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Community Structure and Production in a Marsh on the Southern Branch of the Elizabeth River, Virginia

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COMMUNITY STRUCTURE AND PRODUCTION IN A MARSH ON THE SOUTHERN BRANCH OF THE ELIZABETH RIVER, VIRGINIA

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ABSTRACT

Four different plant communities occur on the Southern Branch of the Elizabeth River, Virginia: 1. Spartina alterniflora, 2. Distichlis spicata - Spartina patens - Juncus roemerianus, 3. Baccharis halimifolia - Iva frutescens and 4. Spartina cynosuroides. The cordgrasses S. alterniflora and S. cynosuroides dominate the marsh.

Based on standing crop estimates S. alterniflora produced 1218.6 grams dry wt/m^2 and S. cynosuroides 1681.3 grams dry wt/m^2, which is much higher than generally assumed for Virginia marshes. Evidence for the presence of two crops of S. alterniflora on the marsh during the growing season is presented.

Two animal associations, composed of typically marsh-associated invertebrates, were defined. The low marsh association was dominated by Uca minax, Modiolus demissus, Sesarma reticulatum, Uca pugnax, Littorina irrorata and Polymesoda caroliniana, and the high marsh by Uca minax, Sesarma cinereum and Melampus bidentatus. Uca minax was the major dominant throughout the marsh.

Frequency of tidal inundation was thought to be the principal factor delineating plant and animal communities. This factor and salinity appeared to be the primary regulator of the density of marsh invertebrates.

Comment is made on communities present in the adjacent river and the influence of the marsh on these waters.

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INTRODUCTION

A complex system of interactions exist within an estuary. This system includes tidal effects, nutrient cycles, salinity gradients, sedimentation and distinct biota, all of which are interwoven to constitute "one ecosystem or production unit" (Odum 1961). The salt marsh represents a unique constituent of the estuary and plays a major role within this system.

The structure of the salt marsh is strongly influenced by estuarine dynamics. The combination of varing tides and salinities creates a harsh environment for most plant species and is linked with the high productivity of those forms present (Teal 1962; Wass and Wright 1969; Good 1972; Steever 1972; Teal 1973). Local salinity variations dictate which forms may occur, while the position of these species within the marsh is primarily limited by the frequency of tidal inundation.

Numerous contributions to the estuary are attributed to the salt marsh. The marsh plants provide habitats for many local and migrating wildlife (McAtee 1941) and produce a dense mat of roots and barrier of shoots which protect the shoreline from erosion. Marshes are known to act as nutrient and sediment traps and thus protect estuarine waters from excessive algal blooms and shifting sediments (Wass and Wright 1969). Most important, the marsh is a primary producer within the estuary, thereby enhancing the fertility of these regions.

The purpose of the present study was to characterize a marsh on the Southern Branch of the Elizabeth River by identifying its major plant and animal communities. In addition, seasonal and distributional relationships within these communities were to be noted to include production of the dominant marsh grasses. Communities present within the Southern Branch of the Elizabeth River were investigated in an attempt to link the marsh with the river.

Description of Study Site

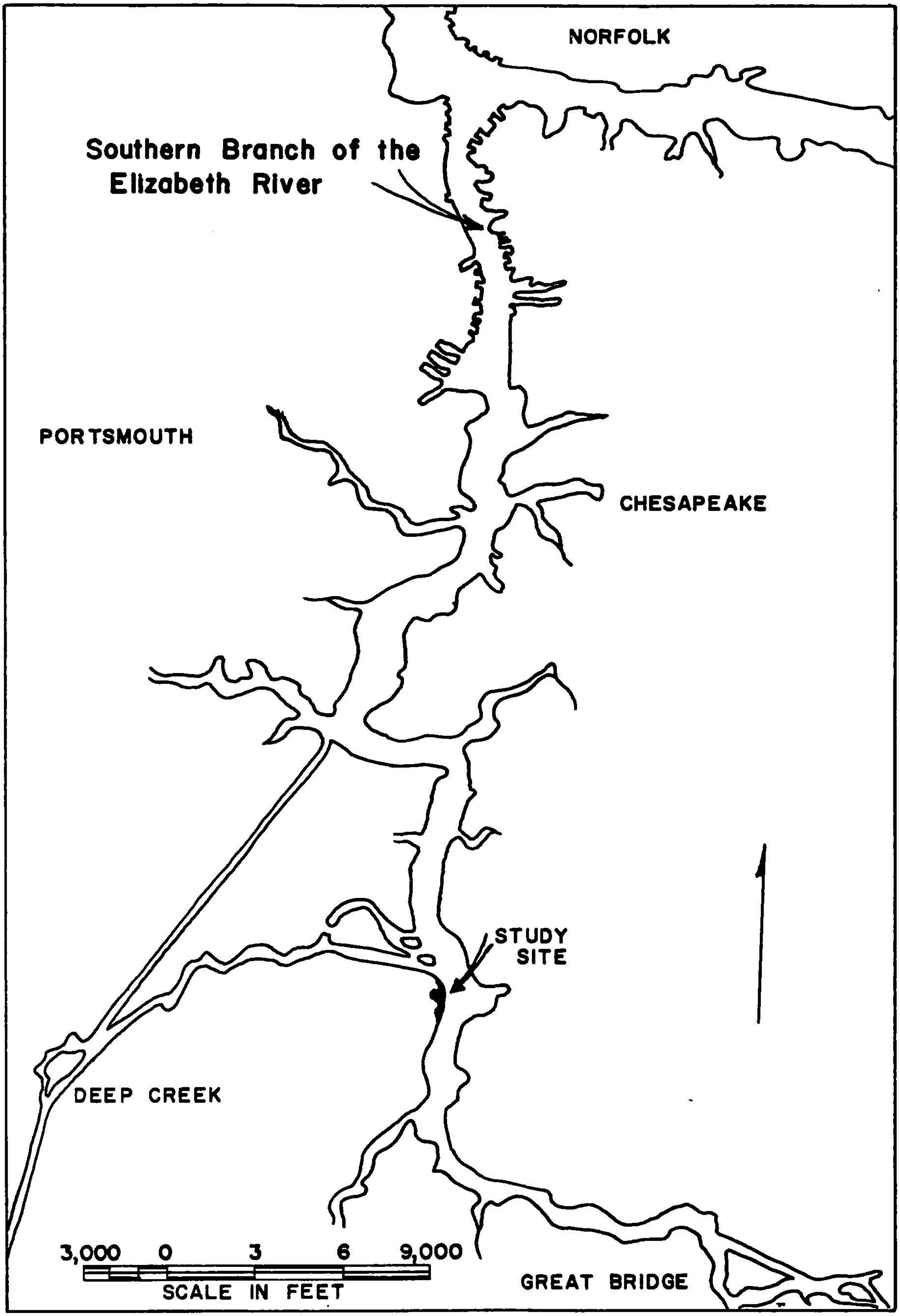
The Southern Branch of the Elizabeth River borders the Southern Virginia cities of Norfolk, Portsmouth, and Chesapeake (see fig. 1). The Southern Branch extends 37.0 km upstream from Hampton Roads where it connects to Currituck Sound via the Albemarle and Chesapeake Canal at Great Bridge, Virginia. The study site is located 6.8 km downstream from Great Bridge at the junction of Deep Creek, which drains waters from the Dismal Swamp, and the Southern Branch of the Elizabeth River.

The study area is typical of this river's upper reaches which are characterized by some barge and construction industry with an occasional home or marina located on its shores. Narrow belts of Spartina-dominated marsh are the predominant

Figure 1

STUDY SITE ON THE SOUTHERN BRANCH
OF THE ELIZABETH RIVER.

Fig. 1


NORFOLK
Southern Branch of the Elizabeth River
PORTSMOUTH
CHESAPEAKE
STUDY SITE
DEEP CREEK
3,000 0 3 6 9,000
SCALE IN FEET
GREAT BRIDGE

natural shore habitat. These marshes often widen into comparatively extensive marshes with an occasional small creek or pond present. The shoreline is most often deeply eroded. Downstream heavier industry includes an electric generating plant (which releases heated effluents), coal loading piers, and numerous waterfront and associated shipping facilities. All natural habitat downstream has either been severely altered or destroyed.

The marsh bordering the river is inundated twice daily to approximately the upper level of *Spartina alterniflora*. Freshwater enters from Currituck Sound while tea-brown freshwater draining through peat substrate in the Dismal Swamp enters the Southern Branch from Deep Creek. Periods of rain result in additional freshwater drainage and reduced salinities.

The Southern Branch, in the region of the study site, is shallow with a soft mud bottom and varies in width up to 350 meters. Greatest depths occur in the channel which passes within 30 meters of the marsh's edge. The channel averages 4 to 5 meters in depth while at low water shallow areas of the river average less than one meter.

LITERATURE REVIEW

General classifications of the salt marshes of the Atlantic coast of the United States have been made by Martin et al. (1953) and Oosting (1954). More recently, Chapman (1960) broadly classified the east coast tidal marshes on the basis of substrate.

Floristic studies which are most often either check-lists of species present or studies dealing with zonation and community structure are common in the literature. The vegetation in the marshes along the Outer Banks of North Carolina are described by Brown (1959). Tidal elevation was considered the major factor in determining zonation within these marshes (Bourdeau and Adams 1956; Beal, Cooper and Adams 1962; Adams 1963). According to Adams, the low marsh is dominated by Spartina alterniflora, with other zones distinguishable that include a Juncus roemerianus zone and a mixed S. alterniflora - Salicornia perenuis - Limonium carolinianum zone. Spartina patens, Distichlis spicata, Borrichia frutescens, Frimbistylis castanea and Aster tenuifolius characterize the high marsh. The marshes of Maryland have also been classified according to community structure (Nicholsen and Van Deusen 1953). More recently, Philip and Brown (1965) have investigated transition zone vascular plants of the South River in Maryland.

Virginia salt marshes have been little studied despite their importance to the Chesapeake Bay. Egler (1942) briefly described the tidal marshes of Seashore State Park at Cape Henry. Floristic checklists have been prepared for several of Virginia's barrier islands. Harvill (1965; 1967) described the vegetation of Parramore and Assateague Islands, while Clovis (1968) reported the vegetation of Smith Island. Hog and Cedar Islands were briefly described by Wass and Wright (1969). Kerwin and Pedigo (1971), during the summer of 1964, quantitatively studied the structure and zonation of Four Point Marsh located on the western shore of Chesapeake Bay. In this latter study, zonation was found to be governed by tidal elevations or environmental factors closely related to the tides.

Kerwin (1966) described and classified the marshes of the Poropotank River, a tributary of the York River, as they passed from salt to fresh water. His classifications, based on relative importance values and community structure were: salt marsh, brackish marsh, slightly brackish and fresh water marsh. Major plant species occurring in this salt marsh classification included S. alterniflora, S. patens, Distichlia spicata, Scirpus robustus and Juncus roemerianus. The dominant species was S. alterniflora. In his brackish water marsh, S. alterniflora, S. cynosuroides, S. patens, and Scirpus robustus. Spartina alterniflora and Polygonum punctatum dominated the slightly brackish marsh type and its dominant community was S. alterniflora - Echinochloa walteri. The most prevalent community consisted of _Z_. _aquatica_ - _E_. _quadrangulata_. _Spartina alterniflora_ which characterizes marshes on the western shore of the Chesapeake Bay also dominates marshes on the Eastern Shore Virginia (Wass and Wright 1969) and those along the entire Atlantic coast (Teal and Teal 1969). The marshes of the Poropotank River and Four Point Marsh show greater similarity to marshes to the north of Chesapeake Bay than to the south (Kerwin 1966; Kerwin and Pedigo 1971). Differences may arise in community structure or species associations, while dominant plants within salt marshes along the Atlantic coast and the Gulf of Mexico are apparently the same or of closely related species (Kerwin 1966).

The animals of the salt marsh have been well investigated. Studies fall primarily into two categories, either descriptive and distributional, or functional. McAtee (1941) mentions common marsh plant species but stresses bird life and coastal marsh bird species. He also briefly mentions reptiles, fish and mammals while ignoring the many invertebrates which occur. Teal and Teal (1969) discuss many of the invertebrates present and their interrelationship with the marsh habitat. Teal (1962) provides an extensive list of species found in Georgia salt marshes and groups them according to distribution and origin.

Perhaps the most characteristic invertebrates of the salt marsh are the fiddler crabs of the genus _Uca_. Crane (1943) describes display and breeding patterns of the fiddlers, while Gray (1942) studied ecological and life history aspects of the red-jointed fiddler, Uca minax. Teal (1958) studied the distribution of U. minax, U. pugnax and U. pugilator relative to marsh type within the salt marsh ecosystem of Sapelo Island, Georgia. Substratum and salinity were found to be important while the presence of food was not thought to be a factor governing distribution on the marsh. Uca pugnax preferred vegetated muddy substratum and salt water while Uca minax preferred fresher water than U. pugnax and U. pugilator, the latter form showing a preference for sandy areas. The crabs, Sesarma reticulatum, Eurytium limosum and Sesarma cinereum, were also investigated by Teal. Kerwin (1971; 1972) studied the distribution of U. minax and Melampus bidentatus relative to marsh grasses in the marshes of the Poropotank River. Both organisms were found in the salt and brackish marsh, but not in the slightly brackish and fresh water marshes.

