

ARTHROPOD FOOD WEB RESTORATION FOLLOWING REMOVAL OF AN INVASIVE WETLAND PLANT

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Abstract. Restoration of habitats impacted by invasive plants is becoming an increasingly important tool in the management of native biodiversity, though most studies do not go beyond monitoring the abundance of particular taxonomic groups, such as the return of native vegetation. Yet, the reestablishment of trophic interactions among organisms in restored habitats is equally important if we are to monitor and understand how ecosystems recover. This study examined whether food web interactions among arthropods (as inferred by abundance of naturally occurring stable isotopes of C [$\delta^{13}\text{C}$] and N [$\delta^{15}\text{N}$]) were reestablished in the restoration of a coastal *Spartina alterniflora* salt marsh that had been invaded by *Phragmites australis*.

From patterns of C and N stable isotopes we infer that trophic interactions among arthropods in the native salt marsh habitats are characterized by reliance on the dominant marsh plant *Spartina* as a basal resource. Herbivores such as delphacid planthoppers and mirid bugs have isotope signatures characteristic of *Spartina*, and predatory arthropods such as dolichopodid flies and spiders likewise have $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures typical of *Spartina*-derived resources (approximately -13‰ and 10‰ , respectively). Stable isotope patterns also suggest that the invasion of *Phragmites* into salt marshes and displacement of *Spartina* significantly alter arthropod food web interactions. Arthropods in *Phragmites*-dominated sites have $\delta^{13}\text{C}$ isotope values between -18‰ and -20‰ , suggesting reliance on detritus and/or benthic microalgae as basal resources and not on *Phragmites*, which has a $\delta^{13}\text{C}$ approximately -26‰ . Since most *Phragmites* herbivores are either feeding internally or are rare transients from nearby *Spartina*, these resources do not provide significant prey resources for other arthropod consumers. Rather, predator isotope signatures in the invaded habitats indicate dependence on detritus/algae as basal resources instead of the dominant vegetation. The reestablishment of *Spartina* after removal of *Phragmites*, however, not only returned species assemblages typical of reference (uninvaded) *Spartina*, but stable isotope signatures suggest that the trophic interactions among the arthropods were also similar in reestablished habitats. Specifically, both herbivores and predators showed characteristic *Spartina* signatures, suggesting the return of the original grazer-based food web structure in the restored habitats.

Key words: Alloway Creek Watershed, New Jersey, USA; *Phragmites*; salt marsh; *Spartina*; stable isotopes.

INTRODUCTION

Invasive plant and animal species present a mounting challenge to the diversity and function of native communities. Species alien to local habitats are becoming established at alarming rates, and the consequences of the establishment of these exotic species on the native flora and fauna are often deleterious (Vitousek et al. 1997), typically reducing native biodiversity in the invaded habitats. However, in many instances the effects of invasive species have not been rigorously documented and may have unforeseen effects on native communities, including the alteration of nutrient cycling, physical structure, and disturbance regimes (Mack and D'Antonio 1998, Lathrop et al. 2003, Windham and Ehrenfeld

2003). In addition, the replacement of native vegetation by invasive plant species can change the resource base for native consumers, potentially altering trophic structure and food web interactions (Gratton and Denno 2005).

Restoration of natural vegetation to areas that have been dominated by invasive plants is becoming an increasingly important tool in the management of natural resources and maintenance of native biological diversity (Zedler 2000, Weinstein et al. 2001). Typically, efforts target the removal of the invasive species (by herbicides or physical means). Subsequently, native vegetation either colonizes naturally or is directly planted into habitats being restored. This “bottom-up” approach focuses on the establishment of the primary producers with the expectation that the native-associated fauna will reestablish from a source pool (Palmer et al. 1997).

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Moreover, targets in restoration have historically centered on the “structural” goals of reestablishing the component species or guilds (Lockwood and Pimm 1999). However, of critical importance to the successful restoration of native habitats is not only the return of the desired flora and fauna, but also the reestablishment of the preexisting trophic interactions among the species, i.e., “functional” target (Vander Zanden et al. 2006). The mere presence of a species in a restored habitat does not ensure that it is performing the same ecological role as in an uninvaded habitat. Although censusing species and determining their relative abundance is straightforward, we require novel approaches and analytical tools to monitor the reestablishment of food web interactions in restored habitats, interactions that are essential for carrying out critical ecosystem functions, such as the movement of energy within the food web (Vander Zanden et al. 2003). In this study, we used the abundance of naturally occurring stable isotopes as a tool to examine community-wide feeding relationships in unimpacted, invaded, and restored wetlands to understand the manner in which trophic interactions among arthropod consumers are affected by an invasive plant and subsequently recover following the removal of the invasive species.

Phragmites invasion of coastal marshes

Along the northeastern and mid-Atlantic coast of the U.S. there has been a rapid expansion of *Phragmites australis* Trin ex. Stuedel (common reed) in coastal wetlands. Many brackish wetlands typically dominated by *Spartina alterniflora* Loos. are now monocultures of *Phragmites* (Weinstein and Balleto 1999). Although *Phragmites* is a natural component of wetland vegetation in Europe and the Middle East, it has been present in North America for at least 3000 years as a relatively minor component of the marsh and wetland communities (Niering and Warren 1977). Yet within the last 100 years, *Phragmites* has expanded at an unprecedented rate throughout North American wetlands. This recent expansion may in part be due to a genotype recently introduced from Europe that is rapidly invading North America (Saltonstall 2002).

