Effects of Common Reed (Phragmites australis) Invasion on Marsh Surface Macrofauna: Response of Fishes and Decapod Crustaceans

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ABSTRACT: The tidally inundated marsh surface is an important site for energy exchanges for many resident and transient species. In many areas along the East Coast of the U.S. the dominant vegetation, Spartina alterniflora, has been replaced by the common reed (Phragmites australis). This shift has caused concern about the impact of Phragmites on marsh fauna but research in this area has been limited. During 1997 and 1998, we examined the effect of Phragmites on fish and decapod crustacean use of the marsh surface in the brackish water reaches of the Mullica River, in southern New Jersey, U.S. Fish and decapod crustaceans were sampled with an array of shallow pit traps (rectangular glass dishes, 27.5 x 17.5 x 3.7 cm) and with flumes (1.3 m wide x 10 m long of 3.2-mm mesh). Fish (2-60 mm TL) dominated pit trap collections with Fundulus heteroclitus and Fundulus luciae significantly more abundant at Spartina sites. Fundulus heteroclitus was also the dominant fish (15-275 mm TL) collected in flumes but collections with this gear, including a number of species not collected in pit traps, showed no distinct preferences for different marsh vegetation types. Decapod crustaceans (1-48 mm CW) collected in pit traps were generally less abundant than fishes with Callinectes sapidus and Palaemonetes spp. most abundant in Spartina, while Rhithropanopeus harrisii was most abundant in Phragmites. The same decapod crustacean species (2-186 mm CW) dominated the flume collections and, similar to the pattern of fish collected by the flumes, there were no distinct habitat preferences for different marsh vegetation types. As a result of these observations, with different sampling techniques, it appears there is an overall negative effect of Phragmites on larval and small juvenile fish but less or no effect on larger fish and decapods crustaceans.

Introduction

The tidally inundated marsh surface is believed to be an important site for energy exchanges for resident and transient fishes and decapod crustaceans (Kneib 1997b; Cicchetti and Diaz 2000; Degan et al. 2000). This is evident based on the great abundance of fishes and decapod crustaceans that typically occur there (Kneib 1984, 1987a,b; Talbot and Able 1984; Rozas and Reed 1993; McIvor and Rozas 1996; Cicchetti and Diaz 2000). One reason for these high abundances is that the marsh surface provides a spawning site for many fish species (Able and Castagna 1975; Taylor et al. 1979; Middaugh and Takita 1983; Taylor and DiMichele 1983; Conover and Kynard 1983; Kneib 1989). In addition, it is an important feeding area for some species (Weisburg and Lotrich 1982) and a refuge from predation for others (Kneib 1987b). The latter helps explain why the marsh surface is such an important nursery for small individuals of species such as Fundulus heteroclitus and Fundulus luciae (Byrne 1978; Taylor et al. 1979; Kneib 1984, 1986, 1987a,b; Talbot and Able 1984; Able and Fahay 1998). This same pattern of marsh surface as habitat for feeding and refuge is also true for some decapod crustaceans including the blue crab (Callinectes sapidus) and shrimps (Welsh 1975; Zimmerman and Minello 1984; Kneib 1987b; Fitz and Wiegert 1991; Rozas and Reed 1993; Peterson and Turner 1994; Minello 1999; Cicchetti and Diaz 2000).

In the northeastern United States especially, salt marshes have been invaded by the common reed, Phragmites australis, which has replaced Spartina alterniflora and other species on the marsh surface. Phragmites was formally a minor component of the tidal marsh vegetation for at least 3,000 yr (Niering and Warren 1977; Orson et al. 1987); in the last several decades it has become much more abundant in many marsh systems along the East Coast of the U.S. This invasion and replacement of other marsh species has been documented for Connect-
icut (Roman et al. 1984), New York (Winogrond 1997), New Jersey (Windham 1995; Windham and Lathrop 1999), Delaware (Hellings and Gallagher 1992; Sneddon et al. 1995), Maryland (Rice and Stevenson 1996), Virginia (Havens et al. 1997; Pyke and Havens 1999), and South Carolina (Stalter and Baden 1994). The increase in the distribution and abundance of *Phragmites* has raised concern about its impact on natural marsh systems, the associated fauna, and energy exchanges between marshes and the adjacent estuary (Roman et al. 1984; Marks et al. 1994; Weinstein and Baletto 1999; Meyerson et al. 2000; Weinstein et al. 2000). For example, the change in vegetation that occurs during this invasion may influence marsh surface topography by raising the substrate level above the water table and smoothing the surface topography because of increased litter production, and thus eliminating the water-filled hollows typically found in *Spartina* dominated marsh surface (Windham and Lathrop 1999). On the other hand, others have suggested that it should be introduced into selected areas to increase marsh elevation in order to compensate for marsh loss due to sea level rise (Stevenson et al. 2000).

