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# Comparison of Fish and Macroinvertebrate Use of *Typha angustifolia, Phragmites australis,* and Treated *Phragmites* Marshes along the Lower Connecticut River

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**ABSTRACT:** Since 1965 large areas of lower Connecticut River tidelands have been converted from high diversity brackish meadow and *Typha angustifolia* marsh to near monocultures of *Phragmites australis.* This study addresses the impact of *Phragmites* invasion on fish and crustacean use of oligohaline high marsh. During spring tides from early June through early September 2000, fishes and crustaceans leaving flooded marsh along 3 km of the Lieutenant River, a lower Connecticut River tributary, were captured with Breder traps at 90 sites, equally distributed among *Phragmites, Typha,* and treated (herbicide and mowing) *Phragmites* areas. Pit traps, 18 per vegetation type in 2000 and 30 each in *Phragmites* and *Typha* in 2001, caught larvae and juveniles at distances of up to 30 m into the marsh interior. There were no significant differences in fish species compositions or abundances among the vegetation types. Size distributions, size specific biomasses, and diets of *Fundulus heteroclitus,* the numerically dominant fish, were also similar. The shrimp *Palaemonetes pugio* was more abundant in *Phragmites* than in other types of vegetation, whereas the fiddler crab *Uca minax* was least numerous in *Phragmites.* Mean numbers of *F. heteroclitus* and *P. pugio* caught per site event were positively correlated with increasing site hydroperiod. Significantly more *F. heteroclitus* were captured along the upper reach of the river where marsh elevations were lower than farther downstream. More *F. heteroclitus* and fewer *P. pugio* and *U. minax* were captured during the day than at night. A relatively small number of larval and juvenile *Fundulus* sp. were captured in pit traps, but consistently fewer in *Phragmites* than in *Typha,* suggesting that *Typha* and brackish meadow marshes may provide better nursery habitat. Vegetation was sampled along a 30 m transect at each trap site in 2000. Plant species diversity was greatest in treated *Phragmites* areas and lowest in *Phragmites* sites.

## Introduction

Many species of fish, in a number of cases up to 20 or more, and decapod crustaceans may be found on the surface of fresh, brackish, and salt marshes flooded by high tides (Rozas and Odum 1987; McIvor and Odum 1988; Hettler 1989; Kneib 1991; Meyer et al. 2001). Along the Atlantic Coast of the United States, the common mummichog *Fundulus heteroclitus* is frequently the numerically dominant fish or at least one of several abundant fish species to use the marsh surface. The daggerblade grass shrimp *Palaemonetes pugio* is often the most numerous natant crustacean on the marsh during high tide. Crabs, including the blue crab *Callinectes sapidus,* may also be abundant. Although many of the nekton typically do not penetrate far into the marsh interior, *F. heteroclitus* and *P. pugio* appear to use all of the marsh surface that is inundated by the tides (Kneib and Wagner 1994; Peterson and Turner 1994; Rozas 1995; Kneib 2000).

Numerous studies have shown that *F. heteroclitus* (Vince et al. 1976; Kneib and Stiven 1978; Joyce and Weisberg 1986; Kneib 1986; Rozas et al. 1988) and *P. pugio* (Morgan 1980; Kneib 1985, 1987; Posey and Hines 1991; Gregg and Fleeger 1998) may feed extensively on marsh surface invertebrates, algae, detritus, and larval resident fish when the marsh is flooded. On an infrequently flooded marsh in Delaware, when *F. heteroclitus* was denied access to the marsh surface by enclosures, its growth was retarded compared to that of fish able to forage on the marsh during high tides (Weisberg and Lotrich 1982). As the tide recedes, *F. heteroclitus* and *P. pugio* retreat to tidal creeks and other subtidal habitats close to the marsh where they are exposed to predation by a number of larger animals including white perch, striped bass, bluefish, summer flounder, blue crabs, terns, herons, and egrets. *F. heteroclitus* and *P. pugio* appear to provide major trophic links between the productive marsh surface and the adjacent open estuary (Kneib 1982; Kneib and Wagner 1994). Many of the predatory fishes and crustaceans also migrate between shallow estuarine and coastal shelf waters (Szedlmayer and Able 1996; Deegan et al. 2000).

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*F. heteroclitus* deposits its eggs in the intertidal marsh (Able and Castagna 1975; Taylor et al. 1977; Taylor 1986), and for as many as 6 to 9 wk following hatching the larvae and small juveniles often inhabit shallow pools on the marsh surface at low tide (Taylor et al. 1979; Talbot and Able 1984; Kneib 1984, 1997; Able and Hagan 2000). There they are isolated from many aquatic predators including larger *F. heteroclitus*. The postlarvae of *P. pugio* may also populate such pools (Kneib 1984, 1987, 1997). The intertidal marsh surface may be an important nursery area for these natant marsh residents, in addition to its roles as foraging area and refuge from predation.

During the past few decades, *Phragmites australis* has rapidly expanded in many brackish and freshwater tidal wetlands along the Atlantic Coast of North America and elsewhere, forming dense, nearly monotypic stands (Chambers et al. 1999; Galatowitsch et al. 1999; Rice et al. 2000; Saltonstall 2002). The ecological impacts of such *Phragmites* expansion are still poorly understood. Plant species diversity is reduced, and in many cases, habitat structure is dramatically altered (Marks et al. 1994; Chambers et al. 1999; Meyerson et al. 2000). Conversion of short-grass meadow marshes or mixed brackish marshes to tall dense reed stands reduces avian species richness (Benoit and Askins 1999). The use of tidal marshes as refuges, foraging areas, and nurseries by estuarine fishes and crustaceans may also be impacted. Weinstein and Balletto (1999) predicted on the basis of demonstrated effects of *Phragmites* on marsh geomorphology that fish use of marsh systems should be adversely affected by the rapid spread of *Phragmites*. For example, it has been shown that fish densities are higher on the intertidal marsh surface in areas where there is a complex dendritic pattern of many small tidal creeks than where there are few larger creek channels (Kneib 1994), and *Phragmites* growth may result in the filling in of many first and second order tidal creeks (Chambers et al. 1999; Weinstein and Balletto 1999). This together with a possible build up of the marsh plain (Windham and Lathrop 1999; Stevenson et al. 2000) may restrict access of fishes and crustaceans to the marsh surface. The smoothing of the marsh surface within *Phragmites* stands appears to substantially reduce the number of shallow pools that may serve as nursery areas during low tide (Able and Hagan 2000; Windham and Lathrop 1999). There are only a few studies comparing fish and crustacean use of *Phragmites*-dominated and largely *Phragmites*-free reference marshes; these suggest that use of the marsh surface by older juvenile and adult nekton may be essentially unaffected by the invasion of *Phragmites*. Fell et al. (1998) found that *Phragmites* marshes and reference (brackish meadow and *Typha angustifolia*-dominated) marshes near the mouth of the Connecticut River were similar with respect to potential macroinvertebrate prey and foraging of *F. heteroclitus* on the flooded marsh surface. Able and Hagan (2000) and Meyer et al. (2001) demonstrated no differences in the numbers of *F. heteroclitus, P. pugio,* and *C. sapidus* caught in flume and Fyke nets in *Spartina alterniflora* and *Phragmites* marshes in New Jersey and Maryland, respectively. Wainright et al. (2000) provide evidence based on stable isotope compositions that *Phragmites* contributes substantially to the production of *F. heteroclitus* in *Phragmites* marshes. Although the use of the intertidal marsh surface by older age classes of *F. heteroclitus* does not appear to be affected by the invasion of *Phragmites*, nursery function for newly hatched young-of-the-year fish appears to be dramatically reduced. Able and Hagan (2000) showed that significantly more larval and young juvenile *F. heteroclitus* were caught by pit traps in *S. alterniflora* than by those in *Phragmites*-dominated areas.

As a continuation of previous work (Fell et al. 1998; Warren et al. 2001), the present study was undertaken to determine whether the invasion of *T. angustifolia*-dominated brackish marshes of the lower Connecticut River estuary by *Phragmites* alters their capacity to serve as fish and crustacean habitat. The abundance and diversity of nekton were compared among three plant community types: *Typha*-dominated marsh, untreated *Phragmites,* and *Phragmites* marsh that had been treated with herbicide and then mowed (as a *Phragmites* control effort by the Connecticut Department of Environmental Protection). The study was conducted along the lower two-thirds (a 3.3 km stretch) of the Lieutenant River, a lower Connecticut River tributary, and for each type of vegetation, collections were made at multiple river and creek edge sites over a range of elevations. Use of these marshes by *F. heteroclitus* for foraging and as a nursery was also examined. Since marsh nekton may exhibit diel variation in abundance (Roundtree and Able 1993), sampling was carried out both during the day and at night.

## Methods

### Study Area

The Lieutenant River opens into the lower Connecticut River estuary 4.5 km upriver from Long Island Sound, in Old Lyme, Connecticut, and continues north another 5.2 km to the head of tide (Fig. 1). About 90 ha of mesohaline to oligohaline tidal marsh border the Lieutenant; these wetlands are continuous with the Upper Island and Great

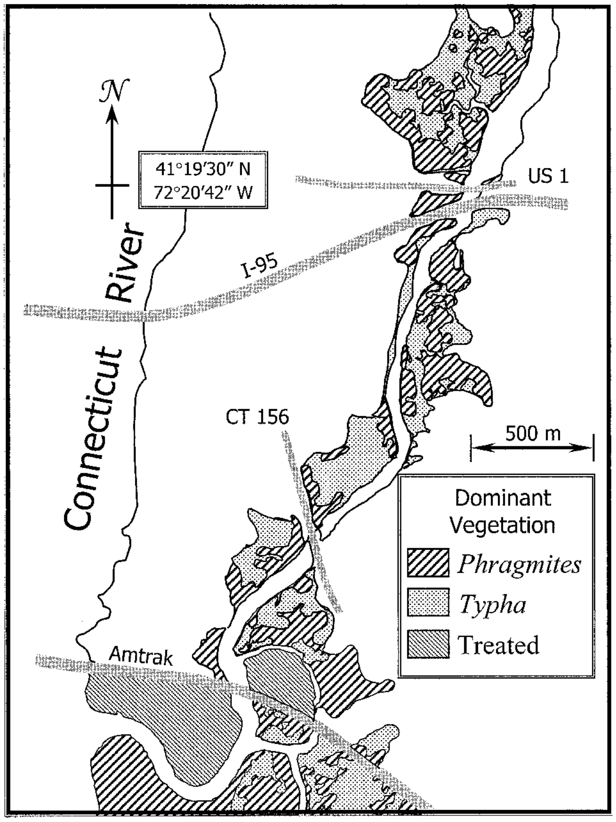


Fig. 1. The Lieutenant River in Old Lyme, Connecticut, showing the distributions of the different types of marsh.

