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Essential Fish Habitat and Wetland Restoration Success: A Tier III Approach to the Biochemical Condition of Common Mummichog *Fundulus heteroclitus* in Common Reed *Phragmites australis*- and Smooth Cordgrass *Spartina alterniflora*-Dominated Salt Marshes

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Abstract A tier III, essential fish habitat analysis was used to evaluate the biochemical condition of common mummichog *Fundulus heteroclitus* residing in two isolated tidal salt marshes, one a relatively undisturbed polyhaline site dominated by *Spartina alterniflora* and the other a meso-oligohaline site dominated by an invasive variety of *Phragmites australis.* Stable isotopes signatures of C, N, and S in whole tissue samples of *F. heteroclitus* were used to compare the trophic spectrum for this species in each marsh as a function of the dominant macrophytes present with additional contributions from phytoplankton and benthic microalgae. Allometry of wet mass and its components, water mass, lean protein mass and lipid mass in individual fish exhibited hyperallometric patterns; and average lipid mass fell within the range reported for most fundulids, including *F. heteroclitus*. Significant differences were also detected in the allocation of lipid classes to energy reserves in the form of triacylglycerols (TAG) and free fatty acids. These reserves, especially TAG, are critical for reproduction, migration, and overwintering survival in many taxa and were significantly lower in fish collected in the *P. australis*-dominated marsh. Relative to the relatively undisturbed *Spartina*-dominated site, we tentatively conclude that the *P. australis*-invaded marsh was an inferior habitat for *F. heteroclitus*.

Keywords Essential fish habitat · *F. heteroclitus* · Salt marshes · Biochemical condition

Introduction

Several years ago, Beck et al. (2001) commented that marine nurseries were places where the “contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur”. The underlying premise for this statement was that habitats varied in their intrinsic quality and that by residing in the best habitats during their first year, some populations experienced higher rates of secondary production and potentially greater recruitment to adult stocks. While this principle can be extended to older life stages as well, its use is confounded in two ways. First, it has been shown that an individual need not spend much time in a given habitat to benefit from it (Weinstein et al. 2005). Because of functional linkages among habitats in the estuarine landscape and the connectivity among system components, habitats do not function in isolation when supporting marine secondary production, but rather are integrated components of larger systems (Childers et al. 2000).

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Moreover, production in the open waters of these systems may be donor-controlled, i.e., a function of the dynamics of external (allochthonous) inputs (Polis et al. 1995; Polis and Strong 1996). In salt marsh-dominated estuaries, export of the products of the salt marsh may support higher levels of productivity in open waters than by in situ production alone.

Second, some species, marine transients in particular (Deegan and Garritt 1997; Deegan et al. 2000), are difficult to define in terms of habitat usage. They are highly mobile and tend to regularly cross habitat boundaries in their quest for food and shelter. Generally, they are not habitat specialists but rather are opportunistic in utilizing resources and treat the estuarine landscape as fine-grained (e.g., see Levins 1968, p. 19). Whatever their adaptive strategy, individuals and populations that live in seasonal environments must address several challenges to reach reproductive age (Post and Parkinson 2001). Foremost among these is the tradeoff between size and the risk of predation and, in northerly latitudes, surviving the winter. The latter interval is a time of scarcity and a period of energy deficits for north-temperate fishes (Hurst 2007). Often, fitness is a function of unique local conditions and the species specific adaptations to them, e.g., strategies used by resident versus transient taxa (Walters and Juanes 1993; Fullerton et al. 2000).

These life history traits can also be evaluated in the context of restoration ecology and essential fish habitat (EFH) by the integration of factors that affect survival and well-being of fish during their life cycle (Able 1999). The degree to which a natural or restored habitat is utilized is presumed dependent on its value. In restored sites, habitat value is maximized once it has reached its restoration asymptote within the "bound of expectation" (Weinstein et al. 1997). The application of EFH to fishery management and restoration design necessitates the analysis of habitat information in a hierarchical or matrix fashion. At the least informative level (tier I), presence or absence information may be used to infer the potential value of habitats, albeit with a high level of uncertainty. At increasingly complex levels, habitat value becomes a function of the relative abundance or density of individuals at different locations (tier II). At the next level, growth, reproduction, and survival rates, if available, are used with the assumption that the habitats contributing the most to productivity should be those that support the highest levels of these parameters (tier III). Finally, production rates can be used to directly relate species or life stages to types, quantity, quality, and location of essential habitats (tier IV). There has been a relatively slow evolution of restoration success criteria to include the upper tiers of EFH (III and IV).

Superimposed on this framework are the negative ecological effects of the invasive variety of the common reed *Phragmites australis* (m-haplotype; Saltonstall 2002) on EFH, i.e., tidal salt marsh functions (Weinstein and Balletto 1999; Weinstein et al. 2003). Modification of habitat quality, and consequently EFH, in brackish salt marshes by non-indigenous common reed has occurred over broad geographic areas of eastern North America (Weinstein et al. 2003). The negative influence of *P. australis* is thought to derive from the plant's ability to influence marsh planform and hydroperiod and, as a result, influence access to the marsh surface by fishes and other biota. Because *P. australis* also affects the area of standing water on the marsh surface, it appears to have severe negative impacts on standing biomass of young finfish (Hagan et al. 2007).

