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Modification of sediments and macrofauna by an invasive marsh plant

T.S. Talley* & L.A. Levin**
Marine Life Research Group, Scripps Institution of Oceanography La Jolla, CA 92093-0218, USA;
**Current address: Department of Environmental Science and Policy, One Shields Ave., University of California, Davis, CA 95616, USA; **Author for correspondence (e-mail: llevin@ucsd.edu; fax: +1-858-822-0562)*

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Abstract

Invasive grasses have recently altered salt marsh ecosystems throughout the northern hemisphere. On the eastern seaboard of the USA, *Phragmites australis* has invaded both brackish and salt marsh habitats. *Phragmites australis* influence on sediments and fauna was investigated along a salinity and invasion-age gradient in marshes of the lower Connecticut River estuary. Typical salinities were about 19–24 ppt in Site I, 9–10 ppt in Site II and 5–7 ppt in Site III. Strongest effects were evident in the least saline settings (II and III) where *Phragmites* has been present the longest and exists in monoculture. Limited influence was evident in the most saline region (I) where *Phragmites* and native salt marsh plants co-occur. The vegetation within *Phragmites* stands in tidal regions of the Connecticut River generally exhibits taller, but less dense shoots, higher above-ground biomass, and lower below-ground biomass than does the un-invaded marsh flora. There were lower sediment organic content, greater litter accumulation and higher sediment chlorophyll *a* concentrations in *Phragmites*- invaded than un-invaded marsh habitat. Epifaunal gastropods (*Succinea wilsoni* and *Stagnicola catascopium*) were less abundant in habitats where *Phragmites* had invaded than in un-invaded marsh habitat. Macro-infaunal densities were lower in the *Phragmites*-invaded than un-invaded habitats at the two least saline sites (II and III). *Phragmites* stands supported more podurid insects, sabellid polychaetes, and peracarid crustaceans, fewer arachnids, midges, tubificid and enchytraeid oligochaetes, and greater habitat-wide taxon richness as measured by rarefaction, than did the un-invaded stands. The magnitude and significance of the compositional differences varied with season and with site; differences were generally greatest at the oldest, least saline sites (II and III) and during May, when faunal densities were higher than in September. However, experimental design and the 1-year study period precluded clear separation of salinity, age, and seasonal effects. Although structural effects of *Phragmites* on salt marsh faunas are evident, further investigation is required to determine the consequences of these effects for ecosystem function.

Introduction

Plant invasions in estuaries are a growing problem (Posey 1988; Callaway and Josselyn 1992; Posey et al. 1993). Habitat modification and degradation have increased the susceptibility of wetlands to invasion and contributed to accelerated rates of invader spread (Nichols et al. 1986; Crooks 1998). The rapid vegetation change associated with plant invasions provides an opportunity to study the effects of plant presence or type on faunal communities. These effects may be direct, such as through alteration of habitat structure

(Peterson 1982; Summerson and Peterson 1984), or may be indirect as through shifts in hydrodynamic or deposition regimes (Fonseca et al. 1982; Peterson et al. 1984; Eckman 1987, 1990). Faunal compositions change when plants invade unvegetated habitat, for example, the invasion of Pacific mudflats by Atlantic cordgrass (*Spartina alterniflora*) (Zipperer 1996) or Japanese eelgrass (*Zostera japonica)* (Posey 1988), or when the composition of existing vegetation changes. Alteration of existing vegetation structure has occurred where the common reed grass (*Phragmites australis*, hereafter referred to as *Phragmites*) has invaded vegetated tidal marsh along the eastern seaboard of the US.

Invasions are generally range expansions over large spatial scales; in marine systems these may involve trans-oceanic expansion. The spread of *Phragmites* is unique in that it has occurred on smaller (within-coast and within-estuary) scales. *Phragmites* has been a feature of marshes on the eastern seaboard of the US for at least 4000 years, but it was limited to upland salt marsh borders and freshwater areas (Niering and Warren 1980a; Warren and Fell 1995). Beginning in the mid-1960s, however, invasions of *Phragmites* into undisturbed, fully tidal brackish marshes were recorded. Since then, monocultures of *Phragmites* have been displacing fresh, brackish and salt marsh plant communities (e.g., *Spartina* spp., other marsh grasses and herbs) in the New England region (Warren and Fell 1995).

Successful invasions depend upon both the properties of the invading species and the environmental conditions of the recipient site (Orians 1986; Ruiz et al. 1997). *Phragmites* has the characteristics of a successful invader as discussed by Orians (1986), including opportunistic growth strategies, generalized pollination and seed dispersal strategies (e.g., Hickman 1993), an ability to outcross and produce successful genotypes (Besitka 1996), and vegetative reproduction (Koppitz 1999; Pellegrin and Hauber 1999; Niering and Warren 1980b). Similar environmental conditions (climate, sediments, plant growth forms) between the recipient and source sites, as occurs within these east coast marshes, also encourage successful invasions (Orians 1986). Proposed catalysts of this recent *Phragmites* invasion include an increase in favorable conditions for *Phragmites* due to increased tidal restrictions (e.g., tidal gates, development) (Rozsa 1995; Chambers et al. 1999). Besitka (1996) suggested that the invasive *Phragmites* genotype differs from the historical *Phragmites*, although this ‘aggressive genotype’ has not yet been found (Chambers et al. 1999).

The spread of *Phragmites* throughout the marshes of the lower Connecticut River estuary (Connecticut, USA) mirrors *Phragmites* invasions occurring in other wetlands along the eastern seaboard and has been both rapid and extensive (Chambers et al. 1999). Areal expansion has occurred at a rate of 1% yr^{-1} in saline marshes and 3% yr^{-1} in brackish marshes (Warren and Fell 1996). The pattern of spread is downstream from oligohaline to more saline areas, so the distance between among reflects not only the estuarine salinity gradient, but also age since invasion.

Effects of *Phragmites australis* spread on salt marsh structure and function are likely to be widespread. Above-ground alteration of canopy architecture (Windham and Lathrop 1999), flow and sediment deposition (Harrison and Bloom 1977; Roman 1978; Takeda and Kurihara 1988), as well as below-ground changes in substrate structure, detrital accumulation and sediment properties (Bart and Hartman 2000; Windham and Lathrop 1999) have been associated with *Phragmites* invasions. These environmental changes have been linked to alterations in trophic structure (Roman 1978; Wilcox and Meeker 1992; Wainright et al. 2000; but see Fell et al. 1998), nutrient cycling (Meyerson et al. 2000) and habitat usage by birds (Roman et al. 1984; Benoit and Askins 1999) and fish (Weinstein and Balletto 1999). There has been little focus on *Phragmites* influence on benthic epifaunal and infaunal assemblages. *Phragmites*-induced changes in above- and below-ground properties would be expected to alter sediment-dwelling fauna (see Levin and Talley 2000 and references therein) and, subsequently, their functional roles in marsh processes (e.g., elemental cycling, trophic support).

This study examined the effects of habitat alteration by the invasive *Phragmites australis* on benthic epifauna and infauna, and their associated environment in Connecticut tidal marshes. Specific goals were to determine whether there were effects of *Phragmites* invasion on (1) above-ground habitat features (canopy architecture, litter biomass, benthic microalgal biomass) and below-ground sediment properties (organic matter content, sand content, root and rhizome biomass and structure, lamination), and (2) macrofaunal community structure (density, biomass, species richness, diversity, dominance, composition), and to assess the extent to which *Phragmites* effects change with salinity regime and/or age of the stand.

