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The Influence of *Phragmites* (Common Reed) on the Distribution, Abundance, and Potential Prey of a Resident Marsh Fish in the Hackensack Meadowlands, New Jersey

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ABSTRACT: This study investigates the influence of *Phragmites australis* (common reed) invasion on the habitat of the resident marsh fish, *Fundulus heteroclitus* (mummichog) in the Hackensack Meadowlands, New Jersey. These abundant fish play an important role in the transfer of energy from the marsh surface to adjacent subtidal waters and thus estuarine food webs. The objectives of this 2-yr study (1999 and 2000) were to compare the distribution and abundance of the eggs, larvae, juveniles, and adults of mummichog and their invertebrate prey inhabiting *Spartina alterniflora*-dominated marshes with *Phragmites*-dominated marshes, and to experimentally investigate the influence of marsh surface microtopography on larval fish abundance within *Phragmites*-dominated marshes. In 2000, we verified that egg deposition does occur in *Phragmites*-dominated marshes. In both years, the abundance of larvae and small juveniles (4–20 mm TL) in *S. alterniflora* was significantly greater than in *Phragmites*-dominated marshes, while larger juveniles and adults (> 20 mm TL) were similarly abundant in both habitat types. The overall abundance of larvae and small juveniles was significantly greater in experimental *Phragmites* plots in which microtopography was manipulated to resemble that of *Spartina* marshes than in *Phragmites* control plots. Major groups of invertebrate taxa differed between marsh types with potential prey for larval fish being significantly more abundant in *S. alterniflora* marshes. *Phragmites*-dominated marshes may not provide the most suitable habitat for the early life-history stages of the mummichog. The low abundance of larvae and small juveniles in *Phragmites* marshes is likely due to inadequate larval habitat and perhaps decreased prey availability for these early life history stages.

Introduction

The expansion of common reed, *Phragmites australis* (hereafter *Phragmites*), into tidal wetlands of the northeastern United States has been extensive over the past century. *Phragmites* has been replacing dominant macrophytes in Atlantic Coast marshes at rates of 1–6% of the marsh surface per year (Chambers et al. 1999; Warren et al. 2001), largely in areas that have undergone disturbance or stress (Marks et al. 1994; Chambers et al. 1999), but also in relatively unaltered areas (Rosza 1995; Windham and Lathrop 1999). *Phragmites* can function positively to ameliorate eutrophication (Templer et al. 1998; Meyerson et al. 1999), stabilize eroding shorelines (Rice et al. 2000; Rooth and Stevenson 2000), and sequester heavy metals (Ye et al. 1997). *Phragmites* invasion also decreases topographic relief (Windham and Lathrop 1999), drainage density (Windham 1995; Weinstein and Balletto 1999; Rooth and Stevenson 2000), and plant diversity (Fell et al. 1998; Chambers et al. 1999; Meyerson et al. 1999; Windham and Lathrop 1999) as well as overall avian species richness (Cross and Fleming 1989; Marks et al. 1994; Benoit and Askins 1999).

Despite these recent findings, there is still insufficient information regarding faunal response to this habitat alteration. The response of resident fishes is important because of the role they play in the trophic transfer of production as a result of the material exchange between the intertidal marsh plain, where production occurs, and the adjacent subtidal waters (Kneib 1997a). Mummichogs (*Fundulus heteroclitus*) are resident fish, completing their entire life cycle within the marsh. On spring tides, the northern subspecies deposits its eggs within the first axils of *Spartina alterniflora* (hereafter *Spartina*; Taylor and DiMichele 1983), the empty shells of the ribbed mussel (*Geukensia demissa*), as well as cracks, crevices, and other small interstices on the marsh surface and along creek banks (Able and Castagna 1975; Able 1984; Able and Hata 1984). After hatching on the following

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spring tide, the larvae reside in shallow pools and depressions on the marsh surface (Taylor et al. 1977; Kneib 1987; Able and Hagan 2000), which may reduce predation rates (Kneib 1987) while providing invertebrate food resources. When the young become too large for these refuges (15–20 mm SL as per Kneib 1986), they adopt the migration patterns of the adults (Kneib 1984, 1997a,b), gaining access to the marsh surface to feed during high tides and returning to adjacent subtidal waters with the ebb tides. The transfer of intertidal marsh production may occur when species such as the mummichog feed within the vegetation on the marsh surface and either excrete material in deeper estuarine waters at low tide or are consumed by predators (Valiela et al. 1977; Weisberg and Lotrich 1982; Deegan 1993; Kneib 1997a). The young-of-the-year may contribute the most to this trophic transfer, because they are the dominant life-history stage on the marsh surface in terms of both abundance and biomass (Taylor et al. 1979; Talbot and Able 1984; Kneib 1986; Smith et al. 2000; Teo and Able 2003), experience the greatest mortality and, having higher food conversion efficiency than adults (Prinslow et al. 1974; Kneib and Parker 1991), are the fastest growing portion of the life cycle (Meredith and Lotrich 1979).

Recent studies investigating fish use of *Phragmites* versus non-*Phragmites* oligo-mesohaline marshes found no significant differences in the relative numbers and biomass of juvenile and adult mummichog that use these habitats (Fell et al. 1998; Able and Hagan 2000; Raichel 2001; Meyer et al. 2001; Warren et al. 2001). Measurements of stable isotopic compositions in juvenile and adult mummichog and other species confirmed that *Phragmites* is contributing to aquatic food webs in Delaware Bay tidal marshes (Wainright et al. 2000), although a recent study in the Mullica River, New Jersey, strongly suggests that *Phragmites* may not provide suitable habitat for larval and small juvenile mummichog (Able and Hagan 2000, 2003).

The hydrological and physical changes that accompany the conversion of a *Spartina*-dominated marsh to a *Phragmites*-dominated marsh may also affect intertidal invertebrates, an important food resource for the mummichog (Weisberg and Lotrich 1982; Kneib 1986; Smith et al. 2000). The types of invertebrates found on or just above the marsh surface may influence the feeding success of mummichogs since some prey may be either too large or too small to be effectively handled by a fish of a given size and thus are unavailable (Kneib 1986). The differences in the invertebrate assemblages of these 2 marsh types are poorly known (but see Angradi et al. 2001).

The objectives of this study were to compare the distribution and abundance of the eggs, larvae, juveniles, and adults of mummichog and their invertebrate prey between *Spartina* and *Phragmites* dominated marshes, and to experimentally investigate the influence of marsh surface microtopography on larval fish abundance within *Phragmites*-dominated marshes.

