



Spatial and temporal shifts in suitable habitat of juvenile southern flounder (*Paralichthys lethostigma*)

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ABSTRACT

Factors influencing suitable habitats of juvenile southern flounder (*Paralichthys lethostigma*) within the Galveston Bay Complex (GBC), Texas, were assessed using generalized additive models (GAM). Fishery independent data collected with bag seines throughout the GBC from 1999 to 2009 were used to predict the probability of southern flounder occurrence. Binomial GAMs were used to assess presence/absence of southern flounder and models included temporal variables, benthic variables such as distance to habitats generated within a geographic information system, and physicochemical conditions of the water column. Separate models were generated for newly settled southern flounder, young-of-the-year (YOY) southern flounder observed in the summer, and YOY southern flounder observed in fall based on size and collection month. Factors affecting southern flounder occurrence changed seasonally, as did the corresponding shifts in the spatial distribution of suitable habitat. Temporal effects (year and month) were retained in all models. Physicochemical conditions (temperature, turbidity, and measures of environmental variability), and the presence of seagrass beds were influential for newly settled southern flounder. Distance to marine and/or freshwater sources were found to be important for YOY southern flounder in the summer and fall seasons. The abundance of brown shrimp was found to only influence the distribution of YOY southern flounder in the fall, when intermediate abundances of the potential prey item increased the occurrence of southern flounder. After model completion, the availability and spatial distribution of suitable habitat within the GBC was predicted using available environmental and spatial data for 2005. Spatial distributions of predicted suitable habitat stress the relative importance of West Bay during the newly settled stage and in the fall season, and Upper Bay during the summer and fall of the first year of life. These models demonstrate the potential dynamics of suitable habitats for juvenile southern flounder and provide insight into ontogenetic shifts in habitat preference during the first year of life.

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1. Introduction

Estuarine habitats support increased densities of many fish and invertebrate species, and are often considered nurseries (Beck et al., 2001; Boesch and Turner, 1984). Within estuaries, site-specific differences in benthic and physicochemical characteristics lead to variability in habitat quality, and subsequent distributions of juveniles (Beck et al., 2001). Identifying factors that influence the distribution and abundance of organisms across estuarine seascapes are needed to define nursery habitats of commercially or recreationally important species. Most studies investigating factors affecting distributions among potential nursery habitats

focus on newly settled individuals immediately after estuarine ingress when mortality is at its highest (Almany and Webster, 2006; Levin, 1991; Victor, 1986). Mortality rates of teleost fishes often remain elevated throughout the juvenile period (Able et al., 2007) and vary as a function of the estuarine habitats used (Minello et al., 2003; Rooker et al., 1998). Furthermore, habitat requirements can change during ontogeny, even within the same estuarine seascape (Grober-Dunsmore et al., 2009). In response, life-stage-specific habitat requirements are needed for the entire period of estuarine residency and, to date, few studies have attempted to simultaneously compare distributions of multiple size/age groups during the juvenile period (but see Stoner et al., 2001).

Habitat distribution models have become a common method to identify factors influencing species' occurrence and subsequently to visualize the spatial arrangement of habitats in estuarine and marine systems (Valavanis et al., 2008). Currently, a number of methods exist for generating habitat distribution models, including classification regression trees, maximum entropy approaches, general linear models, and generalized additive models. Generalized additive models (GAMs) are extensions of general linear models that allow the inclusion of both

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parametric and nonparametric effects of explanatory variables on the response (Wood, 2006; Wood and Augustin, 2002), and GAMs have been used to successfully identify factors influencing habitat requirements of a wide variety of estuarine-dependent fishes, including spotted seatrout (*Cynoscion nebulosus*) (Kupschus, 2003), winter flounder (*Paralichthys pseudoamericanus*) (Stoner et al., 2001), and juvenile Pacific cod (*Gadus macrocephalus*) (Abookire et al., 2007). More recently, GAMs have been used to identify factors influencing suitable estuarine habitats of juvenile flatfish, allowing for the generation of nursery habitat maps in order to guide habitat conservation and fisheries management (Florin et al., 2009; Zucchetto et al., 2010).

The purpose of this study was to develop habitat distribution models for characterizing the spatial occurrence of suitable habitat of juvenile southern flounder (*Paralichthys lethostigma*) across a large estuarine complex. Southern flounder is a recreationally important flatfish found in coastal waters throughout the Gulf of Mexico, and due to recent declines in population numbers (Froeschke et al., 2011), there is a renewed interest in defining essential habitats of this species, particularly during the first year of life when mortality is high and variable for fishes (Houde, 1989; Winemiller, 2005; Winemiller and Rose, 1992). It has been suggested that the coupling of biotic and abiotic factors drives the distribution of juvenile southern flounder within estuarine habitats (Burke, 1995; Fitzhugh et al., 1996). More specifically, benthic types and physicochemical conditions of the water column appear to influence the distribution and possibly growth and survival of southern flounder (Burke et al., 1991; Del Toro-Silva et al., 2008; Minello et al., 1987). Here, we used a GAM framework to examine the relative importance of temporal (seasonal and interannual), physicochemical, and benthic factors on the distribution of newly settled and young-of-the-year southern flounder. By partitioning the first year of life into discrete life history intervals, we comprehensively examine ontogenetic and seasonal changes in species-habitat relationships of southern flounder.

