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Community Structure and Abundance of Benthic Infaunal Invertebrates in Maine Fringing Marsh Ecosystems

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Abstract Fringing marshes are abundant ecosystems that dominate the New England coastline. Despite their abundance, very little baseline data is available from them and few studies have documented the ecosystems services that they provide. This information is important for conservation efforts as well as for an increased understanding of how fringing marshes function compared to larger marsh meadow systems. Benthic infaunal invertebrates were sampled from cores collected from *Spartina alterniflora*-dominated low marsh, *Spartina patens*-dominated high marsh, and *Phragmites australis*-invaded high marsh zones of nine fringing marsh ecosystems in Casco Bay, Maine, USA. Infaunal densities and biomass were generally higher in low marsh than high marsh or *P. australis* cores. Invertebrate community structure was significantly different between low marsh and high marsh and *P. australis* cores, which was attributed to significantly higher pore water salinity, lower organic matter, total plant percent cover, and *S. patens* cover in low marsh zones. There were no differences in invertebrate densities, biomass, or community structure when high marsh and *P. australis* cores were compared. Invertebrate densities and community structure were dominated by oligochaetes in all zones. Oligochaetes were also an important component of infaunal biomass, but the less abundant and larger invertebrates such as green crabs, tanaids, and bivalves were also large contributors to biomass in the low marsh zone. Low marsh invertebrate communities were characterized by significantly higher densities of nematodes, *Nereis virens*, an unidentified oligochaete, the bivalves *Gemma gemma* and *Mya arenaria*, and *Leptochelia rapax*. High marsh invertebrate communities were characterized by higher densities of insects, specifically *Culicoides* sp. ceratopogonid larvae and *Anurida maritima*, as well as an unidentified species of mite. Our results revealed a diverse and abundant infaunal invertebrate community that likely supports similar ecosystem services in fringing marshes as invertebrates in larger marsh meadows.

Keywords Fringing marsh · *Spartina patens* · *Spartina alterniflora* · *Phragmites australis* · Salt marsh · Benthic core · Infaunal invertebrates · Sediment

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Introduction

Fringing salt marshes are a common component of New England coastlines (Jacobsen et al. 1987; Morgan et al. 2009; Roman et al. 2000). Compared to larger *Spartina patens*-dominated marsh meadows, fringing marshes are much smaller in size but have greater edge to area ratios (Morgan et al. 2009). Despite their small size, fringing marshes provide similar ecosystem services to coastal populations of humans as their larger marsh meadow counterparts. Narrow fringing salt marshes that line edges of bays and rivers regulate water quality through the removal of human-induced nitrogen (Tobias et al. 2001; Wigand et al. 2004) and sediment loads (Morgan et al. 2009). These ecosystems can also reduce impacts to coastlines from storm events. *S. patens* dominated fringe marshes reduced wave height by more than 60 %

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(Morgan et al. 2009), while *Spartina alterniflora*-dominated systems reduced mean flow velocities by 40–60 % (Bruno and Kennedy 2000). The latter often resulted in the establishment of diverse beach strand plant communities (Bruno and Kennedy 2000). Fringing marshes also support coastal biodiversity by providing habitat for many species of plants (Morgan et al. 2009), resident and transient nekton (Morgan et al. 2015; Rountree and Able 1992), and marsh birds (Shriver et al. 2004). Fringe marshes likely support abundant and diverse assemblages of benthic infaunal invertebrates that are valuable food resources for higher organisms. However few, if any studies, have documented invertebrate communities in New England fringing or larger marsh meadow ecosystems and what factors influence these communities.

Benthic infaunal invertebrate communities are largely comprised of small invertebrates (i.e., annelids, insects, amphipods) found within or on the sediment of the vegetated marsh surface (Kneib 1984; Rader 1984). Salt marshes are often perceived as supporting nuisance insect species such as mosquitoes, green head flies, and biting no-see-ums. However, salt marshes also support diverse assemblages of insect species that include chironomid midge flies, a salt marsh dragonfly, and a salt marsh caddisfly (MacKenzie 2003; MacKenzie 2005). These diverse invertebrate assemblages support many ecosystems services that marsh ecosystems provide. Marsh invertebrates support provisional services as they are an important food resource for many species of transient and migratory birds and nekton that utilize these habitats (Allen et al. 1994; Deegan and Garritt 1997; MacKenzie and Dionne 2008; Shriver et al. 2004). Many of these fish are of high commercial importance (e.g., winter flounder, American eel, blue fish) (Deegan and Garritt 1997). Benthic macroinvertebrates also indirectly provide food resources by breaking down plant material into more readily available particulate and dissolved food resources for higher trophic groups (Graça et al. 2000). Marsh invertebrates can also support the regulating services provided by plants (e.g., increased water quality, storm protection) by supporting plant growth and community composition. For example, marsh plant productivity can be significantly influenced by top–down control of herbivorous snails and amphipods by predaceous crabs and fish (Pennings and Bertness 2001; Silliman and Bertness 2002), increased oxygen in sediments by burrowing crabs (Andersen and Kristensen 1988), and increased nutrient availability by filter feeders (Bertness 1984; Bertness 1985; Pennings and Bertness 2001).

The nearly 41 ha of fringing salt marsh that make up over 10 % of the Casco Bay shoreline (Morgan et al. 2009) and the majority of marsh habitat found there are expected to provide similar ecosystem services as those described above. A recent report on the status of Casco Bay fringing marshes indicated that while the majority of these marshes are relatively intact, their integrity is threatened from invasive plant species and various human activities (e.g., shoreline development, oil spills, sea level rise) (Hayes et al. 2008). Shifts in hydrological regimes from increased development in this region have altered soil salinity and resulted in the increased spread of both exotic *Phragmites australis* (common reed) (Silliman and Bertness 2004) and *Typha angustifolia* (narrow-leaved cattail) (Burdick et al. 1997), both of which could potentially alter certain habitat values of these ecosystems. For example, significantly lower densities of resident mummichogs (*Fundulus heteroclitus*) have been reported from the surface of *P. australis*-invaded marsh meadows vs. native *S. alterniflora*-dominated ones (Able and Hagan 2000; Able and Hagan 2003; Hunter et al. 2006). Lower densities of larval mummichogs in *P. australis*-invaded marshes were attributed to higher evapotranspiration (ET) rates and litter inputs of *P. australis* compared to *S. alterniflora*. Higher ET rates and increased litter inputs result in fewer water-filled depressions on the marsh surface that provide valuable subtidal refuge for resident fish during low tide (Able and Hagan 2003; Able et al. 2003; Weinstein and Balletto 1999). Invertebrate densities and species richness can also be lower in *P. australis* or *Typha* spp. compared to *S. alterniflora* marshes (Angradi et al. 2001; Gratton and Denno 2006; Talley and Levin 2001; Warren et al. 2002). This was also attributed to reduced standing water and a resulting decrease in microalgal food resources (Angradi et al. 2001). Other studies have reported no changes in biomass, species richness, or overall diversity in invertebrate communities in *P. australis*-invaded marshes (Fell et al. 1998; Warren et al. 2001; Yuhas 2001).

The main objectives of this project were to 1) document the benthic infaunal invertebrate community structure, biomass, and densities in Casco Bay fringe marshes and 2) to determine if these invertebrate parameters differed between high and low fringing marsh areas or between exotic and native plant assemblages. This information also provided a much needed baseline data set that could be used to assess how infaunal communities may change after natural (e.g., hurricane) or human-induced disturbances (e.g., oil spill). Impacts from oil spills are of special concern as Casco Bay is the largest oil port in Northern New England (Hayes et al. 2008). Invertebrate assemblages were compared between high and low marsh zones of nine different fringing marshes. Two of these sites included high marsh areas with established populations of exotic *P. australis*. We hypothesized that invertebrate community structures, biomass, and densities would differ 1) between high and low marsh areas due to differences in plant communities and hydrological influences on sediment properties and 2) between exotic and native high marsh due to homogenization of the marsh surface by high growth of and litter inputs from invasive *P. australis*.

