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ARTICLE

Stable Isotope and Biochemical Composition of White Perch in a *Phragmites* Dominated Salt Marsh and Adjacent Waters

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Abstract Tissue stable isotopes and biochemical condition were compared in two populations of white perch, *Morone americana*, residing in a *Phragmites australis*-dominated tidal salt marsh and adjacent open waters of Haverstraw Bay, in the Hudson River estuary, USA. As reported previously for other taxa in this system, stable isotope composition of *M. americana* was influenced by the dominant vegetation present, in this case a near monoculture of *P. australis* and other C_3 vegetation, mainly deciduous trees, that lined the immediate upland shoreline of the marsh. However, all three stable isotopes, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, differed significantly between the two populations, with all three parameters displaying enrichment in the open water collections. Both fish populations exhibited the expected allometric relationships among mass components (total protein, total lipids, dry weight) but energy reserves in the form of triacylglycerols and total lipids were significantly greater in the Haverstraw Bay population. These results were interpreted to not only be a function of fish size but also to originate from differences in habitat quality at the two locations.

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Introduction

The contributing sources of nutrients to the food web of Atlantic coast estuaries have undergone scrutiny for nearly 50 years. While the fundamental salt marsh paradigm remains intact (Haines 1979), the proportionate contributions of various sources, detritus, benthic macroalgae, phytoplankton, and macrophytes to the trophodynamics of finfish appears to be a function of local conditions—hydrology, geomorphology, vegetation dominance, marsh planform, trophic relays, feeding strategies, food quality, and possibly other factors (Weinstein et al. 2000; Litvin and Weinstein 2004; Weinstein et al. 2005). A published conceptual model for the trophic spectrum of Delaware Bay, for example, suggests that several marine transient and resident finfish, not unexpectedly, benefit from *Spartina alterniflora* production in the lower and mid-Bay giving way to contributions from *Phragmites australis* in the brackish upper Bay (below salinities of about 10 psu; Weinstein et al. 2005). Depending on whether an individual resides in a marsh or open Bay waters, benthic microalgae and phytoplankton (as POM), respectively. dominate the microfloral contributions (Wainright et al. 2000; Weinstein et al. 2000; Currin et al. 2003; Litvin and Weinstein 2003; Litvin and Weinstein, 2004; Weinstein et al. 2005). Recently, Weinstein et al. (2009a, b) extended these findings to the Hudson River estuary, and, for the first time, included evaluation of relative biochemical condition, especially energy reserves, in resident *Fundulus heteroclitus* from *S. alterniflora* versus *P. australis* dominated marshes.

One of the taxa studied in detail in Delaware Bay, the white perch, *Morone americana* similarly benefitted from *P.*

australis in brackish salt marsh habitats, while individual white perch captured in the mid and lower Bay marshes displayed stable isotope signatures that were characteristic of *S. alterniflora*, especially carbon (C) and nitrogen (N) (Weinstein et al. 2000). With one exception, the isotopic composition of white perch in Delaware Bay was not significantly different for all three isotopes among lower-bay locations or between upper-bay brackish habitats (Weinstein et al. 2000). As anticipated, carbon isotope signatures in white perch also differed among upper-bay and both lower bay sites. In upper and mid Bay oligohaline and mesohaline tidal creeks, respectively, 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 (Weinstein et al. 2000). At lower-bay polyhaline sites, however, the pattern shifted to a mixture of *S. alterniflora* and benthic microalgae in the trophodynamic patterns of this species.

In most, if not all, Atlantic coast estuaries, white perch spend virtually their entire life cycle within the confines of the estuary. As young, they are widely distributed and are abundant in tidal creeks throughout the summer and early fall. Although spawning occurs in open waters, early juveniles migrate inshore at about 30 mm TL and occupy shallow waters including tidal creeks throughout the first summer. In the Hudson River estuary, white perch reach a mean length of about 77–90 mm TL during their first year, achieving approximately 40% of their maximum adult size (Able and Fahay 1998). Older juveniles begin moving from the shoal into overwintering habitats in October, and by mid-December a majority of the young-of-year and adults are found in deep mid river channels of the lower estuary and in the fresh and brackish portions of this system. Growth during winter is virtually nil (Able and Fahay 1998).

This life history strategy is common in many fishes occupying estuaries at north temperate latitudes (Hurst 2007). Within these systems, numerous factors interact to affect survival, growth and energy allocation, and ultimately recruitment success (Shuter and Post 1990; Walters and Juanes 1993; Kneib 2003). Early in estuarine residency, predation appears to drive the allocation of energy into somatic growth (Lankford and Targett 1994; Post et al. 1997; Sogard and Spencer 2004), while later in the year preparation for migration and overwintering directs the allocation of energy toward storage in various tissues. Starvation due to energy deficits is considered a major form of mortality in winter with water temperatures and the allometry of metabolic rates determining variability in the magnitude of energy reserves among populations (Post and Lee 1996; Schultz and Conover 1997) and their likelihood of ameliorating overwinter starvation (Hurst 2007). These two sources of mortality, predation and overwinter starvation, generate competing energetic demands with strong size-driven allometries that have important consequences for survival (Conover and Schultz 1997; Post and Parkinson 2001; Hurst and Convover 2003).