2. Methods

2.1. Data used in modeling

Data used in models were based on monthly fishery-independent surveys of the Galveston Bay Complex (GBC) by the Texas Parks and Wildlife Department (TPWD) from 1999 to 2009. Surveys were conducted using bag seines (18.3 m long, 1.8 m deep, 13 mm mesh in the cod end). Bag seines were pulled in shallow water habitats (2 m maximum depth) parallel to shore for a distance of approximately 15 m (Martinez-Andrade et al., 2005). Juvenile southern flounder captured in surveys were enumerated and measured for total length (TL). TPWD recorded location and numerous environmental variables, including water temperature, salinity, dissolved oxygen, sediment types present, and depth. Sediment types recorded by TPWD were simplified to presence of sand, mud, and rocks to reduce the number of explanatory variables used in modeling. Temporal variables of year and month were also retained from TPWD data. In addition, catch data for juvenile southern flounder were separated into three life stages based on size and the months of the year. First, we define the 'newly settled' life stage as individuals captured in the months December through March less than 50 mm total length (TL), which is conservative given growth rates (up to 0.76 mm/day) and hatch dates (predominantly mid December to January) observed by Glass et al. (2008) in Galveston Bay. 'YOY' southern flounder were defined as individuals 50 mm to 200 mm TL and this represents the remainder of the age-0 period well after the winter settlement event. Two YOY life stages were defined using the seasonal periods of April to July and August to November, to further examine ontogenetic and/or seasonal shifts in distribution or habitat use, which for simplicity will be referred to as summer and fall, respectively. Given that the mean size of age-0 southern flounder observed by Stunz et

al. (2000) along the Texas coast was 254 mm TL, we are confident that all individuals in the YOY category were less than one year of age. All survey locations were visualized and all spatial analyses were conducted in ArcGIS 9.3 (ESRI, Redlands CA).

Within a Geographic Information System (GIS), variables of distance to benthic habitats (marsh edge, seagrass, oyster reef) and sources of fresh and marine water (freshwater inlets and tidal inlets) were created for each bag seine sample. Marsh edges were defined from georeferenced National Wetlands Inventory maps (NWI; Cowardin et al., 1979). Marsh habitats were defined as Estuarine Intertidal Emergent Persistent vegetation within the NWI habitat classification scheme (E2EM1; Cowardin et al., 1979). Oyster reef and seagrass locations were downloaded from the National Oceanographic Atmospheric Administration National Coastal Data Development Center (NOAA NCDDC) and were originally defined by the Texas General Land Office (GLO). Distances were calculated between features with the shoreline as a barrier, using the cost-distance function within ArcGIS (ESRI, Redlands CA). In addition, monthly surface freshwater inflow values were generated by Texas Water Development Board (TWDB) hydrography models for Galveston Bay (available at http://midgewater.twdb.state.tx.us/bays_estuaries/hydrologypage.html).

Because unstable habitats may prevent fish from ever experiencing optimal conditions (Peterson, 2003), the variance of a location's physicochemical conditions was estimated and included in the modeling process. Temperature variance was defined as the variance in recorded temperatures from all surveys within the same season (newly settled season, summer, or fall) and within 1 minute (1/60 degree) of latitude and longitude. Variance in dissolved oxygen and salinity were collinear and, as a result, a metric was generated by the summation of variances in the two conditions, using the same temporal and spatial scales as temperature variance.

2.2. Model generation

To examine the factors affecting southern flounder occurrence, generalized additive models (GAMs) were employed (Hastie and Tibshirani, 1990; Wood, 2006). GAMs are a nonparametric extension of general linear models (GLM), and provide the flexibility to model non-parametric relationships that can be seen in ecology. In the case of binomial GAMs with a logit link, the equation takes the form of

$$\ln \left[\frac{1-y^*}{y^*} \right] = \beta_0 + \sum_k f_k x_k$$

Where y^* represents the predicted probability of southern flounder occurrence, β_0 equals the intercept, k equals the number of explanatory variables included in the model, f_k equals the smoothing function for the variable x_k . Penalized cubic regression splines determined the shape of nonparametric functions, with the degree of smoothing selected automatically for models and were generated within the "mgcv" library (Wood, 2006, 2008) using R 2.10 software (R Development Core Team, 2010).

Three different life stages of juvenile southern flounder were modeled: 1) newly settled, 2) YOY-summer, and 3) YOY-fall. Our season and life stage definitions resulted in a total of 2500 surveys from 2455 unique sites, with 196 surveys observing appropriately sized southern flounder (Table 1). Manual backward stepwise selection based on minimization of the Akaike information criterion (AIC; Akaike, 1974) was used to select final models. When GAMs indicated that a linear relationship was appropriate, the smoothed fit was replaced with a linear fit. Prior to model selection, collinearity was explored among abiotic variables using Spearman correlation coefficient (Spearman ρ). When the Spearman ρ between two variables > 0.5, the effect of each variable on southern flounder occurrence was examined alone within a separate GAM. The variable that indicated better model

Table 1

Summary of data used and mean and standard deviation (SD) of explanatory variables evaluated with GAMs to examine habitat-species relationships for juvenile southern flounder. *Prevalence is based on *a priori* size limits for each life stage as described in Methods.