Materials and Methods

Study Design

Thirty-two fringing marsh sites were initially identified along the coastline of Casco Bay, Maine, USA based upon access, marsh condition, unaltered hydrology (e.g., no ditching), and landscape (i.e., distinct low and high marsh areas). Of these 32 sites, seven sites were then randomly selected for sampling (Fig. 1; Appendix 1). Two additional sites were also identified for sampling that had been invaded by *P. australis*. Average elevations of each site ranged from 1.4±0.5 to 4.3±0.4 m (Appendix 1), which were determined by measuring the height of nine random points stratified across each marsh zone within each marsh. Height was then measured relative to a known vertical datum (NAVD88) using Topcon laser surveying equipment. Marsh areas ranged from 910 to 7800 m^2 and were determined by delineating study boundaries using a Geo Explorer GPS receiver, converting boundaries to polygons and then calculating the area. Low marsh areas at each site were dominated by *S. alterniflora*, while high marsh areas of non-invaded sites were dominated by *S. patens* (P. Morgan, unpublished data).

Invertebrate Sampling

Invertebrates were sampled over a 2-day period in June, July, and August of 2002 and 2003. Samples were collected within a 2-h window before and after slack low, spring tides. Sample areas were first randomly selected from within the low marsh, high marsh, and *P. australis*-invaded zones of each of the nine fringing marsh study sites. One person would stand at the marsh ecotone interface (e.g., low marsh-mudflat), look down-slope from the marsh ecotone (e.g., at the mud flat), and throw a flagged rock behind their shoulder. Benthic infaunal invertebrates were then sampled using a 7.7-cm diameter stove pipe corer (Merritt et al. 1984, Turner and Trexler 1997) haphazardly placed in vegetated areas within 1-m from the labeled rock. Triplicate cores were collected from each vegetated zone by carefully inserting the stove pipe corer approximately 20 cm into the marsh surface. Cores were then carefully removed from the marsh surface, extruded on site, and any vegetation present on the surface of the core was carefully removed by clipping. The remaining top 4 cm of the cores were then collected and returned to the lab where they were preserved in a mixture of 90 % formalin and Rose Bengal stain. The top 4 cm were sampled because this is where benthic infaunal invertebrate activity can be the greatest (Rader 1984).

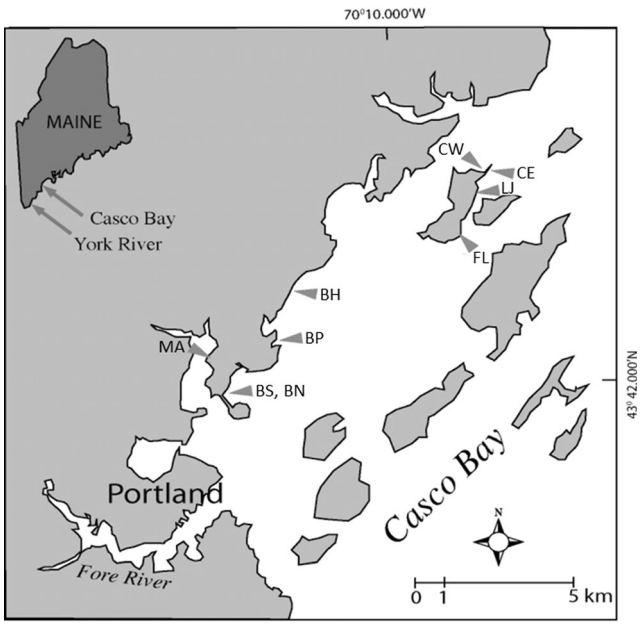

Fig. 1 Map of Casco Bay, Maine, USA showing the nine fringing marshes where benthic infaunal invertebrates were sampled. The BN and BS sites were the two *P. australis*-invaded sites

Preserved core samples were later broken up in the lab and washed through nested 2.0 (coarse) and 0.5-mm (fine) sieves. Sediment material was evenly distributed across the bottom of each sieve and a PVC partition was inserted into the sieve that divided the sieve into four equal quadrats. Two quadrats were then randomly selected from both the coarse and fine sieves for a total of four quadrats. Benthic infaunal invertebrates were then sorted from each quadrat and identified to the lowest practical taxon (Gosner 1971; Merritt and Cummins 1996; Pennak 1953). After a sample had been sorted, it was verified by a second person to ensure that all invertebrates had been successfully removed. For soft-bodied invertebrates that had broken apart (i.e., polychaetes, oligochaetes), only heads were removed from samples and counted. Widths of the fifth setigers were measured from polychaetes and oligochaetes, while total lengths of all remaining invertebrates were measured to the nearest 0.1 mm. Densities (no/m^2) were calculated by first multiplying the total number of invertebrates by two to correct for the quadrats and then divided by the area of the core sampler (46.6 cm^2). Dry biomass (mg) was estimated from either length:mass regressions (Benke et al. 1999; Bouma et al. 2009; Devine and Vanni 2002; Jackson et al. 1985; Kneib 1992; Kristensen 1984; Riisgård et al. 2003; Sabo et al. 2002; Sardá et al. 1995a; Stoffels et al. 2003; Westerbom et al. 2002; Frauendorf, unpublished data) or average biomass values of individuals (Clough et al. 1997; Warwick and Price 1979). Biomass values (mg/m^2) were then calculated following the procedure described above for densities. Invertebrate species richness, evenness (Pielou's *J'*), and diversity (Shannon–Wiener *H'*) were determined using the DIVERSE function in the Primer statistical package (v. 6.1.9 2007) (Clarke 1993) .

Soil Analysis

In July of 2002, an additional core was taken from each site. The top 4 cm of the cores were extruded and returned to the lab where they were weighed, oven dried for 48 h at 60 °C, and then reweighed. Porosity was determined using the following formula:

$$\text{Porosity} = \frac{1}{\left(1 + \text{mass}_{\text{dry}}/2.45 \times \text{mass}_{\text{wet}}\right)} \quad (1.1)$$

where 2.45 represented the density of the soil sample (MacKenzie 2001; Plaster 2013). Bulk density was determined by dividing the total dry mass of the 4 cm core by the total volume of the 4 cm core analyzed. Core samples were then ground into a fine powder using a mortar and pestle and a 0.5-g subsample was combusted at 500 °C for 4 h. Percent organic content was then determined by the loss of mass on ignition.

Soil pore water was extracted once a month from June–August of 2002 and 2003 using soil lysimeters made of 1/4″ PVC pipe inserted into the marsh to a depth of 15 cm. Holes drilled in the PVC allowed water from 10 to 15 cm below the soil surface to enter the lysimeter. The salinity of the water extracted was then determined using a non-temperature-compensated standard refractometer. Salinity values were then averaged across months within each year.

Plant Sampling

The relative abundances of each of the higher plants were assessed once at each site in July of 2002. Nine sampling points were established within each site in a stratified random manner, according to the proportion of high to low marsh. The point intercept method (Morgan et al. 2009; Roman et al. 2001) was then used at each sampling point to determine abundance and percent cover of individual species in 1 m^2 quadrats. Total, *S. patens*, and *S. alterniflora* percent cover were determined by summing up the cover for all plants, *S. patens*, and *S. alterniflora*, respectively, in the low, high, and *P. australis*-dominated marsh sites. Plant species richness, evenness (Pielou's *J′*), and diversity (Shannon–Wiener ′) were determined using the DIVERSE function in Primer 6 (Clarke 1993).

Statistical Design

Invertebrate densities and biomass were first compared across months to determine if there were any significant differences over time using a one-way analysis of variance (ANOVA). Average monthly densities were then compared across marsh zone (high, low), site, and year using a three-way factorial ANOVA. Fixed effects of the model included marsh zone, site, and year, along with all interactions. Average monthly densities were also compared between *P. australis*-invaded and *S. patens*-dominated high marsh areas in both of the invaded sites using a similar three-way factorial ANOVA. Fixed effects for this model included marsh type (invaded vs. native), site, and year, along with all interactions. Densities and biomass of individual invertebrate species that made up at least 5 % of the total invertebrate community were compared across sites and year using a two-way ANOVA. All invertebrate and plant diversity indices, as well as soil and plant parameters, were compared among sites using a one-way ANOVA.

Invertebrate community compositions were compared across marsh zone (high, low, *P. australis*) and year (2002, 2003) using non-metric multi-dimensional scaling (NMDS) and a two-way analysis of similarity (ANOSIM) in PRIMER statistical package (v. 6.1.9 2007) (Clarke 1993). Invertebrate community composition was also compared between *P. australis*-invaded and *S. patens*-dominated marsh cores from the two invaded marshes (Baxter North - BN and Baxter South - BS). A Bray–Curtis similarity matrix was first created from log $(x+1)$-transformed invertebrate densities. NMDS then ordinated sites based upon similarities into a two-dimensional space. Patterns of similarity and the factors responsible for those patterns were visually explored using cluster analyses set at resemblance levels of 20, 40, 60, and 80 % and by changing the factor levels of data points (zone, year). A two-way ANOSIM was then used to statistically compare levels of similarity between zones and years. Species responsible for those differences were identified using a similarity of percentage (SIMPER) procedure in PRIMER 6, which measures dissimilarity by making pairwise comparisons of invertebrate densities between zones and year. Species were then ranked in order of their percent contribution to dissimilarity.

