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RESEARCH ARTICLE

Local-scale characteristics of high-marsh communities next to developed and undeveloped shorelines in an ocean-dominated estuary, Murrells Inlet, SC

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Abstract Anthropogenic alteration of terrestrial shorelines can have pronounced effects on marine environments at the upland-marsh boundary. Possible terrestrial development effects on several physical and biological variables of high-marsh habitats were examined along developed and undeveloped shorelines in an ocean-dominated, southeastern US estuary. Analyses of sediment characteristics suggested development of the upland boundary affected physical conditions within the high-marsh. For example, pore water salinities were greater along undeveloped shorelines during a non-drought period even after rain events. Significant floral and faunal differences also existed between shoreline treatments. Black needle rush stems were significantly taller and marsh periwinkle densities significantly greater, but eastern coffee bean snail densities were significantly reduced along developed shorelines. Benthic infaunal community abundance and composition also were significantly different between shoreline treatments with sand fly larvae, human pest precursors, either only present or present in greater densities along developed shorelines. Sediment respirometry experiments indicated significant differences in heterotrophic and autotrophic processes occurring between shoreline treatments. Greater sediment surface temperatures along developed shorelines provided one possible mechanism driving high-marsh responses to boundary alteration. The history and extent of shoreline development along with a tendency in ocean-dominated southeastern marshes to resist change likely influenced current ecological conditions within our high-marsh study areas. A greater understanding of the driving mechanisms producing localized effects on salt marshes and recognizing regional differences in marsh resistance to change will facilitate predictions of shoreline development consequences and help in proposing effective management strategies for coastal boundaries.

Keywords Benthic respiration · High-marsh · Insect larvae · *Juncus roemerianus* · Shoreline development · Wetland boundary

Introduction

The coastal transition zone (CTZ) is a critical environmental boundary or interface between terrestrial/freshwater and marine systems (e.g., Levin et al. 2001; Talley et al. 2003). Disproportionate to the limited aerial extent globally, the coastal region including the CTZ provides an extensive range of necessary human and ecosystem services (Costanza et al. 1997). Similar to most boundaries (Gosz 1992; Wiens et al. 1985; Yarrow and Marín 2007), the CTZ is defined primarily by abrupt physical gradients (e.g., salinity) and changes in material flux (e.g., nutrients) that occur over local, 10s of meters, to landscape scales, 100s of kilometers. For example, in the southeastern USA, a typical local-scale species gradient from the glycophytic *Morella cerifera* (wax myrtle) to the halophytic *Spartina alterniflora* (cord grass) is contained within the landscape scale gradient between the terrestrial watershed and contiguous estuarine environment. Within estuarine river

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systems, faunal compositions are dependent on changes in two opposing gradients, one from freshwater to marine and the other from marine to freshwater (Attrill and Rundle 2002), which produce a dynamic boundary within estuaries that moves up- and down-stream with changes in climate. Increasingly, both natural and anthropogenic boundaries are recognized as profoundly influencing ecosystem dynamics (e.g., Cadenasso et al. 2003; Ries et al. 2004). Both the alteration of natural boundaries (e.g., removal of native vegetation) and creation of anthropogenic boundaries (e.g., highways, seawalls) are dependent on human activities. Worldwide, coastal environments are being transformed into human-dominated habitats creating and altering boundaries at an increasing rate (Beach 2002). In the USA >50% of the population lives or works within coastal counties (Vernberg et al. 1992), and future population growth along the South Atlantic Bight (e.g., North Carolina, South Carolina and Georgia) is expected to exceed that of all other regions (Bricker et al. 1999). The anticipated population-driven development and resultant changes to terrestrial-marine boundaries could significantly affect one of the region's most ecologically and economically important habitats, the estuarine salt marsh.

Previous research along the eastern USA coast typically has examined the effects of landscape-scale terrestrial development within associated tidal creeks and bays. Nutrient (Mallin et al. 2000a; Valiela and Bowen 2002; Lewitus et al. 2004; White et al. 2008), fecal coliform (Mallin et al. 2000b; DiDonato et al. 2009), and phytoplankton changes in water quality (White et al. 2004) all have been attributed to watershed development. Differences in tidal creek sediment characteristics (Sanger et al. 1999a, b; Van Dolah et al. 2008) and benthic faunal communities (Lerberg et al. 2000; Bilkovic et al. 2006) also have been correlated to landscape-scale change resulting from suburban, urban and industrial alterations of coastal watersheds. Although less studied, local development of the terrestrial-marine boundary also can affect adjacent marine habitats (Wigand et al. 2001; Bertness et al. 2002; Pennings et al. 2002; Silliman and Bertness 2004; Bertness and Silliman 2008; Gedan et al. 2009; Wigand et al. 2010). In the rapidly developing Southeastern USA coastal region, both unknown local- and well-studied landscape-scale changes (e.g., Lerberg et al. 2000; Holland et al. 2004; Lewitus et al. 2004) are likely to have major affects on the terrestrial-marine boundary and adjacent marsh habitats.

Direct, local-scale development of the terrestrial-marine boundary may affect a variety of high marsh physical and biological characteristics. Removal of natural vegetation as a result of shoreline stabilization, suburban landscaping, or other development could alter thermal regimes, surface and below-ground water movements, nutrient and organic inputs, and other factors that contribute to the flux between terrestrial and marine environments. Small scale horizontal differences in high-marsh temperatures resulting from alterations to the thermal environment, such as changes in shading, can influence heat stress levels experienced by intertidal organisms (Jost and Helmuth 2007). Altered anthropogenic nutrient inputs can affect salt marsh plant productivity and benthic microbial activity (Morris 1991; Kiehl et al. 1997; Levine et al. 1998; Morris and Bradley 1999; Van Wijnen and Bakker 1999; Sundareshwar et al. 2003; Hines et al. 2006; Deegan et al. 2007). Nutrient additions also can alter typical patterns of plant zonation and modify normal competitive interactions and community structure (Levine et al. 1998; Emery et al. 2001; Bertness et al. 2002; Pennings et al. 2005; Crain 2007; McFarlin et al. 2008; but also see Brewer 2003). Even the community structure of marsh fauna may be influenced by elevated nutrient inputs (Vince et al. 1981; Stiven and Kuenzler 1982; Silliman and Zieman 2001; Denno et al. 2003; but also see Meany et al. 1976). Anticipated differences in freshwater flux during precipitation events (e.g., Corbett et al. 1997; Wahl et al. 1997) may result in changes in sediment pore-water salinities that affect plant production (Mendelssohn and Morris 2000) and community structure (Pennings and Callaway 1992). Separate from the landscape-scale effects of watershed development, alteration of the terrestrial-marine boundary likely will have major consequences for the dynamics of high-marsh environments.

This paper focuses on identifying the physical (e.g., sediment organic content, pore water salinity, surface temperature) and biological parameters (e.g., plant biomass and richness, macrofauna density and composition, benthic respiration) of a typical southeastern USA high-marsh community that may be affected by development of the associated terrestrial shoreline. Landscape-scale effects are factored out by stratifying selection of developed and undeveloped shorelines within a single marine-dominated estuary surrounded by a watershed of limited aerial extent. Development effects on the high-marsh associated with both barrier land spits and mainland areas were measured. Shoreline development was expected to increase the flux of freshwater and nutrients as in previous studies (Wahl et al. 1997; Bertness et al. 2002; Silliman and Bertness 2004), which would lead to increased autotrophic and heterotrophic production and potentially alter floral and faunal community structure. Results provide the first extensive study of local-scale terrestrial development effects on the high-marsh environment in a region experiencing rapid population growth and increasing terrestrial-marine boundary alteration.