Materials and methods

Three sites (I, II and III) of decreasing salinity (19–24 in I, 9–10 in II and 5–7 in III) were studied in the vegetated marshes along the lower Connecticut River Estuary (Figure 1, Table 1). These were sampled in May (all Sites) and September (Sites I and III only) 1999 for sediments, plants, epifauna and macrofauna (animals $\geq$0.3 mm). Within each site, two 50-m transects were established, one in *Phragmites*-dominated marsh and one in salt marsh grass-dominated marsh (e.g., *Spartina patens*, *Juncus gerardi* and *Distichlis spicata*) (hereafter referred to as un-invaded). Transects ran from the creek edge towards the back of the vegetation patch, except in the un-invaded marsh grass habitats of Sites II and III, which were located in patches behind *Phragmites* bordering the creeks. Transects in these two areas followed the distribution of the patches. Along each 50-m transect, 10 sampling stations were located at 5-m intervals along the transect line and 1–2 m to either side of the line. Field sampling within these stations was conducted during May 7–12 and September 9–17, 1999. Densities of epifauna and plant shoots (number 0.25 m^{-2}), light attenuation through

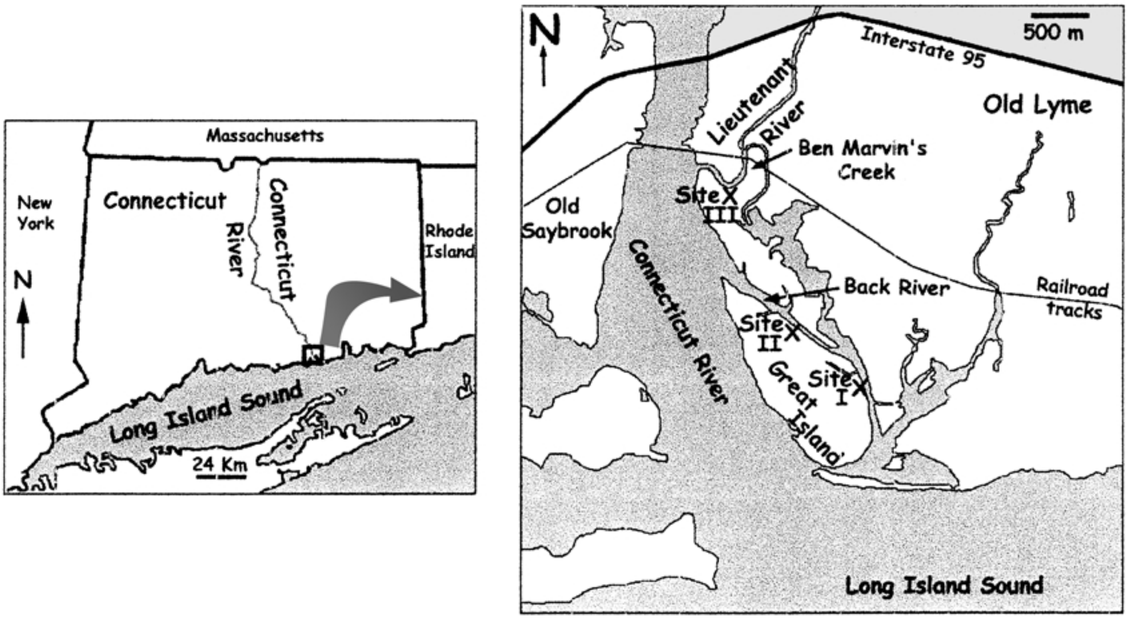

Figure 1. Location of study sites in the lower Connecticut River estuary, Old Lyme, Connecticut, USA.

Table 1. Location, elevation and porewater salinity of each habitat type within each site along the lower Connecticut River estuary during May and September 1999.

	Site I		Site II		Site III	
Latitude	41°17′23″ N		41°17′35″ N		41°18′28″ N	
Longitude	72°19′37″ W		72°20′02″ W		72°20′22″ W	
Location	Back River, Great Island		Back River, Great Island		Lieutenant River & Ben Marvin's Creek	
	Phragmites	Un-invaded	*Phragmites*	Un-invaded	*Phragmites*	Un-invaded
Elevations (cm above MLLW)	106 ± 3	110 ± 3	110 ± 1	110 ± 2	107 ± 2	106 ± 3
Salinity (ppt)						
May	5.2 ± 0.6	4.6 ± 1.6	2.6 ± 0.2	2.0 ± 0.2	0 ± 0	0 ± 0
September	19.8 ± 0.9	23.1 ± 0.9	9.2 ± 0.9	8.9 ± 0.3	5.7 ± 0.8	6.4 ± 0.5

$n = 10$ salinity and 8 elevation samples, values are mean ±1 SE. Salinities in May followed heavy rains. MLLW = mean lower low water.

the plant canopy and litter, and pore water salinity were measured in the field at each station. One sediment core was collected from each station during May and September for macrofaunal analysis ($18\,\text{cm}^2 \times 6\,\text{cm}$ depth) and one core was collected for determination of benthic chlorophyll *a* concentrations ($0.86\,\text{cm}^2 \times 4\,\text{mm}$ depth). In May, one additional core ($18\,\text{cm}^2 \times 6\,\text{cm}$ depth) was collected from each station for analysis of sediment properties. Core sizes were selected based on published methods (see below). Cores collected for macrofaunal analyses that were processed by one particular individual yielded questionable results, so all cores processed by this person were excluded. This resulted in $n = 7$ cores per transect in May and $n = 9$ cores in September. Below-ground plant biomass consisting of live and dead roots, rhizomes and detritus, was sorted and weighed from the macrofaunal cores. Collections of plant litter (shoots and leaves) were made for determination of above-ground litter biomass ($\text{g dw } 400\,\text{cm}^{-2}$) and associated macrofauna (Site III, September only). Standing live and dead shoots of plants were harvested from each station in September for determination of end-of-year above-ground plant biomass ($\text{g dw } 0.25\,\text{m}^{-2}$). Two slabs ($3 \times 12 \times 18\,\text{cm}$ deep) of marsh sediment were collected from each transect in May 1999 for X-radiographic analysis of below-ground sediment structure.

Within each transect, five pitfall traps were installed along the transect line to sample mobile epifauna. Cylindrical pitfall traps ($78.5\,\text{cm}^2 \times 14\,\text{cm}$ deep coffee cans) were inserted flush with the sediment surface. Lids were left on traps until use. Traps were set and sampled during May 11–12, June 30–July 1, July 8–9, 14–15, 22–23, August 5–6, and September 13–14 1999. High tide levels were often high enough to flood some traps and allow the escape of all animals. This variable loss of replication made statistical analysis untenable. These data are therefore presented as a non-quantitative record of mobile epifauna that were missed by sampling with benthic cores and quadrats. Pitfall animals were preserved in 95% ethanol and identified, using a dissecting microscope when necessary.

Light attenuation was measured *in situ* using a Licor hand-held light meter. Light attenuation (μE) was interpreted as the percent decrease in light between ambient and sediment surface (beneath the canopy and any litter that was present) light readings. Pore water salinities were obtained from the top 4 cm of sediment by squeezing the sediment against a filter paper inside of a $10\,\text{cm}^3$ syringe and measuring the salinity (±1 ppt) of the drops of extracted water with a Leica hand-held salinity refractometer.

Sediment cores for macrofaunal analysis were collected and processed following methods described in Levin et al. (1998). Cores were preserved in 8% buffered formalin and stained with Rose Bengal. Sediments were rinsed through 0.3 mm mesh after preservation, and all retained animals were removed and identified to the lowest taxonomic level possible using dissecting and, when necessary, compound microscopes. Animals were stored in 1% buffered formalin, weighed wet using an analytical balance in order to determine biomass, and then transferred into 70% ethanol. Below-ground plant material was also removed from the macrofaunal cores, dried at 60 °C and weighed to determine below-ground biomass.

Sediment cores were collected and processed for combustible organic matter and sand content analyses following methods in Levin et al. (1998). Cores were frozen at −20 °C until analysis. Each sediment core was homogenized. A portion for organic matter analysis was sieved wet through a 2-mm mesh to separate large from fine plant material. The ≤2 mm fraction was dried at 60 °C, weighed, combusted at 550 °C overnight and weighed again to determine loss of organics through combustion. A portion of sediment for sand content analysis was digested with hydrogen peroxide to remove organics. Digested sediments were sieved wet through 2 mm (to remove remaining large plant material) and 63-μm mesh. Both size fractions (≥63μm and <63μm) were dried at 60 °C, weighed, and percent sand (≥63μm) was calculated. The concentration of sediment chlorophyll *a* was determined following methods of Piehler et al. (1998), Wainright et al. (2000) and C. Currin (pers. comm.). Cores were frozen at −20 °C until analysis. Chlorophyll *a* was extracted using 7 ml of a methanol, acetone and deionized water (45 : 45 : 10) solution. Samples were sonicated for 1 min, frozen overnight and then shaken and centrifuged for 3 min at 1500 rpm the next morning. The adsorption or fluorescence of the decanted solution was measured before and after acidification with 5% HCl using a Shimadzu UV 1601 spectrophotometer ($\lambda = 665$ and 750 nm) (May) or a Turner Designs fluorometer (September), depending upon which instrument was available. The fluorometer is routinely used to calibrate the spectrophotometer, so readings from both instruments were comparable. Plant litter and shoots collected for the determination of litter and above-ground biomass were rinsed with fresh water to remove adhering sediments (litter only), dried at

60 °C and weighed. Litter to be used for macrofaunal analysis was collected from two arbitrarily assigned layers; the drier, recently fallen upper layer (about 3–6 cm thick) and the partially decayed bottom layer (about 1–3 cm thick). Litter samples were preserved with 8% buffered formalin, stained with Rose Bengal and rinsed on 0.3 mm mesh. Animals were removed from the plant material, identified using dissecting and compound microscopes and stored in 70% ethanol. Plant material was dried at 60 °C and weighed.