Most of the reports concerning salt marsh organisms deal with trophic position, the flow of energy, net production and possible contributions to the overall marsh-estuary ecosystem. Production figures have been reported for Spartina alterniflora from Louisiana to New York. Kirby (1971) reports values for both inland and streamside S. alterniflora in the region of Barataria Bay, Louisiana. Schelske and Odum (1961), Teal (1962), and Smalley (1959) have indicated the average production values over an entire marsh area in Georgia. Other studies include Williams and Murdock (1969) in North Carolina, Morgan (1961) in Delaware, and Udell *et al.* (1969) in Long Island. Day *et al.* (1972), in reviewing these works, noted a gradient of increasing production southward, possibly due to the increased growing season. Steever (1972) found that net production of *S. alterniflora* increased with tidal amplitude while highest production was also accompanied by narrow salinity fluctuations (Good 1972).

Waits (1967) considered the net primary production of an irregularly flooded salt marsh in North Carolina and included figures on the net production of *Distichlis spicata*, *S. patens* and *S. robustus*. The needlerush, *Juncus roemerianus*, was investigated by Williams and Murdock (1972) who include a review of previous production figures on this species. Studies by Harper (1918) on Long Island present values for the production of *Phragmites communis* and *Juncus roemerianus*. Standing crop estimates of the production of *Ulva lactuca* associated with the salt marshes of Hempstead, Long Island, have been reported by Udell *et al.* (1969). Pomeroy (1959) has measured the production of mud algae, primarily pennate diatoms, in Georgia salt marshes.

In Virginia, only one study has been completed regarding the primary production of marsh grasses. Wass and Wright (1969) measured the net production of fifteen species of marsh grass from peak standing crop estimates. These included *S. alterniflora*, *S. patens*, *S. cynosuroides*, *Juncus roemerianus*, *D. spicata*, *Phragmites* sp. and several less common species.

Several authors have measured the energy requirements of the marsh's primary consumer populations. Much of this work has been done in the salt marshes of Sapelo Island, Georgia. The energy flow of the herbivore populations, primarily the grasshopper, *Orchelimum fidicinium*, and the leafhopper, *Prokelesia marginata*, were studied by Smalley (1959; 1960). It was found that they utilized only 7% of the net production of the marsh. Odum and Smalley (1959) compared the population energy flow of a herbivore, *O. fidicinium*, and a deposit-feeder, *Littorina irrorata*, within the marsh. The structure and energy flow of the ribbed mussel population, *Modiolus demissus*, was reported by Kuenzler (1961). Teal (1957; 1959) investigated the distribution and energy flow of the crab population present in these marshes. Teal (1962) summarized these Sapelo Island studies where he estimated that the consumer populations utilized 55% of the net production of the marsh and that the remaining 45% was exported to the adjacent estuary. Day *et al.* (1972) summarized community energy flow of both the marsh and estuarine populations of the Barataria Bay region of Louisiana. They estimated that the marsh exported 51% of its net production to the estuary.

Odum (1961) states that "most of the tremenduous production of salt marshes is destined to be used in the form of organic detritus." Darnell (1958; 1961; 1962) demonstrated the importantce of detritus as a food source to the fauna of Lake Pontchartrain, Louisiana. Odum (1971) and Heald (1971) in a joint study of a south Florida mangrove estuary demonstrated the dependence of estuarine fauna on organic detritus of mangrove origin. In this study, Odum concluded that the detritus supported a small group of omnivores which supplied energy to higher trophic levels. Odum and de la Cruz (1967) also studied organic detritus in the marsh-estuary ecosystem of Sapelo Island, Georgia. Darnell (1967) and Odum et al. (1972) provide literature reviews of organic detritus as it relates to the estuarine ecosystem.

Virginia marshes have not been studied from a functional point of view. Wassand Wright (1969) measured the productivity of several plant species present in Virginia's marshes but expert was not considered. Van Engel and Joseph (1968) studied the York-Pamunkey River area which they believed to be typical of fish nurseries of the Atlantic coast states.

The Elizabeth River has been studied by Marshall (1967a; 1967b; 1968) who has investigated the phytoplankton, and Richardson (1965) who reported on the macroinvertebrate community as an indicator of pollution in the Elizabeth River. Hillard (1972) describes the prominent algae of the marshes located within the study area.

METHODS

Field Collections

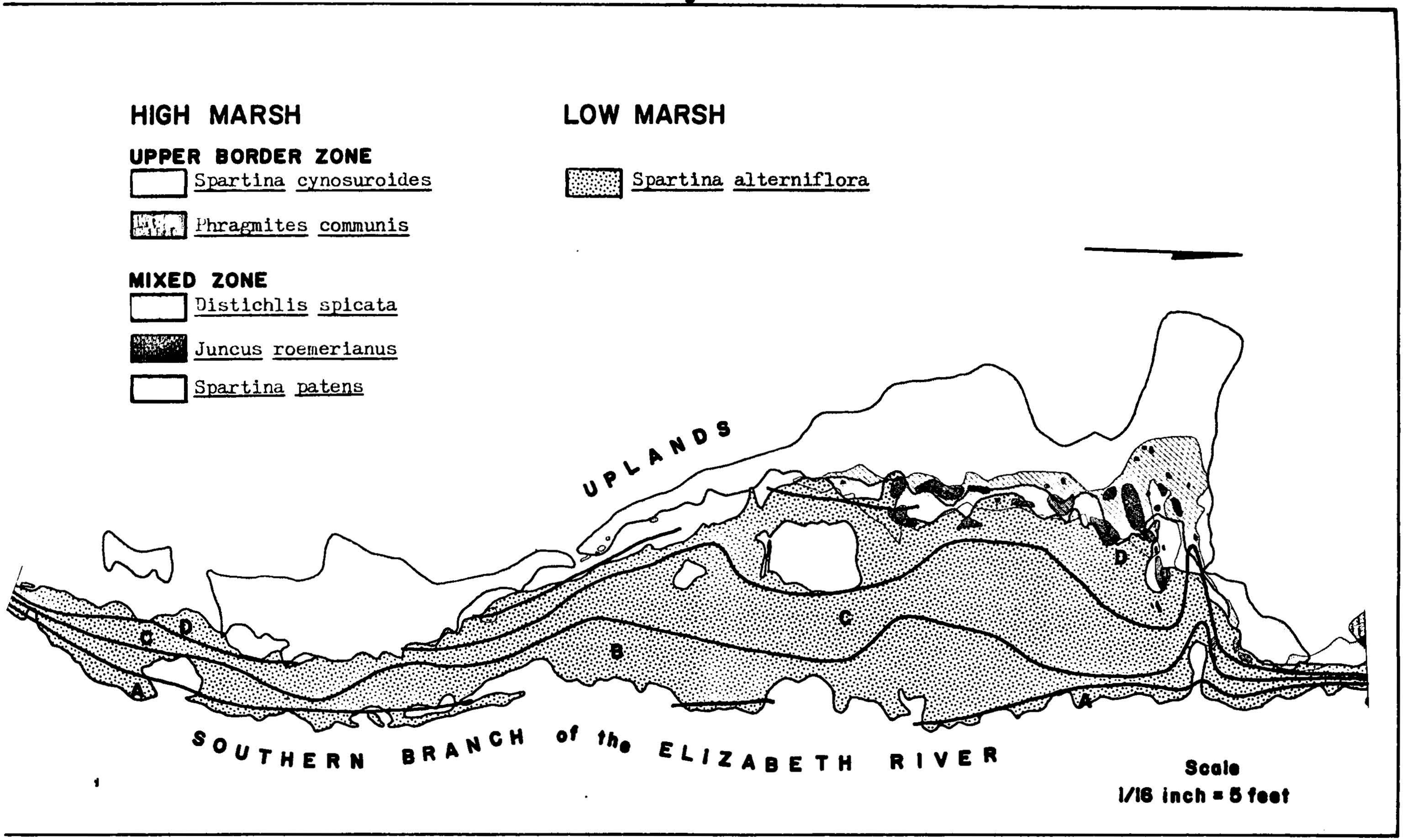
Between January and August 1972, field collections from both marsh and the adjacent river were made. The marsh was initially mapped and points of reference on the marsh determined.(see fig. 2). The dominant plant communities were then plotted along with the relative elevations within the <u>Spartina alterniflora</u> community. A means of quantitatively sampling the marsh was constructed as follows. Between the points of reference a line was stretched and divided into segments 30 meters long. Right angle transects were sent out within each segment through both the low and high marsh. The high marsh segments were staggered 15 meters from the low marsh. The position of the initial transect sampled each month was chosen by random numbers from 1 to 20, each representing 1.5 meters along the line. The remaining transects were spaced at 30 meter intervals across the marsh. The same transects were not repeated in subsequent collections. The right angle transects were then divided into segments 6.3 meters long. By selection random numbers from 1 to 20, each representing a 1/3 meter interval, one sample site was located within each 6.3 meter segment.

At each sample site the above-ground liviing portions of the plants and animals (snails) were collected from a 20 cm^2

Figure 2

FLORAL ZONATION ON THE MARSH ON THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Fig. 2


HIGH MARSH
UPPER BORDER ZONE
Spartina cynosuroides
Phragmites communis
MIXED ZONE
Distichlis spicata
Juncus roemerianus
Spartina patens
LOW MARSH
Spartina alterniflora
UPLANDS
A
B
C
D
SOUTHERN BRANCH of the ELIZABETH RIVER
Scale
1/16 inch = 5 feet

plot. Below-ground portions of plants (rhizomes, roots and peat) and animals (crabs, mussels and clams) were collected with a 15.2 cm diameter core sampler to a depth of approximately 25 cm.

Twice monthly from January through August, random collections were made within the marsh. This afforded a chance to collect insects and other organisms not taken by the quantitative methods previously described, including the trapping of fishes in a small pond which was otherwise inaccessible. Preliminary observations occurred in January and February 1972. The first quantitative samples were collected in March, shortly preceding the first growth of S. alterniflora. Sampling then continued through August at approximately one month intervals.

The river was sampled twice monthly employing a variety of techniques. A 10-foot Otter trawl and boat were employed to sample the channel and shallower areas midstream for fishes and large invertebrates and an 8-foot fine mesh seine net proved most successful for sampling nearshore fishes and invertebrates. Samll minnow traps were used in the early months, but their use was discontinued with April's collections due to the success of seining.

Smaller invertebrates were collected by screening sediment through a fine hardware mesh seive. Shovels were used inshore for sediment collection while in deeper water a small grab sampler was utilized. All living material was preserved in 10% formaldehyde and returned to the laboratory. These methods proved successful for collecting representative species present in the river but inadequate for quantification values, however a relative abundance was calculated.

Sample Analysis

The core samples were returned to the laboratory where they were washed over a hardware mesh screen. The process proved destructive and organisms such as annelids and those smaller (i.e. amphipods and isopods) were not obtained quantitatively. The below-ground portions, including combined rhizomes, roots and peat, were oven-dried at 105° C. The shoots, after counting, were also dried at 105° C. Drying time required to reach a constant weight varied from 24 hours to 10 days in the case of some below-ground samples. Variation was due to differences in quantity and biomass.

The marsh fauna retrieved in the collections were identified, counted, and standard lenghts of specific structures recorded. These included the carpace width of crabs and the body lengths of mussels, snails and clams. These organisms were then oven-dried at 105° C for up to 24 hours.

River invertebrates and fish were examined for abundance and distribution throughout the study period. The standard lengths of the fishes, defined as the distance from the end of the snout to the base of the caudal fin, were measured. In addition, an analysis of the stomach contents of the dominant river species was performed on specimens taken throughout the study period. The entire intestinal tract of the toadfish

Opsanus tau, was examined while in other fish this examination was limited to the stomach. In addition, the buccal cavity was investigated in the blue crab, Callinectes sapidus. Stomach contents were subjectively quantified. First items were identified when possible and counted. Finally, a visual estimate was made as to the relative abundance of each on a percentage basis.

RESULTS

The marsh and adjacent portions of the Southern Branch of the Elizabeth River were sampled from January through August 1972. During this period 102 species of prominent plants and animals were identified (see table 1). Based on sampling records and records of biomass and density, 34 of these were subjectively classified as abundant (A). While the remaining species were either classified as common (C) or rare (R). A characteristic habitat, the location where an organism was most commonly found, was noted for each. In several instances the relative abundance was not known. In these cases, if a characteristic habitat was described, it refers to the location where these organisms were sighted. Several invertebrate species were noted only in the examination of the fish stomachs. Reference to abundance in these would imply their frequency of oocurrence in this stomach analysis.

