Community Metrics and Trophic Dynamics in Tidal Creeks in an Anthropogenically Fragmented, Coastal Landscape

Michael Robert Lowe

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COMMUNITY METRICS AND TROPHIC DYNAMICS IN TIDAL CREEKS IN AN
ANTHROPOGENICALLY FRAGMENTED, COASTAL LANDSCAPE

by

Michael Robert Lowe

Abstract of a Dissertation
Submitted to the Graduate School
of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

May 2013
ABSTRACT

COMMUNITY METRICS AND TROPHIC DYNAMICS IN TIDAL CREEKS IN AN ANTHROPOGENICALLY FRAGMENTED, COASTAL LANDSCAPE

by Michael Robert Lowe

May 2013

Salt marsh landscapes are among the most anthropogenically altered ecosystems in the world. Urbanization (i.e., accumulation of impervious cover and man made structures) of the coastal landscape can disrupt the delivery of numerous ecosystem services. Among the many services provided by salt marsh habitats, they serve as the primary habitats for distinct macroinfauna (i.e., benthic and epibenthic macrofauna) and nekton (i.e., fish and decapod crustaceans) assemblages. In this dissertation, I used a number of metrics to test the overarching hypothesis that coastal urbanization has negative consequences for salt marsh faunal assemblages. Chapter I uses a landscape ecology approach to show that intact natural salt marsh landscapes, coastal landscapes with very little urbanization, host a greater abundance of individual species and nekton assemblages that are different from those in urbanized coastal landscapes (partially fragmented and completely fragmented salt marsh landscapes). The amount of developed shoreline and various metrics related to salt marsh fragmentation were important drivers of observed patterns in both macroinfauna and nekton assemblages. Chapter II examines the growth response of blue crab (*Callinectes sapidus*), brown shrimp (*Farfantepenaeus aztecus*), spot (*Leiostomus xanthurus*), and Gulf killifish (*Fundulus grandis*) to increasing levels of urbanization in salt marsh habitats. Further, the diets of spot and Gulf killifish
were also examined. While blue crab and brown shrimp growth did not differ among the landscapes, spot and Gulf killifish growth dynamics were markedly reduced in the completely fragmented landscapes. Reduced growth, or poor body condition, for both species was related to differences in landscape-specific foraging patterns. Chapter III uses δ¹³C, δ¹⁵N, and δ³⁴S stable isotope ratios and a suite of quantitative stable isotope metrics to relate the composition and configuration of coastal landscapes to the structure of salt marsh food webs. Overall, nekton assemblages in completely fragmented landscapes incorporated a narrower range of autotrophs, had a greater estimated trophic position, and an overall isotopic niche that was markedly reduced compared to both intact natural and partially fragmented salt marsh landscapes. Overall, these results suggest that urban growth that progresses in a manner that both consumes and isolates critical habitats within a human-dominated landscape is unsustainable.
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A Dissertation
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May 2013
ACKNOWLEDGMENTS

I would like to extend my sincerest gratitude to Dr. Mark S. Peterson. On most days we were diametrically opposed. In the end, however, we made a pretty good team and I will never forget that. I would also like to thank my committee members; Dr. Kevin Dillon (USM), Dr. Richard Fulford (EPA), Dr. William T. Slack (USACE), and Dr. Wei Wu (USM). Your advice and expertise provided valuable feedback throughout this project. I would be remiss if I failed to thank all of the individuals that helped out on this project. Brock Houston, Paul Grammer, Erik Lang, Michael Andres, Jeanne Marie Havrylkoff, and Claire Matten were right there with me, covered head-to-toe in mud and ‘noseeums.’ The folks in Dr. Dillon’s Stable Isotope Laboratory helped process more samples than ended up being necessary and, for that, I am very thankful. Dr. Jerry McClelland provided his expertise on benthic ‘critter’ identifications. Beyond that, he displayed extreme patience and understanding. Last, and certainly not least, I have to thank my parents and my friends. I may have never told you in person, but on those days when I felt like a rudderless ship being tossed in a storm, you helped me stay the course. Thank you. We all knew this day would come and it is only fitting that I leave you with this……..

“It’s been a long time leaving…” ~Willie Nelson
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>ii</td>
</tr>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>iv</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>vi</td>
</tr>
<tr>
<td>LIST OF ILLUSTRATIONS</td>
<td>viii</td>
</tr>
<tr>
<td>CHAPTER</td>
<td></td>
</tr>
<tr>
<td>I. GENERAL INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>II. EFFECTS OF HABitat LOSS AND FRAGMENTATION ON SALTMARSH FAUNAL ASSEMBLAGES</td>
<td>4</td>
</tr>
<tr>
<td>Introduction</td>
<td></td>
</tr>
<tr>
<td>Methods</td>
<td></td>
</tr>
<tr>
<td>Results</td>
<td></td>
</tr>
<tr>
<td>Discussion</td>
<td></td>
</tr>
<tr>
<td>III. GROWTH AND DIET PATTERNS OF NEKTOn FROM SALTMARSH HABITATS ARRAYED ALONG A GRADIENT OF ANTRHOPOGENIC ALTERATION</td>
<td>46</td>
</tr>
<tr>
<td>Introduction</td>
<td></td>
</tr>
<tr>
<td>Methods</td>
<td></td>
</tr>
<tr>
<td>Results</td>
<td></td>
</tr>
<tr>
<td>Discussion</td>
<td></td>
</tr>
<tr>
<td>IV. STRUCTURAL CHANGES IN SALT MARSH FOOD WEBS RESULTING FROM URBANIZATION: INFERENCES BASED ON STABLE ISOTOPE ANALYSES</td>
<td>70</td>
</tr>
<tr>
<td>Introduction</td>
<td></td>
</tr>
<tr>
<td>Methods</td>
<td></td>
</tr>
<tr>
<td>Results</td>
<td></td>
</tr>
<tr>
<td>Discussion</td>
<td></td>
</tr>
<tr>
<td>V. OVERALL CONCLUSION</td>
<td>100</td>
</tr>
<tr>
<td>APPENDIXES</td>
<td>107</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>111</td>
</tr>
</tbody>
</table>
LIST OF TABLES

Table

1. Spatial metrics calculated for each spatial extent ........................................ 11

2. Derived spatial metrics for both intact natural (IN), partially fragmented (PF), and completely fragmented (CF) sites in the Biloxi Bay (BB) and Pascagoula (PRE) estuaries at 250 and 750 m spatial extents .................................................. 13

3. Results of permutational multivariate analysis of variance (PERMANOVA) on normalized Euclidean distance matrices based on physical-chemical variables for (a) 250 m and (b) 750 m spatial extents .................................................. 22

4. Mean catch-per-unit-effort (CPUE: # m$^{-2}$) of individual fish collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in both Biloxi Bay (BB) and Pascagoula river (PRE) estuaries............. 24

5. Mean catch-per-unit-effort (CPUE) of decapod crustaceans collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in both Biloxi Bay (BB) and Pascagoula river (PRE) estuaries............. 25

6. Results of permutational multivariate analysis of variance (PERMANOVA) on 4$^{th}$ root transformed Bray-Curtis similarity matrices based on (a) nekton and (b) macroinfaunal assemblages .......................................................... 26

7. Multivariate correlations ($\rho$) between physical-chemical and a) nekton and b) macroinfaunal resemblance matrices .............................................. 31

8. Pearson’s correlation coefficients correlating nekton CPUE and physical-chemical variables identified in the BEST model .............................................. 32

9. Mean density (# m$^{-2}$) of macroinfaunal taxa collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in both Biloxi bay and Pascagoula river estuaries .................................................. 33

10. Pearson’s correlation coefficients correlating macroinfaunal density and physical-chemical variables identified in the BEST model .................................. 34

11. Mean (± S.E.) catch-per-unit-effort (CPUE, total number of individuals during each collection) and number of individuals used in analyses (n) of four nekton species collected from intact, natural (IN), partially fragmented (PF), and completely fragmented (CF) salt marsh landscapes in the a) Biloxi Bay and b) Pascagoula River estuaries .................................................. 51
12. Analysis of covariance results for length-weight relationships for a) blue crab, b) brown shrimp, c) Gulf killifish, and d) spot. ................................................................. 55

13. MANOVA summary comparing autotroph isotope ratios across (a) sites and (b) source. ........................................................................................................... 83

14. MANOVA summary comparing isotope ratios across sites for (a) macroinfauna and (b) nekton................................................................................................. 85

15. Bootstrapped (n = 10,000) estimates of assemblage-level stable isotope metrics (± standard error) for (a) macroinfauna and (b) nekton assemblages .......... 91
LIST OF ILLUSTRATIONS

Figure

1. Map of the study area (a) including the 2005 land-cover data (modified NOAA C-CAP) for both the Biloxi Bay (BB) and Pascagoula River (PRE) estuaries. .......... 9

2. Second stage MDS plots derived from Spearman correlations between first stage Bray-Curtis (4th root transformed) and normalize Euclidean distance matrices of landscape metrics for each spatial extent ................................................................. 17

3. Multi-dimensional scaling (MDS) plots of the landscape metrics and environmental data for the (a) 250 m and (b) 750 m spatial extents ............ 23

4. Multi-dimensional scaling (MDS) plot of the nekton assemblages for each combination of estuary (BB and PRE) and landscapes (IN, PF, and CF) .......... 27

5. Mean CPUE (± SD) of the nekton contributing to 90% of the cumulative variation among landscape-types .............................................................................. 29

6. Mean CPUE (± SD) of the nekton contributing to 90% of the cumulative variation among significant groupings identified by agglomerative hierarchical clustering from Figure 4 ................................................................. 30

7. Multi-dimensional scaling (MDS) plot of the macroinfaunal assemblages for each combination of estuary (BB and PRE) and patch-type (IN, PF, and CF) .......... 35

8. Length-weight relationships for Gulf killifish (a) from intact natural (IN; shaded circles and solid gray line), partially fragmented (PF; shaded squares and dashed gray line), and completely fragmented (CF; triangles and dashed red line) salt marsh landscapes ........................................................................................................ 56

9. Estimated marginal wet weight for a 51.2 mm total length (TL) spot from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) salt marsh landscapes ............................................................................................... 57

10. Mean (± S.E.) frequency of occurrence (FOi) and proportion by number (MNi) of the diet composition of Gulf killifish collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in the Biloxi Bay (BB) and Pascagoula River (PRE) estuaries ................................................................. 58

11. Principal coordinate analyses (PCO) of diet composition of a) Gulf killifish and b) spot collected from intact natural (triangles), partially fragmented (squares), and completely fragmented (circles) salt marsh landscapes in the Biloxi Bay (closed) and Pascagoula River (open) estuaries ................................................................. 60
12. Mean (± S.E.) frequency of occurrence (FOᵢ) and proportion by number (MNᵢ) of the diet composition of spot collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in the Biloxi Bay (BB) and Pascagoula River (PRE) estuaries ................................................................. 62

13. Stable isotope bi-plots of composite δ¹³C and δ¹⁵N macroinfauna and nekton (fish and decapods) samples in relation to autotrophs across sites .............................................. 84

14. δ¹⁵N-based estimates of trophic position (± standard error) for macroinfauna assemblages across sampling sites .................................................................................. 86

15. δ¹⁵N-based estimates of trophic position (± standard error) for a) decapod crustaceans and b) nekton assemblages across sampling sites ......................................... 87

16. Bayesian mixing model estimates of autotroph contributions to a) macroinfauna assemblages using only δ¹³C and δ¹⁵N, b) nekton assemblages using only δ¹³C and δ¹⁵N, and c) nekton assemblages using δ¹³C, δ¹⁵N, and δ³⁴S ............................................. 89
CHAPTER I

GENERAL INTRODUCTION

Salt marshes comprise a suite of shallow, structurally complex habitats arrayed along both abiotic and biotic gradients that vary spatially and temporally (Peterson 2003) and are functionally connected by both the longitudinal and latitudinal axes by energy flows (Odum 1984) and nekton movements (Deegan 1993). Among the many ecosystem services provided by salt marshes (Costanza et al. 1997), they function as critical habitat for a distinct assemblage of ecologically and economically important nekton (i.e., fish and invertebrates; Weinstein 1979; Boesch and Turner 1984; Peterson & Turner 1994; Minello et al. 2003). The value of salt marsh habitats to nekton is attributed to reduced predation risk (Minello et al. 1989; Kneib 1995) and an abundance of benthic and epibenthic macroinfauna (hereafter, macroinfauna) that link salt marsh derived energy to nekton production through complex food web interactions (Kneib 2000).

The value of healthy coastal ecosystems cannot be overstated (Costanza et al. 1997; Duarte et al. 2008; Barbier et al. 2011). Yet, despite this recognition, they are among the most anthropogenically altered ecosystems in the world (Vitousek et al. 1997; Kennish 2001; Lotze et al. 2006; Halpern et al. 2008a; Bromberg Gedan et al. 2009). Much of this alteration can be attributed to the continued urbanization necessary to support human population growth in the coastal zone (Crosset et al. 2004). However, urbanization is outpacing human population growth in coastal areas and is a direct threat to the health of coastal ecosystems (Beach 2002; Allen & Lu 2003; Bromberg Gedan et al. 2009). In Charleston, SC, for example, the population is expected increase 50% by 2030 while the amount of urban area, defined as impervious cover (i.e., artificial
structures), will increase by 247% (Allen & Lu 2003). Not only will 35% of salt marsh habitats and 70% of tidal creeks be lost but also small increases in impervious cover leads to large functional changes in the remaining tidal creek ecosystems (Holland et al. 2004; Van Dolah et al. 2008).

This continued loss of habitat is widely regarded as the largest driver of the declining ecosystem services in terrestrial, aquatic, and marine ecosystem (Dobson et al. 2006; Lotze et al. 2006). However, habitat fragmentation is an emergent property resulting in the serial replacement of salt marsh habitats with man-made surfaces or open water (Peterson & Lowe 2009) and has a long history of study in terrestrial ecosystems (reviewed by Andrén 1994). The ultimate result of fragmentation is the creation of a mosaic of smaller habitat patches, separated by inferior open-water (natural fragmentation) or man-made (anthropogenic fragmentation) habitat, from what was once a more homogenous landscape (Fahrig 2003). Bulkheading (Douglass & Pickel 1999; Peterson et al. 2000; Hendon et al. 2000), dock construction (Sanger et al. 2004), levee building (Reed et al. 2006), and municipal pier and port development (Able et al. 1998, 1999; Duffy-Anderson & Able 1999; Duffy-Anderson et al. 2001) can reduce the functional properties of the salt marsh habitats by both reducing area of high-quality habitat and increasing the distance among habitat patches. Many of these man-made structures, when considered independently, would be defined as ‘local’ or ‘small’ scale in nature (Turner 1990; Kennish 2001). However, as they accumulate across the coastal landscape, salt marsh habitat is reduced and becomes increasingly more fragmented (Peterson & Lowe 2009). Ultimately, nekton (i.e. fish and decapod crustacean) recruitment may be compromised (Eggleston et al. 1998), faunal assemblage structure
and diversity may be altered (Layman et al. 2004; Partyka & Peterson 2008; Goodsell 2009), trophic interactions altered (Layman et al. 2007b) and the production of commercially important nekton may be reduced (Valentine-Rose et al. 2007; Bilkovic & Roggero 2008).

Ultimately, urbanization and accompanying salt marsh fragmentation can disrupt the delivery of numerous economically and ecologically valuable ecosystem services (Sanger et al. 1999a,b; Lerberg et al. 2000; Holland et al. 2004; Bilkovic et al. 2006; Bilkovic & Roggero 2008; Van Dolah et al. 2008; Bromberg Gedan et al. 2009; Long et al. 2011). In the forthcoming chapters, I will use a variety of approaches to evaluate the overarching hypothesis that coastal urbanization leading to habitat fragmentation has negative consequences for salt marsh faunal assemblages. In Chapter I, I use a landscape ecology approach to relate the composition and configuration of coastal salt marsh landscapes to the structure of faunal assemblages. Building on these results, Chapter II examines the growth dynamics and diets of specific fish and decapod crustaceans in different levels of habitat urbanization. Chapter III uses stable isotope ratios to characterize functional differences in food web structure in salt marsh habitats arrayed along a gradient of urbanization.
CHAPTER II
EFFECTS OF HABITAT LOSS AND FragmentATION ON SALT MARSH FAUNAL ASSEMBLAGES

Introduction

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). Both patch composition and configuration within a landscape can significantly influence population and community dynamics (Turner et al. 2001) and, consequently, patterns of faunal distribution and abundance (Wiens 1999). Thus, an important step in the management of these critical ecosystems is to maintain the functional linkages between patches or habitats used by animals at the landscape-level. However, identifying the linkage between complex species interactions and their habitats is often difficult (Thrush et al. 2008) and requires a vigorous approach to linking ecological processes to spatial patterning. Landscape ecology has a long history of application in terrestrial systems (Gustafson 1998; Wiens 1999; Turner 2005) and, fortunately, many of the concepts and spatial pattern metrics can be broadly applied to coastal intertidal habitats, such as salt marshes (Kneib 1994; Wiens 2002; Boström et al. 2011).

Salt marsh ecosystems comprise a suite of shallow, structurally complex habitats arrayed along both abiotic and biotic gradients that vary spatially and temporally (Peterson 2003; Rountree & Able 2007) and are functionally connected by both energy flow and animal movement through tidal creek networks (Odum 1984; Deegan 1993; Kneib 2000; Mallin & Lewitus 2004). These productive ecosystems are viewed as
critical habitat for a number of ecologically and economically important fish and decapod crustaceans (hereafter, nekton; Weinstein 1979; Boesch & Turner 1984; Peterson & Turner 1994; Minello et al. 2003). The structural complexity of salt marsh habitats provides small bodied nekton with refugia from predators (Minello et al. 1989; Kneib 1995) and an abundance of benthic and epibenthic macrofauna (hereafter, macroinfauna) that link salt marsh derived primary production to secondary production through complex food web interactions (Simenstad et al. 1999; Kneib 2000; Dame & Christian 2007). While interactions among nekton, macroinfauna, and salt marsh habitats are spatially complex (Thrush et al. 2008), both faunal components 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 and natural alterations to the coastal environment (Bromberg Gedan et al. 2009; Bulleri & Chapman 2010; Peterson & Lowe 2009; Mee 2011).

Despite early warnings (Mock 1967; Odum 1970, 1982), the potential impacts of urbanization, defined here as coastal development and shoreline hardening, on salt marsh habitats has only recently emerged as a focal area in estuarine ecology. For instance, although a recent review of the cumulative effects of anthropogenic impacts on marine ecosystems did not list salt marshes as impacted habitats or urbanization as a principal driver of change in coastal ecosystems (Halpern et al. 2008a), recent studies have documented the deleterious effects of urbanization on salt marsh ecosystems (Holland et al. 2004; Bilkovic et al. 2006; Bilkovic & Roggero 2008; Van Dolah et al. 2008; Partyka & Peterson 2008; Long et al. 2011). Some consequences of urbanization on salt marsh habitats include reduced stem density (Lathrop et al. 2000; Long & Burke 2007),
sediment contamination (Sanger 1999a,b; Holland et al. 2004; Van Dolah et al. 2008) and altered benthic assemblages (Bilkovic et al. 2006; Seitz et al. 2006); all of which can be linked directly to increases in the amount of impervious surfaces. Moreover, developed shorelines are not functionally equivalent to natural habitats for either benthic (Seitz et al. 2006; Partyka & Peterson 2008; Long et al. 2011) or nekton assemblages (Hendon et al. 2000; Peterson et al. 2000; Bilkovic & Roggero 2008; Long et al. 2011). Consequently, coastal urbanization can impact the production of a number of economically important nekton (Peterson & Lowe 2009). For example, *Callinectes sapidus* (blue crab) growth and survival is markedly decreased in bulkheaded habitats (Long et al. 2011) and the continued increase in the amount of developed shoreline in coastal Alabama is expected to severely reduce *C. sapidus* landings (Jordan et al. 2009). However, neither Long et al. (2011) or Jordan et al. (2009) explicitly examine the impacts of habitat alteration at the landscape-scale which could have important ramifications for population level production.

In addition to the effects on habitat quality, coastal urbanization has significant impacts on the quantity and spatial configuration of salt marsh habitats (Thomas 1995; Lathrop et al. 2000; Peterson & Lowe 2009). As impervious surfaces and hardened shorelines accumulate across coastal landscape, natural salt marsh habitats become increasingly patchy and more isolated within an unsuitable habitat matrix (i.e., fragmentation; Fahrig 2003). Recent examination of the impacts of fragmentation on estuarine habitats has focused predominantly on subtidal habitats (Hovel & Fonseca 2005; Johnson & Heck 2006; Burnfiend & Stunz 2007; Macreadie et al. 2009). However, there is growing evidence that nekton recruitment may be compromised
(Eggleston et al. 1998), faunal assemblage structure and diversity altered (Layman et al. 2004; Partyka & Peterson 2008; Goodsell 2009), the production of commercially important nekton reduced (Valentine-Rose et al. 2007), and trophic interactions modified (Layman et al. 2007b) in intertidal habitats, such as salt marshes, as they become fragmented. Green et al. (2012a) found that salt marsh structural complexity and connectivity were important variables driving fish species richness and density. However, their study centered on natural salt marsh landscapes in northern latitudes and did not include developed surfaces or hardened shorelines.

The main objective of this study is to use a landscape ecology approach to examine the effects of coastal urbanization and salt marsh loss and fragmentation on salt marsh faunal assemblages. I hypothesize that (1) the distribution and abundance of both nekton and macroinfaunal assemblages will differ between non-fragmented and fragmented salt marsh tidal creeks, (2) variation in both nekton and macroinfaunal assemblage structures will be correlated to the composition and configuration of the surrounding landscape at relevant scales, and (3) the associations with landscape structure will vary among individual taxa. Spatial pattern metrics were used to examine the relationships between fauna and the characteristics of coastal landscapes that drive important ecological processes. Such an approach can strengthen our understanding of the consequences of coastal urbanization through both habitat loss (Airoldi & Beck 2007) and fragmentation (Peterson & Lowe 2009; Boström et al. 2011; Green et al. 2012b) on coastal faunal communities.
Methods

**Study Area and Study Site Delineation**

The study area consisted of two large, micro-tidal (tidal range < 0.5 m; Rozas 1995) river estuaries in coastal Mississippi (Figure 1a). The lower Pascagoula River estuary (PRE) is a ~ 15 km long distributary that can be sub-divided 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 with large expanses of intact, natural habitats (Peterson et al. 2007; Partyka & Peterson 2008). The Biloxi Bay estuary (BB) is ~ 21.7 km in length and also consists of both highly impacted and un-impacted shorelines; however, the juxtaposition of the two is spatially more complex than 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 & Lowe 2009). Natural shorelines are comprised mostly of intertidal vegetation dominated by *Spartina alterniflora* (smooth cordgrass) and *Juncus roemarianus* (needlerush) with occasional patches of the invasive *Phragmites australis* (common reed; Peterson & Partyka 2006). Though 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 areas that ranged from natural to highly urbanized salt marsh landscapes (Peterson et al. 2000; Partyka & Peterson 2008). These results were combined with 2007 1 m ortho-rectified color infrared imagery in ArcGIS v10.0 (ESRI) to identify three potential sample sites within each estuary that 1)
Figure 1. Map of the study area (a) including the 2005 land-cover data (modified NOAA C-CAP) for both the Biloxi Bay (BB) and Pascagoula River (PRE) estuaries. Smaller panels are examples of intact natural (IN; b), partially fragmented (PF; c), and completely fragmented (CF; d) landscapes with corresponding aerial imagery. Panels e-g represent the corresponding 250, 500, 750, and 1000 m radial buffers for each landscape with modified C-CAP.
contained a small, first-order salt marsh tidal creek of similar length (all creeks ranged from 26.6 - 32.4 m long) and 2) were arrayed along a gradient of anthropogenic alteration from natural to highly altered local landscapes (Figure 1a). Small, first-order tidal creeks draining large expanses of salt marsh with no evidence of shoreline alteration or development in the immediate vicinity (750-1000 m) were considered intact, natural salt marsh landscapes (IN; Figure 1b). Partially fragmented landscapes (PF) were identified as small, first-order tidal creeks draining marsh systems that were nestled within a moderately developed area with modified shorelines disrupting their natural connection with the main water body (Figure 1c). Small, isolated salt marsh patches, with a small first-order creek, that were surrounded by both altered shorelines and developed surfaces were identified as completely fragmented landscapes (CF; Figure 1d). Each tidal creek and surrounding landscape was examined prior to sampling to ensure the correct assignment to one of the three landscapes.

