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ARTICLE

Effects of Coastal Urbanization on Salt-Marsh Faunal Assemblages in the Northern Gulf of Mexico

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Abstract

Coastal landscapes in the northern Gulf of Mexico, specifically the Mississippi coast, have undergone rapid urbanization that may impact the suitability of salt-marsh ecosystems for maintaining and regulating estuarine faunal communities. We used a landscape ecology approach to quantify the composition and configuration of salt-marsh habitats and developed surfaces at multiple spatial scales surrounding three small, first-order salt-marsh tidal creeks arrayed along a gradient of urbanization in two river-dominated estuaries. From May 3 to June 4, 2010, nekton and macroinfauna were collected weekly at all six sites. Due to the greater abundance of grass shrimp *Palaemonetes* spp., brown shrimp *Farfantepenaeus aztecus*, blue crab *Callinectes sapidus*, Gulf Menhaden *Brevoortia patronus*, and Spot *Leiostomus xanthurus*, tidal creeks in intact natural (IN) salt-marsh landscapes supported a nekton assemblage that was significantly different from those in partially urbanized (PU) or completely urbanized (CU) salt-marsh landscapes. However, PU landscapes still supported an abundant nekton assemblage. In addition, the results illustrated a linkage between life history traits and landscape characteristics. Resident and transient nekton species that have specific habitat requirements are more likely to be impacted in urbanized landscapes than more mobile species that are able to exploit multiple habitats. Patterns were less clear for macroinfaunal assemblages, although they were comparatively less abundant in CU salt-marsh landscapes than in either IN or PU landscapes. The low abundance or absence of several macroinfaunal taxa in CU landscapes may be viewed as an additional indicator of poor habitat quality for nekton. The observed patterns also suggested that benthic sediments in the CU salt-marsh landscapes were altered in comparison with IN or PU landscapes. The amount of developed shoreline and various metrics related to salt marsh fragmentation were important drivers of observed patterns in nekton and macroinfaunal assemblages.

Coastal landscapes are broadly defined, from an ecological perspective, as “spatially heterogeneous areas of the coastal environment that can be perceived as a mosaic of habitat patches” (Boström et al. 2011). Landscape composition and configuration can significantly influence patterns of faunal distribution and abundance (Wiens 1989), thereby influencing population and community dynamics (Turner et al. 2001). Thus, an important step in the management of these critical ecosystems is to maintain the functional linkages among patches or habitats used by animals at the landscape level. However, identification of the linkage between species’ complex interactions and their habitats is often difficult (Thrush et al. 2008).

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Salt-marsh ecosystems comprise a suite of shallow, structurally complex habitats that are arrayed along highly variable abiotic and biotic gradients (Peterson 2003; Rountree and Able 2007) and that are functionally connected by both energy flow and animal movement through tidal creek networks (Odum 1984; Deegan 1993; Kneib 2000; Mallin and Lewitus 2004). These productive ecosystems are viewed as critical habitat for a number of ecologically and economically important fishes and decapod crustaceans (hereafter, "nekton"; Weinstein 1979; Boesch and Turner 1984; Peterson and Turner 1994; Minello et al. 2003). For small-bodied nekton species, the structural complexity of salt-marsh habitats provides protection from predators (Minello et al. 1989; Kneib 1995) and an abundance of benthic and epibenthic macrofaunal prey (hereafter, "macroinfauna") that link salt-marsh-derived primary production to secondary production through complex food web interactions (Kneib 2000; Dame and Christian 2007). Salt-marsh macroinfaunal and nekton assemblages have adapted to a suite of historically stable habitat conditions over the course of millennia (Brush 2009). However, these conditions are rapidly changing as a result of human activities in the coastal zone (Bromberg Gedan et al. 2009; Peterson and Lowe 2009; Bulleri and Chapman 2010; Mee 2011).

Despite early warnings (Mock 1967; Odum 1970, 1982), the potential impacts of urbanization—defined here as the serial replacement of natural habitats with impervious surfaces and hardened shorelines—on salt-marsh habitats have only recently emerged as a focal area in estuarine ecology. In an extensive literature review, Peterson and Lowe (2009) showed that the deleterious effects of urbanization on salt-marsh ecosystems have been clearly documented. Most studies to date have shown that developed shorelines are not functionally equivalent to natural habitats for either benthic assemblages (Bilkovic et al. 2006; Seitz et al. 2006; Partyka and Peterson 2008; Long et al. 2011) or nekton assemblages (Hendon et al. 2000; Peterson et al. 2000; Bilkovic and Roggero 2008; Long et al. 2011). However, few studies have compared habitat value among salt-marsh habitats that have undergone different levels of coastal urbanization.

In addition to the effects on habitat quality, coastal urbanization exerts significant impacts on the quantity and spatial configuration of salt-marsh habitats (Thomas 1995; Lathrop et al. 2000; Peterson and Lowe 2009). As developed surfaces and hardened shorelines accumulate across coastal landscapes, natural salt-marsh habitats become increasingly patchy and isolated within an unsuitable habitat matrix (i.e., fragmentation; Fahrig 2003). This leads to compromised nekton recruitment (Eggleston et al. 1998), altered faunal assemblage structure and diversity (Layman et al. 2004; Partyka and Peterson 2008; Goodsell 2009), reduced production of commercially important nekton species (Valentine-Rose et al. 2007), and modified trophic interactions (Layman et al. 2007) in urbanized and fragmented intertidal habitats, such as salt marshes.

The main objective of this study was to examine the effects of coastal urbanization on salt-marsh faunal assemblages by using a threefold approach. First, we used a landscape ecology approach to quantify the composition and configuration of three replicated coastal landscape types arrayed along a gradient of urbanization from an intact natural salt-marsh landscape to a small salt-marsh patch that was isolated within an urbanized coastal landscape. Second, we examined among-site differences in the distribution and abundance of nekton and macroinfaunal assemblages. Lastly, we related faunal assemblage patterns to the physical and chemical patterns emerging at the landscape level. We hypothesized that if coastal urbanization does have an impact on salt-marsh habitat value, then both the macroinfaunal and nekton assemblages will be discernibly different between the highly urbanized salt-marsh patches and the intact salt-marsh landscape.

METHODS

Study Area and Study Site Delineation

The study area consisted of two large, microtidal (tidal range <0.5 m; Rozas 1995) river estuaries in coastal Mississippi (Figure 1a). The lower Pascagoula River estuary (PRE) is an approximately 15-km-long distributary that can be subdivided into eastern and western branches. The eastern branch has been highly altered and is bordered by intensely developed surfaces and hardened shorelines, while the shorelines of the western branch remain comparatively less modified and possess large expanses of intact natural habitats (Peterson et al. 2007; Partyka and Peterson 2008). The Biloxi Bay estuary (BB) is approximately 21.7 km in length and also consists of both highly impacted and unimpacted shorelines; however, the impacted shorelines are not as aggregated as those in the PRE. In both systems, altered shorelines include erosion control edges in the form of levees, rip-rap, and residential and commercial bulkheads (Peterson and Lowe 2009). Natural shorelines consist mostly of intertidal vegetation dominated by smooth cordgrass *Spartina alterniflora* and needlerush *Juncus roemerianus*, with occasional patches of the invasive common reed *Phragmites australis* (Peterson and Partyka 2006). Although both systems receive considerable freshwater input from upstream watersheds, the Pascagoula River has considerably higher discharge rates than the Biloxi River (Lowe et al. 2012).

Previous work in these estuaries identified salt-marsh landscapes that ranged from natural to highly urbanized (Peterson et al. 2000; Partyka and Peterson 2008). These observations were combined with 2007 1-m orthorectified color infrared imagery in ArcGIS version 10.0 (Environmental Systems Research Institute) to identify within each estuary three potential sample sites that (1) contained small, first-order salt-marsh tidal creeks of similar lengths (all creeks ranged from 26.6 to 32.4 m long) and (2) were arrayed along a gradient of anthropogenic alteration from natural to highly altered local landscapes (Figure 1). Small, first-order tidal creeks draining large expanses of salt marsh with no evidence of shoreline alteration or development in the immediate vicinity (750–1,000 m) were considered intact