There is considerable debate among scientists, managers, and the public regarding the impact that *Phragmites* invasion has on salt marsh ecosystems (Weinstein et al. 2003, Weis and Weis 2003) and on the benefits of restoring invaded marshes to *Spartina* (Teal and Peterson 2005). Studies have found both negative (Able and Hagan 2000) and positive effects of *Phragmites* (Fell et al. 1998) on marsh fauna (fish and other nekton), suggesting that certain species are more sensitive to *Phragmites* than others. Stable isotope evidence suggests that *Phragmites* can be an integral part of estuarine food webs and fish species can derive C and N when this invasive plant dominates the landscape (Wainright et al. 2000, Weinstein and Litvin 2000, Currin et al. 2003). Much less is known about the

manner in which *Phragmites* influences more terrestrial food webs and how restoration affects trophic interactions among terrestrial consumers.

In southern New Jersey at the Alloway Creek Watershed, a (>1000-ha) restoration effort commenced in 1996. A goal of this restoration was the removal of *Phragmites* to restore the native flora (*Spartina* dominated) to marsh habitats (Weinstein et al. 2001). Gratton and Denno (2005) found that free-living arthropods in *Phragmites* at Alloway Creek were dominated by detritivores/algal feeders such as collembola and chironomids, while there were significant decreases in the abundance of dominant marsh spiders such as web-building linyphiids. Yet in areas of the restoration site where *Spartina* has rapidly reestablished as the dominant macrophyte, arthropod assemblages were no different than reference (unimpacted) *Spartina* habitats. These assemblages were characterized by a diverse and abundant guild of free-living externally feeding herbivores such as planthoppers and mirid bugs. These findings suggest that the invasion of *Phragmites* has the potential to alter the trophic structure of arthropod assemblages in *Phragmites*, as indicated by large shifts in the abundance of certain feeding guilds (e.g., detritivores/algivores), but that restoration of *Spartina* can restore the native arthropod assemblages (Gratton and Denno 2005). What remains unknown, however, is whether the return of arthropod biodiversity also restores trophic linkages among species.

This study used natural abundances of stable isotopes to infer the feeding relationships among arthropod consumers within a brackish *Spartina* marsh as a monitoring tool to examine two principle questions: (1) What impact does the invasive plant *Phragmites australis* have on the trophic interactions of marsh arthropods? (2) Can trophic relationships be reestablished with the removal of *Phragmites*? Stable isotopes can offer insights into the interactions between consumers and their resources because of their predictable behavior during trophic transfers (Peterson and Fry 1987). That is, stable isotopes of carbon (^{13}C and ^{12}C , expressed as $\delta^{13}\text{C}$) remain relatively conserved as herbivores feed on plants and as predators feed on herbivores. Hence, the isotope signatures of the basal resources of a food web are propagated relatively unchanged through the consumers (Dawson et al. 2002). In contrast, stable isotopes of N (^{15}N and ^{14}N) become slightly more enriched in the heavier ^{15}N as consumers feed on their resources and thus can be used to infer trophic position within a food web: organisms more enriched in ^{15}N feed higher up in the food chain (Minagawa and Wada 1984, Vander Zanden and Rasmussen 1999).

Moreover, as *Spartina* and *Phragmites* have distinctive $\delta^{13}\text{C}$ isotope signatures due to their differing photosynthetic pathways (C_4 vs. C_3 , respectively), we were able to use stable isotopes to evaluate the effect of *Phragmites* incursion through changes in the $\delta^{13}\text{C}$

signature of resources and salt marsh arthropod consumers. Furthermore, the removal of *Phragmites* and restoration of *Spartina* allowed us to infer whether, in addition to the return of the normal arthropod fauna, trophic interactions among consumers were reestablished, as suggested by changes in isotope signatures.

MATERIALS AND METHODS

Study sites

This study was conducted in the Alloway Creek Watershed (New Jersey, Salem County, 39°30.7' N, 75°28.7' W) in the brackish portion of the Delaware Bay where a large (1138-ha) salt marsh restoration project was undertaken by the Public Service Enterprises Group (PSEG) (Weinstein et al. 1997, 2001). Details of the study site and restoration are provided elsewhere (Weinstein et al. 1997, 2001, Able et al. 2003, Gratton and Denno 2005). Briefly, in 1996 at Alloway Creek, PSEG began the removal of *Phragmites* by applications of the herbicide glyphosate with follow-up spot applications in 1997 and 2000 in areas where *Phragmites* persisted. Areas where *Spartina* was dominant were generally untreated. Most restored (i.e., treated) areas had reverted to *Spartina* within five years.

