

Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs

Sam C. Wainright^{1,*}, Michael P. Weinstein², Kenneth W. Able³, Carolyn A. Currin⁴

¹Institute of Marine and Coastal Sciences, 71 Dudley Road, Rutgers University, New Brunswick, New Jersey 08901-8521, USA

²New Jersey Marine Science Consortium, Bldg. 22, Fort Hancock, New Jersey 07732, USA

³Rutgers University Marine Field Station, 800 Great Bay Blvd., Tuckerton, New Jersey 08087, USA

⁴NOAA Beaufort Laboratory, 101 Pivers Island Road, Beaufort, North Carolina 28516-9722, USA

ABSTRACT: We conducted a study to determine the trophic pathways leading to juvenile fish in 2 mesohaline tidal marshes bordering Delaware Bay. The relative roles of the major primary producers in supplying energy, ultimately, to the mummichog *Fundulus heteroclitus* were assessed by measuring the stable isotopic compositions of juveniles (21 to 56 mm total length, TL; most of which were young-of-the-year) and those of macrophyte vegetation, phytoplankton, and benthic microalgae at each site. We collected samples of primary producers and *F. heteroclitus*, the dominant fish species in this and other marshes along the east coast of the USA, in June and August 1997, at 2 study sites (upstream and downstream) within Mad Horse Creek (a *Spartina alterniflora*-dominated site) and Alloway Creek (a *Phragmites australis*-dominated site), for a total of 4 study sites. Our results indicate that *F. heteroclitus* production is based on a mixture of primary producers, but the mixture depends on the relative abundance of macrophytes. In *S. alterniflora*-dominated marshes, C and S isotope ratios indicate that *F. heteroclitus* production is supported by *S. alterniflora* production (ca 39%, presumably via detritus), while in *P. australis*-dominated marshes, secondary production is based upon *P. australis* (73%). To our knowledge, this finding provides the first evidence that *P. australis* may contribute to aquatic food webs in tidal marshes. Benthic microalgae also contribute to the food chain that leads to *F. heteroclitus* in both marsh types, while phytoplankton may be of lesser importance. Benthic microalgal biomass was lower in the *P. australis*-dominated system, consistent with a greater effect of shading in *P. australis*- versus *S. alterniflora*-based creek systems. Based on the difference in nitrogen isotope values between *F. heteroclitus* and the primary producers, the trophic level of *F. heteroclitus* appears to be similar in the 2 marsh types, despite the differing vegetation types. In summary, the relative roles of the primary producers in supplying energy to *F. heteroclitus* varies locally and, in particular, with respect to the type of marsh macrophyte vegetation.

KEY WORDS: Stable isotopes · $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · $\delta^{34}\text{S}$ · *Fundulus heteroclitus* · Food web

INTRODUCTION

Ecologists are slowly unraveling the complexities of nutrient exchange, and the links between primary pro-

ducers and the fauna in marsh/estuary ecosystems, but our views of marsh function are still undergoing modifications. For example, there are still large gaps in our understanding of how significantly *Spartina* spp. detritus contributes to the secondary production of economically important species (Peterson & Howarth 1987, Mann 1988). In temperate estuaries of the USA, the contribution of the marsh invader *Phragmites australis*

*Present address: US Coast Guard Academy, Science Department, 27 Mohegan Ave., New London, Connecticut 06320, USA.
E-mail: swainright@cga.uscg.mil

(Niering & Warren 1977, Roman et al. 1984, Marks et al. 1993, Fell et al. 1998, Weinstein & Balleto 1999) to the flow of energy in tidal marsh systems is virtually unknown (Schlacher & Wooldridge 1996, Weinstein & Balleto 1999).

Another potential source of carbon, benthic microalgae, has been shown to contribute significantly to marsh food webs (Haines 1979, Haines & Montague 1979, Hughes & Sherr 1983, Sullivan & Moncreiff 1990, Currin et al. 1995). Yet it is not clear how their biomass varies among unvegetated marsh sites versus sites dominated by dense stands of *Spartina* spp. or *Phragmites australis*. From previous isotopic studies in *Spartina* spp. marshes, it appears that the abundant mummichog, *Fundulus heteroclitus*, an omnivore, is likely to derive its carbon (and other elements) ultimately from a mixture of *Spartina* spp., benthic microalgae, and possibly phytoplankton (Peterson & Howarth 1987, Currin et al. 1995). However, the relative contribution of these components and the trophic linkages with consumers may vary among marsh types within an estuarine system (Deegan & Garritt 1997) and within species. For example, based on gut contents, small young-of-the-year (YOY) *F. heteroclitus* (<20 mm standard length, SL) fed primarily on small invertebrates, while slightly larger YOY *F. heteroclitus* (20 to 30 mm SL) had a diet dominated by algae and detrital material (Smith et al. in press).

Fundulus heteroclitus is the dominant fish species in marshes along the east coast of the USA (Bigelow & Schroeder 1953, Able & Fahay 1998) and in Delaware Bay marsh systems (DeSylva et al. 1962, Wang & Kernehan 1979). The YOY have the highest measures of fish production in any natural system (Valiela et al. 1977, Meredith & Lotrich 1979), and are the dominant life-history stage on the marsh surface based on earlier studies in the vicinity of Delaware Bay (Taylor & DiMichele 1983, Talbot & Able 1984, Talbot et al. 1986). This species has a restricted summer home-range, which makes it amenable to studying spatial patterns in trophic utilization (Lotrich 1975, Teo 1999), yet it is abundant along a gradient from interior marsh locations to beaches outside the marsh (Able & Fahay 1998). It is also an important prey species in Delaware Bay. Observations during 1997 to 1998 indicate that this species was a principal prey item in the stomach contents of *Morone saxatilis* (M. Tupper & K.W.A. unpubl.), *Cynoscion regalis* and *Micropogonias undulatus* (D. N. Nemerson & K.W.A. unpubl. data) in marsh creeks.

In a previous study conducted in a New England salt marsh, the $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values of *Fundulus heteroclitus* were very similar to those of *Spartina alterniflora*, indicating that mummichogs were supported by a food chain based largely on that plant (Peterson et al. 1986).

In contrast, when $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were used, the results were not as clear; the $\delta^{15}\text{N}$ values of *F. heteroclitus* indicated a dependence on both *S. alterniflora* and phytoplankton (as particulate matter, PM). The isotopic agreement between *F. heteroclitus* and *S. alterniflora* was not as good in a Georgia salt marsh (Peterson & Howarth 1987), where the use of other sources could not be ruled out. Neither study considered explicitly the nutritional contribution from benthic microalgae. In a more recent study focusing on the roles of benthic microalgae and *Spartina alterniflora* at various stages of senescence, it was concluded that *F. heteroclitus* could ultimately rely on benthic microalgal and standing-dead *S. alterniflora* production (Currin et al. 1995). A similar conclusion was reached by Kneib et al. (1980) in a North Carolina salt marsh.

Our objectives in this study were: (1) to evaluate the trophic linkages between *Fundulus heteroclitus* and the major potential sources of organic matter typical of many mid-Atlantic marsh systems, i.e. macrophytes, benthic microalgae, and phytoplankton (as suspended particulate matter) using a stable isotope approach; (2) to determine whether these trophic linkages differ in a relatively undisturbed *Spartina alterniflora*-dominated marsh versus a *Phragmites australis*-dominated marsh; and (3) to determine whether the relative importance of these organic sources varies temporally and spatially within these marshes. We sampled at the beginning and the end of the macrophyte growing season to test the prediction that if benthic microalgae are a dominant organic source for *F. heteroclitus* then their importance may be greater during the spring, when there is less competition from emergent macrophytes for light and nutrients (Gallagher & Daiber 1974, Sullivan & Daiber 1975, Van Raalte et al. 1976), and at an upstream and a downstream location within each creek.

MATERIALS AND METHODS

Study site. The study was conducted in 2 representative Delaware Bay (USA) marshes (Fig. 1) that differ mainly in their dominant vegetation. The Alloway Creek system was chosen as a system that is dominated by *Phragmites australis* (coverage is ~66%, but is especially high in the area surrounding our 2 study sites: Management Plan Advisory Committee 1997), while Mad Horse Creek is located ~5 km down the bay, and is dominated by *Spartina alterniflora*. The 2 creek systems differ not only in their dominant macrophyte vegetation type but also in their hydrology, and geomorphological features such as drainage density, marsh elevation and creek-bank slopes (Weinstein et al. 1997, Weinstein & Balleto 1999). Additional charac-

