Estuaries and Coasts (2014) 37:339–353
DOI 10.1007/s12237-013-9673-5

The Effects of Plant Invasion and Ecosystem Restoration on Energy Flow through Salt Marsh Food Webs

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Received: 26 October 2012 / Revised: 6 July 2013 / Accepted: 9 July 2013 / Published online: 15 August 2013

Abstract We measured the effects of a plant invasion (*Phragmites australis*) on resident fish (*Fundulus heteroclitus*) in New England salt marshes by assessing diet quality at the food web base and by quantifying the importance of primary producers to secondary production using a recently developed Bayesian mixing model (Stable Isotope Analysis in R, "SIAR"). *Spartina alterniflora*, the dominant native plant, exhibited significantly greater leaf toughness and higher C/N ratios relative to *P. australis*. Benthic microalgae and phytoplankton (as suspended particulate matter) exhibited the lowest C/N indicating higher diet quality. We conducted a sensitivity analysis in SIAR by modeling *F. heteroclitus* at three separate trophic levels (1.5, 2.0, and 2.5) using species-specific discrimination factors to determine basal resource contributions. Overall, the best-fitting models include those that assume *F. heteroclitus* resides approximately 2.0 trophic levels above primary producers. Using discrimination factors from a range of data sources reported in the literature, our analyses revealed that consumers rely less on benthic microalgae and phytoplankton in restricted marshes (7–23 % and 11–44 %, respectively) relative to reference marshes (5–34 % and 23–48 %, respectively), resulting in a shift in diet toward invasive plant consumption (0–27 %). This is likely due to increased *P. australis* cover and marsh surface shading leading to decreased microalgal biomass, combined with reduced flooding of the marsh surface that favors terrestrial invertebrate assemblages. Restoration decreased the quantity of *P. australis* in the food web (0–15 %) and increased the importance of microalgae (1–30 %), phytoplankton (19–48 %), and native plants (23–63 %), indicating a shift in ecological recovery toward reference conditions.

Keywords Diet quality · *Fundulus heteroclitus* · Phenolics · *Phragmites australis* · Sensitivity analysis · SIAR

Communicated by Scott C. Neubauer

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Introduction

Coastal salt marshes are highly productive ecosystems that provide forage, refuge, and nursery habitat for terrestrial and aquatic species worldwide (Beck et al. 2001). Although the importance of detritus from native salt marsh plants to the direct support of near- and off-shore food webs has been debated for decades (Teal 1962; Darnell 1967; Odum 1968; Nixon 1980; Childers et al. 2000), dietary, behavioral, and isotopic evidence indicate that salt marsh organic matter is assimilated by higher trophic levels and is mediated by factors such as geomorphology, tidal attributes, and freshwater input (Deegan et al. 2000). In recent years, the invasion of non-native plant species into coastal salt marshes has generated new questions on how food web support functions change when marshes are colonized by plant invaders (Wainright et al. 2000; Weinstein et al. 2000, 2009; Currin et al. 2003).

Introduced *Phragmites australis* subsp. *australis* (hereafter, "introduced *P. australis*") is replacing native *Spartina alterniflora* along the Atlantic coast of North America (Chambers et al. 1999). The *P. australis* invasion into Atlantic salt marshes provides an excellent model to assess the importance of native versus introduced salt marsh vegetation at the food web base as well as examine trophic response to ecological restoration because, like other invasive species, it is highly plastic, adapts to a wide range of environmental conditions, is globally distributed, and acts as ecosystem engineer post-invasion (Chambers et al. 1999; Meyerson

et al. 2000, 2009). This invasive macrophyte takes advantage of reduced salinity and increased disturbance and nitrogen availability associated with tidal restrictions and coastal development by forming near monocultures that decrease native plant diversity, elevate the marsh surface, and reduce the number of small water-filled marsh pools and depressions (Meyerson et al. 2000, 2009; Able et al. 2003; Rooth et al. 2003).

Turnover of the dominant plant species and subsequent alterations in habitat structure have been shown to alter the trophic structure of arthropod communities, with a shift from externally feeding herbivores in *S. alterniflora* to concealed detritivorous feeders in *P. australis* (Gratton and Denno 2005). This trophic structure shift in feeding guilds may change ecosystem function by decreasing the export of organic material and primary consumers off the marsh surface via predators such as nekton and birds. In addition, tall monocultures of *P. australis* are known to decrease the growth of benthic microalgae ("BMA"; Wainright et al. 2000; Currin et al. 2003) and reduce flooding of the marsh surface (Osgood et al. 2003; and hence deposition of suspended particulate matter, "SPM"), potentially affecting the diets of benthic invertebrates such as polychaetes, oligochaetes, copepods, ostracods, and amphipods (Galván et al. 2008, 2011). Therefore, a change in dominant primary producer may have far-reaching effects up the food chain to higher-level consumers.

Research on the contribution of native and invasive primary producers in salt marsh food webs in the mid-Atlantic region has produced mixed results. Using a multiple stable isotope approach, Gratton and Denno (2006) found that in invaded marshes arthropod food webs are most likely fueled by BMA or SPM and not the invasive plant. Arthropod assemblages and dietary sources are indistinguishable in restored and uninvaded marshes, suggesting that *S. alterniflora* forms the base of the food web (Gratton and Denno 2005, 2006). Other studies concluded that introduced *P. australis* partially supports secondary production for fish such as *F. heteroclitus*, *Anchoa mitchilli*, *Cynoscion regalis*, and *Morone americana* (Wainright et al. 2000; Weinstein et al. 2000, 2009; Litvin and Weinstein 2003, 2004).

In New England, Wozniak et al. (2006) used the carbon isotopic signature ($\delta^{13}C$) of *S. alterniflora* (C_4) and *P. australis* (C_3) to trace the flow of organic matter to consumers in tidally restricted, restored, and reference marshes. They found that secondary consumers (*F. heteroclitus*) have depleted carbon signatures in tidally restricted salt marshes invaded by *P. australis* relative to adjacent unrestricted marshes. The $\delta^{13}C$ in fish tissue became more enriched (i.e., closer to the signature of *S. alterniflora*) as *P. australis* cover was reduced by tidal restoration, providing a useful indicator of the trajectory of ecological change. Therefore, the incorporation of *P. australis* into salt marsh food webs varies by species, study site, and environmental factors, but stable isotopes can be useful in the detection of restoration success.

We investigated whether food web support functions change when invasive plants replace native vegetation in New England salt marshes and determined how restoration influences the assimilation and transfer of organic matter to salt marsh consumers. Specifically, we investigated the contribution of native and invasive primary producers (macrophytes, benthic macroalgae, and phytoplankton) to the production of a resident omnivorous fish (*Fundulus heteroclitus*). To do this, we asked the following questions: (a) Is there a detectable difference in diet quality of the dominant primary producers as measured by leaf toughness, C/N, and phenolic concentration?; (b) What is the relative importance of macrophytes, benthic microalgae, and phytoplankton in driving secondary production in invaded tidally restricted, restored, and reference salt marshes?; and (c) How does the use of different discrimination factors from published literature affect the outcome and interpretation of results from stable isotope mixing models?

Materials and Methods

Study Sites and Sampling Locations

We selected four tidally restricted (hereafter, "restricted") and four tidally restored ("restored") salt marshes invaded by introduced *P. australis* along the Atlantic coast of North America (see figure 1 and Table 1 in Dibble and Meyerson 2012 for a map of study sites and a detailed description of site characteristics). Each restricted or restored site was paired with an adjacent downstream, unrestricted control ("reference") site that was sampled on the same day ($n=16$ marshes total; 4 restricted, 4 restored, 8 reference). At tidally restricted sites, introduced *P. australis* covered approximately 60–88 % of study sites (Orson et al. 2000; Wozniak et al. 2006; personal observations) and 40–62 % of restored sites (Warren et al. 2002; Wozniak et al. 2006; Adamowicz and O'Brien 2012; Golet et al. 2012). Reference sites were primarily colonized by *S. alterniflora*, *S. patens*, and *Distichlis spicata* interspersed with small patches of other native plants (e.g., *Juncus gerardii*, *Limonium nashii*, etc.).

Field Collections

Three stations were randomly selected a priori within each of the 16 marshes ($n=48$ experimental units, "EUs"). Because we employed a matched-pairs experimental design, stations from the restricted marshes were only compared to stations from the adjacent unrestricted (reference) marshes, and stations from the restored marshes were only compared to those from adjacent reference marshes. *Fundulus heteroclitus* typically have a

limited home range and exhibit high site fidelity and limited passage rates between restricted and unrestricted marshes (Fritz et al. 1975; Lotrich 1975; Able et al. 2006; Eberhardt et al. 2011); therefore, fish tissue was expected to reflect resources available within the respective marsh site. We collected samples from one of our study sites (Drakes Island, ME) in summer 2009 (7/10/09, 7/22/09) and fall 2009 (9/1/09) as part of a preliminary research study and collected samples from all 16 marsh sites in summer 2010 (7/12–7/25/10, 7/29/10), fall 2010 (9/22–10/3/10), summer 2011 (7/11–7/23/11), and fall 2011 (9/25–10/7/11). Water quality data (e.g., salinity, temperature, and dissolved oxygen) were collected approximately 1 m from the marsh edge from the top 5 cm of the water column at each site; results and detailed methods are reported in Dibble and Meyerson (2012).