Despite these contradictory concerns, there has been little focused effort to determine the impacts of *Phragmites* on the fauna associated with the salt marsh surface. An exception to this is a recent analysis of the abundance and food habits of *F. heteroclitus* in a variety of reference marshes, dominated by *Juncus gerardii*, *Typha angustifolia*, and *Spartina patens*, relative to *Phragmites*-dominated marshes in the lower Connecticut River (Fell et al. 1998). These authors suggested that marshes with *Phragmites* appeared to be functioning in the same way as nearby reference marshes of variable vegetation based primarily on fish abundance and food habits. Further, an analysis of trophic linkages between *F. heteroclitus* and marsh vegetation indicated that this species derived some of the nutrients in its tissue from *Phragmites* when found in marshes dominated by this vegetation (Wainright et al. 2000).

We examined macrofaunal use of the marsh surface in *Phragmites*-dominated areas largely because this species has shown a marked increase in the relatively undisturbed, low salinity marshes at Mullica River in southern New Jersey in recent years (Windham 1995; Windham and Lathrop 1999). We examined the potential influence of *Phragmites* on the fauna that use the marsh surface as a nursery by comparing the species composition, abundance, and size of fish and decapod crustaceans on *P. australis* versus *S. alterniflora* dominated marsh surfaces. Preliminary results of a portion of this study were presented as an example of the value of pit trap sampling for assessing fish abundance on the marsh surface (Able 1999).

**Methods and Materials**

**STUDY AREA**

Sampling occurred on Hog Islands (Fig. 1) located in the upper reaches of the Mullica River, a portion of the Jacques Cousteau National Estuarine Research Reserve in New Jersey, U.S. (Able et al. 1995), which is an appropriate study area for three reasons. First, the recent invasion of *P. australis* has been thoroughly documented through analysis of aerial photography. The percentage of vegetative cover of this species has increased from 3.2% to 83.1% between 1971–1991 (Ferren et al. 1981; Windham 1995; Windham and Lathrop 1999). Further, this increase in *Phragmites* seems to be representative of other brackish water sites within this estuary (Windham 1995). Second, this estuary and the study area has relatively few human impacts (Able et al. 1996), which could mask the effects of vegetation on macrofaunal use of the marsh surface. Third, the close proximity of the different vegetation types means that interpreta-
TABLE 1. Details of Spartina alterniflora and Phragmites australis surface sampling sites during 1997 and 1998. See Fig. 1 for locations. na = not available.

<table>
<thead>
<tr>
<th>Dominant Vegetation</th>
<th>Years Sampled</th>
<th>Year Phragmites Established</th>
<th>Average Elevation at Pit Traps (m)</th>
<th>Interstitial Costs Percent</th>
<th>Number of Pools</th>
<th>Percent Standing Water</th>
<th>Percent Other Vegetation (dry wt. g)</th>
<th>Other Vegetation Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spartina A</td>
<td>1998</td>
<td>1971</td>
<td>1.09</td>
<td>yes</td>
<td>0</td>
<td>0–10</td>
<td>47 Scirpus americanus, Spartina patentes</td>
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<tr>
<td>Phragmites A</td>
<td>1998</td>
<td>1971</td>
<td>0.97</td>
<td>no</td>
<td>adjacent</td>
<td>0–5</td>
<td>0 none</td>
<td></td>
</tr>
<tr>
<td>Spartina B</td>
<td>1998</td>
<td>1971</td>
<td>1.02</td>
<td>adjacent</td>
<td>0</td>
<td>10–20</td>
<td>21 Scirpus americanus, Spartina patentes</td>
<td></td>
</tr>
<tr>
<td>Phragmites B</td>
<td>1998</td>
<td>1977</td>
<td>1.12</td>
<td>no</td>
<td>0</td>
<td>0</td>
<td>none</td>
<td></td>
</tr>
<tr>
<td>Phragmites Lw</td>
<td>1997</td>
<td>1977</td>
<td>0.86</td>
<td>na</td>
<td>na</td>
<td>0</td>
<td>none</td>
<td></td>
</tr>
<tr>
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<td>1997</td>
<td>1977</td>
<td>0.87</td>
<td>na</td>
<td>na</td>
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</tr>
<tr>
<td>Spartina C</td>
<td>1998</td>
<td>1986</td>
<td>1.02</td>
<td>Adjacent</td>
<td>1</td>
<td>20–40</td>
<td>6 Scirpus americanus, Spartina patentes</td>
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<tr>
<td>Phragmites G</td>
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<td>1986</td>
<td>1.04</td>
<td>yes</td>
<td>0</td>
<td>0</td>
<td>none</td>
<td></td>
</tr>
<tr>
<td>Spartina D</td>
<td>1997</td>
<td>1971</td>
<td>1.02</td>
<td>yes</td>
<td>0</td>
<td>5–15</td>
<td>20 Scirpus americanus, Spartina patentes, Amaranthus cannabinus</td>
<td></td>
</tr>
<tr>
<td>Phragmites D</td>
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<td>1991</td>
<td>1.12</td>
<td>yes</td>
<td>0</td>
<td>0</td>
<td>none</td>
<td></td>
</tr>
</tbody>
</table>

Site Selection and Description

During 1997, four sites were sampled on Hog Islands, two P. australis-dominated areas (Phrag Lw and Phrag Up) and two S. alterniflora-dominated areas (Spart B and Spart D) (Table 1 and Fig. 1). During 1998, a total of eight sites were sampled, four P. australis-dominated areas (Phrag A–D) and four S. alterniflora-dominated areas (Spart A–D). All sites were within an approximately 1.5 km area. Phragmites australis sites were invaded, except Phrag A, after 1971 (Windham personal communication; Table 1). Spartina alterniflora sites at Hog Islands were generally small (< 500 m²) and fragmented, surrounded on all sides by Phragmites.

