

Identification of Important Primary Producers in a Chesapeake Bay Tidal Creek System Using Stable Isotopes of Carbon and Sulfur

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ABSTRACT: The use of multiple stable isotopes in the study of trophic relationships in temperate estuaries has usually been limited to euhaline systems, in which phytoplankton, benthic microalgae, and *Spartina alterniflora* are major sources of organic matter for consumers. Within large estuaries such as Chesapeake Bay, however, many species of consumers are found in the upper mesohaline to oligohaline portions. These lower salinity wetlands have a greater abundance of macrophytes that use C3 photosynthesis to fix carbon, in addition to *S. alterniflora*, which fixes carbon via the C4 photosynthetic pathway. In a broad survey of the biota and sediments of a brackish tidal creek tributary to Chesapeake Bay, combined $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ measurements disclosed a balanced contribution to secondary production from phytoplankton, C3 macrophytes, *Spartina* sp., and benthic microalgae. Surface sediment $\delta^{13}\text{C}$ suggested that the organic matter from C3 plants was derived both from allochthonous sources (terrestrial runoff) and from autochthonous production (marsh macrophytes). Unlike most estuarine systems studied to date, which are dominated by algae (phytoplankton and benthic microalgae) and C4 macrophytes, C3 plants are of greater importance in the diets of consumers in this low-salinity creek system.

Introduction

The natural abundance of multiple stable isotopes has proven to be a valuable tool for the study of estuarine trophic dynamics (Peterson and Fry 1987). Based on the stable isotopic composition of C, N, and S, different primary producers have been shown to provide organic matter for the nutrition of consumers in different estuarine systems. Peterson and Howarth (1987) demonstrated the importance of phytoplankton and *Spartina alterniflora* Loisel in the food web of a Georgia salt marsh, and Peterson et al. (1985) found *S. alterniflora* to be the dominant carbon source in a New England marsh. In a Mississippi estuary, Sullivan and Moncrieff (1990) found evidence for the role of edaphic microalgae as a primary source of organic matter for consumers, and Currin et al. (1995) concluded that microalgae and *S. alterniflora* (specifi-

cally the standing dead plant material) were important to consumers in a North Carolina marsh. All of the above studies focused on higher salinity marshes; investigation of food webs using multiple stable isotopes in lower salinity (brackish to mesohaline) estuaries has been relatively neglected. However, such systems are essential in nurturing commercially important species of consumers, and they are extensive in some coastal areas. In the historically productive Chesapeake Bay, for example, low-salinity marshes constitute 73% of the areal coverage of tidal marshes (Stevenson et al. 1985).

The C4 photosynthetic process used to fix carbon in *S. alterniflora* results in a carbon stable isotopic composition different from that of plants using C3 photosynthesis (Smith and Epstein 1971). One might expect a more important role for C3 plants in the food webs of oligohaline marshes. These marshes have a higher plant species diversity and a greater abundance of C3 macrophytes than

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do coastal salt marshes (Anderson et al. 1968; Odum 1988). Furthermore, their proximity to upland environments should lead to increased input of allochthonous terrestrial detritus, also derived largely from C3 plant production. Such systems are therefore likely to exhibit considerably different trophic relationships, potentially yielding new insights into ecosystem dynamics.

We surveyed the stable isotopic ratios of carbon and sulfur in representative biota of Monie Creek, a brackish tidal creek tributary to Chesapeake Bay. We also examined the $\delta^{13}\text{C}$ of surface sediments to investigate the relative importance of sedimenting carbon from autochthonous and allochthonous production. The objective of this study was to determine whether terrestrial and marsh C3 macrophytes might be more important as sources of organic matter to consumers in a lower salinity marsh.

Methods and Materials

STUDY SITE

Monie Creek is the major tributary of Monie Bay, an embayment on the Wicomico River on the lower eastern shore of Chesapeake Bay (Fig. 1). Historically, this region of Chesapeake Bay has had high commercial finfish and shellfish production (Bundy and Williams 1978). Human influences within the watershed of this relatively pristine creek are largely limited to agriculture and logging. Nutrient concentrations in the waters of the Monie Bay system are low compared with those of other Chesapeake Bay marshes; both nitrogen and phosphorus concentrations reach levels low enough to limit primary production during the growing season (Cornwell et al. 1994).

Monie Creek salinity ranges over space and time from 0‰ to 15‰ (Cornwell et al. 1994). Salinity fluctuations over a normal tidal cycle approach 6‰; the gravitational tidal range is approximately 0.3 m. Meteorological forcing by wind-driven tides and rainfall events can greatly increase the tidal amplitude and the salinity fluctuations. The Monie Bay system as a whole exhibits a close relationship between sediment biogeochemistry and hydrodynamics: concentrations of both sediment organic matter and reduced sulfur compounds increase with decreasing tidal flushing (Cornwell et al. 1994), and, in general, organic matter concentrations in Monie Creek sediments are higher than those in Monie Bay itself (Kearney et al. 1994).

