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THE ECOLOGY OF IRREGULARLY FLOODED SALT MARSHES OF THE NORTHEASTERN GULF OF MEXICO: A Community Profile

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THE ECOLOGY OF IRREGULARLY FLOODED SALT MARSHES OF THE NORTHEASTERN GULF OF MEXICO: A COMMUNITY PROFILE

by

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PREFACE

This community profile is one in a series of Fish and Wildlife Service publications compiled to provide a state-of-the-knowledge synthesis of scientific information and literature available on various coastal habitats. The emphasis of this profile is on irregularly flooded *Juncus roemerianus* marshes along the shores of the northeastern arc of the Gulf of Mexico from the Pearl River, Mississippi, to Cedar Key, Florida.

Information for the profile was gathered from both published literature and, where accessible, numerous graduate research theses and dissertations. Although the majority of marshes in this region are dominated by *Juncus*, research emphasis has been on community structure and function in zones of the marsh dominated by other species such as *Spartina alterniflora*. Some sections of the profile, therefore, focus on selected zones or species in the marsh because of the lack of information on other zones or species. In most cases throughout the profile, the data are representative of marshes of this particular area only.

It is hoped that the profile content and format will be useful to a broad spectrum of users including other scientists, students, resource managers and planners, teachers and interested laypersons. The profile includes structural and functional aspects of the community: its environmental setting, zonation and vascular plant communities, microbial and nonvascular plant communities, marsh fauna, ecological dynamics, and human impact. A brief summary of research needed in this habitat as determined from information lacking in the available literature is provided.

Questions or comments concerning this profile or others in the series should be directed to the following address.

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CONVERSION TABLES

Metric to U.S. Customary

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 (l)	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 (kg)	2.205	pounds
metric tons (mt)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	BTU
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
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
BTU	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius degrees

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ACKNOWLEDGMENTS

I am grateful to the many researchers who braved the Juncus marshes acquiring the information which has allowed me to compile this document. I am responsible for the manner in which their data have been utilized and assimilated here. I am indebted to Richard Heard, Mike Sullivan, Susan Ivester Rees, Bob Shipp, and Dan Holliman for early reviews of portions of the manuscript. The manuscript was further reviewed by Bill Kruczynski, Courtney Hackney, Lionel Eleuterius, Joe Ustach, Howard Marshall, James Barkuloo, Sandy Tucker, Ed Pendleton, and Larry Vinzant. Lynn Bryant persevered through my errors and revisions, holidays, and imminent birth of her child to type and retype the various editions of the manuscript. For her patience and skills I am indeed thankful. All illustrations were prepared by Linda Lutz, including original figures and redrawings of the works of others. Her talents and efforts have been invaluable to the completion of this profile.

The manuscript was edited by Kate Lyster and Rob Brown.

LIST OF ABBREVIATIONS AND SYMBOLS

ha = hectare
m = meter
CFS = cubic feet per second
mm = milimeter
cm = centimeter
ppt = parts per thousand
o/oo = parts per thousand
MLW = mean low water
MHW = mean high water
H' = Shannon-Weiner Diversity
S = total number of species
BI = Biological index
m^2 = meter square area
r = coefficient of correlation between two samples
D = Species Richness
E = Species Equitability
g = gram
mg = milligram
ANPP = Annual net primary productivity
Kg = kilogram
KJ = kilojoule
ml = milliliter
C^o = temperature in degrees centigrade
sq mi = square mile
T(C) = temperature centigrade
S(o/oo) = salinity
R^2 = coefficient of determination in multiple regression
$\bar{x}$ = mean value
Kcal = kilocalorie
^{13}C = isotope of carbon
AFDW = ash free dry weight
MSL = mean sea level

CHAPTER 1

ENVIRONMENTAL SETTING

DISTRIBUTION

The black needlerush (Juncus roemerianus Scheele) occurs along the Atlantic and Gulf of Mexico coasts of North America between latitudes 25° and 42° N, reaching its northern limit along the coast of New Jersey. Of the 3,174,333 ha of marsh area in the eastern United States, 10.06% is dominated by J. roemerianus (Eleuterius 1976a). Table 1 summarizes the areal extent of Juncus roemerianus - dominated marshes in the United States. Though the northeastern gulf (west Florida, Alabama, and Mississippi) contains only 8% of United States marsh area, it represents over 28% of all United States J. roemerianus - dominated marshes as compared to 47% along the Atlantic coast. This three-state arc in the gulf has a greater proportion (52.9%) of its marshlands dominated by the needlerush than any other area of the country.

Large, well-developed, but discontinuous stands of Juncus border the low-energy shorelines, sounds, lagoons, and bays from Cedar Key, Florida, to the Pearl River estuary, Mississippi (Figure 1). South of Florida's Cedar Key, mangrove species begin to codominate with Juncus, and at lower latitudes mangroves far exceed Juncus in abundance and biomass. The Mississippi River discharge and delta system west of the Pearl River in Louisiana creates conditions for extensive marsh development dominated by Spartina alterniflora with abundant Juncus. Only a few large marshes of Juncus are found in Texas, though the species is scattered along the coast into Mexico. Hypersaline conditions in many Texas coastal areas exclude Juncus.

Further discussions of gulf Juncus roemerianus marshes will refer to coastal Mississippi, Alabama, and northwest Florida and to Juncus without the specific epitaph unless other than J. roemerianus.

Irregularly flooded Juncus marshes are classified in the U.S. Fish and Wildlife Service's wetland's classification system (Cowardin et al., 1979) as follows:

System - Estuarine
 Subsystem - Intertidal
  Class - Emergent wetland
   Subclass - Persistent
    Water regime - Irregularly flooded.

CLIMATOLOGY

Gulf coast climatology is characterized by southerly to southeasterly prevailing winds governed by the intensity of circulation about the Azores-Bermuda High. Prevailing onshore winds provide the single most important source of atmospheric moisture to the gulf region of the United States. This prevailing flow is most pronounced in the summer when the high is strongest and furthest north. As the high weakens in winter, the gulf falls under the influence of disturbances in the midlatitudinal westerlies. Intrusions of polar air thrust deep into the region and often stall over coastal areas, producing a stable dome of cold air sometimes far over the gulf (Ward 1980). Winter frost in these coastal marshes prevents the

Table 1. Proportionate distribution of Juncus-dominated marshes of the northeastern Gulf of Mexico to total marsh area: northeastern gulf, total gulf, and gulf and Atlantic coasts of the United States, 1972. (Data from Eleuterius 1976a).

	Marshes		
	Total area (ha)	Juncus-dominated (ha)	Juncus-dominated (% of each total)
NE Gulf of Mexico			
Florida (West Coast)	214,054[a]	60,750[d]	28.38
Alabama	14,019[b]	4,290[b]	30.60
Mississippi	27,107[c]	24,866[c]	91.73
Total	255,180	89,906	35.23
Total U.S. Gulf	2,314,200[d]	170,067[d]	7.35
NE Gulf as % of U.S. Gulf Total	11.03	52.86	
Total U.S. (Atlantic and Gulf)	3,174,333[d]	319,383[d]	10.06
NE Gulf as % of U.S. Total	8.04	28.15	

[a] McNulty et al. 1972.
[b] Crance 1971.
[c] Eleuterius 1972.
[d] Eleuterius 1976.

successful establishment of mangrove species. Mean annual temperatures are approximately 70° F (Table 2A).

The summer climate becomes almost tropical, punctuated by convective airmass thunderstorms and infrequent tropical disturbances, e.g., easterly waves and hurricanes. The interaction between moist, convectively unstable gulf air and frontal systems is a primary mechanism for production of precipitation for the eastern gulf, especially in the summer. This area exhibits a late spring to summer maximum in rainfall and hence, a maximum in freshwater runoff. Mean annual precipitation is from 50 to 67 in. depending on the record station (Table 2B).

Freshwater runoff and its associated sediment input into coastal waters in the northeastern gulf is significant (Table 3). The two largest discharge systems are the Apalachicola in Florida (22,485 cfs) and the Mobile Bay system, Alabama (65,515 cfs); both empty into large estuarine

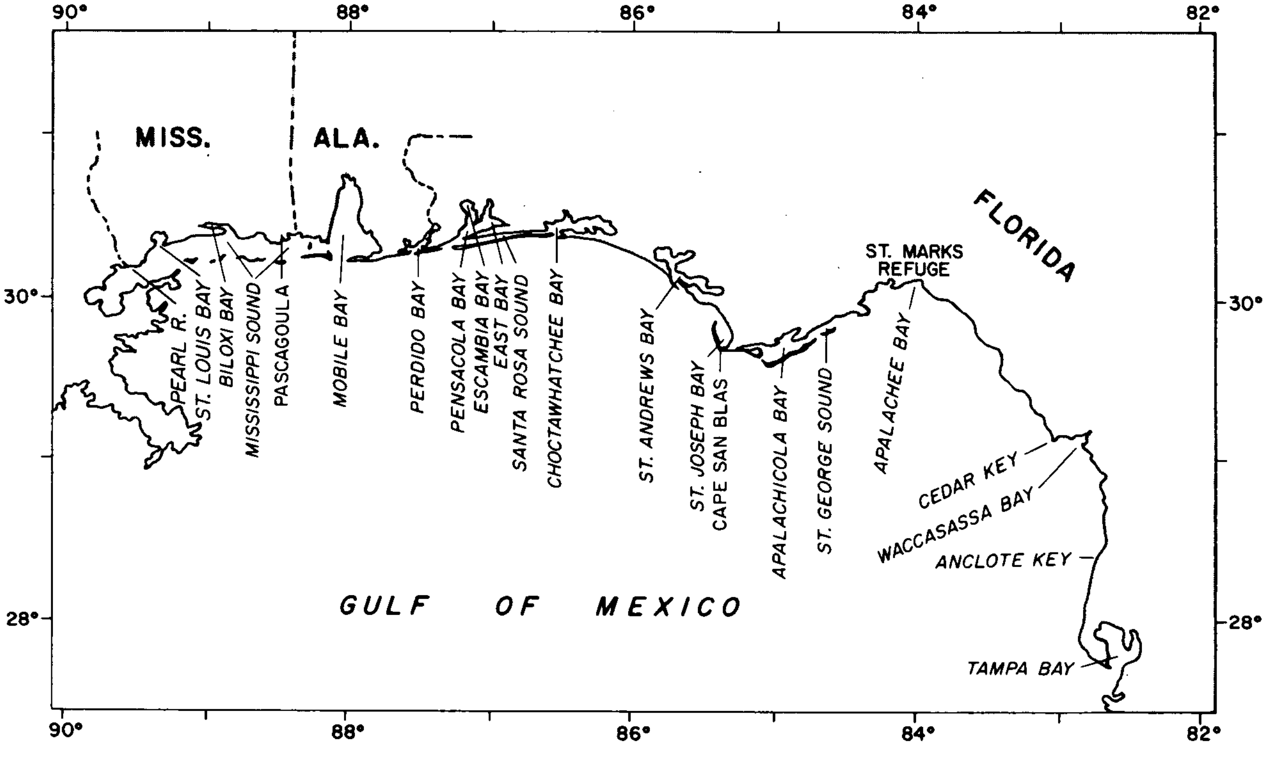


Figure 1. Northeastern Gulf of Mexico showing the location of coastal systems where Juncus roemerianus marshes may be found.

embayments. Other major rivers include the Suwannee and Escambia in Florida and the Pascagoula and Pearl in Mississippi. Between the Apalachicola River and Suwannee River on the Florida west coast there are no major rivers; the smaller rivers empty directly into the Gulf of Mexico.

TIDES AND SEA LEVEL

Tides of the northeastern Gulf of Mexico are of two types: semidiurnal from south Florida to Apalachicola Bay and diurnal (daily) from Apalachicola Bay westward (Figure 2). Semidiurnal tides are mixed with unequal highs and lows and range from 0.67 m to 1.16 m (Provost 1973). Changes in range in semidiurnal tides are correlated with the moon's phase, the greatest range (spring tides) corresponding with the new and full moon and lowest ranges (neap tides) near the times of the moon's first and third quarters. Between spring and neap tides the range may decrease from 20 percent above the average to about 20 percent below the average on a 7.5 day cycle (Marmer 1954).

Daily tides to the west are of less amplitude (0.37-0.52 m) than the semidiurnal tides. The main source of variation in range of the daily tides is associated with the moon's declination. When the moon is over or near the equator the tide has its lowest range and is called an equatorial tide. Tropic tides with the greatest range occur at 13 3/4 day intervals when the moon is near its

Table 2A. Mean monthly and mean annual air temperature (1941-1970) and 1982 departures from normal (°F) (modified from NOAA 1983).

Station	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual total	1982 departure
Tampa, FL	60.4	61.8	66.0	72.0	77.2	81.0	81.9	82.2	80.8	74.7	66.8	61.6	72.2	+ 1.2
Apalachicola, FL	53.7	55.8	60.7	68.3	74.9	80.0	81.4	81.5	78.6	70.8	61.1	55.2	68.5	+ 0.4
Pensacola, FL	52.1	54.8	59.9	68.1	75.2	80.6	81.8	81.8	78.3	70.0	59.5	53.8	68.0	- 0.8
Mobile, AL	51.2	54.0	59.4	67.9	74.8	80.3	81.6	81.5	77.5	68.9	58.5	52.9	67.4	+ 0.3

Table 2B. Mean monthly and mean annual precipitation (1941-1970) and 1982 departures from normal (inches) (modified from NOAA 1983).

Station	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual Total	1982 Departure
Tampa, FL	2.33	2.86	3.89	2.10	2.41	6.49	8.43	8.00	6.35	2.54	1.79	2.19	49.38	+13
Apalachicola, FL	3.07	3.78	4.70	3.61	2.78	5.30	8.02	8.07	9.00	2.88	2.68	3.32	57.21	+26
Pensacola, FL	4.37	4.69	6.31	4.99	4.25	6.30	7.33	6.67	8.15	3.13	3.37	4.66	64.22	- 9
Mobile, AL	4.71	4.76	7.07	5.59	4.52	6.09	8.86	6.93	6.59	2.55	3.39	5.92	69.98	+11

Table 3. Drainage area, annual mean streamflow, 1981-82 percentage of normal flow, and receiving waters of major rivers.

River, State	Drainage area[a] (mi^2)	Normal flow (cfs)	1981-82 flow[b] (percent of normal) 1981	1982	Receiving waters[a]
Suwannee, FL	7,090	10,150	55	80	Gulf of Mexico
Apalachicola, FL	17,100	22,485	56	85	Apalachicola Bay
Escambia, FL	3,817	6,170	62	91	Pensacola Bay
Alabama, AL	22,000	36,011	52	*	Mobile Bay
Tombigbee, AL	8,700	26,504	54	*	Mobile Bay
Pascagoula, MS	6,600	9,770	66	68	Mississippi Sound
Pearl, MS	6,630	9,641	58	66	Lake Borgne

[a] From Kwon 1969
[b] From NOAA 1983
*Data unavailable.

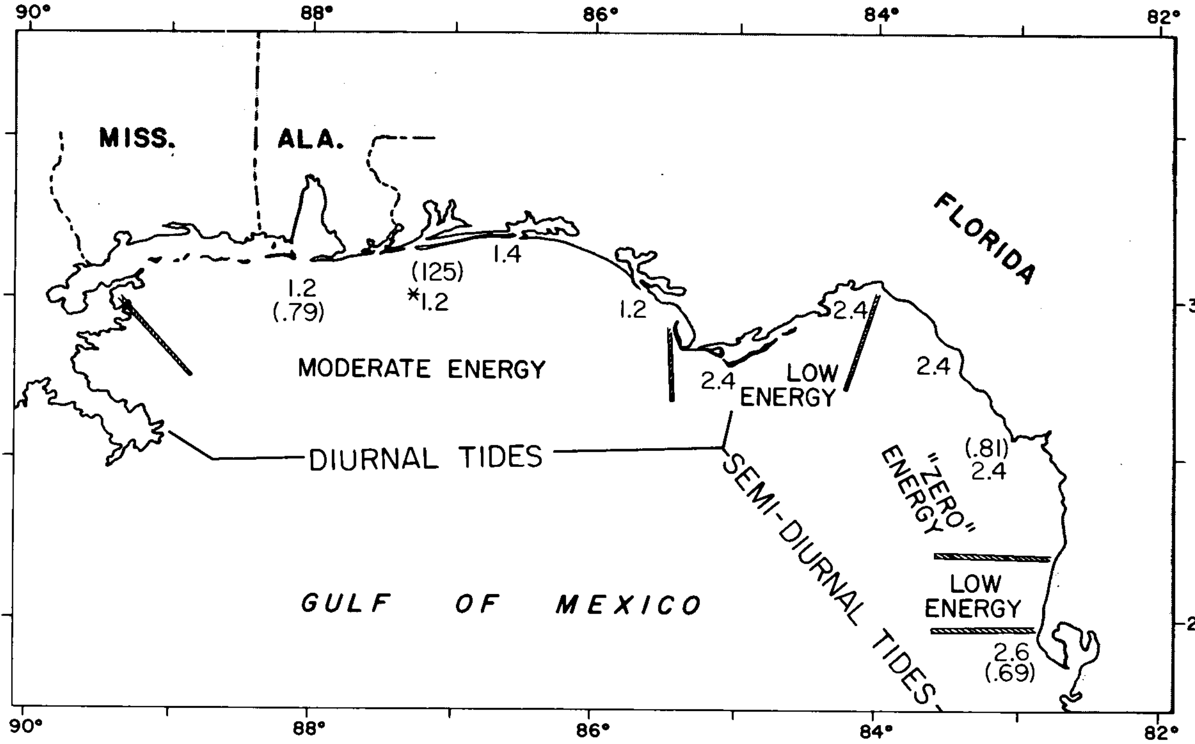


Figure 2. Northeastern Gulf of Mexico tidal characteristics (Coast and Geodetic Survey 1982), energy levels (Tanner 1960), and mean tide intervals (ft) with 100-year sea-level rises in parentheses (Provost 1973).

maximum declination north or south (Provost 1973).

Weak astronomical tides (low amplitude) are often overshadowed by meteorological conditions such as seasonally changing wind directions and summer tropical storms. Tides of the Atlantic marshes are typically semidiurnal with amplitudes of 2.0 m or greater and are maintained by more stable meteorological conditions.

On the northeast gulf coast, monthly sea level rises above the mean annual level beginning in May. It remains above the mean level for half the year (June-December) as compared to the Atlantic coasts, where levels climb rapidly above the mean between August and September and remain elevated for only three months (Provost 1973). Higher sea levels, coupled with southerly winds, result in increased marsh flooding even on neap tides. This coincidence of conditions increases high tide heights causing even the high marsh meadow to remain flooded for considerable periods of time (Provost 1973).

Changes in mean sea level are currently proceeding at a very low rate in the northeastern gulf. Shepard (1960) proposed that sea level rose at an average rate of about 0.85 m per century from 17,000 to 8,000 years before the present. From there the rate decreased to less than 0.3 m per century until about 3,600 years ago when it reached its present level (Coleman and Smith 1964). The current estimated rate of sea level rise for Florida is +2.4 mm yr^{-1} (Provost 1973); on the gulf coast the rate is +1.8 mm yr^{-1} (Aubrey and Emery 1983).

DEVELOPMENT OF COASTAL FEATURES

The shore from Anclote Key to Apalachee Bay is classified as a "zero energy" sector in which wave energy is dampened over the broad, shallow limestone plateau of the gulf bottom (Price 1953; Figure 2). There are no significant sediment sources; hence no barriers have formed; and there is only slight beach development (Figure 3). Shorelines support Juncus marshes directly on the Gulf of Mexico. Scattered mangroves may occur.

West of Apalachee Bay, the Apalachicola River (largest in Florida) and the Ochlockonee River supply alluvium downdrift to the west and across St. Josephs Bay for the construction of a system of beaches, spits, barrier islands, and bars at the river mouths. Within this low-energy zone, marshes are found on the leeside of barriers and within bays protected by wave action (Tanner 1960; Kwon 1969).

Sediment from alluvial and shelf sources is largely lost to coastal deposition west of St. Josephs Bay where the 75-ft. depth contour sweeps into the nearshore zone, directing material from the westward drift into deeper waters. No barriers are found in this zone (Tanner 1960). Moderate energy waves form gulf-front beaches, with marshes restricted to protected bays such as St. Andrews Bay and Choctawhatchee Bay.

Santa Rosa Island and the Mississippi Sound barriers further west receive sediments downdrift from Choctawhatchee Bay and Mobile Bay, respectively, as well as sands from the Continental Shelf (Kwon 1969). Steep mainland bluffs behind Santa Rosa Island do not support broad salt marshes; these are restricted to shorelines of the Pensacola, Escambia, and East Bays. The Mississippi Sound barriers provide protection for the mainland from moderate gulf wave energies and result in extensive marsh development along both shores of the sound.

SUBSTRATE CHARACTERISTICS

Tidal marsh soils of the gulf coast are very diverse, as would be expected with different sediment sources and varied depositional environments. In a study of the marshes of Wakulla County, Florida, Coultas (1969, 1970) found four major groups of soils: haplaquods, psammaquents, haplaquolles, and ochraqualfs. These soils were saline, predominately sandy in texture, and shallow over limestone. Magnesium (Mg) was the predominate cation found. Sodium (Na) was found to be more abundant than potassium (K), contrary to conditions usually found in upland soils. This condition is probably due to the high

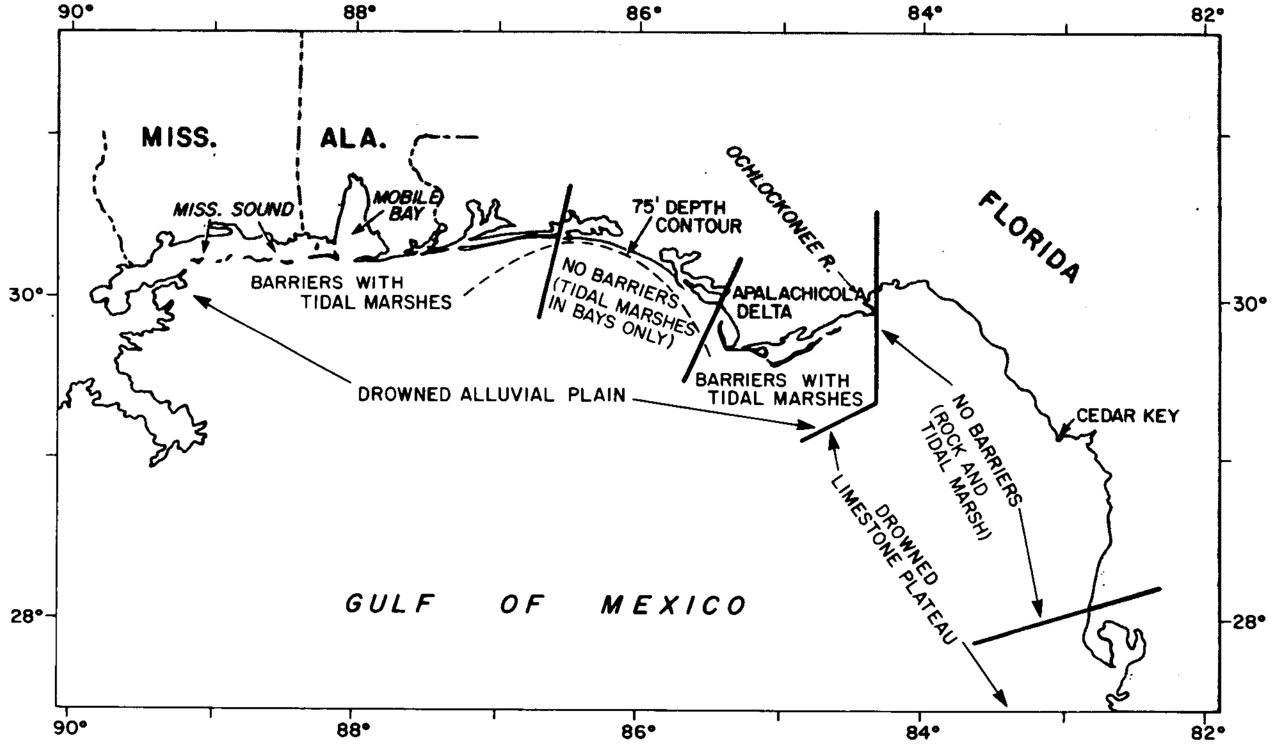


Figure 3. Coastal features of the northeastern Gulf of Mexico (modified from Price 1954 and Tanner 1960).

proportion of Mg and Na salts found in seawater. Sulfidic layers were found in the haplaquolls. Soils were found to be highly mixed at the surface by animals, especially fiddler crabs (Uca spp.). Species of Distichlis predominated on the haplaquods and ochraqualfs, and species of Juncus predominated on psammaquents and haplaquolls (Coultas 1969, 1970).

Three major soil groups were found in other marshes of Apalachee Bay, Florida (Coultas and Gross 1975). Psammaquents and haplaquods occupied a position in the upper marsh adjacent to the uplands. Sulfaquents were typically in a lower marsh position. Both soil organic matter and clay content decreased sharply from lower elevation to higher elevation soils. In the area of sulfaquents, the odor of hydrogen sulfide gas was strong. Air drying of soils produced abrupt decreases in soil pH (2-4 units) with greatest increases in the sulfaquents. Higher content of organic carbon and clay in surface horizons of this soil group along with highly reduced conditions increased the retention of iron sulfides. Calcium was the most abundant extractable base with Na usually more prevalent than K. Psammaquents and haplaquods were sandy. Particle size data indicated deposition of silt and clay marine sediments on the sulfaquents (Coultas and Gross 1975).

Additional sediment analysis in these same marshes along the "zero energy" zone of west Florida revealed peaty sandy mud, carbonaceous muddy sand, or relatively clean sand based upon grain size and amount of organic matter (15-40 %, 4-15% and 0.1-4%, respectively) (Swanson et al. 1972). More than 90% of the inorganic component of the sediment was silt-sized to medium-sized quartz. Pyrite was the second most abundant inorganic mineral. Eighty percent of the organic matter in the sediments was humic material from inland swamps delivered to the marsh by streams. The remaining 20% of the organic matter was also of the humic type, mainly derived from the stalks and root matter of Juncus and to a minor extent from nearby seagrasses such as Thalassia testudinum (Swanson et al. 1972).

The pH and Eh of the sediments are related to organic content - the greater the amount of organic matter, the lower the pH and Eh. Swanson et al. (1972) found marsh soils very acidic and highly reducing. Some metals were enriched in the sediment because of the abundant organic matter and the reduced environment. These included iron, manganese, cobalt, chromium, copper, molybdenum, nickle, and vanadium (except for iron, each less than 0.1% of the sample). Iron sulfide exhibited marked increase with depth.

Mississippi Sound marsh soils grade from generally sandy (e.g., barrier island marshes) to silty with a thin surface layer of muck. Texture analysis by Humphrey (1979) on muddy inshore marsh substrate revealed the following components: 24-28% sand, 40-48% silt, and 24-36% clay. Soil organic matter content ranged from 5 to 13%. The pH values were about 5.2-5.9 in areas dominated by Spartina cynosuroides and 6.2 in Juncus marshes (Hackney and de la Cruz 1978; Faulkner and de la Cruz 1982). Interstitial water salinities ranged from 2.5 to 16.8 ppt and reached about 20 ppt during prolonged dry periods (Hackney and de la Cruz 1978). Both marsh types showed similar orders of relative abundance of nutrient elements (N > Mg > Ca > K > Mn > P > Zn).

SALINITY

As with soils, it is difficult to generalize about marsh salinity levels. Surface water salinities reflect seasonal meteorological conditions and runoff patterns coupled with tidal conditions. Salinity ranges have been measured at 0.0-9.0 ppt (Bishop 1981) and 16.2-27.8 ppt (Sage and Sullivan 1978) in Mississippi marshes, and 13.2-19.1 ppt in Florida marshes (Lindberg and Harris 1973).

Salinities of interstitial waters within the sediments vary not only geographically, reflecting surface water levels, but also within different zones of a single marsh. Mean interstitial salinities near the soil surface (1-4 cm) ranged from 10.1 to 24.4 ppt, while at 22-25 cm depths, salinities were 8.5-12.1 ppt (Lindburg and Harris 1973). Mean interstitial salinities decreased with depth by as much as 50% from a value near the sediment-water interface. This decrease was directly affected by the overlying salinity. Interstitial salinities decreased slightly in response to low-salinity overlying water but increased after exposure to more saline overlying waters, indicating a density gradient-induced exchange across the interface. Interstitial salinities at a depth of 23.5 cm were controlled by response of the fresh groundwater table to varying hydrostatic pressures.

In a Mississippi marsh dominated by Juncus and Spartina cynosuroides, interstitial water salinities also reflected changes in the surface water (Hackney and de la Cruz 1978). The salinity of interstitial water was usually higher, varying between 2.5 and 15.8 ppt, than the nearby surface water which ranged from 0.0 to 11.5 ppt. Maximum flooding of marsh zones was from 0.2 to 12% of the time. Salinity increased as distance of the sampling station from the creek increased, a situation similar to that found in Florida by Kurz and Wagner (1957), Williams (1981), and others (Jackson 1952; Harp 1980).

CHAPTER 2

MARSH ZONATION AND VASCULAR PLANT COMMUNITIES

PLANT COMMUNITY COMPOSITION

In any marsh setting, the most obvious visual impression is one of almost homogenous expanses of dense grass-like plants. In fact, marshes are more often typified by the dominant vascular plant species than by any other feature (i.e., Spartina alterniflora marsh or Juncus marsh). Very few plants have physical and physiological adaptations to grow and reproduce in the conditions of salinity and flooding found in the salt marsh. For this reason, several genera within the grass family (Poaceae), sedge family (Cyperaceae), and rush family (Juncaceae) dominate, represented throughout the world's salt marshes by only a few species. Marsh plant communities are low in species diversity and typically dominated by a small number of species. The remainder of the vascular plant community is comprised of a larger number of incidental species of patchy occurrence and is represented by only a few individuals. Rarer species and diversity increase as freshwater input increases (Figure 4).

A second feature of marsh plant communities is the apparent zonation of both different species and different growth forms. Zonation of different height forms of Spartina alterniflora in marshes of the U.S. Atlantic coast is probably the best documented and studied example of this phenomenon (Anderson and Treshow 1980).

Low tidal amplitudes and low frequency of inundation within the northeastern Gulf of Mexico produce less flooding stress on the plants than along other shorelines (see Chapter 1 for details).

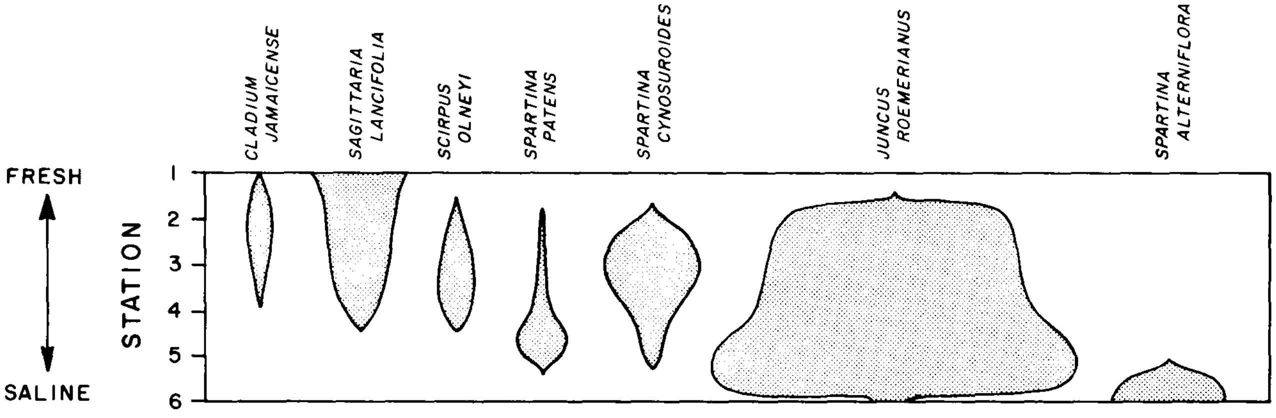


Figure 4. Distribution of dominant plants in a Mississippi estuarine system through the salinity gradient. Width of figures represents the relative abundance of the species in the marshes (modified from Eleuterius 1973).

Long periods of exposure, especially during low rainfall periods, result in an increased importance of vascular plant species' salinity tolerance ranges. Consequently, species composition of the vascular plant community is similar to southeastern United States marshes, but dominance is shifted from intertidal cordgrass (Spartina alterniflora) to the euryhaline black needlerush (Juncus roemerianus) (Figure 5). Along the continuum of marsh environmental variables from the intertidal to the upland, different height forms are found in Juncus and to a lesser extent, also in S. alterniflora. Both species become shorter toward the upland.

