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# Life History Strategies of Estuarine Nekton: The Role of Marsh Macrophytes, Benthic Microalgae, and Phytoplankton in the Trophic Spectrum

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**ABSTRACT:** The stable isotope signatures of marine transient and resident nekton were used to investigate trophic linkages between primary producers, marsh macrophytes, phytoplankton, benthic microalgae, and consumers within the Delaware Bay. A whole estuary approach was used to compare the flux of nutrients from primary producers to juvenile weakfish (*Cynoscion regalis*), bay anchovy (*Anchoa mitchilli*), and white perch (*Morone americana*) in open waters of the lower and upper Bay and adjacent salt marshes dominated by either *Spartina alterniflora* or *Phragmites australis*. Our results suggest that trophic linkages vary significantly along the salinity gradient, reflecting the transition from *Spartina* to *Phragmites*-dominated marshes, and secondarily, in a marsh to open water (offshore) direction at a given salinity. Superimposed on this pattern was a gradient in the proximate use of organic matter that depended on life history traits of each species ranging from pelagic to benthic in the order bay anchovy > weakfish > white perch.

## Introduction

Because they provide abundant food and shelter from predators, tidal salt marshes are thought to serve as essential habitat for nekton (Boesch and Turner 1984). The degree to which individual taxa benefit from salt marshes depends on their life history traits and specificity of habitat use. Life history data for species that use estuaries suggest that there are at least 4 patterns of marsh utilization, and although these are artificial constructs (i.e., punctuations of a continuum), they provide a convenient means of addressing links between marshes and secondary production (Fig. 1). Type I species are marsh residents adapted to a life cycle entirely within these habitats, perhaps to the extent that they may be considered marsh obligates. Type I species include common mummichog (*Fundulus heteroclitus*) and sheepshead minnow (*Cyprinodon variegatus*). Type II, or marsh facultative, taxa appear to have marsh dependent early life stages that may enhance their growth and survival, and include such species as the estuarine resident white perch (*Morone americana*) and the marine transient spot (*Leiostomus xanthurus*). These species may use marsh habitats as primary nurseries in the context defined by Beck et al. (2001).

Although they only occupy marsh habitats for short periods, highly mobile marine transients do

not appear to be particularly adapted to life in the salt marsh but exhibit broad flexibility in diet and habitat utilization (Deegan et al. 2000). While these species benefit from the exchange of marsh products to the open estuary, which become components of their food web, they also use alternative links in the trophic spectrum. In our scheme, Type III marine transients include juvenile weakfish (*Cynoscion regalis*) and bay anchovy (*Anchoa mitchilli*). Finally, Type IV adult marine transients are relatively rare in marshes but via trophic relays and the export of marsh products may also gain benefits from these habitats. An example of Type IV is the adult bluefish, *Pomatomus saltatrix*. As noted in Fig. 1, marsh resident (Type I species) tend to perceive the habitat mosaic as coarse-grained spending much or all of their life cycle in one habitat unit (the marsh) while the other Types tend to increasingly use other habitat units in fine-grained fashion (Levins 1968).

While all of these taxa appear to take advantage of the organic matter produced in salt marshes, the relative contribution to their diet varies with several ontogenetic factors including size (age), feeding strategy, and patterns of habitat utilization. These observations are further mediated by the complexities inherent in estuarine food webs (Peterson et al. 1986; Peterson and Howarth 1987; Polis and Strong 1996; Deegan and Garritt 1997).

We use multiple stable isotopes to address the

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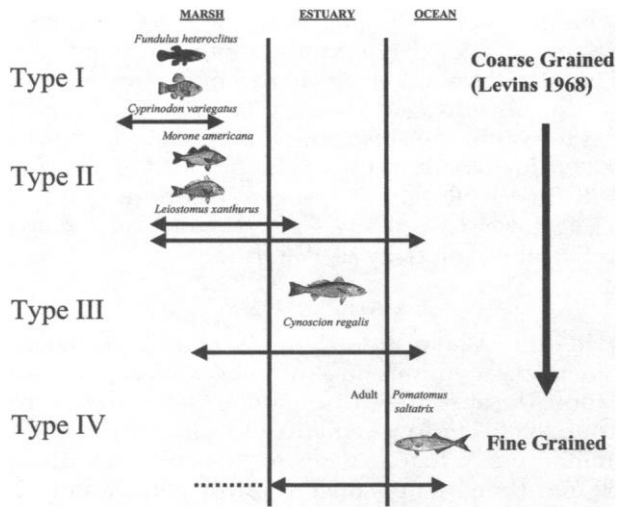


Fig. 1. Spatial distribution of nekton that use tidal salt marsh habitats during all or a part of their life history.

relationship between salt marsh primary production and the flow of nutrients to species exhibiting Types II and III life history strategies. Although the effort focuses on juvenile weakfish, a marine transient predator that uses estuaries as nurseries during their first year of life, observations for white perch and bay anchovy (Weinstein et al. 2000) are re-introduced here in modified form for comparison. A whole estuary approach was adopted for this study, with young weakfish captured throughout the saline portion of the Delaware Bay, United States, and their tissues analyzed for  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$ . Of particular interest was whether or not marsh primary production was available to juvenile weakfish residing in open waters kilometers away from marsh derived organic matter, and in what proportion to other potential sources? Three questions were addressed in this research: what are the trophic linkages between primary producers and Type II-III species? how do these linkages differ among estuarine regions, open waters of the lower and upper Bay and tidal salt marshes dominated by *Spartina alterniflora* and *Phragmites australis*? what were the relative contributions of marsh primary producers and other organic matter sources to the trophic spectrum of Types II and III species?