	Newly settled		YOY-Summer		YOY-Fall	
	Mean	SD	Mean	SD	Mean	SD
number of surveys	865		872		863	
flounder prevalence*	0.09		0.08		0.03	
Temperature (°C)	16.3	4.1	27.9	3.7	26.3	5.2
Salinity (PSU)	16.0	8.8	16.6	9.1	17.9	9.5
Depth (m)	0.4	0.2	0.6	0.3	0.6	0.3
Turbidity (NTU)	39.9	57.6	41.2	55.9	30.2	35.1
dissolved oxygen (ppm)	7.9	1.8	6.1	1.4	6.2	1.7
distance to fresh water (m)	15,193	10,096	14,931	9,830	14,472	9,740
distance to seagrass (m)	13,381	11,724	13,459	11,527	13,155	11,475
distance to tidal inlet (m)	17,874	14,308	17,371	13,706	17,996	13,960
distance to marsh (m)	635	1,174	629	1102	680	1,176
distance to oyster reef (m)	3097	3773	2842	3506	3015	3700
Flow	1,112,625	876,151	1,164,364	965,230	1,021,328	790,498
% mud	76.3		77.3		76.5	
% sand	76.1		77.2		76.6	
% rock	3.9		5.1		3.7	

fit was entered in the initial model prior to backwards selection, while the other variable was discarded (Guisan and Thuiller, 2005).

To prevent overfitting, the gamma parameter was set to 1.4 in all models, as suggested in Wood (2006), and each explanatory variable was given a maximum of number of degrees of freedom (*df*) as suggested in Ciannelli et al. (2008). As the number of *df* increases for each predictor, flexibility increases, as well as the probability of overfitting. The maximum number *df* is decided *a priori*, but the actual limit used varies among studies. Many studies employ a limit of 4 *df* per explanatory variable (Lehmann et al., 2002; Weber and McClatchie, 2010; Zucchetto et al., 2010, and others), but Sandman et al. (2008) suggest a maximum number of degrees of freedom of 2 or 3. Sandman et al. (2008) demonstrated that within model fit generally increases with increasing GAM flexibility, but fit to validation data often decreases simultaneously (indicating a lack of transferability or predictive capabilities).

To examine the effects of varying model complexity, three initial models of increasing complexity (2, 3, or 4 *df* for each continuous explanatory variable) were examined with backward selection for each life stage of interest. After these three models were reduced via backward selection, a final model for each life stage was selected based on model fit to validation data (as described later in 2.3 Model Calibration/Validation). Within-model performance was evaluated by percent deviance explained, AIC, and Area Under the Receiver Operating Characteristic Curve (AUC). AUC values are threshold-independent and range from 0 to 1, and depict a model's ability to determine occurrence or absence at a given site. A value of 0.5 indicates no predictive capability and a value of 1 indicates perfect predictive capability. Within model AUC values were calculated using the ROCR package in R (Sing et al., 2009).

2.3. Model calibration/validation

To evaluate the predictive abilities of GAMs, TPWD data from 1999 to 2009 were randomly split into training and validation datasets, with each dataset having equal number of surveys. Variable selection

for GAMs was conducted using the training data, and the response functions of retained explanatory variables for each life stage were then used to predict responses within the evaluation dataset. Model fits to validation datasets were evaluated by calculating AUC, sensitivity (the proportion of occurrences correctly predicted), and specificity (the proportion of absences correctly predicted) based on the threshold ρ_{fair} , at which the difference between sensitivity and specificity is minimized (Jensen et al. 2005; Jiménez-Valverde and Lobo, 2007). AUC, sensitivity, and specificity, along with corresponding thresholds, were calculated in the “PresenceAbsence” library (Freeman, 2007). From the three models (with 2, 3, or 4 maximum *df* per explanatory variable) for each life stage, sensitivity, specificity, and validation-AUC were compared to choose an optimal model for visualizing the spatial distribution of suitable habitats. Similar to Sandman et al. (2008), models with a maximum of 2 or 3 *df* resulted in the best fit for validation data (Table 2), with the final newly settled and YOY-fall models utilizing a maximum of 2 *df* and the final YOY-summer model utilizing a maximum of 3 *df*.

2.4. Habitat mapping and visualization

After optimal models were selected for each life stage, GAMs were used to predict the probability of southern flounder occurrence across the GBC to visualize habitat suitability. Surfaces of 500 m² resolution were generated for all areas of the GBC less than or equal to 2 m in depth using bathymetry data from NOAA hydrographic sounding surveys (Taylor et al., 2008). This resolution was selected to investigate medium-scale changes in predicted suitability, while preventing misuse of data collected at spatial scales of resolution coarser than the distance between TPWD survey locations. For all locations, distances to benthic habitats and sources of fresh and marine water were calculated. Dissolved oxygen and turbidity were interpolated throughout the GBC using inverse distance weighting from TPWD survey data for each season in 2005. Temperatures were calculated by averaging images derived from blended multiproduct sea surface temperature (SST) data downloaded from the NOAA CoastWatch Live Access Server (Feldman and McClain, 2012; Ocean Watch, 2011). Gaps in SST data were removed via interpolation within the Spatial Analyst Toolbox in ArcGIS (ESRI, Redlands CA). Salinity values were based on monthly bay-wide contours generated by TWDB TxBLEND hydrography models (Longley, 1994). After all explanatory variables were linked to the prediction grids, the “predict.gam” function in the “mgcv” library (Wood, 2006, 2008) was used to predict the probability of southern flounder occurrence given the seasonal conditions of 2005. Once each grid point contained a predicted value, suitable habitats were visualized as raster surfaces with a pixel size of 500 m².

