AN EVALUATION OF THE IMPORTANCE OF ALGAE AND VASCULAR PLANTS IN SALT MARSH FOOD WEBS USING STABLE ISOTOPE ANALYSES

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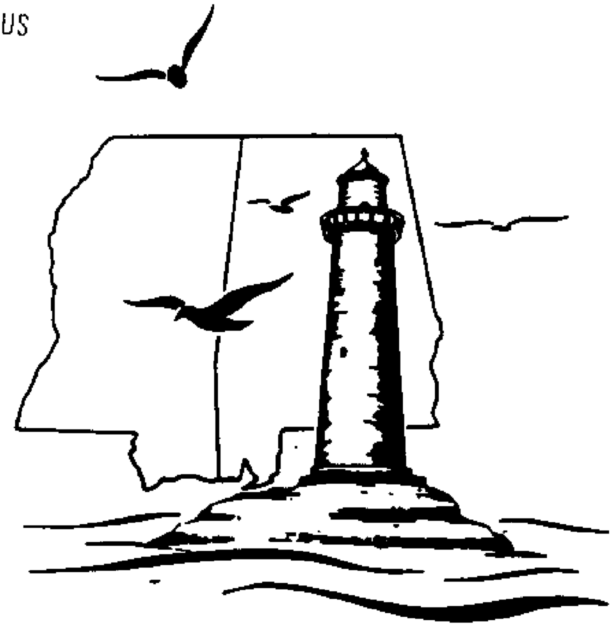

MISSISSIPPI-ALABAMA
SEA GRANT CONSORTIUM

Project No.: R/LR-18

Grant No.: NA85AA-D-SG005

MASGP-88-042

ACKNOWLEDGEMENTS

Many long but memorable hours were spent in the field collecting plants, animals, detritus, and mud. These collecting efforts would not have been successful without the expert boat-handling skills and labors of Bill Demoran, John Cirino, and Steve Breland. The encouragement received from these three individuals and their willingness to go the extra mile are greatly appreciated.

This work is a result of research sponsored in part by NOAA Office of Sea Grant, Department of Commerce under Grant #NA85AA-D-SG005, the Mississippi-Alabama Sea Grant Consortium and Mississippi State University. The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon.

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ABSTRACT

In order to elucidate the flow of organic matter and trophic relationships within Graveline Bay Marsh and bayou system, an irregularly flooded Mississippi salt marsh, stable isotope ratios of carbon ($\delta^{13}C$), sulfur ($\delta^{34}S$), and nitrogen ($\delta^{15}N$) were measured from March 1987 through September 1988. The $\delta^{13}C$ values of the primary producers were distinct: Spartina (-13 °/oo), Juncus (-26 °/oo), and edaphic algae (-21 °/oo). A pure zooplankton sample, which should closely approximate the phytoplankton, had a $\delta^{13}C$ value of -23 °/oo. $\delta^{34}S$ ranged from 0 to +2 °/oo for the vascular plants while those for edaphic algae and zooplankton were +14 and +11 °/oo, respectively; $\delta^{15}N$ for all primary producers ranged from +5 to +6 °/oo. Stable isotope ratios for particulate organic matter and sediments resembled those of the algae rather than Spartina. For 49 of the 56 (88 %) consumers sampled, $\delta^{13}C$ fell within a range of -22 to -18 °/oo; this range centered around edaphic algae and phytoplankton but was distinct from the $\delta^{13}C$ of Spartina. $\delta^{34}S$ for 48 of the 56 (86 %) estuarine consumers ranged from +9 to +16 °/oo, which included edaphic algae and zooplankton but was 8 to 15 °/oo more enriched in ^{34}S than Spartina. The range in $\delta^{15}N$ values for consumers (+6 to +12 °/oo) was more enriched in ^{15}N than any primary producer and proved useful in designating a consumer's relative trophic level. A plot of $\delta^{13}C$ and $\delta^{34}S$ values for primary producers and consumers showed a tight clustering of data points around the edaphic algae and phytoplankton. No consumer even moderately resembled

Spartina or Juncus in its $\delta^{13}C$ and $\delta^{34}S$ values. The stable isotope data indicates that the major food sources for the invertebrate and fish fauna of the Graveline system are the edaphic and phytoplanktonic algae; the contribution of the vascular plants appears to be minor at best. The present study represents the first documentation of the importance of edaphic algae in salt marsh food webs. Comparisons with multiple stable isotope work carried out in Massachusetts and Georgia salt marshes revealed an increasing dependence on phytoplanktonic and benthic algae by salt marsh consumers as one moves south along the Atlantic Coast and then west to the Gulf Coast. Since benthic algae are highly productive, are the preferred food source of many estuarine consumers, and are easily suspended by tidal current to become members of the "phytoplankton", this floral component can no longer be ignored in estuarine food web studies.

INTRODUCTION

Salt marshes are among the most productive ecosystems in the world. The main contributors to the production of salt marshes are the highly visible vascular plants and the microscopic edaphic (sediment-associated) and planktonic algae. The edaphic algae include diatoms, green, yellow-green, and blue-green algae within or on top of the sediments beneath the extensive and dense canopy of vascular plants on the marsh proper, as well as those associated with the exposed and subtidal sediments of tidal creeks. The phytoplankton (which also includes representatives from diverse algal groups) move in and out of salt marsh creeks with each tidal cycle and are widely distributed over the marsh proper when the latter floods.

Despite their microscopic size, the edaphic algae possess significant primary production rates (Sullivan and Moncreiff 1988 and references cited therein). The ratio of annual edaphic algal to vascular plant net aerial production (EAP/VPP) typically ranges from 8 to 33% in coastal salt marshes of the Atlantic and Gulf Coasts. However, an EAP/VPP value of 61% was reported by Sullivan and Moncreiff (1988) in the _Scirpus olneyi_ Gray zone of a Mississippi marsh and Zedler (1980) found values of 76-140% in four vascular plant zones of a California marsh.

Edaphic algae can greatly augment the primary production of the water column in well-mixed shallow estuaries. Shaffer and Sullivan (1988) used K-systems analysis to show that water column productivity was highest when factors operated to displace the benthic microalgae from the sediments of Barataria Estuary, which is ringed by extensive salt marshes. Benthic pennate diatom taxa represented an average of 74 % of all diatom cells in the water column during this study.

Ribelin and Collier (1979) observed that 98 % of the detrital material exported from a Florida Gulf Coast salt marsh to adjacent waters was made up of amorphous aggregates 25-50 μm in diameter, which were produced almost entirely by the edaphic algae. The production of the vascular plants was buried in the marsh rather than exported. This led Ribelin and Collier to seriously question the long-standing dogma that the salt marsh vascular plants supported food webs in adjacent estuarine waters via a detritus-based pathway. Haines (1977), employing stable isotope measurements in a Georgia salt marsh, had earlier hypothesized that the vascular plants were unlikely candidates for the source of detritus exported to coastal waters. Cranford et al. (1987) studied the nature of suspended and sedimentary particulate matter in the Cumberland Basin where _Spartina alterniflora_ Loisel. accounts for approximately 29 % of total estuarine production. Virtually all of the particulate matter in both fractions was comprised of small, organic aggregates less than 100 μm in diameter. _Spartina_ accounted for less than 3 and 1 % of suspended material and sedimentary organic matter, respectively. Bowen (1984) showed that these small amorphous aggregates are formed by precipitation of detrital leachate, are low in refractory matter, and represent an immediately available, high energy food source that does not require a microbial intermediate. In contrast, Spartina must be broken down by microbes because of its high content of refractory organic matter; the microbes rather than the plant itself then serve as the actual food for animals grazing on Spartina detritus.

Haines (1976a) was the first to employ stable carbon isotope analysis to trace the pathway of organic matter flow in salt marshes. Most invertebrates in the Georgia salt marsh being studied had stable carbon values (-19 to -15 °/oo) less than those of Spartina (-13 °/oo) but greater than that of Juncus roemerianus Scheele (-26 °/oo). However, the invertebrate values closely matched those of the edaphic algae (-18 to -16 °/oo). The most significant finding of Haines was that stable carbon isotope values of detritus (-23 to -20 °/oo) in the tidal creeks did not match those of Spartina. Thus, Haines' paper began an extensive reexamination of the dogma that dead Spartina supports food webs in adjacent estuarine waters. This reexamination still continues today and has led to fundamental changes in the ways in which estuarine ecologists view the functioning of salt marshes.

The pioneering work of Haines has been amplified and extended in other studies (Haines 1976b,1977, Haines and Montague 1979, Hackney and Haines 1980, Sherr (formerly Haines) 1982, Hughes and Sherr 1983, Schwinghamer et al. 1983, Mariotti et al. 1983, Jackson et al. 1986, Jackson and Harkness 1987). All of these studies cited above employed a single stable isotope approach and claimed varying importance of Spartina and phytoplankton carbon as a food source for estuarine consumers, with some acknowledging the possible importance of edaphic algae. All with the exception of one study concluded that terrestrial (i.e. upland) plant carbon was of minor importance in the food web. The single exception was that of Hackney and Haines (1980), who found very low stable carbon isotope values in a Gulf Coast salt marsh. They interpreted this to mean that terrestrial plant carbon influx via river flow, rather than phytoplankton, was the major carbon source for the marsh fauna.

Peterson et al. (1985) were the first to employ multiple stable isotopes (two or more elements) for the study of salt marsh food webs. Since carbon isotopic analysis alone cannot provide definitive information on the relative importance of different groups of primary producers to higher trophic levels (particularly when two or more of these groups possess similar or overlapping stable carbon isotope values), the use of multiple stable isotopes may more accurately identify the ultimate source(s) of fixed carbon for consumers at different trophic levels (Fry and Sherr 1984). Peterson et al. measured stable carbon, sulfur, and nitrogen values of Spartina, phytoplankton, and the filter-feeding ribbed mussel Geukensia demissa in a Massachusetts salt marsh. Dual isotope plots (carbon vs. sulfur and carbon vs. nitrogen) for the floral components and the mussel led the authors to conclude that the mussel consumed both Spartina detritus and phytoplankton with the relative proportions of each food source being determined by the location in the marsh (i.e. marsh proper versus lower and higher order tidal creeks). Although the stable carbon values of the mussel ranged from -19 to -16 $^{o}/oo$, the edaphic algae were not considered as a potential food source.

Working in the same salt marsh, Peterson et al. (1986) made an extensive analysis of the stable carbon and sulfur isotope values of macroconsumers (mostly invertebrates and some small fish). Dual isotope plots showed that the majority of the marsh fauna were depleted in ^{34}S and enriched in ^{13}C. The authors concluded that Spartina was the major food source for the marsh macroconsumers with phytoplankton also important, especially for filter feeders in the main marsh channels. Sulfur-oxidizing bacteria were ruled out as a possible food source (see their Fig. 6) but the edaphic algae were again not considered.

Peterson and Howarth (1987) moved south to the Sapelo Island marshes of Georgia where carbon, sulfur, and nitrogen isotope values for producers and macroconsumers were determined and two sets of dual isotope plots made. With regard to the source of organic matter for the macroconsumers, the authors stated that "all of our isotopic data are consistent with a roughly equal contribution by Spartina and by phytoplankton plus perhaps benthic algae." They also made the interesting observation that although Spartina dominates production, the assimilation of Spartina and algal carbon by macroconsumers is equal. Comparisons of food web dynamics between the Massachusetts marsh studied earlier and the Georgia marsh were also made. It was pointed out that the macrofauna in Georgia was relatively more dependent on algal carbon than their counterparts in Massachusetts. The hypotheses was advanced that "perhaps the productivity and availability of plankton or benthic algae relative to Spartina is greater at Sapelo, or perhaps Spartina detritus is more available in Massachusetts."

The present study has taken the multiple stable isotope approach to a Gulf Coast salt marsh. This was done to extend geographic comparisons beyond the Atlantic coast of the United States and because of our belief that the importance of the benthic algae in salt marsh food webs has been underestimated. Also, the only previous stable isotope study conducted in a Gulf Coast salt marsh (Hackney and Haines 1980) employed only carbon and made the singular observation that the major source of organic matter for consumers was not any marsh floral component but terrestrial matter derived from upland plants.

DESCRIPTION OF STUDY SITE

All field work was carried out in Graveline Bay salt marsh, Mississippi (30°21'26" N, 88°40'59" W), located ca. 11 km southeast of the Gulf Coast Research Laboratory at Ocean Springs. Major features of the system and sampling locations described in the sections to follow are shown in Fig. 1. Hydrodynamics (i.e. water levels and movement) within the marsh are dominated by local conditions in adjacent Mississippi Sound and precipitation falling directly on the marsh; there are no other visible inputs of water into the system. Astronomical tidal range is 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.

