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Rates, Patterns, and Impacts of *Phragmites australis* Expansion and Effects of Experimental *Phragmites* Control on Vegetation, Macroinvertebrates, and Fish within Tidelands of the Lower Connecticut River

R. SCOTT WARREN*, PAUL E. FELL, JONNA L. GRIMSBY, ERIKA L. BUCK, G. CHRIS RILLING, and RACHEL A. FERTIK

Goodwin-Niering Center for Conservation Biology and Environmental Studies, Connecticut College Box 5362, 270 Mohegan Avenue, New London, Connecticut 06320–4196

ABSTRACT: ***Phragmites*** **expansion rates (linear at 1–3% yr^{-1}) and impacts of this expansion on high marsh macroinvertebrates, aboveground production, and litter decomposition from *Phragmites* and other marsh graminoids were studied along a polyhaline to oligohaline gradient. These parameters, and fish use of creeks and high marsh, were also studied in *Phragmites* control sites (herbicide, mowing, and combined herbicide/mow treatments). *Phragmites* clones established without obvious site preferences on oligohaline marshes, expanding radially. At higher salinities, *Phragmites* preferentially colonized creekbank levees and disturbed upland borders, then expanded into the central marsh. Hydroperiods, but not salinities or water table, distinguished *Phragmites*-dominated transects. Pooled samples of *Phragmites* leaves, stems, and flowers decompose more slowly than other marsh angiosperms; *Phragmites* leaves alone decompose as or more rapidly than those of cattail. Aboveground *Phragmites* production was 1,300 to 2,400 g m^{-2} (about 23% of this as leaves), versus 600–800 g m^{-2} for polyhaline to mesohaline meadow and 1,300 g m^{-2} for oligohaline cattail-sedge marsh. Macroinvertebrates appear largely unaffected by *Phragmites* expansion or control efforts; distribution and densities are unrelated to elevation or hydroperiod, but densities are positively related to litter cover. Dominant fish captured leaving flooded marsh were *Fundulus heteroclitus* and *Anguilla rostrata*; both preyed heavily on marsh macroinvertebrates. *A. rostrata* and *Morone americana* tended to be more common in *Phragmites*, but otherwise there were no major differences in use patterns between *Phragmites* and brackish meadow vegetation. SAV and macroalgal cover were markedly lower within a *Phragmites*-dominated creek versus one with *Spartina*-dominated banks. The same fish species assemblage was trapped in both, plus a third within the herbicide/mow treatment. Fish biomass was greatest from the *Spartina* creek and lowest from the *Phragmites* creek, reflecting abundances of *F. heteroclitus*. Mowing depressed *Phragmites* aboveground production and increased stem density, but was ineffective for control. *Phragmites*, *Spartina patens*, and *Juncus gerardii* frequencies after herbicide-only treatment were 0.53–0.21; total live cover was < 8% with a heavy litter and dense standing dead stems. After two growing seasons *Agrostis stolonifera*/*S. patens*/*J. gerardii* brackish meadow characterized most of the herbicide/mow treatment area; *Phragmites* frequency here was 0.53, contributing 3% cover. Both values more than doubled after four years; a single treatment is ineffective for long-term *Phragmites* control.**

Introduction

Root and rhizome fragments recovered from three or more meters below today's marsh surfaces demonstrate that *Phragmites australis* (Cav.) Trin ex Steud, common reed grass, has been a component of brackish tidal wetland flora along Long Island Sound, and probably most of the Mid-Atlantic to New England coast, for over three millennia (Niering et al. 1977; Clark 1986; Orson et al. 1987). Both peat cores and historic vegetation descriptions (Torrey 1843; Dame and Collins 1888; Graves et al. 1910; Nichols 1920; Orson 1999) indicate that until relatively recently *Phragmites* has been a minor component of brackish tideland vegetation. Today *Phragmites* is a highly invasive species in tidal and non-tidal wetlands throughout eastern North America, converting the natural vegetation mosaic of these systems into dense, nearly monotypic stands of reed, with stems typically 2 to 3 m tall at densities of 50 to over 100 m^{-2} (Marks et al. 1994; Chambers et al. 1999; Galatowitsch et al. 1999; Windham and Lathrop 1999; Rice et al. 2000). Reasons for such a dramatic increase in the competitive success of *Phragmites* are not well understood, but probably include both the introduction of new genotypes (Besitka 1996; Galatowitsch et al. 1999) and human disturbance of coastal wetlands (Chambers et al. 1999; Bart and Hartman 2000) particularly tidal restrictions (Roman et al. 1984;

* Corresponding author: tele: 860/439-5021; fax: 860/439-2519; e-mail: rswar@conncoll.edu.

Rozsa 1995), which create sites and environments favoring colonization by this grass.

Fell et al. (1998) report that invertebrate prey abundance and foraging on the high marsh by estuarine fish appear to be largely unaffected on marshland dominated by *Phragmites*. Angiosperm and avian biodiversity are significantly reduced in *Phragmites*-invaded marshes (Benoit and Askins 1999) and Windham and Lathrop (1999) report that *Phragmites* invasion of a brackish tidal wetland is correlated with a simplification of marsh surface microrelief, lower soil salinities and water tables, and greater redox potentials. Changes in other ecological functions and environmental factors that might result from conversion of established tidal wetland vegetation to *Phragmites* are not well understood (Marks et al. 1994; Chambers et al. 1999).

This investigation reports on the rates, patterns, and selected ecological consequences of *Phragmites* expansion along a salinity gradient within brackish tidal wetlands of the lower Connecticut River. Findings on vegetation, primary production, fish use of the high marsh, and litter decomposition are considered with the earlier work on fish and macroinvertebrates by Fell et al. (1998).

In response to documented impacts on angiosperms and birds, plus concerns about possible changes to other critical ecosystem functions, the State of Connecticut began a series of *Phragmites*-control treatments, combining mowing and herbicide application, in these same marshes. The impacts of these control efforts on marsh vegetation, primary production, macroinvertebrates, as well as fish use of marsh creeks and the flooded high marsh surface, contribute to understanding the ecological impacts of *Phragmites* invasion, as well as attempts at its control.

Methods

Study Site

This work was done within the complex of tidal wetlands along the eastern shore of the lower Connecticut River (Fig. 1), on the Great Island and Upper Island tidal marshes along the Back River, c. 2.0 km from the mouth of the Connecticut, and marshland bordering the Lieutenant River, which enters the Connecticut 2.5 km further upriver. The marshes of Goose Island and Lord Cove, another 7–8 km upriver, were also included in the study of *Phragmites* invasion rates. Mean tide range at the mouth of the river is 100 cm and 99 cm at the Interstate 95 bridge, 5.7 km upriver.

Spread of *Phragmites*

False color infrared (FCIR) air photos from 1974, 1981, 1986, and 1990 and black and whites from 1994 were enlarged to a scale of 1:4,800. *Phragmites* was identified by color, texture, and ground truth. *Phragmites*-dominated patches of marsh were traced and areas determined by planimetery. Percent of the total marsh area dominated by *Phragmites* on different sections of tideland was determined for each year and used to calculate rates of *Phragmites* spread by linear regression.

Vegetation/Salinity Transects

In 1993 and 1994 seven pairs of 40-m transects, set approximately 90° to the river bank, were distributed along a 5 km salinity gradient from south, on Great Island (season mean peat salinity = 19.3‰) to north, on the west bank of the Lieutenant River (season mean peat salinity = 4.3‰). These were located to sample the range of uninvaded marsh vegetation, from *Spartina patens/Juncus gerardii* salt marsh in the south to cattail/sedge oligohaline marshes to the north. Locations were constrained by the limited reaches of river and creek bank free of *Phragmites*. Transects in each pair were within 150 m of each other. For all but the southernmost pair, one was dominated by *Phragmites* and the other was sited to intercept as little *Phragmites* as possible. The southernmost pair was located below extensive areas of *Phragmites*; one line was completely *Phragmites* free while the second included two small, sparse *Phragmites* patches. Locations of these transects are indicated in Fig. 1.

In 1997 fifteen 40-m vegetation and invertebrate sampling transects were similarly established in the state's *Phragmites* control area by the mouth of the Lieutenant River (Fig. 1). The state did not replicate control treatments over multiple sites but each treatment was sampled in triplicate. Treatments used were: herbicide only (1.25% glyphosate [Rodeo (N Phosphomethylglycine), Pharmica Corporation] in water with an aquatic surfactant [ChemSurf, Chemmose, Inc.] applied at 460 l ha^{-1}) in two plots totaling ca. 1.5 ha (spray), mow only in one plot of ca. 1.3 ha (mow), both in late summer 1996, within three weeks of anthesis, and herbicide in late summer 1995 followed by mowing in spring 1996 in one ca. 16-ha plot, across the river, north of the spray and mow treatments (spray/mow). Untreated *Phragmites* on the southern side of the Lieutenant River (reference) was used as a control and also sampled in triplicate. A fourth transect was established within the spray/mow treatment in an area of sparse angiosperm cover and a single additional line was laid out in a *Phragmites*-free stand of *Typha angustifolia*. By 1997, most of the spray/mow area was dominated by a brackish meadow plant community and this area is also termed restored meadow.