Island marshes, which extend over 230 ha to the south. Salinity along the Lieutenant shows strong seasonal and interannual variability (Warren et al. 2001). Early summer peat and surface water salinities are typically 3–5‰ at the mouth and zero 3.5 km upriver at the furthest Breder trap site; by late summer respective values may rise to 10–15‰ and 3–8‰. In unusually dry years salinities may double and in wet summers they can be less than half. Mean tide range at the mouth of the Connecticut is 100 cm and is 99 cm at the Interstate 95 bridge, 1.2 km upriver from the mouth of the Lieutenant.

Over the past 35 yr *Phragmites* has expanded in the Lieutenant River marshes at the rate of 1.1–1.3% $yr^{-1}$ and near monocultures of this grass now dominate over 70% of the marsh area (Warren et al. 2001). Prior to invasion by *Phragmites,* marsh vegetation was *Spartina patens* dominated brackish meadow at the mouth, grading into cattail-dominated reed marshes (Nichols 1920) within 2 km of the mouth, and by 3.5 km, near monocultures of cattail. In late summer of 1995 c. 10.5 ha of *Phragmites* marsh along the lower Lieutenant was treated once with herbicide (1.25% glyphosate [Rodeo(N Phosphomethylglycine), Pharmica Corporation] in water with an aquatic surfactant [Chem Surf, Chemmose, Inc.] applied at 460 l $ha^{-1}$) and mowed with a mulching mower the following spring. *Phragmites* cover was significantly reduced by the treatment (Warren et al. 2001), but it has become reestablished, particularly along river and creek bank levees, and is expanding rapidly. It should be noted that the herbicide–mow treatment may affect faunal use patterns independently of changes in vegetation, although we have no evidence for this.

### Fish and Crustacean Sampling

During 2000, juvenile and adult fishes and crustaceans were captured on the flooded marsh surface using unbaited Breder traps (Breder 1960). This type of trap consists of a Plexiglas box, 31 × 16 × 15 cm, with a 2-sided funnel, 28 cm wide at the mouth and 1.3 cm wide at the throat, extending from the open end. Prior to high tide, the traps were set 3 m back from the river or creek bank with the mouths facing into the marsh. Plants beneath each trap were clipped so that the trap was even on the marsh surface, but care was taken not to disturb the surrounding vegetation. Each trap was held firmly in place with a cord attached to two chaining pins that were pushed into the peat. The traps were checked soon after the water had drained from the marsh surface, and the fishes and crustaceans were preserved in 10% formalin in river water (Fell et al. 1998).

For each sampling, Breder traps were set out at 90 randomly selected sites, equally distributed among *Phragmites, Typha,* and treated *Phragmites* marsh areas. The traps in *Phragmites* and *Typha* marshes were equally divided among the upper, middle, and lower reaches of the river (Fig. 1). Marsh regions bordering smaller branch creeks were included in the sampling particularly for the lower reach. *Phragmites* and *Typha* areas along a different reach of the river, together with a third of the treated *Phragmites* sites, all along the lower reach, were sampled on 3 consecutive days. Trapping was carried out during spring tides on June 2–4, June 14–16, July 3–5, July 17–19, July 31–August 2, and September 1–3. Because of the asymmetric tides (night tides were often much higher than day tides), night sampling was done for each series of spring tides, whereas day sampling was carried out on July 3–5, July 31–August 2, and September 1–3. A total of 810 Breder traps was set during 9 sampling episodes.

Larval and small juvenile fishes and crustaceans were captured on the high marsh in shallow pit traps: 27.5 × 17.5 × 3.7 cm glass dishes sunk flush with the marsh surface and anchored in place with 2 long tent stakes (Able and Hagan 2000). The pit traps were positioned 1 m away from transect lines set perpendicular to the river or creek bank. In 2000 traps were placed along each transect at 3, 10, and 30 m into the marsh; in 2001 they were set at 10, 20, and 30 m. When setting out and collecting from the pit traps, care was taken to minimally disturb the surrounding vegetation. The traps remained on the marsh for the entire sampling period each year and were emptied prior to high tide for every sampling event. Fishes and crustaceans were collected from the traps during the following low tide and preserved in 95% ethanol.

In 2000, 54 pit traps were equally distributed among the three vegetation types, and for the *Phragmites* and *Typha* marshes, the three reaches of the river. Pit trap sampling occurred during the same spring tides as the Breder trap sampling; pit traps were not set June 2–4 or during the day July 3–5. There was a total of 7 sampling events and 377 individual trap sets. In 2001, 60 pit traps were placed in *Phragmites* and *Typha* marshes along the upper and middle reaches of the river (15 traps in each type of marsh along each reach). Sampling was carried out during spring tides between June 22 and August 22, and a total of 957 individual trap sets were made during 16 sampling events.

Individuals of *F. heteroclitus* captured with both Breder and pit traps were measured to the nearest millimeter total length (TL). Those caught with Breder traps in late July-early August and early September were also weighed to the nearest 0.01 g (wet weight).

### Fish Diet Analysis

Specimens of *F. heteroclitus*, captured with Breder traps during daylight hours in early July, late July-early August, and early September, were kept for gut content analysis. An average of 22 fish (range 7–26) for each vegetation type along each reach of the river was examined for each series of spring tides. The guts of 452 fish that ranged in size from 4.1 to 9.6 cm TL were analyzed: 204 from *Phragmites* marshes, 190 from *Typha* marshes, and 58 from treated *Phragmites* marshes.

Only the contents of the foregut (sections I and II, Babkin and Bowie 1928) were examined. To evaluate the abundance of various food items in the diets of the fish, the relative volume of every type of food in each gut was estimated visually and assigned to one of three categories: $> 50\%$ of the total gut content, 10–50% of the total gut content, and $< 10\%$ of the total gut content (Allen et al. 1994). These categories were given scores of 3, 2, and 1, respectively (James-Pirri et al. 2001). For collections made during late July-early August and early September, a gut fullness index (Hyslop 1980) was calculated for each fish examined. The gut fullness index is the wet weight of the foregut content (difference in weights of full and emptied gut to the nearest 0.01 g) expressed as a percentage of the blotted wet weight of the fish.

### Epibenthic Macroinvertebrate Sampling

Some potential macroinvertebrate prey of *F. heteroclitus* were sampled using litter bags (Scatolini and Zedler 1996). The bags, which measured $29 \times 13.5$ cm, were made of 5 mm Delta weave nylon mesh, and each was filled with 20 g of dried plant material, an equal mixture of *Phragmites* and *Typha* leaves and stems. During two sampling periods, a single litter bag was placed 1-m away from each of the 90 Breder trap sites. The bags were set out with minimal disturbance of the vegetation and were anchored in place with tent stakes. One set of bags was deployed June 14–July 12 and a second set July 19–29. At the time of retrieval, the litter bags were placed individually into plastic shoe boxes, and the boxes were put into an insulated chest for transport back to the laboratory. There 95% ethanol was added to each box, and the macroinvertebrates were separated from the litter and preserved in 95% ethanol. Later they were sorted according to taxon and enumerated.

### Vegetation

After the completion of fish and crustacean trapping on September 3, vegetation was sampled along 30 m transects set normal to river and creek banks at all 90 Breder trap sites. All species present and estimated percent cover of each species were recorded in $3.0 \times 3.0$ m quadrats centered 1.5, 4.5, 10.0, and 28.5 m from the river and creek bank. All taxa were identified to species (Gleason and Cronquist 1991). In 2000, vegetation along the pit trap transects was sampled in the same manner with $3.0 \times 3.0$ m quadrats centered on the individual trap sites at 3, 10, and 30 m.

### Physical Measurements

Depth of tidal flooding was determined at each Breder trap and pit trap site as previously described (Warren et al. 2001) using tide sticks, dead *Phragmites* stems painted with a mixture of water-soluble glue and food coloring, in place of cork dust flooding gauges. Flooding water removes the glue and dye to the height of tide. An earlier study (Bellet 2000) comparing precision of tide sticks to cork dust tidal flooding gauges found measured tide height by the two techniques within 0.5 cm and means of 5 pairs of measurements over a growing season were not significantly different for 10 sites on 5 separate marshes. In this study tide sticks were deployed at each Breder trap and pit trap set. Rain erased readings for a number of dates but

TABLE 1. Flora of the Lieutenant River tidal wetlands recorded on 30-m long transects set normal to the creek bank at each of 90 Breder trap sites. Vegetation types (30 transects each): Tr = treated *Phragmites*, Ta = *Typha angustifolia*, Pa = *Phragmites australis*.

| Recorded Species | | Occurrence Within Vegetation Type | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Lower Reach | | | Middle Reach | | Upper Reach | |
| Scientific Name | Common Name | Tr | Ta | Pa | Ta | Pa | Ta | Pa |
| *Agrostis stolonofera* | Bent grass | X | X | X | X | X | X | X |
| *Amaranthus cannabinus* | Water hemp | X | | X | | X | X | X |
| *Aster* spp. | Salt marsh aster | X | X | | X | | X | |
| *Atriplex patula* | March orach | X | | | X | | | |
| *Calystegia sepium* | Hedge bind weed | | | | | | X | |
| *Caryx stringosus* | Straw-colored umbrella sedge | X | | | | | X | |
| *Echinochloa crusgalli* | Water millet | X | | | | | | X |
| *Eleocharis parvula* | Dwarf spike-rush | X | | X | | | X | |
| *Eleocharis rostellata* | Beaked spike-rush | X | | | X | | X | |
| *Hibiscus palustris* | Marsh mallow | X | X | X | X | X | | |
| *Iponoea sagittata* | Salt marsh morning glory | X | X | | X | X | | |
| *Iva frutescens* | High tide bush | X | | X | | | | |
| *Juncus gerardii* | Black grass | X | | X | X | X | X | X |
| *Lilaeopsis chinensis* | Eastern lilaeopsis | X | | | | | | |
| *Lythrum salicaria* | Purple loostrife | X | | | X | | | |
| *Panicum vergatum* | Switch grass | X | X | X | X | | X | X |
| *Phragmites australis* | Common reed grass | X | X | X | X | X | X | X |
| *Pluchea purpurascens* | Salt marsh fleabane | X | X | X | X | X | X | X |
| *Polygonum airofolium* | Halbred-leaved tear thumb | | | | | | X | |
| *Polygonum punctatum* | Dotted smartweed | X | X | | X | X | X | X |
| *Rumex crispis* | Curley dock | X | | | | | | |
| *Scirpus pungens* | Chairmaker's rush | X | X | X | X | | X | |
| *Scirpus robustus* | Saltmarsh bulrush | X | X | X | X | X | X | X |
| *Scirpus validus* | Soft-stemmed bulrush | X | X | | | X | | |
| *Sium suave* | Water parsnip | | X | X | | | X | |
| *Solidago sempervirens* | Seaside goldenrod | X | | X | X | | | X |
| *Spartina alterniflora* | Smooth cordgrass | X | X | X | X | | X | X |
| *Spartina cynosurosidies* | Giant cordgrass | X | X | X | X | X | X | |
| *Spartina patens* | Salt meadow cordgrass | X | X | X | X | X | X | |
| *Spartina pectinata* | Rough cordgrass | X | X | X | X | X | X | X |
| *Typha angustifolia* | Narrow leaf cattail | X | X | X | X | X | X | X |
| | n = | 28 | 17 | 18 | 20 | 14 | 21 | 13 |
| | | | $\Sigma$ Tr = 28 | | $\Sigma$ Ta = 25 | | $\Sigma$ Pa = 20 | |

additional measures gave each site a minimum of 6 readings between June and September. Flood depth was subtracted from tide height at I-95 bridge (recorded tide height at New London × 1.10, http://www.opsd.nos.noaa.gov/data_res.html) to give relative elevation for the marsh surface at each trap with tidal datum as local mean lower low water. The seasonal mean elevation calculated for each trap and the May 1 to September 1 tidal record were used to estimate frequency and duration of tidal flooding for each site using the program TideMiner 3.0 (http://www.numberstoknowledge.com).

