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Urbanization impacts on production and recruitment of *Fundulus heteroclitus* in salt marsh creeks

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ABSTRACT: It is unclear how urbanization affects secondary biological production in estuaries in the southeastern USA. We estimated production of larval/juvenile *Fundulus heteroclitus* in salt marsh areas of North Carolina tidal creeks and tested for factors influencing production. *F. heteroclitus* were collected with a throw trap in salt marshes of 5 creeks subjected to a range of urbanization intensities. Multiple factor analysis (MFA) was used to reduce dimensionality of habitat and urbanization effects in the creeks and their watersheds. Production was then related to the first 2 dimensions of the MFA, month, and year. Lastly, we determined the relationship between creek-wide larval/juvenile production and abundance from spring and abundance of adults from autumn of the same year. Production in marsh (g m^{-2} d^{-1}) varied between years and was negatively related to the MFA dimension that indexed salt marsh; higher rates of production were related to creeks with higher percentages of marsh. An asymptotic relationship was found between abundance of adults and creek-wide production of larvae/juveniles and an even stronger density-dependent relationship was found between abundance of adults and creek-wide larval/juvenile abundance. Results demonstrate (1) the ability of *F. heteroclitus* to maintain production within salt marsh in creeks with a lesser percentage of marsh as long as this habitat is not removed altogether and (2) a density-dependent link between age-0 production/abundance and subsequent adult recruitment. Given the relationship between production and marsh area, natural resource agencies should consider impacts of development on production when permitting construction in the southeastern USA.

KEY WORDS: Production · *Fundulus heteroclitus* · Salt marsh

1. INTRODUCTION

Secondary biological production in estuaries is the most composite measure of how nekton respond to anthropogenic stressors (Able 1999). It can serve as an indicator of ecological integrity that can be compared among habitats, regions, and types of impacts (Mann & Penczak 1986, Able 1999, Randall & Minns 2000, Rakocinski & Zapfe 2005, Hayes et al. 2007) for coastal management and protection purposes (Beck et al. 2001). Further, estimates of secondary production are valuable for determining the ability of estuaries to serve as nurseries because the process of tissue elaboration over time accounts for density, growth, and mortality (Beck et al. 2001). However, because of the inherent openness of estuarine habitats (Kneib 2003) and the data requirements to estimate production, this metric is not frequently studied in estuaries (Able 1999). This is unfortunate because natural and anthropogenic drivers of production are only recently becoming understood for many fish and invertebrate species inhabiting the rapidly developing coastal zones of the southeastern USA and Gulf of Mexico (Holland et al. 2004, Partyka & Peterson 2008, Peterson & Lowe 2009, Lowe & Peterson 2014). While relationships between fish production (or its

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metrics) and vegetated habitats are used to justify protecting habitats in regions with coastal development (Kneib 2003, Dahlgren et al. 2006), production within these habitats has seldom been compared among waterbodies subjected to various impacts. The expectation is for production of a nekton species to vary among estuaries based on habitat quality at the creek and watershed spatial scales (Able 1999, Kneib 2003, Holland et al. 2004, Krebs et al. 2014).

Urbanization of intact salt marsh mosaics, defined as the severing and serial replacement of these habitats with hardened surfaces and shorelines (Lowe & Peterson 2014), has fragmented them into increasingly smaller and more isolated patches along coastlines of the USA (Holland at et. 2004, Bromberg & Bertness 2005, Lowe & Peterson 2014, Sanger et al. 2015) and other countries (Doody 2004, Duarte et al. 2008, Gedan et al. 2009). Impacts such as habitat fragmentation, shoreline armoring, and dredging have been implicated in affecting the biotic integrity of nekton populations in estuaries along the coasts of the southeastern USA and Gulf of Mexico (Bilkovic & Roggero 2008, Partyka & Peterson 2008, Bilkovic 2011, Gittman et al. 2015, Rudershausen et al. 2016). Impacts from development are most likely to occur in first-order tidal creeks in low-relief coastal areas due to their proximity to the uplands that they drain (Holland et al. 2004, DiDonato et al. 2009). While development in tidal creek watersheds has been implicated in reducing secondary biological production in these systems (Holland et al. 2004, DiDonato et al. 2009), to our knowledge this theory has not been tested along a gradient of urbanization that indexes common human impacts in US coastal zones. Recognizing human encroachment into coastal zones, natural resource agencies in North Carolina (USA) have called for more fishery-independent analyses to determine natural and anthropogenic drivers of estuarine nekton production (NCDMF 2010, Jensen et al. 2014). Effective fisheries management in estuaries requires information relating fish populations to their usage of habitats targeted for protection (Skilleter & Loneragan 2003, Dahlgren et al. 2006), and secondary production is a measure of ecosystem response to stressors (Mann & Penczak 1986, Able 1999, Valentine-Rose et al. 2007). Estimating production and relating it to habitat and urbanization factors in estuaries provides timely information to agencies charged with identifying and mitigating threats to important coastal habitats such as salt marshes. Furthermore, there have been few tests into whether larval and juvenile fish production in estuaries is linked to subsequent recruitment to the adult population (Gillanders & Kingsford 1996, Beck et al. 2001, Kraus & Secor 2005).

Fundulus heteroclitus is the dominant fish species inhabiting salt marshes along the US Atlantic coast. It exhibits monthly peaks in spawning activity; thus, new cohorts are expected monthly in southeastern US tidal creeks (Taylor et al. 1979). This species uses salt marshes for foraging, refuge, reproduction, and as a nursery habitat (Kneib 1986, 1997a). Adult *F. heteroclitus* (≥41 mm total length, TL), while having similar rates of apparent survival among variably altered creeks, have the greatest abundances in creeks with higher percentages of intertidal salt marsh (Rudershausen et al. 2019). This relationship could result from the physical importance of salt marsh for egg deposition (Taylor et al. 1977) and its importance as nursery habitat for larvae and juveniles. Additionally, the absolute amount of salt marsh areal production (g m^{-2} d^{-1}) might be higher in creeks with a higher percentage of salt marsh. Production of age-0 *F. heteroclitus* in salt marsh habitats has been estimated before (Valiela et al. 1977, Meredith & Lotrich 1979, Teo & Able 2003a, Hagan et al. 2007) but, to the best of our knowledge, not along a gradient of urbanization intensity. *F. heteroclitus* is a good model for estimating production and studying impacts on tidal creeks because of its abundance and role in salt marsh trophic dynamics (Kneib 1986, 1997a), small home range, localized recruitment, and site fidelity to home marshes (Lotrich 1975, Sweeney et al. 1998, Skinner et al. 2005).

We estimated larval and juvenile *F. heteroclitus* production in 5 tidal creeks and tested whether it differed as a function of a suite of habitat and urbanization factors. We focused on larval and juvenile *F. heteroclitus* because they contribute the majority of production of this species (Meredith & Lotrich 1979, Teo & Able 2003a, Hagan et al. 2007). Additionally, we tested for relationships between creek-wide larval and juvenile production and creek-wide abundance, respectively, and subsequent adult relative abundance to elucidate a mechanism behind greater abundance of adults in some creeks than others. This project builds on previous studies (Valiela et al. 1977, Meredith & Lotrich 1979, Teo & Able 2003a, Hagan et al. 2007) by examining *F. heteroclitus* production across study areas differentially affected by urbanization.

In this study, areal production was related to multiple habitat and urbanization factors. These factors included percent watershed imperviousness, percent salt marsh in the high tide wetted area of each creek, percent armored intertidal–sub-tidal edge, mean depth of the creek channel at bank-full level, mean creek width of the channel, presence/absence of a

culvert, and percent of marsh downstream of the sampled area in a creek but within a home range (200 m) of adult *F. heteroclitus* (Skinner et al. 2005). Watershed imperviousness is a composite metric of anthropogenic stress to creeks (Wang et al. 2001, Holland et al. 2004, Krebs et al. 2014) while salt marsh is important habitat for spawning, feeding, and refuge by *F. heteroclitus* (Kneib 1997a). Armored shoreline is a common development feature in the southeastern USA that eliminates salt marsh/channel edge (Gittman et al. 2015), important for access to the marsh surface (Peterson & Turner 1994, Minello et al. 2003), and production by salt marsh nekton (Kneib 2003, Roth et al. 2008). Finally, the impacts of culverts and creek channel morphology were examined because culverts alter movement of nekton in tidal creeks (Rudershausen et al. 2016) while channel width and depth can influence nekton use of tidal creeks (Bretsch & Allen 2006, Allen et al. 2007, Rudershausen et al. 2016).

2. MATERIALS AND METHODS

2.1. Study sites

A total of 5 first-order tidal creeks were sampled in mid-coastal (34.7° N, 76.7° W) North Carolina (USA) (Fig. 1). These tidal creeks exhibit impacts to their high-tide areas and watersheds (Table 1) typical of these systems in the southeastern US coastal plain (Holland et al. 2004) and the patchiness of estuarine habitats within developing coastal landscapes (Boström et al. 2011). The vegetative types and tidal characteristics were largely similar among creeks. Production in intertidal areas, such as salt marshes, depends partly on their physical accessibility to consumers (Kneib 2003); the sampled portions of study creeks (above a culvert or above a higher-order waterbody) were positioned within their watersheds such that the duration over which the salt marsh experiences tidal flooding, and thus the time over which it can be accessed by consumers, was roughly equal among them (~3.5 h) (authors' pers. obs.). There was little variation in the times of tidal inundation among study creeks, and thus times over which the marsh flooded were not included in any analyses. The study creeks are considered meso-polyhaline (Table 1). Spooners, Porters, and Atlantic Veneer Creeks (Fig. 1) are 'rivulet' creeks (Rozas et al. 1988, Hettler 1989) with shallow flows roughly 0.1 m deep at low tide that meander through part of their channels. In contrast, the channel in the lower section of Pelletier West Creek is largely covered with water over low tides. Each creek has a fringing marsh dominated by *Spartina alterniflora* (Loisel) (Table 1). Pelletier East Creek is a saltwater pond with a narrow fringing marsh and standing water over all tides due to being dredged in the middle of the 20th century. Below their sampled areas, Pelletier East, Pelletier West, and Spooners Creeks have predominantly armored shorelines with non-existent (Pelletier East) or sparse (Pelletier West and Spooners) *S. alterniflora* coverage. Adult *Fundulus heteroclitus* exhibit similar patterns of high site fidelity among these creeks (Rudershausen et al. 2019).

