

Density-dependent habitat use and growth of an estuarine fish

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Abstract: Density dependence can stabilize or destabilize population size through negative or positive feedback controls operating over different spatial and temporal scales. While many species have been shown to exhibit density dependence, the topic has received little attention in estuaries where environmental variability and larval supply are often considered to be the primary drivers of population dynamics. We used multiple long-term, fishery-independent data sets and a unique modeling approach to test the hypothesis that juvenile red drum (*Sciaenops ocellatus*) exhibit density-dependent habitat use and growth rates in estuaries in North Carolina, USA. Age-1 red drum exhibited density-dependent habitat use after accounting for environmental and landscape variables, disproportionately increasing northward and coastward in the study area at high abundance. Apparent individual growth rates of age-0 and age-1 red drum were generally negatively related to the abundance of their own age classes, but evidence of density-dependent growth rates for age-2 red drum was weak to nonexistent. Changes in spatial distribution of red drum when overall abundance was high did not overcome density-dependent effects on individual growth rates. Thus, density-dependent effects have potential negative feedbacks on population growth in estuaries and should not be ignored in future theoretical or empirical estuarine studies.

Résumé : La dépendance de la densité peut stabiliser ou déstabiliser la taille d'une population par l'entremise de rétroactions négatives ou positives œuvrant à différentes échelles spatiales et temporelles. S'il a été démontré que de nombreuses espèces présentent une dépendance de la densité, le sujet a reçu peu d'attention en ce qui concerne les estuaires, où la variabilité environnementale et l'abondance des larves sont souvent considérées comme les principaux moteurs de la dynamique des populations. Nous avons utilisé de multiples ensembles de données à long terme indépendants de la pêche et une nouvelle approche de modélisation pour tester l'hypothèse selon laquelle l'utilisation de l'habitat et les taux de croissance des tambours ocellés (*Sciaenops ocellatus*) juvéniles dans les estuaires de la Caroline du Nord (États-Unis) sont dépendants de la densité. À forte abondance, l'utilisation de l'habitat des tambours ocellés d'un an était dépendante de la densité si les variables environnementales et du paysage étaient prises en compte, cette dépendance augmentant disproportionnellement vers le nord et les côtes dans la zone d'étude. Les taux de croissance individuels apparents pour les tambours ocellés de zéro et un an présentaient généralement une relation négative avec l'abondance de la classe d'âge concernée, mais les données reflétant des taux de croissance dépendants de la densité pour les tambours ocellés de deux ans étaient rares à non existantes. Des modifications de la répartition géographique des tambours ocellés durant les périodes de grande abondance générale ne compensaient pas les effets dépendants de la densité sur les taux de croissance individuels. Ainsi, les effets dépendants de la densité exercent potentiellement des rétroactions négatives sur la croissance des populations dans les estuaires et devraient être pris en considération dans les études estuariennes théoriques ou empiriques futures.

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Introduction

Density dependence can strongly influence population dynamics by either stabilizing or destabilizing population size through negative or positive feedback controls operating over different spatial and temporal scales (Rose et al. 2001). There are many ways compensatory density dependence can occur, including an increase in mortality (Hixon and Carr 1997) or

movement rates (Abesamis and Russ 2005) or a decrease in individual growth rates (Lorenzen and Enberg 2002) or age-specific fecundity (Ferrer and Donazar 1996) with increasing population density. Although the concept of density dependence is relatively straightforward, no other issue in ecology has generated more debate than the extent to which populations are regulated by density-dependent factors (Hixon et al. 2002).

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Unlike terrestrial systems, determining the extent of population regulation is still an active area of research in aquatic systems (Sale and Tolimieri 2000). Perhaps not surprisingly, density dependence has most frequently been observed for organisms in highly tractable aquatic systems. For instance, in newly settled coral reef fishes where density can be tracked relatively easily, density-dependent mortality has been well-documented (Hixon and Carr 1997; White et al. 2010). Density-dependent growth and habitat use has been found repeatedly in stream-dwelling salmonids (Jenkins et al. 1999; Gibson et al. 2008), likely because of the relative ease of tracking individuals using tagging, manipulation of population densities, and direct observations of competitive interactions in mesocosm experiments. Density dependence has not been found in all processes in all life stages, however (Doherty and Fowler 1994). Osenberg et al. (2002) explained these disparate results by suggesting that density dependence is rarely detected when ambient density of individuals is low and commonly detected when ambient density is high.

In marine fish populations distributed over large spatial scales, density-dependent habitat selection is often examined by comparing the geographical extent of a population over many years with its abundance using spatially and temporally extensive fishery-independent data (Swain and Morin 1996; Petitgas 1998). The geographical distribution of marine fish species is often positively related to its abundance (MacCall 1990; Swain and Wade 1993). Thus, populations tend to expand into potentially suboptimal habitats at high abundance, perhaps because of increased intraspecific competition (Ward et al. 2006; Bartolino et al. 2011; Biesinger et al. 2011). The same theory suggests that overexploited fish populations at historically low levels of abundance may currently be occupying the areas of highest habitat quality (Blanchard et al. 2005). However, Shepherd and Litvak (2004) noted that abundance and geographic area may co-vary with unmeasured density-independent variables, so simply finding a positive relationship between abundance and geographic area is alone not enough to implicate density-dependent habitat selection. Instead, models must be able to account for density-independent variables when relating abundance and distribution (e.g., Bartolino et al. 2011), and some proxy of fitness (e.g., individual growth rate) should also be examined.

Density dependence in estuarine organisms has been relatively understudied compared with organisms in other aquatic habitats like coral reefs, streams, or large marine systems. One possible reason for the lack of attention is because density dependence is often considered less important relative to larval supply or environmental variability in determining local abundance of estuarine organisms (Baltz et al. 1993; Guindon and Miller 1995; Whitfield et al. 2006). Also, estuarine systems are not as amenable to study as coral reefs or small streams because (i) water clarity is often very low in estuaries, so following the fates of individuals using visual assessment is often not possible, (ii) estuarine fishes are generally not site-attached, so manipulative experiments are rarely possible, (iii) estuaries tend to be heavily fished, (iv) estuaries have highly variable environmental conditions, and (v) spatially and temporally extensive fishery-independent data sets are less common in estuaries. Despite these difficulties, some studies have highlighted the importance of density-dependent growth, mortality, or dispersal for estuarine organ-

isms (e.g., Buckel et al. 1999; Cowan et al. 2000; Martino and Houde 2012). The majority of these studies have related individual growth rates or loss rates to annual density estimates; however, there has been little attention paid to the ways in which annual density in combination with density-independent factors influence spatial redistribution patterns of estuarine organisms.

Here we test for the presence of density-dependent habitat use and growth in juvenile red drum (*Sciaenops ocellatus*) in a large USA estuary using spatially and temporally extensive data sets. Multiple fishery-independent data sets were included in our analysis from large-scale gill netting, seining, and tagging programs. Red drum is a long-lived estuarine fish species (maximum age = 56) historically harvested by commercial and recreational fishers in the state (Bacheler et al. 2008a). Adult red drum spawn in lower estuaries, lagoons, inlets, or in nearshore continental shelf habitats during late summer and early fall (Peters and McMichael 1987; Barrios 2004). Larval red drum use tidal or wind-driven currents for transport to marsh edges or seagrass meadows in estuarine habitats (Rooper and Holt 1997; Stunz et al. 2002). Age-0 red drum are often found in a wide variety of shallow estuarine habitats, where they remain for the first 2 or 3 years of life before maturing and joining the adult stock in more coastal waters (Peters and McMichael 1987; Bacheler et al. 2009a).

We first test the hypothesis that juvenile red drum habitat use is density-dependent after accounting for density-independent environmental variation and potential competitors using a unique regression approach. We found evidence for density-dependent habitat selection, so we next tested whether the redistribution of red drum during years with high density mitigated potential negative effects on growth. Individual growth rates of juvenile red drum were related to their own relative abundance using three fishery-independent data sets. Our results provide strong evidence for the importance of density-dependent effects on both habitat use and vital rates of red drum.