Three sampling locations (Fig. 1) were chosen to encompass the salinity gradient, and to include several hydrodynamically different marshes. The first location, designated HWY, is at the uppermost

navigable portion of the creek, below a highway culvert. This point in the creek has the lowest salinity (0–4‰). The marsh surface is flooded on most high tides, and the surficial sediment organic matter content of 26% (based on ash-free dry weight) was highest of all the sites studied (Cornwell et al. 1994). The second sampling location (DB) has higher salinity (2–12‰). We sampled three sites along a transect of this marsh, including a well-drained, elevated creek bank (DB1), a low, flooded interior marsh with reducing sediments (DB2), and the upper marsh edge adjacent to a nontidal wetland forest (DB3). The third location (BAY) is near the mouth of Monie Creek and has the highest salinity (9–12‰). This marsh is low and floods on most high tides.

SAMPLE COLLECTION

We sampled marsh macrophytes and consumers in July and August 1990. Consumers were collected with cast net, hand-fishing line, crab trap, and dip net from the creek adjacent to the HWY, DB1, and BAY sites; however, we did not collect individuals from each species from every site. The consumers included representative molluscs, crustaceans, and planktivorous and predatory fish. For determination of stable isotopic ratios and peak standing crop, aboveground plant biomass was clipped 2 cm above the marsh surface from triplicate 0.25-m² quadrats at each of the five marsh sites. Plant samples were refrigerated and animals were frozen until they could be processed.

We collected a benthic diatom mat from an intertidal mud flat at the BAY site. Terrestrial plant material (pine needles and tree leaves) was sampled from the marsh surface at the HWY site, where it was commonly found. A sample of the submersed aquatic plant *Ruppia maritima* was collected from a small creek at the DB site. Because it is difficult to obtain a pure sample of phytoplankton in a turbid system, we characterized the planktonic algal $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ using estimates derived from water-column dissolved inorganic carbon (DIC) and sulfate. Water was sampled at 5 cm below the surface, filtered with Whatman GFF filters, stored in plastic bottles (sulfate) or in evacuated serum vials (DIC), and frozen prior to analysis. We collected sediment cores from each site with 7.5-cm diameter acrylic core tubes.

SAMPLE PREPARATION AND ANALYSIS

We pooled individual plant shoots (three to six shoots per sample) for stable isotope analysis. *Spartina alterniflora* samples from each sampling site were analyzed separately for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$. We isolated animal muscle tissue when feasible; very