Statistical comparisons of macrofaunal and environmental variables among sites (I, II and III), marsh habitats (un-invaded, *Phragmites*) and dates (May and September 1999) were made using Student's *t*-tests and one-way ANOVAs with *a-posteriori t*-tests (JMP statistical software). Interactions between site (i.e., age and salinity gradient) and habitat affecting macrofaunal and environmental variables were identified using two-way ANOVAs (JMP statistical software). Bonferroni-adjusted α values for the number of comparisons made within each date and variable type (e.g., environmental, macrofaunal) were used. All proportion data were arcsin-square-root transformed and numeric data were $\log_{10}(x + 1)$ transformed prior to statistical analyses.

Macrofaunal diversity was examined at the family level (or higher) using taxon richness per core, as well as the Shannon–Weiner Information index (H'; log base 2), evenness (J') per core, and rarefaction for cores pooled within transects (Biodiversity Pro software; McAleece et al. 1999).

Similarities and differences in macrofaunal communities were explored using non-metric multidimensional scaling (MDS), based on Bray–Curtis similarity indices. Pairwise comparisons between habitat types, sites and dates were made using Analysis of Similarity (ANOSIM; to obtain *P*-values). Similarity Percentages (SIMPER) determined the percent of dissimilarity (or similarity) and the taxa responsible for differences between groups. These multivariate analyses (MDS, ANOSIM, SIMPER) were run using Primer Statistical Software (Clarke and Warwick 1994) on double square-root transformed, unstandardized macrofaunal data.

Results

Vegetation characteristics

Plant shoots in the *Phragmites* habitats were 4–6 times taller ($P < 0.001$, $t_{18} \geq 3.78$) and 2–85 times less dense ($P \leq 0.002$, $t_{18} \geq 3.58$) than the shoots in the un-invaded marsh grass habitats at all sites (Figures 2A,B). The difference in total shoot density and height between the un-invaded and *Phragmites* habitats became greater with distance upstream (decreasing salinity, increasing age since invasion) (Table 2A). This was due to an upstream increase in height and a decrease in density of shoots within the *Phragmites* habitat. The biomass of above-ground plant shoots growing in the *Phragmites* habitats was 4–5 times greater ($P < 0.001$, $t_{18} \geq 4.17$) than the shoots in the un-invaded marsh grass habitats

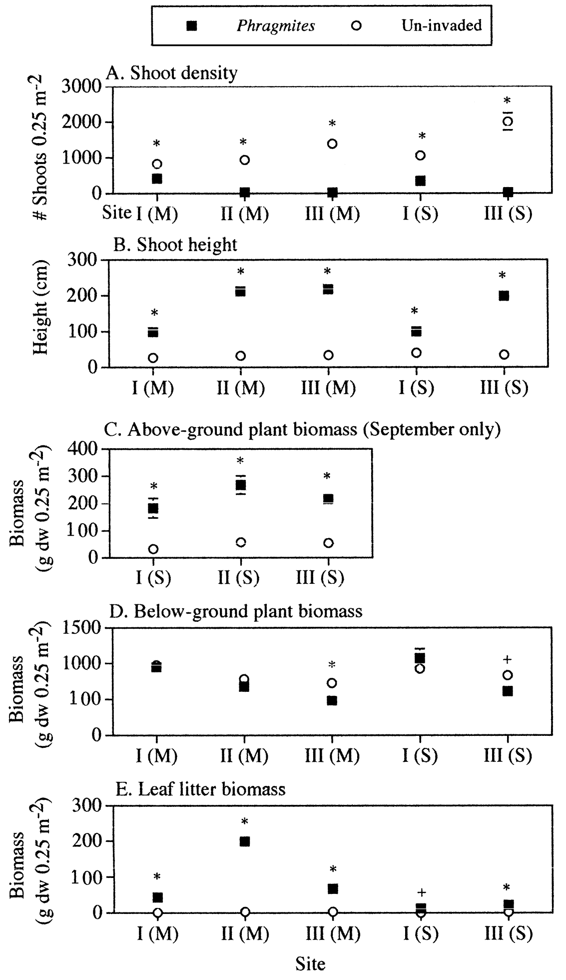

Figure 2. Mean (±1 SE) shoot density (A), shoot height (B), above-ground biomass (C), below-ground biomass (D) and leaf litter biomass (E) found in the *Phragmites* and un-invaded marsh grass habitats at three sites along the lower Connecticut River estuary during May (M) and September (S) 1999. $n = 10$ samples. $* = P \leq 0.006$; $+ = 0.006 < P \leq 0.05$; from *t*-tests between habitats within each site and date. Bonferroni adjusted $\alpha = 0.006$.

Table 2. Results of two-way analyses of variance (ANOVA) for (A) environmental and (B) macrofaunal variables as compared among site (I, II and III), habitat (*Phragmites* and un-invaded), and interaction between site and habitat within the lower Connecticut River estuary; data are from May and September 1999.

		May 1999					September 1999				
		Whole model (df = 5,54)		Site	Habitat	Site × habitat	Whole model (df = 3,36)		Site	Habitat	Site × habitat
		P	*F*	*P*	*P*	*P*	*P*	*F*	*P*	*P*	*P*
A. Environmental variables											
Above-ground properties											
Shoot height		<0.001	160	<0.001	<0.001	<0.001	<0.001	186	<0.001	<0.001	<0.001
Shoot density		<0.001	214	<0.001	<0.001	<0.001	<0.001	141	<0.001	<0.001	<0.001
Shoot biomass		No data					<0.001	54	0.003	<0.001	0.271
Litter biomass		<0.001	241	<0.001	<0.001	<0.001	<0.001	41	<0.001	<0.001	0.080
Open space (%)		<0.001	37	0.312	<0.001	0.312	<0.001	123	<0.001	<0.001	0.080
Sediment properties											
Bg plant biomass		<0.001	9	<0.001	0.005	0.162	0.002	6	0.001	0.293	0.032
% Organic matter		<0.001	21	0.004	<0.001	<0.001	No data				
% Sand		0.692	<1	NS	NS	NS	No data				
Chlorophyll *a*		0.002	4	0.001	0.107	0.120	0.074	2	NS	NS	NS
Light attenuation		0.017	3	0.120	0.392	0.010	0.032	3	0.160	0.022	0.159
Salinity		<0.001	18	<0.001	0.054	0.184	<0.001	99	<0.001	0.056	0.855
B. Macrofaunal variables											
Biomass		0.178	2	NS	NS	NS	0.074	2	NS	NS	NS
Density		<0.001	23	<0.001	0.002	0.181	<0.001	18	<0.001	0.879	0.366
Taxon richness		<0.001	6	<0.001	0.211	0.515	<0.001	15	<0.001	0.254	0.954
Oligochaeta											
Tubificidae	#	<0.001	7	<0.001	0.015	0.348	0.002	6	<0.001	0.354	0.194
	%	0.017	3	0.009	0.056	0.487	0.187	2	NS	NS	NS
Enchytraeidae	#	<0.001	34	<0.001	0.120	0.716	<0.001	17	<0.001	0.274	0.090
	%	<0.001	7	<0.001	0.755	0.695	0.002	6	<0.001	0.220	0.314
Naididae	#	0.015	3	0.003	0.816	0.233	<0.001	9	<0.001	0.065	0.072
	%	0.044	3	0.262	0.058	0.056	0.159	2	NS	NS	NS
Polychaeta											
Sabellidae	#	<0.001	7	<0.001	0.015	0.754	<0.001	13	<0.001	0.002	0.695
	%	0.053	2	0.234	0.005	0.900	<0.001	9	0.265	<0.001	0.016
Other polychaeta	#	0.499	1	NS	NS	NS	0.410	1	NS	NS	NS
	%	0.056	2	0.014	0.419	0.445	0.239	1	NS	NS	NS
Arachnida	#	<0.001	19	<0.001	<0.001	0.021	0.239	1	NS	NS	NS
	%	<0.001	12	<0.001	<0.001	0.036	0.131	2	NS	NS	NS
Insecta											
Midges	#	<0.001	9	<0.001	<0.001	0.954	0.212	2	NS	NS	NS
	%	<0.001	15	<0.001	<0.001	0.848	0.097	2	NS	NS	NS
Poduridae	#	<0.001	60	<0.001	<0.001	<0.001	No poduridae in September				
	%	<0.001	23	<0.001	<0.001	<0.001					
Other insecta	#	0.065	3	NS	NS	NS	0.065	3	NS	NS	NS
	%	0.500	1	NS	NS	NS	0.029	3	0.077	0.066	0.077
Gastropoda	#	0.881	<1	NS	NS	NS	0.482	1	NS	NS	NS
	%	0.783	<1	NS	NS	NS	0.579	<1	NS	NS	NS
Peracarida	#	0.015	3	0.003	0.173	0.532	0.017	4	0.105	0.018	0.105
	%	0.390	1	NS	NS	NS	0.216	2	NS	NS	NS
Nemertea &	#	0.437	1	NS	NS	NS	0.015	4	0.003	0.277	0.376
Turbellaria	%	0.415	1	NS	NS	NS	0.094	2	NS	NS	NS

