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ARTICLE

Habitat Associations and Co-Occurrence Patterns of Two Estuarine-Dependent Predatory Fishes

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Abstract

Estuarine-dependent fishes experience a wide range of environmental conditions, and most species exhibit distinct associations with particular habitats. However, similar species or multiple conspecifics often overlap spatiotemporally, which can result in ecological interactions that have consequences for behaviors that can shape the structure and function of ecosystems. We used a long-term gill-net data set (2001–2015) to investigate the habitat associations and co-occurrence patterns of two estuarine-dependent predatory fishes, Red Drum *Sciaenops ocellatus* and Spotted Seatrout *Cynoscion nebulosus*, in coastal Alabama, USA. Both species were associated with similar environmental conditions, primarily low dissolved oxygen and low salinity, especially when temperature was low. However, differences emerged between the species with respect to the effects of interacting environmental variables on their habitat use patterns, which were likely driven by physiological, biological, and ecological dissimilarities between them. Concerning their biogenic habitat use, extensive submerged aquatic vegetation (SAV) was an important habitat for both species, but Spotted Seatrout appeared to prefer high-salinity SAV beds, while Red Drum associated with SAV regardless of salinity. Spotted Seatrout were associated with extensive emergent marsh edges, and the positive relationship between Red Drum and SAV was diminished when marsh edge was abundant. Co-occurrence was observed primarily in habitats with which both species were associated, most frequently in shallow, prey-rich marsh edges and high-salinity seagrass beds. These observed habitat use patterns elucidate the subtle differences in resource use that allow these species to coexist and suggest potential areas where interactions between them may shape their roles as predators.

Estuaries exhibit steep gradients and broad ranges in environmental conditions, and they can support highly productive and diverse communities due to the variety of habitats that they provide (Day et al. 1989). Within these

heterogeneous landscapes, biogenic habitats such as submerged aquatic vegetation (SAV) and salt marsh edges provide vertical structure in a system that is otherwise primarily dominated by bare substrate. In addition to

Subject editor: Jeffrey A. Buckel, North Carolina State University, Morehead City

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Received March 6, 2019; accepted December 2, 2019

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providing valuable ecosystem services in the form of shoreline stabilization, water filtration, and carbon sequestration (Costanza et al. 1997; Barbier et al. 2011), these habitats serve as critical nursery and foraging grounds for many estuarine-dependent species of fish and invertebrates (Beck et al. 2001). Ecosystem-based management strategies that incorporate habitat considerations, such as marine protected areas, can be highly effective for conserving resources in dynamic coastal systems (Roberts et al. 2001). To maximize the effectiveness of such strategies, it is necessary to determine the habitat requirements of a variety of species, which often requires biological monitoring across large spatiotemporal scales.

The distribution and structure of benthic and nektonic communities in estuaries are generally influenced by abiotic factors such as salinity, temperature, and dissolved oxygen (Dunson and Travis 1991; Jassby et al. 1995; Marshall and Elliott 1998). Additionally, biogenic structured habitats can provide refuge from predation, resulting in generally high prey densities (Summerson and Peterson 1984; Heck et al. 2003). Various predators often associate with these dense and diverse prey assemblages, which can influence the rate and nature of encounters between numerous predator and prey species (Crowder and Cooper 1982; Grabowski and Powers 2004). Mechanisms such as physiological tolerances and prey availability often drive the selection of habitats by estuarine predators, with species often balancing trade-offs to maximize growth while minimizing competitive pressures (Crowder and Magnuson 1983; Kramer 1987; Hughes and Grand 2000).

Given the high diversity and productivity of estuarine ecosystems, multiple predator species often co-occur and use similar resources such as habitats (i.e., foraging grounds or areas with ideal environmental conditions) or food (i.e., shared prey populations). To allow for the co-existence of sympatric species, specialization often emerges over evolutionary timescales to reduce competitive interactions between them (MacArthur 1958; Hutchinson 1959; Schoener 1974). The resulting resource partitioning can allow multiple predators to co-occur while occupying different niches. Some predatory fishes exhibit distinct habitat partitioning, spatially separating themselves from potential competitors (Wheeler and Allen 2003; Fairclough et al. 2008). Others partition trophically, specializing their diet to reduce overlap with similar predators (Hartman and Brandt 1995; Kroetz et al. 2017). Determining the nature and degree of resource partitioning that occurs between sympatric predator species can provide insight into their individual and shared roles in ecosystem function (e.g., Amundsen et al. 2010; Browning et al. 2014).

In estuaries along the U.S. coast of the Gulf of Mexico, two predatory fish species, Red Drum

Sciaenops ocellatus and Spotted Seatrout *Cynoscion nebulosus*, share overlapping distributions and are exploited heavily as recreational sportfish. During their subadult and adult life stages, both species are considered generalist demersal predators that feed on small fishes and crustaceans. However, Spotted Seatrout tend to be more piscivorous, while Red Drum consume a higher proportion of shrimp and crabs (Darnell 1958; Scharf and Schlicht 2000). Both species occur throughout marine, estuarine, and freshwater regions (Peters and McMichael 1987; Helser et al. 1993; Bacheler et al. 2009a), but adult Spotted Seatrout exhibit some seasonally varying aversion to low salinities (Callihan et al. 2015). Red Drum frequently associate with shallow, structured habitats (Bacheler et al. 2009a; Dance and Rooker 2015; Fodrie et al. 2015; Moulton et al. 2017), while Spotted Seatrout generally inhabit deeper waters, bare substrate, loose shell bottom, and seagrass beds (MacRae and Cowan 2010; Moulton et al. 2017). Both species can demonstrate relatively high site fidelity, with many individuals often traveling less than 10 km from their original catch location (Adams and Tremain 2000; Hendon et al. 2002; Dresser and Kneib 2007; Bacheler et al. 2009b).

Few studies have explicitly compared the habitat associations of these two species in estuarine systems, despite the similarities in their life histories and the high likelihood of co-occurrence between them. Using acoustic telemetry, Moulton et al. (2017) determined that Red Drum and Spotted Seatrout differed significantly in their habitat use patterns in a Texas estuary, suggesting habitat-related resource partitioning. The present study compares the habitat associations and co-occurrence patterns of these two species over a longer timescale (thereby capturing interannual variability) and in an estuary with substantially different climatic conditions (most notably higher river discharge), resulting in an improved understanding of the resource needs of these two ecologically and socioeconomically important species. This information can be used to enhance the effectiveness of local, regional, and large-scale management strategies, particularly by determining best practices for conserving essential habitats (Pikitch et al. 2004).