Delineating downstream study area boundaries is often subjective in research of estuarine production (Kneib 2003). Culverts, while manmade, can delineate these boundaries (Stevens et al. 2006). We bounded the downstream sampling limit in each creek by the presence of a culvert or its confluence with a higher-order estuary. The limit of upstream sampling was bounded by the extent of tidal influence or, in the case of Pelletier East Creek, an upstream culvert.

Boundaries and impervious surface percentages for each watershed were estimated by using ArcGIS version 9.3.1 (ESRI). Details of this process are found elsewhere (Rudershausen et al. 2016). We sampled creeks both below and above a threshold level of watershed imperviousness (20–30%) where it is believed that biotic integrity or components of estuarine nekton production (growth and survival) are negatively impacted in tidal creeks (Holland et al. 2004, Bilkovic & Roggero 2008).

2.2. Field sampling and sample processing

Each creek was sampled monthly from April through October in 2012 and 2013 to provide data to estimate production. These are months over which *F. heteroclitus* spawns in this region (Kneib & Stiven 1978, Taylor et al. 1979). Creeks were sampled on different days. Each creek was divided into 10 evenly spaced and contiguous transects; transect size varied among creeks due to creek size. All 10 transects per creek (or a lesser number due to tidal levels in Pelletier East Creek) were sampled the same day each month. Sampling gear was a 1 m^2 square metal frame throw trap with sides 0.6 m high. It was deployed by foot in the flooded marsh. The throw trap is a type of areal sampling gear used to target small nekton in vegetated habitats (Turner & Trexler 1997, Rozas & Minello 1998). When adjusted for catchability, it

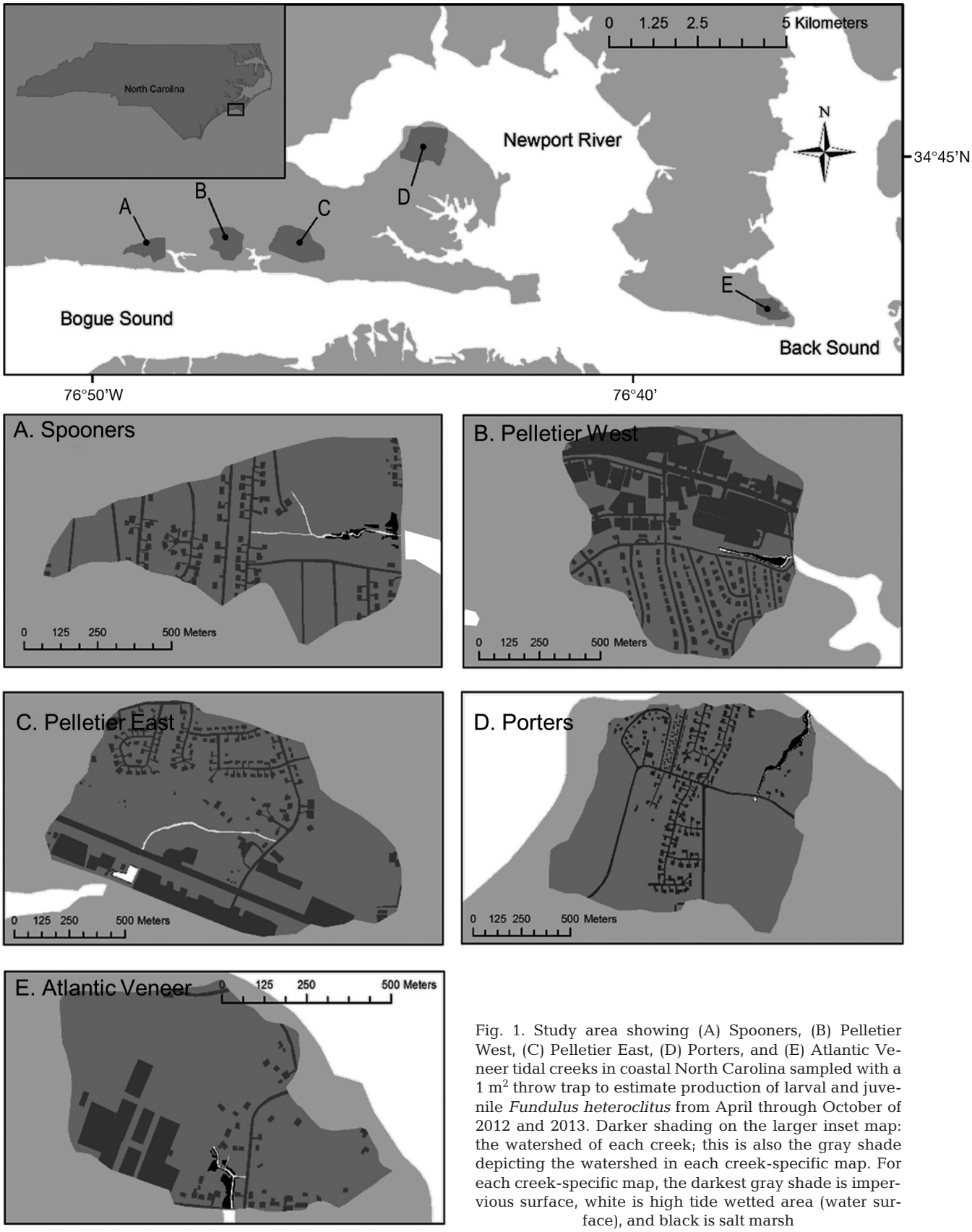

Fig. 1. Study area showing (A) Spooners, (B) Pelletier West, (C) Pelletier East, (D) Porters, and (E) Atlantic Veneer tidal creeks in coastal North Carolina sampled with a 1 m^2 throw trap to estimate production of larval and juvenile *Fundulus heteroclitus* from April through October of 2012 and 2013. Darker shading on the larger inset map: the watershed of each creek; this is also the gray shade depicting the watershed in each creek-specific map. For each creek-specific map, the darkest gray shade is impervious surface, white is high tide wetted area (water surface), and black is salt marsh

Table 1. Watershed, habitat, and water quality characteristics for 5 tidal creeks in coastal North Carolina (USA) that were sampled for larval and juvenile *Fundulus heteroclitus* production from April through October, 2012–2013

Characteristic/measurement	Atlantic Veneer	Porters	Pelletier East	Pelletier West	Spooners
Watershed area (m^2)	414 224	1 095 729	1 127 387	698 413	490 859
Impervious area (m^2)	64 322	110 166	260 740	325 629	64 220
Inter-tidal–sub-tidal vegetated edge (m)	500	1200	145	500	400
Percent watershed imperviousness	15.5	10.0	23.1	46.7	13.0
High tide wetted area (m^2)	5209	15 162	4170	5427	7691
Marsh area (m^2)	4247	9498	112	3707	6324
Percent marsh area instream at high tide	81.5	62.6	2.7	68.3	82.2
Percent marsh area downstream at high tide	91.0	100	0	34.5	37.3
Mean creek channel depth (m)	0.21	0.27	0.96	0.28	0.29
Mean ± SE sampling distance from channel (m)	5.8 ± 0.1	11.25 ± 0.9	0.4 ± 0.1	4.7 ± 0.3	3.5 ± 0.5
Mean ± SE sampling depth (m)	0.19 ± 0.01	0.24 ± 0.01	0.19 ± 0.01	0.19 ± 0.01	0.19 ± 0.01
Mean ± SE vegetative coverage (%)	65.0 ± 1.6	61.7 ± 1.7	72.0 ± 2.4	80.6 ± 1.6	68.3 ± 1.8
Mean ± SE temperature (°C)	24.9 ± 0.4	26.0 ± 0.4	27.6 ± 0.4	26.8 ± 0.4	27.3 ± 0.5
Mean ± SE salinity (psu)	30.0 ± 0.7	25.8 ± 0.5	21.0 ± 0.9	17.6 ± 0.8	25.6 ± 1.0
Mean ± SE dissolved oxygen (mg l^{-1})	4.83 ± 0.12	5.26 ± 0.20	5.7 ± 0.3	5.0 ± 0.27	4.2 ± 0.2

allows for estimating absolute density (Kushlan 1981, Rozas & Minello 1997, Rudershausen et al. 2016).

The throw trap was used to target small (<41 mm TL) *F. heteroclitus* in this study. Variation in the frequency and duration of tidal inundation in salt marshes can influence the density of young *F. heteroclitus* on the marsh surface (Kneib 1997b). For this reason, the throw trap was deployed over high tides using a stratified random sampling design with respect to distance upstream within each transect, left vs. right fringing marsh, and lateral distance into the marsh towards upland. Such a design accounted for variability in nekton densities with lateral distance from creek channels (Kneib & Wagner 1994, Allen et al. 2007). With this sampling design, 10 trap deployments were generally made monthly in each creek (1 transect^{-1}) except for Pelletier East Creek, where the narrowness of the marsh prevented trap deployment in roughly half of the strata each month. Immediately after deployment, the trap was pressed into the sediment to prevent fish from escaping. Water depth (±0.1 m) and visually estimated percent salt marsh vegetation (*S. alterniflora* stem density) in the trap (nearest 10%) were collected with each trap deployment. Each trap set was then swept 50 times with a 0.30 × 0.25 m dipnet possessing 0.72 mm^2 nylon mesh. Netted vegetation was initially removed in the field by sieving the sample through a wash bucket with 0.22 mm^2 mesh. Fauna and remaining organic matter were preserved in 95% ethanol for later sorting, fish identification, and measurement.