To examine arthropod food webs in invaded and restored salt marsh habitats, we sampled arthropod assemblages in four different habitat types along a 5-km stretch of the Alloway Creek restoration area: (1) reference *Spartina*, (2) restored *Spartina*, (3) mixed *Spartina*–*Phragmites*, and (4) *Phragmites*. Detailed vegetation cover maps (1–2 m² resolution) made from digital aerial photographs were available for the entire Alloway Creek restoration site from 1996 through 2000 (PSEG 2000, 2001; PSEG, 1999 permit renewal and application, New Jersey Pollutant Discharge Elimination System [NJPDES] permit number NJ0005622). From these maps we determined the history of vegetation cover and *Phragmites* invasion for a particular sampling location. “Reference” *Spartina* habitats corresponded to areas that had no historical evidence of *Phragmites* invasion (back as far as 1955 [Weinstein and Balletto 1999]) and supported arthropod assemblages representative of undisturbed *Spartina* marshes found along the Atlantic Coast (Davis and Gray 1966, Denno 1977, Döbel et al. 1990, Denno et al. 2003, Gratton and Denno 2005). “Restored” *Spartina* were areas that were previously dominated by *Phragmites* (as evident on 1996 maps) but had since reverted to *Spartina* (>80% cover) following *Phragmites* removal. “Mixed” *Spartina*–*Phragmites* habitats supported a mix of newly established *Spartina* (30–60% cover) and *Phragmites* and represented a successional transition to a monotypic stand of *Spartina*. “*Phragmites*” habitats were persistent stands of >90% *Phragmites* cover. Numerous large patches of each habitat were spatially interspersed along the Alloway Creek. We randomly selected 4–9 replicates (“sites”) of each habitat for sampling by identifying

areas with >30 m² of a particular habitat type. Sampling sites were located a minimum of 10 m from one another.

Arthropod sampling

At each replicate sampling site, arthropods were collected using a D-vac suction sampler (Rincon-Vitova Insectaries, Ventura, California, USA) fitted with a 0.04-m² sampling head (Gratton and Denno 2003). Sampling consisted of haphazardly selecting a starting point within a site and walking a 3–4 m transect while taking eight nonoverlapping (8 seconds each) samples of the vegetation with the D-vac. To sample internal or concealed feeding insects we randomly cut 15 stems from each sampling station and returned them to the laboratory for inspection. Stems were then dissected with a razor blade and internally feeding insects were collected. Arthropod samples were stored at –20°C before being identified to the lowest taxonomic category possible, usually at or below family level or to morphospecies (Oliver and Beattie 1996). Sampling occurred on 18 August 2001 when the arthropod food web was fully developed (Gratton and Denno 2003, 2005).

For stable isotope analysis, we restricted our analysis to the 4–12 most abundant taxa (cumulative abundance >80% of total arthropods in a habitat type) in each of three broad trophic groups in a particular habitat type: detritus/algal feeders, herbivores, and carnivores. The latter group was further subdivided into spiders and non-spider predators, hereafter referred to as “predators” (Appendix A). “Detritus/algal” feeders are common habitat generalists that include collembola (springtails, saprovores/fungal feeders), chironomids (midges, algal filter feeders), ephydriids (shore flies), and gammarid amphipods (scuds, both algae and detritus feeders). *Spartina* herbivores were primarily host-specific species such as delphacid planthoppers, mirids bugs, and stem-boring flies and beetles. *Phragmites* herbivores included a mealybug, aphid, and a stem-mining cecidomyiid. Predators included dolichopodid flies, velliid bugs, mirid egg predators, and predatory beetles. Spiders were treated separately from other arthropod predators because they constitute a taxonomically distinct group and generally act as top arthropod predators in marsh ecosystems (Döbel and Denno 1994, Denno et al. 2003, Finke and Denno 2004).

Stable isotope analysis

When necessary we pooled several individuals of a taxon into a single sample to provide enough material for isotope analysis (0.5–1.0 mg dry mass). This ranged from 20–50 individuals for smaller taxa such as collembola to 1–3 individuals for large spiders such as *Pardosa* sp. We calculated a mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from between two and nine replicate samples of each taxon from within each replicate sampling site. To establish the isotope signature of the resource base we also collected

plant leaf tissue (5–10 randomly selected plants, rinsed with deionized water) from the dominant vegetation at each replicate sampling site, either *Spartina* or *Phragmites*. In addition, a sample of leaf litter (thatch, rinsed with deionized water) from the marsh surface and a soil core (3 cm diameter, 5 cm depth) was returned to the laboratory. Soil samples were rinsed in deionized water and passed through a 500- μm sieve and likely included soil organic matter as well as microalgae and phytoplankton. All samples (arthropod, plant, litter, and soil) were oven-dried at 55°C for 48 h and ground to a powder using a small mortar and pestle or a Wiley Mill (plants and litter; VWR International, West Chester, Pennsylvania, USA).

Samples were analyzed for stable isotopes of C and N using a Thermo-Finnigan DELTA-plus Advantage Mass Spectrometer (Thermo Electron, Waltham, Massachusetts, USA) coupled to a Carlo Erba NC2100 Elemental Analyzer (EA; Carlo Erba, Milan, Italy) at the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff, Arizona, USA). Ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ are expressed relative to a known standard (Vienna Pee Dee Belemnite [VPDB] and atmospheric N, respectively) in per mil notation (e.g., $\delta^{13}\text{C}_{\text{sam}} = [(^{13}\text{C}/^{12}\text{C}_{\text{sam}})/(^{13}\text{C}/^{12}\text{C}_{\text{std}}) - 1] \times 1000$; subscripts “sam” and “std” refer to “sample” and “standard,” respectively). Data were normalized using four International Atomic Energy Association (IAEA) reference standards (CH6, CH7, N1, and N2). An internal laboratory standard (National Institute of Standards and Technology, NIST 1547- peach leaves) was run every 10 samples, and 10% of samples were run in duplicate. Measurement errors on the laboratory standard were approximately $\delta^{13}\text{C} = \pm 0.05\text{‰}$ and $\delta^{15}\text{N} = \pm 0.11\text{‰}$ ($\pm\text{SD}$) while measurement errors on duplicates were approximately $\delta^{13}\text{C} = \pm 0.15\text{‰}$ and $\delta^{15}\text{N} = \pm 0.19\text{‰}$ ($\pm\text{SD}$).