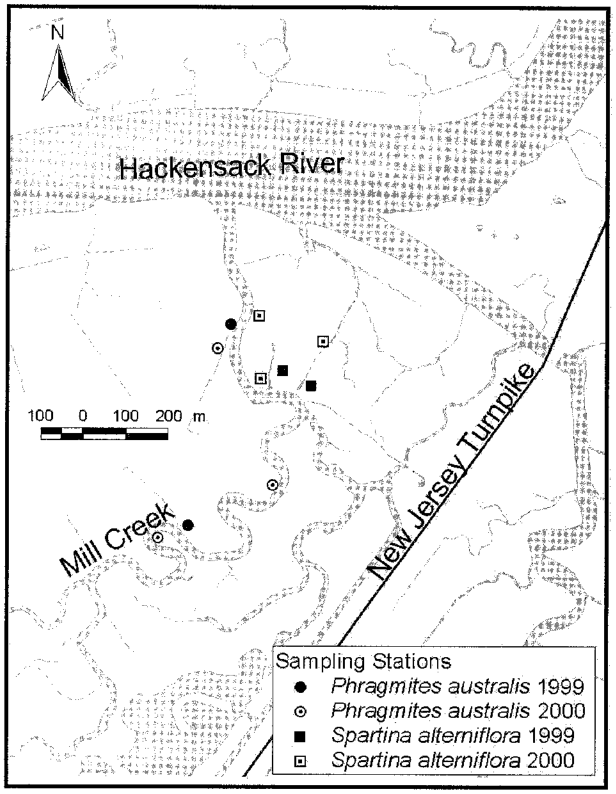

Fig. 1. Mill Creek sampling stations located off the Hackensack River in Secaucus, New Jersey, 40°47′59″N, 74°02′24″W, in 1999 (2 replicate stations marsh type^{-1}) and 2000 (3 replicate stations marsh type^{-1}). Underlined *Phragmites* replicate sampling stations were paired plots in 2000.

Methods and Materials

STUDY SITE

The study site is located in oligo-mesohaline marshes along Mill Creek, which lies within the Hackensack Meadowlands near Secaucus, New Jersey (Fig. 1). The Hackensack Meadowlands District consists of 7,985 ha of predominantly tidal marsh (Quinn 1997) occurring along the Hackensack River in northeastern New Jersey. Marsh elevations range from 0–3.1 m with most areas being less than 1.5 m above mean sea level (Sipple 1971). The Meadowlands has a long history of disturbance and alteration of tidal flow via impoundments, dikes, tide gates, and the construction of the Oradell Dam and New Jersey Turnpike. Most diking occurred in the late 1800s in an effort to reclaim the marshes for salt hay farming, agriculture, and livestock. Other marsh alterations include filling, dumping, and mosquito ditching (Sipple 1971; Quinn 1997). Extensive drainage networks for mosquito control led to domination of the area by *Typha* spp. and *Phragmites* by the early 1930s (Sipple 1971).

At the northern portion of Mill Creek is a 25.5 ha Hartz Mountain Industries mitigation site referred to as Western Brackish Marsh. Prior to 1985, this area was a tidal marsh dominated by *Phragmites*. Analysis of aerial photographs suggests that the *Phragmites* stands along the western side of Mill Creek have been established for at least 30 years. The mitigation design, completed in 1990, incorporated channels, open water, intertidal areas planted with *Spartina*, and upland planted with trees and shrubs. The southern portion of Mill Creek is a 56.7 ha site that was under mitigation during 1999 and 2000. The marshes on the western side of Mill Creek were not part of these mitigations and remain dominated by *Phragmites*. The astronomical tidal range at the study site, as determined by tide charts (Tides and Currents for Windows, Nautical Software, version 2.5b), fell between 0.79–2.10 m during June 4–August 27, 1999, and between 1.48–2.38 m during May 23–August 17, 2000.

SAMPLING STATIONS

During 1999, 4 stations along Mill Creek with similar flood depths (±8 cm) at a distance of 5–9 m from the marsh edge were chosen for sampling. These stations were established in late April, before seasonal macrophyte growth began with 2 replicate stations each of *Spartina*-dominated and *Phragmites*-dominated habitats (Fig. 1). In 2000, a greater effort was taken to locate stations with comparable flood depth and elevation at a uniform distance of 5 m from the marsh edge. Three 2 × 7 m replicate stations of both marsh types (6 stations total) were established (Fig. 1). It should be noted that in 2000, 2 of the *Phragmites* stations had small creeks (~0.7 m wide, 5 m from marsh edge) along the edge of the plots. In both years, all stations were located within 0.56 km. The elevations of the stations were then determined by using global positioning system Real Time Kinematic methods. Each of the 6 plots was divided into a grid of 1.0 m^2 quadrats. Within each plot, 3 quadrats were randomly selected for readings and averaged. Position and elevation accuracy was ±1 and ±3 cm, respectively. Maximum topographic relief was measured within each plot by point estimates of rugosity using a meter stick attached to a combination square with a level that ensured measurements were taken at a 90° angle. The meter stick was laid down horizontally and rested on the highest point of the quadrat while the perpendicular ruler measured the maximum topographic relief. Within each plot, six 1.0 m^2 quadrats were randomly selected for measurements and averaged.

For both years, measurements of salinity, temperature, pH, and dissolved oxygen were taken on 1 day of each pair of sampling dates using a handheld refractometer, a HANNA model HI9023 pH meter, and a portable YSI model 95 dissolved oxygen (DO) meter. Each of these measurements was taken in the creek at a depth of 3–5 cm, at a central location among the sampling stations.

VEGETATION

For both years, plant coverage was estimated within each sampling station and expressed as the total foliage area covered by a species divided by the total habitat area sampled (Brower et al. 1990). Measurements were carried out in 5 random 0.5 × 0.5 m quadrats within each station and averaged. In 2000, basal-area coverage was also determined to provide a more detailed description of the marsh surface with the units of measurement being culms for *Phragmites* and multi-stemmed clumps for *Spartina* and *Pluchea purpurascens*. The diameter of each unit was measured approximately 3–5 cm above the soil surface from 5 random 0.25 m^2 quadrats within each station and averaged (Brower et al. 1990). Basal-area coverage was estimated by the basal area covered by a species divided by the total area sampled.

FISH AND INVERTEBRATE DISTRIBUTION AND ABUNDANCE

In 1999, large juvenile and adult fish were sampled biweekly July 13–August 15. Three rectangular minnow traps (41 × 24 × 24 cm, 2 mm nylon mesh with 3 cm openings at both ends) per station (n = 12 traps) were deployed perpendicular to the marsh edge, spaced at approximately 1-m intervals, on each sampling date just before high tide and collected 1–2 h after high tide. Fish were identified, measured (total length, TL), counted, and released in the field. Small juvenile and larval fish were sampled by installing three shallow pit traps (20.3 × 27.9 × 5.1 cm) at each station. These traps were anchored with tent stakes flush with the marsh substrate at 5–9 m from the marsh edge and spaced at approximately 1-m intervals. Efforts were taken to avoid altering the marsh surface by laying down boards when accessing traps. Samples were collected on a biweekly basis (n = 18 samples) that coincided with spring high tides from June 4 to August 27. In 2000, greater efforts were taken to avoid alteration of the marsh surface while collecting samples by installing boardwalks perpendicular to the marsh edge at each station in April before seasonal macrophyte growth began. At each station, 4 of the same pit traps used in 1999 were placed 0.5 m apart and 5 m (± 0.5 m) from the marsh edge. Pit trap samples were again collected on a spring tide schedule (n = 24 traps) from May 23 to August 17.