Surface water salinities along different reaches of the river were recorded for most sampling periods. Salinity (±1%) was measured with a Goldberg refractometer (American Optical Corp.).

## Results

### Vegetation

A total of 31 different angiosperm species were recorded from the 360 separate 3 × 3 m quadrats along the transects established at each of the Breder trap sites. Twenty-eight species occurred within the treated *Phragmites* area, 25 within *Typha*, and 20 in *Phragmites* (Table 1). The diversity of this flora was significantly different (Shannon-Weaver diversity index, Zar 1984) between the treated *Phragmites* area and both the *Typha* and *Phragmites* for all three reaches. Pooling all reaches, areas treated for *Phragmites* control were similar to *Typha*, but both were different than *Phragmites* (Table 2).

The vegetation within the treated *Phragmites*, *Typha*, and *Phragmites* areas were very similar both within and among reaches, but from creek or river bank into the interior, consistently different among the three communities (Fig. 2). Patterns among the three marsh types and, for each type, among lower, middle, and upper reaches were compared by Kruskal-Wallis using mean cover of *Typha*, *Phragmites*, and combined other species for each transect.

For both species and the combined others, there were no differences in mean cover per transect

TABLE 2. Shannon-Weaver diversity index for the three sampled vegetation types across all river reaches. Values in a column followed by the same letter are not significantly different ($p < 0.05$). b[+] $p = 0.07$.

| | Shannon Diversity Index | | | |
|---|---|---|---|---|
| | Lower | Middle | Upper | Combined |
| Treated* | 1.269 a<br>1.251 a<br>1.168 a | — | — | 1.206 ab |
| *Typha* | 1.050 b | 1.142 b | 1.146 b | 1.1721 b |
| *Phragmites* | 0.938 b | 0.778 b[+] | 0.872 b | 0.916 c |

* All treated transects were on the lower reach in three sets of 10. All were >Pa and two were >Ta.

within each community among lower, middle, and upper reaches. There were differences in *Typha* and combined other among *Phragmites* transects within each reach, but no differences in the consistently high cover of *Phragmites* itself (mean % cover = 84, 89, and 85 for lower, middle, and upper reaches, respectively). Among *Typha* transects there was also some variability in *Typha* and combined other within each reach, but no differences in the consistently low cover of *Phragmites* itself (mean % cover = 8, 10, and 6 for lower, middle, and upper reaches, respectively). The treated transects, all lower reach, are dominated by combined other (mean % cover = 58) and *Phragmites* (mean % cover = 26) with no differences for these two among transects. *Typha* cover within treated transects is low (mean = 10%) but variable, with differences among transects.

Focusing particularly on *Phragmites* versus *Typha*, for all the *Phragmites* transects, *Phragmites* occurred essentially as a monoculture at 1.5, 4.5, and 10.0 m, and still averaged over 75% of the total cover in the 28.5 m quadrats, where *Typha* finally made a measurable contribution (5%) to total cover. In contrast, at *Typha* sites, *Phragmites* increased from under 1% at river and creek banks to less than 5% by 10.0 m and 25% at 28.5 m, whereas *Typha* itself consistently contributed 43–56% of the cover across the length of the transects.

The treated *Phragmites* sites were distinctly different from either, with 40–50% *Phragmites* cover in the first 6 m, falling to about 20% further back from the river; *S. alterniflora* occurred frequently below mean high water, and most of the area between 10 and 30 m was dominated by a mixture of low brackish meadow graminoids, most notably *Agrostis stolonifera, S. patens,* and *Juncus gerardii*. The vegetation along the pit trap transects was essentially the same as along the Breder trap transects in *Phragmites, Typha,* and treated *Phragmites* areas (Fig. 2).

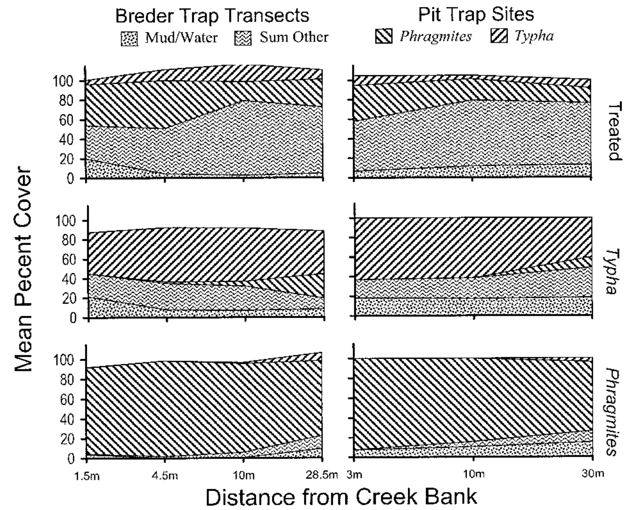


Fig. 2. Plant cover along Breder trap vegetation transects and at pit trap sites in *Phragmites*, *Typha*-dominated, and treated *Phragmites* marshes. For Breder traps 30 transects and for pit traps 6 transects were sampled in each type of vegetation.

## Physical Measurements

Although the mean Breder-trap site elevations in *Phragmites* marshes were consistently somewhat lower than those in *Typha* and treated *Phragmites*, there were no significant differences in site elevations or in site flooding frequencies and durations among the three vegetations types of the lower reach (for elevation, ANOVA, $F = 1.292$, $p = 0.29$) or between *Typha* and *Phragmites* sites for all three reaches (lower: $t = 1.911$, $p = 0.07$; middle: $t = 0.464$, $p = 0.65$; upper: $t = 1.034$, $p = 0.31$). There were also no significant differences among *Typha, Phragmites,* and treated-*Phragmites* comparing all 30 sites for each vegetation type (ANOVA, $F = 2.591$, $p = 0.058$; Fig. 3, Table 3). Elevation and hydroperiod did differ among the three reaches. Upper reach sites were significantly lower (ANOVA, $F = 9.076$, $p < 0.001$) than those along the middle and lower reaches, while flooding frequency and duration were greater (Table 3).

Similarly for the pit trap sites, there were no elevation (ANOVA, $F = 1.370$, $p = 0.284$) or hydroperiod differences among treated *Phragmites* and lower reach *Typha* and lower reach *Phragmites* sites in 2000 (Table 4). Among reaches lower reach sites were on average higher (ANOVA, $F = 10.184$, $p < 0.001$) with correspondingly lower hydroperiod values than those of the middle and upper reaches. Within reaches there were no differences between *Typha* and *Phragmites* site means; for the lower reach, one set of traps in the treated *Phragmites* area was significantly higher than all others. Elevation means at 3, 10, and 30 m were not signifi-

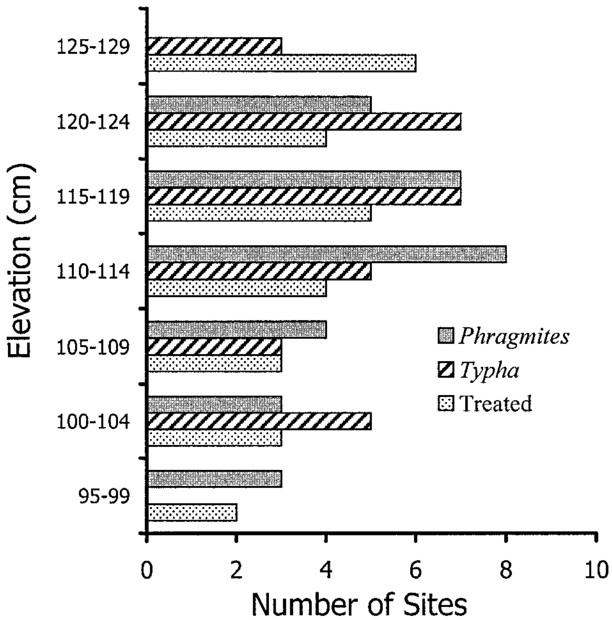


Fig. 3. Distribution of Breder trap site elevations in *Phragmites, Typha,* and treated *Phragmites.*

cantly different sorted by either reach or vegetation.

In 2001 as in 2000, pit trap elevation means of the upper reach did not differ by vegetation ($t$ = 1.44, p = 0.161), but *Typha* sites were higher in the middle reach ($t$ = 2.334, p = 0.027). Pooling vegetation types, there was no difference between reaches ($t$ = 1.416, p = 0.162). Also as in 2000, there was no significant pattern of elevation differences by distance from the river bank. Both by reach and by vegetation, there were also no differences between 2000 and 2001 means (Table 4).

During early June of 2000, surface salinity was 0‰ all along the Lieutenant River. By early July, it had risen to 6‰ along the upper and middle reaches and to 8‰ along the lower reach but then declined. Subsequently surface salinities rose again and in early September they were comparable to those in early July. During late June and early July of 2001, surface salinity was 0‰ along the upper and middle reaches of the river and then rose to 7‰ and 10‰, respectively, by mid-August.

## Marsh Surface Fishes and Crustaceans: Breder Trap Collections

A total of 3,136 fishes representing 11 species and 3,350 crustaceans comprising 5 species were captured in Breder traps during the course of this study. The total numbers of fishes caught per trap in the *Phragmites, Typha,* and treated *Phragmites* marshes were not significantly different (Table 5). Both the frequency of fish capture and the mean number caught per trap were somewhat higher in *Phragmites* than in *Typha* marshes and were lowest in treated *Phragmites* areas that were all restricted to the lower reach of the river (see below). The total number of crustaceans captured per trap was greater in *Phragmites* marshes than at the *Typha* and treated *Phragmites* sites (Table 5, Tukey, p < 0.05). The faunal assemblages in the three types of marsh were similar.

*F. heteroclitus* was the numerically dominant fish, making up 94% of the total number of fish captured (Table 5). The mean numbers of *F. heteroclitus* captured per Breder trap in *Typha* and *Phragmites* areas along all reaches of the river were not significantly different ($t_{58}$ = 0.822, p = 0.415) and the frequencies of capture were similar (Table 5).

