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Comparison of fish and invertebrate assemblages among variably altered tidal creeks in a coastal landscape

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ABSTRACT: We sampled variably altered tidal creeks to determine community structure in a developing coastal (USA) landscape. Throw trapping collected smaller and juvenile nekton in the vegetated marsh while minnow trapping in unvegetated channels targeted relatively larger fishes. Non-metric multidimensional scaling ordinations were used to assess community structure. Environmental factors and species most rank-correlated with community dissimilarities in ordinations were determined through the nonparametric BIOENV analysis. We found differences in community composition among creeks that were largely consistent in 2 years. Juveniles of the dominant salt marsh fish *Fundulus heteroclitus* from throw trapping had a pattern opposite of amphipods and associated with creeks with marsh downstream while larger *F. heteroclitus* (from minnow trapping) associated with creeks with high percentages of marsh coverage and lower watershed imperviousness. A transient fish *Lagodon rhomboides* was associated with creeks with lower marsh percentages. Results indicate that loss of marsh, and breaks in marsh connectivity to areas downstream of tidal creeks, can lead to reduced abundances of a dominant resident marsh fish. In order to maintain production of marsh fishes, planners should prioritize the maintenance of intact salt marsh habitats and natural landforms.

KEY WORDS: Salt marsh · *Fundulus heteroclitus* · BIOENV · Coastal development

INTRODUCTION

Salt marshes provide ecosystem services such as contaminant filtration, nutrient sequestration, and buffering from storm surge (Odum 1970, Costanza et al. 1997, Portnoy 1999, Holland et al. 2004, Barbier et al. 2011). These biologically productive areas also provide vital habitat for resident nekton (Weinstein 1979, McIvor & Odum 1988, Kneib 1997, Teo & Able 2003, Bretsch & Allen 2006) and larger predators that forage in tidally flooded marshes (Minello et al. 2003, Rozas et al. 2007). Salt marshes are geographically positioned in coastal landscapes such that they link physical and chemical processes between upland areas and open estuaries (Holland et al. 2004, Sanger et al. 2015) as well as relay production to higher trophic levels in open estuaries (Teal 1962, Kneib 2000).

Anthropogenic impacts are known to impede the ability of estuaries to serve as nurseries for resident and transient fish species (Hinrichsen 1998). In the USA coastal zone, development is growing 300 to 600 % faster than the human population (Beach 2002) and over half of US salt marshes have been lost, mostly due to human disturbance (Kennish 2001). Human encroachment also threatens the connectivity of these habitats (Kennish 2001, Thrush et al. 2008, Lowe & Peterson 2014) and biological production along the US Atlantic and Gulf of Mexico coastlines (Dame et al. 2000, Seabrook 2012, Krebs et al.

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2014a,b, Lowe & Peterson 2014). Due to displacement from habitats and physiological stress (Sklar & Browder 1998), estuarine nekton assemblages tend to exhibit lower biomass and different community structure in environments that have experienced greater impact.

Among estuarine habitat types, tidal creeks may be particularly threatened by human development due to their proximity to uplands that they drain (Krebs et al. 2014b, Sanger et al. 2015). First-order tidal creeks are apt to show the strongest and most direct biological response to development because they are the geographically most immediate repositories of land-based contaminants (Sanger et al. 1999a,b, 2015, Lerberg et al. 2000, Van Dolah et al. 2008). Specific anthropogenic impacts on tidal creeks include watershed development and imperviousness (Holland et al. 2004, Bilkovic & Roggero 2008), shoreline hardening that eliminates shallow-water habitat (Porter et al. 1997, Hale et al. 2004, Bilkovic & Roggero 2008, Krebs et al. 2014a), greater salinity fluctuations due to freshwater pulses during rain events (Lerberg et al. 2000, Krebs et al. 2014a,b) and fragmentation of marsh habitat (Valentine-Rose et al. 2007, Eberhardt et al. 2011, Lowe & Peterson 2014). Because small tidal creeks receive runoff from neighboring terrestrial areas, they serve as sentinel systems by which to gauge cumulative anthropogenic impacts on estuaries (Holland et al. 2004, Sanger et al. 2015).

The relationship between specific, measurable anthropogenic alterations and metrics of nekton abundance remain poorly understood in tidal creeks (Partyka & Peterson 2008) and less studied than similar impacts on freshwater creeks (Krebs et al. 2014a,b). For example, a recent synthesis of urbanization impacts on aquatic ecosystems did not cite similar research into human impacts on saltwater creeks (Hughes et al. 2014). However, a small but growing body of evidence suggests that the biotic integrity of tidal creeks may be affected by a suite of unique watershed and instream factors, some that are common to both freshwater and tidal creeks, such as watershed imperviousness (Holland et al. 2004) and shoreline development (Bilkovic & Roggero 2008, Partyka & Peterson 2008, Lowe & Peterson 2014), but others that are unique to tidal systems and the fauna under study, such as creek geomorphology (Allen et al. 2007). Compared to studies into impacts on benthic infauna in tidal creeks (Lerberg et al. 2000, Holland et al. 2004, Sanger et al. 2015), studies on impacts on nekton are less common. While research is emerging on the anthropogenic impacts on nekton in tidal creeks (Peterson & Lowe 2009, Krebs et al. 2014b, Lowe & Peterson 2014), further work is needed to strengthen understanding of the relationship between metrics of development and patterns of nekton abundance in them (Sanger et al. 2015). Characterizing biological communities is an effective approach at simultaneously measuring the response of multiple taxa to human stressors (Niemi et al. 2004). Further, understanding how land use relates to patterns of nekton abundance in salt marshes is helpful information for projects intent on identifying or restoring the functional value of these productive habitats (Kneib 1997).

The objective of this study was to relate fish and invertebrate communities to specific, measurable habitat and disturbance metrics in first-order salt marsh tidal creeks in a rapidly developing section of the southeastern US coastline. We sampled variably altered systems possessing instream and watershed-level impacts largely representative of residential and commercial disturbances along the US Atlantic and Gulf of Mexico coastlines. Imperviousness exceeding 20% (Holland et al. 2004) and 20–30% (Lerberg et al. 2000, Krebs et al. 2014a) in tidal creek watersheds has been used as a composite metric of impact and implicated in reducing biological diversity; several of our study sites had imperviousness values in excess of these published threshold levels. We hypothesized that these more altered creeks would have different species assemblages than less impacted creeks nearby.

MATERIALS AND METHODS

Study sites

We sampled 6 first-order tidal systems in coastal North Carolina (USA): Atlantic Veneer, Porters, Pelletier East, Pelletier West, Spooners, and Webb Creeks. These creeks spanned a gradient of habitat characteristics and alterations to their high tide wetted areas and watersheds (Table S1 in the Supplement at www.int-res.com/articles/suppl/m544p015_supp.pdf). Embedded in a landscape undergoing rapid development, the tidal creeks we elected to study epitomize the patchiness of estuarine habitats across spatially heterogeneous coastal landscapes (Boström et al. 2011). Across this landscape these creeks are positioned roughly equally with respect to semidiurnal tidal inundation; the duration over which marsh flooding occurs around high tide is roughly the same among the 5 marsh-fringed intertidal creeks that we sampled.

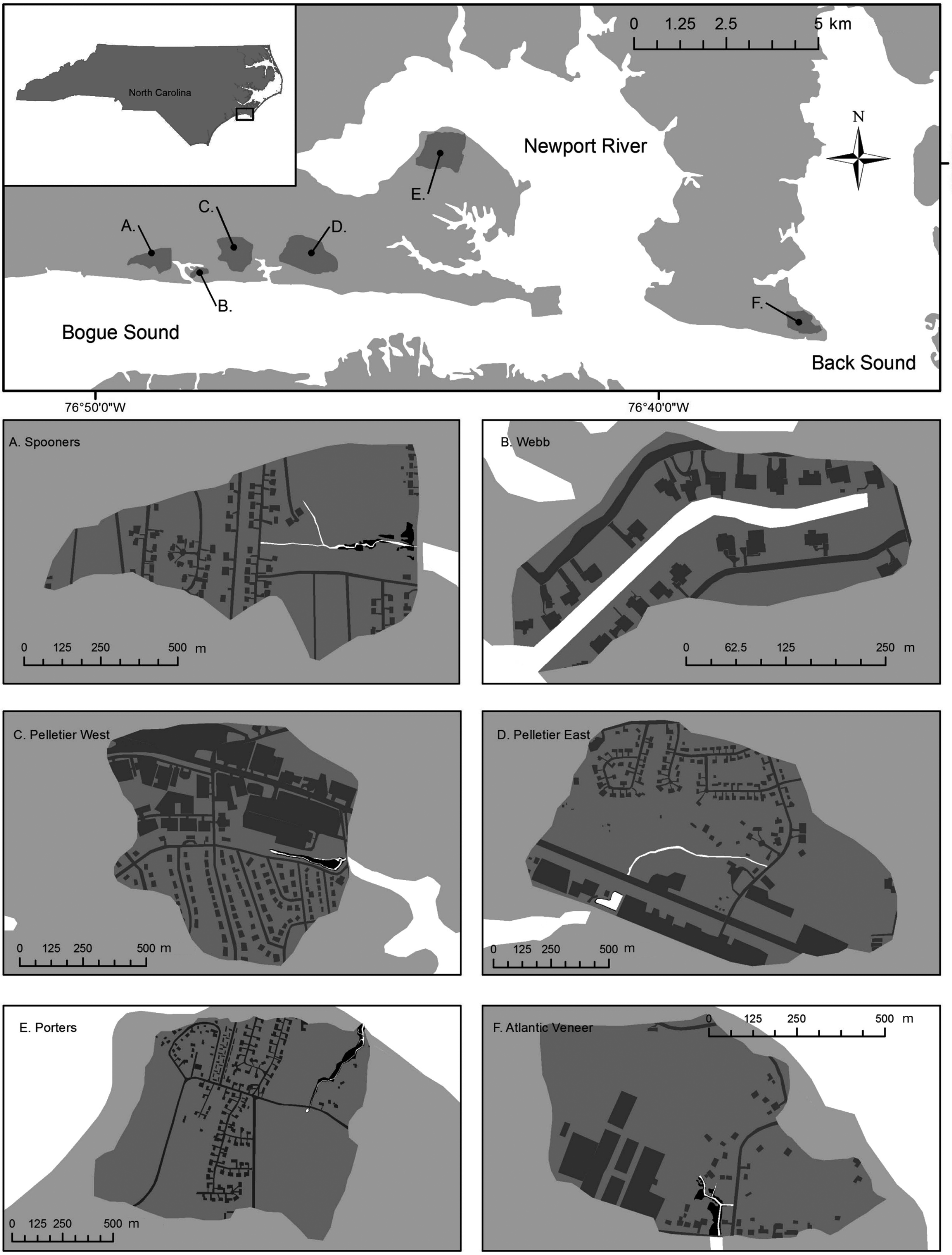
Each sampled creek had a unique combination of environmental and habitat characteristics but also shared some characteristics with other creeks that were studied. All study creeks were considered polyhaline because high tide salinity at the downstream end of the sampled area of each creek is ~30 psu during non-rain periods. Atlantic Veneer, Porters, and Spooners Creeks are considered 'rivulet' marsh creeks in that shallow rivulets of water (~0.1 m deep at low tide) meander through part of each channel at low tide (Rozas et al. 1988, Hettler 1989). The full width of the channels of the other 3 creeks are largely covered with water over average low tides. Except for Webb Creek, each creek has a fringing marsh dominated by *Spartina alterniflora* (Loisel) (Fig. 1; Table S1); Pelletier East Creek has the narrowest fringing marsh due to historic dredging of the marsh to provide road fill. Each creek we studied had a different amount of intertidal-subtidal vegetated edge: the linear distance of marsh edge that faces the creek channel. Each creek experiences semi-diurnal tidal amplitudes of roughly 1.0 m at its downstream end. Of the 5 salt marsh creeks, none has any bulkheaded shoreline within the sampling area; however, Pelletier East and Pelletier West Creeks have predominantly bulkheaded shorelines with no *S. alterniflora* coverage below the sampled area. In studies of tidal marsh production, the delineation of the downstream extent of habitat is often subjective (Kneib 2003). However, culverts can delineate boundaries of salt marshes for sampling (Stevens et al. 2006). We bounded the downstream sampling area by the presence of a culvert or a downstream boundary with a higher order system. Upstream sampling was bounded by the most upstream extent of tidal influence or, in the case of Pelletier East Creek, an upstream culvert. Thus, except for Pelletier East Creek, each creek was sampled from the downstream mouth or culvert to the upstream extent of tidal influence.