Materials and methods

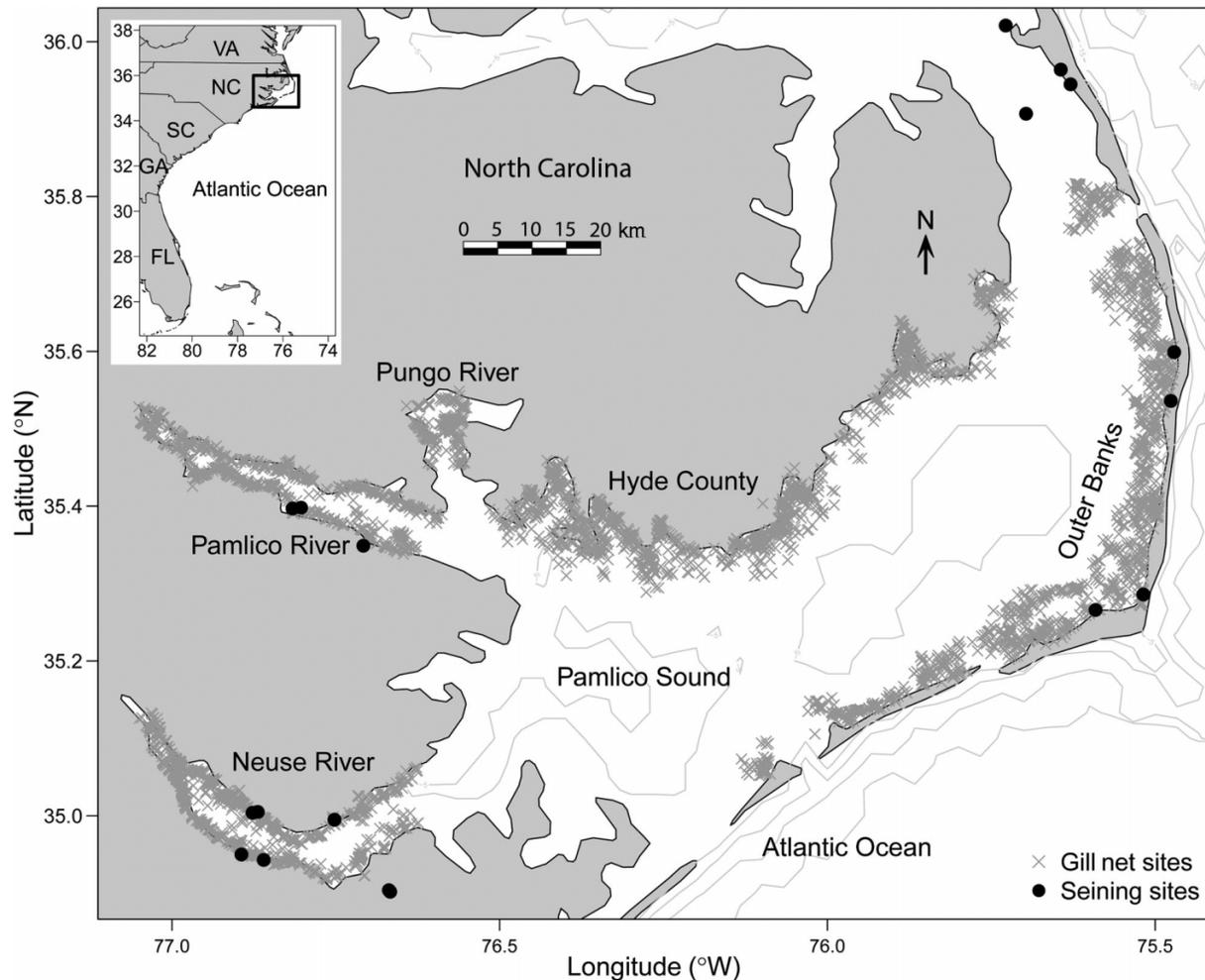
Study area

Red drum habitat use and growth rates were quantified in Pamlico Sound, North Carolina (Fig. 1). Pamlico Sound is the second largest estuary in North America, bordered on the east by the Outer Banks and on the west by mainland North Carolina. The Neuse, Pamlico, and Pungo rivers drain eastern North Carolina and empty into Pamlico Sound. Water level fluctuations in Pamlico Sound are influenced more by wind than lunar tides except within a few kilometres of inlets to the Atlantic Ocean. Pamlico Sound is an important nursery habitat for a wide variety of estuarine species, including juvenile red drum (Bacheler et al. 2008b).

Data collection

Data from three fishery-independent surveys were analyzed in this study to determine whether red drum habitat use or individual growth rates were density-dependent. The first was a fishery-independent gill net survey (IGNS) data set from the North Carolina Division of Marine Fisheries (NCDMF). The IGNS was initiated by the NCDMF to index

Fig. 1. Study area in Pamlico Sound and associated rivers, North Carolina, USA. Red drum (*Sciaenops ocellatus*) independent gill net sites are indicated by the gray “x”, and seining sites are denoted by the solid circles. Gray contour lines denote depths of 5, 10, 15, and 20 m.



abundance and quantify habitat use patterns of a wide variety of estuarine organisms in Pamlico Sound. The IGNS began in Pamlico Sound in May 2001 and in the Pamlico, Neuse, and Pungo rivers in July 2003, and we used data through 2008. The IGNS used a stratified random sampling design (stratified by depth and region), randomly deploying two experimental gill nets within each of 16 regions each month from February through December annually. Gill nets consisted of eight equal length segments of 7.6, 8.9, 10.2, 11.4, 12.7, 14.0, 15.2, and 16.5 cm stretched mesh webbing, totaling 219.5 m in length. Nets were generally deployed within 1 h of sunset and retrieved the next morning, so all soak times were approximately 12 h. Red drum were aged based on their length at capture, and we assumed a 1 January birthday; age-0, age-1, and age-2 red drum in North Carolina were easily distinguished using a 6-month age-length key owing to rapid summertime growth rates (Bacheler et al. 2008a). Because red drum spawn in August and September in North Carolina, the age-0 period only lasts a few months (until 1 January), at which point they become age-1. Therefore, it is important to note that red drum are less than 1 year old for most of their time (8–9 months) as an age-1 fish.

Data from the NCDMF red drum juvenile abundance index (JAI) survey was also used. The NCDMF pulled a single seine at 16 fixed stations in Pamlico Sound biweekly from early September to late November in 1991–2009, resulting in six seine samples per station annually (Fig. 1). These fixed stations were chosen because of their accessibility and productivity from prior scoping work and were assumed to be representative of North Carolina estuaries. Annual mean catch per unit effort (CPUE) of age-0 red drum (number-haul⁻¹) was calculated as the arithmetic mean of the six samples taken at each of the 16 fixed stations.

We also used data from the NCDMF red drum tagging program. The NCDMF has used various methods to collect red drum opportunistically since 1983, including pound nets, hook and line, runaround gill nets, trammel nets, and electrofishing (Bacheler et al. 2008a). All fish were measured to the nearest millimetre by NCDMF biologists. Juvenile red drum were tagged with Floy internal anchor tags inserted into a small abdominal incision made by a scalpel approximately 10 mm posterior to the pelvic fin and dorsal to the midventral line. All tags were labeled with a unique tag number, a reward message, a mailing address, and a telephone

number. During the reporting of a tag, fishers provided information about the fate of the fish, gear used to collect the tagged fish, and location of capture.

