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Assessing the Link Between Coastal Urbanization and the Quality of Nekton Habitat in Mangrove Tidal Tributaries

Justin M. Krebs · Susan S. Bell · Carole C. McIvor

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Abstract To assess the potential influence of coastal development on habitat quality for estuarine nekton, we characterized body condition and reproduction for common nekton from tidal tributaries classified as undeveloped, industrial, urban or man-made (i.e., mosquito-control ditches). We then evaluated these metrics of nekton performance, along with several abundance-based metrics and community structure from a companion paper (Krebs et al. 2013) to determine which metrics best reflected variation in land-use and in-stream habitat among tributaries. Body condition was not significantly different among undeveloped, industrial, and man-made tidal tributaries for six of nine taxa; however, three of those taxa were in significantly better condition in urban compared to undeveloped tributaries. *Palaemonetes* shrimp were the only taxon in significantly poorer condition in urban tributaries. For *Poecilia latipinna*, there was no difference in body condition (length–weight) between undeveloped and urban tributaries, but energetic condition was significantly better in urban tributaries. Reproductive output was reduced for both *P. latipinna* (i.e., fecundity) and grass shrimp (i.e., very low densities, few ovigerous females) in urban tributaries; however a tradeoff between fecundity and offspring size confounded meaningful interpretation of reproduction among land-use classes for *P. latipinna*.

Reproductive allotment by *P. latipinna* did not differ significantly among land-use classes. Canonical correspondence analysis differentiated urban and non-urban tributaries based on greater impervious surface, less natural mangrove shoreline, higher frequency of hypoxia and lower, more variable salinities in urban tributaries. These characteristics explained 36 % of the variation in nekton performance, including high densities of poeciliid fishes, greater energetic condition of sailfin mollies, and low densities of several common nekton and economically important taxa from urban tributaries. While variation among tributaries in our study can be largely explained by impervious surface beyond the shorelines of the tributary, variation in nekton metrics among non-urban tributaries was better explained by habitat factors within the tributary and along the shorelines. Our results support the paradigm that urban development in coastal areas has the potential to alter habitat quality in small tidal tributaries as reflected by variation in nekton performance among tributaries from representative land-use classes.

Keywords Tampa Bay · Tidal creek · *Rhizophora* · Mosquito ditch · Nekton metrics · CCA

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Introduction

Coastal ecosystems are rapidly changing as a result of urban development, prompting an urgent need to understand the ecological response of these natural systems to anthropogenic alterations in the landscape. Within coastal watersheds, tidal tributaries represent a relatively small percentage of all estuarine habitat, but lie at the interface between terrestrial and aquatic realms, where they closely link the physical and functional processes that occur between the surrounding watershed and the open estuary (Holland et al. 2004;

Martinetto et al. 2006; Malkin et al. 2010; Sanger et al. 2011). Small tidal tributaries, often referred to as tidal creeks, have been a relatively understudied element of the estuarine ecosystem, specifically in mangrove-dominated systems. Even less studied are the factors underlying the distribution and habitat associations of nekton in mangrove tidal tributaries. This lack of study is particularly surprising due to the potentially significant ecological role of tidal creeks as habitat for a distinct subset of the nekton community (Mallin and Lewitus 2004; Tuckey and DeHaven 2006; Sherwood 2010) and as a source of primary and secondary production to the estuary (Kneib 2003; Stevens et al. 2006). Despite the apparent ecological and economic value of these systems, relatively little is known about the link between coastal development and the quality of nekton habitat in tidal tributaries.

Although numerous factors may underlie ecological variation among small tributaries (Brown et al. 2009), urbanization has repeatedly been associated with alterations to the quality of stream habitats (Allan 2004 and references therein). These alterations occur through just a few proximate mechanisms that can be directly linked to a larger suite of correlated factors (Allan 2004). For example, increased impervious surface reduces rainwater infiltration and promotes rainwater runoff thereby accelerating the delivery of sediment, nutrients, and chemical contaminants to the tributary (Arnold and Gibbons 1996; Konrad and Booth 2005). The amount of impervious surface in a watershed is believed to be one of the most integrative indicators for assessing the ecological impacts of urbanization (Schueler 1994; Arnold and Gibbons 1996; Xian and Crane 2005; Schueler et al. 2009) along with greater pollutant loading and sedimentation resulting from more extensive urban development (Fulton et al. 1993; Xian et al. 2007). Impervious surface has been used successfully to predict community characteristics of stream fishes (e.g., density, diversity, stress-sensitive taxa) in urbanized freshwater tributaries (Wang et al. 2001; Roy et al. 2005) and in small tidal tributaries (Holland et al. 2004).

Alteration to the surrounding landscape and in-stream habitat of tidal tributaries in developed watersheds may explain variation in nekton-community structure and influence the quality of nekton habitat in these systems compared to undeveloped systems (Krebs et al. 2013). Habitat quality, in this sense, can be defined as the ability of the environment to provide conditions necessary for individual survival and population persistence (*sensu* Hall et al. 1997). Attributes such as a high percentage of urban lands and impervious surface in the surrounding watershed, limited natural structure along the shorelines, disruption of tidal connectivity, frequent hypoxia or greater salinity variation, for example, may elicit a quantifiable response from the nekton community that could be useful in assessing the effects

of coastal development on the quality of the habitat. The biotic response to such alterations may be observed at the species level as reduced growth rate, poor body condition, changes in reproductive strategy (i.e., number and size of offspring) or lower survival (Lloret and Planes 2003; Martin et al. 2009; Piazza and LaPeyre 2010), all of which are quantifiable metrics of the biotic response to coastal development.

Small tidal tributaries in the Tampa Bay estuary on Florida's Gulf coast are found within a larger matrix of undeveloped, industrialized and urbanized land uses and may be of natural or man-made origin. Recent studies of Tampa Bay's tidal tributaries have characterized the nekton community and related it to in-stream habitat and watershed characteristics (Greenwood et al. 2007; Krebs et al. 2007; Greenwood et al. 2008a,b; Sherwood 2008; MacDonald et al. 2010; Sherwood 2010). For example, Krebs et al. (2007) demonstrated that the origin of a tributary (i.e., natural or man-made) may be less predictive of the potential quality of nekton habitat than the environmental conditions that characterize in-stream habitat in a particular type of tributary (i.e., tidal creek, mosquito-control ditch, stormwater-drainage ditch). Although several of these studies have examined variation in nekton-community attributes in the context of watershed land use (Greenwood et al. 2008a,b; Sherwood et al. 2008), a clear association between the nekton community and the surrounding landscape remains elusive. More recently, urbanized tributaries were shown to host a distinct nekton assemblage characterized by high densities of poeciliid fishes and very low densities or absence of otherwise common estuarine taxa including palaemonid grass shrimps and some killifish species (Krebs et al. 2013). Tidal tributaries located in relatively undeveloped watersheds, whether naturally formed or man-made, tended to have higher evenness than urbanized tributaries; however, total nekton density did not differ among land-use classes (Krebs et al. 2013). These studies suggest that spatial variation in community structure among tributaries (and density for some species), and among habitats within a tributary, is related to physicochemical (e.g., salinity, substrate, shoreline structure) and geomorphological (e.g., channel width) features within the tributary and is less directly influenced by landscape characteristics at the watershed level. However, from a functional perspective, trophic pathways within tidal tributaries appear to be determined by nutrient inputs from surrounding land uses as reflected by the stable-isotopic signatures of resident nekton (Malkin et al. 2010). Collectively, these studies indicate that the assessment of nekton-habitat quality in tidal tributaries will require the careful selection of metrics of nekton performance (*sensu* Claireaux and Lefrancoix 2007) that are sensitive to the factors that underlie variation in habitat quality at both in-stream and watershed scales.