Methods

Study area

The study was conducted within the ocean-dominated estuary of Murrells Inlet, South Carolina (33:32.7′ N, 79:2.7 W) where salinities average > 30 ppt (Blood and Vernberg 1991). Within the inlet, approximately equal semidiurnal tides, mean 1.37 m, vary in timing, ca. 30 min delay, but not height of high tide from north to south. Freshwater input is restricted to a relatively small, local watershed (ca. 35.5 km^2) without major riverine influence. Mainland drainage into the estuary can be divided into eight sub-basins, some of which are emptied by small creeklets (Tufford et al. 2003). The estuary covers ca. 26.7 km^2 between the barrier land spits and mainland, almost half of which is salt marsh. A primary inlet stabilized by the construction of two weir jetties in 1977 splits the estuary roughly in half. The cities of Murrells Inlet and Garden City are located on the estuary and have a combined population of 14,876 individuals (2000 USA census). Murrells Inlet housing density in 2000 was 165.8 units km^{-2}. Surrounding Georgetown and Horry County populations have increased by up to 36.5% between 1990 and 2000 (1990 and 2000 USA census). Huntington Beach State Park, an 1,100 ha undeveloped area, forms the southern boundary of the inlet.

Regional rainfall averages 138.4 cm year^{-1} with 115 days year^{-1} of precipitation, but surrounding counties experienced intermittent drought conditions throughout the study period. The South Carolina Department of Natural Resources, Land, Water, and Conservation Division, State Climate Office declared statewide severe to extreme drought conditions ended in April 2003, 2 months prior to the study's start. Incipient drought conditions were declared for Georgetown and Horry counties in June 2004 and downgraded to normal in July 2004. Reduced rainfall amounts from 12 to 25 cm below normal between September and November 2004, encompassing the study's last sampling dates, prompted a November 2004 advisory but no declaration of drought conditions. Average daily temperatures range from a low of 2.3°C in January to a high of 32.4°C in July.

The position of terrestrial-wetland boundary locations ($n = 8$) studied within Murrells Inlet are shown in Fig. 1. Location names, inlet position, development status including type and approximate time since development, coordinates, and sampling dates are found in Table 1. All boundary locations were selected primarily based on a visual assessment of CTZ development status. Undeveloped locations ($n = 4$) were identified by the presence of an extensive overhang of trees and dense stand of shrubs, typically consisting of native oaks (e.g., *Quercus virginiana*), wax myrtle (*Morella cerifera*), yaupon (*Ilex vomitoria*), and southern red cedar (*Juniperus silicicola*)

Fig. 1 Map of South Carolina indicating location of Murrells Inlet (inset), and Google® satellite image of inlet showing sampling locations. Refer to Table 1 for location abbreviations

Table 1 Murrells Inlet locations names, position within the inlet, developmental status including type and approximate age, geographic coordinates, and sampling dates for the current study

Location name (code)	Inlet position	CTZ Status (type/age)	Latitude	Longitude	Dates sampled			
					06/03	10/03	03/04	9/04
Sara J's (SJMD)	Mainland	Developed (Housing/>10 years)	33:34:55.8	79:00:09.9			X	X
MI Road (MRMD)	Mainland	Developed (Road/>10 years)	33:31:46.1	79:03:37.9			X	X
Oyster Recycle (OMD1)	Mainland	Developed (Housing+/<5 years)	33:31:17.4	79:03:53.4	X	X	X	X
Oyster Recycle (OMU1)	Mainland	Undeveloped	33:31:22.0	79:03:48.5	X	X	X	X
Oyster Recycle (OMU2)	Mainland	Undeveloped	33:31:21.4	79:03:49.6			X	X
Huntington (HBMU)	Mainland	Undeveloped	33:30:39.8	79:04:11.6			X	X
Marlin Quay (MQID)	Barrier	Developed (Housing+/>10 years)	33:33:04.0	79:01:10.9		X		
Huntington (HBIU)	Barrier	Undeveloped	33:30:50.1	79:03:22.5		X		

(Fig. 2, top). Developed locations ($n = 4$) had >90% of the boundary vegetation removed (Fig. 2, bottom), including native trees and shrubs that often were replanted with grass or cultivated shrubbery when the type of development was residential housing. A contiguous length (ca. 50 m) of shoreline and high marsh unbroken by tidal creeks, without an upland berm, and with a minimum of 0.2 km of salt marsh between open water and the shoreline boundary was selected at each location. Selection of developed locations with consistently similar characteristics was hampered by a lack of accessible, multiple shorelines of sufficient length within Murrells Inlet having the same extent (>90% of natural vegetation removed), type (e.g., residential, commercial), and age of boundary alteration. The extent of shoreline development did not vary among developed locations, but differences in the type and age of development (Table 1) could affect our results and conclusions (see "Discussion").

Fig. 2 Comparison of undeveloped (top HBIU) and developed (bottom MQID) terrestrial-marsh boundaries from the Murrells Inlet barrier island spit location. Images were taken from the salt marsh facing eastward towards the boundary and upland area

Wetland areas adjacent to the terrestrial boundary at each location consisted of salt marsh species typical of southeastern USA high intertidal elevations; black needle rush (*Juncus roemerianus*), salt hay (*Spartina patens*), marsh elder (*Iva frutescens*), and sea oxeye (*Borrichia frutescens*). Marsh samples from each location were collected from an area <50 m long, to avoid possible edge effects at the ends of developed or undeveloped boundaries, and <15 m wide, to remain in close proximity to the CTZ. All salt marsh areas sampled were shoreward of the short *S. alterniflora* zone in the high marsh just adjacent (<15 m) to the terrestrial boundary. Additionally, in October 2003, samples were collected from within *J. roemerianus* stands located directly adjacent to the boundary to reduce potential variation associated with sampling within a mixed plant community.

Variables sampled

Various physical and biological variables were sampled between June 2003 and September 2004, but data for all variables were not collected at all locations on all dates (Table 1). Sample variation and boundary status effects initially were evaluated in June 2003. Based on June results, a more extensive study was conducted in October 2003 to document boundary treatment differences. Follow-up samples in March and September 2004 were collected to examine significant or unexplained results from the October 2003 study or additional variables. Differences among dates likely affected the variables sampled but not the proportional effects of boundary development on the variables. Only data from individual sampling dates were analyzed statistically to minimize any potential to confound date with boundary development effects (see "Analyses").