Here we examine the stable isotope composition and nutritional biochemistry (Weinstein et al. 2009b) of *M. americana* residing in a brackish tidal creek and adjacent shoals of the Hudson River estuary at Piermont Marsh one of the National Estuarine Research Reserves located at approximately river km 37 near Piermont, New York. The following questions were addressed in this research: Given the size dependent, seasonal movements of white perch, (1) were there any differences in the contribution of primary producers to the trophic spectrum of *M. americana* in the marsh and adjacent open waters; (2) were there any differences in biochemical condition, principally the deposition of energy reserves, in white perch captured seasonally at the two locations; (3) were any differences related to size distributions of individuals in the populations; and (4) could biochemical condition of individuals distinguish between the two sampled populations?

Methods

Study Area and Collections

Details of all of the field and laboratory techniques used for analyzing fish and vegetation were presented in Weinstein et al. (2000, 2009a), Wainright et al. (2000), Currin et al. (2003), and Litvin and Weinstein (2004). Two sampling locations were established in the Hudson River estuary: one at Piermont Marsh, an oligo-mesohaline site (Montalto et al. 2005; Osgood et al. 2006) located in the Hudson River National Estuarine Research Reserve at approximately river km 37 (the southern tip of Manhattan Island is used as the 0-km reference point for the Hudson River; Fig. 1), and the other at an adjacent open water site in Haverstraw Bay. Prior surveys of Piermont Marsh indicated that the C_3 species *P. australis* dominated more than 85% of the total vegetated marsh surface, with much small patches of other vegetation present (primarily *Spartina patens*), permanent tide pools, intertidal flats, and subtidal waters comprising the remainder (Winogrand and Kiviat 1997).

Vegetation

"Baseline" stable isotope values for marsh macrophytes, benthic microalgae, and phytoplankton as suspended particulate matter were presented in earlier studies (Weinstein et al. 2000; Wainright et al. 2000; Currin et al. 2003), and were supplemented with local samples of dominant macrophytes and hardwoods (that lined the shore) at Piermont Marsh (Weinstein et al. 2009a).

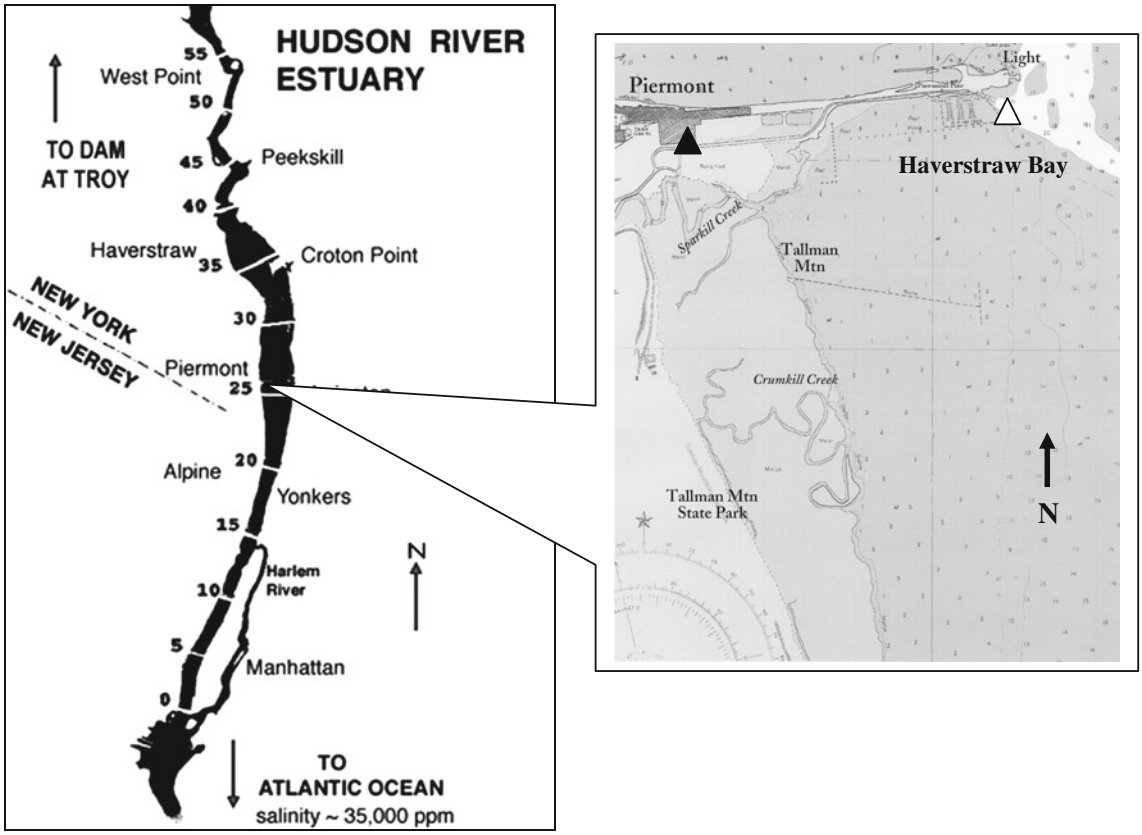


Fig. 1 Sampling locations for white perch (*Morone americana*) in Sparkill Creek, Piermont Marsh (▲) and in open waters (△) of Haverstraw Bay, on the Hudson River

Fish

Populations of *M. americana* were sampled in all collections by 16-m seine (6.5-mm mesh) or 9-m otter trawl (6.5-mm mesh cod end) during July through October–November, at Piermont Marsh and nearby Haverstraw Bay, respectively. Up to 15 randomly selected individuals from each monthly collection were examined for stable isotope composition, dry and wet weight, lean biomass (protein content), and lipid stores. Fish were immediately frozen on dry ice in the field and transferred to −80°C upon return to the laboratory (Weinstein et al. 2000).