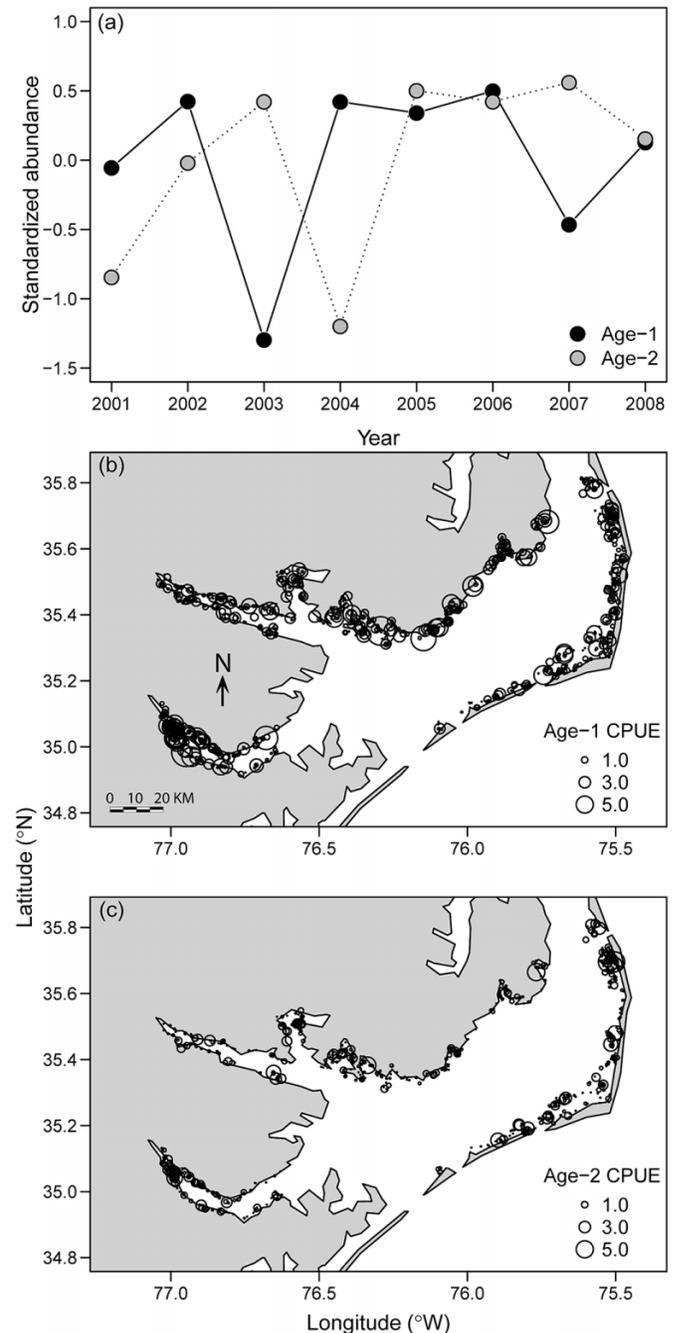
Red drum habitat use

We related age-specific red drum CPUE from the IGNS to various density-dependent and density-independent variables using a spatially explicit variable-coefficient generalized additive model (Bacheler et al. 2009b, 2010a; Bartolino et al. 2011). A generalized additive model (GAM) is a nonlinear, nonparametric regression technique that does not require a priori specification of the functional relationship between the response and predictor variables (Wood 2006). The addition of variable-coefficient terms can be used to determine specific locations where fish are expected to increase or decrease in abundance with changes in any of the predictor variables in the model (Bacheler et al. 2009b). Variable-coefficient terms can be thought of as an interaction between a predictor variable (such as global abundance) and space; in other words, when global abundance increases, where is local abundance predicted to increase the most? We were interested in the ways in which overall (global) red drum abundance influenced their own spatial patterns of habitat use, after accounting for the effects of density-independent environmental variation and potential competitors.

We examined the influence of nine predictor variables on age-1 or age-2 CPUE (number·h⁻¹). Our models built upon the previous modeling work of Bacheler et al. (2009c), who examined how age-1 and age-2 red drum CPUE was related to a variety of abiotic and biotic factors. We added spatially explicit, density-dependent terms to these previously published models. The predictor variables used in the current model were global age-1 red drum abundance, global age-2 red drum abundance, year, bottom habitat type, bottom depth, day of the year, salinity, position (latitude and longitude), and CPUE of potential competitors. Prey availability could not be measured and included as a predictor variable because the sizes of prey of age-1 and age-2 red drum were too small to be captured in the IGNS. Water temperature and dissolved oxygen were not included in the model based on the findings of Bacheler et al. (2009c). A limitation of most previous work is that the same data were used to index both abundance and distribution. Instead, we included age-1 and age-2 red drum abundance in the models as the annual deviations from the overall natural log-transformed mean abundance. These annual abundance values came from a statistical catch-at-age model for North Carolina for years 2001–2008 that overlapped with the IGNS (Fig. 2a; SEDAR 2009) and is hereafter referred to as “global red drum abundance”. Variance estimates were not available for red drum abundance estimates from the catch-at-age model, but the consistency among many different fishery-dependent and fishery-independent data sources was very high (i.e., good and bad year classes were obvious and consistent across all data sources), suggesting that relative abundance estimates were robust. Bottom habitat type was included in the model as a categorical variable with the following levels: seagrass, oyster shell, algae, detritus, or sand and (or) mud.

Although our primary focus was on the presence or absence of density-dependent habitat use, we also quantified the effects of potential competitors of juvenile red drum to

Fig. 2. (a) Standardized global age-1 (black) and age-2 (gray) red drum abundance in North Carolina and used in variable-coefficient generalized additive models, 2001–2008. (b) Age-1 and (c) age-2 red drum catch per unit effort (CPUE; number·h⁻¹) from the North Carolina independent gill net survey, 2001–2008.



explain additional variation in habitat use due to this source. We included as a covariate the pooled natural log-transformed CPUE (number·h⁻¹) of the following five species also caught in the IGNS survey: southern flounder (*Paralichthys lethostigma*), bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), black drum (*Pogonias cromis*), and spotted seatrout (*Cynoscion nebulosus*). Each of these species occurs in the Pamlico Sound and associated rivers, was caught commonly in the IGNS, and is known to have diets consisting of invertebrate and fish prey.

Before developing models, multicollinearity among predictor variables was examined because its presence can cause erratic model behavior and should be avoided (Zar 1999). We assessed the severity of multicollinearity among predictor variables by calculating the variance inflation factor for each variable, which measures the amount of variance that is inflated for each variable owing to its collinearity with other predictor variables. The variance inflation factor for all predictor variables was less than 4.0, well below the level generally acknowledged to be problematic (5–10; Neter et al. 1989), suggesting no multicollinearity among predictor variables in our data set.

The spatially explicit variable-coefficient GAMs were formulated as follows:

$$(1) \quad x_{t,y,(\phi,\lambda)} = a_y + f_1(\text{substr}) + g_1(t) + g_2(d) + g_3(\text{sal}) \\ + g_4(\text{comp}) + g_5(\phi, \lambda) + g_6(\phi, \lambda)N1_y \\ + g_7(\phi, \lambda)N2_y + e_{t,y,(\phi,\lambda)}$$

where $x_{t,y,(\phi,\lambda)}$ is the age-1 or age-2 red drum CPUE on day of the year t in year y at latitude ϕ and longitude λ , a_y is the year-specific intercept, *substr* is the above-bottom habitat type, d is the bottom depth, *sal* is the salinity (psu), *comp* is the log-transformed CPUE of potential competitors, $N1_y$ is global age-1 abundance, $N2_y$ is global age-2 abundance, f_1 is a categorical function, g_{1-7} are nonparametric smoothing functions, and $e_{t,y,(\phi,\lambda)}$ is the random error assumed to be normally distributed with a mean of zero and finite variance. Separate models were created for age-1 and age-2 red drum.

We did not examine within-year changes in habitat use of juvenile red drum. The GAM model corrected for any month or seasonal effects from the inclusion of the day of the year predictor variable. Therefore, the effect of annual global abundance on the annual local CPUE was adjusted to an overall day of the year effect. Most importantly, we assumed that whatever size selectivity might have existed was consistent among years.

We used Akaike information criterion (AIC; Burnham and Anderson 2002) to compare eq. 1 (hereafter “base” model) to a variety of reduced models, and standard model diagnostics were used to evaluate model fit. The AIC approach balances the number of parameters of a model and its log-likelihood (Burnham and Anderson 2002). We computed simple differences (Δ_i) between the best model (AIC_{\min}) and the i th model (AIC_i) as

$$(2) \quad \Delta_i = \text{AIC}_i - \text{AIC}_{\min}$$

We also calculated the Akaike weight (w_i) of the i th model given the data and the set of R models as

$$(3) \quad w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^R \exp\left(-\frac{1}{2}\Delta_r\right)}$$

The w_i can be interpreted as the weight in favor of the i th model being the best model in the data set given that one of the R models must be the best model of the set. In our analyses, we compared our base model with a variety of other models that had predictor variables added or removed inde-

pendently (i.e., not cumulative addition or removal), and the best model in the model set was the one with the lowest AIC score and highest w_i (i.e., $\Delta_i = 0$). For smoothed and variable-coefficient terms, estimated degrees of freedom were chosen using automatic software selection. Models were coded and analyzed using the *mgcv* library (version 1.6-2; Wood 2004) in R version 2.11.1 using the Gaussian family model and identity link function (The R Project for Statistical Computing, <http://www.r-project.org/>). The *gam.check* function in R was used to determine that age-1 and age-2 red drum CPUE required a fourth-root transformation to meet the assumptions of constant variance and normal residuals. Other distribution types were evaluated but compared unfavorably with the fourth-root transformation using the Gaussian distribution based on standard diagnostic plots and AIC. There were no consistent patterns in the relationship between the semivariance of the model residuals and distance between sampling points, indicating negligible spatial autocorrelation in the residuals. Furthermore, there were no obvious trends in residuals over space, suggesting no spatial bias in model fit (see Supplemental Materials¹ for map of residuals plotted across the study area). We also tested two interactions ($\text{sal} \times t$ and $\text{comp} \times t$) to determine if local red drum CPUE was influenced by salinity or potential competitors differently depending on the time of year, but there was no evidence to support their inclusion in final models based on AIC.