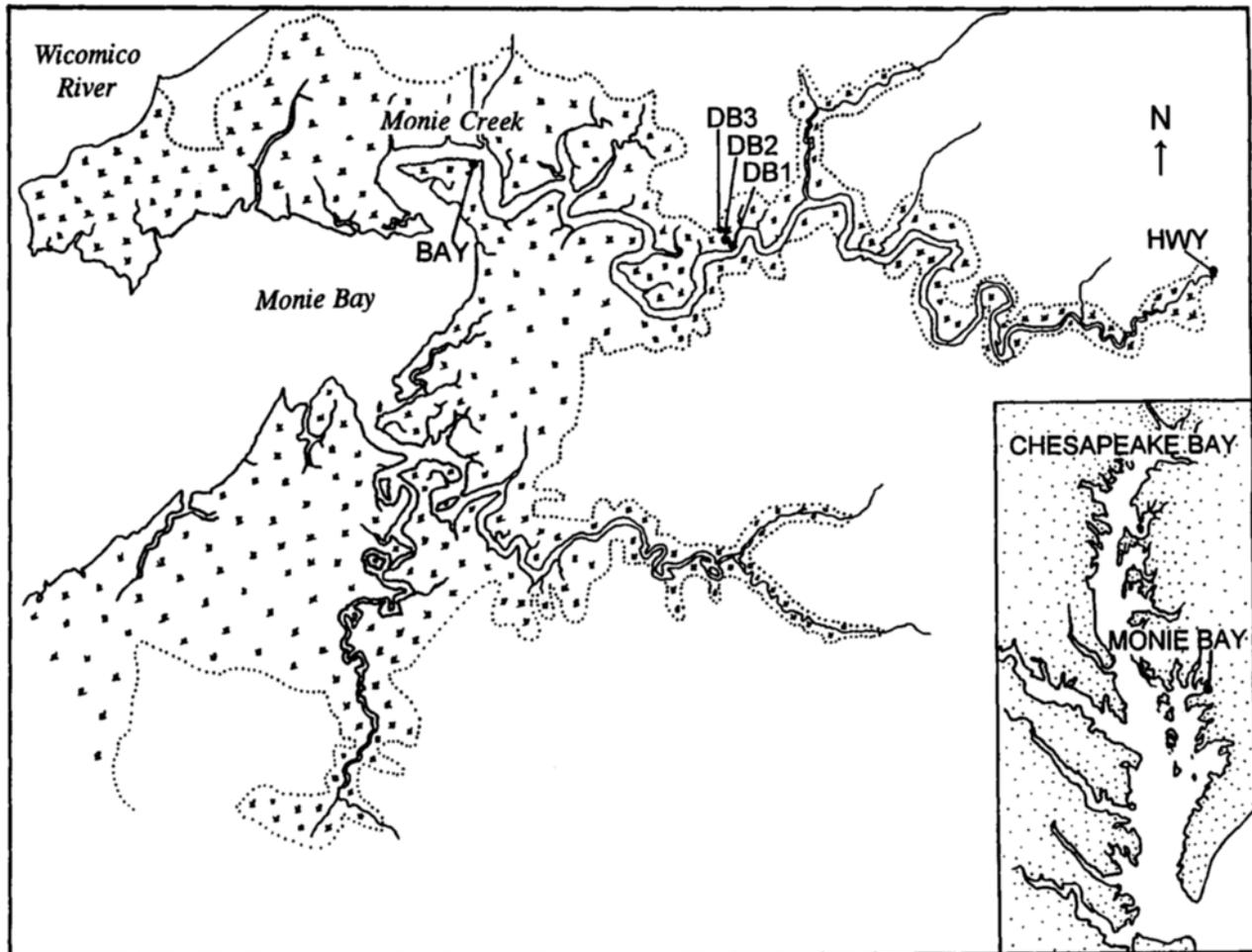


Fig. 1. Location of Monie Creek and of study sites.

small organisms were processed whole and pooled. All samples were soaked in 10% HCl to remove carbonates, rinsed in deionized water, dried in a 65°C oven to constant weight, ground with a mortar and pestle (animals) or in a Wiley Mill with a 40-mesh screen (plants), and placed in a desiccator. Benthic microalgae were washed and filtered sequentially through 100- μm , 83- μm , 55- μm , and 20- μm mesh (Nytex). Microscopic examination showed this to be an almost pure sample of pennate diatoms. We determined sediment $\delta^{13}\text{C}$ using a 2-cm surface section of each sediment core, dried at 65°C and ground with a mortar and pestle.

Water column sulfate was precipitated as BaSO_4 (Hall et al. 1988). Dissolved inorganic carbon samples were acidified, and the CO_2 was stripped with helium and cryogenically trapped. There is a small fractionation of one to two per mil (‰) of sulfur during sulfate uptake by phytoplankton (Trust and Fry 1992), and we estimated the $\delta^{34}\text{S}$ of the phytoplankton to be 1.5‰ lighter than that of the

water column sulfate. Several investigators have estimated the $\delta^{13}\text{C}$ for phytoplankton by assuming a constant fractionation during inorganic carbon assimilation of -20‰ (J. Chanton, The Florida State University, personal communication) or -19‰ (Spiker and Schemel 1979). Although Tan and Strain (1983) caution against the use of a single fractionation factor, in the absence of a pure phytoplankton sample, seston variability probably far outweighs that of DIC fractionation. We assumed a DIC assimilation fractionation of -20‰ .

Preparation of organic and sediment samples for $\delta^{13}\text{C}$ determination followed Boutton (1991a); samples were analyzed on a Finnigan MAT 251 isotope ratio mass spectrometer. Accuracy was within 0.2‰. Stable sulfur isotope analysis was performed at Coastal Science Laboratories, Austin, Texas; accuracy was within 0.5‰. Isotopic data are expressed in conventional δ notation, relative to the Peedee Belemnite standard for carbon and the Canyon Diablo troilite standard for sulfur.

TABLE 1. Biomass (grams dry weight m⁻²) of plant species found in the Monie Creek marshes.

Species	HWY	DB1	DB2	DB3	BAY
(C4)					
<i>Spartina alterniflora</i>	358.7	319.9	243.5	0	237.3
<i>Spartina cynosuroides</i>	20.5	271.5	50.3	0	0
<i>Spartina patens</i>	0	0	0	313.2	0
<i>Distichlis spicata</i>	0	0	0	197.7	0
(C3)					
<i>Amaranthus cannabinus</i>	20.4	193.2	140.7	0	0
<i>Juncus roemerianus</i>	0	0	149.2	0	440.0
<i>Ptilimnium capillaceum</i>	91.7	0	0	0	0
<i>Juncus gerardi</i>	64.4	0	0	0	0
<i>Scirpus americanus</i>	0	0	0	38.4	0
<i>Polygonum punctatum</i>	37.2	0	0	0	0
<i>Atriplex patula</i>	0	23.3	0	0	0
<i>Phragmites australis</i>	0	0	26.9	0	107.6

Results and Discussion

MACROPHYTES

The C4 plants found in the Monie Creek marshes included the three *Spartina* species (*alterniflora*, *patens*, and *cynosuroides*) and *Distichlis spicata*. *Spartina alterniflora* was abundant throughout the tidal portion of the system (Table 1). Based on peak standing crop, *Spartina* species were dominant at all of the four upstream sites (HWY, DB1, DB2, and DB3). The DB3 site was populated almost exclusively by the C4 species *S. patens* and *D. spicata* (Fig. 2).

