FUNCTIONAL IMPORTANCE OF ALGAL PRODUCTIVITY IN MISSISSIPPI SALT MARSHES

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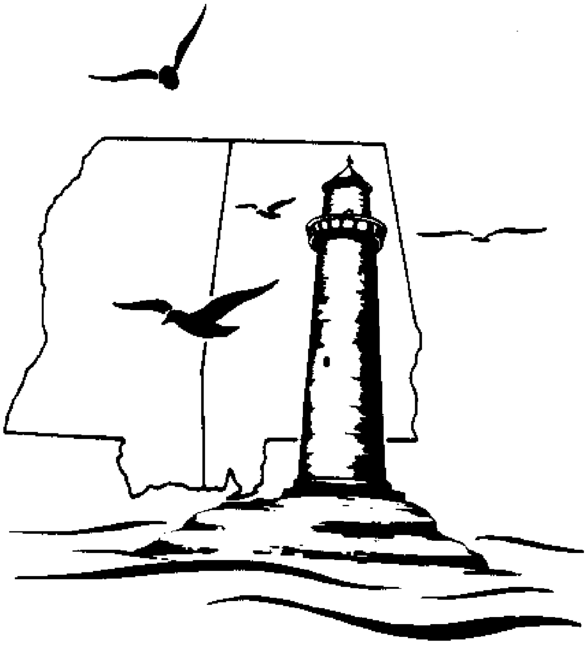

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ABSTRACT

The community structure and primary production rates of edaphic algae beneath five monospecific stands of vascular plants in Graveline Bay Marsh, Mississippi were determined over an annual cycle (April 1985-March 1986). The edaphic algal flora was totally dominated by small, motile pennate diatoms. A total of 155 taxa (species and their varieties) in 30 genera were identified; more than half of these belonged to the genera _Navicula_ and _Nitzschia_. For the most part, the more abundant taxa were widely distributed over the marsh. Functions generated by a stepwise discriminant analysis employing the relative abundances of the 33 most abundant diatom taxa assigned 70% of the cases to the correct community. Mean annual chlorophyll _a_ values for the sediments beneath the five vascular plant canopies ranged from 38-160 mg/m^2. Pheophytin _a_ was undetectable in the sediments beneath _Scirpus olneyi_ and _Spartina alterniflora_ during April and May. Edaphic algal production (as measured by ^{14}C uptake) was generally highest in spring-early summer and lowest in the fall. Hourly rates ranged from a low of 0.4 mg C/m^2 on 16 July in _Spartina patens_ to a high of 164 mg C/m^2 in _Scirpus_. Stepwise multiple regressions identified chlorophyll _a_ and soil moisture as the best variables for predicting hourly edaphic algal production rates; light energy proved of little value. Adding the relative abundances of the 33 diatom taxa to the set of dependent variables only slightly increased the coefficient of determination (R^2), but virtually all variables selected were diatom taxa. No combination of environmental or species variables did a "good job" of predicting hourly production beneath _S. alterniflora_ ($R^2 = 0.38$) but R^2 values ranged from 0.70 to 0.87 for the remaining vascular plant zones. Annual

rates of edaphic algal production (g C/m^2) were estimated as follows: *S. patens* (9), *Juncus roemerianus* (28), *S. alterniflora* (57), *Distichlis spicata* (88), and *Scirpus* (151). The ratio of annual edaphic algal production to annual vascular plant aerial production (EAP/VPP) was only 1% in *S. patens*, 10-12% for *Juncus*, *S. alterniflora*, and *Distichlis*, and 61% in *Scirpus*. Chlorophyll *a* concentrations, annual edaphic algal production rates, and EAP/VPP values were comparable to those previously determined in Texas, Delaware, and Massachusetts salt marshes but lower than those reported for Georgia and California marshes.

INTRODUCTION

Mississippi's Gulf Coast encompasses slightly less than a twentieth of the total northern Gulf perimeter, yet is an extremely productive region. With a total of only 68.8 miles (110.7 km) of coastline divided among three counties comprising a mere 3.8% of the state's total area, the region is home to 11.9% of the total population and virtually all of its commercial marine fisheries (Mississippi Power & Light Co., 1983). Commercial marine fisheries in Mississippi represent an average of 17.8% of all northern Gulf fisheries catches over the past ten years. However, very little is known about the ecosystems supporting this extremely valuable resource, particularly the 27,100 hectares of extensive marshland (Christmas, 1973) that is a dominant natural coastal habitat.

This study was undertaken to initiate work towards an understanding of Mississippi's coastal marsh processes. Specifically, the primary productivity of edaphic algae (microscopic plants which may be the major component of the base of the food webs supporting organisms dependent on coastal wetlands) was studied. Research conducted in other coastal regions and in the laboratory indicate that edaphic algae are an essential dietary requirement for commercially harvested shrimp species (Gleason & Zimmerman, 1984). This is also true for other organisms that are major components of the diets of a wide variety of vertebrates and invertebrates found in coastal marshes at some point in their life cycle (Stuart et al., 1985). Preliminary assessment of the primary production patterns and rates for edaphic algae will help to develop an understanding of the structure and function of wetlands ecosystems at a basic level, as well as provide a reference point for further studies.

It is well known that temperate salt marshes are among the most productive ecosystems in the world. The main contributor to this high rate of productivity are the highly visible vascular plants. However, beneath the often extensive and dense vascular plant canopy a second and equally important productivity component lives on and within the marsh soil--the edaphic (= sediment-associated) algae. Diatoms, blue-green, green, and yellow-green algae are the dominant algal groups inhabiting the sediments of coastal salt marshes. These edaphic algae are largely microscopic, extremely diverse in terms of numbers of resident species, and highly productive in spite of the heavy shading by the vascular plant canopy. Where the canopy is open or lacking, thick mats of edaphic algae may develop and take up the "slack" in productivity due to the paucity or absence of vascular plants (Estrada et al., 1974; Sullivan & Daiber, 1975). This vascular plant/edaphic algal productivity system assures near maximal productivity over the entire marsh surface. Furthermore, the edaphic algae, unlike the overstory vascular plants, are productive on a year-round basis and represent the major source of newly fixed carbon on the marsh when the latter are dormant. Recent work has shown that 98% of the detrital material exported from a Florida Gulf Coast marsh was produced by edaphic algae (Ribelin & Collier, 1979). This, combined with their high palatability, suggests that edaphic algae may be an important food source for consumers both resident within salt marshes and in adjacent estuarine waters. Stable carbon isotope work in salt marshes has shown that the productivity of the vascular plants is buried in the marsh rather than exported (see review by Fry & Sherr, 1984). Thus the importance of the productivity of edaphic algae in salt marsh food webs represents an unknown but intriguing factor (Pomeroy et al., 1981).

Pomeroy (1959) was the first researcher to study the productivity rates of edaphic salt marsh algae. His study was conducted in the Duplin River marshes adjacent to Sapelo Island, Georgia. Productivity was highest during summer and lowest during winter at high tide while the opposite was true for low tide measurements. High and low tide seasonal patterns, as well as those of light and temperature, alternated to give a nearly constant rate of daily production throughout the year. Annual gross primary productivity (GPP) was estimated to be 200 g C/m^2 for the Duplin River system and net primary productivity (NPP) was calculated to be not less than 90% of GPP.

Gallagher & Daiber (1974) measured edaphic algal productivity in five zones of a Delaware salt marsh employing the Winkler technique (dissolved O_2 measurements). Annual GPP in this more northerly marsh was estimated to be 80 g C/m^2. However, much of it occurred when the canopy-forming grasses were dormant, particularly in the zones dominated by tall Spartina alterniflora and Distichlis spicata. Annual algal GPP was approximately equal to one-third the yearly NPP of the vascular plants.

Van Raalte et al. (1976) utilized ^{14}C uptake to measure edaphic algal productivity in a Massachusetts salt marsh. All work was done in the S. alterniflora zone of the low marsh. In general, algal production was lowest in summer and early winter and highest in spring and to a lesser degree fall. The grass canopy reduced irradiance and depleted nutrients, thus severely limiting algal productivity during summer. Their data showed a highly significant, linear relationship beneath light energy reaching the marsh surface and edaphic algal production up to the highest light levels measured (i.e., there was no photoinhibition). Annual algal production for the marsh under study was estimated to be 105 g C/m^2, which was about 25% that of the overstory grass canopy. As in Gallagher & Daiber's (1974) study, much of it occurred when the vascular plants were dormant.

The first study of algal productivity in a Pacific coastal salt marsh was made by Zedler (1980) in the Tijuana Estuary of southern California. She employed the Winkler technique and measured productivity in four marsh zones which differed with respect to elevation as well as the specific identity, height, and density of the vascular plants making up the overstory canopy. Annual algal NPP ranged from 185 to 341 g C/m^2 and the ratio of annual algal NPP to annual vascular plant NPP within a canopy type ranged from 0.76 to 1.40. This ratio varied from 0.25 to 0.33 in the three Atlantic Coast marshes discussed above and may be even lower for Gulf Coast marshes. On a yearly basis, the edaphic algae were responsible for 40-50% of total marsh productivity in the Tijuana Estuary and virtually all productivity was due to the algae from October through February when the vascular plants were dormant. The latter phenomenon parallels that found in Atlantic Coast marshes and suggests that edaphic algal production may be critical for the functioning of estuarine food webs during winter and early spring. Zedler pointed out that algal productivity was much higher than, and vascular plant productivity much lower than, corresponding values for these same components in Atlantic Coast marshes and stated that the Tijuana marshes functioned quite differently than their counterparts in Georgia, Delaware, and Massachusetts.

Recently, experimental work investigating the relationship between environmental factors and edaphic algal productivity in salt marshes has finally begun. Such work has been carried out in the salt marshes of Sapelo Island, Georgia by M. Darley and his associates. They first demonstrated that edaphic diatoms collected form these marshes possess limited heterotrophic capabilities and could obtain up to 1% of their carbon using this nutritional mode if several usable substrates were each available at concentrations of 1 μm (Darley et al., 1979). In another experiment (Darley et al., 1981), they fertilized cores from different areas of the marsh and even made reciprocal transplants. ^{14}C uptake and chlorophyll *a* measurements showed that the edaphic algae of the short *Spartina alterniflora* zone were limited by nitrogen throughout the year whereas edaphic algae of the creekbank marsh were not limited by supplies of this element. Experimental manipulation of irradiance reaching the marsh surface beneath short *Spartina* indicated that the edaphic algae of this marsh zone were not limited by light. In a third experiment (Whitney & Darley, 1983), the relationship between irradiance and edaphic algal productivity was studied in detail. In the vegetated portion of the marsh, maximum production rates occurred at irradiances higher than the average irradiance values beneath the grass canopy. Whitney & Darley concluded that algal productivity in the short *Spartina* zone was light-limited and noted that this finding was in direct opposition to that of an earlier study. At full sunlight, photoinhibition of productivity was detected in contrast to the results of other workers who found little, if any, photoinhibition of edaphic algae from a variety of different intertidal habitats.

It should be readily apparent from this brief review of edaphic algal productivity in salt marshes that although very little research has been done, it has been quite successful in documenting the significant productivity rates of these unseen, microscopic organisms. In addition, it has provided some cursory information on the regulation of algal productivity by environmental factors. However, the productivity of edaphic algae in Gulf Coast salt marshes remains a completely unknown entity. Hall & Fisher (1985) determined the seasonal productivity patterns of a blue-green algal mat in a Texas salt marsh but these algae were continuously exposed on the banks of a drainage canal. Bona fide edaphic salt marsh algae are defined in this study as those forms resident within or on the sediments beneath the overstory canopies of the vascular plants. The seasonal productivity rates and distributional patterns of the understory edaphic algae are inseparably linked with the growth cycles of the vascular plants. This phenomenon is completely absent on mud and sand flats for obvious reasons.

The major objective of the present study was to quantitate the spatial and temporal productivity patterns of edaphic algae in a representative Mississippi salt marsh over an annual cycle. Other objectives were to identify those environmental parameters potentially most important in regulating algal productivity and to compare algal production rates to those of the overstory vascular plant canopy.

DESCRIPTION OF STUDY AREA

Climate

The Gulf Coast region, classified as being humid and semi-tropical, characteristically has long, warm summers and short, mild winters. Moist tropical air predominates over the area, but in winter this may briefly be displaced by polar continental air intrusions. Average annual air temperature is 66.7°F (19.3°C); mean humidity is 78%. Temperatures can be as extreme as -1 to 106°F (-18.3 to 41.1°C); however, the mean range is 50.6 to 81.9°F (10.3 to 27.7°C) with an annual daily maximum of 78.6°F (25.9°C) and a minimum of 54.7°F (12.6°C). Winds are generally from the SSE at a speed of 6.5 mph (10.4 kph). Mean annual precipitation is approximately 60 inches (152.4 cm), with 89.9 days per year with rainfall exceeding 0.1" (0.25 cm). The region experiences 75.7 days with thunderstorms. July is generally the wettest month of the year; October is usually the driest (ONWI, 1983).

A major seasonal Gulf coast weather feature is the occurrence of tropical storms and hurricanes. From 1886 to 1970, a total of 42 tropical cyclones have crossed the Mississippi Gulf Coast; 24 of these storms were hurricanes with wind speeds in excess of 74 mph (119 kph) (Simpson and Lawrence, 1971). This averages out to one tropical cyclone entering the state every two years, of which one every four years was a hurricane.

Geographic Setting

Graveline Bay Marsh is located on the Mississippi Gulf coast between Biloxi Bay and the mouth of the Pascagoula River (Fig. 1) (N30°21'26" W88°40'59"). This area lies on the southeast margin of the Gulf Coast Area River Basin portion of the Coastal Terrace watershed, and is hydrologically affected by drainage from the Pascagoula River Basin. Uplands drainage to the north of the study site occurs primarily via the Pascagoula River and Biloxi Bay tributaries. The area itself is hydrologically isolated by rail lines and local roads, resulting in the domination of hydrodynamics (water levels and movement) in the area by local conditions in Mississippi Sound and precipitation falling directly on the marsh. Horn Island, part of the barrier island chain fronting the Mississippi coast, lies to the SSW and Round and Petit Bois Islands to the SSE; these islands inhibit the exchange of sound waters with the Gulf (MacKenzie, 1977). Astronomical tidal range is 2 feet (0.6 m); aeolian effects on local hydrodynamics generally exceed this, resulting in irregular flooding for most of the marsh areas in the Graveline system.

Soils

Coastal marsh soils of the northern Gulf are characteristically composed of fine-grained clays and silts. These are interspersed with varying amounts of vascular plant detritus, depending on the dominant vascular plant species present. Fine-grained sand may also be a significant fraction of the soil, if available.

Marsh soils in the Graveline system can generally be categorized as silts or mucks, overlying a deeper layer of peat. These soils are usually saturated or submerged throughout most of the year, resulting in extremely reduced conditions with no measurable oxygen content beyond more than a few millimeters into the marsh surface. Gray to black soil colors observed are characteristic of reduced mucks and organic clays (Lytle, 1968). Soil materials are generally silts, silty clays, and clays of recent alluvial origins, plus sand from the adjacent beachfront in the *Spartina patens*-dominated areas.

Seasonal changes in degree of soil oxidation occur in response to fluctuations in temperature and prevailing wind direction, which control drying conditions and tidal depth plus the length of time the marsh is submerged. Winter weather patterns tend to keep the marsh surface free from tidal flooding, leading to drier conditions; they can also occur in summer months during periods of little or no rainfall, high temperatures, and low tides. Saturation persists at most of the study locations year-round, however. Soil pH generally approaches 7.0, due to the buffering effect of products of reducing conditions in waterlogged sediments (Ponnamperuma, 1972).

Vegetation

Mississippi's Gulf Coast is part of the Longleaf-Slash Pine Belt. General forest types adjacent to the Graveline marsh system are longleaf-slash pine and oak-gum-cypress associations. The marsh proper is dominated by extensive stands of *Juncus roemerianus* Scheele and of *Scripus olneyi* Gray, interspersed with regions covered by *Spartina alterniflora* Loisel. and *Distichlis spicata* (L.) Greene. Areas adjoining the beachfront are edged by swales of *Spartina patens* (Ait.) Muhl. Monospecific stands of these vascular plants are common in the Graveline system, with relatively sharp ecotones between communities. Detailed descriptions of the vascular plants found in Mississippi marshes have been published by Hackney & de la Cruz (1982) and de la Cruz (1974).

In addition to the vascular vegetation, occurrence of diverse algal communities beneath the vascular plant canopies and on exposed mudflats has been documented by Sullivan (1978) and Sage and Sullivan (1978). Diatoms dominate the algal communities to the virtual exclusion of all other algal taxa beneath the marsh canopies in the plant stands selected for this study. In the open areas, a variety of filamentous blue-greens and xanthophytes can occur, particularly along paths through the marsh and in other periodically disturbed areas (Sage & Sullivan, 1978).

Fauna

Invertebrates dominate the marsh fauna by virtue of sheer numbers. A plethora of insects are present throughout most of the year, disappearing only briefly following intense tropical storm activity and during the cold polar air intrusions occurring in winter months. Benthic invertebrate communities have been described in detail by Heard (1982). Snails and several types of crabs are regularly observed in all areas of the marsh. The fiddler crab, *Uca pugnax*, is the most visible invertebrate, with extensive burrows in the marsh substrate.

Vertebrate marsh inhabitants are numerous but shy, generally heard more than seen. Snakes in the marsh proper are rare in areas dominated by mud substrate, but are occasionally encountered in regions where a relatively thick, dry layer of detrital material covers the marsh surface. A wide variety of birds select the Graveline system for nesting and feeding. Red-winged blackbirds, marsh sparrows, and gallinules are commonly found on the marsh. Muskrat make extensive use of the *Scirpus olneyi* stands year-round.

