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Michael P. Weinstein^{a b}, Steven Y. Litvin^{a b}, Keith L. Bosley^b, Charlotte M. Fuller^b & Sam C. Wainright^b

^a New Jersey Marine Sciences Consortium, Sandy Hook Field Station, Building 22, Fort Hancock, New Jersey, 07732, USA

^b Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey, 08903, USA

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The Role of Tidal Salt Marsh as an Energy Source for Marine Transient and Resident Finfishes: A Stable Isotope Approach

MICHAEL P. WEINSTEIN* AND STEVEN Y. LITVIN

New Jersey Marine Sciences Consortium, Sandy Hook Field Station,
Building 22, Fort Hancock, New Jersey 07732, and
Institute of Marine and Coastal Sciences,
Rutgers University, New Brunswick, New Jersey 08903, USA

KEITH L. BOSLEY, CHARLOTTE M. FULLER, AND SAM C. WAINRIGHT

Institute of Marine and Coastal Sciences,
Rutgers University, New Brunswick, New Jersey 08903, USA

Abstract.—Stable isotope ratios of carbon, nitrogen, and sulfur ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) in bay anchovy *Anchoa mitchilli* and white perch *Morone americana* from Delaware Bay were a function of capture location and, for restored tidal salt marshes, possibly a function of the relative position of the marsh restoration trajectory. White perch collected in polyhaline restoration and reference (Moore's Beach) sites had stable isotope signatures that reflected contributions from both benthic microalgae and *Spartina alterniflora*. Isotope values from white perch captured at the reference site were slightly enriched compared with those captured at the restoration sites. At upper estuary oligo-mesohaline locations, *Phragmites australis* contributed to the isotopic composition of both species. Although *P. australis* was not dominant at the reference marsh (Mad Horse Creek), it also seemed to influence the flow of nutrients into these species. White perch were not collected in open waters of Delaware Bay, but bay anchovy were abundant at offshore sampling stations. A striking result of this study was that stable isotopes that originated in macrophytes and benthic microalgae of salt marshes occurred ubiquitously among bay anchovy collected several kilometers from shore. Interestingly, fish from Mad Horse Creek, a reference marsh where *Phragmites* was abundant only along creek banks, were intermediate in their isotopic composition. Although benthic microalgal signatures varied both within and among sites, the isotopic composition of bay anchovy and white perch was clearly influenced by these primary producers across all marsh types. Particulate organic matter (POM) appeared to play a lesser role in bay anchovy and white perch nutrition, although depletion of POM sulfur due to the presence of inorganic sulfur may have led to underestimates of the contribution of phytoplankton. Further studies are required to elucidate the relative role of phytoplankton in the trophodynamics of these species.

The relative contributions of various plants to the high levels of secondary production observed in estuaries are poorly documented. External (allochthonous) inputs from the watershed, high in situ production by phytoplankton or benthic microalgae, and abundant biomass of marsh macrophytes made available through a detrital pathway have all been proposed to explain high production of estuarine consumers (Nixon 1980, 1988; Mallin and Paerl 1994).

Stable isotope tracers can be a particularly powerful tool for discriminating among nutrient pathways in estuaries, especially where spatial complexity, variations in water and organic matter exchange, and multiple sources of organic matter all

complicate the unraveling of nutrient fluxes that support finfish production (Deegan and Garritt 1997). For example, competing sources of carbon and other nutrients generated in the open estuary were originally overlooked in marsh studies.

Whereas inputs of particulate organic matter from rivers apparently play a relatively minor role, other studies have shown that phytoplankton and benthic microalgae, with their apparent high palatability and assimilation efficiency, and macrophyte detritus are important sources of estuarine secondary production (Coffin et al. 1989; Couch 1989; Peterson et al. 1994). Nixon (1988), however, demonstrated that in addition to these sources, salt-marsh macrophytes must also be included in total estuarine production to explain fish yields.

Using stable isotopes, Deegan and Garritt (1997) noted that consumers in all regions of their "whole estuary" study at Plum Island Sound,

* Corresponding author: mikew@njmsc.org

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Massachusetts, relied most heavily on locally produced organic matter. Proceeding down estuary, organic sources gradually changed from oligohaline (brackish water) phytoplankton and fresh-marsh organic matter to marine phytoplankton, benthic microalgae, and salt-marsh macrophytes in the lower estuary. Within a region, benthic and pelagic consumers appeared to depend on different sources of organic matter. Benthic fauna had enriched $\delta^{13}\text{C}$ and depleted $\delta^{34}\text{S}$ values, indicative of greater reliance on *Spartina* sp. detritus and benthic microalgae, whereas isotope signatures of pelagic fauna suggested greater reliance on phytoplankton (oligohaline or marine).

Other investigators have argued that energy losses associated with detritus processing would render this source of nutrition virtually meaningless by the time it reaches the open waters of the estuary (Peterson and Howarth 1987; Day et al. 1989). Using stable isotopes and a mass balance approach, Cifuentes et al. (1988) calculated the relative contribution of marsh-derived organic carbon to the suspended particulate organic matter concentration to be only 7% in open waters of Delaware Bay. A potentially important confounding factor is the ratio of marsh to open-water volumes (DeLaune and Lindau 1987); in larger open estuaries the marsh signal tends to be diluted. Coffin et al. (1994) attributed much of the divergent opinion on the role of *Spartina*-derived plant detritus in the open estuary to physical processes, which they concluded undoubtedly control the amount of organic matter available. The latter arguments also do not consider storm-induced pulses as potentially important routes of detrital export (Roman 1982) nor the export of nutrients via migratory species that utilize marshes for varying periods and then emigrate to the estuary and coastal zone (Haines 1979; Weinstein 1981; Deegan 1993).

Here we examine the trophic pathways of carbon, nitrogen, and sulfur in Delaware Bay, USA, as they pass from primary producers to a marine transient species, the bay anchovy *Anchoa mitchilli*, and an estuarine resident, the white perch *Morone americana*. Plants investigated included two salt-marsh macrophytes, *Spartina* spp. and *Phragmites australis*, benthic microalgae, and particulate organic matter (POM). For the first time, we link the fate of nutrients from *P. australis* to marine transient and estuarine resident species.

Methods

Site descriptions, salt marshes.—Two formerly diked salt hay farms (SHF) adjoining polyhaline

waters, Commercial Township SHF (1,688 ha) and Dennis Township SHF (234 ha), are currently undergoing restoration on the New Jersey side of Delaware Bay (Figure 1). Moore's Beach (MB), restored in the early 1980s, is a 480-ha polyhaline salt marsh that serves as a reference marsh for the two salt hay farms. Our study also included two sites in the upper bay comprising an oligo-mesohaline marsh complex: Mad Horse Creek (MHC), a relatively undisturbed 1,558-ha reference marsh, and an ongoing 1,253-ha restoration project in the Alloway Creek (AC) marsh system (Figure 1). *P. australis* predominates the vegetation in most brackish marshes of the upper Delaware Bay. A near monoculture of *Phragmites* presently covers more than 16,000 ha of marsh on the Delaware side of the bay, and the magnitude of coverage is similar on the New Jersey side (Weinstein and Balleto 1999). Before restoration was initiated in 1997, *Phragmites* covered more than 70% of the Alloway Creek marsh. Many ten thousands of hectares of surrounding marsh have become similarly predominated by *Phragmites* in the past 40 years (Figure 1; Weinstein and Balleto 1999).