Up to five plots (0.25 m^2) were positioned haphazardly within the ca. 50 by 15 m sampling area at each developed and undeveloped boundary location. All snails, exclusively *Littoraria irrorata* and *Melampus bidentatus*, were collected and a haphazard subsample of stem heights ($n = 20$) was measured from each plot. Live and standing-dead plant stem densities were enumerated from one 0.0625 m^2 sub-plot within each plot. Plant biomass was determined by removing all above-ground material from each sub-plot, determining dry mass (60°C for 4 days), and calculating ash-free dry mass (AFDM) after loss from ignition (450°C for >4 h). Within the same high-marsh elevation, sediments were sampled ($n = 5$) using a 2.1 cm diameter corer to a depth of 5 cm. Individual cores, either whole or divided into 0–2 and 2–5 cm sections (June 2003 only), immediately were frozen at −20°C for later determination of pore water salinity and sediment grain size and organic content. Pore water salinity (ppt) was measured both in the lab and field. Salinities in the lab were calculated by adding 20–30 ml of distilled water to a thawed sediment sample, repeatedly agitating over 48 h, allowing the sediment to settle, measuring the supernatant salinity with a refractometer, and correcting for dilution. Field salinities were measured using an YSI 85 salinometer within 2–3 surface wells dug to a depth of 30 cm at each site. Sediment grain sizes were determined by measuring the dry mass of wet-sieved standard soil size fractions. The sediment organic content or AFDM (mg g^{-1}) was calculated as the difference between sediments dried at 60°C and then ashed at 450°C for >4 h. An additional five sediment cores were collected using a 2.1 cm diameter corer to a depth of 5 cm to identify benthic infauna. Core samples were preserved with 10% formaldehyde, processed on a 500-μm sieve in the lab, and all organisms identified to major taxon and enumerated.

Sediment samples for benthic respiration incubations were collected in a 10.2 cm diameter acrylic corer to a depth of 3 cm. Only at the barrier island location, three sites 0.0625 m^2 in area were selected haphazardly within developed and undeveloped locations. At each site, three sediment cores were collected and mixed mechanically, any root or rhizome material removed, and dispensed into 250-ml acid-washed Pyrex glass bottles. Sediments were slurried with the addition of 30% by volume of either 0.45 μm filtered seawater (control), filtered seawater with 20 μM nitrogen as ammonium sulphate and 1.25 μM phosphorus as sodium diphosphate, or filtered seawater with 200 μM glucose. Samples were placed within a Percival climate controlled chamber at 28°C and incubated under either light or dark conditions. Benthic respiration measurements were collected multiple times ($n = 4$) during the 3 h incubation using a Columbus Instruments 30 channel respirometer.

Sediment surface temperatures were determined during a 2-week period in September 2004 using HOBO® and Stowaway Tidbit® temperature loggers. Loggers were placed above the highest high tide level on the terrestrial side of the boundary at Murrells Inlet mainland locations (Table 1). Sites where loggers were located differed mainly in the presence or absence of vegetation >1.5 m in height.

Analyses

Data from our initial June 2003 samples were used to conduct a prospective or a priori power analysis using G*Power v3.0 (Faul et al. 2007). Mean differences and variation between developed and undeveloped locations for each variable measured were used to calculate initial effect sizes and estimate appropriate sample sizes to detect significant shoreline treatment effects. Sample sizes were estimated for 2-tailed tests with an error probability or $\alpha = 0.05$, power or $1 - \beta = 0.80$, and based on the calculated effect sizes from the June samples. Future sample sizes and approaches were adjusted based on the results of power analyses and a qualitative assessment of collection and processing costs.

Sediment grain size distributions were analyzed separately for each inlet side using the Kolmogorov–Smirnov Z-test for two independent samples. Sediment pore water salinity and organic content, plant density, height and biomass, snail and benthic infaunal abundance, and benthic respiration rate data all were analyzed using parametric ANOVA models including blocked one-way, nested and two-way analyses. Data were transformed when necessary to satisfy critical assumptions of the ANOVA models. Inlet side (barrier, mainland) in October 2003 and sample dates without rain in March 2004 (see Table 1) were treated as block effects, except for the analysis of benthic respiration which was conducted only at the barrier location. Significant differences between undeveloped barrier and mainland locations, given the range of potential differences between inlet sides (e.g., groundwater discharge, soil properties), and between dates without major rainfall events were anticipated, but inlet side or date differences were not the focus of the current study. Our primary factor of interest was shoreline development.

Differences in the taxonomic composition of benthic infauna were analyzed using PERMANOVA, permutational multivariate analysis of variance (Anderson 2005). The PERMANOVA program provides an ANOVA-like test based on P values generated from permutations of a distance matrix derived from the original species by sample data (Anderson 2001, 2005; McArdle and Anderson 2001). Barrier and mainland location compositional differences were analyzed separately, abundance data were 4th root transformed, and distances were based on Bray-Curtis dissimilarity measures (Anderson 2005).

Results

Prospective power analyses for June 2003 initial data indicated that detectable effect sizes ranged between 0.5 or medium and 0.8 or large (see Cohen 1988), but the total samples required to detect differences at a 0.05 significance level with 80% power often were large (Table 2). In a number of instances (e.g., *L. irrorata*, 3–5 mm AFDM and pore water) the large effect sizes were detectable with relatively few samples (Table 2). Based on initial results, we decided to increase sample sizes where possible to guarantee a minimum of five samples per location for each measurement variable, to increase the number of locations ($n = 2$–3), and to combine 0–2 and 2–5 cm sediment depth data into a single sample in an effort to reduce among sample variability and increase the ability to detect reasonable effect size differences between shoreline treatments.

Analyses of sediment characteristics in October 2003 provided suggestive evidence for the effects of boundary development. No significant difference in sediment particle size distributions (Fig. 3) existed between developed and undeveloped locations for either barrier ($Z = 0.577$, $P > 0.05$) or mainland locations ($Z = 0.289$, $P > 0.05$). Except for the occasional size-class disparity (e.g., >0.125 mm), differences in developed and undeveloped sediment grain size fractions were similar between barrier and mainland locations (Fig. 3). Sediment AFDM exhibited significant block (location) effects ($F_{1,\ 17} = 5.03$, $P < 0.04$) but not a significant shoreline development effect ($F_{1,\ 17} = 1.67$, $P > 0.05$). Mainland compared to barrier sediments contained greater amounts of organic matter, but among sample variation limited detection of a significant development effect on sediment AFDM (Fig. 4). Sediment pore water salinities in October 2003 also exhibited a significant block or location effect ($F_{1,\ 16} = 14.83$, $P < 0.005$) but not a significant shoreline development effect ($F_{1,\ 16} = 0.87$, $P > 0.05$). Barrier sediment salinities were two times mainland values, but no consistent difference between developed and undeveloped locations was identified (Fig. 4). In situ comparison of mainland pore water salinities in March 2004 on two dates 5 days apart after 7+ days without rain resulted in a marginally significant date block effect ($F_{1,\ 20} = 4.10$, $P < 0.057$), no significant shoreline development effect ($F_{1,\ 4} = 4.84$, $P > 0.05$) but a significant site effect ($F_{4,\ 20} = 4.61$, $P < 0.009$). Although unable to detect significant differences, undeveloped location salinities were ca. two times that of developed locations (Fig. 5). Comparison of salinity before and after a 0.64–1.3 cm rain event in March 2004 resulted in nonsignificant development ($F_{1,\ 2} = 3.89$, $P > 0.05$), rain ($F_{1,\ 2} = 5.17$, $P > 0.05$) or interaction effects ($F_{1,\ 2} = 0.05$, $P > 0.05$). However, among site effects again were significant ($F_{2,\ 35} = 4.83$, $P < 0.03$). The rainfall event did not affect pore water salinities significantly, but undeveloped locations consistently had greater pore water salinities before and after the rain event (Fig. 5).