The dominant vascular plants are Juncus roemerianus and Spartina alterniflora. The production dynamics of the edaphic algae on the marsh proper (Sullivan and Moncreiff 1988) and the phytoplankton and subtidal microalgae of tidal creeks (Zimba 1989) have been determined. Graveline Bay marsh supports rich and diverse invertebrate and fish faunas. Fishing is quite good; commercial trapping of blue crabs occurs in Graveline Bayou, and penaeid shrimp are seasonally abundant. A productive oyster reef is present in this same bayou.

MATERIALS AND METHODS

Sampling Strategy

Samples for stable isotope analyses were collected in the Graveline system on 18-19 March, 11-13 May, 25 June, 8-9 July, 21-24 September, 15-16 October 1987, 13-14 January, 6-7 April, 13 June, 18-19 August, and 22 September 1988. The sampling effort was concentrated at three stations. Station 1 was located near the upper end of Graveline Bayou, Station 2 was approximately at the mid-point of the bayou, and Station 3 was immediately upstream of the mouth. The three stations were floristically similar in terms of vascular plant composition. Besides the differences in distance from Mississippi Sound amongst the stations, the only other major difference was that the sediments of Stations 1 and 2 were silts and clays whereas sand was also present at Station 3. Additional samples were collected at the boat launch site upstream from Station 1, from Graveline Bay marsh beach immediately outside the mouth of Graveline Bayou in Mississippi Sound, and from the sites where Sullivan and Moncreiff (1988) measured the primary production rates of edaphic algae beneath monospecific vascular plant canopies.

Stable Isotope Terminology and Background

Because the measurement of absolute isotopic abundances is very difficult, stable isotope ratios are reported with reference to a standard (Fry and Sherr 1984). The difference between the material under consideration and the standard is expressed in parts per thousand or per mil (^{o}/oo) according to the following formula:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3,$$

where X is ^{13}C, ^{34}S, or ^{15}N, R is $^{13}C/^{12}C$, $^{34}S/^{32}S$, or $^{15}N/^{14}N$, and the standards for C, S, and N are Peedee Belemnite, Canyon Diablo troilite, and atmospheric diatomic nitrogen, respectively.

Biological materials are usually depleted in ^{13}C relative to the PDB standard and hence have negative $\delta^{13}C$ values (Fry and Sherr 1984). Table 1 summarizes ranges in $\delta^{13}C$ values that have been reported for salt marsh floral components. C_4 plants such as <u>Spartina</u> discriminate less against the ^{13}C isotope and hence have higher $\delta^{13}C$ values (i.e. are relatively more enriched in ^{13}C) than do C_3 plants such as <u>Juncus</u>. The edaphic algae and phytoplankton, which obtain their inorganic carbon as dissolved bicarbonate instead of gaseous carbon dioxide, have intermediate $\delta^{13}C$ values.

Unlike $\delta^{13}C$ values, those of $\delta^{34}S$ may be positive or negative in the tissues of estuarine plants and animals. Estuarine plants will have positive values if they take up their inorganic sulfur primarily as ionic sulfate and negative if their main sulfur source is inorganic sulfide (Fry et al. 1982). <u>Spartina</u>, which takes up both seawater sulfates (+20 $^{o}/oo$) and depleted sulfides (-24 $^{o}/oo$), has a variable range of $\delta^{34}S$ values centered more or less around 0 $^{o}/oo$ (Table 1). Only one value has been published for <u>Juncus</u> (6 $^{o}/oo$). The few values reported for edaphic algae and phytoplankton show their primary source of sulfur is seawater sulfate.

In contrast to carbon and sulfur, few $\delta^{15}N$ values exist for salt marsh flora and fauna. All such values for marsh plants have proved to be positive (Table 1). Spartina, Juncus, and edaphic algae have $\delta^{15}N$ values less than or equal to 6 °/oo whereas phytoplankton are relatively more enriched in ^{15}N at 9 °/oo.

The old axiom, "you are what you eat (and assimilate)", refers to the finding that the tissues of animals for the most part mirror their diet, at least for $\delta^{13}C$ and $\delta^{34}S$ (Fry and Sherr 1984). This is a powerful tool for evaluating the relative importance of various floral components (i.e. vascular plants, edaphic algae, and phytoplankton) as food sources for estuarine consumers. In order to detail the actual flow of organic matter through estuarine food webs from the primary producers to consumers occupying different trophic levels, a slightly different approach is needed. Recently, Fry (1988) has pointed out that $\delta^{15}N$ values are useful for determining the trophic position of a given consumer since an enrichment in the heavy isotope (^{15}N) of 3-4 °/oo occurs per trophic level. He also stated that the relationship between an animal and its food is nearly 1:1 for $\delta^{34}S$ while enrichment in the ^{13}C isotope from one trophic level to the next is about 1 °/oo. Finally, dual isotope plots ($\delta^{13}C$ vs. $\delta^{34}S$ and $\delta^{13}C$ vs. $\delta^{15}N$), as pioneered by Peterson and co-workers (1985,1986,1987), have proved to be a strategy that significantly improves the resolution of the stable isotope technique in unraveling the great complexity of salt marsh food webs.

Sample Collection

Vascular plants (Spartina, Juncus, Scirpus, Iva) were carefully procured in the field to prevent contamination by the introduction of foreign material to the samples. Only living, aboveground biomass was collected. Samples, stored in plastic bags, were transported to the laboratory for further processing.

Macroalgae were collected whenever available. Samples were placed in plastic bags with a minimal volume of water from the collection site, and kept on ice for transport to the laboratory for identification and processing. Material was frozen as soon as possible upon return to the laboratory if it was not immediately processed.

Edaphic algae were also collected whenever possible. Samples were removed from the marsh surface with care to exclude as much non-algal material as conditions would permit. Transportation to the laboratory in plastic containers on ice was followed by freezing if immediate processing was not possible.

Samples for particulate organic matter and zooplankton were collected on most sampling dates, with a concentrated effort on 13 January 1988. Plankton nets with mesh sizes of 335 μm, 153 μm, and 28 μm were towed for a maximum of 10 minutes; a minimum of two replicate tows was made at each station. Samples were gently washed into the cod ends of the nets with ambient bayou water and stored on ice for immediate processing upon return to the laboratory.

Surface sediments were collected at each station. A hand shovel was used to collect sediments beneath Spartina and Juncus as well as along the creekbank of Graveline Bayou. An Ekman dredge was used to sample subtidal sediments in the bayou.

Consumers (polychaetes, bryozoans, bivalves, gastropods, crustaceans, and a variety of fish species) were collected from as many habitats and trophic levels as possible. Only live, intact organisms were taken to minimize contamination by shell or other foreign material. All samples were placed in clean plastic bags or containers, labelled as to date and location of collection, and placed on ice for transport to the laboratory, where they were frozen for future processing if immediate preparation was not possible.

Bivalves were either collected by hand when encountered in the marsh or with an oyster dredge within a well-established oyster bed in Graveline Bayou. Polychaetes were also collected from this area in conjunction with the bivalve samples.

Crustaceans were also either hand-collected (Callinectes, Clibanarius and Uca spp.) or taken with nets in conjunction with fish samples. Generation of an amphipod sample was attempted by combining material from all collection dates but available biomass was unfortunately not sufficient for a sample.

Fish were collected using a variety of sampling nets. Smaller fish in tidal creeks and shallows were taken with either a 10 ft (3 m) minnow seine of 1/4 inch (6.4 mm) mesh or with a 40 ft (12.2 m), 1/8 inch (3.2 mm) mesh bag seine. Intermediatesized and large fish were obtained with a 16 ft (4.9 m), 1/2 inch (12.7 mm) mesh trawl with a 1/8 inch (3.2 mm) mesh bag or by using a series of gill nets and cast nets in areas where trawling was not possible.

Sample Processing

In the laboratory, vascular plants were sorted to obtain pure samples of each species. All plant stems and leaves were washed free of mud. Samples were then rinsed with distilled water, blotted dry, and oven-dried to a constant weight at 60°C. Samples were stored at this point prior to final processing.

Macroalgae were sorted and picked free of all visible detritus fragments and associated zooplankton and meiofauna. Material was examined under a dissecting microscope (15 and 30X) to assure complete removal of visible contaminants. The final samples were rinsed with a solution of 10% HCl to remove any $CaCO_3$ present on the material; this was followed by several rinses with tap water to a neutral pH, with a final rinse of distilled water. Excess moisture was removed from the samples by vacuum filtration on glass fiber filter paper. Samples were then oven-dried to constant weight at 60°C. The edaphic algae were processed in a similar fashion. Samples were stored and combined by genus for final processing if possible.

Zooplankton were carefully separated from particulate material using a saturated NaCl solution; plankton floated on the surface with the majority of the detritus sinking to the bottom of the processing container. Using a dissecting microscope, all remaining visible detrital material was manually separated from the zooplankton to obtain as pure a sample as possible. The final sample was washed with 10% HCl to remove any traces of $CaCO_3$. This was followed by several rinses with tap water and a final rinse with distilled water under gentle vacuum filtration to remove acid and excess moisture. Samples were dried to a constant weight at 60°C and stored in clean, airtight plastic containers for final processing.

Particulate organic matter samples were processed either intact or following removal of zooplankton. Samples were size-fractionated using mini-sieves equipped with 335 μm, 153 μm, and 28 μm meshes. Retained material was washed with 10 % HCl and then rinsed with tap water to a neutral pH, followed by a final rinse with distilled water, all under gentle vacuum filtration. Samples were oven-dried at 60 C to a constant weight and then stored in clean, airtight plastic containers for final processing.

Sediments were arbitrarily divided into subsamples for analysis as intact sediment and as sediment fractions retained by 1 mm and 63 μm sieves. Meiofauna were removed from the sieved samples for separate analysis (primarily Neanthes spp.) when present. Intact sediment samples were washed with 10 % HCl until no bubbling was observed to remove all traces of $CaCO_3$ present in the samples. Visible shell fragments were removed during this process. Samples were rinsed with tap water to a neutral pH; this was followed by a final rinse with distilled water under gentle vacuum filtration to remove excess moisture prior to drying to constant weight at 60°C. Samples were gently handled to minimize loss of fine particulate material; glass fiber paper was used for filtration. Sieved subsamples were treated in a similar fashion. All samples were stored in clean, airtight containers for final processing.

Consumer samples were handled to minimize contamination with foreign material. Whenever possible, only muscle tissue was used to obtain consistent and comparable samples for each species. Particular care was taken with bivalve samples to exclude shell fragments from the samples. All tissues were washed with 10 % HCl to remove any potential residues of $CaCO_3$, followed by tapwater rinses to a neutral pH and a final rinse with distilled water under gentle vacuum filtration (glass fiber paper). Samples were dried at 60°C to a constant weight and stored in clean, airtight plastic containers for final processing.

Final processing was essentially identical for all sample types. Dried samples were powdered using either a Wiley Mill equipped with a #40 mesh delivery tube, or ground with a mortar and pestle to as fine a consistency as possible.

The actual measurements of stable isotope ratios for all samples were performed by Coastal Science Laboratories of Austin, Texas. The accuracy of the $\delta^{13}C$, $\delta^{34}S$, and $\delta^{15}N$ analyses was 0.2, 0.5, and 0.2 parts per mil (°/oo), respectively. A blind control was included with each set of samples to the commercial firm to test the repeatability of the determinations.

RESULTS

Isotope Ratios of Primary Producers

The stable carbon isotope ratios of the vascular plants and algae were distinct (Table 2). The C_4 plant Spartina had $\delta^{13}C$ values that exhibited very little seasonal variation (-13.9 to -12.8 °/oo) with an average value of -13.2 °/oo. For the C_3 plant Juncus, $\delta^{13}C$ ranged from -26.6 to -24.8 °/oo with an average value of -25.5 °/oo. A single sample of Scirpus olneyi, another C_3 marsh plant, yielded a value of -25.2 °/oo. Iva frutescens L. and Solidago sempervirens L., both of which occur on higher elevations in Graveline Bay Marsh not subjected to tidal flooding, had $\delta^{13}C$ values more characteristic of terrestrial vegetation: -27.7 and -27.2 °/oo, respectively. The composite sample of edaphic algae had a $\delta^{13}C$ value of -20.6 °/oo. Samples of macroalgae collected in the bayou yielded the following $\delta^{13}C$ values: Bostrychia radicans Montagne (-26.2 °/oo), Vaucheria sp. (-19.3 °/oo), Ectocarpus sp. (-18.7 °/oo), and Enteromorpha sp. (-18.4 °/oo). Excepting the very low value for the red alga Bostrychia, $\delta^{13}C$ ranged from -20.6 to -18.4 °/oo for the benthic algae of Graveline Bay Marsh. It was not possible to collect a "pure" phytoplankton sample but a pure zooplankton sample was obtained; its $\delta^{13}C$ value was -23.3 °/oo.