Field collections, fish.—Fish tissue samples were obtained from all marsh sites and from open waters of the Delaware Bay (Figure 1). Bottom otter trawl tows were conducted monthly from June through October 1998 in the marshes and were supplemented by bi-weekly tows at 40 randomly selected stations within the bay. These collections were part of a permit-mandated monitoring study that was required for a power plant located in the upper bay on the New Jersey shore.

The bay anchovy used in this study were captured in open waters of the lower bay and upper bay and in Alloway Creek, Mad Horse Creek, Moore's Beach, Commercial Township SHF, and Dennis Township SHF (Figure 1). Fish were collected in each of five months and sorted into three size-classes (<30 mm, 30–60 mm, >60 mm) that reflected the ontogenetic shifts in feeding that occurs as juveniles include new items in their diet. For each date and location we attempted to analyze up to 15 individuals in each size-class, but this was not always possible. Although not captured in open waters, white perch were obtained from all marsh collections in October. These fish ranged from 105 to 246 mm standard length (SL) and were handled in the same manner as bay anchovy.

Field collection, vegetation.—Predominant vegetation was sampled on three dates: June (when macrophytes were less than 0.5 m in height), Sep-

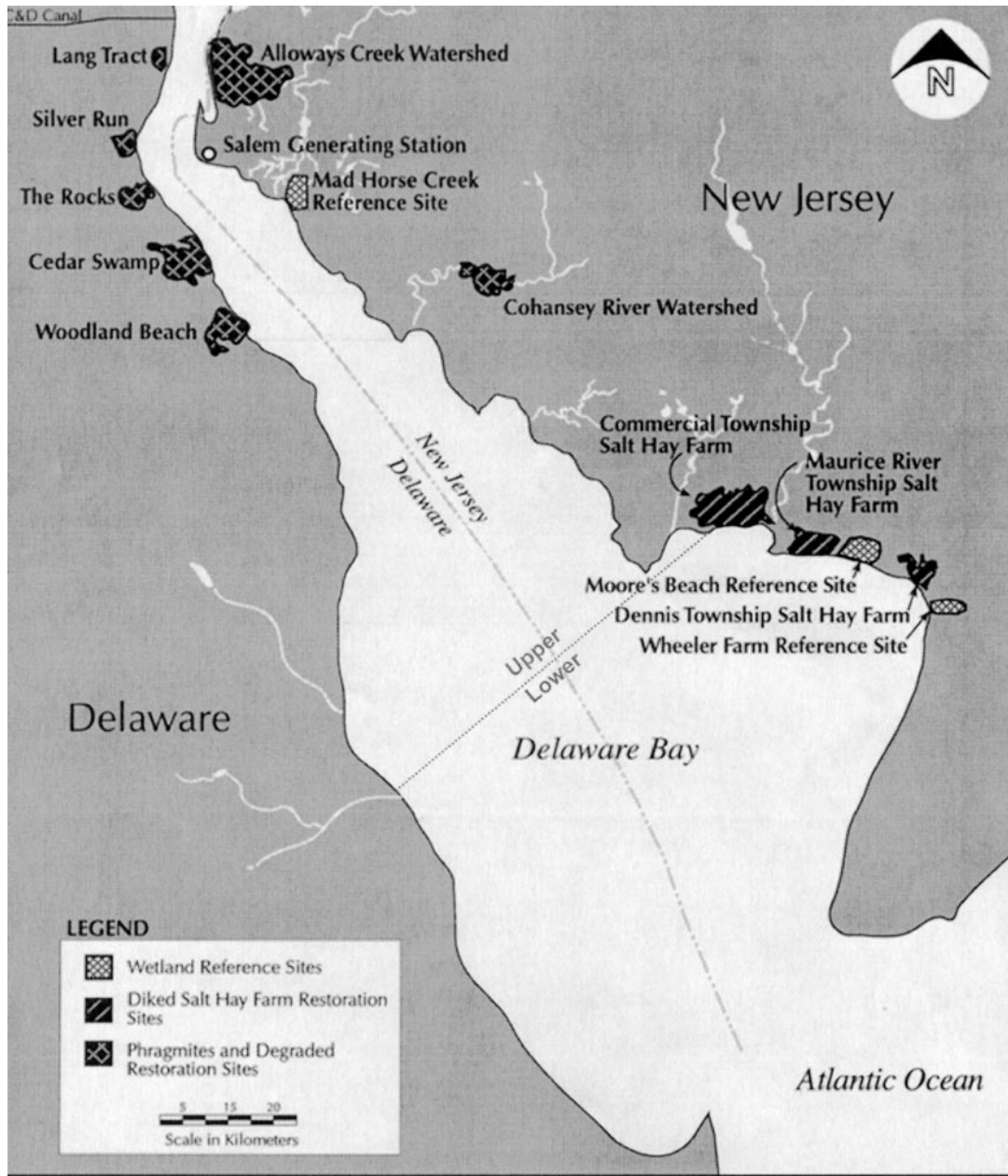


FIGURE 1.—Locations of restored, and reference marshes that formed part of this study. The dotted line denotes the separation between upper, and lower Delaware Bay.

tember (coinciding with early senescence), and October (coinciding with later senescence). Samples were obtained from two locations in Alloway Creek and from Mad Horse Creek and Moore's Beach (Figure 1).

Within each sampling period and when present, *Spartina patens*, *S. cynosuroides*, *S. alterniflora*,

and *P. australis* were collected at three locations on the creek levee and at 30 and 60 m from the creek's edge. At each location, a single leaf was removed from each of five randomly selected plants and combined into a composite sample. During September, additional samples of flowers and dead leaves (lying on the marsh surface, but

still attached to the plant) of each species were collected. In October, sampling was restricted to dead leaves.

Benthic microalgae were sampled in June and September on vegetated and unvegetated (creek-bank and mudflat) areas in the three salt marshes. A "clean" sample of benthic microalgae was obtained by a modification of the techniques of Couch (1989) and Wainright et al. (in press). This technique takes advantage of microalgal vertical migration through 63- μ m Nitex screening.

Field collection, particulate organic matter.—Suspended particulate organic matter was collected in tidal creeks during June and September by filtering known volumes (about 500 mL) of sample water through precombusted glass fiber filters (Whatman GF/F). Surface POM samples were obtained in Alloway Creek, Mad Horse Creek, and Moore's Beach at locations approximately 2 km upstream from the creek mouth on mid-ebb tide and at the creek mouth on mid-flood tide. Mid-flood tide samples were assumed to include a larger influence from open bay sources of POM.