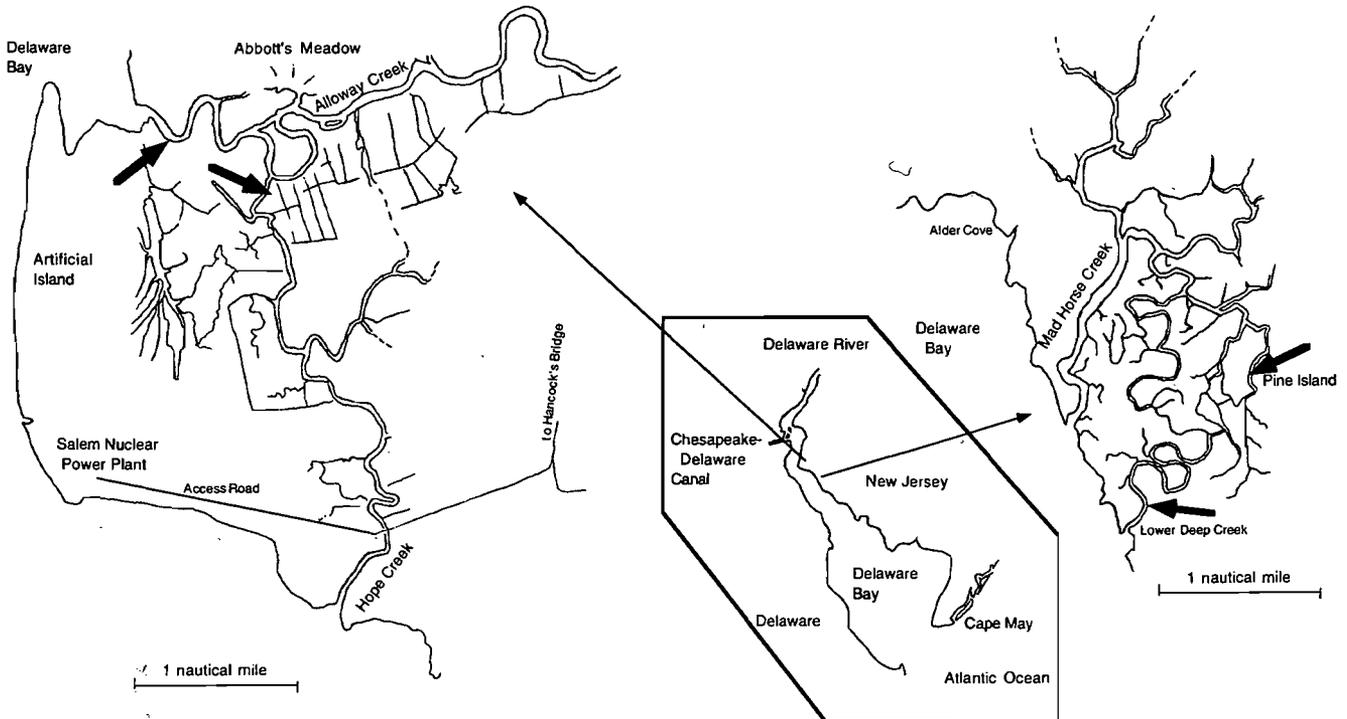


Fig. 1. Map of study area in Delaware Bay. Bold arrows indicate sampling locations

teristics of the Mad Horse Creek study site are described in Able et al. (unpubl.).

Two sites were chosen within each marsh system (Fig. 1). The downstream site in Alloway Creek, hereafter referred to as Lower Alloway Creek ($39^{\circ}30'N$, $75^{\circ}31'40''W$), was within 200 m of the entrance to Delaware Bay. The upstream site, hereafter referred to as Upper Alloway Creek ($39^{\circ}29'40''N$, $75^{\circ}30'40''W$), in a creek that connects Alloway Creek with Hope Creek. Salinities were similar at the 2 Alloway Creek sites (~ 5 to 7%). Vegetation cover was entirely *Phragmites australis* in the vicinity of both of the Alloway Creek sites. Two sites within the Mad Horse Creek system were similarly chosen. The Lower Mad Horse Creek site was located ($38^{\circ}24'40''N$, $75^{\circ}26'30''W$) in a connecting creek (Lower Deep Creek), ~ 300 m upstream of its entrance to Delaware Bay, and the Upper Mad Horse Creek site was located ($39^{\circ}25'20''N$, $75^{\circ}25'40''W$) approximately 3 km upstream. Salinities were $\sim 12.5\%$ at the Mad Horse Creek sites. Vegetation at both Mad Horse Creek sites was dominated by a natural assemblage hereafter referred to as the *Spartina* spp. community (a mixture of *S. alterniflora*, *S. cynosuroides*, *S. patens*, *Distichlis spicata*, and infrequent patches of *P. australis*).

Sample collection. *Fundulus heteroclitus*, marsh macrophytes, benthic algae, and phytoplankton (as sus-

pended particulate matter [PM]) were collected at Alloway Creek and Mad Horse Creek on 2 occasions: in June 1997 at the beginning of the growing season of the macrophytes, and in August 1997 near the end of the growing season.

At each sampling site, leaves of *Spartina alterniflora* or *Phragmites australis*, and several other species of macrophytes (see Table 1) were collected from 5 different plants of each species, and the 5 leaves were pooled before analysis; 3 such pooled samples were collected for each dominant species at each site. Samples of standing-dead plants were also collected because their isotopic composition may differ significantly from that of live plants (Currin et al. 1995) and thus consumers that depend on detrital production may reflect the isotopic composition of plant detritus rather than living plants.

Benthic microalgae were sampled in vegetated, marsh areas and on unvegetated, muddy creek banks at each site. A 'clean' sample of benthic microalgae was obtained by a modification of the technique of Couch (1989), utilizing microalgal vertical migration through nylon screening. Briefly, sediments were covered with a thin layer of pre-combusted silica sand (149 to $420\ \mu\text{m}$ [40 to 100 mesh], Fisher Scientific), a piece of $62\ \mu\text{m}$ Nitex nylon mesh, another thin layer of silica sand, and then moistened with filtered creek water. Treated sediments were shaded from full sun-

light with a single layer of fiberglass window screen. After 1 to 2 h, the Nitex mesh was peeled off the sediment. In the laboratory, the benthic microalgae and silica sand were rinsed from the Nitex with a stream of deionized water, swirled in a beaker, and the suspended (non-sand) material was filtered onto a pre-combusted Whatman GF/F filter. In unvegetated areas (muddy creek banks), clean samples of benthic microalgae for stable isotopic analysis were collected by applying the technique *in situ* (Couch 1989). In macrophyte-vegetated areas, trays of sediment (~1 cm thick) were collected and brought back to the laboratory, and the same technique was applied under artificial lighting for 24 h (4 fluorescent lights suspended within 0.3 m of the sediment surface). We minimized the contribution of inorganic S in these samples by a combination of careful removal of extraneous materials (Currin et al. 1995) and rinsing with deionized water. Benthic microalgal biomass was estimated by analyzing surface sediments (sampled to a depth of 0.3 cm with cores) for chlorophyll *a* using standard fluorometric techniques (Parsons et al. 1984). At least 5 samples were collected at 5 m intervals along transects both on the creek banks and on the marsh surface in the vicinity of sediments used for benthic microalgal vertical migration. Sediments were extracted overnight in 90% acetone before analysis, and the sediments were re-dried and weighed after extraction for expression of chlorophyll content on a weight basis.

Suspended PM for isotopic analysis was collected by filtering known volumes of water samples through pre-combusted glass-fiber filters (Whatman GF/F) until the filters clogged (Wainright & Fry 1994). PM samples at the upstream sites were collected at ebb tide, while those collected at the downstream sites were collected on flood tides to ensure that we covered the range of isotopic compositions for PM between incoming bay water and outgoing marsh creek water. Chlorophyll samples were collected concurrently (100 ml water filtered onto GF/F filters), and were frozen immediately on dry ice. Water samples for analysis of the carbon isotopic composition of dissolved inorganic carbon, DI^{13}C , were preserved with mercuric chloride. Three independent samples of each type were collected at each site.

Fundulus heteroclitus (mostly YOY, 21 to 56 mm TL) were collected with either unbaited wire mesh traps or seines along the edges of creeks at or near low tide. Analyses were done on fish large enough (>25 mm) to provide sufficient tissue for stable isotopic analysis.

Laboratory preparation of stable isotope samples. Plant tissues were cleaned by gently scraping the plants with a scalpel and rinsing with deionized water to remove epiphytes and sediment. Fish were gutted and rinsed with deionized water; the remainder was

used for isotopic analysis. Plant and animal tissues were dried at 50°C, and ground to a fine powder using an automated mortar and pestle (Wig-L-Bug™; Crescent Dental Corp., Lyons, IL). Prior to C and N isotopic analysis, a subsample of the powdered material was pre-treated with dilute HCl (0.1% PtCl_2 in 0.1 N HCl) to remove inorganic carbon (Wainright & Fry 1994). PM filters and benthic microalgae samples that were used for C and N isotopic analysis were first scraped from a filter with a scalpel, dried, powdered by hand in a mortar and pestle, acidified, and then re-dried. Filters for S isotopic analysis were treated similarly, except that they were rinsed with deionized water prior to scraping, and were not acidified.

Stable isotope ratio analysis. Powdered samples were loaded into tin capsules and analyzed on a Europa Scientific continuous-flow, elemental analyzer (ANCA-GSL)/mass spectrometer (20-20) stable-isotope ratio-analysis system. The system determines C and N isotopic ratios and C and N content from a single sample. Sulfur-isotope ratios were determined on separate subsamples. Analytical precision was ~0.1 to 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values, and 0.3‰ for $\delta^{34}\text{S}$ values, based on repeated analysis of the same samples. Secondary organic standard materials (egg powder and aquatic plant from National Institute of Standards and Technology [NIST], for animal and plant material, respectively) and blanks were routinely analyzed for quality control/assurance. DI^{13}C analyses were conducted by acidification (8.5% H_3PO_4 , 0.1 ml per ml sample) of a subsample in a closed vial to release DIC into the headspace as CO_2 . Acidified samples were sonicated in a bath for 10 min to ensure complete release of CO_2 . The CO_2 in the headspace was sampled with a Gilson gas autosampler connected to the ANCA-GSL, and referenced against a reference CO_2 gas cylinder that was calibrated against standard calcium carbonate NBS-19 (from NIST).

Data analysis. Statistical analyses were performed using SuperANOVA software (SAS Inst., Inc., Cary, NC), using a general linear model and Type III sums-of-squares. Month (June, August), creek (Mad Horse, Alloway), and site within creek (upstream, downstream) were the usual effects tested, although we also tested for the effect of creek bank versus marsh surface in our analysis of benthic microalgal biomass data.