Shrinkage in fish lengths due to time lags between collection and sample sorting was examined to estimate original unpreserved lengths (Cunningham et al. 2000). *F. heteroclitus* from 8.9–42.7 mm TL were sampled with a dipnet (separate from trapping), measured (±0.1 mm), and stored in individual vials with 95% ethanol. Each preserved individual was remeasured 36, 196, 485, and 673 d later to encompass times we believed, *a priori*, would be needed to sort trap samples. Shrinkage decreased with time, and the slope of a linear regression fitted to TL vs. time at 196, 485, and 673 d after collection was not different than zero ($p = 0.059$) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m645p187_supp.pdf). The mean proportional decrease in length over these 3 time points was 0.065. Because trap samples were sorted 6–18 mo after collection, we adjusted the length of fish from trapping upwards by 6.95% (preserved length × 1.0695). Shrinkage is independent of fish length among preserved small-bodied fish species (Cunningham et al. 2000), so original fish size was not accounted for when adjusting lengths.

Dry weight (DW) is often used to estimate production of small-bodied fishes, including *F. heteroclitus* (Teo & Able 2003a). However, time lags between trapping and sample sorting prevented recording DWs after capture; thus, DW relationships were developed for each creek to estimate the DW of each individual after correcting lengths from preservation. *F. heteroclitus* were collected from each creek (independent of trapping), measured (±0.1 mm), then dried for 48 h at 60°C and weighed (±0.00001 g). Data on DW and TL were natural logarithm (ln) transformed to establish a linear relationship: $\ln(DW) = a + b \times \ln(TL)$ where a and b are parameters estimated in the model fit. Each

creek's model explained a high proportion of variability (adjusted $r^2 > 0.8$) (Fig. S2). The relationship for each creek was used to estimate the DW of each individual from throw trapping after correcting lengths from preservation.

Catch rates of fish from throw trapping can be biased due to incomplete recovery of all targeted individuals enclosed by the gear (Kushlan 1981, Rozas & Minello 1997). Catchability by an actively deployed trap has 2 components: capture efficiency and recovery efficiency (Rozas & Minello 1997); capture efficiency is the proportion of targeted individuals in a sampling area eventually enclosed by the gear while recovery efficiency is the proportion of individuals recovered relative to those enclosed. Given the small size of larval and juvenile *F. heteroclitus* targeted by the throw trap, we were more concerned about recovery efficiency than capture efficiency. The catch from each trap deployment was adjusted for recovery efficiency to estimate absolute density of *F. heteroclitus*. Methods for estimating throw trap recovery efficiency are found elsewhere (Rudershausen et al. 2016). Briefly, recovery efficiency of *F. heteroclitus* was estimated with a depletion method; efficiency was negatively related to *S. alterniflora* stem density. Absolute density for each trap deployment was then estimated by dividing the catch of *F. heteroclitus* in a trap by the estimated recovery efficiency for each deployment.

2.3. Tracking cohorts

Estimating secondary production incorporates calculations of individual growth. Data on larval and juvenile *F. heteroclitus* growth were obtained by constructing length–frequency histograms to track cohorts across 2 successive months of sampling. Monthly length–frequency histograms of throw-trapped *F. heteroclitus* from each study creek were plotted to identify age-0 cohorts newly recruited to the throw trap and also to estimate growth of age-0 cohorts already recruited in an earlier month (Fig. S3). We estimated growth and production on a cohort-specific basis due to recruitment of new cohorts to the gear throughout the growing season. An advantage to estimating production of larval and juvenile *F. heteroclitus* is that they largely remain on the intertidal marsh surface over all tides (Kneib 1984, Teo & Able 2003b). Thus, adjustments to production to account for immigration to and emigration from study creeks (Stevens et al. 2006) are not needed for these life stages.

We used several criteria to identify and distinguish cohorts of *F. heteroclitus* using length–frequency histograms. Anti-modes in observations (low numbers or no observations per length bin) in monthly histograms were used as guides in selecting the length range of individuals comprising a cohort (Fig. S3). More than one captured individual was required to distinguish a cohort collected from a monthly set of trap samples in a creek. Using these criteria, the same number of cohorts was not necessarily equal among creeks within the same month. Additionally, no cohorts were identified for some creek–month combinations. Owing to concerns about capture efficiencies being less than 100% and to restrict production to age-0 fish, estimates of production were limited to cohorts that had an averaged ≤44.5 mm TL upon the second month of being tracked.

2.4. Calculating production

DW areal production in the salt marsh (g m^{-2} d^{-1}) was calculated for each cohort that could be tracked between 2 consecutive months. We estimated production using a method that incorporates the instantaneous growth rate, G_{inst}, of a cohort and its mean biomass over the tracked period (Ricker 1946); this model choice is consistent with previous estimates of production of *F. heteroclitus* (Valiela et al. 1977, Teo & Able 2003a). G_{inst} for a cohort across successive sampling dates was calculated as:

$$G_{inst} = \frac{\ln(\bar{w}_2) - \ln(\bar{w}_1)}{t_2 - t_1} \quad (1)$$

where ($\bar{w}_1$) and ($\bar{w}_2$) are the mean DWs predicted from TLs of throw-trapped fish upon the first (t_1) and second (t_2) sampling dates.

The other calculation used to estimate production was the mean biomass of a cohort ($\bar{B}$) between successive sampling dates. $\bar{B}$ has 2 components. The first is density; mean monthly density ($\bar{N}$) of each tracked cohort of larvae/juveniles was calculated as the average catch of individuals within a cohort across successive monthly values of density. These calculations assume that $\bar{N}$ is representative of the mean density over a creek's entire salt marsh area (Teo & Able 2003a). The 2.5 and 97.5% confidence intervals (CIs) about $\bar{N}$ in the first month ($\bar{N}_1$) and second month ($\bar{N}_2$) in each creek were also calculated. These CIs about density were used to calculate 2.5 and 97.5% CIs for production (Teo & Able 2003a), since the principal source of error in estimating production arises from variability about density rather than growth

(Chapman 1967, Mann & Penczak 1986, Morin et al. 1987, Teo & Able 2003a). The second component of $\bar{B}$ is the $\bar{w}_1$ and $\bar{w}_2$ of 2 successive sampling occasions. $\bar{B}$ was then calculated as:

$$\bar{B} = \frac{\bar{N}_1\bar{w}_1 + \bar{N}_2\bar{w}_2}{2} \quad (2)$$

Finally, for each tracked cohort, production on the marsh surface between 2 successive sampling events (P) was taken from Ricker (1946) and calculated as:

$$P = G_{\text{inst}} \times \bar{B} \quad (3)$$

As with calculations of $\bar{B}$, the lower and upper CIs of P were calculated; these CIs only capture the uncertainty about $\bar{N}$.

2.5. Relating production to habitat and urbanization factors

Multiple factor analysis (MFA) was used to reduce the dimensionality of the aforementioned habitat and urbanization factors (Fig. 2). MFA is a technique to visualize how study subjects (in this case, tidal creeks) are oriented in graphical space based on loadings of continuous and/or categorical effects (Escofier & Pagés 1994). The MFA output includes the variability about the model fit explained by each plotted dimension. The MFA model was fitted to habitat and urbanization data for each creek (Table 1) using the R package 'FactoMineR' (Husson et al. 2018). Creek-specific values for MFA dimensions 1 (MFA1) and 2 (MFA2) were then used in linear modeling to test for meaningful covariates of production (see below).

Non-spatial variables (not modeled within the MFA) were also considered for their effects on production. Month at the start of each production estimate and year were considered as temporal factors. Although it may affect fish production (Valiela 1984), water temperature (°C) was not modeled because it is related to month. Values for stem density of *S. alterniflora* and water depth from trap deployments were not considered because these data were used in the model describing recovery efficiency (Rudershausen et al. 2016).

