

# Stage-specific variability in habitat associations of juvenile red drum across a latitudinal gradient

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**ABSTRACT:** Long-term fisheries independent data (2000–2014) from bag seine surveys were used to characterize fish–habitat relationships for red drum *Sciaenops ocellatus* at 2 critical life stages during the first year of life: post-settlement (October to December) and early juvenile (overwintering, January to March). Relationships between environmental variables and red drum abundance were examined in 3 estuaries (Galveston Bay, Aransas-Corpus Bay, and Laguna Madre, Texas, USA) along a latitudinal gradient using generalized additive models. Temporal factors were among the most important predictor variables for both life stages, with month and/or year retained in each model. In addition to temporal variability, abundance of post-settlement and early juvenile red drum was influenced by both physicochemical conditions (temperature and salinity) and aquatic vegetation (seagrass and salt marsh coverage). Although fish–habitat relationships were often similar across the 3 estuaries, the relative importance of abiotic and biotic factors to red drum distribution and abundance varied among estuaries and life stages. Likewise, habitat relationships for post-settlement and early juvenile red drum were influenced by variability in habitat availability among estuaries, with abundance at both life stages positively associated with seagrass coverage in seagrass-limited systems and negatively associated in systems where seagrass was more abundant. This study clearly demonstrates that fish–habitat relationships for red drum are life stage-, time- and estuary-specific, and therefore, habitat suitability models that account for such variability are needed to effectively identify and conserve important estuarine nursery areas.

**KEY WORDS:** Nursery habitat · Estuarine · Ontogenetic shifts · Habitat suitability model · Overwintering · Post-settlement · Habitat relationships · Gulf of Mexico · Essential fish habitat

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## INTRODUCTION

Estuaries provide important habitat for a wide variety of organisms during early life, and often serve as nursery areas for marine fishes (Beck et al. 2001, Gillanders et al. 2003). Because subtle fluctuations in life history parameters of fishes during early life can greatly affect recruitment, there is considerable interest in identifying estuarine habitats that improve growth and/or survival (Able 2005, Dahlgren et al. 2006). Currently, many estuarine habitats are in decline due to degradation or alteration and thus,

there is need to identify 'high quality' habitat for estuarine-dependent fishes (Boström et al. 2011). While benthic habitats such as seagrass, mangroves, oyster reef, and salt marsh are known to hold high densities of juvenile fishes (Heck et al. 2003, Boström et al. 2006, 2011), assessing the relative value of these habitats across broad spatial scales is often difficult, as habitat quality is influenced by a variety of abiotic and biotic factors that vary spatially and temporally in estuarine systems (Sheaves et al. 2015).

Habitat suitability models are increasingly used to identify factors influencing the distribution of juve-

nile organisms and have recently been used to classify potentially important nursery areas in estuarine ecosystems (Guisan & Thuiller 2005, Niklitschek & Secor 2005). While species–habitat relationships are often broadly applied across a large geographical area (Johnson et al. 2013), the complex and variable nature of these relationships realistically limits our ability to extrapolate them across both time and space (McAlpine et al. 2008). For many marine fishes, habitat requirements also change with ontogeny (Bartolino et al. 2011, Johnson et al. 2013). Likewise, the degree to which these relationships vary geographically is poorly understood, despite the fact that neighboring estuarine systems may differ in climate, hydrology, physicochemical processes, and anthropogenic impacts. Therefore, spatially explicit approaches that account for multiple life stages may be needed to more effectively assess habitat quality and identify highly suitable habitats within a particular estuarine system.

Here, a generalized additive model (GAM) framework was used to examine stage-specific habitat relationships for red drum *Sciaenops ocellatus* in 3 estuaries along a latitudinal gradient in the northwestern Gulf of Mexico. Red drum is an estuarine-dependent sciaenid of considerable economic value, and is among the most highly targeted recreational finfish in the Gulf of Mexico (Coleman et al. 2004). Adult red drum typically spawn in coastal waters near tidal passes in the fall, with juveniles settling in estuarine habitats, where they remain throughout adolescence (ca. 0 to 3 yr) before joining adult populations in coastal waters (Powers 2012). Differences in density, survival, and growth have been observed among estuarine habitats for newly settled red drum (Rooker & Holt 1997, Rooker et al. 1998a, Stunz et al. 2002b), suggesting that nursery value may vary greatly among habitats within an estuary. Moreover, it is suspected that essential nursery habitat(s) of red drum vary ontogenetically (Bacheler et al. 2009) and among estuarine systems (Stunz et al. 2002a). The purpose of this study was to examine the influence of abiotic and biotic factors on the distribution and abundance of juvenile red drum for 3 estuarine systems (Galveston, Aransas-Corpus Christi, and Laguna Madre, Texas, USA) along a latitudinal gradient, that differ in benthic habitat composition, hydrology, and physicochemical conditions. Furthermore, we explore these relationships across 2 life stages in the first year of life that have been described as potential bottlenecks in recruitment success of marine fishes: post-settlement and overwintering (Hurst 2007, Johnson 2007).

## MATERIALS AND METHODS

The Texas coastline in the northwestern Gulf of Mexico is comprised of a series of estuaries along a latitudinal gradient from north to south, which vary in salinity, temperature, freshwater input, and benthic habitat coverage (Fig. 1). Estuaries in the north are characterized by higher freshwater inflow and lower salinities, while estuaries in the south receive very little freshwater input and are often hypersaline (Tolan 2007). Areal coverage of both seagrass (mixed stands dominated by *Halodule wrightii* and *Thalassia testudinum*) and black mangrove *Avicennia germinans* increases from north to south as well (Sherrod & McMillan 1981, Adair et al. 1994). Given this latitudinal variation in environmental conditions, we chose 3 estuarine systems in different locations of the Texas coast to examine variability in fish–habitat relationships for red drum: the Trinity-San Jacinto Estuary (referred to from hereafter as Galveston Bay) on the north coast, Mission-Aransas/Nueces Estuary (referred to hereafter as Aransas-Corpus Bay) on the middle coast, and the Lower Laguna Madre (referred to from hereafter as Laguna Madre) on the southern coast (Fig. 1). In addition to differences in habitat availability and hydrology, these 3 estuaries also receive varying degrees of anthropogenic pressure, as Galveston Bay is adjacent to and receives effluent from the major metropolitan area of Houston (population >2 million in city limits). In contrast, Aransas-Corpus Bay is bordered to the southwest by the city of Corpus Christi (population >300 000), while the Laguna Madre is largely undeveloped with the exception of the smaller city of Brownsville (population ~175 000) at the southwestern tip of the estuary.

Red drum were collected over a 15-yr period from 2000 to 2014 as part of the Texas Parks & Wildlife Department (TPWD) long-term monthly bag seine surveys. Bag seine surveys were conducted based on a stratified, random sampling design, with each estuary divided into sampling grids (1' latitude by 1' longitude) and a fixed number of samples were taken per month (20 estuary<sup>-1</sup> mo<sup>-1</sup>), providing a broad spatial coverage of representative seascapes within each estuary over the 15 yr examined. Bag seines (18 × 1.8 m, with 13 mm mesh in cod end) were deployed in shallow habitats (<2 m depth) and pulled parallel to shore for approximately 15 m following methods described by Martinez-Andrade et al. (2009). At sites containing hard-bottom habitat or structure (i.e. oyster reefs, pilings), seines were pulled adjacent to, rather than directly over structure to minimize variability in gear efficiency among sampling sites. We