We also tested an alternative hypothesis that could potentially explain annual changes in the spatial distribution of juvenile red drum, which was annual variability in salinity. In other words, we tested whether annual changes in the spatial distribution of juvenile red drum were more likely explained by salinity instead of global abundance. To test this hypothesis, we replaced the variable-coefficient terms for age-1 and age-2 global abundance (g_6 and g_7 in eq. 1) with a variable-coefficient term for salinity. Mean salinity values from all IGNS sets within each year were used for this analysis.

The results from the GAM analysis (see Results below) predicted different regional effects on local juvenile red drum CPUE as a function of global abundance. To help interpret the GAM results, we plotted mean CPUE of age-1 red drum by region for each year (2003–2008). We chose two regions for this analysis, the Neuse River and northern Outer Banks, because global abundance had contrasting effects on local red drum CPUE that were consistent throughout the spatial extent of each region, and these regions have been identified as exporting areas or receiving areas based on movement data from tagging (Bacheler et al. 2009a).

Potential mechanisms for habitat use patterns

The variable-coefficient GAMs indicated a disproportionate increase in age-1 and age-2 red drum CPUE in the northern Outer Banks as global red drum abundance increased (see Results below). Two potential explanations for this result are increased larval supply to the northern Outer Banks and movement of age-1 or age-2 fish into the northern Outer Banks during years of high global abundance. We used Pearson correlation to determine if mean CPUE (from the IGNS) of age-1 red drum in the Neuse River or northern

Outer Banks in year $x + 1$ was related to the mean CPUE of age-0 red drum (from the JAI) in year x in the Neuse River or northern Outer Banks, respectively.

We also examined if, as age-1 or age-2 red drum global abundance increased, a higher proportion of fish tagged outside of the northern Outer Banks region would be recaptured inside the northern Outer Banks using NCDMF tagging data. We included all recaptures occurring within the same calendar year at tagging, excluding only those recaptures occurring within 14 days of tagging to allow for sufficient mixing. We expected a positive relationship if fish move disproportionately more into the northern Outer Banks region during years with high global abundance. Only years for which red drum abundance has been estimated by assessments (1992–2008) and only years when at least ten total recaptures occurred were included in these analyses. Pearson correlation was used to test for an effect of global abundance on the proportion of fish immigrating into the northern Outer Banks.

Red drum growth rates

Apparent individual growth rates were calculated for red drum based on the slope of a linear regression fit to lengths of individuals by date of collection from IGNS, JAI, and tagging surveys in Pamlico Sound. Apparent age-0 red drum growth rates were quantified using collections from the JAI. Red drum spawn in late summer, and age-0 red drum recruit to estuarine habitats in late summer and fall (Bacheler et al. 2008b). Apparent age-0 growth rates (for fall months) were calculated as the linear slope of total length (TL) of individuals collected in the JAI survey from 1 October until 20 November each year. September samples were excluded because of the potential for new recruits to bias growth rate calculations (Bacheler et al. 2008b; Stewart and Scharf 2008), and individuals collected after 20 November each year were excluded because of cold water temperatures after this time that could depress growth rates in some years (Lanier and Scharf 2007). An annual age-0 red drum abundance index was calculated as the arithmetic mean of the six seine samples for each of the 16 Pamlico Sound seining stations in a given year (Bacheler et al. 2008b). We related apparent age-0 red drum growth rates to the age-0 abundance index using a linear model.

Apparent growth rates of age-1 and age-2 red drum were estimated based on the slope of a linear regression fit to lengths of individuals by date of collection using IGNS and tagging data. Only fish collected between 1 June and 31 September were included in this analysis, which corresponds to the peak growth period of juvenile red drum (Facendola and Scharf 2012). The major benefit of using the IGNS survey is that the experimental gill nets (with many different mesh sizes) collect the entire range of sizes of age-1 and age-2 red drum, but the primary drawbacks are that the time series is relatively short (8 years), and in some years sample sizes were small for part of the year. In addition, the majority of age-1 red drum did not fully recruit to the IGNS until late summer. Therefore, we also used data from the NCDMF red drum tagging program. To be consistent with growth rate calculations from the IGNS, apparent growth rates of age-1 and age-2 red drum were calculated as the linear slope of lengths of individuals collected in the tagging program from 1 June through 31 September for each

year. The major benefits of using tagging data to calculate apparent red drum growth rates is that the time series is much longer and more age-1 red drum were collected early in the season, but the downside is that the selectivity patterns of these gears are not known and may not be equal for all sizes of fish (Bacheler et al. 2010b). Apparent red drum growth rates were then compared with global age-1 or age-2 abundance using a linear regression model (Fig. 2a; SEDAR 2009). All analyses were performed in R version 2.11.1 (The R Project for Statistical Computing, <http://www.r-project.org/>).

Results

Red drum habitat use

A total of 5174 age-1 red drum were caught in 4184 samples from the IGNS and included in the variable-coefficient GAM (Fig. 2b). The best overall age-1 model based on AIC scores was the base model; all of the reduced models, including the variable-coefficient salinity model, had Δ AIC values ≥ 7.0 (Table 1). The base model included two factor variables (year, above bottom habitat), five nonparametric smoothed terms (day of the year, bottom depth, salinity, CPUE of potential competitors, and spatial position; see Supplementary Materials¹ for plots showing the fitted effect of spatial position), and two variable-coefficient terms (for global age-1 and age-2 abundance).

Age-1 red drum were related to biotic, landscape, and environmental predictor variables as suggested by the variable-coefficient GAM. Age-1 red drum were positively related to day of the year, negatively related to bottom depth and salinity, and displayed a positive or dome-shaped response to CPUE of potential competitors (Fig. 3). Relative to sand and (or) mud, age-1 red drum were caught most often in bottom habitats of oyster shell, algae, and detritus. We also observed spatially explicit effects of global age-1 and age-2 abundance on age-1 CPUE as measured by the variable-coefficient terms of the GAM (Table 1). As global age-1 abundance increased, age-1 red drum CPUE disproportionately increased in the northern upriver and coastal sections of the study area (i.e., the northern Outer Banks region; Fig. 4a). Since the increases in the northern upriver areas were only marginally significant, hereafter we focus our attention on the northern Outer Banks region. Similarly, an increase in global age-2 abundance was associated with a disproportionate increase of age-1 CPUE behind the northern Outer Banks (Fig. 4b).