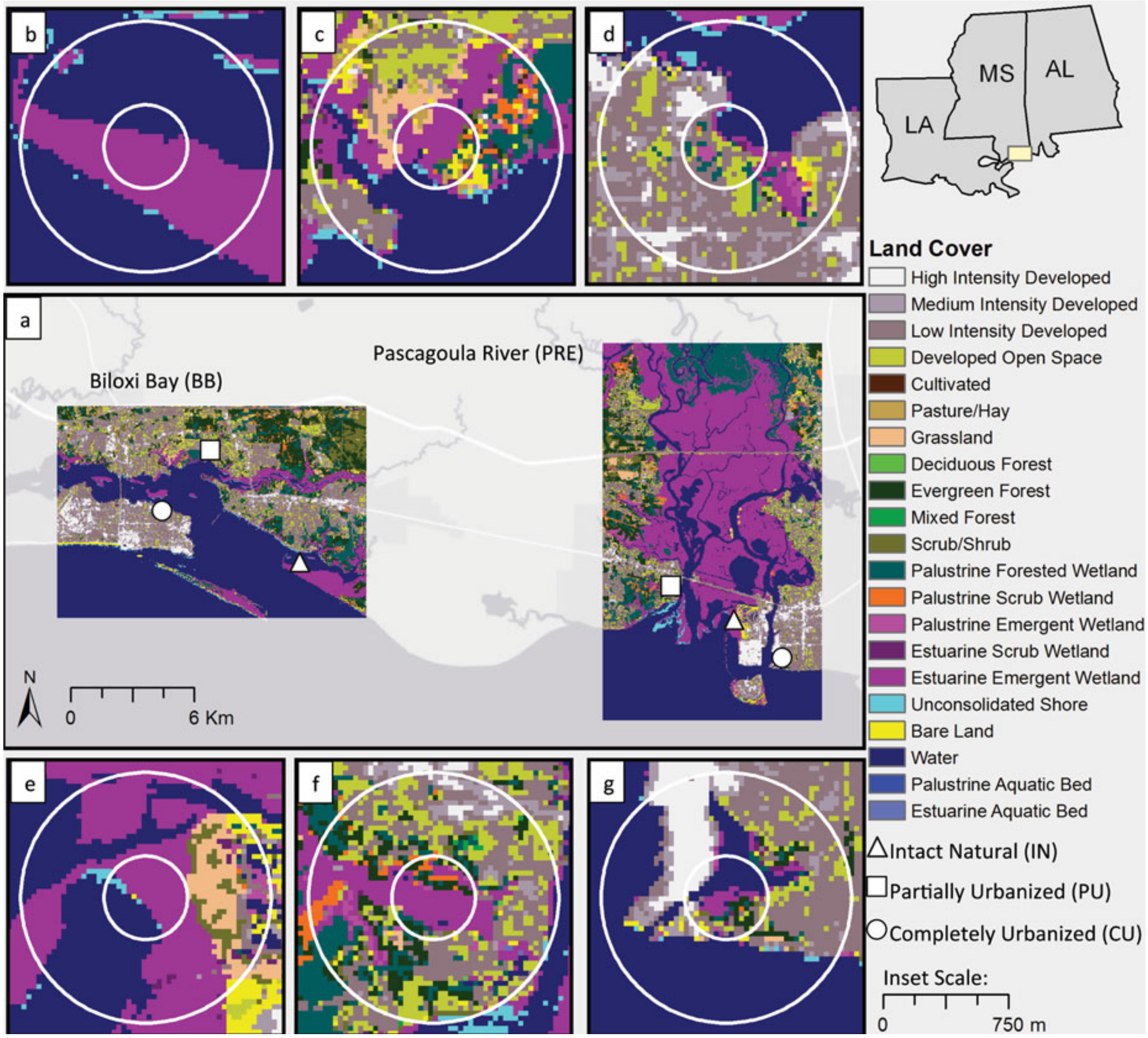

FIGURE 1. **(a)** Map of the study area, including the 2005 land cover data for the Biloxi Bay estuary (BB) and Pascagoula River estuary (PRE), Mississippi (examples of landscape types are shown: triangles = intact natural [IN]; circles = partially urbanized [PU]; squares = completely urbanized [CU]). Inset panels depict examples of each landscape type (represented by symbols in panel a): **(b)** IN landscape in BB; **(c)** PU landscape in BB; **(d)** CU landscape in BB; **(e)** IN landscape in PRE; **(f)** PU landscape in PRE; and **(g)** CU landscape in PRE. Small and large circles in each panel represent the corresponding 250- and 750-m radial buffers used for landscape analyses. For the purpose of this work, the original classes for developed land (e.g., developed open space and high-, medium-, and low-intensity developed class) and estuarine wetlands (i.e., estuarine forested wetland, estuarine scrub or shrub wetland, and estuarine emergent wetland) were reclassified as "developed" and "salt marsh," respectively.

natural (IN) salt-marsh landscapes (Figure 1b, 1e). Partially urbanized (PU) landscapes were identified as small, first-order tidal creeks draining marsh systems that were nestled within a moderately developed area, with modified shorelines disrupting the creeks' natural connection to the main water body (Figure 1c, 1f). Small, isolated salt-marsh patches that contained a small first-order creek and that were surrounded by both altered shorelines and developed surfaces were identified as completely urbanized (CU) landscapes (Figure 1d, 1g). Prior to sampling, each tidal creek and its surrounding landscape were examined to ensure the correct assignment to one of the three landscape types.

Land Cover Data and Landscape Metrics

Land cover data for the study area in 2005 (after Hurricane Katrina; Figure 1a) were obtained from the National Oceanic and Atmospheric Administration's Coastal Change Analysis Program (C-CAP; www.csc.noaa.gov/crs/lca/ccap.html). The C-CAP system classifies 30-m^2 (0.9-ha) pixels into 21 land cover classes at an overall accuracy of 85% (Dobson et al. 1995). For the purpose of this work, the original classes for developed land (e.g., developed open space and high-, medium-, and low-intensity developed class; cells containing 21–100% concrete, asphalt, or other constructed materials) and estuarine wetlands (i.e., estuarine forested wetland, estuarine scrub or shrub wetland, and estuarine emergent wetland) were re-classified as "developed" and "salt marsh," respectively. The remaining classes were not modified.

For each sample site, ArcGIS Model Builder was used to extract a series of circular buffers at different spatial scales (radius = 250 or 750 m) centered on the mouth of each tidal creek (Figure 1e–g). These scales were considered spatially relevant for both less-mobile, resident species (e.g., Able et al. 2012) and more-mobile, transient species (e.g., Weinstein et al. 1984; Wolcott and Hines 1990; Saucerman and Deegan 1999). Within each GIS-rendered spatial extent, the extracted land cover data were used to calculate 10 spatial metrics (Table 1) at the class level and the landscape level by using FRAGSTATS version

TABLE 1. Spatial metrics calculated for each spatial extent (250 and 750 m) in the Biloxi Bay and Pascagoula River estuaries. Composition metrics (PLAND, TE, and TECI) were calculated for water (W), developed (DV), and salt-marsh (SM) classes. Configuration metrics (SHAPE–MESH) were calculated for the SM class only.

Metric	Code	Class	Aspect	Description
Percentage of landscape	PLAND	DV and SM	Area	Percentage of total landscape occupied by a class (unit = %)
Total edge	TE	DV, SM, and W	Edge	Total length of class edge in the landscape (unit = m)
Total edge contrast index	TECI	DV, SM, and W	Edge	Total length of high-contrast class edge scaled proportionally to total edge of class (e.g., TECI_SM[W] = W edge contrasted against SM edge; index of how much of the salt-marsh edge is available to nekton) (unit = proportion)
Area-weighted mean shape index	SHAPE	SM	Shape	SHAPE = 1 when aggregation of cells is square, and value increases with more complex shapes (unit = none)
Contiguity index	CONTIG	SM	Shape	CONTIG = 0 for single-pixel class and increases to 1 as class connectedness increases (unit = none)
Clumpiness index	CLUMPY	SM	Aggregation	CLUMPY = −1 when cells are maximally disaggregated; 0 when cells are randomly distributed; and 1 when cells are maximally aggregated
Creek connectivity index	CONNECT	SM	Isolation	Proportion of tidal creek mouths that are within a 250-m threshold distance of each other; value is 1 when tidal creeks are highly connected (unit = proportion)
Landscape division index	DIVI	SM	Fragmentation	Probability that two randomly chosen pixels are not situated in the same patch. DIVI = 0 when a landscape consists of a single, small patch and increases to 1 as the focal class becomes a single, large patch (unit = proportion)
Splitting index	SPLIT	SM	Fragmentation	The number of patches that results from dividing the landscape into equal-size patches while holding DIVI constant. SPLIT = 1 when a landscape consists of a single patch and increases as the number of focal patches increases and as patch area decreases (unit = none)
Effective mesh size	MESH	SM	Fragmentation	MESH values are minimal when a focal class consists of a single, small patch and are maximized when a landscape consists of a single, large patch

TABLE 2. Derived spatial metrics for intact natural (IN), partially urbanized (PU), and completely urbanized (CU) sites in the Biloxi Bay estuary (BB) and Pascagoula River estuary (PRE) at 250- and 750-m spatial extents. Asterisks denote variables that were used for multivariate analyses. Landscape metrics and their units are defined in Table 1.

	BB-IN		BB-PU		BB-CU		PRE-IN		PRE-PU		PRE-CU	
Metric	250 m	750 m	250 m	750 m	250 m	750 m	250 m	750 m	250 m	750 m	250 m	750 m
PLAND_DV*	0	0	0	18.8	57.3	64.9	0	2.4	6.8	30.3	30	54.2
PLAND_SM*	70	33.9	55.9	24.5	5.5	4.6	64.1	42.6	51.4	37	17.3	3.5
TE_W	600	4,830	660	5,880	690	4,200	750	6,350	1,500	5,970	1,830	7,680
TE_DV	0	0	0	2,880	600	3,840	0	750	300	3,420	810	5,160
TE_SM	600	4,830	1,640	7,260	780	4,440	750	6,090	3,300	7,230	1,230	4,560
TECI_DV(W)*	0	0	0	0.11	0.32	0.42	0	0.075	0.042	0.21	0.27	0.46
TECI_SM(W)*	1	1	0.67	0.52	0.42	0.47	0.96	0.89	0.53	0.51	0.47	0.39
TECI_DV(SM)*	0	0	0	0.31	0.5	0.28	0	0.043	0.075	0.3	0.26	0.36
SHAPE*	1.2	1.6	2	2.1	1.1	1.3	1.5	1.2	1.9	2	1.3	1.3
CLUMPY*	0.93	0.94	0.64	0.65	0.6	0.49	0.88	0.83	0.55	0.6	0.56	0.5
CREEKS	14	51	6	20	1	9	10	31	5	19	1	3
CONNECT*	0.73	0.74	0.51	0.53	0	0.14	0.68	0.64	0.42	0.4	0	0.33
CONTIG*	0.88	0.91	0.74	0.67	0.42	0.54	0.86	0.86	0.68	0.59	0.53	0.43
DIVI	0.54	0.68	0.74	0.93	0.9	0.9	0.56	0.54	0.87	0.93	0.94	0.96
SPLIT*	2	9.6	3.7	63.7	654.1	4,961.3	2.4	13.4	13.9	187.6	68.9	4,348.1
MESH*	9.7	18.6	5.3	2.8	0.03	0.03	8.1	13.3	1.4	0.9	0.3	0

4.0 (McGarigal et al. 2002). Primary emphasis was placed on the composition and configuration of the developed (DV) and salt-marsh (SM) classes in relation to the water (W) class. The percentages of the landscape occupied by the DV class (PLAND_DV) and SM class (PLAND_SM) were calculated for each spatial scale. Total edge (TE) and total edge contrast index (TECI) were used to estimate the relative amount of functional and nonfunctional class edges. For example, the amount of hardened shoreline (TECI_DV[W]) was calculated as W cell edges contrasted against DV cell edges, the amount of natural shoreline (TECI_SM[W]) was calculated as W edge cells contrasted against SM class cells, and the amount of salt-marsh edge that was bordered by developed surfaces (TECI_DV[SM]) was calculated as the amount of SM cell edge contrasted against DV cell edge (see Table 2). For the SM class, the complexity and aggregation of cells were calculated using the area-weighted mean shape index (SHAPE), the contiguity index (CONTIG), and the clumpiness index (CLUMPY). Salt marsh isolation was quantified with the connectivity index (CONNECT), which was used to describe creek connectivity within each spatial scale (proportion of small, first-order creek mouths in each buffer that were located within 250 m of each other; estimated from 2007 1-m orthorectified color infrared imagery in ArcGIS). Three spatial metrics were used to quantify the degree of salt marsh fragmentation (Jaeger 2000). The landscape division index (DIVI) was the probability (D) that two randomly chosen pixels in the landscape are *not* situated in the same salt-marsh patch. The splitting index (SPLIT) was defined as the number of salt-marsh patches (S) that resulted from dividing the landscape by the observed mean salt-marsh patch size while holding D constant. Effective mesh size (MESH) was the mean patch area obtained when the landscape was divided into S patches.