Table 2 Calculations of effect sizes based on a prospective (a priori) power analyses for mainland developed (OMD1) and undeveloped locations (OMU1) sampled in June 2003 using G*Power v3.0

Variable	Mean		SD		n		Effect size (d)	Total samples
	D	U	D	U	D	U		
Juncus density (m^{-2})								
Live stems	499	624	286	149	5	5	0.574	26
Dead stems	294	416	309	323	5	5	0.384	56
Snail density (m^{-2})								
L. irrorata	31	4	26	4	5	3	1.814	5
M. bidentatus	98	65	97	32	5	3	0.500	34
Sediment AFDM (mg g^{-1})								
0–2 cm	183.7	121.3	166.9	70.5	3	3	0.545	32
3–5 cm	164.1	69.1	147.3	21.2	3	3	1.127	9
Pore water (%)								
0–2 cm	46.9	43.9	20.4	12.2	3	3	0.182	234
3–5 cm	47.1	35.0	19.6	5.8	3	3	0.952	11

Total samples needed to detect the effect size were calculated for $\alpha = 0.05$ and $1 - \beta = 0.80$. *D* developed, *U* undeveloped

Characteristics of the predominant high-marsh plant at all locations, *J. roemerianus*, generally did not exhibit the effects of shoreline development. Live and dead stem densities were not significantly different between locations ($F_{1,\ 17} = 7.34$, $P > 0.05$ and $F_{1,\ 17} = 8.96$, $P > 0.05$, respectively) or between shoreline treatments ($F_{1,\ 17} = 0.35$, $P > 0.05$ and $F_{1,\ 17} = 0.48$, $P > 0.05$, respectively). Live stems tended to be more abundant at all developed locations, but dead stems were more numerous at mainland undeveloped locations (Fig. 6). Stem AFDM also was not significantly different between locations ($F_{1,\ 17} = 0.34$, $P > 0.05$) or shoreline treatments ($F_{1,\ 17} = 0.03$, $P > 0.05$). However, stem heights were significantly different between locations ($F_{2,\ 388} = 1{,}765.15$, $P < 0.001$) and shoreline treatments ($F_{1,\ 8} = 6.95$, $P < 0.04$). Stem heights were greater at both mainland and barrier developed locations (Fig. 6).

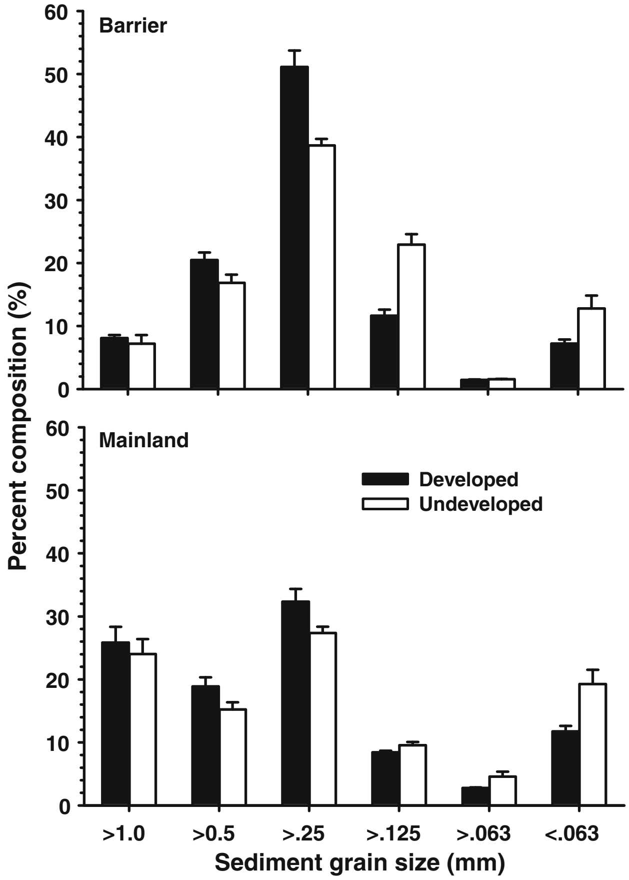

Fig. 3 Percent sediment grain size distributions ($\mu + 1$ se, $n = 5$) for developed and undeveloped locations at Murrells Inlet barrier and mainland locations

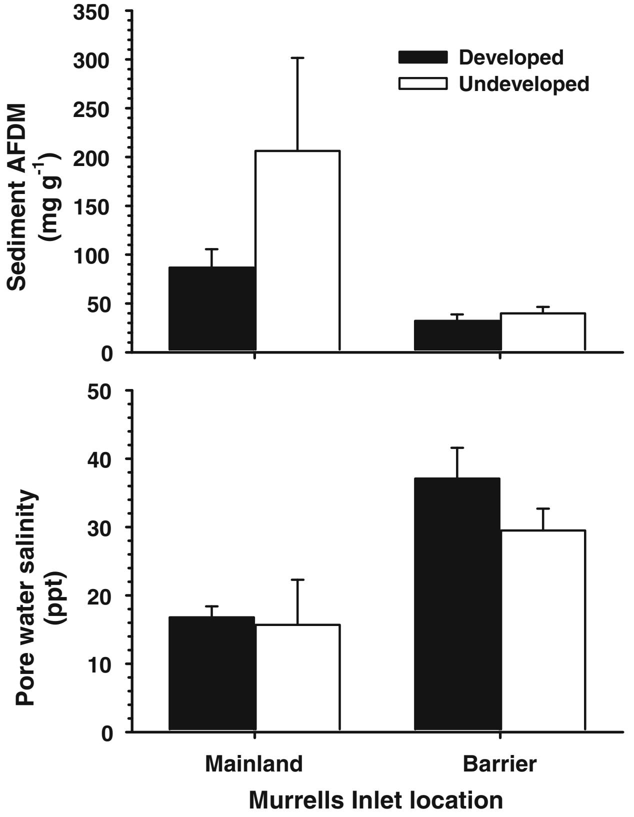

Fig. 4 Differences ($\mu + 1$ se, $n = 5$) in sediment AFDM and pore water salinity for developed and undeveloped locations at barrier and mainland locations

Boundary development also had varying effects on resident marsh fauna. Snail densities exhibited a significant location ($F_{1,\ 17} = 10.52$, $P < 0.006$) and shoreline development effect ($F_{1,\ 17} = 13.73$, $P < 0.003$) for *L. irrorata* but no significant location ($F_{1,\ 17} = 2.87$, $P > 0.05$) or shoreline development effect ($F_{1,\ 17} = 2.95$, $P > 0.05$) for *M. bidentatus*. Periwinkles virtually were absent from mainland locations and densities were greater at developed barrier locations (Fig. 7). However, *M. bidentatus* densities were greater at undeveloped barrier locations (Fig. 7). Benthic infaunal abundances were significantly different by location ($F_{1,\ 17} = 13.18$, $P < 0.003$) and shoreline treatment ($F_{1,\ 17} = 4.73$, $P < 0.045$), but only the barrier island undeveloped site exhibited greater infaunal abundances, ca. fourfold, compared to the developed site (Fig. 7). The similarity of taxonomic compositions analyzed by PERMANOVA also was significantly different between developed and undeveloped shorelines for barrier ($F_{1,\ 8} = 4.38$, $P < 0.02$) and mainland locations ($F_{1,\ 8} = 7.83$, $P < 0.02$). Compositions were more similar among barrier developed, 42.5%, compared to undeveloped shorelines, 28.4%, but were less similar among mainland developed, 45.1%, compared to undeveloped shorelines, 53.2%. Both barrier and mainland undeveloped shorelines had greater abundances of oligochaetes while developed shorelines had greater abundances of ceratopogonid larvae (Table 3). Mainland developed shorelines also, in general, had a greater number of Diptera larvae (e.g., Ceratopogonidae, *Hexatoma*, Chironomidae).