### Materials and Methods

Tidal marshes of the lower Delaware Bay, in salinities generally  $>10\text{‰}$ , are dominated by smooth cordgrass (*S. alterniflora*) in the low marsh and at higher elevations by mixtures of *S. alterniflora*, *S. cynosuroides*, *S. patens*, and *Distichlis spicata*. These wetlands comprise more than 73,000 ha of the Delaware Bay shorefront, but a substantial portion of lower salinity wetlands ( $<10\text{‰}$ ), at least 16,000 ha

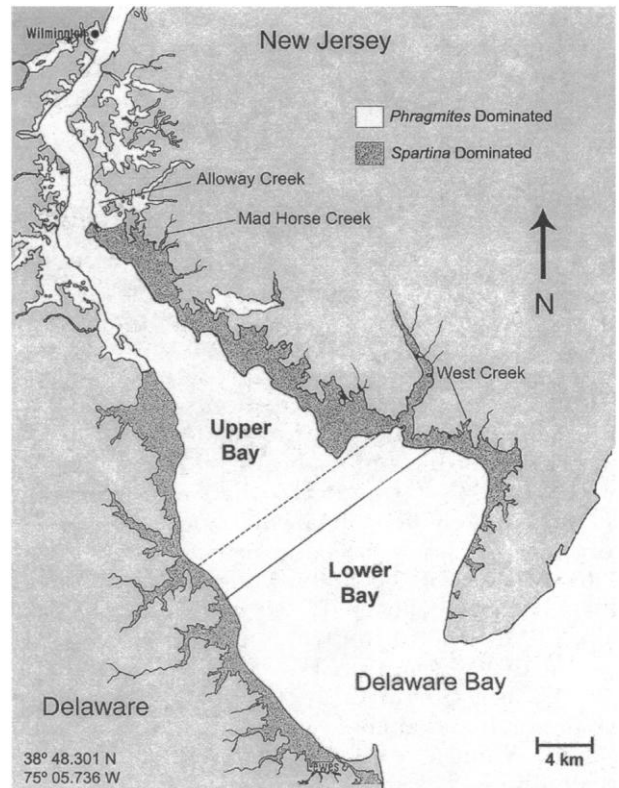


Fig. 2. Locations of the three tidal marsh creeks that formed part of this study (Alloway Creek, Mad Horse Creek, and West Creek). The solid and dotted lines denote the separation between upper and lower Delaware Bay for the anchovy and weakfish collections, respectively.

in Delaware and probably an area of similar magnitude on the New Jersey side, have been recently invaded by an aggressive variety of *P. australis* (Fig. 2). Over a 2-yr period, 1998–1999, we sampled nekton in 3 marshes, Alloway Creek (1,253 ha) and Mad Horse Creek (1,558 ha), both meso-oligohaline, and West Creek (1,234 ha), a polyhaline system. Marsh surface coverage of *P. australis* approached a near monoculture in Alloway Creek, but was generally restricted to small patches along creek banks at Mad Horse Creek, where it comprised  $<4\%$  of the macrophyte community coverage. This species was virtually absent at West Creek, but *P. australis* is generally found further south toward the Bay mouth on the Delaware side of Delaware Bay (Fig. 2). In addition to the dominant macrophytes, benthic microalgae (BMA) and phytoplankton (as suspended particulate matter; SPM) were also collected for analysis (Wainright et al. 2000; Weinstein et al. 2000). Because seagrasses are virtually absent in Delaware Bay, a highly light limited system (Pennock and Sharp 1986), epiphytic algae, the grasses themselves, and other macroal-

gae (also found in very low abundance) were not collected for analysis.

#### FIELD COLLECTIONS

Juvenile weakfish were captured in 1998 and 1999 within open waters of the Delaware Bay, designated lower and upper Bay, and in tidal creeks adjacent to these regions: Alloway Creek (visited only in 1999) and Mad Horse Creek in the upper Bay and West Creek in the lower Bay (Fig. 2). Fish were collected from June through October in near-bottom habitats with a 4.9 m otter trawl; 9.5-mm mesh cod liner, towed near low tide for 10 min during daytime and nighttime hours. On each date and location, an attempt was made to capture at least 15 individuals in each of 3 size classes (<60, 60–100, and >100 mm; SL) that were chosen to reflect ontogenetic shifts in diet and expected differences in isotopic composition (Nemerson 2001). Details of vegetation sample collection and analysis (macrophytes [*P. australis* and *Spartina* spp.], BMA, and phytoplankton measured as SPM) appear in Wainright et al. (2000), Weinstein et al. (2000), and Currin et al. (2003), and details of white perch and anchovy sampling and analysis appear in Weinstein et al. (2000) and are not repeated here.