We examined the concept of habitat quality (EFH) for *Fundulus heteroclitus* in relatively undisturbed and *Phragmites*-dominated tidal salt marshes along the mid-Atlantic Coast of the USA. In addition to our earlier work on the trophic spectrum of this species (Wainright et al. 2000; Currin et al. 2003), an interesting "natural experiment" was available to us because (1) the species spends its entire life cycle within the confines of the marsh and has an extremely small home range (Valiela et al. 1977; Meredith and Lotrich 1979; Teo and Able 2003), and (2) many tidal salt marshes, particularly those with brackish salinities, have become dominated by virtual monocultures of the invasive variety of the common reed that is perceived to reduce habitat quality for *F. heteroclitus* (Weinstein and Balletto 1999; Saltonstall 2002; Hagan et al. 2007). By adopting a whole ecosystem approach, we essentially had a "captive audience", one in each of two isolated marsh complexes, a polyhaline system dominated by *Spartina alterniflora* and a meso-oligohaline system dominated by an invasive variety of *P. australis.*

The following questions were addressed in this study: (1) Were there any differences in the contribution of primary producers to the trophic spectrum of *F. heteroclitus* in the two marshes; (2) were there any differences in biochemical condition, principally the deposition of energy reserves, in mummichogs captured seasonally in the *S. alterniflora*-dominated "natural" and the *P. australis*-invaded salt marshes (Tier III EFH analysis); (3) were any differences related to size distributions of individuals in the populations; (4) were any differences related to the annual reproductive cycle, or the degree of parasitization of individuals; and (5) could biochemical condition ultimately serve as a success criterion to evaluate the *functional* success of wetland restoration?

Materials and 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), Wainright et al. (2000), Currin et al. (2003), and Litvin and Weinstein (2004). Two new sites were established in the Hudson River estuary (Fig. 1): Horseshoe Cove, an isolated polyhaline marsh dominated by the C_4 plant *S. alterniflora* situated at about river km 29 in Sandy Hook Bay (the Battery at the southern tip of Manhattan Island is used as the 0-km reference point for the Hudson River; Fig. 1), and the oligo-mesohaline Piermont Marsh (Montalto et al. 2005; Osgood et al. 2006), also isolated but larger and located in the Hudson River National Estuarine Research Reserve at approximately river km 37. Surveys of Piermont Marsh conducted in 1991 indicated that the C_3 species *P. australis* dominated more than 85% of the total vegetated marsh surface, with small patches of other vegetation (primarily *Spartina patens*), permanent tide pools, intertidal flats, and subtidal waters comprising the remainder (Winogrand and Kiviat 1997). In this estuarine system, it was not possible to locate an undisturbed *Spartina*-dominated marsh in close proximity to Piermont Marsh, nor was it possible to establish collecting sites in the two marsh types within the same salinity regime.

