Monitoring Food Web Changes in Tide-Restored Salt Marshes: A Carbon Stable Isotope Approach

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ABSTRACT: Primary producer (angiosperms, macroalgae, submerged aquatic vegetation), suspended particulate matter, and *Fundulus heteroclitus* isotope values ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) were examined to assess their use as indicators for changes in food web support functions in tidally-restored salt marshes. Study sites, located throughout the southern New England region (USA), ranged from *Spartina alterniflora*-dominated reference marshes, marshes under various regimes and histories of tide restoration, and a severely tide-restricted *Phragmites australis* marsh. *Fundulus* $\delta^{13}C$ values were greater for fish from reference *Spartina* marshes than for fish from adjacent tide-restricted or tide-restored marshes where higher percent cover of C_3 plants, lower water column salinities, and more negative dissolved inorganic $\delta^{13}C$ values were observed. The difference in *Fundulus* $\delta^{13}C$ values between a tide-restricted *Phragmites* marsh and an adjacent reference *Spartina* marsh was great compared to the difference between marshes at various stages of tide restoration and their respective reference marshes, suggesting that food web support functions are restored as the degree of tidal restriction is lessened. While a multiple isotopic approach can provide valuable information for determining specific food sources to consumers, this study demonstrates that monitoring *Fundulus* $\delta^{13}C$ values alone may be useful to evaluate the trajectory of ecological change for marshes undergoing tidal restoration.

Introduction

Salt marshes with altered hydrologic regimes or restricted tidal flow are prevalent throughout the northeastern United States (Roman et al. 1984; Neckles et al. 2002). Numerous efforts to restore ecosystem functions by reintroducing tidal flow or otherwise restoring hydrologic patterns are underway (e.g., Roman et al. 1995; Burdick et al. 1997; Warren et al. 2002). Restoration monitoring often seeks to determine the trajectory of tide-restored marshes toward the ecological condition of reference marshes. Variables, such as vegetation change, nekton community structure, waterbird utilization, and sediment and water chemistry, have been monitored at many restoration and reference sites in the northeast and elsewhere (Burdick et al. 1997; Portnoy 1999; Zedler and Callaway 1999; Talley 2000; Morgan and Short 2002). While these monitoring efforts provide valuable information on the progress of a restoration and are providing knowledge to help guide future restoration efforts, none of these methods directly examines organic matter flow through food webs as salt marshes are in the process of restoration.

Stable isotope analysis has been employed in a variety of studies to trace the flow of organic matter, or food web support to consumers, in salt marshes (Haines 1976; Peterson et al. 1985; Currin et al. 1995). The stable isotope technique has been used to compare energy flow in *Spartina* and *Phragmites*-dominated marshes (Wainright et al 2000; Currin et al. 2003) and suggested as a possible approach for assessing ecological recovery in tide-restored systems (Weinstein et al. 2000; Currin et al. 2003; Moseman et al. 2004). Consumers from *Phragmites*-dominated marshes often show depleted $\delta^{13}C$ signatures reflecting the carbon isotopic signature of the dominant primary producer (Wainright et al. 2000; Currin et al. 2003), while consumers in *Spartina*-dominated systems tend to be relatively enriched in ^{13}C (Peterson and Howarth

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1987; Currin et al. 1995). With tidal restoration there is documented evidence that tide-restricted marshes dominated by *Phragmites,* and often terrestrial species, slowly return to *Spartina*-dominated vegetation (e.g., Dionne et al. 1999; Roman et al. 2002; Warren et al. 2002). Nekton abundance, species composition, and species growth rate have been shown to respond favorably to tidal restoration (Able et al. 2000; Roman et al. 2002; Raposa and Roman 2003; Teo and Able 2003). There is little documentation of trophic transfers from producer to consumer during the marsh restoration process.

The present study examined carbon, nitrogen, and sulfur stable isotope ratios of *Fundulus heteroclitus* (common mummichog) and marsh primary producers to evaluate organic carbon flow to *Fundulus* on six southern New England salt marshes representing tide-restricted, tide-restored, and reference conditions. Primary producer, suspended particulate matter (SPM), and *Fundulus* isotopic signatures were examined as indicators of energy flow patterns with the hypothesis that as isotopic signatures of food sources change from tide-restricted marshes toward tide-restored and reference marsh conditions, isotopic signatures of *Fundulus* would similarly change.

For several reasons *F. heteroclitus* is a good choice as a target or indicator organism for monitoring energy flow processes in tide-restored salt marsh systems. It is a numerically dominant nekton species in East Coast salt marshes (e.g., Nixon and Oviatt 1973; Meredith and Lotrich 1979; Kneib 1997; Raposa and Roman 2001). Gut content studies have revealed that *Fundulus* is an opportunistic benthic omnivore, making it an integrator of trophic levels. Detritus and algae have appeared in the guts of *Fundulus* along with a variety of animal prey items (Vince et al. 1976; Kneib and Stiven 1978; Allen et al. 1994; Fell et al. 1998; James-Pirri et al. 2001). Previous studies employing *Fundulus* as a study consumer in stable isotope trophic studies have provided evidence that *Fundulus* in *Phragmites*-dominated marshes show depleted $\delta^{13}C$ signatures (Wainright et al. 2000; Currin et al. 2003), while those found in *Spartina*-dominated marshes are comparatively enriched in ^{13}C (Peterson and Howarth 1987; Currin et al. 1995). A variety of estuarine predators including *Paralichthys dentatus* (Rountree and Able 1992), *Morone saxatilis* (Tupper and Able 2000), *Anguilla rostrata,* and *Callinectes sapidus* (Meredith and Lotrich 1979), and presumably birds (Burger et al. 1982; Brush et al. 1986), have been reported to prey on *Fundulus.* *Fundulus* occupies a position in salt marsh systems as an integrator of dominant organic matter sources and a link to estuarine predator species.

