Benthic communities of common reed *Phragmites australis* and marsh cordgrass *Spartina alterniflora* marshes in Chesapeake Bay

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ABSTRACT: Invasive species are receiving increased attention both for their direct effects, including competitive displacement and predator–prey interactions, and indirect effects involving ecosystem and habitat alterations. The common reed *Phragmites australis* is spreading along much of the Atlantic and Gulf coasts of the USA. Its spread is particularly apparent in disturbed oligohaline to mesohaline areas, where it may displace the marsh cordgrass *Spartina alterniflora*. Because of the different morphologies of these plants, associated sediment effects, and differences in biogeochemical cycling, there is the potential for significant faunal community changes where macrophyte species replacement occurs. We conducted a study in the mesohaline region of Chesapeake Bay to examine differences between benthic communities associated with *S. alterniflora* and *P. australis* marshes. Paired *P. australis* and *S. alterniflora* marshes were sampled at 4 sites in summer and 2 sites in fall, blocking for tidal height (high marsh versus low marsh) and small-scale topographic features (rivulet and hummock areas in each marsh type). Sediment grain size did not differ between marsh types, and percent organics differed only for *P. australis* hummock sites compared to other habitat types. Benthic microalgal biomass also did not differ among marsh types. There was only a small effect on faunal abundance patterns, with most species exhibiting slightly higher mean density in *Spartina* compared to adjacent *Phragmites* marshes. Much stronger differences in faunal density were observed between hummocks and adjacent rivulets within each marsh type. While macrophyte type had a detectable effect, local microhabitat characteristics had a stronger relation to local faunal abundance patterns. Since such microhabitat characteristics may covary with macrophyte type (although they did not do so in this study), care must be taken in the design and interpretation of comparative marsh studies and more emphasis should be given to including relations of small-scale topographic features with faunal characteristics. In this system and on the scale studied here, macrophyte replacement did not strongly affect the benthic infaunal community.

KEY WORDS: *Phragmites australis* · *Spartina alterniflora* · Benthos · Invasive species · Chesapeake Bay · Marsh topography

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INTRODUCTION

Tidal marshes are widely recognized as an important habitat for a variety of fishes and decapods (Levinton 1982). *Spartina alterniflora* (hereafter referred to as '*Spartina*') marshes and their associated channel com-

plexes support ecologically important resident species (Kneib & Stiven 1978, Kneib 1984, 1988, McIvor & Odum 1988, Minello & Zimmerman 1992) as well as juveniles of transient species, including, on the east coast of the US, commercially important nekton such as spot, croaker, flatfish, penaeid shrimp, and blue

crabs (Boesch & Turner 1984, Zimmerman & Minello 1984, Hettler 1989, Minello & Zimmerman 1992, Minello et al. 1994). Nekton use tidal marsh habitats both as a critical foraging area (Miltner et al. 1995) and for refuge during times of tidal inundation (Peterson & Turner 1994, Rozas & Zimmerman 2000).

A recent concern for the management of oligohaline to mesohaline marshes along the Atlantic coast of the US has been the spread of the common reed *Phragmites australis* (hereafter referred to as '*Phragmites*'). Although *Phragmites* has been an historic constituent of northeastern oligohaline marshes, it began to dramatically spread in the 1960s (Warren & Fell 1995, Rice et al. 2000), possibly reflecting the introduction of a new genotype (Blossey 2002). However, the native distribution and reasons for its recent invasiveness are still uncertain. *Phragmites* is now expanding its range along the whole east coast of the US, especially in disturbed habitats. In many locations, *Phragmites* has replaced oligohaline and mesohaline marsh macrophytes, including *Spartina*, or produced mixed vegetation stands (Havens et al. 1997, Chambers et al. 1999, Rice et al. 2000, Weis & Weis 2000, Talley & Levin 2001).

Replacement of *Spartina* by *Phragmites* has led to concerns about shifts in habitat quality, since faunal patterns may vary with changes in vegetation type (LaSalle & Bishop 1987, Posey et al. 1997, Talley & Levin 1999). *Phragmites* stands present a different physical structure than *Spartina*, with larger but less dense stands of stems and a lower relative below-ground biomass (Meyerson et al. 2000, Windham 2001). Differences in growth form and structure of these plants may be associated with differences in detrital production, potential water flow through the stems, root mass, sediment organic content and nutrient cycling (Meyerson et al. 2000, Talley & Levin 2001, Windham 2001) as well as patterns of sediment deposition within the macrophyte stands (Weinstein & Balleto 1999, Rooth & Stevenson 2000, Leonard et al. 2002).

