
Restoration of Arthropod Assemblages in a *Spartina* Salt Marsh following Removal of the Invasive Plant *Phragmites australis*

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Abstract

Invasive plants are one of the most serious threats to native species assemblages and have been responsible for the degradation of natural habitats worldwide. As a result, removal of invasive species and reestablishment of natural vegetation have been attempted in order to restore biodiversity and ecosystem function. This study examined how native arthropod assemblages, an abundant and functionally important group of organisms in many ecosystems, are affected by the incursion of the invasive wetland plant *Phragmites australis* and if the restoration of the native vegetation in brackish *Spartina alterniflora* marshes results in the reestablishment of the arthropod community. The invasion of *Phragmites* into a coastal *Spartina* marsh in southern New Jersey seriously altered arthropod assemblages and trophic structure by changing the abundance of trophic groups (detritivores, herbivores, carnivores) and their taxonomic composition. Herbivore assemblages shifted from the dominance of external free-living specialists (e.g., planthoppers) in *Spartina* to concealed feeders in *Phragmites* (stem-feeding cecidomyiids). Moreover, free-living arthropods in *Phragmites* became dominated by detritivores such as Collembola and chiro-

nomids. The dominant marsh spiders, web-building linyphiids, were significantly reduced in *Phragmites* habitats, likely caused by differences in the physical environment of the invaded habitats (e.g., lower stem densities). Thus, trophic structure of arthropod assemblages in *Phragmites*, as seen in the large shifts in feeding guilds, was significantly different from that in *Spartina*. Removal of *Phragmites* with the herbicide glyphosate resulted in the rapid return of *Spartina* (≤ 5 yrs). Moreover, return of the dominant vegetation was accompanied by the recovery of most original habitat characteristics (e.g., live and dead plant biomass, water flow rate). The arthropod assemblage associated with *Spartina* also quickly returned to its pre-invasion state and was not distinguishable from that in uninvaded *Spartina* reference sites. This study provides evidence that the reestablishment of native vegetation in areas previously altered by an invasive plant can result in the rapid recovery of the native arthropod assemblage associated with the restored habitat.

Key words: Alloway Creek, arthropod community structure, habitat restoration, invasive plants, *Phragmites*, salt marsh, *Spartina*, trophic structure.

Introduction

Invasive plants are one of the most severe threats to native species assemblages and have been responsible for the degradation of natural habitats worldwide (Vitousek et al. 1997). Invasive plants can directly influence native communities by outcompeting native vegetation as well as by altering nutrient availability and cycling (Windham & Lathrop 1999), by affecting soil erosion and accretion (Lacey et al. 1989; Windham 2001), or by modifying disturbance regimes (Mack & D'Antonio 1998). As a result, restoration of native habitats via the removal of alien invasive plants is becoming an important tool in the management of natural resources and ecosystem services

(Weinstein et al. 1997). Fundamental to our understanding of how to manage invasive species in the environment is documenting the impact that they have on native communities and determining if native communities can be restored following removal of invasives.

Restoration of natural communities often relies on the assumption that with the reestablishment of natural vegetation, either by natural means or transplanting (Zedler & Callaway 1999), will come the reestablishment of the fauna normally associated with the habitat. Although restoration objectives usually include both reestablishment of native vegetation and the entire food web that it supports (Palmer et al. 1997), emphasis is often placed on monitoring the return of only a few target groups such as plants (Zedler & Callaway 2000). In particular, we have little information of how arthropod assemblages are affected by the reintroduction of native flora (but see, Majer et al. 2002), despite the fact that native arthropods play important functional roles in their native habitats (Crooks 2002).

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This study examined (1) how native arthropod assemblages changed with the invasion of *Phragmites australis* (hereafter *Phragmites*), an aggressive plant invading the salt marshes along the east coast of North America and (2) how assemblages of arthropods recovered following *Phragmites* removal and the reestablishment of *Spartina alterniflora* (hereafter *Spartina*), the dominant salt marsh macrophyte in Atlantic coast marshes (Ewanchuk & Bertness 2004). Because many arthropods are intimately associated with the native vegetation or the microhabitats that it creates, a decrease in the dominant plant species and alteration of the physical characteristics of a habitat is generally expected to have negative consequences for the native fauna. For example, *Phragmites* habitats have lower soil salinity, lower water level, less pronounced microtopographic relief, increased flow and sediment deposition, and higher redox potentials compared with neighboring *Spartina* communities (Windham & Lathrop 1999; Bart & Hartman 2000; Able et al. 2003). Because marsh arthropods are sensitive to a variety of plant and habitat variables such as soil characteristics (Scatolini & Zedler 1996; Talley & Levin 2001; Levin & Talley 2002), plant quality (Gratton & Denno 2003), habitat structure (Langellotto & Denno 2004), habitat patchiness (Denno & Grissell 1979), and the presence of higher trophic levels (Posey et al. 1999; Meyer et al. 2001; Denno et al. 2003), they make ideal indicators of the impact of *Phragmites* invasion on community change and of the efficacy of restoration measures on the recovery of the *Spartina* habitats.

Moreover, there has been recent concern regarding the unprecedented expansion of *Phragmites* in North American wetlands (Galatowitsch et al. 1999; Weinstein et al. 2003). Although *Phragmites* has been a minor component of marsh vegetation for at least 3,000 years (Niering & Warren 1977), the recent spread has resulted in the displacement of other dominant marsh plants such as the Cordgrass (*Spartina alterniflora*). Invasion of *Phragmites* has been explained in terms of increased coastal disturbance, pollution, and development, changes in salinity and sulfide concentrations in wetland soils, and recently introduced aggressive genotypes (Marks et al. 1994; Chambers et al. 1999, 2003; Windham & Lathrop 1999; Bart & Hartman 2000; Meyerson et al. 2000; Bertness et al. 2002; Saltonstall 2002). Although *Phragmites* stands are considered important wildlife habitats in Europe (Tscharntke & Greiler 1995), there is considerable debate regarding the impact of *Phragmites* in North American wetlands (Marks et al. 1994; Weinstein & Balleto 1999; Meyer et al. 2001), with studies finding positive (Fell et al. 1998) and negative effects on marsh fauna (Benoit & Askins 1999; Able & Hagan 2000; Able & Ragan 2003). However, there is neither data on how terrestrial arthropod communities in *Spartina* are influenced by *Phragmites* invasion nor information on whether assemblages recover following extirpation of *Phragmites*. The goal of this study was to provide such information.

Materials and Methods

Study Sites

This study was conducted in the Alloway Creek Watershed (Salem County, New Jersey, lat 39°30.7'N, long 75°28.7'W) in the brackish portion of the Delaware Bay where a large (1,138 ha) salt marsh restoration project was undertaken by Public Service Enterprises Group (PSEG) (Weinstein et al. 1997, 2001). In 1996 at Alloway Creek, PSEG began the removal of *Phragmites* via ground and aerial applications of glyphosate and surfactant, followed by burning the dead standing crop. Areas where *Phragmites* reappeared were treated again in 1997 with follow-up spot applications of glyphosate in 2000. Areas where *Spartina* was dominant were generally untreated. Additional site information is provided in Wainright et al. (2000), Weinstein et al. (2001), Able et al. (2003).