Using data from a long-term gill-net sampling program in coastal and estuarine Alabama, the goals of this study were to (1) characterize the individual habitat use patterns of Red Drum and Spotted Seatrout and (2) examine the conditions under which the two species co-occur and potentially interact. These results define the environmental factors that influence the spatiotemporal overlap and habitat use patterns of these predators, which aids in elucidating their ecological roles and provides evidence to support ecosystem-based management strategies.

METHODS

Study area.—This study was conducted in coastal Alabama, primarily in Mobile Bay (Figure 1A). Mobile Bay is a broad, shallow estuary that is approximately 50 km in length (from the northern end to the southern end), with an average width of 20 km and an average depth of 3 m (McPhearson 1970). The Mobile–Tensaw River delta provides fresh water from the north, mixing with Gulf of Mexico waters to the south. The region experiences a diurnal tidal cycle, with an average tidal range of 0.5 m. Salinities range from 0‰ to 34‰, primarily depending on river outflow and wind mixing (Schroeder et al. 1990). The Alabama coast also includes the eastern portion of Mississippi Sound to the west and the western portion of Perdido Bay to the east. Perdido Bay receives considerably less freshwater inflow than Mobile Bay (USEPA 1999),

while northern Mississippi Sound receives a moderate amount of freshwater from the Escatawpa, Pascagoula, Tchoutacabouffa, Biloxi, Wolf, and Jourdan rivers. Both Mississippi Sound and Perdido Bay are separated from the Gulf of Mexico by barrier islands, and both receive tidally driven influxes of marine water through the passes.

The emergent wetlands in coastal Alabama are generally dominated by smooth cordgrass *Spartina alterniflora* and black needlerush *Juncus roemerianus* in the marine-brackish regions, and they transition to include bulrush *Scirpus* spp., cattail *Typhus* spp., and arrowhead *Sagittaria* spp. in the brackish–fresh delta region (Vittor and Stout 1975). Submerged aquatic vegetation (SAV) is relatively sparse, as turbidity is generally quite high. The majority of marine SAV occurs in Mississippi Sound and Perdido Bay, where the beds are dominated by shoalgrass

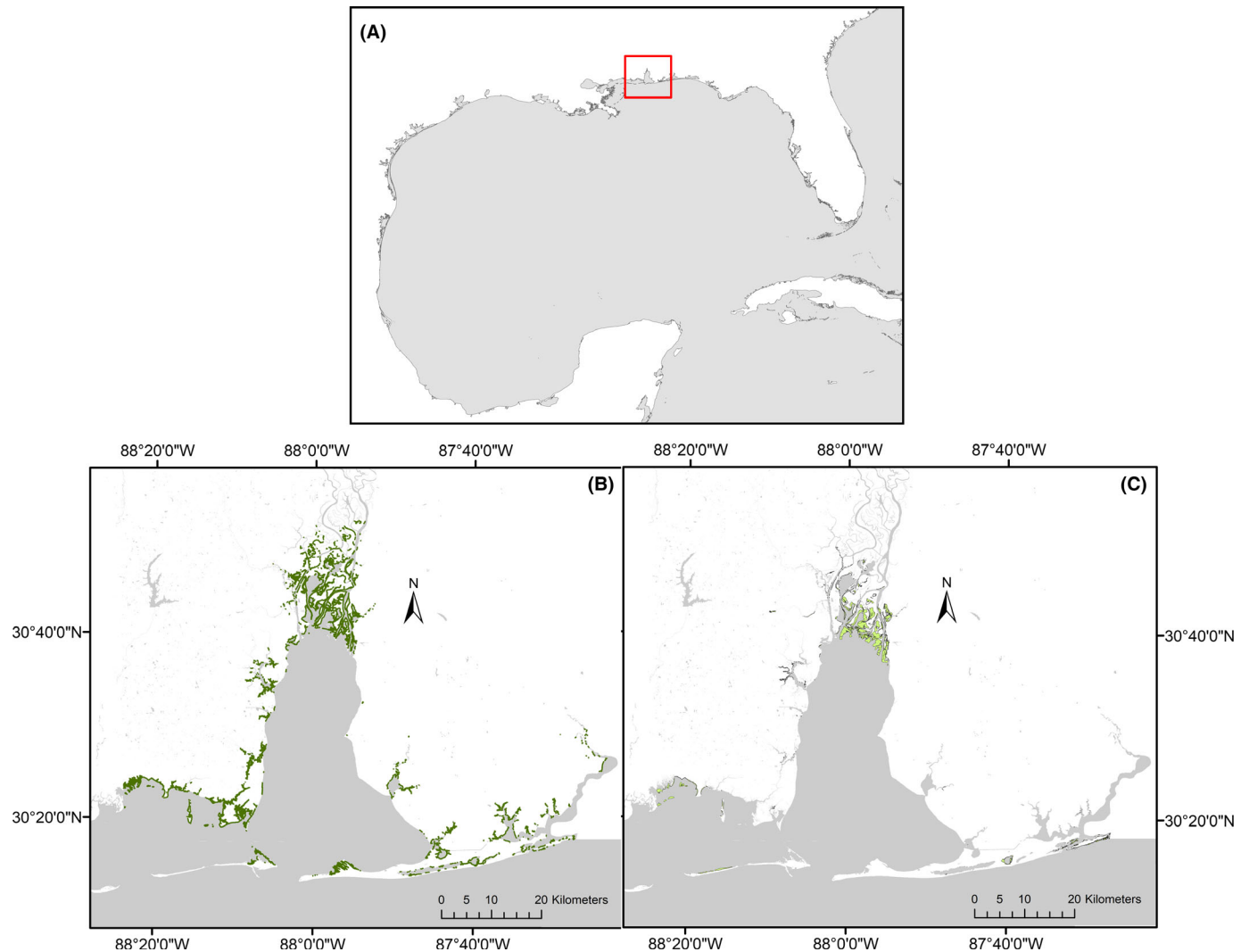


FIGURE 1. Spatial data representing (A) the study site, (B) emergent marsh shoreline, and (C) submerged aquatic vegetation in coastal Alabama used in habitat association analysis.

Halodule wrightii and widgeon grass *Ruppia maritima*. Brackish and freshwater SAV beds are distributed within the river delta in northern Mobile Bay, and they are dominated by native wild celery *Vallisneria spiralis*, non-native Eurasian water milfoil *Myriophyllum spicatum*, and nonnative southern naiad *Najas guadalupensis* (Barry A. Vittor and Associates 2016).