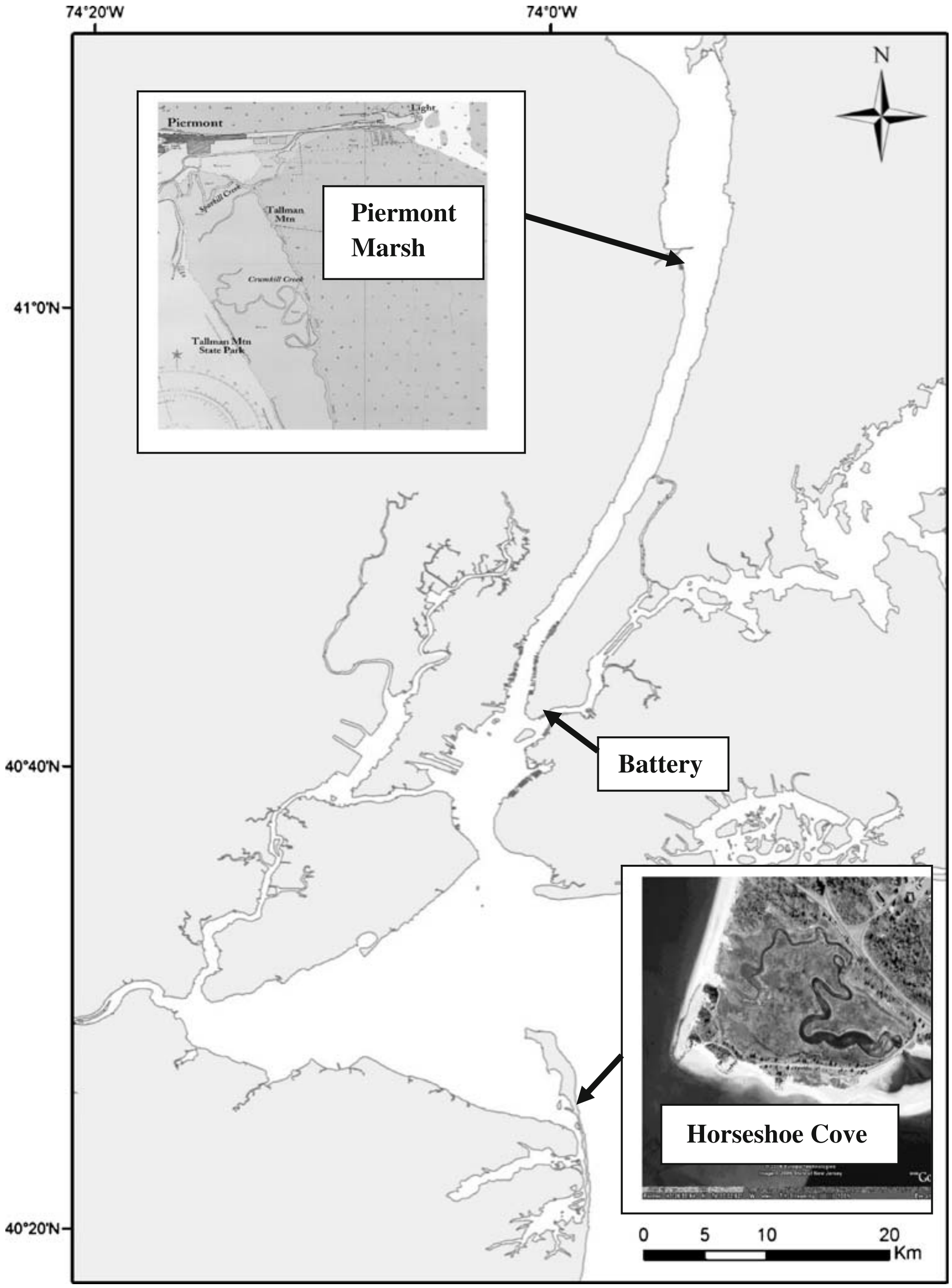

Fig. 1 Sampling locations for common mummichogs (*F. heteroclitus*) captured in the *S. alterniflora*-dominated Horseshoe Cove Marsh and *P. australis*-dominated Piermont Marsh on the Hudson River Estuary

Vegetation

To develop “baseline” stable isotope signatures for dominant macrophytes, leaves from individual *S. alterniflora*, *P. australis*, and hardwoods that lined the landward shore of Piermont Marsh (Fig. 1) were collected from widely dispersed plants located throughout the study area. Each sample for stable isotope analysis consisted of five leaves removed from five individually selected plants and subsequently pooled. These samples were supplemented with three pooled samples of five leaves each taken from the C_3 species Northern red oak (*Quercus rubra*), Norway maple (*Acer platanoides*), and American beech (*Fagus grandifolia*). All pooled samples were placed on dry ice prior to return to the laboratory for storage at −80°C. No new data were collected for benthic microalgae or phytoplankton (estimated by suspended particulate matter) as part of this study.

Fish

Populations of *F. heteroclitus* were sampled in each marsh using a 16-m seine during a 4-month interval, July through October–November. In addition, samples of *F. heteroclitus* were provided by an independent team of investigators from permanent tide pools at Piermont marsh. These pools were created as a by-product of construction of a railroad trestle across the site by the Erie Railroad during the mid-nineteenth century (S. Vincent, person. commun.). All pools had extensive algal growth lining them. Although we were unable to acquire biochemical condition data from these fish (precautions were not taken to preserve them properly for lipid analysis), the data were used to assess nutrient flux from in situ primary producers to this isolated population.

Up to 30 randomly selected individuals from monthly collections were examined for stable isotope composition, sex, gonad condition, dry and wet weight, and water content, lean biomass (protein content), and lipid stores. Because we wished to focus on the accumulation of energy reserves prior to the overwintering period, late July was chosen as a starting date to minimize the confounding influence of energy partitioning during the reproductive cycle in mummichogs collected at this latitude (Hardy 1978). Fish were immediately frozen on dry ice in the field and transferred to −80°C upon return to the laboratory (Wainright et al. 2000).

Laboratory Processing and Analysis

All pooled vegetation samples were rinsed with distilled water, freeze-dried, and ground to a fine powder prior to isotope analysis following methods of Wainright et al. (2000). 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). Ground samples were stored in pre-combusted glass vials 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

Vegetation and 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 carbon, air for nitrogen, and Canyon Diablo triolites for sulfur (Litvin and Weinstein 2004). Macrophyte C, N, and S stable isotopic signatures from previously collected 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 in Fig. 2, whereas new values for *S. alterniflora*, *P. australis*, and the dominant hardwoods *Q. rubra*, *A. platanoides*, and *F. grandifolia* collected in this study are 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 4 days to avoid esterification of fatty acids by methanol in the extraction solvent (Parrish 1987). Fifty micrograms per microliter nonadecane ($C_{19}H_{40}$, 1.000 mg total) internal standard in chloroform was added to each extract, and back extraction in 0.1 M aqueous KCl solution at 5°C was used 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