TABLE 3. Mean elevation (cm), % hours flooded, and % times flooded over the growing season for 90 Breder trap sites: 30 sites per vegetation type with all 30 treated sites in the lower reach and with 10 *Typha* and 10 *Phragmites* sites within each of the lower, middle, and upper river reaches.

| | Vegetation* | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Treated | | | *Typha* | | | Phragmites | | | Means by Reach** | | |
| | Elev | % Hours | % Tides | Elev | % Hours | % Tides | Elev | % Hours | % Tides | Elev | % Hours | % Tides |
| Lower Reach | 112.4 | 7.2 | 35.5 | 112.5 | 5.5 | 31.9 | 107.8 | 8.7 | 44.8 | 111.5 | 7.2 | 36.6 |
| | (1.92) | (1.10) | (4.22) | (1.41) | (0.80) | (4.10) | (2.01) | (1.46) | (5.46) | (1.27) | (0.74) | (2.90) |
| Middle Reach | | | | 113.1 | 6.5 | 33.2 | 111.4 | 6.5 | 34.5 | 112.3 | 6.5 | 33.8 |
| | | | | (2.84) | (1.64) | (7.18) | (2.20) | (1.52) | (5.61) | (1.76) | (1.09) | (4.44) |
| Upper Reach | | | | 104.7 | 11.1 | 52.2 | 101.4 | 13.6 | 60.8 | 103.1 | 12.4 | 56.5 |
| | | | | (2.29) | (1.80) | (5.74) | (2.20) | (1.88) | (4.77) | (1.59) | (1.30) | (3.76) |
| | 112.4 | 7.2 | 35.5 | 110.1 | 7.7 | 39.1 | 106.9 | 9.6 | 46.7 | | | |
| Means by Vegetation | (1.92) | (1.10) | (4.22) | (1.42) | (0.94) | (3.67) | (1.42) | (1.06) | (3.57) | | | |

* Vegetation type means are not significantly different by ANOVA for elevation (F = 2.951, p = 0.058), % hours flooded (F = 1.512, p = 0.226), and % tides flooding (F = 2.215, p = 0.115). *Typha* versus *Phragmites* means alone were also not significantly different for all three parameters ($t$-test, equal variances, $t \leq 1.589$, p $\geq$ 0.118).

** River reach means are significantly different by ANOVA for elevation (F = 8.403, p < 0.001), % hours flooded (F = 6.618, p = 0.002), and % of tides flooding (F = 8.791, p < 0.001).

TABLE 4. Mean pit trap elevations (±SE) by reach and vegetation for 2000 and 2001. Number of trap sites is after parentheses.

| | Vegetation | | | | |
|---|---|---|---|---|---|
| | Treated | *Typha*** | | *Phragmites*** | |
| | 2000 | 2000 | 2001 | 2000 | 2001 |
| Lower Reach* | 116.2 (1.63) 18 | 114.2 (1.15) 6 | | 116.1 (0.46) 6 | |
| Middle Reach** | | 111.0 (2.90) 6 | 110.8 (1.01) 15 | 105.9 (2.17) 6 | 107.2 (2.67) 15 |
| Upper Reach** | | 107.3 (1.39) 6 | 104.7 (1.62) 15 | 105.9 (2.59) 6 | 108.7 (2.23) 15 |

* Mean elevations of combined lower reach sites were significantly greater than middle and upper reach sites by ANOVA ($F = 10.184$, $p < 0.001$).

** There were no significant differences between vegetation types or middle and upper reaches for both years, and for reach and vegetation type, between years.

The number of *F. heteroclitus* caught per trap set ranged from 0 to 70 and the patterns of capture in these two types of marsh were comparable (Kolmogorov-Smirnov, $Z = 0.514$, $p = 0.954$), with 59% of the traps capturing this fish catching 1 to 3 of them. The mean number of *F. heteroclitus* caught in treated *Phragmites* sites (only along the lower reach) was not different from those in *Phragmites* and *Typha* marshes of the lower reach (Table 6, ANOVA, $F = 0.399$, $p = 0.675$), and the numbers captured in *Phragmites* and *Typha* marshes of the middle and upper reaches were not different (middle: $t_{18} = 0.015$, $p = 0.988$; upper: $t_{18} = 0.863$, $p = 0.399$). Although there were no statistical differences in the abundance of *F. heteroclitus* with respect to vegetation, this fish tended to be most numerous and most frequently captured in *Phragmites* (Tables 5 and 6).

*F. heteroclitus* ranged in size from 1.0 to 10.0 cm TL with a median TL of 5.7 cm. The size distribution patterns of *F. heteroclitus* in the *Typha* and *Phragmites* marshes were generally correspondent (Fig. 4, Kolmogorov-Smirnov, $Z = 0.474$, $p = 0.978$). In the treated *Phragmites* marshes there were relatively fewer intermediate size individuals (5.1 to 6.5 cm TL) and somewhat more smaller and larger fish than in the *Typha* and *Phragmites* marshes. The treated *Phragmites* marshes were restricted to the lower reach of the river; the size distributions of *F. heteroclitus* in these marshes and the *Typha* and *Phragmites* areas of the lower reach were more similar (Kolmogorov-Smirnov, *Phragmites* and treated *Phragmites* $Z = 0.474$, $p = 0.978$; *Typha* and treated *Phragmites* $Z = 0.632$, $p = 0.819$). Length-weight regressions of *F. heteroclitus* caught in the three types of vegetation were not significantly different (two sample *t*-test for the equality of slopes: *Phragmites* and *Typha*, $p = 0.42$; *Phragmites* and treated *Phragmites*, $p = 0.59$; *Typha* and treated *Phragmites*, $p = 0.23$).

More *F. heteroclitus* were captured and the frequency of capture was higher at *Typha* and *Phrag-*

TABLE 5. Total number of each species of fish and crustacean caught and mean number (±SE) per trap captured in *Phragmites*-dominated, *Typha*-dominated, and treated *Phragmites* marshes along the Lieutenant River in 2000 using Breder Traps. A = ANOVA, KW = Kruskal-Wallis test. Frequency of capture (percentage of trap sets capturing each species) is after parentheses.

| Species | Number | *Phragmites* (n = 30) | *Typha* (n = 30) | Treated *Phragmites* (n = 30) | Significance |
|---|---|---|---|---|---|
| *Fundulus heteroclitus,* mummichog | 2,959 | 4.60 (0.53) 69 | 3.81 (0.48) 64 | 2.55 (0.26) 51 | A: $F = 2.70$, $p = 0.073$ |
| *Anguilla rostrata,* American eel | 20 | 0.02 (0.01) 1 | 0.02 (0.01) 2 | 0.04 (0.01) 3 | KW: $\chi^2 = 1.91$, $p = 0.385$ |
| *Notropis hudsonius,* spottail shinner | 31 | 0.08 (0.04) 3 | 0.01 (0.01) 1 | 0.03 (0.02) 1 | KW: $\chi^2 = 2.96$, $p = 0.227$ |
| *Apeltes quadracus,* fourspine stickleback | 24 | 0.04 (0.02) 2 | 0.02 (0.01) 1 | 0.04 (0.01) 3 | KW: $\chi^2 = 1.91$, $p = 0.384$ |
| *Lepomis gibbosus,* pumpkinseed | 18 | 0.03 (0.01) 2 | 0.04 (0.02) 2 | <0.01 0.4 | KW: $\chi^2 = 2.92$, $p = 0.233$ |
| *Alosa* sp., shad (small) | 25 | 0.09 (0.09) 0.4 | 0 | 0 | KW: $\chi^2 = 2.00$, $p = 0.368$ |
| *Menidia* spp., silversides (small)* | 40 | 0.01 (0.01) 1 | 0.02 (0.01) 1 | 0.12 (0.10) 2 | KW: $\chi^2 = 3.55$, $p = 0.170$ |
| *Fundulus diaphanus,* banded killifish | 16 | 0.04 (0.01) 2 | 0.02 (0.02) 1 | 0 | KW: $\chi^2 = 5.17$, $p = 0.075$ |
| *Cyprinodon variegatus,* sheepshead minnow | 2 | <0.01 0.4 | 0 | <0.01 0.4 | KW: $\chi^2 = 1.01$, $p = 0.603$ |
| *Pungitius pungitius,* ninespine stickleback | 1 | 0 | <0.01 0.4 | 0 | KW: $\chi^2 = 2.00$, $p = 0.368$ |
| All fishes | 3,136 | 4.90 (0.74) 69 | 3.93 (0.66) 65 | 2.78 (0.58) 56 | A: $F = 2.65$, $p = 0.076$ |
| *Palaemonetes pugio,* grass shrimp | 2,469 | 4.73 (0.70) 40 | 2.09 (0.34) 26 | 2.33 (0.45) 27 | A: $F = 6.55$, $p = 0.002$ |
| *Uca minax,* red-jointed fiddler crab | 464 | 0.36 (0.06) 20 | 0.79 (0.08) 39 | 0.57 (0.6) 35 | A: $F = 7.74$, $p = 0.001$ |
| *Callinectes sapidus,* blue crab | 8 | 0.02 (0.01) 1 | 0.01 (0.01) 1 | 0 | KW: $\chi^2 = 4.01$, $p = 0.135$ |
| *Orchestia grillus,* amphipod | 127 | 0.12 (0.04) 6 | 0.09 (0.03) 5 | 0.26 (0.05) 14 | KW: $\chi^2 = 3.94$, $p = 0.140$ |
| *Gammarus tigrinus,* amphipod | 282 | 0.46 (0.21) 4 | 0.31 (0.20) 3 | 0.28 (0.12) 4 | KW: $\chi^2 = 0.85$, $p = 0.653$ |
| All crustaceans | 3,350 | 5.69 (0.77) 58 | 3.28 (0.45) 60 | 3.44 (0.48) 60 | A: $F = 4.12$, $p = 0.019$ |

* *M. menidia* and *M. beryllina.*

TABLE 6. The influence of river reach on the abundances (mean ± SE per trap) and percentages (number after parentheses) of trap sets capturing *F. heteroclitus*, *P. pugio*, and *U. minax* in different types of marsh bordering the Lieutenant River in 2000.

| | | Reach of River | | | | | |
|---|---|---|---|---|---|---|---|
| Species | Marsh type | Lower | n | Middle | n | Upper | n |
| *F. heteroclitus* | *Phragmites* | 3.06 (0.56) 58 | 10 | 2.86 (0.67) 62 | 10 | 7.89 (1.26) 87 | 10 |
| | *Typha* | 2.24 (0.45) 59 | 10 | 2.83 (0.63) 54 | 10 | 6.34 (1.15) 79 | 10 |
| | Treated *Phragmites* | 2.55 (0.26) 51 | 30 | — | | — | |
| *P. pugio* | *Phragmites* | 8.20 (1.66) 52 | 10 | 2.98 (0.86) 27 | 10 | 3.02 (0.85) 30 | 10 |
| | *Typha* | 2.73 (0.87) 31 | 10 | 2.24 (1.00) 24 | 10 | 1.28 (0.46) 21 | 10 |
| | Treated *Phragmites* | 2.33 (0.45) 27 | 30 | — | | — | |
| *U. minax* | *Phragmites* | 0.20 (0.07) 17 | 10 | 0.51 (0.11) 27 | 10 | 0.36 (0.09) 18 | 10 |
| | *Typha* | 0.78 (0.13) 42 | 10 | 0.97 (0.23) 44 | 10 | 0.62 (0.13) 31 | 10 |
| | Treated *Phragmites* | 0.57 (0.60) 35 | 30 | — | | — | |

*mites* sites along the upper reach of the Lieutenant River, where elevations were lowest, than in those along the middle and lower reaches (Table 6, ANOVA, F = 12.89, p < 0.001, Tukey, p < 0.05, for both types of marsh considered together). For all vegetation types in all reaches of the river there was a positive correlation between the mean number of *F. heteroclitus* caught at each trap site and hydroperiod, the frequency, depth, and duration of marsh flooding (Fig. 5, p < 0.001). The frequency of capture also increased and became less variable as marsh flooding increased (data not shown).