Table 2. Continued

		May 1999					September 1999				
		Whole model (df = 5,54)		Site	Habitat	Site × habitat	Whole model (df = 3,36)		Site	Habitat	Site × habitat
		P	*F*	*P*	*P*	*P*	*P*	*F*	*P*	*P*	*P*
Dwelling groups											
Burrowers	#	<0.001	25	<0.001	0.068	0.384	<0.001	15	<0.001	0.612	0.249
	%	0.002	5	<0.001	0.754	0.315	0.445	1	NS	NS	NS
Tube-builders	#	<0.001	7	<0.001	0.154	0.753	<0.001	13	<0.001	0.002	0.687
	%	0.070	2	NS	NS	NS	<0.001	9	0.261	<0.001	0.015
Errant	#	<0.001	13	<0.001	0.001	0.264	0.368	1	NS	NS	NS
	%	<0.001	9	<0.001	0.005	0.191	0.187	2	NS	NS	NS

$n = 10$ for environmental variables, $n = 7$ for macrofaunal variables in May and $n = 9$ for macrofaunal variables in September. Bonferroni adjusted $\alpha = 0.005$ for environmental variables and $=0.003$ for macrofaunal variables. Results of tests where $P \leq 0.05$ are shown. NS = not significant for whole model tests where $P > 0.05$, Bg = below-ground

(Figure 2C). *Phragmites* was the dominant plant ($\geq$98% of total above-ground biomass) in the *Phragmites* habitats of Sites II and III. At Site I, however, *Phragmites* shoots comprised 82% and native marsh grasses 18% of the shoot biomass in the *Phragmites* habitat. The native grasses found within the *Phragmites* habitat were 13 cm taller and 2–3 times less dense than those found in the un-invaded habitat. The below-ground plant biomass in un-invaded marsh habitat was 36–52% higher than that found in the *Phragmites* habitats of Site III (May, $P = 0.001$, $t_{18} = 3.7$; September, $P = 0.026$, $t_{18} = 2.4$) and similar in Sites I and II (Figure 2D). There was 10–83 times more plant leaf and stem litter on the sediment surface of the *Phragmites* than un-invaded habitats (Figure 2E) ($P \leq 0.001$, $t_{18} \geq 3.7$, except Site I in Sept when $P = 0.009$, $t_{18} = 2.9$). For all of the above comparisons, Bonferroni-adjusted $\alpha = 0.006$.

Sediment properties

Sediments of the un-invaded marsh habitats had 1.5–4 times higher percent combustible organic matter content (54–58%) than the *Phragmites* sediments within Sites II and III ($P < 0.001$, $t_{18} \geq 6.6$); there was no difference in Site I (Figure 3A). The effect of *Phragmites* invasion on sediment organic matter content was stronger in the sites farther upstream (II and III) (Table 2A). Sand content of sediments was similar in the *Phragmites* and un-invaded habitats at all sites (Figure 3B, Table 2A).

Porewater salinities decreased with distance from the mouth of the Connecticut River (I > II > III) on both dates sampled ($P < 0.001$, $F_{2,28} \geq 25.6$) (Table 1). Salinities in May were measured following heavy rains and so were low in all sites with readings between 0 and 5 (Table 1). In September, salinities were 21, 9 and 6 at sites I, II and III, respectively. Within each site there were no differences in salinity between *Phragmites* and un-invaded habitats (Table 1).

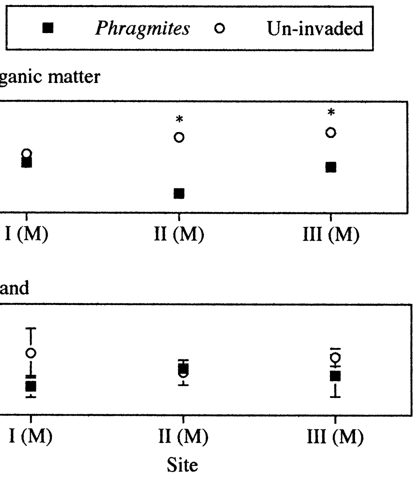

Figure 3. Mean (±1 SE) percent combustible organic matter (A) and sand (B) in the *Phragmites* and un-invaded marsh grass habitats at three sites along the lower Connecticut River estuary during May (M) 1999. $n = 10$ samples. $* = P \leq 0.006$; from t-tests between habitats within each site and date. Bonferroni adjusted $\alpha = 0.006$.

Benthic chlorophyll *a* concentration was 2–3 times higher in the *Phragmites* than un-invaded grass habitats of Site III (May, $P = 0.053$; $t_{18} = 2.1$; September, $P = 0.021$; $t_{18} = 2.5$) although this is not significantly different at Bonferroni adjusted $\alpha = 0.006$ (Figure 4A). There were no differences in chlorophyll *a* concentration between the two habitats in Site I

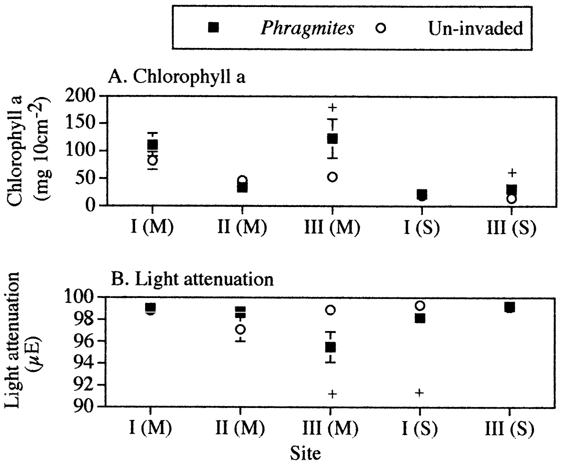

Figure 4. Mean (±1 SE) sediment chlorophyll *a* concentration (A) and light attenuation (B) in the *Phragmites* and un-invaded marsh grass habitats at three sites along the lower Connecticut River estuary during May (M) and September (S) 1999. $n = 10$ samples. $* = P \leq 0.006$; $+ = 0.006 < P \leq 0.05$; from t-tests between habitats within each site and date. Bonferroni adjusted $\alpha = 0.006$.

(Figure 4A). The percent of light attenuated through the *Phragmites* stand (canopy and litter) and the marsh grass canopy was generally similar ($P \geq 0.016$; $t_{18} \leq 2.7$; $\alpha = 0.006$) and ranged between 95 and 99% (Table 2A, Figure 4B).

X-radiographs revealed very different sediment structure in the un-invaded and *Phragmites* habitats. Broad but sparse rhizomes and distinct laminae characterized *Phragmites*-habitat sediments at all sites (Figure 5). Un-invaded marsh sediments exhibited apparent bioturbation (no laminae) and a more dense root mat of thinner rhizomes (Figure 5).