TABLE 1.   Tidal range and percent cover of C_3 plants at study marshes. Data Sources: Roman et al. 1995, 2002; Portnoy et al. 2003; National Park Service unpublished vegetation data.

Marsh	Tidal Range	% C_3 Cover
Herring River		
Tide restricted	0.5 m	82
Reference	2.3 m	na
Sachuest Point		
Tide restored	Pre-restoration: 1–2 cm, Post-restoration: 30 cm	62
Reference	30 cm	37
Hatches Harbor		
Tide restored	Pre-restoration: 26 cm, Post-restoration: 55 cm	55
Reference	65 cm	20

Methods

STUDY SITES AND STUDY DESIGN

Three salt marsh systems in southern New England were selected for this study (Table 1). Each system was bisected by a road or dike during the early part of the 20th century, with a culvert or similar structure allowing reduced or restricted tidal flow to portions of the marsh system upstream of the road or dike. Tidal flows to the marshes located immediately downstream of the road or dike and culvert were unrestricted. Vegetation of the tide-unrestricted marshes for all three systems was dominated by *Spartina alterniflora,* typical of New England marshes (Niering and Warren 1980). Upstream of the tidal restriction, marsh vegetation was dramatically different, dominated by *Phragmites australis* and often terrestrial species.

The Herring River (Wellfleet, Massachusetts; 41°55′52″N, 70°03′52″W) salt marsh is severely tide-restricted upstream of a dike constructed in 1908. Historically, *S. alterniflora* and other salt marsh species dominated the upstream marsh, but with installation of the dike the vegetation converted to *Phragmites,* brackish and freshwater marsh species, terrestrial grasses, and woody species (Portnoy et al. 1987; Roman et al. 1995). *S. alterniflora* dominated the tide-unrestricted downstream marsh. Mean tidal range of the tide-restricted marsh was 0.5 m, compared to 2.3 m for the adjacent tide-unrestricted reference marsh.

A road and small culvert bisected the Sachuest Point Marsh (Middletown, Rhode Island; 41°29′16″N, 70°14′58″W), restricting tidal flow to a 3-ha portion of salt marsh, until 1998 when the culvert was replaced restoring tidal flow. Prior to tidal restoration, tidal range at the tide-restricted marsh was just 1–2 cm, but with tide restoration the mean range was equal to the downstream reference

marsh (30 cm; Roman et al. 2002). Prior to tide restoration, vegetation was dominated by *Phragmites.* Following installation of the new larger culverts *Phragmites* remained a dominant species, but an increased abundance of *S. alterniflora* and *Spartina patens* and a decrease in *Phragmites* cover was documented (Roman et al. 2002). The 6-ha Sachuest Point reference marsh was dominated by species typical of the New England high marsh (short *S. alterniflora, S. patens, Juncus gerardii, Distichlis spicata, Iva frutescens*), but patches of *Phragmites* and *Typha angustifolia* also occurred.

In 1930 a dike bisected the Hatches Harbor salt marsh (Provincetown, Massachusetts; 42°03′55″N, 70°14′09″W) into a 90-ha unrestricted marsh and 80-ha tide-restricted marsh. Mean tidal range of the tide-restricted marsh was 28 cm, compared to 65 cm for the unrestricted marsh. In 1998, the culvert through the dike was enlarged, resulting in a mean tidal range of 55 cm, nearly equivalent to the adjacent tide-unrestricted marsh. Under tide-restricted conditions, *Phragmites* was highly abundant, but salt marsh species (*S. alterniflora, S. patens, J. gerardii*) occupied portions of the marsh. Under a regime of restored tidal flow, *Phragmites* is declining, along with terrestrial species that were dominant throughout the restricted marsh (Portnoy et al. 2003). *S. alterniflora* dominated the tide-unrestricted reference marsh.

Collectively, these marshes represent hydrologic conditions ranging from tide-restricted marsh (Herring River), to tide-restored marshes with varying histories of tide-restriction and varying stages of vegetation change (Sachuest Point and Hatches Harbor), to tide-unrestricted reference salt marshes. Vegetation plot data (1 m²) from previous studies (Herring River: unpublished National Park Service data; Sachuest Point: Roman et al. 2002; Hatches Harbor: Portnoy et al. 2003) revealed that the abundance of C_3 plants was variable at the sites and percent cover of C_3 plants ranged from 20% at the Hatches Harbor reference marsh to 82% at the Herring River tide-restricted marsh (Table 1). Plants using the C_3 pathway of photosynthesis include *Phragmites* and terrestrial plants, while C_4 plants include *Spartina* and other salt marsh dominants. Vegetation plot data were not available for the Herring River reference marsh, but similar to the Hatches Harbor reference marsh, very little C_3 plant cover exists on this marsh.

The Herring River, Sachuest Point, and Hatches Harbor sites were each divided into reference and tide-restored or tide-restricted marshes. The reference marshes were those portions of the marsh system downstream of the tide-restricting structure. The marsh upstream of the structure was tide-restored at Hatches Harbor and Sachuest Point,

while the Herring River upstream marsh was tide-restricted. A total of six marsh areas were sampled.