Marsh surface elevation largely controls the area of marsh surface that is flooded, and the amount of time the marsh surface remains flooded at high tide. Thus, elevation is important in understanding the spatial and temporal availability of marsh surface habitat for fish and nektonic invertebrates. Relative elevation among locations was determined with a tripod-mounted Electronic Distance Machine (EDM), prism pole, and Sokkia surveying program. This method provided benchmarks on sites used during 1997 and potential sites to be selected for 1998 that were relative to other locations. Relative elevation of the marsh surface at each pit trap was then measured with a hand-held level and stadia rod and these elevations were referenced to the benchmarks.

Based on these methods, it was determined that sites selected for the 1997 field season differed in marsh surface elevation between vegetation types (ANOVA: F₁,2 = 2217.58, p = 0.0005) with Phragmites-dominated sites lower (at a location approximately 15 cm from the marsh edge) than Spartina-dominated sites (Fig. 2). Therefore, during 1997, Phragmites-dominated sites were more available to nektonic macrofauna than Spartina-dominated sites. In order to eliminate elevation as a confounding variable, we selected sites for the 1998 field season after reviewing relative elevations determined for potential sites. As a result, during 1998 relative elevation at the pit traps was not significantly different between vegetation type (ANOVA: F₁,6 = 0.36, p = 0.569) (Fig. 2). During both years, elevation for pit traps varied with distance from the marsh edge with a general increase in elevation with increasing distance from the marsh edge (ANOVA 1997: F₁,5 = 20.06, p = 0.0008; 1998: F₁,12 = 39.86, p = 0.0001) (Fig. 2) but those within the same site and distance from the marsh edge generally varied less than 10 cm. Spartina sites were more variable than Phragmites at the higher elevation with two sites similar at the 5.0 and 9.5 m distance from marsh edge while one site was lower and one site was higher.

During 1998, a general description of the marsh surface topography at each site was compiled at the end of the field season. Percent standing water (> 1 mm of water) on the marsh surface was visually determined within a 10 m area encircling the pit trap array and flume. Three individuals qualitatively assessed the amount of standing water on the marsh surface and the range of their estimates were recorded. Measurements were taken just after the tide had receded from the marsh surface, therefore these are maximum estimates of available standing water. A count was also made of any pools of water and any creeks within this area.

Marsh surface topography differed by vegetation...
type (Table 1). Standing water was present on all Spartina-dominated sites and covered as much as 40% of the marsh surface. In Phragmites-dominated sites little or no standing water (0–5%) was present. These estimates were consistent with our observations during the field season, i.e., the marsh surface on Phragmites marshes was always drier. There were some small (< 0.5 m wide), shallow intertidal creeks present on or adjacent to the study sites, however, these were found on both vegetation types.

Physical and Aboveground Vegetation Characteristics

During the entire study period (May 16–October 31, 1997 and May 1–October 8, 1998), water salinity (%), temperature (°C), and pH were recorded every 30 min by a datalogger (Endeco YSI Environmental Monitoring Systems—PC6000). During 1997, the datalogger was placed adjacent to one of the Phragmites sites (Phrag Lw) in 1 m of water (Fig. 1). In 1998, it was placed between the two islands in 2 m of water. There were some extended time periods in which the datalogger was either removed for routine maintenance or it malfunctioned, including June 5–18, 1997, July 4–14, 1997, July 26–31, 1997, September 25–30, 1997, and July 11–18, 1998. Hand-held point estimates of temperature (alcohol field thermometer) and salinity (refractometer) were taken when flume cod ends were set and retrieved. These data were compared with datalogger data to ground truth values and were found comparable.

To characterize vegetation type and biomass, two replicates of aboveground vegetation were taken at three distances from the marsh edge (0.5, 5.0, and 9.5 m) at each sampling site on August 8, 1997 and August 15, 1998. In previous years, this time period proved to be at the peak of growth of these species at this location and therefore represent maximum stem density, biomass, and height (Windham 1995). For each replicate, all live and dead standing stems within 0.25 m² quadrats were clipped at ground level, identified to lowest possible taxa, counted, bagged, and dried to a constant weight (g) to determine biomass. Length (cm) of 10 live random stems from each quadrat were measured before drying.

