin (Table 4). Over the region as a whole, especially in the urban areas, agricultural land has been converted to urban and industrial use without a large net reclamation of new marsh (Table 5).

Table 5. Land use changes, in hectares, in the Mississippi Delta, 1955-78 (Nicker et al. 1980a).

Unit	Urban/industrial area			Agricultural area			Net change
	1955	1978	Change	1955	1978	Change	
II	27,987	55,116	[illegible]79	[illegible]37	23,949	-21,059	
III	1,979	2,058	11,343	13,772	81	44	6,070 123
IV	8,279 / 1,279	19,680 / 12,682	1,402	5,100	14,118	346	11,689
					6,639	1,539	2,941
VI	387	575	188	742	1,043	301	489
Total	2,145	4,364	2,219	41,366	40,772	-594	1,625
							22,937

CHAPTER TWO
TEMPORAL AND SPATIAL GRADIENTS IN DELTA MARSHES

The ecology of a marsh is determined by the biota as constrained by the regional geologic platform on which it develops, and by the water regime. These create physical gradients that are closely related to variations across the delta in marsh vegetation, fauna and ecological processes. Furthermore, in the Mississippi Delta geologic processes are so rapid that the platform cannot be assumed to be constant in the time scale of human yenerations.

As we have seen, a typical delta lobe has a life cycle of about 5,000 years. But the accretionary phase is very rapid. Wells et al. (1982) showed subdelta cycles in the modern birdsfoot delta of 115 - 175 years. In the Atchafalaya Delta about 20 km^2 of new land has appeared since 1973. And with current subsidence rates of about 1 cmlyr even the destructional phase of a delta is rapid; marsh degradation to open water is occurring at a net rate of about 75 km^2/yr for the deltaic plain as a whole. As a result, the spatial gradients are not constant but vary with the age of the delta lobe. In this chapter we will consider the spatial and temporal gradients of Mississippi delta marshes, particularly as they control the physical substrate, water and water chemistry, and vegetation.

TEMPORAL GRADIENTS

Gagliano and Van Beek (1975) suggested that the geologic cycle of delta growth, abandonment, and destruction is paralleled by a cycle of biological productivity. The biotic cycle lags the geologic one so that peak productivity occurs during the delta lobe's destructional phase (Figure 25). In order to throw some further light on this interesting hypothesis, it is pertinent to describe the way marshes develop in the context of whole basin systems.

To do this, I have used data from the delta hydrologic units, arranged by age to get an instant snapshot of a basin's development over time. This approach is not ideal. The hydrologic units are interdistributary, except for the active deltas, and thus represent the active sedimentation of more than one river distributary. For example, the west side of the Barataria basin was formed when the Lafourche distributary was active; the east side is strongly influenced by recent Mississippi River sediments. However, biological data have, in general, been collected by hydrologic unit, and a rough tine sequence of six units can be identified, ranging from modern to about 5,000 years old.

When a delta lobe first begins to form, it is overwhelmingly riverine. The mineral sediment load is high, and water is fresh. As a result,the newly emerged sediments are mineral, and the first marshes to appear are fresh (Figures 26 and 27).

4s the delta grows, the fresh marshes expand. As described in Chapter 1, the expansion is not uniform; as subdeltas are cut off from stream flow,they become more and more influenced by marine tidal waters. Consequently, salinity increases, and brackish and saline marshes begin to appear.

When the river diverts to another delta site, the periphery of the abandoned

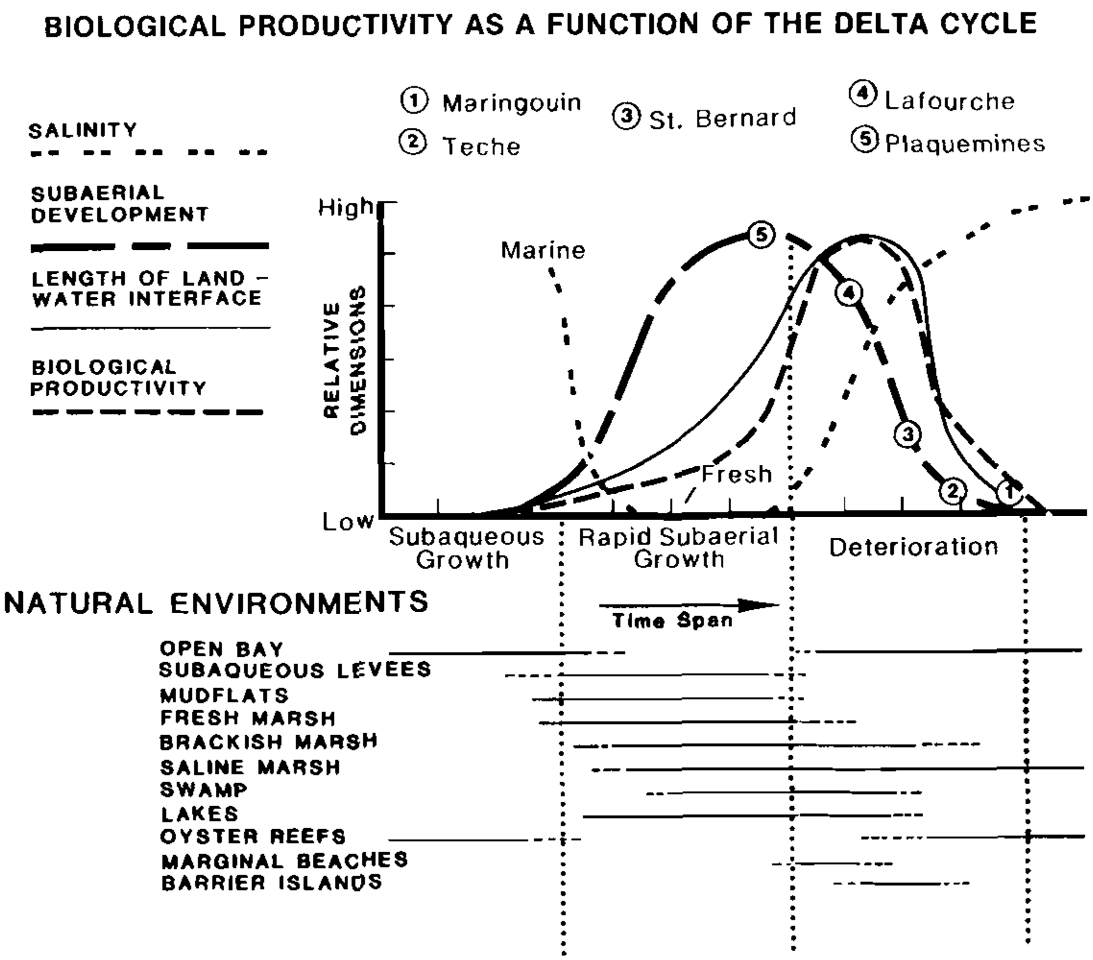


Figure 25. Environmental succession of an idealized delta cycle (Gagliano and Van Beek 1975).

delta becomes saline and is modified by marine processes which typically rework the delta edge into a series of barrier reefs and islands that protect the inner estuary. Riverine hydraulic energy is much reduced and sediment loads decline.

Further marsh development is increasingly controlled by the productivity of the vegetation, which forms peat. This is especially true at the landward edge of the basin. Here, too far from the coast to experience much tidal activity and with the river's sediment supply cut off, organic material produced in situ is the only material available for marsh accretion. Thus, as Figure 26 shows, fresh marshes start out as highly mineral, but as the delta lobe ages become increasingly organic. Salt marsh sediments, subject to frequent, turbid tidal washes, are always fairly high in mineral content.

The general sequence is clear in the figure, but some exceptions deserve comment. Sediment mineral content decreases with distance from the river source (that is, from fresh toward salt marshes) in active deltas (units II and V) but decreases with distance from the marine sediment source in the abandoned basins. This trend is consistent in all basins. However, compared to the low mineral contents in the recently abandoned basins III and IV, marshes of the older basins I and VI have relatively high mineral concentrations. This probably reflects the continued sediment-laden freshwater input into these systems.

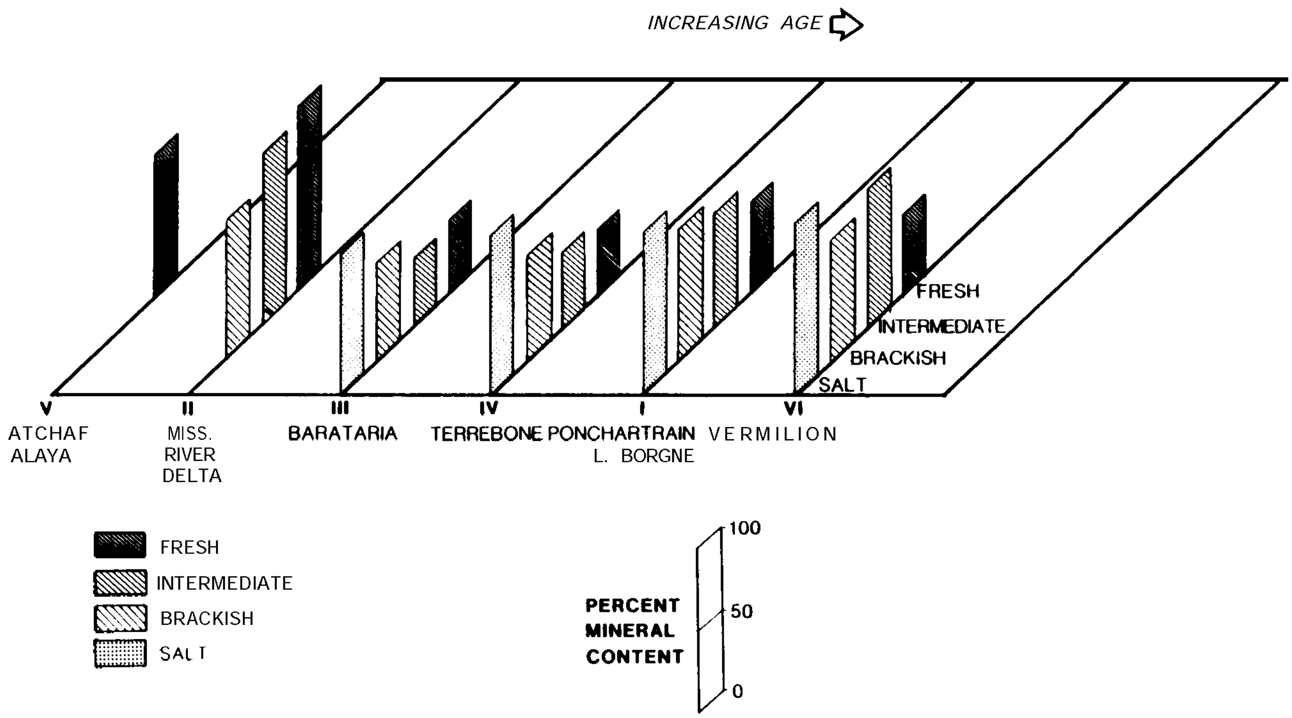


Figure 26. Mineral content of marsh soils in Mississippi delta hydrologic units, arranged in order of increasing age (data from Chabreck 1972).

The Ponchartrain-Lake Borgne basin (Unit I) is fed by a number of small, local streams, by the Pearl River, and periodically by diversion of the Mississippi River through the Bonnet Carre spillway into the lake. The Vermilion basin (Unit VI) is fed by the Vermilion River and also receives significant quantities of fresh Atchafalaya River water flowing into it from the neighboring Atchafalaya Bay across Cote Blanche Bay. This freshwater supply is reflected in the low mean sediment salinity of Unit VI and in its higher-than-expected proportion of fresh marshes (Figure 27).

The Pontchartrain-Lake Borgne unit is exceptional in that the mean salinity is high, but so is the proportion of fresh marshes. This may be a result of the physiography of the system. The gradient is compressed into the lower half of the basin by the location of the mouth of the Pearl River, the primary freshwater source, and by the small passes into Lake Pontchartrain which restrain free flow of saline water into the lake.

Within a hydrologic unit of constant size, wetland area and land:water ratio

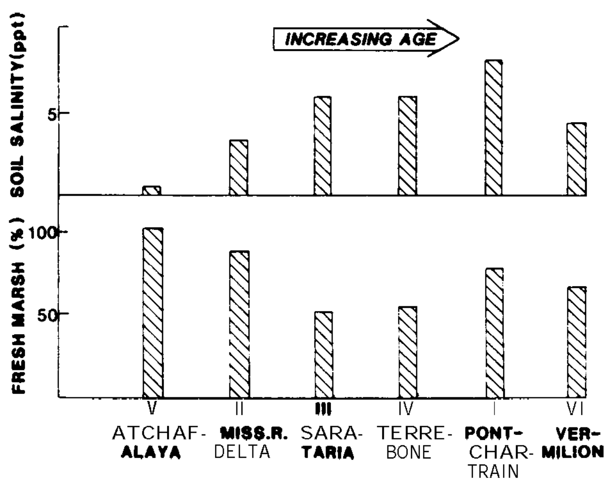


Figure 27. Marsh soil salinity and percent fresh marsh in Mississippi Delta marshes by hydrologic unit, arranged in order of increasing age. Soil salinity is a mean for the whole basin weighted by area of each marsh zone. The fresh marsh is percent of total marsh area (data from Chabreck 1972).

increase during active delta growth to a maximum when the distributary is abandoned, and then decrease as marshes subside and degrade back to open water bodies. The length of the interface between the marsh and adjoining water bodies (the marsh edge) is small in young delta lobes because the new marsh is fairly solid. After abandonment, however, the marsh edge increases as marshes open up and more and more tidal streams interfinger through them.

This is reflected in the ratio of marsh edge length to marsh area (m/m') in different marsh zones. There are no measurements of this ratio available for the delta, but in the neighboring chenier plain's fairly solid fresh and intermediate marshes the ratio is 15 and 17, respectively. As tidal energy increases, the ratio increases to 39 in brackish marshes and 60 in salt marshes (Gosselink et al. 1979). Applying these ratios to the delta hydrologic units., the mean edge length per unit area of marsh, weighted for the area of different marsh zones in a hydrologic unit, increases with the age of the unit (Figure 28). However, because younger units have more marsh, the total length of the marsh edge (the product of the ratio and the marsh area) is greatest in the recently abandoned Barataria and Terrebonne units (III and IV, Figure 28).

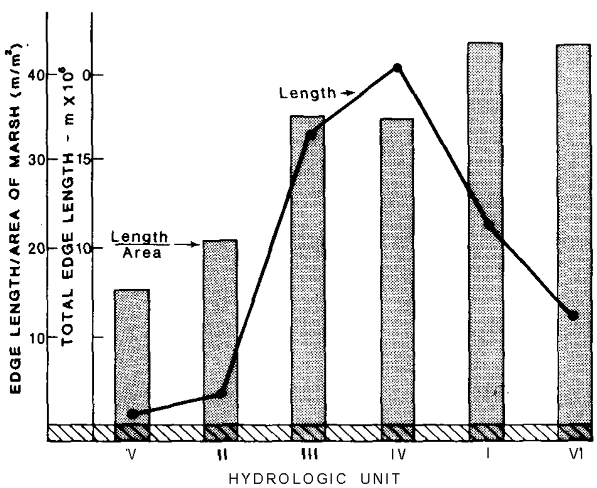


Figure 28. Marsh edge length:area ratio and total marsh edge length for delta hydrologic units. The units are arranged in order of increasing age (data from Chabreck 1972).

How are these differences in the physical characteristics of hydrologic units related to biological productivity? Two measures of productivity are net primary production and the inshore shrimp harvest (Figure 29). Total net productivity is lowest in the active deltas and highest in the Pontchartrain hydrologic unit - mostly a function of the size of the unit. Primary production per unit area, however, is highest in the Barataria and Terrebonne basins. Inshore shrimp yield is also highest in the same basins. Since these basins are in the early destructional phase,these data support the hypothesis of Gagliano and Van Beek (1975).

Regressions of biological productivity on salinity, marsh area, and edge length (Table 5) should be taken with caution because they are based on data from only six hydrologic units. Nevertheless, thev make for interesting speculation. -Average net primary production

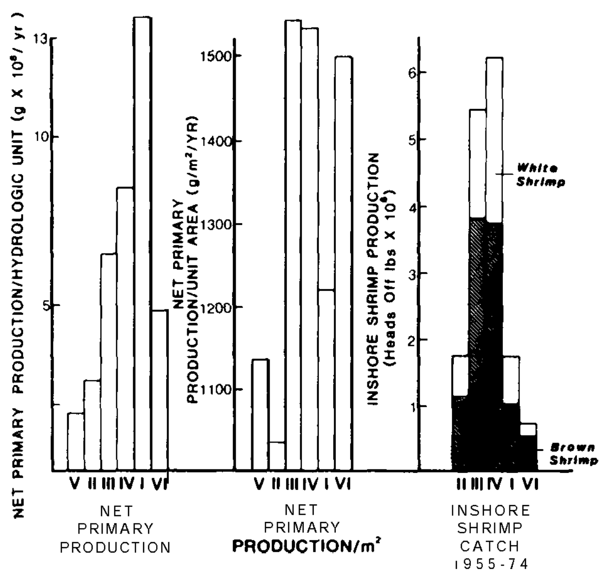


Figure 29. Net primary production and fishery yield of Mississippi River Deltaic Plain hydrologic units. Production calculated from average production of each habitat type and its area in the hydrologic unit. Shrimp data from Barrett and Gillespie (1975). Basins are, in order of increasing age: I - Pontchartrain-Lake Borgne, II - Balize, III - Barataria, IV - Terrebonne, V - Atchafalaya, VI - Vermilion.

Table 6. Regression analyses relating net primary production (NPP) and inshore shrimp production (1955-74) in hydrologic units to various physical parameters. NPP was calculated from the mean productivity and area of each habitat type (Costanza et al. 1983). Shrimp catch is from Barrett and Gillespie (1975). R is the proportion of the variability in the dependent variable accounted for by variations in the independent variable.

Independent variable	Dependent variable					
	NPP		NPP/area		Shrimp catch	
	Equation	R	Equation	R	Equation	R
Total unit area	Y=1.22E5X+0.5	0.96	Not computed		Y=0.2E5X+2.4	0.09
Total marsh area	Y=4.4E5X+0.92	0.72	Y=0.02X+318	0.20	Y=1.04E5X+0.22	0.76
Marsh/total area	Not computed		Y=17.2X+881	0.98	Not computed	
Total brackish & salt	Y=0.1E5X+1.4	0.79	Not computed		Y=1.6E5X-0.01	0.58
Marsh edge length	Y=1.16X+1.2	0.83	Not computed		Y=0.285X-13	0.75
Edge length/area	Y=0.41X-6.5	0.77	Not computed		--	0.01
Mean salinity	Y=1.57X-1.02	0.85	Y=37.5X+1150	0.18	--	cl.01
NPP	--		Not computed		Y=0.25X+1.7	0.20

per unit area is very closely related to the proportion of marsh in the unit because marsh productivity is higher than aquatic productivity; therefore, average productivity increases with the proportion of marsh.

Total net primary production is, as might be expected, closely related to the total area of the hydrologic unit. In contrast, inshore shrimp catch, which in these estuaries is quite a good index of total shrimp yield (R. Condrey, LSU Center for Wetland Resources; pers. comm.), is poorly related to most single factors in the analysis. This may be because of the animal's complex migratory life history. For example, shrimp yield is not related to total hydrologic unit area, nor to total net primary production. The best relationship is to the marsh area and to the total marsh edge length in the unit. This suggests that accessibility to the marsh and marsh refugia are important components of fishery productivity. Accessibility (as indicated by the marsh edge length:marsh area ratio) increases with the age of the delta lobe. Since marsh area decreases as the delta degrades, the total accessible marsh is maximum in the early destructional geologic phase.

These tentative correlations between marsh edge length and fisheries productivity need to be verified with additional research, but the implications are interesting and important. First, they support Gagliano and Van Beek's hypothesis and provide a reason why biological productivity peaks in degrading basins.

Second, if the hypothesis is correct, it has significant implications for the future of Louisiana fisheries. We are currently enjoying the results of past delta building by the Mississippi River. Modifications of the river have significantly affected its ability to build new wetlands. As a result we are not now producing the geological resource for our future fisheries. If there is a significant lag time before new delta growth can support efficient fishery production, we can not afford to wait until the present bounty disappears before encouraging new delta formation.

SPATIAL GRADIENTS

Within any delta basin a spatial gradient is set up by the land's slope and by the source and magnitude of freshwater compared to marine water inflow. In the Barataria basin the mean water slope from the coast to the swamp forests 80 km inland is about 2 mm/km (Byrne et al. 1976). Since coastal marsh elevations approximate the local mean water level

(Sasser 1977; Baumann 1980), the land slope is also exceedingly small. The slope of the water is slightly steeper in the Atchafalaya basin because of the enormous river inflow. Generally, across the coast it is so slight that "downhill" changes daily, depending on the astronomical tide stage, wind direction and strength, rainfall, local runoff, and river flow.

On a smaller scale of meters rather than kilometers, a slope also exists on the marsh surface from the edge of tidal streams inland. Water overflowing stream banks on flood tides slows and drops much of its sediment load near the stream edge as it moves inland, creating a slight crest or levee next to the stream. Because of this, water tends to drain away from streams into small marsh channels that eventually carry the water back through the natural levee. The natural creekbank levee, which is usually measured in centimeters, and the slight marsh surface slope are enough to create a gradient of inundation, water chemistry and biotic activity. These hydraulically mediated gradients are responsible for much of the observed biotic diversity in the delta marshes.

Flooding

Information on the frequency and duration of marsh flooding is rather scarce. Sasser (1977) and Baumann (1980) measured marsh elevations relative to local mean water levels and calculated inundation statistics for a number of different species and associations from nearby tide gauge records. Byrne et al. (1976) plotted frequency and duration of flooding at locations in the Barataria basin corresponding to salt, brackish and fresh marshes. They did not measure the elevation of any marshes relative to these data. However, by interpolating Sasser's elevations on the graphs by Byrne et al. it is possible to come up with several estimates of marsh inundation (Table 7).

Considering the variability in these estimates, it appears that the total duration of flooding during the year is about constant across the whole marsh from coast to upland. But the regular, daily tidal flushing of the salt marsh is replaced by a more infrequent flooding inland where wind tides and upstream runoff play a much larger role. The delta marshes appear to be flooded about 50 percent of the time. The average duration of a flooding increases from 12 to 16 hours at the coast to almost 5 days in fresh marshes. Notice that the streamside marsh, some 10 - 15 cm above the inland marsh, is inundated almost as often but for much shorter time periods, so that it is flooded only about 12 percent of the year.

Baumann (1980) showed that inundation characteristics are not constant throughout the year (Figure 30). Flooding frequency does not vary much, but because the water level varies seasonally, the

Table 7. The annual duration and frequency of inundation of marshes in the Barataria basin, Louisiana. Figures in parentheses indicate the percentage of the year inundated.

Marsh zone	Reference	Duration (hr/yr)	Frequency (No./yr)	Duration/event (hr)
Salt (inland)	Baumann 1980	4396 (50)	263	16
	Byrne et al. 1976	4400 (50)	200	22
	Sasser 1977	4100 (47	150	27
(streamside)	Byrne et al. 1976	1050 (12	160	6.6
Brackish	Byrne et al. 1976	3700 (42	75	50
	Sasser 1977	3500 (40	125	28
Intermediate[a]	Sasser 1977	2300 (26	32	29
Fresh	Byrne et al. 1976	3700 (42	32	115

[a]*Spartina patens* and *Sagittaria falcata* association.

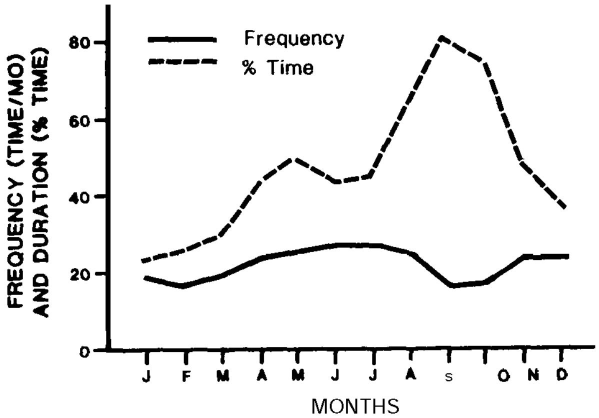


Figure 30. Seasonal salt marsh inundation patterns (Baumann 1980).

water depth over the marsh also varies. There is a sharp peak in duration of flooding in September and October when water levels are highest. During this time the salt marshes are inundated more than 80 percent of the time.

Soils

As discussed in the previous section on changes in an aging delta lobe, the mineral content of marsh soil is directly related to the hydraulic energy of the system. In abandoned interdistributary environments this means that sediment delivery to the marsh decreases inland from the coast (Units III, IV, I, and VI in Figure 26) and also into the marsh from the edge of local tidal streams (Figure 31).

According to Baumann (1980), most of the sediment is deposited during frequent winter storms and rare summer tropical disturbances, probably by redistribution of sediment from bay bottoms (Figure 32). As expected, the sediment size fraction also varies with the hydraulic energy. There is hardly any sand in delta marshes, but the fraction of clays increases inland with decreasing hydraulic energy (Gosselink et al. 1977).

Rates of sediment deposition are rather well known, both from ^{137}Cesium (Cs) profiles and from marker horizons laid down on the surface and tracked over time (Hatton 1981, Table 8). Streamside

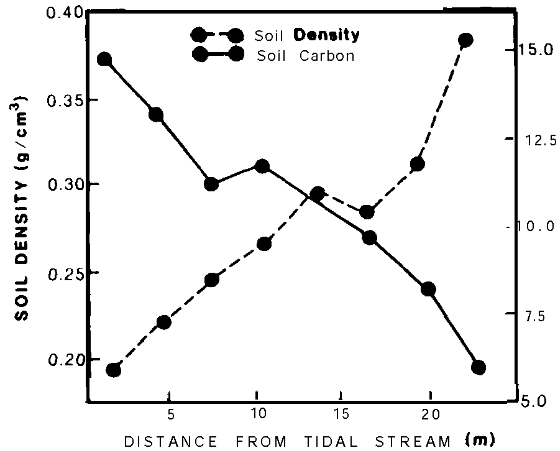


Figure 31. Variation in soil density and soil carbon content with distance inland from the stream edge in a salt marsh in the Barataria basin (Buresh 1978).

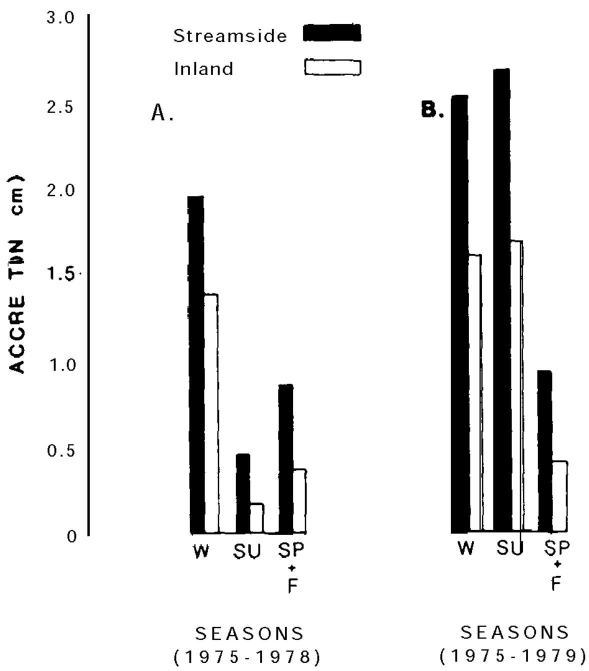


Figure 32. Sedimentation rates on the Barataria saline marsh. (A) Mean seasonal sedimentation 1975 - 78. (B) Mean seasonal sedimentation 1975 - 79. Sedimentation rates were highest during the winders of 1975 - 78. Hurricane Bob and tropical storm Claudette passed through the area during the summer of 1979, resulting in very high desposition rates (Baumann 1980).

rates average about 1.4 cm/yr, while accretion in inland marshes is lower, about 0.75 cm/yr. Table 9 shows the deposition rate of certain soil components as given by Hatton (1981). Mineral deposition, which is directly proportional to bulk density, is much faster in salt than in fresh marshes. Even though the fresh marshes are much more organic than the saline marshes, the rate of deposition of organic carbon is no faster in these marshes. It only appears to be because the organic material deposited is not "diluted" by as much mineral matter.

Salt

One component of the mineral sediment is salt. Despite the earlier discussion of discrete marsh vegetation zones, the salt gradient is horizontally stratified. Rather, sediment salinity decreases gradually from the coast inland (Figure 33). There does not seem to be much of a gradient from the edge of a stream into the marsh interior. In many marshes elsewhere, salinity actually increases inland as elevation increases, and the salts in infrequently flooded soils accumulate because evaporation exceeds rain. But in these delta marshes this does not occur. In fact, impounded marshes typically become less saline as surplus rain gradually leaches out the sediment salts.

Table 8. Accretion rates (mm/yr) in Louisiana delta marshes, based on the 1963 ^{137}Cs fallout peak (S=streamside, I=inland; Hatton 1981).

Marsh zone	Site	N*	Accretion rate Mean	Accretion rate Range
Fresh	S	2	10.6	0
	I	6	6.5	3.1- 6.9
Intermediate	S	3	13.5	13.0-14.0
	I	6	6.4	3.8-10.6
Brackish	S	3	14.0	10.6-16.9
	I	7	5.9	3.8- 8.1
Salt	S	2	13.5	0
	I	6	7.5	5.6- 9.4

* Number of cores represented.

Table 9. Concentration (C) and accumulation rates (A) of organic carbon, nitrogen, phosphorus, iron, and manganese in Louisiana delta marsh soils (Hatton 1981).

Marsh zone	Site*	Vertical accretion rate	Bulk density	Organic carbon C	Organic carbon A	Nitrogen C	Nitrogen A	C:N	Phosphorus C	Phosphorus A	Iron C	Iron A	Manganese C	Manganese A
		(cm/yr)	(g/cm³)	(%)	(g/m²/yr)	(%)	(g/m²/yr)		(µg/g)	(g/m²/yr)	µg/g	g/m² yr	(µg/g)	(g/m²/yr)
Fresh	S	1.06±0.	0.11±0.03	23.1±4.2	250	1.5±0.3	16	15.7±1.5	927±171	1.0	4,729±3,912	19 2	144±52	0.15±0.
	I	0.65 18	0.09±0.01	29.6±3.1	145± 40	1.8±0.2	9±3	16.7±1.0	944± 82	0.5±0.1	9,956±2,007	7± 3	114±12	0.07± 02
Inter-mediate	S	1.35 ±0. 09	0.18±0.04	18.6±3.4	415± 28	1.2±0.18	28±2	15.5±2.3	648± 88	1.5±0.	18,691±2,672	46± 1	69±12	0.17 ±0. 01
	I	0.64±0.16	0.08±0.01	29.4±2.4	154± 38	2.0±0.16	11±3	15.0±1.0	763± 34	0.4±0.	10,079±1,590	6±	60± 7	0.03±0.01
Brackish	S	1.40±0.36	0.27 .02	12.5±1.	469±121	0.7±0.04	25±7	18.8±2.	624±135	2.4±0.	20,831±1,251	79±20	100±1	0.38±0.09
	I	0.59 12	0.14±0.01	23.7±1.6 9	183± 37	1.3±0.10	10±2	18.4±1.0 3	664± 38	0.5±0.6	11,830±1,152	10	77± 2 7	0.06 01
Salt	S**	1.35 ±0.	0.25 ±0	11.2	393 ±	0.6	21	18.1	489	1.7 1	17,735	60 ±	111	0.37 ±0.
	I	0.75±0.14	0.29±0.06	11.4±1.6	200± 37	0.7±0.10	11±2	18.9±1 9	668±112	1.1±0 2	16,857± 855	29± 6	33± 8	0.14±0.03

*S=streamside, I=inland.
**From Delaune et al. (1979).

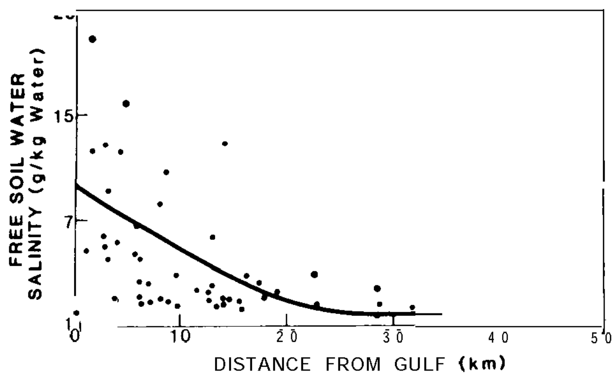


Figure 33. The decrease in free soil water salinity (mg/g) of chenier plain marshes with distance (km) from the gulf (Rainey 1979).

Soil Nutrients

The nutrient content of delta marshes is quite well known from a comprehensive set of surface sediment samples taken across the whole coast by R. H. Chabreck, LSU, in 1968 and analyzed by Srupbacker et al. (1973). Rainey (1979) used the same data set to draw a number of conclusions about the factors controlling sediment nutrient concentrations. Because the density of marsh soils varied from 0.05 to 0.97 in Chabreck's data set, a 20-fold range, Rainey converted all nutrient con-centrations to a volumetric basis as recommended by Boelter and Blake (1964), Clarke and Harmon (1967), and Mehlich (1972, 1973).

When analyzed on a volumetric basis (dry mass/volume wet soil), the distribu-tion of nutrients across the marshes falls into a predictable pattern. As one would expect, the soluble ions associated with sea water [sodium (Na), chloride (Cl), potassium (K), magnesium (Mg), and total soluble salts] are closely controlled by the surface water salinity (Table 10). This is also shown in Table 11, which compares the ratio of soluble nutrients to chloride in seawater and in the different marsh zones. Sodium, K, and Mg ratios in the marsh are never more than twice the seawater ratio.

Compared to the soluble ions, some of the total available ions (the soluble plus the exchangeable fractions) behave some-what differently. Total available Na is closely related to surface water salinity since it is a major component of sea water. However most available K and Mg are held in the soil exchange complex. Therefore, available K and Mg are strongly influenced by the adsorptive capacity of the soil mineral component as indicated by their high regression coefficients with bulk density in Table 10. Phosphorus distribution is also strongly related to the mineral component of the soil. The major source of phosphorus to the marsh is probably from mineral sediment deposits.

Neither total nitrogen (N) nor cal-cium (Ca) (either soluble or exchangeable) are closely related to salinity or to bulk density. Unlike the other soluble cations, Ca is abundant in freshwater, and runoff from the surrounding upland areas into the fresh marsh contains high quantities of Ca. This explains the high Ca/Cl ratios

Table 10. Multiple linear regression models of soil ions showing what factors control their distribution in Louisiana marshes (Rainey 1979). For each nutrient the first soil factor entering the model is shown with its R value. The total proportion of the variability accounted for when salinity, bulk density and or-ganic matter are all entered in the model is also shown. In general, one factor accounts for most of the variability.

Soil nutrient	Soil factor*	R	Total R **
Total soil salts	Salinity	0.741	0.754
Soluble chloride	Salinity	0.748	0.753
Soluble sodium	Salinity	0.760	0.767
Available sodium	Salinity	0.760	0.789
Soluble potassium	Salinity	0.643	0.744
Available potassium	Density	0.673	0.707
Soluble magnesium	Salinity	0.604	0.622
Available magnesium	Density	0.580	0.617
Available phosphorus	Density	0.673	0.707
Total nitrogen	Organic		0.189
Available calcium			0.246

*Independent variable that explains the greatest part of the variability, and the R value associated with it.
**Total proportion of the variability in the dependent variability explained by var-iations in the soil factors.

found in fresh marshes (Table 11). Calcium is tightly bound to organic material. (However, on a volumetric basis neither Ca nor organic content shows a wide range of values, and as a result the statistical association is not strong). Nitrogen distribution is similarly affected. It is relatively constant in organic material (C:N = 16.5; Chabreck 1972), and most of the N in the sediment is tied up in organic form.

Sulfate distribution is interesting because the major source is presumably seawater, but the concentration in marsh sediments is as much as four times that expected from the sulfate:chloride ratio in seawater. However,the biochemistry of sulfur (S) in anaerobic soils is complex; sulfates are reduced to insoluble sulfides that can accumulate in the soil and later be re-oxidized to sulfate.

Summarizing, the distribution of nutrient elements in the delta marsh zones (Figure 34) is understandable in light of the source of each and its soil chemistry. The ions Na, K, and Mg, associated with sea water, decrease from salt to fresh marshes as salinity decreases. Phosphorus also decreases, but for a different reason; it is carried into the marsh with sediment and sedimentation rates decrease inland. Calcium increases inland since it is derived mostly from upland runoff. Nitrogen is fairly constant across the marshes since it is closely associated with organic matter.

Vegetation

I have discussed the physical and chemical traits of the vegetation zones in delta marshes in some detail. It is time now to consider the vegetation itself. Based on a classification from early studies by Penfound and Hathaway (1938), Chabreck surveyed and classified the Louisiana marshes in 1968 and 1978. I

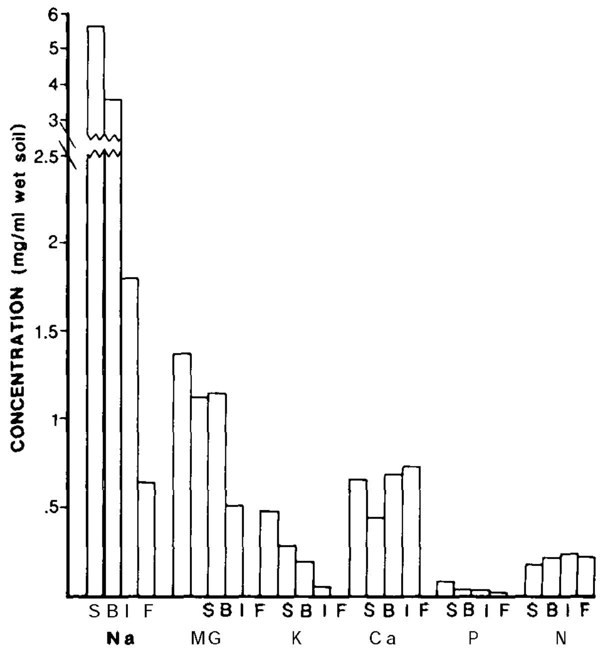


Figure 34. Concentrations of available Na, Ca, K, Mg, P, and N in different marsh zones (Rainey 1979).

Table 11. The ratio of the major cations to the chloride ion in normal seawater and in the saline, brackish, intermediate, and fresh marshes of Louisiana (Rainey 1979).

Cation	Seawater[a]	Marsh zone			
		Salt	Brackish	Intermediate	Saline
Soluble sodium	0.556	0.585	0.576	0.613	0.560
Soluble magnesium	0.067	0.070	0.085	0.090	0.107
Soluble calcium	0.021	0.034	0.040	0.077	0.135
Soluble potassium	0.021	0.028	0.026	0.030	0.040
Soluble sulfate	0.140	0.250	0.341	0.407	0.533

[a]From Riley and Chester (1971).

Table 12. Percent cover of the dominant plant species in major marsh zones of the Louisiana coast (Chabreck 1972).

Species	Marsh zone			
	Salt	Brackish	Intermediate	Fresh
Batis maritima	4.41	0	0	0
Distichlis spicata	14.27	13.32	0.36	0.13
Juncus roemerianus	10.10	3.93	0.72	0.60
Spartina alterniflora	62.14	4.77	0.86	0
Eleocharis parvula	0	2.46	0.49	0.54
Ruppia maritima	0	3.83	0.64	0
Scirpus olneyi	0	4.97	3.26	0.45
Scirpus robustus	0.66	1.78	0.68	0
Spartina patens	5.99	55.22	34.01	3.74
Bacopa monnieri	0	0.92	4.75	1.44
Cyperus odoratus	0	0.84	2.18	1.56
Echinochloa walteri	0	0.36	2.72	0.77
Paspalum vaginatum	0	1.38	4.46	0.35
Phragmites australis	0	0.31	6.63	2.54
Alternanthera philoxeroides	0	0	2.47	5.34
Eleocharis sp.	0	0.82	3.28	10.74
Hydrocotyl unbellata	0	0	0	1.93
Panicum hemitomon	0	0	0.76	25.62
Sagittaria falcata	0	0	6.47	15.15
Other species	2.43	5.09	25.26	29.10
Total	100.00	100.00	100.00	100.00
Total number of species	17	40	54	93

have used his grouping of the marshes into four broad zones in the discussion of temporal and spatial gradients earlier in this chapter. The 1968 survey (Chabreck 1972) is still the best description available of the broad marsh vegetation patterns, including the species associated with each marsh zone and their relative importance as indicated by percent cover (Table 12, Figure 35, Appendix 1).

Spartina alterniflora and S. patens dominate the saline marsh, with Juncus roemerianus, Distichlis spicata and Batis maritima as subdominants (see Frontispiece). Chabreck identified 12 additional species in this vegetation zone. In the brackish zone S. patens is dominant. D. spicata, S. alterniflora, J. roemerianus, and Scirpus olneyi are also common species of this zone. Notice that many of the species are the same in both zones, but their order of dominance is changed. Often the brackish marsh has a distinct "hummocky" appearance associated with the clumped growth of S. patens (Figure 36). Forty species are on the brackish marsh list.

The intermediate marsh is difficult for the novice to identify. The species are not, on the whole, different from those found in the fresh marsh, but all but one of the four dominant species in these two zones are different. Intermediate marsh dominants are again S. patens, with Phragmites australis, Sagittaria falcata, and Bacopa monnieri.

In the fresh marsh the dominants are Panicum hemitomon, S. falcata, Eleocharis spp., and Alternanthera philoxeroides. Species richness increases from salt to fresh marsh and dominance decreases. Fresh marshes are often very diverse with many different species of grasses and broad-leaved annuals waxing and waning throughout the growing season (Figure 37).

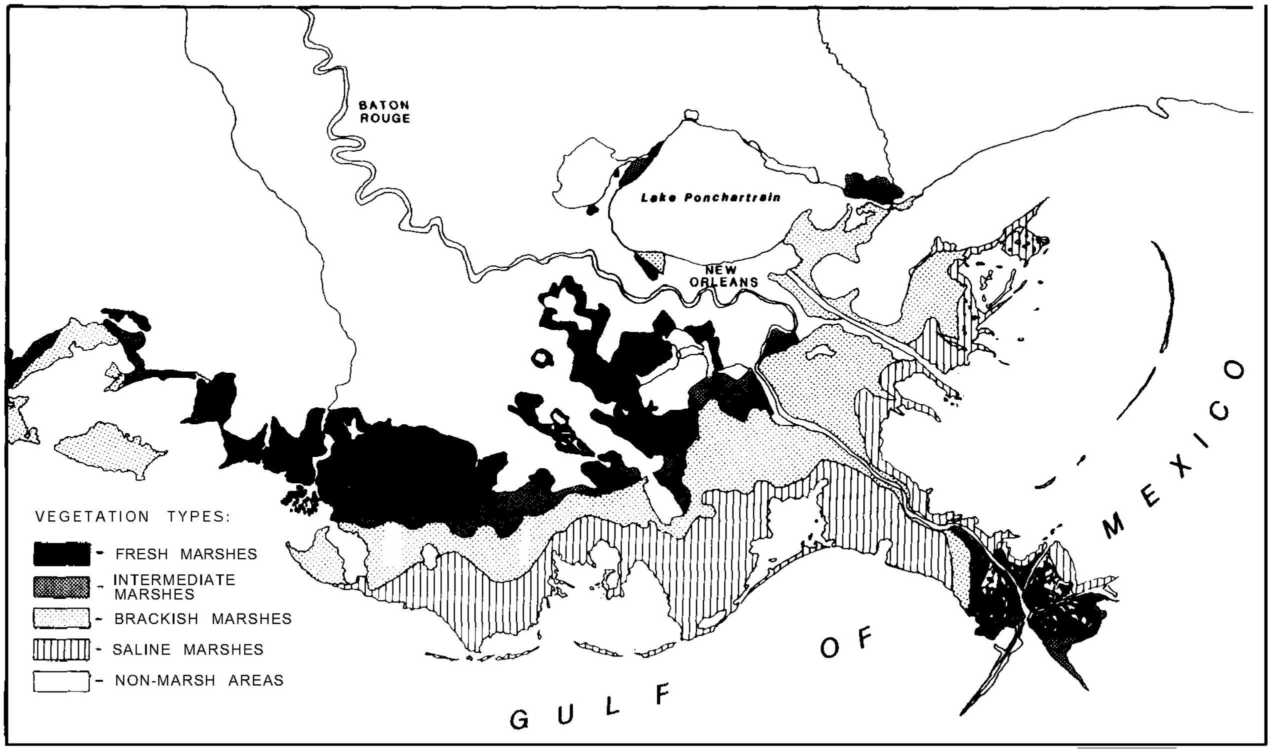


Figure 35. Vegetation zones in the Mississippi River Delta marshes (Chabreck and Linscombe 1978).

Chabreck's data are for the coastal marshes of the whole state. There is some difference in the species found in the western chenier plain compared to the delta, but these are minor. More important is that the species list is a composite from many different. sites. No one site would be expected to contain all the species, especially in the intermediate and fresh marshes. Each major zone is actually a complex mosaic of many sub-associations. The primary zones are, as the names indicate, determined by the salinity tolerance of the plants. Within each zone detailed mosaics result from much more complex factors including soil nutrients and elevation (hence flooding frequency and duration).