Samples were collected in July and August 2002 at low tide from five randomly selected stations along the main tidal creek within each reference, tide-restored, or tide-restricted marsh area. At each station, angiosperm, macroalgae, seagrass, water, and *Fundulus* samples were collected from the tidal creek or adjacent marsh surface as described below. The result was five samples of each available primary producer and *Fundulus* from each of six marsh areas. The isotopic values of these five samples were determined and then averaged to provide one value for that particular marsh area.

Standing dead and live leaves of *S. alterniflora, Phragmites,* and other dominant angiosperms were selected from a minimum of five different plants at each sampling station and the five leaves were then pooled as one sample for analysis. For consistency, only the top 15 cm of leaf tissue was collected from a plant. Table 2 provides a complete listing of the producers sampled at each individual marsh. Dominant macroalgal species and the seagrass, *Ruppia maritima,* were collected in a similar manner from the tidal creek and marsh surface at marshes when present. All of the above samples were put in sealed plastic bags and placed on ice in the dark until prepared for analysis.

SPM samples were collected at each randomly located tidal creek station to establish isotopic signatures for the aggregate of phytoplankton, zooplankton, detritus, and organic and inorganic suspended sediment. Water samples from within 5 cm of the surface were collected from the tidal creek in dark 1-l plastic bottles. Phytoplankton $\delta^{13}C$ values are hypothesized to vary with the dissolved inorganic $\delta^{13}C$ ($DI^{13}C$) in the water column (Chanton and Lewis 1999; Coffin and Cifuentes 1999; Fry 2002), so water column $DI^{13}C$ measurements were performed to determine the degree to which SPM $\delta^{13}C$ values reflected a phytoplankton signature. Water samples (20 ml) were transferred to scintillation vials in the field and preserved with sodium azide for $DI^{13}C$ isotopic analysis. The remaining water was stored frozen in dark plastic bottles until they were vacuum-pumped through precombusted (450°C) Whatman GF/F filters in the laboratory. SPM was scraped from the filters, and this material was saved for analysis. Salinities were recorded at each station using a handheld refractometer.

F. heteroclitus were captured at the tidal creek stations using a seine net (6 m long, 3.2 mm mesh) and sorted into adult and juvenile categories based on size because previous studies have shown that *Fundulus* diet varies with fish length. Isotope studies have shown differences in *Fundulus* $\delta^{13}C$ (Currin et al. 2003) and $\delta^{15}N$ (Griffin and Valiela 2001; Currin

TABLE 2. Primary producers and consumers sampled at each study marsh. Live and standing dead samples were collected for all angiosperm species.

Marsh	Primary Producers
Herring River	
Tide restricted	Angiosperms: *Phragmites australis*
	Submerged aquatic vegetation: *Ruppia maritima*
	Suspended particulate matter (SPM)
Reference	Angiosperms: *Spartina alterniflora*
	Submerged aquatic vegetation: *Ruppia maritima*
	Macroalgae: *Fucus vesiculosus, Ulva lactuca, Gracilaria tikviahae*
	SPM
Sachuest Point	
Tide restored	Angiosperms: *Phragmites australis, Solidago sempervirens, Iva frutescens*
	SPM
Reference	Angiosperms: *Spartina alterniflora, Spartina patens, Distichlis spicata, Juncus gerardii, Iva frutescens*
	SPM
Hatches Harbor	
Tide restored	Angiosperms: *Spartina alterniflora, Juncus gerardii, Phragmites australis*
	Macroalgae: *Chaetomorpha picquotiana*
	SPM
Reference	Angiosperms: *Spartina alterniflora*
	Macroalgae: *Fucus vesiculosus, Ascophyllum nodosum*
	SPM

et al. 2003) with fish length implying different diets, and gut content studies have described smaller *Fundulus* eating less algal and detrital material (Kneib and Stiven 1978) and smaller infauna (Penczak 1985; Kneib 1986) than larger *Fundulus*. Fish less than 40 mm total length were considered juveniles, and fish greater than 50 mm were classified as adults. A minimum of 5 individuals of each size class was caught at each station, and these individuals were combined during sample processing to represent one pooled sample for that particular station.

In late September and early October 2003 1-cm deep (15 mm diameter) cylindrical sediment cores were collected at each study marsh for benthic chlorophyll analysis according to Wainright et al. (2000). Sediment cores taken at five randomly selected stations at each marsh were transferred to centrifuge tubes wrapped in aluminum foil, and placed on ice for benthic chlorophyll *a* analysis. The benthic microalgal community was also sampled following a modification of the Couch (1989) method as described in Wainright et al. (2000). Where bare sediment in the form of mudflat or sandflat habitat was available at low tide, the sediment was covered with a thin layer of precombusted silica sand. An approximately 600-cm² piece of 62-μm Nitex mesh was placed over the sand and covered with another thin layer of sand. The mesh was wetted thoroughly with ambient seawater, and a piece of window screening mounted on a Styrofoam circle was placed over the mesh to shade the surface and induce microalgal vertical migration. This setup was left for 1–2 h before the incoming tide inundated the intertidal habitat. The mesh was then carefully peeled off the ground, and placed on ice in a dark plastic container and brought to the laboratory. At marshes with low mean tidal range and no mudflats or sandflats, plastic trays were filled with thin sections of sediment from within the marsh vegetation. These trays were taken to the lab, and the same method of inducing microalgal vertical migration was applied using either a fluorescent light setup or sunlight entering a greenhouse as a light source. The time allowed for migration varied from 6 to 8 daylight hours in the greenhouse and 4 to 12 h under the fluorescent light.