Laboratory Processing and Analysis

Partially thawed fish were measured to the nearest mm standard length and, after removing gut contents and gently blotting, were wet weighed to the nearest 0.1 g and subsequently freeze-dried to a constant dry weight before being ground to a fine powder (Cyclotec 1100® grinding mill). Larger fish were pre-sectioned into smaller pieces before freeze drying. Powdered samples were stored in pre-combusted glass containers with acid-washed polyethylene caps and purged with N_2 gas to exclude airborne oxygen and prevent lipid peroxidation prior to storage at −80°C.

Isotopic Determinations

Fish samples were analyzed on a Micromass Isochrom Continuous Flow Stable Isotope Mass Spectrometer coupled to a Carla Erba Elemental Analyzer (CHNS-O EA1 108). Standards were Peedee Belemnite for C, air for N, and Canyon Diablo triolites for sulfur (S) (Litvin and Weinstein 2004). Macrophyte C, N, and S stable isotopic signatures from previously collected samples in Delaware Bay samples (Weinstein et al. 2000; Wainright et al. 2000) and Mullica River (Currin et al. 2003) were calculated as 95% confidence ellipses, whereas new values for *S. alterniflora, P. australis,* and the dominant hardwoods *Q. rubra, A. platanoides,* and *F. grandifolia* collected in this study will be shown as discrete data points.

Lipid Class Determination

A 50±5-mg subsample of ground fish tissue (or the entire aliquot if the fish weighed <50 mg) was folded into a 70-mm-diameter Whatman® 541 ashless filter paper and

extracted three times, first in 4.0 ml of 2:1 (v/v) dichloromethane/methanol for 15-h at 5°C (vial headspace purged with N_2), then in 3.0 ml of fresh solvent mixture for 3-h, followed by a final 3-h extraction in 2 ml of fresh solvent mixture. The three sequential extracts were combined and stored at −80°C under N_2 for no more than four days to avoid esterification of fatty acids by methanol in the extraction solvent (Parrish 1987). We added 50 μg μl^{-1} nonadecane ($C_{19}H_{40}$, 1.000 mg total) internal standard in chloroform to each extract, and we used back extraction in 0.1 M aqueous KCl solution at 5°C to remove non-lipid materials (Folch et al. 1957). Back extracted samples were concentrated by evaporating to dryness in a 38°C water bath under a stream of N_2 gas and then reconstituted in 0.5–1.5 ml of dichloromethane, depending on sample size and lipid content.

A modified method of Lochmann et al. (1995) where 1 μl aliquots of lipid extract was spotted on individual Iatron Chromarod III® silica-coated rods and partially developed in three successive HPLC grade solvent systems was used to separate lipid classes. Flame ionization detector (FID) scanning using an Iatroscan® Mark VI and the Peak Simple® software integrator was used for data acquisition. Blanks, a combined synthetic standard that included hydrocarbon (nonadecane), waxy ester (palmitic acid stearyl ester), triacylglycerol (tripalmitin), free fatty acid (palmitic acid), fatty alcohol (1-hexadecanol [cetyl alcohol]), sterol (cholesterol), monoacylglycerol (1-monopalmitoyl-rac-glycerol), phospholipid (phosphatidyl-choline), and one replicate for every seven samples were utilized to determine lipid class concentrations and ensure accuracy.

Conversion of FID peak areas to extract lipid concentrations (mg g^{-1} dry weight) was performed using a segmented third order polynomial calibration model with separate curves generated for each standard and each chromarod used.

Lean Protein Mass

After removing lipids, subsamples were dried at 90°C, placed in a porcelain crucible with the addition of 0.1 ml of mineral oil to promote burning, and ashed in a muffle furnace for 2-h at 550°C. The ash was cooled in a desiccator then weighed. Lean protein mass (LPM) was determined from the subsample using each ash weight (corrected by 0.04 mg for ash mass of filter paper packets), and lipid weight was determined via TLC/FID:

$$\text{LPM} = \text{dry weight} - \text{ash weight} - \text{total lipid weight}$$

This measure of non-lipid structural organic matter has been used to estimate protein content in a variety of fishes and was applied in this study (Montevecchi and Piatt 1984; Schultz and Conover 1999; Slotte 1999; Hurst et al. 2000).

Data Analyses

Stable isotope signatures from individual *M. americana* were compared to dominant marsh grasses at each location and also evaluated in the context of microphyte and hardwood tissue signatures. Biochemical condition of individual *M. americana* was evaluated on the basis of total lipids, triacylglycerols (TAG), free fatty acids (FFA), phospholipids (PL), and the LPM of individuals. Other lipid classes such as cholesterol, fatty alcohols, and wax esters were not examined in detail but included in the calculation of total lipid mass. It is generally accepted that the size of lipid stores can be used to predict whether a fish is ready to migrate, preparing to overwinter, or is likely to have future fecundity and reproductive success (Ackman 1980; Shulman and Love 1999). Previous studies of lipid class dynamics in young teleosts suggest that TAG is the primary form of lipid used in energy storage; therefore, this lipid class was selected as an important indicator of biochemical condition (Ackman and Eaton 1976; Lochmann et al. 1995; Lochman et al. 1996; Lochmann and Ludwig 2003; Heintz et al. 2004). However, free fatty acids and phospholipids can contribute to energy metabolism (Ross and Love 1979; Henderson and Tocher 1987; Yuneva et al. 1991) and may be important in the reproductive cycle (Ackman 1980) and were thus examined in individual fish. TAG, FFA, PL, and total lipids (all expressed in mg g^{-1} dry weight, and LPM (g) for whole fish was extrapolated from extracted subsamples and converted to total storage quantities by adjusting to the dry weight of each fish.