Although C4 plants were widespread, C3 macrophytes were important at most locations as well. A combination of C3 species constituted over 50% of the total peak standing crop of macrophytes at DB2, and approximately 30% at the HWY and DB1 sites (Table 1). The dominant macrophyte at the BAY site was the C3 species *Juncus roemerianus*, which, in combination with *Phragmites australis*, resulted in a total C3 contribution of 70% of peak standing crop at that location.

The stable isotopic compositions of most of the marsh macrophytes in this study (Table 2) were similar to values reported elsewhere (Peterson et al. 1985; Peterson and Howarth 1987; Sullivan and Moncrieff 1990). The major difference was with respect to $\delta^{34}\text{S}$. Plants have been shown to isotopically resemble the source of sulfur incorporated by their roots (Chukhrov et al. 1980), and the $\delta^{34}\text{S}$ of the free sulfur in marsh sediments is influenced by the chemical transformations related to dissimilatory sulfate reduction (Goldhaber and Kaplan 1980; Fry et al. 1982). Hydrodynamic differences within the Monie Bay system are associated with the sulfur stable isotopic composition of the *S. alterniflora* at different locations; plants growing in reducing sediments have lower $\delta^{34}\text{S}$ than do plants from better oxidized sediments (Stribling 1994).

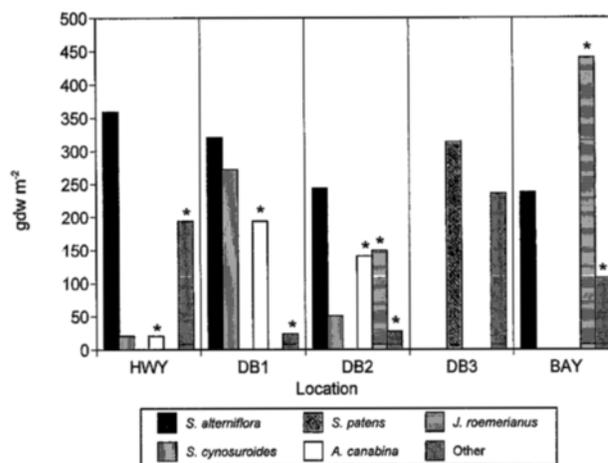


Fig. 2. Plant species composition and peak standing crop for the marsh study sites. Bars representing C3 species are marked *. See Table 1 for listing of all species by location.

Salinity, too, has been shown to influence the $\delta^{34}\text{S}$ of *S. alterniflora* within this system, as it produces variability in the sulfate supply to sediments, and thus in the stable isotopic composition of the reduced sulfur available for plant uptake. Lower salinity locations exhibit sulfate limitation of sulfate reduction, resulting in a higher $\delta^{34}\text{S}$ of the sulfur pool, and consequently of the *S. alterniflora* (Stribling 1994).

As a result, although there was little difference among sampling sites in the $\delta^{13}\text{C}$ of *S. alterniflora*, its $\delta^{34}\text{S}$ values varied widely (Table 2), from -5.6‰ to $+6.6\text{‰}$. The lowest $\delta^{34}\text{S}$ was found for the *S. alterniflora* sample from the BAY site. *Juncus roemerianus* collected at the BAY site was also depleted in

TABLE 2. Primary producer $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ (‰) for Monie Creek, Maryland. Phytoplankton ratios were calculated from the $\delta^{13}\text{C}$ of dissolved inorganic carbon and the $\delta^{34}\text{S}$ of sulfate, both corrected for fractionation (see text). For multiple sample analyses, the range of values is in parentheses.

Species	$\delta^{13}\text{C}$	$\delta^{34}\text{S}$	
(C4 marsh macrophytes)			
<i>Spartina alterniflora</i>	-12.32 (0.19)	1.65 (12.2)	n = 4
<i>Spartina patens</i>	-12.8	4.0	
<i>Spartina cynosuroides</i>	-12.47	1.7	
(C3 marsh macrophytes)			
<i>Juncus roemerianus</i>	-27.34	-1.1	
<i>Phragmites australis</i>	-25.32	-3.9	
<i>Amaranthus cannabinus</i>	-23.67	13.05	
<i>Eleocharis parvula</i>	-23.76		
(Other producers)			
<i>Ruppia maritima</i>	-17.57	14.8	
benthic diatoms	-14.85	5.4	
upland plants	-27.3	7.6	
phytoplankton	-24.08 (3.16)	20.2 (1.9)	n = 3

TABLE 3. Sediment $\delta^{13}\text{C}$ (‰) for top 2 cm.