Primary Producers

We collected the standing live leaves of the dominant plants present at each station (*P. australis*, *S. alterniflora*, *S. patens*, and *D. spicata*). Plant dominance was determined via visual inspection of the marsh surface and surrounding area; any plant species representing >25% (approximate) cover was selected. For consistency, we randomly selected a minimum of five leaves from the top 15 cm of the stem from each dominant species and pooled the samples in the field (Wainright et al. 2000; Weinstein et al. 2000; Wozniak et al. 2006). In the laboratory, we rinsed leaves with deionized water (DI) water and froze, freeze-dried, ground, and stored the samples in a −80 °C freezer. We sampled plants in 2009 at Drakes Island, at all sites in 2010, and at three sites in 2011 (for clarification of 2010 data). In fall 2011, we collected data on leaf toughness using a handheld leaf penetrometer (Chatillon Push/Pull Gauge, Model 719) to test hypotheses on diet quality (Jiménez et al. 2012). At each station where introduced *P. australis* and/or *S. alterniflora* were present, we sampled 10 leaves from randomly selected plants and measured the amount of force (in Newtons) needed to penetrate each leaf.

In summer and fall 2010, we collected a 1-L amber high-density polyethylene bottle of water from the top 5 cm of the water column approximately 1 m from the marsh edge at each station and brought the water back to the laboratory on ice. In the laboratory, we vacuum filtered the water through Whatman binder-free glass microfiber filters (GF/F; 4.7 cm) to collect SPM. Filters were dried in a 40 °C oven and pelleted for stable isotope analysis. Phytoplankton fix water column dissolved inorganic carbon and fractionate that carbon upon uptake, resulting in SPM values that are depleted in $\delta^{13}C$ by ~20‰ (Chanton and Lewis 1999; Fry 2002). To examine dissolved inorganic carbon ($\delta^{13}C$-DIC) in the water column and to determine whether SPM in the water contained a phytoplankton signature, we collected 40 mL of water from the top 5 cm of the water column in I-Chem 200 Series glass scintillation vials, preserved the water with 5–10 mg sodium azide, and capped the vials with Chromatographic Specialties PTFE butyl rubber septa without a headspace to prevent CO_2 equilibration across the air–water interface.

We sampled the BMA community using a modification of the Couch (1989) method, whereby the top 1 cm of bare mudflat, sandflat, or sediment between vegetation at low tide was collected and brought on ice in the dark to the laboratory. We induced microalgal vertical migration in our greenhouse at the University of Rhode Island Greene H. Gardner Crops Research Center by spreading the sediment in trays, covering the wet sediment with a thin layer of Acros Organics precombusted silica sand, covering the sand with Nitex mesh, and then covering the mesh with another layer of sand. Window screening mounted on Styrofoam was placed on top of the sand to shade the surface. After 12 h of daylight, we removed the mesh, rinsed BMA off the mesh with DI water, removed inorganic sediment, and vacuum pumped the water through Whatman GF/F filters (4.7 cm; Wainright et al. 2000; Wozniak et al. 2006). Filters were dried in a 40 °C oven and pelleted for stable isotope analysis.

Fish

At each station, we deployed two Frabill vinyl-coated round minnow traps on flood tide for 30 min, combined the contents from both traps, then randomly selected five male and five female adult fish (>40 mm) representing the largest, smallest, and middle size ranges of adult fish available. We measured (total length, millimeters), weighed (centigrams), and then humanely euthanized the fish via IACUC-sanctioned procedures (URI Protocol #AN-09-05-020). In the laboratory, we removed fish digestive tracts and regurgitated food to ensure the isotopic signature encompassed assimilated food only. We rinsed fish in DI water and then froze, freeze-dried, ground (whole body), and stored the fish in a −80 °C freezer. Due to delayed spawning in the Northeast in 2011, we captured large quantities of gravid fish, providing the opportunity to assess nutrient allocation to reproduction (i.e., whether nutrients from different food sources are preferentially allocated to egg development; O'Brien et al. 2000). We collected the egg sacks from female body cavities, combined the eggs from each station into one sample, and prepared them for stable isotope analysis as we did with the fish and plants above.

Laboratory Analyses

Inorganic Carbon Removal

Carbon incorporated into tissues and carbon in inorganic carbonate originates from different sources and can bias stable isotope results, so it has been common practice to remove inorganic carbon from field samples prior to analysis (Fry

1988; Cloern et al. 2002; Jacob et al. 2005). However, inorganic carbon removal via acidification can affect the $\delta^{15}N$ signature of the sample (Pinnegar and Polunin 1999; Jacob et al. 2005), so we conducted an experiment using plant, fish, BMA, and SPM samples from 2009 field collections to determine whether it was necessary to acidify our samples prior to isotope analysis. Subsamples were treated with dilute (10%) hydrochloric acid, dried in a 40 °C oven (without rinsing, to minimize loss of dissolved organic matter), re-ground with a mortar and pestle, and weighed on a microbalance into Costech tin capsules (3.5 × 5 mm) to the nearest 0.001 mg (Fry 1988; Cloern et al. 2002). We ran the acidified samples for $\delta^{13}C$ using an isotope ratio mass spectrometer at the Environmental Protection Agency, Atlantic Ecology Laboratory in Narragansett, Rhode Island and compared the results to data from the unacidified parent sample.

Lipid Removal

To avoid potential error due to differential fractionation of $\delta^{13}C$ in lipids, carbohydrates, and proteins during tissue synthesis (Post et al. 2007), we removed lipids from individually ground fish samples. Briefly, powdered samples were packed into Whatman cellulose extraction thimbles and washed with a non-polar lipid solvent (petroleum ether) for 6 h using a Soxhlet apparatus (Dobush et al. 1985). After lipid extraction, we composited 10 fish from each EU using a mortar and pestle and weighed three replicates to the nearest 0.001 mg into tin capsules for isotope analysis (Fry et al. 2008). We did not remove lipids from ground eggs due to the limited quantity of material available; instead, we corrected the $\delta^{13}C$ values using an equation based on the relationship between lipid content, C/N ratio, and $\delta^{13}C$ (Eqn. 3; Post et al. 2007).

Stable Isotope, Elemental, and Phenolic Compound Analyses

We determined the isotopic composition ($\delta^{13}C$, $\delta^{15}N$) and elemental composition (%C, %N) of fish, eggs, plants, SPM, and BMA using an Elementar Vario Micro Cube elemental analyzer interfaced to an IsoPrime 100 mass spectrometer (precision = ±0.2 ‰) at the EPA Atlantic Ecology Laboratory. The C and N isotopic composition is expressed as a part per thousand (per mille, ‰) deviation from the reference standard for carbon (PDB) and from the composition of N_2 in the air and was calculated using the following equation:

$$\delta X = \left[\left(R_{\text{sample}} \Big/ R_{\text{standard}}\right) - 1\right] \times 1,000$$

Where X is ^{13}C or ^{15}N and R is the ratio of $^{13}C/^{12}C$ and $^{15}N/^{14}N$. Samples were randomly run in batches of 80–100 due to instrument capacity. Laboratory standards (blue mussel) were placed in duplicate every 20th sample and at the beginning and end of each run to check and correct for instrument drift. We analyzed 10 % of the primary producer samples in duplicate; composited samples of fish and eggs were run in triplicate (Fry et al. 2008). The mean of the duplicate and triplicate samples for each EU/time period was used for statistical analyses to avoid pseudoreplication. Ground samples of fish, eggs, and primary producers were packaged with vanadium pentoxide and analyzed by Iso-Analytical in Crewe, UK for $\delta^{34}S$ and %S, with 10 % run in duplicate.

We sent preserved 40-mL scintillation vials of water to the University of California Davis Stable Isotope Facility for analysis of $\delta^{13}C$-DIC. To examine plant tissue phenolic compounds and verify elemental concentration, we sent ground leaf samples (*S. alterniflora* and *P. australis*) from summer and fall 2010 to the University of Louisiana Agricultural Research and Extension Center, Soil Testing and Plant Analysis Laboratory in Baton Rouge, Louisiana. Percent carbon and nitrogen were determined using a Leco CN Analyzer. Phenolic compounds were extracted using 50 % methanol, after which a 100-μL aliquot of extract was mixed with DI water, Folins Reagent, and sodium carbonate. Absorbance was read at a wavelength of 720 nm. Samples were run in duplicate; if replicate absorbance values were not within 0.020 ODU the replicate was re-analyzed. The phenolics concentration was not broken down into its constituent components; however, the standard curve used to calculate the concentration was constructed using gallic acid (a phenolic compound in plants).