In both years, the pit traps were emptied just prior to high tide and fish and invertebrates in the traps were collected ~2 h after high tide receded. Samples were poured into plastic bags and immediately placed in a cooler on ice. Upon return to the laboratory, samples were passed through a 300-μm sieve to retain macrofauna and large meiofauna. The organisms were then preserved in a buffered 20% formaldehyde solution. After 1 wk, samples were transferred to 70% ethanol with rose bengal stain. After staining, all organisms were sorted from debris under a dissecting microscope, identified to lowest practical taxonomic level using a variety of taxonomic keys (Hardy 1978; Merritt and Cummins 1978; Wang and Kernehan 1979; Weiss 1995; Able and Fahay 1998; Pollock 1998), and enumerated. TL measurements of the fish were made to the nearest 0.1 mm with calipers under a magnifying lens.

LARVAL FISH PREY AVAILABILITY

To evaluate the relationship between invertebrate size and availability as fish prey, measurements of gape widths for fish and invertebrate sizes were carried out using a dissecting microscope with an ocular reticle. Major groups of invertebrates (n = 50 specimens taxon^{-1}) were measured by the narrowest width, assuming the fish can handle the prey so as to minimize width relative to gape for ingestion. Specimens for these measurements were randomly selected from samples collected throughout the sampling months.

HABITAT MANIPULATION EXPERIMENTS

To determine if spawning by mummichogs could occur in *Phragmites*-dominated marshes, egg deposition was investigated (June 18 and July 3, 2000) by deploying 5 anchored scrub brushes (14 × 6.5 × 3.5 cm) per *Phragmites* sampling station (n = 15 brushes sampling date^{-1}). Before sampling, the brushes were set out in the marsh for 2 d to allow them to be coated with marsh biofilms. Brushes were set out 1–5 m from the marsh edge before high tide the day before collection, allowing two high tides for spawning access. At the time of collection, the brushes were placed in plastic bags and then immediately into a cooler with ice. Upon return to lab, eggs were removed from brushes, preserved in 70% ethanol, identified (Armstrong and Child 1965), and counted with the aid of a dissecting microscope.

To determine if changes in marsh surface microtopography would influence larval mummichog abundance, 3 experimental plots were established in 2000 (Fig. 1) in which depressions were created on the marsh surface of *Phragmites*-dominated sites to simulate the microtopography of a *Spartina* marsh (i.e., more small depressions and pools). The collective treatment involved using 3 techniques within each treatment plot that included removing the upper 2 cm of soil from the center of 6 PVC cylinders (10 cm diam and 10 cm deep) installed flush with the marsh surface, physically stamping the substrate to create varying numbers of depressions approximately 10 × 25 × 3 cm in size, and installing 4 shallow pit traps (20.3 × 27.9 × 5.1 cm) flush with the marsh surface. These 3 treatment plots were paired with the unaltered (i.e., control) plots (Fig. 1) and separated by a distance of 3–5 m. Two of the paired plots contained small creeks (~0.7 m wide, 5 m from marsh edge) that separated the control from the treatment. In order to determine whether these techniques adequately altered the microtopography, point estimates of rugosity were measured in both control and treatment plots as described earlier. Boardwalks were installed in April to avoid alteration of the marsh surface within the control plots. The pit traps were used as the sampling device. To separate out the effects of the presence of the pit traps, traps placed in the control plots were kept covered until just before high tide on sampling days. Possible disturbance of water flow by the boardwalks was duplicated in the treatment plots by installing wooden boards to simulate the legs of the boardwalks. Pit trap samples were collected on the 2 days following spring tides (n = 24 traps) from June 18 to August 17.

STATISTICAL ANALYSES

The influence of marsh type on abundance (average catch per sampling unit effort, CPUE) of large juvenile and adult mummichogs in 1999 was tested using a one-way analysis of variance (ANOVA). Marsh type was the treatment (2 replicate sampling stations marsh type^{-1}), mesh traps were the sampling units (3 traps sampling station^{-1}), and abundance was the response variable. The larval and small juvenile fish abundance data (average CPUE) did not meet the normality assumption of ANOVA, so nonparametric Kruskal-Wallis ANOVA (Hollander and Wolfe 1973) was employed on untransformed data to determine the influence of marsh type on abundance (average CPUE) using marsh type as the treatment (3 replicate sampling stations marsh type^{-1}), pit traps as the sam-

TABLE 1. Physical characterization of marsh types along Mill Creek, Hackensack Meadowlands, New Jersey, in 2000. s = standard deviation, n = sample size within each habitat type. One-way ANOVA was used to determine significant differences ($\alpha \leq 0.05$). * denotes the manipulated *Phragmites* stations for comparison between manipulated stations and control stations.

	Spartina-Dominated Marsh	*Phragmites*-Dominated Marsh	F	p
Flood depth	Mean = 11.7 cm s = 2.7 (n = 9)	Mean = 12.0 cm s = 4.1 (n = 9)	0.04	0.85
Elevation above mean sea level	Mean = 0.7 m s = 0.1 (n = 9)	Mean = 0.7 m s = 0.1 (n = 9)	6.49	0.06
Maximum relief	Mean = 4.4 cm s = 1.3 (n = 18)	Mean = 0.4 cm, 5.2 cm* s = 0.6, 1.5* (n = 18)	126.71, 180.86*	<0.0001, <0.0001*
Vegetation dominance	Mean = 86.7% *S. alterniflora* (n = 15)	Mean = 100% *P. australis* (n = 15)	—	—
Vegetative basal-area coverage	353.7 cm^2 0.25 m^{-2} s = 15.1 (n = 15)	82.7 cm^2 0.25 m^{-2} s = 6.4 (n = 15)	2.30	0.0001

pling unit (4 traps station^{-1}), and abundance as the response variable. In the *Phragmites* habitat manipulation experiment, the Kruskal-Wallace ANOVA was also used to determine the influence of created pools and depressions on larval and small juvenile fish abundance (average CPUE) using microtopography as the treatment (3 stations microtopography type^{-1} [i.e., smooth versus hummocky]), pit traps as the sampling unit (4 traps sampling station^{-1}), and abundance as the response variable. In 2000, the abundances (average CPUE) of the 8 major groups of invertebrate taxa collected within each marsh type were compared using the Kruskal-Wallis ANOVA on untransformed data. A Bonferroni correction was then applied to the invertebrate results to correct for multiple testing. All physical parameters were tested with a one-way ANOVA. SAS software (version 7.0, SAS Institute Inc., Cary, North Carolina) was employed for all analyses.

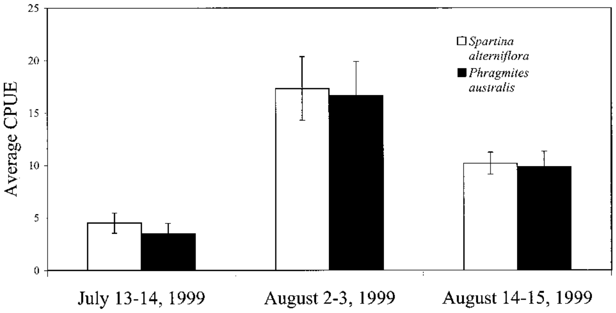

Fig. 2. Mean abundance (average catch per unit effort, CPUE) ± 1 SE, of large juvenile and adult mummichog (*Fundulus heteroclitus*) by marsh type at Mill Creek, New Jersey, in 1999. Samples were collected from 2 replicate stations of each marsh type with 3 minnow traps per station (n = 12 traps).

