



# Relating absolute abundance of an estuarine fish to habitat area in an urbanizing environment

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**ABSTRACT:** Organisms that rely on salt marsh habitat are an important trophic link, helping to maintain estuarine ecosystem productivity. We used GIS to quantify intertidal (assumed salt marsh) area from aerial photographs taken in 1939 and from software-supplied satellite imagery taken in 2021 for tidal creeks in North Carolina (USA) that have experienced minor (<20%), moderate (20–60%), or substantial (>60%) losses of intertidal habitat over the 8 decades. The current (2022) absolute abundance of adult *Fundulus heteroclitus*, a trophically important resident fish in US Atlantic estuaries, was estimated over each season in each creek by fitting a Lincoln-Petersen model to tag–recapture data. Current abundances of *F. heteroclitus* were lowest in creeks with the lowest intertidal area. The median and 2.5/97.5 credible intervals of the posterior probability distribution for the slope of a regression model relating current fish abundance to current intertidal area were positive, demonstrating that intertidal area was a meaningful covariate of abundance. Loss of intertidal area in the creeks between 1939 and 2021 ranged from 8 to 93%. The correlation between current intertidal area and historical loss of this habitat was negative and significant (Pearson  $r = -0.91$ ,  $p = 0.012$ ). Parameters from the regression relating current abundance to intertidal area were used to estimate historic *F. heteroclitus* abundances in each creek using GIS-derived estimates of historic intertidal area. Historic abundances were predicted to have been on average (across study creeks) 7.5 times greater in 1939 than in 2022. Reduced abundances, and thus reduced trophic relay by *F. heteroclitus* to higher-order consumers, can be expected in estuaries that have lost salt marsh due to inter-decadal development.

**KEY WORDS:** Salt marsh · Trophic link · Intertidal · Ecosystem productivity · Urbanization · Habitat loss · *Fundulus* · Killifish

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## 1. INTRODUCTION

The intertidal zone has long been regarded as among the most biologically productive areas within estuarine environments (Teal 1962, Odum 1970, Barber et al. 2011, Baker et al. 2020). Undeveloped intertidal areas along the southeastern US and Gulf of

Mexico coastlines are typically dominated by salt marsh. While they are among the most biologically productive ecosystems on Earth (Kneib 1997, Silliman 2014), salt marsh habitats have been eliminated by humans for centuries (Bromberg & Bertness 2005, Gedan et al. 2009) in favor of landforms deemed to be more aesthetically or financially attractive (Valiela et

al. 2004). Specific anthropogenic impacts on salt marshes include fragmentation (Kennish 2001, Lowe & Peterson 2014), upland development (Holland et al. 2004, Lowe & Peterson 2014), dredging (Johnston 1981, Lee et al. 2006), and construction of vertical shorelines (Peterson & Lowe 2009, Gittman et al. 2015). It is estimated that over 50% of the original salt marsh area in the USA has been lost (Kennish 2001), with loss rates in US coastal zones exceeding human population growth rates in these areas (Beach 2002). Elimination of salt marsh habitats does not bode well for estuarine organisms, given the fact that intact coastal environments are required to maintain estuarine ecosystem productivity (Peterson & Lowe 2009).

Due to the low-relief topography of the southeastern US coastal plain, salt marshes comprise a large percentage of the area within estuaries in this region and provide habitat for numerous resident and non-resident fishes and invertebrates (Kneib 1997, Bloomfield & Gillanders 2005). Among these species is *Fundulus heteroclitus*, a small-bodied resident fish that inhabits estuaries along the US and Canadian Atlantic coasts. It is locally abundant in tidal creeks and sheltered embayments containing salt marshes, which is an essential habitat for the species (Langton et al. 1996). Salt marshes are utilized throughout its lifecycle for foraging, refuge, and reproduction (Kneib 1986, 1997, Able & Fahay 1998). Throughout its range, *F. heteroclitus* is a critical link in the 'trophic relay', whereby salt marsh production is transferred through secondary consumers (Teal 1962, Valiela et al. 2004) to tertiary predators inhabiting seaward waterbodies (Kneib 1986, 2000, Cicchetti & Diaz 2002). *F. heteroclitus* is an ideal species for studying how abundance varies with habitat area due to its obligate use of salt marsh, its importance to estuarine trophics (Kneib 2000), and its numerical dominance in nekton communities in small estuaries along the US Atlantic coast (Valiela et al. 1977, Kneib 1997, Teo & Able 2003). Given its small home range (Lotrich 1975, Meredith & Lotrich 1979, Teo & Able 2003) and high site fidelity (Sweeney et al. 1998, Teo & Able 2003, Skinner et al. 2006), *F. heteroclitus* is a suitable species for studying impacts to salt marshes at the small spatial scales over which human elimination of this habitat often occurs (Holland et al. 2004, Lowe & Peterson 2014).

Absolute abundance (or density) is a key demographic frequently estimated in research on fish and wildlife populations (Williams et al. 2002), yet due to biological or logistical constraints, this metric is infrequently measured in nekton populations inhabiting estuaries (Able 1999). Compared to more frequently collected data on relative abundance (e.g. catch-per-

unit-effort) that is often used to make inferences about the abundance of aquatic species, absolute abundance estimated through the Lincoln-Peterson model and other methods (Williams et al. 2002) quantifies the biological impact of habitat loss in areal units (e.g. waterbody size or number per m<sup>2</sup>) that can be easily interpreted and compared among time periods or study areas that possess a range of impacts or habitat coverages. These are important considerations for natural resource planners tasked with conserving imperiled habitats or evaluating tradeoffs between permitting the conversion of habitats for coastal development while still trying to maintain nekton abundances reflective of undeveloped conditions. Despite being infrequently collected, data used to estimate absolute abundance can often be collected more easily than data used to simply index abundance. For example, absolute abundance estimated from the Lincoln-Peterson model can be obtained from fitting to data on batch tags with no need to account for gear or recovery inefficiencies because capture probabilities are assumed to be equal between tagged and untagged animals. In contrast, capture probability is an issue with many sampling gears that index the abundance of nekton in estuaries, such as enclosure-type samplers deployed in structured or soft-bottom habitats (Kneib 1997, Rozas & Minello 1997, Rudershausen et al. 2016). We are not aware of any previous studies that have related the absolute abundance of *F. heteroclitus* to intertidal habitat area.

The difficulty in relating population demographics (e.g. abundance) to habitat increases the further coastal ecosystems are altered from baseline conditions (Peterson & Lowe 2009). Coastal development invariably leads to declines in the abundance of dominant estuarine nekton (Holland et al. 2004, Bilkovic & Roggero 2008, Peterson & Lowe 2009, Lowe & Peterson 2014). However, there are some estuarine residents, including *F. heteroclitus*, that appear to maintain within-habitat densities and production rates in altered estuaries as long as the habitats that they rely upon are not removed altogether (Rudershausen et al. 2019, Rudershausen & Buckel 2020). Therefore, if losses of estuarine habitats, such as salt marsh, can be quantified and compared versus historic conditions (Rudershausen et al. 2021), one can reconstruct how these habitat losses affect system-wide abundances of species obligated to these habitats because abundances should track the area of habitat remaining. The combination of geographic information systems (GIS) to advance research on salt marsh ecology (Kimball et al. 2021) for examining differences in habitat area between baseline (pre-development)

and current conditions, and the collection of current biological data can allow for relating nekton abundance to habitat area, habitat area to its temporal loss, and estimating historic abundances from historic habitat area. Thus, historic population levels can be 'reconstructed' before the elimination of natural estuarine habitats became a widespread phenomenon. The relationship between salt marsh area and *F. heteroclitus* abundance is expected to be positive, given previous findings of similar relationships between this habitat and the abundance of this fish species (Rudershausen et al. 2016, 2019).

