Cost-effective use of aerial imagery to quantify faunal–habitat associations across multiple spatial scales

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ABSTRACT: We investigated the utility of publicly available map products to identify faunal–habitat associations to inform fisheries management. The influence of structural and abiotic variables on the abundance of 4 focal species (red drum *Sciaenops ocellatus*, spotted seatrout *Cynoscion nebulosus*, blue crab *Callinectes sapidus*, and brown shrimp *Farfantepenaeus aztecus*) was examined at multiple spatial scales in the Mission-Aransas estuary, Texas, USA. Structural habitat data were derived from the 2004 Benthic Atlas of Texas and paired with species abundance and hydrographic data collected by the Texas Parks and Wildlife Department's Fisheries Independent Monitoring program. Blue crab and brown shrimp distributions at the ecosystem scale were driven primarily by abiotic factors such as salinity and distance to inlet, but structural habitat became relatively more important at smaller spatial scales. Variation in spotted seatrout abundance was primarily driven by seagrass and saltmarsh extent at the ecosystem scale but was driven by abiotic factors at the sub-region scale. Red drum distribution was driven primarily by abiotic factors, and association with structural habitats was bay-specific; there was no clear pattern in the influence of spatial scale on the relative importance of structural versus abiotic habitat variables for red drum. Results demonstrate that leveraging existing mapping efforts can allow fisheries managers to incorporate habitat data into fisheries management when funding or logistical challenges may otherwise prevent habitat monitoring at management-relevant scales. More research is warranted to investigate the temporal limitations to this approach, such as identifying the 'shelf life' of historical mapping products for utility in fisheries management.

KEY WORDS: Fish habitat · Habitat relationships · Spatial scale · Estuarine · Fisheries management

1. INTRODUCTION

Estuarine habitats such as seagrasses, marshes, oyster beds, and mangroves provide refuge from predation, increased food resources, and nursery habitat for the fauna that utilize them (Beck et al. 2001, Yoklavich et al. 2010). The quality and quantity of estuarine habitats can significantly affect the survivorship, growth, and recruitment of estuarine-dependent fish and invertebrates (Beck et al. 2001, Dahlgren et al. 2006, Yoklavich et al. 2010, Fonseca et al. 2015, Skern-Mauritzen et al. 2016). For example, juvenile blue crabs *Callinectes sapidus* have higher survival rates in vegetated habitats (Minello et al. 2003), and the failure to incorporate local losses of seagrass and saltmarsh, potentially affecting recruitment, in fisheries management decisions can lead to unsustainable blue crab harvest practices (Jordan et al. 2008). Similarly, mesocosm studies have shown juvenile red drum *Sciaenops ocellatus* mortality to be lower in

seagrass and other structured habitats than it is over bare or unvegetated bottom (Stunz & Minello 2001), indicating that the availability, extent, and quality of seagrass habitats can have a significant impact on red drum recruitment.

Quantifying the relationship between fish abundance and estuarine habitats can be integral to reducing variability and improving the accuracy of modeled recruitment indices and stock carrying capacity estimates (Yoklavich et al. 2010, Foley et al. 2012) as well as improving the identification and conservation of essential fish habitat (Yoklavich et al. 2010). However, the relationship between fishes and their associated habitats is complex and can vary with ontogeny and environmental conditions. For example, salinity can significantly impact selection of vegetated versus non-vegetated habitats by fish and invertebrates (Zimmerman et al. 1990) and influences the distribution of spotted seatrout *Cynoscion nebulosus* within seagrass beds (Flaherty-Walia et al. 2015). Similarly, landscape-scale patterns in habitat availability may influence the selection of vegetated habitats by facultative habitat users such as brown shrimp *Farfantepenaeus aztecus* (Clark et al. 2004, Clarkson & Beseres Pollack 2021). Unfortunately, there is a lack of paired fish–habitat data at the temporal and spatial scales necessary to capture the complexity of these relationships over space and time. This results in high levels of scientific uncertainty about habitat impacts on fish stocks, and consequently most fisheries are managed conservatively using a precautionary approach (Garcia 1994, Yoklavich et al. 2010).

While concurrent collection of *in situ* habitat data and fisheries-independent monitoring could improve managers' understanding of fish–habitat dynamics (Clarkson & Beseres Pollack 2021), *in situ* habitat sampling can have spatiotemporal limitations. *In situ* habitat data collection can be efficient when the methodology is simplified to presence/absence of habitat features at the individual site scale (Clarkson & Beseres Pollack 2021), but assessing large-scale parameters, such as areal extent of habitats, using *in situ* methods would be onerous and inefficient. The scale of observation can influence the interpretation of faunal–habitat associations (Levin 1992), and the complexity of these associations necessitates a multi-scale approach (Mellin et al. 2009) that *in situ* assessment alone cannot achieve. An additional challenge is that assessing trends in fish habitat utilization over large temporal scales requires a historic database of paired fish–habitat *in situ* sampling, which does not exist for most regions.

Remote sensing is the most commonly accepted method for obtaining habitat data at a large spatial scale to inform ecosystem-based fisheries management and improve our understanding of essential fish habitat (Zharikov et al. 2005, Valavanis et al. 2008, Chassot et al. 2011). Remotely sensed habitat map products are often used as inputs into fisheries models (e.g. Ault et al. 1999, 2005, Jordan et al. 2008) and habitat suitability models (Kupschus 2003) that help prioritize conservation and management strategies. These models are often used to describe how target species may be distributed across the mapped region based on fish–habitat associations that have been defined *a priori*. However, there is often a disparity in spatial scale between model input parameters and output parameters, as the sampling data used to determine fish–habitat associations are often collected at a much smaller scale than that of the model output (Mellin et al. 2009). Relatively fewer studies in the Gulf of Mexico have used remotely sensed map products to define fish–habitat associations at larger spatial scales (e.g. Dance & Rooker 2016), despite the availability of numerous aerial imagery and habitat mapping products (e.g. USFWS 1994, Finkbeiner et al. 2009, NOAA & USGS 2019). While remote sensing map products may be updated infrequently, there is often an abundance of historical aerial imagery sets, such as those acquired through the National Agricultural Imagery Program, that can be retroactively assessed for habitat distribution information.

Remote sensing products are likely to remain a funding priority for resource managers due to their diverse utility and application. By evaluating the utility of these map products in various approaches to fisheries-independent modeling, managers can identify how to best leverage existing mapping efforts as a low-cost complement to fisheries monitoring. In this study, we used existing map products and fisheries-independent monitoring (FIM) data to evaluate the utility of remote sensing in identifying the habitat associations of 4 focal species (red drum, spotted seatrout, blue crab, and brown shrimp) at multiple spatial scales in a Texas (USA) estuary. These focal species are recreationally, commercially, and ecologically important within the Gulf of Mexico and have exhibited habitat-dependent distributions within estuaries during their juvenile life stage primarily associated with vegetated habitats (e.g. Holt et al. 1983, Orth & van Montfrans 1987, Patillo et al. 1997, Rozas & Minello 1998, Minello & Rozas 2002, Clark et al. 2004, Neahr et al. 2010, Dance & Rooker 2016, Clarkson & Beseres Pollack 2021).

2. MATERIALS AND METHODS

2.1. Study site

The Mission-Aransas Estuary (Fig. 1) is located within the coastal bend of Texas in the northwestern Gulf of Mexico at approximately 28° N, 97° W and has a total surface area of 46 279 ha and average depth of 2 m (Armstrong 1987). Salinity varies across climatic and spatial gradients, ranging from 0 to >40, with the lowest salinities near the mouth of the Aransas River in Copano Bay (Bittler 2011). The watershed is predominantly rural and receives relatively high amounts of freshwater inflow, with a mean surface inflow of 490 000 acre-feet (~604 415 000 m^3) per year (Schoenbaechler et al. 2011); the National Wildlife Federation cites the Mission-Aransas Estuary as 1 of 2 estuaries in Texas that receive sufficient freshwater inflow to maintain a 'healthy' ecosystem (Morehead et al. 2007). At the time of the most recent comprehensive mapping survey, the estuary contained approximately 10 033 ha of seagrass, 3512 ha of saltmarsh, 1853 ha of oyster reef, and 816 ha of mangroves (Finkbeiner et al. 2009). Within the estuary, Redfish Bay is characterized as one of the most extensive areas of pristine seagrass in Texas (Texas Parks and Wildlife Department 1999).

2.2. Fisheries-independent sampling

Finfish and macroinvertebrates were sampled using bag seines (19 mm mesh in the wings, 13 mm mesh in the cod end) as part of the Texas Parks and Wildlife Department (TPWD) FIM program (Martinez-Andrade et al. 2009). Bag seines assess juvenile fish and invertebrate abundance due to the size selectivity of the gear and thus illustrate post-settlement habitat preference of juvenile fish and invertebrates. Monitoring sites were designated using a stratified random design in which 20 sampling locations were randomly selected from each bay system, each month, according to a 1 × 1 nautical mile sampling grid. During each sampling event, bag seines were extended 12.1 m from shore and pulled along emergent shoreline for a distance of 27.4 m, thus sampling an area of 0.03 ha. All collected fish and invertebrates >5 mm in length were counted, and total length measurements were recorded for 19 individuals per species, per established FIM sampling protocols. Environmental variables were collected at each sampling site and included dissolved oxygen (mg l^{-1}), salinity, water temperature (°C), and turbidity (NTU).

2.3. Habitat data

FIM samples from 2002 to 2006 were assigned habitat attributes using a spatial join to the 2004 NOAA Benthic Atlas map product (Finkbeiner et al. 2009) in ArcGIS 10.6.1 (ESRI). The Benthic Atlas was derived from aerial imagery flown in 2004 and classified using the Florida System for Classifications of Habitats in Estuarine and Marine Environments (Madley et al. 2002) with a 100 m^2 minimum mapping unit, and had 87 % deterministic accuracy (Finkbeiner et al. 2009). Targeted habitats selected for this study include seagrass (patchy and continuous), saltmarsh (typically dominated by smooth cordgrass *Sporobolus alterniflorus*), oyster reef, and mangroves. Each fisheries sampling site was classified by the presence/absence of these target habitats, as well as by the areal extent of each of these habitats within a 300 m buffer (28.3 ha, as in Dance & Rooker 2016) from the fisheries sampling location, determined using the ArcGIS Intersect Tool (Overlay Toolset).
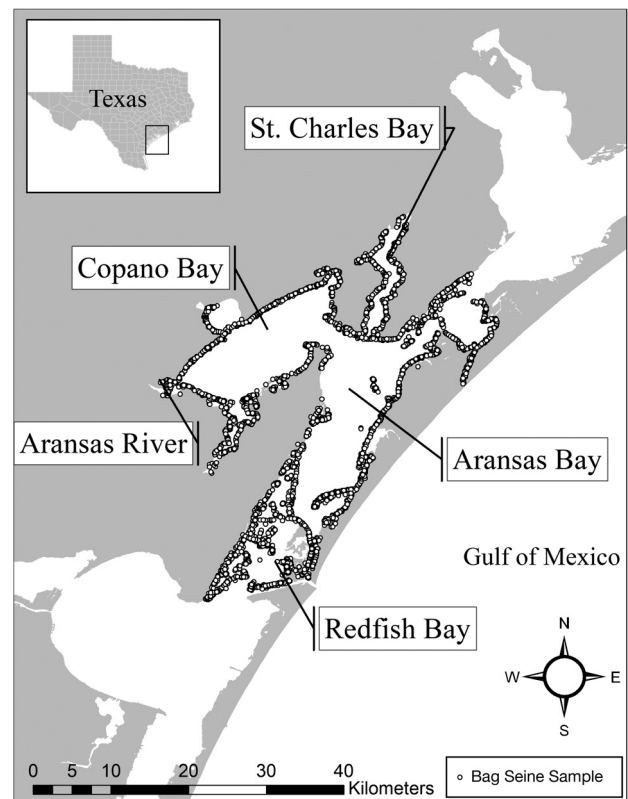

Fig. 1. Fisheries sampling site locations within the Mission-Aransas Estuary, Texas (28° N, 97° W). Each point represents a single bag seine sample. In the 5 yr study period (2002–2006), 1425 bag seine samples were collected as part of Texas Parks and Wildlife Department's Fisheries-Independent Monitoring program

Due to remote sensing limitations, such as turbidity and glare, subtidal habitats were not always visible in the aerial imagery, resulting in approximately 20 000 ha of 'unknown habitat' within the study area and the removal of these samples from the dataset. For this reason, sample size was not consistent between our analyses, but the loss of information was negligible due to the large sample size of each dataset.