A normally distributed linear model was fitted via Bayesian inference (Kéry 2010) to examine the relationship between mean cohort-specific estimates of areal production and the MFA scores as well as 2 temporal factors (month and year). Raw values of production were transformed (ln[P + 1]) to address potential non-linearity between the response data and covariates. An uninformative normal prior prob-

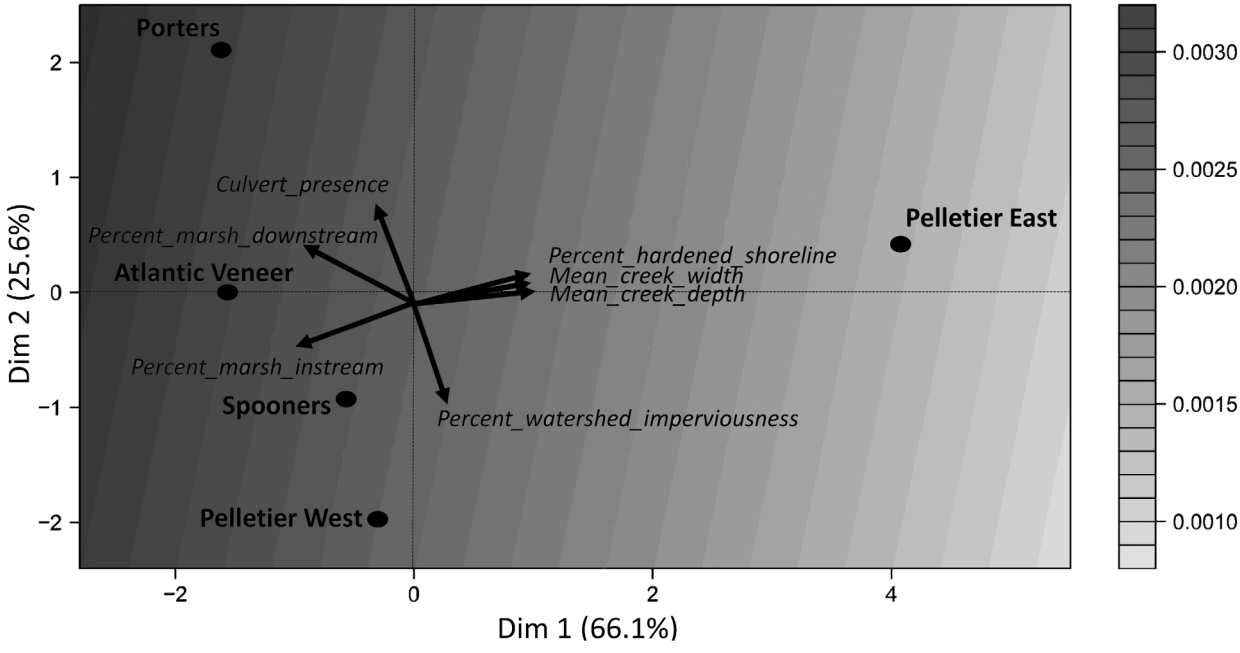

Fig. 2. Results of a multiple factor analysis (MFA) showing the orientation of 5 North Carolina tidal creeks (**bold** font) in 2-dimensional graphical space based on loadings (arrows) of each of 7 habitat/urbanization factors (*italicized* font). Creeks were studied for production of *Fundulus heteroclitus* from April through October of 2012 and 2013. The variability in the MFA model explained by dimensions 1 and 2 is provided with *x*- and *y*-axis labels, respectively. The predicted production (heat plot in grayscale) (g m^{-2} d^{-1}) vs. MFA scores are from a linear model that included MFA1 and year as meaningful covariates of production; the plot shows the prediction for the base year

ability distribution (prior) was assigned to the intercept (alpha) term (mean and precision of 0 and 1×10^{-6}, respectively) as well as each partial regression coefficient (beta) in the model. The model was fitted by fixing the effect of the first year and first month sampled within each year at zero (base levels) and evaluating the effects of the other levels of each of these respective factors relative to the base (Kéry 2010). We fitted a model with all potential covariates that might explain production. A factor was considered meaningful when its 95% credible interval for its partial regression coefficient did not overlap zero. The model was fitted using 'JAGS' version 4.0 (Plummer 2015) in R version 3.5.3 (R Core Team 2019) with the interface package 'R2jags' (Su & Yajima 2015). The model was run using 3 chains of initial values updated 10 000 times. The initial 10% of retained updates of each parameter were discarded as an adaptive phase. Convergence was assessed by computing the Gelman-Rubin statistic ($\hat{R}$) for each model parameter; values <1.1 for $\hat{R}$ suggest convergence to a stable posterior probability distribution (Gelman et al. 1996). A Bayesian p-value, used to assess model goodness of fit, was calculated; values close to 0.5 suggest adequate fit (Kéry 2010).

2.6. Relating adult abundance to larval and juvenile metrics

We examined relationships between 2 larval and juvenile metrics (considered 'stock', S) and an index of adult *F. heteroclitus* abundance (considered subsequent 'recruits', R). The first metric was larval and juvenile production and the second was larval and juvenile abundance. Data used to index adult abundance were mean creek-wide catches of *F. heteroclitus* in September 2012 and September 2013, respectively, using baited Gee-style 6.4 mm mesh wire minnow traps passively fished for 3 h over high tides (catch-per-unit-effort [CPUE] data). This is a time of year when age-0 *F. heteroclitus* dominate the catch in this gear type (Kneib & Stiven 1978, authors' unpubl. data) and thus are most likely to represent catches of recruits of larvae hatched earlier the same year. Additionally, the length–frequency histograms (Fig. S3) suggested that fish tracked for production in the spring each year were age-0 rather than being spawned late in the previous year. Based on growth rates of throw-trapped fish tracked for production (see Section 3.1) and low survival of age-1+ *F. heteroclitus* (Rudershausen et al. 2019), we assumed that minnow trap CPUE linearly indexes densities of larger age-0 (≥41 mm TL) *F. heteroclitus* (Rudershausen et al. 2019). Each of the relationships we examined between larval and juvenile and adult *F. heteroclitus* is described in greater detail below.

We examined the relationship between springtime (April, May, June) larval and juvenile production and adult CPUE. To put the larval and juvenile data on the same spatial scale as the adult abundance index, each mean cohort-specific estimate of areal production within marsh habitat for the April–May and May–June periods was extrapolated to the full high wetted area of each creek; this was computed by multiplying each mean within-marsh production estimate by the proportion of a creek's high tide area comprised of salt marsh (Table 1). We assumed that production of larval and juvenile *F. heteroclitus* is relegated to marsh rather than non-vegetated mud (Kneib 1984, Talbot & Able 1984, Teo & Able 2003b). For this reason, our comparison of production did not include water volume differences among creeks since previous studies have found that larval and juvenile *F. heteroclitus* are relegated to the marsh surface of their natal creeks. Thus, area of marsh is more important than the volume of water.

In exploratory modeling of the creek-wide larval and juvenile production and adult CPUE relationship, we fitted a linear model and found that its slope contained zero, and so pursued alternative models to examine this relationship further. We then fitted a 2-parameter Beverton-Holt model, because the relationship between adult CPUE (i.e. R) and larval and juvenile production (i.e. S) indicated potential density-dependence based on a data plot (see Section 3.3). This model is given as: $R = aS / 1 + bS$, where S is the extrapolated larval and juvenile (creek-wide) production and R was the subsequent minnow trap CPUE, while a and b are parameters estimated via the fit. The model was fitted using nonlinear regression within the 'brms' package (Bürkner 2019); uniform priors were used for a and b that ranged from 0–50 000 for a and 0–3000 for b. The model fit was considered plausible and parameters biologically meaningful if the 95% credible intervals for a and b did not overlap zero.

The second larval and juvenile and adult relationship examined was between spring larval and juvenile abundance and September CPUE because density contributes more than other components to the variability about production (Chapman 1967, Mann & Penczak 1986, Morin et al. 1987, Teo & Able 2003a). We used each unique estimate of $\overline{N}$ in April, May, and June in estimating abundance over the full high tide wetted area of each creek (Table 1) so that these esti-

mates applied to the same area over which adult CPUE data were collected. The relationship between adult CPUE and the larval and juvenile data appeared strongly density-dependent (dome-shaped) based on a plot of these data, so we elected to fit a 2-parameter Ricker stock-recruitment model (Ricker 1975): $R = aSe^{-a[S/[be(1)]]}$, where a and b are parameters estimated using non-linear regression. The priors used within the 'brms' package for a and b were uniform from 1×10^{-10} to 0.3 for a and 1×10^{-10} to 100 for b.

3. RESULTS

3.1. Estimates of density, growth, and production

Areal production estimates were highest in creeks that had a high percentage of salt marsh. Mean (±SD) densities of *Fundulus heteroclitus* within salt marshes across all months sampled were 4.51 ± 5.18, 5.00 ± 5.74, 2.50 ± 2.84, 2.60 ± 3.26, and 2.99 ± 2.98 m^{-2} for Atlantic Veneer, Porters, Pelletier East, Pelletier West and Spooners Creeks, respectively. In general, there was high variability about mean density values (0.20–4.20 ind. m^{-2}) and wide overlap in densities among creeks for cohorts tracked for production (Fig. 3, Table S1).

Cohort-specific absolute growth rates ranged from 0.08–0.72 mm d^{-1} (Table S1). There was variation in absolute growth rates among creeks, but values were generally consistent and averaged 0.34 ± 0.14 mm d^{-1} (Fig. 4). A total of 69 cohort-specific estimates of DW areal production within salt marsh habitat were made. Across all creeks and time intervals, this production averaged 0.0022 ± 0.0022 g m^{-2} d^{-1} (Fig. 5; Table 2). Mean creek-specific estimates of production for Atlantic Veneer, Porters, Pelletier East, Pelletier West, and Spooners Creeks averaged 0.0023 ± 0.0023, 0.0026 ± 0.0024, 0.0010 ± 0.0009, 0.0031 ± 0.0029, and 0.0015 ± 0.0010 g m^{-2} d^{-1}.

3.2. Relating production to habitat and urbanization factors

The MFA resulted in axes describing instream and watershed-level impacts. Axis 1 (MFA 1) largely represented a gradient of instream impacts to salt marsh, with less developed creeks and more intact marsh mosaics having negative values for MFA1. MFA2 represented increasing watershed imperviousness in one direction and presence of culverts in the other (Fig. 2).

We identified covariates that explained variability in our individual estimates of cohort-specific production (95% credible sets of partial regression coefficients not overlapping with zero). These covariates included MFA1, the month of September, and year (Table 3). Specifically, MFA1 (Fig. 2) had a negative effect on production; thus, production was lower in creeks with lower percentages of salt marsh. Additionally, September had higher production than the base (April), and Year 2 had lower production than Year 1. This model had acceptable goodness of fit (Bayesian p = 0.525). Each model parameter converged ($\hat{R} < 1.1$). Development at the watershed scale (watershed imperviousness) did not affect production.