We used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots of arthropod groups to compare arthropod food webs in the different marsh habitats. Differences between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among habitat types were tested separately for each of the trophic groups using a mixed-model ANOVA. Each sampling site was treated as an independent replicate ($n = 4\text{--}9$) of habitat type (*Spartina*, restored *Spartina*, mixed *Spartina*–*Phragmites*, *Phragmites*), and for arthropod analyses mean isotope signatures of each taxon within sites were treated as subsamples. Separate estimates of variance were used for each habitat type if the model fit was improved (as indicated by Akaike’s Information Criterion) over a model using a pooled variance estimate (PROC MIXED, SAS; Littell et al. 1996).

In addition, in each of the four different habitat types a three-source mixing model was used to estimate the relative contribution of detritus/algal feeders, herbivores, and other predators to the diets of spiders. We used assumed fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to be 0.0‰ and 1.5‰, respectively, by relying on spider-specific

fractionation values from the literature (Oelbermann and Scheu 2002) and from laboratory feeding experiments (C. Gratton and R. F. Denno, unpublished data). In establishing the signature of the herbivore endmembers in *Phragmites*, we excluded *Spartina* herbivores that were occasionally collected in these habitats since they are transient and relatively rare (Gratton and Denno 2005) and thus unlikely to be prey of spiders in these habitats. We calculated means and 95% CI of the proportion of each end member in the diet of spiders using the ISOERROR 1.04 spreadsheet program of Phillips and Gregg (2001; available online).⁴

RESULTS

Stable isotope patterns in reference Spartina

Carbon and nitrogen stable isotope patterns suggest that arthropods within reference *Spartina* habitats are dependent in large part on *Spartina*-derived resources. *Spartina* leaf tissues and decomposing leaf litter have $\delta^{13}\text{C}$ signatures characteristic of C_4 plants (mean = -12.9‰ , Appendix B). Soil $\delta^{13}\text{C}$ values are significantly lower than plant tissue (Fig. 1A, -20‰). Herbivore $\delta^{13}\text{C}$ signatures are indistinguishable from the signature of *Spartina* foliage (Fig. 1A, -12.9‰), while predators and spiders have slightly depleted $\delta^{13}\text{C}$ signatures (-14.3‰ and -13.7‰ , respectively) compared to herbivores. In contrast, detritus/algal feeders have significantly depleted $\delta^{13}\text{C}$ (Fig. 1A, -15.5‰), indicating that this group obtains carbon from sources other than *Spartina*. The $\delta^{15}\text{N}$ patterns show an incremental fractionation of consumer $\delta^{15}\text{N}$ relative to their resources, characteristic of ^{15}N becoming more enriched as one moves up the trophic chain. Spiders as a group have the highest $\delta^{15}\text{N}$ values (13.7‰), while other invertebrate predators are slightly lower (12.9‰). On average, herbivores (11.9‰), which are mostly host-specific on *Spartina*, fractionate $\delta^{15}\text{N}$ by $+1.4\text{‰}$ relative to their host plants (10.4‰). Detritus/algal feeders are the most depleted arthropods in $\delta^{15}\text{N}$ (11.0‰ , Appendix B).

Stable isotope patterns in Phragmites

Arthropod isotope patterns in sites that become dominated with *Phragmites* are significantly different than reference *Spartina* sites (Fig. 1B, Appendix 2). *Phragmites* leaf and litter tissues have $\delta^{13}\text{C}$ signatures characteristic of C_3 photosynthesis plants (mean = -26.2‰), while soil $\delta^{13}\text{C}$ values were significantly depleted compared to *Spartina* (-23‰ ; Appendix B). Herbivore signatures, however, are very heterogeneous (Fig. 1B). Concealed-feeding *Phragmites* herbivores, such as the mealybug *Chaetococcus phragmitis* and the cecidomyiid *Lasioptera hungarica*, have carbon signatures similar to that of their host plant (-25.5‰). However, other herbivores recovered in *Phragmites* include accidental emigrants from *Spartina*, including

⁴(http://www.epa.gov/wed/pages/models/isotopes/isoerror1_04.htm)