Table 2

Comparison of fit among models for each season or life stage based on model flexibility (Max *df*). Values in bold indicate the model with best fit to validation data, and thus selected as the final model for the respective life stage/season for use in habitat visualization. Sensitivity and specificity values were calculated based on an optimized threshold, ρ_{fair} , as described in Methods.

Life stage	Newly settled		Young-of-the-year						
	Season		Summer			Fall			
<i>Within model measures of fit</i>									
<i>df</i>	2	3	4	2	3	4	2	3	4
% Dev Explained	40%	42.3%	53.9%	23.4%	27.0%	33.1%	28.6%	42.7%	33.9%
Within Model AUC	0.92	0.93	0.96	0.81	0.84	0.87	0.92	0.96	0.92
<i>Validation measures of fit</i>									
Validation AUC	0.81	0.8	0.78	0.65	0.68	0.67	0.71	0.65	0.62
ρ_{fair}	0.05	0.05	0.05	0.06	0.07	0.07	0.01	0.01	0.01
Sensitivity	0.76	0.68	0.73	0.67	0.63	0.63	0.69	0.54	0.54
Specificity	0.72	0.71	0.66	0.57	0.64	0.62	0.65	0.71	0.67

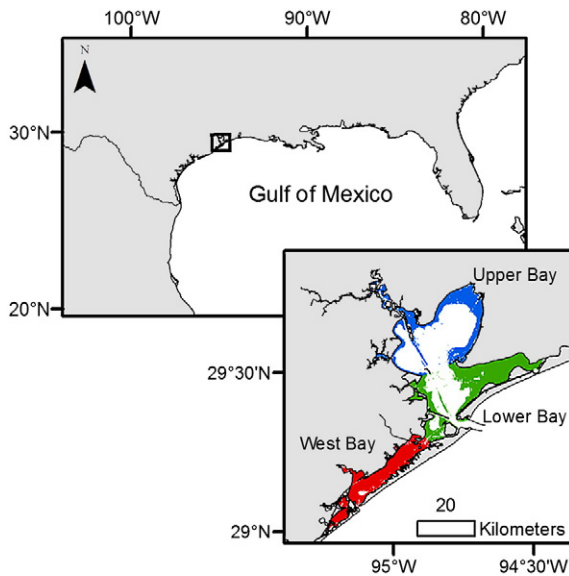


Fig. 1. Galveston Bay Complex (GBC) location within the Gulf of Mexico. Shaded portions denote waters less than 2 m depth, and are separated into three regions for analysis of the spatial distribution of suitable habitats.

The highest 10% of predicted values were labeled as being within of one of three geographic regions of the GBC: Upper Bay, Lower Bay, or West Bay (Fig. 1). Areas of highly suitable habitats within each region were divided by the amount of available habitat (less than 2 m depth) within the same region to provide the proportion of the region that was considered to be highly suitable habitat in 2005.

3. Results

The number of explanatory variables retained within the three final models ranged between five and seven (Fig. 2). Relationships between the presence of mud, presence of sand, and monthly freshwater inflow with both temporal variables (year and month) were found to be collinear (Spearman $\rho > 0.5$). Therefore, only one variable from each pair was allowed to enter the initial models prior to stepwise selection. Only two variables (month and year) were retained in all three final models, while six variables (depth, DO, presence of mud, presence of sand, monthly flow, and distance to marsh) were never retained in any of the final models. Each final model retained at least one variable unique from the other models.

3.1. Temporal effects

Inter-annual variability in the occurrence of southern flounder was detected and the year variable was retained in all models. In general, the occurrence of southern flounder declined throughout the study period for all life stages. Month was also retained in all final models, suggesting that occurrence also varied as a function of season (intra-annual effect). The newly settled model indicated a progressive increase in southern flounder occurrence throughout the season, with occurrence being lowest in December. For the YOY-summer and YOY-fall models, southern flounder occurrence decreased throughout each life stage.

3.2. Benthic effects

Among benthic effects, only distance to seagrass was retained in the newly settled model, and southern flounder occurrence increased at sites near seagrass. In the YOY-summer model, the variable distance to oyster reefs was retained, with areas less than 2 km from oyster reefs having reduced southern flounder occurrence. Within

the YOY-fall model, distance to seagrass was retained, with occurrence peaking at intermediate distances (between approximately 5 and 25 km). In addition, brown shrimp abundance was retained in the YOY-fall model. Southern flounder occurrence increased at sites with intermediate abundances of the decapod.

3.3. Physicochemical effects

For the newly settled life stage, both temperature and turbidity maintained positive relationships with southern flounder occurrence. Temperatures greater than 16 °C and turbidities of greater than 40 NTU resulted in an increased probability of southern flounder occurrence. Within the YOY-fall model, salinity was retained, and southern flounder occurrence increased in regions of the GBC with higher salinities (above 20 ppt).

Both measures of physicochemical variance (temperature variance and abiotic variance) maintained a negative association with southern flounder occurrence in the newly settled model. Abiotic variance was also retained in the YOY-summer model, with decreased southern flounder occurrence when variance was high.