Data Analysis

We analyzed data using SAS (v. 9.2) and the R Statistical Environment (v. 2.15.0); figures were developed using SigmaPlot (v. 9.0). Assumptions of normality and equality of variances within datasets were verified prior to all statistical analyses. We examined whether it was necessary to remove inorganic carbon from samples using a two-sample paired *t* test of means. Regression was used to examine the relationship between salinity, $\delta^{13}C$-SPM, and water column $\delta^{13}C$-DIC. For leaf toughness data collected in fall 2011, we summarized 10 force measurements from each EU prior to analysis. Due to violations of normality and homogeneity of variance, we analyzed leaf toughness and phenolics data from *S. alterniflora* and *P. australis* using Welch's *t* tests. An independent samples *t* test was used to examine differences in C/N of *S. alterniflora* and *P. australis*. We used one-way analysis of variance (ANOVA) with Fisher's protected least significant difference tests to determine whether primary producer sources should be combined for use in stable isotope mixing models. Because we collected fish samples from each EU over time, we analyzed differences in mean $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, %C, %N, and %S in fish tissue using repeated measures mixed model ANOVA. We used SLICES

in the model to examine interaction effects to determine whether there were significant differences in the response after explanatory variables were incorporated into the model (i.e., marsh type, time, and region); mean fish length was used as a covariate to account for trophic level differences associated with $\delta^{15}N$. We used heterogeneous autoregressive (1) as our covariance structure because it assumes that data that are farther apart in time will be less similar and that each time period has its own unique variance.

Stable Isotope Mixing Models

We used a recently developed Bayesian mixing model in the software package SIAR (Stable Isotope Analysis in R; Jackson et al. 2009; Parnell et al. 2010) to assess the importance of native and invasive primary producers to *F. heteroclitus* production. SIAR represents an improvement over previous modeling approaches because it incorporates discrimination factors (i.e., the change in isotope ratio from prey to consumer tissue, $\Delta^{13}C$, $\Delta^{15}N$, and $\Delta^{34}S$) and their variation, the variation in isotopic signatures of each prey source, and source elemental concentrations into the model (Parnell et al. 2010). To date, most studies using isotopic mixing models have assessed the proportions of direct prey items to the tissue sampled (one trophic level). Instead, we estimated the contribution of primary producers to the production of *F. heteroclitus* that resides approximately two trophic levels above primary producers (Currin et al. 1995, 2003; Deegan and Garritt 1997; Wainright et al. 2000), an approach that has been taken for other species in coastal salt marshes (Wainright et al. 2000; Brittain et al. 2012). Brittain et al. (2012) used SIAR to model the contribution of salt marsh versus terrestrial primary producer sources to passerine food webs in Sapelo Island, Georgia, using discrimination factors to estimate dietary proportions 1.5 to 3 trophic levels above the food web base. In the mid-Atlantic region, Wainright et al. (2000) used a two-source mixing model to estimate a 2-trophic-level shift between juvenile *F. heteroclitus* and baseline diet, doubling the discrimination factors for carbon (1 ‰) and assuming a 0‰ shift for sulfur based on values from Peterson and Fry (1987). Since *F. heteroclitus* are known to consume invertebrates and accompanying plant matter (Kneib 1986; Allen et al. 1994; Wainright et al. 2000; James-Pirri et al. 2001) as well as exhibit limited piscivory either through cannibalism or scavenging (Able et al. 2007; Deegan et al. 2007), we also modeled the data at 1.5 and 2.5 trophic levels ("TLs") to ensure we were not making inaccurate assumptions of TL for our study species.

In SIAR, we ran 200,000 iterations with an initial discard of 50,000, thinned by 15, resulting in 10,000 posterior draws. When SIAR has difficulty differentiating between possible sources the posterior samples for the source contributions to diet are likely to be highly negatively correlated, so we assessed model fit by examining the highest correlations between sources in each model. We also assessed model fit by using the 95 % high-density region values for residual variance (standard deviation; i.e., inter-observation variance not described by the model; Parnell et al. 2010). Higher residual variance is attributed to greater variability in the isotopic values of the consumers, *F. heteroclitus*. Because the use of discrimination factors can influence model output (Bond and Diamond 2011), we ran a sensitivity analysis using $\Delta^{13}C$, $\Delta^{15}N$, and $\Delta^{34}S$ values reported from the literature. We adjusted the discrimination factors and errors to account for tissue to diet discrimination between primary consumers (invertebrates) and their diet (primary producers) and secondary consumers (*F. heteroclitus*) and their diet (invertebrates/plant detritus) at 1.5, 2.0, and 2.5 TLs. We believe this is an appropriate approach because the range of discrimination factors used to correct fish to omnivorous prey diets ($\Delta^{13}C = 0.40–3.36$; $\Delta^{15}N = 2.30–3.73$) are similar to those used to correct invertebrate to primary producer diets ($\Delta^{13}C = -0.50–2.50$; $\Delta^{15}N = 1.50–2.70$; Gratton and Denno 2006; Caut et al. 2009; Brittain et al. 2012).

We used six sets of discrimination factors, five of which were reported directly in the literature (Fry 1988; Post 2002; McCutchan et al. 2003; Dennis et al. 2010; Elsdon et al. 2010) and the sixth represents the median value of $\Delta^{13}C$, $\Delta^{15}N$, and $\Delta^{34}S$ compiled from the above literature and from other publications (Peterson and Fry 1987; Vanderklift and Ponsard 2003; Caut et al. 2009; Wyatt et al. 2010; termed "cross-study Δ values"). Discrimination factors from Fry (1988), Post (2002), McCutchan et al. (2003), and Dennis et al. (2010) were experimentally determined primarily using fish and aquatic organisms and differ based on trophic level, species, tissue sampled, diet fed, and sample preparation methodology. Elsdon et al. (2010) experimentally determined discrimination factors for *F. heteroclitus* fed a range of diets in the laboratory; however, we selected the discrimination factors from their study that closely resembled our sample methodology (i.e., lipid-free, non-acidified *F. heteroclitus* muscle tissue from fish fed an omnivorous diet). Source concentration dependence values were not entered into SIAR because the incorporation of Whatman GF/F filter weight into %C, %N, and %S led to lower (and erroneous) elemental concentrations for BMA and SPM in our data set.

Results

Basal Diet Quality

We detected significant differences in the toughness of *S. alterniflora* and *P. australis* leaves ($p<0.0001$, $t_{45.91}=-10.66$), with the former requiring significantly more force to penetrate ($\bar{x} = 14.43 \pm 2.37$ N; $n=47$) than the latter ($\bar{x} = 8.38 \pm 2.11$ N;

n=22). The C/N ratio generated via mass spectrometry at the EPA laboratory closely resembled results from LSU, so we used the latter dataset for analysis of vascular plant C/N. Mirroring leaf toughness results, *S. alterniflora* had a significantly higher ratio of carbon to nitrogen ($\bar{x}$ = 21.05 ± 6.12; n=16) than *P. australis* ($\bar{x}$ = 16.29 ± 3.48; n=17; p=0.0095, t_{31}=−2.76). The mean C/N ratios of BMA ($\bar{x}$ = 8.84 ± 2.29; n=33) and SPM ($\bar{x}$ = 6.95 ± 0.92; n=108) were lower than live vascular plants. Using the leaf samples measured for C/N, we found that the concentration of phenolic compounds in *P. australis* was higher ($\bar{x}$ = 18.56 ± 6.59 mg/g dry weight plant tissue; n=18) than *S. alterniflora* ($\bar{x}$ = 15.55 ± 2.16 mg/g dry weight; n=16), but the difference between plant species was not significant (p=0.0816; $t_{21.02}$=1.83). The phenolic concentration of *P. australis* ranged from 11.14 to 34.97 mg/g in restricted marshes and 11.13–28.64 mg/g in restored marshes, whereas *S. alterniflora* ranged from 13.55 to 19.69 mg/g in reference (restricted) marshes and 10.48–17.35 mg/g in reference (restored) marshes (Table 1).

Stable Isotope Analysis

Primary Producers

We examined the relationships between δ^{13}C-DIC, salinity, and δ^{13}C-SPM to determine whether SPM samples contained a phytoplankton signature and whether that signature was affected by changes in salinity between marsh types. Our data agree with the estimated ~20‰ depletion (Chanton and Lewis 1999; Fry 2002), as δ^{13}C-SPM was depleted by ~18‰ relative to δ^{13}C-DIC (Fig. 1). The mean C/N ratio of SPM was 6.9–7.0 at our stations. We found significant positive relationships between salinity and both δ^{13}C-DIC (r^2=0.81, p<0.0001; n=62) and δ^{13}C-SPM (r^2=0.34, p<0.0001; n=62; Fig. 1). Phytoplankton values are strongly influenced by changes to δ^{13}C-DIC (and hence, salinity) in the water column (r^2=0.52, p<0.0001; n=93; Fig. 2) so we ran separate models for each of the four marsh types to reduce error associated with local environmental conditions.