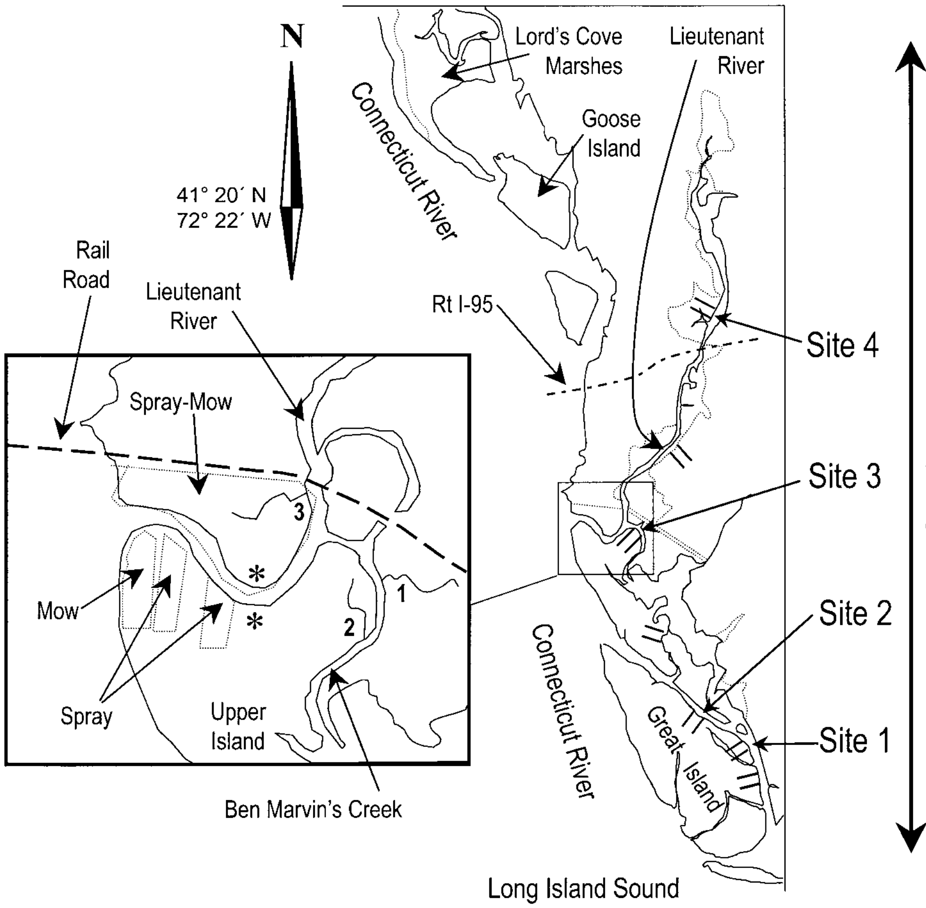

Fig. 1. East shore of the lower Connecticut River estuary from Long Island Sound to Lord's Cove. *Phragmites* expansion was followed at Lord's Cove, Goose Island, the Lieutenant River marshes, Upper Island, and Great Island. Location of the seven 1994 vegetation transect pairs indicated by sets of parallel lines; invertebrates and primary production were also sampled at Sites 1–4. Blow-up is of experimental *Phragmites* control area at the mouth of the Lieutenant River. Numbers here note fish sampling creeks: 1) largely *Phragmites*-free, 2) *Phragmites*-dominated, and 3) brackish meadow restored with herbicide/mow treatment. High marsh fish sampling sites indicated by *.

Salinity and Water Table Measurements

Soil water wells (5 cm diam PVC pipe, perforated beginning 5 cm below the marsh surface and loosely capped to keep out rain and debris) sampling the top 30 cm of peat were set at 3, 10, and 30 m on each transect. Water table depth, well water salinity, and creek surface water salinity were measured weekly from mid June to mid August of 1993 and 1994 for the transect pairs along the salinity gradient and similarly on the *Phragmites* control site transects in 1997. Tide stage at the time of measurements was recorded as Low (predicted time of low tide ± 1.5 h), Flood, High (predicted time of high tide ± 1.5 h), and Ebb.

Elevations

Cork dust tidal flooding gauges were set at 10 and 30 m on each salinity gradient transect in 1994 and all the *Phragmites* control transects in 1997. Depth of flooding during spring tides was measured at least ten times from mid June to mid August; subtracting flood height above the marsh surface from predicted tide height (I-95 bridge station: Tide1, Micronautics, Inc., Rockport, Maine) gave relative elevation for the marsh surface at each gauge; the tidal datum was local mean lower low water. Seasonal means for these calculated marsh surface elevations were used to establish benchmarks for each transect. At the Lieutenant River *Phragmites* control site benchmark relative elevations were further checked with overlapping closed level loops (total length 2.1 km, closing error < 1.5 cm), which included every benchmark. Elevation was measured at 1-m intervals along each transect line by standard surveying techniques. Mean high marsh elevations were calculated using all measurements beyond the point where intertidal *Spartina alterniflora* cover fell to < 50%, which always occurred between 85 and 90 cm. Elevation of each invertebrate sampling plot was also determined from the mean of five points within each plot, one at each corner plus the center.

Vegetation

Species present were recorded in contiguous 1-m^2 quadrats along each transect line in mid to late June. Percent cover for each species was also estimated visually in each quadrat. Transects in the spray/mow treatment area were re-sampled in mid August of 1997.

Primary Production

In 1994 four pairs of transects, designated Sites 1–4 (most to least saline, Fig. 1) were selected for detailed sampling of macroinvertebrate populations (Fell et al. 1998) and estimates of angiosperm primary production. In mid August (ca. peak aboveground live standing crop, PLSC) five 0.25-m^2 quadrats were sampled at each salinity gradient transect by clip harvest. Plant material was sorted into live (current year's growth) and dead. Samples were dried at 100°C to a constant dry weight and mean peak live standing crop was used as a conservative estimate of productivity.

A second estimate of 1994 *Phragmites* production was based on the approach of Morris and Haskin (1990). Transects were sampled for live and dead *Phragmites* stem density and flowering frequency using five 0.25-m^2 quadrats located at 3, 10, 20, 30, and 40 m along each transect. At the same time 10 shoots were randomly collected from each quadrat and returned to the laboratory; shoots were collected from the immediate area to get a total of ten if a quadrat included less than 10 shoots. Shoot height, nodes, persisting leaves, abscised leaves, and flowering frequency were averaged for each transect. Shoots were separated into stems, leaf sheaths, leaf blades, and flowers and each component was dried at 100°C to a constant dry weight. These results were used to calculate mean weight per cm of stem, per leaf sheath, per leaf blade, and per flower; the sum of these was used as total weight per shoot. Productivity was estimated for each site from its mean weight per shoot multiplied by stem density. In 1997 productivity at each *Phragmites* control site transect was estimated by PLSC using clip harvest in mid-August, as above.

Litter Decomposition

Dry weight loss from litter bags was used as a measure of the movement of angiosperm primary production into the detrital food chain. Standing dead samples of *S. alterniflora, S. patens, Spartina cynosuroides, T. angustifolia,* and *Phragmites* were collected in April 1994, oven dried at 100°C for 5 d and stored in plastic bags. Litter was re-dried and placed in 5-mm delta mesh 12 × 30 cm litter bags, 20 g bag^{-1}; six sets of litter bags were moored subtidally, attached c. 2 m apart on nylon line, near each of the four production/invertebrate sites on June 6. Each set consisted of one bag for each species. Three sets were collected on July 6 and the remaining on August 5. In the field each bag was gently placed in a separate 2-l plastic container while still under water, and transported to the laboratory.

In the laboratory litter from each bag was rinsed on 1-mm mesh screens; plant material was separated from macroinvertebrates and dried at 100°C to a constant dry weight. Two-way ANOVA revealed no salinity effect on decomposition so data from all four sites were pooled and analyzed by species.

A second litter loss trial was run from September 9 to October 14 at Site 3. Triplicate bags with 25 g of *T. angustifolia* or *Phragmites* litter from the 1994 growing season, and a comparable set from live leaves, all oven dried immediately after collection, were prepared, deployed, and analyzed as above.

Macroinvertebrate Populations

High marsh surface macroinvertebrates were sampled along the salinity gradient in 1994 (Fell et al. 1998) and at *Phragmites* control sites in 1997. In 1997, using the same procedures as in 1994, eight 0.25-m^2 quadrats, sited c. 2 m off the transect line to avoid human disturbance, were sampled per transect.

Tidal Creek Fish, Macroalgae, and SAV

A pair of tidal creeks, one dominated along its entire length by *Phragmites* (hereafter *Phragmites* creek) and the second with banks and levees dominated by *S. alterniflora* and *T. angustifolia* (hereafter Reference creek), were compared for fish use, macroinvertebrate populations (Fell et al. 1998), and submerged aquatic vascular plants (SAV) and macroalgae. The creeks are located off Ben Marvin's Creek, by the Lieutenant River and near Invertebrate/Production Site 3 (Fig. 1). Both were c. 150 m in length, narrowing to < 1 m wide by 80–100 m and drained c. 1.5 ha of marsh. SAV and macroalgae were sampled July 28 and 29 within 1.5 h ± low tide. At 5-m intervals from creek mouths to 80 m, individual species were recorded by occurrence and estimated percent cover in contiguous 1-m^2 quadrats along lines perpendicular to the main creek axis and extending to the lower limits of *S. alterniflora* or *Phragmites.*

Fish use of the above two creeks was sampled in 1994 (Fell et al. 1998). Fish populations from both creeks were sampled again in 1997, along with a third of comparable dimensions that runs through

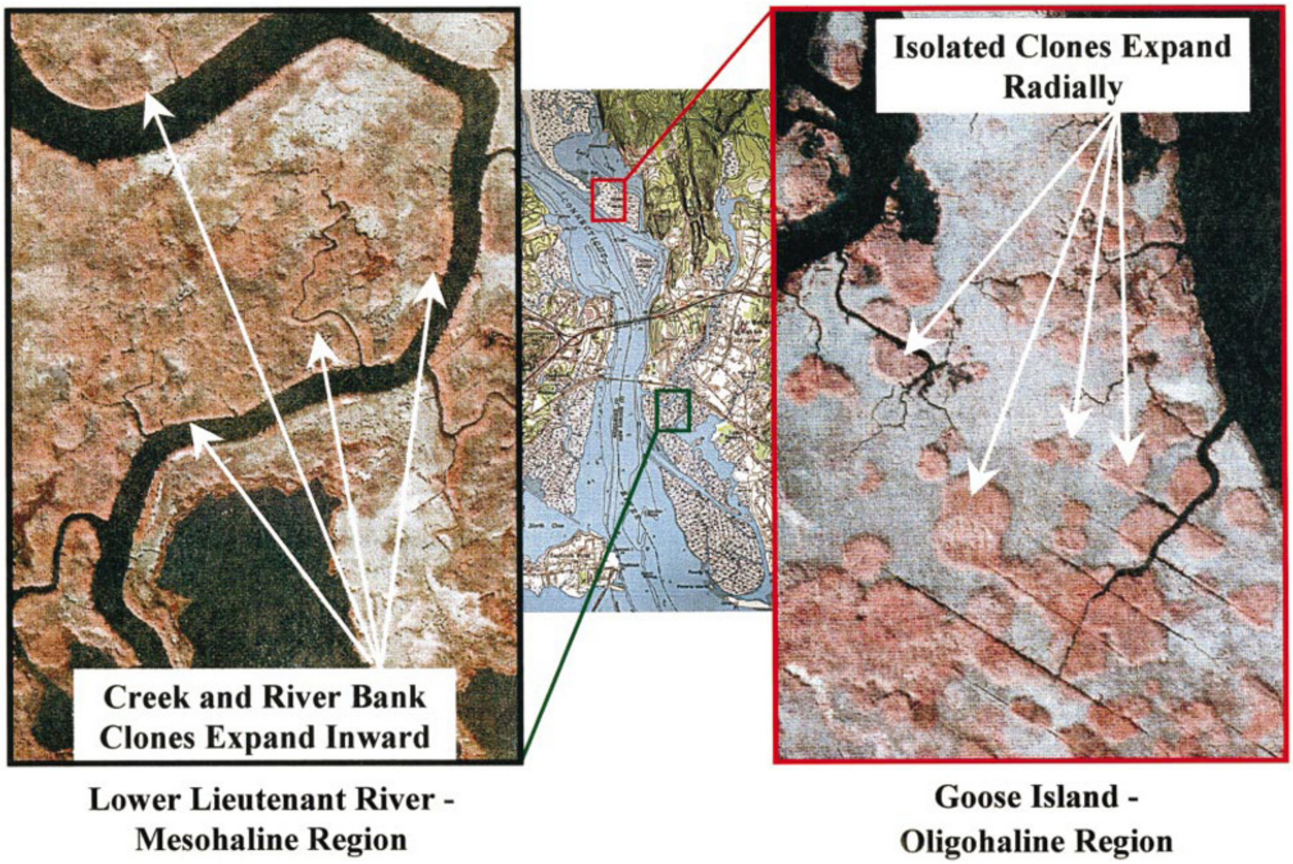

Fig. 2. Portions of Upper Island/Lieutenant River (A) and Goose Island (B) marshes from 1986 false color infrared air photos. Sites of initial *Phragmites* establishment noted with arrows. On Goose Island establishment is random and clones expand radially; along the Lieutenant River *Phragmites* tends to establish first on creek and river banks then expand inward.