Relationships between invertebrate community structures and environmental variables (marsh area, % organic matter content, porosity, soil bulk density, pore water salinity, total % plant cover, % *S. alterniflora* cover, % *S. patens* cover, number of plant species, plant species richness, Shannon–Wiener plant diversity) were examined using the BIO-ENV routine in PRIMER 6. BIO-ENV uses Spearman rank correlation to calculate dissimilarity between Bray–Curtis and Euclidian similarity matrices created from log $(x+1)$-transformed invertebrate densities and square root-transformed environmental variables.

A power analysis was also conducted on invertebrate densities to determine how effective the three cores, and thus our study design, would be at detecting change in invertebrate densities after a major disturbance. The analysis was only done on the 2002 data set as this had a complete data set with three cores from almost every zone, site, and month. Analyses were run using a sample statistic set at 2 from the *t*-distribution for the 95 % confidence interval and the level of change to be detected ranging from 10 to 100 %.

Total and individual invertebrate densities, biomass, salinity, and Shannon–Weiner values did not meet assumptions of normality and equal variance and were transformed (log+1) prior to analysis. Total plant, *S. patens*, and *S. alterniflora* percent cover were arcsine transformed. All data presented in tables, figures, and text are the average values and standard errors. All post hoc analyses were conducted using the Tukey–Kramer method and all ANOVAs were performed in PROC MIXED from SAS 9.1 (2002. SAS Institute, Cary, NC) at an alpha level of 0.05.

Results

Invertebrate Densities

Initial examination of invertebrate densities and biomass across the 3 months sampled could only be conducted on data from 2002 due to the fact that several cores from 2003 had been thrown out (Appendix 1). Because there were no significant differences across months in 2002, we assumed that the use of monthly samples as replicates would provide a robust comparison among individual sites, between marsh zones (high vs. low), and between years (2002 vs. 2003). Average invertebrate densities were significantly different across sites (Fig. 2; $p<0.01$, $F_{8,\ 50}=3.11$). Tukey's post hoc comparison of least squares means revealed that this difference was due to significantly lower invertebrate densities at the Baxter South (BS) site versus Baxter North (BN) ($p<0.01$, $F_{8,\ 52}=14.4$) and Maine Audubon (MA) ($p<0.01$, $F_{8,\ 52}=13.4$); invertebrate densities did not significantly differ across all other sites (Fig. 2). Invertebrate densities averaged (±1 SE) across sites and years were higher in low marsh zones (45,900±4800 no/m^2) than high marsh zones (36,400±4100 no/m^2), which was nearly significant ($p=0.06$, $F_{1,\ 44}=8.01$). This was the general trend when low vs. high marsh zones were compared across individual sites each year (Fig. 2). Invertebrate densities were generally greater in 2003 (45,000±5600 no/m^2) than 2002 (38,400±3500 no/m^2), although this was not significant.

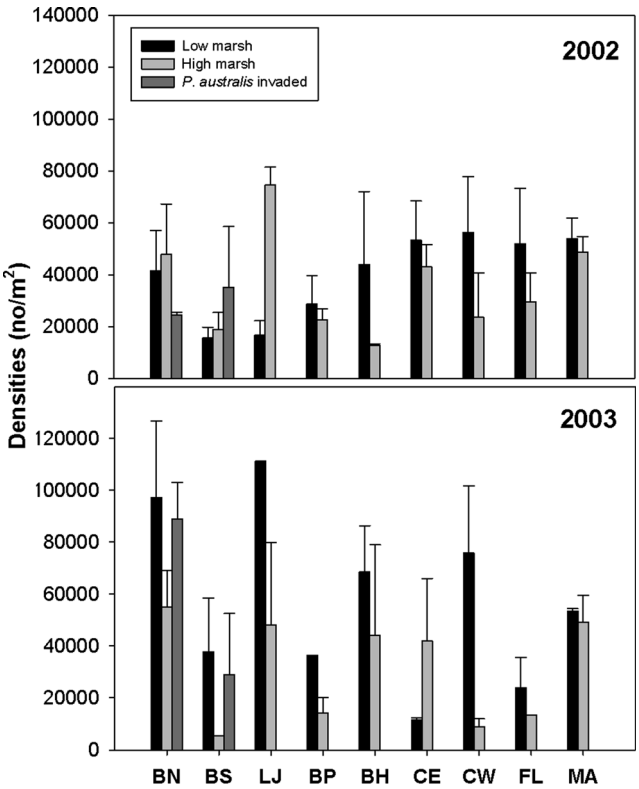

Fig. 2 Average (±1 SE) invertebrate densities from the low marsh, high marsh, and *P. australis*-invaded zones across all nine sites that were sampled from Casco Bay in 2002 and 2003

Average invertebrate densities did not significantly differ between cores from *P. australis*-invaded and adjacent *S. patens*-dominated high marsh areas (Fig. 2). In 2002, average invertebrate densities were higher from *S. patens*-dominated high marsh (37,500±11,000 no/m^2) than *P. australis*-invaded areas (23,300±6300 no/m^2). In 2003, the opposite trend was observed, with average invertebrate densities higher from *P. australis*-invaded areas (40,000±24,300 no/m^2) than *S. patens*-dominated high marsh (22,800±3900 no/m^2).

Invertebrate densities in high marsh areas were dominated by oligochaetes (Naididae, Tubificidae, Oligochaete F, Oligochaete G), which contributed an average of 73.6 % (range 41.9–89.9 %) of total invertebrate abundance from sediment cores in 2002 and 47.1 % (range 7.6–87.1 %) in 2003 (Appendix 2 and 3; Fig. 3). Oligochaetes were also the dominant invertebrate in low marsh areas and comprised an average of 67.8 % (range 26.8–98.7 %) in 2002 and 44.0 % (range 1.0–84.1 %) of invertebrate densities. Oligochaete G had significantly higher densities in low marsh than high marsh or *P. australis* cores ($p<0.01$, $F_{2,\ 32}=6.08$). Densities of Tubificidae were not significantly different across sites but were significantly greater in 2002 than 2003 ($p<0.05$, $F_{1,\ 32}=6.4$). There were no differences across sites or between years for Naididae or Oligochaete F. Other invertebrates that contributed to at least 5 % of total invertebrate abundance in decreasing order of contribution included the following: nematodes, the tanaid *Leptochelia rapax*, the insects *Culicoides* sp. and *Anurida maritima*, the polychaetes *Nereis virens* and *Manyunkia speciosa*, the bivalves *Gemma gemma* and *Mya arenaria*, and the mite species C. Nematodes, *N. virens*, *G. gemma*, *M. arenaria*, and *L. rapax* all had significantly higher densities in low marsh than high marsh or *P. australis* cores ($p<0.05$, $F_{2,\ 32}=3.58$; $p<0.001$, $F_{2,\ 32}=24.33$; $p<0.01$, $F_{2,\ 32}=6.42$; $p<0.001$, $F_{2,\ 32}=6.21$; $p<0.001$, $F_{2,\ 32}=8.8$, respectively). The biting midge, *Culicoides* sp., and mite C had significantly higher densities in high marsh and *P. australis* cores than low marsh cores ($p<0.001$, $F_{2,\ 32}=10.48$; $p<0.01$, $F_{2,\ 32}=5.41$, respectively). None of these species densities were

