Trophic Importance of Epiphytic Algae in Mississippi Seagrass Beds

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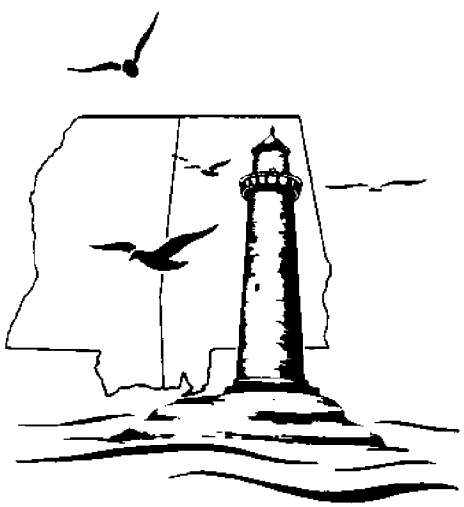

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DEDICATION

This report is dedicated to the memory of Dr. James I. Jones, Director of the Mississippi-Alabama Sea Grant Consortium from 1976 until his death on 10 July 1993.

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TABLE OF CONTENTS

ABSTRACT

Multiple stable isotope analyses were used to examine food web dynamics in Halodule wrightii Aschers. beds located off the northwestern shore of Horn Island in Mississippi Sound. Stable isotope ratios for carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) were measured on material collected from May 1989 through November 1992. The $\delta^{13}C$ and $\delta^{34}S$ values of most consumer organisms clustered near those measured for epiphytes, macroalgae, and plankton, rather than that of the seagrass blades. Trophic levels, as determined by $\delta^{15}N$, could not be clearly separated. Stable isotope data, in combination with high measured rates of primary production, strongly suggest that epiphytic algae are the major source of organic carbon for higher trophic levels in this system. The contribution of H. wrightii appears to be minimal, at best. The overall picture that is emerging based on the present and previous studies is one of the major trophic importance of benthic microalgae (i.e. epiphytes and sediment-associated microflora) in coastal food webs.

INTRODUCTION

Seagrasses and their associated epiphytes are a unique component of the benthic communities of Mississippi Sound. Seagrass beds in the Sound occur primarily in shallow water (1-2 m) along the nearshore margins of the coastal barrier islands. They may also be found in semi-protected regions of coastal embayments and estuaries where substrate, salinity, and light requirements for the various seagrass species are met (Eleuterius 1971, Eleuterius and Miller 1976).

Seagrass beds can be characterized as extremely productive ecosystems in shallow coastal waters. Their complexity with regard to both structure and function is due to the great diversity and abundance of organisms present. The dominant vascular plants are perennial marine angiosperms, termed seagrasses, which are monocots of the families Hydrocharitaceae, Posidoniaceae, Cymodoceaceae, and Zosteraceae (not members of the grass family Poaceae). Seagrasses are rooted in the sediments, which may be either sandy or muddy. A diverse and highly productive epiphytic assemblage, comprised mainly of microscopic algae, is attached to the seagrass leaf blades. This assemblage is dominated by various species of diatoms and red, brown, green, and blue-green algae (Humm 1964, Ballantine and Humm 1975, Sullivan 1979, Thursby and Davis 1984). Sediments beneath and adjacent to the seagrass beds are covered with a microfloral community populated primarily by

species of small pennate diatoms. Seagrasses function as habitat for invertebrate and small vertebrate marine organisms, in addition to acting as a substrate for the epiphytic algal assemblage associated with the beds. Resident fauna associated with seagrass beds includes copepods, amphipods, isopods, shrimp, crabs, other small crustaceans, gastropods, nematodes, polychaetes, echinoderms, and small fish (Morgan and Kitting 1984, Kitting 1984, Kitting et al. 1984). Recent research indicates that the epiphytic algal assemblage may be the primary food source within this community, as opposed to the seagrasses and the detrital material they generate (Fry et al. 1982, Fry 1984, Kitting et al. 1984, Nichols et al. 1985, Gleason 1986, Fry et al. 1987, Dauby 1989).

The dominant seagrasses in the Gulf of Mexico are Halodule wrightii Ascherson (shoal grass), Thalassia testudinum Koenig (turtle grass), and Syringodium filiforme Kuetz. (manatee grass). Studies of seagrasses conducted in Louisiana, Mississippi, and Alabama are summarized by Eleuterius (1987). Extensive beds of these seagrasses have developed off the northern shores of the offshore barrier islands in Mississippi Sound in the past (Eleuterius 1971, Eleuterius and Miller 1976). These beds are assumed to be trophically important to many consumer species in Mississippi Sound, particularly penaeid shrimp and fin fish. This study was designed to evaluate the trophic importance of seagrass beds in Mississippi Sound.

Research efforts heretofore have focused on the productivity and presumed trophic importance of the macroscopic seagrasses themselves; however, recent work

has indicated that the epiphytic algae may be the primary basis of the food web in many seagrass ecosystems. Sand-associated microflora within seagrass beds have been virtually ignored. The primary production rates of epiphytic algae in Mississippi Sound's seagrass beds have been shown to be sufficiently high such that these algae are a potentially significant contributor to the food web (Moncreiff et al. 1992). Previous joint research on these two factors has been carried out in only one seagrass system in all the world's oceans (Morgan and Kitting 1984, Kitting et al. 1984).

Although food webs in seagrass systems are complex, determination of ultimate food sources via stable carbon isotope analysis can be a powerful tool for studying trophic relationships in particular seagrass beds, as indicated by the review of selected literature that follows. Multiple stable isotope analysis, a combination of carbon, nitrogen, and sulfur measurements, greatly increases the resolution of the technique and can provide concrete evidence for the relative importance of seagrasses, epiphytic algae, and phytoplankton in the food web (Fry and Sherr 1984, Peterson and Howarth 1987, Fry et al. 1987).

It is well known that many animals, including commercially important species such as penaeid shrimp and blue crab, use seagrass beds for habitat and feeding during part or all of their life cycles (Kitting et al. 1984, Morgan and Kitting 1984, van Montfrans et al. 1984). Laboratory feeding experiments have shown that penaeid shrimp prefer epiphytic algae over phytoplankton, seagrass, or marsh grass as a primary food source (Gleason and Zimmerman 1984). The preference of

invertebrate grazers for the ephemeral and highly productive epiphytes is illustrated in Figure 2 of Kitting et al. (1984), which is a photograph of the brown shrimp Penaeus aztecus Ives actively foraging in an overgrowth of epiphytic algae in a Halodule wrightii bed at night. Morgan and Kitting (1984) have urged that, because epiphyte growth is translated into a substantial biomass which is heavily grazed, any investigations of production dynamics and food relationships in seagrass systems should include careful evaluation of the role of epiphytic algae.

The major objective of the present study was to assess the trophic importance of seagrass communities in Mississippi Sound. To accomplish this, we employed multiple stable isotope analyses to document the importance of the four components of primary production (the seagrass H. wrightii, its associated epiphytes, the phytoplankton, and the sand microflora) as food sources for not only economically important shellfish and fin fish but also the numerous invertebrate and fish species which support these fisheries.

The survey of the stable isotope literature that follows constitutes a review of the technique and details how it has been used in estuarine and marine ecosystems, focusing on marine seagrasses.

REVIEW OF LITERATURE

Stable Isotope Terminology and Background

Stable isotope analyses provide a means of assessing the trophic importance of various components of primary production. The element carbon (C) occurs in two different stable isotopic forms in the earth's biosphere: ^{12}C and ^{13}C. Approximately 99% of elemental carbon is in the ^{12}C form and 1% in the ^{13}C form (Haines 1977). The $^{13}C/^{12}C$ ratio of various organisms can be quite useful in ecological studies of carbon flow through different trophic levels because significant fractionation of these carbon isotopes occurs during photosynthesis (Haines 1977, Fry and Sherr 1984). This fractionation is dependent on both the source of carbon used (CO_2 or HCO_3^-) and the photosynthetic pathway employed (Benedict 1976). $^{13}C/^{12}C$ ratios are reported with reference to a standard, generally the marine limestone PeeDee belemnite, which is often abbreviated as PDB (Fry and Sherr 1984). Although the supply of this material has been virtually exhausted, there are a number of other reference materials in use at various laboratories that have well-established values relative to this standard (Ehleringer and Rundel 1988). The difference between the material under consideration and the standard is expressed in parts per thousand or per mil (‰) according to the following formula:

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1) \times 10^3,$$

where R is the ratio of ^{13}C to ^{12}C in both the sample and the standard.

Stable carbon isotope fractionation was first used in the 1950's as a research tool by geochemists, and in the early 1970's by plant physiologists to investigate photosynthetic pathways (Benedict 1976, Ehleringer and Rundel 1988). This was followed by use of isotopic fractionation as a means of elucidating ecological relationships and the fate of carbon in estuarine and marine food webs (Haines 1976).

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). Studies have consistently shown that animals have $\delta^{13}C$ values within 2 ‰ of their food sources (Fry and Sherr 1984, DeNiro and Epstein 1978, Peterson and Howarth 1987). Since these values for the tissues of animals mirror their diet, one should be able to trace the pathway of organic matter through seagrass food webs from the primary producers to consumers occupying different trophic levels. The old axiom, "you are what you eat (and assimilate)", should permit one to identify the ultimate food sources for many of the animals inhabiting seagrass beds on a permanent basis or during a particular stage of their life cycle.

Carbon isotopic analysis alone cannot always 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 $\delta^{13}C$ values); therefore 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). Two other stable isotopes that have proved valuable in this regard in studies from Massachusetts, Georgia, and Mississippi salt marshes are those of sulfur and nitrogen (Peterson et al. 1985, Peterson et al. 1986, Peterson and Howarth 1987, Sullivan and Moncreiff 1990).

The element sulfur (S) exists in four different stable isotopic forms in the earth's biosphere, ^{32}S, ^{33}S ^{34}S, and ^{36}S, with ^{32}S being the most abundant isotope (95%) and ^{34}S the most common of the rare forms (4%). As in stable carbon isotopic work, $^{34}S/^{32}S$ ratios are expressed relative to a standard, in this case a troilite (FeS) from the Canyon Diablo meteorite, abbreviated as CD (Ehleringer and Rundel 1988, Krouse 1988). Unlike $\delta^{13}C$ values, those of $\delta^{34}S$ may be positive or negative in the tissues of estuarine and marine plants and animals. Estuarine plants will have positive $\delta^{34}S$ values if they take up their inorganic sulfur primarily as ionic sulfate and negative values if their main sulfur source is inorganic sulfide (Fry at al. 1982). $\delta^{34}S$ values for seawater sulfate and ^{34}S-depleted sedimentary sulfides are +20 ‰ and -10 to -30 ‰, respectively (Fry and Sherr 1984, Fry et al. 1982). Animals typically possess $\delta^{34}S$ values within 2 ‰ of their food source (Peterson and Howarth 1987, Fry 1988).

The element nitrogen, like carbon, also exists in two different stable isotopic forms: ^{14}N and ^{15}N. ^{14}N is the more abundant isotope at 99.6%, with ^{15}N comprising 0.4% of the available element (Ehleringer and Rundel 1988). $\delta^{15}N$ values are also expressed relative to a standard (atmospheric diatomic nitrogen) and are usually

positive (i.e. enriched in ^{15}N relative to the standard) in marine plants and animals (Peterson and Howarth 1987). Stable nitrogen isotope values are good indicators of relative trophic level of a consumer rather than food source (Peterson and Howarth 1987, Fry 1988, Sullivan and Moncreiff 1990) because $\delta^{15}N$ values for different primary producer groups are typically not distinct and consumers fractionate nitrogen by +1 to +5 ‰ per trophic transfer (Peterson and Howarth 1987, Fry 1988).

Haines (1976) was the first investigator to use stable isotope analysis as a tool for examining food webs. Using stable carbon isotope values to trace organic matter flow, she found that most invertebrates sampled in a Georgia salt marsh matched values for edaphic algae, as opposed to those for the dominant vascular plants or detritus.

Peterson et al. (1985) were the first to use multiple stable isotopes to study marine food webs. By measuring stable carbon, nitrogen, and sulfur ratios, and employing dual isotope plots, they concluded that a mixture of food sources fueled the salt marsh food web under study. The use of dual isotope plots allowed unambiguous interpretation of food web relationships employing the stable isotope ratios measured for primary producer and consumer organisms sampled.

Seagrass ecosystem food webs were first examined using stable isotope analysis by Thayer (1978); this and other published studies in seagrasses to date are summarized below.

Stable Isotope Studies in Seagrass Beds

McMillan et al. (1980) summarized $\delta^{13}C$ values for 47 species of seagrasses in 12 genera from the oceans of the world. Values ranged from -3 to -19 ‰ and species of the genus Syringodium (e.g. S. filiforme and S. isoetifolium (Aschers.) Dandy) were most enriched (i.e. least depleted) in ^{13}C. In general tropical species had higher $\delta^{13}C$ values than temperate ones.

Thayer et al. (1978) conducted the first bona fide stable isotope study in a seagrass meadow. $\delta^{13}C$ values for Zostera marina L. and its epiphytes in a North Carolina bed averaged -10 and -16 ‰, respectively. Animals within the eelgrass bed representing different invertebrate groups and fish species possessed $\delta^{13}C$ values which ranged from -15 to -18 ‰. Despite the fact that $\delta^{13}C$ values ranged from -14 to -18 ‰ for the epiphytic algae the authors concluded that the majority of animals were more linked to the plankton-carbon food chain than the seagrass-carbon food chain. In addition, they hypothesized that $\delta^{13}C$ was higher for epiphytic than for planktonic algae (typically -20 to -22 ‰) because it was assumed that the former derived some of their carbon from dissolved organic carbon released by Z. marina leaves.

Fry and Parker (1979) found that shrimp and fish collected in south Texas seagrass beds were significantly enriched in ^{13}C by an average of +3.3 to +5.1 ‰ relative to comparative animals collected offshore in the open waters of the Gulf of Mexico. $\delta^{13}C$ values for the four seagrass species ranged from -5 to -13 ‰; epiphytic algae were not sampled. They concluded that seagrasses and other benthic

plants were major food sources for juvenile shrimp and fish inhabiting the beds.

Fry et al. (1982) recorded nearly identical results relative to enrichment in ^{13}C for animals inhabiting seagrass beds off Nicaragua and St. Croix, U.S. Virgin Islands, as did Fry and Parker (1979). $\delta^{13}C$ values ranged from -4 to -13 ‰ for the four seagrass species. A single epiphyte sample scraped from Thalassia testudinum leaves yielded a value of -12.4 ‰. Most animals ranged from -9 to -16 ‰ and it was estimated that seagrasses and benthic algae (i.e. macroalgae) contributed at least 48 to 76% of the carbon found in fish associated with the seagrass beds. Based on $\delta^{13}C$ values (-10.3 and -11.1 ‰) for two St. Croix ballyhoo fish (Hemiramphus brasiliensis (L.)) which eat only Syringodium filiforme leaves, Fry and Parker (1979) and Fry et al. (1982) first suggested that animals ingest and assimilate epiphytic algae instead of seagrass leaves. They further suggested that consumption of these algae could account for the overall similarity in $\delta^{13}C$ values observed at all study sites.

Fry (1984) then turned his attention to Syringodium filiforme beds in the Indian River Lagoon, Florida. Average $\delta^{13}C$ values for manatee grass and its epiphytes were -8 and -19‰, respectively, and most of the fauna ranged from -16 to -22 ‰. Fry (1984) concluded that the food web was based on algal (i.e. epiphytes and phytoplankton) rather than seagrass carbon and noted that these results contradicted the dogma that seagrass detritus was the dominant carbon source in the food web.

Kitting et al. (1984) supplemented their previously described remote sensing

of grazing (time-lapse photography, microacoustical monitoring, and high resolution gut analyses) with $\delta^{13}C$ determinations of three seagrass species (-2.5 to -11 ‰), epiphytes (-10.5 to -17 ‰), and animals (-9 to -15 ‰) in six seagrass beds in Corpus Christi and Redfish Bays and the lower Laguna Madre of Texas. This study might be considered a landmark study because the data affirmed that invertebrates fed largely on epiphytic algae, even when such algae were scarce, rather than the seagrass leaves. For the sites under study in this system the epiphytic algae were the primary basis of the food web in each seagrass bed monitored. Very strong support for this conclusion came from the fact that animal $\delta^{13}C$ values tracked epiphyte rather than seagrass values when comparisons were made over six sites.

Dauby (1989) determined $\delta^{13}C$ values for floral and faunal components in the Gulf of Calvi, Corsica, where extensive Posidonia oceanica (L.) Delile meadows develop. Average values were as follows for the primary producers: -8 ‰ for the seagrass, -17 ‰ for the epiphytes, -19 ‰ for the macroalgae, and -23 ‰ for the phytoplankton. $\delta^{13}C$ values for animals ranged from -14 to -24 ‰, indicating they feed mainly on benthic algae and phytoplankton. A large fraction of the P. oceanica biomass was exported toward beaches by winter storms and consequently lost to marine consumers as a direct source of carbon.

Nichols et al. (1985) employed $\delta^{13}C$ analysis in southeast Australian seagrass beds where the macrophytes Posidonia australis Hook. f. and Heterozostera tasmanica (Aschers.) den Hartog were dominant. The seagrasses and epiphytic algae were -8 and -9 ‰, respectively, while the animals were -11 to -15 ‰. It was

estimated that the various invertebrate and fish species collected in the bed derived 20-35% of their carbon from seagrasses and 65-80% from epiphytes; phytoplankton (-21 ‰) were not considered important. However, the closeness of the $\delta^{13}C$ values for seagrasses and epiphytes made the above calculations tenuous. Such a situation is clearly an example where a multiple stable isotope approach (i.e. also employing $\delta^{34}S$ and $\delta^{15}N$ analyses) may have greatly assisted in evaluating the relative importance of seagrasses and epiphytic algae as food sources.

There is a paucity of studies dealing with stable sulfur and nitrogen isotope ratios in seagrass beds. Fry et al. (1982) reported $\delta^{34}S$ values of +10 to +15 ‰ for leaves of four seagrass species in Redfish Bay, Texas, whereas their roots, with the exception of one species with a very shallow root system, were -4 to -17 ‰. These values reflected active sulfur uptake by the leaves of seawater sulfate (+20 ‰) and by the roots of ^{34}S-depleted sulfide from the sediment (-10 to -30 ‰). The authors noted that the leaf and root sulfur pools were not well-mixed. A single $\delta^{34}S$ value of +17.4 ‰ (+15.2 ‰ after acid washing) was recorded for the epiphytes on Thalassia testudinum leaves.

Fry et al. (1987) have summarized much of the literature on stable isotope studies conducted in seagrass beds of Texas coastal waters. Consumers in a seagrass meadow had $\delta^{34}S$ values that ranged from +10 to +15 ‰ whereas corresponding ranges for seagrass leaves and algae (3 macroalgal species and 1 epiphytic algal sample) were +10 to +13 ‰ and +15 to +19 ‰, respectively. Although one might conclude that seagrasses were at the base of the food web in

this system, the authors pointed out that one could not discount the possibility that the benthic microflora which may take up ^{34}S-depleted sulfides from the sediments could represent a significant source of organic matter for consumers. Tables 8 and 9 in Fry et al. (1987) represent the first published $\delta^{15}N$ values for seagrasses. A value of +4 ‰ was typical for the leaves of Halodule wrightii, Syringodium filiforme, Thalassia testudinum, and Halophila engelmanni Aschers., while corresponding values for 6 species of macroalgae averaged +8 ‰. Therefore $\delta^{15}N$ values for seagrasses are distinct from those of algae that do not fix nitrogen and these values should be able to function as tracers of organic nitrogen.

DESCRIPTION OF STUDY AREA

Geographic Setting

Horn Island is one of the five islands comprising the barrier island chain off the Mississippi coast. The island extends roughly 22 km (14 mi) from Dog Keys Pass at its western extremity (N 30°15′, W 88°45′) to Horn Island Pass at its eastern end (N 30°13′, W 88°32′). From the coastline south of Ocean Springs, the island lies 11 km (7 mi) offshore in Mississippi Sound, separating the waters of the Sound from the Gulf of Mexico. At its widest point, the island is 1.6 km (1 mi) across; it measures less than 0.16 km (0.1 mi) across at its narrowest point.

Horn Island is hydrologically affected by drainage from the Biloxi Back Bay, the Biloxi River, and the Pascagoula River; degrees of influence are a function of discharge rates and prevailing winds. Upland drainage from the island proper is a very minor factor, as the island is a sand formation and all rainfall tends to percolate into the local water table or accumulates as runoff in a series of island lagoons and marshes.

Astronomical tidal range is 0.6 m (2 ft); the effects of wind on local hydrodynamics generally overrides this and tends to determine local water depth and surface level fluctuations.

Climate

The Gulf Coast region is characterized by high humidity, long warm summers and short mild winters; it is technically classified as being semi- or sub-tropical. Other than brief winter intrusions of polar continental air, moist tropical air predominates over the area. Air temperatures generally range from 10.3 to 27.7°C (50.6 to 81.9°F), with extremes ranging from -18.3 to 41.1° C (-1 to 106°F). Mean annual air temperature is 19.3°C (66.7°F); mean humidity is 78%. Mean annual precipitation averages about 154.2 cm (60 in), resulting primarily from a typical number of 75.7 days with thunderstorms. Winds are generally from the SSE with a mean velocity of 10.4 kph (6.5 mph). October is usually the driest month of the year; July is the wettest (ONWI 1983).

The occurrence of tropical storms and hurricanes is a major feature of Gulf Coast weather, with an average of one tropical cyclone event impacting the state every two years, of which one every four years is a hurricane (Simpson and Lawrence 1971).

Soils

The soils of Horn Island are dominated by sands of varying grain size at its margins and out into the surrounding waters along the northern shore where the island adjoins Mississippi Sound. This sand contains varying amounts of plant detritus and debris of both plant and animal origins resulting from mechanical action of the surf and bioperturbation by various organisms. Degree of sorting of sand

material is a function of these physical and biological activities. The sand is characterized by an upper oxygenated layer, the thickness of which depends on wave action, ambient water temperature and oxygen concentration, salinity, and biological activity. Beneath this oxygenated layer is a gray to black layer of anoxic sand and silt rich in material of biological origin. Dramatic shifts in salinity can result in a die-off of the organisms "cementing" the microlayer of surface sand together, resulting in rearrangement of the sand surface and a marked increase in the depth of the oxygenated layer.

Flora

Horn Island's vegetation features salt-tolerant plants common on beach fronts, marsh plant associations, and stands of slash pine (Pinus elliotii Englmn.). On the side of the island bordering Mississippi Sound, sand flats adjacent to the shoreline are sparsely populated by beds of the marine angiosperm Halodule wrightii. More protected sand flat regions of the shoreline feature denser, larger and more closely spaced H. wrightii beds. In addition to this vascular vegetation, a diverse aquatic flora exists throughout the water column in the form of phytoplankton, epiphytes on the seagrasses, and a microscopic plant community associated with the sand surface, dominated by diatoms.

Fauna

The island proper is inhabited by seasonal and resident bird populations,

rabbits, and other small mammals. Alligators, snakes, nutria, and muskrats inhabit the marshes of the island. Large populations of insects and other invertebrates are found throughout the several habitats of the island.

Waters surrounding the island are home to a variety of invertebrates; the most visible of these are several species of snails, crabs such as the hermit crab (Clibanarius vittatus), sand dollars, and starfish. Vertebrate species in the water include a number of commercial and non-commercial finfish species, small sharks, and porpoises.

Utilization

Horn Island is part of the Gulf Islands National Seashore and is thus a protected resource area. The National Park Service maintains a Ranger outpost on the island. The western end of the island was used as a research site by the U. S. Army from 1943-1945. Primary use of the island is recreational; it is a favorite location for birding, fishing, boating, beachcombing and camping.

MATERIALS AND METHODS

Sampling Strategy

Floral and faunal samples for stable isotope analyses were collected in the Horn Island seagrass beds from May 1989 through November 1992, with the bulk of the samples being collected from June 1991 through November 1992. The sampling effort was concentrated in the grass beds at the northwest end of the island (Figure 1), as these beds were fairly extensive and could be located under most environmental conditions. Also, these beds were in the same area as that previously used for production measurements (Moncreiff et al. 1992) and in some cases were the same beds.

Sample Collection

Epiphytes and Halodule wrightii blades were collected over an annual cycle in conjunction with the primary productivity measurements, in addition to collections made on other dates throughout the study. Both producers and consumers were sampled during each year of the more intensive sampling period, if possible, to determine if any temporal effects could be detected.

The shoal grass Halodule wrightii and its associated epiphytes were collected intact in the field. Material was stored in plastic bags and transported on ice to the

laboratory, where it was frozen prior to further processing.

Macroalgae were collected whenever encountered in sufficient quantity. Samples were placed in plastic bags with a minimal volume of water from the collection site, placed on ice, and transported to the laboratory for identification and processing. Material was frozen on return to the laboratory if immediate processing was not possible.

Plankton samples were collected on several dates (n=6). Plankton nets with mesh sizes of 28 μm and 153 μm were towed for a maximum of 10 min; if a bloom was encountered, as many replicates as possible were collected and combined for a stable isotope sample. Tows were made parallel to the shoreline and just north of the beds at their limit of distribution to avoid possible contamination of the plankton samples with fragments of seagrass blades or epiphytes. Samples were gently washed into the cod ends of the nets with ambient water, concentrated using sieves of appropriate mesh sizes, transferred to water-tight containers, and stored on ice for immediate processing on return to the laboratory.

Consumers, including crustaceans, gastropods, bivalves, echinoderms, bryozoans, polychaetes, and a variety of fish species, were collected using several different types of sampling gear to obtain individuals representative of as many microhabitats and trophic levels within the seagrass system as possible. Only live, intact organisms were included in the samples to minimize contamination by shells or other foreign material. All samples were placed in clean plastic bags, buckets, or other containers, labelled as to date and location of collection, and placed on ice for

transport to the laboratory. Samples were frozen for future processing if immediate preparation was not possible.

Larger crustaceans were collected by hand (Clibanarius vittatus and Pagurus pollicaris) when encountered in the grass beds and vicinity or in nets in conjunction with fish samples (penaeid shrimp, crabs). Smaller specimens (hippolytid shrimp, Tozeuma carolinense) were collected using a beam plankton sampler (BPL), or by sieving sediments using a 1 mm mesh polyethylene sieve (Emerita talpoida, Haustoriidae).

Gastropods and bivalves were collected by hand when encountered in the grass beds and vicinity. Additional gastropod specimens were obtained from stone crab traps set at the northwest end of the island for an ongoing monitoring program of the activities of Menippe spp. in the area (Harriet Perry, GCRL).

Echinoderms, primarily the sand dollar Mellita quinquiesperforata, were collected by hand when encountered in the grass beds and at their immediate margins. The gray sea star Luidia clathrata was observed on 30 June 1989 during the primary production studies, but was not encountered during the collection trips for the stable isotope study. Material collected in 1989 was sufficient for a single sample.

Bryozoans were also collected by hand when encountered. Over the duration of the study, they were present in isolated locations in individual grass beds and were abundant on one sampling date, which comprised the bulk of these samples.

Polychaetes were collected by sieving sediments through a 0.5 mm mesh

polyethylene sieve. Bioturbation of sediments within the seagrass beds, indicative of the presence of a variety of worm-like, tube-forming species, was not evident at the study site. Individual polychaetes were also collected when encountered singly in seagrass or macroalgal samples.

Fish species were collected using a variety of sampling nets. Smaller fish were collected from within the grass beds using a BPL and also along the beachfront in shallow areas using either a 3 m (10 ft) minnow seine with 6.4 mm (1/4 in) mesh or a 12.2 m (40 ft) bag seine with 3.2 mm (1/8 in) mesh. Larger specimens were collected using a 4.9 m (16 ft) otter trawl with a 12.7 mm (1/2 in) mesh and a 3.2 mm (1/8 in) mesh bag or by deploying a series of gill nets and cast nets in areas where trawling was not feasible.

Sample Processing

In the laboratory, Halodule wrightii and its epiphytes were gently rinsed with tap water and then distilled water to remove any traces of salts. Epiphytes were carefully scraped from the H. wrightii blades using a dulled scalpel. Removal efficiencies were at least 95% or better when working with material that had been previously frozen. The separated plant material was then oven-dried at 60°C to a constant weight, and stored in clean airtight plastic bags prior to final processing.

Macroalgae were sorted according to species and picked free of all visible meiofauna and detrital fragments. Any intact organisms taken with these samples were identified, rinsed with distilled water, dried at 60°C to a constant weight,

combined with like species, and stored prior to final processing. The macroalgae were also rinsed with tap and distilled water, dried at 60°C to a constant weight, and stored in clean, airtight plastic containers prior to final processing.

