

Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses

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ABSTRACT: Multiple stable isotope analyses were employed to examine food web dynamics in a northern Gulf of Mexico seagrass system in which epiphytic algae were the single most important primary productivity component, being responsible for 46 and 60 % of total system and benthic primary production, respectively. The seagrass *Halodule wrightii* Ascherson contributed only 13 % to total system primary production on an annual basis. Stable isotope ratios of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) were measured for producer and consumer samples collected from May 1989 through November 1992. Epiphytes and leaves of *H. wrightii* had distinct $\delta^{13}\text{C}$ values (-17.5 vs -12‰ , respectively) as well as distinct $\delta^{34}\text{S}$ values ($+18$ vs $+11\text{‰}$, respectively). $\delta^{13}\text{C}$ values for the sand microflora, occasional macroalgae, and phytoplankton were -16 , -17 , and -22‰ , respectively; $\delta^{15}\text{N}$ values were lowest for epiphytes and *H. wrightii* ($+6\text{‰}$) and highest for phytoplankton ($+10\text{‰}$). Virtually all consumers had $\delta^{13}\text{C}$ values that fell within a narrow range of -20 to -15‰ , which included all $\delta^{13}\text{C}$ values of epiphytes and the sand microflora but none of those for either *H. wrightii* or phytoplankton. Values for $\delta^{15}\text{N}$ for consumers fell within a range of $+8$ to $+16\text{‰}$, spanning herbivorous species with diets of microalgae to carnivorous species feeding at secondary to tertiary levels in the local food webs. Consumer values for $\delta^{34}\text{S}$ ranged from $+4$ to $+20\text{‰}$ (mean = 14.2‰), and indicate a stronger influence of seawater-derived sulfate than sediment-associated sulfides. The stable isotope data, in combination with measured high biomass and primary production rates of the epiphytic algae, strongly suggest that these algae are the primary source of organic matter for higher trophic levels in seagrass beds of Mississippi Sound. The contribution of *H. wrightii* to the food web appears to be minimal. The overall picture that has emerged based on the present and previous stable isotope studies is one of the major trophic importance of benthic microalgae (i.e. epiphytic and sediment-associated) in seagrass beds.

KEY WORDS: Multiple stable isotope analyses · Food web · Seagrass · Trophic relationships

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INTRODUCTION

Seagrass beds constitute 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. A

diverse and highly productive epiphytic assemblage, composed mainly of microscopic algae, is attached to the seagrass leaf blades. This assemblage is dominated by various species of diatoms and red, brown, and green algae, and cyanobacteria (Humm 1964, Ballantine & Humm 1975, Sullivan 1979, Thursby & Davis 1984). Sediments beneath and adjacent to the seagrass beds are covered with a microfloral community populated primarily by species of small pennate diatoms

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(Daehnick et al. 1992). 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 fishes (Kitting 1984, Kitting et al. 1984, Morgan & Kitting 1984, Jernakoff et al. 1996, Jernakoff & Nielsen 1997). Past research in coastal seagrass ecosystems 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. 1982a, 1987, Fry 1984, Kitting et al. 1984, Nichols et al. 1985, Gleason 1986, Dauby 1989, 1995, Stoner & Waite 1991, Klumpp et al. 1992, Pollard & Kogure 1993, Yamamuro 1999).

Although food webs in seagrass systems are complex, determination of ultimate food sources via multiple stable isotope analysis can be a powerful tool for studying trophic relationships in coastal ecosystems (Fry & Sherr 1984, Peterson et al. 1985, Fry et al. 1987, Peterson & Howarth 1987, Sullivan & Moncreiff 1990, Currin et al. 1995, Créach et al. 1997, Deegan & Garritt 1997, Kwak & Zedler 1997, Marguillier et al. 1997). The present study represents the first systematic application of the multiple stable isotope approach to study food webs in a seagrass system. The particular system in question included beds of *Halodule wrightii* Ascheron off Horn Island in Mississippi Sound. Moncreiff et al. (1992) found that microalgae (epiphytes, diatom-dominated sand microflora, and phytoplankton) were responsible for 87% of total system primary production in these beds, with *H. wrightii* contributing only 13% on an annual basis. Epiphytic algae were the single most important productivity component, being responsible for 46 and 60% of total system and benthic primary production, respectively. The high rates of microalgal production suggest that microalgae are the primary source of organic matter for higher trophic levels in this system, and this hypothesis has been tested in the present study using stable isotope ratios of carbon, nitrogen, and sulfur.

MATERIALS AND METHODS

Study area. Horn Island is 1 of 5 islands comprising the barrier island chain off the Mississippi coast, extending approximately 22 km from Dog Keys Pass at its western extremity (30° 15' N, 88° 45' W) to Horn Island Pass at its eastern end (30° 13' N, 88° 32' W) (Fig. 1). From the coastline south of Ocean Springs, the island lies 11 km offshore in Mississippi Sound, sepa-

rating the waters of the Sound from the Gulf of Mexico. Horn Island is hydrologically affected by drainage from the Biloxi Back Bay and the Biloxi and Pascagoula Rivers; degrees of influence are a function of discharge rates and prevailing winds. Astronomical tidal range is 0.6 m. Upland drainage from the island proper is negligible, 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. During the course of this study, the shallow water (<2 m) sand flats on the side of Horn Island bordering Mississippi Sound were populated exclusively by beds of *Halodule wrightii*.

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 most samples collected from June 1991 through November 1992 in the grass beds at the northwest end of the island (Fig. 1). These beds were fairly extensive and could be located under most environmental conditions; they were also in the same area as the beds used for the primary production measurements of Daehnick et al. (1992) and Moncreiff et al. (1992). *Halodule wrightii* collected during 1988 as a preliminary sample for biomass estimates prior to the latter study was also included; associated epiphyte material was insufficient for analysis.

Sample collection. All samples were placed in plastic bags or other containers 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. *Halodule wrightii* and its associated epiphytes were collected intact in the field. Macroalgae were collected whenever encountered in sufficient quantity. Plankton samples were collected with plankton nets with mesh sizes of 28 and 153 µm. Nets 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.

Sand microflora were very difficult to sample directly. We chose, instead, to represent the assemblage of diatoms and bacteria associated with the sand surface by a series of composite samples of the sand dollar *Mellita quinquiesperforata*. A similar approach was employed by Newell et al. (1995), who used microalgae from the stomach of the mudskipper *Boleophthalmus boddarti* as stable isotope material to represent collections of sediment microalgae. Our proxy samples consisted of muscle tissues only; gut