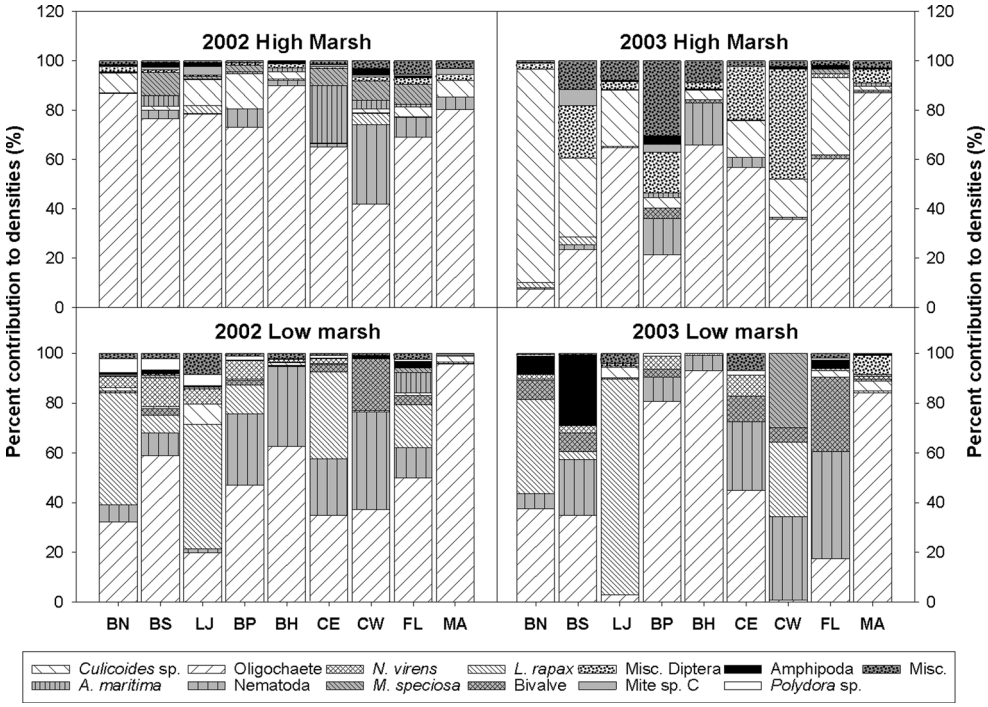

Fig. 3 Stacked bar graph showing the invertebrates that contributed to 5 % or more of the community composition in the low and high marsh zones from 2002 and 2003

significantly different between years. Densities of *A. maritima* were not significantly different across sites but were significantly greater in 2002 than 2003 ($p<0.05$, $F_{2,\ 32}=6.4$; $p<0.01$, $F_{2,\ 23}=7.4$, respectively). There were no differences across sites or between years for *M. speciosa*.

The number of invertebrate species, species richness, evenness (*J'*), and Shannon–Wiener (*H'*) did not significantly differ among sites (Table 1). The number of species and species richness was significantly higher in 2002 than 2003 ($p<0.01$, $F_{1,\ 32}=9.34$ and $p<0.01$, $F_{1,\ 32}=9.19$, respectively). All other invertebrate diversity parameters were similar between years.

Variability in invertebrate densities was quite high across zones, sites, and years (Fig. 2). Results from the power analysis conducted on core data from 2002 revealed that the ability to detect a change within 10, 20, or 50 % of the mean invertebrate densities would require 142±15, 36±4, or 6±1 cores, respectively.

Invertebrate Biomass

Average invertebrate biomass values were significantly different across sites (Fig. 4; $p<0.05$, $F_{8,\ 48}=2.21$). Tukey's post hoc comparison of least squares means revealed that this

Table 1 Average (±1 SE) invertebrate diversity measures from cores taken from the high, low, and *P. australis*-invaded marsh in 2002 and 2003

Metric	Low marsh	High marsh	*P.australis*
2002			
Number of invertebrate species**	17.5±1.3	21.4±2.6	16±4
Invertebrate species richness**	1.9±0.2	2.3±0.3	1.8±0.5
Evenness (Pielou's *J'*)	0.5±0	0.4±0	0.3±0
Shannon–Wiener (*H'*)	1.5±0.2	1.1±0.1	0.9±0.2
2003			
Number of invertebrate species	9.7±1.4	13.9±1.9	14±0
Invertebrate species richness	1±0.2	1.5±0.2	1.5±0.1
Evenness (Pielou's *J'*)	0.5±0.1	0.5±0.1	0.4±0
Shannon–Wiener (*H'*)	1.2±0.2	1.3±0.2	1.2±0.1

There were no significant difference across sites

Asterisks after taxa names mean significant differences between years

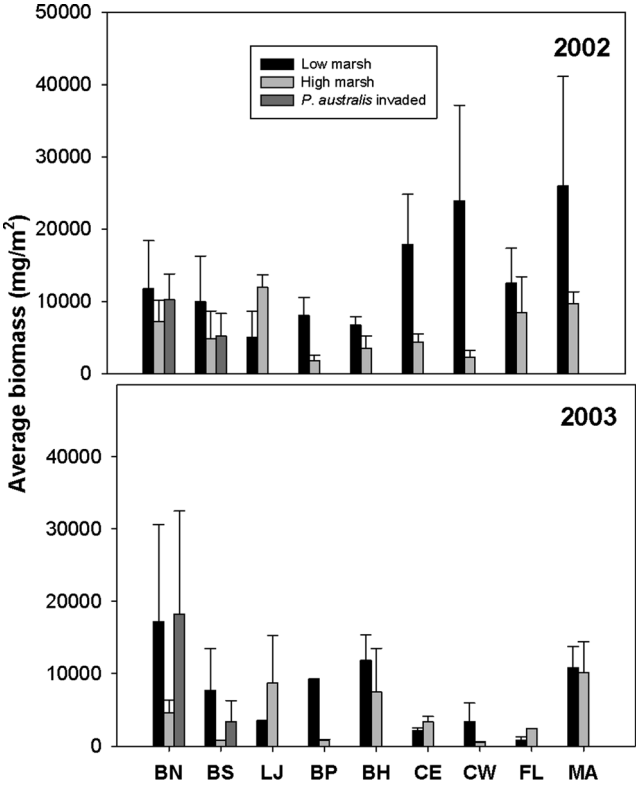

Fig. 4 Average (±1 SE) invertebrate biomass from the low marsh, high marsh, and *P. australis*-invaded zones across all nine sites that were sampled from Casco Bay in 2002 and 2003

difference were only due to significantly higher invertebrate biomass values at Baxter North (BN) site compared to Cornfield West (CW) ($p<0.05$, $F_{8,\ 52}=4.4$) and at Maine Audubon (MA) compared to Bartlett Point ($p<0.05$, $F_{8,\ 52}=6.3$), Cornfield West ($p<0.05$, $F_{8,\ 52}=9.9$), and Ferry Landing ($p<0.05$, $F_{8,\ 52}=9.6$). Invertebrate biomass did not significantly differ across all other sites (Fig. 4). Invertebrate biomass averaged (±1 SE) across sites and years was significantly and 2× greater in low marsh areas (11,200±1900 mg/m^2) than high marsh zones (5500±800 mg/m^2) ($p<0.01$, $F_{1,\ 52}=8.3$). Average invertebrate biomass was also significantly higher in 2002 (10,000±1500 mg/m^2) than in 2002 (5800±1100 mg/m^2) ($p<0.01$, $F_{1,\ 52}=8.6$).

Average invertebrate biomass values were generally higher from *P. australis*-invaded areas than adjacent *S. patens*-dominated high marsh areas (Fig. 4), but this trend was not significant. In 2002, average invertebrate biomass values (±1 SE) were higher from *P. australis*-invaded areas (7800±2400 mg/m^2) than *S. patens*-dominated high mash areas (6000±2200 mg/m^2). In 2003, average invertebrate biomass values (±1 SE) were again higher in *P. australis*-invaded areas (10,800±7300 mg/m^2) than *S. patens*-dominated high marsh (3100±1300 mg/m^2).

Invertebrate biomass in high marsh areas was dominated by oligochaetes, contributing an average of 88.9 % (range 64.8–98.8 %) of the total invertebrate biomass from sediment cores in 2002 and 85.3 % (range 48.2–97.6 %) in 2003 (Fig. 5). Invertebrate biomass in low marsh areas was also dominated by oligochaetes, but only contributed an average of 67.8 % (range 26.8–98.7 %) in 2002 and 60.3 % (range 8.7–99.7 %). Oligochaete biomass averaged across sites and years was significantly greater in low marsh and *P. australis*-invaded areas than high marsh areas ($p<0.001$, $F_{2,\ 34}=70.7$). Other invertebrates contributing to at least 5 % of biomass in cores included amphipods, *A. maritima*, bivalves, *Carcinus maenus*, coleopterans, *Culicoides* sp., *L. rapax*, miscellaneous dipteran species, and *N. virens*. *L. rapax* and *N. virens* biomass was significantly greater in low marsh areas than either high marsh or *P. australis*-invaded areas ($p<0.001$, $F_{2,\ 34}=17.1$ and $p<0.001$, $F_{2,\ 34}=54.6$, respectively). Amphipoda and *Culicoides* sp. biomass were significantly higher in *P. australis* than high marsh areas ($p<0.01$, $F_{2,\ 34}=5.3$ and $p<0.01$, $F_{2,\ 34}=6.4$, respectively). Bivalve's biomass was significantly greater in low marsh areas than high marsh areas ($p<0.001$, $F_{2,\ 34}=11.9$). Coleoptera biomass was significantly greater in high marsh areas than low marsh areas ($p<0.05$, $F_{2,\ 34}=3.3$). *C. maenus* was not different among sites. None of these species biomass values were significantly different between years.