The purpose of the present study was to further investigate the link between coastal urbanization and the quality of small tidal tributaries as nekton habitat using a series of metrics that directly or indirectly reflect nekton performance in these habitats. Here we built upon the results of our companion paper (Krebs et al. 2013), which describes variation in nekton density and community structure among tributaries, by examining several less traditional metrics: body condition and reproduction of common nekton. We then conducted a multivariate analysis to relate nekton performance to various in-stream habitat and watershed-scale variables for 11 tidal tributaries in developed and undeveloped watersheds in Tampa Bay. Based on the assumption that watershed development reduces the ecological value of natural systems (Holland et al. 2004), we predicted that nekton performance would differ between tidal tributaries from undeveloped and developed watersheds as well as man-made tributaries (i.e., mosquito-control ditches). We therefore tested the null hypothesis of no difference in nekton performance (including body condition or reproduction) between undeveloped tributaries (i.e., reference sites) and developed or man-made tributaries; however, we had no a priori expectations related to potential differences in these metrics of nekton performance among tributaries.

Materials and Methods

Site Selection

Selection of study sites was based on a land-use characterization for Tampa Bay tidal tributaries presented in the companion paper by Krebs et al. (2013). Briefly, this characterization included the type and percent composition of land use and land cover within the watershed and within a 100-m shoreline buffer to classify tributaries into general categories, including undeveloped (i.e., predominantly tidal wetlands and intact uplands), agricultural, industrial, urban and other (i.e., rural and recreational) according to classifications defined by the Florida Department of Transportation (1999). To further quantify the degree of land development for each tributary, we estimated percent impervious surface within the 100-m buffer and at the watershed scale using data from Xian and Crane (2005) and calculated the landscape development intensity (LDI) within the buffer to provide an area-weighted, land-use specific estimate of land development (Brown and Vivas 2005). Based on the results of this land-use analysis, we stratified our sample universe by land-use class and selected nine tidal creeks and two mosquito-ditched wetlands as study sites (companion

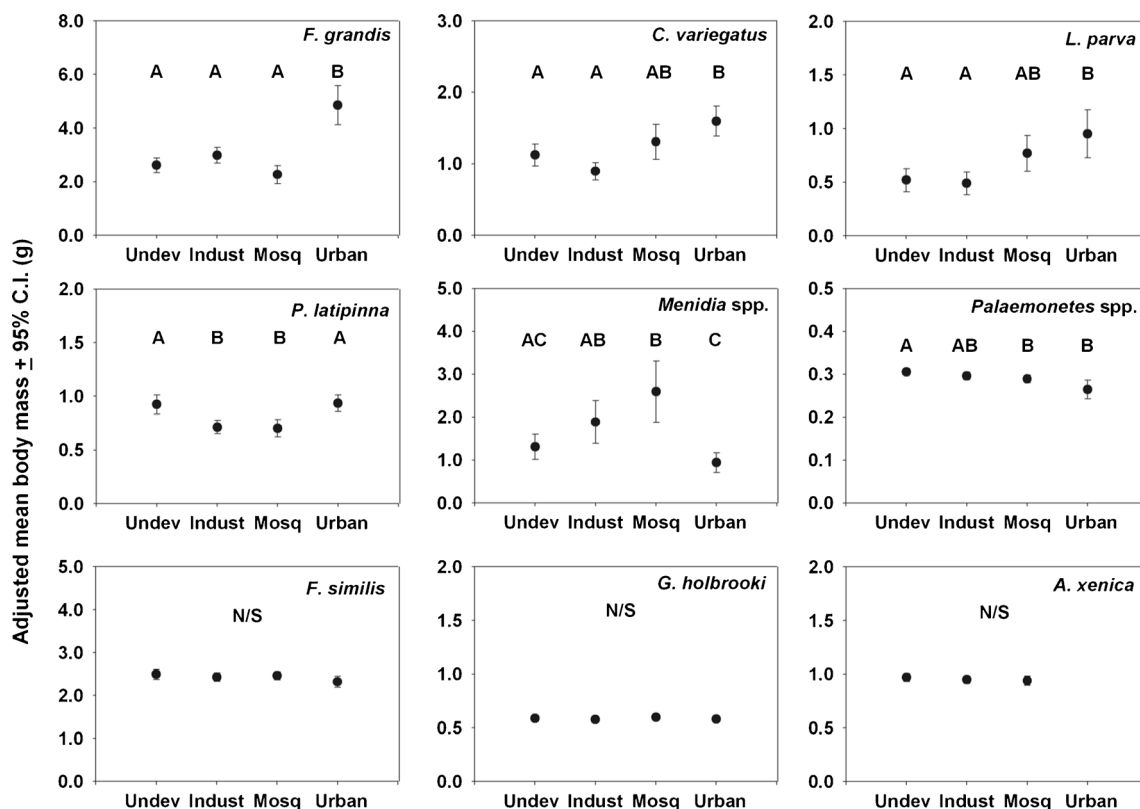


Fig. 1 Body condition of common nekton from tidal tributaries located in undeveloped (*Undev*), industrial (*Indust*), and urban (*Urban*) watersheds and mosquito ditches (*Mosq*). Condition is shown as the

adjusted mean body mass at reproductive maturity as estimated using ANCOVA. Minimum sample size for each land-use class was $n=60$ per species

paper Fig. 1 and Table 1 in Krebs et al. 2013); a third mosquito-ditched location was abandoned due to logistical constraints. We selected three replicates (one each from the upper, mid, and lower regions of the estuary) from watersheds characterized as (1) undeveloped, (2) urban, or (3) industrial. Urban and industrial tributaries were randomly selected from within the land-use and location strata, while two of the three undeveloped tributaries (i.e., Frog and Mobbly) and the mosquito-ditched sites (i.e., Weedon and Mobbly) were included based on long-term study at these sites. We considered tidal creeks from primarily undeveloped watersheds to represent baseline conditions for nekton habitat in Tampa Bay's tidal tributaries and used these as reference sites for comparisons with urban, industrial and mosquito-ditch tributaries.

Sample Collection

Sample collection methods are described in detail in the companion paper (Krebs et al. 2013), but briefly, we collected nekton samples using a "9.1-m raft seine" deployed along the shorelines of each of the 11 tributaries during three sampling events per year between March–October 2007 and 2008. During each event, we sampled six random sites totaling 36 samples from each tributary over 2 years, with the exception of the mosquito ditches at Mobbly Bayou where 30 samples were taken. All nekton were quantified and identified to the lowest practical taxonomic level. For each sample, a subset of nekton was retained for further analysis of body condition and reproduction. During each sampling event, we recorded instantaneous in situ water quality in each tributary and

Table 1 Summary of the nekton community collected from small tidal tributaries in the Tampa Bay estuary (2007–2008)