To examine the effect of *Phragmites* invasion and habitat restoration on native arthropod assemblages, we sampled replicate sites of five different habitat types along a 5-km stretch of the Alloway Creek restoration area: (1) reference *Spartina* ($n = 11$); (2) restored *Spartina* ($n = 12$); (3) mixed *Spartina-Phragmites* ($n = 12$); (4) *Phragmites* ($n = 12$); and (5) long-standing *Phragmites* stands ($n = 5$) that had never been treated with herbicides. Taken together, these habitats provided the framework to examine the effect of *Phragmites* invasion on *Spartina* arthropod communities (e.g., contrast of *Phragmites* and reference *Spartina* habitats) as well as the ability of arthropods to become reestablished following the return of *Spartina* (e.g., contrast of reference vs. restored *Spartina*). Mixed *Spartina-Phragmites* habitats offered a snapshot of the intermediate condition between *Phragmites* removal and complete *Spartina* restoration.

Detailed vegetation cover maps (1- to 2-m² resolution) made from digital aerial photographs were available for the entire Alloway Creek Restoration Site from 1996 through 2000 (PSEG 1999, 2000, 2001). From these maps, and less detailed vegetation cover maps dating back to 1955 (Weinstein and Balleto 1999), we determined the history of vegetation cover and *Phragmites* invasion for a particular sampling station. "Reference" *Spartina* habitats corresponded to areas that had no historical evidence of *Phragmites* invasion (back as far as 1955) and supported arthropod assemblages representative of pristine *Spartina* marshes found along the Atlantic coast (Davis & Gray 1966; Denno 1977; Döbel et al. 1990; Denno et al. 2003). "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. Many areas previously dominated by *Phragmites* continued to receive spot applications of glyphosate through 2000, and some areas existed as unvegetated mud flats before *Spartina* reestablished (PSEG 1999, 2000, 2001). However, most restored areas reverted to *Spartina* cover within 5 years. "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 greater than 90% *Phragmites* cover that were treated but not extirpated by herbicide applications. Finally, “long-standing” *Phragmites* included stands of untreated *Phragmites* adjacent to the Alloway Creek restoration area and served as unsprayed reference *Phragmites*. We haphazardly located a sampling station within replicates of these habitat types ($n = 5\text{--}12$) by identifying areas with greater than 30 m² of a particular habitat type. Sampling stations were a minimum of 10 m from each other, with the location of habitat types spatially interspersed among each other within the Alloway Creek system.

Arthropod Sampling

At each sampling station, arthropods were collected using a D-vac suction sampler (Rincon-Vitova Insectaries, Ventura, CA, U.S.A.) fitted with a 0.04-m² sampling head (Gratton & Denno 2003). Sampling consisted of haphazardly selecting a starting point within a station and walking a 3- to 4-m transect while taking eight nonoverlapping (8 seconds each) samples of the vegetation with the D-vac (approximately 0.32 m² of vegetation sampled). All stations were sampled three times over the course of a summer (16 June, 7 July, 18 August 2001). Arthropod densities were summed and are reported as total number of individuals per square meter. Sampling in *Phragmites* became progressively more difficult because plants grew to greater than 1.5 m. As a result, we sampled *Phragmites* by placing a 56-cm² quadrat (approximately 0.32 m²), forcing the contained vegetation to the ground, and vacuuming it repeatedly for 30 seconds.

Internal or concealed-feeding insects could not be estimated using vacuum sampling. Thus, 15 randomly selected stems from each sampling station were cut at the base and taken to the laboratory for inspection. Stems and leaves were examined carefully for scale insects or leafminers. Stems were then dissected with a razor blade, and internally feeding insects were counted and collected. For gregarious insect species (i.e., those species that had large aggregations of larvae, range of 10–60 individuals), the average number of larvae occupying each stem internode was calculated from a subset of stems. Subsequently, the number of internodes occupied were counted and multiplied by the average number of larvae per internode. This gave an estimate of the total number of larvae per stem. The density (number of individuals/m²) of these internal and concealed feeders was calculated by multiplying the number of individuals per stem by the average number of stems per square meter at that station.

Arthropod samples, stored in 70% ethanol, were identified to family level or below or to morphospecies (Oliver & Beattie 1996). The 153 different taxa collected (Appendix A) were assigned to broad trophic groups (detritivore, herbivore, carnivore) based on the literature

or our knowledge of the biology of the arthropods (Denno et al. 2002; Gratton & Denno 2003). We further subdivided each trophic group into feeding guilds. Detritivores were categorized as either (1) scavengers/shredders or (2) filter feeders, and herbivores were pooled into either (3) free-living chewers; (4) free-living sap feeders; or (5) concealed chewers. For the purpose of analyses, free-living chewing and sap-feeding guilds were combined. Carnivores were divided into (6) predators; (7) parasitoids; or (8) spiders. Spiders were treated separately from other arthropod predators because they constitute a taxonomically distinct group with a consistent feeding mode (extraoral digestion) and generally act as top arthropod predators in marsh ecosystems (Döbel et al. 1990; Denno et al. 2003). Given the diversity of spider taxa, these were further categorized into two subguilds, either (9) web builders or (10) hunters.

Site Characteristics

On the same dates on which arthropods were sampled (see above) and at each sampling station, we measured various environmental characteristics. We measured pore-water salinity by extracting a small soil core (top 2 cm), centrifuging the core, and assessing a drop of supernatant using a hand-held salinity refractometer (VWR International, West Chester, PA, U.S.A.). We used a plaster dissolution method to measure relative rates of water movement through a site (modified from Angradi & Hood 1998). We pinned preweighed plaster casts (161 g) to the marsh surface at each site, and recovered them approximately 1 month later. We then rinsed the casts of superficial silt, air dried them, and reweighed them to determine mass loss per day. A seasonal average ($n = 3$ dates) of pore-water salinity and plaster dissolution was calculated for each sampling station.

At the end of the growing season (September), after plants reached peak biomass (Windham 1995), we determined aboveground biomass. First, we estimated aboveground biomass indirectly by counting the number of stems in three haphazardly placed, 0.25-m² quadrats and estimating stem density per square meter at each sampling station. From each sampled quadrat, we randomly selected 15 stems and dried them at 60°C for 48 hours. We calculated an average live weight per stem and estimated total aboveground biomass (live aboveground biomass/m²) by multiplying average stem mass (g dry weight/stem) × stem density (stems/m²). Second, from a subset of sites (*Phragmites*, $n = 9$ and *Spartina*, $n = 14$), we calculated total aboveground biomass by clipping all stems within a 0.25-m² quadrat placed in each sampling site. From these samples, we counted all plant stems, separated live and dead (litter) aboveground biomass, and dried samples at 60°C for 48 hours. Aboveground biomass was calculated by weighing the live aboveground biomass from the harvest (“direct” estimate). In addition, we also estimated biomass using the “indirect” estimate described above for the same plots. Species-specific regressions (*Phragmites*, $r^2 = 0.87$;

Spartina, $r^2 = 0.66$) between the actual biomass measured (direct measurement) and biomass estimated using the indirect method were used to adjust indirect biomass estimates taken at other sites. From the harvested plant sample, we also calculated total leaf litter (g dry weight dead biomass/m²), and live plant tissue was analyzed for percent N content using a CHN-automated analyzer (Leco, Inc., St. Joseph, MO, U.S.A.). Finally, a sample of soil taken from the top 5 cm of sediment (passed through 250- μ m sieve and dried at 60°C for 48 hours) was analyzed for percent C and percent N.