Plankton samples were examined using both a dissecting microscope and a light microscope to determine the dominant species composition. All visible detrital material was manually removed from the samples with fine forceps to obtain as pure a sample as possible. Cleaned plankton material was rinsed with 10% HCl to remove any traces of $CaCO_3$. This was followed by several tap water rinses and a final rinse of distilled water to remove acid. The plankton was then concentrated using a fine-mesh sieve (153 μm or 28 μm, depending on sample mesh size), transferred to clean aluminum foil pans, and dried at 60°C to a constant weight. The dried plankton was then stored in clean, airtight plastic containers prior to final processing.

All consumer organisms (crustaceans, gastropods, bivalves, echinoderms, bryozoans, polychaetes, and fish) were handled in such a way as to minimize potential contamination with foreign material. Whenever possible, only muscle tissue was used, thereby providing consistent and comparable samples for each species or group. All tissues were washed free of salts with tap water, followed by a final distilled water rinse. When contamination with $CaCO_3$ was possible, tissues were first washed with 10% HCl, and then rinsed with tap water to a neutral pH to remove both acid and salts. This was followed by a final distilled water rinse. Samples were transferred to Al foil pans and dried at 60°C to a constant weight.

The samples thus obtained were stored in clean, airtight plastic containers prior to final processing.

Final processing was virtually identical for all sample types. Dried samples were powdered using either a Wiley mill equipped with a #20 or #40 mesh delivery tube, or ground with a mortar and pestle to as fine a consistency as possible. Samples were then stored in clean, airtight glass vials, capped tightly, and packed for shipping.

The measurements of stable isotope ratios for all samples were performed by Coastal Science Laboratories of Austin, Texas. The accuracy of the $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ analyses was reported to be 0.2, 0.2, and 0.5 parts per mil (‰), respectively. A minimum of one blind control was included with each set of samples sent to Coastal Science Laboratories to test the repeatability of the determinations and to ensure that samples were comparable over time.

Stable isotope values were determined via mass spectroscopy by comparing samples of seagrass system material to known standards, and reporting the difference between the sample and the appropriate standard in parts per thousand or per mil (‰) 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, and R is $^{13}C/^{12}C$, or $^{34}S/^{32}S$, or $^{15}N/^{14}N$. The accepted reference standard materials for C, S, and N are PeeDee belemnite, Canyon Diablo troilite, and atmospheric diatomic nitrogen, respectively; however, supplies of standard reference material from the geologic formations used for C and S are

limited, so other materials are used for routine analysis.

Standards for stable isotope analyses used by Coastal Science Laboratories during the course of this study were as follows: National Bureau of Standards (NBS) carbon standard NBS #22 (oil) for the $\delta^{13}C$ analyses, NBS standards N-1 and N-2 (ammonium sulfates) and N-3 (potassium nitrate) for the $\delta^{15}N$ analyses, and NBS #123 (sphalerite) and OGS (barium sulfate) for the $\delta^{34}S$ sample analyses.

RESULTS AND DISCUSSION

Stable Isotope Ratios of Primary Producers

Stable carbon isotope ratios of Halodule wrightii, its associated epiphytes, plankton, and sand microflora (as represented by the Mellita quinquiesperforata sample) were all distinct (Table 1). Samples of macroalgae collected in the area (Sargassum spp., Gracilaria verrucosa, and Enteromorpha spp.) also had discrete, well-separated $\delta^{13}C$ values in relation to other primary producers.

$\delta^{13}C$ values for Halodule wrightii ranged from -13.6 to -10.6‰ and averaged -12.2‰. Epiphytic algae exhibited values ranging from -19.7 to -15.2‰ and averaged -17.5‰. Thus, there was very good separation between these critical samples.

The average value measured for Halodule wrightii blades in the present study was slightly more depleted than the average $\delta^{13}C$ value for H. wrightii of -10.8‰ reported by McMillan et al. (1980). However, it lies within the range of -12.3 to -8.5‰ reported by these same authors. The average epiphyte $\delta^{13}C$ value is similar to the value of -19‰ measured for Syringodium filiforme epiphytes in Indian River Lagoon, Florida by Fry (1984) and values of -17 to -10.5‰ determined for H. wrightii, S. filiforme, and Thalassia testudinum epiphytes in coastal Texas

embayments by Kitting et al. (1984).

Phytoplankton, represented by the plankton samples consisting of a mixture of diatoms and copepods, had an average $\delta^{13}C$ value of -21.8‰ (range = -23.3 to -21.2‰). This lies between the average reported values of -22‰ and -20‰ for phytoplankton and zooplankton, respectively (Boutton 1991), and is somewhat less depleted in ^{13}C than the -23‰ zooplankton value reported by Sullivan and Moncreiff (1990) for a nearby coastal marsh system. However, a nearly pure phytoplankton bloom was sampled on 30 May and 4 June 1991; this material had a $\delta^{13}C$ value of -23.3‰. The plankton values are also well-separated from those for epiphytes and H. wrightii blades.

Macroalgal samples had the following $\delta^{13}C$ values: Sargassum natans (-16.8‰), Sargassum fluitans (-16.6‰), Enteromorpha spp.(-16.2‰), Gracilaria verrucosa (-17.4‰). Macroalgae in this system were somewhat more depleted in ^{13}C on average than in other systems; the reported average $\delta^{13}C$ value for macroalgae is -15‰ (Boutton 1991).

The sand microflora could not be sampled directly, so evaluation was based on a sample of the soft tissues of the sand dollar Mellita quinquiesperforata. Sand dollars have been reported to subsist on a diet consisting almost exclusively of diatoms and bacteria associated with the surface of the substrate in which M. quinquiesperforata lives (MacGintie and MacGintie 1968, Ruppert and Fox 1988). The $\delta^{13}C$ value for this organism was -16.9‰, which is very close to the benthic microalgal $\delta^{13}C$ value of -16.7‰ reported by Craft et al. (1988).

Stable nitrogen isotope ratios, which are indicative of trophic level, ranged from +5.6‰ to +6.4‰ for Halodule wrightii, with an average $\delta^{15}N$ of 6.0‰, and from +4.6‰ to +6.9‰ for its epiphytes, with an average $\delta^{15}N$ of 5.9‰. The composite samples, representing a full year of collected material, had values of +5.6‰ and +6.9‰ for H. wrightii and its epiphytes, respectively. Fry et al. (1987) reported a $\delta^{15}N$ value of 4‰ for a variety of seagrass species in Australia, Jamaica, Nicaragua, and Texas, with a value of +3.9‰ for H. wrightii in the last location.

The plankton $\delta^{15}N$ values ranged from +8.2‰ to +10.4‰, with an average value of +9.9‰. $\delta^{15}N$ values for the macroalgae sampled were as follows: Sargassum natans (+4.7‰), Sargassum fluitans (+4.5‰), Enteromorpha spp. (+9.8‰), Gracilaria verrucosa (+10.0‰). Fry et al. (1987) reported a $\delta^{15}N$ value of 8‰ for macroalgae, which is bracketed by the data from this study. The sand dollar value, representative of the sand microflora, was +6.6‰. This is enriched in comparison to the $\delta^{15}N$ value of 0.8‰ reported by Craft et al. (1988) for an unidentified sample of benthic microalgae, but within the range of $\delta^{15}N$ values observed for macroalgae in this seagrass system.

Stable sulfur isotope ratios were much more variable than those for carbon or nitrogen. Values for $\delta^{34}S$ ranged from +7.8 to +15.0‰ for Halodule wrightii, averaging 11.5‰, and from +13.0 to +18.3‰ for its epiphytes, with an average of 13.7‰. The composite samples, representing a full year of collected material, had values of +15.0‰ and +18.3‰ for H. wrightii and its epiphytes, respectively. The plankton sample values ranged from +11.5 to +17.6‰, with an average $\delta^{34}S$ value

of +15.4‰. This is more enriched than the value of +10.7‰ reported by Sullivan and Moncreiff (1990) for zooplankton in a nearby coastal Mississippi marsh system, probably indicating the increased influence of sulfate in more marine systems. $\delta^{34}S$ values for the macroalgae sampled were as follows: Sargassum natans (+17.8‰), Sargassum fluitans(+17.9‰), Enteromorpha spp. (+20.6‰), Gracilaria verrucosa(+16.6‰). The sand dollar $\delta^{34}S$ value, representative of the sand microflora, was +8.6‰. This suggests that the sand microflora are making more use of sediment-associated sulfide as a source of sulfur, as opposed to seawater sulfate, than are the epiphytes which are bathed completely by the water column.

Stable Isotope Ratios of Sediments and Associated Detrital Material

The sandy substrate in which Halodule wrightii was rooted had a $\delta^{13}C$ value of -14.7‰, a $\delta^{15}N$ value of +7.8‰, and a $\delta^{34}S$ value of +12.6‰. These were discrete from those of the primary producers (Table 1). The material was free of any visible detrital fragments. However, sand grains are covered with variously sized fissures that are "home" to attached bacteria and microalgae, particularly small, pennate diatom species (Round 1979, Lukatelich and McComb 1986). Thus, this value may also be representative of the sand microflora along with that of the sand dollar Mellita quinquiesperforata.

Samples of detrital material exposed along the beachfront adjacent to the seagrass beds had distinctly different stable isotope values in relation to primary producers. This material appeared to be relict marsh root and stem material,

previously buried, that had been exposed by wave action. A large population of hermit crabs (primarily Clibanarius vittatus) was observed in this area; samples of this organism were also collected from this location.

The $\delta^{13}C$ value for the sandy substrate was -14.7‰. The relict marsh material, which exhibited a high sand content, exhibited a wide range in values, with one set of samples having $\delta^{13}C$ values of -24.5 and -22.7‰ and another set having $\delta^{13}C$ values of -15.2 and -14.5‰. This large difference could be due to the type of marsh detritus sampled, as Juncus roemerianus Scheele and Spartina alterniflora Loisel. material in a geographically close marsh had average $\delta^{13}C$ values of -26 and -13‰, respectively (Sullivan and Moncreiff 1990). The presence of algal material could also contribute to the low value observed in one of the sample sets. However, there was still very good separation among these samples and the primary producers (Table 1).

The stable nitrogen isotope ratio for the sandy substrate was +7.8‰. The relict marsh material exhibited low $\delta^{15}N$ values, with one set of samples having values of +1.4 and +2.0‰, and the other set having values of +0.6 and +2.0‰.

Stable sulfur isotope ratios were much more variable than those for nitrogen. The sandy substrate value for $\delta^{34}S$ was +12.6‰. Values for the relict marsh material were +4.4 and +6.3‰ for one set, and +4.2 and +4.5‰ for the other sample set.

Stable Carbon Isotope Ratios of Consumers

Stable carbon isotope ratios of consumers ranged from -23.0‰ for the Atlantic croaker Micropogon undulatus to -12.7‰ for the white mullet Mugil curema. An average $\delta^{13}C$ value for all animals sampled was -17.1‰; the average for all species sampled was -17.3‰. $\delta^{13}C$ values for all primary producers and consumer organisms are included in Appendix A. Average $\delta^{13}C$ values for each species or type of consumer sampled, arranged alphabetically, are presented in Table 2. When averaged by species or sample type, the white trout Cynoscion arenarius exhibited the lowest $\delta^{13}C$ value (-21.0‰) and a pooled sample of miscellaneous small shrimp species the highest (-13.5‰). Consumers in comparable seagrass systems in Florida and Texas exhibited values ranging from -22 to -16‰ and -15 to -9‰, respectively (Fry 1984, Kitting et al. 1984). However, both of these data sets were generated from coastal lagoons with well-defined inputs from marine and terrestrial sources; the present study was conducted in an open system, which will be discussed in more detail later.

It is important to restate at this point that the $\delta^{13}C$ values of consumer organisms in marine environments tend to reflect the material assimilated from their diets, exhibiting $\delta^{13}C$ values within $\pm$1‰ of their food sources (Peterson et al. 1985, 1986). In some instances, consumers become more enriched (i.e. $\delta^{13}C$ values are less negative) than their food sources with respect to ^{13}C, generally by 1-2‰ per trophic level (Gearing 1991). A total of 129 out of 183 (70%) consumers sampled in this system had $\delta^{13}C$ values falling within a range of -18.8 to -15.4‰. All but 13

of the 183 (93%) consumers sampled fell within a range of -20.1 to -14.1‰. This strongly suggests that the blades of Halodule wrightii, with an average $\delta^{13}C$ value of -12.2‰, are at best a minimal contributor to the base of this food web. The average $\delta^{13}C$ value for consumer species (-17.3‰) is almost identical to average epiphyte (-17.5‰) and sand microflora (-16.9‰) $\delta^{13}C$ values. Stephenson et al. (1986), using stable carbon isotope ratios, also found that seagrasses were not a carbon source for the invertebrate members of a seagrass food web.

Stable Nitrogen Isotope Ratios of Consumers

Stable nitrogen isotope ratios, which are indicative of trophic level, ranged from +6.0‰ for the white mullet Mugil curema (a different specimen than that producing the lowest $\delta^{13}C$ value) to +16.6‰ for the bluefish Pomatomus saltatrix. Average $\delta^{15}N$ for all animals sampled was +12.5‰. $\delta^{15}N$ values for all primary producers and consumer organisms are presented in Appendix A. Table 2 contains an alphabetical listing, by consumer group or species, of average $\delta^{15}N$ values. Average consumer values showed the bivalve Tellina alternata to occupy the lowest trophic position at +7.5‰, and the estuarine squid Lolliguncula brevis with a $\delta^{15}N$ of +15.7‰ to occupy the highest position.

Hobson and Welch (1992) employed $\delta^{15}N$ values in an Arctic marine food web to determine trophic levels using values measured for a known set of predators (polar bears) and their prey (ringed seals). A similar approach can be taken in this subtropical seagrass system using $\delta^{15}N$ values for the portunid crabs Callinectes

sapidus and Portunus gibbesii, and the bonnethead and Atlantic sharpnose sharks Sphyrna tiburo and Rhizoprionodon terranovae. Both shark species were found to have stomach contents consisting almost exclusively of portunid crabs. $\delta^{15}N$ for the two shark species averaged +14.6 ± 0.2‰ (n=7) and +13.1 ± 0.4‰ (n=3) for the portunid crabs. A trophic enrichment factor of 1.5‰ for this seagrass system is established from this relationship; however, sharks are opportunistic feeders, and the limited samples on which this is based likely do not represent their long-term diet. Also, sharks use nitrogenous compounds in osmoregulation, which may reduce the shift in ^{15}N values for their tissues relative to their prey. Additional values for known dietary relationships were determined for clupeid species and plankton, which have a well-established predator-prey relationship. Anchovies (Anchoa mitchilli and Anchoa nasuta) collected during this study had an average $\delta^{15}N$ value of 14.5 ± 0.5‰ (n=4). This produced a trophic enrichment factor of 4.6‰ based on the 9.9‰ average for plankton (n=6). Harengula jaguana and Brevoortia patronus samples averaged 12.7 ± 0.7‰ (n=3) for $\delta^{15}N$, yielding a trophic enrichment factor of 2.8‰ assuming a planktonic diet. Combining all of these values yields an average shift of +3.0‰ per trophic level (TL). This estimated shift is less than that determined at by Hobson and Welch (1992), who used an enrichment value of +3.8‰ per TL based strictly on the polar bear and ringed seal. An additional $\delta^{15}N$ value for particulate organic matter (POM) is needed as a "baseline" value to establish where TL1 lies; averaging the $\delta^{15}N$ values for all primary producers, excluding the plankton, yielded an estimate of +7.0 ± 1.8‰ for POM. Using the

equation of Hobson and Welch (1992) and substituting the values determined for this seagrass system, an equation for the prediction of trophic level is as follows:

$$TL = 1 + (N_m - 7.0)/3.0,$$

where TL is the trophic level of the consumer, N_m is the $\delta^{15}N$ value for muscle tissue of the organism (samples of small whole organisms could also be used in this equation, as values are comparable), and the values 7.0 and 3.0 are the estimates for POM and a trophic enrichment factor for this seagrass system, respectively. Using this equation for the sharks sampled places them at TL 3.5. An average $\delta^{15}N$ value of 10.3‰ for the plankton samples collected on 10 July 1992, a large fraction of which was zooplankton, places this set of samples at TL 2.1. The estuarine squid Lolliguncula brevis and the bluefish Pomatomus saltatrix, with the highest $\delta^{15}N$ values, fall at TL 3.9 and 4.2, respectively. Thus, this model seems to work well for this system, which has no obvious demarcations between trophic levels, as there are no breaks in the cascade of $\delta^{15}N$ values shown in Figure 2. General consumer groups are also indicated on this figure.

Stable Sulfur Isotope Ratios of Consumers

Stable sulfur isotope ratios for consumers in this system ranged from +2.3‰ for the white mullet Mugil curema (the same individual producing the lowest $\delta^{15}N$ value) to +19.6‰ for the jellyfish Aurelia aurita. The average $\delta^{34}S$ value for all animals sampled was 13.8‰. $\delta^{34}S$ values for all primary producer and consumer organisms sampled are shown in Appendix A. An alphabetized list of consumer

groups and species showing their average $\delta^{34}S$ values is given in Table 2. The observed range in these average $\delta^{34}S$ values was from +4.4‰ for beach diggers (Haustorius spp.) in the family Haustoriideae to +19.6‰ for the jellyfish A. aurita. Average $\delta^{34}S$ for seawater sulfate is 20‰, which is very close to that of the jellyfish sample. The sample dominated by Haustorius spp. shows the strongest influence of sulfide (-10 to -30‰) in the organic matter that was assimilated by this group.

Dual Stable Isotope Plots

A series of dual stable isotope plots of $\delta^{13}C$ versus $\delta^{15}N$ and $\delta^{13}C$ versus $\delta^{34}S$ was generated from the set of stable isotope ratios for selected organisms sampled in this seagrass system. The use of dual isotope plots allows interpretation of food web relationships employing stable isotope ratios for primary producer and consumer organisms (Peterson et al. 1985). Plots of $\delta^{15}N$ versus $\delta^{34}S$ were not generated, as information contained in the first two sets of plots was sufficient for basic interpretation of the data. Error bars are not shown for the primary producers as these values are given in Table 1.

Figures 3 and 4 show $\delta^{13}C$ versus $\delta^{15}N$ and $\delta^{13}C$ versus $\delta^{34}S$, respectively, for potential sources of organic matter at the base of the food web in this system. The plot of $\delta^{13}C$ versus $\delta^{15}N$ (Figure 3) shows that the benthic microalgae (epiphytes, sand microflora as represented by the Mellita quinquiesperforata sample) are well separated from both intact and epiphyte-free blades of Halodule wrightii. The microalgae are also distinct from detrital marsh material in the system. The two sets

of relict marsh samples probably originated from stands of C_4 and mixed C_3 and C_4 marsh plants, likely species of Spartina and Juncus based on stable isotope ratios for material collected during a previous study in a geographically close marsh system (Sullivan and Moncreiff 1990). The lower $\delta^{15}N$ values measured in these samples likely result from the greater contribution of atmospheric N_2 to this material of terrestrial origin, plus the depleting effects of bacterial decomposition and leaching (Benner at al. 1987). The plankton values were measured for material comprised of mixed zooplankton and phytoplankton, approximately 50% of each component by volume based on visual inspection during removal of detritus from the samples. The measured $\delta^{15}N$ values are about 3‰ higher than those of the other primary producers, most likely due to the large quantity of zooplankton in the plankton samples.

The plot of $\delta^{13}C$ versus $\delta^{34}S$ (Figure 4) further illustrates the degree of separation among the primary producers and the available pool of detrital material. It also shows the influence of seawater sulfate in most algal samples (phytoplankton, epiphytes, and macroalgae), and the presence of sulfides during the growth of the plant material that comprised the relict marsh samples. The clear separation of the primary producers from one another is evident in this figure and is critical to the interpretation of the results shown in the dual stable isotope plots employing the values measured for consumer organisms.

A major concern in the analysis of trophic relationships is the accuracy of stable isotope ratio measurements. As previously mentioned, blind controls were

included with the material sent to Coastal Science Laboratories (CSL) for determinations of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. Plots of $\delta^{13}C$ versus $\delta^{15}N$ and $\delta^{13}C$ versus $\delta^{34}S$ are shown for these control samples in Figures 5 and 6. Values were extremely consistent for these samples with the exception of the 9 February 1993 sample set value for $\delta^{34}S$. A major equipment breakdown at CSL occurred during the analysis of this set of samples, forcing the use of older, less accurate equipment to complete the results for this set of samples. However, values for other samples in the set seemed to fit well with previously analyzed material, so this outlier may have been anomalous.

Another major concern in stable isotope analysis are the degree of seasonal changes in stable isotope ratios of both primary producers and consumers and the effects of these seasonal shifts on interpretation of results. Samples were collected over several years in this study to determine the potential effects of these shifts. This phenomenon is illustrated for this system in a dual stable isotope plot of $\delta^{13}C$ versus $\delta^{34}S$ for primary producers (Figure 7). There are obvious inter-annual differences for plankton, epiphytes, and H. wrightii that must be taken into consideration when analyzing the consumer stable isotope data. However, the majority of the consumer organisms sampled were 1 yr or older, so the organisms themselves "average" the effects of differences among organic matter sources by the gradual incorporation of these disparate materials into their muscle tissue or the whole organism.

Differences between 1991 versus 1992 collections of consumer organisms

were examined graphically using dual stable isotope plots to assess this physiological "averaging" effect. Plots of $\delta^{13}C$ versus $\delta^{15}N$ for all consumer organisms sampled in 1991 and 1992 (in addition to potential sources of organic matter) are shown in Figures 8 and 9, respectively. Consumers only are shown in Figure 10 for both years. There appear to be no major differences between the 1991 and 1992 samples other than perhaps a tighter clustering of the former; this may be an artifact of the number of samples analyzed from each year, as approximately half as many samples were analyzed from material collected in 1992 (123 versus 63). Overlaying the consumer values from the two years (Figure 10) shows good overlap between the two years. Corresponding plots for $\delta^{13}C$ versus $\delta^{34}S$ are shown in Figures 11 through 13. Again, the clustering of values in 1991 (Figure 11) versus 1992 (Figure 12) is likely an artifact of sample numbers. Figure 13 shows a high degree of overlap in $\delta^{34}S$ values for both years. Based on these results, data from both years were pooled for all further dual isotope plots presented below.

Dual stable isotope plots of $\delta^{13}C$ versus $\delta^{15}N$ and $\delta^{13}C$ versus $\delta^{34}S$ for all consumer organisms sampled (1991-1992) in the system are shown in Figures 14 and 15, respectively. Values for potential sources of organic matter are also shown. These scatter plots show the lack of any clear breaks among trophic levels, other than the separation between primary producers and consumers (Figure 14), and the relative unimportance of Halodule wrightii and relict marsh detritus as sources of organic matter (Figure 15). $\delta^{13}C$ values of consumers are in general centered around those of seagrass epiphytes and the sand microflora, and also the macroalgae.

However, macroalgae were ephemeral contributors to organic matter in the seagrass system, as their presence in the seagrass beds was episodic; Sargassum spp. were encountered in abundance only once during the four years of sampling in the area, and Enteromorpha spp. and Gracilaria spp. were only seasonally abundant. The plankton were apparently of importance in the diets of some organisms such as the white trout Cynoscion arenarius, the Atlantic croaker Micropogon undulatus, and the Florida pompano Trachinotus carolinus.

For ease in interpretation of results, consumers were broken down into eight groups for further analysis using dual isotope plots. These groups are as follows: (1) shrimp species, (2) carnivorous fish, sharks, and rays, (3) omnivorous fish species, (4) a "generic" group of fish referred to as Group 1, (5) a second "generic" group of fish referred to as Group 2, (6) crabs and other crustaceans, (7) mollusks and other non-crustacean invertebrates, and (8) planktivorous fish species. This greatly facilitates not only comparisons within these groups, but also allows the differences among samples of the same species to be easily seen. A key to the species and groups shown is indicated parenthetically for each figure.

The first in this series of plots shows $\delta^{13}C$ versus $\delta^{15}N$ for the shrimp species and potential sources of organic matter (Figure 16; 1=hippolytid shrimp, 2=Penaeus aztecus, 3=P. duorarum, 4=P. setiferus, 5=Sicyonia brevis, 6=Squilla empusa, 7=Trachypenaeus constrictus, 8=T. similis, 9=Tozeuma carolinense, 10=miscellaneous small shrimp). $\delta^{13}C$ values ranged from -19.6‰ for a sample of the white shrimp Penaeus setiferus (n=3) to -13.5‰ for a sample of mixed species

of small shrimp (n=203) sampled over the course of the study. Epiphyte and sand microflora values bracket this group of consumers whereas Halodule wrightii leaves and phytoplankton are outliers. $\delta^{15}N$ ranged from +7.9‰ for hippolytid shrimp, an herbivorous group, to +13.4‰ for the mantis shrimp Squilla empusa, a carnivorous species (n=23). Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ for this group (Figure 17; 1=hippolytid shrimp, 2=Penaeus aztecus, 3=P. duorarum, 4=P. setiferus, 5=Sicyonia brevis, 6=Squilla empusa, 7=Trachypenaeus constrictus, 8=T. similis, 9=Tozeuma carolinense) shows the values for shrimp species to be clustered between those for epiphytes and sand microflora. The sand microflora is composed almost exclusively of diatoms in this system, and the epiphytes on the H. wrightii blades are dominated by filamentous algae which are in turn heavily epiphytized by diatoms, as well as a heavy coating of diatoms attached directly to the blade surface. This is also true for the seagrass blades themselves. The grouping of shrimp species values between these two primary producers suggests either the consumption of both types of food items, or selective grazing and assimilation of diatoms when grazing on epiphytic material. $\delta^{34}S$ values ranged from +10.1‰ for the hippolytid shrimp sample to +14.6‰ for S. empusa. The brown shrimp Penaeus aztecus exhibited a wide range in $\delta^{13}C$ values but a narrow range in $\delta^{34}S$ values; in contrast, Trachypenaeus constrictus exhibited a wide range in $\delta^{34}S$ but a narrow range in $\delta^{13}C$ (Figure 17).

The second set in this series of dual isotope plots shows trophic relationships for carnivorous fish, sharks, and rays. Figure 18 (1=Ancyclopsetta quadrocellata,

2=Cynoscion arenarius, 3=C. nebulosus, 4=Dasyatis sabina, 5=Elops saurus, 6=Gymnothorax ocellatus, 7=Pomatomus saltatrix, 8=Rhizoprionodon terranovae, 9=Synodus foetens, 10=Scomberomorus maculatus, 11=Strongylura marina, 12=Sciaenops ocellata, 13=Sphyrna tiburo, 14=Trachinotus carolinus, 15=juvenile T. carolinus) shows $\delta^{13}C$ versus $\delta^{15}N$ for this group of carnivorous organisms. $\delta^{13}C$ values ranged from -21.7‰ for the white trout Cynoscion arenarius to -14.9‰ for the redfish Sciaenops ocellata. $\delta^{13}C$ values for this group of consumers are bracketed by those of phytoplankton, epiphytes, and sand microflora. $\delta^{15}N$ ranged from +10.5‰ for S. ocellata to +16.6‰ for the bluefish Pomatomus saltatrix. Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ (Figure 19; 1=Ancyclopsetta quadrocellata, 2=Cynoscion arenarius, 3=C. nebulosus, 4=Dasyatis sabina, 5=Elops saurus, 6=Gymnothorax ocellatus, 7=Pomatomus saltatrix, 8=Rhizoprionodon terranovae, 9=Synodus foetens, 10=Scomberomorus maculatus, 11=Strongylura marina, 12=Sciaenops ocellata, 13=Sphyrna tiburo, 14=Trachinotus carolinus, 15=juvenile T. carolinus) shows the $\delta^{34}S$ values for these carnivores to be clustered between those for epiphytes and macroalgae and those for the sand microflora. The grouping of values around these primary producers suggests the consumption of other organisms which are in turn consuming these items, either directly or indirectly. As mentioned earlier, however, the presence of macroalgae was episodic; it is thus of much less importance than indicated by the graphical results. $\delta^{34}S$ values ranged from +6.2‰ for S. ocellata to +17.8‰ for the inshore lizardfish Synodus foetens. Elops saurus, the ladyfish, exhibited a wide range in both $\delta^{13}C$

and $\delta^{34}S$ values. There was also a large difference between juveniles and adults in the Florida pompano Trachinotus carolinus, likely a result of differences in feeding strategies among age classes which is a common occurrence in fish species (Figure 19).

