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Population dynamics, relative abundance, and habitat suitability for adult red drum (*Sciaenops ocellatus*) in nearshore waters of the north-central Gulf of Mexico

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Abstract—In the Gulf of Mexico, the red drum (*Sciaenops ocellatus*) is an immensely popular sportfish, yet the Gulf of Mexico stock is currently managed as data-limited in federal waters. The results of the federal stock assessment conducted in 2016 for Gulf of Mexico red drum were not recommended for providing management advice. Consequently, we sought to address data gaps highlighted in the assessment by producing up-to-date overall and sex-specific growth models, standardized indices of relative abundance, and predictions of habitat suitability and by updating estimates of natural mortality. Using a time series for the period of 2006–2018, we assigned ages of 0–36 years to 1178 red drum. A negative binomial generalized linear model including variables for year, depth, surface temperature, dissolved oxygen, and bottom salinity was used to standardize an index of relative abundance. Examination of catch per unit of effort revealed that adult red drum were significantly more abundant in state waters than in federal waters. These findings were explained by habitat suitability models, which were used to identify surface current velocity, surface temperature, and depth as the strongest predictors of relative abundance. The results of our investigation reveal that the adult spawning stock of red drum in the Gulf of Mexico is not fully protected by the catch moratorium in federal waters.

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Advances in approaches to data collection and statistical techniques have ushered in the next generation of stock assessments (Lynch et al., 2018). For data-rich species, stock assessments can incorporate ecosystem-based inputs (Lynch et al., 2018), often through the use of spatially explicit approaches (e.g., Goethel et al., 2011; Berger et al., 2017). Despite these advances, more than half of U.S. stocks remain data-limited (Newman et al., 2015). Enhancing basic data inputs is imperative for improving assessments for these stocks. For stocks under aggressive rebuilding schedules, those for which catch data may not reflect population trends or for which catch is completely restricted, the need for reliable time series that track abundance is even more critical.

In the Gulf of Mexico (GOM), the red drum (*Sciaenops ocellatus*) is a highly prized species supporting valuable recreational fisheries. Recreational catch of red drum is permitted in all state waters in the GOM (out to 3 nautical miles [nmi] in Louisiana, Mississippi, and Alabama and out to 9 nmi in Texas and Florida), but a catch moratorium in federal waters has been in place since 1987. In addition, commercial fishing of this species is prohibited in all GOM states except Mississippi. Consequently, the data sources that would be useful for assessing GOM red drum (e.g., commercial landings) are lacking (Powers et al., 2012). Therefore, despite a wealth of knowledge on population connectivity (e.g., Rooker et al., 2010), movement and recruitment (e.g., Burnsed et al., 2020), and

spawning (e.g., Lowerre-Barbieri et al., 2019), the red drum in the Gulf of Mexico is classified by the National Marine Fisheries Service as a "data-limited species" (SEDAR, 2016).

The reauthorization in 2006 of the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens . . . 2021) required development and implementation of annual catch limits for all federally managed stocks, a mandate that spurred significant advances in the development of methods for assessment of data-limited stocks (Newman et al., 2015). One of these methods, as implemented in the R package DLMtool (vers. 3.2.1; Carruthers and Hordyk, 2018), was recently used to assess a suite of data-limited species in the GOM, including the lane snapper (*Lutjanus synagris*), wenchman (*Pristipomoides aquilonaris*), yellowmouth grouper (*Mycteroperca interstitialis*), speckled hind (*Epinephelus drummondhayi*), snowy grouper (*Hyporthodus niveatus*), almaco jack (*Seriola rivoliana*), lesser amberjack (*S. fasciata*), and red drum (SEDAR, 2016). During this assessment, at least one method for data-limited species was identified as having preferable performance compared to the status quo for every species examined, with the notable exception of red drum (SEDAR, 2016). Therefore, despite new tools tailored to the assessment of data-limited species and a wealth of information about the population biology and ecology of red drum, the results from this assessment were not recommended for providing management advice for red drum (SEDAR, 2016).

Careful consideration of existing data sets can improve our ability to assess stocks like the GOM stock of red drum. Specific data recommendations from the most recent assessment of red drum include 1) expansion of efforts to collect samples, for analysis of age and length, at varying sizes, seasons, months, and locations, particularly for offshore fish; 2) identification or optimization of fishery-independent surveys to characterize relative abundance in federal waters; and 3) exploration of ways to increase data collection from existing fishery-independent surveys (SEDAR, 2016). To those ends, the goals of this study were to combine data from fishery-independent surveys operating throughout the year and across the continental shelf to produce up-to-date overall and sex-specific growth models, update estimates of the instantaneous natural mortality rate (M), generate standardized indices of relative abundance, and provide predictions of habitat suitability for red drum in the north-central GOM, with the expectation that the results of these efforts can be used to optimize future fishery-independent surveys.