LABORATORY PROCEDURES

All angiosperm, macroalgal, and *Fundulus* samples were rinsed with tap water to remove any sediment or other extraneous material that could confound isotopic analyses. Prior to processing, fish were measured from the tip of the tail to the mouth. Mean lengths of adult and juvenile *Fundulus* were 60 and 31 mm, respectively. The head and gut were discarded and the remainder was used for analysis to ensure that the isotopic signatures reflected assimilated tissue as opposed to recently ingested food items. All samples intended for isotope analyses were dried in an oven at 65°C for at least 24 h. All samples were then homogenized to a powder using either a Wiley Mill or a Crescent Wig-L-Bug amalgamating machine (Crescent Dental Corp., Lyons, Illinois). Powdered samples were weighed on a microbalance and placed in tin capsules for isotopic analysis.

Sediment core chlorophyll *a* analysis was performed with an adaptation to the procedures outlined in Oviatt and Hindle (1994) using a Turner Designs Model 10 fluorometer. Chlorophyll *a* was extracted from the top 1 cm of the sediment core. For isolation of the benthic microalgal community the Nitex mesh was placed in a plastic receiving container and sprayed with deionized water from top to bottom to transfer the sample from the mesh to the container. The water in the container was swirled and filtered onto Whatman GF/F filters. These filters were then folded, placed in aluminum foil, and refrigerated. Upon microscopic analysis it was determined that the filters did contain benthic diatoms. The microalgal community was not plentiful, and the majority of the filter material was determined to be suspended sediment.

ISOTOPIC ANALYSIS

Carbon and nitrogen isotopic analyses were performed at the U.S. Environmental Protection Agency Atlantic Ecology Division laboratory using a Carlo-Erba NA 1500 Series II Elemental Analyzer interfaced to a Micromass Optima Mass Spectrometer. Dried samples were combusted (1020°C, chromic oxide catalyst) sending CO_2 (or N_2) to the mass spectrometer for determination of isotopic ratios. Sulfur isotopic analyses were performed by Iso-Analytical Ltd. (Cheshire, U.K.) using an EA-C-CF-IRMS (elemental analyzer combustion continuous flow isotope ratio mass spectrometry). $DI^{13}C$ analyses were conducted at the U.S. Coast Guard Academy on a Gilson gas autosampler connected to a Europa ANCA-GSL preparation unit and 20-20 mass spectrometer stable isotope ratio-analysis system as described in Wainright et al. (2000). Isotopic ratios of sample material are reported as ‰ differences from accepted standards ($\delta^{13}C$: Peedee Belemnite standard, Craig 1957; $\delta^{15}N$: atmospheric N_2 gas; $\delta^{34}S$: the Canyon Diablo troilite) as:

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

where X is ^{13}C, ^{15}N, or ^{34}S and R is the ratio $^{13}C/^{12}C$, $^{15}N/^{14}N$, or $^{34}S/^{32}S$. Sample precision for duplicate analyses was always less than 0.35‰.

Results and Discussion

TIDE RESTORATION EFFECTS ON $\delta^{13}C$ VALUES OF *FUNDULUS* AND ORGANIC MATTER SOURCES

Restoration of tidal flow to tide-restricted salt marshes in the northeastern U.S. often results in increased tidal creek and marsh porewater salinity and a conversion from C_3 angiosperms (e.g., *Phragmites*) that often dominate tide-restricted marshes to C_4 *Spartina*-dominated vegetation (Sinicrope et al. 1990; Burdick et al. 1997; Dionne et al.

1999; Roman et al. 2002; Warren et al. 2002). The conversion from C_3 to C_4 vegetation results in organic matter sources enriched in ^{13}C. The two photosynthetic pathways fractionate carbon differently during uptake of atmospheric CO_2 (Peterson and Fry 1987). C_3-photosynthesizing plants, like *Phragmites*, preferentially exclude $^{13}CO_2$ to a greater extent and have more negative $\delta^{13}C$ values (−23‰ to −31‰; Table 3; Peterson and Howarth 1987; Sullivan and Moncreiff 1990; Stribling and Cornwell 1997; Wainright et al. 2000), while *S. alterniflora* and other C_4 plants have values near −13‰, enriched in ^{13}C relative to C_3 plants (Table 3; e.g., Haines and Montague 1979; Fry and Sherr 1984; Peterson and Fry 1987; Wainright et al. 2000).

Regarding the change in salinity with tide restoration, previous studies have found both SPM and water column $DI^{13}C$ values to increase with increasing salinity (Chanton and Lewis 1999; Coffin and Cifuentes 1999; Fry 2002), as do our data (Fig. 1). Regressions of SPM $\delta^{13}C$ versus salinity and $DI^{13}C$ versus salinity were both significant (p < 0.001). SPM samples contain phytoplankton and detritus, both of which contribute to the $\delta^{13}C$ signal of SPM. A regression of SPM $\delta^{13}C$ versus $DI^{13}C$ was highly significant with a slope very close to 1 (p < 0.001; Fig. 2). Phytoplankton fix water column DIC and fractionate this carbon upon uptake resulting in isotopic compositions depleted by approximately 20‰ relative to DIC (Chanton and Lewis 1999; Wainright et al. 2000). Figure 2 indicates that the SPM $\delta^{13}C$ values are strongly influenced by water column $DI^{13}C$ with a difference in $\delta^{13}C$ values of about −16‰. This difference is less than the phytoplankton-associated fractionation cited in other studies (Tan and Strain 1983; Chanton and Lewis 1999) and is possibly due to an actual difference in phytoplankton carbon fractionation or additional carbon sources besides phytoplankton in the SPM.