Distance to freshwater sources was retained in the YOY-summer model, with southern flounder occurrence highest at locations close to (<1 km) or farther removed (>3.5 km) from a freshwater source in the summer. The YOY-fall model also indicated that southern flounder occurrence was higher near freshwater sources, with occurrence declining at distances greater than 20 km from the freshwater source. An association with sources of marine water (tidal inlets) was also observed in the YOY-fall model, and distances greater than 20 km from tidal inlets resulted in an increased occurrence.

3.4. Spatial distribution of habitat suitability

The spatial distribution of predicted suitable habitat for 2005 across the GBC varied seasonally (Fig. 3). The newly settled model predicted both a single large (>20 km²) patch and multiple smaller patches (1–9 km²) of “highly suitable” habitat within West Bay, and these habitats accounted for 29% of this bay (Fig. 3, Fig. 4). For the YOY-summer model, a large patch (51 km²) of “highly suitable” habitat was predicted near the Trinity River inlet along with a number of small patches (<5 km²) near the San Jacinto River inlet within the Upper Bay. A large area of contiguous patches (43 km²) of “highly suitable” habitats by the San Jacinto River inlet in Upper Bay was also predicted by the YOY-fall model in addition to a patch of 18 km² in West Bay. Thirty percent of West Bay contained “highly suitable” habitat for the YOY-summer life stage of 2005, while these habitats were found in 19% of West Bay for the YOY-fall life stage. Predicted suitability was relatively low in the Lower Bay during all three seasons, with only 4% of this bay containing highly suitable habitat in February 2005, and both YOY life stages containing even less (Fig. 3, Fig. 4).

3.5. Final model fit and validation

Within-model fit, measured by AUC, was greater than 0.83 for all models (Table 2). Final models for southern flounder maximized validation AUC values, and the three models explained between 27.0% and 40.0% of residual deviance. Model fit to validation data were slightly lower, with a validation AUC values of 0.81, 0.68, and 0.71 for the newly settled, YOY-fall, and YOY-summer models, respectively. Sensitivity (percent of occurrences correctly predicted) ranged between 0.63 and 0.76, and specificity (percent of absences correctly predicted) ranged between 0.64 and 0.72. All measures of fit to validation data (validation AUC, sensitivity, and specificity) were highest for the newly settled model, and lowest for the YOY-summer model.