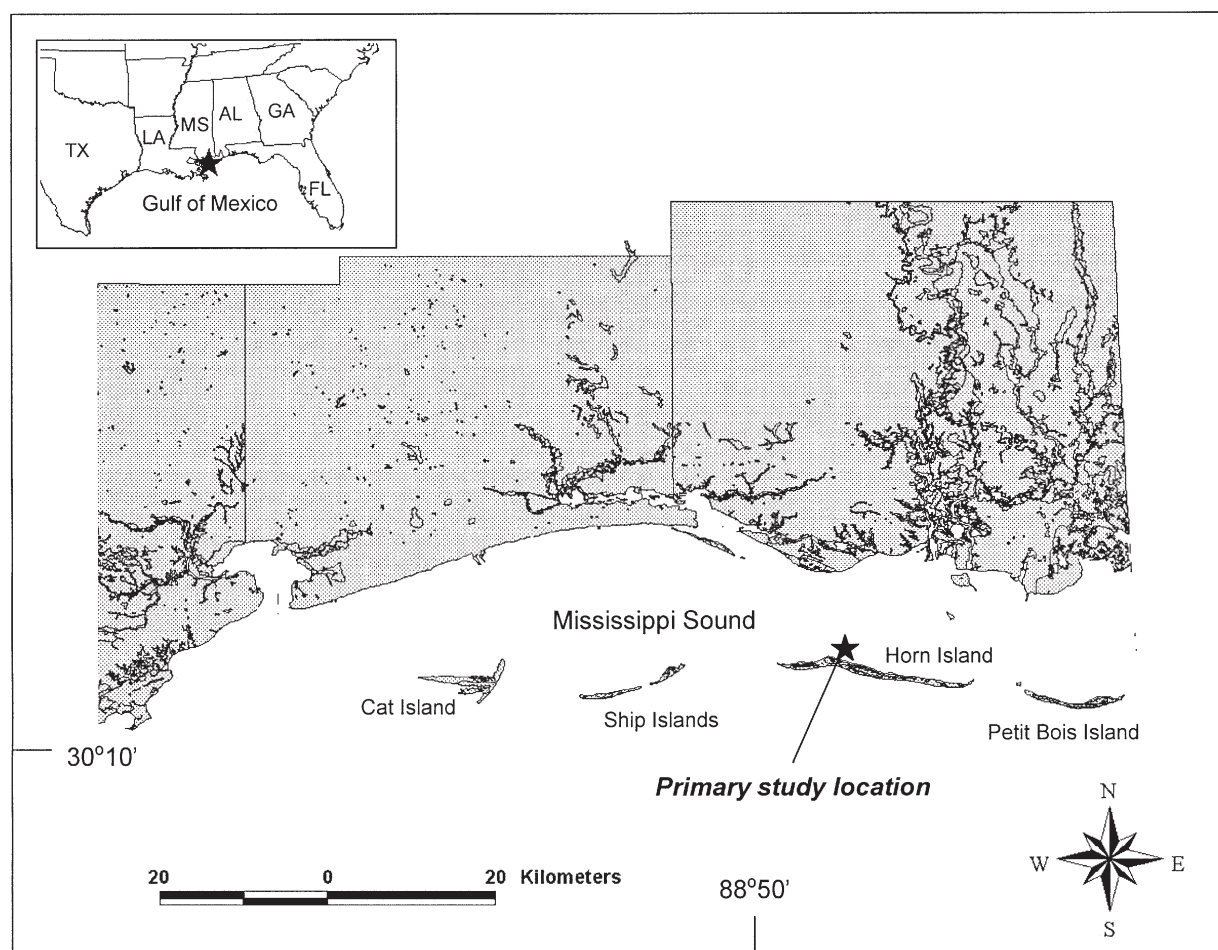


Fig. 1. Map of Mississippi Sound (USA) and the northern Gulf of Mexico indicating location of the study area

contents were discarded. Sand dollars have been reported to subsist on a diet consisting almost exclusively of sand-associated diatoms and bacteria (MacGinitie & MacGinitie 1949, Gosner 1971, Ruppert & Fox 1988). Sediment-associated bacteria have been shown to rely on carbon sources other than macrophyte carbon, perhaps using material of algal origin as their dominant carbon source (Boschker et al. 1999). A similar relationship could be expected in seagrass systems for bacteria also, so that any bacterial material ingested by *M. quinquiesperforata* should also have an algal-based isotopic signature. The $\delta^{13}\text{C}$ value for this organism was -16.9‰ , which was only slightly enriched compared to the mean $\delta^{13}\text{C}$ value for epiphytes. A second value for the diatom-dominated sand microflora was obtained from detritus-free substrate collected within seagrass beds; this material had a $\delta^{13}\text{C}$ value of -14.7‰ .

Consumers were collected using several different types of sampling gear to obtain individuals represen-

tative of as many microhabitats and trophic levels within the seagrass system as possible. To minimize contamination by shells or other foreign material, only live, intact organisms were included in the samples. Larger crustaceans were collected by hand from the grass beds and vicinity or in nets in conjunction with fish samples (penaeid shrimps, crabs). Smaller specimens (hippolytid shrimps *Tozeuma carolinense*) were collected using a beam plankton sampler (BPL), or by sieving sediments with a 1 mm-mesh polyethylene sieve (*Emerita talpoida*, Haustoriidae). Gastropods, bivalves, echinoderms (primarily the sand dollar *Mellita quinquiesperforata*), and bryozoans 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. Polychaetes were collected by sieving sediments through a 0.5 mm-mesh polyethylene sieve. Individual polychaetes were also collected when encountered singly in seagrass or macroalgal samples.

Fish species were collected using a variety of sampling gear, including a BPL, seines, trawls, gill nets, and cast nets.

Sample processing. All biological materials were gently rinsed with tap water to remove salts, followed by a final rinse with distilled water. In the laboratory, epiphytes were carefully scraped from fresh or frozen *Halodule wrightii* blades using a dull scalpel prior to drying. Microscopic examination showed that removal efficiencies were at least 95 % when working with material that had been previously frozen. Although time-consuming, the efficiency of epiphyte removal by scraping has been well documented (see Fig. 5 in Dauby & Poulicek 1995 and references therein). Macroalgae were sorted according to species and picked free of all visible meiofauna and detrital fragments. Plankton samples were examined to determine the dominant species composition, and all visible detrital material was manually removed from the samples with a fine forceps to obtain as pure a sample as possible. Cleaned plankton material was rinsed with 10 % HCl to remove any traces of CaCO₃ before rinsing with distilled water, and was then concentrated using a fine-mesh sieve (153 or 28 µm, depending on sample mesh size).

Consumer samples were carefully processed to minimize contamination with foreign material. Whenever possible, only muscle tissue was used to obtain consistent and comparable samples for each species or group. When contamination with CaCO₃ was likely, tissues were washed in 10 % HCl before rinsing with tap and distilled water. Although there are some questions regarding the use of HCl in processing tissues for stable isotope analysis (Bunn et al. 1995), removal of CaCO₃ as a contaminant was critical for some organisms, particularly gastropods that could only be sampled by crushing their shells. Chanton & Lewis (1999) reported no significant effects on C or N stable isotope ratios as a result of using HCl in tissue-sample processing. Any animal tissues that required acid washing were treated prior to drying and grinding, which has much less of an effect on stable isotope ratios (Bunn et al. 1995) and in most cases is not ecologically significant (Bunn et al. 1995, Chanton & Lewis 1999). Samples were then oven-dried to constant weight at 60°C.

Final processing was essentially 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 actual measurements of stable isotope ratios for all samples were performed by the Coastal Science Laboratories of Austin, Texas. The accuracy of the

δ¹³C, δ¹⁵N, and δ³⁴S analyses was 0.2, 0.2, and 0.5 parts per mil (‰), respectively. A minimum of 1 blind control was included with each set of samples sent to the Coastal Science Laboratories to test the repeatability of the determinations and to insure that samples were comparable over time.

Stable isotope values were determined via mass spectroscopy by comparing samples to known standards and recording the difference between the sample and the appropriate standard in parts per thousand or per mil (‰) according to the formula

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

where X is ¹³C, ¹⁵N, or ³⁴S, and R is ¹³C/¹²C, ¹⁵N/¹⁴N or ³⁴S/³²S. Standards for C, N, and S are Pee Dee belemnite, atmospheric diatomic nitrogen, and Canyon Diablo troilite, respectively.

Trophic levels were calculated for selected samples according to the approach of Hobson & Welch (1992) using values determined for this seagrass system, and their equation for the prediction of trophic level:

$$TL = 1 + (N_m - 7.0)/3.0 \quad (2)$$

where TL is the trophic level of the consumer, N_m is the δ¹⁵N 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.

RESULTS

Stable isotope ratios of producers

Stable carbon isotope ratios of *Halodule wrightii* and its associated epiphytes (mainly araphid and biraphid diatom taxa and the red alga *Acrochaetium flexuosum* Vickers) were distinct (Table 1). The mean δ¹³C value for *H. wrightii* was −12.2‰ (range = −13.6 to −10.6‰), while that for epiphytes was −17.5‰ (range = −19.7 to −15.2‰). Thus, there was very good separation between these critical samples. The sand microflora (almost exclusively small, pennate diatoms), represented by proxy samples of the sand dollar *Mellita quinquiesperforata* and by detritus-free, diatom-rich seagrass substrate, had an average δ¹³C value of −15.8‰, which was only slightly enriched compared to the mean δ¹³C value for epiphytes. Phytoplankton, represented by plankton samples consisting of a mixture of diatoms and copepods, had a mean δ¹³C value of −21.8‰, with a range of −23.3 to −21.2‰. Thus, phytoplankton values were reasonably well separated from those for epiphytes and particularly *H. wrightii* blades.