Results

PHYSICAL AND VEGETATION PARAMETERS

Flood depth and elevation did not vary significantly between marsh types ($F = 0.04$, $p = 0.85$; $F = 6.49$, $p = 0.06$; Table 1). Rugosity was significantly greater in the *Spartina*-dominated marshes ($F = 126.71$, $p < 0.0001$; Table 1), and this measure was also significantly greater in the created microtopography within the *Phragmites* treatment plots than that in the control plots ($F = 180.86$, $p < 0.0001$). The average salinity varied between years (1999: 11‰; 2000: 5‰), as well as DO (1999: 6.6 mg l^{-1}; 2000: 4.3 mg l^{-1}). Mean temperature (1999: 25.7°C; 2000: 26.2°C) and pH (1999: 7.3; 2000: 7.3) were similar between years. Vegetation dominance was characterized as > 70% coverage in both *Phragmites* and *Spartina* marsh types. *P. purpurascens* (9.1%), *Eleocharis* spp. (3.7%), and *Scirpus americanus* (0.5%) were also present at the *Spartina* sites. The average basal-area coverage of the vegetation in the *Spartina* marshes (353.7 cm^2 0.25 m^{-2}) was significantly higher than in *Phragmites*-dominated marshes (82.7 cm^2 0.25 m^{-2}; ANOVA: $F = 2.30$, $p = 0.0001$).

FISH DISTRIBUTION AND ABUNDANCE

The abundance (average CPUE) of large juveniles and adult mummichogs as sampled by minnow traps, was similar in both marsh types in 1999 (Fig. 2). There were no significant differences in abundance on any of the 3 sampling dates ($F = 0.31$, $p = 0.63$; $F = 0.01$, $p = 0.92$; $F = 0.54$, $p = 0.84$). Total length of mummichogs from both habitats ranged from 20–104 mm over the sampling period (mean = 43.30 mm, SD = 12.57).

In both years, larvae and small juvenile mummichogs as sampled by pit traps, were consistently

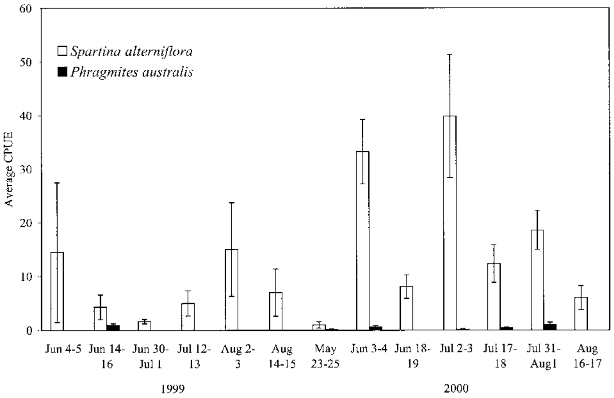

Fig. 3. Mean abundance (average catch per unit effort, CPUE) ± 1 SE, of larval and small juvenile mummichog (*Fundulus heteroclitus*) at Mill Creek, New Jersey, in 1999 and 2000. In 1999, samples were collected biweekly from 2 replicate stations of each marsh type with 3 pit traps per station (n = 12 traps) from June 4–5 to August 14–15. In 2000, samples were collected biweekly from 3 replicate stations of each marsh type with 4 pit traps per station (n = 12 traps) from May 23–25 to August 16–17. See Fig. 1 for sampling stations.

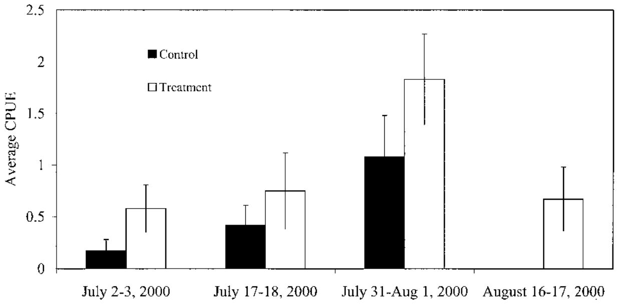

Fig. 4. Mean abundance (average catch per unit effort, CPUE) of larval and small juvenile mummichogs in *Phragmites* control plots versus *Phragmites* treatment plots as collected by pit traps at Mill Creek, New Jersey, in 2000. Samples were collected biweekly coinciding with spring high tides from 4 pit traps at 3 replicate stations each in *Phragmites* control plots and *Phragmites* treatment plots. Treatments involved creating a microtopography similar to that of *Spartina alterniflora* (i.e., more depressions and small pools) within a *Phragmites*-dominated marsh.

more abundant in *Spartina* than in *Phragmites* habitats (Fig. 3). In 1999, mummichogs made up 100% of the pit trap collections in both marsh types but the average CPUE differed dramatically between them with abundance significantly higher in *Spartina* (Kruskal-Wallis: $\chi^2 = 5.32$, $p = 0.04$). Total length ranged from 5.10–25.80 mm (mean = 12.03, SD = 5.05) and was similar between the 2 habitats. In 2000, mummichogs again made up 100% of the pit trap collections. Abundance was significantly higher in *Spartina* marsh (CPUE = 17.01) relative to *Phragmites* (CPUE = 0.35) over the sampling period (Kruskal-Wallis: $\chi^2 = 90.79$, $p < 0.0001$; Fig. 3). Out of the total 1,469 fish collected, only 29 young-of-the-year individuals were captured in *Phragmites*-dominated marsh. The TL ranged from 4.50–26.40 mm (mean = 8.83, SD = 3.22) and again was similar between the 2 habitats.

HABITAT MANIPULATIONS

Mummichog eggs (n = 891) were collected from artificial spawning sites (scrub brushes) in *Phragmites*-dominated marshes. A total of 98 eggs were collected on June 28, 2000, and a total of 793 eggs were collected on July 3, 2000. With the exception of the 16 eggs collected on July 3, all eggs were deposited ~2 m landward from the marsh edge and only collected from the 2 stations with creeks adjacent to them.

In the marsh surface habitat manipulation experiment, there was a trend for higher larval mummichog abundance within the *Phragmites* treatment plots versus the *Phragmites* control plots over the sampling periods (Fig. 4). Overall differences were significant (Kruskal-Wallis: $\chi^2 = 5.03$, $p = 0.02$) with the more rugose plots in the manipulated habitats having a greater abundance of mummichog.

