

Fragmentation of habitat affects communities and movement of nekton in salt marsh tidal creeks

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ABSTRACT: The specific biological impacts of anthropogenic activities and associated fragmentation of estuarine habitats remain understudied. We compared nekton communities and fish movement at 9 road crossings (with culverts) and a tenth crossing ('reference' crossing that lacked a road or a culvert) in first-order *Spartina alterniflora*-dominated tidal creeks in coastal North Carolina. Sample sites were located on both sides of each crossing. Percent salt marsh and increasing water depth were factors that most contributed to dissimilarities in biological communities among sample sites; the resident salt marsh fish *Fundulus heteroclitus* dominated the catch at sites with high percentages of marsh and inherently shallow depths while a transient species *Lagodon rhomboides* dominated at deeper sites where marsh was absent. *F. heteroclitus* was marked with injectable elastomer to determine factors influencing its movement probability to sites on sides of crossings opposite from where it was tagged. The probability of *F. heteroclitus* moving was positively related to the percentage of marsh-fringed shoreline within its published home range and was highest at intermediate water depths. The results show that preserving salt marsh adjacent to road crossings will maintain communities and movement rates reflective of non-impacted habitats in tidal creeks in the US South Atlantic coastal plain and emphasize habitat connectivity as an ecological factor important to community structure and movement.

KEY WORDS: Salt marsh · *Fundulus heteroclitus* · Habitat fragmentation · Culverts

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INTRODUCTION

Habitat connectivity is an integral part of seascape structure and important for sustaining populations of estuarine nekton (Eggleston et al. 1999, Micheli & Peterson 1999, Roth et al. 2008). In the context of landscape or seascape ecology, connectivity is 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al. 1993, p. 571). Connectivity has implications for habitat patch use by estuarine nekton (Micheli & Peterson 1999) and transfer of production from salt marshes (Kneib 2000, Stevens et al. 2006), and may explain a substantial proportion of fish production in estuaries (Meynecke et al. 2008, Valentine-Rose et al. 2011).

Reduced connectivity between habitat patches, or fragmentation, represents an anthropogenic threat to

biodiversity worldwide (Collinge 1996) and can dramatically alter fish community composition in tidal creeks (Layman et al. 2004). Estuarine habitat fragmentation can be viewed as a change in the structural arrangement of patches (Peterson 2003). Despite the importance of habitat connectivity, the influence of fragmentation in specific habitats and on specific taxa remains an understudied area of marine and estuarine ecology (Grober-Dunsmore et al. 2009).

Anthropogenic impacts to tidal creeks along the US South Atlantic coast include changes to sub-tidal habitat features and fragmentation of formerly connected habitats across intertidal areas due to development practices such as road construction and shoreline armoring (Forman et al. 2003, Valentine-Rose et al. 2007a, Eberhardt et al. 2011, Lowe & Peterson 2014). Shoreline armoring of estuaries is an

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example of 'structural fragmentation' that eliminates intertidal salt marsh habitat (Peterson & Lowe 2009) and has been found to reduce the integrity (Bilkovic & Roggero 2008) and density (Torre & Targett 2016) of estuarine fishes near armored sites. Fragmentation can also be hydrological, in which case the anthropogenic impediment to water flow also blocks the flow of organisms, matter, or energy (Valentine-Rose et al. 2007b). Road building and associated culvert placement is one example of hydrological fragmentation that poses a behavioral and physical deterrent to fish movement in both freshwater (Warren & Pardew 1998) and estuarine environments (Eberhardt et al. 2011).

Vegetated salt marsh is critical to the energy flow (Teal 1962) and ecology (Kneib 1997) of tidal creeks in the US South Atlantic region. Water depth is an important determinant of nekton use of intertidal salt marsh creeks along the US South Atlantic coast (Allen et al. 2007, Rudershausen et al. 2016) and metrics of channel morphology (such as water depth) influence nekton movement through these corridors (Rozas et al. 1988, Visintainer et al. 2006, Allen et al. 2007, Boström et al. 2011). Culverts, dredging, and shoreline armoring are common anthropogenic impacts on salt marshes (Lee et al. 2006), deepening these inherently shallow creeks. However, state and federal natural resource agencies lack information on the extent of these types of anthropogenic impacts on critical salt marsh habitats (North Carolina Division of Marine Fisheries 2010, Environmental Protection Agency 2017). Despite the potential for fragmentation to alter movement patterns of nekton, the specific effects of fragmentation on movement of estuarine nekton species remain largely unknown (Minello & Rozas 2002, Meynecke et al. 2008).

In this study, we examine how fragmentation within tidal creeks influences nekton communities and whether culverts and instream habitat features influence the probability of movement of a dominant fish species, *Fundulus heteroclitus*. For the community analyses, our goal was to determine whether factors at small (within-creek) spatial scales contributed to differences in nekton community assemblages between paired sites in close proximity to each other. For the movement analyses, we sought to determine whether road culverts were barriers to connectivity or whether *F. heteroclitus* could pass these culverts but elected not to due to site-specific factors. The fish's ability to move through a culvert thus defined whether a culvert or similar break in salt marsh habitat from development results in a loss of connectivity in these systems.

MATERIALS AND METHODS

Study sites

We sampled in 10 first-order tidal creeks in Carteret County, coastal North Carolina (USA) from April 2015 to July 2016. The study creeks epitomize patchy estuarine habitats found in heterogeneous and developing coastal landscapes (Boström et al. 2011). These creeks generally have salinities greater than 20 psu during non-rain events with a range of 0 to 36 psu (Rudershausen et al. 2016). Each of the studied crossings experiences semi-diurnal tides. Tidal amplitudes in this region of the US Atlantic coast are roughly 1 m in range (Kirby-Smith & Costlow 1989). The study creeks are located in close geographic proximity to one another (<35 km) and some are substantially altered from development.

Similar to Eberhardt et al. (2011), we defined a 'crossing' as a longitudinal segment of tidal creek where there was a culvert under a road or a reference segment of creek (no culvert) of similar length to a culvert. Thus, each creek crossing consisted of a longitudinal creek segment whose length was the distance between fixed trap sample sites located immediately at each end of the segment. All but 1 of the 10 crossings had a culvert (Fig. 1, Table 1).

Crossings with culverts varied as to whether *Spartina alterniflora* salt marsh was present on both sides of the culvert or only on one side. The reference crossing had salt marsh on both sides. Among the 10 creeks and 20 sites that were sampled, as well as other areas along the US South Atlantic coast, reduced or eliminated salt marsh at a site can be a consequence of shoreline armoring (Kennish 2001, Gittman et al. 2015), dredging (Kennish 2001), and culvert scour that often widens and deepens sub-tidal habitats adjacent to culverts (Wargo & Weisman 2006, authors' pers. obs.). The distance from each sample site to the nearest patch of salt marsh was 0 on both sides of 6 crossings. For the other 4 crossings, this distance was 0 on one side of the crossing but greater than 0 on the side of the crossing lacking physical connectivity to salt marsh (range from 6 to 430 m).

The physical characteristics of the 9 culverts across which we sampled typify those found bisecting tidal creeks in coastal North Carolina (authors' pers. obs.). The bottom of the full length of each culvert remains covered with water at low tides. Most of the culvert crossings exhibited scour pools at the downstream sample site except for Wading Creek (scour pools at both the upstream and downstream sample sites) and Town Creek (no obvious scour pools from the culvert).