the northeastern portion of the spray/mow treatment of the *Phragmites* control area (Fig. 2). A 1-m diam Fyke (hoop) net (6-mm mesh) with 3-m wings extending to both creek banks captured fish leaving the creeks during ebb tide (Fell et al. 1998). The net was set at slack high water of a spring tide and fished continuously at 0.5-h intervals for 2.5 to 4.0 h. After each 0.5 h the net was emptied and reset; this took less than 5 min. Fish captured during each sampling interval were immediately sorted by species, enumerated and, when total weight of a species was about 20 g or more, the sample was weighed to obtain fresh biomass. Each creek was sampled once each in early June, early July, and early August; for each month, a different creek was sampled during three consecutive days.

Fish on the High Marsh

Fish using the high marsh of the herbicide/mow *Phragmites* control site (8.4 ha between the Lieutenant River to the south and, c. 250 m north, a railroad embankment), and of a reference *Phragmites* area across the Lieutenant on Upper Island (55 ha marsh island, about 75% *Phragmites* dominated, Fig. 1) were sampled with a 6-mm mesh tarred nylon mesh flume net (Hettler 1989) during spring tides in August, September, and October 1997. The net was set at slack high water with its mouth (3 m wide by 1 m high) positioned just at the lower limit of *S. alterniflora*; the 7 m-long tail, equipped with a funnel and attached float, extended into the river and was tethered to weights resting on the river bottom. On each side of the mouth a 1-m high wing extended forward and laterally (ca. 45°) about 4 m from the mouth and then onto the marsh and perpendicular to the river bank for another 10 m. Starting at the edge of the mouth, 5-cm diam PVC pipes were attached to the wings every 3–4 m; in setting the net these were slipped over permanent stakes driven into the marsh. At the start of the study vegetation was trimmed in a 5–10 cm strip immediately in front of the mouth and where the wings contacted the marsh surface and plastic garden border sections were sunk, elevated slightly above the marsh sur-

TABLE 1. Rates of *Phragmites australis* expansion in different regions of the lower Connecticut River estuary. Slopes followed by the same letter are not significantly different.

Region	Salinity Regime	Expansion Rate (% yr^{-1})	r^2
Great Island/Back River	Polyhaline	1.07	0.86[a]
Upper Island/Lower Lieutenant River	Mesohaline	1.10	0.83[a]
Upper Lieutenant River	Low Mesohaline	1.32	0.92[b]
Goose Island	Oligohaline	2.73	0.95[c]
Lords Cove	Oligohaline-Fresh Tidal	2.92	0.85[c]

face, permanently into the marsh along the trimmed path. As the net was set, the lead line at the base of the wings and mouth was staked tightly against the border. When employed the net spanned 10 m of river bank.

Fish and crustaceans were removed from the net after the water had completely drained from the marsh surface, usually about 3 h following peak high tide. Fish were preserved in formalin in the field and returned to the laboratory for gut content analysis. Only foregut contents were examined; this restricted analysis to organisms consumed during the previous 2–3 h on the high marsh. In most cases little or no digestion was evident and prey were readily counted and identified to species. Ninety *Fundulus heteroclitus,* 30 from each sampling session, were randomly selected from the reference *Phragmites* site and from the herbicide/mow site catches. Most *Anguilla rostrata* from both sites were also analyzed.

Litter and High Marsh Macroinvertebrates

Litter was quantified within three areas of the *Phragmites* control site: untreated reference *Phragmites,* herbicide only *Phragmites,* and mow only *Phragmites*. All the litter covering the marsh surface, principally dead *Phragmites* stems and decomposing leaves, was collected from eight 0.25-m^2 quadrats located c. 5 m apart along one transect in each treatment. Litter samples were dried at 100°C to a constant weight.

On July 29, 1997 all litter was removed from eight 1.0-m^2 plots positioned c. 5 m apart within the spray *Phragmites* area. This was done with minimal disturbance of the standing dead stems. Three days later macroinvertebrates were sampled in eight 0.25-m^2 quadrats placed in the center of the cleared plots as well as in eight reference plots situated midway between the experimental plots.

Also during late July, litter from the cleared plots described above was added to eight 1.0-m^2 plots within the mow *Phragmites* area. These plots were positioned c. 5 m apart and 15 m from the border of the herbicide only treatment area. Each plot was surrounded by a 28 cm high, 5 cm mesh chicken wire fence, staked at each corner, to help retain added litter. Litter was placed on the marsh surface with minimal disturbance of shoots within and bordering the plots; final litter density approximated that found in reference and herbicide only areas. On September 12 marsh surface macroinvertebrates were sampled in 0.25-m^2 quadrats located in the center of each litter-augmented plot, and in eight reference quadrats situated midway between these plots. Sampling was done as described above (Fell et al. 1998). During the interval between litter additions and invertebrate sampling, tides removed varying amounts of litter from the plots.

Results

Rates and Patterns of *Phragmites* Expansion

Phragmites expansion rates, change in percent of marsh area identified on air photos as dominated by *Phragmites* versus time, were determined for five separate regions of the lower Connecticut River estuary, from the polyhaline brackish meadows of Great Island in the south to the oligohaline-fresh tidal reed and cattail marshes of Lord's Cove, 10 km upriver to the north. Expansion rates on all areas were strongly linear and increased up the salinity gradient from c. 1% yr^{-1} at Great Island to nearly 3% yr^{-1} at Lord's Cove (Table 1). Regression lines of total *Phragmites* cover for all sites extrapolated back to zero between 1968 and 1973.

Several individual clones on Goose Island and Lord's Cove could be followed over all four photo sets; expansion rates were all strongly linear ($r^2 \geq 0.91$) but varied considerably. Differences between the slowest (33 and 51 m^{-2} yr^{-1}) and most rapidly expanding (855 and 1,630 m^{-2} yr^{-1}) clones varied by more than an order of magnitude. The oldest of these extrapolated back to zero cover in the early 1950s; using these extrapolated ages, new clones established every three to five years until a burst of new clones between 1967 and 1973.

Patterns of initial invasion and subsequent spread also differed between the lower salinity Lord's Cove/Goose Island marshes and higher salinity areas of Great and Upper Islands. These are seen in Fig. 2, a pair of 1986 FCIR air photos from Goose Island and Upper Island. In oligohaline and fresh tidal marshes, as found on Goose Island, *Phragmites* clones appear to initiate at random lo-

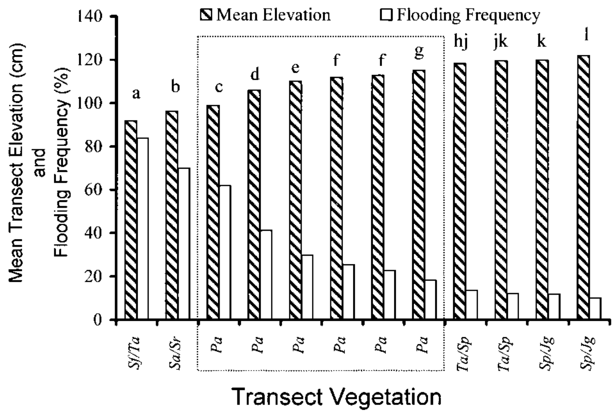

Fig. 3. Elevations and flooding frequencies (% of tides predicted to reach or exceed the mean transect elevation between May 1 and September 1, 1994) of *Phragmites*-free and *Phragmites*-dominated transects along the Back and Lieutenant Rivers.

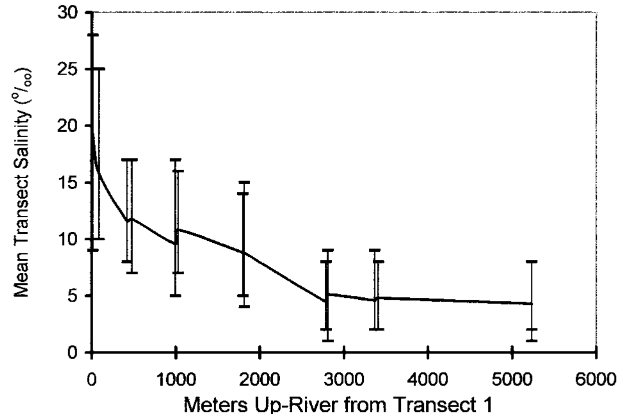

Fig. 4. Mean transect soil water well salinity (3 wells per transect) ± maximum and minimum readings June–August 1994.

cations within the existing *Typha/Scirpus* vegetation matrix and expand radially outward (radius increase averaging ca. 2.0 m yr^{-1} between 1974 and 1981, slowing to ca. 1.6 m yr^{-1} between 1986 and 1990), forming nearly circular patches. In mesohaline and polyhaline regions *Phragmites* tends to invade first on river, creek, and ditch bank levees, then expand back into the brackish meadows. Human disturbance along upland borders also provided establishment sites along the Lieutenant River.

Mean elevations of the paired vegetation transects (excluding the highest salinity pair) also reveal a pattern for *Phragmites* establishment, resistance to encroachment by *Phragmites,* or both (Fig. 3). Elevations and resulting hydroperiods of *Phragmites*-dominated transects cluster in a range of 99 to 118 cm, representing a mean growing season flooding frequency of 40%. *Phragmites*-free transects, in contrast, were either significantly higher (120 cm mean elevation flooded by 15% of seasonal high tides) or lower (94 cm and a flooding frequency of 94%).