Species	Mean	Species	Mean density
<i>Poecilia latipinna</i>	30.5	<i>Oreochromis aureus</i>	0.04
<i>Palaemonetes</i> spp.	23.1	<i>Tilapia</i> spp.	0.04
<i>Lucania parva</i>	20.6	<i>Leiostomus xanthurus</i> ^a	0.04
<i>Cyprinodon variegatus</i>	11.1	<i>Belonesox belizanus</i>	0.03
<i>Anchoa mitchilli</i>	9.8	<i>Cichlasoma urophthalmus</i>	0.03
<i>Gambusia holbrooki</i>	9.1	<i>Dorosoma petenense</i>	0.03
<i>Menidia</i> spp.	8.3	<i>Gobiosoma bosc</i>	0.03
<i>Fundulus grandis</i>	6.0	<i>Achirus lineatus</i>	0.03
<i>Floridichthys carpio</i>	3.1	<i>Cichlasoma</i> spp.	0.02
<i>Eucinostomus</i> spp.	1.3	<i>Strongylura</i> spp.	0.02
<i>Adinia xenica</i>	1.1	<i>Strongylura notata</i>	0.02
<i>Microgobius gulosus</i>	1.1	<i>Mugil gyrans</i> ^a	0.02
<i>Fundulus similis</i>	0.9	<i>Anchoa</i> spp.	0.01
<i>Sarotherodon melanothron</i>	0.6	<i>Oligoplites saurus</i>	0.01
<i>Fundulus confluentus</i>	0.5	<i>Pogonias cromis</i> ^a	0.01
<i>Mugil cephalus</i> ^a	0.4	<i>Bathygobius soporator</i>	0.01
<i>Eucinostomus harengulus</i>	0.3	<i>Ctenogobius smaragdus</i>	0.01
<i>Archosargus probatocephalus</i> ^a	0.3	<i>Cynoscion nebulosus</i> ^a	0.01
<i>Lagodon rhomboides</i>	0.3	<i>Lophogobius cyprinoides</i>	0.01
<i>Callinectes sapidus</i> ^a	0.3	<i>Cynoscion arenarius</i> ^a	0.01
<i>Gobiosoma</i> spp.	0.3	Loricariidae	0.01
<i>Centropomus undecimalis</i> ^a	0.2	<i>Lucania goodei</i>	0.01
<i>Eugerres plumieri</i> ^a	0.2	<i>Micropterus salmoides</i> ^a	0.01
<i>Farfantepenaeus duorarum</i> ^a	0.1	<i>Chaetodipterus faber</i>	<0.01
<i>Trinectes maculatus</i>	0.1	<i>Chasmodes sabburrae</i>	<0.01
<i>Cichlid</i> spp.	0.09	<i>Cichlasoma bimaculatum</i>	<0.01
<i>Elops saurus</i> ^a	0.08	<i>Cichlasoma octofasciatum</i>	<0.01
<i>Eucinostomus gula</i>	0.07	<i>Lepomis macrochirus</i> ^a	<0.01
<i>Brevoortia</i> spp.	0.07	<i>Lutjanus griseus</i> ^a	<0.01
<i>Opsanus beta</i>	0.06	<i>Mugil curema</i> ^a	<0.01
<i>Fundulus</i> spp.	0.04	<i>Mugil</i> spp. ^a	<0.01
<i>Heterandria formosa</i>	0.04	<i>Sciaenops ocellatus</i> ^a	<0.01

Densities are reported as mean nekton 10 m⁻²

^a Economic species

characterized shoreline habitat by estimating percent cover of physical structure (e.g., oyster, seawall, mangrove prop roots), shoreline vegetation (e.g., mangrove, emergent grass), and "altered" shoreline (i.e., seawall, rip-rap, terrestrial lawn grasses, invasive vegetation).

Metrics of Nekton Performance

To evaluate the quality of tidal tributaries as habitat for nekton, we examined 11 metrics that characterized various aspects of nekton performance such as abundance, community structure, body condition and reproduction. Abundance-based metrics included: (1) total nekton density; (2) taxon-specific density of common taxa; (3) species richness; (4) percent composition of economically important species (i.e., commercial or recreational fishery species); (5) proportion of exotic taxa (i.e., non-native species); and (6) community similarity to the average community defined by the three reference sites. We also estimated body condition for nine of the most common nekton species using: (7) length–weight relationships derived from analysis of covariance (ANCOVA) that compared body mass among tributaries (described below) and (8) lipid energy reserves for sailfin mollies (*Poecilia latipinna*), which were quantified as dry-weight standardized triacylglycerols (TAG) using thin-layer chromatography with flame-ionization detection methods described by Litvin et al. (2011). Finally, we described reproduction for up to 20 gravid *P. latipinna* and ten ovigerous palaemonid grass shrimp (*Palaemonetes* spp.) per sampling event for each tributary. Reproductive metrics for both species included: (9) fecundity and, for *P. latipinna*: (10) offspring size (mg), and (11) reproductive allotment, which we defined as the proportion of total maternal mass represented by embryos. Details of the reproductive methods for *P. latipinna* are provided by Krebs and Bell (2012).

Statistical Analysis

We compared body condition for nine numerically dominant nekton taxa using the GLM procedure in SAS to perform ANCOVA (SAS Institute, Inc. 2005). Using the weighted least-square approach described by Vila-Gispert and Moreno-Amich (2001), we tested for differences in length-standardized mean body mass among land-use classes and tributaries nested within land-use class. We used the following model statement for these and subsequent ANCOVAs:

$$\ln Y_i = \text{LU} + \text{Trib}(\text{LU}) + \text{Time} + \ln \text{Size} + \text{LU} * \ln \text{Size},$$

where $\ln Y_i$ is the natural log transformed body mass or reproductive metric for species i , LU is the land-use class, Trib (LU) is the tidal tributary nested within land-use class, Time is the sample period in which fish samples were

collected, $\ln \text{Size}$ is the natural log transformed standard length or body mass as a covariate.

We natural log transformed both the dependent variable (body mass) and the covariate (body length) prior to analysis and tested for homogeneity of slopes by including a treatment-by-covariate interaction effect. When slopes were heterogeneous, we tested body mass at the length of reproductive maturity, which was determined by examination of body size and reproductive status and by using literature values of size-at-maturity (Hildebrand and Schroeder 1928; Middaugh and Hemmer 1992; Nordlie 2000; Wallace and Waters 2004). The range of body sizes for each species spanned the range from early juvenile through reproductive maturity. When there were significant differences in body condition among land-use classes, we performed multiple comparisons, which were adjusted using the studentized maximum modulus (PDIFF option with ADJUST = SMM in SAS). For each species, a minimum sample size of 20 individuals per tributary was used for condition analysis. We also used ANCOVA to compare energetic condition for juvenile *P. latipinna* among land-use classes with TAG content in milligrams as the dependent variable and SL as the covariate. We performed this ANCOVA on the rank transformed values of the dependent variable and covariate as described by Conover and Iman (1982) because the data did not meet the assumption of homogeneity of variance. Comparisons of TAG content between land-use classes were made at the grand mean rank SL by specifying the value of the grand mean rank in the LSMEANS statement.

To examine variation in reproductive traits for *P. latipinna* and *Palaemonetes* spp., we used three separate ANCOVAs to test for differences in fecundity, offspring size and reproductive allotment among land-use classes. *Palaemonetes* spp. from urban creeks was excluded from this analysis because of the extremely low densities of ovigerous females in this land-use class. To allow for comparison among individuals of different sizes and stages of embryo development, we standardized fecundity, offspring size and reproductive allotment using maternal mass and embryo stage as covariates. As described above for body condition, adjusted multiple comparisons were conducted when significant differences were observed among land-use classes. Back-transformed least-square (i.e., adjusted) means from the ANCOVA analyses for body condition and reproduction were plotted in the figures and used in the multivariate CCA described below. To assess the variation in nekton performance (i.e., body condition and reproduction) as a function of coastal development, we used simple linear regression to relate the adjusted means for each performance metric with the intensity of landscape development (LDI index) for each tributary.