A number of studies provide an overall view of plant species composition and zonation in marshes of Florida (Kurz and Wagner 1957), Alabama (Sapp et al. 1976; Stout 1979; Stout and de la Cruz 1981a) and Mississippi (Eleuterius 1972, 1973, 1978). Eleuterius (1973) identified approximately 60 plant species as occurring in brackish, saline, or hypersaline Mississippi marshes. Forty species of marsh plants were found by Hackney and de la Cruz (1982) in an oligohaline brackish Juncus marsh in Mississippi (Table 4). Most of the species were incidentals and rarely contributed significantly to cover or biomass. Twelve

Figure 5. Black needlerush (Juncus roemerianus). Photo by J. Stout.

Table 4. Species composition of a brackish study marsh in St. Louis Bay Estuary (Hackney and de la Cruz 1982).

Taxonomic family and scientific name	Common name
Juncaceae	
Juncus roemerianus	Needlerush
Juncus effusus	
Gramineae	
Spartina alterniflora	Smooth cordgrass
Spartina cynosuroides	Giant cordgrass
Spartina patens	Saltmeadow cordgrass
Distichlis spicata	Salt grass
Panicum virgatum	Switch grass
Panicum amarulum	Shoredune panicum
Zizaniopsis miliaceae	Water millet
Phragmites australis	Common reed
Cyperaceae	
Scirpus americanus	Bulrush
Scirpus robustus	Leafy sedge
Scirpus californicus	
Scirpus olneyi	Three square sedge
Scirpus validus	Bull whip
Scirpus sp.	
Cladium jamaicense	Sawgrass
Fimbristylis castanea	
Fimbristylis caroliniana	
Carex hyalinolepis	
Eleocharis cellulosa	Spike rush
Eleocharis intermedia	Spike rush
Cyperus odoratus	Umbrella sedge
Asteraceae	
Aster tenuifolius	Startwort
Aster subulatus	
Aster sp.	
Solidago sempervirens	Seaside golden rod
Ambrosia artemisiifolia	Hog weed
Iva frutescens	Marsh elder
Boltonia asteroides	

(continued)

Table 4. Concluded.

Taxonomic family and scientific name	Common name
Alismaceae	
Sagittaria falcata Sagittaria lancifolia	Arrow head
Amaryllidaceae	
Crinum americanum	Marsh lily
Apiaceae	
Lilaeopsis chinensis	
Vitaceae	
Ampelopsis sp.	Pepper vine
Iridaceae	
Iris virginica	Southern blue flag
Convolvulacea	
Ipoema sagittata	Morning glory
Lythraceae	
Lythrum lineare	Loose strife
Asclepiadaceae	
Asclepias curassavica	
Campanulaceae	
Lobelia cardinalis	Cardinal flower

species were most abundant in Juncus-dominated marshes (Table 5). Many incidental species were absent in the hypersaline and saline marshes, but their members and density increased under more oligohaline conditions.

Table 5. Most frequently occurring vascular plants in Juncus marshes of the north eastern Gulf of Mexico.

Species	Common name
Juncus roemerianus	Black needlerush
Spartina alterniflora	Smooth cordgrass, oyster grass
S. patens	Saltmeadow hay, saltmeadow cordgrass
S. cynosuroides	Giant cordgrass, rough cordgrass
Distichlis spicata	Salt grass
Scirpus olneyi	Three square sedge
Salicornia bigelovii	Annual glasswort
Sa. virginica	Perennial glasswort
Batis maritima	Saltwort
Phragmites australis	Common cane, roseau cane
Baccharis halimifolia	Sea myrtle
Iva frutescens	Marsh elder

Three different plant communities can be described for Juncus-dominated marshes: (1) saline marshes experiencing little significant dilution of tidal waters, (2) brackish marshes where tidal waters are routinely diluted before flooding the marsh, and (3) a transitional community between brackish and freshwater marshes. The latter has been termed "Intermediate Marsh" (Eleuterius 1972, 1973) or "Brackish Marsh II" (Stout 1979) (Figure 6). General characteristics of the plant communities of each type are presented in Table 6.

ZONES

Vascular plants demonstrate obvious and distinctive patterns of species zonation within the salt and brackish marshes. Various authors have described and named these zones. Uhler and Hotchkiss (1968) identify the irregularly flooded salt marsh, the salt flat, and the salt

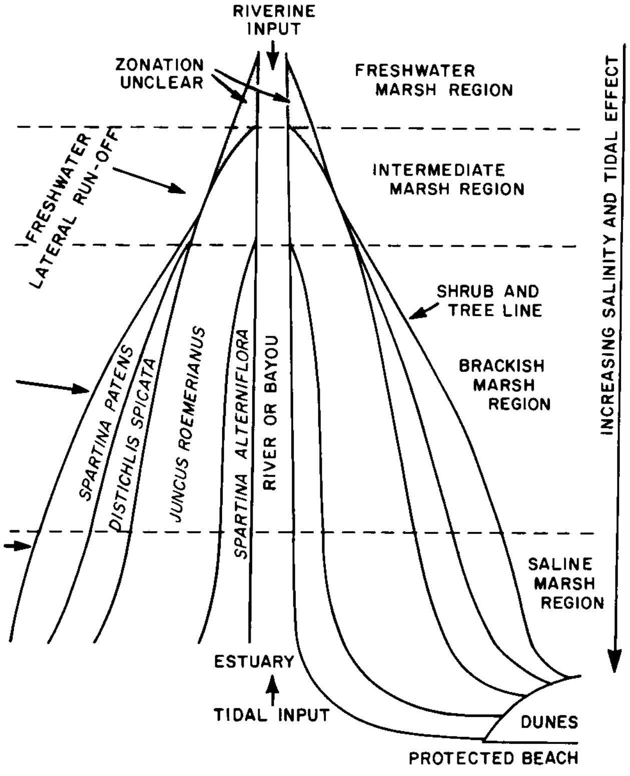


Figure 6. Marsh zonation within gulf coastal estuaries (modified from Eleuterius 1973).

Table 6. Dominant species of marsh plant communities in three *Juncus* marsh types(from Stout 1979; Sapp et al. 1976; and Eleuterius 1972, 1973).

Marsh type	Scientific name	Common name	Notes
Saline marsh	*Juncus roemerianus*	Black needlerush	Low diversity
	Spartina alterniflora	Smooth cordgrass	Great homogeneity of stands
	S. patens	Saltmeadow cordgrass	
	S. cynosuroides	Giant cordgrass	
	Distichlis spicata	Salt grass	
	Salicornia spp.	Saltworts	
	Scirpus olneyi	Three-square	
	Sc. robustus	Leafy sedge	
Brackish marsh	*Juncus roemerianus*		Greatly diminished
	Spartina alterniflora		*S. alterniflora*
	S. cynosuroides		Increased abundance of
	S. patens		*S. cynosuroides* &
	Limonium caroliniana	Sea lavender	*S. patens*
	Scirpus olneyi		*D. spicata* and *Salicornia*
	Sagittaria latifolia	Arrow leaf	spp. absent
Intermediate marsh (Brackish II (Stout 1979)	*Juncus roemerianus*		Absence of *S. alterniflora*,
	Phragmites australis	Roseau cane	*S. patens*, *Sc. olneyi*, and
	Cladium jamaicense	Saw grass	*Sc. robustus*
	Scirpus validus	Bullwhip	Increased diversity
	Iris virginica	Blue flag	Mixed stands

meadow. Subrahmanyam and Drake (1975) subdivided the marsh into low marsh, upper marsh, and high marsh based upon soil conditions, elevation, and species assemblages. Regardless of names applied to the zones, the distribution of species along a transect from water to upland can be generalized. For the purpose of this profile, four ecological zones will be discussed: *Spartina alterniflora*, *Juncus roemerianus*, salt flat, and high meadow.

Spartina alterniflora Zone

Spartina alterniflora forms a border along the open water within the intertidal zone (Figure 7). This fringe may extend above mean high water (MHW) depending on local conditions (Figure 8). Eleuterius and Eleuterius (1979) found this species between -0.24 m to 0.54 m (MLW), an elevational range of 0.78 m. If the shoreline is broad and gently sloping, *S. alterniflora* plants may exhibit differences in growth form and in flowering (Figure 9 A). Taller plants with flower heads occur in the lower elevations of the zone, while shorter, sterile plants occupy the upper area. The *Spartina* band is usually monospecific and may be from less than a meter to tens of meters wide. On shorelines with a greater initial slope, *S. alterniflora* can be found only as individuals mixed in with *Juncus roemerianus*.

Along shorelines which receive greater wave energy, a levee may form just upslope from the *Spartina alterniflora* fringe (Figure 9B). In this case, the pattern of *S. alterniflora* abutting a *Juncus* zone is interrupted by a band of

Figure 7. *Spartina alterniflora* at low tide. Photo by J. Stout.

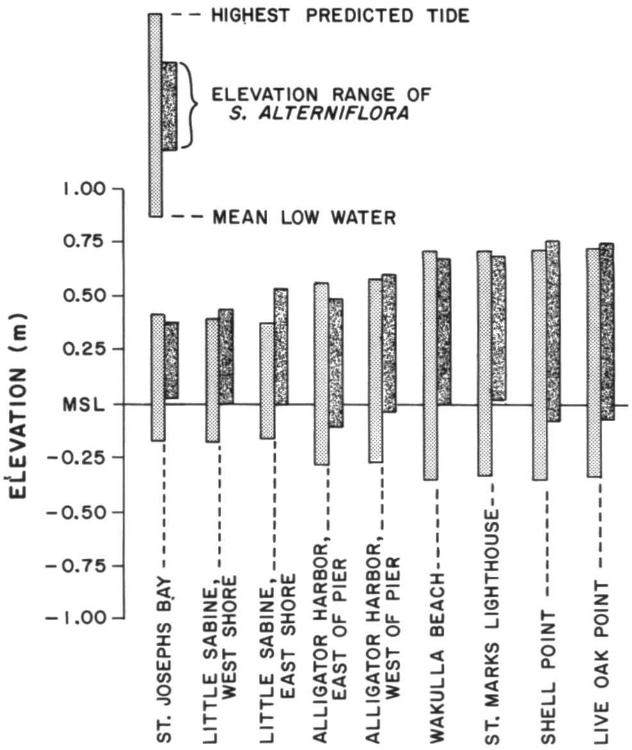


Figure 8. Elevation range of *Spartina alterniflora* in relation to tides along the northwest Florida gulf coast (modified from Kurz and Wagner 1957).

vegetation comprised of species typically adapted to higher elevation. These may include *S. patens*, *Borrichia frutescens*, *Distichlis spicata*, and the salt shrubs *Baccharis halimifolia* and *Iva frutescens*. The relatively higher energy of wave movement onto shorelines such as this is evidenced in coarse substrates, often of shell hash, and in dense wrack-lines of heavier materials on the facing slope of the levee. Where tidal creeks penetrate the levee or breaks in the levee occur, a second zone of *S. alterniflora*, with shorter plants than those in front of the levee, may be found before reaching the *Juncus* zone. The shorter *S. alterniflora* zone rarely produces flowers and is inundated less frequently and for shorter durations than in front of the levee. If the levee is continuous, without breaks, *Juncus* will be found immediately behind the levee.

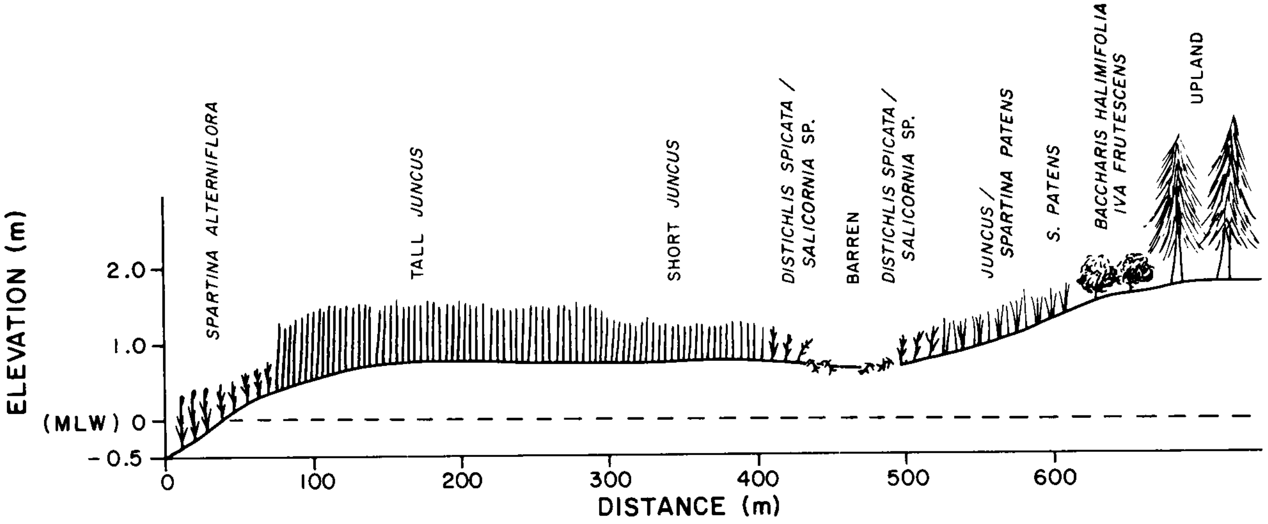
In brackish marshes, the density of *Spartina alterniflora* is diminished, and the lower marsh zone may be codominated or entirely comprised of *Spartina cynosuroides* (Figure 10). *Spartina cynosuroides* can occur at higher elevations, such as low levees, than *S. alterniflora* and may be found scattered among the *Juncus* or in other irregularly flooded brackish marshes (Jackson 1952; Eleuterius 1973; Sapp et al. 1976; Hackney and de la Cruz 1982) (Figure 11).

Intermediate marshes have no *S. alterniflora* zone and distinct zonation is obscure.

Juncus roemerianus Zone

Juncus roemerianus comprises the largest vegetated zone and the bulk of

(A) PROTECTED LOW ENERGY SHORELINE



(B) OPEN MODERATE ENERGY SHORELINE

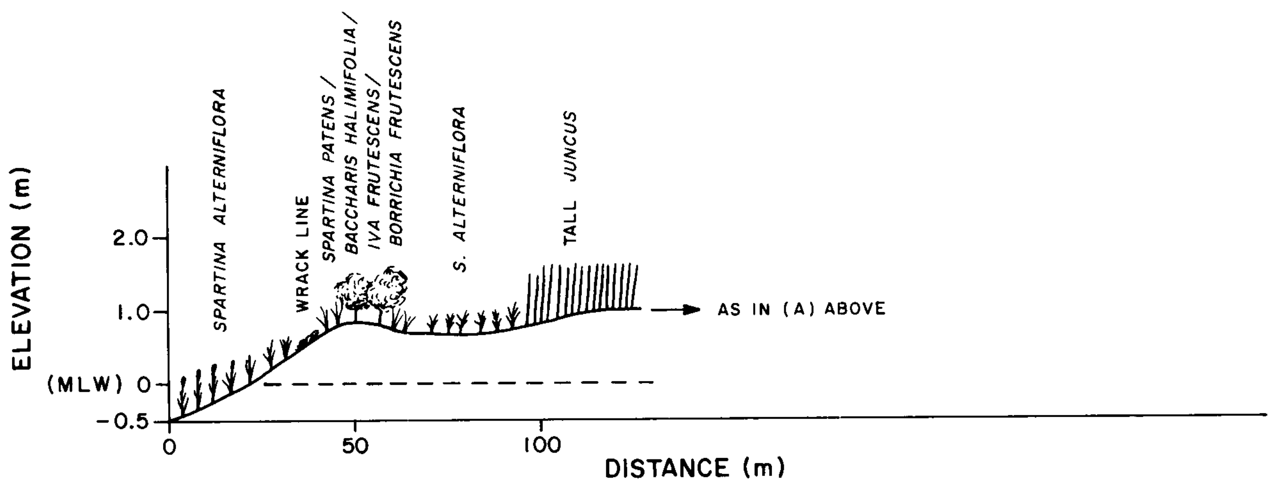


Figure 9. Generalized diagrams of gulf coast salt marshes on protected low energy shorelines and open moderate energy shorelines.

biomass in most marshes on the northeast gulf coast. An abrupt demarcation usually exists between the lower *Spartina* zone and the *Juncus* zone (Figure 12). This boundary line has been suggested as an indicator of mean high water (Sapp et al. 1976), but the differences in the physical environment on either side of the line are not nearly as distinct as the differences between plant communities. Eleuterius and Eleuterius (1979) found that the upper quarter of the elevation zone occupied by *S. alterniflora* was more similar to the lower quarter of the *Juncus* zone when details of innundation frequency and duration were examined (Figure 13). Thirty-eight percent of high tides carried water into the upper *Spartina* zone (S4) and 26% into low *Juncus* (J1). However, 78% reached the next lower *Spartina* zone (S3). Thus the separation of species in *Spartina* and *Juncus* zones involves more than simple tidal inundation. Edaphic conditions and biotic factors may also be important.

Figure 10. Inflorescence of giant cordgrass (*Spartina cynosuroides*). Photo by J. Stout.

Figure 12. Abrupt boundary between *Spartina alterniflora* (foreground) and *Juncus roemerianus*. Photo by J. Stout.

The broad expanses of *Juncus* occupy a much narrower elevational range but typically greater horizontal distances than *S. alterniflora* in the northeast Gulf. The *Juncus* zone of Eleuterius and Eleuterius (1979) covered an elevational range of 0.21 m, from 0.54 m to 0.75 m (MLW). The zone may be several hundred meters to several miles wide (Swanson et al. 1972).

Tidal inundation of this entire zone is very irregular, and higher elevations may be flooded only during spring tides and storm events. At a Mississippi site, the entire *Juncus* zone was flooded only 16 times out of 368 predicted high tides for

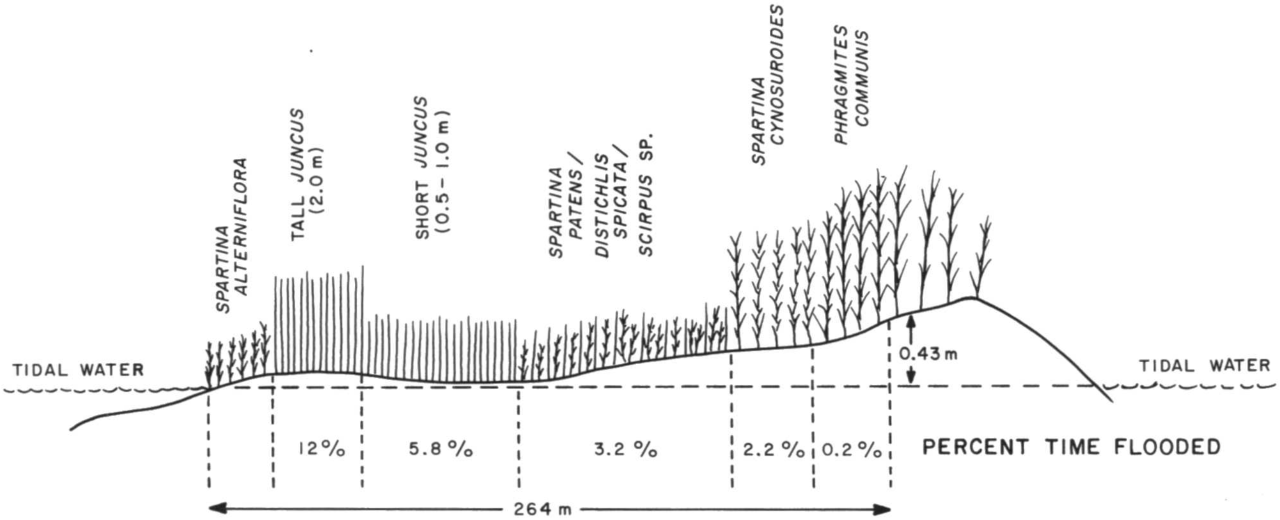
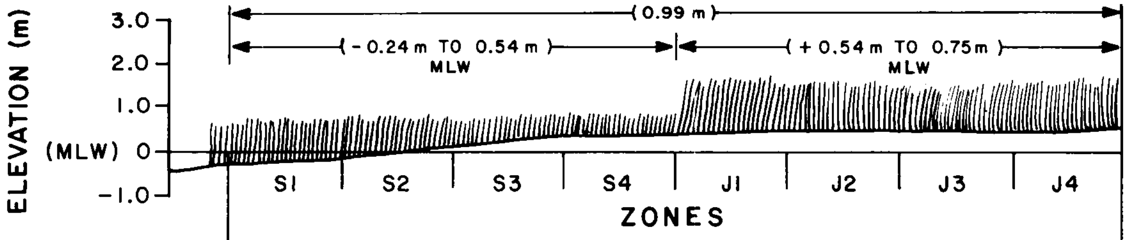


Figure 11. Composite profile diagram of a Mississippi brackish *Juncus* marsh (compiled from Hackney and de la Cruz 1978, 1982).



	S1	S2	S3	S4	J1	J2	J3	J4
NUMBER OF FLOODINGS (OUT OF 368)	362	351	297	144	99	60	31	16
DIFFERENCE IN FLOODINGS		11	64	148	45	39	29	15
PERCENT OF TOTAL HIGHS	98	95	78	38	26	16	8	4
PERCENT OF TOTAL TIME FLOODED (8,750 HOURS)	87	66	35	10	5.4	2.9	1.3	0.86

Figure 13. Profile of the distribution of *Spartina alterniflora* (S) and *Juncus roemerianus* (J) along an elevation gradient with respective flooding conditions. Plant heights are not to scale, but approximate relative growth forms in each zone. Zones are of unequal width, but represent equal portions of the range of elevation for each species (data from Eleuterius and Eleuterius 1979).

the year. Portions of the *Juncus* zone were inundated from 0.86% to 5.4% of the total time that any portion of the marsh was covered by water during the year. The upper portion of the zone was exposed continuously for over 720 hours during late November and December (Eleuterius and Eleuterius 1979) (Figure 13). Although elevations in the *Juncus* zone may fall within the range of local tidal amplitude, tides of those heights or higher may or may not reach a particular area due to levees and other topographic restrictions, percolation into the substrates at lower elevations, and increased resistance to flow induced by friction with the sediment and dense vegetation (Kurz and Wagner 1957).

Because of longer and more frequent periods of exposure and evaporation, interstitial water salinities may be higher in *Juncus* than *S. alterniflora* zones (Hackney and de la Cruz 1978). High organic content and acid conditions of *Juncus* soils have also been noted (Kurz and Wagner 1957; Coultas and Gross 1975). Organic content may impede percolation of both tidal water and rainwater into the substrate. Field pH as low as 4.3 was measured by Kurz and Wagner (1957) in Florida *Juncus* marsh soils. Upon drying of similar soils, Coultas and Gross (1975) observed drops in pH values of 0.5 to 3.7 pH units with resulting pH ranging from 2.5 to 7.2.

As previously mentioned, the *Juncus* zone is often comprised of two or more height forms reflecting microhabitat differences across the zone. Two heights, tall (2.0 m) and short (0.5-1.0 m), were found in the brackish marsh studied by Hackney and de la Cruz (1978); the tallest plants were nearest the tidal source and more frequently flooded (Figure 11). Table 7 presents a summary of differences in gross morphology and population parameters of *Juncus* in three subzones (low, upper, and high marsh) of *Juncus* marshes in northwest Florida. Though stem height and diameter decrease with distance from the shore, stem densities and new leaf production increase with distance inland (Kruczynski et al. 1978a). Differences in soil texture and salinity were noted for different height forms in Mississippi marshes (Eleuterius and Caldwell 1981a). Tall plants (mean = 142 cm) were found in highly organic soils, composed primarily of peat with salinities of 0-6 ppt; and short plants (mean = 26 cm) in sandy soils underlain at 2-4 feet by clay and with high salinities of 60-300 ppt; and intermediate height plants (mean = 104 cm) in sandy clay of 5-20 ppt

Table 7. Morphological features (annual mean values) of Juncus from three marsh zones (from Kruczynski et al. 1978a).

Feature	Marsh zones		
	Low marsh	Upper marsh	High marsh
Mean density/m^2 (total)	1,660	2,097	4,719
Mean density/m^2 (live)	885	993	1,692
Mean density/m^2 (dead)	776	1,164	3,029
Mean height (cm)	102	88	78
Mean diameter (mm)	3.6	2.9	1.9
New leaves/20 plants/year	26	39	44
Height of bracts with flowers (cm)	70	66	54
Number of flowers/m^2	40	46	7
Perfect flowers (%)	57	17	8

salinity. There is a decline in sexual reproduction in Juncus plants at higher elevations similar to that seen in Spartina alterniflora (Kruczynski et al. 1978a). Shortest (< 0.5 m) Juncus plants, usually sterile, are found adjacent to salt flats (Eleuterius and Caldwell 1981a). These differences, within what may at first glance appear to be a fairly uniform and homogeneous stand, must be recognized in terms of evaluating species functions, stress impacts, and management in Juncus marshes.

Salt Flats

The term "salt flat" will be used to describe a zone of sandy, hypersaline soil just upland of the Juncus zone. The salt flat includes the portions of the zone vegetated by halophytic species and portions called "barrens," which are devoid of vascular plants (see Kurz and Wagner 1957, and Coultas and Gross 1975). This zone is rarely inundated by tidal water, and when inundated, the water quickly percolates through the coarse substrate. Barrens within the salt flat receive tidal input least frequently. Low rates of tidal recharge, long periods of exposure, high evaporation, and concentration of soluble salts result in extremely high interstitial water salinities. Evaporation is high because of several factors including: (1) coarse sediments with large interstices, (2) greater wind velocities due to sparse or no vegetation, and (3) higher surface temperatures also related to minimal shading by a plant canopy. Salt flats develop at a critical level above frequent flooding, but not high enough in elevation to allow for effective leaching by rainfall, which contributes further to the high salinities (Kurz and Wagner 1957). More research is needed to delineate the physicochemical dynamics of this zone and the biotic reactions to the microhabitat that are created.

The margins, seaward and upland, of the salt flat usually present mirror-image plant communities on either side of the barrens. *Distichlis spicata* extends in parallel strands by rhizomes from the upper edge of the *Juncus* and the lower edge of the high meadow into the salt flat. As salinities become higher toward the barrens, *Distichlis* no longer grows and adjacent rhizomes appear about equal in length (Figure 14). *Distichlis* forms a low profile carpet on either side of the barrens. Infrequent individuals of other species found among the *Distichlis* may include *Limonium carolinianum*, *Agalinus maritima*, *A. purpurea*, *Sabatia dodecandra*, *S. stellaris*, and *Atriplex arenaria* (personal collections). At slightly lower elevations where rainwater may pool, or nearer to the freshwater table, *Scirpus olneyi* may occur in small stands among the *Distichlis*. Individual clumps of *Spartina spartinae* may also occur, often established on a small hummock on the *Distichlis* margin, such as those created over rotted relic tree stumps.

Interior to the *Distichlis* margins of the salt flat only three species are found: *Salicornia virginica* (a perennial), *S. bigelovii* (an annual), and *Batis maritima*. Both *S. virginica* and *Batis* trail across the substrate as prostrate stems (Figure 15). *S. bigelovii* grows in stands of individual, erect, tree-like stems (Figure 15). All three species are obligate halophytes and do not live in lower salinity areas of a marsh or in brackish or intermediate marshes. These succulent species have internal fluids which are hypertonic (osmotically more concentrated) relative to salinities of external environmental fluids and are thus able to take in water in this physiologically xeric setting. Internal salinities may reach 80-95 ppt (personal observation). Slight differences in height may be found between individuals of these species located nearest the barrens and those located near the *Distichlis* fringe (Kurz and Wagner 1957).

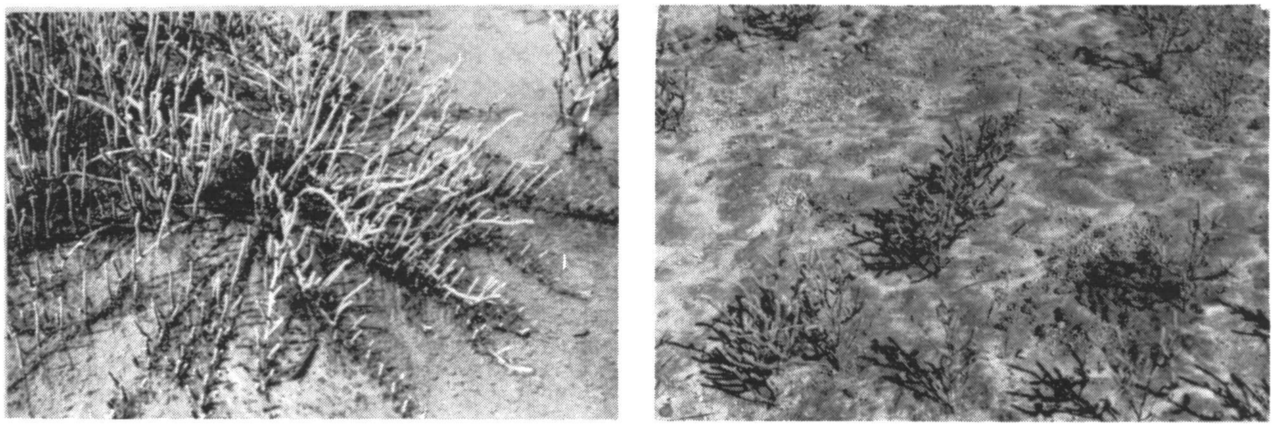
Figure 14. Salt flat zone with *Juncus* (rear), *Distichlis spicata*, *Salicornia bigelovii*, and barren soil. Photo by J. Stout.

The barrens are devoid of vascular plants because of salinity conditions. The size of the barrens varies with local conditions and may even change over short periods of time with increased or decreased rainfall, tidal inundation, or changes in elevation. If salinity decreases, seedlings of the annual *Salicornia bigelovii* and rhizomes of the other salt flat species can quickly invade the barrens. Increased salinities can, however, also result in the expansion of the barrens at the loss of plant coverage.

High Meadow

The high meadow or high marsh may vary greatly in its areal extent, from a narrowly vegetated fringe between the salt flat and upland vegetation, to a broad meadow of grasslike vegetation (Figure 16). *Juncus* is again very abundant in this zone, sharing dominance to varying degrees with *Spartina patens*. *Spartina patens* dominates nearest the upland border. Numerous incidental species are found in this zone which grades into a shrub/forb ecotone between the marsh and the upland forest. This zone contributes most to the diversity of plant species over the entire marsh. Other species include *Fimbristylis caroliniana*, *Scirpus robustus*, *Aster tenuifolius*, *Phragmites australis*, *Cynanchum angustifolium*, *Pluchea* sp., and the shrubs *Baccharis halimifolia*, *Iva frutescens*, and *Myrica cerifera* (Figure 17).

Salt grass (**Distichlis** spicata) Glasswort (Batis maritima)



Perennial saltwort (Salicornia virginica) Annual glasswort (Salicornia bigelovii)

Figure 15. Common plant species of zones within Juncus-dominated marshes. Photos by J. Stout.

JUNCUS ROEMERIANUS LIFE HISTORY

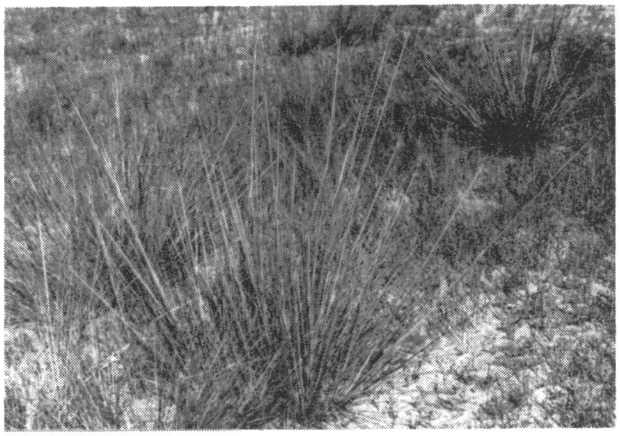
The marshes of Mississippi Sound have been well studied, and the taxonomy and life history studies of Juncus roemerianus in these marshes are well known (Eleuterius 1974a,b, 1975, 1976b, 1978; Eleuterius and McDaniel 1978; Eleuterius and Caldwell 1981a).

Similar to other marsh spermatophytes, Juncus roemerianus spreads by vigorous rhizome growth, and a single plant may therefore cover large areas of the marsh surface. Rhizomatous growth makes J. roemerianus unique among rushes. Study of the rhizomes during anthesis shows that they bear leaves with inflorescenses composed exclusively of pistillate or bisexual flowers. Transplanted clonal material from unisexual and bisexual plants produced only the respective flower type for five years. No staminate flowers have been found along the gulf coast (Eleuterius 1974a; Eleuterius and McDaniel 1978). Plants grown from seeds also consistently produced a single flower type (Eleuterius 1984). Unisexual flowers are the results of stamen abortion in immature flowers

(Eleuterius and McDaniels 1978). Flower types may be mixed in marshes where rhizomes of different shoots intermingle or may be in homogeneous stands of a single flower type. In the St. Marks Refuge (Florida) marshes, there was a significantly greater proportion (57%) of bisexual flowers in low marsh (X^2, $P < 0.01$), and no significant difference in proportion of the two flower types between high marsh (8%) and upper marsh (17%) (Kruczynski et al. 1978a). Dimorphic flowers (pistillate and bisexual) in Juncus roemerianus are also unique among species of Juncus, where bisexual flowers are the rule. Bisexual plants must serve

Figure 16. Salt flat with barrens (center), high meadow upland (left), and low Juncus marsh (right). Photo by J. Stout.