Laboratory preparation of samples, fish.—After removal of their gut, fish were processed, depending on their size, by one of three methods: (1) skin and scales were removed from larger fish and a sample of muscle tissue was excised, (2) heads were removed from smaller fish and the remaining carcass used whole, and (3) postlarvae and early juveniles were randomly selected and pooled whole to supply sufficient tissue for the analyses. A roughly equal quantity of tissue, by weight, from each fish constituted the composite.

Tissue samples were dried to constant weight at 60°C for approximately 48 h and then ground to a fine powder in a Wig-L-Bug automated mortar and pestle (Crescent Inc.) or a Spex/CertiPrep 5100 mixer mill.

Laboratory preparation of samples, vegetation.—The distal two-thirds to three-quarters of each leaf was lightly scraped with a scalpel, then rinsed with deionized water to remove epiphytes. Each leaf was dried in an oven (60°C) to constant weight, and then ground to a fine powder. Approximately 20 mg of ground material was acidified with 1% PtCl₂ in 1 N HCl and then dried at 60°C for 12–24 h. Inorganic sulfur was excluded from benthic microalgal samples by a combination of careful sorting (Currin et al. 1995) and rinsing with isotonic NaCl solution.

Laboratory preparation of samples, particulate organic matter.—All filters were rinsed with deionized water to wash into precombusted shell vi-

als as much of the POM as possible, which was then dried to constant weight. Dried material was then ground and, for the C and N samples, acidified with PtCl₂ in 1 N HCl. Sulfur samples were not acidified.

Preparation of samples for stable isotope analysis.—Samples were weighed to the nearest microgram (Sartorius Micro Scale, model M2P) and loaded into 8 × 5-mm tin capsules (Microanalysis, Inc.). Before use, capsules were rinsed in methanol for 5–10 min, methylene chloride for another 5–10 min, and allowed to dry under a hood. Replicate samples were analyzed for every 8th sample.

Stable isotope analysis.—Isotopic composition is expressed in terms of δ values. The δ notation indicates depletion (–) or enrichment (+) of the heavy isotope relative to the lighter isotope in the following relationship:

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

where $X = {}^{13}\text{C}$, ${}^{34}\text{S}$, or ${}^{15}\text{N}$ and $R = {}^{13}\text{C}/{}^{12}\text{C}$, ${}^{34}\text{S}/{}^{32}\text{S}$, or ${}^{15}\text{N}/{}^{14}\text{N}$ of the samples and the standards. Because measurements are subject to day-to-day fluctuations in sample preparation and instrument performance, the isotopic ratio in a sample is typically compared with a standard so that any fluctuations will be reflected equally well.

Vegetation was analyzed at the Institute of Marine and Coastal Sciences, Rutgers University on a Europa Scientific continuous-flow, elemental analysis system. Sulfur isotope ratios were determined on separate subsamples (about 10 μ g S with V₂O₅ added). Instrument precision is 0.1–0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values and 0.5‰ for $\delta^{34}\text{S}$ (S. Wainright, unpublished data). Fish tissue samples were analyzed at the Environmental Isotope Laboratory, University of Waterloo on a Micro-mass Isochrom Continuous Flow Stable Isotope Mass Spectrometer coupled to a Carla Erba Elemental Analyzer (CHNS-O EA1108). Instrument precision is $\pm 0.2\text{‰}$ for C and $\pm 0.3\text{‰}$ for N.

Data analyses.—Pooled data were examined for normality using Kolmogorov–Smirnov one-sample tests. Main effects were tested with 1-way analysis of variance (ANOVA) and residuals examined for homogeneity of variance. Because the assumptions for parametric ANOVA could not be met in a few instances, a nonparametric approach was adopted for all pair-wise comparisons except fish length (bay anchovy): Kruskal–Wallis k -sample tests with Bonferroni adjustments to 34 values ($34 = 0.05/\text{the number of pair-wise comparisons in the data set}$).

Results

Stable Isotopes Composition of Vegetation and Particulate Organic Matter

Although considerable variation sometimes occurred within taxa, species-specific vegetation and organic matter sources were readily distinguishable on the dual isotope plots (^{13}C versus ^{15}N and ^{13}C versus ^{34}S axes; Figure 2). *Spartina* spp., a C_4 plant, displayed the heaviest (enriched) $\delta^{13}\text{C}$ values, roughly -11‰ to -14‰ , and displayed few differences among species. *Phragmites australis*, a C_3 plant, had depleted $\delta^{13}\text{C}$ values, the lowest (-25‰ to -28‰) among all vegetation categories. Generally, the range of $\delta^{15}\text{N}$ values was smaller, $+5\text{‰}$ to $+15\text{‰}$, and there was more overlap among primary producers than $\delta^{13}\text{C}$ (-11‰ to -28‰) or $\delta^{34}\text{S}$ (-5‰ to $+25\text{‰}$).

Given the variable nature of water column and sediment sources of nutrients, it was not surprising that isotopic values in benthic microalgae that reside at the sediment-water column interface were the widest among all vegetation categories ($+1$ SD ellipses; Figure 2). Benthic microalgae and particulate organic matter could be readily distinguished on the sulfur axis, an observation that might be related to relative availability of sulfate (in the water column) and sulfide (from sediments) to these taxa.

The composition of POM samples differed among sites for all three isotopes (Kruskal-Wallis for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$, respectively: TS = 14.075, 9.384, 25.875; $P = 0.001, 0.009, < 0.001$). Greatest differences were observed between Alloway Creek and Moore's Beach, where all three isotopes differed significantly between the two locations ($P = 0.006, 0.006, < 0.001$ for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$, respectively). POM isotope values for $\delta^{34}\text{S}$ were similar in Alloway Creek and Mad Horse Creek, but both differed from Moore's Beach in the lower Bay ($P = < 0.001$ for AC versus MB; $P = < 0.001$ for MHC versus MB). In general, POM varied less within a marsh than among marshes where the isotope values seemed to be influenced by organic matter from the predominant primary producers. Such variation is shown by the location of the POM isotope values relative to those of primary producers, especially as differentiated by $\delta^{34}\text{S}$ (Figure 2). Particulate organic matter $\delta^{13}\text{C}$ values did not differ between the *S. alterniflora*-predominated Mad Horse Creek and Moore's Beach sites, but they were significantly different from the *Phragmites australis*-predominated Alloway Creek ($P = < 0.001$ for MHC ver-