Omnivorous fish species are represented by the third set of dual isotope plots (Figures 20 and 21). $\delta^{13}C$ values ranged from -19.9‰ for the hardhead catfish Arius felis to -12.7‰ for the white mullet Mugil curema. Primary producer values bracketing this group of consumers are the epiphytes and sand microflora (Figure 20; 1=Arius felis, 2=A. felis liver tissue, 3=juvenile A. felis, 4=Lagodon rhomboides, 5=Mugil cephalus, 6=M. curema). The only exception to this is the individual M. curema sample referred to previously which overlies values for H. wrightii. Mullet are reported to be detritovores; however, it is possible that this individual consumed quantities of seagrass material sufficient to produce this stable isotope signature. $\delta^{15}N$ ranged from +6.0‰ for another white mullet to +15.7‰ for A. felis (the same individual was the outlier). Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ (Figure 21; 1=Arius felis, 2=A. felis liver tissue, 3=juvenile A. felis, 4=Lagodon rhomboides, 5=Mugil cephalus, 6=M. curema) shows the values for this group of omnivores to be widely scattered, surrounded by the plankton, epiphytes, macroalgae, and sand microflora. The scattering of values between these primary producers suggests consumption of a mixture of food sources, which would be expected by definition, as this is a set of values for omnivorous fish. Again, it should be noted that the presence of macroalgae was sporadic, with Sargassum spp.

being encountered in quantity only once during the study, and Enteromorpha and Gracilaria spp. being only seasonally abundant. ^{34}S values ranged from +2.3°/oo for M. curema (the same individual with the lowest $\delta^{15}N$ value) to +16.2°/oo for A. felis. M. curema exhibited the widest variation in both $\delta^{13}C$ and $\delta^{34}S$ values; however, M. cephalus, the striped mullet, exhibited the least variation in $\delta^{34}S$ and $\delta^{13}C$ among this group of fish (Figure 21), illustrating that differences in feeding strategies may exist within the same genus.

The first "generic" group of fish, referred to as Group 1, is shown in the fourth set of dual isotope plots. Figure 22 (1=Citharichthys spilopterus, 2=Diplectrum bivittatum, 3=D. formosum, 4=Leiostomus xanthurus, 5=Micropogon undulatus, 6=Orthopristis chrysoptera, 7=Prionotus tribulus, 8=Symphurus plagiusa) shows $\delta^{13}C$ versus $\delta^{15}N$ to illustrate trophic levels within this set of fish species. Interestingly, this haphazard grouping appears to lie within the same basic TL due to the relatively narrow range in $\delta^{15}N$ values; $\delta^{15}N$ ranged from +12.2°/oo for the Atlantic croaker Micropogon undulatus to +14.2°/oo for the sand perch Diplectrum formosum (n=4). Using the formula presented earlier (Hobson and Welch 1992), fish in this figure fall into TL's 2.7 to 3.4. $\delta^{13}C$ values ranged from -23.0°/oo for the Atlantic croaker M. undulatus to -15.7°/oo for spot, Leiostomus xanthurus. The $\delta^{13}C$ values of epiphytes, macroalgae, and sand microflora bracket this group of consumers, with the exception of the croaker. Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ for this group (Figure 23; 1=Citharichthys spilopterus, 2=Diplectrum bivittatum, 3=D. formosum, 4=Leiostomus xanthurus, 5=Micropogon undulatus,

6=Orthopristis chrysoptera, 7=Prionotus tribulus, 8=Symphurus plagiusa) shows the values for this group to be clustered primarily between those for plankton, epiphytes, sand microflora, and macroalgae, with the values lying closer to those for macroalgae and epiphytes. The grouping of values between these primary producers suggests direct or indirect consumption of these food sources. However, macroalgae, as stated earlier, were an extremely limited resource. $\delta^{34}S$ values ranged from +12.0‰ for the pigfish Orthopristis chrysoptera (its young are reported to live in seagrass beds, according to Hoese and Moore 1977) to +16.3‰ for the bighead sea robin Prionotus tribulus. As mentioned above, an individual specimen of the Atlantic croaker M. undulatus was an outlier with respect to $\delta^{13}C$ values (Figure 23), but was intermediate within this group in its $\delta^{34}S$ value. This individual may have been a transient in the system, or it may have exhibited the lowest $\delta^{13}C$ value recorded in this study due to its ripe reproductive condition.

A second "generic" group of fish, again chosen arbitrarily from the remaining species once the obvious omnivores, carnivores, and planktivores were assigned to their respective groups, is referred to as Group 2. $\delta^{13}C$ versus $\delta^{15}N$ is shown in Figure 24 (1=Chloroscombrus chrysurus, 2=Chaetodipterus faber, 3=Fundulus similis, 4=Lutjanus campechanus, 5=L. griseus, 6=L. synagris, 7=Menticirrhus americanus). $\delta^{13}C$ values ranged from -21.2‰ for an individual gray snapper Lutjanus griseus to -14.0‰ for the longnose killifish Fundulus similis (n=10). As with the Group 1 fishes, plankton, epiphytes, macroalgae, and sand microflora values bracket the $\delta^{13}C$ values of Group 2. $\delta^{15}N$ ranged from +11.8‰ for F. similis to

+15.3‰ for the Atlantic spadefish Chaetodipterus faber. Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ for Group 2 (Figure 25; 1=Chloroscombrus chrysurus, 2=Chaetodipterus faber, 3=Fundulus similis, 4=Lutjanus campechanus, 5=L. griseus, 6=L. synagris, 7=Menticirrhus americanus) shows the values to be clustered around those for epiphytes and macroalgae, with a definite planktonic influence in the samples of C. faber and L. griseus. The grouping of the majority of values near the epiphytes and macroalgae strongly suggests these plants as primary sources of organic matter for most Group 2 fish. However, the macroalgae were a limited resource, indicating the importance of epiphytes to this group as a whole. $\delta^{34}S$ values ranged from +9.6‰ for F. similis to +18.7‰ for the Atlantic bumper Chloroscombrus chrysurus. The longnose killifish F. similis was an outlier with respect to both $\delta^{13}C$ and $\delta^{34}S$ in Group 2 (Figure 25); these individuals were quite likely immigrants from a tidal creek on Horn Island adjacent to the study area, as specimens were collected there for an unrelated project on 31 July 1992.

Trophic relations for crabs and other crustaceans are illustrated in the sixth set of dual isotope plots. The plot of $\delta^{13}C$ versus $\delta^{15}N$ (Figure 26; 1=Chelonibia patula, 2=Callinectes sapidus, 3=Clibanarius vittatus, 4=Emerita talpoida, 5=Haustoriidae, 6=Hepatus epheliticus, 7=Libinia dubia, 8=L. emarginata, 9=Limulus polyphemus, 10=Menippe mercenaria, 11=mysids, 12=Portunus gibbesii, 13=Pagurus polycaris) for this broadly-based group shows three clusterings of organisms. The upper grouping includes the portunid and spider crabs, the central group consists exclusively of the horseshoe crab Limulus polyphemus, and the lower

group is comprised exclusively of benthic organisms. $\delta^{13}C$ values ranged from -20.0‰ for a sample of the barnacle Chelonibia patula (n=25) to -14.3‰ for a sample of the family Haustoriideae (n > 100). Again, epiphyte, macroalgae, and sand microflora $\delta^{13}C$ values bracket this group of consumers. $\delta^{15}N$ ranged from +8.4‰ for the haustoriid sample to +14.1‰ for samples of the stone crab Menippe mercenaria and the calico box crab Hepatus epheliticus. Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ for this group (Figure 27; 1=Chelonibia patula, 2=Callinectes sapidus, 3=Clibanarius vittatus, 4=Emerita talpoida, 5=Haustoriidae, 6=Hepatus epheliticus, 7=Libinia dubia, 8=L. emarginata, 9=Limulus polyphemus, 10=Menippe mercenaria, 11=mysids, 12=Portunus gibbesii, 13=Pagurus polycaris) shows the values for this group to be clustered between those for the epiphytes and macroalgae and the sand microflora, with the exception of C. patula (which lies very close to an extreme epiphyte value and to the plankton) and the haustoriids and mysids. Once again, the grouping of values in relation to these primary producers suggests the benthic microalgae as primary sources of organic matter, either directly or indirectly, although the importance of macroalgae is limited due to its unavailability in any quantity throughout most of the year. $\delta^{34}S$ values ranged from +4.4‰ for the haustoriids to +19.5‰ for C. patula, illustrating the varying importance of sulfide and seawater sulfate in their respective diets. The haustoriid sample point lies virtually on top of the values for marsh detritus (Figure 27), strongly suggesting this as a food source for this infaunal member of the beachfront fauna. The mysid values are intermediate between these values and the sand microflora, suggesting

consumption of a mix of these materials (Figure 27).

Molluscs and other non-crustacean invertebrates are shown in the seventh set of dual isotope plots. A plot of $\delta^{13}C$ versus $\delta^{15}N$ for these invertebrates is shown in Figure 28 (1=Aurelia aurita, 2=Busycon contrarum, 3=Crepidula plana, 4=Calliactis tricolor, 5=Lolliguncula brevis, 6=Mercenaria campechiensis, 7=Nassarius vibex, 8=Polynices duplicatus, 9=Pisania tincta, 10=polychaetes, 11=Tellina alternata, 12=Thais haemostoma, 13=Luida clathrata). $\delta^{13}C$ values ranged from -19.5‰ for a sample of the moon jellyfish Aurelia aurita (n=12) to -15.5‰ for the hermit crab anemone Calliactis tricolor (n=13). Primary producers bracketing this group of consumers as regards $\delta^{13}C$ values are again the epiphytes, macroalgae, and sand microflora. $\delta^{15}N$ ranged from +7.5‰ for the bivalve Tellina alternata to +16.5‰ for the estuarine squid Lolliguncula brevis (n=33). Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ for this group (Figure 29; 1=Aurelia aurita, 2=Busycon contrarum, 3=Crepidula plana, 4=Calliactis tricolor, 5=Lolliguncula brevis, 6=Mercenaria campechiensis, 7=Nassarius vibex, 8=Polynices duplicatus, 9=Pisania tincta, 10=polychaetes, 11=Tellina alternata, 12=Thais haemostoma, 13=Luida clathrata) reveals the values to be closely associated with those for epiphytes and macroalgae, indicating the probable consumption of this material as an ultimate food source. However, the macroalgae were a limited resource as a result of their sporadic abundance. $\delta^{34}S$ values ranged from +13.0‰ for the white slipper snail Crepidula plana to 19.6‰ for A. aurita. Interestingly, A. aurita lies near the same epiphyte outlier value as the barnacle Chelonibia patula (compare Figures 27 and 29).

Because jellyfish are transients in this seagrass system, this epiphyte value may be near to that of plankton originating offshore, which could also potentially be consumed by the barnacle C. patula. Both of these species feed exclusively on particulate material and plankton in the water column.

The final pair of dual isotope plots details trophic relationships for planktivorous fish species. Figure 30 (1=Anchoa mitchilli, 2=A. nasuta, 3=Brevoortia patronus, 4=Harengula jaguana, 5=larval clupeids, 6=Menidia beryllina, 7=non-clupeid larval fish) shows $\delta^{13}C$ versus $\delta^{15}N$ for this group. $\delta^{13}C$ values ranged from -19.4‰ for larval clupeids (n=35) to -15.7‰ for a sample of non-clupeid larval fish (n=137). $\delta^{15}N$ ranged from +10.2‰ for the non-clupeid larval fish to +15.0‰ for a sample of the bay anchovy Anchoa mitchilli collected in 1992 (n=75). Using the formula of Hobson and Welch (1992) presented earlier, non-clupeid larval fish and A. mitchilli possess TL values of 2.1 and 3.7, respectively. As in previous sample sets, epiphyte, macroalgae, and sand microflora values bracket this consumer group. Examination of the plot of $\delta^{13}C$ versus $\delta^{34}S$ for this group (Figure 31; 1=Anchoa mitchilli, 2=A. nasuta, 3=Brevoortia patronus, 4=Harengula jaguana, 5=larval clupeids, 6=Menidia beryllina, 7=non-clupeid larval fish) shows the values for planktivorous fish to be clustered among those for plankton, macroalgae, and epiphytes. Once again, the grouping of values between these primary producers suggests consumption of these materials, although macroalgae are likely to be of limited importance as a result of sporadic availability. Fragments of macroalgae and epiphytes may be present in the plankton for direct

consumption, or the zooplankton eaten by these fish could in turn consume these items, in addition to phytoplankton cells. $\delta^{34}S$ values ranged from +12.4‰ for the tidewater silverside Menidia beryllina to +17.7‰ for the scaled sardine Harengula jaguana.

The consistent theme that emerges from this detailed examination of the consumers sampled in the Horn Island seagrass system is one of the overall importance of epiphytes and possibly macroalgae as primary sources of organic matter for higher trophic levels, with sand microflora and plankton also contributing to this pool. As mentioned previously, however, the presence of macroalgae was episodic; accordingly its importance is much less than that suggested by the graphical results. The most striking fact is that the direct contribution of Halodule wrightii to the food web appears to be minimal at best.

The relatively close match of the $\delta^{13}C$ and $\delta^{34}S$ values of primary producers and consumers in this seagrass system is very interesting. The northwest shore of Horn Island is influenced by a number of hydrologic features: Mississippi Sound, Biloxi Bay, the Pascagoula River, and the Gulf of Mexico via Dog Keys Pass at its west end and Petit Bois Pass at its east end. In contrast to this, most stable isotope studies to date have been performed in ecosystems with well-defined boundaries. Results of the stable isotope analysis performed here did not seem to be overly influenced by the totally open nature of the Horn Island seagrass system.

SUMMARY AND CONCLUSIONS

Summary

Stable Isotope Ratios of Primary Producers

Stable carbon isotope ratios of Halodule wrightii and its associated epiphytes were distinct. $\delta^{13}C$ values for H. wrightii averaged -12.2‰ (range = -13.6 to -10.6‰). Epiphytic algae $\delta^{13}C$ values averaged -17.5‰ (range = -19.7 to -15.2‰). Thus, there was very good separation between these two critical samples. Phytoplankton had an average $\delta^{13}C$ value of -21.8‰ (range = -23.3 to -21.2‰). The plankton values were distinct from those for the epiphytes and H. wrightii blades.

$\delta^{13}C$ values for the algae epiphytic on H. wrightii, macroalgae, and the sand microflora (as represented by the Mellita quinquiesperforata sample) all overlapped. However, use of stable nitrogen and sulfur values allowed these primary producers to be separated with respect to their contributions to the overall food web.

Macroalgal samples had the following average $\delta^{13}C$ values: Sargassum natans (-16.8‰), Sargassum fluitans (-16.6‰), Enteromorpha spp.(-16.2‰), Gracilaria verrucosa (-17.4‰). These algae were of minor importance as sources of organic matter due to their limited availability.

The sand microflora could not be sampled directly, and were thus represented

by a sample of the sand dollar Mellita quinquiesperforata, which subsists on a diet consisting almost exclusively of sand-associated diatoms and bacteria. The $\delta^{13}C$ value for this organism was -16.9‰.

Stable nitrogen isotope ratios, indicative of trophic level, averaged +6.0‰ for H. wrightii and +5.9‰ for its epiphytes. The plankton sample $\delta^{15}N$ values averaged +9.9‰. $\delta^{15}N$ values for the macroalgae sampled were as follows: Sargassum natans (+4.7‰), Sargassum fluitans (+4.5‰), Enteromorpha spp. (+9.8‰), Gracilaria verrucosa (+10.0‰). The sand dollar value, representative of the sand microflora, was +6.6‰.

Stable sulfur isotope ratios were much more variable than those for carbon or nitrogen. Values for $\delta^{34}S$ averaged +11.5‰ for H. wrightii and +13.7‰ for its epiphytes. The average $\delta^{34}S$ value of the plankton samples was +15.4‰. $\delta^{34}S$ values for the macroalgae sampled were as follows: Sargassum natans (+17.8‰), Sargassum fluitans (+17.9‰), Enteromorpha spp. (+20.55‰), Gracilaria verrucosa (+16.6‰). The sand dollar $\delta^{34}S$ value, representative of the sand microflora, was +8.6‰.

Stable Isotope Ratios of Consumers

Stable carbon isotope ratios of consumers ranged from -23.0‰ for the Atlantic croaker Micropogon undulatus to -12.7‰ for the white mullet Mugil curema. The average $\delta^{13}C$ value for all animals sampled was -17.1‰. When averaged by species or sample type a pooled sample of miscellaneous small shrimp species exhibited the highest $\delta^{13}C$ value (-13.5‰) and the white trout Cynoscion

arenarius the lowest (-21.0°/oo) . The average $\delta^{13}C$ value for all organisms sampled grouped by species or type was -17.3°/oo.

A total of 129 out of 183 (70%) consumers sampled in this system had $\delta^{13}C$ values falling within the range of -18.8 to -15.4°/oo. All but 13 of the 183 (93%) consumer organisms sampled fell within the range of -20.1°/oo to -14.1°/oo. This strongly suggests that Halodule wrightii, with an average $\delta^{13}C$ value of -12.2°/oo, was a minimal contributor to the base of this food web.

Stable nitrogen isotope ratios, indicative of trophic level, ranged from +6.0°/oo for the white mullet Mugil curema (a different specimen than that producing the lowest $\delta^{13}C$ value) to +16.6°/oo for the bluefish Pomatomus saltatrix. Average $\delta^{15}N$ for all animals sampled was 12.5°/oo. Averaging consumer values by species or sample type showed the bivalve Tellina alternata to occupy the lowest trophic position at 7.5°/oo, and the estuarine squid Lolliguncula brevis with a $\delta^{15}N$ of 15.7°/oo to occupy the highest position. The average $\delta^{15}N$ value for all organisms sampled by species or type was also +12.5°/oo.

Stable sulfur isotope ratios for consumers in this system ranged from +2.3°/oo for the white mullet Mugil curema to +19.6°/oo for the moon jelly Aurelia aurita. The average $\delta^{34}S$ value for all animals sampled was 13.8°/oo. The observed range in $\delta^{34}S$ values when averaged by species or sample type was from +4.4°/oo for beach diggers in the family Haustoriideae to +19.6°/oo for the moon jelly Aurelia aurita. The average $\delta^{34}S$ value for the consumer organisms sampled, by species or type, was +14.2°/oo.

Dual Stable Isotope Plots

Multiple stable isotope analyses were employed to examine food web dynamics in this seagrass ecosystem. Stable isotope ratios for carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) were measured on material collected from May 1989 through November 1992. For most organisms sampled, values for $\delta^{13}C$ and $\delta^{34}S$ clustered around those measured for seagrass epiphytes, macroalgae, and plankton, rather than the seagrass blades. Trophic levels, as determined by $\delta^{15}N$, were not well delineated. The overall picture that emerges from this detailed examination of the consumers sampled in the Horn Island seagrass system is one of the overall importance of epiphytes as organic matter sources, with sand microflora and plankton also contributing to this pool. Macroalgae are additional but ephemeral contributors, as their presence in the seagrass beds is an episodic event; Sargassum spp. were encountered in abundance only once during the four years of study in the area, and Enteromorpha spp. and Gracilaria verrucosa were limited in abundance throughout most of the year. The most striking fact is the virtual absence of Halodule wrightii stable isotope signatures from this food web.

Conclusions

Multiple stable isotope analyses, the results of which were used to produce dual stable isotope plots, showed that Halodule wrightii, its associated epiphytes, plankton, and the sand microflora (as represented by the Mellita quinquiesperforata sample) were all distinct when stable carbon and sulfur isotope ratios were employed

in combination. Use of $\delta^{13}C$ alone did not provide sufficient resolution to allow for separation of the algal components of the system. Also, although the $\delta^{13}C$ values of epiphytes and plankton differed, their $\delta^{34}S$ values were close. Macroalgae present in the area (Sargassum spp., Gracilaria verrucosa, and Enteromorpha spp.) exhibited similar stable carbon isotope signatures. They too had discrete, well-separated $\delta^{13}C$ and $\delta^{34}S$ values in relation to other primary producers only when the dual isotope approach was used. $\delta^{15}N$ values were not distinctly separate, with the exception of the plankton, as these primary producers all represent the same trophic level.

A series of dual isotope plots were used to examine food web relationships during this multi-year study. Although values for consumers were influenced by organism size and age, temporal factors, and geographic location, none of these factors interfered significantly with interpretation of the results. Epiphytes, sand microflora, macroalgae, and plankton were all potentially important sources of organic matter to varying degrees. Halodule wrightii blades essentially served as attachment sites for a high diversity of epiphytic algal species.

The relatively close match of the $\delta^{13}C$ and $\delta^{34}S$ values of primary producers and consumers despite the open nature of the system is noteworthy. The northwest shore of Horn Island is influenced by Mississippi Sound, Biloxi Bay, the Pascagoula River, and the Gulf of Mexico via Dog Keys Pass at its west end and Petit Bois Pass at its east end. Most stable isotope studies to date have been performed in relatively well-defined systems with definite boundaries. Lack of definition in the boundaries of this seagrass system did not seem to overly influence the identification of benthic

microalgae as a primary food source.

Based on the sizes of samples that were collected during this study in relation to the areal extent of the seagrass beds sampled, seagrass beds function both as structural habitat and as a food source via their associated benthic algae.

As stated earlier, the overall conclusion that emerges from this detailed examination of the food web in the Horn Island seagrass system is one of the overwhelming importance of epiphytes (and macroalgae when present) as organic matter sources for higher trophic levels. Sand microflora (as represented by the sand dollar Mellita quinquiesperforata) and plankton also contribute to the organic matter pool at the base of this food web. The most striking fact is the virtual absence of Halodule wrightii as a component of energy transfer to higher trophic levels in the food web of this system.

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Table 1. Stable C, N, and S Isotope Ratios of Primary Producers

Sample type		del 13C	del 15N	del 34S
Sargassum natans		-16.8	4.7	17.8
Sargassum fluitans		-16.6	4.5	17.9
	Averages =	-16.7	4.6	17.9
	std.dev. =	0.1	0.1	0.0
Plankton				
30-V & 4-VI-91		-23.3	8.2	11.5
10-VII-92, mixed		-21.5	11.1	17.6
10-VII-92, 26 um		-21.3	9.8	13.0
10-VII-92, 26 um		-21.6	10.4	17.6
10-VII-92, 153 um		-21.7	10.0	16.7
10-VII-92, 153 um		-21.2	10.0	15.9
	Averages =	-21.8	9.9	15.4
	std.dev. =	0.7	0.9	2.3
'89-'90 epiphyte sample		-18.5	6.9	18.3
'91 epiphyte sample		-15.2	6.2	-
'92 epiphyte sample		-16.8	4.4	16.1
'92 epiphyte sample (older)		-19.7	5.9	20.2
	Averages =	-17.5	5.9	13.7
	std.dev. =	1.7	0.9	8.0
'88 H. wrightii sample		-13.6	6.4	15.0
'89-'90 H. wrightii sample		-12.9	5.7	15.0
'91 H. wrightii sample		-10.6	4.6	7.4
'92 H. wrightii sample		-11.7	7.5	8.5
	Averages =	-12.2	6.0	11.5
	std.dev. =	1.2	1.1	3.5
Enteromorpha spp., VII-92		-16.5	9.8	20.6
Enteromorpha spp., X-92		-16.0	7.8	20.2
	Averages =	-16.3	8.8	20.4
	std.dev. =	0.3	1.0	0.2
Gracilaria verrucosa		-17.4	10.0	16.6
Sand microflora (Mellita quinquiesperforata)		-16.9	6.7	8.6

Table 2. Average C, N, and S Stable Isotope Ratios For Consumer Species and Groups

Genus and Species or Group	del 13C	del 15N	del 34S
Anchoa mitchilli	-19.1	14.8	16.7
Anchoa nasuta	-18.4	14.3	17.0
Ancyclopsetta quadrocellata	-16.0	13.7	13.6
Anguinella palmata	-19.2	9.0	14.3
Arius felis	-17.0	13.6	11.6
Arius felis liver tissue	-19.2	13.9	16.0
Aurelia aurita	-19.5	15.0	19.6
Ballistes capricus	-16.7	11.9	15.8
Brevoortia patronus	-19.6	11.9	14.9
Busycon contrarum	-17.1	11.6	16.7
Calliactis tricolor	-16.0	12.0	16.7
Callinectes sapidus	-18.0	13.1	14.7
Chaetodipterus faber	-19.2	14.9	15.9
Chelonibia patula	-20.1	11.7	19.5
Chloroscombrus chrysurus	-17.8	14.5	17.4
Citharichthys spilopterus	-16.8	13.1	15.4
Clibanarius vittatus	-15.1	9.6	15.7
Crepidula plana	-19.3	8.7	13.0
Cynoscion arenarius	-21.0	14.2	16.5
Cynoscion nebulosus	-17.5	14.6	12.4
Dasyatis sabina	-16.2	12.2	12.1
Diplectrum bivitattum	-17.5	13.4	15.4
Diplectrum formosum	-17.1	14.2	16.2

Echeneis neucratoides	-17.4	14.1	14.2
Elops saurus	-19.5	12.7	9.4
Emerita talpoida	-15.3	8.9	14.7
Eucinostomus argenteus	-17.8	12.5	11.5
Fundulus similis	-14.1	11.8	9.6
Fundulus similis eggs	-15.1	10.9	10.0
Gymnothorax ocellatus	-17.5	14.4	14.0
Harengula jaguana (f. pensacolae)	-18.2	13.1	17.8
Haustoriidae	-14.3	8.4	4.4
Hepatus epheliticus	-16.2	14.1	15.8
Hippolytid shrimp	-15.1	7.9	10.1
Lagodon rhomboides	-16.1	12.2	11.8
Larval clupeids	-19.4	12.0	ins.[a]
Leiostomus xanthurus	-17.4	13.5	13.8
Libinia dubia	-17.2	13.9	16.6
Libinia emarginata	-17.3	13.7	17.1
Limulus polyphemus	-15.7	12.1	13.1
Limulus eggs	-18.2	12.1	11.5
Lolliguncula brevis	-17.8	15.7	15.7
Luida clathrata	-17.3	9.3	15.5
Lutjanus campechanus	-16.8	14.1	15.8
Lutjanus griseus	-20.1	14.4	14.0
Lutjanus synagris	-16.7	14.2	16.9
Mercenaria campechiensis	-18.5	10.8	15.6
Menippe mercenaria	-16.5	14.1	18.0
Menidia beryllina	-17.1	13.0	13.3

Menticirrhus americanus	-15.8	13.8	14.7
Micropogon undulatus	-20.1	12.7	13.5
Miscl. small shrimp	-13.5	10.6	ins.
Monocanthus setifer	-17.0	12.8	15.8
Mugil cephalus	-14.6	10.2	9.2
Mugil curema	-15.7	9.8	9.6
Mysids	-15.9	9.6	6.3
Nassarius vibex	-16.3	14.1	ins.
Non-clupeid larval fish	-15.7	10.2	ins.
Orthpristis chrysoptera	-16.5	13.5	12.7
Pagurus pollicaris	-15.6	11.6	15.0
Penaeus aztecus	-17.7	11.0	11.8
Penaeus duorarum	-16.5	11.2	12.1
Penaeus setiferus	-19.6	11.4	12.2
Pisania tincta	-19.2	12.6	13.7
Polychaetes	-17.7	11.6	13.5
Polynices duplicatus	-16.5	11.4	15.1
Pomatomus saltatrix	-18.9	15.6	15.0
Portunus gibbesii	-17.3	13.2	15.1
Prionotus tribulus	-16.5	13.4	14.2
Rhizoprionodon terranovae	-16.9	14.8	15.2
Sciaenops ocellata	-16.2	11.4	6.7
Scomberomorus maculatus	-17.7	15.1	16.3
Sicyonia brevirostris	-16.4	10.9	14.4
Sphoeroides parvus	-17.2	13.5	14.8
Sphyrna tiburo	-16.3	14.5	15.6

Squilla empusa	-16.9	13.1	14.6
Strongylura marina	-19.9	14.6	17.6
Symphurus plagiusa	-18.2	12.7	13.1
Synodus foetens	-17.0	15.3	17.0
Tellina alternata	-19.2	7.5	ins.
Thais haemastoma	-16.6	13.7	15.7
Tozeuma carolinense	-14.7	10.1	10.9
Trachinotus carolinus	-19.4	12.2	14.9
Trachypenaeus constrictus	-16.7	11.4	13.2
Trachypenaeus similis	-17.9	11.8	13.5
AVERAGE VALUES FOR ALL CONSUMERS	*-17.1*	*12.5*	*13.8*