Estimates of watershed and impervious surface areas

Mapping and spatial analysis from ArcGIS (version 9.3.1) were used to estimate watershed area of the creeks and impervious surface contained within each watershed (Fig. 1; Table S1). The primary data used for this analysis were digital elevation models (DEM) developed from light detection and ranging (LiDAR) data, field survey data, and aerial photographs. Watershed area for each of the study creeks was estimated using the 'watershed' spatial analysis tool in the hydrology toolset in ArcToolbox®. Extraction of relevant features (hill slopes and flow paths) from the DEM layers was performed using the 'flow direction' tool, creating a new layer where flow direction and channeling points were represented. This layer was then used as the input for the 'watershed' tool which created a layer delineating watersheds for each study site. From this layer, watershed area (m^2) for each study creek could be estimated from the layer's attributes. Due to the low elevation of the study sites and minimal elevation change across the sites, the watershed delineation procedure in ArcGIS had trouble correctly assigning watershed boundaries for some of the creeks. Because of this, the watershed layers were corrected by hand to conform to obvious contour changes in the landscape inferred from site visits and contour data layers. Recent satellite imagery from Google Earth® (images captured in 2010) was overlaid on the watershed areas and used to estimate land use within the watershed. Impervious surface was estimated by manually drawing polygons over hardened (impervious) surface areas (i.e. buildings, driveways, walkways, and roads) within the watershed of each creek (Fig. 1).

Fish and invertebrate sampling

Tidal creeks were sampled from spring through fall in 2012 and 2013. Sampling over the bulk of the spring and summer provides the most representative characterization of nekton communities in shallow-water estuaries in this region (Bilkovic & Roggero 2008). Each creek was divided into 10 measured and evenly spaced strata that were sampled monthly with 2 different gear types: an actively deployed throw trap and passively deployed wire-mesh minnow traps. The throw trap targets small and juvenile fishes and epibenthic crustaceans (Turner & Trexler 1997, Rozas & Minello 1998) less than roughly 30 mm total length that use the marsh platform for foraging and refuge over most tides and that would not be retained by minnow traps if they elected to enter them. When adjusted for catchability (see below), throw trapping provides estimates of absolute densities of small fishes and invertebrates inhabiting salt marshes (Kushlan 1981, Rozas & Minello 1997). In contrast, minnow traps collect relatively larger fishes (40–110 mm total length) (authors' unpubl. data) that typically make tidally mediated migrations between the vegetated and unvegetated portions of salt marsh creeks (Allen et al. 2007). Sampling with both gears allowed us to develop a more composite picture of


North Carolina
0 1.25 2.5 5 km
N
Newport River
34°45'0"N
E.
C.
A.
D.
B.
F.
Bogue Sound
Back Sound
76°50'0"W
76°40'0"W
A. Spooners
0 125 250 500 m
B. Webb
0 62.5 125 250 m
C. Pelletier West
0 125 250 500 m
D. Pelletier East
0 125 250 500 m
E. Porters
0 125 250 500 m
F. Atlantic Veneer
0 125 250 500 m

both small and large resident and transient fauna inhabiting multiple habitats in tidal creeks.

The throw trap was a 1 m^2 square by 0.6 m high aluminum frame with solid sides and an open top and bottom. The throw trap was deployed by foot during high tide in the marsh and used monthly in the 5 salt marshes (but not in sub-tidal Webb Creek) by employing a stratified random sampling design. Distances upstream in each stratum and laterally into the fringing marsh, as well as left- vs. right-fringing marshes, were randomly selected for throw trap sampling. We generally made 10 throw trap deployments monthly in each creek, except in Pelletier East Creek, where the narrowness of the fringing marsh and steepness of the slope from the marsh to subtidal areas prevented throw trap deployment in roughly half of the strata (depending on high tide amplitude). Immediately after deployment, the trap frame was pressed into the sediment to prevent escapement of fishes and epibenthic crustaceans. Water depth was measured (nearest 0.1 m) and percent vegetation (*S. alterniflora* stem density) in the trap was visually estimated (nearest 10%) in conjunction with each deployment. Water temperature (°C), salinity (psu) and dissolved oxygen concentration (mg l^{-1}) were measured in the lower, middle, and upper creek reaches during monthly throw trap- and minnow trap collections (below). We swept each throw trap deployment 50 times with a 0.30 × 0.25 m dip net made of 0.72 mm^2 mesh and initially removed vegetation by sieving each trap's sample through a wash bucket with 0.22 mm^2 mesh. All fauna and remaining organic matter were preserved in 95% denatured ethanol for subsequent identification and enumeration.

Our goal was to use throw trapping to estimate fish and invertebrate density. Sampling bias, due to differing recovery efficiencies (Rozas & Minello 1997) (see below) for different species or environmental factors (e.g. vegetation density, water depth), may exist when researchers use actively deployed enclosure-type samplers (Kushlan 1981, Rozas & Minello 1997). To account for these potential biases, a subset of throw trap samples (from September 2013) was used to estimate species-specific recovery efficiency across a range of water depths and vegetation densities. For each stratum sampled during this month, we preserved each set of 10 sweeps in a separate jar to determine the rate of decline of catch of each targeted taxon with successive units of effort. This resulted in 5 jars preserved per throw trap deployment during this month (Sweeps 1–10, 11–20, 21–30, 31–40, and 41–50). Estimates of taxon-specific recovery efficiencies and environmental conditions from September 2013 samples were used to develop models that were used to estimate recovery efficiencies by taxon for all trap deployments from the full study.

Gee-style wire mesh minnow traps (6.4 mm square mesh) baited with dried pet food were deployed in channels of each stratum for 3 h soak times around high tide. Traps were deployed using a stratified random sampling design whereby distance upstream into each stratum to deploy each trap (by thirds) was randomly selected. We generally fished one minnow trap per stratum except for Porters Creek, where we fished 2 traps per stratum because of its relatively large size. We assumed independence among minnow trap deployments. Deployment of minnow traps in channels insured that trap entrances remained submerged during high tide sampling and could be retrieved by boat at the conclusion of 3 h soaks. All minnow-trapped individuals were identified, counted, and released.

Data analysis: estimating absolute abundance from throw trap collections

Catch efficiency (or catchability) relates absolute abundance to catch (Arreguín-Sánchez 1996). Throw trap catch efficiency has 2 components: gear capture efficiency and recovery efficiency (Rozas & Minello 1997). Gear capture efficiency is the proportion of the target animals in an area that were then enclosed by the trap while recovery efficiency is the proportion of animals recovered of those enclosed. We estimated absolute abundance, $\widehat{N}$, of common fauna collected by throw traps because we suspected that the catch after sweeping each throw trap 50 times did not completely recover all target individuals (recovery effi-

Fig. 1. Six tidal creeks in coastal North Carolina, USA, sampled with a 1 m^2 throw trap and 6.4 mm wire mesh minnow traps to estimate densities and relative abundances of epibenthic fishes and crustaceans from spring through fall of 2012 and 2013. Darker shading on larger inset map represents the watershed of each creek; this is also the shade showing watersheds of each creek-specific map (A–F). The darkest gray shade for each creek map represents impervious surface. The white and black within the watersted of each creek map is the area of creek channel and marsh surface, respectively. Minnow trapping was conducted in all 6 creeks. Throw trapping was conducted in each creek except Webb Creek

ciency <1). This approach required us to save and process samples of every 10 successive sweeps for the depletion analysis. Given this laborious process, we only empirically determined absolute abundance and overall recovery efficiency ($q_{\text{deployment}}$) during September 2013. Additionally, the analysis was limited to 4 taxa collected by the throw trap (*Fundulus heteroclitus*, *Gambusia holbrooki*, *Palaemonetes* spp., and Amphipoda) in those instances where we had a non-zero catch of that taxon in a trap. The cases of non-zero trap catches for other species was not sufficiently high (n > 10) to allow estimation of absolute abundance.

Absolute abundance of *F. heteroclitus*, *G. holbrooki*, *Palaemonetes* spp., and Amphipoda from throw trapping was estimated in several steps. First, we used the Leslie-Davis depletion estimator (Leslie & Davis 1939) to estimate density ($\widehat{N}$, ind. m^{-2}) for each September 2013 trap deployment. The depletion estimator was implemented in the Program R (R Development Core Team 2011) using the *fishmethods* package (Nelson 2011). Catch data from the 5 successive units of effort (1 unit of effort = 10 net sweeps) were used to estimate q_{effort}, the recovery efficiency between successive effort units. We then calculated $q_{\text{deployment}}$ for each September 2013 trap deployment and taxon by dividing cumulative catch over the 50 sweeps by the estimate of $\widehat{N}$ from each deployment. Thus, $q_{\text{deployment}}$ represents the cumulative recovery efficiency for a particular taxon after 50 sweeps of the net within the trap and is synonymous with the term 'efficiency' used for similar gear types commonly deployed in estuaries (Kushlan 1981, Rozas and Minello 1997). Third, we used normally distributed general linear models to determine the relationship between $q_{\text{deployment}}$ and 2 potential covariates that were collected during throw trap sampling: water depth, percent emergent vegetation (*S. alterniflora*) in each trap deployment, and the interaction between these 2 factors. Plots of the raw data as well as post-hoc residual plots revealed no unusual patterns from the use of normal distributions for these model fits. Thus, 5 models of $q_{\text{deployment}t}$, including an intercept-only model, were developed for each of the 4 taxa (see 'Results'). We used Akaike Information Criteria (AIC; Burnham & Anderson 2002) to evaluate model parsimony and determine the factor(s) most influential on $q_{\text{deployment}}$. Checks of the dispersion parameter, $\hat{c}$, revealed that these data were not overly dispersed. Chi-square goodness of fit (GOF) testing was used to assess the adequacy (if the probability level exceeded 0.05) of each model fit. We used results of best fitting models (determined through AIC) to calculate the $q_{\text{deployment}}$ for each main taxon in each trap deployment over the course of the full study. Finally, $\widehat{N}$ was estimated for each main taxon in each deployment over the full study by dividing catch of a taxon in each trap deployment by the estimated $q_{\text{deployment}}$ for that deployment. We could not estimate recovery efficiencies for less abundant species, given sample size constraints, and assumed that catch was representative of absolute abundance.