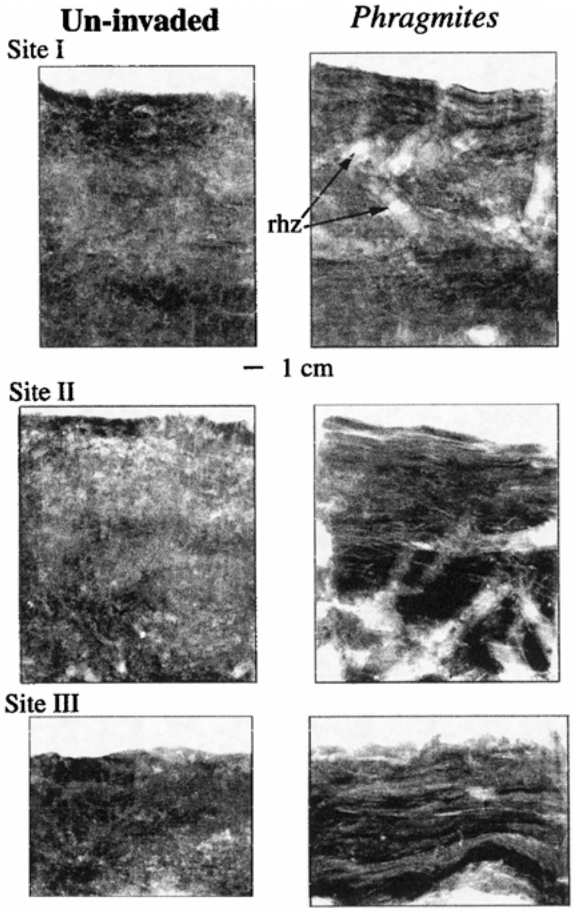

Figure 5. X-radiographs of the un-invaded marsh grass and *Phragmites* sediments from three sites along the lower Connecticut River estuary. Light areas indicate lower density sediments than darker areas. Characteristic thick *Phragmites* rhizomes (rhz) are indicated in the Site I *Phragmites* X-radiograph.

Epifauna

Epifauna consisted primarily of gastropods, peracarid and decapod crustaceans, insects and arachnids. Common gastropods at all sites (*Phragmites* and un-invaded habitats combined) included the pulmonate *Melampus bidentatus*, which had highest densities (mean ± 1 SE) at Site I (20 ± 7 individuals m^{-2} in May; 8 ± 3 individuals m^{-2} in September), *Succinea wilsoni* which had highest densities at Site III (116 ± 18 individuals m^{-2} in May; 20 ± 6 individuals m^{-2} in September), and *Stagnicola catascopium,* which only occurred at Site III during May (44 ± 16 individuals m^{-2}). Densities of *S. wilsoni* were generally higher in the un-invaded habitat, while densities of *M. bidentatus* did not differ between the un-invaded and *Phragmites* habitats of any site during May or September (Table 3). Density of *S. catascopium* in Site III was higher in the un-invaded than *Phragmites* habitat, where it was absent.

Pitfall trap taxa that had not been seen in the benthic cores or quadrats included a grasshopper (family Tettigoniidae), a cricket (family Gryllidae), an ant (family Formicidae), the fiddler crabs *Uca minax* and *U. pugnax* and the green crab *Carcinus maenas* (Table 4). The pitfall traps also collected taxa similar to those found in the benthic cores: the arachnids *Pardosa* spp. and mites, the beetle *Enochrus hamiltoni*, an unidentified beetle larvae, podurids (Collembola), tabanid dipteran larvae, the amphipod *Orchestia grillus* and the isopod *Philloscia vittata* (Table 4). At the end

Table 3. Densities (individuals m^{-2}) of gastropods found in the un-invaded marsh grass and *Phragmites* habitats in three sites along the lower Connecticut River estuary during May and September 1999.

	Site I				Site II				Site III			
	Un-invaded		*Phragmites*		Un-invaded		*Phragmites*		Un-invaded		*Phragmites*	
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE
May 1999												
Melampus bidentatus	28	12	12	6	22	10	5	3	0	0	0	0
Succinea wilsoni	100	32[a]	12	8	168	40[a]	8	8	115	18	116	32
Stagnicola catascopium	0	0	0	0	0	0	0	0	88	24[a]	0	0
September 1999												
Melampus bidentatus	51	23	14	8	10	5	3	2	0	0	0	0
Succinea wilsoni	2	2	3	3	24	8[a]	0	0	165	35[a]	0	0
Stagnicola catascopium	0	0	0	0	0	0	0	0	0	0	0	0

$n = 10$ quadrats.

[a] significance ($P < 0.006$) between habitats (within site and date). Bonferroni adjusted $\alpha = 0.006$. No symbol represents no significant difference ($P > 0.05$).

of the survey, over 4 times as many crabs (*Uca pugnax*, *U. minax* and *C. maenas*) had been caught in the *Phragmites* than un-invaded habitats of Sites I (9 versus 2 crabs) and III (18 versus 4 crabs). No crabs were captured at Site II (Table 4). These data suggest that differences in densities of mobile fauna (e.g., crabs) might exist between *Phragmites* and un-invaded marshes. However, these pitfall trap data cannot be quantitatively analyzed because of the loss of various replicates during each sampling period when several traps flooded and animals escaped. High replication and better designed (e.g., draining) pitfall traps could be valuable for determining mobile faunal communities.

Litter fauna. The dense litter in the *Phragmites* habitat of Site III during September hosted faunal communities of 4784 ± 1483 individuals m^{-2} (8 ± 3 individuals g dw^{-1}) and 19 taxa per site compared with the 3008 ± 633 individuals m^{-2} and 13 taxa per site found in the *Phragmites* sediments (macro-infauna) on the same date (Table 5). The litter contained 4 taxa (Chelonethidan [pseudoscorpions], an unidentified adult and unidentified larval coleopteran and Staphylinidae) which were not collected in the sediments (Table 5). The *Phragmites* litter fauna consisted mostly of enchytraeid and naidid oligochaetes (45%), coleopteran and dipteran larvae (20%), and the peracarid crustaceans *Orchestia grillus* and *Philoscia vittata* (17%). Also present were arachnids (7%), turbellarians (6%), sabellid worms (4%) and the gastropod *Succinea wilsoni* (3%). Density of fauna in the bottom layer of litter was 3× higher than in the top layer and was dominated by both burrowers (49%) and errant fauna (47%), whereas errant fauna dominated the top litter layers (67%). Most taxa were found in both layers. However, sabellid polychaetes, dolichopodid and muscid insect larvae and chelonethids were found only in the bottom layer, and the spider *Grammonota trivittata*, soldier beetles (Cantharidae) and rove beetles (Staphylinidae), as well as unidentified beetle larvae, were found only in the top layer (Table 5).

Macro-infauna

Abundance, composition and diversity. Densities of total macro-infauna (hereafter referred to as macrofauna) ranged from 6000 to 142,000 individuals m^{-2} in May and 3000 to 27,000 individuals m^{-2} in September. Highest densities occurred at Site I, intermediate values at Site II (May only) and lowest densities at Site III (May: ANOVA $P < 0.001$, $F_{2,18} = 32.1$; September: $P < 0.001$, $t_{16} = 5.2$) (Table 5). Total macrofaunal biomass did not differ between sites or habitats and ranged from 11 to 47 g wet wt. m^{-2} in May and 1 to 6 g wet wt. m^{-2} in September.

Major macrofaunal taxa within the marsh habitats included tubificid, enchytraeid and naidid oligochaetes (20–68%), insects (1–73%), especially podurids and midge (chironomid and ceratopogonid) larvae, polychaetes (4–42%), especially sabellids, and arachnids (0–16%, mainly mites) (Table 2). In May, when densities were highest, the un-invaded areas of all 3 sites hosted different macrofaunal communities than the *Phragmites* areas (ANOSIM, $P < 0.004$) (Figure 6, Table 6). Un-invaded sediments contained 2–3 times greater densities of total macrofauna (Site II, $P = 0.040$; $t_{12} = 2.3$ and III, $P = 0.02$, $t_{12} = 2.7$) although these differences were

Table 4. Presence (+) or absence (blank) of each taxon found in the pitfall traps of the invasive *Phragmites* (P.a.) and un-invaded marsh grass (Un) habitats in three sites along the lower Connecticut River estuary from May through September 1999. No animals were found during the July 14 and 22 samplings.