Invertebrate Community Structure

Invertebrate assemblages from the majority of core samples clustered into two distinct groups at the 45 % similarity level at a stress value of 0.19 (Fig. 6), although there were five outliers. While this stress value is moderately high (e.g., >0.1) and influenced the ordination, the patterns observed were still considered to provide a useful and relatively unbiased interpretation of the ordination (Clarke 1993). Visual examination of year and site revealed that site was more influential in structuring invertebrate community assemblages, with low marsh and the combination of high marsh and *P. australis* sites clustering into two distinct larger groups (Fig. 6). Oligochaetes were the most abundant invertebrates in low, high, and *P. australis* cores. Species from the Naididae family represented 40.5, 69.8, and 75.8 % of all invertebrates from low, high, and *P. australis* cores, respectively, in 2002. In 2003, Naididae represented 35.2, 47.2, and 46.6 % of invertebrates from low, high, and *P. australis* cores, respectively, in 2003. Lower percent contributions by Naididae were due to higher densities and thus increased percent contribution by *Culicoides* sp. ceratopogonid larvae, which represented 1.0, 27.2, and 37.7 % of invertebrates from low, high, and *P. australis* cores, respectively, in 2003.

Invertebrate community structure significantly differed across low marsh, high marsh, and *P. australis* cores (ANOSIM, $R=0.50$, $p<0.01$). This was due to significant differences between high and low marsh cores ($R=0.60$, $p<0.01$)

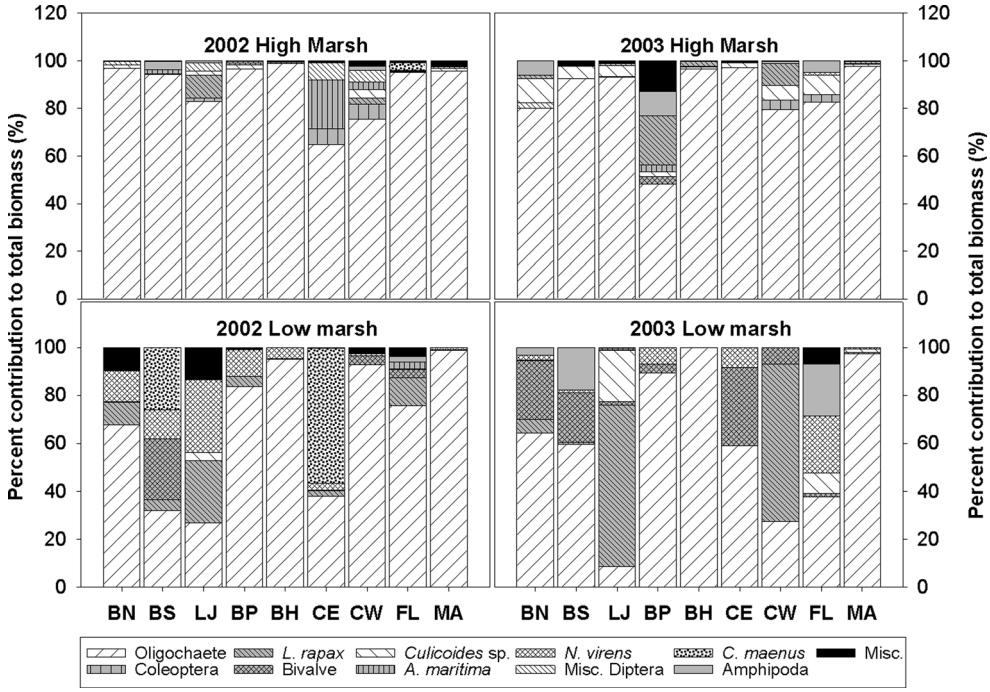

Fig. 5 Stacked bar graph showing the invertebrates that contributed to 5 % or more of invertebrate biomass in the low and high marsh zones from 2002 and 2003

and between *P. australis* and low marsh cores (R=0.58, p<0.05). There were no significant differences between high marsh and *P. australis* cores. Higher densities of polychaetes (*N. virens*, *Polydora* sp.), oligochaetes (Tubificidae, oligochaete sp. C), amphipods (*L. rapax*), bivalves (*M. arenaria*, *G. gemma*), and nematodes in low marsh cores accounted for nearly 30 % of the difference between high and low marsh. Higher densities of dipterans (*Culicoides* sp., dolichopodid flies, various dipteran pupae), springtails (*A. maritima*), *M. speciosa* polychaetes, and mite sp. C in high marsh cores accounted for 16 % of the difference between high and low marsh cores. Similar patterns were observed between low marsh and *P. australis* cores. Invertebrate community assemblages were also weakly but significantly different between 2002 and 2003 (R=0.38, p<0.01). Higher average densities of oligochaetes, amphipods (*L. rapax*, *Hyale* sp.), *M. speciosa*, nematodes, and *Culicoides* sp. flies in 2002 accounted for 35 % of differences observed between years.

With the exception of pore water salinity, all environmental parameters were only measured in 2002. However, it was assumed that these parameters (e.g., percent organic matter, plant species richness) would not differ significantly across years. Therefore, values from 2002 were also used for 2003 in the BIO-ENV routine. Salinity and total plant percent cover

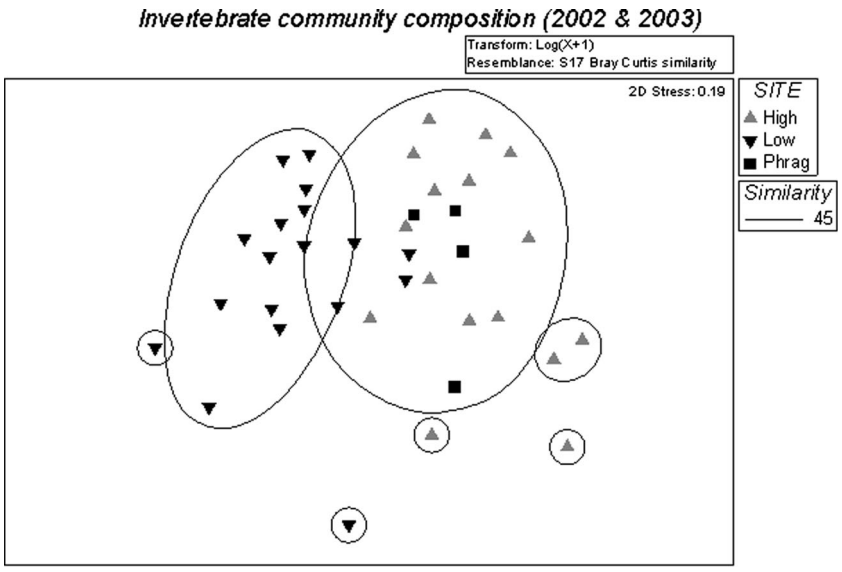

Fig. 6 Nonmetric multidimensional scaling plots (NMDS) of invertebrate communities from core samples collected from low marsh, high marsh, and *P. australis* zones. Marsh zone (low vs. high) clustered data into two distinct large groups at the 45 % similarity level

were the best environmental variables that were weakly, but significantly correlated to the observed invertebrate community composition (ρ=0.24, p<0.05). The next two best environmental variables were percent soil organic matter (ρ=0.24) and *S. patens* percent cover (ρ=0.23).

Soil Analyses

Percent organic content was significantly higher while pore water salinity was significantly lower in high marsh and *P. australis* cores compared to low marsh cores (Table 2) (p<0.001, $F_{2,\ 16}$=10.84 and p<0.001, F=10.49, df=2, respectively). Porosity was also higher in high marsh and *P. australis* cores compared to low marsh cores, while bulk density was higher in *P. australis* cores compared to high or low marsh cores. Neither of these patterns was significant.