We then analyzed the full set of nekton metrics to determine which aspects of nekton performance best reflected

variation in in-stream nekton habitat and land-use characteristics within the surrounding watershed. We examined the relation between nekton metrics and measures of nekton habitat using canonical correspondence analysis (CCA) conducted with the vegan package in R statistical software (Oksanen et al. 2010). Nineteen environmental variables were used to characterize nekton habitat in tidal tributaries (Table 1 in the companion paper by Krebs et al. 2013). Ten of these variables described in-stream habitat (i.e., structural features and water quality). The other nine variables described land use within the surrounding watershed (e.g., percent land-use cover, impervious surface), tributary length and basin size. Prior to CCA analysis, we performed correlations to identify redundancies in the environmental dataset. We minimized multicollinearity by removing variables that were correlated at a level ≥ 0.7 and by sequential removal of environmental variables with variance inflation factors (VIF) > 15 . The VIF is a measure of the amount of variance that can be explained by multicollinearity among variables in a multiple regression model. Environmental variables were $\log(x+1)$ transformed (Palmer 1993), except for percent-composition variables, which were arcsine-square root transformed prior to analysis. Using vegan's "anova.cca" function, we performed non-parametric Monte Carlo permutation tests to evaluate the statistical significance of each CCA axis as a function of its constraining habitat and land-use variables and to estimate the significance of each constraining variable. For significant axes, we determined the strength of the correlation with nekton metrics using vegan's species–environment function "spenvcor". When interpreting results, we excluded statistically non-significant variables.

Results

Characteristics of Tidal Tributaries

Six of the watershed and in-stream habitat variables used to characterize tidal tributaries were highly correlated (i.e., positively) with the extent of impervious surface in the 100-m buffer along tributary shorelines. More specifically, tributaries with high imperviousness in the buffer were typically located in watersheds that had greater percentages of urban lands ($r=0.94$) and watershed imperviousness ($r=0.83$), greater LDI ($r=0.91$), more altered shoreline ($r=0.86$), less undeveloped lands in the buffer ($r=-0.84$) and lower mean salinity ($r=-0.79$) than tributaries with lower buffer imperviousness. In contrast, tributaries characterized by low buffer imperviousness (i.e., red mangroves as the dominant landscape feature) were located in watersheds with a high percentage of undeveloped lands ($r=0.42$) and low LDI ($r=-0.65$). These tributaries usually had more oysters along the shoreline ($r=0.62$), higher average salinities ($r=0.80$) and

dissolved oxygen (DO) concentrations ($r=0.66$) and fewer hypoxic events ($r=-0.41$) than tributaries with high buffer imperviousness.

Common Nekton

The nekton community in these tidal tributaries was largely dominated by nine taxa (Table 1), which represented 86 % of all nekton collected. Four of these taxa: sailfin molly (*P. latipinna*), grass shrimp (*Palaemonetes* spp.), rainwater killifish (*Lucania parva*), and sheepshead minnow (*Cyprinodon variegatus*) were collected in all tributaries and represented 65 % of all individuals. The other five taxa: eastern mosquitofish (*Gambusia holbrooki*), silverside (*Menidia* spp.), gulf killifish (*Fundulus grandis*), goldspotted killifish (*Floridichthys carpio*), and diamond killifish (*Adinia xenica*) made up an additional 21 % (Krebs et al. 2013).

Body Condition of Common Nekton

Body condition was significantly better in urban creeks for three of nine common nekton species (*F. grandis*, *C. variegatus*, and *L. parva*) compared to undeveloped creeks (ANCOVA, Table 2, Fig. 1); these species were 42–86 % larger by mass in urban creeks. In contrast, *Palaemonetes* spp. was in significantly poorer condition (13 % smaller) in urban creeks compared to undeveloped creeks. Condition for the remaining five taxa did not differ between undeveloped and urban creeks as most taxa had < 7 % difference in body mass between land-use classes. With the exception of *P. latipinna*, which displayed significantly poorer condition (30 % smaller) in industrial creeks, body condition did not differ for common nekton between undeveloped and industrial creeks. Similarly, there was no difference in condition for nekton in undeveloped creeks and mosquito ditches, except for *P. latipinna* (31 % larger by mass in undeveloped creeks), *Menidia* spp. (98 % larger by mass in mosquito ditches), and *Palaemonetes* spp. (5 % smaller by mass in mosquito ditches). No significant differences in body condition were found among land-use classes for *F. similis*, *G. holbrooki*, and *A. xenica*, which differed by only 3–7 % in body mass among tributaries. Finally, energetic condition for juvenile *P. latipinna* was significantly different among land-use classes (ANCOVA, Table 2, Fig. 2) and was highest in urban creeks. Compared to undeveloped creeks, energetic condition was significantly higher in urban creeks, not significantly different than industrial creeks ($p=0.99$), and significantly less than mosquito ditches ($p=0.026$).

Body condition was not significantly related to LDI for eight of the nine taxa examined (all $r^2 < 0.05$, $p=0.07$ – 1.00). For *L. parva*, however, condition decreased significantly with increasing intensity of landscape development ($r^2=0.15$, $p=0.005$).

Table 2 Results of analysis of covariance (ANCOVA) comparing body condition of common nekton from mangrove tidal tributaries in watersheds classified as undeveloped, industrial, and urban and mosquito-ditch land-use classes

Taxon	ANCOVA			Undeveloped vs.		
	SL (mm)	<i>F</i>	<i>p</i>	Industrial	Mosquito	Urban
Adjusted mean body mass						
<i>Fundulus grandis</i>	50 ^a	13.10	<0.0001	0.55	0.75	<0.0001**
<i>Cyprinodon variegatus</i>	30 ^b	8.30	<0.0001	0.32	0.88	0.018*
<i>Lucania parva</i>	30 ^c	4.62	0.0032	1.00	0.19	0.018*
<i>Poecilia latipinna</i>	30 ^d	7.42	<0.0001	0.009*	0.019*	1.00
<i>Menidia</i> spp.	50 ^e	7.38	<0.0001	0.62	0.020*	0.52
<i>Palaemonetes</i> grass shrimp	7.5 ^a	5.30	0.0012	0.35	0.016*	0.0099*
<i>Fundulus similis</i>	—	1.89	0.13	—	—	—
<i>Gambusia holbrooki</i>	—	1.37	0.25	—	—	—
<i>Adinia xenica</i>	—	0.73	0.48	—	—	—
Adjusted mean TAG content						
<i>Poecilia latipinna</i>	—	13.50	<0.0001	0.99	0.026*	<0.0001**

Condition was estimated as body mass at reproductive maturity and triacylglycerol (TAG) with standard length as the covariate. The *p* values are shown for multiple comparisons of each land-use class relative to undeveloped tributaries. SL for *Palaemonetes* spp. was measured as post-orbital head length. Significance reported as: - ns, * <0.05 , ** <0.005

^a Size-at-maturity was determined from Wallace and Waters (2004)

^b Size-at-maturity was determined from Nordlie (2000)

^c Size-at-maturity was determined from Hildebrand and Schroeder (1928)

^d Size-at-maturity was determined from Krebs (unpublished data)

^e Size-at-maturity was determined from Middaugh and Hemmer (1992)

Reproductive Traits

Some performance measures based on reproduction differed among land-use classes for the two taxa examined. For *P. latipinna* (31–70 mm SL), fecundity, which ranged from 26 to 42 offspring across tributaries, differed among land-use