Among other factors, increased water column salinity and a shift from C_3 to C_4 plant communities contribute to enriched organic matter sources and ultimate enrichment in *Fundulus* $\delta^{13}C$ tissue values. For Hatches Harbor, Herring River, and Sachuest Point, adult and juvenile *Fundulus* from the tide-restricted or tide-restored marshes always had more negative $\delta^{13}C$ values when compared to their adjacent unrestricted reference marsh (Fig. 3). In general, the tide-restricted or tide-restored marshes had lower $\delta^{13}C$ values compared to reference marshes (Fig. 3). *Fundulus* from the Sachuest Point reference marsh deviate significantly from the other reference marshes presumably due to organic matter sources depleted in ^{13}C as evidenced by a higher cover of C_3 producers (Table 1) and a more negative SPM $\delta^{13}C$ value (Table 3). This lower SPM

TABLE 3. $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ (‰) values for angiosperms, macroalgae, submerged aquatic vegetation, suspended particulate matter, and *Fundulus heteroclitus* collected at the three study marshes. Mean values (SE, n) are presented. - indicates sample type not found.

	Reference			Tide Restricted		
Marsh and sample type	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Herring River						
C$_4$ Plants						
Spartina alterniflora (live)	−13.3 (0.2, 5)	6.3 (0.7, 5)	1.1 (6.8, 5)	–	–	–
Spartina alterniflora (standing dead)	−12.9 (0.2, 5)	6.2 (0.5, 5)	11.8 (2.5, 4)	–	–	–
C$_3$ Plants						
Phragmites australis (live)	–	–	–	−26.7 (0.3, 5)	6.5 (0.5, 5)	3.3 (1.5, 5)
Phragmites australis (standing dead)	–	–	–	−26.3 (0.4, 5)	4.4 (0.9, 5)	3.2 (2.3, 5)
Macroalgae						
Fucus vesiculosus	−14.7 (0.4, 5)	5.7 (0.3, 5)	18.9 (0.1, 5)	–	–	–
Gracilaria tikviahae	−16.9 (0.1, 4)	6.4 (0.2, 5	18.2 (0.1, 5)	–	–	–
Ulva lactuca	−9.0 (0.3 4)	7.4 (0.1, 3)	16.4 (0.5, 4)	–	–	–
Ruppia maritima	−9.4 (0.3, 5)	2.5 (0.4, 5)	6.1 (1.8, 5)	−22.5 (0.2, 5)	5.8 (0.2, 5)	14.0 (1.9, 5)
Suspended particulates	−19.7 (0.4, 5)	4.4 (0.0, 1)	3.2 (0.0, 1)	−32.6 (0.7, 5)	5.8 (0.0, 1)	−1.8 (0.0, 1)
Adult *Fundulus heteroclitus*	−14.6 (0.1, 4)	10.0 (.2, 5)	8.2 (0.3, 5)	−21.3 (0.2, 5)	11.1 (0, 5)	9.2 (0.3, 5)
Juvenile *Fundulus heteroclitus*	−13.9 (0.4, 5)	9.3 (0.0, 5)	6.7 (0.3, 5)	−21.3 (0.4, 5)	10.3 (.1, 5)	8.7 (0.0, 5)
Sachuest Point						
C$_4$ Plants						
Distichlis spicata (live)	−14.1 (0.2, 3)	5.7 (1.0, 3)	11.5 (1.7, 3)	–	–	–
Distichlis spicata (standing dead)	−14.0 (0.4, 5)	2.4 (0.7, 5)	13.2 (1.3, 5)	–	–	–
Spartina patens (live)	−13.3 (0.2, 5)	4.0 (0.7, 5)	18.1 (0.3, 5)	–	–	–
Spartina patens (standing dead)	−13.3 (0.1, 5)	2.9 (0.8, 4)	15.9 (0.5, 5)	–	–	–
Spartina alterniflora (live)	−13.0 (0.1, 5)	7.7 (0.5, 5)	5.6 (2.0, 5)	–	–	–
Spartina alterniflora (standing dead)	−12.4 (0.2, 5)	7.3 (1.0, 5)	9.0 (0.2, 5)	–	–	–
C$_3$ Plants						
Solidago sempervirens (live)	–	–	–	−29.7 (0.2, 5)	0.3 (0.5, 5)	18.5 (0.6, 2)
Solidago sempervirens (standing dead)	–	–	–	−30.8 (0.3, 4)	0.8 (0.4, 4)	18.3 (0.5, 3)
Iva frutescens (live)	−27.0 (0.1, 5	2.2 (0.4, 5)	19.8 (0.2, 5)	−28.9 (0.4, 5)	1.0 (0.8, 5)	19.7 (0.3, 5)
Iva frutescens (standing dead)	−27.0 (0.2, 5)	3.2 (0.6, 5)	20.0 (0.1, 5)	−30.3 (0.2, 3)	1.0 (0.9, 3)	19.7 (0.1, 5)
Phragmites australis (live)	–	–	–	−25.0 (0.1, 5)	3.1 (0.3, 5)	2.8 (3.0, 5)
Phragmites australis (standing dead)	–	–	–	−25.6 (0.1, 5)	0.9 (0.3, 5)	11.0 (0.6, 5)
Juncus gerardii (live)	−27.4 (0.4, 4)	3.5 (0.6, 4)	19.6 (0.2, 4)	–	–	–
Juncus gerardii (standing dead)	−26.0 (0.6, 5)	3.1 (0.9, 5)	17.3 (0.5, 5)	–	–	–
Suspended particulates	−23.9 (0.4, 5)	9.4 (0.7, 4)	0.2 (0.0, 1)	−28.1 (0.5, 5)	4.8 (0.5, 4)	−5.5(0.0, 1)
Adult *Fundulus heteroclitus*	−20.8 (0.6, 5)	11.3 (0.4, 5)	7.8 (0.9, 5)	−24.1 (0.3, 5)	10.8 (0.2, 5)	2.9 (0.5, 5)
Juvenile *Fundulus heteroclitus*	−18.3 (0.5, 5)	11.3 (0.1, 5)	3.1 (0.6, 5)	−23.5 (0.3, 4)	10.4 (0.2, 5)	0.2 (0.1, 4)
Hatches Harbor						
C$_4$ Plants						
Spartina alterniflora (live)	−13.3 (0.1, 6)	5.7 (0.3, 6)	14.9 (2.2, 6)	−13.2 (0.0, 5)	4.9 (0.3, 5)	10.6 (2.4, 5)
Spartina alterniflora (standing dead)	−12.2 (0.1, 6)	4.0 (0.1, 6)	15.8 (0.9, 6)	−12.4 (0.2, 5)	2.1 (0.4, 5)	10.2 (1.3, 5)
C$_3$ Plants						
Phragmites australis (live)	–	–	–	−23.4 (0.2, 4)	4.7 (0.4, 4)	9.0 (2.4, 4)
Phragmites australis (standing dead)	–	–	–	−24.2 (0.2, 5)	2.8 (0.6, 4)	7.2 (2.2, 5)
Juncus gerardii (live)	–	–	–	−23.4 (0.1, 5)	2.0 (0.2, 5)	16.4 (2.0, 5)
Juncus gerardii (standing dead)	–	–	–	−23.4 (0.1, 4)	2.1 (0.2, 4)	9.0 (2.4, 4)
Macroalgae						
Ascophyllum nodosum	−17.4 (0.3, 5)	5.1 (0.3, 4)	20.1 (0.0, 5)	–	–	–
Chaetomorpha picquotiana	–	–	–	−19.6 (0.9, 5)	3.2 (0.3, 5)	20.2 (0.3, 5)
Fucus vesiculosus	−17.7 (0.1, 5)	4.2 (0.2, 5)	19.9 (0.1, 5)	–	–	–
Suspended particulates	−19.0 (0.7, 1)	7.5 (0.0, 1)	17.6 (0.0, 1)	−19.4 (0.5, 5)	3.6 (0.0, 1)	4.0 (0.0, 1)
Adult *Fundulus heteroclitus*	−15.3 (0.4, 3)	8.5 (0.3, 3)	17.0 (0.5, 3)	−17.5 (0.3, 5)	7.8 (0.2, 5)	16.6 (0.6, 5)
Juvenile *Fundulus heteroclitus*	−15.4 (0.4, 5)	8.1 (0.1, 5)	15.6 (0.4, 5)	−18.3 (0.4, 5)	7.5 (0.0, 5)	15.6 (0.3, 5)