Data analysis: community assessment

We tested whether creeks differed in community composition and determined environmental and habitat factors that explained differences in creek communities by gear. Non-metric multi-dimensional scaling (NMDS) was used to graphically depict fish and invertebrate communities of each creek. NMDS is an ordination technique for graphical representation of community relationships of non-normal or discontinuous data (Clarke 1993, McCune & Grace 2002). NMDS arranges samples so that the rank-order correlation between distance measures and distance in ordination space is maximized, while also minimizing stress: a measure of fit between ordination space and multi-dimensional space (McCune & Grace 2002). We conducted a separate NMDS ordination for each gear and year. The Bray-Curtis coefficient was used to construct similarity matrices for the sample-by-species matrix on counts of individuals from throw trap and minnow trap collections, which were square-root transformed to diminish the influence of numerically dominant taxa. To balance uniform exclusion versus inclusion of rare species (Poos & Jackson 2012), we elected to include species in each gear-specific NMDS that comprised at least 0.1% of the total abundance for that gear type (by year). Each individual sample by a gear type was considered a 'sample' for NMDS; however, deployments with zero data across all the taxa considered in the ordination (those >0.1% in numerical abundance in our case) cannot be evaluated. For throw trap data, NMDS was performed using density, $\widehat{N}$, for the 4 taxa on which recovery efficiency was computed and using catch data for the other taxa that met the 0.1% inclusion threshold. NMDS for minnow trap collections was performed using catch data. Fit (stress) was computed as part of each gear-specific NMDS ordination to determine how well the Euclidean distances preserved the Bray-Curtis sample dissimilarities (Kruskal 1964, McCune & Grace 2002): stress levels <~0.2 are considered reasonable (Clarke & Warwick 2001). Relatively high stress (>0.2) can potentially lead to misinterpreting scaling distances (Clarke & Warwick 2001). An ANOSIM procedure was conducted in conjunction with each NMDS to provide a quantitative interpretation of whether biological communities differed among creeks. The ANOSIM test statistic, R, varies from −1 to 1 but most typically from 0 to 1; increasingly greater positive values indicate greater differences among sites while a value of 0 for R indicates no dissimilarities among sites (Chapman & Underwood 1999).

Urbanization includes factors that can be difficult to summarize (Wang et al. 2001). We measured numerous habitat and environmental factors at the creek and watershed levels. For these reasons, we sought to determine a subset of environmental and habitat factors most related to differences in biological communities among creeks for each collection gear and year of data. This was done through the nonparametric BIOENV analysis (Clarke & Ainsworth 1993) that determines the suite of environmental variables that show the greatest rank correlation with sample dissimilarities. BIOENV can be conducted with environmental/habitat data as well as biological data; the latter can be used to determine the group of taxa showing the greatest rank correlation with sample dissimilarities. We conducted BIOENV analysis with each type of data, using a 'forward selection/backward elimination approach' where the rank correlation in sample similarities between a subset of environmental variables/taxa and the full data set of environmental variables/taxa was set at 0.95 (Clarke & Warwick 1998). Euclidean distances among sample items were calculated as part of each BIOENV procedure; this distance measure can be applied to both categorical and continuous environmental/habitat data (McCune & Grace 2002). A Spearman correlation coefficient (rho) is calculated for the best fitting suite of taxa and environmental/habitat factors.

BIOENV analysis allows environmental variables and taxa that are most correlated with sample similarities to be plotted in NMDS ordination space. Each continuous environmental/habitat factor in the most parsimonious BIOENV model is plotted as a vector while each level of a categorical factor in the model is plotted as a point. Each taxon in the best fitting BIOENV analysis of biological data is plotted as a vector. Continuous environmental/habitat factors considered in the throw trap and minnow trap BIOENV analyses included percent watershed imperviousness, percentage of each creek's high tide wetted area that was vegetated, water temperature, salinity, dissolved oxygen, and mean creek channel depth at bank-full level. We included mean creek channel depth because it has been found to be an important geomorphological determinant of nekton use of intertidal salt marsh creeks in the US southeast (Allen et al. 2007), and metrics of channel morphology (such as depth) influence nekton movement through these corridors (Rozas et al. 1988, Visintainer et al. 2006, Allen et al. 2007, Boström et al. 2011). Categorical factors considered in each BIOENV analysis included stratum number (distance upstream: 1–10) as well as the presence/absence of (1) a culvert, and (2) contiguous marsh found immediately downstream of the creek's mouth or culvert. An additional factor incorporated into the throw trap BIOENV analysis included the lateral distance into the marsh (closest to the inter-tidal channel, in the middle marsh, or closest to the high marsh) where each trap deployment occurred. Shoreline hardening ('bulkheading') was a categorical factor only in the minnow trap BIOENV analysis because of the addition of Webb Creek to that analysis. Standing water was considered a categorical factor in preliminary model runs but was eliminated from subsequent runs because of its perfect negative correlation with the presence of marsh downstream. Water depth and percent vegetation in each throw trap sample were not considered environmental factors in the throw trap BIOENV analysis because they were considered covariates of recovery efficiency (above). NMDS, BIOENV, and fitting of environmental variables and taxa groupings was done through the Program R package *vegan* using the *metaMDS*, *bioenv*, and *envfit* functions, respectively (Oksanen 2014). The *envfit* function was also used to evaluate the significance of each individual environmental/habitat factor included in each best fitting BIOENV model through a permutation test.

We ran follow-up univariate models after the BIOENV procedures to determine whether habitat and environmental factors most responsible for community differences among creeks influenced the abundance of dominant taxa that contributed to among-creek community differences. Each model that we constructed focused on predictor variables (habitat/environmental factors) and response variables (dominant taxa) that each year's BIOENV analysis for a gear type showed via loadings on ordination plots as contributing to community differences among creeks. Dominant taxa included *F. heteroclitus*, *Cyprinodon variegatus*, *Lagodon rhomboides*, and the combined density/catch data from *Palae-*

monetes spp. and *Callinectes sapidus*. We elected to combine data from these latter 2 taxa due to the similar manner in which they loaded on throw trap ordinations (see 'Results'). We compared the mean abundance of each main taxa for binary and continuous predictors. Each model included data from both 2012 and 2013. Comparisons with binary predictors used unpaired *t*-tests on untransformed data when a Bartlett's test did not reveal heterogeneity between group variances ($p > 0.05$) and on logarithmically transformed data ($\ln(x+1)$) when it did. Linear models regressing each taxa against a continuous predictor were conducted using logarithmically transformed data.

RESULTS

A total of 640 throw trap and 1001 minnow trap deployments were made during the study. Mean monthly water temperature and dissolved oxygen concentration generally overlapped among creeks during each of the 2 sampling seasons (Fig. 2). However, mean monthly salinity was generally lower in Pelletier East and Pelletier West Creeks than in the other creeks (Fig. 2B). Average percent *Spartina alterniflora* coverage in throw traps, a proxy for stem density, differed among creeks and was (mean ± SE) 61.1 ± 0.5, 65.2 ± 0.4, 68.6 ± 0.3, 72.4 ± 0.8, and 80.6 ± 0.3% for Porters, Atlantic Veneer, Spooners, Pelletier East, and Pelletier West Creeks, respectively.

Fundulus heteroclitus, *Gambusia holbrooki*, *Cyprinodon variegatus*, *Palaemonetes* spp., and Amphipoda — all resident fish and crustacean taxa to US Atlantic coastal salt marshes (Kneib 1997) — were the 5 most abundant species from throw traps and accounted for 96.3% of the cumulative catch from this gear (Table 1). *F. heteroclitus*, *G. holbrooki*, and *C. variegatus* were 3 of the 4 most abundant species captured from minnow traps; they accounted for 95.2% of the cumulative catch from minnow traps (Table 2; Table S2 in the Supplement at www.int-res.com/articles/suppl/m544p015_supp.pdf). Transient taxa were caught in relatively low numbers by each gear; *Farfantepenaeus* spp. was the most abundant transient taxa caught in the throw trap and accounted for 0.8% of the catch from that gear while *Lagodon rhomboides* was the most abundant transient taxa collected from minnow traps and accounted for 4.3% of the individuals from that gear type. The sizes of *F. heteroclitus*, *G. holbrooki*, and *C. variegatus* were smaller from throw trap than minnow trap samples (Table 3, Table S3 in the Supplement).

Recovery efficiency ($q_{\text{deployment}}$) as measured in our September 2013 throw trapping was relatively high but differed among taxons. *F. heteroclitus* and Amphipoda had a correspondingly lower mean (±SD) $q_{\text{deployment}}$ (0.88 ± 0.20 and 0.82 ± 0.22, respectively) than *G. holbrooki* (0.98 ± 0.07) and *Palaemonetes* spp. (0.99 ± 0.29). Covariates important to throw trap recovery efficiency differed among taxons. For *F. heteroclitus*, $q_{\text{deployment}}$ was negatively related to the percentage of *S. alterniflora* while recovery efficiency of *Palaemonetes* spp. was reduced with increasing water depths (Table 4). *S. alterniflora* and water depth did not influence $q_{\text{deployment}}$ of *G. holbrooki* or Amphipoda (Table 4).

NMDS ordinations were conducted on data from the 628 throw trap samples and 678 minnow trap samples. Eleven and 13 taxa met the relative abundance threshold for inclusion in each ordination for throw trap collections in 2012 and 2013, respectively (Table 1). Four and 6 different taxa were included in the 2012 and 2013 minnow trap ordinations, respectively (Table 2).

There were differences in community assemblages among creeks. For throw trap ordinations, Porters and Atlantic Veneer Creeks separated out from the other 3 creeks which had more overlap in each year (Figs. 3A & 4A). Minnow trap ordinations displayed less community overlap among creeks than throw trap ordinations; Pelletier East and Webb Creeks separated out from the other 4 creeks, which largely overlapped (Figs. 5A & 6A).