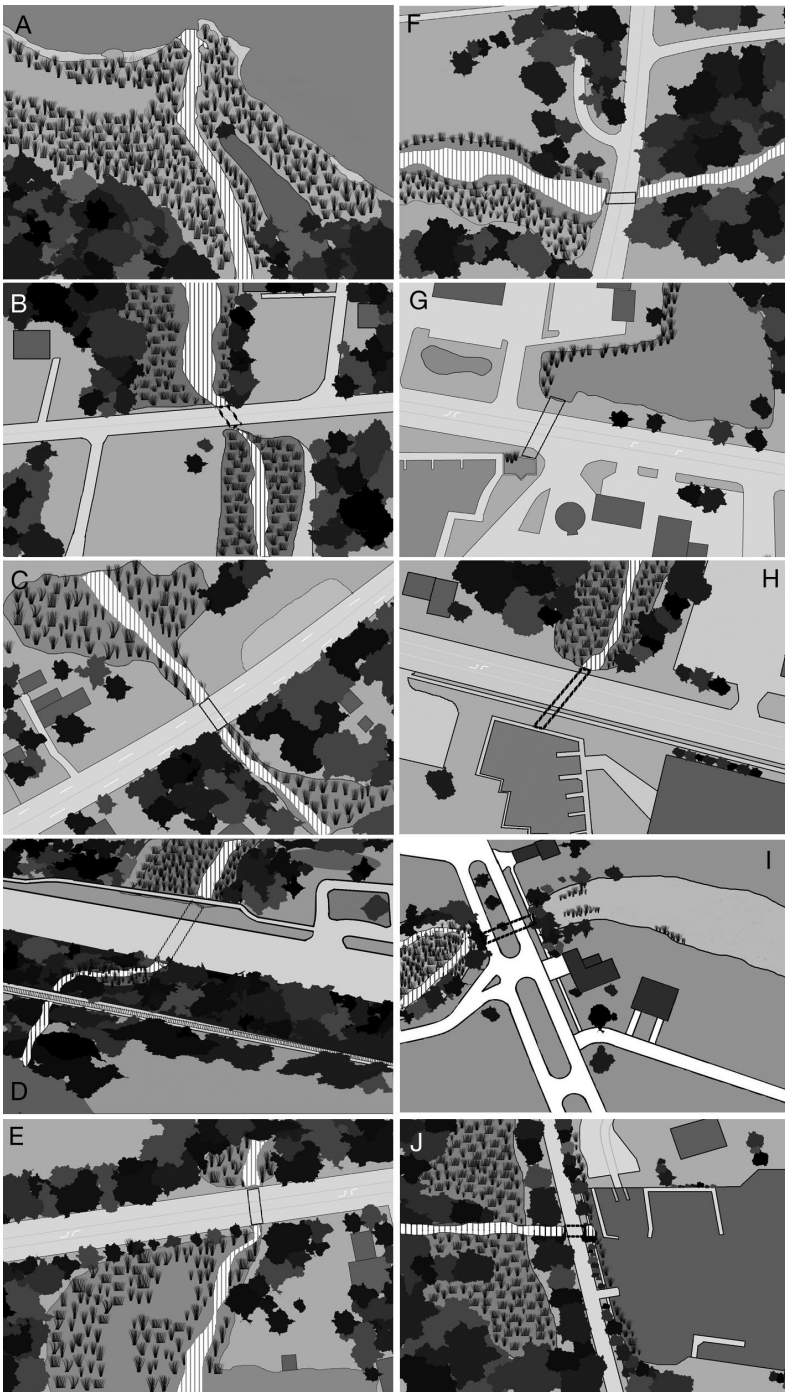


Fig. 1. 'Birds-eye view' sketches of 10 crossings in first-order tidal creeks in coastal North Carolina studied for nekton communities and movement rates of *Fundulus heteroclitus* in 2015–2016. The reference crossing represented in panel A did not have a culvert. The rectangular outlines on panels B–J denote the culvert crossings for those sites. Sample sites for panels A–D were considered non-impacted while one sample site at each of the crossings in panels E–J was considered impacted by instream development. Road surfaces are represented by the lightest gray shade, upland by the next lightest gray, buildings by gray rectangles, standing water by darker gray, sub-tidal creek channels by white with black hatching, and salt marsh by gray with black tussocks. Blotched multiple grayscale shading represents tree cover

We measured anthropogenic and habitat features that had the potential to influence community structure and *Fundulus heteroclitus* movement probability. Fixed factors recorded at each site included percent fringing salt marsh (described below), presence or absence of salt marsh connected to a site, distance to the nearest marsh from each site on the same side of the crossing, presence or absence of bulkheading at a site, and water depth. Culvert length, a shared metric between the 2 sites at each crossing, was also recorded. Current velocity at each crossing, over both ebb and flood tides, was measured with a General Oceanics model 2135 flowmeter (General Oceanics) over several occasions at each crossing.

We used the percent of vegetated marsh edge above upstream sample sites and below downstream sample sites as a metric of marsh integrity (Baltz et al. 1993). We measured the combined percentage of marsh that fringed both shorelines to a distance of 200 m away from each site. This 200 m distance (via creek meander) was selected because it is an approximate maximum home range distance (Skinner et al. 2005) for the dominant salt marsh fish species in this region, *F. heteroclitus* (Able & Fahay 1998). Sites without development had 100% marsh edge. The length of each crossing (distance between sample sites) was far less than the published home range distance of *F. heteroclitus*, increasing the probability that any patterns of *F. heteroclitus* would not be due to its limited dispersal.

Nekton sampling for effects of habitat fragmentation on community structure

Each site was sampled with Gee-style wire mesh minnow traps. All traps had 6.4 mm square mesh and funnel openings 20 mm in diameter. Traps were baited with whole dead

Table 1. Habitat and anthropogenic characteristics of 10 crossings (abbreviations as in Fig. 1) in first-order tidal creeks in coastal North Carolina sampled for nekton communities and movement rates of *Fundulus heteroclitus* in 2015–2016. Latitude and longitude for each crossing are provided. Site types above and below each crossing were classified as: (1) lacking a culvert and having no impact (reference: R), (2) having a culvert next to them but otherwise having no impact (non-impacted: N-I), and (3) having a culvert next to them and impacted by development (impacted: I). 'Marsh percent' is the percentage of salt marsh in the published home range of *Fundulus heteroclitus* on the side of the crossing where the site was located. Culvert types are: none (reference crossing), pipe, box, or both. Ebb- and flood-tide current velocities as well as water depths ('depth') were measured at mid-tide. 'Area' depicts the cross-sectional area of the culvert pipe or channel.

Crossing name (abbreviation)	Latitude (°N)	Longitude (°W)	Site type, marsh percent		Culvert		Depth at sample site (m)		Current velocity (m s ⁻¹)		
			Above	Below	Type	Length (m)	Area (m ²)	Upstream	Downstream	Ebb	Flood
Porters (A)	34.759664	76.721992	R, 100	R, 100	(None)	30	1.8	0.50	0.68	0.27	0.12
Atlantic Veneer (B)	34.709431	76.622672	N-I, 100	N-I, 91	Pipe	13	0.8	0.40	0.58	0.23	0.34
Town (C)	34.721722	76.649936	N-I, 100	N-I, 100	Both	28	10.2	0.39	0.37	0.13	0.10
Bridges (D)	34.730064	76.772750	N-I, 100	N-I, 100	Box	46	2.4	0.20	0.40	0.01	0.01
Goose (E)	34.703928	77.017822	N-I, 100	I, 100	Box	29	2.3	0.70	1.20	0.06	0.04
Wading (F)	34.748875	76.651181	I, 5	N-I, 100	Box	11	1.6	0.90	1.00	0.73	0.46
Pelletier East (G)	34.729111	76.774806	N-I, 50	I, 1	Box	36	2.4	0.40	0.78	0.47	0.10
Pelletier North (H)	34.731567	76.781633	N-I, 100	I, 12	Box	38	1.7	0.23	1.68	0.04	0.09
Pelletier West (I)	34.731278	76.785772	N-I, 100	I, 35	Pipe	30	2.5	0.70	0.84	0.20	0.07
Spooners (J)	34.730867	76.809553	N-I, 100	I, 37	Pipe	19	4.5	0.79	0.90	0.38	0.07