Removal of inorganic carbon from primary producer and consumer samples using 10 % hydrochloric acid did not significantly affect δ^{13}C (p=0.0935; t_{36}=−1.72), so we did not remove inorganic carbon from samples used in our primary analysis. The mean isotopic composition, elemental concentration, and C/N ratio of primary producer sources are reported in Table 2. We combined the dominant salt marsh grasses *S. alterniflora*, *S. patens*, and *D. spicata* into one native "salt marsh plant" source for use in SIAR because we found no significant difference in mean isotopic composition between all three plant sources for δ^{34}S (p=0.2320; $F_{2,79}$=1.49; n=82), between *S. alterniflora* and *D. spicata* for δ^{15}N (p=0.2073; n=201), and between *S. alterniflora* and *S. patens* for δ^{13}C (p=0.2907; n=221). In addition, the variability associated with the combined salt marsh plant source was low relative to the other plant sources. Overall, mean δ^{13}C was distinct for the salt marsh plant ($\bar{x}$ = −14.34 ± 0.57), BMA ($\bar{x}$ = −19.74 ± 2.98), SPM ($\bar{x}$ = −21.10 ± 2.69), and *P. australis* ($\bar{x}$ = −26.12 ± 1.20) sources. Mean δ^{15}N was distinct for SPM ($\bar{x}$ = 3.72 ± 3.06) but indistinguishable between salt marsh plants ($\bar{x}$ = 6.07 ± 2.09), BMA ($\bar{x}$ = 7.17 ± 4.06), and *P. australis* ($\bar{x}$ = 6.68 ± 1.90). Sulfur isotopes were highly variable but distinguished BMA ($\bar{x}$ = −3.51 ± 10.41) and SPM ($\bar{x}$ = 13.71 ± 6.09) from salt marsh plants ($\bar{x}$ = 3.94 ± 9.82) and *P. australis* ($\bar{x}$ = 2.35 ± 9.52). Stable isotope biplots show the relationship between the four dominant plant sources in restricted, restored, and reference marsh food webs as well as their relationship to secondary consumers (*F. heteroclitus*) in the system (Figs. 3 and 4a, b).

Fish

We captured 1,920 adult *F. heteroclitus* from 48 stations in the summer and fall seasons from 2010 to 2011, totaling 192 composited lipid-free whole-body samples. We found significant differences in the isotopic signature of fish inhabiting tidally restricted versus reference marsh sites for δ^{13}C (p<0.0001, t_{40}=7.83) and δ^{15}N (p=0.0366, t_{40}=−2.16) but not for δ^{34}S, %C, %N, or %S (p>0.05; Table 2). Results for differences between the restricted and reference systems

Table 1 Summary of phenolic concentrations in *P. australis* and *S. alterniflora* (mg/g dry plant matter) by marsh site[a]

	P. australis	*S. alterniflora*	Marsh type
Barn Island, CT	15.46 (3.91)	17.06 (0.41)	Restored/reference
Drakes Island, ME	21.86 (7.82)	12.22 (2.45)	Restored/reference
Galilee, RI	14.01 (3.44)	15.46 (2.39)	Restored/reference
Hatches Harbor, MA	17.72 (2.88)	15.33 (2.45)	Restored/reference
Herring River, MA	18.15 (0.68)	15.67 (0.01)	Restricted/reference
Stony Brook, MA	13.96 (0.02)	17.21 (3.50)	Restricted/reference
Sybil Creek, CT	13.99 (4.02)	15.41 (2.62)	Restricted/reference
Sluice Creek, CT	30.03 (6.98)	16.06 (0.41)	Restricted/reference

[a] Data are means±standard deviations (in parentheses)

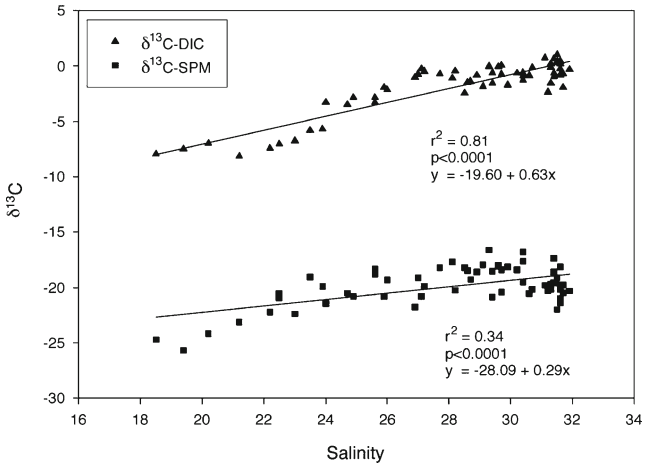

Fig. 1 Carbon stable isotope composition of suspended particulate matter (SPM) and dissolved inorganic carbon (DIC) vs. water column salinity for all study sites

for $\delta^{13}C$ were significant and in agreement in the Long Island Sound (LIS) and Gulf of Maine (GOM) regions and in all four time periods sampled ($p<0.05$). The significant difference in fish $\delta^{15}N$ signatures in the restricted versus reference marshes was driven by samples collected in LIS in the summer ($p=0.0510$, $t_{119}=-1.97$) and fall of 2010 ($p=0.0098$, $t_{119}=-2.63$). For fish residing in the tidally restored versus reference marsh sites, we found significant differences in the $\delta^{13}C$ ($p=0.0370$, $t_{40}=2.16$) and %S ($p=0.0358$, $t_{40}=2.17$) in fish tissue but not for $\delta^{15}N$, $\delta^{34}S$, %C, or %N ($p>0.05$; Table 2). Overall differences in $\delta^{13}C$ were driven by differences in carbon source for one time period and region only: summer 2011 in the GOM ($p=0.0291$, $t_{119}=2.21$). The isotopic composition of whole-body *F. heteroclitus* was similar to eggs although egg tissue was ~1–1.5‰ depleted in $\delta^{13}C$, which could be an artifact of differences in methodology used to correct for lipid content (direct lipid removal vs. C/N correction).

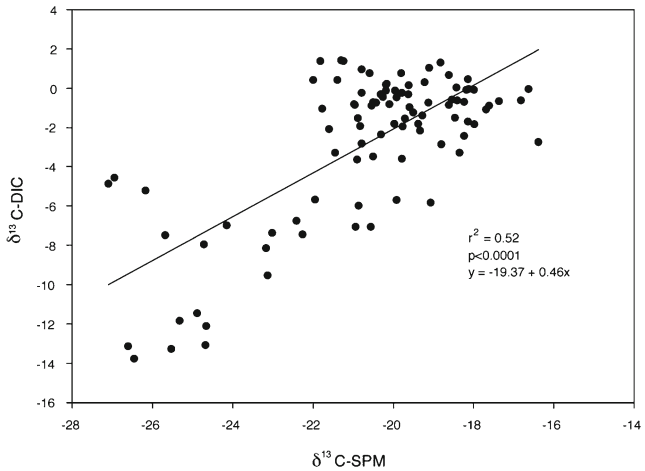

Fig. 2 Relationship between the carbon isotopic composition of suspended particulate matter (SPM) and dissolved inorganic carbon (DIC) in the water column for all study sites

Basal Diet Proportions

SIAR model performance using our data can be considered moderate based on source correlation coefficients in the range 0.3–0.7 (Bond and Diamond 2011; Doucette et al. 2011). Overall, the lowest residual variance across all models was found for the models run at 2.0 trophic levels, with the 95% high-density region values overlapping zero in 65 of 72 models (Table 3). When the data were modeled at 1.5 and 2.5 TLs, 61 and 62 models overlapped zero, respectively. In addition, the cross-study Δ values, which integrated a large number of discrimination factors across a range of studies, largely yielded the lowest residual variance within the 2.0 TL category across the three isotopes. Hereafter, we focus on models produced by modeling *F. heteroclitus* at 2.0 TLs (Tables 3 and 4).

The discrimination factor inputs experimentally measured for *F. heteroclitus* by Elsdon et al. (2010) that represent the closest tissue preparation methodology relative to our study resulted in the poorest fit overall (95 % HDR range = 0.00–7.12), with results deviating significantly from the model outputs for Fry 1988, Post 2002, McCutchan et al. 2003, Dennis et al. 2010, and the cross-study Δ values (Tables 3–4). Results revealed that benthic microalgae contributed the least to basal diet in restricted (1–13 %) and restored (3–25 %) marshes, with higher contributions in reference marshes adjacent to the restricted and restored sites (12–30 % and 27–43 %, respectively). Introduced *P. australis* contributed 25–43 % and 23–40 % to basal diet in restricted and restored marshes, respectively, and SPM was equally important in all marshes (~40–62 %). Salt marsh plants represented a smaller fraction of basal resources in restricted (0–8 %), restored (0–7 %), and reference marshes adjacent to restricted and restored sites (13–40 % and 8–27 %, respectively; Table 4).