Stable sulfur isotope ratios were much more variable than those of carbon (Table 2). The average $\delta^{34}S$ value for Spartina was +1.4 °/oo but such values ranged from -8.5 to +13.9 °/oo over an annual cycle. However, with the exception of two high values,

$\delta^{34}S$ was always less than +8 °/oo. The range in $\delta^{34}S$ for Juncus (-4.8 to +5.4 °/oo) was less than that for Spartina, with an average value of +0.4 °/oo being recorded for the former. The edaphic algae composite had a $\delta^{34}S$ value of +14.3 °/oo whereas the pure zooplankton sample was more depleted in ^{34}S with a value of +10.7 °/oo. A single collection of the brown alga Ectocarpus yielded a value of +13.1 °/oo.

Stable nitrogen isotope values ranged from +3.4 to +6.7 °/oo and +3.7 to +7.3 °/oo for Spartina and Juncus, respectively. Mean $\delta^{15}N$ values for these two vascular plants were +5.2 and +5.3 °/oo, respectively (Table 2). The edaphic algae composite had a $\delta^{15}N$ value of +6.1 °/oo whereas the pure zooplankton sample was +7.1 °/oo. Samples of macroalgae collected in the bayou yielded the following values: Vaucheria (+4.7 °/oo), Bostrychia (+6.5 °/oo), Enteromorpha (+9.0 °/oo), and Ectocarpus (+10.6 °/oo).

Isotope Ratios of Particulate Organic Matter

Different size class fractions of particulate organic matter (POM) had similar $\delta^{13}C$ values (Table 3). The average ranged from -25 to -23 °/oo which was similar to values for the edaphic algae (-21 °/oo), pure zooplankton sample (-23 °/oo), and Juncus (-25 °/oo).

POM fractions were more variable in their sulfur isotope ratios (Table 3). All values were negative and ranged from -12.5 to -3 °/oo. These values were much closer to those of the vascular plants (0 to +2 °/oo for Spartina and Juncus) than to those for the pure zooplankton sample (+11 °/oo) or the edaphic algae (+14 °/oo).

Stable nitrogen isotope ratios were very similar for all size class fractions of POM and averaged +5.2 °/oo (Table 3). This value is essentially identical to that for Spartina and Juncus (+5 °/oo) but less than that of edaphic algae (+6 °/oo) and the pure zooplankton sample (+7 °/oo).

Isotope Ratios of Sediments

Sediment samples were taken in March, May, and July 1987. Temporal variability was so low that stable isotope ratios were combined for the three months and the data summarized over all stations, size fractions, and marsh zone. Table 4 lists the average $\delta^{13}C$ and $\delta^{34}S$ values for the three stations. Values for $\delta^{13}C$ were very similar for all three stations and the grand mean (-23.2 °/oo) was nearly identical to that for all POM fractions combined (-23.8 °/oo). Stations 1 and 2 had $\delta^{34}S$ values that were very close but the sediments near the mouth of Graveline Bayou (Station 3), which contain some sand, had a less depleted value of -6.0 °/oo. The grand mean for sediment $\delta^{34}S$ (-11.3 °/oo) was somewhat less than that for all POM fractions combined (-8.0 °/oo).

The three different sediment size fractions had $\delta^{13}C$ values that ranged from -22.4 to -23.6 °/oo (Table 5). $\delta^{34}S$ was greatest in the 1 mm fraction and approximately the same in the unsieved and 63 μm fractions.

When the data are grouped by marsh zone (Table 6), patterns for $\delta^{13}C$ are again the same, namely very little variability in the data. $\delta^{13}C$ ranged from -23.6 to -22.7 °/oo for the four marsh zones. Values for $\delta^{34}S$ were more variable and ranged from -14.9 to -7.3 °/oo. The sediments beneath Juncus were least depleted in ^{34}S whereas creekbank sediments were the most depleted. Values for $\delta^{15}N$ were obtained only for sediments beneath the two vascular plants. Spartina and Juncus sediments had $\delta^{15}N$ values of +2.9 and +2.8 °/oo, respectively, which was less than that for all POM fractions combined (+5.2 °/oo).

Stable Carbon Isotope Ratios of Consumers

Table 7 and Fig. 2 summarize the $\delta^{13}C$ data for consumers sampled in the Graveline Bay Marsh system. Forty-nine of the 56 (88%) $\delta^{13}C$ values listed in Table 7 fell within a range of -22 to -18 °/oo. The largemouth bass (Micropterus salmoides), which was collected from a freshwater spillway at the head of the Graveline system, had the lowest $\delta^{13}C$ value of -25.1 °/oo, whereas the deposit-feeding Uca (fiddler) crabs had the highest $\delta^{13}C$ value (-15.0 °/oo) of any consumer. The pure zooplankton sample possessed one of the lowest $\delta^{13}C$ values (-23.3 °/oo) of any consumer. Filter-feeding bivalves (Polymesoda, Rangia, Ischadium, Geukensia, and Crassostrea) exhibited a very narrow range of -22 to -21 °/oo; this range is slightly more enriched in ^{13}C than the zooplankton in the Graveline system and approximately the same as that of phytoplankton in most estuarine systems (Gearing et al. 1984).

Of the 56 consumer categories listed in Table 7, 34 (61 %) of these fell within a range of -22 to -20 °/oo (see Fig. 2

also). This range must be very close to that separating the $\delta^{13}C$ values of phytoplankton and edaphic algae in the Graveline system. These 34 consumer categories include all filter-feeding bivalves, the algal grazer Littorina, bryozoans, nereid worms, both penaeid shrimp species, squid, and fish occupying different trophic levels such as the Gulf menhaden, bay anchovy, both silverside species, spot, southern flounder, speckled trout, and redfish. These last three fish species are probably among the top carnivores in the system neglecting fish-eating birds and alligators.

One can also define a second group of 12 consumers with $\delta^{13}C$ values between -19.6 and -18.6 °/oo (Table 7, Fig. 2). These included species such as the striped hermit crab, blue crab, grass shrimp, longnose anchovy, two species of killifish, striped mullet, and silver perch.

Four species defined a third group with $\delta^{13}C$ values ranging between -18.1 and -17.8 °/oo (Table 7, Fig. 2). Members of this last group were the moon snail, longnose killifish, sailfin molly, and scaled sardine.

Differences between adults and larvae/juveniles of the same fish species (see Table 7) were as follows: redfish (-1.3 °/oo), Gulf menhaden (-1.0 °/oo), rough silverside (-0.2 °/oo), and striped mullet (+0.3 °/oo). Only in the last species were the adults more enriched in ^{13}C than the larvae/juveniles.

Stable Sulfur Isotope Ratios of Consumers

Table 7 and Fig. 3 summarize the $\delta^{34}S$ data for consumers.

As expected, the range in $\delta^{34}S$ values (+6.2 to +16.4 °/oo) for marsh consumers was the greatest of the three isotope ratios. The freshwater largemouth bass (Micropterus) was an outlier with a $\delta^{34}S$ value of +3.6 °/oo.

Two artificial groups may be distinguished: the first includes 7 consumer categories (12 % of total) with a range of +6 to +8 °/oo and the second includes the remaining 48 consumer categories (86 % of total) with a range of +9 to +16 °/oo. The first group is comprised of the grass shrimp, nereid worms, two species of killifish, hogchoker, black drum, and the roe of the Atlantic croaker. The $\delta^{34}S$ of roe is difficult to interpret because of its high lipid content; protein from muscle tissue was analyzed in larval, juvenile, and adult fish. While some of these had the lowest $\delta^{13}C$ values of all consumers (hogchoker, croaker roe), others had among the highest $\delta^{13}C$ values (two species of killifish, grass shrimp). Zooplankton, which belonged to the second group, possessed a surprisingly low $\delta^{34}S$ value of 11 °/oo.

Examination of Table 7 and Fig. 5 reveals that there was no consistent relationship between a consumer's $\delta^{13}C$ and $\delta^{34}S$ value. The only possible exceptions were the three species of Fundulus (killifish), all of which had among the highest $\delta^{13}C$ values and lowest $\delta^{34}S$ values. In contrast, Uca crabs and the scaled sardine possessed among the highest $\delta^{13}C$ and $\delta^{34}S$ values.

Stable Nitrogen Isotope Ratios of Consumers

Table 7 and Fig. 4 summarize the $\delta^{15}N$ data for consumers.

Such data was obtained for 45 of the 56 consumer categories. Two groups may distinguished. The first (+6 to +10 °/oo) is made up of 30 consumers and includes all invertebrate species (zooplankton, 5 species of filter-feeding bivalves, nereid worms, 2 bryozoan genera, grass shrimp, and 3 crab species). The species most depleted in ^{15}N was the sailfin molly (+6.2 °/oo). The occurrence of the southern flounder (+9 °/oo) and redfish (+10 °/oo) was quite unexpected.

The second group (+11 to +12.4) was made up of 15 consumers and all were fish. The highest $\delta^{15}N$ values, all of which were $\geq$ 12 °/oo, belonged to the two anchovy species, scaled sardine, and silver perch. The scaled sardine, which is a member of the herring family along with the Gulf menhaden, was exceptional in that its $\delta^{13}C$, $\delta^{34}S$, and $\delta^{15}N$ values were all among the highest recorded during the study. However, the former was only collected once at the mouth of the Graveline system, and is most likely not a resident species. For the most part, the second group included higher-level predators and omnivores while the first group included deposit and suspension feeders.

Dual Isotope Plots

Three different dual isotope plots were made (Figs. 4-6). Each plot includes the stable isotope values for the consumer categories listed in Table 7 in addition to those of *Spartina*, *Juncus*, and edaphic algae. Error bars were not plotted around the means for *Spartina* and *Juncus* since only a single value for the edaphic algae was obtained. The pure zooplankton sample was considered to very closely match corresponding stable isotope values of the phytoplankton. However, it should be pointed out that its $\delta^{34}S$ value of +11 °/oo is much lower than the +19 °/oo employed by Peterson and co-workers (1985, 1986, 1987) in their dual isotope plots.

The most useful plot is that employing $\delta^{13}C$ and $\delta^{34}S$ (Fig. 5) since isotope shifts of +4 °/oo may occur during assimilation of nitrogen (Fry 1988). Particularly striking is the tight clustering of data points around the edaphic algae and zooplankton values. None of the consumers even moderately resemble the $\delta^{13}C$ and $\delta^{34}S$ values for either _Spartina_ or _Juncus_. The single data point near _Juncus_ is that for the freshwater largemouth bass (_Micropterus_) and hence can be ignored for the present discussion. No consumer was more depleted in ^{13}C than the zooplankton. As stated previously, all filter-feeding bivalves had $\delta^{13}C$ values between -22 and -21 °/oo and hence were only slightly enriched in ^{13}C relative to the zooplankton. In addition, the filter-feeding bivalves were also only slightly enriched in ^{34}S (range = +11 to +12.5 °/oo for four species and +14 °/oo for the oyster, see Table 7) as compared to the zooplankton. All this strongly suggests that the $\delta^{13}C$ and $\delta^{34}S$ values of the zooplankton are very close to those actually characterizing the phytoplankton in the Graveline system, despite its low $\delta^{34}S$ value.

Only three consumers (grass shrimp, bayou killifish, and longnose killifish) appeared to exhibit any displacement toward

Spartina (Fig. 5). These species are characteristically found in shallower areas well within the marsh where bacterial degradation of Spartina may affect the stable isotope ratios of available pools of organic matter. Neglecting these consumers, the distribution of $\delta^{13}C$ and $\delta^{34}S$ values indicated that the consumers in the Graveline system for the most part closely match the $\delta^{13}C$ and $\delta^{34}S$ values of the phytoplankton and edaphic algae. Uca crabs were nearly 6 °/oo more enriched in $\delta^{13}C$ than the edaphic algae; however, their $\delta^{34}S$ value of +15 °/oo almost exactly matched that of edaphic algae and was more than 13 °/oo higher than the mean $\delta^{34}S$ value of Spartina. The algal-grazing marsh periwinkle (Littorina) differed from the edaphic algae only in its $\delta^{13}C$ value, which was a mere 1 °/oo less.