Brevoortia tyrannus and fished roughly twice per month over 24 h soak times from April 2015 to July 2016. Exceptions to trap sampling occurred in instances of lost or opened traps, which were not counted, and 3 crossings that were first sampled after the study started; Bridges Creek was first sampled in August 2015 while Goose and Wading creek crossings were first sampled in March 2016. During each 24 h soak time, we deployed one trap in the sub-tidal creek channel at both the upstream and downstream ends of each culvert. In the case of the reference crossing, traps were deployed a distance apart from each other that was an approximate average distance separating sites at the culvert crossings (Table 1). At the conclusion of each trap deployment, individuals were identified, counted, and released (except for tagged *F. heteroclitus*; see below). Most individuals were identified to species but some were identified to genus or family levels in instances where multiple closely related species in a higher order taxa were known to occur in this geographic region (for *Gobiosoma* spp., *Mugil* spp., *Eleotridae*, *Palaemonetes* spp., *Farfantepenaeus* spp., and *Xanthidae*).

Like all sampling gears, minnow traps are size selective. By virtue of the sizes of their trap meshes and funnel entrances, respectively, minnow traps have lower and upper limits of size selectivity. However, this gear is nonetheless one by which numerous salt marsh nekton species can be sampled for relative abundances while minimally impacting habitat (Talley 2000, Rudershausen et al. 2016). Minnow traps retain fishes of roughly 40–110 mm total length, depending on species (West & Zedler 2000, Teo & Able 2003, Rudershausen et al. 2016), and crustaceans over roughly the same size range (authors' pers. obs).

Analyses of nekton communities

We tested for differences in nekton communities among site types and determined habitat and anthropogenic factors most responsible for these differences. The community analysis was conducted using data from the full study period (when not all creeks were sampled in early months). It was also done for the portion of the study (March 2016–July 2016) when data were collected simultaneously in all 10 creeks to determine whether the results changed compared with analyzing the full dataset collected over the entire study.

For the community analysis, we used published studies (Bretsch & Allen 2006, Allen et al. 2007, Bilkovic 2011, Rudershausen et al. 2016) that have

identified important habitat and physical determinants of tidal creek nekton communities along the US South Atlantic coast (salt marsh, shoreline armoring, and water depth) to separate sites into 3 groups. These 3 groups were (1) a site that lacked a culvert and had no visible physical impact ('reference'), (2) sites with a culvert next to them but otherwise having no impact ('non-impacted'), and (3) sites with a culvert and obviously impacted by development (reduction or complete loss of salt marsh from one or more causes and/or obvious change in creek morphology) ('impacted') (Table 1). We focused our sampling effort on crossings with one or more anthropogenic impacts to better understand their effects on nekton communities and movement. In addition to the community analysis, we compared catch rates of each dominant species among the 3 site types using 1-way ANOVA on logarithmically transformed data ($\ln(x + 1)$) and using Tukey's HSD post-hoc test for pairwise comparisons between site types.

Non-metric multi-dimensional scaling (NMDS) was used to graphically depict the community of nekton captured for each of the 3 site types. NMDS is an ordination technique well suited for visualizing non-normal or discontinuous data in 2-dimensional graphical space (Clarke 1993, McCune & Grace 2002). The NMDS algorithm seeks to minimize stress, a measure of fit that determines how well the Euclidean distances preserve sample dissimilarities (Kruskal 1964, McCune & Grace 2002).

We conducted NMDS with each individual trap sample as its own community (data point) in the ordination. The Bray-Curtis coefficient was used to construct similarity matrices for the sample-by-species matrix on counts of individuals from minnow trap collections, which were square-root transformed to diminish the influence of numerically dominant taxa. We elected to balance the inclusion versus exclusion of rare species by conducting NMDS on species that occurred in at least 1% of the collections across all 3 site types. While each individual trap was considered a 'sample' for NMDS, traps with a zero catch across all taxa that met the 1% inclusion threshold cannot be evaluated and thus were eliminated from the analysis. Stress was computed as part of the NMDS. Stress levels $< \sim 0.2$ are considered reasonable while levels $> \sim 0.2$ can potentially lead to misinterpretation of scaling distances (Clarke & Warwick 2001). Following ordination model runs, we constructed NMDS plots depicting the centroid and standard deviation ellipse of each site's community.

Following NMDS, ANOSIM was conducted to quantify whether biological communities differed be-

tween the 2 sites at each creek. Increasingly more positive values of the ANOSIM test statistic, R , indicate greater differences in the nekton community among sites while an R value of 0 indicates no dissimilarities among sites (Chapman & Underwood 1999). A significant ($p \leq 0.05$) but low ($< \sim 0.2$) R value indicates effects that are relatively unimportant (compared with higher R values) and can result from large sample sizes. SIMPER analysis was conducted to determine the most influential taxa contributing to the overall Bray-Curtis dissimilarity between pairs of communities (McCune & Grace 2002).

In conjunction with NMDS, we determined whether the number of samples collected was sufficient to describe the community at each site. This was done by computing a pseudo multivariate dissimilarity-based standard error (multSE) (Lefchek 2015) and determining at what sample size at each site the error about the multSE value overlaps with the computed error for the final (highest) number of samples integrated into the multivariate analysis (in this case, NMDS) (Anderson & Santana-Garcon 2015). This analysis was implemented through the 'multSE' function (Lefchek 2015) run through R software (R Core Team 2015).

We tested for the influence of habitat and anthropogenic factors on nekton communities using the non-parametric BIOENV approach (Clarke & Ainsworth 1993). Habitat and anthropogenic factors tested included the presence or absence of salt marsh, percentage of salt marsh in the home range of *F. heteroclitus* on the same side of the crossing as where each site was located, distance from each site to the nearest salt marsh on the same side of the crossing, presence or absence of a culvert, culvert type, presence or absence of bulkheading, water depth at each site, presence or absence of standing water (across all tides) at each site, and water temperature, salinity and dissolved oxygen were taken upon each sample at a site. These different factors were considered due to the potential for taxa to respond differently to fragmentation and at different spatial scales (Eggleston et al. 1998, Minello & Rozas 2002).

BIOENV determines the suite of environmental and habitat factors with the greatest rank correlation with sample dissimilarities of the biological community analyzed through ordination. We conducted the BIOENV analyses using a 'forward selection, backward elimination approach' where the rank correlation of sample dissimilarities between a subset of environmental variables or taxa and the full dataset of environmental variables or 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 and habitat data (McCune & Grace 2002). A non-parametric Spearman rank correlation coefficient (ρ) is calculated for each suite of habitat and anthropogenic factors. After the group of best-fitting factors is determined (greatest ρ value), they can be plotted in NMDS ordination space. Each continuous environmental and habitat factor in the most parsimonious BIOENV model is plotted as a vector, while each level of a categorical factor is plotted as a point. Following the determination of the best-fitting suite of environmental and habitat factors, a permutation test was used to determine whether each factor in the most parsimonious BIOENV model was significantly rank-correlated ($\alpha = 0.05$) with ordination sample dissimilarities.

BIOENV can also be conducted with biological data. We used this approach to determine the group of nekton taxa that showed the greatest rank correlation with sample dissimilarities. Each taxon in the best-fitting BIOENV analysis is plotted as a vector. The NMDS ordination, BIOENV, fitting of environmental and habitat variables and taxa, and permutation tests were conducted with R software (R Core Team 2015) using the 'vegan' package (Oksanen et al. 2016).