2.4. Statistical analysis

Data were analyzed at 3 spatial scales (from smallest to largest: site level, sub-region, and ecosystem level). The site level scale was used to assess faunal utilization within discrete habitat classifications so that results can be comparable to other *in situ* studies that stratify faunal sampling by habitat type (e.g. Thomas et al. 1990, Clark et al. 2004, Neahr et al. 2010), and includes assessment of habitat within the 0.03 ha FIM sampling area only. Specifically, these results can be compared to those from Clarkson & Beseres Pollack (2021), who assessed the same faunal–habitat comparisons using *in situ* methods, to compare faunal–habitat associations detected through remote sensing versus *in situ* sampling. The larger-scale (ecosystem level and sub-regional level) analytical approach incorporates multiple large-scale ecological drivers to describe faunal distribution more fully across habitats and environmental conditions and includes habitat characterization within an expanded range (300 m; 23.8 ha) surrounding the TPWD FIM sampling site. In contrast to the site-level approach that can be used to compare our results to previous *in situ* efforts, the 2 larger spatial scale analyses were used to assess how the spatial scale of observation affects interpretation of faunal–habitat associations.

For the site-level analysis, the effects of habitat composition on focal species occurrence were analyzed using generalized linear mixed effects models (GLMMs) with a binomial distribution and a logit link function (R v. 3.4.3, 'lme4' package, Bates et al. 2015). Habitat composition was defined by the presence/absence of target habitat features within the FIM sampling site. Responses of focal species were assessed across the following habitat comparisons: (1) vegetated versus unvegetated shorelines; (2) mangrove-dominated versus saltmarsh-dominated shorelines; (3) seagrass presence versus seagrass absence at site; and (4) the heterogeneity of vegetated habitat (i.e. comparison between the following categories: 'no vegetation'; 'presence of emergent vegetation only'; 'presence of submerged vegetation only'; 'presence of both emergent and submerged vegetation'). Fisheries-independent data were simplified to a binomial presence–absence response variable due to zero-inflation and poor goodness-of-fit for abundance-based GLMMs, and were further truncated to include only data from months where a minimum of 1 focal organism, on average, was captured throughout the study area (Table 1) in order to satisfy goodness-of-fit tests and reduce zero-inflation. Therefore, the results of this analysis represent habitat associations that are driven by species' occurrence rather than abundance. Model fit was assessed using chi-squared goodness-of-fit tests in R (R Core Team 2015) and was determined acceptable at $\alpha > 0.05$. Because salinity may impact the occurrence of target species (Zimmerman et al. 1990) and our fisheries data spanned multiple years and varying salinity regimes, salinity was used as a blocking factor in the GLMM. Salinity was binned into 'low' (<15), 'moderate' (15–25), and 'high' (>25), and the bins correlated roughly with the 25th, 50th, and 75th percentiles of salinity distribution for the project period, respectively. To determine predictor variable significance, a likelihood

Table 1. Average abundance (no. of organisms per sample) of focal species in bag seine samples throughout the 5 yr study period, by month. Values highlighted in **bold** indicate the months that were selected as 'recruitment periods' for the site-level analysis

	Red drum	Spotted seatrout	Blue crab	Brown shrimp
January	**1.38**	0	**2.13**	0.06
February	**4.33**	0.02	**3.46**	0.15
March	**1.71**	0	**3.81**	**5.44**
April	**1.96**	0	**4.86**	**54.47**
May	**1.07**	0.2	**3.95**	**71.72**
June	0.35	0.33	**3.83**	**28.88**
July	0.19	**1.26**	**3.66**	**12.65**
August	0.06	**1.08**	**1.91**	**5.14**
September	0.04	**2**	**2.66**	**8.18**
October	0.78	**1.23**	**2.65**	**5.52**
November	**3**	**1.51**	**4.69**	**4.09**
December	**4.1**	0.3	**4.03**	0.65

ratio test was used; a null model was built in which the fixed effect predictor variable (habitat class) was removed and compared to the treatment model using ANOVA, and p-values were obtained from the ANOVA summary. For tests with more than 2 independent factor levels, a Tukey-type multiple comparisons test was conducted with a Westfall adjustment of p-values using the 'multcomp' package (Hothorn et al. 2008). Results were considered significant at p < 0.05.

For the sub-region and ecosystem-level analysis, faunal response to multiple system drivers was examined to represent large-scale trends in habitat selection. The abundance of focal species in each sample was used as a response variable. Predictor variables included areal extent of habitats within a 300 m buffer (28.3 ha) around the sampling site (see Section 2.3), distance from nearest inlet, salinity, month, and year. Distance from nearest inlet was calculated using the 'Cost Distance' function in ArcGIS (v. 10.6.1, ESRI), with emergent habitats (as classified by the NOAA Benthic Atlas) included as a cost barrier. Because the relationship between predictive and response factors was expected to be non-linear, the response of faunal abundance to these habitat parameters was modeled with a generalized additive model (GAM) with a negative binomial family, log link function, and thin plate spline (Wood 2006, R Core Team 2015). Degrees of freedom of the smooth term (k) were initially set at 10 and then reduced or increased as needed based on the 'true' order of the polynomial relationship (Wood 2006) and to optimize the model restricted maximum likelihood estimate. For final models, k ranged from 3 to 10. Model fit was evaluated using regression plots with the 'gam.check' function in the 'mgcv' library, and the 'concurvity' function in the 'mgcv' library was used to ensure that prediction factors did not co-vary (Wood 2006). A manual stepwise removal process was used to evaluate each predictor variable for significance and relative impact on the percent of deviance explained (DE) by the model (Kupschus 2003, Dance & Rooker 2016). Predictor variables were considered significant if their removal from the model resulted in an increase in Akaike's information criterion (AIC, Akaike 1974) of ≥2. Contrary to previous studies (Dance & Rooker 2016), predictor variables were retained in the final model even if 'insignificant', as long as their inclusion improved overall model AIC and DE. Using species abundance as a response variable necessitated the use of a presence-only model to satisfy goodness of fit evaluation. Presence-only models are effective with zero-inflated fisheries-independent data (Hirzel

et al. 2001, Froeschke & Froeschke 2016). Consequently, the results of this analysis represent habitat associations driven by species' abundance rather than occurrence, complementary to the site-level analysis that examines species occurrence as a response variable. While using the same response variable for both analyses would have been more consistent, response variables were selected to maximize goodness of fit tests for each modeling approach.

For the sub-region analysis, the data were subset by ecologically distinct regions to examine the effect of differing spatial scales on the interpretation of faunal–habitat associations, while the ecosystem-level analysis was completed on the entire pooled dataset and not subset by region. Redfish Bay, St. Charles Bay, and Aransas Bay (Fig. 1) were selected for the sub-region analysis to capture a spectrum of habitat composition and environmental parameters. Redfish Bay is situated directly adjacent to the main tidal inlet of the estuary (~0 to 15 km distance) and is characterized by expansive seagrass beds and mangrove-dominated shorelines. Aransas Bay lies immediately eastward of Redfish Bay (~5 to 35 km from the inlet), and is characterized by an intermediate amount of seagrasses, vegetated shorelines (salt-marsh and mangroves), and subtidal oyster reefs. St. Charles Bay is situated at a maximum distance from the inlet (~31 to 48 km) but adjacent to a minor source of freshwater inflow, contains no mangroves, and is dominated by subtidal oyster reefs, seagrasses, and a mixture of saltmarsh-dominated shorelines and clay bluff shorelines. Average salinities in the sub-bays during the sampling period were 25.5, 19.8, and 9.6 for Redfish Bay, Aransas Bay, and St. Charles Bay, respectively. Low abundance of focal species and resulting small sample size in the remaining sub-regions (i.e. Copano Bay and Mesquite Bay) precluded these areas from analysis. The results from the sub-region GAMs were compared to the ecosystem-level analysis results to examine how spatial scale of observation influences environmental drivers of faunal abundance.

3. RESULTS

3.1. Habitat and faunal composition

In total, 1455 FIM observations were made from 2002 to 2006; exclusion of sites with 'unknown habitat' truncated the overall sample size to 1403 and 1402 for shoreline and aquatic habitat analyses, respectively. Of the 1403 sampling sites at which

shoreline was characterized, 530 sites (37%) had shoreline vegetation present. The areal extent of intertidal vegetation (mangroves or saltmarsh) within 300 m of the sampling site ranged from 0 to 15 ha and averaged 2.4 ha. Of the 530 sampling sites with vegetated shorelines, 109 (20%) were dominated by mangroves and 421 (80%) were dominated by saltmarsh. The areal extent of mangroves within 300 m of the sampling site ranged from 0 to 13 ha and averaged 0.5 ha, while the areal extent of saltmarsh ranged from 0 to 15 ha, with an average of 1.9 ha. Of the 1402 sampling sites at which aquatic habitat was classified, 980 sites (70%) had seagrass present. The areal extent of seagrass within 300 m of the sampling site ranged from 0 to 25 ha and averaged 6 ha. Both submerged and emergent habitats were classified at 1392 sites. Both submerged vegetation (seagrass) and emergent vegetation (saltmarsh or mangroves) were present at 389 sites (28%). Emergent vegetation only was present at 140 sites (10%), and submerged vegetation only was present at 581 sites (42%). Neither submerged nor emergent vegetation was present at 282 sites (20%). Salinity during the study ranged from 0.1 to 36.9, with an average of 17.3.

3.2. Red drum

Red drum were present in 245 of 1455 samples. A total of 1276 red drum were captured during the study, with an average total length of 92.7 mm. At the site level, juvenile red drum occurrence was not correlated with the overall presence of shoreline vegetation (p = 0.15, Fig. 2A). Within vegetated habitats, however, juvenile red drum occurrence was higher at sites adjacent to mangroves as compared to saltmarsh (p = 0.002, Fig. 2B). Red drum occurrence was positively correlated with seagrass presence (p = 0.012, Fig. 2C) and was not influenced by vegetated habitat heterogeneity (p = 0.064, Fig. 2D).