Marsh Sampling

In November of 1972 the zones delimited by the dominant plants were mapped (see fig. 2). Based on floral zonation and relative degrees of tidal inundation, this marsh was divided into a low and a high marsh area. The low marsh,

Table 1

THE DOMINANT FLORA AND FAUNA AT THE SALT MARSH SITE ON THE SOUTHERN BRANCH OF THE ELIZABETH RIVER*

Species	Abundance	Characteristic habitat**
A. Prominant marsh algae (after Hillard, 1972)		
Anabaena sp.	A	Formed a carpet through the low marsh (A & B zones) January-April
Enteromorpha intestinales	C	Shoreline attached to soil, Spartina, protruding roots and debris
Melosira sp.	C	Intertidal pools
Vaucheria sp.	C	Intertidal pools
Cladophora albida	R	Intertidal pools
Monostroma oxyspernum	R	Marsh edge
B. Prominant vascular plants		
Spartina alterniflora	A	Intertidal zone of marsh
S. cynosuroides	A	Upper border of marsh
Distichlis spicata	A	Mixed zone, debris line
Baccharis halimifolia	C	Lower edge of upper border
Iva frutescens	C	Lower edge of upper border
Scripus robustus	C	Intertidal zone of marsh
Juncus roemerianus	C	Upper intertidal, mixed zone
S. patens	R	Mixed zone, upper debris line
Phragmites communis	R	Upper border of marsh
Pluchea purpurescens	R	High marsh
Aster tenuifolius	R	High marsh

*Abundance was determined on the basis of biomass and density. A-abundant, C-common, R-rare.
**Characteristic habitat refers to the location where an organism was most commonly found, a time period is given when appropriate.

Table 1 (con't)

Species	Abundance	Characteristic habitat
C. Marsh meiobenthos*		
Cyathura polita	-	Marsh edge
Gammarus sp.	-	Marsh edge, base of *Spartina* shoots
Orchestia grillus	A	Mixed zone, under *Spartina* thatch
Neris succinea	-	Intertidal zone
Capitella capitata	-	Intertidal zone
D. Marsh macrofauna		
Melampus bidentatus	A	Upper edge of intertidal through lower edge of upper border zone
Modiolus demissus	A	Forward edge of marsh
Lycosa sp.	A	Upper border zone, mixed zone under *Spartina* thatch
Concephalus allardi	A	Throughout marsh, late June to early August
Sesarma reticulatum	A	Forward edge of marsh
Uca minax	A	Throughout marsh
Littorina irrorata	C	Intertidal zone
Polymesoda caroliniana	C	Upper edge of low marsh, mixed zone
Clinocephalus elegans	C	Throughout marsh, late June to early August
Balanus improvisus	C	Boards associated with forward edge of marsh
Palaemonetes pugio	C	Tide pools formed at low tide, forward edge of marsh
Sesarma cinereum	C	Mixed zone, lower edge of upper border zone
Callinectes sapidus	C	Tide pools formed at low tide
Uca pugnax	C	Low marsh, intertidal zone

*Polycheates included in this group because they were small enough not to be collected quantitatively. Abundance absent because of the sampling technique.

Table 1 (con't)

Species	Abundance	Characteristic habitat
E. Higher carnivores*		
Malachemys centrata	C	Intertidal zone, May-August
Chelydra serpentina	-	Marsh edge, one taken
Terpene carolinia	-	Lower edge of upper border
Rana pipiens	C	Intertidal pools and low marsh zone
Rallus crepitans	C	Marsh edge, intertidal and upper border
Herodiaus egretta	-	Marsh edge and pond
Ardea herodias	-	Upper border and tree line
Procyron lotor	-	
Ondatra zibethieus	-	Two sighted, marsh edge

*Where the species is not accompanied by a relative abundance assume that the characteristic habitat is the area in which the organism was sighted. The presence of mammals was assumed by observing scats, tracks, droppings and runs.

dominated by *Spartina alterniflora*, was inundated by daily tides, while the high marsh, dominated by *Distichlis spicata* and *S. cynosuroides* was inundated only by spring or storm tides. The average vertical range of the tides for this location was approximately 1.2 to 1.6 meters. Dominance was determined on the basis of biomass determinations (see table 2).

Low Marsh

The low marsh encompassed the largest floral zone within the marsh, representing approximately two-thirds to three-fourths of its area. This was an intertidal zone, with the frequency of tidal inundation a major factor. Considering this, the zone was subdivided by relative elevation below the debris line (see fig. 2). Zones A through D varied with elevation, each corresponding to a 15 cm range. Zone D was characterized by being flooded fewer times than other zones within this intertidal community or only by the highest tides. From January through April, this area was covered by a thick layer of Spartina thatch which was moved to higher ground by the higher spring tides. Zone C and B differed slightly. The period of tidal inundation was shorter for zone C than B, while zone B bordered the river in some areas. Zone A was a narrow strip which bordered the river along most of the site. Present in zones A, and in B, where it bordered the river, was a steeply eroded marsh edge, up to four feet in height. This section had been frequently undercut by wave action along its length and had consequently collapsed.

Table 2

DISTRIBUTION OF STANDING CROP IN GRAMS DRY WT/M^2 PER DENSITY NUMBER/M^2
OF DOMINANT MARSH FLORA

	Low Marsh				High Marsh	
	Zone A	B	C	D	Mixed	Upper border
March						
Total marsh	52.7**					
April						
Total marsh	87.6**					
May						
Spartina alterniflora	755.0/1600	424.2/515.0	419.5/432.5	308.0/730.0	236.7/159.2	
Distichlis spicata				5.5/30.0	55.2/209.2	
Spartina cynosuroides		46.5/2.2				238.2/42.7
July						
Spartina alterniflora	530.0/616.5	615.5/553.0	895.0/779.0	577.7/666.5	25.7/8.3	
Distichlis spicata					140.2/517.5	

**Figure represents average standing crop for marsh.

Table 2 (con't)

	Low Marsh				High Marsh	
	Zone A	B	C	D	Mixed	Upper border
July (con't)						
Spartina cynosuroides					46.1/8.3	915.0/50.0
Spartina patens					101.0/180.5	
August						
Spartina alterniflora	1267.5/850.0	1658.8/657	1055.0/502.5	1169.0/908.2	461.5/245.0	
Distichlis spicata				22.5/87.5	136.0/390.0	
Spartina cynosuroides						1749.2/61.0

Spartina alterniflora dominated the low marsh. Standing crops were generally higher in zones A and B along the river's edge (see table 2). First growth of this dominant vascular plant was observed in mid-March. Previous to this time a low carpet of Spartina alterniflora (approximately 4 cm in height) had been present throughout the winter. Associated with this grass was a prominent algal community dominated by a minute blue-green, Anabaena sp., which formed a carpet up to 3 cm in thickness on the floor of the marsh and was most common in zones A and B. Enteromorpha intestinales was common in the low marsh, with Vaucheria sp. associated with the filamentous diatom Melosira sp. in small intertidal pools (Hillard 1972). Generally with higher temperatures and increased growth of S. alterniflora these species were shaded out.

Other vascular marsh plants occurred occasionally throughout the low marsh area, most commonly in the higher elevations (zones C and D). Those occurring most often were: Distichlis spicata, Scripus robustus, Juncus roemerianus, Spartina cynosuroides and Spartina patens. All of these are prominent members of plant communities present in higher zones of the marsh with the exception of Scripus robustus. This plant was found exclusively within the intertidal zone, most often in zones B and C. Easily sighted, S. robustus was a prominent member of the low marsh community, but was present in concentrations too small to have been quantitatively sampled.

The animals present within this zone are quite similar to those that have been described in Georgia (Teal 1962), in Louisiana (Day et al. 1972) and in Virginia's marshes (Wass and Wright 1969). Uca minax, the red-jointed fiddler, dominated here and throughout the entire marsh. Other crabs were present, including Uca pugnax, Callinectes sapidus and Sesarma reticulatum. Sesarma cinereum, the wood crab, was observed within this intertidal zone but not sampled, implying that it may feed here but does not burrow. Modiolus demissus, the ribbed mussel, dominated the forward edge of the marsh (zones A and B), although it was also present throughout the low marsh area. Littorina irrorata, the marsh periwinkle, was present exclusively within this intertidal zone while the clam, Polymesoda caroliniana, and the salt marsh snail, Melampus bidentatus occupied positions within its higher elevations (zones C and D).

Other species, either not taken quantitatively or occurring less commonly, were also present. Two annelids were collected, Capitella capitata and Neris succinea. The isopod Cyathura polita and the amphipods Gammarus sp. and Orchestia grillus were also taken. The latter was most common under Spartina thatch.

In late June a sharp rise in the insect community was noted. Representatives of the orders Hemiptera (bugs), Homoptera (leaf hoppers), Diptera (flies), Coleoptera (beetles) and Odonata (dragonflies) were common. Two prominent members of this community were the grasshoppers (order Orthoptera), Clinocephalus elegans and Conocephalus allardi. They were observed to feed heavily upon the flowers of the cordgrasses. Coinciding with the increase in insects was the appearance in early July of the leopard frog, Rana pipiens. The diamond-back terrapin, Malchemys centrata first appeared in late May and was seen occasionally for the remainder of the study period. The diamondback terrapin is also present in the more saline marshes of Eastern Shore Virginia.

The clapper rail, Rallus cerpitans proved to be common on the marsh throughout the study period. The American egret, Herodiaus egretta, was seen occasionally in low numbers, while Ardea herodias, the great blue heron, was seen on one occasion. They fed along the shoreline or in the shallow pond located on the marsh. Two muskrats, Ondatra zeibethieus, were sighted, while evidence for the presence of the racoon, Proyron lotor, was common.

At low tide, small pools appeared along the forward edge of the marsh (zones A and B). These pools normally were no more than a few meters in diameter. Zone C contained a large shallow pond approximately 20 meters square in area. Within these pools the juveniles of two fishes were common: Fundulus heteroclitus, the mummichog, and Fundulus majalis, the striped killifish. The mummichog was by far the more abundant, as it also was within the nearshore river community. Cyprinodon variegatus, the sheepshead minnow, occurred in low numbers throughout the study period but most commonly in the small marsh pools in late May. Two crustaceans were also commonly in these pools: the small grass shrimp Palaemonetes pugio and young blue crabs, Callinectes sapidus.

High Marsh

The high marsh was characterized as being inundated only by spring and storm tides. Two zones based on relative tidal inundation were present: the mixed zone, dominated by Distichlis spicata and inundated by both spring and storm tides, and the upper border zone, dominated by Spartina cynosuroides and inundated only by storm tides.

The mixed zone represented approximately one-twelth of the total marsh area in which a prominent debris line was present. The zone's width varied from two meters to 15 meters. Presenting a varied habitat, this zone consisted in part of mud flats, areas covered by Spartina thatch, and areas dominated by marsh spike-grass, Distichlis spicata, which also contained small patches of S. patens and clumps of J. roemerianus. Spartina alterniflora and S. cynosuroides Both encroached on this zone and dominated it on the basis of biomass. However, Distichlis spicata and Spartina patens attained their greatest biomasses here, while Juncus roemerianus achieved its greatest prominence.(see table 2). Needlerush, J. roemerianus, a clumping species, was not common enough to be sampled quantitatively yet was prominent, much as was the case with Scripus robustus.

No animal was present exclusively within the mixed zone. Dominant species included Sesarma cinereum and Melampus bidentatus, each with their greatest biomass and density values in this zone. Orchestia grillus was present in its largest numbers beneath the Spartina thatch common to the debris line. Uca minax was also present, with Polymesoda caroliniana occurring only sparsely.

The upper border zone represented from one-fourth to one-third of the total marsh area. At its widest it was approximately 35 meters deep while in other areas it thinned and disappeared. Dominating this zone was Spartina cynosuroides. This species occurs in most brackish marshes, increasing in dominance up rivers toward the fresher waters to eventually replace S. alterniflora (Wass and Wright 1969).

In comparison with the low marsh and the mixed zone, the upper border zone was barren. Its lower edge adjacent to the mixed zone contained several characteristic plants including Baccharis halimifolia, and Iva frutescens. More colorful inhabitants include Aster tenuifolius, the salt-marsh aster, and Pluchea purpurascens, the marsh-fleabane. Prominent plants of the mixed zone encroached on this lower edge, while Phragmites communis, reed grass, which is a similarly appearing plant, replaced S. cynosuroides in one small area.

Three major marsh animals occurred within this zone. Uca minax was the only marsh animal present throughout most of the zone, while Melampus bidentatus and Sesarma cinereum occurred along its lower edge. The wolfe spider, Lycosa sp., was common throughout the year.

Distribution and Production of Dominant Marsh Grasses

The above and below ground portions of the dominant marsh grasses were sampled from March through August. The distribution of these grasses is given in Table 2 for each zone in relation to standing crop and density. There were 235 samples collected, averaging 47 per monthly collection. The data is expressed as grams dry wt/m^2. In Table 2 all values represent averages for each zone.