For example, a 90-km^2 site in the intermediate marsh in the Barataria basin was mapped from aerial imagery, and intensive ground surveys were conducted. Six plant associations were identified using statistical clustering techniques (Figure 38), and even more complex visual patterns are seen in the aerial imagery.

The observed patterns seem to result from the interaction of brackish water entering the marsh from the east and south, and fresh upland runoff from the west, combined with slight elevation differences (Sasser et al. 1982).

Vegetation studies in the Atchafalaya basin fresh marshes show the importance of elevation and exposure to direct river flow versus stagnating backwater flooding in controlling the species distribution (Johnson et al., LSU Center for Wetland Resources; unpublished). Greenhouse studies on salt marsh species from the delta clearly show differences in the ability of different species to tolerate floodinq (Parrondo et al. 1978). In these studies; although S. alterniflora and S. cynosuroides appeared to be equally well adapted to salt, the latter was far less tolerant of flooding (Figure 39). The greenhouse studies quantify qualitative observations that S. cynosuroides is found in slightly elevated locations in the marsh.

Figure 36. A deltaic plain brackish marsh. Note the "hummocky" appearance which is typical of Spartina patens stands. The birds with black-tipped wings are white pelicans, the smaller ones ducks, mostly teal (Photograph by Robert Abernathy).

The roles of chance and competition in marsh plant distribution have not been extensively studied in the delta marshes. We usually assume that seed sources are abundant so that a supply of propagules does not limit invasion by a species and the presence of one species does not prevent another adapted species from invading. In fact, competition is probably a very strong distribution factor. With the exception of a few true obligate halophytes (represented on the gulf coast by Batis maritima and several species of Salicornia), the salt-tolerant species will all grow well in fresh or nearly fresh substrates. Since these species are not found in salt-free areas, presumably they are confined to saline areas because they cannot compete well with fresh marsh species in a fresh environment. Another example of competition is the observation that the thick layer of dead vegetation covering a stand of the perennial grass S. patens excludes S. olneyi and annual grasses. It is common to burn S. patens stands to encourage these other species which are more desirable as food for ducks and muskrats (Hoffpauir 1968).

In early literature on delta marsh plants it was assumed that the vegetation modified the landscape so that the environment was changed, allowing other species to invade. For example, Penfound and Hathaway (1938) outlined a successional sequence from saline through fresh marshes to upland forests. The sequence was based on the idea that marsh plants, by producing peat, could elevate the sites they grew on until upland species could invade and survive there. This idea of autogenic succession arose before we understood the rapidity of subsidence on the gulf coast. It is clear now, I think, that most vegetation changes in the delta marshes occur because of allogenic processes. In a sense, the most the biota can do is resist and slow down the inevitable change from

Figure 37. A diverse deltaic plain fresh marsh scene. Species are: _Sagittaria falcata_ (foreground), _Typha_ sp. (right edge), mixed grasses and vines, _Myrica_ shrubs in rear (Photograph by Charles Sasser).

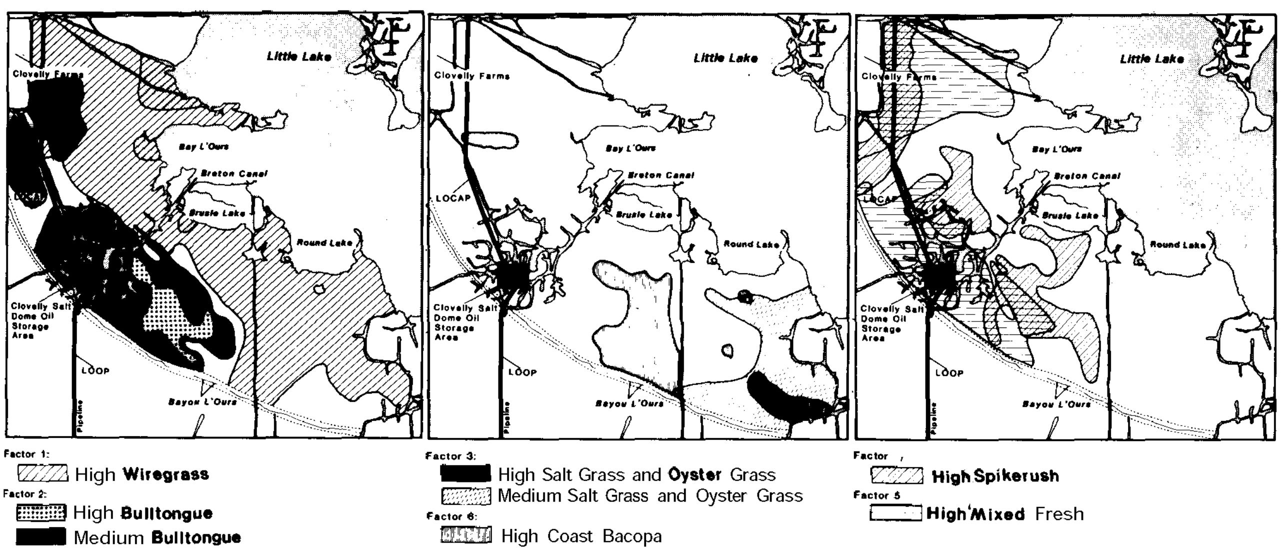


Figure 38. Vegetation zonation in an intermediate marsh transition zone in the Barataria basin (Sasser et al. 1982). Factors arise from statistical clustering techniques and are identified by the dominant species.

fresh to saline conditions associated with the overriding geomorphic processes.

Perhaps one exception to this generalization is the fresh floating marsh. This marsh is a thick (up to 1 m) mat of interwoven roots binding decaying peat into a platform that floats on the water. It supports a diverse flora of emergent species dominated by Panicum hemitomon. The origins of these mats is not known. Russell (1942) suggested that they arise by growing out into lakes from the shoreline. O'Neil (1949) thought that they began as anchored marshes that broke loose from their substrate during a high-water period because of the bouyant force of the mat. The fresh floating marshes are in many respects highly self-controlled. Since they float they are never deeply flooded, but by the same token the water level is always near the marsh surface. The production of organic matter maintains the floating mat. Thus the vagaries of water supply are effectively controlled, and the hydrologic environment of the floating marsh is nearly constant.

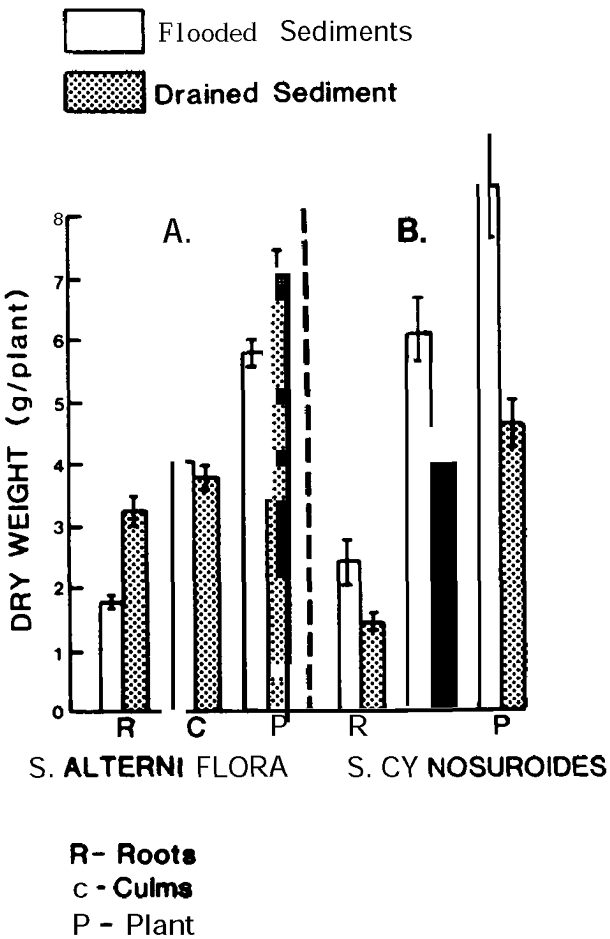


Figure 39. Effects of substrate drainage conditions on the dry weight accumulation by (A) Spartina alterniflora and (B) S. cynosuroides (reproduced from Bot. Gazette, 1978 by R.T. Parrando, J.G. Gosselink, and C.S. Hopkinson with permission of The University of Chicago).

CHAPTER THREE
ECOLOGICAL PROCESSES IN DELTA MARSHES

In the previous chapter, I considered marsh changes across spatial gradients and also those temporal changes that are measured in hundreds or thousands of years. But within any fairly homogeneous patch of marsh, many complex interacting processes occur and reoccur in cycles that are measured in days and seasons. In order to understand the marsh ecosystem, it is necessary to understand how these processes operate and how they interact. However, it is not clear how best to study them. One can analyze the individual components of the system and from these attempt to reconstruct the whole. Or conversely, it is possible to examine the system from a "macroscopic' point of view, almost as an independent organism which acts as an integrated individual. Both approaches have their strengths and weaknesses. The latter "systems" approach has been emphasized in Mississippi delta marshes in studies supported by the Louisiana Sea Grant program, and I will draw heavily on them in this chapter. In addition,much excellent research has also focused on individual species, especially fish, mammals, and birds. Without these studies it would not have been possible to draw as complete a picture as we now have.

In the systems approach one often relies heavily on ecosystem models which conceptually organize and simplify the ecosystem under study. Although more sophisticated, quantitative models of delta marshes have been published (Day et al. 1973; Hopkinson and Day 1977; Costanza et al. 1983), I will use a simple conceptual model to focus the reader's attention on the most important components and processes in the marsh ecosystem. Each of these will then be considered further. This model (Figure 40) emphasizes the importance of (1) primary production and its control, (2) decomposition, detritus, and the role of micro-organisms, (3) the benthos, (4) the food chain to vertebrates - fish, waterfowl, and fur animals, and (5) nutrient cycles.

Throughout this discussion the role of hydrology will be emphasized. This property makes wetlands unique. Nearly everything that happens in wetlands is influenced by the flooding properties of the site. Some of these - flooding dynamics, chemical and physical properties of the substrate, vegetation zones - have already been considered. In addition, each of the five groups of processes emphasized in Figure 40 is influenced by hydrology. The extent of hydrology's influence should become increasingly clear in the following discussion.

PRIMARY PRODUCTION

It is convenient to consider marsh plants in four different groups. (1) The most extensively studied are the emergent vascular plants, most of them grasses which are responsible for most marsh photosynthesis. (2) Almost always associated with the emergent plants on the mud surface, and especially on the lower parts of the vascular plant stems, is an active community of epiphytic filamentous algae and diatoms along with many microscopic consumers. (3) The benthic algal community in marsh ponds, almost always submerged, is a rich surface coating of diatoms and other unicellular green and blue-green algae. (4) Finally, in many marsh ponds submerged macrophytes such as <u>Ruppia maritima</u>, <u>Eleocharis</u>

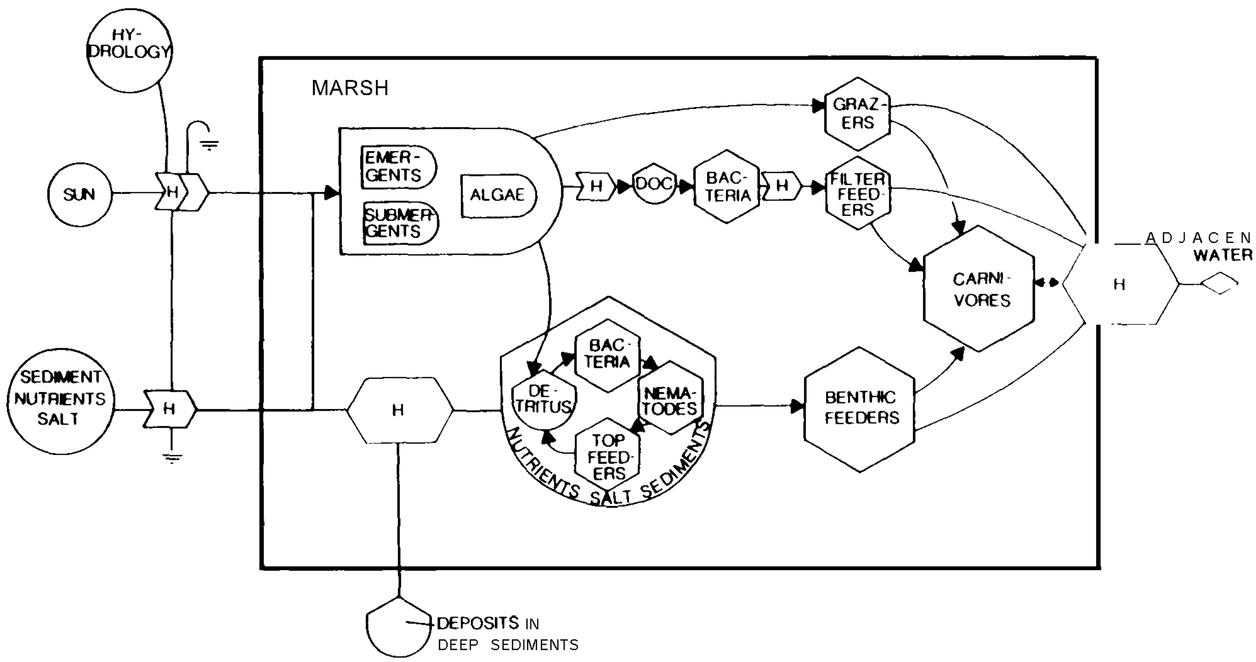


Figure 40. A conceptual model of a typical wetland ecosystem, showing major components and processes.

parvula, Chara vulgaris and Potomageton spp. are found.

Emergent Vascular Plants

The emergent vascular plants are by far the most intensively studied of these four groups. Much plant biomass information about delta marsh species has been generated during the past decade. Seven studies of marsh grass productivity covering nine plant species have been performed (Table 13).

The most common information related to production is peak end-of-season biomass. In more northerly climates where all growth ceases and the plants are killed to the ground during the winter, this is often an excellent estimate of true net production. But in the subtropical climate of the gulf coast peak biomass has been shown to underestimate production by a factor of 1.6 to over 4, even in those species that have a single growth cycle each year (Hopkinson et al. 1978a). As a result,one must interpret peak biomass data with caution. Table 13 shows production estimates vary considerably, but most estimates are very high compared to studies in other localities in the temperate zone. This is because production yenerally increases with decreasing latitude (Turner 1976).

The seasonal growth of marsh plants in Louisiana shows two patterns (Figure 41). One is characteristic of annual plants and many species with perennial roots that die to the ground every winter. These species have a single, smooth growth curve which builds from near zero in January to a peak sometime between July and September. Each year almost all of the new stems emerge at once when growth commences in the spring. In Figure 41 P. australis illustrates this group. For species like this, peak biomass represents about 40 - 60 percent of annual net production. The rest is accounted for by shedding of leaves during the spring and some continued growth into the fall that is masked by mortality after the peak is attained. Sagittaria falcata appears to follow the same growth pattern, but actually the individual leaves of this species have a short lifespan and are replaced constantly throughout the year.

Table 13. Production of marsh vascular plant species in the Mississippi Delta (g dw/m^2 biomass and g dw/m^2/yr production).

Species	Site	Yr	Peak live biomass	Production: Different techniques	Production: Best estimate	Ref.
Salt marsh						
Spartina alterniflora						
Streamside	Barataria	70	1,018	1,410 a		
				2,645 b	2,645	1
Inland	Barataria	70	788	1,006 a		
				1,323 b	1,323	1
Intennediate or unstated	Barataria	74-5	754	1,000 a		
				1,673 c		
				1,381 d		
				2,178 b	2,178	2
	Barataria	80	831	1,086 a		
				1,494 b		
				1,445 e		
				2,220 f	1,445	3
	Lake Borgne	75	1,070	1,527 a		
				2,895 b	2,895	4
Distichlis spicata	Barataria	74-5	991	700 a		
				1,010 c		
				1,967 d		
				2,881 b	2,881	2
	Lake Borgne	75	750	1,291 a		
				1,162 b	1,291	4
Juncus roemerianus	Barataria	74-5	1,240	1,200 a		
				1,850 c		
				3,295 d		
				3,257 b	3,257	2
	Lake Borgne	75	1,550	1,740 a		
				1,806 b	1,806	4
Spartina cynosuroides	Barataria	74-5	808	1,767 b		
				1,134 d		
				398 c	1,134	2
Brackish marsh						
Spartina patens	Terrebonne	74	1,376	2,000 a		
				2,500 c		
				4,159 d		
				5,812 b	4,159	2
	Lake Borgne	75	1,350	1,342 a		
				1,428 b	1,428	4
	Terrebonne	74	800	2,128 a	2,128	5
	Lake Pont-char-train N.O. East	78	1,248	2,605 a		
				3,056 b		
				3,053 b+	3,053	6
	Walker Canal	78	2,159	4,411 a		
				3,464 b		
				5,509 b+	5,509	6

(Continued)

Table 13. Concluded.

Species	Site	Yr	Peak live biomass	Production: Different techniques	Production: Best estimate	Ref.
	Goose Point	78	2,130	2,541 a		
				2,487 b		
				3,075 b+	3,075	6
	Irish Bayou	78	2,466	3,192 a		
				2,861 b		
				3,595 b+	3,595	6
Intermediate marsh						
Phragmites communis	Barataria	74-5	990	2,364 b	2,364	2
Sagittaria falcata	Terrebonne	74-5	648	1,402 b		
				2,310 d		
				1,113 c		
				700 a	2,310	2
	Terrebonne	74	360	608 a	608	5
Fresh marsh						
Scirpus validus	Terrebonne	74	800	1,261 a	1,261	5
Panicum hemitomon	Barataria	80	1,160	1,700 b		
				1,810 f	1,700	7

Techniques:
a - Smalley 1958
b - Wiegert and Evans 1964
b+- Wiegert and Evans 1964, modified
c - Mortality, Hopkinson et al. 1980
d - Williams and Murdoch 1972
e - Lomnicki et al. 1968
f - Density and longevity, Sasser et al. 1982

Reference:
1 - Kirby and Gosselink 1976
2 - Hopkinson et al. 1980
3 - Kaswadji 1982
4 - White et al. 1978
5 - Payonk 1975
6 - Cramer and Day 1980
7 - Sasser et al. 1982

At the other extreme, Spartina patens is an example of a species that grows throughout the year, continuously adding foliage and losing it through death in a kind of steady state. Biomass fluctuates widely around a mean, and there is little if any seasonal pattern. For species like these, peak biomass tells almost nothing about annual production, which is three to four times higher. S. alterniflora falls between these two extremes. It continues to grow slowly during the winter and always has some green foliage, but superimposed on this is a distinct seasonal cycle.

Figure 42 contrasts the monthly growth pattern of S. alterniflora with that of the fresh marsh species Panicum hemitomon. The latter has a broad peak in its growth rate during the spring; growth

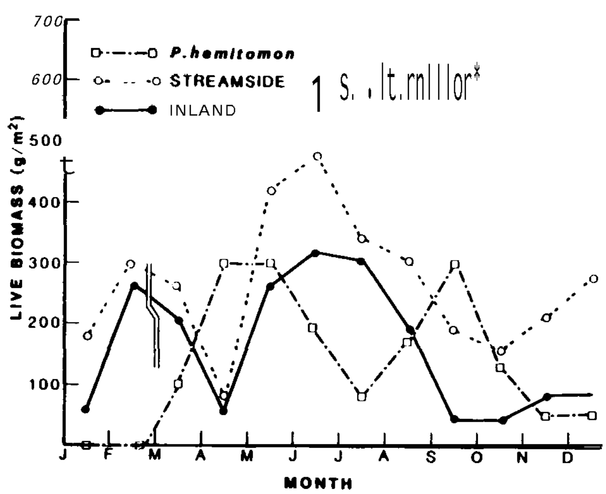


Figure 41. Monthly growth rates of Panicum hernitomon (Sasser et al. 1982) and Spartina alterniflora (Kirby 1971).

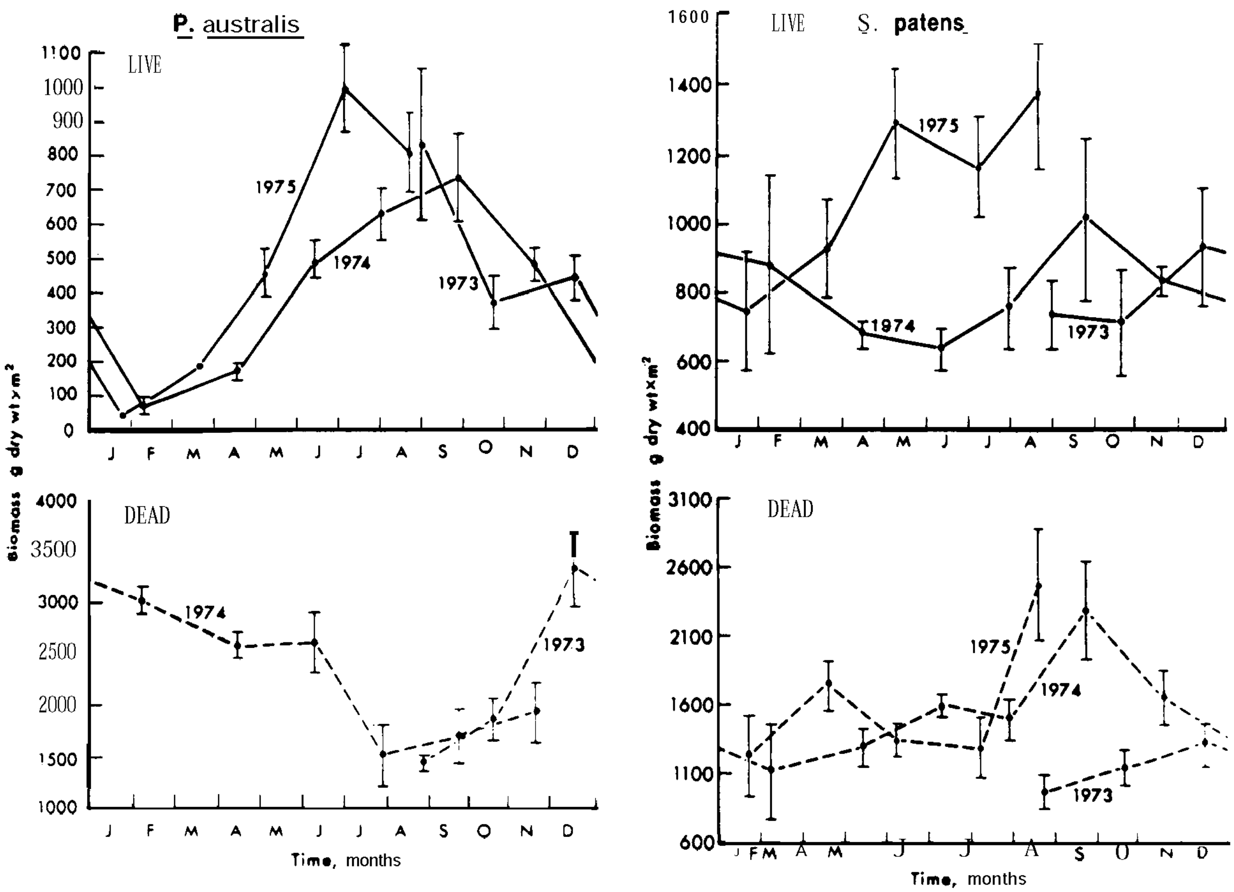


Figure 42. Seasonal changes in live and dead biomass of Phragmites australisand Spartina patens during 1973 - 1975 (Copyright. Reprinted from "Aboveground-production of seven coastal marsh plant species in coastal Louisiana " in Ecology, 1978, by C.S. Hopkinson, J.G. Gosselink, and R.T. Parrondo with permission of Ecological Society of America).

gradually tapers into the fall with a resurgence after the hottest months, and the plants die to the ground each winter. S. alterniflora maintains active growth throughout the year, with a maximum rate during the early summer. The pattern of streamside and inland plants is similar, but the inland rates are lower.

All the production data reported so far have been for aboveground growth. Root production is difficult to measure because it is difficult to determine, in a substrate that is nearly all root material, which roots are living. Table 14 lists reports of root biomass from a number of studies in the delta. The reported biomass varies widely, partly as a result of differences in techniques. Fresh and brackish marsh species in established, highly organic marshes have enormous belowground biomass, whereas the same species (for example, Saqittaria spp., Table 14) in the mineral sediments of the Atchafalaya Delta produce few roots.

Outside of the delta, root production measurements have been almost as variable. Good et al. (1982) reported S. alterniflora root production estimates ranging from 220 to 3500 $g/m^2/yr$ for tall form (streamside) locations and 420 to 6200 $g/m^2/yr$ for short form (inland) locations. High root:shoot ratios have been considered indicative of unfavorable soil conditions requiring greater root surface area to support a unit of aboveground material (Shaver and Billings 1975). This relationship seems to hold in marshes

Table 14. Belowground biomass of Mississippi Delta marsh plant species (g dw/m[2]).

Species	Month	Biomass	Percent*	Comment	Ref.
Salt marsh					
Spartina alterniflora		100-250+	25	Lake Borgne	a
Brackish marsh					
Spartina patens	Oct.	1,375	57	Terrebonne	b
	Jan.	1,957	58	"	
Scirpus validus	Oct.	3,598	73	"	
	Jan.	11,917	96	"	
Intermediate marsh					
Sagittaria falcata	Oct.	2,775	96	Terrebonne	b
	Jan.	7,093	99	"	
Fresh marsh					
Panicum hemitomon	Mean	8,000	90	Barataria	c
Cyperus difformis	Fall	62	39	Atchafalaya	d
	Prod./yr	117		"	e
Sagittaria latifolia	Prod./yr	140		"	e
Sagittaria sp.	Fall	114		"	d
Typha latifolia	Fall	214		"	d

*Percentage of total biomass.

References:
a - White et al. 1978
b - Payonk 1975
c - Sasser et al., LSU, unpubl.
d - Johnson et al. LSU, unpubl.
e - Mendelssohn, LSU, unpubl.

where, for example, *S. alterniflora* root:shoot ratios increase from 1 - 8 streamside to 1.2 - 49 inland (Good et al. 1982).

As with root biomass estimates, aboveground production estimates vary widely, even for a single species. Again this is partly because of methodological problems. Production is calculated from at least two sets of measurements - biomass and sone measure of mortality during the interval between sampling. The latter introduces a large element of uncertainty in the estimate. One study can generate several estimates that vary from each other by as much as a factor of three, depending on the assumptions made. Shew et al. (1981) have an excellent discussion of this topic. For example Kaswadji's (1982) study was designed to compare four different techniques for determining production in a *S. alterniflora* marsh. The four methods resulted in estimates of annual production (g/m2) varying from 641 to 2,220 (Table 15). The higher estimates are commonly, but not universally, considered the more realistic in gulf coast marshes.

Aside from the variation in reported production due to the methods of analysis,

Table 15. Production estimates for a *Spartina alterniflora* stand based on different techniques (Kaswadji 1982).

Technique	Estimate ($g/m^2/yr$)
Milner & Hughes[a]	641
Peak standing live biomass	831
Smalley	1086
Wiegert-Evans	1496
Lomnicki	1445
Stem longevity/density	2220

[a]See Table 13 for references to techniques.

there is still a good deal of real variation in the productivity of a single species in different environments. This is best shown by differences in peak biomass, which although not equivalent to production are a pretty good index of relative production. These differences are temporal as well as spatial. At Airplane Lake in the Barataria basin, peak bianass has varied by over 300 g/m^2 from year to year (Table 16).

Turner (1979) found a positive relationship between biomass and potential evaporation (which is in turn related to the average air temperature) durinq the growing season. By implication, differences in biomass among years at one location should be related to annual differences in the accumulated potential evaporation. While this kind of relationship has been confirmed for many agricultural crops, it has not been studied in marshes, perhaps because long-term data sets are not available.

Spatial variations in biomass have been the subject of many investigations, both to determine the correlation of biomass with environmental variables and to identify the physiological mechanisms of adaptation to the marsh environment. Figures 43, 44, and 45 show three typical examples of spatial variations in marsh biomass. It is instructive to examine them because they throw light on the physiological responses of plants.

The first of these is the "tidal subsidy", discussed by Odum and Fanning (1973) as a reason for the high productivity of coastal marshes. Tides mediate such plant growth-influencing factors as nutrient supply, sediment grain size, drainage, soil oxygenation, and secondary chemical changes. In this illustration, peak plant biomass along the north Atlantic coast is directly proportional to the tide range. Notice that biomass from one Louisiana delta study does not fit the trend. Biomass is much higher than expected considering the tidal range.

Table 16. Year-to-year variation in peak live biomass of Spartina alterniflora at a single site in the Barataria basin.

Year	Biomass. (g/m^2)	n	Source
1970	903	10	Kirby 1971
1976	701±246	6	Buresh 1978
1978	700	10	Sasser et al. 1982
1979	700	10	"
1980	790	10	"
1981	748±377	10	"
1982	1,047±190	10	"

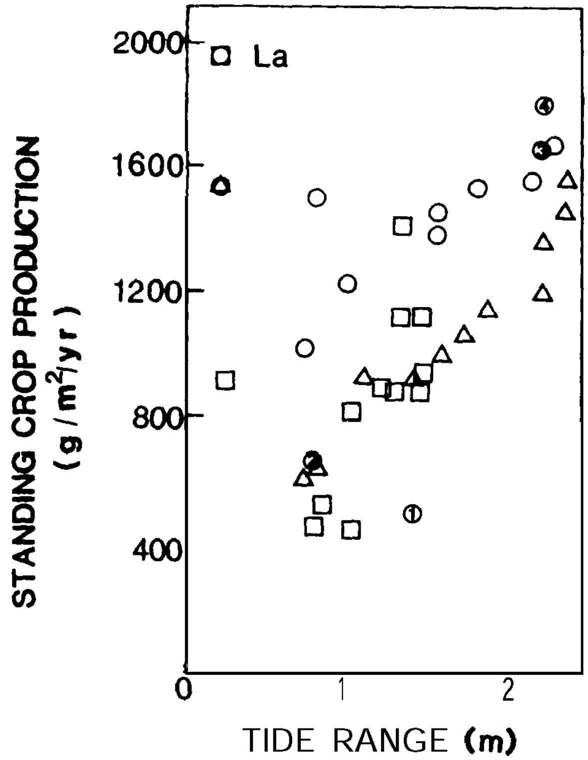


Figure 43. Production of intertidal S. alterniflora vs. mean tide range for various Atlantic coastal marshes. Different symbols represent different data sources (adapted from Steever et al. 1976). Note the position of Mississippi delta marshes on the graph.

The second example illustrates the well-known "streamside" effect - the stimulation of growth along the edge of natural streams, or conversely its inhibition inland. This effect is similar to the tidal subsidy in that tidal action is weaker inland than streamside so the plants receive less "subsidy."

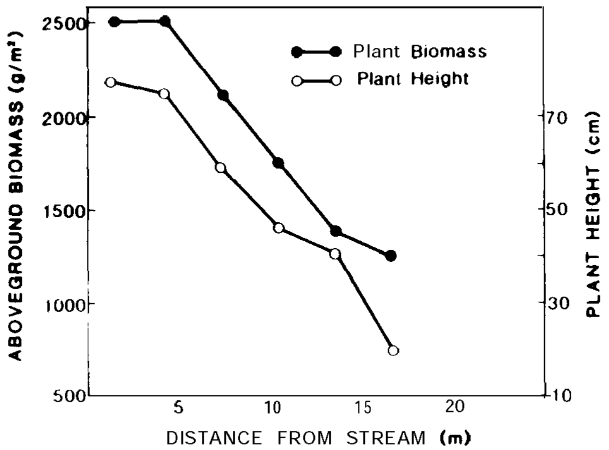


Figure 44. Variation in total aboveground biomass and height of Spartina alterniflora with distance inland from the marsh edge in a Barataria basin salt marsh (Buresh 1978).

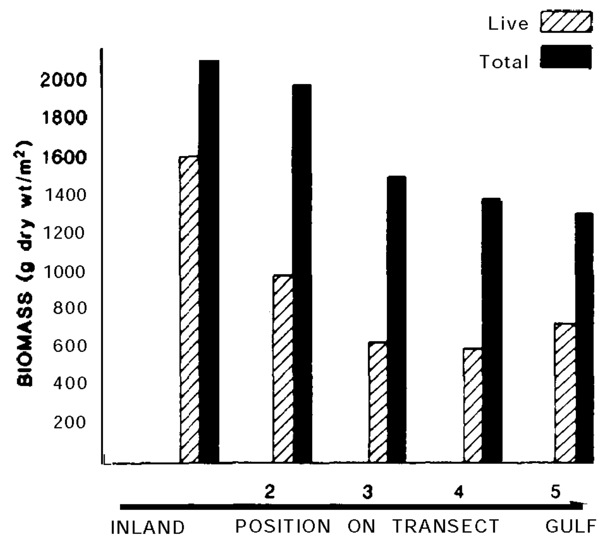


Figure 45. Gulf-inland variations in live and total biomass in Spartina alterniflora marshes (Gosselink et al. 1977).

The third example shows the increase in biomass from the coast inland. The first two examples illustrate complex gradients in the physiological sense; the last may be due simply to a gradient of decreasing salinity.

Physiologically a plant growing in a marsh has to solve one or both of two problems. All marsh plants are periodically exposed to high salt concentrations and to anoxic soil conditions and accompanying sediment chemical changes.

As indicated earlier, the dominant salt and brackish marsh plants are salt tolerant rather than salt requiring. Generally, growth is depressed as salt concentration increases (Parrondo et al. 1978). One reason for this is that the high concentration of salt surrounding the roots makes it osmotically difficult for plant cells to absorb water.

The plant could get around this problem by simply absorbing salt to decrease the internal osmotic potential. But this leads to biochemical problems because the Na and Cl ions interfere with the activity of many enzymes, probably through steric effects. For example, the enzyme-mediated absorption of the radiotracer, rubidium (Rb) by excised roots of S. alterniflora and D. spicata is strongly inhibited by salt in the root medium (Figure 46). This may occur because Na replaces Ca, which has been shown to stimulate ion uptake, on the cell membranes.

Plants have adapted to the problems posed by salt in a number of ways. These all involve mechanisms to exclude or selectively absorb only certain ions, to raise the osmotic concentration of the plant cells to overcome the water uptake problem, and/or to secrete unwanted ions. S. alterniflora has apparently evolved all three mechanisms. The osmotic concentration of its cells is always slightly higher than the substrate concentration, creating a favorable gradient for water flow into the plant. This is accomplished both by absorption of salts from the external medium and by production of osmotically active organic compounds.

The absorption of salt is not a passive process. The relative concentrations of different ions within the plant cells indicate that absorption is selective, with the exclusion of Na and

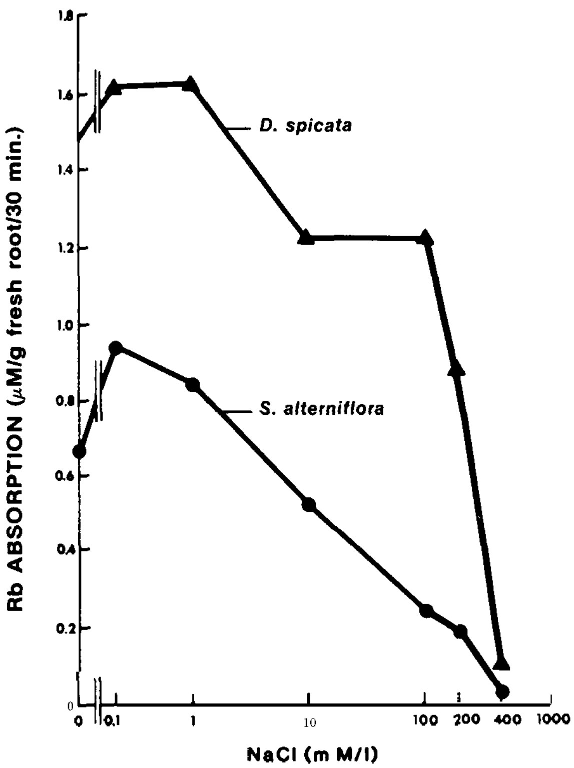


Figure 46. Effects of NaCl concentration in the root medium on the rate of Rb absorption by excised root tissue of S. alterniflora and D. spicata (1 mM Rb; 2 mM Ca; reprinted from Bot. Gazette, 1981, by R.T. Parrando, J.G. Gosselink, and C.S. Hopkinson with permission of The University of Chicago).

the concentration of other ions such as K (Smart and Barko 1978). Finally, the plant leaves have secretory glands called hydathodes which selectively secrete certain ions. All this regulatory activity requires extra energy expenditure by the plant. It is not surprising then that the growth rate decreases as the external salt concentration increases.

The problem of anoxia is complex because it affects not only the plant itself but also the microbially mediated biochemical reactions that occur in the soil around the roots. Oxygen is required as an electron acceptor in aerobic cell respiration. Its presence allows the efficient oxidation of organic sugars to carbon dioxide and water to produce high energy-reduced organic compounds and the cell's ready energy currency adenosine triphosphate (ATP).

In the absence of oxygen, cell metabolism is incomplete; less energy is released from an equivalent amount of sugar (1 mole of glucose yields 2 moles of ATP under anaerobic conditions compared to 36 moles under aerobic conditions); and organic "waste products" like ethanol and lactic acid accumulate because they cannot be oxidized to carbon dioxide (Figure 47).

In the surrounding root medium, when oxygen is depleted, other materials act as electron acceptors, almost always through some microbial intermediary rather than through strictly inorganic chemical transformations. Many ionic species are reduced. The reduced form of metallic ions such as manganese and iron is more soluble than the oxidized form, and the ions can accumulate to toxic levels. At very low reduction potentials, sulfate is reduced to the highly toxic sulfide. Since the substrate is largely organic and micro-organisms are active, organic toxins such as ethylene can also potentially be produced.

Marsh plant species have developed a number of adaptations to cope with anoxia, but even with these the plants are stressed by sublethal effects of anaerobiosis (Mendelssohn and McKee 1982). One of the main adaptations of nearly all wetland plant species is the extensive development of aerenchyna tissues in the leaves, stems, and roots, which allow the diffusion of oxygen from aerial plant parts into the roots (Etherington 1975, Teal and Kanwisher 1966). There is evidence that this oxygen source is normally enough to satisfy the root metabolic requirements of wetland plants. In addition, diffusion of oxygen out of the roots can buffer the effect of soil anoxia by creating a thin, oxidized layer in the rhizosphere. Mendelssohn and Postek (1982) eloquently demonstrated through scanning electron microscopy and x-ray microanalysis that the brown precipitate often seen surrounding S. alterniflora roots is indeed highly enriched in oxidized iron (Fe) and manganese (Mn).

Another adaptation of wetland plants to anoxia is the evolution of the ability

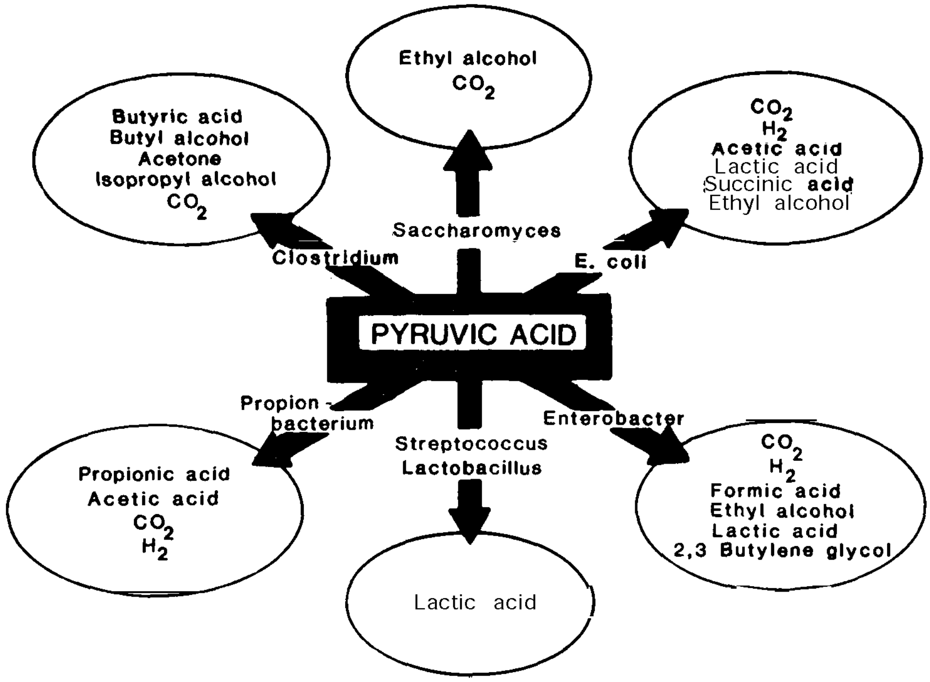


Figure 47. Metabolic conversions of pyruvic acid. This "key" intermediate in metabolism can be converted to a variety of end products, depending on the organism and the electron acceptors available (Nester et al. 1973).

to shift from aerobic to anaerobic (fermentation) metabolism. In one study, enzymatic alcohol dehydrogenase (ADH) activity, a measure of the cells' ability to convert acetaldehyde to ethanol during alcoholic fermentation, was much higher in inland sites where the soil reduction potential was intense than in a nearby less-reduced streamside marsh (Table 17). Alcohol did not accumulate in inland plant tissues in spite of the high ADH activity, indicating that it was able to diffuse out of the roots.

Table 17. Spartina alterniflora root alcohol dehydrogenase (ADH) activity, adenosine triphosphate (ATP) and ethanol concentrations, and soil Eh in a Louisiana salt marsh (Mendelssohn et al. 1982).

Variable	Unit	Location: Streamside	Inland
ADH	μmoles NADH oxidized/g fw/hr	36 ± 9	325 ±71[a]
ATP	μmoles/g dw	218 ±23	248 ±25
Ethanol	μmoles/g fw	1.17± .07	1.10± .08
Eh	mV	174 ±30	-131 ±22

[a]Mean±standard error of mean.

In spite of these adaptations marsh plants in highly reduced environments are stressed, as shown by reduced growth rates, and in severe cases, death. Comparison of streamside to inland sites in the salt marsh provides good examples of the intensity of the stressing agents, their relationship to tidal flooding, and their effects on plant growth. Figure 48 shows schematically a few of the transformations that result from tidal action, and their effects on plant growth. When the tide rises it carries minerals, both particulate and dissolved, onto the marsh. Because the water slows as it crosses the natural levee, most of the sediment is deposited close to the stream bank, less inland (Table 9). At the same time, flooding water reduces the diffusion rate of oxygen into the marsh soil. The result is usually anoxic soils, especially where organic concentration is high. The streamside area is flooded as regularly as

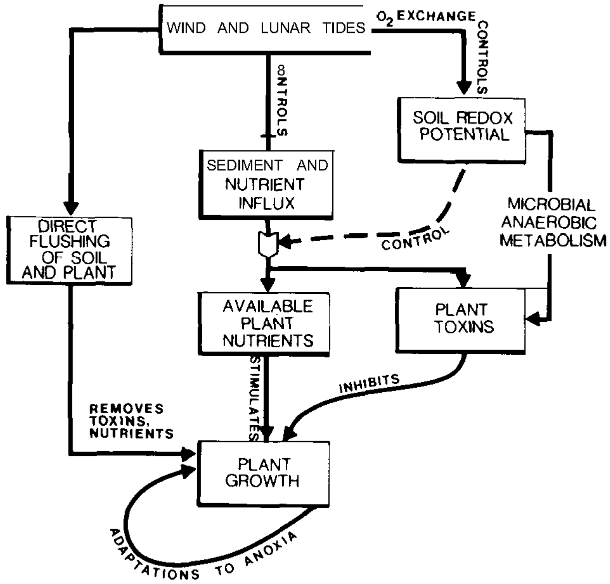


Figure 48. Marsh soil transformations that result from tidal flooding.

inland, but for shorter periods of time (Table 7), and the inland floodwaters are more slowly exchanged. Furthermore, the streamside marshes drain better on falling tides because their sediments are coarser. They also contain more reducible mineral ions to buffer redox changes. All these factors lead to stronger reducing potentials in inland marshes than streamside.

The chemistry of many minerals is strongly influenced by the redox potential. Phosphorus, a key plant nutrient, is much more soluble (and hence available to plants) under reduced than oxidized conditions (Delaune et al. 1981). Inorganic nitrogen, the primary limiting nutrient in marshes, is reduced to the ammonium ion which is readily absorbed by plant roots. More nutrients are delivered to streamside than to inland sites; this should favor streamside plant growth rates. Organic nitrogen is also more rapidly mineralized to ammonium in streamside sites (Brannon 1973).

Other minerals may be transformed to toxins or accumulate in toxic concentrations (for example,sulfide) (Hollis 1967). Toxic byproducts of anaerobic microbial metabolism may accumulate. In general, the levels of these potential toxins are higher in inland marshes than streamside marshes, increasing the stress on inland plants. Finally, referring again to Figure 48, the direct flushing of marsh soils and the leaching of olant leaves can dilute toxic materials, reducing their activity. Flushing occurs more readily in streamside sites, reducing the potential for accumulation of toxins. With all these potential effects it is not surprising that plant production is higher along streams than inland.

Soil analyses can, at times, mislead. For example, it has been found that ammonium in marsh soil interstitial water is more concentrated inland than streamside. This is not expected, considering the higher rates of ammonium production in streamside areas. Apparently, however, the interstitial water concentration is controlled by the rate of plant root uptake. The concentration is maintained at low levels by streamside plants; it accumulates in inland sites because the less robust inland plants are unable to use all the ammonium available to them.

Figure 49 summarizes typical seasonal patterns for various physical and biological processes in marsh soils. Soil water salinity is highest during the summer but probably does not reach levels that are biologically limiting for the euryhaline marsh species. The low winter and early spring salinities correspond with winter rains and low transpiration rates, indicating flushing of the marsh by rainwater.