Macroalgal species had $\delta^{13}\text{C}$ values which ranged from -17.4 to -16.2 ‰; this range overlapped $\delta^{13}\text{C}$ values for epiphytes and sand microflora (Table 1).

Stable nitrogen isotope ratios were similar for *Halodule wrightii*, its epiphytes, and the sand microflora as mean values ranged from $+5.9$ to $+7.2$ ‰ (Table 1). The plankton samples had $\delta^{15}\text{N}$ values that were consistently higher than those of the above 3 producers (range = $+8.2$ to 11.1 ‰, mean = $+9.9$ ‰). $\delta^{15}\text{N}$ values for the macroalgae showed the greatest variability and ranged from $+4.5$ to 10.0 ‰, with a mean value of 7.0 ‰ for the 4 species.

Stable sulfur isotope ratios were much more variable than those for carbon or nitrogen (Table 1). The mean $\delta^{34}\text{S}$ value for *Halodule wrightii* was $+11.5$ ‰ and for its epiphytes $+18.2$ ‰. However, the range of these values was greater for the former (7.6 compared to 4.1 ‰). The sand microflora had the lowest $\delta^{34}\text{S}$ value ($+10.6$ ‰). The mean $\delta^{34}\text{S}$ value for the macroalgae was identical to that for epiphytes ($+18.2$ ‰) as was the range, whereas $\delta^{34}\text{S}$ values for phytoplankton (mean = $+15.4$ ‰, range = $+11.5$ to $+17.6$ ‰) were intermediate between those for *H. wrightii* and its epiphytes.

Stable isotope ratios of consumers

Table 2 summarizes the $\delta^{13}\text{C}$ data for consumers of the Horn Island seagrass beds; all values in this table are means. The individual $\delta^{13}\text{C}$ values for each of 186 consumer samples, as well as matching values for $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$, can be found in Appendix A of Sullivan & Moncreiff (1993); like values for all primary producer samples are also given here. Stable carbon isotope ratios for individual organisms ranged from -23.0 ‰ for the Atlantic croaker *Micropogon undulatus* to -12.7 ‰ for the white mullet *Mugil curema*. When averaged by species or sample type, a pooled sample of miscellaneous small shrimp species exhibited the highest $\delta^{13}\text{C}$ value (-13.5 ‰) and the white trout *Cynoscion arenarius* the lowest (-21.0 ‰). The mean $\delta^{13}\text{C}$ value for all consumers sampled was -17.3 ‰. A total of 129 out of 186 (70%) consumer samples in this system had $\delta^{13}\text{C}$ values falling within a range of -18.8 to -15.4 ‰. All but 13 of the 186 (93%) consumer samples fell within a range of -20.1 to -14.1 ‰. Neither of these ranges includes the mean $\delta^{13}\text{C}$ values of -12.2 and -21.8 ‰ for *Halodule wrightii* and phytoplankton, respectively. Tissues of consumer species mirror their diet with respect to $\delta^{13}\text{C}$, although enrichment of 1 ‰ may occur from one trophic level to the next (DeNiro & Epstein 1978, Fry 1984, Peterson et al. 1985, 1986, Currin et al. 1995).

Table 1. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values (‰) for primary producers in seagrass beds of Horn Island. \bar{x} = mean; SD = standard deviation; nd = not determined

Producer	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
<i>Halodule wrightii</i>			
1988 sample	-13.6	6.4	15.0
1989–90 sample	-12.9	5.7	15.0
1991 sample	-10.6	4.6	7.4
1992 sample	-11.7	7.5	8.5
\bar{x}	-12.2	6.0	11.5
SD	1.2	1.1	3.5
Epiphytic algae			
1989–90 sample	-18.5	6.9	18.3
1991 sample	-15.2	6.2	nd
1992 sample	-16.8	4.4	16.1
1992 sample	-19.7	5.9	20.2
\bar{x}	-17.5	5.9	18.2
SD	1.7	0.9	2.1
Sand microflora proxies			
<i>Mellita quinquiesperforata</i> (1992)	-16.9	6.7	8.6
Diatom-rich seagrass substrate (1992)	-14.7	7.8	12.6
\bar{x}	-15.8	7.2	10.6
SD	1.1	0.6	2.0
Phytoplankton			
1991 sample	-23.3	8.2	11.5
1992, 28 μm	-21.3	9.8	13.0
1992, 28 μm	-21.6	10.4	17.6
1992, 153 μm	-21.7	10.0	16.7
1992, 153 μm	-21.2	10.0	15.9
1992, mixed	-21.5	11.1	17.6
\bar{x}	-21.8	9.9	15.4
SD	0.7	0.9	2.3
Macroalgae			
<i>Enteromorpha</i> sp.	-16.2	8.8	20.4
<i>Sargassum natans</i>	-16.8	4.7	17.8
<i>Sargassum fluitans</i>	-16.6	4.5	17.9
<i>Gracilaria verrucosa</i>	-17.4	10.0	16.6
\bar{x}	-16.8	7.0	18.2
SD	0.5	2.8	1.6

Stable nitrogen isotope ratios, indicative of trophic level, ranged from $+6.0$ ‰ for the white mullet *Mugil curema* (a different specimen from that producing the lowest $\delta^{13}\text{C}$ value) to $+16.6$ ‰ for the bluefish *Pomatomus saltatrix* for individual organisms. Averaging $\delta^{15}\text{N}$ values for consumers by species or sample type showed the bivalve *Tellina alternata* to occupy the lowest trophic position at 7.5 ‰, and the estuarine squid *Lolliguncula brevis* with a value of 15.7 ‰ to occupy the highest position (Table 2). The mean $\delta^{15}\text{N}$ value for all consumers sampled was $+12.5$ ‰.

Hobson & Welch (1992) employed $\delta^{15}\text{N}$ 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

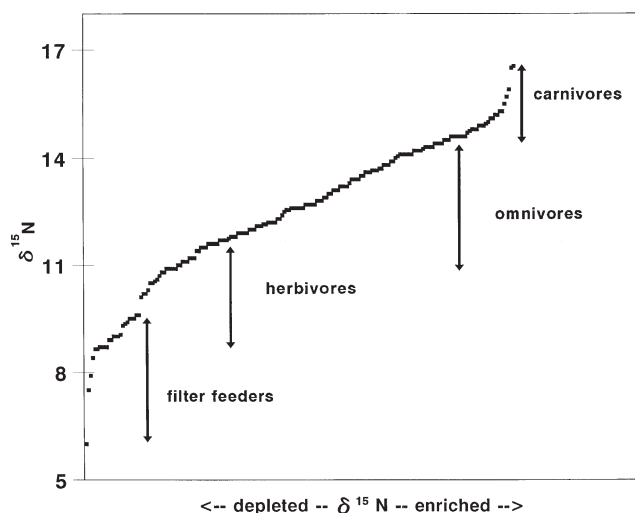


Fig. 2. Plot of $\delta^{15}\text{N}$ (‰) for all consumer samples collected in 1991 and 1992 (combined data) from Horn Island seagrass beds

can be taken in this subtropical seagrass system. Averaging the $\delta^{15}\text{N}$ values for all primary producers, excluding the plankton, yielded an estimate of $+7.0 \pm 1.8\text{‰}$ for POM as a 'baseline' value to establish where TL1 lies. Using the previously described equation of Hobson & Welch as adapted for this seagrass system (Eq. 2), the shark species sampled lie at TL 3.5. An average $\delta^{15}\text{N}$ value of $+10.3\text{‰}$ for the plankton samples collected on 10 July 1992, a large fraction of which were copepods, places this set of samples at TL 2.1. The estuarine squid *Lolliguncula brevis* and the bluefish *Pomatomus saltatrix*, with the highest $\delta^{15}\text{N}$ values, lie at TL 3.9. Thus, this type of model seems to work well for this system, which has no obvious demarcations between trophic levels as there are very few breaks in the cascade of the $\delta^{15}\text{N}$ values shown in Fig. 2. General consumer groups are also indicated in this figure.