The standing crop estimates indicate the distribution and dominance of the major plant species. Spartina alterniflora dominated the low marsh while Spartina cynosuroides dominated the upper, landward border. Both plants represented a considerable biomass within the mixed zone, yet far less than they did within their respective zones. For example, in August S. alterniflora averaged 1265.6 grams dry wt/m^2 within the low marsh, while in the mixed zone this plant represented only 461.5 grams dry wt/m^2. Distichlis spicata achieved its highest monthly biomass (140.2 grams dry wt/m^2) within this zone. Other prominent plants included S. patens and Juncus roemerianus. Spartina patens was sampled only in July with an estimated standing crop within the mixed zone of 101.0 grams dry wt/m^2.

Production by the dominant marsh grasses, Spartina alterniflora, Spartina cynosuroides and Distichlis spicata is represented in Table 3. Spartina alterniflora achieved an estimated net production of 1218.6 grams dry wt/m^2 or

Table 3

NET PRODUCTION OF THE DOMINANT MARSH FLORA IN GRAMS DRY WT/M^2

A. Net production of dominant species

Species	March*	April*	May	July	August	Net Production
Spartina alterniflora	34.7	72.0	493.1	699.3	1253.3	1218.6
Spartina cynosuroides	4.7	12.5	172.5	806.2	1681.3	1681.3
Distichlis spicata	0.4	6.5	117.5	252.5	226.5	252.5

B. Net production of the dominant species as a marsh average

Species	March*	April*	May	July	August	Net Production
Spartina alterniflora	50.1	78.8	321.1	428.1	886.5	836.4
Spartina cynosuroides	2.1	7.0	50.7	312.9	410.1	410.1
Distichlis spicata	0.5	2.2	10.9	21.4	19.9	21.4

*Total marsh biomass was collected in March and April. On the basis of observation production values were assigned to the various species as follows: *S. alterniflora* - 95% in March and 90% in April; *S. cynosuroides* - 4% in March and 8% in April; *D. spicata* - 1% in March and 2% in April.

5.47 tons/acre. Greatest production occurred during the period July-August and was estimated at 18.3 grams dry wt/m^2 per day. Net production of S. alterniflora was assumed to equal the August standing crop minus that of March. The March standing crop represented the smooth cordgrass that had wintered over on the marsh. Net production of Spartina cynosuroides was estimated at 1681.3 grams dry wt/m^2 or 7.47 tons/acre. Greatest production occurred during the period July-August with an estimated rate of production of 27.1 grams dry wt/m^2 per day. Distichlis spicata played a relatively minor role on the Southern Branch. Starting slowly this species reached a peak standing crop in July of 252.5 grams dry wt/m^2 or 1.13 tons/acre. Net production for both S. cynosuroides and D. spicata was based upon an assumed zero production prior to the growing season.

The marsh as a whole produced an average of 1267.9 grams dry wt/m^2 or 5.59 tons/acre. The dominant grasses contributed to this total as follows: S. alterniflora, 836.4 grams dry wt/m^2; S. cynosuroides, 410.1 grams dry wt/m^2; and Distichlis spicata, 21.4 grams dry wt/m^2. These figures represent both the natural growth characteristics of the grasses as well as their relative coverage within the marsh, and thus their relative importance.

Below ground standing crop was measured in conjunction with shoot sampling. Data is presented in Table 4. Standing crop data includes the combined contributions of peat, roots and rhizomes to a depth of 25 cm.

Table 4

DISTRIBUTION OF BELOW GROUND STANDING CROP OF THE DOMINANT MARSH FLORA TO A DEPTH OF 25 CM IN GRAMS DRY WT/M^2

	Low Marsh				High Marsh	
	Zone A	B	C	D	Mixed	Upper border
March	15831.6	15672.2	11397.8	12179.9	1019.1	7262.7
April	20419.0	16529.6	14100.8	15829.2	10300.8	8633.4
May	12091.7	11827.3	10259.1	12125.1	9550.5	7370.2
July	14860.5	12130.1	9673.9	10481.8	6196.4	5533.3
August	12706.0	12253.5	11007.3	12045.1	10185.6	5550.8

Considerable amounts of organic matter were present below the surface within the marsh. In August this biomass ranged from 56.6 tons/acre in the low marsh (zone A) to 24.7 tons/acre in the upper border zone. In general, a decrease in biomass occurred landward. This trend included a decrease in peat and an increase in sand content. The former disappeared entirely within the upper border zone. Mixed zone samples indicated an average standing crop of approximately 10,000 grams dry wt/m^2 or 44.1 tons/acre. Standing crop within this zone was highly variable depending on the amount of *Spartina alterniflora* sampled. In July *D. spicata* dominated the mixed zone sampling and the standing crop amounted to only 6196.4 grams dry wt/m^2 or 27.6 tons/acre. In August the sampling was dominated by *S. alterniflora* and *S. cynosuroides*. The resulting standing crop was 10185.6 grams dry wt/m^2 or approximately 45.0 tons/acre.

Major Invertebrate Species of the Marsh

Eight species of marsh invertebrates dominated this marsh. Dominance was based on biomass and density values. This data is expressed as grams dry wt/m^2 with shell and carpace weights included or number/m^2. Values represent the average biomass or density for each species within each zone. In addition, monthly averages for each zone and each collection are given followed by an average for the entire study period.

Table 5

DISTRIBUTION OF BIOMASS PER DENSITY OF THE DOMINANT MARSH FAUNA*

Uca minax

	Low Marsh				High Marsh		
	Zone A	B	C	D	Mixed	Upper border	Average
March	2.7/91.1	1.1/9.9			0.5/36.2	9.9/19.7	2.7/16.5
April		3.8/6.0	2.1/9.0	2.1/27.4	0.1/21.9	9.3/24.7	3.5/12.3
May		21.9/9.9	7.8/32.0	33.5/78.4	2.7/20.3	1.6/23.0	10.6/30.0
July		5.5/27.4	14.3/27.4	8.2/36.2	0.5/6.6	8.8/19.7	6.5/21.3
August	3.4/13.7	68.8/23.0	29.1/39.5	3.3/8.8	6.1/54.9	36.1/68.6	26.3/34.9
Average	1.3/18.3	17.9/14.3	11.8/23.5	7.2/24.4	1.9/25.7	11.6/29.7	10.0/22.4**

Uca pugnax

	Zone A	B	C	D	Mixed	Upper border	Average
March	3.8/18.1		0.4/6.0				0.3/2.2
April				0.3/3.5			0.1/1.1
May				1.8/11.0			0.2/1.3
July							
August	4.4/13.7	1.3/7.7					0.7/2.5
Average	1.6/6.1	0.2/1.2	0.1/1.2	0.3/3.0			0.2/1.4**

*Biomass in grams dry wt/m^2, density in number/m^2.
**Average biomass/density of study.

Table 6

DISTRIBUTION OF BIOMASS PER DENSITY OF THE DOMINANT MARSH FAUNA*

Sesarma reticulatum

	Low Marsh				High Marsh		
	Zone A	B	C	D	Mixed	Upper border	Average
March	1.6/18.1		4.4/6.0				1.0/2.2
April	29.1/87.7	3.3/6.0					2.4/6.7
May		6.0/19.7					1.6/1.3
July	12.1/18.1	4.9/6.6					1.6/2.2
August			0.5/4.9				0.1/3.0
Average	7.2/21.3	3.1/7.2	1.3/3.0				1.4/3.0**

Sesarma cinereum

	Zone A	B	C	D	Mixed	Upper border	Average
March							
April						0.2/4.9	0.1/1.1
May					0.9/6.9		0.2/1.3
July					2.7/6.6		0.5/1.1
August						0.8/6.9	0.1/0.2
Average					0.9/3.4	0.2/2.3	0.2/0.9**

*Biomass in grams dry wt/m^2, density in number/m^2.
**Average biomass/density of study period.

Three species of fiddler crab (genus *Uca*) occur within Virginia's salt marshes. On the Southern Branch of the Elizabeth River *Uca minax* was the dominant crab present, occurring throughout the marsh (see table 5). Over the study period biomass ranged from an average of 2.7 grams dry wt/m^2 in March to 26.3 grams dry wt/m^2 in August, averaging 10.0 grams dry wt/m^2 overall. The population varied from a low of 12.3/m^2 as sampled in April to a high of 34.9/m^2 in August. The average number was 22.4/m^2. In general, concentrations increased with elevation although there were some evidence of seasonal migration within the *Uca minax* population. In March the greatest numbers were found in the low marsh zone A (91.1/m^2). No further crabs were taken in this zone until August. In May a dense population was noted in ther higher elevations of zone D in the low marsh with values of 78.4/m^2 and a biomass of 33.5 grams dry wt/m^2. In August, the *Uca minax* population was largest within the mixed and upper border zones with densities of 54.9/m^2 and 68.6/m^2 respectively.

Uca pugnax occurred only in the low marsh. Its greatest concentrations were in zone A of the low marsh (see table 5) where it averaged 1.6 grams dry wt/m^2 and 6.1/m^2.

Two species of crab of the genus *Sesarma* occur on this coast (Gosner 1971). Both were commonly collected on this marsh (see table 6). At the collection site *Sesarma reticulatum* was found only in zones A through C of the low marsh nearest to the marsh's edge. Greatest abundance occurred in zone A with an average density of $21.3/m^2$ and biomass of 7.2 grams dry wt/m^2. Generally, with higher elevation, these values decreased. Sesarma cinereum was most abundant in the high marsh (mixed zone and lower edge of upper border). Greatest concentrations and biomass occurred within the mixed zone (0.9 grams dry wt/m^2, $3.4/m^2$) while overall the average biomass was only 0.2 grams dry wt/m^2 and density only $0.9/m^2$.

Both M. bidentatus and L. irrorata were present during this study (see table 7). Melampus bidentatus was common within the mixed zone associating with Distichlis spicata, Spartina patens and J. roemerianus. The density of snails in this zone averaged $36.7/m^2$ while the biomass averaged 1.7 grams dry wt/m^2. The biomass and density averaged 0.5 grams dry wt/m^2 and $8.0/m^2$. Littorina irrorata was present only within the S. alterniflora zone and these in very low number. It was first observed on the marsh in April and was first sampled in May. The overall mean biomass and density of the marsh periwinkle was 0.4 grams dry wt/m^2 and $0.3/m^2$.

The ribbed mussel, Modiolus demissus, was the most abundant animal found on the study site, averaging through the study period a density of $62.5/m^2$ and a biomass of 73.9 grams dry wt/m^2, including shell (see table 8). Greatest numbers were found in the marsh edge habitat, zones A and B, with densities averaging $234.8/m^2$ and $181.2/m^2$.

Table 7

DISTRIBUTION OF BIOMASS PER DENSITY OF THE DOMINANT MARSH FAUNA*

Melampus bidentatus

	Low Marsh				High Marsh		
	Zone A	B	C	D	Mixed	Upper border	Average
March			0.1/2.8		0.1/29.0	0.1/9.0	0.1/6.0
April			0.1/8.3	0.5/2.5	0.2/15.0	0.1/2.6	0.1/3.6
May			1.4/7.5		4.5/37.5		1.2/9.0
July			1.3/8.3		1.8/75.0	0.3/11.3	0.7/15.8
August		0.5/7.0		2.4/16.5	0.4/3.0	0.2/3.1	0.5/4.5
Average		0.1/1.1	0.6/5.1	0.6/5.1	1.7/36.7	0.1/5.7	0.5/8.0**

Littorina irrorata

	Zone A	B	C	D	Mixed	Upper border	Average
March							
April							
May		4.2/37.5					1.1/0.6
July		3.5/3.0					0.6/1.1
August			2.7/2.3				0.7/0.6
Average		1.6/1.1	0.6/0.5				0.4/0.3**

*Biomass in grams dry wt/m^2, density in number/m^2.
**Average biomass/density of study period.

Table 8

DISTRIBUTION OF BIOMASS PER DENSITY OF THE DOMINANT MARSH FAUNA*

<u>Modiolus demissus</u>

	Low Marsh				High Marsh		
	Zone A	B	C	D	Mixed	Upper border	Average
March	28.0/87.8	528.2/418.5	23.6/36.2	3.3/6.6			122.8/105.
April	504.6/731.2	35.1/24.1	19.5/36.2				39.8/53.
May	108.1/131.6	136.5/119.6					48.7/47.
July	213.9/219.4	178.3/171.1	109.2/41.1				69.1/51.
August	53/8/54.9	153.0/117.4	230.4/69.7	2.2/3.0			87.2/51.
Average	166.5/243.8	220.3/181.2	85.3/55.5	1.2/3.0			75.9/62.

<u>Polymesoda caroliniana</u>

	Zone A	B	C	D	Mixed	Upper border	Average
March			53.6/12.1	74.0/13.7			21.4/4.4
April		19.8/6.0					4.1/1.2
May				83.9/11.0	6.0/6.9		11.0/2.6
July		24.1/23.7	50.0/13.7	32.9/8.8			18.3/5.6
August			8.0/5.0	25.8/18.1	14.8/11.0		5.4/5.1
Average		6.0/2.4	22.2/6.7	33.8/9.1	3.8/3.4		12.1/3.8

*Biomass in grams dry wt/m^2, density in number/m^2.
**Average biomass/density of study period.