Sampling design and data collection.—To determine the habitat use patterns of Red Drum and Spotted Seatrout throughout coastal Alabama, data were used from an ongoing stratified random gill-net survey that was conducted by the Alabama Department of Conservation and Natural Resources, Marine Resources Division from 2001 to 2015. The survey included four major zones: eastern Mississippi Sound, western Perdido Bay, and two zones of approximately equal area in Mobile Bay (in the northern and southern areas). Each zone contained five subzones of approximately equal area. Stratified random sampling occurred monthly, but the number of gill-net sets per month (sample size) was unequal, ranging from 8 to 13. The sample sizes were allocated by comparing the monthly coefficients of variation to maximize sampling efficiency. Each month, the subzones were randomly selected for the allocated sample size of that month, with a total of 240 gill-net sets conducted annually. Two experimental gill nets were used, and they were generally set separately but concurrently. The first consisted of five 45.72-m panels (228.6 m total length), each with distinct mesh sizes (5-, 6-, 8-, 9-, and 10-cm stretch). The other was composed of four 45.72-m panels (182.88 m total length), with mesh sizes of 11-, 13-, 14-, and 15-cm stretch. All of the nets were 2.45 m in height. The gill nets were typically set with the small-mesh panels

perpendicular to shore and the large-mesh panels parallel to shore unless obstructions prevented this configuration. The gill nets were allowed to soak for 1 h within the selected 24-h sampling period, with most sets being conducted during daylight. Water temperature, salinity, dissolved oxygen, and water depth were recorded during each gill-net set at the surface of the water column. All of the animals were extracted from the gill net and identified to the lowest taxonomic level possible (typically species).

To investigate the associations of Red Drum and Spotted Seatrout with biogenic habitats, the gill-net catch data were combined with publicly available habitat data. Quantifications of the spatial extent of specific biogenic habitats in the coastal waters of Alabama were collected from the National Oceanic and Atmospheric Administration (NOAA) and the Mobile Bay National Estuary Program (MBNEP). Spatial data in the form of ArcGIS polyline shapefiles were obtained for marsh shoreline based on the NOAA's environmental sensitivity index classification scheme (NOAA NOS Office of Response and Restoration, Emergency Response Division 2007). The shoreline classifications were determined by digitizing orthorectified aerial photographs from October 2006. The NOAA data included categorizations for all shore types, including non-marsh shorelines, so the data were filtered to include only the lines that were categorized as emergent marsh (either fresh or brackish) or salt marsh (Figure 1B). Spatial data for SAV in the form of polygons were also obtained from the MBNEP, and it included fresh, brackish, and marine species (Barry A. Vittor and Associates 2016). These polygons were digitized based on orthorectified aerial photographs from July and August 2015 (Figure 1C). All of the layers (gill-net points, marsh lines, and SAV polygons)

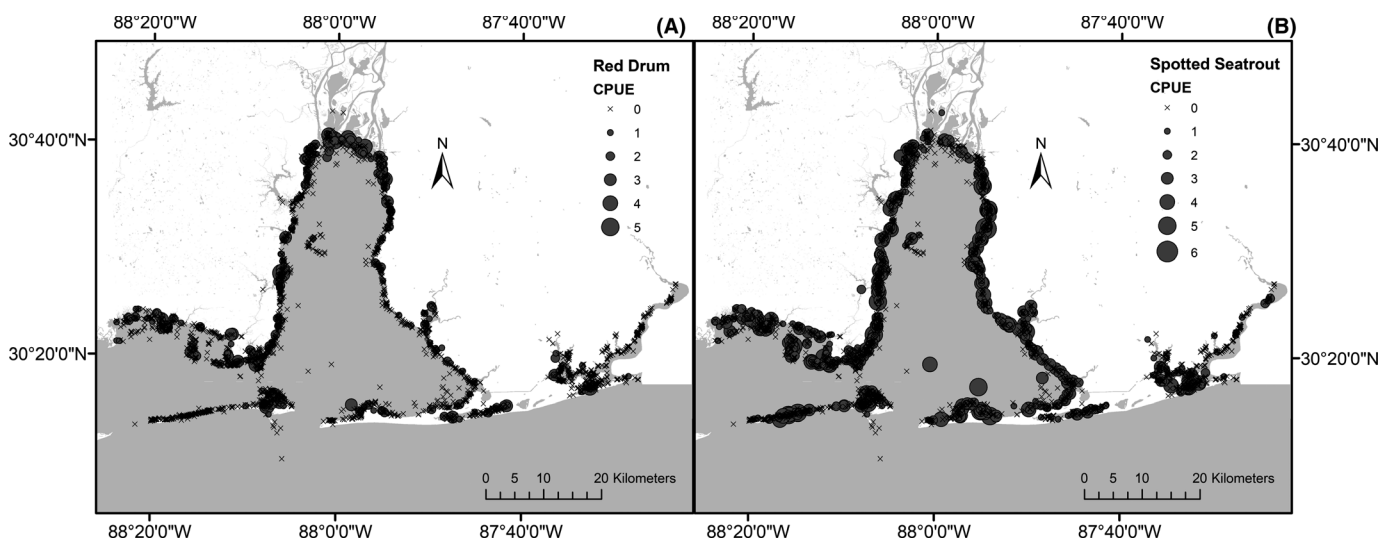


FIGURE 2. Distribution of CPUE (number of individuals per gill net) for (A) Red Drum (B) and Spotted Seatrout in coastal Alabama.

were mapped in ArcGIS 10.3 and projected to the same coordinate system, WGS 84 / UTM zone 16N, for spatial consistency.

The distributions of Red Drum and Spotted Seatrout CPUE were then mapped separately using ArcMap 10.3 (Figure 2). The gill-net locations were visually examined for points that were located in unreasonable areas such as on land or far from the region, indicating incorrect coordinates. Locations that were on land and greater than 500 m from a water body were removed, and those that fell within that range were moved to the shoreline of the nearest water body. To estimate the habitat associations of Red Drum and Spotted Seatrout, all of the gill-net set locations were overlaid on the SAV and marsh edge habitat data layers. Using ArcMap 10.3 Model Builder, a workflow was produced to create a circular buffer with a 2.5-km radius (5-km diameter) around each gill-net set location and any available habitat within that buffer was extracted and assigned to the corresponding gill-net sample. This buffer distance was selected as an estimate of daily to weekly movement for these species, considering their generally high site fidelity but immense variability in movement patterns (Baker and Matlock 1993; Dresser and Kneib 2007; Bacheler et al. 2009b; Moulton et al. 2017).

Data analysis.—To examine the environmental and habitat conditions that influenced the distribution of Red Drum, Spotted Seatrout, and their interspecific co-occurrence events, generalized linear models with binomial error distributions (logistic regressions) were fitted, with presence or absence of either Red Drum, Spotted Seatrout, or a co-occurrence event as the response and abiotic, seasonal, and biogenic habitat variables as predictors. The potential predictors included water depth (m), surface water temperature (°C), surface salinity, surface dissolved oxygen (mg/L), season (winter: December, January, and February; spring: March, April, and May; summer: June, July, August; and fall: September, October, and November), area of SAV (m²), and length of marsh edge (m). Seasons were defined based on the timing of ecologically relevant changes in temperature in the region (Carassou et al. 2012). Outlier values were observed for water depth and dissolved oxygen, so those parameters were censored to include only water depths of 3 m or less and dissolved oxygen concentrations of 10 mg/L or less.