Population parameters and the biochemical condition of white perch were compared among collection dates and collection locations. Extreme outliers, defined as values with absolute Studentized residuals ranging from −6.8 to 3.91 (n=12<3% of the total components analyzed), were removed from the data set prior to analysis (Sutton et al. 2000). Because not all parametric statistical assumptions could be met in every instance, a non-parametric approach was also adopted where necessary, utilizing Kruskal–Wallis one-way ANOVA, Mann–Whitney two-sample tests, and Kolmogorov-Smirnov two-sample tests. All statistical tests were conducted with SYSTAT 12 (SPSS 2007).

Results

Length Distributions

As anticipated, *M. americana* collected in open waters in Haverstraw Bay were larger on average than fish collected in the marsh (Fig. 2; Kolmogorov-Smirnov two sided probability; p<0.0001). However, fish smaller than 101 mm SL, those largely responsible for this difference

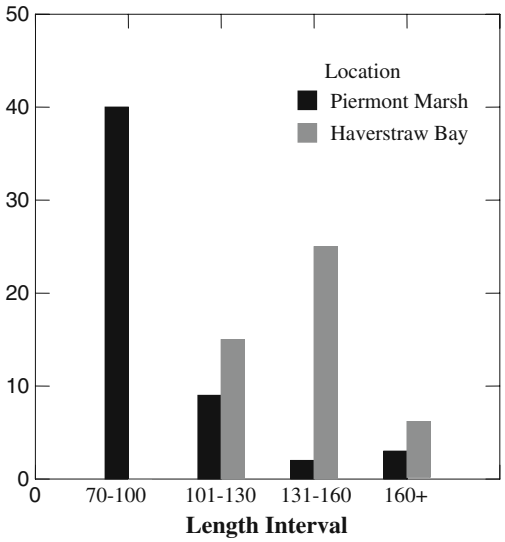


Fig. 2 Length frequency distribution (%) as a function of standard length for white perch (*Morone americana*) captured in Piermont Marsh and adjacent open waters of Haverstraw Bay, Hudson River estuary

were absent in the Haverstraw Bay samples. This trend was in keeping with younger fish moving to shallow waters in spring and larger individuals emigrating first to open waters as the season progressed (Able and Fahay 1998). In addition, both sites included fish larger than 1-year olds, using 90 mm as a rough measure of growth during the first year (Able and Fahay 1998).

Isotopic Signatures

Lipid concentrations in white perch averaged 2.4%, ranging from 0.3% to 13.2%, suggesting that the stable isotope values could be compared directly without adjusting for lipid content (Post et. al. 2007). Earlier, Weinstein et al. (2009a) reported that overall, stable isotope values for *P. australis* collected in this study were broadly similar to those established in our previous work on Delaware Bay and the Mullica River estuary. Sulfur values, however, were slightly ^{34}S-enriched in *P. australis* sampled in Piermont Marsh. In contrast, ^{15}N signatures in *P. australis* were slightly depleted in Piermont Marsh compared to sites in the Delaware Bay and the Mullica River (Weinstein et al. 2000; Currin et al. 2003; Weinstein et al. 2009a). While S values for northern red oak (*Q. rubra*) overlapped those of *P. australis,* all three deciduous C_3 species were readily distinguished from *P. australis* by their N stable isotope values (Fig. 3). Similar results were reported in our work on *F. heteroclitus* captured in similar habitats in three different estuarine systems (Wainright et al. 2000; Currin et al. 2003; Weinstein et al. 2009a) suggesting that the method is robust in examining nutrient flux from primary producers to consumers.

Overall, isotopic values for *M. americana* tissues overlapped substantially when visual comparisons were made among fish collected in marsh creeks and open waters of the Hudson and Delaware Bay sites (Fig. 3). Although no direct statistical comparisons were made between *M. americana* collections from the two estuaries, the 95% confidence ellipses for fish collected at Alloway Creek and its nearby shoals (Fig. 3) suggest that some qualified differences occur. Fish captured at both the Alloway Creek and shoal sites displayed enriched δ^{15}N values that were similar to Hudson River *M. americana* collected in Haverstraw Bay but greater than fish collected in Piermont Marsh. Similarly, there appeared to be enriched δ^{13}C values at both Delaware sites and Haverstraw Bay while δ^{13}C values from fish collected in Piermont Marsh were relatively depleted.