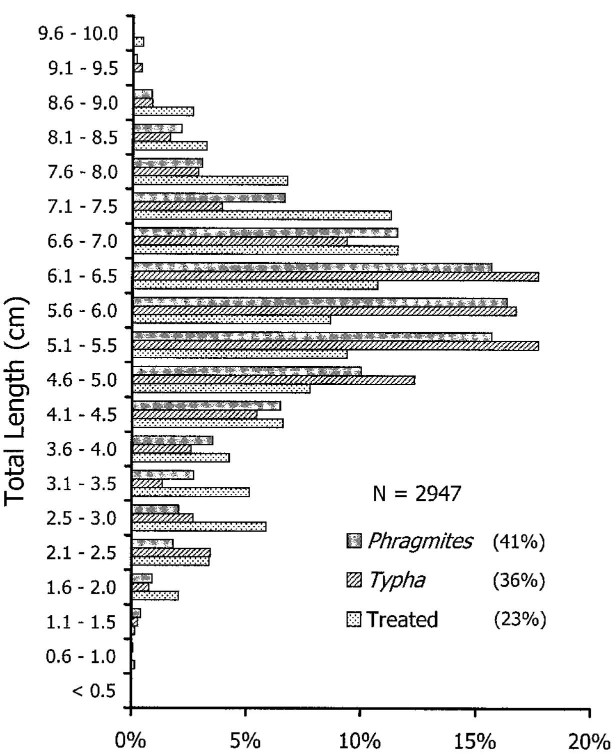


Fig. 4. Size frequency distribution of *F. heteroclitus* captured with Breder traps in *Phragmites, Typha,* and treated *Phragmites* marshes.

The mean number of *F. heteroclitus* caught per trap during daytime high tides was greater than that during nighttime high tides despite the fact that flooding depths were often greater at night (for all 90 traps on dates when coupled day-night sampling was done, $t = 8.05$, p < 0.001). Although this pattern was evident in all marshes along all reaches of the river, it was especially striking in *Phragmites* and *Typha* marshes of the upper reach where the mean number of *F. heteroclitus* caught per trap during the day was 16.2 ± 2.1 compared with 1.7 ± 0.3 at night. In fact, the influence of river reach on the abundance of *F. heteroclitus* was primarily a daytime phenomenon (for both marsh types considered together: ANOVA, day: F = 15.28, p < 0.001; night: F = 2.16, p = 0.125). The numbers of *F. heteroclitus* captured at night remained nearly constant from June 2 through September 3, whereas the numbers trapped during the day were higher and more variable (Fig. 6).

*P. pugio* was the most abundant crustacean, representing 74% of those caught. The mean number of *P. pugio* captured per trap was greater in *Phragmites* than in *Typha* areas (all reaches combined, $t_{58} = 3.094$, p = 0.003) and the frequency of capture

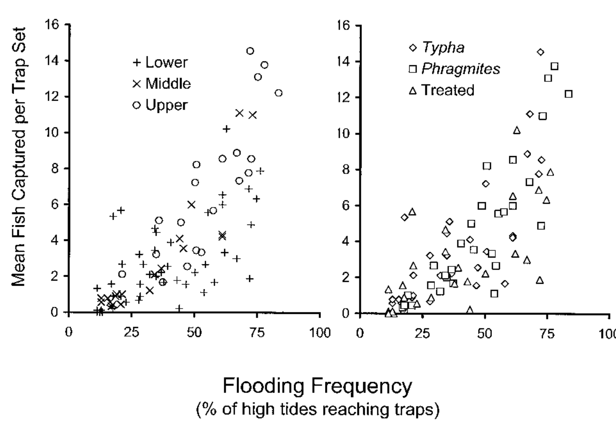


Fig. 5. Mean number of *F. heteroclitus* caught at each of the 90 Breder trap sites in relation to flooding frequency.

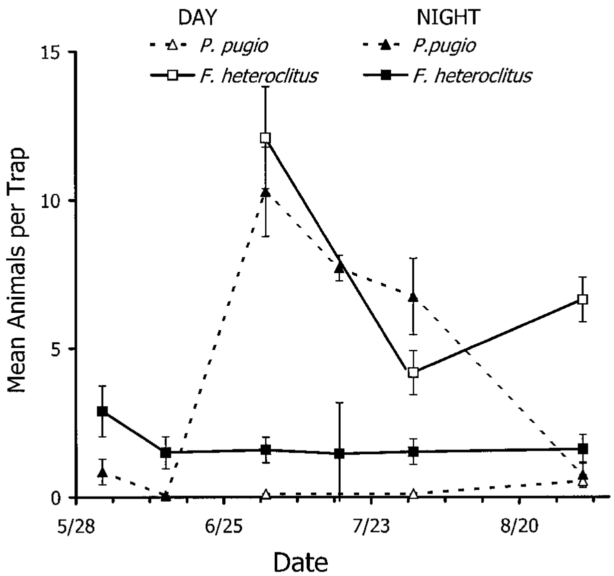


Fig. 6. Mean numbers (± SE) of *F. heteroclitus* and *P. pugio* collected in Breder traps during daytime and nighttime high tides at various times during the late spring and summer of 2000. Each date is the first day of a 3-d sampling sequence.

also was higher in *Phragmites* (Table 5). This shrimp was more abundant in *Phragmites* marshes along the lower reach of the river than in those along the middle and upper reaches (Table 6, ANOVA, F = 9.075, $p = 0.001$, Tukey, $p < 0.05$). The number of *P. pugio* trapped at *Typha* sites along the three reaches were not significantly different (ANOVA, F = 0.851, $p = 0.438$). More *P. pugio* were captured in *Phragmites* marshes of the lower reach than in *Typha* and treated *Phragmites* marshes along this reach (Table 6, ANOVA, F = 15.936, $p < 0.001$, Tukey, $p < 0.05$). Although *P. pugio* tended to be somewhat more numerous in *Phragmites* than in *Typha* marshes along the middle and upper reaches, these differences were not significant (middle: $t = 0.499$, $p = 0.624$; upper: $t = 1.936$, $p = 0.069$). The mean number of *P. pugio* caught per trap was positively correlated with marsh hydroperiod ($p = 0.001$). Unlike *F. heteroclitus*, more *P. pugio* were caught during nighttime high tides than during daytime high tides (Fig. 6, for all 90 traps on dates when coupled day-night sampling was done: Kruskal-Wallis, $\chi^2 = 72.373$, $p < 0.001$); this was true for marshes along all reaches of the river. The numbers of *P. pugio* captured during the night in July and early August were relatively large, but only few shrimp were trapped at night in June and early September (Fig. 6).

*Uca minax*, a permanent marsh resident, made up 14% of the crustacean catch. This crab was more abundant in *Typha* than in *Phragmites* (all reaches combined, $t_{58} = 3.843$, $p < 0.001$) and the frequency of capture was nearly 2-fold greater in *Typha* (Table 5). The numbers of *U. minax* trapped in marshes along the three reaches of the river were not significantly different (Table 6, *Phragmites* marshes: ANOVA, F = 2.985, $p = 0.067$; *Typha* marshes: ANOVA, F = 1.024, $p = 0.373$). More *U. minax* were caught in lower-reach *Typha* and treated *Phragmites* than in lower-reach *Phragmites* (Table 6, ANOVA, F = 6.017, $p = 0.005$, Tukey, $p < 0.05$); the numbers trapped in *Typha* and *Phragmites* marshes of the middle and upper reaches were not significantly different (middle: $t = 1.820$, $p = 0.092$; upper: $t = 1.697$, $p = 0.107$). The mean number of fiddler crabs captured per trap was positively correlated with elevation ($p < 0.001$). Larger numbers of *U. minax* were caught at night than during the day (Kruskal-Wallis, $\chi^2 = 75.871$, $p < 0.001$).

Only a small number of *C. sapidus* were caught on the marsh surface. All were captured during June, and they ranged in carapace width from 4.2 to 5.6 cm (median 4.6 cm). In addition to grass shrimp and crabs, two amphipods, *Gammarus tigrinus* and the permanent marsh resident *Orchestia grillus*, were captured by Breder traps. The numbers of these crustaceans trapped in the different types of marsh were not significantly different (Table 5).

## Marsh Surface Fishes and Crustaceans: Pit Trap Collections

During 2000 and 2001, 94 and 346 larval-juvenile fishes, respectively, were captured in pit traps placed on the high marsh (Table 7). *Fundulus* sp. made up > 99% of the fish catch. This fish ranged in size from 0.3 to 5.5 cm TL with a median TL of 0.7 cm (73% were 0.6 to 1.0 cm TL). The numbers of *Fundulus* caught in the different types of marsh during 2000 were not significantly different (Kruskal-Wallis, $\chi^2 = 3.92$, $p = 0.141$), even though 10 times as many were captured in *Typha* marshes as in *Phragmites*. Only 14 of the 54 traps (26%) caught any fish: 7 in *Typha*, 5 in treated *Phragmites*, and 2 in *Phragmites*. In fact, 72% of the *Fundulus* were from just four traps. In 2001 when more extensive sampling was done, 37% of the pit traps in *Phragmites* marshes and 87% of those in *Typha* marshes captured *Fundulus*, and the numbers of fish caught in the two types of marsh (Table 7) were significantly different (Kruskal-Wallis, $\chi^2 = 20.80$, $p < 0.001$).

Considering all types of marsh, more *Fundulus* were captured at 30 m than at 3 m from the river or creek bank in 2000 (Fig. 7, Kruskal-Wallis, $\chi^2 = 8.34$, $p = 0.015$). During both years, the number of *Fundulus* trapped at 30 m into the marsh interior tended to be greater than that at 10 m.