While physical and geochemical differences among *Phragmites* and *Spartina* marshes have been noted, the influence of these macrophytes on fauna is less clear, and comparisons between the 2 marsh types have provided mixed results. Some studies of marsh utilization by nekton have indicated no detectable difference among these marsh types (Fell et al. 1998, Able et al. 2001, Meyer et al. 2001), yet other studies have indicated lower abundances of certain species and of certain life stages within *Phragmites* compared to *Spartina* marshes (Weinstein & Balleto 1999, Able & Hagan 2000). Bird abundance and species richness were lower in a *P. australis* marsh than in an *S. alterniflora* marsh (Benoit & Askins 1999). Laboratory studies have suggested some behavioral avoidance of *Phragmites* by juvenile fishes (Weis & Weis 2000). Talley &

Levin (2001) found that certain benthic fauna were less dense within northeastern *Phragmites* compared to *Spartina* marshes (specifically gastropods, midges and oligochaetes) while other taxa were more common (sabellid polychaetes in *Phragmites*). However, Fell et al. (1998) found no evidence for significant differences in prey-resource availability for mummichogs (mostly surface-oriented infauna and selected epifauna) among the 2 marsh types. Possible reasons for variability in macro-infaunal response may involve interactions among macrophyte type and landscape aspects, nutrient and sediment regimes, and local invertebrate species pools. In some locations, *P. australis* marshes may serve as sediment sinks, even forming mounded areas (Rooth & Stevenson 2000). However, such effects are variable among *P. australis* marsh sites and also may occur in *S. alterniflora*-dominated marshes (Meyer et al. 2001).

Studies evaluating both functional characteristics of *Phragmites* (e.g. habitat provision) and comparisons of fauna among vegetation types are limited. This underscores the need for additional information on the potential effects of *Phragmites* replacement of *Spartina* on associated communities. Differences between these marsh types may depend on covariate factors interacting with structural aspects of each plant type. Among the possible reasons for variability in abundance are variations in surface topography among the vegetation types (Weinstein & Balleto 1999) or geographic variations in background faunal availability. While studies have independently examined aspects of topography within a marsh type (usually *Spartina*) or have compared fauna among marsh types, few studies have examined the relative effects of plant type, topography and location in combination.

We compared the benthic macrofaunal communities from adjacent *Phragmites* and *Spartina* marshes at 4 sites in the mesohaline region of Chesapeake Bay, controlling for topographic variability among the vegetation types through stratified sampling in both rivulet and hummock areas and at 2 marsh elevations for each site. The general study area is a good location for the study of *Phragmites* effects because of the close occurrence of monospecific stands of both *Phragmites* and *Spartina* (allowing a paired-site sampling design) as well as the presence of rivulet and hummock features in both marsh types (allowing observation of topographic effects independent of the dominant macrophyte species).

MATERIALS AND METHODS

Study sites. The study was conducted within the Chester River and Prospect Bay regions of Chesa-

apeake Bay, an area of mesohaline to oligohaline salinities (Meyer et al. 2001; present Fig. 1). Within this region we sampled 4 sites with paired *Phragmites* and *Spartina* marshes: (1) Muddy Creek (MUD), (2) Marshy Creek North (MCN), (3) Marshy Creek East (MCE), and (4) Marshy Creek South (MCS). The paired marshes within a site were 100 to 400 m distant from each other, and each site was 1 to 2 km from the next nearest site. Sampling within a marsh was conducted within an area that was 10 m across and extended 6 m from the water's edge into the marsh interior. This area contained numerous vegetated hummocks interspersed by small (~20 to 30 cm wide) sinuous rivulets. Hummocks are raised, vegetated areas 5 to 10 cm higher than adjacent rivulets and separated by the unvegetated rivulets (small drainage channels). All areas drained at low tide. Percent

rivulet versus hummock varied among sites, but was similar for different plant (marsh) types within a site (Fig. 2). Paired marshes were located in the same creek and were chosen to have similar tidal elevations, creek order, salinity and hydroperiod (Meyer et al. 2001). *Spartina* marshes had *Distichis spicata* as a subdominant in the upper marsh, while *Phragmites* marshes were >90% dominated by this 1 macrophyte species (measured by stem density; Meyer et al. 2001). Sampling within a marsh was stratified by topography (rivulet versus hummock) and marsh elevation (high marsh and low marsh—an average elevation difference of 20 cm, with high-marsh areas located 4 to 6 m horizontally into the marsh and low marsh areas located within the first 2 m). There were 4 subsites within a marsh, representing full combinations of the 2 elevations and 2 topography types.