Faunal Sampling Techniques

At each site, larval and juvenile fish and decapod crustaceans were passively collected on the marsh surface with shallow pit traps, rectangular glass dishes (27.5 × 17.5 × 5.7 cm) that were sunk flush with the marsh surface. These traps served as mimics of the shallow water habitats typically used by larval and small juvenile fish and crustaceans during periods in which the marsh is not inundated and were functionally similar to those used to collect fish on the marsh surface in North Carolina (Kneib 1978), Georgia (Kneib 1984, 1987b, 1997a), and New Jersey (Talbot and Able 1984;
Martinsdottir 1991). At each site, a total of nine traps were arranged in three parallel rows at three distances (0.5, 5.0, and 9.5 m) from the marsh edge. Pit traps within each row were placed 0.5 m apart. An elevated boardwalk was installed in early spring before vegetation developed and this gave access to the pit traps without altering the marsh surface. On each sampling date, pit traps were completely emptied at low tide prior to flooding at high tide. After the water receded from the marsh surface on the next low tide, the contents of the traps were emptied into bags and refrigerated for several hours before being sorted in the laboratory. All fish and decapod crustaceans were preserved in 95% ETOH. Fish and crabs were measured to the nearest 0.1 mm total length (TL) or carapace width (CW), respectively, using callipers. Panulirus spp. were identified using descriptions compiled by Hardy (1978) and Able and Fahay (1998). Pit trap sampling occurred twice each month at or near daytime spring tides from June through October 1997 (total of 10 sampling dates and 355 individual pit trap sets) and April through October 1998 (total of 11 sampling dates and 782 individual pit trap sets). A total of 5 pit traps in 1997 (1.5% of 1997 total sets) and a total of 10 pit traps in 1998 (1.3% of 1998 total sets) did not flood due to unusually low spring high tides and these were excluded from analyses.

Larger juvenile and adult fish and decapods using the marsh surface were collected at each site with a single flume net (McIvor and Odum 1986), adjacent to the pit trap arrays. The flumes consisted of two parallel (1.3 m apart) walls (1 m high × 10 m long of 3.2-mm mesh) extended perpendicularly from the marsh edge. The back of the flume was blocked with similarly sized mesh. At high tide, a weighted mesh bag cod end (1.3 m × 1.3 m with 3.2-mm mesh) was attached to the flume to enclose the sampling area. As the tide receded, transient fauna that occurred on the marsh surface at high tide moved into the cod end. The cod end was retrieved at low tide. We attempted to increase capture success within each flume with modified Gee minnow traps (length = 45 cm, diam = 23 cm, mesh = 0.64 cm²), which were positioned inside each flume after the cod end was in place. Although some animals were collected in these traps, the overall catch rates were not dramatically enhanced. As a result, trap catches were combined with flume data for all analyses. Flume sampling occurred from April through October 1998 (total of 11 sampling periods and 264 sets). Each sampling period included three consecutive days (at or near spring tides) of flume sampling on daytime high tides. All fish and selected decapod crustaceans were identified, counted, and measured in the field. Fish were measured either to the closest millimeter total length (TL) or fork length (FL). Decapod crustaceans were measured to the closest millimeter carapace width (CW). All fork lengths of fish were converted to total lengths for comparison using regressions from Able and Fahay (1998).

**Analysis**

Analysis of variance (ANOVA) was used to test for the effect of vegetation type and other factors on relative marsh surface elevation, stem density (live and dead), aboveground biomass (live and dead), live stem height, and overall fish and decapod abundance collected by flume. The unit of replication was a pit trap for elevation, quadrat for vegetation, and flume set for fish and decapod analyses. Our blocked factorial design included vegetation type (Spartina or Phragmites) and distance from marsh edge (0.5, 5.0, or 9.5 m) and interactions with location blocked for elevation and vegetation analyses. The model for flume analysis differed with the exception of distance from marsh edge and inclusion of month (April–October). Aboveground biomass and overall fish and decapod abundance collected by flume was log-transformed and stem height was square root transformed in order to meet the assumptions of the ANOVA. Separate analyses were conducted for each year (1997 and 1998).

Since the assumptions necessary for ANOVA were not met for some sampling techniques, overall abundance of fish and decapods collected by pit trap and species specific comparisons of fish and decapods collected by both pit trap and flume were analyzed with nonparametric statistics. Separate Kruskal-Wallis tests were performed to examine differences between vegetation type (Spartina and Phragmites) and distance from marsh edge (0.5, 5.0, and 9.5 m) within each vegetation type for pit trap collections, while flume collections were only tested between vegetation type.

**Results**

**Physical and Vegetation Characteristics**

During the sampling period the datalogger deployed in the sampling area recorded seasonally variable values of salinity and temperature (Fig. 3). Some of the variability between years may have resulted from the different depths of deployment, i.e., 1 m in 1997 and 2 m in 1998. Mean salinities were similar between years and the range of values were similar as well (1997: mean = 7.0%, range = 0.0–19.1; 1998: mean = 8.1%, range = 0.0–18.8). The timing of minimum and maximum values varied somewhat between years. In 1997, salinities < 5.0% occurred in May, June, and August
while in 1998 these values occurred in May, June, and July. Maximum values (> 15.0%) in 1997 occurred in July, August, and October while in 1998 these values were in July, August, September, and October. Temperatures followed a seasonal pattern in both years with lowest mean temperatures in May and highest in July (Table 2). Mean temperatures were higher in 1998 (23.3°C) than in 1997 (20.6°C) even though the datalogger was at greater depth in 1998. pH was variable in this system with similar mean (6.6 and 6.7) and overall range (4.1-7.7) of values for 1997 and 1998, respectively. In general, the lowest pH was associated with increased river runoff and low salinities (Able unpublished data).