Salinity and Water Table

In both 1993 and 1994 salinities increased linearly ($r^2 > 0.79$) from early June to mid August and decreased with the log of the distance up-river of Transect 1 ($r^2 > 0.87$; Fig. 4). There were no differences in seasonal mean salinities among the three soil water wells within individual transects. There were also no differences between mean well salinity in any *Phragmites*-dominated versus *Phragmites*-free transect pair.

Pooling all wells, averaged over growing season, soil water table depths varied with tide stage in both 1993 and 1994, with a mean range of ca. 12 cm. Also pooling all transects, water table was significantly different among wells ($p \leq 0.05$ by Tukey's) and deeper (1994 mean ± SE) at the 3-m point (14.8 ± 1.15 cm) than at 10 m (11.2 ± 0.98 cm) and at 30 m (7.1 ± 0.98 cm). There were no consistent patterns in soil water table between transect pairs that could be related to vegetation, and ANOVA revealed no significant differences in water table depths when wells were sorted by dominant vegetation or location along the salinity gradient.

Vegetation

Salinity Gradient Transects

Changes in frequency of high marsh dominants along the salinity gradient are seen in Fig. 5. At the southern, polyhaline end of the gradient (Site 1) vegetation along *Phragmites*-free transects were characterized by *S. alterniflora* low marsh with scattered *Scirpus robustus* and *S. patens/J. gerardii* dominated high marsh brackish meadows. At lower salinities along the Back River (Site 2) the annual forb *Amaranthus cannabina* occurred occasionally

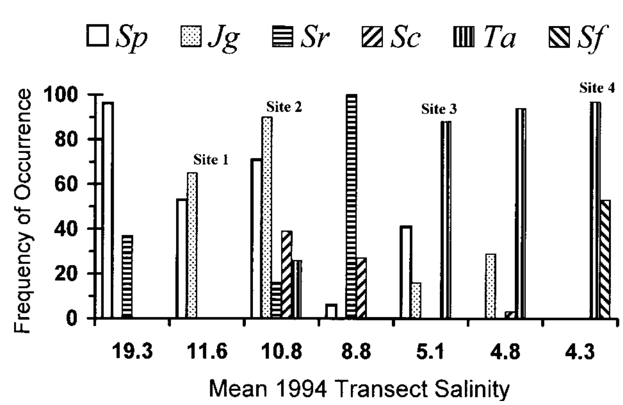

Fig. 5. Frequency of occurrence of dominant angiosperms along *Phragmites*-free transect lines in 1994. Sites sampled for primary production and macroinvertebrates are identified.

TABLE 2. Frequency and cover of dominant angiosperms in the *Phragmites* control treatment areas.

Species	Treatment/Vegetation									
	Herbicide/Mow									
	Brackish Meadow		Bare		Reference *Phragmites*		Mow *Phragmites*		Herbicide *Phragmites*	
	Freq	% Cover	Freq	% Cover	Freq	% Cover	Freq	% Cover	Freq	% Cover
Agrositis stolonifera	0.93	31.6	0.93	2.2	0.28	0.9	0.69	0.7	0.01	0.0
Eleocharis parvula	0.00	0.0	0.85	25.2	0.01	0.3	0.02	0.0	0.04	0.2
Eleocharis rostellata	0.22	9.8	0.15	0.1	0.08	0.1	0.00	0.0	0.03	1.5
Juncus gerardii	0.52	13.6	0.90	7.7	0.31	4.1	0.64	2.0	0.21	0.8
Panicum virgatum	0.33	6.4	0.18	0.3	0.20	3.8	0.00	0.0	0.00	0.0
Phragmites australis	0.54	3.0	0.58	0.3	0.98	72.0	0.97	85.5	0.53	2.3
Pluchea purpurascens	0.51	0.8	0.98	6.8	0.00	0.0	0.48	0.7	0.09	0.0
Polygonum punctatum	0.00	0.0	0.30	0.8	0.00	0.0	0.00	0.0	0.00	0.0
Scirpus pungens	0.36	1.1	0.20	0.5	0.07	0.0	0.00	0.0	0.05	0.0
Scirpus robustus	0.17	0.1	0.73	0.8	0.00	0.0	0.02	0.0	0.09	0.0
Solidago sempervirens	0.44	2.1	0.23	0.1	0.13	0.6	0.37	0.1	0.03	0.0
Spartina patens	0.43	36.1	0.00	0.1	0.27	10.5	0.01	0.0	0.25	2.8
Typha angustifolia	0.27	0.3	0.95	1.1	0.21	0.5	0.18	0.1	0.12	0.1
Total Cover		104.9		45.9		92.8		89.1		7.7

in the low marsh; *S. cynosuroides, T. angustifolia,* and *Agrostis stolonifera* appeared on creek and river bank levees and, while graminoid species diversity increased in high marsh meadows, *S. patens* and *J. gerardii* remained dominant. *Spartina pectinata* was an additional minor component of the mesohaline lower Lieutenant River (Site 3) low marsh; high marsh here was a mosaic of largely pure *T. angustifolia* stands, *S. robustus* at lower elevations, mixed with high diversity *S. patens/J. gerardii* meadow. Nearly pure stands of *T. angustifolia* and *Scirpus fuvulatulus* dominated high marsh elevations of the oligohaline upper Lieutenant River (Site 4) while in the low marsh *S. alterniflora* was patchy and heavily mixed with *S. robustus* and *S. pectinata.*

A total of 19 angiosperm species were recorded along all 14 transect lines. Species diversity was consistently higher on the five mid-salinity *Phragmites*-free transects (6 to 12 per transect with an average of 9.4) than those at the two extremes (2 and 4 species per transect).

Experimental Phragmites Control Sites

The state's experimental *Phragmites* control area was in the region of Site 3 from 1994. Thirty-one different species were found in 1997; frequency and cover of dominants within the various treatments/vegetation types are presented in Table 2.

Vegetation patterns revealed from the 1997 *Phragmites* transects in this mesohaline region of the Lieutenant River marshes are consistent with the single *Phragmites* line sampled here in 1994. Stem density (80 versus 125 m^{-2}) and mean end-of season shoot heights (208 versus 248 cm) were both less in 1997 (Tables 3 and 4) but this probably reflects the diversity of sites (three versus one) and increased sample size in 1997. *Phragmites* is particularly dense and pure along river bank levees, where it initially established 20–30 yr earlier. Moving back, brackish meadow graminoids may survive as a sparse understory, dominated by *A. stolonifera, J. gerardii, S. patens,* and *Panicum virgatum.* These often persist at frequencies of 20–30% each, but rarely combined for more than c. 20% of the total live plant cover along a typical 40-m transect.

This pattern of understory graminoid frequencies was similar, except for the complete lack of *S. patens,* on mowed *Phragmites* transects. In this area, however, total understory cover was rarely more than a few percent.

Total angiosperm cover in the herbicide treatment areas was c. 8%. Live *Phragmites* shoots were found in half the quadrats sampled, but few grew to more than a meter tall and total *Phragmites* cover was just 2%. Herbicide completely eliminated *A. stolonifera* and *P. virgatum.* Frequencies of both *S.*

TABLE 3. Aboveground production, mean (SE), for different treatments/vegetation types in the 1997 experimental *Phragmites* control area. Within categories, values followed by the same letter are not significantly different ($p \leq 0.05$ by Tukey's test).

Treatment/Vegetation	Peak Live Standing Crop ($g\ m^{-2}$)	*Phragmites* Stems m^{-2}	*Phragmites* Stem Height (cm)
Reference *Phragmites*	1,310 (202)^{a}	80 (5.4)^{a}	208 (9.5)^{a}
Mowed *Phragmites*	1,094 (86)^{b}	165 (19.6)^{b}	163 (9.5)^{b}
T. angustafolia	1,057 (67)^{bc}	0 (0.0)^{c}	0 (0.0)^{c}
Herbicide-Mowed Brackish Meadow	862 (58)^{c}	12 (6.7)^{d}	80 (5.0)^{d}
Herbicide Only *Phragmites*	30 (25)^{d}	3 (2.2)^{e}	24 (2.5)^{e}

TABLE 4. Mean elevations (SE) of points (n = 120 for each treatment: 5 points $plot^{-1}$ × 8 plots $transect^{-1}$ × 3 transects $treatment^{-1}$) for invertebrate sampling plots and vegetation transect points (n = 120 for each treatment: 40 points $transect^{-1}$ × 3 transects $treatment^{-1}$). Within sample sets treatment means followed by the same letter are not significantly different (Tukey's test, $p \leq 0.05$). Plot versus transect means compared by *t*-test.

Treatment	Invertebrate Plot Points	Transect Points	Plots versus Transects
Typha	102.8 (1.23)[a]	102.5 (0.75)[a]	ns
Spray/Mow Bare	106.7 (0.91)[b]	109.2 (0.05)[b]	ns
Reference *Phragmites*	108.3 (0.24)[b]	108.8 (0.28)[b]	ns
Sprayed *Phragmites*	108.6 (0.40)[b]	111.9 (0.67)[c]	$p < 0.001$
Spray/Mow Meadow	108.8 (0..8)[b]	109.0 (0.34)[b]	ns
Mowed *Phragmites*	121.5 (0.33)[c]	120.0 (0.44)[d]	$p < 0.01$

patens and *J. gerardii* were similar to reference *Phragmites* transects but with greatly reduced cover; shoots emerged from surviving rhizome/rootstock. *T. angustifolia* seedlings were found in 12% of the sampled quadrats.

A brackish meadow with *A. stolonifera, S. patens, J. gerardii,* and *P. virgatum* combining for over 80% of the total cover, had become established over most of the herbicide/mow treatment area. *Phragmites,* however, had not been eliminated; although contributing only 3% to total plant cover, it occurred in about half the sampled quadrats.

In contrast to the essentially complete cover of the meadow, a small (c. 2 ha) area along the eastern most river edge was nearly devoid of angiosperms at the start of the 1997 growing season. By mid-August plant cover had increased to c. 45%; over half of that was the diminutive sedge *Eleocharis parvula,* with seedling establishment and growth accounting for most of the balance (Table 2). The most frequently occurring seedlings were *Pluchea purpurascens, T. angustifolia, A. stolonifera, J. gerardii,* and *Scirpus* spp. *Phragmites* occurrence along this transect (0.58) was similar to the brackish meadow (0.54) and the spray treatment transects (0.53). Species diversity was very high here; 14 different angiosperms occurred in transect quadrats, and wider sampling found seven additional species.