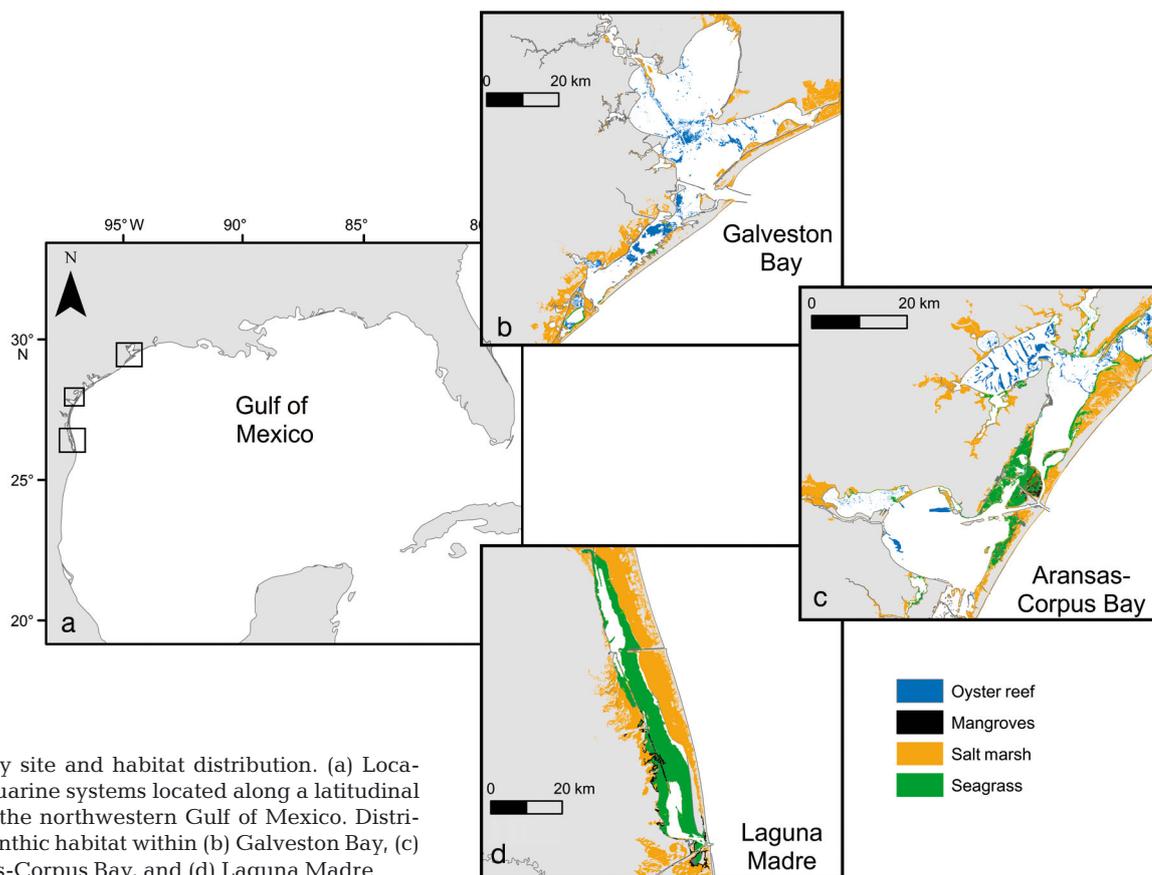


Fig. 1. Study site and habitat distribution. (a) Location of 3 estuarine systems located along a latitudinal gradient in the northwestern Gulf of Mexico. Distribution of benthic habitat within (b) Galveston Bay, (c) Aransas-Corpus Bay, and (d) Laguna Madre

acknowledge that catchability could vary as a function of habitat type (e.g. Lauretta et al. 2013, Bacheler et al. 2014); however, given the methodology it was assumed to be negligible. Red drum captured in each seine haul were enumerated and measured to the nearest mm total length (TL). This particular sampling gear targets juvenile red drum and is not particularly effective for larger more mobile individuals (age 1+); thus, all individuals captured were presumed to be first-year juveniles. Juvenile red drum catch data were partitioned into 2 life stages for modeling purposes. Post-settlement red drum were defined as individuals captured from October through December, which corresponds with documented settlement patterns of the species (Rooker et al. 1998b), while early juvenile red drum were defined as individuals captured from January through March, corresponding to the first 'overwintering' period. Spatial and temporal differences in mean length of red drum at each life stage were compared across estuaries and years with a 2-way ANOVA.

Environmental variables were used to investigate the influence of physicochemical processes and habitat on red drum distribution and abundance in each

estuary. Dissolved oxygen ( $\text{mg l}^{-1}$ ), salinity, water temperature ( $^{\circ}\text{C}$ ), and turbidity (nephelometric turbidity units, NTU) were recorded from surface waters at each site by the TPWD during sampling. Minimum and maximum depth of each seine haul, as well as sampling date and geolocation were also recorded. For the purposes of this study, depth was defined as the mean depth of each seine haul. Distance to both freshwater sources and tidal inlets were estimated to examine the influence of freshwater and saltwater inflow on juvenile red drum distribution and abundance. Distance to a particular feature was calculated with the shoreline as a barrier using the cost-distance function in ArcGIS 10.2 (ESRI). To account for the influence of adjacent or surrounding habitats on red drum abundance, benthic habitat coverage of a particular site was classified as the areal coverage of a particular habitat (seagrass, oyster, or salt marsh) within a 300 m radius of a sampling location and was calculated using Geospatial Modelling Environment (Beyer 2012) and ArcGIS 10.2. Seagrass, mangrove, and oyster reef habitat layers were obtained from the National Oceanic Atmospheric Administration National Coastal Data Development Center. Marsh

habitat was defined as 'estuarine intertidal emergent persistent vegetation' within the habitat classification scheme from georeferenced National Wetlands Inventory maps from the United States Fish & Wildlife Service.

GAMs were used to investigate the influence of environmental variables on post-settlement and early juvenile red drum abundance for Galveston Bay, Aransas-Corpus Bay, and Laguna Madre. Catch per unit effort (CPUE; individuals per seine haul, ca. 300 m<sup>2</sup>) at each station was modeled as a count variable. GAMs are non-parametric extensions of generalized linear models (GLM) that allow for non-linear relationships between predictor and response variables that are common to ecological data (Guisan et al. 2002). General GAM construction is given by the equation:

$$E[y] = g^{-1} \left[ \beta_0 + \sum_k S_k(x_k) \right] \quad (1)$$

where  $E[y]$  is equal to the expected value of the response variable (CPUE),  $g$  is the link function,  $\beta_0$  is the intercept,  $x$  represents one of  $k$  predictor variables, and  $S_k$  is the smoothing function of the predictor variable,  $x_k$ . Negative binomial models with a logarithm link were fit with cubic regression splines using the *mgcv* library in R version 3.1.3 (Wood 2006, R Core Team 2015). Cubic regression splines were automatically penalized from a specified maximum degrees of freedom and the degree of smoothing selected by minimizing the generalized cross validation (GCV) score (Wood 2011). In the current study, cubic splines were restricted to a maximum of 3 degrees of freedom for all predictor variables to prevent overfitting (i.e. unrealistic ecological responses) (Ciannelli et al. 2008, Sundblad et al. 2009).

Predictor variables influencing juvenile red drum CPUE were selected for final models using a manual backwards stepwise procedure based on minimizing the Akaike information criterion (AIC; Akaike 1974), which measures goodness of fit, while accounting for model complexity (number of variables). Approximate significance of smoothed predictor variables (p-values) was used to guide the backwards selection procedure, where the variable with the highest p-value was removed first. When removal of a predictor variable resulted in a reduced model with a lower AIC, this variable was excluded from analysis. Stepwise selection continued until removal of any of the remaining predictor variables resulted in an increase in model AIC. Non-significant terms ( $p > 0.05$ ) retained in the final model were removed if model AIC was comparable ( $< 2$ ) after removal (Burnham & Anderson 2002, Rooper et al. 2012). Prior to variable

selection, Spearman's  $\rho$  was used to test for collinearity between predictor variables. If Spearman's  $\rho$  was  $> 0.5$  between 2 variables, each variable was tested alone in separate GAMs and the variable that indicated better model fit (lower AIC) was included in the initial model prior to backwards selection. In addition to AIC, overall model fit was assessed with percent deviance explained:  $DE = [(null\ deviance - residual\ deviance) / null\ deviance] \times 100$ . The relative influence of each predictor variable was assessed by removing each variable individually from the final model and comparing percent change in DE ( $\Delta DE$ ) and change in AIC ( $\Delta AIC$ ).