	11 May 1999						30 June 1999						8 July 1999						5 August 1999						14 September 1999					
	Site I		Site II		Site III		Site I		Site II		Site III		Site I		Site II		Site III		Site I		Site II		Site III		Site I		Site II		Site III	
	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un	P.a.	Un
Arachnida																														
Pardosa sp.	+		+	+																					+		+	+		+
Mite												+																		
Insecta																														
Enochrus hamiltoni				+																										
Coleopteran larvae								+																						
Tabanus sp. larvae																+												+		
Tettigoniidae																+														
Gryllidae																+											+			
Poduridae	+																													
Formicidae						+																								
Crustacea																														
Orchestia grillus	+		+	+		+	+	+					+	+	+	+	+	+							+	+	+	+	+	
Philoscia vittata	+																								+	+	+			
Uca minax											+	+					+	+											+	
Uca pugnax													+							+										
Carcinus maenas																									+	+				

Table 5. Density of each macrofaunal taxon found in the un-invaded marsh grass and *Phragmites* stands within three sites of the lower Connecticut River estuary during May and September 1999. Values are average (±1 SE) number of individuals m^{-2}, $n = 7$ benthic samples in May, and 9 benthic and 10 litter samples in September 1999.

	Site I				Site II				Site III			
	Un-invaded		*Phragmites*		Un-invaded		*Phragmites*		Un-invaded		*Phragmites*	
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE
May 1999												
Annelida												
Polychaeta												
Capitella spp.	158	158	0	0	79	79	0	0	237	164	316	164
Sabellidae	9,717	2,963	20,224	4,432	3,081	2,990	12,245	7,220	0	0	1,343	1,092
cf. *Arenicola* sp.	0	0	0	0	0	0	0	0	79	79	0	0
Ampharetidae	0	0	0	0	0	0	237	237	0	0	0	0
Oligochaeta												
Tubificidae	9,480	2,626	7,189	2,189	20,461	8,115	3,476	1,223	5,135	4,598	158	158
Naididae	2,370	549	2,765	973	3,160	701	2,212	818	158	102	1,185	504
Enchytraeidae	56,248	13,284	46,531	11,358	14,852	3,599	9,164	2,531	1,501	901	316	112
Nemertea	79	79	0	0	0	0	0	0	0	0	0	0
Platyhelminthes	237	164	79	79	0	0	316	237	79	79	158	102
Mollusca												
Gastropoda												
Hydrobia totteni	0	0	0	0	0	0	0	0	0	0	0	0
Melampus bidentatus	0	0	79	79	0	0	79	79	0	0	0	0
Succinea wilsoni	237	164	237	164	316	237	0	0	158	158	79	79
Stagnicola catascopium	0	0	0	0	0	0	0	0	0	0	79	79
Arthropoda												
Arachnida												
Chelonethida	0	0	0	0	0	0	0	0	0	0	0	0
Grammonota spp.	0	0	79	79	0	0	0	0	0	0	0	0
Pardosa spp.	0	0	0	0	0	0	0	0	158	158	0	0
Mites	25,833	8,835	7,505	3,273	9,401	4,725	0	0	237	164	0	0
Crustacea												
Orchestia grillus	0	0	79	79	0	0	0	0	0	0	0	0
Philoscia vittata	158	102	237	112	0	0	0	0	0	0	79	79
Insecta												
Coleoptera (unid adult)	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera (unid larvae)	0	0	0	0	0	0	0	0	0	0	0	0
Cantharidae	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus hamiltoni	79	79	0	0	0	0	0	0	0	0	0	0
Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0
Poduridae	79	79	23,226	5,819	0	0	1,185	371	79	79	0	0
Dipteran (unid pupae)	0	0	79	79	0	0	316	237	0	0	79	79
Ceratopogonid larvae	1,580	306	0	0	474	254	474	254	2,370	868	395	395
Chironomid larvae	35,866	11,314	13,272	5,744	8,848	4,015	395	395	9,243	2,643	1,817	395
Dolichopodid larvae	0	0	158	102	0	0	237	164	0	0	0	0
Dytiscid larvae	0	0	0	0	0	0	0	0	0	0	0	0
Muscid larvae	0	0	0	0	0	0	79	79	79	79	79	79
Homoptera	0	0	0	0	79	79	0	0	0	0	0	0
Aphidae	79	79	0	0	316	112	0	0	0	0	0	0
Coccoidea	0	0	0	0	0	0	0	0	632	474	0	0
No. macrofauna m^{-2}	142,200	23,611	121,739	21,905	61,067	9,657	30,415	8,670	20,145	7,174	6,083	1,182
Biomass g wet wt. m^{-2}	47	31	16	3	40	16	6	2	11	5	7	4
No. species per site	15		15		11		13		14		13	

Table 5. Continued

	Site I				Site III				Site III			
	Un-invaded		*Phragmites*		Un-invaded		*Phragmites*		*Phragmites* litter fauna			
									Top layer		Bottom layer	
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE
September 1999												
Annelida												
Polychaeta												
Capitella spp.	0	0	184	130	246	163	0	0	0	0	0	0
Sabellidae	3,134	1,431	6,513	2,450	0	0	1,229	430	0	0	281	235
cf. *Arenicola* sp.	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	0	0	0	0	0	0	0	0	0	0	0	0
Oligochaeta												
Tubificidae	2,642	878	3,564	1,506	1,659	975	184	130	0	0	0	0
Naididae	4,178	1,159	1,659	583	676	273	553	160	128	80	552	181
Enchytraeidae	3,994	854	13,211	6,827	676	329	307	97	180	52	1,224	537
Nemertea	0	0	0	0	0	0	0	0	0	0	0	0
Platyhelminthes	614	194	676	222	0	0	307	187	32	32	479	347
Mollusca												
Gastropoda												
Hydrobia totteni	799	799	0	0	0	0	0	0	0	0	0	0
Melampus bidentatus	0	0	0	0	0	0	0	0	0	0	0	0
Succinea wilsoni	61	61	0	0	61	61	0	0	63	37	24	24
Stagnicola catascopium	0	0	0	0	0	0	0	0	0	0	0	0
Arthropoda												
Arachnida												
Chelonethida	0	0	0	0	0	0	0	0	0	0	21	21
Grammonota spp.	0	0	0	0	0	0	0	0	109	71	0	0
Pardosa spp.	61	61	0	0	123	123	0	0	11	11	38	26
Mites	492	268	123	81	307	163	0	0	13	13	29	20
Crustacea												
Orchestia grillus	0	0	123	81	0	0	61	61	239	113	146	79
Philoscia vittata	0	0	246	134	0	0	0	0	135	68	73	44
Insecta												
Coleoptera (unid adult)	0	0	0	0	0	0	0	0	0	0	12	12
Coleoptera (unid larvae)	0	0	0	0	0	0	0	0	16	16	0	0
Cantharidae	0	0	0	0	0	0	0	0	21	21	0	0
Enochrus hamiltoni	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae	0	0	0	0	0	0	0	0	8	8	0	0
Poduridae	0	0	0	0	0	0	0	0	0	0	0	0
Dipteran (unid pupae)	0	0	0	0	0	0	0	0	27	27	0	0
Ceratopogonid larvae	0	0	0	0	0	0	0	0	0	0	0	0
Chironomid larvae	61	61	307	187	0	0	369	244	66	33	709	367
Dolichopodid larvae	0	0	61	61	0	0	0	0	0	0	112	61
Dytiscid larvae	0	0	0	0	61	61	0	0	0	0	0	0
Muscid larvae	0	0	0	0	0	0	0	0	0	0	42	35
Homoptera	0	0	0	0	0	0	0	0	0	0	0	0
Aphidae	0	0	0	0	0	0	0	0	0	0	0	0
Coccoidea	0	0	0	0	430	316	0	0	0	0	0	0
No. macrofauna m^{-2}	16,092	2,157	26,728	11,259	4,240	1,005	3,008	633	1,041	249	3,743	1,390
Biomass g wet wt. m^{-2}	4	1	6	2	3	1	1	1	No data			
No. species per site	10		11		9		7		19			

Un-invaded = salt marsh grasses (*Spartina patens, Distichlis spicata, Juncus gerardii*); *Phragmites* = *Phragmites australis*; unid = unidentified; SE = standard error.