Creek Bottom Vegetation

Two macroalgal (*Enteromorpha* sp. and *Vaucheria* sp.) and two angiosperm (*Ruppia maritima* and *E. parvula*) species were found on low-tide exposed mud flats and channel bottoms of the *Phragmites* creek and nearby Reference creek. Frequency of occurrence and percent cover for all four species were significantly greater in the Reference creek than in the *Phragmites* creek (Table 5).

Litter Decomposition

Two-way ANOVA revealed no salinity effect but significant species effects on litter decomposition rates over both the first and second 4-wk sampling intervals. Data pooled from all four sites are summarized in Table 6. Weight loss rates from *S. patens* and *S. alterniflora* samples were more than twice those from *S. cynosuroides* and *Phragmites*; *T. angustifolia* was intermediate but closer to the latter two.

By the August sampling, leaf blade and sheath material in the *S. cynosuroides* and *Phragmites* bags was largely gone while woody stem sections remained essentially intact. The second, early fall, decomposition experiment compared dead and live leaves only from just *Phragmites* and *T. angustifolia* over 35 d, from September 9 to October 14 (Table 7). For both species, leaves collected live and dried just before the experiment decomposed faster than those collected as dead litter. In contrast to the pooled mix of plant parts used in the summer, the fall decomposition rate of *Phragmites* leaves was significantly greater than that of *T. angustifolia* leaves for both live and dead samples.

Primary Production

Aboveground 1994 peak live standing crop primary production estimates, measured stand characteristics, and calculated production using the mean g $shoot^{-1}$ multiplied by mean stem density

TABLE 5. Mud flat and channel bottom vegetation, mean cover (SE), in the Reference and *Phragmites* creeks.

	Creek Drainage Basin Vegetation			
	Reference (*Spartina/Typha*)		*Phragmites*	
Species	% Cover	Frequency	% Cover	Frequency
Ruppia	8.38 (1.49)	0.67	1.88 (0.53)	0.58
Eleocharis	2.36 (1.02)	0.43	0.07 (0.00)	0.07
Enteromorpha sp.	1.92 (0.37)	0.71	0.42 (0.13)	0.49
Vaucheria sp.	0.77 (2.79)	0.15	0.02 (na)*	0.01

* Occurred in only one quadrat.

TABLE 6. Mean (SE) and percent dry weight loss from litter bags over two intervals totaling 58 d during midsummer. Within intervals, rates followed by the same letter are not significantly different ($p \leq 0.05$ by Tukey's test). Sp = *Spartina patens,* Sa = *Spartina alterniflora,* Ta = *Typha angustifolia,* Sc = *Spartina cynosuroides,* and Pa = *Phragmites.*

	Dry Weight Loss mg d^{-1} (SE) and % d^{-1}			
Species	June 8–July 5		July 6–August 5	
Sp	348 (17)[a]	1.39%	92 (8)[a]	0.60%
Sa	300 (29)[b]	1.20%	155 (19)[b]	0.93%
Ta	179 (11)[c]	0.72%	37 (3)[cd]	0.18%
Sc	152 (10)[c]	0.61%	39 (4)[c]	0.19%
Pa	150 (6)[c]	0.60%	20 (5)[d]	0.10%

are summarized in Table 8. Peak live standing crop, *Phragmites* height, and *Phragmites* stem density for the 1997 experimental *Phragmites* control treatments, Site 3 from 1994, are in Table 3.

Aboveground Resource Allocation by *Phragmites*

Averaged over all four sites and including leaves dropped during the growing season, a typical *Phragmites* shoot produced 24.9 net grams of dry weight. The distribution of this production among aboveground organs is seen in Fig. 6. Leaves contribute about a quarter of the total aboveground dry weight, with nearly 23% of this shed over the May to September growing season. Converting these percentages into grams m^{-2}, average leaf production is 501 g m^{-2}, with 115 g of this added to the litter layer during the growing season. These estimates should be compared to the peak live standing crop production measures of 530 and 680 g m^{-2} for the Site 1 *S. patens/J. gerardii* brackish meadow and the *S. patens/J. gerardii/T. angustifolia* mosaic of Site 2, respectively (Table 3).

Invertebrates at Control Sites

Mean invertebrate sampling plot elevations for transects were significantly different within all but the spray *Phragmites* treatment (data not shown).

TABLE 7. Mean dry weight loss (SE) from litter bags over 35 d during late summer/early fall. Rates followed by the same letter are not significantly different ($p \leq 0.05$ by Tukey's test).

Species	Dry Weight Loss mg d^{-1} (SE) and % d^{-1}	
Phragmites Live	147 (4)[a]	1.47%
Phragmites Dead	108 (3)[b]	1.08%
Typha angustifolia Live	129 (7)[c]	1.29%
Typha angustifolia Dead	80 (7)[d]	0.80%

Pooling all plots within treatments, however, showed no significant differences among reference *Phragmites,* spray *Phragmites,* and restored meadow areas, all of which were significantly lower than plots along the mowed *Phragmites* transects; *Typha* transect plots averaged significantly lower than all other treatments. In addition, invertebrate sample plot elevations were very close to those taken along transects for vegetation samples (Table 4).

During June 1997, the amphipod *Orchestia grillus,* the isopod *Philoscia vittata,* and the snail *Succinea* sp. were among the most abundant macroinvertebrates within the studied marsh areas along the lower Lieutenant River (Table 9). The snails *Melampus bidentatus* and *Stagnicola catascopium* and the fiddler crab *Uca minax* generally occurred at lower densities. Because young *Succinea* and *Stagnicola* were hatching out during the course of the sampling period, only snails > 6 mm in shell length were used in comparing various marsh regions; however, the abundances of small snails reflected those of the larger ones. *Orchestia, Philoscia, Succinea,* and *Uca* were widely distributed throughout the marshes, whereas *Melampus* and *Stagnicola* exhibited a more limited distribution, with *Melampus* most abundant in the spray *Phragmites* treatment area and *Stagnicola* in the restored meadow (Table 9).

In general these invertebrates were typically most abundant in regions with relatively dense plant and/or litter cover (see below). There were no relationships between species abundances and

TABLE 8. 1994 aboveground production for all transects estimated by peak live standing crop clip harvest and for *Phragmites* transects by calculation using shoot density and g $shoot^{-1}$. Within categories, values followed by the same letter are not significantly different ($p \leq 0.05$ by Tukey's test). Pa = *Phragmites,* Sp = *Spartina patens,* Jg = *Juncus gerardii,* Ta = *Typha angustifolia,* and Sf = *Scirpus fuvulatulus.*

			Peak Live Standing Crop (g m^{-2})			*Phragmites* Stand Characteristics			
			Pa Transects		Pa-free Transects	Plant Height (cm)	Mean g $shoot^{-1}$	Shoots m^{-2}	Calculated g m^{-2}
Site	Vegetation of Pa-free Transect	Mean Salinity (‰)	1993	1994	1994	1994			
1	Sp/Jg	11.8[a]	1,148[a]	814[a]	560[a]	188[a]	19.9[a]	54[a]	1,075
2	Sp/Jg	10.8[a]	968[a]	944[a]	630[b]	234[b]	20.4[b]	100[b]	2,040
3	Ta	4.5[b]	1,885[b]	1,786[b]	1,280[c]	248[b]	29.3[c]	125[b]	3,663
4	Ta/Sf	4.3[b]		1,751[b]	1,340[c]	281[c]	32.3[b]	89[b]	2,875
Mean			1,334	1,324	953	238	25.5	92	2,413

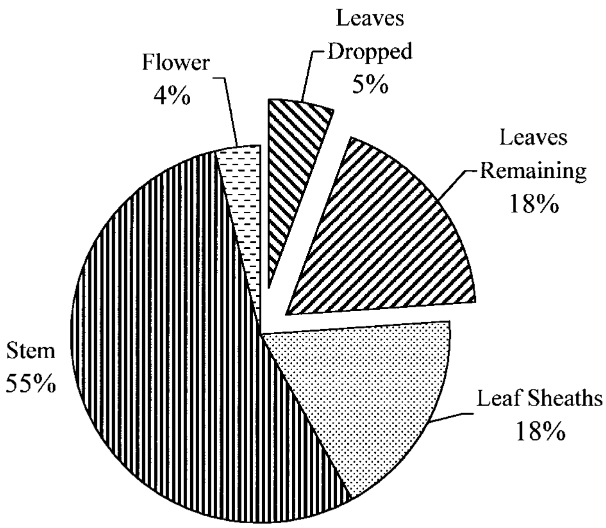

Fig. 6. Allocation of aboveground dry weight production over the May to September 1994 growing season for a typical (averaged over all four sites) *Phragmites* shoot.

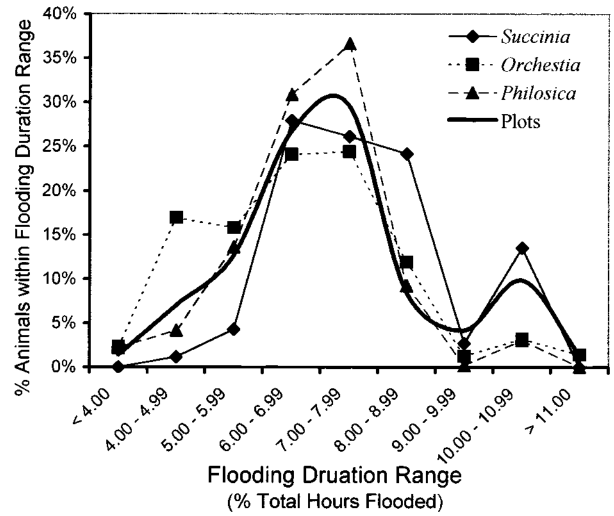

Fig. 7. Frequency distribution of animals captured and plots sampled across the flooding duration range of the total plots from Reference *Phragmites,* Spray *Phragmites,* and Spray-Mow/Meadow treatment areas. Three transects per area, eight plots sampled per transect.

elevation/hydroperiod. This is apparent both from frequency distributions of mean sampling plot hydroperiods and the relative number of animals found within hydroperiod ranges (Fig. 7) and from the lack of significance in regressions of hydroperiod versus population density for all species (data not shown).

Orchestia was most abundant in the sprayed *Phragmites* treatment area, and its densities in reference *Phragmites* and the restored meadow (spray-mow) area were not significantly different. *Orchestia* was less abundant in mowed *Phragmites* than in either the reference or sprayed *Phragmites* sites, but its density in the mowed *Phragmites* marsh was not significantly lower than in the restored meadow. *Philoscia* occurred at the highest densities in the reference *Phragmites* and sprayed *Phragmites* marshes and was equally abundant in the mowed *Phragmites* marsh and the restored meadow marsh. On the other hand, *Succinea* was more abundant in the restored meadow than in the other sampled marsh regions. However, the densities of particular invertebrate species often varied widely among the three transects in each type of marsh (Table 10), and there were frequently no clear differences in the abundances of these animals in relation to vegetation or *Phragmites* control treatment.