## RESULTS

Overall, 8395 juvenile red drum were collected in the 3 estuarine systems over the 15-yr period analyzed. Mean length of post-settlement red drum decreased from north to south among the estuaries investigated (ANOVA;  $p < 0.001$ ), with the largest individuals in Galveston Bay ( $48.8 \pm 0.6$  mm; mean  $\pm$  SE), followed by Aransas-Corpus Bay ( $44.9 \pm 0.5$  mm), and Laguna Madre ( $41.3 \pm 0.6$  mm) (Tukey's HSD;  $p < 0.001$ ) (Table 1). Mean length did not vary across years for the post-settlement stage, and no interaction was detected between estuary and year (ANOVA;  $p > 0.05$ ). While mean length differed among estuaries for early juvenile red drum (ANOVA;  $p < 0.001$ ), it also varied among years and a significant interaction between estuary and year was detected (ANOVA;  $p < 0.05$ ), indicating that estuary-specific differences in mean length among bays during this life stage were not consistent across years. Mean CPUE (SE) for post-settlement red drum ranged from 0.63 (0.07) in Galveston Bay to 0.93 (0.14) and 0.94 (0.13) in Aransas-Corpus Bay and Laguna Madre, respectively. Mean CPUE (SE) for early juvenile red drum decreased from north to south, ranging from 3.03 (1.00) in Laguna Madre to 1.00 (0.02) and 0.88 (0.11) in Aransas-Corpus and Galveston Bays, respectively.

Intra- and inter-annual variability in CPUE of juvenile red drum was observed for all 3 estuarine systems. Annual CPUE for post-settlement red drum ranged from 0.23 (year = 2010) to 1.00 (2008) in Galveston Bay, from 0.05 (2011) to 2.60 (2014) in Aransas-Corpus Bay, and from 0.05 (2011) to 2.47 in Laguna Madre (2012) (Fig. 2). The abundance of post-settlers peaked earlier in Galveston Bay, in November (CPUE = 0.84)/December (0.85), relative to Aransas-Corpus Bay (December [1.68]) and Laguna

Table 1. Red drum catch data and associated abiotic variables of both post-settlement (October–December) and early juvenile (January–March) life stages in 3 estuaries from the northwestern Gulf of Mexico from 2000 to 2014. Estuaries sampled were Galveston Bay (n = 900), Aransas-Corpus Bay (n = 1800), and Laguna Madre (n = 900). n = number of seine hauls

Surveys	Galveston		Aransas-Corpus		Laguna Madre	
	Mean	SD	Mean	SD	Mean	SD
<b>Post-settlement</b>						
CPUE	0.63	2.11	0.93	5.84	0.94	4.03
Total length (mm)	48.83	14.33	44.86	15.63	41.33	16.40
Temperature (°C)	20.10	5.27	21.76	5.60	23.17	5.23
Salinity	18.99	8.81	24.85	10.48	30.33	8.70
Dissolved oxygen (mg l <sup>-1</sup> )	7.89	1.84	8.53	2.34	7.07	2.42
Turbidity (NTU)	32.08	55.86	21.59	35.85	25.55	42.53
Depth (m)	0.33	0.19	0.26	0.14	0.18	0.07
Distance to freshwater (km)	11.19	7.76	18.63	10.79	19.89	13.40
Distance to tidal inlet (km)	21.65	15.26	28.41	14.76	20.63	9.28
<b>Early juvenile</b>						
CPUE	0.88	3.18	1.00	5.59	3.03	30.13
Total length (mm)	61.98	25.27	68.32	23.21	61.77	27.66
Temperature (°C)	16.72	4.18	17.69	3.98	19.52	4.14
Salinity	17.73	8.74	24.02	8.35	31.53	7.21
Dissolved oxygen (mg l <sup>-1</sup> )	8.41	1.73	8.38	1.96	7.82	1.91
Turbidity (NTU)	37.05	55.15	18.82	29.67	33.77	60.67
Depth (m)	0.28	0.14	0.20	0.11	0.15	0.07
Distance to freshwater (km)	11.55	7.75	18.59	11.05	20.44	13.34
Distance to tidal inlet (km)	21.48	15.98	28.02	14.88	20.52	9.29

Madre (December [1.55]) (Fig. 3). Annual CPUE was also variable during the early juvenile stage and ranged from 0.20 (year = 2004) to 1.97 (2001) in Galveston Bay, from 0.13 (2013) to 2.17 (2005) in Aransas-Corpus Bay, and from 0.17 (2000) to 28.83

(2014) in Laguna Madre. In contrast, monthly CPUE of early juvenile red drum followed the opposite pattern of the post-settlement stage, and peaked earlier in Aransas-Corpus Bay (February) and Laguna Madre (February) than in Galveston Bay (March).

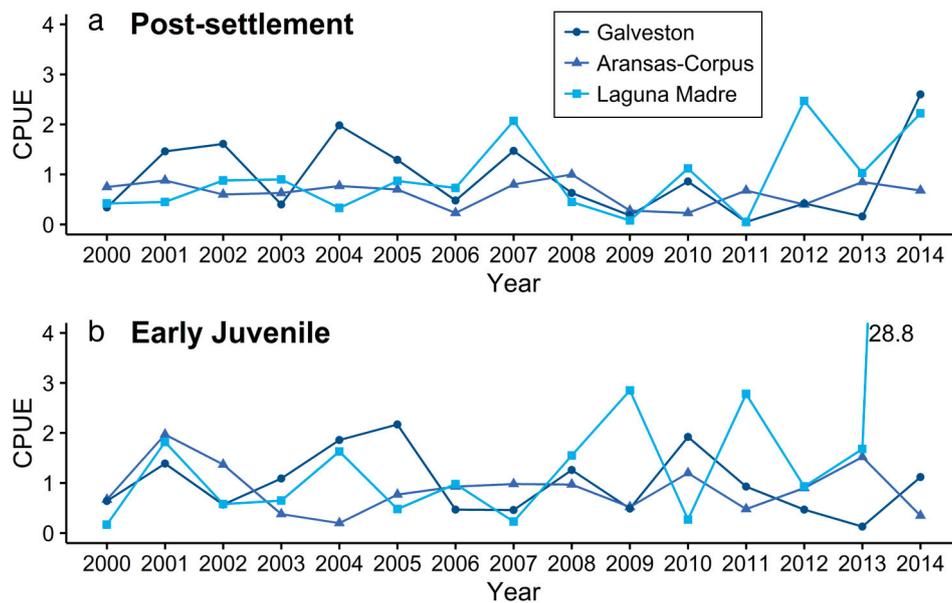


Fig. 2. Mean annual CPUE of red drum in Galveston Bay, Aransas-Corpus Bay, and Laguna Madre between 2000 and 2014 during the (a) post-settlement (October–December) and (b) early juvenile (January–March) life stages. CPUE was recorded as the number of individuals per seine haul (~300 m<sup>2</sup>)