ANOSIM results were consistent with visual assessments of ordination plots. There were significant differences in faunal assemblages for annual throw trap data (2012; $R = 0.258$, $p = 0.001$ 2013: $R = 0.182$, $p = 0.001$) and minnow trap data (2012: $R = 0.345$, $p = 0.001$; 2013: $R = 0.393$, $p = 0.001$). Stress was 0.189 and 0.231 for 2012 and 2013 throw trap ordinations and 0.063 and 0.087 for 2012 and 2013 minnow trap ordinations, respectively. One ordination (2013 throw trap) had relatively high stress (>0.2). However, we believe that this did not hinder our interpretation of the result due to the similarities in throw trap ordinations between the 2 years.

For each gear type, the suite of fish and invertebrate taxa that most correlated with dissimilarities among samples was consistent between years. The 5 numerical dominant taxa in the throw trap (Table 1), as well as *Callinectes sapidus*, were most correlated with sample dissimilarities for the throw trap ordination in 2012 (Fig. 3B) and 2013 (Fig. 4B). *Lagodon rhomboides*, *F. diaphanus, Dormitator maculatus*, *Mugil* spp. and Xanthidae were additional taxa in the

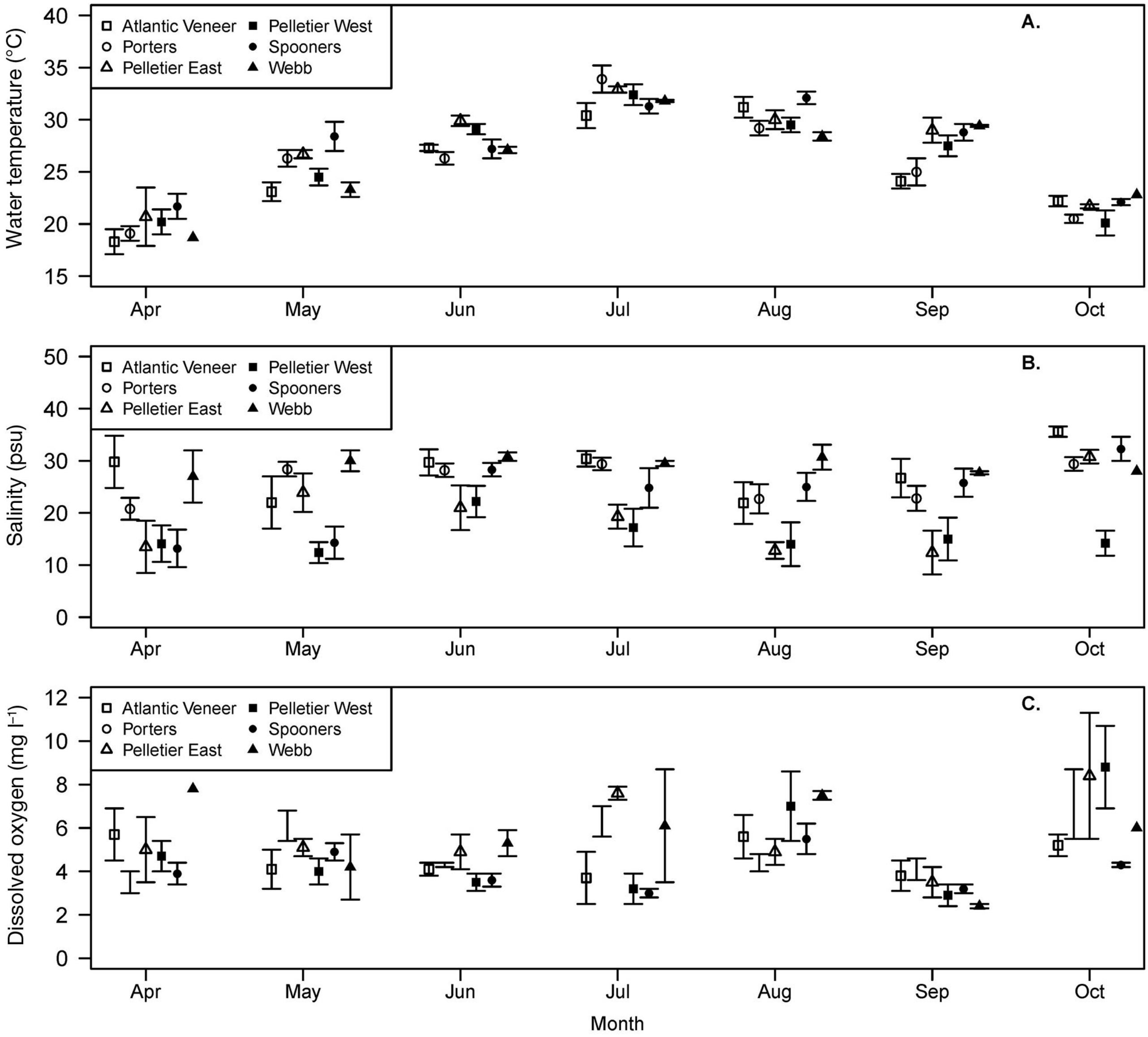


Fig. 2. Mean (±SE) (A) monthly water temperature, (B) salinity, and (C) dissolved oxygen concentration in 6 tidal creeks in coastal North Carolina, USA, sampled from April through October in 2012 and 2013. Symbols for each creek are jittered around monthly tick marks

best fitting throw trap model for 2013 (Fig. 4B). Best fitting BIOENV models for minnow trap ordinations in 2012 (Fig. 5B) and 2013 (Fig. 6B) included only 2 species: *F. heteroclitus* and *L. rhomboides*. Spearman rho values were 0.847 and 0.803 for throw trap taxa correlations in 2012 and 2013, and 0.966 and 0.917 for minnow throw trap taxa correlations in 2012 and 2013, respectively. Trends among creeks in throw trap densities and minnow trap catches of each main species (Fig. 7) were consistent with ordination results.

For each gear type, the suite of environmental/habitat factors that showed the greatest rank correlation with sample dissimilarities was similar between years. The presence/absence of a culvert, the presence/absence of contiguous marsh downstream, and mean creek depth were in the best fitting correlation with sample dissimilarities for the throw trap ordination in each year (Figs. 3C & 4C). Percent watershed imperviousness and marsh percentage in each creek were factors in best fitting models for minnow trap ordinations in each year (Figs. 5C & 6C). The presence/absence of contiguous marsh downstream, salinity and dissolved oxygen were additional factors in the best BIOENV model fit to the minnow trap ordination in 2013 (Fig. 6C). Permutation tests found that

Table 1. Number (n) and percent frequency (%) of fish and invertebrate taxa captured by a 1 m^2 throw trap actively deployed on the marsh surface (n = 640 deployments) in 5 tidal creeks in coastal North Carolina, USA, from spring through autumn of 2012 and 2013. Species in **bold** are those for which catch data were analyzed with non-metric multidimensional scaling

Species	2012		2013	
	n	%	n	%
Amphipoda	4250	61.55	3547	57.37
Fundulus heteroclitus	1065	15.42	1004	16.24
***Palaemonetes* spp.**	791	11.46	602	9.74
Gambusia holbrooki	581	8.41	579	9.36
Cyprinodon variegatus	102	1.48	84	1.36
Xanthidae	4	0.06	169	2.73
***Farfantepenaeus* spp.**	16	0.23	89	1.44
Callinectes sapidus	25	0.36	20	0.32
Fundulus diaphanus	19	0.28	22	0.36
Dormitator maculatus	16	0.23	20	0.32
***Mugil* spp.**	22	0.32	11	0.18
Menidia menidia	8	0.12	12	0.19
Lagodon rhomboides	1	0.01	15	0.24
Leiostomus xanthurus	2	0.03	5	0.08
Gobiosoma spp.	2	0.03	1	0.02
Anguilla rostrata	–	–	2	0.03
Eucinostomus argenteus	–	–	1	0.02
Centropomus undecimalis	1	0.01	–	–

Table 2. Number (n) and percent frequency (%) of fish and invertebrate taxa captured by 6.4 mm wire mesh minnow traps passively deployed (n = 1001 deployments) in unvegetated channels of 6 tidal creeks in coastal North Carolina, USA, from spring through autumn of 2012 and 2013. Species in **bold** are those for which catch data were analyzed with non-metric multidimensional scaling

Species	2012		2013	
	n	%	n	%
Fundulus heteroclitus	14915	87.24	14355	93.00
Lagodon rhomboides	846	4.95	562	3.64
Cyprinodon variegatus	1154	6.75	250	1.62
Gambusia holbrooki	119	0.70	175	1.13
***Gobiosoma* spp.**	16	0.09	37	0.25
Dormitator maculatus	10	0.06	27	0.17
Palaemonetes spp.	10	0.06	4	0.03
Fundulus diaphanus	6	0.04	5	0.03
Callinectes sapidus	3	0.02	5	0.03
Mugil spp.	4	0.02	2	0.01
Farfantepenaeus spp.	3	0.02	3	0.02
Leiostomus xanthurus	1	<0.01	5	0.03
Orthopristis chrysoptera	5	0.03	–	–
Anguilla rostrate	1	<0.01	1	<0.01
Lutjanus griseus	–	–	1	<0.01
Cynoscion nebulosus	–	–	1	<0.01
Eucinostomus argenteus	1	<0.01	–	–
Paralichthys lethostigma	1	<0.01	–	–
Bairdiella chrysoura	1	<0.01	–	–
Elops saurus	–	–	1	<0.01
Xanthidae	–	–	1	<0.01

almost all individual environmental/habitat factors in the 4 best fitting BIOENV models were significantly rank correlated ($p < 0.01$) with ordination sample dissimilarities for the respective ordination; the only exception was dissolved oxygen, which was not significantly correlated with ordination of 2013 minnow trap data ($p = 0.109$). Spearman rho values were 0.222 and 0.193 for throw trap environmental/habitat correlations in 2012 and 2013, and 0.540 and 0.576 for minnow throw trap environmental/habitat correlations in 2012 and 2013, respectively.

For each gear, the direction and strength of gradients for fish and invertebrate taxa (Figs. 3B, 4B, 5B & 6B) showed consistent trends with environmental/habitat gradients (Figs. 3C, 4C, 5C & 6C) across years. For invertebrates captured in throw trap samples, amphipods were an important contributor to creek dissimilarities, being more abundant in creeks that had no marsh downstream while *Palaemonetes* spp. and *Callinectes sapidus* were consistently a part of the community in 2 creeks that had little impact (Porters Creek) and extensive impact (Pelletier East Creek). The dominant fish across gears/years and in best fitting BIOENV models, *F. heteroclitus*, was most closely associated with creeks having high percentages of marsh, contiguous marsh downstream of the sampled area for small individuals caught in throw traps, as well as shallower mean channel depth and lower watershed imperviousness for large individuals caught in minnow traps. The transient fish *L. rhomboides* (minnow trap) associated with creeks with lower percentages of vegetated marsh. This species loaded on 2013 throw trap and minnow trap ordinations similar to mean channel water depth. Throw trap-caught *G. holbrooki* and *Cyprinodon variegatus* were consistently related to sample dissimilarities in both years and were predominantly found in 2 culverted creeks (Pelletier East and Pelletier West) that lacked marsh downstream. These 2 species loaded on 2013 throw trap ordination in a manner almost identical to mean channel water depth.