Roseau cane (Phragmites australis) in flower



Spartina spartinae

Salt shrubs (Baccharis halimifolia) on hummock in high meadow

Three-corner sedge (Scirpus robustus)

Figure 17. Incidental plant species common to Juncus marshes. Photos by J. Stout.

as the pollen source for unisexual pistillate plants by cross pollination.

Juncus roemerianus produces flowers in the northeastern gulf from midwinter to midspring (January - April) (Figure 18). This reduces the possibility of hybridization with *J. effusus* which may co-occur in fresher marshes, but initiates flowering in April (Eleuterius 1974a). *J. roemerianus* seeds are shed simultaneously. Although seeds are highly viable (mean ≥ 90%), they have a high light and moisture requirement and produce seedlings generally only on barren, sandy substrate. Progeny of the bisexual plant type are less vigorous than the unisexual type. Once established, *J. roemerianus* maintains itself in the marsh through vegetative growth. Therefore, sexual reproduction is important primarily for colonization of new habitats (Eleuterius 1974b).

Juncus roemerianus plants mature from seedlings in about 12 months, although plants are usually 18-24 months old before they flower. Prolific flower production begins at about three years (Eleuterius 1974a).

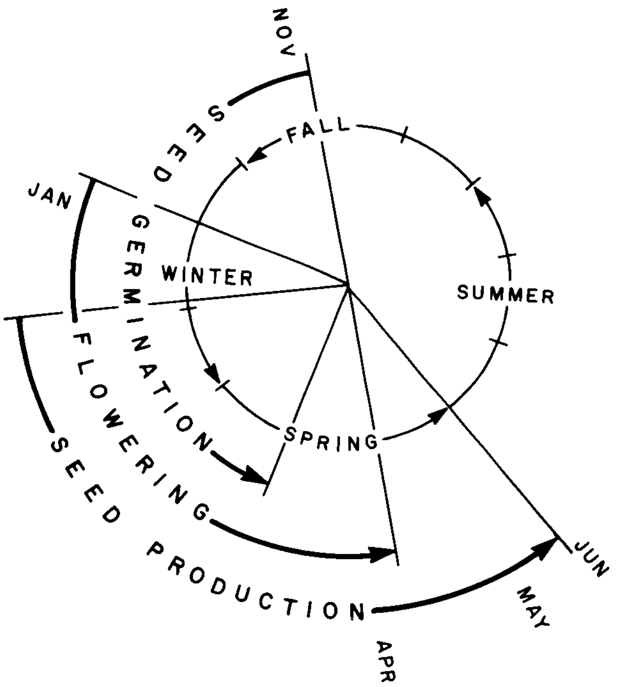


Figure 18. The life cycle of *Juncus roemerianus* in relation to the seasons in Mississippi (from Eleuterius 1975).

Eleuterius and Caldwell (1981a) showed that shoot age, number of leaves produced, plastochron (time interval between initiation of sequential leaves), and leaf longevity varied considerably between populations of *J. roemerianus* living under different environmental conditions. All populations, however, exhibited: (1) cessation of growth of first leaf when growth of the second leaf was initiated, (2) death of leaves from the tip downward, and (3) growth rates of leaves within a population equalling their death rates during maximum growth periods. In this study, however, tall and intermediate plant populations produced more leaves per shoot annually (four) than short populations (two), had longer leaf life (14 and 16 months, respectively) than short forms (7.5 months), and had greater average shoot longevity (21 months and 25 months) as compared to short plants (11 months). Some vegetative shoots of the intermediate height form may live four years or longer (Eleuterius and Caldwell 1981a).

Short populations of *J. roemerianus* may appear less productive than taller forms when productivity estimates do not adequately account for biomass turn over. Eleuterius and Caldwell (1981a) found that in some short stands, two entire crops of shoots may turnover every 22 months, while in taller forms a complete vegetational turnover may require up to 4 years. Rapid turnover and higher stem density in short plants may indicate an equal or greater biomass value of these plants relative to taller plants (Eleuterius and Caldwell 1981a). Since short plants are typically at higher elevations in the marsh (see Zones), recognition of the potential importance of shorter plants must be considered before advocating a more relaxed attitude about marsh alterations in higher marshes.

CHAPTER 3

MICROBIAL AND NONVASCULAR PLANT COMMUNITY

Little is known about the species composition and functional contributions of nonvascular floral communities within Juncus marshes. Diverse canopies of tall spermatophyte species limit light availability at the marsh surface but also moderate extreme environmental fluctuations. Benthic algal communities have received the greatest attention. However, marsh substrates also provide habitats for epiphytic microfloral communities.

MICROBIAL COMMUNITIES

In order to identify the organisms potentially active in the decomposition process, Brown and Landers (1978) isolated pure cultures of micro-organisms from aboveground and belowground litter bags of detritus of Spartina alterniflora, S. cynosuroides, Distichlis spicata and Juncus roemerianus of six different ages. Samples were obtained from coastal Juncus marshes in Mississippi and Alabama. All counts were carried out under aerobic conditions, and therefore, obligate anaerobes were not detected. Sixty species of fungi, yeasts, and actinomycetes were isolated. Plate counts were always highest in aboveground bags. Counts in belowground samples of S. alterniflora were lower than counts from all other species. Count results are summarized in Table 8.

Twenty-five species of filamentous fungi are identified as occurring on Spartina spp. in the marshes of Mississippi, Alabama and Florida (Table 9) (Gessner and Kohlmeyer 1976). All fungi isolated by Gessner and Kohlmeyer, and not determined only from the literature, were found growing on the aboveground parts of the plants. Spartina alterniflora was host to the greatest number of fungal species. Of the microbial species found in the northeast gulf, several have a wide geographical range, occurring wherever the host is found. These include Buergenerula spartinae, Claviceps purpurea, Leptosphaeria albopunctata, L obiones, Lulworthia medusa var. medusa, Phaeosphaeria typharum, Pleospora pelagica, Puccinia sparganioides, Phoma sp., and Stagonospora sp.

Tracy and Earle (1895) reported the ascomycetous ergot fungus, Claviceps purpurea, on Spartina alterniflora in Mississippi tidal marshes. Claviceps has also been reported utilizing salt grass (Distichlis spicata) as a host species (Parris 1959). Eleuterius and Meyers (1974) found the ergot fungus on S. alterniflora throughout Atlantic and gulf coast marshes and also frequently on S. patens and S. cynosuroides. Infection of the three Spartina species is sequential. Sclerotial germination is simultaneous with flowering in Spartina patens and spores are then spread by insects to later-flowering S. cynosuroides and S. alterniflora. Conidia may also be dispersed by the wind to open flowers. Absence of the ergot in adjacent Spartina spartinae may be explained by the closed spikelets, without exserted stigmas or stamens to facilitate infection.

Investigations of S. alterniflora stands in Mississippi reveal that the incidence of ergot infection varies with location. Barren spoil areas and manmade beaches about 3-4 ft. above mean low water show 100% panicle infection with 95% of the seeds replaced by sclerotia. Plants

Table 8. Mean plate counts of marsh microflora on different spermatophyte detritus and at two depths in the sediment (data from Brown and Landers 1978).

Spermatophyte	Total	Fungi	Yeasts	Actinomycetes
Aboveground				
Juncus roemerianus (MS)	8.3×10^7	6.2×10^6	3.6×10^6	8.5×10^6
Spartina cynosuroides	2.1×10^8	1.2×10^7	1.7×10^6	1.8×10^7
S. patens	2.4×10^8	3.2×10^7	4.9×10^6	2.8×10^7
J. roemerianus (AL)	1.7×10^8	3.3×10^6	1.3×10^6	4.4×10^7
S. alterniflora	8.0×10^8	6.0×10^5	8.3×10^5	3.8×10^7
Distichlis spicata	7.4×10^8	8.9×10^6	5.7×10^6	2.9×10^7
Belowground - 5 cm				
J. roemerianus (MS)	8.0×10^7	1.0×10^6	4.4×10^5	2.7×10^6
S. cynosuroides	8.3×10^7	2.1×10^6	9.3×10^5	1.1×10^7
J. roemerianus (AL)	9.2×10^7	4.5×10^5	3.5×10^5	2.9×10^7
S. alterniflora	7.2×10^6	1.6×10^5	3.4×10^4	7.7×10^6
Belowground - 10 cm				
J. roemerianus (MS)	8.0×10^6	3.6×10^5	2.9×10^5	2.8×10^6
S. cynosuroides	1.3×10^7	6.9×10^5	4.4×10^5	1.2×10^6
J. roemerianus (AL)	5.9×10^7	9.6×10^5	4.4×10^5	1.2×10^7
S. alterniflora	3.1×10^6	1.1×10^5	3.3×10^3	8.5×10^6

from undisturbed marshes show a 10% infection rate with less than 1% of the seeds lost. Natural marsh levees represent an intermediate condition having an infection rate of 62% and seed loss of 5%. Greater exposure, aeration, and periodic drying of the substrate at higher elevations may favor ergot germination and dissemination on the spoil and beach sites (Eleuterius and Meyers 1974).

There are several implications of the ergot infections of Spartina species within the marsh: 1) heavy infections may produce yields of ergot great enough to make harvest for pharmaceuticals economically appealing, 2) human alterations of natural wetlands and creation of artificial marshes may create conditions suitable for widespread infection, and 3) extensive loss of viable seeds will reduce

Table 9. Higher filamentous fungi reported from *Spartina* spp. from the northeastern Gulf of Mexico by direct observation, including their geographical distribution and literature citations. Host code: A, *Spartina alterniflora*; C, *S. cynosuroides*; P, *S. patens*; and S, *Spartina* sp. (unidentified from marine habitats) (modified from Gessner and Kohlmeyer 1976).

Fungus	Host	Location	Literature
I. Ascomycetes			
Anthostomella sp.	A	RI, Conn, NC, Fla, Arg	Gessner and Goos 1973b; Gessner and Kohlmeyer 1976
Buergenerula spartinae Kohlmeyer et Gessner	A	Me, NH, RI, Conn, NJ, Va, NC, Fla, Arg	Webber 1970; Gessner and Goos 1973a, 1973b, Gessner 1976; Gessner and Kohlmeyer 1976
Claviceps purpurea (Fr.) Tul.	A	Me, NH, Mass, RI, NY, NJ, Del, Md, Va, NC, SC, Ga, Fla, Ala, La, Miss, Tex, Arg, Uru	Seymour 1929; Sprague 1950; U.S. Dep. Agric. 1960; Gessner and Goos 1973b; Eleuterius and Meyers 1974; Gessner 1976; Lindquist (unpublished); Gessner and Kohlmeyer 1976
	C	NY, Fla, Miss	Seymour 1929; Sprague 1950; U.S. Dep. Agric. 1960; Eleuterius and Meyers 1974
	P	Md, Miss	Seymour 1929; Sprague 1950; U.S. Dep. Agric. 1960; Eleuterius and Meyers 1974
Halosphaeria hamata (Hohnk) Kohlm	A	Me, RI, Fla	Gessner and Goos 1973a, 1973b; Gessner 1976; Gessner and Kohlmeyer 1976
Leptosphaeria albopunctata (Westend.) Sacc.	A	RI, Conn, NJ, Va, NC, Fla, Arg	Johnson 1956a; Johnson and Sparrow 1961; Gessner and Goos 1973b; Gessner 1976; Gessner and Kohlmeyer, 1976
L. arundinacea (Sow.) Sacc.	S	NC, Fla	Johnson and Sparrow 1961
L. herpotrichoides deNot	P	NC, Fla	Johnson and Sparrow 1961
L. lacustris (Fuckel) Wint.	S	NC, Fla	Johnson and Sparrow 1961
L. obiones (Crouan et Crouan) Sacc.	A	Me, RI, Conn, Mass, NJ, Md, Va, NC, SC, Fla, Miss, Tex	Johnson 1956a; Johnson and Sparrow 1961; Wagner 1969; Webber 1970; Gessner and Goos 1973a, 1973b; Gessner 1976

(continued)

Table 9. Continued.

Fungus	Host	Location	Literature
L. oraemaris Linder	A	Mass, RI, NC, Fla, Tex	Johnson 1956a; Johnson and Sparrow 1961; Webber 1966; Gessner and Kohlmeyer 1976
L. scirpina Wint.	S	NC, Fla	Johnson and Sparrow 1961
L. vagans Karsten	S	NC, Fla	Johnson and Sparrow 1961
L. medusa var. medusa (Ell, et Everh.) Cribb et Cribb	A	Va, NC, SC, Fla, Tex	Johnson 1956b; Johnson and Sparrow 1961
Phaeosphaeria typharum (Desmaz.) Holm	A	Can, Me, RI, Conn, NJ, Va, NC, Fla, Arg	Gessner and Goos 1973b; Gessner 1976; Gessner and Kohlmeyer 1976
Pleospora pelagica Johnson	A	RI, NC, Fla	Johnson 1956a; Johnson and Sparrow 1961; Gessner 1976; Gessner and Kohlmeyer,1976
II. Basidiomycetes			
Puccinia seymouriana Arth.	A	NY, Miss	Seymour 1929; U.S. Dep. Agric. 1960; Arthur and Cummins 1962; Cummins 1971
P. sparganioides Ell. et Barth.	A	Me,NH, Mass, RI, Del, Va, NC, Fla, Miss	Seymour 1929; U.S. Dep. Agric. 1960; Arthur and Cummins 1962; Cummins 1971
	C	NJ, Del, Md, SC, Fla, La	Seymour 1929; U.S. Dep. Agric. 1960; Arthur and Cummins 1962
Uromyces acuminatus Arth.	A	Me, NH, Mass, Conn, NY, NJ, Del, Md, Fla	Seymour 1929; U.S. Dep. Agric. 1960; Cummins 1971
	C	Fla	Seymour 1929; U.S. Dep. Agric. 1960
	P	Me, Mass, Conn, NH, NY, NJ, Del, Md, Fla	Seymour 1929; U.S. Dep. Agric. 1960
U. argutus Kern	A	Fla, Fr	Seymour 1929; U.S. Dep. Agric. 1960; Cummins 1971

(continued)

Table 9. Concluded.

Fungus	Host	Location	Literature
III. Fungi Imperfecti			
A. Coelomycetes			
Phoma sp. and spermogonia	A	Can, Me, RI,Conn, NJ, Va, NC, Fla, La, Arg	Meyers et al. 1970; Gessner and Goos 1973a, 1973b; Gessner 1976; Gessner and Kohlmeyer 1976
Stagonospora sp. II	A	Can, Me, RI, Conn, NJ, Va, NC, Fla, Arg	Gessner and Goos 1973b; Gessner 1976; Gessner and Kohlmeyer 1976
Tracyella spartinae (Pk.) Tassi	P	Miss	Seymour 1929; U.S. Dep. Agric. 1960
B. Hyphomycetes			
Alternaria alternata (Fr.) Keissl.	A	Me, RI, Conn, Va, Fla	Gessner 1976; Gessner and Kohlmeyer 1976
Drechslera halodes (Drechsl.) Subram. et Jain	A	RI, NC, Fla	Gessner 1976; Gessner and Kohlmeyer 1976
Epicoccum nigrum Link	A	Conn, RI, Va, Fla	Gessner and Goos 1973b; Gessner 1976; Gessner and Kohlmeyer 1976

the availability of propagules and thus inhibit natural colonization of new substrates and dieback areas by sexual reproduction of the *Spartina*. Long-term impacts of ergot infection on marsh maintenance, expansion, and function within estuarine systems may be significant.

The rust fungus *Puccinia sparganioides* has been reported on *S. alterniflora* in Mississippi and Florida as well as other states (USDA 1960). No data are available on the patterns of its distribution or extent of infection. In North Carolina, Van Dyke and Amerson (1976) found an inverse relationship between the percentages of infected plants and interstitial water salinities. It may, therefore, be expected that the incidence of rust infection would be low in northeastern gulf marshes that exhibit seasonal periods of high soil salinity due to exposure and evaporation.

ALGAE

Only the diatom and blue-green algal communities of *Juncus* marshes have been studied. There is no information on the functional roles of these two groups and other algae within the marsh ecosystem.

Kurz and Wagner (1957) tabulated the zonal relationship of algal species with marsh spermatophyte communities. As can be seen in Table 10, few species were observed, but the most frequently noted were epiphytic *Bostrychia* and *Enteromorpha* and unidentified soil diatoms. Sage and Sullivan (1978) found the green algae *Rhizoclonium riparium* var. *implexum* and *R. kerneri* only in winter and spring as a mat attached to *Juncus*. In a subsequent study, Sullivan (1982a) found epiphytic diatoms on *Bostrychia radicans* and *Caloglossa lepriurri* attached to dead stems of *Spartina alterniflora*.

Sage and Sullivan (1978) described a single nearly homogeneous community of blue-green algae throughout the different angiosperm zones of a Mississippi marsh. The five angiosperm canopies were *Distichlis spicata*, *Scirpus olneyi*, *Spartina patens*, *Spartina alterniflora*, and *Juncus roemerianus*. Each zone represented a different set of environmental conditions (Table 11). Twenty-five species of blue-green algae were identified, but the community was strongly dominated by only three species: *Schizothrix calcicola* (40.5% annual relative abundance), *Anacystis montana* (17.4% annual relative abundance), and *A. aeruginosa* (16.4% annual relative abundance). A high of 20 species was associated with *Juncus*, and a low of 14 species was associated with *S. patens*. Seven species were found only once during the study, whereas 20 species were found in all habitats (Sage and Sullivan 1978). (Numbers of individuals found in *S. alterniflora* and *Juncus* are presented in Table 11.) Seasonal abundance was highest (802 individuals) in June and lowest (290) in January, indicating a seasonality in standing crop.

This Mississippi marsh has an almost continuous angiosperm canopy; thus, there

Table 10. Zonal relationships of algae with spermatophyte communities in Florida marshes (modified from Kurz and Wagner 1957).

Spermatophyte community	Dominant algae	Location
Spartina alterniflora	*Bostrychia*, *Enteromorpha flexuosa*, *Melosira*	Attached to culms
	Microcoleus chthonoplastes	Channel bottom
	Phormidium fragile, *Lyngbya confervoides*	Attached to oyster shells
	Soil diatoms	
	Chondria, *Digenia*, *Enteromorpha*, *Sargassum*, *Polysiphonia*, *Champia*, *Fosliella*	Drift fragments
Juncus roemerianus	*Bostrychia*, *Cladophora*, *Chaetomorpha*, *Enteromorpha*, *Lyngbya aestuarii*	Attached to culms
Distichlis spicata	*Bostrychia*, *Cladophora*, *Chaetomorpha*, *Enteromorpha*, *Lyngbya aestuarii*, *Enteromorpha*	Attached to culms

Table 11. Abundance of blue-green alga species collected in Graveline Bay Marsh, Mississippi, with physical characteristics of each habitat (0 = not collected) (Sage and Sullivan 1978).

Blue-green algae	Marsh habitat[a]					
	DS	SO	SP	SA	JR	TOTAL
Anabaena oscillarioides Bory	5	3	6	3	46	63
Anacystis aeruginosa (Zanard.) Dr. & Daily	40	49	58	159	77	386
A. dimidiata (Kurtz) Dr. & Daily	8	5	2	2	3	20
A. marina (Hansg.) Dr. & Daily	22	46	27	45	47	187
A. montana (Lightf.) Dr. & Daily f. *montana*	99	58	77	93	80	407
Calothrix crustacea Schousb. & Thur.	0	1	0	0	0	1
Coccochloris aeruginosa (Nag) Dr. & Daily	0	1	0	0	3	4
C. stagnina Spreng.	7	2	7	20	35	71
Entophysalis conferta (Kutz.) Dr. & Daily	1	3	2	8	2	16
E. deusta (Menegh.) Dr. & Daily	32	19	25	31	17	124
Gomphosphaeria aponina Kutz	0	0	1	2	3	6
Johannesbaptista pellucida (Dickie) W. R. Taylor & Dr.	2	3	1	5	1	12
Microcoleus lyngbyaceus (Kutz.) Crouan	1	0	0	0	0	1
Nostoc commune Vauch.	0	0	0	5	1	6
N. spumigena (Mert.) Dr.	0	0	0	0	1	1
Oscillatoria lutea Ag.	1	4	2	6	12	25
O. submembranocea Ard. & Straff.	2	0	0	0	3	5
Porphyrosiphon miniatus (Hauck) Dr.	0	0	0	0	1	1
P. notarisii (Menegh.) Kutz.	1	0	0	0	0	1
Schizothrix arenaria (Berk.) Gom.	1	0	0	0	0	1
S. calcicola (Ag.) Gom.	101	175	155	266	250	947
S. mexicana Gom.	2	1	0	0	0	3
Scytonema hofmannii Ag.	0	0	0	0	1	1
Spirulina subsalsa Oerst.	15	11	6	5	2	39
Stichosiphon sansibaricus (Híeron.) Dr. & Daily	2	3	1	6	3	15
Totals: individuals	342	384	370	656	588	2,343
species	18	16	14	15	20	25

	N	DS	SO	SP	SA	JR
Marsh surface temp (^{o}C)	12	21.2	21.0	21.8	23.0	22.8
Salinity (ppt)	12	23.8	17.1	16.2	18.8	27.8
Canopy height (cm)	12	36	109	72	81	146
Standing water (cm) on 1 Sept. 1977	5	5.4	8.7	10.0	7.6	7.5

N = Number of observations
[a] DS = *Distichlis spicata*
SO = *Scirpus olneyi*
SP = *Spartina patens*
SA = *Sp. alterniflora*
JR = *Juncus roemerianus*

were few open areas suitable for supporting algal mat development. Where small mats were found they consisted primarily of Microcoleus lyngbyaceus, Schizothrix calcicola, and S. arenaria (Sage and Sullivan 1978). Open areas with mat communities are much more extensive in many Alabama and Florida marshes, but have not been studied.

Maples (1982) found similar low diversity values for blue-green algae in Louisiana marshes salt flats devoid of a spermatophyte canopy. In six salt flats, seven genera of Chrysophycophyta, eleven genera of Cyanochloronta, and seventeen genera of the Chlorophycophyta were found (Table 12). The most abundant algae were Oscillatoria sp. High soil pH within the salt pannes may be an important factor influencing the frequency and occurrence of soil algae. Blue-green algae are particularly sensitive to low pH, whereas green algae are the least sensitive (Maples and Watson 1979).

Blue-green algae demonstrate an ability to survive in a wide variety of habitats. The only significant community changes in the blue-green algae were between areas either shaded by canopy vegetation or lacking cover. Light intensity is then a major factor influencing the distribution of blue-green algae within salt marshes (Sage and Sullivan 1978).

Diatoms (Figure 19) exhibit a continuous benthic marsh cover both in areas with and without a spermatophyte canopy. Sullivan (1978) identified 119 diatom taxa in a Mississippi marsh with variations in community composition beneath five canopy species (as listed above for blue-green algae). Within the Mississippi marsh, the most abundant diatom species was Navicula tripunctata, which accounted for 21.5% of the individuals identified. The greatest number of species (89) was found in Distichlis spicata and the lowest in Juncus. Only seven species were restricted to a single spermatophyte canopy. Significant differences were demonstrated between the five habitats with regard to species diversity (H') and the number of taxa in a sample (S). The presence of restricted taxa indicates that differences do exist among the edaphic habitats beneath different canopy species (Sullivan 1978). Diversity values were high for all communities (H' = 3.348 - 4.246 and S = 35.3 - 43.0) of diatoms in contrast to the low diversity of spermatophytes. Sullivan (1978) suggested that salt marsh sediments do not constitute a stressful environment for the well-adapted diatom communities. The highly dynamic nature of the marsh and heterogeneity of the marsh sediments create various microniches such that no single taxon completely dominates a community. A large number of diatom species identified are motile, pennate forms able to adjust to changing conditions through locomotion (Sullivan 1978).

One hundred of the Mississippi diatom taxa have also been reported in the marshes of Delaware and/or New Jersey (Sullivan 1975 and Sullivan 1977, respectively), which suggests that a single, basic edaphic diatom community indigenous to Atlantic and gulf coast salt marshes may exist.

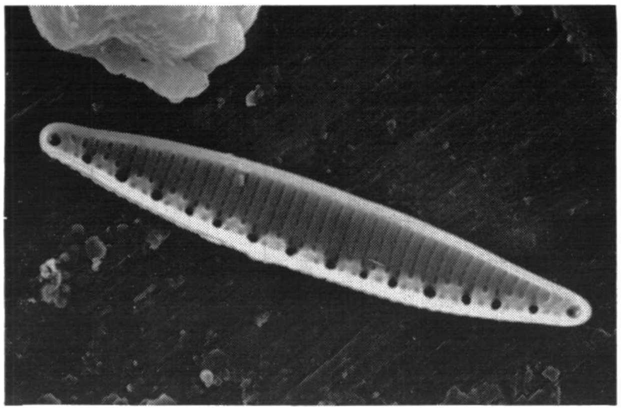
Canonical correlation analysis of marsh diatom data indicates that distributions are primarily regulated by marsh surface elevation and canopy height. Of the two, canopy characteristics are most complex as they relate to quality and quantity of light and relative humidity at the marsh surface (Sullivan 1982b). Other parameters such as ammonia nitrogen, far red light energy, and soil moisture can be important in determining the structural organization of edaphic diatom communities (Sullivan 1978).

Experimental removal of a canopy of Distichlis spicata reduced diatom species diversity (H') and the number of taxa in a sample (S). Nine preexisting taxa were eliminated and three new taxa introduced to the community (Sullivan 1981). Therefore, marsh alterations which affect canopy characteristics may have significant impacts upon the benthic communities through alterations of the algal community structure.

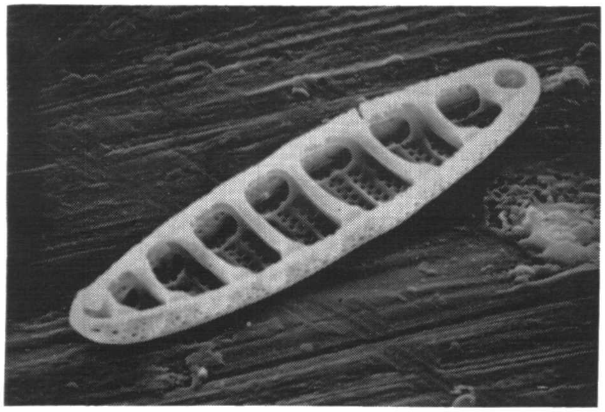
Enrichment of the Mississippi Juncus marsh with nitrogen had positive impacts on diatom community organization and did

Table 12. Distribution of microalgae found in six salt flats along the coast of southwestern Louisiana. (Maples and Watson 1979).

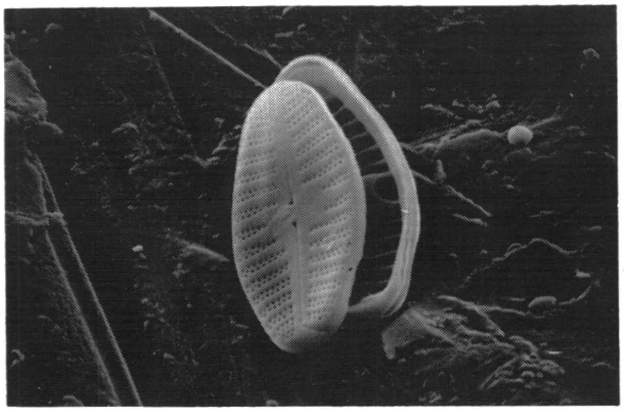
Classification	November 1978 site no.						April 1979 site no.					
	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Chlorophycophyta												
Ankistrodesmus							+		+	+	+	
Bracteococcus			+		+			+				
Chlamydomonas	+	+	+			+	+	+				+
Chlorococcum	+	+	+		+	+	+	+	+	+	+	+
Chlorosarcina						+						
Chlorosarcinopsis	+		+	+	+	+	+	+	+	+	+	+
Gleocystis												+
Klebsormidium		+	+									+
Microspora											+	
Pedimonas		+										
Pleuastrum		+	+					+				
Radiosphaera											+	
Rhizoclonium					+	+						+
Spongiochloris											+	
Stigeoclonium						+		+				+
Tetracystis	+	+	+	+			+		+	+		
Ulothrix						+						
Chrysophycophyta												
Amphora		+		+				+		+		
Botrydiopsis			+									
Chrysosarcinia				+								
Fragilaria		+				+		+				+
Navicula	+	+	+	+	+	+	+	+	+	+	+	+
Nitzschia	+					+	+					+
Ochromonas				+			+		+			+
Cyanochloronta												
Anabaena	+	+	+	+	+		+	+		+	+	
Aphanotheca	+			+			+					
Calothrix			+						+			+
Chroococcus	+		+				+				+	
Microcoleus					+							
Microcystis			+	+								+
Nodularia			+	+							+	
Nostoc			+						+			+
Oscillatoria	+	+	+	+	+	+	+	+	+	+	+	+
Schizothrix	+	+	+	+	+	+	+		+	+	+	+
Spirulina	+	+	+				+	+	+			
Totals	12	13	18	12	9	12	14	12	11	9	12	16



Nitzschia minutula inside valve (6000X, 0° tilt)



Denticula subtilis inside valve (10,000X, 45° tilt)



Achnanthes lanceolata raphe and araphid valves (6500X, 45° tilt)

Figure 19. Juncus marsh diatoms. Photos

not eliminate taxa (Sullivan 1981). High light intensity caused by canopy removal in conjunction with nitrogen enrichment increased the relative abundance of *N. gandersheimiensis* from fall through spring, while natural light intensity and nitrogen enrichment under an undisturbed canopy greatly stimulated *N. perversa* growth in spring and summer (Sullivan 1981).

Sullivan (1982a) compared the structure of an epiphytic and edaphic diatom community within the same stand of *Spartina alterniflora* in Mississippi. Epiphytic diatoms were examined from two red algal species, *Bostrychia radicans* and *Caloglossa leprieurii*, which were associated with dead *S. alterniflora* stems. The dominant taxa of both edaphic and epiphytic communities were *Anaulus balticus*, *Fragilaria atomus*, *F. pinnata* and *Nitzchia minutula*. Totals of 31 epiphytic and 43 edaphic taxa were encountered. Species diversity (H') and the number of taxa in a sample (S) were similar in October and January for both habitats. Edaphic communities exhibited higher diversity, but comparison of the species structure of the two communities revealed that they shared 63.2% of the maximum similarity possible.

Multicellular algae of northeast gulf marshes are poorly known. In addition to observations previously mentioned, Pecora (1978, 1980) described five species of *Vaucheria* (Xanthophyceae) from *Juncus* marshes in Mississippi and western Florida (Table 13). This genus is a major component of the algal flora in diverse habitats of these marshes during winter. *Vaucheria velutina* is the most abundant *Vaucheria* species in the northern gulf coast region (Pecora 1980).

In addition, Humm and Caylor (1957) listed two cyanophytes (*Microcoleus chthonoplastes* and *Nodularia harveyana*), two chlorophytes (*Cladophora gracilis* and *Rhizoclonium riparium*) and three rhodophytes (*Saloglossa leprieurii*, *Bostrichia radicans*, and *B. tenella*) as components of the summer salt marsh flora

Table 13. Occurrence of *Vaucheria* species (Xanthophyceae) in marshes of the northeastern Gulf of Mexico (data from Pecora 1978, 1980).

Species	Location	Soil water salinity	Occurrence
V. lii[a]	St. Louis Bay, MS	4.5 ppt	Shaded soil among *Spartina cynosuroides*
V. adela[a]	St. Louis Bay, MS	5.5-8.0 ppt	Open, nonshaded areas of a *Juncus roemerianus* marsh
V. arcassionensis[a]	St. Marks State Park, Wakulla Co., FL	25 ppt	Exposed edge of *J. roemerianus* marsh with filaments of *Cladophora* sp. and *Dichotomosiphon tuberosus*
V. prolifera var. *reticulospora*[b]	Buccaneer St. Park, Hancock Co., MS	9.5 ppt	Compacted plant debris at edge of *J. roemerianus* marsh
V. velutina	Buccaneer St. Park, Hancock Co., MS	2.0 ppt	Exposed mud in *Spartina patens*
	Buccaneer St. Park, Hancock Co., MS	9.0 ppt	In mud of *J. roemerianus*
	Bayside Dr., Miss. Sound, Hancock Co., MS		Dry soil of burned *J. roemerianus* and *Distichlis spicata*

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[a] First report from Gulf of Mexico.
[b] First report from North America.

CHAPTER 4

MARSH FAUNA

ZOOPLANKTON

Very little information is available on zooplankton of gulf coast *Juncus* marshes. The only available study is of decapod larvae (Shipp 1977). Decapod larvae make up a major portion of the total meroplankton and seasonally are an important part of the total zooplankters. Adult decapods are major marsh detritivores and may significantly control detrital energy flow.