3.3. Relating adult abundance to larval and juvenile metrics

The relationship between R in September of each year (recruitment) and S production in spring of that same year (stock) was variable. However, the Beverton-Holt model fit these data reasonably well, showing density-dependence at higher larval and juvenile production levels (Fig. 6A). The median value (±2.5 and 97.5% credible intervals) for a from fitting a 2 parameter Beverton-Holt stock-recruitment model was 33 730 (9761, 49 282) while the median value for b was 1600 (276, 2899); thus, the credible set for each parameter was meaningful in that it did not contain zero. Each model parameter converged ($\hat{R} < 1.1$).

The relationship between R in September of each year and estimated S abundance over the high tide wetted area of each creek was even more density-dependent with a dome-shape; the Ricker model fitted these data well (Fig. 6B). The median value (±2.5 and 97.5% credible intervals) for a from fitting a 2 parameter Ricker stock-recruitment model was 0.02 (0.01, 0.04) while the median value for b was 23.4 (15.4, 31.6); thus, the credible set for each parameter was meaningful in that it did not contain zero. Each model parameter converged ($\hat{R} < 1.1$).

4. DISCUSSION

4.1. Importance of salt marsh habitat to production

We estimated production of larval and juvenile *Fundulus heteroclitus* in multiple tidal creeks and related these estimates to a number of potentially meaningful

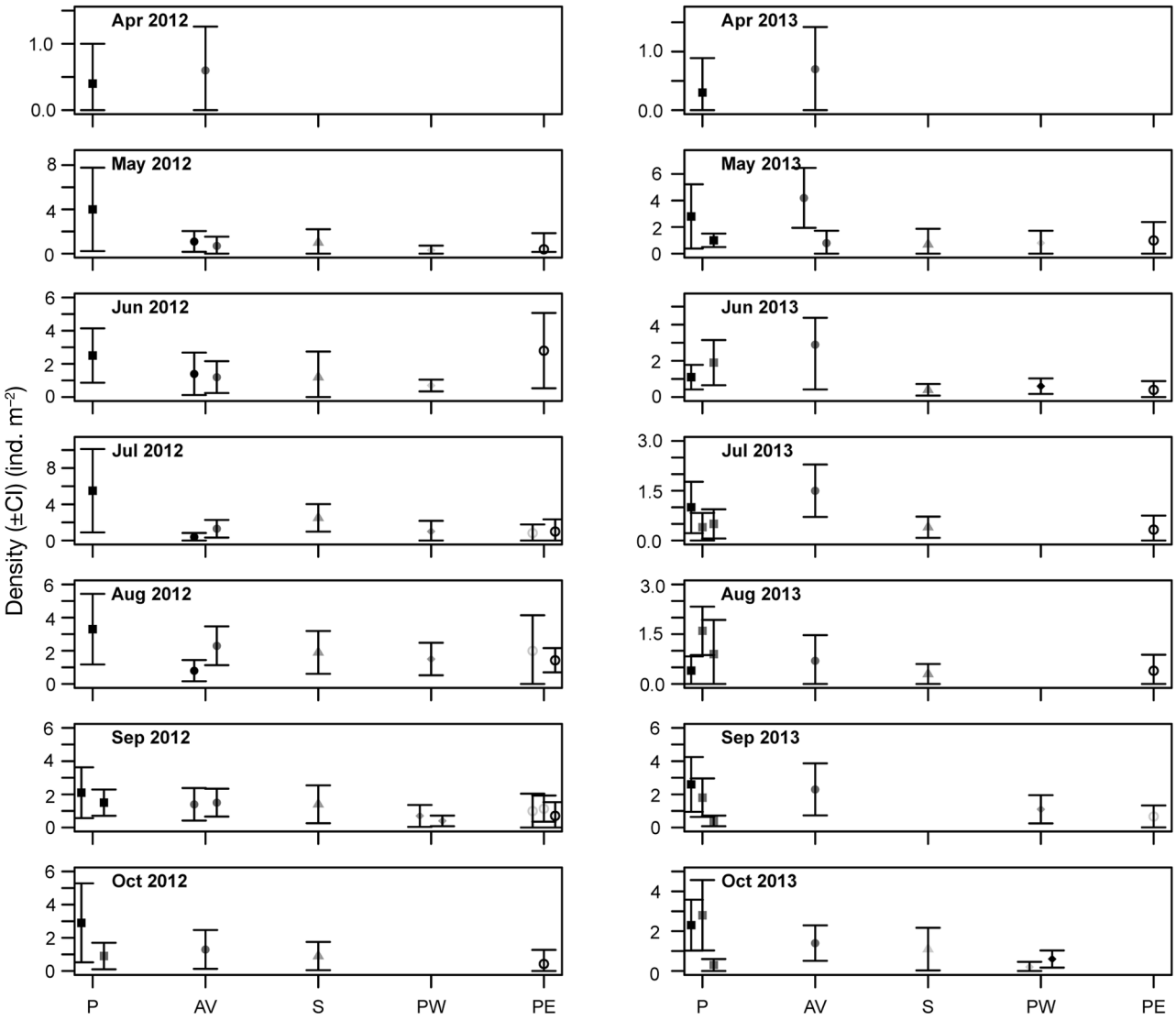

Fig. 3. Cohort-specific estimates of mean density of *Fundulus heteroclitus* averaged over the salt marsh area for 7 mo and 2 yr of sampling. Fish were captured with a 1-m^2 throw trap deployed in the salt marsh of 5 tidal creeks (*x*-axis) in coastal North Carolina in 2012 (left column) and 2013 (right column). Different numbers of cohorts were tracked over successive months within and among creeks; some creeks/months did not have cohorts that were tracked. The *x*-axis is identical among panels; the scale of the *y*-axis differs. Creeks are ordered from left to right on the *x*-axis by increasing MFA1 value (see Fig. 2). AV: Atlantic Veneer; P: Porters; PE: Pelletier East; PW: Pelletier West; S: Spooners. Creek-specific values are jittered around the *x*-axis to avoid overlap for time intervals when more than one cohort was tracked

environmental factors. These factors included habitat features (salt marsh area and creek morphology), common instream development types (shoreline armoring, culverts), and a composite metric of impact (watershed imperviousness). Creeks with intact marsh benefited from not only more marsh habitat, but also higher areal production within that habitat. This relationship was largely driven by a single creek, Pelletier East, which had low areal production (in both study years) and reduced salt marsh (as indexed by MFA1). The low areal production in Pelletier East was not a result of our inability to assign individual fish to a cohort, as Pelletier East had a relatively small percentage of unassigned individuals relative to other creeks. Replicating a creek like Pelletier East that had lost part of its marsh surface as a result of development would have been ideal in order to strengthen our interpretation of this trend; we encourage other researchers to investigate the effect of habitat size on areal production. Although Pelletier East had lost