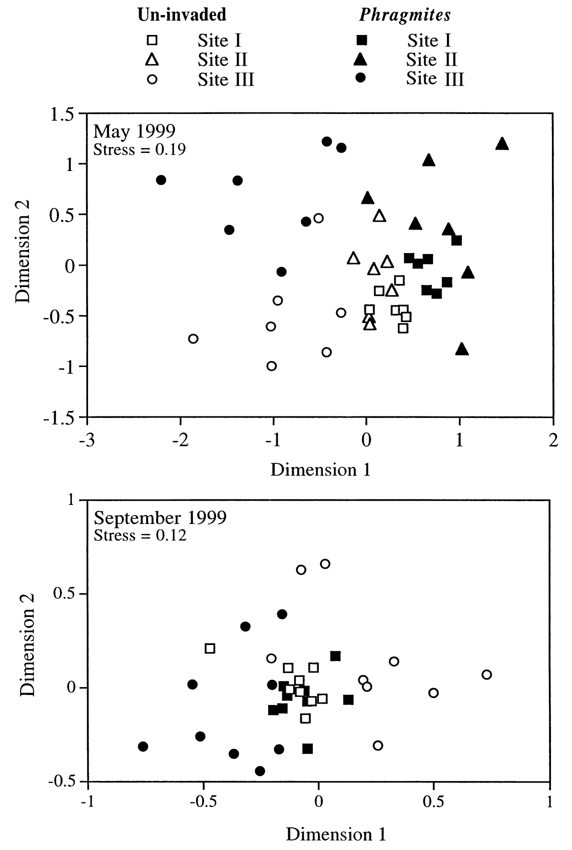

Figure 6. Multidimensional scaling of macrofaunal abundances from the *Phragmites* and un-invaded marsh grass habitats located in three locations along the lower Connecticut River Estuary during May and September 1999. Each point represents the assemblage within one core.

Table 6. Comparisons of macrofaunal assemblages from the invasive *Phragmites* and un-invaded marsh grass habitats within three sites along the lower Connecticut River estuary during May and September 1999. Shown are pairwise Analysis of Similarity (ANOSIM) probabilities and SIMPER between-site percent similarities.

Date	Site	ANOSIM *P*	SIMPER % Similarity
May	I	0.001	65
	II	0.001	45
	III	0.004	38
September	I	0.07	70
	III	0.003	25

Significance was set at $\alpha = 0.010$ based on Bonferroni adjustment for the number of pairwise comparisons. $n = 7$ (18 cm^2 × 6 cm deep) cores for May 1999, $n = 9$ cores for September.

not significant at the Bonferroni adjusted α of 0.003 (Table 5). The un-invaded compared to *Phragmites* areas had higher densities of arachnids (Sites I and II only), midges and tubificid oligochaetes (Site II only), and lower densities of podurids (Sites I and II only) ($P \leq 0.003$, $t_{12} \geq 3.70$) (Table 2). *Phragmites*-habitat sediments exhibited higher densities of the sabellid worm (Site I only) and lower densities of enchytraeid oligochaetes (Site III only) contributing to differences in the macrofaunal communities between the two habitats (SIMPER, Figure 6). Macrofaunal communities of the *Phragmites* and un-invaded areas were the most similar at Site I (65% similarity, SIMPER), intermediate at Site II (45%), and least similar at Site III (38%) during May (Table 6). Differences between the *Phragmites*- and un-invaded-habitat macrofauna changed along the salinity/age gradient in May with respect to density and proportion of arachnids and podurids (Table 2B). Differences in the abundance of both taxa between the *Phragmites* and un-invaded habitats diminished with distance upstream due to concurrent decreases in density in both habitats (Table 5).

Lower macrofaunal densities in September caused many of these differences to disappear. There were, however, fewer sabellids (Site III only; $P = 0.001$, $t_{16} = 4.03$) in the un-invaded compared with the *Phragmites* habitats (Table 5). Assemblage differences between the *Phragmites* and un-invaded macrofaunal communities evident in MDS plots (Figure 6) were additionally attributed to higher densities of arachnids, and tubificid and enchytraeid oligochaetes in the un-invaded relative to the *Phragmites* habitat (SIMPER). Macrofaunal communities in the *Phragmites* and un-invaded areas were similar (ANOSIM $P = 0.07$; SIMPER 70% similarity) at Site I and different (ANOSIM $P = 0.003$; SIMPER 25%) at Site III during September (Figure 6; Table 6). Differences in the proportion of naidids, sabellids and total tube-builders between the *Phragmites* and un-invaded habitats were greater at Site III than Site I in September (Table 2B); their proportions increased upstream within the *Phragmites* habitat, but decreased upstream in the un-invaded habitats.

There were 29 macrofaunal taxa found in the *Phragmites* habitat and un-invaded-sediments throughout this study; 9 were found exclusively in the un-invaded habitat and 4 exclusively in the *Phragmites* habitat (Table 5). Common taxa exclusive to each habitat included coccoidean and aphid insects, the spider *Pardosa* sp. and the gastropod *Hydrobia totteni* in the

Table 7. Macrofaunal taxon richness, evenness and dominance in the un-invaded marsh grass and *Phragmites* habitats at three sites along the lower Connecticut River estuary during May and September 1999.

	Site I				Site II				Site III			
	Un-invaded		*Phragmites*		Un-invaded		*Phragmites*		Un-invaded		*Phragmites*	
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE
May 1999												
Taxon richness per core	8.0	0.5	8.3	0.5	6.7	0.5	5.7	1.0	5.1	1.0	4.0	0.6
Shannon–Weiner H'	2.00	0.13	2.16	0.08	1.71	0.22	1.69	0.21	1.62	0.20	1.65	0.25
Evenness J'	0.67	0.03	0.67	0.02	0.62	0.06	0.71	0.06	0.74	0.05	0.86	0.05
Rank 1 dominance	49	5	42	3	55	8	56	8	55	6	48	6
September 1999												
Taxon richness per core	5.3	0.4	6.1	0.5					7.7	0.3	5.4	0.4
Shannon–Weiner H'	1.95	0.12	1.95	0.08			No data		1.19	0.16	1.39	0.17
Evenness J'	0.83	0.02	0.78	0.03					0.86	0.05	0.91	0.03
Rank 1 dominance	45	3	48	3					62	8	57	7

$n = 7$ cores in May and $n = 9$ in September. $H' = H' \log_2$. No differences were found between the *Phragmites* and un-invaded habitats within each site during each date.

un-invaded habitat, and dolichopodid fly larvae and dipteran pupae in the *Phragmites* habitat (Table 5).

Because some groups were not identified to the species level (e.g., oligochaete families, insect families or orders), we examined diversity at higher levels of organization (see taxa list in Table 5), hereafter referred to as taxa. Overall taxon richness per unit area (number of taxa per core), diversity (Shannon–Weiner H') and evenness (J') were similar in the un-invaded marsh grass and *Phragmites* habitats of all sites on both sampling dates (Table 7). While Site I had higher taxon richness per core than the other sites (May, $P = 0.002$, $F_{2,18} = 8.5$; September, $P < 0.001$, $t_{16} = 4.3$; $\alpha = 0.003$), there were no site differences in diversity (H') or evenness (J') on either date (Table 7). Total taxonomic richness per transect, standardized to number of individuals using rarefaction (Hurlbert 1971), appeared higher in the *Phragmites* relative to un-invaded sediments of Sites II and III, but similar at Site I during May (Figure 7). Transect-wide taxonomic richness was more similar among sites and habitats in September than in May (Figure 7). The percent of total macrofaunal individuals belonging to the dominant taxon in each habitat (Rank 1 dominance) was between 42 and 62% and did not differ between the *Phragmites* and un-invaded habitats within each site on either date (Table 7). Rank 1 dominance did not differ among sites and ranged from 43 to 56% in May and 45 to 62% in September.

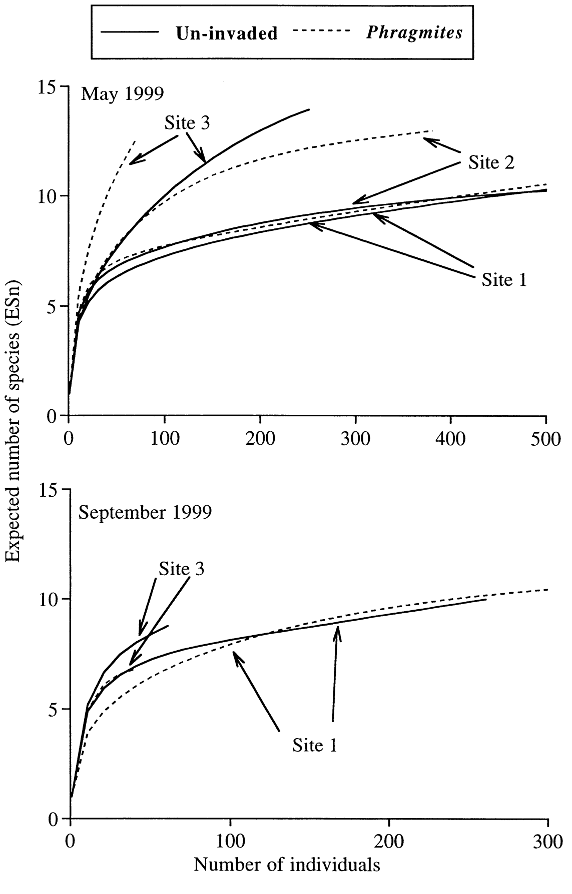

Figure 7. Rarefaction curves of macrofauna from the un-invaded marsh grass and *Phragmites* habitats in three sites along the lower Connecticut River estuary during May and September 1999. Data from each transect were pooled for analyses.