In follow-up univariate tests of species and environmental factors, we found that throw trapped *F. heteroclitus* had a significantly greater mean abundance in creeks with marsh downstream ($t = -3.40$, df = 626, $p < 0.001$) while the opposite was found for *C. variegatus* ($t = 7.64$, degrees of freedom (df) = 626, $p < 0.001$). The regression of combined abundances of throw trapped *Palaemonetes* spp. and *Callinectes sapidus* against water depth showed that the coefficient for water depth was significant (adjusted $r^2 = 0.096$, df = 626, $p < 0.001$). Finally, we

Table 3. Annual mean (±SD) and range of total length (mm) of the fishes *Fundulus heteroclitus*, *Gambusia holbrooki*, and *Cyprinodon variegatus* captured by a 1 m^2 minnow trap and wire mesh minnow traps fished in North Carolina, USA, tidal creeks in 2012 and 2013

Species	Throw trap				Minnow trap			
	2012		2013		2012		2013	
	Mean (±SD)	Range	Mean (±SD)	Range	Mean (±SD)	Range	Mean (±SD)	Range
F. heteroclitus	26.8 (13.6)	2.5–91.0	23.0 (15.0)	3.4–92.0	57.7 (12.1)	28.0–103.0	58.6 (10.8)	27.0–110.0
G. holbrooki	22.4 (9.3)	4.2–48.0	21.8 (10.5)	3.6–48.0	41.6 (2.9)	35.0–50.0	41.8 (2.9)	31.0–47.0
C. variegatus	37.9 (13.2)	5.9–60.0	33.7 (14.7)	6.1–62.0	46.6 (6.3)	27.0–64.0	49.4 (5.5)	34.0–61.0

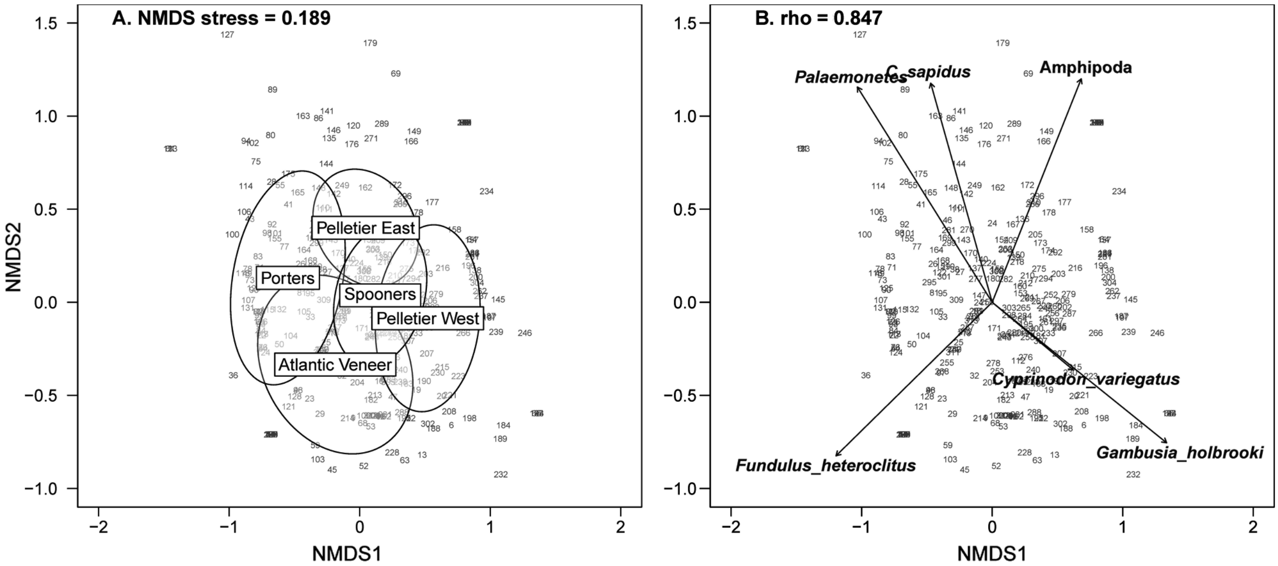
regressed catches of minnow trapped *F. heteroclitus* and *L. rhomboides* against the percentage of marsh in the creeks and found that the coefficient for marsh percentage was significantly positive for the model that included *F. heteroclitus* (adjusted r^2 = 0.420, df = 683, p < 0.001) and significantly negative for the model that included *L. rhomboides* (adjusted r^2 = 0.440, df = 683, p < 0.001).

Table 4. Results of fitting normally distributed general linear models to cumulative recovery efficiency ($q_{\text{deployment}}$) of 4 resident salt marsh taxa by a 1 m^2 throw trap. Covariates of $q_{\text{deployment}}$ considered in each model set included water depth (depth), percent *Spartina alterniflora* stem coverage in each trap (*Spartina*), and the interaction between these factors. AIC: Akaike Information Criteria. ΔAIC value for each model was calculated as the difference between the value of any particular model (AIC$_i$) and the minimum AIC (best fitting model) in the taxon-specific model set. Number of model parameters = k. Akaike weight = w_i. Intercepts and regression coefficients are listed in parentheses for the best fitting model in each set

Model	k	AIC	ΔAIC	w_i
Fundulus heteroclitus				
(1.084) *Spartina* (–0.003)	2	–11.02	0	0.42
Null	1	–10.03	0.99	0.25
Depth + *Spartina*	3	–9.08	1.94	0.16
Depth	2	–8.37	2.65	0.11
Depth + *Spartina* + Depth × *Spartina*	4	–7.12	3.90	0.06
Gambusia holbrooki				
Null (0.975)	1	–52.80	0	0.42
Depth	2	–51.07	1.73	0.18
Spartina	2	–50.92	1.88	0.16
Depth + *Spartina* + Depth × *Spartina*	4	–50.88	1.92	0.16
Depth + *Spartina*	3	–49.31	3.49	0.07
***Palaemonetes* spp.**				
(1.304) Depth (-1.221)	2	5.77	0	0.54
Depth + *Spartina*	3	7.77	1.92	0.20
Depth + *Spartina* + Depth × *Spartina*	4	8.89	3.84	0.11
Null	1	9.47	6.55	0.09
Spartina	2	10.19	7.32	0.06
Amphipoda				
Null (0.821)	1	–3.37	0	0.33
Spartina	2	–2.86	0.51	0.26
Depth + *Spartina*	3	–2.37	1.00	0.20
Depth	2	–1.49	1.88	0.13
Depth + *Spartina* + Depth × *Spartina*	4	–0.38	2.99	0.07

DISCUSSION

Differences in biological communities among saltwater creeks along the US Atlantic and Gulf of Mexico coastlines have been related to human alterations (Holland et al. 2004, Krebs et al. 2014b, Lowe & Peterson 2014). However, variability of nekton density within a creek and sampling seasons makes the detection of anthropogenic impacts difficult among creeks (Rose 2000, Ellis & Bell 2013). The performance of bio-indicators of habitat condition in tidal creeks may be improved by accounting for spatiotemporal variation of fauna in these systems in sampling designs (Shenker & Dean 1979, Talbot & Able 1984, Allen et al. 2007). In this study we sampled across tidal creeks possessing objectively measured attributes believed to be important to distributions of tidal creek nekton potentially impacted by disturbances (Stewart-Oaten 1996). Our sampling was consistent across sites, tides, and biologically productive seasons to help lessen the influence of spatial and temporal variability of nekton on our interpretation of biological pattern. Using a multivariate ordination approach, we found differences in community assemblages among creeks largely consistent across years and that appear attributable to habitat and watershed characteristics. Some of these characteristics reflect anthropogenic impacts on tidal creeks in a developing landscape. Our multivariate analyses support the hypothesis that loss of marsh and severing the physical connectivity of marsh habitat to areas downstream of first-order tidal creeks can lead to reduced abundances of dominant resident nekton. Despite the difference in sample gears, regions, and sizes



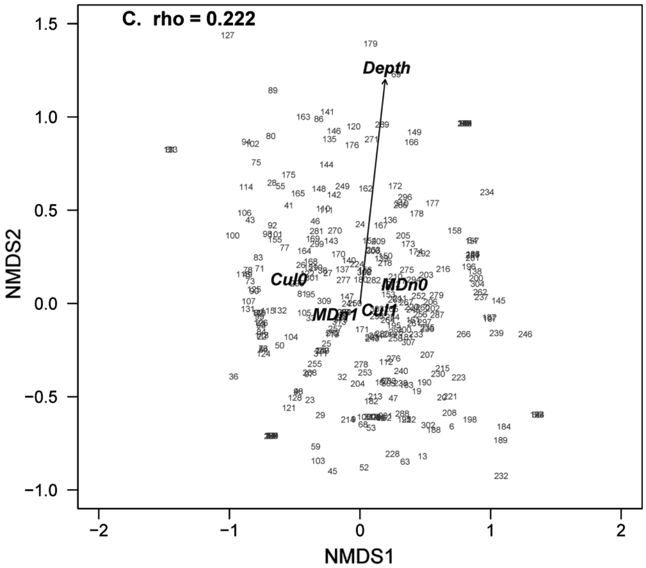


Fig. 3. Non-metric multidimensional scaling (NMDS) ordinations of 2012 throw trap samples among 5 salt marsh creeks. (A) Sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses. (B) Direction and strength of the group of fish and invertebrate densities that showed the greatest rank-correlation with sample dissimilarities. *C_sapidus*: *Callinectes sapidus*, *Palaemonetes*: *Palaemonetes* spp. (C) Direction and strength (length of arrow) of continuous environmental variables, and the centroid (location) of each class of binary environmental variables that were most rank-correlated with sample dissimilarities. Cul: culvert; MDn: marsh downstream of sample area (1 indicates presence of a binary variable; 0 indicates absence of it). The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C). Samples from each trap deployment are shown in small gray numbers

of study areas, our results are consistent with recent Gulf of Mexico analyses that identified creek and watershed-level anthropogenic impacts as factors influencing nekton community composition in that region (Sanger et al. 2011, Lowe & Peterson 2014).