At the sub-regional scale, juvenile red drum density was highest in Redfish Bay, followed by Aransas and St. Charles bays. Within Redfish Bay, red drum abundance was significantly explained by salinity (ΔAIC = 12.8; DE = 14%), distance to inlet (ΔAIC = 9.4; DE = 12.5%), areal extent of oyster reef (ΔAIC = 6.0; DE = 6.2%), and month (ΔAIC = 4.8; DE = 3.0%). Red drum abundance was negatively and linearly correlated with oyster reef, was highest at salinities less than 25, and was highest at distances ~13 km from the inlet in Redfish Bay. The full model for Redfish Bay (48.8% DE, Fig. 3) included significant predictors as well as saltmarsh extent. Although in-

significant, saltmarsh extent improved DE by 1.4%. Within Aransas Bay, red drum abundance was significantly explained by areal extent of saltmarsh (ΔAIC = 8.8; DE = 8.1%), salinity (ΔAIC = 4.2; DE = 10.8%), and month (ΔAIC = 3.5; DE = 11.8%). Red drum was positively and linearly correlated with saltmarsh extent and salinity in Aransas Bay. The final model (59.5% DE, Fig. 3) included significant predictors as well as distance to inlet (ΔAIC = 1.7; DE = 9.1%) and year (ΔAIC = 1.8; DE = 9.1%), as the inclusion of these 2 factors improved DE by 17.7%. Within St. Charles, red drum abundance was significantly explained by areal extent of seagrass (ΔAIC = 2.4; DE = 8.2%) and month (ΔAIC = 2.9; DE = 21.7%) only. Red drum abundance was positively and linearly correlated with seagrass extent in St. Charles Bay. The final model for St. Charles (34.7% DE, Fig. 3) included significant predictors as well as salinity (ΔAIC = 1.0; DE = 2.2%) and year (ΔAIC = 1.1; DE = 8.4%), as the inclusion of these 2 factors improved DE by 10.3%.

At the ecosystem level, variation in juvenile red drum abundance was significantly explained by year (ΔAIC = 14.2; DE = 5.1%), mangrove extent (ΔAIC = 12; DE = 5.3%), distance from inlet (ΔAIC =9.3; DE = 3.9%), saltmarsh extent (ΔAIC = 4.6, DE = 2.5%), salinity (ΔAIC = 3.6; DE = 1.3%), and month (ΔAIC = 5.9; DE = 0.6%). The full model (Fig. 4) included only significant predictors (44.6% DE); the inclusion of insignificant predictor variables did not improve model performance. Red drum abundance showed a negative relationship with distance from inlet and a non-linear relationship with habitat coverage, where abundance was highest at sites with intermediate (5 ha) extent of mangroves and slightly greater (6–8 ha) extent of saltmarsh. Red drum abundance was also non-linearly related to salinity with peak abundance occurring at salinities ranging from 20 to 25. Red drum abundance peaked in winter months (November–January).

3.3. Spotted seatrout

Spotted seatrout were present in 200 of 1455 samples, and a total of 547 spotted seatrout were captured throughout the study. The average total length of spotted seatrout was 73.5 mm. At the site level, juvenile spotted seatrout occurrence was positively correlated with shoreline vegetation presence (p < 0.001, Fig. 2A), and was higher along saltmarsh-dominated shorelines than mangrove-dominated shorelines (p = 0.02, Fig. 2B). Spotted seatrout occurrence was positively correlated with seagrass presence (p = 0.009, Fig. 2C) and was affected by vege-
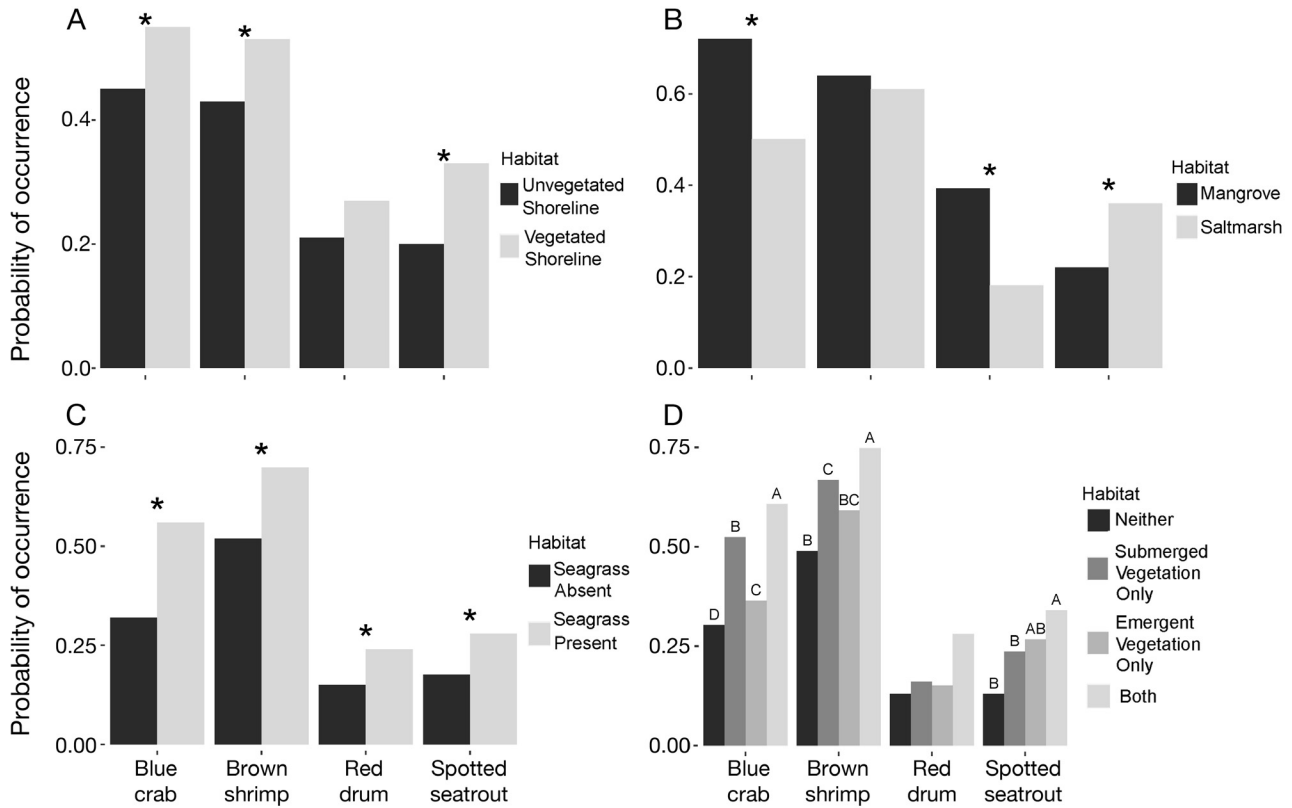
Fig. 2. Site-level model-predicted occurrence of juvenile focal species between (A) sites adjacent to unvegetated shoreline versus vegetated shoreline, (B) sites adjacent to saltmarsh versus mangrove dominated shorelines, (C) sites where seagrass was present versus absent, and (D) sites that had no vegetation, subtidal vegetation only, intertidal vegetation only, or both subtidal and intertidal vegetation. Focal species were collected with a bag seine as part of Texas Parks and Wildlife Department's Fisheries Independent Monitoring program, and habitat was determined using the NOAA Benthic Atlas map product (Finkbeiner et al. 2009). A presence/absence (binomial) generalized linear mixed effects model was used to determine significant between-habitat comparisons. Significance is indicated with an asterisk (*) in panels A–C, and with differing letters in panel D. Comparisons were only made between habitat factors for each species; differences of occurrence between species were not tested

tated habitat heterogeneity (p < 0.001, Fig. 2D). Tukey's comparisons indicated that the occurrence of spotted seatrout was higher at sites that had both submerged and emergent vegetation as compared to sites that had only submerged vegetation (p = 0.049) or no vegetation (p < 0.001). Spotted seatrout occurrence was similar at sites with both vegetation types and those with only emergent vegetation, and between sites with emergent-only and submerged-only vegetation. Sites with only emergent vegetation (p = 0.01) or only submerged vegetation (p = 0.034) had higher spotted seatrout occurrence than sites with no vegetation.

At the sub-region scale, juvenile spotted seatrout were ubiquitously distributed within the bay system. Within Redfish Bay, variation in spotted seatrout abundance was significantly explained by salinity (ΔAIC = 5.6; DE = 3.4 %) and year (ΔAIC = 4.4; DE = 11.7 %) only, with peak abundances occurring at lower salinities. The full model for Redfish Bay

(35.8 % DE, Fig. 5) included significant predictors as well as seagrass extent. Although insignificant, seagrass extent improved DE by 6.4 %. Within Aransas Bay, variation in spotted seatrout abundance was significantly explained by seagrass extent (ΔAIC = 4.9; DE = 17.2 %) and year (ΔAIC = 3.4; DE = 13.1 %) only. Spotted seatrout abundance in Aransas Bay was highest at sites with an intermediate extent (6 to 10 ha) of seagrass. The full model for Aransas Bay (43 % DE, Fig. 5) included significant predictors as well as saltmarsh extent; while saltmarsh extent was insignificant, its inclusion improved DE by 9.5 %. In St. Charles Bay, spotted seatrout abundance was significantly explained by distance to inlet (ΔAIC = 10.5; DE = 18.3 %), salinity (ΔAIC = 8.2; DE = 15.8 %), year (ΔAIC = 3.5; DE = 5.6 %), and extent of saltmarsh (ΔAIC = 2.3; DE = 1.7 %). The full model for St. Charles Bay (86.7 % DE, Fig. 5) included significant predictors as well as extent of seagrass, and month; while these factors were not individually significant,
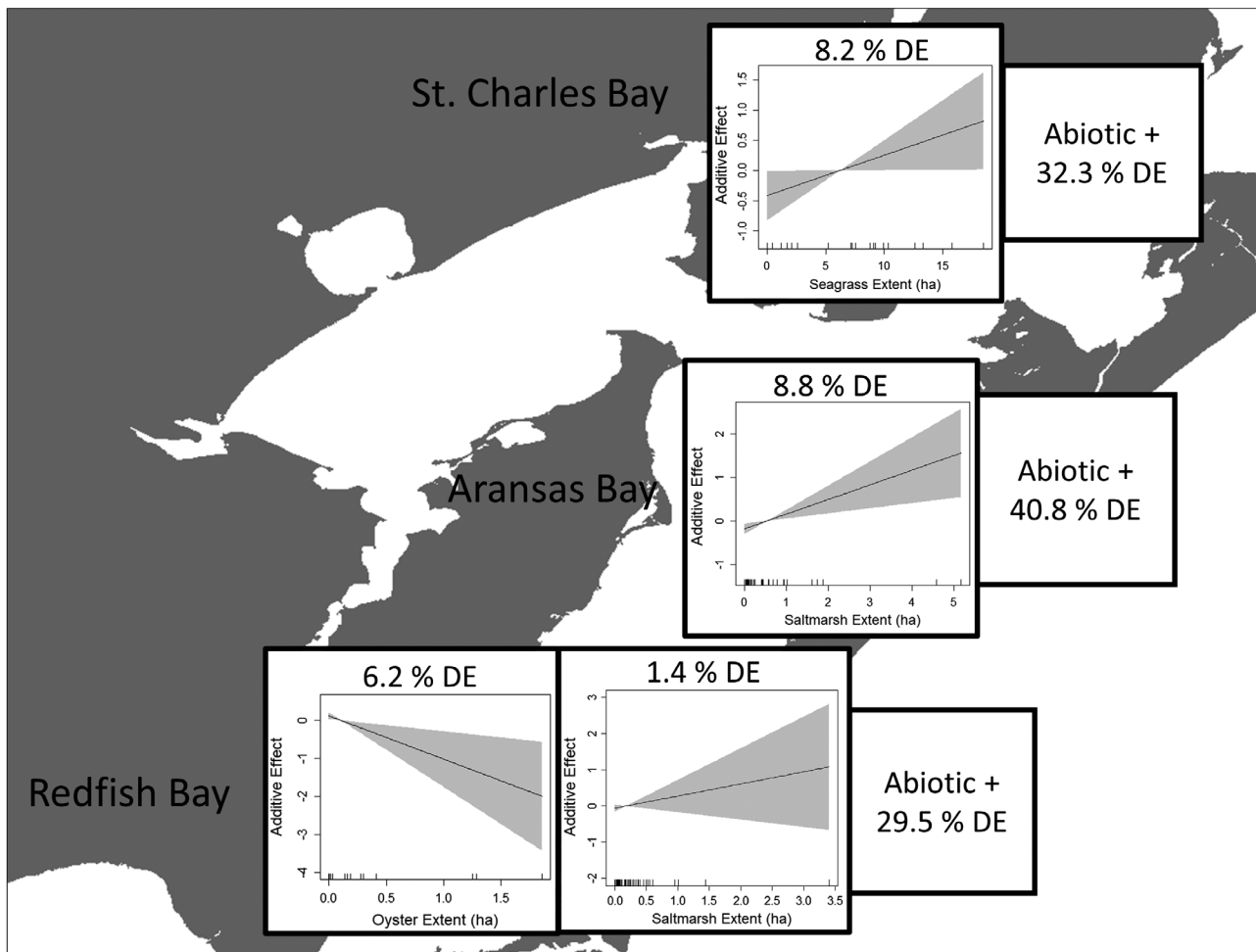
Fig. 3. Generalized additive model response plots showing influence of structural habitat model variables on the abundance of juvenile red drum at the sub-region scale in Redfish Bay, Aransas Bay, and St. Charles Bay. Spatial extent of habitats was determined within a 300 m (28.3 ha) buffer around the sampling site using habitat data from the 2004 NOAA Benthic Atlas. Shaded areas represent 95% confidence intervals around the smoothed variable response (solid line). The dashed lines (or rug plots) along the *x*-axis represent sample distribution across the range of the predictor variable. Structural habitat variables are presented in order of decreasing AIC scores. 'Abiotic +' represents the influence of all abiotic variables combined on faunal response. DE: deviance explained