#### SAMPLE PROCESSING AND ISOTOPE ANALYSIS

After removing gut contents from individual weakfish, two methods were used to analyze tissue stable isotope composition. In 1998, whole fish were dried to constant weight at 60°C and ground to a fine powder in a Spex/CertiPrep 5100 mill. To facilitate the simultaneous analysis of lipids and protein content for a concurrent biochemical condition study (Litvin and Weinstein unpublished data), all juvenile weakfish collected in 1999 were freeze-dried whole (Labconco Inc. Model #7758000) prior to grinding.

In 1998, stable isotopes in weakfish were analyzed at two locations, the Institute of Marine and Coastal Sciences, Rutgers University, on a Europa Scientific continuous-flow, elemental analyzer (ANCA-GSL)/mass spectrometer stable isotope system, and at the Environmental Isotope Laboratory, University of Waterloo, on a Micromass Isochrom Continuous Flow Stable Isotope Mass Spectrometer coupled to a Carla Erba Elemental Analyzer (CHNS-O EA1 108). All fish sampled in 1999 were analyzed at the University of Waterloo. Isotopic composition is expressed in  $\delta$  notation that 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. The standards are Peedee Belemnite for carbon (C), air for nitrogen (N), and Canyon Diablo troilites for sulfur (S). Instrument precision was  $\pm 0.1$ – $0.2\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, and  $\pm 0.5\text{‰}$  for  $\delta^{34}\text{S}$  for the Rutgers University laboratory and  $\pm 0.2\text{‰}$  for  $\delta^{13}\text{C}$ ,  $\pm 0.3\text{‰}$  for  $\delta^{15}\text{N}$ , and  $\pm 0.5\text{‰}$  for  $\delta^{34}\text{S}$  at the University of Waterloo.

#### DATA ANALYSIS

Because stable isotope ratios were expected to reflect the confounding influences of capture location (local sources of organic matter; Weinstein et al. 2000) and movements of individual fish, we limited our initial analyses to juvenile weakfish < 60 mm (hereinafter small weakfish). Small individuals feed at approximately the same trophic level (Nemerson 2001) and are relatively less mobile than larger juveniles that tend to migrate down bay as they grow (Grecay and Targett 1996). The results for small weakfish were then compared to bay anchovy and white perch collected within the same tidal creek or open bay location.

Pooled stable isotope data for small weakfish at a given site were tested for normality and homogeneity of variance using Kolmogorov-Smirnov one-sample tests and analysis of variance (ANOVA) applied to residuals. Because the assumptions for parametric ANOVA could not be met in a few instances (despite attempts to transform the data), a nonparametric approach was adopted for all pairwise comparisons, with the data for each species also pooled by collection location; Mann-Whitney two sample tests with Bonferroni adjustments to  $\alpha$  values ( $\alpha = 0.05/\text{the number of pairwise comparisons in the data set}$ ,  $\alpha = 0.05/78 = 0.00064$ ). Differences and variability in the isotopic data ( $\delta^{15}\text{N}$  or  $\delta^{34}\text{S}$  versus  $\delta^{13}\text{C}$ ) for individual nekton were also examined by locally weighted curves (distance weighted least squares, DWLS;  $t = 0.5$ ; McClain [1976]; SPSS [1998]) fit over the  $\delta^{13}\text{C}$  range for each species from all tidal marsh or open water locations.

Prior to statistical analysis, isotope values were adjusted for anticipated fractionation among trophic levels (Peterson and Howarth 1987; Post 2002). In Delaware Bay, white perch between 105 and 205 mm feed at approximately one trophic level higher than small weakfish and bay anchovy, and due to increasing proportions of fish in their diet, weakfish between 60 and 100 mm feed at approximately 0.15 trophic level above the latter species (Smith et al. 1984; Nemerson 2001). Consumers generally display average  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values that are about 1‰ (or less) enriched relative to their food, while the corresponding fractionation

TABLE 1. Stable isotope and length data for juvenile weakfish, bay anchovy, and white perch collected in the tidal creeks and open waters of Delaware Bay. Isotope values for white perch and juvenile whitefish from Alloway Creek are adjusted for the expected isotope fractionation due to trophic differences.

	Juvenile Weakfish					Bay Anchovy					White Perch				
	n	SL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$	n	SL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$	n	SL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
Alloway Creek															
Min	18	61	-22.5	10.7	13.0	67	20	-24.6	11.5	12.8	15	105	-27.6	11.4	4.5
Max		94	-18.3	18.4	16.6		58	-17.2	20.7	18.6		184	-21.4	-24.0	1.7
Mean		74.8	-20.5	14.2	14.7		39.2	-21.1	15.0	16.0		133.7	-24.0	14.0	9.3
SD		10.2	1.2	2.1	1.0		8.5	1.7	2.2	1.4		21.2	1.7	2.3	3.3
Mad Horse Creek															
Min	86	11	-22.2	9.6	12.9	63	20	-21.9	12.4	14.9	15	116	-26.3	11.1	5.6
Max		59	-16.7	20.2	20.8		58	-17.1	17.3	22.9		174	-20.0	17.7	12.7
Mean		38.6	-19.1	14.7	15.9		35.4	-19.4	13.9	17.1		139.5	-23.2	13.7	10.5
SD		12.4	1.3	2.3	1.5		7.9	1.1	0.9	1.1		17.2	1.7	1.8	2.3
West Creek															
Min	9	33	-18.0	14.2	15.7	27	33	-21.3	14.0	16.8	7	174	-23.1	11.8	10.1
Max		56	-16.7	15.0	16.6		52	-17.1	17.3	18.6		205	-17.3	16.7	15.1
Mean		42.3	-17.3	14.5	16.3		40.8	-19.5	15.3	17.4		187.7	-19.1	13.5	12.4
SD		9.4	0.4	0.3	0.3		5.4	1.1	1.0	0.5		11.8	2.0	1.5	1.6