Materials and methods

Data collection

Catch data for adult red drum were collected during fishery-independent bottom longline surveys conducted in all seasons in the north-central GOM during 2006–2018 (Fig. 1). The locations for bottom longline surveys were selected by using a stratified-random sampling design and were sampled following standardized methods described in Drymon et al. (2013, 2020). Briefly, the mainline consisted of 1.85 km (1 nmi) of 4-mm monofilament (545 kg test) that was set with 100 gangions. Gangions consisted of a longline snap and a 15/0 circle hook baited with Atlantic mackerel (*Scomber scombrus*). Each gangion was made of 3.66 m of 3-mm monofilament (320 kg test). All sets were soaked for 1 h, and mid-set measurements of surface and bottom temperatures (in degrees Celsius), salinity, and bottom dissolved oxygen (in milligrams per liter), as well as of depth at the start and end of each set (in meters), were recorded. During the retrieval of the bottom longline, all red drum encountered were measured to the nearest millimeter (maximum total length [TL]), weighed, and retained, and their sex was determined. Sagittal otoliths were extracted for age and growth analyses. Catch data were converted to catch per unit of effort (CPUE), expressed as the number of individuals per 100 hooks per hour.

To augment the samples of adult red drum from the bottom longline survey, smaller red drum were collected from the monthly gill-net survey of the Alabama Department of Conservation and Natural Resources, Marine Resources Division, during 2006–2018; these additional samples were aged. This survey includes areas of coastal Alabama from eastern Mississippi Sound to western Perdido Bay and Mobile Bay (Fig. 1) (Livernois et al., 2020). The gill-net survey of the Marine Resources Division involves 2 different nets: a small-mesh gill net and a large-mesh gill net. The small-mesh gill net consists of 5 panels that are 45.0 m long by 2.4 m deep, each containing stretch meshes in sizes of 5.1–10.2 cm. The large-mesh gill net consists of 4 panels that are also 45.0 m long by 2.4 m deep, with stretch meshes in sizes of 11.4–15.2 cm. Red drum caught in either gill net were measured to the nearest millimeter (maximum TL) and weighed, and their sex was determined. Sagittal otoliths were extracted for age and growth analyses.

For fish of all ages combined (from both longline and gill-net surveys), 2-sample Kolmogorov–Smirnov tests were used to examine differences in length and weight distributions between sexes. Some red drum collected with longlines were not measured for TL. For red drum from longline surveys that had both maximum total and fork length (FL) measurements, linear regression was used to examine the relationship of maximum TL to FL, resulting in this equation:

$$TL = 1.04(FL) + 23.53, \quad (1)$$

where TLs and FLs are expressed in millimeters (number of samples [n]=346, coefficient of multiple determination [R^2]=0.96). This regression was used to estimate the TLs of red drum from the longline survey that were lacking a maximum TL measurement (n=238). Differences in sex ratio were tested by using a chi-square test (Pearson, 1900) against an expected 1:1 male-to-female ratio.