For Hudson River collections alone, all mean (±SE) isotopic values for *M. americana* differed significantly (Fig. 4; Kruskal-Wallis test; $P<0.0001$; all parameters)

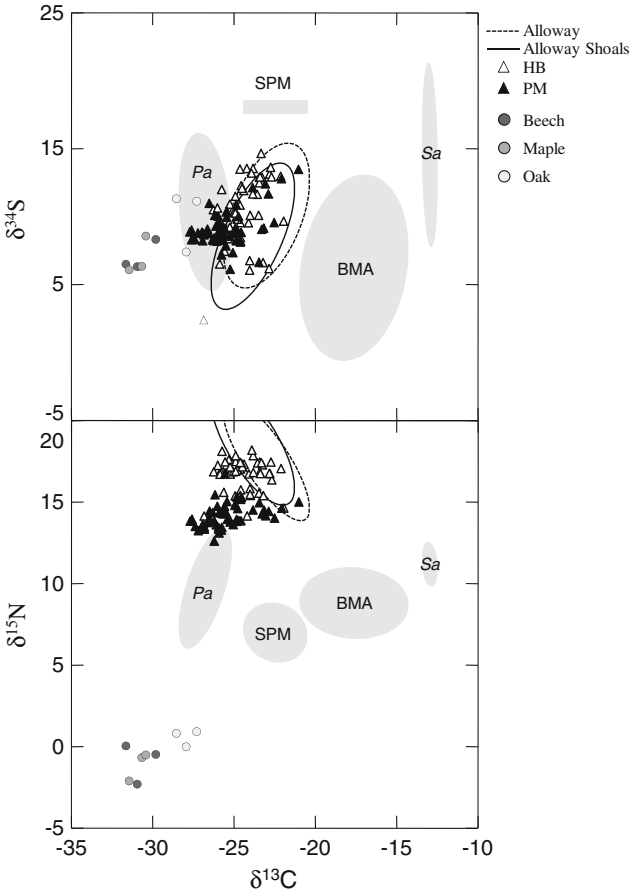


Fig. 3 Stable isotope signatures (CNS) for white perch (*Morone americana*) captured in PM—Piermont Marsh (▲), HB—Haverstraw Bay (△). Vegetation ellipses: SPM—suspended particulate matter (surrogate for phytoplankton), *BMA* benthic microalgae, *Sa Spartina alterniflora*, *Pa Phragmites australis*, *Beech* American beech, *F. grandifolia*, *Maple* Norway maple, *A. platanoides*, and *Oak* northern red oak, *Q. rubra*. For comparison, stable isotope values for white perch collected in a Delaware Bay tidal creek (– – –) and adjacent shoals (———) are also shown as 95% confidence ellipses

between Piermont Marsh and the adjacent open waters of Haverstraw Bay; $\delta^{13}C$=−25.37 (1.44), −24.42 (1.10); $\delta^{34}S$= 9.10 (1.39), 10.24 (2.46); and $\delta^{15}N$=14.11 (0.73), 16.55 (1.05); respectively. Upon further examination, it was clear that the differences were largely a function of capture location and size differences in the two populations (Fig. 5). Although ontogenetic feeding patterns change with size in *M. americana*; as is the case with many other fish taxa (Smith et al. 1985; Nemerson 2001), larger individuals captured in Piermont Marsh, although a small sample of four fish, did not display the sort of trophic fractionation for N anticipated in larger individuals (as suggested by the "trophic breakpoint" between length intervals II and III shown in Fig. 5; see below).

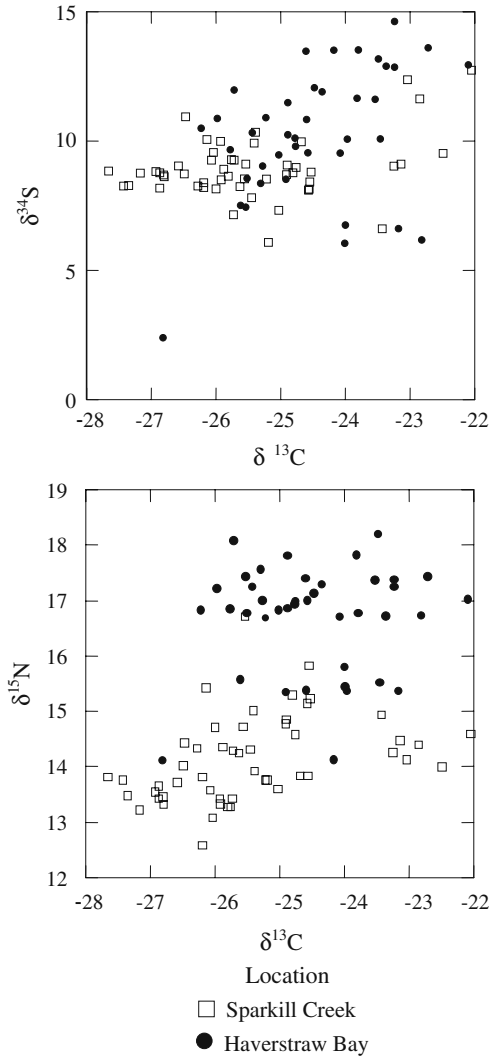


Fig. 4 Stable isotope values bi-plot, $\delta^{34}S$ and $\delta^{15}N$ versus $\delta^{13}C$ in white perch (*Morone americana*) captured in Sparkill Creek (□), Piermont Marsh and adjacent open waters of Haverstraw Bay (●), Hudson River

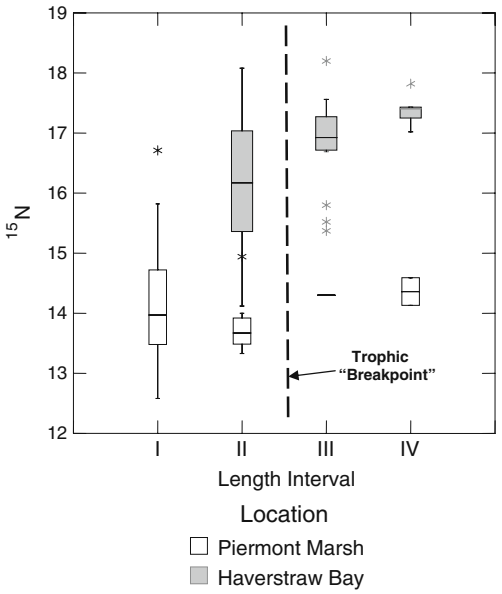


Fig. 5 Nitrogen stable isotope composition ($\delta^{15}N$) of white perch (*Morone Americana*) characterized by standard length interval; *I*=70–100 mm, *II*=101–130, *III*=131–160, *IV*=161+. Vertical broken line shows "trophic breakpoint" where young white perch exhibit an ontogenetic shift to more fish in their diet