Soil-reducing potential (Eh) is least negative (least anaerobic) during the winter, but even during this period it is too low to support any free oxygen. The seasonal Eh curve is the inverse of the temperature curve - the soil becomes more and more reduced as temperatures rise and biological activity increases. Soils begin to become less anoxic in late summer as temperature drops, even though the marsh is flooded almost all the time during these months. Free sulfide follows the redox curve closely. It is generally highest when the Eh is lowest. Extractable manganese is an example of a metal ion that is fairly easily reduced. The substrate is always anoxic enough to reduce the manganic ion and the reduced fonn is present year round. Free ammonium is the only form of inorganic nitrogen available to plants in these reduced soils. In streamside marshes it is maintained at a low level of 1 - 2 μg/ml by plant uptake during the spring and summer, building up in the fall when plant growth tapers off.

Epiphytic Algae

Where emergent grasses and algae grow together the grass is probably nearly always the dominant producer. Certainly it develops the largest biomass, but this is not a good criterion for comparison because the turnover rate of algae is much faster than that of grass. In a study in which the carbon dioxide uptake of both of these groups was measured simultaneously (Gosselink et al. 1977), the algal community was responsible for only 4 - 11 percent of the photosynthesis but 64 - 76 percent of the total respiration (Table 18). It has not been possible to separate out from the plants the respiratory activity associated with the active consumers - bacteria, fungi, protozoans, and other invertebrates - found in this community.

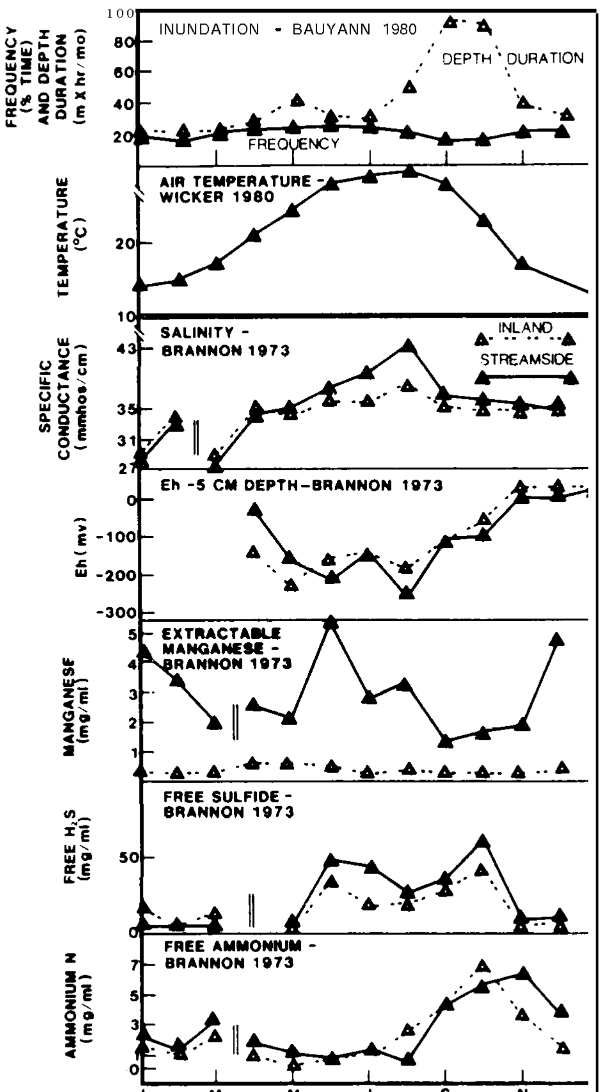


Figure 49. Seasonal changes in various physical, chemical, and biotic factors in a Barataria basin salt marsh.

Stowe (1972) found that only along the edges of the marsh where adequate light penetrated did photosynthesis exceed respiration (Figure 50). He estimated that net carbon (C) fixation amounted to about 60 g C/m^2 annually at the water's edge, compared to -18 g C/m^2 inland. The inland community was consuming more organic carbon than it produced. Nearly all of the photosynthetic activity was associated with organisms growing on the base of S. alterniflora culms rather than on the sediment surface.

Filamentous algal production was dominated by the genera Enteromorpha and Ectocarpus in the winter and Bostrichia and Polysiphonia in the summer. The diatom community was also abundant; the cells clustered on the intertidal portion of the culms, decreasing in concentration upward into the drier environment (Figure 51). Although quantitatively the algal community appears to be rather insignificant, the cells are much higher

Table 18. Percentage of marsh community metabolism by Spartina alterniflora (Gosselink et al. 1977).

	December 1975	March 1976	May 1976
Gross photosynthes	89± 6[a]	92±6	96±3
Respiration	36±11	36±5	24±9

[a]Mean±standard deviation.

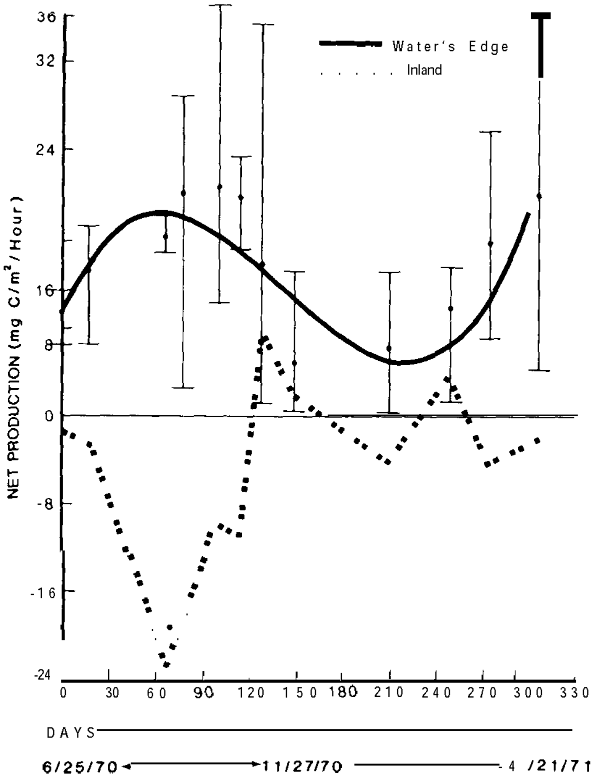


Figure 50. Net epiphytic production on stems of Spqrtina alterniflora collected at the water s edge and inland 1.5 m with the averaqes, extremes, and fitted curve for the water's edge production superimposed (Stowe 1972).

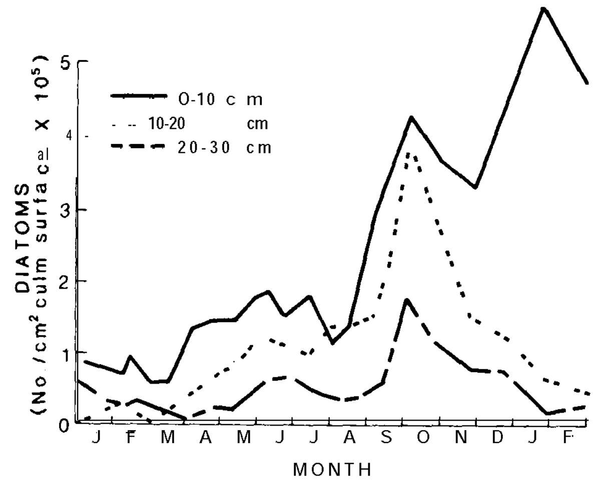


Figure 51. Number of shore-line epiphytic diatoms/cm culm surface area of Spartina alterniflora. Results are pooled averages for four stations and height classes (Stowe 1982).

in protein than the dominant grasses. Furthermore the diatoms are already "bite-sized" and may he much more readily available to the consuming members of the community. Therefore they may be more important metabolically than has been commonly realized.

Benthic Microflora in Marsh Ponds

There have been no studies on the gulf coast of the benthic flora found in marsh ponds. Most individuals who have taken the trouble to examine these ponds when they are exposed at low tide can testify that there is almost always a golden sheen to the mud surface. Under the microscope this sheen is resolved into a dense layer of diatoms of many species.

Recently Moncreiff (1983) studied the algal mats found on the edges of the freshwater marshes in the Atchafalaya Delta, and Shaffer (LSU Department of Marine Sciences; pers. comm.) measured metabolic rates of algae on mud flats adjoining salt marshes in Barataria Bay. Both measured high rates of production and respiration. Moncreiff reported net production rates of about 400 g $C/m^2/yr$ with individual measurements as high as 300 mg $C/m^2/hr$.

Submerged Grasses in Marsh Ponds

There have been no measurements of productivity of submerged plants in marsh ponds. Chabreck (1971a) identified the species found there (Table 19), and it is known that growth is enhanced by stabilizing the water level at shallow depths (Chabreck 1975), as is done with weirs. Periodic water drawdowns also stimulate growth by consolidating the substrate to reduce turbidity. This is a fertile field for further research.

DECOMPOSITION

One of the important insights that has developed in ecology in the past 25 years has been that the major flow of organic energy in most ecosystems is through a detrital food chain. Open oceanic ecosystems are one exception;

these are usually considered grazing food chains from phytoplankters to herbaceous zooplankton to larger consumers. Terrestrial grasslands are another. In these, the grazers are large mammals, ruminants that are able to digest the rather refractory cellulose that is the major structural material in plants because their digestive tracts harbor bacteria and protozoa that can break it down to simpler compounds.

Marshes are often called wet grasslands, but they differ from their terrestrial counterparts in that large mammals are not common. The microbial equivalents to the digestive microflora of the ruminants are bound up in the decomposing grass and sediment on and in the marsh. Much research has been devoted to elucidation of this pathway of energy flow in marshes, and I will try to summarize the major current ideas about how it works.

Before considering decomposition, however, let us pause to consider whether herbivory is really as insignificant as it

Table 19. Submerged aquatic plant species composition of ponds and lakes by marsh zone along the Louisiana coast (August 1968, Chabreck 1971a).

Plant species	Marsh zone[a]			Entire coast
	Brackish	Intermediate	Fresh	
	- - -	- percent	cover - - -	- - -
Alternanthera philoxeroides	...	...	1.29	0.89
Azolla caroliniana	...	...	0.59	0.40
Bacopa caroliniana	...	...	0.35	0.24
Bacopa monnieri	4.97	11.69	0.35	2.46
Brasetiia schreberi	...	...	2.23	1.54
Cabomba caroliniana	...	...	3.64	2.51
Centella erecta	...	...	0.63	0.44
Ceratophyllum demersum	...	...	11.15	7.68
Chara vulgaris	...	32.47	8.10	8.81
Eichhornia crassipes	...	...	4.53	3.12
Eleocharis parvula	23.01	10.07	1.60	6.97
Eleocharis sp.	3.98	6.82	11.27	9.28
Hydrocotyl bonariensis	...	...	0.12	0.08
Hydrocotyl umbellata	...	...	1.67	1.15
Hymenocallis occidentalis	...	...	0.47	0.32
Jussiaea alterniflora	...	...	0.23	0.16
Lemna minor	...	2.43	15.26	10.75
Limnobium spongia	...	...	1.13	0.78
Myriophyllum spicatum	3.06	8.93	11.03	9.14
Myriophyllum heterophyllum	...	...	0.47	0.32
Najas quadolupensis	...	8.93	5.75	4.85
Nelumbo lutea	...	...	1.88	1.29
Nymphaea odorata	...	...	4.98	3.40
Potamogeton nodosus	...	...	0.23	0.16
Potamogeton pusillus	...	4.87	2.70	2.34
Ruppia maritima	62.29	12.98	0.23	14.72
Sagittaria falcata	...	...	1.24	0.86
Scirpus californicus	...	0.81	...	0.08
Spirodela polyrhiza	...	...	0.94	0.65
Utricularia cornuta	...	...	5.99	4.12

[a]No vegetation in salt marsh zone.

is usually considered to be. The idea that herbivory is not important in marshes stems partially from our qualitative observations that we do not see cows, deer, buffalo, and other large grazers in the marsh very often.

Smalley (1960) quantified energy flow through the grasshopper (Orchelimum fidicinium) and concluded that it grazed less than 10 percent of the net production of its host, S. alterniflora. Parsons and de la Cruz (1980) estimated that consumption by grasshoppers in a Mississippi coast marsh was only about 5.4 $g/m^2/yr$. Other investigators have identified a broad diversity of insects in marshes but little is known about their importance in controlling the flow of organic energy.

Common invertebrates of the Louisiana coast have been enumerated (Gosselink et al. 1979), but quantitative studies of productivity and consumption are lacking. Invertebrates other than grasshoppers may ingest significant amounts of live grass tissue, even though this is an accidental component of their diets. For example, the marsh snail (Littorina irrorata) grazes up and down S. alterniflora stems, skimming off the dead organic material and epiphytes. It also scrapes off living rass tissue in this process. Alexander 41976) estimated that about 4 percent of the marsh snail's diet is living tissue, which amounts to less than 1 percent of the production of that plant. In fresh marshes insect herbivory is thought to be more important than in salt marshes, because there appear to be more insects in that environment. However, no supporting data are available in the delta.

In the delta marshes larger consumers such as snow geese, muskrats, and nutria probably are responsible for more grass consumption or destruction than insects. For example, Smith (1982) reported that snow geese grazing in Atlantic coast marshes can reduce the plant cover by two-thirds where they concentrate and virtually destroy the plants by digging up their roots. This results in significant changes in plant composition the next year.

Similarly, O'Neil (1949) indicated that dense concentrations of nutria and/or muskrats can "eat out" a marsh area. These mammals are attracted to stands of Scirpus olneeyi, Typha spp., P. hemitomon and other species. They are reported to eat up to one-third of their weight per day (O'Neil 1949) and destroy much more vegetation than they eat.

Although grazing can be locally important in marshes, most discussions of marsh processes ignore it and assume that over the marsh as a whole it is negligible. The bulk of the organic matter produced by the emergent macrophytes dies and falls to the marsh surface. The decomposition of this material can be divided into two phases: an initial rapid loss of easily soluble organic compounds, followed by a longer, slower decomposition rate.

The first phase takes only about 2 weeks. The rapid release of easily soluble metabolites from the grass tissue and the continuous leaching of organic compounds from the live grass (Turner 1978) represent a significant flow of organic energy, perhaps as much as 20 - 30 percent of aboveground primary production (Teal 1983). The fate of this material has not been studied in gulf coast marshes, but a number of investigations were conducted in Georgia (Pomeroy and Wiegert 1981). There, much of the dissolved organic carbon (DOC) in the water column is refractory, probably released from later stages of decay of the marsh detritus. It is likely that the readily soluble compounds released when the grass cells die are easily metabolized by micro-organisms and disappear rapidly from the water column.

In a recent review article Ducklow (1983) assembled evidence that bacterial production in the ocean is not only high but is also a significant food supply for planktonic zooflagellates and ciliates. Most of these bacteria are apparently using DOC as an energy source since they are not associated with particulate matter. We need to know much more about this pathway of energy flow in coastal marshes. If Ducklow's model for the ocean and continental shelf is any guide, the food chain from grass to DOC to bacteria to microzooplankton and eventually to such filter feeders as mollusks and menhaden may be more significant than has been realized.

The second phase of decomposition often takes a year or more, depending on the environment and the plant species (Valiela et al. 1982). At the end of this period about 10 percent of the original detrital biomass may remain as refractory organic compounds.

A common way to investigate the loss rates is by enclosing dead plant material in litter bags (small nylon mesh bags with 2 to 5-mm holes), suspending the bags in the marsh, and retrieving them at intervals to examine the amount of material remaining. Decomposition is not the only thing measured by this technique. As soon as the plant fragments become small enough to escape from the bags, they may be lost by the flushing action of flooding water. In addition, usually larvae of many invertebrates find their way into the bags and prosper on the detritus. Their action in fragmenting the detritus is undoubtedly important in the loss rate.

A number of decomposition studies carried out in the delta are summarized in Appendix 2. In this Appendix and the figures and tables that follow, decomposition rates have been standardized by assuming an exponential decay rate (Wiegert and Evans 1964). The data are reported as loss rates, r [mg dry weight (dw) lost/g dw detritus/&y], defined as [ln(initial mass/final mass)]/time interval.

These studies support results found elsewhere: the three main factors controlling decomposition are temperature, location in the intertidal zone, and the plant species. Nutrient levels and the presence of macro-invertebrates that shred the detritus are also important.

Figure 52 shows that the decomposition rate of S. patens detritus decreases with time. This could happen for two reasons. First, this study was initiated in June, and the rate declined as the air temperature declined. Second, one would expect the more easily decomposed material to disappear first, leaving the more refractory, slowly decomposing compounds.

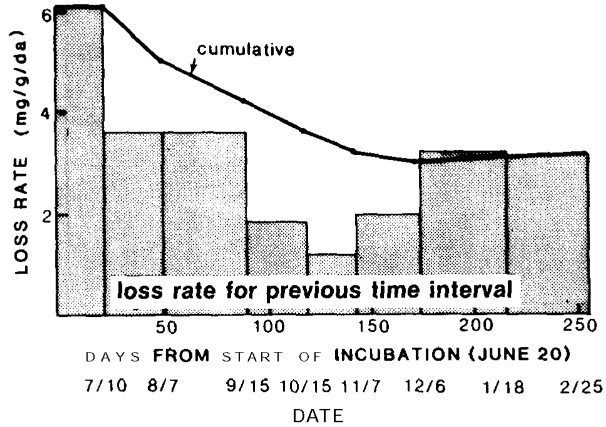


Figure 52. Disappearance of S. patens litter from litter bags in the Pontchartrain-Borgne basin (data from Cramer and Day 1980).

Both of these factors are probably reflected in this graph. The histogram showing the changing rate for each successive interval of time indicates that the initial rapid rate was declining as early as August before air temperature dropped significantly. This implies a change in the kind of material being decomposed. On the other hand, the rate began to increase again at the end of the experiment when the remaining materials would be most refractory; this coincided with the early spring increase in the ambient temperatures.

Figure 53 shows mean loss rates of S. alterniflora detritus from litterbags submerged but susoended off the bottom in a tidal stream, on the surface of a streamside marsh, and on the marsh surface further inland. Decomposition was fastest in flowing water, second where tidal flushing was vigorous, and slowest where the bags tended to be submerged most of the time in stagnant water. The figure also demonstrates the temperature (seasonal) effect.

Finally, Table 20 summarizes the species-dependency of the decomposition rate. Variability is high, but I believe the means are fairly reliable indicators of the relative rates of decomposition of different species. S. alterniflora is the most easily broken down of the grasses, but they all tend to be fairly fibrous and

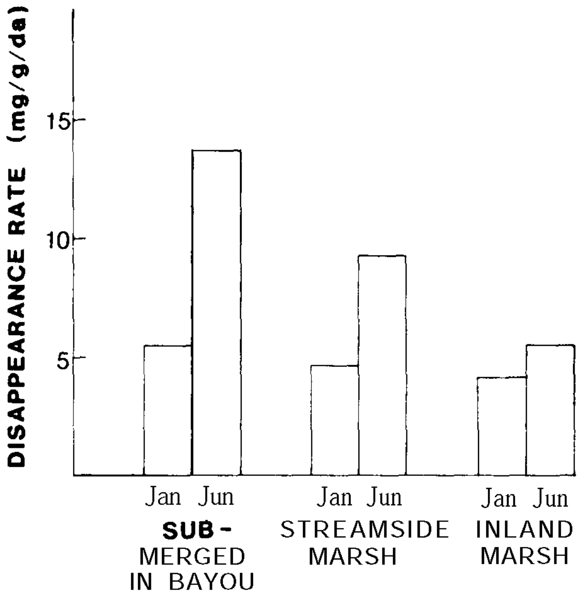


Figure 53. Decomposition rates (mg/g/day) of S. alterniflora litter incubated in 2-mm-mesh bags in different locations (Kirby 1971).

slow to decompose. J. roemerianus decomposes rapidly for a-species with a low surface to volume ratio. S. falcata, a broad-leaved monocot with- high leaf N content, decomposes extremely rapidly, apparently at any temperature.

Nitrogen availability often limits the decay rate of detritus (Teal 1983). Since most animals have low C:N ratios (under 10) while litter from such plants as S. alterniflora has a ratio well over 20, the decomposers must either. select high N residues from the litter or supplement the litter with N from other sources.

In a laboratory test Gosselink and Kirby (1974) found that litter became increasingly fragmented as it decomposed, and that the C:N ratio, after an initial increase, dropped rapidly so that the finely decomposed material had a N content up to 8 percent (C:N = 6). This increase in N was not simply a concentration of litter N by respiration of the C. Rather, N was absorbed from inorganic sources in the environment. This is not surprising since it has been known for many years that when a mulch is used in an agricultural crop the soil micro-organisms use it as an energy substrate and compete with the crop plant for available nitrogen.

Table 20. Range and mean loss rates (mg/g/day) of litter from different marsh plant species (summarized from Appendix 2).

Species	Range	Mean
Salt marsh		
Spartina alterniflora	4.0-21.9	8.4
Spartina cynosuroides	2.7- 6.4	4.6
Distichlis spicata	2.2- 9.0	4.6
Juncus roemerianus	5.9-14.4	9.3
Brackish marsh		
Spartina patens	2.8- 6.4	6.0
Intermediate & fresh marsh		
Phragmites australis	1.3- 6.2	3.8
Sagittaria falcata	24.1-25.7	24.9

Although this laboratory test suggested that litter can be converted to high protein microbial biomass efficiently, several recent studies showed that the bacterial and fungal biomass associated with detritus is quite small (Rublee et al. 1978, Wiebe and Pomeroy 1972). This may be at least partially because the bacteria are cropped as rapidly as they are produced by the meiofauna.

Other forms of nitrogen are extracellular compounds produced by microbes and proteins bound to oxidized phenolic compounds (degradation products of plant lignins). Many of these compounds are relatively resistant to decomposition and poor sources of organic energy to detritus feeders.

The aerobic decomposers comprise a bewildering array of species and physiological strains. Meyers et al. (1971) identified the species Pichia spartinae and Kluyveromyces drosophilarum as dominant yeasts in the salt marsh sediment surface. Hood and Colmer (1971) characterized a number of physiological groups of bacteria. They found that the soil-root interface of the grass was the site of most intense microbial activity. Maltby (1982) found that the ratios of actinomycetes to bacteria and of filamentous fungi to yeasts changed predictably in different wetlands depending on their history.

Mixed with these decomposers on the soil surface is an active community of autotrophic algae, chiefly diatoms, that enter the food web at the same level as the decomposers and may he an important additional energy source. Most investigators, however, are concerned more with the biochemical activity mediated by the microbiota than with species identification. They are satisfied to get some relative index of microbial biomass like that afforded by total ATP activity, or to characterize the microbiota by their chemical activity (White et al. 1979).

The decomposition of underground biomass has been studied very little. No studies are available from the Louisiana delta marshes. The best information on the subject comes from studies in Atlantic coast salt marshes summarized by Valiela et al. (1982), Teal (1983), and Howarth and Hobbie (1982).

Since the soil environment is anoxic, most of the decomposition must be anaerobic. The leaching phase of decomposition is the same as aboveground, but subsequently the disappearance of organic material is slower. Nitrogen stimulates the decomposition rate, indicating that it is limiting belowground as well as in an aerobic environment. One reason is that nitrate may control the metabolic rate by acting as an electron acceptor in the absence of oxygen. Most underground production, however, is decomposed through the fermentation and sulfate reduction pathways (Howarth and Teal 1979).

CONSUMERS

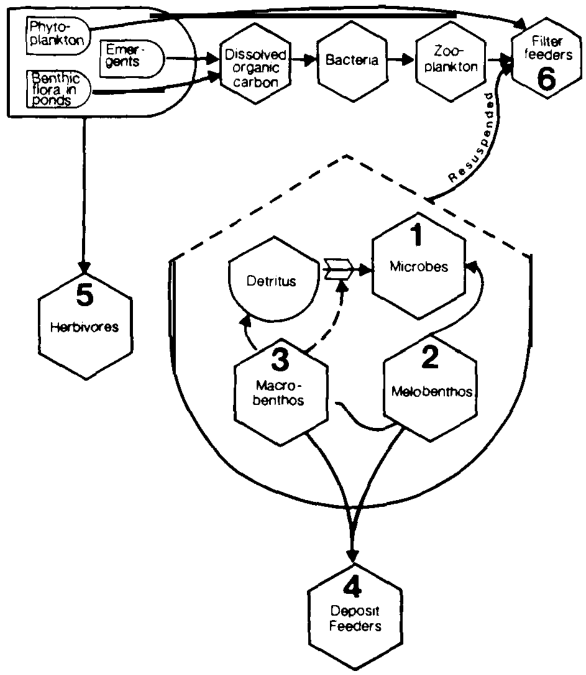
Benthos

In terms of energy transfer it is assumed that' the microflora act as the intermediary between the organic production of the higher plants and the higher trophic levels. At first investigators thought that the macroscopic deposit feeders were ingesting bacteria-laden detritus; skimming the bacteria from it; and fragmenting, packaging, and inoculating the detritus with bacteria in fecal pellets.

It appears now that bacterial density is too low on most detrital material to provide a sufficient food source for the macro-benthos (Wiebe and Pomeroy 1972). This change in viewpoint is reflected in the trophic diagram of Figure 54. The meiofauna are seen to have a crucial role in energy transfer (1 in Figure 54). They are distinguished from macrofauna primarily by size. Both are found in or on the substrate during all or part of their life cycles. Meiobenthos are generally microscopic; macrobenthos are larger and include such taxonomic groups as snails, mussels, and crabs.

Sikora et al. (1977) found that meiobenthic nematodes account for 70 - 90 percent of the sediment ATP, indicating that nearly all living biomass in anoxic marsh sediments is meiofaunal, not bacterial. These organisms are thought to be small enough to graze the bacteria efficiently and "package" that organic energy supply in bite-sized portions for slightly larger macrobenthic deposit feeders (3 in Figure 54).

Sikora (1977) showed that the chelae of the grass shrimp (Paleomonetes spp.) are about the right size to capture nematodes and speculated that grass shrimp are more likely to use this food than detritus. Bell's study (1980) supports this idea. She found that meiobenthic polychaete and copepod densities increased in caged exclosures that reduced macrofaunal predation. Gut analyses seldom turn up nematodes, the dominant meiofaunal taxon, but this is probably because their soft bodies are dissolved rapidly. Macrobenthic deposit feeders are thus ingesting and using as an energy source meiofauna, which in turn have been cropping bacteria, The deposit feeders themselves are prey for the many small fish, shellfish, and birds that use the marsh, marsh creeks, and small marsh ponds (3 and 4, Figure 54). Although apparently each step in this energy transfer can be quite efficient - net growth efficiencies up to 50 percent for bacteria (Payne 1970), 38 percent for nematodes (Marchant and Nicholas 1974) - the trophic pathway from detritus to microbes to meiofauna to



1
Bacteria
Fungi
Protozoa

2
Nematodes
Turbellarians
Gastrotrichs
Polychaete larvae
Harpacticoid copepods
Ostracods

3
Polychaetes
Amphipods
Oligochaetes
Tenaiads
Isopods
Melampus sp.
Caridean shrimp
Fiddler crabs
Small blue crabs
Littorina snails
Neritina snails
Carolina marsh clam

4
Penaeid shrimp
Blue crab
Sea catfish
Blue catfish
Channel catfish
Largemouth bass
Black drum
Red drum
Striped mullet
Silver perch
Spotted gar
Alligator gar
Yellow bass

Speckled trout
Gizzard shad
Hogchoker
Pinfish (juvenile)
spot
Tidewater silverside
Atlantic croaker

American alligator
Snapping turtle
Mississippi mud turtle
Red-eared turtle
Graham's water snake
Western ribbon snake

Brown snake
Garter snake

Pied-billed grebe
Eared grebe
Great blue heron
Little blue heron
Green heron
Snowy egret
Great egret
Glossy ibis
White ibis
King rail
Virginia rail

Clapper rail
Sora
Belted kingfisher
Fish crow
Black duck
Least bittern
Northern shoveler
Hooded merganser
American avocet
Western sandpiper
Solitary sandpiper
Wilson's phalarope
Common snipe
Dunlin
Piping plover
Killdeer

Muskrat
Raccoon
Mink
River otter

5
Southern painted turtle
Sheepshead
Pinfish
American coot
Canada goose
Seaside sparrow
Nutria

6
Oyster
Mussels
Clams

Gulf menhaden
Threadfin shad
Sand seatrout
Bay anchovy
Atlantic croaker
(< 25 mm)

Figure 54. Major pathways of organic energy flow in a Mississippi River deltaic salt marsh and associated water bodies.

macrofauna to fish is long. The overall energy transferred to the nektonic level is a small fraction of primary production.

Figure 54 also shows a feedback loop from macrobenthos to detritus. Macrobenthic animals actively shred and break up detritus in their feeding activity, increasing its surface area and making it more readily decomposed. For example, Valiela et al. (1982) estimated that exclosures that keep detritivores away from decaying litter reduce the decomposition rate by as much as 30-50 percent.

Nekton

Numerous fish species are found in the delta marshes (Appendix 3). These include a broad array of year-round residents with varying salinity tolerance and migrating species that use the marsh as juveniles for a nursery. Many of these species are benthic feeders and represent the next link in the benthic food chain described in the previous section.

Ruebsamen (1972) studied the stomach contents of fish captured by seine in small, shallow intertidal marsh ponds in the Barataria basin (Table 21). Of the nine most abundant species, six were described as feeding on benthic infauna such as copepods, amphipods, ostracods, mysidaceans, polychaetes, tendipedid larvae, nematodes, and annelid worms. Two were described as detritus eaters, (which probably means that they were using the meiofauna in the sediment). The small marsh ponds are frequented primarily by resident fish, while migratory fish are found in the deeper marsh creeks. In Ruebsamen's study of small marsh ponds, spot (Leiostomus xanthurus) was the only migratory species found in large numbers.

Variation in the particular species reported to use marsh ponds is often related to differences in gear used and definitions of what comprises a marsh pond. Nevertheless, much evidence points to heavy use of the marsh by nekton for both food and shelter. Ruebsamen (1972) found only the small fish in the intertidal marsh ponds. As they grew they usually disappeared from the samples.

Table 21. Monthly occurrence and abundance of the fish species collected in small salt marsh ponds (Ruebsamen 1972).

Species	Month (A S O N D J F M A M J J A)	Relative abundance[a]
Cyprinodon variegatus	-----------*******------[b]	14,353
Adinia xenica	----*******-- --	4,763
Menidia beryllina	-----------------******--	2,662
Fundulus grandis	-----------****--*****----	2,272
Poecilia latipinna	----------*-------****---	2,064
Fundulus pulvereus	-------------	348
Lucania parva	____ __________________	304
Leiostomus xanthurus	-----------	212
Fundulus similis	----- -----------------	139
Mugil cephalus	---_____	86
Gobionellus boleosoma	----	35
Anchoa mitchilli	--	28
Lagodon rhomboides	______	27
Gambusia affinis	___	22
Brevoortia patronus	---	12
Sciaenops ocellatus		7
Cynoscion nebulosus		5
Achirus lineatus		4
Evorthodus lyricus		3
Elops saurus		2
Sphaeroides parvus		2
Archosargus probatocephalus		2
Gobiosoma bosci		2
Lepisosteus sp.		1
Syngnaathus scovelli		1
Pogonias cromis		1
Microgobius gulosus		1

[a] Total caught during study.
[b] Present, ***** abundant.

Hinchee (1977) found 20 to 25-mm menhaden along the edges of Lake Ponchartrain, apparently as they moved into the estuary from the gulf. These small juveniles moved into the marsh where they stayed until they reached about 50 mm, after which they began their emigration back out through the lake to the open gulf (Figure 55).

When conditions permit, many nektonic organisms move up into the marsh itself. Sikora (1977) found this true for the grass shrimp in Georgia, and Werme (1981) found 30 percent of the silverside (Menidia menidia) and mummichog (Fundulus heteroclitus) in a north Atlantic estuary up in the marsh at high tide.

Kelley (1965) sampled fish in marsh ponds in the active Balize Delta. In this nearly freshwater area he found mullet and blue catfish the most abundant, but he also reported plentiful croaker, spot, sand seatrout, spotted seatrout, and menhaden. It is interestinq that

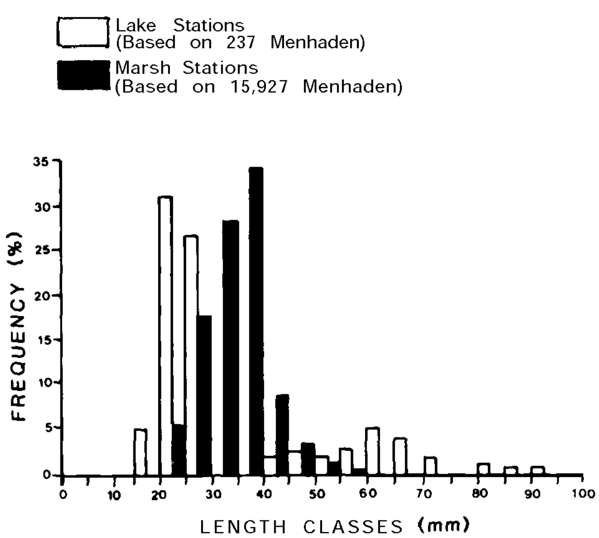


Figure 55. Length class frequency of gulf menhaden captured in and near Lake Pontchartrain (Hinchee 1977).

freshwater coastal marsh/aquatic systems represented by the Balize and Atchafalaya Deltas are found to function in very much the same way as saline estuaries, with the same suite of marine/estuarine fish and shellfish. In addition, freshwater species like gars (Lepisosteus spp.), gizzard shad (Dorosoma cepedianum), and blue (Ictalurus furcatus) are common 1965, Thompson and Deegan 1983).

Even when they are seldom found up in the marsh itself or in the small marsh ponds, other species concentrate along the marsh edges where food is abundant and shelter is available in the streamside grass stems. For example, Peterson (LSU; pers. comm.) was unsuccessful in capturing larval spotted sea trout until he began to seine along the very edge of marshes as compared to more open aquatic environments. Spotted sea trout are just one example of the concentration of both the food supply and the aquatic organisms that depend on it.

Biological activity is concentrated at the marsh edge (Figure 56). For reasons already discussed, plant production is highest along the marsh edge. Finely decomposed detritus from the previous year's plant crop is flushed from the marsh during the winter and accumulates along the marsh edge in deep deposits known to local shrimpers as "coffee grounds." Nematode numbers are highest here as are the concentrations of small deposit feeders. It is no wonder that larger invertebrates - shrimp and crabs - and larval and juvenile fish are also attracted to this feast. Virtually every kind of organism enumerated has been found to concentrate along marsh edges.

This benthic food pyramid is the dominant one in salt marshes. Yeiofauna, particularly nematodes, graze the bacteria on decomposing grass, are ingested in turn by deposit feeders which are a major source of food to nektonic fish, shellfish and birds. The marsh-dependent fish, especially the very small ones, graze and shelter up in the marsh when it is flooded and lie in the small marsh ponds and along the edges of fine feeder creeks at other times. As they grow they frequent deeper, more open water.

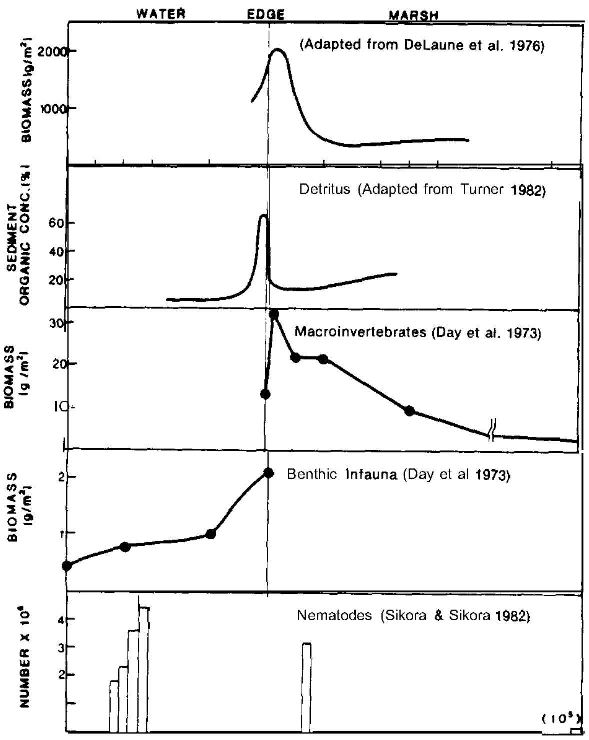


Figure 56. Density of vegetation, detritus and consumers at the edge of the salt marsh.

The importance of this energy flow pathway in marshes can be seen qualitatively by comparing the list of nektonic species in Figure 54 that use the benthic pathway predominantly with those that use the planktonic pathway. Of the abundant species only the gulf menhaden, the bay anchovy, and the juvenile Atlantic croaker are filter feeders. Crabs, shrimp, drum, gar, mullet and nearly all the small resident marsh fish are benthic feeders.

Wildlife

Wildlife species that use Mississippi delta marshes are abundant. Table 22 summarizes the species of different taxonomic groups that are likely to be found in different marsh zones in the chenier plain region of southwestern Louisiana. The deltaic plain has about the same species. In general, species richness is highest in the fresh marsh, decreasing into saline areas. No amphibians and only 4 reptile species are found

Table 22. Wildlife species richness (number of species) in the chenier plain marshes (Gosselink et al. 1979).

Wildlife group	Swamp	Marsh zone			
		Fresh	Intenediate	Brackish	Salt
Amphibians	18	18	6	5	0
Reptiles	32	24	16	16	4
Birds	120	84	89	89	92
Mammals	25	14	11	10	8

in salt marshes, for example, whereas 13 amphibian and 24 reptilian species inhabit the fresh marsh. Bird species richness does not vary much over these zones, perhaps because birds are mobile and can easily move from one area to another. The richness of swamp forest habitats is included in the table for comparison. It is higher for all groups, probably reflecting the higher structural heterogeneity of that hdbitat.

Although preferred habitat conditions vary with individual species, Weller (1973) suggested that the following characteristics can lead to increased wetland use: (1) Diversity of plant communities. Wildlife are usually more densely distributed where several different plant zones occur than in homogeneous stands. The structure of the habitat is apparently more important for nesting than the particular taxonomic makeup. Bird species that prefer tall, robust veyetation, for example, seem to be equally satisfied with cattails, bulrushes, or small willows. This is not true for feeding since decided preferences are found, especially for annual plants such as millets with abundant seed and for tuberous species. (2) High edge zone:marsh ratio. Apparently both the edges between different vegetation zones and between vegetation and water are important. For example, the ideal in midwestern pothole marshes appears to be a "henimarsh" that has a 1:1 or 1:2 ratio of marsh to water with good interspersion between the two (Weller 1973). For' waterfowl, the size and depth of shallow marsh ponds is particularly important.

In the delta marshes, waterfowl studies have emphasized their distribution with respect to the broad vegetation zones of the coast. Studies of local marsh:water relationships, marsh breakup, and plant diversity as they relate to waterfowl are rare. Perhaps this is inevitable in a wetland area as large as the Mississippi Delta. The availability, in the past few years, of good remote sensing data and new technologies to process large data sets gives us the capability of examining in much greater detail the complex wildlife:habitat relationships.

In midwestern pothole marshes,habitat quality for wildlife is closely bound to an approximate lo-year cycle of emergent-floating-submergent vegetation succession that seems to be controlled by water levels and herbivory, especially muskrat herbivory. In Louisiana's coastal marshes, water levels controlled by the level of the Gulf of Mexico are more stable in that time scale, and the dominant trend is a long-term (100+ year) change from fresh to saline and from solid marsh to broken-up marsh to open water. However, within this long tine frame O'Neil (1949) identified 10- to 14-year cycles that are related to severe storms and muskrat and goose "eat-outs."

Alligators. One of the most dramatic success stories in wildlife conservation in Louisiana is the return of the alligator from a threatened classification (Endangered Species Tech. Bull. 2(2), Feb. 1977) to the present abundance that makes possible a controlled harvest each year. The species was threatened by severe hunting pressure, not habitat loss. When that pressure was removed, its numbers increased rapidly.

Alligators are abundant in fresh and slightly brackish bayous and lakes. They reach their highest densities in intermediate wetland zones (Joanen and McNease 1972). They build nests in marshes and on levees. One favorite microhabitat is the wax myrtle thickets common in fresh marshes. In 1932 we counted 23 nests in a fresh floating marsh fringing a small shallow lake; a night count along a fresh marsh bayou revealed over four alligators per km (Sasser et al. 1932).

Crawfish, and in brackish areas blue crabs, are major alligator foods, but alligators are also reported to eat birds, fiddler crabs, fish, insects, muskrats, nutria, turtles, shrimp, snails, and grasses (Chabreck 1971b). In the Florida Everglades they make "wallows" that are ecologically important for fish during the dry season, but this has not been reported in delta marshes.

Muskrat and nutria. The muskrat (Ondatra zibethicus) and the nutria (Myocastor coypus), both herbivores, are the dominant mammals in the delta marshes. The nutria is an introduced species. It is debatable whether muskrats are native or not. O'Neil (1949) stated that although early surveyors' records provide an unconfirmed record of high density muskrat populations in the Barataria-Lafitte area in 1840, fur harvesting did not begin until the first years of the twentieth century, and old-time trappers all claimed that no "rats" were seen much prior to that time. However, Arthur (1931), in a Louisiana Department of Conservation Bulletin, quotes from the journal of Father Jacques Gravier describing travels down the Mississippi River. He described the dress of the Tunica Indians in a November, 1700 entry:

"Most of the men have long hair and have no dress but a wretched deerskin. Sometimes they, as well as the women, also have mantels of turkey feathers or muskrat skins well woven and worked."

About the Houmas Indians he stated:

"The women wear a fringed skirt, which covers them from the waist to below the knee. When they go out of their cabins they wear a robe of muskrat skins or of turkey feathers."

These reports seem to indicate that the muskrat has been abundant in the coastal region for at least several hundred years.

The nutria is a native of South America. It was introduced by the McIlhennys to Avery Island; it escaped in 1938 and rapidly spread throughout the Louisiana coast. Whereas the muskrat is found most abundantly in brackish marshes (Figure 57), the nutria prefers fresh marsh and swamp forests and often ventures into nearby ricefields to feed. There is some evidence (Lowery 1974) that the present muskrat distribution results from the invasion of fresh marshes by the more robust nutria which displace muskrats into less desirable brackish areas. Although both species often exist side-by-side in the same area, they appear to have very much the same food habits, and it has been noted that when nutria are heavily trapped, the muskrat population can soar (Evans 1970).

Muskrats often seem to be the primary agents in a 10- to 14-year cycle of marsh growth and collapse (Figure 58). They

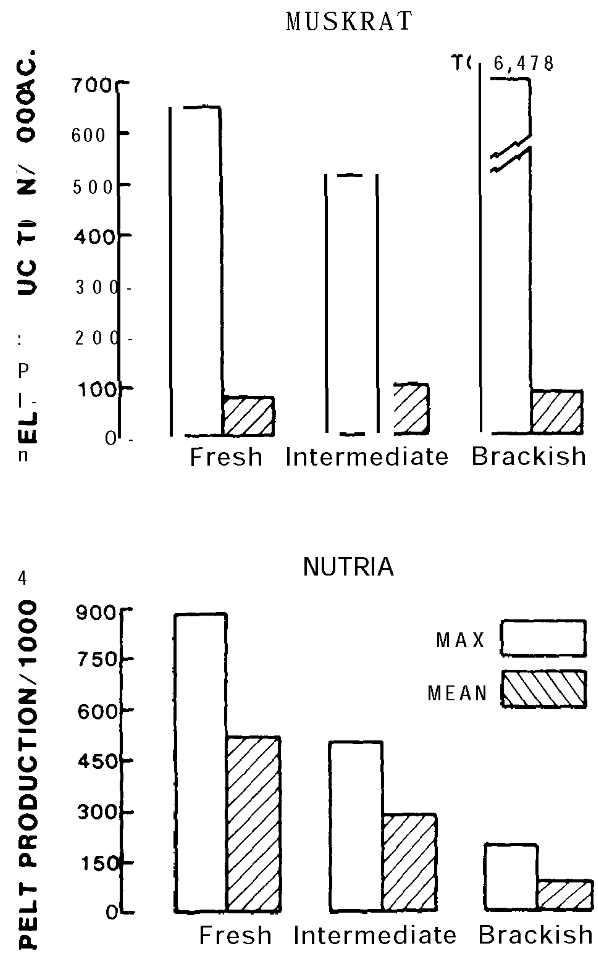


Figure 57. Pelt production from marsh zones in coastal Louisiana (Palmisano 1972).

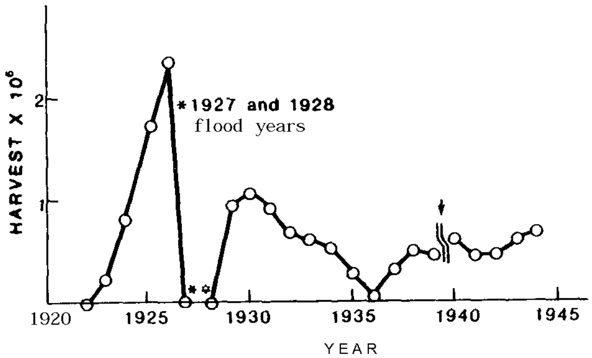


Figure 58. Annual muskrat harvest from a 52,200-ha brackish Scirpus olneyi marsh in the Mississippi Delta (O'Neil 1949).

kill much vegetation digging for the preferred roots. In addition, their house-building activity, underground runs, and surface trails (Figure 59) destroy much more marsh than is directly eaten. For example, in a 10-ha brackish marsh area that contained 24 active and 30 inactive houses in April 1982, 31 new houses were built and 10 "refurbished" during the next year (Table 23). Sixty percent of the active houses and 57 percent of the inactive ones simply disappeared.