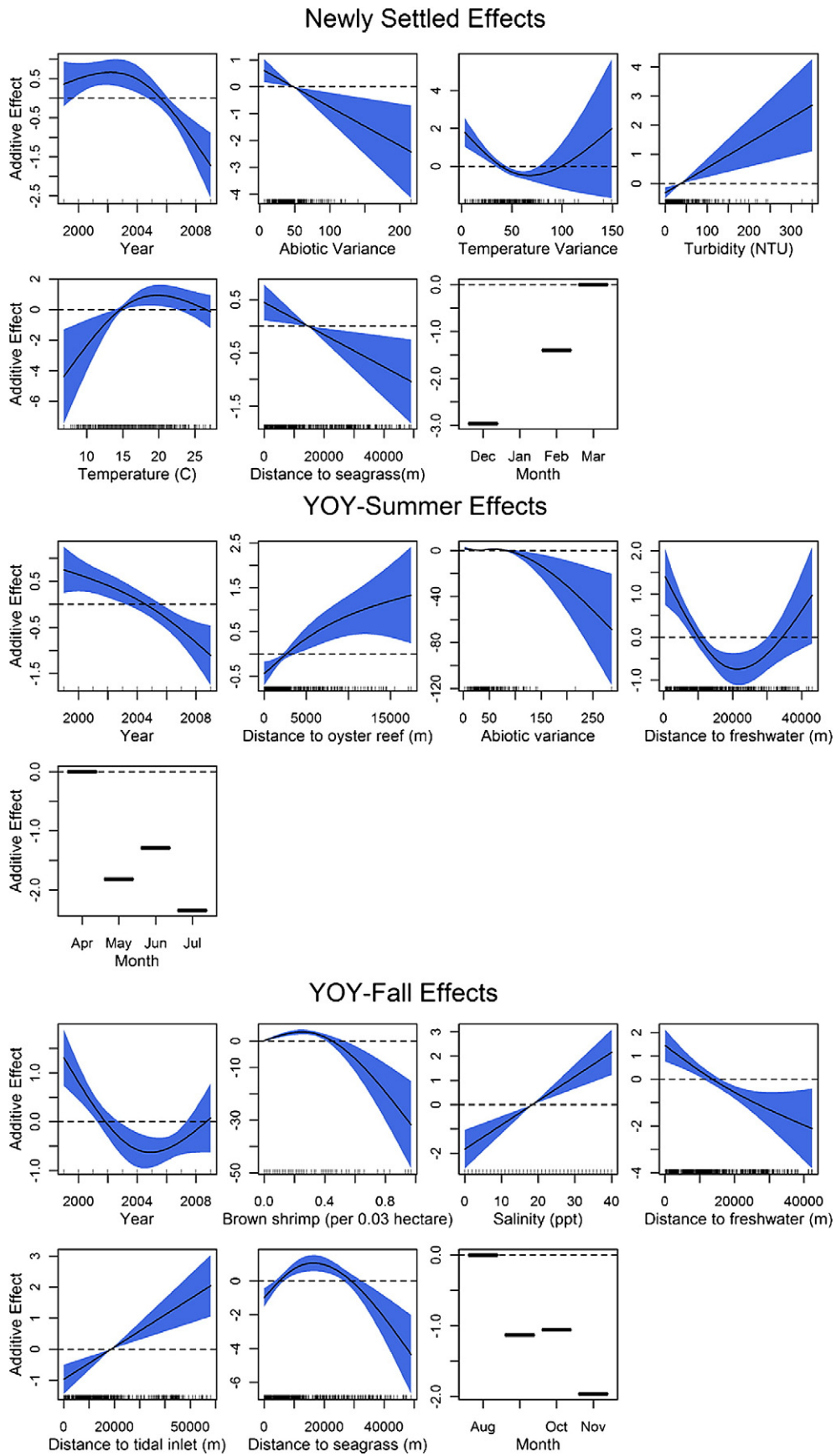


Fig. 2. Response curves of the relationships among explanatory variables and juvenile southern flounder occurrence for each life stage as generated through generalized additive models.

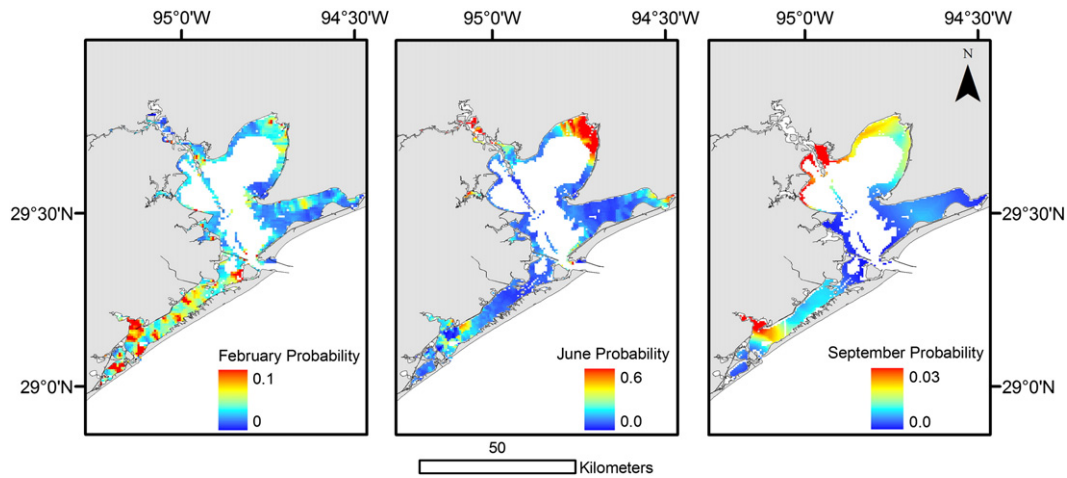


Fig. 3. Spatial distribution of predicted habitat suitability for juvenile southern flounder across the Galveston Bay Complex (GBC) in February, June, and September of 2005, corresponding to models generated for the newly settled, YOY-summer, and YOY-fall life stages, respectively.

4. Discussion

The occurrence of juvenile southern flounder in the large estuarine seascape of the GBC varied both within and across years and both temporal variables (year and month) were retained in all three final models. Response curves indicated a relative decline in southern flounder occurrence within the GBC for all life stages, which is in accord with other studies reporting declines in the abundance of juvenile southern flounder in Texas (Froeschke et al., 2011; Nañez-James, 2009). Newly settled southern flounder increased in occurrence throughout the season, corresponding to the timing of larval influx into the estuary and subsequent winter settlement, and it appears that southern flounder are fully recruited to the estuary by the end of March. Both the YOY-summer and YOY-fall models are characterized by a general decline in southern flounder occurrence over time, which is expected due to natural mortality experienced by each cohort. Both intra- and inter-annual variations in occurrence suggest that other factors may influence the distribution and abundance of southern flounder population within the GBC. Taylor et al. (2010) found that winter winds and freshwater discharge heavily influenced recruitment variability of southern flounder in North Carolina estuaries. Although unexamined in the current study, we expect that physical processes could also influence the transport of southern flounder prior to settlement, thus influencing their distribution in

the GBC. Studies modeling transport have demonstrated strong correlations between larval fish pulses into Texas bay systems and physical processes occurring along the Texas coast, further indicating the influence of physical transport on recruitment success (Brown et al., 2004, 2005).

Specific estuarine habitats can enhance the growth and/or survival of juvenile fishes, resulting in higher abundances of newly settled and YOY individuals within these habitats (Minello et al., 2003). The distance to specific habitat types was shown to affect southern flounder occurrence within the GBC. Distance to seagrass was retained in the model for newly settled southern flounder, and occurrences were elevated near seagrass beds. Seagrass beds have been shown to support high densities of juveniles within estuaries (Heck et al., 2003) because these habitats provide shelter from predators and are often associated with elevated prey biomass (Beck et al., 2001). It appears that seagrass beds within the GBC are important habitats for newly settled southern flounder when compared to other potential nursery habitats (marsh edge or oyster reef), as was suggested by Nañez-James (2009). Distance to seagrass was also retained in the YOY-fall model; however, it appears that this habitat's importance decreases with ontogeny, even within the first year of life. Other nursery habitat types investigated included salt marshes and oyster reefs. Distance to salt marsh edge was never retained, and although salt marshes have been identified as important nursery habitat for crustaceans and fishes (Minello et al., 2003), they did not appear to influence the distribution of juvenile southern flounder within the GBC over the years investigated. Oyster reefs were only retained in one model (YOY-summer), and our finding of reduced occurrence near oyster reefs is in accord with other studies, which may be due to reductions in prey or increases in predation pressure near this habitat (Robillard et al., 2010). In addition, the availability of benthic substrates has been shown to influence habitat selection and distribution of juvenile flatfish (Ryer et al., 2004; Stoner and Abookire, 2002). Unlike other modeling analyses of flatfish habitat use (Florin et al., 2009; Loots et al., 2010; Simpson and Walsh, 2004; Zucchetto et al., 2010), our models did not retain sediment type variables. This may be due to the quality of data used because all sediment types were binomially represented without mention of a dominant sediment type or percent composition.