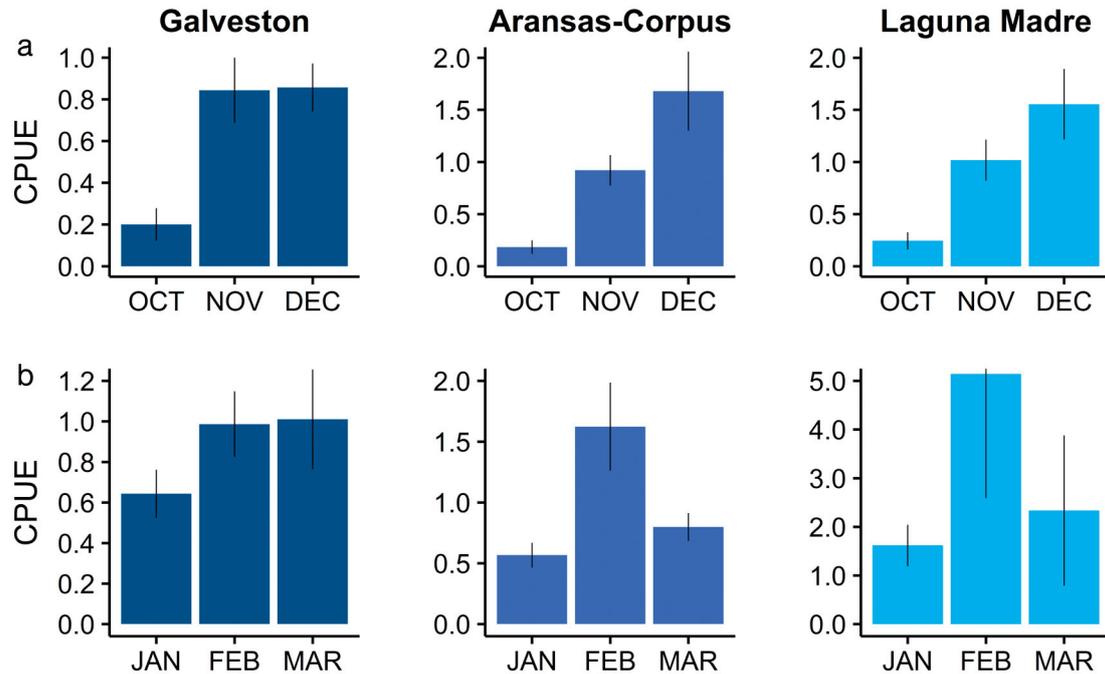


Fig. 3. Plots of intra-annual variability in red drum abundance during (a) post-settlement (October–December) and (b) early juvenile (January–March) life stages for Galveston Bay, Aransas-Corpus Bay, and Laguna Madre. CPUE was recorded as the number of individuals per seine haul (~300 m<sup>2</sup>). Note different scales on each plot

#### Post-settlement models

The final model for post-settlement red drum in Galveston Bay included month ( $\Delta\text{AIC} = 70.7$ ), seagrass coverage (61.4), salinity (30.8), year (22.1), salt marsh coverage (17.2), turbidity (13.7), depth (6.9), oyster coverage (5.8), and temperature (3.3) with an overall DE of 27.3% (Table 2). Similar to  $\Delta\text{AIC}$ ,  $\Delta\text{DE}$  (%) indicated that the 4 most influential predictor variables were month (5.8%), seagrass coverage (4.8%), year (3.8%), and salinity (2.9%). Response plots indicated that CPUE of post-settlement red drum was reduced at higher salinities (>25) and at greater depth (>0.6 m), but was positively related to temperature (greatest above 25°C) (Fig. 4). CPUE of post-settlement red drum was also influenced by benthic habitat structure, with abundance higher in areas of moderate marsh coverage (30 to 60%) and positively related to areal seagrass coverage (Fig. 5). Finally, abundance of post-settlers was negatively related to oyster coverage and turbidity.

In Aransas-Corpus Bay, the final model for post-settlement red drum (DE = 44%) indicated that year ( $\Delta\text{AIC} = 185.6$ ), depth (105.0), month (64.7), seagrass coverage (63.4), distance to freshwater (62.4), salt marsh coverage (57.8), and temperature (48.8) were the most influential variables with turbidity (30.6), oyster coverage (17.9), and salinity (14.4) also con-

tributing to the final model (Table 2). Findings were similar using  $\Delta\text{DE}$ , with year (5.8%), depth (3.1%), month (1.9%), seagrass coverage (1.9%), and distance to freshwater (1.9%) being the most influential variables. Response plots indicated that post-settlers in Aransas-Corpus Bay were in greater abundance in shallow to moderate depths (0.1 to 0.5 m), far from freshwater sources (>10 km), at moderate temperatures (15 to 25°C) and salinities >10 (Fig. 4). CPUE was also influenced by benthic habitat structure, with higher catches in areas with low to moderate seagrass coverage (20 to 50%) and moderate to high coverage of marsh habitat (30 to 70%) (Fig. 5). In addition, post-settlement red drum abundance was reduced in areas with greater turbidity (>100 NTU) and moderate to high oyster reef coverage (>25%), relative to other areas surveyed.

The final model for post-settlement red drum in Laguna Madre (DE = 42.1%) included year ( $\Delta\text{AIC} = 119.9$ ), distance to inlet (55.6), month (35.9), salinity (27.1), temperature (26.2), mangrove coverage (14.1), oyster coverage (10.3), turbidity (8.0), and distance to freshwater (7.4) (Table 2).  $\Delta\text{DE}$  was in general agreement with the  $\Delta\text{AIC}$  method, and indicated that year (8.8%), distance to inlet (3.4%), month (2.4%), salinity (1.9%), and temperature (1.9%) were the most influential variables on post-settler abundance. Response plots indicated that CPUE of post-settlement

Table 2. Temporal and environmental variables retained in final generalized additive models for post-settlement and early juvenile red drum in 3 estuaries in the northwestern Gulf of Mexico. Estuaries include Galveston Bay, Aransas-Corpus Bay, and Laguna Madre. Model fit was assessed with Akaike's information criterion (AIC) and % deviance explained (DE). Relative importance of each predictor variable is given by the difference in AIC ( $\Delta$ AIC) and DE ( $\Delta$ DE) when this variable was removed from the final model. Explanatory variables that were included as categorical factors in models are denoted by (f)

Variable	Galveston		Aransas-Corpus		Laguna Madre	
	$\Delta$ AIC	$\Delta$ DE	$\Delta$ AIC	$\Delta$ DE	$\Delta$ AIC	$\Delta$ DE
<b>Post-settlement</b>						
	AIC = 1672.6	DE = 27.3	AIC = 3285.4	DE = 44.0	AIC = 1781.4	DE = 42.1
Month (f)	70.7	5.8	64.7	1.9	35.9	2.4
Year (f)	22.1	3.8	185.6	5.8	119.9	8.8
Temp	3.3	0.4	48.8	1.6	26.2	1.9
Salinity	30.8	2.9	14.4	0.6	27.1	1.9
Turbidity	13.7	1.3	30.6	1.0	8.0	0.8
Tidal inlet					52.6	3.4
Freshwater			62.4	1.9	7.4	0.7
Salt marsh	17.2	1.4	57.8	1.8		
Seagrass	61.4	4.8	63.4	1.9		
Oyster	5.8	0.6	17.9	0.7	10.3	0.9
Mangrove					14.1	1.1
Depth	6.9	0.8	105.0	3.1		
<b>Early juvenile</b>						
	AIC = 2069.5	DE = 22.2	AIC = 3958.9	DE = 31.6	AIC = 2240.2	DE = 61.0
Month (f)	0.3	0.3	42.9	1.3	53.4	1.8
Year (f)	55.3	5.3	360.3	11.2	413.6	14.2
Temp	43.5	3.3	92.2	2.8	11.7	0.5
Salinity			96.0	2.9	29.9	1
Turbidity			4.5	0.3	11.7	0.5
Tidal inlet	3.7	0.7			18.7	0.6
Freshwater	10.0	1.2	44.6	1.4		
Salt marsh	10.0	0.9	18.5	0.7	32.8	1.1
Seagrass	32.7	2.6	62.9	1.9	76.4	2.4
Oyster	1.3	0.2	33.0	1.1	11.6	0.5
Mangrove			36.4	1.1	7.8	0.3
Depth	55.2	4.1	15.4	0.6	153.8	5

red drum was highest at moderate temperatures (15 to 25°C) and salinities (10 to 30) far from tidal inlets (>15km) and relatively close to freshwater sources (<5 km) (Fig. 4). Abundance of post-settlement red drum also decreased with greater areal coverage of both mangrove (>15%) and oyster (>10%) habitat (Fig. 5).

### Early juvenile models

The final model for early juvenile red drum in Galveston Bay included 9 variables (DE = 22.2%), with year ( $\Delta$ AIC = 55.3), depth (55.2), temperature (43.5), seagrass coverage (32.7), and distance to freshwater (10.0) comprising the most influential variables retained in the model (Table 2). The  $\Delta$ DE for these variables ranged from 1.2 to 5.3%, and was <1% for the remaining 4 variables (salt marsh coverage, distance to inlet, month, and oyster coverage). Response

plots indicated that early juvenile red drum were more abundant in areas near freshwater sources with warmer temperatures (>15°C) and shallow to moderate depths (<0.6 m) (Fig. 6). CPUE of early juvenile red drum was positively related to seagrass coverage and, to a lesser extent, oyster reef coverage, and greater abundance was observed in areas with low to moderate areal coverage of salt marsh habitat (10 to 50%), relative to other areas surveyed (Fig. 7). A more complex relationship was observed with distance to tidal inlet, with greater CPUE of early juveniles at both moderate (10 to 25 km) and large distances (>55km) from tidal inlets.