The Influence of Litter on Invertebrate Abundances

There was no significant difference between the amounts of litter collected in the sprayed *Phragmites* marsh and the reference *Phragmites* marsh (Table 11), but the mowed *Phragmites* marsh had significantly less litter than the other two marsh regions (Tukey's test, F = 14.544, df = 2, p = 0.005). In general, the abundances of *Orchestia,*

TABLE 9. Mean densities, no. (SE) 0.25 m^{-2} of six marsh invertebrates in different marsh regions along the lower Lieutenant River during June 1997; n = number of 0.25 m^2 quadrats sampled). For each species, values indicated by the same letter are not significantly different at the 0.05 level (Tukey's test). Frequency (%) of occurrence is in parentheses.

Species	*Phragmites* Reference 24	*Phragmites* Sprayed 24	*Phragmites* Mowed 24	Restored Meadow 24	Typha 8	Bare Area 8
Orchestia	11.2 ± 2.4^{a} (100)	18.3 ± 4.7^{b} (100)	4.0 ± 1.0^{c} (83)	7.7 ± 1.4^{ac} (100)	1.5 ± 0.5^{d} (63)	0.01 ± 0.1^{e} (13)
Philoscia	11.3 ± 2.1^{a} (92)	9.8 ± 1.2^{a} (100)	1.2 ± 0.4^{b} (33)	2.0 ± 0.7^{b} (54)	2.5 ± 1.7^{c} (50)	0
Succinea (>6 mm)	0.4 ± 0.2^{a} (17)	0.9 ± 0.2^{b} (54)	0.1 ± 0.1^{a} (8)	1.7 ± 0.4^{c} (67)	0.6 ± 0.3^{d} (50)	0.1 ± 0.1^{a} (13)
Succinea (<6 mm)	5.2 ± 3.1 (21)	3.6 ± 1.8 (33)	0.2 ± 0.1 (13)	20.1 ± 8.0 (54)	5.9 ± 2.8 (75)	0.3 ± 0.3 (13)
Uca	0.8 ± 2.3^{a} (50)	1.0 ± 0.3^{a} (54)	0.9 ± 0.2^{a} (54)	0.3 ± 0.21^{b} (17)	1.0 ± 0.3^{a} (63)	0
Melampus	0.2 ± 0.1^{a} (13)	5.5 ± 1.8^{b} (50)	0.3 ± 0.3^{a} (13)	0	0	0
Stagnicola (>6 mm)	0.04 ± 0.04^{a} (4)	0	0	0.8 ± 0.3^{b} (29)	0.1 ± 0.1^{c} (13)	0.1 ± 0.1^{c} (13)
Stagnicola (<6 mm)	0.2 ± 0.2 (4)	0	0	20.3 ± 16.7 (17)	0	0

TABLE 10. Mean densities, no. (SE) 0.25 m^{-2}, n = 8, of three marsh invertebrates along fourteen transects in the marshes of the lower Lieutenant River. Values followed by the same letter are not significantly different ($p \leq 0.05$ by Tukey's test).

Orchestia grillus		*Philosica vittata*		*Succinea* sp. (>6 mm)	
Transect	Density	Transect	Density	Transect	Density
Spray A	41.8 (9.6)^{a}	*Phragmites* A	17.4 (3.9)^{a}	Meadow A	2.0 (0.6)^{a}
Phragmites A	20.0 (5.3)^{b}	*Phragmites* B	14.0 (3.0)^{b}	Meadow C	1.9 (0.9)^{a}
Meadow A	10.0 (2.5)^{c}	Spray C	10.3 (2.1)^{c}	Spray B	1.5 (0.5)^{ab}
Phragmites B	9.8 (2.5)^{c}	Spray B	10.1 (2.5)^{c}	Meadow B	1.3 (0.6)^{b}
Spray C	8.8 (2.2)^{cd}	Spray A	8.9 (1.7)^{c}	Spray A	1.1 (0.4)^{bc}
Meadow C	8.0 (2.7)^{cde}	Meadow A	2.8 (1.4)^{d}	*Phragmites* A	1.0 (0.7)^{bc}
Mow C	7.0 (2.5)^{cdef}	*Phragmites* C	2.6 (0.9)^{d}	*Typha*	0.6 (0.3)^{cd}
Meadow B	5.1 (1.7)^{defg}	*Typha*	2.5 (1.7)^{d}	Mow C	0.3 (0.2)^{de}
Spray B	4.5 (0.9)^{defg}	Mow C	2.0 (1.0)^{de}	*Phragmites* B	0.3 (0.2)^{de}
Phragmites C	3.9 (1.9)^{efgh}	Meadow C	1.9 (1.5)^{de}	Spray C	0.1 (0.1)^{de}
Mow B	3.3 (0.9)^{fgh}	Mow B	1.5 (0.8)^{de}	Bare	0.1 (0.1)^{de}
Mow A	1.9 (0.7)^{gh}	Meadow B	1.4 (0.6)^{de}	Mow A	0^{e}
Typha	1.5 (0.5)^{gh}	Mow A	0^{e}	Mow B	0^{e}
Bare	0.1 (0.1)^{h}	Bare	0^{e}	*Phragmites* C	0^{e}

Philoscia, and *Succinea* were positively correlated with the amount of litter. With respect to the areas in which the litter was sampled, the densities of these invertebrates were significantly lower in the mowed *Phragmites* marsh than in the sprayed *Phragmites* and the reference *Phragmites* (Table 10 A transects and Table 11).

In both types of litter manipulation experiments, *Orchestia, Philoscia,* and *Succinea* occurred at significantly higher densities in quadrats with greater amounts of litter (Table 11). *Melampus* also was more abundant in the sprayed *Phragmites* quadrats with typical amounts of litter than in those from which litter had been removed 3 d earlier. Although not significantly different, *Melampus* density tended to be higher in mowed *Phragmites* plots to which litter had been added than in the reference quadrats.

Tidal Creek and Marsh Surface Fish at *Phragmites* Control Sites

A total of 15 fish species were caught with the fyke net in the three intertidal creeks near the mouth of the Lieutenant River (Table 12). Fish assemblages within these creeks were very similar. *F. heteroclitus* (mummichog) was the dominant fish, comprising 89% to 96% of the total number and 80% to 96% of the total fresh biomass of fish caught in each creek. This fish was much more abundant in Creeks 1 (*S. alterniflora/T. angustifolia*) and 3 (restored meadow) than in Creek 2 (*Phragmites*); 53%, 38%, and 9% of the total number of captured mummichogs were from creeks 1, 3, and 2, respectively. *Morone americana* (white perch), *Notropis hudsonius* (spottail shinner), *Lepomis gibbosus* (pumpkinseed), *Menidia beryllina* (tidewaer silverside), and young *Alosa* spp. (herring and shad) were common in all three creeks. White perch and spottail shiners were most abundant in Creeks 1 and 2, whereas young alosids were most numerous in Creek 3. It is worth noting that widgeon grass, *R. maritima,* appeared to be as abundant in the creek that courses through the restored meadow (Creek 3) as in that still bordered by *S. alterniflora* and *T. angustifolia* (Creek 1); apparently herbicide treatment did not adversely affect this submerged aquatic plant.

Nine species of fish were caught with the flume net on flooded areas of high marsh; all occurred on the reference *Phragmites* area while just four were trapped from the restored meadow (Table 12). Mummichogs represented 96% of the fish

TABLE 11. Litter biomass (g dry weight (SE) 0.25 m^{-2}; n = 8) in treated and reference *Phragmites* stands and density (no. (SE) 0.25 m^{-2}) of selected macroinvertebrates in sprayed and mowed *Phragmites* areas in relation to the amount of litter (p from *t*-test).

Litter Biomass	Reference *Phragmites* 245 (51)	Sprayed *Phragmites* 222 (11)		Mowed *Phragmites* 31 (9)	
		Not Manipulated	Litter Removed	Not Manipulated	Litter Added
Orchestria		10.6 (1.4)	3.2 (0.8)	14.2 (4.3)	65.4 (18.6)
		p = 0.002		p = 0.024	
Philosica		3.4 (1.8)	0.0	0.4 (0.2)	3.4 (0.8)
		p = 0.051		p = 0.004	
Melampus		4.7 (1.9)	0.1 (0.1)	0.6 (0.3)	2.5 (1.3)
		p = 0.024		p = 0.118	
Succinea		8.6 (3.3)	0.6 (0.6)	2.2 (1.1)	9.7 (2.4)
		p = 0.016		p = 0.007	

TABLE 12. Fishes caught in intertidal creeks (June, July, August) and on the flooded marsh surface (August, September, October) near the mouth of the Lieutenant River during 1997. Species caught in two of the creeks during 1994 (Fell et al. 1998) are indicated by asterisks. Fresh fish biomass (kg) is in parentheses.

	Creeks			Marsh Surface	
Species	*S. alterniflora/Typha* (1)	*Phragmites* (2)	Restored Meadow (3)	*Phragmites*	Restored Meadow
Fundulus heteroclitus	16,051 (55.12)*	2,742 (12.61)*	11,349 (40.51)	210 (1.02)	279 (1.06)
Alosa spp. (young)	97 (0.08)*	12*	409 (0.35)	1	1
Morone americana	213 (2.66)*	158 (2.90)*	47 (0.19)	53 (0.14)	
Menidia beryllina[a]	128 (0.17)*	57 (0.06)*	28 (0.05)	2	
Notropis hudsonius	89 (0.40)*	88 (0.38)*	3 (0.01)		
Lepomis gibbosus	45 (0.45)*	18 (0.09)*	33 (0.22)	1	
Apeltes quadracus	19*	4*	15	1	
Gasterosteus aculeatus	12*	2	10		
Pomatomus saltatrix	7 (0.12)*	4 (0.07)	10 (0.06)		
Fundulus diaphanus	2*	1*	2		
Notropis cornutus	*	*	4 (0.01)		
Caranx hippos	*	*	2		
Microgadus tomcod		1			
Cyprinodon variegatus			1	2	
Anguilla rostrata	*	*		30 (0.80)	11 (0.29)
Fundulus majalis				1	1
Syngnathus fuscus	*				
Pungitius pungitius	*				
Total	16,663 (58.35)	3,087 (15.67)	11,913 (41.36)	301 (1.97)	292 (1.38)

[a] In 1994 both *Menidia beryllina* and *Menidia menidia* (Atlantic silverside) were caught in both creeks.

trapped on restored meadow marsh and 70% of those caught on the *Phragmites* marsh. *Anguilla rostrata* (American eel) was also found in both areas, but fewer were caught from the restored meadow. White perch (4 to 8 cm TL), the second most abundant species, were trapped only from *Phragmites*. The total biomass of mummichogs caught on the two marsh areas were similar; mummichogs, however, comprised only 52% of the fish biomass from *Phragmites* compared to 77% from the restored meadow. This difference was due in large part to the greater biomass of eels trapped from the reference *Phragmites*.