INVERTEBRATE DISTRIBUTION AND AVAILABILITY

The pit traps used in this study sampled the invertebrates associated with habitats on or just above the marsh surface and those suspended in the water column during incoming tides. The traps sampled the organisms that would be available as prey for mummichogs, which move onto the marsh surface during high tides to feed. Thirty-nine invertebrate taxa were identified from the pit trap collections, with a total of 13,109 individuals collected in *Spartina* habitat while a significantly lower number, 7,182 individuals, were collected from *Phragmites* habitat (Kruskal-Wallis: $\chi^2 = 12.39$, $p < 0.0004$; Table 2). The major invertebrate groups (those taxa that comprised > 2% of the total organisms collected) also differed significantly in abundance between the 2 habitat types (Fig. 5), with the exception of nematodes (Kruskal-Wallace: $\chi^2 = 5.14$, kp = 0.16). Harpacticoid copepods, oligochaetes, ostracods, and the sabellid polychaete *Manayunkia aestuarina* were all significantly greater in abundance within the *Spartina* pit trap collections (Kruskal-Wallis: $\chi^2 = 55.65$, kp < 0.0008; $\chi^2 = 15.69$, kp < 0.0008; $\chi^2 = 23.19$, kp < 0.0008; $\chi^2 = 11.43$, kp = 0.0056) while chironomids, gastropods, predominantly *Hydrobia* spp., and gammarids were significantly more abundant in the *Phragmites*-dominated marshes (Kruskal-Wallis: $\chi^2 = 14.61$, kp = 0.0008; $\chi^2 = 38.00$, kp < 0.0008; $\chi^2 = 15.46$, kp < 0.0008).

The relationship between mummichog gape width and invertebrate size indicated that prey for

TABLE 2. Species composition and abundance (total individuals) of prey taxa in *Phragmites* and *Spartina*-dominated marshes as collected by pit traps (n = 54 samples marsh type^{-1}) from May 23–August 17, 2000, at Mill Creek, Hackensack Meadowlands, New Jersey.

Phylum Class	Taxonomic Group	*Phragmites*	*Spartina*
Annelida			
Oligochaetae	Oligochaete	850	1,899
Polychaetae	*Manayunkia aestuarina*	82	196
	Hobsonia florida	5	1
	Spionidae	0	1
	Capitellidae	3	0
Arthropoda			
Arachnida	Acarina	83	67
	Araneae	30	3
	Pseudoscorpiones	7	0
Crustacea	Calanoid copepod	58	46
	Cyclopoid copepod	501	1,275
	Harpacticoid copepod	243	2,756
	Argulus sp.	1	22
	Ostracoda	982	5,018
	Gammaridae	771	130
	Talitridae	74	2
	Corophium sp.	3	3
	Cyathura polita	2	1
	Philoscia vittata	6	0
Insecta	Hydrophilidae	13	4
	Ephydridae	0	11
	Tipulidae	9	1
	Ceratopogonidae	15	23
	Chironomidae	266	87
	Dolichipodidae	3	6
	Stratiomyidae	0	7
	Chloropidae	8	33
	Corixidae	0	11
	Erythrodiplax berenice	0	9
	Collembola	60	207
	Unidentified larvae	24	29
Chordata			
Osteichthyes	*Fundulus heteroclitus*	29	1,440
Cnidaria			
Anthozoa	Anthozoa	89	11
Mollusca			
Bivalvia	*Macoma baltica*	5	0
Gastropoda	Hydrobia sp.	2,600	688
	Succinea wilsonii	29	18
	Melampus bidentata	1	0
Nematoda	Nematoda	219	403
Platyhelminthes			
Turbellaria	Turbellaria	125	104
Sarcomastigophora	Foraminifera	14	39

larval fish were more available in *Spartina* marsh than in *Phragmites* marsh. There was a positive correlation (r = 0.987) between fish total length and gape width measurements. In keeping with the positive relationship between fish size class, gape width, and invertebrate size, the prey available to the smallest fish (6.5 mm TL) included harpacticoid copepods, *M. aestuarina*, nematodes, oligochaetes, and ostracods (Table 3). These taxa were significantly more abundant in pit trap collections from *Spartina* marsh. On average, gammarids and gastropods, which were found to be most abundant in *Phragmites* marsh, would not be available to fish <14 mm total length due to gape limitations.

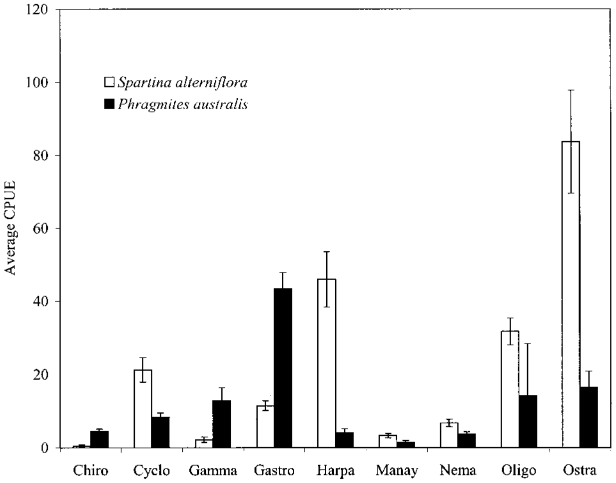

Fig. 5. A comparison of major invertebrate groups (taxa that comprise over 2% of the total organisms collected) from *Spartina alterniflora* or *Phragmites australis* pit trap collections (n = 54 samples marsh type^{-1}) at Mill Creek, New Jersey, in 2000. Chiro = chironomidae, Cyclo = cyclopoid copepod, Gamma = gammaridae, Gastro = gastropoda, Harpa = harpacticoid copepod, Manay = *Manayunkia aestuarina*, Nema = nematoda, Oligo = oligochaetae, Ostra = ostracoda.

Discussion

Several parameters investigated in this study suggest that *Phragmites*-dominated marshes may not provide suitable habitat for mummichog larvae and small juveniles. The low abundances of these early life history stages observed in *Phragmites*, in contrast to *Spartina* habitat in both 1999 and 2000, corroborates earlier comparisons between these marsh types in the Mullica River in southern New Jersey (Able and Hagan 2000, 2003). On the other hand, the abundance and distribution of the larger juveniles and adults in Mill Creek seems to indicate that these size classes are using the 2 marsh types similarly. This portion of the results corresponds to findings in the Connecticut River (Fell et al. 1998; Warren et al. 2001), the upper Chesapeake Bay (Meyer et al. 2001), and the Mullica River, New Jersey (Able and Hagan 2000). It is important to note that in each of the aforementioned studies, *Phragmites* sampling sites were in close proximity to *Spartina* sampling sites, the latter of which may have been serving as larval habitat and hence a source for the larger size-classes collected in *Phragmites*. Once the young fish are large enough to migrate on and off of the marsh surface (~15–20 mm

TABLE 3. Mouth gape width (mm TL) of larval and juvenile mummichog (*Fundulus heteroclitus*) and sizes (mm) of representative potential prey. All measurements were made under a dissecting microscope to the nearest 0.01 mm. For all invertebrate taxa, the narrowest width was measured. H = harpacticoid copepod, M = *Manayunkia aestuarina,* N = Nematoda, Ol = Oligochaetae, Os = Ostracoda, Gm = Gammaridae, and Gs = Gastropoda.

	Gape Width			Invertebrate Size						
	6.1–8.4	8.5–14.4	14.5–25.5	H	M	N	Ol	Os	Gm	Gs
Average	0.93	1.40	2.32	0.24	0.17	0.09	0.30	0.32	1.89	1.74
n	43	31	18	50	50	50	50	50	50	50
SE	0.01	0.04	0.10	0.01	0.01	0.00	0.01	0.01	0.16	0.08

standard length as per Kneib 1986) and feed on larger prey, they may then use both marsh types similarly.