Shipp (1977) identified decapod larval stages representing 9 families, 14 species, and 12 genera in an Alabama *Juncus* marsh complex. *Uca* spp., *Rhithropanopeus harrisii*, *Sesarma reticulatum* and *Sesarma cinereum* were the most commonly collected forms (Table 14), with *Uca* spp. making up 86% of the total collection. Larvae were abundant April through September with the most species (eight) collected in September, a period of moderate temperatures (22.9-23.8 °C) and broad salinity ranges (3-22 ppt).

In the Alabama study different species showed different seasonal peaks of abundance. *Rhithropanopeus harrisii* larvae were most abundant in June. *Palaemonetes* spp. and *Eurypanopeus depressus* also showed peak abundance in June, but these two species had a second peak in August - September and September, respectively. The xanthid larvae *Panopeus herbstii*/ *Eurythium limosum* had a single peak of abundance in September. *Sesarma cinereum* and *Uca* spp. peaked in August. *Sesarma reticulatum* was most numerous in August but had a smaller second peak abundance in May (Shipp 1977).

Salinity appeared to play a role in distribution of decapod larvae. Shipp (1977) found four taxa throughout the range of salinity (0.6-22.0 ppt): *Uca* spp., *Sesarma reticulatum*, *S. cinereum*, and *Rhithropanopeus harrisii* (Table 15). *Ogyrides limicola* and *Upogebia affinis* were collected only at the highest salinity station (4.1-22.0 ppt). Salinity ranges for other species were *Palaemonetes* spp. (1.4-22.0 ppt); *Eurypanopeus depressus* and *Panopeus herbstii*/*Eurytium limosum* (1.6-22.0 ppt); and *Alpheus* sp. and *Callianassa* sp. (1.6-18 ppt).

Several species of decapod larvae showed a consistent pattern of greater abundance in bottom samples over 24-hour collection periods and in night samples. These include *Sesarma reticulatum*, *Rhithropanopeus harrisii*, and *Palaemonetes* sp. There was also a greater abundance of progressively older stages in bottom collections except for megalops of *Callinectes sapidus*. Vertical migration was noted for all species collected in any numbers during the 24-hour samples (Shipp 1977).

More information is needed on environmental controls of distribution and success of larval forms in order to understand the ecology of the adults. Studies of zooplankton, other than decapods, are sorely needed.

MEIOFAUNA

Meiofaunal communities have received attention in Gulf of Mexico *Juncus* marshes recently. Information is available on species composition and short-term

Table 14. Larval decapod crustacean species and abundance in the zooplankton of an Alabama *Juncus* marsh (data from Shipp 1977). Species names in parentheses indicate probable species identification.

Species	Abundance	Relative abundance (%)	Salinity ranges (ppt)
Palaemonetes spp.	366	0.44	1.4-22.0
Alpheus sp. (*heterochaelis*)	11	0.01	1.6-18.0
Alpheus sp.	6	0.01	1.6-18.0
Ogyrides limicola	8	0.01	4.1-22.0
Leptochela sp.	1	0.01	-
Callianassa sp. (*jamaicense*)	81	0.10	1.6-18.0
Upogebia affinis	4	0.01	4.1-22.0
Sesarma cinereum	1,265	1.51	0.6-22.0
Sesarma reticulatum	3,149	3.76	0.6-22.0
Uca spp.	72,085	86.05	0.6-22.0
Rhithropanopeus harrisii	5,873	7.01	0.6-22.0
Eurypanopeus depressus	485	0.58	1.6-22.0
Panopeus herbstii/ *Eurytium limosum*	335	0.40	1.6-22.0
Callinectes sapidus	101	0.12	-
Total	83,770		

fluctuations (1-2 yr), but no work has been done on their ecological role or long-term community dynamics.

In comparison to other marsh systems, Harp (1980) found Alabama marsh areas with *Juncus roemerianus* and *Spartina alterniflora* canopies depauperate in both total abundance and number of copepod species present. Ten major taxa comprised the total meiofauna community. Of these taxa, nematodes dominated both habitats.

In *S. alterniflora*, nematodes contributed 62% and 77% of the total meiofauna for two years, harpacticoid copepods 25%, and oligochaetes 2% (Table 15). Abundance peaked in March, fell to a minimum in June, then increased through the fall and winter. Nematode and copepod

Table 15. Meiofaunal communities, dominant copepods, copepod abundance, and copepod diversity in Alabama coastal marshes.

Spermatophyte canopy	Community composition[a]	Dominant copepods[b]	Copepod abundance	Copepod diversity (H')
Spartina alterniflora	Nematoda 62-77% Harpacticoid Copepods 25% Oligochaeta 2% Total Taxa - 11	Microarthridion littorale (49.5%) Enhydrosoma propinquum Onychocamptus mohammed Nannopus palustris	Spring & fall peaks minimum summer	Low, decreasing in spring and fall
Juncus roemerianus	Nematoda 52-57% Harpacticoid Copepods 26% Oligochaeta 10% Polychaeta 3% Total Taxa - 10	Schizopera sp. (44.7%) Nannopus palustris Microarthridion littorale Halicyclops sp. Phyllopodopsyllus aegypticus	Spring peaks, minimum summer	Low, variable over year

[a] Ivester 1978.
[b] Harp 1980.

abundance variations were similar to those of the total meiofauna (Figure 20).

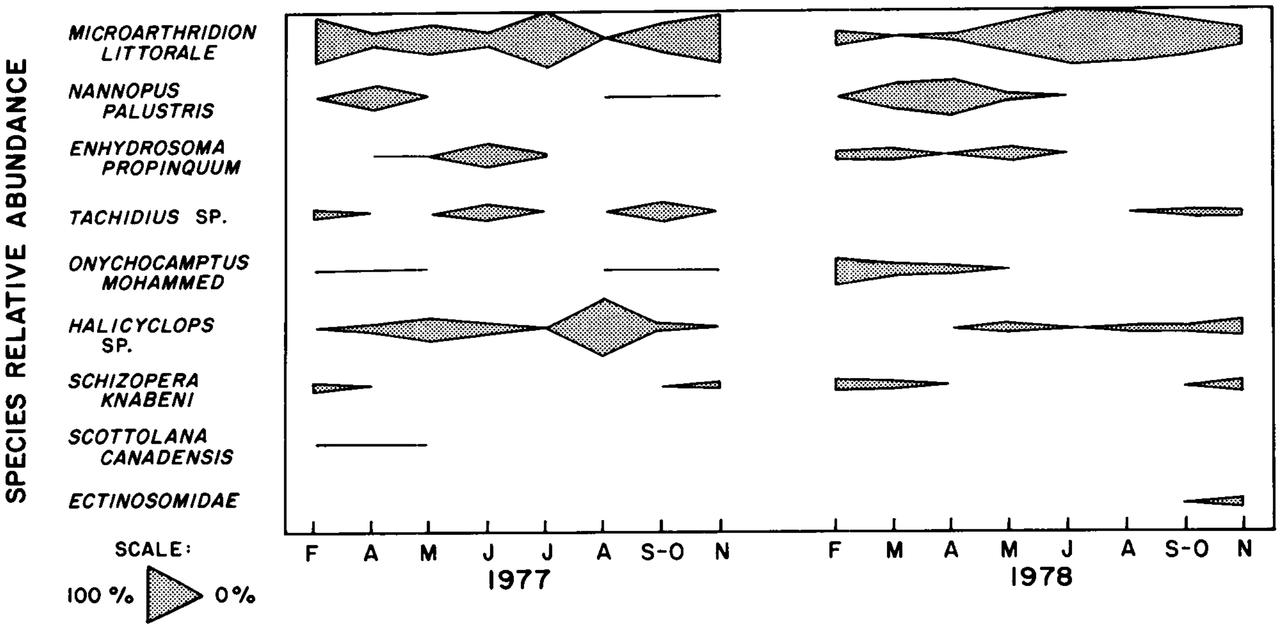
Meiofauna of Juncus habitats was also dominated by nematodes (52-57%), with harpacticoid copepods comprising 26%, oligochaetes 10%, and polychaetes 3% of the total number of individuals. The polychaete Manyunkia aestuarina was more numerous in Juncus than in Spartina, but did not fluctuate as widely over the year in Juncus areas.

Harp (1980) identified 14 harpacticoid and 1 cyclopoid copepod species. Twelve species were found under Spartina alterniflora and Juncus canopies. Three species (Schizopera sp., Phyllopodopsyllus aegypticus, and Robertsonia sp.) were restricted to Juncus, and four species (Schizopera knabeni, Pseudostenhelia wellsi, Nitocra sp. and Tachidius sp.) were restricted to Spartina sites (Table 16). Dominant species were different between the two spermatophyte covers. Comparisons of species composition of the two communities and seasonal variations in abundance are presented in Figure 20.

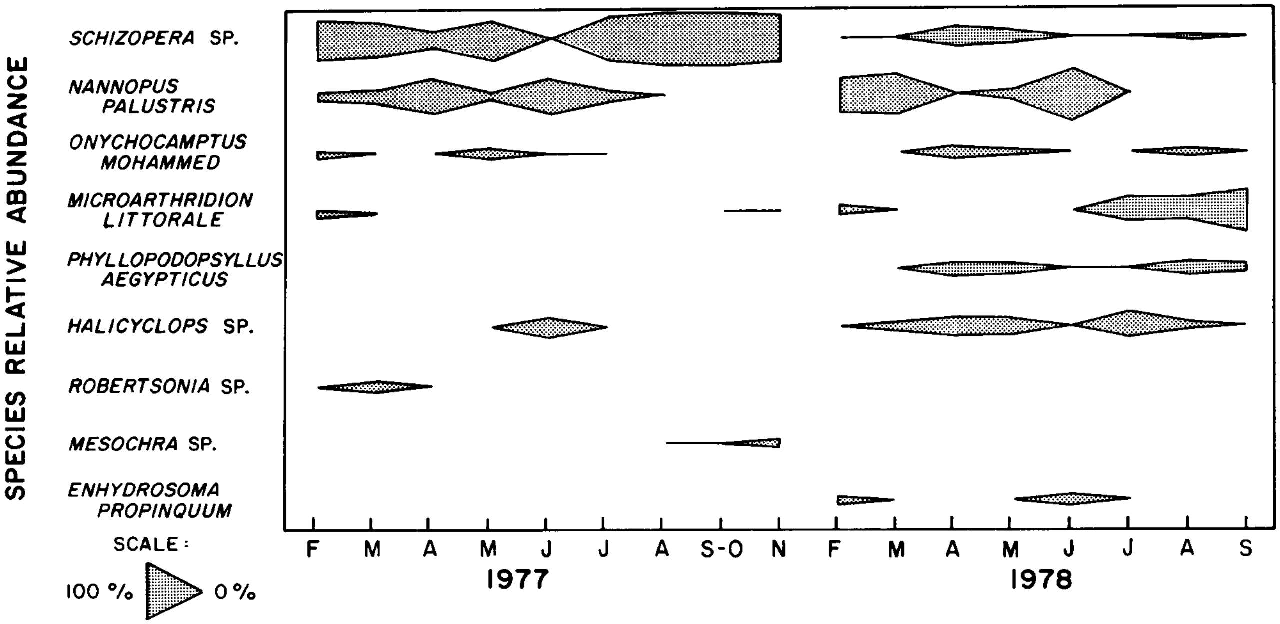
Although the two marsh copepod communities differed in species structure and dynamics, species diversities were not significantly different. This has been noted in other areas at different depth zones of subtidal marsh sites (Coull and Fleeger 1977; Bell 1979) and in regions where sedimentological regimes differ greatly (Ivester 1980). Ivester (1975) indicated that numerical equivalence of diversity indices masks the fact that each community is composed of different species partitioning resources in different ways. Further studies are needed to understand the ecological differences between marsh meiofauna communities.

A number of mechanisms have been suggested as controlling copepod community dynamics. Among these factors are food resource availability, predation, and physicochemical factors.

Though salt marshes usually have high primary production, feeding strategies of some copepod species are highly specialized. In South Carolina marshes, Stenhellia bifidia populations were found



SPARTINA ALTERNIFLORA



JUNCUS ROEMERIANUS

Figure 20. Relative abundance of the dominant copepod species under Spartina alterniflora and Juncus roemerianus (from Harp 1980).

Table 16. Benthic copepod species under *Spartina alterniflora* and *Juncus roemerianus* (modified from Harp 1980).

Canopy species	
Spartina	*Juncus*
Schizopera knabeni[a]	*Schizopera* sp.
Pseudostenhelia wellsi[a]	*Robertsonia* sp.
Nannopus palustris	*Nannopus palustris*
Enhydrosoma propinquum	*Enhydrosoma propinquum*
Onychocamptus mohammed	*Onychocamptus mohammed*
Microarthridion littorale	*Phyllopodosyllus aegypticus*[a]
Tachidius sp.[a]	*Microarthridion littorale*
Scottolana canadensis	*Scottolana canadensis*
Mesochra sp.	*Mesochra* sp.
Nitocra sp.[a]	*Nitocra* sp.
Halicyclops sp.	*Halicyclops* sp.
Ectinosomidae	Ectinosomidae

[a] Species restricted to either *Spartina* or *Juncus* stands.

to be density dependent (Fleeger 1979). However, population densities in Alabama *Juncus* marshes were so low that competition for food here seems unlikely to be a limiting factor, although seasonal availability of specific food items (i.e., algae, bacteria, etc.) may be limiting.

Macrofauna predation and/or disturbance may have an important role in regulating copepod communities. This is especially true in zones frequently inundated and, therefore, vulnerable to aquatic macrofauna such as the grass shrimp (*Palaemonetes pugio*) (Sikora 1977; Bell and Coull 1978). Gulf coast *Juncus* marsh meiofauna may be less susceptible because of irregular and infrequent tidal flooding and exposure patterns. Harp (1980) found no significant association between copepod and macrofauna abundance patterns.

Marsh substrates represent great spatial heterogeneity due in part to biogenic activity. Macrofauna burrows, especially those of *Uca*, may affect copepod densities (Bell et al. 1978). Root biomass may limit meiofauna abundance by occupying available space (Bell 1979). Harp's *Spartina* site, however, had the greatest belowground biomass of plant material, the greatest density of *Uca* sp., and highest copepod abundance. Thus, the effect of biological action on habitat heterogeneity and availability is unclear in gulf *Juncus* marshes.

Horizontal community zonation may reflect differences in physicochemical factors. The lower intertidal zone occupied by *S. alterniflora* is more regularly flooded than higher zones and is, consequently, subjected to shorter periods of sediment exposure, less drying, and less solar heating. This in part compensates for less shading of substrates by the spermatophyte canopy of this zone and smaller quantities of protective litter on the substrate surface. On the other hand, *Juncus* areas provide a dense shading canopy and heavy litter cover, but are susceptible to periods of severe dessication and resulting elevated interstitial salinities.

Juncus marshes located in embayments and river mouths, instead of directly on the coastline, represent a less saline environment and reduced seasonal extremes in fluctuating salinities. Within the lower salinity marshes, pH, salinity, nitrogen, and phosphorus are important abiotic variables explaining the variability in the density and diversity of meiofauna (Humphrey 1979).

In a brackish marsh of St. Louis Bay, Mississippi, Humphrey (1979) found meiofauna dispersed throughout the marsh with a high degree of similarity among plant associations. Within stands of short and tall *Juncus roemerianus*, *Spartina patens*, *Spartina cynosuroides*, and *Phragmites australis*, eight major taxa were observed. Meiofauna were dominated by nematods and foraminiferans. Other abundant taxa included polychaetes, crustaceans (harpacticoids and ostracods), and insect larvae. Low elevation sites contained greater densities, and individuals were more equitably distributed among the component species in these zones. Densities were higher during the spring and lower in the winter with declines during the summer and fall. However, no significant differences between seasons were measured.

Because the marsh environment of the northeast gulf is so dependent on seasonal and annual fluctuations in meteorological conditions (i.e., winds and rainfall), long-term community analyses are necessary to explain meiofauna population and community dynamics. Benthic environmental conditions will differ between coastal saline Juncus marshes and brackish Juncus marshes. Differences may be attributed to source(s) of flood waters, sediments, and nutrients and will be manifested in the meiofaunal communities. More work is necessary to understand the meiofauna community dynamics and environmental controls along the entire range of conditions in which Juncus marshes are found along the northeastern gulf coast.

MACROINVERTEBRATES

Macroinvertebrates comprise a large and diverse group of organisms closely linked to the abiotic marsh environment and uniquely adapted to its rigors and variations. Heard (1979) compiled a guide to 88 species of macroinvertebrates which have been observed and reported in marshes of the northeastern Gulf of Mexico. The species listing would be greatly expanded with the addition of oligochaetes and insects, taxa that are abundant in the marshes but present difficulties in systematics and identification.

Species range in size from small annelids and crustaceans less than 1 mm in size to large bivalve mollusks and crabs over 100 mm wide. They are found as both benthic epifauna and infauna and are pelagic as well as in tidal creeks and ponds. Occurrence over time varies from permanent to seasonal to tidal depending upon such aspects of the specific life history as feeding strategy, respiratory physiology, and reproductive patterns. Spatial distributions reflect adaptations of each species in regards to osmotic regulation, dessication, oxygen levels, and pH as well as respiration, sediment preference, and reproductive and feeding demands.

As highly productive systems, marshes provide ample nutrients in a variety of forms to suit the various invertebrate feeding mechanisms. Abundant living plant material, especially benthic algae and epiphytes, support grazers such as gastropods. Bivalve suspension feeders consume abundant detrital material within the tidal "soup." Most invertebrates of the marsh are detritivores or omnivores and provide an important link at the base of the food chain, concentrating the food values of detritus, algae, and meiofauna for transfer to higher trophic levels.

Macroinvertebrate Community Studies

Subrahmanyam et al. (1976) provide the only comprehensive picture of the macroinvertebrate community in Juncus marshes. Two Florida Juncus marshes, Wakulla and St. Marks, were each divided into low marsh, upper marsh, and high marsh zones based on soil characteristics and elevation. Tidal creeks represent a fourth zone. The low marsh and upper marsh were sampled with traps and all three zones by random transects. Tidal creeks were sampled with seines.

Four major taxa comprised the invertebrate community, mollusca (31%), annelida (24%), insect larvae (1%), and crustacea (44%). Traps yielded a total of 48 species, 40 at St. Marks with 63% common to low and upper marshes, and 43 at Wakulla with a low and upper marsh species similarity of 53%. Nineteen species (39%) were found in all four zones, whereas 11 species were found in only one zone. Unique species were typically estuarine forms found in the marsh only on flooding tides (e.g., Haminoea succinea, Taphromysis bowmani, and Mysidopsis almyra). Sixteen species were designated abundant resident species, occurring in at least three seasons and with a mean density of greater than $3/m^2$/season (Table 17).

Pooled mean densities of all four zones exhibited a bimodal distribution that peaked in February-April, with a smaller peak in September. Both peaks showed higher species diversity with increased densities of some species (Subrahmanyam et al. 1976). Maximum late winter density ($578/m^2$) corresponded with species breeding patterns. At this time recruitment of juveniles of the mollusks Littorina irrorata, Cyathura polita, Sesarma reticulatum, Melampus bidentatus, Modiolus demissus (= Geukensia demissus), and Cyrenoidea floridana was common. Densities were lowest in summer ($375/m^2$)

Table 17. Rankings (R), frequency of occurrence (F/12), and Biological Index values (BI) of the 10 most important species of macroinvertebrates in the two marsh zones of St. Marks and Wakulla, Florida, based on densities/m^2 in trap samples (Subrahmanyam et al. 1976).

	Marsh zones[a]											
	WLM			SLM			WUM			SUM		
Species	R	F/12	BI	R	F/12	BI	R	F/12	BI	R	F/12	BI
Littorina irrorata	1	12	96	1	52	104	1	10	89	2	12	92
Cyathura polita	2	10	86	2	22	81	2	9	75	1	11	101
Apseudes sp.	3	8	70	7	5	41	7	4	33	-	-	-
Scoloplos fragilis	4	6	57	4	8	57	6	5	39	4	8	63
Sesarma reticulatum	5	8	37	-	-	-	9	5	26	-	-	-
Modiolus demissus	6	6	36	-	-	-	4	6	42	-	-	-
Neanthes succinea	7	6	36	5	8	51	3	6	48	-	-	-
Leptochelia sp.	8	6	33	8	5	34	-	-	-	3	11	81
Insect larvae	9	5	33	-	-	-	-	-	-	-	-	-
Uca spp.	10	3	24	10	5	30	-	-	-	9	6	32
Heleobops sp.	-	-	-	3	8	65	-	-	-	7	5	39
Cyrenoidea floridana	-	-	-	6	1	47	-	-	-	8	5	34
Amphicteis gunneri	-	-	-	9	5	31	-	-	-	6	7	40
Laeonereis culveri	-	-	-	-	-	-	5	6	41	5	8	59
Polymesoda caroliniana	-	-	-	-	-	-	8	5	30	-	-	-
Cerithidea scalariformis	-	-	-	-	-	-	10	4	20	-	-	-
Melampus bidentatus	-		-	-	-	-	-	-	-	10	5	30

[a] WLM = Wakulla low marsh, SLM = St Marks low marsh, WUM = Wakulla upper marsh, SUM = St.Marks upper marsh.

due to predation by fish. Subrahmanyam and Coultas (1980) provided correlation coefficients between evenness and diversity of fish and invertebrates which also implied a mutual regulation between the two groups. High temperatures, low oxygen, and low moisture may also diminish summer densities, as has been suggested for *Halmyrapseudes bahamensis*, a tanaidacea (Sieg et al. 1982).

No significant monthly density variations were detected, indicating fairly stable invertebrate populations (Subrahmanyam et al. 1976). However, low marsh zones had significantly more species than did the upper marsh. This may be caused by greater accessibility of the low marsh to estuarine organisms. The homogeneity index (HI) on density was 33-38% between the two zones, i.e., one third of the density of the two zones was made up of the same species. Zone differences were also seen in higher diversity in the low marsh than in the upper marsh. A second contributing factor to higher density and diversity within the low marsh may be the greater availability of organic detritus in this zone (Coultas 1969).

When the Biological Index (BI), a function of frequency and relative density of species between samples is used, the marsh periwinkle (*Littorina irrorata*), the isopod *Cyathura polita*, and the polychaete *Scoloplos fragilis* dominated both marshes (Table 17). Based on biomass instead of density, *L. irrorata* contributed 81% of the total, and therefore, any seasonal changes in community biomass parallel those of *Littorina* (Subrahmanyam and Coultas 1980) (Figure 21).

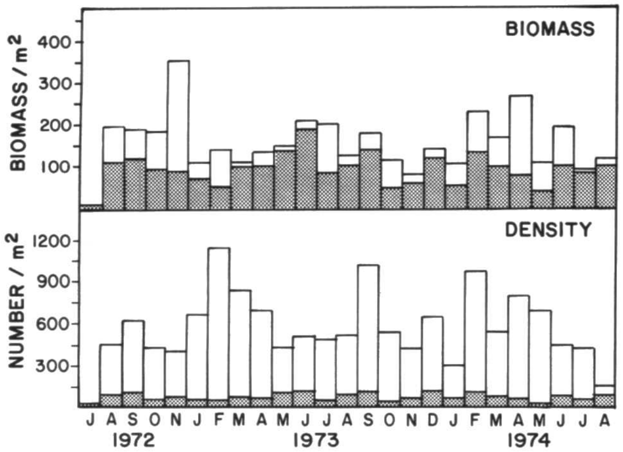


Figure 21. Seasonal fluctuations of biomass and density of macroinvertebrates in Florida marsh zones. Stippled areas represent Littorina irrorata (redrawn from Subrahmanyam and Coultas 1980).

Species relative abundance showed seasonal succession with Cyathura polita peaking in fall, and the tanaidacean Halmyrapseudes bahamensis (= Apseudes) and polychaete Scoloplos fragilis most abundant in the spring. Scoloplos was replaced by Neanthes succinea in the fall (Subrahmanyam and Coultas 1980).

Significant community changes were seen near the salt flat dividing the marsh into two distinct invertebrate species communities. They were characterized by Subrahmanyam et al. (1976) as a low marsh/upper marsh community dominated by Littorina irrorata, Cyathura polita, and tanaidaceans, with several abundant polychaetes (Scoloplos fragilis, Neanthes succinea, and Laeonereis culveri). Mollusk populations increased toward the salt flat. A high marsh community existed with abundant fiddler crabs (Uca spp.) and the gastropods Melampus bidentatus and Cerithidea scalariformis (Figure 22 and Table 18).

Spatial distribution of benthic faunal specimens may be governed by substrate properties. An optimum grain size for suspension feeders (0.18 mm with 50-90% silt-clay fraction) may exist (Sanders 1958). However, the north Florida marshes had a preponderance of deposit feeders and a sand fraction from 34-79%; therefore, other factors must also govern distribution of species. (Subrahmanyan and Coultas 1980).

Mollusks and arthropods dominated a Juncus marsh at Bay St. Louis, Mississippi (Humphrey 1979). Five stations were sampled based upon the species of vascular plant present: short and tall Juncus, Spartina cynosuroides, S. patens, and a mixed community of S. cynosuroides, S. alterniflora, and Phragmites australis.

As in north Florida, the low marsh Juncus contained the greatest diversity and density of invertebrates. Soil pH, phosphorus content, and free soil water were positively correlated with abundance. Dominant species by both density and biomass were: low marsh Juncus - the bivalves Polymesoda caroliniana and Geukensia demissa, and the snail Neritina usnea (= Neritina reclivata) and high

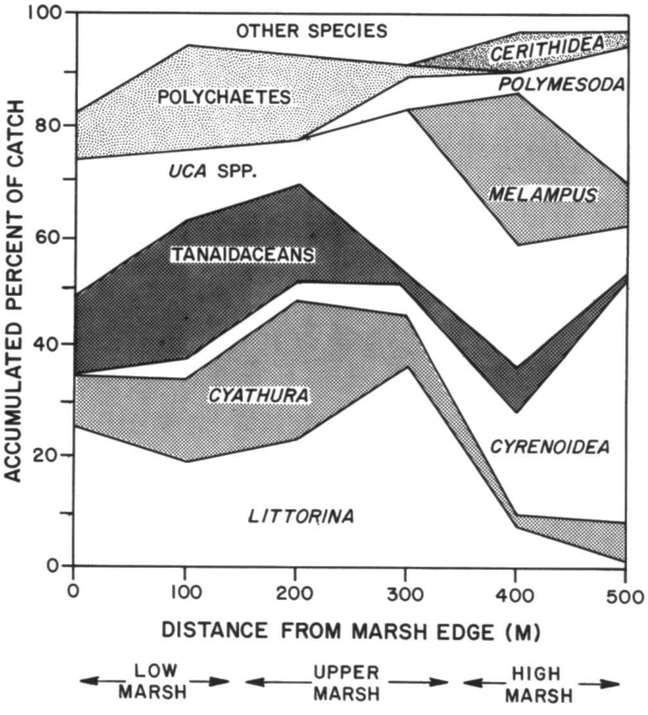


Figure 22. Horizontal distribution of macroinvertebrates in St. Marks and Wakulla tidal marshes based on transect sampling (redrawn from Subrahmanyam et al. 1976).

Table 18. Horizontal distribution and relative abundance of macroinvertebrates of two *Juncus* marshes. Abundant species occurred in at least three seasons at densities greater than 3/m^2, scarce species in at least two seasons at densities greater than 1/m^2, and rare species in one or two seasons at densities less than 1/m^2. LM = lower marsh, UM = upper marsh, HM = high marsh (Subrahmanyam et al. 21976).

Abundance	LM (0-100 m)	LM / UM (0-300 m)	UM (200-300 m)	UM / HM (200-500 m)	HM (400-500 m)	Ubiquitous (0-500 m)
Abundant		*L. irrorata* *C. polita* *Apseudes* sp. *Leptochelia* sp. *S. fragilis* *L. culveri* *N. succinea* *A. gunneri* *M. demissus* *S. reticulatum* *G. bonnieroides* *Uca* spp. *N. abiuma*			*M. bidentatus*	*C. floridana*
Scarce	*S. quadridentatum* *E. limnosum* *L. palustris*	*G. mucronatus* *U. longisignalis* *U. speciosa* *O. grillus* Talitrid	*M. nitida*	*N. reclivata* *P. caroliniana* *U. pugilator*	*C. scalariformis*	Insect larvae *Oligochaetes* *L. pontica*[a]
Rare	*T. bowmani* *M. almyra* *P. pugio* *C. fragilis* *M. corona* *H. succinea* *A. papyria* *T. plebius* *E. heteropoda*[a] *M. sanguinea*[a] *C. capitata* *Notomastis* sp.	*C. louisianum* *P. herbstii* *E. rupicolum*	*S. cinereum* *L. hyalina*	*P. floridana*		

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[a] Denotes species found only in transect samples.

marsh *Juncus* - *Melampus bidentatus*, *Uca* sp., and *Polymesoda caroliniana*. *Littorina irrorata* were of minimal importance, found only infrequently in samples, perhaps because of the lower salinities (x = 7.58 ppt) compared to the north Florida marsh (x = 15 o/oo) (Humphrey 1979). Diversity was also low, with maximum H' = 0.77 in low marsh *Juncus*, compared to the Florida marshes where H' = 2.49 (Subrahmanyam et al. 1976). The Mississippi marsh may represent the lower end of salinity tolerences for many estuarine and marsh organisms; and yet it is still too salty for most freshwater or terrestrial species. Mean density (26/m^2) of the two *Juncus* zones was lower than 475/m^2 found by Subrahmanyam et al. (1976), but biomass ranged within values for north Florida (Figure 23). This may be explained by the community dominance in Mississippi of larger bivalve mollusks and the scarcity of *Littorina irrorata*.

In a third community study of macroinvertebrates, pure stands of *Juncus roemerianus*, intertidal *Spartina alterniflora*, and *Distichlis spicata* along a salt flat in Alabama were sampled by Ivester (1978) for macroinvertebrate community comparisons. A total of 18 species were identified along with unidentified oligochaetes, insects, and a capitellid polychaete (Table 19). Oligochaetes dominated each of the three communities ranging in relative abundance from 80% in *Spartina alterniflora* to 53% in *Distichlis spicata* (Table 20). Six macroinvertebrate species composed over 90% of total numbers of the community in each zone, though species and relative abundance differed between zones. *Littorina irrorata* and *Guekensia demissa* were important only in *Spartina* stands. *L. irrorata* was replaced by *Melampus bidentatus* and increased numbers of *Neritina reclivata* in *Juncus* and *Distichlis*. *Polymesoda caroliniana* was the prevalent bivalve of the *Juncus* zone, as seen in both north Florida and Mississippi (Subrahmanyam et al. 1976; Humphrey 1979). There was no abundant bivalve found near the Mississippi salt flat (Humphrey 1979).

Macroinvertebrate diversity (H') in Alabama *Juncus* (0.69) and *Distichlis* (0.66) marshes was similar to Humphrey's (1979)findings in Mississippi. Alabama *Spartina alterniflora* had the lowest macroinvertebrate diversity (0.37); diversity declined in both late winter-early spring and in early fall (Ivester 1978).

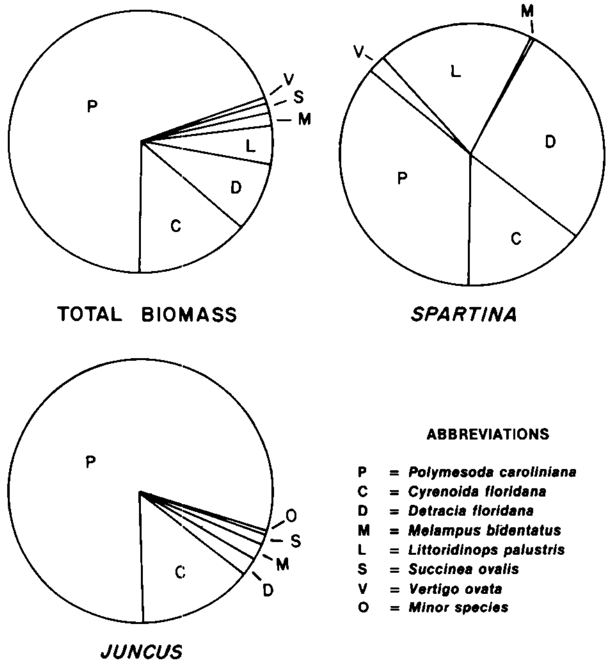


Figure 23. Percentage contribution of the dominant mollusk species to total mollusk biomass (g dry wt. m^{2}) in Mississippi *Juncus roemerianus* and *Spartina cynosuroides* marshes (redrawn from Bishop 1981).

Marsh tidal creek communities have marked seasonal fluctuations in macroinvertebrate species abundance. Grass shrimp (*Palaemonetes pugio*, *P. intermedius*) and blue crabs (*Callinectes sapidus*) were found dominating creeks in spring and summer, while mysid shrimp were most abundant in spring (Subrahmanyam et al. 1976; Subrahmanyam and Coultas 1980). Eight of the thirty-eight species collected in creeks were abundant enough to be considered dominants. Densities were highest during warmer months due to an increase in young decapod crustaceans. Creek samples yielded 15 species not found in marsh zones (Table 21).