Faunal Collections

Weekly from May 3 to June 4, 2010, nekton and macroinfauna were collected and environmental variables were measured in each of the six tidal creeks (2 estuaries × 3 landscape types). Modified fyke nets with two 0.91-m-diameter steel hoops positioned 1 m apart and with a single throat located on the first hoop (Memphis Net and Twine) were used to collect nekton in each creek. Fyke nets consisted of two wings (3 m long, 1.8 m high) and a mouth (3 m wide, 1.8 m high). Each net (including the wings and mouth) was constructed of 5-mm stretched nylon mesh, and the bottom of the net's leading edge was constructed with double-weighted lead line. Nekton were collected by placing the fyke net across the wet cross-sectional area of the tidal creek mouth at slack high tide (depth = 35.0–59.0 cm) and extending each wing onto the salt-marsh platform at an approximate 45° angle. Poles (10 cm in diameter, 4.0 m long) driven into the marsh platform were attached to the net at the float and lead lines on each side of the net mouth and at the end of each wing. Estuaries in the northern Gulf of Mexico are microtidal, and salt-marsh tidal creeks rarely drain completely except during extreme meteorological events (Rozas 1995). Therefore, once the tide had ebbed and all water had drained from the marsh surface (∼6 h after high tide), a 4.9-m minnow seine (3.2-mm stretched mesh) was pulled through about 75% of the total creek length (coinciding with the low-water mark) and into the mouth of the fyke net. The lead line was lifted out of the water, and nektonic organisms, including those in the wings, were funneled into the net mouth. Due to time constraints, a maximum of two creeks in the same estuary could be sampled on a given day. All nekton were removed from the cod end of the fyke net, placed on ice in the field, and returned to the laboratory, where they were frozen until they could be identified and enumerated. Nekton abundance in each fyke net was considered the CPUE.

Concomitant with nekton collections, environmental data (i.e., depth; temperature, °C; salinity, ‰; and dissolved oxygen [DO], mg/L; all measured with a hand-held YSI 85 meter) and macroinfauna were collected weekly at the mouth, middle, and head of each tidal creek (2 estuaries × 3 creeks × 4 weeks × 3 locations within a creek = 72 samples). Each macroinfaunal sample was taken from mid-channel by using a pole-mounted Ekman grab (0.024 m^2); the sample was washed through a 500-μm sieve in the field to remove excess mud, preserved in 7% buffered formalin containing rose bengal stain, and returned to the laboratory. Macroinfauna were sorted from each sample by using one of two methods. Samples with a high volume of detrital material were fluidized with 3.8–7.6 L (1–2 gal) of water and were quartered into approximately equal-volume samples with a Motodo plankton splitter; macroinfauna were then isolated from two of the four samples. Thirty-eight samples were split, and the mean difference in abundance between the two splits within a creek ranged from 3.1 to 4.0 total individuals (range of SD = 1.25–3.87; range of CV = 22–35%). The remaining 34 samples contained a low volume of detrital material, so macroinfauna were obtained from these samples in their entirety. All macroinfaunal samples were examined in random order in groups of eight samples, from which one sample was randomly selected for quality control. If the number of missed animals in a quality control sample was greater than 10% of the total animals that were observed during the first sorting event, then all eight samples were re-examined. Based on this criterion, one group of samples was re-examined and the percentage of animals that were missed ranged from 0.0% to 3.8%, with the initial quality control sample having missed 4 (11%) of 36 individuals. The remaining quality control samples ranged from 0% to 3% of animals missed. All macroinfaunal animals were identified to the lowest possible taxonomic level. Most individuals were identifiable to the species level. However, in taxonomic groups for which it was not possible to identify every individual to the species level, the lowest confirmed taxonomic level was used for classification purposes. To facilitate comparisons with other studies, macroinfaunal densities were scaled to 1 m^2 for all analyses.

Statistical Analyses

Univariate analyses.—Taxonomic richness and Simpson's evenness index ($1-\lambda$; Clarke and Gorley 2006) were calculated for both nekton and macroinfaunal assemblages and were compared between estuaries (BB and PRE) and among landscapes (IN, PU, and CU) by using two-way ANOVA. An initial three-way ANOVA indicated that diversity measures for macroinfauna did not differ among locations within each creek ($P > 0.05$); as a result, the pooled samples for each week were treated as replicates.

Water temperature, salinity, DO, and depth were averaged across weeks and compared between estuaries and among landscapes and locations within the tidal creek (mouth, middle, and head) by using three-way ANOVA. For all univariate ANOVAs, relative F-values and associated effect size (partial η^2) values were used to assess the importance of significant interactions between main effects (Green and Salkind 2008). If the effect size of the interaction term was small (partial $\eta^2 \leq 0.3$; Field 2005) relative to the main effect or if there was no interaction, Tukey's honestly significant difference (HSD) post hoc test was used to examine significant differences among treatments for each variable. All variables used in univariate analyses were $\log_{10}$ transformed and met the assumptions of normality (Kolmogorov–Smirnov test) and homogeneity (Levene's test). All univariate analyses were performed at an α level of 0.05 in SPSS version 20 (IBM).

Multivariate analyses.—Initial analysis of both nekton and macroinfaunal data indicated that collection week was not significant in any model and had negative variance component estimates (Fletcher and Underwood 2002). Therefore, samples were pooled across weeks for all multivariate analyses. Furthermore, macroinfaunal assemblages did not differ among locations within creeks (permutational multivariate ANOVA [PERMANOVA]: pseudo-$P > 0.05$) and were summed across all three locations for a given week to facilitate multivariate correlations with physical-chemical data by maintaining resemblance matrices of equal size. For both spatial scales, stationary landscape metrics were coupled with the dynamic environmental variables averaged weekly within each creek into a set of physical-chemical variables and were used to construct a resemblance matrix based on normalized Euclidean distance measures.

Rare taxa (those comprising less than 0.2% of total abundance for each assemblage) were removed, and a resemblance matrix of Bray–Curtis similarity values for each sample was created from fourth-root-transformed CPUE data (for nekton) or density (for macroinfauna) to downweight the importance of numerically dominant taxa (Clarke and Gorley 2006). Levels of similarity among samples (physical-chemical, nekton, and macroinfauna) were statistically compared between estuaries and among landscapes by using a full-factorial PERMANOVA (permutations = 999; Anderson et al. 2008). Due to issues associated with pseudoreplication, PERMANOVA is prone to type I errors (Atkinson et al. 2011). Therefore, conservative pseudo-F ratios, which were computed using the interaction error term as the denominator, were used in lieu of conventional pseudo-F ratios to assess the level of significance. Estimated variance components were used to assess the importance of significant main effects and interaction terms. Pairwise a posteriori comparisons using the multivariate analog of the t-test (pseudo-t) were made for each level of significantly different main effects and interaction terms. Patterns based on group average cluster analysis (CLUSTER) and similarity profiles (SIMPROF) were projected onto two-dimensional multidimensional scaling (MDS) ordination plots to examine the relationships among samples and to identify well-differentiated groupings. Rank dissimilarities (SIMPER) for nekton and macroinfaunal assemblages were used to identify characteristic taxa that were driving differences among (1) significant factors identified by PERMANOVA tests and (2) significant clusters identified by the CLUSTER and SIMPROF analyses.

The statistical agreement between physical-chemical and assemblage resemblance matrices was assessed with a nonparametric form of the Mantel test (RELATE; permutations = 999). Multivariate correlation (BEST; permutations = 999) was used to quantitatively examine the agreement between faunal assemblages and physical-chemical variables. The BEST procedure conducted rank correlations (coefficient ρ) to determine the scale of pattern matching between the physical-chemical resemblance matrix and each of the resemblance matrices for the nekton and macroinfaunal assemblages. This approach searches all possible combinations of physical-chemical variables (BIOENV function) to identify the subset of physical-chemical variables that give the best correlative explanation of the assemblage structure. The best subsets of physical-chemical variables were further investigated by using Pearson's product-moment correlations to relate individual species' abundances to the landscape and environmental factors. All multivariate analyses were performed using PRIMER version 6.0 (Clark and Gorley 2006). Pearson's product-moment correlations were performed in SPSS.