The characteristics of the vegetation at the different marsh types was consistent between years although it varied somewhat among locations (Table 1). Phragmites sites were monotypic stands of *P. australis* while the Spartina sites were dominated by *S. alterniflora* with *S. patens*, *Scirpus americanus*, and *Amaranthus cannabifolius* present to a lesser degree. Several vegetation characteristics differed markedly between the Phragmites and Spartina sites (Fig. 4). In 1997 and 1998, the average density of live stems was significantly greater at the Spartina sites than for Phragmites (ANOVA 1997: $F_{1,2} = 108.5, p = 0.009$; 1998: $F_{1,8} = 14.1, p = 0.006$); while the

![Graphs showing temperature and salinity over time](image)

**Fig. 3.** Average temperature and salinity of subtidal waters that flooded the marsh surface on high tides during the sampling period based on datalogger records.

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**TABLE 2.** Species composition and abundance of fish and selected decapod crustaceans collected from *Spartina* and *Phragmites* vegetated marsh surfaces in pit traps at Hog Islands during June–October 1997 and April–October 1998. Catch per unit effort (CPUE) = number collected per individual pit trap set or flume set. * = significant difference ($p < 0.05$) Kruskal-Wallis test ($x^2$) between vegetation types within year and gear.

<table>
<thead>
<tr>
<th>Species</th>
<th>1997</th>
<th>1998</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pit trap</td>
<td>CPUE</td>
</tr>
<tr>
<td></td>
<td>Total Collected</td>
<td>Phragmites</td>
</tr>
<tr>
<td><strong>Decapod crustaceans</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Callinectes sapidus</td>
<td>89</td>
<td>0.69</td>
</tr>
<tr>
<td>Palomoides spp.</td>
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<td>0</td>
</tr>
<tr>
<td>Rhithropanopeus harrisi</td>
<td>66</td>
<td>0.83*</td>
</tr>
<tr>
<td>Sesarma reticulatum</td>
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<td>—</td>
</tr>
<tr>
<td><em>Uca</em> spp.</td>
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</tr>
<tr>
<td>Total</td>
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<td>0.43</td>
</tr>
<tr>
<td><strong>Fish</strong></td>
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</tr>
<tr>
<td>Anchovia mitchelli</td>
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<tr>
<td>Anguilla rostrata</td>
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<tr>
<td>Ethostoma alabastroides</td>
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<td>Pandinus diaphanus</td>
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</tr>
<tr>
<td>Pandinus heterochirus</td>
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<td>0.08</td>
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<td>Pandus lucioperca</td>
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<td>0</td>
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<tr>
<td>gobio marinus</td>
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<tr>
<td>Gobiomorus sp.</td>
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</tr>
<tr>
<td>Menidia menidia</td>
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<td>—</td>
</tr>
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<td>Morone americana</td>
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<td>Sygnathus fasciatus</td>
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<tr>
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<td>—</td>
</tr>
<tr>
<td>Unknown fish</td>
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<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>521</td>
<td>0.08</td>
</tr>
</tbody>
</table>
Density of dead stems was similar between vegetation types during both years (ANOVA 1997: $F_{1,2} = 0.58$, $p = 0.527$; 1998: $F_{1,8} = 2.16$, $p = 0.180$). The average live biomass (ANOVA 1997: $F_{1,2} = 38.49$, $p = 0.025$; 1998: $F_{1,8} = 89.45$, $p = 0.0001$) and the average height (ANOVA 1997: $F_{1,2} = 254.56$, $p = 0.004$; 1998: $F_{1,8} = 185.57$, $p = 0.0001$) of aboveground vegetation was consistently greater for Phragmites than for Spartina sites in both years.

**Size Composition of the Fauna**

Although the size composition of fish and decapod crustaceans varied with sampling gear, patterns were similar regardless of vegetation type (Figs. 5 and 6). Pit traps caught smaller fishes and decapod crustaceans than flumes. For fishes, the mean size in pit traps was 14.5 mm TL while fishes in flumes were much larger (mean = 59.4 mm TL). Thus, individuals collected in pit traps were predominantly recently hatched young-of-the-year, while those collected in flumes represented large young-of-the-year and older age classes. There was some overlap in size of fishes in these two gears from approximately 19–61 mm TL, but these represented a relatively small proportion of the fish collected in pit traps. For decapod crustaceans, the differences in size by collecting gear were not as pronounced. The mean size was 7.8 mm CW in pit traps and 30.0 mm CW in flumes but there was considerable overlap in the range of sizes from approximately 3–22 mm CW.

**Distribution and Abundance of Fauna**

Overall fish use of Spartina-dominated marsh was significantly and consistently higher than for Phragmites-dominated marsh for small fishes based on pit trap collections in both years (Kruskal-Wallis 1997: $x^2 = 86.8$, $p = 0.0001$; 1998: $x^2 = 183.14$, $p = 0.0001$) (Table 2 and Figs. 7 and 8). The rarity of fish in Phragmites-dominated marshes is evident by the fact that only 15 individuals were collected in 1997 and 33 individuals in 1998 of the 1,600 individuals captured in both years (Table 2). The spatial pattern of fish use within these vegetation
types was similar for both years based on pit trap collections (Fig. 7). Distance from the marsh edge within Spartina marshes had a significant effect on fish, i.e., Fundulus spp., abundance with pit traps positioned 0.5 m from the marsh edge typically capturing fewer fish than pit traps at 5.0 m and 9.5 m from the marsh edge (Kruskal-Wallis 1997: $\chi^2 = 35.95, p = 0.0001$; 1998: $\chi^2 = 106.52, p = 0.0001$) (Fig. 7). So few fish were captured at the Phragmites-dominated sites that no pattern was discernible. No significant differences (ANOVA: $F_{1,8} = 0.24, p = 0.641$) occurred in flume collections where the abundance of larger fish typically caught in this year averaged 3.6 ± 0.3 individuals per 1.3 m of marsh edge in Spartina and 2.8 ± 0.5 in Phragmites (Table 2 and Fig. 9).