Stable sulfur isotope ratios of consumers ranged from $+2.3\text{‰}$ for the white mullet *Mugil curema* to $+19.6\text{‰}$ for the moon jellyfish *Aurelia aurita* for individual samples. The observed range in $\delta^{34}\text{S}$ values when averaged by species or sample type was $+4.4\text{‰}$ for beach diggers in the family Haustoriidae to $+19.6\text{‰}$ for *A. aurita*. The mean $\delta^{34}\text{S}$ value for all consumers sampled was $+14.2\text{‰}$. Stable sulfur isotope ratios of consumers tend to closely reflect their diets (Peterson et al. 1985, 1986). The observed range and average for consumer $\delta^{34}\text{S}$ values indicates that a variety of algal food sources are being used by the organisms found within the seagrass beds. A diet consisting of a mix of food items including epiphytic algae, sand microflora, and phytoplankton in equal amounts would have a $\delta^{34}\text{S}$ value of $+14.7\text{‰}$, which is very close to the average value for all con-

sumers. However, the results do not rule out the potential for indirect contributions of seagrass to the overall food web, perhaps as detritus, as is the case for *Spartina alterniflora* in North Carolina (Currin et al. 1995).

Dual isotope plots

A series of dual isotope plots of $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ were generated from the pool of stable isotope data. Fig. 3 is a $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ plot for all consumers sampled during the study. There was a close match between the 1991 and 1992 samples, except for a slightly tighter clustering of the former. This, however, may simply be an artifact of the number of samples analyzed from each year (125 in 1991 vs 53 in 1992). As the majority of consumer organisms sampled were at least 1 yr old, the consumers were 'averaging out' seasonal and interannual differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the potential sources of organic matter listed in Table 1. Fig. 4 plots $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ values for all 1991 and 1992 consumer samples and reveals essentially the same pattern as seen in Fig. 3. The greatest disparity between years involved organisms with low $\delta^{34}\text{S}$ values; however, the majority of these were either sampled in 1 yr only or were collected from the nearby beach rather than from *Halodule wrightii* beds. Again, it is assumed that consumers greater than 1 yr old were exposed to all seasonal differences in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values of potential organic matter sources.

The $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ plots shown in Fig. 5 include the primary producer samples listed in Table 1 and all consumer samples collected in 1991 and 1992. In both

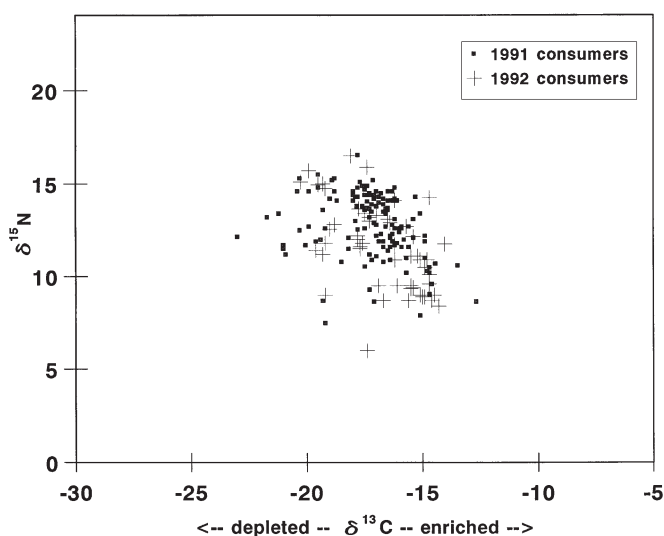


Fig. 3. Plot of $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ (‰) for all consumer samples collected in 1991 and 1992 from Horn Island seagrass beds

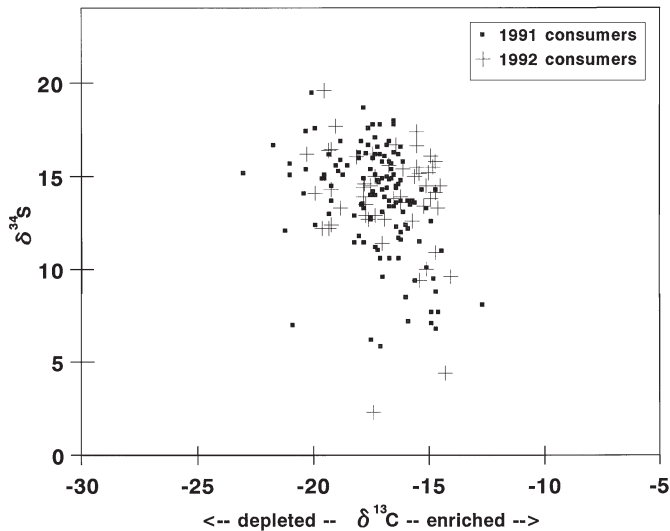


Fig. 4. Plot of $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ (‰) for all consumer samples collected in 1991 and 1992 from Horn Island seagrass beds

plots, the $\delta^{13}\text{C}$ values for virtually all consumers fall within a range of -20 to -15 ‰; this range includes all $\delta^{13}\text{C}$ values for epiphytic algae, sand microflora, and macroalgae but none of those for *Halodule wrightii* or phytoplankton. Neither plot reveals any discontinuities in the $\delta^{15}\text{N}$ data for consumers, but rather a continuum of values; hence, delineation of distinct trophic levels is not possible in this data set.

Fig. 6 shows dual isotope plots of the $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ data for primary producers and consumers in 1991 and 1992. Virtually all data points for consumers in both years are bracketed by the epiphytic algae, sand microflora, and macroalgae. The data points for *Halodule wrightii* and phytoplankton are outliers.

DISCUSSION

Stable isotope ratios of producers

Stable carbon isotope values for *Halodule wrightii* and for its epiphytes in Mississippi Sound fell within the range of previously reported values for at least 8 species of seagrasses (Table 3). Hemminga & Mateo (1996) summarized $\delta^{13}\text{C}$ values from the literature for 195 seagrass values, and reported an average value of -11 ‰ for all species, with values ranging from -12 to -11.2 ‰ for *Halodule* species based on the work of McMillan et al. (1980); we found a mean value of -12.2 ‰ (Table 1). As previously stated, the $\delta^{13}\text{C}$ value for the sand microflora (-15.8 ‰) was the average for samples of the sand dollar *Mellita quinquiesperforata* and a diatom-dominated seagrass-substrate sample.

Dauby (1995) recorded a mean $\delta^{13}\text{C}$ value of -18.0 ‰ for the sand microflora (mostly diatoms) in a *Posidonia oceanica* (L.) Delile bed, while Stoner & Waite (1991) reported -19 ‰ for a cyanobacterial mat in a Bahamas seagrass bed. Phytoplankton in Mississippi Sound had a mean $\delta^{13}\text{C}$ value of -21.8 ‰, very close to the -23 ‰ reported by Sullivan & Moncreiff (1990) for a pure zooplankton sample collected in Graveline Bay Marsh 11 km to the north of the Horn Island seagrass beds.