Discrimination factor inputs from the five other models yielded a much better fit and were consistent in model output; therefore, results based on Fry 1988, Post 2002, McCutchan et al. 2003, Dennis et al. 2010, and the cross-study Δ values will be collectively evaluated in the discussion. Overall, BMA contributed 7–23 % to *F. heteroclitus* production in restricted marshes, with an additional 0–27 % originating from *P. australis*, 11–44 % from SPM, and 26–55 % from fringing salt marsh plants (Table 4). In adjacent reference marshes, BMA and SPM constituted a larger proportion of the food web (5–34 % and 23–48 %, respectively) with additional contributions from salt marsh plants (25–62 %). Hydrologic restoration decreased the contribution of *P. australis* in the food web (0–15 %) and increased the proportion of BMA, SPM, and native salt marsh plants (1–30 %, 19–48 %, and 23–63 %, respectively). Benthic microalgae and salt marsh plants contributed the most to *F. heteroclitus* production in reference marshes adjacent to restored sites (4–35 % and 29–62 %, respectively), with additional contributions from SPM (21–45 %; Table 4).

Table 2 Summary of data for primary producers, fish, and eggs by marsh type[a]

Marsh type	Producer and consumer species	$\delta^{13}C$ (±SD)[b]	$\delta^{15}N$ (±SD)	$\delta^{34}S$ (±SD)	%C (±SD)	%N (±SD)	%S (±SD)	C/N	*n*
Restricted	Benthic microalgae (BMA)	−21.49 (1.82)	8.66 (4.37)	−7.65 (8.95)	–	–	–	9.1	10
	D. spicata	−15.49 (0.32)	8.68 (2.16)	11.18 (9.61)	42.93 (1.39)	1.71 (0.24)	0.46 (0.16)	25.5	7
	P. australis	−26.61 (1.23)	7.47 (2.00)	2.82 (7.96)	41.70 (3.78)	2.88 (0.58)	0.53 (0.34)	15.0	28
	Phytoplankton (SPM)	−23.98 (2.53)	3.96 (3.35)	11.65 (5.83)	–	–	–	6.9	30
	S. alterniflora	−14.23 (0.48)	7.90 (2.89)	11.16 (5.30)	41.37 (4.12)	1.98 (0.66)	0.41 (0.07)	23.1	27
	S. patens	−14.80 (0.49)	6.94 (1.09)	15.12 (2.06)	42.39 (1.73)	1.26 (0.16)	0.18 (0.02)	34.0	5
	F. heteroclitus (whole body)	−17.91 (1.65)	12.10 (1.63)	8.52 (1.66)	35.43 (2.01)	11.28 (0.60)	1.09 (0.16)	3.1	48
	F. heteroclitus (eggs)	−19.48 (0.79)	13.49 (2.85)	6.94 (3.19)	47.24 (1.15)	9.94 (0.56)	0.65 (0.16)	4.8	4
Reference (restricted)	Benthic microalgae (BMA)	−19.07 (1.77)	8.84 (4.11)	−6.17 (8.22)	–	–	–	9.5	10
	D. spicata	−15.19 (0.39)	7.78 (2.67)	0.5 (3.15)	43.24 (2.95)	1.63 (0.35)	0.45 (0.11)	27.0	17
	Phytoplankton (SPM)	−20.31 (1.54)	4.23 (3.92)	10.19 (7.01)	–	–	–	7.0	30
	S. alterniflora	−14.45 (0.48)	7.40 (2.20)	3.86 (7.80)	41.72 (3.6)	2.38 (0.55)	0.65 (0.30)	18.2	30
	S. patens	−14.44 (0.48)	5.99 (2.10)	0.74 (3.88)	41.16 (3.71)	1.20 (0.35)	0.28 (0.06)	37.0	20
	F. heteroclitus (whole body)	−15.64 (1.58)	11.50 (1.33)	7.81 (1.72)	35.83 (2.07)	11.36 (0.57)	1.08 (0.15)	3.2	48
	F. heteroclitus (eggs)	−16.67 (1.73)	11.64 (1.32)	11.53 (5.93)	47.99 (1.81)	9.53 (0.40)	0.85 (0.10)	5.0	7
Restored	Benthic microalgae (BMA)	−19.59 (3.93)	4.26 (1.43)	−0.69 (10.94)	–	–	–	8.2	9
	D. spicata	−15.36 (0.47)	4.49 (0.92)	4.13 (5.76)	39.35 (6.95)	1.43 (0.32)	0.35 (0.09)	28.8	11
	P. australis	−25.63 (0.99)	5.74 (1.28)	1.82 (11.33)	44.90 (5.96)	2.70 (0.46)	0.45 (0.23)	17.0	22
	Phytoplankton (SPM)	−20.62 (2.35)	3.45 (2.42)	15.25 (4.32)	–	–	–	7.0	27
	S. alterniflora	−13.90 (0.54)	6.20 (1.61)	3.61 (11.01)	40.73 (4.50)	1.93 (0.46)	0.59 (0.28)	22.1	29
	S. patens	−14.06 (0.83)	4.22 (2.10)	10.58 (10.68)	42.58 (3.24)	1.13 (0.30)	0.25 (0.08)	40.8	20
	F. heteroclitus (whole body)	−15.46 (1.48)	9.29 (1.09)	9.15 (5.04)	36.65 (2.64)	11.57 (0.73)	1.18 (0.18)	3.2	48
	F. heteroclitus (eggs)	−16.42 (1.65)	9.51 (1.48)	10.14 (5.69)	49.95 (1.40)	9.46 (0.31)	0.85 (0.05)	5.3	11
Reference (restored)	Benthic microalgae (BMA)	−18.70 (3.59)	6.58 (4.22)	0.48 (12.82)	–	–	–	8.3	9
	D. spicata	−15.07 (0.67)	3.84 (1.50)	−2.36 (7.55)	44.38 (1.84)	1.35 (0.23)	0.32 (0.13)	33.8	9
	Phytoplankton (SPM)	−19.74 (2.00)	3.20 (2.23)	17.49 (4.32)	–	–	–	7.0	31
	S. alterniflora	−14.20 (0.49)	5.42 (1.52)	−0.79 (12.68)	40.70 (3.98)	2.29 (0.74)	0.89 (0.37)	19.5	29
	S. patens	−14.23 (0.59)	3.85 (2.12)	7.35 (6.03)	43.16 (2.76)	1.11 (0.26)	0.16 (0.04)	41.0	18
	F. heteroclitus (whole body)	−14.72 (1.45)	9.17 (1.18)	9.56 (4.83)	36.79 (2.10)	11.63 (0.59)	1.23 (0.19)	3.2	48
	F. heteroclitus (eggs)	−15.68 (0.85)	9.83 (0.84)	7.10 (5.05)	50.32 (0.88)	9.71 (0.29)	0.84 (0.08)	5.2	8

[a] Data are means±standard deviations (in parentheses)

[b] Composited *F. heteroclitus* $\delta^{13}C$ values corrected by lipid extraction; egg tissue $\delta^{13}C$ corrected mathematically (Post et al. 2007)

Discussion

Basal Diet Quality

The flow of energy through salt marsh food webs is partially influenced by the diet quality of primary producers at the base of the food web (Wainright and Fry 1994; Parker et al. 2008). The C/N ratio is often used as an indicator of the nutritional value of plant sources, with higher %N values (i.e., lower C/N ratio, hence higher protein content) indicating a higher quality diet (Wainright and Fry 1994; Jiménez et al. 2012). In our study systems, SPM and BMA exhibited the lowest C/N and vascular plants exhibited the highest C/N. Therefore, SPM and BMA are nutritionally superior to vascular plants and are more likely to be preferentially consumed by primary consumers. This is likely due to high palatability and digestibility associated with algal-based food webs leading to higher trophic levels (Deegan et al. 2000), especially for BMA that is rich in fatty acids and high in nitrogen (Tenore 1988). Fish tissue from reference marshes contained high proportions of nutrients from resources exhibiting low C/N ratios, indicating that primary consumers target high-quality and palatable dietary items. Using stable isotope tracers, other studies have found that invertebrates such as amphipods, copepods, isopods, polychaetes, oligochaetes, insects, and snails (the primary diet items of *F. heteroclitus*) preferentially graze on BMA and SPM (Currin et al. 2003; Gratton and Denno 2006; Deegan et al. 2007; Galván et al. 2008, 2011) and are consumed by *F. heteroclitus* (Kneib 1986; Allen et al. 1994; James-Pirri et al. 2001), providing a mechanism behind the relay of BMA and SPM into the tissue of higher trophic levels. This lends