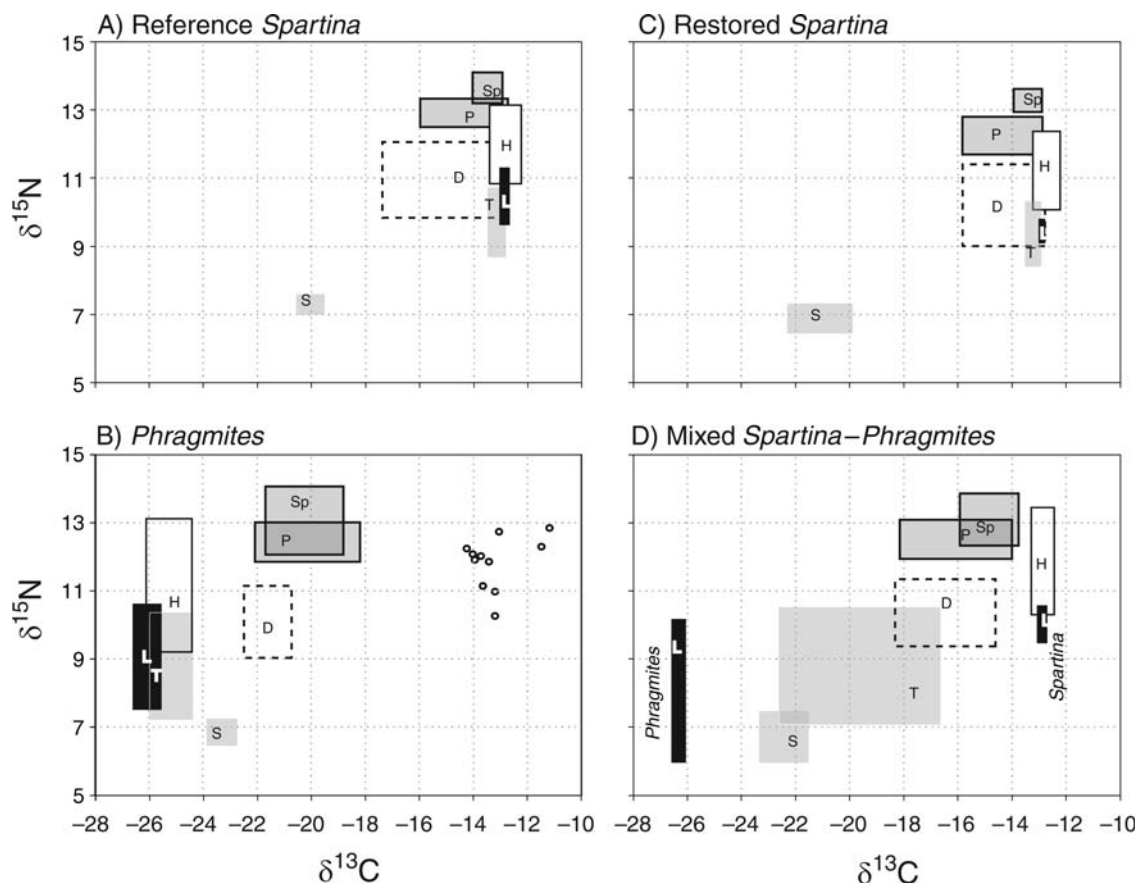


FIG. 1. Bi-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes for the major arthropod trophic groups in the main habitat types at the Alloway Creek, Salem County, New Jersey, USA, restoration site: (A) reference *Spartina*, (B) *Phragmites*, (C) restored *Spartina*, and (D) mixed *Spartina-Phragmites*. Trophic groups include H, herbivores; D, detritus/algal feeders; P, non-spider predators; and Sp, spiders. Basal resources are L, leaves of the dominant macrophytes; T, thatchy leaf litter; and S, soil. Letters are on the median of each group, and boxes bound the 25–75% interquartile range. In *Phragmites* habitats (B), accidental *Spartina* herbivores are shown as open symbols and are not included in the calculation of the herbivore median and interquartile range.

the specialist planthoppers *Prokelisia* spp. and *Megamelus lobatus*, the stem-boring fly *Cheotopsis*, and the mirid *Trigonotylus uhleri*, all of which have characteristic *Spartina* $\delta^{13}\text{C}$ signatures approximately -13‰ (Fig. 1B, circles). Detritus/algal feeders have a carbon signature that is significantly enriched relative to *Phragmites* (-21.7‰ ; Appendix B). Spiders and predators have a $\delta^{13}\text{C}$ signature significantly depleted compared to those same species collected in nearby *Spartina* habitats (-20.4‰ and -20.6‰ , respectively; Appendix B). As in *Spartina* habitats, the $\delta^{15}\text{N}$ pattern of arthropods in *Phragmites* shows an incremental trophic enrichment from detritus/algal feeders, herbivores, predators, and spiders: 9.9‰ , 11.4‰ , 12.48‰ , and 13.17‰ , respectively (Fig. 1A, Appendix B). In general, $\delta^{15}\text{N}$ values across all resource and trophic groups are similar between *Spartina* and *Phragmites*, making this isotope less informative on its own for inferring resource use by consumers.

Stable isotope patterns in restored *Spartina* and mixed *Spartina-Phragmites*

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ patterns of both resources and consumers were the same between reference *Spartina* and restored *Spartina* habitats (Fig. 1A, C, Appendix B). In contrast, spiders, predators, and detritus/algal feeders in mixed *Spartina-Phragmites* habitats (Fig. 1D) had $\delta^{13}\text{C}$ signatures that were slightly more depleted relative to reference and restored *Spartina* (Fig. 1A, C), but only spiders were significantly lower than reference *Spartina* (Appendix B). Leaf litter and soil collected in mixed habitats were intermediate between *Phragmites* and *Spartina* with regard to carbon isotope signature (Fig. 1D, Appendix B).