Overall decapod crustacean use varied among marsh-surface pit trap collections (Table 2 and Figs. 7 and 9). During 1997, vegetation type did not have a significant effect on decapod abundance (Kruskal-Wallis: $\chi^2 = 1.229, p = 0.268$); while vegetation was significant in 1998 (Kruskal-Wallis: $\chi^2 = 9.471, p = 0.002$). Similarly, during 1997, distance from marsh edge did not significantly affect decapod distribution on either Spartina (Kruskal-Wallis: $\chi^2 = 2.23, p = 0.328$) or Phragmites (Kruskal-Wallis: $\chi^2 = 5.705, p = 0.0577$) marshes; while in 1998, it did (Kruskal-Wallis Spartina: $\chi^2 = 16.80, p = 0.0002$; Phragmites: $\chi^2 = 21.866, p = 0.0001$) (Fig. 7). These differing patterns of significance between years may have been the result of a smaller sample size in 1997 than 1998. There was no significant difference in abundance of decapods in flume collections between Spartina and Phragmites sites ($F_{1,6} = 0.25, p = 0.635$) (Table 2 and Fig. 9).

The temporal pattern of fish and decapod abundance was generally similar between vegetation types and collecting gears (Figs. 8 and 9). For fishes collected in pit traps at Spartina sites, catches were low or zero in May, June, September, and October (Fig. 8). Peak abundance was in midsummer, early July in 1997 and late July in 1998, with abundance slightly greater in 1997 (12.1 ± 2.4) than in 1998 (9.0 ± 1.4) (Fig. 8). For decapod crustaceans in Spartina, abundance peaked in August 1997 and September in 1998 (Fig. 9). Peak catches in Phragmites were most noticeable in 1997 in June and October (Fig. 9). No peaks were observed in Phragmites in 1998. For flume collections, patterns of abundance varied with the faunal group. For fish-
Fig. 9. Abundance (± SE) of all decapod crustaceans collected in pit traps by date on Hog Islands during June–October 1997 (n = 10 sampling dates, n = 4 sites) and pit traps (n = 11 sampling dates, n = 8 sites) and flumes (n = 11 sampling dates, n = 8 sites) during April–October 1998. For pit traps, data were averaged across vegetative types, irrespective of distance from marsh edge.

In *Spartina* marshes, no fish species collected by pit trap was dominant in *Phragmites* (Table 2). The composition of decapod crustaceans in pit traps varied between years and with vegetation type (Table 2). In 1997, two crabs, *Callinectes sapidus* (56.0%) and *Rhithropanopeus harrisii* (41.5%), made up the vast majority of the individuals collected (n = 159 total decapods). In 1998, *Palaeomonetes* spp. (85.5%) made up much of the catch (n = 675 total decapods) even though only a single individual was collected in 1997. Other contributors included *Uca* spp. (7.4%), *R. harrisii* (3.8%), and *C. sapidus* (3.0%). The distribution of these species relative to vegetation type was species specific (Table 2). During both years, *Callinectes sapidus* was consistently more abundant in collections in *Spartina* (1997: 81%; 1998: 95%) (Kruskal-Wallis 1997: χ² = 13.686, p = 0.0002; 1998: χ² = 16.138, p = 0.0001). During 1997, *R. harrisii* (91%) was significantly more abundant in *Phragmites* (Kruskal-Wallis: χ² = 31.60, p = 0.0001). During 1998, *Palaeomonetes* spp. were collected exclusively in *Spartina* (Kruskal-Wallis: χ² = 49.72, p = 0.0001), while most *Uca* spp. (80%) were collected in *Phragmites* (Kruskal-Wallis: χ² = 13.856, p = 0.0002).

The overall species composition of the fauna collected with flumes was similar to the pit traps for decapod crustaceans but differed markedly for fishes (Table 2). *Fundulus heteroclitus* was still the dominant fish (84.2% of 848 total fish) collected in flumes. *F. luciae* (1.5%) also occurred. Other species unique to flume collections included *Morange americana* (4.4%), *Menidia menidia* (2.9%), *Gobiosoma bosci* (2.6%), *Anguilla rostrata* (2.2%), and *Gobiosoma* spp. (1.1%). With flume sampling, *F. heteroclitus* was evenly distributed between *Spartina* (55%) and *Phragmites* (45%) (Kruskal-Wallis: χ² = 3.820, p = 0.0507). This pattern was similar for all other fish species except *A. rostrata* which was significantly more abundant in *Spartina* (Kruskal-Wallis: χ² = 4.305, p = 0.038). Most decapod species collected by flume were evenly distributed by vegetation type except for *R. harrisii* which was more abundant in *Spartina* (Kruskal-Wallis: χ² = 5.247, p = 0.022).