Statistical Analyses

Univariate diversity indexes were used to examine differences in arthropod assemblages between habitats. For each site, we calculated N (total abundance of arthropods), S (total species/taxon richness), and species/taxon richness as a function of the number of individuals sampled (rarefaction index). In addition, we calculated a Shannon diversity index (H') and Pielou's evenness index (J'). Because conclusions are identical whether S or rarefaction index and H' or J' are examined, we will only present S and H' . Differences between habitats were tested by analysis of variance (ANOVA), and pairwise tests were conducted by Tukey's honestly significant difference.

Multivariate analyses were used to examine differences in the arthropod species assemblage between habitats. For all pairs of sites, we first computed a Bray–Curtis similarity index on the square root–transformed abundance of each taxon, from which a rank-similarity matrix was constructed (Clarke & Greene 1988). Nonmetric multidimensional scaling (MDS) was then used to create a graphical representation of the between-site rank-similarity matrix. The MDS algorithm plots sites that are most similar (based on their rank similarities) closer to each other in a two-dimensional ordination space, whereas sites that are more different are placed further apart. As the MDS procedure is known to be influenced by outlying points, the procedure was rerun using data from only the *Spartina* sites. An independent assessment of the site groupings was performed by cluster analysis (group average method) on the Bray–Curtis similarity matrix. Cluster membership of sites with greater than 50% similarity were overlaid on the MDS plot.

To test statistically for differences in arthropod assemblages between habitats, randomization tests were used using the R test statistic, which evaluates differences in rank similarity among replicate sites within a habitat to the average rank similarity arising from all pairs of sites between habitats (Clarke & Greene 1988; Manly 1997; see Clarke & Warwick 2001, for details). A value of $R = 1$ implies that all replicates within a habitat are more similar to each other than to any replicate from different habitats. $R \approx 0$ under the null hypothesis that similarities between replicate sites within and between habitats are the same. For each randomization, habitat type was randomly

assigned to each site and a new R statistic computed (repeated 999 times). The probability (p) of randomly observing values of R greater than or equal to the value calculated from the original (unshuffled) data was calculated. Pairwise comparisons between habitats were evaluated using a Bonferroni adjustment of the critical value alpha ($\alpha_{\text{critical}} = 0.05/10 = 0.005$). Similarities among habitats were calculated using a Bray–Curtis similarity index for square root transformed and presence–absence (0/1) transformation of taxon abundance. In addition, to determine if certain groups of arthropods were more affected than others across the different habitats sampled, analyses were repeated for similarity matrices computed for taxa within each trophic group, guild, and subguild separately. MDS and randomizations (ANOSIM procedure) were carried out using PRIMER software (version 5.2, PRIMER-E, Ltd., Plymouth, U.K.; Clarke & Warwick 2001). Taxa responsible for major differences between habitats were identified using the SIMPER procedure on PRIMER software. This procedure examines the overall percentage of contribution each taxon makes to the average dissimilarity between groups (Clarke & Warwick 2001).

Variation in environmental parameters (aboveground live and dead biomass, stem density, leaf percent N, soil percent N and percent C, salinity, and plaster weight loss) between habitats was examined using ANOVA and multiple comparisons using Tukey's HSD. All univariate analyses were performed in JMP 5.0 (SAS Institute 2003).

Results

Differences in Abundance, Diversity, and Community Structure Between Invaded and Restored Habitats

Three broad patterns emerged from analyses of arthropod assemblages across habitats (Fig. 1). First, arthropod assemblages in *Spartina*-containing habitats were not significantly different from each other. Both MDS plots and cluster analyses place sites containing *Spartina* (reference, restored, and mixed) close to each other in ordination space, indicating that the arthropod communities associated with these habitats are more similar to each other than to the ones containing *Phragmites* (Fig. 1A). There were no differences in arthropod abundance or any index of species diversity between reference, restored *Spartina*, or mixed *Spartina*–*Phragmites* habitats (Table 1), and randomization tests of species similarity matrices do not reject the hypothesis that arthropod assemblages found in reference and restored *Spartina* are different ($R = 0.09$, $p = 0.062$, $\alpha_{\text{critical}} = 0.005$). Second, in *Phragmites* habitats, species richness and diversity were lower (Table 1) and arthropod assemblages were significantly different from those associated with *Spartina* and long-standing *Phragmites* sites (Fig. 1A, $R = 0.75$ – 0.82 , $p < 0.001$). Finally, the arthropod community associated with long-standing *Phragmites* habitats (i.e., areas never treated with glyphosate) was most different with respect to those in all other

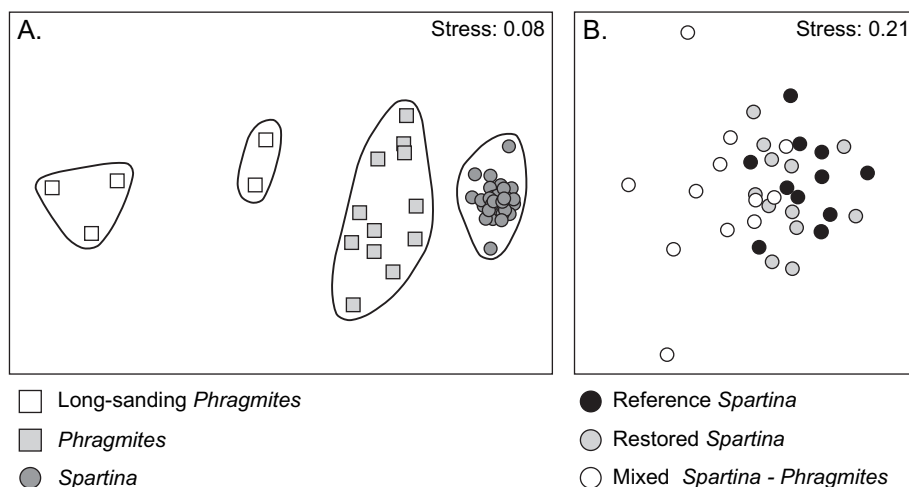


Figure 1. MDS plot of between-site rank-similarity matrix (Bray–Curtis, square root–transformed arthropod abundance) for (A) all sites and (B) for *Spartina*-containing sites only (i.e., reference, restored, and mixed). The relative distance between points (sampling stations) within the ordination space represents the degree of similarity of arthropod assemblages between sampling sites (points closer together have more similar species assemblages). Stress indexes are a measure of fit between the rank-similarity matrix and the two-dimensional representation of the similarity matrix (<0.10 excellent fit). Lines around points in A are groupings independently determined by cluster analysis (group average method, >50% similarity).

habitats, and it showed substantial within-habitat heterogeneity as well (Fig. 1A, $R > 0.99$, $p < 0.001$). Species richness, diversity, and abundance was about one-third that of reference *Spartina* habitats (Table 1).

Differences in Trophic Structure Between Invaded and Restored Habitats

The overall differences in species assemblages between *Spartina* and *Phragmites* habitats were reflected in changes in the relative abundance of particular trophic groups (Fig. 2). In general there were no differences in any trophic categories between reference and restored *Spartina* habitats (Fig. 2, $R = -0.40$ to 0.13 , $p = 0.06$ – 0.74). A closer examination of *Spartina* habitats (Fig. 1B), however, revealed that mixed *Spartina*–*Phragmites* habitats

had slightly different species assemblages than reference *Spartina* (Fig. 2, $R = 0.214$, $p = 0.001$). In particular, mixed sites had a slightly different assemblage of concealed-feeding herbivores (e.g., the absence or rarity of *Languria taedata* and *Haliopsis spartinae*, Appendix A) and web-building spiders than monotypic stands of *Spartina* (restored and reference, Appendix A). In addition, the numerically dominant spider in reference *Spartina*, *Grammonota trivittata* (approximately 1,386 individuals/m²), was only half as abundant in mixed habitats (approximately 550 individuals/m², Appendix A). Overall, the structure of other feeding guilds, such as predators and parasitoids, was not significantly different among the three *Spartina*-containing sites ($R = -0.06$ to 0.1 , $p = 0.03$ – 0.84).