Table 19. Occurrence of macroinvertebrates in Alabama coastal marshes (data from Ivester 1978). C = class; F = family; O = order.

Invertebrates	Zones of occurrence *Juncus romerianus*	 *Spartina alterniflora*	 *Distichlis spicata*
Annelida			
F. Capitellidae	X		X
Heteromastus filiformis		X Rare	
F. Nereidae			
Lycastopsis sp.	X		
Nereis succinea	X	X	X
C. Oligochaetae	X	X	X
Mollusca			
Littorina irrorata	X Rare	X	X Rare
Melampus bidentata	X	X Rare	X
Neritina reclivata	X	X	X
Geukensia demissa	X Rare	X	X
Polymesoda caroliniana	X	X Rare	
Rangia cuneata			X Rare
Crustacea			
Aramadillum vulgare	X		X
Gammarus mucronatus	X	X	
Orchestia grillus	X		X
Sesarma reticulatum	X	X	
Uca sp. A	X	X	X
Uca longisignalis		X	
Uca minax	X	X	X
Uca pugilator		X	X
Uca virens	X	X	X
Insecta			
O. Coleoptera	X		X
O. Odonta			X
F. Chironomidae	X	X	X

Hackney and de la Cruz (1981a) found only six species of invertebrates in an oligohaline marsh creek in Mississippi. All were macrocrustaceans; *Penaeus aztecus* and the parasitic isopod *Probopyrus pandalicola* were most abundant. The mud crab (*Rhithropanopeus harrisii*) was an abundant Mississippi species not listed for the north Florida marshes (Table 22; Figures 24, 25, 26).

Isolated ponds within the marsh receive tidal input and recruit species during spring tides and storms. Table 23 compares the common invertebrate species of an isolated pond with marsh creeks and an open bay. Among the six invertebrate species in ponds, *Palaemonetes pugio* and *Callinectes sapidus* were dominant (Subrahmanyam and Coultas 1980). These same two species were dominant in creeks

Table 20. Relative abundance of dominant macroinvertebrates in three zones of a northeastern gulf coast marsh (data from Ivester 1978).

Zone					
Spartina alterniflora		*Juncus roemerianus*		*Distichlis spicata*	
Oligochaeta	80%	Oligochaeta	54%	Oligochaeta	53%
Nereis succinea[a]	7%	*Nereis succinea*	13%	*Neritina reclivata*	25%
Littorina irrorata	5%	Unident. capitellidae	10%	*Melampus bidentatus*	3%
Neritina reclivata	2%	*Melampus bidentatus*	8%	*Uca* sp.	5%
Geukensia demissa	2%	*Polymesoda caroliniana*	3%	*Orchestia grillus*	3%
Uca sp.	2%	*Uca* sp.	3%	Unident. capitellidae	3%
Total	98%		91%		92%

[a] Syn. *Neanthes succinea*.

Table 21. Species of macroinvertebrates collected in tidal creeks of St. Marks and Wakulla *Juncus* marshes (Subrahmanyam et al. 1976).

Bivalvia

Tagelus plebius
Macoma constricta[a]
Modiolus demissus
Gemma purpurea[a]
Crassostrea virginica[a]

Gastropoda

Melongena corona
Cantharus tinctus[a]
Epitonium rupicolum
Haminoea succinea
Nassarius vibex[a]
Neritina reclivata
Bulla striata[a]
Cerithidea scalariformis
Polinices duplicatus[a]
Odostomia sp.[a]
Cerithidea costata
Melampus bidentatus

Polychaeta

Neanthes succinea
Scoloplos fragilis
Cistenides gouldii[a]

Cirripedia

Chthamalus fragilis
Balanus amphitrite[a]

Isopoda

Spaeroma quadridentatum

Amphipoda

Corophium louisianum
Corophium ellisi[a]
Talitrid
Orchestia grillus
Gammarus mucronatus

Mysidacea

Taphromysis bowmani
Mysidopsis almyra

Decapoda

Penaeus aztecus[a]
Penaeus duorarum
Palaemonetes pugio
P. vulgaris[a]
P. intermedius[a]
Palaemon floridanus[a]
Callinectes sapidus
Panopeus herbstii
Uca spp.
Sesarma reticulatum

[a] Not found in marsh zones.

(Subrahmanyam and Coultas 1980) and in Apalachicola Bay (Livingston 1976).

Mollusk Communities

Mollusk species are important members of the marsh community in terms of their abundance, biomass, and roles in the food chain. Nine species of mollusks were found in *Juncus roemerianus* and *Spartina cynosuroides* stands in a Mississippi oligohaline marsh (Bishop 1981). Eighty-five percent of the individuals collected in the *Juncus* stand were of three gastropod species: *Detracia floridana*, *Melampus bidentatus*, and *Succinea ovalis*. A small gastropod, *Onobops jacksoni*, was collected in relatively large numbers; this snail may have been missed in the north Florida studies because of the larger mesh size of the collecting gear. A typically terrestrial species, *Vertigo ovata*, was found in *Juncus* as well.

Gastropods were much less abundant in *Juncus* stands than in *Spartina cynosuroides* stands. Whereas total numbers peaked at 103 individuals/m^2 in July in *Juncus*, a single species, *Littoridinops palustris*, attained densities in June of over 1,500/m^2 in *Spartina*. *Detracia* and *Vertigo* were also

Table 22. Crustacean species in an oligohaline Mississippi tidal creek (data from Hackney and de la Cruz 1981a).

Abundance	Species
Abundant	Palaemonetes pugio Callinectes sapidus Rithropanopeus harrisii Uca longisignalis
Infrequent	Penaeus aztecus Probopyrus pandalicola

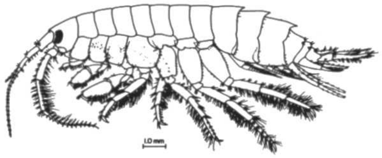
common in Spartina, but Melampus, Onobops, and Succinea were not found there (Figure 27).

Three bivalve mollusks species were found by Bishop (1981) (Figure 28). Polymesoda caroliniana and Cyrenoida floridana were found in Juncus and Spartina zones. Geukensia demissa granosissima was found in Juncus only. Cyrenoida floridana was the dominant species, comprising 94.8% and 86.6% of Juncus and Spartina bivalves collected, respectively. There were more bivalves in Juncus (1,099 individuals) than in Spartina (201 individuals).

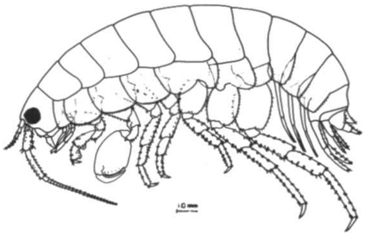
Total molluskan biomass was significantly greater in Juncus (10.4 g dry wt. m^{-2}yr^{-1}) than in Spartina (3.4 g dry wt. m^{-2}yr^{-1}. Approximately 83% of the total biomass was provided by the two dominant bivalves. Gastropod species accounted for approximately 17% of the total biomass, even though they were more numerous (Bishop 1981).

Species Notes

Neritina usnea (= Neritina reclivata) (Figure 27) is a gill-breathing gastropod in intertidal habitats throughout the Gulf of Mexico. Lehman and Hamilton (1980) determined a salinity tolerance of 1-19% for the snail and a marked preference for solid substrates. Neritina usnea was found to ingest only epiphytic algae from the substrate plants and not sand or plant biomass.

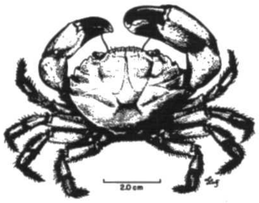


Gammarus mucronatus (Amphipoda)

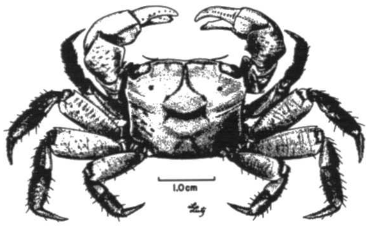


Orchestia grillas (Isopoda)

Clibanarius vittatus (Decapoda)



Panopeus herbstii-simpsoni (Decapoda)



Sesarma reticulatum

Figure 24. Common crustaceans of gulf Juncus marshes (from Heard 1982).

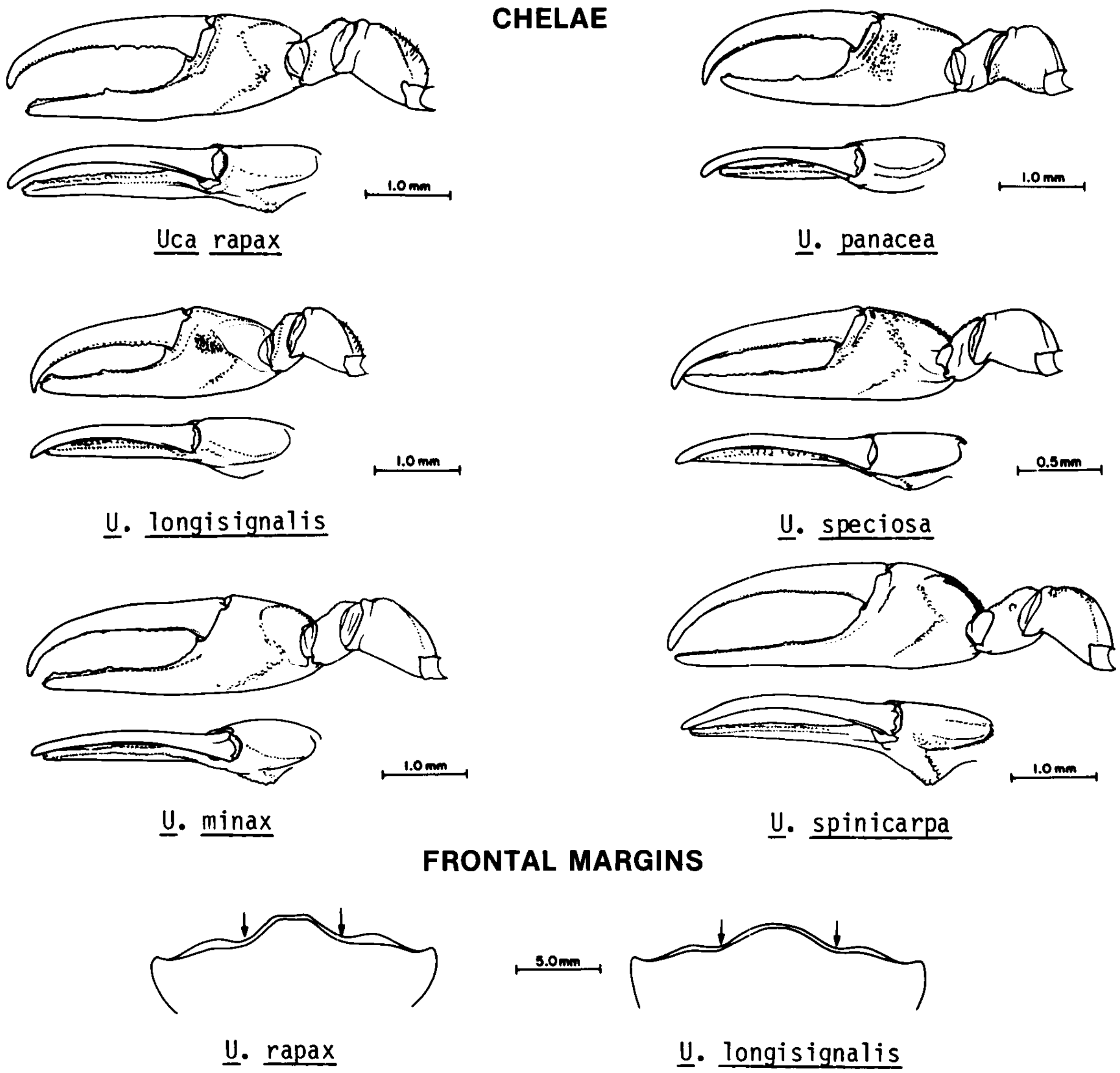


Figure 25. Chelae and frontal margins of Uca species found in gulf coast Juncus marshes (from Heard 1982).

Melampus bidentatus was described by Russell-Hunter et al. (1972) as amphibious. Respiration is by breathing air through a pneumostome and lungs. However, reproduction is like that of primitive marine snails, with production of a large number of small eggs and a planktonic veliger larvae. Egg-laying and hatching are, therefore, synchronous with spring tides. Wilder (1979) observed aggregation, copulation, and egg-laying at two-week intervals in phase with spring tides.

Harlos (1976) found Melampus bidentatus only within 1.0 m on either side of the Juncus edge of a Florida salt flat. Wilder (1979) found greatest densities in mixed vegetation dominated by Juncus and determined a significant relationship between plant density and snail density.

Figure 26. Small blue crab (*Callinectes sapidus*) seeking refuge among *S. alterniflora* at low tide. Photo by J. Stout.

When submerged, *Melampus bidentatus* suffers heavy predation from *Fundulus grandis*, *F. similis*, *Panopeus herbstii*, and *Callinectes sapidus* (Harlos 1976). Individuals in the high marsh have been observed being eaten by clapper rails (Howell 1932; Heard 1982) and *Sesarma reticulatum* (Wilder 1979).

Melampus lacks an operculum and has no ability to burrow or form an epiphragm to resist desiccation (Price and Russel-Hunter 1975). Though they can survive up to 80% weight loss by desiccation (Price 1976), the snails avoid desiccation by several behavioral adaptations including aggregation (Price and Russell-Hunter 1975) and positive geotaxis during dry spells by hiding in burrows, under rocks and detritus (Price and Russell-Hunter 1975; Wilder 1979).

Littorina irrorata, the marsh periwinkle, is probably the best known salt marsh invertebrate of southeastern North America. Although they have gills, *L.*

Table 23. Comparison of the dominant species of epifaunal invertebrates in a bay, marsh creeks, and isolated ponds based on numerical abundance (Subrahmanyam and Coultas 1980).

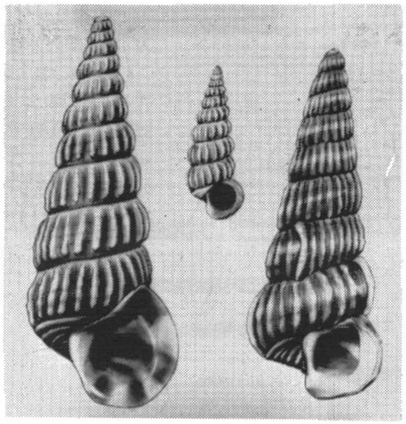
Bay system[a]	Marsh creeks[b]	Ponds[b]
Callinectes sapidus	*P. pugio*	*P. pugio*
Trachypenaeus constrictus	*Palaemonetes intermedius*	*P. intermedius*
Penaeus duorarum	*C. sapidus*	*C. sapidus*
Penaeus setiferus	*Taphromysis bowmani*	*P. vulgaris*
Chrysaora quinquecirrha[c]	*P. duorarum*	*P. duorarum*
Penaeus aztecus	*Gammarus mucronatus*	
Lolliguncula brevis[c]	*P. vulgaris*	
Palaemonetes vulgaris	*Mysidopsis almyra*	
Portunus gibbesii[c]	*Nassarius vibex*	
Stomolophus meleagris[c]	*Panopeus herbstii*	
Palaemonetes pugio	*Melongena corona*	
Squilla empusa	*Orchestia grillus*	

[a] Livingston 1976.

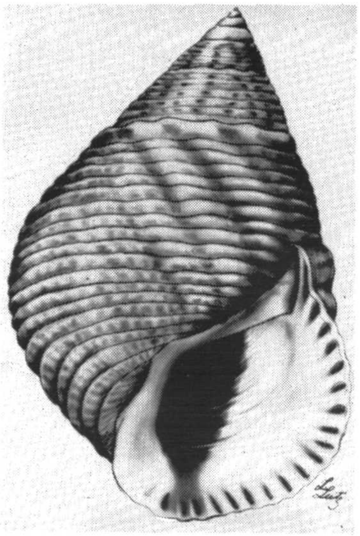
[b] Subrahmanyam and Coultas 1980.

[c] Species not recorded in marsh creeks or ponds.

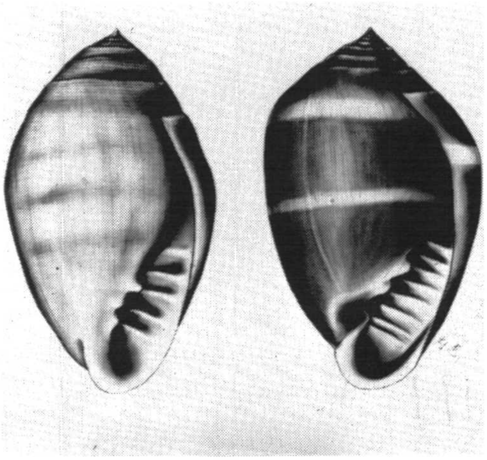
Neritina usnea



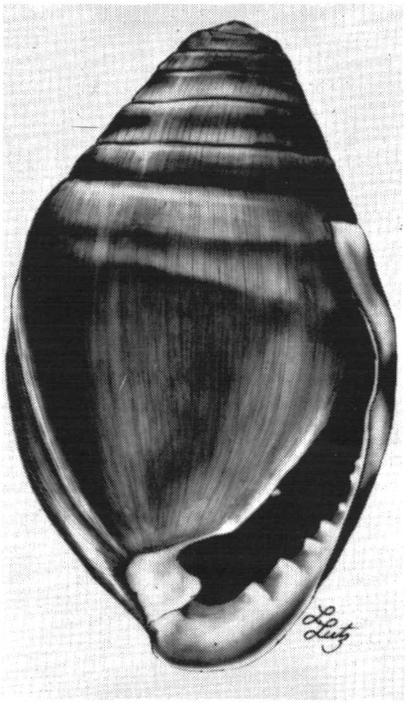
Cerithidea spp.



Littorina irrorata

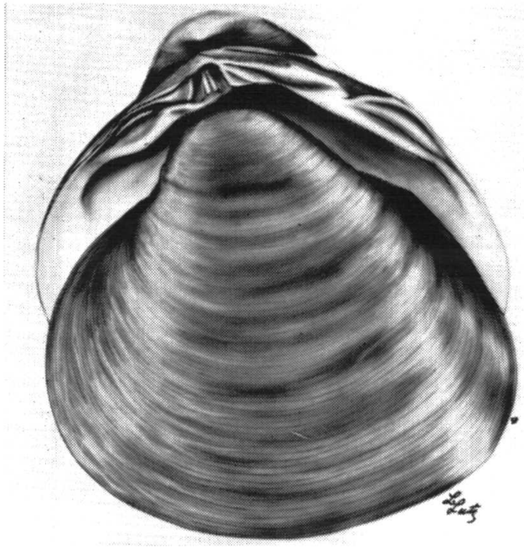


Melampus spp.

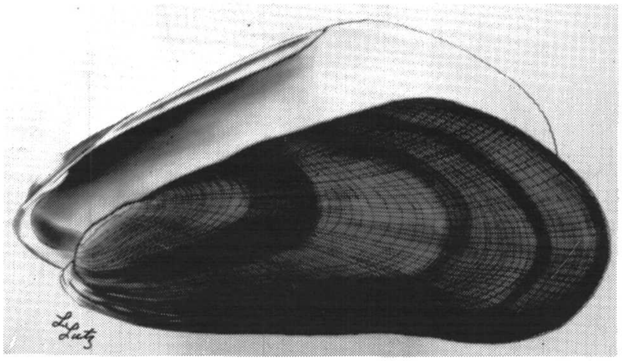


Detracia floridana

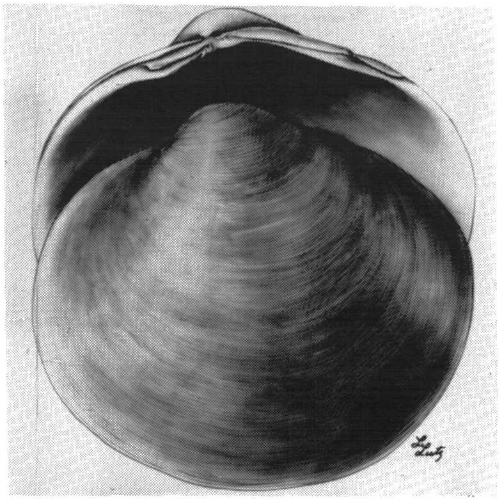
Figure 27. Common marsh gastropod species (from Heard 1982).



Polymesoda caroliniana



Geukensia demissa



Cyrinoidea floridana

Figure 28. Bivalve mollusks common to *Juncus* marshes (from Heard 1982).

irrorata rarely enter the water. They feed on the marsh floor during low tides and climb plant stems as the tides rise (Figure 29). However, larger snails may spend more time in the water than smaller snails. Stanhope et al. (1982) described a size-specific response to submergence due to differential predation on smaller snails by the blue crab (*Callinectes sapidus*). Periwinkles 5-7 mm in shell height were regularly eaten by blue crabs.

Figure 29. Periwinkles (*Littorina irrorata*) feeding on marsh surface (top) and on *Juncus* stems (bottom). Photos by J. Stout.

Of snails 10-16 mm, about 25% bore fracture marks indicative of unsuccessful attacks by blue crabs; those less than 5 mm in height were not attacked.

Periwinkles exhibit an upslope movement pattern apparently toward vegetational refuges. Hamilton (1977, 1978) demonstrated that the direction of movement is mediated by visual perception, especially of vegetation, on the horizon.

Littorina irrorata pair and spawn during new and full moons; spawning is correlated with the time of high tide. Females submerge for two to four successive days to release pelagic egg cases. Metamorphosis to a crawling supratidal snail is preceeded by a planktonic veliger stage (Gallagher and Reid 1974).

Bingham (1972) found Littorina irrorata unevenly distributed over the marsh with a sharp decline in total population density and large adult snails at the upper marsh. Adults required a salinity of 15 ppt or greater, and lower salinities of the upper marsh probably limited distribution. Subrahmanyam et al. (1976) collected more young snails (1-11 mm) in the lower marsh (415/yr) than in the upper marsh (34/yr).

The anthurid isopod Cyathura polita is considered euryokous because of its nearly ubiquitous distribution in many salinity, temperature, and sediment regimes from Maine to Louisiana. Adults can withstand salinities from 0 to 140 ppt, a pH of 3.4 to 11, and temperatures from -8 to 45 °C for up to 12 hours, but they die quickly in water with little oxygen (Burbanck 1961). Kruczynski and Subrahmanyam (1978) found there was no significant variation in densities of the isopod between low and upper marsh zones of a north Florida Juncus marsh. No C. polita were collected landward of the salt flats.

Cyathura polita probably has a 2-yr. life cycle in northern Florida (Kruczynski and Subrahmanyam 1978). Males matured first and made up 100% of the sexually mature population in winter. The percentage of males declined in spring as females with oostigites appeared in the population. Reproduction was from April through June. There was evidence for protogynous hermaphroditism in the isopod. Large males may have functioned as females during the preceding spring and summer.

Additional general life history details of most invertebrates of the northeastern gulf marshes may be found in Heard (1979).

Insects

Though species from all major insect orders have been reported from salt marshes, the Diptera, Coleoptera, and Hemiptera predominate.

The definition of "salt marsh insects" is complicated by a large number of transient species, i.e., species which may range into salt marshes but are common in other habitats. In this profile, only those species that have a habitual requirement for some part of the saltmarsh environment at some stage of their life cycle are considered.

The insect fauna can conveniently be divided into aquatic, subterranean, and surface-living groups. Aquatic species are invaders of freshwater origin and include dipteran larvae (especially those of the Culicidae, Chironomidae, and Ceratopogonidae), heteropterans, coleopterans, and certain trichopteran larvae. The subterranean and surface-living forms are regarded as being of terrestrial origin and include representatives of most major insect orders (Foster and Treherne 1976).

The insect populations of a Mississippi Juncus-dominated marsh were assessed by Parsons (1978). Two hundred sixty-five species representing 72 families and 9 orders were collected using standard sweepnet techniques. Only four Diptera, one Hymenoptera, and one Hemiptera occurred consistently throughout the year. Numerically, the dipterans and hymenopterans were codominants throughout the year and were joined during the warmer months by the equally abundant homopterans. The total number of species of hymenopterans collected (71) was greater than the dipteran count (64), yet only one species of a single family (Formicidae) accounted for the large number of the Hymenoptera.

Overall insect abundance was greatest in the late spring-early summer (April, May, and June). Two seasonal peaks in insect species diversity were found, one in May, (H' = 4.7) and the other in September (H' = 5.25). The spring peak coincided with the time when there were large quantities of fresh, new vegetation and the second peak when the senescence of most marsh vegetation began (Parsons 1978). This effect was especially pronounced in massive population increases observed among homopterans and dipterans. The insect assemblage is determined by the nature and amount of shelter and food supply. Species diversity increases with vegetation structural complexity.

While insects as a group are considered r-selectors compared to vertebrates, some insects are k-selectors (i.e., culicids). Cameron (1972) defined species which remain in the marsh throughout the year in adult form as "persistent" and those associated with seasonal or high energy inputs as "seasonal" species. These essentially are the k- and r-selectors, respectively. The r-selectors are responsible for increased richness and diversity in the insect community when they respond to increased resources during reproductive cycles.

Of approximately 208 species of adult insects collected by Parsons (1978), only six species representing three orders and six families (Diptera: Otitidae, Chloropidae, Dolichopodidae, Sciomyzidae; Hymenoptera: Formicidae; Hemiptera: Lygaeidae) were collected with enough frequency and consistency to be considered persistent, year-round resident species.

VERTEBRATES

Fish

Fish communities of the Juncus marsh are notable both in their species diversity and abundance of individuals. Seasonal changes in local environmental conditions of temperature and salinity, as well as tide-related changes in habitat availability, couple with species tolerances, life histories, habitat preferences, and feeding strategies to produce a dynamic community.

The community is dominated by physiologically euryhaline and holeuryhaline fish (Kilby 1955; Subrahmanyam and Drake 1975; Subrahmanyam and Coultas 1980; Hackney and de la Cruz 1981a). Of 49 species collected in a Florida Juncus marsh by Kilby (1955), over two-thirds were predominantly freshwater to brackish water species. These species comprised approximately 87.7% of the total number of individuals collected. An oligohaline (0.5-5.0 ppt) marsh in Mississippi was distinctive in that freshwater centrarchids (Micropterus salmoides and Lepomis macrochirus) were major predator species (Hackney and de la Cruz 1981a).

The marsh landscape provides diverse fish habitats. The availability of each habitat varies tidally and seasonally. Most obvious are the tidal creeks which wind and branch throughout the marsh. Deeper, primary creeks may provide permanent habitat though the overall total area is tide dependent. Intertidal creeks are available to fish only on flooding and high tides and may be partially unavailable during seasons with low tidal amplitude.

Depressions and ponds within the marsh may represent persistent habitats if deep enough and flooded frequently, or may only have standing water during limited periods of the year. Pond communities are isolated from the remainder of the marsh except on spring tides or storm tides which provide an avenue for immigration or emigration as well as replenishing nutrients, food organisms, and oxygen within the ponds.

Tidal range and specific marsh topography will determine the areal extent and temporal availability of the marsh surface as fish habitat. This habitat is difficult to sample because of the vegetation. The dynamics and details of utilization need further elucidation to determine the value of the marsh itself to fish.

Over 80 species of fish have been reported from creeks, ponds, and open waters of *Juncus* marshes of the northeastern gulf (see Table 24). Using the terminology of Subrahmanyam and Drake (1975), these species include permanent residents which spend their entire lives in the marsh, juveniles of nonresident species, adult migrants, individuals foraging from outside the marsh, and rare sporadic visitors.

Table 24. Fish species collected from *Juncus roemerianus* dominated marshes of the northeastern Gulf of Mexico with references for each.

Species	Reference[a]
Dasyatis sabina	1, 4
Lepisosteus platyrhincus	1
L. oculatus	5
Anguilla rostrata	5
Myrophis punctatus	4
B. patronus	3, 4, 5
Harengula jaguana	3
H. pensacolae	4
Dorosoma petenense	4
Anchoa mitchilli	3, 4, 5
A. hepsetus	3, 4
Notropis petersoni	1
Notemigonus c.	1
Arius felis (= *Galeichthys felis*)	5
Ictalurus punctatus	5
Synodus foetens	3, 4, 5
Hyporhampus unifasciatus	1, 3, 4
Strongylura notata	1, 2, 3, 4
S. timicu	1, 2
S. marina	3, 4, 5
Fundulus chrysotus	1
F. similis	1, 2, 3, 4
F. grandis	1, 2, 3, 4, 5
F. confluentus	1, 3, 4, 5
Adinia xenica	1, 3, 4, 5
Lucania parva	1, 2, 3, 4, 5
Chriopoeps goodei (= *Lucania goodei*)	1
Cyprinodon variegatus	1, 2, 3, 4, 5
Floridichthys carpio	1, 2
Jordanella floridae	1
Gambusia affinis	1,
Poecilia latipinna (= *Mollienesia latipinna*)	1, 3, 4, 5
Heterandria formosa	1
Syngnathus scovelli	1, 2, 3, 4
S. louisianae	5
Micrognathus crinigerus	2
Sphyraena barracuda	1
Mugil cephalus	1, 3, 4, 5
M. curema	1, 4
Prionotus scitulus	4
P. tribulus	3, 4

(continued)

Table 24. Concluded.

Species	Reference
Menidia beryllina	1, 2, 3, 4
Membras martinica	5
Micropterus salmoides	1, 5
Lepomis punctatus	1
L. macrochirus	5
L. microlophus	1, 5
Chaenobryttus coronarius (=*L. gulosus*)	1
Elassoma evergladei	*1*
Lutjanus griseus	1
Oligoplites saurus	2, *3*, 4, *5*
Trachinotus falcatus	2
Caranx hippos	*4*
Selene vomer	*4*
Seriola zonata	*4*
Eucinostomus argenteus	1, 2, 4
E. gula	1, 2, 3, 4
Polydactylus octonemus	2, 3, 4
Orthopristis chrysopterus	*1*, *3*, *4*
Lagodon rhomboides	1, 2, 3, 4
Archosargus probatocephalus	*1*, *5*
Chaetodipterus faber	4
Bairdiella chrysura sp.	*1*, *3*, *4*
Cynoscion nebulosus	*1*, 4, *5*
C. arenarius	3, *4*, *5*
Leiostomus xanthurus	1, 2, 3, 4, *5*
Sciaenops oscellata	1, *3*
Menticirrhus americanus	*4*
Opsanus beta	1, 2
Microgobius gulosus	1, 2, 4
M. thalassinus	*5*
Gobiosoma robustum	*1*, 2, *4*
G. bosci	*3*, 4, 5
Gobionellus boleosoma	*3*
Evorthodus lyricus	5
Eleotris pisonis	*5*
Chasmodes saburrae	*1*
Achirus lineatus	*1*, 2, *3*, 4, 5
Paralichthys lethostigma	3, *4*
P. albigutta	2
Symphurus plagiusa	2, *3*, 4
Citharichthys spilopterus	4
Sphoeroides nephelus	2, 4

1 = Kilby 1955
2 = Cherr 1974
3 = Subrahmanyam and Drake 1975
4 = Subrahmanyam and Coultas 1980
5 = Hackney and de la Cruz 1981a

[a] Uncommon occurrences in references are underlined.

Residents are dominated by cyprinodont species. Subrahmanyam and Drake (1975) attributed 53%-90% of total monthly biomass to adults of Fundulus similis, F. grandis, and Cyprinodon variegatus. Less common were Adinia xenica, Poecilia latipinna, Lucania parva, and F. confluentus (Figure 30). Variation in seasonal abundance of these dominants was positively correlated with temperature but not with salinity. Most resident species have protracted or continuous spawning seasons as evidenced by the year-round presence of juveniles and by species life history studies (Kilby 1955; Harrington 1959; Martin and Finucane 1969; Subrahmanyam and Drake 1975; Hardy 1978; de Vlaming et al. 1978). Additional species, including Mugil cephalus, Anchoa mitchilli, Membras martinica and Brevoortia patronus were persistent in an oligohaline marsh creek in Mississippi and contributed up to 99.9% of total catches in spring and winter (Hackney 1977).

Marsh resident species are typically opportunistic omnivores, capable of utilizing different food depending on availability. Harrington and Harrington (1961) found that resident species made heavy use of sudden hatches of mosquito larvae, then returned to other foods as the mosquitos were depleted (e.g., Lucania parva ate copepods; Cyprinodon variegatus and Poecilia latipinna ate plant materials). Foraging species, however, did not eat the abundant mosquitos, but stayed with basic food sources.