Utilization

The region of the Graveline Bay marsh system studied is relatively unimpacted by human activities. Trapping of furbearers and hunting in the immediate area is almost non-existent (M. McCaffrey, pers. comm.).

Graveline Bay and Bayou are popular locally for shrimping, oystering, and rod and reel fishing in season. The western third of the beachfront ecotone area has been destroyed by construction of a minimum grade roadbed and a mixture of seasonal and year-round dwellings. To the west, the marsh boundary is defined by a canal maintained for boating access to Graveline Bay. This receives light to moderate seasonal use.

METHODS AND MATERIALS

Sampling Strategy

All sampling was carried out in five monospecific stands of vascular plants in Graveline Bay Marsh and included: *Juncus roemerianus* (black needle rush), *Spartina alterniflora* (smooth cordgrass), *S. patens* (salt hay), *Distichlis spicata* (spikegrass), and *Scirpus olneyi* (bulrush). An area 1 x 4 m was roped off in each vascular plant zone and subdivided into 16 quadrats that were 0.5 x 0.5 m each. Quadrats were selected for sampling within each roped-off area by employing a modified random block design. Samples were collected on a monthly basis from 12 April 1985 through 26 March 1986. It was impossible to sample during the months of August and November because of two major hurricanes. Hurricane Elena roared ashore on 2 September 1985 with winds of 125 mph while Hurricane Juan battered the coast on 28 October 1985 with winds in excess of 80 mph. The eye of both hurricanes passed within 2 km of Graveline Bay Marsh and both deposited several cm of fine-grained sediments over the marsh surface. The beach overwash associated with each storm buried the *S. patens* sampling area; therefore, the results presented for this vascular plant zone are from three different sampling areas within the same monospecific stand.

Edaphic Algal Primary Production

Edaphic algal production was estimated by a ^{14}C uptake technique described by Van Raalte et al. (1974) designed specifically for sediment-associated algae in salt marshes. The technique, as modified, is described below.

1. *Cores - Incubation*

Cores were taken to a depth in excess of 5 mm using a modified 2.1 cm diam. disposable syringe. Each core was extruded from the syringe until only the upper 5 mm was retained; the excess was discarded. Retaining its original orientation, the upper layer was then placed in an incubation chamber with an approximate total volume of 70 ml (3.6 cm diam x 7 cm high). To the chamber was added 9 ml of filtered Mississippi Sound water (0.45 µm nitrocellulose membrane filter plus prefilter) and 1 ml of labelled $NaH^{14}CO_3$ (5 µCi/ml, New England Nuclear). Each chamber was covered with a circle of transparent plastic wrap which was secured with a size 8 rubber band; this effectively sealed the chambers during incubation. Following an incubation period of 3 hours, buffered formalin was added to a concentration of 4% to stop uptake. Chambers were then capped at this point.

This procedure was carried out in situ beneath each vascular plant canopy; remaining steps took place in the laboratory. Cores were transported to the laboratory in their chambers on ice to further ensure cessation of active carbon-14 uptake, and were stored under refrigeration at 4°C until processing.

2. Removal of Adsorbed Label

In the laboratory, cores were removed from the chambers by washing them onto 0.45 µm nitrocellulose filters. Unincorporated $NaH^{14}CO_3$ was removed from the samples by washing with a minimum of 50 ml of 2% HCl under a fume hood. All core material was collected on the filter, which was then placed in a 125 ml wide mouth Erlenmeyer flask for digestion. Van Raalte et al. (1974) scraped their samples off the filters; in our samples there was no measurable retention of label in the filters so they were included in the digestion to facilitate sample processing.

3. Digestion

Ten milliters of concentrated nitric acid (analytical grade) were added to each sample which was then allowed to stand at room temperature ("cold" nitric acid digestion) for 6 hr under a fume hood; at this point, a smooth digest was obtained. Other workers have indicated a need for shorter or longer digestion periods to reach this stage as smoothness of the digest, and thus length of digestion, is dependent on the amount and condition of vascular plant detritus in the sample. Shimmel and Darley (1985) found digestion periods of 5-12 hr were necessary to completely breakup cores with increasing amounts of vascular plant material present.

4. Sample Preparation

Following digestion, samples were decanted into 15 ml polyethylene tubes and centrifuged for 10 min at 1000 rpm. A 1 ml subsample of the supernate was added to 9 ml of 0.75M tris buffer; 1 ml of this was combined with 10 ml of Solvent-Free (Isolab), a scintillation cocktail designed for aqueous samples, which possesses a high efficiency for ^{14}C counting.

5. Scintillation Counting

Samples were counted using a Beckman LS 3801 liquid scintillation counter programmed for "wide window" counting (color/chemical quench correction); counting times of 5 minutes or less were required. Count rates were obtained in disintegrations per minute (dpm).

6. Correction for Carbon Update in the Dark

A total of 6 cores were taken in each vascular plant zone on each sampling date and each core was placed beneath the canopy in the position it formerly occupied. Five of the cores were incubated with the isotope only, while the sixth core received the isotope and dichlorophenyl dimethyl urea (DCMU) (Legendre et al., 1983). DCMU is a herbicide which inhibits the operation of Photosystem II and thus active carbon uptake, and was used to generate a "blank" for determination of absolute active uptake of ^{14}C. Within each vascular plant zone, inactive ^{14}C uptake was relatively constant, so that only one blank was run for each marsh type. DCMU values were subtracted from those values measured in the cores that received the isotope only.

7. Calculation of Uptake Rates

Disintegrations per minute were converted to hourly rates of carbon uptake via a combination of the formulas used by Strickland and Parsons (1968) and by Leach (1970). Productivity was calculated for each individual sample and extrapolated to a value per square meter of mud surface by the following equations:

$$\text{sample uptake} = \frac{(\text{dpm} - \text{DCMU}) \times (\text{act})/(\text{alk}) \times 1.064 \times 100}{t}$$

and uptake/m^2 mud surface = sample uptake x 2886.84, where

dpm = disintegrations per minute for the sample
DCMU = dpm for "blank"
act = added activity (constant for this study and equal to 5 μCi)
alk = alkalinity factor
1.064 = differential isotopic uptake correction factor
100 = dilution factor
t = length of incubation in hr
2886.84 = factor converting uptake for sample area to m^2.

Chlorophyll Determinations

A total of 6 sediment cores were taken in each vascular zone on each sampling date in order to estimate the "biomass" of edaphic algae as chlorophyll (chl.) a. All chl. a samples were processed according to the technique developed by Whitney and Darley (1979) for the extraction of pigments in salt marsh sediments.

Samples were collected using sharpened aluminum corers 1.6 cm inside diam and approximately 5 cm in length, excluding the sharpened, angled cutting edge. Following the addition of $MgCO_3$, cores were wrapped intact with aluminum foil and placed on ice. Samples were frozen as soon as possible after collection. All further handling of the samples was carried out with minimal exposure to any type of light source. For processing, cores were thawed just sufficiently to permit slicing. The upper 0.5 cm of each core, assumed to contain all the chlorophyll-containing cells, was separated from remaining sediment material using a sharp knife. Each sample was extracted according to the following protocol:

1) Sediment cores were suspended in 100% acetone and allowed to stand overnight under refrigeration in the dark.
2) Sediment was removed from the extract by centrifugation for 10 min at 1000 rpm; the supernatant was collected and the pellet resuspended in 90% acetone for an additional 2 hours of extraction under refrigeration, which was again followed by centrifugation and collection of the supernatant.
3) Extracts for each sample were pooled and then partitioned with hexane. For each sample, 10 ml of the acetone extract was placed in a 60 ml separatory funnel and 3.5 ml of 0.05% NaCl and 13.5 ml of hexane were added.

4) The separatory funnel was shaken for 5 minutes (ca. 60 cpm). This time proved to be sufficient for maximum separation.

5) The acetone hypophase was drained off and the hexane hyperphase collected in 20 ml glass vials.

6) Approximately 1.0 g anhydrous sodium sulfate was added to each vial to dry the hexane.

7) Absorbance was measured against a hexane blank for each sample at 663 and 750 nm using a spectrophotometer (Beckman Model DB-G).

8) Following these measurements, one drop of concentrated HCl was mixed well with each sample to convert all chl. a to pheophytin a. The absorbance was determined again at each wavelength.

Chl. a concentrations in the original sediment core samples were calculated using the following equation:

$$\text{mg chl. } \underline{a} = \frac{1.81 \times 11.05\ (A - Ac) \times 1.6}{4} \times 0.01 \times \frac{Va}{10}, \text{ where}$$

1.81 = factor equating reduction in absorbancy to initial chl. a concentration (hexanes versus acetone)

11.05 = absorption coefficient of chl. a in hexane

A = corrected unacidified absorbance at 663 nm

Ac = corrected acidified absorbance at 663 nm

1.6 = factor to correct for acetone and hexane volume differences

4 = cuvette path length in cm

0.01 = factor converting mg/l to mg/10 ml

Va = volume of acetone used for sample extraction

10 = volume of acetone used in partitioning step.

To calculate the concentration of pheophytin (pheo.) a per sediment sample, the corrected unacidified absorbance at 663 nm (term A in previous equation) was multiplied by 2.23. This correction factor is the ratio of before to after acidification absorbance of pure chl. a in hexane.

Chl. a and pheo. a concentrations per square meter of marsh surface were calculated according to the following formulas:

chl. a/m^2 = mg chl. a/sample x 4972.65

pheo. a/m^2 = mg pheo. a./ sample x 4972.65

where

4972.65 = constant converting mg pigment per sample to mg pigment per square meter (core area = 2.011 cm^2).

Some minor changes were made in the technique of Whitney & Darley (1979). Hexanes were not redistilled; they were used as received from the manufacturer and were of spectrophotometric quality. Use of approximately the last half-liter in each 8-liter bottle was avoided to eliminate interference from visible impurities. Acetone (spectrophotometric grade) was dried prior to use with anhydrous Na_2SO_4. Slightly more than the recommended amount of anhydrous Na_2SO_4 was required on occasion to eliminate clouding of the hexane extracts following acidification with concentrated HCl. Samples were read at each wavelength, acidified, and absorbance measured again; separate acidified samples were not used.

Diatom Sampling

As discussed later in the Results section, diatoms dominate the edaphic algal flora of Graveline Bay Marsh to the virtual exclusion of all other algal taxa. Whenever macroscopic growths of green, blue-green, or yellow-green algae were observed, they were collected and then identified upon return to the laboratory. On each of the 10 sampling dates of this study, edaphic diatoms were collected from beneath the 5 vascular plant canopies with the use of 7 cm diam. acrylic glass tubes which were pushed at least 8 cm into the marsh soil. Only edaphic diatoms were sampled as care was taken to exclude the vascular plant shoots. Cores were stored in a lightly iced styrofoam chest, out of direct sunlight, for 24 hr or less before processing.

Upon return to the laboratory, the top 1 cm of each core was sliced off and placed in a petri dish. A sheet of lens paper was then laid on the surface of each soil sample and moistened with filtered (0.45 μm) seawater. At 1000 hr the next morning the edaphic diatoms were "harvested" from the sample by removal of the lens paper with a pair of tweezers (Eaton & Moss, 1966). The diatoms were cleaned (i.e. all organic matter in the cells was oxidized) by boiling in 20% HNO_3 and $K_2Cr_2O_7$. Following a series of 6 settlings, decantings, and rinses with distilled water, the diatoms were mounted in Hyrax for identification purposes.

The sampling method just described does not collect epipsammic diatoms, but this is of little concern as the marsh sediments are composed exclusively of silts and clays in all habitats except <u>Spartina patens</u> where a small amount of sand is present. Although permanent diatom slides were prepared each month for S. patens, no counts were made for this area because of the paucity of diatoms and the very low and nearly constant edaphic algal production values throughout the entire year. The term edaphic as used in this study refers to both the motile and non-motile components of the diatom flora associated with the sediments. It is thus not strictly synonymous with the term epipelic.

Diatom Community Structure Analysis

Exactly 300 valves were counted and identified to species or varietal rank in each of the 40 samples (4 vascular plant zones x 10 dates) using a Zeiss phase contrast light microscope equipped with an oil immersion lens (1000X; NA = 1.25) and an Optovar. After a sample had been analyzed taxonomically, its species diversity was calculated by the Shannon-Wiener informational index (H') using tables prepared by Lloyd et al. (1968). The number of taxa in each sample of 300 valves (S) was also determined. The structure of selected pairs of edaphic diatom samples was compared by means of the Czekanowski (CZ) Quantitative Index:

$$CZ = \frac{2\sum_{i=1}^{s} \min (P_{ij}, P_{in})}{\sum_{i=1}^{s} (P_{ij} + P_{in})},$$

where $\min (P_{ij}, P_{in})$ is the minimum relative abundance of the i-th taxon in the j-th and n-th samples and $(P_{ij} + P_{in})$ is the sum of the relative abundances of the i-th taxon in the j-th and n-th samples (Bloom, 1981). If the two samples being compared share no taxa in common, CZ will have a minimum value of 0; whereas, if the taxa present and their relative abundances are identical in both samples, CZ will have its maximum value of 1. According to Bloom (1981), the CZ index is one of the few indices that measure true similarity between samples.

Environmental Factors

During each sampling date, several environmental factors were measured for later correlation with the biological data. Air and sediment temperatures were measured in each vascular plant zone at the beginning and end of the ^{14}C incubations with a YSI Model 42SC Tele-Thermometer. The data presented in Table 1 are the means of the beginning and end of incubation values. Salinity of the upper 2 mm of marsh sediment was obtained by scraping the marsh surface, wrapping the soil surface in No. 2 filter paper, and then squeezing it in a syringe until enough drops of sediment-free water were obtained for a reading in an AO Goldberg T/C Refractometer, Model 10419. Light energy above the vascular plant canopy and that reaching the sediment surface below was measured as photosynthetically active radiation (400-700 nm) with a LI-COR Quantum/Radiometer/Photometer, Model LI-185B. The meter was equipped with a LI-COR underwater quantum sensor, Model LI-192SB. Light energy readings were taken at the beginning and end of each ^{14}C incubation period; these values were averaged and form the basis of Table 3. Canopy height measurements represent the average height of each vascular plant stand.

RESULTS AND DISCUSSION

Environmental Factors

Temperature

As might be expected, there was a strong positive correlation ($r = 0.97$) between air and sediment temperature (Table 1). In addition, the temperature of the marsh sediment beneath all five vascular plant canopies was always less than that of the air except in *Scirpus* on 13 February. Air temperature was lowest on this collection date and standing water was present only in the *Scirpus* habitat.

Salinity

Sediment surface salinity is affected by temperature, precipitation, frequency of tidal flooding, and moisture content of the sediments. This last factor was only weakly correlated with salinity ($r = 0.20$). Table 2 lists the salinity and moisture content of the surface sediments in all five edaphic habitats. Salinity was usually less than 30 $^{o}/oo$ and tended to reach its lowest values in February and March. Highest salinity values occurred from June through September. Hypersaline conditions existed in the *Scirpus* habitat on 12 June when salinity rose to 71 $^{o}/oo$. In completely exposed sediments adjacent to *Scirpus* a salinity value of 132 $^{o}/oo$ was recorded. On other dates, salinity beneath *Scirpus* tended to be equal to or less than that beneath the remaining vascular plant canopies.

The arbitrary moisture index employed (see Table 2) shows that *Scirpus* was the wettest and *S. patens* the driest habitat. Standing water was present in the *Scirpus* habitat on 7 out of the 10 sampling dates whereas this never occurred beneath the *S. patens* canopy. Based on the moisture index and measurements of standing water the five habitats can be ranked in the following order as regards elevation: Scirpus < S. alterniflora ≤ Juncus < Distichlis < S. patens.

Light Energy

Photosynthetically active radiation (PAR = 400-700 nm) reaching the marsh surface is a function of the height and density of the vascular plant canopy. Table 3 lists PAR above each vascular plant and that reaching the marsh surface beneath its canopy. PAR was lowest beneath the extremely dense S. patens and Juncus canopies. The % incident PAR was always less than 10% beneath S. patens. On 16 July PAR was 1900 $\mu E/m^2/s$ above the S. patens canopy and only 9 $\mu E/m^2/s$ at the marsh surface; therefore, only 0.47% of full sunlight reached the edaphic algae. Percent incident radiation never exceeded 20% beneath the Juncus canopy and was less than 10% on 6 of the 10 sampling dates. Light energy reaching the marsh surface was highest beneath either the Distichlis or Scirpus canopies on all dates except 16 July when the highest value (1160 $\mu E/m^2/s$) of the entire study was recorded beneath S. alterniflora. The highest percent incident radiation reaching the marsh surface was measured beneath Scirpus on 13 February and was 77.4%.

Canopy Height

Although one could argue canopy height should be treated as a biological factor, the physical stature of each vascular plant species has a profound effect on the quantity of light energy reaching the marsh surface. Canopy heights are listed in Table 4. The tall Juncus stand was a mature one and changed little in height over an annual cycle. The same was true of S. alterniflora, although new plants were observed and canopy height tended to be highest from July through October. The tremendous decrease in height of the S. patens canopy measured on

19 September was due to the destruction of the original stand by Hurricane Elena on 2 September. All other vascular plant canopies exhibited a slight decrease in height because of sediment deposition over the marsh surface caused by this powerful storm. The *Distichlis* canopy, which was always the shortest one, exhibited considerable die-back during the winter months. In contrast to the other four vascular plants, the shoots of *Scirpus* live for only a single growing season. Measurements listed in Table 4 from 24 October to 13 February are those of dead *Scirpus* stems. New growth was first apparent on 13 February and measured 35 cm. By 26 March the previous year's growth had completely collapsed and the new growth was 80 cm in height. Light energy reaching the marsh surface beneath the *Scirpus* canopy was 1025 and 400 $\mu E/m^2/s$ on 13 February and 26 March, respectively.