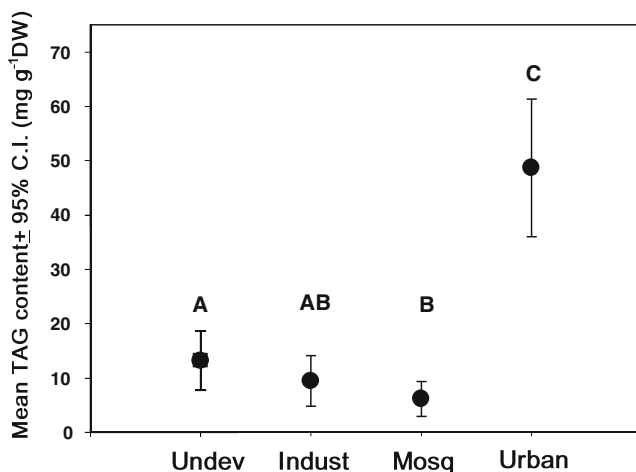


Fig. 2 Energetic condition for juvenile *P. latipinna* from tidal tributaries located in undeveloped (Undev; $n=58$), industrial (Indust; $n=51$), and urban (Urban; $n=53$) watersheds and mosquito ditches (Mosq; $n=32$)

classes (ANCOVA, $F=10.03$, $p\leq 0.0001$). Compared to fecundity in undeveloped creeks, fecundity was similar for *P. latipinna* in industrial creeks ($p=0.31$), lower in urban creeks ($p=0.063$), and significantly lower in mosquito ditches ($p=0.015$; Fig. 3a). Offspring size for *P. latipinna* ranged from 18.5 to 28.1 mg across tributaries and was significantly different among land-use classes (ANCOVA, $F=21.53$, $p<0.0001$, Fig. 3b). Specifically, significantly larger offspring were observed in urban creeks ($p<0.0001$) and mosquito ditches ($p<0.0001$) than in undeveloped creeks. Offspring size did not differ between undeveloped and industrial creeks ($p=1.00$). Mean reproductive allotment for *P. latipinna* ranged from 14.7 % to 21.5 % of maternal body mass across tributaries and did not differ among land-use classes (ANCOVA, $F=2.03$, $p=0.11$, Fig. 3c). Fecundity for *Palaemonetes* spp. differed among land-use classes (ANCOVA, $F=3.46$, $p=0.033$), but relative to undeveloped creeks (197 oocytes), there was no difference for industrial creeks (190 oocytes, $p=0.53$) or mosquito ditches (204 oocytes, $p=0.45$); very few ovigerous *Palaemonetes* spp. were collected in urban creeks. Within the same watershed, adjusted mean fecundity of *Palaemonetes* spp. was nearly identical ($p=1.00$) between the undeveloped tidal creek (MB, 204 oocytes) and the mosquito ditches (MM, 199 oocytes). Reproductive traits were not closely associated with

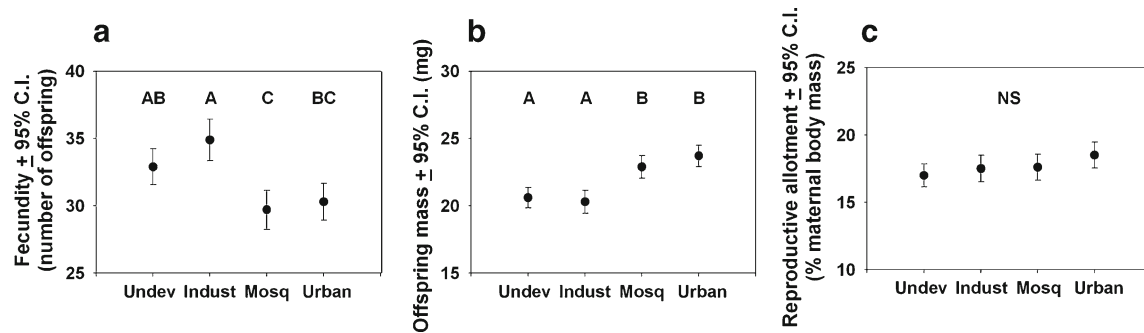


Fig. 3 Reproductive metrics for *P. latipinna* from tidal tributaries located in undeveloped (*Undev*; $n=178$), industrial (*Indust*; $n=152$), and urban (*Urban*; $n=157$) watersheds and mosquito ditches (*Mosq*;

$n=116$). Reproduction was estimated as the adjusted mean **a** fecundity, **b** offspring size, and **c** reproductive allotment using ANCOVA

LDI for fecundity ($r^2=0.02$, $p=0.66$), offspring size ($r^2=0.004$, $p=0.86$) or reproductive allotment ($r^2=0.03$, $p=0.64$) for *P. latipinna*. Fecundity for *Palaemonetes* spp. decreased with increasing LDI, but this trend was not statistically significant ($r^2=0.47$, $p=0.13$).

Canonical Correspondence Analysis

Six of 19 environmental variables were removed prior to CCA analysis (Table 1 in the companion paper by Krebs et al. 2013) due to their high correlation with buffer imperviousness and two additional variables, mean DO and percent oyster along the shoreline, were removed from the CCA model following

the initial analysis because of high VIFs indicating multicollinearity. Ordination of nekton metrics with the remaining 11 variables explained 54 % of the total variation in the weighted averages of nekton metrics among tributaries. Approximately 35 % of the total variation was accounted for by the first two axes, CC1 and CC2 (Table 3). Each of the environmental variables had higher biplot scores on the first axis (>0.40) compared to the second axis. Environmental variables describing in-stream nekton habitat were better predictors of variation in nekton performance as five of six habitat variables were statistically significant in terms of the null distribution (Monte Carlo, $p<0.05$; Table 3), in contrast to only one of the five watershed variables. Frequency of

Table 3 Summary of results from canonical correspondence analysis for 22 nekton metrics of habitat quality in relation to in-stream habitat and watershed characteristics

		Axis 1 (CC1)	Axis 2 (CC2)
Summary statistics			
Eigenvalue		0.13	0.064
Statistical significance of CC axes		0.005	0.005
Variance in species data			
% variance explained		0.23	0.12
Cumulative % variance explained		0.23	0.35
Weighted correlation for species and habitat		0.94	0.73
Variables		Biplot scores	
Watershed			
	<i>p</i>		
Basin size (BSNSZ)	0.14	−0.38	−0.15
Tributary length (CRKLEN)	0.26	−0.41	−0.05
Impervious surface (IMPBUF)	0.005	0.85	−0.20
Industrial (IND)	0.1	−0.36	0.18
Agricultural (AG)	0.09	−0.22	−0.37
Fish habitat			
Red mangrove (RM)	0.015	− 0.69	0.25
White mangrove (WM)	0.005	− 0.69	− 0.45
Mean water temperature (TEMP)	0.33	−0.003	0.29
Instantaneous salinity (SAL)	0.005	− 0.49	−0.004
Salinity variability (SAL_SD)	0.04	−0.02	−0.08
Frequency of hypoxic events (DO_HYPFRQ)	0.01	0.78	−0.19

Variable abbreviations correspond to those used in the CCA plots (Fig. 4)

p values indicate significance of watershed and fish habitat variables from the Monte Carlo permutation test

Statistically significant ($p<0.05$) biplot scores that were >0.40 were considered important in defining an axis and are indicated in bold

hypoxia, instantaneous salinity, salinity variability, percentage of red and white mangrove and percent buffer imperviousness best explained the observed variation in nekton metrics among tributaries. The remaining variables, including water temperature, tributary length, basin size, industrial development in the buffer, and agricultural development in the buffer were not statistically significant at $\alpha=0.05$, explained little variation in the nekton metrics, and are not considered further. Five of the 12 abundance-based metrics of nekton performance scored highest on CC1 (Table 4) reflecting the variation in species-level density and community structure between urban and non-urban tributaries. Body condition for many of the common nekton (e.g., Con_Plat), species-level densities for *L. parva* (Lpar) and *Menidia* silversides (Menspp), and the proportion of exotic/non-native taxa (Exotic) scored higher on CC2.