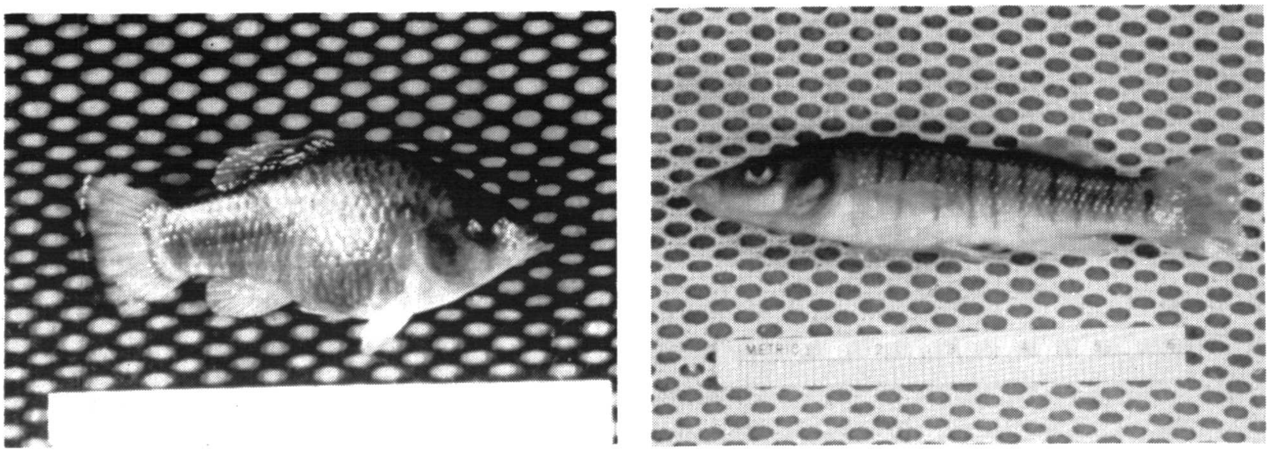
A relatively small number of species dominate the marsh fish community on an annual basis. The marsh fish community structure (i.e., diversity and evenness) may be markedly influenced by the nursery role played by these habitats. Nursery utilizers may be represented by only juveniles on both tides or by adults as well at high tides (Subrahmanyam and Drake 1975). Along with the resident cyprinodonts in the north Florida marshes, juveniles of four nursery species contributed significantly to fish community structure (Kilby 1955; Subrahmanyam and Drake 1975).

In the north Florida studies, Menidia beryllina made up 26-72% of the catches by number and occurred throughout the year. Leiostomus xanthurus juveniles were common in spring and late fall, accounting for 16-90% of catch by numbers and biomass. Abundance was negatively correlated with temperature ($r = 0.381$, $p < 0.01$) and positively correlated with salinity ($r = 0.351$, $p < 0.05$). Adults were caught in high tide samples in summer and fall. Juvenile mojarras (Eucinostomus argenteus) occurred primarily in fall, comprising 14-72% of the catch by numbers (Subrahmanyam and Drake 1975). Anchoa mitchilli was represented in most catches by juveniles only between March and September. Variations in abundance were not related to temperature or salinity. Two other nursery utilizers, Mugil cephalus and Lagodon rhomboides were seasonally abundant (Subrahmanyam and Drake 1975). Most juveniles of these two species and Leiostomus xanthurus leave the marsh creeks by June (Zilberberg 1966).

Foraging species are captured only on high tides as they make use of increased feeding habitat during tidal flooding of the marsh surface. Most foragers are estuarine residents and their numbers and diversity depend upon the proximity of the marsh to estuarine or nearshore waters. Eight species were categorized by Subrahmanyam and Drake (1975) as foragers. Dominants included Hyporhamphus unifasciatus, Bairdiella chrysura, and Cynoscion arenarius.

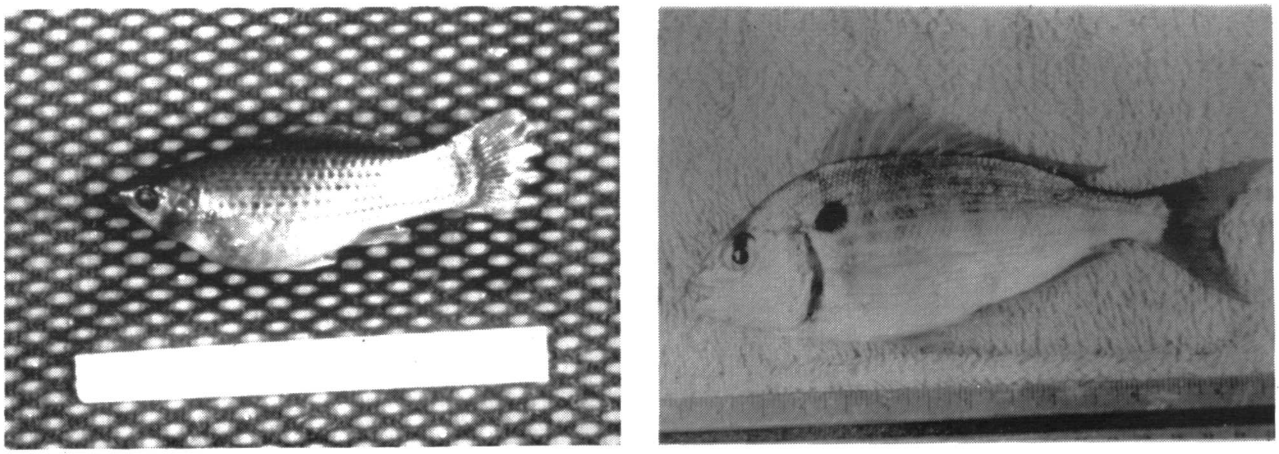
Species categorized as sporadic visitors include Polydactylus octonemus (Subrahmanyam and Drake 1975), Anguilla rostrata, Archosargus probatocephalus, Cynoscion nebulosus, Arius felis, and Sphyraena barracuda (Kilby 1955; Hackney and de la Cruz 1981a) (see Table 24 for uncommon species).

Different species may have other than seasonal differences contributing to their abundance or occurrence. Cherr (1974) found both day/night species preferences and high tide/low tide species preferences in a Juncus marsh creek in Apalachee Bay, Florida (Table 25).



Sheepshead minnow (*Cyprinodon variegatus*)

Longnose killifish (*Fundulus similis*)



Sailfin molly (*Poecilia latipinna*)

Pinfish (*Lagodon rhomboides*)

Figure 30. Common marsh fishes. Photos courtesy of R. Shipp.

Species dominance is also different between habitats. Fewer species are found in isolated ponds than in creeks. Common pond dominants include *Poecilia latipinna*, *Cyprinodon variegatus*, *Lucania parva*, *Adinia xenica*, *Fundulus confluentus*, and *Leiostomus xanthurus*. Freshwater forms such as *Gambusia affinis* and *Lepomis* sp. may also be present. (Kilby 1955; Subrahmanyam and Coultas 1980) (Table 26).

Juncus marsh fish community structure is influenced by: (1) season and tides, (2) species breeding activity, (3) species feeding behavior, (4) habitat diversity and available space, and (5) proximity to the estuary and nearshore waters. Subrahmanyam and Drake (1975) found significant seasonal changes in fish diversity (H'), species richness (D), and equitability (E), but no differences in these indices between tides. Diversity and species richness were higher in spring and fall and lower in winter and summer. Changes in species equitability were related to the seasonal abundance of a few

Table 25. Fish species preference based on occurrence (% of total of that species caught under given condition) for (A) day/night and (B) high tide/low tide, Live Oak Point, Florida (data from Cherr 1974).

Species	%	Species	%
A) Night		Day	
Strongylura notata	85.3	*Lucania parva*	86.4
S. timica	94.7	*Eucinostomus argenteus*	72.5
Menidia beryllina	85.1	*E. gula*	72.8
Oligoplites saurus	80.0	*Sphoeroides nephelus*	87.5
Trachinotus falcatus	75.9		
Leiostomus xanthurus	99.6		
Polydactylus octonemus	65.7		
B) High tide		Low tide	
Opsanus beta	92.9	*Oligoplites saurus*	66.7
Cyprinodon variegatus	97.6	*Polydactylus octonemus*	84.6
Floridichthys carpio	92.9		
Fundulus grandis	91.9		
F. similis	91.4		
Lucania parva	100.0		
Eucinostomus argenteus	84.7		
Paralichthys albigutta	90.9		
Symphurus plagiusa	77.8		

species such as *Anchoa mitchilli* (Subrahmanyam and Coultas 1980). The major temporal changes appeared to be related to the breeding patterns of the fish with a sequence of juvenile nursery users being noted. *Leiostomus xanthurus* dominated winter and spring collections, followed in the spring and summer by *Anchoa mitchilli* and *Menidia beryllina*. Fall collections were dominated by *Eucinostomus* sp. and *Lagodon rhomboides*. Temporal succession avoids niche overlap between these species with feeding similarities (Subrahmanyam and Drake 1975, Subrahmanyam and Coultas 1980). Abundance per unit of effort per month varied from 62 to 6,973 individuals (Subrahmanyam and Coultas 1980).

Total fish biomass also reflects periods of breeding and juvenile activity in the marsh. There is significantly higher biomass during the warm months; this can be attributed to the greater number of species and juveniles present, and to larger individuals in the resident fish population. Three species - *Cyprinodon variegatus*, *Menidia beryllina*, and *Leiostomus xanthurus* account for low winter biomass levels. Monthly biomass varied from 98.8 g to 5,168 g per unit of effort (Subrahmanyam and Drake 1975).

Total abundance was significantly different between high and low tides but was not correlated with temperature or salinity. Average low-tide catches were greater than high tide when the community could occupy a larger habitat space as it spread across the marsh surface. High tide collections were composed mostly of juveniles of nursery species with a few adults and subadults of foraging species. Many resident species left the creeks and spread with tidal waters across the marsh surface. Juveniles and adults of resident

Table 26. Comparison of the 10 dominant fish species in an estuary, salt marsh tidal creeks, and isolated ponds in salt marshes in north Florida. (Subrahmanyam and Coultas 1980).

Apalachicola Bay[e]	Marsh tidal creeks[f]	Isolated ponds[f]
Anchoa mitchelli	A. mitchilli[b]	L. xanthurus
Micropogon undulatus[a]	L. xanthurus	Poecilia latipinna[c,d]
Cynoscion arenarius[c]	Fundulus similis[d]	C. variegatus[d]
Leiostomus xanthurus	F. grandis	A. xenica[d]
Chloroscombrus chrysurus[a]	Cyprinodon variegatus[d]	Mugil cephalus[c]
Menticirrhus americanus[c]	Adinia xenica	F. confluentus[c,d]
Symphurus plagiusa	Eucinostomus argenteus	F. grandis[d]
Polydactylus octonemus	Menidia beryllina[d]	Lucania parva[c]
Arius felis[a]	Lagodon rhomboides[d]	F. similis
Prionotus tribulus[c]	F. confluentus	Microgobius gulosus[c,d]

[a] Not recorded in marsh tidal creeks or ponds.

[b] Rare in isolated ponds.

[c] Rare in tidal creeks.

[d] Rare in estuary.

[e] Livingston 1976.

[f] Subrahmanyam and Coultas 1980.

species contributed significantly to low tide collections as marsh surface water drained away into the creeks (Subrahmanyam and Drake 1975).

Though many marsh fish species have little commercial importance, their diverse food habits and intense utilization of marsh creeks may make them especially important in transferring energy from the marsh to the estuary and coastal waters and thus to commercially valuable species. Nursery species and foraging species consume detritus, larvae, and plankton at the base of the food chain in the marsh and then introduce this energy to the estuarine and nearshore food chains when they leave the marsh. Foraging carnivores also provide a trophic link between the marsh and adjacent ecosystems (see Table 27).

Reptiles and Amphibians

Only a few reptile species have adapted to the conditions of the Juncus marsh (Table 28). With the exception of the American alligator, marsh reptile species have very limited geographic distributions and, along with the alligator, have been designated for special status or concern by the states where they are found (Figure 31). No information is available on marsh amphibians.

Birds

Juncus marshes of the northeastern Gulf of Mexico have, in addition to a rich local resident bird fauna, seasonal influxes of species migrating through the Mississippi Flyway. Within the marsh

Table 27. Food habits of dominant fish species of the *Juncus* marsh.

Species	Herbivore/ detritivore	Detritivore/ carnivore	Plankton feeders	Carnivores Larvivores	Carnivores General	Carnivores Piscivores
Cyprinodon variegatus	1,2			1		
Leiostomus xanthurus	2					
Mugil cephalus	1,2		1			
Poecilia latipinna	1			1		
Eucinostomus sp.		2				
Fundulus grandis		2		1		
F. similis		2				
Hyporhamphus unifasciatus		2				
Lagodon rhomboides		2,6				
Menidia beryllina		2				
Strongylura sp.		2				
Cynoscion arenarius					2	
Oligoplites saurus					2	
Megalops atlantica			1			1
Diapturus			1			
Lucania parva			1	1		
Elops saurus			1			1
Fundulus confluentus		5		1		
Gambusia affinis				1		
Centropomus undecimalis						1
Cynoscion nebulosus					3,4	
Lepomis macrochirus						7
Micropterus salmoides						7

1 = Harrington and Harrington 1961
2 = Subrahmanyam and Drake 1975
3 = Moody 1950
4 = Lorio and Schafer 1965
5 = Harrington and Harrington 1972
6 = Hansen 1969
7 = Hackney and de la Cruz 1981a

system, birds comprise one of the larger herbivore groups and are also significant at higher trophic levels as top carnivores in both the immediate marsh and estuarine food chains. The *Juncus* marsh supports year-round residents (e.g., clapper rail and great blue heron), summer-nesting species (e.g., least bittern), migrants (e.g., short-billed marsh wren, sedge wren and American wigeon), casual feeders (e.g., great white herons), and summer visitors (white ibis).

In their summary of coastal birds of the Gulf of Mexico, Lowery and Newman (1954) found that of 125 coastal species, all but 19 have been recorded all along the shorelines of the gulf. Their geographic variance is primarily a matter of season. No species of bird is endemic to the marshes of the northeastern gulf area alone. Five subspecies of marsh birds are restricted to marshes of the Gulf of Mexico: two seaside sparrows, *Ammodramus maritimus juncicola* from Taylor County to St. Andrews Bay, Florida, and *A. m. fisheri* from the coast of Alabama to *High Island*, Texas; the Louisiana clapper rail (*Rallus longirostris saturatus*) from Alabama to Texas, and two marsh wrens, *Cistothorus palustris marianae* from *Charlotte Harbor, Florida to Mobile*, Alabama, and *C. p. thryophilus* of the coasts of *Mississippi, Louisiana*, and Texas.

Table 28. Reptiles of the coastal marshes of the northeastern Gulf of Mexico.

Name	Distribution
Mississippi diamondback terrapin (Malaclemys terrapin pileata)	Florida panhandle to western Louisiana
Alabama red-bellied turtle (Pseudemys alabamensis)	Apalachee Bay, Florida, to Mobile Bay, Alabama
Florida cooter (Pseudemys floridana floridana)	Florida west to Mobile Bay, Alabama
American alligator (Alligator mississippiensis)	Ubiquitous
Gulf salt marsh water snake (Nerodia fasciata clarkii)	West central Florida to central Texas

Figure 31. Mississippi diamondback terrapin (Malaclemys terrapin pileata) and the gulf salt marsh snake (Nerodia fasciata clarkii). Photo by J. Stout.

Over 60 species of birds use habitats within Juncus - dominated marshes (Table 29). Few of these are permanent residents of the marsh, but make use of abundant food sources, resting areas, and refuges within the marsh. Wading birds, and shorebirds more typical of beaches and bars, are often observed feeding in the marsh intertidal zone, in creeks, or on sandy berms along the shore. Salt flats also provide good feeding areas for these species and for migrants. Woody vegetation of berms and hummocks provides nesting habitat for perching birds (Figure 32).

Only clapper rails and seaside sparrows nest in pure Juncus stands. Most other nests are found in small trees and shrubs on shell and sand berms and spoil deposits within the marshes. This probably provides some protection from predators as well as from the effects of tidal inundation.

Portnoy (1977) found that the snowy egret and great egret were the most abundant nesting species in brackish marshes, and tricolored herons were the most abundant species in salt marshes

Table 29. Birds associated with salt and brackish marsh environments in Alabama.

Name	Occurrence[a]	Special status[b]
Falconiformes		
Turkey vulture (*Cathartes aura*)	PB	
Northern harrier (*Circus cyaneus*)	W	
Gruiformes		
King rail (*Rallus elegans*)	PB	
Clapper rail (*R. longirostris*)	PB	
Virginia rail (*Rallus limicola*)	MW	
Sora (*Porzana carolina*)	MW	
Yellow rail (*Coturnicops noveboracensis*)	W	
Purple gallinule (*Porphyrula martinica*)	SB	
Common moor hen (*Gallinula chloropus*)	SB	
Charadriiformes		
Gull-billed tern (*Sterna nilotica*)	M	
Forster's tern (*S. forsteri*)	PB	
Caspian tern (*S. caspia*)	W	
American oystercatcher (*Haematopus palliatus*)	PB	
Semipalmated plover (*Charadrius semipalmatus*)	W	
Piping plover (*C. melodus*)	W	
Snowy plover (*C. alexandrinus*)	PB	
Wilson's plover (*C. wilsonia*)	SB	
Killdeer (*C. vociferus*)	PB	
Black-bellied plover (*Pluvialis squatarola*)	WM	
Ruddy turnstone (*Arenaria interpres*)	WM	
Long-billed curlew (*Numenius americanus*)	WM	
Whimbrell (*N. paheopus*)	SM	
Willet (*Catoptrophorus semipalmatus*)	MB	
Greater yellowlegs (*Tringa melanoleucus*)	M	
Redknot (*Calidris canutus*)	M	
Baird's sandpiper (*C. bairdii*)	C	
Least sandpiper (*C. minutilla*)	WM	
Dunlin (*C. alpinna*)	WM	
Short-billed dowitcher (*C. griseus*)	SM	
Stilt sandpiper (*C. himantopus*)	M	
Semipalmated sandpiper (*C. purillus*)	M	
Western sandpiper (*C. mauri*)	WM	
American avocet (*Recurvirostra americana*)	M	
Ciconiiformes		
Great white heron (*Ardea herodias occidentalis*)	CS	F(T)
Great blue heron (*A. herodias*)	PB	
Green-backed heron (*Butorides virescens*)	SB	
Little blue heron (*Egretta caerulea*)	SB	A(S)
Great egret (*Casmerodius albus*)	PB	
Snowy egret (*Egretta thula*)	PB	
Tricolored heron (*E. tricolor*)	SB	
Black-crowned night heron (*Nycticorax nycticorax*)	PB	A(S)

(continued)

Table 29. Concluded.

Name	Occurrence[a]	Special status[b]
Least bittern (*Ixobrychus exilis*)	SB	
American bittern (*Botaurus lentiginosus*)	M	
White-faced ibis (*Plegadis chihi*)	C	
White ibis (*Eudocimus albus*)	S	
Anseriformes		
Fulvous whistling duck (*Dendrocygna bicolor*)	CW	
Mallard (*Anas platyrhynchos*)	W	
American black duck (*A. rubripes*)	W	
Mottled duck (*A. fulvigula*)	PB	A(T)
Gadwall (*A. strepera*)	W	
Northern pintail (*A. acuta*)	W	
Green-winged teal (*A. crecca*)	W	
Blue-winged teal (*A. discors*)	M	
American wigeon (*A. americana*)	W	
Northern shoveler (*A. clypeata*)	W	
Redhead (*Aythya americana*)	MW	
Lesser scaup (*Aythya affinis*)	MW	
Surf scoler (*Melanitta perspicillata*)	W	
Red-breasted merganser (*Mergus serrator*)	?	
Passeriformes		
Tree swallow (*Tachycineta bicolor*)	M	
Fish crow (*Corvus ossifragus*)	PB	
Marsh wren (*Cistothorus palustris*)	PB	
Sedge wren (*C. platensis*)	W	
Eastern meadowlark (*Sturnella magna*)	PB	
Western meadowlark (*S. neglecta*)	W	
Red-winged black bird (*Agelatis phoeniceus*)	PB	
Boat-tailed grackle (*Cassidix mexicanus*)	PB	
Sharp-tailed sparrow (*Ammodramus caudacutus*)	PB	
Seaside sparrow (*A. maritimus*)	PB	

[a] Occurrence (from Chermock 1974; Imhoff 1976).
P=Permanent resident; M=Migrant; W=Winter visitor; S=Summer resident; C=Casual; B=Breeding population.

[b] Special status (from Christman and Lippincott 1978)
F=Florida list; A=Alabama list; T=Threatened; S=Special concern.

(Table 30). Two periods of incubation were determined for these various species (Figure 33). The snowy egret, great egret, little blue heron, tricolored heron, and Forster's tern incubate eggs during the spring. Summer incubation is typical of the white ibis, white-faced ibis, cattle egret, and least tern. Tricolored herons begin incubation in early spring, and eggs may be found in some nests through midsummer. Two separate incubation periods, in spring and again in mid-summer, are exhibited by blackcrowned night herons and little blue herons (Figure 33) (Portnoy 1977).

Many coastal birds nest in freshwater deltas and use the *Juncus* marsh habitats

Figure 32. Nestling herons in shrubs of a Juncus marsh. Photo by J. Stout.

as secondary breeding and dispersal areas. The marsh provides an ideal environment for breeding birds. Dense vegetation and the isolated nature of many marsh tracts restrict access by predators, especially the raccoon (Procyon lotor). Small fish as well as numerous, abundant invertebrate species provide food for both adults and young fledglings.

Of the species found in the marshes of this region only the clapper rail (Rallus longirostris) has been studied in detail. Though the clapper rail, or marsh hen, is a popular sport species in marshes in other regions of the United States, it is not so along the gulf coast. Holliman (1978) attributed the absence of hunter pressure to inaccessibility caused by low tides and lack of extensive areas of habitat. Nest sites and higher population densities are found in large open areas of S. alterniflora. In most northeastern gulf coast marshes, S. alterniflora occurs only as a fringe, and the marsh expanse is dominated by Juncus with significantly fewer rails per ha. In Alabama, rail densities ranged from 2.64/ha in an insular marsh with 85% S. alterniflora cover to 0.12/ha in an insular marsh with 95% Juncus and 3% Spartina (Holliman 1978). Examination of hurricane impacts on populations of clapper rails indicated significant population reduction in coastal marshes where storm overwash caused sediments to bury the S. alterniflora habitat (Holliman 1981).

Rails build a platform nest of Spartina alterniflora stem fragments woven among standing live stems. Nests are usually in areas close to secondary and tertiary tidal creeks, about 15-25 cm above the marsh floor. Nest height seems to accommodate average tide heights, but Holliman (1978) found a number of nests destroyed by storm tides. In this study no nests were found in pure Juncus stands or in areas where there was a mixture of only Distichlis and Spartina. However, rail activity is evidenced in Juncus stands by trails worn between the leaves

Table 30. Abundance of some colonial nesting birds of salt and brackish marshes, Louisiana-Mississippi-Alabama coasts, 1976 (adapted from Portnoy 1977).

Species	Breeding adults	
	Brackish marsh	Salt marsh
Olivaceous cormorant	788	0
Great egret	15,138	20,564
Snowy egret	15,932	53,018
Cattle egret	2,400	2,212
Tricolored heron	13,294	112,000
Little blue heron	250	2,206
Black-crowned night heron	4,604	14,729
White ibis	134	11,095
White-faced ibis	0	6,909
Roseate spoonbill	1,346	0
Laughing gull	0	14,318
Gull-billed tern	0	20
Forster's tern	6,768	12,196
Least tern	1,280	14
Caspian tern	0	326
Royal tern	0	584
Black skimmer	2,831	4,353

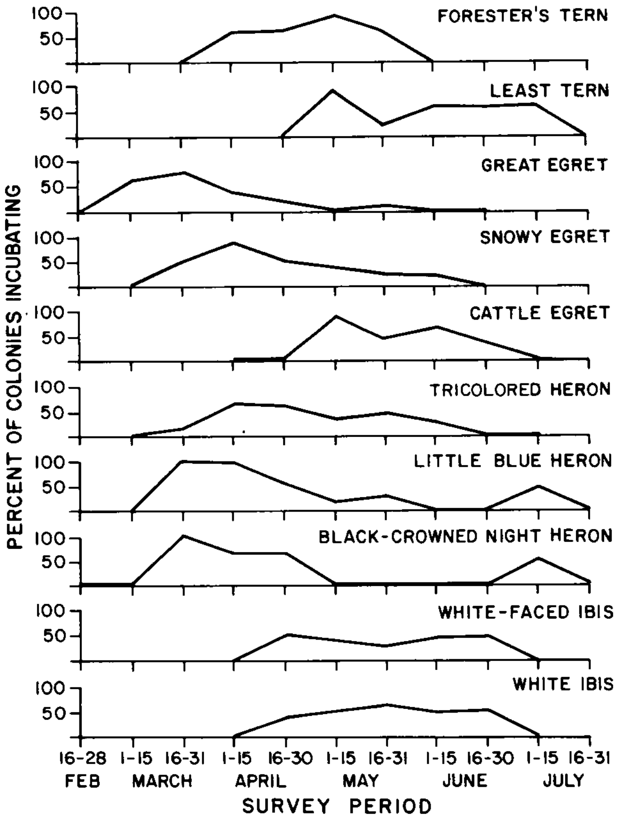


Figure 33. Seasonal timing of incubation for common wading birds and seabirds nesting in salt and brackish marshes of the northeastern Gulf of Mexico. (Modified from Portnoy 1977).

and plants by frequent repeated passages. of the birds.

Rails are opportunistic omnivores, occupying a broad feeding niche in marshes. Food habits of clapper rails have been examined for both the Louisiana rail (Rallus longirostris saturatus; Alabama to Texas) and the Florida clapper rail (R. l. scotti). Howell (1932) listed four species of decapod crustaceans and one species of insect eaten by Florida clapper rails in western Florida. Nine genera of food organisms were identified from a Louisiana clapper rail stomach by Bateman (1965). Uca, Littorina, and Sesarma occurred most frequently (74%, 49%, and 38% of stomachs, respectively). Stomachs of Alabama birds yielded Uca and seeds (Holliman 1978).

Heard (1982) described food and feeding habits of five subspecies of clapper rails of the gulf and Atlantic coasts. Though there were some differences in dietary items due to zoogeography and habitat type, all five subspecies ate basically the same kinds of food. Fiddler crabs (Uca) were the most commonly occurring food in approximately 70% of the rail's stomachs. Sesarma were found in 20% of the stomachs of both subspecies. Relative abundance of the two crab genera in the diet varied with season and tidal conditions. Uca are generally less active and in their burrows during the winter (Teal 1958). Sesarma are more terrestrial than Uca and may avoid the high-tide waters by taking refuge on detrital rafts or on living plants where they are more vulnerable to predation. Rails taken by Heard appeared to have been feeding throughout the tidal cycle; most feeding was during low tide.

Littorina irrorata and Melampus bidentatus were the second most abundant component of the clapper rails' diet. These mollusks were found in 25% of the stomachs of the Louisiana clapper and 15% of the Florida clapper rail. These may be major food items during cold periods when Uca and other crabs are less accessible. Minor components of the diet include polychaete worms, insects, and plant materials, all of which may be more important during winter feeding. Vertebrates have rarely been reported from clapper rail stomach analyses, but fish remains were found by Heard (1982) in R. l. saturatus. Heard's unpublished data on helminth parasites of the rail suggest that fish are of some importance.

Four species of marsh birds have been given special status by the States of Florida or Alabama. Alabama has indicated that both the little blue heron (Egretta caerulea) and the black-crowned night heron (Nycticorax nycticorax) are of "Special concern." "Threatened" status has been given to the great white heron (Ardea herodias occidentalis) in Florida and to the mottled duck (Anas fulvigula) in Alabama. All species using habitats within the Juncus marshes are, however, somewhat threatened by the limited amount of suitable marsh available and by increasing pressures to develop marshes. Breeding birds are especially susceptible to human disturbances since most are very secretive and require isolation for nesting.

Mammals

Mammals of the *Juncus* marsh may be categorized into three groups: (1) marsh residents, (2) inhabitants of the marsh/upland interface, and (3) upland mammals entering the marsh to feed (Table 31).

Marsh residents include the nutria, Louisiana muskrat, and marsh rabbit, all of which are strong swimmers. Their behavior includes nesting among plant stems or building dens with elevated floors to keep their young above tidal waters (Figure 34). All are herbivores feeding upon herbaceous leaves, stems, and roots. Their large size and voracious appetites may result in significant damage to plants if animal population densities are high. The nutria is successful in freshwater as well as in the *Juncus* marshes. The muskrat (Figure 35) and nutria support a fur-trapping industry, especially in Mississippi marshes.

Table 31. Common mammals associated with *Juncus roemerianus* marshes of the northeastern Gulf of Mexico.

Marsh rabbit (*Sylvilagus palustris palustris*)

Rice rat (*Oryzomys palustris palustris*)[a]

Cotton rat (*Sigmodon hispidus*)[a]

Louisiana muskrat (*Ondatra zibethicus rivalicius*)

Nutria (*Myocastor coypus bonariensis*)

Raccoon (*Procyon lotor varius*)[b]

Southern mink (*Mustella vison mink*)[b]

Otter (*Lutra c. canadensis*)[b]

Red fox (*Vulpes fulva*)[b]

Long-tailed weasel (*Mustela frenata*)[b]

Bobcat (*Lynx rufus*)[b]

Deer (*Odocoileus* sp.)[a]

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[a] Marsh upland interface inhabitants.

[b] Predators from upland habitats.

Figure 34. **Nutria nest in short *Spartina alterniflora*. Photo by J. Stout.**

The cotton rat is more terrestrial in nesting habit and prefers the higher, less frequently flooded marsh upland interface. The rice rat is the most abundant of all the coastal marsh mammals. The rice rat is a good swimmer and may be observed feeding in the lower marsh. To escape flooding waters, they use emergent vegetation and floating debris as temporary refuges. Wolfe (1982) found that population size of the rice rat showed no noticeable change

Figure 35. Common muskrat (*Ondatra zibethicus*). Photo by J. Wolf.

following marsh flooding by a storm and two hurricanes within a six-month period in 1979. These granivorous species are a primary food for larger predators that visit the marsh to feed.

Predator species include the raccoon, mink, long-tailed weasel, and otter who only visit the marsh for feeding (Figure 36). All have mixed diets of small mammals, such as the rats above; young muskrat, nutria and birds; and benthic invertebrates and fish in the tidal creeks. Debris mats and abandoned nutria or muskrat dens serve as feeding stations.

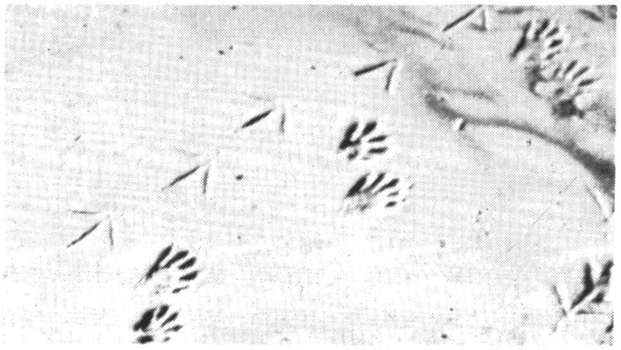

Figure 36. Heron and raccoon tracks at low tide. Photo by J. Stout.

CHAPTER 5

ECOLOGICAL DYNAMICS

Marshes have historically been viewed as vital primary production sites that serve as the base of detrital food chains (Odum and de la Cruz 1967; de la Cruz 1973). High levels of productivity have been attributed to a variety of marsh types (see reviews by Keefe 1972 and Turner 1976); three components contribute to these high levels: phytoplankton, algae on the sediments and plants, and vascular plants.

Marsh detritus produced by biological decomposition, as well as mechanical breakdown of dead plants, is reported as a rich and abundant food source for marsh and estuarine organisms (de la Cruz and Gabriel 1974; de la Cruz 1975; de la Cruz and Poe 1975b). Studies of patterns and significance of transport of detritus to estuaries have yielded disparate results and demonstrate that the energy dynamics of different marsh/estuarine systems may vary greatly (Nixon and Oviatt 1973; Day et al. 1973; Hackney 1977).

Recent information (Nixon 1980; Haines 1976, 1977) questions long-held dogma regarding marshes as nutrient pools and primary sources of detritus for the food chain. Very few comprehensive studies have addressed the functional role of salt marshes in the estuarine ecosystem, and even less information is available to assess the role of gulf coast *Juncus* marshes. This role cannot be interpolated from data on other types of marsh systems (i.e., *Spartina alterniflora*) because of the lower tidal energy inputs on the gulf coast, irregular tidal flooding, and differences in *Juncus* tissue composition. There is a critical need to clarify the role of these marshes in food chains in order to determine their value.

PRIMARY PRODUCTION

No data are available on primary production in the phytoplankton and attached algal components of *Juncus* marsh flora. Therefore, estimates of marsh primary productivity are for vascular plants only and are underestimates of biomass produced by the entire primary-producer community.