Location	HWY	DB1	DB2	DB3	BAY
$\delta^{13}\text{C}$	-21.1	-19.2	-20.0	-22.9	-20.5

^{34}S (-1.1‰) compared with other published values for this species (i.e., $+6.1\text{‰}$; Peterson and Howarth 1987). These results are consistent with the extremely low (-22.8‰) $\delta^{34}\text{S}$ of total reduced sulfur in the BAY site sediments (8–10 cm depth) by Cornwell et al. (1990). The highest sediment $\delta^{34}\text{S}$ values measured by Cornwell et al. were at the low-salinity HWY site (1.3‰) and at the elevated DB3 site (-0.1‰), consistent with the higher $\delta^{34}\text{S}$ of *S. alterniflora* at the HWY site (3.0‰) and of *S. patens* from DB3 (4.0‰). The highest $\delta^{34}\text{S}$ of any marsh or terrestrial primary producer sampled (13.0‰) was found for *Amaranthus cannabinus*, also collected from the elevated HWY site.

The $\delta^{13}\text{C}$ values of the three *Spartina* species were very close ($-12.3\text{‰} \pm 0.19$). The stable isotopic ratios of the other C4 plant in the Monie Bay system, *D. spicata*, were not determined in this study; its $\delta^{13}\text{C}$ has been reported at -13.1‰ (Haines 1976). However, the plants (*D. spicata* and *S. patens*) growing at the DB3 site are likely to be of little importance as food sources for aquatic consumers because this site is remote from tidal influence. The limited export of detritus from DB3 was evidenced by the large standing crop of dead plant material at the peak of the growing season (660 g m^{-2} versus 549 g m^{-2} for live shoots).

SURFACE SEDIMENT CARBON

The $\delta^{13}\text{C}$ of surface sediment generally resembles that of the dominant plant species on a site (Chmura et al. 1987); however, it is influenced by differential decomposition of plant fractions with different stable isotopic signatures (cf. Benner et al. 1991; Haddad et al. 1992). Nevertheless, differences between C3 and C4 $\delta^{13}\text{C}$ values are of sufficient magnitude that it should be possible to detect the influence of allochthonous inputs of organic carbon. Surface sediment $\delta^{13}\text{C}$ may thus provide indirect evidence for the relative importance of marsh macrophytes and terrestrial plant material as C3 carbon sources.

The Monie Creek values increased in the order DB3, HWY, BAY, DB2, DB1 (Table 3). This pattern of surface sediment $\delta^{13}\text{C}$ did not always reflect the dominant macrophytes at each location. *Spartina* species were dominant at both the HWY and DB3 sites (Fig. 2), yet both locations had relatively light sediment $\delta^{13}\text{C}$ values, suggesting C3 input as well. The DB3 site is only a few meters from a shrub community and forest, where C3 plants are abun-

dant. The HWY portion of Monie Creek also receives large amounts of terrestrially-derived organic matter; decomposing tree leaves were frequently found on the marsh surface, and the water entering the system from upstream was deeply colored with tannin. Terrestrial (allochthonous) organic matter thus appears to be a major source of surface sediment carbon inputs at the HWY and DB3 locations.

The BAY site also had a relatively light sediment $\delta^{13}\text{C}$ signal; however, this portion of the creek is distant from the terrestrial input of the freshwater and upland reaches. In this case, much of the sedimenting carbon appears to be of autochthonous origin because C3 marsh macrophytes were dominant at this site (Fig. 2).

The heaviest $\delta^{13}\text{C}$ of surface sediments was at the DB1 site. This, too, is consistent with autochthonous carbon input, as *Spartina* species were the dominant macrophytes at this location (Fig. 2). The DB2 site was intermediate both in its surface sediment $\delta^{13}\text{C}$ and in the representation of C3 and *Spartina* species. The sites closest to upland inputs (HWY and DB3) thus appear to accumulate terrestrial carbon in the surface sediments, whereas the more remote sites (DB1, DB2, and especially BAY) exhibit sediment carbon $\delta^{13}\text{C}$ values more consistent with the dominant macrophytes at those locations.