Several factors may be contributing to the dramatic differences in larval and small juvenile mummichog abundances within *Phragmites*-dominated and *Spartina*-dominated marshes. Although physical features such as elevation and flood depth affect fish utilization of the marsh surface (Rozas et al. 1988; Kneib and Wagner 1994; Rozas 1995; Minnello and Webb 1997), these potentially confounding factors were kept similar between marsh types and cannot be responsible for the differences in abundance observed between the 2 habitats. *Phragmites* dominance would influence available spawning substrate for mummichogs that use the first axils of *S. alterniflora* for egg deposition (Taylor and DiMichele 1983), as well as other cracks, crevices, and small interstices (Able and Castagna 1975; Able 1984; Able and Hata 1984). *Phragmites* leaves are attached to the stems with tightly bound culm sheaths, rendering these inaccessible as egg deposition sites. Egg deposition has been observed in broken dead culms short enough to be submerged at high tide with the number of eggs positively correlating with stem diameter (Able and Hagan 2003). The results of the spawning substrate trial in this study also showed that these fish will spawn within *Phragmites* marshes, given adequate substrate. It is interesting to note that eggs were collected only from the *Phragmites* plots with creeks adjacent to them. This finding suggests the potential importance of creeks and rivulets on the marsh surface (i.e., drainage density) as access points for spawning (Rozas and Odum 1987; Rozas et al. 1988; Kneib and Wagner 1994; Rozas 1995; Kneib 1997a,b; Minnello and Webb 1997; West and Zedler 2000). These topographic features are reduced as a result of *Phragmites* establishment (Weinstein and Balletto 1999; Windham and Lathrop 1999; Rooth and Stevenson 2000) and may influence marsh fish accessibility and hence abundance over the long term.

Shallow pools and depressions on the marsh surface have been observed to be an important habitat component for the larval stage of mummichog development (Taylor et al. 1979; Talbot and Able 1984; Yozzo et al. 1994; Kneib 1997a,b). These microhabitats, as small as 1 cm deep and 10 cm wide (Taylor et al. 1979), are thought to serve as refuges from predators while providing invertebrate food resources (Kneib 1984, 1987). In contrast to the hummock-building morphology of *Spartina, Phragmites* communities have much less pronounced microtopographic relief (Windham 1995; Windham and Lathrop 1999; Able and Hagan 2000, 2003; Raichel 2001) and may not provide the standing water refuge necessary for larvae. The smooth microtopography of *Phragmites*-dominated marshes may be influenced by the water-flow conditions dictated by the morphology of the plant (Leonard and Luther 1995), as well as by the increased amount of litter production, which fills in hollows and rivulets (Chambers et al. 1999; Windham and Lathrop 1999). The degree of marsh surface rugosity seems to have an inverse relationship with the length of time *Phragmites* has been established (Windham and Lathrop 1999). In this study, the experimental creation of microhabitats (i.e., increasing rugosity and amount of standing water) on the *Phragmites* marsh surface appeared to improve larval habitat based on larval abundance but cannot be interpreted as the only important habitat feature.

Hydrologic features may precede the issue of microtopography in terms of larval fish habitat. Since mean flow speed over the marsh surface has an inverse relationship with plant density (Leonard and Luther 1995), it would follow that the conversion of a *Spartina*-dominated marsh to the significantly lower basal-area coverage of a *Phragmites*-dominated marsh would alter this hydrologic feature. The influence plant morphology has on deposition and erosion patterns in tidal marshes (Pethick 1992; Leonard and Luther 1995) is also an important consideration in the resulting spatial distribution of water velocity (i.e., small creeks and rivulets in *Spartina* marsh versus sheet flow in *Phragmites* marsh). Since *Phragmites* causes a smoothed marsh surface (Windham and Lathrop 1999), possibly promotes faster flow speed (Leonard and Luther 1995) relative to *Spartina* (Angradi et al. 2001), and has an ability to wick moisture away from the marsh surface (Amsberry 1997; Stevenson et al. 2000), this type of marsh could potentially influence larval transport off the marsh surface during ebb tides. During the course of this study, considerable numbers of mummichog larvae were frequently observed (n = 18 d) along the edges of each *Phragmites* marsh (n = 5 sites) after the marsh surface had drained, possibly making them more vulnerable to predation by aquatic predators.

The conversion of a *Spartina* marsh to a *Phragmites* marsh gradually changes the microtopography from hummocky to smooth (Windham and Lathrop 1999), possibly by means of altering the marsh surface hydrology. We speculate that the resultant change in microtopography, and possibly water flow across the marsh surface, has a negative effect on larval habitat (i.e., reduced standing water refuge on the marsh surface) and that these alterations potentially affect larval survivorship. A recent study investigating marsh surface flow dynamics and sedimentation in *Phragmites* and *Spartina* marshes (Leonard et al. 2002) found no significant differences between the 2 marsh types, although the study site in upper Chesapeake Bay is a very low energy system with a flow depth of < 12 cm in *Phragmites* and < 8 cm in *Spartina* (lower than the lowermost leaves). The same results may not apply to higher energy systems, such as the Mill Creek site, where flood depths averaged 12 cm in both marsh types, and plant morphology may have more of an influence on marsh surface flow dynamics and microtopography. The morphology of *Phragmites* may also have an influence on predators exploiting the marsh surface since its widely spaced stems may interfere less with their movement and foraging activity than the higher basal-area coverage of grasses such as *Spartina* (Vince et al. 1976; Van Dolah 1978; West and Williams 1986).

Food availability may also influence the distribution and abundance of larval and small juvenile mummichogs (5–25 mm TL), which are largely carnivorous and show size-specific preferences for certain prey (Kneib and Stiven 1978; Kneib 1986). The types and sizes of invertebrates available on or just above the marsh surface may influence feeding success since some prey may be either too large or too small to be effectively handled by a fish of a given size and are unavailable (Kneib 1986). In a Delaware Bay marsh, meiofauna (copepods, foraminiferans, ostracods, and nematodes) were found to compose the majority of the smallest fishes diets, but declined in occurrence in fish > 20 mm SL; the relative importance of crustaceans (primarily amphipods) tended to increase with fish size (Smith et al. 2000). In a Georgia salt marsh, harpacticoid copepods, tanaids, and sabellid polychaetes (*M. aestuarina* and *Fabricia* spp.) were the most abundant taxa in the diets of young mummichogs, while *Nereis succinea* and amphipods occurred only in the guts of the larger individuals (Kneib 1986). The results of this study suggest that availability of larval fish prey items may be greater in *Spartina* marsh in comparison to *Phragmites* marsh. Larval mummichog prey such as harpacticoid copepods, nematodes, *M. aestuarina*, and ostracods (Kneib and Stiven 1978; Smith et al. 2000) were significantly more available in the *Spartina*-dominated marshes than in *Phragmites*-dominated marshes. The relationship between invertebrate size and gape width of mummichogs indicates that these organisms are available to the smallest size classes (6–14 mm TL). The taxa found to be dominant in the *Phragmites*-dominated marshes (i.e., amphipods and gastropods) are known to be prey of larger individuals (Kneib and Stiven 1978; Fell et al. 1998; Smith et al. 2000). These prey-size differences might help explain differences in abundances of fish size-classes between marsh types in this study. In general, the total number of individuals collected in the pit traps was significantly higher in *Spartina* marsh. The greater abundance of benthic taxa such as nematodes, *M. aestuarina*, and oligochaetes in *Spartina* pit trap collections could be attributed to a greater amount of suspended sediments in these marshes (Raichel personal observation). Low numbers of copepods in *Phragmites* marsh, in contrast with numbers found in *Spartina* marsh, may be due to the decrease in light penetration to the marsh surface as a result of dense aerial production. This decrease in light would influence diatom production (Thurman 1991) and limit a food resource for the copepods, which in turn are important prey for the mummichog.