The $\delta^{13}C$ vs. $\delta^{15}N$ plot (Fig. 6) is less informative because the $\delta^{15}N$ values of the primary producers differ by less than 1 °/oo (Table 2). It does however show the tight clustering of $\delta^{13}C$ values around the edaphic algae and phytoplankton. Also evident is a slight break in $\delta^{15}N$ values between 10 and 11 °/oo. As discussed earlier, all deposit and suspension feeders had $\delta^{15}N$ values less than 10 °/oo and all consumers with $\delta^{15}N$ values greater than 11 °/oo were carnivorous or omnivorous fish.

The plot of $\delta^{34}S$ vs. $\delta^{15}N$ (Fig. 7) reveals no new insights but does again emphasize the fact that the stable isotope ratios of the consumers are very unlike those of the vascular plants.

DISCUSSION

Isotope Ratios of Primary Producers

The $\delta^{13}C$ values of Spartina and Juncus fell within previously reported ranges (compare Tables 1 and 2). Edaphic algae in Graveline Bay Marsh were more depleted in ^{13}C than previously reported with a $\delta^{13}C$ value of -20.6 °/oo. Peterson and Howarth (1987) reported a value of -17 °/oo for creekbank algae in a Georgia salt marsh, whereas Rodelli et al. (1984) found ranges of -20 to -18 °/oo for four benthic diatom species and -22 to -18 °/oo for filamentous green algae attached to the roots of Malaysian mangroves. Craft et al. (1988) measured $\delta^{13}C$ values of -19 to -14 °/oo for benthic and floating algae in a North Carolina salt marsh. With the exception of one species, $\delta^{13}C$ ranged from -19 to -18 °/oo for macroalgae collected in Graveline Bay Marsh. Therefore, $\delta^{13}C$ for benthic algae in the Graveline system ranged from -21 to -18 °/oo.

As previously mentioned, a pure zooplankton sample was obtained which had a $\delta^{13}C$ value of -23.3 °/oo. Gearing et al. (1984) found from extensive sampling in Narragansett Bay that the zooplankton were enriched in ^{13}C relative to °/oo by 0.6 °/oo. If this is also the case in the Mississippi marsh then the phytoplankton would be -24 °/oo, which is only slightly lower than the range reported in Table 1. Although Peterson et al. (1985) have used an average phytoplankton value of -21 °/oo in their salt marsh work, they obtained a measurement of -20 °/oo for a plankton tow (300 μm mesh) of large mixed diatoms and copepods taken in the Woods Hole passage.

The average $\delta^{34}S$ value of Spartina (+1.4 °/oo) in Graveline Bay Marsh fell within the middle of the range of reported values listed in Table 1. This mean value compared well with mean values measured by Peterson and co-workers (1985,1986,1987), which ranged from -4 to +1 °/oo in Massachusetts and Georgia salt marshes. A single value of +6 °/oo for Juncus is all that existed before the present study (Peterson and Howarth 1987). Juncus in Graveline Bay Marsh had an average $\delta^{34}S$ value of +0.4 °/oo. Edaphic algae with their value of +14 °/oo fell within the lower part of the range listed in Table 1. These algae must therefore obtain most of their sulfur as seawater sulfate which has a $\delta^{34}S$ value of +20 °/oo rather than as depleted sulfides which are -24 °/oo (Fry et al. 1982). Zooplankton were +11 °/oo which is much lower than the values of +19 and +20 °/oo measured by Peterson et al. (1985,1986). All detritus was hand-picked from the zooplankton sample so the question naturally arises as to whether or not phytoplankton in the Graveline system are more depleted in ^{34}S than their Atlantic counterparts. A "pure" phytoplankton sample was not collected in the present study but the filter-feeding bivalves in the marsh were only slightly enriched in ^{34}S relative to the zooplankton (see Table 7).

Stable nitrogen isotope values for Spartina and Juncus were within previously reported ranges, whereas the edaphic algae were higher by 1 °/oo (compare Tables 1 and 2). Macroalgae, however, exhibited a range of +5 to +11 °/oo in this same system. The zooplankton, with their $\delta^{15}N$ vale of +7 °/oo, were more depleted than the literature value of 9 °/oo. Presumably the phytoplankton in the Graveline system should have a $\delta^{15}N$ value equal to or less than that of the edaphic algae.

Isotope Ratios of Particulate Organic Matter

Particulate organic matter (POM) fractions yielded $\delta^{13}C$ values of -25 to -22 °/oo (Table 3), which fell within ranges reported by Haines (1976a, 1977) and Sherr (1982) for a Georgia salt marsh. This range encompassed values near those of zooplankton, edaphic algae, and Juncus, but was much more depleted than organic carbon from Spartina. POM was depleted in ^{34}S; no corresponding literature values exist for comparison. The $\delta^{15}N$ values for POM are close to those of the vascular plants and edaphic algae (compare Tables 2 and 3). Mariotti et al. (1983) reported a value of +4 °/oo and Peterson and Howarth (1987) measured a value of +8 °/oo for POM in Georgia salt marshes.

Isotope Ratios of Sediments

The sediments in all four marsh zones had more or less the same $\delta^{13}C$ value of -23 °/oo (Table 6). Despite the fact that Spartina is a C_4 plant and Juncus is a C_3 plant, the $\delta^{13}C$ values for sediments beneath their canopies were essentially identical and matched that of the zooplankton and edaphic algae. Haines (1976a) measured values of -23 to -16 °/oo and Sherr (1982) recorded -20 to -14 °/oo for intertidal and -21 to -19 °/oo for subtidal marsh sediments. Hackney and Haines (1980) found values for sediments beneath Spartina to be -21 °/oo and those beneath Juncus to range from -23 to -21 °/oo in a salt marsh in western Mississippi. Stable sulfur isotope values were depleted in ^{34}S and were close to the $\delta^{34}S$ value of -9 °/oo measured for Spartina roots by Fry et al. (1982). Whereas $\delta^{13}C$ values for sediments and POM were nearly identical, $\delta^{34}S$ values for the former were on average 3 °/oo more depleted than the latter. Few $\delta^{15}N$ values for salt marsh sediments have been published; our value of +3 °/oo is very close to the +4 °/oo recorded by Mariotti et al. (1983). The latter study found that sediments and POM had identical $\delta^{15}N$ values, whereas in the present study the former were depleted in ^{15}N by 2 °/oo relative to the latter.

Stable Isotope Ratios of Consumers

Stable carbon isotope values for the consumers of Graveline Bay Marsh were more depleted in ^{13}C than their counterparts in a Massachusetts (Great Sippewissett) and Georgia (Sapelo Island) salt marsh. Forty-nine of the 56 (88 %) consumer categories listed in Table 7 (see also Fig. 2) had $\delta^{13}C$ values between -22 and -18 °/oo. Of these 49 consumers, 34 fell within a narrower range of -22 to -20 °/oo. At Great Sippewissett, the marsh fauna fell between -17 and -10 °/oo (Peterson et al. 1986) while in Sapelo Island the range for consumers was -18 to -15 °/oo (Peterson and Howarth 1987). The $\delta^{13}C$ values of the Mississippi consumers therefore do not even overlap those of their counterparts in the two Atlantic salt marshes. In general, all consumers were more depleted in ^{13}C than zooplankton and their

$\delta^{13}C$ values centered around that for the edaphic algae (Fig. 2). As previously mentioned, $\delta^{13}C$ for all benthic algae in the Graveline system ranged from -21 to -18 °/oo, which would include the greater majority of consumers. The five species of filter-feeding bivalves all fell within a range of -22 to -21 °/oo which was only slightly more enriched in ^{13}C than the zooplankton.

Hackney and Haines (1980) conducted the only other stable isotope study in a Gulf Coast salt marsh. Consumers ranged from -28 to -16 °/oo, but most had $\delta^{13}C$ values less than -22 °/oo. Rangia, Geukensia, and Polymesoda possessed $\delta^{13}C$ values of -28 to -26 °/oo. These values indicate a fauna very depleted in ^{13}C relative to that in the Graveline system. Because of these low $\delta^{13}C$ values and the nearby proximity of the Jourdan River to this western Mississippi marsh, Hackney and Haines concluded that terrestrial plant matter rather than phytoplankton was the dominant food source for the marsh fauna. Freshwater inputs to the Graveline system are negligible and the stable isotope ratios of POM and consumers indicate that organic matter from upland plants is not a significant part of the base of the food web.

The consumers of Graveline Bay Marsh were slightly more enriched in ^{34}S than their counterparts in a Georgia salt marsh. Forty-eight of the Mississippi consumers (86 % of total) fell within a range of +9 to +16 °/oo (Table 7, Fig. 3). Most of the marsh fauna at Sapelo Island had $\delta^{13}C$ values between +6 and +14 °/oo (Peterson and Howarth 1987). Among the consumers with the highest $\delta^{34}S$ values were Uca crabs, Littorina, and oysters; this was also true in our study. Peterson and Howarth considered it unlikely that phytoplankton were the main source of sulfur for Uca and Littorina but that edaphic and epiphytic algae, which also obtain most of their sulfur from seawater sulfate, were their major ultimate source of organic matter. This is also probably true of the majority of consumers in the Graveline system, as 86% of all consumers were 8 to 15 °/oo more enriched in ^{34}S than Spartina. In contrast, Fry (1988) stated that $\delta^{34}S$ values of +11 to +14 °/oo for benthic invertebrates are probably associated with production of ^{34}S-depleted sulfides during sulfate reduction in muddy sediments. Finally, Peterson et al. (1986) found that all fauna in the northeastern Great Sippewissett salt marsh had $\delta^{34}S$ values between 0 and 10 °/oo. Such values are intermediate between those for Spartina and for benthic and phytoplanktonic algae.

The only other study in which comprehensive $\delta^{15}N$ measurements were made is that of Peterson and Howarth (1987) in the salt marshes of Sapelo Island. They observed that the $\delta^{15}N$ values for consumers (+7 to +11 °/oo) centered around the phytoplankton (+9 °/oo). In Graveline Bay Marsh virtually all consumers (+6 to +12 °/oo) were enriched in ^{15}N compared to the vascular plants (+5 °/oo) and edaphic algae (+6 °/oo), and all but three consumers were enriched relative to the zooplankton (+7 °/oo). Peterson and Howarth (1987) found that fiddler crabs (Uca) and small mullet generally had the lowest $\delta^{15}N$ values which was also true in our study.

Stable nitrogen isotope ratios are good indicators of trophic level whereas those of carbon and sulfur are not (Fry 1988). Peterson and Howarth (1987) found that consumers fractionate nitrogen by +1 to +5 °/oo per trophic transfer; fractionation of carbon or sulfur was slight and could be in either the positive or negative direction (see their Table 3). Peterson and Howarth divided the marsh fauna of Sapelo Island into two groups: one with $\delta^{15}N$ values less than 9 °/oo which included deposit and suspension feeders, and a second with $\delta^{15}N$ values greater than 9 °/oo which included predators and omnivores. Consumers belonging to the deposit/suspension feeding group were <u>Uca</u> crabs, small mullet, <u>Geukensia</u>, <u>Littorina</u>, and oysters. Consumers belonging to the predator/omnivore group were the grass shrimp, white shrimp, silver perch, blue crab, <u>Fundulus</u>, and large mullet. Such an arbitrary division would seem also to characterize the fauna of Graveline Bay Marsh quite well (see Table 7). The five filter-feeding bivalves belong to the first group as do <u>Uca</u> crabs, nereid worms, and both bryozoans. The blue crab and grass shrimp had $\delta^{15}N$ values very close to 9 °/oo; however, both species are highly omnivorous and thus utilize a variety of food sources. All fish species except the black drum, sailfin molly, and bayou killifish fall into the second predator/omnivore group based on their $\delta^{15}N$ values which is generally consistent with their biology. Thus, $\delta^{15}N$ measurements appear in the Mississippi marsh to be an excellent indicator of a consumer's relative trophic level.

Dual Isotope Plots

In contrast to previous studies (Peterson et al. 1986, Peterson and Howarth 1987), a plot employing $\delta^{13}C$ and $\delta^{34}S$ values of primary producers and consumers did not result in a broad band of values lying between phytoplankton and Spartina. Instead, this dual isotope procedure for Graveline Bay Marsh produced a tight clustering of data points around the edaphic algae and zooplankton (≈ phytoplankton) (Fig. 5). The consumers varied from moderately to greatly depleted in ^{13}C and enriched in ^{34}S relative to both Spartina and Juncus. The marsh periwinkle (Littorina), which is known to graze on edaphic algae, was essentially identical to the latter in both its $\delta^{13}C$ and $\delta^{34}S$ values. An inescapable conclusion from the stable isotope data is that the major food sources for the fauna of Graveline Bay Marsh are the edaphic and planktonic algae; the contribution of vascular plants is either minor or negligible. This does not mean of course that all consumers are actually eating algae, but that the algae are the very basis of the food web in Graveline Bay Marsh. Kitting et al. (1984) used stable carbon isotope analysis to show that epiphytic algal carbon, rather than that of seagrasses, formed the primary basis of the food web in Texas seagrass beds; very little of the seagrass leaf biomass was ingested by any invertebrate species.