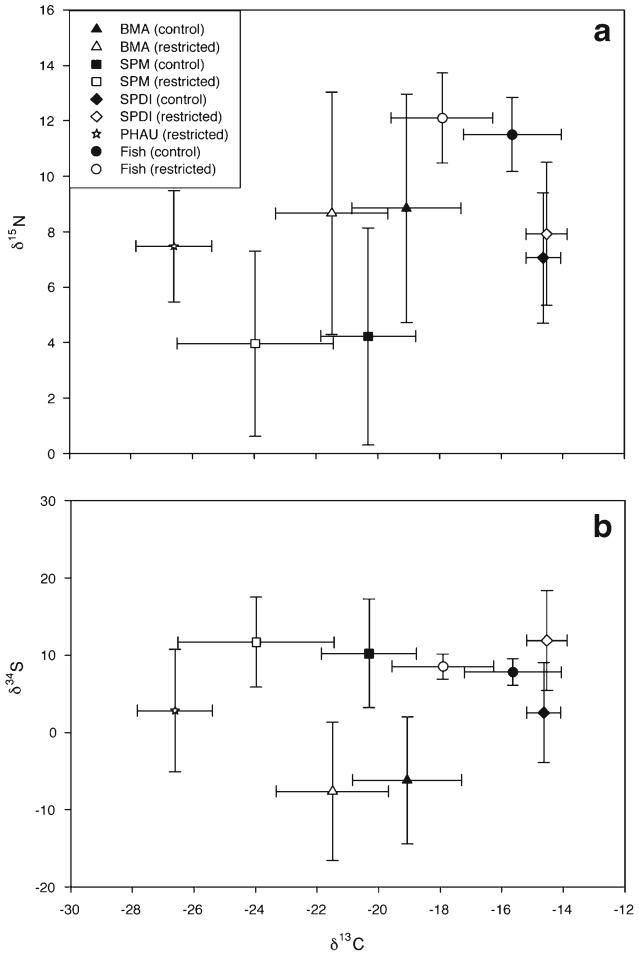

Fig. 3 Stable isotope biplots for **a** $\delta^{13}C$ vs. $\delta^{15}N$ and **b** $\delta^{13}C$ vs. $\delta^{34}S$ for the restricted vs. reference (control) marsh sites. Data for sources are means ± standard deviations and are separated by marsh type. Key: *Fish—F. heteroclitus* (whole body, lipid-free), *BMA*—benthic microalgae, *SPM*—phytoplankton, *SPDI*—salt marsh plants *Spartina alterniflora, S. patens*, and *Distichlis spicata*, *PHAU—Phragmites australis*. Fish data are not corrected for discrimination in these plots

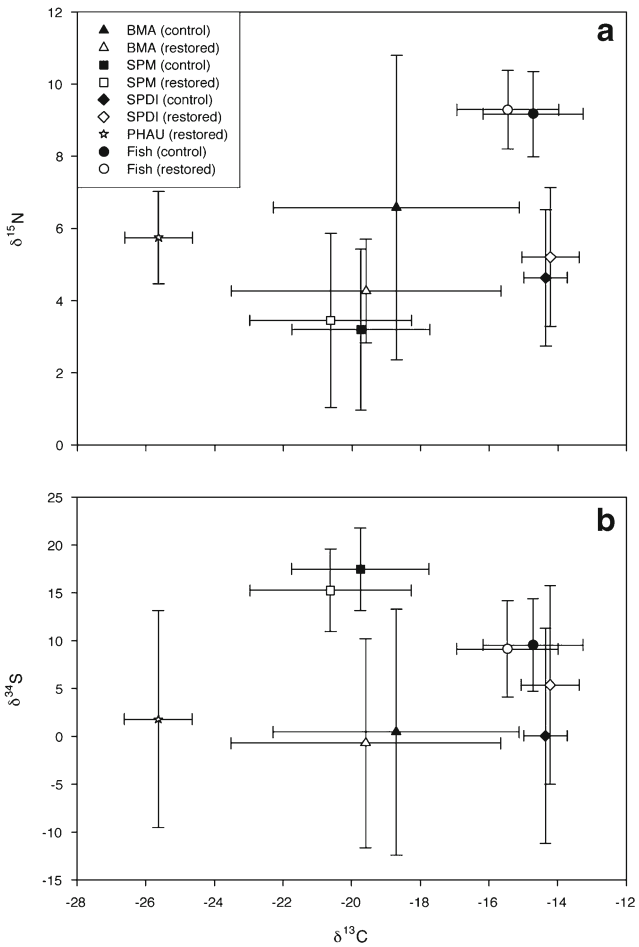

Fig. 4 Stable isotope biplots for **a** $\delta^{13}C$ vs. $\delta^{15}N$ and **b** $\delta^{13}C$ vs. $\delta^{34}S$ for the restored vs. reference (control) marsh sites. Data for sources are means ± standard deviations and are separated by marsh type. Key: *Fish—F. heteroclitus* (whole body, lipid-free), *BMA*—benthic microalgae, *SPM*—phytoplankton, *SPDI*—salt marsh plants *Spartina alterniflora, S. patens*, and *Distichlis spicata*, *PHAU—Phragmites australis*. Fish data are not corrected for discrimination in these plots

Table 3 The 95% high-density region values for residual variance (standard deviation) from SIAR models as a measure of model fitness

		1.5 Trophic levels						2.0 Trophic levels						2.5 Trophic levels					
Reference	Marsh type	SD ^{13}C Low 95%	SD ^{13}C High 95%	SD ^{15}N Low 95%	SD ^{15}N High 95%	SD ^{34}S Low 95%	SD ^{34}S High 95%	SD ^{13}C Low 95%	SD ^{13}C High 95%	SD ^{15}N Low 95%	SD ^{15}N High 95%	SD ^{34}S Low 95%	SD ^{34}S High 95%	SD ^{13}C Low 95%	SD ^{13}C High 95%	SD ^{15}N Low 95%	SD ^{15}N High 95%	SD ^{34}S Low 95%	SD ^{34}S High 95%
Fry 1988	Restricted	0.05	1.47	0.00	0.94	0.00	1.30	0.00	1.05	0.00	1.16	0.00	1.34	0.00	0.95	0.00	2.15	0.00	1.42
Post 2002		0.05	1.53	0.00	0.93	0.00	1.38	0.00	1.15	0.00	1.51	0.00	1.45	0.00	1.06	1.53	3.87	0.00	1.50
McCutchan et al. 2003		0.14	1.53	0.00	1.21	0.00	1.46	0.00	1.18	0.00	0.95	0.00	1.44	0.00	1.06	0.00	1.01	0.00	1.47
Dennis et al. 2010		1.12	1.92	0.00	1.06	0.00	1.36	0.94	1.85	0.00	0.97	0.00	1.33	0.58	1.75	0.00	1.43	0.00	1.45
Elsdon et al. 2010		0.27	1.69	0.00	1.02	0.00	1.33	0.00	1.06	0.00	1.13	0.00	1.54	0.00	1.63	0.07	3.03	0.00	1.72
Cross-Study Δ Values		0.31	1.62	0.00	1.07	0.00	1.38	0.00	1.09	0.00	0.97	0.00	1.32	0.00	0.96	0.00	1.57	0.00	1.39
Fry 1988	Reference (restricted)	0.00	1.23	0.00	1.37	0.00	1.45	0.00	1.08	0.00	1.43	0.00	1.41	0.00	1.21	0.00	1.65	0.00	1.48
Post 2002		0.00	1.28	0.00	1.33	0.00	1.66	0.00	1.10	0.00	1.48	0.00	1.51	0.00	1.04	0.00	1.69	0.00	1.47
McCutchan et al. 2003		0.00	1.22	0.00	1.42	0.00	1.67	0.00	1.02	0.00	1.20	0.00	1.48	0.00	0.95	0.00	1.24	0.00	1.42
Dennis et al. 2010		1.07	1.84	0.00	1.80	0.00	1.58	0.95	1.78	0.00	1.58	0.00	1.48	0.72	1.78	0.00	1.64	0.00	1.42
Elsdon et al. 2010		0.00	2.66	0.00	2.39	0.00	1.63	2.29	5.17	0.00	1.83	0.00	1.57	3.98	7.12	0.00	1.90	0.00	1.50
Cross-Study Δ Values		0.00	1.22	0.00	1.48	0.00	1.57	0.00	0.95	0.00	1.38	0.00	1.46	0.00	0.93	0.00	1.50	0.00	1.49
Fry 1988	Restored	0.00	0.93	0.00	0.72	0.00	3.29	0.00	0.86	0.00	1.29	0.00	3.48	0.00	0.86	0.40	3.81	0.00	3.48
Post 2002		0.00	1.12	0.00	0.68	0.00	2.94	0.00	1.03	0.16	2.18	0.00	2.90	0.00	1.01	2.45	4.38	0.00	2.84
McCutchan et al. 2003		0.00	1.00	0.00	0.87	0.00	3.04	0.00	0.99	0.00	0.76	0.00	2.92	0.00	1.00	0.00	0.92	0.00	2.92
Dennis et al. 2010		0.47	1.63	0.00	0.66	0.00	3.09	0.01	1.28	0.00	0.80	0.00	3.11	0.00	1.08	0.00	1.99	0.00	3.24
Elsdon et al. 2010		0.00	0.95	0.00	0.74	0.05	4.19	0.00	0.91	1.42	3.06	0.00	3.33	0.00	1.10	3.53	5.78	0.00	2.90
Cross-Study Δ Values		0.00	0.99	0.00	0.66	0.00	3.08	0.00	0.87	0.00	0.79	0.00	3.17	0.00	0.90	0.13	2.42	0.00	3.30
Fry 1988	Reference (restored)	0.00	0.85	0.00	1.14	0.00	2.78	0.00	0.85	0.00	1.31	0.00	2.94	0.00	1.03	0.00	1.56	0.00	3.11
Post 2002		0.00	1.56	0.00	1.20	0.00	3.17	0.00	1.39	0.00	1.42	0.00	2.88	0.00	1.23	0.00	1.64	0.00	2.88
McCutchan et al. 2003		0.00	1.15	0.00	1.20	0.00	3.24	0.00	1.08	0.00	1.07	0.00	2.88	0.00	1.01	0.00	1.17	0.00	2.73
Dennis et al. 2010		0.68	1.58	0.00	1.42	0.00	3.08	0.07	1.33	0.00	1.33	0.00	2.84	0.00	1.02	0.00	1.46	0.00	2.81
Elsdon et al. 2010		0.00	1.42	0.00	1.58	0.00	3.11	0.00	3.05	0.00	1.64	0.00	2.95	1.20	5.87	0.00	1.83	0.00	2.94
Cross-Study Δ Values		0.00	0.98	0.00	1.18	0.00	2.99	0.00	0.83	0.00	1.21	0.00	2.84	0.00	0.83	0.00	1.37	0.00	2.88