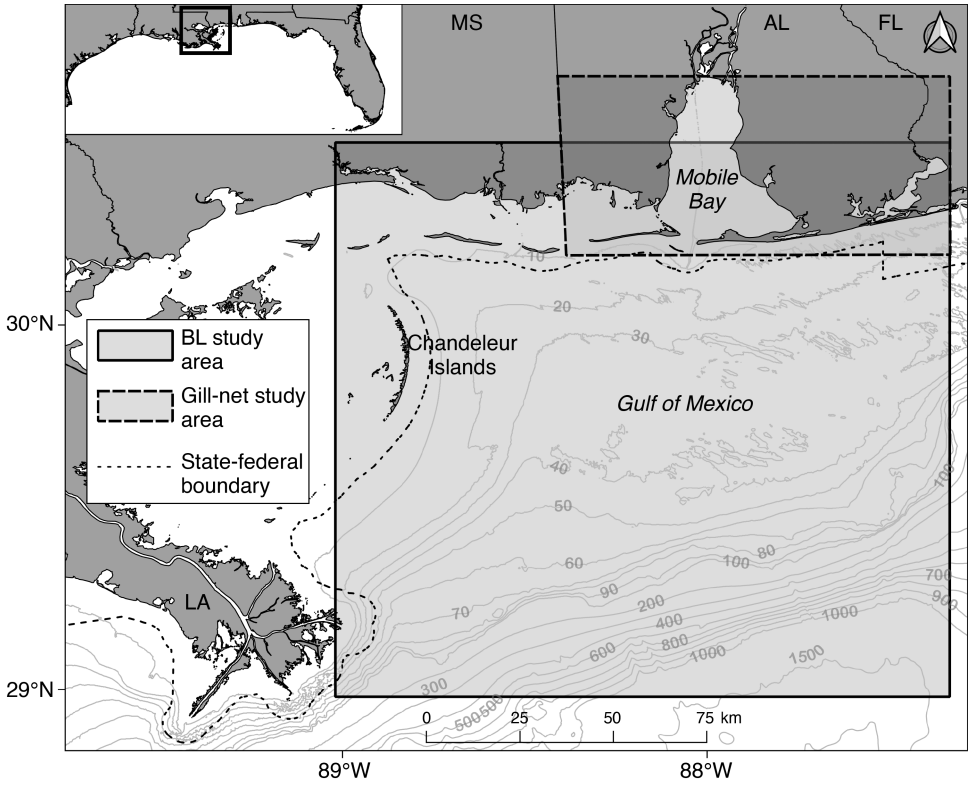

Figure 1

Map of the study areas in the north-central Gulf of Mexico where red drum (*Sciaenops ocellatus*) were collected during fishery-independent bottom longline (BL) and gill-net surveys from 2006 through 2018. The dashed line that follows the coastline indicates the boundary between state and federal waters. Gray lines indicate depth contours. LA=Louisiana; MS=Mississippi; AL=Alabama; FL=Florida.

Otolith processing and aging

All otoliths were processed following procedures detailed in Powers et al. (2012) and VanderKooy et al.[1] A portion of the fish aged in Powers et al. (2012) were also included in our study; however, these fish were aged again as part of this study for consistency. Once otoliths were processed, aging was conducted by 2 readers independently (without consultation between readers) and blindly (without knowledge of fish capture date or size). Each otolith section was viewed with an Olympus[2] SZX16 stereomicroscope (Olympus Corp., Tokyo, Japan) with transmitted light (brightfield illumination). The number of opaque zones was counted along the ventral edge of the sulcus acusticus. A margin code (1–4) was assigned to the otolith margin, according to the otolith manual of the Gulf States Marine Fisheries Commission (VanderKooy et al.[1]).

Whole age, in years, was calculated for each fish according to guidelines of the Gulf States Marine Fisheries Commission. If the collection month was January–June and the margin code was 3 or 4, the whole age equaled the number of opaque zones, plus 1. If the collection month was October–December and the margin code was 1 or 2, the whole age equaled the number of opaque zones, minus 1. For all other combinations of capture month and margin code, the whole age equaled the number of opaque zones. Next, the number of days between the capture date and October 1 (the assumed birth date of red drum; Ditty, 1986) of the previous year was calculated. This number was then divided by the total number of days in the capture year, and the result was added to the whole age to yield the fractional age.

If the readers assigned different whole ages to any otolith, the readers consulted with each other or a third reader aged the otolith. If the 2 initial readers did not reach an agreement or if the third reader did not agree with 1 of the 2 initial ages, the otolith was excluded from further analysis. Average percent error was calculated for all whole ages to

[1] VanderKooy, S., J. Carroll, S. Elzey, J. Gilmore, and J. Kipp (eds.). 2020. A practical handbook for determining the ages of Gulf of Mexico and Atlantic Coast fishes, 3rd ed. Gulf States Mar. Fish. Comm., Publ. 300, 248 p. [Available from website.]

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

evaluate between-reader precision (Beamish and Fournier, 1981; Campana, 2001). Two-sample Kolmogorov–Smirnov tests were used to examine differences in fractional age distributions between sexes.

Modeling growth

To estimate growth parameters for red drum in this study, the von Bertalanffy growth function (VBGF) was fit to female and male red drum and to red drum of unknown sex for the complete data set, the fishery-independent Marine Resources Division gill-net data set, and the bottom longline data set, by using the following equation (von Bertalanffy, 1938):

$$L_t = L_\infty(1 - e^{-K(t - t_0)}), \quad (2)$$

where L_t = the predicted TL in millimeters;
L_∞ = the mean asymptotic length in millimeters;
K = the Brody growth coefficient (years^{-1});
t = the time (fractional age) in years; and
t_0 = the hypothetical age in years at which length equals 0.

The VBGF was used to model sex-specific growth. Eight candidate versions of the VBGF were fit to the sex-specific fractional age data: a general version, where all 3 parameters (L_∞, K, and t_0) could vary between sexes; 3 versions where 2 of the 3 parameters could vary between sexes; 3 versions where only 1 parameter could vary between sexes; and a common version where all 3 parameters were held constant between sexes (Ogle, 2016; Nelson et al., 2018; Jefferson et al., 2019). Akaike information criterion (AIC) values were used to rank these models on the basis of fit and to identify the best-fitting version (Akaike, 1998; Katsanevakis and Maravelias, 2008; Ogle, 2016). All growth parameters were modeled in statistical software R, vers. 4.1.0 (R Core Team, 2021), with the add-on packages FSA (vers. 0.9.1; Ogle et al., 2021) and nlstools (vers. 1.0-2; Baty et al., 2015).