Edaphic Algal Distribution

General Comments

The edaphic algal communities beneath all five vascular plant canopies were totally dominated by small, motile pennate diatoms to the virtual exclusion of all other algal taxa. Therefore, when considering the chlorophyll and productivity data one can assume for all practical purposes that the only contributors were edaphic diatoms. Following Hurricane Elena in early September, the marsh surface was always a golden-brown color due to a continued surface bloom of edaphic algae. It was surprising to this investigator how resilient both the vascular plants and diatoms were and how quickly both recovered following each hurricane.

The Non-Diatom Flora

Very occasional growths of filamentous algae were observed and these for the most part were limited to areas that had been sampled during previous sampling trips. The blue-greens *Anabaena torulosa* (Carmichael) Lagerheim and *Spirulina* sp. were abundant on 14 May in trampled areas of the *Scirpus* stand. The green alga *Rhizoclonium tortuosum* Kützing was rare on the base of *Scirpus* stems forming skeins on 16 July. On 19 September the blue-green *Lyngbya semiplana* (C.Ag.) J.Ag. was found as an epiphyte on a dead stem of *Scirpus* and *Anabaena fertilissima* Rao formed patches in areas of the *Scirpus* stand that had been trampled. An unidentified species of the yellow-green alga *Vaucheria* was very abundant in trampled areas of *Juncus*, *S. alterniflora*, and *Scirpus* on 13 February. Also present along with *Vaucheria* were the blue-greens *A. torulosa* and *Nodularia harveyana* (Thwaites) Thuret. On the last collection date (26 March), only a blue-green alga lacking akinetes with characteristics intermediate between those of *A. torulosa* and *A. fertilissima* was abundant in the trampled areas discussed above as *Vaucheria* had disappeared. In addition, the blue-green *Porphyrosiphon notarisii* (Meneghini) Kützing was evident as rare filaments during March. It should be noted that the most abundant non-diatom algae were heterocystous blue-green algal genera (*Anabaena* and *Nodularia*) known to be efficient nitrogen fixers.

The Diatom Flora

A total of 155 diatom taxa (species and their varieties) in 30 genera were identified as constituents of the edaphic diatom flora of Graveline Bay Marsh (Table 5). One-third (i.e. 53 taxa) of these taxa were new records for Mississippi based on a checklist published by Sullivan (1981). By far the greatest number of taxa belonged to the genera *Navicula* (47) and *Nitzschia* (40). These two genera accounted for 56% of all taxa encountered. The next most abundant genera in terms of number of taxa were *Amphora* (11), *Gyrosigma* (8), and *Diploneis* (5). In a previous study (Sullivan, 1978) of Graveline Bay Marsh, where the edaphic diatoms beneath the same four vascular plant stands and *S. patens* were sampled once during each of the traditional four seasons, a total of 119 taxa in 29 genera were identified.

Table 6 lists the 48 most abundant edaphic diatom taxa of Graveline Bay Marsh during the present study. With the exception of two taxa, this table includes all taxa with an overall relative abundance greater than 0.3% (i.e. $N_t \geq 36$ valves). Furthermore, the 48 taxa accounted for 87% of a total valve count of 12,000. Considering only those taxa in Table 6, a low of 39 were members of the *Scirpus* community while a high of 46 were encountered beneath the *S. alterniflora* canopy. Only two taxa were restricted in occurrence to a single edaphic diatom community; *Nitzschia habirshawii* and *Nitz. petitiana* were found only beneath *Scirpus*, but accounted for only 2.6% of the 3,000 valves counted from this edaphic habitat. In contrast, 35 taxa were members of all four edaphic diatom communities and hence were widely distributed over the marsh surface. Notable absences of a diatom taxon from only one community were *Navicula binodulosa*, *N. infaceta*, *N. iranensis*, *Nitzschia granulata*, *Nitz. laevis*, and *Nitz. levidensis* from *Scirpus*, and *Nitz. serpenticula* from *Distichlis*. Of interest is the fact that *N. binodulosa*, *Nitz. granulata*, and *Nitz. laevis* were restricted in occurrence to *Distichlis* in my earlier study (Sullivan, 1978).

The three most abundant taxa in each community were as follows (see Table 6): *Juncus* - *N. salinicola*, *N. ammophila*, *F. hyalina*; *S.*

alterniflora - *N. sydowii*, *N. salinicola*, *N. ammophila*; *Distichlis* - *N. salinicola*, *N. ammophila*, *N. binodulosa*; and *Scirpus* - *N. sydowii*, *N. hudsonis*, *Amphora coffeaeformis*. *Navicula salinicola* and *N. ammophila* were among the three most abundant taxa in all but the *Scirpus* community, and together accounted for nearly 1 out of every 5 valves counted during the study.

The character of the diatom flora observed in the present study was very different from that seen in 1976-77 (Sullivan, 1978). *Navicula tripunctata* (Müll.) Bory was the single most abundant diatom in the earlier study accounting for 21.5% of all valves counted. In the present study this taxon was split into two taxa (*N. ammophila* and *N. normaloides*) which together accounted for 9.8% of all valves counted. *Navicula salinicola* was among the three most abundant taxa beneath the *Distichlis* and *Juncus* canopies in the earlier study. *Nitzschia obsidialis* Hust. and *Nitz. pseudoamphioxys* Hust. were dominants in the previous study but not a single valve was encountered in the present study. *Achnanthes rostrata* (synonym = *A. lanceolata* var. *dubia* Grun.) was the second most abundant diatom beneath the *Juncus* and *Scirpus* canopies in 1976-77 but accounted for less than 2% of all valves counted in both habitats in 1985-86. Taxa such as *Denticula subtilis*, *Navicula peregrina*, *N. pseudocrassirostris*, *Nitzschia bilobata* var. *ambigua* Manguin, *Nitz. perversa*, *Nitz. scalaris*, and *Stauroneis amphioxys* var. *obtusa* Hendey were abundant (i.e. overall abundance > 0.7%) in the previous study but were either extremely rare or completely absent in the present one. Conversely, 10 of the 48 taxa listed in Table 6 were not observed even once during the earlier study; collectively they accounted for 14.3% of all valves counted.

Some remarks concerning the temporal and spatial distribution of selected edaphic diatom taxa should be made. *Fragilaria hyalina*, *F. obtusa*, and *F. pinnata* were first observed in the collection immediately following Hurricane Elena. The first two taxa were not observed in the previous study but *F. hyalina* was found to be the most abundant diatom taxon on offshore seagrasses of Mississippi Sound (Sullivan, 1979). All three *Fragilaria* taxa were relatively abundant immediately after both Hurricane Elena and Juan and then steadily decreased in abundance during the remaining months of the study. *Fragilaria* was least abundant beneath *Scirpus*. Taxa that became most abundant after Hurricane Elena were *Navicula ammophila*, *N. flanatica*, and *Pinnularia ambigua*, whereas *Nitzschia petitiana* was first collected after Hurricane Juan. Taxa with winter and early spring maxima were *N. hudsonis*, *N. salinarum*, and *Nitz. filiformis*. Finally, *N. normaloides*, *N. phyllepta*, and *Nitz. quadrangula* were most abundant in spring and summer. A contrasting pattern was exhibited by *Amphora coffeaeformis*, *A. exigua*, *N. salinicola*, and *Plagiogramma tenuissimum*, which were equally abundant over an annual cycle.

Diatoms which showed a marked "preference" for one particular habitat were *N. obsoleta* for *Juncus*, *Nitz. siliqua* for *Distichlis*, and *N. hudsonis*, *N. consentanea*, *N. flanatica*, *N. phyllepta*, and *N. salinarum* for *Scirpus*. As previously mentioned, *Nitz. habirshawii* and *Nitz. petitiana* were restricted to the sediments beneath *Scirpus*. No taxon showed a marked preference for *S. alterniflora*. Furthermore, the preferences listed above did not correspond to spatial patterns observed in the earlier study of Sullivan (1978). Finally, *N. binodulosa* showed distinct "preferences" for *Juncus* and *Distichlis*, whereas *N. sydowii* was the most abundant diatom beneath *S. alterniflora* and *Scirpus* but extremely rare in the remaining two habitats. It should be pointed out for the latter diatom taxon that the June and July samples yielded 329 out of the 402 valves counted in *S. alterniflora* and 342 of the 343 valves from *Scirpus*. In the previous study, *N. binodulosa* was restricted to the *Distichlis* community and *N. sydowii* (synonym = *N. incerta* Grun.) was a member of only the *Distichlis* and *S. patens* communities, where it was very rare.

Community Diversity

Values for species diversity (H') and the number of diatom taxa in a sample (S) of 300 valves are given in Tables 7 and 8, respectively. H' ranged from a low of 2.471 to a high of 5.184 while S ranged from 24 to 57. The low H' values characterizing the *S. alterniflora* and *Scirpus* communities on 12 June and 16 July were associated with large populations of *Navicula sydowii*. The lowest H' value for the *Distichlis* community was associated with a large bloom of *N. ammophila* on 19 September following Hurricane Elena. The highest H' value in each habitat occurred on 5 December except for *Distichlis* where this occurred in the next month. In general, highest community diversity values were observed during winter, which is typical of sediment-associated diatom communities.

The average H' and S values ($n = 10$) did not differ greatly among the four edaphic diatom communities. *Juncus* tended to be slightly more diverse while *Distichlis* and *Scirpus* tended to be the least diverse. This is opposite to the situation that existed in my 1976-77 study, where *Distichlis* harbored the most diverse diatom community and *Juncus* and *S. alterniflora* the least diverse ones. In this previous study, H'

ranged from 2.825 to 4.397 and S from 28 to 48. These ranges were smaller than those found in the present study and it would probably be safe to add that edaphic diatom community diversity appears to be higher in Graveline Bay Marsh at the present time than in 1976-77.

Community Similarity

The structural similarity between selected pairs of edaphic diatom communities was objectively measured by use of the Czekanowski Quantitative Index (CZ) previously described. CZ values were calculated for both the data of the present study and that of my previous study (Sullivan, 1978) and these results are presented in Table 9. The *Juncus* & *Distichlis* communities were structurally most similar and shared 74% of the maximum similarity possible. The lowest CZ values resulted when the *Scirpus* community was part of the comparison. Such values were less than 0.400 except for the *Scirpus* & *S. alterniflora* comparison which was 0.546. As previously mentioned, *Navicula sydowii* was the dominant diatom in both communities, but was abundant only in June and July. If one were to delete this diatom from the calculations then CZ would drop to 0.483. In the previous study, *Scirpus* & *Juncus* and *Scirpus* & *S. alterniflora* were the most similar community pairs and *Distichlis* & *S. alterniflora* the most dissimilar pair. Examination of Table 9 shows that this is not true for the diatom communities sampled in 1985-86.

Canonical Correlation Analysis

Since the diatom taxa composing a given edaphic diatom community on each sampling date and the environmental factors that regulate the spatial and temporal distribution of each taxon represent multivariate data sets, a canonical correlation analysis was performed (Dixon & Brown, 1979: BMDP6M program) on the entire data set. The 33 most abundant diatom taxa constituted the variables of the first set and 10 "environmental" variables made up the second set. Table 10 summarizes the results of the canonical correlation analysis.

The first canonical variable (CV1) had a high positive correlation ($r = 0.716$) with productivity and a moderate positive correlation ($r = 0.522$) with chlorophyll *a*. Taxa with high positive correlations with CV1 (*Navicula salinarum* and *Nitz. alexandrica*) tended to be most abundant in those areas and on those dates where hourly production rates and chlorophyll *a* concentrations were highest. No taxon possessed a negative correlation with CV1 greater than -0.5. The two *Fragilaria* species that had the highest negative correlations with CV1 were most abundant when productivity and chlorophyll *a* were lowest however.

The second canonical variable (CV2) had a positive correlation ($r = 0.620$) with chlorophyll *a* and a negative correlation ($r = -0.722$) with moisture content of the marsh sediments. Taxa that have high positive correlations with CV2 should be abundant when both soil moisture (see Table 2) and chlorophyll *a* concentrations are high. This was true for the two taxa with the highest positive correlations with CV2, *Navicula consentanea* and *Amphora coffeneformis*. In contrast, *N. contenta* tended to be most abundant in dry sediments with low chlorophyll *a* concentrations; its correlation coefficient with CV2 was -0.575.

In a previous study of edaphic diatom distribution in Graveline Bay Marsh (Sullivan, 1982), canonical correlation analysis was also performed. Only the first two canonical variables were biologically interpretable as in the present study, but in the former CV1 was negatively correlated ($r = -0.920$) with relative elevation and CV2 was negatively correlated ($r = -0.876$) with canopy height. Elevation was not included in the present study as this variable was changed twice by sediment deposition from two hurricanes. Canopy height showed only weak correlations with CV1 and CV2 in the present work (Table 10).

The canonical correlation analysis indicated that the redundancy in the species given the environmental data was 0.467 (Table 10). This compares well with redundancy values of 0.412 (McIntire, 1978) and 0.498 (Amspoker & McIntire, 1978) for canonical correlation analysis of benthic diatom distribution in Oregon estuaries. The combined redundancy for CV1 and CV2 was only 17% (i.e., 36% of the total redundancy -- see Table 10) and this explains in part the low correlations between the species data and the canonical variables. In addition, the lack of high R^2 values for taxa possessing the highest negative correlations with CV1 may also explain this. McIntire (1978) found a redundancy of 31% for CV1 and CV2 while this value was 29% in Amspoker & McIntire's (1978) study. In Sullivan's (1982) previous study, redundancy associated with CV1 and CV2 was 23%, and several taxa exhibited high negative correlations (i.e. $r > -0.5$) with CV1. As pointed out in this last paper, environmental gradients are at best difficult to perceive in salt marshes where a few steps may allow one to traverse two or three monospecific stands of vascular plants. In spite of this, the current canonical correlation analysis collapsed the multidimensionality of the data into two interpretable, orthogonal (uncorrelated) dimensions and identified productivity, chlorophyll *a*, and soil moisture content as potentially related to the distribution of edaphic diatoms across Graveline Bay Marsh.

Edaphic Algal Functioning

Chlorophyll a

Chlorophyll a concentrations (hereafter referred to as chl. a) beneath each of the five vascular plant canopies are listed in Table 11. Chl. a ranged from a low of only 2 mg/m^2 in S. patens on 16 July to a high of 400 mg/m^2 in Scirpus on 14 May. The Scirpus habitat had the highest chl. a values on all 10 sampling dates while chl. a was lowest beneath S. patens on 7 out of 10 dates. Chl. a exhibited very similar temporal patterns in all edaphic habitats (Figs. 2-6). It tended to be highest in April and May, dropped to its lowest values in June and July when the vascular plant canopies were tallest and densest, and starting in October began a steady increase which leveled off in March. Following Hurricane Elena, chl. a rose greatly in the S. patens habitat. Perhaps this was a response to storm-related deposition of fine sediments to replace the high sand content that existed at this habitat before Elena roared ashore.

Table 11 also lists the mean chl. a value for each edaphic habitat of Graveline Bay Marsh. The lowest such value was 38 mg/m^2 for S. patens and the highest 160 mg/m^2 for Scirpus. Very few data on chl. a in salt marsh sediments have been published. Gallagher (1971) measured concentrations of 111, 127, and 92 mg/m^2 for tall S. alterniflora, short S. alterniflora, and Distichlis, respectively in a Delaware salt marsh. In this same marsh, Sullivan & Daiber (1975) found mean annual chl. a beneath short S. alterniflora to be 95 mg/m^2, which is identical to the mean value characterizing a stand of medium S. alterniflora in Mississippi. Estrada et al. (1974) published chl. a values of 95 mg/m^2 for short S. alterniflora and 193 mg/m^2 for a mixed stand of S. patens and *Distichlis* in a Massachusetts salt marsh. The three previous studies cited above used the traditional acetone extraction method, whereas we employed hexane partitioning following acetone extraction according to the technique of Whitney & Darley (1979). The former technique measures chlorophyllide *a* along with "active" chl. *a*, while the latter corrects for all degradation products of chl. *a*. Varela & Penas (1985) used the acetone/hexane technique to determine pigment concentrations on an intertidal sand flat in northwest Spain. On the average, "total" chl. *a* consisted of 15% "active" chl. *a*, 12% chlorophyllide *a*, 54% pheophytin *a*, and 19% pheophorbide *a*. In their study 85% of "total" chl. *a* was in a degraded form. Therefore, it is likely that the chl. *a* values reported for Delaware and Massachusetts marshes are overestimates. Whatever the case may be, it is clear that chl. *a* concentrations beneath the vascular plant canopies in Mississippi marshes are comparable to those of their Atlantic counterparts.

Table 12 lists values for one of the three degradation products of chl. *a*, in this case pheophytin *a*, which has lost the magnesium atom from the central porphyrin ring. The most striking feature about the distribution of pheophytin *a* is the fact that it was either undetectable or near zero during April and May beneath the *S. alterniflora* and *Scirpus* canopies. It was during these two months that the highest chl. *a* concentrations of the study were recorded. Chl. *a* and pheophytin *a* were negatively correlated for the data taken over all sampling dates and vascular plant zones ($r = -0.624$, $p<0.01$). The highest pheophytin *a* concentrations were measured in all edaphic habitats on 19 September, which with the exception of *S. patens* was the time of lowest chl. *a* concentrations. In *Juncus*, *S. patens*, and *Distichlis* pheophytin *a* concentrations were almost always higher than those of chl. a. In contrast, the opposite was true on 6 out of 10 dates in S. alterniflora and 8 out of 10 dates in Scirpus. It is not possible to compare the pheophytin a values reported here with those previous studies since both pheophytin a and pheophorbide a were measured together as "pheopigments" in the latter. However, the very low to undetectable concentrations of pheophytin a in S. alterniflora and Scirpus from April to July have not been reported in other marine sedimentary environments and the explanation for such low values is at present unknown.