The modeling procedure did not include a spatial component (i.e., including zone as a predictor variable or creating individual models for each zone) because the goal was to determine large-scale habitat use patterns in an estuarine complex. Modeling the estuary as constituent parts would likely create more accurate models for each zone (e.g., Bacheler et al. 2009a), but it may reduce the study's applicability to other estuarine systems. Furthermore, Mobile Bay is a particularly dynamic estuary with

complex hydrographic processes. For example, the salinity flux in Mobile Bay is highly variable, depending primarily on river discharge and secondarily on wind speed, wind direction, and tides (Coogan and Dzwonkowski 2018). Therefore, it is most effective to analyze the habitat use patterns of species in this system in a general, region-wide manner.

Prior to model selection, variance inflation factors were calculated for all of the predictors in each model to determine the degree of collinearity between variables. No variables exhibited a variance inflation factor above 2.5, which is well below the established cutoff value of 5 (Hair et al. 1995). All of the models were optimized using a backwards stepwise “leave-one-out” variable selection method to determine which set of predictors best explained the response. The full models included all of the possible predictors as well as all of the two-way interactions between them. The significance of the predictors was determined using single-term deletions and subsequent likelihood ratio testing between the nested models. A predictor was considered significant at $\alpha = 0.05$ if its deletion from the model significantly reduced the model fit. Comparisons of model fit via Akaike's information criterion (AIC) were also assessed for a drop of more than 2 (Burnham and Anderson 2002), and they were in agreement with the likelihood ratio tests. In a stepwise manner (starting with the term with the highest *P*-value), nonsignificant two-way interactions and main effects were removed, leaving models that included only significant single predictors and interaction terms.

To visually represent the results from each of the best-fitting models, the predicted responses and 95% confidence intervals were plotted against each predictor while holding all of the other predictors at their mean values. For the models in which season (a categorical variable) was significant, we also fitted simplified models that excluded season and any significant interactions between season and the other predictors. These simplified models were used to produce predicted responses and confidence intervals across the other significant predictors for plotting purposes. To visualize the effect of interaction terms on the response, the model predictions were plotted against one of the interacting predictors at the 25th quantile (referred to as “low”) and 75th quantile (referred to as “high”) of the other interacting predictor.

Finally, to create a simple characterization of the frequency of inter- and intraspecific co-occurrence, the data were partitioned into three different catch event types: (1) interspecific, where at least one individual of both species were caught together, (2) Red Drum intraspecific, where two or more Red Drum were caught (Spotted Seatrout could be present), and (3) Spotted Seatrout intraspecific, where two or more Spotted Seatrout were caught (Red

Drum could be present). The number of each event type was then summed, and a percentage was calculated for each to determine the proportion of their occurrences. All analyses and data visualizations were conducted in R using the R packages MASS, stats, and ggplot2.

RESULTS

Summary of Catch Data

In total, 527 Red Drum (mean standard length \pm SE = 424.42 ± 6.12 mm) and 1,399 Spotted Seatrout (397.27 ± 2.40 mm) were caught, and 32.5% of gill nets caught Red Drum and/or Spotted Seatrout. The catch event type with the highest percentage of occurrence was Spotted Seatrout intraspecific (13.3%), while Red Drum intraspecific was the least common (4.2%). This indicates that Spotted Seatrout were generally caught more often and experienced higher instances of intraspecific co-occurrence than Red Drum. The percentage of gill nets with interspecific co-occurrence events was only 5.4%, suggesting that overlap between these species occurs relatively infrequently as compared to the percentage of gill nets that caught either of them (32.5%).

Habitat Associations of Red Drum and Spotted Seatrout

The probability of Red Drum presence was influenced by the interaction between dissolved oxygen and temperature (Figure 3A; $P=0.039$), the interaction between water depth and salinity (Figure 3B; $P=0.005$), the interaction between salinity and dissolved oxygen (Figure 3C; $P=0.022$), the interaction between area of SAV and marsh edge extent (Figure 3D; $P=0.001$), and season (Figure 3E; $P<0.001$). The probability of Red Drum presence was negatively related to dissolved oxygen but only when temperature was low (19.6°C). Red Drum presence was negatively related to water depth, but this relationship was more pronounced when salinity was high (21.0‰) compared to when salinity was low (8.1‰). Similarly, a negative relationship was observed with salinity but was slightly stronger when dissolved oxygen was high (8.3 mg/L) compared to when dissolved oxygen was low (6.0 mg/L). Red Drum presence was positively related to increasing area of SAV, but this relationship was more pronounced when marsh edge extent was low (1,496.5 m) compared to when marsh edge extent was high (15,598.2 m). The probability of Red Drum presence was lowest in the winter, moderate during the spring and summer, and highest in the fall.

The probability of Spotted Seatrout presence was influenced by the interaction between dissolved oxygen and temperature (Figure 4A; $P<0.001$), the interaction between salinity and temperature (Figure 4B; $P<0.01$), the length of marsh edge (Figure 4C; $P=0.001$), the

interaction between area of SAV and salinity (Figure 4D; $P<0.001$), and the interaction between area of SAV and season (Figure 4E; $P=0.002$). Spotted Seatrout presence was negatively related to both dissolved oxygen and salinity when temperature was low (19.6°C), but presence was slightly positively related to both predictors when temperature was high (29.2°C). Spotted Seatrout presence exhibited a positive relationship with the length of emergent marsh edge. A similar positive relationship was observed with area of SAV but only under high-salinity conditions (21.0‰). The presence of Spotted Seatrout was positively related to increasing area of SAV in the winter, summer, and fall but exhibited a negative relationship in the spring.

Conditions for Co-Occurrence

The probability of an interspecific co-occurrence event was influenced by the interaction between dissolved oxygen and temperature (Figure 5A; $P=0.047$), the interaction between water depth and temperature (Figure 5B; $P=0.009$), the length of marsh edge (Figure 5C; $P=0.045$), and the interaction between area of SAV and salinity (Figure 5D; $P=0.009$). The probability of a co-occurrence event was negatively related to dissolved oxygen when temperature was low (19.6°C) but not when temperature was high (29.2°C). A similar negative relationship was observed with water depth when temperature was high but not when temperature was low. Co-occurrence events were positively related to increasing length of marsh edge and increasing area of SAV. However, this positive relationship with SAV was more pronounced under high-salinity conditions (21.0‰).