Stable nitrogen isotope values were essentially identical for *Halodule wrightii*, its epiphytes, and the sand microflora (means = $+6$ to $+7$ ‰; see our Table 1). The absence of cyanobacteria from *H. wrightii* leaves

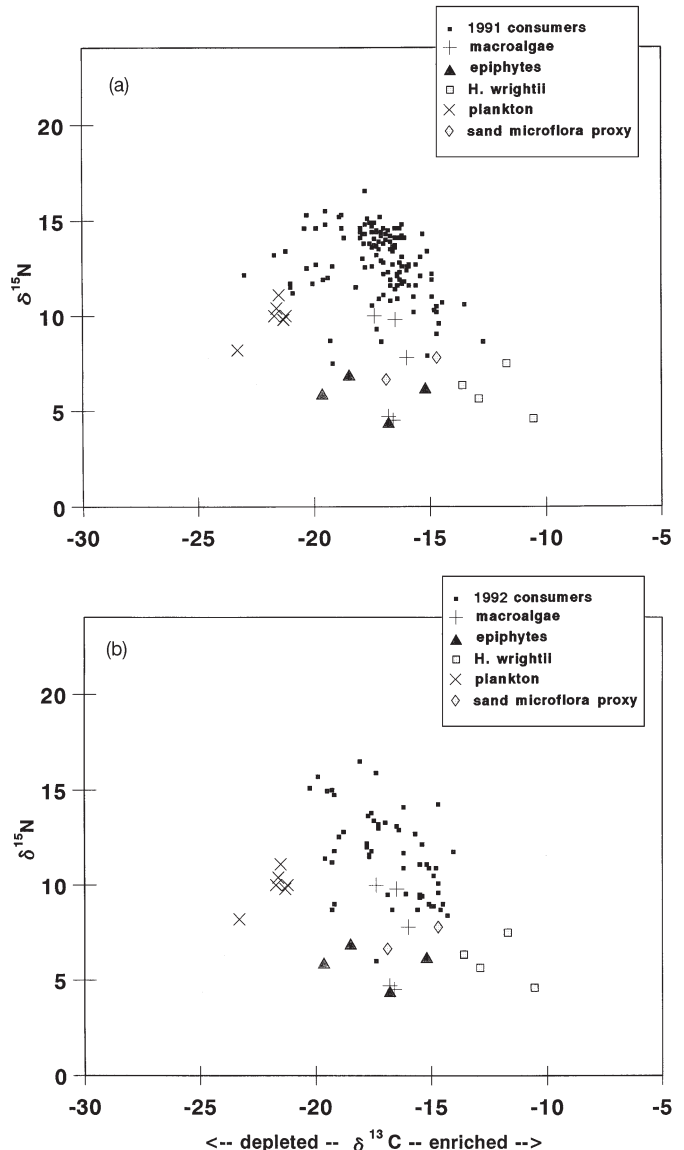


Fig. 5. Plots of $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ (‰) for primary producers and consumers collected from Horn Island seagrass beds in (a) 1991 and (b) 1992. Each small square represents an individual consumer sample

in Mississippi Sound (Moncreiff et al. 1992) eliminated the possibility of nitrogen-fixing cyanobacteria in the epiphytic assemblage influencing the $\delta^{15}\text{N}$ values of seagrass leaves (Fry et al. 1987). In contrast, Yamamuro (1999) reported a range in $\delta^{15}\text{N}$ values of -2 to -1 ‰ for a cyanobacteria-dominated epiphytic assemblage on the seagrass *Syringodium isoetifolium* Dandy. Phytoplankton had a mean $\delta^{15}\text{N}$ value of $+10$ ‰ which compares well to values of $+7$ ‰ (Sullivan & Moncreiff 1990), $+8$ ‰ (Fry et al. 1987), and $+9$ ‰ (Peterson & Howarth 1987).

Stable sulfur isotope values of *Halodule wrightii* and its epiphytes were distinct (mean $\delta^{34}\text{S}$ values = $+11$ and $+18$ ‰, respectively; see our Table 1) in Mississippi Sound. Macroalgae collected in Mississippi Sound had the same mean $\delta^{34}\text{S}$ value and range of values as the epiphytes. This closely approximates the situation in Texas seagrass beds (Fry et al. 1982b; see also Table 10 in Fry et al. 1987). Thus, epiphytes and macroalgae obtain more of their sulfur from seawater sulfate ($\delta^{34}\text{S} = +20$ ‰) than do seagrass leaves, which obtain at least some of their sulfur from $\delta^{34}\text{S}$ -depleted sulfides (range = -30 to -10 ‰) following uptake from the sediments by the roots. Phytoplankton in Mississippi Sound had a mean $\delta^{34}\text{S}$ value of $+15$ ‰, which is intermediate between values of $+11$ ‰ measured for a pure zooplankton sample in Graveline Bay Marsh by Sullivan & Moncreiff (1990) and $+19$ ‰ for a plankton sample from Woods Hole Passage by Peterson et al. (1985, 1986). The $\delta^{34}\text{S}$ value of $+10.6$ ‰ for the sand microflora proxies of the Horn Island seagrass beds is more depleted in $\delta^{34}\text{S}$ than the value of $+14$ ‰ obtained for edaphic algae of Graveline Bay Marsh by Sullivan & Moncreiff (1990). However, Currin et al. (1995) reported a $\delta^{34}\text{S}$ value of $+4$ ‰ for sediment-associated microalgae of a North Carolina salt marsh. A notable problem with these 3 measurements is that $n = 1$ for the cited studies and $n = 2$ for the present study, so that the variability in benthic microalgal $\delta^{34}\text{S}$ values is unknown.

Table 2. Summary of mean $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values (‰) for consumers in seagrass beds of Horn Island. Organisms are arranged by functional groups. See Sullivan & Moncreiff (1993) for complete sample record. nd = not determined; n = number of individual organisms sampled