Mixing model analysis of spider diet

Utilizing both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of detritus/algal feeders, herbivores, and predators as end-member resources for spiders, a three-source mixing model found

TABLE 1. Mixing model estimates of proportion (mean \pm SE and 95% CI) of arthropod resources (detritus/algal feeders, herbivores, and non-spider predators) in the diets of spiders collected in four different habitat types at the Alloway Creek Restoration site, Salem County, New Jersey, USA, in August 2001.

Resources	Reference <i>Spartina</i>		Restored <i>Spartina</i>		Mixed <i>Spartina-Phragmites</i>		<i>Phragmites</i>	
	Mean \pm SE	95% CI	Mean \pm SE	95% CI	Mean \pm SE	95% CI	Mean \pm SE	95% CI
Detritus/ algal feeders	0.129 \pm 0.119	0.00–0.37	0.1272 \pm 0.138	0.00–0.40	0.4391 \pm 0.113	0.21–0.66	0.3689 \pm 0.129	0.11–0.62
Herbivores	0.5073 \pm 0.17	0.17–0.85	0.4574 \pm 0.157	0.14–0.77	0.3078 \pm 0.12	0.07–0.55	–0.13 \pm 0.15	0.00–0.16
Predators	0.3637 \pm 0.168	0.03–0.70	0.4154 \pm 0.132	0.15–0.68	0.2531 \pm 0.151	0.00–0.55	0.7654 \pm 0.11	0.55–0.98

that in reference *Spartina* habitats, herbivores (17–85%, 95% CI) and predators (3–70%) were likely the most important resources in the diet of salt marsh spiders (Table 1). Detritus/algal feeders represented a relatively small fraction (0–37%) of the diet of spiders in uninvaded habitats. In restored habitats, herbivores and predators represented the largest fraction of resources in the diet of spiders (~14–77%), with detritus/algal feeders still representing at most 40% of the spider diet (Table 1). As *Phragmites* becomes common within the salt marsh environment, the isotope signatures of spiders indicate a greater reliance on detritus/algal feeders (21–66% and 11–62% of diet in mixed and *Phragmites* habitats, respectively) with a decrease in the importance of herbivores (maximum of 55% and 16%, mixed and *Phragmites* habitats, respectively; Table 1). This pattern can also be seen in a shift in the $\delta^{13}\text{C}$ position of spiders from one suggesting use of *Spartina*-based resources (Fig. 1A) to one in which the $\delta^{13}\text{C}$ signatures of spiders are more similar to those of the detritus/algal feeders (Fig. 1B). Moreover, in *Phragmites* habitats the large difference between the $\delta^{15}\text{N}$ of detritus/algal feeders (10.1‰) and predators (12.5‰) and the high $\delta^{15}\text{N}$ of spiders (13.2‰, Fig. 1B) suggests that spiders in these habitats may be more dependent on predators relative to detritus/algal feeders (Table 1). It is important to note that the spider taxa examined in the different habitats were largely the same (Appendix A), so differences in mixing model results is not due to differences in the species examined, rather they were likely due to differences in basal resources across habitats.

DISCUSSION

Invasion by Phragmites and restoration of Spartina

The elimination of *Spartina* from salt marsh habitats with the incursion of the invasive grass *Phragmites* has significant consequences for the interactions among salt marsh arthropods. Evidence from naturally occurring patterns of C and N stable isotopes strongly suggests that arthropod food webs shift from dependence on the native plant *Spartina* to a mostly detritus-based food web in the *Phragmites*-invaded habitats. Most of the arthropods in undisturbed *Spartina* habitats have $\delta^{13}\text{C}$ signatures that resemble that of *Spartina* (Fig. 1A) and

the mixing model analysis of the top consumers (spiders) indicate little use of detritus/algal feeders as prey items (maximum of 37% diet of spiders). In contrast, although *Phragmites* does support large numbers of concealed-feeding herbivores (Gratton and Denno 2005), these herbivores are not accessible to the vast majority of predators and spiders, and there is little evidence that salt marsh predators and spiders derive much of their energy from these prey. The result is a food web that is more dependent on detritus/algal feeders and detrital resources (Fig. 1B). For example, spiders collected in *Phragmites* habitats are unlikely to derive much of their diet from herbivores (maximum of 16%) and utilize primarily other predators or detritus/algal feeders (Table 1, Fig. 1B), neither of which have a *Phragmites* or *Spartina* signature. An alternative explanation for this pattern could be that spiders are highly vagile and move readily between *Spartina* and *Phragmites* and the intermediate signature of these spiders between the two plant $\delta^{13}\text{C}$ values is reflected in the tissues of these consumers. If this were the case, then spiders collected within adjacent *Spartina* areas should also have intermediate signatures since they would also be part of this large panmictic population. Since spiders collected in *Spartina* do not have depleted $\delta^{13}\text{C}$ values, feeding on detritus-based resources is a more likely explanation of the lower $\delta^{13}\text{C}$ values observed in *Phragmites*. Consistent with this pattern is also the fact that detritus/algal feeders are the most abundant free-living arthropod prey within *Phragmites* (Gratton and Denno 2005).