More conspicuous were differences in trophic structure between *Spartina* and *Phragmites*. *Phragmites* herbivores,

Table 1. Summary of univariate diversity indexes (mean \pm SEM) and ANOVA F test for arthropod assemblages collected in summer 2001 in reference *Spartina*, restored *Spartina*, mixed *Spartina*–*Phragmites*, *Phragmites*, and long-standing *Phragmites* habitats at the Alloway Creek Restoration Site (New Jersey).

Habitat	n^a	Abundance (N) ^b	Richness (S) ^c	Shannon (H') ^d
Reference <i>Spartina</i>	11	3,085.87 \pm 248.84 a	78.55 \pm 2.10 ab	3.28 \pm 0.06 a
Restored <i>Spartina</i>	12	3,345.14 \pm 223.14 a	82.67 \pm 2.24 a	3.34 \pm 0.05 a
Mixed <i>Spartina</i> – <i>Phragmites</i>	12	2,786.76 \pm 176.62 a	83.00 \pm 2.19 a	3.31 \pm 0.09 a
<i>Phragmites</i>	12	2,766.71 \pm 427.14 a	73.17 \pm 2.17 b	2.67 \pm 0.18 b
Long-standing <i>Phragmites</i>	5	1,154.56 \pm 245.47 b	33.80 \pm 4.72 c	1.62 \pm 0.35 c
$F_{[4,47], p}$		4.94, 0.002	41.86, <0.0001	19.58, <0.0001

Column means with different letters indicate significant differences (Tukey's HSD, $p < 0.05$).

^aNumber of sites sampled in each habitat.

^bCumulative number of individuals (per m²) collected over season.

^cTotal number of species.

^dShannon diversity index, $H' = -\sum_i p_i \ln(p_i)$, p_i is proportion of total of i th species.

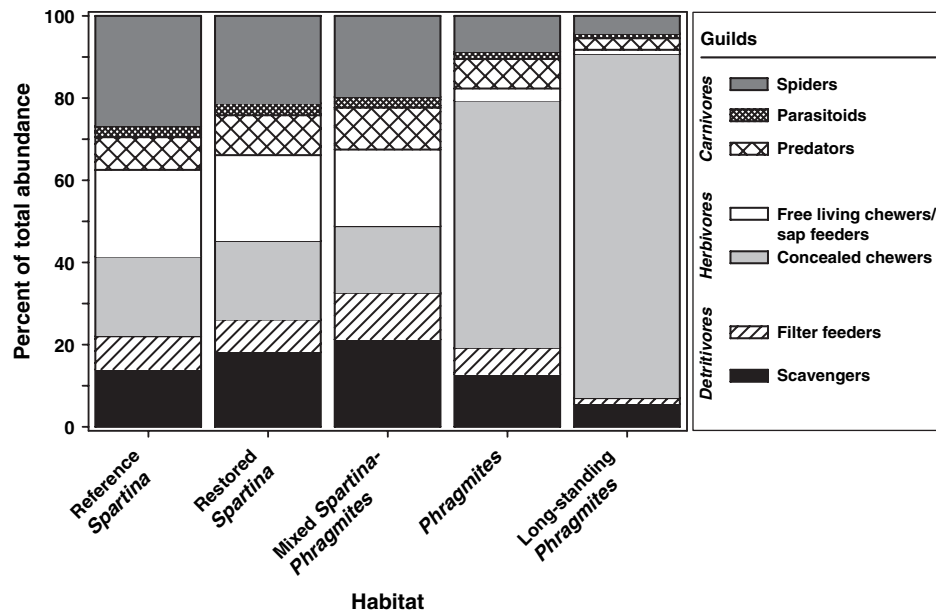


Figure 2. Proportion of total abundance of arthropod trophic groups collected in reference *Spartina*, restored *Spartina*, mixed *Spartina-Phragmites*, *Phragmites*, and long-standing *Phragmites* habitats at the Alloway Creek Restoration Site (Salem County, NJ) in summer 2001. Arthropods are categorized as carnivores (spiders, parasitoids, predators), herbivores (free-living and concealed), and detritivores (filter feeders and scavengers).

for example, were dominated by concealed, stem-feeding herbivores (62% of total abundance), dominated by one species of stem-feeding fly, *Lasioptera hungarica* (Cecidomyiidae, Appendix A), whereas *Spartina* had a diverse assemblage of host-specific, free-living herbivores such as the planthoppers, *Prokelisia* spp. and *Megamelus lobatus*; the mirid bug, *Trigonotylus uhleri*; as well as a stem-boring fly, *Chaetopsis* sp. These herbivores were virtually absent from *Phragmites* (Appendix A). Excluding the numerically abundant concealed feeders of *Phragmites* (Fig. 2), arthropods in *Phragmites* habitats were mostly detritivores (46%) and carnivores (45%, primarily generalist predators), followed by free-living herbivores (7%). In contrast, detritivores, herbivores, and carnivores (mostly spiders) represented 22, 32, and 45%, respectively, of total arthropod abundance in reference *Spartina*, suggesting a significant shift in trophic structure between the invaded and native habitats. Differences in the assemblage of the carnivore groups were mostly attributable to differences in spider assemblages between the two habitats: web builders (mostly *G. trivittata*) were 80% less abundant in *Phragmites* than in *Spartina*, whereas hunting spiders (e.g., lycosids and clubionids) were only slightly less abundant (25%). Assemblages of other carnivores (i.e., predators and parasitoids) also differed between *Phragmites* and *Spartina* habitats ($R = 0.28-0.55$, $p = -0.001$ to 0.002). For example, predators were only about half as numerous in *Phragmites* (approximately 226 individuals/m² vs. 478 individuals/m² in reference *Spartina*), and taxa such as *Achalca* sp. (Dolichopodidae), the most common nonspider carnivore in *Spartina* (approximately 237 individuals/m²), was rare in *Phragmites* (approximately 29 individuals/m², Appendix

A). Detritivores were the only trophic group whose species assemblage did not differ significantly between *Phragmites* and *Spartina* sites ($R = 0.2-0.16$, $p = 0.01-0.33$). Detritivores common to all habitats included *Collembola*, *Gammarus* sp., chironomids, and ephydrid flies.

Environmental Variables

Reference *Spartina* habitats did not differ from restored *Spartina* with regard to most site characteristics (Table 2). Reference *Spartina* sites, however, tended to have lower stem densities than either restored *Spartina* or mixed *Spartina-Phragmites* habitats. In addition, mixed habitats experienced less plaster mass loss than reference *Spartina* habitats. In general, *Phragmites* habitats were characterized by low stem density and long-standing *Phragmites* had higher water flow rates (as measured by plaster dissolution) and lower soil percent N than *Spartina* (Table 2). *Phragmites* leaves had significantly higher total leaf percent N than *Spartina*, and although total aboveground biomass of *Phragmites* tended to be higher, there was significant variation among sites. There were no differences in salinity and total soil percent C among habitats.