When muskrat populations are dense, all this activity can decimate a marsh, creating large "eat-outs" especially in the favored brackish marsh three-corner grass (Scirpus olneyi) (Figure 60). Subsequently the local population, with no

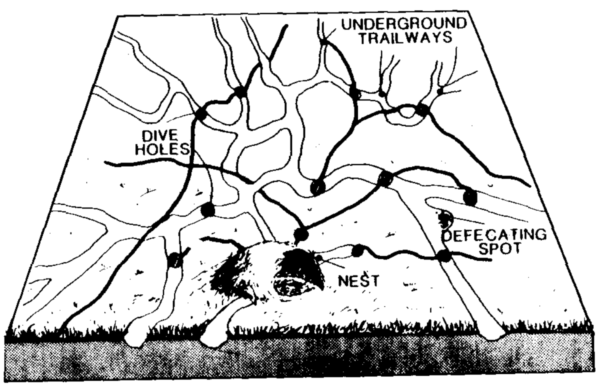


Figure 59. Ground plan of a typical muskrat house with underground runways and surface trails (barred lines) (Arthur 1931).

food, crashes. If water levels are low for a year or two to allow regrowth of the vegetation,the marsh may recover (and the muskrat population with it), but often the damage extends so deeply into the marsh that recovery is poor at best. Severe storms may reset this cycle by destroying nests and burrows and drowning the predatory disease organisms they harbor. The muskrat population often comes back strongly after these storms (O'Neill 1949).

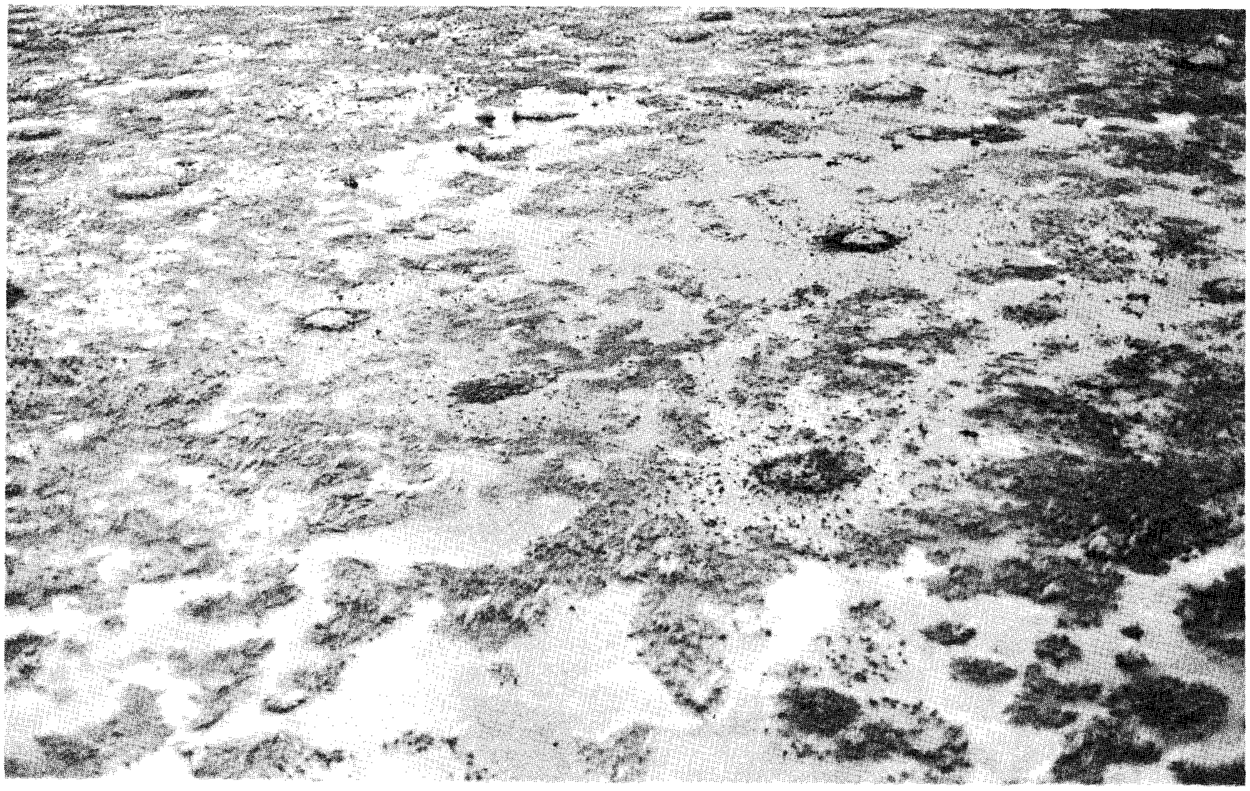
It is interesting that "eat-outs" are seldom found outside of brackish marshes and are always attributed to muskrats, not nutria (O'Neil 1949). The nutria has a much longer gestation period (130 days compared to 28 days for the muskrat) so that its potential for response to environmental change is much slower than the muskrat's, Consequently, its population is more stable. Muskrat "eat-outs" in fresh marshes have been recorded (O'Neil 1949) but the preference for brackish marsh makes this a more likely site. "Eat-outs" are much rarer today than in the 20's and 30's because trapping keeps the population down to nondamaging levels.

In light of the apparent local importance of plant-eating furbearers and the earlier discussion of the relative lack of herbivory in marshes, it is informative to reconsider the importance

Table 23. Ctuskrat house-building activity in 10-ha brackish and salt marsh areas in Barataria basin (Sasser et al. 1982).

Status	Number of houses			
	Brackish		Salt	
	Apr. 1982	Apr. 1983	Apr. 1982	Apr. 1983
Active	24	47	26	40
Inactive	30	22	12	8
Total	54	69	38	48

Status change	Brackish	Salt
Active to active	6 (25%)	19 (73%)
Active to inactive	3 (12%)	3 (12%)
Active to gone	15 (62%)	4 (15%)
Inactive to active	10 (33%)	1 (8%)
Inactive to inactive	3 (10%)	0 (0%)
Inactive to gone	17 (57%)	11 (92%)
New active	31	20
New inactive	16	5



Fisure 60. A muskrat "eat-out" in the brackish marsh in the Earataria basin. Note the high density of muskrat houses (Photograph by Robert Abernathy).

of herbivory. Muskrats are reported to eat one-third of their weight per day (O'Neil 1949), and a nutria consumes 1.5 - 2 kg of vegetation each day (Lowery 1974). The average population of nutrias and muskrats from Point au Chien Wildlife Management Area in the delta, from 1973 to 1981, was 1.2 and 0.8/ha, respectively (from Sasser et al. 1982, assuming the population is double the catch (O'Neil 1949).

If a nutria eats 2 kg/day, a muskrat 0.3 kg/day (a muskrat weighs about a kilogram), and the vegetation is 20 percent dry weight, then their combined intake is about 150 kg/ha/yr, compared to a plant productivity of about 30,000 kg/ha/yr. Direct grazing is thus less than 1 percent of production. O'Neil (1949) reported a peak harvest of 46 muskrats/ha in a brackish marsh (Figure 59). With the same assumptions, that many animals would eat as much as 7 percent of the vegetation. If damage from burrowing, building nests, and digging for roots was 10 times greater than ingestion, it is easy to see that a significant portion of the vegetation would be destroyed.

Deer. Although one-third of Louisiana's white-tailed deer (*Odocoileus virginianus*) population is reported to live in the coastal marshes (which comprise only 13 percent of the state) (St. Amant 1959), very few studies have been made of their feeding and habitat requirements in this environment. Apparently, fresh marshes are preferred almost to the exclusion of brackish and saline marshes.

Based upon data gathered over 20 years, J. B. Kidd (La. Wildlife and Fisheries Commission), in a 1972 letter (as reported in Self 1975), estimated that the "potential" density of deer by marsh type was one deer per 12 ha in the fresh marsh, 1 per 330 ha in the brackish marsh, and 1 per 2900 ha in the salt marsh. This assessment of carrying capacity for fresh marsh agrees well with observations by Jessie Fontenot (Morgan City, La., 1983; pers. comm.) about the deer density in his 1600-ha hunting lease in a fresh marsh in the Atchafalaya hydrologic unit. He reported 180 deer (about one per 9 ha) on his lease, which he said was overstocked.

White-tailed deer prefer areas slightly elevated above the marsh such as natural levees and spoil banks which can be used for travel, bedding, and fawning. From a browse study made on spoil levees in the fresh marsh in the Rockefeller Wildlife Refuge in the chenier plain of Louisiana, and from rumen analyses of deer killed in that area, Self (1975) determined that deer ate nearly any plants that were succulent and green.

Important food plants during the fall were Alternanthera philoxeriodes, Bacopa halimifolia, Vigna luteola, Salix nigra, B. monnieri, Echinochloa walterii, Kosteletzkya virginica, Leptochloa fascicularis, Panicum dicotomiflorum, and Paspalum vaginatum. During the spring and summer the same species and Phragmites australis, Iva annua, Cyperus virens, and Typha angustifolia were browsed. All these species are found in fresh and intermediate marshes. The brackish marsh grass Spartina patens was grazed in proportion to its abundance but was not a preferred species.

Waterfowl, coots, and wading birds. Functionally, birds that use Louisiana's delta marshes can be divided into dabbling or puddle ducks and coots, diving ducks, geese, wading birds, birds of prey, and other marsh birds (Appendix 4). The waterfowl and coots are by far the most abundant. They are mostly winter residents that migrate as far north as the Arctic Circle each summer. Of this group, only the mottled duck breeds in Louisiana marshes with any regularity. Duck populations are highly variable in censuses because of their mobility, but peak populations in the deltaic plain are usually over 2 million birds. Table 24 shows the density of the most common species along transects through Barataria basin. Gadwall (Anas strepera), blue-winged teal (A. discors), and mallard (A. platyrhynchos) were the most common

Table 24. Density of waterfowl (number/100 ha) by marsh zone in the Barataria basin in 1980-81 (total for 13 flights; Sasser et al. 1982).

Species[a]	Marsh zone		
	Salt	Brackish	Fresh[b]
Gadwall	90.0	212.2	11.2
American Coot	25.8	198.4	82.2
Blue-winged Teal	30.8	65.5	25.3
Mallard	10.3	24.0	26.3
Northern Pintail	11.2	53.8	3.5
Green-winged Teal	17.3	1.5	0.0
Mottled Duck	3.8	12.6	12.2
Northern Shoveler	4.5	9.4	0.3
American Wigeon	1.7	2.9	0.7
Red-breasted Merganser	2.1	0.0	0.1
Hooded Merganser	1.7	0.2	0.0
Scaup spp.	0.4	0.9	0.1
Bufflehead	0.2	0.0	0.0
Ruddy Duck	0.1	0.0	0.0
Ringneck Duck	0.1	0.0	0.0
Common Goldeneye	0.02	0.0	0.0
Total Density[c]	199.9	579.9	161.7
Flight Mean[d]	15.4	44.6	12.4

[a]For scientific names see Appendix 4.
[b]Includes intermediate marsh.
[c]Total number of ducks/13 flights/100 ha.
[d]Total density divided by number of survey flights.

puddle ducks in this study (Sasser et al. 1982). In Louisiana Department of Wildlife and Fisheries surveys taken over the past 10 years in the same area, the green-winged teal (A. crecca) replaces the blue-winged teal. The American coot (Fulica americana), which is also very common, is not a duck but in the rail family. However, because of its habits it is usually included with the puddle ducks. The diving ducks - scaup (Aythya spp.), ring-necked duck (A. collaris) and hooded merganser (Lophodytes cucullatus) - are also common. Generally, geese are found only in the active Balize Delta. They are much more common along the southwestern coast of Louisiana.

Puddle ducks prefer marshes interspersed with small, shallow ponds (less than 5 ha) from a few centimeters to about one-half meter deep. They are primarily herbivores, and good stands of submerged grasses improve the quality of the habitat. Ruppia maritima (widgeongrass) is the preferred food in brackish ponds; Potamogeton pusillus (pondweed), Najas quadalupensis (naiad), and Lemna spp. (duckweed) in freshwater ponds. In brackish marshes Scirpus olneyi (three-cornered grass), Bacopa monnieri (water hyssop), and Eleocharis parvula (dwarf spikerush) are desirable foods. Echinochloa walteri (wild millet), Leptochloa fascicularis (sprangletop), Panicum sp. (fall panicum), and other annuals that produce abundant seeds are good fresh marsh foods. The succulent roots and tubers of species such as S. olneyi and Sagittaria 'platyphylla (delta duck potato) are also favorite foods. especially for geese.

It is easy to see why fresh and brackish marshes in the delta support so many dabbling ducks. There are thousands of small marsh ponds in all salinity zones (Table 25), and the dominant plant species in brackish to fresh ponds are considered excellent duck food. Ponds 0.4 - 4 ha in size have the best growth of submerged grasses, possibly because wind-induced turbulence is low in these small ponds. Saline ponds are poorly vegetated (Table 26). Because of this and because the plant species of this marsh zone make poor duck foods, the saline marshes are relatively poor puddle duck habitat.

Much attention has been focused on the habitat conditions of arctic and subarctic nesting grounds and their influence on the growth of duck populations. Much less attention has been directed toward the importance of wintering grounds for reproductive success. A recent study by iieitmeyer and Fredrickson (1981), however, emphasized this important aspect of wintering grounds. They found a direct linear relationshio between winter precipitation in the Mississippi delta riparian hardwoods (an index of pond number and hence habitat quality) and reproductive success of mallards as measured by the ratio of young to mature mallards. In their multiple regression models both the wintering ground quality index and the numbers of ponds in the nesting area in May and June were significantly positively related to mallard age ratios. The study implies that the quality of deltaic plain marshes may also be important in duck reproductive success.

In contrast to puddle ducks, diving ducks usually prefer deep water. They are carnivores, diving to depths of over 10 meters in some cases to obtain their food. Because of this preference they are usually found in open water and along the nearshore zone. However, they are also known to feed on the vegetation of shallow

Table 25. Density of ponds and lakes of various size classes in marsh zones along the Louisiana coast in August, 1968 (Chabreck 1971a).

Pond and lake size class	Marsh zone			
	Salt	Brackish	Intermediate	Fresh
(acres)	(number per 100,000 acres)			
0.01	27,700.2	118,841.7	55,952.2	59,181.2
0.01-0.10	16,749.0	62,162.2	45,024.0	47,637.4
0.10-1.0	4,702.6	14,139.0	10,432.8	9,796.8
1.0-10	700.0	1,376.1	759.1	1,070.5
10-80	132.2	179.5	73.2	108.8
80-640	30.2	12.4	2.6	25.1
640-3,200	5.2	3.2	0	4.5
3,200-16,000	0.5	0.6	0	0.2
16,000-32,000	0	0.2	0	0.3
64,000	0	0.1	0	0

Table 26. The percent of the area of ponds and lakes covered with subnerged vegetation in August, 1968 (Chabreck 1971a).

Pond and lake size class	Marsh zone				Entire coast
	Salt	Brackish	Intermediate	Fresh	
(acres)	(percent)				
0.01	0	8.6	11.4	53.2	20.0
0.01-0.10	0	15.4	29.1	75.6	35.4
0.10-1.0	0	8.1	37.7	71.7	31.1
1 .o-10	0	10.7	19.5	56.4	23.9
10-80	0	16.3	13.1	28.4	16.0
30-640	0	7.1	0	29.6	15.1
640-3,200	0	7.9	0	4.0	3.8
3,200-16,000	0	0	0	0	0
16,000-32,000	0	0	0	0	0
64,000	0	0	0	0	0

ponds (Bellrose 1980) and in this case are associated with marsh habitats.

Compared to ducks,much less information is available about wading bird ecology in delta marshes. This is surprising when it is considered that they are abundant year-round residents. The herons and egrets (Table 27) are mostly carnivorous, catching frogs, small fish, snakes, crawfish, and a wide assortment of worms and insects (Mabie 1976). They prefer to fish in very shallow marsh ponds and along the bayous that drain marshes. They also nest in marshes or in close-by mangrove thickets, wax myrtles, and uplands. They appear to prefer the brackish marsh zone for feeding. Oensities range up to 103 or more per 100 ha, and average from 6 to 26 per 100 ha (Sasser et al. 1982). A number of heronries occur in the delta marshes (Portnoy 1977). They are abandoned and reformed in other places fairly frequently. For example, of 27 sites identified by Portnoy (1977) in the Barataria basin only 17 were active in 1982, and at least 4 new nesting colonies were found (Sasser et al. 1982). It would be interesting to know whether the nesting of wading birds in a congested area made much impact on the local nutrient cycles. Certainly this has been shown for other birds, especially where huge guano deposits have resulted (Deevey 1970).

Rails (Rallus spp.), the seaside sparrow (Anmospiza maritima), the great-

Table 27. Density of wading birds and pelicans (number/100 ha) by marsh zone, in the Barataria basin, 1980-81 (total for 6 flights; Sasser et al. 1982).

Species[a]	Marsh zone		
	Salt	Brackish	Fresh[b]
Snowy Egret	8.2	23.9	35.5
Great Common Egret	9.4	25.9	23.1
American White Pelican	8.6	39.3	1.3
White-faced Ibis	1.1	31.9	16.1
White Ibis	2.2	21.1	14.7
Great Blue Heron	3.6	5.3	3.6
Little Blue Heron	2.4	8.0	4.8
Louisiana Heron	1.4	2.7	1.3
Cattle Egret	0.02	1.5	4.2
Black-crowned Night Heron	1.0	1.1	0.8
Reddish Egret	0.04	0	0
Brown Pelican	0.02	0	0
Total Density[c]	38.0	160.6	105.4
Flight Mean[d]	6.3	26.8	17.6

[a]For scientific names see Appendix 4.
[b]Includes intermediate marsh.
[c]Total number of ducks/6 flights/100 ha.
[d]Total density divided by number of survey flights.

tailed grackle (Quiscalus mexicanus) and the red-winged blackbird (Agelaius phoeniceus) are the most numerous of the other marsh birds. The latter two species, especially, are abundant during the spring breeding season. They are migratory and are absent during the winter. Northern harriers are also seen frequently in all marsh environments.

Some of these species are endangered or rare (Table 28). The beautiful brown pelican, in particular, has been almost lost from the delta (King et al. 1977). It has been reintroduced from Florida and is found in two nesting colonies on mangroves on Queen Bess Island in Barataria Bay and North Island just west of the Chandeleur Island chain.

Carbon Budget

One way of summarizing quantitatively the productivity and trophic relations discussed is with a C budget. Most c budgets are primarily input-output budgets that treat the ecosystem under study as a black box so that internal details of the trophic structure are ignored, and metabolism of all consumers is lumped as community respiration. In particular, higher consumers contribute little to community respiration and are usually ignored. Both Day et al. (1973) and Costanza et al. (1983) are exceptions to this generalization; they calculated metabolic rates for a number of consumer groups. However, I will consider the overall input-output budget without this detail. Unfortunately, several key flows in the budget are still not quantified. As a result, any carbon balance must be considered tentative even today.

Table 28. Birds of the Mississippi Deltaic Plain on the Audubon Society "Blue List," indicating that their populations are declining (Mabie 1976).

Brown Pelican (Pelecanus occidentalis) [a]
American White Pelican (P. erythrorhynchos)
Reddish Egret (Egretta rufescens)
White-faced Ibis (Plegadis chihi)
White Ibis (Eudocimus albus)
Black-crowned Night Heron (Nycticorax nycticorax)
Red-shouldered Hawk (Buteo lineatus)
Northern Harrier (Circus cyaneus)
Osprey (Pandion haliaetus)
Black vulture (Coragyps atratus)
Loggerhead Shrike (Lanius ludovicianus)

[a] Endangered species.

Day et al. (1973) published the first budget for a delta salt marsh. It was based almost entirely on aboveground primary production, benthic comrnmunity respiration, and calculated energy flow through the abundant consumers. Loss to deep sediments was assumed to come from root production, and both were ignored in the balance. These authors concluded that 50 percent of net production was exported from the marsh. It has not been possible to measure this organic export directly.

Happ et al. (1977) calculated the export of total organic carbon (TOC) from the Barataria estuary to the nearshore gulf from the gradient of decreasing TOC across the passes and an estimate of the turnover rate of bay water. They estimated that the export of TOC was about 150 $g/m^2/yr$. Since aquatic primary production and community respiration in the bay appear to be about equal (Allen 1975), this export from the estuary must reflect marsh export. It amounted to about one-half of the Day et al. estimate.

Hopkinson et al. published additional salt marsh respiration data in 1978. Since then Smith et al. (1982) published an incomplete carbon budget for the same area which includes estimates of methane evolution and new data on CO_2 evolution. I have attempted to create a new budget from all this information and some direct carbon dioxide flux measurements of photosynthesis that include root production (Gosselink et al. 1977). The weakest links in all these budgets are the paucity of root production information and our inability to measure marsh export directly.

Figure 61 shows measurements of CO_2 flux through a S. alterniflora stand at different seasons. The cuvette used to collect these data enclosed 0.07 m^2 of marsh, including sediment and aboveground vegetation, so the data should represent the whole community. Notice that nearly

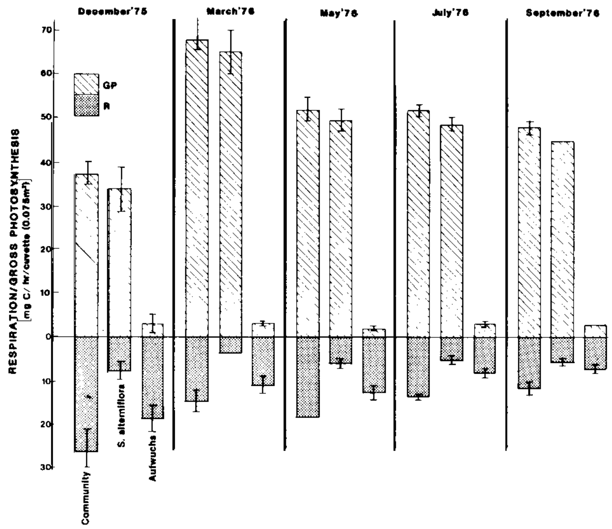


Figure 6.. Carbon dioxide flux measurements in a deltaic salt marsh community (unpublished data; see Gosselink et al. 1977).

all the production can he attributed to the grass.

Most of the respiration is associated with the diatom and microbial community (aufwuchs) on the base of the plant culms and sediment surface. In Figure 62 I show annual C fluxes calculated from these data, adjusted for the difference in average biomass in the cuvette compared to the surrounding marsh but not corrected for light intensity, marsh flooding, and temperature variation (see Gosselink et al. 1977 for details of the technique).

Comparable data from other delta salt marsh studies is displayed for comparison in Table 29. Organic matter has been converted to carbon by multiplying by 0.4 (Smith et al. 1932a). The differences from earlier budgets are startling. Gross community production was estimated to be

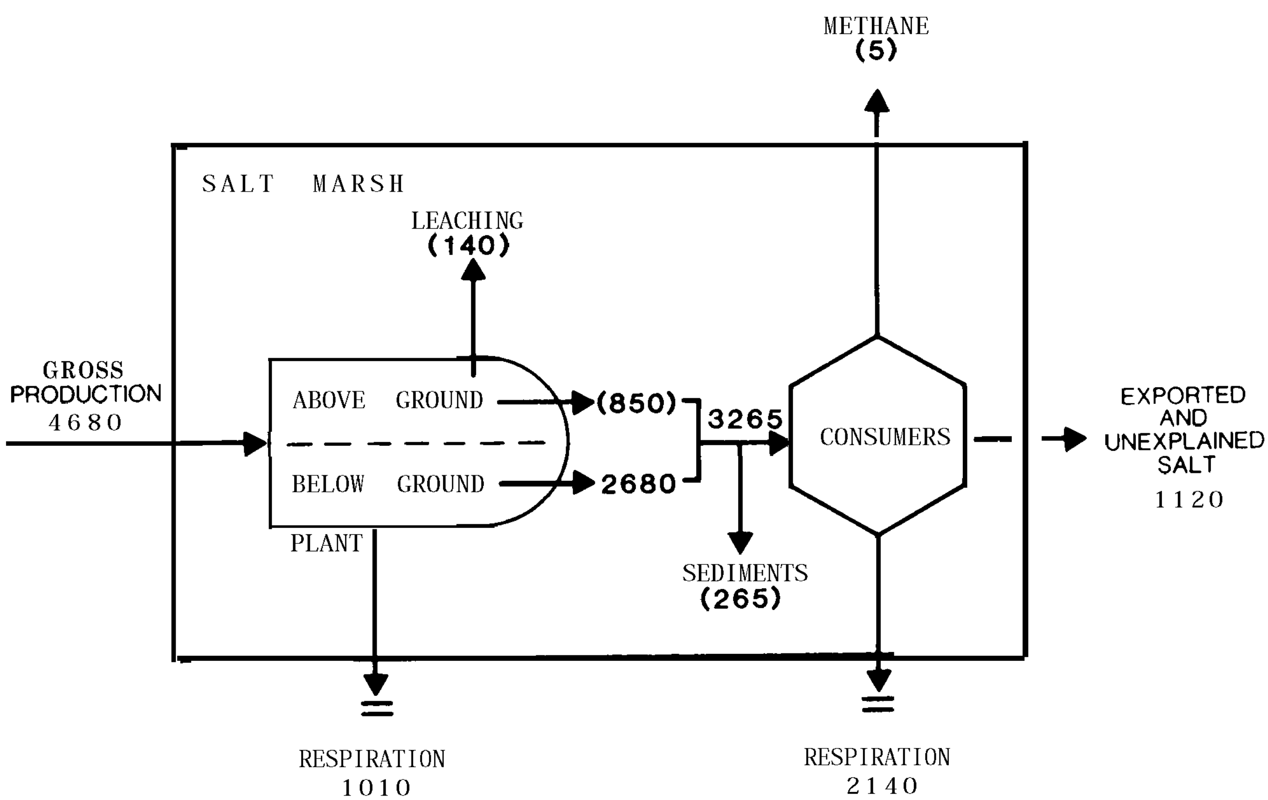


Figure 62. Carbon budget of a Mississippi River deltaic salt marsh (see Table 29 for sources). Rates (g $C/m^2/yr$) are from CO_2 flux measurements, except numbers in parentheses, which are from other sources.

4,680 g $C/m^2/yr$, most of which is due to the emergent grass. Net primary production was 3,670 $g/m^2/yr$. There are no other figures comparable to these from direct measurement.

Net aboveground production from clip plot studies is only about 850 $g/m^2/yr$, leaving an estimated 2,800 $g/m^2/yr$ underground production. That is not impossible but is certainly very high. Community respiration was about 3,150 $g/m^2/yr$, which is not too different from the estimates of Day et al. (1973) and Hopkinson and Day (1977) of around 3000 $g/m^2/yr$; but in their studies 90 percent of this was plant

Table 29. Estimates of different components of the carbon budget of a Mississippi deltaic salt marsh community (g $C/m^2/yr$).

		Carbon flux	Technique	Reference
Input				
Gross community primary production		4,680	CO_2 flux	a
Net plant primary production (above and belowground)		3,670	" "	a
Aboveground emergents	793		Clip plot	b
	578		" "	c
	871		" "	d
	1,158		" "	
Mean		850	" "	Mean
Belowground production		2,820	Difference (3,670-850)	
output				
Community respiration		3,150	CO_2 flux	a
		3,081	Sed. oxygen flux & calc. plant resp.	f,g
Emergent plant respiration		1,010	CO_2 flux	a
		2,760	calculated from other studies	f,g
Consumers		2,140	CO_2 difference	a
		302 -3 16	Oxygen flux & calc. for large consumers	f,g
Leaching from live plants		140	Leaching studies	i
Methane production		5	Methane flux	h
Lost to deep sediments		265	Subsidence rate x sed. C content	j
Balance (export and unaccounted)				
Net community production		1,260	from CO,	a
		300	from organic balance	f,g
		300	from N balance	j
		150	from estuary export & bay P:R ratio	k

References:

a - Gosselink et al. 1977 and unpubl.
b - Kirby 1971
c - Kaswadji 1982
d - Hopkinson et al. 1978
e - White et al. 1978
f - Hopkinson and Day 1977
g - Day et al. 1973
h - Smith et al. 1982
i - Turner 1978
j - DeLaune and Patrick 1979
k - Happ et al. 1977

respiration (calculated from literature values). In the CO_2 flux studies, two-thirds is associated with the aufwuchs community and the sediments. The experimentally determined data for consumer respiration are 2,140 g/m^2/yr from CO_2 flux measurements and about 300 g/m^2/yr from O_2 flux. The CO_2 flux was determined with the marsh unflooded, the O_2 flux when the marsh surface was submerged. About 140 g/m^2/yr may be lost through leaching, 265 g/m^2/yr are lost to deep sediments, and another 5 g/m^2/yr are lost as methane.

Over the whole community the net balance unaccounted for (that is, the organic C available for export) is 1,120 g/m^2/yr. Export of all the aboveground production would not equal this. Hopkinson's estimate of about 330 g exported/m*/yr is also the balance left over when all other inputs and outputs are considered. It is a reasonable figure in that it matches the estimate of Happ et al. (1977). Furthermore, the N budget (see Nutrient Cycling), which is derived from different assumptions and measurements, also makes a value of about 330 g C reasonable, assuming that the exported N is all organic with a C:N ratio of 21.6 (Delaune et al. 1981).

The discrepancy between 300 and 1,120 g/m^2/yr is large. The best that can be said for the C balance in deltaic salt marshes at present is that there appears to be a large amount of organic production for which the fate is unknown. Part of it is certainly exported, but we do not know how much. Methodological differences certainly contribute to the uncertainty.

We know even less about C balances in zones other than the salt marsh. Burial of C in deep sediments does not vary much from salt to fresh marshes. However, as sulfate availability decreases, methane production increases. The annual loss of C as methane increases from 5 g/m^2 in salt marshes to 73 g/m^2 in brackish marshes and 160 g/m^2 in fresh marshes (Smith et al. 1982a).

On the other hand, because flushing energies are lower than in salt marshes one would expect waterborne organic export to decrease toward fresh areas. The brackish marsh, in particular, is very poorly understood. Its production is high, probably higher than the salt marsh. Because flushing energy is low, export is expected to be low also. This suggests that respiration must be very high, but decomposition studies (White et al. 1978) show slower loss rates than in salt marshes.

NUTRIENT CYCLES

In coastal marsh ecosystems, as in other types, organic productivity depends on the availability of inorganic nutrients in the right proportions at the right times. Growth limitation due to both nutrient limitation and toxicity can and probably do occur in marshes. However, of the 12 inorganic minerals known to be required by plants, only N appears to be regularly limiting to marsh plant growth.

Iron limitations have been reported (Adams 1963), but subsequent studies have not supported this observation (Haines and Dunn 1976). In fact Fe and Mn are much more likely to be in toxic concentrations in marsh soils because of their increased availability under anaerobic conditions. For example, Fe is found in marsh plant tissues in concentrations up to 1,800 ppm (Haines and Dunn 1976), which is well over 10 times the concentration in most agricultural crops.

Marshes are open systems, and the absorption and release of nutrients can have strong effects on adjacent waters. Marshes have been said to reduce eutrophication by removing nutrients from these water bodies and, conversely, to be a source of nutrients that supplements aquatic production. The evidence for Mississippi delta salt marshes is that they are sinks for all nutrients, that they absorb inorganic N and release part of it as reduced ammonia and organic forms, and that they export organic C. Ecologically the most important nutrients in the marsh are N, P, and S.

Nitrogen

Nitrogen, as mentioned earlier, has been found to limit growth in most marshes (see Mendelssohn et al. 1982). Nitrogen chemistry in anoxic soils is extremely complex and is made even more so by the proximity of aerobic and anaerobic layers in marsh sediments (Figure 63). In the aerobic layer, oxidation of ammonium to nitrate occurs. This is an extremely thin layer in most delta marshes because the rate of diffusion of oxygen into the flooded soil is not fast enough to supply the demand by the large microbial population. The nitrate can diffuse down into the anaerobic zone where it is reduced to nitrous oxide and nitrogen gas and lost from the marsh ecosystem.

Nitrate can also be reduced all the way to ammonium, and perhaps as much as 50 percent of it is reduced to this form under the environmental conditions of a delta salt marsh (Smith et al. 1982a). Either the oxidized nitrate or the reduced ammonium can be taken up by the emergent grasses, but free nitrate is present in only the thin aerobic layer. Undoubtedly, nearly all the N absorbed by the marsh plants is ammonium. The nitrification of ammonium and its subsequent denitrification to N_2 is facilitated by the vertical movement of the aerobic-anaerobic interface as the tide rises and falls. The ions do not even have to diffuse from one zone to another - the zones migrate to the ions.

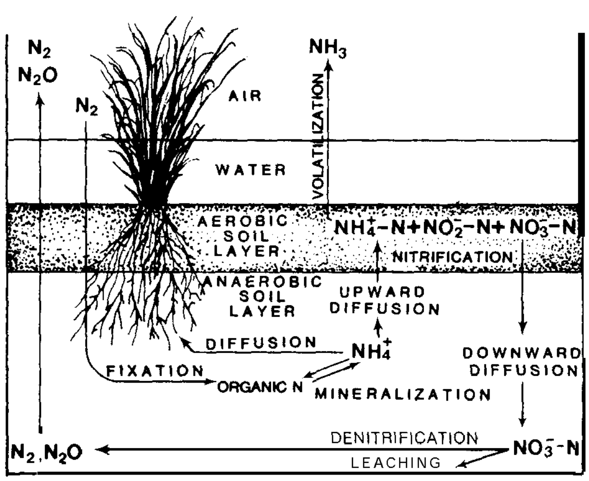


Figure 63. A schematic outline of the redox zones in a submerged soil showing some of the N transformations. The aerobic layer has been drawn thick for clarity. In reality, it is seldom over 1-2 mm in flooded marshes. (Patrick 1982. Copyright. Reprinted from "Nitrogen in Agricultural Soils," with permission of the American Society of Agronomy.)

Most of the N in the substrate is organic; mineralization (the decomposition of organic material and release of inorganic nutrients) of this material yields nearly all of the ammonium available for absorption and for nitrification (Patrick 1982). As much as 3.8 µg N/ml soil/week (inland) to 11.1 µg/ml/week (streamside) is mineralized under optimum conditions (Brannon 1973). This compares to a peak demand by S. alterniflora of about 2.1 µg/ml/week based on the maximinum growth rates determined by Kirby (1971). Kirby's estimate does not include root production so it is an underestimate, but the indication is that mineralization can provide nearly all the inorganic N that the plant takes up. Delaune and Patrick (1979) came to the same conclusion based on average annual rates.

It is likely, for two reasons, that plant uptake tracks mineralization closely during the active part of the growing season: (1) Nitrogen is limiting plant growth so the plants would be expected to take it up as it became available. (2) During the active growing season, sediment ammonium-N remains at a very low concentration of less than 1 µg/ml, increasing to higher levels of 6 - 7 µg/ml during October and November when the plant growth demand is much reduced (Brannon 1973).

Ammonium not taken up by plants is likely to be lost through denitrification. Vegetated marsh plots retained 93 - 94 percent of added labelled ammonium-N in the plant and soil, whereas in soil cores without plants only 56 percent of the labelled N was recovered (Table 30). However, denitrification and other gaseous losses of N are reported to be low in delta salt marshes, probably because plants absorb ammonium before it can be denitrified. Smith et al. (1982a) reported that only about 50 mg N/m^2/yr are released as N_2O, and estimated that about 5 g N/m^2/yr is released as N_2 through denitrification. Nitrogen fixation is also relatively minor. Casselinan et al. (1981) measured fixation rates of 15 and 4.5 g N/m^2/yr in a streamside and an inland marsh, respectively.

Table 30. Influence of Spartina alterniflora plants on recovery of ^{15}N-ammonium added over 18 weeks to soil cores (Buresh et al. 1982).

	Recovery of added N		
	Soil[a]	Aboveground tissue	Total
Soil core with plants	42±2.3	51±3.5	93±4
Bare soil core	56		56

[a]Includes belowground tissue.

The overall N budget for a salt marsh is summarized in Figure 64. There is a large reserve in the sediment. New N is introduced in particulate form in tidal water. DeLaune et al. (1981) estimated this source to be about 23 g/m^2/yr from the N concentration in sediment trapped in shallow pans set into the marsh, multiplied by the sedimentation rate determined from ^{137}Cs profiles. The deep sediments are a sink for N, because the marshes are subsiding. This loss, known quite accurately from ^{137}Cs profiles, is about 16 g/m^2/yr. Nitrogen export in surface water, the amount needed to balance the budget, is 14 g/m^2/yr. Presumably this is primarily bound up in organic form. Notice that there are no estimates of the flux of dissolved N in the water column. Nobody has made even a first order estimate of that.

Phosphorus

At first glance the P budget appears to be much less complex than the N budget.

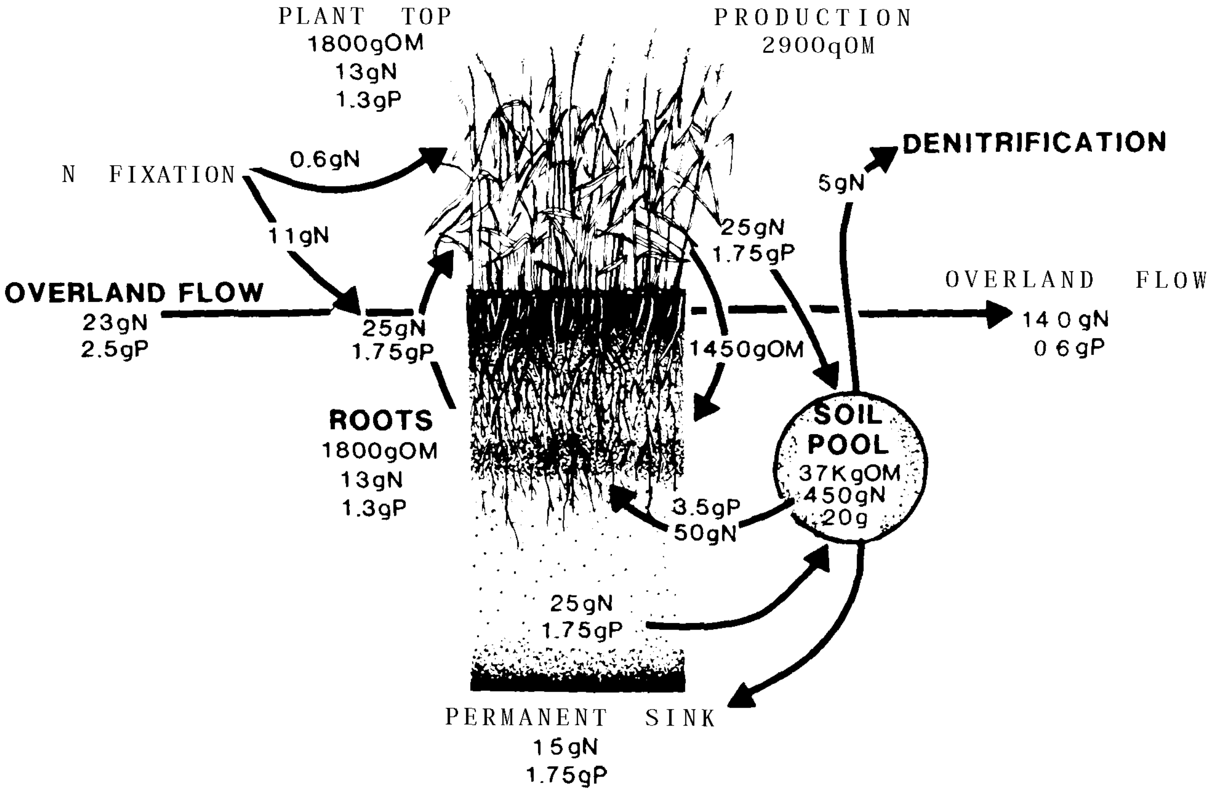


Figure 64. Nitrogen and phosphorus budgets for a Mississippi deltaic Salt marsh (adapted from DeLaune and Patrick 1979).

Phosphorus has no volatile forms, so sources and losses must occur through water flow across the marsh. Studies in Georgia salt marshes have shown that P accumulates in estuarine sediments, forming an enormous reservoir of many years supply (Pomeroy and Wiegert 1981).

In aerobic soils P rapidly becomes unavailable because it is tied up with Fe, Ca and aluminum (Al). But under anoxic conditions the ferric phosphates are reduced to the more soluble ferrous form, phosphate anions can exchange between clay and organic anions, sulfides can replace phosphate in ferric phosphates, and hydrolysis of phosphate compounds can occur.

The P budget for a delta salt marsh is presented in Figure 64. Extractable (and presumably available) P averages between 4 and 8 g/m^2 in the sediment over the year (Brannon 1973). Since the annual demand for P by the emergent plants is only about 2.6 g/m^2 there does not seem to be any lack of P for plant growth. About 2.3 g/m^2 is brought in with sediments, and 1.7 g/m^2 is lost to deep sediments. This leaves a balance of 0.6 g P/m^2 exported, again probably as organic P.

Sulfur

The S cycle is interesting not because S has been reported to limit plant growth in marshes, but because of its important role in energy transfer. This is a new and still not fully understood role. When oxygen and nitrate are depleted in flooded soils, sulfate can act as a terminal electron acceptor and is reduced to sulfide in the process. (This gives the marsh its characteristic rotten egg odor).

In anoxic salt marshes sulfate is a major electron acceptor. In fresh marshes where the supply of sulfate is limited, C is reduced to methane instead. The sulfide radical is a form of stored energy that can be tapped by S bacteria in the presence of oxygen or other oxidants (Howarth et al. 1983).

In a northeast Atlantic coast marsh the energy flow through reduced inorganic S compounds was equivalent to 70 percent of the net belowground primary productivity of the dominant grasses. Apparently most of the stored sulfides are reoxidized annually, by oxygen diffusing into the substrate from the marsh grass roots (Howarth and Teal 1979), but there is a possibility of soluble sulfides being flushed from the marsh to become a source of biological energy elsewhere. In the marsh cited above, Howarth et al. (1983) estimated that 2.5 to 5.3 moles of reduced $S/m^2/yr$ are exported by pore water exchange with adjacent creeks. This amounts to about 3 - 7 percent of the S reduced in the sediment, and as much as 20 - 40 percent of net aboveground production.

No one has investigated whether the export of reduced S compounds is significant in Mississippi delta marshes. Brannon (1973) measured the total S content of salt marsh sediments (Figure 49) and found the same kind of seasonal variation reported by Howarth et al. (1983). A crude estimate of the amount of reduced S lost to deep sediments by marsh subsidence shows it to be in the neighborhood of 1 g (0.3 mol)$/m^2/yr$. This is about the same amount of S deposited by precipitation in southeastern forests (Swank et al. 1984). We have no idea of the reduced S flux from the marsh.

STORMS

The role of severe storms on marshes has received little attention, mostly because their occurrence is unpredictable and their immediate effects difficult to document. Storms occur with remarkable frequency on the delta plain. A 1.5-m wind tide occurs about every 8 years. (Figure 12), and smaller storms are annual events. Yost of the sediment is deposited in the coastal marshes during these high water periods or during winter storms (Figure 32).

Day et al. (1977) reported that Hurricane Carmen in 1974 defoliated swamp forests in its path two months earlier than normal leaf fall. A large amount of organic C, N, and P was flushed from the swamp to the fresh, brackish, and salt marshes of the lower estuary by the accompanying torrential rains. Part of this material undoubtedly resulted from the early defoliation, but visual evidence pointed to thorough flushing of stored detritus from the swamp floor which would not wash out under notmal weather conditions.

On the other hand, a survey of salt marsh biomass in the Barataria and Terrebonne basins in progress at the time of the same hurricane (Gosselink et al. 1977) showed no evidence that dead biomass collected from the marsh surface was any different in plots sampled before the hurricane than after.

Short-term effects of Hurricane Camille on species composition in fresh and brackish marshes near the mouth of the Mississippi River were described by Chabreck and Palmisano (1973). They found that an increase in salinity caused by the hurricane tide was ephemeral. The major effect seemed to be widespread destruction of vegetation, especially woody species, by wind and water which uprooted and ripped apart stands of plants. Recovery of most species was rapid so that prehurricane levels of abundance were approached within a year. In the small lakes and ponds, however, the submerged and floating vegetation was slow to recover.

Probably the most dramatic alteration documented in marshes is that described by Valentine (1977) in the chenier plain of southwestern Louisiana. One hundred sixty thousand ha of Cladium jamaicense (sawgrass) were killed by the saline tide of Hurricane Audrey "in 1957. The following year 86 percent of this area was open water. During the drought years of the early 60's annual grasses and sedges became abundant. By 1972 Sagittaria falcata (bulltongue) occupied 74 percent of the area and Nymphaea odorata (white water-lily) 11 percent. C. jamaicense never reestablished itself in any extensive areas, oerhaps because seed viability was very low. Secondary effects of these vegetation changes on duck feeding habits were dramatic. Prior to 1959 C. jamaicense seeds were an important component of duck diets. In the years immediately following the hurricane, duck stomachs contained primarily rice seeds, indicating heavy dependence on agricultural areas outside the marshes. During succeeding drought years, when the marshes produced large quantities of annual grass seeds, large numbers of both ducks and geese were attracted to these habitats. It seems likely, therefore, that hurricanes are major forces on gulf coast marshes, initiating changes that can have significant consequences for years following the storm.