for  $\delta^{15}\text{N}$  averages 3.4‰ between trophic levels (Peterson and Howarth 1987; Post 2002). Consequently, 1.0 ‰  $\delta^{13}\text{C}$ , 3.4 ‰  $\delta^{15}\text{N}$ , and 0.5 ‰  $\delta^{34}\text{S}$  were selected to represent the fractionation associated with a one trophic level difference in feeding regimes and this relationship was used to adjust the isotope values of white perch and weakfish between 60 and 100 mm by 1.0‰  $\delta^{13}\text{C}$ , 3.4‰  $\delta^{15}\text{N}$ , and 0.5‰  $\delta^{34}\text{S}$  and 0.15‰  $\delta^{13}\text{C}$ , 0.51‰  $\delta^{15}\text{N}$ , and 0.08‰  $\delta^{34}\text{S}$ , respectively.

## Results

### PRIMARY PRODUCER STABLE ISOTOPIC SIGNATURES

Stable isotope signatures for the primary producers examined in this study were published earlier (Wainright et al. 2000; Weinstein et al. 2000) and, with the exception of SPM S, are repeated here in the dual isotope plots. Phytoplankton  $\delta^{34}\text{S}$  values generally reflect those of seawater sulfate, 18‰ to 21‰, their primary source of sulfate throughout the estuary except in the immediate vicinity of the freshwater-saltwater interface (Fry 2002). Because the whole water SPM samples collected may also reflect the confounding influence of inorganic S contamination (Chanton and Lewis 1999; Currin et al. 2003), we chose to substitute a literature value, 18.8‰  $\pm$  0.6, for our earlier results (Peterson et al. 1986).

### WEAKFISH STABLE ISOTOPIC SIGNATURES

The isotopic content of juvenile weakfish (n = 222) appeared to be largely a function of capture location and for the smallest fish, their degree of site fidelity (Table 1, Fig. 3). C, N, and S content of whole body tissues varied among locations (Kruskal-Wallis; TS = 65.8, 131.3, 43.5; all p <

0.0001), but not within the lower Bay, and tissue differences in  $\delta^{13}\text{C}$  were more variable than  $\delta^{15}\text{N}$  or  $\delta^{34}\text{S}$  (Table 2). Within a collection location, however, variability in isotope ratios was greater in the upper Bay and was especially evident in tissue N values (Table 1).

Small weakfish captured in open waters of the upper and lower Bay differed in their C and N isotopic content (Table 2), and although mean values were not significantly different, fish from the upper Bay were characterized by depleted S ratios (Table 1). Small weakfish captured in open waters of the upper Bay also differed from those collected in the adjacent Mad Horse Creek (C, N, and S, Table 2). The stable isotope composition of small weakfish sampled in Alloway Creek was indistinguishable from those individuals collected in upper Bay open waters. We anticipated that these individuals would display elevated  $\delta^{15}\text{N}$  and depleted  $\delta^{34}\text{S}$  values relative to small weakfish from the open estuary, reflecting the contribution of *P. australis* in Alloway Creek and possibly an anthropogenic source of N (Weinstein et al. 2000). Because small weakfish were collected in two consecutive tows in August 1999 and not on any other date, they may have been recently recruited to Alloway Creek and not resident long enough to acquire the local isotopic signatures.

Because juvenile weakfish 60 to 100 mm exhibited the anticipated ratios, i.e., elevated  $\delta^{15}\text{N}$  and depleted  $\delta^{34}\text{S}$  relative to weakfish resident in open waters of the upper Bay, we chose this size class to represent the locally available organic matter sources in Alloway Creek (Tables 1 and 2). These larger fish were significantly depleted in  $^{13}\text{C}$  relative to small individuals from Mad Horse Creek,