**Discussion**

**Influence of Sampling Technique**

The patterns of distribution and abundance of fishes and decapod crustaceans in this study varied between collecting gears and vegetation type. The influence of sampling technique is especially critical in interpreting faunal use patterns on the topographically complex marsh surface, especially for the very small, early life history stages of fishes. In this study we relied on two sampling approaches...
to help characterize the nekton in the different vegetation types, flumes and pit traps. The advantages of flumes are that they presumably provide a quantitative measure of abundance for nekton that move onto the marsh surface with flooding tides (McVoy and Rozas 1996; Rozas and Minello 1997). Typically, the mesh sizes in prior studies, as in this one, are too large to retain recently hatched larvae and small juvenile fishes (see Fig. 5). Pit traps are non-quantitative samplers (Kneib 1987a, 1997a) and these and other techniques used to sample marsh surface nekton may be biased by a variety of factors (Fulling et al. 1999).

On the other hand, pit traps offer the advantage that they appear to mimic natural water-filled depressions on the marsh surface, and thus may introduce fewer artifacts into a sampling program targeting young-of-the-year Fundulus spp. than constructing large structures such as flumes which influence the direction and location of capture (Kneib 1991; Kneib and Wagner 1994; Kneib and Knowlton 1995). Clearly, these two sampling approaches influenced the size and species composition of the fishes and decapods captured. As a result, pit traps consistently captured smaller individuals of fewer species (primarily F. heteroclitus), while flumes captured larger and a more diverse group of fishes and decapods. Thus, gear type strongly influenced the interpretation of the nekton using the marsh surface. As a result, if we had only sampled with flumes we may have concluded that the size and faunal composition of fishes and decapods of Phragmites versus Spartina marshes is similar and that vegetation type does not influence the fauna. The primary reason that fish abundance in flumes appeared similar between vegetation types is that the overwhelming dominant species, i.e., large juvenile and adult F. heteroclitus (mean = 58.1 ± 0.6 mm TL), were evenly distributed between vegetation types. However, other species had greater abundance in Spartina relative to Phragmites. For example, G. osceola and Gobiosoma spp. (probably the same species because the only other Gobiosoma in this estuary [G. ginsburgi] is distributed in higher salinities; Duval and Able 1998), and A. rostrata were significantly more abundant or exclusively found (F. luciae) in Spartina (Table 2). The only fish species that appeared more abundant in Phragmites was M. menidia. Unfortunately, the only other study that addresses faunal use of the marsh surface in Phragmites-dominated marshes (Fell et al. 1998) used a different sampling technique (Breder traps; Breder 1960) of unstated mesh size to capture fishes moving onto the marsh surface. Perhaps because Breder traps were used to capture fishes as they moved on and off the marsh surface, they had a species composition similar to our

Influence of Vegetation Type

The patterns of decapod use of the Spartina and Phragmites-dominated marsh surface varied between years and sampling techniques, as previously discussed. The species composition in pit traps differed markedly between years and differences probably reflected differences in availability. The large numbers of Palaemonetes spp. in 1998 accounted for the peak in decapod abundance in September and October and this occurred at the same time as a dramatic increase in salinity and decrease in pH at the study area (Fig. 3). This suggests that high salinity (Table 2) water from lower in the estuary brought large numbers of Palaemonetes and/or their larvae into the Hog Islands area. This pattern was reflected in increased catches of shrimp in the flumes as well. The abundance relative to vegetation type varied with individual species in the pit trap collections (Table 2). In both years, C. sapidus was more abundant in Spartina and R. harrisii was more abundant in Phragmites. In 1998, the Palaemonetes spp. were exclusively found in Spartina. We suspect that these patterns by C. sapidus and Palaemonetes are due to a behavioral preference as they move onto the marsh surface on flooding tides.

The overall species composition of decapods was similar between pit traps and flumes in 1998. Two possible exceptions were that C. sapidus was relatively much more abundant and Uca spp. were less abundant in flume collections relative to pit trap collections. These exceptions may be the result of
differences in life history patterns of these species. Calamoeces sapidus is a transient on the marsh surface (Fitz and Wiegert 1991; Cicchetti and Diaz 2000) and therefore is more susceptible to the flume gear which collects animals as they are leaving the marsh surface; while Uca spp. reside on the marsh surface regardless of tide and are less susceptible. Differences relative to vegetation type were not so clear within flume collections with most species of similar relative abundance regardless of vegetation type.

Others have determined that some of the same species of decapods use the marsh surface. For C. sapidus, this was documented in Texas (Minello and Zimmerman 1992), Louisiana (Rozas and Reed 1993), Georgia (Fitz and Wiegert 1991), and South Carolina (Mense and Wenner 1989) marshes, and now we have confirmed that it occurs in New Jersey as well. The same pattern of use of the marsh surface is evident for Palaeonetes spp. in Texas (Minello and Zimmerman 1992), Louisiana (Rozas and Reed 1993; Peterson and Turner 1994), and Georgia (Kneib and Wagner 1994), and we have identified that this occurs on New Jersey salt marsh surfaces, although it varied annually at our typically low-salinity study area. Taken together it appears that decapod crustaceans can make up a significant component of the marsh surface fauna in New Jersey and elsewhere and should be considered as potentially important mediators of energy flow and trophic interactions from the marsh surface to adjacent intertidal and subtidal habitats (see Cicchetti and Diaz 2000).