Sampling for *F. heteroclitus* movement past crossings

We estimated movement probabilities of adult *F. heteroclitus* past the crossings. The process to estimate movement probability involved batch-tagging *F. heteroclitus* caught after each 24 h soak of minnow traps. Fish from the upstream site were tagged with a different color of visible implanted elastomer (VIE) tag (Northwest Marine Technology) and different body location than fish from the downstream site. Tagged fish were released back to the site from which they were captured. Subsequent sampling (24 h soaks) to collect movement data on each batch of tagged fish occurred on both sides of the crossing at least 1 wk after each tagging exercise and lasted until at least 8 wk post-tagging. We recorded the total number of tagged individuals of each tag color and body location at each site. Using this information, we classified each recaptured fish as a mover (to the opposite side of the crossing from where it was tagged) or a non-mover.

Analysis of *F. heteroclitus* movement

We sought to identify factors influencing *F. heteroclitus* movement past crossings. This process involved fitting binomially distributed random-intercept generalized linear models (generalized linear mixed models: GLMMs) with logit links. Mixed models allow the researcher to extend the model results from studies with at least 5–10 study 'subjects' to a larger population of 'subjects' (in this case, tidal creek crossings) that have similar characteristics (Kéry 2010).

For the data to which GLMMs were fitted, C (number of successes) represented the number of tagged individuals that had subsequently moved to the side of a crossing opposite from the side they were tagged, while N (number of trials) represented the total number of recaptured individuals, regardless of whether they moved or not. C was assumed to conform to an underlying binomial distribution (see Kéry 2010) with success probability p . For each crossing, we only used C and N data for the first sampling visit that a unique tag color and body location combination (from a single tagging event) was recaptured. This insured data from the same individual was not used twice in the analysis and reduced the chances that some recaptured individuals had made round-trip movements without intervening recapture on the side of a crossing opposite to the side at which they were originally tagged.

Before model fitting to movement data, we initially considered characteristics of both sites and crossings. Data for site-specific covariates considered in GLMMs were for the side of the crossing that C individuals moved to (the side opposite to which they were tagged and released). Site-level covariates initially considered included presence or absence of salt marsh at each site, the percentage of vegetated marsh edge within the *F. heteroclitus* home range of each sample site, and water depth.

Other covariates initially considered in movement models were attributes of the crossing separating the sites and thus had a shared value between the 2 sites: crossing length and current velocity. For current velocity, we averaged values across ebb and flood tidal currents at each crossing.

Collinearity between pairs of factors potentially explaining fish movement was examined with the Spearman rank correlation coefficient (when one factor in a pair was categorical) or the Pearson correlation coefficient (when both factors in a pair were continuous). The presence or absence of salt marsh at each site and percent salt marsh edge within the

published *F. heteroclitus* home range were strongly correlated (Spearman $\rho = 0.537$, $p < 0.001$); marsh presence or absence was dropped in favor of percent marsh edge in the home range due to potential movement of *F. heteroclitus* not only to specific sample sites but also over wider home range areas (Skinner et al. 2005). Percent marsh edge within the home range and culvert length were inversely correlated (Pearson $r = -0.254$, $p = 0.017$) owing to the fact less-developed marsh mosaics in this region are more likely to be bisected by narrower roads (authors' pers. obs.). However, this relationship was weak (low absolute value for the correlation coefficient), so we retained both factors. Percent marsh edge within the home range and site water depth were found to be inversely correlated (Pearson $r = -0.751$, $p < 0.001$) owing to a typical pattern along the US Atlantic coastal plain whereby water depth increases with conversion of salt marsh to developed shoreline (Hartig et al. 2002). For this reason, these 2 factors were not included in the same model but were included in separate models owing to the importance of each of them in dictating movements and abundance of tidal creek species (Allen et al. 2007, Rudershausen et al. 2016). Current velocity and crossing length were not included in the same model because they were negatively correlated (Pearson $r = -0.731$, $p < 0.001$). However, current velocity and crossing length were incorporated into each of the 2 full models. Each of these 4 factors was also tested alone in its own model.

Observed rates of movement displayed a linear pattern with percent marsh edge within the *F. heteroclitus* home range but a dome-shaped relationship with water depth, current velocity, and crossing length. Thus, models fitted to movement data simultaneously incorporated linear and quadratic terms for water depth, current velocity, and crossing length, respectively, and just a linear term for the percent of vegetated marsh edge within the *F. heteroclitus* home range. Before model fitting (outside of each model run), we centered values for each continuous covariate and the squared values for the water depth, current velocity, and crossing length covariates, a technique that improves the efficiency of the Markov chain Monte Carlo sampler when fitting a probabilistic model (McCarthy 2007). The 8 GLMMs of *F. heteroclitus* movement as well as a null (intercept-only) model were fitted via Bayesian inference using published prior probability distributions and likelihoods (Kéry 2010) (see code in the Supplement at www.int-res.com/articles/suppl/m586p057_supp.pdf).

Each GLMM was fitted by calling JAGS software version 4.0 (Plummer 2015) from R software using the

package 'R2jags' (Su & Yajima 2015) and run using 3 chains of initial values updated 100 000 times, a burn-in of 10 000, and thin of 10. Convergence was determined by computing the Gelman-Rubin statistic; values $< \sim 1.1$ suggest convergence to a stable posterior probability distribution (Gelman 1996).

The goodness of fit for each model fitted to *F. heteroclitus* movement data was assessed by computing a Bayesian probability (p) value (Gelman et al. 1996) (see code in the Supplement). This computation involves constructing a replicate dataset using parameter estimates obtained from the model fitted to the actual data (Kéry 2010). Chi-square was used as the discrepancy (goodness of fit) measure for both the actual and replicated data sets. This p -value computes the proportion of instances when the chi-square value for replicated dataset exceeds that for the actual dataset; Bayesian p -values of ~ 0.5 suggest an adequate model fit while values near 0 or 1 suggest a poor fit of the model to the data (Kéry 2010).

We used the Bayes factor (K) as a method of comparing parsimony of mixed models (Kass & Raftery 1995, Rouder et al. 2012) among the 8 models. The value for K for each model containing potential explanatory factors (relative to the null model) was computed using the function 'lmBF' in the R package 'BayesFactor' (Morey et al. 2015). Values for K in the range of 0–1, 1–3, 3–20, and > 20 respectively indicate negative, inconsequential, positive, and strong support for a model (Kass & Raftery 1995).

RESULTS

Analysis of nekton communities

A total of 500 trap samples were collected from the 20 sites. Of these, 32 traps were empty, resulting in 468 samples analyzed for community composition with NMDS. The number of replicate samples at each site adequately characterized the community; multivariate dissimilarity-based standard error calculations revealed the estimated minimum number of samples needed to characterize the community was exceeded for each site.

Two taxa dominated collections from the 10 crossings studied for community structure; the fish species *Fundulus heteroclitus* and *Lagodon rhomboides* comprised 93.3% of all individuals. Mean catch rates differed among sites for both *F. heteroclitus* ($F = 113.3$, $p < 0.001$, residual $df = 465$) and *L. rhomboides* ($F = 41.2$, $p < 0.001$, $df = 465$). The catch rates of each of these 2 species differed significantly between ref-

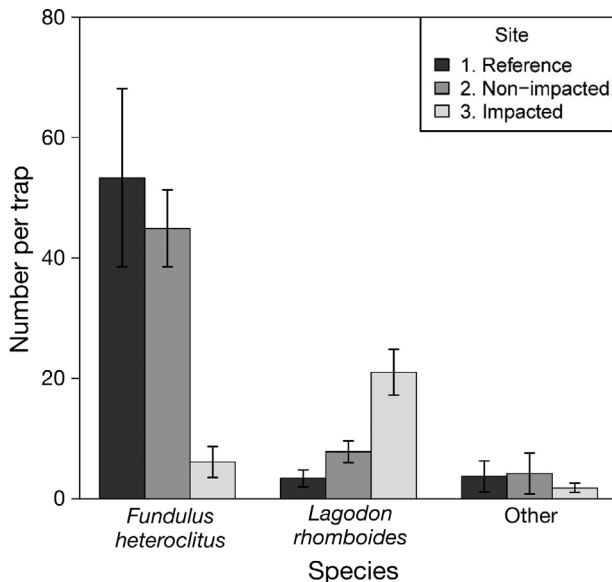


Fig. 2. Abundance (mean \pm SE) of 3 taxa groupings of nekton collected by wire mesh minnow traps at 3 types of sites in tidal creeks in North Carolina: sites (1) lacking a culvert and having no impact (reference = no culvert), (2) having a culvert next to them but otherwise having no impact (non-impacted), and (3) having a culvert next to them and impacted by development (impacted)

reference and impacted sites as well as between non-impacted and impacted sites ($p < 0.001$ in each case), but not between reference and non-impacted sites (*F. heteroclitus*, $p = 0.968$; *L. rhomboides*, $p = 0.470$) (Fig. 2).