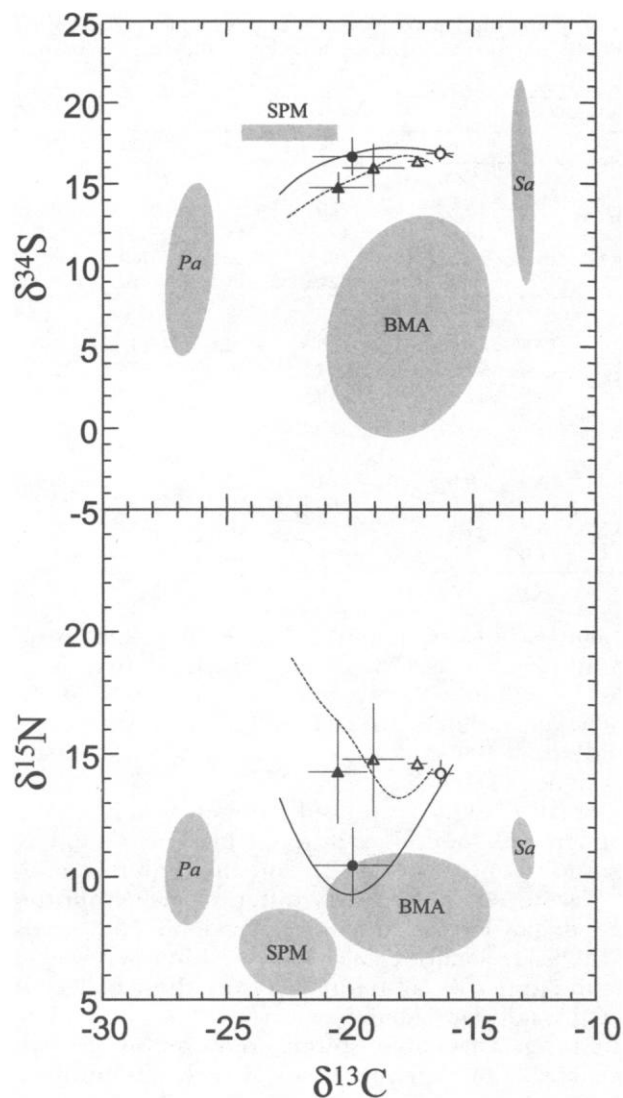


Fig. 3. Dual isotope plots of  $\delta^{34}\text{S}$  on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  on  $\delta^{13}\text{C}$  for juvenile weakfish, *Cynoscion regalis*, collected in West Creek (open triangle), Mad Horse Creek (half filled triangle), Alloway Creek (filled triangle), and the open waters of lower (open circle) and upper (filled circle) Delaware Bay (all values are mean  $\pm$  one standard deviation) and primary producers collected in salt marshes (suspended particulate matter [SPM], benthic micro algae [BMA] *Phragmites australis* [Pa], and *Spartina alterniflora* [Sa], all presented as  $\pm$  one standard deviation ellipses; Weinstein 2000). Lines represent locally weighted curves (distance weighted least squares;  $t = 0.5$ ; McClain 1976) fit over the  $\delta^{13}\text{C}$  range for individuals from all tidal marsh (dashed line) or open water (solid line) locations.

which, in turn, were significantly depleted relative to small individuals captured in West Creek (Tables 1 and 2).

In addition to the mean  $\delta^{13}\text{C}$  values becoming progressively depleted in the upper Bay direction,  $\delta^{34}\text{S}$  values were depleted in juvenile weakfish captured in the upper Bay tidal creeks (Fig. 3). Larger

juveniles from Alloway Creek were significantly depleted in  $\delta^{34}\text{S}$  relative to their smaller counterparts in West Creek (Tables 1 and 2) and depleted, but not significantly so (Mann-Whitney;  $p = 0.00078$ ), relative to small fish collected in Mad Horse Creek (Table 1). Although there were no significant differences in the  $\delta^{15}\text{N}$  signatures of juveniles from tidal creeks, fish from Alloway Creek and Mad Horse Creek exhibited a wider range of N ratios (Table 1) and increased  $\delta^{15}\text{N}$  values as  $\delta^{13}\text{C}$  values decreased (Fig. 3).

#### COMPARISON OF WEAKFISH, ANCHOVY, AND WHITE PERCH ISOTOPE SIGNATURES

The isotope composition of weakfish (including individuals 60–100 mm from Alloway Creek), bay anchovy ( $n = 266$ ) and white perch ( $n = 37$ ) collected at the same location differed both within tidal creeks and open waters of Delaware Bay (Fig. 4). In tidal creeks, significant differences in  $\delta^{34}\text{S}$  values varied in the direction bay anchovy > weakfish > white perch (Tables 1 and 2). Differences in  $\delta^{13}\text{C}$  values were not consistent across locations; in West Creek weakfish  $\delta^{13}\text{C}$  was enriched relative to bay anchovy and white perch while in Mad Horse Creek and Alloway Creek, white perch  $\delta^{13}\text{C}$  content was depleted relative to the other species (Fig. 4, Table 2). All 3 species exhibited a similar pattern of increasing  $\delta^{15}\text{N}$  with decreasing  $\delta^{13}\text{C}$  in the upper Bay tidal creeks. Although there were few significant differences in the isotopic content of species collected in the open waters of Delaware Bay, juvenile weakfish and bay anchovy differed in their  $\delta^{13}\text{C}$  content in the lower Bay and  $\delta^{15}\text{N}$  content in upper Bay (Table 2), the relationships among their individual  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were strikingly different (DWLS curves, Fig. 4).