The best overall age-2 model, based upon the catch of 3120 age-2 red drum (Fig. 2c), was a reduced model excluding year and the variable-coefficient term for global age-2 abundance (Table 1). There was no support for the variable-coefficient salinity model to describe age-2 red drum habitat use (Table 1). Age-2 red drum were influenced by bottom habitat, day of the year, bottom depth, salinity, CPUE of potential competitors, spatial position, and global age-1 abundance. Age-2 red drum were negatively related to day of the year, depth, and salinity and positively related to CPUE of potential competitors (Fig. 3). The same bottom habitats that were important to age-1 red drum were important to age-2 red drum. Moreover, age-2 red drum CPUE disproportion-

Table 1. Model selection for the variable-coefficient generalized additive models of age-1 and age-2 red drum (*Sciaenops ocellatus*) in Pamlico Sound, North Carolina, 2001–2008.

| Model | Dev. exp. | Log-likelihood | edf | AIC | Δ AIC | w_i |
|--|-----------|----------------|------|--------|--------------|-------|
| Age-1 | | | | | | |
| Base | 41.2 | -23.2 | 41.2 | 163.6 | 0.0 | 0.96 |
| Base minus $g_7(\phi, \lambda)N_{2y}$ | 41.0 | -30.1 | 55.2 | 170.7 | 7.0 | 0.03 |
| Base minus $f_1(\text{substr})$ | 41.0 | -31.2 | 55.7 | 173.8 | 10.2 | 0.01 |
| Base minus $g_6(\phi, \lambda)N_{1y}$ | 40.9 | -37.9 | 49.3 | 174.5 | 10.9 | 0.00 |
| Base minus $g_6(\phi, \lambda)N_{1y}$ and $g_7(\phi, \lambda)N_{2y}$; plus $g_8(\phi, \lambda)\text{sal}_y$ | 40.7 | -41.6 | 47.3 | 177.9 | 14.3 | 0.00 |
| Base minus a_y | 40.7 | -41.2 | 52.3 | 186.9 | 23.3 | 0.00 |
| Base minus $g_3(\text{sal})$ | 40.7 | -42.3 | 57.3 | 199.1 | 35.5 | 0.00 |
| Base minus $g_4(\text{comp})$ | 40.6 | -47.2 | 54.2 | 202.8 | 39.2 | 0.00 |
| Base minus $g_5(\phi, \lambda)$ | 40.4 | -53.3 | 50.2 | 207.0 | 43.4 | 0.00 |
| Base minus $g_2(d)$ | 32.0 | -326.1 | 52.9 | 757.8 | 594.2 | 0.00 |
| Base minus $g_1(t)$ | 21.2 | -634.8 | 53.5 | 1376.5 | 1212.9 | 0.00 |
| Age-2 | | | | | | |
| Base minus $g_7(\phi, \lambda)N_{2y}$ | 23.1 | 320.5 | 36.9 | -567.2 | 0.0 | 0.41 |
| Base minus a_y | 22.8 | 319.2 | 36.1 | -566.3 | 0.9 | 0.26 |
| Base | 23.6 | 322.7 | 39.9 | -565.6 | 1.6 | 0.18 |
| Base minus $g_3(\text{sal})$ | 23.1 | 320.4 | 38.1 | -564.5 | 2.7 | 0.11 |
| Base minus $g_5(\phi, \lambda)$ | 22.1 | 316.2 | 34.8 | -562.6 | 4.6 | 0.04 |
| Base minus $f_1(\text{substr})$ | 22.2 | 316.6 | 37.2 | -558.8 | 8.5 | 0.00 |
| Base minus $g_6(\phi, \lambda)N_{1y}$ and $g_7(\phi, \lambda)N_{2y}$; plus $g_8(\phi, \lambda)\text{sal}_y$ | 21.8 | 313.5 | 34.2 | -558.5 | 8.7 | 0.00 |
| Base minus $g_6(\phi, \lambda)N_{1y}$ | 22.1 | 315.8 | 37.1 | -557.4 | 9.8 | 0.00 |
| Base minus $g_2(d)$ | 21.6 | 313.7 | 37.9 | -551.5 | 15.7 | 0.00 |
| Base minus $g_4(\text{comp})$ | 21.0 | 309.9 | 36.8 | -546.1 | 21.2 | 0.00 |
| Base minus $g_1(t)$ | 19.1 | 305.1 | 37.6 | -535.0 | 32.2 | 0.00 |

Note: Base is as follows: $x_{t,y}(\phi, \lambda) = a_y + f_1(\text{substr}) + g_1(t) + g_2(d) + g_3(\text{sal}) + g_4(\text{comp}) + g_5(\phi, \lambda) + g_6(\phi, \lambda)N_{1y} + g_7(\phi, \lambda)N_{2y} + e_{t,y}(\phi, \lambda)$, where x = red drum CPUE, a_y = year-specific intercept, f = categorical function, g = nonparametric smoothing function, substr = above bottom habitat type, t = day of the year, d = bottom depth, sal = bottom salinity, sal_y = annual bottom salinity, comp = log-transformed CPUE of potential competitors, ϕ = latitude, λ = longitude, N_{1y} = annual global age-1 abundance, N_{2y} = annual global age-2 abundance, and $e_{t,y}(\phi, \lambda)$ = random error. Dev. exp. = deviance explained; edf = estimated degrees of freedom.

ately increased behind the northern Outer Banks with increases in global age-1 abundance (Fig. 4c).

There were contrasting effects of global age-1 red drum abundance on observed regional mean age-1 CPUE (Fig. 5). In the Neuse River, mean age-1 CPUE was minimally influenced by global age-1 abundance, whereas changes in global age-1 abundance influenced local age-1 CPUE in the northern Outer Banks substantially. This pattern resulted in a significant interaction between global abundance and region on mean age-1 CPUE (two-way analysis of variance, ANOVA: $F_{[1,8]} = 8.10$; $P = 0.022$). Thus, global age-1 abundance had a dramatic effect on age-1 CPUE in the northern Outer Banks region but a significantly reduced effect in the Neuse River where local CPUE was higher and more consistent.

Potential mechanisms for habitat use patterns

Mean age-0 red drum CPUE in year x was not related to age-1 CPUE in year $x + 1$ for either the Neuse River ($r = 0.49$; $P = 0.32$) or Outer Banks ($r = 0.65$; $P = 0.16$), although positive relationships were observed in both instances. Likewise, the proportion of tagged age-1 red drum immigrating into the Outer Banks was not significantly related to the global abundance of age-1 red drum, but a positive relationship was observed ($r = 0.37$, $P = 0.36$; 8 out of 16 years had sufficient recaptures). The proportion of age-2 red drum immigrating into the Outer Banks was not related

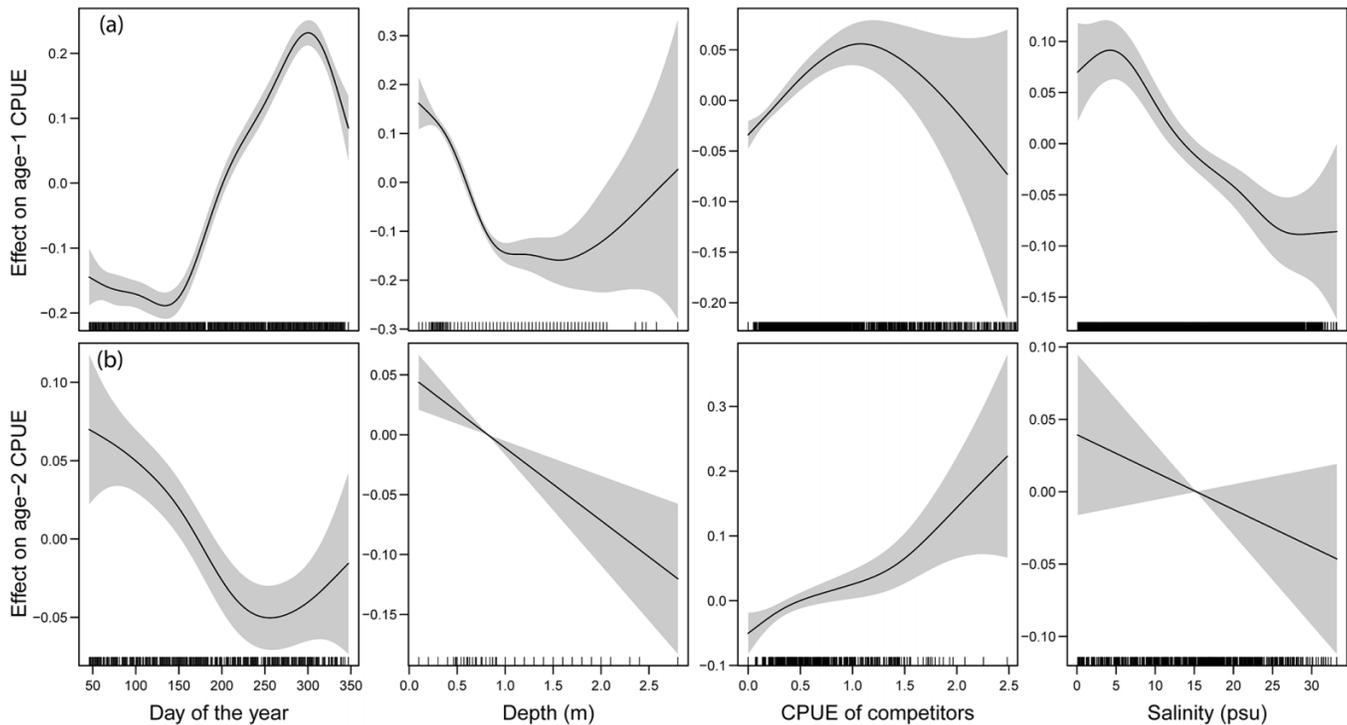
to the global abundance of age-2 red drum ($r = -0.13$, $P = 0.73$; 13 out of 16 years had sufficient recaptures).