Consumer group, species, and common name	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
Planktivorous fish species			
<i>Anchoa mitchilli</i> (bay anchovy), n = 119	-19.1	14.8	16.7
<i>Anchoa nasuta</i> (longnose anchovy), n = 24	-18.4	14.3	17.0
<i>Brevoortia patronus</i> (Gulf menhaden), n = 2	-19.6	11.9	14.9
<i>Harengula jaguana</i> (scaled sardine), n = 220	-18.2	13.1	17.8
Larval clupeids, n = 35	-19.4	12.0	nd
<i>Menidia beryllina</i> (tidewater silverside), n = 69	-17.1	13.0	13.3
Non-clupeid larval fish, n = 137	-15.7	10.2	nd
Benthic carnivorous fish species			
<i>Ancyclopsetta quadrocellata</i> (ocellated flounder), n = 2	-16.0	13.7	13.6
<i>Dasyatis sabina</i> (Atlantic stingray), n = 4	-16.2	12.2	12.1
<i>Citharichthys spilopterus</i> (bay whiff), n = 16	-16.8	13.1	15.4
<i>Cynoscion arenarius</i> (white trout), n = 2	-21.0	14.2	16.5
<i>Diplectrum bivittatum</i> (dwarf sand perch), n = 29	-17.5	13.4	15.4
<i>Diplectrum formosum</i> (sand perch), n = 4	-17.1	14.2	16.2
<i>Eucinostomus argenteus</i> (spotfin mojarra), n = 17	-17.8	12.5	11.5
<i>Gymnothorax ocellatus</i> (ocellated moray), n = 1	-17.5	14.4	14.0
<i>Lutjanus campechanus</i> (red snapper), n = 12	-16.8	14.1	15.8
<i>Lutjanus griseus</i> (gray snapper), n = 3	-20.1	14.4	14.0
<i>Lutjanus synagris</i> (candy snapper), n = 3	-16.7	14.2	16.9
<i>Menticirrhus americanus</i> (southern kingfish), n = 3	-15.8	13.8	14.7
<i>Micropogon undulatus</i> (Atlantic croaker), n = 5	-20.1	12.7	13.5
<i>Prionotus tribulus</i> (bighead sea robin), n = 8	-16.5	13.4	14.2
<i>Sciaenops ocellata</i> (redfish), n = 2	-16.2	11.4	6.7
<i>Sphoeroides parvus</i> (least puffer), n = 10	-17.2	13.5	14.8
<i>Symphurus plagiusa</i> (blackcheek tonguefish), n = 13	-18.2	12.7	13.1
<i>Synodus foetens</i> (inshore lizardfish), n = 5	-17.0	15.3	17.0
Pelagic carnivorous fish species			
<i>Chaetodipterus faber</i> (Atlantic spadefish), n = 3	-19.2	14.9	15.9
<i>Chloroscombrus chrysurus</i> (Atlantic bumper), n = 3	-17.8	14.5	17.4
<i>Cynoscion nebulosus</i> (speckled trout), n = 3	-17.5	14.6	12.4
<i>Elops saurus</i> (ladyfish), n = 3	-19.5	12.7	9.4
<i>Echeneis neucratoides</i> (sharksucker), n = 2	-17.4	14.1	14.2
<i>Pomatomus saltatrix</i> (bluefish), n = 3	-18.9	15.6	15.0
<i>Strongylura marina</i> (Atlantic needlefish), n = 1	-19.9	14.6	17.6
<i>Trachinotus carolinus</i> (Florida pompano), n = 7	-19.4	12.2	14.9
<i>Scomberomorus maculatus</i> (Spanish mackerel), n = 1	-17.7	15.1	16.3
Carnivorous/benthic scavengers			
<i>Arius felis</i> (hardhead catfish), n = 25	-17.0	13.6	11.6
<i>Rhizoprionodon terranova</i> (Atlantic sharpnose shark), n = 3	-16.9	14.8	15.2
<i>Sphyrna tiburo</i> (bonnethead shark), n = 4	-16.3	14.5	15.6
'Generic' omnivorous fish species			
<i>Balistes capricus</i> (gray triggerfish), n = 1	-16.7	11.9	15.8
<i>Leiostomus xanthurus</i> (spot; flat croaker), n = 4	-17.4	13.5	13.8
<i>Monacanthus setifer</i> (pygmy filefish), n = 1	-17.0	12.8	15.8
Benthic omnivorous fish species			
<i>Fundulus similis</i> (longnose killifish), n = 10	-14.1	11.8	9.6
<i>Lagodon rhomboides</i> (pinfish), n = 13	-16.1	12.2	11.8
<i>Mugil cephalus</i> (striped mullet), n = 3	-14.6	10.2	9.2
<i>Mugil curema</i> (white mullet), n = 6	-15.7	9.8	9.6
<i>Orthopristis chrysoptera</i> (pigfish), n = 2	-16.5	13.5	12.7

Table 2 (continued)

Consumer group, species, and common name	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
Benthic/pelagic crabs and crustaceans			
<i>Callinectes sapidus</i> (blue crab), n = 11	-18.0	13.1	14.7
<i>Chelonibia patula</i> (crab barnacle), n = 25	-20.1	11.7	19.5
<i>Hepatus epheliticus</i> (calico box crab), n = 2	-16.2	14.1	15.8
<i>Libinia dubia</i> (spider crab), n = 2	-17.2	13.9	16.6
<i>Libinia emarginata</i> (spider crab), n = 2	-17.3	13.7	17.1
<i>Menippe mercenaria</i> (stone crab), n = 1	-16.5	14.1	18.0
<i>Portunus gibbesii</i> (purple swimming crab), n = 18	-17.3	13.2	15.1
Nearshore crabs and crustaceans			
<i>Clibanarius vittatus</i> (striped hermit crab), n = 72	-15.1	9.6	15.7
<i>Emerita talpoida</i> (common mole crab), n = 191	-15.3	8.9	14.7
Haustoriidae (beach diggers), n > 100	-14.3	8.4	4.4
<i>Limulus polyphemus</i> (horseshoe crab), n = 5	-15.7	12.1	13.1
<i>Pagurus pollicaris</i> (flat-clawed hermit crab), n = 25	-15.6	11.6	15.0
Shrimp species			
Hippolytid shrimp, n > 1,500	-15.1	7.9	10.1
Miscellaneous small shrimp, n = 203	-13.5	10.6	nd
Mysids, n > 500	-15.9	9.6	6.3
<i>Farfantepenaeus aztecus</i> (brown shrimp), n = 40	-17.7	11.0	11.8
<i>Farfantepenaeus duorarum</i> (pink shrimp), n = 8	-16.5	11.2	12.1
<i>Litopenaeus setiferus</i> (white shrimp), n = 3	-19.6	11.4	12.2
<i>Sicyonia brevirostris</i> (brown rock shrimp), n = 9	-16.4	10.9	14.4
<i>Squilla empusa</i> (mantis shrimp), n = 23	-16.9	13.1	14.6
<i>Tozeuma carolinense</i> (arrow shrimp), n = 297	-14.7	10.1	10.9
<i>Rimapenaeus constrictus</i> (roughneck shrimp), n = 29	-16.7	11.4	13.2
<i>Rimapenaeus similis</i> (yellow roughneck shrimp), n = 97	-17.9	11.8	13.5
Miscellaneous invertebrate species			
<i>Anguinella palmata</i> (brown bushy bryozoan), n = 10	-19.2	9.0	14.3
<i>Aurelia aurita</i> (moon jelly), n = 12	-19.5	15.0	19.6
<i>Calliactis tricolor</i> (hermit crab anemone), n = 22	-16.0	12.0	16.7
<i>Lolliguncula brevis</i> (Atlantic brief squid), n = 48	-17.8	15.7	15.7
<i>Luidia clathrata</i> (grey sea star), n = 7	-17.3	9.3	15.5
<i>Mellita quinquesperforata</i> (sand dollar), n = 99	-16.9	6.7	8.6
Polychaetes, n > 100	-17.7	11.6	13.5
Bivalves and gastropods			
<i>Busycon contrarium</i> (lightning whelk), n = 2	-17.1	11.6	16.7
<i>Crepidula plana</i> (white slipper snail), n = 177	-19.3	8.7	13.0
<i>Mercenaria campechiensis</i> (southern quahog), n = 2	-18.5	10.8	15.6
<i>Nassarius vibex</i> (eastern nassa snail), n = 79	-16.3	14.1	nd
<i>Pisania tinctoria</i> (tinted cantharus), n = 54	-19.2	12.6	13.7
<i>Polynices duplicatus</i> (Atlantic moon snail), n = 1	-16.5	11.4	15.1
<i>Tellina alternata</i> (telling clam), n = 1	-19.2	7.5	nd
<i>Thais haemastoma</i> (rock snail), n = 20	-16.6	13.7	15.7

Trophic importance of benthic microalgae

Plots employing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 5) or $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values (Fig. 6) of primary producers and consumers from the Horn Island seagrass beds strongly argue in favor of a food web based on epiphytic algae, sand microflora, and macroalgae. Production rates of the first 2 primary producers are known to be substantial in these beds (see discussions in Daehnick et al. 1992 and Moncreiff et al. 1992). No attempt was made to determine primary production rates of macroalgae, since their occurrence in the beds was at best occa-

sional and hence their contribution to annual system production was negligible. Thus, although the stable isotope ratios of macroalgae and epiphytes were similar for all 3 elements examined, the former must be regarded as a purely opportunistic rather than a long-term food source for consumers in seagrass beds of Mississippi Sound.