#### Discussion

For more than 40 years, estuarine ecologists have debated the role of tidal salt marshes in providing trophic support for nekton, especially the link between macrophytes and marine transients (Teal 1962; Odum 1968; Haines 1979; Nixon 1980; Deegan et al. 2000). We used a stable isotope approach to better understand the importance of salt marsh primary production in the flux of nutrients to higher consumers. We were particularly interested in examining the interactive effects of life history with the availability of local organic matter along the estuarine salinity gradient.

Two major trends were evident in our data (Figs. 3 and 4): the first trend linked the availability of organic matter on a landscape scale to the dominance of either *Spartina* spp. or *P. australis* along the estuarine salinity gradient, with the latter species providing a ready source of nutrients to con-



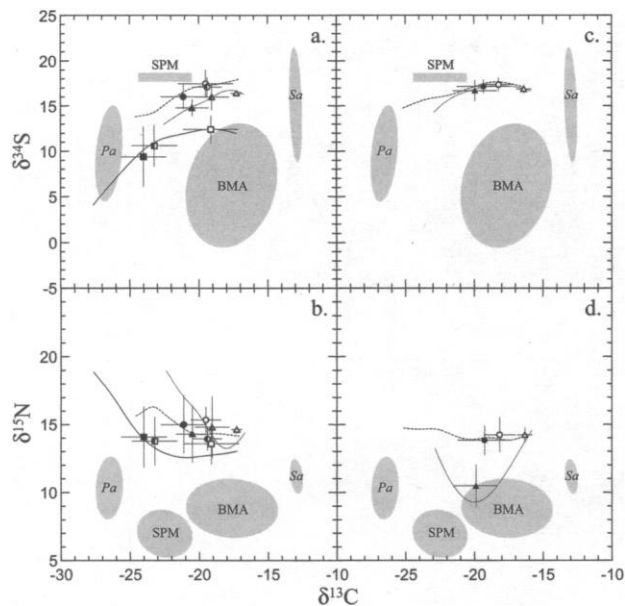


Fig. 4. Dual isotope plots of  $\delta^{34}\text{S}$  on  $\delta^{13}\text{C}$  (a) and  $\delta^{15}\text{N}$  on  $\delta^{13}\text{C}$  (b) for juvenile weakfish, *Cynoscion regalis* (triangles), bay anchovy, *Anchoa mitchilli* (circles), and white perch, *Morone americana* (squares) collected in West Creek (open symbols), Mad Horse Creek (half filled symbols), and Alloway Creek (filled symbols). Similar plots,  $\delta^{34}\text{S}$  on  $\delta^{13}\text{C}$  (c) and  $\delta^{15}\text{N}$  on  $\delta^{13}\text{C}$  (d) for juvenile weakfish, *Cynoscion regalis* (triangles) and bay anchovy, *Anchoa mitchilli* (circles) collected in the open waters of lower (open symbols) and upper (filled symbols) Delaware Bay (all values are mean  $\pm$  one standard deviation). Lines represent locally weighted curves (distance weighted least squares;  $t = 0.5$ ; McClain 1976) fit over the  $\delta^{13}\text{C}$  range for bay anchovy (dashed), juvenile weakfish (dotted) and white perch (solid) from all tidal marsh ([a] and [b]) or open water ([c] and [d]) locations. Primary producers collected in salt marshes are presented as  $\pm$  one standard deviation ellipses (suspended particulate matter [SPM], benthic microalgae [BMA], *Phragmites australis* [Pa], and *Spartina alterniflora* [Sa]; Weinstein 2000).

sumers in the upper Bay. We also observed a trophodynamic link between the availability of organic matter in the water column and the life history traits of individual organisms. Species with a pelagic orientation, such as bay anchovy and young weakfish, had proportionally greater contributions in their diet that originated in the phytoplankton, whereas benthically oriented white perch and mummichog (Currin et al. 2003) appeared to depend more on macrophyte detritus and benthic microalgae.

#### THE IMPORTANCE OF MARSH MACROPHYTE AND ALGAL ORGANIC MATTER SOURCES FOR JUVENILE WEAKFISH

Patterns of overlapping  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values in juvenile weakfish collected in West Creek and the open waters of the lower Delaware Bay suggested that fish from this region took advantage of similar

organic matter sources (Fig. 3). All individuals displayed  $\delta^{13}\text{C}$  values intermediate between SPM and *Spartina* spp. and enriched  $\delta^{34}\text{S}$  values relative to benthic microalgae (Fig. 3). Because extensive stands of *P. australis* were absent in the lower Bay (Fig. 2), these fish likely derived the majority of their nutrition from a mixture of predominately *Spartina* spp. and SPM.

A very different pattern emerged in juvenile weakfish nutrition in the upper Bay. Fish captured here exhibited progressively depleted  $\delta^{13}\text{C}$  content with distance from the bay mouth (Table 1, Fig. 3). This trend can be explained either by a transition in the contribution of marsh macrophyte organic matter from *Spartina* spp. to *P. australis*, mirroring the change in dominant macrophytes along the salinity gradient or the contribution of phytoplankton with depleted  $\delta^{13}\text{C}$  values (Fogel et al. 1992; Fry 2002; but see below). Although C isotope data alone could not separate these effects, the addition of S isotopes provided a greater degree of resolution and suggested two lines of evidence that variability in the  $\delta^{13}\text{C}$  values of juvenile weakfish was not driven by variations in phytoplankton  $\delta^{13}\text{C}$  alone. Mean  $\delta^{34}\text{S}$  values for weakfish at all locations were depleted relative to SPM indicating that the latter was not the sole or necessarily dominant source of organic matter used (Fig. 3). Because SPM  $\delta^{34}\text{S}$  should not exhibit a location effect in the salinity regime where our samples were collected (Fry 2002), the significant effect of collection location on juvenile weakfish  $\delta^{34}\text{S}$  also suggested that SPM was not the sole organic source used (Fig. 3, Table 2).