Juncus roemerianus and *Spartina alterniflora* have been the most frequently investigated species on the gulf coast. Different techniques for computing estimated annual net aboveground primary production (ANPP) yield widely varying results and make comparisons between different studies difficult if not impossible (Table 32). Estimates of standing crop as an indicator of production provide more similar results between studies. Little data is available on belowground primary production, although this production component may be very important ecologically.

Aboveground net primary production estimates for *Spartina alterniflora* (130-2,029 g dry wt m^{-2} yr^{-1}) and for *Spartina patens* (1,242 and 1,922 g dry wt m^{-2} yr^{-1}) on the gulf coast are greater than estimates from studies in Atlantic coast marshes (Stroud and Cooper 1968; Williams and Murdoch 1972; Waits 1967; Wass and Wright 1969; Steever 1972). A wide range of values for *Distichlis spicata* (63-1,484 g dry wt m^{-2} yr^{-1}) from a limited number of studies is difficult to evaluate.

Table 32. Estimates of productivity for various salt marsh plants of the northeastern Gulf of Mexico coasts.

Species	State	Above ANPP (g/m^2)	Below ANPP (g/m^2)	Total ANPP (g/m^2)	Above standing crop (g/m^2)	Below standing crop (g/m^2)	Total standing crop	References
Juncus roemerianus								
	MS				2,000[c]			Eleuterius 1972
	MS				1,300[b]			de la Cruz 1974
		1,697[a]						
	MS	390[b]						Gabriel and de la Cruz 1974
	MS	1,700[e]			1,360[e]			de la Cruz and Hackney 1977
	MS	460-580[e]				5,000-7,000[c]		
	AL	1,745[c]	6,340[c]	8,085				Stout 1978
		1,449[d]	4,425[d]	5,874				
		3,078[a]	7,578[a]	10,656				
		1,180[b]	5,212[b]	6,392				
	AL	580[e]				2,000-4,000[c]		Hackney et al. 1978
	FL (LM)	949[g]			530[f]	4,573[d]	5,103	Kruczynski et al. 1978a
	(UM)	595[g]			481[f]	4,063[d]	4,544	
	(HM)	243[g]			351[f]	5,140[d]	5,591	
Spartina alterniflora	AL	2,029[a]	6,218[a]	8,247	1,275[c]	5,033[c]	6,308	Stout 1978
		657[b]	6,051[b]	6,708	1,030[d]	3,595[d]	4,625	
	AL	175[e]				3,000-7,000		Hackney et al. 1978
	MS (Tall)				1,473[b]			de la Cruz 1974
					1,964[a]			
	(Short)				1,089[b]			
	FL (LM)	700[g]						Kruczynski et al. 1978a
	(UM)	335[g]						
	(HM)	130[g]						

(continued)

Table 32. Concluded.

Species	State	Above ANPP (g/m²)	Below ANPP (g/m²)	Total ANPP (g/m²)	Above standing crop (g/m²)	Below standing crop (g/m²)	Total standing crop	References
Spartina patens	MS				1,242[b]			de la Cruz 1974
					1,922[a]			
Spartina cynosuroides	MS	475[b]						Gabriel and de la Cruz 1974
	MS	1,740[e]				6,000-9,000[c]		Hackney et al. 1978
		1,988[e]						
Distichlis spicata	MS				1,072[b]			de la Cruz 1974
					1,484[a]			
	MS	63[b]						Gabriel and de la Cruz 1974
		100[e]						Hackney et al. 1978
	FL (HM)				610[c]			Kruczynski et al. 1978a
Scirpus robustus	MS	1,056[b]						de la Cruz 1974
Scirpus olneyi	MS				495[c]	12,000[c]	12,695	Hall and Faulkner 1980
Mixed species	MS	1,051[b]						de la Cruz 1974

Method of Calculation

[a] Smalley 1959
[b] Milner & Hughes 1968
[c] Peak standing crop
[d] Mean monthly standing crop

[e] Periodic max.-min. model (Hackney and Hackney 1977; 1978)
[f] End of season live
[g] Weigert and Evans 1964

MS = Mississippi
AL = Alabama
FL = Florida

LM = Low Marsh
UM = Upper Marsh
HM = High Marsh

Of the species listed in Table 32, *Distichlis spicata*, *Spartina cynosuroides*, and *Scirpus* spp. have a well-defined growing season from early spring to fall. No significant winter production of new tissues occurs in any of these species. However, unlike most Atlantic coast marshes, gulf marshes support measurable productivity in all months with new live tissues being produced by *Juncus*, *Spartina alterniflora* and *S. patens*. Biomass production has a different seasonal pattern for each of these species. Dead and partially decaying biomass are greater than living biomass through the winter months (Gabriel and de la Cruz 1974; Stout 1978; Kruczynski et al. 1978a).

Belowground productivity of marsh plants is difficult to accurately assess because of problems in separating living and dead material and thus, in determining rates of loss by death and decomposition. Attempts at estimating belowground ANPP have resulted in 1.1-7.6 kg m^{-2} for Juncus and 3.5-6.2 kg m^{-2} for S. alterniflora (Stout 1978). Standing crop estimates for all species studied indicated that total (living and dead) belowground biomass exceeded aboveground biomass three to ten times (Figure 37). Stout (1978) and de la Cruz and Hackney (1977) found that most root and rhizome material is in the upper 20 cm with as much as 80% in the 0-10 cm layer (Figure 38). This large pool of biomass may provide valuable energy if it finds its way into the food web. Some may be lost through respiration or in the anaerobic production of methane and other anaerobic byproducts by microorganisms. Organic materials within the substrate could be removed by bioturbation, erosion, subsurface drainage, or through seepage as dissolved organics. Because of the significant contribution of belowground production to total marsh plant biomass, it is necessary to determine more about its fate and role in the ecosystem.

Productivity of both Juncus and Spartina alterniflora may differ in different zones of the marsh. Kruczynski et al. (1978a) found that total net aboveground Juncus production decreased landward for Juncus (low marsh = 700 g m^{-2} yr^{-1}, upper marsh = 335 g m^{-2} yr^{-1} and high marsh = 130 g m^{-2} yr^{-1}). Highest annual mean belowground biomass in Juncus was in the high marsh (8.7 times aboveground), while low marsh and upper marsh had similar belowground to aboveground ratios (3.7 and 3.8, respectively) (Table 32).

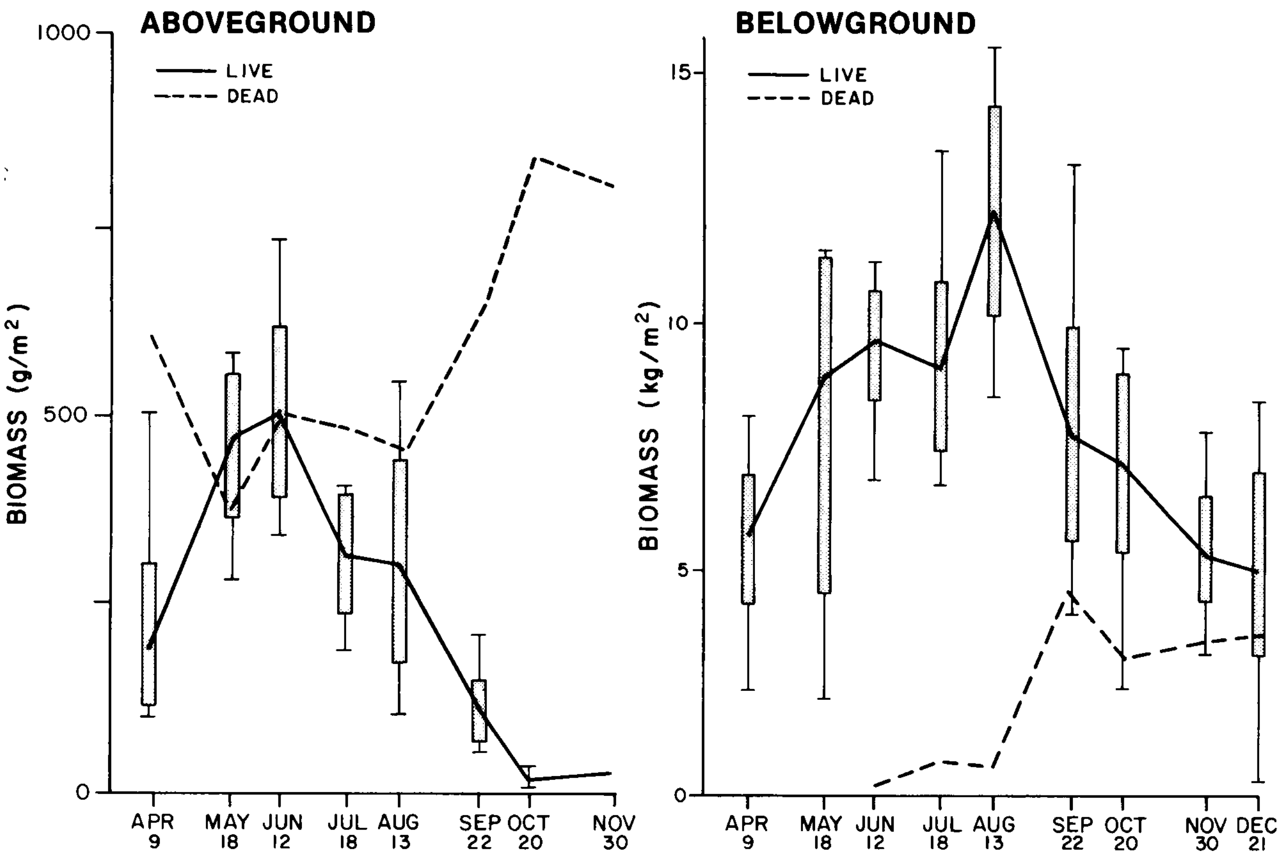

Figure 37. Standing crop measurements of aboveground and belowground Scirpus olneyi. Vertical bars represent maximum and minimum values per sample period. Shaded bars represent ± standard deviation (from Hall and Faulkner 1980).

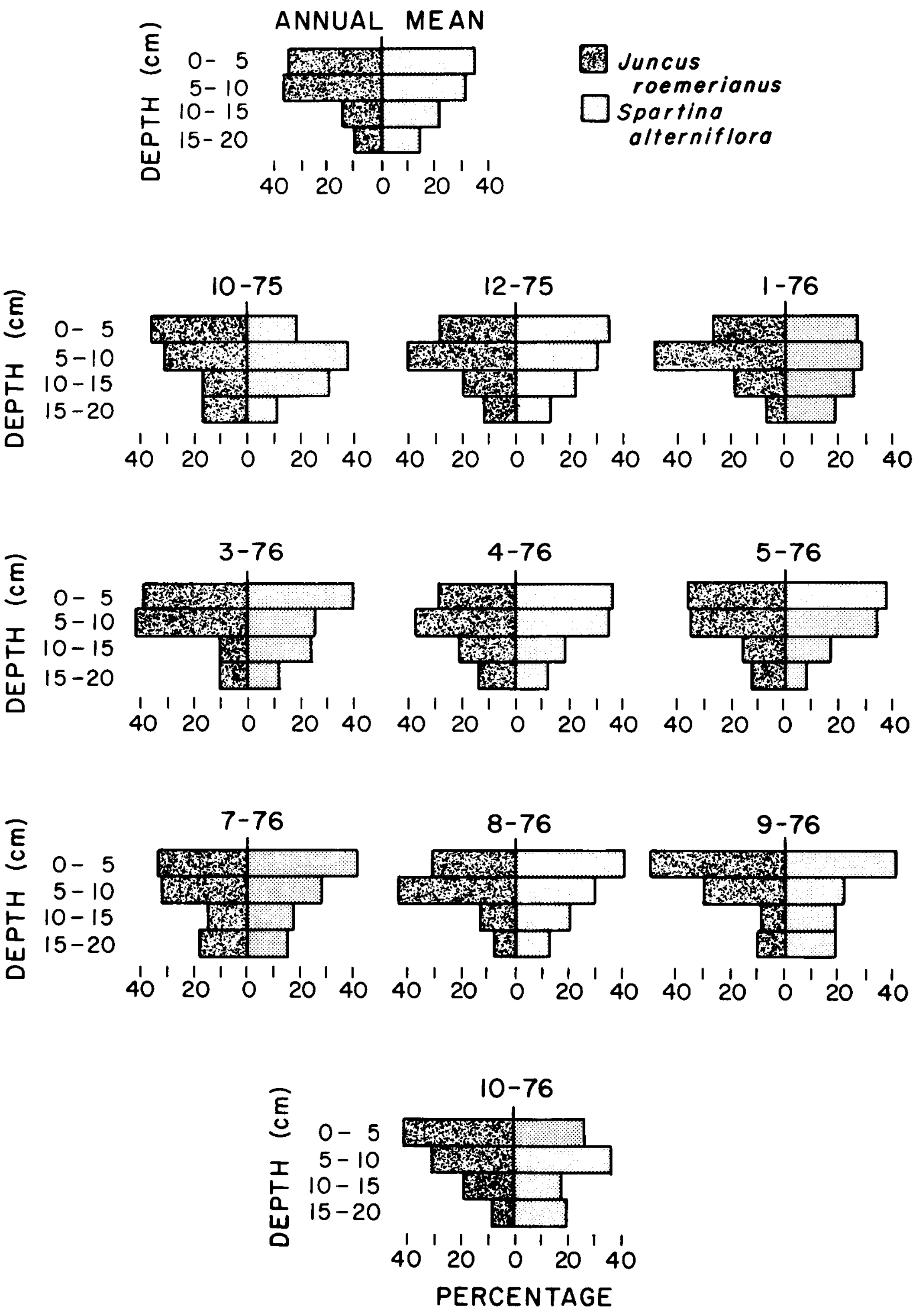

Figure 38. Depth distribution of annual mean and monthly mean below-ground biomass of *Juncus roemerianus* and *Spartina alterniflora* (from Stout 1978).

TISSUE NUTRIENTS

Concentrations of amino acids, nutrients, and protein are higher in *Juncus roemerianus*, a C_3 species, than in C_4 species which have been examined (i.e., *S. alterniflora*, *S. cynosuroides*, *S. patens*, and *Distichlis spicata*) (Table 33). This may imply a potential herbivore preference for this more nutritious species and certainly indicates a large pool of high-quality food material as a result of its high productivity and extensive coverage (de la Cruz and Poe 1975a).

Nutrient content may vary considerably between populations. Twenty-two free amino acids were isolated by Eleuterius (1979) from dwarf *Juncus* plants (30 cm), while only 18 were found in either medium (120 cm) or tall (210 cm) plant populations. Free amino acid content of dwarf plants was twice as great as in other populations (Table 33).

Juncus may, however, have natural defenses against fungal and insect attack. High levels of silica were found in the leaves and rhizomes in all three populations (Table 34) (Lanning and Eleuterius 1978). Rhizome silica content was directly related to available silica in the soil, but leaf concentrations were similar for all three height forms. Both leaves and rhizomes exhibited increased silica content with age.

DECOMPOSITION AND FOOD VALUE OF DETRITUS

Great variability exists in the decomposition of different marsh plants (Figure 39) due to differences in tissue make-up and environmental conditions where the species occur. Dead leaves and stems of *Spartina alterniflora* break down most rapidly of all species studied (Table 35). When leaf decomposition is taking place on the marsh surface, 80-90% of initial biomass may be lost from litter bags in a year. Within creeks, *S. alterniflora* litter may lose up to 95% of its initial biomass in a year (Kruczynski et al. 1978b) (Figure 40). Occurring in or near intertidal areas, this loss by decomposition provides an almost complete annual turnover of aboveground plant production to detritus by this species.

Other species studied have decomposition rates significantly lower than *S. alterniflora*. Higher, drier marsh species *S. patens* and *Distichlis spicata* were slowest to decompose with 36% and 38-54% losses per year in marshes of Mississippi Sound (Stout and de la Cruz 1981b). When placed in the moist conditions of a creek, up to 73% of *Distichlis spicata* was lost (de la Cruz 1975).

Table 33. Amino acid and crude protein (mg/g) in salt marsh plants (shoot/root) (modified from de la Cruz and Poe 1975a).

	Plant species					
Parameter	*Distichlis spicata*	*Phragmites australis*	*Spartina alterniflora*	*Spartina cynosuroides*	*Spartina patens*	*Juncus roemerianus*
Total amino acid (AA)	48.5/27.3	42.8/26.4	40.4/27.6	36.9/30.2	48.1/47.8	74.3/37.9
Crude protein (CP)	69.2/58.7	46.5/50.6	55.8/44.0	46.9/55.8	72.0/84.0	79.0/59.2
% AA in CP	70.1/46.5	92.0/52.2	72.4/62.7	78.7/54.1	66.8/56.9	94.1/64.0

Table 34. Variation in amino acid (A) and silica and ash content (B) of tissues from three populations of *Juncus roemerianus* (compiled from Eleuterius 1979 and Lanning and Eleuterius 1978, respectively).

Population	Free amino acids (mg/g)	Protein-bound amino acids (mg/g)	Number amino acids
(A)			
Tall (210 cm)	0.781	113.0	18
Medium (120 cm)	0.651	113.5	18
Short (30 cm)	1.383	108.2	22

	Rhizome silica (% dry wt.)	mg soil silica/ 100g soil	Leaf silica (% dry wt.)
(B)			
Tall	0.34	29.7	0.93
Medium	0.20	17.0	0.87
Short	0.60	169.6	0.90

Decomposition loss was intermediate for *Juncus* though higher in Florida (65%) than in Mississippi Sound (40-48%). Rates for *S. cynosuroides* are more variable (26-57%). Similar to *S. alterniflora* and *S. patens*, decomposition was enhanced by moist creek conditions resulting in a net loss for *S. cynosuroides* of 61% (de la Cruz 1975).

Belowground biomass has much slower rates of decomposition than aboveground material for the same species. Limited results are available, and more information is needed for an ecological interpretation of the data. Faster decomposition in the upper 10 cm of substrate has been demonstrated for *Juncus* and *S. cynosuroides*, but not for *S. alterniflora* (Hackney and de la Cruz 1980). Greater aeration within this layer creates more favorable conditions for decomposing biota. A maximum of 25% loss annually is seen for *Juncus* in the top 10 cm with a minimum loss of 8% in the 10-20 cm layer for *Juncus* and *S. cynosuroides* (Stout and de la Cruz 1981a; Hackney and de la Cruz 1980).

Analysis of dead, decomposing, and detrital tissues of marsh species indicates several general patterns of tissue composition changes during decomposition: (1) increase in amino acids and/or proteins; (2) retention or increase in caloric content; (3) declines in crude fiber, carbohydrates, fats, and organic content; and (4) increased bacterial respiration (de la Cruz 1975; de la Cruz and Poe 1975b; de la Cruz and Gabriel

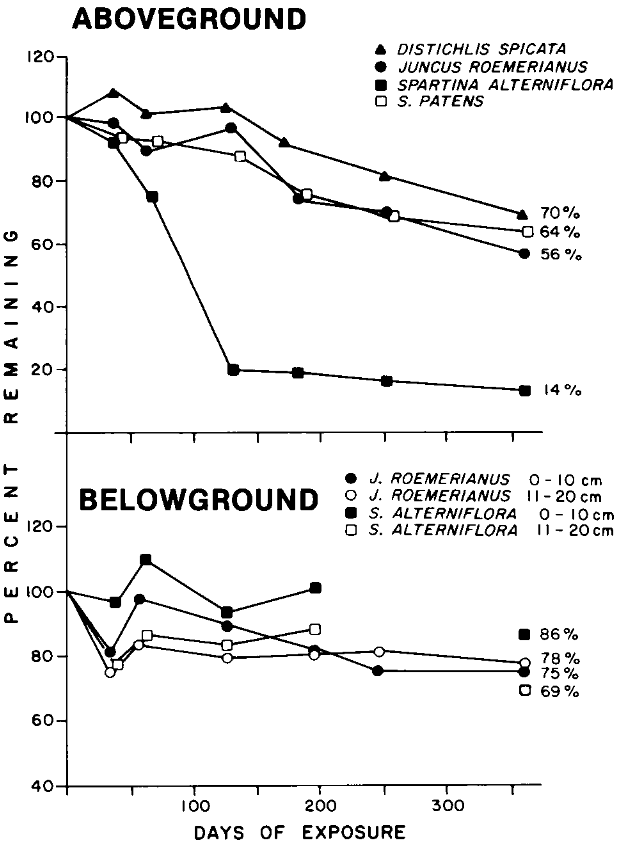

Figure 39. Decomposition of aboveground and belowground plant material of Juncus roemerianus and Spartina alterniflora and aboveground Distichlis spicata and S. patens (modified from Stout and de la Cruz 1978).

1974; Brown et al. 1978; Kruckzynski et al. 1978b). All of these imply a rich nutrient source, readily assimilable to detritivores.

Examination of changes in tissue composition for Spartina alteriflora, Distichlis spicata, and Scirpus americana indicated that these species retain 60-70% organic matter during decomposition. Caloric values remained the same or increased slightly. Protein showed a 96-300% increase from dead plants to particulate detritus stage, while crude fiber, carbohydrates, and fats declined (de la Cruz 1975). Similar patterns were seen for Juncus when particulate detritus from litterbags was further decomposed in incubation flasks (de la Cruz and Gabriel 1974). Increases in nitrogen (0.44%-1.21%) and respiration rates (0.11-1.10 mg O_2 hr^{-1} ash free g^{-1}) were accompanied by decreases in organic content (67%-32%) and carbon (5.6%-3.2%). The increase in detrital nitrogen was attributed to the conversion of plant tissue to microbial protoplasm as evidenced by increased respiration rates (de la Cruz and Gabriel 1974).

In vitro decomposition of particles (250 μm) of Spartina cynosuroides resulted in an increase in crude protein, total amino acids, and essential amino acids from 19.0 to 31.0 mg/g, 11.1 to 17.6 mg/g, and 5.8 to 8.1 mg/g, respectively, over a 36-day period (de la Cruz et al. 1975). When compared to the increment in crude protein in the in situ studies (de la Cruz and Poe 1975b), in vitro results are lower, suggesting additional sources of nitrogen in the natural environment (e.g., adsorbed and/or absorbed soluble nutrients [de la Cruz et al. 1975]). Following decomposition, Juncus roemerianus detritus has notably higher total amino acids, crude protein, and amino acid/crude protein ratios than other marsh plant species (Table 36).

Changes during decomposition of belowground material have indicated no distinct trends for nutrients or energy value (Stout and de la Cruz 1978; Hackney and de la Cruz 1980).

TRANSPORT OF ORGANIC MATTER

High primary production, rapid rate of decomposition, efficient formation of marsh plant detritus, and import of allochthonous organic materials characterize the fertility of estuarine and coastal systems. The actual linkages in the marsh-estuary food web have not been demonstrated, but information is becoming available which indicates some of the possible mechanisms and pathways of energy and nutrient transfers.

Freshwater outflow from major rivers into the northern Gulf of Mexico transports large quantities of carbon and produces variable low salinity conditions in areas such as Mississippi Sound. Post and de la Cruz (1977) estimated that the

Table 35. Annual decomposition rates (as percentage of total loss) of dominant marsh plants.

Species	State	Marsh zone	Mesh size (mm)	Aboveground % loss/ year	Belowground % loss/ year	References
Juncus roemerianus	MS		5.0	40		de la Cruz & Gabriel 1974
	MS		3.0	48	5 cm = 17.5 15 cm = 7.9	Hackney & de la Cruz 1980
	FL		5.0	65		Kruczynski et al. 1978b
	AL		1.25	44	10 cm = 25 20 cm = 22	Stout & de la Cruz 1978, 1981
Spartina alterniflora	FL	High marsh	5.0	80		Kruczynski et al. 1978b
	FL	Midmarsh	5.0	87		Kruczynski et al. 1978b
	FL	Low marsh	5.0	91		Kruczynski et al. 1978b
	FL	Creek	5.0	95		Kruczynski et al. 1978b
	AL	Low marsh	1.25	86	10 cm = 14 20 cm = 31	Stout & de la Cruz 1978, 1981b
Spartina cynosuroides	MS	High marsh	5.0	57		de la Cruz 1975
	MS	Creek	5.0	61		de la Cruz 1975
	MS	High marsh	3.0	26	5 cm = 20.5 15 cm = 6.7	Hackney & de la Cruz 1980
Spartina patens	MS	High marsh	3.0	36		Stout & de la Cruz 1978, 1981
Distichlis spicata	AL	Midmarsh	1.25	38		Stout & de la Cruz 1978, 1981
	MS	Marsh	5.0	54		de la Cruz 1975
	MS	Creek	5.0	73		de la Cruz 1975

Jourdan River, for example, transported 688,000 kg yr^{-1} of particulate organic matter into St. Louis Bay Estuary, Mississippi. They estimated that this transport could be as much as 921,000 kg yr^{-1} or as little as 450,000 kg yr^{-1} depending on rainfall and tides. This particulate carbon is of terrestrial origin from forests that surround the numerous small streams which flow into the Jourdan River (de la Cruz and Post 1977).

Hackney (1977) quantified the flux of suspended organic detritus, floating debris, and animal biomass over both diurnal and semidiurnal tidal periods in a

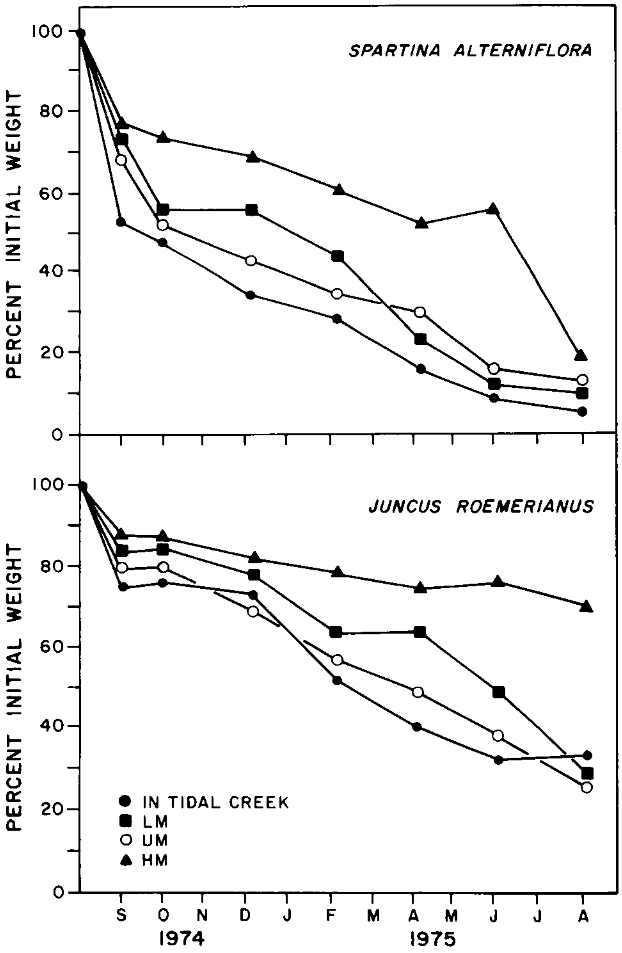

Figure 40. Rate of disappearance of Juncus and Spartina in litterbags placed in a Florida tidal creek (redrawn from Kruczynski et al. 1978a).

small tidal creek in a Bay St. Louis, Mississippi marsh. His results indicate: (1) a net annual export of floating debris (3.1 kg); (2) a net annual import of suspended particulate detritus (38.5 kg); and (3) an annual net import of 4 million kilojoules of energy for the 5.8-ha drainage basin. Hackney and de la Cruz (1979) found that for this marsh there was a total net import of 39.32 kg of particulate organic detritus and 292.51 kg of suspended inorganic detritus. This was equivalent to 168 g m^2 yr^{-1} of detrital material to the marsh of which 16 % was carbon. Imports to the marsh occurred during high river discharge with the marsh exporting during low river discharge periods. The marsh may then serve to dampen oscillations in detritus availability to the estuary instead of providing a constant input or export.

There was a small, but important net export of living biomass (0-5 kg yr^{-1}) from the Bay St. Louis marsh, Mississippi (Hackney 1977). This is probably a gross underestimate because it does not include the large numbers of animals removed by predators, larger organisms able to avoid the collection nets and smaller organisms passing through the net.

Stout (1978) found high levels of dead biomass remaining on marshes instead of being removed. This was especially true for Juncus with a live to dead ratio in June of 0.56. The passage of Hurricane Bob over the Mississippi coast in July, 1979, resulted in a net removal of 218 x 10^3 kg of dead plant material (wrack) from a 96-ha study area (Hackney and Bishop 1981). It may be that within Mississippi Sound marshes which experience low tidal amplitude, the marsh acts as an energy reservoir, and storm surges may account for substantial portions of the total annual export of organic detritus from the marsh. Similar information is not available on other gulf coast marsh/estuarine systems. In a North Carolina Juncus marsh, Kuenzler and Marshall (1973) reported removal of 270 g^{-1} m^2 of Juncus by a tropical storm but no significant effect of the subsequent passage of a hurricane through the same area.

Hackney and Haines (1980) compared $^{13}C/^{12}C$ isotope ratios in the tissue of the fauna of a marsh dominated by C_3 Juncus with a marsh dominated by C_4 S. cynosuroides to determine possible food sources (Table 37). Faunal tissue ratios should reflect the same carbon ratios found in the plant species grazed on or producing detrital food. Marsh fauna exhibited no significant differences attributable to type of dominant plant cover. Hackney and Haines (1980) proposed that the carbon ratios observed may reflect a significant input of allochthonous terrestrial material by river flow. Sediment carbon ratios were intermediate between the two marsh communities (Figure 41). This ratio could also be

Table 36. Total amino acid and crude protein content (mg g^{-1}) for live, dead, and decayed marsh plants and detritus decomposed *in situ* (modified from de la Cruz and Poe 1975b).

Species	Component	Total amino acid (AA)	Crude protein (CP)	% AA in CP
Juncus roemerianus				
	Live	74.2	79.0	94.05
	Dead	34.3	49.5	69.39
	Detritus	65.1	87.1	74.74
Spartina cynosuroides				
	Live	36.9	46.9	76.68
	Dead	12.0	19.0	63.16
	Detritus	32.3	44.4	68.02
Scirpus americanus				
	Live	85.0	100.3	84.75
	Dead	32.1	30.7	75.23
	Detritus	41.3	64.4	64.13
Distichlis spicata				
	Live	48.5	69.2	70.09
	Dead	20.2	29.8	67.79
	Detritus	45.7	72.3	63.21

attributed to marsh algae and perhaps reflects the trophic importance of this little-known marsh component.

Ribelin and Collier (1979) found that 98% of particulate detrital material smaller than 0.064 mm ("nano detritus" of Odum and de la Cruz 1967) from a Florida *Juncus* marsh was made up of amorphous aggregates. These detrital aggregates, averaging 25-50 µm in diameter, were derived from the benthic microflora of the marsh rather than produced by microbial decomposition of *Juncus*. Particles were aggregates of diatom frustule fragments; species of the benthic genera *Nitzschia* and *Navicula* were most common. Many small (1 µm) unidentifiable inclusions, all bound together by an adhesive substance, were also present. Visual observations and cellulose-staining techniques indicated that vascular plant fragments comprised less than 1% of the total suspended load.

Table 37. Carbon isotope composition of fauna and organic material collected in Juncus and Spartina marshes in a Mississippi estuary (from Hackney and Haines 1980).

		^{13}C (o/oo)(PDB)[a]	
Trophic level	Species	Juncus marsh	Spartina marsh
Herbivore	Orchelimum sp., grasshopper	-16.9	
Detritivore	Uca longisignalis, fiddler crab	-19.0	-17.5
	Littorina irrorata, periwinkle snail		-19.5
	Neritina reclivata, mud snail	-23.2	-23.5
	Membras martinica, rough silverside	-25.2	
	Anchoa mitchilli, anchovy		-26.3
	Mugil cephalus, mullet	-19.0	
Filter feeder	Polymesoda caroliniana, Carolina marsh clam	-27.1	-27.4
	Rangia cuneata, broadclam	-27.7	
	Geukensia demissus, ribbed mussel	-25.9	-27.5
Omnivore	Sesarma reticulatum, squareback crab	-23.2	
	Callinectes sapidus, blue crab	-22.0	-19.3
	Penaeus aztecus, brown shrimp	-25.8	-23.6
	Rhithropanopeus harrisii, mud crab	-22.3	
	Lucania parva, rainwater killifish	-24.2	
	Fundulus confluentus, killifish	-23.0	
Top carnivore	Micropterus salmoides, largemouth bass	-21.0	
	Archosargus probatocephalus, sheepshead		-22.4
Plants	Juncus roemerianus	-26.2	
	Spartina cynosuroides		-12.4
Sediment		-23.2 to -20.7	-21.0
Suspended detritus		-26.7	-25.0

[a] Isotopic ratios relative to Chicago PDB standard isotopic bicarbonate reference material.