DISCUSSION

Spatiotemporal overlap between predators often results in ecological interactions, such as shifts in trophic dynamics, which can shape the roles of predators in their shared ecosystem (Sih et al. 1998). Here, we used a long-term gill-net sampling data set to reveal similarities in habitat use between Red Drum and Spotted Seatrout, but our results also indicated that these sympatric estuarine predator species exhibit subtle habitat partitioning. Both species associated with similar environmental conditions, but the predictors often had interactive effects with other variables. The nature of these interactions suggested specialization in the species' associations with biogenic habitats and differences in their responses to compounding stressors. The habitats in which interspecific co-occurrence was observed most frequently generally aligned with the habitat associations that were shared by both species. These results clarify the influence of abiotic and biotic variables on the distribution and abundance of these species and suggest mechanisms by which they are able to co-exist.

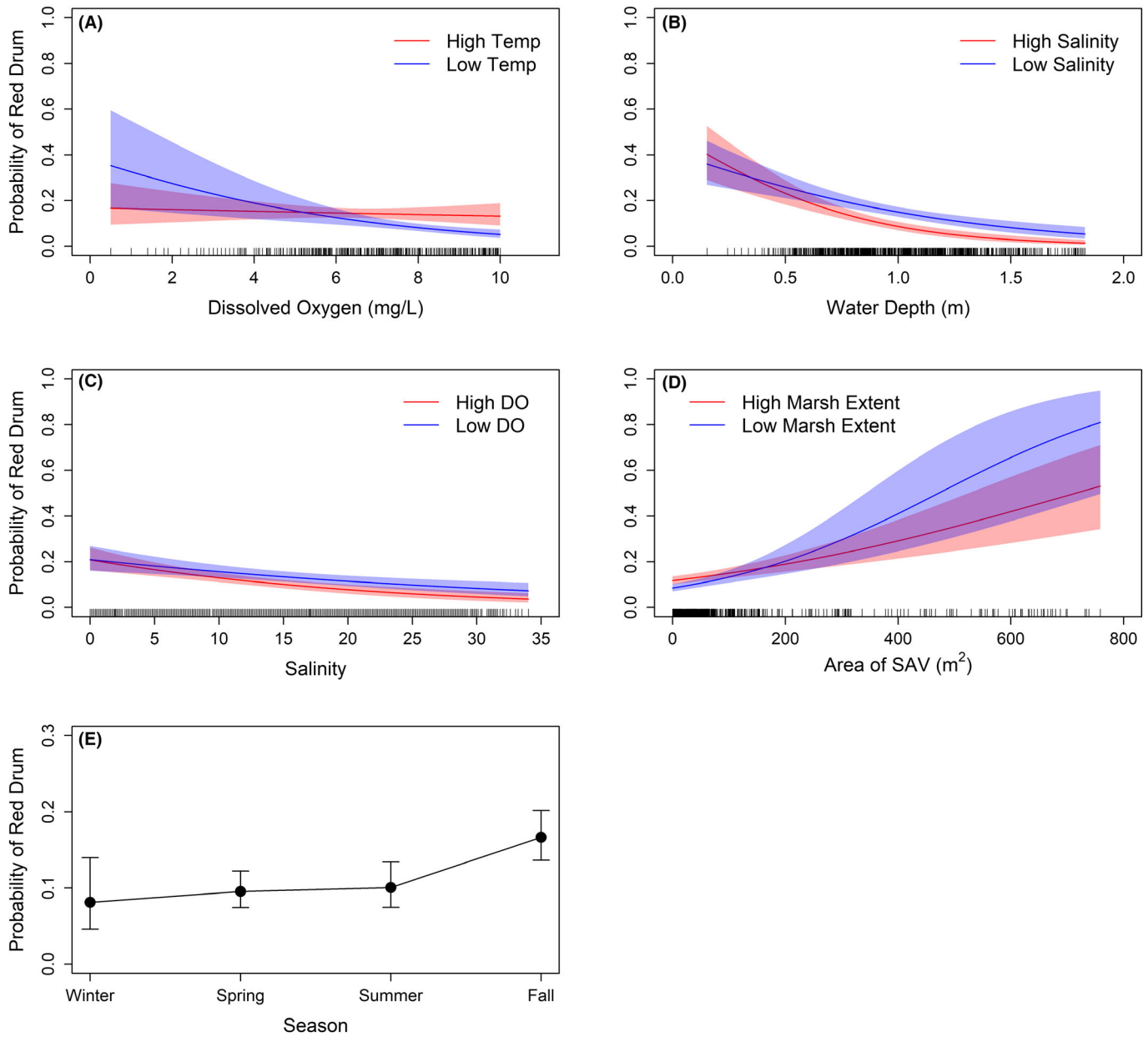


FIGURE 3. Red Drum presence or absence as predicted by (A) the interaction between dissolved oxygen and temperature, (B) the interaction between water depth and salinity, (C) the interaction between salinity and dissolved oxygen, (D) the interaction between SAV and marsh extent, and (E) season. Plots represent predicted probabilities and 95% confidence intervals from a logistic regression with statistically significant predictors only. The values in (A), (B), (C), and (D) are from a separate model without season.

Spotted Seatrout were encountered more frequently than Red Drum throughout the sampling period, suggesting that Spotted Seatrout are the more abundant species in this estuarine system. It is possible that inherent differences in body shape and movement patterns between Red Drum and Spotted Seatrout influenced their catchability in the gill nets. However, this remains to be tested and the wide range of gill-net mesh sizes used in this study (5–15-cm stretch) reduces the likelihood that species selectivity

influenced the observed catch rates. Potentially as a result of their generally high densities, intraspecific co-occurrence was observed frequently for Spotted Seatrout. When multiple conspecifics are present at one location in the estuary, behavioral interactions between them have the potential to impact their ecological roles (Abrams and Ginzburg 2000). Both Red Drum and Spotted Seatrout have been observed to alter their trophic dynamics when two conspecifics forage together as compared to when single