A stepwise multiple regression was performed (Dixon & Brown, 1979: BMDP2R program) to determine the relative importance of 8 independent variables in explaining the variation in chl. a concentrations beneath each vascular plant canopy. Table 13 lists the variables employed in this analysis as well as other multiple regressions and discriminant analyses to be discussed later. The stepwise procedure used here will cease adding variables to the regression equation when none of the remaining variables has an F value to enter greater than or equal to 4.0. In the three most productive areas (S. alterniflora, Distichlis, Scirpus), pheophytin a was the first variable to enter and in all cases the sign of its regression coefficient was negative (Table 14). This inverse relationship between chl. a and pheophytin a was expected based on the discussion in the previous paragraph. Soil moisture appeared in the regression equation in the S. patens, Distichlis, and Scirpus habitats. Surprisingly, light energy reaching the marsh surface appeared only twice and in both cases was the third and last variable to enter. The coefficient of determination (R^2) ranged from 0.43 in Distichlis to 0.68 in S. alterniflora and S. patens (i.e. the 8 environmental variables "explained" between 43 and 68% of the variability in chl. a concentrations). In general terms, higher chl. a values tend to be associated with both lower pheophytin a concentrations and lower sediment salinity.

Hourly Production

Hourly edaphic algal primary productivity rates are listed in Table 15 and presented graphically in Figs. 2-6. Hourly production was lowest beneath *S. patens*, reaching values as low as 0.4 mg C/m^2/h on 16 July, when the grass canopy was densest and light energy reaching the marsh surface was lowest. Productivity, on an hourly basis, was highest in the *Distichlis* and *Scirpus* habitats. It skyrocketed in *Scirpus* to 163.6 mg C/m^2/h on 26 March, which is equivalent to an annual rate of 716.6 g C/m^2/yr according to procedures to be described later.

With the exception of *S. patens*, where productivity was essentially a straight line parallel to the X-axis, temporal productivity patterns were very similar beneath the different vascular plant canopies (Figs. 2-6). In all four remaining areas, productivity decreased from April to May and then rebounded to a peak summer value in June. With the exception of *Juncus*, a precipitous linear decline marked the months of July and September. Hourly productivity values tended to reach their lowest values in September and October following Hurricane Elena. In all areas but *Distichlis* production rose again in December following Hurricane Juan. January and February 1986 were abnormally cold months on the Mississippi Gulf Coast, and productivity was less than 10 mg C/m^2/h during these two months in all areas except *Scirpus* where a value of 33.7 mg C/m^2/h was measured on 13 February (Table 15). In all habitats productivity greatly increased with the return of warm spring temperatures in March.

Comparisons of the temporal patterns of edaphic algal productivity observed in Graveline Bay Marsh with those of other marshes are of interest, but caution must be used in view of the fact that three major hurricanes impacted the former marsh. In general, algal productivity in the Mississippi marsh was highest during spring and early summer with lowest productivity rates being recorded in fall (Figs. 2-6). In addition, productivity exhibited a pronounced secondary peak in December in most vascular plant zones. Farther north in Delaware, Gallagher (1971) found that algal productivity was highest beneath short S. alterniflora and Distichlis during spring and/or summer while production peaked in tall S. alterniflora during late winter and early spring. Production was lowest beneath all three canopies in fall as in the present study. Van Raalte et al. (1976) measured highest productivity in spring and fall and lowest rates in summer and early winter beneath the vascular plants of a Massachusetts salt marsh. In southern California, Zedler (1980) found algal productivity to be highest in summer and lowest in spring. Thus, the study temporally most similar to that of the present one was that of Gallagher (1971).

The hourly productivity data, subjected to a 2-way ANOVA (Dixon & Brown, 1979: BMDP2V program), produced a 2-way interaction term (site x month) that was highly significant ($p < 0.0001$). S. patens was not included in the ANOVA since productivity here was so low and did not exhibit any detectable temporal variation. The mean hourly values for the remaining four edaphic habitats during each month were compared by calculating the least significant difference (LSD = 14.25) at the 0.05 level of significance; these results are shown in Table 15. During May and from September through January, hourly production was statistically equivalent beneath all four vascular plant canopies. In February and March, *Scirpus* was significantly greater than the remaining three habitats, which did not differ in their productivity rates. *Scirpus* was significantly different from *Juncus* during April whereas no two edaphic algal communities had statistically equivalent productivity rates in June. In July, *Juncus* was significantly lower than the remaining three areas, and *Distichlis* was significantly higher than *S. alterniflora*. This pattern is very similar to that seen in June.

To determine if a linear relationship existed between hourly productivity and community diversity, simple linear regressions (Dixon & Brown, 1979: BMDP6D program) were run employing either species diversity (H') or the number of diatom taxa in a sample (S) as the independent variable. A linear relationship between S and production was observed only in *S. alterniflora* ($p = 0.03$; $r^2 = 0.37$) and *Distichlis* ($p = 0.01$; $r^2 = 0.48$). The regression equations were $\hat{Y} = 31.52 - 0.46X$ and $\hat{Y} = 79.93 - 1.63X$ in *S. alterniflora* and *Distichlis*, respectively, where $\hat{Y} = \text{mg C/m}^2\text{/h}$ and X = number of diatom taxa in a count of 300 valves. Since the slope is negative in both cases, algal productivity is predicted to decrease as the number of diatom taxa increases. A linear relationship between H' and production did not exist in any vascular plant zone.

Stepwise multiple regressions were performed (Dixon & Brown, 1979: BMDP2R program) to determine the relative importance of environmental factors alone and both environmental factors and various attributes of community structure in explaining the variation in hourly edaphic algal productivity rates. The first set of multiple regressions, employing environmental factors only, is shown in Table 16. The coefficient of multiple determination (R^2) ranged from a low of 0.39 in *S. alterniflora* to a high of 0.86 in *Scirpus*. Moistness of the sediment surface and chl. *a* concentration were useful predictor variables in four and three, respectively of the regression equations and in all cases had positive regression coefficients. It should be pointed out that chl. *a* entered the regression equation for *Distichlis* at Step 2 (making the cumulative $R^2 = 0.51$) but was removed at Step 6. Chl. *a* was the first variable to enter for both *Juncus* and *S. patens*. Examination of Figs. 2 and 4 indicates a weak linear relationship between chl. *a* and production in these two habitats. Since all light energy fixed in the photosynthetic process must pass through the chl. *a* molecule, it is not surprising to find that chl. *a* proved to be a good predictor of algal productivity in the present study. This has been found in virtually all studies of algal productivity in marine benthic environments. Moistness was the first variable to enter the regression equation for *S. alterniflora* and *Scirpus* and the second one for *Distichlis*. Since the sign of regression coefficient for moistness was positive in all cases, this indicates that as the marsh surface dries out algal productivity is predicted to increase. In September and October algal production was at a minimum (Figs. 2-6) when all habitats except *S. patens* were submerged (see Table 2 where the moistness index was 0). In general, the highest productivity rates were associated with a moisture index of 3 or 4 in each habitat. Holmes & Mahall (1982), who worked with high intertidal sediments in a California lagoon, found that the productivity of the benthic microflora (motile diatoms and filamentous blue-greens) was maximal in moist sediments. Minimum rates were measured for flooded sediments. Their findings are in agreement with those of the present study.

As in the regressions for chl. a (Table 14), light energy reaching the marsh surface was a poor predictor variable for algal production, appearing only in the Distichlis equation where canopy height was the first variable to enter (Table 16). This contrasts with the findings of Van Raalte et al. (1976), who found a highly significant, linear relationship between light energy reaching the marsh surface and edaphic algal production in a Massachusetts salt marsh; however it agrees with those of van Es (1982) and Colijn & de Jonge (1984), who found no correlation between light energy and benthic microalgal production in the sediments of the Ems-Dollard Estuary. Van Raalte et al. reported no correlation existed between temperature and algal production. In the present study, air and/or sediment temperatures were the last variables to enter in three of the regression equations, with the largest increase in R^2 being 0.10 in the case of Juncus (Table 16).

The second set of stepwise multiple regressions on hourly algal production, employing both environmental and species variables, is summarized in Table 17. The coefficient of multiple determination (R^2) ranged from a low of 0.38 in S. alterniflora to a high of 0.87 in Scirpus. The remaining two habitats had R^2 values > 0.80. When H', S, and the relative abundances of the 33 most numerous diatoms were added to the 8 environmental variables, the former predominated as predictor variables in the regression equations at the expense of the latter (compare Tables 16 and 17). However, R^2 was either identical or only slightly increased by the addition of the species data (Table 18). The 8 environmental variables accounted for 79 and 70% of the variability in hourly algal production in *Juncus* and *Distichlis*, respectively, whereas the addition of the species data increased this to 85 and 82%, respectively. R^2 actually decreased by 1% in *S. alterniflora* and increased 1% in *Scirpus* when the species data was added (Table 18). Note that *S. patens* is not included in either Table 17 or 18 since diatom counts were not made in this unproductive habitat.

The only environmental variables to enter the regression equations were air temperature and light for *Juncus* and *Distichlis*, respectively (Table 17). These same variables were included when only environmental factors were considered (Table 16) and entered the equations in approximately the same positions in both the absence and addition of the species variables. Number of taxa in a sample (S) entered the regression equation first for *S. alterniflora*, as it did for *Distichlis* ($R^2 = 0.40$), but in the latter case was removed at Step 6. As previously mentioned, a significant linear (and negative) relationship between hourly productivity and S was found only in these two habitats.

Of all the diatom taxa listed in Table 17, only *Nitzschia alexandrica* (SP23) and *Nitz. pubens* (SP28) appeared in more than one regression equation. In 11 of 14 cases, the sign of the regression coefficient (which is multiplied by the relative abundance of the taxon in question) was positive. In some cases, the diatom taxa selected as predictor variables were abundant (e.g. *Navicula obsoleta* (SP18) in *Juncus* and *Nitz. quadrangula* (SP29) in *Distichlis*), while in other cases the taxa were not abundant (e.g. *Pinnularia ambigua* (SP32) in *Distichlis* and *Nitz. alexandrica* (SP23) in *Scirpus*) (see Tables 6 and 17). No one combination of environmental factors or species relative abundances was a good predictor of algal production in *S. alterniflora*, whereas either set of variables did a "good job" of predicting production in the remaining three habitats. To the author's knowledge, this is the first attempt to determine how well the relative abundances of diatom taxa (or for that matter all other algal taxa as well) can "explain" the variability recorded for algal productivity in any marine benthic environment. Dixit (1986) carried out a series of multiple regressions to estimate lake-water pH using various attributes of diatom community structure from the sedimentary record. The best predictor variables were the relative abundances of selected diatom taxa ($R^2 = 0.96$) rather than equations involving the proportions of individuals belonging to arbitrarily defined groups differing in their pH optima. It is hoped that more studies of the kind reported here may show that marine benthic diatoms are as useful in predicting productivity as their freshwater counterparts are in inferring pH of recent and fossil lake-water pH.

Annual Production Estimates

Extrapolating from hourly production rates to daily, monthly, and annual values is subject to many sources of error. In the present study a simplistic approach was taken: for each vascular plant zone the average hourly productivity rate (see Table 15) was multiplied by the average photoperiod length during the study (12h), which was then multiplied by 365 days. Rizzo & Wetzel (1986) found that monthly measurements (as employed in the present study) were adequate for estimation of annual productivity rates for benthic microalgae in the sediments of the York River Estuary in Virginia. In contrast, Shaffer & Onuf (1985) state that this simplistic approach (their Formula A) overestimates productivity by ca. 30%. However, they do note that where light saturation of benthic microalgal production occurs at low light intensities, the simplistic approach taken above introduces little systematic error. Preliminary photosynthesis-irradiance work in Graveline Bay Marsh has shown that the resident edaphic algal communities are very efficient at low light levels and are photoinhibited to a significant degree in full sunlight. Hall & Fisher (1985) found identical annual rates for the simplistic approach and integration of the area beneath daily curves (71.84 vs. 71.04 g C/m^2) in their study of a blue-green algal mat inhabiting the unvegetated sediments of a Texas salt marsh. We therefore feel our simplistic approach provides a reasonable estimate of algal productivity over a yearly cycle.

Annual production rates of edaphic algae in Graveline Bay Marsh ranged from a very low 8.8 g C/m^2/yr in _S. patens_ to a quite respectable 150.7 g C/m^2/yr in _Scirpus_ (Table 19). _Distichlis_ and _S. alterniflora_ were somewhat intermediate while _Juncus_ was towards the lower end of the scale. Table 20 compares annual edaphic algal production from different salt marshes of the United States (no such studies have been carried out in Canadian or European marshes). The figure given by Van Raalte et al. (1976), which has been cited often in the literature, may be in error, as examination of their paper (p. 871) suggests that they had converted g C/m^2/yr to g dry wt/m^2/yr. In any event, the range (28-151) for the present study is broader than but compares favorably with those reported for Delaware, Massachusetts, and Texas marshes. Note that data for the _S. patens_ habitat was not included in Table 20 because this area was destroyed twice by hurricanes and it was not studied in any of the other investigations. The edaphic algae were clearly most productive in the Georgia and California studies. Table 4 of Colijn & de Jonge (1984) contains a summary of edaphic microalgal production from intertidal flats and shallow coastal areas around the world. Colijn & de Jonge point out that, on a global scale, most annual production values are within a narrow range from 50 to 200 g C/m^2. They ascribe this to the dynamic nature of the marine sedimentary environment in tidal areas, which limits the formation of a considerable algal biomass and hence their production. Except for S. patens and Juncus (Table 19), the annual production determined for the remaining edaphic algal communities fall within Colijn & de Jonge's range.

One of the major objectives of the study was to compare algal production rates to those of the overstory vascular plant canopy. This was accomplished by using literature values based on studies conducted in Mississippi (Table 21). Except for one study (that involving Scirpus where all aboveground biomass dies and completely collapses during winter), all others employed a harvest method and monthly measurements to arrive at a realistic estimate of total annual net aerial production of each vascular plant species. To convert annual algal production in g C/m^2 to g ash-free dry wt/m^2 the former values were multiplied by 2 (Gallagher & Daiber, 1974). A ratio of annual edaphic algal to vascular plant production (EAP/VPP) was then calculated and gave the following values: Juncus (10%), S. alterniflora (11%), S. patens (1%), Distichlis (12%), and Scirpus (61%). For reasons previously cited, the very low EAP/VPP value for S. patens was excluded from Table 20. Despite large differences in canopy stature and productivity, as well as in abiotic factors, the production of edaphic algal communities beneath Juncus, S. alterniflora, and Distichlis was 10-12% that of the overstory canopy on an annual basis. The aerial shoots of Scirpus are annual and form localized clumps; this, together with high edaphic algal production, produced an EAP/VPP of 61%.

EAP/VPP values for salt marshes in the United States are given in Table 20. The 10-12% range for the three vascular plant zones of Graveline Bay Marsh discussed above is the same as that found for a Texas marsh, but less than that found for Delaware, Massachusetts, and Georgia marshes. The 61% value associated with the Scirpus habitat is considerably greater than that reported for all other marshes except those in California where annual algal production equaled or exceeded that of the overstory canopy in two of four vascular plant zones studied (Zedler, 1980). The edaphic algae in Zedler's marsh formed mats on the sediment surface up to 5 mm thick and were dominated by filamentous green and blue-green algae, but diatoms were also abundant. Furthermore, these mats grew up the vascular plant stems for 5-10 cm. The large algal biomass and reduction in vascular plant production caused by the arid environment and hypersaline saline soils were cited by Zedler as the main reasons for such high algal production rates. Since the production rates of vascular plants in salt marshes of the southeastern United States are higher than those from other geographical areas, an EAP/VPP value of 10% indicates that the edaphic algae contribute significantly to total marsh productivity.

Discriminant Analyses

Discriminant analysis is a powerful multivariate technique that allows one to study how well a set of variables can differentiate cases belonging to preassigned groups. Discriminant analysis also allows the investigator to analyze differences between groups, and provides a means to classify an individual case into the group it most closely resembles (Klecka, 1980).

In the present study, stepwise discriminant analyses (Dixon & Brown, 1979: BMDP7M program) were performed using *Juncus*, *S. alterniflora*, *Distichlis*, and *Scirpus* as the groups, and the variables listed in Table 13 as discriminators. In the first discriminant analysis, all environmental factors except canopy height were employed as discriminating variables. Canopy height was omitted because the four vascular plant zones fell into more or less distinct height categories (see Table 4); thus canopy height was essentially equal to the name of the vascular plant species. Environmental factors alone did a poor job of discriminating between the four vascular plant zones as the eigenvalue and canonical correlation coefficient for the first discriminant function were only 0.712 and 0.64, respectively. A plot of group centroids and individual cases in discriminant space (i.e. canonical variable 1 vs. 2) showed poor separation. A total of 55% of cases were correctly classified by the discriminant functions.

The second discriminant analysis employed only the species data (H', S, and relative abundances of the 33 most abundant diatom taxa -- see Table 13) as the discriminating variables. Table 22 lists information relevant to the discriminating power of the discriminant functions (only three can be derived since there are four groups). Approximately 90% of discriminating power resides in the first function and only 8% in the second function. There is virtually no discriminating power in the third function and it need not be considered further. Only the eigenvalue and canonical correlation coefficient associated with the first function can be considered "high". Based on calculations of Mahalanobis squared-distance for each case from each of the four group centroids, 70% of all cases were correctly classified (Table 23). Only 1 out of 10 cases for both *Distichlis* and *Scirpus* were incorrectly classified while the number of incorrect classifications was 4 for *Juncus* and 6 for *S. alterniflora* (see also Fig. 7). Table 24 lists the stepwise entry of selected variables where the F value to enter was greater than or equal to 4.0. Note that the variables SP21 (*Navicula salinicola*) and SP31 (*Nitzschia siliqua*) were removed at Steps 7 and 9. Their contribution to discrimination of groups was duplicated by either combinations of variables selected later, or by combinations of those variables selected later with SP18, hence their removal (see Klecka, 1980).