TABLE 7. Total number of each species of fish and crustacean caught and mean number (±SE) per tap captured in *Phragmites*-dominated, *Typha*-dominated, and treated *Phragmites* marshes along the Lieutenant River in 2000 and 2001, using pit traps.

| | 2000 | | | | 2001 | | |
|---|---|---|---|---|---|---|---|
| Species | No. | *Phragmites* (n = 18) | *Typha* (n = 18) | Treated *Phragmites* (n = 18) | No. | *Phragmites* (n = 30) | *Typha* (n = 30) |
| *Fundulus* sp. | 93 | 0.04 (0.03) | 0.42 (0.20) | 0.28 (0.17) | 346 | 0.10 (0.03) | 0.62 (0.12) |
| *Menidia* sp. | 1 | 0.01 (0.01) | | | 0 | | |
| *Palaemonetes pugio* | 0 | | | | 4 | 0.01 (0.01) | <0.01 |
| *Uca minax* | 151 | 0.23 (0.06) | 0.56 (0.11) | 0.41 (0.08) | 155 | 0.17 (0.03) | 0.15 (0.03) |
| *Orchestia grillus* | 383 | 0.90 (0.81) | 0.02 (0.01) | 2.12 (0.73) | 296 | 0.29 (0.12) | 0.33 (0.20) |

Depending upon the year, larval and juvenile *Fundulus* were captured in pit traps from late June or mid-July through mid-August or early September, the latest sampling period. The numbers of fish trapped tended to be greatest during the last half of July and early August (Fig. 8). In 2001 the mean number of *Fundulus* captured per trap site was significantly greater during the July 20 series than both earlier and later (Kruskal-Wallis, $\chi^2 = 54.27$, $p < 0.001$).

During 2 yr of sampling, only 4 postlarval *P. pugio* were caught in pit traps (Table 7). Other crustaceans captured in these traps were the permanent marsh residents *U. minax* and *O. grillus*. *U. minax*, which was found in 80% of the traps in 2000 and 88% of them in 2001, represented 28% and 34%, respectively, of the crustacean catch. Although this crab tended to be more abundant in *Typha* than in *Phragmites* in 2000, the numbers caught in the different types of marsh were not significantly different either year (Kruskal-Wallis, $\chi^2 = 5.13$, $p = 0.077$ and $\chi^2 = 0.14$, $p = 0.710$). There were no differences in the numbers of *U. minax* captured at 3, 10, and 30 m from the river or creek bank in 2000 (Kruskal-Wallis, $\chi^2 = 2.43$, $p = 0.296$) or at 10, 20, and 30 m in 2001 ($\chi^2 = 0.64$, $p = 0.727$).

*O. grillus* comprised at least 65% of the total number of crustaceans caught in pit traps each year; however, only 43% of the traps in 2000 and 35% in 2001 captured this amphipod. In 2000, more *O. grillus* were trapped in the treated *Phragmites* marshes than in *Typha* and *Phragmites* (Table 7, Kruskal-Wallis, $\chi^2 = 12.81$, $p = 0.002$). The treated *Phragmites* sites were restricted to the lower reach of the river and 99% of the *O. grillus* caught were from this reach. The numbers of *O. grillus* trapped in *Typha* and *Phragmites* marshes in 2001

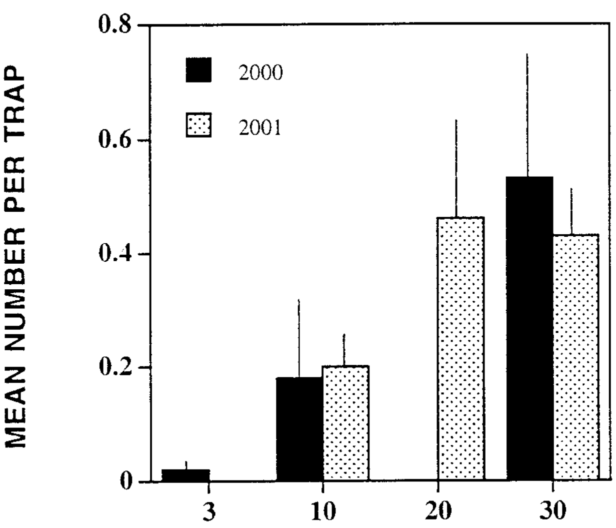


Fig. 7. Mean numbers (±SE) of *F. heteroclitus* caught in pit traps at different distances from the river and creek edge. Data from the different types of marsh were pooled for each year.

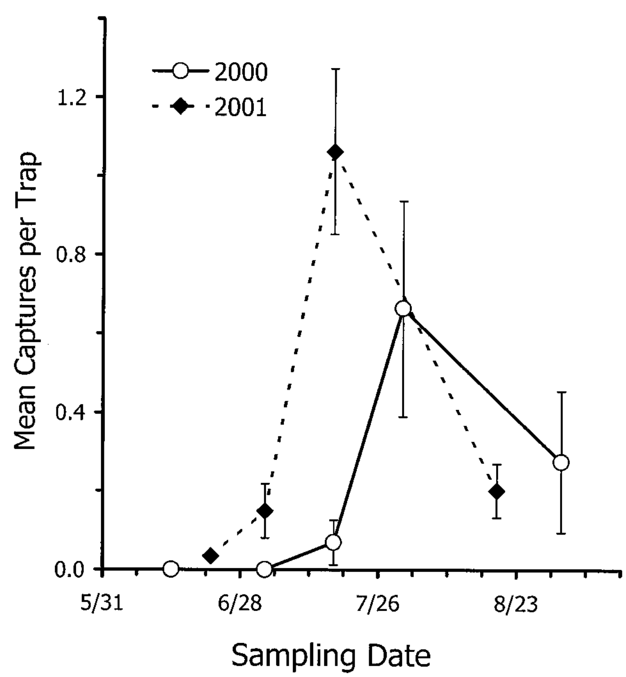


Fig. 8. Mean numbers (±SE) of larval and juvenile *F. heteroclitus* caught in pit traps at various times during the late spring and summer of 2000 and 2001. Each date is the first day of a sampling sequence.

TABLE 8. Macroinvertebrates collected in litter bags placed on the marsh surface at each of 90 Breder trap sites. For each sampling period the total number of each kind of animal and the mean number (± SE) per bag in each type of marsh are given.

| | June 14–July 12 | | | | July 19–29 | | | |
|---|---|---|---|---|---|---|---|---|
| | No. | *Phragmites* (n = 30) | *Typha* (n = 30) | Treated (n = 30) | No. | *Phragmites* (n = 30) | *Typha* (n = 30) | Treated (n = 30) |
| Amphipods (*Orchestia*) | 155 | 2.23 (0.49) | 1.27 (0.28) | 1.67 (0.33) | 252 | 2.87 (0.76) | 4.07 (1.11) | 1.47 (0.29) |
| Isopods (*Philoscia*) | 41 | 0.10 (0.06) | 0.53 (0.18) | 0.73 (0.27) | 91 | 0.10 (0.06) | 2.00 (0.75) | 0.93 (0.57) |
| Insects | 1,295 | 5.90 (2.36) | 24.93 (14.10) | 12.33 (5.44) | 477 | 4.13 (2.19) | 8.93 (4.08) | 2.83 (0.44) |
| Dipterans (flies) | 72 | 0.93 (0.47) | 0.23 (0.09) | 1.23 (0.50) | 33 | 0.07 (0.05) | 0.80 (0.35) | 0.23 (0.10) |
| Coleopterans (beetles) | 44 | 0.17 (0.08) | 0.63 (0.17) | 0.67 (0.13) | 60 | 0.30 (0.11) | 0.53 (0.14) | 1.17 (0.27) |
| Hymenopterans (ants) | 35 | 0 | 1.10 (1.10) | 0.07 (0.05) | 98 | 0 | 3.23 (3.13) | 0.03 (0.03) |
| Orthopterans (crickets) | 20 | 0.10 (0.07) | 0.40 (0.27) | 0.17 (0.08) | 50 | 0.60 (0.33) | 0.80 (0.24) | 0.27 (0.08) |
| Collembolans (springtails) | 1,104 | 4.50 (2.33) | 22.40 (14.12) | 9.90 (5.40) | 215 | 2.73 (2.19) | 3.50 (2.89) | 0.93 (0.33) |
| Hemipterans (bugs) | 3 | 0.03 (0.03) | 0.03 (0.03) | 0.03 (0.03) | 13 | 0.33 (0.17) | 0.03 (0.03) | 0.07 (0.05) |
| Other | 17 | | | | 8 | | | |
| Spiders | 74 | 0.33 (0.09) | 0.83 (0.28) | 1.30 (0.28) | 78 | 0.33 (0.11) | 1.13 (0.24) | 1.13 (0.27) |
| Mites | 22 | 0.03 (0.03) | 0.07 (0.05) | 0.63 (0.29) | 7 | 0.10 (0.06) | 0.10 (0.07) | 0.03 (0.03) |
| Gastropods | 465 | 4.57 (2.37) | 5.57 (1.88) | 5.37 (1.27) | 379 | 3.47 (1.39) | 4.40 (1.52) | 4.77 (1.52) |
| *Succinea* | 121 | 0.03 (0.03) | 0.87 (0.38) | 3.13 (1.04) | 193 | 0.03 (0.03) | 2.03 (0.67) | 4.37 (1.55) |
| Hydrobiids | 340 | 4.53 (2.37) | 4.70 (1.90) | 2.10 (0.97) | 186 | 3.43 (1.39) | 2.37 (1.48) | 0.40 (0.21) |
| Other | 4 | | | | 0 | | | |
| Oligochaetes | 72 | 0.23 (0.21) | 1.63 (0.68) | 0.53 (0.22) | 2 | 0.03 (0.03) | 0.03 (0.03) | 0 |
| Nematodes | 25 | 0.03 (0.03) | 0.23 (0.14) | 0.57 (0.47) | 0 | 0 | 0 | 0 |
| Total | 2,149 | 13.43 (3.12) | 35.07 (14.31) | 23.13 (6.46) | 1,287 | 11.03 (2.46) | 20.67 (5.22) | 11.20 (2.04) |

were not significantly different (Kruskal-Wallis, $\chi^2 = 1.88$, p = 0.170). There were no differences in the numbers of this amphipod captured at different distances from the river or creek bank either year (Kruskal-Wallis, $\chi^2 = 0.13$, p = 0.983 and $\chi^2 = 2.09$, p = 0.352).

## Marsh Surface Macroinvertebrates

A total of 3,436 invertebrates was collected from the litter bags. Although the mean number of invertebrates per litter bag tended to be highest in *Typha* marshes for both sampling periods (Table 8), differences between *Typha* and *Phragmites* areas were not significant. The mean numbers of invertebrates per litter bag did not differ between the two sampling periods in collections made along different reaches of the river in *Phragmites* (upper: $t = 1.165$, p = 0.259; middle: $t = 0.450$, p = 0.658; lower: $t = 1.329$, p = 0.200) or *Typha* (upper: $t = 0.478$, p = 0.639; middle: $t = 1.064$, p = 0.301; lower: $t = 2.048$, p = 0.061) or in treated *Phragmites* of the lower reach ($t = 1.734$, p = 0.092). In the combined collections from the two periods, there were no differences between the numbers in *Phragmites* and *Typha*-dominated areas of the upper ($t = 0.817$, p = 0.419) or middle ($t = 1.705$, p = 0.103) reaches or among those in treated *Phragmites*, *Phragmites*, and *Typha* marshes of the lower reach (ANOVA, F = 1.606, p = 0.206).