The pattern of fish species composition varied with vegetation type, based on pit trap sampling, perhaps as a result of the differences in marsh topography associated with vegetation. Fundulus heteroclitus was captured exclusively in Spartina marsh, perhaps because it lives in shallow depressions on the marsh surface (Able et al. 1983). If future studies confirm its absence in Phragmites marshes, that would be one example of how this vegetation type reduces biodiversity.

The much reduced abundance of small, recently hatched F. heteroclitus in Phragmites-dominated marshes merits special attention because this is probably the most important fish species in marshes along the East Coast of North America due to its abundance and the roles it plays in marsh trophodynamics both as predator and prey (Kneib 1986, 1997b). Additionally, the habitat use, growth, and survival of the larvae and small juveniles may be particularly important to the population dynamics of this species (Kneib 1993, 1997a) as occurs for many other species of fish (e.g., Able and Fahay 1998). The greater abundance of F. heteroclitus larvae and small juveniles in Spartina relative to Phragmites-dominated marsh may be due to several factors. First, the patterns of abundance may reflect spawning site preference. It is well documented that F. heteroclitus deposits its eggs as it moves onto the marsh surface in Spartina marshes at the base of Spartina stems (Taylor et al. 1977) and in ribbed mussel (Geukensia demissa) shells (Able and Castagna 1975; Able 1984; Able and Hata 1984). This effect could be enhanced if there is fidelity to the spawning site by the larvae. Second, differential survival of eggs and larvae could also account for the differences observed, as could preference of larvae for Spartina marshes.

Perhaps the simplest explanations are that F. heteroclitus prefer to spawn in Spartina dominated marshes and the larvae have a high degree of fidelity to these sites. The first suggestion has yet to be tested. However with regard to the latter, there are numerous examples of the use of intertidal marsh surface puddles and depressions as microhabitat for larvae and small juveniles of F. heteroclitus in New Jersey (Talbot and Able 1984), Delaware (Taylor et al. 1979), North Carolina (Kneib and Stiven 1978), and Georgia (Kneib 1984, 1986, 1987a, 1997a). Thus, these likely serve as essential habitats for early life history stages. These habitat types were present in the variable topography of the Spartina sites in this study but infrequently in the Phragmites sites where standing water was seldom present (Table 1). The flat “table top” topography appears to be characteristic of Phragmites marsh surfaces at Hog Islands (Windham and Lathrop 1999), and in marshes along Delaware Bay (Weinstein and Balletto 1999). Our own extensive observations in a variety of Phragmites-dominated marshes in Delaware Bay (Able et al. unpublished data) confirm the difference in marsh topography between these vegetation types. Perhaps, as suggested by Windham and Lathrop (1999), the high litter production in Phragmites marshes may fill depressions in the marsh surface, thus raising the soil level above the water table, as well as smoothing the surface topography. Both of these would reduce the number and size of depressions and thus serve to eliminate the nursery habitat for recently hatched Fundulus spp. as noted above. Furthermore, if Phragmites causes the marsh surface to be elevated, as has been suggested (Stevenson et al. 2000), it may reduce access to the marsh surface in general and eliminate it as a feeding and nursery area. If this process varies with age of Phragmites, i.e., older stands have flatter topography, then all of the above effects may vary among stands of Phragmites and confound interpretation of effects on the fauna unless age or other factors that influence marsh surface topography are taken into consideration. However, even when we created
standing water on the *Phragmites* marsh surface with pit traps, we caught very few fish, suggesting that there are few in the *Phragmites* marsh sites in general.

Clearly, the sources of larvae, i.e., local reproduction or movement from adjacent sources, needs to be resolved for this and other *Phragmites*—*Spartina* marsh comparisons to see if our results for larvae and small juveniles can be confirmed. Additionally, the possibility of differential larval preference and survival needs to be investigated further to determine the source of these differences in distribution and abundance.

Other physical characteristics and faunal components also differ across these vegetation types at some of the same study sites (Angradi et al. unpublished data). In their study, benthic macroinvertebrate density and richness was greater in *Spartina* than *Phragmites*. In the *Phragmites* marshes, detrital biomass was higher, as was water velocity. Both variables may be responses to vegetation type and density. Also, species composition varied across vegetation types, perhaps because of large amounts of standing water on the marsh surface at their *Spartina* sites and generally drier conditions in *Phragmites* marshes (Bertness 1999).

In summary, vegetation type and associated microtopography influenced fish and decapod use of the marsh surface at Hog Islands, especially for *F. heteroclitus* an important component of marsh trophic relays. However, more studies at a variety of sites need to be completed before we can confirm the patterns observed in this study. These future attempts to evaluate the effects of *Phragmites* should incorporate detailed site analysis including microtopography, elevation, and soil characteristics as well as age of *Phragmites* sites. Clearly, faunal sampling techniques are a major consideration.

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