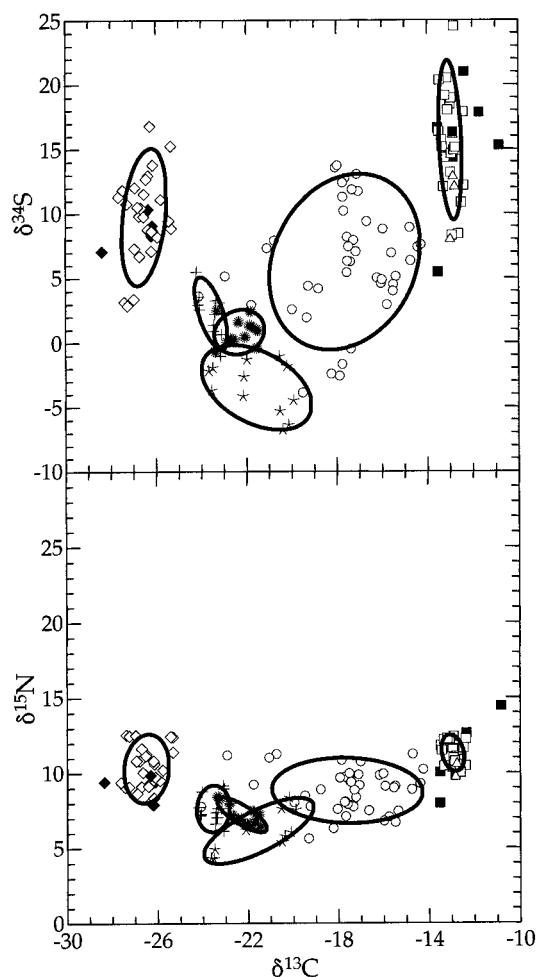


FIGURE 2.—Dual isotope plots of $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ on $\delta^{13}\text{C}$ for primary producers collected within reference and restored marshes. Data for macrophytes and benthic microalgae are pooled across sites, but particulate organic matter (POM) values from each sampled marsh are shown separately. Plots include enthic microalgae (open circles) *Phragmites australis* (open diamonds), *Phragmites australis* as detritus and senescent leaves (solid diamonds), *Spartina alterniflora* (open squares), *Spartina alterniflora* as detritus and senescent leaves (solid squares), *Spartina cynosuroides* (open triangles), POM for Alloway Creek (plus signs), POM for Moore's Beach (stars), and POM for Mad Horse Creek (asterisks). Ellipses represent mean values $+1$ standard deviation.

us AC; $P = 0.006$ for MB versus AC). The general absence of overlap in isotopic composition between POM and primary producers suggests the presence of a strong, if not dominant, phytoplankton component in these samples.

The POM sulfur values reported in this study were depleted compared with those previously re-

TABLE 1.—Summary of Kruskal–Wallis two-way tests for effect of location on stable isotope values of bay anchovy (Bonferroni-adjusted $\alpha = 0.002$); NS = not significant.

Location	Isotope	Alloway Creek	Commercial Township salt hay farm	Dennis Township salt hay farm	Mad Horse Creek	Moore's Beach	Lower bay
Commercial Township salt hay farm	$\delta^{13}\text{C}$	<0.001					
	$\delta^{15}\text{N}$	NS					
	$\delta^{34}\text{S}$	<0.001					
Dennis Township salt hay farm	$\delta^{13}\text{C}$	<0.001	<0.001				
	$\delta^{15}\text{N}$	NS	<0.001				
	$\delta^{34}\text{S}$	<0.001	<0.001				
Mad Horse Creek	$\delta^{13}\text{C}$	<0.001	<0.001	NS			
	$\delta^{15}\text{N}$	NS	NS	<0.001			
	$\delta^{34}\text{S}$	<0.001	NS	NS			
Moore's Beach	$\delta^{13}\text{C}$	<0.001	<0.001	<0.001	0.001		
	$\delta^{15}\text{N}$	NS	NS	NS	<0.001		
	$\delta^{34}\text{S}$	NS	NS	<0.001	NS		
Lower bay	$\delta^{13}\text{C}$	<0.001	NS	<0.001	<0.001	NS	
	$\delta^{15}\text{N}$	NS	NS	NS	NS	0.002	
	$\delta^{34}\text{S}$	<0.001	NS	NS	NS	<0.001	
Upper bay	$\delta^{13}\text{C}$	<0.001	<0.001	NS	NS	NS	NS
	$\delta^{15}\text{N}$	0.001	NS	<0.001	NS	<0.001	NS
	$\delta^{34}\text{S}$	<0.001	NS	NS	NS	NS	NS

corded for marine phytoplankton. This observation may result from residual inorganic and sedimentary sulfur in these estuarine samples, although our values overlap with the lower end of the range reported by (Chanton and Lewis 1999).

Stable Isotopes in Bay Anchovy

Stable isotopes were analyzed in 272 bay anchovy from collections in June and August through October at restoration sites in Alloway Creek, Dennis Township SHF, and Commercial Township SHF, and from reference marshes in Mad Horse Creek and Moore's Beach. An additional 124 fish from the upper and lower bay, at depths generally exceeding 4 m (the exception was one collection at 2.5 m in September offshore of the mouth of Moore's Beach), were also analyzed. Because fish were provided on an as-available basis, not all size classes were represented in each month or at each location. Although juveniles were captured on each sampling date, it was clear that the 23 specimens obtained in June at lower bay sites and Moore's Beach were adults (Able and Fahay 1998).

Analysis of carbon isotopic composition across size-classes indicated that adult bay anchovy captured in June differed significantly from the other two groups (Bonferroni post hoc t -test, $\alpha = 0.05$). For this reason, adults captured in this month were not included in further statistical comparisons but are included qualitatively in this paper. In addition, carbon, nitrogen, and sulfur isotope values for four fish, one each from Alloway Creek and Mad Horse

Creek and two from Commercial Township SHF, were shown to be outliers ($p < 0.05$) and were therefore excluded from further analysis (Grubbs and Beck 1972).

The isotopic composition of bay anchovy samples differed among sites for all three isotopes (Kruskal–Wallis for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$: TS = 149.228, 55.720, 58.923; all $P < 0.001$) with differences in carbon more variable than either nitrogen or sulfur (Table 1). Significant differences in sulfur isotope ratios were largely restricted to Alloway Creek, and among the three isotopes generally displayed the fewest differences in intersite comparisons. Across all sites, the isotope composition of bay anchovy captured in Alloway Creek was most often significantly different from other locations.

Isotope composition of anchovy from Mad Horse Creek and Moore's Beach differed in most parameters from Alloway Creek (Table 1), perhaps indicative of the predominance of *P. australis* in Alloway Creek. However, fish from the two reference sites, Mad Horse Creek and Moore's Beach (both *S. alterniflora*-predominated marshes), also differed in their C and N isotopic content. Although fish captured in open waters of the lower bay and the upper bay did not differ (Table 1; Figure 3), they sometimes displayed differences compared with nearby salt marshes in each region. For example, nitrogen isotope values for fish captured in Dennis Township SHF and Moore's Beach, two of the salt marshes in the lower bay region, differed significantly from values for fish