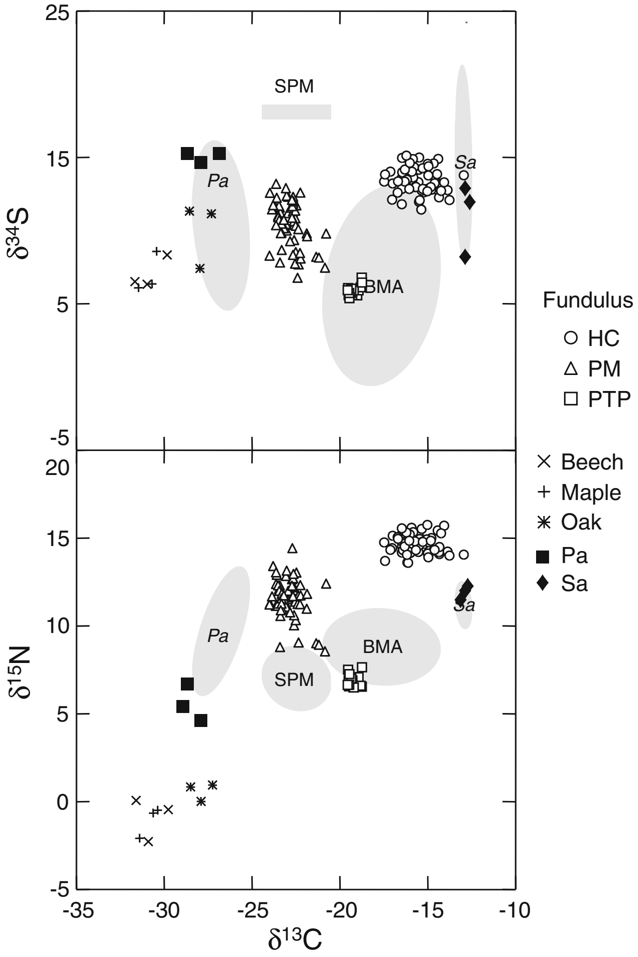

Fig. 2 Stable isotope signatures (CNS) for common mummichog *F. heteroclitus* and vegetation: *SPM* suspended particulate matter (surrogate for phytoplankton), *BMA* benthic microalgae, *Sa S. alterniflora*, *Pa P. australis*, *Beech* American beech *F. grandifolia*, *Maple* Norway maple *A. platanoides*, and *Oak* northern red oak *Q. rubra*. *Confidence ellipses* are shown for macrophytes and benthic microalgae collected in earlier studies by the authors. *Fundulus F. heteroclitus*, *HC* Horseshoe Cove Marsh, *PM* Piermont Marsh, *PTP* Piermont Marsh Tide Pools

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 (milligrams per gram 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 (Montevecchi and Piatt 1984; Schultz and Conover 1999; Slotte 1999; Hurst et al. 2000).

Data Analyses

Stable isotope signatures in individual *F. heteroclitus* were compared to dominant marsh grasses at each location and also evaluated in the context of microphyte and hardwood tissue signatures. Fish collected in the Piermont marsh tide pools were treated separately from those collected in marsh creeks.

Biochemical condition of individual *F. heteroclitus* 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, 1996; Lochmann and Ludwig 2003; Heintz et al. 2004). However, free fatty acids and phospholipids can contribute to energy metabolism (Ross and Love 1979; Yuneva et al. 1991; Henderson and Tocher 1987) 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 milligrams per gram dry weight, and LPM (expressed in grams) 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 mummichogs were compared among collection dates and collection locations. Extreme outliers, defined as values with absolute Studentized residuals ranging from 3.8 to 13.1 (n=13, ~5% of the total sample), were removed from the data set prior to analysis (Sutton et. al 2000). Dry weight versus standard length of all fish was analyzed by ANCOVA with location and sex as covariates. 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 or Mann–Whitney two-sample tests. All statistical tests were conducted with SYSTAT 12 (SPSS 2007).

Results

Isotopic Signatures

Overall, stable isotope values for *P. australis* and *S. alterniflora* samples collected in this study were similar to those established in our previous studies (Fig. 2). Sulfur values, however, were slightly ^{34}S-enriched in *P. australis* collected in Piermont Marsh. The opposite was true for ^{34}S values in *S. alterniflora* samples; they were slightly depleted in Horseshoe Cove compared to Delaware Bay and the Mullica River. In contrast, ^{15}N signatures in *P. australis* were slightly depleted in Piermont Marsh compared to the other sites and slightly enriched in Horseshoe Cove. While S values were overlapping among the C_3 species, *P. australis* and *Q. rubra* exhibited enriched δ^{13}C values relative to *A. platanoides* and *F. grandifolia*, and all three tree species were readily distinguished from *P. australis* by their N stable isotope values (Fig. 2).

Mean (±SE) isotopic values for *F. heteroclitus* differed significantly (Fig. 2; Kruskal–Wallis one-way ANOVA; $p<0.000$) among Piermont and Horseshoe Cove marshes, and the isolated tide pool at Piermont marsh; $\delta^{13}C=-22.82$ (0.09), −15.00 (0.55), −19.55 (0.05); $\delta^{34}S=10.44$ (0.20), 13.42 (0.11), 5.37 (0.05); and $\delta^{15}N=11.56$ (0.15), 14.63 (0.07), 6.47 (0.05); respectively.

Biochemical Condition

No differences were detected in the log–log relationships between length or dry weight versus standard length in *F. heteroclitus* populations residing at Horseshoe Cove Marsh and Piermont Marsh when sex and location were included as covariables (ANCOVA, interaction terms; p=0.300 [location]; and p=0.158 [sex]). Similarly, LPM did not differ significantly between locations (Fig. 3; Mann–Whitney U, p=0.916). Thus, from a morphometric standpoint, mummichogs in both marshes appeared to be of the same average length, and relative condition in terms of total body or protein mass at a given length.