they improved DE by 5.4%. Spotted seatrout abundance in St. Charles Bay was highest at sites with intermediate (6 to 10 ha) extent of saltmarsh and at greater distances from the inlet.

At the ecosystem level, variation in juvenile spotted seatrout abundance was significantly explained by areal extent of seagrass (ΔAIC = 5.7; DE = 6.1%) and areal extent of saltmarsh (ΔAIC = 4.3; DE = 3.2%) only (Fig. 6). Spotted seatrout abundance was linearly and positively correlated with saltmarsh and was highest at sites with low to intermediate (5 to 10 ha) extent of seagrass. The full model (14% DE) included significant predictors as well as mangrove extent, salinity, and distance from inlet; while these were all individually insignificant predictors, their inclusion improved DE by 3.1%.

3.4. Brown shrimp

Brown shrimp were present in 669 of 1455 samples and were the most abundant species observed during the study, with a total catch of 20 380 and an average of 14 shrimp captured per sample. The average total length of captured brown shrimp was 55.5 mm. At the site level, brown shrimp occurrence was positively related to presence of shoreline vegetation (p = 0.001, Fig. 2A) and was similar between mangrove-dominated and saltmarsh-dominated sites (Fig. 2B). Juvenile brown shrimp occurrence was positively correlated with seagrass presence (p < 0.001, Fig. 2C), and was significantly influenced by vegetated habitat heterogeneity (p < 0.001, Fig. 2D). Tukey's comparisons indicate that the occurrence of brown shrimp
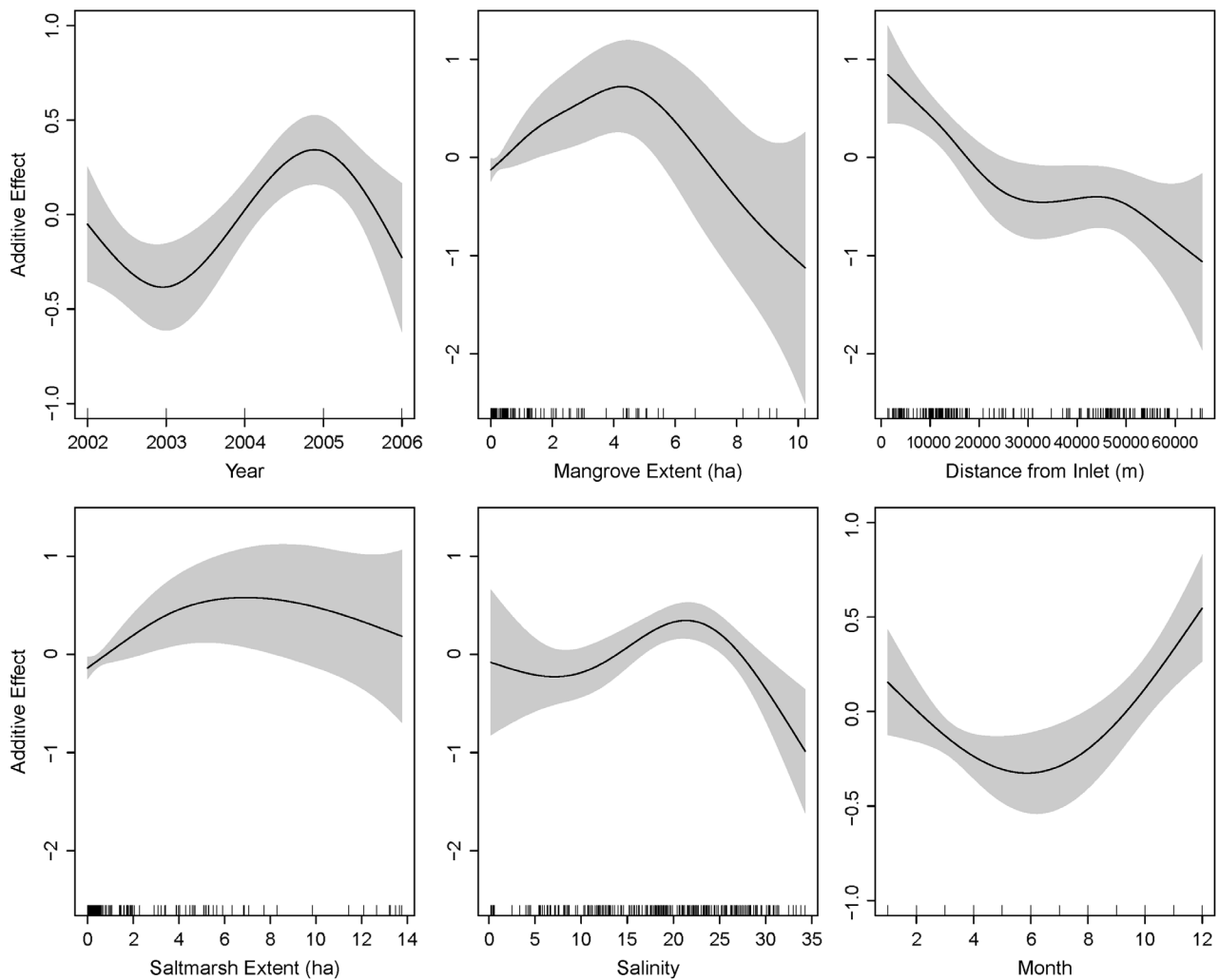
Fig. 4. Generalized additive model response plots showing influence of significant (ΔAIC > 2) model variables on the abundance of juvenile red drum at the ecosystem scale. Other details as in Fig. 3

was higher at sites that had both submerged and emergent vegetation as compared to only emergent vegetation (p = 0.005), only submerged vegetation (p = 0.042), or no vegetation (p < 0.001), and higher at sites with submerged vegetation only than at sites with no vegetation (p < 0.001). Brown shrimp occurrence was similar between sites with emergent-only and submerged-only vegetation and between sites with emergent vegetation only and no vegetation.

At the sub-region level, juvenile brown shrimp density was highest in Redfish Bay and St. Charles Bay and intermediate in Aransas Bay. Within Redfish Bay, variation in brown shrimp abundance was significantly explained by seagrass extent (ΔAIC = 14.8; DE = 9.6%), mangrove extent (ΔAIC = 23.9; DE = 3.9%), distance from inlet (ΔAIC = 6.1; DE = 5.0%), and month (ΔAIC = 96.0; DE = 35.9%). Brown shrimp abundance was highest at sites with more than 5 ha