PHYTOPLANKTON

Phytoplankton abundance, as estimated from chlorophyll *a* levels, was several times higher at the HWY site than downstream (Stribling unpublished data). Samples collected monthly from April to October averaged $30.3 \mu\text{g l}^{-1}$ at the HWY site and $9.2 \mu\text{g l}^{-1}$ at the DB1 site (chlorophyll samples were not collected at the BAY site). Because the HWY site is near the turbidity maximum for Monie Creek, the increased phytoplankton abundance at this site probably results from both greater nutrient inputs and a longer particle residence time. The isotopic composition of phytoplankton, as estimated from surface water DIC and sulfate, was depleted in ^{13}C and enriched in ^{34}S compared with phytoplankton in coastal estuaries (i.e., Peterson et al. 1985). Both features are consistent with the low salinity and high sediment organic content of the Monie Creek system. River water DIC is commonly depleted in ^{13}C relative to seawater (Tan and Strain 1983), and the high rates of sulfate reduction found in very organic estuarine sediments result in an enrichment of the sulfate pool with ^{34}S in late summer (Goldhaber and Kaplan 1974; Carlson and Forrest 1982; Stribling 1994).

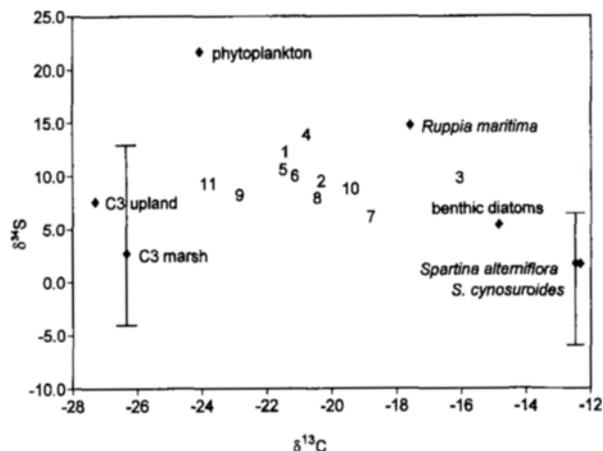


Fig. 3. Combined $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ for producers (\blacklozenge) and consumers (numerals). Numerals are presented in Table 2. The ranges of values for C3 marsh macrophytes and for *Spartina alterniflora* are shown.

BENTHIC MICROALGAE

Few stable isotopic data are available for benthic microalgae, and most studies have used a sample collected in one location to represent edaphic microalgae for an entire system. However, benthic microalgae, like many aquatic plants, have a wide range of reported $\delta^{13}\text{C}$ values (Fry and Sherr 1984; Currin et al. 1995), and the few studies reporting $\delta^{34}\text{S}$ of benthic microalgae (Sullivan and Moncrieff 1988; Currin et al. 1995; this study) encompass a range of 10.4‰. It is possible that the variability in $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ for these primary producers is in part related to differences in the chemistry of the edaphic environment. In addition to atmospheric CO_2 , benthic microalgae may fix dissolved inorganic carbon from the water column; this DIC pool varies in $\delta^{13}\text{C}$ as a result of fluxes from the sediments. The latter carbon sources are both enriched in ^{13}C (Boutton 1991b; Des Marais and Canfield 1994); their relative availability may substantially influence the $\delta^{13}\text{C}$ of this primary producer. With respect to sulfur, differences in the chemistry of the edaphic environment may also generate variability in the $\delta^{34}\text{S}$ of the sulfur source for benthic microalgae, as is the case for *S. alterniflora*. In highly organic, reducing sediments, sulfate derived from oxidation of isotopically light sulfide might represent a substantial portion of the sulfate pool available to these organisms. Our benthic diatom sample was obtained from such a location; the $\delta^{34}\text{S}$ of total reduced sulfur (mainly pyrite) in the sediment in the BAY marsh was -22.8‰ (Cornwell et al. 1990). However, as noted above, Monie Creek sediment $\delta^{34}\text{S}$ was variable (Cornwell et al. 1990), and without samples from different environments, it is not reasonable to assume that the benthic algal

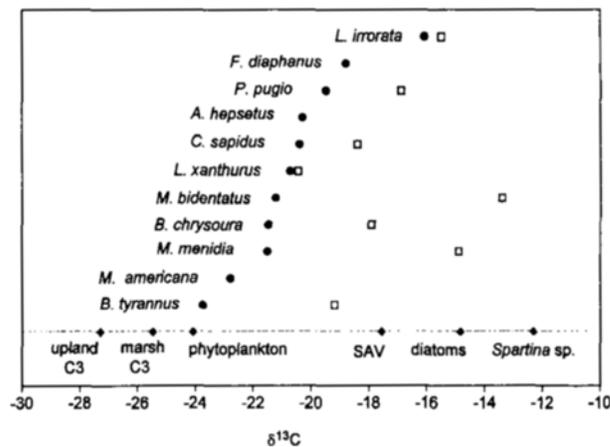


Fig. 4. $\delta^{13}\text{C}$ for consumers (\bullet) and producers (\blacklozenge). Literature values for consumers (\square), where available, are means calculated from data presented in Table 4.

sample in this study is representative of this producer throughout the system.