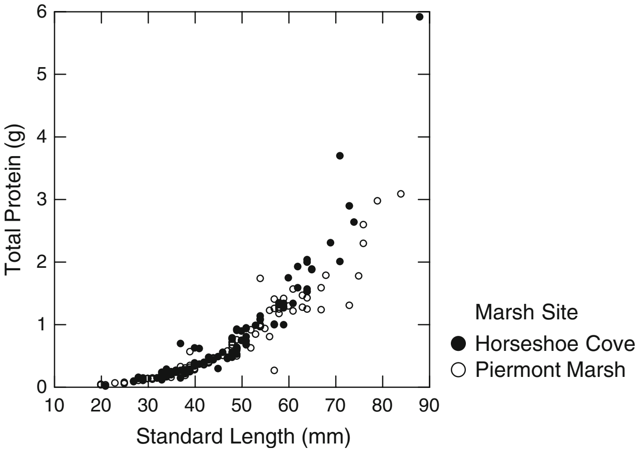

Fig. 3 Total protein (grams dry mass) versus standard length (millimeters) for common mummichogs (*F. heteroclitus*) captured at Horseshoe Cove and Piermont Marshes

Allometry of wet mass and its components, water mass, LPM, and lipid mass, exhibited the anticipated hyperallometric patterns commonly found in many teleosts and other taxa (Fig. 4; Post and Parkinson 2001) and were best described by the following equations for log-transformed wet weight (grams), water mass (grams), total protein mass as lean ash-free dry weight (grams), and total lipid mass (milligrams) against the log of standard length (millimeters):

$$\log(\text{wet mass}) = -4.994 + 3.215\log(\text{standard length});\quad r^2 = 0.964$$

$$\log(\text{water mass}) = -5.089 + 3.202\log(\text{standard length});\quad r^2 = 0.961$$

$$\log(\text{lean protein mass}) = -5.933 + 3.400\log(\text{standard length});\quad r^2 = 0.943$$

$$\log(\text{lipid mass}) = -4.667 + 3.452\log(\text{standard length});\quad r^2 = 0.732$$

Lipid mass as a percentage of total mass was best expressed in milligrams per gram (Fig. 5) and was within the range previously reported for whole-body homogenates of fundulids (De Vlaming et al. 1978; Weld and Meier 1984) or for muscle tissue of *F. heteroclitus* (Fangue et al. 2008). The values described here, however, may have been influenced by an unexplained laboratory artifact: Rather than nonadecane ($C_{19}H_{40}$) standard additions being ~1.0 mg as expected, the values in this study were inconsistent,

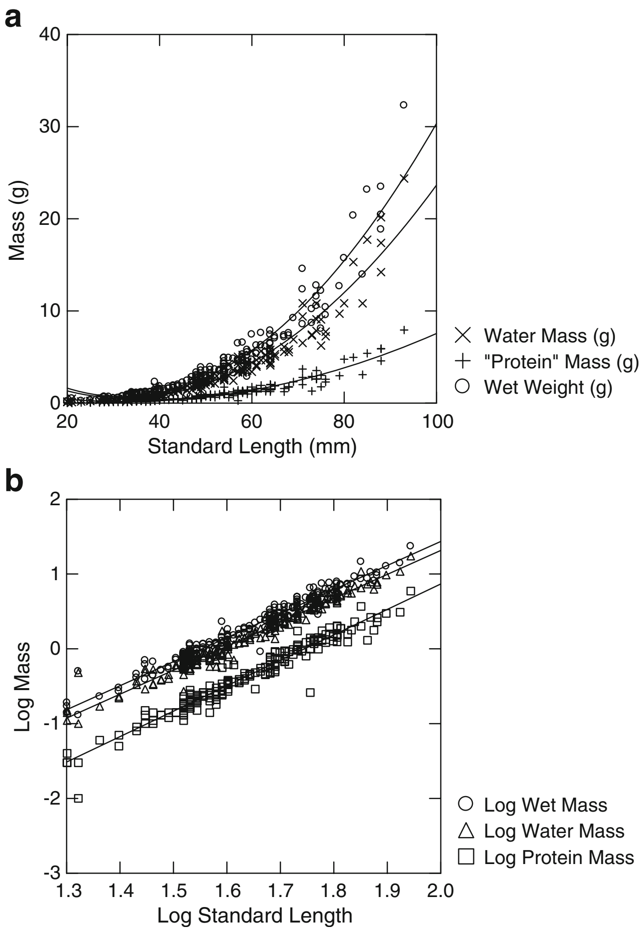

Fig. 4 **a** Water mass, protein mass, and wet weight in grams versus standard length (millimeters) for pooled collections of common mummichogs (*F. heteroclitus*) recorded in this study; **b** log–log plot of water mass, protein mass, and wet weight versus standard length (millimeters) for pooled collection of common mummichogs (*F. heteroclitus*) recorded in this study

averaging 3.14±0.81 (SD) mg. We used the actual measured standard value 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 should be interpreted with caution.

Before comparing biochemical condition of individual fish among habitats, we first examined the influence of gonad ripeness on lipid stores, defined for purposes of this study, as females or males with advanced gonad development consisting minimally of enlarged organs and visible eggs (Snyder 1983). Only two ripe individuals, both female, were collected in Piermont Marsh and, due to this small sample size, were not analyzed further. However, ten ripe mummichog were captured at Horseshoe Cove, and these individuals were found to be deficient in TAG and FFA stores ($p<0.01$ and $p=0.05$, respectively; Mann–Whitney *U*). An unexpected but interesting observation in this study was the presence of parasites encysted within the body cavity of mummichogs collected in Piermont Marsh. They were not present in any fish collected at Horseshoe Cove. As reported by Weisburg et al. (1986), mummichogs appeared to be intermediate hosts for these organisms that were likely larvae of the genus *Eustronglylides* (Nematoda). Although 12% of the sample population collected in Piermont marsh was parasitized, no significant difference in TAG concentration among parasitized and parasite-free individuals was detected (Fig. 5; Mann–Whitney *U*, $p=0.797$).