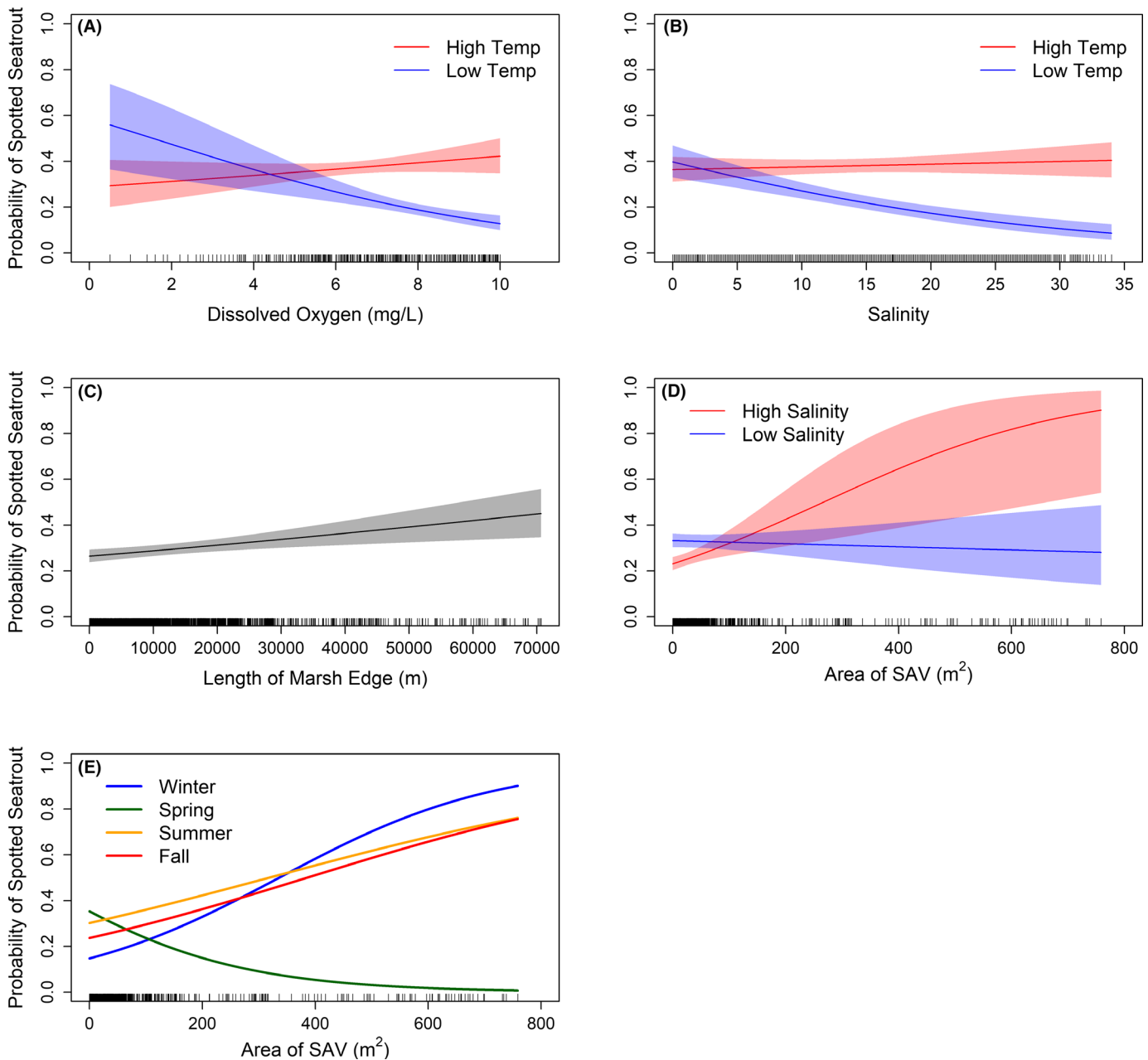


FIGURE 4. Spotted Seatrout presence or absence as predicted by (A) the interaction between dissolved oxygen and temperature, (B) the interaction between salinity and temperature, (C) the length of marsh edge, (D) the interaction between SAV and salinity, and (E) the interaction between SAV and season. Plots represent the predicted probabilities and 95% confidence intervals from a logistic regression with statistically significant predictors only. The values in (A), (B), (C), and (D) are from a separate model without season.

individuals forage alone. In the presence of a conspecific, Spotted Seatrout often reduce their per capita prey consumption, whereas Red Drum often increase their per capita prey consumption (Livernois et al. 2019). Numerous studies have similarly documented either positive or negative effects of conspecific predator density on predation rates for a variety of marine and coastal species, including reef-associated fishes (Stallings and Dingeldein 2012; Stier

and White 2014) and estuarine invertebrates (Booth et al. 2018). Therefore, behavioral interactions between conspecific predators are likely to be important factors shaping predation pressures in this estuarine system, especially for predators like Spotted Seatrout that co-occur frequently.

Surprisingly, both Red Drum and Spotted Seatrout were observed to be negatively associated with increasing