Estimating mortality

By using whole ages of fish sampled in bottom longline surveys, an age-based catch curve (Chapman and Robson, 1960) was created for calculating total mortality; however, graphical examination of the catch curve revealed that critical assumptions necessary for estimating instantaneous total mortality had been violated (Tuckey et al., 2007; Smith et al., 2012). Specifically, red drum did not appear to fully recruit to the gear until age 20; therefore, any mortality estimates generated from this catch curve would not be representative of the stock. Although total mortality estimates were unattainable, M was calculated by using 3 empirical methods (Then et al., 2015; Ogle, 2016):

1. Hoenig$_{\text{fishes}}$, Hoenig's (1983) log-transformed linear regression for fish species,

$$M = e^{1.46 - 1.01\log_e(t_{max})}, \quad (3)$$

where t_{max} = the maximum age of the animal in years;

2. the Hoenig$_{\text{nls}}$ (nonlinear least squares) estimator (Then et al., 2015),

$$M = 4.899t_{max}^{-0.916}; \text{ and} \quad (4)$$

3. the Pauly$_{\text{nls–T}}$ (nonlinear least squares, omitting temperature) estimator (Pauly, 1980; Then et al., 2015),

$$M = 4.118K^{0.73}L_\infty^{-0.333}, \quad (5)$$

where K and L_∞ are parameters from the combined VBGF. All mortality analyses were conducted with FSA in R.

Relative abundance

Yearly changes in CPUE for red drum sampled during bottom longline surveys were examined by generating a nominal index of relative abundance. To standardize the index of relative abundance, a negative binomial generalized linear model (Hardin and Hilbe, 2007) was fit to the CPUE data by using the glmmTMB package (vers. 1.1.2; Brooks et al., 2017) in R. Abiotic variables thought to influence CPUE were added to the model by using forward stepwise model selection. Akaike information criterion values were used to identify the best-fitting model. Model fit was examined by using the DHARMa package (vers. 0.4.3; Hartig, 2021) in R to check for uniformity, outliers, dispersion, and zero inflation. Multicollinearity was tested by using the performance package (vers. 0.7.3; Lüdecke et al., 2021) in R, with variance inflation factors less than 10 signifying low correlation (Dormann et al., 2013). To create a standardized yearly index, the abiotic variables thought to influence CPUE were set to their median values.

Spatial analysis

The index of relative abundance generated as described above was used to examine trends in relative abundance of red drum. First, minimum distance from shore (in kilometers) was calculated in QGIS, vers. 3.8.1 (QGIS Development Team, 2019). Then, nominal CPUE was calculated for 4 discrete areas: <3 nmi from shore (i.e., state waters), 3–6 nmi from shore, 6–9 nmi from shore, and >9 nmi from shore. Finally, a one-way analysis of variance, followed by a Tukey's multiple-pairwise-comparison test, was used to test for differences in nominal CPUE between these 4 areas. Age and length were examined in relation to distance from shore to identify the composition of red drum vulnerable to recreational fishermen in state waters versus that of those protected in federal waters.

Habitat modeling

Boosted regression trees (BRTs) were used to describe the relationships between the CPUE of red drum from bottom longline surveys and environmental variables potentially influencing distribution and abundance. Specifically, BRTs were fit for 3 seasons (meteorological spring, summer, and autumn); winter data were not included in BRT analysis

given that few red drum were captured (n=35) and effort was relatively low (70 stations). Boosted regression trees use machine learning to fit complex, nonlinear relationships and to offer predictive advantages over generalized linear or additive models. For a complete description of BRTs and the methods used in this study, see Drymon et al. (2020).

Results of preliminary analyses indicate a high proportion of zero values (i.e., zero-inflated data). To account for the preponderance of zeros, a 2-step (i.e., delta or hurdle) process was chosen to model catch data. Probability of presence and absence was modeled by using a BRT with a binary distribution, and continuous non-zero (i.e., abundance) probability was modeled by using a BRT with a Gaussian distribution. Because the catch data also contain some instances of anomalously high catch (i.e., long-tailed data), non-zero data were natural log-transformed. Predictions were reverse log-transformed so that the final model is a product of the binary and Gaussian BRTs (Lo et al., 1992).