Residual variance modeled for *Fundulus heteroclitus* at three trophic levels. Lower values indicate a better fitting model

Table 4 Discrimination factors used in sensitivity analysis, with model output by marsh type

	Discrimination factors[a]			SIAR model output: basal diet proportions[c]				
Reference	$\Delta^{13}C$ (±SD)	$\Delta^{15}N$ (±SD)	$\Delta^{34}S$ (±SD)	Marsh type	Benthic microalgae	*Phragmites australis*	Phytoplankton (SPM)	Salt marsh plants
Fry 1988	1.60 (1.35)	3.40 (1.95)	[b]	Restricted	0.13 (0.07–0.19)	0.19 (0.11–0.27)	0.36 (0.29–0.44)	0.31 (0.26–0.36)
Post 2002	0.40 (1.30)	3.40 (1.00)	[b]	Restricted	0.16 (0.10–0.22)	0.04 (0.00–0.10)	0.33 (0.25–0.40)	0.47 (0.41–0.52)
McCutchan et al. 2003	0.50 (1.30)	2.30 (1.55)	0.50 (1.95)	Restricted	0.17 (0.10–0.23)	0.14 (0.05–0.22)	0.20 (0.11–0.28)	0.50 (0.45–0.55)
Dennis et al. 2010	1.10 (0.30)	2.90 (1.20)	[b]	Restricted	0.15 (0.08–0.21)	0.15 (0.06–0.23)	0.31 (0.23–0.40)	0.39 (0.34–0.44)
Elsdon et al. 2010	3.36 (0.80)	3.73 (0.80)	[b]	Restricted	0.07 (0.01–0.13)	0.34 (0.25–0.43)	0.55 (0.47–0.62)	0.04 (0.00–0.08)
Cross-study Δ values	1.19 (1.30)	2.90 (1.10)	0.50 (1.83)	Restricted	0.14 (0.08–0.21)	0.16 (0.09–0.25)	0.31 (0.24–0.39)	0.38 (0.33–0.43)
Fry 1988	1.60 (1.35)	3.40 (1.95)	[b]	Reference (restricted)	0.27 (0.20–0.34)	n/a	0.42 (0.35–0.48)	0.32 (0.25–0.39)
Post 2002	0.40 (1.30)	3.40 (1.00)	[b]	Reference (restricted)	0.11 (0.05–0.18)	n/a	0.35 (0.28–0.41)	0.54 (0.47–0.62)
McCutchan et al. 2003	0.50 (1.30)	2.30 (1.55)	0.50 (1.95)	Reference (restricted)	0.16 (0.09–0.23)	n/a	0.29 (0.23–0.36)	0.55 (0.47–0.62)
Dennis et al. 2010	1.10 (0.30)	2.90 (1.20)	[b]	Reference (restricted)	0.17 (0.10–0.24)	n/a	0.39 (0.32–0.45)	0.45 (0.38–0.51)
Elsdon et al. 2010	3.36 (0.80)	3.73 (0.80)	[b]	Reference (restricted)	0.21 (0.12–0.30)	n/a	0.52 (0.43–0.62)	0.27 (0.13–0.40)
Cross-Study Δ Values	1.19 (1.30)	2.90 (1.10)	0.50 (1.83)	Reference (restricted)	0.19 (0.12–0.25)	n/a	0.42 (0.36–0.48)	0.40 (0.33–0.47)
Fry 1988	1.60 (1.35)	3.40 (1.95)	[b]	Restored	0.20 (0.08–0.30)	0.08 (0.01–0.15)	0.40 (0.32–0.48)	0.32 (0.23–0.41)
Post 2002	0.40 (1.30)	3.40 (1.00)	[b]	Restored	0.10 (0.01–0.19)	0.01 (0.00–0.04)	0.34 (0.24–0.43)	0.55 (0.46–0.63)
McCutchan et al. 2003	0.50 (1.30)	2.30 (1.55)	0.50 (1.95)	Restored	0.16 (0.07–0.26)	0.03 (0.00–0.08)	0.27 (0.19–0.36)	0.53 (0.45–0.61)
Dennis et al. 2010	1.10 (0.30)	2.90 (1.20)	[b]	Restored	0.21 (0.10–0.31)	0.02 (0.00–0.06)	0.37 (0.29–0.45)	0.40 (0.33–0.48)
Elsdon et al. 2010	3.36 (0.80)	3.73 (0.80)	[b]	Restored	0.14 (0.03–0.25)	0.32 (0.23–0.40)	0.51 (0.42–0.61)	0.03 (0.00–0.07)
Cross-Study Δ Values	1.19 (1.30)	2.90 (1.10)	0.50 (1.83)	Restored	0.19 (0.09–0.29)	0.04 (0.00–0.09)	0.38 (0.30–0.46)	0.38 (0.31–0.47)
Fry 1988	1.60 (1.35)	3.40 (1.95)	[b]	Reference (restored)	0.27 (0.19–0.35)	n/a	0.37 (0.31–0.43)	0.36 (0.29–0.43)
Post 2002	0.40 (1.30)	3.40 (1.00)	[b]	Reference (restored)	0.13 (0.04–0.23)	n/a	0.34 (0.25–0.42)	0.53 (0.45–0.62)
McCutchan et al. 2003	0.50 (1.30)	2.30 (1.55)	0.50 (1.95)	Reference (restored)	0.17 (0.07–0.26)	n/a	0.29 (0.21–0.37)	0.54 (0.47–0.62)
Dennis et al. 2010	1.10 (0.30)	2.90 (1.20)	[b]	Reference (restored)	0.20 (0.10–0.29)	n/a	0.35 (0.27–0.42)	0.45 (0.39–0.52)
Elsdon et al. 2010	3.36 (0.80)	3.73 (0.80)	[b]	Reference (restored)	0.35 (0.27–0.43)	n/a	0.48 (0.40–0.55)	0.17 (0.08–0.27)
Cross-study Δ values	1.19 (1.30)	2.90 (1.10)	0.50 (1.83)	Reference (restored)	0.21 (0.13–0.30)	n/a	0.38 (0.32–0.45)	0.41 (0.33–0.48)

Output modeled for *Fundulus heteroclitus* at 2.0 trophic levels above primary producers

[a] These values represent discrimination between diet and consumer (1 trophic level). We doubled discrimination factor values and errors to simulate two trophic levels between *F. heteroclitus* and primary producers

[b] Used cross-study sulfur discrimination values (0.50±1.83) in model because individual study authors did not quantify sulfur discrimination

[c] Basal diet proportions represent the source contributions from 10,000 posterior draws generated using discrimination factors from each reference. Dietary proportions are reported as the median with 95% credibility intervals in parentheses

credence to our finding of the importance of these more palatable dietary items in salt marsh food webs, especially for fish using reference marshes.