In Aransas-Corpus Bay, the final model for early juvenile red drum included 11 variables (DE = 31.6%), and comparison of  $\Delta$ AIC indicated that year ( $\Delta$ AIC = 360.3), salinity (96.0), temperature (92.2), seagrass coverage (62.9), distance to freshwater (44.6), and month (42.9) were the most influential variables (Table 2). Similarly,  $\Delta$ DE values were highest for year

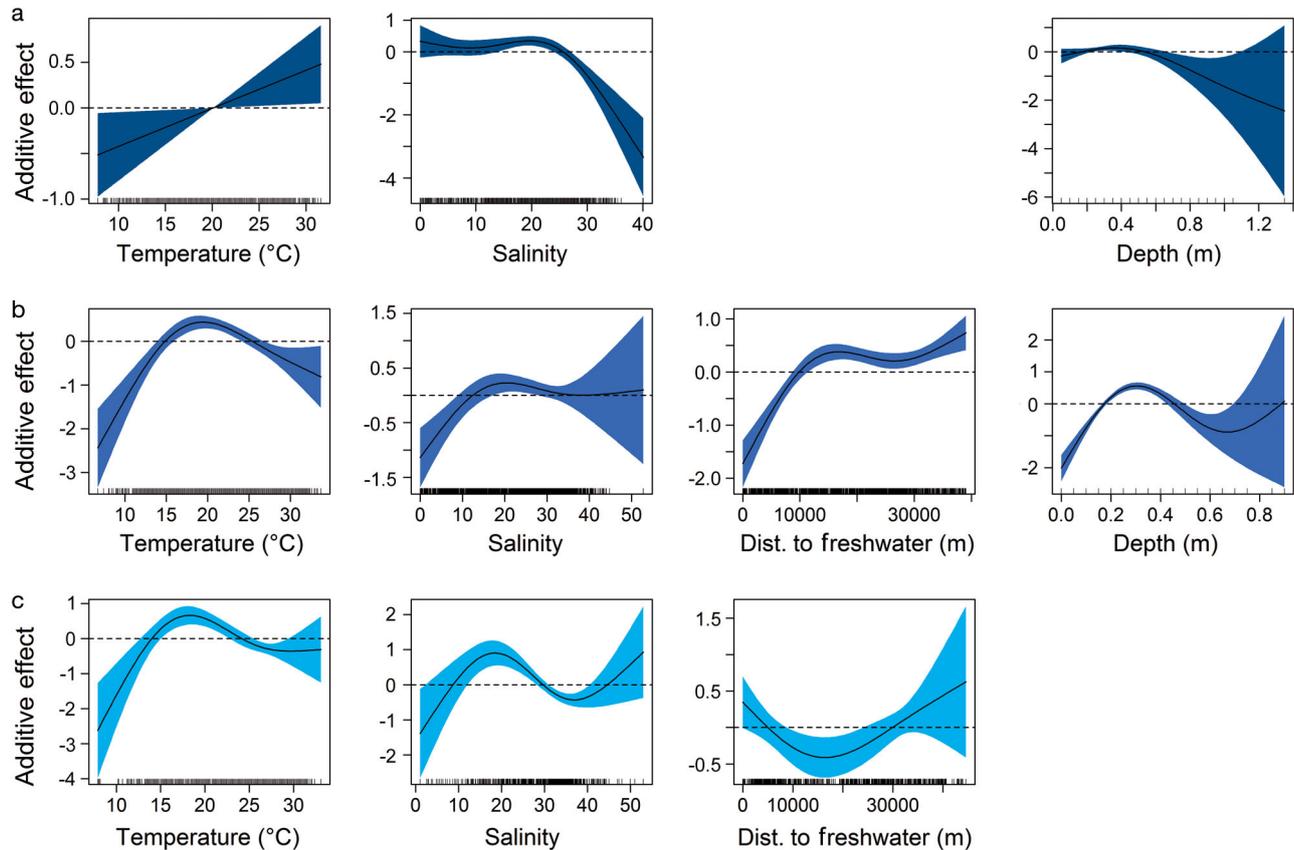


Fig. 4. Response plots showing the influence of retained abiotic variables on the abundance of post-settlement red drum in (a) Galveston Bay, (b) Aransas-Corpus Bay, and (c) Laguna Madre from final generalized additive models. Variables shown include temperature, salinity, distance to freshwater, and depth. Solid lines represent smoothed values, and shaded areas represent 95% confidence intervals

( $\Delta DE = 11.2\%$ ), salinity (2.9%), temperature (2.8%), and seagrass coverage (1.9%). Response plots from the final GAM indicated that early juvenile red drum in Aransas-Corpus Bay were most abundant in areas far from freshwater sources (>25 km) with low to moderate seagrass coverage (10 to 40% cover) and moderate to high salt marsh coverage (30 to 75% cover) relative to other areas surveyed (Figs. 6 & 7). CPUE of early juvenile red drum was also positively related to salinity, temperature, and areal coverage of mangrove habitat, with higher abundance at temperatures >15°C and salinities >29. In addition, early juvenile red drum abundance was negatively related to areal coverage of oyster reef habitat.

The most influential variables in the final model ( $DE = 61.0\%$ ) for early juvenile red drum in Laguna Madre (based on  $\Delta AIC$ ) included year ( $\Delta AIC = 413.6$ ), depth (153.8), seagrass coverage (76.4), month (53.4), salt marsh coverage (32.8), and salinity (29.9), with distance to inlet (18.7), temperature (11.7), turbidity (11.7), oyster coverage (11.6), and mangrove coverage (7.8) also contributing (Table 2). The most influ-

ential variables according to  $\Delta DE$  were similar, with the highest values observed for year ( $\Delta DE = 14.2\%$ ), depth (5%), seagrass coverage (2.4%), and salt marsh coverage (1.1%). Response plots indicated that early juvenile red drum in Laguna Madre were most abundant in shallow to moderate depths (0.2 to 0.8 m) far from tidal inlets (>15 km) (Fig. 6). CPUE was highest in areas with low seagrass coverage (<20%) and was reduced in areas of high seagrass coverage (>60%) (Fig. 7). Early juvenile abundance was greatest at temperatures between 18 and 24°C, and was positively related to salinity. In addition, abundance was negatively related to mangrove coverage, and was lower in areas with greater areal coverage of salt marsh (>20%) and oyster reef (>10%).

## DISCUSSION

Intra-annual variability in abundance of juvenile fishes is often reflective of the timing of recruitment to the nursery (Rooker et al. 1998b). Peak abundance