Land-cover Data and Landscape Metrics

Post-Hurricane Katrina (2005) land-cover data for the study area (Figure 1a) was obtained from the National Oceanic and Atmospheric Administration Coastal Change Analysis Program (NOAA C-CAP; http://www.csc.noaa.gov/crs/lca/ccap.html). The C-CAP system classifies 0.9 ha (30 m²) 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/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 (250, 500, 750, and 1000 m radius) centered on the mouth of each tidal creek (Figure 1; see panels e, f, & g). Within each GIS-rendered spatial scale, extracted land-cover data was used to calculate 10 spatial metrics (Table 1).

Table 1

<table>
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<th>Spatial metrics calculated for each spatial extent.</th>
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<td>Metric</td>
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<tr>
<td>Percentage of Landscape</td>
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<tr>
<td>Total Edge</td>
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<tr>
<td>Total Edge Contrast Index</td>
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<tr>
<td>Area-weighted Mean Shape Index</td>
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<td>Splitting Index</td>
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<td>Effective Mesh Size</td>
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</table>

Note. Composition metrics (PLAND, TE and TECI) were calculated for water (W), developed (DV), and saltmarsh (SM) classes. Configuration metrics (SHAPE-MESH) were calculated for the saltmarsh class only.
at both the class- and landscape-level using FRAGSTATS version 4.0 (McGarigal et al. 2002). Primary emphasis was placed on the composition and configuration of developed (DV) and salt marsh (SM) classes in relation to water (W). The percentage of the landscape occupied by developed and salt marsh classes (PLAND_DV, PLAND_SM) was calculated for each spatial scale. Both total edge (TE) and total edge contrast index (TECI) were used to estimate the relative amount of both functional and non-functional class edges. For example, the amount of hardened shoreline (TECI_DV(W)) was calculated as water cell edges contrasted against developed cell edge, natural shoreline (TECI_SM(W)) was calculated as water edge cells contrasted against salt marsh class cells, and the amount of salt marsh edge that was bordered by developed surfaces (TECI_DV(SM)) was calculated as the amount salt marsh cell edge contrasted against developed cell edge (see Table 2). For the salt marsh class, the complexity and aggregation of cells was calculated using the area weighted mean shape index (SHAPE), contiguity index (CONTIG), and clumpiness index (CLUMPY). Salt marsh isolation was quantified using 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 ortho-rectified color infrared imagery in ArcGIS). Three metrics were calculated to quantify the degree of salt marsh fragmentation (Jaeger 2000). Landscape division index (DIVI) is the probability ($D$) that two randomly chosen pixels in the landscape are not situated the same patch of a corresponding cell type (i.e., the same salt marsh patch). Splitting index (SPLIT) is defined as the number of salt marsh patches ($S$) that result from dividing the landscape by the observed mean salt marsh patch size while holding $D$ constant.
Table 2

Derived spatial metrics for intact natural (IN), partially fragmented (PF), and completely fragmented (CF) sites in the Biloxi Bay (BB) and Pascagoula (PRE) estuaries at 250 and 750 m spatial extents.

<table>
<thead>
<tr>
<th></th>
<th>BB-IN</th>
<th>BB-PF</th>
<th>BB-CF</th>
<th>PRE-IN</th>
<th>PRE-PF</th>
<th>PRE-CF</th>
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<tr>
<td></td>
<td>PLAND</td>
<td>DV*</td>
<td>TE</td>
<td>PLAND</td>
<td>DV*</td>
<td>TE</td>
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<td>250</td>
<td>0.0</td>
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<td>70.0</td>
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</tr>
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<td>0.0</td>
<td>4830.0</td>
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<td>100.0</td>
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<td>1.0</td>
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<tr>
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<td>66.8</td>
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<td>2.1</td>
<td>20.0</td>
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<td>5880.0</td>
<td>10.8</td>
<td>51.9</td>
<td>24.5</td>
<td>7260.0</td>
</tr>
<tr>
<td></td>
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<td>3.0</td>
<td>0.6</td>
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<tr>
<td>250</td>
<td>57.3</td>
<td>31.6</td>
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<td>780.0</td>
<td>50.0</td>
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<tr>
<td>750</td>
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<td>4200.0</td>
<td>41.6</td>
<td>47.4</td>
<td>4.6</td>
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</tr>
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<td>1.3</td>
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<tr>
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<td>0.0</td>
<td>750.0</td>
<td>95.7</td>
<td>64.1</td>
<td>750.0</td>
<td>0.0</td>
</tr>
<tr>
<td>750</td>
<td>2.4</td>
<td>6350.0</td>
<td>7.5</td>
<td>89.0</td>
<td>42.6</td>
<td>6090.0</td>
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<td>1.2</td>
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<tr>
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<td>4.2</td>
<td>52.8</td>
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<td>3300.0</td>
</tr>
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<td>750</td>
<td>30.3</td>
<td>5970.0</td>
<td>20.6</td>
<td>51.3</td>
<td>37.0</td>
<td>7230.0</td>
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<tr>
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<td>29.6</td>
<td>2.0</td>
</tr>
<tr>
<td>250</td>
<td>30.0</td>
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<td>27.4</td>
<td>46.6</td>
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<td>1230.0</td>
</tr>
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<td>750</td>
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<td>46.2</td>
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</tr>
<tr>
<td>PRE-CF</td>
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<td></td>
<td></td>
<td>36.2</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Note. Landscape metrics defined in Table 1.

Effective mesh size (MESH) is the mean patch area when the landscape is divided into $S$ patches. Each spatial scale was compared in multivariate space in order to identify the spatial scale at which the composition and configuration of the surrounding landscapes showed the greatest heterogeneity (see *Statistical Analyses*).

**Faunal Collections**

From 3 May to 4 June 2010, nekton, macroinfauna, and environmental parameters were collected weekly in each tidal creek. Modified Fyke nets with two 0.91 m diameter steel hoops positioned 1 m apart 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 and 1.8 m high) and a mouth (3 m wide and 1.8 m high). All nets, wings and the mouth were constructed with 5 mm stretched nylon mesh and the bottom of the
leading edge of each net 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 ~ 45 degree angle. Poles (10 cm dia., 4.0 m length), driven into the marsh platform, were attached to the net at the float and lead line on each side of the net mouth and at the end of each wing. Estuaries in the northern Gulf of Mexico are micro-tidal 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 hours post-high tide), a 4.9 m minnow seine (3.2 mm stretched mesh) was pulled through ~75 % of the total creek length (coinciding with the low water mark) into the mouth of the Fyke net. The lead line was lifted out of the water and nekton, including those in the wings, were funneled into the net mouth. 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 to the lowest possible taxonomic-unit (i.e., species) and enumerated. Nekton abundance from each Fyke net was considered catch-per-unit-effort (CPUE).

Concomitant with nekton collections, environmental data (i.e., depth, temperature (°C), salinity, and dissolved oxygen (mg/L); hand-held YSI-85) and macroinfauna were collected weekly at the mouth, middle, and head of each tidal creek (2 estuaries x 3 creeks x 4 weeks x 3 locations within a creek = 72 samples). Each macroinfaunal sample was taken mid-channel using a pole-mounted Ekman grab (0.024 m²), washed through a 500-µm sieve in the field to remove excess mud, preserved in 7% buffered formalin containing Rose Bengal, and returned to the laboratory. Macroinfauna were picked from
each sample using one of two methods. Samples with a high volume of detrital material were quartered into approximately equal volume samples with a Motodo plankton splitter and macroinfauna were picked from 2 of the 4 samples. Thirty-eight samples were split and the mean difference between the 2 splits within a creek ranged from 3.1 to 4.0 total individuals (range S.D. = 1.25 – 3.87; range C.V. = 22-35%). The remaining 34 samples contained a low volume of detrital material and macroinfauna were picked in their entirety. All macroinfaunal samples were picked in random order in groups of 8 samples, from which one sample was randomly selected for quality control (QC). If the number of missed animals in a QC’d sample was greater than 10% of the total animals observed in the first pick, all 8 samples were re-picked. Based on this criterion, one group was re-picked and the percentage of animals missed ranged from 0 to 3.8% with the initial QC’d sample having missed 4 of 36 individuals (11%). The remaining QC’d 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 where every individual could not be identified 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 m² for all analyses.

Statistical Analyses

Univariate Analyses. Taxonomic richness (S) and Simpsons evenness index (1-λ; Clarke & Gorley 2006) were calculated for both nekton and macroinfaunal assemblages and compared between estuaries (BB and PRE) and among landscapes (IN, PF, and CF) using a 2-way analysis of variance (ANOVA). An initial 3-way ANOVA indicated that
diversity measures for macroinfaunal did not differ among locations within each creek (p > 0.05) and the three samples were averaged for each week.

Water temperature, salinity, dissolved oxygen, and depth were averaged across weeks and compared between estuaries and among landscapes and locations within the tidal creek (mouth, middle, and head) using a 3-way ANOVA. For all univariate ANOVAs, relative F-values and associated effect size (partial η²) values were used to assess the importance of significant interactions between main effects (Green & Salkind 2008). If the effect size of the interaction term was small (≤ 0.3; Field 2005) relative to the main effect or if there was no interaction, Tukey’s HSD post hoc test was used to examine significant differences among treatments for each variable. All variables used in univariate analyses failed to meet the assumptions of normality (Kolmogorov-Smirnov test) and homogeneity (Levene’s test) and, as a result, were log (base 10) transformed. All univariate analyses were performed at a significance level of 0.05 in SPSS v20 (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. Therefore, week was removed from all multivariate analyses (Fletcher & Underwood 2002) and each of the four sample weeks were treated as replicates in a repeated-measures design (Gurevitch & Chester 1986). Further, macroinfaunal assemblages did not differ among locations within creeks (p > 0.05) and were averaged for all three locations for a given week to facilitate multivariate correlations with physical-chemical data by maintaining resemblance matrices of equal size.
Normalized Euclidean distance and Bray-Curtis similarity matrices based on spatial metrics (Table 1) were calculated for each spatial scale and compared using ‘second stage’ multidimensional scaling (MDS; Clarke et al. 2006). ‘Second stage’ MDS provided a measure of concordance among the different spatial scales by generating a ‘second’ similarity matrix based on Spearman rank correlations ($\rho$) between each matrix (i.e., a similarity matrix of similarity matrices). The resulting rank correlation matrix was plotted in multivariate space and indicated that 1) differences among the matrices were maximized using Euclidean-based distances, 2) the 250 m scale was the most different (as indicated by the length of the dashed arrow), and 3) the 500, 750, and 1000 m scales were relatively similar (Figure 2). However, the scales at which aquatic animals perceive their environment is a function of their mobility. Therefore, the 250 and 750 m spatial

![Figure 2](image)

**Figure 2.** Second stage MDS plots derived from Spearman correlations between first stage Bray-Curtis (4th root transformed) and normalize Euclidean distance matrices of landscape metrics for each spatial extent. Each point represents the multivariate landscape structure for the full set of sites and arrows indicate the magnitude and direction of differences in multivariate space that occurs with increasing spatial extent.
scales were deemed the most appropriate scales for less mobile, resident species (e.g., Able et al. 2012) and more mobile, transient species (e.g., Weinstein et al. 1984; Wolcott & Hines 1990; Saucerman & Deegan 1991), respectively, and were used for further analyses. 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 used to construct a resemblance matrix based on normalized Euclidean distance measures.

For each faunal assemblage, rare taxa comprising less than 0.2% of total abundance were removed and a resemblance matrix of Bray-Curtis similarity values for each sample was created from the 4th root transformed CPUE data for nekton and density for macroinfauna to down-weight numerically dominant taxa. Levels of similarity among samples (physical-chemical, nekton, and macroinfaunal) were statistically compared between estuaries and among landscapes using a full-factorial permutational multivariate ANOVA (PERMANOVA; permutations = 999; Anderson et al. 2008). Due to issues associated with pseudo-replication, 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. Estimated variance components were used to assess the importance of significant main effects and interaction terms. Pair-wise $a$ posteriori comparisons, using the multivariate analogue 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 MDS ordination plots to examine the relationships among samples and
identify well differentiated groupings. Rank dissimilarities (SIMPER) for both faunal assemblages were used to identify characteristic taxa 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 non-parametric 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. BEST conducts rank correlations (\( \rho \)) 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) in order to identify the subset of physical-chemical variables that give the best correlative explanation of the assemblage structure. The best subsets of physical-chemical parameters were further investigated using Pearson’s correlations to relate individual species abundances to the landscape/environmental factors. All multivariate analyses were performed using PRIMER version 6.0 (Clarke & Gorley 2006). Pearson’s correlations were performed in SPSS.

Results

Environmental parameters varied spatially throughout the study area and within the tidal creeks. Mean water depth at high tide ranged from 17-45 cm and differed only among locations within creeks (ANOVA, \( p = 0.003 \)) with the head of the tidal creek being significantly shallower than the mouth (Tukey’s HSD, \( p = 0.002 \)). Water
temperature (range 27.1 to 30.4 °C) differed both between estuaries (ANOVA, p = 0.001) and among landscapes (ANOVA, p = 0.04). On average, the PRE was ~ 1.0 °C warmer than the BB (Tukey’s HSD, p = 0.03) and PF landscapes were ~ 1.5 °C cooler than both IN and CF landscapes (Tukey’s HSD, p = 0.03). Though dissolved oxygen concentrations (DO; 2.5 to 6.6 mg l⁻¹) fell within suitable range for most estuarine nekton (Wannamaker & Rice 2000), they 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 η² = 0.152; estuary*landscape, partial η² = 0.141) and precluded post hoc comparison of the main effect. Overall, DO concentrations were lower in BB (mean = 3.4, S.E. = 0.7 mg l⁻¹) than in PRE (mean = 4.2, S.E. = 0.5 mg l⁻¹) and this difference was further exacerbated by the lowest DO concentrations in BB-PF landscapes (mean = 2.7, S.E. = 0.4 mg l⁻¹).

Similarly, salinity differed among landscapes (ANOVA, p < 0.001, partial η² = 0.474) and there was a significant estuary*landscape interaction (ANOVA, p < 0.001, partial η² = 0.455). Both IN and CF landscapes were more saline than PF landscapes (Tukey’s HSD, p < 0.001) and the interaction was driven by higher salinities observed at the PRE-CF site (mean = 6.4, S.E. = 1.0) relative to the BB-CF site (mean = 2.2, S.E. = 1.0) and the BB-IN site (mean = 6.7, S.E. = 1.7) compared to the PRE-IN site (mean = 2.6, S.E. = 0.9). However, observed mean salinities at all sites (1.9 to 8.4) fell within the oligohaline range for estuarine organisms (Bulger et al. 1993).

Regardless of estuary, clear landscape metric patterns were evident for each landscape-type at both the 250 and 750 m scales (Table 2). In the IN landscape, salt marsh was the dominant class (PLAND_SM). As a result, shoreline consisted almost
exclusively of natural, salt marsh shoreline (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). Further, tidal creeks were more connected at both the 250 and 750 m spatial scales (CONNECT; 63.7 – 74.4 %) and unfragmented (DIVI, MESH, SPLIT). In both BB and PRE estuaries, PF landscapes were dominated by the salt marsh class at the 250 m spatial scale (PLAND_SM; 64.1 and 55.9%, respectively). However, at 750 m, PF landscapes were a mix of developed (PLAND_DV, 18.8 and 50.3%) and salt marsh classes (PLAND_SM, 24.5 and 42.6). Overall, PF landscapes had more salt marsh edge (TE) than either the IN or CF due to the large, convoluted creeks that are a dominant feature of the landscape and lent to their greater shape complexity (AM_SHAPE, 1.9-2.1). However, the amount of natural shoreline (TECI_SM(W)) decreased inversely with the amount of developed surface (PLAND_DV) and hardened shoreline (TECI_DV(W)) resulting in salt marsh landscapes that were more fragmented (DIVI, MESH, and SPLIT) at the 750 m spatial scale. On the other hand, CF landscapes were dominated by the developed class (PLAND_DV, 30.0-64.9 %) and hardened shorelines (TECI_DV(W) constituted 42.3 to 52.8 % of the shoreline in this landscape. Salt marsh patches tended to be small (PLAND_SM, 3.5-17.3 %), simply shaped (AM_SHAPE, 1.1-1.3), moderately aggregated (CLUMPY, 0.5-0.6), and highly fragmented (DIVI, MESH, and SPLIT).

The conventional PERMANOVA indicated that physical-chemical variables differed between estuaries, among landscape-types, and there was a significant interaction for both spatial scales (Table 3). However, variance components attribute most of the model variation to the landscape-level and the conservative model suggested
Table 3

Results of permutational multivariate analysis of variance (PERMANOVA) on normalized Euclidean distance matrices based on physical-chemical variables for (a) 250 m and (b) 750 m spatial extents.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MSE</th>
<th>Conventional Pseudo-F</th>
<th>Conservative Pseudo-F</th>
<th>Variance component</th>
<th>Pairwise comparisons</th>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estuary (E)</td>
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<td>1.32ns</td>
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<td>29.42***</td>
<td>8.85**</td>
<td>3.48</td>
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</tr>
<tr>
<td>Total</td>
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</tr>
<tr>
<td>(b)</td>
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<tr>
<td>Estuary (E)</td>
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<td>14.70</td>
<td>4.32*</td>
<td>0.95ns</td>
<td>0.98</td>
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</tr>
<tr>
<td>Landscape (L)</td>
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<td>95.01</td>
<td>28.21***</td>
<td>6.13**</td>
<td>5.40</td>
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<td>E*L</td>
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<td>4.56*</td>
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<tr>
<td>Total</td>
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<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Pairwise comparisons based on pseudo-t test. * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001, and ns = not significant.

that physical-chemical variables differed only among landscape-types. Pair-wise comparisons showed that all three landscapes 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 due to the variation in environmental variables discussed previously. These results are corroborated by the MDS plots that showed significant separation among the landscapes with 4 significant groupings at 250 m and 3 groupings at 750 m (Figure 3).

A total of 26,379 individual fish were collected across 36 species (Table 4). Six species comprised ~ 94% of the total catch; *Brevoortia patronus* (Gulf menhaden), *Anchoa mitchilli* (bay anchovy), *Mugil cephalus* (striped mullet), *Fundulus grandis* (Gulf killifish), *Leiostomus xanthurus* (spot), and *Cynoscion arenarius* (sand trout). Decapod crustaceans were represented by 35,714 individuals from 6 species (Table 5). *Palaemonetes* spp. (grass shrimp; 75.3%), *Farfantepenaeus aztecus* (brown shrimp;
Figure 3. Multi-dimensional scaling (MDS) plots of the phyico-chemical data for the (a) 250 m and (b) 750 m spatial extents. Dashed contours identify significant clusters (based on Euclidean distance) from agglomerative hierarchical clustering (CLUSTER) and similarity profiles (SIMPROF).
Table 4

Mean catch-per-unit-effort (CPUE; # sample) of individual fish collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in both Biloxi Bay (BB) and Pascagoula river (PRE) estuaries.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>IN</th>
<th>PF</th>
<th>CF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lepisosteus oculatus</td>
<td>0.3&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>0.1&lt;sup&gt;Z&lt;/sup&gt;</td>
</tr>
<tr>
<td>Elops saurus</td>
<td></td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Anguilla rostrata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Myrophis punctatus</td>
<td>0.1&lt;sup&gt;Z&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brevoortia patronus*</td>
<td>2225.6&lt;sup&gt;X&lt;/sup&gt;</td>
<td>140.9&lt;sup&gt;X&lt;/sup&gt;</td>
<td>148.1&lt;sup&gt;X&lt;/sup&gt;</td>
</tr>
<tr>
<td>Anchoa mitchilli*</td>
<td>96.0&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>15.9&lt;sup&gt;X&lt;/sup&gt;</td>
<td>0.4&lt;sup&gt;X&lt;/sup&gt;</td>
</tr>
<tr>
<td>Mugil cephalus*</td>
<td>43.0&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>22.0&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>35.4&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Fundulus grandis*</td>
<td>40.8&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>22.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>15.6&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Fundulus jenkinsi*</td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fundulus pulvereus</td>
<td></td>
<td></td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Fundulus similis*</td>
<td>0.5&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>7.6&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>6.4&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Adinia xenica*</td>
<td>6.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>7.6&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>6.4&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lucania parva</td>
<td></td>
<td>1.1&lt;sup&gt;Z&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Cyprinodon variegatus*</td>
<td>1.6&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>1.9&lt;sup&gt;X&lt;/sup&gt;</td>
<td>14.0&lt;sup&gt;X&lt;/sup&gt;</td>
</tr>
<tr>
<td>Poecilia latipinna*</td>
<td>1.3&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>8.1&lt;sup&gt;X&lt;/sup&gt;</td>
<td>17.1&lt;sup&gt;X&lt;/sup&gt;</td>
</tr>
<tr>
<td>Gambusia affinis</td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>0.5&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>0.8&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Menidia beryllina*</td>
<td>8.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>7.9&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>2.4&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lepomis macrochirus</td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepomis microlophus*</td>
<td></td>
<td>1.0&lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Micropterus salmoides</td>
<td>0.4&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>2.0&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>0.6&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Syngnathus louisianae</td>
<td>0.1&lt;sup&gt;Z&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagodon rhomboides*</td>
<td>6.3&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>12.0&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>7.4&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Leiostomus xanthurus*</td>
<td>91.5&lt;sup&gt;X&lt;/sup&gt;</td>
<td>85.6&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>50.5&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Sciaenops ocellatus</td>
<td></td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Pogonias cromis</td>
<td>2.1&lt;sup&gt;Z&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cynoscion arenarius*</td>
<td>50.3&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>0.8&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>2.6&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Cynoscion nebulosus</td>
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<tr>
<td>Bairdiella chrysoura</td>
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<td></td>
<td>0.3&lt;sup&gt;Y&lt;/sup&gt;</td>
</tr>
<tr>
<td>Micropogonias undulatus</td>
<td>0.5&lt;sup&gt;Y&lt;/sup&gt;</td>
<td>0.1&lt;sup&gt;Y&lt;/sup&gt;</td>
<td></td>
</tr>
</tbody>
</table>

21.4%), and *Callinectes sapidus* (blue crab; 3.3%) dominated the total decapod crustacean catch. Nekton species richness (S) differed only among the landscapes (ANOVA, p < 0.001) and was greater in PF landscapes (Tukey’s HSD; 18.1 ± 0.7) than either IN (15.6 ± 1.2) or CF (15.3 ± 1.4) landscapes; PF landscapes, however, contained...
Table 4 (continued)

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>IN</th>
<th>PF</th>
<th>CF</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ctenogobius shufeldti</em></td>
<td>23.4Y</td>
<td>0.3Y</td>
<td></td>
</tr>
<tr>
<td><em>Ctenogobius boleosoma</em></td>
<td>0.1Y</td>
<td>2.1Y</td>
<td></td>
</tr>
<tr>
<td><em>Gobiosoma bosc</em></td>
<td>0.1Z</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Evorthodus lyricus</em></td>
<td>0.3X</td>
<td>0.9Y</td>
<td>1.1Z</td>
</tr>
<tr>
<td><em>Gobionellus oceanicus</em></td>
<td>1.3Z</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Paralichthys lethostigma</em></td>
<td>3.1X</td>
<td>2.9X</td>
<td>4.5X</td>
</tr>
<tr>
<td><em>Citharichthys spilopterus</em></td>
<td>5.6X</td>
<td>3.8X</td>
<td>1.5X</td>
</tr>
<tr>
<td><em>Sphoeroides parvus</em></td>
<td>6.4Z</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Asterisks indicate species used in multivariate analyses (≥ 0.2 % of total abundance). Collected in both estuaries (X), only PRE (Y), and only BB (Z).