Discussion

Influence of *Phragmites* Invasion on Marsh Arthropod Assemblages

The progressive invasion of *Phragmites* into salt marsh habitats alters plant species composition and physical structure of the habitat and radically changes arthropod

Table 2. Environmental variables (mean \pm SEM) and ANOVA *F* test for measurements taken in the summer of 2001 in reference *Spartina*, restored *Spartina*, mixed *Spartina*–*Phragmites*, *Phragmites*, and long-standing *Phragmites* habitats at the Alloway Creek Restoration Site (New Jersey).

Habitat	Stem Density (no./m ²)	Aboveground Live Biomass (g dry weight/m ²)	Litter Biomass (g dry weight/m ²)	Total Leaf N (%)	Salinity (ppt) ^a	Plaster Mass Loss (g/day) ^a	Total Soil N (%)	Total Soil C (%)
Reference <i>Spartina</i>	289.23 \pm 16.99 b	1,071.45 \pm 150.79	316.37 \pm 31.15 b	1.47 \pm 0.09 a	1.79 \pm 0.13	1.86 \pm 0.16 b	0.46 \pm 0.03 ab	5.09 \pm 0.34
Restored <i>Spartina</i>	395.10 \pm 31.94 a	1,068.41 \pm 147.58	333.57 \pm 67.63 b	1.50 \pm 0.15 a	1.94 \pm 0.13	1.50 \pm 0.17 bc	0.44 \pm 0.01 ab	4.75 \pm 0.17
Mixed <i>Spartina</i> – <i>Phragmites</i>	402.04 \pm 28.99 a	825.77 \pm 102.20	171.53 \pm 81.22 b	1.51 \pm 0.06 a	2.14 \pm 0.13	1.20 \pm 0.08 c	0.52 \pm 0.04 a	5.58 \pm 0.54
<i>Phragmites</i>	153.27 \pm 24.22 c	1,021.90 \pm 223.44	502.62 \pm 167.01 b	2.71 \pm 0.15 b	2.00 \pm 0.21	1.30 \pm 0.13 c	0.47 \pm 0.04 ab	5.21 \pm 0.32
Long-standing <i>Phragmites</i>	90.59 \pm 30.36 c	2,267.81 \pm 927.42	1,366.36 \pm 142.44 a	2.59 \pm 0.08 b	1.53 \pm 0.03	2.94 \pm 0.28 a	0.35 \pm 0.01 b	3.86 \pm 0.14
<i>F</i> _{[4,47], <i>P</i>}	22.2, <0.0001	1.46, 0.23	12.25, <0.0001	29.52, <0.0001	1.57, 0.20	13.32, <0.0001	3.03, 0.04	2.26, 0.10

Column means with different letters indicate significant differences (Tukey's HSD, *p* < 0.05).

^aAverage of measurements taken three times over the course of the summer. Other variables were measured once at the end of the growing season (September).

assemblages native to these habitats (Fig. 1A). Yet, the removal of *Phragmites* by herbicide application resulted in the rapid return of *Spartina* stands with an associated arthropod assemblage not distinguishable from that in uninvaded *Spartina* sites (Fig. 1B). Species diversity, abundance, and overall assemblage structure in restored *Spartina* were not statistically different from those in reference habitats less than 5 years after removal of *Phragmites*. In general, these findings support the view that reestablishment of native vegetation in areas previously altered or dominated by an invasive plant can result in rapid restoration of a significant component of native fauna, namely, the arthropod assemblage (Williams 1993; Palmer et al. 1997).

Changes in the trophic structure of arthropod assemblages accompany the invasion of *Phragmites*. In *Phragmites*, the lack of free-living herbivores, reduced predator abundances, differences in composition of the spider guilds, and dominance of detritivores suggest that trophic structure is significantly different than that in the native *Spartina* habitats. Because the numerically most abundant *Spartina* herbivores in this study and other Atlantic coast marshes are host specialists such as *Prokelisia* planthoppers and the mirid bug *Trigonotylus uhleri* (Davis & Gray 1966; Denno 1977; Denno et al. 2003), the displacement of *Spartina* by *Phragmites* eliminates these important salt marsh consumers. In contrast, *Phragmites* herbivores are dominated by concealed feeders, a guild dominated by one stem-feeding species. Of the few free-living herbivores occasionally found in *Phragmites*, most were transients from *Spartina* habitats. Thus, the structure of the herbivore guild shifted from external free-living feeders in *Spartina* to internal concealed feeders in *Phragmites* likely altering the availability and distribution of prey for arthropod carnivores.

The composition of the carnivore assemblages also changed with the incursion of *Phragmites*. In this study, notably absent from *Phragmites* was *Grammonota trivittata* (Linyphiidae), the numerically dominant spider species in *Spartina* (see also, Döbel et al. 1990). Alteration of the physical environment on the marsh could influence species that are affected by habitat structure, such as spiders (Langellotto & Denno 2004). The vegetative structure of *Phragmites* is significantly different from that of *Spartina*. *Phragmites* grows as large-diameter stems spaced far apart, whereas *Spartina* grows with small-diameter stems at higher densities. In addition, *Phragmites* habitats had the highest rates of mass loss from plaster casts, indicating that these areas had relatively greater flows of water, a feature correlated to changes in the surface topography (Angradi et al. 2001; Able et al. 2003). Such changes in the physical environment at the marsh surface could be stressful for spiders such as *Grammonota* that build complex sheet webs at the base of *Spartina* stems, near the soil surface. These and other surface-dwelling organisms are likely to be affected by the altered hydrologic regimes and vegetation structure and are less capable of persisting in

Phragmites habitats (Angradi et al. 2001). Hunting spiders such as lycosids, by contrast, are known to accumulate in litter-rich areas (Denno et al. 2002), and the accumulation of dead plant biomass in *Phragmites* habitats may buffer them against the loss of organisms that benefit from habitat structure.

Detritivores were least affected by *Phragmites* invasion. Detritivores comprised a trophic group that included saprophages (Collembola), filter feeders (culicids and chironomids), and shredders (amphipods), which tend to be trophic generalists with broad habitat requirements (Hughes et al. 2000). Detritivores became proportionally the most abundant free-living arthropod assemblage in *Phragmites* because of the rarity of free-living herbivores.

The significant change in predator and prey assemblages, driven by differences in the web-building spiders, herbivores, and detritivores, suggests that trophic interactions among arthropods are likely impacted when *Phragmites* invades coastal communities. In *Phragmites*, a trophic shift from free-living herbivores to detritivores and a reduction in the numerically dominant spiders will likely have an effect on food-web interactions and the flow of energy in invaded habitats. Thus, the notion that *Phragmites* habitats are functionally equivalent to those of *Spartina* is not likely to hold with respect to arthropod food webs. In examining the effects of habitat restoration in a southern California marsh, Boyer and Zedler (1996) found that the lack of important predators resulted in the outbreak of herbivore populations in restored *Spartina foliosa*, showing that restoration of vegetation without the full complement of arthropods could influence the ability to restore communities. As insects and other arthropods are significant components of the diet of fish (*Fundulus heteroclitus*, James et al. 2001), an important marsh consumer and link to open-water habitats (Wainright et al. 2000), it is likely that changes in arthropod assemblages will also impact food resources of a variety of estuarine consumers. Studies of food-web interactions in this system using stable isotopes further indicate that feeding interactions among arthropods are also restored in *Spartina* while *Phragmites* consumers are deriving most of their resources from detritus and detritivores (Gratton and Denno, unpublished data). Thus, the return of arthropods to newly established *Spartina* not only restores the native arthropod diversity but also recreates the trophic structure, an aspect important to the restoration of these habitats.