$\delta^{13}C$ value is likely due to the lower salinity observed at Sachuest Point (Fig. 1, Table 1).

Another way to interpret the data is to evaluate differences in *Fundulus* $\delta^{13}C$ values between unrestricted reference marshes and adjacent tide-restored or tide-restricted marshes. This reveals that the magnitude of differences decreased as the tide restriction lessened (Fig. 4). The greatest differences were observed in both adult and juvenile Fundulus from the severely tide-restricted Herring River marsh and the adjacent Herring River reference marsh, with smaller differences at Sachu-
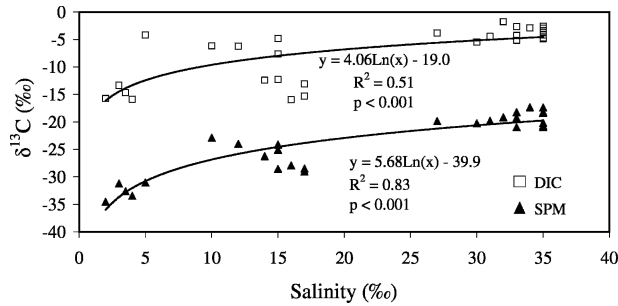
Fig. 1.   Suspended particulate matter (triangles) and dissolved inorganic carbon (squares) $\delta^{13}C$ values (‰) plotted against tidal creek salinity (‰). Data are from all six study marshes (n = 29).

est Point and Hatches Harbor, marshes that are in the restoration process. As noted in Figs. 3 and 4, there is a trend suggesting that as restoration proceeds from tide-restricted and recently tide-restored marsh conditions toward reference marsh conditions, there is an enrichment in *Fundulus* $\delta^{13}C$ values.