Large expanses of *Phragmites* monocultures may not provide adequate habitat to sustain abundant populations of the resident mummichog. Because this fish is frequently consumed by many estuarine species, it would follow that a population size reduction could have profound impacts on salt marsh food webs and the trophic relay (Kneib 1997a) of production from the marsh surface to the adjacent subtidal waters.

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LITERATURE CITED

ABLE, K. W. 1984. Variation in spawning site selection of the mummichog *Fundulus heteroclitus*. *Copeia* 1984:522–525.

ABLE, K. W. AND M. CASTAGNA. 1975. Aspects of an undescribed reproductive behavior in *Fundulus heteroclitus* (Pisces: Cyprinodontidae) from Virginia. *Chesapeake Science* 16:282–284.

ABLE, K. W. AND M. P. FAHAY. 1998. The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, New Jersey.

ABLE, K. W. AND S. M. HAGAN. 2000. Effects of common reed (*Phragmites australis*) invasion on marsh surface macrofauna: Response of fishes and decapod crustaceans. *Estuaries* 23:633–646.

ABLE, K. W. AND S. M. HAGAN. 2003. The impact of common reed, *Phragmites australis,* on essential fish habitat: Influence on reproduction, embryological development, and larval abundance of mummichog (*Fundulus heteroclitus*). *Estuaries* 26: 40–50.

ABLE, K. W. AND D. HATA. 1984. Reproductive behavior in the *Fundulus heteroclitus-F. grandis* complex. *Copeia* 1984:820–825.

AMSBERRY, L. 1997. Factors regulating the invasion of *Phragmites australis* into southern New England salt marshes. Master's Thesis, Brown University, Providence, Rhode Island.

ANGRADI, T. R., S. M. HAGAN, AND K. W. ABLE. 2001. Vegetation type and the intertidal macroinvertebrate fauna of a brackish marsh: *Phragmites* vs. *Spartina*. *Wetlands* 21:75–92.

ARMSTRONG, P. B. AND J. S. CHILD. 1965. Stages in the normal development of *Fundulus heteroclitus*. *Biological Bulletin* 128: 143–168.

BENOIT, L. K. AND R. A. ASKINS. 1999. Impact of the spread of *Phragmites australis* on the distribution of birds in Connecticut tidal marshes. *Wetlands* 19:194–208.

BROWER, J. E., J. H. ZAR, AND C. N. VON ENDE. 1990. Field and Laboratory Methods for General Ecology, 3rd edition. William C. Brown Publishers, Dubuque, Iowa.

CHAMBERS, R. M., L. A. MEYERSON, AND K. SALTONSTALL. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany* 64:261–273.

CROSS, D. H. AND K. L. FLEMING. 1989. Control of *Phragmites* or common reed. U.S. Fish and Wildlife Service, Office of Information Transfer, Fort Collins, Colorado. FWS/OIT-13.4.12: 1–15.

DEEGAN, L. A. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Sciences* 50:74–79.

FELL, P. E., S. P. WEISSBACH, D. A. JONES, M. A. FALLON, J. A. ZEPPIERI, E. K. FAISON, K. A. LENNON, K. J. NEWBERRY, AND L. K. REDDINGTON. 1998. Does invasion of oligohaline tidal marshes by reed grass, *Phragmites australis* (Cav.) Trin. ex Steud., affect the availability of prey resources for the mummichog, *Fundulus heteroclitus* L.? *Journal of Experimental Marine Biology and Ecology* 222:59–77.

HARDY, JR., J. D. 1978. Development of Fishes of the Mid-Atlantic Bight. An Atlas of Egg, Larval and Juvenile Stages, Volume II. U.S. Fish and Wildlife Service Publication FWS/OBS-78/ 12. Center for Environmental and Estuarine Studies of the University of Maryland, Cambridge, Maryland.

HOLLANDER, M. AND D. A. WOLFE. 1973. Nonparametric Statistical Methods. John Wiley and Sons, Inc., New York.

KNEIB, R. T. 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). *Journal of Experimental Marine Biology and Ecology* 83:41–51.

KNEIB, R. T. 1986. The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. *American Zoologist* 26:259–269.

KNEIB, R. T. 1987. Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology* 68:379–386.

KNEIB, R. T. 1997a. The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology: An Annual Review* 35:163–220.

KNEIB, R. T. 1997b. Early life stages of resident nekton in intertidal marshes. *Estuaries* 20:214–230.

KNEIB, R. T. AND J. H. PARKER. 1991. Gross conversion efficiencies of mummichog and spotfin killifish larvae from a Georgia salt marsh. *Transactions of the American Fisheries Society* 120:803–809.

KNEIB, R. T. AND A. E. STIVEN. 1978. Growth, reproduction and feeding of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. *Journal of Experimental Marine Biology and Ecology* 31: 121–140.

KNEIB, R. T. AND S. L. WAGNER. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* 106:227–238.

LEONARD, L. A., P. A. ANSLEY, AND R. L. BEAVERS. 2002. Flow dynamics and sedimentation in *Spartina alterniflora* and *Phragmites australis* marshes on the Chesapeake Bay. *Wetlands* 22: 415–424.

LEONARD, L. A. AND M. E. LUTHER. 1995. Flow hydrodynamics in tidal marsh canopies. *Limnology and Oceanography* 40:1474–1484.

MARKS, M., B. LAPIN, AND J. RANDALL. 1994. Element Stewardship Abstract for *Phragmites australis*. The Nature Conservancy, Arlington, Virginia.

MEREDITH, W. H. AND V. A. LOTRICH. 1979. Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). *Estuarine and Coastal Marine Science* 8:99–118.

MERRITT, R. W. AND K. W. CUMMINS (EDS.). 1978. An Introduction to the Aquatic Insects of North America, 2nd edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

MEYER, D. L., J. M. JOHNSON, AND J. W. GILL. 2001. Comparison of nekton use of *Phragmites australis* and *Spartina alterniflora* marshes in the Chesapeake Bay, USA. *Marine Ecology Progress Series* 209:71–83.

MEYERSON, L. A., K. A. VOGT, AND R. M. CHAMBERS. 1999. The effects of *Phragmites* removal on nutrient pools in a freshwater tidal marsh ecosystem. *Biological Invasions* 1:129–136.

MINELLO, T. J. AND J. W. WEBB, JR. 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Marine Ecology Progress Series* 151:165–179.

PETHICK, J. S. 1992. Saltmarsh geomorphology, p. 41–62. *In* L. Allen and K. Pye (eds.), Saltmarshes, Morphodynamics, Conservation and Engineering Significance. Cambridge University Press, Cambridge, U.K.