In this study, we quantified intertidal habitat area and fish abundance. We address the question of whether historical loss of salt marsh is related to reduced abundances of *F. heteroclitus* and reasoned that reduced salt marsh area from 1939 to the present would result in reduced abundances of *F. heteroclitus*. To the best of our knowledge, this is the first study to

investigate absolute abundance along a continuum of vegetated habitat areas and losses for a habitat type critical for *F. heteroclitus* and other estuarine nekton species (Kneib 1997, Ziegler et al. 2021). Studies such as this are valuable for understanding the relationship between demographics and habitat area of important estuarine nekton and determining the population-level impacts of changing area of habitats that are considered critical for estuarine nekton production.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

We studied 6 first-order polyhaline tidal creeks in the Morehead City/Beaufort micropolitan area of coastal North Carolina (Fig. 1). This is a region of the southeastern US coast that has experienced a variety

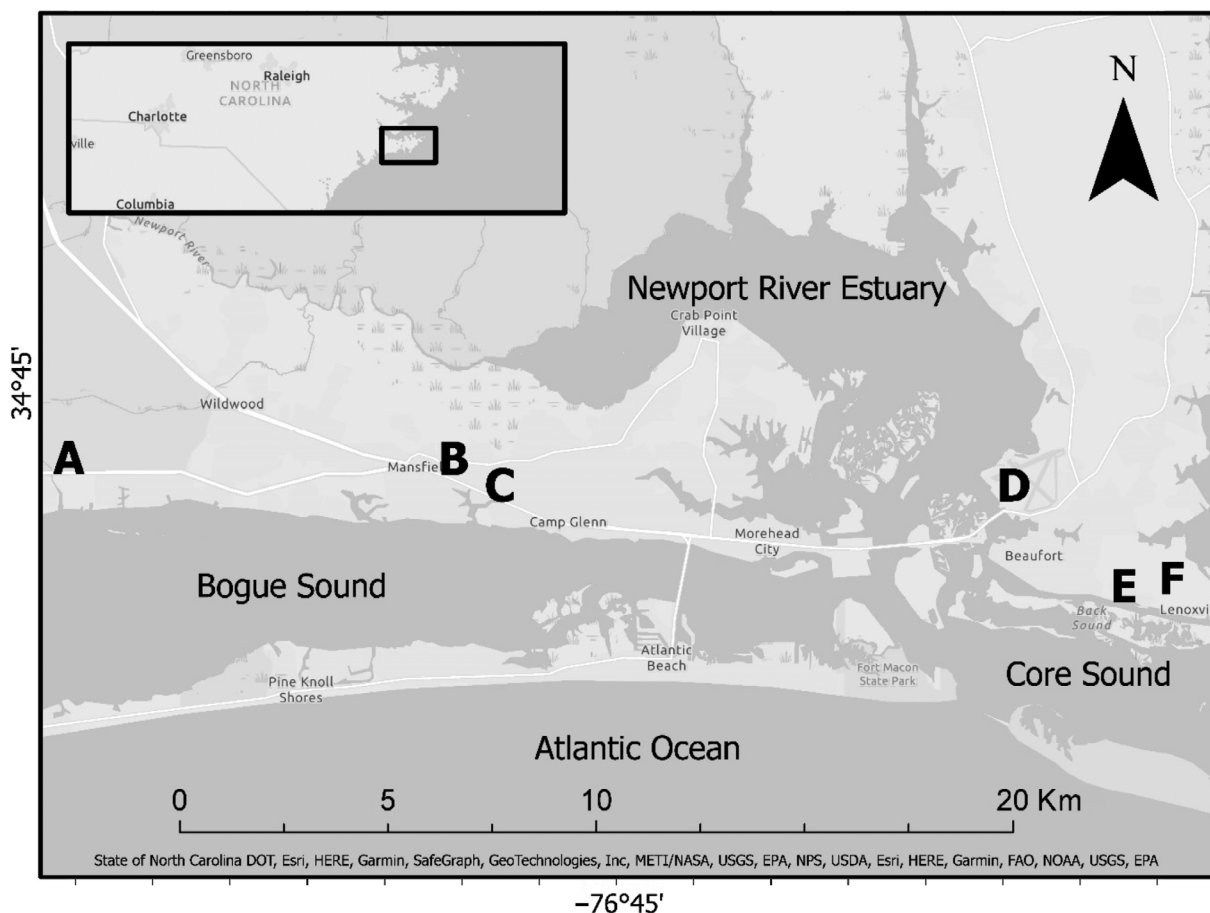


Fig. 1. General area of North Carolina (USA) studied for a relationship between adult *Fundulus heteroclitus* abundance and intertidal area in 6 tidal creeks. Small black box within the inset map: approximate study location. Letters (A–F) show approximate locations of the study creeks in Morehead City and Beaufort, North Carolina; these letters correspond to maps of intertidal area of the respective creeks shown in Fig. 2. From west to east, these creeks are (A) Jumping Run, (B) Pelletier North, (C) Pelletier East, (D) Wading, (E) Front Street, and (F) Atlantic Veneer

of anthropogenic impacts due to 20th and 21st century development (Kennish 2001, Peterson & Lowe 2009, Seabrook 2012). These creeks in their unaltered conditions are largely intertidal and fringed by salt marsh chiefly comprised of *Spartina alterniflora*. The 6 creeks were studied based on the availability of historic (1939) imagery and the fact that they were largely undeveloped in 1939 but now have a range of impacts representative of small estuaries in the larger coastal region of the southeastern USA. Patterns of nekton usage of salt marsh tidal creeks along the southeastern US and Gulf of Mexico coasts are influenced by geomorphic (landscape) and hydrographic (tidal) factors (Kneib 1997, Allen et al. 2007); we controlled for these factors by studying creeks roughly equally positioned within the surrounding landscape (all first-order systems) with approximately equal semi-diurnal tidal amplitudes (1 m) and periods when the salt marsh is flooded (roughly half of each tidal cycle) (Kirby-Smith & Costlow 1989). Except for Jumping Run, each study creek was separated from the downstream estuarine area by a culvert. Culverts can impede movements of estuarine nekton within tidal creeks (Eberhardt et al. 2011, Rudershausen et al. 2016), thus potentially isolating upstream portions of tidal creeks from their downstream counterparts.

## 2.2. Estimating inter-decadal salt marsh loss with GIS

We used GIS to determine the extent of inter-decadal salt marsh loss within each creek. All GIS analyses were performed with ArcGIS Pro version 2.9 (ESRI 2021). Historic aerial photography of each creek, taken in 1939 during a flyover of Carteret County, North Carolina (USA), by the US Department of Agriculture at a scale of 1:38 265 (SANC 2022), was georeferenced by establishing control points at known locations (e.g. road crossings) that could be located within both the 1939 (historic) and 2021 (current) base map imagery (provided by the software); for this analysis, we assumed no change in salt marsh loss between 2021 and 2023. The historic aerial photographs used to estimate salt marsh loss within each creek included (from west to east) BUS-105-48 (Jumping Run Creek), BUS-105-3 (Pelletier North and Pelletier East Creeks), BUS-104-7 (Wading Creek), and BUS-110-45 (Front Street and Atlantic Veneer Creeks) (SANC 2022).

Low and high tide areas in each creek were digitized to create both historic and current low tide and

high tide polygon feature classes. Low and high tide areas were respectively defined as the amount of area inundated by low and high tide. This was accomplished by digitizing outlines of low tide (vegetated and unvegetated edges of subtidal creek channels) and high tide features (high tide or upland edge) using the 'freehand' tool. Following the creation of low tide and high tide feature classes for each period, the 'dissolve' tool was used to eliminate overlapping areas among the drawn polygons comprising each feature class. A shapefile of the intertidal area within each creek and period was created using the 'erase' tool to subtract the low tide from the high tide area. The resulting intertidal area (m<sup>2</sup>) of each creek was then calculated using the 'calculate geometry' tool. We assumed that the intertidal area comprised salt marsh in each time period rather than unvegetated mud; this assumption was supported by ground-truthing the intertidal area that appeared in the current imagery. The 'erase' tool was then used to subtract the intertidal area within the current period from that of the historic period. Finally, the percentage of lost intertidal area within each creek was computed by subtracting the intertidal area in the current period from that of the historic period, dividing this difference by the value in the historic period, and multiplying by 100.