CHAPTER FOUR
THE MARSH IN THE COASTAL BASIN

Marshes are open ecosystems; that is, they are not isolated islands out of touch with their surroundings. Quite the contrary, the main reason that they are of particular interest to environmentalists and conservationists is because they are strongly coupled with surrounding ecosystems. In Chapter 2 we say that the main physical driving forces for marshes are the upstream river and the downstream ocean. Both are outside the marsh, but the annual variation in river flow, the periodic switching of its channel and thereby its nutrients and sediment, and the periodic variation in the gulf water level and salinity all determine the character of the marsh. Similarly, marshes are open biotically - they contribute biologically to many other ecosystems. Figure 65 illustrates these couplings with other ecosystems: marsh zone to marsh zone; marsh to estuary; marsh/estuary to gulf, river and adjacent uplands; and intercontinental couplings.

COUPLINGS AMONG ECOSYSTEMS

Intra-Basin Couplings

The coastal basin can be viewed as a set of coupled subsystems, for indeed the marshes, bays and streams in the basin are tightly coupled. A typical basin is organized by the internal freshwater-salt

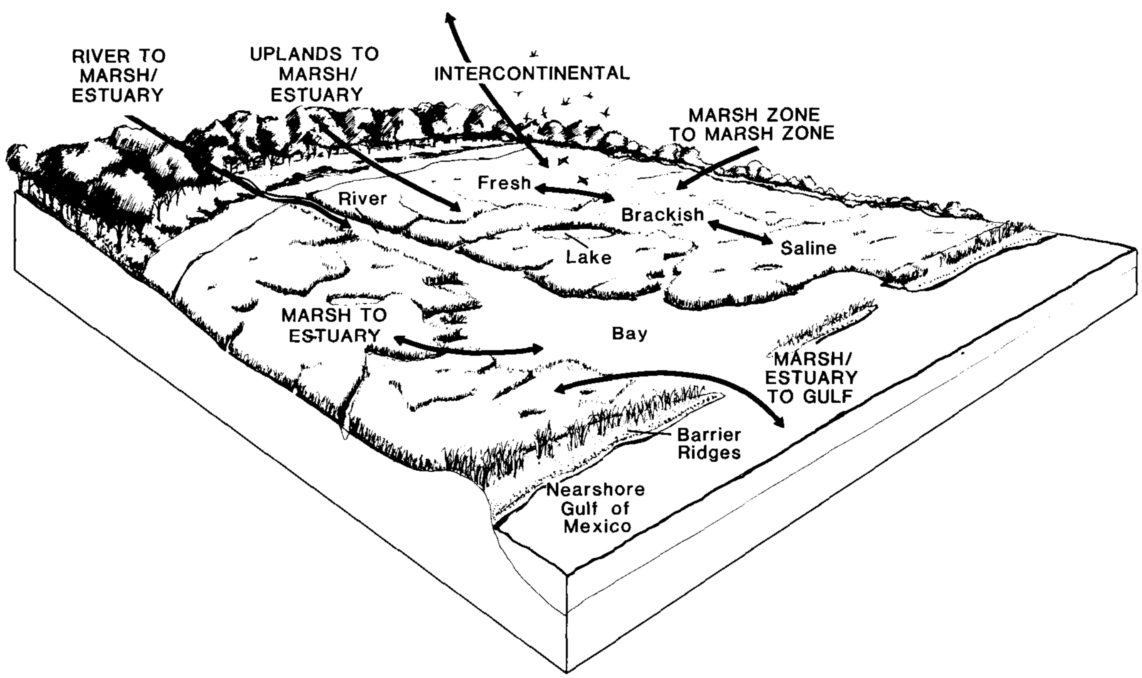


Figure 65. Conceptual diagram illustrating the coupling of delta marshes to other ecosystems.

water gradient. We take the organization for granted, but brackish areas are always between fresh and salt areas. The marshes next to the uplands are usually fresher than marshes in the interior of the basin because they receive rain runoff; salt marshes are more naturally dissected by channels than fresh marshes because they receive stronger tidal energy, and so forth.

Similarly, biotic assemblages are organized along these gradients. We have seen that one of the chief consumer groups in the marsh, the waterfowl, partitions itself within the different marsh zones according to the tolerance of individual species for salt and preference for available foods, marsh ponds, and water depths. But these preferences are only average ones. On any single aerial bird census, individual flocks may be found in fresh marsh or in salt marsh. They move freely among the different marsh zones, taking advantage of favorably changing conditions. The increased waterfowl density when marshes changed from sawgrass to annuals, mentioned in the previous chapter, is an example of the mobility of the fauna among marsh zones. The possible displacement of muskrats toward saline marshes by the invading nutria is another.

Nektonic organisms provide particularly good examples of the use of multiple subsystems within the coastal basin (Figure 66). Many year-round residents of the estuary are euryhaline and move freely throughout the basin. Such species as the bay anchovy, mullet, alligator gar, rainwater killifish, and tidewater silverside are found from salt to freshwater, many of them in the small creeks that border the marshes. Others, like the threadfin shad, the blue and channel catfish, and the river shrimp move down basin during the fall and winter as brackish areas freshen. The marine-spawned croaker, menhaden, and blue crab use the whole estuary as a nursery area, penetrating all the way through salt and brackish zones to fresh marshes in their migrations.

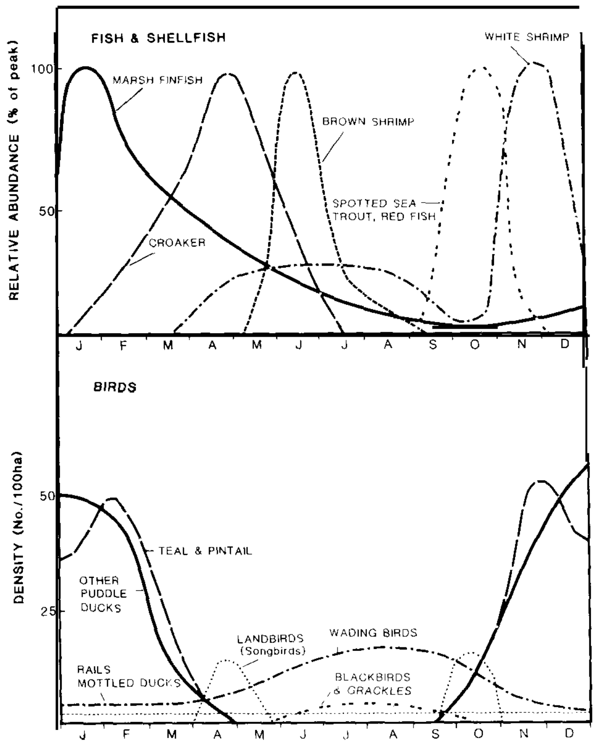


Figure 66. Patterns of estuarine use by nektonic organisms and waterfowl in the Barataria basin, LA (Chambers 1980).

Extra-Basin Couplings

The marine-spawned, estuarine-dependent fish and shellfish mentioned above are, from an economic point of view, the most important group of consumers that frequent the coastal marshes. Typically they spawn on the continental shelf, move into estuaries as juveniles, and return to the Gulf of Mexico as adults to continue the cycle. Nearly all the commercially important nektonic species on the gulf coast are estuarine-dependent (Gunter 1967). Within the estuary marsh habitat is crucial for these species. For example, Turner (1977) showed that both along the gulf coast and worldwide, the commercial shrimp harvest is directly related to the marsh area in the inshore nursery. The relationship is to the total marsh area - not just salt marsh; the relationship of yield to the inshore open water area is poor.

The brown shrimp life cycle is typical for these estuarine-dependent species (Figure 67). Early in their juvenile stage they can be found deep in the marsh in small bayous and ponds. As they increase in size,they move slowly out into

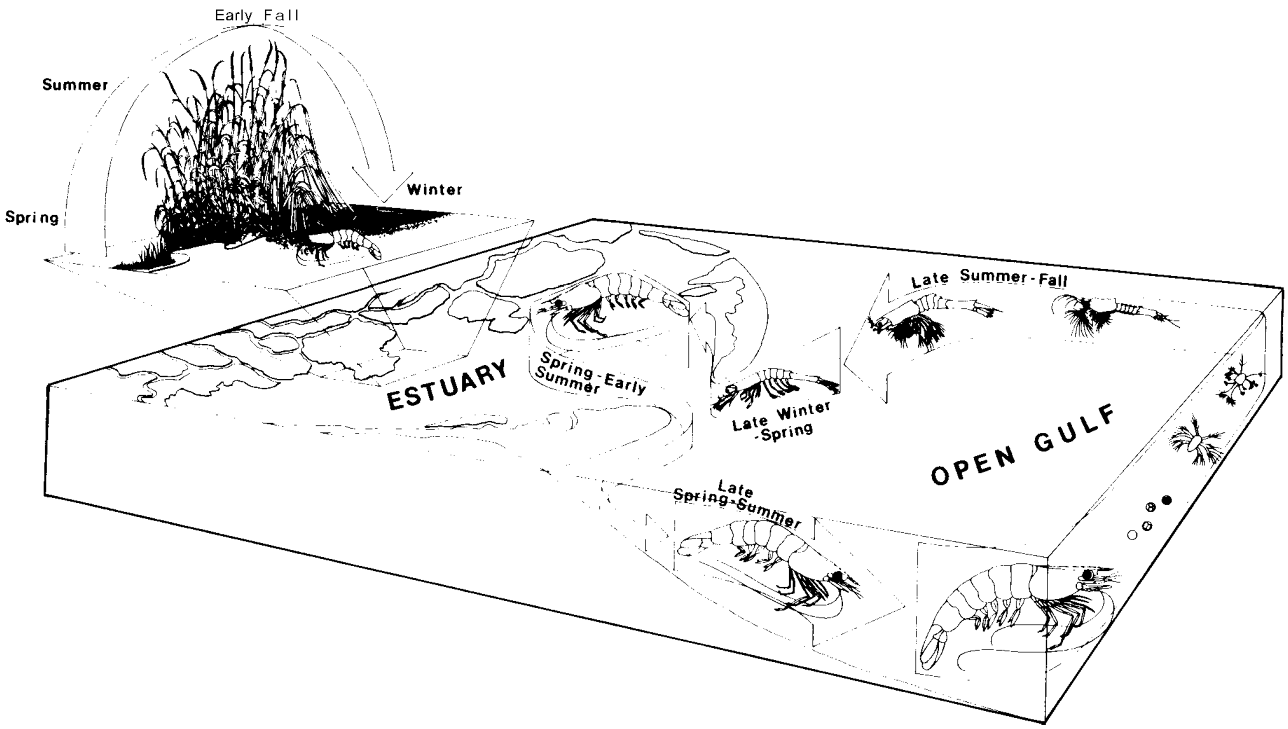


Figure 67. The life cycle of the brown shrimp (Gosselink 1980).

larger, deeper water bodies which they appear to use as "staging areas" for emigration. These emigrations occur primarily at night and are keyed to the phase of the lunar tidal cycle, with greatest movement duriny periods of highest tides (Blackmon 1974).

In the Mississippi Delta there appear to be no fish species that spawn in fresh water and move to the ocean as they mature. But in other locations these species make extensive use of the marshes through which they pass on these migrations.

A different kind of migratory use of marshes is that of numerous bird species which move daily in and out of the marshes to feed. Wading birds, for example, may nest in adjacent upland areas and along beach rims but feed along the marsh edges and in marsh ponds during the day. Their daily travels may cover many miles. One member of this group, the white ibis, has been reported to travel as much as 80 km from its nesting site to feed (Lowery 1960). In a similar vein,Tamasier (1976) found wintering green-winged teal and pintail resting during the day on large, shallow ponds. The birds then spread out to forage elsewhere at night. Deer and other mammals may also venture out into marshes to forage from upland resting areas (Schitoskey and Linder 1979).

Intercontinental Couplings

The most dramatic inter-ecosystem couplings are those of the migratory birds that link Canadian and Alaskan pothole wetlands to gulf coast marshes. The Mississippi delta wetlands are at the southern extreme of the major duck and goose migration corridors (Figure 68). Many songbird species winter further south and are found moving through the delta marshes only during fall and spring migrations. As mentioned earlier,we have very poor information about the importance of winter-habitat quality of birds that nest in the far north, but all indications are that it is extremely important for nesting success.

TEMPORAL USE OF MARSHES

It is interesting to observe how different migrating species use coastal wetlands at different times. (Figure 69).

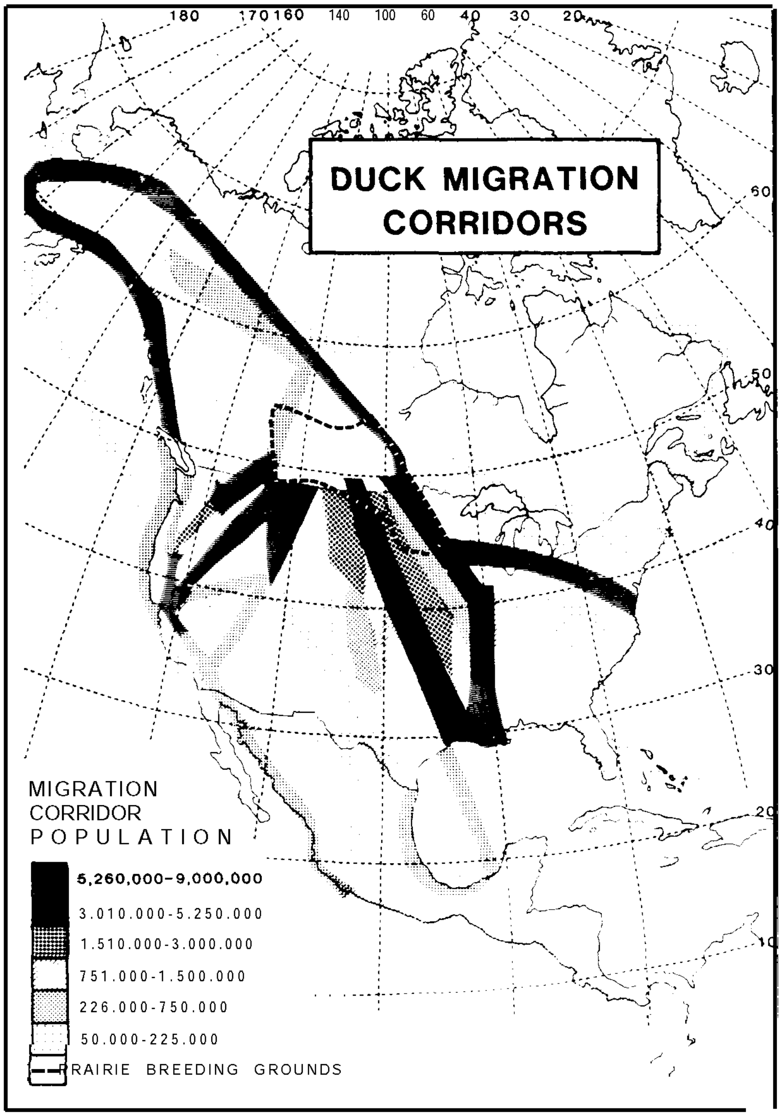


Figure 68. Major duck migration corridors to gulf coast marshes (Bellrose 1980).

Bird populations are largest during the winter when ducks and geese are abundant. It is misleading to group all these species, however, as some migrate on through to South America, as shown for the pintail and teals. These two species reach peak abundance late in the year and again in the spring, apparently because a large proportion of the population moves south across the gulf in mid-winter.

Wading bird densities in the marsh peak during the summer. Although they are year-round residents, they appear to be much more active in marshy areas during the summer (Mabie 1976). About 60 species of land birds, mostly songbirds, migrate through the delta to South America each year. They do not use the marsh extensively, but usually fly over it. However, during northward spring migrations they frequently encounter strong head winds and take refuge on the first landing sites, the cheniers and slightly elevated marsh ridges. During these occasions their densities can be very high, and the marshes can be important for their survival. Some of these songbirds, like the red-winged blackbird and the great-tailed grackle, nest in the coastal marshes in

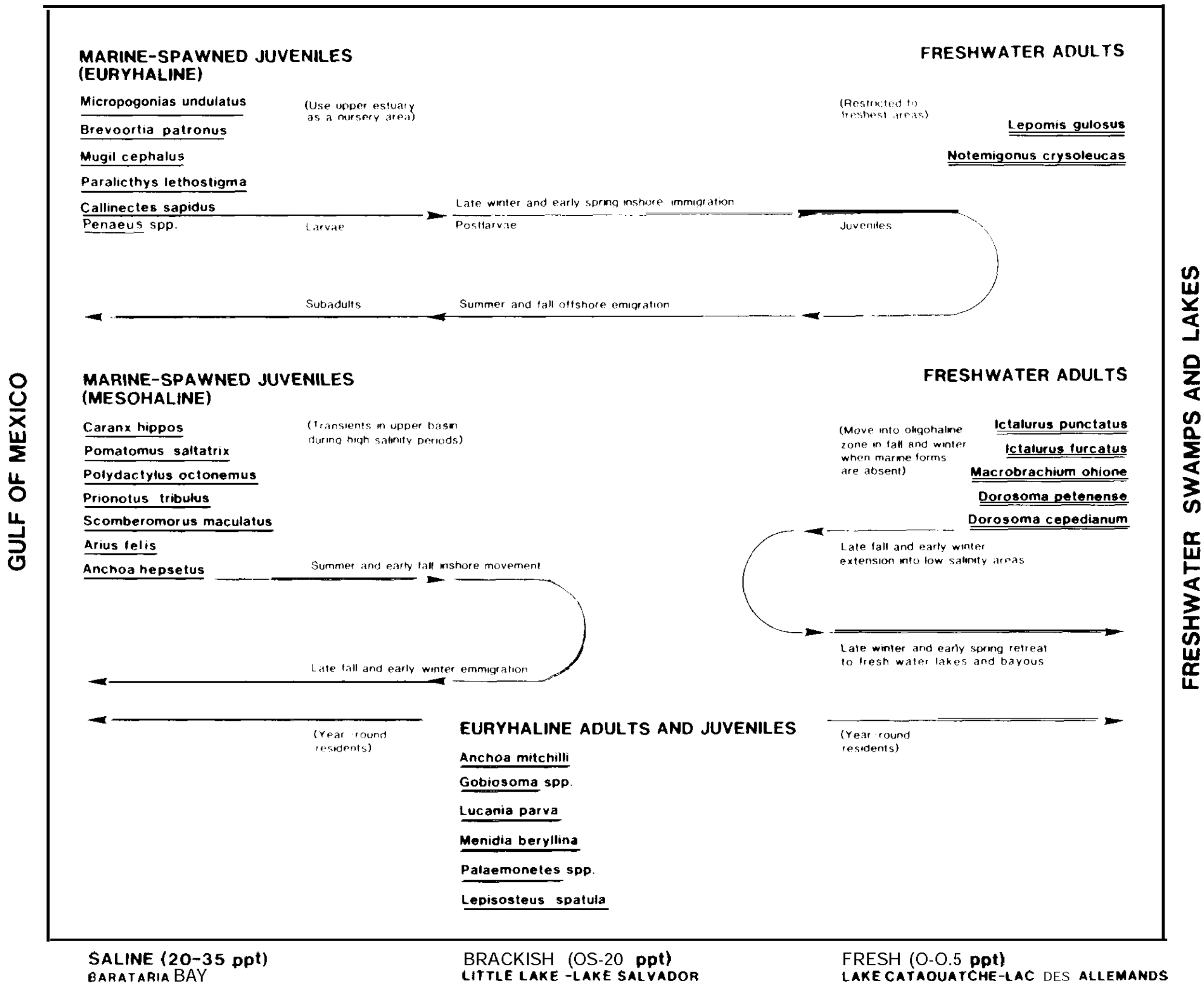


Figure 69. Seasonal use of wetlands by migratory birds, shellfish, and fish.

large numbers. They disappear during the winter when they migrate south.

Similarly, nektonic species appear to partition the marsh ponds and creeks seasonally. The most abundant commercial species peak in May and June (brown shrimp), October to December (white shrimp), and March to May (croaker and menhaden). The top carnivores, spotted seatrout and red drum, reach greatest densities in September and October. Up in the shallow marsh ponds, the year-round residents peak in early spring (Ruebsamen 1972). The hot months of July and August seem to be the periods of least activity in the marsh, perhaps because many species move into deeper, cooler bay waters during that time.

The migratory habits of the many species that inhabit the delta marshes emphasize the importance of management objectives that take into account the high degree of coupling of the marsh with other ecosystems. Marshes cannot be managed in isolation.

CHAPTER FIVE
WETLAND VALUES, HUMAN IMPACTS, AND MANAGEMENT

The term "value" imposes an anthropocentric orientation on the discussion of marshes. The term can be used in an ecological sense to refer to functional processes, for example, when we speak of the "value" of primary production in providing the food energy thdt drives the ecosystem or the "value" of a predator in controlling the size of herbivore populations. But it is important to distinguish this use of the term from its ordinary use which refers to the services wetlands perform for man.

The reasons that wetlands are legally protected have to do with their value to society, not with any abstruse ecological processes that proceed therein; this is the sense in which "value" is used in this chapter. These perceived values arise out of the functional ecological processes described in the previous chapters, but are determined also by the location of a particular marsh, the human population pressures on it, and the extent of the resource.

The extent of the marsh, in particular, has been one factor that has lowered the value of gulf coast marshes in human eyes. There is so much marsh that losing a few acres for any specific project has not been seen to be of much consequence. In this chapter I will first review the services natural wetland systems provide for society, then discuss the problems of trying to compare the values of natural ecosystems with more conventional economic systems. Finally, I will outline what appear to me to be the major management issues in Mississippi delta marshes.

WETLAND VALUES

Wetland Harvest

The easiest wetland value to discuss and quantify is the harvest of animals thdt depend on it. Aside from the important fur animals, most commercially important species associated with wetlands are migratory, requiring habitats in addition to marsh to complete their life cycles. This group includes all commercially important fish and shellfish, recreational fish species, and hunted waterfowl. Qualitatively, it is clear that delta marshes are important habitats for these species, and the completion of their normal life cycles depends on the marshes.

This dependence has been the rationale for imputing the whole economic value of the harvest to the marsh, although this is not without problems from an economist's point of view. The Louisiana coast fishery harvest is the largest in poundage in the country, and the wild fur harvest is also without equal. Sport fishing dnd recreational hunting generate comparable revenues, The per acre dollar value of these harvests has been determined by a number of individuals. The figures in Table 31 for the Barataria basin are representative. Cited values usually range from $50 to $200/ha/yr, depending on the geographic area and the assumptions made. Other measures of wetland value for harvested species would be the weight of harvested animals or the number of hides and carcasses. These measures would not be subject to year-to-year variability in prices, but from an economic point of view they are not much good for comparison to other commodities.

Table 31. The estimated economic value of harvests from the Barataria basin, Louisiana (Mumphrey et al. 1978).

Activity	Annual return	Present value[a]
	($/acre)	($)
Commercial fishing	286.36	5,540
Noncommercial fishing	3.19	46
Commercial trapping	11.69	170
Recreation		
Economic impact of recreation expenditures	60.08	874
Economic value of user-benefits	104.33	2,428
Total	$465.65	$9,058

[a] Capitalized value for indicated annual return.

Environmental Quality

Another set of values society receives from wetlands can be grouped under the heading of environmental quality. This includes a number of ecological functions of coastal wetlands that contribute to the improvement of water and air quality taken in the broadest sense. Much has been made of the ability of wetlands to remove organic and inorganic nutrients and toxic materials from the water that flows across them. In the delta, Meo et al.(1975) found that fresh marshes effectively removed nearly all the organic material and most of the nutrients from a menhaden processing plant's effluent when that effluent was allowed to filter throuqh the marsh. There have been similar reports of efficient waste-water treatment from a number of other studies elsewhere (Bastian and Reed 1979; Kadlec 1979; Kadlec and Kadlec 1979). Nevertheless, these reports can not be taken uncritically. Most studies have been short term, and there is a persisting question of what happens if and when the system becomes saturated with the pollutant. The answer depends on the circumstances. In some systems the pollutants begin to appear in the outflow. Other marshes have been used for 20 - 50 years and still seem to function effectively.

Where environmental circumstances are appropriate, nitrogen may be denitrified and lost to the air. But other pollutants such as heavy metals and phosphorus must accumulate or be washed out. There have been no long-term studies in the Mississippi delta, but the capacity for permanent storage of nutrients in these marshes is unusually high because of the rapid subsidence rate. Craig et al. (1977) showed that the upper part of the Barataria basin was heavily polluted, but that water quality rapidly improved downstream. This improvement would not have occurred if the marshes and streams were unable to "remove" the pollutants from the water. In spite of this cleansing capacity, the delta marshes are not used explicitly, with one or two minor exceptions. for water quality improvement.

Marshes function in the maintenance of water and air quality on a much broader scale. Nitrogen and S are good examples. The natural supply of ecologically useful N comes from the fixation of atmospheric nitrogen gas (N_2) by a small group of plants and microorganisms that can convert it into organic form. Today the production of ammonia from N_2 for fertilizers is about equal to all natural fixation (Delwiche 1970). Wetlands may be important in returning part of this "excess" N to the atmosphere through denitrification. The close proximity of an aerobic and a reducing environment, such as the marsh surface, is ideal for denitrification as discussed in Chapter 3. The denitrification rate seems to increase with the nitrate supply (Reddy et al. 1980; Engler et al. 1976). Because coastal wetlands are the downstream receivers of fertilizer-enriched river runoff and are ideal environments for denitrification,it is likely that they are important in the world's fixed N balance.

Sulfur is another element whose cycle has been modified by man. The atmospheric sulfate load has been greatly increased by fossil fuel burning. When sulfates are washed out of the atmosphere by rain they acidify oligotrophic lakes and streams. tiowever, when washed into marshes, the intensely reducing environment of the sediment reduces them to sulfides which form insoluble complexes with phosphate and metal ions. In salt marshes this effect is masked hy the abundance of sulfate in seawater, so perhaps sulfide accumulation in freshwater wetlands is a better index of atmospheric input. In delta fresh marshes about 20 mg $S/m^2/yr$ as sulfide is sequestered in deep sediments (Hatton 1981). This is more or less permanently removed from circulation in the S cycle.

Marshes are also valuable because they act as giant water reservoirs during floods. The vegetation may provide some resistance to the flow of water, slowing it down and thus protecting inland areas, but most of the benefit is probably its storage capacity. This is best seen on rivers where large riparian areas store storm waters and decrease the river stage downstream, reducing flood damage.

On the Charles River inllassachusetts, this role was deemed effective enough by the U.S. Army Engineers that they purchased the river flood plain rather than build expensive flood-control structures to protect Boston (U.S. Army Engineers 1972). The broad, coastal expanse of the Mississippi Delta acts more as a storm buffer. Its value has to be seen in the context of marsh conservation VS. development. The full fury of a coastal storm hits the barrier islands and marshes first and it attenuated as it crosses them, damaging little property of societal value. Buildings and other structures in this coastal zone are vulnerable to the same storms, and damage is often high. Inevitably the public pays much of the cost of this damage through taxes for relief, rebuilding public services such as road:; and utilities, and federally guaranteed nsurance.

Esthetics

A very real but difficult aspect of the marsh to capture is its esthetic value, often hidden under the dry term "nonconsumptive use values", which simply means that people enjoy being out in marshes. The Mississippi delta marshes are a rich source of information on our cultural heritage. The remains of prehistoric Indian villages, mounds of shells or middens, have contributed to our understanding of both their culture and the physical yeography of the delta (McIntire 1959).

Smardon (1979) described wetlands as visually and educationally rich environments because of their ecological interest and diversity. Their complexity makes wetlands excellent sites for research. Many artists have been drawn to them, notably the Georgia poet Sidney Lanier, the painters John Constable and John Singer Sargent, the Louisiana photographer Clyde Lockwood, and many other artists of lesser public recognition. Each year thousands of these artists paint and photograph marshes. I suspect that many wetland visitors use hunting and fishing only as excuses to experience its wildness and solitude, expressing that frontier pioneering instinct that may lurk in us all.

Conflicting Values

With this long list of marsh values one might expect marsh conservation to be an issue that everyone would support. This is not so, and the reason is simple. The private owner of a marsh tract benefits financially from very few of these services. In Louisiana land can be leased to trappers and hunters for perhaps $25/ha/yr (Chabreck, LSU School of Forestry and Wildlife Management; pers. comm.). The owner has no monopoly on, and cannot sell, the fishery resources and the improved air and water quality associated with the marshes.

To the owner the wetland is valuable primarily for development - drainage for construction or agriculture, or dredging and drilling for subsurface mineral resources - that can bring in thousands of dollars per hectare annually. This conflict between private ownership and public services is becoming more intense everywhere as population density increases, but it is particularly impassioned in wetlands for several reasons. First, population density and development pressure are particularly high on coasts; second, marshes are open systems that cannot be considered in isolation; and third, marsh development is essentially irreversible.

Recognizing the value of wetlands and educating the public and public officials to these values are important milestones that have led to legislation (particularly Section 404 of the Clean Water Act of 1977) protecting marshes from unconsidered modification. Wetland management did not begin with this legislation, but certainly the Clean Water Act has focused attention on many wetland issues. Some of these issues, particularly those that relate directly to Mississippi delta marshes, will be discussed in the rest of this chapter.

WETLAND EVALUATION

One important component of wetland management is the evaluation of proposed actions in wetlands. Under Section 404 of the Clean Water Act of 1977 a permit is required for wetland activities that might affect water quality. For activities that require an environmental impact statement (as required by the National Environmental Policy Act) two different kinds of evaluation are involved. First, the ecological value of the area in question is determined - that is, the quality of the site as compared to other similar sites or its suitability for supporting wildlife. Second, the ecological value of the habitat is compared to the economic value of some proposed activity that would destroy or modify the habitat - in other words, a benefit:cost analysis. Both procedures are fraught with difficulties. Both require an evaluation of the relative values of different commodities, like comparing apples and oranges. Above all,both require numerous value judgments about what is ecologically desirable.

Essentially all procedures now in use assess the relative value of wildlife habitat. Lonard et al. (1981) evaluated '20 different wetland valuation systems. The emphasis in all of them was overwhelmingly on the evaluation of the ecological habitat function of wetlands. Hydrology functions are poorly documeted and difficult to quantify. Evaluation of silviculture, heritage, and recreation functions are also considered open for improvement (Lonard et al. 1981).

Probably the most used instruments for ecological evaluations in general are the U.S. Fish and Wildlife Service Habitat Evaluation Procedures (HEP, USFWS 1980) and the U. S. Army Engineers Habitat Evaluation System (HES, USAE 1980). Both 'were developed for upland sites. HES has not been adapted for wetlands, and HEP wetland applications are still evolving. These procedures are most valuable when used to compare two different areas or to compare an area before modification to the expected state afterward.

The HEP procedure, probably the more detailed, illustrates both the potential and the problems of evaluation. In this procedure the suitability of a site is evaluted for a number of different game species, commercially important species, and species of special interest for ecosystem structure or function. For each species, habitat suitability is evaluated on a scale of 0 - 1.0 for a number of habitat characteristics. These Habitat Suitability Indices (HSI's) are multiplied by the area of each species' habitat under consideration to yield Habitat Units (HU's). Thus both habitat quality and area are combined in one number. Schamberger et al. (1979) listed the assumptions of the system: (1) habitat value can be quantified; (2) habitat suitability for a species of concern can be evaluated from habitat characteristics; (3) overall habitat value can be determined by assessing suitability for selected species; (4) habitat quantity and quality are directly related to animal numbers. It is apparent that the community HSI's depend on the species selected for evaluation.

The result of the HEP analysis is a set of HU's for individual species for the site or sites in question. The HU's can be compared within a site or among sites for determining best management scenarios. The values can be used to help make a management decision about the site, as for instance, offsetting project impacts through mitigation. In this case, sites with equal value in terms of HU's are created or set aside for use by the species in question.

This or any other evaluation system must play off bewildering detail against simplifying integrations to facilitate the decisionmaking process. The evaluator must integrate mentally the information about a number of different individual species in order to make the decision. The ideal solution is a compromise between extremes - simple enough to allow a decision to be made, but detailed enough for the decisionmaker to feel confident about it.

All procedures developed to make decisions about wetlands are based on human values and human judgments about what is good and what is not. They reflect what humans think is important, and that fact is a basic ingredient in all management. In the case of HEP, the procedures have been standardized, individuals can be trained and certified to carry them out, and reproducibility is quite good. These facts often make us forget the value-laden nature of the whole enterprise.

When habitat values are monetized for benefit:cost analyses, a whole new set of assumptions are superimposed on the ecological evaluation. I do not intend to discuss these because they are well covered by several other authors (Shabman and Ratie 1979; McAllister 1982). The methodology has evolve3 From economic theory that assumes that in a free economy the market price reflects the value of a commodity (the willingness-to-pay approach).

This leads to real problems in monetizing nonmarket commodities like pure water and air, and in pricing marshes whose monetary value in the marketplace is determined by their value as real estate, not their "free services" to society. Consequently, attempts to monetize marsh values have generally emphasized the commercial "crops" from marshes - fish, shellfish, furs, and recreational fishing and hunting for which pricing methodologies are available. As Odum (1979) pointed out, this kind of pricing ignores ecosystem-level values related to hydrology and productivity, and global values related to clean air dnd water and other "life support" functions.

One controversial approach uses the idea that energy flow through an ecosystem or the similar concept "embodied energy" (the total energy required to produce the commodity, Costanza 1980) is a valid index of the totality of ecosystem functions; and that furthermore, this index is applicable to human systems as well. Thus natural and human systems can he evaluated on the basis of one common currency: "embodied energy." (Since there is a linear relationship between embodied energy and dollars, that more familiar currency can also be used.)

The general response to this kind of approach is probably fairly summed up by Reppert and Sigleo (1979): "Certain aspects of the evaluation structure .... are too theoretical and unsubstantiated to be considered for general application, particularly those involving the analysis of energy flows and the conversion of energy values to monetary values." However, in recent years both the theoretical base and the methodology have been much improved.

Using better assumptions, Costanza (1983) showed that the economist's willingness-to-pay approach and energy analysis converge to a surprising degree. In Table 32 the average gross benefits arrived at by summing the gross economic value of different marsh resources ($342/acre/yr) are roughly equivalent to the latest value arrived at from the embodied energy of biological productivity ($300/acre/yr). This convergence suggests an integrated methodological framework for evaluation. The approach has the real merit of being equally applicable to both natural and human systems, hut like every other approach it simplifies by converting everything into one currency.

Since the purpose of the exercise is to compare apples to oranges or oil wells to marshes, some kind of equivalence must be established, hut it seems to me dangerous to lose sight of the real

Table 32. Estimates of the economic value of Louisiana's coastal wetlands comparing willingness-to-pay approaches with energy analysis approaches (Costanza 1983).

Approach	Shadow value*	Reference
	(1979 $/acre/yr)	
Willingness-to-pay approaches		
Consumer surplus	155	a
Gross benefits	241	b
	352	c
	544	a
	231	a
Average of gross benefits	342	
Net benefits	237	d
Replacement value	25,662	b
	3,120	d
Energy Analysis approaches		
Biological productivity	7,374	b
	300	d

*Price that would prevail in a perfect market.

References:

a - Mumphrey et al. 1978
b - Gosselink et al. 1974
c - Vora 1974
d - Costanza 1983

structures involved. One compromise has been suggested by Lichfield et al. (1975), who used a planning balance sheet to list the major commodities exchanged and to identify the recipients of the cost and the benefits. This procedure ensures that the important factors in the benefit:cost analysis are explicitly recognized rather than being lumped into a single dollar value.

WETLAND MANAGEMENT

In the Mississippi River Deltaic Plain the major wetland management issues are marsh loss, salt intrusion, and the maintenance of habitat and water quality. These are interrelated problems. They are affected by a number of human activities, but the major ones can be grouped as either development or conservation-oriented (Table 33). I will discuss briefly each major issue or problem, bringing in the role of the various human activities as they apply. Since habitat loss (marsh loss) is by far the most pressing problem, it will receive the major emphasis.

Marsh Loss and Salt Intrusion

As discussed in Chapter 1 (Figure 23), the rate of marsh loss to open water has been accelerating over the past 50 years to the present rate of about 1.5 percent of the delta marshes being lost annually. Although the circumstances leading to this loss are complex and involve natural processes beyond human control, there is good evidence that a significant part of the problem is a result of human modification of the Mississippi River and the deltaic plain. This discussion will be limited to these latter factors, that is, those which man can hope to manage on a regional scale.

All the development activites listed in Table 33 contribute to marsh loss. Reclamation does so because it impounds and drains wetlands, essentially turning them into upland habitat. Although marsh "reclamation" is still occurring, the pace of development is much slower than it was early in this century (Gosselink et al. 1979), and the cost of impounding, draining and maintaining an area is becoming so prohibitive that economics

Table 33. Major wetland issues and human impacts in Mississippi delta wetlands.

		ENVIRONMENTAL ISSUES			
		MARSH AREA DEGRADATION	MARSH WATER QUALITY	SALT INTRUSION	HABITAT QUALITY
DEVELOPMENT	MINERAL EXTRACTION	=	–	–	–
	FLOOD CONTROL	–	+ ?	–	–
	NAVIGATION	–	–	=	–
	RECLAMATION	–	0		–
CONSERVATION	HABITAT PROTECTION & ENHANCING	?	0 +	+	
	HABITAT CREATION	+	?	+	+

dictates against this practice for most purposes.

The impact of mineral extraction, flood control, and navigation on marsh loss occurs primarily through the canals dredyed for these operations. Table 34 lists the major ecological effects of canals in the deltaic marshes, the kinds of mechanisms that should minimize these ecological impacts, and the specific management practices that are being used or could be used to implement these mechanisms. Because good experimental evidence is often lacking, many of the effects and mitigation procedures are inferred. I will document those statements that can be documented. Rut many are merely reasonable extrapolations from what is known.

Canals alter marshes by accelerating salt intrusion, changing hydrology, and affecting benthic and aquatic organisms. Salt intrusion is closely tied to changes in hydrology. It occurs when deep, straight channels connect low-salinity areas to high-salinity zones. Large navigation channels that link the marshes directly to the gulf are particularly efficient in allowing salt intrusion (Gosselink et al. 1979), but a channel from a saline bay into a less sdline marsh also allows salt intrusion.

Salt intrusion into fresh and intermediate marshes stresses the vegetation. We do not know exactly how the fairly subtle changes in salinity operate, but the result is often death of the plants and, as the roots die, loss of their peat-binding capacity. If the salinity changes so rapidly that the plants are not replaced immediately by more salt-tolerant species, often the underlying peat rapidly erodes and large, shallow lakes appear (Dozier 1933). These changes are linked to biochemical and microbial changes in the peat associated with salt intrusion (Dozier 1933).

Canals also change hydrologic patterns that modify a marsh independently of any salt effect. Straight, deep canals in shallow bays, lakes, and marshes capture flow, depriving the natural channels of water (L. Gosselink 1954; Turner, pers. comm.). Canals are hydrologically efficient, allowing more rapid runoff of fresh water than the normal sinuous channels. As a result, water levels fluctuate more rapidly than in unmodified marshes, and minimum levels are lowered (Light 1976). Sheet flow of water across the marsh surface is reduced by the spoil banks that almost always line a canal. Consequently,the sediment supply to the marsh is reduced, and the water on the marsh is more likely to stagnate than when freely flooded.

Since canals change the marsh water budget, the salt budget, and the sediment supply, any mechanisms that can influence these three factors might be useful ways of minimizing the effects of canals. Table 34 lists several mechanisms. Generally, an increased freshwater supply

Table 34. Impacts of canals in Louisiana coastal marshes leading to habitat loss, and mechanisms and management practices to minimize these impacts.

Type of impact	Mechanisms to minimize impacts	Management practices
1. Salt intrusion	1. Increase fresh water supply	1. Fresh water diversion
2. Hydrologic change	2. Increase sediment supply	2. Reduce number of canals
	3. Reduce salt intrusion	3. Control canal location
	4. Maintain slow, sinuous natural water flows	4. Improve engineering design
	5. Maintain overland flow	5. Backfill canals
	6. Maintain water levels	6. Require mitigation fee for lost resources

to a marsh also increases the sediment load since rain runoff and river water are both generally quite turbid. Mechanisms that maintain slow, sinuous, shallow natural channels and overland flow will generally also reduce salt intrusion and stabilize water levels. They may also reduce the sediment-carrying capacity of the water, but this has to be balanced against the increased overland flow.

A number of practices are already being used or are potentially useful to minimize marsh loss (Table 34). They can be grouped as those that build new marshes to replace those lost and those that minimize the loss of existing marshes.

Day and Craig (1982) assessed the potential for reduction in wetland loss by several mitigation techniques. They concluded that diversion of fresh water to build new marshes could only create 1 - 3 km^2 of marsh a year, and the Atchafalaya had the potential of building about 18 km^2/yr. The largest potential for saving marshlands (30 - 40 km^2/yr), therefore, was by strict regulatory control of new canals.

We have little experimental experience on which to outline the best canaling technology. Prohibition against new canals would be the best solution, but prohibition against crossing barrier islands, connecting basin interiors to the periphery, and creating canals that shunt upland runoff around [marshes would be partial solutions.

Directional drilling is a well-established technology that would eliminate the need to dredge canals for many well heads. It has not been used often in the coastal marshes, and good studies comparing the extra cost of directional drilling against the environmental cost of the canal are needed.

Another technology that needs to be explored is the use of air cushion vehicles to traverse the marshes. These are used in the tundra and might provide a way to approach well sites and even transport drilling rigs without damaging the marsh extensively and without the need for canal dredging.

There are also possibilities for better design of canals. Where possible, they should follow natural channels in order to maintain natural circulation patterns. Spoil deposits are usually placed on both sides of the canal, isolating the canal from the adjacent marsh. Any design that breaks the spoil barrier to allow better exchange with the marsh would probably be an improvement. Unfortunately, there are no studies upon which to base detailed recommendations.

It is common practice to require that when canals cross natural streams and other canals,they must be blocked to minimize the danger that the new canal will capture the flow of the other channels and/or allow salt intrusion. Some fairly straightforward engineering work is needed to improve the design of these barriers. Earth fill, shell, or rock are usually used. These materials have densities much greater than the organic marsh, and their weight tends to settle and load down the adjacent marsh. As a result, the barriers are constantly breaching, especially at their ends. It would seem that an inert plastic material of the same density as the surrounding marsh, perhaps anchored into place with a minimum number of pilings, could be more effective.

Many canals can be backfilled - certainly all those dredged for pipelines and also many that lead to dry or depleted wells. Yet we know little about the relative value of backfilling compared to open canals. Work in progress (Mendelssohn, Sikora and Turner, Center for Wetland Resources, LSU) points to the effectiveness of backfilling canals because the practice removes spoil banks and also raises the bottom of the canal (although it seldom fills it completely because of the oxidation and dissipation of sediments when they are exposed in spoil banks) to a depth where the water column does not stratify. Oxygen is then available to the sediments, and a healthy benthic infauna can grow. In addition, there is some evidence that these shallow ditches, if left open in areas where marsh circulation is poor, can improve the quality of adjacent marshes. Such research on canals can yield major benefits to the State by providing practical means of reducing marsh degradation.

Recently some permits for dredging in the delta marshes have included requirements for marsh improvement elsewhere to mitigate the damage in the permit area. This is a creative mechanism for conserving marsh, although at the expense of other marsh tracts. Unfortunately, the methodology for assessing the true environmental cost of canals is rudimentary, so the relationship between the canal damage and the mitigation effort is somewhat arbitrary.

If environmental costs of development in wetlands are to be internalized by the developer, we need much better information about how to assess these costs. In a recent article Amft et al. (in review) present a methodology and make a benefit:cost assessment of an oil well access canal in the chenier plain. Based on their methodology, they suggest that a conservative estimate of the environmental cost for a typical exploratory well is $380,000 (1981 dollars) per kilometer of access canal.

A word needs to be said about some current practices that do not seen to effectively retard marsh loss. One of these is channelizing upland runoff. In fairness, this practice is not used to minimize marsh loss, but it is a common flood control measure. The impact on marshes is negative because it shunts the sediments of rivers and runoff away from marshes, both by leveeing rivers to prevent overbank flooding and by digging deep-dredged channels to deliver flood water through and around marshes instead of over them. This is a case of conflicting interests in the coastal zone. Until recently, flood control interests took ascendancy over marsh loss concerns. A more balanced evaluation of this "solution" to flooding is needed.

Another common practice is the construction of levees and impoundments to prevent marsh loss. In recent years, all over the deltaic and the chenier plain marshes small levees no more than a meter high have been thrown up by private land owners. Marsh impoundments are also common in State and Federal wildlife management areas where they were created to improve habitat for waterfowl and fur animals. These levees are much more common in the chenier plain than in the delta, primarily because the firmer substrate in the cheniers makes levee construction much less expensive and more effective.

The idea behind these impoundments is to prevent salt intrusion and thus retard marsh loss. Unfortunately, there is little evidence to show that they are effective, and some evidence to suggest that they are not. Baumann, Conner, and Gosselink (LSU Center for Wetland Resources; unpubl. MS.) analyzed marsh loss rates in impoundments compared to adjacent unimpounded areas, and concluded that loss rates were actually higher in impoundments than outside them (Figure 70). Wicker et al. (1983) also [measured marsh loss rates in different kinds of impoundments in the Rockefeller Wildlife Refuge. Although they presented no comparative data, it is apparent from their maps that marsh degradation is occurring in all the impoundments except perhaps those with pumps for water level control.