Table 5

Mean catch-per-unit-effort (CPUE; # sample) of decapod crustaceans collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in both Biloxi Bay (BB) and Pascagoula river (PRE) estuaries.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>IN</th>
<th>PF</th>
<th>CF</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Callinectes sapidus</em></td>
<td>56.9X</td>
<td>53.0X</td>
<td>36.4X</td>
</tr>
<tr>
<td>Uca spp.</td>
<td>0.6X</td>
<td>1.4X</td>
<td>0.9X</td>
</tr>
<tr>
<td><em>Farfantepenaeus aztecus</em></td>
<td>835.8X</td>
<td>81.6X</td>
<td>37.4X</td>
</tr>
<tr>
<td><em>Litopenaeus setiferus</em></td>
<td>0.3Y</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaemonetes spp.*</td>
<td>2212.3X</td>
<td>1021.1X</td>
<td>126.9X</td>
</tr>
<tr>
<td><em>Macrobrachium ohione</em></td>
<td>0.1Y</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Asterisks indicate species used in multivariate analyses (≥ 0.2 % of total abundance). Collected in both estuaries (X), only PRE (Y), and only BB (Z).

(ANOVA, p < 0.001) and was greater in PF landscapes (Tukey’s HSD; 18.1 ± 0.7) than either IN (15.6 ± 1.2) or CF (15.3 ± 1.4) landscapes; PF landscapes, however, contained more freshwater species (e.g., *Lepomis macrochirus* (bluegill), *L. microlophus* (readear sunfish), and *Micropterus salmoides* (largemouth bass)) due to the lower salinity.

Simpsons evenness index (1-λ) differed only among landscapes (ANOVA, p < 0.01) and the nekton assemblage in CF (Tukey’s HSD; 0.68 ± 0.063) were more evenly distributed than either IN (0.57 ± 0.023) or PF (0.59 ± 0.031) landscapes due to the presence of
highly abundant species (e.g., *B. patronus* and *Palaemonetes* spp.) in the latter two landscapes.

Once rare species were removed from the data, 21 nekton species were retained for multivariate analyses (Tables 4 and 5). Nekton assemblage composition differed between estuaries, among landscapes, and there was a significant estuary*landscape interaction (PERMANOVA, Table 6a). However, the conventional test is compromised by a lack of independence among sampling units (i.e., weeks) and 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-PF landscape and BB-PF differed markedly in the composition of their nekton assemblages. MDS plots showed a

---

**Results of permutational multivariate analysis of variance (PERMANOVA) on 4th root transformed Bray-Curtis similarity matrices based on (a) nekton and (b) macroinfaunal assemblages.**

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MSE</th>
<th>Conventional Pseudo-(F)</th>
<th>Conservative Pseudo-(F)</th>
<th>Variance component</th>
<th>Pair-wise comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estuary (E)</td>
<td>1</td>
<td>615.38</td>
<td>2.37*</td>
<td>0.72ns</td>
<td>5.45</td>
<td></td>
</tr>
<tr>
<td>Landscape (L)</td>
<td>2</td>
<td>2394.52</td>
<td>9.23***</td>
<td>2.81*</td>
<td>16.36</td>
<td>IN ≠ PF ≠ CF</td>
</tr>
<tr>
<td>E*L</td>
<td>2</td>
<td>853.51</td>
<td>3.29**</td>
<td></td>
<td>12.19</td>
<td>BB-PF ≠ PRE-PF</td>
</tr>
<tr>
<td>Residual</td>
<td>18</td>
<td>259.52</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MSE</th>
<th>Conventional Pseudo-(F)</th>
<th>Conservative Pseudo-(F)</th>
<th>Variance component</th>
<th>Pair-wise comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>(b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estuary (E)</td>
<td>1</td>
<td>3033.50</td>
<td>2.92*</td>
<td>0.65ns</td>
<td>12.89</td>
<td>IN ≠ PF ≠ CF</td>
</tr>
<tr>
<td>Landscape (L)</td>
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<td>5902.20</td>
<td>5.68***</td>
<td>1.26ns</td>
<td>24.65</td>
<td>IN ≠ PF ≠ CF</td>
</tr>
<tr>
<td>E*L</td>
<td>2</td>
<td>4688.44</td>
<td>4.51*</td>
<td></td>
<td>30.20</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>18</td>
<td>1039.60</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Pairwise comparisons based on pseudo-t test. * \(p \leq 0.05\), ** \(p \leq 0.01\), *** \(p \leq 0.001\), and ns = not significant.
similar differentiation among landscapes with two significant groupings at 65% similarity (CLUSTER); group 1 contained all of the IN samples, the PRE-PF samples, and a single BB-CF sample and group 2 contained the remaining PF and CF samples (Figure 4).

Nekton

Figure 4. Multi-dimensional scaling (MDS) plot of the nekton assemblages for each combination of estuary (BB and PRE) and landscapes (IN, PF, and CF). Dashed contours identify significant clusters (based on Bray-Curtis similarity) from agglomerative hierarchical clustering (CLUSTER) and similarity profiles (SIMPROF).

assemblages in IN and CF landscapes were most dissimilar (SIMPER, mean dissimilarity = 71.86 %) followed by IN and PF (mean dissimilarity = 58.39%) and PF and CF (mean dissimilarity = 56.30%). Further, the CPUE of a few species (e.g., Palaemonetes spp., Brevoortia patronus, Farfantepenaeus azteca, Leiostomus xanthurus, Callinectes sapidus) contributed to 90% of the dissimilarity among landscapes (Figure 5) and between the 2 significant clusters (mean dissimilarity = 61.79%; Figure 6).
Nekton assemblage patterns were significantly correlated to the physical-chemical patterns at both 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 (TECI_SM(W)), developed shoreline (TECI_DEV(W)), and salt marsh habitat (PLAND_SM) were commonly correlated to the nekton assemblage patterns (Table 7). Though the three variable model (TECI_SM(W), PLAND_SM, CONNECT) had the highest correlation (BEST, ρ = 0.571) with nekton patterns at the 250 m spatial scale, CONNECT alone was similarly correlated (BEST, ρ = 0.569). At the larger spatial scale, salt marsh fragmentation (SPLIT) was an important correlate of nekton patterns. For most nekton, CPUE increased significantly with both the amount of natural shoreline and salt marsh habitat and creek connectivity and significantly decreased with increasing fragmentation (e.g., Brevoortia patronus, Anchoa mitchilli, Fundulus grandis, Palaemonetes spp., and Farfantepenaeus aztecs; Table 8). Conversely, both Cyprinodon variegatus (sheepshead minnow) and Poecilia latipinna (sailfin molly) were negatively and positively correlated to creek connectivity and salt marsh fragmentation, respectively. Several species showed no correlation to any of these spatial metrics (e.g., Fundulus jenkinsi (saltmarsh topminnow), Leistomus xanthurus, Paralichthys lethostigma (southern flounder), and Callinectes sapidus.

A total of 4,480 individual macroinfauna representing 25 taxa were collected in 72 Eckman samples (Table 9). Mean macroinfaunal densities (scaled to m²) ranged from 0.0 to 17,001.4 individuals m². During the sampling period, the macroinfaunal assemblage was dominated by 7 taxa: the insect family Chironomidae (29.87 %), polychaete worm family Capitellidae (20.38%), oligochaete worm family Tubificidae (17.66 %),
Figure 5. Mean CPUE (± SD) of the nekton contributing to 90% of the cumulative variation among landscape-types. Mean dissimilarity (SIMPER) between landscapes shown in the upper left corner of each plot and mean dissimilarity (± SD) attributed to each species indicated by the black circles. Note the difference in CPUE scale for the bottom panel. GSHP = *Palaemonetes* spp., BSHP = *Farfantepenaeus aztecus*, GMEN = *Brevoortia patronus*, SPOT = *Leiostomus xanthurus*, BLCB = *Callinectes sapidus*, SMUL = *Mugil cephalus*, SHMN = *Cyprinodon variegatus*, PINF = *Lagodon rhomboides*. 


Note the difference in CPUE scale for the bottom panel.
Figure 6. Mean CPUE (± SD) of the nekton contributing to 90% of the cumulative variation among significant groupings identified by agglomerative hierarchical clustering from Figure 4. Mean dissimilarity (SIMPER) between groups shown in the upper left corner of each plot and mean dissimilarity (± SD) attributed to each species indicated by the black circles. GSHP = Palaemonetes spp., BSHP = Farfantepenaeus aztecus, GMEN = Brevoortia patronus, SPOT = Leiostomus xanthurus, BLCB = Callinectes sapidus, SMUL = Mugil cephalus, MOLL = Poecilia latipinna.

Gammarus spp. (7.12%), Amphecteis floridus (7.01%), polychaete worm family Nereididae (6.78%), and Streblospio spp. (6.41%; Table 9). Taxonomic richness (S) did not differ between estuaries (PRE = 6.50 ± 0.78; BB = 5.91 ± 1.01; ANOVA, p = 0.63) or among landscapes (IN = 7.38 ± 1.27; PF = 6.13 ± 0.90; CF = 5.63 ± 0.92; ANOVA, p = 0.25), nor was there a significant estuary*landscape interaction (ANOVA, p = 0.15). Simpson’s evenness index (1 – λ) did not differ between estuaries (PRE = 0.55 ± 0.066; BB = 0.58 ± 0.042; ANOVA, p = 0.17) but was significantly different among landscapes (ANOVA, p = 0.008, partial η² = 0.42) and there was a significant interaction
Table 7

Multivariate correlations ($\rho$) between physical-chemical and a) nekton and b) macroinfaunal resemblance matrices.

<table>
<thead>
<tr>
<th>Number Variables</th>
<th>$\rho$</th>
<th>Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) 250 m</td>
<td>3</td>
<td>0.571</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.569</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.563</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.559</td>
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<tr>
<td>750 m</td>
<td>2</td>
<td>0.700</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.660</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.659</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.651</td>
</tr>
<tr>
<td>b) 250 m</td>
<td>3</td>
<td>0.395</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.391</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.390</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.385</td>
</tr>
<tr>
<td>750 m</td>
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<td>0.282</td>
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<tr>
<td></td>
<td>6</td>
<td>0.282</td>
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<td></td>
<td>5</td>
<td>0.279</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.279</td>
</tr>
</tbody>
</table>

Note. Displayed are top 4 models from the BEST output. Variable definitions found in Table 1.

(ANOVA, $p = 0.02$, partial $\eta^2 = 0.36$) that accounted for a similar proportion of model variance. Though both macroinfaunal assemblages were more evenly distributed in IN ($0.64 \pm 0.047$) and PF ($0.57 \pm 0.089$) than in CF ($0.42 \pm 0.060$), taxa were more evenly distributed in BB-PF ($0.71 \pm 0.039$) than PRE-PF ($0.42 \pm 0.079$).

Removal of rare taxa resulted in 13 taxa being retained for multivariate analyses (Table 10). Though the conventional PERMANOVA indicated significant differences in macroinfaunal assemblages at all levels including a significant estuary*landscape interaction (Table 6b), the conservative estimate of the pseudo-$F$ test indicated that
Macroinfaunal assemblage structure did not differ between estuaries or among landscapes. Further, both the residuals and interaction term accounted for a large proportion of the model variation suggesting that macroinfaunal assemblages differ markedly among samples within sites and that differences in macroinfaunal assemblages were not consistent across either estuaries or landscapes. The MDS ordination of the macroinfaunal resemblance data corroborates the PERMANOVA results (Figure 7) and six significant clusters were identified at 40% similarity.

Despite a clear lack of patterning, the macroinfaunal assemblage showed a significant correlation to 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.

### Table 8

**Pearson’s correlation coefficients correlating nekton CPUE and physical-chemical variables identified in the BEST model.**

<table>
<thead>
<tr>
<th>Species</th>
<th>TECI_SM(W)</th>
<th>PLAND_SM</th>
<th>CONNECT</th>
<th>TECI_SM(W)</th>
<th>SPLIT</th>
</tr>
</thead>
<tbody>
<tr>
<td>GMEN</td>
<td>0.47*</td>
<td>0.35*</td>
<td>0.38*</td>
<td>0.55**</td>
<td>-0.24</td>
</tr>
<tr>
<td>BAYA</td>
<td>0.55**</td>
<td>0.46*</td>
<td>0.48**</td>
<td>0.60**</td>
<td>-0.36*</td>
</tr>
<tr>
<td>SMUL</td>
<td>0.085</td>
<td>-0.001</td>
<td>0.034</td>
<td>0.21</td>
<td>0.048</td>
</tr>
<tr>
<td>FUNG</td>
<td>0.51**</td>
<td>0.44*</td>
<td>0.46*</td>
<td>0.55**</td>
<td>-0.35*</td>
</tr>
<tr>
<td>FUNJ</td>
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<td>0.15</td>
<td>0.080</td>
<td>-0.21</td>
<td>-0.28</td>
</tr>
<tr>
<td>SHMN</td>
<td>-0.42*</td>
<td>-0.54**</td>
<td>-0.59*</td>
<td>-0.44*</td>
<td>0.60**</td>
</tr>
<tr>
<td>MOLL</td>
<td>-0.37*</td>
<td>-0.43*</td>
<td>-0.37*</td>
<td>-0.29</td>
<td>0.39*</td>
</tr>
<tr>
<td>SPOT</td>
<td>0.19</td>
<td>0.22</td>
<td>0.25</td>
<td>0.17</td>
<td>-0.26</td>
</tr>
<tr>
<td>WTRO</td>
<td>0.57**</td>
<td>0.41*</td>
<td>0.45*</td>
<td>0.62***</td>
<td>-0.29</td>
</tr>
<tr>
<td>FLDR</td>
<td>-0.20</td>
<td>-0.24</td>
<td>-0.23</td>
<td>-0.094</td>
<td>0.24</td>
</tr>
<tr>
<td>GSHP</td>
<td>0.62***</td>
<td>0.61***</td>
<td>0.63***</td>
<td>0.65***</td>
<td>-0.54*</td>
</tr>
<tr>
<td>BSHP</td>
<td>0.66***</td>
<td>0.48**</td>
<td>0.54**</td>
<td>0.64***</td>
<td>-0.39*</td>
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<tr>
<td>BLCB</td>
<td>0.20</td>
<td>0.19</td>
<td>0.15</td>
<td>0.19</td>
<td>0.19</td>
</tr>
</tbody>
</table>

Note. * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001. GMEN = Brevoortia patronus, BAYA = Anchoa mitchilli, SMUL = Mugil cephalus, FUNG = Fundulus grandis, FUNJ = Fundulus jenkinsi, SHMN = Cyprinodon variegatus, MOLL = Poecilia latipinna, SPOT = Leioptomus xanthurus, WTRO = Cynoscion arenarius, FLDR = Paralichthys lethostigma, GSHP = Palaemonetes spp., BSHP = Farfantepenaeus aztecus, and BLCB = Callinectes sapidus. Landscape metrics defined in Table 1.
m spatial scale, the amount of amount of salt marsh edge that was bordered by developed surfaces (TECI_DV(SM)), salt marsh fragmentation (SPLIT), and salinity were

Table 9

Mean density (# m⁻²) of macroinfaunal taxa collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in both Biloxi bay and Pascagoula river estuaries.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>IN</th>
<th>PF</th>
<th>CF</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Family: Chironomidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaemonetes spp. (post-larval)*</td>
<td>2031.8 X</td>
<td>5133.1 X</td>
<td>26.9 X</td>
</tr>
<tr>
<td>Grandidierella bonnieroides</td>
<td>311.8 X</td>
<td>143.2 X</td>
<td>26.9 X</td>
</tr>
<tr>
<td>Gammarus spp.*</td>
<td>1617.9 X</td>
<td>698.8 X</td>
<td>26.9 X</td>
</tr>
<tr>
<td>Ampelisca spp.</td>
<td>16.1 Z</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apocorophium spp.*</td>
<td>279.5 X</td>
<td>231.1 X</td>
<td>21.5 Y</td>
</tr>
<tr>
<td>Edotea montosa*</td>
<td>327.9 X</td>
<td>21.5 Y</td>
<td></td>
</tr>
<tr>
<td>Hargeria rapax*</td>
<td>96.8 Y</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melita spp.*</td>
<td>236.5 Y</td>
<td></td>
<td>16.1 Y</td>
</tr>
<tr>
<td><strong>Family: Tubificidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Streblospio benedicti*</td>
<td>365.5 X</td>
<td>1397.5 X</td>
<td>1198.6 X</td>
</tr>
<tr>
<td><strong>Family: Capitellidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capitella capitata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mediomastus californiensis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heteromastus filiformis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phylum: Nemertea</td>
<td>5.4 Z</td>
<td></td>
<td>10.8 Y</td>
</tr>
<tr>
<td>Leitoscoloplos fragilis</td>
<td>5.4 Z</td>
<td></td>
<td>5.4 Y</td>
</tr>
<tr>
<td>Eteone heteropoda*</td>
<td>75.3 Y</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Family: Nereididae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neanthes succinea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Laeonereis culveri</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stenonereis martini</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphicteis floridus*</td>
<td>80.6 X</td>
<td>1596.4 X</td>
<td>10.8 X</td>
</tr>
<tr>
<td>Polydora cornuta*</td>
<td>16.1 Y</td>
<td>86.0 Z</td>
<td>5.4 Z</td>
</tr>
<tr>
<td><strong>Family: Piscicolidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macoma mitchelli</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mulinia lateralis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tagelus plebius</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Asterisks indicate taxa used in multivariate analyses (≥ 0.2 % of total abundance). Collected in both estuaries (X), only PRE (Y), and only BB (Z).

commonly correlated (BEST, ρ = 0.395) to macroinfaunal patterns (Table 7b). The amount of hardened shoreline (TECI_DV(W)), percentage of the landscape that was salt marsh (PLAND_SM), salt marsh fragmentation (SPLIT), and environmental variables
Table 10

*Pearson’s correlation coefficients correlating macroinfaunal density and physical-chemical variables identified in the BEST model.*

<table>
<thead>
<tr>
<th>Species</th>
<th>PLAND_SM</th>
<th>TECI_DV(SM)</th>
<th>Salinity</th>
<th>TECI_DV(SM)</th>
<th>SPLIT</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHIR</td>
<td>0.24</td>
<td>-0.25</td>
<td>-0.24*</td>
<td>0.036</td>
<td>-0.35*</td>
</tr>
<tr>
<td>GAMM</td>
<td>0.24</td>
<td>-0.21</td>
<td>0.12</td>
<td>-0.39*</td>
<td>-0.21</td>
</tr>
<tr>
<td>APOC</td>
<td>0.21</td>
<td>-0.24</td>
<td>0.47*</td>
<td>-0.11</td>
<td>-0.11</td>
</tr>
<tr>
<td>EDOT</td>
<td>0.30*</td>
<td>-0.22</td>
<td>0.40*</td>
<td>-0.040*</td>
<td>-0.095</td>
</tr>
<tr>
<td>MELI</td>
<td>0.18</td>
<td>-0.16</td>
<td>0.16</td>
<td>-0.27</td>
<td>-0.16</td>
</tr>
<tr>
<td>OLIG</td>
<td>-0.34*</td>
<td>0.33*</td>
<td>-0.37*</td>
<td>0.30*</td>
<td>-0.32*</td>
</tr>
<tr>
<td>STRE</td>
<td>0.41*</td>
<td>-0.31**</td>
<td>0.16</td>
<td>-0.53**</td>
<td>-0.29**</td>
</tr>
<tr>
<td>CAPT</td>
<td>0.008</td>
<td>0.46*</td>
<td>0.44*</td>
<td>0.40*</td>
<td>0.13</td>
</tr>
<tr>
<td>ETEO</td>
<td>0.28</td>
<td>-0.21</td>
<td>0.051</td>
<td>-0.15</td>
<td>-0.20</td>
</tr>
<tr>
<td>NERD</td>
<td>-0.11</td>
<td>-0.20</td>
<td>0.15</td>
<td>0.32</td>
<td>0.13</td>
</tr>
<tr>
<td>AMPH</td>
<td>0.25</td>
<td>-0.35*</td>
<td>-0.37*</td>
<td>0.31</td>
<td>-0.39*</td>
</tr>
<tr>
<td>POLY</td>
<td>0.11</td>
<td>-0.16</td>
<td>-0.20</td>
<td>0.095</td>
<td>-0.15</td>
</tr>
<tr>
<td>MOLU</td>
<td>0.30</td>
<td>0.27</td>
<td>-0.077</td>
<td>-0.25</td>
<td>-0.26</td>
</tr>
</tbody>
</table>

Note. * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001. CHIR = Chironomidae, GAMM = Gammarus spp., APOC = Apocorophium spp., EDOT = Edotia triloba, MELI = Melita spp., OLIG = Tubificid Oligochaetes, STRE = Streblospio benedicti, CAPT = Capitellid polychaetes, ETEO = Eteone heteropoda, NERD = Nereididae, AMPH = Amphicecis floridus, POLY = Polydora cornuta, MOLU = molluscs. Landscape metrics defined in Table 1.

were weakly correlated (BEST, ρ = 0.282) to the macroinfaunal assemblage at 750 m.

However, at this spatial scale, only combinations of 5 and 6 variables were correlated to macroinfaunal patterns suggesting that a parsimonious solution could not be found.