Red drum growth rates

Overall, 12 451 age-0 red drum were collected and 9509 were measured in the seining survey between 1991 and 2009 (Supplemental Fig. S2¹), ranging in size from 11 to 104 mm TL (mean = 40.0, SD = 14.8). The annual age-0 index of abundance (number-haul⁻¹) ranged from a low of 1.0 in 1999 to 16.1 in 1991. Apparent growth rates of age-0 red drum were highly variable among years, ranging from a low of 0.1 mm-day⁻¹ in 1994 to 0.6 mm-day⁻¹ in 2001 (Supplemental Fig. S2¹). Apparent growth rates of age-0 red drum were negatively related to the age-0 abundance index (linear model: $F_{[1,17]} = 4.72$, $P = 0.04$; Fig. 6).

Apparent growth rates of age-1 and age-2 red drum were also variable over time. A total of 5070 age-1 and 3604 age-2 red drum were measured from 4184 samples from the IGNS and used to calculate apparent growth rates in 2001–2008 (Supplemental Fig. S2¹). Apparent age-1 growth rates varied from a low of 0.7 mm-day⁻¹ in 2002 to 1.9 mm-day⁻¹ in 2003 from the IGNS, while apparent age-2 growth rates varied from 1.1 mm-day⁻¹ in 2007 to 1.7 mm-day⁻¹ in 2001 (Supplemental Fig. S2¹). Based on the measurements of 11 667 age-1 and 3756 age-2 red drum from the long-term tagging database, apparent age-1 growth rates varied from 0.8 mm-day⁻¹ in 2005 to 2.1 mm-day⁻¹ in 1997, while ap-

Fig. 3. Partial effects of day of the year, bottom depth, catch per unit effort (CPUE) of potential competitors, and salinity on the CPUE (number·h⁻¹) of age-1 (a) or age-2 (b) red drum from the spatially explicit, variable-coefficient generalized additive models. Shaded areas indicate 95% confidence intervals, and tick marks on the *x* axis indicate sampling intensity.



parent age-2 growth rates ranged from 1.1 mm·day⁻¹ in 2002 to 1.8 mm·day⁻¹ in 1993 (Supplemental Fig. S2¹).

The relationships between apparent growth rate of age-1 or age-2 red drum (calculated from the long-term tagging program or the IGNS; Supplemental Fig. S2¹) and age-1 or age-2 abundance were mixed (Fig. 7). There was a significant negative relationship between apparent growth rates of age-1 red drum and age-1 ($P = 0.04$), age-2 ($P < 0.01$), and combined age-1 and age-2 abundance ($P < 0.01$) using tagging data (Fig. 7). None of these relationships were significant using IGNS data (all $P \geq 0.05$), although the slopes were negative and similar to long-term tagging results in two of three cases despite lower sample sizes (Fig. 7). Apparent age-2 growth rate was negatively related to age-2 abundance using IGNS data ($P = 0.05$), but no other relationships were significant ($P > 0.05$) using either tagging or IGNS data.

Discussion

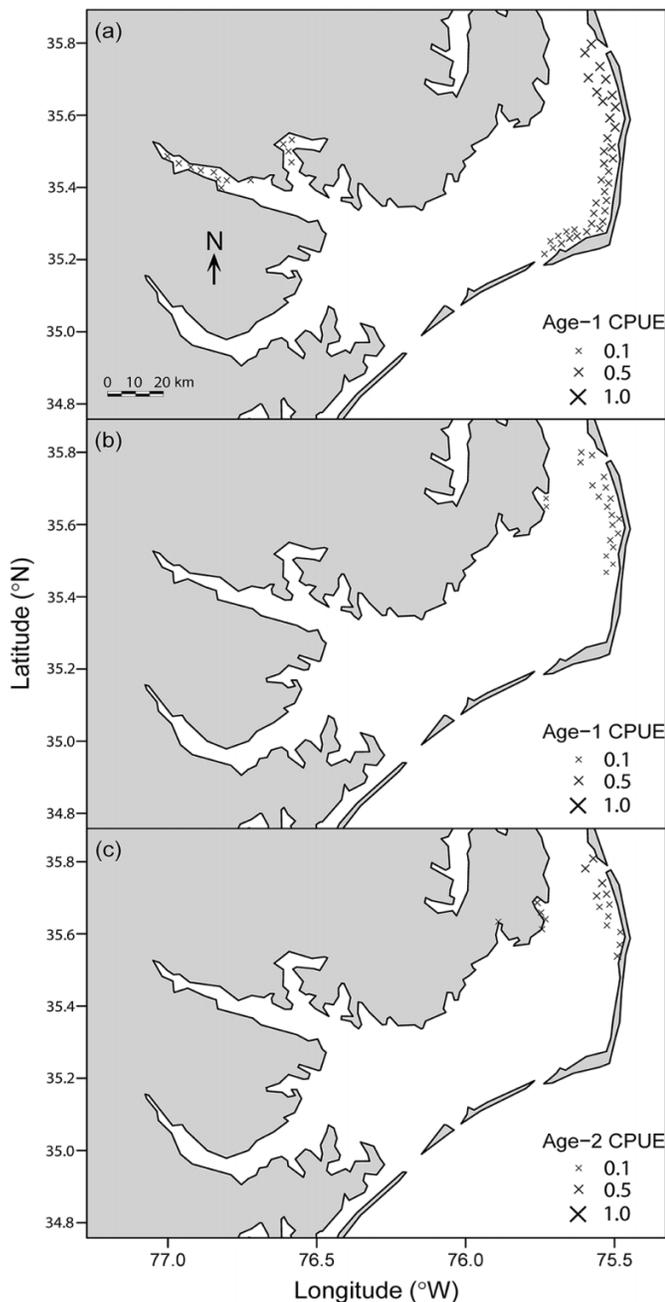
Across the estuarine landscape, we found that global conspecific abundance influenced local juvenile red drum distribution and relative abundance. Juvenile red drum exhibited density-dependent habitat use, whereby local CPUE in northern and coastal areas of Pamlico Sound increased disproportionately when their own global abundance was high. We also observed density-dependent growth rates of juvenile red drum despite density-dependent population redistribution. Density-dependent effects were more obvious for younger compared with older juvenile red drum, likely because older juveniles occurred at lower densities because of exploitation by fishers and more time over which to experience natural

deaths. Although we were unable to control for prey availability across the estuarine landscape, we did control for other density-independent variables, including salinity, day of year, depth, and substrate type.

Estuaries are often considered undersaturated environments where organisms are primarily limited by fluctuating environmental conditions or larval supply but not competition (Guindon and Miller 1995; Kamermans et al. 1995). Alternatively, our results are more consistent with a recent body of work suggesting that estuarine organisms are not immune to density-dependent effects (e.g., Buckel et al. 1999; Craig et al. 2007; Martino and Houde 2012). For instance, Craig et al. (2007) documented reductions in growth and increased mortality in high density treatments of spot (*Leiostomus xanthurus*). Craig et al. (2007) found that prey density for spot was negatively related to spot density, suggesting that competition for food was the underlying mechanism. Likewise, we documented two- to eight-fold differences in apparent growth rates among years that were negatively related to juvenile red drum relative abundance. These results suggest that density dependence may be more related to the absolute global abundance of the species or size class under study (Osenberg et al. 2002) than the type of system in which the species occurs. Density-dependent growth rates may lead to density-dependent mortality by increasing the amount of time individuals spend at vulnerable (i.e., small) sizes (Houde 1989). Because red drum are managed with a slot limit, density-dependent growth rates in age-1 and age-2 fish also have consequences for time of entry into, and length of time within, the exploitable size window.