Although there was some overlap with conspecifics captured in the lower Bay, juvenile weakfish collected in the upper Bay most likely derived a majority of their nutrition from phytoplankton with varying contributions from *P. australis* (DWLS curves, Fig. 3). Similar spatial heterogeneity in utilization of organic matter sources was observed in the tidal creeks, but depleted juvenile weakfish S isotope values indicated increasing contributions from tidal marsh production (Fig. 3). The trend in declining C and S isotope values in individuals from West Creek > Mad Horse Creek > Alloway Creek also reflected the increasing contribution of *P. australis* to the trophic spectrum of juvenile weakfish with distance from the Bay mouth, and mirrored the importance of macrophyte production to fish collected in adjacent open waters. The products of marsh production are reaching juvenile weakfish residing in the open Bay, many of which may not have ventured into a marsh during their first year of life (Fig. 3, Table 2). As in other studies, significant differences in the isotopic signatures of individuals from both tidal marshes and



open waters signified the importance of local organic matter sources (Peterson et al. 1985, 1986; Deegan and Garritt 1997; Chanton and Lewis 2002).

#### VARIABILITY IN THE IMPORTANCE OF MARSH MACROPHYTE AND ALGAL ORGANIC MATTER FOR TYPE I–III SPECIES

While the importance of marsh primary production among estuaries will be influenced by geomorphology, variations in tidal range, relative area of marsh to open water and freshwater inputs (Odum et al. 1979; Deegan et al. 1983), the sphere of influence (*sensu* Deegan et al. 2000) of marsh production within an estuary will vary with life history characteristics of individual species including their feeding strategy and patterns of habitat utilization (i.e., Type I–IV strategies). Like juvenile weakfish, the isotopic composition of white perch (Type II species) and bay anchovy (Type III species) varied in a manner that also reflected the dominance of locally produced organic matter (Fig. 4).

Our results confirm those of Deegan and Garritt (1997) and Chanton and Lewis (2002), in that significant enrichment of  $^{34}\text{S}$  in pelagic versus benthic taxa suggest the relative importance of phytoplankton (SPM) is greater for bay anchovy and juvenile weakfish when they are present in tidal marshes, while *P. australis* and benthic microalgae are relatively more important to demersally oriented taxa such as white perch (Fig. 4). Mummichog, a Type I resident species captured in Mad Horse Creek and Alloway Creek, had S isotope values similar to white perch and derived a portion of their nutrition from BMA (Sullivan and Montcrieff 1990; Wainright et al. 2000; Currin et al. 2003). Although BMA contributed to the stable isotope signatures of all species, pelagic taxa (bay anchovy and juvenile weakfish) appeared to be less dependent on this source of primary production (Fig. 4). The contribution of BMA to the nutrition of the species studied likely decreases in the order mummichog (see also Currin et al. 2003) and white perch > juvenile weakfish > bay anchovy.

The role of marsh macrophytes in support of nekton production is also reflected in the complex interactions between feeding strategy and patterns of movements within and among locations, i.e., the landscape grain (Levins 1968). With the highest degree of site fidelity (Lotrich 1975; Teo 1999), *F. heteroclitus* appear to use the marsh habitat mosaic at the coarsest level of the taxa studied, i.e., occupy fewer habitat units than other species (Levins 1968). The organic matter they assimilate will vary with the relative production of marsh macrophytes and BMA at the specific localities they inhabit

(Wainright et al. 2000; Currin et al. 2003). As facultative marsh residents, but moving relatively freely throughout the marsh drainage (Weinstein personal observations), white perch tend to use the marsh macrophytes and BMA that contribute to the benthic food web throughout the tidal creek systems in which they reside.

Type III marine transients, juvenile weakfish and bay anchovy, appeared to integrate organic matter sources on a landscape scale. Though they may never enter a tidal creek during their first year, marsh production, including nutrients derived from the *P. australis* that now covers nearly one-third of the fringing marshes, appear to reach young weakfish and bay anchovy in open waters of Delaware Bay via several potential routes: trophic relays (Kneib 1997), pulsing events (Odum 2000), continuous detritus export (Nixon 1980; Childers et al. 2000), dissolved organic matter (DOM) pathways (especially where the marsh to open water ratio is >0.8; Eldridge and Cifuentes 2000), or other mechanisms. The reduced effect of location on the  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values of bay anchovy (Table 2), especially between individuals collected in the upper and lower open Bay, suggests that bay anchovy display the least site fidelity among the 4 species investigated. As they grow and increase their mobility, we anticipate that weakfish would also treat the estuary as increasingly fine grained (Grecay and Targett 1996).