Virtually all consumers sampled in this study had $\delta^{13}\text{C}$ values that fell between -20 and -15‰, with an overall average of -17.3‰; this is very close to the average literature value of -17.1‰ for organisms reported by Stribling & Cornwell (1997). This range of values includes all $\delta^{13}\text{C}$ values for epiphytes and sand microflora listed in Table 1, but none of those for either *Halodule wrightii* or phytoplankton. This strongly suggests that direct contribution of organic matter by *H. wrightii* to higher trophic levels of the food web was minimal relative to the biomass of seagrass versus epiphytes available to consumers within the system. An earlier study for the seagrasses in this locality (Moncreiff et al. 1992) showed that biomasses of seagrass and epiphytes are roughly equal when averaged over that part of the year during which data was collected. Using the pinfish *Lagodon rhomboides* ($\delta^{13}\text{C}$ = -16.1‰) as an example for a 'mixing model' for $\delta^{13}\text{C}$, and assuming equal contributions of seagrass and epiphytes, this organism would have a $\delta^{13}\text{C}$ value of -14.8‰. Setting contributions of seagrass at 25% and that of epiphytes at 75% would yield a $\delta^{13}\text{C}$ value of -16.2‰, which is nearly identical to the measured value for this organism. Equal contributions to $\delta^{13}\text{C}$

from the sand microflora and from epiphytes would yield a $\delta^{13}\text{C}$ value of -16.6‰, again close to the measured value. Estimated $\delta^{13}\text{C}$ would be -15.2‰ for an organism consuming food items deriving nutrition equally from seagrass, epiphytes, and sand microflora, again less than the value observed for *L. rhomboides*, which can only be compensated for by increasing the relative contributions of epiphytes (or phytoplankton) to the base of this fish's diet. Thus, epiphytes would appear to make a larger contribution to this fish species' diet than relative biomass values for the primary producers would indicate. This could be a result of

Table 3. Stable carbon isotope values (‰) for primary producers and consumers in seagrass systems

Component	δ ¹³ C	Location	Source
<i>Zostera marina</i>	−10	North Carolina, USA	Thayer et al. (1978)
Epiphytes	−18 to −14		
Animals	−18 to −15		
<i>Syringodium filiforme</i>	−5	St. Croix, US Virgin Islands	Fry et al. (1982a)
<i>Thalassia testudinum</i>	−10		
<i>Halophila decipiens</i>	−9		
Epiphytes	−12	Florida, USA	Fry (1984)
Animals	−16 to −9		
<i>Syringodium filiforme</i>	−8		
Epiphytes	−22 to −17	Texas, USA	Kitting et al. (1984)
Animals	−22 to −16		
<i>Halodule wrightii</i>	−11 to −2		
<i>Syringodium filiforme</i>			
<i>Thalassia testudinum</i>			
Epiphytes	−17 to −10	Australia	Nichols et al. (1985)
Animals	−15 to −9		
<i>Posidonia australis</i>	−8		
<i>Heterozostera tasmanica</i>	−8	Gulf of Calvi, Corsica	Dauby (1989)
Epiphytes	−9		
Phytoplankton	−21		
Animals	−15 to −11	Bahamas	Stoner & Waite (1991)
<i>Posidonia oceanica</i>	−8		
<i>Cymodocea nodosa</i>	−9		
Epiphytes	−20 to −14	Gulf of Calvi, Corsica	Dauby (1995)
Macroalgae	−31 to −10		
Phytoplankton	−23		
Animals	−24 to −14	Gulf of Carpentaria, Australia	Loneragan et al. (1997)
<i>Thalassia testudinum</i>	−5		
<i>Syringodium filiforme</i>	−3		
Epiphytes	−16	Dravuni Island, Fiji	Yamamuro (1999)
Cyanobacteria mat	−19		
Macroalgae	−17 to −11		
<i>Strombus gigas</i>	−11	Mississippi, USA	This study
Juveniles (40–45 mm)			
Juveniles (120–140 mm)	−10		
<i>Posidonia oceanica</i>	−12 to −9	Mississippi, USA	This study
Epiphytes	−17.5		
Sand microflora	−18		
Macroalgae	−20 to −16	Mississippi, USA	This study
Phytoplankton	−24 to −20		
Mysid shrimps	−20 to −17		
<i>Enhalus acoroides</i>	−9	Mississippi, USA	This study
<i>Halodule uninervis</i>	−12		
<i>Halophila ovalis</i>	−11		
Epiphytes	−13	Mississippi, USA	This study
Macroalgae	−23 to −20		
Seston	−22 to −19		
Juvenile prawns	−13 to −9	Mississippi, USA	This study
<i>Syringodium isoetifolium</i>	−5 to −3		
Epiphytes	−14 to −13		
Macroalgae	−13	Mississippi, USA	This study
Herbivores	−17 to −10		
<i>Halodule wrightii</i>	−12		
Epiphytes	−20 to −15	Mississippi, USA	This study
Sand microflora proxies	−16		
Macroalgae	−17		
Phytoplankton	−22	Mississippi, USA	This study
Animals	−20 to −15		

preferential assimilation of algal material, selective grazing by organisms within the local food web, or greater available biomass during the year due to shorter turnover rates for epiphytes than for seagrasses (Borum 1987). Similar mixing models can be devised for most of the organisms sampled during this project with similar results: for most of the animals sampled, seagrass epiphytes and sand microflora contribute more to the base of the food web than *H. wrightii*. Contributions of the phytoplankton to the diets of seagrass-associated organisms is also likely to be much less than the contributions of epiphytic algae and the sand microflora. Therefore, one of the more important functions of *H. wrightii* in Mississippi Sound is to provide habitats with a 3-dimensional structure, and also to serve as attachment sites for the highly diverse and productive epiphytic algae (see Moncreiff et al. 1992), and habitat and structure for the sand- and seagrass-associated invertebrates that constitute the diets of many organisms within seagrass systems.

The mean $\delta^{13}\text{C}$ values for epiphytes, sand microflora, and consumers were -17.5 , -15.8 , and -17.3 ‰, respectively, whereas corresponding mean $\delta^{34}\text{S}$ values were $+18.2$, $+10.6$, and $+14.2$ ‰, respectively. Using a mixing model approach with equal contributions to a $\delta^{34}\text{S}$ value for a hypothetical organism that would draw equally from seagrass, epiphytes, and sand microflora for its food web base, a $\delta^{34}\text{S}$ value of $+13.4$ ‰ would be predicted. Again, on average, a larger contribution from epiphytes to the overall food web is needed to achieve the observed average $\delta^{34}\text{S}$ value for all organisms. Using the pinfish *Lagodon rhomboides* ($\delta^{34}\text{S} = +11.8$ ‰) as an example, and assuming that $\delta^{34}\text{S}$ values of organisms mirror their diets, a mixing model for $\delta^{34}\text{S}$ would require a greater contribution from the sand microflora at the base of the components of the diet of this organism; in combination with its $\delta^{13}\text{C}$ value, a diet based strongly on benthic organisms which consume sand microflora, plus additional contributions from epiphyte-based nutrition could be predicted. A large contribution from seagrass to the diet of this species is not supported by $\delta^{34}\text{S}$ values in combination with $\delta^{13}\text{C}$ values; however, bacteria and yeasts that are often associated with the digestive systems of herbivorous fish species have been demonstrated to have cellulase activity, which may play a major role in the observed $\delta^{34}\text{S}$ value (Stickney & Shumway 1974, Deegan et al. 1990). Cellulase activity in pinfish digestive tracts has been well-documented by Luczkovich & Stellwag (1993) and Stellwag et al. (1995).