Another bivalve occurring in the marshes on the Southern Branch was Polymesoda caroliniana, which occurs from Chesapeake Bay southward (Gosner 1971). In the study area, the greatest numbers were found in zone D of the low marsh area, averaging $9.1/m^2$ (see table 8). Here also the greatest biomass, 33.8 grams dry wt/m^2, was found. This clam was present throughout the study period in areas of low-lying water or on soft mud exposed at low tide.

RIVER SAMPLING

The river communities were far more complex than those of the marsh. Table 9 lists 63 species collected within the Southern Branch of the Elizabeth River during the study period, 34 from the invertebrate community. Callinectes sapidus was the most prominent member of this community, not solely for its size but also for its numbers. It was present in the river throughout the sampling period in both the channel and in the shallow, nearshore habitat.

The channel was dominated by several invertebrate species. The amemone, Diadumene leucolena, and the hydroid, Calyptospadix cerulea, were both common in the debris brought up in the trawl, as were the mussels, Musculus niger and Modiolus modiolus. The former was by far the more abundant, attached in clusters to logs and other debris. The amphipods, Gammarus sp. and Corophium laclustre, were associated with the hydroid, C. cerula, logs, and fine root

Table 9

PROMINENT INVERTEBRATES AND FISHES CAPTURED AT THE STUDY STATION ON THE SOUTHERN BRANCH OF THE ELIZABETH, JANUARY-AUGUST

Species	Abundance	Characteristic habitat
A. Invertebrates		
Coelenterata		
Calyptospadix cerulea	C	Channel, May-August
Diadumene leucolena	A	Attached to debris in channel
Chrysaora quinquecirrha	-	Observed in river in July
Ctenophora		
Mnemiopsis leidyi	A	River, late May-June
Mollusca		
Hydrobia sp.*		
Modiolus modiolus	C	Small, attached to debris in channel
Musculus niger	A	Associated with *M. modiolus* on debris
Crassostrea virginica	R	Spat found only, July-August
Tagelus plebeius	R	Burrowing in near shore sand flat
Tellina versicolor	A	Burrowing in near shore sediment, also common in stomach contents
Annelida		
Capitella capitata	A	Most common of polycheates, present throughout river and study period
Neris succinea	A	Near shore sediments, present on marsh
Neris virens	A	Channel sediments
Etone sp.*	R	January-March
Scaloplos sp.*	R	
Arthropoda		
Balanus eburness	C	Attached to debris in channel

*Known from stomach contents only.

Table 9 (con't)

Species	Abundance	Characteristic habitat
Arthropoda (con't)		
Balanus improvisus	C	Shoreline, attached to stakes and pilings
Cyathura polita	A	Present in near shore sediments, common in stomach contents
*Edotea montosa**	-	Present throughout study period
Corophium laclustre	A	Near shore sediments, common in stomach contents June-August
*Gamarus murcronatus**	-	February-May
Gammarus sp.	-	April-August
Melita nitida	A	Near shore, late May-August
Leptocherius plumulosus	R	Near shore sediments, stomach contents in July
*Monocludes edwardsi**	-	February-July
*Neomysis americana**	-	
Crangon septemspinosa	A	River channel throughout study period
Palaemonetes pugio	A	River January-March; near shore throughout study period
Palaemonetes pugio	R	Near shore on one occasion
Callinectes sapidus	A	Abundant throughout study period
Neopanope texana sayi	R	River channel
Panopeus herbstii	C	River channel, May-August
Rhithropanopeus harrisii	A	Near shore and channel of river, associating with debris in channel
Penaeus durarum	C	River channel
B. Fishes		
Menidia beryllina	A	Shoreline
Fundulus heteroclitus	A	Shoreline, marsh pools and pond

Table 9 (con't)

Species	Abundance	Characteristic habitat
Fishes (con't)		
F. majalis	A	Shoreline, marsh pools and ponds
Anchoa mitchilli	A	River channel, January-March; common inshore throughout study period
Leiostomus xanthurus	A	River, abundant throughout study period
Trinectes maculatus	A	River channel, abundant throughout study period
Anguilla rostrata	C	Throughout river
Opsanus tau	C	Channel, more common in summer June-August
Cyprinodon variegatus	C	Abundant in marsh pools late May, taken in low numbers near shore May-July
Paralichthys dentatus	R	River channel
Alosa mediocris	R	River channel
Alosa sapidissima	R	River channel, most common January-February
Brevoortia tyrannus	R	River channel
Opisthonema oglinum	R	River channel
Symphurus plagiusa	R	River channel
Lucania parva	R	Shoreline and low tide pools
Gobiosoma bosci	R	Shoreline
Mugil cephalus	R	River channel
Morone saxatilus	R	River, common in river December-February
Perca flavescens	R	River channel
Gambusia affinis	R	Shoreline
Bairdiella chrysura	R	River channel
Urophycis reguis	R	River channel
Cynoscion regalis	R	River channel
Sciaenops oscellata	R	River
Prionotus carolinus	R	River channel

Table 9 (contt)

Species	Abundance	Characteristic habitat
C. Higher carnivores		
Larus atricilla	A	Abundant especially May-August
Larus argentatus	A	Abundant especially January-March.

masses which had apparently originiated in adjacent marshes. The polychaete, Neris virens, also occurred in the channel. The sand shrimp, Crangon septemspinosa, was present in the river throught the study period, while Penaeus duorarum, the pink shrimp, was taken in low numbers from March through August. In addition to the blue crab, other crabs included the common mud crab, Rhithropanopeus harrisii, and two other xanthid crabs, Panopeus herbstii and Neopanope texana sayi.

The nearshore community differed in several dominant organisms. Palaemonetes pugio was present in large numbers adjacent to the marsh. The amphipod Melita nitida was very abundant May through August with Corophium laclustre. The isopod Cyathura polita was found in both the marsh's forward edge and the nearshore community. The annelids Neris succinea and Capitella capitata were common in the shallow water sediments, as was the frail, white bivalve, Tellina versicolor. Capitella capitata was the most abundant annelid from both collections and stomach analyses.

The nearshore shallow water community was dominated by the mummichog, Fundulus heteroclitus, and the striped killifish, F. majalis, The striped killifish characteristically was found in deeper waters than F. heteroclitus. Occurring nearshore were the bay anchovy, Anchoa mitchilli, and the tidewater silverside, Menidia beryllina. Anchoa mitchilli was most common nearshore from June through August, while in January through March large numbers of this fish were caught in deeper waters. The bay anchovy accounted for 24.2% of the fishes taken at stations in the Southern Branch. The sheepshead minnow, Cyprinodon variegatus, the rainwater killifish, Lucania parva, the spottail goby, Gobiosoma bosci, and the mosquitofish, Gambusis affinis, were also collected nearshore.

The croaker, Micropogon undulatus, and the spot, Leiostomus xanthurus, present in the river as both juveniles and sub-adults, dominated the channel trawls. The hogchoker, Trinectes maculatus, best characterized this community as being abundant all through the study period. The toadfish was taken in greatest numbers during the summer months. Other species were taken only occasionally (see table 9).

Feeding Habits of Major River Fauna

Eight species of fish represented 96.5% of the 2,863 fish collected during the study. These were the hogchoker, Trinectes maculatus; the toadfish, Opsanus tau; the mummichog, Fundulus heteroclitus; the striped killifish, Fundulus majalis; the atlantic croaker, Micropogon undulatus; the spot, Leiostomus xanthurus; the bay anchovy, Anchoa mitchilli; and the tidewater silverside, Menidia beryllina. The first six of these were chosen for a detailed food analysis. In addition, the buccal cavity of the blue crab, Callinectes sapidus, was investigated. Feeding habits of Anchoa mitchilli and Menidia beryllina will be briefly covered from the literature.

Whenever possible the identification of a food item was to the specific level. The importance of food items in the diet was expressed in terms of the percent of occurrence and an estimated percent of the total volume per species.

Trinectes maculatus - the Hogchoker

Hildebrand and Schroeder (1928) examined the stomachs of 17 hogchokers from Chesapeake Bay and concluded that this fish fed primarily upon annelids and occasionally on small crustaceans and algae. Darnell (1958) in examining 3 hogchokers collected in Lake Pontchartrain, found that about 50% of their diet consisted of amphipods of the genus, *Corophium*. In Virginia on the York and Pamunkey Rivers, polychaete worms were found to be the single most important food source for *Trinectes maculatus*. Amphipods constituted the second most important source, while the isopod *Cyathura* polita formed the third (Van Engel and Joseph 1968).

At stations in the Southern Branch of the Elizabeth River, the hogchoker, ranging in size from 41 mm to 116 mm, constituted 16.2% of the fish taken during the study period. A total of 74.4% of the stomach contents consisted of annelids. Cyathura polita was a prominent food item (16.5%) and was most common in small hogchokers of less than 72 mm. Amphipods were present in only 2.4% of the fish examined and represented 0.2% of the hogchoker's diet (see table 10.)

Table 10

STOMACH CONTENTS OF THE HOGCHOKER, *TRINECTES MACULATUS*, FROM STATIONS IN THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Food item	Per cent occurrence	Per cent total volume
Amphipoda	2.4	0.2
Isopoda *Cyathura polita*	26.3	16.5
Annelida *Neris* sp. *Capitella capitata*	90.2	74.4
Plant material	14.6	2.0
Unidentified	34.1	6.7
Sand	4.9	0.5

68 fish analysed, 27 empty. Length 41 mm - 116 mm, average 83 mm.

Opsanus tau - the Toadfish

Hildebrand and Schroeder (1928) found that small crabs and other crustaceans were the primary food of the toadfish while smaller fish ate amphipods and isopods. Twenty-nine Opsanus tau were examined from the Southern Branch. They ranged in size from 59 to 224 mm, with the average being 121 mm. Decapod crustaceans, including Palaemonetes pugio, Rhithropanopeus harrisii, Crangon septemspinosa and Callinectes sapidus, made up 37.6% of the toadfish's diet. Fish remains, including Fundulus sp., contributed another 12.0% (see table 11).

Fundulus heteroclitus - the Mummichog

Mummichog's from the Chesapeake Bay were found to have a varied diet including small crustaceans, small mollusks, annelid worms, insects, small fish and a variety of plant material (Hildebrand and Schroeder 1928). The stomachs of 35 Fundulus heteroclitus were examined during the study period with nine being found empty. The fishes ranged in size from 40 to 79 mm, the average being 62 mm. This species represented 10.0% of those taken on the Southern Branch. The diet of the mummichog, located on or near the marsh, was dominated by plant material (27.1%) and amphipods (22.6%). The amphipod, Corophium laclustre, dominated the latter. Insects contributed 18.6% of the diet while annelids accounted for an additional 9.3% (see table 12).

Table 11

STOMACH CONTENTS OF THE TOADFISH, *OPSANUS TAU*, FROM STATIONS IN THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Food item	Per cent occurrence	Per cent total volume
Amphipoda *Corophium laclustre* *Gammarus* sp.	56.0	33.4
Decapoda *Palaemonetes pugio* *Rhithropanopeus harrisii* *Crangon septemspinosa* *Callinectes sapidus*	40.0	37.6
Mollusca *Modiolus modiolus* *Musculus niger*	24.0	6.2
Annelida	26.0	4.9
Gastropoda	4.0	0.2
Fish *Fundulus* sp.	12.0	12.0
Unidentified	16.0	5.7

29 fish analysed, 5 empty. Length 59 mm - 224 mm, average 121 mm.

Table 12

STOMACH CONTENTS OF THE MUMMICHOG, *FUNDULUS HETEROCLITUS*, FROM STATIONS IN THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Food item	Per cent occurrence	Per cent total volume
Cumaceans	3.8	0.1
Isopoda *Cyathura polita*	7.7	0.1
Amphipoda *Corophium laclustre* *Gammarus* sp.	53.8	22.6
Annelida *Neris* sp. *C. capitata*	34.6	9.3
Mollusca *Tellina* sp.	3.8	1.2
Insecta	23.1	18.7
Plant material	61.5	27.1
Unidentified	53.8	20.8
Sand	11.5	0.2

35 fish analysed, 9 empty. Length 40 mm - 79 mm, average 62 mm.

Fundulus majalis - the Striped Killifish

Hildebrand and Schroeder (1928) found that the diet of the striped killifish consisted of small mollusks, crustaceans, fish insects as well as insect larvae.

Fundulus majalis occupies a position in somewhat deeper waters than F. heteroclitus. The stomachs of 25 striped killifish were examined with three stomachs found empty. These fish ranged in size from 27 mm to 89 mm, averaging 70 mm and constituted 3.5% of the fish captured in the Southern Branch of the Elizabeth. Occurring in 77.5% of the stomachs containing food items, amphipods were found to represent 44.5% of the diet of the fish. Gammarus sp. dominated this amphipod material. In addition, 11.5% of the diet consisted of annelids, 6.8% insects and 5.2% mollusks (Tellina sp.). (See table 13).