The problem, I think, is that sediment input is a key element in the ability of a marsh to accrete fast enough to keep up with subsidence. Impounding

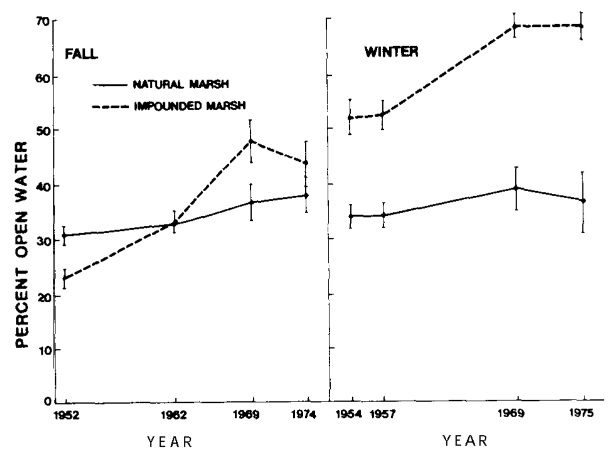


Figure 70. The increase in open water in natural and impounded wetlands. The pattern of gredter wetland loss in impoundments is consistent in both fall, when water levels are low, and winter, when impoundments are flooded (W. Conner and R. Baumann, Center for Wetland Resources, Louisiana State University; pers. comm.).

cuts off the sediment supply. In interdistributary basins which have very little surface fresh water input,most of the sediments come from tidal action. Under these circumstances attempts to retard salt intrusion also restrict sediment input.

In addition to marsh loss caused by salt intrusion and hydrologic changes, canals also directly change benthic and nektonic habitat quality (Table 34). The deep canals are depauperate in benthic organisms because, at least in bulkheaded channels, the lower part of the water column and the sediments are anoxic most of the year (W. Sikora, LSU Center for Wetland Resources; pers. comm.).

On the other hand,canals might enable nektonic organisms to penetrate marsh areas where they previously had no access, although the presence of spoil banks would cancel this benefit. Fish can use the deep water of canals as a refuge during cold spells when the shallow natural streams become almost as cold as the air above them.

tiabitat Quality

In the wildlife management areas of the delta (Figure 71) several kinds of marsh nodifications are practiced to improve habitat quality. Generally this means improved quality for waterfowl and fur animals, sometimes at the expense of fishery species. But in recent years the aim has been a diversified habitat that will support a broad range of species.

Where water level management is active, the opening and closing of water control structures is timed to increase the availability of the managed area to migratory fish and shellfish species. The simplest control structure is the weir (Figure 72); this is a common device found all over the coastal zone, especially in areas managed by State or Federal authorities. It is a dam placed in tidal creeks to maintain a minimum water level in the marshes drained by the creek. Usually the top of the weir is about 15 cm below the average marsh surface. The purpose of the weir is to stabilize water levels to encourage the growth of submerged aquatic plants and reduce marsh erosion by keeping the marsh from drying out and oxidizing. Weirs seem fairly effective for stabilizing water levels (Figure 73) and for promoting growth of submerged aquatic plants (Chabreck 1968).

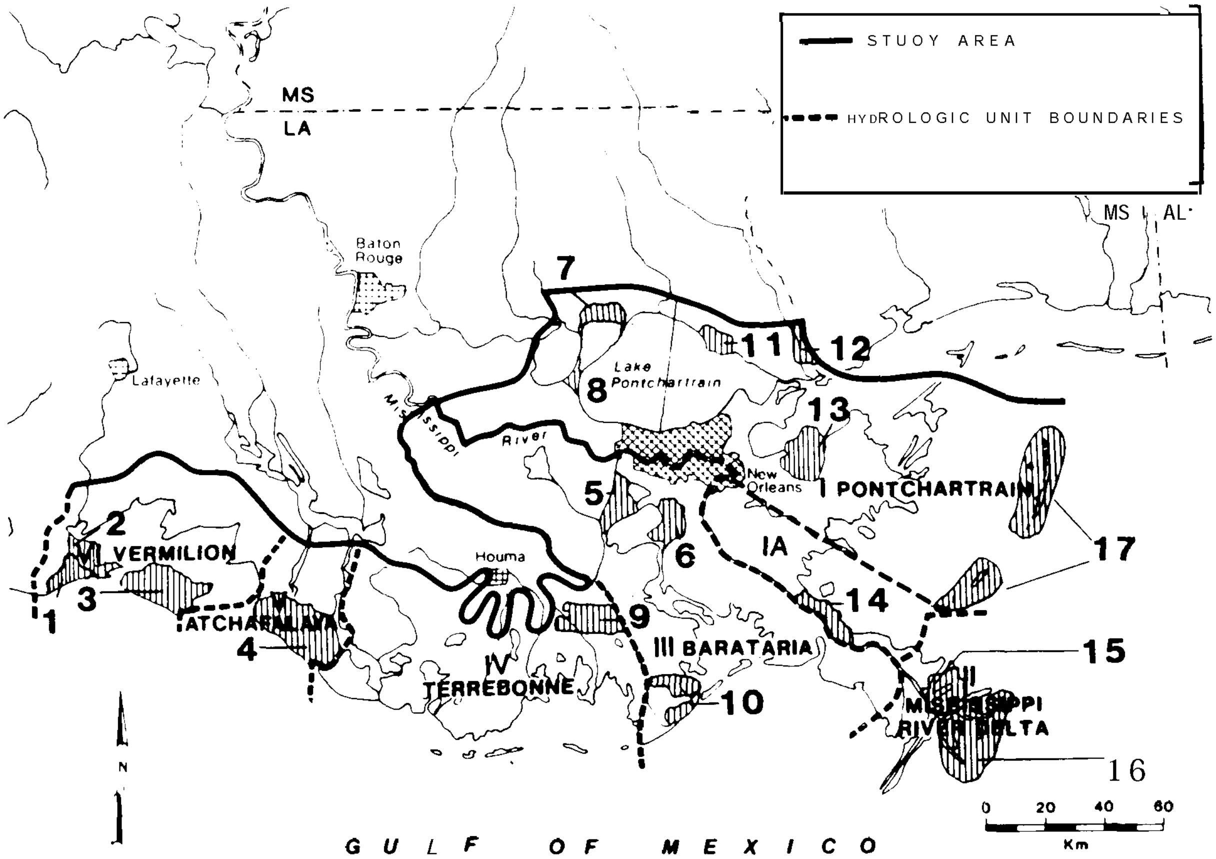
On the other hand, the evidence from the study of Steever et al. (1976; see Figure 43) that marsh plant biomass is directly proportional to tide range makes it likely that marsh productivity is reduced by these structures. As far as erosion prevention is considered, there is no evidence that weirs are effective. Weirs are the cheapest kind of marsh management. Because of the increase in submerged vegetation, the ponds behind weirs attract more wintering waterfowl than unweired ponds (Spiller 1975). They also improve conditions for fur animals.

The next level of control device is the flap gate and/or variable level dam in a completely impounded marsh. The flap gate allows water to flow one way through the control structure. Modern ones are reversible, but in Louisiana,with its high rainfall, they are usually set to allow freshwater to flow out of the impoundment and to prevent saltwater from moving in. Because of the surplus rainfall, all impounded areas become fresher with time.

The variable height device, which is often incorporated in the same structure, allows the manager to set minimum water levels behind the weir. With this "gravity drainage" system, if the weather cooperates it is possible to draw down the water in the spring to allow seeds of annual emergents to germinate. It can then be raised in the winter to make shallow ponds for ducks.

The most sophisticated water level control is obtained by pumping water out of or into the impoundment (forced drainage). The effectiveness of these management measures can be judged by the kinds and diversity of vegetation produced (habitat quality) and the use of the impoundment by birds, fur animals, fish, and shellfish.

Wicker et al. (1983) summarized the effectiveness of impoundments in the Rockefeller Wildlife Refuge. Annual vegetation surveys carried out since 1958



1 PAUL J. RAINEY WILDLIFE REFUGE

2 LOUISIANA STATE WILDLIFE REFUGE

3 RUSSELL SAGE FOUNDATION WILDLIFE REFUGE

4 ATCHAFALAYA WMA

5 SALVADOR STATE WMA

6 JEAN LAFITTE NATIONAL HISTORICAL PARK

7 JOYCE WMA

8 MANCHAC STATE WMA

9 POINTE -AU- CHIEN STATE WMA

10 WISNER STATE WMA

11 ST. TAMMANY STATE WMA

12 PEARL RIVER WMA

13 BILOXI WMA

14 BOHEMIA STATE WMA

15 DELTA NATIONAL WILDLIFE REFUGE

16 PASS A LOUTRE STATE WMA

17 BRETON NATIONAL WILDLIFE REFUGE

Figure 71. Wildlife management areas in the Mississippi Delta.

Figure 72. A weir in the deltaic plain marshes. The strong flow of water across the weir is an indication of the effectiveness of the barrier. These structures are favorite sport fishing spots (Photograph by Robert Chabreck).

show that the production of the desired emergent annuals and aquatic plants was variable. Even with pumps it was not possible to control water level in very rainy years like 1973, and the level of control decreased as the sophistication of the control devices decreased. In general, the better the water level management, the greater the diversity and desirability of the vegetation (Figure 74).

Water level management in the Rockefeller Wildlife Refuge is credited with increasing waterfowl use from a peak population of about 75,000 ducks in 1951 - 1952 to over 400,000 dabbling ducks, 40,000 coots and 10,000 diving ducks in 1958 - 1959 when the control structures were put into use (Chabreck 1961). The freshwater impoundments attract the most ducks; use of brackish water impoundments (usually areas in which water exchange with the surrounding marsh is not completely cut off) is comparable to unmanaged marshes (Chabreck et al. 1975; Davidson and Chabreck 1983).

The value of freshwater impoundments for species other than ducks is not as clear; fur animals, geese, and marine organisms are not benefitted (Chabreck 1975). However, crawfish can be successfully raised · impoundments managed for ducks (Perry et al. 1970). Brackish marsh impoundments seem to yield excellent crops of marine shellfish and fish if the control gates are managed to allow the juvenile organisms access during their immigration periods (Davidson and Chabreck 1983). Figure 75 summarizes the effectiveness of impoundments.

Marshes, inside impoundments and out, are often burned as a management practice.

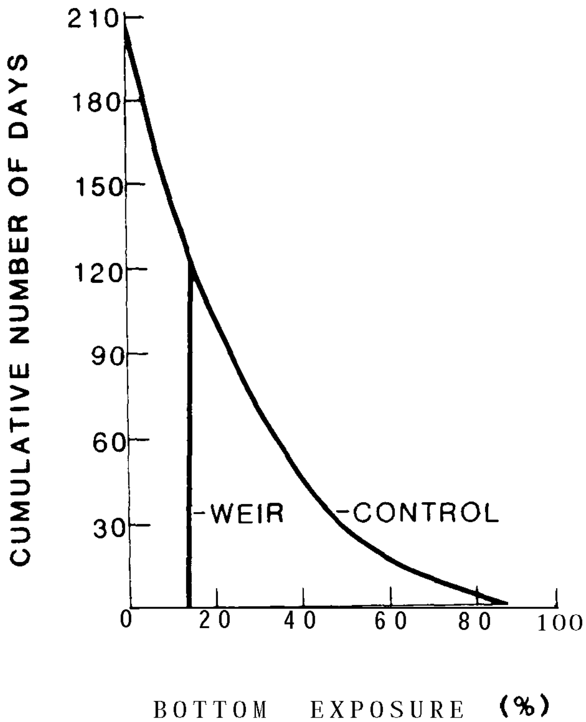


Figure 73. Cumulative number of days per year that ponds in the study area will equal or exceed certain percentages of bottom exposure. Based on depth contours of 48 ponds and 20 years of tide data on the central Louisiana coast (Chabreck 1979).

Chabreck (1975) questioned the value of most of this effort. However, he acknowledged that burning can be useful to remove a heavy vegetation thatch to allow annual species to germinate and to give three-cornered grass an earlier start during the growing season. Burning is widely practiced to attract snow geese to an area. Trappers find burned areas much easier walking, and animal trails are much more noticeable. However, nutria and raccoon often move from a burned marsh because of the lack of adequate cover.

Water Quality

Water quality is a major issue in Louisiana wetlands as in many other areas of the country, but it has received relatively little attention, probably because the much more pressing issue of marsh loss has taken the spotlight. The source of delta sediments, the Mississippi River itself, is heavily polluted with exotic chemicals which become incorporated in the sediments of any marshes created.

From here they can be magnified into the food chain, leading to the kind of effects on individual species that occurred with the brown pelican. That species was extirpated from the delta because of the effect of chlorinated hydrocarbon pesticides on egg shell strength; it has only recently been reintroduced from Florida (Blus et al. 1975).

Local runoff from urban and agricultural areas is also a serious problem. Seaton and Day (1979), Seaton and Day (1980), and Kemp (1973) documented the effects of urban runoff from the New Orleans area into the Barataria basin and Lake Pontchartrain. Gael and Hopkinson (1979) showed that eutrophication of water bodies is accelerated by canals which shunt the water around marshes instead of over them. High coliform counts have resulted in oyster bed closures in much of the estuarine area south of New Orleans and east of the Mississippi River. In all these examples the primary concern has been with the quality of water in the coastal lakes and bays. If more runoff water was allowed to flow across the marshes instead of bypassing it through flood drainage canals, it is likely that water quality would improve significantly.

With all the oil and gas production activity in wetlands, it is surprising that so little is known about the effect of oilspills on wetlands. In the delta only one group of studies is available. This research showed that chronic, low-level oilspills resulted in fairly high levels of hydrocarbons in marsh sediments (Bishop et al. 1976) in the Leeville oilfield.

These high concentrations are reflected in the aromatic hydrocarbon concentration in tissues of benthic organisms such as oysters and mussels. The emergent grasses and free-swimming organisms such as the grass shrimp and killifish had high concentrations of unresolved hydrocarbon components (Milan and Whelan 1979). The influence of this pollution on biota could not be separated

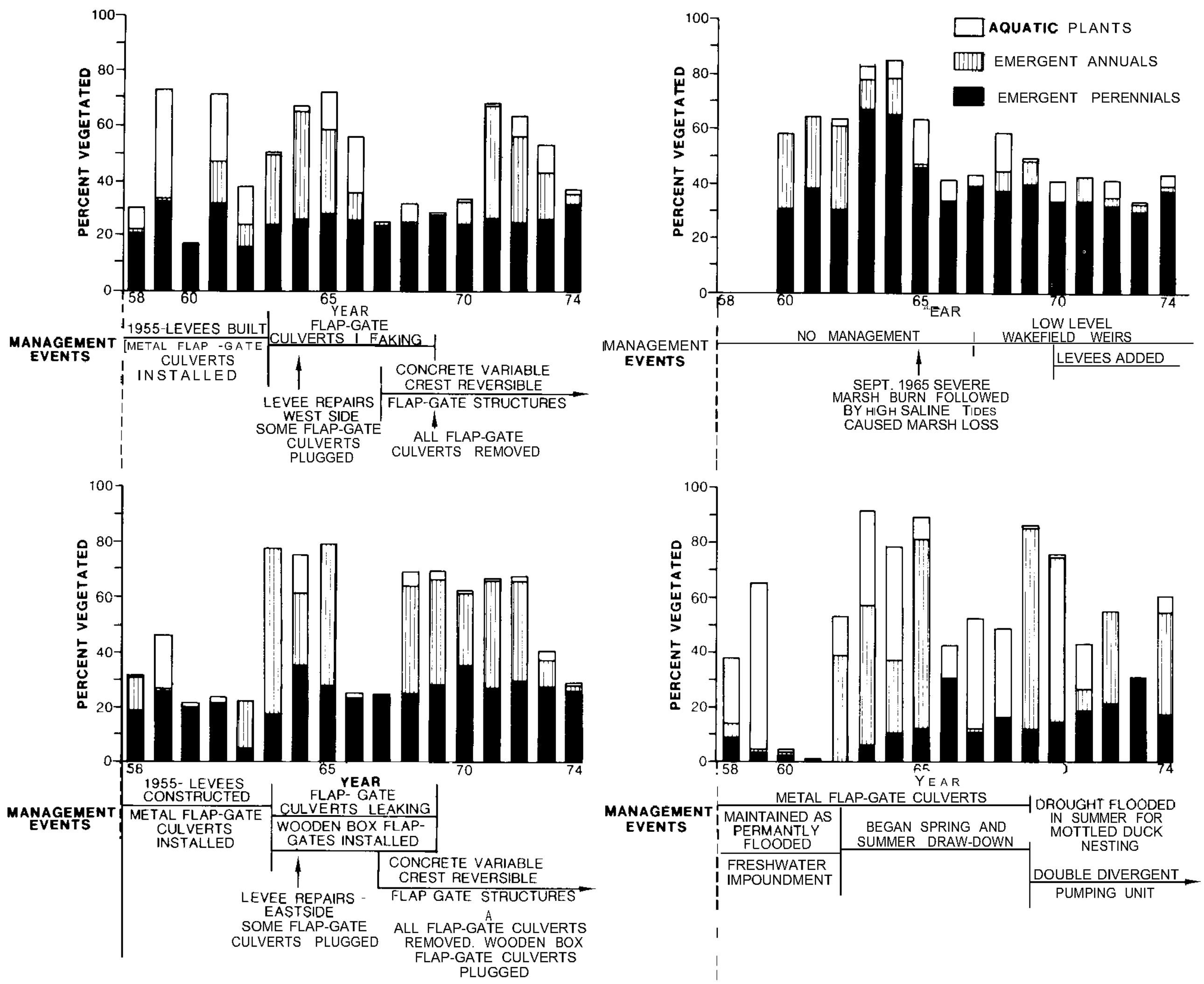


Figure 74. The percentage of different types of vegetation in impoundments in the Rockefeller State Wildlife Refuge (Wicker et al. 1983).

from the effect of the associated dense network of canals and spoil banks, but the density of marsh grass culms and average height was lower than in control areas (R. E. Turner; pers. comm.).

Amphipods, total crustaceans, and total benthic organisms were reduced 50 percent compared to non-oil field control areas (Lindstedt 1978). Killifish abundance was substantially less in oil-field marsh ponds than at control sites, although not statistically so because of the large confidence limits. However, the fecundity of Fundulus grandis in oilfield marshes was significantly lower than at control sites, especially the condition index of females 61-80 mm long (May 1977). It is apparent that we need to know much more about the effects of chronic low-level oilspills.

From a management point of view, water pollution is a good example of the need to manage on many different levels. Water quality of the Mississippi River must be improved. This is a problem national in scope because of the river's enormous watershed.

The control of urban runoff in the delta itself is a regional problem that affects marshes and estuaries in the New Orleans area more than other delta

TARGET HABITAT TYPE[1]	WATER MANAGEMENT PROGRAMS					
	PASSIVE ESTUARINE	CONTROLLED ESTUARINE		GRAVITY DRAINAGE	FORCED DRAINAGE	UNCONTROLLED
	Wakefield Weirs at -0.5 ft MSL	Concrete Variable Crest Reversible Flap-Gates	Concrete Radial Lift Gates	36-in and 48-in Flap-Gates Concrete Variable Crest Reversible Flap-Gates	Pumps	Nonexisting or Nonoperable Structures
EMERGENT PERENNIAL VEGETATION:						
Fresh	Ve-A	"e-A	Ve-A	"e-A	Ve-A	Ve-H[3]; Du-P, Mu-P, Nu-P
Intermediate	Ve-A	Ve-M; Du-P, Mu-F, Nu-F, Ge-F	Ve-H; Ge-G, Du-P, Mu-F, Nu-G, De-F	Ve-M; Du-P, Mu-F, Ge-G, Nu-F, De-P	Ve-L; Du-P, Mu-P, Nu-P, De-P	Ve-A
Brackish	Ve-M; Du-P, Mu-F[2], Ge-F. Nu-F	Ve-M; Du-P, Mu-F, Nu-F, De-P, Ge-F	"e-H; Du-P, Mu-F, Nu-F, De-P, Ge-G	Ve-M; Du-P, Mu-F, Ge-G, Nu-F, De-P,	Ve-A	Ve-H; Du-P, Mu-F Nu-F, Ge-G
Saline	Ve-H; Du-P, Mu-P, Nu-P, Ge-G	Ve-A	Ve-A	Ve-A	Ve-A	Ve-H; Du-P, Mu-P, Nu-P, Ge-G
EMRGENT ANNUAL VEGETATION:						
Fresh	Ve-A	Ve-A	Ve-A	Ve-A	"e-A	Ve-A
Intermediate	Ve-A	Ve-M; Du-G, Nu-F, Mu-P	Ve-L; Du-F, Mu-P, Nu-P, Ge-P	Ve-H; Du-E, Mu-P, Gr-P, Nu-F, De-F	Ve-H[4]; Du-E, Mu-P, Nu-F, De-F	Ve-A
Brackish	Ve-L; Du-F, Nu-P, Ge-P	Ve-M; Du-G, Mu-P, Nu-F, De-P, Ge-P	Ve-L; Du-F Mu-P, Nu-P, De-P, Ge-P	Ve-H; Du-E, Mu-P, Nu-F, De-F, Ge-P	Ve-A	Ve-L; Du-F, Mu-P, Nu-P, Ge-P
Saline	Ve-L; Du-P, Mu-P, Nu-P, Ge-P	"e-A	Ve-A	Ve-A	Ve-A	Ve-l; Du-F, Mu-P, Nu-P, Ge-P
AQUATIC VEGETATION:						
Fresh	"e-A	Ve-A	Ve-A	Ve-A	"e-A	Ve-M[3]; Du-G; Mu-P, Nu-P
Intermediate	Ve-A	Ve-M; Du-G, Mu-P, Nu-F, Ge-P	Ve-L; Du-f, Mu-P, Ge-F, Nu-P, De-P	Ve-L; Du-F, Mu-P, Ge-P, Nu-P, De-P	Ve-M; Du-G, Mu-P, Nu-G, De-F	Ve-A
Brackish	Ve-H; Du-G, Nu-F, Mu-P, Ge-P	Ve-M; Du-G, Mu-P, Nu-F, De-P, Ge-F	Ve-L; Du-F, Mu-P, Nu-P, De-P, Ge-P	Ve-L, Du-F, Mu-P, Ge-P, Nu-P, De-P	Ve-A	Ve-L; Du-F, Mu-P, Nu-P. Ge-P
Saline	Ve-A	Ve-A	Ve-A	Ve-A	Ve-A	Ve-A
FRESH-TO-INTERMEDIATE WATER BODIES		Ff-G, Cr-P, Wb-E, Al-E, Ot-G		Ff-P, Cr-P, Ot-P, Al-F, W-P	Cr-G, Ff-P, Wb-G, Wb-G, Al-F, Ot-P	Ff-G[3], Cr-F[3], Al-F, Ot-F, Wb-P
ESTUARINE WATER BODIES	Ef-E., Al-F. Sh-E. Ot-G, "b-E; Sb-G	Ef-E, Sh-E, Ot-G, Al-G, WI-E, Sb-F		Ef-P, Ot-P, Al-P, Wb-F		Ef-G, Sh-G, Al-P, Ot-F, Sb-E, W-G

SPECIES SYMBOLS

Vegetation	Ve
Geese	Ge
Dabbling ducks	Du
Shorebirds	Sb
Wading birds	Wb
Muskrats	Mu
Nutria	Nu
Deer	De
Alligators	Al
Shrimp	Sh
Crayfish	Cr
Freshwater Fish	Ff
Estuarine Fish	Ef
Otters	Ot

RATING OF MANAGEMENT TECHNIQUE FOR PRODUCING FLORA AND FAUNA

FLORA (Relative vegetative cover):

High	H
Medium	M
Low	L
Absent	A

FAUNA (Habitat value):

Excellent	E
Good	G
Fair	F
Poor	P

SPECIAL NOTES

[1] Water salinities in these zones are as follows:

Fresh	o-2 ppt
Intermediate	2-5 ppt
Brackish	5-15 ppt
Saline	over 15 ppt

[2] Fur-hearer populations on Rockefeller are presently at a low point in their cycle, but this management technique has bee" successfully used in other areas, especially with proper burning.

[3] This aplies only to Unit 9

[4] All forced drainage units are of intermediate salinities.

Figure 75. Habitat type, vegetative cover, and fish and wildlife values achieved with water management programs operating on the Rockefeller Refuge (Wicker et al. 1983).

wetlands. Local marsh management cannot solve that problem. The recommendation to route upland runoff across wetlands rather than around them in order to take advantage of marshes' ability to intercept pollutants is a basin-level problem that involves local, State and Federal management agencies. Finally, closer control of oilspills, oxidation ponds or drilling mud disposal in wetlands are problems that involve not only the local, State and iederal enforcement agencies but also single industries in site-specific problems.

REFERENCES

Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44:445-456.

Adams, R. D., B. B. Barrett, J. H. Blackmon, B. W. Gane, and W. G. McIntire. 1976. Barataria basin: yeoloyic processes and framework. Center for Wetland Resources, Louisiana State University, Baton Rouge. Sea Grant Publ. LSU-T-76-006.

Alexander, S. K. 1975. Relationship of macrophyte detritus to the salt marsh periwinkle, Littorina irrorata Say. Ph.D. Thesis. Louisiana State University, Baton Rouge. 104 pp.

Allan, P. F. 1950. Ecological gases for land use planning in gulf coast marshlands. J. Soil Water Conserv. 5:57-62, 05.

Allen, R. 1975. Aquatic primary productivity in various marsh environments in Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge. 50 pp.

American Ornithologists' Union. 1983. The A. O. U. Check-list of North American Birds. 6th ed. Allen Press, Inc. Lawrence, Kansas. 877 QQ.

Amft, J. A;, J. G. Gosselink, J. M. Caffrey, K. G. Teague, C. A. Moncrieff, J. H. Cowan, and C. A. Alexander. In review. An environmental/economic evaluation of a proposed canal in Cameron Parish, Louisiana, utilizing a cost-benefit technique. J. Coastal Zone Manage.

Arbib, R. 1978. The blue list for 1978. Am. Birds 31:1087-1096.

Arthur, S. C., compiler. 1931. The fur animals of Louisiana. La. Dep. Conserv. Bull. 18 (revised).

Audubon, J. J. 1867. The birds of America. Vols. I-III. Dover Publications, New York.

Barrett, B. B., and M. C. Gillespie. 1975. 1975 environmental conditions relative to shrimp production in coastal Louisiana. La. Wildl. Fish. Comm. Tech. Rull. 15. 22 QQ.

Bastian, R. K., and S. C. Reed. 1979. Aquaculture systems for wastewater treatments. Seminar proceedings and engineering assessment. U.S. Environmental Protection Administration, Office of Water Programs Operations, Washington, DC. 485 pp.

Baumann, R. H. 1980. Mechanisms of maintaining marsh elevation in a subsiding environment. M.S. Thesis. Louisiana State University, Baton Rouge. 91 pp.

Bell, S.S. 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. Ecol. Monogr. 50:487-505.

Bellrose, F. C. 1980. Ducks, geese and swans of North America. 3rd ed. Wildlife Management Institute and Illinois Natural Yistory Museum, Washington, D.C. 540 pp.

Beyer, G. E. 1900. The avifauna of Louisiana, with an annotated list of the birds of the state. Proc. La. Soc. Nat. 1897-1899:75-120.

Bishop, W., F. Bishop, M. Hood, and T. Whelan. 1976. Hydrocarbons. Vol. 3, App. 6.2 in J. G. Gosselink, R. Miller, M. Hood, and L. M. Bahr, eds. Louisiana offshore oil port: environmental baseline study. Center for Wetland Resources, Louisiana State University, Baton Rouge. Prepared for Louisiana Offshore Oil Port, Inc., New Orleans.

Blackmon, J. H. 1974. Observations on the emigration of the brown shrimp, Penaeus aztecus, through a tidal pass in the Caminada bay, Louisiana area. M.S. Thesis. Louisiana State University, Baton Rouge.

Blus, L. J., T. Joanen, A. A. Belisle, and R. M. Prouty. 1975. Brown pelicans and certain environmental pollutants in Louisiana. Bull. Environ. Contam. Toxicol. 13:646-655.

Boelter, D. H., and G. R. Blake. 1964. Importance of volumetric expression of water contents of organic soils. Soil Sci. Soc. Am. Proc. 28:176-178.

Brannon, J. M. 1973. Seasonal variation of nutrients and physicochemical properties in the salt marsh soils of Barataria bay, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge. 130 pp.

Brown, C. A. 1936. The vegetation of the Indian mounds, middens, and marshes in Plaquemines and St. Bernard parishes. La. Dep. Conserv. Bull. 8:423-440.

Brown, C. A. 1944. Historical commentary on the distribution of vegetation in Louisiana and some recent observations. Proc. La. Acad. Sci. 8:35-47.

Brupbacher, R. H., J. E. Sedberry, Jr., and W. H. Willis. 1973. The coastal marshlands of Louisiana: chemical properties of the soil materials. La. Agric. Exp. Stn., Baton Rouge. Bull. 672.

Buresh, R. J. 1978. Nitrogen transformations and utilization by Spartina alterniflora in a Louisiana salt marsh. Ph.D. Thesis. Louisiana State University, Baton Rouge.

Buresh, R. J., R. D. DeLaune, and W. H. Patrick, Jr. 1981. Influence of Spartina alterniflora on nitrogen loss from marsh soil. Soil Sci. Soc. Amer. J. 45:660-661.

Byrne, P., M. Borengasser, G. Drew, R. Muller, B. L. Smith, Jr., and C. Wax. 1976. Barataria basin: hydrologic and climatologic processes. Center for Wetland Resources, Louisiana State University, Baton Rouge. Sea Grant Publ. LSU-T-76-012. 175 pp.

Cary, L. R. 1907. The cultivation of oysters in Louisiana. Gulf Biol. Stn., Cameron, La. Bull. 8. 56 pp.

Casselman, M. E., W. H. Patrick, Jr., and R. D. DeLaune. 1981. Nitrogen fixation in a gulf coast salt marsh. Soil Sci. Soc. Amer. J. 45:51-56.

Chabreck, R. H. 1961. Coastal marsh impoundments for ducks in Louisiana. Proc. 14th Annu. Conf. Southeast. Assoc. Game Fish Comm. 14:24-29.

Chabreck, R. H. 1968. Weirs, plugs and artificial potholes for the management of wildlife in coastal marshes. Pages 178-192 in J. D. Newsom, ed. Proceedings of marsh and estuary management symposium. Division of Continuing Education, Louisiana State University, Baton Rouge.

Chabreck, R. H. 1971a. Ponds and lakes of the Louisiana coastal marshes and their value to fish and wildlife. Proc. 25th Annu. Conf. Southeast. Assoc. Game Fish Comm. 25:206-215.

Chabreck, R. H. 1971b. The foods and feeding habits of alligators from fresh and saline environments in Louisiana. Proc. 25th Annu. Conf. Southeast. Assoc. Game Fish Comm. Unpubl. MS.

Chabreck, R.H. 1972. Vegetation, water and soil characteristics of the Louisiana coastal region. La. Agric. Exp. Stn., Baton Rouge. Bull. 664. 72 pp.

Chabreck, R. H. 1975. Management of wetlands for wildlife habitat improvement. Proc. 3rd Bienn. Conf. Estuarine Res. Fed. Galveston, Tex.

Chabreck, R.H., and A. W. Palmisano. 1973. The effects of Hurricane Camille on tile marshes of the Mississippi River delta. Ecology 54:1118-1123.

Chabreck, R. H., R. K. Yancey, and L. McNease. 1975. Duck usage of management units in the Louisiana coatal marsh. Proc. 28th Annu. Conf. Southeast. Assoc. Game Fish Comm. 28:507-516.

Chabreck, R. H., and G. Linscombe. 1978. Vegetative type map of the Louisiana coastal marshes. Louisiana Department of Wildlife and Fisheries, New Orleans.

Chabreck, R. H., R. J. Hoar, and W. D. Larrick, Jr. 1979. Soil and water characteristics of coastal marshes influenced by weirs. Pages 129-145 in J. W. Day, Jr., D. D. Culley, Jr., R. E. Turner, and A. J. Mumphrey, Jr., eds. Proc. 3rd Coastal Marsh Estuary Manage. Symp. Division of Continuing Education, Louisiana State University, Baton Rouge. 511 pp.

Chambers, D. G. 1980. An analysis of nekton communities in the upper Barataria basin, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge. 286 pp.

Clarke, L., and N. J. Hannon. 1967. The mangrove swamp and salt marsh communities of the Sydney district. I. Vegetation, soils and climate. J. Ecol. 55:753-771.

Chew, F. 1962. Sea level changes along the northern coast of the Gulf of Mexico. Trans. Am. Geophys. Union 45:272-280.

Coates, D.R., ed. 1972. Environmental geomorphology and landscape conservation. Vol 1. Page 350 in Benchmark papers in geology. Dowden, Hutchinson and Ross, Stroudsburg, Pa.

Cocks, R. S. 1907. The flora of the Gulf Biologic Station. Gulf Biol. Stn. Cameron, La. Bull. 7.

Coleman, J. M. 1976. Deltas: processes of deposition and models for exploration. Continuing Education Publishing Company, Inc. Champaign, Ill. 132 pp.

Coleman, J. M., and S. M. Cagliano. 1964. Cyclic sedimentation in the Mississippi River deltaic plain. Gulf Coast Assoc. Geol. Soc. Trans. 14:67-80.

Collins, J. T., R. Conant, J. E. Huheey, J. L. Knight, E. M. Rundquist, and H. M. Smith. 1982. Standard common and current scientific names for North American amphibians and reptiles. 2nd ed. Society for the Study of Amphibians and Reptiles, Department of Zoology, Miami University, Oxford, Ohio.

Conner, W. H., and J. W. Day, Jr. 1982. The ecology of forested wetlands in the southeastern United States. Pages 59-87 in B. Gopal, R. E. Turner, R. G. Wetzel, and D. F. Whigham, eds. Wetlands ecology and management. National Institute of Ecology and International Science Publications. Jaipur, India.

Costanza, R. 1980. Embodied energy and economic valuation. Science 210: 1319-1224.

Costanza, R. 1983. Natural resource valuation and management: toward an integrated approach. Center for Wetland Resources. Louisiana State University, Baton Rouge. Unpublished MS.

Costanza, R., and C. J. Cleveland. 1984. Ultimate recoverable hydrocarbons in Louisiana: a net energy approach. Scient (in press).

Costanza, R., C. Neill, S.G. Leibowitz, J. R. Fruci, L. M. Bahr, Jr., and J. W. Day, Jr. 1983. Ecological models of the Mississippi deltaic plain region: data collection and presentation. U.S. Fish Wildl. Serv. Div. Biol.

Serv., Washington, D.C. FWS/OBS-82/68. 342 pp.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U. S. Fish Wildl. Serv., Div. Biol. Serv., Washington, D.C. FWS/OBS-79/31. 103 pp.

Craig, N. J., J. W. Day, Jr., A. Seaton, P. Kemp, and W. G. Smith. 1977. Eutrophication. Pages 1-97 in N. J. Craig and J. W. Day, Jr., eds. Cumulative impact studies in the Louisiana coastal zone. Part I. Center for Wetland Resources, Louisiana State University, Baton Rouge.

Cramer, G. W., and J. W. Day, Jr. 1980. Productivity of the swamps and marshes surrounding Lake Pontchartrain, La. Pages 593-545 in Stone, J. H., ed. Environmental analysis of Lake Pontchartain, Louisiana, its surrounding wetlands, and selected land uses. Vol 2. Coastal Ecology Lab., Center for Wetland Resources, Louisiana State University, Baton Rouge. Prepared for U.S. Army Engineers District, New Orleans. Contract DACW 29-77-C-0253.

Crowe, P. R. 1971. Concepts of climatology. Longman Group Ltd., London. 589 pp.

Davidson, R. B., and R. H. Chabreck. 1983. Fish, wildlife and recreational values of brackish marsh impoundments. Proceedings of water quality and wetland management conference. New Orleans, La. Aug. 4, 1983.

Davis, W. M. 1899. The geographical cycle. Geogr. J. 14:481-504.

Day, J. W., Jr., W. G. Smith, P. Wagner, and W. Stowe. 1973. Community structure and carbon budget in a salt marsh and shallow bay estuarine system in Louisiana. Center for Wetland Resources, Louisiana State University, Baton Rouge. Sea Grant Publ. LSU-SG-72-04. 30 pp.

Day, J. W., Jr., T. J. Butler, and W. H. Conner. 1977. Productivity and nutrient export studies in a cypress swamp and lake system in Louisiana. Pages 255-259 in M. Wiley, ed. Estuarine processes. Vol 2. Academic Press, New York.

Day, J. W., Jr., and N. J. Craig. 1982. Comparison of the effectiveness of [management options for wetland loss in the coastal zone of Louisiana. Pages 232-239 in D. F. Boesch, ed. Proceedings of a conference on coastal erosion and wetland modification in Louisiana: causes, consequences, and options. U. S. Fish Wildl. Serv. Biol. Serv. Program, Washington, D.C. FWS/OBS-82/59. 256 pp.

Day, J. W., Jr., C. S. Hopkinson, and W. H. Conner. 1982. An analysis of environmental factors regulating community metabolism and fisheries production in a Louisiana estuary. Pages 121-136 in V. S. Kennedy, ed. Estuarine comparisons. Academic Press, New York. 709 pp.

Deegan, L. A., H.M. Kennedy, and R. Costanza. 1983. Factors contributing to marsh land loss in Louisiana's coastal zone. Pages 915-920 in W. K. Lauenroth, G. V. Skogerboe, and M. Flug, eds. Analysis of ecological systems: state of the art in ecological modeling. Elsevier Publishing co., New York. 992 pp.

Deegan, L. A., and B. A. Thompson. 1984. The ecology of fish communities of the Mississippi River Deltaic Plain reqion. In Yanet-Arancibia, A., ed. Fish community ecology in estuaries and coastal lagoons. Universidad Nacional Autonoma De Mexico, Mexico City, Mexico. (in press).

Deevey, E. S., Jr. 1970. Mineral cycles. Sci. Am. 223:148-158.

DeLaune, R. D., and W. H. Patrick, Jr. 1979. Nitrogen and phosphorus cycling in a gulf coast salt marsh. Pages 143-151 in Proc. 5th Bienn. Int. Estuarine Res. Conf. Jekyll Island, Ga. October 7-12, 1979.

Delaune, R. D., R. J. Buresh, and W. H.

Patrick, Jr. 1979. Relationship of soil properties to standing crop biomass of Spartina alterniflora in a Louisiana marsh. Estuarine Coastal Mar. Sci. 8:477-487.

DeLaune, R. D., C. N. Reddy, and W. H. Patrick, Jr. 1981. Accumulation of plant nutrients and heavy metals through sedimentation processes and accretion in a Louisiana marsh. Estuaries 4:328-334.

DeLaune, R. D., R. H. Raumann, and J. G. Gosselink. 1983. Relationships among vertical accretion, apparent sea level rise and land loss in a Louisiana gulf coast marsh. J. Sediment. Petrol. 53:147-157.

Delwiche, C. C. 1970. The nitrogen cycle. Sci. Am. 223:137-146.

Dozier, M. D. 1983. Assessment of Chdnge in the marshes of southwestern Barataria basin; Louisiana, using historical aerial photographs and a spatidl information system. M. S. Thesis. Louisiana State University, Baton Rouge. 102 pp.

Ducklow, H. W. 1983. Production and fate of bacteria in the oceans. Bioscience 33:494-501.

Engler, R. M., E. A. Antie, and W. H. Patrick, Jr. 1976. Effect of dissolved oxygen on redox potential and nitrate removal in flooded swamp and marsh soils. J. Environ. Dual. 5:230-235.

Ethrington, J. R. 1975. Environment and plant ecology. John Wiley and Sons, London. 347 pp.

Evans, J. 1970. About nutria and their control. U.S. Bur. Sport Fish. Wildl. Denver, Colo. 65 pp.

Fenchel, T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass Thalassia testudinum. Limnol. Oceanogr. 15:14-20.

Fisk, H. N. 1939. Depositional terrace slopes in Louisiana. J. Geomorph. 2:181-199.

Fisk, H. N., 1944. Geological investigation of the alluvial valley of the lower Mississippi River. U. S. Army Engineers, Mississippi River Commission, Vicksburg, Miss.

Fisk, H. N. 1952. Geological investigations of the Atchafalaya basin and problems of Mississippi River diversion. U. S. Army Engineers, Mississippi River Commission, Vicksburg, Miss. 145 pp.

Fisk, H. N. 1956. Nearshore sediments of the continental shelf off Louisiana. Pages 1-23 in Proc. 8th Tex. Conf. Soil Mech. Found. Eng.

Fisk, H. N., and E. McFarlan, Jr. 1955. Late quarternary deltaic deposits of the Mississippi River. Crust of the earth. Geol. Soc. Am. Spec. Pao. 62:279-302.

Frazier, D. E. 1967. Recent deltaic deposits of the Mississippi River, their development and chronology. Gulf Coast Assoc. Geol. Soc. Trans. 17:287-315.

Gael, B. T., and C. S. Hopkinson. 1979. Drainage density, land-use and eutrophication in Barataria basin, Louisiana. Pages 147-163 in J. W. Day, Jr., D. D. Culley, Jr., R. E. Turner, and A. J. Mumphrey, Jr., eds. Environmental conditions in the coastal zone. Proc. 3rd Coastal Marsh Estuary Manage. Symp. Division of Continuing Education, Louisiana State University, Baton Rouge. 511 pp.

Gayliano, S. M., and J. L. Van Beek. 1970. Geologic and geomorphic aspects of deltaic processes, Mississippi delta system. Hydrologic and geologic studies of coastal Louisiana. Center for Wetland Resources, Louisiana State University, Baton Rouge. Rep. 1.

Gagliano, S. M., and J. L. Van Beek. 1975. An approach to inultiuse management in the Mississippi delta system. Pages 223-238 in M. L. Broussard, ed. Deltas, models for exploration. Houston Geological Society. Houston, Tex.

Gagliano, S. M., P. Culley, D. W. Earle, P. King, C. Latiolais, P. Light, A. Rowland, R. Shlemon, and J. L. Van Beek. 1973. Environmental atlas and multiuse management plan for south-central Louisiana. Center for Wetland Resources, Louisiana State University, Baton Rouge. Coastal Resour. Unit Rep. 18, Vol. 2.

Gagliano, S. M., K. J. Meyer-Arendt, and K. M. Wicker. 1981. Land loss in the Mississippi River Deltaic Plain. Trans. Gulf Coast Assoc. Geol. Soc. 31:295-300.

Gaudet, J. J. 1982. Nutrient dynamics of papyrus swamps. Pages 305-319 in B. Gopal, R. E. Turner, R. G. Wetzel, and D. F. Whigham, eds. Wetlands ecology and management. National Institute of Ecology and International Science Publications. Jaipur, India. 514 pp.

Giles, L. W. 1966. Relationship of vegetation to salinity in a southeast Louisiana coastal marsh. Rureau of Sport Fisheries and Wildlife, Division of River Basin Studies. Vicksburg, Miss. 26 pp.

Good, R. E., N. F. Good, and B. R. Frasco. 1982. A review of primary production and decomposition dynamics of the belowground marsh component. Pages 139-157 in V. S. 'Kennedy, ed. Estuarine comparisons. Academic Press, New York.' 709 pp.

Gosselink, J. G. 1980. Tidal marshes - the boundary between land and ocean. U. S. Fish Wildl. Serv., Biol. Serv. Program, Washington, D.C. FWS/OBS-80/15. 13 pp.

Gosselink, J. G., and C. J. Kirby. 1974. Decomposition of salt marsh grass, Spartina alterniflora, Loisel. Limnol. Oceanogr. 19:825-832.

Gosselink, J. G., E. P. Odum, and R. M. Pope. 1974. The value of the tidal marsh. Center for Wetland Resources, Louisiana State University, Baton Rouge. Sea Grant Publ. LSU-SG-74-03.

Gosselink, J. G., C. S. Hopkinson, Jr., and R. T. Parrondo. 1977. Common marsh plant species of the gulf coast area. Center for Wetland Resources, Louisiana State University, Baton Rouge. Prepared for Dredged Material Research Program, U. S. Army Engineers Waterways Experiment Station, Vicksburg, Miss. Tech. Rep. D-77-44.

Gosselink, J. G., C. L. Cordes, and J. W. Parsons. 1979. An ecological characterization study of the Chenier Plain coastal ecosystem of Louisiana and Texas. 3 vols. U.S. Fish Wildl. Serv., Biol. Serv. Program, Washington, D.C. FWS/OBS-78/9 through 78/11.

Gosselink, L. 1984. Hydrology and the effects of canals in Western Terrebonne parish marsh, La. M.S. Thesis, Louisiana State University, Baton Rouge.

Gowanloch, H. N. 1933. Fishes and fishing in Louisiana. La. Dep. Conserv. Bull. 23. 638 pp.

Gunter, G. 1938. Seasonal variations in abundance of certain estuarine and marine fishes in Louisiana, with particular reference to life histories. Monogr. 8. Ecology 3:313-346.

Gunter, G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. Pages 621-638 in G. H. Lauff, ed. Estuaries. Am. Assoc. Adv. Sci. Publ. 83.

Haines, E. B., and E. L. Dunn. 1976. Growth and resource allocation responses of Spartina alterniflora Loisel. to three levels of NH,-N, Fe and NaCl in solution culture. Bot. Gaz. 137:224-230.

Happ, G., J. G. Gosselink, and J. W. Day, Jr. 1977. The seasonal distribution of organic carbon in a Louisiana estuary. J. Estuarine Coastal Mar. sci. 5:695-705.