[a] ins. = insufficient sample size for analysis

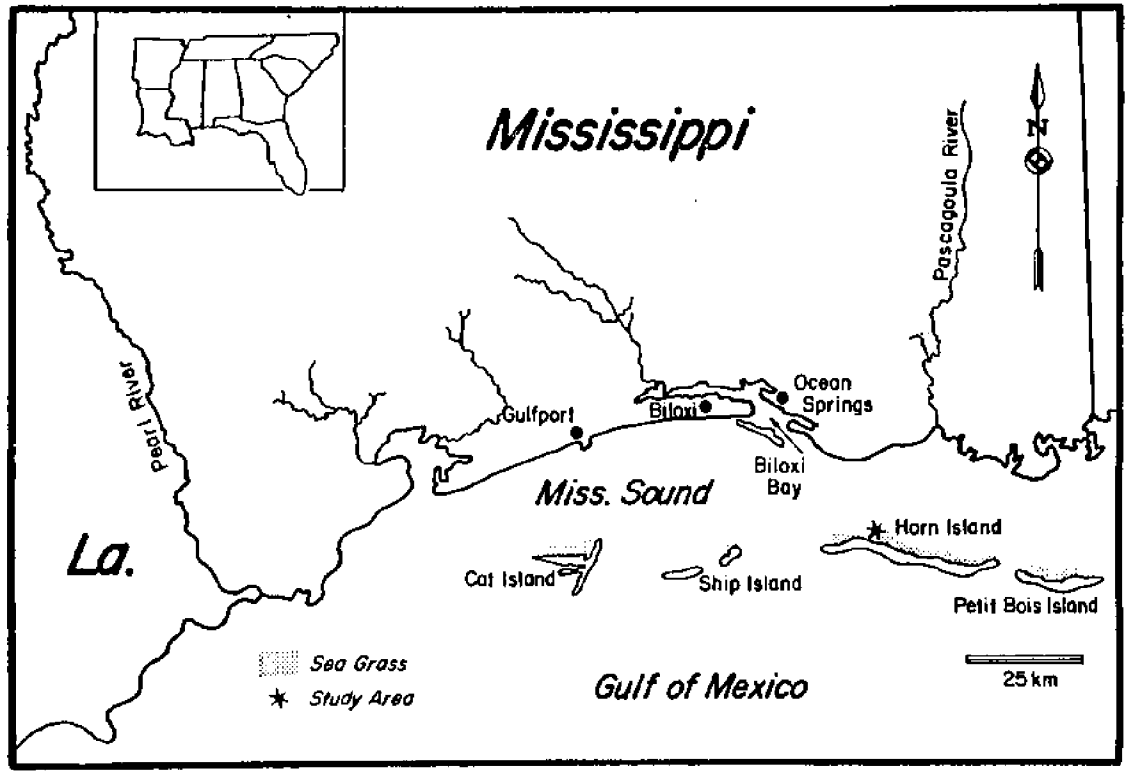

Mississippi
Pascagoula River
N
Pearl River
Gulfport
Biloxi
Ocean Springs
Biloxi Bay
Miss. Sound
La.
Horn Island
Cat Island
Ship Island
Petit Bois Island
Sea Grass
Study Area
Gulf of Mexico
25 km

Figure 1

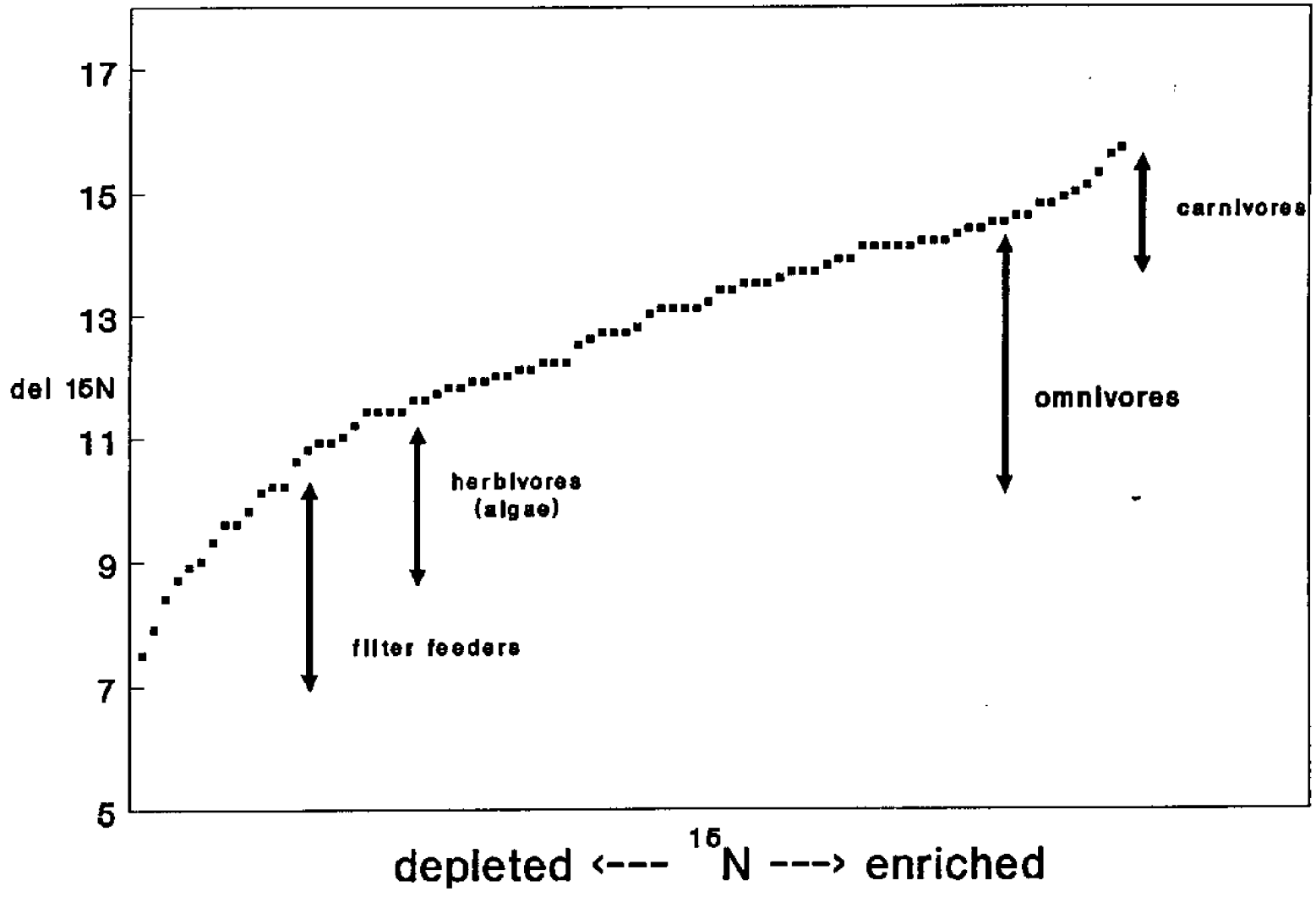
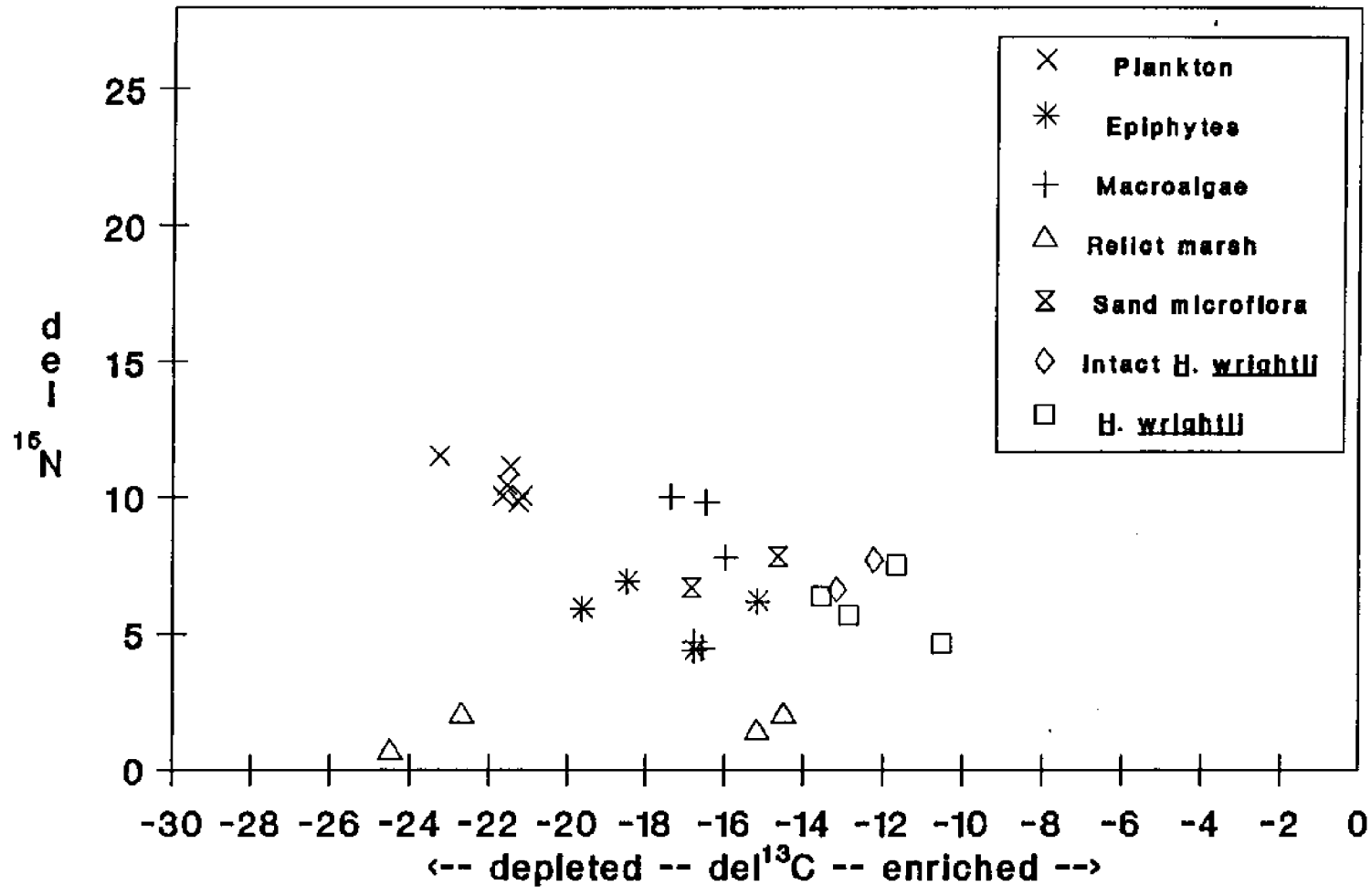
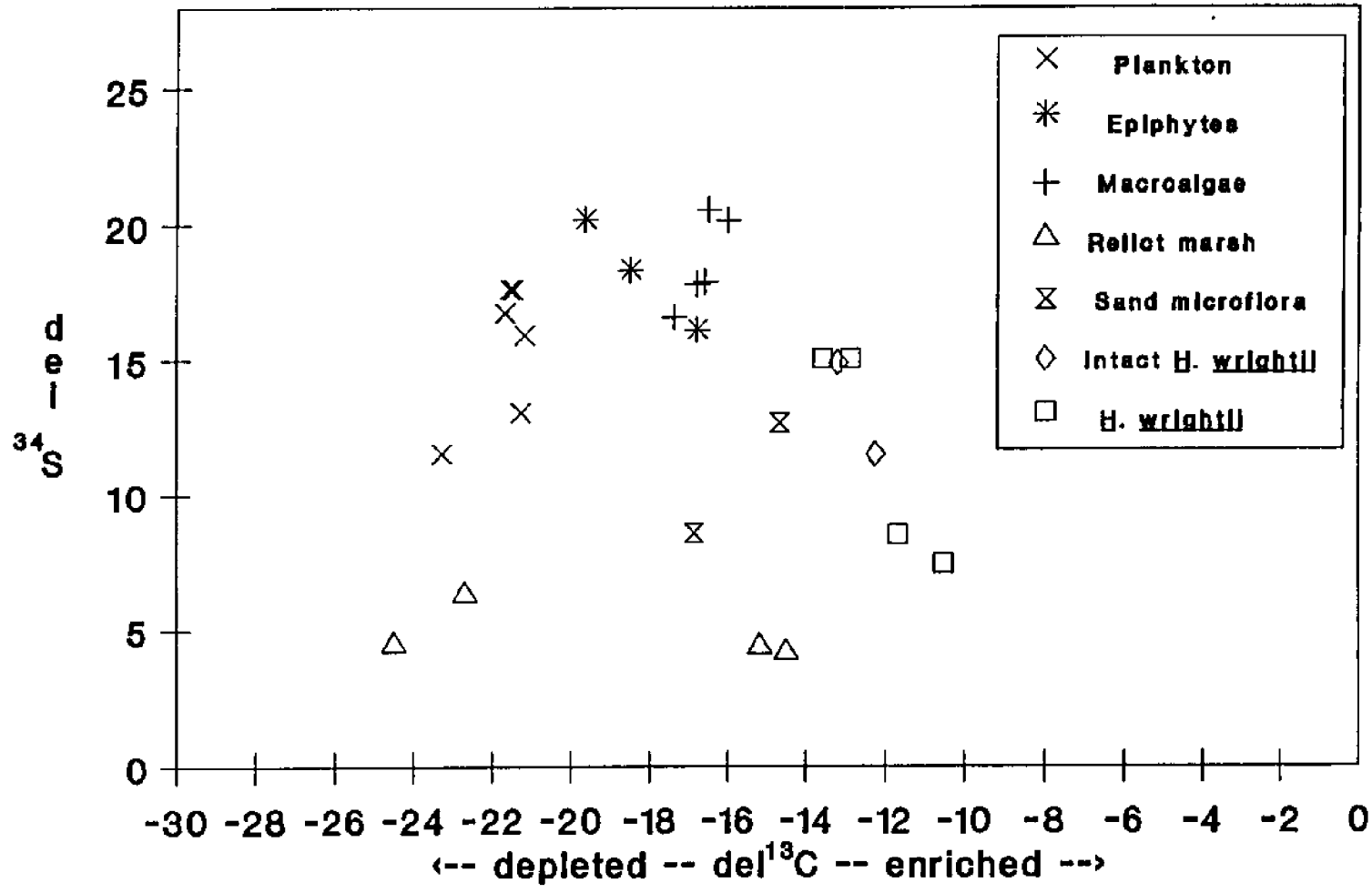

17
15
13
del 15N
11
9
7
5
carnivores
omnivores
herbivores
(algae)
filter feeders
depleted <--- 15N ---> enriched

Figure 2



Primary Producers

Figure 3



Primary Producers

Figure 4

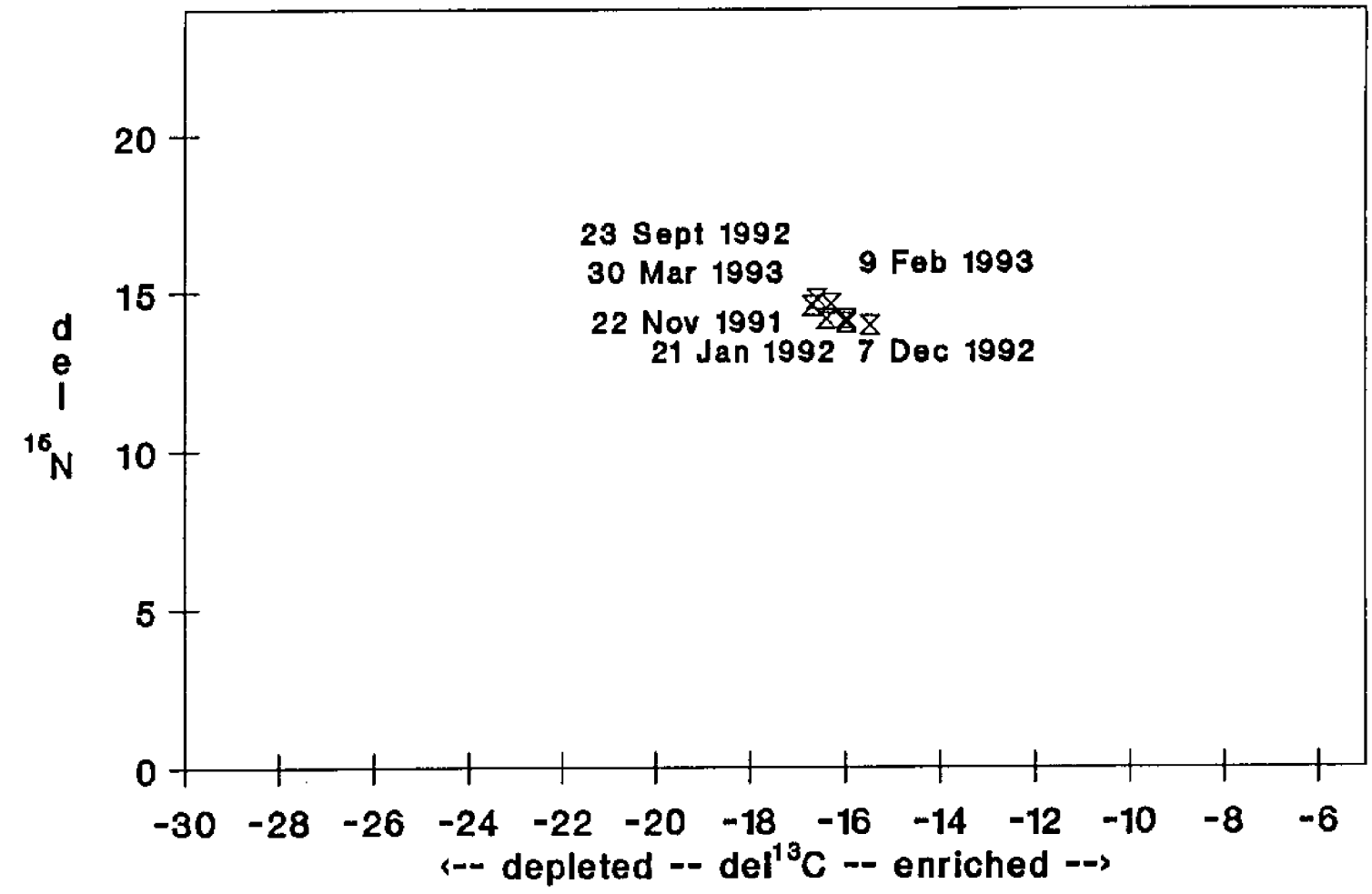

20
15
10
5
0
del
15N
23 Sept 1992
30 Mar 1993
9 Feb 1993
22 Nov 1991
21 Jan 1992
7 Dec 1992
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del13C -- enriched -->
Control Samples

Figure 5

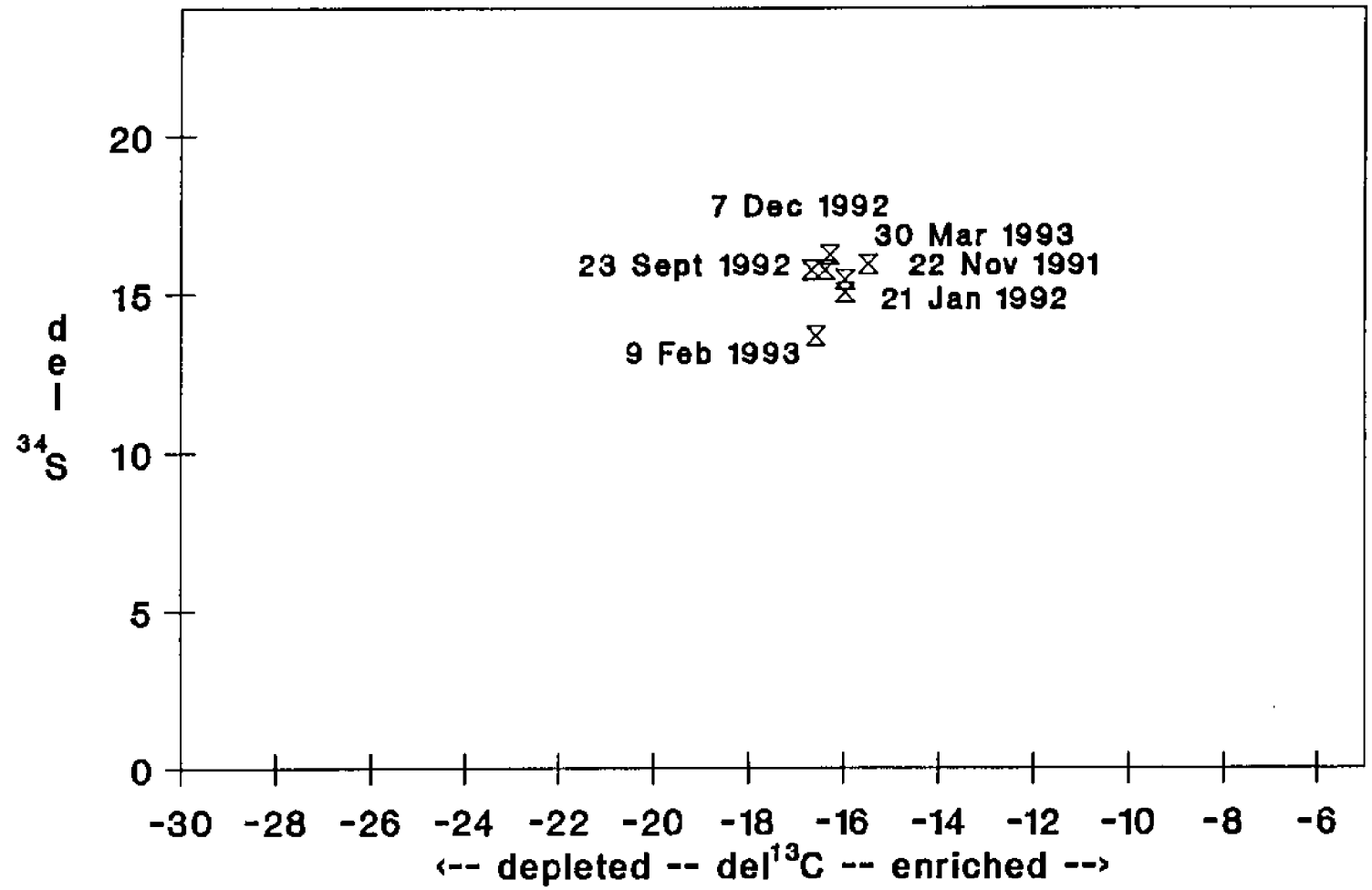

20
15
10
5
0
del
34S
7 Dec 1992
30 Mar 1993
23 Sept 1992
22 Nov 1991
21 Jan 1992
9 Feb 1993
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
‹-- depleted -- del13C -- enriched --›
Control Samples

Figure 6

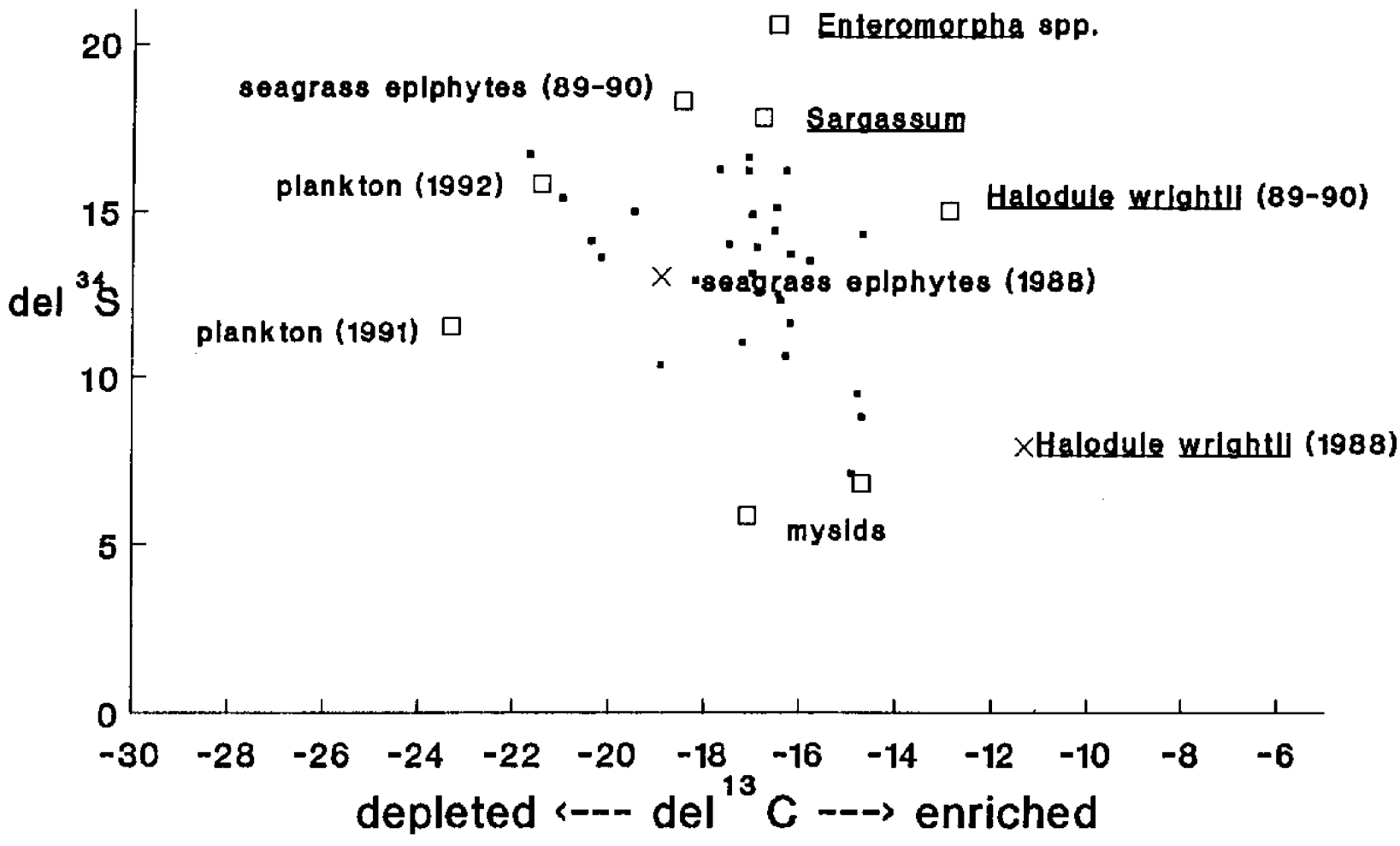

del 13C vs. del 34S
Enteromorpha spp.
seagrass epiphytes (89-90)
Sargassum
plankton (1992)
Halodule wrightii (89-90)
seagrass epiphytes (1988)
plankton (1991)
Halodule wrightii (1988)
mysids
del 34S
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
depleted <--- del 13C ---> enriched