Because of the significant differences observed, the 12 ripe fish were removed from the data set leaving 209 individuals from the two sites for additional analyses. Mummichogs captured in Horseshoe Cove exhibited significantly greater concentrations of TAG ($p<0.01$) and FFA ($p<0.05$) in whole-body tissues than fish from Piermont Marsh (Fig. 6), but total lipid ($p=0.067$) and PL ($p=0.240$) concentrations did not differ significantly between the two populations.

Discussion

Carnivorous fishes are reliable indicators of the condition of complex ecosystems as they are the tertiary link in the food chain. Thus, the magnitude of protein and fat deposition and the level of fat reserves can not only be used to assess the "degree of well being" of fishes but can also serve to integrate the overall value of habitats to their production. In this study, we compared the quality of marshes dominated by the native macrophyte *S. alterniflora* versus the invasive variety of *P. australis* as habitat for *F. heteroclitus*. Stable isotope signatures were used to assess the contribution of primary producers to *F. heteroclitus* production. The condition and whole-body composition of juvenile and

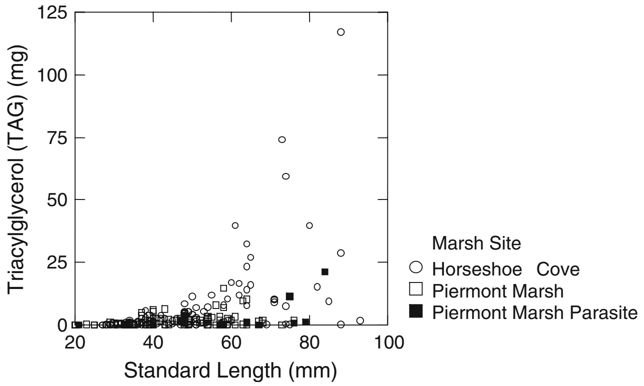

Fig. 5 TAG content (milligrams) in individual common mummichogs (*F. heteroclitus*) versus standard length (millimeters) from collections in Horseshoe Cove and Piermont marshes. Individual *F. heteroclitus* parasitized by *Eustrongylides* sp. are shown separately in collections from Piermont Marsh

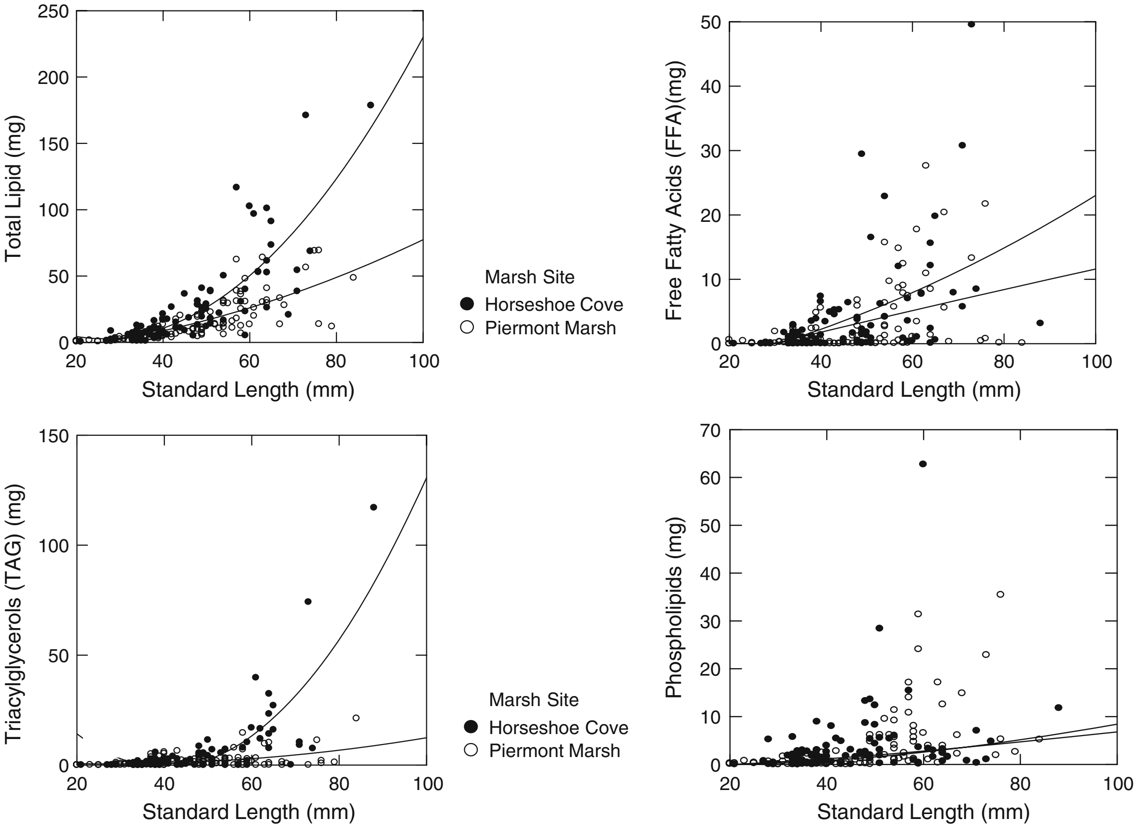

Fig. 6 Total lipids (milligrams), free fatty acids (*FFA*, milligrams), triacylglycerol (*TAG*, milligrams), and phospholipids (milligrams) shown separately versus standard length (millimeters) in individual mummichogs (*F. heteroclitus*) captured at Horseshoe Cove and Piermont Marshes

adult mummichog were investigated by traditional morphometric methods (tier II analysis, essential fish habitat) that were supplemented with tier III biochemical condition analysis (availability and allocation of energy reserves).