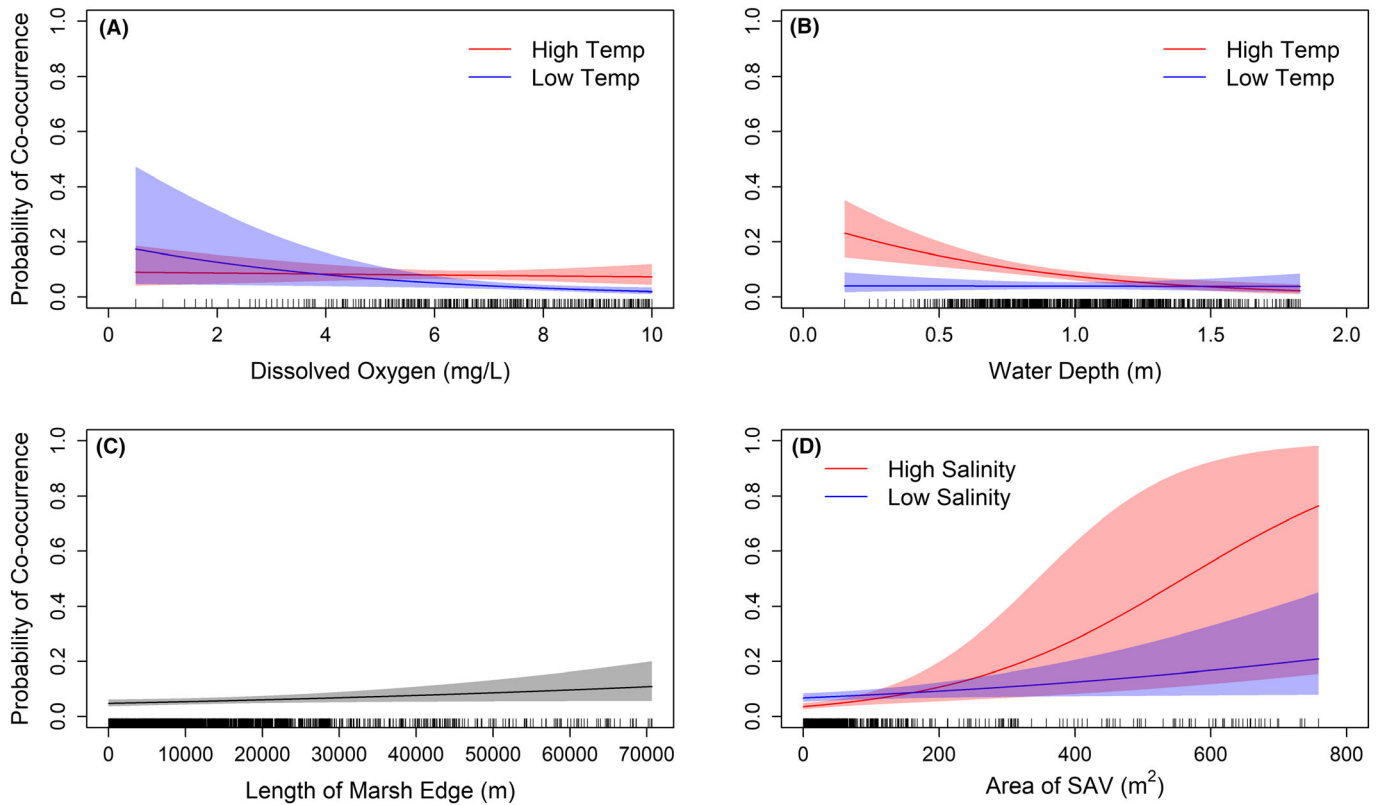


FIGURE 5. Probability of a co-occurrence event (presence of both Red Drum and Spotted Seatrout) as predicted by (A) the interaction between dissolved oxygen and temperature, (B) the interaction between water depth and temperature, (C) the length of marsh edge, and (D) the interaction between area of SAV and salinity. Plots represent the predicted probabilities and 95% confidence intervals from a logistic regression with statistically significant predictors only.

dissolved oxygen concentrations. Hypoxia (dissolved oxygen less than 2 mg/L) is deleterious to the health of most marine organisms, and many mobile species will actively avoid those conditions (Breitburg 2002). The observed association of both Red Drum and Spotted Seatrout with low surface water dissolved oxygen is thus unexpected but may be indicative of a tradeoff between stress (low oxygen) and an ecological benefit. Multiple elasmobranch and teleost predators have exhibited a similar ability to inhabit hypoxic zones, and some appear to continue feeding in those conditions (Jorgensen et al. 2009; Craig et al. 2010; Mohan and Walther 2016; Navarro et al. 2016). Furthermore, prey have been observed to experience increased predation pressure in low dissolved oxygen conditions (Rahel and Kolar 1990), so the movement of predators into hypoxic zones may be a strategy to increase feeding opportunities or avoid competitors. Hypoxic events are expected to increase in size, frequency, and duration in the northern Gulf of Mexico (Diaz and Breitburg 2009; Laurent et al. 2018), and understanding the effects of varying oxygen concentration on predator behavior can aid in predicting ecosystem-level responses to those changes.

Similar to the negative effects of dissolved oxygen, elevated water temperatures can cause acute stress in ectothermic organisms, generally due to increased physiological demands (Madeira et al. 2013). Though both species frequently appeared in low dissolved oxygen conditions, this relationship had an interactive effect with temperature, which was more pronounced for Spotted Seatrout than for Red Drum. Therefore, areas with low dissolved oxygen concentrations and high temperatures are especially stressful, and it appears as though Spotted Seatrout avoided those conditions. These results suggest that Red Drum and Spotted Seatrout differ in their ability to tolerate multiple compounding stressors, and Red Drum appear to be more robust to those conditions. Similar patterns have been observed in other estuarine fish communities, with differences emerging between species in their ability to tolerate the combination of low dissolved oxygen and high temperature. As a result, fish community structure in regions experiencing those multiple compounding stressors is often dominated by species with elevated physiological tolerances (Layman et al. 2000; Smith and Able 2003). Additionally, the probability of co-

occurrence between Red Drum and Spotted Seatrout was increased in low dissolved oxygen conditions but only when temperature was low. Therefore, any ecological or biological benefit that individuals might experience in those conditions is likely shared by both species, but increased temperature may exclude Spotted Seatrout. Water temperatures have been increasing in the northern Gulf of Mexico over the last four decades (Turner et al. 2017), a trend that may alter the distribution of species that are sensitive to temperature stress (e.g., Gulf of Mexico Spotted Seatrout). Continued monitoring of Red Drum and Spotted Seatrout populations will be necessary to determine best practices for management under changing environmental conditions.

Throughout their life history, Red Drum are known to use low-salinity areas and can physiologically tolerate freshwater, as evidenced by the maintenance of their osmotic balance during low-salinity exposure (Watson et al. 2014). However, adult Spotted Seatrout have been observed to make directional movements away from intense freshwater flow events (Callihan et al. 2015), and they exhibit reduced metabolic scope and swimming velocity at salinities of 10‰ or less (Wohlschlag and Wakeman 1978). Although the osmoregulatory abilities of these species have not been explicitly compared, it appears as though low-salinity conditions are likely to be more stressful for Spotted Seatrout than for Red Drum. In the present study, Spotted Seatrout were observed less frequently in low-salinity conditions when temperature was high, considering both of those variables as potential stressors. Therefore, the ability of Spotted Seatrout to use freshwater-dominated habitats appears to be limited when compounding stressors are present (i.e., elevated temperature), whereas Red Drum appear to tolerate low salinities regardless of other potential stressors. A similar pattern of salinity-dependent co-occurrence was observed for Bull Sharks *Carcharhinus leucas* and Blacktip Sharks *Carcharhinus limbatus* along the Texas coast (Matich et al. 2017). Bull Sharks are euryhaline (similar to Red Drum), while Blacktip Sharks generally prefer moderate to high salinities (similar to Spotted Seatrout). Co-occurrence of these species was observed in higher salinities compared to single-species catch events, suggesting that overlap between them was limited in low-salinity regions, where Blacktip Sharks were potentially excluded by physiological constraints and competitive interactions (Matich et al. 2017). Differences in the osmoregulatory and physiological tolerances of Red Drum and Spotted Seatrout may thus influence their co-occurrence patterns in estuaries like Mobile Bay, where salinities are highly variable in both space and time.

Beyond physiological limitations, there are other possible explanations for the observed temperature-dependent salinity associations of Spotted Seatrout. For example,

adult Spotted Seatrout spawn when temperatures increase in the spring and summer, and the optimal salinity observed for their larvae is around 20‰ (Froeschke and Froeschke 2011). Therefore, the lack of relationship between Spotted Seatrout abundance and salinity at high temperatures may be related to the selection of moderate- to high-salinity habitats by spawning adults during warm conditions. A variety of other unmeasured factors may also influence the movement of Spotted Seatrout into low-salinity water, such as prey availability or temperature refuge in riverine and deltaic regions during the winter, so further study is necessary to understand the mechanisms behind the observed patterns of salinity-driven habitat use.