Figure 7

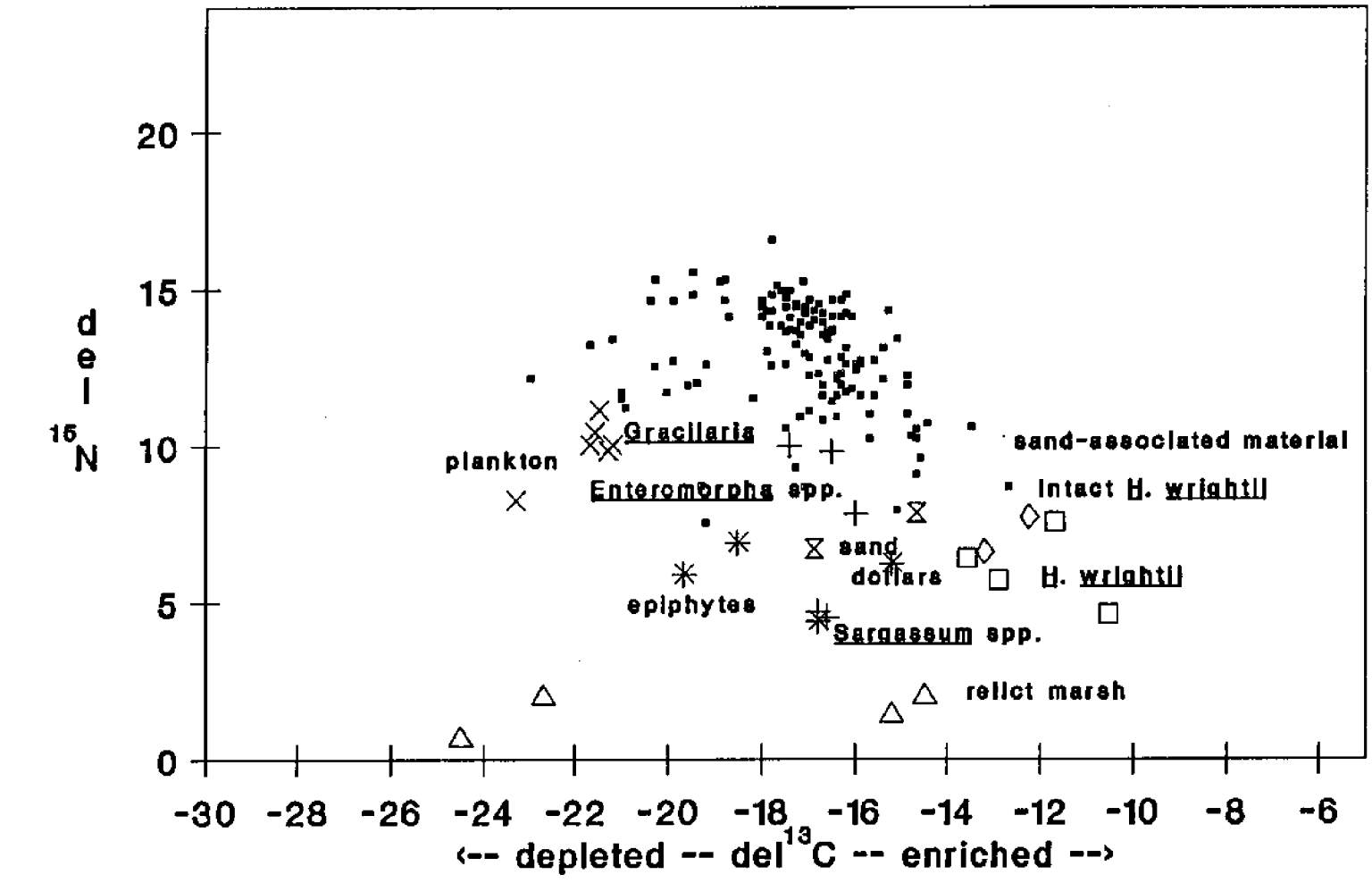
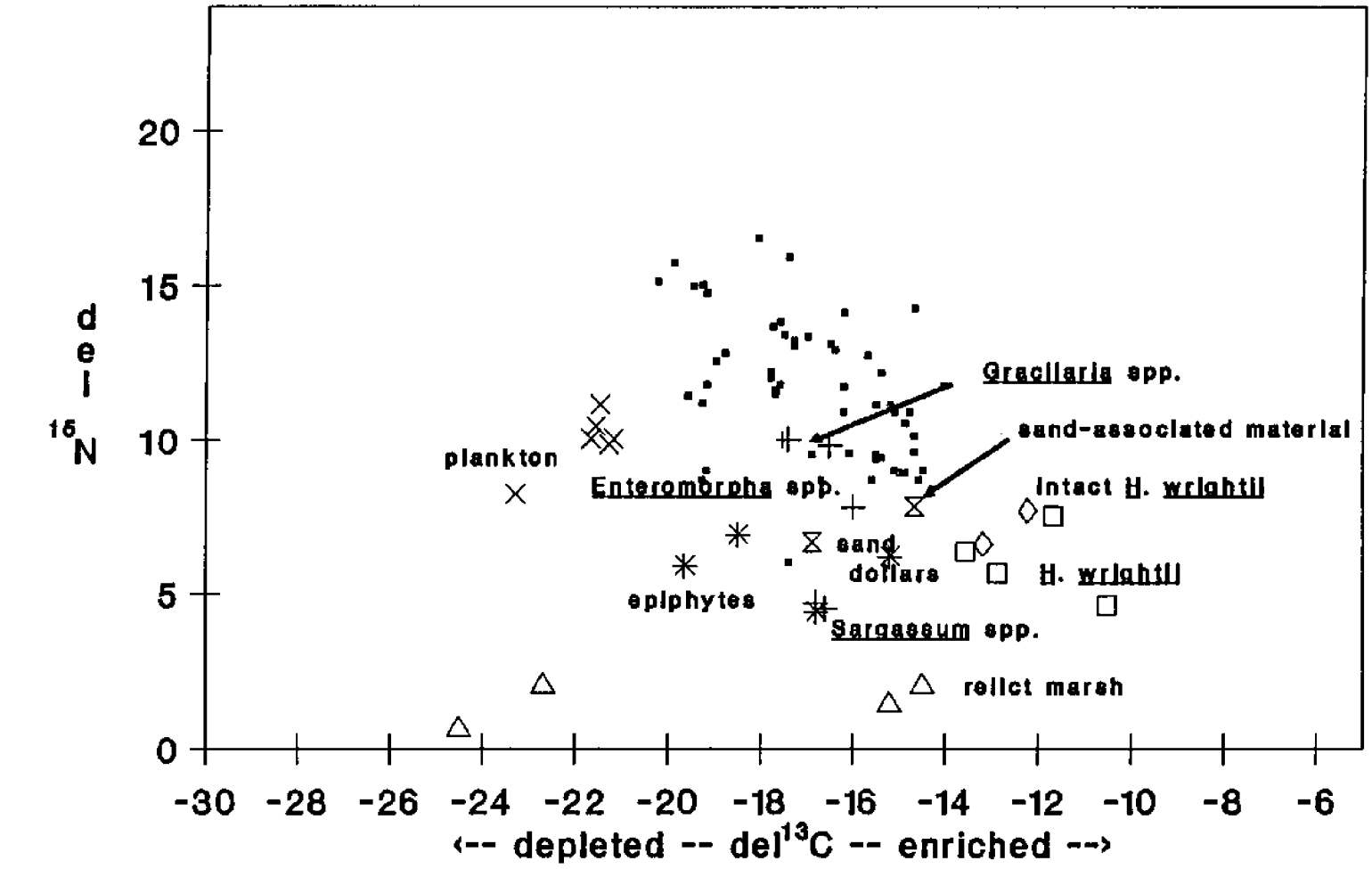
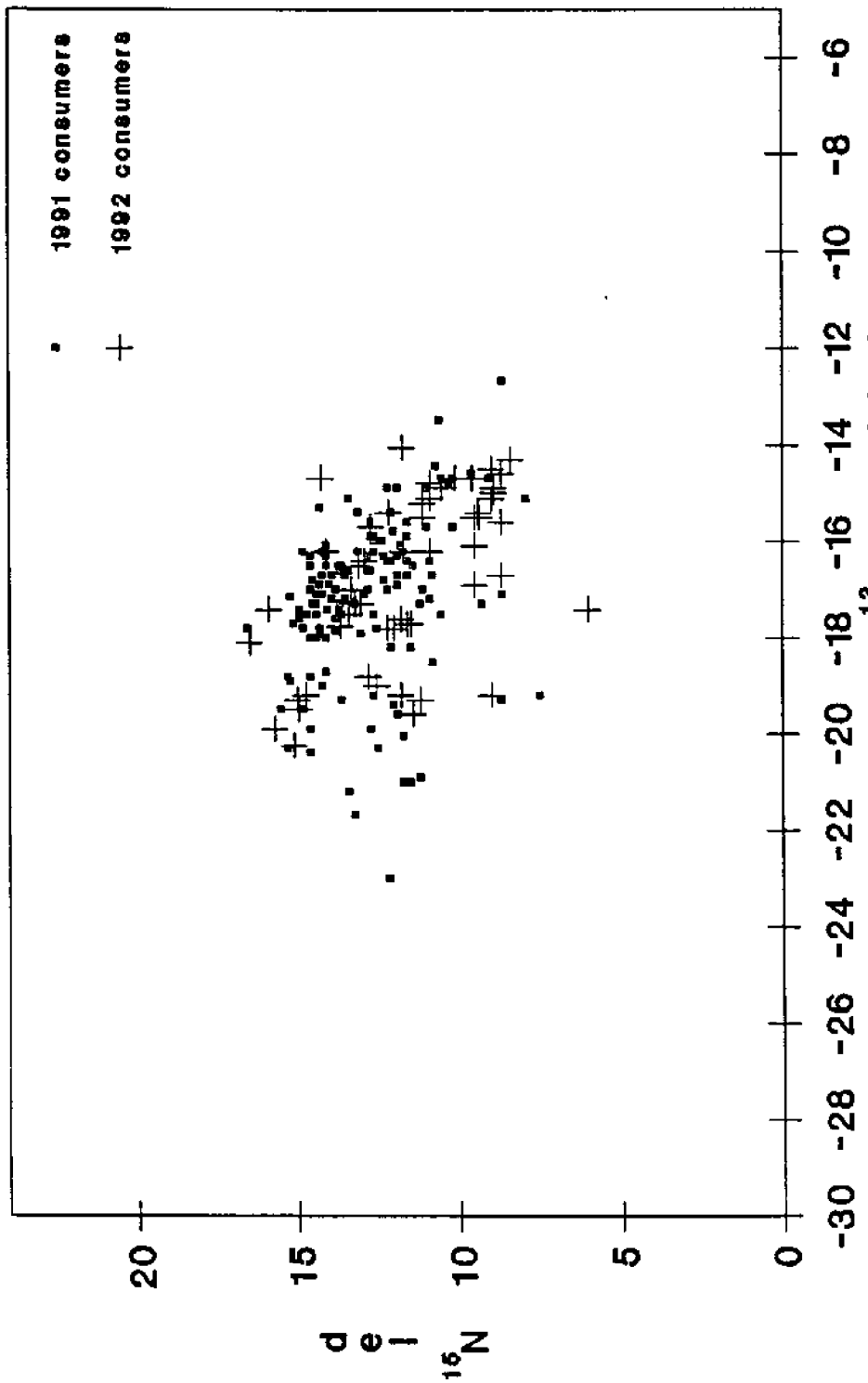

20
15
10
5
0
del
15N
Gracilaria
plankton
Enteromorpha spp.
sand-associated material
intact H. wrightii
sand
dollars
H. wrightii
epiphytes
Sargassum spp.
relict marsh
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del 13C -- enriched -->
1991 Consumers

Figure 8



1992 Consumers

Figure 9


1991 consumers
1992 consumers
del ^{15}N
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del^{13}C -- enriched -->
Figure 10

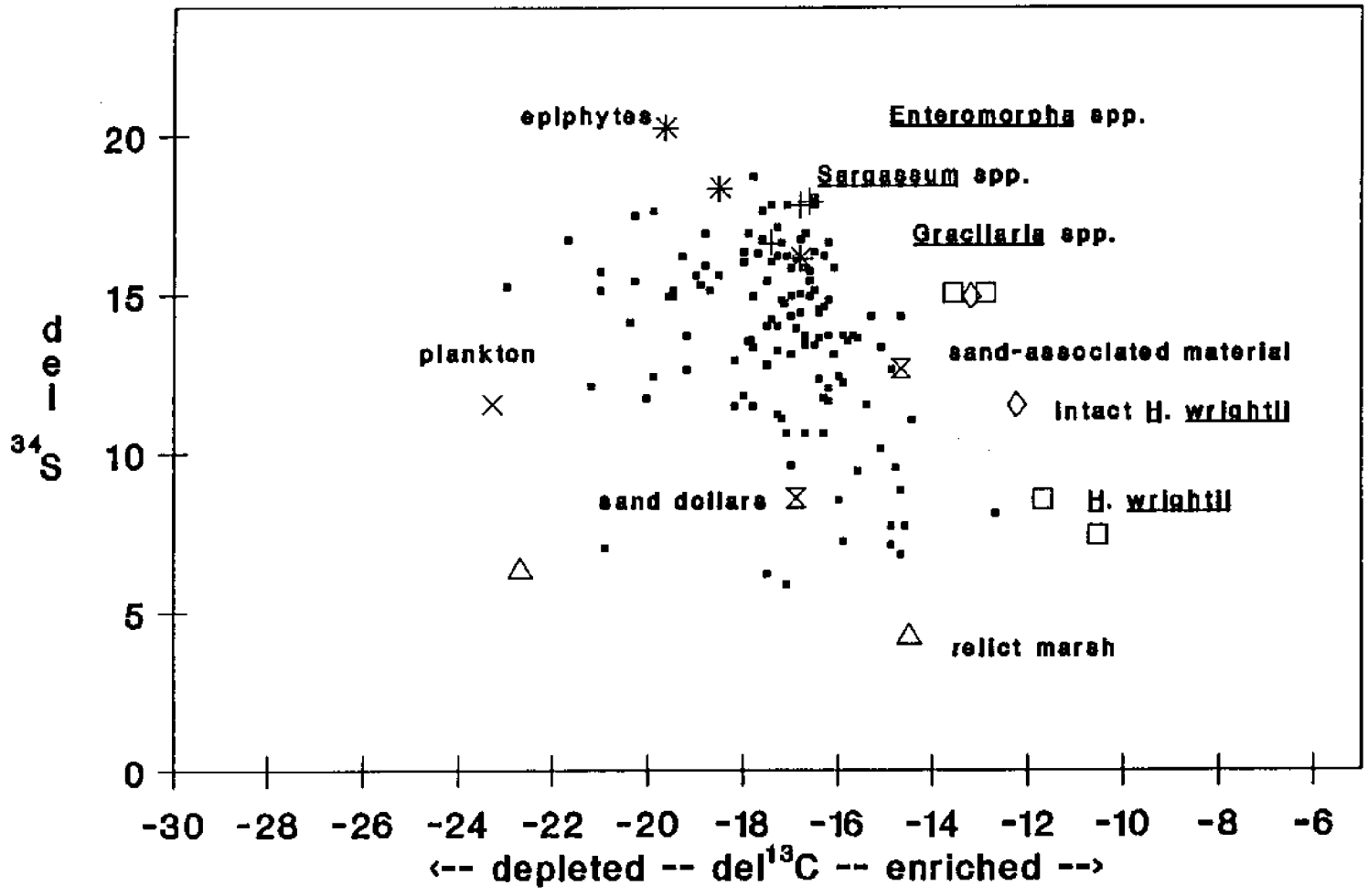

epiphytes
Enteromorpha spp.
Sargassum spp.
Gracilaria spp.
plankton
sand-associated material
intact H. wrightii
sand dollars
H. wrightii
relict marsh
del 34S
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del13C -- enriched -->
1991 Consumers

Figure 11

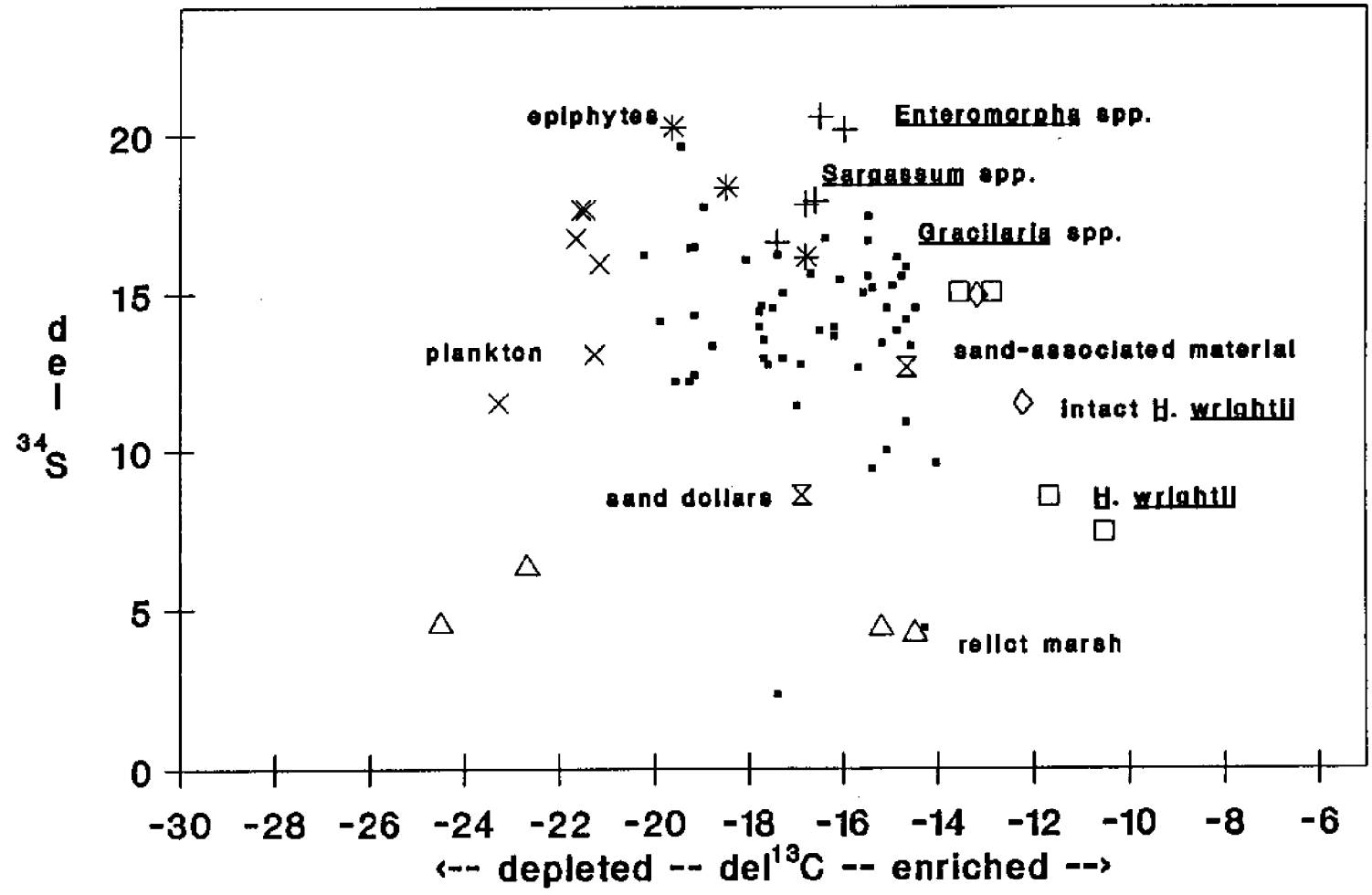
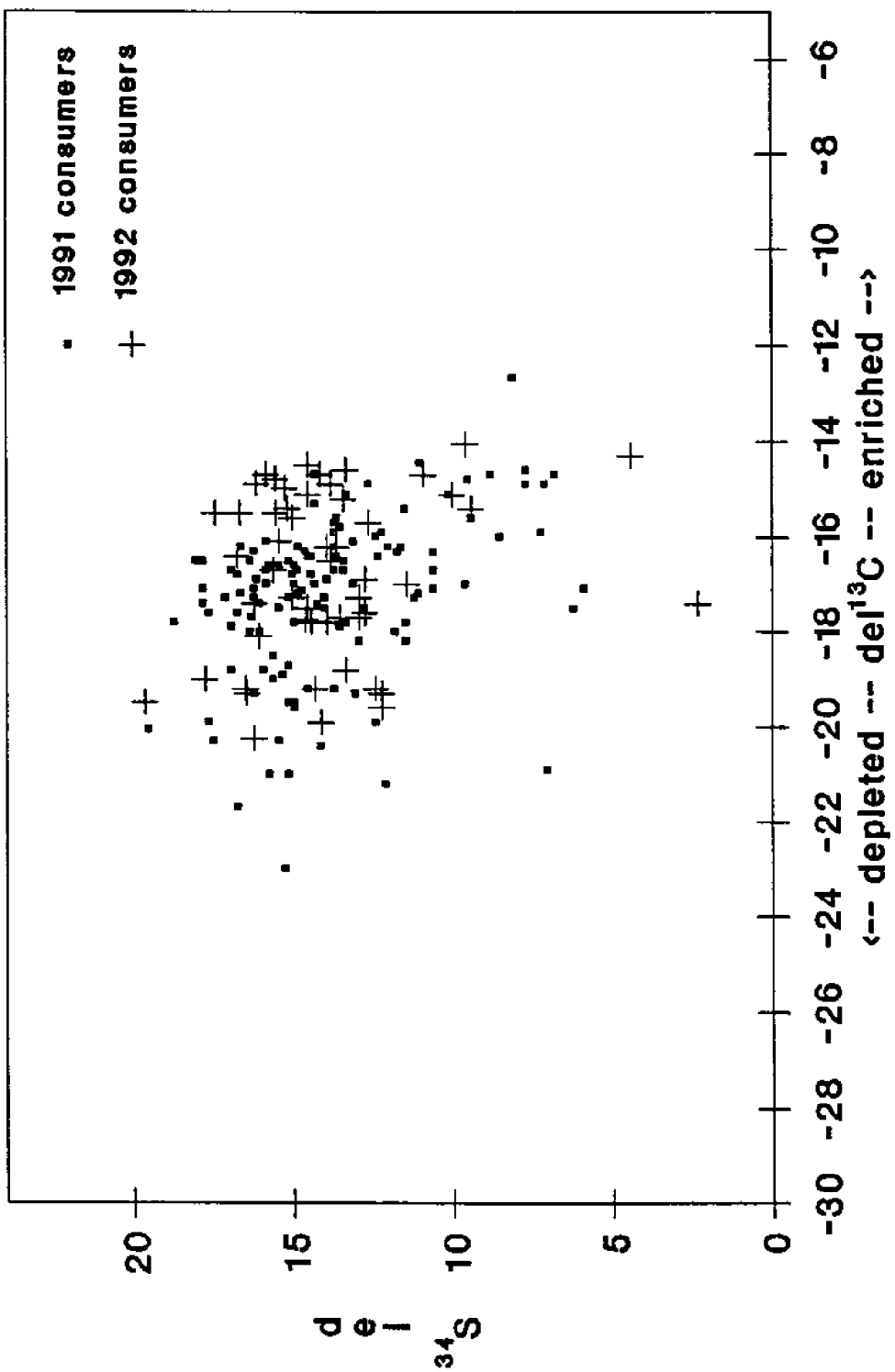

epiphytes
Enteromorpha spp.
Sargassum spp.
Gracilaria spp.
plankton
sand-associated material
intact H. wrightii
sand dollars
H. wrightii
relict marsh
del 34S
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del13C -- enriched -->
1992 Consumers

Figure 12


1991 consumers
1992 consumers
del ^{34}S
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del ^{13}C -- enriched -->
Figure 13

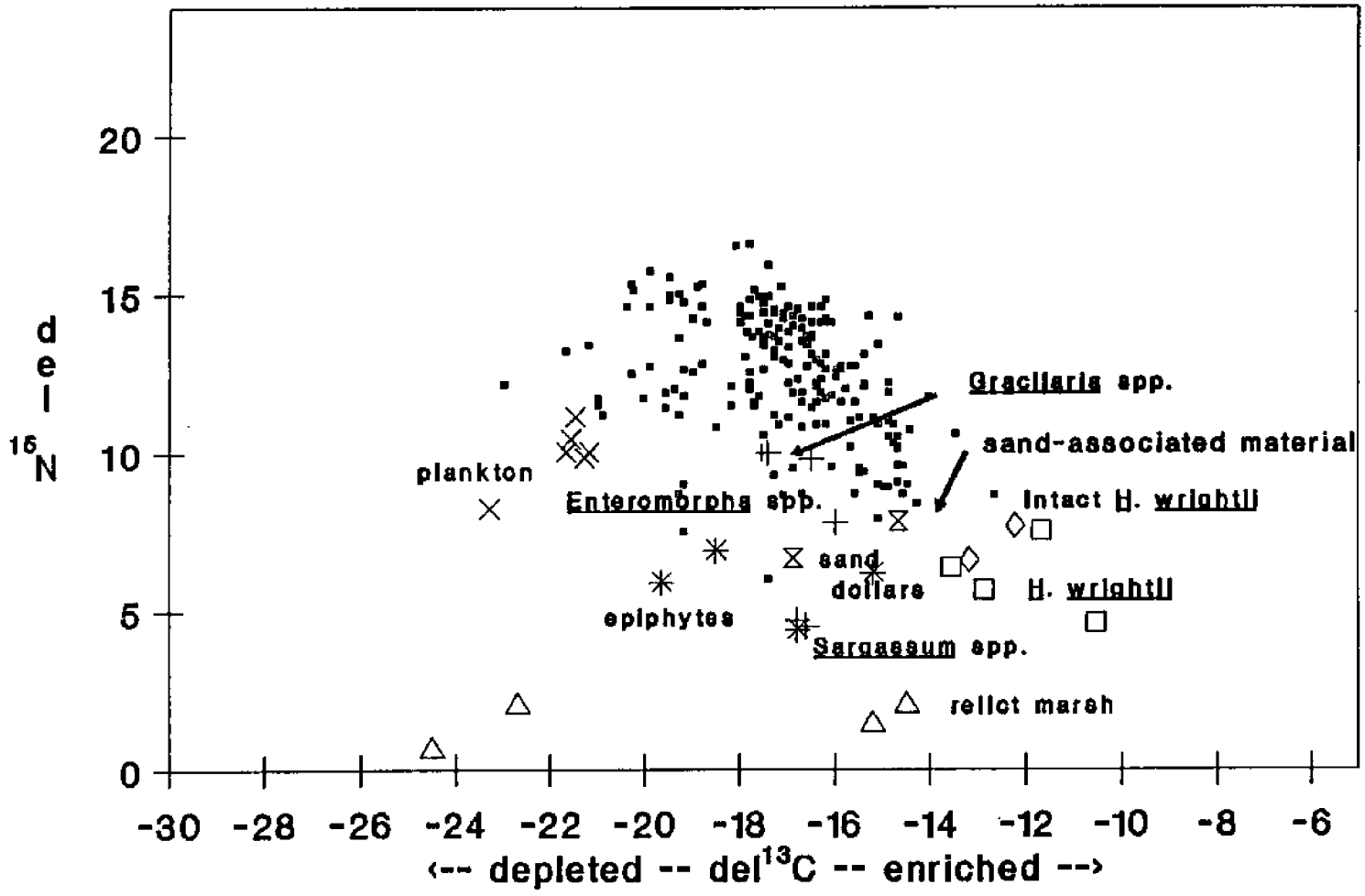

20
15
10
5
0
del 15N
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del13C -- enriched -->
Gracilaria spp.
sand-associated material
plankton
Enteromorpha spp.
Intact H. wrightii
sand dollars
H. wrightii
epiphytes
Sargassum spp.
relict marsh

Figure 14

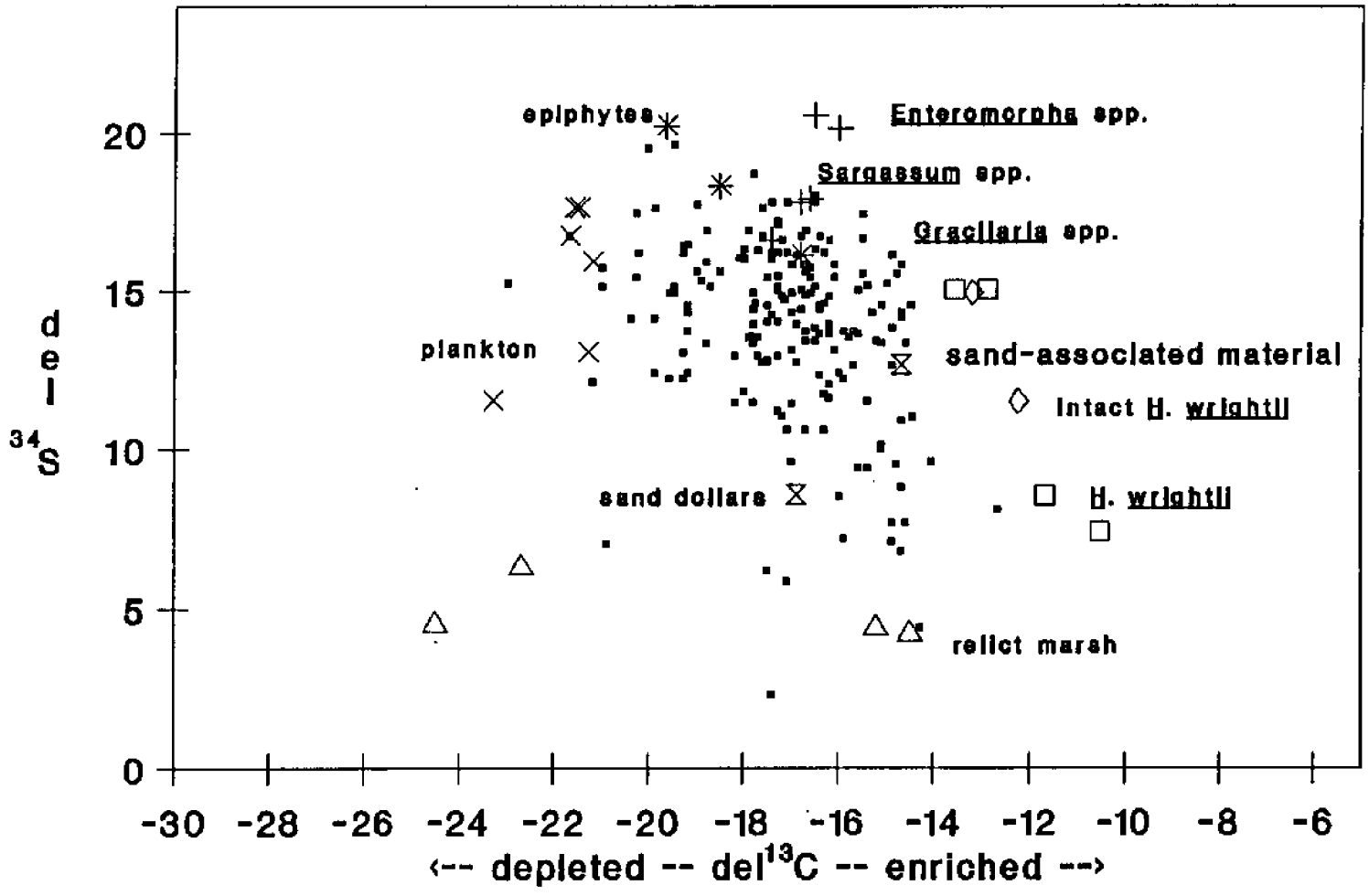

epiphytes
Enteromorpha spp.
Sargassum spp.
Gracilaria spp.
plankton
sand-associated material
Intact H. wrightii
sand dollars
H. wrightii
relict marsh
20
15
10
5
0
d
e
l
34S
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6
<-- depleted -- del13C -- enriched -->
78