## 2.3. Tag-recapture fish sampling

We estimated the abundance of adult *Fundulus heteroclitus* within each creek during each of 4 separate tag-recapture sampling events. Sampling events occurred in winter (February–March), spring (April–May), summer (July–August), and fall (November–December) 2022. The 4 sampling events were intended to account for seasonally dynamic adult abundances of this species in tidal creeks (Rudershausen et al. 2019). Each tag-recapture event consisted of passively fishing up to 8 Gee-style 6.4 mm square wire mesh minnow traps baited with previously frozen *Brevoortia tyrannus* for roughly 24 h within the sub-tidal channel of each creek. Using a tag-recapture approach allows for estimating the absolute abundance of salt marsh nekton and avoids the challenges of estimating capture and recovery efficiency when sampling with actively fished enclosure-type samplers to collect relative abundance data in low-energy habitats such as salt marshes (Kneib 1997, Rozas & Minello 1997). Previous research has shown that the Gee-style trap type almost exclusively selects for adult *F. heteroclitus* (Ruders-

hausen et al. 2019), which are  $\geq 41$  mm total length (TL) (Kneib & Stiven 1978).

Within each creek and season, traps were fished over 4 consecutive days (4 sampling events). Capture of fish for tagging occurred between the first and second days while recapture of both tagged and untagged fish occurred between the third and fourth days. Thus, deployment of baited traps occurred on Days 1 and 3 while retrieval of traps occurred on Days 2 and 4. For each season and creek, fish were batch tagged (no individual identification) with a single color of visible implant elastomer (VIE) (Northwest Marine Technologies). For each creek, a different VIE color was used each season. Due to variable trap catches, the number of fish tagged within each creek varied by creek and season. The precision of a Lincoln-Petersen estimate of absolute abundance increases when more individuals are tagged and recaptured. Therefore, we tagged as many fish as catch rates would allow. For recapture sampling, we set multiple traps instream and one trap immediately ( $< 5$  m) outside each creek mouth. The trap set outside the creek was used to collect data to evaluate potential violations of the assumption of population closure over the duration of each tag–recapture event.

#### 2.4. Estimating *F. heteroclitus* abundances and relating them to habitat area

We estimated the absolute abundance of adult *F. heteroclitus* from each tag–recapture sampling event using a modified (Bayes) version of the Lincoln-Petersen model (Sethi & Tanner 2014). We fitted a Lincoln-Petersen model because it is well suited for data where the researcher can efficiently batch tag many individuals of the target species when working in environments that are physically difficult to sample. The Lincoln-Petersen estimator of absolute abundance  $\hat{N}$  of a closed population is given by the equation:

$$\hat{N} = \frac{R(N+1)}{(N+1)} \quad (1)$$

where  $R$  is the number of tagged individuals released into the population,  $N$  is the total number of individuals (both tagged and untagged) in the recapture sample, and  $M$  is the number of tagged individuals in the recapture sample. The above formula, with additions of 1 to  $N$  and  $M$ , is useful for cases where  $M$  is small ( $< \sim 10$ ) (Bailey 1951, Begon 1974). The standard error (SE) of the estimated abundance of the population is given by the equation:

$$SE = \left( \frac{R^2(N+1)(N-M)}{(M+1)^2(M+2)} \right)^{0.5} \quad (2)$$

The Lincoln-Petersen estimator has a number of assumptions. It assumes that the population is closed and that all individuals in the population have equal and independent capture probabilities. It also assumes that tagging does not affect capture probability and that tags are not lost between tagging and recapture (Skinner et al. 2006). Finally, it assumes that tagged individuals mix throughout the population before recapture (Begon 1974, Pollock et al. 1990). Given that adult *F. heteroclitus* undertake tidally mediated movements (Allen et al. 2007, Rudershausen et al. 2014), we allowed 24 h (2 tidal cycles) between trapping for tagging and then soaking traps for recapture, so that mixing could occur.

A Lincoln-Petersen model to estimate creek- and season-specific absolute abundance was fitted through Bayesian inference (Sethi & Tanner 2014). The variant of the fitted Lincoln-Petersen model defines a catchability coefficient,  $p$ , as a parameter estimated in the model run. The number of tagged and untagged animals in the recapture sample are each modeled using a binomial distribution with  $p$  (catchability coefficient: success probability) and number of trials respectively represented by the (known) number of tagged individuals  $M$  in the recapture sample and the (unknown) number of untagged individuals  $U$  in the population.  $U$  can be estimated by assuming equal capture probabilities between tagged and untagged animals. Thus, catchability, assumed equivalent between tagged and untagged portions of the population when fitting the model, is estimated regardless of the tagged vs. untagged status of an animal. Without pre-existing information on catchability or population size in each creek, the stochastic elements in the model ( $p$  and  $U$ ) were assigned non-informative uniform prior probability distributions (priors) with minimum and maximum values of (0, 1) and (0, 1 000 000), respectively.  $\hat{N}$  was a calculated value in the model and was computed as the addition of  $M$  and  $U$ . Finally, density within each creek (number per  $m^2$ ) was calculated within each model run by dividing  $\hat{N}$  by the high tide wetted area for a creek obtained from using GIS to create a high tide feature class from current imagery. High tide area was used to calculate density because it represents the maximum area available for adult *F. heteroclitus* spawning, foraging, and refuge (Kneib 1997). Thus,  $R$ ,  $M$ ,  $N$ , and high tide area were the data to which each model was fitted.

Each creek- and season-specific Lincoln-Petersen model (as well as other models; see below) was fitted

by calling 'OpenBUGS' software (version 3.2.1; Spiegelhalter et al. 2010) in R software (R Core Team 2019) using the software interface 'R2OpenBUGS' (Gelman 2020) to obtain median and associated 2.5 and 97.5 credible intervals for the posterior probability distribution (posterior) of each parameter and calculated value. For each model, 3 Markov chains (independent sample sets) each generated 100 000 updates with every tenth iteration saved, with the first 10 000 updates discarded as burn-in. Convergence of the chains to stationarity was verified by examining software-generated history plots for adequate mixing of model chains of retained updates of each parameter (McCarthy 2007, Lunn et al. 2013) and a Gelman-Rubin statistic ( $\hat{R}$ ) for each parameter; values  $< \sim 1.05$  for this statistic suggest adequate convergence to a stable posterior (Gelman 1996).

The assumption of population closure when fitting the Lincoln-Petersen model was evaluated by comparing ratios of tagged:untagged *F. heteroclitus* in-stream vs. downstream of each study creek during recapture sampling in each season. These ratios were evaluated through R software using a test of independence ( $\chi^2$  test statistic) to evaluate whether to reject the null hypothesis that the ratios did not differ from each other. The statistical significance of these tests was set at  $\alpha = 0.05$ . To be performed, the test requires non-zero count data for each condition (trap location) (Zar 1984).