Fig. 1. (A) Location of study sites in central Chesapeake Bay. MUD: Muddy Creek, MCN: Marshy Creek North; MCE: Marshy Creek East; MCS: Marshy Creek South; subsites representing *Phragmites australis* marsh (*) and *Spartina alterniflora* marsh (■) are identified within each site. (B) Summary of variables examined indicating stratification of main factors

Fig. 2. *Phragmites australis* and *Spartina alterniflora* marshes. Relative elevation and rivulet/hummock patterns at 2 representative sites (MCE and MUD). Note that relative cover of hummock areas and elevation patterns are more similar for different macrophyte types within a site than for the same macrophyte types between sites

Methodology. Organics and sediment composition:

Cores for percent organics and sediment grain-size composition were taken at paired rivulet/hummock areas within high- and low-marsh locations in each paired marsh type at a site (paired *Phragmites* and *Spartina* marshes at each of 4 sites) during summer 1998. The samples were placed immediately on ice and subsequently frozen. Sediment samples were analyzed for percent silt/clay and organic content for each of the treatments across all the sites according to the methods described by Royce (1970).

Size fractions for the sediment were determined by washing a 5 g subsample of sediment through a standard sieve series. Each sediment fraction was dried for 24 h at 100°C and percent composition determined by

relative dry weight. Percent silt/clay was determined using the filtrate obtained from wet-sieving. This filtrate was placed in a graduated cylinder, 20 ml of sodium hexametaphosphate was added to prevent flocculation, and the remaining volume of the 1000 ml cylinder was filled with deionized water and homogenized. After 24 h the sample was rehomogenized, and after 20 s three 40 ml subsamples were taken. These subsamples were dried for 24 h at 100°C, and the percent silt/clay was determined relative to the total sample dry weight.

For percent organics, a preweighed subsample of sediment was dried at 100°C for 24 h; the sample was then ground into a fine powder using a mortar and pestle and combusted at 500°C for 24 h. Percent or-

ganics was determined as a ratio of weight loss after combustion to dry weight before combustion.

Benthic chlorophyll a: Benthic chlorophyll *a* for each site was collected in April 1998 and concurrent with infaunal collections in July/October 1998 (see next subsection). We collected 3 surface sediment cores, measuring 1.1 cm diameter $\times$ 1.0 cm deep for each elevation (high marsh 3 to 6 m from the front fringe, low marsh 0 to 2 m from the front fringe) and microhabitat type (rivulet and hummock) from each paired vegetation type at a site. The total number of samples taken within each paired vegetation type at a site was 12. Benthic chlorophyll *a* and pheopigments were determined spectrophotometrically based on methods employed by Pinckney & Zingmark (1993). A 45:45:10 acetone:methanol:distilled water mixture was added to samples and sonicated to liberate and extract pigments. After 24 h extractions, the samples were centrifuged and the solvent was extracted for spectrophotometric analyses. The Lorenzen equations (Lorenzen 1967) were used to calculate chlorophyll *a* and pheopigment content.

Percent (proportion) silt content, percent organics and chlorophyll *a* concentration were compared among macrophyte type, topographic features and tidal levels blocking for marsh locations using analysis of variance (ANOVA) with 2- and 3-way interactions. Because proportions were all less than 0.05 and data for both sediment characteristics and chlorophyll *a* concentrations were normally distributed with non-heterogeneous variance, no transformation was necessary. Where interactions occurred (the only interaction was a weak plant type $\times$ topography interaction for % organics), effects were examined separately by macrophyte type and topographic characteristics.

Macro-infaunal community patterns: Macro-infauna was sampled using 0.007 m² $\times$ 12 cm deep cores taken at low tide. As with sediment and chlorophyll *a* samples, cores were taken at paired rivulet/hummock areas within high- and low-marsh locations in each marsh type (paired *Phragmites* and *Spartina* marshes at each of 2 to 4 sites). All 4 sites were sampled in July 1998, while 2 sites (MUD and MCN) were sampled in October 1998. At each sampling location, 2 cores were taken (between stems for hummock areas), but these were combined for later statistical analyses because of possible non-independence at that spatial scale. Cores were preserved in 10 % formalin solution with added rose bengal dye. Cores were left in formalin for at least 1 wk; the contents were then sieved through a 0.5 mm screen, and the residue was transferred to 50 % isopropanol for storage until identification. Animals were removed from the root matrix under a dissecting microscope.