RESULTS

Physical-Chemical Analyses

Environmental characteristics varied spatially throughout the study area and within the tidal creeks. Mean water depth at high tide ranged from 17 to 45 cm and differed only among locations within tidal creeks (ANOVA: $P = 0.003$), with the creek head being significantly shallower than the creek mouth (Tukey's HSD test: $P = 0.002$). Water temperature (range = 27.1–30.4°C) differed between estuaries (ANOVA: $P = 0.001$) and among landscape types (ANOVA: $P = 0.04$). On average, PRE was approximately 1.0°C warmer than BB (Tukey's HSD test: $P = 0.03$), and PU landscapes were about 1.5°C cooler than IN and CU landscapes (Tukey's HSD test: $P = 0.03$). Although DO concentrations (2.5–6.6 mg/L) fell within a suitable range for most estuarine nekton species (Wannamaker and Rice 2000), DO differed between estuaries (ANOVA: $P = 0.003$) and there was a significant estuary × landscape interaction (ANOVA: $P = 0.017$). However, both factors accounted for a similar amount of model variation (estuary: partial $\eta^2 = 0.152$; estuary × landscape: partial $\eta^2 = 0.141$) and precluded post hoc comparison of the main effect. Overall, DO concentrations were lower in BB (mean ± SE = 3.4 ± 0.7 mg/L) than in PRE (4.2 ± 0.5 mg/L), and this difference was further exacerbated by the lowest DO concentrations observed in BB-PU landscapes (2.7 ± 0.4 mg/L). Similarly, salinity differed among landscapes (ANOVA: $P < 0.001$; partial $\eta^2 = 0.474$), and there was a significant estuary × landscape interaction (ANOVA: $P < 0.001$; partial $\eta^2 = 0.455$). Both IN and CU landscapes were more saline than PU landscapes (Tukey's HSD test: $P < 0.001$), and the interaction was driven by higher salinities observed at the PRE-CU site (mean ± SE = 6.4 ± 1.0‰) relative to the BB-CU site (2.2 ± 1.0‰) and at the BB-IN site (6.7 ± 1.7‰) relative to the PRE-IN site (2.6 ± 0.9‰). However, observed mean salinities at all sites (1.9–8.4‰) fell within the oligohaline range for estuarine organisms (Bulger et al. 1993).

Regardless of estuary, the composition and configuration of the three coastal landscape types in this study were clearly different at both the 250- and 750-m scales (Table 2). In the IN landscape, SM was the dominant class (PLAND_SM). As a result, shoreline consisted almost exclusively of natural salt-marsh edge (TECI_SM[W] = 89–100%). Salt-marsh cells within the IN landscapes tended to be aggregated (CLUMPY ≥ 0.8) and simply shaped (SHAPE = 1.2–2.0). Furthermore, tidal creeks were more connected at both the 250- and 750-m spatial scales (CONNECT = 63.7–74.4%) and were unfragmented (DIVI, MESH, and SPLIT). In both BB and PRE, PU landscapes were dominated by the SM class at the 250-m spatial scale (PLAND_SM = 64.1% and 55.9%, respectively). However, at the 750-m scale, PU landscapes were a mix of DV (PLAND_DV = 18.8% for BB and 50.3% for PRE) and SM (PLAND_SM = 24.5% for BB and 42.6% for PRE) classes. Overall, PU landscapes had more salt-marsh edge (i.e., TE) than either the IN or CU landscapes due to the large, convoluted creeks that are a dominant feature of the landscape and resulted in greater shape complexity (SHAPE = 1.9–2.1). However, the amount of natural shoreline (TECI_SM[W]) decreased inversely with the amounts of developed surface (PLAND_DV) and hardened shoreline (TECI_DV[W]), resulting in salt-marsh landscapes that were more urbanized (DIVI, MESH, and SPLIT) at the 750-m spatial scale. On the other hand, CU landscapes were dominated by the DV class (PLAND_DV = 30.0–64.9%), and hardened shorelines (TECI_DV[W]) constituted 42.3–52.8% of the shoreline in this landscape type. Salt-marsh patches in CU landscapes tended to be small (PLAND_SM = 3.5–17.3%), simply shaped (SHAPE = 1.1–1.3), moderately aggregated (CLUMPY = 0.5–0.6), and highly urbanized (DIVI, MESH, and SPLIT).

The conventional PERMANOVA indicated that physical-chemical variables differed between estuaries and among landscape types and that there was a significant interaction for both spatial scales (Table 3). However, variance components attributed most of the model variation to the landscape level, and the conservative model suggested that physical-chemical variables differed only among landscape types. In pairwise comparisons, all three landscape types were dissimilar at both the 250- and 750-m spatial scales. Further, due to the stationary nature of the landscape variables, all of the residual variance (i.e., within replicate) was attributable to the variation

TABLE 3. Results of permutational multivariate ANOVA on normalized Euclidean distance matrices based on physical-chemical variables for 250- and 750-m spatial extents (landscape types: IN = intact natural; PU = partially urbanized; CU = completely urbanized) in the Biloxi Bay estuary (BB) and Pascagoula River estuary (PRE). Pairwise comparisons are the results of pseudo-*t*-tests (MSE = mean square error; $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$).

Source	df	MSE	Conventional pseudo-*F*	Conservative pseudo-*F*	Variance component	Pairwise comparisons
			250-m spatial extent			
Estuary	1	14.86	4.35*	1.32	0.54	
Landscape	2	100.13	29.42**	8.85**	3.48	IN ≠ PU ≠ CU
Estuary × landscape	2	11.31	3.32*		1.41	BB-CU ≠ PRE-CU
Residual	18	3.40				
Total	23					
			750-m spatial extent			
Estuary	1	14.70	4.32*	0.95	0.98	
Landscape	2	95.01	28.21***	6.13	5.4	IN ≠ PU ≠ CU
Estuary × landscape	2	15.51	4.56*		1.74	BB-IN ≠ PRE-IN
Residual	18	3.40				
Total	23					

in environmental variables discussed previously. These results are corroborated by the MDS plots, which showed significant separation among the landscape types: four significant groupings were observed at the 250-m scale, and three significant groupings were observed at the 750-m scale (Figure 2).

Nekton Assemblage Analyses

In total, 26,379 individual fish representing 36 species were collected (Table 4). Six species comprised approximately 94% of the total catch: Gulf Menhaden, Bay Anchovy, White Mullet, Gulf Killifish, Spot, and Sand Seatrout. Decapod crustaceans were represented by 35,714 individuals from six species (Table 5). Grass shrimp *Palaemonetes* spp. (73.3%), brown shrimp *Farfantepenaeus aztecus* (21.4%), and blue crab *Callinectes sapidus* (3.3%) dominated the total decapod crustacean catch. Nekton species richness differed only among the landscape types (ANOVA: $P < 0.001$) and was greater in PU landscapes (Tukey's HSD test; richness [mean ± SE] = 18.1 ± 0.7) than in the IN (15.6 ± 1.2) or CU (15.3 ± 1.4) landscapes; PU landscapes, however, contained more freshwater species (e.g., Bluegill, Redear Sunfish, and Largemouth Bass) due to the lower salinity. Simpson's evenness index ($1 - \lambda$) differed only among landscapes (ANOVA: $P < 0.01$), and the nekton assemblage in CU landscapes (Tukey's HSD; evenness index [mean ± SE] = 0.68 ± 0.063) was more evenly distributed than that in either the IN landscapes (0.57 ± 0.023) or the PU landscapes (0.59 ± 0.031) due to the presence of highly abundant species (e.g., Gulf Menhaden and grass shrimp) in the latter two landscape types.

Once the rare species were removed from the data, 21 nekton species were retained for multivariate analyses (Tables 4, 5). Nekton assemblage composition differed between estuaries and among landscapes, and there was a significant estuary × landscape interaction (PERMANOVA; Table 6a). However,

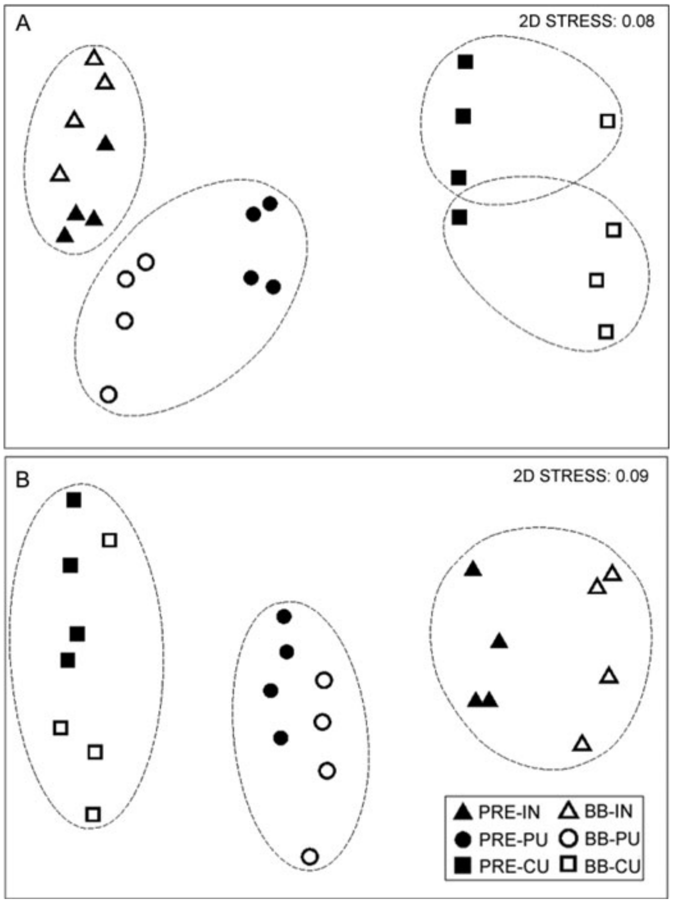

FIGURE 2. Multidimensional scaling (MDS) plots of the physical-chemical data for the **(a)** 250-m spatial extent and **(b)** 750-m spatial extent (landscape types: IN = intact natural; PU = partially urbanized; CU = completely urbanized) in the Biloxi Bay estuary (BB) and Pascagoula River estuary (PRE). Dashed contours identify significant clusters (based on Euclidean distance) from agglomerative hierarchical clustering and similarity profiles.

TABLE 4. Mean (± SE) CPUE (individuals/sample) of fish species collected from intact natural (IN), partially urbanized (PU), and completely urbanized (CU) landscapes in the Biloxi Bay and Pascagoula River estuaries. Asterisks indicate species that were used in multivariate analyses (i.e., species comprising ≥ 0.2% of total abundance).