The most abundant prey in the forguts of *F. heteroclitus* trapped leaving flooded high marsh, both reference *Phragmites* and restored (herbicide/mow) brackish meadow areas, were *Succinea, Orchestia, Philosica,* and insects (Table 13). Greater numbers of *Orchestia* and *Philosica* and fewer insects were consumed by *F. heteroclitus* on the reference *Phragmites* marsh than on the restored meadow (*t*-tests, $p < 0.05$). *A. rostrata* fed primarily on *Orchestia* and insects while almost completely avoiding snails. The mean numbers of *Orchestia* per gut were nearly identical in the two marsh habitats, but insects appeared to be consumed in greater quantities in the herbicide/mow meadow. It should also be noted that all of the sampled white perch had empty guts.

Discussion

Rates and Patterns of *Phragmites* Expansion

Although *Phragmites* invasion of tidal marshes is often associated with tidal restriction or other dis-

TABLE 13. Relative abundance (%) and total numbers of invertebrate prey and seeds in the foreguts of *Fundulus heteroclitus* and *Anguilala rostrata* caught in flume nets leaving spring-tide-flooded reference *Phragmites* and herbicide/mow treatment brackish meadow sites near the mouth of the Lieutenant River during August–October 1997.

	Fundulus				*Anguilla*			
	Reference Phragmites n = 90		Herbicide/Mow Meadow n = 90		Reference Phragmites n = 22		Herbicide/Mow Meadow n = 10	
Food Organisms	%	Number	%	Number	%	Number	%	Number
Succinae	48	561	51	808	1	2	—	0
Orchestia	30	353	11	167	79	142	57	68
Philosica	15	171	3	43	2	3	—	0
Palaemonetes	<1	3	—	0	3	5	—	0
Uca	<1	4	<1	1	5	9	—	0
Stagnicola	2	20	<1	2	—	0	—	0
Spiders	1	8	5	80	1	1	—	0
Insects	5	58	18	275	9	17	43	52
Seeds	<1	1	12	195	—	0	—	0

turbance (Roman et al. 1984; Chambers et al. 1999) these factors appear to have played little or no role in the rapid invasion and expansion of this grass in marshes of the lower Connecticut River estuary. A few clones became established between 1940 and 1960, with numbers increasing rapidly beginning in the late 1960s to early 1970s, about the same time period in which Windham and Lathrop (1999) report that *Phragmites* was first recorded on the oligohaline Hog Island marsh in New Jersey.

Both the rates and patterns of invasion and consequent spread on Connecticut River tidelands are clearly influenced by salinity. Sites of establishment were scattered with no apparent pattern in the oligohaline to nearly fresh *Typha/Scirpus* marshes of Goose Island and Lord's Cove, where clones tended to expand radially outward. This is similar to the pattern of establishment (Ferren et al. 1981) and spread (Windham and Lathrop 1999) reported for Hog Island. Creek-bank levees, and to a lesser extent upland edge, were preferred establishment sites in mesohaline to polyhaline reed marshes and brackish meadows of the Lieutenant River, Upper Island, and Great Island tidelands, where *Phragmites* expanded as a front into the established plant communities (Fig. 2). This is analogous to the pattern described by Bart and Hartman (2000) for the Hackensack Meadowlands, Secaucus, New Jersey, where *Phragmites* initially established on ditch edges then expanded into the marsh interior.

Conversion of existing plant communities to *Phragmites* was strongly linear at all sites and nearly three times as rapid on the lowest salinity, oligohaline, marshes at Lord's Cove as on the polyhaline *Spartina/Juncus* meadows of Great Island (Table 1). A similar pattern of *Phragmites* expansion rates has been reported by Rice et al. (2000) for several Chesapeake Bay tidal marshes. Although area increase in most of their sites was strongly linear, they calculated intrinsic growth rate, *r,* assuming geometric growth with the equation

$$N = N_0 e^{rt}$$

when N and N_0 are final and initial areas over time interval t, and e is the natural log base. From the 1970s to 1990s, mean r for their two oligohaline sites averaged 0.165 yr^{-1} and 0.064 yr^{-1} on two mesohaline marshes. Using the same assumptions of geometric growth, between 1974 to 1990 r from the oligohaline Lords Cove and Goose Island marshes was 0.119 yr^{-1} and averaged 0.065 yr^{-1} for the mesohaline to polyhaline marshes of the Lieutenant River and Great Island.

Intertidal estuarine mud-flats in northern California, Oregon, and Washington are facing analogous invasions by *S. alterniflora,* first introduced from Atlantic estuaries around the turn of the century (Frenkel 1987). Rates and patterns in more northern sites (Feist and Simenstad 2000) reflect those for *Phragmites* reported here and in the Chesapeake (Rice et al. 2000). In a detailed study of *S. alterniflora* at four sites in Willapa Bay, Washington, Feist and Simenstad (2000) report steady recruitment of new clones from ca. 1955 to the early 1970s, followed by a second round of establishment in the 1980s in the area of oldest colonization. Other Willapa Bay areas were similar to *Phragmites* in this study, with scattered older clones and rapid establishment of new clones 20 to 30 years ago. Like oligohaline *Phragmites, S alterniflora* patches remained nearly circular for 20 years as diameters increased linearly (mean = ca. 0.79 m yr^{-1}), but more slowly than *Phragmites* (mean from this study = 4.77 m yr^{-1}). *Spartina* expansion rates and patterns on the Pacific coast can be quite variable, making comparisons to Atlantic coast *Phragmites* difficult. In several southern San Francisco Bay sites, in contrast to Willapa Bay, *S alterniflora* became well established within a decade, and over a single year clone diameters increased an order of magnitude more rapidly, c. 10–20 m yr^{-1} (Callaway and Josselyn 1992).

Comparing *Phragmites*-dominated transects and their relatively *Phragmites*-free pairs, no consistent differences in either peat salinity or water table depth were found over both the 1993 and 1994 growing seasons. This is in contrast to the findings of Windham and Lathrop (1999) at Hog Island; they report lower soil salinities (6‰ versus 8‰) and deeper water tables (− 4 versus + 4 cm) in established *Phragmites* stands compared to adjacent *S. patens/Distichlis spicata* meadow.

Sampling quadrats from all transects, *Phragmites* occurred over a greater range of predicted tidal flooding frequency than any other angiosperm (100% to 6%), but its mean was not significantly different than other high marsh dominants (data not shown). Despite this broad range of occurrence, the only abiotic factor found distinguishing *Phragmites*-dominated versus *Phragmites*-free transects was mean elevation, which translates into hydroperiod. Tidal flooding frequencies for *Phragmites*-dominated transects (25% to 67% of growing season high tides, mean = 40%) were distinctly different from those that had resisted *Phragmites* invasion; the former were bracketed by and significantly different from the *Phragmites*-free lines (Fig. 3); the wettest two transects remained *Phragmites*-free; they also had the lowest salinities, which otherwise might be expected to favor *Phragmites.* It is also notable that in 1997 the *Typha* transect, which sampled one of the few plant communities along the lower Lieutenant River that had resisted *Phrag-*

mites invasion, was significantly lower than the 14 others established that year (predicted 1997 flooding frequency = 54%), while the highest sites (all three mowed transects: c. 22% predicted 1997 flooding frequency) were completely dominated by *Phragmites*. Over the long term *Phragmites* expansion is unlikely to be limited by hydroperiod up to elevations of nearly extreme spring high water. Greater hydroperiod may slow or stop its spread into lower elevation sites, particularly at higher salinities. This prediction from field observations is consistent with experimental findings (Hellings and Gallagher 1992) on the effects of submergence, salinity and cutting on *Phragmites* growth and survival.

Despite the information presented here and recent work of others (Chambers et al. 1999; Rice et al. 2000) on rates and patterns of *Phragmites* expansion, there is little to suggest why this species, which had been a relatively minor component of brackish tidal marsh plant communities for at least three millennia (Orson 1999), began to expand so aggressively just a few decades ago. One contributing factor is likely human activities, particularly tidal restrictions and upper border disturbance resulting from coastal development (Niering and Warren 1980; Roman et al. 1984; Rozsa 1995; Bart and Hartman 2000), which have created sites and conditions particularly favorable to colonization by *Phragmites*. The resulting new populations greatly increased the supply of both seed and vegetative propagules. It is difficult to argue that increased potential invasion sites and propagules alone could have driven the explosive expansion of *Phragmites* in largely undisturbed marshes such as those of the lower Connecticut River. Evidence presented by Besitka (1996) argues compellingly that another factor helping to drive this phenomenon is the introduction of European, tetraploid, strains of the grass, which in their new North American environment, became highly invasive. The order of magnitude range of expansion rates among clones in essentially identical sites is consistent with a model of a population with a wide range of genetic potentials. Increased opportunity for establishment resulting from coastal zone development, coupled with highly aggressive introductions from Europe is a reasonable, testable causal explanation for the rapid expansion of *Phragmites* reported here and elsewhere.

Impacts of *Phragmites* Invasion on Selected Ecosystem Functions

Angiosperm Biodiversity and Macro-Scale Habitat Structure

In just three decades, over 90% of Nichols' (1920) *Typha/Scirpus* reed marshes have become near or complete *Phragmites* monocultures. Creek and river banks and the upland border of the brackish meadow complex are now almost entirely *Phragmites* dominated. Although vestiges of the initial meadow community may persist as understory for a decade or more, well over half of this species rich vegetation has become low diversity *Phragmites* marsh.

At the reed marsh end of this spectrum, *Phragmites* does not seem to significantly alter macroscale habitat structure as perceived by some bird species (Benoit and Askins 1999). The lower palatability of *Phragmites* has probably contributed to a decline in muskrat populations in these areas (Marks et al. 1994; Benoit and Askins 1999). Muskrat dens with surrounding eat-out areas, common features on historic air photos of Lord's Cove and Goose Island, are now rare and angiosperm species dependant upon such open, disturbed sites are in all probability much less frequent today than 30 years ago. Where *Phragmites* has invaded *Spartina/Juncus* brackish meadow, dense stands of reed 1.5 to 2 m or more tall have replaced structurally more complex and floristically rich grasslands, dramatically altering bird use of these marshes (Marks et al. 1994; Benoit and Askins 1999).