POLLOCK, L. W. 1998. A Practical Guide to the Marine Animals of Northeastern North America. Rutgers University Press, New Brunswick, New Jersey.

PRINSLOW, T. E., I. VALIELA, AND J. M. TEAL. 1974. The effect of detritus and ration size on the growth of *Fundulus heteroclitus* (L.). *Journal of Experimental Marine Biology and Ecology* 16:1–10.

QUINN, J. R. 1997. Fields of Sun and Grass: An Artist's Journal of the New Jersey Meadowlands. Rutgers University Press, New Brunswick, New Jersey.

RAICHEL, D. L. 2001. The influence of *Phragmites* dominance on a marsh resident fish in the Hackensack Meadowlands, New Jersey. Master's Thesis, Rutgers University, New Brunswick, New Jersey.

RICE, D., J. ROOTH, AND J. C. STEVENSON. 2000. Colonization and expansion of *Phragmites australis* in upper Chesapeake Bay tidal marshes. *Wetlands* 20:280–299.

ROOTH, J. E. AND J. C. STEVENSON. 2000. Sediment deposition patterns in *Phragmites australis* communities: Implications for coastal areas threatened by rising sea-level. *Wetlands Ecology and Management* 8:173–183.

ROSZA, R. 1995. Human impacts on tidal wetlands: History and regulations. *In* G. D. Dreyer and W. A. Niering (eds.), Tidal Marshes of Long Island Sound: Ecology, History, and Restoration. Bulletin No. 34. Connecticut College Arboretum, New London, Connecticut.

ROZAS, L. P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: A pulsing ecosystem. *Estuaries* 18:579–590.

ROZAS, L. P., C. C. MCIVOR, AND W. E. ODUM. 1988. Intertidal rivulets and creekbanks: Corridors between tidal creeks and marshes. *Marine Ecology Progress Series* 47:303–307.

ROZAS, L. P. AND W. E. ODUM. 1987. Use of tidal freshwater marshes by fishes and macrofaunal crustaceans along a marsh stream-order gradient. *Estuaries* 10:36–43.

SIPPLE, W. 1971. The past and present flora and vegetation of the Hackensack Meadows, NJ, and suggestions for management. Master's of Regional Planning Thesis, University of Pennsylvania, Philadelphia, Pennsylvania.

SMITH, K. J., G. L. TAGHON, AND K. W. ABLE. 2000. Trophic linkages in marshes: Ontogenetic changes in diet for young-of-the-year mummichog, *Fundulus heteroclitus,* p. 221–237. *In* M. P. Weinstein and D. A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.

STEVENSON, J. C., M. S. KEARNEY, AND K. L. SUNDBERG. 2000. The health and long-term stability of natural and restored marshes in Chesapeake Bay, p. 709–735. *In* M. P. Weinstein and D. A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishing, Dordrecht, The Netherlands.

TALBOT, C. W. AND K. W. ABLE. 1984. Composition and distribution of larval fishes in New Jersey high marshes. *Estuaries* 7:434–443.

TAYLOR, M. H. AND L. H. DIMICHELE. 1983. Spawning site utilization in a Delaware population of *Fundulus heteroclitus* (Pisces: Cyprinodontidae). *Copeia* 1983:719–725.

TAYLOR, M. H., L. DIMICHELE, AND G. J. LEACH. 1977. Egg stranding in the life cycle of the mummichog, *Fundulus heteroclitus. Copeia* 2:397–399.

TAYLOR, M. H., G. J. LEACH, L. H. DIMICHELE, W. M. LEVIAN, AND W. F. JACOB. 1979. Lunar spawning in the mummichog, *Fundulus heteroclitus* (Pisces: Cyprinodontidae). *Copeia* 1979: 291–297.

TEMPLER, P., S. FINDLAY, AND C. WIGAND. 1998. Sediment chemistry associated with native and non-native emergent macrophytes of a Hudson River marsh ecosystem. *Wetlands* 18:70–78.

TEO, S. L. H. AND K. W. ABLE. 2003. Growth and reproduction of the common mummichog (*Fundulus heteroclitus*) in a restored salt marsh. Estuaries 26:51–63.

THURMAN, H. V. 1991. Chapter 13, The marine environment, p. 333–335. *In* R. A. McConnin (ed.), Oceanography, 6th edition. Macmillan Publishing Company, New York.

VALIELA, I., J. E. WRIGHT, J. M. TEAL, AND S. B. VOLKMANN. 1977. Growth, production and energy transformations in the salt marsh killifish *Fundulus heteroclitus. Marine Biology* 40:135–144.

VAN DOLAH, R. F. 1978. Factors regulating the distribution and population dynamics of the amphipod (*Gammarus palustris*) in an intertidal salt marsh community. *Ecological Monographs* 48:191–217.

VINCE, S., I. VALIELA, N. BACKUS, AND J. M. TEAL. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: Consequences for prey distribution and abundance. *Journal of Marine Biology and Ecology* 23:255–266.

WAINRIGHT, S. C., M. P. WEINSTEIN, K. W. ABLE, AND C. A. CURRIN. 2000. Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. *Marine Ecology Progress Series* 200:77–91.

WANG, J. C. S. AND R. J. KERNEHAN. 1979. Fishes of the Delaware Estuaries: A Guide to the Early Life Histories. EA Communications, Ecological Analysts, Inc., Towson, Maryland.

WARREN, R. S., P. E. FELL, J. L. GRIMSBY, E. L. BUCK, C. G. RILLING, AND R. A. FERTIK. 2001. Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within the tidelands of the lower Connecticut River. *Estuaries* 24:90–107.

WEINSTEIN, M. P. AND J. H. BALLETTO. 1999. Does the common reed, *Phragmites australis,* affect essential fish habitat? *Estuaries* 22:793–802.

WEISBERG, S. B. AND V. A. LOTRICH. 1982. The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog *Fundulus heteroclitus.* An experimental approach. *Marine Biology* 66:307–310.

WEISS, H. M. 1995. Marine Animals of Southern New England and New York. State Geological and Natural History Survey of Connecticut Bulletin 115, Department of Environmental Protection, Hartford, Connecticut.

WEST, D. L. AND A. H. WILLIAMS. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology* 100:75–95.

WEST, J. M. AND J. B. ZEDLER. 2000. Fish use of tidal creek habitats in two southern California salt marshes. *Ecological Engineering* 14:233–252.

WINDHAM, L. 1995. Effects of *Phragmites australis* invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. Master's Thesis, Rutgers University, New Brunswick, New Jersey.

WINDHAM, L. AND R. LATHROP. 1999. Effects of *Phragmites australis* (common reed) invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. *Estuaries* 22:927–935.

YE, Z. H., A. J. M. BAKER, AND M. H. WONG. 1997. Zinc, lead and cadmium tolerance, uptake and accumulation by the common reed, *Phragmites australis* (Cav.) Trin ex Steudel. *Annals of Botany* 80:363–370.

YOZZO, D. J., A. MANNING, AND D. E. SMITH. 1994. Midsummer abundance of resident sub-adult marsh nekton at the Virginia Coast Reserve. *Virginia Journal of Science* 45:21–30.

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