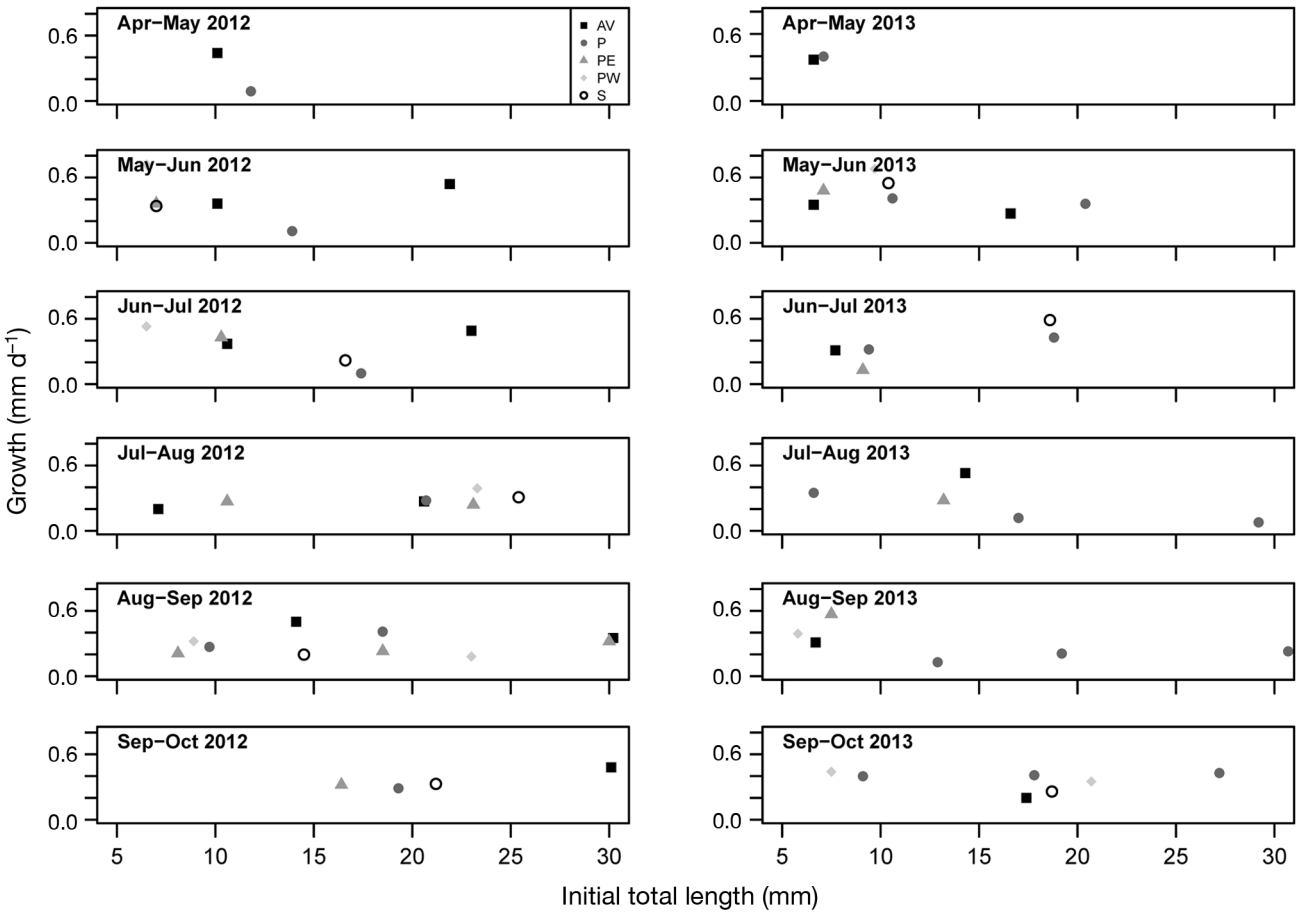

Fig. 4. Calculations of mean absolute growth rate (mm total length d^{-1}) over 6 inter-monthly time intervals for *Fundulus heteroclitus* captured with a 1 m^2 throw trap deployed in salt marsh of 5 tidal creeks in coastal North Carolina in 2012 (left column) and 2013 (right column). Growth rate was calculated as the difference in mean sizes of individuals comprising a cohort between successive months. For each panel, fish are separated by initial mean total length at the start of the interval (*x*-axis). Different numbers of cohorts were tracked over successive months within and among creeks. The scales of both the *x*- and *y*-axes are identical among panels. AV: Atlantic Veneer; P: Porters; PE: Pelletier East; PW: Pelletier West; S: Spooners. The legend applies to all panels

marsh area, it still retained linear marsh–creek edge found to be important for secondary production of this species (Kneib 2003). The results demonstrate the capacity for *F. heteroclitus* to maintain larval and juvenile production within developed salt marsh, at albeit compromised levels. We reached this conclusion because watershed imperviousness (indexed by MFA2), believed to be a composite metric of watershed urbanization (development, conversion of vegetative cover classes, nutrient loading, etc.) (Wang et al. 2001, Holland et al. 2004, Bilkovic & Roggero 2008), was not related to areal production. It is possible that research on different or a larger number of study creeks would reveal potential impacts of watershed-level development on the production of *F. heteroclitus*. In contrast, month and year effects were important covariates describing variability in production, given the temporal dynamics of shallow estuaries in temperate climates (Able 1999). These temporal effects were important to control for when examining spatial covariates.

4.2. Relating adult abundance to larval and juvenile metrics

Valiela et al. (1977) suggested that the catch of larval and juvenile *F. heteroclitus* could predict subsequent adult recruitment. We confirmed a positive relationship between larvae and juveniles and adults (≥41 mm age-0 fish) using creek-wide larval and juvenile production or abundance as the predictor ('stock') variable; however, the relationship showed evidence of density-dependence which was particularly strong when using numbers. Rudershausen et

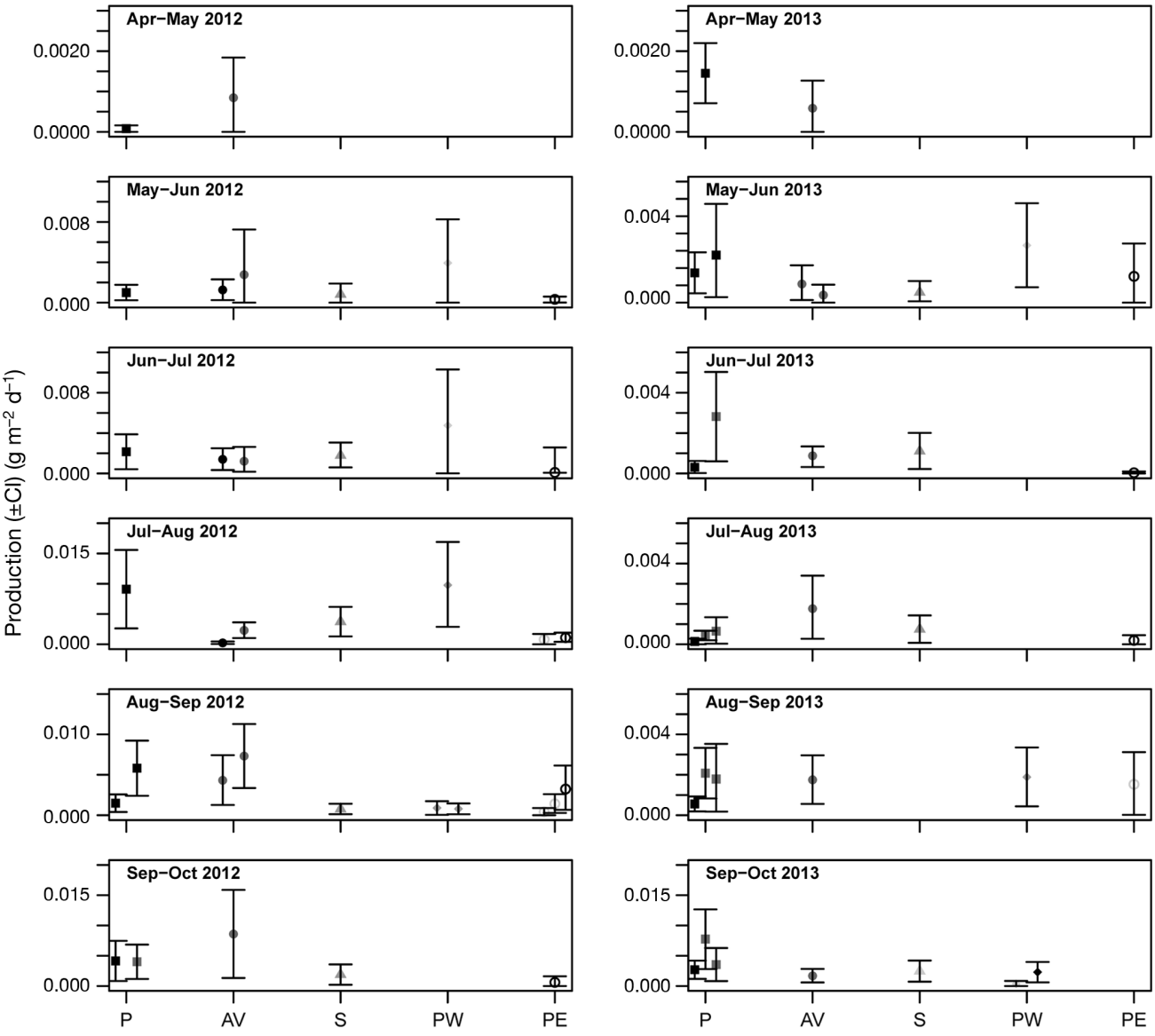

Fig. 5. Cohort-specific estimates of dry weight production (mean ± CI) (*y*-axis) averaged over the creek-wide marsh area for *Fundulus heteroclitus* captured by a 1 m^2 throw trap is salt marsh of 5 tidal creeks (*x*-axis) in coastal North Carolina in 2012 (left column) and 2013 (right column). Different numbers of cohorts were tracked over successive months within and among creeks; some creek/time combinations did not have cohorts that were tracked. The *x*-axis is identical among panels; the scale of the y-axis differs. AV: Atlantic Veneer; P: Porters; PE: Pelletier East; PW: Pelletier West; S: Spooners. Creeks are ordered from left to right on the *x*-axis by increasing MFA1 value (see Fig. 2). Creek-specific values are jittered around the *x*-axis to avoid overlap where more than one cohort is tracked for a creek

al. (2019) speculated that the relationship between catch rates of adult *F. heteroclitus* and percent marsh coverage in the same creeks studied here resulted from differential larval and juvenile production given the obligate use of salt marsh by larval and juvenile *F. heteroclitus*. The relationship between larval and juvenile areal production and salt marsh coverage, as well as the relationship between creek-wide larval and juvenile production and adult CPUE, supports this mechanism. Pelletier East Creek, which has minimal amount of marsh coverage, had low creek-wide production (or numbers) of larval and juveniles and had low adult CPUE while Atlantic Veneer creek had high instream marsh coverage, higher larval and juvenile production/abundance, and high adult CPUE. However, some of the highest production and numerical estimates were from Porters Creek, which had low adult CPUE estimates. This may be due to

Table 2. Estimated biomass and production for cohorts of *Fundulus heteroclitus* sampled with a 1 m^2 throw trap from April through October, 2012–2013 around high tides in the salt marsh of 5 tidal creeks in coastal North Carolina. Data include the 2.5% confidence interval (CI), mean (m), and 97.5% CI of dry weight ($\bar{B}$, g) across successive months as well as the 2.5% CI, mean, and 97.5% CI of cohort-specific areal dry weight production on the marsh surface (P, g m^{-2} d^{-1}). AV: Atlantic Veneer; P: Porters; PE: Pelletier East; PW: Pelletier West; S: Spooners