Micropogon undulatus - the Atlantic Croaker

Darnell (1958) found smaller croaker feeding primarily on small crustaceans while the larger fish preferred mollusks, larger crabs, shrimp and fish. Annelids played a small role in the diet of the atlantic croaker from Lake Pontchartrain. Amphipods, Neomysis americana and copepods constituted 86.0% of the fish's diet in the York and Paumunkey Rivers (Van Engel and Joseph 1968).

Croakers collected on the Southern Branch ranged in size from 32 to 136 mm and averaged 107 mm. Annelids accounted

Table 13

STOMACH CONTENTS OF THE STRIPED KILLIFISH, *FUNDULUS MAJALIS*, FROM STATIONS IN THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Food item	Per cent occurrence	Per cent total volume
Copepoda	4.5	[illegible]
Amphipoda *Corophium* sp. *Gammarus* sp.	77.3	[illegible]
Isopoda *Cyathura polita*	22.7	4.0
Annelida *Neris* sp. *C. capitata*	40.9	11.5
Mollusca *Tellina* sp.	27.3	[illegible]
Gastropoda *Hydrobia* sp.	18.2	[illegible]
Insecta	9.1	6.8
Plant material	36.4	1.4
Unidentified	45.6	[illegible]
Sand	36.4	[illegible]

25 fish analysed, 3 empty. Length 27 mm - 89 mm, average 70 mm.

for 57.0% of their diet and crustaceans, including copepods, cumaceans, isopods, and amphipods, constituted 10.7%. Gammarus murcronatus and Cyathura polita were most common. Fish play a minor role in the diet of M. undulatus as 4.1% of analysed material consisted of fish remains, including Anchoa mitchilli. Plant material accounted for another 3.9% of the food intake (see table 14).

Leiostomus xanthurus - the Spot

Darnell (1958) found that small spot depended heavily on copepods, mysid shrimp, isopods and amphipods. With an increase in size L. xanthurus shifts to a diet of bottom burrowers. Detritus also formed a substantial portion of this fish's diet. Van Engel and Joseph (1968) examined 162 spot from the York-Pawmunkey River area of Virginia. Copepods were present in 93% of the stomachs analysed but constituted only 8% of their diet. Amphipods and polychaete worms contributed 44% of the diet, while small pelecypods accounted for 18.4%.

Spot collected from the Southern Branch ranged in size from 74 to 154 mm, averaging 104 mm. Annelids, including most prominently Capitella capitata, accounted for 38.6% of this fish's diet, while small crustaceans, amphipods and isopods constituted 6.3%. Copepods occurred in 70.7% of the fish sampled while accounting for 13.4% of the spot's diet (see table 15).

Table 14

STOMACH CONTENTS OF THE ATLANTIC CROAKER, MICROPOGON UNDULATUS FROM STATIONS IN THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Food item	Per cent occurrence	Per cent total volume
Copepoda	35.6	4.8
Cumacens	4.7	0.3
Mysidacea	4.7	0.8
Neomysis americana		
Isopoda	23.4	2.4
Edotea montosa		
Cyathura polita		
Amphipoda	23.4	3.2
Gammarus murcronatus		
Gammarus sp.		
Corophium sp.		
Annelida	95.3	57.6
Capitella capitata		
Neris sp.		
Etone sp.		
Decapoda	6.3	1.8
Palaemonetes pugio		
Crangon septemspinosa		
Mollusca	6.3	1.5
Tellina sp.		
Modiolus sp.		
Fish	7.8	4.1
M. beryllina		
Anchoa mitchilli		
Plant material	34.4	3.9
Unidentified	64.0	19.8
Sand	17.2	0.5

68 fish analysed, 4 empty. Length 32 mm - 136 mm, average 107 mm.

Table 15

STOMACH CONTENTS OF THE SPOT, LEIOSTOMUS XANTHURUS FROM STATIONS IN THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Food item	Per cent occurrence	Per cent total volume
Copepoda	70.7	13.4
Cumaceans	17.1	0.2
Isopoda *Edotea montosa* *Cyathura polita*	24.4	2.4
Amphipoda *Monocludes edwardsi* *Corophium* sp. *Leptocherius plumlosus* *Gammarus* sp. *Gammarus murcronatus*	39.0	3.9
Annelida *C. capitata* *Neris* sp. *Etone* sp.	75.6	38.6
Decapoda	2.4	0.1
Mollusca *Tellina* sp.	14.6	0.9
Fish *A. mitchilli* scales eggs	14.6	2.2
Plant material	56.1	3.3
Unidentified	80.5	33.9
Sand	39.0	1.0

43 fish analysed, 2 empty. Length 74 mm - 154 mm, average 104 mm.

Anchoa mitchilli - the Bay Anchovy and Menidia beryllina - the Tidewater Silverside

Anchoa mitchilli and Menidia beryllina are both resident fish within the Elizabeth River, and were present during the entire study. They represented 24.2% and 9.2% respectively, of the fishes taken.

Darnell (1958) examined 92 Anchoa mitchilli and found that copepods and mysid shrimp were the most important food items, while in larger specimens, larval fishes constituted a larger portion of the diet. Detritus as a food item was present in all size ranges. Van Engel and Joseph (1968) state that the Bay Anchovy is strictly a pelagic feeder. They found that copepods occurred in A. mitchilli and constituted 98% of the total food. Larger crustaceans, amphipods, mysids and isopods were also present but only as smaller forms. Day et al. (1972) found in the bay anchovies of Barataria Bay, Louisiana, that crab megalops and zooplankton were most important.

Day et al. (1972) noted that Menidia beryllina fed primarily on zooplankton, insect larvae and fish remains. Darnell (1958) found that tidewater silversides fed primarily on amphipods, isopods and insect pupae. In Chesapeake Bay, Hildebrand and Schroeder (1928) reported the principal foods to be small crustaceans and mollusks, insects, and worms along with some algae. Odum (1971) reported that Menidia beryllina fed predominantly at night and that day and night feeding differed. During the day terrestial insects, copepods and chironomid larvae dominated the diet while at night mysid shrimp dominated.

Callinectes sapidus - the Blue Crab

Darnell (1958), examining blue crabs from Lake Pontchartrain, Louisiana, indicated that mollusks accounted for 63.4% of the diet of large crabs, with 10.4% including crabs or crustacean material. Detritus accounted for about 11% of their diet. Smaller crabs depended more heavily on crustaceans than older crabs, eating more mollusks as they matured. Tagatz (1968) examined 668 crabs from St. John's River, Florida. They showed a similar diet, with mollusks accounting for 39.0%, 19.4% for fish and 15.9% crustacean. *Rhithropanopeus harrisii* was a preferred crustacean. Odum (1971) noted that *Callinectes sapidus* ate food items in the following order of preference: Mollusks, crustaceans, fish, sand, and a small amount of plant detritus.

The dominant invertebrate at the Elizabeth River stations throughout the study period was *Callinectes sapidus*. The buccal cavity contents of ten blue crabs were analyzed that ranged in size from 50 to 151 mm, with an average of 106 mm. These blue crabs primarily ate mollusks (46.6%), while 25.2% of their diet consisted of crustaceans, including *Rhithropanopeus harrisii*, *Uca minax* and *C. sapidus* (see table 16).

Table 16

BUCCAL CAVITY CONTENTS OF THE BLUE CRAB, CALLINECTES SAPIDUS, FROM STATION IN THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Food item	Per cent occurrence	Per cent total volume
Mollusca	100.0	42.6
M. Modiolus		
M. niger		
Annelida	11.1	2.3
Neris sp.		
Arthropoda	77.8	25.2
Rhithropanopeus harrisii		
Cyathura polita		
Corophium sp,		
Callinectes sapidus		
Uca minax		
Hydroid	33.3	0.1
Unidentified	88.9	29.5
Sand	33.3	0.3

10 crabs were analysed, 1 buccal cavity empty
Size ranged from 50 mm to 151 mm, average analysed were 106 mm in carpace width.

DISCUSSION and CONCLUSIONS

The salt marsh as an ecosystem is strongly influenced by physical and chemical parameters, of which the most important are the tides and their accompanying salinities. Salinity tolerances limit the species which may occur on the marsh, while the frequency of tidal inundation influences the distribution of these species within the marsh. The result is a horizontal stratification or zonation of communities containing relatively few, yet characteristic plants and animals.

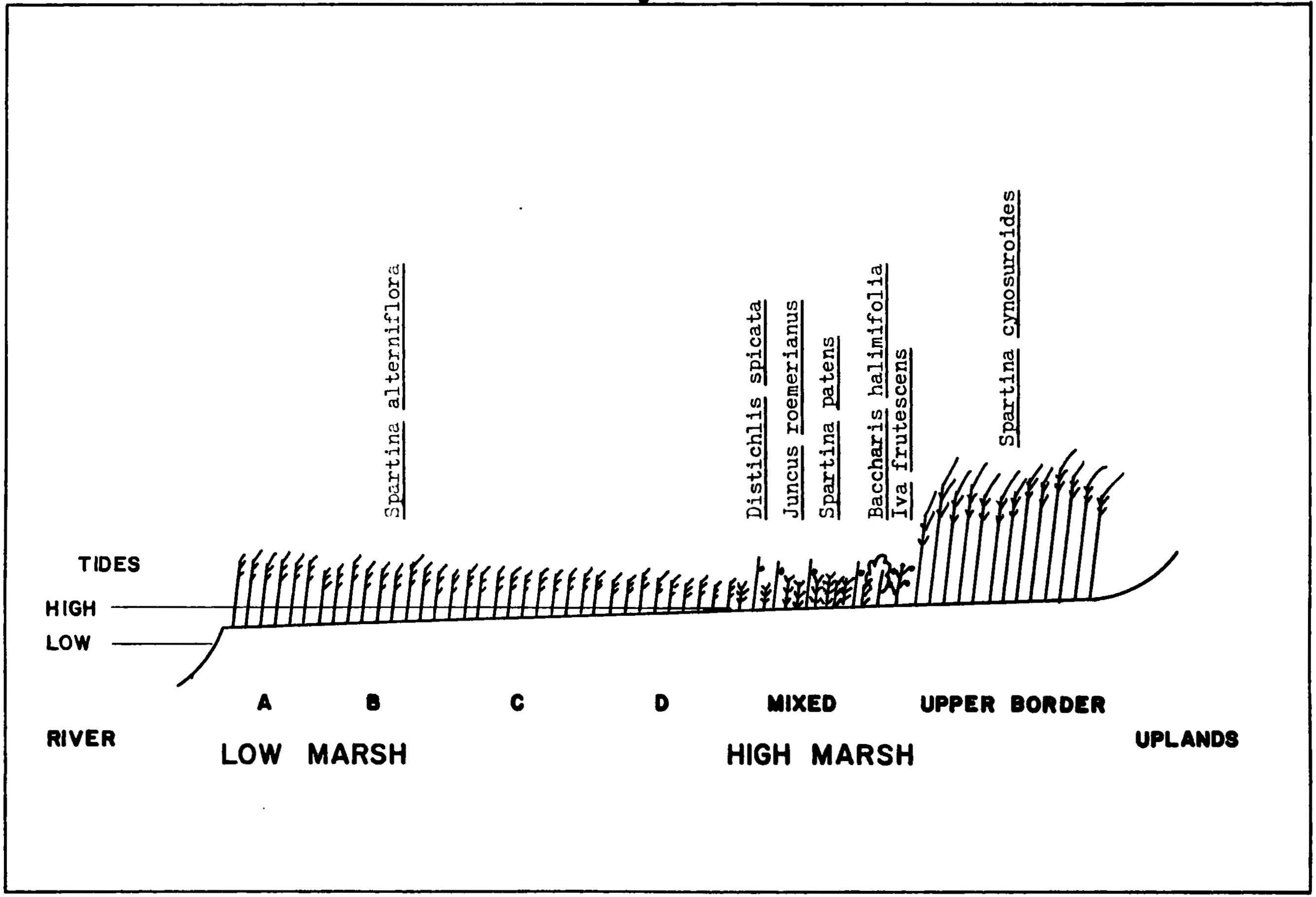
Present within this marsh on the Southern Branch of the Elizabeth River were four distinct floral communities (see Fig. 3). Spartina alterniflora dominated the intertidal low marsh and was associated with the saltmarsh bulrush, Scripus robustus. Distichlis spicata was found next in the landward progression in association with Spartina patens and the needlerush, Juncus roemerianus. The marsh elder, Iva frutescens, and the groundsel tree, Baccharis halimifolia, comprised a narrow, but prominent bush community, which was then followed by the luxuriant Spartina cynosuroides, or giant cordgrass community, forming the marsh's upper border.