The responses of benthic autotrophic and heterotrophic communities at the barrier location varied between undeveloped and developed shorelines (Fig. 8). A significant interaction between sediment and shoreline treatments affected respiration rates under natural light conditions ($F_{2,\ 12} = 5.41$, $P < 0.03$). Heterotrophic consumption was greater in developed compared to undeveloped control sediments but was decreased in N & P addition sediments (Fig. 8). Dark incubations resulted in no significant interaction ($F_{2,\ 12} = 1.67$, $P > 0.05$) or sediment treatment effects ($F_{2,\ 12} = 1.90$, $P > 0.05$) but a significant shoreline treatment effect ($F_{1,\ 12} = 28.82$, $P < 0.001$). Undeveloped shoreline heterotrophic oxygen consumption was greater in all sediment treatments (Fig. 8).

The maximum and range of sediment surface temperatures varied over the 2-week period sampled at mainland developed and undeveloped locations (Fig. 9). A

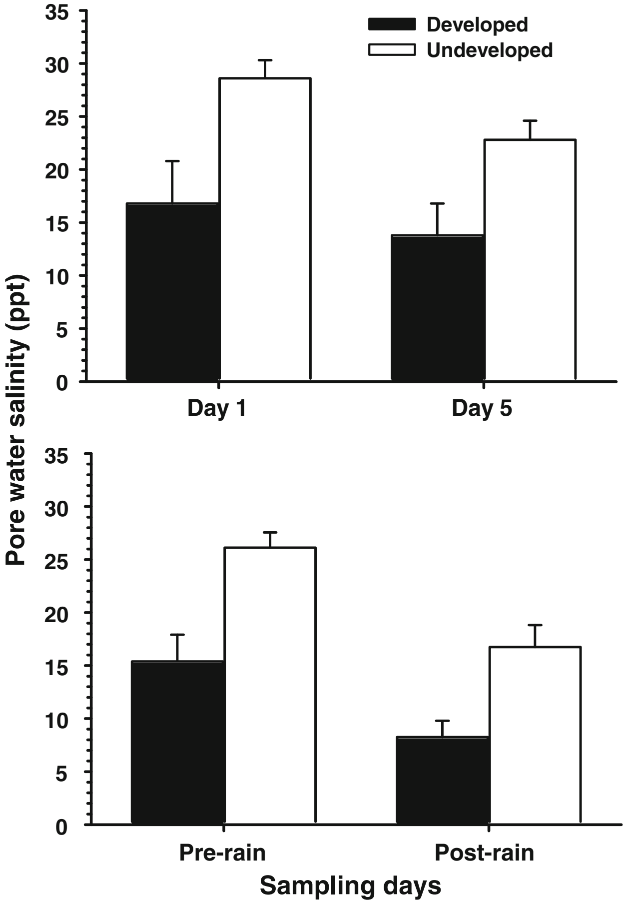

Fig. 5 Mainland sediment pore water salinity ($\mu + 1$ se) for developed and undeveloped locations ($n = 3$) on multiple dates during a period without precipitation (*top*) and before and after a March 2004 precipitation event (*bottom*)

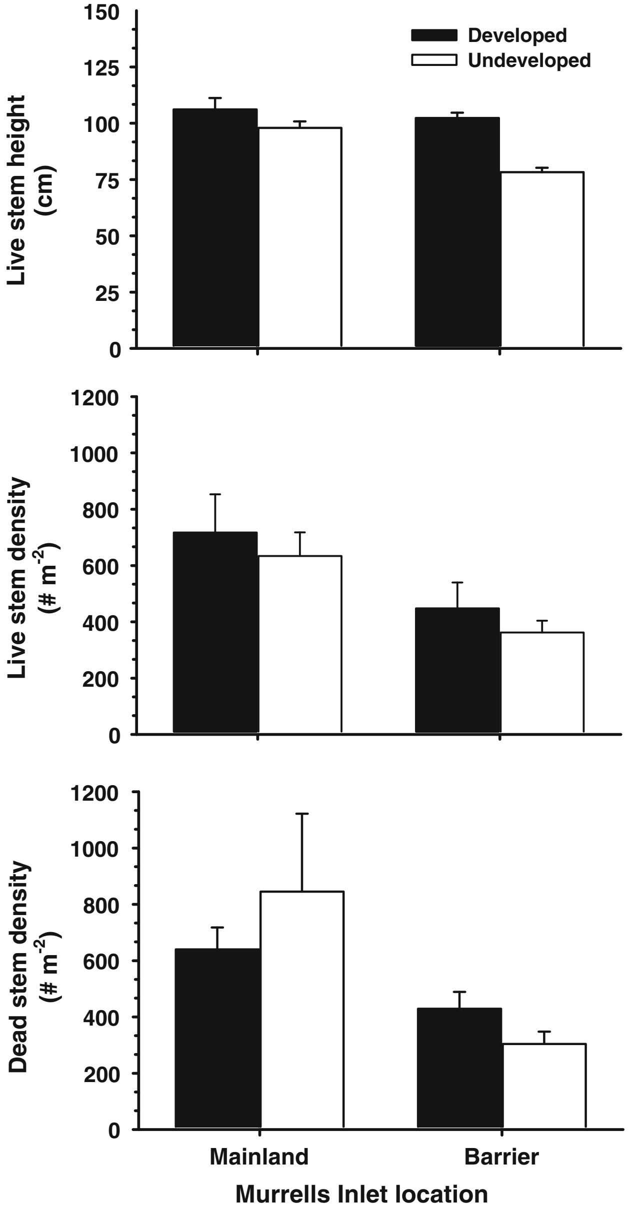

Fig. 6 Live and standing-dead mean (+1 se) J. roemerianus stem densities ($n = 5$) and live stem heights ($n = 25$) from developed and undeveloped locations within Murrells Inlet barrier and mainland locations

significant interaction between date and boundary development existed for maximum temperatures ($F_{13,\ 56} = 1.94$, $P < 0.05$), but while temperatures varied between 25 and 40°C, on no date did undeveloped exceed developed (Fig. 9). No significant interaction ($F_{13,\ 56} = 1.79$, $P > 0.05$) but significant date ($F_{13,\ 13} = 17.08$, $P < 0.001$) and boundary treatment effect ($F_{1,\ 13} = 26.79$, $P < 0.001$) existed for daily temperature ranges. Day–night temperatures varied between 5 and 18°C, but the range was always greater at the developed locations (Fig. 9).

A summary of the ecological attributes measured and shoreline alteration effects determined in the present study are compared with observed or predicted effects of shoreline development from previous studies in Table 4. Shoreline development has or is expected to increase freshwater inflow and both inorganic and organic loading in the high salt marsh environment (see Wahl et al. 1997; Bertness et al. 2002; Silliman and Bertness 2004). Expected or predicted changes occurred in only 50% of the ecological attributes measured in Murrells Inlet (Table 4). Typically significant differences between developed and undeveloped shorelines were not detected (e.g., plant density, benthic species richness), but in a few instances (e.g., sediment organic content) the observed trend contradicted expectations (Table 4).