*Streblospio benedicti* density was positively correlated to the amount of salt marsh habitat in the landscape and negatively correlated to the amount of salt marsh edge contrasted with developed surfaces and salt marsh fragmentation (Pearson’s r, Table 10). Both tubificid oligochaete worms and capitellid polychaete worms were positively correlated to the amount of salt marsh edge bordered by developed surfaces. Further, the density of a number of taxa was positively (*Apocorophium* spp., *Edotia triloba*, and capitellid polychaetes) and negatively (Chironomidae, tubificid oligochaetes, and *Amphicecis*
floridus) correlated to salinity. The density of chironomids, tubificid oligochaetes, Streblasio benedicti, and Amphectes floridus was negatively correlated to salt marsh fragmentation.

![Figure 7. Multi-dimensional scaling (MDS) plot of the macroinfaunal assemblages for each combination of estuary (BB and PRE) and patch-type (IN, PF, and CF). Dashed contour identifies significant groupings 40% similarity, respectively, from agglomerative hierarchical clustering (CLUSTER) and similarity profiles (SIMPROF).]

Discussion

I used a landscape ecology approach to show that although salt marsh landscapes arrayed along a gradient of urbanization hosted a similar suite of organisms there were clear compositional differences in nekton and, to a lesser extent, macroinfaunal assemblages. I demonstrated that the amount of salt marsh habitat, amount of natural shoreline (defined as the salt marsh-water interface), and both tidal creek connectivity and salt marsh fragmentation were consistent correlates of CPUE for a number of
species; the results were not always consistent across assemblages and warrant further examination. However, these results continue to build on the growing paradigm that, while the amount of salt marsh habitat is a driver of both nekton and macroinfaunal production (Weinstein 1979; Boesch & Turner 1984), the composition and configuration of the surrounding landscape is equally important (Guest & Connolly 2006; Meynecke et al. 2008; Roth et al. 2008; Meyer & Posey 2009; Green et al. 2012b).

Though it has been suggested that fish are poor indicators of habitat quality (Ellis & Bell 2013), the most conspicuous difference in this study occurred in the more mobile nekton assemblage. While natural salt marsh landscapes (IN) supported a significantly greater nekton CPUE, both in aggregate and on a species-specific basis, than either moderately (PF) or heavily urbanized (CF) landscapes there is evidence that suggests that moderately urbanized coastal landscapes are still viable habitats for nekton. Most likely, the relative value of the salt marsh habitat in moderately urbanized landscapes relates to the greater amount of salt marsh edge (TE for salt marsh class) that occurred as a result of the large tidal creek network that was a dominant feature of the landscape. Numerous studies have identified salt marsh edge as an important habitat for estuarine-dependent nekton (Peterson & Turner 1994; Minello & Rozas 2002; Minello et al. 2003). Both Browder et al. (1989) and Roth et al. (2008) found that 1) the length of salt marsh edge was a strong predictor of the abundance and production of *Farfantepenaeus aztecus* 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. However, there are limits to the amount of edge habitat that can be created as salt marsh habitat is lost (Chesney et al. 2000). Further, neither Browder et al. (1989) nor Roth et
al. (2008) explicitly examined the effects of anthropogenic habitat loss and fragmentation by substituting salt marsh habitats with developed surfaces and shorelines and sets upper limits on the amount of natural salt marsh edge.

The observed patterns in the relationships between the nekton CPUE and spatial metrics also suggest a linkage between life-history and landscape characteristics. Specifically, both resident (species that complete life-cycle in salt marsh habitats) and transient (species that spend only a portion of life in salt marsh habitats) nekton displayed different relationships with spatial metrics and these relationships were not consistent across species within each group. Resident and transient nekton differ markedly in both their tolerance of stressful conditions and ability to move amongst suitable habitat patches (Weinstein et al. 1984; Chitty & Able 2004; Rountree & Able 2007; Haas et al. 2009; Able et al. 2012) and this has strong implications for nekton distribution patterns in salt marsh habitats. The inner marsh serves as habitat for resident salt marsh nekton (e.g., Fundulus grandis, Cyprinodon variegatus, Poecilia latipinna, and Palaemonetes spp.; Kneib 2000; Minello & Rozas 2002). These smaller-bodied species use tidal creeks and rivulets along the marsh edge to access the inner marsh at high tide (Rozas et al. 1988; Kneib 2000; Bretsch & Allen 2006; Lopez et al. 2010) and inter-patch movements are spatially limited (Chitty & Able 2004; Able et al. 2012). Thus, anthropogenic salt marsh fragmentation would limit their access to primary habitats and negate inter-patch movements. However, while both F. grandis and Palaemonetes spp. were negatively correlated to salt marsh loss and fragmentation, C. variegatus and P. latipinna CPUE increased. Both F. grandis and Palaemonetes spp. are the dominant nekton 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 species have similar niche requirements and, as a result, a decrease in the abundance of *F. grandis* and *Palaemonetes* spp. under stressful conditions would likely result in a competitive release for more tolerant species, such as *C. variegatus* (e.g. Rowe & Dunson 1995).

Transient nekton (e.g., *Brevoortia patronus*, *Farfantepenaeus aztecus*, and *Callinectes sapidus*), on the other hand, use a variety of estuarine habitats, including tidal creeks and salt marsh edge, for a portion of their life-cycle (Rozas & Minello 1998; O’Connell et al. 2005). The amount of time spent in salt marsh habitats varies by species and life-stage (Kneib 1995; Hines 2007). Thus, some transients may visit salt marsh habitat sporadically (Deegan 1990); others may have a prolonged period of temporary residency (Weinstein et al. 1984; Haas et al. 2005), while more mobile transient nekton may supplement their habitat requirements with other, potentially less suitable, habitats. For example, both *B. patronus* and *F. aztecus* CPUE was positively correlated to patch-size and inversely correlated to fragmentation whereas *C. sapidus* showed no correlation to any of the spatial metrics. Juvenile *B. patronus* are a migratory schooling species that move amongst tidal creeks to maximize foraging opportunities (Deegan 1990) and their diets are a mixed composition of detrital and phytoplankton sources (Deegan et al. 1990). While this would require moving short distances through vegetated corridors in natural salt marsh landscapes (i.e., IN), *B. patronus* would have to move large distances through unsuitable habitat and would likely experience increased predation (*sensu* Simenstad et al. 1999; Long et al. 2011) in search of other salt marsh patches in urbanized landscapes (i.e., CF landscapes). Unlike *B. patronus*, once *F. aztecus* 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 & Turner 1994; Rozas & Zimmerman 2000; Haas et al. 2005). Both salt marsh loss and the addition of developed shorelines can significantly reduce the amount of habitat (Browder et al. 1985; Chesney et al. 2000; Peterson & Lowe 2009) for *F. azteca*. *Callinectes sapidus*, on the other hand, shift among habitats according to life stage and movements are highly variable ranging from 50 m d\(^{-1}\) after molting to 200 m d\(^{-1}\) for juveniles to several km d\(^{-1}\) for adults (Hines 2007). As a result, transient species that have specific habitat requirements (i.e., *B. patronus* and *F. azteca*) are more likely to be impacted in urbanized landscapes than species that are able to exploit multiple habitats (i.e., *C. sapidus*). Interestingly, several studies have shown developed shorelines to be sub-optimal habitats for *C. sapidus* (Kemp et al. 2005; King et al. 2005; Seitz et al. 2006; Long et al. 2011), suggesting that maintaining some marsh habitat in urbanized landscapes, at least, is better than total habitat loss (Partyka & Peterson 2008).

Though patterns were less clear, macroinfaunal assemblages in completely fragmented salt marsh landscapes were comparatively more depauperate than either assemblage in intact natural or partially fragmented landscapes (mean total density of all taxa decreased from IN (3545.6 ± 172.7 #ind m\(^{-2}\)), PF (2899.9 ± 111.3 #ind m\(^{-2}\)), and CF (1813.5 ± 88.6 #ind m\(^{-2}\))). The density of annelid worms, most notably tubificid oligochaetes and capitellid polychaetes, was positively correlated to the amount of salt marsh edge that was shared with hardened edge (TECI_DV(SM)) and displayed conflicting correlations to salinity. Thus, tubificid oligochaetes were the dominant taxa in urbanized, low salinity salt marsh habitats (i.e., BB-CF) while capitellid polychaetes were dominant in urbanized salt marshes with elevated salinity (i.e., PRE-CF). In their
development of a benthic index for estuarine ecosystem health in the GOM, Engle et al. (1994) found that the relative proportion of tubificid oligochaetes combined with a measure of benthic diversity was a good discriminator between healthy and degraded benthic habitats. Previous studies have established that both taxa are opportunistic colonizers of degraded habitats (Sarda et. al 1996; Rakocinski et al. 1997; Weinstein & Sanger 2003; Holland et al. 2004; Dean 2008). However, tubificid oligochaetes are typically more abundant in low salinity, freshwater habitats while capitellid oligochaetes are more commonly found toward the marine end of the estuarine gradient (Engle et al. 1994). Additionally, *Streblospio benedicti* displayed a strong, negative correlation with the amount of salt marsh edge adjacent developed surfaces. Though 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 both sediment contamination (e.g., PAHs) and hypoxia (Sarda et al. 1996; Lerberg et al. 2000; Weinstein & Sanger 2003; Holland et al. 2004). Combined, these correlations suggest that benthic sediments in the highly urbanized, CF salt marsh landscapes are more degraded than either IN or PF landscapes. However, these patterns are unlikely to be a direct consequence of processes occurring at the landscape-scale most likely reflect benthic degradation due to the influence of developed (i.e., impervious) surfaces adjacent the salt marsh patches (Sanger et al. 1999a,b; Lerberg et al. 2000; Holland et al. 2004; Van Dolah et al. 2008).

While the coarse resolution of the macroinfaunal identifications prevents direct comparisons with similar studies, the densities of both amphipod crustaceans (e.g., *Gammarus* spp., *Ampelisca* spp., *Apocorophium* spp., *Edotia montosa*, and *Hargeria* spp.,...
rapax) and bivalves (e.g., *Macoma mitchelli*, *Mulinia lateralis*, and *Tageulus plebius*) were conspicuously low in CF landscapes, which was also noted in a similar study in the Pascagoula River estuary (Partyka & Peterson 2008). Both taxa are important components of nekton diets (Hines et al. 1990; Rozas & LaSalle 1990; McTigue & Zimmerman 1991; Nemerson & Able 2004) and their low abundance may also be viewed as an additional indicator of poor habitat quality for nekton (Partyka & Peterson 2008; Goto & Wallace 2010). Decreased prey availability not only diminishes the value of salt marsh habitats (Weinstein 1979; Boesch & Turner 1984) but also disrupt 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 CF landscapes could offset the potentially altered trophic pathways for nekton. Goto and Wallace (2010) showed that *Fundulus heteroclitus* (mummichog), a congener of *F. grandis*, was able to offset the metabolic costs of altered prey sources by increasing consumption rates and there is evidence that this species may undertake long distance migrations in salt marsh landscapes to optimize growth (Haas et al. 2009).

Seitz et al. (2006) suggested that degraded benthic assemblages could arise from altered trophic dynamics due to decreased allochthonous carbon input in salt marsh habitats with restricted shorelines. In their study, the abundance of deposit feeding infauna (e.g., *Macoma baltica*) was lower than that of suspension feeding infauna (e.g., *Tageulus plebius*) in restricted salt marsh sites. While similar bivalves were notably absent from the urbanized salt marshes in our study, exploratory grouping of the remaining taxa into appropriate feeding guilds (Fauchald & Jumars 1979; Ferdette & Diaz 1986; Gaston & Nasci 1988; Stocks & Grassle 2001) revealed that both deposit
feeding (e.g., tubificid oligochaetes and capitellid polychaetes) and suspension feeding (e.g., *Streblospio benedicti* and some amphipod crustaceans) macroinfauna were present in our study. However, based on feeding strategy, our observations are counterintuitive to the hypothesis of Seitz et al. (2006) and we suggest that this is an artifact of both season and sampling design. Seitz et al. (2006) sampled in benthic habitats in subestuaries of Chesapeake Bay during a period (June – August) when aboveground biomass of live and dead (detritus) plant material is approaching its maximum and minimum (Valiela et al. 1975; Dame & Kenny 1986), respectively. Thus, they hypothesized that suspension feeders would do well in altered habitats due to allochthonous food sources in the water column. Our samples, however, were collected in a one-month snap-shot during a period when regional patterns in aboveground production of live biomass is starting to build up and dead biomass is still readily available (Kirby & Gosselink 1976). Thus, had we extended our sampling longer into the primary growth season we may have observed turnover in the benthic assemblage from deposit feeding annelid worms to suspension feeding infauna that would also coincide the benthic assemblage switching from reliance on autochthonous derived production to more allochthonous production.

There are several limitations associated with the results presented in this study that warrant discussion. First, the coarse resolution (i.e., grain) of the land-cover data for the study area (30 m² pixels) is likely to influence “area-sensitive” metrics (e.g., edge and shape metrics; Moilanen & Nieminen 2002). However, all landscapes and spatial scales were examined at the same resolution and thus the relative differences in metrics are viable. Further, the connectivity measures used in this study (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; with the current resolution, the minimum edge depth value would correspond to the smallest unit of measurement (i.e., 30 m). Resident and transient nekton, are commonly found in inner and edge (< 5m) salt marsh habitats, respectively, at high tide (Minello & Rozas 2002) and finer resolution land-cover data would allow for a more accurate calculation of edge and core area metrics (McGagrial et al. 2002). Lastly, my approach admittedly violates the assumption of sample independence (i.e., I was unable to appropriately replicate each landscape and treated weekly samples as the unit of measure) and is a pseudo-replicated 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 1 error (Hurlbert & White 1993). However, it has been argued that pseudo-replication is, oftentimes, unavoidable in experimental ecology (Stewart-Oaten & Murdoch 1986; Hargrove & Pickering 1992; Oksanen 2001) and while my results are difficult to extrapolate to other systems, I feel that the causal inferences made in this study are strengthened by their generality (Beck 1997). As such, the aggregated faunal responses in this study are an abbreviated representation of the complex interactions between salt marsh and urban ecosystems (Halpern et al. 2008b). At a minimum, these results generate a core set of hypotheses for future work. As more detailed information is acquired, salt marsh ecologists can move from simply matching landscape pattern to ecological patterns such as this to providing more detailed mechanistic linkages between salt marsh habitats, their faunal components, and the surrounding landscape.
Despite these limitations, our results have broad implications for salt marsh habitat restoration and management. I recognize the obligatory nature of population growth (Crossett et al. 2004; European Environmental Agency 2006) and accompanying infrastructure (Beach 2002; Living Shoreline 2006) in the coastal zone, and suggest, as do others (Thom et al. 2005; Swann 2008; Peterson & Lowe 2009; Bulleri & Chapman 2010; Browne & Chapman 2011; Chapman & Underwood 2011), that identifying and maintaining the functional properties of natural landscapes (i.e., habitat quality and connectivity) is critical to the future health of coastal ecosystems and continued delivery of ecosystem services. Based on my results, coastal landscapes consisting of several smaller, connected salt marsh patches have faunal components similar to those in natural salt marsh landscapes (sensu Partyka & Peterson 2008; Green et al. 2012). Thus, management and restoration efforts aimed at maintaining faunal assemblages and secondary production could benefit from focusing on promoting functional connectivity among several smaller patches (i.e., SLoSS concept; Moy & 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 & 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 ecologist, engineers, managers, and decision makers to make
well-informed science-based decisions regarding future growth in the coastal zone. Growth that progresses in a manner that both consumes and isolates critical habitats within a human-dominated landscape is unsustainable and 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).
CHAPTER III
RELATIVE CONDITION AND DIET COMPOSITION OF SELECT NEKTON IN URBANIZED SALT MARSH LANDSCAPES

Introduction

Salt marsh estuaries are highly productive features of temperate coastal landscapes. The consistency of estuarine primary production has led to the long-standing axiom that salt marshes support abundant fish and decapod crustacean (i.e., nekton) populations through reduced predation, increased individual growth, and increased foraging opportunities (Shenker & Dean 1979, Weinstein 1979, Kneib 1982, Peterson & Turner 1994, Beck et al. 2001). Many of the nekton that utilize salt marsh habitats for a portion of their life (i.e., estuarine-dependent nekton) are either ecologically or economically important (Weinstein 1979, Boesch & Turner 1984, Kneib 2000, Minello et al. 2003, O’Connell et al. 2005) and, as a result, healthy salt marsh ecosystems are a valuable economic commodity (Costanza et al. 1997, Heinz Center 2002, U.S. Commission on Ocean Policy 2004). Yet, despite the clear linkage between healthy coastal ecosystems and economically valuable fisheries production, salt marsh estuaries are among the most degraded and altered ecosystems in the world (Vitousek et al. 1997, Valiela et al. 2004, Lotze et al. 2006).

As the human population continues to grow in the coastal zone (Crossett et al. 2004, European Environmental Agency 2006) salt marsh habitats are degraded, lost, fragmented and/or replaced with developed surfaces and hardened shorelines (i.e., urbanization, Bromberg Gedan et al. 2009, Peterson & Lowe 2009, Mee 2010). Though it is well established that coastal urbanization has negative consequences for the long-
term sustainability of nekton communities (Peterson & Lowe 2009), the bulk of research to date has focused on the comparative value of natural salt marsh habitats and their man-made counterparts (i.e., flood control structures and armored shorelines, Able et al. 1999, Hendon et al. 2000, Peterson et al. 2000, Bilkovic & Roggero 2008, Long et al. 2011). Often times, coastal urbanization progresses additively (Odum 1970, 1982) in a manner that results in various degrees of salt marsh loss and increasingly fragmented salt marsh habitats nestled within urbanized landscapes (Chapter II). While there is empirical evidence suggesting that anthropogenically fragmented salt marsh landscapes harbor altered faunal assemblages (i.e., nekton and macrobenthic, Partyka and Peterson 2008, Chapter II), neither the mechanisms nor the ultimate consequences of these patterns are well understood. For example, Chapter II found that not only did nekton assemblages differ among salt marsh landscapes arrayed along a gradient of urbanization and fragmentation, but also that the benthic macroinfaunal (i.e., benthic and epibenthic fauna) assemblages differed as well. Specifically, the densities of several taxa (e.g., chironomids, amphipod crustaceans, and bivalves), common prey items for nekton, were notably low or absent in highly urbanized, fragmented salt marsh habitats. The reduced prey density may result in altered trophic dynamics and, consequently, reduced nekton growth in urbanized landscapes.

While the mechanisms contributing to variable growth patterns in estuarine dependent-nekton are numerous (Sogard 1992; Fitzhugh et al. 1996; Rakocinski et al. 2006), somatic growth is ultimately constrained by both prey availability and foraging efficiency. Habitats that provide increased foraging opportunities are likely to facilitate growth and, thus, confer a number of ecological advantages (Werner & Gilliam 1984;
Sogard 1997). Such habitats are vital to the maintenance of coastal nekton populations (Levin et al. 1997, Craig & Crowder 2000, Stunz et al. 2002) and should contribute disproportionately more individuals to later life-stages (Houde 1989) than sub-optimal habitats (Beck et al. 2001). However, the relative value, in terms of growth and feeding, of salt marsh habitats arrayed along a gradient of urbanization has received little attention outside of the impacts of pollution (Toppin et al. 1987, Weis & Kahn 1991, Weis et al. 2011).

The primary goal of this work is to examine the effects of urbanization and fragmentation of salt marsh habitats on select nekton populations. The specific objectives of this work are two-fold. First, I used length-weight relationships to examine the growth dynamics (i.e., relative condition) of nekton populations collected from salt marsh habitats arrayed along a gradient of urbanization and fragmentation. Secondly, I quantified the diet composition of selected nekton populations in each salt marsh landscapes and related these patterns to growth dynamics.

Methods

Study Area and Site Description

The study area consisted of two large, micro-tidal river estuaries in coastal Mississippi (Chapter II, Figure 1). The lower Pascagoula River estuary (PRE) is a ~15 km long distributary that can be further sub-divided 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 with large expanses of intact, natural habitats (Peterson et al. 2007, Partyka & Peterson 2008). The Biloxi Bay estuary (BB) is ~21.7 km in length and
consists of both highly impacted and un-impacted shorelines, however, the juxtaposition of the two is spatially more complex than 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 & Lowe 2009) and natural shorelines are comprised mostly of intertidal vegetation dominated by *Spartina alterniflora* (smooth cordgrass) and *Juncus romerianus* (black needlerush) with occasional landscapes of the invasive *Phragmites australis* (common reed, Peterson & Partyka 2006). Though both systems receive considerable freshwater input from upstream watersheds, the PRE has considerably higher discharge rates than the BB (Lowe et al. 2012).

Though the full recount is beyond the scope of this paper, and can be found in Chapter II, a brief synopsis of those methods and results is warranted. I used a landscape ecology approach to quantify both the composition and configuration of the associated landscapes at multiple spatial scales surrounding 3 small, first-order salt marsh tidal creeks arrayed along a gradient of increasing urbanization and salt marsh fragmentation in each estuary. Intact natural landscapes (IN, Figure 1) were dominated by unfragmented salt marsh with a high degree of connectivity among small first-order tidal creeks. There was little evidence of urbanization within these landscapes at multiple GIS rendered spatial scales. Partially fragmented landscapes (PF, Figure 1) were a mix of urbanized surfaces and salt marsh classes. Overall, a large tidal creek network was the prominent feature of both PF salt marsh landscapes and, as a result, PF landscapes had more salt marsh edge (i.e., natural shoreline) than either the IN or completely fragmented (CF, Fig 1) landscapes. However, the amount of salt marsh edge decreased inversely with the amount of urbanized surface and hardened shoreline resulting in moderately
fragmented salt marsh patches. Completely fragmented landscapes, on the other hand, were dominated by urbanized surfaces and hardened shorelines. Salt marsh patches in these landscapes tended to be small, simply shaped, moderately aggregated, and highly fragmented. Based on several landscape metrics, the three landscape types were significantly different from one another (Chapter II).

Nekton Collections and Relative Condition

From 3 May to 4 June 2010, nekton were collected weekly in each tidal creek (2 estuaries \( \times 3 \) creeks \( \times 4 \) weeks = 24 collections) using modified Fyke nets (Memphis Net and Twine). Specific details on the net dimensions and deployment can be found in Chapter II. Fyke nets were placed across the wet cross-sectional area of each tidal creek mouth at slack high tide (depth 35.0 – 59.0 cm) and nekton were collected on the ebbing tide as they exited the marsh surface by pulling a 4.9 m minnow seine (3.2 mm stretched mesh) through \( \sim 75 \% \) of the total creek length (corresponding to low water), into the mouth of the net. All captured nekton were removed from the cod-end of the net, placed on ice in the field, and returned to the laboratory where they were frozen until they could be identified to the lowest possible taxonomic-unit (i.e., species) and enumerated. Blue crab (Callinectes sapidus), brown shrimp (Farfantepenaeus aztecus), Gulf killifish (Fundulus grandis), and spot (Leiostomus xanthurus) were consistently among the most abundant economically and ecologically important species in each collection (Table 11).

Abundance, in this case, is equal to total number of individuals in each collection (i.e., catch-per-unit-effort, CPUE). For each of the four species, up to 30 individuals from each collection including both the largest and smallest individuals were randomly subsampled, measured (carapace width (CW) for blue crab, carapace length (CL) for
brown shrimp, total length (TL) for Gulf killifish and spot, ± 0.1 mm) and weighed (wet weight (WW), ± 0.001 g).