Thirteen taxa exceeded the threshold frequency of occurrence for inclusion in ordination modeling. These taxa were the fishes *F. heteroclitus*, *L. rhomboides*, *Cyprinodon variegatus*, *Gambusia holbrooki*, *Gobiosoma* spp., *Anguilla rostrata*, *Mugil* spp., *Leiostomus xanthurus*, and *Eleotriidae*, as well as the crustaceans *Palaemonetes* spp., *Callinectes sapidus*, *Farfantepenaeus* spp., and *Xanthidae* spp.

Community composition overlapped between reference and non-impacted sites (ANOSIM $R < 0.2$) even though the p -value for this ANOSIM test statistic was marginally significant ($p = 0.046$; Table 2). Relatively high ANOSIM R values (>0.2) as well as significant p -values for these test statistics indicated less overlap between reference and impacted sites and between non-impacted

and impacted sites, respectively. NMDS plots also showed more overlap between reference and non-impacted sites than between each of these site types and impacted sites (Fig. 3A). The ordination stress was reasonably low (0.158). SIMPER analysis revealed that *F. heteroclitus* was the most influential species contributing to sample dissimilarities for each pair of site types (Table 2).

The NMDS, ANOSIM, and SIMPER results were largely similar when model fitting to the data collected simultaneously in all 10 creeks (March 2016–July 2016). The one exception was that the ANOSIM R value was not significant ($p = 0.070$) when communities were compared between reference and non-impacted sites using the reduced dataset.

The BIOENV analysis of environmental and habitat variables revealed 2 factors in the model that showed the greatest rank correlation (Spearman $\rho = 0.226$) with sample dissimilarities of the nekton community. Percent salt marsh and water depth at each site were continuous factors in this model that best fitted the data on habitat, environmental, and anthropogenic effects (Fig. 3B). Permutation testing found that each of these factors was significantly rank-correlated ($p < 0.01$) with ordination sample dissimilarities. The results were similar when BIOENV models were fitted to the reduced dataset collected simultaneously in all 10 creeks; both percent salt marsh and water depth were factors in the model that best fitted the reduced dataset.

The BIOENV analysis of species included in the NMDS ordination found that 9 of the taxa in the model showed the greatest rank-correlation with sample dissimilarities (Spearman $\rho = 0.762$) (Fig. 3C). The 2 dominant species, *F. heteroclitus* and *L. rhomboides*, were part of this suite of taxa and

Table 2. Results of ANOSIM testing for pairwise differences in nekton communities among 3 types of sites in North Carolina tidal creeks. Site types were classified as: (1) lacking a culvert and having no impact (reference), (2) having a culvert next to them but otherwise having no impact (non-impacted), and (3) having a culvert next to them and impacted by development (impacted). Sites were sampled with wire mesh minnow traps on both sides of 10 crossings in first-order tidal creeks in coastal North Carolina in 2015–2016. ANOSIM R values > 0.2 were considered to indicate community differences. Results from SIMPER analysis show the species making the greatest proportional contribution to nekton community differences for each significant ANOSIM result

Site pairing	–ANOSIM–		— SIMPER —	
	R	p	Taxa	Proportion
Reference vs. non-impacted	0.075	0.046	<i>Fundulus heteroclitus</i>	0.715
Reference vs. impacted	0.324	0.001	<i>Fundulus heteroclitus</i>	0.559
Non-impacted vs. impacted	0.382	0.001	<i>Fundulus heteroclitus</i>	0.551