We did not find conclusive evidence about whether the increased CPUE of age-1 fish in northern Outer Banks at

Fig. 4. Spatially explicit, variable-coefficient generalized additive model plots for the effects of global red drum abundance on local red drum catch per unit effort (CPUE; number·h⁻¹) from the North Carolina independent gill net survey, 2001–2008. (a) Effect of global age-1 abundance on local age-1 CPUE. (b) Effect of global age-2 abundance on local age-1 CPUE. (c) Effect of global age-1 abundance on local age-2 CPUE. In each plot, an “x” indicates an expected increase in red drum CPUE with a one-unit increase in global red drum abundance; there were no predicted negative effects. Size of the “x” is scaled to the size of the effect, and effects not significantly different from zero were excluded.



higher levels of global abundance was driven by density-dependent movement or by above average recruitment of settling juveniles in those years. The tagging analyses were limited to a small number of years because of low numbers of tagged fish; this prevented a robust analysis of the population

redistribution (i.e., movement) mechanism, although the trends were suggestive. This mechanism is supported by previous tagging analyses that show a net movement of red drum from western to eastern Pamlico Sound (Bacheler et al. 2009a). Also suggestive were the trends in age-0 and age-1 red drum abundance. Thus, larval supply may be another mechanism that is partly responsible for increased local abundance. Clearly, the causes of density-dependent habitat use require more attention.

Although prey availability was not measured in the field, circumstantial evidence suggests that competition for food resources may have been the primary mechanism underlying density-dependent growth rates of juvenile red drum. There is increasing evidence that estuaries may be food-limited (e.g., Kneib 1997; Kimmerer et al. 2000), especially for species with high predatory demands. Juvenile red drum are a likely candidate to experience food limitation in estuaries because they exhibit high predatory demand (Facendola and Scharf 2012), high individual growth rates (Scharf 2000; Laniar and Scharf 2007), and tend to aggregate at small and medium spatial scales (Bacheler et al. 2008b; Arnott et al. 2010). Juvenile red drum may also exhibit interference competition, as has been found in other sciaenid species (Gibbard et al. 1979). Our results strengthen the evidence that competition among estuarine organisms may be important. Similarly, density-dependent growth rates were found in 9 out of 16 fish populations examined in freshwater and marine habitats, and attributes of these nine populations were consistent with predictions from a modeled population that was regulated solely by density-dependent growth (Lorenzen and Enberg 2002). Thus, an understanding of the population dynamics of estuarine organisms will likely be improved by the inclusion of density-dependent processes.

Juvenile red drum were associated with potential competitors and season in unique ways. Juvenile red drum CPUE was generally positively related to the CPUE of potential competitors, suggesting that red drum may respond to similar habitat conditions as their competitors or gain an advantage in feeding through facilitation with heterospecifics (Hixon and Carr 1997). Seasonal relationships, whereby age-1 red drum increased and age-2 red drum decreased throughout the year, were likely due to changing gear selectivity, migratory behavior of juvenile red drum, and fishery removals and are consistent with the findings of Bacheler et al. (2009c).

Our results also indicate possible competitive interactions between age classes (cohorts) of juvenile red drum. Competitive interactions between cohorts primarily occur when prey consumed is similar and spatial and temporal overlap of cohorts is high (Scharf et al. 2006; Einum and Kvingedal 2011). Age-1 red drum appeared to influence the habitat use of age-2 red drum, suggesting competitive interactions between these two age classes. Age-1 and age-2 red drum consume similar types of prey (Scharf and Schlicht 2000); since age-1 red drum in Pamlico Sound were generally more abundant, it is not surprising that the abundance of age-1 red drum may have influenced the abundance and distribution patterns of age-2 red drum.

Juvenile red drum did not use all available estuarine habitats equally. Our habitat modeling suggested that the core juvenile red drum habitat occurred in the lower rivers of western Pamlico Sound, but when global abundance in-

Fig. 5. Mean regional catch per unit effort (CPUE; number·h⁻¹) of age-1 red drum at different levels of global age-1 abundance in Neuse River and northern Outer Banks, North Carolina. Each line represents a single year between 2003 and 2008. Low global abundance = dotted lines; medium global abundance = dashed line; high global abundance = solid lines.

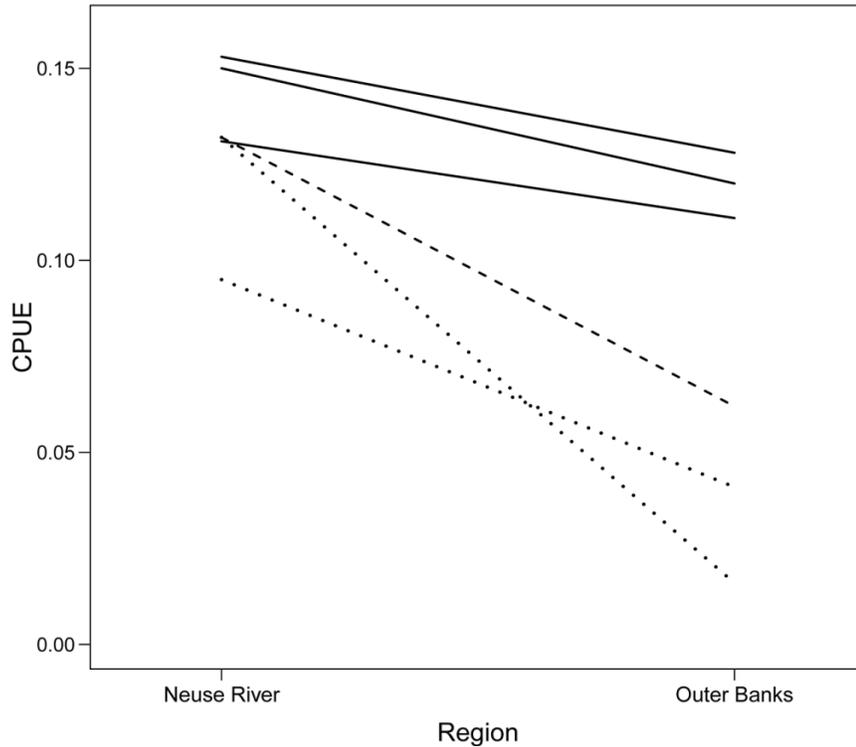
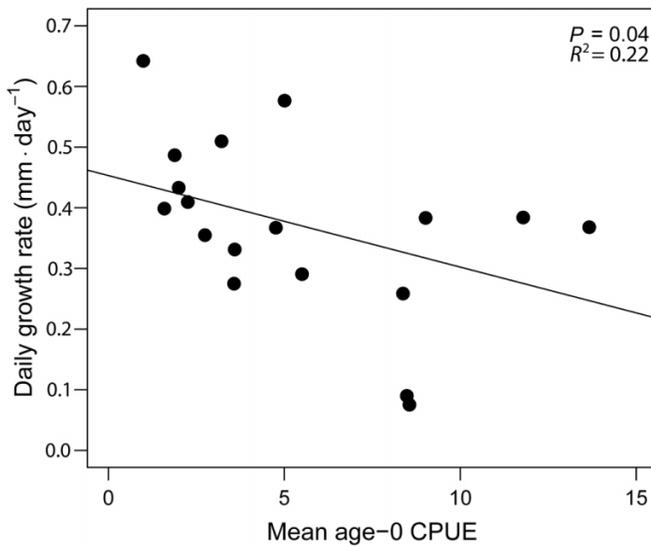


Fig. 6. Relationship between apparent age-0 growth rate (mm·day⁻¹) and mean catch per unit effort (CPUE; number·haul⁻¹) of age-0 red drum caught in the North Carolina seining survey, 1991–2009. Trendline indicates least squares linear model fit. Standard errors (SEs) for growth rates are provided in the online Supplementary Materials¹.