Species	IN	PU	CU
Spotted Gar *Lepisosteus oculatus*		0.3 (0.1)	
Ladyfish *Elops saurus*	0.1 (0.1)	0.1 (0.1)	
American Eel *Anguilla rostrata*			0.1 (0.1)
Speckled Worm Eel *Myrophis punctatus*		0.1 (0.1)	
Gulf Menhaden *Brevoortia patronus**	2,225.6 (1,061.9)	170.4 (95.2)	148.1 (163.7)
Bay Anchovy *Anchoa mitchilli**	96.0 (46.9)	15.9 (6.3)	0.4 (0.3)
White Mullet *Mugil curema**	43.0 (21.7)	22.0 (11.9)	35.4 (20.2)
Gulf Killifish *Fundulus grandis**	40.8 (11.8)	22.1 (5.1)	15.6 (5.3)
Saltmarsh Topminnow *Fundulus jenkinsi**	0.1 (0.1)	27.3 (13.5)	
Bayou Killifish *Fundulus pulvereus*			0.1 (0.1)
Longnose Killifish *Fundulus similis**	0.5 (0.6)		5.8 (3.3)
Diamond Killifish *Adinia xenica**	6.1 (3.5)	7.6 (4.3)	6.4 (2.2)
Rainwater Killifish *Lucania parva*		1.1 (1.0)	
Sheepshead Minnow *Cyprinodon variegatus**	1.6 (0.9)	1.9 (0.9)	14.0 (5.1)
Sailfin Molly *Poecilia latipinna**	1.3 (1.0)	8.1 (2.4)	17.1 (11.4)
Western Mosquitofish *Gambusia affinis*		0.5 (0.2)	0.8 (0.6)
Inland Silverside *Menidia beryllina**	8.1 (5.4)	7.9 (4.6)	2.4 (1.7)
Bluegill *Lepomis macrochirus*		0.1 (0.1)	
Redear Sunfish *Lepomis microlophus**		1.0 (1.0)	
Largemouth Bass *Micropterus salmoides*	0.4 (0.4)	2.0 (1.0)	0.6 (0.5)
Chain Pipefish *Syngnathus louisianae*	0.1 (0.1)	2.0 (1.0)	
Pinfish *Lagodon rhomboides**	6.3 (2.4)	12.0 (7.5)	7.4 (5.7)
Spot *Leiostomus xanthurus**	91.5 (34.4)	85.6 (23.3)	50.5 (25.3)
Red Drum *Sciaenops ocellatus*		0.1 (0.1)	
Black Drum *Pogonias cromis*	2.1 (2.4)		
Sand Seatrout *Cynoscion arenarius**	50.3 (23.2)	0.8 (0.6)	2.6 (1.8)
Spotted Seatrout *Cynoscion nebulosus*	0.1 (0.1)		
Silver Perch *Bairdiella chrysoura*	1.0 (0.8)		0.3 (0.3)
Atlantic Croaker *Micropogonias undulatus*		0.5 (0.4)	0.1 (0.1)
Freshwater Goby *Ctenogobius shufeldti**		23.4 (21.7)	0.3 (0.3)
Darter Goby *Ctenogobius boleosoma**		0.1 (0.1)	2.1 (1.5)
Naked Goby *Gobiosoma bosc*	0.1 (0.1)		
Lyre Goby *Evorthodus lyricus**	0.3 (0.2)	0.9 (0.7)	1.1 (0.7)
Highfin Goby *Gobionellus oceanicus*		1.3 (0.9)	
Southern Flounder *Paralichthys lethostigma**	3.1 (1.2)	2.9 (1.1)	4.5 (1.6)
Bay Whiff *Citharichthys spilopterus**	5.6 (2.4)	3.8 (2.2)	1.5 (0.5)
Least Puffer *Sphoeroides parvus*	6.4 (6.4)		

the conventional pseudo-*F*-test was compromised by a lack of independence among sampling units (i.e., weeks); the conservative pseudo-*F*-test showed that nekton assemblage composition differed among landscapes but not between estuaries. Despite attributing most of the model variation to the landscape level and residual error term, the interaction still accounted for a large portion of the variation, suggesting that the magnitude of the difference in nekton assemblages among landscapes was not similar across estuaries. Indeed, the PRE-PU and BB-PU landscapes differed markedly in the composition of their nekton assemblages. The MDS plots showed a similar differentiation among landscapes, with two significant groupings at 65% similarity (CLUSTER): group 1 contained all of the IN samples, the PRE-PU samples, and a single BB-CU sample; and group 2 contained the remaining PU and CU samples (Figure 3). Nekton assemblages in the IN and CU landscapes were most dissimilar (SIMPER; mean dissimilarity = 71.86%), followed by IN versus PU (mean dissimilarity = 58.39%) and PU versus CU (mean dissimilarity = 56.30%). Furthermore, the CPUEs of a few species (e.g., grass shrimp, Gulf Menhaden,

TABLE 5. Mean (±SE) CPUE (individuals/sample) of decapod crustaceans collected from intact natural (IN), partially urbanized (PU), and completely urbanized (CU) landscapes in the Biloxi Bay and Pascagoula River estuaries. Asterisks indicate species that were used in multivariate analyses (i.e., species comprising $\geq 0.2\%$ of total abundance).

Taxon	IN	PU	CU
Blue crab*	56.9 (9.4)	53.0 (17.0)	36.4 (12.5)
Fiddler crabs *Uca* spp.	0.6 (0.5)	1.4 (0.7)	0.9 (0.9)
Brown shrimp*	835.8 (282.4)	81.6 (37.8)	37.4 (13.2)
White shrimp *Litopenaeus setiferus*	0.3 (0.1)		
Grass shrimp*	2,212.3 (435.7)	1,021.1 (374.6)	126.9 (24.9)
Ohio shrimp *Macrobrachium ohione*	0.1 (0.1)		

brown shrimp, Spot, and blue crab) contributed much of the dissimilarity among landscape types (Figure 4) and between the two significant clusters (Figure 5).

Relationships between Nekton Assemblage and Physical-Chemical Patterns

Nekton assemblage patterns were significantly correlated with the physical-chemical patterns at the 250-m (BEST: global $R = 0.59$, $P = 0.01$) and 750-m (BEST: global $R = 0.68$, $P = 0.01$) spatial scales. For both spatial scales, the relative amounts of both natural salt-marsh edge (i.e., TECI_SM[W]) and developed shoreline (TECI_DV[W]) and the amount of salt-marsh habitat (PLAND_SM) were commonly correlated with the nekton assemblage patterns (Table 7). The three-variable model that included TECI_SM(W), PLAND_SM, and tidal creek connectivity (CONNECT) had the highest correlation with nekton patterns at the 250-m spatial scale (BEST: $\rho = 0.571$), but CONNECT alone was similarly correlated (BEST: $\rho = 0.569$). At the 750-m spatial scale, salt marsh fragmentation (SPLIT) was an important correlate of nekton patterns. For most nekton species, CPUE increased significantly with TECI_SM(W), PLAND_SM, and CONNECT and significantly decreased with increasing SPLIT (e.g., Gulf Menhaden, Bay Anchovy, Gulf Killifish, grass shrimp, and brown shrimp; Table 8). Conversely, the Sheepshead Minnow and Sailfin Molly were negatively correlated with CONNECT and positively correlated with SPLIT. Several species showed no correlation with any of these spatial metrics (e.g., Saltmarsh Topminnow, Spot, Southern Flounder, and blue crab).

Macroinfaunal Assemblage Analyses

In total, 4,480 individual macroinfauna representing 25 taxa were collected in 72 Eckman samples (Table 9). Mean macroinfaunal densities (scaled to m^2) ranged from 0.0 to 17,001.4 individuals/m^2. During the sampling period, the macroinfaunal assemblage was dominated by seven taxa: Chironomidae (midges; 29.87%), Capitellidae (polychaetes, 20.38%; includes *Capitella capitata*, *Mediomastus californiensis*, and *Heteromastus filiformis*), Tubificidae (oligochaetes; 17.66%), scuds *Gammarus* spp. (7.12%), the polychaete *Amphicteis floridus* (7.01%), Nereididae (polychaetes, 6.78%; includes *Neanthes succinea*, *Laeonereis culveri*, and *Stenonineris martini*), and the

TABLE 6. Results of permutational multivariate ANOVA on fourth-root-transformed Bray–Curtis similarity matrices for nekton and macroinfaunal assemblages (landscape types: IN = intact natural; PU = partially urbanized; CU = completely urbanized) in the Biloxi Bay estuary (BB) and Pascagoula River estuary (PRE). Pairwise comparisons are the results of pseudo-*t*-tests (MSE = mean square error; $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$).

Source	df	MSE	Conventional pseudo-*F*	Conservative pseudo-*F*	Variance component	Pairwise comparisons
Nekton assemblage						
Estuary	1	615.38	2.37*	0.72	5.45	
Landscape	2	2,394.52	9.23***	2.81*	16.36	IN ≠ PU ≠ CU
Estuary × landscape	2	853.51	3.29**		12.19	BB-PU ≠ PRE-PU
Residual	18	259.52				
Total	23					
Macroinfaunal assemblage						
Estuary	1	3,033.50	2.92*	0.65	12.89	
Landscape	2	5,902.20	5.68***	1.26	24.65	
Estuary × landscape	2	4,688.44	4.51*		30.2	BB-CU ≠ PRE-CU
Residual	18	1,039.60				
Total	23					

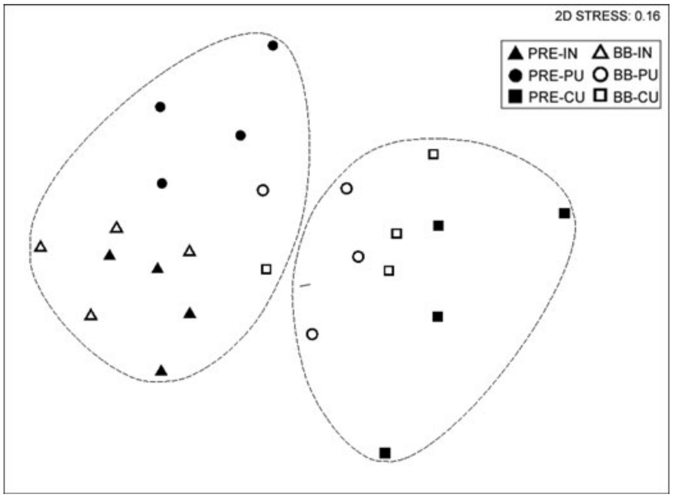

FIGURE 3. Multidimensional scaling (MDS) plot of the nekton assemblages for each combination of estuary (Biloxi Bay estuary [BB]; Pascagoula River estuary [PRE]) and landscape type (IN = intact natural; PU = partially urbanized; CU = completely urbanized). Dashed contours identify significant clusters (based on Bray–Curtis similarity) from agglomerative hierarchical clustering and similarity profiles.