Southern flounder are a predominant predator of brown shrimp, a benthic crustacean, in Galveston Bay from March through September (Minello et al., 1989). Abundance of brown shrimp was only retained in the YOY-fall model, in which intermediate abundances of brown shrimp increased the occurrence of southern flounder. Although high densities of brown shrimp did not result in increased southern flounder

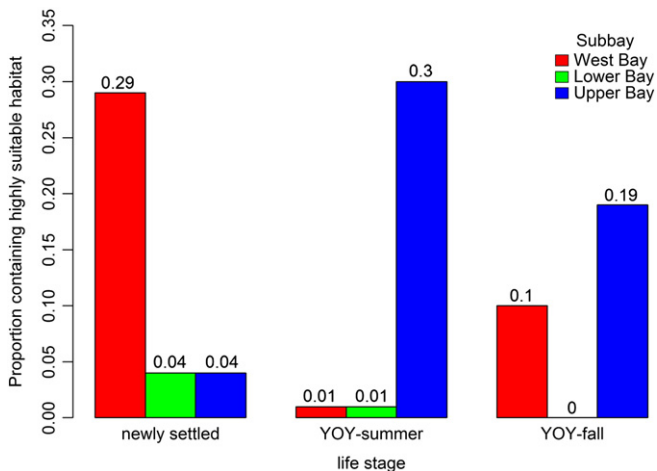


Fig. 4. The proportion of each region within the Galveston Bay Complex (GBC) that contains highly suitable habitat (top 10% of predicted values per life stage).

occurrence, increased use of marsh edge and seagrass habitats by brown shrimp in the fall (Clark et al., 2004) may allow for some separation in the distribution of the two species within the GBC. Brown shrimp abundance was not retained in the newly settled or YOY-summer models, and this is likely due to the fact that southern flounder in these life stages are too small to utilize brown shrimp as a prey resource, as indicated by stomach content analyses (Kamermans et al., 1995).

In addition to benthic conditions, physicochemical parameters such as temperature can structure estuarine fish assemblage composition (Attrill and Power, 2002), and higher temperatures in the GBC increased southern flounder occurrence during the newly settled life stage. Although juvenile southern flounder can tolerate a wide range of temperatures, with a minimum tolerance of at least 4 °C (Taylor et al., 2000), growth may be inhibited at temperatures less than 20 °C (White and Stickney, 1973), potentially explaining the negative effect of lower temperatures on the occurrence of newly settled southern flounder. Increased variability of temperature also decreased occurrence of newly settled southern flounder. Increased stability in temperature has been suggested to help facilitate recruitment of estuarine species (Drake et al., 2002). Temperature was not retained in either YOY models, and this may be due increased physiological tolerance with ontogeny or the elevated temperatures present bay-wide during the summer and fall.

Salinity is also regarded as an important environmental scalar, and it can directly or indirectly influence the distribution of suitable nursery habitat within an estuary (Secor and Rooker, 2000). Our results support this premise and GAMs indicated that salinity played an important role in determining the distribution of YOY southern flounder in the GBC. Within the YOY-fall model, occurrence of YOY southern flounder in the GBC increased at higher salinities, potentially to prepare the body for higher salinity of coastal waters that will be inhabited during the winter. This result, however, contrasts with our finding that southern flounder occurred near freshwater inlets and far from tidal inputs within the same YOY-fall model. Increased use of areas within 10 km of freshwater inlets also occurred during the preceding YOY-summer life stage. The conflicting results observed during the YOY-fall life stage between salinity and distance to water sources may represent the use of multiple habitat types during the first year of life. Starting in November and peaking in December, southern flounder aggregate at tidal passes and subsequently in coastal waters for reproduction (GSMFC–Gulf States Marine Fisheries Commission, 2000). It is therefore possible that southern flounder are utilizing areas near freshwater inlets for part of the YOY-fall life stage prior to moving into higher salinity waters to prepare for emigration out of the bay. Recent otolith microchemistry analyses also indicate that variation exists in the extent and timing of freshwater use by southern flounder within the first year of life (Lowe et al., 2011). Salinity was not retained in the newly settled model, and this may be because southern flounder are euryhaline as larvae (Deubler, 1960). Increased variability in salinity, however, reduced the occurrence of southern flounder within both the newly settled and YOY-summer models, potentially indicating the physiological costs of increased environmental variability (Aranguren-Riano et al., 2011; Death and Winterbourn, 1995).