It is not possible to evaluate the relative importance of edaphic algae and phytoplankton since their $\delta^{13}C$ values are so close and the $\delta^{34}S$ value of the latter in Graveline Bay Marsh is not precisely known. What is evident however, is that this represents the first study to conclusively document the importance of edaphic algae in salt marsh food webs and to show that Spartina may be of little trophic importance in at least some marsh systems. Hopefully, the data presented here will encourage other investigators to consider the benthic algae as a potentially important source of organic matter in all future studies of trophic relationships in salt marshes and other estuarine systems. This becomes even more important when one considers that much of the water column productivity (i.e. "planktonic" productivity) in shallow estuarine systems is due to displaced benthic diatoms and other microalgae (Shaffer and Sullivan 1988).

Although a plot of $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 6) for primary producers and consumers is less informative, it does corroborate conclusions drawn from the $\delta^{13}C$ and $\delta^{34}S$ plot. Instead of a vertical band of values falling between phytoplankton and Spartina as in the work of Peterson and Howarth (1987), $\delta^{15}N$ values of the Graveline Bay Marsh fauna form a vertical band between the $\delta^{13}C$ values of zooplankton (≈ phytoplankton) and edaphic algae. Again, this strongly suggests that the base of the food web is a mixture of these two algal groups and that neither Spartina nor Juncus is important. As noted by Peterson and Howarth (1987), the vertical extension of $\delta^{15}N$ values beyond those of the algae represents the fractionation of nitrogen occurring at the various trophic levels as organic matter is processed by consumers.

Regional Comparisons

The only other studies employing multiple isotopes in salt marshes are those of Peterson et al. (1986) for Great Sippewissett Marsh in Massachusetts and Peterson and Howarth (1987) for Sapelo Island marshes in Georgia. The present study makes possible a comparison of a Gulf Coast marsh with two widely separated Atlantic marshes. It is profitable to begin with a comparison of the stable isotope values of consumers listed in both Table 7 of the present study and Table 4 of Peterson and Howarth (1987). All but one (Uca) of the 11 species common to both studies was more depleted in ^{13}C in the Mississippi marsh. The Graveline Bay Marsh fauna was on average 2.7 °/oo more depleted than the Sapelo Island fauna ($\delta^{13}C$ means = -19.8 and -17.1 °/oo, respectively). The opposite was true for $\delta^{34}S$; all but one (grass shrimp) Mississippi consumer was more enriched in ^{34}S than the same species in Georgia. The average enrichment was 2.1 °/oo ($\delta^{34}S$ means = +11.6 and +9.5 °/oo, respectively). The average $\delta^{15}N$ value for these consumers was 8.9 and 8.4 °/oo in Mississippi and Georgia, respectively. The difference is only 0.5 °/oo, which probably does not represent a significant enrichment and agrees with previous findings that $\delta^{15}N$ is most useful as an indicator of trophic level rather than food source.

As one moves from Massachusetts to Georgia to Mississippi the following trends confront an observer (see also Table 5 of

Peterson and Howarth 1987): 1) $\delta^{13}C$ values for Spartina stay constant at -13 $^{o}/oo$ whereas those for edaphic algae (and perhaps phytoplankton) become increasingly more negative; 2) the marsh fauna becomes increasingly depleted in ^{13}C and increasingly enriched in ^{34}S; and 3) although $\delta^{15}N$ values for consumers increase slightly the differences are insignificant compared to those for carbon and sulfur. Peterson and Howarth (1987) interpreted these trends as indicating that consumers in Sapelo Island were more dependent on phytoplankton and perhaps benthic algae than the fauna at Great Sippewissett. They stated that the contributions of Spartina and algae to the food web at Sapelo Island were "roughly equal" whereas their previous isotope work (Peterson et al. 1986) at Sippewissett led to the conclusion that Spartina was the major food source but phytoplankton were also important. The benthic algae were not considered in their earlier study. In the Mississippi marsh we move more or less 180 degrees from the conclusions of the Sippewissett study in that phytoplanktonic and benthic algae are major food sources and Spartina presumably plays a very minor role.

Why the relative importance of algae and Spartina should change so dramatically as one moves south along the Atlantic Coast and then west to the Gulf Coast is an important question, since it relates to possible differences in the functioning of salt marshes from different geographical regions. Peterson and Howarth (1987) hypothesized that algae would be expected to be more important in Georgia than in Massachusetts if their productivity and availability relative to *Spartina* were higher in the more southerly marsh. The productivity rates of edaphic algae on the marsh proper (Sullivan and Moncreiff 1988) and in the subtidal sediments of Graveline Bayou and lower-order tidal creeks (Zimba 1989) are quite significant. These algae are known to be the preferred food source for a host of estuarine consumers at lower trophic levels including harpacticoid copepods, nematodes, ostracods, mollusks, juvenile shrimp, and certain fish species (Gleason and Zimmerman 1984, Montagna 1984, Gleason 1986, Plante-Cuny and Plante 1986, Decho 1988). It should be pointed out that there are differences in basic hydrology between the three systems discussed above. Such differences include tidal range, regularity of tidal flooding, and possible freshwater and upland terrestrial inputs. Factors of this type could also be key components leading to the observed differences in stable isotope ratios. However, the bottom line is that the edaphic and other benthic algae can no longer be ignored in estuarine food web studies.

SUMMARY

1. To elucidate ultimate sources of organic matter and trophic relationships within a salt marsh food web the stable isotope ratios of the flora and fauna of an irregularly flooded Mississippi salt marsh were examined.

2. The stable carbon isotope ratios ($\delta^{13}C$) of the primary producers were distinct: _Spartina_ (-13 °/oo), _Juncus_ (-26 °/oo), and edaphic algae (-21 °/oo). Benthic algae, including macroalgal species, ranged from -21 to -18 °/oo. A pure zooplankton sample, which should closely approximate the phytoplankton, had a $\delta^{13}C$ value of -23 °/oo. Stable sulfur isotope ratios ($\delta^{34}S$) for the vascular plants ranged from 0 to +2 °/oo while those for the edaphic algae and zooplankton were +14 and +11 °/oo, respectively. The main source of sulfur for the algae is seawater sulfate. Stable nitrogen isotope ratios ($\delta^{15}N$) for all primary producers showed a narrow range of +5 to +6 °/oo.

3. The average $\delta^{13}C$, $\delta^{34}S$, and $\delta^{15}N$ values for particulate organic matter were -24, -8, and +5 °/oo, respectively. The $\delta^{13}C$ and $\delta^{15}N$ values are close to those of the algae but distinct from those of _Spartina_.

4. $\delta^{13}C$ values for sediments collected from beneath _Spartina_ and _Juncus_ and from the creekbank and subtidal reaches of

Graveline Bayou were all identical (-23 °/oo). $\delta^{34}S$ averaged -11 °/oo which is close to that of Spartina (and probably also Juncus) roots. $\delta^{15}N$ for sediments beneath the two vascular plants was +3 °/oo. Particulate organic matter and sediments had the same $\delta^{13}C$ values, whereas the latter had only slightly lower $\delta^{34}S$ and $\delta^{15}N$ values than the former.

5. The $\delta^{13}C$ values for 49 of 56 (88 %) consumers sampled in Graveline Bay Marsh ranged from -22 to -18 °/oo. Of these 49 consumers, 34 fell within an even narrower range of -22 to -20 °/oo. These $\delta^{13}C$ values centered around the edaphic algae and were slightly depleted in ^{13}C relative to zooplankton. The $\delta^{13}C$ values of the fauna were quite distinct from those of Spartina and Juncus.

6. The $\delta^{34}S$ values for 48 of 56 (86 %) consumers ranged from +9 to +16 °/oo. These consumers were 8 to 15 °/oo more enriched in ^{34}S than Spartina. It appears then that the major ultimate source of organic sulfur for the flora is seawater sulfate rather than ^{34}S-depleted sulfides.

7. $\delta^{15}N$ for the fauna ranged from +6 to +12 °/oo; thus all consumers were enriched in ^{15}N relative to phytoplankton, edaphic algae, and the vascular plants. The designation of a $\delta^{15}N$ value of +9 °/oo as a dividing line between deposit/suspension feeders and predators/omnivores advocated

in previous work appears to apply equally well to the consumer species of Graveline Bay Marsh. The value of $\delta^{15}N$ analyses thus lies in the area of determining a consumer's relative trophic level.

8. In contrast to previous studies, a plot of $\delta^{13}C$ and $\delta^{34}S$ values for primary producers and consumers resulted in a tight clustering of data points around the edaphic algae and phytoplankton, rather than in a broad band of values lying between phytoplankton and Spartina. No consumer even moderately resembled Spartina in its $\delta^{13}C$ and $\delta^{34}S$ values. Hence, an inescapable conclusion from the stable isotope work is that the major food sources for the fauna of Graveline Bay Marsh are the edaphic and planktonic algae; the contribution of the vascular plants appears to be minor at best. The present study represents the first documentation of the importance of edaphic algae in salt marsh food webs.

9. A plot of $\delta^{13}C$ and $\delta^{15}N$ values corroborated conclusions drawn from the $\delta^{13}C$ vs. $\delta^{34}S$ plot. This second plot showed a vertical band of $\delta^{15}N$ values lying between the $\delta^{13}C$ values of phytoplankton and edaphic algae. The fractionation of nitrogen by consumers at different trophic levels was also obvious in this plot.

10. Multiple stable isotope approaches have now been employed in salt marshes of Massachusetts, Georgia, and Mississippi. Regional comparisons reveal the following as one moves south along the Atlantic Coast and then west to the Gulf Coast: i) $\delta^{13}C$ values of Spartina remain constant but those for edaphic algae become increasingly more negative; ii) the marsh fauna becomes increasingly depleted in ^{13}C and increasingly enriched in ^{34}S; and iii) differences in $\delta^{15}N$ values between these three widely separated marshes are too small to be significant. These regional trends indicate an increasing dependence on phytoplanktonic and benthic algae by salt marsh consumers as one moves from Massachusetts to Georgia to Mississippi, with Spartina presumably playing a very minor role as a food source in the Mississippi marsh.

11. Previous work in the Graveline system has shown the edaphic algae beneath the vascular plant canopies and those associated with subtidal sediments in the main bayou and lower-order tidal creeks to possess significant production rates. Since these algae are the preferred food source of many estuarine consumers and are easily suspended by tidal currents to become members of the "phytoplankton", the edaphic and other benthic algae can no longer be ignored in estuarine food web studies.

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Table 1. Summary of $\delta^{13}C$, $\delta^{34}S$, and $\delta^{15}N$ values from the literature for salt marsh floral components in parts per mil (°/oo).

Plant group	$\delta^{13}C$	$\delta^{34}S$	$\delta^{15}N$	References[a]
Spartina	-13 to -12	-10 to +8	+4 to +6	1,3,4,6-10
Edaphic algae	-18 to -14	+13 to +18	+4 to +5	3,6,8-11
Phytoplankton	-23 to -19	+19 to +20	+9	2-4,7-10
Juncus	-26 to -24	+6	+3 to +5	1,5,6,9

[a] Key to references: 1. Hackney & Haines (1980); 2. Gearing et al. (1984); 3. Haines (1976a); 4. Haines & Montague (1979); 5. Hughes & Sherr (1983); 6. Mariotti et al. (1983); 7. Peterson et al. (1985); 8. Peterson et al. (1986); 9. Peterson & Howarth (1987); 10. Schwinghamer et al. (1983); 11. Zimba (1989)

Table 2. Summary of $\delta^{13}C$, $\delta^{34}S$, and $\delta^{15}N$ values for primary producers of Graveline Bay Marsh in parts per mil (°/oo). Each mean is followed by its standard error and the number of samples (N).

Producers	$\delta^{13}C$	$\delta^{34}S$	$\delta^{15}N$
Spartina	-13.2 ± 0.1 (12)	+1.4 ± 2.2 (12)	+5.2 ± 0.5 (6)
Juncus	-25.5 ± 0.2 (12)	+0.4 ± 0.8 (12)	+5.3 ± 0.8 (4)
Edaphic algae	-20.6 (1)	+14.3 (1)	+6.1 (1)

Table 3. Mean values for $\delta^{13}C$, $\delta^{34}S$, and $\delta^{15}N$ characterizing different size fractions of particulate organic matter in Graveline Bay Marsh in parts per mil ($^{o}/oo$).