Table 11

*Mean (± S.E.) catch-per-unit-effort (CPUE, total number of individuals during each collection) and number of individuals used in analyses (n) of four nekton species collected from intact, natural (IN), partially fragmented (PF), and completely fragmented (CF) salt marsh landscapes in the a) Biloxi bay and b) Pascagoula River estuaries.*

<table>
<thead>
<tr>
<th></th>
<th>Blue crab</th>
<th>Brown shrimp</th>
<th>Gulf killifish</th>
<th>Spot</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) IN</td>
<td>59.8 ± 14.2</td>
<td>559.5 ± 252.6</td>
<td>54.5 ± 18.3</td>
<td>54.5 ± 18.3</td>
</tr>
<tr>
<td>n = 120</td>
<td>n = 114</td>
<td>n = 101</td>
<td>n = 113</td>
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</tr>
<tr>
<td>PF</td>
<td>67.3 ± 48.0</td>
<td>109.3 ± 32.3</td>
<td>32.0 ± 8.8</td>
<td>32.0 ± 8.3</td>
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<tr>
<td>n = 120</td>
<td>n = 98</td>
<td>n = 88</td>
<td>n = 108</td>
<td></td>
</tr>
<tr>
<td>CF</td>
<td>53.8 ± 18.4</td>
<td>37.8 ± 19.7</td>
<td>14.3 ± 5.6</td>
<td>29.5 ± 3.6</td>
</tr>
<tr>
<td>n = 101</td>
<td>n = 81</td>
<td>n = 57</td>
<td>n = 111</td>
<td></td>
</tr>
</tbody>
</table>

|                |            |              |                |              |
|                |            |              |                |              |
| b) IN          | 54.0 ± 10.3| 1112.0 ± 405.3| 27.0 ± 5.5     | 34.5 ± 1.8   |
| n = 136        | n = 120    | n = 112      | n = 119        |
| PF             | 38.8 ± 12.6| 54.3 ± 18.0  | 21.3 ± 3.6     | 31.3 ± 3.5   |
| n = 116        | n = 102    | n = 84       | n = 108        |
| CF             | 29.0 ± 3.4 | 37.0 ± 15.5  | 14.3 ± 3.6     | 27.3 ± 2.8   |
| n = 78         | n = 71     | n = 68       | n = 116        |

**Diet Analyses**

Stomach contents were removed from individual Gulf killifish and spot for comparative diet analyses. For the former, stomach contents were taken from the first turn of the intestine, consisting of the area between the esophagus and the distal end of the stomach (Lopez et al. 2010). Stomach contents were preserved in 7% buffered formalin containing Rose Bengal and maintained in solution until individual prey items could be identified to the lowest possible taxonomic level (Heard 1982, Abel & Kim 1986, Thorp & Covich 1991) using a dissecting microscope. Both occurrence (O<sub>i</sub>) and proportion by number (N<sub>i</sub>) of each prey item was calculated for each individual (j) and
then averaged for all diets in a collection week (n) to provide a mean proportion by number (MN$_i$) and frequency of occurrence (FO$_i$) for each prey item, as well as empty stomachs, using the following equations:

$$MN_{ij} = \frac{N_{ij}}{\sum_{i=1}^{n} N_{ij}} \times 100,$$ and

$$FO_{ij} = \frac{O_{ij}}{\sum_{i=1}^{n} O_{ij}} \times 100.$$  

To examine differences in the relative amount of food eaten (i.e., feeding intensity), each individual stomach was weighed (SW, ± 0.001 g) prior to content analyses and used to calculate an index of feeding intensity (IFI, Weitkamp & Sturdevant 2008, Daly et al. 2009):

$$IFI = \left( \frac{SW}{WW - SW} \right) \times 100.$$  

**Statistical Analyses**

In order to make comparisons of relative condition, WW, with the appropriate length measurement (CW, CL, or TL) as the covariate, was compared at both the estuary- and landscape-levels with a one-way analysis of covariance (ANCOVA) for each species separately. Prior to analyses, the relationships were linearized by log-transforming (base 10) both WW (LogWW) and length (LogCW, LogCL, or LogTL). A significant interaction between the main effect (estuary or landscape) and the covariate was examined using pairwise t-tests (t-test) to compare slope values for each level of the main effect. In the absence of a significant interaction, the interaction term was removed and the reduced model was used to examine main-effects on L-W relationships. Significant
main-effects were further examined by making Sidak-adjusted pairwise comparisons on estimated marginal mean WW (Green & Salkind 2008) and un-transformed values are reported in the text for clarity.

A two-way analysis of variance (ANOVA) was used to quantify differences in IFI values with estuary and landscape as the main-effects. In order to ensure that empty stomachs did not bias IFI values, these analyses were restricted only to individual stomachs that contained prey items. Further, IFI data failed to meet the assumptions of normality (Kolmogorov-Smirnov test) and homogeneity (Levene’s test) and were, consequently, normalized using the arcsin square root transformation. Significant main-effects were further examined with Sidak multiple comparisons for each level of the main effect. Because the diets of both Gulf killifish and spot typically contained several taxa, we used a multiivariate approach to examine diet similarities between estuaries and among landscapes. The unit of comparison for these analyses was FOᵢ for each collection week. Prior to analyses, FOᵢ data were square root transformed and used to calculate pairwise similarities between samples using the Bray-Curtis similarity coefficient (Clarke & Gorley 2006). I tested for differences in diets for each species for each main effect using a full-factorial permutational multivariate analysis of variance (PERMANOVA, permutations = 999, Anderson et al. 2008). Pairwise comparisons among all levels of a significant main effect were obtained using a multivariate analog of the univariate t-test (pseudo-t) in which the P-values are based on permutations (permutated-P, Anderson et al. 2008). Principal coordinates analyses (PCO) based on the Bray-Curtis similarity matrices were used to reduce the dimensionality of the prey FOᵢ data and project each sample point in multivariate space. In addition, vector overlays based on Pearson’s correlations
were included in each plot to examine the linear relationship between prey taxa and ordination axes. The strength of each relationship is indicated by the length and direction of each vector. All univariate analyses were performed at a significance level of 0.05 in SPSS v20 (IBM). All multivariate analyses were performed using PRIMER version 6.0 (Clarke & Gorley 2006).

Results

In 24 samples, 1170 blue crab, 7638 brown shrimp, 628 Gulf killifish, and 1821 spot were collected and from those, 721, 596, 510, and 675 individuals, respectively, were used for analyses (Table 1). Blue crab (range = 6.2 – 153.2 mm CW) L-W relationships differed only between estuaries, however, there was a significant estuary × LogCW interaction (Table 12a) suggesting that blue crab accrued more weight as they grew in the PRE estuary (PRE slope = 2.83, BB slope = 2.68). Blue crab L-W relationships did not differ among landscapes in either the full- or reduced-model. The L-W relationships for brown shrimp (range = 7.4 – 36.3 mm CL) differed between estuaries but not landscapes (Table 12b). Post hoc comparisons of the estimated mean marginal WW indicated that, for a given CL (16.9 mm CL), brown shrimp were significantly heavier in PRE (0.71 ± 0.011 g WW) than in BB (0.63 ± 0.010 g WW).

Length-weight relationships for Gulf killifish (17.6 – 110.2 mm TL) did not differ among estuaries in either the full- or reduced-model (Table 12c). However, there was a significant landscape × LogTL interaction suggesting that as Gulf killifish grow they accrue body weight at a significantly lower rate in CF landscapes than in either IN or PF landscapes, both of which have similar slopes (Figure 8a & b). Additionally, the L-W relationships for spot did not differ between estuaries in either model (Table 12d).
Table 12

Analysis of covariance results for length-weight relationships for a) blue crab, b) brown shrimp, c) Gulf killifish, and d) spot.

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Estuary</th>
<th>Landscape</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>MS</td>
<td>$P$</td>
<td>df</td>
</tr>
<tr>
<td>a)</td>
<td>1</td>
<td>0.361</td>
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<td>2</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>450.903</td>
<td>$&lt;0.001$</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.335</td>
<td>0.010</td>
<td>2</td>
</tr>
<tr>
<td>Error</td>
<td>717</td>
<td>0.050</td>
<td></td>
<td>715</td>
</tr>
<tr>
<td>b)</td>
<td>1</td>
<td>0.134</td>
<td>0.022</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>70.142</td>
<td>$&lt;0.001$</td>
<td>1</td>
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<tr>
<td></td>
<td>1</td>
<td>0.071</td>
<td>0.062</td>
<td>2</td>
</tr>
<tr>
<td>Error</td>
<td>592</td>
<td>0.025</td>
<td></td>
<td>590</td>
</tr>
<tr>
<td>c)</td>
<td>1</td>
<td>0.276</td>
<td>0.001</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>70.932</td>
<td>$&lt;0.001$</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.071</td>
<td>0.062</td>
<td>2</td>
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<tr>
<td>Error</td>
<td>593</td>
<td>0.026</td>
<td></td>
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</tr>
<tr>
<td>d)</td>
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<td>0.063</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>55.988</td>
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</tr>
<tr>
<td></td>
<td>1</td>
<td>0.014</td>
<td>0.077</td>
<td>2</td>
</tr>
<tr>
<td>Error</td>
<td>506</td>
<td>0.004</td>
<td></td>
<td>504</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.009</td>
<td>0.153</td>
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</tr>
<tr>
<td></td>
<td>1</td>
<td>55.976</td>
<td>$&lt;0.001$</td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>507</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Main effects are Estuary (Biloxi Bay or Pascagoula River) and Landscape (intact natural (IN), partially fragmented (PF), or completely (CF)). Shown are the full- and reduced-models with and without the interaction term, respectively.

However, there was a significant landscape effect in the reduced-model. Based on post hoc examination of the estimated marginal WW (Figure 9), a 51.2 mm TL spot in IN
landscapes (3.23 ± 0.07 g WW) was significantly heavier than in CF landscapes (3.03 ± 0.05 g WW). However, the estimated marginal WW for spot from PF landscapes (3.13 ± 0.06 g WW) was similar to both IN and CF (Figure 9).

Figure 8. Length-weight relationships for Gulf killifish (a) from intact natural (IN; shaded circles and solid gray line), partially fragmented (PF; shaded squares and dashed gray line), and completely fragmented (CF; triangles and dashed red line) salt marsh landscapes. ANCOVA (Table 2c) indicated a significant interaction between landscapes and log total length (LogTL). Pairwise comparisons (b) indicated that the slope of the L-W relationship was significantly lower in CF landscapes than either IN or PF.

Gulf killifish consumed a wide variety of taxa including meiofauna (nematodes, cladocerans, and copepods), macroinfauna (annelid worms, chironomids, and amphipods), decapod crustaceans (shrimp and crabs), molluscs (gastropods and bivalves), and fish (mostly unidentifiable, but including Clupeidae, Engraulidae, and Gobiidae, Figure 4). Based on MNi, macroinfauna and decapod crustaceans were the numerically
abundant prey groups in the Gulf killifish diets (Figure 10). Patterns of feeding intensity (IFI) differed markedly between estuaries (ANOVA, $df = 1, 329, F = 7.72, p = 0.006$),

\[ IFI_{BB} = 0.265 \pm 0.079 \]
\[ IFI_{PRE} = 0.243 \pm 0.055 \]

\[ \text{Diet composition differed only among landscapes (PERMANOVA, } df = 2, 18, \text{ pseudo-}F = 8.14, \text{ permuted-}P = 0.001). \]

Figure 9. Estimated marginal wet weight for a 51.2 mm total length (TL) spot from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) salt marsh landscapes. Capital letters (A & B) indicate significant differences between patch-types based on Sidak pairwise comparison. All analyses were performed on log-transformed variables; un-transformed values are presented in the figure for clarity.

but the differences among the landscapes ($df = 2, 329, F = 0.79, p = 0.45$) and the interaction between the main effects ($df = 2, 329, F = 2.03, p = 0.13$) were not significant. Stomach weights were a greater proportion of body weight (i.e., feeding intensity was greater) in BB ($IFI = 0.265 \pm 0.079$) than in PRE ($IFI = 0.243 \pm 0.055$). Diet composition differed only among landscapes (PERMANOVA, $df = 2, 18$, pseudo-$F = 8.14$, permuted-$P = 0.001$). Pairwise comparisons showed a high degree of similarity in Gulf killifish
Figure 10. Mean (± S.E.) frequency of occurrence (FOi) and proportion by number (MNi) of the diet composition of Gulf killifish collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in the Biloxi Bay (BB) and Pascagoula River (PRE) estuaries. Number of individual diets examined (n).

Diet composition between IN and PF landscapes (similarity = 71.8 %, pseudo-t = 1.067, permuted-P = 0.359). The composition of Gulf killifish diets in CF landscapes was significantly different from both IN (similarity = 53.3
%, pseudo-t = 3.771, permuted-P = 0.001) and PF (similarity = 54.5 %, pseudo-t = 3.027, permuted-P = 0.001). The first 2 axes of the PCO explained 64.1% of the total variation in Gulf killifish diets among the
24 samples and showed a similar pattern of separation among the landscapes (Fig 11a). Landscape-specific differences in diet composition were driven principally by the increased FO\textsubscript{i} of both empty stomachs (Pearson’s r = -0.86) and brown shrimp (r = -0.77) in CF landscapes and grass shrimp (r = 0.87) and fish (r = 0.70) in IN and PF landscapes (Figure 11a).

Spot diets contained a similar breadth of taxa (Figure 12). However, meiofauna (nematodes and cyclopoid, calanoid, and harpactacoid copepods) and chironomids were the numerically dominant component (MN\textsubscript{i}) of spot diets. Stomach weights were a significantly greater proportion of body weight ($df$ = 1, 431, $F$ = 11.01, $p = 0.001$) in PRE (IFI = 0.128 ± 0.038) than BB (IFI = 0.117 ± 0.031). Additionally, feeding intensity differed among landscapes ($df$ = 2, 431, $F$ = 5.05, $p = 0.007$) and was greater in CF (IFI = 0.128 ± 0.035), followed by PF (IFI = 0.123 ± 0.037) and IN (IFI = 0.115 ± 0.033).

However, differences in IFI values at both the estuary and landscape-level likely result from the greater FO\textsubscript{i} of sand in the diets of spot from the CF site in the PRE (Figure 6, lower right panel) which inflated their individual stomach weights. The composition of spot diets differed at both the estuary- (PERMANOVA, $df$ = 2, 18, pseudo-$F$ = 4.54, permuted-$P$ = 0.008) and landscape-level ($df$ = 2, 18, pseudo-$F$ = 13.79, permuted-$P$ = 0.001). At the landscape-level, pairwise comparisons indicated that spot diets in IN
**Figure 11.** Principal coordinate analyses (PCO) of diet composition of a) Gulf killifish and b) spot collected from intact natural (triangles), partially fragmented (squares), and completely fragmented (circles) salt marsh landscapes in the Biloxi Bay (closed) and Pascagoula River (open) estuaries. Based on mean frequency of occurrence (FOi) for each collection week. Pearson’s correlations (vectors) are shown for each prey taxa contributing to differences among samples ($\geq 0.70$). Note the different scales on both the PCO1 and PCO2 axes for each plot.
landscapes were dissimilar to both PF (similarity = 55.4%, pseudo-t = 2.14, permuted-P = 0.001) and CF (similarity = 58.3%, pseudo-t = 4.13, permuted-P = 0.003) landscapes and both PF and CF landscapes were also dissimilar (similarity = 61.5%, pseudo-t = 4.36, permuted-P = 0.001). These patterns are also evident in the PCO in which the first two axes explain 67.1% of the total variation in diet composition among sites (Figure 11b). Similar to Gulf killifish, empty stomachs were correlated with spot diets (r = -0.87) in CF landscapes and annelid worms (r = 0.89), large chironomids (r = 0.76), amphipods (r = 0.73), and grass shrimp (r = 0.77) were associated with spot diets in both IN and PF landscapes. Further, the difference between estuaries was driven largely by the presence of both nauplii and ostracods in the diets of spot from the BB estuary (Figure 11b & 12).

Discussion

Understanding the linkage between both habitat quality and quantity and nekton production is an important step mitigating the impacts of urbanization and habitat loss in coastal ecosystems (Peterson 2003). Although the apparent impacts of urbanization and fragmentation on salt marsh habitats and their implications for nekton resources is well documented (Peterson & Lowe 2009), many studies have emphasized comparisons between natural salt marsh habitats and man-made structures (Able et al. 1999, Hendon et al. 2000, Peterson et al. 2000, Bilkovic & Roggero 2008, Long et al. 2011). Fewer studies, however, have specifically examined the relative role of salt marsh habitats arrayed along a gradient of alteration (Partyka & Peterson 2008). By making such comparisons in this study, I have provided evidence that 1) estuarine-dependent nekton respond differently to the urbanized and fragmented salt marsh habitats compared to less altered landscapes and 2) highly altered and fragmented salt marsh habitats do not
Figure 12. Mean (± S.E.) frequency of occurrence (FO) and proportion by number (MN) of the diet composition of spot collected from intact natural (IN), partially fragmented (PF), and completely fragmented (CF) landscapes in the Biloxi Bay (BB) and Pascagoula River (PRE) estuaries. Black bars are for descriptive purposes only and are diet items not used in statistical analyses. Number of individual diets examined (n).

provide the similar functional support nekton as in intact natural landscapes.

Although growth dynamics for both blue crab and brown shrimp in this study differed spatially between estuaries, equivalent growth dynamics at the landscape-level
suggest that even highly urbanized salt marshes provide sufficient resources to support the growth of both species. However, the functional value of salt marsh habitats for nekton is predicated on both the greater abundance of a given species and increased individual growth derived from increased foraging (Shenker & Dean 1979, Weinstein 1979, Kneib 1982, Peterson & Turner 1994, Beck et al. 2001). Chapter II showed that while blue crab CPUE did not differ among landscapes, brown shrimp CPUE was significantly lower in CF landscapes than in either IN or PF landscapes. So while highly urbanized salt marsh landscapes may sufficiently support blue crabs at abundances commensurate with other studies in the northern Gulf of Mexico (Zimmerman et al. 2000, Heck et al. 2001, Rakocinski et al. 2003), brown shrimp production in small, fragmented salt marsh landscapes is likely compromised at densities approaching those found in natural, intact salt marsh landscapes.

Conversely, highly urbanized and fragmented salt marsh landscapes did not support similar growth dynamics for either Gulf killifish or spot and these differences are likely linked to landscape-specific foraging patterns. Compared to both IN and PF landscapes, Gulf killifish in CF landscapes accrued weight at a slower rate as they grew and, thus, larger individuals were in comparatively poorer condition. In CF landscapes, empty stomachs and larger brown shrimp were characteristic of Gulf killifish diets while smaller grass shrimp and fish were key diet components in IN and PF landscapes. Rozas & LaSalle (1990) showed that peak consumption occurred prior to Gulf killifish leaving the salt marsh surface, so it is unlikely that the high incidence of empty stomachs is a sampling artifact. Further, numerous studies have noted the broad diets of Gulf killifish, including decapod crustaceans (Harrington & Harrington 1961, Perschbacher & Strawn
1986, Rozas & LaSalle 1990), yet this is the first time penaeid shrimp have been noted in the diets of Gulf killifish. In habitats where forage species (e.g., grass shrimp) are not readily abundant, such as the CF salt marsh landscapes in this study (Chapter II), Gulf killifish tended to supplement their diets with larger bodied brown shrimp. While the energetic density of both grass shrimp and brown shrimp is similar (deMutsert 2010), the energetic cost of handling larger bodied prey has never been examined for Gulf killifish and it is likely that the energetic return from increased handling time would be lower (Schoener 1971, Stein 1977). However, mummichog (*Fundulus heteroclitus*), a congener of Gulf killifish, fed diets of grass shrimp, fiddler crabs (*Uca pugnax*), or annelid worms had very high assimilation efficiencies (~87%, Weisberg & Lotrich 1982) which could be an indication that resource scarcity (i.e., empty stomachs) may be driving Gulf killifish growth dynamics.

Spot were in markedly better condition (i.e., heavier for a given length) in natural salt marsh landscapes relative to urbanized and fragmented landscapes and these results mirrored diet patterns. Though spot diets were similar to observations elsewhere (O’Neil & Weinstein 1987, Nemerson & Able 2004, Zapfe & Rakocinski 2008), larger-bodied macroinfauna and grass shrimp were common diet components in both IN and PF landscapes while meiofauna were a numerically dominant component and empty stomachs were more frequently observed in CF landscapes. Like Gulf killifish, spot feed on the marsh surface during the flood tide (Miller & Dunn 1980, Zapfe & Rakocinski 2008) and the higher frequency of empty stomachs in CF landscapes is not likely to be an artifact of sampling. Additionally, several studies have noted an apparent ontogenetic shift from feeding on meiofauna at smaller sizes to ingesting more macroinfaunal
organisms with increasing size (Sheridan 1979, Livingston 1982, O’Neil & Weinstein 1987). As a result, the greater occurrence of meiofauna in spot diets indicates that ontogenetic shifts in prey preference may be delayed in urbanized and fragmented salt marshes and potentially drives growth dynamics in these habitats (Buckel et al. 1998).

Alternatively, the greater prevalence of empty stomachs in both Gulf killifish and spot could reflect sublethal exposure to contaminants. Nekton have a wide range of behavioral responses to pollution that can have negative ecological consequences (Sandheinrich & Atchison 1990, Weis et al. 2011). For example, mummichog’s prey (grass shrimp) capture ability is hampered in polluted salt marsh habitats and, as a result, empty stomachs are more frequent (Weis & Kahn 1991). Mummichog diets generally contained fewer prey items and more sediment and detritus in contaminated sites (Smith & Weis 1997) and, as a result, fish did not grow as well compared to uncontaminated salt marsh habitats (Toppin et al. 1987). Similar responses have been noted for grass shrimp (Perez & Wallace 2004) and blue crab (Reichmuth et al. 2009). However, blue crab growth in our study did not differ among landscapes and there may be species- or trait-specific responses to contaminants (Weis et al. 2011).

Observed growth and diet patterns could result from competition for limited food resources in urbanized coastal landscapes. Though the diets of blue crab and brown shrimp were not quantified in this study, previous diet descriptions for both species suggests that there is some diet overlap with Gulf killifish and spot (Hines et al. 1990, Zimmerman et al. 2000, Meise & Stehlik 2003) and other species not examined in this study (Hsueh et al 1992, Lopez et al. 2010). Interspecific competition in salt marsh habitats is difficult to document because it requires 1) knowledge regarding the
availability of resources (i.e., food) and 2) that common resources be limiting for at least one of the consumers. In Chapter II, I showed that common forage species (e.g., Gulf menhaden (*Brevoortia patronus*), grass shrimp, chironomids, amphipod crustaceans, and bivalves) were significantly less abundant in CF salt marsh landscapes compared to both IN and PF landscapes. However, the benthic sampling method used in that work may have used a sieve (500 µm) that was inappropriate for the quantification of meiofauna densities. Assuming that the macroinfaunal patterns observed in Chapter II are representative of prey availability in each salt marsh landscape-type, competition for food may play a pivotal role in structuring the nekton community in urbanized salt marsh landscapes. For example, all four species examined in this study feed primarily on the intertidal marsh surface, there is, however, some habitat partitioning with spot, blue crab, and brown shrimp using the salt marsh edge at the water interface and Gulf killifish using the inner marsh (Kneib 2000, Minello & Rozas 2002). Thus, competition could be a strong structuring mechanism among spot, blue crab, and brown shrimp populations co-occurring in fragmented salt marsh landscapes.