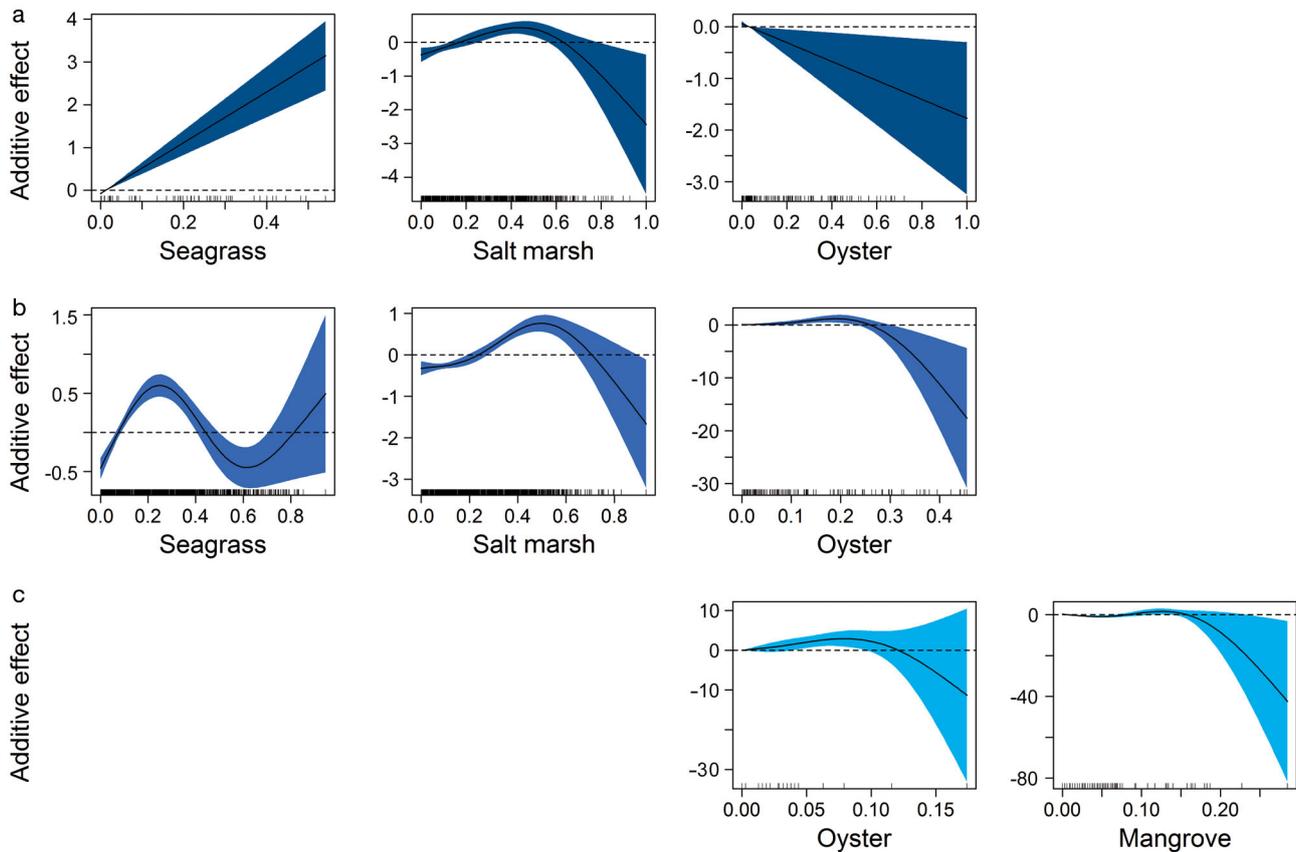


Fig. 5. Response plots showing the influence of retained biotic variables on the abundance of post-settlement red drum in (a) Galveston Bay, (b) Aransas-Corpus Bay, and (c) Laguna Madre from final generalized additive models. Variables shown include proportion of seagrass, salt marsh, oyster, and mangrove coverage within a 300 m radius of the sampling site. Solid lines represent smoothed values, and shaded areas represent 95% confidence intervals

of post-settlement red drum occurred earlier in Galveston Bay (November–December) than in the 2 southern estuaries (December), suggesting that recruitment to estuarine nurseries may be staggered from north to south along the Texas coast. Red drum spawning is temperature dependent (Wilson & Nieland 1994, Lowerre-Barbieri et al. 2008) and is estimated to occur when coastal temperatures begin to drop from 27–29° to 24–25°C, as both hatching success and larval survival is optimal at about 25°C (Holt et al. 1981, Stewart & Scharf 2008). This typically corresponds to a spawning season that can begin as early as late August and run through October (Wilson & Nieland 1994, Rooker & Holt 1997, Lowerre-Barbieri et al. 2008). Estuarine temperature varied by 1.5°C between each estuary along the latitudinal gradient during the study (lowest temperatures in Galveston Bay), suggesting that the optimal temperature range for spawning likely occurred earlier in Galveston Bay. This notion of an earlier spawning period and hence longer growing season in Galveston Bay appears to be supported by our finding that

mean length of post-settlement red drum decreased with latitude (from 48 mm in Galveston Bay to 41 mm in Laguna Madre) despite the fact that growth rates are higher in the southern estuaries (Scharf 2000). Latitudinal variation in spawning period and growth are known to occur in estuarine fishes, and this is especially common for fall spawning fishes, which may use this strategy to maximize growth prior to winter as overwinter mortality is often size selective (Conover 1992, Sogard 1997, Hurst 2007). Field experiments indicate that red drum growth decreases dramatically as temperatures decline in late fall and winter (Lanier & Scharf 2007), and therefore an earlier onset to spawning in Galveston Bay would be advantageous as it would allow for an extended growing period to maximize overwinter survival (Anderson & Scharf 2014).

Inter-annual variability in the abundance of juvenile fishes is often high in marine and estuarine systems (Fogarty et al. 1991, Myers et al. 1997), and year was among the most influential variables in models for post-settlement red drum. Similar to our results,

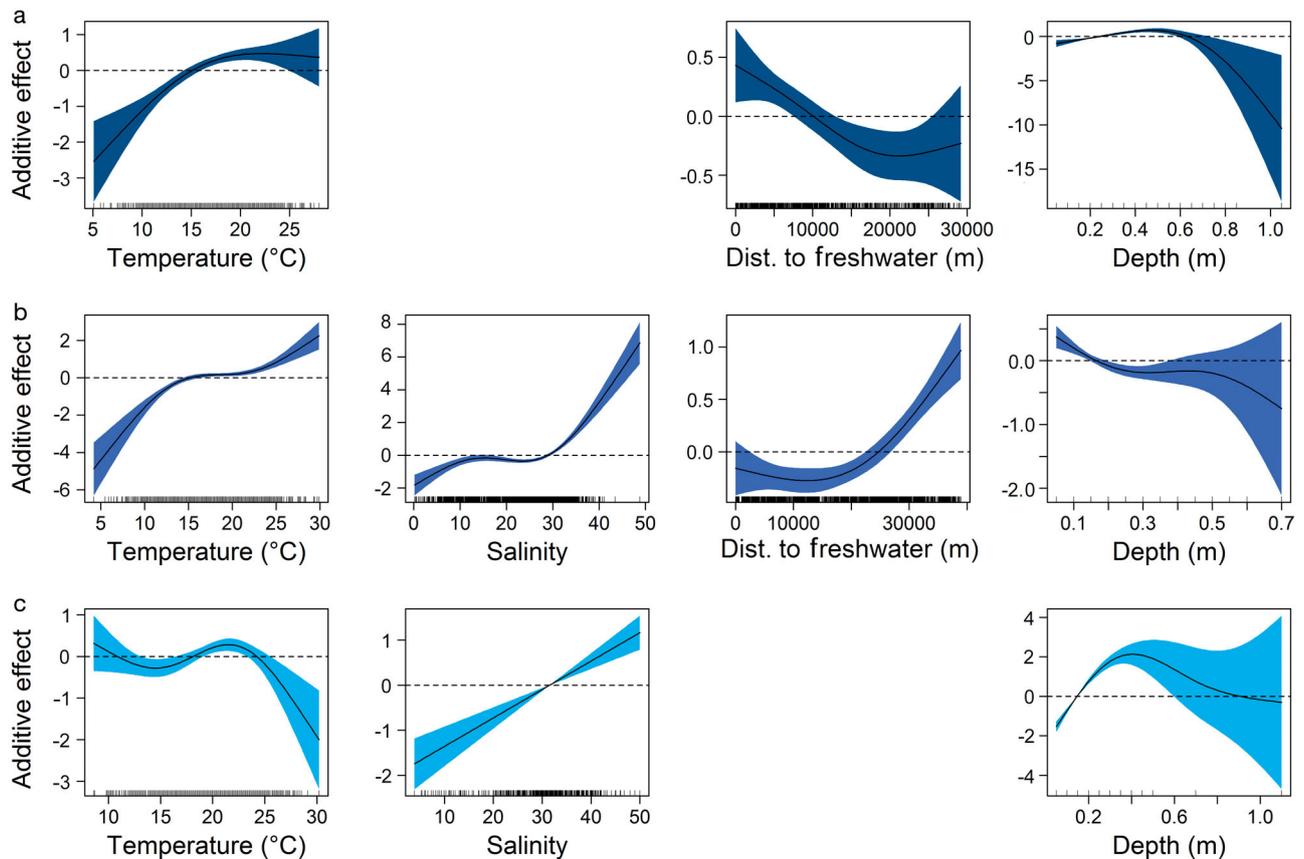


Fig. 6. Response plots showing the influence of retained abiotic variables on the abundance of early juvenile red drum in (a) Galveston Bay, (b) Aransas-Corpus Bay, and (c) Laguna Madre from final generalized additive models. Variables shown include temperature, salinity, distance to freshwater sources, and depth. Solid lines represent smoothed values, and shaded areas represent 95% confidence intervals