Ecosystem heterogeneity over space and time (Brown et al. 2004) is one of the dominant themes in ecology (Wu 2006). Such variability can mask the detection of environmental impact (Wiens 1989), particularly in highly dynamic habitats such as tidal creeks (Able 1999). Complicating the interpretation of ecological pattern is the fact that human impacts are not necessarily destructive from the organism's perspective; more heterogeneous habitats are apt to provide a greater number of niches (MacArthur & Wilson 1967), and human disturbance can create spatial heterogeneity at multiple scales (Turner 2005). In this project we sampled across multiple temporal and spatial scales to attempt to account for ecosystem variability and determine ecological pattern. Our sampling efforts produced relatively robust sample sizes over some scales (e.g. number of samples per creek) but low sample sizes over others (e.g. numbers of creeks sampled). We found some factors were statistically meaningful covariates of community patterns. Increasing the sample sizes over some of the spatial scales or sampling a different suite of creeks may have revealed different or more apparent patterns than those that we observed and may have helped to explain more of the variability in community patterns (relatively low ANOSIM test statistics (<0.4)).

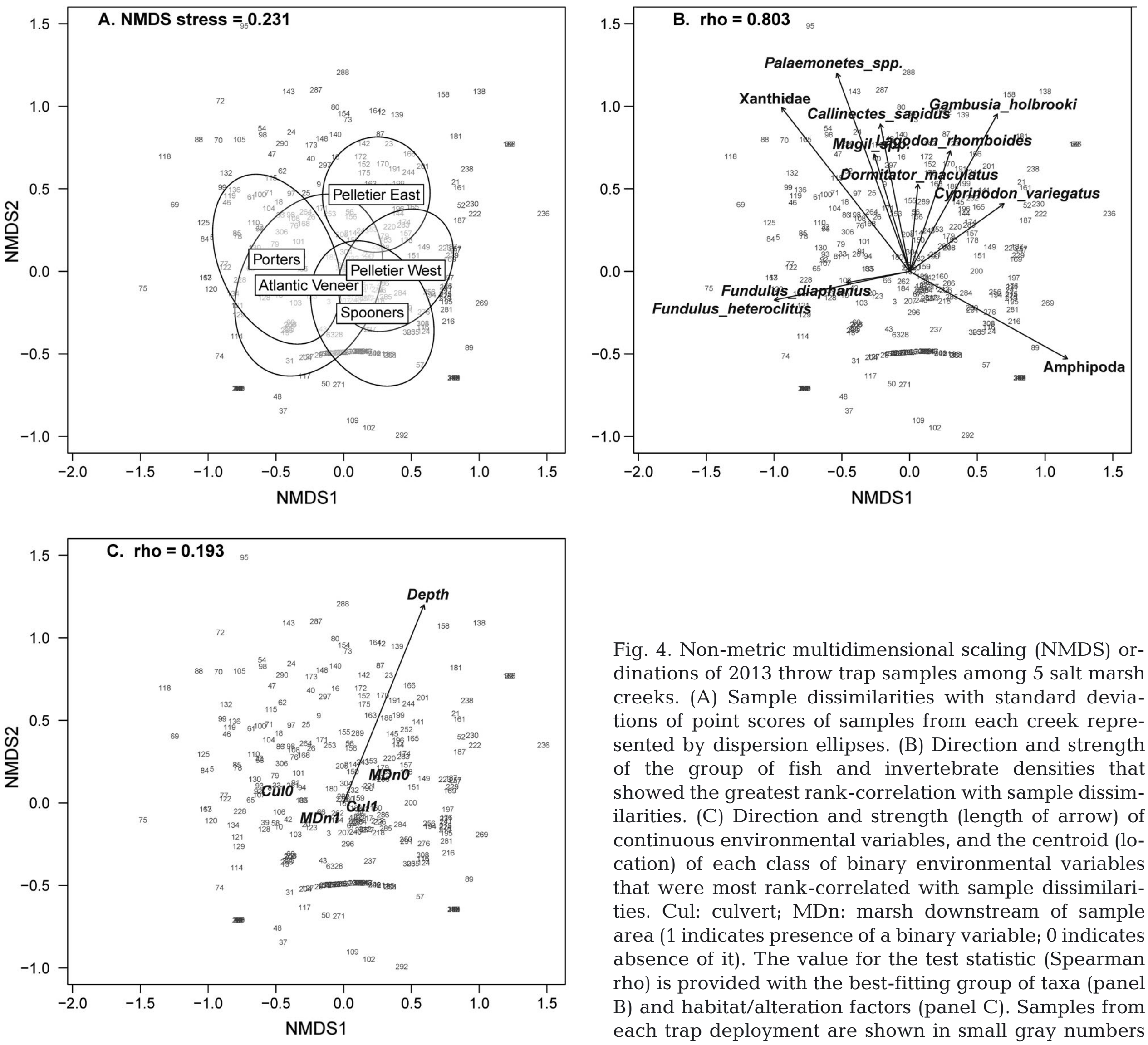


Fig. 4. Non-metric multidimensional scaling (NMDS) ordinations of 2013 throw trap samples among 5 salt marsh creeks. (A) Sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses. (B) Direction and strength of the group of fish and invertebrate densities that showed the greatest rank-correlation with sample dissimilarities. (C) Direction and strength (length of arrow) of continuous environmental variables, and the centroid (location) of each class of binary environmental variables that were most rank-correlated with sample dissimilarities. Cul: culvert; MDn: marsh downstream of sample area (1 indicates presence of a binary variable; 0 indicates absence of it). The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C). Samples from each trap deployment are shown in small gray numbers

Urbanized tidal creeks have been characterized by increased watershed imperviousness (Holland et al. 2004), reduced marsh coverage (Lowe & Peterson 2014), reduced or eliminated vegetated buffers (Uphoff et al. 2011, Krebs et al. 2014a,b), hardened shoreline (Bilkovic & Roggero 2008, Lowe & Peterson 2014), and fragmented habitat due to infrastructure (e.g. culverts; Porter et al. 1997, Eberhardt et al. 2011, Krebs et al. 2014a). We examined if some of these urbanization factors — those that BIOENV analyses identified as creating community dissimilarities among our study creeks — influenced patterns of nekton abundance and found that they did.

Community assemblages differed among the tidal creeks we sampled. Biologically speaking, these differences were largely driven by a limited number of species such as *Fundulus heteroclitus*, the dominant fish species in US Atlantic coastal salt marshes (Kneib 1986, 1987, 1997). Estimated densities of small *F. heteroclitus* (throw trap) and catches of larger conspecifics (minnow trap) were greater in creeks with higher percentages of marsh, lower percentages of watershed imperviousness, and continuous marsh below creek mouths/culverts.

The dependency of *F. heteroclitus* on *Spartina alterniflora* salt marsh is well established (Kneib 1984, 1986, Teo & Able 2003, Meyer & Posey 2009). *F. heteroclitus* is known to use this marsh type for foraging and refuge (Weinstein 1979, Kneib 1997, Rozas & Minello 1998, Teo & Able 2003, Allen et al. 2007) as well as reproduction (Taylor et al. 1977, 1979). The percentage of vegetated marsh surface in creeks was

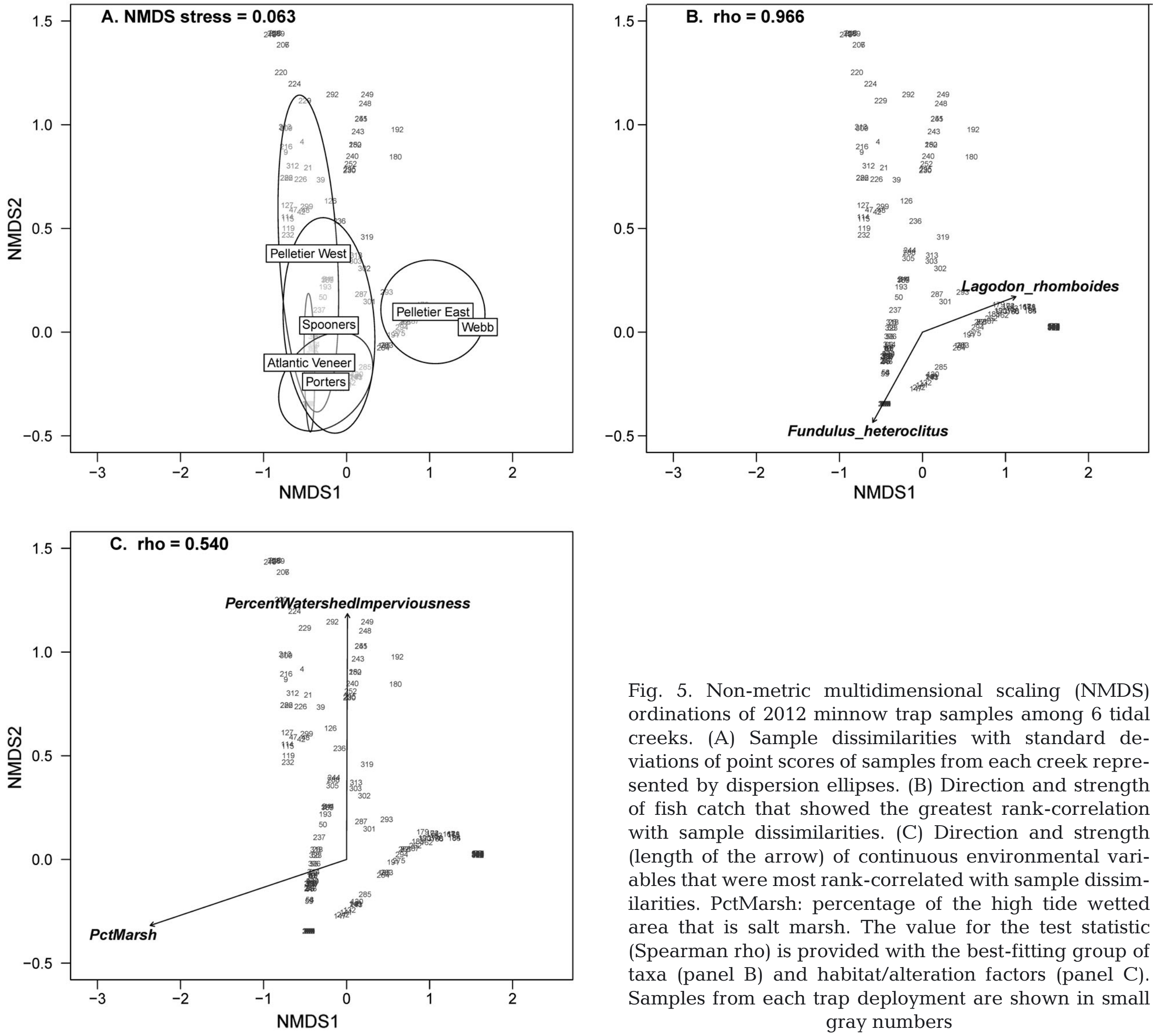


Fig. 5. Non-metric multidimensional scaling (NMDS) ordinations of 2012 minnow trap samples among 6 tidal creeks. (A) Sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses. (B) Direction and strength of fish catch that showed the greatest rank-correlation with sample dissimilarities. (C) Direction and strength (length of the arrow) of continuous environmental variables that were most rank-correlated with sample dissimilarities. PctMarsh: percentage of the high tide wetted area that is salt marsh. The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C). Samples from each trap deployment are shown in small gray numbers

a significant factor in minnow trap analyses and associated closely with *F. heteroclitus* in ordination space. Our results associating this marsh resident species with less altered habitats are consistent with those of Lowe & Peterson (2014), who found a congener, *F. grandis*, in greater abundance in less urbanized Gulf of Mexico tidal creeks. Intertidal marsh surface is recognized as facilitating secondary production in tidal creeks (Kneib 2000, Teo & Able 2003) by providing an enhanced refuge from predation and greater trophic support than unvegetated channels (Kneib 1987, McIvor & Odum 1988, Kneib 2003).