Figure 15

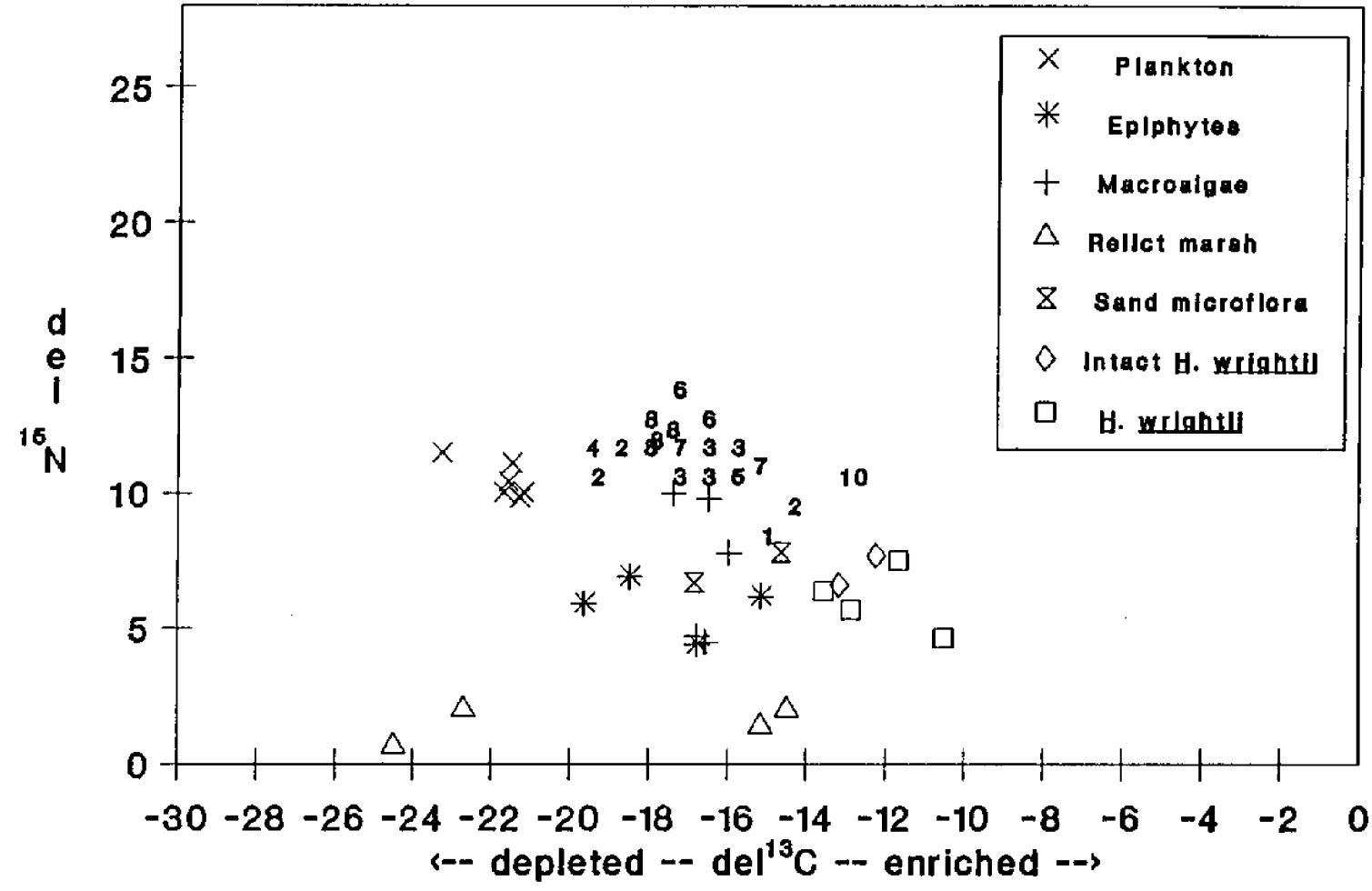

Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 15N
25
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Shrimp Species

Figure 16

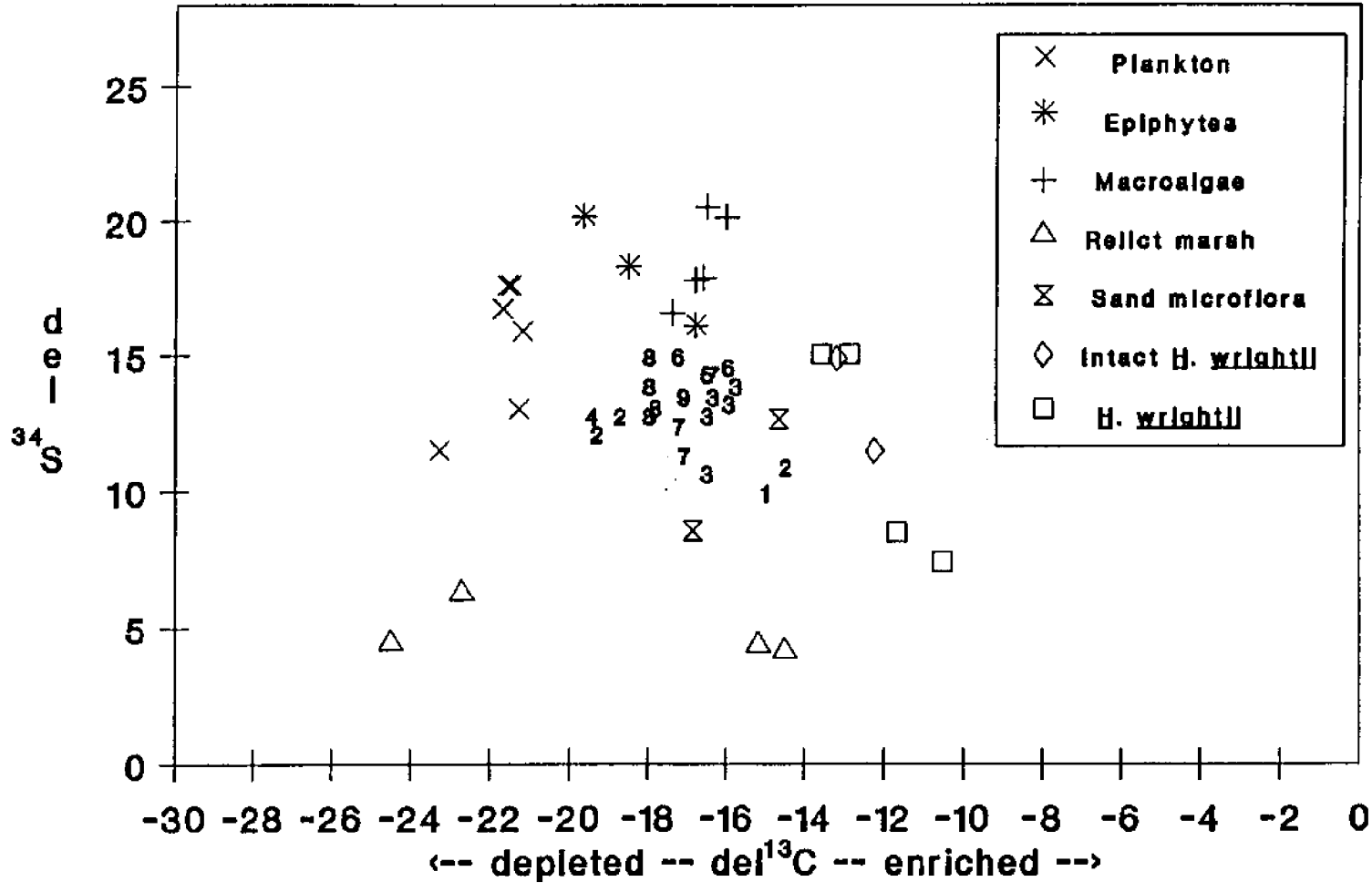

Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 34S
25
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Shrimp species

Figure 17

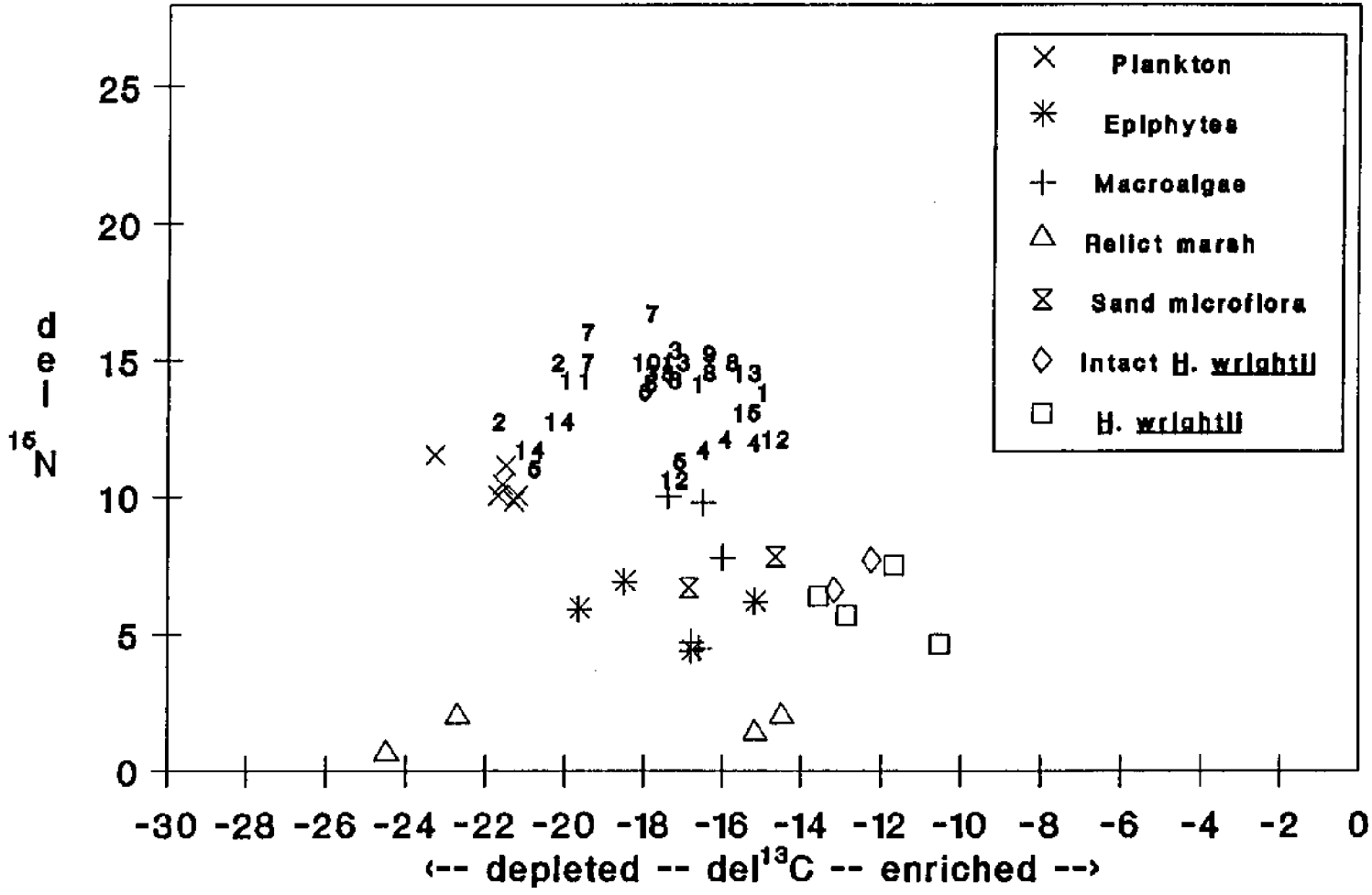

Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 15N
25
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Carnivorous fish and rays

Figure 18

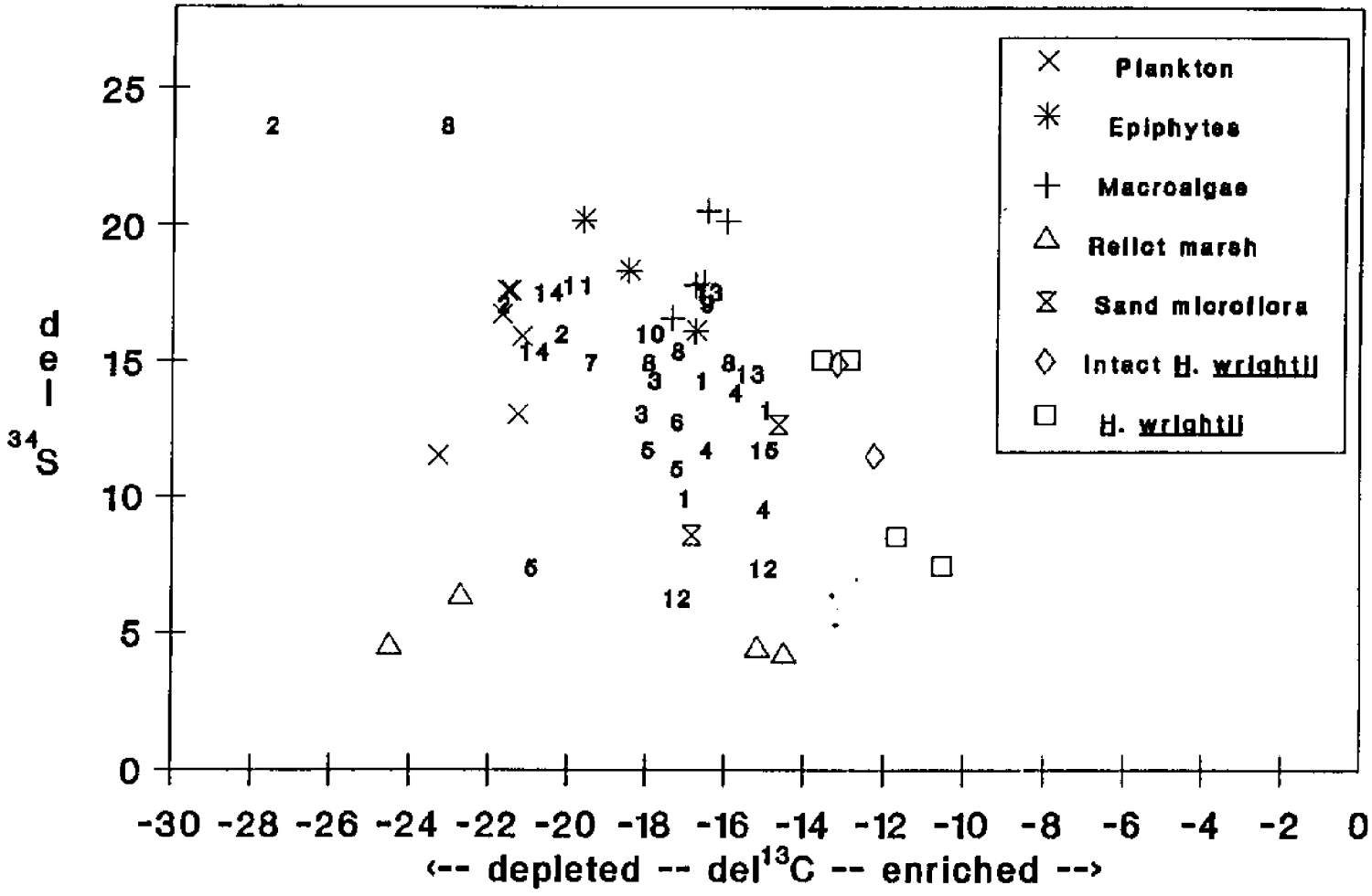
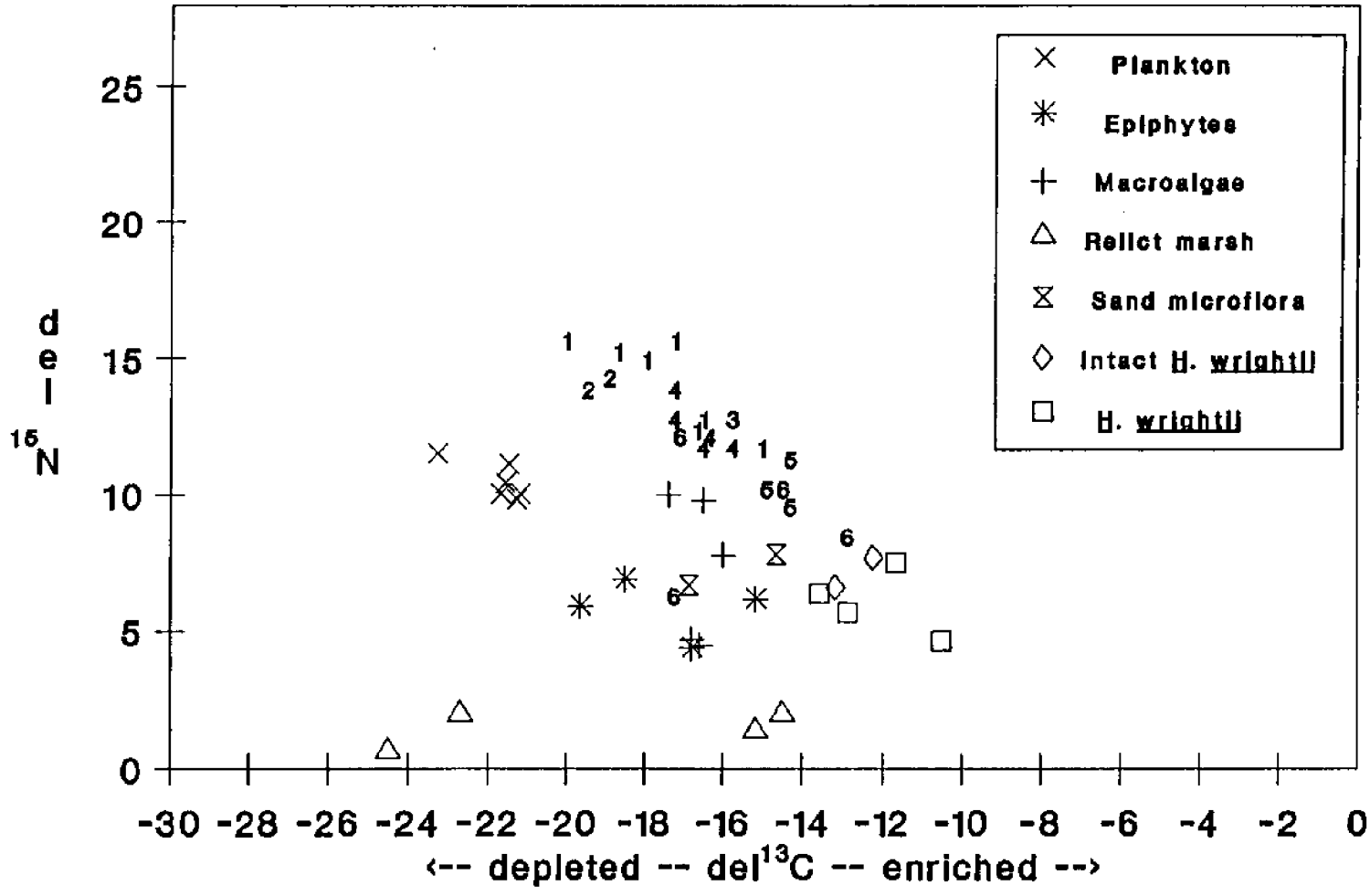

Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 34S
25
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Carnivorous fish and rays

Figure 19



"Omnivorous" fish species

Figure 20

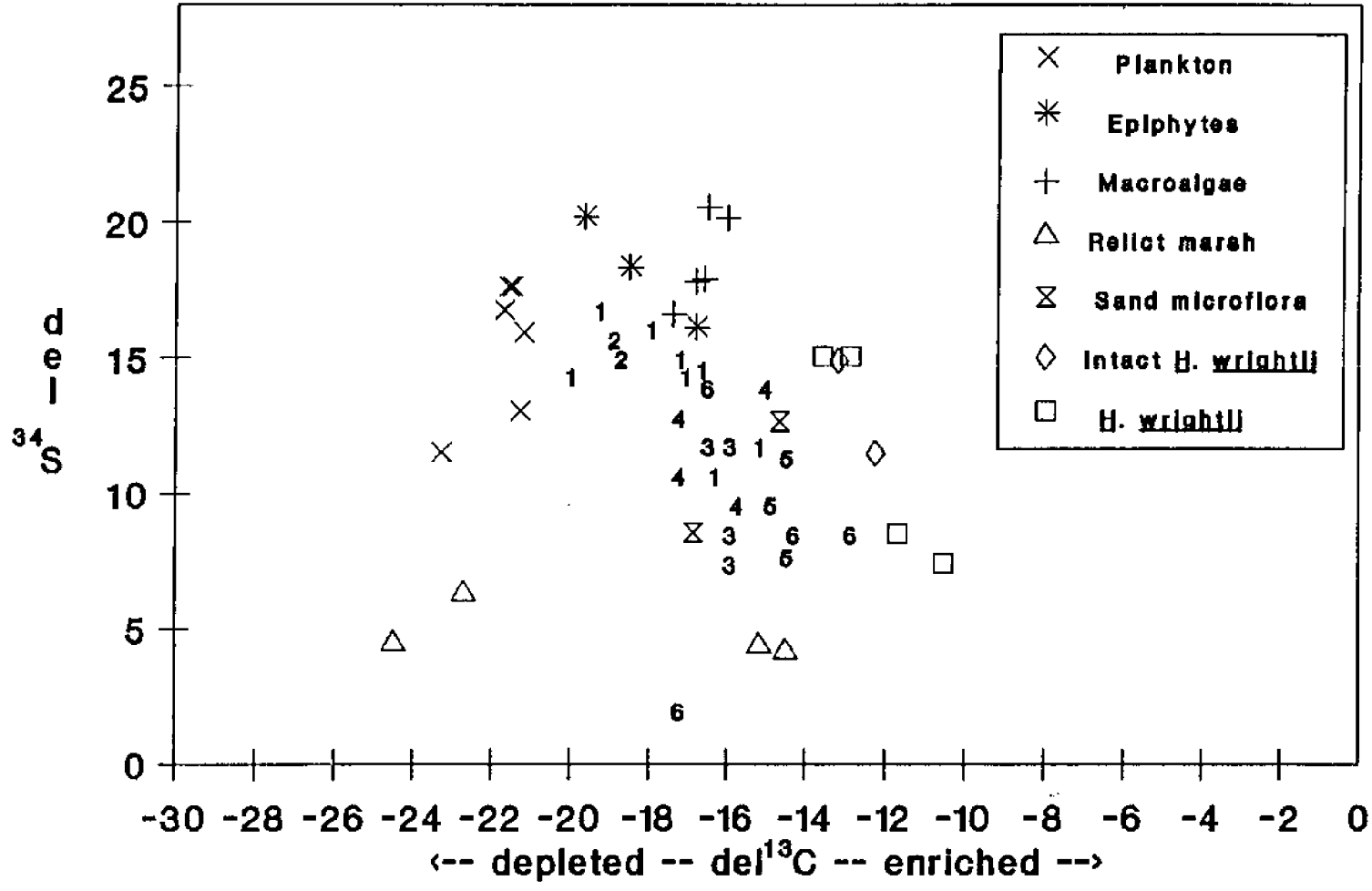

Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 34S
25
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
"Omnivorous" fish

Figure 21

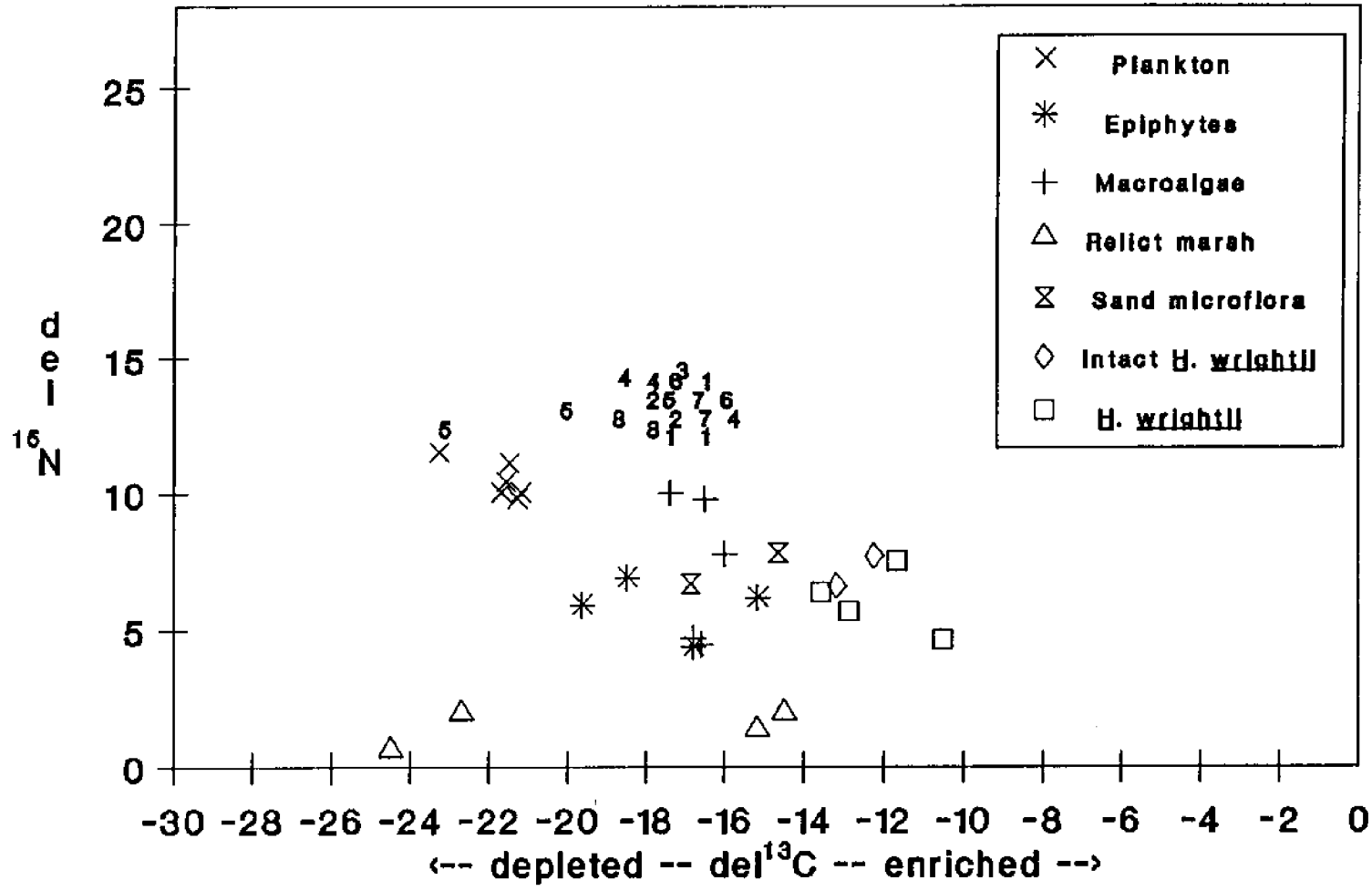

Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 15N
25
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Group 1 fish species