Our results confirm our previous observations that *P. australis* contributes nutrients (C, N, and S) to the trophic spectrum of resident *F. heteroclitus* and other marine transient species (Weinstein et al. 2000, 2005; Wainright et al. 2000; Litvin and Weinstein 2003; Currin et al. 2003). Also, of interest is the potential role of other dominant C_3 species on land adjacent to these coastal marshes. Within the scope of the present study, we have demonstrated that the isotopic signature of dominant trees—northern red oak, Norway maple, and American beech—are sufficiently distinct (Fig. 2) as to allow future analysis of the contribution from this source to marsh secondary production of resident and/or transient finfish.

Similarly, the significantly disproportionate contribution from benthic algae to mummichogs residing in the permanent tide pools on the Piermont marsh surface is noteworthy (Fig. 2). Unfortunately, we were unable to acquire biochemical condition data from these fish because they were not collected as part of this study, and precautions were not taken to preserve them properly for lipid analysis. Clearly, the role of these "specialized" habitats warrants further investigation, especially since they may serve as temperature refugia during the wintertime (Smith and Able 1994).

Both populations of *F. heteroclitus* examined in this investigation displayed hyperallometric length/wet mass relationships with increasing size (Fig. 3). This trend was significant for all measures of mass (Fig. 4). As noted by Post and Parkinson (2001), larger-bodied individuals and those with greater energy storage in utilizable forms (primarily lipids, Post and Parkinson 2001) are more likely to survive periods of resource scarcity. In this context, it is likely that the larger lipid reserves observed in *F. heteroclitus* collected in the *Spartina*-dominated Horseshoe Cove would better prepare these individuals for the rigors of wintertime scarcity than populations in the *Phragmites*-invaded Piermont Marsh. In addition, numerous authors have described the tradeoffs between energy allocation for growth and predator avoidance, reproduction, and the laying down of sufficient storage reserves for periods of resource scarcity as "competing demands" in pre-reproductive organisms living in seasonal environments (Walters and Juanes 1993; Fullerton et al. 2000; Post and Parkinson 2001). This is especially important in north-temperate fishes because experimental and field data suggest that energy availability is often limiting, i.e., fish in their natural environments tend to grow at less than their physiological optimum at a given temperature (Post and Parkinson 2001). Similarly, for sexually mature fish, including those observed here, energy utilized for the reproductive cycle may occur at the expense of somatic growth and energy storage. This has been clearly observed in mature *F. heteroclitus* individuals examined in this study (TAG and FFA stores were significantly lower in ripe fish (Mann–Whitney *U*); $p<0.01$ and $p=0.05$, respectively). When ripe fish were removed from the collections, the observed patterns of energy allocation followed the pattern observed in juvenile (pre-reproductive) finfish, i.e., early rapid growth with little accumulation of energy reserves and later in the growing season, rapid hyperallometric accumulation of lipid stores in the form of TAG, and free fatty acids (Fig. 6; Shulman and Love 1999; Hurst et al. 2000; Lochmann and Ludwig 2003).

Potential Confounding Influences of Salinity and Anthropological Stress

In addition to the ecological effects induced by the invasion by *P. australis*, especially the qualitative and quantitative differences associated with reduced access to the marsh surface, increased detrital biomass production, dramatic changes in vegetation density and "architecture", flow velocity reduction, and the likelihood of altered exchange of organic materials with the surrounding drainage (Weinstein and Balletto 1999; Angradi et al. 2001; Able et al. 2003), other geomorphological and functional changes associated with the presence of *P. australis*, particularly in "mature" stands where the plant has been present for long periods, have been documented (Hunter et al. 2006; Osgood et al. 2006). These included an elevated marsh surface that dramatically reduces micro-topographic relief and consequently affects flow rates (hydrodynamics; Hanson et al. 2002), hydrology, and hydroperiod (Weinstein and Balletto 1999; Windham and Lathrop 1999; Hanson et al. 2002; Able et al. 2003; Montalto et al. 2005; Hagan et al. 2007). One result of these differences is the qualitative and quantitative changes observed in macrofaunal composition in adjacent *Spartina*- and *Phragmites*-dominated systems (Angradi et al. 2001; Posey et al. 2003; Raichel et al. 2003). We believe that the influence of *P. australis* on geomorphological and hydrological characteristics of the marsh, translated into altered habitat quality—less frequent flooding, fewer refugia for young fish, reduced access to the intertidal marsh plain by adults, and reduced flow rates affecting exchange of materials—were the primary influences affecting the ability of *F. heteroclitus* to attain and partition surplus energy into long-term storage products for reproduction, migration, and overwintering.

This discussion, however, would not be complete without consideration of the potentially confounding influences of salinity and anthropologically induced stress on the biochemical condition of *F. heteroclitus*. We do not believe that either factor was the dominating influence in creating the biochemical condition differences observed and expect that additional studies will support this conclusion.