Of particular interest in discriminant analysis are the standardized (rather than absolute) discriminant coefficients for each of the selected variables. The magnitude of these standardized coefficients can be used to indicate which variables contribute most to determining scores on each discriminant function (Klecka, 1980). For function 1, *Navicula flanatica* (SP14), *N. hudsonis* (SP15), and *N. phyllepta* (SP19) made the greatest contribution (the sign is ignored) (Table 25). These three diatom taxa showed a marked preference for the *Scirpus* habitat (Table 6). Examination of Fig. 7 shows that the first function is separating *Scirpus* from the other three habitats. Only *N. obsoleta* (SP18) makes a major contribution to determining scores on function 2 (Table 25). This diatom was abundant beneath *Juncus* but either extremely rare or absent elsewhere (Table 6). Fig. 7 shows that the second function is separating *Juncus* from both *S. alterniflora* and *Distichlis*. None of the variables had high standardized coefficients for function 3 (Table 25), which is expected considering its lack of discriminating power (see Table 22). *N. sydowii* (SP22) was the last variable to enter (Table 24), but none of its standardized coefficients were high for any function (Table 25). This taxon was a dominant in both the *S. alterniflora* and *Scirpus* communities but extremely rare elsewhere (Table 6). Perhaps this variable was responsible for the slight separation between *S. alterniflora* and *Distichlis* along the first canonical discriminant function (Fig. 7).

The last discriminant analysis involved using all variables (except canopy height) listed in Table 13 as discriminators (i.e. all environmental and species data). The results were essentially identical to the analysis where only the species data was used, except that the percent of cases correctly classified increased from 70 to 88. The stepwise entry of variables was exactly the same as that shown in Table 24 except that light energy entered in Step 10 with an F value of 4.3; however, its standardized discriminant coefficient ranged from only 0.006 to 0.080 on the three functions. The improvement in correct classifications appears to reside in the fact that functions 2 and 3 had more discriminating power (10.5 and 2.9%, respectively) than when only species data were used. In addition, *N. obsoleta* (SP18) and *N. sydowii* (SP22) had standardized coefficients of 1.857 and 0.516, respectively on the third discriminant function.

SUMMARY

1. Temporal and spatial patterns of edaphic algal productivity in the sediments beneath the canopies of *Juncus roemerianus*, *Spartina alterniflora*, *S. patens*, *Distichlis spicata*, and *Scirpus olneyi* were determined over an annual cycle in a representative Mississippi salt marsh. This is the first such study for any Gulf Coast marsh.

2. A series of environmental factors were measured for correlation with the biological data. Sediment salinity was almost always less than 30 ^{o}/oo in all edaphic habitats. Light energy (400-700 nm) reaching the marsh surface was least beneath the *Juncus* and *S. patens* canopy and greatest beneath *Distichlis* and *Scirpus*. The tallest canopies were those of *Juncus* and *Scirpus* while the shortest belonged to *Distichlis*.

3. The edaphic diatom community beneath each vascular plant canopy was totally dominated by small, motile pennate diatoms. Filamentous non-diatom algae were occasionally abundant in trampled areas of the marsh and were mostly heterocystous blue-green algae.

4. A total of 155 taxa (species and their varieties) in 30 genera were constituents of the edaphic diatom flora of Graveline Bay Marsh. More than half of these taxa belonged to the genera *Navicula* and *Nitzschia*; 53 taxa were new records for Mississippi. Only two of the more abundant taxa were restricted to a particular vascular plant zone - *Nitz. habirshawii* and *Nitz. petitiana* in *Scirpus*. For

the most part, the more abundant taxa were widely distributed over the marsh; however, many of these showed a "preference" for either one or two habitats.

5. *Navicula salinicola* and *N. ammophila* were among the 3 most abundant diatoms in all habitats except *Scirpus* and collectively accounted for nearly 1 out of every 5 valves counted during the study. *N. sydowii* was the most abundant diatom in both the *S. alterniflora* and *Scirpus* communities. Hurricane Elena introduced 3 species of *Fragilaria* into the Graveline system. Floristic comparisons with a 1976-77 study done by the author indicate that the character of the edaphic diatom flora has changed substantially.

6. The edaphic diatom communities beneath all 4 vascular plant communities were quite diverse ($\bar{H}' = 4.072 \pm 0.207$ bits/individual and $\bar{S} = 39.1 \pm 2.4$ taxa/300 valves). Comparison of community similarity by the Czekanowski Quantitative Index showed that *Juncus* and *Distichlis* were most similar, while the community least similar to the rest was *Scirpus*. A canonical correlation analysis collapsed the data base into 2 interpretable, orthogonal dimensions and identified productivity, chlorophyll *a*, and soil moisture content as potentially related to the distribution of edaphic diatoms across Graveline Bay Marsh. A stepwise discriminant analysis employing the relative abundances of the 33 most abundant diatom taxa assigned 70% of the cases to the correct community. Of the 4 discriminator taxa selected, 3 showed a distinct preference for *Scirpus* and 1 a distinct preference for *Juncus*.

7. The concentration of chl. a was always highest in Scirpus (max. value = 400 mg/m^2) and usually lowest beneath S. patens (min. value = 2 mg/m^2). In all habitats, chl. a was highest in spring, and lowest in summer when the vascular plant canopies were tallest and densest. Mean annual chl. a values were 38 to 160 mg/m^2 for the 5 habitats, which were comparable to those reported (92-127 mg/m^2) for Delaware and Massachusetts marshes. Pheophytin a concentrations were undetectable during April and May in S. alterniflora and Scirpus, and were typically less than those of chl. a in these same 2 habitats in other months. A stepwise multiple regression of chl. a on 8 environmental variables showed pheophytin a, soil moisture, and salinity to be the best predictor variables. All 3 predictor variables had negative regression coefficients. R^2 ranged from 0.43 to 0.68 in the 5 vascular plant zones.

8. Hourly edaphic algal production was always lowest beneath S. patens (min. value = 0.4 mg C/m^2/h) and highest beneath Distichlis and Scirpus. Hourly production skyrocketed to 164 mg C/m^2 in Scirpus on 26 March, however its mean hourly value in this habitat for all 10 months was 34 mg C/m^2. In all areas except S. patens (where production was low and more or less constant), hourly productivity was highest in spring-early summer and lowest in the fall. Hurricane Elena, which came ashore on 2 September, was probably responsible for the very low production rates measured across Graveline Bay Marsh in September and October.

9. Stepwise multiple regressions were run with hourly edaphic algal production as the dependent variable. The first set of regressions, which employed 8 environmental variables as the independent variables, generated R^2 values of 0.39 - 0.86 for the 5 vascular plant zones. The best predictor variables were chl. *a* and soil moisture, both of which always had positive regression coefficients. Light energy reaching the sediment surface proved of little value. In the second set of regressions, the relative abundances of the 33 most abundant diatom taxa were added to the list of independent variables. Adding the species data slightly increased R^2 in some cases (range = 0.38 - 0.87). Virtually all predictor variables were diatom taxa. These taxa were different in the different vascular plant zones, were either abundant or not, and most had positive regression coefficients. No combination of environmental or species variables did a "good job" of predicting hourly rates in *S. alterniflora*, but R^2 values ranged from 0.70 to 0.87 in the remaining habitats.

10. Hourly edaphic algal production rates were converted to annual rates. These rates in g $C/m^2/yr$ were as follows: *S. patens* (9), *Juncus* (28), *S. alterniflora* (57), *Distichlis* (88), and *Scirpus* (151). The range in annual values for Graveline Bay Marsh is broader than those reported for Delaware, Massachusetts, and Texas marshes (61-105), but less than those measured in California and Georgia marshes (200-341). This difference in productivity may be related to differences in edaphic algal community composition. Annual edaphic algal production rates (EAP) were compared to the

annual net aerial production rates (VPP) of the overstory canopies. EAP/VPP values (x 100%) were as follows: *S. patens* (1), *Juncus* (10), *S. alterniflora* (11), *Distichlis* (12), and *Scirpus* (61). The values for *Juncus*, *S. alterniflora*, and *Distichlis* are equal to those reported for a Texas marsh (8-13), but less than those characterizing marshes in Delaware, Massachusetts, and Delaware (25-33). Only the EAP/VPP value for *Scirpus* approached those (76-140) reported for California marshes, where the highest edaphic algal production rates have been measured.

CONCLUSIONS

The present study has shown that the edaphic algae of Graveline Bay Marsh, despite living constantly in the shade of the macroscopic vascular plant canopies, possess significant primary production rates. These rates were shown to be comparable to those of their counterparts in salt marshes of Delaware, Massachusetts, and Texas. The question naturally arises as to whether or not edaphic algal production is important as a food source for consumers within the marsh itself and in adjacent estuarine waters; their importance will hopefully be shown in our next Sea Grant project (R/LR-18) where stable carbon and sulfur isotope analyses of marsh flora, fauna, and sediments will be determined. It is well known that intertidal edaphic diatoms are easily suspended by tidal currents (Williams, 1962; Gallagher, 1975; Baillie & Welsh, 1980; Varela & Penas, 1985; Shaffer & Sullivan, manuscript in preparation) and hence potentially available to consumers. Numerous studies have shown that salt marsh animals do indeed seek out and ingest edaphic algae (e.g. Brenner et al., 1976; Pace et al., 1979; Connor & Edgar, 1982; Gleason & Zimmerman, 1984; Stuart et al., 1985; Decho, 1986). Therefore, the edaphic algae could be a major food source for animals that are dependent on salt marshes for at least part of their life cycle. This floral component is productive on a year-round basis and is immediately available for consumption as it does not have to enter a detrital pathway as would vascular plant production. Stable isotope studies (summarized by Fry & Sherr, 1984) and detritus work (Ribelin & Collier, 1979) have shown that virtually all vascular plant production is buried in the marsh sediments rather than exported.

Hence, the productivity rates of edaphic algae may be much more important than their magnitude would indicate because of their high turnover rates and palatability.

Stepwise multiple regressions suggested that edaphic algal production rates are controlled primarily by standing crop (measured as chl. *a* with correction for all degradation products) and soil moisture. Light energy apparently has little effect on production, as the edaphic algae of Graveline Bay Marsh appear to saturate at very low light levels. Chl. *a* concentrations in turn were most related to pheophytin *a*, soil moisture, and salinity; again light energy was a poor predictor variable in the stepwise multiple regression analyses. From a management standpoint, edaphic algal production is expected to be highest when chl. *a* concentrations are highest and no standing water is present on a marsh surface which has dried out slightly. Chl. *a* concentrations (i.e. standing crop) are expected to be highest under the moisture conditions described above and when both pheophytin *a* and salinity values are toward the lower end of the scale. Therefore, as a general statement, edaphic algal productivity should be highest in salt marshes that are brackish and well-drained. Such conditions should favor the development of large and extensive edaphic diatom populations.

Those marshes which have the largest stands of *Scirpus*, *Distichlis*, and *S. alterniflora* will have the highest edaphic algal production rates. *Scirpus* stands are heavily utilized as habitat and feeding grounds by fur-bearing animals (nutria and muskrats) whereas the other vascular plant zones receive little use. By far the highest edaphic algal production rates were in *Scirpus*, and on numerous occasions we observed large numbers of small fish and invertebrates grazing on the abundant edaphic diatoms, which were easily visible as a striking, golden-brown hue on the sediments. Whether or not this observed consumption is transferred to higher trophic levels is the subject of future research. It is probably safe to conclude, however, that from a management point of view, *Scirpus* marshes are highly desirable: the production of fur-bearing animals is high, the edaphic algae are the most productive here, and herbivore activity on the marsh appears to be more intense here than elsewhere. It may be entirely coincidental but the edaphic diatom community beneath *Scirpus* is most distinct in terms of the specific identity and abundance of the more abundant taxa. Hence this area of the marsh stands out from the rest because of the structure and functioning of both the overstory canopy and understory, microscopic edaphic algal vegetation.

Two major hurricanes (Elena and Juan) directly impacted Graveline Bay Marsh during the course of the study. The resiliency of the marsh flora was remarkable. With the exception of a portion of the *S. patens* stand which was buried by an overwash of beach sand, the vascular plants seemed to be little affected by the hurricanes except for the removal of dead standing material. Edaphic algal productivity was sharply reduced in September and October following Hurricane Elena, and three species of the offshore diatom genus *Fragilaria* were introduced to the marsh. However, following both hurricanes, the entire marsh surface was a deep golden-brown color due to an accelerated growth of edaphic diatoms. In the last two months of the study (February and March), edaphic algal production began to rise sharply beneath the vascular plant canopies and increased markedly in the *Scirpus* habitat. Data collected suggest that annual edaphic algal production estimates would have been much higher if the study had been started one year later. It therefore would appear that hurricanes may have beneficial effects on the macroscopic and microscopic flora of irregularly flooded Gulf Coast salt marshes.

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Table 1. Air and sediment temperature (°C) in each vascular plant zone of Graveline Bay Marsh from 12 April 1985 - 26 March 1986.

	4/12		5/14		6/12		7/16		9/19		10/24		12/5		1/8		2/13		3/26	
Habitat	Air	Sed	Air	Sed	Air	Sed	Air	Sed	Air	Sed	Air	Sed	Air	Sed	Air	Sed	Air	Sed	Air	Sed
Juncus	26	20	35	28	32	26	35	28	28	27	29	27	23	16	13	10	10	7	24	22
S. alterniflora	25	22	34	29	31	28	35	30	32	27	32	27	22	15	14	10	10	6	26	21
S. patens	24	20	36	30	32	29	37	29	34	27	32	27	22	16	15	9	10	8	24	20
Distichlis	26	22	38	33	33	30	35	32	31	29	32	29	20	17	17	11	11	8	27	24
Scirpus	25	23	36	35	34	32	36	31	31	30	31	28	19	18	15	12	11	13	27	26

Table 2. Salinity ($^{o}/oo$) and moistness of sediment surface in each vascular plant zone of Graveline Bay Marsh from 12 April 1985-26 March 1986. Moistness arbitrarily expressed according to the following scale: 0 = submerged, 1 = slurry, 2 = very wet, 3 = wet, 4 = moist, 5 = relatively dry, 6 = dry, 7 = very dry.

	4/12		5/14		6/12		7/16		9/19		10/24		12/5		1/8		2/13		3/26	
Habitat	Sal	Mst	Sal	Mst	Sal	Mst	Sal	Mst	Sal	Mst	Sal	Mst	Sal	Mst	Sal	Mst	Sal	Mst	Sal	Mst
Juncus	13	3	20	2	34	5	28	5	24	0	20	0	16	5	16	4	10	3	11	4
S. alterniflora	16	2	20	2	36	5	24	4	23	0	18	0	18	5	16	4	14	3	12	4
S. patens	8	3	16	5	20	7	10	4	35	4	22	2	24	4	16	7	18	4	9	4
Distichlis	16	3	18	1	32	6	24	6	32	0	20	0	20	5	17	4	13	2	12	4
Scirpus	14	1	16	0	71	4	18	2	28	0	18	0	16	0	13	0	11	0	10	3

Table 3. Light energy ($\mu E/cm^2/s$) above the canopy (full) and that reaching the marsh surface (w/in) in each vascular plant zone of Graveline Bay Marsh from 12 April 1985 - 26 March 1986.

Habitat	4/12		5/14		6/12		7/16		9/19		10/24		12/5		1/8		2/13		3/26	
	full	w/in	full	w/in	full	w/in	full	w/in	full	w/in	full	w/in	full	w/in	full	w/in	full	w/in	full	w/in
Juncus	1025	128	1775	29	1055	41	1210	24	1575	235	1310	160	1050	68	1100	38	1400	48	1410	166
S. alterniflora	820	202	1375	170	925	152	2050	1160	1650	455	1330	292	1250	48	1150	90	1450	112	1525	95
S. patens	680	56	1775	110	1085	45	1900	9	1750	38	1395	40	1075	26	1025	21	1400	19	1850	49
Distichlis	870	230	1925	800	1475	520	1600	475	1750	575	1480	378	815	64	1275	115	1450	625	1825	825
Scirpus	1040	320	1925	875	1500	855	1725	885	1575	212	1480	335	585	120	1175	325	1325	1025	1325	400

Table 4. Height (cm) of each vascular plant canopy in Graveline Bay Marsh from 12 April 1985 - 26 March 1986.

Habitat	4/12	5/14	6/12	7/16	9/19	10/24	12/5	1/8	2/13	3/26
Juncus	125	120	135	118	110	110	115	115	110	110
S. alterniflora	60	64	77	67	70	70	60	58	60	57
S. patens	63	78	75	88	42	38	40	60	55	50
Distichlis	40	38	38	37	26	24	20	25	20	34
Scirpus	87	96	90	85	72	66	65	55	50	80

Table 5. An alphabetical list of the 155 edaphic diatom taxa identified from the sediments of Graveline Bay Marsh from 12 April 1985 through 26 March 1986. An * indicates taxon new record for Mississippi based on checklist of Sullivan (1981).

Achnanthes _brevipes_ var. _intermedia_ (Kütz.) Cl.
_A._ _curvirostrum_ Brun
_A._ _delicatulum_ (Kütz.) Grunow ssp. _delicatula_
_A._ _rostrata_ ϕstrup

Amphiprora _alata_ (Ehr.) Kütz.*
_A._ _duplex_ Donkin
_A._ _paludosa_ W.Sm.
_A._ _similis_ Hust.