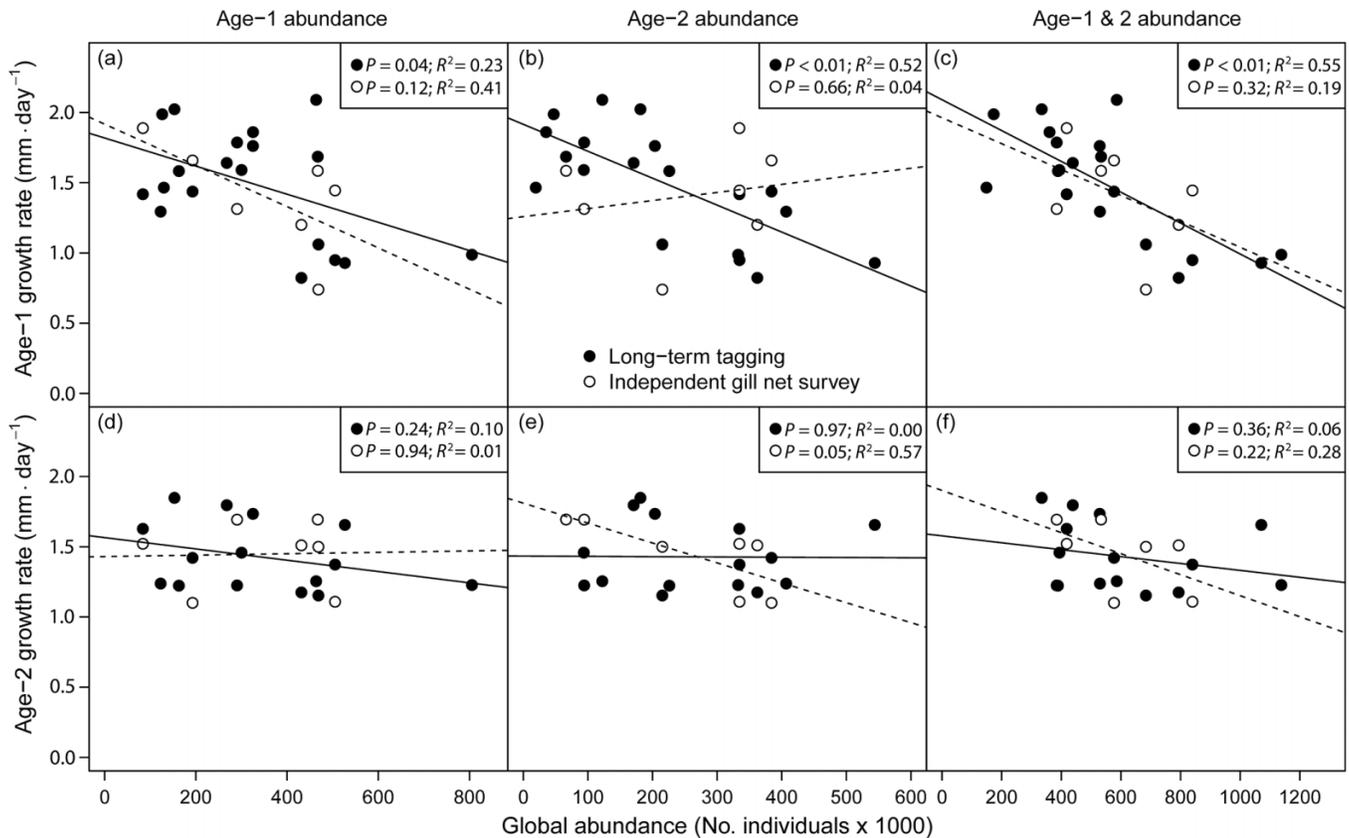
creased, individuals expanded towards the north and the coast. Shackell et al. (2005) showed that areas occupied during periods of low regional abundance may reflect core areas, except when fishing is heavy enough in high density areas to cause localized depletions and when recolonization

rates are low. Neither is likely the case for juvenile red drum. Thus, our results support MacCall’s (1990) basin model; during years with high global abundance, red drum “spill over” into other habitats, but that redistribution does not allow a fitness character (i.e., individual growth rate) to be maintained at levels observed in low global abundance years.

Variable-coefficient GAMs are a useful approach to detect density-dependent habitat use in the presence of density-independent environmental variability. For instance, Bacheler et al. (2009b) used variable-coefficient GAMs to show that walleye pollock (*Theragra chalcogramma*) spawning distribution contracted during periods of low spawning stock biomass, after accounting for the effects of ocean transport and sea surface temperature. Similarly, Bartolino et al. (2011) documented expansion of yellowfin sole (*Limanda aspera*) into marginal, peripheral habitats at high overall abundance levels in the eastern Bering Sea. We highly recommend the use of variable-coefficient GAMs to evaluate density-dependent spatial dynamics because they are able to control for density-independent environmental variation, they are flexible and can be adapted to a variety of unique situations, and the results can be straightforward to interpret.

Our results have implications for many aspects of sustainable fisheries management. For instance, managers have often attempted to augment estuarine populations using stock enhancements, but results have been mixed as to whether stocking has increased ambient densities over moderate spatial or temporal scales (Scharf 2000; Jenkins et al. 2004; Tringali et al. 2008). Our results suggest that the ideal candi-

Fig. 7. Apparent growth rate ($\text{mm}\cdot\text{day}^{-1}$) of age-1 (top row) and age-2 (bottom row) red drum as a function of the global abundance of age-1 (left column), age-2 (middle column), or age-1 and age-2 red drum (right column) in Pamlico Sound, North Carolina. Apparent growth rate was estimated from collections made by either the North Carolina independent gill net survey (open circles, dotted trendline) or the North Carolina long-term tagging program (solid circles, solid trendline). Abundance of age-1 and age-2 red drum was estimated from a statistical catch-at-age stock assessment (SEDAR 2009). Trendline indicates least squares linear model fit. Standard errors (SEs) for growth rates are provided in the online Supplementary Materials¹.



dates for stock enhancement are those species currently at very low population abundance levels (i.e., highly overfished) to minimize competitive interactions with wild fish, not a species like red drum whose juvenile abundance is high enough in some years to saturate their estuarine environment. Our results also have implications for marine reserve design. Given that estuarine fish abundance can be influenced by both density-dependent and density-independent factors, both need to be considered when choosing the proper placement and size of marine reserves.

There were some potential limitations of our study. For instance, estimating apparent growth rates using lengths of fish sampled throughout the year is dependent upon the selectivity patterns of the sampling gears. We consider the collection of age-0 red drum by seines to be relatively nonselective over the range of lengths encountered in this study (11–104 mm TL). Gill nets can be highly size-selective when a single or minimum mesh size is used (Bacheler et al. 2010b); however, the gill nets used in our study consisted of a wide range of mesh sizes, likely minimizing size-selectivity effects within an age class. Because sample sizes were limited for the gill net survey (e.g., length of time series was short, number of red drum caught within some years was modest), we also analyzed length data from a long-term tagging program that used multiple gears to collect red drum, and selectivity pat-

terns of these combined gears was unknown. In five of six cases, the slopes of the apparent growth rate versus abundance plots were very similar between long-term tagging and gill net collection gears, suggesting that biases in apparent growth rate due to gear selectivity issues were minimal. Another potential limitation is that density-dependent growth rates might also be observed if larger, but not smaller, individuals happen to experience higher mortality rates during years of higher global abundance. We consider this alternative explanation unlikely because we cannot think of any source of mortality that would act selectively on larger individuals within an unfished cohort. One source of mortality of older (age-2) red drum is the recreational or commercial fishery, but that fishery does not operate on age-0 or age-1 fish, where we saw evidence of density-dependent growth. The last limitation of our study was that age-0 density-dependent habitat use could not be tested for because age-0 red drum were too small to be collected by the IGNS, and the JAI survey consisted of a low number of seining stations across Pamlico Sound ($N = 16$).

We have shown that compensatory density dependence must be accounted for to fully understand the population dynamics of an estuarine species. Density dependence can either regulate populations by offsetting the losses of individuals from exploitation or density-independent mortal-

ity (Rose et al. 2001), or it can destabilize populations and perhaps even drive them towards extinction (Myers et al. 1995). Although some have urged an end to the density-dependence debate (Turchin 1995), we agree with Rose et al. (2001) that understanding the magnitude of density dependence in specific populations continues to be critical for a complete understanding of population dynamics. Productive areas of research include the effect of density-dependent growth and habitat use on population regulation (and causal mechanisms), the most appropriate spatial scale over which to model population dynamics given density dependence, and the densities at which competition begins to affect growth, mortality, and movement.

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