Figure 22

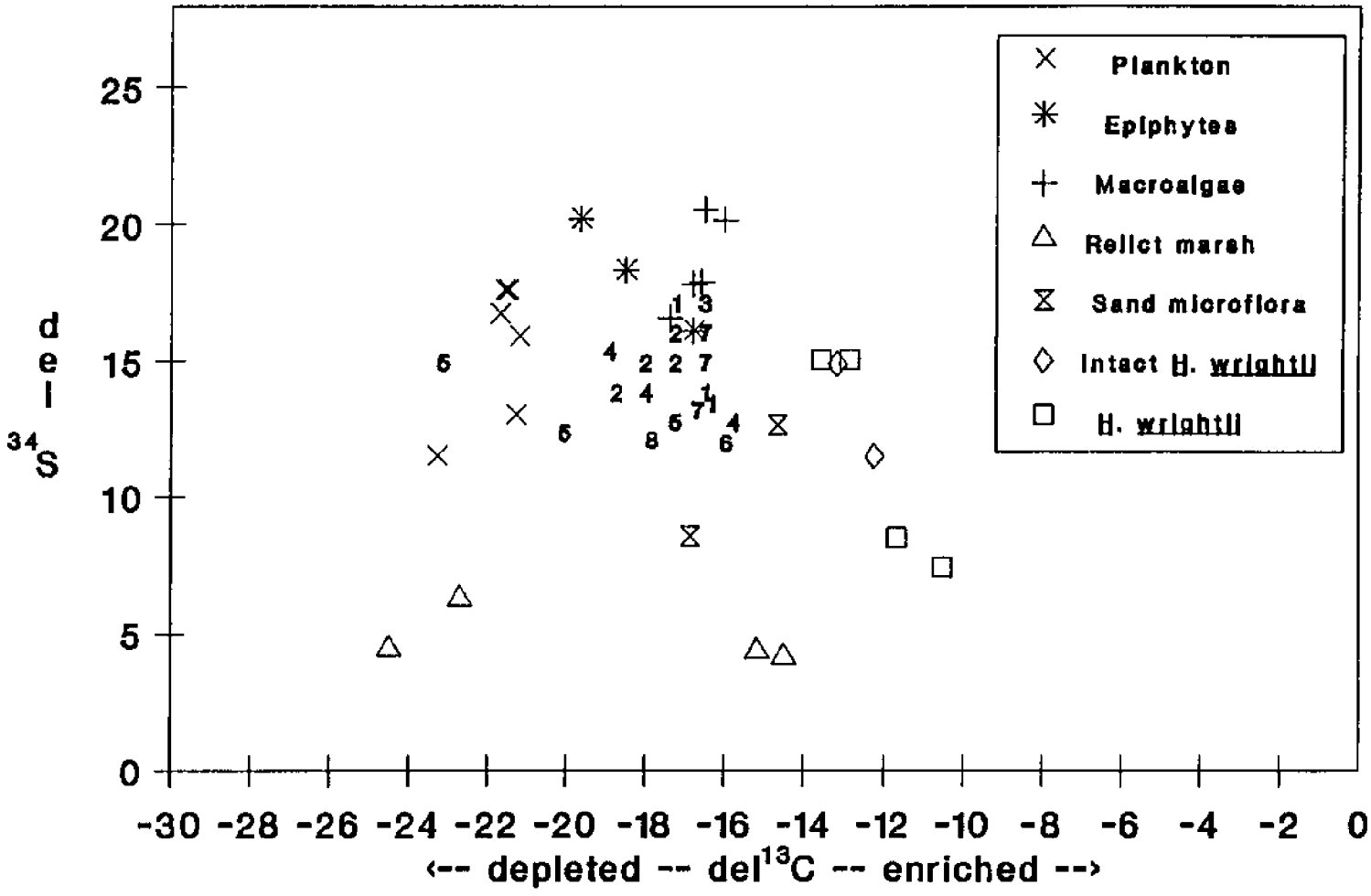
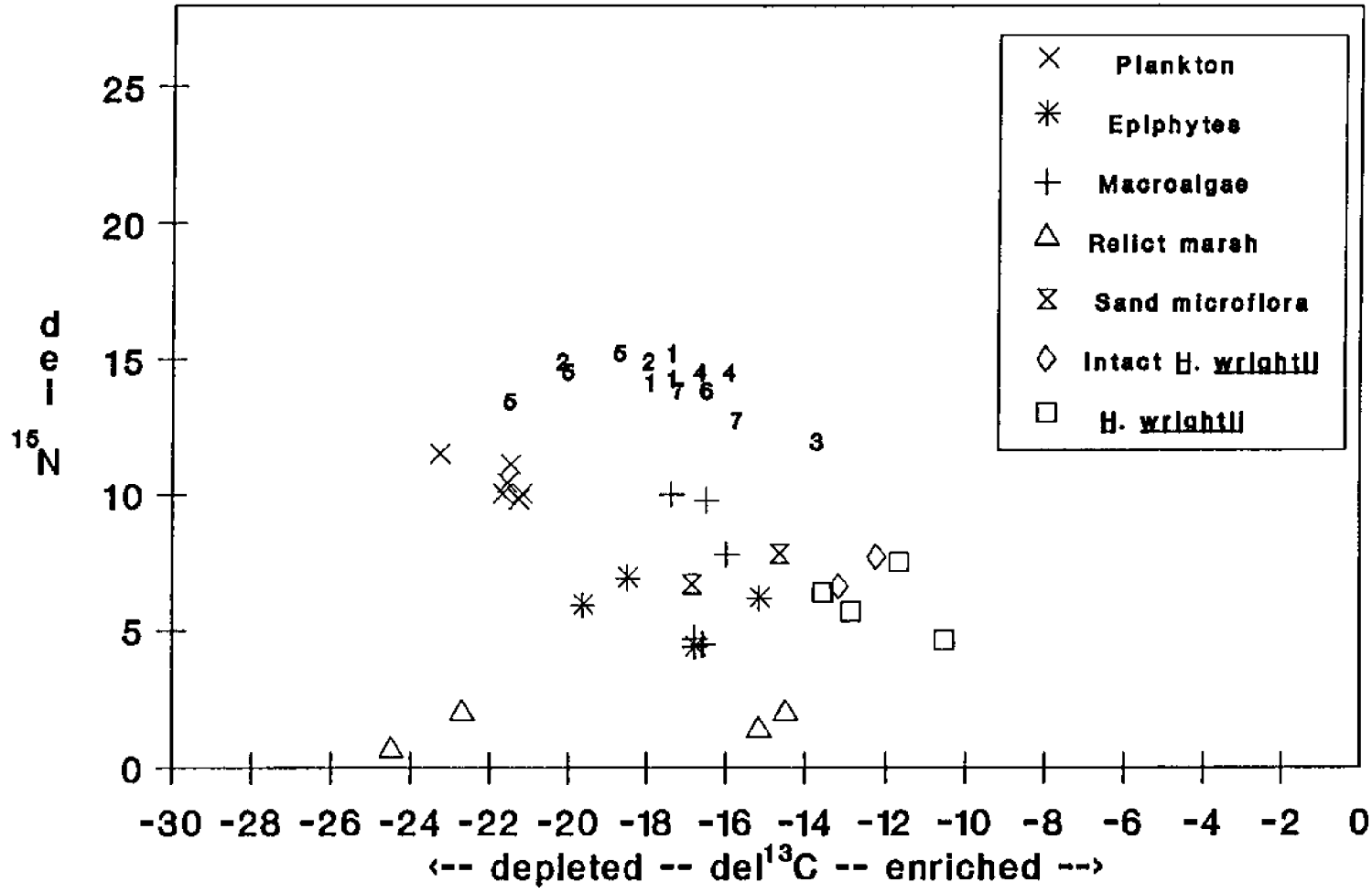
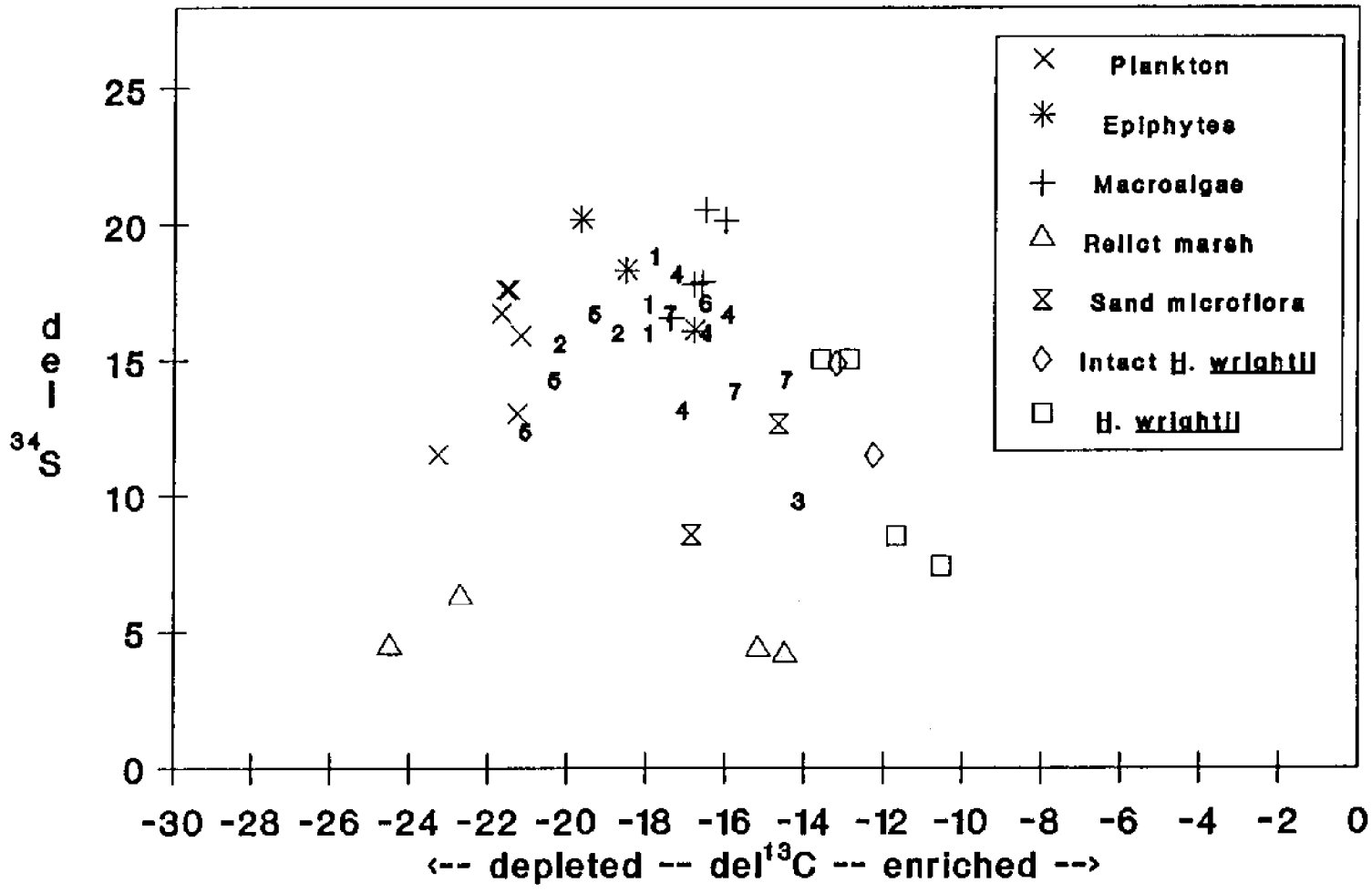

Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del ^{34}S
25
20
15
10
5
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del^{13}C -- enriched -->
Fish species group 1

Figure 23



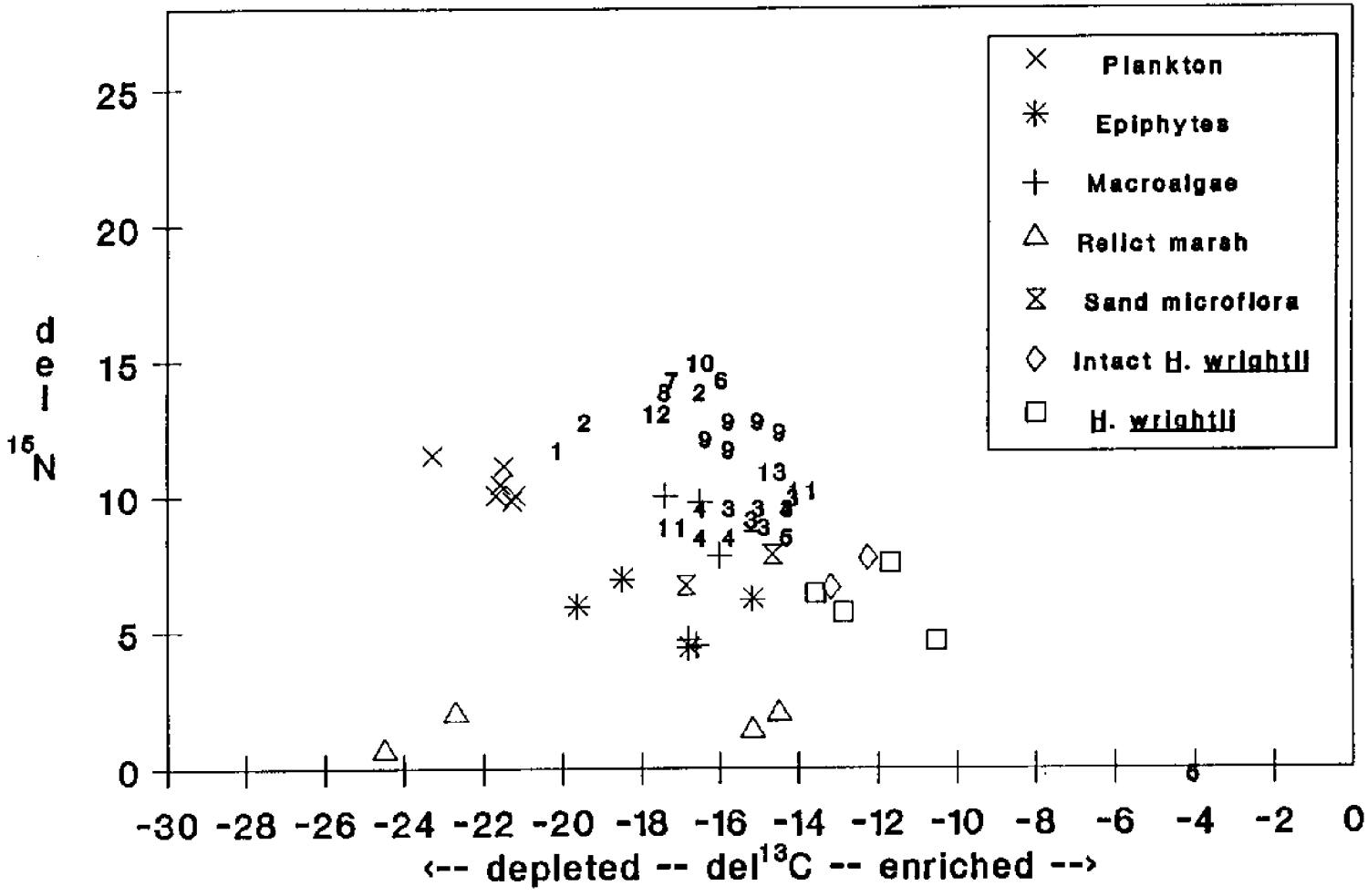
Fish species group 2

Figure 24



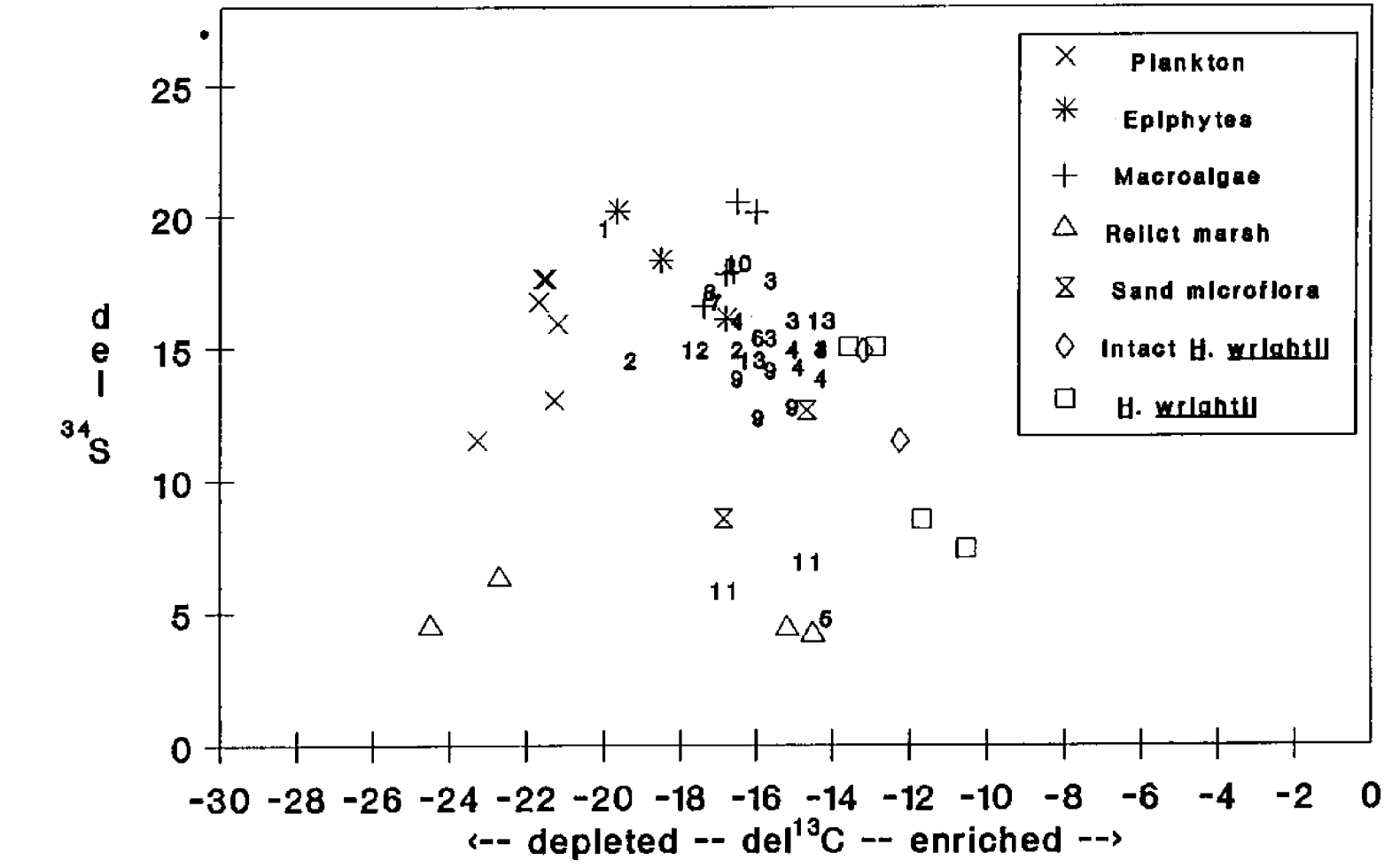
Fish species group 2

Figure 25



Crabs and other crustaceans

Figure 26


Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 34S
25
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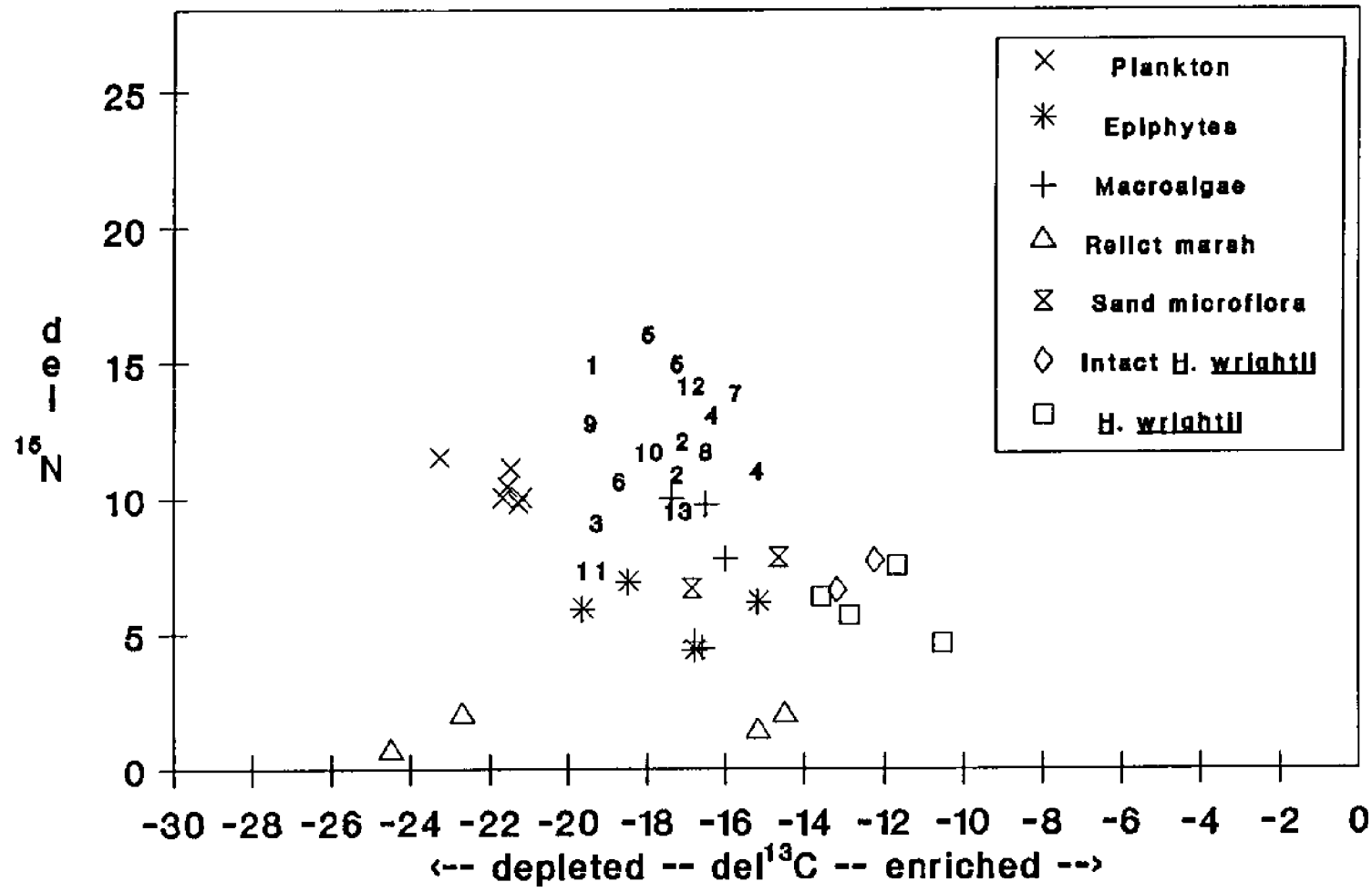
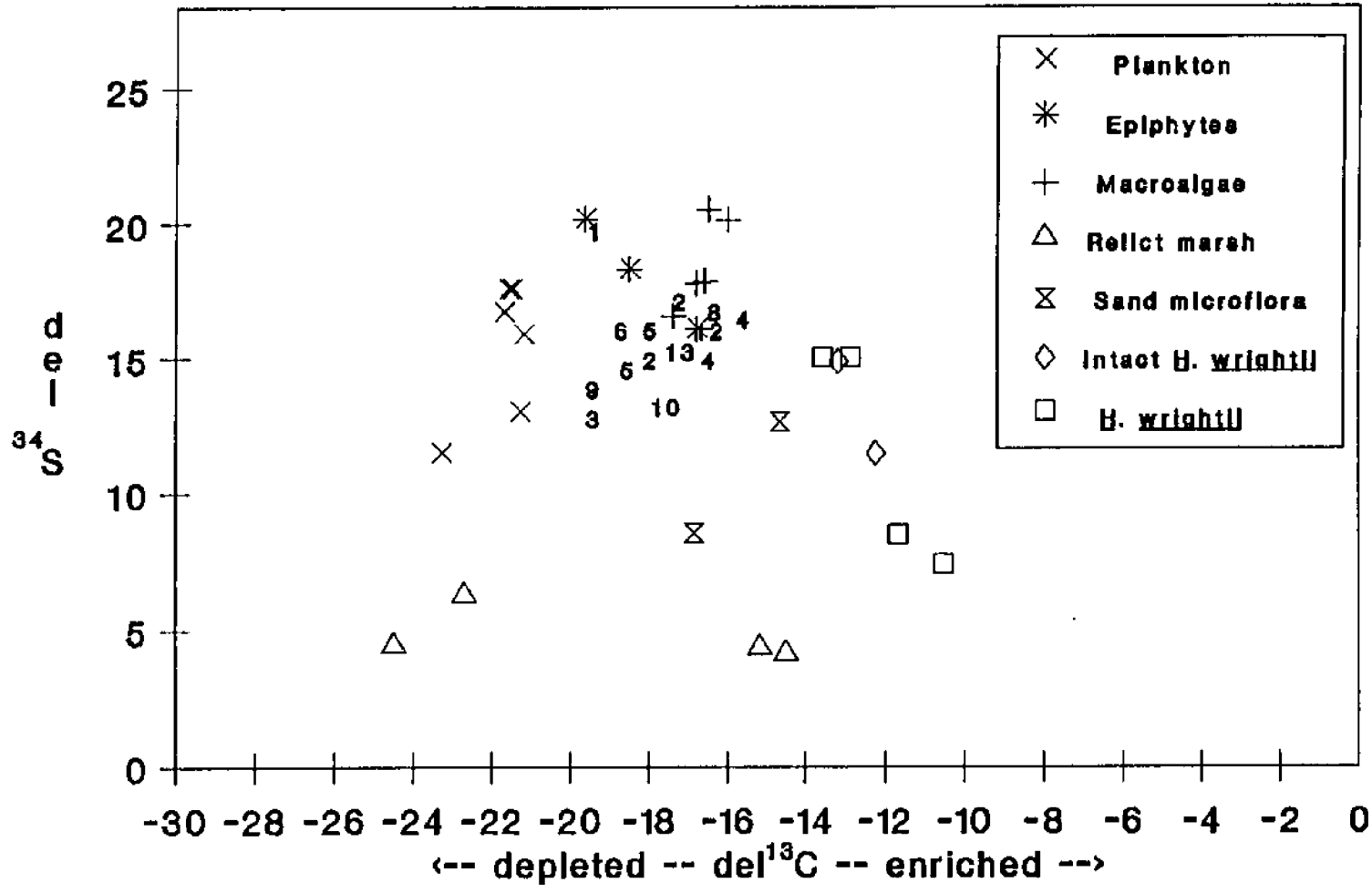
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Crabs and other crustaceans

Figure 27



Molluscs and other Invertebrates

Figure 28


Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 34S
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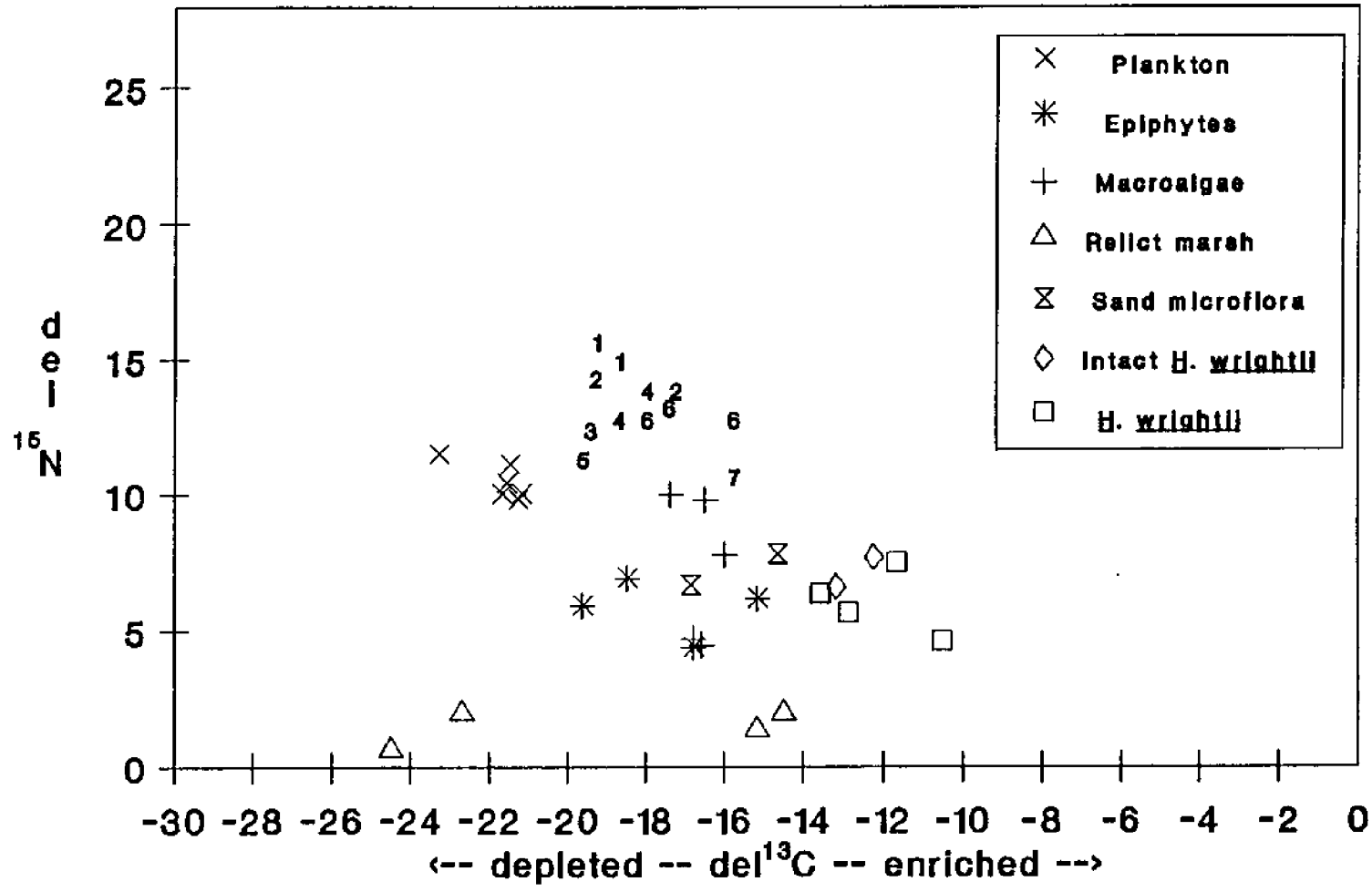
0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Molluscs and other invertebrates