The actual resource base that was likely used by the detritivore/algal-feeding group was only indirectly measured in this study (i.e., soil and thatch) as these consumers probably fed on benthic microalgae and/or phytoplankton and decaying plant tissue. In *Phragmites*, the highly depleted $\delta^{13}\text{C}$ values of detritus/algal feeders compared to those same taxa in *Spartina* suggests that they may be utilizing different carbon resources. Our analysis of soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ found isotope values (Fig. 1) similar to those Currin et al. (2003) found from this same study site for benthic microalgae on the marsh surface ($\delta^{13}\text{C} \approx -21\text{‰}$; $\delta^{15}\text{N} \approx 9\text{‰}$). Together with isotope values of microalgae from creekbanks and mudflats ($\delta^{13}\text{C} \approx -17.5\text{‰}$; $\delta^{15}\text{N} \approx 8\text{‰}$; Currin et al. 2003), these potential resource signatures significantly

overlap the isotope values of the detritus/algal-feeding trophic group examined in this study. In *Phragmites* habitats, detritus/algal feeders could also be increasing their reliance on suspended organic matter (a proxy for phytoplankton; $\delta^{13}\text{C} \approx -25\text{‰}$ to -19‰ ; $\delta^{15}\text{N} \approx 5\text{‰}$ – 8‰) which could further deplete the $\delta^{13}\text{C}$ values (Currin et al. 2003). The enrichment of $\delta^{13}\text{C}$ in detritus/algal-feeding organisms in *Spartina* (Fig. 1A, C, D; “D” group) relative to those in *Phragmites* (Fig. 1B) suggests a shift in the resource base even for these taxa not directly associated with macrophytes. These organisms may be depending on decaying macrophytes and their associated microbes to a greater extent than in *Phragmites* or on benthic microalgae with more enriched isotopic signatures (Currin et al. 2003). In general, these data support the notion that *Phragmites* resources are not directly fueling trophic interactions among arthropods in the invaded habitats, but that other forms of productivity such as benthic microalgae or suspended organic matter are the most likely basal resources for the arthropod food web. Moreover, the relatively high $\delta^{15}\text{N}$ signature of spiders in *Phragmites* habitats suggests a large proportion of their diet may be derived from other predators (intraguild prey) or possibly that spiders may be more cannibalistic in these herbivore-scarce habitats. Thus, the invasion of *Phragmites* not only alters the resource base of the arthropod food web, but also changes trophic interactions in the food web.

Habitats in which *Phragmites* was actively removed as part of the restoration program experienced a rapid return of *Spartina* (<5 yr) and with it the typically associated arthropod fauna (Gratton and Denno 2005). Furthermore, the interactions among arthropods within these newly restored habitats, as inferred by the stable isotope patterns, are also indistinguishable from those in the undisturbed *Spartina* habitats (Fig. 1C). This suggests that not only is the assemblage of arthropods reestablished with the return of the native vegetation, but so are the linkages among the species that result in similar flows of C and N within these reestablished food webs (Vander Zanden et al. 2003). Mixed *Phragmites*–*Spartina* habitats (Fig. 1D) had spider signatures that indicated a greater dependence on detritivores (Table 1) than in habitats dominated by *Spartina* (reference and restored). Mixed habitats have a slightly greater abundance of detritus/algal feeders compared to habitats with no *Phragmites* and also have higher stem densities of *Spartina* (Gratton and Denno 2005). Such a change in the habitat structure may facilitate foraging on the marsh surface by spiders (Langellotto and Denno 2004), thus enhancing the likelihood of encounter and capture of surface-dwelling detritus/algal feeders and a greater proportional representation in their diets. Notably though, as the physical structure of the habitat returns and the native species assemblages are reestablished, the feeding interactions among arthropods are also restored.

Effects of Phragmites on native food webs

The invasion of *Phragmites* into *Spartina* marshes has been shown to alter habitat structure (Windham 2001, Able et al. 2003), ecosystem processes (Windham and Ehrenfeld 2003), and faunal assemblages (Grothues and Able 2003, Gratton and Denno 2005). Habitat modification has been implicated in changes in arthropod assemblages (Gratton and Denno 2005) and mummichog (*Fundulus heteroclitus*) abundance (Able and Hagan 2003). Angradi et al. (2001) and Robertson and Weis (2005) generally found higher abundance and diversity of microinvertebrate epifauna and benthic infauna in brackish *Spartina* habitats relative to *Phragmites*, although certain groups tended to be more abundant in *Phragmites* (e.g., Collembola; Angradi et al. 2001, Talley and Levin 2001). That *Phragmites* can alter faunal communities within invaded habitats is not under dispute. However, the consequence of these faunal changes to the trophic dynamics of marsh ecosystems has remained largely unexplored.