Sixteen variables with data from multiple sources were considered for the BRTs (see table 1 in Drymon et al., 2020). Although data for some variables (e.g., temperature, salinity, and dissolved oxygen) were collected on-site during bottom longline sampling, all predictor data were obtained following methods outlined in Drymon et al. (2020) to facilitate comparisons with previous habitat modeling in the same region. Surface and bottom temperatures (in degrees Celsius), salinity, and 3-dimensional surface and bottom current velocities (surface, northward, and upward, in meters per second), as well as sea-surface height (in meters), were obtained from the Hybrid Coordinate Ocean Model data server (4-km resolution; HYCOM consortium, available from website, accessed January 2020). Bottom dissolved oxygen (in milligrams per liter) was obtained from Gulf of Mexico Hypoxia Watch maps (NOAA National Centers for Environmental Information, available from website, accessed January 2020) and interpolated across ~100–250 survey stations (the number of stations varied by year). Depth (in meters) and substrate grain size (in millimeters) were obtained from the Coastal Relief Model bathymetry for the Gulf of Mexico (resolution of 0.33 arc seconds or ~10 m; Buczkowski et al., 2006; U.S. Geological Survey, gmx_grd.zip, available from website). Day length (in minutes) was calculated in R by using code by S. Dedman (available from GitHub, accessed January 2020).

Given the quantity of potential predictor data considered within the BRTs, some degree of spatial autocorrelation was anticipated (e.g., between distance from shore and depth, between surface and bottom temperatures); however, BRTs are robust despite autocorrelation among independent variables (Abeare, 2009). All BRTs were fit by using the package gbm.auto (vers. 1.4.1; Dedman et al., 2017) in R. Learning rate, bag fraction, and tree contribution are parameters that are used in concert to determine minimum predictive error (Elith et al., 2008). These parameters were optimized by using gbm.auto for the model run for each season.

Model performance and interpretation

The BRT modeling approach allowed automatic partitioning of the data into training and testing sets, at a ratio dictated by the bag fraction. Ten-fold cross validation was then performed, with the members of the training and testing sets randomized each time. Performance metrics included training and testing correlation, cross-validation deviance (and standard error [SE]), and correlation (and SE), as well as area under receiver-operator curve (AUC) (Hanley and McNeil, 1982) and its cross-validation and cross-validation SE for the binary models (Parisien and Moritz, 2009). The final Gaussian fitted functions from the BRT were visualized by using marginal effect plots to indicate the effect of a particular variable on the response after accounting for the average effects of other model variables (Elith et al., 2008).

Habitat suitability

The distribution of suitable habitat was predicted by using the BRTs described previously. Environmental data for model predictions were obtained as detailed previously, except that Hybrid Coordinate Ocean Model data were extracted for one representative date per season (the monthly groupings for the seasons were March–May, June–August, and September–November). Representative dates for environmental data were selected by ranking the absolute value of the differences between values for all sites for all variables against the mean for those variables, then by identifying the date within each season that most closely matched those values. The BRTs then were used to predict CPUE values for each 2-by-2-km cell. These values were then then mapped in QGIS by using the heatmap setting to produce color points weighted by the predicted abundances generated from the BRT. By using gbm.auto, the coefficient of variance was calculated for the predicted abundance values for each 2-by-2-km cell to represent model variance.

Results

Catch data

Between May 2006 and November 2018, 1296 bottom longline sets were conducted and 815 red drum were caught (Fig. 2), with 741 of those red drum measured and 472 fish kept for otolith collection. Approximately 100 stations were sampled each year (mean: 100 stations [standard deviation 22]; range: 80–143 stations), and survey effort (number of sets) was relatively well distributed across the 3 seasons examined in the BRTs: spring (460 sets), summer (405 sets), and autumn (361 sets). Red drum caught on bottom longlines were primarily encountered in state waters across all seasons (Fig. 2) and were exclusively larger than the size at 50% maturity reported by Bennetts et al. (2019) (Fig. 3A).

To supplement the otoliths taken from the 472 red drum retained from the bottom longline surveys, otoliths from