ANOVA was used to compare abundances of common fauna (individual taxa representing at least 1 % of the total individuals sampled during either summer or fall) using a Type III Model ANOVA (Sokal & Rohlf 1981) including the main effects of macrophyte type (*Phragmites* vs *Spartina*; *F*₁ variable: SAS Institute 1990), topography (rivulet vs hummock), elevation (high vs low marsh), and site, as well as 2-way and 3-way interactive effects among these variables. Analyses were conducted separately for summer and fall samples because of seasonal differences in faunal composition and fewer sites sampled in the fall. Data were log-transformed before analysis to meet assumptions of non-heterogeneity of variances and normality (*F*_{max} test; Sokal & Rohlf 1981). Significant interactions were only detected among 7 comparisons (Tables 1 & 2)

Table 1. *Phragmites australis* and *Spartina alterniflora* marshes. Main and interactive effects of plant type, topography, topo (rivulet vs hummock), elevation, elev (high vs low marsh) and site (MUD, MCN, MCE, MCS) for dominant macrofaunal species (those taxa comprising at least 1 % of individuals) during summer samples. Shown are *F*-values with significance levels in parentheses (significant relations are indicated by bold type). All interactions not shown were non-significant for all taxa. Error: df = 17.

See Fig. 1 legend for explanation of site acronyms

Taxon	Plant type (1 df)	Topography (1 df)	Elevation (1 df)	Site (3 df)	Plant $\times$ topo (1 df)	Plant $\times$ elev (1 df)	Topo $\times$ elev (1 df)	Plant $\times$ site (3 df)
<i>Capitella capitata</i>	2.80 (0.11)	0.20 (0.66)	0.01 (0.93)	0.94 (0.44)	0.01 (0.99)	0.26 (0.62)	1.01 (0.33)	0.88 (0.47)
<i>Chironomus</i> spp.	0.56 (0.47)	4.51 (0.049)	5.34 (0.034)	12.54 (0.0001)	0.10 (0.75)	1.18 (0.29)	0.14 (0.72)	1.13 (0.37)
<i>Cyrenoida</i>	1.04 (0.32)	0.95 (0.34)	0.03 (0.86)	0.76 (0.53)	0.91 (0.35)	0.20 (0.66)	1.34 (0.26)	0.26 (0.86)
<i>Diptera</i>	1.21 (0.29)	1.17 (0.20)	1.75 (0.20)	9.64 (0.0006)	1.06 (0.32)	<0.01 (0.998)	0.66 (0.43)	0.91 (0.45)
<i>Gammarus mucronatus</i>	0.05 (0.82)	1.79 (0.20)	0.29 (0.60)	0.15 (0.93)	2.10 (0.17)	0.41 (0.53)	2.86 (0.11)	0.09 (0.96)
<i>Hobsonia florida</i>	4.18 (0.05)	12.81 (0.002)	1.87 (0.19)	2.05 (0.15)	8.36 (0.01)	0.87 (0.36)	0.24 (0.63)	0.15 (0.93)
<i>Hydrobia minuta</i>	1.57 (0.23)	9.95 (0.006)	0.40 (0.54)	2.06 (0.14)	2.19 (0.16)	0.24 (0.63)	0.29 (0.60)	0.17 (0.91)
<i>Laonereis culveri</i>	17.53 (0.0006)	24.91 (0.0001)	1.08 (0.31)	1.11 (0.37)	20.31 (0.0003)	0.53 (0.48)	4.59 (0.047)	3.88 (0.028)
<i>Leptochelia dubia</i>	3.50 (0.079)	11.24 (0.004)	1.76 (0.20)	4.72 (0.014)	1.15 (0.30)	0.01 (0.92)	4.49 (0.049)	0.48 (0.70)
Acarina	1.78 (0.20)	23.15 (0.0002)	4.56 (0.048)	0.62 (0.61)	1.19 (0.26)	1.35 (0.26)	0.04 (0.85)	2.17 (0.13)
Oligochaeta	0.29 (0.60)	11.63 (0.003)	0.24 (0.63)	3.79 (0.03)	0.35 (0.56)	0.01 (0.94)	0.01 (0.94)	0.11 (0.95)
Total fauna	0.01 (0.91)	3.55 (0.077)	0.98 (0.34)	0.09 (0.96)	0.89 (0.36)	0.35 (0.56)	0.45 (0.51)	0.36 (0.79)
	4.02 (0.061)	1.52 (0.23)	<0.01 (0.95)	0.18 (0.91)	0.47 (0.50)	0.39 (0.54)	2.02 (0.17)	1.79 (0.19)