polychaete *Streblospio benedicti* (6.41%; Table 9). Taxonomic richness did not differ between estuaries (richness [mean ± SE] = 6.50 ± 0.78 for PRE and 5.91 ± 1.01 for BB; ANOVA: $P = 0.63$) or among landscapes (richness [mean ± SE] = 7.38 ± 1.27 for IN, 6.13 ± 0.90 for PU, and 5.63 ± 0.92 for CU; ANOVA: $P = 0.25$), and there was no significant estuary × landscape interaction (ANOVA: $P = 0.15$). Simpson's evenness index ($1 - \lambda$) did not differ between estuaries (evenness index [mean ± SE] = 0.55 ± 0.066 for PRE and 0.58 ± 0.042 for BB; ANOVA: $P = 0.17$) but was significantly different among landscapes (ANOVA: $P = 0.008$; partial $\eta^2 = 0.42$), and there was a significant interaction (ANOVA: $P = 0.02$; partial $\eta^2 = 0.36$) that accounted for a similar proportion of model variance. Although macroinfaunal assemblages in both PRE and BB were more evenly distributed in the IN (evenness index [mean ± SE] = 0.64 ± 0.047) and PU (0.57 ± 0.089) landscapes than in CU landscapes (0.42 ± 0.060), taxa were more evenly distributed in BB-PU (0.71 ± 0.039) than in PRE-PU (0.42 ± 0.079).

After the removal of rare macroinfaunal taxa, 13 taxa were retained for multivariate analyses (Table 10). The conventional PERMANOVA indicated significant differences in macroinfaunal assemblages at all levels, including a significant estuary × landscape interaction (Table 6b); however, the estimate from the conservative pseudo-F-test indicated that macroinfaunal assemblage structure did not differ between estuaries or among landscapes. Both the residuals and interaction term accounted for a large proportion of the model variation, suggesting that (1) macroinfaunal assemblages differed markedly among samples within sites and (2) differences in macroinfaunal assemblages were not consistent either across estuaries or across landscape types. The MDS ordination of the macroinfaunal resemblance data corroborated the PERMANOVA results (Figure 6), and six significant clusters were identified at 40% similarity.

TABLE 7. Multivariate correlation coefficients (ρ) between physical-chemical variables and the nekton or macroinfaunal resemblance matrices. Displayed are the top-four models from the multivariate correlation analysis (i.e., BEST) output (TEMP = temperature; SAL = salinity; other variables are defined in Table 1).

Number of variables	ρ	Variables
Nekton assemblage, 250-m extent		
3	0.571	TECI_SM(W), PLAND_SM, CONNECT
1	0.569	CONNECT
2	0.563	TECI_SM(W), CONNECT
2	0.559	TECI_DV(W), CONNECT
Nekton assemblage, 750-m extent		
2	0.700	TECI_DV(W), SPLIT
3	0.660	TECI_SM(W), PLAND_SM, SPLIT
3	0.659	PLAND_SM, TECI_DV(SM), SPLIT
2	0.651	PLAND_SM, SPLIT
Macroinfaunal assemblage, 250-m extent		
3	0.395	PLAND_SM, TECI_DV(SM), SAL
3	0.391	TECI_DV(W), TECI_DV(SM), SPLIT
4	0.390	TECI_DV(SM), SPLIT, TEMP, SAL
5	0.385	PLAND_SM, TECI_DV(SM), SPLIT, TEMP, SAL
Macroinfaunal assemblage, 750-m extent		
6	0.282	TECI_DV(W), PLAND_SM, TECI_DV(SM), SPLIT, TEMP, SAL
6	0.282	TECI_DV(W), PLAND_SM, TECI_DV(SM), SPLIT, DEPTH, SAL
5	0.279	TECI_DV(W), PLAND_SM, TECI_DV(SM), TEMP, SAL
5	0.279	TECI_DV(W), PLAND_SM, TECI_DV(SM), SPLIT, SAL

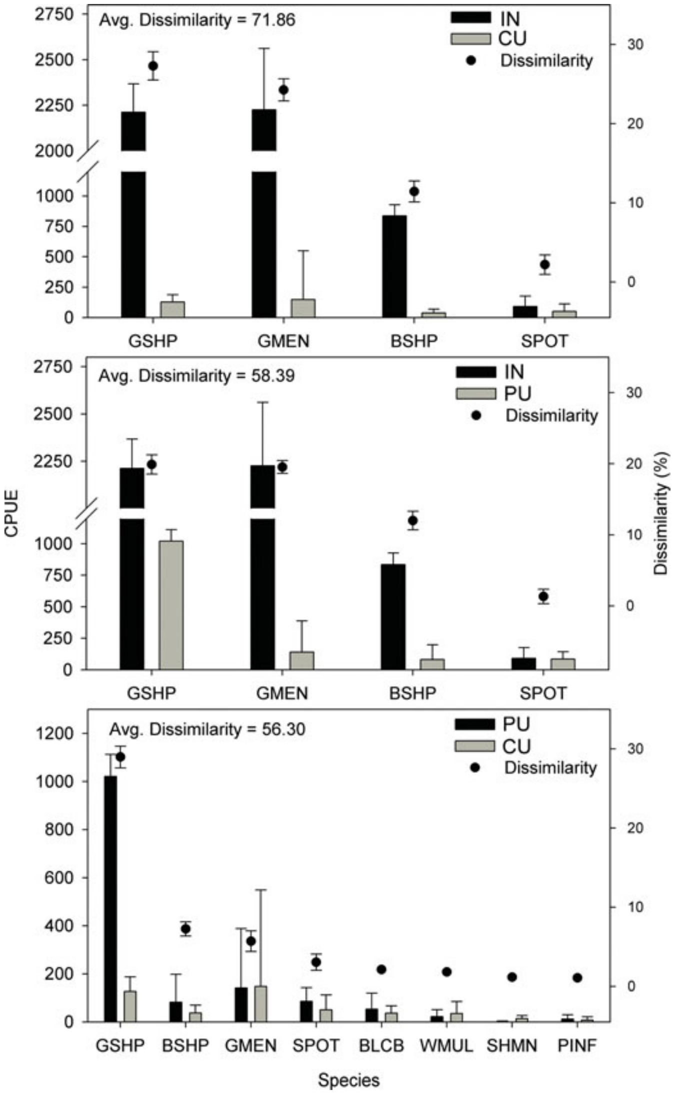

FIGURE 4. Mean (± SD) CPUE (individuals/sample) of the nekton species contributing to 90% of the cumulative variation among landscape types (IN = intact natural; PU = partially urbanized; CU = completely urbanized) in the Biloxi Bay and Pascagoula River estuaries. Mean dissimilarity between landscapes is shown in the upper left corner of each plot; mean (± SD) dissimilarity attributed to each species is indicated by the black circles. Note the difference in CPUE scale for the bottom panel (GSHP = grass shrimp; BSHP = brown shrimp; GMEN = Gulf Menhaden; SPOT = Spot; BLCB = blue crab; WMUL = White Mullet; SHMN = Sheepshead Minnow; PINF = Pinfish).

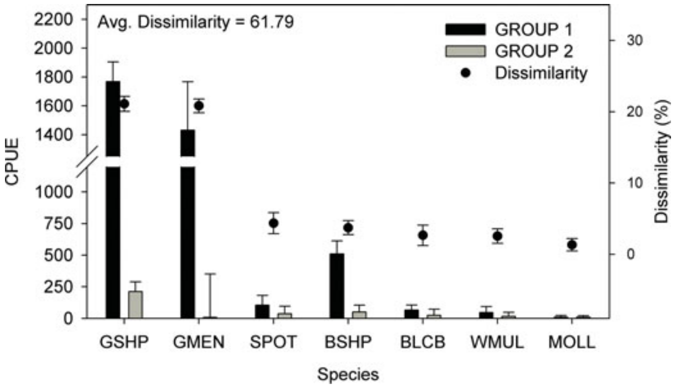

FIGURE 5. Mean (± SD) CPUE (individuals/sample) of the nekton species contributing to 90% of the cumulative variation among significant groupings identified by agglomerative hierarchical clustering (see Figure 3). Mean dissimilarity between groups is shown in the upper left corner of each plot; mean (± SD) dissimilarity attributed to each species is indicated by the black circles (GSHP = grass shrimp; GMEN = Gulf Menhaden; SPOT = Spot; BSHP = brown shrimp; BLCB = blue crab; WMUL = White Mullet; MOLL = Sailfin Molly).

Relationships between Macroinfaunal Assemblage and Physical-Chemical Patterns

Despite the absence of a clear pattern, the macroinfaunal assemblage patterns were significantly correlated with the physical-chemical data at both the 250-m (BEST: global $R = 0.32$, $P = 0.01$) and 750-m (BEST: global $R = 0.28$, $P = 0.01$) spatial scales. For the 250-m spatial scale, three variables (TECI_DV[SM], SPLIT, and salinity) were commonly correlated (BEST: $\rho = 0.395$) with macroinfaunal patterns (Table 7b). The variables TECI_DV(W), PLAND_SM, SPLIT, temperature, and salinity were weakly correlated (BEST: $\rho = 0.282$) with the macroinfaunal assemblage at the 750-m scale. However, at this spatial scale, only combinations of five or six variables were correlated with macroinfaunal patterns, suggesting that a parsimonious solution could not be found. The density of *S. benedicti* was positively correlated with PLAND_SM and negatively correlated with TECI_DV(SM) and SPLIT (Pearson's *r*; Table 10). Densities of tubificid oligochaetes and capitellid polychaetes were positively correlated with TECI_DV(SM). Furthermore, the densities of a number of taxa were positively (amphipods *Apocorophium* spp., the amphipod *Edotea triloba*, and capitellid polychaetes) or negatively (Chironomidae, tubificid oligochaetes, and *A. floridus*) correlated with salinity. The densities of chironomids, tubificid oligochaetes, *S. benedicti*, and *A. floridus* were negatively correlated with SPLIT.