Imperviousness is an integrated metric of urbanization in watersheds (Schueler 1994, Arnold & Gibbons 1996, Wang et al. 1997, 2001, Schueler et al. 2009, Coleman et al. 2011) that can lead to contamination to tidal creeks (Kennish 1991, Sanger et. al. 1999a,b). Watershed imperviousness was a significant factor in minnow trap BIOENV models. Three study creeks (Pelletier West, Pelletier East, and Webb Creeks) lie in watersheds with imperviousness exceeding 20% (Table S1 in the Supplement), and these were the least related to *F. heteroclitus* abundance in both throw trap and minnow trap ordinations.

The presence of contiguous marsh downstream of sampled areas was also a factor that associated with *F. heteroclitus* densities. This finding is consistent with the view that marsh configuration and structural connectivity, not merely presence/absence, is important in determining nekton patterns in tidal creeks (Partyka & Peterson 2008, Green et al. 2012, Lowe & Peterson 2014). Fragmentation of formerly continu-

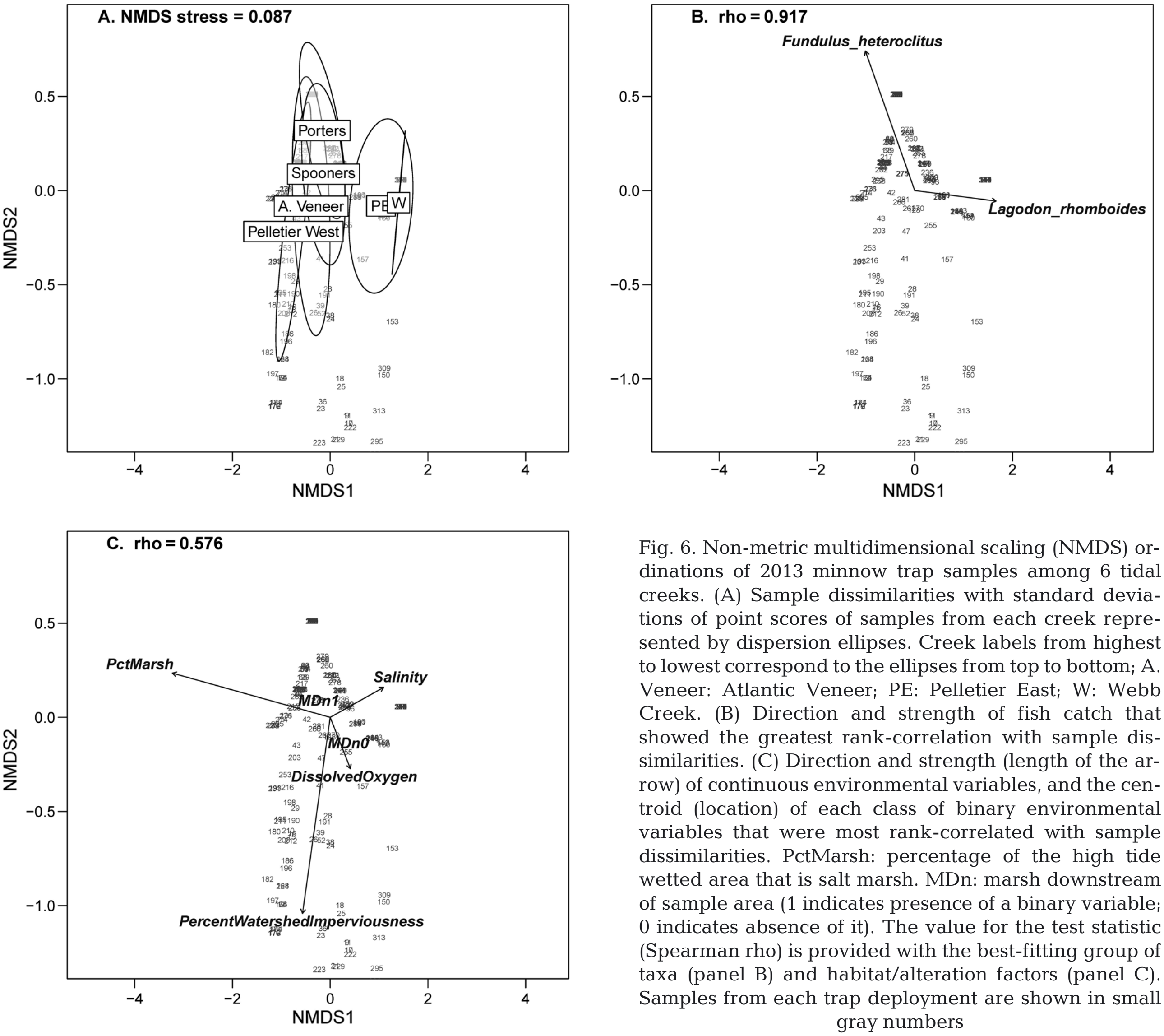


Fig. 6. Non-metric multidimensional scaling (NMDS) ordinations of 2013 minnow trap samples among 6 tidal creeks. (A) Sample dissimilarities with standard deviations of point scores of samples from each creek represented by dispersion ellipses. Creek labels from highest to lowest correspond to the ellipses from top to bottom; A. Veneer: Atlantic Veneer; PE: Pelletier East; W: Webb Creek. (B) Direction and strength of fish catch that showed the greatest rank-correlation with sample dissimilarities. (C) Direction and strength (length of the arrow) of continuous environmental variables, and the centroid (location) of each class of binary environmental variables that were most rank-correlated with sample dissimilarities. PctMarsh: percentage of the high tide wetted area that is salt marsh. MDn: marsh downstream of sample area (1 indicates presence of a binary variable; 0 indicates absence of it). The value for the test statistic (Spearman rho) is provided with the best-fitting group of taxa (panel B) and habitat/alteration factors (panel C). Samples from each trap deployment are shown in small gray numbers

ous marsh area into discontinuous patches has been identified as contributing to reduced abundances of fishes and crustaceans in first-order salt marsh creek systems in other areas in the western Atlantic (Valentine-Rose et al. 2007, Lowe & Peterson 2014); this anthropogenic change is more likely to affect smaller less mobile organisms such as the cyprinodont fishes (Lowe & Peterson 2014, present study). Habitat connectivity appears to be a factor influencing residency and movement of *F. heteroclitus* in salt marsh seascapes (Rozas et al. 1988, Able et al. 2012).

Related to the presence/absence of contiguous marsh, culverts were also in best fitting throw trap BIOENV models. These structures can act as barriers to animal movement in salt marsh creeks (Stevens et al. 2006, Eberhardt et al. 2011) and fragment formerly continuous marsh habitat (Kennish 2001). In North Carolina, culverts are considered an anthropogenic factor compromising the quality of estuarine fish habitat (Deaton et al. 2006). Culverts may impede downstream movement of resident fishes or upstream movement of transient estuarine predators, effectively trapping fish biomass above them (Stevens et al. 2006). One creek with a short culvert (Atlantic Veneer) had catch rates of both small and large *F. heteroclitus* that were higher than the 2 unculverted study sites (Porters and Webb Creeks). Thus, the impact of culverts on resident species remains unclear. Sampling logistics restricted our throw trap sampling to only one creek (Porters Creek) lacking a culvert. We elected not to include culverting as a categorical factor in follow-up univariate models