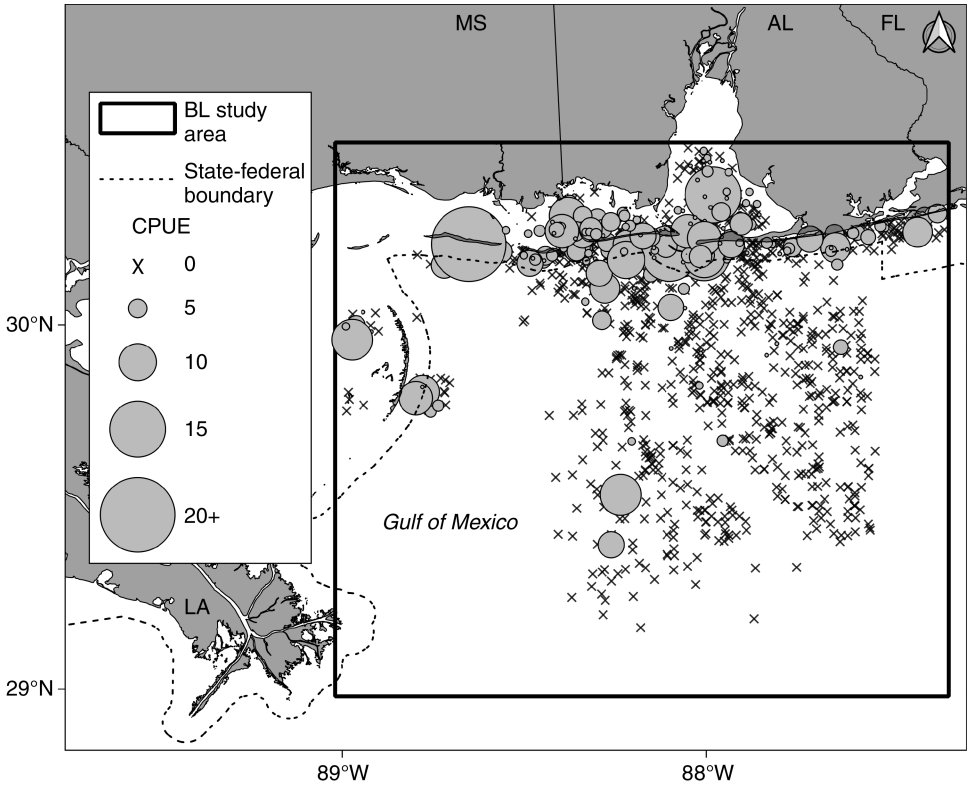

Figure 2

Map of the study area in the north-central Gulf of Mexico showing catch per unit of effort (CPUE) of red drum (*Sciaenops ocellatus*) for the bottom longline (BL) surveys conducted in spring, summer, and autumn during 2006–2018. Size of circles is proportional to CPUE, defined as the number of fish per 100 hooks per hour. The symbol × indicates effort with no catch of red drum. The dashed line that follows the coastline indicates the boundary between state and federal waters.

an additional 709 red drum captured in gill nets were analyzed; therefore, a total of 1181 red drum were used for age and growth analyses. Of these fish, 392 red drum were female, 369 fish were male, and 420 fish were of unknown sex. The female-to-male ratio was 1.06:1.00 and did not differ significantly from a 1:1 ratio (χ^2=0.70, df=1, P=0.40). Total lengths of red drum were 80–1102 mm (Fig. 3B). The average TL of all fish examined (those caught with bottom longlines and gill nets combined) was 619.13 mm (SE 8.22). Results from Kolmogorov–Smirnov tests indicate that females were significantly longer (D=0.20, P<0.01) and heavier (D=0.18, P<0.01) than males.

Age

Ages were assigned to 1178 red drum. Otoliths from the remaining 3 fish (0.25% of all red drum from which otoliths were taken) were deemed unreadable and were omitted from further analysis. Four fish had no length measurements and were also omitted from further analysis. The between-reader percent agreement was 93.46%, and the between-reader average percent error was 4.52%; these estimates are largely driven by differences in the margin codes assigned to age-0 fish. Whole ages ranged from 0 to 36 years, and fractional ages ranged from 0.37 to 36.53 years. The maximum age of both sexes was 36 years; however, results of Kolmogorov–Smirnov tests indicate that fractional age distributions differed significantly by sex (D=0.15, P<0.01). The mean ages of females and males were 11.72 and 9.90 years, respectively.

Growth and mortality

The VBGF for all age data combined (including females, males, and fish of unknown sex) is as follows:

$$L_t = 950.45(1 - e^{-0.31(t-(-0.26))}) \text{ (Fig. 4A).} \quad (6)$$

For the sex-specific data, the model version that allowed L_∞ and t_0 to vary by sex best fit the data. This model version was followed closely by the version in which L_∞ and K vary (difference in AIC values [ΔAIC] between these 2 models: 1.7) and the version that allowed all parameters to vary (ΔAIC for the best fit version and this version: 1.7). On the basis of predictions from the best-fit model, females