CONSUMERS

The heaviest $\delta^{13}\text{C}$ was exhibited by the marsh periwinkle, *Littorina irrorata*, which grazes the leaves of *S. alterniflora* and the marsh surface, and is unlikely to ingest either phytoplankton or C3 plants. Values for this species were similar to those reported by Currin et al. (1995), who concluded that standing dead *Spartina alterniflora*, its associated fungi, and benthic microalgae were important food sources for *L. irrorata* in a North Carolina marsh. With the exception of *L. irrorata*, the combined $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ of consumers fell intermediately among the isotopic signatures of the major producers. The primary producers appear to form a rough triangle around most of the consumers, with *Spartina* and benthic microalgae exhibiting generally higher $\delta^{13}\text{C}$ and lower $\delta^{34}\text{S}$, phytoplankton representing higher $\delta^{34}\text{S}$, and C3 upland and marsh plants representing low ratios of both stable isotopes (Fig. 3). Each of these primary producers is potentially an important food source for higher trophic levels in the Monie Creek system.

The consumers collected for this study included several species (*Fundulus diaphanus*, *Anchoa hepsetus*, and *Morone americana*) for which carbon stable isotopic compositions have not previously been reported. The distributions of *F. diaphanus* and *M. americana* are limited to fresh to brackish salinities; however, the other species collected from Monie Creek are also found in euhaline marshes (Hardy 1978). For species that have been investigated elsewhere, the Monie Creek $\delta^{13}\text{C}$ values were lower (Fig. 4), and the mean $\delta^{13}\text{C}$ for all Monie Creek consumers (Table 4) of -20.6‰ was lighter than

TABLE 4. Consumer $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ (‰) for Monie Creek, Maryland, including sampling location. "No." corresponds to numerals used in Fig. 3.

No.	Species	$\delta^{13}\text{C}$	$\delta^{34}\text{S}$	Location
1	<i>Bairdiella chrysoura</i> (silver perch)	-21.5	11.9	BAY
2	<i>Anchoa hepsetus</i> (striped anchovy)	-20.3	9.4	DB
3	<i>Littorina irrorata</i> (marsh periwinkle)	-16.1	9.7	BAY
4	<i>Leiostomus xanthurus</i> (spot)	-22.1	13.8	DB
	<i>Leiostomus xanthurus</i>	-19.4		HWY
5	<i>Menidia menidia</i> (silversides)	-21.5	10.7	BAY
6	<i>Melampus bidentatus</i> (salt-marsh snail)	-21.2	10.5	DB
7	<i>Fundulus diaphanus</i> (banded killifish)	-18.8	6.2	DB
8	<i>Callinectes sapidus</i> (blue crab)	-21.0	8.6	HWY
	<i>Callinectes sapidus</i>	-19.9	8.5	DB
	<i>Callinectes sapidus</i>	-20.3	7.3	BAY
9	<i>Morone americana</i> (white perch)	-22.8	8.2	HWY
10	<i>Palaemonetes pugio</i> (shore shrimp)	-20.3	8.9	DB
	<i>Palaemonetes pugio</i>	-18.7	8.1	BAY
11	<i>Brevoortia tyrannus</i> (Atlantic menhaden)	-23.7	9.0	HWY

the -17.1‰ mean of literature values for the reported species (Table 5). The lighter $\delta^{13}\text{C}$ of consumers suggests a greater diversity of important primary producers in the trophic dynamics of this system.

The submersed macrophyte *Ruppia maritima* was not found in abundance and probably is not a major food source for consumers in Monie Creek. Phytoplankton, as the only producer with a high $\delta^{34}\text{S}$, is almost certainly important. There is an increase in the $\delta^{34}\text{S}$ of *S. alterniflora* leaves with senescence; standing dead leaves, the primary form of *S. alterniflora* available to consumers, have been shown to range in $\delta^{34}\text{S}$ from 8.4–12.9‰ (Currin et al. 1995). An upward shift of this magnitude for the Monie Creek *Spartina* would place these pro-

ducers much closer in $\delta^{34}\text{S}$ to all of the consumers sampled, and might signify a smaller contribution by phytoplankton to the diets of Monie Creek consumers.

The relative importance of the *Spartina* species and benthic microalgae as food sources for consumers was not possible to determine from their stable isotopic signatures. Rates of primary production comparable with those of marsh macrophytes have been demonstrated for benthic microalgae in salt marshes (Zedler 1980; Sullivan and Moncreiff 1988; Pinckney and Zingmark 1993), and it is likely that both producers are important to consumers in this system.