The cordgrass communities of Spartina alterniflora and Spartina cynosuroides dominated this marsh; smooth cordgrass

Figure 3

COMMUNITY STRUCTURE OF THE DOMINANT MARSH FLORA OF THE STUDY SITE ON THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Fig. 3



Spartina alterniflora
Distichlis spicata
Juncus roemerianus
Spartina patens
Baccharis halimifolia
Iva frutescens
Spartina cynosuroides
TIDES
HIGH
LOW
A
B
C
D
MIXED
UPPER BORDER
RIVER
LOW MARSH
HIGH MARSH
UPLANDS

dominating the low marsh, intertidal zone, and giant cordgrass dominating the high marsh, upper border zone. In general this was true of the marshes present on the Southern Branch of the Elizabeth River.

Within this smooth cordgrass community three forms of S. alterniflora were present, although the tall form was often missing. Its absence at the study site appears to be the result of considerable shoreline erosion. Kerwin and Pedigo (1971) observed a similarly eroded marsh edge and attributed this state to wave action. They also mention the theories of Marmer (1948; 1951) who felt that an increase in sea level accounted for such erosion. The erosion present on the Southern Branch appears also to be most directly the result of wave action. The channel has been cut to within 30 meters of some marshes and along these shores erosion was most severe.

The presence of the saltmarsh bulrush, Scripus robustus, within the S. alterniflora community has been noted for the marshes of the Poropotank River. Kerwin (1966) describes this community, S. alterniflora - S. robustus, as the dominant classification in his brackish marsh type and as being present within his altwater marsh classification, occupying a similar position. In the latter, the presence of S. robustus was not significant to the community's structure as was the case found on this marsh on the Southern Branch of the Elizabeth.

Spartina alterniflora has been credited with two crops annually in Georgia marshes (Odum 1961; Schelske and Odum 1961). During this study one crop overlapped two growing seasons. Thus, two crops were present on the marsh each year. In July a late summer or fall crop of S. alterniflora began development. Due to the shortness of the remaining growing season and possibly in part as a result of shading by taller smooth cordgrass already present, this crop failed to develop higher than a low-lying carpet (50.1 grams dry wt/m^2 in March). It was this July crop of S. alterniflora which wintered over on the marsh forming the spring or early summer crop that then dominated the marsh throughout the following growing season. Again, in the following July the process was repeated.

Spartina cynosuroides occurs in most brackish marshes (salinities less than 15°/oo, optimum 5-10°/oo) and is known to dominate the lower marshes of the Pamunkey and Mattaponi Rivers (Wass and Wright 1969). Kerwin (1966) considered giant cordgrass to be an indicator species and a co-dominant with S. alterniflora for his brackish water marsh type. On the Southern Branch of the Elizabeth River it often occurred quite densely along small tidal creeks and was occasionally prominent within the smooth cordgrass community. The reedgrass, Phragmites communis, occasionally occupied a similar position within these marshes, however, it was most common along Deep Creek. These two species were not observed mixed although separate stands could be found adjacent to each other.

The two intermediate communities of D. spicata - S. patens - J. roemerianus and I. frutescens - B. halimifolia represented only one-twelth or less of the total marsh area. In general, this was true of all marshes present on the river. Often the S. alterniflora community merged directly with the giant cordgrass or even reached to the wood's edge. Zonation is dependent upon the topography of a particular marsh and the local vertical range in tides which then influence the degree of tidal inundation, and thus the relative ratios of the various floral communities present. For example, Four Point Marsh, a marsh quite similar to those found on the Southern Branch, was dominated by Distichlis spicata (Kerwin and Pedigo 1971).

The presence of J. roemerianus within the D. spicata - S. patens community was contrary to patterns of zonation as observed by Kerwin (1966) and Kerwin and Pedigo (1971) in Virginia marshes. In these studies J. roemerianus occupies a zone adjacent to and on slightly higher ground than the D. spicata - S. patens zone.

The method employed in this study to measure net production is essentially a peak standing crop method. There are several criticisms to this approach. Wiegert and Evans (1964) stress two. First, it does not account for the mortality of green plants before the peak standing crop is attained. This growth not measured by individual standing crop estimates. Also, growth which may occur after the peak during the decline of standing crop is not measured. Second, this method does not account for the differences in the time at which varying species reach their peak standing crops. As a result standing crop estimates of net production should be considered low.

Net production within these communities by the dominant marsh grasses, S. alterniflora, S. cynosuroides and D. spicata, totaled 1267.9 grams dry wt/m^2 averaged over the marsh as a whole. The relative contribution to this total by each dominant was as follows: S. alterniflora, 836.4 grams dry wt/m^2; S. cynosuroides, 410.1 grams dry wt/m^2; and D. spicata, 21.4 grams dry wt/m^2. These figures re-emphasize the dominance of the cordgrasses.

Generally, the assumption is made that net production of marsh grasses decreases northward along the Atlantic coast with the length of the growing season. There is evidence that production within Virginia's smooth cord-grass marshes is higher than this generalization would imply (Wass and Wright 1969). Kirby (1971) estimated annual net production of Spartina alterniflora in a Louisiana marsh as 2800 grams dry wt/m^2 for streamside and 1950 grams dry wt/m^2 inland (Smalley 1959). In Georgia production estimates ranged from 2000 grams dry wt/m^2 (Odum and Schelske 1961) to 973 grams dry wt/m^2(Smalley 1959). In North Carolina net production of this cordgrass was fixed at 650 grams dry wt/m^2 (Williams and Murdock 1969) while a value of 443 grams dry wt/m^2 was reported by Morgan (1961) in Delaware. Within this general scheme, the smooth cordgrass community in Virginia would be expected to produce approximately 500 grams dry wt/m^2 or 2.3 tons/acre (Wass and Wright 1969), less than North Carolina yet higher than Delaware. Contrary to this, Wass and Wright (1969) report a net production of 1140 grams dry wt/m^2 (5.1 tons/acre) compiled from standing crop estimates taken at large within Virginia's marshes. In the present study the net production of Spartina alterniflora totaled 1218.6 grams dry wt/m^2 or 5.47 tons/acre.

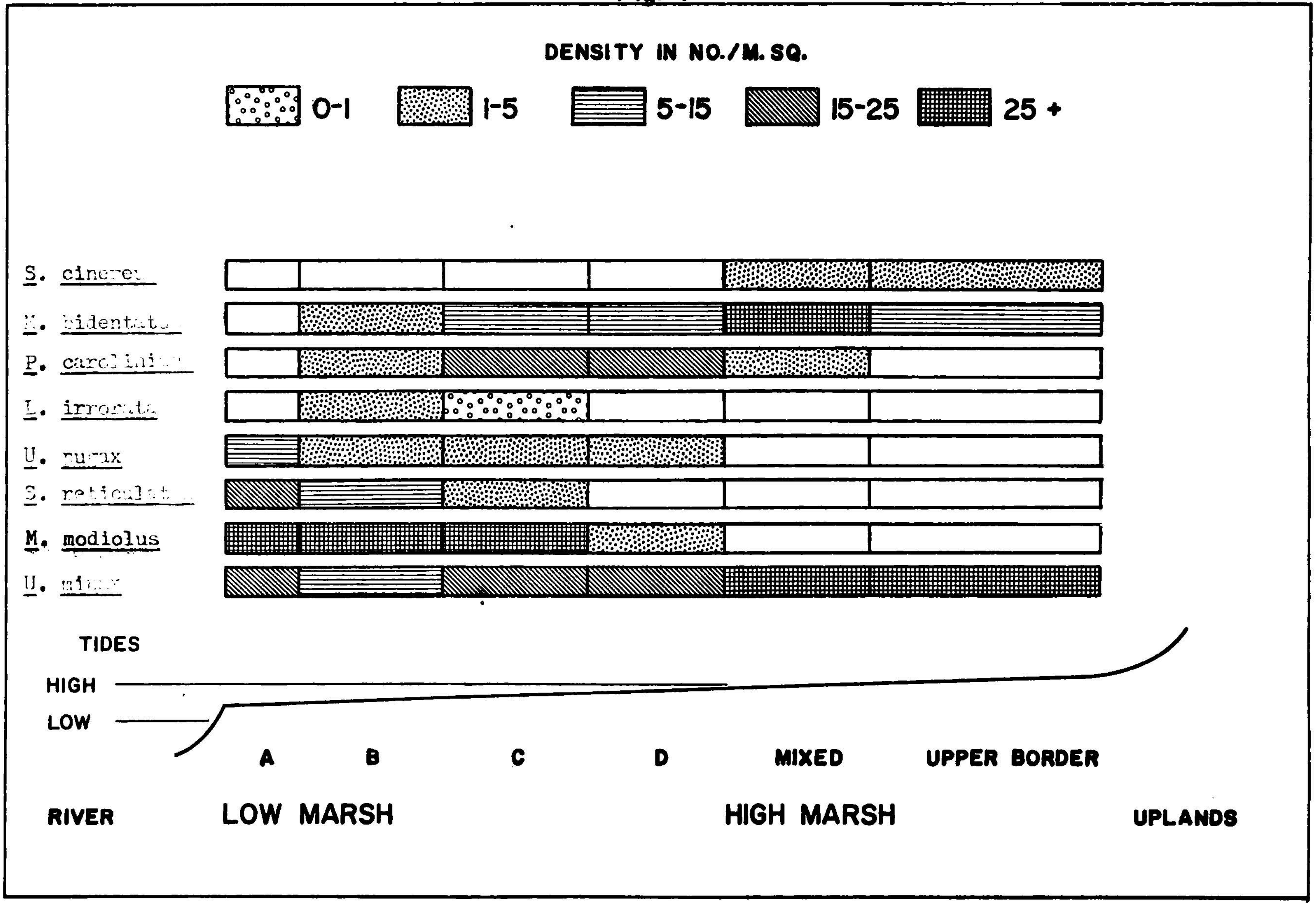
Giant cordgrass, Spartina cynosuroides, is also a high yield producer. Wass and Wright (1969) estimated the net production of this species at 1454.1 grams dry wt/m^2 or 6.5 tons/acre. At the Southern Branch site, net production was estimated at 1681.3 grams dry wt/m^2 or 7.47 tons/acre.

Within these floral communities, distinct animal associations were present (see Fig. 4). Uca minax, the red-jointed fiddler, occurred throughout both the low and high marsh, dominating all but the marsh edge of the low marsh community. The marsh edge was dominated by Modiolus demissus, the ribbed mussel; Sesarma reticulatum, the square-backed crab; and the fiddler crab, Uca pugnax. Littorina irrorata generally occurred in low numbers throughout this intertidal low marsh while Polymesoda caroliniana was present at higher eleveations. In addition to Uca minax, the high marsh communities were dominated by Sesarma cinereum, the wood crab, and Melampus bidentatus, the salt marsh snail. The latter was also present sparsely within the low marsh.

Figure 4

COMMUNITY STRUCTURE OF THE DOMINANT MARSH FAUNA OF THE STUDY SITE ON THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Fig. 4


DENSITY IN NO./M. SQ.
0-1
1-5
5-15
15-25
25 +
M. modiolus
TIDES
HIGH
LOW
A
B
C
D
MIXED
UPPER BORDER
RIVER
LOW MARSH
HIGH MARSH
UPLANDS

Uca minax dominated this marsh and is generally thought to be typical of brackish marshes in Virginia (Wass and Wright 1969). Kerwin (1971), in his study of the Poropotank River, found this fiddler crab in both his brackish water marsh type (salinity, 4.11-9.39°/oo) and salt water marsh type (salinity, 9.38-14.72°/oo) and occurring with S. alterniflora, Scripus robustus, D. spicata, S. patens and S. cynosuroides more than 20% of the time. Gray (1942) noted typical Uca minax colonies associated with S. cynosuroides and Paspalum sp. near Solomons Island, Maryland. Teal (1958) in higher salinity marshes of Sapelo Island, Georgia, found U. minax only within the short Spartina high marsh zone. In this marsh Teal found several factors to be important in governing the distribution of Uca minax, primarily, substratum, salinity and competition by other species. U. minax preferred muddy substrate, yet within these Georgia marshes it had been limited by competition with U. pugnax and U. pugilator to high sandy areas of the marsh where, due to frequent land runoff, lower salinities occurred and only Uca minax could survive.

In this study the distribution of the red-jointed fiddler seemed largely due to its preference for low salinities and to competition with other species. The salinity ranged from 7.3°/oo to 17.1°/oo throughout the study period while a mean density of $22.4/m^2$ was maintained overall. Kerwin (1971) had observed mean densities of $7.88/m^2$ in his brackish water marsh type and $14.35/m^2$ in his salt water marsh type. Generally the population decreased with increased frequency of tidal inundation. Largest concentrations ($29.7/m^2$) occurred within the S. cynosuroides community where infrequent tidal inundation and greater land runoff would enhance lower salinities.

Competition also appeared as a factor affecting this crab's local distribution. Lowest numbers were present on the marsh edge of the low marsh community. Here Uca pugnax and Sesarma reticulatum reached their greatest densities of 6.1 and $21.3/m^2$, respectively. Uca pugnax is known as a strong competitor with Uca minax for burrowing space (Teal 1958). Indeed, Uca minax occurred in its greatest concentrations within the S. cynosuroides community where otherwise only S. cinereum occurred. S. cinereum was present only along the lower edge of this community and in very low numbers (2.3 crabs/m^2).