Restoration of Arthropod Assemblages

Our study supports the notion that restoration of native vegetation can promote the reestablishment of the associated native arthropod community (Palmer et al. 1997). However, restoration of native vegetation in general has had mixed success regarding the reestablishment of arthropods assemblages. Some arthropod communities are quick to reestablish even after a short time. For example, Williams (1993) showed that replanting riparian vegeta-

tion along stream banks resulted in arthropod communities that had similar species and guild composition after 3 years, although abundances tended to be significantly lower when compared with reference sites. In contrast, arthropod assemblages in restored coastal sage scrub communities in California were slow to recover (Longcore 2003), and trophic structure was different (more predators) on replanted sagebrush (Burger et al. 2003). Similarly, studies of mine reclamation suggest that arthropod species richness and abundance were consistently lower in restored sites (Parmenter et al. 1991) even for as long as 20 years after restoration (Bisevac & Majer 1999).

Rapid recovery of *Spartina* arthropod assemblages at Alloway Creek may have been facilitated by several factors. A local or regional source from which arthropod colonists could disperse and colonize newly established vegetation was likely available. Colonists may have originated locally from reference *Spartina* patches present within the Alloway Creek site or from nearby marshes where *Spartina* dominates (e.g., Grothues & Able 2003). In this regard, the dispersal abilities of arthropods have been long appreciated (Taylor & Taylor 1983; Gatehouse 1997). The dominant *Spartina* herbivores, *Prokelisia marginata* planthoppers, are known to undertake long-distance migrations annually to colonize overwintering habitats (Denno & Grissell 1979). Linyphiid (e.g., *Grammonota*) and lycosid spiders are capable of aerially ballooning on silken strands and dispersing several kilometers (Thomas & Jepson 1999). Levin and Talley (2002) found that macrobenthic species colonized reconstructed marshes in southern California by rafting on algal and detrital wrack originating from nearby *Spartina*. Conversely, the slow recovery of particular arthropod groups (e.g., carabids, Blake et al. 1996) in some restorations may be in part attributable to their limited dispersal abilities (Brady et al. 2002).

Finally, the return of *Spartina* to the Alloway Creek site following *Phragmites* removal restored habitat features of the marsh to a state similar to those of reference *Spartina*. Thus, both the reestablishment of native plants and the return of physical characteristics of the marsh permitted the establishment and persistence of the native arthropods in the restored habitats. The small but lingering differences between arthropod assemblages in the mixed *Spartina-Phragmites* habitats suggest that other features of the habitat may affect arthropod community restoration. For example, the rarity of concealed-feeding herbivores in *Spartina* growing in mixed stands suggest that associational resistance may result from the proximity of *Phragmites* (Hamback et al. 2000). Some species, such as stem-boring languriid beetles and scale insects, may be more sensitive to subtle differences in plant quality or may change oviposition behavior in the presence of nonhost plants, thereby affecting their abundance in partially invaded habitats. Nevertheless, with the reestablishment of pure stands of *Spartina*, concealed feeders ultimately achieve reference densities, suggesting that the effect of *Phragmites* is reversible even for more sensitive *Spartina* taxa.

Conclusions

The increasing disappearance and degradation of natural environments has generated a need to conserve and restore biological diversity. This study documented that arthropod assemblages are seriously altered with the invasion of *Phragmites* into coastal habitats that were historically dominated by *Spartina* cordgrass. However, the removal of *Phragmites* results in the rapid reestablishment of *Spartina* as well as the entire arthropod assemblage associated with this habitat. Restoration of already existing (although degraded) marsh habitats may thus be a viable strategy for restoring native biodiversity because the native plants were able to quickly reestablish and the physical structure of the marsh likewise recovered. Furthermore, successful restoration of arthropod assemblages will depend in part on maintaining large undisturbed refuges of *Spartina* marsh that act as local and regional sources of potential immigrants that have the dispersal abilities to colonize restored habitats.

Acknowledgments

We thank D. Finke, J. Hines, A. Huberty, G. Langellotto, and D. Lewis for field assistance, and we greatly appreciated the many hours of sample collection and processing by S. Ferrenberg and J. Sanchez. We would like to thank the numerous colleagues who helped with identifications of arthropods: B. Blossey (*Phragmites* herbivores), C. Desjardins (Hymenoptera), M. Drany (spiders), R. Hurley (Dolichopodids), and I. Winkler (Diptera). In addition, B. Cardinale, M. Weinstein, and J. Zedler reviewed drafts of this manuscript, and we hope to have incorporated their many insightful suggestions. Ken Strait (PSEG) facilitated our research at the Alloway Creek Restoration Site. This research was supported by funds from Maryland Sea Grant in collaboration with the New Jersey Sea Grant Program (Marsh Ecology Research Program, National Oceanic and Atmospheric Association award NA06RG101) to C.G. and R.F.D. and from National Science Foundation grants (DEB-9903601 and DEB-0313903) to R.F.D.

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Appendix A. Mean abundance (cumulative number of individuals/m²) of arthropods collected by vacuum sampling and stem dissections in reference *Spartina*, restored *Spartina*, mixed *Spartina*-*Phragmites*, *Phragmites*, and long-standing *Phragmites* marsh habitats at Alloway Creek Restoration Site, New Jersey, in 2001.