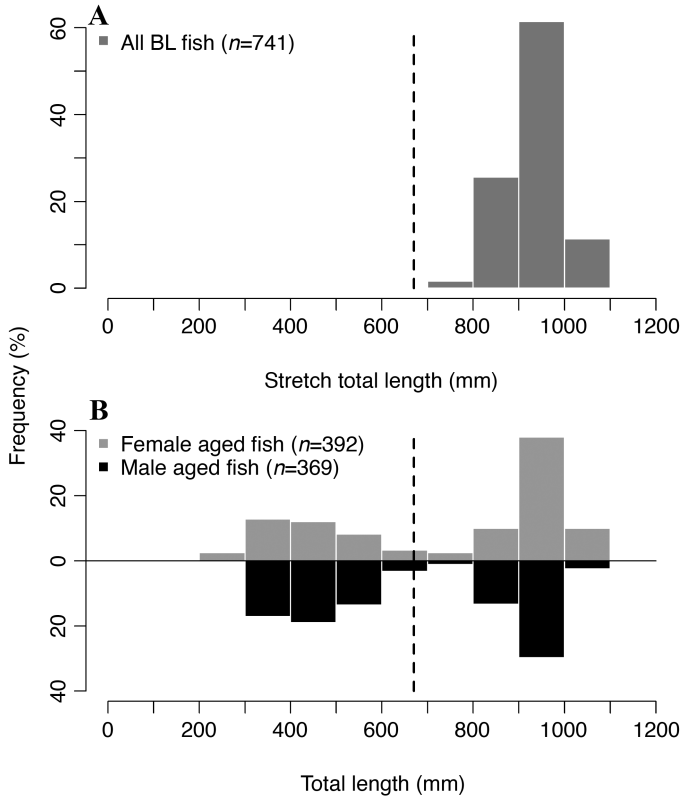

Figure 3

Length–frequency distributions for (**A**) red drum (*Sciaenops ocellatus*) encountered during bottom longline (BL) surveys (sexes combined) and (**B**) red drum encountered during BL and gill-net surveys (by sex) in the north-central Gulf of Mexico from 2006 through 2018. The vertical dashed line represents size at 50% maturity, reported by Bennetts et al. (2019). *n*=number of samples.

have a higher L_∞ value compared with that of males. The VBGF versions for female (F) and male (M) red drum, respectively, are as follows:

$$L_{t(F)} = 969.63(1 - e^{-0.30(t-(-0.35))}); \text{ and} \quad (7)$$

$$L_{t(M)} = 932.71(1 - e^{-0.30(t-(-0.45))}) \text{ (Fig. 4B).} \quad (8)$$

All VBGF parameter estimates from this study are listed in Table 1. Estimates of M were 0.12 for the $\text{Hoenig}_{\text{fishes}}$ method, 0.14 for the $\text{Hoenig}_{\text{nls}}$ method, and 0.39 for the $\text{Pauly}_{\text{nls-T}}$ method.

Relative abundance

The final version of the negative binomial generalized linear model included variables for year, depth, surface temperature, dissolved oxygen, and bottom salinity. The variables for latitude, longitude, bottom temperature, surface salinity, and day length were also tested but were excluded from the final version of the model. Model fit was deemed appropriate because the model did not suffer from deviations from uniformity, outliers (Suppl. Fig. 1), dispersion (P=0.92), or zero inflation (P=0.87). The results of the variance inflation factor analysis indicate a lack of multicollinearity, given that all variance inflation factors were less than 2. The variable for year was not significant (P=0.13), and there were no trends within the standardized index (Fig. 5), indicating that the declines in the nominal CPUE data for 2007–2010 reflect increases in offshore sampling effort beginning in 2010 rather than changes in relative abundance of red drum.

Spatial analysis

During 2006–2018, bottom longline sets were distributed fairly evenly between state (46%) and federal (54%) waters. Nominal CPUE was highest less than 3 nmi from shore (1.13 [SE 0.10], 602 stations), followed by 3–6 nmi from shore (0.72 [SE 0.18], 103 stations), 6–9 nmi from shore (0.35 [SE 0.19], 58 stations), and greater than 9 nmi from shore (0.08 [SE 0.03], 533 stations). The one-way analysis of variance found that distance from shore was significant (P<0.01). The results from the Tukey's multiple-pairwise-comparison test indicate that nominal CPUE was significantly higher less than 3 nmi from shore compared with 6–9 nmi from shore (P<0.01) and greater than 9 nmi from shore (P<0.01). Nominal CPUE was also significantly higher 3–6 nmi from shore than greater than 9 nmi from shore (P<0.01). Both ages (D=0.41, P<0.01) and length distributions (D=0.42, P<0.01) were significantly different for red drum caught in state versus federal waters. Notably, fish were older and larger in state waters (average age of 18 years and average total length of 938 mm) than in federal waters (average age of 12 years and average total length of 887 mm). Further examination revealed a negative correlation between age and distance from shore (coefficient of correlation [r]=–0.239, P<0.01) and between size and distance from shore (r=–0.274, P<0.01).

Model performance and interpretation

Model performance was assessed for all red drum across the 3 sampling seasons: spring, summer, and autumn. The AUC scores for training data were high across all seasons (0.90), indicating "very good" model performance according to criteria defined in Lane et al. (2009) (Table 2). Cross-validated AUC scores were 0.85–0.86 (SE 0.01), indicating that model overfitting was negligible (Hijmans and Elith, 2013).

Habitat suitability

Across all seasons, northward velocity of the surface current, surface temperature, and depth were the 3 most influential predictors of abundance of red drum (Table 2).