Insects, primarily represented by 6 orders, made up the dominant group, comprising 52% of the individuals collected; among the insects collembolans (springtails) were present in greatest numbers (Table 8). Although collembolans constituted 74% of the total number of insects, their distribution was patchy as was that of hymenopterans (ants). Orthopterans (crickets) and larval and adult dipterans (flies) and coleopterans (beetles) tended to be more evenly distributed in small numbers. Following the insects in abundance were gastropod molluscs and the high marsh amphipod *O. grillus.* These animals represented 25% and 12% of the total number, respectively. The two most prominent gastropods were *Succinea* sp. and hydrobiids. *Succinea* tended to be most abundant in *Typha* and treated *Phragmites* marshes along the lower reach of the river. On the other hand, the hydrobiids tended to occur in greatest numbers in upper reach *Typha* and *Phragmites.* A small number of *Melampus bidentatus* was limited to the treated *Phragmites* marshes. Other invertebrates included the high marsh isopod *Philoscia vittata,* spiders, mites oligochaetes, and nematodes.

## Feeding by *F. heteroclitus* on the Marsh Surface

Specimens of *F. heteroclitus,* caught in Breder traps as they left the marsh surface on the ebbing tide, often had substantial amounts of food in their guts (Table 9). There were no significant differences between the gut fullness indices of *F. heteroclitus* captured in *Phragmites* and *Typha* marshes bordering the upper ($t_{96} = 1.63$, p = 0.107), middle ($t_{78} = 1.48$, p = 0.142), and lower ($t_{40} = 1.81$,

TABLE 9. Frequency (%) of occurrence of gut content components of *Fundulus heteroclitus* trapped in *Phragmites* marshes, *Typha* marshes, and treated *Phragmites* marshes situated along the lower, middle, and upper reaches of the Lieutenant River during high spring tides. The frequency with which various components represented more than half of the total gut content volume is given in parentheses. n = the number of fish guts examined.

| | Upper | | Middle | | Lower | | |
|---|---|---|---|---|---|---|---|
| Components | *Phragmites* (n = 76) | *Typha* (n = 75) | *Phragmites* (n = 68) | *Typha* (n = 63) | *Phragmites* (n = 60) | *Typha* (n = 52) | Treated (n = 58) |
| Major components | | | | | | | |
| Insects | 49 (24) | 52 (25) | 46 (18) | 35 (17) | 43 (15) | 33 (19) | 48 (17) |
| Amphipods | 16 (9) | 13 (5) | 10 (4) | 14 (11) | 20 (8) | 8 (4) | 19 (12) |
| Gastropods | 13 (5) | 5 (4) | 15 (1) | 11 (3) | 20 (8) | 17 (12) | 33 (10) |
| Detritus | 58 (21) | 39 (13) | 34 (13) | 25 (13) | 33 (10) | 38 (13) | 21 (3) |
| Algae | 29 (4) | 25 (12) | 31 (13) | 40 (17) | 22 (5) | 19 (10) | 28 (12) |
| Minor components | | | | | | | |
| Crabs | 11 (5) | 5 (1) | 1 (0) | 5 (3) | 8 (5) | 4 (2) | 2 (0) |
| Shrimp | 1 (1) | 3 (3) | 7 (0) | 5 (2) | 5 (2) | 2 (2) | 12 (12) |
| Isopods | 0 | 0 | 0 | 3 (0) | 0 | 0 | 2 (2) |
| Spiders | 4 (3) | 7 (0) | 6 (3) | 10 (3) | 3 (0) | 10 (2) | 5 (0) |
| Mites | 1 (0) | 4 (0) | 4 (4) | 3 (2) | 0 | 0 | 0 |
| Nematodes | 0 | 5 (0) | 1 (0) | 2 (0) | 7 (0) | 2 (0) | 0 |
| Fish | 0 | 1 (1) | 0 | 0 | 0 | 0 | 3 (3) |
| Eggs | 1 (1) | 5 (3) | 3 (0) | 2 (2) | 3 (2) | 6 (4) | 7 (5) |
| Unrecognizable | 12 (1) | 11 (4) | 12 (6) | 13 (5) | 20 (7) | 13 (2) | 22 (3) |
| Empty (%) | 12 | 9 | 18 | 16 | 17 | 19 | 12 |
| Gut fullness index* | 2.40 (0.28) n = 49 | 1.79 (0.24) n = 49 | 2.07 (0.35) n = 42 | 2.79 (0.33) n = 38 | 1.48 (0.19) n = 35 | 2.21 (0.36) n = 27 | 2.86 (0.41) n = 32 |

* Determined for fish caught during late July–early August and early September.

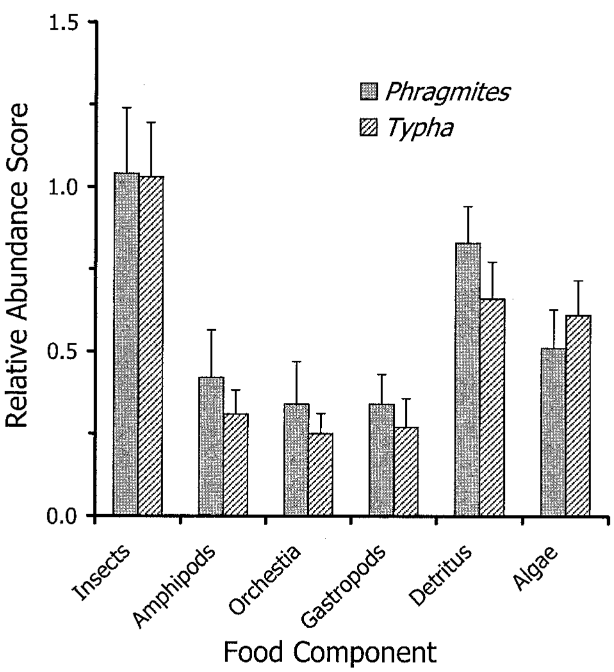


Fig. 9. Mean relative abundance scores (±SE) for major food components in the guts of *F. heteroclitus* caught in *Phragmites* and *Typha* marshes along the Lieutenant River.

p = 0.078) reaches of the river. The gut fullness indices of *F. heteroclitus* captured in *Phragmites* and *Typha* marshes along the different reaches of the river were also not significantly different (ANOVA, F = 2.46, p = 0.090, and F = 3.07, p = 0.050, respectively). There were significant differences among the gut fullness indices of this fish from *Phragmites*, *Typha*, and treated *Phragmites* areas of the lower reach (ANOVA, F = 4.94, p = 0.009).

Diets of *F. heteroclitus* from the different types of marsh were generally similar (Table 9). The major dietary components were insects, amphipods, gastropods, detritus, and algae. Other organisms including crabs, shrimp, and spiders contributed a lesser portion. Relative abundance scores of the major dietary components were not different for *F. heteroclitus* trapped in the *Typha* and *Phragmites* marshes (Fig. 9). Insects, including beetles, aphids, and dipteran and other larvae, constituted the greatest part of the diet, followed by detritus and algae. *Orchestia* was the dominant amphipod in the gut contents of *F. heteroclitus*. Of the fish with amphipods in their guts, 77% had consumed *Orchestia*. The most commonly occurring gastropod molluscs in the diet were *Succinea* and hydrobiids. *Succinea* tended to occur most often in the guts of *F. heteroclitus* from the lower reach of the river. Shrimp were found infrequently in the guts of *F. heteroclitus*, but all that could be identified were *P. pugio*.

Although the diets of *F. heteroclitus* from the different marshes were generally similar, there were some specific differences. In late July and early August aphids were a prominent food in 35% of the *F. heteroclitus* trapped in *Phragmites* along the upper reach of the river, whereas these insects were found in only one fish (4%) from *Typha*-dominated areas. Small lepidopteran larvae were numerous in the guts of many *F. heteroclitus* captured in *Phragmites* marshes in early September, but were not found in the guts of fish from *Typha* marshes.

## Discussion

### Nekton Sampling Gears

In the present study, Breder traps were used to sample fishes and crustaceans moving off the flooded marsh surface with the ebbing tide. Because these traps are relatively inexpensive and easy to set and retrieve, a fairly large number of them can be used simultaneously, allowing greater replication than is feasible with many other types of gear. Breder traps appear to be well suited for comparing the abundances of most resident marsh nekton at closely situated sites that are sampled at the same time (Sargent and Carlson 1987; Fulling et al. 1999). The disadvantages of this gear are that the sampled area cannot be defined, larger fishes and crustaceans are excluded, and some nekton may readily avoid capture (Sargent and Carlson 1987; Rozas and Minello 1997).

Another potential problem with Breder traps is trap saturation, reaching a number of captured fish beyond which no more fish will enter. In two cases, 69 and 70 *F. heteroclitus* were captured in Breder traps, once each in *Phragmites* and *Typha*. We do not know if this number is at or near the saturation level; however, only 2% (11 out of 497) of the traps that captured *F. heteroclitus* caught more than half this number and fewer than 50% of them caught more than three.

The assemblage of fishes and crustaceans captured with Breder traps in this study was generally similar to that caught using flume nets in New Jersey marshes (Able and Hagan 2000). A major difference was the capture of large numbers of *C. sapidus* in the New Jersey study. The range in TL and the median TL of *F. heteroclitus*, the numerically dominant fish, were comparable in the two studies.

Use of the marsh interior, at distances of up to 30 m from the river and creek bank, as nursery areas by marsh nekton was examined using shallow pit traps. *Fundulus* spp., ranging from 0.3 to 5.5 cm TL, was found in the traps at low tide. The pit traps retained primarily larval and young juvenile *Fundulus*, whereas the Breder traps captured both juveniles and adults (up to 10.0 cm TL). The sizes of *F. heteroclitus* caught with the two gears overlapped in the range of 1.0 to 5.5 cm TL. These results are similar to those of Able and Hagan (2000).