of seagrass and increased linearly with mangrove coverage in Redfish Bay. The full model for Redfish Bay (55.7% DE, Fig. 7) included significant predictors as well as saltmarsh extent and year; while these factors were individually insignificant, they improved DE by 6.7%. Within Aransas Bay, variation in brown shrimp abundance was significantly explained by seagrass extent (ΔAIC = 3.1; DE = 2.1%), saltmarsh extent (ΔAIC = 4.0; DE = 2.4%), mangrove extent (ΔAIC = 3.0; DE = 1.4%), salinity (ΔAIC = 3.1; DE = 0.7%), distance from inlet (ΔAIC = 8.4; DE = 5.3%), and month (ΔAIC = 23.4; DE = 10.0%). Brown shrimp abundance increased linearly with coverage of each habitat type as well as with increasing salinity. The full model for Aransas Bay included only significant predictors (38.3% DE, Fig. 7); the inclusion of insignificant predictor variables did not improve model performance. Within St. Charles Bay, variation in
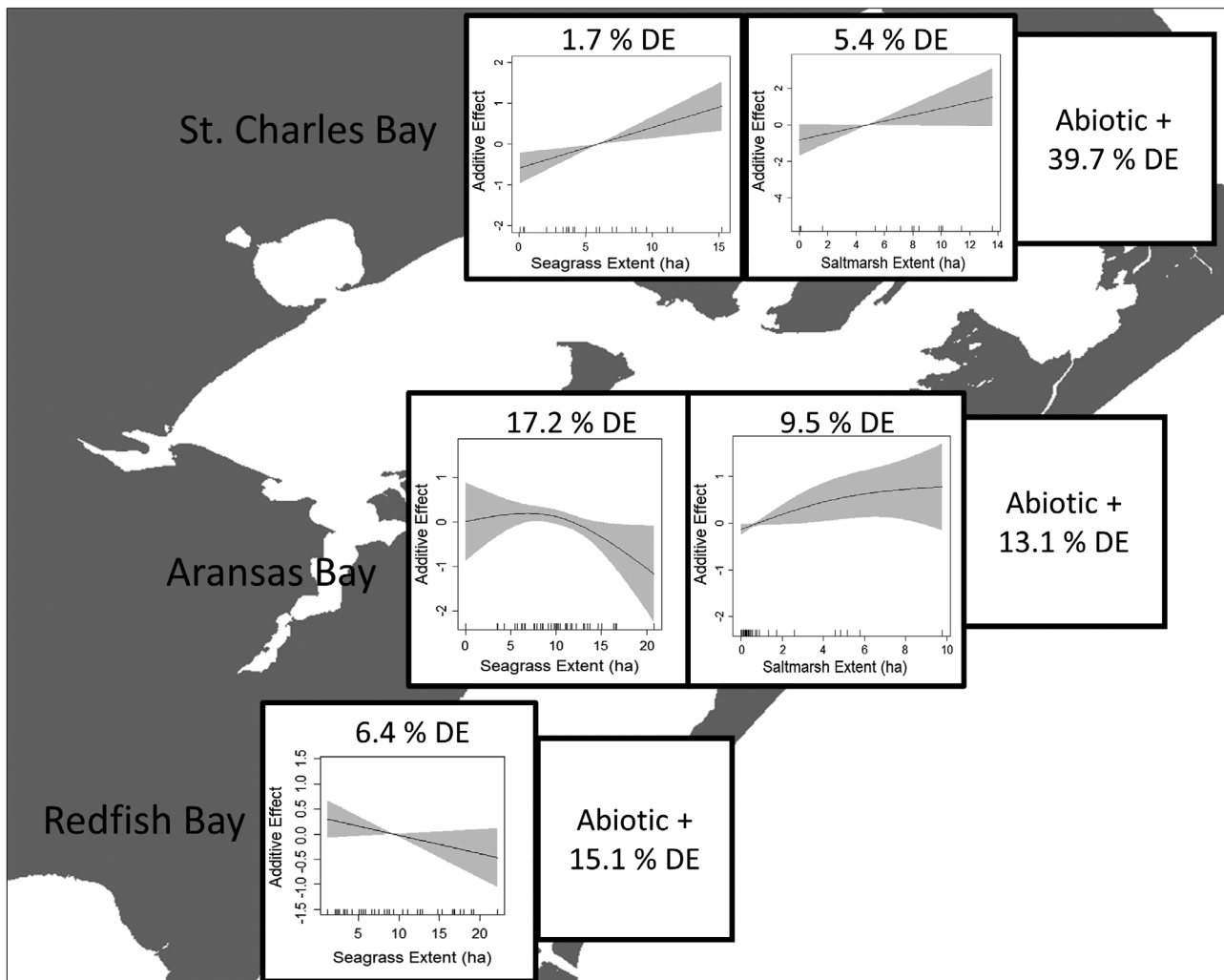
Fig. 5. Generalized additive model response plots showing influence of structural habitat model variables on the abundance of juvenile spotted seatrout at the sub-region scale in Redfish Bay, Aransas Bay, and St. Charles Bay. Other details as in Fig. 3

brown shrimp abundance was explained only by salinity (ΔAIC = 4.4; DE = 0.5%) and month (ΔAIC = 14.9; DE = 5.3%). Brown shrimp abundance in St. Charles Bay was linearly and negatively correlated with salinity. The full model for St. Charles Bay included only significant predictors (26.7% DE, Fig. 7); the inclusion of insignificant predictor variables did not improve model performance.

At the ecosystem level, variation in juvenile brown shrimp abundance was significantly explained by month (ΔAIC = 255; DE = 25.3%), distance from inlet (ΔAIC = 5.5; DE = 2.2%), mangrove extent (ΔAIC = 5.2; DE = 1.4%), and salinity (ΔAIC = 2.6; DE = 0.9%) (Fig. 8). The full model (34.3% DE) included significant predictors as well as seagrass extent, saltmarsh extent, and year; while these factors were individually insignificant, they improved DE by 1.1%.

3.5. Blue crab

Blue crabs were present in 702 of 1455 samples, and a total of 3602 blue crabs were captured throughout the study period. The average total length of captured blue crabs was 33.8 mm. At the site level, blue crab occurrence was positively correlated with presence of shoreline vegetation (p < 0.001, Fig. 2A) and was higher at sites adjacent to mangroves as compared to saltmarsh (p = 0.004, Fig. 2B). Blue crab occurrence was positively correlated with seagrass presence (p < 0.001, Fig. 2C) and was significantly impacted by vegetated habitat heterogeneity (p < 0.001, Fig. 2D). Tukey's comparisons indicate that the occurrence of blue crabs was higher at sites that had both submerged and emergent vegetation as compared to sites that had only submerged (p = 0.02),
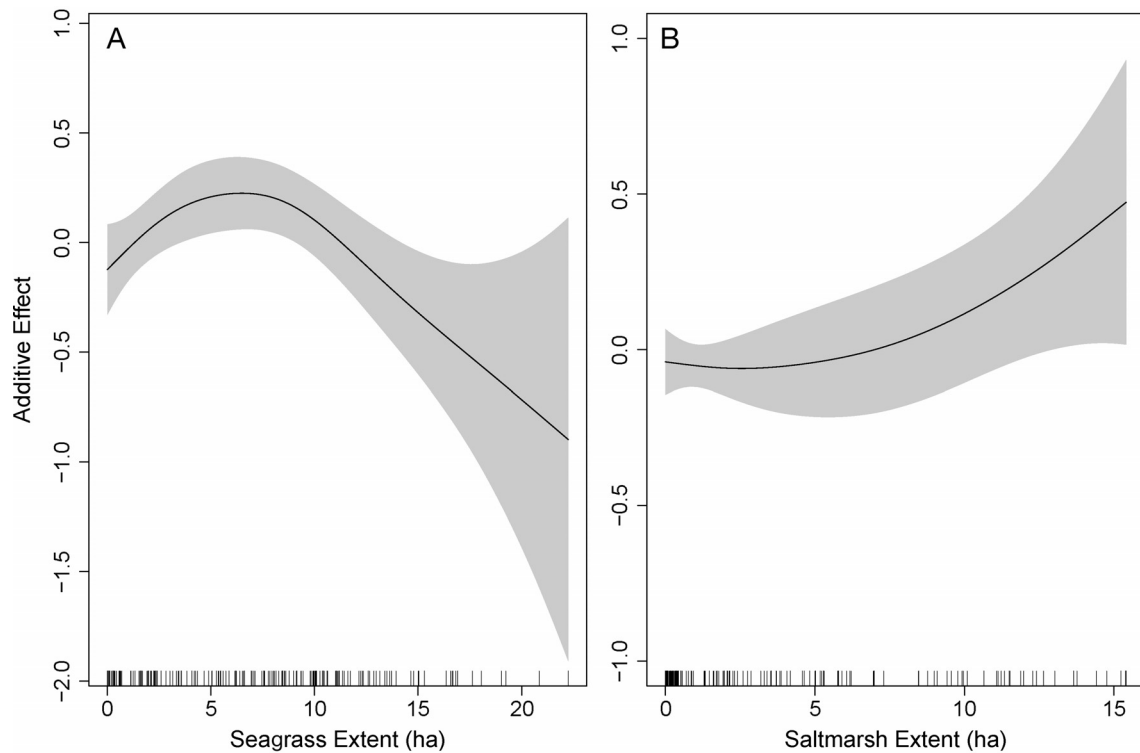
Fig. 6. Generalized additive model response plots showing influence of significant (ΔAIC > 2) model variables on the abundance of juvenile spotted seatrout at the ecosystem scale. Other details as in Fig. 3

emergent (p < 0.001), or no vegetation (p < 0.001). Blue crab occurrence was higher at sites with submerged vegetation than at those with emergent vegetation (p = 0.001) or no vegetation (p < 0.001).

At the sub-region scale, blue crab density was highest in Redfish Bay and St. Charles Bay and intermediate in Aransas. Within Redfish Bay, variation in blue crab abundance was significantly explained by month (ΔAIC = 3.3; DE = 4.0%) only. The full model for Redfish Bay (15.8% DE, Fig. 9) included the significant predictor variables as well as mangrove extent and year; while these factors were individually insignificant, they improved DE by 5.9%. Within Aransas Bay, variation in blue crab abundance was significantly explained by distance from inlet (ΔAIC = 3.9; DE = 4.6%), saltmarsh extent (ΔAIC = 4.0; DE = 4.4%), mangrove extent (ΔAIC = 2.6; DE = 3.8%), and seagrass extent (ΔAIC = 2.3; DE = 3.4%). Blue crab abundance increased linearly with saltmarsh extent, was highest at sites with low (~3 ha) mangrove extent, and had a biomodal relationship with seagrass extent, with highest abundance at low (<5 ha) and high (>20 ha) coverage of seagrass. The full model for Aransas Bay (17.9% DE, Fig. 9) included significant predictors as well as year; while year was not significant, it improved DE by 2.6%. Within St. Charles Bay, variation in blue crab abundance was

significantly explained by year (ΔAIC = 3.8; DE = 1.8%) only. The full model for St. Charles Bay (27.2% DE, Fig. 9) also included month; while month was not significant, it improved DE by 11.3%.

At the ecosystem scale, variation in blue crab abundance was explained by month (ΔAIC = 15.5; DE = 2.9%), salinity (ΔAIC = 7.8; DE = 1.9%), year (ΔAIC = 7.5; DE = 1.5%), distance to inlet (ΔAIC = 6.1; DE = 0.9%), and saltmarsh extent (ΔAIC = 6.0; DE = 0.8%) (Fig. 10). Blue crab abundance was positively correlated with saltmarsh extent, negatively correlated with distance from inlet, and peaked in the spring (March–May). The full model (15.9% DE) included significant predictors as well as mangrove extent. While mangrove extent was an insignificant predictor, including it in the final model improved DE by 0.6%.