Table 2. *Phragmites australis* and *Spartina alterniflora* marshes. Main and interactive effects of plant type, topography, topo (rivulet vs hummock), elevation, elev (high vs low marsh) and site (MUD, MCN) for dominant macrofaunal species (those taxa comprising at least 1% of individuals) during fall samples. Shown are *F*-values with significance levels in parentheses (significant relations indicated by bold type). All interactions not shown were non-significant for all taxa. Error: df = 6. See Fig.1 legend for explanation of site acronyms

Taxon	Plant type (1 df)	Topography (1 df)	Elevation (1 df)	Site (1 df)	Plant × topo (1 df)	Plant × elev (1 df)	Topo × elev (1 df)	Plant × site (1 df)
<i>Capitella capitata</i>	3.57 (0.11)	0.53 (0.49)	0.12 (0.75)	8.44 (0.03)	0.29 (0.61)	0.73 (0.43)	0.90 (0.38)	0.20 (0.67)
<i>Chironomus</i> spp.	0.30 (0.60)	30.30 (0.0015)	6.74 (0.041)	0.04 (0.84)	0.21 (0.66)	0.51 (0.50)	0.06 (0.82)	7.03 (0.04)
<i>Cyrenoida</i>	0.05 (0.84)	3.44 (0.11)	0.04 (0.85)	0.27 (0.62)	0.09 (0.78)	0.53 (0.49)	0.56 (0.48)	3.23 (0.12)
<i>Diptera</i>	2.23 (0.19)	22.56 (0.003)	0.06 (0.82)	0.49 (0.51)	3.06 (0.13)	0.01 (0.93)	2.29 (0.18)	1.84 (0.22)
<i>Gammarus mucronatus</i>	0.52 (0.50)	8.99 (0.024)	0.35 (0.57)	0.05 (0.83)	0.12 (0.74)	0.99 (0.36)	0.90 (0.38)	1.20 (0.31)
<i>Hobsonia florida</i>	1.38 (0.28)	19.35 (0.0046)	1.52 (0.26)	0.24 (0.64)	0.13 (0.73)	0.56 (0.48)	0.18 (0.69)	1.36 (0.29)
<i>Hydrobia minuta</i>	0.26 (0.63)	5.05 (0.066)	1.41 (0.28)	1.28 (0.30)	0.67 (0.45)	0.24 (0.65)	<0.01 (0.98)	0.01 (0.93)
<i>Laonereis culveri</i>	8.12 (0.029)	25.31 (0.0024)	0.88 (0.39)	0.05 (0.84)	0.50 (0.51)	2.46 (0.17)	0.57 (0.48)	2.44 (0.17)
<i>Leptochelia dubia</i>	0.01 (0.93)	0.18 (0.68)	2.02 (0.21)	2.75 (0.15)	1.40 (0.28)	0.08 (0.78)	0.11 (0.75)	1.01 (0.35)
Acarina	1.83 (0.23)	7.43 (0.034)	0.48 (0.51)	0.58 (0.47)	0.03 (0.88)	1.14 (0.33)	<0.01 (0.98)	0.08 (0.79)
Oligochaeta	0.10 (0.77)	25.64 (0.0023)	4.75 (0.072)	1.14 (0.33)	0.94 (0.37)	<0.01 (0.95)	8.57 (0.026)	2.85 (0.14)
Total fauna	0.02 (0.89)	0.36 (0.57)	0.07 (0.80)	2.76 (0.15)	0.08 (0.79)	0.38 (0.56)	0.95 (0.37)	0.19 (0.67)
	<0.01 (0.99)	1.47 (0.27)	1.34 (0.29)	0.55 (0.49)	0.01 (0.93)	<0.01 (0.99)	0.15 (0.71)	0.22 (0.66)

and 6 of these were small relative to main effects ($p > 0.025$). Where interactions were strong relative to main effects (this occurred only for *Hydrobia minuta* in summer, involving a plant type × topography 2-way interaction), effects were examined separately by plant type and by topographic characterization. Where main effects were detected, a Student-Newman-Keuls (SNK) post hoc test was used to distinguish effects. Because high variability in faunal abundances may obscure subtle patterns in faunal distribution, Friedman's test (Posey & Ambrose 1984, Holland et al 1987) was used to examine general trends in rank abundance of fauna among macrophyte types or topographic regimes. This test examines the hypothesis that, on a whole-community scale, the species in the site will consistently have higher rank abundance in one macrophyte type or under a certain topographic regime. Friedman's test was conducted separately for each season. Principal components analysis (PCA) was used to determine if samples were grouped by macrophyte type, topographic regime, elevation or site. PCA was conducted using the SAS statistical package (SAS Institute 1990), and a biplot was constructed from the first 2 eigenvectors (De'ath 1999). Wards minimum cluster analysis was used to detect significant groupings of samples (De'ath 1999, Posey et al. 2002).