We explored the relationship between current (2022) adult *F. heteroclitus* abundance and current (2021) intertidal area by fitting linear models through Bayesian inference. Data on fish abundance and habitat area was logarithmically transformed ( $\ln[x]$ ) before model fitting because preliminary models fitted to raw data showed poor Bayesian goodness of fit (GOF). For these models, abundance was defined as a normally distributed random variable with mean  $\mu$  and precision  $\tau$  ( $1 / SD^2$ ). We assigned an uninformative normally distributed prior with a mean and precision of 0 and 0.001, respectively, to both the regression intercept and slope. A uniform prior (minimum and maximum values of 0 and 100, respectively) was assigned to the modeled SD. In total, 5 models were fitted to the tag-recapture data. One model included the main effects of area and season (main effects analysis of covariance [ANCOVA]) while another included main effects plus their interaction (interaction effects ANCOVA). Models were also fitted to abundance vs. area regardless of season (regression), abundance vs. season (ANOVA), and finally an intercept-only model. Parsimony among the 5 models was evaluated by using software-gener-

ated values for the deviance information criterion (DIC) (Spiegelhalter et al. 2002); the model with the lowest DIC was considered best fitting. Proportional model support for each model  $i$  in the set (summing to a value of 1 across all models) was evaluated by computing its Akaike weight ( $w_i$ ); the most parsimonious model in the set (based on information criteria) should receive more support than any other candidate model. The GOF of each model was evaluated by computing a sum-of-squares discrepancy measure between the observed data and a replicate data set generated using the parameter estimates produced from model fitting to the real data (Kéry 2010). GOF testing within a Bayesian framework involve computing a Bayesian probability (p) value (Gelman et al. 1996). This p-value (distinct from probability values synonymous with hypothesis testing) computes the proportion of instances when the discrepancy measure for the replicated data set exceeds that for the observed data set; a p-value of roughly 0.5 suggests an adequately fitting model while a value closer to 0 or 1 suggests a poorer fit and that an alternate model structure should be considered (Kéry 2010). For the most parsimonious model, the meaningfulness of each parameter was evaluated by determining whether its posterior 95% credible set overlapped zero; lack of overlap with zero indicates either a meaningfully positive (direct) or negative (inverse) relationship between the response variable and the covariate. Within the run of the best-fitting model, back-transformed estimates of abundance were calculated to visualize (graph), in untransformed space, both the observed and predicted values of current abundance over the range of values of the current intertidal area.

Back-transformed historic (1939) abundances of adult *F. heteroclitus* were estimated within the model that best fitted the current abundance vs. current intertidal area data. Historic abundance in each creek (regardless of season) was calculated using the single value of the historic intertidal area for each creek obtained from digitizing it in GIS from 1939 aerial imagery. In the 'OpenBUGS' software, estimating a value for a missing response datum is obtained by setting the estimate of interest (in this case, a historic estimate of abundance) to 'NA' in the vector of data for the response variable (Lunn et al. 2013). This exercise of estimating historic fish abundance in each creek assumed that density-dependent effects regulating adult *F. heteroclitus* abundance remained constant between 1939 and 2021. Thus, we assumed that the difference in abundance in each creek resulted from a difference in intertidal habitat area. For each creek, a

ratio of the modeled abundance in the historic period (1939) to the mean Lincoln-Peterson estimate of abundance in the current period was calculated after averaging the 4 median abundance values (one per season) from fitting the Lincoln-Peterson model for current estimates of abundance.

### 3. RESULTS

Inter-decadal salt marsh loss ranged from 8 to 93 % within the 6 study creeks (Fig. 2, Table 1). Two of the study creeks experienced minor (<20%), one experienced moderate (20–60%), and 3 experienced substantial (>60%) salt marsh loss over the 8 decade period between 1939 and 2021.

Stationarity to a stable posterior was achieved for the parameters estimated in fitting each Lincoln-Petersen model to tag–recapture data and for the models relating logarithmically transformed absolute abundance of adult *Fundulus heteroclitus* to transformed current intertidal habitat area. Greater abundances were generally found in creeks with greater intertidal habitat areas (Table 2, Fig. 3). Among 5 models fitted to current abundance vs. habitat area, a regression model was best fitting based on its DIC value and proportional support (Table 3). The main effects ANCOVA model, which contained season as a factor, received the second most support. The median value of the intercept for the regression model relating fish abundance to current habitat area was  $-1.035$ , with its 2.5 and 97.5 credible intervals overlapping zero ( $-4.675$ ,  $2.579$ ). The median value of the slope of this model was  $0.956$ , and its 2.5 and 97.5 credible intervals did not overlap zero ( $0.465$ ,  $1.452$ ). Thus, there was a trend for increasing abundance with increasing intertidal area (Fig. 3).

The ratio of tagged:untagged *F. heteroclitus* caught instream vs. downstream generally varied between sampling seasons and creeks (Table 4). In 10 of 24 cases, one or more tagged individuals were recaptured in the downstream trap. Six tests of independence were significant ( $p < 0.05$ ); 5 showed that the ratio of tagged:untagged *F. heteroclitus* was greater instream of a study creek than downstream while the opposite was true for the other case. Eight sampling events did not catch *F. heteroclitus* in the downstream trap so a test of independence could not be conducted. Each of the other 10 tests did not reject the null hypothesis of no difference in the ratio of tagged:untagged fish within the study creek vs. downstream (Table 4).

The correlation between current intertidal area and loss of intertidal area was negative and significant (Pearson's  $r = -0.91$ ,  $p = 0.012$ ) (Fig. 4). The ratios of estimated historic (1939) to current abundance of adult *F. heteroclitus* averaged over the 4 seasons in 2022 were 30.0, 0.9, 10.5, 1.3, 1.8, and 0.4 for Jumping Run, Pelletier North, Pelletier East, Wading, Front Street, and Atlantic Veneer Creeks, respectively (Fig. 5). Averaged across the 6 creeks, the mean ratio of historic:current abundance was 7.5.

### 4. DISCUSSION

This study quantified the area of intertidal habitat in southeastern US tidal creeks and its impact on absolute abundances of adult *Fundulus heteroclitus*, an ecologically important fish resident in US Atlantic estuaries. We asked the question of whether fish abundances were related to salt marsh habitat area and found that current abundances (densities)

Table 1. Estimated high tide, low tide, and intertidal area ( $m^2$ ) in 6 first-order North Carolina (USA) tidal creeks studied with geographic information systems (GIS) to examine loss of intertidal area between 1939 and 2021. Intertidal area for each year was computed as the difference between GIS-digitized high tide and low tide areas. Creeks are tabled in the order that they appear (from west to east) in Fig. 1

Creek	High tide area: 1939	Low tide area: 1939	Intertidal area: 1939	High tide area: 2021	Low tide area: 2021	Intertidal area: 2021	Percent change in intertidal area between 1939 and 2021
Jumping Run	25445	3917	21529	12329	10866	1462	−93
Pelletier North	2631	654	1978	1110	165	945	−52
Pelletier East	6270	288	5982	4875	4386	489	−92
Wading	6191	743	5448	6947	1953	4994	−8
Front Street	3652	972	2680	3898	3303	595	−78
Atlantic Veneer	5729	386	5343	5269	425	4844	−9