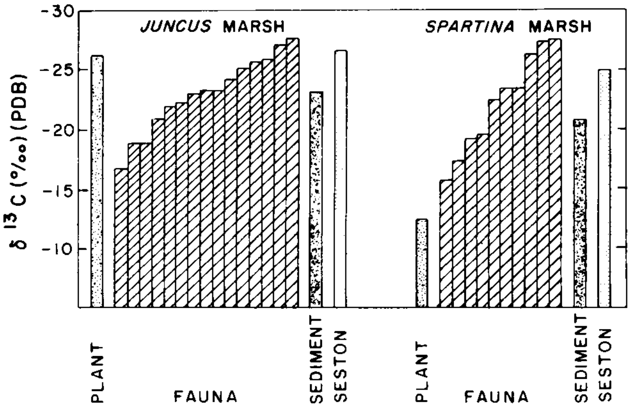

Figure 41. Decomposition of δ ^{13}C values for biota, seston, and sediment in two Mississippi marshes (redrawn from Hackney and Haines 1980).

An examination of floating surface films and of surface films upon the marsh sediment revealed a mixture of materials essentially identical to the components of the suspended particulates (Harriss et al. 1980). Rising tides lifted the films of aggregate material from the sediment algae carpet and ebbing tides transported the floating films into tidal creeks. Mild water surface disturbances dispersed the films, which sank as detrital aggregates into the water column.

Harriss et al. (1980) summarized tidally related characteristics of suspended aggregates as follows: (1) The concentrations of suspended particulates in ebb-tide waters are typically greater than concentrations measured in flood-tide waters. (2) The concentration of suspended particulates is commonly higher in daytime ebb-tide waters than in nighttime ebb-tide waters. (3) The rate of change in suspended particulate concentrations reaches values up to approximately 9 mg/l hr^{-1} during the transition from flood to ebb or vice versa when other factors (e.g., wind, benthic animal activity) are at a minimum.

Seasonally, concentrations of detrital aggregates are lower in the winter months and increase through the spring and early summer to maximum values in August and September. The scale of the seasonal variability in suspended particulate concentrations was similar to the variability observed on an hourly to daily basis during intensive sampling periods. Suspended particulate concentrations in flood-tide water typically did not vary by more than a factor of two on a daily or seasonal basis. The suspended particulate concentrations in ebb-tide waters vary by an order of magnitude on a seasonal basis. Qualitatively these data suggest that the Juncus marsh probably exports particulates to estuarine waters during approximately 9 months of the year (Harriss et al. 1980).

A hypothesis for the absence of detrital Juncus material in ebb-tide waters is provided by Ribelin and Collier (1979). Older leaves of Juncus plants seldom die and drop to the marsh floor as single pieces. Instead, dry, dead tissue is normally found at the tips of many leaves and can extend downward for up to 25 cm. Small pieces of this dead region break off, often as a result of mechanical abrasion, and fall to the marsh floor. Their scarcity in the tidal streams is probably due to the dense growth of Juncus that serves as a highly effective filter, retaining the dead fragments in the marsh. If the leaf fragments are left in contact with the mud surface after an ebbing tide, they quickly become waterlogged and soon collect small amounts of redeposited, previously floating films which loosely cement them to the mud surface. Within two or three days, filaments from the dense filamentous algae and fungi grow over the dead leaf fragments. This network provides additional attachments that prevent the removal of dead plant material from the marsh on subsequent ebbing tides. A thin layer of benthic diatoms and mucilaginous material soon appears, completely covering the leaf fragment. Juncus tissue therefore appears to be rapidly covered over by the marsh benthic microfloral community and is incorporated in the surface of the marsh floor. The tissue is then decomposed beneath the layer of benthic algae and is thereby retained in the marsh (Ribelin and Collier 1979).

It is obvious that more research is needed to elaborate the complex coupling of marsh primary production and estuarine food chains.

CONSUMER ECOLOGY

Consumer ecology and details of energy flow through marsh fauna and into estuarine food chains have not been studied or documented in northeast gulf marshes. A single study by Parsons and de la Cruz (1980), however, provides some insight into primary consumption and sêcondary production within the marsh. Three species of conocephaline grasshoppers (Tettigoniidae) were the major insect herbivores grazing on the leaves of Juncus in a Mississippi marsh (Parsons and de la Cruz 1980). They ingested 105 kilojoules $(kJ)m^{-2}$ of the 31.62 kJ m^{-2} net annual aboveground production of the Juncus. Practically all grazing occurred in summer and was localized on the distal portion of the leaves (Figure 42). Following the grazing season, the distal portion of the leaves died and fell to the marsh floor, representing the addition of 245.7 kJ m^{-2} yr^{-1} of Juncus material to the heterotrophic food chain prior to the death and decomposition of the entire Juncus leaf.

Assimilation of ingested Juncus tissue was 60.7 kJ m^{-2} yr^{-1}, and production of new tissue by the grasshoppers was 9.6 kJ m^{-2} yr^{-1}, which represented 0.03% of net primary production (Parsons and de la Cruz 1980). Juncus contained approximately twice the amino acid concentrations measured in Spartina cynosuroides for nine of the ten essential amino acids required by insects. Stable carbon isotope ratios in the subadult grasshoppers indicated that approximately one-third of their diet was Juncus (Hackney and Haines 1980).

Figure 42. Grazed portions of *Juncus* leaves (top) and *Spartina alterniflora* leaves (bottom). Photos by J. Stout.

The area of the leaf normally grazed by the grasshoppers contained proportionally greater amounts of most amino acids than either the tip or bottom portions. Two nonessential amino acids, glutamic acid and proline, were higher in the grazed portions than either tips or bottoms. These compounds are exceedingly important in the metabolic mechanisms of flight. Timing of ingestion by subadults coincides with the physiological development necessary for flight.

SUMMARY

It is obvious from the above discussion that a good deal of information is available on primary production rates and rates of carbon and mineral loss during *in situ* decay of aerial plant tissues of dominant species such as *Juncus* and *Spartina alterniflora*. Most other plant species are the subject of only one study at a single location along the gulf. Only preliminary data is available on belowground pools of materials, and the technology and methodology to assess the production component is still quite primitive. Mechanisms and forms of export or storage of primary production from marsh plants are poorly understood and existing information is at best variable, if not contradictory. Answers are needed to questions pertaining to detritus utilization and its impact on secondary production; the fate and turnover rate of the nutrients released in decomposition; the impact of meteorological, sedimentary, and geomorphological events on nutrient utilization and accretion; and nutrient translocation between shoots and roots prior to death and decomposition.

CHAPTER 6

HUMAN IMPACT

Natural marsh functions are multifaceted and valuable for food and nutrient sources, faunal habitat, water purification, shoreline stabilization, storm buffers, and recreation. They are also important for marsh products (e.g., potential drugs, food, and craft meterials), and aquaculture, fur trapping, and energy potentials. Many of the values may be maintained with multiple use by compatible activities; however, significant loss of value accompanies certain individual uses. An evaluation of monetary value attributed to different uses is summarized in Table 38 (de la Cruz 1976). Values attributed to the natural functioning of the marsh-estuarine system range from an annual return of $481/ha for nutrient and habitat input to dependent fisheries, to $7,452/ha for total life support. Respective income-capitalized (7%) values for the above functions were $6,878 and $106,457/ha. These values are significantly higher than those proposed by Gosselink et al. (1973) and illustrate the difficulties in placing a finite economic value on biological functioning. Lynne and Prochaska (1981) attempted to estimate the marginal (economic) values of the Juncus marsh in fish and shellfish production (specifically blue crabs) by developing an aggregate production function model relating marsh to blue crab population dynamics. The derived dockside value of $0.30 per acre when capitalized yields an annual value of $3.00 per acre in blue crab production. More information is needed to quantify with precision the linkages of marsh functions and their associated economic values.

Table 38. Examples of monetary evaluation for Juncus-dominated marshes (from de la Cruz 1976).

Approach	Approximate annual return per hectare	Income-capitalized value per hectare at 7% interest[a]
Cattle production based on grazing capacity	$ 70	$ 1,000
Pulp production for paper making	174	2,486
Production of dependent fishery (e.g., Miss.)	481	6,878
Natural use in tertiary treatment of sewage[b]	2,470	13,232
Potential development for aquaculture[b]	2,964	42,343
Life support value based on primary production[b]	7,452	106,457

[a] Income capitalized value is based on the formula V = R/i where V represents the value of a parcel of land, R is annual return for it, and i the approximate interest rate.

[b] Estimates of Gosselink et al. (1973).

MARSH ALTERATION AND LOSSES

For a long time marshlands were viewed as lands with very little value or use. Consequently, the value of marshland acreage was only enhanced by conversion (consequently destruction) to more "productive" uses. In Mississippi Sound, Stout and de la Cruz (1981 a) estimated a loss of 4,040 hectares (9,978 acres) or 11.5% of total marsh acreage by conversion to open water by dredging or to upland dry ground by filling. They considered this an underestimate as data were not complete, and only large sites were included. Net loss of marsh acreage in Mobile Bay due to dredging activities alone was 1,596 ha prior to 1979 (Stout 1979). This loss was equivalent to 22% of total marsh acreage within the bay.

McNulty et al. (1972) determined that 9,527 ha of west Florida estuaries had been filled for spoil disposal, causeways, and residential or industrial use. An additional 10,800 ha had been drained. The amount of marsh included in these totals is not provided.

Loss due to human activities becomes more critical when losses attributed to erosion are also considered. Minimal estimates of annual marsh erosion in Alabama along Mississippi Sound were 16-31 ha.

The gradual but continuing loss of marsh acreage should be of concern when viewed as a total loss of marsh functions and value.

FIRE

A small fur industry in coastal Mississippi and Alabama depends upon nutria and muskrat. Occasional raccoon, fox, opossum, and mink may also be taken. Fur sales in Mississippi were $2,529 for muskrat and $468 for nutria in 1975-76, a decline from 1974-75 values of $10,706 and $582, respectively. Since average prices per pelt remained the same, the decline in total number of pelts taken accounts for the reduction (de la Cruz 1976).

Trappers think frequent burning of the coastal marsh makes trapping easier and food abundant for preferred pelt mammals.

The effects of fire in two Mississippi tidal marshes from 1976 to 1980 provide insight into the impact of this practice on marsh structure and function (Hackney and de la Cruz 1981b). Fire increased the net primary production (ANPP) of the aerial portion in *Juncus* and *Spartina cynosuroides* communities 56% and 49% respectively, over controls. Increased production of *Juncus* communities may be attributed to: (1) remobilization of energy and nutrients from roots and rhizomes to aboveground tissues, (2) increased light availability, and (3) removal of accumulated dead material with subsequent ash deposition. Repeated removal of vegetation by three annual fires resulted in a decline in vigor and growth of *Juncus*. Total community biomass was maintained by increased growth of other species which took advantage of improved light and space conditions. However, *Scirpus* spp. (which might improve the habitat for fur bearers) did not increase in abundance (Hackney and de la Cruz 1981b).

Production of *S. cynosuroides* did not decline with repeated burnings, but an increase in the production of the associated species *Panicum virgatum* changed the relative contribution of plant species and increased biomass.

Release of nutrients following fires in the two marsh communities resulted in increased calcium (Ca) and phosphorus (P) at both sites and magnesium (Mg) at the *S. cynosuroides* site. Estimated nitrogen (N) losses from aboveground standing crops were 70% at both sites. Potassium (K) losses were 35 and 38%, respectively, for the *Juncus* and *S. cynosuroides* communities (Faulkner and de la Cruz 1982).

Enhancement of the sediment nutrient pool was limited to the top 2 cm of sediment. Surface pH was elevated in both sites following burning due to the high input of basic cation oxides and carbonates (primarily K^+, Ca^+, and Mg^{2+}). The pH elevation was shortlived in *Juncus*, but persisted in the *Spartina*. Extractable soil P and K increased after burning and remained elevated at both sites. Extractable Ca increased over 30% and remained elevated at the *Spartina* site. Magnesium at both sites and Ca at the *Juncus* site appeared to increase over time. Levels of sediment N remained unchanged at both sites (Faulkner and de la Cruz 1982).

The Hackney and de la Cruz (1981b) study points out the impact of fire and its implications on the management of these marshes:

1. Loss of *Juncus* growth and reduced density after repeated burns will reduce the dense living root/rhizome mat and may

cause the sediments to become unconsolidated and subject to erosion.

2. Fire destroys a large quantity of plant biomass, some of which is probably destined for export to nearby aquatic ecosystems.

3. Removal of vegetation by fire exposes the marsh surface and its associated flora and fauna to increased solar insolation and evaporation and may increase predation pressures.

4. Frequently repeated marsh burns will result in community succession. The details of succession and impacts on marsh functioning are not known.

It is suggested that fires only be used as a management tool every 4 or 5 years and that portions of marshes, rather than entire marshes, be burned in a rotation (Hackney and de la Cruz 1981b).

PETROLEUM POLLUTION

Because of their location, Juncus marshes are susceptible to oil pollution--indirectly by residual oils in land runoff and directly by massive quantities of oil spilled in gulf and estuarine waters. In experimental marsh ponds, the primary production of the phytoplankton community was reduced by 44 to 65% and respiration was reduced 30 to 50% two weeks after an experimental "spill" of Empire Mix crude oil (1.45 mg/per liter of water). Two months after the spill, primary productivity and respiration in the oiled pond were 17% and 7% lower, respectively, than in control ponds (de la Cruz 1982).

On the marsh surface, contamination is usually restricted to the outer 1 or 2 m of marsh fringe, unless the area is totally submerged. Contamination occurs on the surfaces of the substrate, lower plant stems, and leaves, and may penetrate the substrate through worm tubes and burrows. Photosynthetic portions of the plants extending above the high-tide level usually are not contaminated. When the plants are totally covered, mortality may occur, plants partially contaminated by residual and low toxicity oils can be expected to recover (Castle 1977).

A low-level dose of Empire Mix crude oil (250-600 ml m^{-2}) initially affected the primary productivity of a Mississippi Juncus marsh. A single heavy dose of 1,500 ml m^{-2} of Saudi Arabian oil killed most plants and completely suppressed growth in survivors for 1-2 years (de la Cruz et al. 1981).

The impact of oil on marsh fauna can be acute or chronic. Heavy concentrations of crude oil have resulted in massive killing of birds, fish, and invertebrates associated with wetlands. Low-level but chronic dosages (25-75 mg l^{-1}) of Empire Mix and Saudi Arabian oils have been shown to retard growth and cause severe fin rot in the striped mullet (Mugil cephalus) (Minchew and Yarbrough 1977). Shrimp (Penaeus spp.) showed behavioral changes when exposed to low concentrations of crude oil. Nigerian oil was most toxic to shrimp and resulted in uncoordinated swimming behavior and spiralling motion (Brown 1978). Oysters responded to oil contamination by closing of valves and ceasing of pumping. Barszcz et al. (1978) observed that oysters reduced their intake and/or assimilation of food when exposed chronically to single, low-level (4 ppm) doses of Empire Mix, Saudi Arabian, and Nigerian crude oils. Histological alterations in the connective tissues associated with the body wall, mantles, and food groove were also observed. Oil exposure may reduce reproductive potential in oysters as indicated by reduction in the development of the germinal tissues (Barszcz et al. 1978).

Further study is needed on oilspill impacts and on other components of the marsh biota.

PULP-MILL EFFLUENTS

Livingston (1975), in a 2-yr study of the impact of kraft pulp-mill effluents (KME) on fish fauna in the Apalachee Bay area of Florida, found that marsh fish assemblages in areas of acute dosage were severely reduced in numbers of both individuals and species. Polluted areas showed changes in community structure, i.e., decreased dominance as well as qualitative differences in species composition when compared to control areas.

An associated study comparing the bird populations in the marsh areas (Weiser 1973) pointed out reduced numbers of species and individuals in the KME-polluted areas.

MITIGATION

Since marshes play a unique and critical role in coastal ecosystems, it is important that they be preserved and even restored where possible; their contributions must be recognized, evaluated, and enhanced.

Recent experiments have analyzed the success of harvest and artificial fertilization in enhancing the primary productivity of dominant plant species in the Mississippi-Alabama marshes (de la Cruz et al. 1981b). Indications are that fertilization, either with commercial fertilizer or nitrogen-rich wastes, may increase plant production and enhance the food chain role of remaining marshes. Fertilization with commercial NH_4NO_3 (126g m^{-2}) in a single, late-winter application increased primary production of Juncus by 59-74%, Spartina alterniflora by 82%, and S. cynosuroides by 24%. Harvesting was of questionable value because of lack of technology and resultant extreme disruption of the substrate (Stout et al. 1980). However, if any of the recent work on chemical derivatives (Miles and de la Cruz 1976; Mody et al. 1975) and on the potential of marsh plants (de la Cruz and Lightsey Unpubl. MS.) proves to be of economic value, certain plants may be regularly harvested for certain plants for chemicals, cellulose, and other by-products.

Demand for suitable dredge material disposal sites and apparent successes with marsh creation on spoil may meet a need to both preserve remaining marsh and replace lost marsh acreage. Eleuterius (1974a) successfully transplanted Spartina patens, Distichlis spicata, S. cynosuroides, S. alterniflora, Phragmites australis, and Juncus on spoil sites in Mississippi Sound. Extensive investigations by the U.S. Army Corps of Engineers' Waterways Experiment Station at Vicksburg, Mississippi, resulted in detailed guidelines for marsh plant establishment. The reader is referred to their summary publications for further information (see Kadlec and Wentz 1974; Wentz et al. 1974).

Two attempts have been made in northwestern Florida to create salt marshes by planting dredge spoil (Figure 43). The intertidal area of Panacea Island, at Dickerson Bay, was planted with Juncus, Distichlis spicata, and Spartina alterniflora culms (Coultas et al. 1978; Krucyznski and Huffman 1978). Only a few clumps of S. alterniflora were present 17 months after planting. Losses were attributed to attrition and erosion. Spartina alterniflora transplants survived well at Drake Wilson Island in Apalachicola Bay, achieving full cover of the 7-acre intertidal area within 15 months after planting. At elevations from 1.0 m to 1.4 m above MSL, bare-root culms of S. patens survived well on Drake Wilson Island. Xeric, nutrient-poor sediments can be rapidly stabilized through planting of this species.

Eleuterius (1974a) and Eleuterius and Caldwell (1981b) transplanted marsh species onto barren spoil areas at Horn Island, Simmons Bayou, and Ship and Petit Bois Islands, Mississippi. Species used included S. alterniflora, S. patens, S. cynosuroides, D. spicata, Juncus, and Phragmites australis. Both Distichlis and S. patens had good survival when planted in peat pellets. This method did not work well for other species which showed greater survival success when transplanted as culms or plant sprigs.

Eleuterius and Caldwell (1981b) found that colonies and immature stands of S. alterniflora spread centrifugally at first, then predominantly downward on the tidal plane. Four or more years may be required before this species reaches the lowest limit of vertical distribution. From a single transplant in Davis and Biloxi Bays, Mississippi, 0.2 ha was completely covered by S. alterniflora in two years. D. spicata was observed to rapidly colonize barren spoil islands and generally replace S. alterniflora as that species grows down the tidal plane.

Juncus was very slow to naturally colonize spoil islands in Mississippi (Eleuterius and Caldwell 1981b). It may

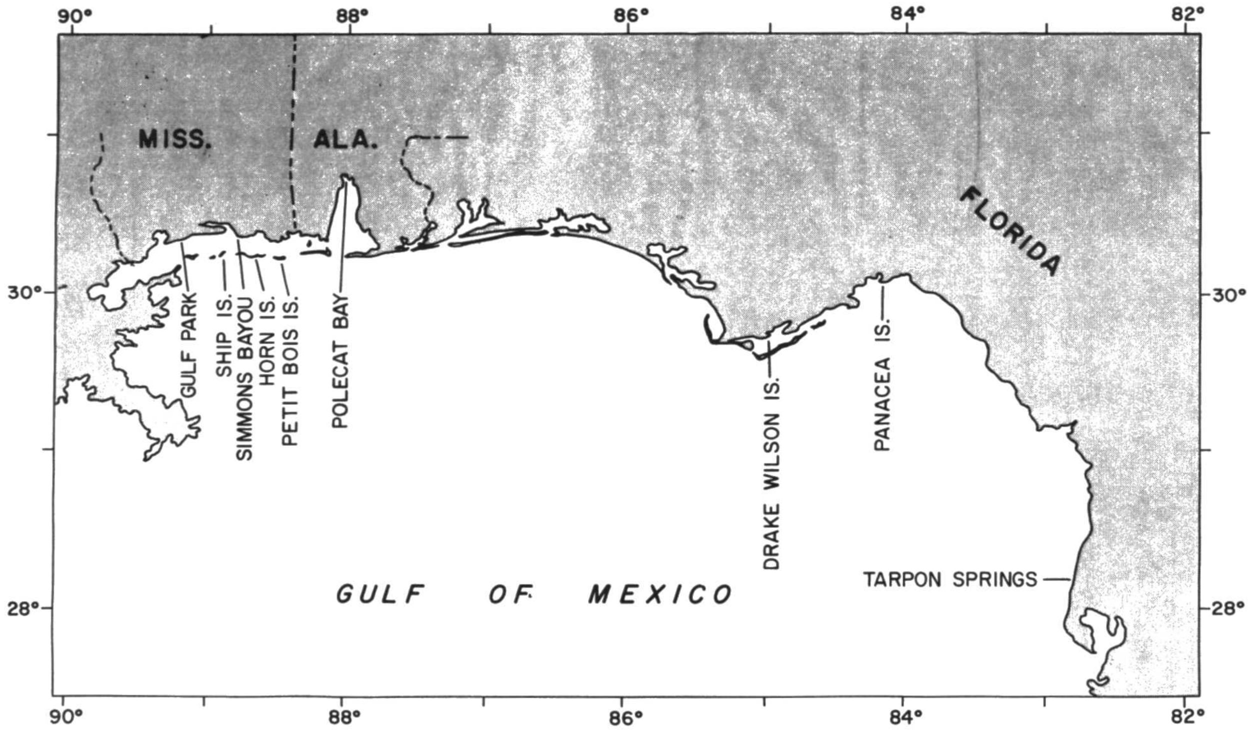

Figure 43. Marsh creation projects, northeastern Gulf of Mexico (after Kruczynski 1982).

take 10 years before this species begins to be observed, often in the D. spicata zone. Juncus may also become established at the upper edge of the S. alterniflora zone, eventually crowding out the latter species. Juncus grows very slowly compared to S. alterniflora and D. spicata, but once it becomes established in an area, no other species seems to be able to replace it. Eleuterius and Caldwell (1981b) estimated that from 16 to 35 yrs. may be required for Juncus to colonize spoil and form a closed stand. In contrast, culms planted at 4-foot centers formed a closed stand in 5 years.

Transplants of S. cynosuroides at Simmons Bayou, Mississippi, were slow growing but did not form closed stands 8 years after planting (Eleuterius and Gill 1981). Similar growth and cover rates were found for Phragmites australis in the same study.

According to Eleuterius (1974b,) factors affecting transplant success, in decreasing order of importance, were erosion by wind or water, available soil water, soil water salinity, and soil nutrients. Potential marsh-creation sites should be surveyed for topographic and soils information before transplanting. A waiting period of 1-2 years may be required on new spoil to allow for normal settling of sediments. Hay bales were recommended to reduce wave erosion while still allowing tidal exchange.

New marshes can be created and damaged marshes restored by a well-planned and timed revegetation program if local environmental conditions are suitable. However, many sites are not suitable because of one or more factors mentioned above; therefore, this approach must be considered on a case-by-case basis.

Currently, mitigation options are limited. The value of Juncus marshes and their continued deterioration and loss mandate that new viable options be investigated and exercised.

CHAPTER 7

RESEARCH NEEDS

As can be seen in preceding chapters, considerable information has been developed concerning the structure and function of *Juncus*-dominated marsh ecosystems on the coasts of the northeastern Gulf of Mexico. There is much more not known, and numerous basic and applied studies are needed to satisfactorily evaluate the importance of these systems and to further understand the functioning of the marshes in the overall ecology of the estuaries and coastal waters of the region. Significant data gaps include the following:

(1) Phytoplankton - community dynamics, environmental tolerances, primary productivity in marsh creeks. Comparative importance vs. benthic macroalgae vs. macrophytes.

(2) Benthic algae - community structure, substrate requirements, environmental relationships, primary productivity, food chain role.

(3) Belowground biomass - productivity, decomposition, role in nutrient and energy flow.

(4) Microbiota - role in detritus and decomposition processes, environmental controls, action in nutrient cycling.

(5) Zooplankton - utilization of marshes, secondary productivity, environmental tolerances.

(6) Macrofauna - population dynamics, energy budgets, habitat requirements, interactions for dominant species of mollusks, arthropods, birds, and mammals.

(7) Commercial species - quantification of marsh role in food requirements and habitat utilization.

(8) Fish - feeding and breeding chronologies and marsh dependency, utilization of marsh detritus.

(9) Hydrological studies - freshwater discharge patterns, nutrient and sediment fluxes, toxic materials transport.

(10) Inter-relationships of freshwater wetlands and *Juncus* coastal marshes.

(11) Nutrient contributions of *Juncus*-dominated coastal marshes to estuarine communities.

(12) Creation and success of man-made marshes.

(13) Long-term studies to evaluate long-term cycles and aperiodic events.

(14) Impact studies, i.e., thin layer spoil disposal, ditching, elevated construction.

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GLOSSARY

Actinomycetes- filamentous bacteria

Anthesis- flowering

Ascomycetes- a group of fungi including yeasts, molds, and powdery mildews

Basidiomycetes- a group of fungi including rusts, jelly fungi, and mushrooms

Biological Index- a measure of species importance determined by assigning scores to species in the order of abundance in a sample

Biomass- weight of living or previously living material expressed in wet weight, dry weight, or ash-free dry weight

Bisexual flower- a flower with both male (stamens) and female (pistil) reproductive organs

Bracts- a modified leaf existing in a much reduced form, often scalelike

C_3 species- plants which fix carbon by the Calvin cycle of photosynthesis and produce two three-carbon molecules of 3-phosphoglyceric acid from one molecule of carbon dioxide

C_4 species- plants which fix carbon by way of the C-4 dicarboxylic acid pathway, forming malic acid and aspartic acid

Carnivore- an organism whose principal food source is living animal tissue

Chlorophycophyta- the green algae

Chrysophycophyta- the algae division including diatoms

Conidia- asexual reproductive spores in yeasts

Culm- the stem of grasses

Cyanochloronta- the blue-green algae

Detritivore- an organism whose principal food source is fragments of previously living tissue (detritus)

Diurnal tide- having one high and one low tide in each 24-hour period

Eh- a measure of electron activity expressed in millivolts as a measure of oxidation - reduction potential of a substance

Edaphic- related to the soil

Epifauna- animals living on the surface of the soil

Epiphytic- living on plant surfaces

Eutrophication- nutrient enrichment of a system resulting in increased primary production of organic material

Euryhaline- having a broad tolerance of fluctuating salinities from seawater to 15 ppt or lower

Euryokous- broad tolerance of a variety of environmental parameters

Gynodioecious- having two types of flowers on separate plants, one with bisexual flowers, one with female only

Hectare- a metric unit of area equivalent to 10,000 square meters (2.47 acres)

Herbivore- an organism which derives its nutrition primarily from living plant material

Holeuryhaline- animals with broad salinity tolerance who spend all of their lives in the estuary such as cyprinodont fishes

Hypersaline- salinity greater than 35 ppt

Interstitial water- water contained within spaces, as between soil particles

Kilojoule- 1,000 joules, a unit of work or energy; 1 joule = 10^7 ergs or approximately 0.7375 foot pounds

Megalops- larval stage just before the adult stage in marine crabs

Meiofauna- animals in the size range from 1.0 mm to 0.1 mm

Meroplankton- organisms which spend only a part of their life cycles in the plankton

Oligohaline- brackish, 15.0 - 5.0 ppt

Omnivore- an organism with a broad diet of both animal and plant tissue

Oostigites- plate-like processes from the bases of the thoracic legs of peracaridan crustaceans for brooding young

Panicle- a form of flower arrangement in a branching pattern

Pelagic- pertaining to the open water of the ocean

Perfect flower- a flower with both male and female reproductive organs

Pneumostome- pulmonary aperture in some gastropods

Protogynous hermaphroditism- an organism existing initially as a sexual female converting at a later age to a functional male, especially found in fish

Rhizome- an underground stem

Sclerotia- a hard, dormant stage of some fungi

Semidiurnal tide- having 2 high and 2 low tides each 24-hour period

Spermatophyte- a flowering plant producing true seeds

Staminate flower- a flower with only male reproductive organs (stamens)

Supratidal- above mean high water

Xeric- very low in moisture for life support

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15. Supplementary Notes

16. Abstract (Limit: 200 words)

The salt marshes of the northeastern Gulf of Mexico are distinguished by irregular flooding, low energy wave and tidal action, and long periods of exposure. The plant community is most often dominated by black needlerush (*Juncus roemerianus*), the species of focus in this synthesis. Distinct marsh zones include those dominated by *Juncus* and *Spartina alterniflora* at low elevations, sparsely vegetated salt flats, and higher elevation salt meadows of *Juncus* and *Spartina patens*. A diverse microbial and algal assemblage is also present.

A diverse fauna has adapted to the physical rigors of these marshes. Zooplankton are dominated by the larvae of fiddler crabs and other decapods. The meiofauna consist primarily of nematodes and harpacticoid copepods. Macroinvertebrates are represented by crustaceans (especially mollusks and crabs), annelids, and insects. Grass shrimp, blue crabs, and other crustaceans are seasonally abundant in marsh creeks, as are a number of resident and migratory fish species. Birds comprise one of the larger herbivore groups and are also significant at higher tropic levels as top carnivores. Muskrat and nutria are important mammals.

Our knowledge of the relationships of these marshes to coastal ecosystems is still incomplete. Further information is needed in light of development pressures and stresses.

17. Document Analysis a. Descriptors
Primary biological productivity, fishes, birds, fires, furbearers

b. Identifiers/Open-Ended Terms
Salt marshes, human impacts, *Juncus roemerianus*, *Spartina alterniflora*, *Spartina patens* *Distichlis spicata*, Salt flats, high meadows, dredge and fill activities

c. COSATI Field/Group

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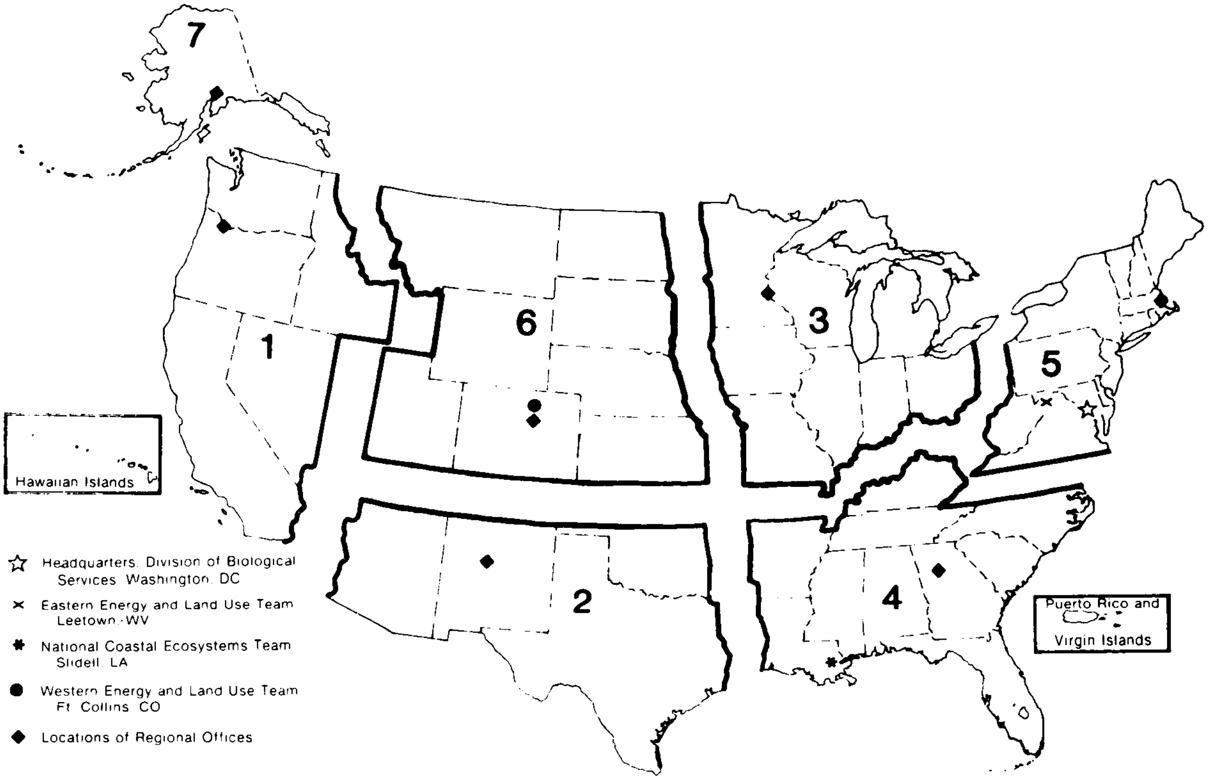

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