Creek	Year	Months	$\bar{B}_{2.5}$	$\bar{B}_m$	$\bar{B}_{97.5}$	$P_{2.5}$	P_m	$P_{97.5}$
AV	2012	Apr–May	0.0000	0.0135	0.0293	0.0000	0.0009	0.0018
		May–Jun	0.0049	0.0256	0.0462	0.0003	0.0013	0.0023
		May–Jun	0.0000	0.0687	0.1795	0.0000	0.0028	0.0073
		Jun–Jul	0.0059	0.0243	0.0427	0.0003	0.0014	0.0025
		Jun–Jul	0.0044	0.0324	0.0701	0.0002	0.0012	0.0026
		Jul–Aug	0.0010	0.0055	0.0100	0.0001	0.0003	0.0005
		Jul–Aug	0.0441	0.0996	0.1550	0.0010	0.0023	0.0036
		Aug–Sep	0.0209	0.0715	0.1221	0.0013	0.0043	0.0074
		Aug–Sep	0.1295	0.2811	0.4328	0.0034	0.0073	0.0113
		Sep–Oct	0.0375	0.2433	0.4491	0.0013	0.0086	0.0159
	2013	Apr–May	0.0000	0.0075	0.0160	0.0000	0.0006	0.0013
		May–Jun	0.0019	0.0143	0.0284	0.0002	0.0011	0.0022
		May–Jun	0.0000	0.0146	0.0341	0.0000	0.0005	0.0010
		Jun–Jul	0.0050	0.0138	0.0210	0.0003	0.0009	0.0013
		Jul–Aug	0.0043	0.0289	0.0555	0.0003	0.0018	0.0034
		Aug–Sep	0.0079	0.0248	0.0418	0.0006	0.0018	0.0030
		Sep–Oct	0.0212	0.0614	0.1015	0.0006	0.0017	0.0028
P	2012	Apr–May	0.0006	0.0119	0.0237	0.0000	0.0001	0.0002
		May–Jun	0.0072	0.0303	0.0532	0.0002	0.0010	0.0018
		Jun–Jul	0.0202	0.1034	0.1866	0.0004	0.0022	0.0039
		Jul–Aug	0.0704	0.2444	0.4183	0.0026	0.0091	0.0156
		Aug–Sep	0.0062	0.0228	0.0394	0.0004	0.0015	0.0026
		Aug–Sep	0.0448	0.1080	0.1711	0.0024	0.0058	0.0092
		Sep–Oct	0.0191	0.0960	0.1728	0.0008	0.0041	0.0075
		Sep–Oct	0.0509	0.1738	0.2968	0.0012	0.0040	0.0068
	2013	Apr–May	0.0057	0.0118	0.0178	0.0007	0.0015	0.0022
		May–Jun	0.0062	0.0200	0.0338	0.0005	0.0017	0.0029
		May–Jun	0.0057	0.0494	0.1024	0.0003	0.0028	0.0057
		Jun–Jul	0.0003	0.0032	0.0063	0.0000	0.0003	0.0006
		Jun–Jul	0.0087	0.0408	0.0728	0.0006	0.0028	0.0050
		Jul–Aug	0.0000	0.0010	0.0019	0.0000	0.0001	0.0003
		Jul–Aug	0.0084	0.0180	0.0278	0.0002	0.0004	0.0007
		Jul–Aug	0.0028	0.0736	0.1515	0.0000	0.0007	0.0013
		Aug–Sep	0.0068	0.0197	0.0326	0.0002	0.0006	0.0009
		Aug–Sep	0.0276	0.0694	0.1112	0.0008	0.0021	0.0033
		Aug–Sep	0.0082	0.0804	0.1583	0.0002	0.0018	0.0035
		Sep–Oct	0.0129	0.0293	0.0458	0.0012	0.0027	0.0042
		Sep–Oct	0.0474	0.1310	0.2139	0.0028	0.0078	0.0127
		Sep–Oct	0.0195	0.0844	0.1496	0.0008	0.0035	0.0063
PE	2012	May–Jun	0.0001	0.0046	0.0082	0.0000	0.0003	0.0006
		Jun–Jul	0.0011	0.0194	0.0423	0.0001	0.0012	0.0026
		Jul–Aug	0.0000	0.0166	0.0344	0.0000	0.0008	0.0017
		Jul–Aug	0.0179	0.0499	0.0864	0.0004	0.0011	0.0019
		Aug–Sep	0.0000	0.0074	0.0153	0.0000	0.0004	0.0009
		Aug–Sep	0.0096	0.0487	0.0891	0.0003	0.0014	0.0026
		Aug–Sep	0.0257	0.1246	0.2348	0.0007	0.0033	0.0061
		Sep–Oct	0.0000	0.0148	0.0378	0.0000	0.0006	0.0016
	2013	May–Jun	0.0000	0.0138	0.0309	0.0000	0.0015	0.0034
		Jun–Jul	0.0000	0.0015	0.0033	0.0000	0.0000	0.0001
		Jul–Aug	0.0000	0.0041	0.0090	0.0000	0.0002	0.0005
		Aug–Sep	0.0002	0.0127	0.0258	0.0000	0.0015	0.0031

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the openness of Porters (lack of culvert) relative to the other creeks. Estimates of larval and juvenile production on the marsh surface extrapolated to the full high-tide area can be useful for comparing the ability of creeks to trophically relay nekton production to open-water estuaries (Kneib 2000); on average, this is greater in creeks possessing marsh mosaics less impacted by urbanization.

Caution is advised when comparing production estimates from this study to others. In this study, not all throw-trapped individuals could be assigned to a cohort and thus not all of them were used to estimate production between successive months (cumulative areal production was not estimated). Additionally, some studies of *F. heteroclitus* production have collected samples over seasons (fall–winter) (e.g. Teo & Able 2003a) when data were not collected for this study. Hagan et al. (2007) may have DW production estimates most comparable to ours because those data were collected over the summer, in similar habitats, and over similar sizes of *F. heteroclitus*. In the Hagan et al. (2007) study, mean estimates of areal production within salt marsh (converting monthly G_{inst} to daily rates for their small fish: <30 mm standard length) were 0.024, 0.059, and 0.090 g m^{-2} d^{-1} for 3 inter-monthly summertime periods. These estimates are higher than values in our study even when mean production estimates (Table 2) are summed across cohorts and for creeks/inter-monthly periods where all collected larval and juvenile fish could be used to estimate production; our mean production estimate (across creeks) was 0.0023 ± 0.0016 g m^{-2} d^{-1} for these specific data (n = 17).

Density appears to vary widely for larval and juvenile *F. heteroclitus* collected in salt marshes and

Table 2. (continued)

Creek	Year	Months	$\bar{B}_{2.5}$	$\bar{B}_m$	$\bar{B}_{97.5}$	$P_{2.5}$	P_m	$P_{97.5}$
PW	2012	May–Jun	0.0000	0.0193	0.0405	0.0000	0.0039	0.0083
		Jun–Jul	0.0001	0.0303	0.0657	0.0000	0.0048	0.0103
		Jul–Aug	0.0601	0.2037	0.3523	0.0029	0.0098	0.0169
		Aug–Sep	0.0007	0.0121	0.0235	0.0001	0.0009	0.0017
		Aug–Sep	0.0064	0.0420	0.0775	0.0001	0.0008	0.0015
	2013	May–Jun	0.0064	0.0240	0.0418	0.0009	0.0033	0.0058
		Aug–Sep	0.0040	0.0174	0.0308	0.0004	0.0019	0.0034
		Sep–Oct	0.0000	0.0035	0.0080	0.0000	0.0004	0.0008
		Sep–Oct	0.0140	0.0529	0.0918	0.0006	0.0023	0.0040
S	2012	May–Jun	0.0000	0.0114	0.0258	0.0000	0.0008	0.0019
		Jun–Jul	0.0234	0.0699	0.1193	0.0006	0.0018	0.0031
		Jul–Aug	0.0536	0.1537	0.2538	0.0013	0.0037	0.0062
		Aug–Sep	0.0046	0.0277	0.0507	0.0001	0.0008	0.0014
		Sep–Oct	0.0058	0.0524	0.0989	0.0002	0.0019	0.0036
	2013	May–Jun	0.0009	0.0068	0.0142	0.0001	0.0006	0.0013
		Jun–Jul	0.0041	0.0207	0.0373	0.0002	0.0011	0.0020
		Jul–Aug	0.0032	0.0363	0.0693	0.0001	0.0008	0.0014
		Sep–Oct	0.0238	0.0810	0.1382	0.0007	0.0025	0.0042

offers an explanation for differences in production between this study and others. Production is difficult to accurately measure due to the high variability about density. For example, the mean density of larval and juvenile *F. heteroclitus* was estimated to be 7.2 m^{-2} in a Georgia salt marsh, but that estimate used passive sampling gear and included data across all cohorts (Kneib 1997b). Two studies using a throw trap in New Jersey salt marshes estimated densities of 15.1 m^{-2} (Teo & Able 2003a) and 20.2 m^{-2} (Hagan et al. 2007), respectively. These densities are higher than the highest mean creek-specific density in this study (5 m^{-2}). It is unknown why densities of age-0 fish were higher in the New Jersey study compared to ours but this difference could be due to sampling techniques. Deploying a throw trap around low tide, as done in the aforementioned New Jersey studies, would tend to minimize the escape of fish from the sampling area (capture efficiency: Rozas & Minello 1997) due to shallow depths. Thus, if capture efficiency is an issue in using a throw trap to collect small *F. heteroclitus*, it is likely more so around high tides (such as in this study) where chances of escape before trap deployment are theoretically higher. We purposefully sampled around high tide to accurately estimate fish density over the full wetted marsh area in each creek; while larval and juvenile *F. heteroclitus* are mostly relegated to the marsh surface even over low tides (Kneib 1984, Talbot & Able 1984, Teo & Able 2003b), this could be an issue in sampling individuals of larger sizes over the size range we used for production estimates if they move into creek channels over low tides.