Plant Community Structure

Total plant cover was generally higher in high marsh and *P. australis* zones compared to low marsh zones (Table 2). *S. patens* cover was highest in high marsh areas, while *S. alterniflora* was highest in low marsh areas. *S. alterniflora* cover was the only response variable that was significantly affected by zone as a factor (p<0.001, $F_{2,\ 16}$=24.6). Total number of plant species, species richness, and diversity (H') were all significantly higher in high marsh areas than *P. australis* areas (Table 2) (p<0.05, $F_{2,\ 16}$=5.56; p<0.05, $F_{2,\ 16}$=5.52; p<0.01, $F_{2,\ 16}$=7.0, respectively). Evenness (J') was significantly higher in high marsh areas than low marsh or *P. australis* areas (p<0.01, $F_{2,\ 16}$=8.0). These parameters were also generally higher in high marsh than low marsh areas, although these trends were not significant.

Discussion

Densities and biomass of invertebrates from fringe marsh cores reported here (5300–127,000 no/m^2 and 320–55,000 mg/m^2) were within the range of densities and biomass reported from other larger marsh meadows along the southern Atlantic and Gulf coasts (Bell 1979; Jackson et al. 1985; Kneib 1984; Plante-Cuny et al. 1993; Rader 1984; Sardá et al. 1995b; Whaley and Minello 2002). Similar values between our sites and larger marsh meadows suggests that fringing marsh ecosystems could provide an important feeding area for transient and resident fish species that access these ecosystems at high tide (Deegan et al. 2000; MacKenzie and Dionne 2008; Weisberg and Lotrich 1982). Indeed, many of the same species reported using larger marsh meadows were observed leaving our study sites with the receding tides during this study (Morgan et al. 2015). Many of the invertebrates that were abundant in our cores (e.g., oligochaetes, polychaetes, aquatic insects) have been found in the gut contents of fish known to access the marsh surface during high tide (Burdick et al. 1997; Haas et al. 2009; James-Pirri et al. 2001; Weisberg et al. 1981). These invertebrates also likely provide an important food resource for birds, crabs, and shrimp (Kneib and Stiven 1982; MacKenzie 2005). This underscores the potential ecological importance of a relatively understudied component of fringing marsh ecosystems commonly found along New England coastlines. Cores from high marsh *S. patens* and *P. australis* areas were dominated by infaunal assemblages of oligochaetes (49.4–87.4 %) and dipteran larvae (7.9–39.1 %), while cores from low marsh *S. alterniflora* zones were dominated by assemblages of oligochaetes (39.8–51.3 %) and *L. rapax* (17.0–23.2 %). Invertebrate densities and biomass were generally higher from low marsh

Table 2 Average (±1 SE) soil and plant metrics from the high, low, and *P. australis*-invaded marsh in 2002 and 2003

	Low marsh	High marsh	*P. australis*
Area (m^2)	1880±240	1640±550	2510±0
% Organic content	*0.03*±0.01^{b}	*0.13±0.01*^{a}	*0.13±0.08*^{a}***
Porosity	0.0029±0.0004	0.0004±0.0037	0.0037±0.002
Bulk density (mg/L)	0.77±0.14	0.77±0.09	0.86±0.51
Salinity (2002)	*27.9±2.3*^{b}	*14.8±2.6*^{a}	*8.9±0*^{a}***
Salinity (2003)	*25.5±2.2*^{b}	*15.4±4.0*^{a}	*8.3±0*^{a}***
% *S. alterniflora* cover	*69.7±5.5*^{b}	*14.1*±7.6^{a}	*0.0±0.0*^{a}***
% *S. patens* cover	7.5±3.6	22.6±10.2	0.0±0.0
Total plant cover	90.8±5.3	108.1±12.1	100±0.0
Plant species richness	*0.7±0.2*^{ab}	*1.0±0.1*^{a}	*0.0±0.0*^{b}*
Evenness (Pielou's J')	*0.5±0.2*^{a}	*0.6±0.1*^{b}	*0.0±0.0*^{a}**
Total plant species	*4.3±0.8*^{ab}	*5.8±0.4*^{a}	*1.0±1.0*^{b}*
Shannon–Wiener (H')	*0.6±0.2*^{b}	*1.1±0.1*^{b}	*0.0±0.0*^{a}**

Italicized values indicate significant differences across sites determined using a two-way ANOVA (*p<0.05, **p<0.01, ***p<0.001), and different letters indicate significant Tukey's post hoc comparisons

cores than high marsh or *P. australis* cores; high marsh cores generally had more species and higher species richness compared to low marsh cores. Thus, marsh zone (i.e., high vs. low) appeared to play an important role in structuring invertebrate assemblages between both high marsh *S. patens* and *P. australis* and low marsh *S. alterniflora* areas. These general trends only partially supported our first hypothesis that invertebrate communities would significantly differ between high and low marsh zones. Our second hypothesis that there would be differences between invertebrate densities, biomass, or community structure from high marsh *S. patens* and *P. australis* cores was rejected due to lack of significant results.

Influence of Marsh Zonation on Invertebrate Community Structure

Marsh zonation was expected to have a large influence on the abundance, biomass, and community composition of invertebrates in fringing marsh ecosystems. Higher densities of invertebrates have previously been reported from the marsh edge (e.g., near the marsh–water interface) than marsh interior in both freshwater (Cardinale et al. 1997; MacKenzie and Kaster 2004; MacKenzie et al. 2004) and saltwater ecosystems (Kneib 1984; MacKenzie 2005; Rader 1984). This pattern has been attributed to the marsh–water interface receiving higher rates of deposited food resources, larval invertebrate recruitment, and inundation from adjacent open waters (Kneib 1984; Kneib and Stiven 1982; MacKenzie et al. 2004; Rader 1984). Alternatively, this has been attributed to higher rates of predation in the marsh interior (Kneib and Stiven 1982) as well as desiccation that results from less frequent tidal inundation of higher elevations (Kneib 1984).

The lack of significant differences in overall fringe marsh invertebrate densities across marsh zones was likely due to differences observed in invertebrate community composition. For example, the patterns reported by Kneib (1984) were largely driven by nematodes, whose contributions to overall invertebrate densities decreased from 80.7 % in the marsh edge to 4.6 % in the marsh interior. Nematode densities were also significantly lower in our high marsh *S. patens* and *P. australis* cores compared to low marsh *S. alterniflora* cores. However, lower nematode densities in high marsh cores were replaced by higher densities of oligochaetes and various dipteran larvae (Appendix 2 and 3; Fig. 3), a pattern that differed from those reported by Kneib (1984). This discrepancy could be explained by the fact that Kneib was comparing invertebrate communities across a *S. alterniflora*-dominated marsh, while we were comparing invertebrate communities between high (*S. patens*-dominated) and low (*S. alterniflora*-dominated) marsh zones that not only varied in plant community structure but also in hydrological regime influenced by marsh elevation (e.g., flooding frequency) (Bertness and Ellison 1987). The significant correlation between pore water salinity and invertebrate community composition suggests that, of the parameters we measured, salinity was the strongest driver influencing invertebrate community composition. Salinity has been shown in other studies to be an important factor influencing invertebrate community composition (Arnold and Ormerod 1997; Kneib 1984; Quintino et al. 2011). Certain invertebrate species in the high marsh areas, particularly dipterans, likely had higher densities than the low marsh because they are less-adapted to the higher pore water salinity conditions that were observed in the lower marsh areas (MacKenzie 2005). Salinity also influenced invertebrate community composition within three European reed swamps. In this study, saline sites supported higher densities of fewer invertebrate species, while lower saline sites had lower densities of speciose assemblages dominated by insects (Arnold and Ormerod 1997). Finally, the lack of differences we observed between zones could have been due to the high variability we observed in infaunal densities across sites. This was likely influenced by the differences in marsh elevation among our sites as well as their physical location along the coast. For examples, some sites were well protected, while others were more exposed to storm and tidal surge which could have impacted infaunal communities.

Percent organic content was another factor we measured that significantly influenced invertebrate structure. Significantly higher percent organic content in high marsh cores were partially due to higher rates of organic matter buildup (i.e., roots and stems of marsh plants) and lower rates of decomposition in high marsh compared to low marsh areas (Bricker-Urso et al. 1989; Ellison et al. 1986). Lower percent soil organic matter from low marsh cores was also attributed to higher deposition of heavier inorganic material compared to organic matter that occurs at the marsh–water ecotone (Bricker-Urso et al. 1989; Morgan et al. 2009; Stumpf 1983). This suggests that deposition of suspended organic material from inundating tidal waters was also greater in the low marsh zone. This would provide food resources for the higher densities of omnivorous polychaetes (*N. virens*) as well as surface-deposit feeding amphipods (*L. rapax*) (Kneib 1992) and other polychaetes (*Spiophanes* sp., *Streblospio benedicti*, *Manyunkia aesturina*) (Montagna 1984; Nielson et al. 1995; Rader 1984) we observed in the low marsh zone. Suspended particles in inundating tidal water would also provide important food resources for *G. gemma* and *M. arenaria*, two filter feeding bivalves that had higher densities in the low marsh than the high marsh, although this was only significant for *G. gemma* in 2003 and *M. arenaria* in 2002.