#### VARIABILITY IN ISOTOPE END MEMBERS IN DELAWARE BAY AND THE INTERPRETATION OF THE RELATIVE IMPORTANCE OF MARSH DERIVED ORGANIC MATTER

Despite some shortcomings, stable isotopes have proven highly useful for tracking the fate of primary production in estuaries. Recent data suggest that the overlap among C isotopic signatures from different plant sources and anthropogenic inputs, especially in the brackish portions of estuaries, tend to confound the interpretation of mixed sources at higher trophic levels (Cifuentes et al. 1988; Cloern et al. 2002; Currin et al. 2003). Balancing this constraint is the oft-quoted observation that local sources of nutrients are the most important driver of isotope signatures in higher order consumers (Fry and Sherr 1984; Deegan and Garritt 1997; Chanton and Lewis 1999).

C in particular may sometimes be problematic because phytoplankton in more confined regions of the upper estuary may display  $^{13}\text{C}$  depleted values when they use  $\text{CO}_2$  produced by respiration of organic C (Fry and Sherr 1984) or when there are seasonal patterns in species composition (Gearing et al. 1984). This may be especially true in warm weather when heterotrophic respiration can be a

potentially important CO<sub>2</sub> source (Spiker and Schemel 1979; Cifuentes et al. 1988; Fogel et al. 1992; Fry 2002). In a long-term study conducted in Delaware Bay, for example, Fogel et al. (1992) reported summertime phytoplankton C signatures in the upper estuary as depleted as -31‰ (1987–1988), while several years earlier (1984–1985) the investigators reported lower summertime limits of only -24‰ in the same region of the estuary (Cifuentes et al. 1988). Conservative mixing of marine and freshwater dissolved inorganic C end members alone (Fry 2002) does not seem to account for a significant portion of the observed differences. Monthly springtime (March–April) freshwater flow during the study period averaged 439 m<sup>-3</sup> s<sup>-1</sup> and 576 m<sup>-3</sup> s<sup>-1</sup> in 1984–1985 (Cifuentes et al. 1988) and 1987–1988 (Fogel et al. 1992), respectively, while the corresponding figures for June and July were only 294 m<sup>-3</sup> s<sup>-1</sup> and 165 m<sup>-3</sup> s<sup>-1</sup> (U.S. Geological Survey 2002). Not only were the most depleted δ<sup>13</sup>C values observed during low flow periods, but also freshwater flow of similar magnitude during the summer months resulted in very different minimum δ<sup>13</sup>C values (-24‰ versus -31‰).

Two alternative explanations for the observed depleted C values seem feasible. delGiorgio and Newell (in review) observed consistently higher bacterial growth efficiency in Delaware Bay tidal salt marshes over a 5-yr period compared to the open Bay. For the upper Delaware Bay, in the region of the estuary where the marsh area:open water ratio is 0.8 or greater and more than 32,000 ha of *Phragmites*-dominated marshes are present, we posit a potential C pathway from *P. australis* DOM and SPM production in tidal creeks through heterotrophes to phytoplankton (Eldridge and Cifuentes 2000). A potential trophic linkage between marsh macrophyte production and a heterotroph→phytoplankton pathway should be examined in greater detail (Holmes et al. 2000).

Our δ<sup>15</sup>N data from earlier marsh studies at the same Delaware Bay locations also suggests that N isotope values are elevated in both white perch and bay anchovy collected within the brackish Alloway Creek, compared to N values in the same species collected in the open Bay or in down-bay polyhaline marshes (Weinstein et al. 2000). White perch, a species that appears to have greater affinity for marsh habitats than bay anchovy, displays greater enrichment in mean δ<sup>15</sup>N values (see below; Weinstein et al. 2000). There appears to be a natural gradient in δ<sup>15</sup>N isotope signatures in species categorized by Type II-III life history strategies with white perch collected in Alloway Creek displaying the most enriched mean values, and bay anchovy and weakfish, the least. Such results implicate anthropogenic inputs (Cifuentes et al. 1988), possibly

sewage effluent, as a potential source of nutrients. Several sewage treatment plant outfalls are located on Alloway Creek, both upstream and in the immediate vicinity of our sampling sites (e.g., the towns of Quinton and Alloway [ $<6$  km distant] and at Hancocks Bridge, New Jersey). The most depleted SPM δ<sup>13</sup>C value measured in Alloway Creek, -27.1‰, was recorded at the dock at Hancocks Bridge (Currin et al. 2003), where a sewage treatment plant outfall located  $<50$  m downstream of the sampling location produces an average summertime flow rate of about 590 m<sup>3</sup> d<sup>-1</sup>. The reported dock value is consistent with the lower range of depleted sewage values (-25.2‰ to -26.2‰) reported elsewhere (Burnett and Schaeffer 1980; Waldron et al. 2001). In addition to phytoplankton, our SPM stable isotope signatures are likely influenced by anthropogenic sources as well as depleted C that may have originated from marsh macrophytes through a heterotrophic pathway.

Although anthropogenic inputs from upriver may play a minor role in mid and lower Delaware Bay (Cifuentes et al. 1988), local inputs in tidal tributaries are important, and detectable.

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