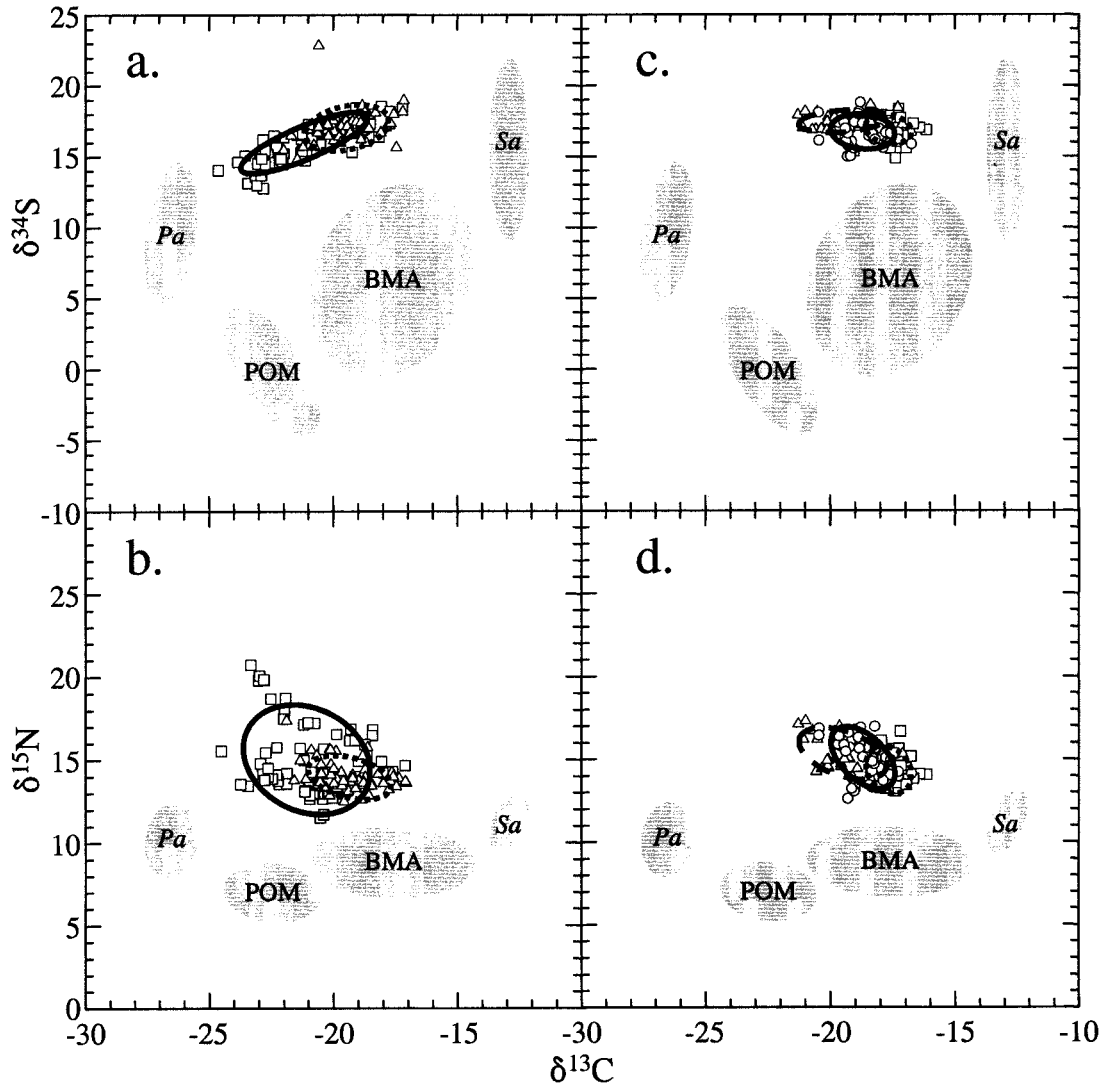


FIGURE 3.—Dual isotope plots for bay anchovy of $\delta^{34}\text{S}$ on $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ on $\delta^{13}\text{C}$ (b) for Alloway Creek (open squares; solid line for mean value + SD ellipse) and Mad Horse Creek (open triangles; dotted line for mean value + SD ellipse), and primary producers collected in salt marshes: particulate organic matter (POM), benthic microalgae (BMA), *Phragmites australis* (Pa), and *Spartina alterniflora* (Sa). Similar plots, $\delta^{34}\text{S}$ on $\delta^{13}\text{C}$ (c) and $\delta^{15}\text{N}$ on $\delta^{13}\text{C}$ (d), for Moores Beach (open circles; solid line for mean value + SD ellipse), Dennis Township Salt Hay Farm (open triangles; dashed line for mean value + SD ellipse), and Commercial Township Salt Hay Farm (open squares; dotted line for mean value + SD ellipse).

taken in open waters of the upper bay (Table 1). Similarly, fish from Dennis Township SHF differed in carbon isotope composition compared with fish from open waters of the lower bay.

The relationships between stable isotope patterns of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ in bay anchovy and vegetation from various marsh locations are depicted in Figure 4. In upper bay marshes, significant differences in carbon and sulfur isotope com-

position of bay anchovy from Alloway Creek and Mad Horse Creek appeared to be most influenced by *P. australis* (Figure 4a) and *S. alterniflora* (Figure 4b). If POM and benthic microalgae contributed to bay anchovy isotopic composition in either creek, it was likely to be minor addition. This is especially evident along the $\delta^{34}\text{S}$ axis.

The pattern is quite different in the lower bay marshes, where *P. australis* is a minor component

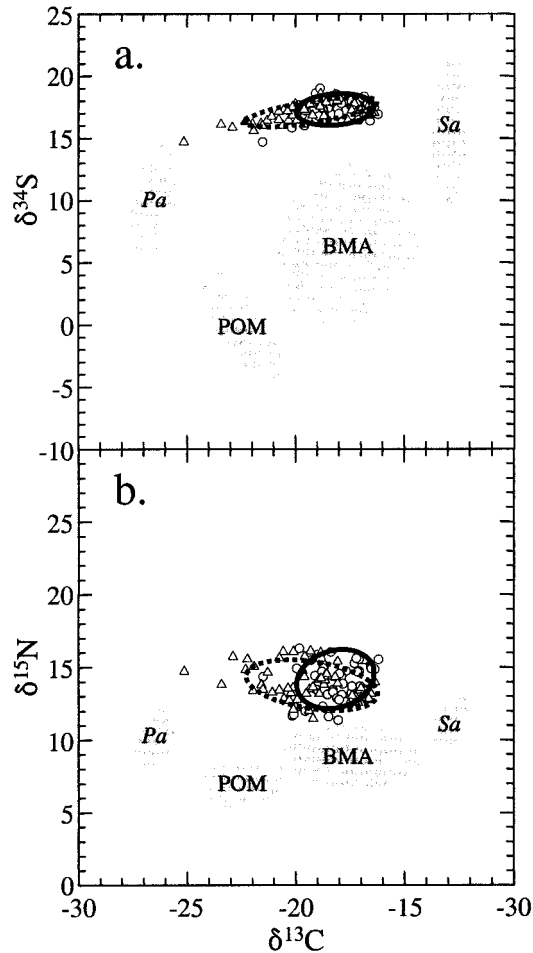


FIGURE 4.—Dual isotope plots of $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ on $\delta^{13}\text{C}$ for bay anchovy, *Anchoa mitchilli*, collected in the open waters of the lower bay (open circles; solid line for mean value + SD ellipse) and upper bay (open triangles; dotted line for mean value + SD ellipse), and primary producers collected in salt marshes: particulate organic matter (POM), benthic microalgae (BMA), *Phragmites australis* (Pa), and *Spartina alterniflora* (Sa).

of the vegetation community. Here, the stable isotopic compositions of bay anchovy from reference and restoration marshes were generally uniform (Figure 4c, d) and were linked to a mixture of benthic microalgae and *S. alterniflora* sources.