Amphora _acutiuscula_ Kütz.*
_A._ _angusta_ var. _oblongella_ (Grun.) Cl.
_A._ _bigibba_ Grun.*
_A._ _caroliniana_ Giffen
_A._ _coffeaeformis_ (Ag.) Kütz.
_A._ _exigua_ Greg.
_A._ _micrometra_ Giffen*
_A._ _proteus_ Greg.
_A._ _sabyii_ Salah
_A._ _tenerrima_ Aleem & Hust.
_A._ _tenuissima_ Hust.

Anorthoneis _hummii_ Hust.*

Bacillaria _paradoxa_ Gmelin

Caloneis _westii_ (W.Sm.) Hendey

Campylosira _alexandrica_ Salah
_C._ _cymbelliformis_ (A.S.) Grun.

Cocconeis _deperdita_ Giffen
_C._ _disculoides_ Hust.

Cyclotella _atomus_ Hust.*
_C._ _caspia_ Grun.
_C._ _meneghiniana_ Kütz.
_C._ _stylorum_ Brightwell

Cylindrotheca _gracilis_ (Bréb.) Grun.

Cymatosira _belgica_ Grun.
_C._ _lorenziana_ Grun.*

Cymbella pusilla Grun.

Denticula subtilis Grun.

Dimeregramma minor (Greg.) Ralfs

Diploneis bombus Ehr.*
D. gruendleri (A.S.) Cl.
D. pseudovalis Hust.
D. suborbicularis (Greg.) Cl.
D. weissflogii (A.S.) Cl.*

Eunotogramma laeve Grun.

Fragilaria gessneri Hust.
F. hyalina (Kütz.) Grun.
F. obtusa Hust.
F. pinnata Ehr.

Gyrosigma beaufortianum Hust.
G. distortum (W.Sm.) Griff. & Henfr.*
G. fasciola (Ehr.) Griff. & Henfr.*
G. macrum (W.Sm.) Griff. & Henfr.
G. obliquum (Grun.) Boyer
G. peisonis Hust.

Mastogloia elliptica var. dansei (Thw.) Cl.*

Navicula abunda Hust.
N. accomoda Hust.
N. acutissima Hust.*
N. aequorea Hust.
N. alpha Cl.
N. ammophila Grun.
N. amphipleuroides Hust.
N. arenicola Grun.*
N. binodulosa Sulliv. & Reim.
N. cancellata f. minuta Grun.*
N. cincta (Ehr.) Ralfs*
N. circumtexta Meister
N. clamans Hust.
N. clementis Grun.
N. consentanea Hust.*
N. contenta Grun.*
N. diserta Hust.
N. flanatica Grun.
N. forcipata Greville*
N. gregaria Donkin
N. hagelsteinii Hust.*
N. hudsonis Grun.
N. hyalinula De Toni
N. incomposita Hagelstein
N. infaceta Cholnoky*
N. iranensis Hust.*

N. marina Ralfs*
N. mutica Kütz.
N. normaloides Cholnoky*
N. obsoleta Hust.
N. peregrina (Ehr.) Kütz.
N. perminuta Grun.*
N. phyllepta Kütz.
N. pseudocrassirostris Hust.
N. punctigera Hust.*
N. salinarum Grun.
N. salinicola Hust.
N. spicula (Hickie) Cl.
N. subhamulata Grun.*
N. subinflatoides Hust.*
N. sydowii Cholnoky (= *N. incerta* Grun.)
N. tenera Hust.
N. teneloides Hust.*
N. umpatica Cholnoky*
N. viminoides Giffen*
N. virginalis Hust.
N. yarrensis Grun.

Nitzschia alexandrica (Choln.) Lange-B. & Simonsen*
N. angularis W.Sm.
N. apiculata (Greg.) Grun.
N. aremonica Archibald*
N. calida Grun.
N. closterium (Ehr.) W.Sm.
N. dissipata (Kütz.) Grun.
N. dubia W.Sm.
N. fasciculata (Grun.) Grun.
N. filiformis (W.Sm.) Schütt
N. fontifuga Cholnoky*
N. gandersheimiensis Krasske
N. granulata Grun.
N. habirshawwi Febiger ex Cl. & Möller*
N. hungarica Grun.
N. hustedtiana Salah
N. hybrida Grun.*
N. laevis Hust.*
N. lanceola (Grun.) Grun.*
N. levidensis (W.Sm.) V.H.
N. lorenziana var. *subtilis* Grun.
N. microcephala Grun.
N. obtusa W.Sm. var. *obtusa*
N. obtusa var. *nana* Grun.
N. ovalis Arnott ex Grun.*
N. panduriformis Greg. var. *panduriformis*
N. panduriformis var. *continua* Grun.
N. perspicua Cholnoky*
N. perversa Grun.
N. petitiana Grun.*
N. pubens Cholnoky*
N. quadrangula (Kütz.) Lange-B.*

N. rhopalodioides Hust.*
N. rufitorrentis Cholnoky*
N. scalaris (Ehr.) W.Sm.
N. serpenticula Cholnoky*
N. sigma (Kütz.) W.Sm.
N. siliqua Archibald*
N. tryblionella Hantz.
N. vitrea var. *salinarum* Grun.

Opephora pacifica (Grun.) Petit
O. parva (Grun.) Krasske
O. schwarzii (Grun.) Petit

Pinnularia ambigua Cl.*

Plagiogramma tenuissimum Hust.*

Pleurosigma formosum W.Sm.*
P. salinarum (Grun.) Grun.

Rhopalodia gibberula (Ehr.) Müll.

Stauroneis amphioxys Greg.
S. salina W.Sm.

Surirella atomus Hust.

Thalassiosira decipiens (Grun.) Jørgensen*
T. eccentrica (Ehr.) Cl.

Tropidoneis pusilla (Greg.) Cl.*
T. semistriata (Grun.) Cl.*

Table 6. A list of the 48 most abundant edaphic diatom taxa of Graveline Bay Marsh and their relative abundance (expressed as number of valves) beneath the *Juncus* (JR), *S. alterniflora* (SA), *Distichlis* (DS), and *Scirpus* (SO) canopies from 12 April 1985 to 26 March 1986. A (--) indicates taxon not collected whereas an * indicates not observed during previous study of Sullivan (1978).

Diatom Taxon	JR	SA	DS	SO	Marsh
Achnanthes delicatula	65	121	60	35	281
A. rostrata	53	46	42	59	200
Amphora coffeaeformis	78	65	92	195	430
A. exigua	65	87	51	104	307
A. micrometra*	100	133	42	19	294
A. tenerrima	40	45	13	20	118
Bacillaria paradoxa	132	42	8	72	254
Fragilaria hyalina*	192	199	145	74	610
F. obtusa*	43	33	119	19	214
F. pinnata	12	54	--	--	66
Gyrosigma peisonis	14	10	5	9	38
Navicula ammophila	279	259	335	115	988
N. binodulosa	154	11	274	--	439
N. consentanea	20	36	36	102	194
N. contenta	57	10	26	5	98
N. flanatica	6	2	7	162	177
N. hudsonis	--	25	2	197	224
N. infaceta	9	7	20	--	36
N. iranensis	35	68	58	--	161
N. normaloides	72	67	35	21	195
N. obsoleta	125	4	--	--	129
N. perminuta	31	9	31	1	72
N. phyllepta	10	7	15	128	160
N. salinarum	6	27	34	146	213
N. salinicola	529	260	448	79	1316
N. sydowii	3	402	14	343	762
N. sp. #1	11	33	6	15	65
N. sp. #2*	4	11	9	39	63
Nitzschia alexandrica	10	64	15	40	129
N. angularis	56	42	15	43	156
N. closterium	4	27	6	33	70
N. filiformis	20	18	2	92	132
N. fontifuga*	36	68	70	22	196
N. granulata	29	3	98	--	130
N. habirshawii*	--	--	--	35	35
N. hungarica	15	3	7	6	31
N. laevis	3	14	21	--	38
N. levidensis	1	18	22	--	41
N. petitiana*	--	--	--	42	42

N. pubens	30	25	41	4	100
N. quadrangula	123	83	159	120	485
N. serpenticula*	2	15	--	72	89
N. sigma	12	45	7	6	70
N. siliqua	--	4	88	--	92
Pinnularia ambigua*	14	21	60	17	112
Plagiogramma tenuissimum	76	103	76	27	282
Pleurosigma salinarum	9	8	26	1	44
Surirella atomus*	26	12	21	2	61
Total no. taxa	44	46	43	39	48
% valve count of all taxa	87.0	88.2	88.7	84.0	87.0
Total no. valves counted	2611	2646	2661	2521	10439
No. restricted taxa	--	--	--	2	2
% contribution of restricted taxa	--	--	--	2.6	2.6

Table 7. Species diversity values (H' in bits/individual) for each edaphic diatom community of Graveline Bay Marsh from 12 April 1985 to 26 March 1986.

Habitat	4/12	5/14	6/12	7/16	9/19	10/24	12/5	1/8	2/13	3/26	X ± S.E.
Juncus	4.072	4.491	4.170	4.097	4.103	4.119	4.914	4.185	4.009	4.208	4.237 ± 0.086
S. alterniflora	4.803	4.406	3.034	2.471	3.386	4.023	5.184	4.960	4.402	3.776	4.044 ± 0.278
Distichlis	4.322	4.466	3.625	3.106	3.048	4.249	4.066	4.644	4.589	4.186	4.030 ± 0.183
Scirpus	4.328	4.273	2.520	2.871	3.697	4.426	4.691	4.565	4.189	4.212	3.977 ± 0.231
											4.072 ± 0.207

Table 8. Number of diatom taxa (S) in a sample of 300 valves for each edaphic diatom community of Graveline Bay Marsh from 12 April 1985 to 26 March 1986.

Habitat	4/12	5/14	6/12	7/16	9/19	10/24	12/5	1/8	2/13	3/26	X ± S.E.
Juncus	39	41	37	37	40	41	55	49	38	39	41.6 ± 1.8
S. alterniflora	46	36	26	26	37	41	54	57	42	32	39.7 ± 3.4
Distichlis	36	44	31	24	37	45	33	44	42	31	36.7 ± 2.2
Scirpus	38	40	35	28	34	42	45	47	39	36	38.4 ± 1.8
											39.1 ± 2.4

Table 9. Matrix of similarity values (CZ) comparing edaphic diatom communities of Graveline Bay Marsh in the present study (first value) and in 1976-77 (second value). In the present study each CZ value calculated after 10 samples for each habitat pooled to yield a single sample whereas CZ values for 1976-77 calculated directly from Table 2 of Sullivan (1978); all values X10^3.

	Distichlis	*S. alterniflora*	*Scirpus*
Juncus	738(550)	661(554)	392(696)
Distichlis		601(347)	365(435)
S. alterniflora			546(698)

Table 10. Correlations of original observations of species and environmental data with canonical variable one (CV1) and two (CV2); the canonical correlation coefficients (R_c) and redundancy in the species data given the environmental data for CV1 and CV2; and the proportion of variation in each species variable (R^2) that can be associated with all 10 environmental variables by multiple regression.

Variables	CV1	CV2	R^2
Taxa:			
Navicula salinarum	0.705	0.323	0.698
Nitzschia alexandrica	0.669	0.123	0.569
Achnanthes rostrata	0.471	0.153	0.698
Nitzschia quadrangula	0.466	-0.154	0.539
Amphora exigua	0.403	0.232	0.594
Navicula hudsonis	0.360	0.320	0.657
Navicula phyllepta	0.332	0.367	0.654
Navicula normaloides	0.278	-0.451	0.469
Navicula consentanea	0.224	0.527	0.573
Nitzschia pubens	0.200	-0.453	0.657
Nitzschia angularis	0.141	-0.023	0.394
Nitzschia granulata	0.120	-0.304	0.387
Amphora coffeaeformis	0.075	0.487	0.497
Navicula contenta	0.075	-0.575	0.466
Achnanthes delicatula	0.034	-0.020	0.270
Navicula sydowii	0.030	-0.315	0.714
Navicula binodulosa	0.014	-0.407	0.433
Navicula obsoleta	-0.110	-0.320	0.426
Nitzschia filiformis	-0.110	0.346	0.370
Navicula flanatica	-0.126	0.356	0.409
Navicula salinicola	-0.153	-0.355	0.610
Nitzschia serpenticula	-0.159	0.144	0.337
Nitzschia siliqua	-0.168	0.071	0.334
Plagiogramma tenuissimum	-0.174	0.067	0.499
Navicula iranensis	-0.185	-0.009	0.368
Nitzschia fontifuga	-0.186	0.246	0.216
Amphora tenerrima	-0.221	-0.005	0.223
Amphora micrometra	-0.227	0.063	0.347
Bacillaria paradoxa	-0.230	0.000	0.348
Navicula ammophila	-0.235	-0.023	0.531
Pinnularia ambigua	-0.287	0.220	0.286
Fragilaria obtusa	-0.385	0.188	0.373
Fragilaria hyalina	-0.454	0.174	0.474
Environmental:			
Canopy height	0.132	-0.387	
Sediment salinity	-0.154	-0.324	
Moisture	0.065	-0.722	
Productivity	0.716	-0.031	
Chlorophyll *a*	0.522	0.620	
Pheophytin *a*	-0.467	-0.085	
Julian date	-0.414	0.206	
Light energy	0.206	0.160	
Air temperature	0.369	-0.137	
Sediment temperature	0.405	-0.024	
R_c	1.000	1.000	
Redundancy (CVS/CVE)	0.087	0.083	0.467

Table 11. Chlorophyll *a* concentrations (mg/m^2) beneath each vascular plant canopy of Graveline Bay Marsh from 12 April 1985 to 26 March 1986. Each monthly value is the mean of 6 observations.

Habitat	4/12	5/14	6/12	7/16	9/19	10/24	12/5	1/8	2/13	3/26	X ± S.E.
Juncus	105	44	37	27	44	48	77	57	70	86	59 ± 8
S. alterniflora	199	311	58	39	35	48	86	66	80	67	95 ± 29
S. patens	25	12	3	2	49	40	42	46	76	81	38 ± 9
Distichlis	81	103	58	41	31	48	48	48	64	50	57 ± 7
Scirpus	310	400	110	56	62	118	140	125	135	146	160 ± 34

Table 12. Pheophytin *a* concentrations (mg/m^2) beneath each vascular plant canopy of Graveline Bay Marsh from 12 April 1985 to 26 March 1986. Each monthly value is the mean of 6 observations.

Habitat	4/12	5/14	6/12	7/16	9/19	10/24	12/5	1/8	2/13	3/26	X ± S.E.
Juncus	57	80	74	86	134	94	99	96	100	119	94 ± 7
S. alterniflora	0	0	4	21	107	71	67	85	74	100	59 ± 13
S. patens	50	65	57	19	129	79	54	72	67	96	69 ± 9
Distichlis	38	57	71	66	128	115	90	84	82	116	85 ± 9
Scirpus	3	0	28	44	147	132	79	82	62	107	68 ± 16

Table 13. A list of variables and their abbreviations employed in the multiple regression analyses and discriminant analyses.

Environmental:	
HTCAN	Canopy height
SEDSALT	Sediment salinity
MOIST	Soil moisture
LIGHT	Photosynthetically active radiation reaching marsh surface (400-700 nm)
AVEAIR	Air temperature
AVESED	Sediment temperature
PROD	Hourly algal production
CHL	Chlorophyll *a* concentration
PHEO	Pheophytin *a* concentration
Species:	
DIVER	Species diversity (H')
NO. TAXA	Number diatom taxa in a sample
SP 1-33	Relative abundances of 33 most abundant diatoms
SP1	*Achnanthes delicatula*
SP2	*A. rostrata*
SP3	*Amphora coffeaeformis*
SP4	*A. exigua*
SP5	*A. micrometra*
SP6	*A. tenerrima*
SP7	*Bacillaria paradoxa*
SP8	*Fragilaria hyalina*
SP9	*F. obtusa*
SP10	*Navicula ammophila*
SP11	*N. binodulosa*
SP12	*N. consentanea*
SP13	*N. contenta*
SP14	*N. flanatica*
SP15	*N. hudsonis*
SP16	*N. iranensis*
SP17	*N. normaloides*
SP18	*N. obsoleta*
SP19	*N. phyllepta*
SP20	*N. salinarum*
SP21	*N. salinicola*
SP22	*N. sydowii*
SP23	*Nitzschia alexandrica*
SP24	*N. angularis*
SP25	*N. filiformis*
SP26	*N. fontifuga*
SP27	*N. granulata*
SP28	*N. pubens*
SP29	*N. quadrangula*
SP30	*N. serpenticula*
SP31	*N. siliqua*
SP32	*Pinnularia ambigua*
SP33	*Plagiogramma tenuissimum*

Table 14. Cumulative R^2 values and F values for each variable (and the sign of its regression coefficient) to enter the stepwise multiple regression employing chlorophyll *a* as the dependent value and 8 environmental variables listed in Table 13 as the independent variables for each vascular plant zone.

Marsh Area	Variable		R^2	F value
Juncus	SEDSALT	(-)	0.43	44.2
	HTCAN	(+)	0.54	13.9
	LIGHT	(+)	0.64	14.0
S. alterniflora	PHEO	(-)	0.45	47.0
	SEDSALT	(-)	0.63	28.8
	AVEAIR	(+)	0.68	8.7
S. patens	AVEAIR	(-)	0.52	18.6
	PROD	(+)	0.60	12.0
	PHEO	(+)	0.64	5.4
	MOIST	(-)	0.68	10.0
Distichlis	PHEO	(-)	0.26	20.5
	MOIST	(-)	0.38	10.9
	LIGHT	(+)	0.43	5.2
Scirpus	PHEO	(-)	0.27	21.1
	MOIST	(-)	0.35	7.5
	HTCAN	(+)	0.43	7.9
	PROD	(+)	0.52	10.5

Table 15. Hourly edaphic algal productivity rates (mg $C/m^2/h$) beneath each vascular plant canopy of Graveline Bay Marsh from 12 April 1985 to 26 March 1986. Each monthly value is the mean of 5 observations. Means for the same month followed by the same letter are not statistically different ($P = 0.05$).