DISCUSSION

We used a landscape ecology approach to show that although salt-marsh landscapes arrayed along a gradient of urbanization hosted similar suites of species, there were clear compositional differences in nekton assemblages and, to a lesser extent, macroinfaunal assemblages. We have demonstrated that the amount of salt-marsh habitat, amount of natural shoreline (defined as the salt marsh–water interface), tidal creek connectivity, and salt marsh fragmentation were consistent correlates of abundance for a number of species. Despite inconsistent results across assemblages, this work continues to build on the growing paradigm that although the amount of salt-marsh habitat is a driver of both nekton and macroinfaunal production (Weinstein 1979; Boesch and Turner 1984), the composition and configuration of the surrounding landscape are equally important (Guest

TABLE 8. Pearson's product-moment correlation coefficients for nekton CPUEs in relation to physical-chemical variables identified in the multivariate correlation analysis (i.e., BEST model; $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$). Landscape metrics are defined in Table 1.

	250-m extent		750-m extent		
Species	TECI_SM(W)	PLAND_SM	CONNECT	TECI_SM(W)	SPLIT
Gulf Menhaden	0.47*	0.35*	0.38*	0.55**	−0.24
Bay Anchovy	0.55**	0.46*	0.48**	0.60**	−0.36*
White Mullet	0.085	−0.0011	0.034	0.21	0.048
Gulf Killifish	0.51**	0.44*	0.46	0.55**	−0.35*
Saltmarsh Topminnow	−0.20	0.15	0.080	−0.21	−0.28
Sheepshead Minnow	−0.42*	−0.54**	−0.59*	−0.44*	0.60**
Sailfin Molly	−0.37*	−0.43*	−0.37*	−0.29	0.39*
Spot	−0.19	0.22	0.25	0.17	−0.26
Sand Seatrout	0.57**	0.41*	0.45*	0.62***	−0.29
Southern Flounder	−0.20	−0.24	−0.23	−0.094	0.24
Grass shrimp	0.62**	0.61***	0.63***	0.65***	−0.54**
Brown shrimp	0.66**	0.48***	0.54***	0.64***	−0.39*
Blue crab	0.20	0.19	0.15	0.19	0.19

TABLE 9. Mean (± SE) density (individuals/m^2) of macroinfaunal taxa collected from intact natural (IN), partially urbanized (PU), and completely urbanized (CU) landscapes in the Biloxi Bay and Pascagoula River estuaries. Asterisks indicate taxa that were used in multivariate analyses (taxa that comprised $\geq$ 0.2% of total abundance).

Taxon	IN	PU	CU
Insecta			
Chironomidae (midges)*	656.2 (325.7)	1,658.1 (675.1)	8.7 (10.0)
Decapoda			
Grass shrimp (postlarval)*	100.7 (38.4)	53.9 (15.3)	7.7 (7.9)
Tanaidacea			
*Hargeria rapax**	13.9 (11.6)		6.9 (5.8)
Amphipoda			
Grandidierella bonnieroides		1.7 (2.5)	
Gammarus spp.*	522.6 (338.7)	22.6 (4.6)	7.1 (8.7)
Ampelisca spp.	5.2 (7.4)		
Apocorophium spp.*	99.3 (90.3)	74.7 (36.5)	6.9 (5.8)
Melita spp.*	132.4 (97.2)		
Isopoda			
*Edotia triloba**	105.9 (74.8)	6.9 (6.8)	
Oligochaeta			
Tubificidae*	644.1 (348.2)	451.4 (175.3)	385.5 (286.4)
Polychaeta			
*Streblospio benedicti**	442.7 (201.7)	45.1 (28.3)	12.2 (7.5)
Capitellidae*	585.1 (225.9)	20.8 (17.7)	1,010.5 (447.1)
Leitoscoloplos fragilis	1.8 (2.5)		1.8 (2.5)
Hypereteone (*Eteone*) *heteropoda**	24.3 (21.5)		
Nereididae*	52.1 (44.1)	105.9 (38.9)	118.1 (57.6)
*Amphicteis floridus**	26.0 (18.0)	515.7 (168.5)	3.5 (3.4)
*Polydora cornuta**	5.2 (7.4)	27.8 (19.3)	1.7 (2.5)
Nemertea (ribbon worms)	1.7 (2.4)		3.5 (4.9)
Piscicolidae (marine leeches)	3.4 (4.9)		1.7 (2.3)
Mollusca*	14.8 (12.2)	6.95 (3.8)	

TABLE 10. Pearson's product-moment correlation coefficients for macroinfaunal densities in relation to physical-chemical variables identified in the multivariate correlation analysis (i.e., BEST model; $^*P \le 0.05$, $^{**}P \le 0.01$).

	250-m extent		750-m extent		
Taxon	PLAND_SM	TECI_DV(SM)	Salinity	TECI_DV(SM)	SPLIT
Chironomidae	0.24	−0.25	−0.24*	0.036	−0.35*
Gammarus spp.	0.24	−0.21	0.12	−0.39*	−0.21
Apocorophium spp.	0.21	−0.24	0.47*	−0.11	−0.11
Edotia triloba	0.30*	−0.22	0.40*	−0.40*	−0.095
Melita spp.	0.18	−0.16	0.16	−0.27	−0.16
Tubificidae	−0.34*	0.33*	−0.37*	0.30*	−0.32*
Streblospio benedicti	0.41*	−0.31**	0.16	−0.53**	−0.29**
Capitellidae	0.018	0.46*	0.44*	0.40*	0.13
Hypereteone (*Eteone*) *heteropoda*	0.38	−0.21	0.051	−0.15	−0.20
Nereididae	−0.11	−0.20	0.15	0.32	0.13
Amphicteis floridus	0.25	−0.35*	−0.37*	0.31	−0.39*
Polydora cornuta	0.11	−0.16	−0.20	0.095	−0.15
Mollusca	0.30	0.27	−0.077	−0.25	−0.26

and Connolly 2006; Meynecke et al. 2008; Roth et al. 2008; Meyer and Posey 2009; Green et al. 2012).

Patterns in the Nekton Assemblage

It has been suggested that intertidal fishes are poor indicators of habitat quality (Ellis and Bell 2013); however, the most conspicuous difference in this study occurred in the more mobile nekton assemblage. The IN salt-marsh landscapes supported significantly greater nekton CPUEs, both in aggregate and on a species-specific basis, than either PU or CU landscapes. However, our results also suggest that salt-marsh landscapes can retain some of their habitat value with moderate amounts of urbanization. The relative value of the salt-marsh habitat in both the IN and PU landscapes relates to the greater amount of salt-marsh edge (i.e., TE for the SM class). Numerous studies have identified salt-marsh edge as an important habitat for estuarine-dependent nekton species (Baltz et al. 1993; Peterson and Turner 1994; Minello and Rozas 2002; Minello et al. 2003). Browder et al. (1989) and Roth et al. (2008) showed that (1) the length of salt-marsh edge was a strong predictor of the abundance and production of brown shrimp in coastal Louisiana and (2) the effects of salt-marsh habitat loss were ameliorated by the creation of additional edge habitats through changes in perimeter–area relationships. Nevertheless, there are limits to the amount of edge habitat that can be created through salt-marsh habitat loss (Chesney et al. 2000). However, neither Browder et al. (1989) nor Roth et al. (2008) explicitly examined the effects of anthropogenic habitat loss and fragmentation. The serial replacement of salt-marsh habitats with developed surfaces and shorelines sets the upper limits on the amount of natural salt-marsh edge in a landscape and, ultimately, the amount of production that can be expected.

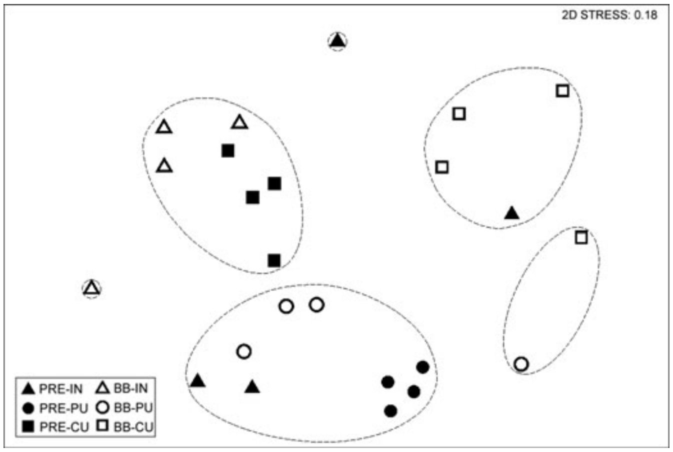

FIGURE 6. Multidimensional scaling (MDS) plot of the macroinfaunal assemblages for each combination of estuary (Biloxi Bay estuary [BB]; Pascagoula River estuary [PRE]) and landscape type (IN = intact natural; PU = partially urbanized; CU = completely urbanized). The dashed contour identifies significant groupings (40% similarity) based on agglomerative hierarchical clustering and similarity profiles.