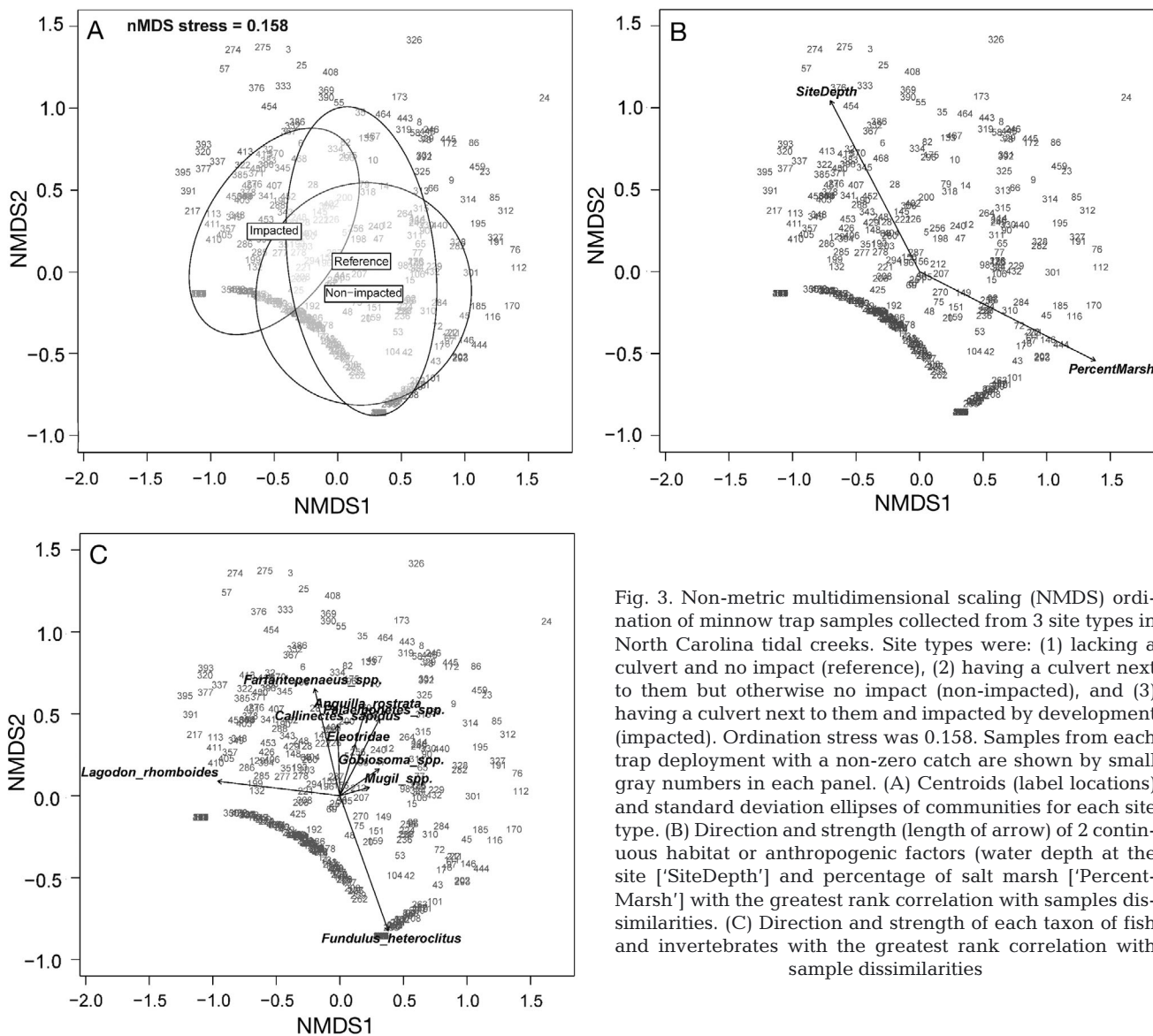


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of minnow trap samples collected from 3 site types in North Carolina tidal creeks. Site types were: (1) lacking a culvert and no impact (reference), (2) having a culvert next to them but otherwise no impact (non-impacted), and (3) having a culvert next to them and impacted by development (impacted). Ordination stress was 0.158. Samples from each trap deployment with a non-zero catch are shown by small gray numbers in each panel. (A) Centroids (label locations) and standard deviation ellipses of communities for each site type. (B) Direction and strength (length of arrow) of 2 continuous habitat or anthropogenic factors (water depth at the site ['SiteDepth'] and percentage of salt marsh ['PercentMarsh'] with the greatest rank correlation with samples dissimilarities. (C) Direction and strength of each taxon of fish and invertebrates with the greatest rank correlation with sample dissimilarities

loaded on the ordination at roughly equal strengths but in different directions. *F. heteroclitus* loaded in a direction similar to samples from reference and non-impacted sites that were typically shallow and close to salt marsh habitat. In contrast, *L. rhomboides* loaded in a direction similar to samples from impacted sites, which were typically deeper, had bulkheads, and were further removed from salt marsh. None of the other 8 taxa in the best-fitting model loaded in a direction similar to *F. heteroclitus* or *L. rhomboides*. *Palaemonetes* spp., a dominant crustacean taxa in tidal creeks in this region (Welsh 1975), loaded in a direction similar to samples from deeper sites but at an intermediate distance to salt marsh. The majority of the 6 other taxa in the best-fitting model loaded in a direction generally similar

to *Palaemonetes* spp. (Fig. 3C) but were more closely associated with shallower sites that were located closer to the nearest salt marsh than *Palaemonetes* spp. BIOENV results on important taxa loadings were similar when models were fitted to data collected over the period when all 10 creeks were sampled simultaneously; the same 9 taxa were included in the ordination model when fitting to the full and reduced datasets and *Gambusia holbrooki* was an additional species in the model that best fitted the reduced dataset.

To summarize, impacted sites had nekton communities dominated by *L. rhomboides*. These were anthropogenically deepened sites further removed from salt marsh due to scour and/or having bulkheads (Figs. 2 & 3B). In contrast, communities at the

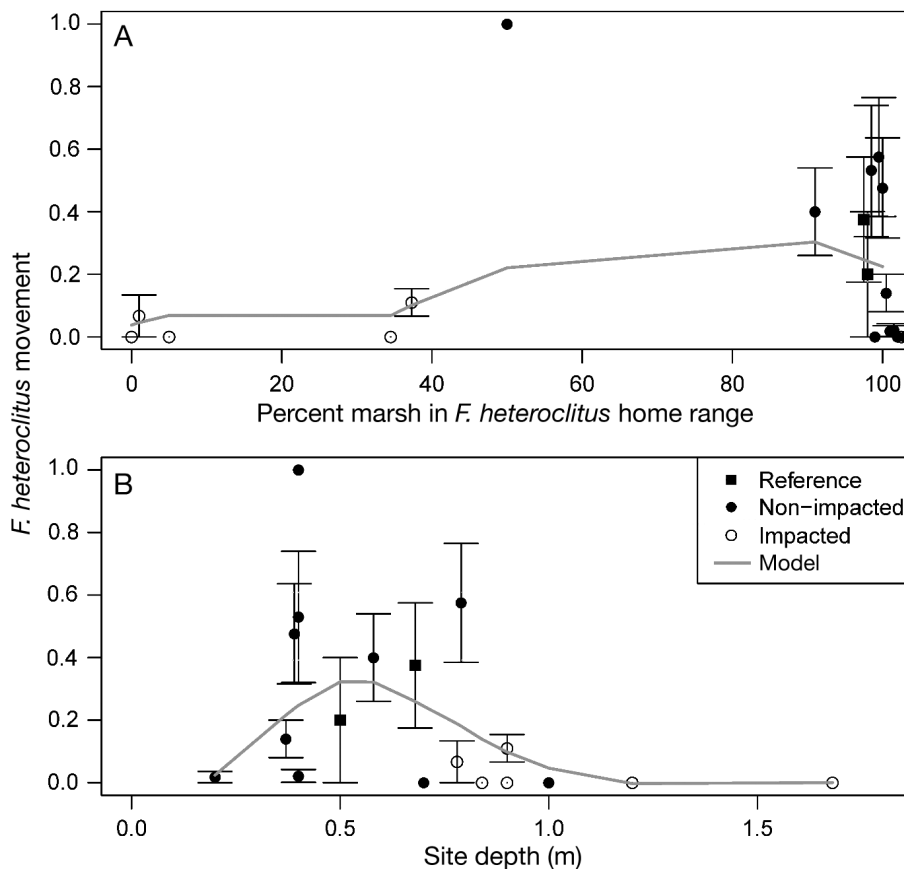


Fig. 4. Mean observed proportional movement (\pm SE) (symbols and vertical error bars) and predicted proportional movement (gray lines) of *Fundulus heteroclitus* past tidal creek crossings in coastal North Carolina as a function of (A) percent marsh-fringed shoreline within the species home range at sites to where individuals moved and (B) water depth at sites to where individuals moved. Predictions are from the 2 generalized linear models that best fitted the data (see values for Bayes factors, Table 3). The predicted line in each panel was plotted using a smoothing parameter whose value was set to 0.5. For different symbols among site types, the single legend applies to both panels

reference and non-impacted sites were dominated by *F. heteroclitus*; these sites were further removed from metrics of anthropogenic impact.

Movement of *F. heteroclitus*

A total of 2311 *F. heteroclitus* were tagged to study movement of this species past tidal creek crossings. The range of total lengths of VIE-tagged individuals widely overlapped between the 2 sides of each crossing and also among crossings. There were 96 sampling events that had recaptured *F. heteroclitus* whose markings were tag colors and body locations from a unique batch tagging event that had not previously been recaptured at each crossing ($n = 285$ recaptures). There was generally high variability in rates of *F. heteroclitus* movement past each crossing (Fig. 4).

Of the 8 movement models that included covariates, 7 had values for Bayes factors (K) that showed either positive or strong support relative to the null model (Table 3). Bayesian p-values for each model suggested reasonable fit although some values were ~ 0.3 . The convergence statistic for each estimated

parameter indicated adequate convergence to a stable posterior probability distribution.

The 2 covariates that consistently (i.e. in multiple models) had coefficients with 2.5 and 97.5 credible intervals that did not overlap with zero were the percent marsh within the home range of *F. heteroclitus* (Table 3, Fig. 4A) and water depth (Table 3, Fig. 4B). Percent salt marsh had a positive effect on movement probability. Movement rates to the shallowest and deepest sites were lowest while the highest rates of movement occurred at intermediate water depths. Thus, *F. heteroclitus* moved through culverts as long as the habitat on the opposite side of a crossing contained marsh and was not too shallow or too deep.