The potential for prey resources to be a limiting factor also highlights the potential role of biological controls on structuring salt marsh communities (Valiela et al. 2004). Both bottom-up and top-down controls on community structure have been studied extensively in salt marsh ecosystems with mixed results (Valiela et al. 2004, Deegan et al. 2007). In a previous study in the Pascagoula River estuary, it was suggested that absence of amphipod crustaceans, a key diet component of juvenile nekton, from highly altered salt marsh habitats may also be viewed an additional indicator of poor habitat quality for nekton (Partyka & Peterson 2008). While bottom-up
controls may be an important mechanism determining the distribution and abundance of nekton in salt marsh habitats, the results shown here, combined with Chapter II, indicate that consumers regulate benthic community through top-down control as well. For example, large chironomids were abundant in benthic samples and spot diets from both IN and PF landscapes and only small chironomids (< 500 µm) were present in spot diets from CF landscapes. Increased predation may prevent chironomids from growing to later life-stages in urbanized and fragmented salt marshes. Kneib (1992) showed that the mummichog could significantly reduce benthic harpacticoid copepod abundance within a patch without impacting the prey population in the overall salt marsh landscape.

Interestingly, these findings contradict recent work relating the structure of coastal landscapes to both brown shrimp and blue crab production in the northern Gulf of Mexico. Roth et al. (2008) used a spatially explicit, individual-based simulation model to investigate the potential impacts of tidal inundation and fragmentation on brown shrimp production derived from salt marsh habitats. They showed that tidal inundation was relatively more important than marsh configuration for brown shrimp production. However, they implicitly assumed that all salt marsh edge cells (1 m²) had similar habitat value in terms of growth and feeding potential and, as a result, brown shrimp production increased with increasing levels of fragmentation (creation of more edge habitat) and significantly declined in open water systems. The results of this study, in concert with Chapter II, suggest that all salt marsh landscapes do not have the same habitat value and I suspect that salt marsh habitat in urbanized landscapes would produce (i.e., biomass and number of individuals) fewer brown shrimp than cells in natural landscapes. Further, brown shrimp production would likely be more skewed towards natural landscapes when
scaled up to the landscape level as in Roth et al. (2008). Jordan et al. (2009), on the other hand, used a population model embedded with in a coarse-grained (~55.2 km$^2$ polygons) habitat model to simulate the long-term effects of cumulative shoreline alteration on blue crab landings in Mobile Bay, Al. Under the scenario where an additional 10% of the shoreline was hardened, their model showed that simulated blue crab landings would significantly decrease below baseline conditions (i.e., no change in current state of Mobile Bay). However, their model explicitly examined changes in summed totals for each land-cover class (e.g., marsh edge, nonvegetated bottom, and submerged aquatic vegetation) for each cell and did not consider either the composition or the spatial configuration of the target habitats within the landscape. Depending on the initial state of each cell, replacing 10% of salt marsh habitat with hardened shoreline could result in a variety of different spatial configurations of salt marsh habitat (Cushman et al. 2012, Rubio & Saura 2012, With & Pavuk 2012). In all likelihood, some configurations could offset the effect of habitat loss by maintaining functional connectivity amongst smaller habitat patches (Moy & Levin 1991, Fonseca et al. 1997, Green et al. 2012). Though the results of both studies are intuitively reasonable, the processes driving secondary production in salt marsh habitats are inherently complex (Peterson 2003) and constantly degrading as a result of urbanization (Bromberg Gedan et al 2009, Peterson & Lowe 2009; Bulleri & Chapman 2010). Ultimately, these contradictions emphasize the need to better understand the mechanistic linkages between coastal development, salt marsh habitat mosaics, and nekton production on a species-specific basis.

Beck et al. (2001) proposed that the relative value of a habitat for estuarine-dependent nekton is based on the greater contribution of that habitat to the adult
population relative to other habitats. Thus, the value of the habitat is derived from the ability to support increased density, growth, and survival of juveniles. Growth, in particular, is vital and habitats where growth is compromised due to reduced trophic support are unlikely to contribute substantially to the adult population. In this context, the habitat value of small fragmented salt marsh landscapes nestled within urbanized landscapes would likely vary from species to species but would, ultimately, be reduced relative to healthy, natural salt marshes.
CHAPTER IV

STRUCTURAL CHANGES IN SALT MARSH FOOD WEBS RESULTING FROM URBANIZATION: INFERENCES BASED ON STABLE ISOTOPE ANALYSES

Introduction

Despite cognizance of their value (Costanza et al. 1997; Duarte et al. 2009; Barbier et al. 2011), coastal habitats are among the most anthropogenically altered ecosystems in the world (Vitousek et al. 1997; Kennish 2001; Lotze et al. 2006; Halpern et al. 2008b; Bromberg Gedan et al. 2009). Pervasive human population growth and its accompanying infrastructure (i.e., urbanization) is now a major driver of change in coastal ecosystems (Peterson & Lowe 2009; Mee 2011). Salt marshes, in particular, have a long history of anthropogenic alteration (Bromberg Gedan et al. 2009) that has led to global declines in both habitat quantity (Allen & Lu 2003) and quality (Holland et al. 2004; Van Dolah et al. 2008). Salt marsh ecosystems operate at the nexus of marine, freshwater, terrestrial, and urban landscapes and, as a result, are vulnerable to a number of stressors that potentially disrupt the delivery of ecosystem services (Sanger et al. 1999a,b; Lerberg et al. 2000; Holland et al. 2004; Bilkovic et al. 2006; Bilkovic & Roggero 2008; Van Dolah et al. 2008; Bromberg Gedan et al. 2009; Long et al. 2011; Chapter II & III).

Among the many ecosystem services provided by salt marshes, they function as critical habitat for a distinct assemblage of ecologically and economically important nekton (i.e., fish and invertebrates; Weinstein 1979; Boesch & Turner 1984; Peterson & Turner 1994; Minello et al. 2003). The value of salt marsh habitats to nekton is attributed to reduced predation risk (Minello et al. 1989; Kneib 1995) and an abundance of benthic
and epibenthic macroinfauna (hereafter, macroinfauna) that link salt marsh derived energy to nekton production through complex food web interactions (Kneib 1994, 2000). Therefore, the upper limit to nekton production is set by the amount of material that enters the base of the food web (Kneib 2000) and trophic interactions are critical to the continued ecological functioning of these habitats. However, numerous studies have illustrated the deleterious effect of coastal urbanization on salt marsh faunal communities (Holland et al. 2004; Bilkovic et al. 2006; Bilkovic & Roggero 2008; Van Dolah et al. 2008; Partyka & Peterson 2008; Long et al. 2011). For example, Chapter II demonstrated an inverse relationship between the abundance of select organisms with several metrics related to coastal urbanization. Though few studies have attempted to relate the observed patterns to changes in food web structure (Long et al. 2011; Chapter III), changes at the landscape-level (i.e., urbanization) can significantly alter or reduce the flux of energy between habitats (Holt 2002; Doi et al. 2010; Olsen et al. 2010).

A central organizing theme in ecology is the identification of the patterns in the relative importance of primary producers that contribute to consumer diets and ultimately form the base of the food web (Polis et al. 1997). While inferences based on diet descriptions alone are hindered by a number of caveats (Shepard & Mills 1996; Waggy et al. 2007; Cortés 1997), stomach content analysis can serve as a reliable snapshot of the food choices made by nekton over relatively short temporal scales (Chapter III). Alternatively, stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$), nitrogen ($^{15}\text{N}/^{14}\text{N}$ or $\delta^{15}\text{N}$), and sulfur ($^{34}\text{S}/^{33}\text{S}$ or $\delta^{34}\text{S}$) represent a time-integrated measure of the materials assimilated by macroinfauna and nekton and, thus, are not influenced by the caveats of stomach content analysis (Dalerum & Angerbjörn 2005). As a result, they have
commonly been used for mapping energy flow through salt marsh food webs (Peterson & Fry 1987; Peterson & Howarth 1987), infer importance on specific energy sources (Howe & Simenstad 2007; Jackson et al. 2012), and consumer trophic position (Post 2002).

Oftentimes, however, our understanding of salt marsh food web structure has been hampered by the inherent limitations of the various quantitative approaches that have recently been developed (Phillips 2001; Phillips & Gregg 2001, 2003; Parnell et al. 2010). In simple systems with few sources, for example, simple linear mixing models are appropriate for estimating the relative contribution of an assimilated dietary source to a consumers tissues (Philips 2001). However, linear mixing models assume fixed source isotope ratios and are unsuitable for under-determined systems (i.e., more sources than isotopes; Phillips & Gregg 2001, 2003; Fry 2013). Further, our understanding of the trophic fractionation of isotope ratios also hampers inferences based on stable isotopes (Martínez del Rio et al. 2009; Caut et al. 2009). Trophic isotope fractionation, the preferential incorporation of heavier isotopes over lighter isotopes into consumer tissues, can vary widely across organisms and is often inferred from extensive literatures reviews (Vander Zanden & Rasmussen 2001; McCutchan et al. 2003; Caut et al. 2009). Thus, it is imperative to include this source of uncertainty when using surrogate estimates of trophic fractionation factors based on literature estimates.

Recent advances in stable isotope ecology have seen the inclusion of a Bayesian inference framework into isotope mixing models (Moore & Semmens 2008; Parnell et al. 2010; Hopkins & Ferguson 2012; Parnell et al. 2012). Bayesian isotope mixing models allow ecologist to incorporate multiple sources of uncertainty and a priori information
(e.g., constraining solutions to known diet items) to estimate proportional contributions of each source to consumer diets. Such models have proven flexible across a broad range of ecological questions related to food web dynamics (Boyle et al. 2012; Briggs et al. 2012; Jackson et al. 2012; Miranda & Perissinotto 2012; Pomerleau et al. 2012). For example, Grey & Jackson (2012) showed that invasive crayfish were able to persist during periods of resource limitation and increased competition with native assemblages by leaving aquatic habitats and directly incorporating live terrestrial plants into their diets.

Another advancement in stable isotope ecology has been the recognition that points in isotope space (e.g., δ^{13}C and δ^{15}N biplots) represent a subset of the Hutchinsonian niche concept (Bolnick et al. 2003; Bearhop et al. 2004; Newsome et al. 2007). In this context, the isotopic niche of an individual is linked to its trophic niche through strong relationships between stable isotope values and dietary history (Rodríguez & Herrera 2012). Based on these linkages, individuals should occupy a larger isotopic niche (i.e., realized niche) in habitats where competition for space and resources are weakest. Layman et al. (2007a) suggested a suite of isotope metrics for making inferences regarding food web structure at the individual, population, or assemblage level. Though these metrics are subject to spurious results under certain situations (Hoeinghaus & Zeug 2008) they have been used widely in ecological studies (Layman et al. 2007b; Jackson et al. 2012; Layman et al. 2012; McHugh et al. 2012; Rodríguez & Herrera 2012). Using these metrics, Layman et al. (2007b) showed that grey snapper (*Lutjanus griseus*) occupied a smaller isotopic niche in fragmented tidal creeks compared to tidal creeks that maintained their natural connection with open water.
The goal of this work is to relate structural changes at the landscape level (i.e., fragmentation due to urbanization) to functional changes in food web structure in salt marsh habitats. I use stable isotope data in a Bayesian framework to make inferences regarding food web structure in salt marsh habitats arrayed along a gradient of urbanization. Specifically, I test the hypothesis that food web structure differs between less-altered and highly-altered salt marsh sites and that these differences are manifested in the relative contribution of various autotrophs to consumer diets and in the isotopic niche of macroinfauna and nekton assemblages.

Methods

Study Area and Site Description

The study region consisted of two large, micro-tidal river estuaries in coastal Mississippi (Chapter II, Figure 1). The lower Pascagoula River estuary (PRE) is a ~ 15 km long distributary that can be divided into highly urbanized eastern and more natural western branches (Peterson et al. 2007; Partyka & Peterson 2008). The Biloxi Bay estuary (BB) is ~ 21.7 km in length and consists of both highly urbanized and vegetated shorelines bordering a single river channel. In both estuaries, urbanized shorelines consist of erosion control edges in the form of levees, rip-rap, and residential and commercial bulkheads (Peterson & Lowe 2009) and natural shorelines are comprised of intertidal emergent vegetation (Peterson & Partyka 2006). Though both systems receive considerable freshwater input from upstream watersheds, the PRE has considerably higher discharge rates than the BB (Lowe et al. 2012).

Previous work in the region used a landscape ecology approach to characterize three different salt marsh landscape-types (hereafter, landscape) in each estuary (see
Chapter II. Briefly, I quantified both the composition and configuration of the associated coastal landscapes at multiple spatial scales surrounding three small first-order salt marsh tidal creeks arrayed along a gradient of increasing urbanization and subsequent salt marsh fragmentation in each estuary. Intact natural landscapes (IN; Chapter I, Figure 1) were dominated by unfragmented salt marsh patches and there was a high degree of connectivity among small first-order tidal creeks. There was little evidence of urbanization within these landscapes at any spatial scale. *Spartina alterniflora* (smooth cordgrass) was the abundant macrophyte at these sites with intermixed stands of *Juncus romerianus* (black needle rush). Partially fragmented landscapes (PF; Chapter I, Figure 1) were a mix of urbanized surfaces and salt marsh classes. Within these landscapes, salt marsh patches consisted mostly of *J. romerianus* (abundant) with sparse clumps of *S. alterniflora*. A large tidal creek network was the prominent feature of both PF salt marsh landscapes and, as a result, PF landscapes had more salt marsh edge (i.e., natural shoreline) than either the IN or completely fragmented (CF; Chapter I, Fig 1) landscapes. However, the amount of salt marsh edge decreased inversely with the amount of urbanized surface and hardened shoreline resulting in moderately fragmented salt marsh patches. Completely fragmented landscapes, on the other hand, were dominated by urbanized surfaces and hardened shorelines. Salt marsh patches in these landscapes were comprised mostly of *S. alterniflora* (abundant) with sparse stands of *J. romerianus* and tended to be small, simply shaped, moderately aggregated, and highly fragmented.

*Sample Collection and Stable Isotope Analyses*

From 3 May to 21 May 2010, the most conspicuous and abundant autotrophs, macroinfauna, and nekton were collected weekly from each site for stable isotope
analyses. Four groups of autotrophs were targeted at each site; benthic microalgae (BMA), emergent macrophytes utilizing the C3 (C3; *Juncus romerianus*) and C4 (C4; *Spartina alterniflora*) photosynthetic pathways, and particulate organic matter (POM). Benthic macroalgae were collected by placing 3 sets of glass plates (58.2 cm\(^2\); 2 plates cemented together with ~3 mm gap between the plates to prevent grazing) perpendicularly into the sediment-water interface at the mouth of each creek. Plates were deployed for one week to allow sufficient colonization. Three replicate POM samples were collected by filtering 1 L of water across a pre-combusted 45 µm Whatman filter using a peristaltic water pump. Six individual emergent macrophytes (C3 and C4) were collected along the edge of each tidal creek. All autotrophs samples used in stable isotope analyses were collected during the second week (10 – 14 May). In the laboratory, BMA plates were, separated, washed with distilled water to remove loose dirt, rinsed three times with 10% HCL to remove carbonates, rinsed again with distilled water, and attached BMA was removed with an acid washed razor blade. All POM samples were examined under a dissecting microscope to remove all large zooplankton and then fumed with concentrated HCL in a glass desiccator for 24 hr to remove inorganic carbonates. Emergent vegetation samples were scraped with an acid washed razor blade to remove surface epiphytes, rinsed with distilled water, and cut into small pieces.

Macroinfauna were collected from each creek using a pole mounted Ekman grab (0.024 m\(^2\)); details can be found in Chapter II. Due to coarse taxonomic resolution and variable abundances across all sampling sites (Chapter II), similar taxa were grouped into functional feeding groups (Fauchald & Jumars 1979; Ferdette & Diaz 1986; Gaston & Nasci 1988; Stocks & Grassle 2001) and pooled across all three sampling weeks to
increase sample sizes. In all, 6 feeding groups were identified and included meiofauna (nematodes, copepods, and ostracods), surface deposit feeding worms (SDFW; capitellid polychaetes and tubificid oligochaetes), surface deposit feeding chironomids (SDFC; dipteran insect family Chironomidae), omnivorous worms (OW; nereid polychaete worms), suspension feeding worms (SFW; *Amphicteis floridus*), and suspension feeding amphipods (SFA; *Gammarus* spp. and *Apocorophium* spp.). Grab samples were sieved through a 500 µm stainless steel sieve and meiofauna were poorly represented (Chapter II). Thus, meiofauna were sampled directly from spot (*Leiostomus xanthurus*) diets and used in lieu of samples from grab samples. For stable isotope analyses (SIA), each feeding group consisted of multiple individuals based on body size; small-bodied meiofauna, moderately sized SFA, and larger-bodied SDFW samples were comprised of > 100, > 20 and > 10 individuals per site, respectively.

Nekton were collected from each creek using a modified Fyke net (Chapter II). Specific details regarding macroinfauna and nekton collections can be found in Chapter II. Three species of fishes (i.e., Gulf killifish (*Fundulus grandis*), spot, and southern flounder (*Paralichthys lethostigma*)) and three species of decapod crustaceans (i.e., grass shrimp (*Palaemonetes* spp.), brown shrimp (*Farfantepenaeus aztecus*) and blue crab (*Callinectes sapidus*) were consistently abundant at all six sites and were used for SIA. In order to account for the potential effects of ontogenetic diet shifts, species with a broad size range (e.g., Gulf killifish, brown shrimp, and blue crab) were split into size classes reflecting diet preferences (Jones 1973; Perschbacher and Strawn 1986; Hines 2007). Stable isotope samples consisted of muscle tissue from 8-10 individuals from a site taken from the following locations; dorsal muscle tissue for fish, muscle tissue from the first
abdominal segment for both grass shrimp and brown shrimp, and flank muscle tissue
(adjacent to the 5th swimming leg inside the carapace) for blue crab. Pooling multiple
individuals into a single sample reduces complexity associated with individual variability
and creates a representative composite that is more applicable to looking at differences
among sites at the assemblage level.

Autotroph and macroinfauna samples were dried at 60°C in a drying oven while
nekton were freeze-dried for ≥ 24 h. All decapod crustacean samples were acid washed
to remove carbonates and re-dried. Dried samples (except POM) were ground into a fine
powder using a Wig-L bug encapsulated amalgamator and stored in clean glass vials. For
POM samples, the surface material was dissected from each filter using an acid-washed
scalpel and transferred to a clean glass vial. Each sample was sub-sampled, weighed
(nearest 0.001 mg; ≥ 2.0 mg for BMA, C3, and C4; ≥ 7.5 mg for POM; ≥ 0.5 mg for
macroinfauna and nekton; sample weights based on nitrogen concentration in preliminary
analyses) and packed into Ultra-pure tin capsules (Costech, Valencia, CA) for SIA. The
analyses of carbon and nitrogen stable isotopes (autotrophs, macroinfauna, and nekton)
were conducted at the Stable Isotope Laboratory at the University of Southern
Mississippi while sulphur isotope analyses (autotrophs and nekton only) occurred at the
University of California-Davis’ Stable Isotope Facility. All results are presented in delta
notation (parts per thousand or per mil deviation from a standard reference material):
\[ \delta^{13}C, \delta^{15}N, \text{and } \delta^{34}S = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000; \text{ where } R = \frac{^{13}C}{^{12}C}, \frac{^{15}N}{^{14}N}, \text{ or } \frac{^{34}S}{^{32}S}. \]
Standard reference material for carbon, nitrogen, and sulfur is Pee Dee Belemnite
limestone, atmospheric nitrogen, and Canon Diablo meteorite, respectively. Isotope
values were not mathematically normalized for lipid concentration because C:N ratios were consistently $\leq 3.5$ (Post et al. 2007).

**Stable Isotope Mixing Model and Statistical analyses**

For all statistical analyses, estuaries (i.e., BB and PRE) and landscapes (i.e., IN, PF, CF) were combined into six independent sites (Site) for the purpose of simplification. This allowed us to focus only on functionally meaningful pairwise comparisons (e.g., differences among sites). Carbon, nitrogen, and sulfur isotope ratios of aggregated autotroph, macroinfauna, and nekton assemblages were compared among sites using multivariate analysis of variance (MANOVA). For autotrophs, two omnibus MANOVAs were conducted; one using only $\delta^{13}C$ and $\delta^{15}N$ for all four sources and one using all three isotope ratios for only BMA, C3, and C4 sources. Similarly, only $\delta^{13}C$ and $\delta^{15}N$ were used in the macroinfauna model while $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were used in the nekton model. Further, because one of the requirements of isotopic mixing models is that each autotroph has a unique isotopic ratio (Ward et al. 2011), a separate MANOVA was conducted for autotrophs at the taxonomic level. Significant results were followed up with a series of protected one-way ANOVAs and Tukey’s HSD tests (Tabachnick & Fidell 2000) using individual isotope ratios as the dependent variable. Prior to analyses, isotope ratios were found to violate the assumption of multivariate normality (Shapiro-Wilk test) and, as a result, equality of covariance matrices (Box’s test). Subsequent transformations failed to satisfactorily normalize the data. Therefore, data were not transformed for analyses and Pillai’s trace ($V$) was used as the primary test statistic given its robustness to violations of multivariate normality (Field 2005).
The trophic position (TP) of each consumer at a given site was determined using the equation of Post (2002):

\[ TP = \left[ \left( \delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}} \right) / \Delta^{15}N \right] + \lambda ; \]

where \( \delta^{15}N_{\text{consumer}} \) is the nitrogen isotope ratio of the consumer, \( \delta^{15}N_{\text{baseline}} \) is the site-specific nitrogen isotope ratio for a resident organism at the base of the food web with known trophic position (\( \lambda \)). The mean \( \delta^{15}N \) of all autotrophs (\( \lambda = 1 \); base of the food web) and marsh periwinkles (\( Littorina irrorata \); \( \lambda = 2 \); feed directly on autotrophs) within a site were treated as the baseline organisms for calculating the trophic position of macroinfauna and nekton, respectively. The denominator value (\( \Delta^{15}N \)) is the assumed trophic fractionation factor (+2.4 ‰) of \( \delta^{15}N \) that occurs with each step in the food web (McCutchan et al. 2003) and the value used in all subsequent isotope mixing models.