RESULTS

Primary producers

The $\delta^{13}\text{C}$ values of primary producers varied over a relatively wide range of ~14‰ (Table 1, Figs. 2 & 3). Suspended PM always had slightly heavier $\delta^{13}\text{C}$ val-

Table 1. *Spartina* spp. and *Phragmites australis*. Stable isotopic compositions of marsh macrophytes. Values are averages in ‰ (SD; n). LMHC, UMHC: Lower and Upper Mad Horse Creek, respectively; LAC, UAC: Lower and Upper Alloway Creek, respectively (see Fig. 1 for study-site locations). Macrophyte samples from Upper Mad Horse Creek in June were not available

Site	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
LMHC				
Jun	<i>S. alterniflora</i>	-12.47 (0.31; 3)	9.02 (0.98; 3)	13.77 (2.58; 3)
	Detritus	-12.27	8.39	15.77
	<i>S. cynosuroides</i>	-12.76	12.04	10.09
	<i>S. patens</i>	-12.78	11.73	10.48
	<i>Scirpus</i> sp.	-25.04	8.69	15.09
Aug	<i>S. alterniflora</i>	-12.50 (0.35; 3)	8.75 (0.58; 3)	11.31 (4.42; 3)
	Detritus	-12.18 (0.08; 2)	6.79 (0.74; 2)	15.62 (1.71; 2)
	<i>S. patens</i>	-13.29 (0.65; 3)	10.39 (0.59; 3)	12.08 (3.56; 3)
	<i>S. cynosuroides</i>	-13.32 (0.12; 3)	10.96 (0.56; 3)	9.57 (2.13; 3)
	Detritus	-12.37	5.92	11.37
UMHC				
Aug	<i>S. alterniflora</i>	-12.49 (0.05; 3)	11.47 (0.88; 3)	17.76 (2.49; 3)
	Detritus	-12.61 (0.46; 3)	10.88 (0.29; 3)	8.26 (2.54; 3)
	<i>S. patens</i>	-12.89 (0.12; 3)	10.47 (1.63; 3)	11.92 (3.45; 3)
	<i>S. cynosuroides</i>	-12.86 (0.03; 3)	12.13 (0.47; 3)	9.63 (1.12; 3)
	<i>P. australis</i>	-25.72 (0.07; 3)	10.35 (1.81; 3)	10.36 (2.19; 3)
LAC				
Jun	<i>P. australis</i>	-26.50 (0.39; 3)	9.62 (1.16; 3)	8.68 (3.85; 3)
	Detritus	-23.84 (2.17; 2)	11.29 (1.50; 2)	13.35 (4.41; 2)
Aug	<i>P. australis</i>	-26.59 (0.52; 3)	9.38 (1.25; 3)	9.40 (0.56; 3)
UAC				
Jun	<i>P. australis</i>	-26.55 (0.74; 3)	10.79 (0.97; 3)	11.64 (3.80; 3)
Aug	<i>P. australis</i>	-26.21 (0.40; 3)	9.59 (0.44; 3)	13.43 (2.22; 3)

ues than *Phragmites australis* values and benthic microalgae always had heavier $\delta^{13}\text{C}$ values than suspended PM but lighter than *Spartina* spp. Nitrogen isotopic compositions of all plant types averaged $\sim 10\text{‰}$, and were less variable than $\delta^{13}\text{C}$ values. At most sites, the $\delta^{15}\text{N}$ values of the various primary producers overlapped substantially. The one exception was the Upper Alloway Creek site in August. The $\delta^{15}\text{N}$ variation and overlap in primary producers may be attributable to the variable sources of dissolved inorganic nitrogen available to all types of primary producers within a creek system (e.g. Wainright et al. 1996, McLelland et al. 1997). The $\delta^{34}\text{S}$ values of all primary producers extended over a range of up to 19‰ at a given site. While there was relatively wide variation within plant taxa (e.g. *S. alterniflora*), there were usually significant differences among taxa. The significant differences in sulfur isotope values between taxa compared with the overlap in nitrogen-isotope values suggested that sulfur isotopes might be more useful in discriminating between organic sources of *Fundulus heteroclitus*. The macrophytes generally had relatively high $\delta^{34}\text{S}$ values (Table 1), while suspended PM had the lowest $\delta^{34}\text{S}$ values (Fig. 2); benthic microalgae (Fig. 3) were often intermediate, and were variable. The relatively large isotopic variation

associated with the benthic microalgae samples is not unlike that reported previously and can be expected given their occurrence at the sediment-water interface (Currin et al. 1995).

Macrophytes

The *Spartina* species had enriched $\delta^{13}\text{C}$ values (Table 1), characteristic of plants with the C_4 photosynthetic pathway (Smith & Epstein 1971). The $\delta^{13}\text{C}$ values were remarkably consistent among the species of *Spartina*, and there was little difference in $\delta^{13}\text{C}$ between June and August for *Spartina* spp. species in the Mad Horse Creek system. In contrast, *Phragmites australis* had relatively light $\delta^{13}\text{C}$ values, typical of C_3 plants, and similar to those reported by Schlacher & Wooldridge (1996). The $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values of macrophytes were more variable than $\delta^{13}\text{C}$ values. This variation most probably reflects site-specific differences in the sources of N and S and their isotopic compositions, as well as hydrology (Mariotti et al. 1984, Cifuentes et al. 1989, McLelland et al. 1997, Stribling et al. 1998). The $\delta^{13}\text{C}$ values of standing-dead *Spartina* spp. were similar to those of live plants (Table 1), but $\delta^{15}\text{N}$ values were lower in standing-dead plants, as has been noted

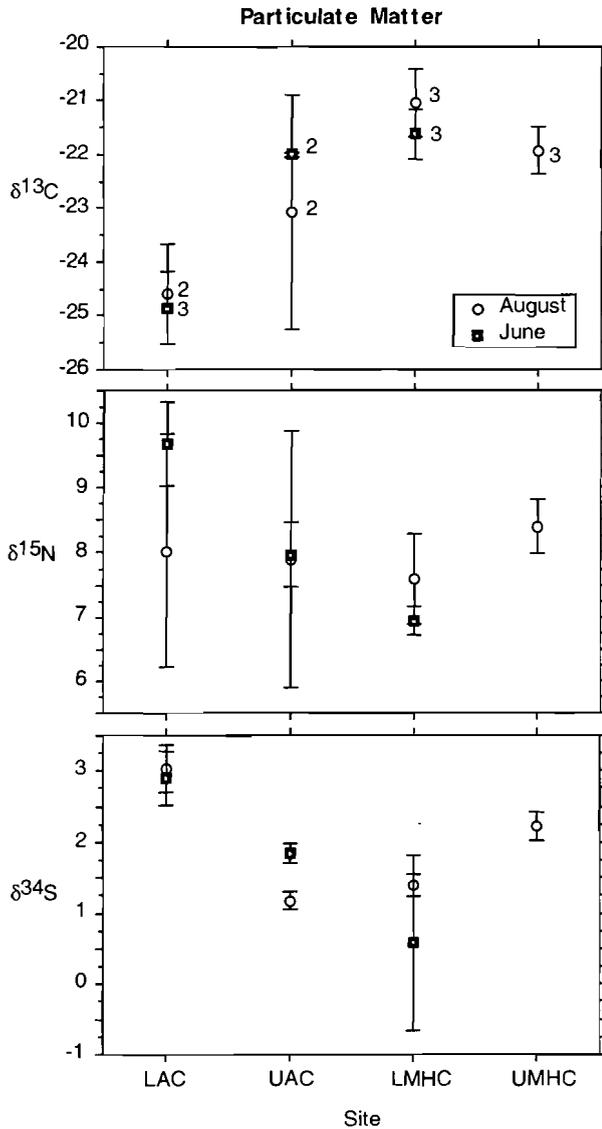


Fig. 2. Stable-isotope compositions (‰) of suspended particulate matter arranged by site and collection date. Error bars = 1 SD of mean; sample size (same for C, N, and S) is given next to each mean value in top panel. LAC: Lower Alloway Creek; UAC: Upper Alloway Creek; LMHC: Lower Mad Horse Creek; UMHC: Upper Mad Horse Creek (see Fig. 1 for study-site locations)

previously (Currin et al. 1995). This detrital depletion in ^{15}N was found in *S. alterniflora* (3 live vs detritus comparisons; the difference was significant: $F_{1,11} = 6.98$, $p = 0.023$) and in *S. cynosuroides* (one comparison), but not in *P. australis* (one comparison; see Table 1). Standing dead *Spartina* spp. had somewhat higher $\delta^{34}\text{S}$ values than live plants at Lower Mad Horse Creek, consistent with the findings of Currin et al. (1995), but this pattern was not apparent in *S. alterniflora* collected at Upper Mad Horse Creek.

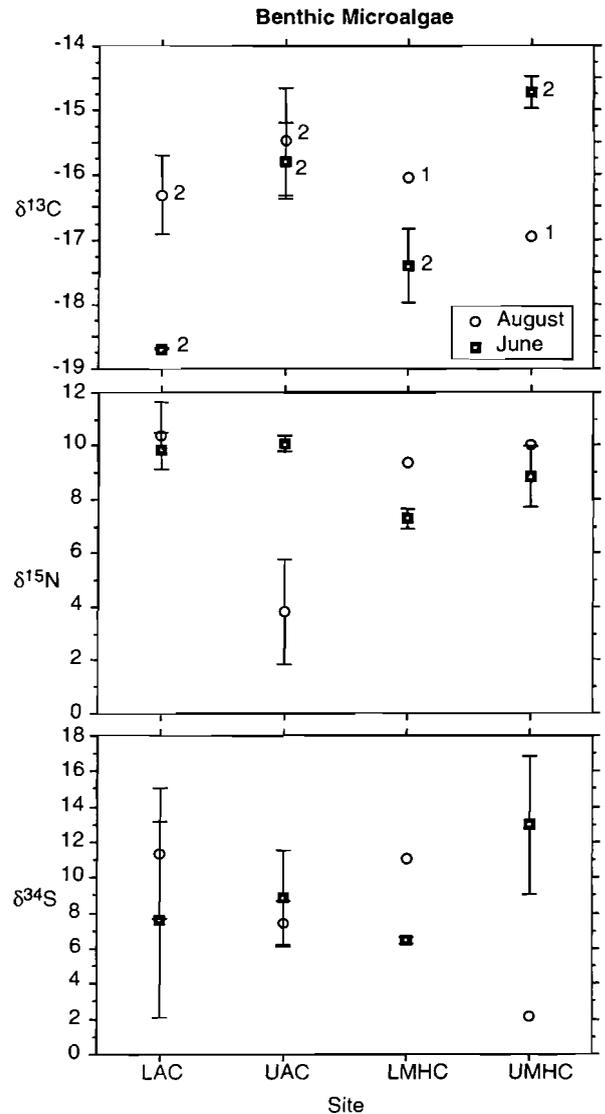


Fig. 3. Stable-isotope compositions (‰) of benthic microalgae arranged by site and collection date. Error bars = 1 SD of mean; sample size (same for C, N, and S) is given next to each mean value in top panel. Site abbreviations as in Fig. 2