Because the salinity regime of salt marsh habitats routinely undergoes dramatic changes, resident finfishes must adapt to dynamically regulating ion balance in their natural environments (Scott et al. 2008). Among estuarine residents, *F. heteroclitus* is renowned for both its salinity and temperature tolerances (Griffith 1974; Burnett et al. 2007), readily adapting to widely ranging conditions from ion-poor to hypersaline (nearly four times that of seawater) and temperatures between 7°C and 23°C without impairment of swimming performance (Fangue et al. 2008). In addition to its broad eurythermal and euryhaline adaptability, *F. heteroclitus* tolerates low oxygen conditions better than most resident marsh fishes with little or no mortality occurring a oxygen tensions above 1 mg l^{-1} (Wannamaker and Rice 2000; Smith and Able 2003; Burnett et al. 2007). Thus, *F. heteroclitus* seems to manage the vagaries of its thermo-haline regime without apparent ill effects nor substantial influence on its productivity (Griffith 1974).

Similarly, there is nothing that leads us to believe that the spectrum of anthropogenic stresses on the *F. heteroclitus* populations residing in Piermont Marsh contributes differentially to the biochemical condition of these individuals (Wolfe et al. 1996). Virtually, the entire Hudson River Estuary is described as being in "fair condition" at best, exhibiting relatively poor benthic indices (Weisburg et al. 1997) and sediment contaminants often exceeding the effects range medium (Long et al. 1995) and national sediment quality criteria (USEPA 1994) values for many metals, pesticides, and PAHs/PCBs (USEPA 2001). The most impacted areas of the Hudson River Estuary, in terms of contaminants, include Sandy Hook Bay, the location of Horseshoe Cove (Wolfe et al. 1996). If anything, the USEPA (2001) notes that the Raritan Estuary adjacent to Sandy Hook Bay is one of the most contaminated areas in the region. On the other hand, there is no indication that Piermont Marsh is an acutely contaminated location within the Hudson River Estuary (Wolfe et al. 1996).

An examination of *F. heteroclitus* density and growth rates in other estuarine systems is telling in this regard. Hagan et al. (2007) were able to colocate *Spartina* and "late stage" (i.e., without standing water on the marsh plain) *Phragmites*-dominated sites in the brackish marshes of Delaware Bay. Sites examined in their study *did not differ significantly* in mean salinity or salinity variance (Hagan et al. 2007). Among their findings were significantly lower growth rates in “large” (mean standard length, 36.5 mm) *F. heteroclitus* captured in the *P. australis*-dominated marsh versus sites where *S. alterniflora* predominated. While population density for large fish did not differ significantly in the two marsh types marshes, densities (number per square meter) of the “small” (mean standard length, 24.1 mm) life stages were significantly lower at the *Phragmites* sites (see also Hunter et al. 2006). Similarly, standing crops (grams dry weight per square meter) measured over the growing season for large *F. heteroclitus* were significantly higher in the *Spartina*-dominated marsh. The similar standing crops of adult mummichog in the two marsh types as determined by seine-haul catch per unit effort, combined with lower observed absolute growth rate of *F. heteroclitus* in the *Phragmites*-dominated marsh, however, suggests that the *size* of the average adult was smaller at the *Phragmites*-dominated site. In contrast, our results clearly indicate that size distributions, length, and dry weight at length (accounting for sex and location) did not differ significantly in the two populations. Unfortunately, the approach used by Hagan et al. (2007) to estimate production could not actually employ the Jolly–Seber method because it failed to allow for *unique* identification of individuals during the re-capture–release phase (Seber 1973). As a result of their efforts, Hagan et al. 2007 concluded “density, growth, biomass, and production of mummichog are affected by the invasion of *Phragmites* onto natural *Spartina* intertidal marsh”. With the minor exception of their production estimates, we concur.

The tier II studies conducted by Hagan et al. (2007) and in this study (examining dry weight at length with location and sex as covariables) have demonstrably contributed to understanding the impacts of *Phragmites* on potential recruitment success of marsh dependent fishes. Yet, the tier II approach fails to fully address the question: How do these habitats contribute to the ultimate fitness of fishes produced by each marsh type, i.e., were individuals produced in a *Phragmites*-dominated marsh as well off as those from marshes free of this invasive plant?

Although our comparisons on a dry weight basis (morphometric basis) alone did not detect differences in condition of *F. heteroclitus* populations sampled in the two marshes, the examination of energy reserves in these fish after removing the potential confounding influences of the reproductive cycle and parasitization clearly indicated that significant differences occurred in TAG and free fatty acids levels (milligrams per gram dry weight; Fig. 6). Thus, supplementing tier II data with a tier III biochemical condition approach was a more sensitive measure of the condition of individuals produced in these habitats. This conclusion is supported by Mommsen (1998) who suggested that a 100-g fish acquiring 1 g of lipid was unlikely to change in length, and its weight gain was hardly detectable in the statistical noise, yet the fish has added a statistically significant amount of energy.

By focusing on energy reserves, principally TAG, we have been able to demonstrate that mummichogs residing in a polyhaline *S. alterniflora*-dominated tidal salt marsh were better able to acquire energy reserves for reproduction and overwintering survival than fish residing in a *Phragmites*-dominated marsh. Thus, *Phragmites* invasion and its consequent habitat impacts (Weinstein and Balletto 1999; Hagan et al. 2007) appear to have contributed in lower quality EFH for mummichogs.

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