Stable Isotopes in White Perch

We obtained all 55 white perch for this study from marsh collections in October (none were captured in open waters of the bay). Previously published data for white perch collected in Delaware River and Delaware Bay in October confirms that the size frequency distributions observed in this

study (105–246 mm SL) included age-0 fish, although most were larger, older fish (yearlings and older; Able and Fahay 1998).

Fish densities were lower in October at the Commercial Township SHF and Dennis Township SHF restoration sites (repeated trawling at other sites failed to yield the desired number of fish). However, combined with the 15 individuals captured at the nearby Moore's Beach reference site, valid inferences can be made comparing lower-bay with upper-bay marsh locations.

The isotopic composition of white perch samples differed among sites for carbon and nitrogen isotopes (Kruskal–Wallis for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$, respectively: $TS = 36.336, 17.976, 5.554$; $P = < 0.001, 0.001, 0.235$). With one exception, the isotopic composition of white perch was not significantly different for all three isotopes among lower-bay locations (Commercial Township SHF, Dennis Township SHF, and Moore's Beach West) or between upper-bay locations (Alloway Creek, Mad Horse Creek; Table 2). White perch collected in Alloway Creek and Mad Horse Creek exhibited the most variability compared with the other sites, especially in $\delta^{13}\text{C}$ values. Carbon isotope signatures in white perch also differed between the upper-bay sites and both the Dennis Township SHF and Moore's Beach sites in the lower bay (Table 2).

In Alloway Creek and Mad Horse Creek, trophic pathways between primary producers and white perch appeared to be dominated by *P. australis* and POM-derived organic matter, with lesser influence from benthic microalgae (Figure 5a, b). In lower-bay salt hay farms and the Moore's Beach reference site (Figure 5c, d), the picture shifted again, and a mixture of *S. alterniflora* and benthic microalgae appeared to dominate the trophodynamics of this species.

Discussion and Conclusions

Tidal salt marshes are an integral link between estuaries and coastal fisheries. Marshes contribute to the success of juvenile marine finfishes that benefit from the abundant food and perhaps fewer large predators in these habitats. One of the difficulties in identifying trophic pathways from primary producers to fish, however, is the lag associated with the processing of organic carbon from marsh plants to consumers higher in the food web. Also, despite the consumption of phytoplankton and benthic microalgae and their efficient use in short, algae-based food chains, tracking the flow of nutrients from these taxa to higher-order con-

TABLE 2.—Summary of Kruskal–Wallis two way tests for effect of location on stable isotope values of white perch (Bonferroni-adjusted $\alpha = 0.005$); NS = not significant.

Location	Isotope	Alloway Creek	Commercial Township salt hay farm	Dennis Township salt hay farm	Mad Horse Creek
Commercial Township salt hay farm	$\delta^{13}\text{C}$	NS			
	$\delta^{15}\text{N}$	NS			
	$\delta^{34}\text{S}$	NS			
Dennis township salt hay farm	$\delta^{13}\text{C}$	0.001	NS		
	$\delta^{15}\text{N}$	NS	NS		
	$\delta^{34}\text{S}$	NS	NS		
Mad Horse Creek	$\delta^{13}\text{C}$	NS	NS	0.002	
	$\delta^{15}\text{N}$	NS	NS	NS	
	$\delta^{34}\text{S}$	NS	NS	NS	
Moore's Beach	$\delta^{13}\text{C}$	<0.001	NS	NS	<0.001
	$\delta^{15}\text{N}$	0.001	NS	0.003	<0.001
	$\delta^{34}\text{S}$	NS	NS	NS	NS

sumers under field conditions has been difficult (Keller et al. 1990; Deegan and Garritt 1997).

These are reasons why it has taken so long to effectively test Teal's (1962) hypothesis that salt-marsh production may drive much of the secondary production in estuaries. Teal's (1962) idea was first modified by Haines (1979) and Nixon (1980), who recognized that finfish, as well as phytoplankton production and organic matter export, are important contributors to nutrient flux from the salt marsh to the estuary and coastal zone. This relationship was first quantified by Deegan (1993) for Atlantic menhaden *Brevoortia tyrannus*, but applies equally well to other marine transients—i.e., species that spawn on the continental shelf and the young move into estuaries during their first year of life. The emigration of maturing individuals back to the ocean completes a cycle that has sometimes been referred to as a “conveyor belt” between the estuary and shelf waters (E. Houde, personal communication).

Despite regional and site-specific differences, salt marshes clearly contribute to the production of many marine transient species in temperate estuaries of the eastern United States. The consumption of marsh products in situ, the export of dissolved and detrital organic carbon (and other nutrients), and the movement of fish and shellfish along this coastal conveyor belt all contribute to secondary production of transient and resident species in estuarine and coastal waters.

By using multiple stable isotopes to examine trophic pathways, we conclude that carbon, nitrogen, and sulfur originating in the emergent macrophytes and benthic microalgae of salt marshes contribute to the production of marine transient and resident estuarine species and, consequently,

contribute to the export process. If contamination by sedimentary or inorganic sulfur indeed mask the phytoplankton signal in POM (Chanton and Lewis 1999), then we may have underestimated the contribution of phytoplankton nutrients to bay anchovy and white perch. Although senescent leaves of *P. australis* and *S. alterniflora* collected from the marsh plain were heavily laden with sediments and probably inorganic sulfur, their $\delta^{34}\text{S}$ values fell within the range of fresh leaves collected from the upper portions of these plants (Figure 2). Apparently, our laboratory methods removed the effects of inorganic sulfur from these samples and should have been equally successful in the POM analyses. Clearly, more study of the subject is required.

The enriched $\delta^{15}\text{N}$ values reported here suggest that anthropogenic sources of nitrogen may influence the N stable isotope composition of organic matter at the base of the food web and may be available to secondary consumers in Delaware Bay (Lipschultz et al. 1986; McClelland et al. 1997). Results similar to ours were also reported for striped bass (*Morone saxatilis*) captured in the lower Delaware River at the head of the estuary by Wainright et al. (1996).

Critical to all of our observations, however, is the assumption that the species we examined exhibit site fidelity—i.e., that they were present at some locations long enough to acquire the dominant signal at that site. Moreover, these and our earlier studies on a resident marsh species (mummichog *Fundulus heteroclitus*; Wainright et al., in press), confirm that nutrients from *P. australis* contribute to this process.