Marsh vegetation was also identified as an important factor influencing invertebrate community structure. Community structure of invertebrates has been correlated to increased plant cover/structural complexity in other marsh ecosystems (Batzer 2013; Braga et al. 2009; DeSzalay and Resh 2000; MacKenzie 2005; Sueiro et al. 2012). The *S. patens* vegetation that dominated our high marsh zones likely provided

above- and belowground tertiary structure that could have influenced fringing marsh infaunal invertebrate community structure. Aboveground, *S. patens* tiller densities and heights are significantly denser and higher, respectively, compared to *S. alterniflora* (Bertness and Ellison 1987; Buchsbaum et al. 2009). This increased plant structural complexity may have positively influenced invertebrate community structure through provision of food (Campeau et al. 1994) or protection from predation (Compte et al. 2011; Dionne and Folt 1991; Schriver et al. 1995). Plant structure can also provide shelter from extreme temperatures or desiccation either directly (Bertness and Leonard 1997; Canepuccia et al. 2007) or indirectly though the provision of materials to build protective retreats (e.g., caddisfly cases) (MacKenzie 2005). Finally, several species of insects (e.g., culicids, ephydrids, syrphids) prefer to oviposit in marsh areas with dense plant cover (DeSzalay and Resh 2000). This would have influenced invertebrate community composition, resulting in the higher densities of insect larvae observed in the high marsh zone.

The significant higher infaunal biomass in the low marsh compared to the high marsh or *P. australis* zones was due to the contribution of larger and heavier organisms that were not as abundant as the lighter oligochaetes, polychaetes, and nematodes. Therefore, these results do not necessarily indicate a greater food supply in the lower marsh, only those larger organisms (e.g., green crabs (*C. maenus*), tanaiads (*L. rapax*), bivalves) contributed more to total infaunal biomass in the cores that we collected. Despite the fact that these animals typically represented <5 % of invertebrate abundances, their heavy carapace and shells resulted in higher contributions to total infaunal biomass.

Invertebrate Communities in *P. australis*-Invaded High Marsh

The invasion of *S. alterniflora* and *S. patens* marshes by *P. australis* has resulted in altered marsh elevation, substrate, and hydrology (Osgood et al. 2003). As a result, we expected to see differences in benthic infaunal invertebrate community composition, densities, and biomass based on the influence of plant structure on invertebrate communities discussed above. However, we saw no differences in any of these invertebrate metrics when *S. patens* high marsh cores were compared to *P. australis* high marsh cores from the Baxter North and South fringing marshes. Similar results have been reported from other studies that have compared epifaunal and infaunal invertebrate communities between *P. australis* and *S. alterniflora* (Fell et al. 1998; Posey et al. 2003; Warren et al. 2001; Yuhas 2001) or *T. angustifolia* (Yozzo and Osgood 2013). Our results, coupled with results from these studies, suggest that *P. australis* is having a minimal impact on abundance, biomass, and diversity of benthic infaunal and epifaunal invertebrate communities. A recent meta-analysis suggested that impacts of *P. australis* on resident fauna varies by region and habitat (Dibble et al. 2013). The greatest negative impacts occur in the mid-Atlantic, but not New England, where we conducted our study. Greater impacts to mid-Atlantic marshes were due to two potential mechanisms. First, *P. australis* invasion of mid-Atlantic marshes are in a later invasional stage compared to New England marshes. Second, the lower salinities of mid-Atlantic study sites (<16 ppt) compared to New England sites (>16 ppt) may have contributed to greater spread of *P. australis* in the mid-Atlantic (Dibble et al. 2013). They also found that nekton appeared to be more impacted by *P. australis* invasion than invertebrates. Posey et al. (2003) reported that, while there were no obvious differences when benthic invertebrates were compared between *S. alterniflora* and *P. australis* cores, there were differences within sites when microhabitats were compared. They suggest that future studies include small-scale topographic features to minimize variance in comparisons.

Conclusion

Our study was one of the first studies to document benthic infaunal invertebrate communities in fringing marsh ecosystems, a dominant coastal habitat throughout New England (Morgan et al. 2009; Roman et al. 2000). Casco Bay fringing marsh ecosystems provide important habitat for an abundant and diverse assemblage of benthic infaunal invertebrates residing within marsh sediments. Salinity, soil organic matter, and plant community structure were important factors influencing invertebrate communities in fringing marshes. Our data also underscored the need to protect and preserve fringing marsh ecosystems from long-term (e.g., coastal development) and short-term (e.g., oil spills) impacts that could negatively impact marsh invertebrate communities and the many ecosystem services that these invertebrates provide. While the support of ecosystem services by infaunal invertebrates has yet to be documented from fringing marshes, studies from larger marsh meadows have shown that benthic invertebrates play important roles in organic matter decomposition (D' Avanzo and Valiela 1990; Valiela et al. 1985), nutrient and organic matter cycling (Boyer and Fong 2005), marsh sediment oxygenation (Gribsholt et al. 2003), and provision of food resources for many species of resident and transient fish species (Allen et al. 1994; Deegan et al. 2000; MacKenzie and Dionne 2008; Weisberg and Lotrich 1982). Similar services are expected to be provided by fringing marsh ecosystems.

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Appendix 1

Table 3 Average elevations (elev.) (±1 SE) and areas of the nine fringing marshes (site name abbreviation)

Site	Elev. (m)	Area (m^2)	2002			2003		
			June	July	Aug	June	July	Aug
Baxter North (BN)	4.2±0.8							
Low marsh		1300	3	3	3	3	–	1
High marsh		2500	3	3	3	2	1	1
P. australis			3	3	3	2	1	–
Baxter South (BS)	4.2±0.8							
Low marsh		1300	3	3	3	3	–	1
High marsh		2500	2	3	3	3	1	–
P. australis			3	3	3	2	2	–
Little John (LJ)	3.0±0.7							
Low marsh		2600	3	3	3	–	–	1
High marsh		5200	3	3	3	1	1	1
Bartlett Point (BP)	3.3±0.3							
Low marsh		2600	3	3	3	2	–	–
High marsh		1700	3	3	3	3	–	1
Boat House (BH)	2.9±0.3							
Low marsh		2800	–	3	3	1	1	–
High marsh		980	–	3	3	2	–	1
Cornfield East (CE)	2.2±0.3							
Low marsh		1300	3	3	3	2	–	–
High marsh		130	2	3	3	2	1	–
Cornfield West (CW)	1.5±0.4							
Low marsh		2200	3	3	3	1	1	–
High marsh		180	3	3	3	3	1	–
Ferry Landing (FL)	3.0±0.4							
Low marsh		2100	3	3	3	2	1	1
High marsh		1500	3	3	3	2	–	–
Maine Audubon (MA)	3.6±0.2							
Low marsh		880	3	3	3	2	–	1
High marsh		30	3	3	3	3	1	–

Triplicate cores were collected in June, July, and August of 2002 and 2003 from the low and high marsh zones in all nine sites; triplicate cores were also collected from *P. australis*-invaded marsh zones in two of the sites. Numbers represent the numbers of sediment cores successfully processed and should equal three. Lower numbers were due to cores that had been lost when we moved between labs

Appendix 2

Table 4 Average (±1 SE) invertebrate densities (no/m^2) from cores taken in 2002 from the high, low, and *P. australis*-invaded marshes

Taxa	Average (±1 SE) invertebrate densities (no/m^2)		
	Low marsh	High marsh	*P. australis*
Protista			
Foraminifera	–	260±130 (0.7)	–
Cnidaria	30±20 (0.1)	20±20 (0)	–
Platyhelminthes			
Turbellaria	–	10±10 (0)	–

Table 4 (continued)