RESULTS

Sediment and chlorophyll a characteristics

As reflected by percent silt and clay composition (Fig. 3), sediment grain size did not differ among vari-

ous macrophyte types, topographic features, or marsh elevation. All sediments were dominated by fine sands. However, percent organics was affected significantly by topography ($F = 6.02$, $p < 0.023$) and an interactive effect between topography and macrophyte type ($F = 5.68$, $p < 0.027$). Percent organics was greater in *Phragmites* hummock subsites compared to *Phragmites* rivulet or *Spartina* subsites (rivulet or hummock). *Phragmites* and *Spartina* rivulet subsites did not differ significantly in percent organics nor did *Spartina* rivulet and hummock subsites (Fig. 3). A significant site × macrophyte interaction ($F = 6.17$, $p < 0.004$) reflected stronger, although still non-significant, macrophyte type influences at MCN ($F = 7.88$, $p < 0.068$) and MCE ($F = 7.36$, $p < 0.074$) compared to MUD ($F = 2.94$, $p <$

Fig. 3. *Phragmites australis* and *Spartina alterniflora* marshes. Percent organic and percent silt fraction for sediments collected from rivulet and hummock areas (averaged over all sites). Bars indicate mean percent (+1 SE)

Fig. 4. *Phragmites australis* and *Spartina alterniflora* marshes. Chlorophyll *a* concentrations in rivulet and hummock areas for April, July and October sampling. Bars indicate means (+SE). Concentrations do not differ among macrophyte type but differ between rivulet and hummock areas for all sampling periods

0.19) and MCS ($F = 1.68$, $p < 0.29$). For both MCN and MCE, higher percent organics occurred in *Phragmites* marshes.

Benthic chlorophyll *a* concentrations differed between rivulet versus hummock subsites for all sampling periods (April, July, October) in both macrophyte types (Fig. 4, April: $F = 28.13$, $p < 0.0001$; July: $F = 9.98$, $p < 0.0043$; October: $F = 5.72$, $p < 0.022$ —MUD and MCN sites only). Chlorophyll *a* concentrations were higher in hummock subsites during April and July, but patterns were reversed in October. No other significant main effects nor any significant interactive effects were detected.

Benthic macro-infaunal patterns

The benthic macro-infaunal community at the 4 paired marsh sites was numerically dominated by a typical mesohaline assemblage, including the polychaetes *Capitella capitata*, *Hobsonia florida* and *Laeonereis culveri*, oligochaetes, insect larvae (especially *Chironomus* spp.), clam (*Cyrenoidea* sp.) and the gastropod *Hydrobia minuta* (Tables 1 & 2). During summer, strong interactions were apparent only for the gastropod *H. minuta*, between topography and macrophyte type (Table 1). *H. minuta* was more common in *Spartina* than in *Phragmites* marshes (Fig. 5), with strongest effects observed in rivulet habitats because of low occurrence of this snail

on the hummocks (Fig. 6). The only other taxa to show significant differences among macrophyte type was the amphipod *Gammarus mucronatus*, which was also more common in *Spartina* marshes. Although differences in abundance for most individual taxa among macrophyte types were not significant, due to high variability in numbers, most taxa had higher overall mean numbers in *Spartina* versus *Phragmites* marshes. Friedman's test indicated a significant overall community trend towards higher rank abundance of fauna in *Spartina* versus *Phragmites* marshes (10 of 12 species more common in *Spartina*: Fig. 5). This test compared rank abundance for all species in *Phragmites* versus *Spartina* marshes to determine if there were a consistent overall pattern in rank abundance for all species considered together.

While there were few differences among macrophyte types for individual taxa, several taxa exhibited differences in abundance related to small-scale topography. *Chironomus* (isopod), *Gammarus mucronatus* (amphipod), *Leptochelia dubia* (tanaid), and *Acarina* (mites) were all more common in hummock than in rivulet microhabitats (Fig. 6). *Hobsonia florida* (polychaete), *Hydrobia minuta* (gastropod), and *Laeonereis* (polychaete) were more common in rivulet areas than in hummock microhabitats. Few differences were observed between high and low tidal areas, but among-site effects were strong for both *Chironomus* and *Cyrenoidea* (bivalve); higher abundances of both species occurred at MUD and MCN sites than at MCE and MCS. Relative abundance between *Phragmites* and *Spartina* marshes for both species was consistent across all sites.