Order Family	Taxon Name ^d	Trophic Group ^b	Guild (Subguild) ^c	Reference <i>Spartina</i>		Restored <i>Spartina</i>		Mixed <i>Spartina</i> - <i>Phragmites</i>		Long-Standing <i>Phragmites</i>	
				Mean (SE), n = 11	Mean (SE), n = 12	Mean (SE), n = 12	Mean (SE), n = 12	Mean (SE), n = 12	Mean (SE), n = 5		
Acari											
Erythraeidae	Erythraeidae	C	Pr	20.6 (6.2)	9.7 (2.4)	21.0 (8.7)	72.3 (39.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Arachnida											
Anyphaenidae	<i>Oxysoxa cubana</i>	C	Sp (Hunt)	4.6 (2.9)	9.7 (2.7)	4.2 (1.6)	2.9 (1.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Araneidae	<i>Larinia directa</i>	C	Sp (Web)	20.0 (4.8)	13.6 (2.7)	13.4 (3.5)	5.0 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	<i>Singa eugeni</i>	C	Sp (Web)	96.1 (18.5)	61.1 (10.3)	79.1 (17.1)	19.7 (6.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Clubionidae	<i>Clubiona littoralis</i>	C	Sp (Hunt)	20.9 (3.2)	15.2 (2.8)	9.2 (2.4)	7.6 (3.8)	6.9 (6.2)	6.9 (6.2)	6.9 (6.2)	6.9 (6.2)
	<i>Clubiona maritima</i>	C	Sp (Hunt)	27.2 (5.3)	14.9 (3.0)	13.9 (3.3)	5.8 (1.8)	1.3 (0.8)	1.3 (0.8)	1.3 (0.8)	1.3 (0.8)
	<i>Clubiona</i> imm.	C	Sp (Hunt)	108.6 (7.3)	93.0 (13.2)	80.7 (10.6)	32.8 (6.0)	5.0 (2.1)	5.0 (2.1)	5.0 (2.1)	5.0 (2.1)
Gnaphosidae	<i>Sergiolus</i> sp.	C	Sp (Hunt)	11.7 (3.6)	15.2 (2.9)	13.1 (2.8)	7.3 (1.7)	4.4 (2.9)	4.4 (2.9)	4.4 (2.9)	4.4 (2.9)
Linyphiidae	<i>Agyreta</i> sp.	C	Sp (Web)	18.0 (5.8)	27.3 (6.7)	13.1 (7.0)	16.5 (6.0)	1.9 (1.3)	1.9 (1.3)	1.9 (1.3)	1.9 (1.3)
	<i>Agyreta/Dicynidae</i> imm.	C	Sp (Web)	6.0 (2.9)	5.8 (2.3)	6.0 (3.1)	2.6 (1.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	<i>Glenognatha foxi</i>	C	Sp (Web)	6.3 (1.9)	14.7 (4.3)	9.2 (3.1)	2.6 (1.4)	0.6 (0.6)	0.6 (0.6)	0.6 (0.6)	0.6 (0.6)
	<i>Grammonota genitilis</i>	C	Sp (Web)	13.4 (2.5)	4.2 (2.1)	4.7 (1.8)	1.0 (0.4)	1.3 (1.3)	1.3 (1.3)	1.3 (1.3)	1.3 (1.3)
	<i>Grammonota trivittata</i>	C	Sp (Web)	1,385.9 (218.2)	994.0 (126.4)	550.3 (98.6)	175.1 (52.5)	39.6 (23.6)	39.6 (23.6)	39.6 (23.6)	39.6 (23.6)
	<i>Scotinotylus</i> sp.	C	Sp (Web)	1.1 (0.9)	0.3 (0.3)	1.6 (0.9)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	<i>Spider</i> sp. B	C	Sp (Web)	3.4 (2.1)	2.1 (0.9)	2.1 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Lycosidae	<i>Walkeraeria/Anibontes</i>	C	Sp (Web)	6.9 (2.4)	10.2 (2.9)	5.2 (1.7)	5.2 (1.7)	2.5 (2.5)	2.5 (2.5)	2.5 (2.5)	2.5 (2.5)
	<i>Hogna</i> sp.	C	Sp (Hunt)	12.3 (3.9)	7.3 (3.0)	17.6 (6.2)	12.6 (5.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	<i>Pardosa</i> sp.	C	Sp (Hunt)	97.5 (29.0)	128.4 (26.4)	149.6 (26.8)	107.7 (15.1)	34.6 (14.5)	34.6 (14.5)	34.6 (14.5)	34.6 (14.5)
	<i>Pirata</i> sp.	C	Sp (Hunt)	3.7 (1.2)	6.3 (2.1)	7.1 (3.5)	9.4 (2.4)	4.4 (2.7)	4.4 (2.7)	4.4 (2.7)	4.4 (2.7)
	<i>Lycosid</i> imm.	C	Sp (Hunt)	51.7 (16.4)	73.1 (17.3)	70.8 (11.9)	41.4 (8.5)	7.5 (3.1)	7.5 (3.1)	7.5 (3.1)	7.5 (3.1)
Philodromidae	<i>Philodromus</i> sp.	C	Sp (Hunt)	9.4 (3.1)	15.5 (5.8)	10.2 (2.7)	6.8 (3.2)	5.0 (2.1)	5.0 (2.1)	5.0 (2.1)	5.0 (2.1)
	<i>Tibellus</i> sp.	C	Sp (Hunt)	0.6 (0.4)	1.6 (1.6)	11.5 (5.5)	0.8 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Pisuridae	<i>Dolomedes</i> sp.	C	Sp (Hunt)	9.4 (2.4)	14.2 (3.6)	12.3 (3.6)	1.8 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Salticidae	<i>Hentzia mitrata</i>	C	Sp (Hunt)	3.4 (1.7)	5.5 (1.4)	4.2 (1.3)	18.1 (12.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	<i>Hentzia palmarum</i>	C	Sp (Hunt)	1.1 (0.5)	2.1 (0.9)	3.9 (1.0)	6.0 (1.1)	1.3 (1.3)	1.3 (1.3)	1.3 (1.3)	1.3 (1.3)
	<i>Hentzia</i> imm.	C	Sp (Hunt)	55.7 (8.0)	47.4 (5.9)	63.4 (8.4)	61.6 (7.9)	4.4 (1.6)	4.4 (1.6)	4.4 (1.6)	4.4 (1.6)
	<i>Marpissa</i> sp.	C	Sp (Hunt)	9.4 (3.9)	1.3 (0.8)	3.4 (1.5)	0.5 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Salticidae A	C	Sp (Hunt)	6.0 (1.5)	2.6 (1.2)	4.5 (1.7)	1.8 (0.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Tetragnathidae	<i>Pachygnatha brevis</i>	C	Sp (Web)	32.0 (7.1)	59.2 (7.0)	38.0 (9.5)	7.3 (2.4)	6.9 (6.9)	6.9 (6.9)	6.9 (6.9)	6.9 (6.9)
	<i>Pachygnatha</i> imm.	C	Sp (Web)	116.4 (21.2)	135.0 (15.5)	132.3 (23.1)	32.5 (7.4)	3.8 (2.3)	3.8 (2.3)	3.8 (2.3)	3.8 (2.3)
	<i>Tetragnatha caudata</i>	C	Sp (Web)	47.2 (7.2)	47.7 (7.3)	42.2 (8.7)	14.7 (2.6)	4.4 (2.1)	4.4 (2.1)	4.4 (2.1)	4.4 (2.1)
	<i>Tetragnatha pallescens</i>	C	Sp (Web)	6.0 (1.3)	8.4 (1.8)	9.2 (1.6)	5.0 (1.4)	1.3 (0.8)	1.3 (0.8)	1.3 (0.8)	1.3 (0.8)
	<i>Tetragnatha</i> imm.	C	Sp (Web)	194.4 (23.3)	199.2 (21.4)	174.3 (23.3)	89.6 (16.8)	6.9 (3.0)	6.9 (3.0)	6.9 (3.0)	6.9 (3.0)
Unknown	Spider A	C	Sp	26.6 (5.9)	14.2 (5.2)	11.8 (4.5)	6.8 (2.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Spider B	C	Sp	2.3 (1.2)	4.2 (1.2)	2.9 (0.9)	1.8 (0.7)	0.6 (0.6)	0.6 (0.6)	0.6 (0.6)	0.6 (0.6)
	Spider misc.	C	Sp	39.7 (6.6)	54.5 (13.0)	38.5 (7.5)	12.6 (4.1)	4.4 (2.1)	4.4 (2.1)	4.4 (2.1)	4.4 (2.1)
Pseudoscorpiones											
Pseudoscorpionidae	Pseudoscorpionidae	C	Pr	37.7 (13.3)	11.8 (4.8)	56.6 (16.3)	35.4 (14.6)	10.7 (6.9)	10.7 (6.9)	10.7 (6.9)	10.7 (6.9)
Amphipoda											
Gammaridae	<i>Gammarus</i> sp.	D	Scv/Shr	361.9 (106.0)	320.2 (103.1)	201.5 (54.6)	213.3 (57.3)	21.4 (8.9)	21.4 (8.9)	21.4 (8.9)	21.4 (8.9)