DISCUSSION

Fragmentation of salt marsh influences nekton community assemblage

The presence or absence of *Spartina alterniflora*-dominated salt marsh determined nekton communities over spatial scales smaller than the home range of *Fundulus heteroclitus*. Crossings with sites lacking

connectivity to marsh and sites further removed from the nearest marsh had different community assemblages and lower percentages of marsh residents on the impacted sides of these crossings. Thus, anthropogenic impacts appear to be species specific in tidal creeks (Layman et al. 2004, Krebs et al. 2014). These results are also consistent with a recent creek-wide analysis of nekton communities in many of these same creeks that found salt marsh attributes (e.g. percent marsh) were important factors underpinning community differences at creek-wide spatial scales (Rudershausen et al. 2016). At sites that lacked connectivity in this study, a dominant species and obligate marsh resident, *F. heteroclitus*, was replaced by *Lagodon rhomboides*. *L. rhomboides* was the dominant transient species in this study and a habitat generalist (Jordan et al. 1997). Ordination results for *Callinectes sapidus* and *Palaemonetes* spp., crustaceans important to salt marsh trophic dynamics (Welsh 1975, Kneib & Knowlton 1995, Silliman & Bertness 2002), suggest that they also respond to common types of instream development in salt marsh systems. This is consistent with recent studies that

have found that shoreline armoring reduces the habitat value for *C. sapidus* (Long et al. 2011) and that intact salt marsh mosaics support greater abundances of *Palaemonetes* spp. than impacted marsh systems (Lowe & Peterson 2014).

Factors influencing the abundance of *F. heteroclitus* at sample sites were consistent with factors influencing its movement probability. This species had low or zero rates of movement to sites with reduced percentages of salt marsh or elimination of this habitat. In contrast to our findings, Eberhardt et al. (2011) found culvert presence and hydrological regime did not affect tidal creek fish communities collected from the upstream side of New England road crossings relative to reference crossings; however, they did not sample artificially deepened scour pools given their gear type used (fyke nets). Eberhardt et al. (2011) did not mention whether the salt marsh mosaics sampled in their study were intact or altered at each of their sample sites.

Any management efforts to maintain the landward-to-seaward connectivity among marsh patches are likely to help maintain communities of marsh residents

Table 3. Bayesian probability values (p), Bayes factors (K), and the 2.5, median and 97.5 credible intervals of partial regression coefficients from fitting each of 8 binomially distributed generalized linear mixed models to data on movement of *Fundulus heteroclitus* through road and reference crossings in tidal creeks in coastal North Carolina. Models are listed in descending order of their K values. See 'Materials and methods' for a description of covariates

Model	Covariate	p	K	2.5	Median	97.5
1	Percent marsh edge	0.300	232.33	0.010	0.030	0.050
	Current velocity			9.439	36.048	100.940
	Current velocity ²			-259.873	-75.761	-13.865
	Percent marsh edge × current velocity ²			-0.948	-0.293	0.717
2	Water depth	0.328	107.87	2.981	21.818	42.882
	Water depth ²			-39.149	-22.526	-6.806
	Current velocity			-43.721	31.005	114.227
	Current velocity ²			-283.964	-70.858	101.131
	Water depth ² × current velocity ²			-189.497	-15.210	137.489
3	Percent marsh edge	0.321	24.80	0.012	0.049	0.123
	Crossing length			-1.606	0.313	2.760
	Crossing length ²			-0.050	-0.006	0.031
	Percent marsh edge × crossing length ²			0.000	0.001	0.002
4	Water depth	0.391	17.57	2.809	17.645	35.250
	Water depth ²			-33.443	-18.464	-6.611
	Crossing length			-0.861	0.252	2.095
	Crossing length ²			-0.037	-0.006	0.016
	Water depth ² × crossing length ²			-0.010	-0.003	0.004
5	Current velocity	0.291	9.92	-20.749	40.298	169.178
	Current velocity ²			-420.672	-93.286	48.219
6	Percent marsh edge	0.349	6.91	0.007	0.025	0.046
7	Crossing length	0.297	2.33	-1.269	0.074	1.778
	Crossing length ²			-0.032	-0.002	0.023
8	Water depth	0.443	0.67	2.114	15.267	34.196
	Water depth ²			-31.333	-15.108	-4.771

in these and similarly configured estuaries and thus sustain the 'trophic relay' (Kneib 2000, Stevens et al. 2006) by marsh-resident nekton to higher-level predators in nearby open-water estuaries. A recent community analysis of nekton in Gulf of Mexico estuaries similarly concluded that preserving functional connectivity among marsh patches helps maintain communities and secondary production reflective of unimpacted salt marsh mosaics (Lowe & Peterson 2014).

The multivariate community analysis included common habitat and development features to test their influence on how communities separated in ordination space. Some of these features are widespread anthropogenic impacts in North Carolina tidal creeks (Jensen et al. 2014) and other tidal creeks along the US coastline (Kennish 2001, Holland et al. 2004, Lowe & Peterson 2014), and were part of the BIOENV model that best correlated with community dissimilarities. Anthropogenic impacts to salt marshes can increase the distance separating habitat patches and this distance was a metric incorporated into community models. Among sites sampled in this study, this distance is greater than 0 due exclusively to anthropogenic activities that have eliminated salt marsh. Anthropogenically eliminated salt marsh and shoreline armoring are 'cost' factors assumed to negatively affect estuarine nekton populations in North Carolina (Jensen et al. 2014) and our results support this assumption.

There are several common construction types that can lead to reduced area of salt marsh in tidal creeks. Bulkheads are commonly used structures to armor shoreline (Gittman et al. 2015). These structures fragment salt marsh and reduce the diversity and integrity of estuarine fish communities (Peterson et al. 2000, Bilkovic & Roggero 2008, Peterson & Lowe 2009). Water depth at each site was also a factor in the best-fitting BIOENV model; increased depth at the sites we sampled most often results from dredging to create boat basins and from scouring due to water flow through inappropriately sized or shaped culverts (Wargo & Weisman 2006).

It is uncertain whether the catch rates of the 2 dominant species in this study, *F. heteroclitus* and *L. rhomboides*, are driven by habitat preferences or interactions outside or within the traps. The relationship between their community dominance and habitat factors (Fig. 3B,C) leads us to believe that catch rates of these 2 species are mostly driven by different habitat preferences. We are not aware of any studies that have examined the interaction between these 2 species but recommend this topic as a useful area of future research.

Community differences at our sampling sites could result from habitat-specific attributes but could also be influenced by the ability of fish to move to those sites. That is, culverts may impede movements to upstream or downstream locations. As described in the next section, the movements of *F. heteroclitus* through culverts suggest that habitat characteristics are more important than culvert-related factors in dictating rates of movement of this species.

Factors influencing *F. heteroclitus* movement

Our analysis of fish movement suggests that fragmentation of salt marsh leads to reduced connectivity for *F. heteroclitus* in US South Atlantic tidal creeks. This species showed a higher probability of movement to sites with greater percentages of marsh-fringed shoreline and had limited or no movement to sites lacking marsh. Similarly, Doak et al. (1992) concluded that disruption of dispersal ability by nekton is a consequence of habitat fragmentation. There is also evidence from our data that water depth affects rates of movement of this species despite the fact the 2 sites on either side of each crossing had adequate water levels to hold *F. heteroclitus* over all tidal levels. The effect of water depth on movement rates was not as strong as percent marsh but we found a lower proportional recapture rate at the shallowest sites and also at the deepest sites. This suggests that anthropogenic activities that result in scour as well as siltation may result in reduced movement rates of this species.

Fragmentation of salt marsh habitat appears to be a main mechanism for lower movement rates of *F. heteroclitus* to sites lacking salt marsh. In a separate (authors' unpubl.) tagging study across tidal creek reaches lacking culverts, we found that (depending on creek) few or no adult *F. heteroclitus* were recaptured in salt marsh within their home range as they were disconnected from tagging sites due to fragmentation.