Discussion

The alteration of terrestrial shoreline characteristics affected a number of ecological attributes in the high-marsh

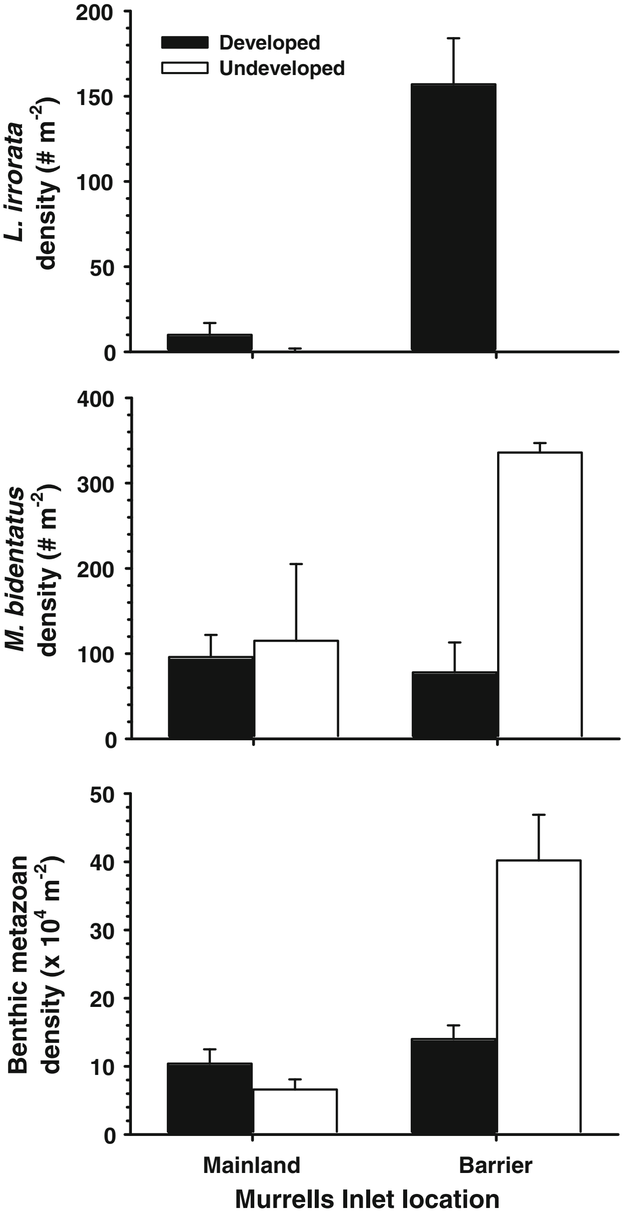

Fig. 7 Total benthic infaunal, L. irrorata and M. bidentatus densities ($\mu + 1$ se, $n = 5$) from developed and undeveloped shoreline locations within Murrells Inlet barrier and mainland locations

environment within an ocean-dominated, southeastern USA estuary. Faunal densities and composition, sediment surface temperatures, benthic microbial respiration rates and plant height all exhibited predictable, significant differences between developed and undeveloped shorelines. Densities of *L. irrorata*, *J. roemerianus* stem height, and both temperature maxima and range were significantly greater while night-time microbial oxygen consumption was significantly reduced at developed shoreline locations. Increased densities of *L. irrorata* can have cascading effects within salt marshes (Silliman and Zieman 2001; Silliman and Bertness 2002), and anthropogenic development can lead to consumer control of marsh productivity (Bertness et al. 2008; Bertness and Silliman 2008). Although few effects of consumer control were evident at Murrells Inlet locations (Walters et al. pers. obs.), *L. irrorata* densities even along developed shorelines were <50% of the numbers reported in studies where consumers do affect marsh productivity (Silliman and Zieman 2001; Bertness and Silliman 2008). Autumn marsh periwinkle densities from undeveloped locations also were low compared to spring snail densities of just the year before (Hutchens and Walters 2006). Typically undeveloped, high marsh shorelines in northern South Carolina tend to have low *L. irrorata* densities but increased biomass in spring relative to mid- and low-marsh elevations (Hutchens and Walters 2006). Summer recruitment and growth in blue crabs, *Callinectes sapidus*, a major predator on *L. irrorata* (Schindler et al. 1994; Lewis and Eby 2002), could account for observed snail density differences between spring and autumn. Increased crab numbers or size could increase predation pressure on snail populations in the fall of the year, but would not account for density differences between adjacent developed and undeveloped shorelines. However, crab predation might reduce overall autumn snail densities within Murrells Inlet marshes so that snail populations along developed shorelines do not increase to densities sufficient to produce catastrophic cascade effects on the marsh.

The benthic infauna was dominated by oligochaetes and nematodes at all marsh locations, but barrier island side densities were greater along the undeveloped shoreline. Average total metazoan densities at all shorelines (66–401 ind/10 cm^2) were ca. 50% less than densities in the preserved North Inlet marshes (Bell 1980). Taxonomic similarity among samples varied most at undeveloped locations possibly indicating a more patchily distributed fauna. The most conspicuous difference between developed and undeveloped locations was the order of magnitude greater proportion of larval ceratopogonids collected along developed shorelines. Ceratopogonid larvae were absent from barrier undeveloped shorelines but comprised 13% of total metazoan abundance (14 ind/10 cm^2) at the developed shoreline. Increased densities of larvae suggest that altered shoreline conditions may lead to unanticipated environmental management issues for Murrells Inlet residents and tourists. Adult ceratopogonids (sand flies, no-see-ums) are serious mammalian pests and can vector livestock diseases (e.g., blue tongue) as a result of the female's biting behavior. Developed locations also contained two other groups of Diptera flies absent from undeveloped locations: Chironomidae or midge flies and *Hexatoma* (Tipulidae) or crane flies. Coastal environments that vary widely in salinity (e.g., oligohaline marshes to saline pools) typically contain increased densities of

Table 3 Percent taxonomic composition identified from October 2004 infaunal samples collected at barrier and mainland developed and undeveloped locations in Murrells Inlet

Taxa	Mainland		Barrier beach	
	Undeveloped	Developed	Undeveloped	Developed
Oligochaeta	60.5	38.9	51.4	34.2
Polychaeta	0.9	2.2	0.3	1.6
Nematoda	31.6	21.1	46.9	47.7
Mite	0.9	1.1	0.3	0.4
Bivalvia	0.0	11.1	0.1	0.0
Copepoda	0.9	0.0	0.9	2.1
Ceratopogonidae	4.4	19.4	0.0	13.2
Collembola	0.0	0.0	0.1	0.0
Gastropoda	0.0	0.0	0.0	0.0
Crab	0.0	0.0	0.0	0.4
Shrimp	0.9	0.0	0.0	0.4
Hexatoma	0.0	1.1	0.0	0.0
Amphipoda	0.0	1.1	0.0	0.0
Chironomidae	0.0	0.6	0.0	0.0
Total abundance ($n = 5$)	114	180	695	245