With respect to the food web taken as a whole, the relatively low $\delta^{34}\text{S}$ values for the sand microflora proxies suggest that the epiphytic algae dominate the base of the food web in the *Halodule wrightii* beds of Mississippi Sound. Their annual production rates are

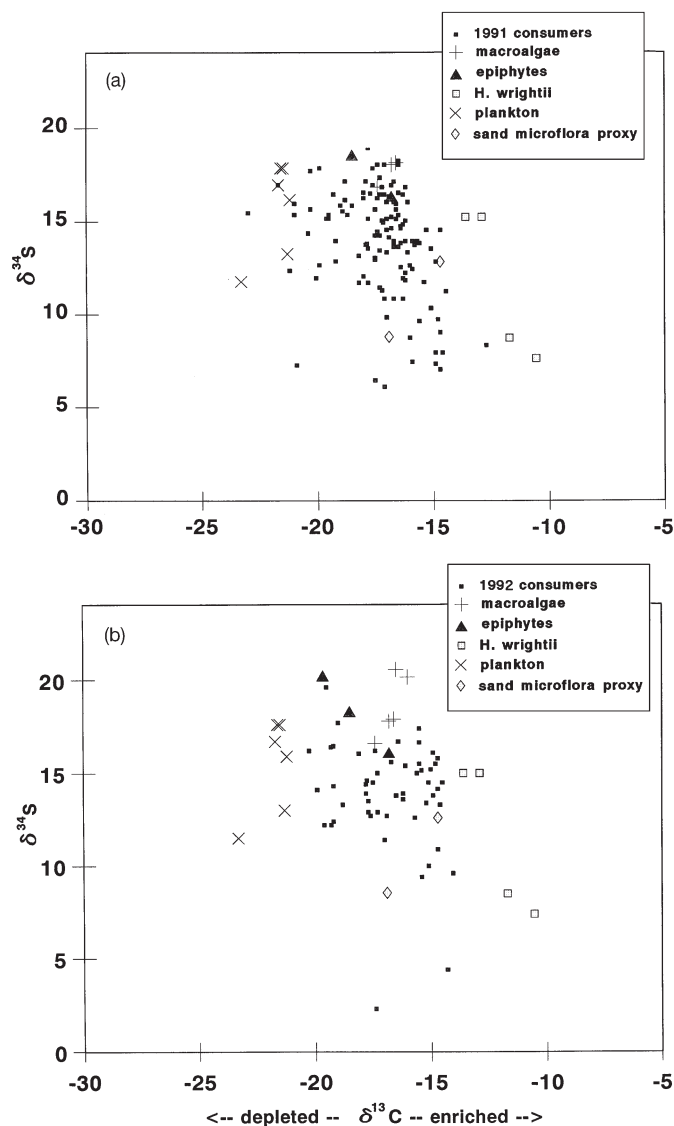


Fig. 6. Plots of $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ (‰) for primary producers and consumers collected from Horn Island seagrass beds in (a) 1991 and (b) 1992. Each small square represents an individual consumer sample

nearly 3 times greater than that of the sand microflora within these beds (Daehnick et al. 1992, Moncreiff et al. 1992). However, Fry et al. (1987) indicated that very little is known regarding the $\delta^{34}\text{S}$ values of sediment-associated microalgae and bacteria; the situation remains little changed today. These authors point out that low $\delta^{34}\text{S}$ values in consumers may well reflect consumption of benthic microflora rather than seagrasses, so that interpretations of food web dynamics based on $\delta^{34}\text{S}$ data must be made with caution. Stoner & Waite (1991) employed stable isotope ratios of carbon and nitrogen to study organic matter sources for growth of juvenile queen conch *Strombus gigas* in the

Bahamas. Although stomach contents revealed large amounts of seagrass detritus, $\delta^{13}\text{C}$ values indicated that this detritus was not assimilated. $\delta^{13}\text{C}$ values for conch foot muscle matched those of macroalgae (mainly the red algae in the genus *Laurencia* sp. and the green alga *Batophora* sp.) and sedimentary organic matter, the carbon sources used by this gastropod for growth. In the case of the sediments, it was suggested that juvenile conch process large amounts of sand to extract diatoms and other organic matter from the surface sediments. Hence, the importance of the sand microflora to the food web in *H. wrightii* beds of Mississippi Sound may be much greater than suggested by $\delta^{34}\text{S}$ data alone.

Recent work employing multiple stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) has confirmed the importance of the microscopic benthic algae in salt-marsh food webs, although vascular plants do contribute as much as 50 % to the nutrition of consumers in some systems (Peterson & Howarth 1987, Sullivan & Moncreiff 1990, Currin et al. 1995, Kwak & Zedler 1997). Dependence on seagrasses and their associated macroalgae as organic matter sources for fishes has also been documented using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Marguillier et al. 1997). The present report represents the first systematic application of the multiple stable isotope approach to the study of food webs in seagrass beds, and the importance of the benthic microalgae has also been confirmed in this system. Contributions from the dominant vascular plant in this study to overall consumer nutrition appear to be substantially less than those observed in salt-marsh ecosystems. Furthermore, systems such as the one we studied, which are characterized by low tidal amplitude typically have an algae-based food web (Deegan & Garritt 1997).

A progression of stable isotope studies since that of Thayer et al. (1978) has established a new paradigm for food web structure in seagrass systems, and these are summarized in Table 3. Similar results for the importance of algal as opposed to detrital carbon sources have been found in mangrove and mangrove-seagrass systems (Newell et al. 1995, Primavera 1996). Fry et al. (1982a) had earlier suggested that animals feeding in seagrass beds ingest and assimilate epiphytic algae rather than seagrass leaves. Klumpp et al. (1992) reported that 20 to 62 % of the net production of epiphytes was consumed by epifaunal organisms in a tropical seagrass bed, and concluded that epiphytic algae played a major role in the trophic flux of this system. With the exception of the studies of Nichols et al. (1985) and Loneragan et al. (1997), all studies listed in Table 3 that determined stable isotope ratios for a diversity of animals occupying different trophic levels demonstrate the striking similarity in $\delta^{13}\text{C}$ values between epiphytic algae and consumers. In most cases,

$\delta^{13}\text{C}$ values for seagrass leaves are quite distinct from those of consumers (Table 3). Kitting et al. (1984) found that animal $\delta^{13}\text{C}$ values tracked epiphyte values, and their remote sensing of grazing activities affirmed that invertebrates fed primarily on epiphytic algae, even when such algae were scarce, with very little feeding on seagrass leaves or detritus. As in the seagrass beds of Mississippi Sound, the biomass and primary production rates of the epiphytic algae are very high, providing an abundant food source for grazers; therefore, epiphytic algae in these 2 systems at least are the primary basis of the food web.

Fry et al. (1987) emphasized that nutrient availability may govern the trophic importance of epiphytic algae in seagrass meadows. Eutrophic conditions would favor food webs based on algae whereas oligotrophic conditions would favor seagrass detritus (but see Yamamuro 1999). Production of organic matter by epiphytic algae has been shown to equal or exceed that of their seagrass hosts in temperate (Thom 1990), subtropical (Morgan & Kitting 1984, Moncreiff et al. 1992), and tropical (Klumpp et al. 1992, Loneragan et al. 1997) systems. In such cases, the epiphytic algae (dominated by diatoms in our system) represent a reliable and highly nutritious food source (Montagna 1984, Gleason 1986, Plante-Cuny & Plante 1986, Decho 1988, Klumpp et al. 1992, Jernakoff et al. 1996, Créach et al. 1997). Even in more oligotrophic conditions, epiphytic algae may nonetheless be trophically important because diatoms can completely coat seagrass leaves, forming an 'epiphytic felt' (Dauby & Poulicek 1995) and yet be invisible to the naked eye (see Fig. 2 in Koch 1994 and Fig. 1 in Dauby & Poulicek 1995). Furthermore, the benthic microalgae in sandy sediments (which is typically dominated by diatoms; Rao & Lewin 1976, Sundbäck 1983, 1984, Delgado 1989, Dauby 1995) may also contribute significantly to the food web in seagrass systems. A significant portion of water column productivity (i.e. 'phytoplankton' production) in shallow systems may sometimes be due to displaced benthic diatoms and other microalgae (Riaux-Gobin 1987, Shaffer & Sullivan 1988). A recently completed ecosystem-network analysis by Christian & Luczkovich (1999) strongly suggests a major role for sediment-associated microalgae in *Halodule wrightii* meadows in nearby Apalachee Bay, Florida. Since the diatom taxa epiphytic on seagrass leaves and in the sediments are different (Sullivan 1979, Daehnick et al. 1992, Moncreiff et al. 1992), a determination of the identity and abundance of diatoms in the guts of primary consumers would help address this question. At present, the overall picture that has emerged is one of the major trophic importance of benthic microalgae in seagrass beds.

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