Mean estimated trophic positions of macroinfauna and nekton assemblages were compared among sites and functional group or species using a two-way ANOVA without the interaction term. Given the large number of total comparisons (906 for nekton alone) and previous work that indicated a number of significant interactions driven by species differences across sites, we elected to compare estimated TPs for a given species across sites using a one-way ANOVA. Significant main-effects were followed up with pairwise comparisons using Tukey’s HSD. To increase sample size and improve replication across sites, all SDFW and SDFC were pooled into surface deposit feeders (SDF) and SFW and SFA were pooled into suspension feeders (SF) for analyses. Estimated trophic position values violated the assumption of normality and were log_{10}-transformed for analyses; however, untransformed estimates are presented for clarity.
In order to estimate the relative importance of each autotroph to the diets of macroinfauna and nekton, two separate Bayesian stable isotope mixing models (SIAR v 4.0; Parnell et al. 2010) were run; a two-isotope model using only \( \delta^{13}C \) and \( \delta^{15}N \) (macroinfauna and nekton, separately) and a three-isotope model using \( \delta^{13}C \), \( \delta^{15}N \), and \( \delta^{34}S \) (nekton only). All models used uninformative priors, site-specific mean (± SD) autotroph isotope ratios, composite isotope samples for consumers, and trophic fractionation values based on literature estimates (\( \Delta^{13}C = 0.4 \%_o \pm 0.22 \), \( \Delta^{15}N = 2.4 \%_o \pm 0.42 \), and \( \Delta^{34}S = 1.9 \%_o \pm 0.51 \); McCutchan et al. 2003). Estimated autotroph contributions to each consumer (i.e., taxa or species) within an assemblage (i.e., macroinfauna or nekton) were based on posterior distributions showing the most feasible contribution. For both macroinfauna and nekton assemblages, mixing model estimates were compared among sites and functional group/species using a 2-way permutational MANOVA (PERMANOVA; permutations = 999; Anderson et al. 2008). Due to a lack of replication for functional groups or species within a site, interaction terms could not be calculated. Significant differences among independent variables were further examined through pairwise comparisons using a multivariate analog of the univariate t-test (pseudo-\( t \)) in which the \( P \)-values are based on permutations (permuted-\( P \); Anderson et al. 2008).

Autotrophs, macroinfauna, and nekton were plotted in isotope space (i.e., \( \delta^{13}C \) and \( \delta^{15}N \) biplots) and SIBER (Stable Isotope Bayesian Ellipses in R) was used to calculate bootstrapped estimates (n = 10000) of 4 assemblage-level trophic metrics for macroinfauna and nekton in order to compare the food web structure among sites (Layman et al. 2007a; Jackson et al. 2011). Standard ellipse area, a measure of assemblage isotopic niche, was calculated from the variance and covariance matrices of
$\delta^{13}C$ and $\delta^{15}N$ data with each ellipse containing ~40% of the data points in isotope space. The SEA has the same properties and interpretation as the univariate standard deviation. Both $\delta^{13}C$ range and $\delta^{15}N$ range were calculated as the distance between the most enriched and depleted samples within each assemblage and were interpreted as the breadth of autotrophs incorporated into consumer diets (larger values indicate integration of more basal resources) and the vertical structure of the food web within each assemblage (larger values indicate more trophic positions), respectively. Mean nearest neighbor distance, based on the average Euclidean distance of each sample in each assemblage to the $\delta^{13}C$ and $\delta^{15}N$ centroid, was used to infer the density of species packing. Using this metric, assemblages with small mean nearest neighbor distance values would have a high degree of functional redundancy. For each metric, I tested the hypothesis that the absolute value of the difference between pairwise site comparisons was equal to 0. For example, if standard ellipse area is significantly different from 0 for a pairwise comparison, then the assemblage with the larger standard ellipse area occupies a larger isotopic niche than the other. Mixing models, MANOVAs, and ANOVAs were performed in R (version 2.15.1) and PERMANOVAs were carried out in Primer version 6.0 with PERMANOVA add-on (Clarke & Gorley 2006; Anderson et al. 2008).

Results

A total of 590 and 229 samples (i.e., autotroph, macroinfauna, and nekton) were analyzed for $\delta^{13}C/\delta^{15}N$ and $\delta^{34}S$, respectively (Appendix A). Mean isotopic ratios of autotrophs ranged between -33.2 ‰ (POM) and -13.5 ‰ (C4) for $\delta^{13}C$, 4.6 ‰ (POM) and 6.6 ‰ (C4) for $\delta^{15}N$, 2.2 ‰ (C3) and 7.6 ‰ (BMA) for $\delta^{34}S$. The isotopic ratios of aggregated autotroph assemblages differed across sites (Table 13a); $\delta^{15}N$ was more
depleted in PRE-CF than all other sites. As a result, site-specific autotroph isotope ratios were used for all subsequent mixing models. In addition, BMA and C3 were isotopically indistinguishable using only δ^{15}N and C3 and C4 were similar using δ^{34}S (Table 13b).

Table 13

**MANOVA summary comparing autotroph isotope ratios across (a) sites and (b) source.**

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>V</th>
<th>F</th>
<th>p</th>
<th>Pairwise comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>5</td>
<td>4.6</td>
<td>2.19</td>
<td>&lt; 0.001</td>
<td>PRE-CF  PRE-PF  BB-IN  BB-PF  PRE-IN  BB-CF</td>
</tr>
<tr>
<td>δ^{13}C</td>
<td>1</td>
<td>0.13</td>
<td>0.98</td>
<td></td>
<td></td>
</tr>
<tr>
<td>δ^{15}N</td>
<td>4.96</td>
<td>4.96</td>
<td>&lt; 0.001</td>
<td>PRE-CF  PRE-PF  BB-IN  BB-PF  PRE-IN  BB-CF</td>
<td></td>
</tr>
<tr>
<td>δ^{34}S</td>
<td>0.37</td>
<td>0.37</td>
<td>0.87</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>5.94</td>
<td>0.45</td>
<td>7.37</td>
<td>&lt; 0.0001</td>
<td>PRE-CF  PRE-PF  BB-IN  BB-PF  PRE-IN  BB-CF</td>
</tr>
<tr>
<td>δ^{13}C</td>
<td>0.26</td>
<td>0.26</td>
<td>0.93</td>
<td></td>
<td></td>
</tr>
<tr>
<td>δ^{15}N</td>
<td>7.36</td>
<td>7.36</td>
<td>&lt; 0.0001</td>
<td>PRE-CF  PRE-PF  BB-IN  BB-PF  PRE-IN  BB-CF</td>
<td></td>
</tr>
<tr>
<td>(b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Source</td>
<td>2.49</td>
<td>1.8</td>
<td>175.6</td>
<td>&lt; 0.0001</td>
<td>C3  BMA  C4</td>
</tr>
<tr>
<td>δ^{13}C</td>
<td>602.7</td>
<td>602.7</td>
<td>&lt; 0.0001</td>
<td>C3  BMA  C4</td>
<td></td>
</tr>
<tr>
<td>δ^{15}N</td>
<td>15.13</td>
<td>15.13</td>
<td>&lt; 0.0001</td>
<td>C3  BMA  C4</td>
<td></td>
</tr>
<tr>
<td>δ^{34}S</td>
<td>0.37</td>
<td>0.37</td>
<td>0.93</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Source</td>
<td>3.96</td>
<td>0.99</td>
<td>31.09</td>
<td>&lt; 0.0001</td>
<td>C3  C4  BMA</td>
</tr>
<tr>
<td>δ^{13}C</td>
<td>1439</td>
<td>1439</td>
<td>&lt; 0.0001</td>
<td>POM  C3  BMA  C4</td>
<td></td>
</tr>
<tr>
<td>δ^{15}N</td>
<td>10.78</td>
<td>10.78</td>
<td>&lt; 0.0001</td>
<td>POM  C3  BMA  C4</td>
<td></td>
</tr>
</tbody>
</table>

Note. Significant omnibus models were followed by protected ANOVA models and pairwise comparisons using Tukey’s HSD. Pascagoula River estuary (PRE), Biloxi Bay (BB), intact natural salt marsh landscapes (IN), partially fragmented salt marsh landscapes (PF), completely fragmented salt marsh landscapes (CF), benthic microalgae (BMA), Juncus romerianus (C3), Spartina alterniflora (C4), and particulate organic matter (POM). In pairwise comparisons, sites or sources are ordered from left to right from most depleted to most enriched values. Shared underline signifies no difference at p < 0.05.

Macroinfauna assemblages had mean δ^{13}C ranging from -27.0 ‰ to -20.3 ‰ and mean δ^{15}N ranging from 6.1‰ to 9.3 ‰ (Appendix A; Figure 13). Aggregated isotope ratios differed among the sites with macroinfauna assemblages in PRE-PF having markedly depleted δ^{13}C and δ^{15}N values relative to all other sites (Figure 13; Table 14a). Nekton isotope ratios displayed a similar pattern for δ^{13}C (range, -24.1 ‰ to -17.3 ‰) and δ^{15}N (range, 10.3 ‰ to 13.2 ‰; Appendix A; Figure 13). Likewise, δ^{34}S (range, 7.8 ‰ to 10.3 ‰) was enriched relative to both autotrophs and macroinfauna (Appendix A). Aggregated isotope ratios differed among sites for all three isotopes (Table 14b). Nekton
assemblages in BB-IN, PRE-IN, and BB-CF had similar $\delta^{13}$C, however all other pairwise comparisons were

\[\text{Figure 13. Stable isotope bi-plots of composite } \delta^{13}\text{C and } \delta^{15}\text{N macroinfauna and nekton (fish and decapods) samples in relation to autotrophs across sites. See Appendix A for functional group- or species-specific isotope values.}\]
statistically different. Nitrogen isotope ratios for the nekton assemblage at BB-CF were significantly enriched compared to all other sites and $\delta^{34}$S differed haphazardly among sites.

Table 14

MANOVA summary comparing isotope ratios across sites for (a) macroinfauna and (b) nekton.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>$V$</th>
<th>$F$</th>
<th>$p$</th>
<th>Pairwise comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>5,91</td>
<td>0.88</td>
<td>14.36</td>
<td>&lt; 0.0001</td>
<td>PRE-PF BB-CF BB-F PRE-CF BB-IN PRE-IN</td>
</tr>
<tr>
<td>$\delta^{13}$C</td>
<td>38.82</td>
<td>&lt; 0.0001</td>
<td>PRE-PF BB-CF BB-F PRE-CF BB-IN PRE-IN</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\delta^{15}$N</td>
<td>7.09</td>
<td>&lt; 0.0001</td>
<td>PRE-PF BB-CF BB-F PRE-CF BB-IN PRE-IN</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>5,153</td>
<td>1.4</td>
<td>175.6</td>
<td>&lt; 0.0001</td>
<td>PRE-PF BB-PF BB-IN PRE-IN BB-CF PRE-CF</td>
</tr>
<tr>
<td>$\delta^{13}$C</td>
<td>154.3</td>
<td>&lt; 0.0001</td>
<td>PRE-CF PRE-IN PRE-PF BB-IN BB-PF BB-CF</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\delta^{15}$N</td>
<td>22.86</td>
<td>&lt; 0.0001</td>
<td>PRE-CF PRE-IN PRE-PF BB-IN BB-PF BB-CF</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\delta^{34}$S</td>
<td>7.08</td>
<td>&lt; 0.0001</td>
<td>PRE-CF PRE-IN PRE-PF BB-IN PRE-PF BB-CF</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Significant omnibus models were followed by protected ANOVA models and pairwise comparisons using Tukey’s HSD. Pascagoula River estuary (PRE), Biloxi Bay (BB), intact natural salt marsh landscapes (IN), partially fragmented salt marsh landscapes (PF), and completely fragmented salt marsh landscapes (CF). In pairwise comparisons, sites are ordered from left to right from most depleted to most enriched values. Shared underline signifies no difference at $p < 0.05$.

Though estimated trophic position for macroinfauna was lower at the PRE-PF site compared to all others (Figure 14), trophic position differed only among functional feeding groups (ANOVA; $df = 3,77; F = 20.35; P < 0.001$). Meiofauna (MEIF) fed at the lowest trophic position while omnivorous worms (OW) tended to feed higher in the food chain and both SDF and SF fed at an intermediate trophic position (Figure 14).

Estimated trophic position for decapod crustaceans (Figure 5a) differed among sites ($df = 5,253; F = 222.50; P < 0.001$) and species ($df = 5,253; F = 38.55; P < 0.001$). At the species level, grass shrimp, brown shrimp, and small blue crabs (< 60 mm CW) fed at a similar trophic position (~3.0) while larger blue crabs (> 60 mm CW) fed at a higher
trophic position (~3.5). Within each estuary, decapod crustaceans generally fed at a higher trophic

**Figure 14.** δ¹⁵N-based estimates of trophic position (± standard error) for macroinfauna assemblages across sampling sites. Sites with similar upper-case letters (in figure key) are not different. Horizontal black bars indicate significantly different trophic position estimates at the functional feeding group-level. Within feeding groups, trophic position did not differ among sites. Meiofauna (MEIF), suspension feeders (SF), surface deposit feeders (SDF), and omnivorous worms (OW).

position in CF landscapes compared to both IN and PF and these results were corroborated by among-site comparisons within species (lower case letters; Figure 15a). Fish, on the other hand, fed at a higher trophic position (> 3.0) and mean TLs differed both among sites (df = 5,135; F = 81.23; P < 0.001) and species (df = 3,135; F = 17.64; P < 0.001). As with decapod crustaceans, fish assemblages in CF landscapes fed at significantly higher trophic position compared to both IN and PF sites within an estuary and this result was nearly consistent across the four species (Figure 15b). Additionally, both size classes of Gulf killifish fed at a similar trophic position with the larger size class (> 60 mm TL) feeding at a trophic position that was similar to both spot and southern
Figure 15. δ¹⁵N-based estimates of trophic position (± standard error) for a) decapod crustaceans and b) nekton assemblages across sampling sites. Sites with similar upper-case letters (in figure key) are not different. Horizontal black bars indicate significantly different trophic position estimates at the species-level. Within species, estimates with different lower-case letters are significantly different. Grass shrimp (GSHP), brown shrimp < 20 mm carapace length (BSHPA), brown shrimp > 20 mm carapace length (BSHPB), blue crab < 30 mm carapace width (BLCBA), blue crab 30-60 mm carapace width (BLCBB), blue crab > 60 mm carapace width (BLCBC), Gulf killifish < 60 mm total length (FUNGA), Gulf killifish > 60 mm total length (FUNGB), spot (SPOT), and southern flounder (FLDR).
flounder.

All four autotrophs (BMA, C3, C4, and POM) contributed to macroinfaunal assemblages across all sites (Figure 16a; Appendix B). The contribution of POM, however, was minimal at most sites. However, due to similar $\delta^{15}$N values for both BMA and C3 (Table 13b), the two-isotope mixing model could not adequately separate the two autotrophs for the purpose of estimating their contribution to both macroinfauna and nekton diets. Internal model diagnostics (not shown) indicated a consistently strong, negative correlation (-0.71 to -0.86) between BMA and C3 in model outputs that suggested the mixing model could only increase the contribution of either BMA or C3 at the expense of the other autotroph. Though it is advisable to combine similar sources into a single group (Ward et al. 2011), I acknowledge that estimates for BMA and C3 in the two-isotope mixing model are likely biased towards either over- or underestimation but feel that their relative values still provide a useful metric for examining trophic dynamics in each site. Estimated autotroph contributions to macroinfauna diets differed among sites (PERMANOVA; $df = 5, 27$; pseudo-$F = 8.49$; permuted-$P = 0.001$; Figure 16a) but not functional feeding groups ($df = 5, 27$; pseudo-$F = 1.8$; permuted-$P = 0.095$; Appendix B). At the PRE-PF site, C4 autotrophs contributed a significantly smaller proportion to macroinfauna diets compared to all other sites (similarity = 61.01 – 75.95%; all pseudo-$t \geq 2.7$; all permuted-$P \leq 0.028$; Figure 16a). Further, autotroph contributions to macroinfauna diets differed between IN and CF sites within each estuary (BB, similarity = 70.18%; pseudo-$t = 2.8$; permuted-$P = 0.002$; PRE, similarity = 71.4%; pseudo-$t = 2.9$; permuted-$P = 0.042$). In CF landscapes, C4 was the most important contributor to macroinfauna diets (47 – 63%) while contributions were spread more
Figure 16. Bayesian mixing model estimates of autotroph contributions to a) macroinfauna assemblages using only $\delta^{13}$C and $\delta^{15}$N, b) nekton assemblages using only $\delta^{13}$C and $\delta^{15}$N, and c) nekton assemblages using $\delta^{13}$C, $\delta^{15}$N, and $\delta^{34}$S. Symbols are designated as the estimated modal contribution and vertical lines represent the 95% credible interval. Species or taxa specific contributions can be found in Appendices B-D.

Evenly among the BMA, C3, and C4 autotrophs in the IN sites (Figure 5a; Appendix B).

Based on the two-isotope mixing model, autotroph contributions to nekton diets differed among sites ($df = 5, 49$; pseudo-$F = 20.51$; permuted-$P = 0.001$; Figure 16b) but
not species ($df = 10, 49$; pseudo-$F = 1.2$; permuted-$P = 0.31$; Appendix C & D). As with macroinfauna, C4 autotrophs contributed a significantly smaller proportion to macroinfauna diets at the PRE-PF site, which was different from all other sites (similarity = 52.67 – 69.33%; all pseudo-$t \geq 2.08$; all permuted-$P \leq 0.023$) with the exception of BB-PF (similarity = 79.67%; pseudo-$t \geq 1.65$; permuted-$P \leq 0.083$; Figure 16b). Likewise, autotroph contributions to nekton diets in CF sites were markedly different from all other sites (similarity = 52.67 – 74.19%; all pseudo-$t \geq 1.86$; all permuted-$P \leq 0.045$). Though POM contributed minimally to nekton diets across all sites, C4 autotrophs provided the bulk of the contribution at CF sites while different combinations of BMA, C3, and C4 autotrophs contributed to nekton diets in the IN and PF sites (Figure 16b). The three-isotope mixing model revealed similar patterns where autotroph contributions differed among sites ($df = 5, 44$; pseudo-$F = 21.98$; permuted-$P = 0.001$; Figure 16c) but not species ($df = 9, 44$; pseudo-$F = 3.17$; permuted-$P = 0.04$; Appendix C & D). With the exception of both IN sites (similarity = 84.77%; pseudo-$t = 0.24$; permuted-$P = 0.94$; Figure 16c), all sites differed in terms of autotroph contributions to nekton assemblage diets (similarity = 54.91 – 74.77%; all pseudo-$t \geq 2.29$; all permuted-$P \leq 0.033$).

However, the most conspicuous differences occurred when CF sites were compared to IN (BB, similarity = 57.93%; PRE, similarity = 58.27%) and PF (BB, similarity = 60.54%; PRE, similarity = 54.91%) sites within an estuary. All three autotrophs (BMA, C3, and C4) contributed similarly to nekton diets in both IN sites and the BB-PF site. On the other hand, two autotrophs comprised nekton diets in BB-CF (BMA and C4) and PRE-PF (BMA and C3) sites while a single autotroph (C4) was the primary source in the PRE-CF site (Figure 16c).
Bootstrapped estimates of assemblage-level trophic metrics indicate that food web dynamics in both macroinfauna and nekton assemblages differ among sites (Table 3). However, the results were highly variable and no consistent pattern emerged for macroinfauna assemblages (Table 15a). All macroinfaunal assemblages appeared to integrate a similar range of autotroph resources (CR) and have similar number of functional groups with similar trophic niches (MNND). On the other hand, patterns were clearer for the nekton assemblages and most metrics changed with levels of landscape urbanization (Table 15b). For example, both the isotopic niche (SEA) and integration of

<table>
<thead>
<tr>
<th></th>
<th>SEA (‰^2)</th>
<th>NR (‰)</th>
<th>CR (‰)</th>
<th>MNND</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BB-IN</td>
<td>7.94 (1.04)</td>
<td>5.96 (2.47)</td>
<td>8.92 (3.24)</td>
<td>1.21 (0.13)</td>
</tr>
<tr>
<td>BB-PF</td>
<td>2.60 (0.48)</td>
<td>4.60 (3.42)</td>
<td>4.51 (3.71)</td>
<td>0.79 (0.11)</td>
</tr>
<tr>
<td>BB-CF</td>
<td>3.51 (1.14)</td>
<td>4.15 (1.28)</td>
<td>6.98 (1.17)</td>
<td>1.17 (0.13)</td>
</tr>
<tr>
<td>PRE-IN</td>
<td>4.93 (0.44)</td>
<td>4.18 (1.30)</td>
<td>4.43 (1.43)</td>
<td>0.65 (0.13)</td>
</tr>
<tr>
<td>PRE-PF</td>
<td>5.36 (0.87)</td>
<td>4.78 (2.89)</td>
<td>5.69 (3.92)</td>
<td>0.61 (0.13)</td>
</tr>
<tr>
<td>PRE-CF</td>
<td>4.77 (0.81)</td>
<td>3.20 (1.10)</td>
<td>6.99 (1.23)</td>
<td>0.99 (0.12)</td>
</tr>
</tbody>
</table>

| (b)   |          |            |            |           |
| BB-IN | 3.01 (0.46) | 4.89 (0.41) | 5.13 (0.47) | 0.75 (0.09) |
| BB-PF | 2.88 (0.44) | 4.10 (0.35) | 4.43 (0.49) | 0.74 (0.08) |
| BB-CF | 2.44 (0.47) | 6.02 (0.43) | 4.03 (0.44) | 1.05 (0.09) |
| PRE-IN| 3.55 (0.51) | 3.55 (0.41) | 4.89 (0.45) | 0.84 (0.11) |
| PRE-PF| 4.88 (0.49) | 3.28 (0.34) | 4.75 (0.48) | 0.83 (1.0)   |
| PRE-CF| 2.11 (0.43) | 5.37 (0.46) | 3.93 (0.43) | 0.90 (0.00)  |

Note. Results of the pairwise comparison (i.e., absolute value of the difference = 0) are indicated with capitalized superscript letters. Values with different superscript letters are significantly different at p < 0.05. Pascagoula River estuary (PRE), Biloxi Bay (BB), intact natural salt marsh landscapes (IN), partially fragmented salt marsh landscapes (PF), and completely fragmented salt marsh landscapes (CF). SEA = standard ellipse area, a measure of isotopic niche space, NR = δ¹⁵N range, a measure of the vertical food web structure, CR = δ¹³C range, MNND = mean nearest neighbor distance, used to infer density of species packing.
basal resources to nekton diets (CR) decreased with increasing urbanization. Likewise, nekton assemblages in CF landscapes had more trophic positions (NR).

Discussion

Numerous stable isotope-based metrics presented in this study illustrate a complex interaction between increased urbanization and food web structure, particularly for nekton. Firstly, this work highlights the importance of autochthonous salt marsh production (i.e., BMA, C3, and C4) for macroinfauna and nekton production across all sites. However, assemblages in CF landscapes integrated a narrower range of autotrophs into their diets compared to assemblages in either IN or PF landscapes. Secondly, nekton assemblages in CF landscapes had a significantly greater estimated trophic position and nitrogen range. While these results appear to suggest increased food chain length in these assemblages, it is more likely a stress response to poor foraging conditions. Thirdly, there was a considerable reduction in isotopic niche for nekton and, to a lesser degree, macroinfauna assemblages in CF sites. However, linking the observed patterns to urbanization is not straightforward and requires careful examination. Thus, I discuss the potential linkages and explore the implications of altered food web dynamics for nekton resources.