4. DISCUSSION

While *in situ* observations are often considered the most accurate representation of biological data, we have demonstrated that remote sensing can be used to describe estuarine faunal–habitat associations. The faunal–habitat associations identified using this remote sensing approach are comparable to previous
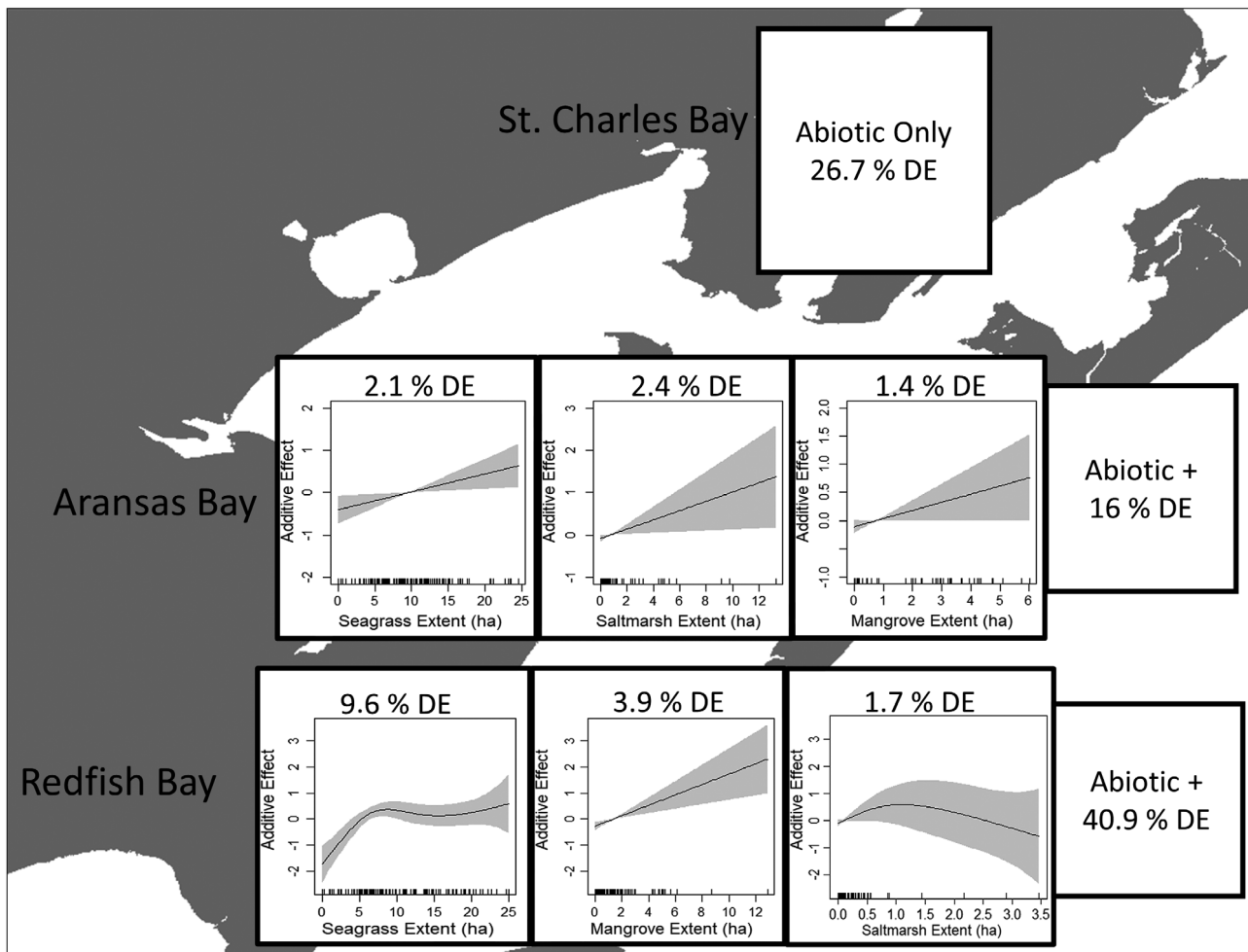
Fig. 7. Generalized additive model response plots showing influence of structural habitat model variables on the abundance of juvenile brown shrimp at the sub-region scale in Redfish Bay, Aransas Bay, and St. Charles Bay. Other details as in Fig. 3

studies that have used *in situ* observations to characterize habitat use or have stratified fisheries sampling by habitat. For example, our results support previous *in situ* findings that the abundance of red drum, spotted seatrout, blue crabs, and brown shrimp increases in areas adjacent to or within vegetated (i.e. saltmarsh or seagrass) habitats (Thomas et al. 1990, Stunz et al. 2002, Clark et al. 2004, Neahr et al. 2010, Clarkson & Beseres Pollack 2021). Beyond detecting faunal response to simplistic metrics of vegetation presence, this approach was also effective in identifying more complex patterns of faunal distribution between different types of vegetated habitats. For example, we observed increased abundance of blue crabs in seagrass as compared to marsh edge, supporting previous findings (Thomas et al. 1990, Clarkson & Beseres Pollack 2021) and indicating that saltmarshes may be used as nursery habitats when seagrasses are limited (Thomas et al. 1990). Impres-

sively, the probability of blue crab occurrence within different types of vegetated habitats observed in this study exhibits the same pattern as in Clarkson & Beseres Pollack (2021), despite the 2 studies using different methodology (*in situ* versus remote sensing) and being separated by more than a decade (Fig. 11). The corroboration of these results suggests that remotely sensed habitat data can be integrated with FIM datasets to detect faunal–habitat associations at multiple spatial scales, which can be an critical to informing management decisions when funding or resource limitations prevent *in situ* habitat data collection.

The influence of spatial scale on the interpretation of faunal–habitat associations is clearly demonstrated by our results, as the importance of predictor variables for focal species abundance changed across spatial scales. Brown shrimp and blue crab abundance was predominantly driven by abiotic factors at the ecosystem scale but was more influenced by
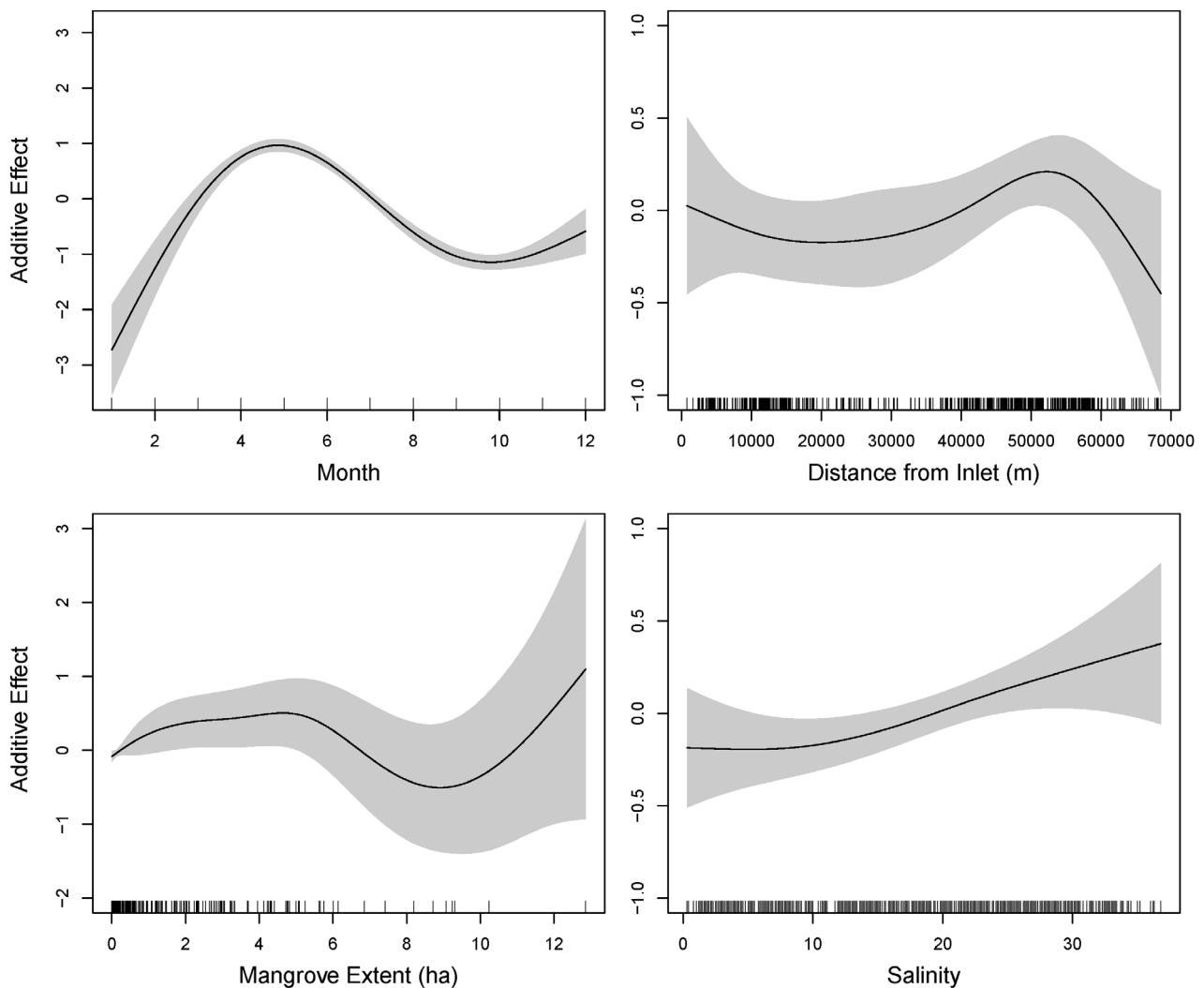
Fig. 8. Generalized additive model response plots showing influence of significant (ΔAIC > 2) model variables on the abundance of juvenile brown shrimp at the ecosystem scale. Other details as in Fig. 3

structural habitat factors at the sub-region scale based on the availability of habitat. Conversely, spotted seatrout distribution was ubiquitous across the ecosystem and primarily driven by habitat at the ecosystem scale, supporting previous findings that spotted seatrout select vegetated habitats across large spatial scales (e.g. the northwestern Gulf of Mexico, Neahr et al. 2010). However, in sub-regions where preferred habitats (i.e. seagrass and saltmarsh) were abundant and evenly distributed, such as in Redfish Bay, micro-scale patterns in spatial distribution of spotted seatrout were driven more by abiotic factors (i.e. salinity). The inverse pattern in scale-dependent habitat associations of spotted seatrout versus decapod crustaceans may be driven by patterns of physiological tolerance. Both juvenile brown shrimp and blue crab have narrower ranges of salinity prefer-