Taxa	Average (±1 SE) invertebrate densities (no/m^2)		
	Low marsh	High marsh	*P. australis*
Nemertea	30±20 (0.1)	–	–
Nematoda	*7100±2200* (*18.0*)[a]	*1100±330* (*2.8*)[ab]	*100±50* (*0.4*)[b]*
Annelida			
Clitellata	–	20±20 (0.1)	–
Oligochaete sp. E	70±40 (0.2)	100±60 (0.3)	–
Oligochaete sp. F	640±270 (1.6)	70±50 (0.2)	200±2005 (0.9)[ns]
Oligochaete sp. G	*1200±610* (3)[a]	*100±50* (*0.3*)[b]	*50±50* (*0.2*)[b]**
Oligochaete sp. H	540±190 (1.4)	410±130 (1.1)	240±50 (1)
Naididae	16,000±4400 (40.5)	27,000±6100 (72.5)	18,000±600 (75.8)[ns]
Tubificidae*	1800±500 (4.6)	1100±230 (2.8)	2200±710 (9.5)[ns]
Polychaeta	810±400 (2.1)	70±60 (0.2)	20±20 (0.1)
Nereididae			
Nereis virens	*970±280* (*2.5*)[b]	*30±30* (*0.1*)[a]	–[a]***
Sabellidae			
Manayunkia speciosa	160±100 (0.4)	1100±400 (3)	20±20 (0.1)[ns]
Spionidae	50.0±20 (0.1)	–	–
Spiophanes sp.	100±90 (0.3)	–	–
Streblospio benedicti	180±120 (0.4)	–	–
Mollusca			
Bivalva	220±110 (0.6)	–	–
Gemma gemma	*630±610* (*1.6*)[b]	–[a]	–[a]**
Modiolus modiolus	20±20 (0.1)	–	–
Mya arenaria	*750±370* (*1.9*)[b]	–[a]	–[a]***
Gastropoda	15±10 (0)	6±6 (0)	–
Arthropoda	–	50±50 (0.1)	–
Araneae	–	9±8 (0)	20±20 (0.1)
Acarina	10±10 (0)	70±60 (0.2)	50±50 (0.2)
Mite sp. A	–	30±10 (0.1)	20±20 (0.1)
Mite sp. C	*20±20* (*0*)[a]	*510*.0±*300* (*1.4*)[b]	*50±50* (*0.2*)[a]*
Malacostraca			
Amphipoda	30±30 (0.1)	60±50 (0.2)	140±140 (0.6)
Corophium sp.	180±140 (0.4)	–	–
Rivulogammarus sp.	30±20 (0.1)	6±6 (0)	–
Hyale sp.	40±10 (0.1)	260±120 (0.7)	170±170 (0.7)
Maera danae	10±7 (0)	–	–
Isopoda	10±10 (0)	–	–
Jaera sp.	5±5 (0)	40±40 (0.1)	–
Tanaidacea			
Leptochelia rapax	*6600±2500* (*17*)[b]	*300±260* (*0.8*)[a]	–[a]***
Insecta	10±10 (0)	–	50±0 (0.2)
Coleoptera	–	20±20 (0.1)	–
Elodes sp.	–	10±7 (0)	–
Collembola			
*Anurida maritima***	520±470 (1.3)	1500±1200 (3.9)	120±70 (0.5)[ns]
Diptera	15±10 (0)	190±120 (0.5)	20±20 (0.1)
Ceratopogonidae	10±7 (0)	100±50 (0.3)	–
Bezzia sp.	–	30±20 (0.1)	50±50 (0.2)

Table 4 (continued)

Taxa	Average (±1 SE) invertebrate densities (no/m^2)		
	Low marsh	High marsh	*P. australis*
Culicoides sp.	*490±180 (1.3)*[b]	*2500±870 (6.7)*[a]	*2000±1020 (8.7)*[a]***
Chironomidae	–	90±80 (0.2)	50±0 (0.2)
Dolichopodidae	15±10 (0)	100±50 (0.3)	20±20 (0.1)
Tabanidae	–	6±6 (0)	–
Tabanus sp.	10±10 (0)	50±303 (0.1)	–
Hemiptera	–	10±10 (0)	–
Homoptera	–	20±10 (0.1)	–
Total	39,000±14,000 (100)	37,500±11,000 (100)	23,000±6300 (100)

Values in parentheses represent percent contribution of that species, family, or order to the overall invertebrate community from that area. Italicized values indicate significant differences across sites determined using a two-way ANOVA (*p<0.05, **p<0.01, ***p<0.001), and different letters indicate significant Tukey's post hoc comparisons. Asterisks after taxa names mean significant differences between years (Table 2)

Appendix 3

Table 5 Average (±1 SE) invertebrate densities (no/m^2) from cores taken in 2003 from the high, low, and *P. australis*-invaded marshes

Taxa	Average (±1SE) invertebrate densities		
	Low marsh	High marsh	*P. australis*
Protista			
Foraminifera	–	120±80 (0.5)	210±210 (0.5)
Platyhelminthes			
Turbellaria	–	–	50±50 (0.1)
Nematoda	*7000±3600 (15.8)*[a]	*1100±600 (5)*[ab]	*160±160 (0.4)*[b]*
Clitellata	290±290 (0.6)	–	–
Oligochaete sp. F	50±50 (0.1)	30±30 (0.1)	1600±1600 (4.1)[ns]
Oligochaete sp. G	*820±560 (1.9)*[a]	–[b]	*50±50 (0.1)*[b]**
Oligochaete sp. H	–	60±50 (0.2)	–
Naididae	15,600±5600 (35.2)	10,900±3800 (47.7)	18,600±6900 (46.6)[ns]
Tubificidae*	890±600 (2)	350±190 (1.5)	2200±1900 (5.4)[ns]
Polychaeta	200±100 (0.4)	120±120 (0.5)	–
Nereis virens	*700±220 (1.6)*[b]	*30±25 (0.1)*[a]	*50±50 (0.1)*[a]***
Manayunkia speciosa	3500±3500 (7.9)	60±40 (0.3)	160±160 (0.4)[ns]
Mollusca			
Bivalva	20±20 (0)	–	–
Gemma gemma	*860±460 (1.9)* [b]	*30±30 (0.1)*[a]	–[a]*
Modiolus modiolus	10±10 (0)	50±50 (0.2)	–
Mya arenaria	*1500±660 (3.3)*[b]	*80±40 (0.4)*[a]	*50±50 (0.1)*[a]***
Gastropoda	140±140 (0.3)	70±60 (0.3)	–
Arthropoda	140±130 (0.3)	40±40 (0.2)	50±50 (0.1)
Araneae	–	30±30 (0.1)	50±50 (0.1)
Acarina	–	170±110 (0.8)	–
Mite sp. A	–	30±30 (0.1)	–
Mite sp. C	–[b]	*130±70 (0.5)*[a]	*50±50 (0.1)*[a]**

Table 5 (continued)

Taxa	Average (±1SE) invertebrate densities		
	Low marsh	High marsh	*P. australis*
Amphipoda	60±60 (0.1)	170±130 (0.7)	430±430 (1.1)
Corophium sp.	1500±970 (3.4)	10±10 (0)	–
Isopoda			
Jaera sp.	10±10 (0)	–	–
Tanaidacea			
Leptochelia rapax	*10,300±5100 (23.2)*[b]	*160±100 (0.7)*[a]	–[a]***
Insecta	–	590±480 (2.6)	210±210 (0.5)
Coleoptera	–	60±50 (0.3)	–
Collembolan	–	–	50±50 (0.1)
*Anurida maritima***	20±20 (0.1)	100±60 (0.5)	–[ns]
Diptera	–	1500±1100 (6.4)	320±320 (0.8)
Ceratopogonidae			
Bezzia sp.	290±290 (0.6)	–	–
Culicoides sp.	*430±220 (1)*[b]	*6300±3800 (27.7)*[a]	*15,100±13,700 (37.7)*[a]***
Chironomidae	–	–	270±270 (0.7)
Dolichopodidae	50±50 (0.1)	450±170 (2)	270±50 (0.7)
Tabanidae	–	30±30 (0.1)	–
Hemiptera	–	40±30 (0.2)	–
Total	44,300±9600 (100)	22,800±3900 (100)	40,000±24,300 (100)

Values in parentheses represent percent contribution of that species, family, or order to the overall invertebrate community from that area. Italicized values indicate significant differences across sites determined using a two-way ANOVA (*$p<0.05$, **$p<0.01$, ***$p<0.001$), and different letters indicate significant Tukey's post hoc comparisons. Asterisks after taxa names mean significant differences between years (Table 1)

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