Hathaway, E. S., and W. T. Penfound. 1936. The relation of salinity to plant communities in southeastern Louisiana. Proc. La. Acad. Sci. 3:63-71.

Hatton, R. S. 1981. Aspects of marsh accretion and geochemistry: Barataria basin, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge. 115 pp.

Heitmeyer, M. E., and L. H. Fredrickson. 1981. Do wetland conditions in the Mississippi delta hardwoods influence mallard recruitment? Pages 44-57 in Trans. 46th N. Am. Wildl. Nat. Resour. Conf.

Hicks, S. D. 1978. An average geopotential sea level series for the United States. J. Geophys. Res. 83:1377-1379.

Hinchee, R. E. 1977. Selected aspects of the biology of Lake Pontchartrain, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge. 75 pp.

Hoffpauir, C. M. 1968. Burning for coastal marsh management. Pages 134-139 in J. D. Newsom, ed. Marsh and estuary management symposium. Louisiana State University, Baton Rouge.

Hollis, J. P. 1967. Toxicant diseases of rice. La. Agric. Exp. Stn. Bull. 614. Baton Rouge.

Hood, M. A., and A. R. Colmer. 1971. Seasonal bacterial studies in Barataria bay. Center for Wetland Resources, Louisiana State University, Baton Rouge. Coastal Stud. Bull. 6:16-26.

Hopkinson, C. S., Jr., and J. W. Day, Jr. 1977. A model of the Barataria bay salt marsh ecosystem. Pages 235-265 in C. A. S. Hall and J. W. Day, Jr., eds. Ecosystem modeling in theory and practice. John Wiley and Sons, New York. 684 pp.

Hopkinson, C. S., J. W. Day, Jr., and B. T. Gael. 1978a. Respiration studies in a Louisiana salt marsh. An. Centro. Cienc. del Mar. Y Limnol. Univ. 4uton. Mexico 5:225-238.

Hopkinson, C. S., Jr., J. G. Gosselink, and R. T. Parrondo. 19785. Aboveground production of seven marsh plant species in coastal Louisiana. Ecology 59:760-769.

Hopkinson, C. S., J. G. Gosselink, and R. T. Parrondo. 1980. Production of coastal Louisiana marsh plants calculated from phenometric techniques. Ecology 61:1091-1098.

Howarth, R. W., and J. M. Teal. 1979. Sulfate reduction in a New England salt marsh. Limnol. Oceanogr. 24:999-1013.

Howarth, R. W., and J. E. Hobbie. 1982. The regulation of decomposition and heterotrophic microbial activity in salt marsh soils: a review. Pages 183-207 in V. S. Kennedy, ed. Estuarine comparisons. Academic Press, New York.

Howarth, R. W., A. Giblin, J. Gale, B. J. Peterson, and G. W. Luther III. 1983. Reduced sulfur compounds in the pore waters of a New England salt marsh. Ecol. Bull. (Stockholm) 35:135-152.

Joanen, T., and L. McNease. 1972. Population distribution of alligators with special reference to the Louisiana coastal marsh zones. Symposium of the American Alligator Council, Lake Charles, La. Unpubl. MS.

Johnson, W. B., and J. G. Gosselink. 1982. Wetland loss directly associated with dredging in the Louisiana coastal zone. Pages 60-72 in D. F. Boesch, ed. Proceedings of a conference on coastal erosion and wetland modification in Louisiana: causes, consequences, and options. U.S. Fish Wildl. Serv., Biol. Serv. Program, Washington, D.C. FWS/OBS-82/59. 256 pp.

Jones, J. K., Jr., D. C. Carter, and

H. H. Genoways. 1975. Revised checklist of North American mammals north of Mexico. Occas. Pap. Mus. Tex. Tech. Univ. No. 28. 14 pp.

Kadlec, R. H. 1979. Wetlands for tertiary treatment. Pages 490-504 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. 674 pp.

Kadlec, R. H., and J. A. Kadlec. 1979. Wetlands and water quality. Pages 436-456 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. 674 pp.

Kane, H. T. 1943. The bayous of Louisiana. William Morrow and Co., New York. 341 pp.

Kaswadji, R. F. 1982. The estimation of primary production using five different methods in a Spartina alterniflora salt marsh in Barataria bay, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge. 39 pp.

Kelley, J. R. 1965. A taxonomic survey of the fishes of Delta National Wildlife Refuge with emphasis upon distribution and abundance. M.S. Thesis. Louisiana State University, Baton Rouge. 133 pp.

Kellogg, J. L. 1905. Upon the marine food mollusks of Louisiana. Gulf Biol. Stn., Cameron, La. Bull. 3. 43 pp.

Kemp, G. P. 1978. Agricultural runoff and nutrient dynamics of a swamp forest in Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge.

Keown, M. P., E. A. Dardeau, and E. M. Causey. 1980. Characterization of the suspended-sediment regime and bed-material gradation of the Mississippi River basin. Environmental Laboratory, U.S. Army Engineers Waterways Experiment Station., Vicksburg, Miss. Prepared for U.S. Army Engineers District, New Orleans, La. Potamology Invest. Rep. 221.

King, K. A., E.L. Flickinger, and H. H. Hildebrand. 1977. The decline of brown pelicans on the Louisiana and Texas gulf coast. Southwest. Nat. 2:417-431.

Kirby, C. J. 1971. The annual net primary production and decomposition of the salt marsh grass Spartina alterniflora Loisel. in the Barataria bay estuary of Louisiana. Ph.D. Thesis. Louisiana State University, Baton Rouge. 74. pp.

Kjerfve, B. J. 1972. Circulation and salinity distribution in a marsh-lake system in coastal Louisiana. Center for Wetland Resources, Louisiana State University, Baton Rouge. Sea Grant Publ. LSU-SG-72-06. 54 pp.

Yniffen, F. B. 1968. Louisiana, its land and people. Louisiana State University Press, Baton Rouge.

Kolb, C. R., and J. R. Van Lopik. 1958. Geology of the Mississippi deltaic plain - southeastern Louisiana. U.S. Army Eng. Waterways Exp. Stn. Tech, Rep. 2:3-482.

Lemaire, R. J. 1960. Preliminary report of marsh vegetation study, Mississippi River-Gulf Outlet navigation project, Orleans and St. Bernard Parishes, La. U.S. Army Engineers, Branch of River Basin Studies, Vicksburg, Miss. Prepared for U.S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Region 4, Atlanta, Ga. 35 pp.

Le Page du Pratz, A. S. 1758. Histoire de la Louisiane, contenant la decoverte de ce vaste pays. 3 vols. Paris.

Lerch, O., W. W. Clendenin, and W. C. Stubbs. 1892. Geology and agriculture of Louisiana. Louisiana Agricultural Experiment Station., Baton Rouge. 295 pp.

Lichfield, N., P. Kettle, and M. Whitbread. 1975. Evaluation in the planning process. Pergamon Press, Oxford.

Light, P. 1976. Hydrology. Ch. 2 in J. G. Gosselink, R. R. Miller, M. Hood, and L. M. Bahr, Jr., eds. Louisiana offshore oil port: environmental baseline study. Vol. II. Technical Appendices. Center for Wetland Resources, Louisiana State University, Baton Rouge. Prepared for Louisiana Offshore Oil Port, Inc., New Orleans.

Lindstedt, D. M. 1978. Effects of long term oil-recovery operations on macrobenthic communities near marsh-estuarine creek banks. M.S. Thesis. Louisiana State University, Baton Rouge. 67 pp.

Lisitzin, E., and J. G. Pattullo. 1961. The principal factors influencing the seasonal oscillation of sea level. J. Geophys. Res. 66:845-852.

Lomincki, A., E. Randola, and J. Jankowa-ska. 1968. Modification of the Wiegert-Evans [method for estimation of net primary production. Ecology 49:147-149.

Lonard, R., E. J. Clairain, R. T. Huffman, J. W. Hardy, L. D. Brown, P. E. Ballard, and J. W. Watts. 1981. Analysis of methodologies used for the assessment of wetlands values. Environmental Laboratory, U.S. Army Engineers Waterways Experiment Station, Vicksburg, Miss. Prepared for U.S. Water Resource Council, Washington, O.C. 68 pp.

Louisiana Department of Conservation. 1931. The birds of Louisiana. Dep. Conserv. Bull. 20. 598 pp.

Lowery, G. H. 1960. Louisiana birds. Louisiana State University Press, Baton Rouge. 567 pp.

Lowery, G. H. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge. 565 pp.

Mabie, D. W. 1976. 4vifauna. Vol. 3, App. 6, Sec. 12 in J. G. Gosselink, R. R. Miller, M. A. Hood, and L. M. Bahr, Jr., eds. Louisiana offshore oil port: environmental baseline study. Center for Wetland Resources, Louisiana State University, Baton Rouge. Prepared for Louisiana Offshore Oil Port, Inc., New Orleans.

Maltby, E. 1982. Changes in microbial numbers resulting from alternative management strategies in wetland and related habitats in southern Louisiana. Pages 477-506 in B. Gopal, R. E. Turner, R. G. Wetzel, and D. F. Whigham, eds. Wetlands ecology and management. National Institute of Ecology and International Science Publications, Jaipur, India. 514 pp.

Marchant, R., and W. L. Nicholas. 1974. An energy budget for the free-living nematode Pelodora (Rhabditidae). Oecologia 16:237-252.

May, L. N. 1977. The effects of oil-recovery operations on the biology and ecology of killifishes in a Louisiana salt marsh. M.S. Thesis. Louisiana State University, Baton Rouge. 80 pp.

McAllister, D. M. 1982. Evaluation in environmental planning. Massachusetts Institute of Technology Press, Cambridge.

McIntire, W. G. 1959. Methods of correlating cultural remains with stayes of coastal development. Pages 340-359 in 2nd Coastal Geogr. Conf. Coastal Studies Institute, Center for Wetland Resources, Louisiana State University, Baton Rouge.

Mehlich, 4. 1972. Unifonnity of expressing soil test results. A case for calculating results on a volume basis. Commun. Soil Sci. Plant Anal. 3:417-424.

Mehlich, A. 1973. Uniformity of soil test results as influenced by volume weight. Commun. Soil Sci. Plant Anal. 4:475-486.

Mendelssohn, E. A., and M. T. Postek. 1982. Elemental analysis of deaosits on the roots of Spartina alterniflora Loisel. Am. J. Bot. 69:904-912.

Yendelssohn, I. A., K. L. McKee, and M. T. Postek. 1982. Sublethal stresses controlling Spartina alterniflora productivity. Pages 223-242 in B. Gopal, R. E. Turner, R. G. Wetzel and D. F. Whigham, eds. Wetlands ecology and management. National Institute of Ecology and International Science Publications, Jaipur, India. 514 pp.

Meo, M., J. W. Day, Jr., and T. Ford. 1975. Overland flow in the Louisiana coastal zone. Center for Wetland Resources, Louisiana State University, Baton Rouge. Sea Grant Publ. LSU-SG-T-75-04.

Meyers, S. J., D. G. Ahearn, and P. C. Miles. 1971. Characterization of yeasts. Center for Wetland Resources, Louisiana State University, Baton Rouge. Coastal Stud. Bull. 6:7-15.

Milan, C. S., and T. Whelan. 1979. Accumulation of petroleum hydrocarbons in a salt marsh ecosystem exposed to steady state oil input. Pages 65-87 in J. W. Day, Jr., D. D. Culley, Jr., R. E. Turner, and A. J. Mumphrey, Jr., eds. Proc. 3rd Coastal Marsh Estuary Manage. Symp. Division of Continuing Education, Louisiana State University, Baton Rouge. 511 pp.

Milner, C., and R. E. Hughes. 1968. Method for the measurement of the primary production of grasslands. Int. Biol. Programme Handb. 6. Blackwell Scientific Publications, Oxford, England. 70 pp.

Moncreiff, C. A. 1983. Filamentous algal mat communities in the Atchafalaya River delta. M.S. Thesis. Louisiana State University, Baton Rouge. 129 pp.

Montz, G. N. 1976. Botanical elements. Reports to the file, U. S. Army Engineers District, New Orleans.

Mumphrey, A. J., J. S. Brooks, T. D. Fox, C. 3. Fromherz, R. J. Marak, and J. D. Wilkinson. 1978. The valuation of wetlands in the Barataria basin. Urban Studies Institute, University of New Orleans. Prepared for Louisiana Department of Transportation and Development, Baton Rouge.

National Research Council. 1982. Impacts of emerging agricultural trends on fish and wildlife habitat. National Academic Press, Washington, D.C. 244 pp.

National Oceanic and Atmospheric Agency. 1979. local climatological data, annual summary for Louisiana. U.S. Department of Commerce, Washington, D.C.

Nester, E. Y., C. E. Roberts, B. J. McCarthy, and N. N. Pearsall. 1973. Microbiology. Molecules, microbes and man. Holt, Rinehart and Winston, Inc. New York. 719 pp.

Nixon, S. W. 1982. The ecology of New England high salt marshes: a community profile. U. S. Fish Wildl. Serv., Biol. Serv. Program, Washington, D.C. FWS/OBS-81/55. 70 PP.

Odum, E. P. 1979. The value of wetlands: a hierarchical approach. Pages 16-25 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. 674 pp.

Odum, E. P., and M. E. Fanning. 1973. Comparison of the productivity of Spartina alterniflora and Spartina cynosuroides in Georgia coastal marshes. Ga. Acad. Sci. Bull. 31:1-12.

Odum, H. T., and R. C. Pinkerton. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. Am. Sci. 43:331-343.

O'Neil, T. 1949. The muskrat in the

Louisiana coastal marsh. Louisiana Department of Wildlife and Fisheries, New Orleans. 152 pp.

Palmisano, A. W. Jr., 1971. Commercial wildlife work unit report to Wildlife and Fisheries Commission, study of the Louisiana coast at the Atchafalaya basin. Louisiana Wildlife and Fisheries Commission, Vol. 1. 180 pp.

Palmisano, A. W. 1972. Habitat preference of waterfowl and fur animals in the northern gulf coast marshes. Pages 163-190 in R. H. Chabreck, ed. Coastal marsh and estuary management symposium proceedings, Division of Continuing Education and School of Forestry, Louisiana State University, Baton Rouge. 315 pp.

Parrondo, R. T., J. G. Gosselink, and C.S. Hopkinson. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. Rot. Gaz. 139:102-107.

Parrondo, R. T., J. G. Gosselink, and C. S. Hopkinson, Jr. 1981. Infuence of salinity on the absorption of rubidium by Spartina alterniflora and Distichlis spicata. Rot. Gaz. 142:402-407.

Parsons, K. A., and A. A. de la Cruz. 1980. Energy flow and grazing behaviour of conocephaline grasshoppers in a Juncus roenerianus marsh. Ecology 61:1045-1050

Patrick, W. H., Jr. 1982. Nitrogen transformations in submerged soils. Pages 449-465 in F. J. Stevenson, ed. Nitrogen in agricultural soils. Am. Soc. Agron. Monogr. 22. American Society of Agronomy, Madison, Wis.

Payne, W. J. 1970. Energy yields and growth of heterotrophs. Annu. Rev. Microbiol. 24:17-52.

Payonk, P. M. 1975. The response of three species of marsh macrophytes to artificial enrichment at Dulac, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge. 122 pp.

Penfound, W. T. 1944. Plant distribution in relation to the geology of Louisiana. Proc. La. Acad. Sci. 8:25-34.

Penfound, W. T., and E. S. Hathaway. 1936. Plant communities of the southeastern Louisiana marshes. Proc. La. Acad. Sci. 3:61-62.

Penfound, W. T., and E. S. Hathaway. 1938. Plant communities in the marshlands of southeastern Louisiana. Ecol. Monogr. 8:1-56.

Perry, W. G., Jr., T. Joanen, and L. McNease. 1970. Crawfish-waterfowl, a [multiple use concept for impounded marshes. Proc. 24th Annu. Conf. Southeast. Assoc. Game Fish Comm. 23: 178-188.

Pomeroy, L. R., and R. G. Wiegert, eds. 1981. The ecology of a salt marsh. Springer-Verlag, Inc., New York. 271 pp.

Portnoy, J. W. 1977. Nesting colonies of seabirds and wading birds in coastal Louisiana, Mississippi and Alabama. U.S. Fish Wildl. Serv. Biol. Serv. Program, Washington, D.C. FWS/OBS-77/07.

Rainey, G. B. 1979. Factors affecting nutrient chemistry distribution in Louisiana coastal marshes. M.S. Thesis. Louisiana State University, Baton Rouge. 103 pp.

Reddy, K. R., W. H. Patrick, Jr., and R. E. Phillips. 1980. Evaluation of selected processes controlling nitrogen loss in flooded soil. Soil Sci. Soc. Am. J. 44:1241-1246.

Reppert, R. T., and W. R. Sigleo. 1979. Concepts and methods for wetlands evaluation under development by the U. S. Army Corps of Engineers. Pages 57-62 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. 674 pp.

Riley, G. 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. J. Mar. Res. 1:60-74.

Riley, J. P., and R. Chester. 1971. Introduction to marine chemistry. Academic Press, London.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Rrooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada. An. Fish. Soc. Soec. Publ. No. 12. 174 pp.

Rublee, P. A., L.M. Cammen, and J. E. Hobbie. 1978. Bacteria in a North Carolina salt marsh: standing crop and importance in the decomposition of Spartina alterniflora. Univ. North Carolina Sea Grant Publ. NCU-T-78-004. Raleigh.

Ruebsamen, R. N. 1972. Some ecological aspects of the fish fauna of a Louisiana intertidal pond system. M.S. Thesis. Louisiana State University, Baton Rouge. 80 pp.

Russell, R. J. 1936. Lower Mississippi River delta, reports on the geology of Plaquemines and St. Bernard parishes. La. Dep. Conserv. Geol. Bull. 8:3-199.

Russell, R. J. 1942. Flotant. Geogr. Rev. 32:74-98.

Russell, R. J. 1967. River and delta morphology. Louisiana State University Press, Baton Rouge. 55 PP.

Sasser, C. E. 1977. Distribution of vegetation in Louisiana coastal marshes as response to tidal flooding. M.S. Thesis. Louisiana State University, Baton Rouye. 40 PP.

Sasser, C. E., G. W. Peterson, D. A. Fuller, R. K. Abernethy, and J. G. Gosselink. 1982. Environmental monitoring program. Louisiana offshore oil port pipeline. 1981 Annual Report. Coastal Ecology Laboratory Center for Wetland Resources, Louisiana State University, Baton Rouge. 299 pp.

Schamberger, M. L., C. Short, and A. Farmer. 1979. Evaluation wetlands as wildlife habitats. Pages 74-83 in P.E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. 674 pp.

Schitoskey, F., Jr., and R. L. Linder. 1979. Use of wetlands by upland wildlife. Pages 307-311 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. 674 pp.

Scruton, P. C. 1960. Delta building and the deltaic sequence. Pages 82-102 in F. P. Shepard et al., eds. Recent sediments , northwest Gulf of Mexico. American Association of Petroleum Geologists. Tulsa, Okla.

Seaton, A. M., and J. W. Day, Jr. 1979. The development of a trophic state index for the quantification of eutrophication in the Barataria basin. Pages 113-125 in J. W. Day, Jr., D. D. Culleg, Jr.,% E. Turner, and A. J. Yumphrey, Jr., eds. Environmental conditions in the Louisiana coastal zone. Proc. 3rd Coastal Marsh Estuary Manage. Symp., Division of Continuing Education and School of Forestry, Louisiana State University, Baton Rouge. 511 pp.

Seaton, A. W., and J. W. Day, Jr. 1980. A trophic analysis of Lake Pontchartrain, Louisiana, and surrounding wetland tributaries. Pages 31-37 in J. H. Stone, ed. Environmental analysis of Lake Pontchartrain, Louisiana, its surrounding wetlands, and selected land uses. Coastal Ecology Laboratory, Center for Wetland Resources, Louisiana State University, Baton Rouge. Prepared for U.S. Army Engineers District, New Orleans.Contract No.DACW29-77-C-0253.

Self, C. A. 1975. Marsh plants as food for captive white-tailed deer (Odocoileus virginianus), fallow deer

(Dama, and sika deer (Cervus nippon). M.S. Thesis. Louisiana State University, Baton Rouge.

Shabman, L. A., and S. S. Batie. 1978. Economic value of natural coastal wetlands: a critique. Coastal Zone Manage. J. 4:231-247.

Shaver, G. R., and W. D. Billings. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. Ecology 56:401-409.

Shew, D. M., R. A. Linthurst, and E. D. Seneca. 1981. Comparison of production computation methods in a southeastern North Carolina Spartina alterniflora salt marsh. Estuaries 4:97-109.

Sikora, J. P., W. B. Sikora, C. W. Erkenbrecher, and B. C. Coull. 1977. Significance of ATP, carbon, and caloric content of meiobenthic nematodes in partitioning benthic biomass. Mar. Biol. 44:7-14.

Sikora, W. B. 1977. The ecology of Paleomonetes pugio in a southeastern salt marsh ecosystem with particular emphasis on production and trophic relationships. Ph.D. Thesis. University of South Carolina, Columbia. 122 pp.

Sikora, W. B., and J. P. Sikora. 1982. Ecological implications of the vertical distribution of meiofauna in salt marsh sediments. Pages 269-282 in V. S. Kennedy, ed. Estuarine comparisons. Academic Press, New York. 709 pp.

Sklar, F. 1983. Water budget, benthological characterization, and simulation of aquatic material flows in a Louisiana freshwater swamp. Ph.D. Thesis. Louisiana State University, Baton Rouge.

Smalley, A. E. 1958. The role of two invertebrate populations, Li ttorina irrorata and Orchelium fidiciniun, in the energy flow of a salt marsh ecosys tem. Ph.D. Thesis. University of Georgia, Athens.

Smalley, A. E. 1960. Energy flow of a salt marsh grasshopper. Ecology 41:785-790.

Smardon, R. C. 1979. Visual-cultural values of wetlands. Pages 535-544 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. 674 pp.

Smart, R. M., and J. W. Barko. 1978. Influence of sediment salinity and nutrients on the physiological ecology of selected salt marsh plants. Estuarine Coastal Mar. Sci. 7:487-495.

Smith, C. J., R. D. DeLaune, and W. H. Patrick, Jr. 1982a. Nitrate reduction in Spartina alterniflora marsh soil. Soil Sci. Soc. Am. J. 46:748-750.

Smith, C. J., R. D. DeLaune, and W. H. Patrick, Jr, 1982b. Carbon and nitrogen cycling in a Spartina alterniflora salt marsh. Pages 97-104 in J. R. Freney, and I. E. Galvally, eds. The cycling of carbon, nitrogen, sulfur and phosphorus in terrestrial and aquatic ecosystems. Springer-Vet-lag, New York.

Smith, T. J., III. 1982. Herbivore-induced changes in salt marsh plant community structure. Pages 131-149 in B. Gopal, R. E. Turner, Q. G. Wetzel, and D. F. Whigham, eds. Wetlands ecology and management. National Institute of Ecology and International Science Publications, Jaipur, India. 514 pp.

Spaulding, M. H. 1908. Preliminary report on the life history and habits of the "Lake shrimp" (Pennaeus setiferus). Gulf Biol. Stn.., Cameron, La., Bull. 11.

Spiller, S. F. 1975. A comparison of wildlife abundance between areas influenced by weirs and control areas. M.S. Thesis. Louisiana State University, Baton Rouge. 94 pp.

St. Amant, L. S. 1959. Louisiana wildlife inventory and management plan. Louisiana Wildlife and Fisheries Commission, New Orleans. 329 pp.

Steever, E. Z., R. S. Warren, and W. A. Niering. 1976. Tidal energy subsidy and standing crop production of Spartina alterniflora. Estuarine Coastal Mar. Sci. 4:473478.

Stowe, W. C. 1972. Community structure and productivity of the epiphytic algae in the Barataria bay area of Louisiana. Ph.D. Thesis. Louisiana State University, Baton Rouge. 84 pp.

Stowe, W. C. 1982. Diatoms epiphytic on the emergent grass Spartina. alterniflora in a Louisiana salt marsh. Trans. Am. Microsc. Soc.101:162-173.

Swank, W. T., J. W. Fitzgerald, and J. T. Ash. 1984. Microbial transformation of sulfate in forest soils. Science 223:182184.

Tamisier, A. 1976. Diurnal activities of green-winged teal and pintail wintering in Louisiana. Wildfowl 27:19-32.

Teal, J. M. 1984. Tidal salt marshes of eastern North America: the ecology of the low salt marsh. U.S. Fish Wildl. Serv., Office Biol. Serv. Washington, D.C. FWS/OBS- (in press).

Teal, J. M., and J. W. Kanwisher. 1966. Gas transport in the marsh grass, Spartina alterniflora. J. Exp. Bot. 17:355-361.

Thompson, B., and L. Deegan. 1983. The Atchafalaya River delta: a new fishery nursery, with recommendations for management. Pages 217-239 in Proc. 10th Annu. Conf. Wetlands Restoration Creation.

Thornthwaite, C. W., and J. R. Mather. 1955. The water balance. Publications in Climatology 8(1). Drexel Institute of Technology, Philadelphia, Pa. 86 pp.

Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: a review. Contrib. Mar. Sci. 20:47-68.

Turner, R. E. 1977. Intertidal vegetation and commercial yield of penaeid shrimp. Trans. Am. Fish. Soc. 106: 411-416.

Turner, R. E. 1978. Community plankton respiration in a salt marsh estuary and the importance of macrophytic leachates. Limnol. Oceanogr. 23:442-451.

Turner, R. E. 1979. A simple model of the seasonal growth of Spartina alterniflora and Spartina patens. Contrib. Mar. Sci. 22:137147.

Turner, R. E., R. Costanza, and W. Scaife. 1952. Canals and wetland erosion rates in coastal Louisiana. Pages 73-84 in D. F. Boesch, ed. Proceedings of a conference on coastal erosion and wetland modification in Louisiana: causes, consequences, and options. U. S. Fish Wildl. Serv., Off. Biol. Serv., Washington. D.C. FWS/OBS-82/59. 256 pp.

U.S. Army Engineers. 1972. Charles River watershed, Mass. New England Division, Waltham, Mass. 65 pp.

U. S. Army Engineers. 1974. Pages II-19 to II-36 in draft environmental statement, deep draft access to the ports of New Orleans and Baton Rouge, Louisiana. New Orleans District.

U. S. Army Engineers. 1980. A habitat evaluation system (HES) for water resources planning. Lower Mississippi Valley Division, Vicksburg, Miss.

U. S. Department of Agriculture. No date. Gulf coast wetlands handbook. Soil Conservation Service, Alexandria, La.

U. S. Fish and Wildlife Service. 1980. Habitat evaluation proceduress (HEP) manual. Off. Biol. Serv., Washington, D.C.

U.S. Geological Survey. 1978. Water resources data for Louisiana. Water year 1978. Vol. 3. Coastal Louisiana. Water Resources Division, Baton Rouge, La. U.S. Geol. Surv. Water-Data Rep. LA-78-3.

Valentine, J. M. 1977. Plant succession after saw-grass mortality in southwestern Louisiana. Proc. Conf. Southeast. Assoc. Game Fish Comm. 30:634-640.

Valiela, I., B. Howes, R. Howarth, 4. Giblin, K. Foreman, J. Teal, and J. E. Hobbie. 1982. The regulation of primary production and decomposition in a salt marsh ecosystem. Pages 151-168 in B. Gopal, R. E. Turner, R. G. Wetzel, and D. F. Whigham, eds. Wetlands ecology and management. National Institute of Ecology and International Science Publications, Jaipur, India. 514 pp.

Van Heerden, I. Ll. 1983. Deltaic sedimentation in eastern Atchafalaya bay, Louisiana. Ph.D. Thesis. Louisiana State University, Baton Rouge.

Van Heerden, I. Ll., and H. H. Roberts. 1980. The Atchafalaya delta: rapid progrddation along a traditionally retreating coast (south-central Louisiana). Z. Geomorph. N.F. 34: 225-240.

Viosca, P. 1927. Flood control in the Mississippi valley and its relation to Louisiana fisheries. Trans. Am. Fish. Soc. 57:49-61.

Vora, S. M. 1974. Optimization of natural systems. Ph.D. Thesis. Louisiana State University, Baton Rouge.

Walker, R. E. 1940. Biotic succession in a coastal salt marsh. Proc. Okla. Acad. Sci. 20:95-97.

Wax, C. L., M. J. Borengasser, and R. A. Muller. 1978. Barataria basin: synoptic weather types and environmental response. Center for Wetland Resources, Louisiana State University, Baton Rouge. Sea Grant Publ. LSU-T-78-001.

Weller, M. W. 1978. Management of freshwater marshes for wildlife. Pages 267-284 in R. E. Good, D. F. Whigham, and R. L. Simpson, eds. Freshwater wetlands: ecological processes and management potential. Academic Press, New York. 378 pp.

Wells, J. T., S. J. Chinburg, and J. M. Coleman. 1982. Development of the Atchafalaya River deltas: generic analysis. Coastal Studies Institute, Center for Wetland Resources, Louisiana State University, Baton Rouge. Prepared for U.S. Army Engineers Waterways Experiment Station, Vicksburg, Miss. 91 pp.

Werme, C. E. 1981. Resource partitioning in the salt marsh fish community. Ph.D. Thesis. Boston University, Boston, Mass. 126 pp.

White, D. A., and J. M. Trapani. 1981. Factors influencing disappearance of *Spartina alterniflora* from litterbags. Ecology 63:242-245.

White, D. A., T. E. Weiss, J. M. Trapani, and L. B. Thien. 1978. Productivity and decomposition of the dominant salt marsh plants in Louisiana. Ecology 59:751-759.

White, D. C., R. J. Livingston, R. J. Bobbie, and J. S. Nickels. 1979. Effects of surface composition, water column chemistry, and time of exposure on the composition of the detrital microflora and associated macrofauna in Apalachicola Bay, Fla. Pages 83-116 in R. J. Livingston, ed. Ecological processes in coastal and marine systems. Plenum Press, New York. 548 pp.

Wicker, K. M. 1980. Mississippi deltaic plain region ecological characterization: a habitat mapping study. A user's guide to the habitat maps. U.S. Fish Wildl. Serv., Off. Biol. Serv., Washington, D.C. FWS/OBS-79/07.

Wicker, K. M., et al. 1980a. The Mississippi deltaic plain region habitat mapping study:habitat area data tapes. U.S. Fish Wildl. Serv., Off. Biol. Serv., Washington, D.C. FWS/OBS-79/07.

Wicker, K. M., et al. 1980b. The Mississippi deltaic plain region habitat mapping study. 464 maps. U.S. Fish Wildl. Serv., Off. Biol. Serv., Washington, D.C. FWS/OBS-79/07.

Wicker, K. M., G. C. Castille, D. J. Davis, S. M. Gagliano, D. W. Roberts, D. S. Sabin, and R. A. Weinstein. 1982. St. Bernard parish: a study in wetland management. Coastal Environments, Inc., Baton Rouge, La.

Wicker, K. M., D. Davis, and D. Roberts. 1983. Rockefeller State Wildlife Refuge and Game Preserve: evaluation of wetland management techniques. Coastal Environments, Inc., Baton Rouge, La. Prepared for Coastal Management Section, Louisiana Department of Natural Resources, Baton Rouge.

Wiebe, W. J., and L. R. Pomeroy. 1972. Microorganisms and their association with aggregates and detritus in the sea: a microscopic study. Mem. 1st. Ital. Idrobiol. 29 (suppl.): 325-352.

Wiegert, R.G., and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation in an old field in southwestern Michigan. Ecology 45:49-63.

Williams, R. B., and M. B. Murdoch. 1972. Compartmental analysis of the production of Juncus roemerianus in a North Carolina salt marsh. Chesapeake Sci. 13:69-79.

Wright, R., J. Sperry, and D. Huss. 1960. Vegetation type mapping studies of the marshes of southeastern Louisiana. Texas A and M Research Fd., College Station. Project 191. Prepared for U.S. Bur. Sport Fish. Wildl., U.S. Dep. Inter. Contract 14-16-003-538. 42 pp.

Appendix 1. Plant species composition of salinity zones in the Louisiana coastal marshes (Chabreck 1972). Scientific names conform with the National List of Scientific Plant Names (Soil Conservation Service 1982).

Species	Common name	Vegetative type			
		Saline	Brackish	Intermediate	Fresh
		Percent			
Aeschynomene virginica	Sensitive jointweed	--	--	--	.07
Alternanthera philoxeroides	Alligator-weed	--	--	2.47	5.34
Amaranthus australis	Belle-dame	--	.10	.30	.02
Aster sp.	Aster	--	.08	.44	.13
Avicennia germinans	Black mangrove	.60	--	--	--
Arolla caroliniana	Water fern	--	--	--	--
Baccharis halimifolia	Backbrush	--	.10	.56	.02
Bacopa caroliniana	Carolina bacopa	--	--	.28	.34
Bacopa monnieri	Water hyssop	--	.92	4.75	1.44
Bacopa rotundifolia	Round leaf bacopa	--	.11	.32	--
Batis maritima	Batis	4.11	--	--	--
Bidens laevis	Bur-marigold	--	-	--	.08
Eorrichia frutescens	Sea-oxeye	.67	.11	--	--
Brasenia schreberi	Water shield	--	--	--	.67
Cabomba caroliniana	Fan wort	--	--	--	.71
Carex sp.	Carex	--	--	--	.02
Centella erecta		--	--	.16	.12
Cephalanthus occidentalis	Button-bush	--	--	--	.21
Ceratophyllum demersum	Coontail	--	--	--	1.50
Cladium jamaicense	Saw-grass	--	--	--	.84
Colocasia antiquorum	Elephantsear	--	--	--	.39
Cuscuta indecora	Dodder	--	.02	--	--
Cynodon dactylon	Bermuda grass	-	--	--	.10
Cyperus compressus	Sedge	--	--	--	.02
Cyperus odoratus		--	.84	2.18	1.56
Decodon verticillatus	Water willow	--	--	--	.51
Dichromena colorata	Star sedge	--	--	--	.03
Distichlis spicata	Salt grass	14.27	13.32	.36	.13
Echinochloa walteri	Walter's millet	--	.36	2.72	.77
Eichhornia crassipes	Water hyacinth	--	--	--	1.43
Eleocharis parvula	Dwarf spikerush	--	2.46	.49	.54
Eleocharis sp.	Spikerush	--	.82	3.28	10.74
Eupatorium capillifolium	Yankee weed	--	--	--	.05
Eupatorium sp.	Boneset	--	--	.08	.03
Fimbristylis castanea	Sand rush	.04	.11	.12	--
Gerardia maritima		.01	.08	--	--
Heliotropium curassavicum	Seaside heliotrope	--	.02	--	--
Hibiscus moscheutos	Marsh mallow	--	--	.10	.05
Hydrocotyle bonariensis		--	--	--	.02
Hydrocotyle ranunculoides		--	--	--	.11
Hydrocotyle umbellata	Water pennywort	--	--	--	1.93
Hymenocallis occidentalis	Spider lily	--	--	.04	.14
Ipomoea stolonifera	Morning glory	--	--	--	.03
Ipomoed sagittata	Morning glory	--	.13	.84	.19
Iva frutescens	Marsh elder	.03	.10	--	--
Juncus effusus	Soft rush	--	--	--	.11
Juncus roemerianus	Black rush	10.10	3.93	.72	.60
Kosteletzkya virginica	Pink hibiscus	--	.02	.18	.07
Lemna minor	Duckweed	--	.02	.16	2.31
Leptochloa fascicularis	Sprangle top	--	.32	2.17	.49
Leptochloa filiformis	Red sprangle top	--	--	.04	--
Limnobium spongia	Frogbit	--	--	--	.16
Ludwigia suffruticosa	Water primrose	--	--	--	.24
Ludwigia sp.	Willow primrose	--	--	--	.84
Lycium carolinianum	Salt matrimony vine	.07	--	--	--
Lythrum lineare	Loosestrife	.01	.16	.18	.07
Myrica cerifera	Wax myrtle	--	--	--	.16
Myriophyllum heterophyllum	Eurasian watermill foil	--	--	--	.19
Myriophyllum spicatum	Variable watermill foil	--	.15	.44	1.56

(Continued)

Appendix 1. Concluded.

Species	Common Name	Vegetative Type			
		Saline	Brackish	Intermediate	Fresh
		Percent			
Najas guadalupensis	Southern naiad	--	--	1.03	1.07
Nelumbo lutea	American lotus	--	--	--	.54
Nymphaea odorata/tuberosa	White water lily	--	--	--	1.15
Nymphoides aquatica	Floating hedrt	--	--	--	.11
Osmunda regal is	Royal fern	--	--	.16	.43
Ottelia alismoides		--	--	--	.03
Panicum hemitomon	Maidencane	--	--	.76	25.62
Panicum repens	Dog tooth grass	--	--	.92	.24
Panicum virgatum	Feather grass	--	.14	2.51	.45
Panictdn sp.		--	--	--	.10
Paspalum dissectum		--	--	.40	.42
Paspalum vaginatum		--	1.38	4.46	.35
Philoxerus vennicularis	Salt alligator weed	--	--	.oa	.01
Phragmites australis	Roseau	--	.31	6.63	2.54
Phyla nodiflora		--	--	--	.06
Pluchea foetida	Stinking fleabane	--	--	--	.02
Pluchea camphorata	Camphorweed	--	.87	2.26	.36
Polygonum sp.	Smartweed	--	--	--	.56
Pontederia cordata	Pickerelweed	--	--	--	.01
Potamogeton nodosus	Longleaf pondweed	--	--	.28	.03
Potamogeton pusillus	Slender pondweed	--	--	.24	.62
Ruppia maritima	Widgeongrass	--	3.83	.64	--
Sacciolepis striata	Bagscale	--	--	--	.05
Sagittaria falcata	Bull tongue	--	--	5.47	15.15
Sagittarla latifolia	Wapato	--	--	--	.21
Sagittaria platyphylla	Delta duckpotato	--	--	--	.23
Sagittaria sp.		--	--	.08	--
Salicornia bigelovii	Glasswort	.13	--	--	--
Salicornia virginica	Glasswort	.63	--	--	--
Salix nigra	Black willow	--	--	--	.05
Saururus cernuus	Lizzard's tail	--	--	--	.16
Scirpus americanus	Freshwater three square	--	--	1.27	.13
Scirpus californicus	Hardstem bullrush	--	--	1.83	.42
Scirpus olneyi	Three-cornered grass	--	4.97	3.26	.45
Scirpus robustus	Leafy three square	.66	1.78	.68	--
Scirpus validus	Soft stem bulrush	--	.oa	--	--
Sesbania exaltata		--	.06	.20	--
Sesbania sp.	Rattlebox	--	--	.04	.17
Sesuvium portulacastrum	Marsh purslane	--	.04	--	--
Setaria glauca	Yellow foxtail	--	.06	--	--
Setaria magna	Giant foxtail	--	--	--	.03
Solidago sp.	Goldenrod	--	--	.04	.oa
Spartina alterniflora	Oyster grass	62.14	4.77	.86	--
Spartina cynosuroides	Hog cane	--	.a9	1.19	.02
Spartina patens	Marsh hay cordgrass	5.99	55.22	34.01	3.74
Spartina spartinae		.01	.04	1.48	--
Spirodela polyrhiza	Duckweed	--	--	--	.20
Suaeda linearis	Sea-blite	.23	--	--	--
Taraxacum officinale	Dandelion	--	--	.02	--
Taxodium distichum	Baldcypress	--	--	--	.02
Thelypteris thelypteroides	Southern marsh fern				
Triadenum virginicum	Marsh St. John's wort	--	--	--	.07
Typha spp.	Cattail	--	--	.98	1.57
Utricularia cornuta	Horned bladderwort	--	--	--	1.68
Utricularia subulata	Zigzag bladderwort	--	--	--	.21
Vallisneria americana	Wildcelery	--	.08	--	--
Vigna luteola	Deerpea	--	1.20	3.84	1.43
Woodwardia virginica	Virginia chain fern	--	--	--	.28
Zizaniopsis miliacea	Giant cutgrass	--	--	--	1.20

Appendix 2. Marsh plant decomposition rates, Mississippi River delta marshes.

Species	Month initiated	Loss rate (mg/g/day)	Comment	Citation
Distichlis spicata				
	June	6.6	5-mm mesh bags on marsh	3
	September	4.2		
	December	2.2		
	Summer	9.0	Open plots in marsh	4
	Winter	5.7		
Juncus roenerianus				
	June	7.7	5-mm mesh bags on marsh	3
	Summer	14.4	Open plots in marsh	4
	Winter	5.9		
Phragmites australis				
	Summer	6.2	Open plots in marsh	4
	Winter	1.3		
Sagittaria falcata				
	Summer	25.7	Open plots in marsh	4
	Winter	24.1		
Spartina alterniflora				
	March	8.2	5-mm mesh bags on marsh	1
	July	12.6		
	September	10.1		
	December	5.6		
	June	13.8	2-mm mesh bags in bayou	2
	January	5.5		
	June	9.2	2-mm mesh bags, streamside marsh	
	January	4.6		
	June	5.5	2-mm mesh bags, inland marsh	
	January	4.2		
	May	21.9	5-mm mesh bags on marsh	3
	September	9.2		
	December	4.3		
	Summer	7.0	Open plots in marsh	4
	Winter	4.0		
Spartina cynosuroides				
	Summer	6.4	Open plots on marsh	4
	Winter	2.7		

(Continued)

Appendix 2. Concluded.

Species	Month initiated	Loss rate	Comment	Citation
Spartina patens				
	June	4.6	5-mm mesh bags on marsh	3
	Summer	11.9	Open plots in marsh	4
	Winter	9.1		
	June	2.8-3.0	2-mm mesh bags on marsh	5

Citations:

1 - White and Trapani 1982
2 - Kirby 1971
3 - White et al. 1978
4 - Hopkinson et al. 1978
5 - Cramer and Day 1980

Appendix 3. Fishes of the Mississippi River Deltaic Plain that are found in marshes and associated water bodies (compiled by Gosselink et al. 1979; Deegan and Thompson 1984; see these documents for original sources). Scientific and common names conform to Robins et al. (1980).

	Ecological[a] affinity	Trophic relations	Local distribution	Relative and seasonal abundance	Economic importance
FAMILY DASYATIDAE STINGRAYS					
Dasyatis sabina (Lesueur) Atlantic Stingray	MA	Carnivore; predator on meiofauna	Broadly euryhaline; to freshwater; widespread	Abundant, especially in open bay areas, larger canals	None
FAMILY LEPISOSTEIDAE GARS					
Lepisosteus oculatus (Winchell) spotted Gar	FW	Carnivore; predator/ scavenger on fishes, macroinvertebrates	Fresh to brackish areas, principally in protected areas; swamps, bayous, canals	Locally abundant, especially in fresh swamps, bayous, canals	Limited value as commercial fish (trammel nets); much less important than other gars
Lepisosteus osseus (Linnaeus) Longnose Gar	FW	Carnivore; predator on fishes, macro- and micro-fauna	Broadly euryhaline; widespread, but mainly in freshwater areas; rivers, canals, lakes	Moderately abundant in rivers, canals, lakes	Minor value as commercial fish (trammel nets)
Lepisosteus spatula Lacepede Alligator Gar	FW	Carnivore; predator/ scavenger on fishes, larger invertebrates	see longnose gar entry; less rheophilic than osseus	Moderately abundant in upper bays, canals, lakes, bayous	Moderate value as commercial fish (trammel nets) (most important of gars)
FAMILY AMIIDAE BOWFINS					
Amia calva (Linnaeus) Bowfin	FW	Carnivore; predator/ scavenger on fishes. amphibians, macroinvertebrates	Fresh to slightly brackish areas only; mainly in quiet water, swamps, canals, ditches, bayous, fresh lakes	Locally abundant	Limited value as gamefish
FAMILY ELOPIDAE TARPONS					
Elops saurus (Linnaeus) Ladyfish - Adults	ESM	Carnivore; predator on small fishes, invertebrates. zooplankton	Pelagic; mainly in high salinity areas; lower passes	Locally abundant	None
Ladyfish - Young		Same as adults	Pelagic; broadly euryhaline; to fresh areas; larvae and juveniles widespread in inland open-water areas	Moderately abundant along marsh edges, April-June	None
FAMILY ANGUILLIDAE FRESHWATER EELS					
Anguilla rostrata (Lesueur) American Eel - Adults	MA	Carnivorous; predators on fishes, macroinvertebrates	Demersal; broadly euryhaline but mainly in brackish to fresh areas except during spawning migration; river channel, upper bay, larger bayous	Sparse; very cryptic; occasionally take" in trawls, seines. hook and line	None
American Eel - Young			Planktonic larvae mainly offshore; demersal elvers widespread in bays, bayous, lakes	Sparse; very cryptic; occasionally taken by trawls, seines	
FAMILY CLUPEIDAE HERRINGS					
Alosa chrysochloris (Rafinesque) Skipjack Herring - Adults	FW	Carnivore: predator on fishes; invertebrates, -forage species	Broadly euryhaline, hut mainly-in fresher areas; river channels, upper bays, fresh lakes	Very cyclic; year-class strengths seen to fluctuate radically; can be moderately abundant in some years	Limited value as haitfish (diplines), crawfish traps
Skipjack Herring - Young		-forage species	Platonic larvae mainly in rivers	See above entry; in "good" years larvae moderately abundant April - July; juveniles moderately abundant June - October	None

(Continued)

Appendix 3. Continued.