Distinguishing between C3 marsh and C3 upland macrophytes as food sources is also not possible from their stable isotopic ratios. Monie Creek receives a considerable amount of upland runoff, and a major source of C3 organic carbon from macrophytes is probably terrestrial plant material. However, the abundance of C3 species at the BAY and DB2 sites (70% and >50% of peak standing crop, respectively) suggests these two locations may supply isotopically light carbon from autochthonous sources to consumers within Monie Creek. Consumer data for the same species from different locations were too limited to show any clear associations with collection site (Table 4), but mean $\delta^{13}\text{C}$ values for consumers from the three sites (excluding *Littorina irrorata*) reflected the pattern exhibited by sediment carbon (Fig. 5), increasing in the order HWY (-21.7), BAY (-21.0), and DB (-20.1). These consumer and sediment data collectively support the hypothesis that both marsh and terrestrial C3 plants are important as food sources.

Haines (1977) proposed that organic carbon from terrestrial C3 plants might be a major nutri-

TABLE 5. Literature values for consumer $\delta^{13}\text{C}$ (‰).

Species	$\delta^{13}\text{C}$	Reference(s)
<i>Bairdiella chrysoura</i>	-17.6	Hughes and Sherr 1983
	-16.6	Peterson and Howarth 1987
	-19.4	Sullivan and Moncreiff 1988
<i>Littorina irrorata</i>	-13.6	Haines 1976
	-21.6	Haines and Montague 1979
	-12.6	Schwinghamer et al. 1983
	-16.1	Peterson and Howarth 1987
	-11.9	Sullivan and Moncreiff 1988
<i>Leiostomus xanthurus</i>	-16.3	Currin et al. 1995
	-19.9	Hughes and Sherr 1983
	-21.0	Sullivan and Moncreiff 1988
<i>Menidia menidia</i>	-14.9	Schwinghamer et al. 1983
<i>Melampus bidentatus</i>	-13.4	Haines and Montague 1979
<i>Callinectes sapidus</i>	-19.9	Hughes and Sherr 1983
	-21.0	Sullivan and Moncreiff 1988
<i>Palaemonetes pugio</i>	-13.6	Haines 1976
	-14.9	Haines and Montague 1979
	-18.8	Hughes and Sherr 1983
	-17.1	Peterson and Howarth 1987
	-19.4	Sullivan and Moncreiff 1988
<i>Brevoortia tyrannus</i>	-21.7	Hughes and Sherr 1983
	-16.7	Peterson and Howarth 1987

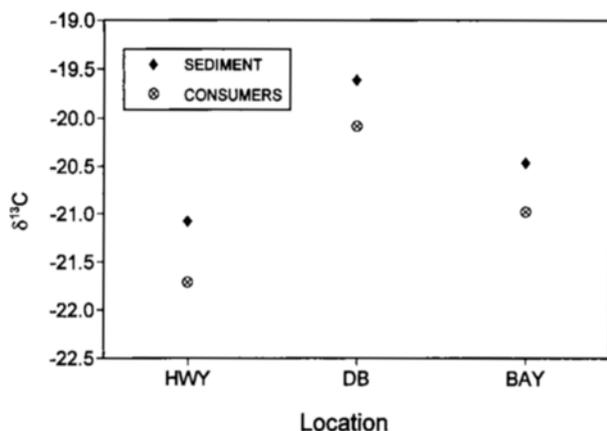


Fig. 5. Comparison of sediment and consumer $\delta^{13}\text{C}$. Sediment value for DB is the mean of DB1 and DB2; DB3 is assumed to contribute little organic matter to consumers in Monie Creek.

tional source in a Georgia salt marsh, and C3 mangrove detritus is a principal food source for consumers within mangrove wetlands (Fleming et al. 1990; Newell et al. 1995). Hackney and Haines (1980) investigated a *Juncus roemerianus* (C3) marsh in Mississippi, but they did not find a local signal of marsh plant carbon in the $\delta^{13}\text{C}$ of consumers. The importance of C3 marsh plants has not heretofore been demonstrated in estuarine food webs. The greater abundance of these plants in lower salinity systems argues for more intensive study of the carbon sources for consumers within brackish estuaries.

Summary

Our study of trophic relationships illustrates the combined importance of C3 plants, phytoplankton, *S. alterniflora* and benthic diatoms to consumers in a lower salinity marsh system. In comparison with higher salinity coastal estuaries, the consumers in this study reflected a greater diversity of food sources and a greater dependence on C3 carbon. Terrestrial plants are certainly major contributors to the C3 macrophyte carbon pool in Monie Creek, and autochthonous C3 carbon may be significant as well. The potential for marsh C3 plants to represent a carbon source for consumers in coastal marsh environments has not previously been shown. Further investigation of low-salinity estuarine systems should be pursued, both because they may differ from the well-studied salt marsh estuaries and because of their importance in such key consumer habitats as Chesapeake Bay.

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