Urban creeks were clearly distinguished from undeveloped and industrial creeks and mosquito ditches (i.e., non-urban tributaries) along the first axis (CC1) ($r=0.94$, Table 3, Fig. 4a). The distinction between urban creeks (PM, WC,

and TC) and non-urban tributaries was based on greater buffer imperviousness, higher frequency of hypoxia, lower instantaneous salinities (<20 psu in 83 % of samples) and considerably fewer mangroves along the shoreline in urban creeks (Fig. 4a, Table 1 in Krebs et al. 2013). Mangrove shorelines in urban creeks had largely been replaced by seawalls and terrestrial grasses. High densities of *G. holbrooki* (Ghol) and *P. latipinna* (Plat) and low densities of *Palaemonetes* grass shrimp (Palspp), *Menidia* silversides (Menspp), *F. grandis* (Fgra) and economically important taxa (Economic) were associated with urban creeks along CC1 (Fig. 4b, Table 4). In addition, *P. latipinna* in urban creeks had greater amounts of stored energy (TAG_Plat) than *P. latipinna* from non-urban tributaries. At the opposite end of this gradient were the non-urban tributaries, which had more mangroves, less impervious surface, lower frequency of hypoxia and higher salinities.

Non-urban tributaries were further separated along the second axis (CC2) based on the type of mangrove shoreline (Fig. 4a, Table 3). Three of eight non-urban tributaries (AC,

Table 4 Summary of metric scores from canonical correspondence analysis for nekton metrics of habitat quality in relation to in-stream habitat and watershed characteristics

Nekton metrics	Abbreviation	Axis 1 (CC1)	Axis 2 (CC2)
Abundance			
Total nekton density	Nekton	0.03	0.09
Density of			
<i>Cyprinodon variegatus</i>	Cvar	0.07	0.22
<i>Fundulus grandis</i>	Fgra	−0.36	−0.29
<i>Gambusia holbrooki</i>	Ghol	1.08	−0.21
<i>Lucania parva</i>	Lpar	−0.08	0.49
<i>Menidia</i> spp.	Menspp	−0.42	−0.60
<i>Palaemonetes</i> grass shrimp	Palspp	−0.64	0.31
<i>Poecilia latipinna</i>	Plat	0.57	0.11
Number of species	Rich	−0.21	−0.19
Percent of taxa that are economically important	Economic	−0.40	−0.13
Proportion of taxa that are exotic/non-native	Exotic	−0.03	−0.57
Community similarity with reference community	Comm_sim	−0.22	−0.25
Body condition			
Adjusted mean body mass for			
<i>C. variegatus</i>	Con_Cvar	−0.16	−0.40
<i>F. grandis</i>	Con_Fgra	−0.15	−0.42
<i>L. parva</i>	Con_Lpar	−0.15	−0.40
<i>Menidia</i> spp.	Con_Men	−0.13	−0.40
<i>Palaemonetes</i> grass shrimp	Con_Pal	−0.16	−0.41
<i>P. latipinna</i>	Con_Plat	−0.17	−0.42
Lipid energy reserves for <i>P. latipinna</i>	TAG_Plat	0.77	−0.35
Reproduction			
Number of offspring	N off_Plat	−0.20	−0.48
Offspring size	Sz off_Plat	0.05	−0.33
Reproductive allotment	RA_Plat	−0.11	−0.41

Metric abbreviations correspond to those used in the CCA plots (Fig. 4)

Metric scores (in bold) were considered to be responsive to the environmental gradient and were included in our interpretation of the axis

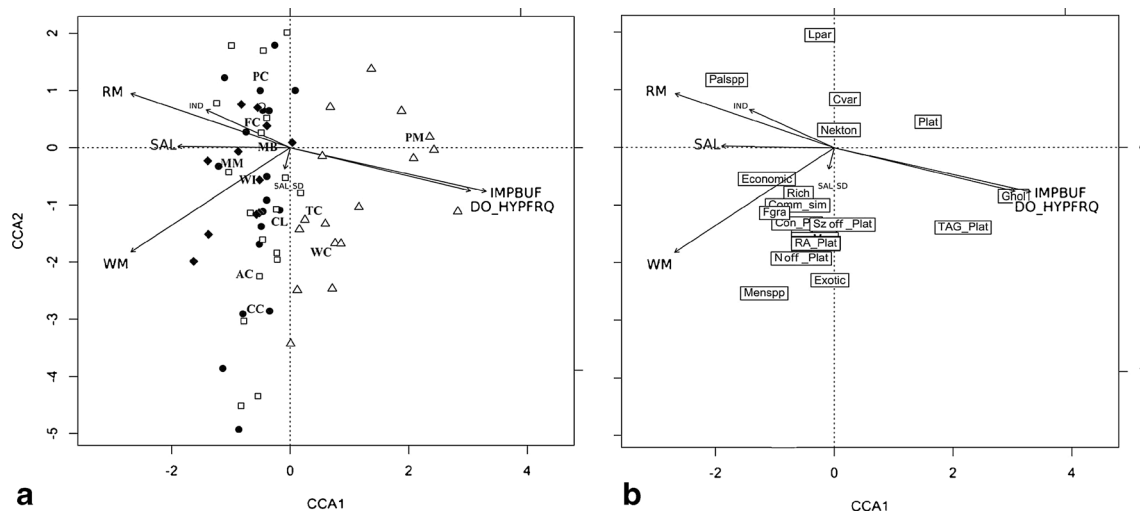


Fig. 4 Canonical correspondence analysis relating in-stream habitat and land-use variables with metrics of nekton-habitat quality in mangrove tidal tributaries. Environmental variables with coefficients >0.40 are displayed in a larger font than less explanatory variables. Gradients are plotted as vectors with **a** tidal tributaries as symbols and with **b** nekton metrics as labels within boxes. Each point in panel **a** represents a sampling event with six events at each tributary. The average location

of each tributary is indicated by its two-letter abbreviation, which corresponds to Fig. 1 in the companion paper (Krebs et al. 2013). Land-use classes are plotted by symbol for undeveloped (circles), industrial (squares) and urban (triangles) tributaries and for mosquito ditches (diamonds). Labels for body condition for six nekton taxa (e.g., Con_Plat) in panel **b** were plotted in the same location and are overlapping

CC, CL) had a greater percentage of white mangroves than the other tributaries, which were largely dominated by red mangroves (Table 1). Many of the white-mangrove tributaries had a greater than average proportion of exotic taxa in samples (Exotic) and greater than average densities of *Menidia* silversides (Menspp), lower densities of several common nekton including *L. parva* (Lpar), *C. variegatus* (Cvar) and *P. latipinna* (Plat) and high fecundity for *P. latipinna* (Noff_Plat, Table 4). At the opposite end of the gradient was a group of tributaries including FC, PC, MB and to a lesser extent the mosquito ditches at WI and MM, all of which had shorelines dominated by red mangroves with relatively few white mangroves (Fig. 4a, Table 1 in Krebs et al. 2013). Higher densities of *L. parva* (Lpar) and *Palaemonetes* spp. (Palspp) were found in these tributaries relative to those characterized by white mangrove shorelines (Table 4).

Several performance metrics were not well associated with any of the environmental gradients (i.e., based on the centralized position of these metrics on the ordination) (Table 4, Fig. 4b). Total nekton density (Nekton), in particular, was located at the plot origin indicating that it was not strongly related to any of the axes, in contrast to species-specific densities, which were more sensitive to variation in environmental conditions among tributaries and better indicators of such variation (Table 4, Fig. 4b). Species richness (Rich), community similarity (Comm_sim) and body condition of six taxa of common nekton (e.g., Con_Plat) were also less sensitive to variation in land use and in-stream habitat variables, based on their low scores, than were the other metrics discussed above.

Discussion

Our analysis of nekton performance in mangrove tidal tributaries revealed that the quality of these habitats was largely correlated with urbanization immediately adjacent to each tributary. Variation among tributaries was described through multivariate analysis as a gradient of urbanization reflecting the intensity of coastal development in the adjacent watershed (i.e., impervious surface, LDI index) and its link to nekton habitat within the tributaries (i.e., through differences in salinity and DO). Variation was further explained at a more localized scale as a function of shoreline habitat within the tributary and salinity regime, which was likely related to freshwater inputs, distance from the estuary and tidal connectivity. Collectively, factors characteristic of urbanized lands, specifically high impervious surface, altered shorelines, low mean salinities and frequent hypoxia relative to less urban watersheds, best explained the observed variation in many of the nekton metrics among tidal tributaries.