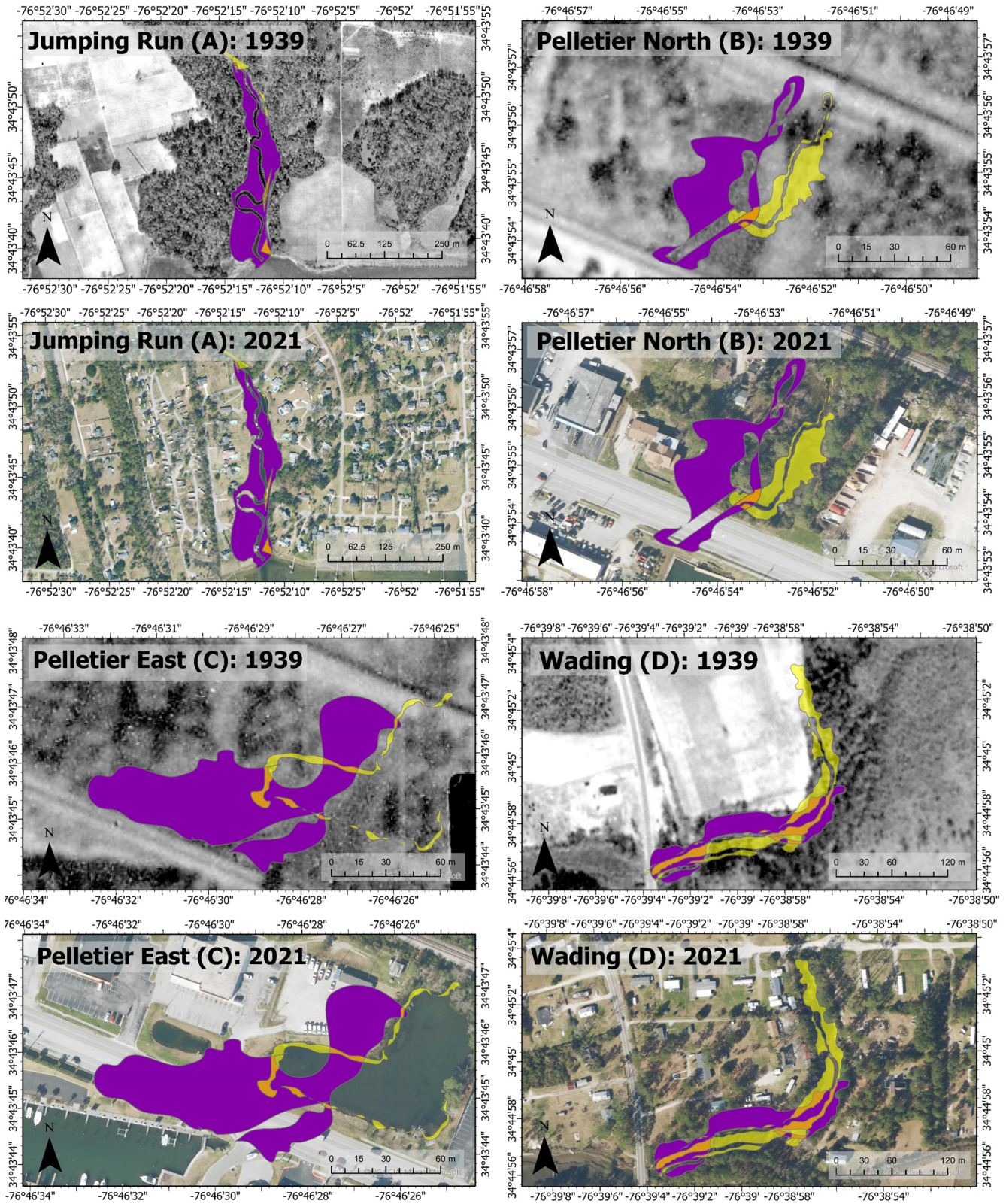


Fig. 2. (Above and next page) Intertidal area of 6 first-order tidal creeks in Morehead City and Beaufort, North Carolina, USA: (A) Jumping Run; (B) Pelletier North; (C) Pelletier East; (D) Wading; (E) Front Street; and (F) Atlantic Veneer. See Fig. 1 for creek locations. The panels show the intertidal area estimated by using orthoimagery in 1939 (purple shading) (top) overlaid with the estimated intertidal area in 2021 (bottom). Semitransparent yellow shading in each panel: areas with no overlap in intertidal area between periods; orange shading: areas with overlap in intertidal area between periods



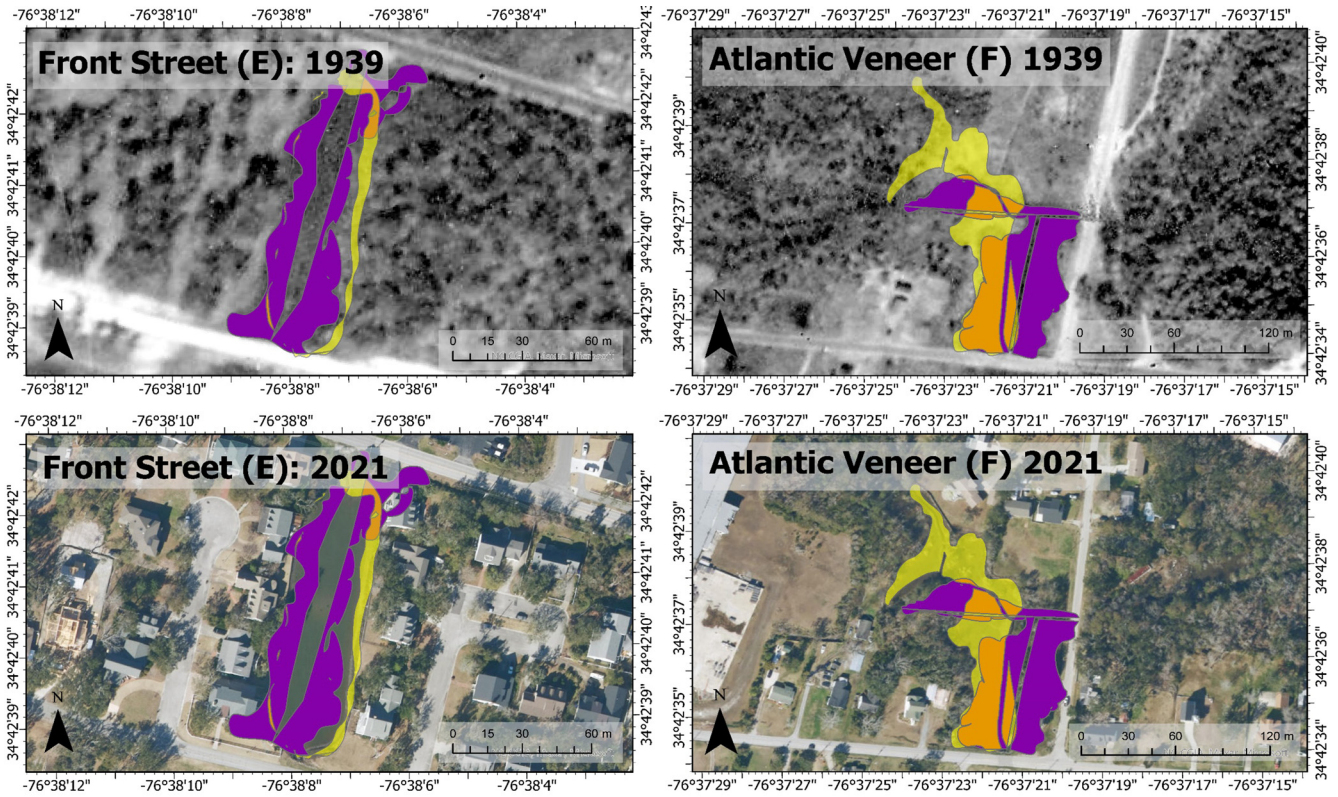


Fig. 2. (continued)

Table 2. Number tagged adult *Fundulus heteroclitus* released into the population ( $R$ ), total number (tagged and untagged) in the recapture sample ( $N$ ), number of tagged in the recapture sample ( $M$ ), and median ( $\pm$  credible interval [CI]) estimated abundance  $\hat{N}$ , and density (ind.  $m^{-2}$ ) within the high tide wetted area of 6 tidal creeks in coastal North Carolina (USA) studied to determine the relationship between their abundance and intertidal area. *F. heteroclitus* abundance was estimated 4 times within each creek: once per season in 2022. Density was calculated in each model run as  $\hat{N}$  divided by the high tide wetted area in 2021.  $\hat{N}$  was estimated from a Lincoln-Petersen model fitted through Bayesian inference, and high tide area was estimated with GIS