Macroinvertebrate Populations

In contrast to the loss of angiosperm and bird diversity, there is no evidence that *Phragmites* has significantly affected high marsh macroinvertebrates along the Great Island-Lieutenant River salinity gradient. This conclusion by Fell et al. (1998) is supported by findings from the experimental *Phragmites* control area: although there are differences among treatment areas and differences within treatments can be significant (Table 10), as a whole the reference *Phragmites* sites supported densities of dominant macroinvertebrates comparable to or greater than restored meadow and uninvaded *Typha* marsh, and very similar to those found in 1994. Macroinvertebrate distributions and densities also appear largely unrelated to hydroperiod. None of the dominants in the 1997 sampling of the *Phragmites* control areas exhibit any clear relationship between population density and elevation, and the frequency distributions of hydroperiod ranges sampled closely parallels invertebrate frequencies within those ranges (Fig. 7). Litter on the marsh surface is an extremely important factor limiting the distribution and density of these animals. Both macroinvertebrate densities (Tables 9 and 10) and surface litter (Table 11) were extremely low on the closed-canopy, mowed *Phragmites* site and on the sparsely vegetated-open bare area of the spray-mow treatment. Population densities dropped significantly where litter was removed from the herbicide treatment area and increased significantly where litter was added in the adjacent mow treatment. Litter probably helps support higher population densities by reducing evaporative water loss, providing cover from predators, and providing nutrition in the form of detritus; the relative importance of these factors probably differs among species.

Production and Decomposition

Patterns of production and litter decomposition by *Phragmites,* coupled with the importance of litter to macroinvertebrates, may help explain why the shift in the plant community and resultant macrohabitat structure reported here has such little influence on high marsh invertebrates. Although estimates of aboveground *Phragmites* production made by clip-harvest at peak standing crop are consistently much lower than those calculated using weight per shoot and stem density, with 1,000 g m^{-2} at even the highest salinity sites, *Phragmites* forms a highly productive plant community (Tables 3 and 8). Most of this production is heavily lignified, decay resistant stem tissue (Table 6) and not a ready source of detritus. Nearly one quarter of aboveground production, however, is leaves (Fig. 6), which were lost from litter bags, and presumably moved into the detrital food web, more rapidly than *Typha* (Table 7). At 23% of total aboveground production (Fig. 6) annual leaf production estimates for *Phragmites* are 300–555 g m^{-2}, comparable to regional high salt marsh (Steever 1972) and brackish meadow (Table 8, also Windham and Lathrop 1999). *Phragmites* loses 20% of its leaf production to the litter layer during the growing season; the rest drops and becomes part of the litter supply over the winter. Stems and leaves combined for c. 1,000 g m^{-2} of litter in 1997 reference *Phragmites* stands (Table 11), a significant portion of which was leaf material. This high production of biomass that is at least as labile as *Typha* leaves may help explain why *Phragmites* appears to have little impact on populations of high marsh macroinvertebrates, which graze principally on detritus and microalgae (Thompson 1984).

Fish Use of Creeks and High Marsh

The same set of submerged vascular plants (*R. maritima* and *E. parvula*) and macroalgae (*Enteromorpha* sp. and the filamentous *Vaucheria*) occupied bottoms of the *Phragmites*-dominated and the reference *S. alterniflora/Typha* creeks; however, frequency of occurrence and cover were significantly greater in the reference creek than the *Phragmites* creek (Table 5) This probably reflects heavy shading from 2 m or taller *Phragmites* along the creek bank. The difference in algal densities was clearly reflected in gut contents of *Fundulus* leaving these creeks in July 1994 (Fell et al. 1998). There was little difference in creek macroinvertebrate populations sampled using litter bags or found in guts of *Fundulus* trapped leaving creeks on ebb tides during June and August. These authors also reported similar fish species assemblages and abundances in the two creeks. The more intensive 1997 sampling of fish leaving the initial two creeks plus a third in the spray/mow meadow restoration site again found *Fundulus* as the dominant species with essentially the same species diversity in all three creeks and few differences between the two years. Results from 1997 suggest that *Phragmites* on the high marsh and creek banks may have a negative impact on fish populations in adjacent creeks. Numbers and fresh biomass of *Fundulus* were very different among the three creeks (Table 12) with the greatest numbers and biomass (53% and 51% of totals, respectively) from the *S. alterniflora/Typha* creek and the least (9% and 12%) from the *Phragmites* creek. *Fundulus* is considered a major vehicle for transfer of marsh, epibenthic, and water column production to higher trophic levels (Weisberg and Lotrich 1982; Kneib 1986). So, although these results represent a limited number of sampling sessions in only three creeks over a single summer, they suggest a possible major impact of *Phragmites* invasion on ecosystem function. Additional work addressing this question should be a priority in understanding the impact of *Phragmites* invasions on brackish and fresh tidal wetlands.

During late summer and fall spring tides *Fundulus* and *Anguilla* foraged on macroinvertebrates from *Phragmites* and restored brackish meadow high marsh. *Fundulus* biomass was comparable in both plant communities (Table 12) and their gut contents generally reflected relative prey abundance (Table 13). These findings are consistent with those of Fell et al. (1998) for *Phragmites*-dominated and largely *Phragmites*-free areas from the higher salinity Site 1 in 1994. Intensive sampling with Breder traps in *Typha*-dominated and *Phragmites*-dominated reaches of marsh along the Lieutenant River during 2000 has revealed no clear difference in fish use between these two community types (Fell and Warren work in progress). In 1997 we found that *Anguilla* preyed primarily upon *Orchestia* and insects in the restored high marsh and *Orchestia* in the *Phragmites* marsh. Young-of-the-year *M. americana* were the second most abundant fish trapped leaving the high marsh and were only captured from *Phragmites* (Table 12). In contrast to *Fundulus* and *Anguilla* this species was not feeding on the marsh; all fish examined had empty guts. The *Phragmites* marsh, with its relatively widely spaced stems, in contrast to the fine, dense shoots of the brackish meadow community, may serve this species principally as a refuge from predation.

Plant Community Responses to *Phragmites* Control

Phragmites is extremely sensitive to glyphosate as applied in this study. One and two years after application (spray and spray/mow treatments) *Phragmites* frequency was c. 0.50, with cover of 2–3% and stem densities of 3–12 m^{-2}. These surviving culms provide *Phragmites* the ability to regain dominance. In a 1999 re-survey of the 1997 spray/mow transect lines both frequency and mean percent cover in the brackish meadow area increased (frequency = 0.54 to 0.67; cover = 3% to 6%, $p < 0.0001$ for percent cover by paired *t*-test); for the bare area transect the increase in *Phragmites* importance was even greater with frequency and cover going from 0.58% and 0.3% to 0.93% and 15% ($p < 0.0001$ for percent cover) over the two years. Non-quantitative 1999 observations in herbicide only treatment areas also found *Phragmites* to be an important component of the vegetation. Effective long-term control of *Phragmites* will likely be much more effective with a follow-up second year spot-application of herbicide to surviving culms. Control with regular herbicide application may be practical but eradication of this grass from brackish tidal marshes is not a realistic goal.

In contrast to herbicide treatments, a single season of mowing alone did little to decrease the dominance of *Phragmites*. Mowing did change some stand characteristics; stem density was doubled while height and production decreased significantly (Table 7).

Extant relic marshland that remains uninvaded by *Phragmites,* along with historic vegetation descriptions (Nichols 1920; Niering and Warren 1975) suggest that *Agrostis,* now dominating the highly productive (Table 3) brackish meadow which developed following the spray-mow treatment, is probably a much more important member of this community now than prior to *Phragmites* invasion. In the two years from 1997 to 1999, however, frequency and cover of *Agrostis* declined (0.93 to 0.71 and 32% to 24% cover, $p = 0.04$) while *Panicum* in particular increased by both measures (0.33 to 0.42 and 6% to 12% cover, $p < 0.001$). The other major trends were frequency increases by *S. robustus* (0.17–0.29), *Scirpus pungens* (0.36–0.43), and *Typha* (0.27–0.35). Together these trends suggest that *Agrostis* importance will decrease with time. The high sensitivity to glyphosate of *Agrostis* and *Panicum* seen in the herbicide only transect and the relatively high survival rate of *Juncus* and *S. patens* suggest that the former became re-established principally by seed.

Although this study integrated several ecological functions over a large salinity, spatial, and temporal range, the long-term impacts of *Phragmites* invasion and expansion within Connecticut River brackish tidelands are not yet completely clear. Our findings demonstrate that several ecological functions and attributes are clearly being altered while the fate of others remains more difficult to predict. Angiosperm biodiversity is being reduced, particularly in mesohaline regions of the system, characterized 30 years ago by brackish meadow plant communities. Angiosperm and macroalgal populations in narrow tidal creeks and channels are also reduced when creek banks come to be dominated by *Phragmites.* Total aboveground angiosperm production increases as brackish meadows and *Typha/Scirpus* reed marshland is converted to *Phragmites,* though much less than half of this increased production is readily converted to detritus for potential transfer to higher trophic levels. Macroinvertebrates appear to be largely unaffected when either brackish meadows or *Typha/Scirpus* marsh is converted to *Phragmites,* while both *Fundulus* and *Anguilla* forage for invertebrate prey with equal effectiveness in *Phragmites* and brackish meadow vegetation. Although fish species assemblages and gut contents revealed no consistent differences between fish leaving *Phragmites*-dominated versus reference creeks, this study suggests possible differences in total fish use, with much greater fish biomass from the relatively *Phragmites*-free creek.

Finally, late summer herbicide followed by spring mowing of *Phragmites* can re-establish brackish meadow vegetation with little or no impacts on the macroinvertebrate community or fish use of the high marsh. The mow-only treatment was not an effective method of *Phragmites* control and any eventual restoration of a brackish meadow is likely to be much slower if herbicide treatment is not coupled with mowing of standing dead shoots. Brackish meadow was restored within two to three years of herbicide/mow treatment. In contrast to the pre-invasion community, *Agrostis* is the dominant graminoid of the restored meadow. It is also significant that some *Phragmites* culms survived the herbicide/mow treatment and *Phragmites* is again expanding in this area. Its growth and spread is particularly apparent along the river bank levees, the site of initial invasion approximately three decades ago. Long-term control of *Phragmites* in brackish tidal marshes will likely require ongoing management.

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