Appendix A. Continued

Staphilinidae	Staphilinidae A	C	Pr	34.6 (13.7)	60.8 (21.5)	41.4 (8.4)	38.0 (9.8)	3.8 (1.8)
Staphilinidae B	Staphilinidae B	C	Pr	0.3 (0.3)	9.4 (5.4)	3.1 (1.8)	0.8 (0.8)	0.0 (0.0)
Staphilinidae C	Staphilinidae C	C	Pr	0.8 (0.8)	0.8 (0.8)	0.8 (0.8)	1.6 (1.6)	0.6 (0.6)
Staphilinidae D	Staphilinidae D	C	Pr	0.0 (0.0)	1.6 (1.6)	1.0 (0.8)	0.0 (0.0)	0.0 (0.0)
Coleoptera	Coleoptera F			29.2 (8.0)	29.1 (8.6)	42.7 (15.5)	3.9 (1.4)	0.6 (0.6)
Misc.	Misc.			12.3 (3.6)	6.3 (1.8)	10.5 (3.7)	2.9 (1.4)	0.0 (0.0)
Diptera								
Cecidomyiidae	Cecidomyiidae	H	Con-Ch	38.6 (7.6)	54.0 (9.4)	24.4 (6.5)	22.0 (8.6)	5.7 (3.8)
	<i>Calamomyia spartinae</i> (larvae)	H	Con-Ch	18.0 (18.0)	0.0 (0.0)	66.8 (56.1)	0.0 (0.0)	0.0 (0.0)
	<i>Lasioptera hungarica</i> (larvae)	H	Con-Ch	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1,900.4 (1,116.3)	0.0 (0.0)
Ceratopogonidae	Ceratopogonidae	D	Filt	101.8 (22.1)	132.3 (46.1)	65.0 (16.9)	87.8 (29.5)	5.7 (5.7)
Chironomidae	Chironomidae	D	Filt	596.9 (116.0)	604.3 (114.8)	850.9 (398.3)	399.1 (71.5)	32.1 (12.0)
Chloropidae	Chloropidae A	H	Con-Ch	42.6 (5.9)	79.4 (11.9)	87.3 (22.5)	54.8 (15.9)	8.2 (5.3)
	Chloropidae B	H	Con-Ch	396.2 (73.1)	447.9 (73.3)	285.6 (46.4)	77.8 (19.0)	11.9 (6.7)
	Chloropidae misc.	H	Con-Ch	5.2 (2.7)	14.2 (4.7)	6.3 (2.7)	3.4 (1.8)	0.0 (0.0)
	<i>Liparia ?rufitarsis</i> (larvae)	H	Con-Ch	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	18.0 (6.8)	6.4 (6.4)
	<i>Liparia ?similis</i> (larvae)	H	Con-Ch	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.6 (1.8)
Culicidae	Culicidae	D	Filt	37.7 (11.6)	58.7 (22.9)	21.0 (5.6)	43.8 (9.6)	9.4 (7.3)
Dolichopodidae	<i>Achalcus</i> undescr. sp.	C	Pr	237.1 (22.7)	241.2 (13.0)	127.1 (27.5)	29.2 (7.9)	4.4 (1.6)
	<i>Tachytrechus</i> sp.	C	Pr	61.5 (8.9)	124.5 (20.4)	111.6 (16.5)	32.5 (11.4)	0.0 (0.0)
	Dolichopodidae C	C	Pr	42.9 (8.7)	46.9 (9.9)	60.3 (10.2)	18.1 (4.1)	3.8 (2.3)
	Dolichopodidae D	C	Pr	2.6 (1.8)	1.6 (1.1)	2.4 (1.2)	0.0 (0.0)	0.0 (0.0)
	Dolichopodidae misc.	C	Pr	0.0 (0.0)	0.8 (0.8)	2.4 (1.7)	0.8 (0.8)	0.6 (0.6)
Ephydriidae	Ephydriidae A	D	Scv/Shr	82.6 (33.6)	178.2 (53.6)	77.8 (35.3)	14.9 (4.2)	0.0 (0.0)
	Ephydriidae B	D	Scv/Shr	25.7 (7.5)	16.5 (6.5)	23.8 (5.8)	49.8 (25.1)	3.8 (3.8)
	Ephydriidae C	D	Scv/Shr	6.9 (3.4)	20.4 (7.7)	11.0 (5.5)	6.3 (2.7)	0.0 (0.0)
	Ephydriidae D	D	Scv/Shr	54.0 (10.1)	65.5 (18.8)	50.1 (7.0)	27.3 (5.6)	0.0 (0.0)
	Ephydriidae E	D	Scv/Shr	90.1 (18.0)	184.2 (28.7)	246.1 (48.9)	91.7 (18.1)	5.0 (1.9)
	Ephydriidae F	D	Scv/Shr	8.0 (2.2)	12.6 (9.5)	16.0 (5.2)	8.1 (4.1)	0.0 (0.0)
	Ephydriidae misc.	D	Scv/Shr	8.6 (4.7)	10.2 (4.6)	7.3 (2.6)	8.1 (2.5)	0.0 (0.0)
Lauxaniidae	Lauxaniidae	D	Scv/Shr	0.8 (0.8)	5.5 (4.7)	3.9 (3.9)	0.8 (0.8)	0.0 (0.0)
Otitidae	Chaetopsis A	H	Con-Ch	74.9 (7.7)	70.5 (9.4)	66.8 (11.4)	10.0 (3.0)	0.0 (0.0)
	Otitidae B	H	Con-Ch	0.8 (0.8)	3.1 (1.4)	7.9 (4.6)	0.8 (0.8)	0.0 (0.0)
Sciomyzidae	Sciomyzidae	C	Pr	9.4 (3.6)	8.9 (3.1)	12.6 (3.1)	4.7 (1.8)	0.0 (0.0)
Tabanidae	Tabanidae	C	Pr	0.0 (0.0)	1.6 (1.1)	0.8 (0.8)	0.8 (0.8)	0.0 (0.0)
Tipulidae	Tipulidae A	D	Scv/Shr	17.5 (4.3)	31.2 (8.1)	54.0 (15.2)	18.9 (6.8)	1.9 (1.9)
	Tipulidae B	D	Scv/Shr	95.2 (29.3)	97.2 (24.1)	69.2 (16.5)	64.2 (14.8)	42.1 (25.5)
	Tipulidae (larvae)	D	Scv/Shr	0.8 (0.8)	0.8 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Unknown	Diptera A	D		6.9 (2.2)	11.0 (3.1)	11.0 (3.2)	3.9 (1.8)	1.9 (1.9)
	Diptera B			6.0 (2.9)	14.2 (4.8)	19.7 (4.8)	10.8 (3.2)	0.0 (0.0)
	Diptera C			37.5 (16.3)	45.8 (11.7)	44.0 (10.1)	11.0 (5.1)	0.0 (0.0)
	Diptera H			11.7 (4.3)	12.0 (3.3)	19.7 (8.9)	10.2 (4.0)	0.0 (0.0)
	Diptera misc.			7.4 (2.7)	11.0 (2.5)	26.2 (7.1)	16.5 (5.5)	0.6 (0.6)
	Diptera larvae			4.3 (2.3)	1.6 (1.1)	0.8 (0.8)	2.4 (2.4)	1.9 (1.9)
Lepidoptera								
Pyralidae	<i>Chilo demotellus</i> (larvae)	H	Con-Ch	1.1 (0.9)	1.6 (1.1)	0.8 (0.8)	3.9 (3.2)	0.6 (0.6)
Elachistidae	<i>Dicranoctetes saccharella</i> (larvae)	H	Con-Ch	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	43.4 (28.1)	287.5 (73.0)