Habitat	4/12	5/14	6/12	7/16	9/19	10/24	12/5	1/8	2/13	3/26	X ± S.E.
Juncus	7.7 a	1.5 a	5.2 a	1.4 a	5.7 a	3.2 a	15.1 a	3.0 a	2.2 a	18.5 a	6.4 ± 1.9
S. alterniflora	18.8 a,b	12.8 a	27.0 b	19.7 b	5.0 a	3.0 a	10.6 a	5.8 a	7.1 a	20.9 a	13.1 ± 2.6
S. patens	2.6	0.5	0.5	0.4	1.5	0.6	2.1	2.6	0.9	7.9	2.0 ± 0.7
Distichlis	18.3 a,b	13.4 a	56.7 d	36.6 c	12.6 a	11.5 a	6.6 a	4.8 a	9.4 a	31.7 a	20.2 ± 5.2
Scirpus	30.8 b	9.5 a	41.3 c	25.4 b,c	7.6 a	3.9 a	20.8 a	7.0 a	33.7 b	163.6 b	34.4 ± 14.9
											15.2 ± 7.2

Table 16. Cumulative R^2 values and F values for each variable (and the sign of its regression coefficient) to enter the stepwise multiple regression employing hourly edaphic algal production as the dependent variable and 8 environmental variables listed in Table 13 as the independent variables for each vascular plant zone.

Marsh Area	Variable		R^2	F Value
Juncus	CHL	(+)	0.34	24.4
	PHEO	(+)	0.47	11.2
	MOIST	(+)	0.69	13.0
	AVEAIR	(+)	0.79	21.6
S. alterniflora	MOIST	(+)	0.15	8.5
	AVESED	(+)	0.31	10.8
	AVEAIR	(-)	0.39	6.1
S. patens	CHL	(+)	0.31	21.2
	SEDSALT	(-)	0.46	13.2
	PHEO	(+)	0.57	12.1
Distichlis	HTCAN	(+)	0.36	27.6
	MOIST	(+)	0.58	7.3
	LIGHT	(+)	0.66	10.9
	SEDSALT	(+)	0.70	7.7
Scirpus	MOIST	(+)	0.34	24.5
	SEDSALT	(-)	0.65	42.1
	PHEO	(+)	0.70	8.4
	CHL	(+)	0.77	12.6
	AVEAIR	(-)	0.83	14.6
	AVESED	(+)	0.86	11.2

Table 17. Cumulative R^2 values and F values for each variable (and the sign of its regression coefficient) to enter the stepwise multiple regression employing hourly edaphic algal production as the dependent variable and the 8 environmental variables and 35 community structure variables listed in Table 13 as the independent variables for each vascular plant zone.

Marsh area	Variable		R^2	F value
Juncus	SP32	(+)	0.37	28.2
	SP6	(-)	0.61	28.9
	SP18	(+)	0.75	26.7
	AVEAIR	(-)	0.82	18.3
	SP23	(+)	0.85	7.6
S. alterniflora	NO. TAXA	(-)	0.27	7.2
	SP28	(+)	0.34	4.8
	SP25	(+)	0.38	6.7
Distichlis	SP29	(+)	0.56	16.3
	LIGHT	(+)	0.65	12.2
	SP21	(+)	0.75	18.7
	SP11	(+)	0.80	10.6
	SP10	(+)	0.82	5.8
Scirpus	SP23	(+)	0.72	126.1
	SP28	(-)	0.82	25.6
	SP14	(-)	0.85	9.4
	SP8	(+)	0.87	7.0

Table 18. Comparison of R^2 values for environmental vs. environmental and species (all) variables listed in Table 13 as the independent variables and hourly edaphic algal production as the dependent variable in stepwise multiple regressions.

Marsh Area	Env. R^2	All R^2	ΔR^2
Juncus	0.79	0.85	+0.06
S. alterniflora	0.39	0.38	-0.01
Distichlis	0.70	0.82	+0.12
Scirpus	0.86	0.87	+0.01

Table 19. Annual production rates (g $C/m^2/yr$) of edaphic algae beneath monospecific vascular plant canopies of Graveline Bay Marsh.

Vascular Plant	Annual Rate
Juncus	28.0
S. alterniflora	57.4
S. patens	8.8
Distichlis	88.4
Scirpus	150.7

Table 20. Comparison of annual edaphic algal production (g C/m^2/yr) and ratio of annual edaphic algal to vascular plant aerial production (EAP/VPP X 100%) from different salt marshes of the United States.

State	Algal Prod.	EAP/VPP	Reference
Georgia	200	25	Pomeroy (1959)
Delaware	61-99	33	Gallagher & Daiber (1974)
Massachusetts	105	25	Van Raalte et al. (1976)
California	185-341	76-140	Zedler (1980)
Texas	71	8-13	Hall & Fisher (1985)
Mississippi	28-151	10-61	This study

Table 21. Annual aerial productivity (g dry wt/m^2/yr) of vascular plant species in Mississippi salt marshes.

Vascular Plant	Prod.	Reference
Juncus	557	Hackney & de la Cruz (1982)
S. alterniflora	1089	de la Cruz (1974)
S. patens	1922	de la Cruz (1974)
Distichlis	1484	de la Cruz (1974)
Scirpus	495	Hall & Faulkner (1980)

Table 22. Eigenvalue, relative percent of discriminating power, and canonical correlation coefficient (R_c) associated with each discriminant function.

Function	Eigenvalue	Rel. %	R_c
1	8.749	90.9	.95
2	.781	8.1	.66
3	.096	1.0	.30

Table 23. Classification matrix for stepwise discriminant analysis with *Juncus* (JR), *S. alterniflora* (SA), *Distichlis* (DS), and *Scirpus* (SO) as the groups and the 35 species variables listed in Table 13 as discriminating variables.

	Predicted Group			
Original Group	JR	SA	DS	SO
JR	6	0	4	0
SA	0	4	6	0
DS	0	1	9	0
SO	0	1	0	9

Table 24. Stepwise entry of variables into the discriminant functions, their F value to enter or remove, and Wilks' lambda (U-statistic) at each step.

Step	Variable	F value	U-statistic
1	SP 18	11.7	.5070
2	SP 21	10.6	.2656
3	SP 31	5.2	.1823
4	SP 14	4.8	.1269
5	SP 15	6.0	.0811
6	SP 19	6.8	.0488
7	SP 31 removed	3.9	.0675
8	SP 22	5.8	.0433
9	SP 21 removed	2.2	.0525

Table 25. Standardized discriminant coefficients for each variable entering the three discriminant functions.

Variable	Function 1	Function 2	Function 3
SP 14	-.809	.192	-.046
SP 15	-.673	.144	.155
SP 18	.266	1.266	.324
SP 19	-.710	.173	-.457
SP 22	-.102	-.001	.192

FIGURE LEGENDS

Fig. 1. Map of the Mississippi Gulf Coast showing location of Graveline Bay Marsh.

Figs. 2-6. Hourly primary production (solid line = mg C/m^2/h) and chlorophyll *a* concentrations (dashed line = mg/m^2) beneath each of the five vascular plant canopies of Graveline Bay Marsh (12 April 1985 - 26 March 1986).

Fig. 2. Primary production and chl. *a* beneath the *Juncus roemerianus* canopy.

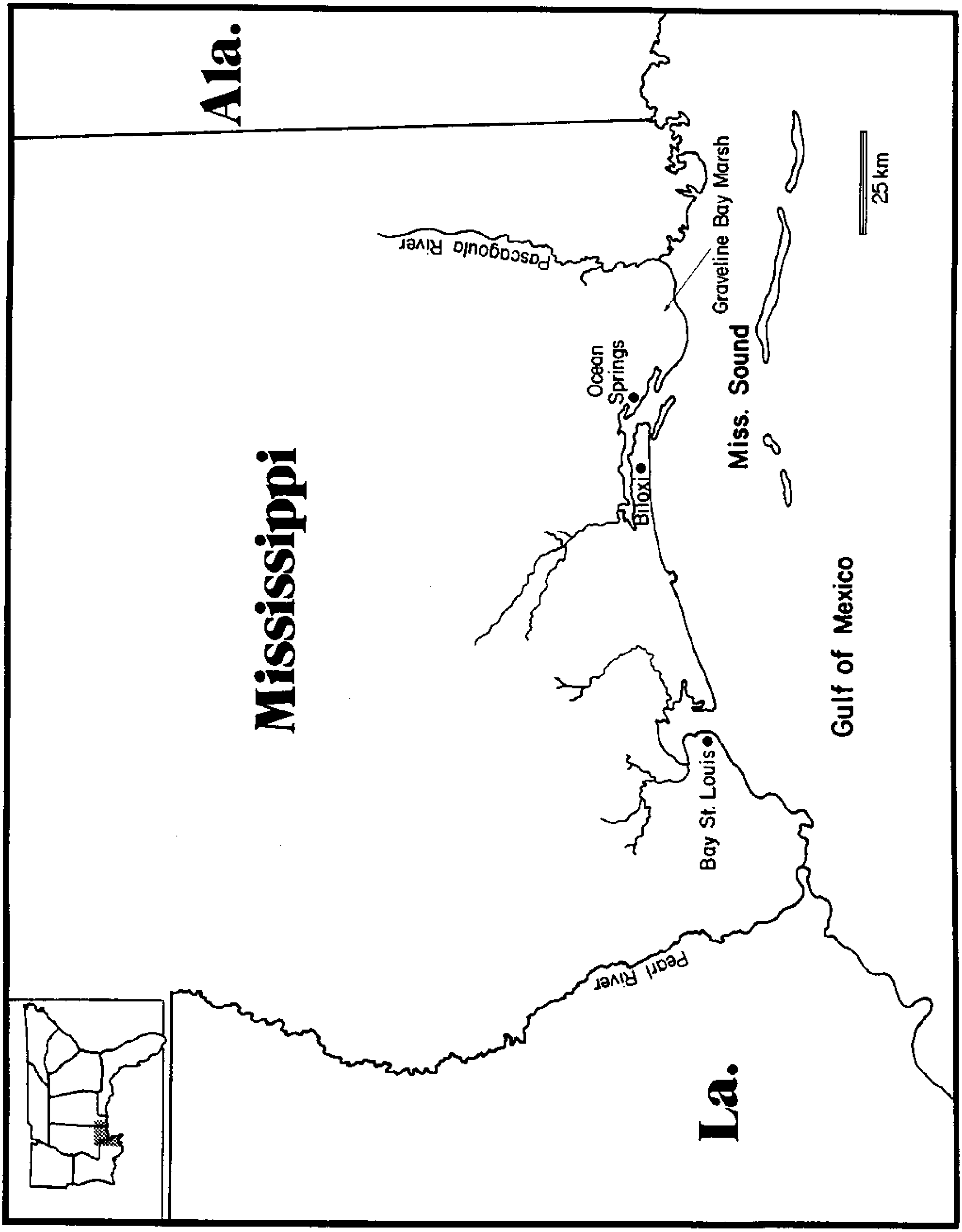
Fig. 3. Primary production and chl. *a* beneath the *Spartina alterniflora* canopy.

Fig. 4. Primary production and chl. *a* beneath the *Spartina patens* canopy.

Fig. 5. Primary production and chl. *a* beneath the *Distichlis spicata* canopy.

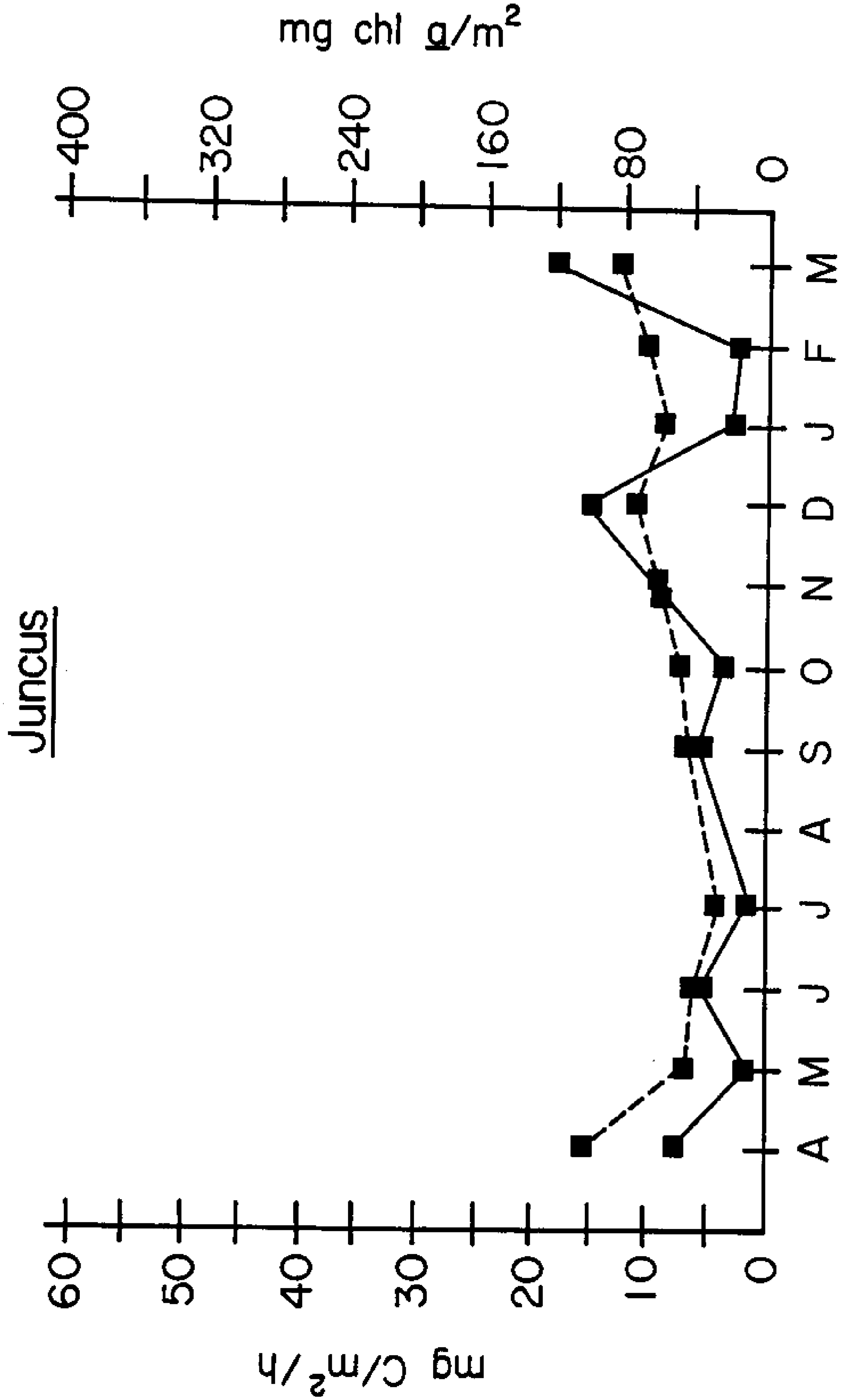
Fig. 6. Primary production and chl. *a* beneath the *Scirpus olneyi* canopy.

Fig. 7. Plot of the scores on canonical variables 1 and 2 for the diatom species data in discriminant space; abbreviations: A = *Juncus roemerianus*, B = *Spartina alterniflora*, C = *Distichlis spicata*, and D = *Scirpus olneyi*. See text for details.