The stable isotope ratios reported here generally conformed to expectations with regard to vege-

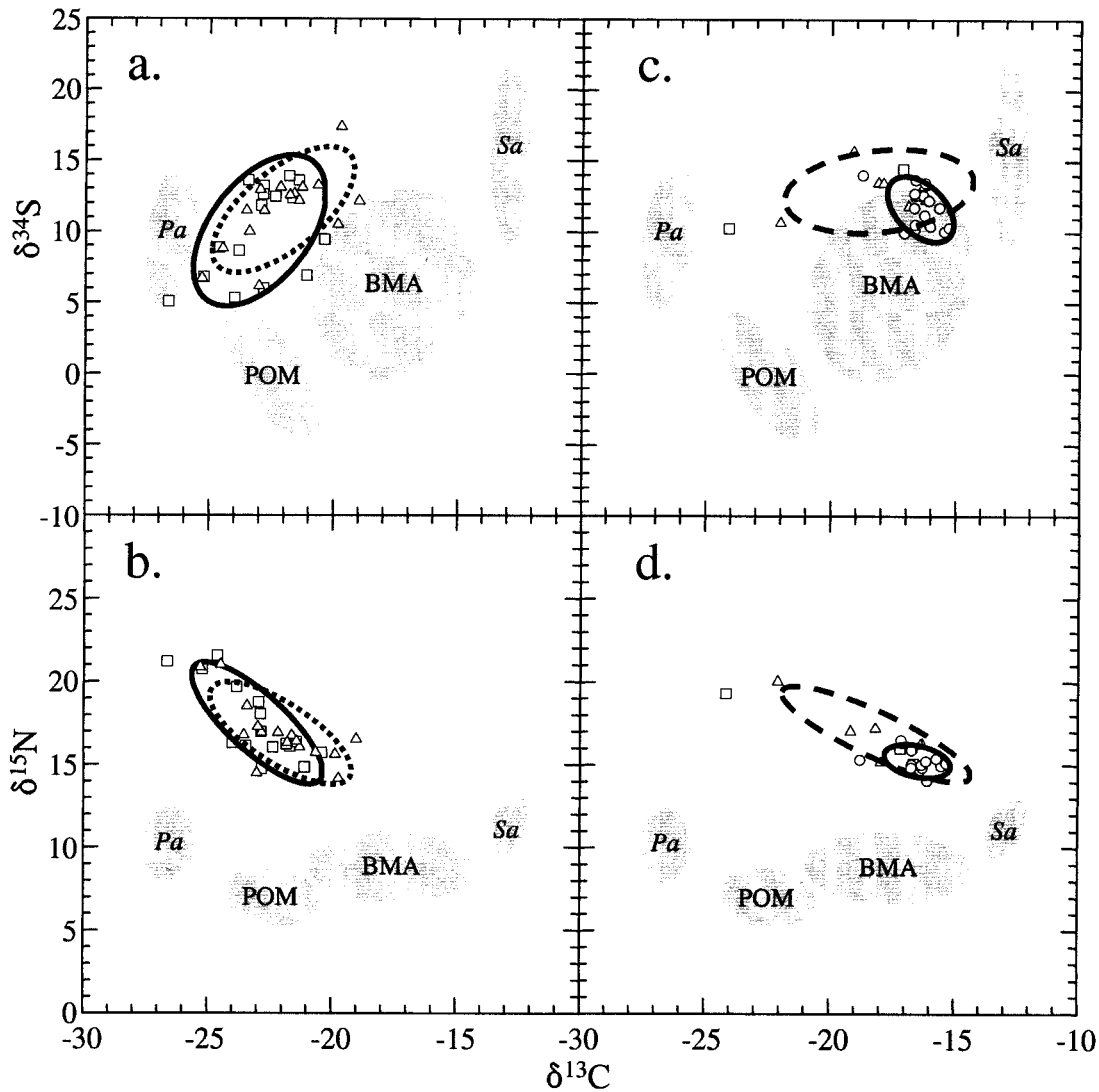


FIGURE 5.—Dual isotope plots for white perch of $\delta^{34}\text{S}$ on $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ on $\delta^{13}\text{C}$ (b) for Alloway Creek (open squares; solid line for mean value + SD ellipse) and Mad Horse Creek (open triangles; dashed line for mean value + SD ellipse), and primary producers collected in salt marshes: particulate organic matter (POM), benthic microalgae (BMA), *Phragmites australis* (Pa), and *Spartina alterniflora* (Sa). Similar plots, $\delta^{34}\text{S}$ on $\delta^{13}\text{C}$ (c) and $\delta^{15}\text{N}$ on $\delta^{13}\text{C}$ (d), for Moores Beach (open circles; solid line for mean value + SD ellipse), Dennis Township Salt Hay Farm (open triangles; dashed line for mean value + SD ellipse), and Commercial Township Salt Hay Farm (open squares; no ellipse shown).

tation type and inorganic matter sources. With the exception of phytoplankton POM, most isotope values fell within previously cited limits (Peterson and Fry 1987; Sullivan and Moncreiff 1990; Schlacher and Woolridge 1996). Although we recognize that other primary producers, and perhaps pyrite-inorganic sulfur, influences POM at our sites, the $\delta^{34}\text{S}$ values were often significantly different from those of macrophytes. Spatial and sea-

sonal differences within creeks also suggested that either different primary producers contributed to POM or that the phytoplankton component had alternative inorganic sources of nutrients (Wainright et al., in press).

Our results also confirm that each category of primary producer or organic matter (marsh grasses, benthic microalgae, and POM) has a unique isotopic signature based on the three isotopes an-

alyzed, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$. These differences, and the observed fractionation patterns between trophic levels, can be effectively combined to trace nutrient pathways from plants to consumers, including the target species.

For Delaware Bay, the relationships between primary producers in the marsh and bay and the species investigated are summarized in Figure 6. White perch spend virtually their entire life cycle within the confines of the estuary. As young, they are widely distributed over most of the Delaware Bay and are abundant in tidal creeks throughout the summer and early fall. They overwinter in deep channels of the lower bay and in the fresh and brackish portions of the Delaware River.

The power of the multiple stable isotope approach in distinguishing trophic linkages for white perch are demonstrated in Figure 6. The differences may relate to the generally greater availability of *P. australis* carbon at upper bay locations, fish movements between sites, and difference in the relative abundance and carbon isotopic composition of other plants in these brackish versus polyhaline sites. For example, the mean values for $\delta^{13}\text{C}$ in white perch and bay anchovy captured in Alloway and Mad Horse creeks fall within the range for POM values, approximately -22% to -24% . If sulfur and nitrogen data were not available, it might be concluded that POM is a significant contributor to white perch and bay anchovy nutrition in these two marshes. That this is unlikely is very clearly indicated by the $\delta^{34}\text{S}$ data, which suggest that a mixture of benthic microalgal and macrophyte organic matter, rather than POM, are the key contributors to white perch and bay anchovy biomass (Figure 6).