Mass

Allometry of wet mass and its components, dry mass, LPM, and lipid mass exhibited the anticipated hyperallometric patterns observed in many teleosts and other taxa (Fig. 6a; Post and Parkinson 2001), and were best described by the following equations for log-transformed wet weight (g), dry weight (g), lean protein mass (g), and total lipid mass (mg) against the log of standard length (millimeters):

$$\log(\text{wet mass, g}) = -4.117 + 2.765\log(\text{standard length}); \quad r^2 = 0.978$$

$$\log(\text{dry mass, g}) = -4.785 + 2.816\log(\text{standard length}); \quad r^2 = 0.969$$

$$\log(\text{lean protein mass, g}) = -4.733 + 2.734\log(\text{standard length}); \quad r^2 = 0.954$$

$$\log(\text{lipid mass, mg}) = -1.5524 + 1.840\log(\text{standard length}); \quad r^2 = 0.439$$

Because of its lower concentrations, lipid mass as a percentage of total wet mass was best expressed in

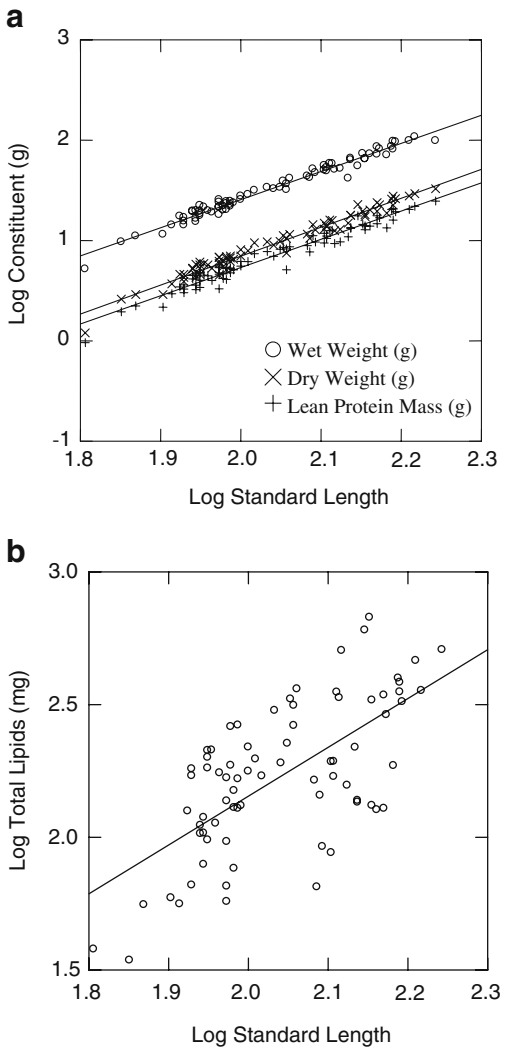


Fig. 6 **a** Log-log plot of wet weight (○), dry weight (×) and lean protein mass (+) in grams versus standard length (mm) for pooled collections of white perch (*Morone americana*); **b** Log–log plot of total lipids (mg) versus standard length (mm) for pooled collections of white perch recorded in this study

mg g^{-1} (Fig. 6b) and most values fell within the range reported for other moronids (Hurst et al. 2000; Hurst and Convover 2003). Not surprisingly, lipid values were characterized by greater variability in individual values compared to the other components (r^2=0.439). As noted previously (Weinstein et al. 2009a), the lipid values described here were also uniformly influenced by an unexplained laboratory artifact at the time of analysis: rather than nonadecane ($C_{19}H_{40}$) standard additions being about 1.0 mg as expected, the values calculated in this study were inconsistent, averaging 4.6±2.1 (SD) mg. We used the actual measured standard values recorded on each chromarod to adjust the area under the standard curves. Although this procedure is believed to have retained the relative lipid values among individual fish, the absolute values reported here, despite falling within the range reported by others, should be interpreted with caution.