Season	Creek	$R$	$N$	$M$	$\hat{N}$ (CI)	Density (CI)
Winter	Jumping Run	17	7	2	75 (31, 450)	0.006 (0.003, 0.037)
	Pelletier North	130	92	22	555 (411, 812)	0.500 (0.370, 0.732)
	Pelletier East	68	5	3	135 (80, 463)	0.027 (0.016, 0.095)
	Wading	205	145	12	2534 (1604, 4610)	0.365 (0.231, 0.664)
	Front Street	198	99	17	1186 (815, 1887)	0.304 (0.209, 0.484)
	Atlantic Veneer	254	429	16	6909 (4438, 11620)	1.311 (0.842, 2.206)
Spring	Jumping Run	74	107	37	216 (184, 269)	0.018 (0.015, 0.022)
	Pelletier North	71	100	15	483 (335, 787)	0.435 (0.302, 0.709)
	Pelletier East	106	52	22	255 (200, 356)	0.052 (0.041, 0.073)
	Wading	230	53	12	1050 (685, 1835)	0.151 (0.099, 0.264)
	Front Street	12	7	2	53 (23, 302)	0.014 (0.006, 0.077)
	Atlantic Veneer	210	253	19	2835 (1935, 4455)	0.538 (0.367, 0.846)
Summer	Jumping Run	33	40	13	105 (78, 168)	0.009 (0.006, 0.014)
	Pelletier North	152	122	38	494 (400, 640)	0.445 (0.360, 0.577)
	Pelletier East	51	38	28	70 (63, 83)	0.014 (0.013, 0.017)
	Wading	282	60	31	555 (452, 722)	0.080 (0.065, 0.104)
	Front Street	26	20	10	54 (41, 87)	0.014 (0.011, 0.022)
	Atlantic Veneer	215	353	46	1664 (1338, 2161)	0.316 (0.254, 0.410)
Fall	Jumping Run	18	38	3	263 (115, 960)	0.021 (0.009, 0.078)
	Pelletier North	250	172	66	656 (564, 784)	0.591 (0.508, 0.706)
	Pelletier East	46	21	21	94 (78, 123)	0.019 (0.016, 0.025)
	Wading	39	6	2	149 (63, 862)	0.021 (0.009, 0.124)
	Front Street	23	124	14	208 (162, 312)	0.053 (0.042, 0.080)
	Atlantic Veneer	555	261	87	1674 (1443, 1984)	0.318 (0.274, 0.377)

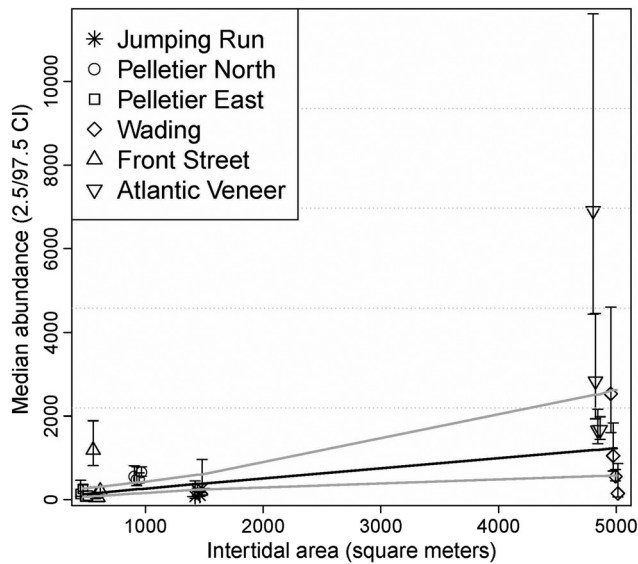


Fig. 3. Median estimated absolute abundance (points)  $\pm 2.5/97.5$  credible intervals [CIs] of adult *Fundulus heteroclitus* in 6 tidal creeks in coastal North Carolina in 2022 vs. current (2021) intertidal area and median predicted abundance (black line)  $\pm 2.5/97.5$  CI for predictions (lower and upper gray lines) obtained from fitting a linear regression model to the fish abundance vs. current intertidal area data. The estimated abundances (points and vertical lines) were obtained by fitting a Lincoln-Peterson model to tag-recapture data in each creek and are jittered around their true x-values to reduce overlap among each creek's symbols. Creeks are listed in the legend in order how they appear (from west to east) in Fig. 1

increased with increasing habitat area within an urbanizing coastal landscape. Furthermore, current intertidal area was negatively correlated with loss rates of this habitat over a roughly 80 yr period, and

historic creek-specific abundance estimates were greater in 5 of the 6 creeks than they are now. To the best of our knowledge, this is the first study to estimate the absolute abundances of *F. heteroclitus* over a continuum of habitat areas and to estimate historic abundance from the current abundance vs. area relationships. As such, this study presents an easily interpretable tradeoff between habitat loss and absolute abundances of an important estuarine species so that resource planners can make informed decisions regarding the conservation of imperiled estuarine habitats along the southeastern US coast, where salt marsh loss is predicted to continue for the remainder of this century (Mattheus et al. 2010, Gittman et al. 2015). Maintaining the natural characteristics of the coastal landscape is essential to ensuring that these habitats continue to provide ecosystem services (Barbier et al. 2011, Lowe & Peterson 2014); our results show that the ecosystem services provided by intertidal areas, such as maintaining pre-development abundances of resident nekton, are diminished with loss of this habitat.

Unfortunately, historic (20th century) records of *F. heteroclitus* densities do not exist for the study creeks. Therefore, we cannot definitively state that creek-specific densities of this species were greater in the 1930s than today or that the greater intertidal area historically vs. currently is solely responsible for this trend in 5 of the 6 study creeks. Other factors besides loss of salt marsh habitat may have caused *F. heteroclitus* abundances to change over time. For example, developing lands in estuarine watersheds are subjected to environmental toxicants (Sanger et al. 1999, Brinson et al. 2013, Anderson et al. 2014),

Table 3. Results from fitting 5 different normally distributed linear models to adult *Fundulus heteroclitus* absolute abundance estimates made from data collected over 4 seasons in 2022 vs. 2021 intertidal area (area) estimated using GIS within 6 study creeks in coastal North Carolina (USA). Season was considered a categorical covariate. Models were fitted to logarithmically transformed data on abundance and area to ensure adequate goodness-of-fit. Models are listed in ascending order of values for the deviance information criterion (DIC) and descending order of proportional support (Akaike weight:  $w_i$ ). ANCOVA: analysis of covariance. A Bayesian goodness of fit p-value is provided for each model. Linear regression tests the null hypothesis of no statistically meaningful relationship between the predictor (marsh area) and response (fish abundance). ANOVA tests the null hypothesis of no difference among group (seasonal) means of abundance. ANCOVA tests the null hypothesis of no difference among group means when controlling for the covariate (marsh area)

Model name	Description of parameters	Structure of the likelihood	DIC	$w_i$	p
Linear regression	One intercept, one slope	$\alpha + \beta \times \text{area}[i]$	74.69	0.75	0.543
Main effects ANCOVA	Multiple intercepts, shared slope	$\alpha[\text{season}[i]] + \beta \times \text{area}[i]$	77.34	0.20	0.541
ANOVA	Multiple intercepts	$\alpha[\text{season}[i]]$	81.06	0.03	0.543
Interaction ANCOVA	Multiple intercepts, multiple slopes	$\alpha[\text{season}[i]] + \beta [\text{season}[i]] \times \text{area}[i]$	82.92	0.02	0.556
Intercept	One intercept	$\alpha$	86.33	0.00	0.541

Table 4. Ratios of tagged:untagged adult *Fundulus heteroclitus* (parentheses: proportions) collected in recapture samples in-stream and downstream of 6 tidal creeks in coastal North Carolina (USA) where absolute abundances were estimated in each season of 2022. The  $\chi^2$  statistic and associated probability (p) values are from tests of independence evaluating whether the ratio of tagged:untagged fish within each creek and season was independent of the sampling location (instream vs. downstream); a ratio shown in **bold** was significantly different than the other ratio for that creek and season. A dash (–) indicates that a test of independence could not be performed due to zero catch of *F. heteroclitus* in the downstream sample