The majority of models in our sensitivity analysis indicated that emergent native salt marsh vegetation was also an important resource at the base of the food web (23–63 %), regardless of system studied. Although the importance of salt marsh detritus to secondary production varies across systems (Deegan and Garritt 1997; Deegan et al. 2000; Galván et al. 2008, 2011), our results indicate that native vegetation is being incorporated into the food web, likely through detrital pathways driven by fungi and bacteria and consumption by intermediaries such as herbivores and benthic/epibenthic organisms (Kneib 1986, 2003; Deegan et al. 2000). Invertebrates such as the common salt marsh amphipod *Gammarus palustris* and omnivorous marsh crab *Armases cinereum* will consume live *S. alterniflora* but only after the destruction of its toughness by physical or microbial pathways (Pennings et al. 1998; Parker et al. 2008). Our data and those of others show that leaf toughness correlates with C/N (Parker et al. 2008; Jiménez et al. 2012), so the vascular plant detritus most likely to enter into salt marsh food webs in invaded marshes will have low leaf toughness and C/N ratios (i.e., *P. australis*). However, invertebrates that consume live vascular plants and detritus can be deterred from consumption if the plant contains phenolic compounds such as tannin and gallic acid (Hendricks et al. 2011).

Invasive plants can contain higher concentrations of phenolic compounds relative to native plants (Callaway and Ridenour 2004; Orr et al. 2005), a potential mechanism to deter herbivory (Grosholz 2010; Hendricks et al. 2011). It has been suggested that gallic acid, a compound secreted by *P. australis*, can inhibit the growth of native plants such as *S. alterniflora* (Rudrappa et al. 2007) and deter consumption, but recent evidence suggests that an unknown, moderately polar compound within the crude extract may deter invertebrate herbivory and native plant growth (Hendricks et al. 2011; Weidenhamer et al. 2013). We compared phenolic concentrations in the leaves of the dominant vascular plants and found a lower (but non-significant) concentration in native versus invasive plant species, which could be due to high variability in our data both within and between sites (Table 1). The coefficient of variation of the phenolic concentration in *P. australis* leaves in restricted and restored marshes was 0.40 and 0.33, respectively, relative to 0.11 and 0.16 in *S. alterniflora* leaves in adjacent reference marshes. Hendricks et al. (2011) examined the feeding preferences of a common salt marsh invertebrate, *Littoraria irrorata*, on the leaves of introduced *P. australis* and native *S. alterniflora* and found that the snail consumed 26× more *S. alterniflora* than *P. australis* even though the native plant was 1.3× tougher, suggesting a chemical deterrent against herbivory. Although *P. australis* at our study sites exhibited lower C/N and leaf toughness measurements than *S. alterniflora*, the variable phenolic concentrations and chemical constituents in *P. australis* extracts at the site level (our study; Rudrappa et al. 2007; Weidenhamer et al. 2013) may deter herbivory and its incorporation into the food web via primary consumers. This could explain the relatively high incorporation of fringing salt marsh plant material (26–55 %) relative to *P. australis* (0–27 %) in restricted marsh food webs.

Basal Diet Proportions

In salt marshes the isotopic composition of primary producers is highly influenced by environmental variables such as salinity (Peterson 1999). Dissolved inorganic carbon (δ^{13}C-DIC) is isotopically lighter (δ^{13}C depleted) in riverine water because it is derived from the remineralization of organic materials combined with carbonate from the soil; however, in marine environments δ^{13}C-DIC is enriched (~0–2.5 ‰) because it is near isotopic equilibrium with atmospheric CO_2 (Gruber et al. 1999). Therefore, primary producers that obtain δ^{13}C from their surrounding environment (such as BMA and SPM) will reflect a δ^{13}C signature that is influenced by salinity, especially in estuaries where riverine and marine waters mix. In addition, marine sulfate is the primary source of planktonic sulfur (δ^{34}S enriched), but sedimentary sulfide depletes the δ^{34}S of SPM in estuaries. Sulfur in salt marshes is often highly variable because plants, bacteria, and macroconsumers are exposed to δ^{34}S enriched seawater sulfate and δ^{34}S depleted porewater sulfide (Peterson 1999). In tidally restricted, restored, and reference marshes, primary producers and secondary consumers will be δ^{34}S and δ^{13}C enriched/depleted depending on the specific environment they reside in, so we separated the SIAR model into four marsh treatments to minimize the cross-system variability that would accompany consolidation of sources across systems to improve model output.

Our results support previous studies in invaded study systems that have linked reductions in BMA to increased shading from *P. australis* (Wainright et al. 2000; Currin et al. 2003; Weis 2005; Bushaw-Newton et al. 2008). Notably, we found that the importance of BMA as a food source declined in tidally restricted marshes (7–23 %) but was highest in reference (uninvaded) marshes where there is less shading by overhanging plants (4–35 %). Restoration enhanced the quantity of BMA within New England salt marsh food webs (1–30 %) and was intermediate to biomass quantified in restricted and reference marshes. Therefore, plant invasion and tidal restriction can reduce the availability of BMA to salt marsh consumers, but restoration can re-establish this food source over a relatively short time scale (11–22 years post-restoration).

The frequency and duration of tidal flooding can directly influence the type of intertidal production available to invertebrate assemblages and higher-level consumers (Kneib

2003). Marshes with higher tidal amplitude and frequent flooding can support a diverse and abundant invertebrate community composed of detritivores that feed on *S. alterniflora* production (Deegan and Garritt 1997) and deposit and filter feeders such as polychaetes, oligochaetes, and copepods that consume SPM deposited on flood tide (Galván et al. 2008, 2011). Daily tidal inundation of the marsh surface has been linked to enhanced phytoplankton production (~25 %) in nearshore waters due to an increase in the surface area of the estuarine euphotic zone (Haines 1977). Relative to reference marshes, SPM in tidally restricted food webs decreased from 23–48 % to 11–44 %, but increased in restored marshes (19–48 %), which could be due to enhanced flooding of the marsh surface post-restoration. Therefore, two factors that influence tidal marsh flooding at our study sites may influence phytoplankton productivity in nearshore waters and the pathways by which SPM is incorporated into salt marsh food webs.

Phragmites australis does not appear to be an important plant at the food web base at our restricted study sites. In a highly invaded tidal creek in the mid-Atlantic (>66% *P. australis*), Wainright et al. (2000) estimated that ~73 % of *F. heteroclitus* production originates from *P. australis* carbon sources. In our tidally restricted New England study sites, invasive plant cover is approximately 60–88 % but *F. heteroclitus* incorporate a lower proportion of carbon, nitrogen, and sulfur from *P. australis* (0–27 %). This low incorporation of *P. australis* into the food web may be related to phenolic concentrations, as discussed earlier, but it could also be due to decreased consumer access to the marsh platform. Tidal restriction reduces tidal amplitude and invertebrate and nekton access to the marsh surface (Warren et al. 2002; Raposa and Roman 2003), thereby inhibiting the trophic relay from marsh to nearshore food webs (Kneib 1997). Given the fact that native salt marsh plants contributed more to *F. heteroclitus* production in restricted marshes (26–55 %) than *P. australis*, it is possible that fringing marshes that typically develop along the main tidal creek in these systems are especially important to the production of salt marsh nekton (Kneib 2003).

Relative to restricted marshes, the contribution of *P. australis* to the food web decreased even further at restored marsh sites (0–15 %). This is likely due to the replacement of undersized culverts that increase marsh salinity (>25) and stunt *P. australis* growth (Roman et al. 2002; Smith et al. 2009), resulting in decreased plant cover (40–62 %) over time. Restoration of tidal flow increased food web reliance on BMA and SPM, likely due to physical changes such as decreased shading of the marsh surface and increased tidal range. Benthic microalgal productivity can rival that of *Spartina* spp. and has long been noted to be an important component of salt marsh food webs readily available to primary consumers that support higher trophic levels (Zedler 1980; Currin et al. 1995, 2003; Galván et al. 2008, 2011). Collectively, our results indicate that algae, plankton, and salt marsh detritus drive trophic support functions at our restricted, restored, and reference marsh sites. Therefore, the removal of invasive plants and restoration of ecosystem function is critically important to supporting secondary production in coastal ecosystems.

Acknowledgments We thank Rick McKinney at the Environmental Protection Agency (EPA) Atlantic Ecology Laboratory for use of the isotope ratio mass spectrometer, guidance on preparing samples, and for the interpretation of IRMS output. Many thanks to Jim Cronin and Warwick Allen at Louisiana State University for leaf chemistry analysis. The following agencies and organizations provided support to KLD: EPA STAR Graduate Fellowship (FP-91710001-0), National Oceanic and Atmospheric Administration NERR Graduate Fellowship (NA09NOS4200041), National Science Foundation (NSF) IGERT Grant to the Coastal Institute at URI (0504103), Philanthropic Educational Organization (Lellis-Dib3158688), Northeast Aquatic Plant Management Society, Rhode Island Natural History Survey and The Nature Conservancy of Rhode Island (Lellis-Dibble 05-30-09), and the URI Coastal Fellows Program. To LAM: US NSF DEB Award (1049914), URI Agricultural Experiment Station (RI00H-332, 311000-6044), and the U.S. and Czech Fulbright Commissions.

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