previous time series analyses of red drum recruitment over multi-decadal scales along the Texas coast documented high inter-annual variability in the abundance of post-settlement red drum for these estuaries (Scharf 2000). Recruitment of pelagic larvae to benthic juvenile habitat is dependent on physical factors (i.e. currents, wind, freshwater inflow) affecting larval transport into the estuary (Brown et al. 2004, 2005) as well as biotic factors such as foraging success, growth, and survival (Fuiman & Cowan 2003, Fuiman et al. 2006). While the availability of suitable juvenile habitat is likely to influence the abundance of post-settlers and early juveniles, variability in physical and biotic factors influencing larval supply is often a much stronger driver of recruitment variability (Brown et al. 2005). High inter-annual variability in red drum abundance was also observed during the early juvenile stage; however, there was little to no correlation in abundance between the 2 life stages in any of the estuaries (Dance 2016). This may indicate that the transition

between post-settlement and early juvenile stages represents an important recruitment bottleneck and that year class strength may be determined by survival through the first winter of life rather than at settlement (Hurst 2007). Overwinter mortality is known to be an important determinant of year class strength in temperate fishes (Hurst & Conover 1998) and has been suggested previously as a likely source of mortality in early juvenile red drum (Stewart & Scharf 2008, Anderson & Scharf 2014). Alternatively, high overall mean abundance of early juveniles across all 3 estuaries could indicate low overwinter mortality; however, this trend was variable across years, with higher abundance in the post-settlement stage in some years, suggesting that high overwinter mortality for early juveniles is likely episodic (Stewart & Scharf 2008).

Temperature is an important factor influencing both growth and survival of juvenile fishes (Lankford & Targett 1994, Anderson & Scharf 2014) and was retained in 5 of the 6 models (exception early juve-

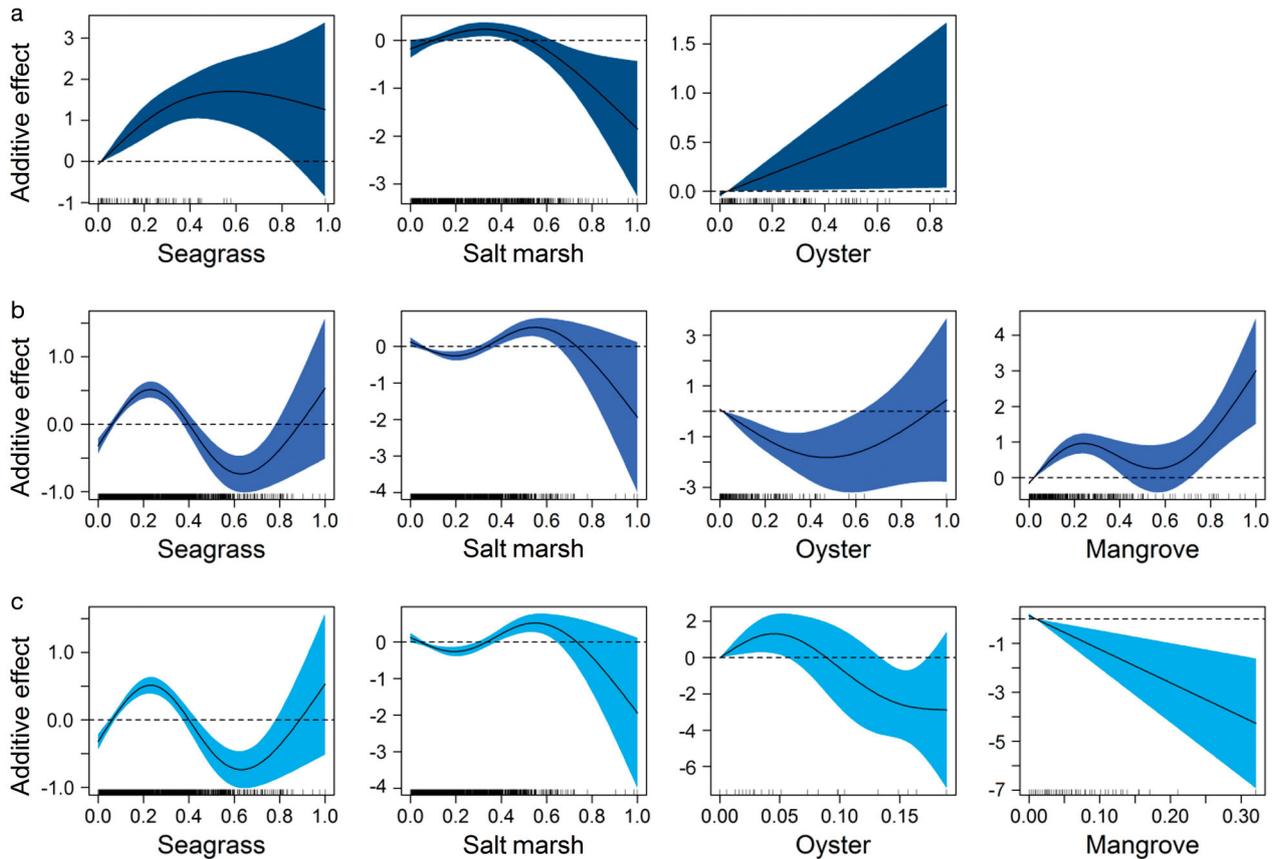


Fig. 7. Response plots showing the influence of retained biotic variables on the abundance of early juvenile red drum in (a) Galveston Bay, (b) Aransas-Corpus Bay, and (c) Laguna Madre from final generalized additive models. Variables shown include proportion of seagrass, salt marsh, oyster, and mangrove coverage within a 300 m radius of the sampling site. Solid lines represent smoothed values, and shaded areas represent 95% confidence intervals

niles in Laguna Madre). Despite differences in mean temperatures among the estuaries, similar patterns in abundance were observed across the 3 systems for each life stage, with both stages of red drum most abundant in areas of the estuaries with water temperatures between 15 and 25°C; individuals were rarely caught in areas with water temperatures <15°C. Similar to our findings, previous large-scale studies in North Carolina described a peak in abundance between 15 and 25°C for juvenile red drum in estuarine habitats (Bacheler et al. 2008), suggesting this temperature range may represent an optimal range of available water temperatures for red drum during the post-settlement and early juvenile stages. While laboratory trials indicate that the minimum cold tolerance of red drum can range from 2 to 5°C (Anderson & Scharf 2014), other studies have shown that winter growth is negligible or even negative at water temperatures <15°C (Lanier & Scharf 2007). Therefore, red drum may preferentially select habitats with water temperatures >15°C to optimize growth and

survival during fall and winter. Abundance of post-settlement red drum was higher at temperatures >25°C in Galveston Bay, which appears to reflect the aforementioned earlier onset of spawning and hence an earlier settlement period relative to the more southern estuaries. Decreased abundance of red drum at water temperatures >25°C in Aransas-Corpus Bay and Laguna Madre may be more reflective of the later timing of recruitment in these estuaries.