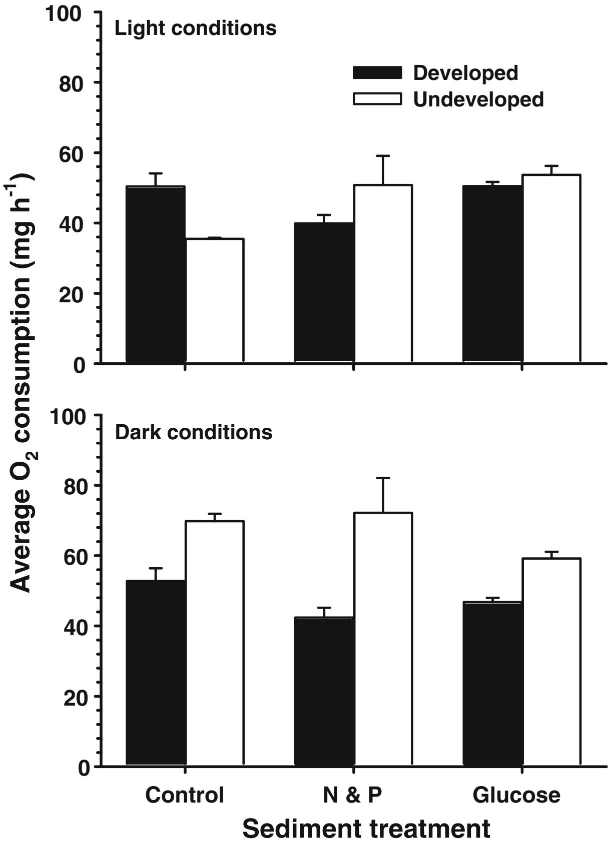

Fig. 8 The mean (+1 se) benthic oxygen consumption rate ($n = 3$) for seawater, nitrogen and phosphorus nutrient and glucose addition light and dark incubations over 3 h of sediment from barrier developed and undeveloped locations

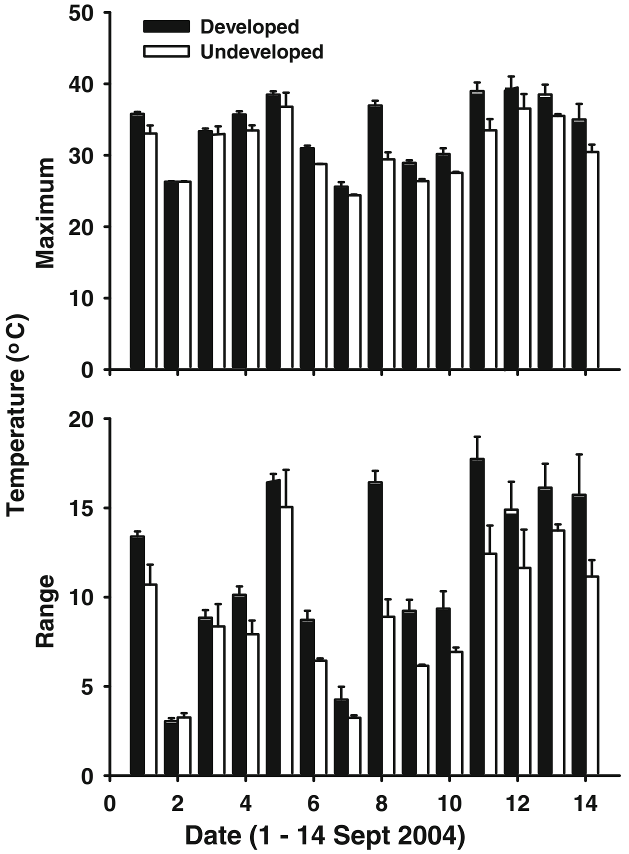

Fig. 9 The mean (+1 se) range and maximum sediment surface temperatures ($n = 3$) for 14 days (1–14 Sept 2004) at mainland developed and undeveloped locations

Table 4 Previously identified ecological attributes affected or possibly affected by shoreline development (see Wahl et al. 1997 [W], Bertness et al. 2002 [B], Silliman and Bertness 2004 [S]; letters denote studies showing respective effects listed below), the observed or predicted high salt marsh effects of development, and identified effects of shoreline alteration in the current Murrells Inlet study

Ecological attribute	Predicted effect	Identified effect
Sediment characteristics		
Sediment grain size	↑	NS Barrier ↓NS Mainland
Sediment organic content	↑ or ↓	NS Barrier ↓NS Mainland
Nutrient concentration	↑ (W, B, S)	NM
Pore water salinity	↓ (S)	NS Oct. 2003 ↓NS Mar. 2004
Sediment surface temperatures	↑	↑ Maximum ↑ Range
Floral characteristics		
Plant density	↑	NS
Plant height	↑ (B)	↑
Plant standing crop	↑ (B)	NS
Plant species richness	↓ (B, S)	NM
Faunal Characteristics		
Snail density	↑	↑ *L. irrorata* ↓NS *M. bidentatus*
Snail biomass	↑	NM
Benthic invertebrate density	↑	↑ Barrier
Benthic species richness	↓	NS
Benthic community similarity	↓	↑ Barrier ↓ Mainland
Microbial characteristics		
Chlorophyll concentrations	↑	NM
Bacterial abundance	↓	NM
Microbial substrate utilization	↑ or ↓	NM
Net primary production	↑	NM
Microbial respiration	↑ or ↓	↓ Dark Barrier

↑ = D > U, ↓ = D < U

NS no significant difference, (↑ or ↓) *NS* trending but not significant, *NM* not measured

nematocerous dipterans, both biting and non-biting species (LaSalle and Bishop 1987; Giberson et al. 2001). Although not statistically significant between shoreline treatments, salinities varied most along developed shorelines (from <10 to >35 ppt) and the variation may be what enables greater densities of Diptera larvae to persist. Whatever the reason, shoreline development appears to contribute to an increase in insect pests and the potential need for greater management efforts (e.g., pesticide spraying).

Shoreline development resulted in consistently greater daily temperature maxima and greater day–night ranges at the sediment surface. Intertidal temperature patterns can be variable and unpredictable both spatially and temporally (Helmuth and Hofmann 2001; Helmuth et al. 2002; Helmuth et al. 2006), but differences in temperature experienced by organisms lead to dramatic differences in distributions, selective pressure and behavior (Helmuth et al. 2006; Jost and Helmuth 2007; Schneider and Helmuth 2007; Pincebourde et al. 2008). Although only documented over a relatively short, 2-week period, the persistent temperature difference between developed and undeveloped marsh shorelines is likely to affect organisms typically inhabiting the high marsh. Ribbed mussels, *Geukensia demissa*, experienced thermal stress and mortality under natural conditions along an undeveloped high marsh shoreline in North Inlet, ca. 25 km south of Murrells Inlet (Jost and Helmuth 2007). High marsh mussels were uncommon in our samples, but temperature differences between developed and undeveloped locations may have affected the coffee bean snail, *Melampus bidentatus*, another high marsh resident. The coffee bean snail has no operculum and is believed to bury in the sediments or invade crab burrows to minimize thermal stress (McMahon and Russell-Hunter 1981). Coffee bean snails experience increased mortality (McMahon and Russell-Hunter 1981) at air temperatures similar to or below (ca. 40°C) the body temperatures that cause increased mortality in ribbed marsh mussels (Jost and Helmuth 2007). *Melampus bidentatus* were significantly more abundant along undeveloped shorelines, especially on the barrier island side of Murrells Inlet. The greater thermal stress of developed shorelines may result in either increased mortality or emigration possibly explaining the observed significant difference in snail densities.