At upper estuary locations, *P. australis* appeared to contribute to the nutrition of white perch and bay anchovy (Figures 3–5), whether they were captured in salt marshes or in the open bay. This was especially true for white perch collected from the two upper estuary marshes, where the signatures for all three isotopes were not significantly different and the fish could not readily be distinguished (Figure 5). However, in Mad Horse Creek another C_3 plant was also present, *Amaranthus cannibus*, that has a carbon signature similar to that of *P. australis*, about -23.7% ($\delta^{34}\text{S} = 13.0\%$; Stribling and Cornwell 1997). Together, these macrophytes composed about 10–15% of the coverage of the marsh plain, virtually all of it adjacent to tidal creeks. It is possible that plants growing along creek banks may contribute disproportionately to nutrient flow into finfish (see below).

Isotopic composition of bay anchovy captured in *Phragmites*-predominated Alloway Creek was significantly different for carbon and sulfur compared with those of Mad Horse Creek (Table 1; Figure 3). This was not the same case for white perch (albeit sample sizes were smaller for white perch; Figure 5). This observation is intriguing because the isotopic compositions of bay anchovy and white perch collected in Mad Horse Creek was intermediate between the *Phragmites*-predominated Alloway Creek and the lower-bay marshes (Figure 4). The interplay of several factors may lead to this observation, including the greater degree of residency of white perch in salt marshes, their movement between marshes, a disproportionate isotopic-signature contribution to white perch by *P. australis* (and possibly *Amaranthus cannibus*) in Mad Horse Creek, and the potentially confounding influence of upland (allochthonous) inputs of nutrients.

The distinction between carbon values in fish captured at Dennis Township SHF versus Commercial Township SHF is not readily explained. It may relate to the differences in the restoration trajectories at the two sites; e.g., *S. alterniflora* coverage is already extensive at Dennis Township SHF (about 50–60%), whereas coverage is less than 5% at Commercial Township SHF. Thus, the availability of *Spartina* production in the marsh food web is far greater in Dennis Township SHF.

Although further studies are needed, a potential explanation or hypothesis for these results rests in the spatial distribution of *P. australis* in Mad Horse Creek. This site is a reference marsh predominated by *S. alterniflora*, and *S. cynosuroides* is abundant along creek banks. However, much of the *Phragmites* present is also found along creek levees, including higher order channels. Perhaps the differences discussed above point out the importance of edge in the interface between tidal creeks and the marsh plain. The observation that exchange of marsh products with adjacent tidal creeks is facilitated by maximum edge is well known (Weigert and Pomeroy 1981; McIvor and Odum 1988; Zimmerman et al., in press). Moreover, most marine transients do not penetrate great distances into the marsh plain from the edge of the tidal creeks (Rozas et al. 1988; Hettler 1989; Zimmerman et al., in press).

Bay anchovy are perhaps the most pelagically oriented of the two species, spending more time feeding in the water column than white perch (Smith et al. 1984). Yet, bay anchovy isotopic signatures generally mirrored those of white perch

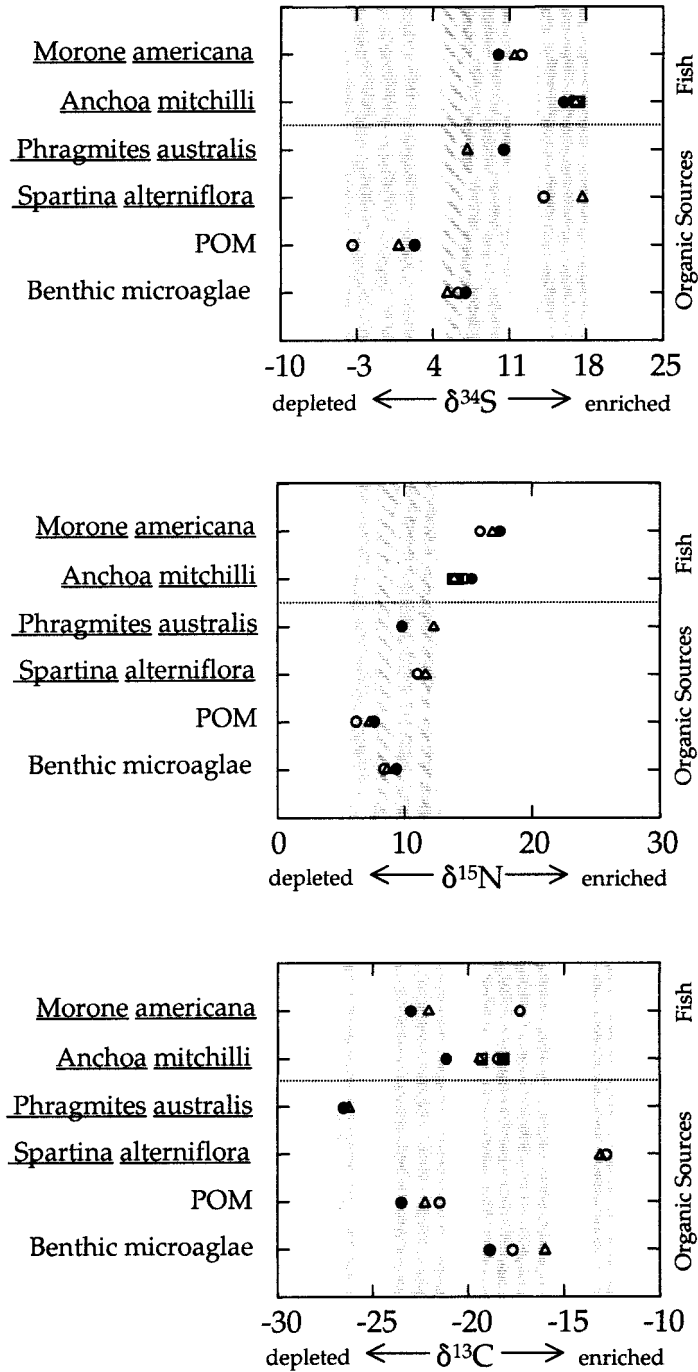


FIGURE 6.—Mean values of $\delta^{13}\text{C}$ (lower panel), $\delta^{15}\text{N}$ (middle panel), and $\delta^{34}\text{S}$ (upper panel) for white perch and bay anchovy and for primary producers (shaded areas) collected in Alloway Creek (solid circles), Mad Horse Creek (open triangles), lower-bay creeks (open circles; Moore's Beach, Commercial Township Salt Hay Farm, and Dennis Township Salt Hay Farm), and the lower (solid squares) and upper bay (open squares).

and were dominated by *S. alterniflora* in lower-bay marshes (Figure 4 c, d). Like white perch, bay anchovy displayed an increasing influence from *Phragmites* as sampling proceeded up estuary to Mad Horse and Alloway creeks (Figure 4a and b).

Although white perch were not obtained from tows in open waters of Delaware Bay, numerous bay anchovy were collected at offshore sampling stations (Figure 3). One of the most striking results of this study is the widespread occurrence of stable isotopes in these species that probably originated in macrophytes and benthic microalgae of salt marshes. Carbon, nitrogen, and sulfur isotopes from marsh macrophytes and benthic microalgae are abundant in bay anchovy and white perch whether they were captured in the marsh or, in the case of anchovies, several kilometers or more from the shore.

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