Salinity often influences the distribution of estuarine organisms (Kimmerer 2002), and response to salinity differed between the 2 life stages and among the 3 estuaries in the current study. Abundance of post-settlement red drum generally peaked at salinities near 20 in all 3 estuaries, but were also abundant at low to moderate salinity (0–25) in Galveston Bay. While the isosmotic salinity for red drum is between 10 and 11, this species is able to tolerate a wide range of salinities, from marine to freshwater, and field experiments with post-settlement red drum suggest

that growth is optimized at mesohaline conditions (Lanier & Scharf 2007). A similar preference for mesohaline waters during the post-settlement stage has been described for other estuarine species such as weakfish *Cynoscion regalis* (Lankford & Targett 1994) and spotted seatrout *C. nebulosus* (Kupschus 2003). Likewise, laboratory trials indicate that the metabolic costs of osmoregulation for post-settlement red drum and perhaps other estuarine-dependent sciaenids, are minimized at moderate salinities (~20), increasing the metabolic scope for growth (Wakeman & Wohlschlag 1983, Lankford & Targett 1994, Lanier & Scharf 2007). Therefore, because of the importance of fast growth in maximizing size prior to winter (Sogard 1997), it may be advantageous for post-settlement fishes such as red drum to recruit to mesohaline nurseries to optimize growth potential. Conversely, the abundance of early juvenile red drum was positively related to salinity in both Aransas-Corpus Bay and Laguna Madre, with high abundances occurring at near marine salinities (30+). These 2 estuaries receive very little freshwater input relative to Galveston Bay, and Laguna Madre is considered a negative estuary (Tolan 2007); therefore, the majority of available juvenile habitat within both Aransas-Corpus Bay and Laguna Madre occurs in higher salinity waters, which could explain the increase in abundance with salinity.

Estuarine ecosystems are uniquely affected by both marine and freshwater inputs, and thus proximity to tidal passes and/or freshwater sources can additionally influence the value of nursery habitats (Froeschke et al. 2010, Furey & Rooker 2013, Whaley et al. 2016). Because adult red drum are known to spawn in coastal waters, it might be expected that the abundance of post-settlement and even early juvenile red drum would be higher in areas near tidal inlets where larvae first enter the estuary; however, our models indicated that red drum abundance at both life stages was either unrelated to proximity to tidal inlets or increased with greater distance from tidal inlets, a finding supported by previous studies in the eastern Gulf of Mexico (Whaley et al. 2007, 2016). Distance to freshwater sources was retained in 4 of the 6 models, suggesting that proximity to freshwater inflow was a more useful predictor of red drum abundance at both life stages. Abundance of post-settlers in Laguna Madre and early juveniles in Galveston Bay were greater near freshwater sources, which is in agreement with previous studies in the eastern Gulf of Mexico linking increased abundance of juvenile red drum to freshwater inflow (Whaley et al. 2016). In contrast, both life stages were generally

less abundant near freshwater sources in Aransas-Corpus Bay. This discrepancy may be a function of the distribution of complex benthic habitat in Aransas-Corpus Bay, which was most abundant in the lower to mid-estuary, but may also be reflective of estuary-specific differences in freshwater inflow among the 3 systems (Tolan 2007).

Seagrass coverage was among the most important predictors of red drum abundance in our models; however, the relationship between seagrass coverage and red drum abundance was estuary-specific. This is not surprising given that the availability of seagrass varies along a latitudinal gradient on the Texas coast. Seagrass coverage is limited in Galveston Bay, but increases from north to south by greater than 3 orders of magnitude from Galveston Bay to Laguna Madre. In the current study, we found that red drum abundance was associated with greater seagrass coverage in Galveston Bay, moderate coverage in Aransas-Corpus Bay, and lower coverage in Laguna Madre. The observed differences may be reflective of the preference for seagrass edge habitats by juvenile red drum, as ecotones at the edges of seagrass beds often provide greater foraging opportunities while still affording protection from predators (Holt et al. 1983, Bologna & Heck 2002). Previous research has shown that abundance of a variety of juvenile fishes and invertebrates (e.g. amphipods, polychaetes, scallops) is typically higher near the edge of seagrass beds relative to the interior (Holt et al. 1983, Bologna & Heck 1999, 2002, Moore & Hovel 2010), a notion that is also supported by recent telemetry studies with juvenile red drum (Dance & Rooker 2015). Therefore, in estuaries where seagrass is ubiquitous and present in large continuous stands such as in Laguna Madre, areas with reduced seagrass coverage may provide more edge habitat preferred by red drum. Conversely, our finding that juvenile red drum abundance increased with coverage of seagrass in Galveston Bay, suggests that the influence of seagrass on red drum distribution is likely stronger in estuaries where the areal coverage of seagrass is limited.

In addition to seagrass, other estuarine habitats such as salt marsh, oyster reef, and mangrove are frequently cited as important early life habitats for juvenile fishes and invertebrates (Stunz et al. 2002a, Minello et al. 2003, Mumby et al. 2004). Salt marsh coverage was retained in 5 of the 6 final models, and red drum abundance at both life stages was generally higher in areas with low to moderate coverage of salt marsh habitat. In temperate and subtropical regions, salt marshes are known to serve as nursery habitats

for fishes and invertebrates (Minello et al. 2003), and previous studies suggest that salt marshes act as an alternative habitat for juvenile fishes (e.g. red drum, spotted seatrout, pinfish *Lagodon rhomboides*) when seagrass coverage is limited (Stunz & Minello 2001, Stunz et al. 2002b, Minello et al. 2003). Fish abundance is known to be highest in areas within 1 m of the salt marsh edge relative to the marsh interior (Minello et al. 2003), and thus lower abundance of red drum observed here at collection sites with high marsh coverage is likely due the fact that these areas were comprised of less edge habitat or heterogeneity. In contrast, areas of moderate salt marsh coverage corresponded to areas with greater marsh edge that is more suitable for juvenile red drum. Moreover, the finding that red drum were more abundant in areas of low to moderate coverage of both seagrass and salt marsh in Aransas-Corpus Bay and Laguna Madre suggests that areas containing mixtures of habitat types (i.e. seagrass adjacent to salt marsh) may enhance nursery habitat value (Levin & Stunz 2005, Baillie et al. 2015). Oyster reef coverage was retained in all models, but was not among the most important variables in any, as post-settlement and early juvenile red drum abundance was generally higher in areas where oyster reef habitat was absent or less prevalent. Similar findings have been described for estuarine fishes in other studies (Stunz et al. 2002a, Geraldini et al. 2009, Furey & Rooker 2013), and it may be that oyster reefs do not offer comparable forage resources to those found in submerged aquatic vegetation, as growth of juvenile red drum inhabiting oyster reefs is often reduced relative to seagrass and salt marsh (Stunz et al. 2002b). Oyster reefs also hold high densities of larger estuarine predators (Robillard et al. 2010), which may increase predation risk and reduce the nursery value of this habitat. In recent years, mangrove habitats have expanded northward along the Texas coast, and have become increasingly prevalent in Laguna Madre and Aransas-Corpus Bay (Armitage et al. 2015). In the current study, abundance of early juvenile red drum was greater in areas with mangrove coverage in Aransas-Corpus Bay, while abundance at both life stages were typically reduced in areas with higher mangrove coverage in Laguna Madre. Relatively little is known about the effects of mangrove expansion on the distribution and abundance of estuarine fauna in the Gulf of Mexico, and it is possible that the reduced use of mangroves in Laguna Madre could be related to competition from tropical fauna that are typically associated with mangroves (Gericke et al. 2014) and are more common in Laguna Madre than the other estuarine systems to the north.

Here we show that the suitability of nursery habitats for post-settlement and early juvenile red drum is life-stage specific and regulated by complex relationships among several environmental factors. Benthic habitat structure and physicochemical conditions in the water (e.g. salinity and temperature) were the key determinants of habitat quality for both life stages, and the relative importance of each parameter was time- and estuary-specific. In response, future efforts to identify and conserve critical nursery areas of red drum and perhaps other estuarine-dependent species will require an understanding of the complexities in fish–habitat relationships and the potential for tradeoffs between parameters that define nursery habitat value in estuarine systems.

*Acknowledgements.* We thank Mark Fisher of Texas Parks & Wildlife Department for contributing catch data. We would like to thank N. Furey for discussions that improved this study. We also thank A. Armitage, J. Gold, G. Stunz, and anonymous reviewers for comments on earlier drafts that improved the quality of the manuscript.

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Editorial responsibility: Janet Ley,  
St. Petersburg, Florida, USA

Submitted: May 9, 2016; Accepted: August 17, 2016  
Proofs received from author(s): September 17, 2016