The observed patterns in the relationships between nekton CPUE and spatial metrics also suggest a linkage between life history and landscape characteristics. Specifically, resident nekton (species that complete their life cycle in salt-marsh habitats) and transient nekton (species that spend only a portion of their life cycle in salt-marsh habitats) displayed different relationships with spatial metrics, and these relationships were not consistent across species within each group. Resident and transient nekton differ markedly in their tolerance of stressful conditions and in their ability to move among suitable habitat patches (Weinstein et al. 1984; Chitty and Able 2004; Rountree and Able 2007; Haas et al. 2009; Able et al. 2012), and these differences have strong implications for nekton distribution patterns in salt-marsh habitats. The inner marsh serves as habitat for resident salt-marsh nekton (e.g., Gulf Killifish, Sheepshead Minnow, Sailfin Molly, and grass shrimp; Kneib 2000; Minello and Rozas 2002). These smaller-bodied nekton species use tidal creeks and rivulets along the marsh edge to access the inner marsh at high tide (Rozas et al. 1988; Kneib 1994; Bretsch and Allen 2006; Lopez et al. 2010), and their interpatch movements are spatially limited (Chitty and Able 2004; Able et al. 2012). Thus, anthropogenic fragmentation of salt-marsh habitat would limit these species' access to primary habitats and would negate small-scale, interpatch movements. However, although the CPUEs of Gulf Killifish and grass shrimp were negatively correlated with salt marsh loss and fragmentation, the CPUEs of the Sheepshead Minnow and Sailfin Molly increased with salt marsh loss and fragmentation. Gulf Killifish and grass shrimp are the dominant nekton taxa in salt-marsh habitats and are often considered sentinel indicators of salt marsh health (Key et al. 2006; Vivian et al. 2012). Further, all four of these resident nekton species have similar niche requirements; therefore, a decrease in the abundances of Gulf Killifish and grass shrimp under stressful conditions would likely result in a competitive release for more tolerant species, such as the Sheepshead Minnow (e.g., Rowe and Dunson 1995).

Transient nekton species (e.g., Gulf Menhaden, brown shrimp, and blue crab) use a variety of estuarine habitats, including salt-marsh tidal creeks and salt-marsh edge, for a portion of their life cycle (Rozas and Minello 1998; O'Connell et al. 2005). The amount of time spent in salt-marsh habitats varies depending on the species and life stage (Kneib 1995; Hines 2007). Thus, some transient nekton species may visit salt-marsh habitat only sporadically (Deegan 1990) and others may have a prolonged period of temporary residency (Weinstein et al. 1984; Haas et al. 2005), whereas the more mobile transient species may supplement their habitat requirements with other, potentially less-suitable habitats. For example, the CPUEs of Gulf Menhaden and brown shrimp were positively correlated with patch size and inversely correlated with fragmentation, whereas the CPUE of blue crabs showed no correlation with any of the spatial metrics. As juveniles, Gulf Menhaden are migratory schooling fish that move among tidal creeks to maximize foraging opportunities (Deegan 1990), and their diets are a mixed composition of detrital and phytoplankton sources (Deegan et al. 1990). This would require moving short distances through vegetated corridors in natural (IN) salt-marsh landscapes, whereas in urbanized (CU) landscapes, the Gulf Menhaden would have to move large distances through unsuitable habitat and would likely experience increased predation (sensu Simenstad et al. 1999; Long et al. 2011) while searching for other salt-marsh patches. Unlike Gulf Menhaden, once brown shrimp recruit into salt-marsh habitats, their movements are confined to within a few meters of the edge habitat for a prolonged period of time until they grow to a certain size and migrate offshore (Peterson and Turner 1994; Rozas and Zimmerman 2000; Haas et al. 2005). Both salt marsh loss and the addition of developed shorelines can significantly reduce the amount of habitat for brown shrimp (Browder et al. 1989; Chesney et al. 2000; Peterson and Lowe 2009). On the other hand, blue crabs exhibit shifts among habitats according to life stage, and their movements are highly variable, ranging from 50 m/d after molting to 200 m/d for juveniles and several kilometers per day for adults (Hines 2007). As a result, transient nekton species that have specific habitat requirements (i.e., Gulf Menhaden and brown shrimp) are more likely to be impacted in urbanized landscapes than nekton species that are able to exploit multiple habitats (i.e., blue crab). Interestingly, several studies have shown that developed shorelines are suboptimal habitats for blue crabs (Kemp et al. 2005; King et al. 2005; Seitz et al. 2006; Long et al. 2011), suggesting that the maintenance of some marsh habitat in urbanized landscapes, at least, is better than total habitat loss (Partyka and Peterson 2008).

Patterns in the Macroinfaunal Assemblage

Though patterns were less clear, macroinfaunal assemblages in CU salt-marsh landscapes were comparatively less abundant than assemblages in the IN or PU landscapes (total density [mean ± SE] of all taxa decreased from 3,545.6 ± 172.7 individuals/m^2 in the IN landscapes to 2,899.9 ± 111.3 individuals/m^2 in PU landscapes and 1,813.5 ± 88.6 individuals/m^2 in CU landscapes). Tubificid oligochaetes were the dominant taxon in CU, low-salinity salt-marsh landscapes (i.e., BB-CU), whereas capitellid polychaetes were dominant in urbanized salt marshes with elevated salinity (i.e., PRE-CU). Previous studies have established that tubificids and capitellids are opportunistic colonizers of altered habitats (Engle et al. 1994; Sarda et. al 1996; Rakocinski et al. 1997; Weinstein and Sanger 2003; Holland et al. 2004; Dean 2008). However, tubificids are typically less tolerant of marine conditions than capitellids (Engle et al. 1994). Additionally, *S. benedicti* displayed a strong negative correlation with the amount of developed surface adjacent to salt-marsh edge. Although early work classified *S. benedicti* as a stress-tolerant species (Rakocinski et al. 1997; Van Dolah et al. 1999), there is a growing consensus that *S. benedicti* is highly susceptible to sediment contamination and hypoxia (Sarda et al. 1996; Lerberg et al. 2000; Weinstein and Sanger 2003; Holland et al. 2004). Combined, these correlations suggest that benthic sediments in the CU salt-marsh landscapes are more altered than those in the IN or PU landscapes. However, these patterns most likely reflect the influence of developed surfaces adjacent to the salt-marsh habitats (Sanger et al. 1999a, 1999b; Lerberg et al. 2000; Holland et al. 2004; Van Dolah et al. 2008).

The coarse resolution of our macroinfaunal identifications prevents direct comparisons with similar studies; however, amphipod crustaceans (e.g., *Gammarus* spp., *Ampelisca* spp., *Apocorophium* spp., and *E. triloba*), the tanaid crustacean *Hargeria rapax*, and bivalves (e.g., Matagorda macoma *Macoma mitchelli*, dwarf surf clam *Mulinia lateralis*, and stout razor clam *Tagelus plebius*) were either conspicuously absent or present at low abundances in CU landscapes. Similar patterns have been noted for the PRE (Partyka and Peterson 2008) and tributaries of Chesapeake Bay (Seitz et al. 2006; Long et al. 2011). Amphipod crustaceans and bivalves are important components of nekton diets (Hines et al. 1990; Rozas and LaSalle 1990; McTigue and Zimmerman 1991; Nemerson and Able 2004), and their low abundance or absence may be viewed as an additional indicator of poor habitat quality for nekton (Partyka and Peterson 2008; Goto and Wallace 2010). Decreased prey availability not only diminishes the value of salt-marsh habitats (Weinstein 1979; Boesch and Turner 1984) but also disrupts important production transfers from the salt marsh to open waters (Kneib 2000). However, the generality of nekton feeding patterns and increased density of annelid worms in CU landscapes could offset the potentially altered trophic pathways for nekton.

Caveats and Limitations

Several limitations associated with the results presented here warrant discussion. First, the coarse resolution (i.e., grain) of the land cover data for the study area (30-m^2 pixels) is likely to influence "area-sensitive" metrics (e.g., edge and shape metrics; Moilanen and Nieminen 2002). However, all metrics were examined at the same resolution, and the connectivity measures we used (i.e., CONNECT, DIVI, SPLIT, and MESH) are insensitive to the grain of the data (Jaeger 2000). Secondly, the coarse grain allowed for an approximation of habitat or class edge and prevented the inclusion of edge depth in the analyses. Given the current resolution, the minimum edge depth value would correspond to 30 m. Resident and transient nekton species are commonly found in inner and edge (<5-m) salt-marsh habitats at high tide (Minello and Rozas 2002), and finer-resolution land cover data would allow for a more accurate calculation of edge and core area metrics (McGarigal et al. 2002). Lastly, our approach admittedly violates the assumption of sample independence and is a pseudoreplicated design (Hurlbert 1984). Where possible, a conservative approach was used so that our results were not weakened by an inflated probability of committing a type I error (Hurlbert and White 1993). As such, the aggregated faunal responses in this study are an abbreviated representation of the complex interactions between salt-marsh and urban ecosystems.

Conclusions

Despite the aforementioned limitations, our results have broad implications for salt-marsh habitat restoration and management. We recognize the obligatory nature of population growth (Crossett 2004; European Environmental Agency 2006) and accompanying infrastructure (Beach 2002; Living Shoreline Steering Committee 2008) in the coastal zone. However, we suggest, as others have (Thom et al. 2005; Swann 2008; Peterson and Lowe 2009; Bulleri and Chapman 2010; Browne and Chapman 2011; Chapman and Underwood 2011), that identifying and maintaining the functional properties of natural landscapes (i.e., habitat quality and connectivity) are critical to the future health of coastal ecosystems and the continued delivery of ecosystem services. Based on our results, coastal landscapes consisting of several smaller, connected salt-marsh patches have faunal components similar to those in natural salt-marsh landscapes (sensu Partyka and Peterson 2008; Green et al. 2012). Thus, management and restoration efforts aimed at maintaining faunal assemblages and secondary production could benefit from a focus on promoting functional connectivity among several smaller patches (i.e., "single large or several small" [SLOSS] concept; Moy and Levin 1991; Fonseca et al. 1997; Eggleston et al. 1998; Green et al. 2012). However, the efficacy of salt marsh restoration is still contested (Moy and Levin 1991; Frisk et al. 2011; Minello et al. 2012), and the landscape processes necessary for habitat maintenance and connectivity are likely disrupted in highly urbanized coastal habitats (Thom et al. 2005).

The reality of coastal urbanization is that restoration efforts aimed at returning to baseline conditions are likely prohibited in most coastal areas, and an alternate baseline that promotes sustainable ecosystem services may be a plausible solution (Duarte et al. 2008). Therefore, the future of salt-marsh landscapes and other intertidal habitat continuums depends heavily on the synergistic efforts among ecologists, engineers, managers, and decision makers to make well-informed, science-based decisions regarding future growth in the coastal zone. Growth progressing in a manner that consumes and isolates critical habitats within a human-dominated landscape is unsustainable. Every effort should be made to promote ecosystem health, the continued delivery of goods and services, and, where possible, net ecosystem improvement (Thom et al. 2005).

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