Size fraction	$\delta^{13}C$	$\delta^{34}S$	$\delta^{15}N$
335 µm	-25.0	-3.2	+4.5
153 µm	-24.0	-12.5	+5.8
28 µm	-22.4	-9.8	+5.4
Grand mean	-23.8	-8.0	+5.2

Table 4. $\delta^{13}C$ and $\delta^{34}S$ values for sediments at the three stations of Graveline Bay Marsh averaged over different size fractions in parts per mil °/oo).

Station	$\delta^{13}C$	$\delta^{34}S$
1	-22.7	-12.9
2	-24.0	-10.5
3	-22.8	-6.0
Grand mean	-23.2	-11.3

Table 5. $\delta^{13}C$ and $\delta^{34}S$ values for different size fractions of sediments in Graveline Bay Marsh averaged over the three stations in parts per mil °/oo).

Size fraction	$\delta^{13}C$	$\delta^{34}S$
Unsieved	-23.1	-11.4
63 µm	-23.6	-11.8
1 mm	-22.4	-8.6
Grand mean	-23.2	-11.3

Table 6. $\delta^{13}C$, $\delta^{34}S$, and $\delta^{15}N$ values for sediments in different marsh zones of Graveline Bay Marsh averaged over all stations and size fractions in parts per mil (°/oo).

Marsh zone	$\delta^{13}C$	$\delta^{34}S$	$\delta^{15}N$
Spartina	-22.7	-11.2	+2.9
Juncus	-23.0	-7.3	+2.8
Creekbank	-23.3	-14.9	N.D.
Subtidal	-23.6	-10.8	N.D.
Grand mean	-23.2	-11.3	+2.9

TABLE 7. Summary of stable isotope ratios for consumers of Graveline Bay Marsh. Numbers for C,S and N indicate number of samples. Values are in parts per mil ($^{o}/oo$).

Consumer	$\delta^{13}C$	$\delta^{34}S$	$\delta^{15}N$	C,S	N
Micropterus salmoides (largemouth bass)	-25.1	3.6	6.7	1	1
Micropogon undulatus roe	-23.4	7.4	8.1	1	1
Trinectes maculatus (hogchoker)	-23.3	8.1	---	2	-
Zooplankton, all species	-23.3	10.7	7.1	1	1
Micropogon undulatus (Atlantic croaker)	-22.4	10.9	10.2	13	6
Polymesoda caroliniana (marsh clam)	-22.0	11.3	8.5	1	1
Lagodon rhomboides (pinfish)	-22.0	12.4	10.1	7	4
Rangia cuneata	-21.9	12.0	7.2	1	1
Ischadium recurvum (hooked mussel)	-21.9	12.4	6.6	6	4
Geukensia demissa (ribbed mussel)	-21.8	11.2	7.3	2	2
Littorina irrorata (marsh periwinkle)	-21.6	14.3	---	4	-
Crassostrea virginica (American oyster)	-21.4	13.9	8.1	6	3
Brevoortia patronus (Gulf menhaden)	-21.3	14.5	11.3	7	6
Elops saurus (ladyfish)	-21.3	10.5	---	2	-
Archosargus probatocephalus (sheepshead)	-21.2	12.4	10.0	6	6
Pogonias cromis (black drum)	-21.1	8.2	8.4	1	1
Brevoortia patronus roe	-21.1	14.0	10.0	1	1
Leiostomus xanthurus (spot)	-21.0	9.9	11.2	7	7
Penaeus setiferus (white shrimp)	-21.0	9.9	---	15	-
Neanthes spp. (nereid worms)	-20.9	8.2	8.2	1	1
Anguinella palmata (bryozoan)	-20.8	13.5	8.1	1	1
Stellifer lanceolatus (star drum)	-20.8	11.5	10.2	1	1
Cynoscion nebulosus (speckled trout)	-20.7	12.2	11.8	11	1
Mugil cephalus roe	-20.6	10.8	7.1	1	1
Anchoa mitchilli (bay anchovy)	-20.6	14.5	12.0	3	2
Penaeus aztecus (brown shrimp)	-20.5	10.7	---	10	-
Cynoscion arenarius larval/juv. (white trout)	-20.4	12.8	11.0	2	2
Bugula sp. (bryozoan)	-20.4	14.0	8.9	1	1
Arius felis (hardhead catfish)	-20.3	12.7	11.5	11	7
Brevoortia patronus, larval	-20.3	10.0	---	3,2	-
Membras/Menidia, juv.	-20.2	13.6	---	1	-
Lolliguncula brevis (estuarine squid)	-20.2	13.2	11.1	2	2
Menidia beryllina (tidewater silverside)	-20.2	12.3	11.2	10	7
Membras martinica (rough silverside)	-20.2	16.0	11.9	3	1
Larval clupeids	-20.1	15.4	11.5	3	3
Paralichthys lethostigma (southern flounder)	-20.0	10.9	9.7	6	2
Sciaenops ocellatus (redfish)	-20.0	9.8	10.2	9	7
Symphurus plagiusa (blackcheek tonguefish)	-20.0	9.3	---	1	-
Membras martinica, larval/juv.	-20.0	14.4	11.5	1	1
Clibanarius vittatus (striped hermit crab)	-19.6	14.2	9.4	2	1
Callinectes sapidus (blue crab)	-19.6	10.7	8.6	10	5
Anchoa nasuta (longnose anchovy)	-19.5	14.0	12.4	1	1
Bairdiella chrysura (silver perch)	-19.4	13.1	12.2	7	4
Paleomonetes pugio (grass shrimp)	-19.4	6.2	8.6	4,3	2
Mugil cephalus, juv.	-19.3	10.3	6.4	2	1
Fundulus pulvereus (bayou killifish)	-19.1	7.3	7.8	1	1
Mugil cephalus (striped mullet)	-18.9	10.3	8.0	7	1
Menticirrhus sp. (kingfish)	-18.8	11.5	11.1	1	1
Sciaenops ocellatus, juv.	-18.7	12.9	---	1	-
Fundulus majalis (longnose killifish)	-18.6	7.8	9.6	3	2
Larval spot/croaker	-18.6	14.6	---	1	-
Poecilia latipinna (sailfin molly)	-18.1	10.0	6.2	1	1
Fundulus grandis (Gulf killifish)	-18.1	9.6	---	1	-
Polinices duplicatus (moon snail)	-18.1	10.5	8.4	1	1
Harengula pensacolae (scaled sardine)	-17.8	16.4	12.1	1	1
Uca spp. (fiddler crabs)	-15.0	14.9	7.2	1	1

FIGURE LEGENDS

Figure 1. Map of Graveline Bay Marsh showing location of the sampling stations.

Figure 2. $\delta^{13}C$ values of consumers in Graveline Bay Marsh in parts per mil (°/oo).

Figure 3. $\delta^{34}S$ values of consumers in Graveline Bay Marsh in parts per mil (°/oo).

Figure 4. $\delta^{15}N$ values of consumers in Graveline Bay Marsh in parts per mil (°/oo).

Figure 5. Plot of $\delta^{34}S$ values as a function of $\delta^{13}C$ for primary producers and consumers of Graveline Bay Marsh in parts per mil (°/oo).

Figure 6. Plot of $\delta^{15}N$ values as a function of $\delta^{13}C$ for primary producers and consumers of Graveline Bay Marsh in parts per mil (°/oo).

Figure 7. Plot of $\delta^{15}N$ values as a function of $\delta^{34}S$ for primary producers and consumers of Graveline Bay Marsh in parts per mil (°/oo).

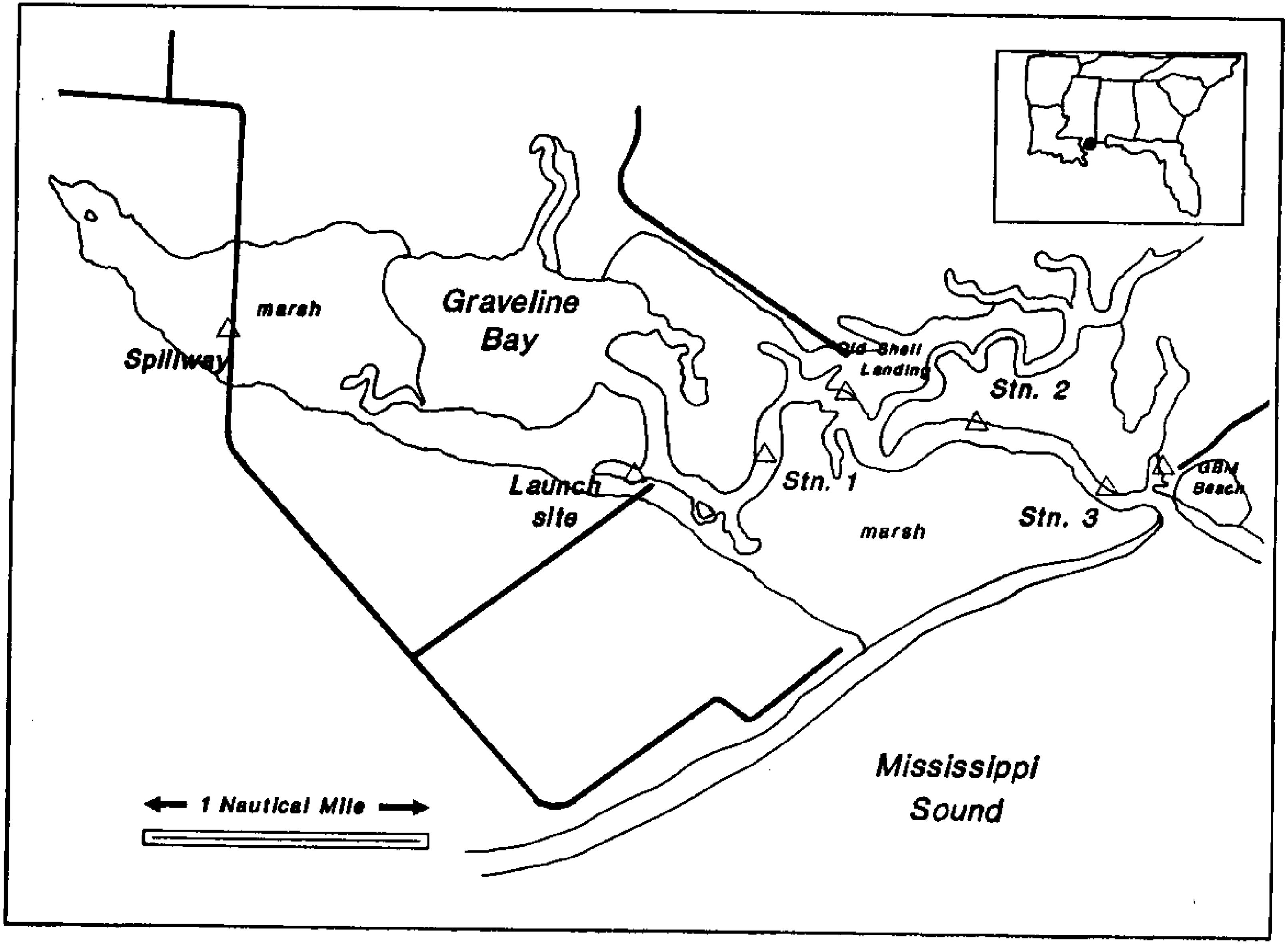
Graveline Bay
marsh
Spillway
Old Shell Landing
Stn. 2
Stn. 1
Launch site
marsh
Stn. 3
GBM Beach
Mississippi Sound
1 Nautical Mile