ence than spotted seatrout and red drum (Patillo et al. 1997), which may explain why large-scale patterns in their distribution are predominantly driven by abiotic factors for these species. For example, juvenile brown shrimp demonstrate preference for salinities ranging from 17 to 35 (Doerr et al. 2016) and exhibit relatively low survivorship in response to rapid decreases in salinity (Saoud & Davis 2003), which may explain the large-scale importance of abiotic factors (e.g. salinity) to brown shrimp distribution. In contrast, spotted seatrout can acclimate to hyposaline conditions at 9 d old (Banks et al. 1991), which may explain the more ubiquitous distribution of spotted seatrout throughout the estuary, including within the low-salinity regions at maximum distances from the inlet such as Copano and St. Charles Bays. Alternatively, the differences in large-scale
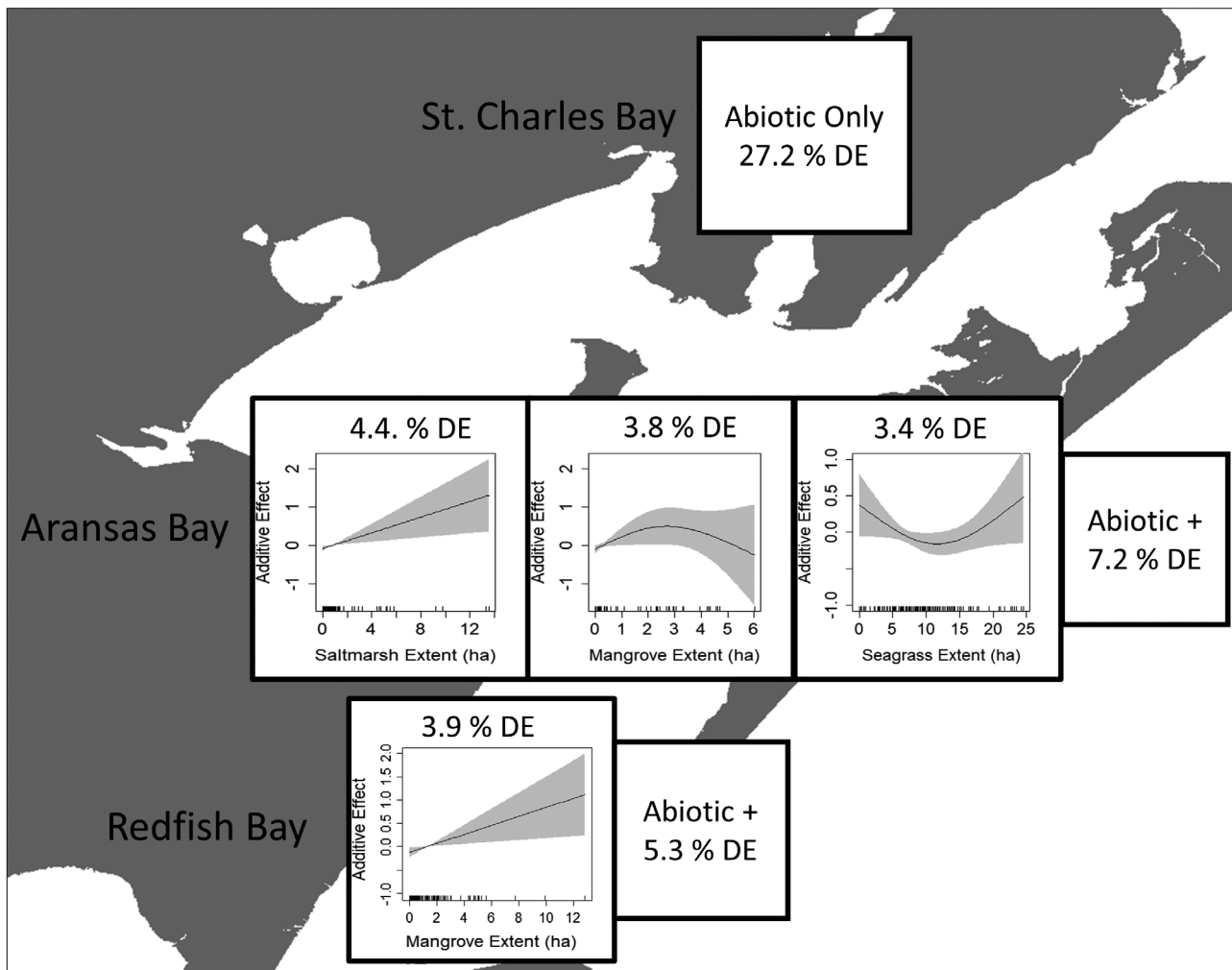
Fig. 9. Generalized additive model response plots showing influence of structural habitat model variables on the abundance of juvenile blue crab at the sub-region scale in Redfish Bay, Aransas Bay, and St. Charles Bay. Other details as in Fig. 3

distribution of our focal species may also be driven by differences in motility between the species. Decapod crustaceans typically have much smaller ranges of daily movement than finfish; for example, blue crabs disperse an average of 130 m per day while red drum and spotted seatrout move an average of 3 to 1.6 km, respectively (Wolcott & Hines 1990, Moulton 2017). This reduced movement may constrain the availability of certain abiotic and structural habitats to decapod crustaceans and inflate the importance of structural habitats near points of ingress. This was exemplified in our results by the significant influence of mangrove habitats on brown shrimp abundance at the ecosystem scale, as mangrove habitats are dominant within Redfish Bay where brown shrimp abundance was highest.

Unlike the other focal species, red drum did not demonstrate a scale-dependent shift in response to abiotic versus structural habitat factors. Red drum distribution was driven by both abiotic and structural habitat factors at both estuarine and sub-region scales, and abiotic factors explained the most deviance at both spatial scales. The similarly wide range of salinity tolerance of juvenile red drum and spotted seatrout indicates that the difference between the scale-dependent selection of abiotic versus structural habitat factors by these 2 species may instead be driven by life history; red drum spawn offshore (Patillo et al. 1997), and the higher density of juvenile red drum in Redfish Bay may be driven by ingress into the estuary. Spotted seatrout are estuarine spawners (Patillo et al. 1997), and their resulting ubiquitous distribution within the estuary is not restricted by patterns of dispersion into the estuary.

The spatially-dependent patterns of habitat utilization by brown shrimp at the sub-region scale are
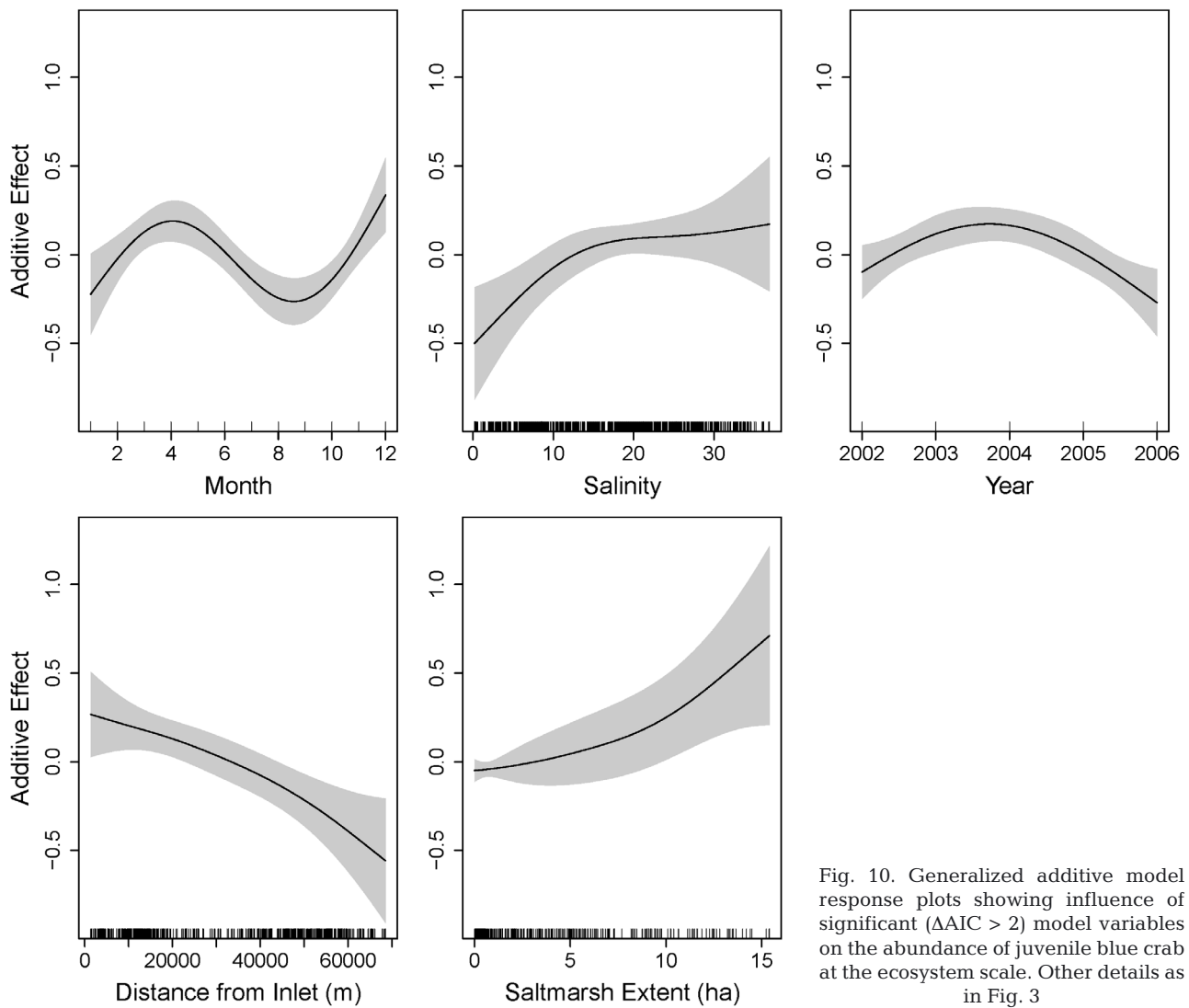
Fig. 10. Generalized additive model response plots showing influence of significant (ΔAIC > 2) model variables on the abundance of juvenile blue crab at the ecosystem scale. Other details as in Fig. 3

indicative of facultative habitat use. Brown shrimp abundance was explained predominantly by abiotic factors (salinity, distance from inlet, and month) at the ecosystem scale, with a greater influence of structural habitat at the sub-regional scale. At the sub-region scale, the significance of habitat as a predictor for brown shrimp abundance was reflected by the relative availability of the habitat within the sub-region. For example, Redfish Bay contains the most extensive seagrass and mangrove habitats in the entire estuary, with relatively less saltmarsh-dominated shorelines. Consequentially, seagrass and mangroves explained more deviance in the dataset (9.6 and 3.9%, respectively) in Redfish Bay than in any other sub-region. Saltmarsh supersedes mangrove as the dominant emergent vegetation in Aransas Bay, and was a significant predictor of brown shrimp abundance in Aransas Bay. Seagrass

and mangrove habitats remained significant predictors in Aransas Bay, but explained less deviance than they did in Redfish Bay (2.1 and 1.4%, respectively). This indicates that brown shrimp facultatively utilize vegetated habitats based on their availability, supporting previous studies with similar findings (Clark et al. 2004, Clarkson & Beseres Pollack 2021). A similar pattern was observed with red drum, where abundance was driven by saltmarsh in Aransas Bay but seagrass in St. Charles Bay, supporting previous findings that red drum facultatively utilize both vegetated habitats depending on their availability (Stunz et al. 2002). Our results indicate that the importance of estuarine habitats to facultative habitat users such as brown shrimp and red drum is dependent on estuarine habitat composition, which highlights the importance of spatially explicit monitoring.
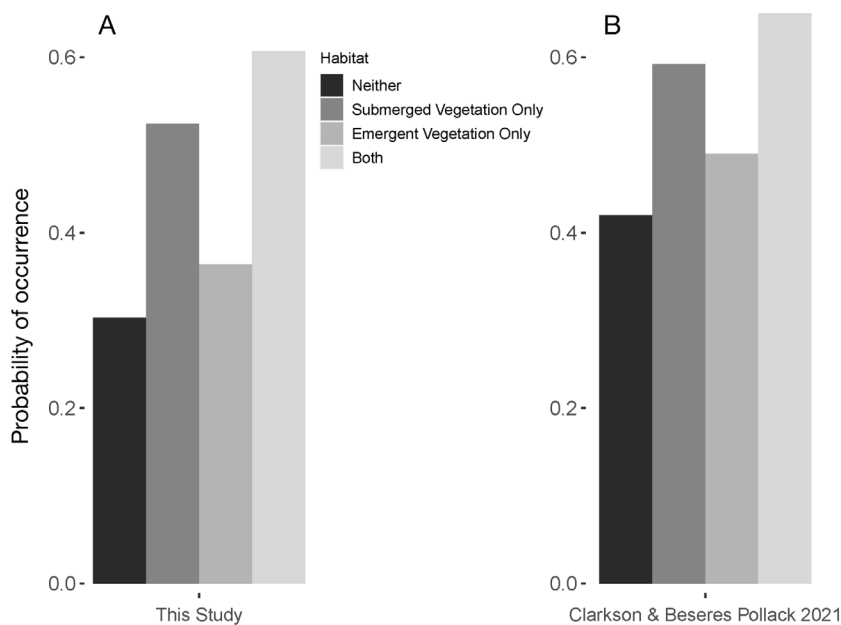
Fig. 11. Model-predicted occurrence of blue crab between vegetated habitat types observed in (A) this study and (B) Clarkson & Beseres Pollack (2021). While both studies used faunal occurrence data from bag seines collected from Texas Parks and Wildlife Department's Fisheries Independent Monitoring program, the present study utilized remotely sensed habitat data from 2002 to 2006, and Clarkson & Beseres Pollack (2021) used *in situ* habitat observations from 2016