Fig. 5. *Phragmites australis* and *Spartina alterniflora* marshes. Mean faunal densities ($n = 32$, +SE) in July. Significant differences between macrophyte type are indicated above pairs of bars (* $p < 0.05$, *** $p < 0.001$). Friedman's test results are for rank abundance patterns of all species combined, indicating general whole-community trend for greater rank abundance in *Spartina*.

Full specific names as in Table 1

Fig. 6. *Phragmites australis* and *Spartina alterniflora* marshes. Mean faunal densities ($n = 32$, +SE) for rivulet and hummock habitats in July. Significant differences between rivulet and hummock habitats are indicated above pairs of bars (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$). Friedman's test results are for rank abundance patterns of all species combined

Principal components analysis for summer samples revealed 2 major patterns (Fig. 7). The first was dominated by rivulet versus hummock effects, with similar topographies clustering together. The second pattern represented overall site differences, whereby pairs of *Phragmites* and *Spartina* marshes at the MCE and MCS sites tended to separate from those at the MUD and MCN sites. The MCS and MCE sites are both located in the upper part of Marshy Creek (Fig. 1), so the site patterns may reflect estuarine location effects. However, these divisions were weak, with the first 2 components representing only 49.8% of the total variance.

We detected no strong interactions in fall samples (Table 2). Only *Hydrobia minuta* showed significant differences in abundance among macrophyte types; it was more common in *Spartina* than in *Phragmites*

marshes (Fig. 8). Unlike summer, during the fall we did not detect a significant trend towards higher rank abundance in *Spartina* marshes, with only 7 of 12 taxa having higher mean abundance in *Spartina*. The reduced influence of macrophyte-type effects appeared to be related to greater densities (although not significantly so) of several taxa within *Phragmites* stands during fall than in summer (Figs. 5 & 8). Fewer sites in the fall analyses may also have contributed to a decreased ability to detect small-magnitude differences among macrophyte types. An analysis of the summer data, considering only MUD and MCN sites (the sites sampled in fall) indicated higher rank abundance for most fauna in *Spartina*; however, the trend was not significant ($\chi^2 = 1.33$). In the fall, 7 taxa exhibited significant differences among topographic features (Fig. 9). *Chironomus*, *Cyrenoida*, *Gammarus mucronatus*, *Leptochelia dubia* and *Acarina* were more common in hummock than in rivulet habitats (4 of these taxa also showed the same pattern for summer samples). Diptera larvae (excluding *Chironomus* spp.) and *Hydrobia minuta* were more common in rivulet than in hummock microhabitats. As with summer samples, elevation was not associated with strong variations in abundance, and there was little difference in overall abundance between the 2 sites sampled in the fall.

DISCUSSION

Plant-type effects were detectable in this study, but were not strong relative to topographic effects. For the sediment and chlorophyll *a* measurements, only percent

Fig. 7. *Phragmites australis* and *Spartina alterniflora* marshes. Biplot of first 2 principal components for samples separated by species composition. The sample characteristics (macrophyte type and habitat type) indicated by different symbols and groupings were determined by cluster analysis. First component was dominated by habitat type (hummock vs rivulet topography), second component was dominated by site (gradient from MCE/MCS to MUD/MCN)

Fig. 8. *Phragmites australis* and *Spartina alterniflora* marshes. Mean faunal densities ($n = 16$, +SE) in October. Significant differences between macrophyte type indicated above pair of bars (* $p < 0.05$). Friedman's test results are for rank abundance patterns of all species combined

organics displayed a difference among sites, and this only in hummock microhabitats. Among individual macro-infaunal species, only the snail *Hydrobia minuta* (both seasons) and *Gammarus mucronatus* (summer only) showed significant macrophyte-type effects, both being more common in *Spartina* than in *Phragmites* stands. *H. minuta* has previously been found to be uncommon/absent in marshes recently invaded by *Phragmites* (Talley & Levin 2001). Rank tests also indicated a significant trend towards lower rank mean abundance of species in *Phragmites* than in *Spartina* marshes. The results of our study are consistent with others that have found small detectable effects or mixed effects of *Phragmites* invasion on macro-infaunal abundances. In comparisons of macrofauna between *Phragmites* and *Spartina* marshes, Warren et al. (2001) found no direct effect of *Phragmites*, but rather found a correlation with litter that might itself vary with plant type (Windham & Lathrop 1999). Weis & Weis (2000) found little behavioral affinity differences of *Uca pugnax* between *Phragmites* versus *Spartina* in laboratory arenas, although nektonic fishes and decapods displayed some differences. Fell et al. (1998) did not find evidence of differences in macrofaunal prey resources for mummichogs between *Phragmites* and *Spartina* marshes. Talley & Levin (2001) observed shifts in faunal abundance patterns, with several burrowing taxa having reduced abundance and several surface-feeding forms having greater abundances in *Phragmites*-invaded areas than in adjacent

non-invaded areas. These shifts were accompanied by shifts in organic matter and plant biomass. Indirect effects on macrofauna may relate to differential predator abundances among macrophyte types (Able & Hagan 2000), but Meyer et al. (2001) found no significant differences in nekton between *Phragmites* and *Spartina* marshes at our study locations.