Table 3. Median along with 2.5 and 97.5% credible intervals (CI) of partial regression coefficients from fitting a linear model using Bayesian methods to mean cohort-specific areal dry weight production (g m^{-2} d^{-1}) of larval and juvenile *Fundulus heteroclitus* in salt marshes in 5 first-order tidal creeks in coastal North Carolina during 2012–2013. For time covariates (month and year), the effect of the first level was fixed at zero. MFA1 and MFA2 are dimensions 1 and 2, respectively, of a multiple factor analysis (MFA) model fitted to reduce the dimensionality of a suite of habitat and urbanization factors (see Fig. 2). See Section 2.5 for a description of covariates and MFA. Factor levels were not applicable (NA) to the MFA continuous effects

Covariate	Level	2.5% CI	Median	97.5% CI	Comment
MFA1	NA	−0.0005	−0.0003	−0.0001	
MFA2	NA	−0.0003	0.0001	0.0004	
Month	Apr	0	0	0	Level fixed at zero
	May	−0.0011	0.0013	0.0037	
	Jun	−0.0012	0.0012	0.0020	
	Jul	−0.0003	0.0020	0.0044	
	Aug	−0.0005	0.0018	0.0053	
	Sep	0.0005	0.0029	0.0053	
Year	2012	0	0	0	Level fixed at zero
	2013	−0.0023	−0.0013	−0.0003	

Variability about growth appears to be less important than variability about density in contributing to discrepancies in production between this study and others since growth rates are similar between studies. For example, the mean absolute growth rate here (0.34 mm d^{-1} across all creeks) was similar to 3 New Jersey studies that estimated absolute growth of juveniles (Rountree 1992, Teo & Able 2003a, Hagan et al. 2007). Teo & Able (2003a) reported a range of absolute growth rates of *F. heteroclitus* <30 mm standard length to be between roughly 0.23 and 0.30 mm d^{-1} while Rountree (1992) and Hagan et al. (2007) respectively reported average (±SE) absolute growth of age-0 fish to be 0.26 ± 0.02 mm d^{-1} and 0.17 mm d^{-1} in salt marsh habitats. The mean (±SD) G_{inst} across all creeks and time intervals in this study, when converted to a monthly time step (1.73 ± 1.14), was

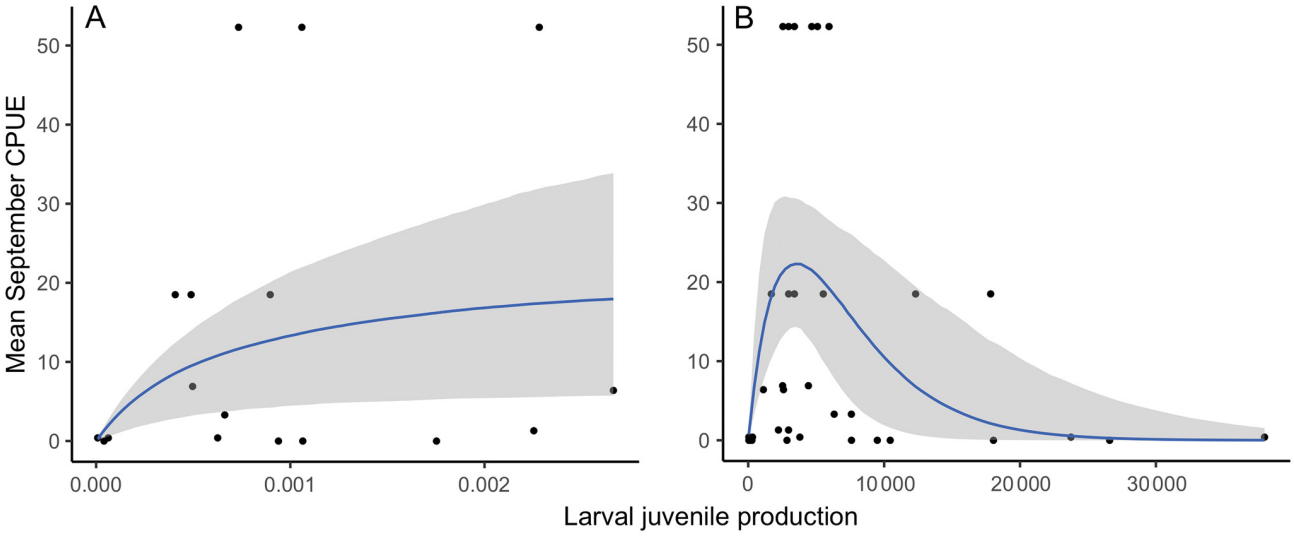

Fig. 6. Relationships between larval and juvenile and adult *Fundulus heteroclitus* in North Carolina tidal creeks. (A) April–June age-0 larval and juvenile dry weight production (g m^{-2} d^{-1}) over the high tide area of each creek (production [stock], *x*-axis) and September minnow trap catch per unit effort of adult *Fundulus heteroclitus* (CPUE [recruitment], *y*-axis) that were modeled by fitting a 2 parameter Beverton-Holt stock-recruitment relationship. (B) April, May, and June numerical abundance of age-0 larvae and juveniles over the high tide area of each creek (Abundance [stock], *x*-axis) and the same recruitment data as (A), which were modeled with a 2-parameter Ricker stock–recruitment relationship. Each panel displays observed data (filled symbols) along with predictions (median: blue line; 95% credible interval: gray shading). See Section 2.6 for details on data inputs and model fitting

roughly 2-fold higher than those found by Hagan et al. (2007) for age-0 fish from a New Jersey salt marsh but within the range (1.06–2.26) that Teo & Able (2003a) found for this age class.

4.3. Potential sources of error

Estimating secondary production is prone to error (Valiela 1984). Error in this study may have arisen from binning individuals into incorrect cohorts, underestimating densities in marshes if larvae and juveniles were over unvegetated mud during sampling, potentially different size-selective mortality among creeks, differential recruitment that could impact the numbers and sizes of individuals in the length–frequency plots, and sampling over different days among study creeks within each lunar (spawning) cycle. Some of these potential issues are discussed below.

We were unable to assign all individual larvae/juveniles to a cohort particularly in later months within a sampling year. Thus, these individuals were not used to estimate production between successive monthly samples. We did not employ a quantitative approach to assign cohorts owing to the continual production of *F. heteroclitus* over the growing season and the inability of the Electronic Length Frequency Analysis program (Pauly 1987) to identify cohorts in exploratory analyses using length–frequency data. We established simple rules to identify and track cohorts. Using these rules, we were able to successfully assign cohort membership for the majority of age-0 individuals captured in each creek (Fig. S3). Most of the remaining individuals that were not assigned to a cohort, and thus not used to estimate production, were either small age-1 fish hatched the year before their capture or caught in a month where production was not estimated. We estimated production only in instances where we had age-0 cohorts that could be clearly identified, and assumed that the cohorts for which we could estimate production were representative of other age-0 cohorts produced in the study creeks.

Production was estimated using the change in average size of individuals within a cohort over time. Changes in average length between samples may not be due to changes in the length of individuals found within a study area but rather via recruitment from outside of a sampling area (Bozeman & Dean 1980). However, larval and juvenile *F. heteroclitus* are mostly relegated to the marsh surface even over low tides (Kneib 1984, Talbot & Able 1984, Teo & Able 2003b). The residency of these young fish to the marsh surface decreases the possibility that sampled individuals were recruits that were spawned elsewhere.

Temporal changes in the average length of individuals comprising a population between samples may also be due to size-selective mortality (Sogard 1997). Analyses into changes in the size distribution of a cohort over time, such as in this study, may confound changes in size distributions due to growth versus mortality (Munch et al. 2003). Thus, our comparisons among salt marsh creeks assume that this bias is consistent across systems or does not occur. Further, different sizes of fish among creeks, due to sampling them at different periods within a lunar cycle one or more months after a cohort was spawned, may have contributed to differences in densities among creeks if capture efficiencies were less than 100% for larger, more mobile individuals.

4.4. Conclusions

Beck et al. (2001) refined the definition of 'nursery habitat' to refer to habitats that make a greater-than-average contribution to adult populations. Although *Fundulus* sp. were identified as a group that does not have nursery habitats because they lack separate adult habitats (see Beck et al. 2001), we believe that the Beck et al. (2001) concepts remain useful when considering the impacts of urbanization on the habitats of resident estuarine fishes. Estimates of *F. heteroclitus* larval and juvenile production, which incorporates important population factors (density, growth, survival) identified in the Beck et al. (2001) paper, had a positive relationship with adult recruitment; this finding likely explains the mechanism between increased salt marsh coverage and adult abundance in this species. We conclude that testing habitat contribution to adult populations is informative and potentially more tractable for resident fishes because it removes the difficult-to-measure but critical movement/contribution portions of 'nursery habitat' or 'effective juvenile habitat' studies (Beck et al. 2001, Dahlgren et al. 2006).

The results from this study are useful to agencies tasked with planning and permitting coastal development. Areal salt marsh production of larval and juvenile *F. heteroclitus*, the numerically dominant nekton in salt marsh habitats in Atlantic coastal tidal creeks, was not affected by watershed development but was affected by reductions in creek-wide salt marsh habitat. Thus, reductions in the percentage of salt marsh in a tidal creek compromises the creek-wide trophic export provided by resident salt marsh nekton (Kneib 2003) not only by having less salt marsh but by reducing areal production. Our observations are mostly that headwater tidal creeks in this region either have intact marshes or, in contrast, have had their marsh area completely developed; in the latter case, we assume that the production of *F. heteroclitus* is eliminated with complete loss of marsh. This assumption is likely correct given that our previous work found zero adult *F. heteroclitus* in a fabricated tidal creek that contained no marsh (Rudershausen et al. 2019). It is forecasted that anthropogenic land-use change in tidal creek watersheds and intertidal zones will further eliminate salt marshes along US coastlines (Kennish 2001, Mattheus et al. 2010, Gittman et al. 2015). These stressors increase the importance of preserving and restoring salt marsh coverage to maintain rates of secondary production reflective of undisturbed systems. Given that *F. heteroclitus* is a relatively tolerant species (Reid et al. 2016), the benefits of conserving habitats important for its production are likely to extend to other estuarine nekton species.

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