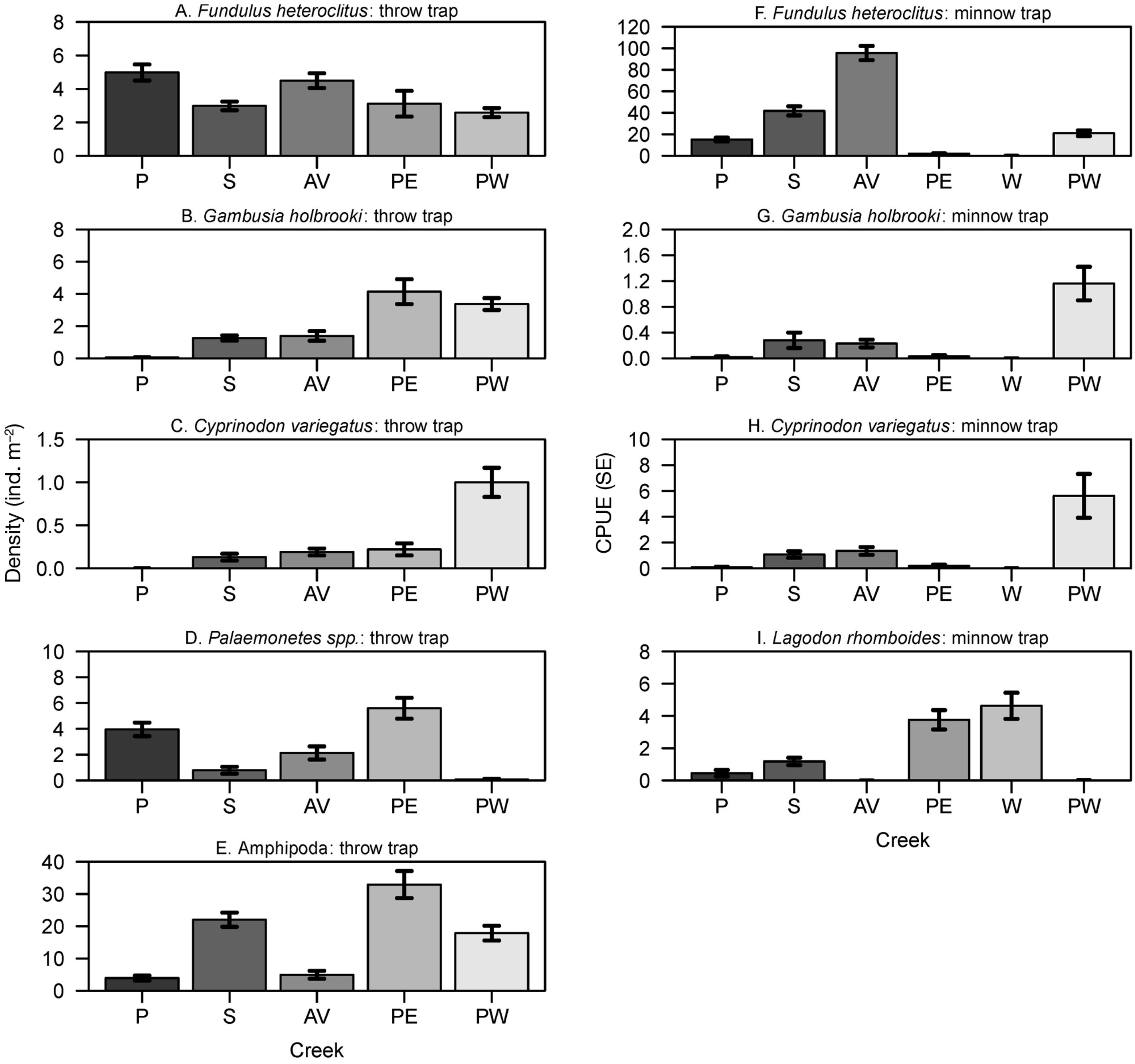


Fig. 7. (A–E) Density (mean ± SE) of dominant macrofauna collected with a 1 m^2 throw trap in 5 tidal creeks and (F–I) catch-per-unit-effort (CPUE, mean ± SE) of dominant macrofauna from wire mesh minnow traps set on 3 h soak times in 6 tidal creeks sampled in coastal North Carolina, USA, in 2012 and 2013. Creeks are listed in order of increasing greater watershed imperviousness: Porters (P), Spooners (S), Atlantic Veneer (AV), Pelletier East (PE), Webb (W) and Pelletier West (PW). Throw trapping was not conducted in Webb Creek

because it did not separate creek communities as strongly as the presence/lack of marsh connectivity and there was only one creek where we throw trapped that lacked a culvert.

Water depth also appears to be an important determinant of nekton abundances in tidal creeks (Allen et al. 2007). This geomorphological metric was associated with community differences in throw trap samples. *F. heteroclitus* prefers shallow, largely intertidal creeks (Ruiz et al. 1993, Smith & Able 1994, Bretsch & Allen 2006, Allen et al. 2007, Meyer & Posey 2009). Our shallow study sites included Atlantic Veneer, Porters, Pelletier West, and Spooners Creeks, which had high or moderate abundances of *F. heteroclitus.* Atlantic Veneer, the creek with the shallowest mean channel depth, consistently had the greatest number catch of minnow-trapped *F. heteroclitus.* In contrast, we found minnow-trapped *Lagodon rhomboides* to be most abundant in creeks with greater mean channel depths (Pelletier East and

Webb Creeks), which is consistent with previous observations that this species prefers deeper waters than marsh residents such as *F. heteroclitus* (Bretsch & Allen 2006, Meyer & Posey 2009).

Visually estimated stem coverage of *S. alterniflora* is a possible explanation for differences in abundances of resident nekton among study creeks. This habitat factor was not considered as a factor in throw trap BIOENV analyses because it was incorporated into estimates of catchability for dominant taxa collected by this gear type. For amphipods that attach themselves to stems of emergent marsh vegetation (Covi & Kneib 1995), this could offer an explanation for higher densities of this taxon in Pelletier East and Pelletier West Creeks. However, it would not simultaneously explain lower densities of *F. heteroclitus* from these creeks; while *F. heteroclitus* is a species that relies heavily on *S. alterniflora* for refuge (Kneib 1986), it was found in greater densities in creeks with the lowest stem density of *S. alterniflora*. Amphipods may respond to vegetation density on more localized scales than *F. heteroclitus* or it may be that *F. heteroclitus* prefers lower stem densities.

Contrasting patterns of abundance between *F. heteroclitus* and one of its prey types (amphipods) suggest that, in addition to habitat or environmental factors, predator–prey interactions might influence densities of nekton in small saltwater creeks (Bass et al. 2001). Amphipods, the most abundant species in throw trap samples, are common prey of both adult and juvenile *F. heteroclitus* (Nixon & Oviatt 1973, Kneib 1986, Allen et al. 1994) and were at their lowest densities in creeks with highest *F. heteroclitus* abundances. Predator–prey dynamics may also explain why the abundance of another prey taxon of adult *F. heteroclitus* (Kneib 1986), *Palaemonetes* spp., did not directly relate to creek alteration levels despite research showing that it is more abundant in creeks with less development, more extensive *S. alterniflora* marsh, and lower percentages of hardened shoreline (Fulton et al. 1996, Porter et al. 1997, Key et al. 2006, Krebs et al. 2014b).

Researchers have found the amount of marsh edge to be a determinant of nekton abundance in salt marsh creeks (Baltz et al. 1993, Minello et al. 1994, Peterson & Turner 1994, Kneib 2003, Visintainer et al. 2006). As an interface between 2 different habitat types, edge represents access to the marsh by nekton and its value to these species is often evaluated by examining the ratio of linear edge to vegetated marsh area in a system (Boström et al. 2011). The ratio of edge to vegetated habitat area is greater for small areas than large ones (Wiens et al. 1993). In our creeks, the ratio of edge to area was predictably negatively correlated with proportional marsh area (Spearman r = –0.90, p = 0.005). Thus, proportional marsh area represented both the edge and vegetation effects. Creeks such as Porters and Pelletier East, with relatively low amounts of proportional marsh area, had relatively high proportional edge compared to the other 3 marsh creeks that were sampled. This may offer an explanation for the continued production of some estuarine species in altered coastal habitats (Chesney et al. 2000) and, in our study, for the close association of the decapod *Callinectes sapidus* with the sparsely vegetated- and highly altered Pelletier East Creek. Our throw trap sampling in this creek was restricted to a laterally narrow swath of marsh there. *C. sapidus* tends to be more abundant near edges (Peterson & Turner 1994, Minello 1999) and also forages more successfully in these spaces (Lewis & Eby 2002). *L. rhomboides*, *Mugil* spp. and xanthid crabs also appear to prefer marsh edge (Peterson & Turner 1994) and were closely associated with Pelletier East in the 2013 throw trap ordination.

For the smaller fish caught in throw traps, 2 cyprinodontiformes fishes, *Gambusia holbrooki* and *Cyprinodon variegatus*, were more closely associated with creeks with more altered characteristics such as high watershed imperviousness, culverts, and discontinuous marsh downstream. This was also seen for larger-sized *G. holbrooki* and *C. variegatus* in minnow traps (Fig. 7, Table 3), but these 2 species were not in best fitting minnow trap BIOENV models in either year. *G. holbrooki* is a species found in lower densities at higher salinities (Alcaraz & Garcia-Berthou 2007) and appears to optimize individual growth in marsh habitats with artificial freshwater pulses (Piazza & LaPeyre 2010); this would explain why this species associated most closely with Pelletier West, the creek with the greatest imperviousness and lowest salinity. *C. variegatus* is a species that utilizes *S. alterniflora* marshes for habitat (Peterson & Turner 1994, Rozas & Zimmerman 2000). However, as was the case in this study, *C. variegatus* has been found in disturbed creeks in Gulf of Mexico estuaries (Lowe & Peterson 2014), potentially due to its ability to withstand highly variable water quality (Nordlie 1985) or due to a release from competition with *Fundulus* spp. (Lowe & Peterson 2014). Additionally, *G. holbrooki, C. variegatus* and *L. rhomboides* were found in greater abundances in creeks possessing standing water than those lacking it.

Transient species were relatively rare in our study. *L. rhomboides*, an omnivorous fish (Muncy 1984) and the only transient taxon caught in abundance by either gear, associated most closely with creeks that were deeper, having little or no marsh surface, and possessing alterations at the creek (low percentages of marsh, shoreline hardening) and watershed levels (high imperviousness). Lowe & Peterson (2014) found *L. rhomboides* to be more abundant in urbanized tidal creeks along the US Gulf of Mexico coastline and described this species as being able to exploit altered estuarine habitats. The high abundance of *L. rhomboides* in unvegetated Webb Creek does not support the previous assertion that marsh habitat is a critical nursery area for this species (Shervette & Gelwick 2007). Differences in recruitment levels among creeks appears to be an unlikely explanation for differences in catch rates, given that creeks differing markedly in catch rates were in geographically close proximity.

Recovery efficiency of the throw trap varied among taxa. We adjusted catch so that the community analyses were not biased to fauna with high recovery efficiencies. Rozas & Minello (1997) reviewed throw trap catch efficiencies (a combination of gear capture efficiency and recovery efficiency) and found them to be high and invariant by habitat type. We also found recovery efficiency to be high but influenced by water depth and vegetation stem density. Given that estimated absolute densities (corrected for recovery efficiency) were roughly 25 and 35 % higher than cumulative catch for *F. heteroclitus* and Amphipoda, respectively, we suggest that future research using enclosure sampling (e.g. throw trapping) in marsh or other heterogeneous habitats employ these or similar methods to estimate recovery efficiencies for main species and habitat types. It is important to point out that the method we used to estimate absolute abundances addresses a bias in failing to collect the full number of fauna enclosed by the throw trap (recovery efficiency) but does not address 'gear capture efficiency' (Rozas & Minello 1997). This is one reason why we sampled with 2 different gear types in this study.

Initiatives to maintain the biological integrity of developing watersheds require understanding the relationship between metrics of urbanization and biological integrity (Wang et al. 1997). Studies into the state and trends of biological production become more difficult the further estuarine habitats become altered from baseline conditions (Peterson & Lowe 2009). While each creek had a unique suite of habitat and anthropogenic characteristics, we recognize that, across study sites, some factors were correlated or were not replicated. Increasing the number of study sites and then conducting similar analyses would further elucidate the influence of specific habitat and urbanization factors, and combinations of factors, on biological communities in tidal creeks in this region.

Coastal development will continue to place anthropogenic stress on *S. alterniflora* salt marsh creeks that are vital to fish and crustacean production in the US Atlantic coastal plain. Roughly 12% of salt marsh habitats in the US South Atlantic region have been lost to development (Gedan & Silliman 2009) and the locations of creeks sampled for this study are forecast to continue increasing in human population. Our findings in the southeast USA can be viewed as the minimum human impact that can be anticipated if the forecasted coastal development to this geographic area continues. Our results predict that densities of dominant resident salt marsh nekton, such as *F. heteroclitus* and *Palaemonetes* spp., are likely to decline and densities of habitat generalist species, such as *L. rhomboides*, are likely to remain with the loss of marsh and continued conversion of upland from vegetated to impervious surfaces. Agencies charged with permitting coastal development should consider the impacts on nekton communities from projects that reduce marsh area and sever the connectivity between marshes patches across the US South Atlantic coastal landscape.

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