Suspended PM

The $\delta^{13}\text{C}$ values of suspended PM were lower at Lower Alloway Creek than at Mad Horse Creek, while PM from Upper Alloway Creek had intermediate $\delta^{13}\text{C}$ values (Fig. 2), possibly because of a greater contribution from *Spartina* spp. because of its greater coverage upstream of our study sites. The $\delta^{15}\text{N}$ values of suspended PM were often higher in the Alloway Creek system than in Mad Horse Creek, particularly at Lower Alloway Creek. The $\delta^{34}\text{S}$ values of suspended PM were more enriched at Lower Alloway Creek than in Mad Horse Creek, while PM from Upper Alloway Creek

had lower $\delta^{34}\text{S}$ values, similar to those of Mad Horse Creek. Seasonal changes in the C, N, or S isotopic composition of PM sometimes occurred, but the direction and magnitude varied between sites. A 2-way ANOVA, using site (4 sites = 2 creeks \times 2 sites within each creek) and date as the 2 main factors showed a highly significant site effect for C and S isotopes ($F_{3,11} = 14.53, 11.34, p = 0.0004$ and 0.0011 , respectively), a nearly significant site effect for $\delta^{15}\text{N}$ values ($F_{3,11} = 2.90, p = 0.08$), and no significant date effect ($F_{1,11} = 0.28, 0.53, 0.10, p = 0.87, 0.48, 0.76$; C, N, S isotopes, respectively) nor site \times date interaction ($F_{2,11} = 1.16, 2.05, 1.99, p = 0.35, 0.17, 0.18$, respectively). Phytoplankton were abundant, with suspended chlorophyll concentrations ranging from ~ 6 to $30 \mu\text{g l}^{-1}$ and chlorophyll/phaeophytin ratios were usually >1 (Table 2).

Benthic microalgae

Benthic microalgal biomass (as chlorophyll) varied between and within creek systems, (Fig. 4). Biomass was higher on muddy creek banks than in sediments amongst macrophyte stems on the marsh surface in both creek systems (4-way ANOVA with creek, month, site within a creek, marsh surface vs creek bank as 4 factors; $F_{1,81} = 18.47, p < 0.0001$), which is consistent with our initial hypothesis that shading by macrophytes

Table 2. Concentrations of chlorophyll *a* (chl *a*), phaeopigments (both in mg m^{-3}) and ratio of chlorophyll to phaeopigments in creek water at the 4 sampling stations. LMHC, UMHC: Lower and Upper Mad Horse Creek, respectively; LAC, UAC: Lower and Upper Alloway Creek, respectively (see Fig. 1 for study-site locations). Standard deviations ($n = 3$) are given in parentheses below each mean

Site	Chl <i>a</i>	Phaeopigments	Chlor/phaeo
June 1997			
LMHC	6.40 (0.75)	16.43 (0.55)	0.39 (0.06)
UMHC	22.62 (0.60)	17.80 (1.55)	1.28 (0.12)
LAC	9.95 (0.67)	7.29 (0.27)	1.37 (0.09)
UAC	9.67 (0.95)	10.67 (0.78)	0.91 (0.16)
August 1997			
LMHC	21.06 (1.30)	18.82 (1.56)	1.13 (0.16)
UMHC	29.40 (0.72)	18.40 (1.77)	1.61 (0.14)
LAC	10.72 (1.09)	7.90 (1.02)	1.36 (0.08)
UAC	13.18 (1.45)	12.03 (0.70)	1.10 (0.12)

may limit the biomass of benthic microalgae in both systems (Gallagher & Daiber 1974, Sullivan & Daiber 1975, Van Raalte et al. 1976). This shading effect appears to be greater in *Phragmites australis* marshes than in *Spartina* spp. marshes. When the 2 creek systems were analyzed separately, the creek bank sediments at Alloway Creek, where *P. australis* dominates, had approximately double the benthic chlorophyll as sediments on the marsh surface ($F_{1,37} = 28.06, p < 0.0001$). The creek bank versus marsh surface difference was only marginally significant in Mad Horse Creek, where the *Spartina* spp. community dominates ($F_{1,40} = 3.79, p = 0.059$), and there was a significant month \times site interaction ($F_{1,40} = 4.44, p = 0.042$) because a difference existed in June but not August. Overall, the biomass of benthic microalgae was higher at Mad Horse Creek sites than in Alloway Creek ($F_{1,81} = 8.77,$

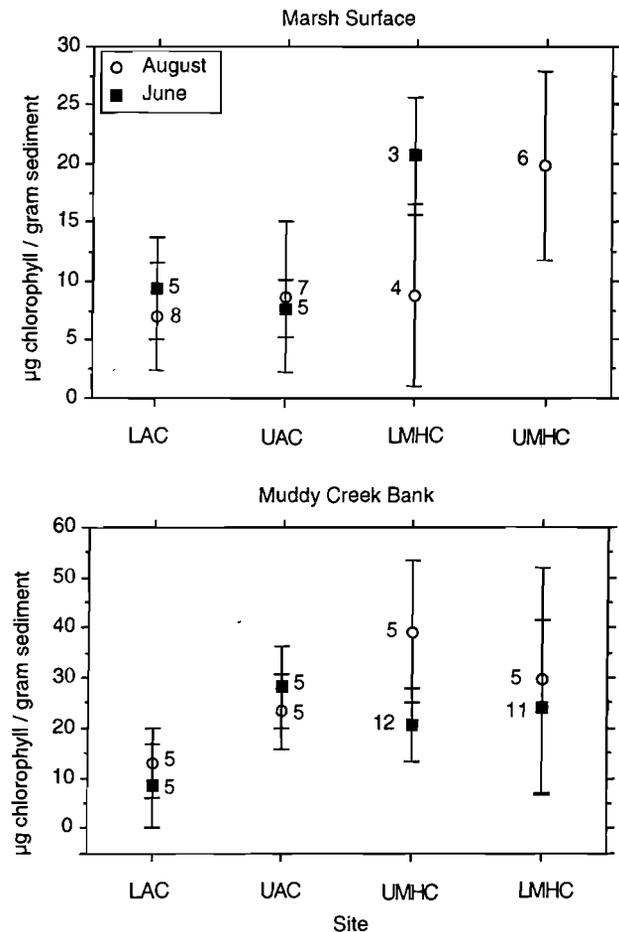


Fig. 4. Sediment chlorophyll concentrations ($\mu\text{g g}^{-1}$ dry sediment) in uppermost 0.3 cm of sediment on marsh surface, and on muddy creek bank (note different scales). Error bars = 1 SD of mean, sample size is given next to each mean value. Site abbreviations as in Fig. 2

$p = 0.004$), both on the marsh surface and on the muddy creek banks. However, benthic microalgal biomass was highly variable within sites. For example, when data from all sites were combined, the muddy creek banks at upstream sites had more benthic microalgal biomass than downstream sites ($F_{1,45} = 5.38$, $p < 0.025$). We could not detect a significant difference in benthic microalgal biomass between June and August in either creek system ($F_{1,40} = 0.17$ and $F_{1,40} = 0.05$ for Mad Horse and Alloway Creeks, respectively, $p > 0.05$). The ratio of chlorophyll to phaeophytin was higher when biomass was higher ($r^2 = 0.64$, $n = 85$; all sites combined; $p < 0.0001$), suggesting that when biomass is greater it may be less degraded.

The benthic microalgae C and N isotopic data revealed significant site effects ($F_{3,6} = 9.38$ and 5.90 , $p = 0.01$ and 0.03 , respectively) and significant site \times date interactions ($F_{3,6} = 10.16$ and 10.71 , $p = 0.009$ and 0.008 , respectively). Most of our samples were from the muddy creek bank, and so we did not have sufficient replication to determine whether there were isotopic differences between microalgae from that habitat versus the marsh surface. Variation among sites was greater in June for C isotopes and in August for N isotopes (Fig. 3), but there was not a consistent isotopic difference for C or N between creek systems. Increases in $\delta^{13}\text{C}$ as the summer progressed were more apparent at the downstream sites in both creek systems.

Fundulus heteroclitus

Fundulus heteroclitus data revealed significant site effects for C, N, and S isotopes ($F_{3,108} = 397$, 23.4 , 2.99 , $p = 0.0001$ and 0.0001 , and 0.03 , respectively), significant date effects for N and S isotopes ($F_{1,108} = 17.11$, 89.36 , $p = 0.0001$ and 0.0001 , respectively) and significant site \times date interactions for C and N isotopes ($F_{3,108} = 5.44$, 21.43 , $p = 0.0016$ and 0.0001 , respectively). The isotopic composition of *F. heteroclitus* was relatively consistent within a site, with a range of 2 to 3‰ in C, N, and S isotope values. Site differences in $\delta^{13}\text{C}$ values were apparent among but not within creeks (i.e. Lower and Upper sites were not distinguishable within a creek: Fig. 5). Significant differences in $\delta^{15}\text{N}$ values existed both among and within creek systems. The $\delta^{15}\text{N}$ values showed a seasonal decrease at Upper Mad Horse Creek and at Upper Alloway Creek. The $\delta^{34}\text{S}$ values of *F. heteroclitus* showed a consistent, and highly significant, seasonal increase at all sites (Fig. 5). The most likely explanation for this seasonal difference is a seasonal increase in the importance of macrophyte detritus in the food web leading to *F. heteroclitus* (see subsection 'Trophic linkages in *Phragmites australis*-dominated marsh').