Lifestyles. The most common dwelling habit of macrofauna in all sites was burrowing (22–69%). Proportion

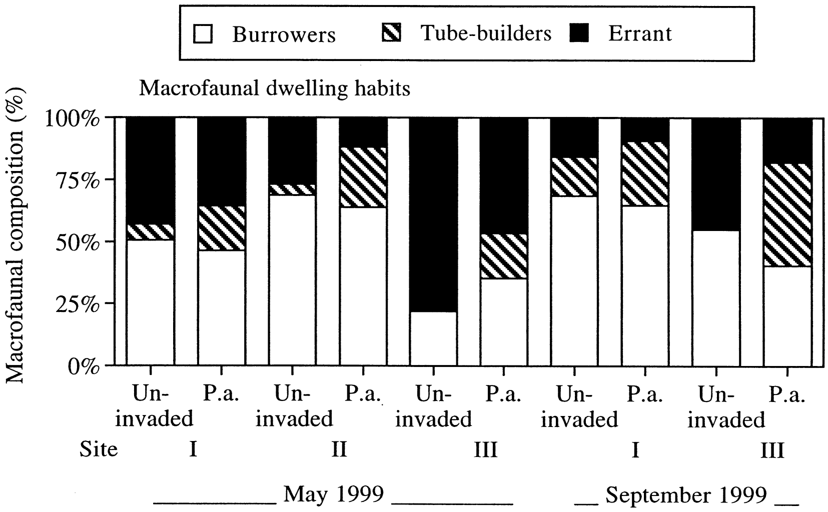

Figure 8. Mean percent abundance of each macrofaunal dwelling group within the un-invaded marsh grass and *Phragmites* (P.a.) habitats of three sites along the lower Connecticut River estuary during May and September 1999. $n = 7$ samples in May and $n = 9$ in September.

of burrowers was similar in the *Phragmites* and un-invaded areas (Figure 8). *Phragmites* habitats often had higher densities of tube-builders (Site I in May, $P = 0.030$, $t_{12} = 2.5$; Site III in September, $P = 0.001$, $t_{16} = 4.0$) and lower densities of errant fauna (Sites III in May, $P = 0.019$, $t_{12} = 2.7$) than un-invaded habitats (Figure 8). For the above lifestyle comparisons, Bonferroni-adjusted $\alpha = 0.020$.

Discussion

Phragmites influence on sediments and fauna

Evaluation of the consequences of invasion for sediment faunas requires an understanding of habitat change. Stands of *Phragmites* have historically been limited to upland borders of tidal marshes (Niering et al. 1977; Niering and Warren 1980a) and so until recently have remained spatially separated from most salt marsh grass habitats. The invasion of *Phragmites* into these more saline marsh grass areas dramatically changes sediment properties and plant composition and structure; there are often shifts to *Phragmites* monocultures (Windham and Lathrop 1999; Bart and Hartman 2000, this study). These differences in environmental variables are reflected in the macrofaunal density and composition of *Phragmites*-invaded and un-invaded marsh sediments in the lower Connecticut River estuary. However, the mechanisms of influence have not been identified. Natural *Typha angustifolia* (cattail) and *Phragmites* stands, which are dominated by plants with similar growth morphologies, exhibit similar sedimentary properties (organic matter, sand, presence of laminations; Levin et al. unpublished data); suggesting that plant structure plays a significant role in shaping the sedimentary environment.

The shifts in macrofaunal composition that accompany *Phragmites* invasion involve loss of burrowing oligochaetes and midges and an increase in surface-feeding forms (sabellid polychaetes and podurids). Higher combustible organic matter content in the un-invaded stands was linked to extremely dense mats of roots and rhizomes found associated with the salt marsh grasses. This dense matrix of roots appears to promote oligochaetes (especially enchytraeids) (Levin et al. 1998), but may inhibit larger burrowers. Abundances of surface (errant) species (mostly arachnids and insects) were reduced in the *Phragmites* stands relative to un-invaded habitat. Sparser roots and rhizomes (less cohesive substratum), and increased trapping of organic matter by slowed flow and litter layers are possible explanations for greater abundances of tube-builders (mostly sabellid polychaetes) in the *Phragmites* relative to un-invaded stands. A dominant sabellid, *Fabricia sabella,* is a facultative surface deposit and suspension feeder capable of consuming particles in a range of flow regimes. Higher deposition rates, reduced sediment aeration by roots and rhizomes, and limited water circulation beneath litter probably generate the laminations observed in the X-radiographs of *Phragmites* stands (see Figure 5). *Phragmites*-induced differences in below-ground and sediment-surface structure may contribute to altered nutrient cycling (Nijburg and Laanbroek 1997; Brulisauer and Klotzli 1998).

Influence of age, salinity and season

The results of this study indicate that the extent of influence of an invasive wetland plant can vary with age, salinity and season. We predicted that *Phragmites* effects should have been minimal at low salinities, where marsh faunas should exhibit greatest affinities with freshwater forms occupying traditional *Phragmites* habitat. However, the reverse was observed, probably because the least saline site had also been invaded the longest (ca. 26 yrs), and the most saline site was invaded fairly recently (<10 yrs). Unfortunately, the experimental design, involving three *Phragmites* sites, each with a different salinity and different time since invasion, did not allow a replicated test of salinity or age influence on *Phragmites*.

Seasonality plays a key role in detection of invasive plant effects on fauna. During September, when densities were greatly reduced, few significant faunal differences were observed between *Phragmites* and un-invaded stands. Had sampling been limited to a single date in Fall, our conclusions may have differed from those presented here. Although two sampling periods are insufficient to adequately characterize seasonality in any system, the trends we observed reflect typical temperate-marsh, seasonal shifts (e.g., Levin 1984; Frid and James 1989; Marsh and Tenore 1990; Trueblood et al. 1994; Sarda et al. 1995). The seasonality in *Phragmites* influence on macrofauna suggests that consequences for consumers of macrofauna should also be seasonal. Alternatively, the density reductions observed between May and September may have been generated by extensive predation in both *Phragmites* and un-invaded marsh habitats. Many fish and shellfish utilize these habitats as feeding grounds and nurseries during summer (blue crabs, grass shrimp, snapper blues, stripers, killifish, sticklebacks) and feed extensively on marsh macrofauna (Kneib 1985, 1986; Weinstein and Balletto 1999).

Consequences of Phragmites *invasion*

The finding that *Phragmites*-invaded stands exhibit modified vegetation, sediment and faunal properties is not surprising. Wetland plant invasions typically have significant influence on animal community structure (Posey 1988; Posey et al. 1993). More problematic is an understanding of the consequences of these modifications for salt marsh ecosystem function. The invertebrate taxa displaced by *Phragmites* (i.e., gastropods, oligochaetes, midges) almost certainly play key roles in organic matter and nutrient cycling and provide trophic support for fish and shellfish within the marsh. It is unknown whether their roles differ from those of the sabellid polychaetes and podurid insects that replaced them. The reduced density of invertebrates within *Phragmites* stands found in this study may represent a lost food base for consumers at the less saline sites. Investigations by Weinstein and Balletto (1999) and Wainright et al. (2000) in mid-Atlantic *Spartina alterniflora* marshes indicate that fishes occupying *Phragmites*-invaded habitat obtain nutrition from animals that feed on *Phragmites* detritus. We do not know anything, however, about the relative efficiency of energy transfer, nor the relative nutritional values of animals dominant in *Phragmites* versus un-invaded marsh grass habitats. Laboratory studies and field experiments that focus on functional attributes of marshes (e.g., primary and secondary production, animal growth rates, trophic transfer efficiency) will be required to address these issues.

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