We did not find an effect of culvert characteristics on *F. heteroclitus* movement. This contrasts with previous work on fish movement in freshwater creeks (Warren & Pardew 1998, Poplar-Jeffers et al. 2009) and a study of fish passage through culverts bisecting New England (US) salt marshes (Eberhardt et al. 2011). Eberhardt et al. (2011) provided strong evidence for the effects of water current velocity through culverts and culvert size (cross-sectional area and length) on *F. heteroclitus* movement. However, the large range of culvert lengths (78.8 m) and current velocities ($\sim 1.5 \text{ m s}^{-1}$) in that study relative to ours may have enabled those researchers to detect

pronounced effects of these 2 factors on movement. Other studies researching movement of small-bodied fishes have concluded that increased water velocities from undersized ('flow-constricted') culverts can reduce movement rates (Warren & Pardew 1998, Eberhardt et al. 2011, Januchowski-Hartley et al. 2014). Water current velocities $>0.4 \text{ m s}^{-1}$ have been found to deter movements of freshwater fundulids (Warren & Pardew 1998). The crossing with the second highest average current velocity in this study (Atlantic Veneer) had the highest movement rates but current velocities there were below the 0.4 m s^{-1} threshold identified by Warren & Pardew (1998) and below the highest current velocities ($\sim 1.5 \text{ m s}^{-1}$) where Eberhardt et al. (2011) observed reduced passage rates of *F. heteroclitus* in New England. The crossing with the highest velocity (Wading) lacked movement of tagged fish and had current velocities above the published threshold for fundulids (Warren & Pardew 1998). This potentially indicates that there is a threshold velocity above which *F. heteroclitus* will not pass through culverts in this area. However, it appears from our sampling and observations in this region of coastal North Carolina that the number of culverts with current velocities exceeding 0.4 m s^{-1} is low. Given the lack of movement at the Wading Creek crossing, potentially due to high current velocities, this could mask the effect of habitat features important to the movement probability of this species.

The natural habitat and anthropogenic alteration characteristics of crossings sampled in this study are largely representative of those found along the low-relief US South Atlantic coast (authors' pers. obs.) and likely other areas of the world where salt marshes have been altered. The results from this study are likely applicable to other micro-tidal areas of coastline where tidal ranges are $<2 \text{ m}$. Some other regions of the US South Atlantic coast (e.g. South Carolina and Georgia coastlines) have substantially greater semi-diurnal tidal amplitudes than coastal North Carolina (Wiegert & Freeman 1990). It is more likely that culverts in tidal creeks in these other areas have current velocities exceeding any passage thresholds for *F. heteroclitus* and other small-bodied nekton species. We are not aware of any other studies from these macro-tidal areas of the US South Atlantic coast (with tidal ranges $>2 \text{ m}$) that have measured current velocities through tidal creek culverts or the responses of nekton species to them.

We sampled across 2 culvert types (box and pipe) that had a range of culvert cross-sectional areas and current velocities. In analyzing the movement data, we elected to model fit to current velocity rather than

culvert diameter due to the inverse relationship between these 2 metrics and also given that Eberhardt et al. (2011) examined current speed and found that movement rates of *F. heteroclitus* were a function of current velocity through culverts in New England (USA) salt marshes. In contrast, culvert type does not influence passage rates in the systems that we studied; there were low and high movement rates at pipe as well as box culverts.

To our knowledge, this is only the third study of fish movement past crossings in tidal creeks (Bowron et al. 2011, Eberhardt et al. 2011). Our study builds on this earlier research by examining not only crossing-level attributes but also sample site-level characteristics influencing nekton movement due to fish passage being a function of the nekton species under study, culvert characteristics, and also one or more site-level factors operating over multiple spatial scales (Januchowski-Hartley et al. 2014). Bowron et al. (2011) found culvert widening increased the relative abundance of *F. heteroclitus* in a macro-tidal area in the Bay of Fundy and attributed that fish response to increased high tide wetted area rather than the characteristics of the single crossing that was researched in that study. In contrast, culverts do not appear to limit upstream high-tide water coverage in the micro-tidal region of the US South Atlantic coast where this study took place (authors' pers. obs.). Thus, road projects and instream development in this area are likely to affect attributes of the crossings themselves (depth, current, culvert length) and the quality of inter-tidal habitat (vegetated vs. non-vegetated) but not change the amount of high-tide wetted area landward of the culvert that is available for foraging or refuge by nekton.

Culverts did indirectly affect movement probability due to scouring (deepening) of soft-bottomed creek channels at crossings we studied. Inappropriately sized or shaped culverts can scour soft-bottom stream channels and adjacent vegetated habitats (Abt et al. 1984). This altered probability of movement by *F. heteroclitus* past crossings could be due to a lack of preferred habitat at these deeper sites, intentional avoidance of increased risk of predation at these anthropogenically deepened sites (Ruiz et al. 1993), predation mortality, or a combination of these factors. *F. heteroclitus* is known to prefer shallow water and intertidal salt marsh habitats (Able & Hagan 2003, Allen et al. 2007, Rudershausen et al. 2016) over deepwater habitats within the same marsh mosaic (Halpin 1997), but adults appear to take a risk-averse movement strategy to avoid stranding over very shallow depths (Rudershausen et al. 2014).

We considered the number of trials (N in the binomial distribution) to be only those instances when fish of a unique tag color and tagging location on the body were first recaptured. For each sampling event, N constituted the sum of recaptured fish of that tag color and body location at both the upstream and downstream sample sites. Because the data on movement of *F. heteroclitus* past crossings was restricted to sample events with a non-zero number of recaptures, the number of data points (trials) is limited for some crossings (<10) despite intensive trapping and tagging effort. High variability in biological response data is common in dynamic ecosystems such as salt marshes and necessitates high spatial replication to detect an ecological effect (Lee et al. 2006). Further work on this topic may reveal other factors important to the movement of *F. heteroclitus* past crossings. In addition, research into the ability of other important estuarine nekton species (e.g. *L. rhomboides*) to pass culvert crossings in tidal creeks is warranted.

Conclusions

Over the range of culvert characteristics examined in this study, we found that 2 sites in close proximity to each other will have similar communities as long as their biological and physical habitats are similar, regardless of the characteristics of the culvert that separates them. The results from this study show common anthropogenic impacts in the US South Atlantic coastal zone—marsh fragmentation, bulk-heading, and increased water depths from instream development—will affect nekton species composition and movement more than culverts by themselves, within the range of culvert characteristics included in this study.

It is forecasted that anthropogenic activities in tidal creek watersheds and intertidal zones will further fragment salt marsh habitats along US coastlines (Kennish 2001, Mattheus et al. 2010, Gittman et al. 2015). For example, the percentage of armored shoreline is predicted to double by 2100 (Gittman et al. 2015). Pressure from ongoing development heightens the importance of managing estuarine habitats to maintain connectivity among patches (Meynecke et al. 2008).

To lessen the impacts of development on marsh-resident nekton, natural resource managers would be well served to prioritize measures that preserve or restore salt marsh connectivity, reduce the rate of installation of armored shoreline by expanding the 'living shorelines' approach (Gittman et al. 2016),

and consider novel culvert designs (Wargo & Weisman 2006) to help reduce scour in low-energy tidal creeks. Since culverts are often replaced and upgraded as part of road maintenance projects (Kemp & O'Hanley 2010, Januchowski-Hartley et al. 2013), coastal planners and transportation agencies will have ongoing opportunities to restore salt marsh connectivity and improve fish passage as new roadworks projects arise in this region.

Acknowledgements. This study was funded by North Carolina Sea Grant, award # R/12-HCE-1. We thank E. Barnett, L. Huffstetler, and L. Lee for assistance with field sampling, and J. E. Hightower for recommendations on modeling. Thanks to T. Dubreuil for producing the creek images. S. Binion-Rock and 2 anonymous reviewers greatly improved the quality of the manuscript.

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