	Ecological[a] affinity	Trophic relations	Local distribution	Relative and seasonal abundance	Econaic importance
Brevoortia patronus Goode Gulf Menhaden	ESM	Filter feeder on plankton, suspended benthic algae, and detritus	Euryhaline; juveniles found from fresh to saline marshes	Very abundant	
Dorosoma cepedianum (Lesueur) Gizzard Shad - Adults	FW	Omnivore: filter feeder of plankton detritus, benthic algae	Broadly euryhaline, hut mainly in fresher areas, where very widespread	Abundant, 1 ocally	Moderate value in spring dipnet fishery for bait, troutlines, and crawfish traps
Gizzard Shad - Young		-forage species	Planktonic larvae mainly in rivers	Larvae abundant late March - June; juveniles moderately abundant June - October	None
Dorosoma petenense (Gunther)	FW	Omnivore; strainer of plankton, detritus, benthic algae	Same as gizzard shad	Same as gizzard shad	Limited value as baitfish
Threadfin Shad - Adults		-forage species			
Threadfin Shad - Young		-forage species	Same as gizzard shad	Larvae abundant May - September; juveniles abundant June - November	None
FAMILY ENGRAULIDAE ANCHOVIES					
Anchoa mitchilli (Valenciennes) Bay Anchovy - Adults	ESM	Carnivore; predator on fishes, invertebrates -forage species	Pelagic; broadly euryhaline to fresh water; widespread	Abundant; increasingly so in summer; usually taken in seines, trawls, cast-nets	None
Bay Anchovy - Young		-forage species	Planktonic larvae widespread; juveniles as adults	Abundant year-round, peak usually in early summer	None
FAMILY CYPRINIDAE MINNOWS AND CARPS					
Cyprinus carpio Linnaeus Carp	FW	Omnivore; grazer/sucker-type feeder on plants, benthic invertebrates, detritus, carrion	Fresh to brackish areas; widespread, larvae planktonic; post larvae and juveniles mainly in temporarily flooded areas	Moderately abundant in fresh areas; young abundant late March through summer	Minor component of freshwater hoopnet fishery
Notemigonus crysoleucas (Mitchill) Golden Shiner	FW	Omnivore; midwater and surface grazer/predator on zooplankton, filamentous algae, periphyton, fouling invertebrates -forage species	Fresh to brackish areas; widespread	Locally abundant	None; (those sold as bait brought in from minnow farms outside the area)
FAMILY ICTALURIDAE BULLHEAD CATFISHES					
Ictalurus furcatus (Lesueur) Blue Catfish - Adults	FW	Omnivore; [mainly carnivorous; predator/grazer on fishes, macro-invertebrates, carrion	Fresh to moderate salinity areas; mainly in fresh and brackish areas; river channel, bayous, upper hay, marsh lakes	Abundant; often taken in trawls, commercial nets, hook and line	Popular gamefish major component of inland troutline, hoopnet, trammel net catches; used in local fish culture
Blue Catfish - Young		Omnivore; similar to adults but using more insect larvae, smaller invertebrates, detritus	Essentially as adults but preferring fresh areas; river channel	Locally abundant; see hahitat entry	None
Ictalurus natalis (Lesueur) Yellow Bullhead	FW	Omnivore, predator/grazer on benthic invertebrates, carrion, detritus	Fresh to slightly brackish; swamps, bayous, canals, ditches	Locally abundant, especially in small canals, ditches, swamps	
Ictalurus punctatus (Rafinesque) Channel Catfish - Adults	FW	See blue catfish entry	See blue catfish entry; this species slightly less salt-tolerant and tends to prefer quieter water areas than I. furcatus	See blue catfish entry; tends to predominate in fresher areas	See blue catfish entry; this species tends to predominate in fresher areas and more benthic situations

(Continued)

Appendix 3. Continued.

	Ecological affinity	Trophic relations	Local distribution	Relative and seasonal abundance	Economic importance
Pylodictis olivaris (Rafinesque) Flathead Catfish	FW	Carnivore; predator on fishes, macro-invertebrates	Fresh to brackish areas; mainly in river channel	Sparse	Popular game-fish; minor component of inland hoopnet and trotline catch
FAMILY ARIIDAE SEA CATFISHES					
Arius felis (Linnaeus) Hardhead Catfish	ESM	Omnivore; grazer/scavenger on carrion, detritus, macro- and meio-benthos	Broadly euryhaline, but mainly in high to moderate salinity areas;	Locally abundant, mainly during warm months	8-10% of industrial bottom-fish catch
Bagre marinus (Mitchill) Gafftopsail Catfish	ESM	Omnivore; grazer/scavenger on carrion, detritus, macro- and meio-benthos	To moderate salinity areas; mainly limited to high salinity; lower bays, passes	Sparse; found in and around (marshes in warm months only	Minor component of bottom-fish catch; not distinguished from Sea Cat-fish
FAMILY GOBIESOCIDAE CLINGFISHES					
Gobiesox strumosus Cope Skilletfish	ESM	Carnivore; feeds on macro- and meio-benthos	High to moderate salinity areas; mainly near reefs, pilings, jetties	Sparse; occasionally taken in trawls, dredges; larvae in plankton near reefs, late winter, spring	None
FAMILY BELONIDAE NEEDLEFISHES					
Strongylura marina (Walbaum) Atlantic Needlefish	ESM	Carnivore; predator on fishes, macro-invertebrates	Broadly euryhaline; to freshwater; widespread	Moderately abundant but seldom concentrated; often taken in seine, castnets	None
FAMILY CYPRINODONTIDAE KILLFISHES					
Adinia xenica (Jordan and Gilbert) Diamond Killifish	ES	Omnivore; mainly herbivorous; grazer on algae, periphyton, detritus	Broadly euryhaline; to freshwater, but mainly in high to moderate salinities; mainly along edges of protected areas (marshes); ponds, ditches, canals	Locally abundant, especially in winter and spring	
Cyprinodon variegatus Lacepede Sheepshead Minnow	ES	Omnivore; primarily herbivorous; grazer on algae, detritus, benthic invertebrates, periphyton -forage species	Broadly euryhaline; wide-spread along shores and in protected marsh waters	Abundant, peaks observed in winter and spring	Minor value as baitfish
Fundulus chrysotus (Gunther) Golden Topminnow	ES	-forage species	Fresh to slightly brackish areas; mainly in fresh swamps, ditches, canals, borrow pits	Locally abundant; especially quiet (marshy areas	None
Fundulus grandis Baird and Girard Gulf Killifish	ES	Omnivore; mainly carnivorous; predator/grazer on small invertebrates, fishes, detritus -forage species	See sheepshead minnow entry	See sheepshead minnow entry	Minor value as baitfish
Fundulus jenkinsi (Evermann) Saltmarsh Topminnow	ES	-forage species	Broadly euryhaline; in protected marsh areas	Rare, occasionally seined in marsh ditches, ponds	None
Fundulus pulvereus (Evermann) Bayou Killifish	ES	Carnivore; predator/grazer on small invertebrates	Broadly euryhaline; in protected marsh areas; bayous, canals, ditches, ponds	Locally abundant, winter through spring	None
Fundulus similis (Baird and Girard) Longnose Killifish	ES	Omnivore; predator/grazer on benthic invertebrates, detritus	Broadly euryhaline but greatest concentrations in moderate to high salinities; along beaches, edges of marsh lakes, bayous	Locally abundant; lower bays, high salinity marshes	

(Continued)

	Ecological affinity	Trophic relations	Local distribution	Relative and seasonal abundance	Economic importance
Lucania parva (Baird) Rainwater Killifish	ES	Omnivore; primarily carnivorous; predator/grazer on invertebrates, detritus -forage species	Same as sheepshead minnow	Locally abundant; peaks in summer	None
FAMILY POECILIIDAE LIVERBEARERS					
Gambusia affinis (Baird and Girard) Mosquitofish	FW	Omnivore; primarily carnivorous; predator/grazer on invertebrates -forage species	Broadly euryhaline, but mainly in fresh to brackish areas; along Edges Of protected areas. swamps, marshes, canals, ditches, bayous, ponds	Locally abundant; especially in fresh areas	None
Heterandria formosa Agassiz Least Killifish	FW	Herbivore; grazer on epiphytes, benthic algae -forage species	Fresh and brackish areas only; swamps, ditches, borrow pits; usually in marshy areas	Rare; occasionally taken in ditches, hoi-row pits	None
Poecilia latipinna (Lesueur) Sailfin Molly	FW	Herbivore; grazer on epiphytes, benthic algae, detritus	Broadly euryhaline to freshwater; widespread along protected shores, open beaches, bayous, ditches, canals, ponds	Locally abundant year-round	None
FAMILY ATHERINIDAE SILVERSIDES					
Labidesthes sicculus (Cope) Brook Silverside	FW	Carnivore; predator on neustonic invertebrates, zooplankton -forage species	Fresh areas only; swamps, small streams	Locally abundant in fresh areas	None
Membras martinica (Valenciennes) Rough Silverside	ES	Carnivore; predator on small invertebrates -forage species	Broadly euryhaline; to freshwater; mainly along marshy shores of bays, lakes, large canals, bayous	Locally abundant during summer	None
Menidia beryllina (Cope) Inland Silverside	ES	Carnivore; predator/grazer on ronplankton, other small invertebrates -forage species	Broadly euryhaline, widespread	Abundant, peaks in summer	None
FAMILY SYNGNATHIDAE PIPEFISHES AND SEAHORSES					
Syngnathus louisianae Gunther Chain Pipefish	ESM	Carnivore; predator on small invertebrates	High to moderate salinity areas; mainly associated with vegetation	Rare; occasionally token by seines in higher salinity marsh ponds, ditches	None
Syngnathus scovelli (Evermann and Kendall) Gulf Pipefish	ES	Carnivore, predator on small Invertebrates	Broadly euryhaline; to freshwater; widespread along edges and areas having dense vegetation; ditches, canals, ponds	Locally abundant	None
FAMILY PERCICHTHYIDAE TEMPERATE BASSES					
Morone chrysops (Rafinesque) White Bass	FW	Carnivore, predator mainly on fishes	Broadly euryhaline but mainly in fresh and brackish areas; pelagic in open waters of river channel, large bayous, canals, lakes, upper bays	Locally abundant in fresher areas	Minor value as gamefish
Morone mississippiensis Jordan and Eigenmann Yellow Bass	FW	Carnivore; predator mainly on fishes	See white bass entry; this form slightly more salt tolerant and more common in smaller water bodies	Locally abundant; mainly in fresh areas, river channel, swamps	Minor value as gamefish
Morone saxatilis (Walbaum) Striped Bass	FW	Carnivore; voracious predator on small fish	Mainly in inland waters	Rare; occasionally caught by hook and line, trammel nets	Limited value as gamefish

(Continued)

Appendix 3. Continued.

	Ecological[a] affinity	Trophic relations	Local distribution	Relative and seasonal abundance	Economic importance
FAMILY CENTRARCHIOAE SUNFISHES					
Centrarchus macropterus (Lacepede) Flier	FW	Carnivore; predator on small fishes, macro-invertebrates	Fresh to slightly brackish areas; swamps, marshes, bayous, sluggish streams	Sparse	Limited value as gamefish
Lepomis cyanellus Rafinesque Green Sunfish	FW	Carnivore; predator on fishes, macro-invertebrates	Fresh to brackish areas; backwaters of streams, swamps, ditches, canals	sparse	None
Lepomis gulosus (Cuvier) War-mouth	FW	Carnivore; predator on fishes, macro-invertebrates	Fresh to brackish areas; swamps, borrow pits, canals, bayous	Locally abundant; especially in swamps	Minor value as gamefish
Lepomis macrochirus Rafinesque Bluegill	FW	Omnivore; predator/grazer on invertebrates, algae	Fresh to brackish areas; widespread in fresh habitats	Locally abundant	Minor value as gamefish
Lepomis marginatus (Holbrook) Dollar Sunfish	FW		Fresh to brackish areas; especially swamps, borrow pits	Locally abundant in fresh areas	None
Lepomis megalotis (Rafinesque) Longear Sunfish	FW	Carnivore; predator/grazer on invertebrates, especially insects	Fresh areas only; mainly in rivers, creeks	sparse	None
Lepomis microlophus (Gunther) Redear Sunfish	Fh	Omnivore; primarily carnivorous; predator/grazer on invertebrates, mainly mollusks	Fresh to brackish areas; mainly in swamps, borrow pits, canals, bayous, lakes	Moderately abundant in fresh lakes, ponds, horrow oits	Minor value as gamefish
Lepomis punctatus (Valenciennes) Spotted Sunfish	FW	See redear sunfish entry	Fresh areas only; mainly in swamps	Sparse	Minor value as qamefish
Lepomis symmetricus Forbes Bantam Sunfish	FW		Fresh to brackish areas; common in swamps, borrow pits, ditches	Locally abundant	None
Micropterus salmoides (Lacepede) Largemouth Bass - Adults	FW	Carnivore; predator mainly on fishes, macroinvertebrates	Fresh to brackish; widespread in lentic situations, especially in areas of low turbidity	Abundant in lentic habitats, sluggish streams, canals, bayous	Popular qamefish; large quantities caught in marsh ponds, impoundments
Largemouth Bass - Young		Carnivore; predator on zooplankton. later insects, small fishes	Minimally in fresh areas; shallow marginal zones of swamps, stream backwaters	Moderately abundant In lentic freshwater areas, April through summer	none
Pomoxis nigromaculatus (Lesueur) Black Crappie	FW	Carnivore; predator on fishes, macro-invertebrates; larvae feed on zooplankton	Fresh to brackish; widespread in low turbid lentic situations	Moderately abundant In fresh areas, especially quiet, weedy areas	Popular gameflsh
FAMILY CARANGIDAE JACKS					
Oligoplites saurus (Schneider) Leatherjacket - Young	ESM	carnivore; predator on small fishes, invertebrates	Broadly euryhaline; to freshwater, bet mainly moderate to high salinity areas; bay shores, bayous, marsh lakes	Moderately abundant during warm months	None
FAMILY GERREIDAE MOJARRAS					
Eucinostomus argenteus Baird Spotfin Mojarra - Young	ESM	carnivore; predator/grazer on benthic invertebrates	Broadly euryhaline, hut mainly In moderate to high salinities; widespread	Moderately abundant In shore seines during warm months	None
FAMILY SPARIDAE PORGIES					
Archosargus probatocephalus (Walbaum) Sheepshead - Adults	ESM	Omnivore; grazer/predator on perlphyton. macroinvertebrates, especially barnacles, hermit crabs	Mainly In high salinity areas, lower bays, tidal passes; near pilings. reefs	Moderately abundant, year-round; often taken by anglers, trammel nets	Minor value as commercial fish (trammel net); popular gameflsh

(Continued)

	Ecological[a] affinity	Trophic relations	Local distribution	Relative and seasonal abundance	Economic importance
Sheepshead - Young			Broadly euryhaline; wide-spread in protected waters, marsh bayous, canals, lakes	Moderately abundant, mainly spring, early summer	None
Lagodon rhomboides (Linnaeus) Pinfish - Adults	ES	Omnivore; predator/ grazer on fishes, detritus, inverte-brates, algae	Broadly euryhaline, but mainly in high to moderate salinity areas; lower bays, bayous	Moderately abundant. especially during warm months	None
Pinfish - Young			Broadly euryhaline; to freshwater; widespread along shores and in marsh bayous, ditches, ponds	Abundant. late winter through summer	None
FAMILY SCIAENIDAE DRUMS					
Aplodinotus grunniens Rafinesque Freshwater Drum - Adults	FW	Carnivore; predator/ grazer on benthic invertebrates, espe-cially mollusks, and fishes	Fresh to brackish areas; especially river channel	Locally abundant year-round	Major component Of Inland hoop-net catch; minor gamefish
Freshwater Drum - Young		Omnivore; larvae predators on zooplank-ton; juveniles grazers on benthic inverte-brates, detritus	Larvae planktonic in river, upper bays, demersal, especially over soft mud/detritus bottoms	Locally abundant, May through early fall	None
Bairdiella chrysoura (Lacepede) Silver Perch	ESM	Carnivore; adults predatory on small fishes, benthic invertebrates	Broadly euryhaline but mainly In moderate to high salinity; widespread	Locally abundant, especially as postlarval and early juveniles. April through early summer	None
Cynoscion arenarius Ginsburg Sand Seatrout - Adults	ESM	Carnivore; predator on fishes, macro-invertebrates	Moderate to high salinity areas; widespread in bays, marsh lakes. bayous	Moderately abundant. declining in cold months	Popular game-fish; minor com-ponent of inland trammel net catch
Sand Seatrout - Young			Broadly euryhaline; wide-spread; very small juveniles prefer protected marsh waters	Abundant, April through early Fall	None
Cynoscion nebulosus (Cuvier) Spotted Seatrout	ESM	Carnivore; predator on fishes and macro-invertebrates	Abundant schooling fish In saline and brackish areas, often found in marsh bayous and shallow lakes. especially juveniles	Abundant year-round, except winter	Popular sport-fish
Leiostomus xanthurus Lacepede spot - Young	ESM	Omnivore; primarily carnivorous on zoo-plankton; grazer an detritus	Broadly euryhaline, but mainly in moderate to high salinity areas; postlarvae and early juveniles mainly In protected marsh waters; older juveniles widespread	Abundant. especially late spring through summer	5-7% of indus-trial bottomfish catch in spring and summer; moderately valu-able as gamefish
spot - Adults		Graze on benthic invertebrates and detritus	Adults move offshore in fall		
Micropogonias undulatus (Linnaeus) Atlantic Croaker	ESM	Omnivores; grazers on benthic Invertebrates. detritus, small fishes; young subsist on zooplankton	Euryhaline, preferring salinity areas around marshes-as juveniles, moving to saline areas with maturity	Very abundant; moving offshore in winter	More than ½ of industrial bottomfish catch
Pogonias cromis (Linnaeus) Black Drum - Adults	ESM	carnivore predator/ grazer on benthic invertebrates. espe-cially bivalue mollusks	Broadly euryhaline, but mainly in high to moderate salinity areas; lower passes; mainly near reefs	Moderately abundant, often taken by trammel nets, hook and line	Same value as sportfish and and commercial fish
Black Drum - Young		Predatory on small benthic Invertebrates	larvae mainly in offshore areas; postlarvae and juveniles occasionally entering bays, lower marshes	Sparse; occasionally taken In seines	None

(Continued)

Appendix 3. Continued.

	Ecological[a] affinity	Trophic relations	Local distribution	Relative and seasonal abundance	Economic importance
Sciaenops ocellatus (Linnaeus) Red Drum	ESM	Carnivores; predators on fishes and crustaceans	Widespread in saline and brackish areas, often in shallow marsh, ponds. and streams	Abundant especially in fall and early winter	Valuable game-fish
Stellifer lanceolatus (Holbrook) star Drum	ESM		Mainly in high salinity areas; lower bays, passes	Sparse; occasionally taken in trawls	None
FAMILY EPHIPPIDAE SPADEFISHES					
Chaetodipterus faber Atlantic Spadefish - Young	ESM	Omnivore; grazer on attached algae. fouling invertebrates	Mainly in high salinity areas, near tidal passes	Moderately abundant, locally, especially during summer and fall	None
FAMILY MUGILIDAE MULLETS					
Mugil cephalus Linnaeus Striped kllet - Adults	ESM	Omnivore; primarily herbivorous; -forage species	Broadly euryhaline; to freshwater;	Abundant. war-round	None
Striped kllet - Young		Omnivore; primarily herbivorous	Broadlv eurvhaline; to freshwater;-widespread; planktonic larvae offshore	Abundant. especially late winter. early spring	None
FAMILY ELEOTRIDAE SLEEPERS					
Dormitator maculatus (Bloch) Fat Sleeper	ES	Carnivore; predator on fishes, macro-invertebrates	Broadly euryhaline; mainly in ditches, canals, bayous	Moderately abundant, locally	None
Eleotris pisonis (Gmelin) Spinycheek Sleeper	ES	Same as fat sleeper	Broadly euryhaline; hut mainly in fresh or brackish areas; canals. ditches	Very rare	NOW
FAMILY GOBIIDAE GOBIES					
Evorthodus lyricus (Girard) Lyre Goby	ES		Broadly euryhaline; but mainly in moderate to high salinity areas; ditches, canals. marsh ponds	Locally abundant	None
Gobioides broussoneti Lacepede Violet Goby	ES		Broadly euryhaline; but mainly in high salinity areas; open bays, bayous. marsh lakes	Sparse; occasionally taken in trawls	None
Gobionellus boleosoma (Jordan and Gilbert) Darter Goby	ES		Broadly euryhaline; widespread	Locally abundant. especially during cold months	None
Gobionellus hastatus Girard Sharptail Goby	ES	Omnivore; grazer on algae. benthic invertebrates	Broadly euryhaline; widespread	Sparse; occasionally taken in trawls	None
Gobionellus shufeldti (Jordan and Eigenmann) Freshwater Goby	ES		Broadly euryhaline. hut mainly in fresh to brackish areas. where widespread	Locally abundant	None
Gobiosoma bosci (Lacepede) Naked Goby	ES	Carnivore; predator/ scavenger on benthic invertebrates, carrion	Broadly euryhaline. widespread	Locally abundant. on reefs. marsh ponds, ditches	None
Gobiosoma robustum Ginsburg Code Goby	ES	Carnivore; predator/ grazer on benthic invertebrates	Broadly euryhaline, hut mainly in moderate to high salinities; mainly associated with vegetation	Sparse, occasionally taken in seines	None
Microgobius gulosus (Girard) Clown Goby	ES	Omnivore; predator/ grazer on benthic invertebrates. algae	Broadly euryhaline. widespread; mainly "ear vegetation	Sparse; occasionally taken in trawls, seines	None
Microgobius thalassinus (Jordan and Gilbert) Green Goby	ES		Broadly euryhaline, but mainly in high salinity areas; "ear vegetation	very rare; occasionally taken in seines	None

(Continued)

Appendix 3. Concluded.

	Ecological affinity[a]	Trophic relations	Local distribution	Relative and seasonal abundance	Economic Importance
FAMILY BOTHIDAE LEFTEYE FLOUNDERS					
Cithrrichthys macrops Dresel Spotted Whiff	ESM	Carnivore; predator on small crustaceans	Limited to high salinity areas; lower bays, passes	Rare; occasionally taken in trawls	None
Paralichthys lethostigma Jordan and Gilbert Southern Flounder	ESM	Carnivore; predator on small fishes, macroinvertebrates	Euryhaline; juveniles and adults found from freshwater to gulf salinities. in tidal channels and shallow lakes; larvae offshore	Fairly abundant, esoecially during warm months	Valuable snort and commercial fish
FAMILY SOLEIDAE SOLES					
Achirus lineatus (Linnaeus) Lined Sole			Broadly euryhaline, but mainly in high to moderate salinity; widespread	Moderately abundant, late summer, fall	None
Trinectes maculatus (Bloch and Schneider) Hogchoker - Adults	ES	Grazer on meio- and macro-benthos. detritus	Broadly euryhaline; to freshwater, but mainly in brackish to high salinity	Abundant, mainly spring and summer	None
Symphurus plagiusa (Linnaeus) Blackcheek Tonguefish	MA	Carnivore; predator on benthic invertebrates	Broadly euryhaline, but mainly in moderate to high salinity; widespread	Abundant, mainly in spring	None

[a]
FW = freshwater
MA = marine
ES = estuarine
ESM = estuarine-marine (migratory)

Appendix 4. Representative vertebrate species of marsh habitats in the Mississippi River Deltaic Plain (compiled by Mabie, 1976 and Gosselink et al. 1979; see these documents for original sources) (F = Fresh, I = Intermediate, B = Brackish, S = Saline). Scientific and common names of amphibians and reptiles conform to Collins et al. (19821; birds to American Ornithologists' Union (19831; and mammals to Jones et al. (1975).

Species	Marsh zone	Food	Seasonal peaks of abundance or activity	Remarks
AMPHIBIANS				
Ambystoma opacum Marbled salamander	F			
Ambystoma texanum Smallmouth salamander	F			
Notophthdlmus viridescens Central newt	F			
Amphiuma tridactylum Three-toed amphiuma	F			
Siren intermedia Lesser				
Eurycea quadridigitata Dwarf salamander	FI			
Bufo vallicepr Gulf coast toad				
Bufo woodhousel Woodhouse's toad	FIB			
Acris crepitans Northern cricket frog	F			
Hyla cinerea Green treefrog	FI	Insects		
Hyla crucifer Spring peeper	F			
Hyla squirella Squirrel treefrog	F			
Pseudacris triseriata Upland chorus frog				
Rana catesbeiana Bullfrog	F			
Rana clamitans Bronze frog	FIB			
Rand qrylio Pig frog				
Rana sphenocephala Southern leopard frog	FIB			
Gastrophryne carolinensis Eastern narrowmouth toad	FIB			
REPTILES				
Alligator mississippiensis American alligator	FIBS	61% crayfish; also birds, fiddler crabs, fish, insects. (muskrats. turtles, shrimp. grasses, snails		Endangered - Tex Threatened - Id.
Chelydra serpentina Snapping turtle	FIB	Fish (35.4%), other vertebrates (1.1%), carrion (19.6%). invertebrates (7.8%), plant material (36.2%)		
Macroclemys temminckii Alligator snapping turtle	F	Fish, frogs, snakes, other turtles, mussels, various aquatic grasses		
Malaclemys terrapin Diamondback terrapin	BS	Fish, crustaceans. mollusks, insects		
Kinosternon subrubrum Eastern mud turtle	FIB	Insects. small snails		
Sternotherus odoratus Stinkpot	FI	Fish (46.3%). mollusks (40.1%). also crayfish, insects, plant material for Michigan		

(Continued)

Appendix 4. Continued.

Species	Marsh zone	Food	Seasonal peaks of abundance or activity	Remarks
Pseudemys concinna River cooter	S	Largely aquatic vegetation		
Pseudemys floridana Missouri slider	FIB	Largely aquatic vegetation		
Pseudemys picta Southern painted turtle	F	Juvenile: 13% plant, 85% animal Adult: 88% plant, 10% animal		
Pseudemys scripta Red-eared turtle	F	Juvenile: 30% plant, 70% animal (e.g., amphipods) Adult: 89% plant, 11% animal (e.g., crayfish)		
Deirochelys reticularia Chicken turtle	FIB	Tadpoles, crayfish, plant material		
Graptemys kohnii Mississippi map turtle	F			
Graptemys pseudogeographica hbine map turtle	F			
Trionyx spiniferus Spiny softshell	F	Carnivorous		
Anolis caroliniensis Green anole		Insects and spiders		
Coluber constrictor Racer	FIB	Insects, frogs, snakes, young birds	Breeds: May Hatch: July-Sept.	
Farancia abacura Mud snake	F	Amphiuma, Siren, frogs		
Lampropeltis getulus Speckled king snake	FIB	Other snakes, small birds, lizards, mice, rats		
Nerodia cyclopion Green water snake	FIB	Gambusia (77.6%); other fish (18.6%); tadpoles (3.5%)	Mar.-Oct.	
Nerodia fasciata clarkii Gulf salt marsh snake	BS	Fish, fiddler crab		
Nerodia fasciata confluens Broad-banded water snake	FIB	Fish (86.9%); frogs and toads (6.4%); tadpoles (4.3%)	Mar.-Sept.	
Nerodia rhombifera Diamondback water snake	FIB	Fish (92.7%); frogs and toads (1.0%); tadpoles (6.1%)	Mar.-Oct.	
Regina grahamii Graham's crayfish snake	FI	Crayfish (100%)	Mar.-Sept.	
Regina rigida Glossy crayfish snake	FIB	Siren, fish, crayfish		
Storeria a y i Brown snake	FIB	Earthworms. snails, Insects, small frogs, fish		
Thamnophis proximus Western ribbon snake	FIB	Insects, fish. frogs, salamanders, mice, toads		
Thamnophis sirtalis Common garter snake	FI	Earthworms. mollusks, insects, fish, salamanders. toads, frogs, small mammals, small birds		
Agkistrodon piscivorus Cottonmouth	FIB	Fish. salamanders, frogs. reptiles, birds, mammals		
BIRDS				
GREBES & WATERFOWL				
Podilymbus podiceps Pied-billed grebe	FIBS	kstly animal: aquatic worms and insects, snails. small frogs and fish. plants: seeds and soft parts	Oct.-Apr.	
Podiceps nigricollis Eared grebe	FIBS	Insects, shrimp, some water plants. feathers	Oct.-May	
Dendrocygna bicolor Fulvous whistling-duck	FIBS	Mostly seeds of grasses and weeds; also grasses. grain	Apr.-Sept.	

(Continued)

Appendix 4. Continued.

Species	Marsh zone	Food	Seasonal peaks of abundance or activity	Remarks
Anser slbifrons Greater white-fronted goose	FIBS	Grain, tender shoots, occasional insects	Nov.-Mar.	
Anas strepera Gadwall	FIBS	Principally plants	Oct.-Mar.	
Anas americana American wigeon	FIBS	90% plant, 10% animal (from Sept.-Apr.)	Oct.-Apr.	
Aythya collaris Ring-necked duck	FIBS	19% animal: insects, mollusks; 81% plant: aquatic plants, sedges, grasses. smartweeds	Oct.-Apr.	
Aythya affinis Lesser scaup	FIBS	Similar to A. marila	Oct.-Apr.	
Bucephala albeola Bufflehead	FIBS	79% animal: insects, crustaceans, mollusks, fish; 21% plant: pondweeds. misc.	Nov.-Mar.	
Lophodytes cucullatus Hooded merganser	FI	Mostly insects; also small fish, frogs, mollusks, crayfish. roots of aquatic plants, seeds, grain	Nov.-Apr.	
Oxyura jamaicensis Ruddy duck	FIBS	72% plant: aquatic plants. grasses, sedges; 28% animal: insects, mollusks, crustaceans	Nov.-Apr.	
Porphyrula martinica Purple gallinule	F	Rice, other seeds. worms, mollusks	Apr.-Sept.	
Gallinula chloropus Common moorhen	FIB	Seeds. roots. soft parts of aquatic plants, snails insects, worms	Apr.-Nov.	
Fulica americana American coot	FIB	Leaves. fronds, seeds and roots of aquatic plants; wild celery, algae; worms, snails, insects, small fish, tadpoles	Sept.-Apr.	
Chen caerulescens Snow goose	FIBS	Almost wholly plants: grain. roots and culms of grasses; some insects. mollusks	Oct.-Apr.	
Branta canadensis Canada goose	FIBS	Almost wholly plants: aquatic plants, marsh grasses sedges; some mollusks, crustaceans	Oct.-Feb.	
Anas crecca Green-winged teal	FIBS	10% animal: insects, mollusks, crustaceans 90% plant: sedges, pondweeds and grasses (62%); other (28%)	Oct.-Mar.	
Anas rubripes American black duck	FIBS	Mast, grain. mollusks, crustaceans	Oct.-Mar.	
Anas fulvigula Mottled duck	FIBS	40% animal: mollusks, insects, crayfish, small fish; 60% plant: mostly grasses (plants and seeds)	Year-round	
Anas platyrhynchos Mallard	FIBS	90% plant: sedges, grasses. smartweeds. pondweeds, duckweeds, tubers. mast; 10% animal: insects, crustaceans. mollusks, fish	Oct.-Mar.	
Anas a Northern pintail	FIBS	13% animal: mollusks, crustaceans, insects 87% plant: pondweed, sedges and grasses (60%); other (27%)	Oct.-Mar.	
Anas discors Blue-winged teal	FIBS	30% animal: worms, mollusks. insects, tadpoles 70% plant: sedges. pondweeds and grasses (43.6%); other (26.4%)	Feb.-Apr.; Sept.-Nov.	
Anas clypeata Northern shoveler	FIBS	Animal: worms, small mollusks, insects. shrimp. small fish, small frogs. Plant: buds and young shoots of rushes and other aquatics; grasses	Oct.-Apr.	
WADING BIRDS				
Botaurus lentiginosus American bittern	FIB	Mollusks, crayfish, insects, small fish, frogs. lizards, small snakes. mice	Oct.-May	"Blue List" Natl. Aud. Soc. (1976)
Ixobrychus exilis Least bittern	FIBS	Slugs, leeches, insects. small fish, tadpoles, small frogs. lizards. small mammals	Apr.-Sept.	
Ardea herodias Great blue heron	FIBS	Mostly fish; also crustaceans. insects. frogs. lizards, snakes, birds, small mammals	Year-Round	
Casmerodius albus Great egret	FIBS	Small fish, snails, fiddlers, insects. frogs, lizards, small snakes, mice, some plant material	Mar.-Nov.	

(Continued)

Appendix 4. Continued.

Species	Marsh zone	Food	Seasonal peaks of abundance or activity	Remarks
Eqretta thulr Snowy egret	FIBS	Shrimp, small fish, fiddlers, snails, insects. crayfish, small lizards, small frogs, small snakes	Mar.-Oct.	
caerulea Little blue heron	FIBS	Crayfish, small crabs, insects, fish, frogs, lizards	Mar.-Oct.	
Eqretta c o l o r Tricolored heron	FIBS	Slugs, snails, crayfish, insects, small fish, lizards, frogs	Mar.-Nov.	
Eqretta rufescens Reddish egret	BS		Mar.-Oct.	"Blue List" Natl. Aud. Soc. (1976)
Bubulcus ibis Cattle egret	FIBS	Insects	Year-Round	
Butorides striatus Green-backed heron	FIBS	Small fish, earthworms, insects. tadpoles, frogs, snakes, small mammals	Mar.-Oct.	
Nycticorax nycticorax Black-crowned night-heron	FIBS	Mostly fish (alive or dead), worms, crustaceans, insects	Mar.-Sept.	"Blue List" Natl. Aud. Soc. (1976)
Nycticorax violaceus Yellow-crowned night heron	FIBS	Snails, crayfish. crabs, fish, small reptiles, small mammals and birds	Mar.-Sept.	
Eudocimus albus White ibis	FBS	Mostly crayfish; also other crustaceans, slugs snails. small snakes. insects	Mar.-Sept.	"Blue List" Natl. Aud. Soc. (1976)
Plegadis falcinellus Glossy ibis	FIBS	Insects, crayfish. young snakes		
Plegadis chihi White-faced ibis	FIBS	Earthworms, crayfish, mollusks, insects, small fish and frogs, newts. leeches	Year-Round	"Blue List" Natl. Aud. Soc. (1976)
Mycteria americana Wood stork	FIB	Fish, aquatic reptiles, insects	Jun.-Sept.	"Blue List" Natl. Aud. Soc. (1976)
SHORE BIRDS				
Pluvialis squatarola Black-bellied plover	FIBS	Marine worms, small mollusks, crustaceans, insects, sane plant material	Sept.-May	
Charadrius semipalmatus Semipalmated plover	S	Worms, small mollusks, crusteans, insects	Sept.-Hay	
Himantopus mexicanus Black-necked stilt	FIBS	99% animal: mostly insects; also crayfish, snails, tiny fish; 1% plant: seeds of aquatic and marsh plants	Mar.-Oct.	
Recurvirostra americana American avocet	FIBS	65% animal: insects. 35% plant: seeds of aquatic and marsh plants	Sept.-May	
Tringa melanoleuca Greater yellawlegs	FIBS	hall fish, occasionally insects	Feb.-May; Aug.-Nov.	
Tringa flavipes Lesser yellowlegs	FIBS	Mostly insects; also small crustaceans, small fish, worms	Feb.-May; Aug.-Nov.	
Tringa solitaria Solitary sandpiper	FIBS	Insects, spiders. worms, small crustaceans, small frogs	Mar.-Apr.; Aug.-Oct.	
Catoptrophorus sanipalmatus Willet	IBS	Worms, insects, small crabs, small mollusks, small fish, grasses, tender roots, seeds	Year-Round	
Actitis macularia Spotted sandpiper	FIBS	Insects, occasionally small fish	Mar.-Apr.; Pug.-Oct.	
Numenius phaeopus Whimbrel	FIBS	Earthworms. sandworms, Insects. mollusks, small crustaceans, sane plant material	Apr.-May	
Limosa haemastica Hudsonian godwit	FIBS	Worms, mollusks, various insects, crustaceans, other small marine life	Apr.-June	
Calidris pusilla Semipalmated sandpiper	IBS	Small mollusks, worms, insects, plant material	Apr.-May; Sept.-Nov.	

(Continued)

Appendix 4. Continued.

Species	Marsh zone	Food	Seasonal peaks of abundance or activity	Remarks
Calidris mauri Western sandpiper	FIBS	Insects, marine worms, small snails	Aug.-May	
Calidris minutilla Least sandpiper	FIBS	Mostly insects; also small crustaceans. worms	Aug.-Apr.	
Calidris bairdii Baird's sandpiper	FIBS	Insects, amphipods. algae	Mar.-May; July-Oct.	
Calidris alpina Dunlin	FIBS	Small mollusks, small crustaceans. insects. marine worms, occasionally seeds	Oct.-May	
Calidris himantopus Stilt sandpiper	FIBS	Animal (70%): small worms, mollusks, insects Plant (30%): seeds	Apr.-May	
Limnodromus griseus Short-billed dowitcher	FIBS	Worms, insects. fish eggs, small mollusks, seeds and roots of aquatic plants	Mar.-May; Sept.-Nov.	
Limnodromus scolopaceus Long-billed dowitcher	FIBS	Insect larvae, some plant material	Oct.-May	
Gallinago gallinago Common snipe	FIBS	Mostly earthworms, also other worms, insects, sane seeds of marsh plants	Oct.-Apr.	
Phalaropus tricolor Wilson's phalarope	FIBS	Aquatic insects and their larvae; amphipods; seeds of aquatic plants	Apr.-May; July-Sept.	
FISHING BIRDS				
Pelecanus erythrorhynchus American white pelican	BS	Fish	Sent.-by	
Larus atricilla Laughing gull	IBS	Mostly small fish; also eggs of other seahirds, refuse	Year-Round	
Sterna nilotica Gull-billed tern	IBS	Insects	Oct.-Apr.	"Blue List" Natl. Aud. Soc. (1976)
sterna caspia Caspian tern	IBS	Almost wholly small fish; also shrimp and other surface-swimming aquatic life	Year-Round	
Sterna forsteri Forster's tern	IBS	Insects. floating carrion	Year-Round	
Childonias niger Black tern	FI	Small fish, insects	Apr.-Sept. (nonbreeding)	
Ceryle alcyon Belted kingfisher	FIBS	Almost wholly fish; also insects, crustaceans, mollusks, amphibians, small reptiles, birds. mice, herries	Sept.-Apr.	
BIRDS OF PREY				
Circus cyaneus Northern harrier	FIBS	Small mammals, herons, ducks, coots, rails, shorebirds, songbirds	Sept.-Apr.	"Blue List' Natl. Aud. Soc. (1976)
Falco sparverius American kestrel	FIBS	Insects. amphibians, reptiles, birds. mammals	Sept.-May	"Blue List" Natl. Aud. Soc. (1976)
Falco colunbarius Merlin	FIBS	Mostly birds: green-winged teal. shorebirds, small chickens, various songbirds; also insects. spiders. reptiles, mice, pocket gophers, squirrels, hats	Sept.-May	"Blue List" Natl. Aud. Soc. (1976)
Falco peregrinus Peregrine falcon	IBS	Primarily birds; also small mammals, insects	Sept.-May	Endangered
Asio flammeus Short-eared owl	FIBS	Mostly small mammals, also small birds. insects	Oct.-Clay	"Blue List" Natl. Aud. Soc. (1976)

(Continued)

Appendix 4. Continued.

Species	Marsh zone	Food	Seasonal peaks of abundance or activity	Remarks
OTHER MARSH BIRDS				
Chordeiles minor Common nighthawk	FIBS	Insects, mostly flying	Apr.-Oct.	"Blue List" Natl. Aud. Soc. (1976)
Coturnicops noveboracensis Yellow rail	FIBS		Oct.-May	
Laterallus jamaicensis Black rail	FIBS		Nov.-Apr.	
Rallus longirostris Clapper rail	BS			
Rallus elegans King rail	FIB	Grass seeds, insects, slugs, leeches, tadpoles, crayfish	Year-Round	
Rallus limicola Virginia rail	FIBS	Earthworms, crayfish, insects, snails, small fish, sane grass seeds	Oct.-Apr.	
Porzana carolina Sora	FIBS	hall mollusks, insects, seeds	Sept.-Hay	
Tachycineta bicolor Tree swallow	FIBS	81% animal: insects and spiders 21% plant: seeds and berries	Sept.-May	
Riparia riparia Bank swallow	FIBS	Insects	Apr.-May; July-Oct.	
Hirundo pyrrhonota Cliff swallow	IBS		Apr.-June	
Hirundo rustica Barn swallow	FIBS	99% animal: insects; sane spiders and snails	Mar.-May; Aug.-Nov.	
Corvus ossifraqus Fish crow	FIBS	Carrion, crustaceans, fish, hird eggs, insects; berries. tree fruits. seeds, sane grain	Year-Round	
Cistothorus platensis Sedge wren	FIBS	Insects, spiders	Oct.-Mar.	
Cistothorus palustris Marsh wren	FIBS	Insects; especially Coleoptera and Diptera	Year-Round	
Anthus spinoletta Water pipit	FIBS		Nov.-Mar.	
Geothlypis trichas Common yellowthroat	FIBS	Mostly insects, a few seeds	Mar.-Oct.	
Passerculus sandwichensis Savannah sparrow	FIBS	92% plant: seeds; 8% animal: mostly insects (winter)	Oct.-Apr.	
Ammodramus caudacutus Sharp-tailed sparrow	BS	81% animal: insects, amphipods, spiders. snails 19% plant: grasses, seeds	Nov.-Mar.	
Ammodramus maritimus Seaside sparrow	S	Marine worms, crustaceans, insects, spiders, mollusks. weed and grass seeds	Year-Round	
Melospiza georgiana Swamp sparrow	FI	55% insects; 45% seeds	Sept.-May	
Dolichonyx oryzivorus Bobolink	FIBS	57% animal: insects, spiders, myriapods; 43% plant: weed seeds. grain	May	
Agelaius phoeniceus Red-winged blackbird	FIBS	73% plant: weed seeds, grain, fruit; 21% animal: mostly insects and spiders	Year-Round	
Quiscalus major Boat-tailed grackle	FIBS	Insects, spiders, small fish, tadpoles	Year-Round	
MAMMALS				
Didelphis virginiana Virginia opossum	FIBS	Insects, birds. carrion, plant material	Breeds in Jan.-Feb.	

(Continued)

Appendix 4. Concluded.

Species	Marsh zone	Food	Seasonal peaks of abundance or activity	Remarks
Myotis austroriparius Southeastern myotis		Insects	Active year-round in warm weather; mating in spring	
Lasiurus borealis Red bat	F	Insects	Active year-round in warm weather; young born May-June	
Lasiurus seminolus Seminole bat	F	Insects	Active year-round in warm weather; young born in June	
Dasypus novemcinctus Nine-banded armadillo	FIBS	Insects, plant material	Breeds in July-Auq.	
Sylvilagus aquaticus Swamp rabbit	FIBS	Green plants	Breeds Jan.-Sept.	
Oryzomys palustris Marsh rice rat	FIBS	Plant material, insects, crustaceans, bird eggs and young	Breeds Mar.-Oct.	
Ondatra zibethicus Common muskrat	FIBS	61% crayfish; also crabs, birds, fish, insects	Active year-round; breeding peaks Nov. and Mar.	
Myocastor coypus Nutria	FI	Aquatic vegetation		
Procyon lotor Northern raccoon	FIBS	Animals and plant material	Breeds Dec.-Jan.	
Mustela vison Mink	FIB	Crayfish, rodents, birds, fish, crabs, frogs	Active year-round, young born in early spring	
Lutra canadensis River	FIBS	Crabs, crayfish, fish, frogs, turtles. snakes	Breeds in late fall	
Odocoileus virginianus White-tailed deer	FIB	Plant material	Breeds in Sept.-Mar.	

50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. FWS/OBS-84/09	3. Recipient's Accession No.

4. Title and Subtitle
The Ecology of Delta Marshes of Coastal Louisiana: A Community Profile

5. Report Date
May 1984

6.

7. Author(s)
James Gosselink

8. Performing Organization Rept. No.

9. Author's Affiliation

Center for Wetland Resources
Louisiana State University
Baton Rouge, LA 70803

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.
(C)
(G)

12. Sponsoring Organization Name and Address
Fish and Wildlife Service
Division of Biological Services
Department of the Interior
Washington, D.C. 20240

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

This document reviews and synthesizes ecological information and data on the extensive marshes of the Mississippi River Deltaic Plain. Over the past 6,000 years the river has built a delta onto the Continental Shelf of the Gulf of Mexico covering about 23,900 km^2. This low land is primarily marshes and represents about 22% of the total coastal wetland area of the 48 contenninous United States. The delta is notable for its high primary productivity, its valuable fishery and fur industry, and the recreational fishing and hunting it supports.

The Mississippi River delta marshes are subject to the unique problem of extremely rapid marsh degradation due to a complex mixture of natural processes and human activities that include worldwide sea-level rise; subsidence; navigation and extractive industry canal dredging; flood control measures that channel the river; and pollution from domestic sewage, exotic organic chemicals, and heavy metals.

17. Document Analysis a. Descriptors
Marshes, ponds, aquatic plants

b. Identifiers/Open Ended Terms
Miss.issippi River Delta, tidal marshes, subsidence, sea-level rise, furbearers, marsh ponds, emergent vascular plants, nutrient cycles, marsh loss, wetlands, waterfowl.

c. COSATI Field/Group

18. Availability Statement	19. Security Class (This Report)	21. No. of Pages
Unlimited	Unclassified	134
	20. Security Class (This Page) Unclassified	22. Price

(See ANSI-Z39.18)

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce

☆ U.S. GOVERNMENT PRINTING OFFICE: 1986—659-142/40000

DEPARTMENT OF THE INTERIOR

U.S. FISH AND WILDLIFE SERVICE

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.