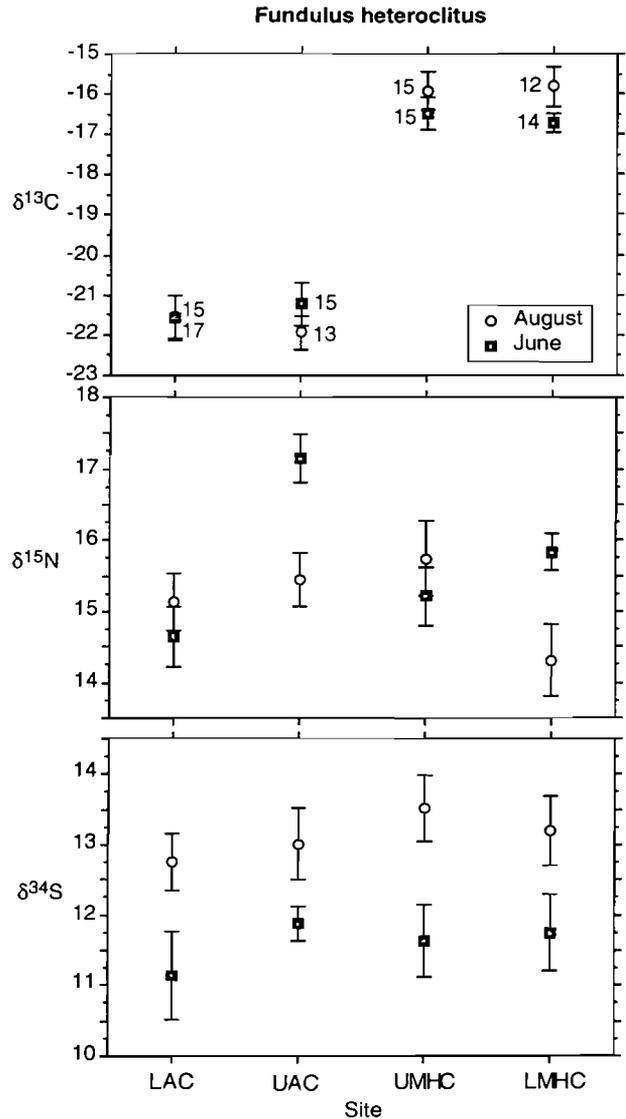


Fig. 5. *Fundulus heteroclitus*. Stable-isotope compositions (‰) of juveniles arranged by site and collection date. Error bars = 95% confidence intervals, sample size (same for C, N, and S) is given next to each mean value in top panel. Site abbreviations as in Fig. 2

DISCUSSION

Trophic linkages in *Spartina alterniflora*-dominated marsh

Ideally, 2 isotope ratios would be sufficient to identify the proportions of 3 food sources in a mixture, but only if those sources occupy a plane, rather than a line, in 2-dimensional isotopic space (see also Fry & Sherr 1984). In June 1997 at Lower Mad Horse Creek (Fig. 6a), the primary producers all fell along a relatively straight line on a plot of $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ values, i.e.,

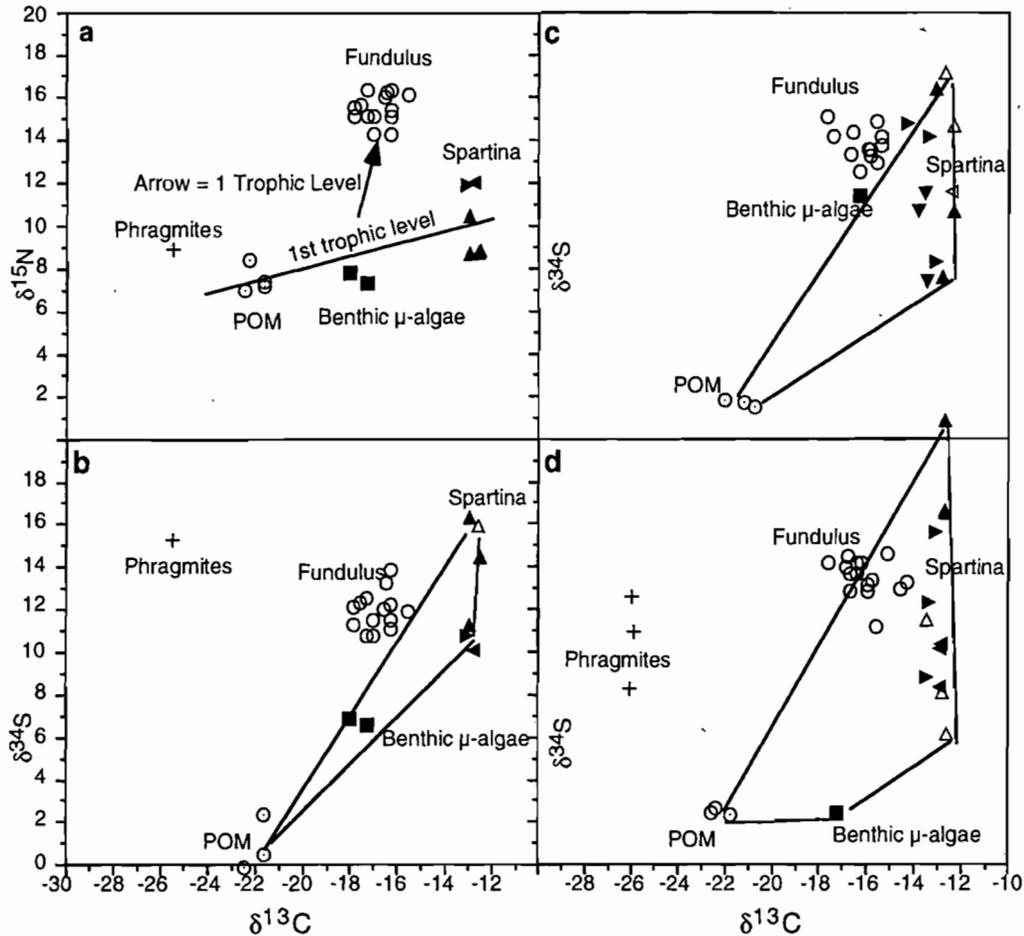


Fig. 6. Two-dimensional isotope plots (‰) of *Fundulus heteroclitus* (O) and primary producers, showing trophic linkages in Mad Horse Creek (see Fig. 1). (a, b) $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ plots of data from Lower Mad Horse Creek, June 1997; (c, d) $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ plots of data from Lower Mad Horse Creek and Upper Mad Horse Creek, August 1997, respectively. (\blacktriangle) *Spartina alterniflora*, (\blacktriangleleft) *S. cynosuroides*, (\blacktriangleright) *S. patens*, (Δ , \triangleleft , \triangleright) detritus of these species; (+) *Phragmites australis* (which occurs in this creek system in low densities); (O) particulate organic matter (POM); (\blacksquare) benthic microalgae; arrows: trophic enrichment

not a plane. Therefore, even though the arrow in Fig. 6a (representing the enrichment in C and N isotope values associated with a shift of 1 trophic level) can be followed backwards from *Fundulus heteroclitus* to benthic microalgae as the source, there are other solutions to the problem. For example, a mixture of the other 2 primary producers (*Spartina* spp. and PM), or all 3, could have the same isotopic composition as benthic microalgae. In contrast, sulfur and carbon isotopic data (Fig. 6b) suggest that *Spartina* spp. is ultimately a significant source of C and S to *F. heteroclitus*. If this is true, however, then either PM or benthic microalgae would need to be added to balance the extremely high $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values of *Spartina* spp., and thus to produce a mixture with the $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ compositions of *F. heteroclitus*. A similar picture emerged in August at Lower Mad Horse Creek (Fig. 6c) and Upper Mad

Horse Creek (Fig. 6d), except that the $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ compositions of *F. heteroclitus* were even more closely aligned with those of *Spartina* spp. (Macrophyte samples for June 1997 at Upper Mad Horse Creek were not available.)

We used 2-source mixing models, with *Spartina* spp. and PM as the 2 sources, and trophic-enrichment factors from the literature to calculate the relative importance of the primary producers (Table 3). Using this approach, a contribution of 35 to 45% of the carbon and virtually all the sulfur in the tissues of *Fundulus heteroclitus* in the Mad Horse Creek system is derived from *Spartina* spp. When *Spartina* spp. and benthic microalgae were used as the 2 sources, we estimated a negative contribution of *Spartina* spp.-derived carbon in the tissues of *F. heteroclitus* and a 66% contribution of *Spartina* spp.-derived S. The relatively large nega-

Table 3. Relative contribution (Rel. contr.) of marsh macrophytes (1.0 = complete dependence, 0.0 = no contribution) to diet of *Fundulus heteroclitus* in Lower and Upper Alloway Creek (LAC and UAC; dominant macrophyte = *Phragmites australis*) and in Lower and Upper Mad Horse Creek (LMHC and UMHC; dominant macrophyte = *Spartina* spp.) (see Fig. 1). Contributions based on 2-source mixing-models, using macrophytes as one endmember and PM or BMA as the other endmember. Separate models were run for C and S isotopes. Endmember isotopic compositions are site-specific means given in Table 1 and Figs. 2 & 3. Model assumes trophic enrichment of 1‰ for each of 2 trophic levels for C isotopes, and no trophic enrichment for S isotopes (Peterson & Fry 1987). Macrophyte data includes standing-dead plants. Mean contributions >1 (>100%) are not significantly different from 1.0 (Sokal & Rohlf 1981). Negative mean contributions indicate those 2 sources alone do not account for that element

Site/month	Suspended particulate matter (PM)		Benthic microalgae (BMA)	
	Rel. contr. C	Rel. contr. S	Rel. contr. C	Rel. contr. S
Mad Horse Creek				
LMHC/Jun	0.35	0.87	-0.22	0.47
LMHC/Aug	0.36	1.17	-0.90	0.59
UMHC/Aug	0.45	1.13	0.05	0.93
Mean (SD)	0.39 (0.05)	1.06 (0.16)	-0.36 (0.49)	0.66 (0.24)
Alloway Creek				
LAC/Jun	-2.21	0.82	0.72	1.20
LAC/Aug	-0.51	1.21	0.71	-0.70
UAC/Jun	0.29	0.82	0.69	1.08
UAC/Aug	0.27	0.80	0.79	0.93
Mean (SD)	-0.54 (1.18)	0.91 (0.20)	0.73 (0.04)	0.63 (0.89)

tive contribution indicates that those 2 sources did not adequately explain the isotopic composition of *F. heteroclitus*. The different results for C versus S isotopes is interesting, and suggests that consumers may assimilate elements from different sources in different proportions. For example, *F. heteroclitus* may utilize organic matter derived from *Spartina* spp. for a relatively large proportion of its protein synthesis (based on S isotopes), while a smaller proportion of other compounds are derived from that source (based on C isotopes). Nitrogen-isotope values might also be good indicators of the source of protein, but in this study nitrogen isotopes were not suitable for distinguishing among primary producers.