Sympatric predators can exhibit depth-related habitat partitioning, which is often related to differences in trophic ecology between the species. For example, Hixon (1980) described a mechanism of coexistence for two sympatric species of surfperch *Embiotoca* in a California reef system: the two species exhibited depth-related habitat partitioning, which was driven primarily by the availability of different prey sources along a depth gradient. The dominant competitor in the system capitalized on shallow, food-rich regions, while the subordinate species found refuge from competition in the deeper, less productive habitats (Hixon 1980). We observed similar differences between Red Drum and Spotted Seatrout in their associations with water depth; Red Drum were caught more frequently in shallow water, whereas Spotted Seatrout exhibited no relationship with depth. Moulton et al. (2017) determined that in a Texas estuary, Red Drum generally inhabited shallower waters than Spotted Seatrout; the results presented here provide further evidence that these species exhibit depth-related differences in habitat use. Both species are demersal predators, but Red Drum are thought to be mainly oriented with the benthos. Red Drum feed primarily on benthic invertebrates, such as small shrimp and crabs that inhabit shallow waters, while Spotted Seatrout consume similar shallow-water prey in addition to a greater proportion of midwater fishes (e.g., menhaden *Brevoortia* spp. and mullets *Mugil* spp.; Llano et al. 1998). The probability of co-occurrence was increased in shallow waters when temperature was high, but co-occurrence was infrequent in deeper waters regardless of temperature. These results suggest that the use of deep water by Spotted Seatrout reduces the likelihood of encountering a Red Drum, thus alleviating potential competitive interactions between them that may occur in shallow water.

Similarities arose between Red Drum and Spotted Seatrout in their use of biogenic habitats, but slight differences were observed that indicated subtle habitat partitioning. Red Drum and Spotted Seatrout were both positively associated with extensive SAV, but this relationship was only true in high-salinity conditions for Spotted

Seatrout. This indicates an association of Spotted Seatrout with marine seagrasses as opposed to brackish and fresh-water SAV. Submerged vegetation provides critical refuge and foraging habitat for Red Drum and Spotted Seatrout at their postsettlement to juvenile life stages (McMichael and Peters 1989; Rooker et al. 1998), and the results of this study indicate that SAV continues to be an important habitat for subadult and adult individuals. Adult Red Drum and (to a lesser extent) Spotted Seatrout have been observed using seagrass habitats in other estuaries in the Gulf of Mexico and along the U.S. Atlantic coast (Fodrie et al. 2015; Moulton et al. 2017). However, salinity-dependent use of SAV by Spotted Seatrout has not been described previously and may be an important factor in the selection of habitats by this species in river-dominated estuaries like Mobile Bay.

Both habitat partitioning and trophic partitioning are important factors structuring species assemblages in estuaries (Ross 1986), but these niche separations can be confounded with one another (i.e., different habitats can harbor distinct prey assemblages). In this study, Spotted Seatrout appeared to inhabit areas with extensive emergent marsh edges. Our results also suggested that marsh edges are important habitats for Red Drum, considering that their positive association with SAV was diminished when marsh edge was extensive. Since both Red Drum and Spotted Seatrout were associated with marsh edges and high-salinity SAV, co-occurrence probability was unsurprisingly high in those habitats. Both of these predators consume prey that are known to inhabit marsh edges and seagrass beds, such as penaeid shrimps and small structure-associated finfish (Rozas and Reed 1993; Heck et al. 2003). Trophic interactions between them are thus likely to occur in these prey-rich, shallow biogenic habitats, which could alter their foraging strategies or the pressures they impose on common shared prey populations (Sih et al. 1998). However, marine seagrass beds are found primarily in the coastal reaches of this estuarine system (Mississippi Sound and Perdido Bay), while extensive low-salinity SAV beds exist in the northern river delta. These freshwater and brackish-water SAV beds may provide Red Drum with refuge and foraging grounds free from Spotted Seatrout—a potential competitor for resources that exhibits limited use of this habitat. Ecosystem-based management initiatives should consider these region-specific habitat associations, as critical ecological value can likely be gained by conserving habitats that may provide refuge from competition for sympatric predators.

Red Drum and Spotted Seatrout commonly exhibit seasonal patterns in movement and habitat use, which can be related to temperature (Moulton et al. 2017) and spawning activities (Nieland et al. 2002; Powers et al. 2012). A seasonal pattern of SAV use was observed for Spotted Seatrout, with individuals primarily inhabiting areas with

minimal SAV coverage in the spring. River discharge in Mobile Bay generally reaches its maximum in the late winter to early spring (Stumpf et al. 1993), so it is possible that Spotted Seatrout are displaced from coastal seagrass beds by dramatic decreases in salinity due to freshwater inflow. Concurrently, Spotted Seatrout form spawning aggregations in the spring and summer (beginning in April), often in regions within estuaries characterized by moderate to high salinity and deep water, where SAV is unlikely to thrive due to lack of light availability (Saucier and Baltz 1993; Kenworthy and Fonseca 1996; Brown-Peterson and Warren 2001). A seasonal pattern was also observed for Red Drum, with their probability of presence being highest in the fall. This temporal trend aligns with the timing of Red Drum spawning, usually from late September to early October (Powers et al. 2012). Gill nets used in this study were selective for subadult and adult individuals, so an annual influx of new (year 1) recruits to the system each fall could have driven the observed trend.

The results presented in this study elucidate the habitat associations and coexistence patterns of Red Drum and Spotted Seatrout at their subadult to adult size range. It is critical to understand the habitat requirements of individuals at this intermediate age, when the two species are coexisting within the estuary while they grow and develop. Determining the habitats that support each species independently, as well as when and where they are most likely to co-occur, suggests how these sympatric species are able to coexist. This information can also guide multispecies management efforts, which emphasize the protection of habitats that are critical to a variety of species. Our results suggest that both Red Drum and Spotted Seatrout rely on biogenic habitats (wetlands and SAV), which have been degraded considerably by coastal development, climate change, and sea level rise (Lotze et al. 2006). Not only do these biogenic habitats provide critical nursery and foraging habitats for estuarine fish, such as Red Drum and Spotted Seatrout, they also protect against shoreline erosion and aid in carbon sequestration and water filtration (Costanza et al. 1997; Barbier et al. 2011). Conservation and restoration efforts that focus on these critical biogenic habitats will likely benefit multiple estuarine predator species while enhancing overall ecosystem functioning and health.

ACKNOWLEDGMENTS

We thank the staff of the Alabama Department of Conservation and Natural Resources, Marine Resources Division for their efforts in collecting the gill-net data used in this study. Additional data were provided by MBNEP and the National Oceanic and Atmospheric Administration. Thank you to D. Byron, R. Collini, and J. Kudullis at MBNEP for providing access to the SAV coverage

data. We thank S. Bosarge for assisting with GIS. This manuscript was greatly improved by the thoughtful comments of the anonymous reviewers. M.C.L. was supported by a grant (USA 272504) from the Bureau of Ocean Energy Management. There is no conflict of interest declared in this article.

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