Biochemical Condition

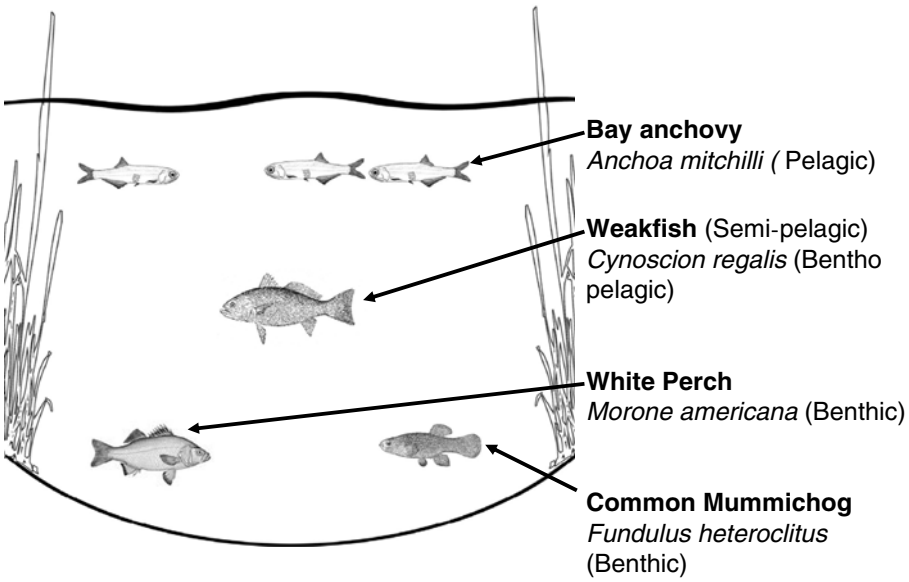
No significant interactions were detected between standard length and sample site for four of five biochemical condition parameters used in this study (Table 1). However, the SL*site interaction probability value for free fatty acids was p=0.0001, thus precluding direct comparisons for this component. Among the four categories compared, only TAG and total lipid concentrations differed significantly in the marsh-Bay comparisons (Mann–Whitney U; $p<$ 0.0001). Similar results were recorded in our previous study on *F. heteroclitus* (Weinstein et al. 2009a)

Discussion

Despite some shortcomings, stable isotope analysis has proven to be an important tool for examining the trophodynamics of estuarine finfish including those species whose young use estuarine habitats as primary nurseries (Weinstein 1979). We have applied our methods with demonstrable success to four estuarine species, a marsh "facultative", *M. americana*; marsh resident, *F. heteroclitus*; and two marsh transients, weakfish, *Cynoscion regalis*, and bay anchovy, *Anchoa mitchilli* in order to revisit the salt marsh paradigm (Haines 1979). By themselves, stable isotope signatures have proven to be a remarkably sensitive and robust indicator of site fidelity, feeding strategies and habitat specific nutrient sources in these species (Wainright et al. 2000; Weinstein et al. 2000; Currin et al 2003; Litvin and Weinstein 2003; Litvin and Weinstein 2004; Weinstein et al. 2005; Weinstein et al. 2009a, b). Using earlier reported results, we have identified what we described as a "feeding compass" for juvenile weakfish in Delaware Bay (Litvin and Weinstein 2004). The stable isotope signatures in fish captured in lower and upper bay tidal creeks were dominated by macrophytes (*S. alterniflora* in the lower bay and an invasive variety of *P.australis* in the upper bay) with additional contributions from benthic microalgae. Fish captured outside of the marshes in open Bay waters, while exhibiting the same patterns of macrophyte end-member contributions depending on whether they spent more time up or down Bay, also displayed a clear shift to increased contributions from phytoplankton (reported as suspended particulate matter, SPM)(Litvin and Weinstein 2004). While we have not yet addressed the issue of proportionate contributions of various end-members (work in progress) the patterns of both site fidelity and nutrients sources examined in these four species has been compelling (Wainright et al. 2000; Weinstein et al. 2000; Currin et al.

Table 1 Marsh-Bay comparisons in biochemical condition of *Morone americana* collected in Piermont Marsh and the adjacent Haverstraw Bay. *SL* standard length

	n	SL		SL*Site	
		t	p	t	p
Lean protein mass (g)	80	9.898	0.0001	−0.229	ns
Total lipids (mg)	86	3.895	0.0001	−1.132	ns
Total TAG (mg)	86	3.307	0.0440	0.403	ns
Total FFA (mg)	80	3.751	0.0001	−3.464	0.001
Total phospholipid (mg)	86	1.623	ns	−0.314	ns