Season	Creek	Instream	Downstream	$\chi^2$	p
Winter	Jumping Run	2:5 (0.40)	0:1 (0)	0.38	0.537
	Pelletier North	22:70 (0.31)	0:0 (0)	–	–
	Pelletier East	3:2 (1.50)	0:0 (0)	–	–
	Wading	12:133 (0.090)	4:111 (0.036)	2.56	0.110
	Front Street	17:82 (0.21)	0:0 (0)	–	–
	Atlantic Veneer	16:413 (0.039)	4:123 (0.033)	0.10	0.758
Spring	Jumping Run	37:70 (0.53)	2:2 (1.00)	0.40	0.526
	Pelletier North	15:85 (0.18)	1:1 (1.00)	1.81	0.178
	Pelletier East	22:30 (0.73)	4:5 (0.80)	0.01	0.905
	Wading	12:241 (0.050)	2:69 (0.029)	0.50	0.481
	Front Street	<b>2:5 (0.29)</b>	0:27 (0)	8.20	0.004
	Atlantic Veneer	19:234 (0.081)	<b>9:35 (0.257)</b>	7.36	0.006
Summer	Jumping Run	13:27 (0.481)	2:12 (0.167)	1.71	0.190
	Pelletier North	38:84 (0.452)	0:0 (0)	–	–
	Pelletier East	28:10 (2.80)	0:0 (0)	–	–
	Wading	31:29 (1.07)	0:0 (0)	–	–
	Front Street	<b>10:10 (1.0)</b>	0:6 (0)	4.88	0.027
	Atlantic Veneer	46:307 (0.150)	1:26 (0.038)	2.01	0.156
Fall	Jumping Run	3:35 (0.086)	0:6 (0)	0.51	0.476
	Pelletier North	66:106 (0.623)	0:0 (0)	–	–
	Pelletier East	21:21 (1.0)	0:0 (0)	–	–
	Wading	<b>2:4 (0.50)</b>	0:13 (0)	4.84	0.028
	Front Street	<b>14:110 (0.127)</b>	0:87 (0)	10.52	0.001
	Atlantic Veneer	<b>87:174 (0.50)</b>	9:43 (0.209)	5.24	0.022

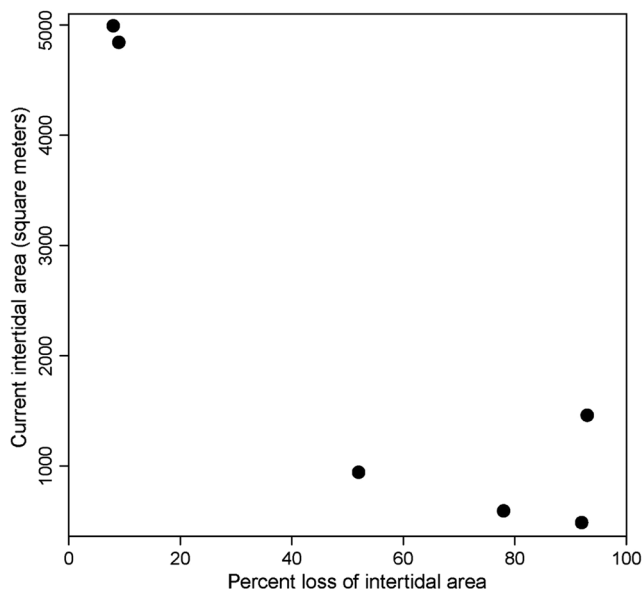


Fig. 4. Current (2021) intertidal area vs. percent loss of intertidal area (between 1939 and 2021) for 6 tidal creeks in coastal North Carolina studied for changes in salt marsh coverage and absolute abundances of adult *Fundulus heteroclitus*

which can have lethal or sub-lethal effects on *F. heteroclitus* (e.g. Weis et al. 2001). This would provide an alternate explanation to habitat loss for temporal changes in the abundance of this species. However, variable survival rates of adult *F. heteroclitus* within the study creeks likely do not explain patterns in abundance given that rates of apparent survival have been found to be similar across a range of watershed conditions (watershed imperviousness, percent hardened shoreline) in southeastern US tidal creeks (Rudershausen et al. 2019). Additionally, the study creeks are not located within heavily industrialized watersheds, which appears to be a prerequisite for lethal toxicity to occur in adults of this species (Smith & Weis 1997). Percent watershed imperviousness, which can lead to excess runoff and reduced dissolved oxygen in estuaries (Uphoff et al. 2011), does not appear to offer an explanation for *F. heteroclitus* densities in this study given that it did not influence them in a previous study in some of the same study creeks (Rudershausen et al. 2019). Another factor potentially influencing temporal changes in fish abundance could be fishery-induced trophic cas-

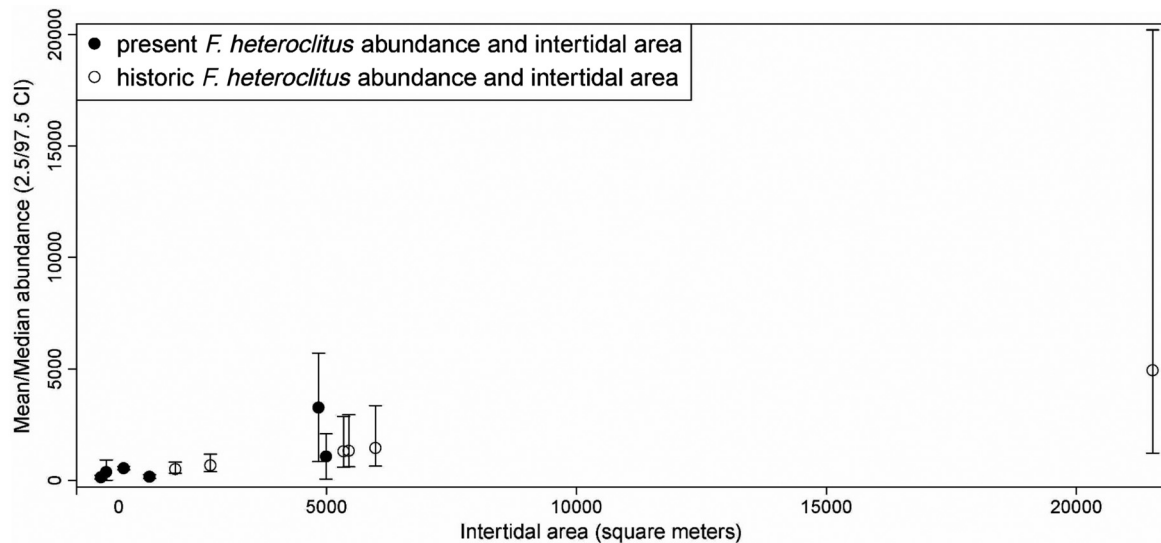


Fig. 5. Estimated absolute abundance of adult *Fundulus heteroclitus* vs. intertidal habitat area in 6 North Carolina tidal creeks. For each creek, filled symbols represent current (2021) estimates of intertidal area and current (2022) mean ( $\pm 95$  credible interval: CI) fish abundance while open symbols represent historic (1939) estimates of intertidal area and median ( $\pm 95$  credible interval: CI) fish abundance. Current fish abundance for each creek was estimated with a Lincoln-Peterson model and then averaged across seasons. Historic fish abundance was estimated by back-transforming estimates obtained from a linear regression model relating logarithmically transformed data on current *F. heteroclitus* abundance vs. current area (see Section 3)

cedes in marine environments (Salomon et al. 2010) that may have changed the abundances of common predators of *F. heteroclitus* either historically or currently. Climate change may have also affected fish abundance. It is possible that changing climate could have affected *F. heteroclitus* abundance over time by, for example, affecting water quality in tidal creeks. Unfortunately, no historic data are available on water quality in the creeks that we studied. *F. heteroclitus* has high tolerances to widely ranging temperatures (Griffith 1974, Nordlie 2006, Fanguie et al. 2008, Chung & Schulte 2015), salinities (Griffith 1974, Nordlie 2006), and values of dissolved oxygen (Nordlie 2006). However, climate change could affect habitat quantity in tidal creeks. Climate change is affecting sea level rise on the North Carolina coast (Kopp et al. 2015). In turn, sea level rise is contributing to the loss of salt marsh in estuaries (Feagin et al. 2010). Given the heavy reliance of *F. heteroclitus* on intertidal salt marsh habitats over its life cycle (Kneib 1997, Able & Fahay 1998) and the fact that each creek lost a percentage of its intertidal area, we can reasonably assume that loss of this habitat is a dominant mechanism for temporal changes in *F. heteroclitus* abundances within these systems.