Whether *Phragmites* marshes are functionally equivalent to uninvaded *Spartina* marshes is a subject of debate (Weis and Weis 2003). Although *Phragmites* represents a large amount of biomass in these salt marshes (Windham 2001) and may increase resources for some consumers, from the perspective of the plant-feeding arthropods this invasive plant is not functionally integrated into the local food web. We suggest this is likely due to the absence of an abundant and diverse free-living herbivore assemblage on *Phragmites* (Gratton and Denno 2005). The absence of this trophic group acts to decouple the invasive plant from the rest of the arthropod food web. In contrast, Weinstein and Litvin (2000), Wainright et al. (2000), and Currin et al. (2003), also using stable isotopes, found evidence that *Phragmites* was incorporated into the estuarine food web supporting *F. heteroclitus* (mummichog), *Morone americana* (white perch), and *Anchoa mitchilli* (bay anchovy) in the Alloway Creek and upper Delaware Bay. In habitats dominated by *Phragmites* the relative importance of benthic microalgae decreased and macrophyte production increased compared to *Spartina*, where most of the *F. heteroclitus* diet was derived from algae. This difference between the incorporation of *Phragmites* into aquatic vs. terrestrial food webs likely is due to the broader and more omnivorous host range of estuarine fish compared to the host specificity of arthropod herbivores, which are unlikely to feed on plants in two different subfamilies (Strong et al. 1984). The dominant arthropod primary consumers present on the marsh surface in *Phragmites* are those capable of consuming algae, phytoplankton, and to a lesser extent detritus, an effect that is propagated to the remainder of the arthropod food web. Thus, whether invasive species affect native food webs will vary depending on the trophic groups considered.

Stable isotopes in restoration ecology

Stable isotope approaches offer a relatively quick and inexpensive means of exploring what resources are being used by consumers (Hobson 1999). In a restoration ecology context, this can be a powerful tool for analyzing diverse assemblages under different management scenarios or states of degradation and for tracking how management strategies change the flow of C or N within food webs. Implicit in this approach is the assumption that trophic interactions are responsible for the isotope patterns that we observe among consumers. This technique has only recently been adopted in studies of invasive species (Vander Zanden et al. 1999) and ecological restoration (Currin et al. 2003, Vander Zanden et al. 2003, Moseman et al. 2004), but has not been used previously to investigate the structure of restored arthropod food webs. Stable isotopes complement the use of more traditional biodiversity data (Gratton and Denno 2005) to tell us whether feeding interactions were qualitatively similar between restored and reference marsh habitats and what the impact of an invasive plant was on the trophic relationships among native salt marsh arthropods. Stable isotopes therefore give us an indirect view of how the food web behaves within different spatial contexts (Finlay et al. 2002).

The use of stable isotopes to infer feeding interactions must be tempered by the assumptions that are made regarding how organisms utilize resources, incorporate heavy and light atoms into tissues and excrete wastes, and how rapidly tissues turn over in their isotope signatures (Gannes et al. 1997, Hobson 1999). In this study, isotope signatures were measured only once at the end of the growing season (August), albeit at a time when maximum arthropod diversity occurs in *Spartina* (Gratton and Denno 2005). We make the assumption that the isotope values of the taxa sampled reflect the resources they had been consuming over the course of the summer. This assumption is probably valid for long-lived organisms such as spiders and for host-specific herbivores, which, although having multiple generations, do not change their plants hosts. Whether this assumption is valid for all organisms in our study is unknown. Moreover, it is uncertain whether this same pattern would hold true at other times of the year. For example, spiders may have access to different resources (other prey) in the spring or late fall in *Phragmites* habitats, which were outside of the time frame of this study (Gratton and Denno 2005). Thus we cannot categorically exclude the possibility that *Phragmites* supports arthropod food webs at other times of the year. However, given the phenology of most *Spartina* arthropods (Döbel et al. 1990, Gratton and Denno 2003), this possibility seems unlikely. Moreover, since we do not have information regarding isotope patterns before restoration activities took place, it should be stressed that patterns of stable isotopes in salt marsh consumers can only be used to infer changes in food web interactions due to invasion and restoration and do not

constitute causal evidence of changes due to management actions.

CONCLUSIONS

The goal of restoration ecology is to recreate ecosystems that are structurally and functionally similar to those previously degraded or lost (Palmer et al. 1997). At the Alloway Creek restoration site from a stable isotope analysis of the arthropod assemblages, we inferred that trophic interactions among arthropods were substantially altered with the invasion of *Phragmites*. Compared to uninvaded *Spartina* habitats, *Phragmites* arthropod assemblages were not trophically linked to the dominant macrophytes, but rather to detritus and algal resources, while the *Spartina* arthropod food web was supported by the native plant. The removal of the invasive *Phragmites* was followed by the return of the dominant native vegetation (*Spartina*) and reestablishment of arthropod species assemblages (Gratton and Denno 2005). The rapid reestablishment of this arthropod assemblage is in part due to the life history traits of many of the dominant arthropods in *Spartina* that have high dispersal capabilities and short generation times and are multivoltine (Döbel et al. 1990, Denno et al. 2003). Thus, the trophic structure of this assemblage can rebuild quickly and, as inferred from the stable isotope data, feeding interactions can also rapidly reestablish. The stable isotope approach was made possible by the differences in photosynthetic pathways between the native *Spartina* (C₄) and alien *Phragmites* (C₃) that allowed the discrimination of carbon sources in consumers. Thus, for arthropod assemblages, it was possible to restore trophically comparable food webs within a short period of time through the reestablishment of native vegetation.

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APPENDIX A

A taxon list of dominant arthropods in different trophic categories analyzed in each habitat type at the Alloway Creek restoration site, Salem County, New Jersey, USA, in August 2001 (*Ecological Archives* A016-026-A1).

APPENDIX B

Mean of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and summary of mixed-model ANOVA for basal resources and arthropod trophic groups analyzed in each habitat type at the Alloway Creek restoration site in August 2001 (*Ecological Archives* A016-026-A2).