We conclude that the organic-matter source for *Fundulus heteroclitus* in the *Spartina* spp.-dominated marsh at Mad Horse Creek is a mixture of *Spartina* spp. plus 1 or both of the other 2 primary producers. The importance of multiple organic sources to *F. heteroclitus* was apparent at 2 sites within the Mad Horse Creek system, and on 2 dates. This result is similar to those obtained in other *Spartina* spp.-dominated systems (Kneib et al. 1980, Peterson et al. 1985, 1986, Currin et al. 1995, Deegan & Garritt 1997, Stribling & Cornwell 1997).

Using a similar approach, Peterson et al. (1985) demonstrated that the relative importance of organic sources to ribbed mussels, *Guekensia demissa*, depended on their location within a marsh. For example, mussels collected at interior-marsh locations had isotopic signatures reflecting a diet based upon 80% *Spartina* spp., while mussels collected near the open estuary had diets based upon 70% plankton and 30%

Spartina spp. The authors suggested that the diet of consumers may be qualitatively different at various locations. Their findings support the concept that marsh detritus is distributed along a gradient, and may be more important to consumers in the smallest marsh creeks relative to larger creeks nearer the ocean. Our results did not show large differences between our Lower and Upper sites, perhaps because our Upper sites were larger creeks than those of Peterson et al. (1985), or because our sites had lower salinities. Our results also differ from those of Sullivan & Moncreiff (1990), who found a minor contribution of *Spartina* spp. relative to benthic microalgae in the isotopic composition of *Fundulus heteroclitus*.

Trophic linkages in *Phragmites australis*-dominated marsh

At both the Lower and Upper sites in Alloway Creek, in both June and August, the majority of the C and S in the tissues of *Fundulus heteroclitus* appeared to be derived from a combination of *Phragmites australis* and benthic microalgae (Fig. 7). As in Mad Horse Creek, the primary producers fell approximately along a straight line in the $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ plots, making it impossible to distinguish their relative importance to *F. heteroclitus* using carbon and nitrogen isotopes alone (data not shown). However, the $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ plots (Fig. 7) suggest that PM is relatively unimportant and macrophytes are very important at both Upper and Lower Alloway Creek sites. If the $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ values of PM accurately reflect the isotopic composition of

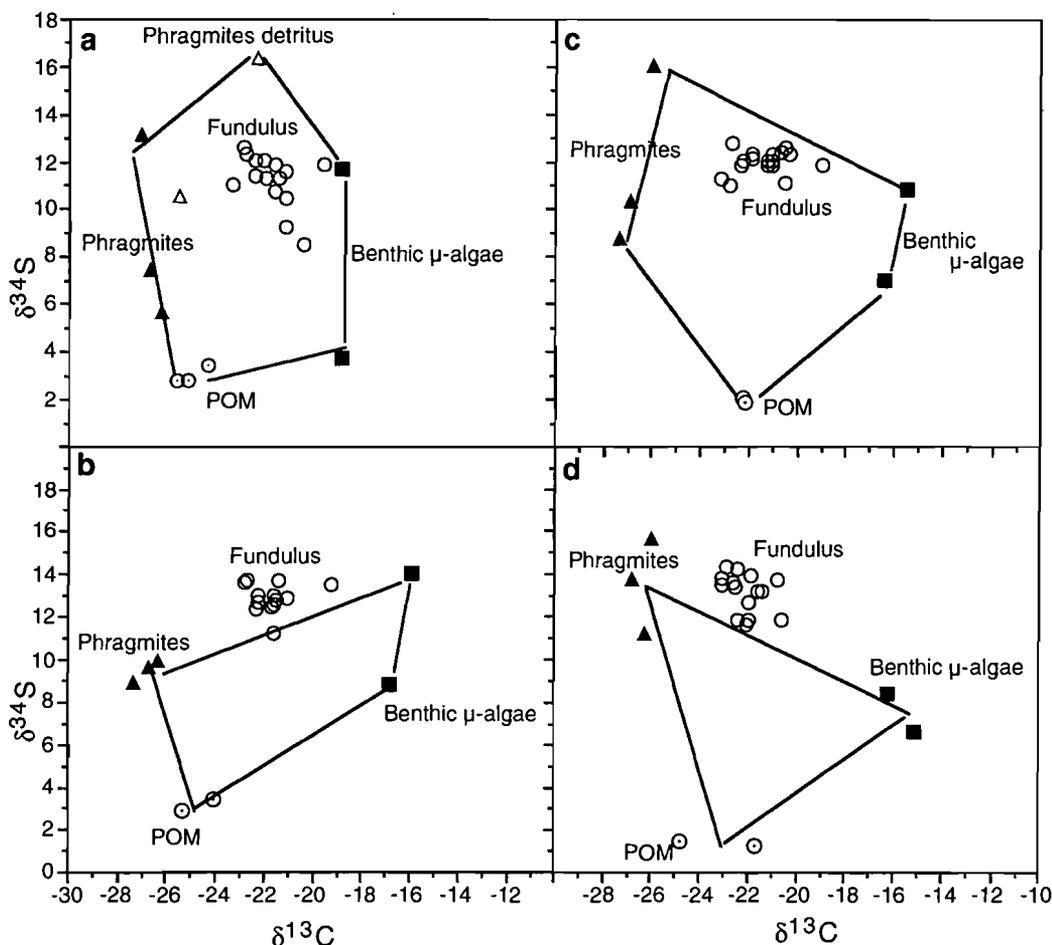


Fig. 7. Two-dimensional isotope plots of *Fundulus heteroclitus* (O) and primary producers, showing trophic linkages in Alloway Creek (see Fig. 1). (a, b) $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ plots for Lower Alloway Creek, June and August 1997, respectively; and (c, d) $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ plots for Upper Alloway Creek, June and August 1997, respectively. (\blacktriangle) *Phragmites australis*, (\triangle) detritus of *P. australis*; (\circ) particulate organic matter (POM); (\blacksquare) benthic microalgae

phytoplankton (see subsection 'Sources and isotopic composition of PM', below) then phytoplankton appear to be of relatively minor importance in *F. heteroclitus* food webs in both creek systems.

In the Alloway Creek system, 2-source mixing models, using *Phragmites australis* and benthic microalgae as the 2 sources, indicated that 69 to 79% of the carbon and 63% of the sulfur in the tissues of *Fundulus heteroclitus* was derived, ultimately, from *P. australis* (Table 3). Similar mixing models, but using *P. australis* and PM as the sources, indicated that *P. australis* made a negative contribution (-54%) to the carbon and a 91% contribution to the sulfur in *F. heteroclitus*. Again, the negative contribution indicates that these 2 sources are not the only organic sources of *F. heteroclitus*. The greater importance of macrophyte detritus in Alloway Creek conforms to our initial hypothesis that benthic microalgae are less important in *P. australis*- than in *Spartina* spp.-dominated systems. However, the over-

lap in isotopic signatures of benthic microalgae and PM in Mad Horse Creek prevents us from eliminating phytoplankton as an important source in that system. If *F. heteroclitus* actually depends upon benthic microalgae to a similar extent in *P. australis* and *Spartina* spp. marshes, this may indicate preferential use of habitats where benthic microalgae are available to the food web, such as frequently flooded marsh-edges (Weisberg 1986, Baltz et al. 1993, Smith et al. in press), or a marsh surface that is not severely shaded by macrophytes.

We believe that the highly significant seasonal increase in $\delta^{34}\text{S}$ values of *Fundulus heteroclitus* at all sites (Fig. 5) most probably represents an increase in the relative importance of macrophyte detritus in the food web. Our June sampling period was at the beginning of the macrophyte growing season, and therefore, available macrophyte detritus would have been principally from the previous growing season, and presum-

ably relatively refractory. Both *Spartina* spp. and *Phragmites australis* have enriched $\delta^{34}\text{S}$ values compared with the other organic sources, and therefore their lack of importance would lead to relatively depleted $\delta^{34}\text{S}$ values (characteristic of other sources) in consumers during that season. Later in the growing season, when labile detrital inputs from macrophytes become more important, the $\delta^{34}\text{S}$ values of consumers would increase.