$\delta^{13}C$ VERSUS A MULTIPLE ISOTOPE APPROACH

In this study we use carbon isotopic signatures to track organic matter flow because the isotopic signatures of marine, estuarine, and terrestrial primary producers are predictable and cover a wide range of values (23‰; Table 3; Fry and Sherr 1984; Peterson 1999). The changes in water column salinity and marsh vegetation patterns that accompany the reintroduction of tidal flow can be expected to result in considerable changes in $\delta^{13}C$ values of organic matter sources. The various organic matter source $\delta^{15}N$ values generally cover a narrow range of values in relation to other isotopic forms (9‰, Table 3; Cloern et al. 2002; Connolly et al. 2004) and can vary over this narrow range seasonally (Cloern et al. 2002). Within the context of tidal restoration, $\delta^{15}N$ values of primary producers do not change in a predictable manner as
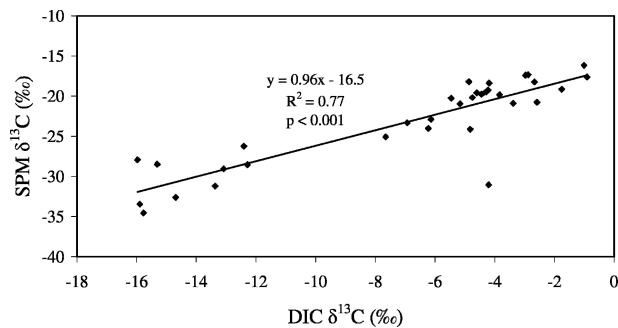

Fig. 2.   Suspended particulate matter $\delta^{13}C$ values plotted against corresponding dissolved inorganic carbon $\delta^{13}C$ values (‰). Data are from all six study marshes (n = 33).

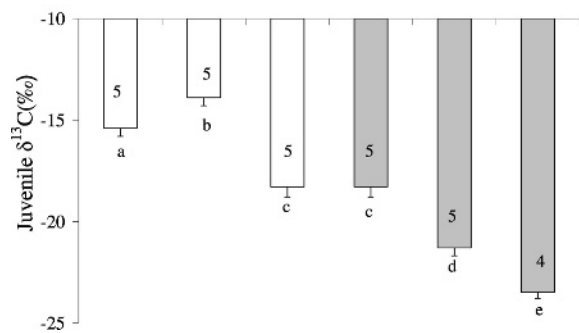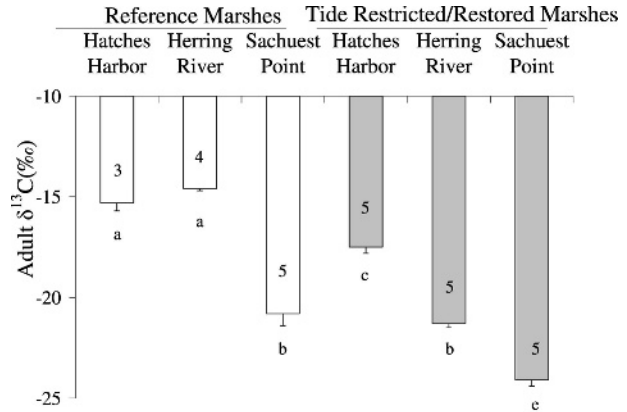

Fig. 3. $\delta^{13}C$ values (‰) for adult (>50 cm) and juvenile (<40 cm) *Fundulus heteroclitus* at Hatches Harbor, Herring River, and Sachuest Point reference, tide-restored, and tide-restricted marshes. Standard errors are presented with sample size indicated. Statistical significance determined by ANOVA (p < 0.05), with a post-hoc Least Square Means test. Values with different letters are statistically different.

demonstrated for $\delta^{13}C$ values. To illustrate this point, note the $\delta^{15}N$ values of organic matter sources at Herring River (Table 3). Organic matter source $\delta^{15}N$ values from the tide-restricted marsh
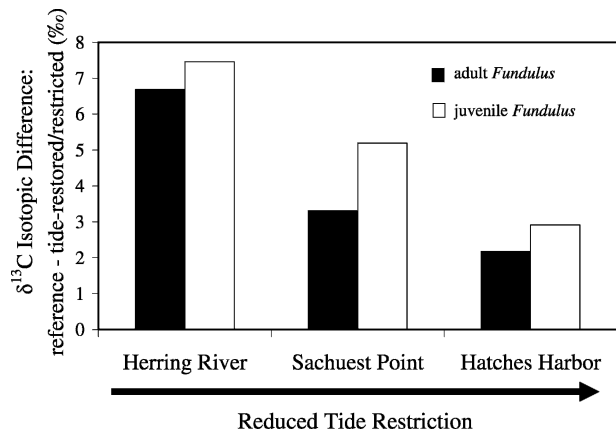

Fig. 4.   Differences in $\delta^{13}C$ values (‰) of adult and juvenile *Fundulus heteroclitus* from tide-restricted and tide-restored marshes and adjacent reference marshes are plotted for each study site.

TABLE 4. Benthic chlorophyll *a* concentrations at salt marsh habitats throughout the East Coast of the United States.

Source	Location	Date	Habitat	Chl *a* (mg chl *a* m^{-2})
This study	Massachusetts, Rhode Island	October 2003	Mudflat	16
			Phragmites marsh	11–29
			Spartina marsh	15–24
			Sandflat	15
Cammen (1991)	Maine	1984–1985	Intertidal sandflat	50–100
			Intertidal mudflat	30–140
Currin et al. (2003)	New Jersey	August 1998, August 1999	*Phragmites* marsh	14
			Spartina marsh	70
			Restored marsh	31
			Mudflat	47–50
Gould and Gallagher (1990)	Massachusetts	1986–1987	Mudflat	50–325
Pinckney and Zingmark (1993)	South Carolina	1990–1991	Sand	77
			Intertidal mudflat	72
			Tall *Spartina*	102
			Short *Spartina*	73
Sullivan and Daiber (1975)	Delaware	1971–1972	Dwarf *Spartina* marsh	79–133