Figure 29


Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
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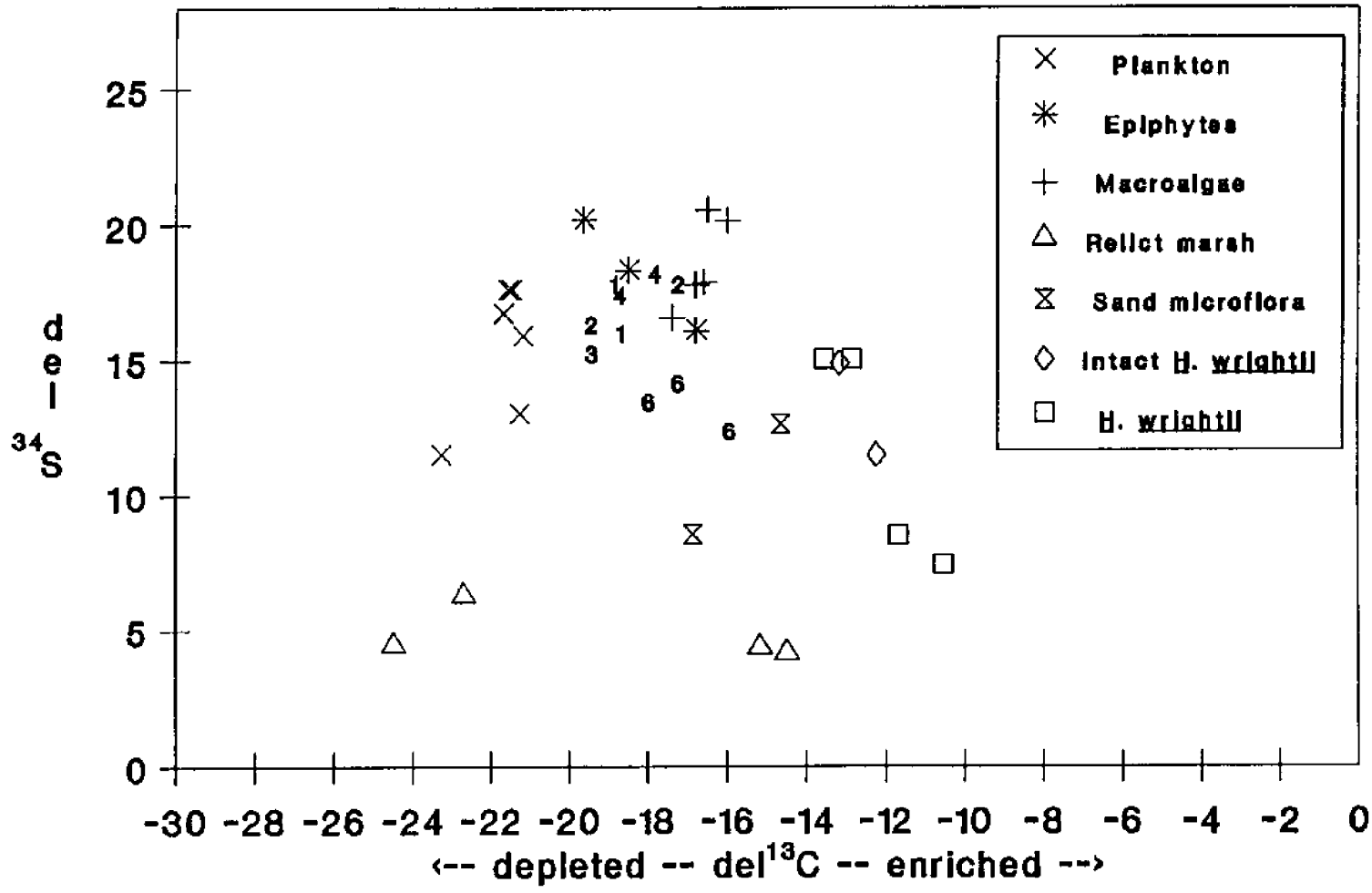
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Planktivorous fish

Figure 30


Plankton
Epiphytes
Macroalgae
Relict marsh
Sand microflora
Intact H. wrightii
H. wrightii
del 34S
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0
-30 -28 -26 -24 -22 -20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0
<-- depleted -- del13C -- enriched -->
Planktivorous fish

Figure 31

APPENDIX A

STABLE ISOTOPE SAMPLE RECORD

Sample Number	Type and Date	$\delta^{13}C$ (PDB)	$\delta^{15}N$ (air)	$\delta^{34}S$ (CDT)
1	Sargassum natans, Petit Bois Island, 30-V-91	-16.8	+4.7	+17.8
2	Sargassum fluitans, Petit Bois Island, 30-V-91	-16.6	+4.5	+18.0, +17.8
3	Solidago sempervirens CONTROL(#229)	-26.5, -26.6	+4.3, +4.0	+12.5
4	Plankton sample Petit Bois Island, 30-V and 4-VI-91	-23.3, -23.3	+8.5, +7.9	+11.5
5	Mysids, BPL's 1 and 2, 30-VII-91	-14.7	+10.5	+6.9, +6.7
6	Composite Halodule wrightii **epiphyte sample** (^{14}C study)	-18.5	+6.9	+18.3
7	Composite Halodule wrightii sample (^{14}C study)	-12.9	+5.5, +5.8	+15.0
8	Additional Halodule wrightii (1988 material)	-13.6	+6.2, +6.5	+15.0
9	Lagodon rhomboides, Cat Island, 16-X-91	-17.5	+13.6	+12.8
10	Lagodon rhomboides, 18-IX-91	-16.2	+12.6	+11.6
11	Lagodon rhomboides, 17-IX-91	-15.6	+11.6	+9.4
12	Arius felis #2, 18-IX-91	-15.4	+12.1	+11.5
13	Arius felis #2, 17-IX-91	-17.1	+12.9	+10.6
14	Arius felis #1, 17-IX-91	-16.3	+12.3	+10.6
15	Arius felis #1, 18-IX-91	-14.9	+11.0	+7.5, +7.9
16	Trachinotus carolinus #3, 26-IX-91	-21.0	+11.7	+15.7

17	Trachinotus carolinus #2, 26-IX-91	-21.0	+11.5	+15.1
18	Trachinotus carolinus #1, 26-IX-91 (least oily)	-20.3	+12.5	+17.2, +17.7
19	Pomatomus saltatrix #3, 26-IX-91 (least oily)	-17.8	+16.6, +16.5	+14.9
20	Pomatomus saltatrix #2, 26-IX-91 (oiliest)	-19.5	+14.8	+15.1
21	Pomatomus saltatrix #1, 26-IX-91	-19.5	+15.5	+14.9
22	Mugil cephalus #3, Cat Island, 16-X-91	-14.7	+10.2	+8.8
23	Mugil cephalus #2, Cat Island, 16-X-91	-14.5, -14.4	+10.7	+11.0
24	Mugil cephalus #1, Cat Island, 16-X-91	-14.6	+9.6, +9.6	+7.4, +8.0
25	Trachypeneus similis, n=33, trawls, 3-X-91	-18.2	+11.5	+12.9
26	Ancyclopsetta quadrocellata #2, trawls, 3-X-91	-16.9	+14.0	+13.9
27	Ancyclopsetta quadrocellata #1, trawls, 3-X-91	-15.1	+13.4	+13.3
28	Penaeus duorarum, n=3, trawls, 3-X-91	-17.2	+10.9	+11.0, +11.1
29	Mugil curema, 17-IX-91	-14.8	+10.3	+9.5
30	Mugil curema #3, 14-X-91	-16.8	+12.3	+14.4
31	Mugil curema #2, 14-X-91	-16.7	+11.6	+13.7
32	Mugil curema #1, 14-X-91	-12.7 -12.7	+8.9, +8.4	+8.2, +8.0
33	Penaeus duorarum #3 and #4 (comb.), trawls, 3-X-91	-16.7	+10.8	+10.6
34	Penaeus duorarum #2, trawls, 3-X-91	-16.1	+11.8	+13.1

35	Penaeus duorarum #1, trawls, 3-X-91	-16.4	+11.6	+12.3
36	Busycon contrarum, 1-VI-89	-16.9	+11.9	+16.1
37	Busycon contrarum, 30-VI-89	-17.3	+11.2	+17.2
38	Cynoscion arenarius, trawls, 3-X-91	-21.6, -21.8	+13.2	+16.7
39	Orthopristis chrysoptera #2, trawls, 3-X-91	-16.2	+13.1	+12.1, +11.9
40	Orthopristis chrysoptera #1, trawls, 3-X-91	-16.7	+13.9	+13.4
41	Prionotus tribulus, n=1, trawls, 3-X-91	-16.5	+13.6	+13.4
42	Prionotus tribulus, n=6, trawls, 3-X-91	-16.6	+13.4	+15.4
43	Clibanarius vittatus, n=9, 18-IX-91	-14.7	+9.1, +9.0	+14.3
44	Polynices duplicatus, n=1, trawls, 3-X-91	-16.5	+11.4	+15.1
45	Gymnothorax ocellatus, trawls, 3-X-91	-17.5	+14.4	+14.0
46	Diplectrum formosum, n=4, trawls, 3-X-91	-17.1	+14.2	+16.2
47	Sphyrna tiburo, 17-IX-91	-16.8	+14.5	+16.7
48	Sphyrna tiburo #2, 18-IX-91	-16.8	+14.5	+15.0
49	Sphyrna tiburo #1, 18-IX-91	-16.3	+14.6	+16.2
50	Sphyrna tiburo, 26-IX-91	-15.3	+14.3, +14.3	+14.3
51	Limulus polyphemus, 30-VI-90	-15.8	+12.0	+13.5
52	Dasyatis sabina, shoreline, 24-IX-91	-16.2	+11.7	+13.7
53	Lutjanus campechanus, 26-IX-91	-17.0	+13.8	+13.1

54	Rhizoprionodon terraenovae #3, 26-IX-91	-17.4	+14.9	+16.0
55	Rhizoprionodon terraenovae #2, 26-IX-91	-16.2	+14.8	+14.8
56	Rhizoprionodon terraenovae #1, 26-IX-91	-17.0	+14.6	+14.9
57	Scomberomorus maculatus, 18-IX-91	-17.7	+15.1, +15.1	+16.4, +16.1
58	Sciaenops ocellata #2, 26-IX-91	-17.5	+10.5, +10.6	+6.0, +6.4
59	Sciaenops ocellata #1, 26-IX-91	-14.8, -15.0	+12.2	+7.1, +7.1
60	Cynoscion nebulosus #1, 26-IX-91	-17.3	+14.4	+11.2
61	Cynoscion nebulosus #2, 26-IX-91	-17.8	+14.8	+13.3
62	Cynoscion nebulosus #3, 26-IX-91	-17.5	+14.7	+12.7
63	Lutjanus griseus #1, 26-IX-91	-20.4	+14.6	+14.1
64	Lutjanus griseus #2, 26-IX-91	-21.1 -21.3	+13.6, +13.2	+12.1
65	Lutjanus griseus #3, 26-IX-91	-18.8	+15.3	+15.9
66	CONTROL - Menidia beryllina sample #364 ('87-'88 SGP)	-20.5	+12.8, +13.0	+13.7
67	CONTROL - Sphyrna tiburo, sample #48	-16.0	+14.1	+15.0
68	Arius felis #1, 26-IX-91, 47 cm; muscle tissue	-18.0	+14.6	+16.0
69	Chaetodipterus faber, 11 cm juvenile, 26-IX-91	-20.3	+15.3	+15.4
70	Elops saurus #1, 26-IX-91, 23 cm	-17.0	+11.1	+9.6

71	Arius felis #1, as above, 26-IX-91, liver tissue (No. 68)	-19.3	+13.6	+16.2
72	Elops saurus #2, 26-IX-91, 23 cm	-20.8, -21.0	+11.2	+7.0
73	Elops saurus #3, 26-IX-91, 25.5 cm	-18.0	+14.1	+11.8
74	Arius felis #2, 26-IX-91, 31.5 cm, muscle tissue	-17.3, -17.0	+15.2	+14.7
75	Arius felis #3, 26-IX-91, 31.5 cm, muscle tissue	-18.9	+15.2	+15.3
76	Arius felis, **liver**, combined sample for Nos. 75 and 76	-19.0	+14.2	+15.6
77	Arius felis, juvenile, 26-IX-91, 18.0 cm	-16.0	+12.6	+8.5
78	Arius felis, juvenile, n=2, 26-IX-91	-15.9	+12.6	+7.2
79	Chloroscombrus chrysurus #1, 26-IX-91, 17 cm	-17.6	+14.9	+16.7
80	C. chrysurus #2, 26-IX-91, 16 cm, female with eggs	-17.9	+14.3	+16.9
81	C. chrysurus #3, 26-IX-91, 16.5cm, female with eggs	-17.8	+14.3	+18.7
82	Micropogon undulatus, 26-IX-91, 16 cm, female with eggs	-22.9, -23.1	+12.2	+15.2
83	Leiostomus xanthurus, 26-IX-91, from gut of Cynoscion nebulosus #1	-18.7	+14.1	+15.1
84	Libinia emarginata, n=2, trawls, 3-X-91 (females)	-17.3	+13.6	+17.1
85	Libinia dubia, n=2, trawls, 3-X-91 (male and female)	-17.2	+13.9	+16.6
86	Hepatus epheliticus, 3-X-91, trawls, 89 mm female	-16.1	+14.1	+15.8
87	Menippe mercenaria, 3-X-91, trawls, 74 mm female	-16.5	+14.1	+18.0

88	Limulus polyphemus #1, 26-IX-91	-14.8, -15.0	+11.9	+12.6
89	L. polyphemus #2, 26-IX-91, female with many eggs	-15.6	+12.7	+13.6
90	L. polyphemus #3, 26-IX-91	-15.9	+11.6	+12.2
91	L. polyphemus #4, 26-IX-91	-16.4	+12.1	+13.6
92	Limulus eggs, from No. 89, 26-IX-91	-18.2, -18.2	+12.1	+11.4
93	Mercenaria campechiensis, 5-IV-90	-18.5	+10.8	+15.6
94	Squilla empusa, n=12, trawls, 3-X-91	-16.3	+12.8	+14.6
95	CONTROL - Sphyrna tiburo #2 (No. 48)	-16.0	+14.0	+15.4
96	Mysids, BPL's, 24-IX-91	-17.1	+8.6	+5.8
97	Menidia beryllina, n=29, 12-VIII-91, Petit Bois Island	-16.0	+12.4	+12.4
98	Lutjanus campechanus, juveniles, n=9, trawls, 3-X-91	-17.1	+14.4	+17.8
99	Lutjanus campechanus, juveniles, n=2, trawls, 3-X-91	-16.2	+14.2	+16.6
100	Lutjanus synagris, juveniles, n=3, trawls, 3-X-91	-16.7	+14.2	+16.9
101	Menticirrhus americanus, 3-X-91, trawls, juvenile, 13.8 cm	-16.9	+14.3	+16.1
102	Synodus foetens, n=2, 3-X-91 trawls	-16.5	+14.6	+17.8
103	Strongylura marina, 30-VII-91, beach seines	-19.9	+14.6	+17.6
104	Lagodon rhomboides, 30-VII-91, beach seines	-17.0	+12.2	+14.3
105	Lagodon rhomboides, juv., n=6, 30-VII-91, beach seines	-16.3	+11.9	+11.7

106	Menidia beryllina, n=30, 30-VII-91, beach seines	-17.9	+13.0	+13.5
107	Harengula pensacolae, n=20, 30-VII-91, beach seines	-17.4	+13.7	+17.8
108	Menidia beryllina, n=10, 30-VII-91, beach seines	-17.3 -17.3	+13.7	+14.0
109	CONTROL - Sphyrna tiburo #1 (No. 49), 18-IX-91	-16.7	14.6 14.4	15.7
110	CONTROL - Solidago sempervirens ('87-'88 SGP, #299)	-26.6	3.8	13.4
111	Enteromorpha spp., 1-VII-92	-16.5	9.8	20.6
112	Plankton sample, 26 and 153 µm nets, 10-VII-92	-21.5	11.1	17.6
113	Plankton sample #2, 26 µm net, 10-VII-92	-21.3	9.8	13.0
114	Plankton sample #1, 26 µm net, 10-VII-92	-21.6	10.4	17.6
115	Plankton sample #2, 153 µm net, 10-VII-92	-21.7	10.0	16.7
116	Plankton sample #1, 153 µm net, 10-VII-92	-21.2	10.0	15.9
117	Dasyatis sabina #1, 31-VII-92	-15.4	12.2	9.4
118	Dasyatis sabina #2, 31-VII-92	-16.2	11.7	13.9
119	Dasyatis sabina #3, juvenile, 31-VII-92	-17.0	13.3	11.4
120	Clibanarius vittatus, 6 & 7-VIII-92, n=16	-15.4	9.4	15.2
121	Clibanarius vittatus, 6 & 7-VIII-92, n=21	-15.5	9.3	15.5
122	Harengula jaguana, juv., n=200, 6-VIII-92, beach seines	-19.0	12.6	17.7
123	Emerita talpoida, individuals ~2cm, n=13, 7-VIII-92	-15.1	9.0	14.5

124	Emerita talpoida, muscle tissue, individuals ≥2.5 cm, n=24, 7-VIII-92	-16.1	9.5	15.4
125	Fundulus similis, beach seines, n=10, 6-VIII-92	-14.0	11.8	9.6
126	Fundulus similis eggs, from fish in #125, n=9, 6-VIII-92	-15.1	10.9	10.0
127	Tozeuma carolinense, n=297, 30-VII-92 (BPL's)	-16.9	9.5	12.7
128	Penaeus aztecus, muscle, n=16, 30-VII-92 (BPL's)	-14.7	10.1	10.9
129	Halodule wrightii **and epiphytes**, 30-VII-92 (from BPL's)	-12.2	7.7	11.5
130	Halodule wrightii **and epiphytes**, 16-X-92, stems washed up along beach	-13.2	6.6	14.9
131	Peaty marsh material, beachfront, 16-X-92 (w/ large C. vittatus population)	-14.5	2.0	4.2
132	Peat/marsh residual, from beachfront, 15-X-92	-22.7	2.0	6.3
133	Emerita talpoida, n=54, beach sieves, individuals >1-≤1.5 cm, 16-X-92	-16.7	8.7	15.6
134	Emerita talpoida, individuals >2cm, beach sieves, 16-X-92	-15.0	8.9	15.2
135	Calliactis tricolor, with pagurids, n=13, 16-X-92	-15.5	11.1	16.6
136	Pagurus pollicaris, n=16, muscle, 16-X-92	-14.8	10.9	15.5
137	Clibanarius vittatus, n=3, grass beds, muscle, 15 & 16-X-92	-14.7	9.6	15.8
138	Clibanarius vittatus, n=4, beachfront, muscle, 15 & 16-X-92	-14.9	10.5	16.1

139	Menticirrhus americanus, 29 cm, female with eggs, 16-X-92	-14.7	14.2	14.2
140	Clibanarius vittatus, n=28, beachfront, muscle only, 16-X-92	-15.5	9.5	17.4
141	Enteromorpha spp., attached to substrates along beachfront, 15-X-92	-16.0	7.8	20.2
142	Aurelia aurita, in H_2O column, 16-X-92, n~=12	-19.5	14.9	19.6
143	Haustoriidae, beach sieves, n>100, 7-VIII-92	-14.3	8.4	4.4
144	Polychaetes, combined from sieves, 7-VIII-92 & 16-X-92	-17.7	11.6	13.5
145	Emerita talpoida, individuals <1cm length, beach sieves, 7-VIII-92 & 16-X-92	-15.6	8.7	15.0
146	Emerita talpoida, individuals ~1cm length, beach sieves, 7-VIII-92	-14.9	8.9	13.8
147	Emerita talpoida, individuals ≥2 cm length, beach sieves, 7-VIII-92	-14.5	9.0	14.5
148	Emerita talpoida, individuals ~1.5 cm length, beach sieves, 7-VIII-92	-14.6	8.7	13.3
149	**CONTROL**, Sphyrna tiburo #49 & #109	-15.5	13.9	15.9
150	**CONTROL**, Sphyrna tiburo # 49	-16.6	14.8	13.6
151	Mellita quinquiesperforata tests (cleaned), 9-VII & 16-X-92, grass beds, n=48	-16.8	6.3	ins.
152	Anguinella palmata, 29-VII-92, H_2O column	-19.2	9.0	14.3
153	Gracilaria verrucosa, 29-VII-92, beds & H_2O column	-17.4	10.0	16.5

154	Anchoa mitchilli, 23-XI-92, trawls, n=75	-19.3	15.0	16.4
155	Squilla empusa, 23-XI-92, trawls, n=11	-17.5	13.4	14.5
156	Trachypenaeus similis, 23-XI-92, trawls, n=28	-17.8	12.2	13.9
157	Trachypenaeus similis, 23-XI-92, trawls, n=10	-17.7	11.5	12.9
158	Trachypenaeus similis, 23-XI-92, trawls, n=26	-17.8	12.0	14.4
159	Penaeus setiferus, 23-XI-92, trawls, n=3	-19.6	11.4	12.2
160	Penaeus aztecus, 23-XI-92, trawls, n=12, rep. #1	-19.3	11.2	12.2
161	Penaeus duorarum, 23-XI-92, trawls, n=1	-16.2	10.9	13.6
162	Penaeus aztecus, 23-XI-92, trawls, n=12, rep. #2	-19.2	11.8	12.4
163	Mellita quinquiesperforata, 9-VII & 16-X-92, grass beds, n=51, soft tissues	-16.9	6.6	8.6
164	Diplectrum bivitattum, 23-XI-92, trawls, n=14	-17.8	13.6	14.6
165	Symphurus plagiusa, trawls, 23-XI-92, n=5	-18.8	12.8	13.3
166	Lolligunculus brevis, 23-XI-92 trawls, n=33	-18.1	16.5	16.0
167	Citharichthys spilopterus, 23-XI-92 trawls, n=5	-17.3	13.0	15.0
168	Calliactis tricolor, 23-XI-92 trawls, n=9	-16.4	12.9	16.7
169	Halodule wrightii, cleaned, from beds, 10-VII-92	-11.7	7.5	8.5
170	**Epiphytes**, 10-VII-92, removed from H. wrightii from beds	-16.8	4.4	16.1

171	**Epiphytes**, 1-VII-92, removed from H. wrightii from beachfront	-19.6	5.9	20.2
172	Hippolytid shrimps, miscellaneous dates, primarily 1991 BPL's, n > 1500 individuals	-15.1	7.9	10.1
173	Non-clupeid larval fish, miscellaneous dates, 1991 BPL's, n=137	-15.7	10.2	ins.
174	Miscellaneous small shrimp, n=203, 24-IX-91 BPL's	-13.5	10.6	ins.
175	Larval clupeids, 30-VII & 3-X-91, n=35	-19.4	12.0	ins.
176	Menticirrhus americanus, 3-X-91 trawls, 10.1 cm juvenile, muscle tissue only	-15.9	12.7	13.7
177	Sicyonia brevirostris, 3-X-91 trawls, n=9	-16.4	10.9	14.4
178	Echeneis neucratoides, 26-X-91, stone crab trap	-17.4	14.0	14.2
179	Tellina alternata, 1-VI-89, vicinity of grass beds (n=1)	-19.2	7.5	ins.
180	Monocanthus setifer, trawls, 3-X-91, n=2	-17.0	12.8	15.8
181	Balistes capricus, trawls, 3-X-91, n=1	-16.7	11.9	15.8
182	Pagurus pollicaris, 3-X-91 trawls, n=9	-16.4	12.2	14.5
183	Trachinotus carolinus, 30-VII-91 seines, n=4 (juveniles)	-15.4	13.1	11.5
184	Trachypenaeus constrictus, 3-X-91 trawls, n=9	-15.7	11.0	13.7
185	Prionotus tribulus,23-XI-92 trawls, n=1	-16.5	13.1	13.8
186	Synodus foetens, 23-XI-92 trawls, n=3	-17.4	15.9	16.2

187	Arius felis, 23-XI-92 trawls, n=15	-19.9	15.7	14.1
188	Anchoa nasuta, 23-XI-92 trawls, n=9	-19.2	14.7	16.4
189	Leiostomus xanthurus,23-XI-92 trawls, n=2	-15.7	12.7	12.6
190	Micropogon undulatus, 23-XI-92 trawls, n=3	-17.3	13.2	12.9
191	Lagodon rhomboides, 10-VII & 23-XI-92, n=3	-15.2	11.1	13.4
192	Trachypenaeus constrictus, 23-XI-92 trawls, n=20	-17.6	11.8	12.7
193	Hepatus epheliticus, 23-XI-92 trawls, 80 mm	-16.2	14.1	ins.
194	Cynoscion arenarius, 23-XI-92 trawls, n=2	-20.2	15.1	16.2
195	Anchoa nasuta, 3-X-91 trawls, n=14	-17.6	13.8	17.6
196	Anchoa mitchilli, 3-X-91 trawls, n=44	-18.8	14.6	16.9
197	Sphoeroides parvus, 3-X-91 trawls, n=10	-17.2	13.5	14.8
198	Mugil curema, 10-VII-92 seines, n=2	-17.4	6.0	2.2, 2.4
199	Symphurus plagiusa, 3-X-91 trawls, n=8	-17.5	12.6	12.8
200	Citharichthys spilopterus, 3-X-91 trawls, n=10	-16.6	12.7	14.9
201	Citharichthys spilopterus, 3-X-91 trawls, 103 mm	-16.5	13.7	16.3
202	Chaetodipterus faber, 26-IX & 3-X-91, n=2	-18.0	14.4	16.3
203	Brevoortia patronus, 3-X-91 trawls, 102 mm	-19.6	11.9	14.9
204	Lolliguncula brevis, 3-X-91 trawls, n=15	-17.5	14.9	15.4

205	Diplectrum bivittatum, 3-X-91 trawls, n=15	-17.3	13.2	16.2
206	Eucinostomus argenteus, 3-X-91 trawls, n=17	-17.8	12.5	11.7, 11.2
207	Pisania tincta, 26-IX-91, stone crab traps, n=29	-19.2	12.6	13.7
208	Thais haemastoma, 26-IX-91, stone crab traps, n=20	-16.6	13.5, 13.8	15.7
209	Nassarius vibex, 5-IV-90, in beds on blades, n=79	-16.3	14.1	ins.
210	Crepidula plana, miscellaneous dates, n=177	-19.3	8.7	13.0
211	Micropogon undulatus, 3-X-91 trawls, n=1	-19.9	12.7	12.4
212	Leiostomus xanthurus, 3-X-91 trawls, n=1	-17.8	13.8	13.6
213	Peat/marsh residual, 15-X-92 (REPEAT, #132)	-24.6, -24.4	0.5, 0.8	4.5
214	Peat/marsh residual, 16-X-92 (REPEAT, #131)	-15.2	1.4	4.4
215	**CONTROL** - Sphyrna tiburo sample #49	-16.4	14.2, 14.0	15.7
216	Seagrass substrate, 7-VIII-92	-14.7	7.8	12.6
217	Halodule wrightii, 1991 material	-10.6, -10.5	4.6, 4.6	7.4
218	**Epiphytes**, 1991 material	-15.2	6.3, 6.1	ins.
219	Luida clathrata, 30-VI-89, n=7	-17.3	9.3	15.4
220	Callinectes sapidus, 3 females, 26-IX-91, 127-165 mm, stone crab traps	-19.2	12.6	14.5
221	Portunus gibbesii, 3-X-91 trawls, n=18, 40-51 mm	-17.3	13.2	15.1

222	Chelonibia patula, 26-IX-91, on backs of C. sapidus (#220), n=25	-20.1, -20.0	11.8, 11.6	19.5
223	Callinectes sapidus, 3-X-91 trawls, 55-56 mm, n=8	-16.7	13.5	14.8
	AVERAGE VALUES FOR ALL CONSUMER SAMPLES	-17.1 ± 1.7	12.5 ± 2.0	13.8 ± 2.9