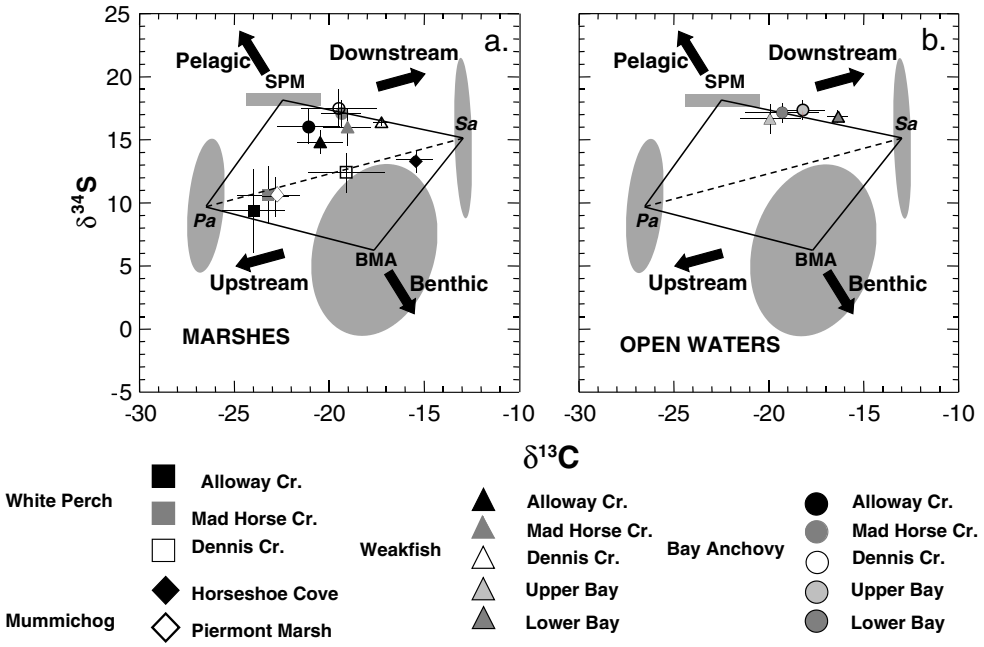


Fig. 7 Water column feeding strategies in four marine finfish, bay anchovy (*Anchoa mitchilli*), white perch (*Morone americana*), weakfish (*Cynoscion regalis*) and common mummichog (*Fundulus heteroclitus*) and their stable isotope signatures based on capture location, Delaware and Hudson River estuaries. In addition to the influence of dominant macrophytes (*Spartina alterniflora*, Sa and *Phragmites australis*, Pa) stable isotope values of benthic feeders were also influence by benthic microalgae (Bμa), while those of bentho-pelagic and pelagic species have a greater proportionate signature associated with phytoplankton (as SPM)

2003; Litvin and Weinstein 2003; Litvin and Weinstein 2004; Weinstein et al. 2005; Weinstein et al. 2009a, b; Fig. 7 this study).

We can extend these findings with a consideration of water column-specific feeding strategies in these same four taxa. White perch and mummichogs are generally considered to be bottom feeders, weakfish bentho-pelagic (or semi-pelagic), and bay anchovy pelagic (Fig. 7) (Able and Fahay 1998). These feeding strategies are clearly confirmed in the stable isotope values shown for each taxon whether they were captured in the marsh or in the case of the two transients, in open waters. Both benthic feeding species, white perch and mummichogs appeared to benefit from benthic microalgal production, while the semi- and pelagic taxa had proportionately greater contributions from phytoplankton, especially in open waters (for details of the statistical comparisons, see Litvin and Weinstein 2003). The arrows represent the "tug" from different end-members in the trophic compass and stable isotopic composition of tissues from these samples.

White perch in this study displayed the characteristic habitat use patterns that we and others have come to call the "coastal conveyor belt" early life-history strategy. Young perch were recruited to the tidal creeks of Piermont Marsh from the main estuary in summer and generally resided here, but with an apparent bleeding off of larger individuals as time passed (Fig. 2). Additionally, the smallest size classes were absent in adjacent shoal waters throughout the period of collection, and as expected, a larger proportion of larger individuals were present on the shoals compared to in creek waters (Fig. 2). Interestingly, a small proportion of larger fish were present throughout the sampling period (see below), until such time as falling temperatures moved the majority of individuals offshore in late autumn; no white perch were collected at Piermont Marsh in our November sampling event.

Young *M. americana* also exhibited some interesting differences in body composition of stable isotopes compared to our findings from the Delaware Bay. Mean values for all three isotopes examined in this study, $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, differed significantly, with fish captured in open waters outside of the marsh enriched in all three isotopes (Figs. 3 and 4). On the other hand, stable isotope values in white perch captured in upper versus lower Delaware Bay tidal creeks (no white perch were collected in adjacent open waters at either location) displayed the expectedly different $\delta^{13}C$ values associated with the dominant macrophytes, upper bay creeks were dominated by *P. australis*, while lower bay creeks were dominated by *S. alterniflora.* Yet, with one exception for N in a lower bay creek (Moore's Beach), neither $\delta^{15}N$ nor $\delta^{34}S$ isotope values differed in white perch among Delaware Bay collections. There, thus, appears to be some fundamental differences in available nutrients for the same species residing in the two habitats, tidal creeks versus adjacent open waters. The source of these differences is not presently clear.

Although white perch were significantly larger in open waters, it also does not appear that trophic fractionation alone accounted for these differences. As noted in Fig. 5, a trophic "breakpoint" occurs in the size categories between II and III associated with a shift to much larger proportions of fish in the diet (Smith et al. 1985; Nemerson 2001). All four individuals in size classes III and IV that were captured in the tidal creek displayed depleted $\delta^{15}N$ values compared to similar sized individuals captured outside of the marsh (Fig. 5). We speculate two possible causes for these patterns, the C shift in fish from the creek might be associated with allochthonous inputs of depleted C from trees lining the upland shore of the marsh. As noted in Fig. 3, maples, oaks and beech were all depleted in $\delta^{13}C$ values compared to *P. australis*, and secondly, in addition to any trophic shift that might be a factor, fish spending the majority of their time offshore might be exposed to additional anthropogenic sources of N associated with the villages of Piermont, Nyack, and Tarrytown located around Haverstraw Bay. Unraveling the details of these differences must await additional research.

The size-driven allometries reported here coincide with our earlier reported results for common mummichog, *F. heteroclitus* collected in Piermont Marsh, and generally, reflects the patterns in other north-temperate species (Post and Parkinson 2001). Larger individuals, those that exhibit greater energy storage in utilizable form (primarily lipids) have a greater likelihood of surviving periods of intense resource scarcity (Post and Parkinson 2001); moreover, individuals entering the winter with enhanced energy stores are more likely to survive until the next growing season (Hurst 2007). White perch collected in Piermont marsh were observed to have significantly lower concentrations of TAG and total lipids as energy stores than their larger conspecifics captured either in open waters of Haverstraw Bay; or those few larger individuals that appeared to stay in the tidal creeks all season (Fig. 5). We suspect that the same competing allometries for rapid somatic growth to avoid gape-limited predators versus allocation to energy reserves to survive the winter are operating in this species (Post and Parkinson 2001; Weinstein et al. 2009a, b).

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