Nekton performance most prominently reflected contrasts among tidal tributaries with divergent watershed and in-stream habitat characteristics through: (1) variation in species-level densities for common taxa, particularly poeciliids, grass shrimp, and exotic species, (2) better energetic condition of *P. latipinna* in urban tributaries relative to conspecifics from non-urban tributaries, and to some extent, (3) fecundity of *P. latipinna* and reproductive potential (i.e., density and fecundity) of *Palaemonetes* spp. Variation in species-level densities and taxonomic composition among

tributaries resulted in the differences in nekton-community structure that we reported previously (Krebs et al. 2013). Total nekton density, however, was a poor indicator of habitat quality as it showed little association with land use and in-stream habitat as demonstrated by the CCA and by trends in abundance reported by Krebs et al. (2013). In general, urban creeks supported a less diverse nekton community composed of fewer taxa, low abundance or absence of palaemonid grass shrimp (which were in poor condition and not reproductively active), and lower densities of economically important taxa than observed in non-urban tributaries. Interestingly, several nekton taxa were in better condition in urban creeks. Moreover, *P. latipinna*, a numerically dominant species and ecologically important link between primary production and upper trophic levels (Stevens et al. 2006) had higher energy reserves (i.e., TAG lipids) in urban tributaries compared to non-urban tributaries. These findings suggest that nekton metrics representing community structure, body condition and reproduction may be more meaningful indicators of habitat quality for tidal tributaries than traditionally applied metrics of total abundance.

Body Condition and Reproduction as Metrics of Habitat Quality in Tidal Tributaries

We observed few differences in body condition for common nekton as a function of land use when we compared developed or man-made tributaries to undeveloped tributaries. Body condition was similar for six of nine common nekton taxa from tidal tributaries in undeveloped and industrial watersheds and mosquito ditches. We rejected our null hypothesis that body condition would be similar among tributaries for *F. grandis*, *C. variegatus*, and *L. parva* — three of the four most common nekton taxa in mangrove tidal tributaries — based on the results of the ANCOVA comparisons of body condition among land-use classes (Table 2; Fig. 1) that showed these taxa were in better condition in urban compared to undeveloped tributaries. This trend for better condition in urban tributaries was further supported by results from the regression analysis of condition and LDI for *L. parva*. Only *Palaemonetes* spp. was in significantly poorer condition in urban versus other creek types, based upon ANCOVA results. Greenwood et al. (2008b) reported significantly poorer condition for *A. mitchilli* (8–16 % smaller by mass) and poorer, but not statistically significant, condition for *C. variegatus* (3–7 %) and *L. parva* (2 %) in the most urbanized tributaries, although they found no difference for six other nekton taxa, including *P. latipinna*, as a function of LDI in the surrounding watershed for Tampa Bay tidal tributaries. For those nekton taxa that exhibited significant differences in condition among land-use classes, we observed differences of greater than 30 % by mass. In comparison, Piazza and LaPeyre (2010) observed only a 9 % difference in length–

weight condition for mosquitofish that had been starved for 10 days compared to mosquitofish fed to satiation over the same time period. Mediterranean barbel (*Barbel meridionalis*) from freshwater streams with dense riparian vegetation and high DO concentrations ($>11 \text{ mg l}^{-1}$) were 6–16 % larger by mass than individuals from streams with sparse vegetation and low DO ($<6 \text{ mg l}^{-1}$; Vila-Gispert and Moreno-Amich 2001). Both of these studies provide context for our results by demonstrating the expected magnitude of differences in condition when small-bodied fishes are exposed to factors such as low food or stressful physicochemical conditions, which can be attributed to poor habitat quality.

Variation in length–weight condition of common nekton was not well explained by any of the habitat variables in the multivariate analysis (Table 4). These results suggest that species-specific habitat requirements (beyond those included in our study) may be required to explain contrasting patterns in body condition among tributaries and land-use classes and may prevent generalization across taxa within the nekton community. Alternatively, length–weight condition may simply not be reflective of variation in habitat quality for some nekton in tidal tributaries.

In contrast to the equivocal results for length–weight condition, we observed that juvenile *P. latipinna* from urban creeks had significantly greater stored energy (TAG content) than individuals from undeveloped creeks. We hypothesize that the lower salinities observed in urban creeks resulted in a high-quality food source (i.e., TAG-rich benthic microalgae) for *P. latipinna*. In contrast, higher salinities in undeveloped creeks elicited a growth response by benthic microalgae to more favorable growing conditions, which resulted in less TAG storage as the energy was used for growth (de Castro Araujo and Garcia 2005; Hu et al. 2008). The fact that juvenile *P. latipinna* had more stored energy in urban versus undeveloped creeks suggests a link between energetic condition and land use that was not observed based on length–weight condition. Similar results were reported by Weinstein et al. (2009) who observed no difference in length–weight condition for mummichogs (*F. heteroclitus*), but found significantly greater storage lipids for fish from *Spartina* marshes compared to those from marshes dominated by the invasive reed, *Phragmites australis*. Given the contrasting conclusions derived from length–weight versus energetic condition for these two species, caution is advised when using length–weight condition to assess habitat quality. Energetic condition is more biologically meaningful than length–weight condition as it can be directly related to survival (i.e., stored energy), while the underlying contribution of water, lipid, and protein mass to body mass is unknown when length–weight alone is measured.

The observed trend towards reduced reproductive output for both *P. latipinna* (i.e., fewer offspring) and *Palaemonetes* spp. (i.e., very low densities and fewer ovigerous females) in

urban creeks is aligned with findings from previous studies in other locations. Specifically, among these findings are: decreased size and age-at-maturity (Fraker et al. 2002), reduced breeding activity and production of fewer eggs (Weber and Bannerman 2004), lower spawning success (Limburg and Schmidt 1990) or increased pre-spawn mortality (Bilby and Mollet 2008) for fishes from urban tributaries relative to non-urban tributaries. However, considerable variation in metrics of reproductive performance among tributaries in our study obscured any clear relationships resulting from differences in land use. Reproductive tradeoffs exhibited by *P. latipinna* (e.g., trading high fecundity for fewer, larger offspring) confounded the relation between habitat quality and reproductive metrics for this species. That is, low fecundity might be expected to indicate poor quality habitat, but was offset by increased offspring size to compensate, and was thus not useful for assessing habitat quality. For reproductive allotment, the absence of a clear relationship with land use for *P. latipinna* suggests that localized ecological factors within tributaries, and not measured in the present study, (e.g., direct biotic effects of predation risk or food availability/quality; Krebs and Bell 2012) may play a greater role than land use in determining reproductive strategy for *P. latipinna*. However, the consistently low reproductive success (i.e., few reproductive individuals) and lower fecundity in tributaries with higher LDI for *Palaemonetes* grass shrimp in urban tributaries suggests poor habitat quality as a result (direct or indirect) of urbanization. Given the confounding effect of reproductive tradeoffs on the use of individual performance metrics such as fecundity and offspring size, it may be worth evaluating habitat quality in terms of metrics that describe population-level reproductive output such as the percentage of reproductively active individuals in a tributary.