### Distribution and Abundance of Fishes and Crustaceans

The numbers of fishes (all species combined) caught with Breder traps in *Phragmites, Typha,* and treated *Phragmites* marshes were not significantly different. *F. heteroclitus*, the numerically dominant fish, was essentially equally distributed among the three vegetation types. No significant differences in the abundances of *F. heteroclitus* in the various types of marsh were found; however, this fish tended to be somewhat more numerous in *Phragmites* than in *Typha* and treated *Phragmites*. Although Breder traps do not permit calculation of fish density per unit area of marsh, the number of fish leaving the marsh per unit length of marsh edge can be estimated. The mean number of *F. heteroclitus* per meter of marsh edge was 16 $\pm$ 1.9 and 14 $\pm$ 1.7 for *Phragmites* and *Typha* (all reaches), respectively, and 8.6 $\pm$ 1.6 to 11 $\pm$ 2.0 per meter of marsh edge for the different types of marsh, including treated *Phragmites*, along the lower reach. Size distributions of this fish in the different marshes were similar as were length-weight regressions. Hanson et al. (2002) and Osgood (personal communication), using bottomless lift nets, have demonstrated no difference in the abundance of *F. heteroclitus* in brackish *Typha* and *Phragmites* marshes along the Hudson River. These findings are in agreement with those of Able and Hagan (2000) and Meyer et al. (2001), who showed that the number of older juvenile and adult *F. heteroclitus* caught with flume and Fyke nets in *S. alterniflora* and *Phragmites* marshes were not significantly different. The size distributions (Able and Hagan 2000) and total biomass (Meyer et al. 2001) of *F. heteroclitus* from the two types of marsh were also comparable. The latter study indicated a tendency for individuals of *F. heteroclitus* and other fishes to be somewhat larger in *Phragmites* marshes than in *S. alterniflora* marshes. Even though vegetation may be an important factor contributing to habitat quality for fishes (Rozas 1995), it appears that in many cases changes in vegetation alone, without changes in abiotic factors such as tidal flooding, have little effect upon older fish use (Meyer et al. 2001). To the extent that *Phragmites* eventually causes the filling in of small creeks or an elevation of the marsh surface, a reduction in fish and natant crustacean use would be expected (Weinstein and Balletto 1999).

Although older stages of *F. heteroclitus* showed no clear preference among different types of vegetation, more *F. heteroclitus* were caught in *Phragmites* and *Typha* marshes along the upper reach of the Lieutenant River than in those bordering the middle and lower reaches. This is probably related to the fact that marsh elevations were generally lower along the upper reach of the river than further downstream. The marshes along the upper reach are flooded more frequently and for longer periods of time, providing greater access to fishes and other natant fauna (Kneib 1994; Kneib and Wagner 1994; Rozas 1995). In addition to the influence of river reach on hydroperiod and fish use of the marsh, there was a positive correlation between the number of *F. heteroclitus* caught per Breder trap and hydroperiod within each reach and each type of vegetation.

While the number of *F. heteroclitus* captured in Breder traps on the marsh surface was positively correlated with flooding depth and hydroperiod (flooding frequency and duration), more *F. heteroclitus* were caught during daytime high tides than during nighttime high tides, even when the night tides were of greater amplitude. There have been few studies that have carried out both day and night sampling of fishes in marsh habitats (Reis and Dean 1981; Weisberg et al. 1981; Rountree and Able 1993; Kneib and Wagner 1994) and to our knowledge no previous study has found strong diel differences in the abundance of *F. heteroclitus*. A greater movement of this fish onto the flooded marsh surface during the day may be to escape visual predators and to feed. Weisberg et al. (1981) have shown that *F. heteroclitus* feeds primarily during the day at the time of high tide, irrespective of marsh flooding. Many *F. heteroclitus* trapped during the day as they were leaving marshes along the Lieutenant River had marsh-surface invertebrates and other foods in their guts; it appears that the diel pattern of fish abundance on the marsh may be related in large part to foraging (see below).

*P. pugio* was more abundant in *Phragmites*-dominated areas than in *Typha* and treated *Phragmites* marshes and was more numerous in *Phragmites* marshes along the lower reach of the river than in those situated further upstream. Able and Hagan (2000) and Meyer et al. (2001) found no significant difference in the number of grass shrimp captured with flume and Fyke nets in *Phragmites* and *S. alterniflora* marshes, although in the latter study *P. pugio* tended to be more abundant in the *Phragmites* marshes during the fall. The distribution of *P. pugio* along the length of the river may be related, at least in part, to salinity. In sampling tidal creeks situated along the salinity gradient of the Lieutenant and Back Rivers, Fell (unpublished data) found *P. pugio* to be most abundant where surface salinities were relatively high (14–28‰). Similarly both Able and Hagen (2000) and Meyer et al. (2001) observed an increase in the abundance of grass shrimp during the fall when salinities were highest.

*P. pugio* sometimes exhibited a diel pattern of abundance opposite that of *F. heteroclitus*. During July and early August, many more shrimp were captured at night than during the day. It is possible that the temporal and spatial patterns in the distribution of *P. pugio* may reflect the avoidance of *F. heteroclitus*, a known predator (Nixon and Oviatt 1973; Heck and Thoman 1981; Knieb 1988, 2000; Posey and Hines 1991; Everett and Ruiz 1993). To the extent that *P. pugio* feeds on the marsh surface only at night to avoid predation, it forfeits many foraging opportunities (Kneib and Wagner 1994).

In the present study, *Fundulus* sp. was essentially the only fish that was found in pit traps on the marsh surface. Somewhat more larval and juvenile *Fundulus* were captured in pit traps placed in *Typha* than in those situated in *Phragmites*. For both years, a total of 350 *Fundulus* was captured in *Typha* as compared with only 54 individuals in *Phragmites*. Although the numbers of fish caught in the two types of vegetation were not significantly different in 2000, they differed in 2001, when a higher proportion of the traps captured fish. These findings are consistent with those of Able and Hagen (2000) who showed that small fishes preferentially used *S. alterniflora*-dominated marshes with numerous small surface pools over *Phragmites* marshes where there was little standing water during low tide. While the presence of shallow pools on the marsh surface appears to be of primary importance for nursery habitat, other factors that may influence the use of marshes by larval and small juvenile fish include food availability and cover (stem density, canopy thickness, etc., providing protection from predators and physical stresses such as elevated temperatures and possibly influencing fish mobility). These were not examined in the present study. Talley and Levin (2001) have shown that within brackish wetlands of the lower Connecticut River macroinfauna, potential food for small fish, are less abundant in *Phragmites*-invaded than in uninvaded sites and compositional differences also exist. It is not yet clear where most fish inhabiting these marshes spend the larval period. Larval and small juvenile *Fundulus* may use as nursery areas submerged aquatic vegetation in the tidal creeks and river (Orth and Heck 1980).

*Fundulus* was captured in pit traps up to 30 m into the marsh interior. In fact, during 2000, more individuals were trapped at 30 m (72% of the total number) than at 3 m from the river or creek bank; during both years, there tended to be more fish caught at 30 m than at 10 m. In *S. alterniflora* marshes, Kneib (1984) found that relatively few larval and juvenile fundulids were caught in pit traps located on the bank of a tidal creek, whereas many were trapped at distances ranging from about 10 m to about 135 m into the marsh interior. Able and Hagan (2000) showed that fewer of these fishes were captured in pit traps situated 0.5 m from the marsh edge than in those positioned at 5 and 9.5 m. It appears that most, if not all, of the intertidal marsh surface may potentially be used as nursery habitat provided shallow pools and perhaps also adequate plant cover are present.

In 2 yr of sampling with pit traps, only 4 postlarval *P. pugio* were captured, even though during 2000 adult *P. pugio* were sometimes caught with Breder traps in large numbers. It is possible that none of the examined marsh types constitute favorable nursery habitat for *P. pugio* or very likely that small grass shrimp simply were not abundant in the Lieutenant River during the sampling periods. Using the same type of trap, Able and Hagan (2000) collected a single *Palaemonetes* sp. during one year but many in late summer and fall of the following year when salinities were higher. In their study all shrimp captures with pit traps were made in *S. alterniflora* marshes, none being in *Phragmites* marshes. It appears that while *S. alterniflora* marshes provide good nursery habitat for both *Fundulus* spp. and *Palaemonetes* spp. (also see Kneib 1984, 1997), *Phragmites* marshes do not.

### Epibentic Invertebrates and Foraging by *F. heteroclitus*

Litter bags were used as the primary method of invertebrate sampling, although some invertebrates were also captured in Breder and pit traps. Depending upon the vegetation and the period of sampling, the mean number of invertebrates per litter bag ranged from 11 ± 2.3 to 35 ± 14.3. Even taking into account differences in the size of the bags and the amount and type of litter, these numbers appear to be low compared to other marshes that have been sampled in the same way (Scatolini and Zedler 1996; Angradi et al. 2001; Pakenham and Fell unpublished data). This may be due in part to the fact that sampling was restricted to a zone close to the marsh edge where environmental conditions may be less favorable for some animals and levels of predation may be especially high. The amount of natural litter present may also influence the effectiveness of litter bags in collecting invertebrates.

Insects, including springtails, ants, and larval and adult beetles and flies, constituted the largest group of marsh fauna collected in litter bags. Gastropods, represented primarily by *Succinea* sp. and hydrobiids, were also relatively abundant as was the high marsh amphipod *O. grillus*. Spiders, the high marsh isopod *P. vittata*, and oligochaetes were present in smaller numbers. *O. grillus* and the fiddler crab *U. minax* were also collected in the fish sampling gears. These results are similar to those obtained in the same general areas with different sampling methods (Fell et al. 1998; Talley and Levin 2001; Warren et al. 2001).

*F. heteroclitus* foraged extensively in all three types of marsh; the gut fullness indicies of this fish from *Typha* and *Phragmites* marshes were not significantly different. The diets of *F. heteroclitus* in the different marshes were also similar. Larval and adult insects constituted the greatest portion of the diet with detritus, algae, amphipods, and gastropods also making substantial contributions. Previous studies by Fell et al. (1998) and Warren et al. (2001) provide similar data on the diets of this fish in *Phragmites* and other marshes in the lower Connecticut estuary.

Although there was a general correspondence between the relative abundances of certain major groups of macroinvertebrates on the marshes (sampled with litter bags) and the prominence of these animals in the diet of *F. heteroclitus*, some notable differences were apparent with respect to specific taxa. Collembolans were the most numerous insects colonizing litter bags on the marsh surface, but they were not observed in the gut contents of *F. heteroclitus*. Aphids and lepidopteran larvae, which were sometimes major components in the diet of this fish in *Phragmites* marshes, did not appear in litter bag collections. However, lepidopteran larvae were consumed by *F. heteroclitus* later in the year after litter bag sampling was completed. Clearly only some of the potential prey resources of fishes were sampled. Certain epibenthic invertebrates, including some snails and fiddler crabs, are not sampled effectively with litter bags (Scatolini and Zedler 1996), and epiphytic animals associated with plant stems and infauna were not collected with this sampling method.

The invasion of brackish cattail marshes by *Phragmites* appears to have no major impact on the use of these marshes by juvenile and adult fishes and shrimp, which were at least as abundant in the invaded as in the uninvaded marsh areas. The numerically dominant fish, *F. heteroclitus*, fed extensively in both types of marsh during high spring tides, and the diets of this fish in *Phragmites* and *Typha* marshes were generally similar. Much more extensive studies will be required to determine whether trophic transfer from the marsh to the adjacent estuary by fishes and crustaceans is affected by the change to *Phragmites* dominance. Fishes and shrimp may also use these marshes as a refuge from predators. *Phragmites*-dominated marshes appear to be less favorable nursery habitats for larval and small juvenile *F. heteroclitus* than uninvaded brackish marsh.

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