Trophic level

The trophic level of juvenile *Fundulus heteroclitus* can be estimated using $\delta^{15}\text{N}$ trophic enrichment factors from the literature (Peterson & Fry 1987, Michener & Schell 1994). In our study, this was done by extending the trophic enrichment arrows in Fig. 6a (and similar figures for other sites) backwards from the mean of the *F. heteroclitus* data points to the line that joins the primary producers (calculated by linear regression of $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ plots using *Phragmites australis* and benthic microalgae for Alloway Creek, *Spartina* spp., benthic microalgae and PM for Mad Horse Creek). The trophic level was 2.7 ± 0.3 (SD, $n = 4$) for the Alloway Creek sites, and 2.8 ± 0.5 (SD, $n = 3$) for the Mad Horse Creek sites. This suggests that *F. heteroclitus* feeds relatively low in the food chain, mostly on herbivores (trophic level = 2), supplemented perhaps with plant material (trophic level = 1). Although previous studies have shown that *F. heteroclitus* does not grow while fed on a diet of *Spartina* spp. detritus alone (Prinslow et al. 1974), our results show that under field conditions a substantial portion of the carbon and sulfur in the tissues of *F. heteroclitus* is attributable, ultimately if not directly, to macrophyte production. Unidentifiable detrital material was the dominant item in the guts of YOY *F. heteroclitus* at a different Delaware Bay *Spartina* spp. marsh site (Smith et al. in press), followed by harpacticoid copepods, annelid worms, crustaceans and insects. Given the focus of that study on the ingested diet of *F. heteroclitus*, Smith et al.'s results may have included detritus ingested incidentally, whereas the present study emphasizes the assimilated portion of the diet.

Sources and isotopic composition of PM

While estuarine suspended organic matter may have multiple sources, several lines of evidence suggest that the PM in our study was composed principally of phytoplankton.

First, the DI^{13}C values of water samples collected concurrently with the suspended PM were lower in

Alloway Creek than in Mad Horse Creek. Depleted DI^{13}C values have been reported previously for nearby low salinity environments (Stribling & Cornwell 1997, Wainright et al. 1999) where *Phragmites australis* tends to occur. Assuming a fractionation of 20‰ between DIC and phytoplankton (Fry & Wainright 1991, Fogel et al. 1992, Fry 1996, Chanton & Lewis 1999), the $\delta^{13}\text{C}$ of suspended PM was consistent with the predicted $\delta^{13}\text{C}$ value of phytoplankton that assimilate that DIC (Table 4, Fig. 2).

Another potential explanation for the lower $\delta^{13}\text{C}$ values of suspended PM in Alloway Creek is the input of detrital *Phragmites australis* (a C_3 plant, with relatively depleted $\delta^{13}\text{C}$ values). However, if macrophyte detritus contributed strongly to the suspended PM, then one might expect a relatively large isotopic difference between the suspended PM from those 2 creeks, reflecting the ca 13 to 14‰ difference in $\delta^{13}\text{C}$ between *Spartina* spp. and *P. australis* (Table 1). The measured difference was much smaller (ca 2 to 4‰; Fig. 2).

Thirdly, the ratio of particulate organic carbon to chlorophyll (POC/chlor) was generally <200 (Table 4) and the C/N ratio of PM was 8.3 ± 0.8 (data not shown). These ratios were used previously in the Delaware River estuarine system (Cifuentes et al. 1988) to distinguish POM dominated by phytoplankton (POC/chlor <200, POC/PN ~8) from that composed principally of degraded detrital material (POC/chlor: 200 to 600, POC/PN > 8). For comparison, the POC/PN ratios of macrophytes (including detritus) in our study were 34 ± 25 . We acknowledge that C/N ratios of ~8 would not

Table 4. Data pertaining to phytoplankton content of particulate matter (PM) at 4 study sites. Estimation of $\delta^{13}\text{C}$ of phytoplankton ($\delta^{13}\text{C}$ -phyto) from DI^{13}C . Phytoplankton $\delta^{13}\text{C}$ was estimated by assuming 20‰ fractionation of CO_2 upon uptake by phytoplankton (Fry & Wainright 1991, Fogel et al. 1992, Fry 1996). Ratio of POC/chlorophyll (POC/chlor) is expressed on weight basis. Values up to 200 are associated with relatively undegraded phytoplankton, values >200 contain significant amounts of degraded detrital material (Cifuentes et al. 1988)

Site	DI^{13}C (‰)	SD	n	Predicted $\delta^{13}\text{C}$ -phyto	POC/chlor
June					
LMHC	-1.78	0.56	6	-21.78	346
UMHC	-2.47	1.54	3	-22.47	
LAC	-3.75	0.30	3	-23.75	115
UAC	-3.64	0.99	9	-23.64	293
August					
LMHC	-1.49	0.28	3	-21.49	170
UMHC	-2.92	0.10	3	-22.92	80
LAC	-3.76	0.44	3	-23.76	79
UAC	-3.64	1.27	3	-23.85	172

distinguish between phytoplankton and resuspended benthic microalgae.

Finally, the $\delta^{34}\text{S}$ values of suspended PM were distinctly depleted compared with those of macrophytes, suggesting that macrophyte detritus (the other likely contributor) was not the source of the suspended PM. Alternative explanations for the depleted $\delta^{34}\text{S}$ values include possible contamination by reduced inorganic S (Chanton & Lewis 1999) and/or inclusion of resuspended benthic microalgae in the PM (Shaffer & Sullivan 1988, Tester et al. 1995). While there is also the possibility that our benthic microalgae samples could be contaminated with inorganic S, the collection technique gave us more control over the purity of the sample than did the collection technique for PM.

Whereas marine phytoplankton typically have $\delta^{34}\text{S}$ values around 18.6‰ (similar to the $\delta^{34}\text{S}$ values of the abundant sulfate in seawater; Peterson et al. 1986), the availability of sulfate at our study sites, which all had low salinities, was presumably much lower. Furthermore, sulfate-reducing sedimentary bacteria strongly fractionate S isotopes (30 to 70‰; Peterson & Fry 1987) and may significantly alter the relative sizes and isotopic compositions of dissolved inorganic sulfur pools in porewaters, particularly late in the growing season. This could produce an isotopic effect in macrophytes that utilize that sulfur (Peterson et al. 1986, Stribling et al. 1998). However, we do not have sufficient information to know whether or not the $\delta^{34}\text{S}$ values of phytoplankton would be affected. It is noteworthy that sediments at the study sites did not have the 'rotten egg' odor characteristic of salt-marsh sediments where sulfate reduction is a dominant process, again suggesting relatively low availability of sulfate (Odum 1988).

Concluding remarks

Given the current controversy over the relative value of *Phragmites australis* versus *Spartina* spp.-dominated marsh systems in terms of habitat for marsh consumers, and the lack of isotopic data pertaining to this issue, our findings are significant. *P. australis* is the dominant marsh plant in a large proportion of the marshes in the Delaware Bay estuary (Hollings & Gallagher 1992, Sneddon et al. 1995) and in many other estuaries in the northeastern USA (Niering & Warren 1977, Roman et al. 1984, Marks et al. 1993). Its perceived poor value as habitat for consumers is a main reason behind current efforts to 'restore' *P. australis*-dominated marshes back to marshes dominated by *Spartina* spp. (Jones & Lehman 1987, Marks et al. 1993, Weinstein et al. 1997, Weinstein & Balleto 1999). Yet, issues other than food quality per se, such as access to the marsh surface, or refuge from predators may

clearly be involved (Weinstein & Balleto 1999). Previous studies conducted to evaluate the value of *P. australis* habitats, using abundances of invertebrates (Fell et al. 1998) and vertebrates (Fell et al. 1998, Able 1999, L. K. Benoit unpubl.) and their food habits as surrogates of habitat quality, have shown mixed results. Studies of fishes (primarily *Fundulus heteroclitus*) in Connecticut River marshes collected within 5 m of the creek bank suggested that the juvenile and adult fish were of similar abundance in a variety of vegetation types including *Spartina* spp. and *P. australis*, and that the diet of *F. heteroclitus* was similar in these vegetation types (Fell et al. 1998). However, in a comparison of the abundances of larval and juvenile fishes (primarily *F. heteroclitus*) on marsh surfaces dominated by *Spartina* spp. versus *P. australis* in the Mullica River in southern New Jersey, fish abundance was drastically reduced at *P. australis* sites during extensive sampling with pit traps in 1997 and 1998 (Able 1999, Able & Hagan unpubl. data). As a result of these variable results, more research is needed to evaluate the habitat use and production of consumers in *P. australis* marshes relative to marshes dominated by other marsh vegetation.

Acknowledgements. This study was made possible by grants from the Marsh Ecology Research Program and New Jersey's Public Service Electric and Gas Company. We thank B. Bush, B. Lemasson, M. Mehlig, K. Bosley, C. Fuller and S. Litvin for their assistance with field sampling and sample preparation. The manuscript benefited from critical reviews by K. Bosley, C. Fuller and 2 anonymous reviewers. The bulk of the carbon and nitrogen stable isotopic analyses were performed at the University of Alaska by N. Haubenstock, while sulfur isotopic analyses were done in the laboratory of C. Scrimgeour (Scottish Crop Institute) through an agreement with Europa Scientific, Inc. This is Contribution No. 2000-02 of the Institute of Marine and Coastal Sciences, Rutgers University, and Report 09-99 of the U.S. Coast Guard Academy's Center for Advanced Studies.