Vegetational cover also limited the distribution of at least a part of the U. minax population. Adult U. minax were conspicuously absent from the mixed zone of the high marsh where vegetation was sparse or lacking. A dense population averaging $25.7/m^2$ was present within this zone throughout the study period, however the average biomass maintained was only 1.9 grams dry wt/m^2, indicating the predominance of juvenile crabs. Large numbers of adult crabs were observed feeding in this zone yet they apparently did not burrow. Schwartz and Satir (1915) reported that Uca pugnax preferred to burrow where vegetative cover was available.

The marsh edge of the low marsh area was similar to those in Louisiana (Day *et al*. 1972) and in Georgia (Teal 1962) with the exception of the presence of *Uca minax*. Dominating this area of the study site were *Modiolus demissus*, *Sesarma reticulatum* and *Uca pugnax*.

The distribution of the filter feeder *M. demissus* was limited by the frequency of tidaliinundation. At the Southern Branch site, the ribbed mussel occurred throughout the low marsh community but most abundantly at the marsh's forward edge (zones A and B). Here biomass and densities were estimated to be as high as 504.6 grams dry wt/m^2 and 418.5/m^2. Zone D, corresponding to that area of the low marsh inundated most infrequently and for the least amount of time, achieved throughout the study period as average biomass of only 1.2 grams dry wt/m^2 and a density of 3.0/m^2.

The density of the *M. demissus* population was far greater than observed elsewhere. In the Louisiana study the highest densities occurred 10 meters from shore while averaging 3.2 grams/m^2 over the forward 50 meters of the marsh. Kuenzler (1961) reported that in Georgia marshes of the greatest concentrations (32/m^2) were associated with tall *S. alterniflora* at creek heads with an average density of 7.8/m^2 for the entire inhabited marsh. At those sites the biomass averaged 4.55 grams/m^2. Day *et al*. (1972) noted that where the ribbed mussel population was densest the individual mussels were mostly small. In the present study the density of the inhabited marsh was 89.3/m^2 over the study period, the biomass (excluding shell weight) was 7.5 grams dry wt/m^2. The average length of a mussel was 26.1 mm with 66.1% of the population sampled being smaller. The largest specimen taken during the study period was 78.2 mm in length.

Typical also of this marsh edge habitat was the square-backed crab, Sesarma reticulatum. This species was found only within the forward three zones of the low marsh community and only within those where they were closest to the shore. Similarly, S. reticulatum was confined to the marsh's edge in Georgia (Teal 1958) and in Louisiana (Day et al. 1972).

Teal (1958) noted that the distribution of Uca pugnax was limited mainly by its preference for a muddy substrate and vegetative cover. For this reason U. pugnax burrowed commonly throughout the marsh near Sapelo Island, Georgia, with the exception of the exposed creek banks and the dry sandy Salicornia - Distichlis marsh. In Louisiana this fiddler crab was present in the forward 50 meters of the S. alterniflora marsh (Day et al. 1972). In the Southern Branch study site Uca pugnax occurred only within the intertidal, low marsh community most commonly within the marsh edge habitat (A zone). Biomass was estimated at 1.6 grams dry wt/m^2 and density at 6.1/m^2. In Georgia greatest concentrations occurred within the medium Spartina levee marsh (61/m^2) while biomass ranged from 5.7 to 54.3 grams/m^2.

Uca pugnax is considered a member of the saltmarsh cordgrass community present in the higher salinity marshes of lower Chesapeake Bay (Wass and Wright 1969). Its presence in low numbers on this Southern Branch marsh, dominated by Uca minax, indicates the marsh's transitional position between high salinity marshes and the brackish water marshes common to the rivers that empty into the Chesapeake Bay. The salinity range (7.3°/oo to 17.1°/oo) present over the study period probably represents the lower salinity limits tolerated by U. pugnax. Kerwin (1971) in a similar marsh located on the Poropotank River (salinity range of 9.38°/oo to 14.72°/oo) noted the absence of Uca pugnax and dominance of Uca minax.

Polymesoda caroliniana dominated the higher elevations of the low marsh. A filter feeder, this clam was found in areas of lwo-lying water or soft mud exposed at low tide. Teal (1962) noted the presence of this clam in the marshes near Sapelo Island, Georgia.

Littorina irrorata is typical of intertidal salt marshes and was present sparsely within the low marsh community. Over the study period its average biomass was estimated at 0.4 grams dry wt/m^2 and density at 0.3/m^2. In Louisiana L. irrorata was considered the most important snail present, with biomass ranging from 1.1 to 16.9 grams/m^2. It was most abundant within the marsh edge community. This population included densities estimated as high as 196/m^2. In Georgia, L. irrorata averaged about 10 grams dry wt/m^2 (without shell). The highest numbers occurred in the high Spartina marsh (Smalley 1959). Apparently the marsh periwinkle population decreased with decreasing salinity. Kerwin

(1972) noted that this anail was present only sparsely in the marshes of the Poropotank River, and the same was noted for the present study. Densities within higher salinity marshes in Virginia (those of Lynnhaven Bay) have been observed by the author as high as 300/square yard.

The high marsh differed from the low marsh by being inundated only by the highest of tides. Sesarma cinereum and Melampus bidentatus were most common here. S. cinereum was observed within the low marsh community but was quantitatively taken only in the high marsh community of the Southern Branch, indicating it only burrowed in the sandier and drier regions of the marsh. Teal (1958) notes, similarly, that S. cinereum was usually abundant within the Salicornia - Distichlis and J. roemerianus marsh in Georgia.

Melampus bidentatus was reported by Day et al. (1972) in both the high and low marsh. Kerwin (1972) noted that this snail occurred more than 50% of the time with Distichlis spicata, Spartina patens and the short form of S. alterniflora. on the Poropotank River. Association with these species would limit this snail to a mid-marsh position as it occupied on the Southern Branch. Greatest biomass and density occurred within the mixed zone of the high marsh community (average biomass of 1.7 grams dry wt/m^2 and density of 36.7/m^2). Kerwin (1972) noted mean densities of 0.23/m^2 within his brackish water marsh type and 7.24/m^2 in the salt water marsh type on the Poropotank River. On this marsh under study a mean density of $8.0/m^2$ was estimated. Day *et al.* (1972) in higher salinity marshes of Louisiana estimated populations as high as $1088/m^2$.

Degree of tidal inundation appeared to be the single most important factor deliniating plant and animal associations on the marsh. *Spartina alterniflora* was limited to an intertidal position as were *M. demissus*, *S. reticulatum*, *L. irrorata* and *P. caroliniana*. *Distichlis spicata*, *S. patens* and *J. roemerianus* were limited to areas inundated only infrequently along with *S. cinereum* and *M. bidentatus*. *Iva frutescens*, *B. halimifolia* and *S. cynosuroides* are limited to areas inundated only by storm tides. The presence of *Spartina cynosuroides* was probably due to lower salinities created by infrequent tidal inundation and the occurrence of land runoff.

The densities of the *Uca minax* and *Uca pugnax* populations were influenced by the frequency of tidal inundation. Day *et al.* (1972) state that animal biomass is correlated with high tide levels in Louisiana marshes. On the Southern Branch marsh only the fiddler crabs appeared affected. Densest concentrations of *U. minax* shifted from the marsh edge in March to the high marsh community in August just as the tide levels increased through this period. A similar pattern was observed for the *U. pugnax* population.

Salinity also affected the density of marsh organisms. *Uca pugnax*, *Littorina irrorata* and *Melampus bidentatus* were present sparsely on this marsh in the Southern Branch. These species are normally abundant in high salinity marshes. Conversely, *Uca minax*, present only sparsely within higher salinity marshes, dominated this low salinity marsh site.

In general, the plant and animal communities present at the Southern Branch marsh were typical of other tidal marshes, and specifically similar to the higher salinity marshes present on the western shore of the Chesapeake Bay. The co-dominance of *Spartina alterniflora* and *Spartina cynosuroides*, as well as the dominance of *Uca minax*, the red-jointed fiddler, indicates the study area was a brackish water marsh. The presence of *Aster tenuifolius* and *Pluchea purpurescens* support this concept, as do the low densities of *Uca pugnax*, *Littorina irrorata* and *Melampus bidentatus*.

Significance of the Marsh to the Area

A salt marsh is an integral part of the estuarine system. Besides providing habitat for marsh-associated organisms which would otherwise not be present, it significantly affects the waterway on which it occurs. Locally, erosion, sedimentation and nutrient concentrations are reduced while, most importantly, the fertility of adjacent waters is enhanced with resultant far-reaching effects.

As a primary producer within the estuary the salt marsh grasses produce considerable organic material each year. *Spartina alterniflora* for this marsh on the Southern Branch of the Elizabeth River has been estimated to have a net production of 5.47 tons/acre while that of *Spartina cynosuroides* amounted to 6.5 tons/acre. Present below-ground were larger quantities of organic material (as high as 56.6 tons/acre in August) although the significance of this material is not fully known.

Teal (1962) and Day *et al*. (1972) estimated that approximately one-half of the net production of the marsh grasses was exported to adjacent waters by the tides where it was utilized in the form of detritus. The remaining material on the marsh was either consumed by grazing herbivores or detrital feeders. On this basis, this marsh on the Southern Branch of the Elizabeth could export to the river 5.5 tons/acre of detritus per year. Detritus consists of decomposed plant and animal material rich in bacteria and microalgae. It serves as a rich source of energy and provides an alternative to the grazing food chain at the base of which are herbivores.

Odum (1971) indicates the estuarine waters contain an array of consumers that derive much of their nourishment from a diet of vascular plant detritus and small quantities of fresh algae. From the adjacent waters of the Southern Branch of the Elizabeth River, species, among others, which would be included in such a group are listed in Table 17. These organisms serve as food for higher consumers present in these waters composed of both resident and migrating species.

Table 17

PROMINENT DETRITAL FEEDERS PRESENT AT THIS STATION ON THE SOUTHERN BRANCH OF THE ELIZABETH RIVER

Mollusks

- *Modiolus modiolus*
- *Musculus niger*
- *Tellina* sp.

Annelids

- *Neris* sp.
- *Capitella capitata*

Crustaceans

- Microcrustaceans
- *Cyathura polita*
- *Corophium laclustre*
- *Gammarus* sp.
- *Palaemontes pugio*
- *Rhithropanopeus harrisii*

Fish

- *Cyprinodon variegatus*

Higher carnivores present in the Southern Branch include large numbers of juvenile and sub-adult fishes which are sought commercially elsewhere. Most commonly, the spot Leiostomus xanthurus and the croaker, Micropogon undulatus, are present. Both the spot and croaker depend heavily upon organisms for food, which are listed in Table 17. Annelids, most prominently Capitella capitata and Neris sp., accounted for 38.6% and 57.6% of the diets of spot and croaker respectively. The blue crab, Callinectes sapidus, which is sought on a commercial basis on the Southern Branch, depended upon mollusks for 42.6% of its diet.

Detrital feeders also support large populations of small resident fishes. Some, Fundulus spp. and Cyprinodon variegatus are closely associated with the salt marsh and utilize significant amounts of algal and detrital material directly. Others, most prominently, Menidia beryllina and Anchoa mitchilli are found throughout the river. These small fishes in turn serve as food for larger predators including the striped bass, Morone saxatilus, the weakfish, Cynoscion regalis, the racoon and many of the birds present on the Southern Branch.

SUMMARY

1. Four distinct plant communities were identified in the salt marsh: a) *Spartina alterniflora*, b) *Distichlis spicata* - *Spartina patens* - *Juncus roemerianus*, c) *Baccharis halimifolia* - *Iva frutescens* and d) *Spartina cynosuroides*.

2. Two distinct animal associations existed. The low marsh was dominated by *Uca minax*, *Modiolus demissus*, *Uca pugnax*, *Sesarma reticulatum*, *Littorina irrorata* and *Polymesoda caroliniana*. The high marsh was dominated by *Uca minax*, *Sesarma cinereum* and *Melampus bidentatus*.

3. Net production by the dominant marsh grasses were as follows: Spartina alterniflora at 1218.6 grams dry wt/m^2 and *Spartina cynosuroides* with 1681.3 grams dry wt/m^2.

4. Evidence would indicate that production is higher within Virginia's marshes than is commonly assumed.

5. Two crops of *Spartina alterniflora* were present on this marsh during each growing season: A spring crop which dominated the marsh throughout the growing season, and a late-summer, early-fall crop which wintered over on the marsh.

6. The standing crop of the below-ground portions of marsh grasses were found to have considerable biomass. In August the standing crop ranged from 56.6 to 24.7 tons/acre on the marsh.

7. The degree of tidal inundation was apparently the principal factor delineating both plant and animal communities on the marsh. This degree of tidal inundation and salinity also affected the density of marsh organisms.

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