In contrast to brown shrimp and red drum, blue crabs did not display patterns of facultative habitat use. The relationship between blue crab abundance and vegetated habitat type has been consistent across time and survey methodologies (see Clarkson & Beseres Pollack 2021; Fig. 11), suggesting that the importance of vegetated habitat type to blue crab populations is less dependent on local habitat composition, although scale-dependent differences in habitat associations were still observed. At the estuary scale, blue crab abundance was explained mostly by abiotic variables (salinity, distance, month, and year), while only a minority of deviance was explained by habitat (saltmarsh extent). In the sub-region of Aransas Bay, however, model deviance was evenly described by structural habitat predictor variables (extent of saltmarsh, seagrass, and mangrove) and abiotic factors (distance from inlet). In Redfish Bay, the only significant predictor of blue crab abundance was month. This spatially explicit habitat utilization pattern is likely related to the life history of blue crabs and ingress into the bay. Blue crab megalopae recruit into the bay through the tidal inlet near Port Aransas, where they immediately settle into Redfish Bay (Greer 2010, Fowler 2017). Megalopae typically settle into seagrass beds (Orth & van Montfrans 1987), which are ubiquitously distributed across

Redfish Bay and thus may not limit blue crab abundance. As blue crabs move out of Redfish Bay and into Aransas Bay, where habitats are less expansive and more fragmented (i.e. patchy rather than continuous seagrass beds), relatively more of the variation in their abundance is described by habitat availability. The increased importance of seagrasses in Aransas Bay may also correspond to higher blue crab survival rates in sparse or patchy seagrass (Hovel & Fonseca 2005), which are typical in the Aransas Bay sub-region.

The spatially explicit habitat associations exhibited by these 4 focal species highlights the importance of considering the spatial scale of fisheries management when incorporating habitat into fisheries-independent monitoring. The majority of fish–habitat associations are determined by *in situ* pairwise comparisons between habitats at a small spatial scale, but management decisions are often based on a larger spatial unit (Mellin et al. 2009). By utilizing remote sensing to pair habitat and fisheries-independent monitoring at multiple spatial scales, variation in species abundance can be explained more precisely. For example, structural habitat availability was one of the most influential factors for juvenile spotted seatrout abundance at the ecosystem scale at which fisheries are managed in Texas. However, this correlation would not be identified if *in situ* sampling only occurred within a sub-region where this relationship is not prevalent, such as within Redfish Bay. Conversely, if associations between seagrass extent and blue crab abundance were determined via sampling in Aransas Bay and extrapolated to infer ecosystem-level trends, it may artificially inflate the perceived impact of seagrass habitat on blue crab recruitment at the fisheries management scale. To truly inform fisheries management, fish-habitat monitoring needs to occur throughout the management area and not only within a sub-region. Clarkson & Beseres Pollack (2021) demonstrated an efficient, rapid *in situ* assessment approach to large-scale habitat monitoring, while the current study demonstrates that remote sensing can be equally effective in identifying faunal–habitat associations at a large spatial scale. That is not to say that monitoring at the sub-region or site-level does not provide valuable information — understanding the regional importance

of habitats can help prioritize areas for conservation, but the spatial scale of monitoring should reflect the spatial scale of management and conservation action.

Not only does remote sensing allow for the examination of faunal–habitat associations across multiple spatial scales, but it is also the most efficient way to characterize the relationship between fish and large-scale habitat features, such as the areal extent of habitat. While many previous studies have identified correlations between our focal species and the presence of a focal habitat (such as seagrass or saltmarsh; e.g. Zimmerman et al. 1984, Thomas et al. 1990, Rozas & Minello 1998, Stunz et al. 2002, Clark et al. 2004, Neahr et al. 2010, Clarkson & Beseres Pollack 2021), few have quantified the relationship between focal species and the areal extent of available habitat (e.g. Dance & Rooker 2016, Livernois et al. 2020). The current framework for faunal–habitat monitoring leads to structural habitats being represented as discrete factors (presence/absence) in habitat suitability models (e.g. Rubec et al. 2001, Kupschus 2003, Bacheler et al. 2009), rather than employing the typical regression-based approach commonly used to model species occurrence across continuous variables (Hirzel & Lay 2008). Assessing the response of a species to habitat as a continuous rather than discrete factor allows for the identification of the appropriate scale for observation, which can significantly impact how we interpret species–habitat relationships (Levin 1992). Our results can be used to identify the linearity of the relationship between species and extent of habitats at various scales, which can inform how habitat data can be incorporated into stock models. For example, the relationship between all focal species and saltmarsh extent appears to be linear at multiple spatial scales, while most of our focal species (i.e. red drum, brown shrimp, blue crab) experience a polynomial relationship with mangrove extent. While a mangrove habitat suitability threshold exists within the 300 m scale, there is no upper threshold to the suitability of saltmarsh extent at the same scale. This indicates that overall suitable intertidal habitats for red drum, brown shrimp, and blue crab may decrease as mangrove habitats continue to expand and displace saltmarsh in south Texas.

By combining site-level (e.g. habitat presence) and large-scale (e.g. habitat extent) observations, we can make inferences about how species may be using habitats across the estuarine landscape. In our study, red drum showed a preference for sites where seagrass was present, but red drum abundance was not correlated with areal extent of seagrass at the fisheries management scale (ecosystem) scale. In an estuary that is characterized by expansive seagrass habitats, this may signify the relative importance of seagrass edge habitat (Holt et al. 1983, Dance & Rooker 2016, Moulton 2017). Preference for edge habitat is not unique to red drum. Previous studies have shown that marsh edge habitat may be more beneficial than the low-edge marsh interior for brown shrimp (Faller 1979, Zimmerman et al. 1984, Minello & Rozas 2002, Haas et al. 2004), and that brown shrimp survival and recruitment differ on the order of 5–10% between high-edge and low-edge marsh habitats (Haas et al. 2004). Use of marsh edge and intertidal habitat can be affected by additional environmental factors, such as tidal amplitude (Minello et al. 2003, Haas et al. 2004), marsh configuration (Zimmerman et al. 1984), and salinity, as demonstrated by the significant interaction between salinity and intertidal habitat use by blue crabs in this study. For species where interior and edge habitats contribute differently to fisheries stocks, spatial extent of vegetated habitat must be incorporated into fisheries models with caution. Because of the complex interactions with edge and salinity observed in our study and in the literature, incorporating the spatial extent of seagrass and vegetated intertidal habitat into red drum and blue crab stock modeling, respectively, may be challenging. However, the results of our abundance-based GAMs suggest that structural habitat (seagrass and saltmarsh) data could explain up to 10% of variation in spotted seatrout abundance at the fisheries management spatial scale, and thus may improve stock modeling for this species.

Our efforts represent a retroactive assessment of faunal habitat preferences during an interval where paired fisheries–habitat data were unavailable. This approach lends itself to informing current management issues that arise from long-term coastal change for which monitoring data are scarce. For example, poleward expansion of black mangroves and subsequent displacement of saltmarshes is altering subtropical and temperate ecosystems (Cavanaugh et al. 2014, Saintilan et al. 2014, Armitage et al. 2015), necessitating long-term monitoring of fish–habitat associations to inform adaptive management. Our study region experienced a 74% increase of mangrove and a 24% loss of saltmarsh from 1990 to 2010 (Armitage et al. 2015), but limited information is available on large-scale faunal–mangrove associations in Texas prior to this expansion. Recent studies (after 2010) report a negative correlation between mangrove presence and blue crab occurrence (Smee et al. 2017, Clarkson & Beseres Pollack 2021), yet our results (2002–2006) demonstrate increased blue crab occur-

rence in mangrove compared to saltmarsh. While this disparity may be due to differences in sampling methodology, it is likely that the relationship between blue crabs and vegetated intertidal habitat has varied with changing habitat extent and condition over time. Our GAM spline shows a peak in habitat suitability at around 3 ha of mangrove within the sample area in Aransas Bay (Fig. 9). Expansion of mangrove may have exceeded the extent that is suitable for blue crabs, shifting blue crab preference toward cordgrass-dominated saltmarsh in recent years. This result may have also been influenced by differences in salinity during the study period. We found a significant interaction between salinity and habitat type (saltmarsh vs. mangroves), where blue crab occurrence was positively correlated with saltmarsh extent at low salinities (<17) only, and with mangrove extent at moderate and high salinities (>17) only. Average salinity in the present study was 17.3, as compared to an average of 15.4 for the same study area in Clarkson & Beseres Pollack (2021), which may explain differences in the blue crab–mangrove relationship identified in the 2 studies.

While this approach allows us to retroactively examine historic faunal–habitat associations, more research is needed to quantify the long- and short-term temporal limitations of this approach. For example, research is warranted to identify the 'shelf life' of aerial imagery for fisheries analysis, as inter- and intra-annual variability in habitats may impact the observed relationship between fish and habitats. We retroactively paired 5 years of fisheries data to a static map product based on similar methods in the literature (Olsen 2019) to reduce potential error introduced by temporal mismatch between the map product and long-term environmental change, while other studies have paired a longer timeframe of fisheries data to static map data (Dance & Rooker 2016). We also paired fisheries-independent data from all seasons rather than only those that aligned with the seasonality of the aerial imagery acquisition. The significance of our results indicates that inter-annual variation in habitat was not prohibitive to the detection of faunal–habitat associations, but more research is needed to quantify potential effects of imagery seasonality on the ability to pair fisheries-independent data and static habitat products. In addition to long-term (e.g. seasonal, annual) effects, more research is warranted to determine the effects of short-term temporal changes (e.g. tidal elevation) on the accuracy of faunal–habitat associations described with remotely sensed habitat data. For example, tidal elevation is likely to influence faunal access to intertidal habitats, such as saltmarshes and

mangroves. Because the tidal range in our study region is relatively small and can be more influenced by winds than astronomical tides (Evans et al. 2012), the interaction between faunal habitat utilization and tidal amplitude was not assessed. However, more research is warranted to see how short-term temporal effects, such as tidal amplitude, may impact habitat–faunal associations identified with remotely sensed habitat data in other regions that experience large tidal fluctuations.

5. CONCLUSIONS

We have demonstrated that freely available remote sensing products can be leveraged to enhance our understanding of faunal–habitat associations, which can improve the efficiency with which habitat data are incorporated into fisheries management. Remote sensing allows for the examination of faunal–habitat associations at multiple spatial scales, which is critical to the comprehensive understanding of estuarine dynamics. Specifically, remote sensing can be used to accomplish habitat monitoring at the larger spatial scales that are often used for fisheries management decisions. The ability to monitor faunal–habitat associations at multiple spatial scales is critical, as our results indicate that the relationship between faunal abundance and habitat availability is spatially explicit and changes across spatial scales. Finally, remote sensing can be used to retroactively assess faunal–habitat associations for historic data sets that do not have paired fish–habitat observations. More research is needed to evaluate the limits of the utility of remote sensing for resource management, specifically to identify the 'shelf life' of an aerial imagery product regarding its ability to be integrated into fisheries monitoring.

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