Inspection of current GIS imagery coupled with ground-truthing creeks in 2022 indicates that creeks with moderate or substantial declines in intertidal area experienced a direct conversion of this habitat

to permanently sub-tidal areas for uses such as boating access (e.g. Jumping Run Creek) or because they were dredged to provide fill for construction (e.g. Pelletier East Creek). With these habitat loss scenarios, the low tide area in a tidal creek increases to more closely match the high tide area (similar wetted areas across tides). However, it is possible that loss of intertidal area could have occurred through other mechanisms. For example, as mentioned above, rising sea level coupled with nearby upland (terrestrial) development (such as road construction or residential development) can inhibit long-term landward migration of salt marshes and ultimately cause them to drown (Reed & Cahoon 1992, Feagin et al. 2010, Mattheus et al. 2010, Mudd 2011).

*F. heteroclitus* has long been recognized as a key link in trophic relay in US Atlantic estuaries (Kneib 2000, Lesser et al. 2021) and the focal species in many studies of estuarine ecology within this region. However, there are few published estimates of absolute abundances of this species. Our study shows that these population estimates need to be viewed in the context of the amount of intertidal area available to them. Therefore, unless previous studies quantified intertidal area, comparing abundances to values among studies is problematic. Further, tides over which sampling occurs (Allen et al. 2007) and gear efficiency and selectivity issues (for data collection types different than ours) could also affect compar-

isons (Rozas & Minello 1997, Rudershausen et al. 2016). For example, Valiela et al. (1977) estimated a mean density of 3.1 adult *F. heteroclitus* m<sup>-2</sup> over high tide areas in Massachusetts (USA) salt marshes but recaptured tagged fish by deploying traps at constriction points on ebb tides as they egressed from the salt marsh. That sampling design, coupled with potential trap shyness by individuals tagged earlier the same day (due to recovery from the tagging procedure, which would positively bias density estimates), may have contributed to the observed differences in densities between that study and ours. Teo & Able (2003) estimated a density of 2.9 ind. m<sup>-2</sup> over both high and low tide sampling in New Jersey (USA) salt marshes, but their density estimate comprised both adult and sub-adult fish (20–40 mm TL). By contrast, there was a mean ( $\pm$ SD) estimated adult density of 0.44  $\pm$  0.79 ind. m<sup>-2</sup> averaged over high tide wetted areas in 4 largely undeveloped North Carolina (USA) first-order tidal creeks studied by Rudershausen et al. (2019) with tag–recapture techniques. Finally, the density estimates in this study accounted for full high tide wetted areas within the study creeks but a percentage of this area (within sub-tidal creek channels) comprised non-vegetated mud bottom, a poorer habitat than salt marsh for adult *F. heteroclitus* (Hettler 1989, Teo & Able 2003, Allen et al. 2007). Therefore, any sampling design (such as in this study) intended to reflect densities over the full high tide area of each creek would theoretically have had lower densities of *F. heteroclitus* than studies that sampled exclusively within *Spartina alterniflora* marsh, its preferred habitat (Kneib 1997). As previously mentioned, our sampling design was not affected by capture or recovery efficiency, habitat type, or tidal stage because we used a passive gear along with a batch tag–recapture approach that assumes equal capture probability between tagged and untagged individuals, and we allowed tagged individuals to disperse with the remainder of the population over the high tide area of each creek. Given the aforementioned nuances associated with sampling *F. heteroclitus* with active gears, we advise using the efficient batch tag–recapture sampling technique that we used in this study, along with passive gears (e.g. traps), if researchers wish to estimate the absolute abundance (density) of this or other nekton species in tidal creek habitats. The aforementioned caveats should be considered when comparing density estimates of adult *F. heteroclitus* between other studies and ours (Table 2).

An assumption of the Lincoln-Petersen estimator, that each creek's population of *F. heteroclitus* was

closed over the duration of each sampling event, was violated based upon the catch of tagged individuals in the downstream trap in 10 out of 24 cases. We are uncertain about the magnitude of the bias that violations of the closure assumption introduced in estimating absolute abundance here. However, animal movement in and out of a study area does not bias population estimates when using closed methods such as the Lincoln-Petersen when it is random but there is bias in estimating abundance when each animal is allowed only a single instance of departure from or entry to a study area (Kendall 1999). This differs from the case of estuarine creeks where *F. heteroclitus* undertakes tidally mediated movements, meaning that individuals are not relegated to a single instance of exit from or entry back into each study creek. With the exception of one creek that lacked a culvert, we tagged fish within those portions of tidal creeks located upstream of a culvert; we assumed, based on research into the impacts of culverts on tidal creek nekton (Eberhardt et al. 2011, Rudershausen et al. 2016), that this would have reduced the probability that the closure assumption would have been violated over the period between tagging and recapture within each seasonal sampling event. However, we found in the majority of cases that numbers of *F. heteroclitus* caught in the downstream trap were very low or zero, indicating that the number of emigrants was likely low during each sampling event. In cases where no fish were caught in the downstream sample, it is possible that this reflects poorer habitat, so emigration from instream habitats may have been unlikely. Given the small home range size of adult *F. heteroclitus* (Lotrich 1975, Meredith & Lotrich 1979, Teo & Able 2003) and the short duration between tagging and recapture, it is possible that dispersal of instream fish to downstream areas was either to the culvert scour pool immediately below a study creek or to a limited distance downstream (<~100 m; Rudershausen et al. 2019). Given that this species undertakes tidal movements within creeks with unimpeded (non-culvert) flows (Rudershausen et al. 2014), it is also possible that tagged fish captured downstream of study areas were temporary emigrants from creeks in which they were tagged. Therefore, the bias resulting from violating the assumption of closure would be small.

The Lincoln-Petersen model also makes assumptions about capture probabilities and tag retention. Specifically, it assumes that all individuals in a population, regardless of tagging status, have equal and independent capture probabilities. We have no reason to believe that recapture probabilities differed

between tagged and untagged individuals, and no data exist on trap happiness or shyness for this species. *F. heteroclitus* has high survival (100%) and tag retention (98.5%) after marking with VIE tags (Skinner et al. 2006) so it appears that the assumptions of post-tagging survival and tag retention were satisfied. The assumption of the Lincoln-Petersen model that tagged individuals became randomly distributed throughout the population was likely met, given the relatively small length of the study creeks (<~300 m), tagging of fish throughout each creek, and the fact that adult *F. heteroclitus* undertake tidally mediated movements within tidal creeks (Bretsch & Allen 2006, Rudershausen et al. 2014).

Conserving living marine resources requires that habitats important for fisheries production are protected from development (Peterson 2003). The relationship between nekton abundance and area of critical habitat is often used as justification for protecting habitats in regions experiencing coastal development (Kneib 2003, Dahlgren et al. 2006). However, managers often lack information on abundance vs. habitat tradeoffs across a quantified range of impacts. This study coupled GIS with an efficient and portable tag-recapture technique to quantify the relationship between absolute abundance and intertidal habitat area. It not only found a meaningful direct relationship between fish abundance and habitat area, but in the majority of cases, estuary-specific abundances were predicted to have been greater historically than currently. Since the study creeks are embedded within an urbanizing environment, we anticipate further losses of intertidal area. Thus, there is an opportunity for future research to consider a full longitudinal (through-time) approach, whereby the researcher, by virtue of this study, possesses historical data on nekton abundance that can complement habitat data over the same time period. We particularly encourage research in tidal creeks, which are among the most impacted types of estuaries along the southeastern US and Gulf of Mexico coastlines (Holland et al. 2004, Peterson & Lowe 2009, Krebs et al. 2014, Sanger et al. 2015). Such research will help us to understand, on an areal basis, how nekton respond to habitat loss, one of the most significant and longstanding anthropogenic threats to temperate coastal marine communities (Odum 1970, Suchanek 1994).

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