Ala.
Mississippi
La.
Pascagoula River
Graveline Bay Marsh
Ocean Springs
Biloxi
Miss. Sound
Gulf of Mexico
Bay St. Louis
Pearl River
25 km

Fig. 1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mg chl a/m^2
400
320
240
160
80
0
mg C/m^2/h
60
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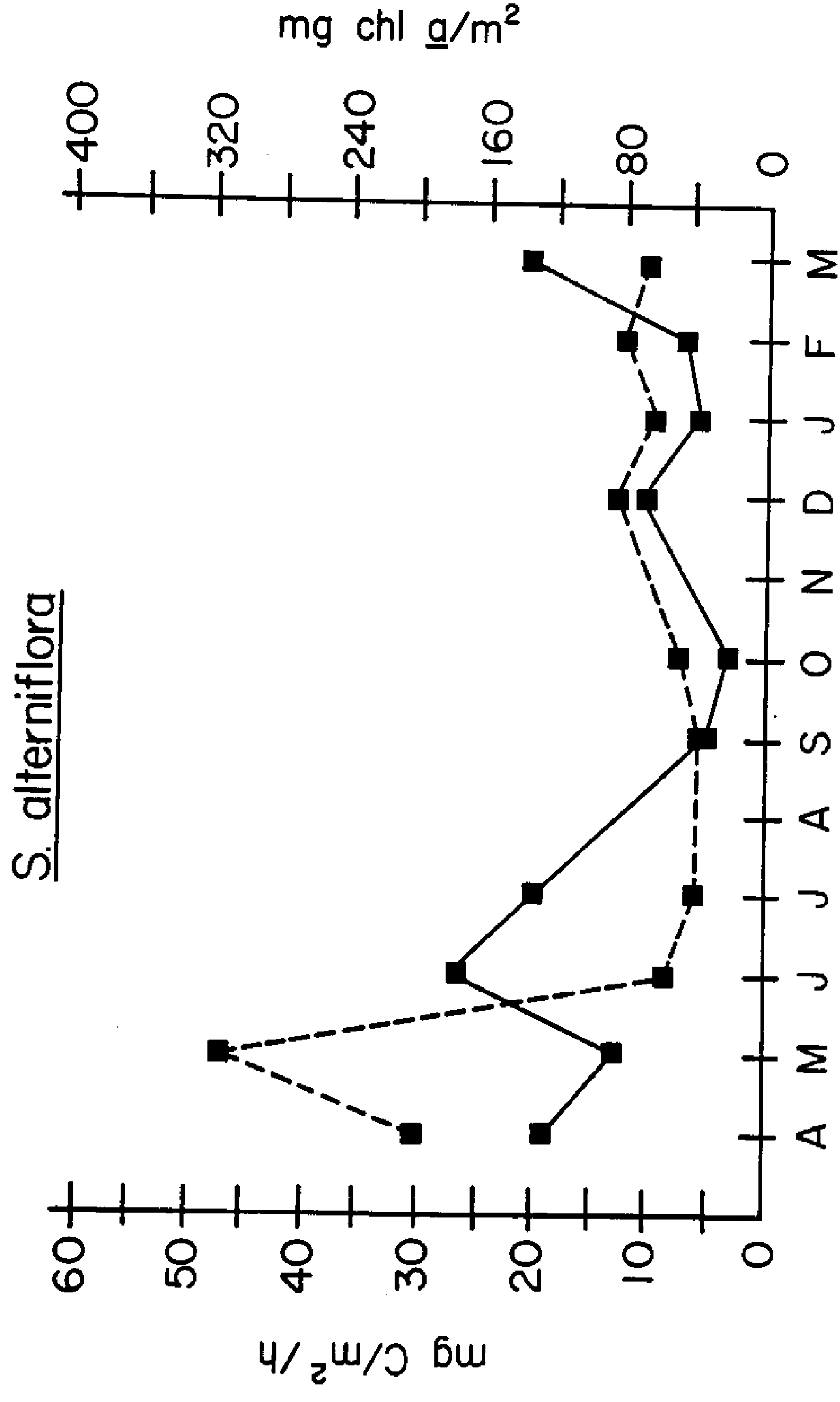
10
0
A
M
J
J
A
S
O
N
D
J
F
M

Fig. 2


S. alterniflora
mg chl a/m²
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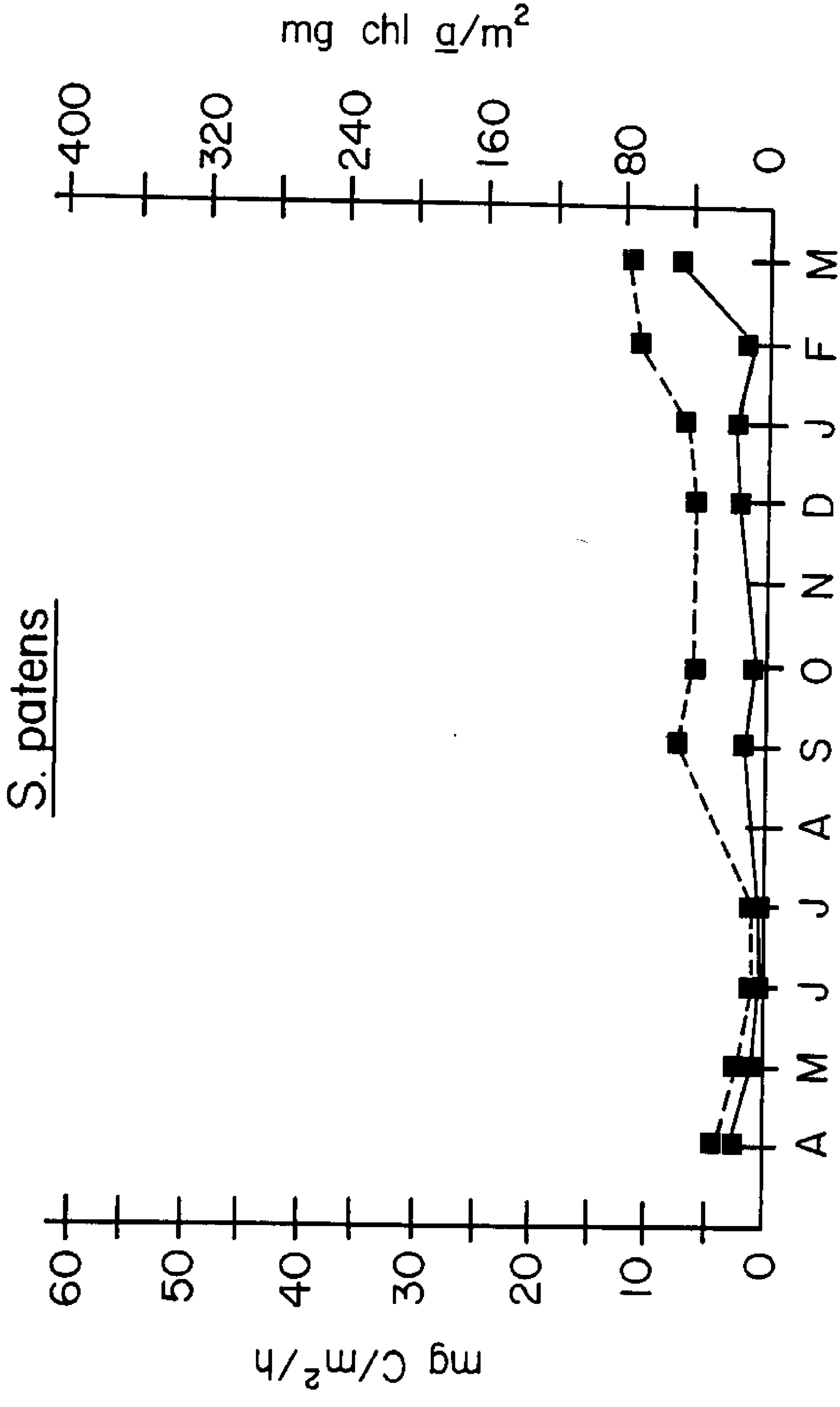
320
240
160
80
0
mg C/m²/h
60
50
40
30
20
10
0
A
M
J
J
A
S
O
N
D
J
F
M

Fig. 3


S. patens
mg C/m²/h
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10
20
30
40
50
60
mg chl a/m²
0
80
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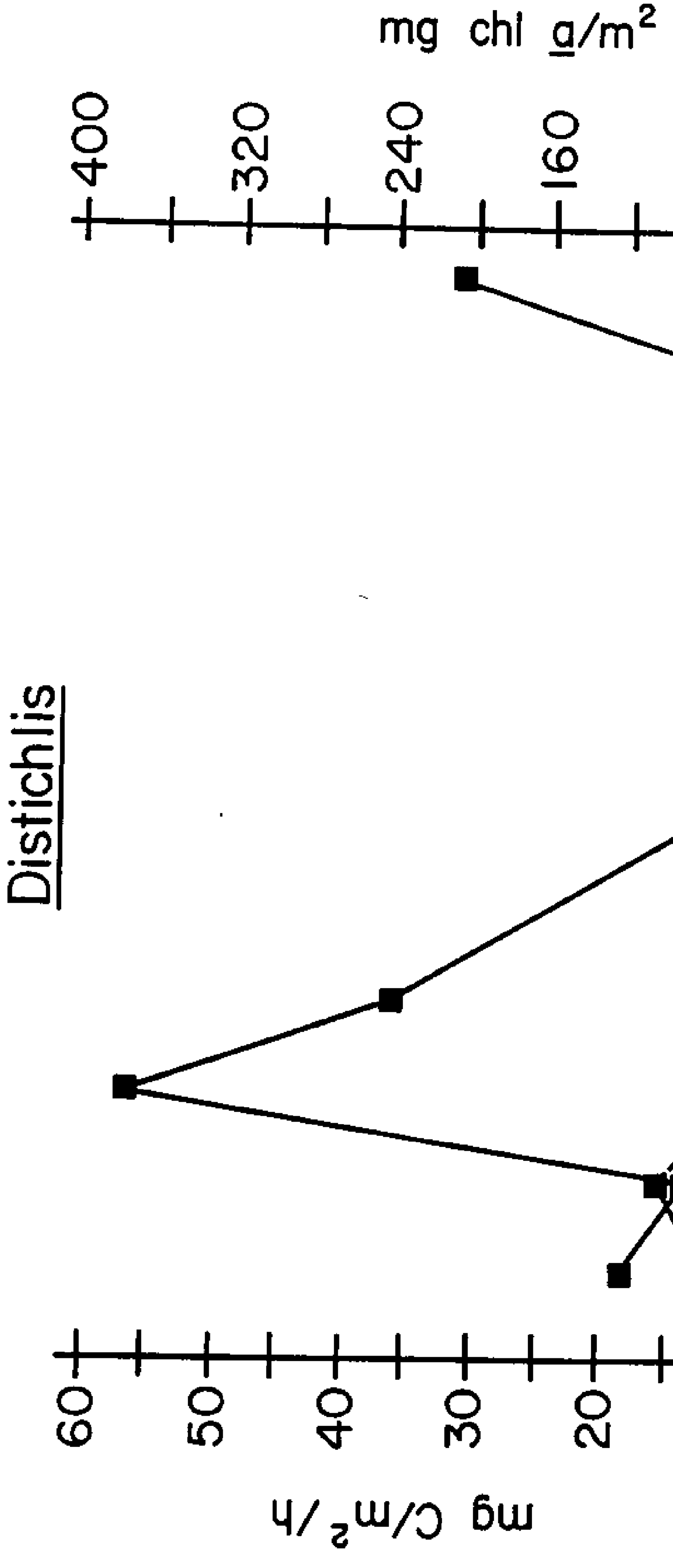
240
320
400
A
M
J
J
A
S
O
N
D
J
F
M

Fig. 4


Distichlis
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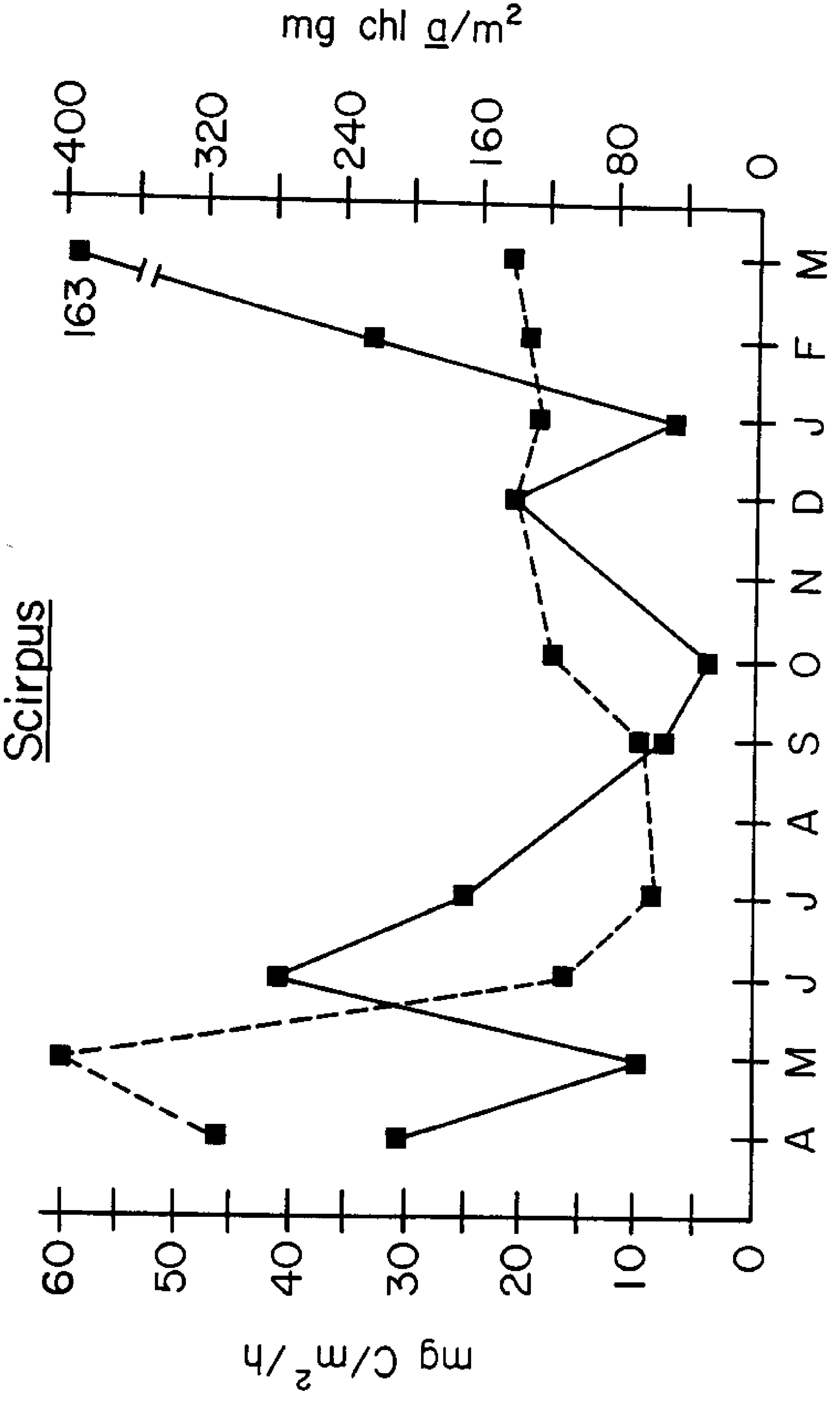
400
320
240
160
80
0
mg C/m²/h
60
50
40
30
20
10
0
A
M
J
J
A
S
O
N
D
J
F
M

Fig. 5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320
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80
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163
A
M
J
J
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S
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D
J
F
M
mg C/m²/h
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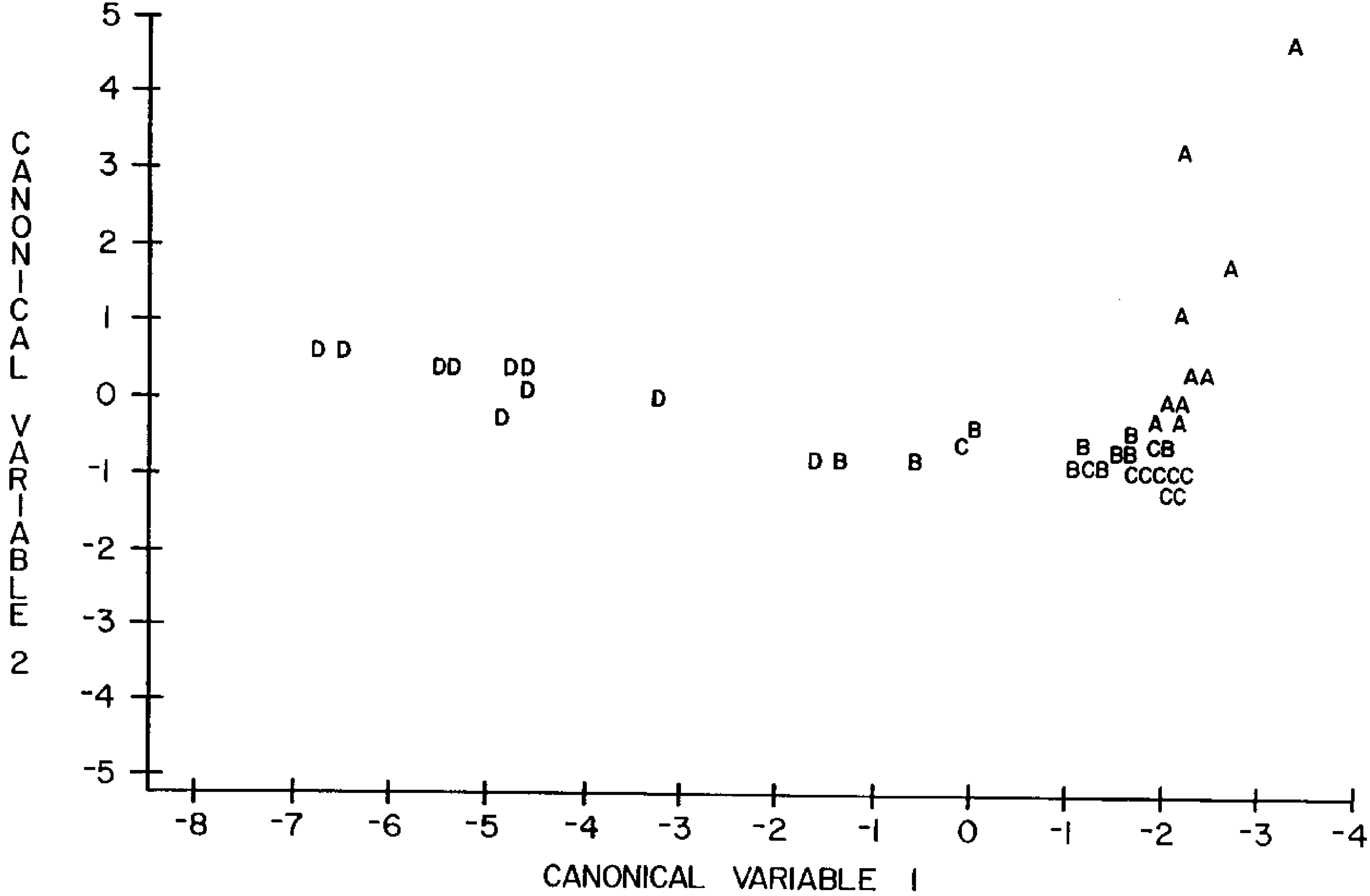
50
40
30
20
10
0

Fig. 6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0
-1
-2
-3
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A
B
C
D

Fig. 7