Our observation of higher southern flounder occurrences in areas of turbidity higher than 30 NTU during the newly settled life stage suggests that these habitats may enhance the growth or survival of southern flounder. Other studies have hypothesized that turbidity levels in Gulf of Mexico estuaries may provide protection from predators for juvenile fishes (Blaber and Blaber, 1980), and other work has documented that predation is reduced in areas of moderate to high turbidity (Gregory and Levings, 1998), with little impact on foraging success on small, slow-moving prey (De Robertis et al., 2003). Increased turbidity, however, may decrease foraging success for larger, YOY southern flounder feeding on more mobile prey, and the subsequent tradeoffs between prey capture and predation risk may negate

the benefits realized by newly settled southern flounder. These tradeoffs may explain why turbidity was not retained in either the YOY-summer or YOY-fall models.

Spatial arrangement of suitable habitat predicted for GBC varied among life stages, with an increasing presence of large contiguous patches of suitable habitat being more common for older or larger southern flounder. Localized patches of suitable habitats during the newly settled life stage may be related to the increased occurrence of southern flounder at seagrass beds. Complex habitats such as seagrass can reduce predation risk by providing a visual or physical impediment between predator and prey (Rooker et al., 1998), and seagrass beds can maintain high densities of juvenile fishes (Orth et al., 1984). The decreasing localization of predicted suitable habitats with successive life stages may be attributed to a decreasing importance of using specific habitat types such as seagrass beds, increasing physiological tolerance, or ontogenetic changes in behavior. Mobility of southern flounder is expected to increase with ontogeny (body size), and the establishment of home range may occur during the first year of life, which can decrease patchiness of spatial distributions in fish in comparison to settlement stages if home ranges have little overlap among individuals (Methven et al., 2003). In addition, physiological tolerance may increase with ontogeny, as the number of physicochemical parameters retained in models decreased after the newly settled life stage. Decreased patchiness in the distribution of southern flounder may also help to explain the reduced model fit for the two YOY models in comparison the newly settled model, as the ability to generate strong species-habitat relationships is decreased for species or life stages with greater spatial ranges and greater physiological tolerances (Planque et al., 2007; Sundblad et al., 2009).

The differences in habitat suitability among West Bay, Lower Bay, and Upper Bay can be attributed to their differences in benthic habitats, physicochemical conditions, and position relative to water sources within the GBC. West Bay contains the only known remaining seagrass beds in the GBC, as the beds in Upper and Lower bays were eradicated by the 1980s due to hurricanes, dredging, and urban development (Pulich and White, 1991). These seagrass beds are predicted to provide favorable habitat to newly settled southern flounder, lending West Bay to being favorable during this life stage. Oyster reefs decreased southern flounder occurrence within the YOY-summer model, and are primarily located in West Bay and Lower Bay, resulting in these regions' low predicted suitability during this life stage. Lower Bay is also characterized by high environmental variability as predicted by spatial interpolations of TPWD data, lending the region to low predicted suitability during the newly settled and YOY-summer life stages. Upper Bay areas are a minimum of 20 km from tidal inlets, and this region has the greatest freshwater influence in the GBC, containing inlets for the Trinity and San Jacinto rivers (annual discharge rates during the study period of 13.1 m³/s and 217.8 m³/s, respectively; USGS–United States Geological Survey, 2012), and these areas represent suitable habitats for YOY-summer and YOY-fall life stages.

Due to the great distances among sub-bays (minimum 20 km between West Bay and Upper Bays), it may be infeasible for juvenile southern flounder to successfully migrate among regions between stages or seasons, especially given the locations of high quality habitats between newly settled and YOY Summer models. If southern flounder are unable to locate optimal habitats on the bay-scale, spatiotemporal connectivity among suitable patches may play great roles in determining mortality rates and subsequent year class success, as medium-scale spatial connectivity among habitats have been linked to high fishery output of adults (Meynecke et al., 2008). Furthermore, an absence of persistent suitable habitat at the sub-bay scale may generate space and age dependent bottlenecks (Lough, 2010; Ziegeweid et al., 2008), leading to high mortality rates within sub-bays at specific stages of ontogeny. The potential

for movements among sub-bays to select suitable habitats, however, increases with body size as home ranges of fishes can expand with mass or length both within (Koehn et al., 2009; Marshall et al., 2011) and across (Kramer and Chapman, 1999) species. Therefore there is a possibility of some of the changes in predicted suitability to be driven by movement rather than mortality, especially between YOY-summer and YOY-fall life stages. Although the spatial and temporal extents of available data on physicochemical conditions for the Galveston Bay complex limited our analyses, rigorous comparisons of suitable habitat distributions across spatial scales (month-to-month and year-to-year) would provide information on the importance of habitat connectivity, post-settlement processes, as well as the potential variability of habitat suitability within bay systems.

5. Conclusions

Here we show that a mix of temporal, benthic, and physicochemical characteristics influence habitat suitability of juvenile southern flounder within the GBC. Factors influencing habitat suitability changed with season and ontogeny, indicating that suitable habitats used by juvenile southern flounder are dynamic. Suitable habitats of newly settled southern flounder that arrive to the GBC in the winter are near seagrass beds with higher temperatures and increased environmental stability, while habitats of older YOY fish in the summer and fall are away from tidal inlets and near sources of fresh water. The changes in habitat requirements for juvenile southern flounder during ontogeny indicate a necessity to identify life-stage specific EFH. Habitat distribution models that incorporate a variety of dynamic and static environmental characteristics will improve our predictive capabilities and lead to more spatially resolved conservation and management of estuarine fishes and the habitats required by these species to complete their first year of life.

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