Linking Impervious Surface and Habitat Quality in Tidal Tributaries

Percent impervious surface within the 100-m shoreline buffer was identified as the best predictor of variation in nekton metrics (i.e., biplot score=0.85) in our multivariate analysis (Table 3). Impervious surface has often been cited as a significant predictor of urbanization-related impacts to aquatic habitats through its physical connection between watershed processes and in-stream pollutants and its correlation with physicochemical and biological variation in aquatic communities (Paul and Meyer 2001; Wang et al. 2001; Holland et al. 2004; Roy et al. 2005; Wenger et al. 2008). As with previous studies on the effects of urbanization in freshwater streams, our results suggest a link between impervious surface and nekton habitat in tidal tributaries as reflected by variation in nekton community structure, lower densities of palaemonid grass shrimp, *Menidia* silversides and

gulf killifish and higher densities of poeciliid fishes, better energetic condition of *P. latipinna* and low reproductive potential of palaemonid grass shrimp (Fig. 4). Thus, efforts to improve habitat quality would benefit from actions to reduce or buffer the connection between impervious surface and tidal tributaries.

The link between imperviousness and degradation of aquatic communities appears to occur at a similar threshold for freshwater and tidal tributaries beyond which biological communities begin to show adverse effects (e.g., Klein 1979; Wang et al. 2000; Holland et al. 2004). In our tidal tributaries, percent imperviousness ranged from 6 % to 41 % of the watershed and was <20 % for each of the non-urban sites except Mobbly Bayou which was only slightly greater than 20 % (Table 1 in Krebs et al. 2013). The three urban watersheds were considerably more impervious and ranged from 30 % to 41 % suggesting a threshold between 20 % and 30 % imperviousness beyond which the nekton response to development within the watershed becomes apparent. In freshwater tributaries, where the majority of studies have been focused, a lower threshold of 5–10 % impervious surface has been related to a drop in species richness (Wang et al. 2000, 2001), lower probability of occurrence for some species (Wenger et al. 2008) and a loss of intolerant species (Wang et al. 2000). A slightly higher threshold of 10–20 % was reported in association with a decline in fish diversity in Maryland freshwater streams (Klein 1979). However, our results are better aligned with those of Holland et al. (2004) who observed declining densities of penaeid shrimp and spot (*Leiostomus xanthurus*) in South Carolina tidal creeks as imperviousness approached 20 %.

Altered Shoreline Habitat

Although impervious surface is often invoked to explain variation in stream-fish communities, such variation has also been attributed to the more localized losses of natural habitat along altered shorelines (Sanger et al. 2004), often following the removal of shoreline vegetation (Mwandya et al. 2009) or the construction of seawalls, docks and rip-rap (Sanger et al. 2004; Bilkovic and Roggero 2008). Shoreline alteration in these studies has been associated with statistically significant reductions in nekton abundance, richness and community structure in many of these cases. We observed the same type of habitat alteration for urban tributaries, in which seawalls or artificially steep banks created by dredging were the characteristic shoreline features, in contrast to gently sloping, mangrove-vegetated intertidal habitat observed in non-urban tributaries. Among the eight non-urban tributaries in our study, shorelines were either dominated by red mangrove, white mangrove or both (Table 1 in Krebs et al. 2013). In tidal tributaries with white mangroves as the dominant or co-dominant shoreline feature (CC, TC, AC, CL), we observed

low densities of many, otherwise common, nekton species. We also observed higher fecundity for *P. latipinna* in these tributaries (Krebs and Bell 2012). Low densities and high fecundity have been associated with higher predation in these (Krebs and Bell 2012) and other systems (Werner and Peacor 2003). Numerous species of nekton utilize red mangrove shorelines (e.g., Ellis and Bell 2008), perhaps related to the structural complexity of prop roots unique to red mangroves (Thayer et al. 1987) and enhanced refuge effects. White mangroves, which lack prop roots, may provide less complex habitat suggesting that the relative refuge value of white mangroves may be inferior to that provided by red mangroves. The absence of structural complexity provided by natural shoreline habitat may partially account for the apparently poor habitat quality for grass shrimp in urban tributaries. Porter et al. (1997) reported significantly and consistently higher densities of *Palaemonetes* grass shrimp along *Spartina* shorelines in both undeveloped and urbanized tidal creeks compared to altered shorelines within the urban creek. Our results, along with previous studies, suggest that differences in shoreline habitat are a defining characteristic of habitat quality in tidal tributaries.

Explaining Variation in Nekton Metrics Among Non-urban Tidal Tributaries

We observed considerable variation in metrics of nekton performance among eight non-urban tributaries as illustrated by the range of metric scores along CC2 in the multivariate analysis (Fig. 4b). Much of this variation appeared to be related to the undeveloped Cockroach Creek, which, despite very little physical modification to the creek and the surrounding mangrove wetlands, was located in a drainage basin characterized by greater agricultural land uses than the other ten tributaries (Table 1 in Krebs et al. 2013). Observations of hypoxia (Table 1 in Krebs et al. 2013; Greenwood et al. 2008b), low densities of total nekton, few decapod crustaceans, low species richness (Krebs et al. 2013), and the occurrence of a fish kill there in 2007 (M.F.D. Greenwood, personal communication) suggest that watershed influences may have affected habitat quality in this tidal creek and distinguished it from the other two undeveloped tidal creeks in the multivariate analysis. Industrial creeks, on the other hand, were generally more similar to undeveloped creeks in terms of nekton performance metrics than to creeks developed for urban land uses (Fig. 4b). Specifically, we observed no statistically significant differences between industrialized and undeveloped creeks in terms of reproductive metrics for *P. latipinna* and body condition for all but one of the common nekton taxa. A high percentage of natural land cover in the 100-m buffer, unaltered geomorphology and natural shoreline vegetation characterized these tributaries.

Allen et al. (2007) demonstrated the importance of channel geomorphology in determining patterns of nekton use in saltmarsh tidal creeks citing water depth, bank steepness and flow velocity as most highly correlated with inter-creek variation in species-level nekton densities. Krebs et al. (2007) reported a similar relationship between nekton-community structure and three types of naturally formed and man-made tidal tributaries that differed in channel geomorphology (i.e., tidal creeks, mosquito-control ditches and stormwater-drainage ditches). Both studies illustrate the importance of localized habitat features rather than landscape-scale features in determining the environmental characteristics and thus, the habitat quality of some tidal tributaries. Similarly, the relatively dense mangrove canopy over mosquito ditches compared to undeveloped tidal creeks in our study likely limited light penetration and thus light availability for benthic microalgae and resulted in lower primary production in mosquito ditches in terms of benthic chlorophyll *a* (Krebs unpublished data). This would have translated to poor-quality foraging habitat for benthic herbivores like *P. latipinna* and may explain the significantly lower energetic condition for juvenile *P. latipinna* in mosquito ditches compared to undeveloped tidal creeks (Fig. 2). While overall variation among tidal tributaries in our study can be largely explained by impervious surface beyond the shorelines of the tributary, variation in nekton performance among non-urban tributaries was more of a function of factors operating within and along the tributary shorelines, specifically differences in shoreline habitat (i.e., red vs. white mangroves) and mangrove canopy.

In the Tampa Bay watershed, more than two-thirds of the small tidal tributaries have experienced moderate to intense development (Krebs et al. 2013). The spatial extent of urban areas and impervious surface has tripled since 1990 and is predicted to increase from 27 % to 38 % by 2020 in this already heavily populated coastal watershed (Xian and Crane 2005; Xian et al. 2007). For the Tampa Bay estuary and other urbanizing areas, a clearer understanding of the relation between landscape development and the ecology of tidal tributaries, in the context of natural variability among systems, sets the stage for better-informed land-management decisions and more successful habitat conservation and restoration efforts. Metrics that emphasize biological traits relevant to population persistence should be more ecologically informative than abundance in assessing differences in environmental quality among habitats. The use of metrics such as individual growth rate, biochemical condition, reproduction and ultimately, contribution of individuals from specific tidal tributaries to reproductive adult populations should continue to be pursued (Beck et al. 2001; Shervette and Gelwick 2008; Weinstein et al. 2009).

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