Figure 1

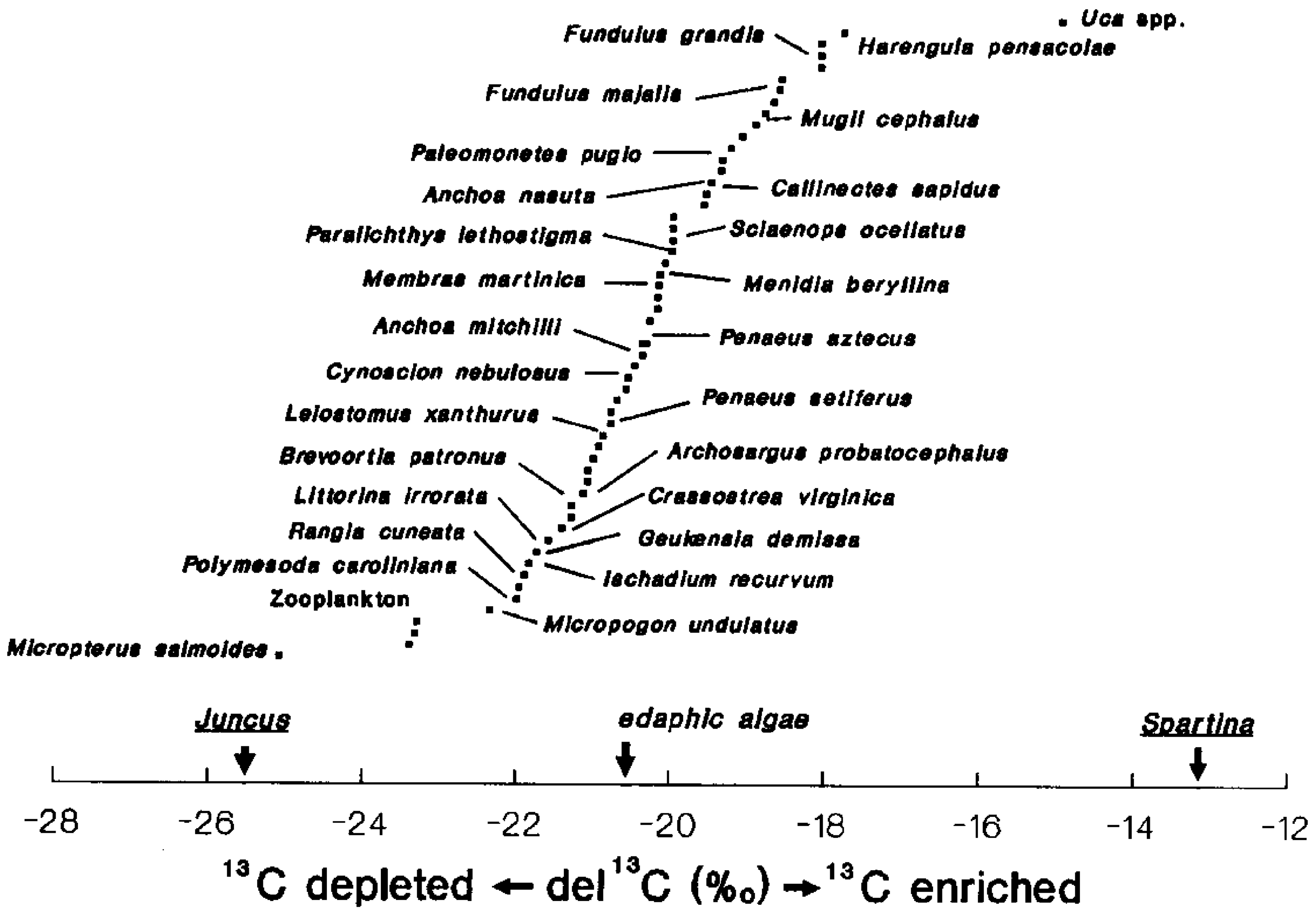
Uca spp.
Fundulus grandis
Harengula pensacolae
Fundulus majalis
Mugil cephalus
Paleomonetes pugio
Anchoa nasuta
Callinectes sapidus
Paralichthys lethostigma
Sciaenops ocellatus
Membras martinica
Menidia beryllina
Anchoa mitchilli
Penaeus aztecus
Cynoscion nebulosus
Penaeus setiferus
Leiostomus xanthurus
Brevoortia patronus
Archosargus probatocephalus
Littorina irrorata
Crassostrea virginica
Rangia cuneata
Geukensia demissa
Polymesoda caroliniana
Ischadium recurvum
Zooplankton
Micropogon undulatus
Micropterus salmoides
Juncus
edaphic algae
Spartina
-28
-26
-24
-22
-20
-18
-16
-14
-12
^{13}C depleted ← del^{13}C (‰) → ^{13}C enriched

Figure 2

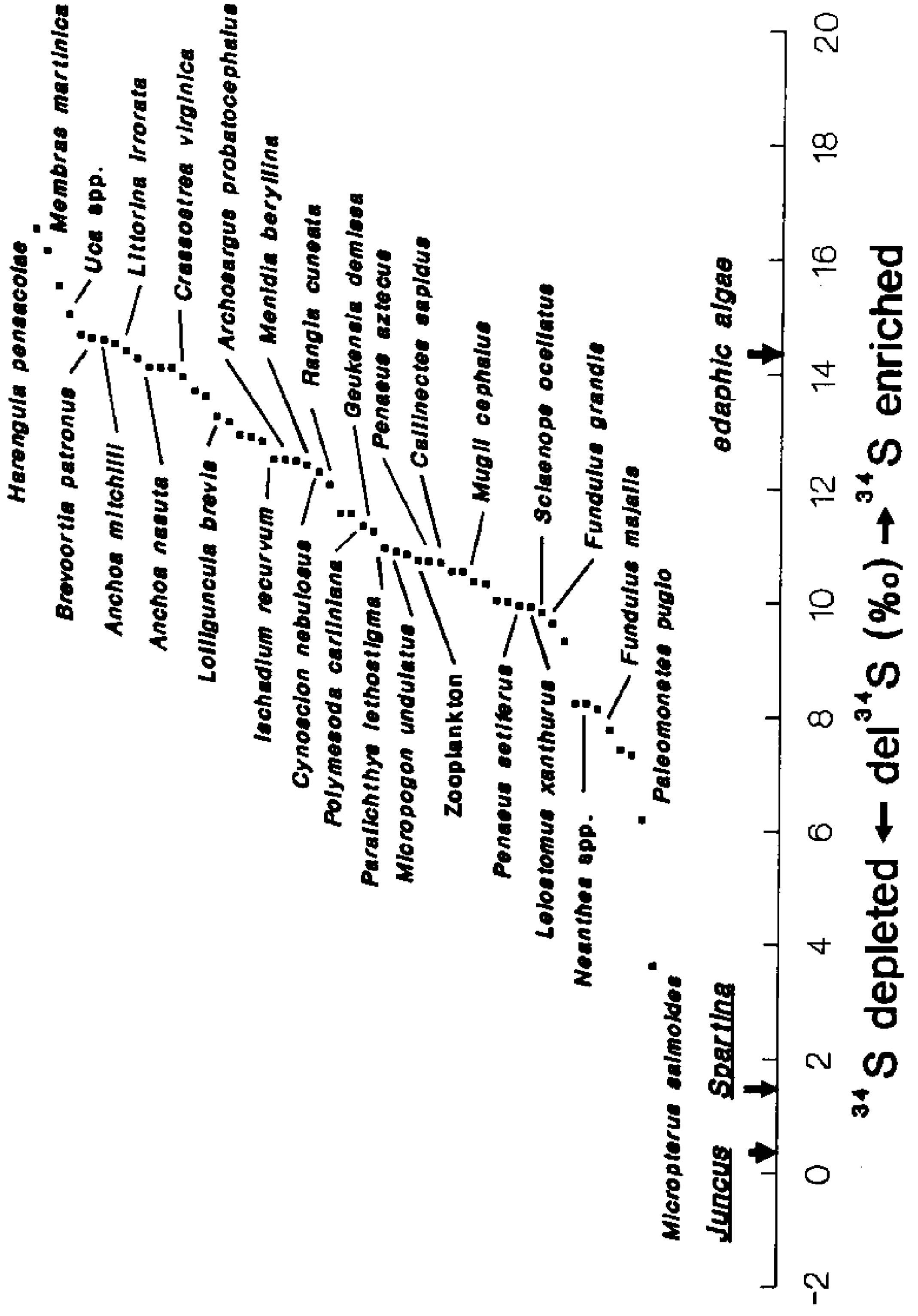
Harengula pensacolae
Membras martinica
Uca spp.
Littorina irrorata
Crassostrea virginica
Archosargus probatocephalus
Menidia beryllina
Rangia cuneata
Geukensia demissa
Penaeus aztecus
Callinectes sapidus
Mugil cephalus
Sciaenops ocellatus
Fundulus grandis
Fundulus majalis
Paleomonetes pugio
Brevoortia patronus
Anchoa mitchilli
Anchoa nasuta
Lolliguncula brevis
Ischadium recurvum
Cynoscion nebulosus
Polymesoda caroliniana
Paralichthys lethostigma
Micropogon undulatus
Zooplankton
Penaeus setiferus
Leiostomus xanthurus
Neanthes spp.
Micropterus salmoides
Juncus
Spartina
edaphic algae
-2
0
2
4
6
8
10
12
14
16
18
20
^{34}S depleted ← del^{34}S (‰) → ^{34}S enriched

Figure 3

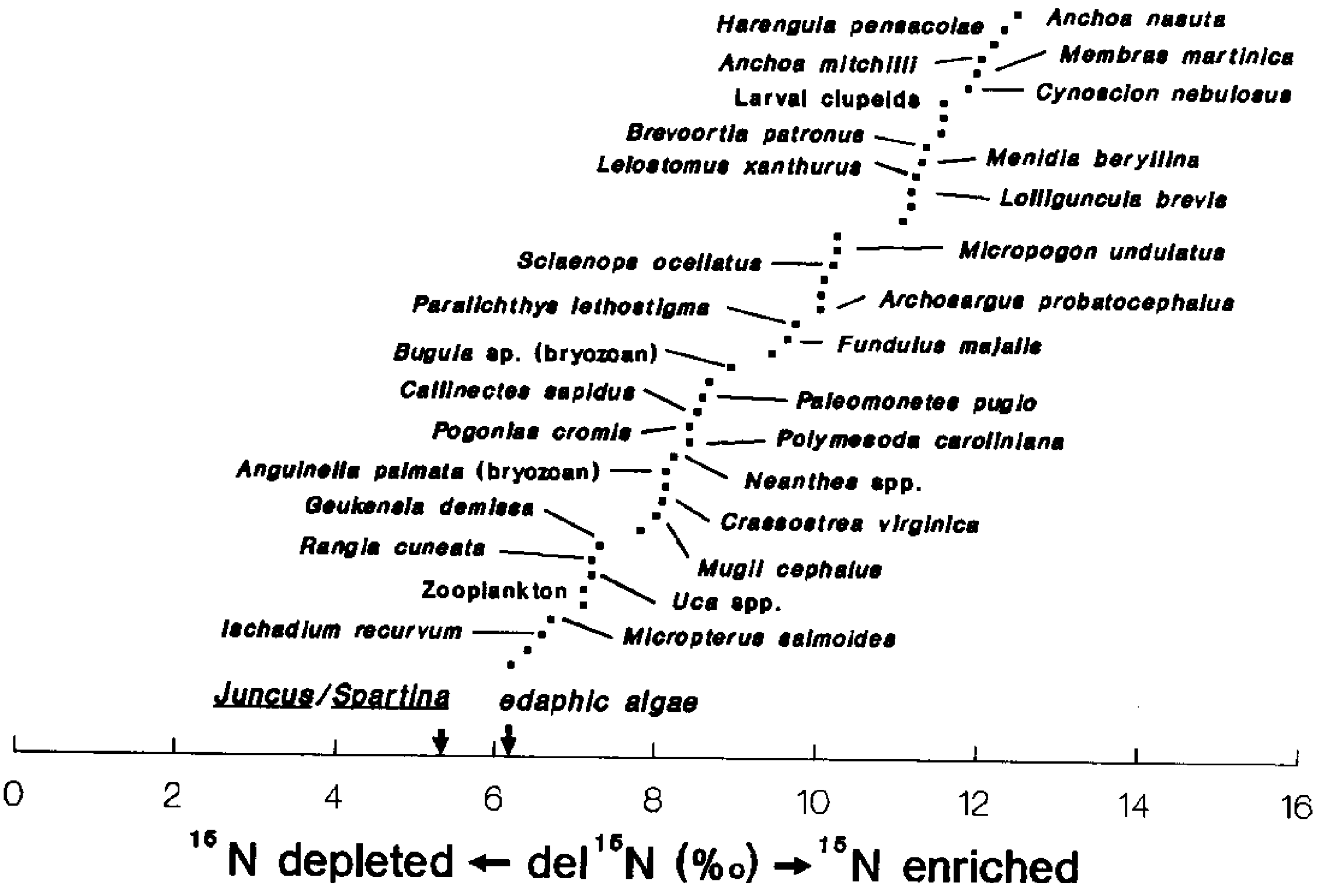
Harengula pensacolae
Anchoa nasuta
Anchoa mitchilli
Membras martinica
Larval clupeids
Cynoscion nebulosus
Brevoortia patronus
Menidia beryllina
Leiostomus xanthurus
Lolliguncula brevis
Micropogon undulatus
Sciaenops ocellatus
Archosargus probatocephalus
Paralichthys lethostigma
Fundulus majalis
Bugula sp. (bryozoan)
Callinectes sapidus
Paleomonetes pugio
Pogonias cromis
Polymesoda caroliniana
Anguinella palmata (bryozoan)
Neanthes spp.
Geukensia demissa
Crassostrea virginica
Rangia cuneata
Mugil cephalus
Zooplankton
Uca spp.
Ischadium recurvum
Micropterus salmoides
Juncus/Spartina
edaphic algae
0
2
4
6
8
10
12
14
16
15N depleted ← del15N (‰) → 15N enriched