There has been considerable concern about potential community changes associated with the spread of *Phragmites* (Havens et al. 1997, Chambers et al. 1999, Rice et al. 2000, Weis & Weis 2000, Talley & Levin 2001). While differences were detectable between paired *Spartina* and *Phragmites* marshes in this study, these differences were not strong, as measured by absolute differences in the mean abundance of species between these plant types as well as the number of taxa exhibiting significant density effects. Although greater replication might have revealed more significant patterns, the influence of macrophyte type was less than that of general site location or microhabitat. A question raised by this and other studies (Fell et al. 1998, Weinstein & Balleto 1999, Able & Hagan 2000, Able et al. 2001, Meyer et al. 2001, Talley & Levin 2001, Warren et al. 2001) is whether such differences represent significant ecological changes. While there were few differences observed in this study for individual taxa, there is evidence for cumulative community differences between *Phragmites*- and *Spartina*-dominated marshes in mesohaline Chesapeake Bay.

Fig. 9. *Phragmites australis* and *Spartina alterniflora* marshes. Mean faunal densities ($n = 16$, +SE) for rivulet and hummock habitats in October. Significant differences between rivulet and hummock habitats are indicated above pairs of bars (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Friedman's test results are for rank abundance patterns of all species combined

In contrast to macrophyte-type effects, small-scale topography had strong effects on macro-infaunal abundance even over the scale of centimeters sampled in this study: 7 of 12 species showed differences between rivulet and hummock areas in summer and 7 taxa also exhibited differences among these habitats in fall (9 taxa overall). Surface-dwelling crustaceans (*Chironomus*, *Gammarus mucronatus*, *Leptochelia dubia*), mites and juvenile bivalves (*Cyrenoida*) were more abundant in hummock than in rivulet areas, whereas polychaetes (*Hobsonia florida*, *Laonereis culveri*), a surface feeding snail (*Hydrobia minuta*), and insect larvae were more numerous in rivulet than hummock areas. Benthic chlorophyll *a* also differed among rivulet and hummock areas, although the pattern changed temporally. Among the major differences between rivulets and hummocks are that hummocks are vegetated, several centimeters higher in elevation, and have root material present, whereas rivulets are unvegetated, lower, and have no root material but some detrital material. Although tidal location can clearly influence marsh macro-invertebrate abundance and species composition (e.g. LaSalle & Bishop 1987, Lin 1999), we did not detect a strong influence of tidal height/distance into the marsh on macrofaunal densities over the ranges examined here, as evidenced by high- versus low-marsh comparisons. Whaley & Minello (2002) suggested that factors affecting predator access, such as distance into a marsh for their Gulf of Mexico marshes, may have greater effects on infaunal abundances over small elevational gradients. Our results suggest that local effects of vegetation presence may be more responsible for the observed differences in faunal abundance patterns. Even on local scales (centimeters), the presence of vegetation may affect immediate sediment deposition and current patterns (Leonard et al. 2002), detrital and sediment organic levels, accessibility to predators (predation pressure), and physical structure. The crustaceans that were more abundant on hummocks have epibenthic foraging habits and may be responding to local structure (reduced predator accessibility), the presence of benthic microalgal food resources near plant stems, and detrital deposits (though there was no significant difference in percent organics between rivulets and hummocks in this study). Small-scale sampling and experimental manipulations of structure would be necessary to determine mechanisms of response.

The results of our study comparing macrophyte influence on benthic macrofauna document the importance of small-scale topographic features in controlling macrofaunal distributions. Topographic features (rivulet vs hummock) on the scale of centimeters common in many marsh systems, along with broad site-location differences, had a greater influence on faunal abun-

dances than macrophyte type. Such small-scale features are often overlooked, or at least not explicitly discussed, in comparisons of marsh systems. These small-scale features may have important influences, and variations in the frequency with which they are sampled among marshes may lead to spurious differences between sites. While topography was similar among marsh types sampled in our study, it may vary between marshes or with dominant macrophyte type. Such features need to be stratified in sampling designs comparing functional attributes of marshes.

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