LITERATURE CITED

- Able KW (1999) Measures of juvenile fish habitat quality: examples from a national estuarine research reserve. In: Benaka LR (ed) Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Bethesda, MD, Symp No. 22
- Able KW, Fahay MP (1998) The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, NJ
- Baltz DM, Rakocinski C, Fleeger JW (1993) Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Env Biol Fish* 36:109-126
- Bigelow HB, Schroeder WC (1953) Fishes of the Gulf of Maine. *Fishery Bull Fish Wildl Serv US* 74:1-576
- Chanton JP, Lewis FG (1999) Plankton and dissolved inorganic carbon isotopic composition in a river-dominated estuary: Apalachicola Bay, Florida. *Estuaries* 22:575-583

- Cifuentes LA, Sharp JH, Fogel ML (1988) Stable carbon and nitrogen isotope biogeochemistry in the Delaware estuary. *Limnol Oceanogr* 33:1102–1115
- Cifuentes LA, Fogel ML, Pennock JR, Sharp JH (1989) Biogeochemical factors that influence the stable nitrogen isotope ratio of dissolved ammonium in the Delaware estuary. *Geochim Cosmochim Acta* 53:2713–2721
- Couch CA (1989) Carbon and nitrogen stable isotopes of meiobenthos and their food resources. *Estuar Coast Shelf Sci* 28:433–441
- Currin CA, Newell SY, Paerl HW (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Mar Ecol Prog Ser* 121:99–116
- Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. *Mar Ecol Prog Ser* 147:31–47
- DeSylva DP, Kalber FA Jr, Schuster CN (1962) Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper water. University of Delaware Marine Laboratory, Information Series Publications 5:1–64
- Fell PF and 8 co-authors (1998) Does invasion of oligohaline marshes by reed grass, *Phragmites australis* (Cav.) Trin. ex Steud., affect the availability of prey resources for the mummichog, *Fundulus heteroclitus* L.? *J Exp Mar Biol Ecol* 222: 59–77
- Fogel ML, Cifuentes LA, Velinsky DJ, Sharp JH (1992) Relationship of carbon availability in estuarine phytoplankton to isotopic composition. *Mar Ecol Prog Ser* 82:291–300
- Fry B (1996) $^{13}\text{C}/^{12}\text{C}$ fractionation by marine diatoms. *Mar Ecol Prog Ser* 134:283–294
- Fry B, Sherr EB (1984) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contr Mar Sci Univ Tex* 27:13–47
- Fry B, Wainright SC (1991) Diatom sources of ^{13}C -rich carbon in marine food webs. *Mar Ecol Prog Ser* 76:149–157
- Gallagher JL, Daiber FC (1974) Primary production of edaphic algal communities in a Delaware salt marsh. *Limnol Oceanogr* 19:390–395
- Haines EB (1979) Interaction between Georgia salt marshes and coastal waters: a changing paradigm. In: Livingston RJ (ed) *Ecological processes in coastal and marine systems*. Plenum, New York, p 35–46
- Haines EB, Montague CL (1979) Food sources of estuarine invertebrates analyzed using $^{13}\text{C}/^{12}\text{C}$ ratios. *Ecology* 60: 48–56
- Hellings SE, Gallagher JL (1992) The effects of salinity and flooding on *Phragmites australis*. *J Appl Ecol* 29:41–49
- Hughes ER, Sherr EB (1983) Subtidal food webs in a Georgia estuary: ^{13}C analysis. *J Exp Mar Biol Ecol* 67:227–242
- Jones WL, Lehman WC (1987) *Phragmites* control and revegetation following aerial applications of glyphosate in Delaware. In: Whitman WR, Meredith WH (eds) *Waterfowl and Wetlands Symposium*. Delaware Coastal Management Program, Delaware Department of Natural Resources and Environmental Control, Dover, Delaware, p 15–24
- Kneib RT, Stiven AE, Haines EB (1980) Stable carbon isotope ratios in *Fundulus heteroclitus* (L.) muscle tissue and gut contents from a North Carolina *Spartina* marsh. *J Exp Mar Biol Ecol* 46:89–98
- Lotrich VA (1975) Summer home range and movements of *Fundulus heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. *Ecology* 56:191–198
- Management Plan Advisory Committee (1997) *New Jersey Phragmites-dominated site maps*. Brian A. Parent Center at Holly Orchard, Millville, NJ
- Mann KH (1988) Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. *Limnol Oceanogr* 33:910–930
- Mariotti A, Lancelot C, Billen G (1984) Natural isotopic composition of nitrogen as a tracer of origin for suspended organic matter in the Scheldt estuary. *Geochim Cosmochim Acta* 48:549–555
- Marks M, Lapin B, Randall J (1993) Element stewardship abstract for *Phragmites australis*. *Nat Areas J* 14:285–294
- McLelland JW, Valiela I, Michener RH (1997) Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. *Limnol Oceanogr* 42:930–937
- Meredith WH, Lotrich VA (1979) Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). *Estuar Coast Mar Sci* 9:99–118
- Michener RH, Schell DM (1994) Stable isotope ratios as tracers in aquatic food webs. In: Lajtha K, Michener RH (eds) *Stable isotopes in ecology and environmental science*. Blackwell, Cambridge, p 138–157
- Niering WA, Warren RS (1977) Our dynamic tidal marshes: vegetation changes as revealed by peat analysis. *Bull Arboretum Conn* 12:1–22
- Odum WE (1988) Comparative ecology of tidal freshwater and salt marshes. *Annu Rev Ecol Syst* 19:147–176
- Parsons TR, Maita Y, Lalli CM (1984) *A manual of chemical and biological methods for seawater analysis*. Pergamon Press, New York
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 181:293–320
- Peterson BJ, Howarth RW (1987) Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. *Limnol Oceanogr* 32:1195–1213
- Peterson BJ, Howarth RW, Garritt RW (1985) Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227:1361–1363
- Peterson BJ, Howarth RW, Garritt RH (1986) Sulfur and carbon isotopes as tracers of salt-marsh organic matter flow. *Ecology* 67:865–874
- Prinslow TE, Valiela I, Teal JM (1974) The effect of detritus and ration size on the growth of *Fundulus heteroclitus* (L.). *J Exp Mar Biol Ecol* 16:1–10
- Roman CT, Niering WA, Warren RS (1984) Salt marsh vegetation change in response to tidal restriction. *Environ Mgmt* 8:141–150
- Schlacher TA, Wooldridge TH (1996) Origin and trophic importance of detritus—evidence from stable isotopes in the benthos of a small, temperate estuary. *Oecologia* 106:382–388
- Shaffer GP, Sullivan MJ (1988) Water column productivity attributable to displaced benthic diatoms in well-mixed shallow estuaries. *J Phycol* 24:132–140
- Smith BN, Epstein S (1971) Two categories of $^{13}\text{C}/^{12}\text{C}$ ratios for higher plants. *Pl Physiol* 47:380–384
- Smith K, Taghon GL, Able KW (in press) Trophic linkages in marshes: ontogenetic changes in diet for young-of-the-year mummichog, *Fundulus heteroclitus*. In: Weinstein M, Kreeger D (ed) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Amsterdam
- Sneddon LA, Metzler KJ, Anderson M (1995) A classification and description of natural community alliances and community elements of the Delaware Estuary (summary). In: Dove LE, Nyman RM (eds) *Living resources of the Delaware Estuary*. The Delaware Estuary Program, p 3–24
- Sokal RR, Rohlf FJ (1981) *Biometry*. The principles and prac-

- tice of statistics in biological research, 2nd edn. WH Freeman & Co, New York
- Stribling JM, Cornwell JC (1997) Identification of important primary producers in a Chesapeake Bay tidal creek system using stable isotopes of carbon and sulfur. *Estuaries* 20:77–85
- Stribling JM, Cornwell JC, Currin C (1998) Variability of stable sulfur isotopic ratios in *Spartina alterniflora*. *Mar Ecol Prog Ser* 166:73–81
- Sullivan MJ, Daiber FC (1975) Light, nitrogen, and phosphorus limitation of edaphic algae in a Delaware salt marsh. *J Exp Mar Biol Ecol* 18:79–88
- Sullivan MJ, Moncreiff CA (1990) Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. *Mar Ecol Prog Ser* 62:149–159
- Talbot CW, Able KW (1984) Composition and distribution of larval fishes in New Jersey high marshes. *Estuaries* 7:434–443
- Talbot CW, Able KW, Shisler JK (1986) Fish species composition in New Jersey salt marshes: effects of alterations for mosquito control. *Trans Am Fish Soc* 115:269–278
- Taylor MH, DiMichele L (1983) Spawning site utilization in a Delaware population of *Fundulus heteroclitus* (Pisces: Cyprinodontidae). *Copeia* 1983:719–725
- Teo SLH (1999) Movements and population dynamics of the mummichog, *Fundulus heteroclitus*, in a restored salt marsh in New Jersey. MS thesis, Rutgers University, New Brunswick, NJ
- Tester PA, Geesey ME, Guo C, Paerl HW, Millie DF (1995) Evaluating phytoplankton dynamics in the Newport River estuary (North Carolina, USA) by HPLC-derived pigment profiles. *Mar Ecol Prog Ser* 124:237–245
- Valiela I, Wright JE, Teal JM, Volkman SB (1977) Growth, production and energy transformations in the salt-marsh killifish *Fundulus heteroclitus*. *Mar Biol* 40:135–144
- Van Raalte C, Valiela I, Teal JM (1976) Production of epibenthic salt marsh algae: light and nutrient limitation. *Limnol Oceanogr* 21:862–872
- Wainright SC, Fry B (1994) Seasonal variation of the stable isotope compositions of plankton from Woods Hole, Massachusetts, USA, and Georges Bank. *Estuaries* 17:552–560
- Wainright SC, Fuller CM, Michener RE, Richards RA (1996) Spatial variations of growth rate and trophic position of juvenile striped bass (*Morone saxatilis*) in the Delaware River. *Can J Fish Aquat Sci* 53:685–692
- Wainright SC, Fuller CM, McGuinness L (1999) Stable isotopic composition of suspended organic matter in the Mullica River/Great Bay estuary (Southern New Jersey, USA). *Bull NJ Acad Sci* 44:1–11
- Wang JCS, Kernehan RJ (1979) Fishes of the Delaware estuaries: a guide to the early life histories. Ecological Analysis Communications, Towson, MD
- Weinstein MP, Balletto JH (1999) Does the common reed, *Phragmites australis* affect essential fish habitat? *Estuaries* 22:63–72
- Weinstein MP, Balletto JH, Teal JM, Ludwig DF (1997) Success criteria and adaptive management for a large-scale wetland restoration project. *Wetlands Ecol Mgmt* 4:111–127
- Weisberg SB (1986) Competition and coexistence among four estuarine species of *Fundulus*. *Am Zool* 26:249–257

Editorial responsibility: Lisa Levin (Contributing Editor), La Jolla, California, USA

Submitted: April 1, 1999; Accepted: December 13, 1999
Proofs received from author(s): June 13, 2000