Figure 4

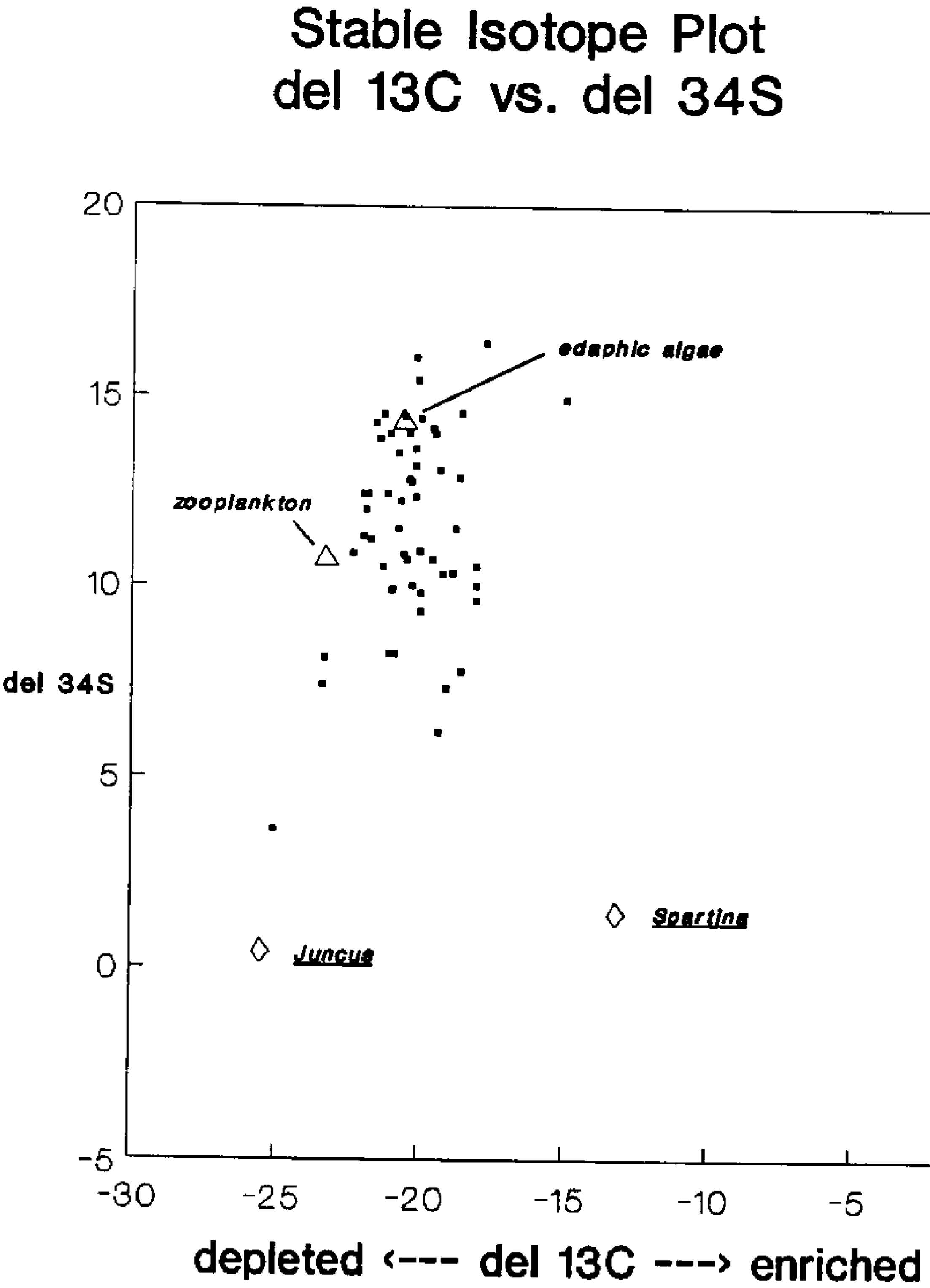
Stable Isotope Plot
del 13C vs. del 34S
20
15
10
5
0
-5
-30
-25
-20
-15
-10
-5
0
del 34S
depleted <--- del 13C ---> enriched
edaphic algae
zooplankton
Spartina
Juncus

Figure 5

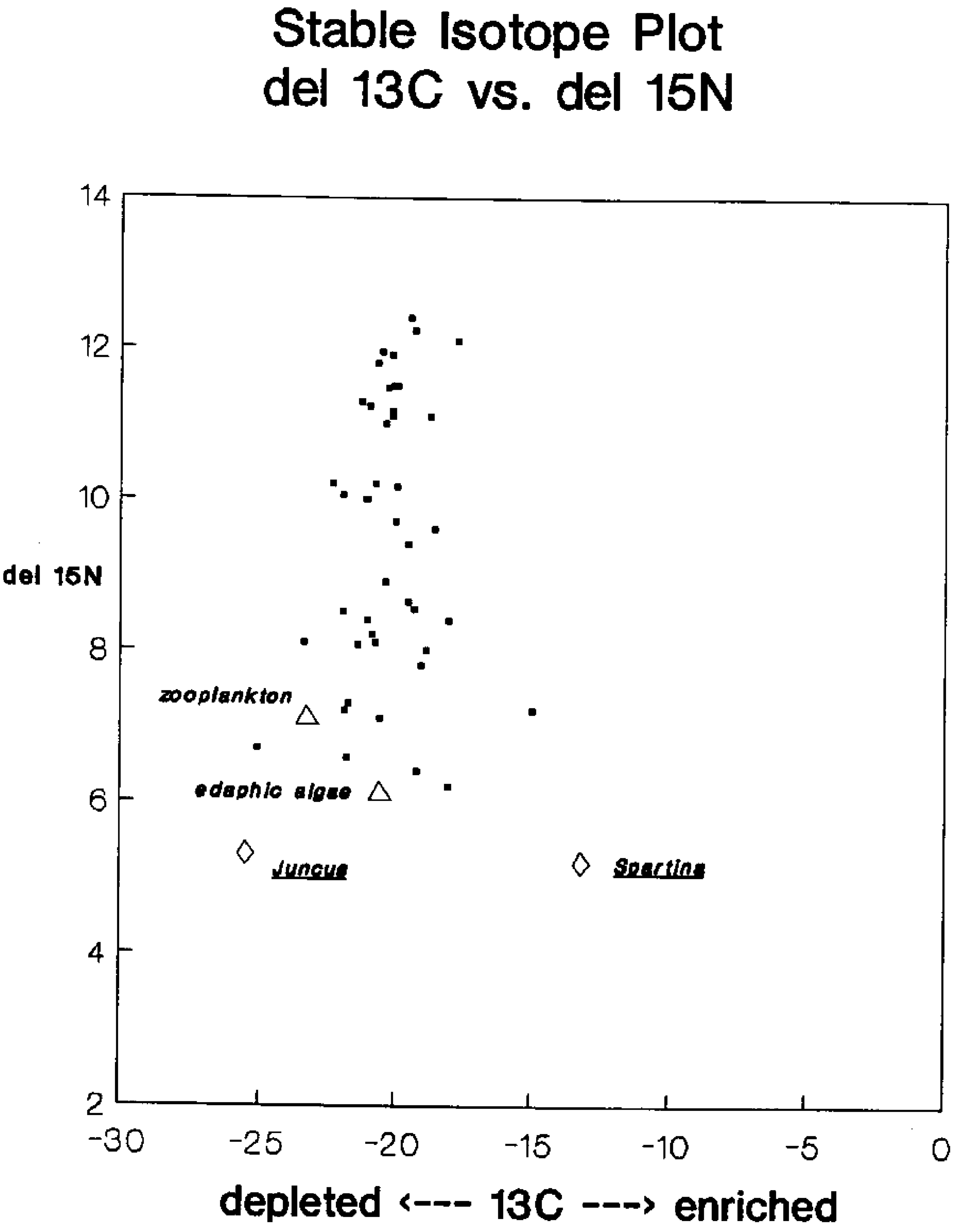
Stable Isotope Plot
del 13C vs. del 15N
14
12
10
8
6
4
2
del 15N
zooplankton
edaphic algae
Juncus
Spartina
-30
-25
-20
-15
-10
-5
0
depleted <--- 13C ---> enriched

Figure 6

Stable Isotope Plot
del 34S vs. del 15N

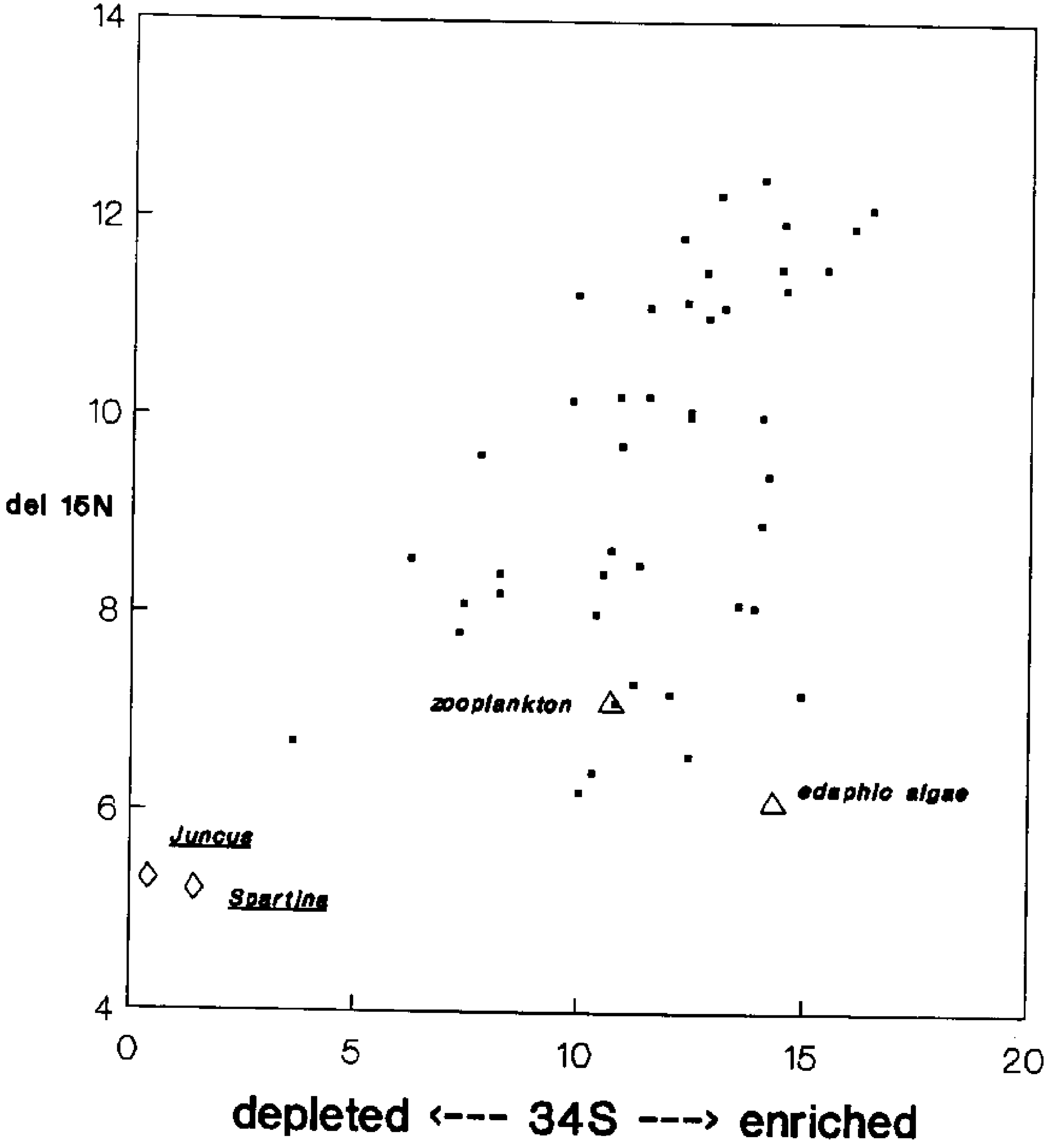

Figure 7