Shifts in the relative contributions of autotrophs and changes in breadth of autotrophs incorporated into consumer diets track increasing levels of urbanization. While numerous factors could contribute to the observed patterns, alterations in the movement of material through salt marsh food webs likely result from habitat reduction and fragmentation. Several studies have related food web alterations to coastal habitat reduction (Guest & Connolly 2006) and fragmentation (Seitz et al. 2006; Layman et al.
2007b). However, the exact mechanisms leading to such alterations remain unclear. In the present study, autotroph contributions (shown in 2- and 3-isotope Bayesian mixing models) to both macroinfauna and nekton diets were more heterogeneous (≥ 3 sources) in IN and PF landscapes and consumers, particularly nekton, incorporated fewer autotrophs into their diets in CF landscapes. The landscapes used in this study were arrayed along a gradient of urbanization such that both salt marsh area and connectivity were greatest in IN and PF landscapes and markedly reduced in the CF landscapes (Chapter II). Given that the stable isotope ratios of an autotroph can vary spatially at small scales (Deegan & Garritt 1997; Cloern et al 2002), a reduction in habitat size may also decrease the opportunity for mobile organisms to exploit isotopically heterogeneous prey resources within a salt marsh. Further, the accumulation of man-made surfaces and developed shoreline isolates salt marsh habitats from other natural habitats and not only negates inter-patch movement by less mobile organisms (Chitty & Able 2004; Able et al. 2012; Green et al. 2012a,b; Chapter II) but also disrupts the flow of allochthonous inputs from other salt marshes (Seitz et al. 2006; Doi et al. 2010; Olsen et al. 2010).

Though trophic position estimates are highly variable, they suggest a general food web structure of grazing by most macroinfauna, secondary consumption by omnivorous worms and smaller decapod crustaceans, and mixed feeding at higher trophic levels by larger blue crabs and fish. Other studies have also noted large variability in trophic position estimates (Fry et al. 1999; Vander Zanden et al. 2000; Anderson & Cabana 2009) and attributed such variability to changes in the structure of the underlying food web (Post & Takimoto 2007). In this study, there are two lines of evidence that suggest increased food chain length in CF landscapes and both metrics suggest that the disruption
is occurring at higher trophic levels. First, estimates of $\delta^{15}$N-based trophic position for nekton assemblages, but not macroinfauna, were significantly greater in the CF landscapes despite similar $\delta^{15}$N baselines (marsh periwinkle) across sites. Akin and Winemiller (2008) used the same approach, with a larger fractionation factor ($\Delta^{15}$N = 3.35), to estimate trophic position for the same suite of similarly sized nekton. While their estimates are lower than those in this study, a reflection of model sensitivity to different levels of $\Delta^{15}$N (Post 2002), their overall patterns are commensurate with estimates of trophic position in IN landscapes. Secondly, the vertical food web structure (NR) within nekton assemblages was significantly larger in CF landscapes where autotroph incorporation was more homogeneous. This result constrasts work in the Bahamas where food chain length was reduced in fragmented tidal creeks with reduced autotroph diversity (CR; Layman et al. 2007b).

The observed increase in food chain length, however, is likely an artifact of greater $\Delta^{15}$N resulting from poor foraging opportunities in CF landscapes (Chapters II & III). Numerous studies have shown greater $\Delta^{15}$N in nutritionally stressed animals (Oelbermann & Scheu 2002; Olive et al. 2003; McCutchan et al. 2003; Haubert et al. 2005) via $^{15}$N excretion and $^{14}$N assimilation during tissue catabolism (Scrimgeour et al. 1995; Adams & Sterner 2000). Conversely, $\Delta^{13}$C and $\Delta^{34}$S appear relatively robust to such stressors (Kempster et al. 2007). Colborne and Robinson (2012) recently showed that pumpkinseed sunfish ($Lepomis gibbosus$) fed rations below minimum daily requirements had elevated $\delta^{15}$N, with no difference in $\delta^{13}$C, compared to fish fed ad libitum. Further, $\delta^{15}$N increased as pumpkinseed sunfish body condition decreased. Previous work in this system showed Gulf killifish offset the low abundance of common
forage species (i.e., nereid worms and grass shrimp) in CF landscapes by supplementing their diets with larger-bodied brown shrimp. Similarly, spot appeared to delay ontogenetic shifts from feeding on meiofauna to larger prey upon recruitment to salt marsh habitats in CF landscapes (Chapter III). For both species, empty stomachs were more prevalent and growth and body condition was reduced in individuals collected from the CF landscapes. However, the manifestation of nutritional stress may be strongest in species with prolonged periods of residency (i.e., grass shrimp, brown shrimp, Gulf killifish, and spot) and ameliorated in species that are capable of feeding in multiple habitats (i.e., southern flounder and larger blue crabs).

The isotopic niche (i.e., SEA) of nekton assemblages was markedly reduced in CF landscapes, despite increased $\delta^{15}N$ range, and parallels the reduction in $\delta^{13}C$ range. However, inflated $\delta^{15}N$ range values in CF landscapes suggest that among-site differences in the isotopic niche of nekton assemblages are likely underestimated. Regardless, the reduced isotopic niche is a synergistic response to the factors discussed in previous paragraphs (i.e., habitat reduction, fragmentation, and prey availability). Based on these results, nekton assemblages in less-altered salt marsh landscapes have much broader isotopic niches because prey resources are more abundant and consumers are able to incorporate a wider variety of isotopically distinct autotrophs into their diets. However, in the CF landscapes, where salt marsh habitat is reduced and fragmented, resources are more scarce (Chapter II) and prey selection is constrained leading to a reduced niche. Similar results have been observed in food webs in fragmented Bahamian tidal creeks (Layman et al. 2007b).
Interestingly, the macroinfaunal assemblage showed a weak response to urbanization. While several studies have noted weak macroinfaunal responses to manipulated top-down and bottom controls (Kneib & Stiven 1982; Posey et al. 2002; Johnson & Fleeger 2009), Seitz et al. (2006) hypothesized that deposit feeding infauna would do poorly in altered salt marsh habitats due to a lack of allochthonous food sources. However, the results presented here contradict that hypothesis and deposit feeders constituted the bulk of the macroinfauna assemblages in the CF landscapes (Chapter II, Appendix B). That said, the contribution of POM to the diets of deposit feeding worms and chironomids was greater in the IN and PF landscapes than the CF landscapes. Determining source contributions to macroinfauna diets can be complicated by their small body size and a variety of feeding modes that allow them to exploit both living and dead autotrophs that can be produced in situ or tidally-imported (Fauchald & Jumars 1979; Connolly et al. 2005). Further, feeding modes have been shown to change spatially and temporally with the quality and quantity of food sources (Kihslinger & Woodin 2000; Carman & Fry 2002). Ultimately, natural abundance stable isotopes may be limited in resolving issues of source contributions to macroinfauna diets (Carman & Fry 2002; Galván et al. 2011). Using dual isotope tracers, Galván et al. (2011) showed that algal resources were more important than macrophyte detritus to the diets of macroinfauna.

There are several methodological limitations to the inferences drawn from the results of this work that require some further discussion. Firstly, trophic fractionation of $\delta^{13}$C, $\delta^{15}$N, and $\delta^{34}$S can vary substantially due to inherent sources of variation (Vander Zanden & Rasmussen 2001; McCutchan et al. 2003; Caut et al. 2009). While trophic
position estimates are clearly sensitive to different levels of $\Delta^{15}\text{N}$ (Post 2002), Bayesian stable isotope mixing models also appear sensitive to uncertainty in fractionation factors (Bond & Diamond 2011). However, reflecting this uncertainty by increasing the variance around the fractionation factors in the model input simply results in larger uncertainty around estimated proportions (i.e., posterior distributions) while providing a similar pattern (Lowe, unpublished data). Thus, modal estimates alone can be misleading and should be accompanied by the 95% credible interval as this gives an indication of the highest density region in the posterior distributions. Further, there is some basis for expecting $\Delta^{15}\text{N}$ to vary systematically among sites, as greater, stress-induced $\Delta^{15}\text{N}$ would be expected for some species, but not all, in CF landscapes. However, more detailed experimental work is needed in order to understand the full-effect of nutritional stress on model estimates of autotroph contributions in this study. Secondly, though the SIAR model used in this study can adequately deal with “undetermined systems” (more sources than isotopes; Parnell et al. 2010), by focusing on the dominant autotrophs in each salt marsh I may have inadvertently excluded the contribution of other important carbon sources such as terrestrial litter (Attrill et al. 2009). However, only the PF landscapes were in close proximity to forested areas (Chapter II) and, therefore, comparisons between IN and CF landscapes are likely still valid. Lastly, the isotope-based niche metrics used in this study are prone to spurious results that can hamper interpretation (Hoeinghaus & Zeug 2008). However, many of my inferences are based on redundant (this study) or complementary information (Chapters II & III). For example, while a difference of ~1-2 ‰ for CR alone is not necessarily biologically meaningful, the same pattern is corroborated in mixing model outputs. In addition, isotopic niche reduction can
result from a truncated autotroph pool (Hoeinghaus & Zeug 2008). However, niche width inferences based on stable isotope data were also supported by diet data for two species (Chapter III). Overall, I feel that the inferences in this study regarding food web alterations in CF landscapes are driven by prey availability and not spurious model results.

These results, despite their potential limitations, have broad implications for nekton resources and salt marsh habitat restoration and management. The relative value of salt marsh habitats for nekton is derived from the ability to support increased juvenile density, growth, survival, and subsequent recruitment to adult populations (Beck et al. 2001). Highly altered salt marsh habitats (i.e., CF landscapes) support compositionally different faunal assemblages (Chapter II), altered growth dynamics for ecologically and economically important species (Chapter III), and trophic support is functionally altered (Chapter III and here). These results continue to build on the growing paradigm that, while the amount of salt marsh habitat is a driver of both nekton and macroinfaunal production (Weinstein 1979; Boesch & Turner 1984; Zimmerman et al. 2000), the composition and configuration of the surrounding landscape is equally important (Guest & Connolly 2006; Meynecke et al. 2008; Roth et al. 2008; Meyer & Posey 2009; Green et al. 2012a,b).

Recognizing that population growth (Crossett 2004; European Environmental Agency 2006) and accompanying urbanization (Beach 2002; Living Shoreline 2006) are necessary components of growth in the coastal zone, I urge planners and decision makers to recognize that coastal urbanization can disrupt the flow of energy and material through aquatic food webs (Doi et al. 2010; Olsen et al. 2010). Coastal development that
progresses in a manner that both consumes and isolates salt marsh habitats within a human-dominated landscape is unlikely to be sustainable and 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). I suggest, as do others (Swann 2008; Peterson & Lowe 2009; Bulleri & Chapman 2010; Browne & Chapman 2011; Chapman & Underwood 2011), that maintaining the functional properties of natural landscapes (i.e., habitat quality and connectivity) is critical to the future health of coastal ecosystems and continued delivery of ecosystem services. Habitat reduction and fragmentation do not operate independently on food web dynamics and maintaining functional connectivity with other natural habitats would likely offset the impact of habitat reduction (Guest & Connolly 2006; Partyka & Peterson 2008; Green et al. 2012b; Chapter III). Thus, management and restoration efforts aimed at maintaining faunal assemblages and secondary production could benefit from focusing on promoting functional connectivity among several smaller natural habitat patches (i.e., SLoSS concept; Moy & Levin 1991; Fonseca et al. 1997; Eggleston et al. 1998; Green et al. 2012b).
CHAPTER V
OVERALL CONCLUSION

Consistent differences in faunal assemblages, reduced growth for some, but not all nekton, and evidence of altered trophic structure indicate that reduced habitat functionality appears to be an emergent property of urbanized coastal landscapes. Though salt marsh function can be broadly defined (Costanza et al. 1997; Barbier et al. 2011), the primary focus of this dissertation has been on their function as critical habitat for a suite of economically and ecologically important estuarine fauna (Boesch & Turner 1984; Minello et al. 2003). Ultimately, the functional value of a habitat to a species or assemblage is derived from those factors that improve individual condition and survival (Able et al. 1999; Beck et al. 2001; Levin & Stunz 2005). Oftentimes, the relative importance (i.e., functionality) of a particular habitat for fauna can be quantified using a suite of metrics (Beck et al. 2001; Rountree & Able 2007; Weinstein et al. 2009), which can be assessed hierarchically in space and time (Johnson 1980).

Relative abundance or density, for example, has commonly been used to infer value on coastal habitats for both nekton and macroinfauna assemblages. In an extensive literature review, Minello et al. (2003) used nekton density estimates to rank coastal habitats in the following order of importance for transient nekton; seagrass > marsh edge > nonvegetated bottom, open water, macroalgae > inner marsh > oyster reef. However, historical seagrass coverage in coastal Mississippi, particularly in the estuaries used in this study, is sparse further emphasizing the importance of salt marsh habitats in the maintenance of faunal assemblages. While elucidating the mechanisms driving unequal spatial distributions of faunal assemblages across coastal landscapes can be difficult
(Craig & Crowder 2000), Fretwell and Lucas’ (1970) Ideal Free Distribution model hypothesizes that the relative abundance or density of organisms in a habitat (i.e., tidal creeks) reflects the suitability of that habitat. Thus, higher quality or fully functional habitats should support more individuals than lower quality, less functional habitats (Kramer & Chapman 1999). Thus, nekton or macroinfauna selecting for salt marsh habitats in CF landscapes would have little flexibility in terms of maximizing fitness by redistributing themselves among available habitats.

Based on the 10 spatial metrics quantified in this study, the relative abundance and density of nekton and macroinfauna, respectively, was strongly correlated to the composition and configuration of the coastal landscape. Multiple nekton species (e.g., grass shrimp, brown shrimp, blue crab, Gulf menhaden, and spot) were most abundant in IN salt marsh landscapes where salt marsh habitats were expansive, natural edge habitat was readily available, and tidal creeks were highly connected and least abundant in CF landscapes where salt marsh habitat was small and largely isolated in an urbanized landscape (Chapter II). These results support the combined findings of other studies that have noted differences in nekton assemblage composition between natural salt marsh and man-made habitats (Able et al. 1998; Hendon et al. 2000; Peterson et al. 2000; Bilkovic & Roggero 2008; Long et al. 2011) and linked nekton assemblage patterns to the geomorphology of and the composition and configuration of natural salt marsh landscapes (Allen et al. 2007; Partyka & Peterson 2008; Green et al. 2012b) and to coastal watershed land use (King et al. 2005).

At the same time, mean total density (#ind m$^{-2}$) of taxa within macroinfaunal assemblages decreased in salt marsh habitats as the level of urbanization increased (IN =
354.6 ± 17.2, PF = 2899.9 ± 111.3, and CF = 1813.5 ± 88.6). Though not specifically addressed in this work, previous studies in these two estuaries have shown that total organic carbon tends to be low (Partyka & Peterson 2008) and sediment pollution threat highest (Lytle & Lytle 1985) in benthic sediments at the CF sites. Thus, the dominance of tolerant taxa (i.e., tubificid oligochaetes and capitellid polychaetes) and relative absence of sensitive taxa (i.e., *Streblospio* spp., amphipod crustaceans, and bivalves) in CF salt marsh landscapes is likely an indicator of degraded benthic conditions resulting from developed (i.e., impervious) surfaces adjacent the salt marsh habitats (Sanger et al. 1999a,b; Lerberg et al. 2000; Holland et al. 2004; Van Dolah et al. 2008). However, without accounting for natural gradients in macroinfaunal assemblage distribution patterns it is difficult to discern a direct response to salt marsh alteration (Rakocinski et al. 1997). That said, degraded sediments would explain reduced density and altered taxa composition in CF landscapes (Dauer 1993).

The second line of evidence supporting reduced habitat functionality in urbanized coastal landscapes comes in the form of reduced growth dynamics for both spot and Gulf killifish (Chapter III). While habitat specific growth is an important component of habitat function for nekton (Beck et al. 2001; Minello et al. 2003), growth results tend to be highly variable due to individual variation and experimental artifacts (Underwood 1997). Numerous studies have shown the importance of salt marsh habitats, relative to other natural habitats, in supporting nekton growth (Rooker et al. 1999; Stunz et al. 2002; Minello et al. 2003). Moreover, nekton growth rates are reduced in man-made habitats compared to natural habitats (Duffy-Anderson & Able 1999; Schindler et al. 2000). For example, Able et al. (1999) growth rates for both winter flounder (*Pseudopleuronectes*
Americanus) and tautog (Tautoga onitis) were reduced in altered habitats of the Hudson River estuary. However, Long et al. (2011) showed that blue crab growth did not differ between hardened shoreline habitats and both natural Spartina alterniflora and invasive Phragmites australis shorelines. In this study, growth dynamics did not differ for either blue crab or brown shrimp. Yet, despite a lack of growth differences, it does not appear that urbanized coastal landscapes can support either species at abundances similar to those found in less altered systems (King et al. 2005; Chapter II).

Lastly, several metrics in this dissertation also suggest that trophic structure is likewise altered in urbanized coastal landscapes (Chapters III & IV). Reduced growth for both spot and Gulf killifish was attributed to suboptimal foraging choices (i.e., meiofauna vs. larger prey items for spot; brown shrimp vs. grass shrimp for Gulf killifish) and a higher prevalence of empty stomachs in CF landscapes (Chapter III). Morley et al. (2012) showed similar results for chum salmon (Oncorhynchus keta) foraging patterns in armored and unarmored shorelines. Chum salmon diets consisted of more benthic prey items in unarmored sites (i.e., natural riparian shorelines) than in armored sites (i.e., rip-rap). However, they did not observe diet differences for Chinook salmon (O. tshawytscha) largely because this species was capable of foraging in other areas. Long et al. (2011), on the other hand, showed that despite differences in prey availability, caged blue crab diets did not differ among vegetated and armored (i.e., rip rap) shorelines; although blue crabs did consume more xanthid mud crabs in the armored habitats. Further, diet patterns in this study appear to reflect macroinfaunal densities at each site (Chapter II). Thus, in small, restricted systems with homogenous habitat choices (i.e., CF salt marsh landscapes) consumer diets are likely to overlap (Persson 1983) resulting in
increased competition for limited prey resources. Given the level of production typically attributed to salt marsh estuaries, competition for plentiful food resources is typically not viewed as a major factor in structuring nekton assemblages (Adams 1976).

Likewise, stable isotope analyses also revealed altered trophic structure in CF salt marsh landscapes. In particular, nekton assemblages tended to rely on a much narrower range of autotroph production centered on C4 plants and there was evidence suggesting that they were nutritionally stressed and occupied a much smaller isotopic niche. While stable isotope analyses have only recently been applied to questions of this nature, this work provides similar results to studies in other systems. Connolly (2003) showed that nekton rely on a different subset of autotrophic production in artificial habitats compared to adjacent natural salt marshes. Likewise, Layman et al. (2007) found that the niche width of grey snapper *Lutjanus griseus*, a generalist predator, was truncated in fragmented (i.e., reduced hydrologic connectivity due to road construction) mangrove tidal creeks when compared to natural creeks. This result appeared to mirror a decrease in prey diversity (Layman et al. 2004). However, the role of changes in relative abundance of both nekton and macroinfauna at CF sites (Chapter II) on trophic structure cannot be overlooked. In a Finnish lake, manipulated reduction in fish abundance to improve water quality resulted in a shift from reliance on littoral sources to pelagic production (Syväranta et al. 2011); there was also a concomitant increase in nitrogen range and isotopic niche space for most fish. Overall, these results suggest that alterations to both the coastal landscape and faunal assemblages can have deleterious impacts on salt marsh food web structure.
These results also have important ramifications for the management and maintenance of commercially and recreationally important nekton. The declining state of marine capture fisheries (Worm & Branch 2012; Watson & Pauly 2013) is often linked to fishing (Jackson et al. 2001); however, other anthropogenic impacts must be considered (Hilborn et al. 2003; Peterson & Lowe 2009). In the northern GOM, fisheries are tightly linked to the amount of salt marsh habitat (Boesch & Turner 1984) and the three largest commercial fisheries target species that rely on salt marsh habitats for a portion of their life (i.e., gulf menhaden, blue crab, and brown shrimp; O’Connell et al. 2005). As a result, there have been a number of attempts to understand the impact of salt marsh loss in the northern GOM on the production of economically important nekton (Browder et al. 1985; Chesney et al. 2000; Minello & Rozas 2002). Roth et al. (2008) showed that brown shrimp production increased with increasing levels of fragmentation (more edge habitat = more production potential) and significantly declined with conversion to an open water systems. Further, Jordan et al. (2009) used a population model embedded within a coarse-grained (~55.2 km² polygons) habitat model to simulate the long-term effects of cumulative shoreline alteration on blue crab landings in Mobile Bay, Al. They were able to show that simulated blue crab landings would decrease significantly with conversion of 10% of contemporary salt marsh habitat to hardened shoreline. However, both studies assumed that all salt marsh habitats functioned similarly, in terms of growth and feeding potential. The results presented here suggest that models that assume similar functionality for all salt marsh habitats are likely to overestimate production potential at the landscape level.
The combined results of my dissertation support the overall hypothesis that urbanization in coastal landscapes functionally alter the value of salt marsh habitats for macroinfauna and nekton assemblages. In this context, the habitat value of small fragmented salt marsh landscapes nestled within urbanized landscapes would likely vary from species to species but would, ultimately, be reduced relative to healthy, natural salt marshes. Coastal urbanization, in all likelihood, prohibits sustainability over the long-term and likely negates restoration efforts aimed at returning to baseline conditions. Therefore, the future of salt marsh landscapes, and other intertidal habitat continuums, depends heavily on the synergistic efforts among ecologist, engineers, managers, and decision-makers to make well-informed science-based decisions regarding future growth in the coastal zone. Growth that progresses in a manner that both consumes and isolates critical habitats within a human-dominated landscape is unsustainable and every effort should be made to promote ecosystem health and the continued delivery of goods and services.
Note: Intact natural (IN), partially fragmented (PF), and completely fragmented (CF) salt marsh landscapes in both the Biloxi Bay (BB) and Pascagoula River (PRE) estuaries. Sample size for each isotope is indicated by \( n (\delta^{13}S \text{ in parentheses}) \). Benthic microalgae (BMA), *Juncus roemerianus* (C3), *Spartina alterniflora* (C4), and particulate organic matter (POM), surface deposit feeding worms (SDFW), surface deposit feeding chironomids (SDFC), omnivorous worms (OW), suspension feeding worms (SFW), and suspension feeding crustaceans (SFC).
APPENDIX B

BAYESIAN MIXING MODEL ESTIMATES OF AUTOTROPH CONTRIBUTIONS TO MACROINFAUNA DIETS ACROSS SITES USING ONLY $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$.

Meiofauna

Surface deposit feeding worms

Surface deposit feeding chironomids

Omnivorous worms

Suspension feeding worms

Suspension feeding crustaceans

BB-IN  BB-PF  BB-CF  PRE-IN  PRE-PF  PRE-CF
APPENDIX C

BAYESIAN MIXING MODEL ESTIMATES OF AUTOTROPH CONTRIBUTIONS TO DECAPOD CRUSTACEAN DIETS USING BOTH $\delta^{13}C$ AND $\delta^{15}N$ (LARGE PIE) AND $\delta^{13}C$, $\delta^{15}N$, AND $\delta^{34}S$ (SMALL PIE).
APPENDIX D

BAYESIAN MIXING MODEL ESTIMATES OF AUTOTROPH CONTRIBUTIONS TO FISH DIETS USING BOTH $\delta^{13}C$ AND $\delta^{15}N$ (LARGE PIE) AND $\delta^{13}C$, $\delta^{15}N$, AND $\delta^{34}S$ (SMALL PIE).
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