Oxygen consumption within sediments, primarily the result of heterotrophic bacteria, was affected by shoreline development. Although consumption rates suggested heterotrophy predominated production pathways along both barrier island shorelines, both heterotrophic (dark) and autotrophic production rates (light–dark) were greater at the undeveloped location. Heterotrophic bacterial production in salt marsh soils generally is understood to be phosphorus limited, but continued phosphorus loading may shift the bacterial population to a carbon-limited status (Sundareshwar et al. 2003). Typical of many environments, the structure of salt marsh microbial communities is sensitive to increases in anthropogenic pollutants (Cao et al. 2006). Darby and Turner (2008) also suggest that phosphorus loading and the resulting competition with microbes can decrease belowground *Spartina* tissue production and be detrimental to long-term salt marsh maintenance. Although difficult to reconcile definitively based on the comparison of barrier island shorelines, the greater oxygen demand, greater metazoan abundance, and the trend towards greater organic matter in undeveloped sediments suggests the presence of a more productive benthic food web.

The significantly greater heights of *J. roemerianus* stems suggest shoreline development is associated with increased production in the adjacent salt marsh. *Juncus roemerianus* is a generalist species tolerating a wide range of conditions (Woerner and Hackney 1997; Brinson and Christian 1999), but previous research indicates that biomass production is greater when grown at relatively low soil salinities (Pennings et al. 2005). Compared to *J. roemerianus* populations further from the shoreline, Touchette (2006) also demonstrated that high marsh plants primarily fed by upland freshwater were less stressed and had greater biomass. Although runoff from areas adjacent to our study locations was not measured directly, salinity results from before and after a rain event suggest that development and the concomitant increased freshwater runoff may be responsible for decreased pore water salinity and improved growing conditions for *J. roemerianus*. In New England, shoreline development is associated with dramatic changes in plant community composition, including the aggressive invasion by *Phragmites australis*, a non-native reed (Bertness et al. 2002, 2008, 2009; Silliman and Bertness 2004). Although present in the area (Luken and Walters 2009), shoreline development in Murrells Inlet has not resulted in an invasion by *P. australis* (Walters et al. pers. obs.). A number of factors including limits on chance dispersal and lack of habitat disturbance (e.g., wrack) could account for the absence of *P. australis* in Murrells Inlet. Alternatively, shoreline development in southeastern marshes may lead to more subtle changes that modify natural environmental gradients and trophic structure but do not necessarily alter the composition of the salt marsh plant community.

The increased freshwater runoff associated with shoreline development also is accompanied typically with increased nitrogen loading (Bowen and Valiela 2001; Bertness et al. 2002, 2009; Wigand et al. 2003) and alteration in the timing of release of mineral nitrogen to associated near shore habitats (Wahl et al. 1997; Gorman et al. 2009). In communities comprised of *S. alterniflora* and *S. patens*, nitrogen loading will alter plant growth, change vegetation structure and modify competitive interactions (Bertness et al. 2002; Wigand et al. 2003). The common presence of a *J. roemerianus* zone adjacent to the upland/marsh boundary in many southeastern marshes suggests a relatively high degree of plant diversity as a result of natural gradients in flooding and salinity (Pennings et al. 2005). As the closest marsh plant to the terrestrial boundary, the *J. roemerianus* zone may be viewed as a secondary buffer that receives and processes the various effects of shoreline development and possibly mitigates anticipated consequences on other marsh species. The regional differences in resistance to shoreline development, specifically the types and prevalence of plant species that may serve as buffers to changing environmental conditions, may explain many of the unanticipated results in our current study.

Even given the possible regional differences, almost 50% of the predicted effects of shoreline development were not observed in Murrells Inlet. Aside from variables not measured or not measured with sufficient power, a number of factors previously not considered in studies of shoreline development may have contributed to our inability to predict consistently the effects of shoreline development in southeastern marshes: the extent and history of shoreline modification. The extent of shoreline modification can vary from no alteration or no removal of the native salt-shrub thicket bordering a marsh to severe alteration or removal of all native vegetation and bulk-heading, channeling, ditching or other modification of the normal tidal flow taking place. Differences also can occur within a modification category. In suburbanized Murrells Inlet, housing developments along the marshes can range from no alteration of the native vegetation, at least directly along the marsh/upland boarder, to complete removal of all native vegetation and alternative landscaping including extensive planting of turf grasses. Depending on the mindset or economy, individual households where complete removal of native vegetation occurs, additionally may experience weekly, monthly, seasonally, or no nitrogen supplements in the form of fertilizers along with the possible additional application of pesticides and herbicides. Although each Murrells Inlet developed shoreline represented a residential alteration of the existing habitat, the extent of the boundary's modification ranged from minimal alteration to complete removal of native vegetation. Differences in the extent of shoreline modification likely made detection of predicted effects difficult.

Any ecological effects of shoreline development also are likely dependent on the history of boundary alteration. Significant high-marsh changes may not have had time to take place along newly altered shorelines depending on the variable being measured. Based on salt marsh restoration studies, plant biomass (Broome et al. 1986; Roman et al. 2002), genetic diversity (Travis et al. 2002), fish utilization (Roman et al. 2002; Able et al. 2004), and sediment salinities (Walters 2009) can change rapidly within newly planted marshes, while changes in sediment organic content (Craft et al. 1999), nutrient cycling (Thompson et al. 1995; Craft et al. 1999), infauna (Sacco et al. 1994; Levin et al. 1996), and plant canopy (Zedler 1993) tend to require significant time if not decades. Ecological changes in Narragansett Bay salt marshes only were detected after two decades of urbanization (Wigand et al. 2010). The developed shoreline we studied, OMD1, consisted of recently built (<5 years) and ongoing building and therefore was a newly developed shoreline along which high-marsh changes may not have been expected to have occurred. In contrast, the barrier island shoreline was developed for at least 20 years and any differences between shoreline locations (e.g., benthic infaunal densities) may be explained in part by the age of boundary development. The same may be true for any differences between observed and expected boundary development effects. Basing predicted effects on studies from Northeastern marshes, historically experiencing greater impacts from increasing populations, may not be justified. Southeastern marshes may be at the very beginning of the shoreline development trajectory leading ultimately to negative effects on high-marsh environments.

Historically, humans have either directly or indirectly altered salt marsh environments (e.g., Gedan et al. 2009), making an accurate assessment of cumulative historical effects difficult. From the earliest days of European colonization, South Carolina marshes have been ditched, dredged, filled and altered to support numerous commercial or residential pursuits (Gedan et al. 2009). Although overt direct impacts to South Carolina salt marshes are now less common, residential development adjacent to salt marshes is on the increase; there are few signs that development of land adjacent to salt marshes will be curtailed in the future as such lots offer numerous amenities (e.g., scenic vistas, recreation opportunities, investment return). Our research suggests that development of the marsh shoreline may produce subtle changes to the adjacent salt marsh. These subtle changes can be contrasted with the more dramatic changes in northeastern USA marshes that presumably are linked to residential development (Bertness et al. 2002, 2008, 2009; Silliman and Bertness 2004).

Future research might focus on two different but related salt marsh issues. First, our data suggest regional differences in the resistance (stability) of salt marshes. Although salt marshes are relatively simple systems and share many of the same characteristics, understanding why regional differences occur is important to making effective management decisions. Experimental results suggest salinity is an important factor affecting the speed of marsh recovery following disturbance (Crain et al. 2008), and regional differences in factors affecting salinity (e.g., drought periods) may influence the impacts of shoreline development. Second, the effects of small changes to marshes may be cumulative and eventually bring the system to a point where the marsh will experience a major change. The invasion of northeast salt marshes by *Phragmites australis* is one example where small, cumulative changes in the nutrient status of marshes eventually set the stage for a larger ecosystem change (Silliman and Bertness 2004). Both lines of research are important for understanding how to manage residential development of shorelines in order to minimize potential negative effects on coastal marshes.

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