(range: 4.4–6.5‰,) fall within the range of values for the reference marsh (range: 2.5–7.4‰); one would not expect that tide restoration would provide a shift in organic matter source δ^{15}N values. *Fundulus* δ^{15}N values at the Herring River reference marsh were less than those from the Herring River tide-restricted marsh, while *Fundulus* values from Sachuest Point and Hatches Harbor reference marshes were greater than at tide-restored marshes, demonstrating no clear trend (Table 3). There also was no consistent trend for Fundulus δ^{34}S values (Table 3). It is noted that the variability for primary producer δ^{34}S values was often high (e.g., *S. alterniflora* at all sites, *P. australis* at the Hatches Harbor tide-restored marsh, *R. maritima* at the Herring River tide-restricted and reference marshes; Table 3). δ^{34}S signatures of primary producers are quite variable within and among species both spatially and temporally (Stribling et al. 1998; Connolly et al. 2004) and this unpredictability limits our confidence in attributing changes in consumer δ^{34}S signatures to the effects of tide restoration as opposed to natural variability. While nitrogen and sulfur isotopic information can provide valuable information in the context of determining specific food sources to consumers (e.g., Peterson et al. 1986; Couch 1989; Deegan and Garritt 1997; Wainright et al. 2000), carbon isotopes alone may be useful as an indicator of changes due to tide restoration.

OTHER ORGANIC MATTER SOURCES

In the present study, we examined changes in organic carbon flow to *Fundulus* with respect to SPM and marsh angiosperms, but there are other organic carbon sources that may contribute to the diet of *Fundulus*. Seagrass, benthic microalgae, and macroalgae, may be important to the diets of consumers in these and other systems. Carbon isotopic

signatures from the literature and this study indicate that as salinity and water column DI^{13}C increase so do the carbon isotopic signatures of the submerged seagrass, *R. maritima*. *Ruppia* from oligohaline waters show depleted δ^{13}C signatures (-23.6‰ in Apalachicola Bay, Florida, Chanton and Lewis 2002; -22.5‰ in the Herring River, Table 3, this study), while at a mesohaline portion of the Chesapeake Bay, its carbon isotopic composition was -17.6‰ (Stribling and Cornwell 1997). Following this pattern of increasing *Ruppia* δ^{13}C with increasing salinity, the marine-influenced Herring River reference marsh had *Ruppia* δ^{13}C values averaging -9.4‰ (Table 3). It appears that tidal restoration, by way of increased water column salinity and higher DI^{13}C, is likely to increase *Ruppia* δ^{13}C values. Were *Ruppia* a significant food resource at the base of a consumer's food web, an increase in *Ruppia* δ^{13}C due to tidal restoration would act to increase that consumer's δ^{13}C signature, a change consistent with those described for SPM and salt marsh angiosperms above. Research on other seagrass species is needed to determine whether this is a general pattern.

A number of studies have investigated the importance of benthic microalgae to salt marsh consumers (e.g., Currin et al. 1995, 2003; Wainright et al. 2000; Moseman et al. 2004), and report considerable variability in δ^{13}C values. One study in New Jersey marshes reported benthic microalgae δ^{13}C values that ranged from -17‰ to -24‰ (Currin et al. 2003), but how these values might change with tidal restoration has not been studied. Benthic microalgal δ^{13}C values might be expected to vary with DI^{13}C as is observed for phytoplankton. If this were the case, our DI^{13}C data indicate that tide restoration would result in an increase in benthic microalgal δ^{13}C values similar to what occurs in SPM. In this study we collected benthic microalgae

from tidal creek intertidal habitats, following the methods of Couch (1989) and Wainright et al. (2000), but the quantity of material collected was insufficient for δ^{13}C analysis. Sediment chlorophyll *a* values from cores taken in this study ranged from 11 to 29 mg m^{-2}, whereas values measured in other studies were typically much higher (Table 4). Benthic microalgal importance is clearly evident in other systems, and changes in microalgal δ^{13}C values with restoration deserves further exploration.

Macroalgal δ^{13}C values reported in the literature are quite variable. Values for *Ulva* sp. have ranged between -4.9‰ (Schwinghamer et al. 1983) and -21.5‰ (Chanton and Lewis 2002). *Fucus vesiculosus* from a Nova Scotia site varied between -13.4‰ and -21.9‰ (Schwinghamer et al. 1983). Values from this study were within these ranges (Table 3). The main carbon source for macroalgae is water column DIC so one might expect macroalgal δ^{13}C values to vary with salinity similar to *Ruppia*, but we do not have adequate data to support this. Until the mechanisms controlling this variability are known, it is unclear what effects tide restoration would have on microalgal and macroalgal δ^{13}C values or what the resultant effects on consumer δ^{13}C values would be. In the present study, these additional organic matter sources do not appear to affect the conclusion that *Fundulus* δ^{13}C values will increase as the effects of tide restoration proceed.

Our data provide evidence that differences in the δ^{13}C values of organic matter sources inherent to tide-restricted and tide-restored salt marshes lead to differences in the δ^{13}C values of *Fundulus*. These data also indicate that differences in *Fundulus* δ^{13}C values from adjacent reference and tide-restricted marshes may lessen with tide restoration that provides food sources with higher δ^{13}C signals. With restoration of salt marshes it is important to select monitoring variables that assess the trajectory of tide-restored marshes towards achieving functional equivalency with reference marshes. Monitoring δ^{13}C values in resident fish along with dominant organic matter sources provides a reasonable indication of how food web support functions change in response to tide restoration.

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SOURCE OF UNPUBLISHED MATERIALS

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