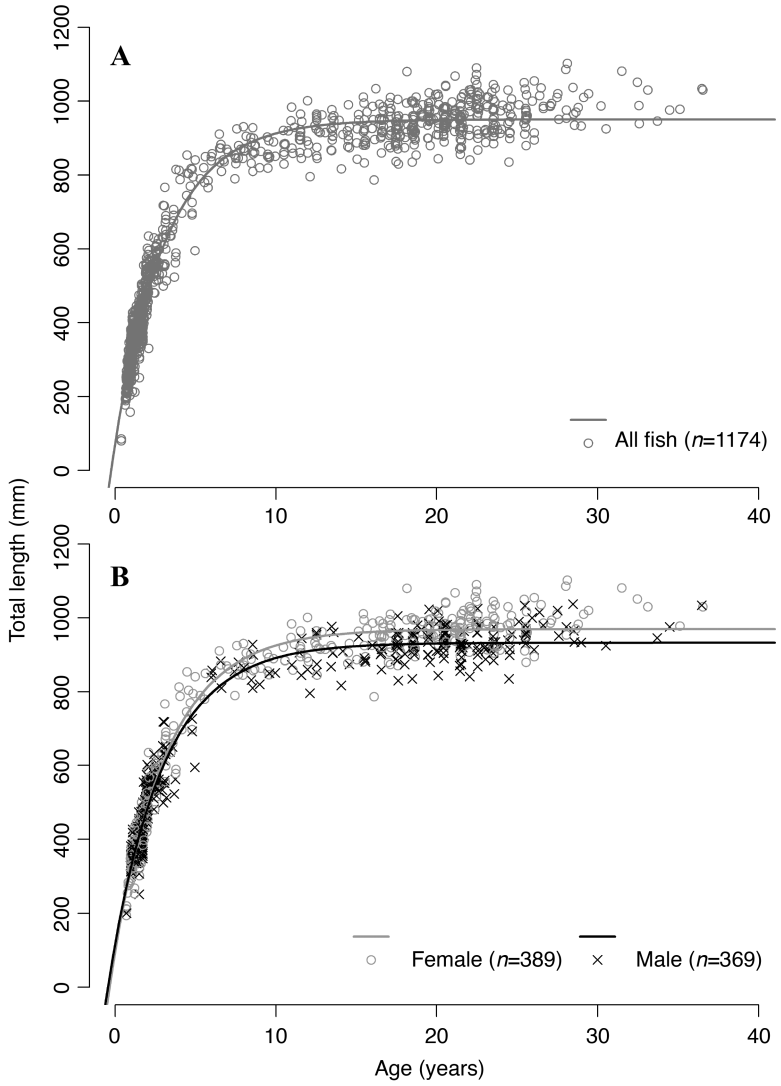

Figure 4

von Bertalanffy growth curves for red drum (*Sciaenops ocellatus*) sampled in the north-central Gulf of Mexico from 2006 through 2018, (**A**) for sexes combined, including fish of unknown sex, and (**B**) for males and females separately. *n*=number of samples.

In particular, red drum had a preference for surface current northward velocities greater than 0 m/s, with high preferences for velocities greater than 0.1 m/s (Fig. 6, A, D, and G). Preferences for surface temperatures less than 22°C (Fig. 6, B, E, and H) and depths between 5 and 17 m (Fig. 6, C, F, and I) were also apparent. These predictors were consistent across seasons. In general, the most suitable habitat for red drum was predominately within state waters. A seasonal shift in predicted habitat suitability was detected, indicating that red drum prefer shallow (<10 m) habitats in the spring and autumn and deep (>30 m) waters during the summer (Fig. 7). Coefficients of variance of the predicted relative abundance were low, but were highest in deep waters (Suppl. Fig. 2). Because all fish in the BRT analysis were larger than the estimated size at 50% maturity (Fig. 3A), we are confident that these results do not confound localized spatial preferences with life history shifts in habitat use.

Discussion

Our findings, based on a large sample size and broad size distribution, support results of previous studies indicating that the red drum is a relatively long-lived, slow-growing species in the GOM. Perhaps not surprisingly, our findings are most similar to those of Bennetts et al. (2019); 3-parameter VBGFs were used in both studies to model sex-specific growth from a similar number and size range of fish collected in Mississippi and Alabama. However, the maximum age in our study is notably older than the maximum age reported by Bennetts et al. (2019) (36 years

Table 1

Mean estimates for parameters of the von Bertalanffy growth function, by sex, based on age data for red drum (*Sciaenops ocellatus*) collected from 2006 through 2018 during fishery-independent bottom longline and gill-net surveys in the north-central Gulf of Mexico. Parameters include mean asymptotic length (L_∞), Brody growth coefficient (K), and hypothetical age at which length equals 0 (t_0). The category for sexes combined includes fish of unknown sex. Standard errors of the mean (SE) are provided in parentheses.

Sex	L_∞ (mm)	K (years^{-1})	t_0 (years)
Combined	950.45 (2.35)	0.31 (0.01)	−0.26 (0.03)
Female	969.63 (3.42)	0.30 (0.01)	−0.35 (0.05)
Male	932.71 (3.78)	0.30 (0.01)	−0.45 (0.06)

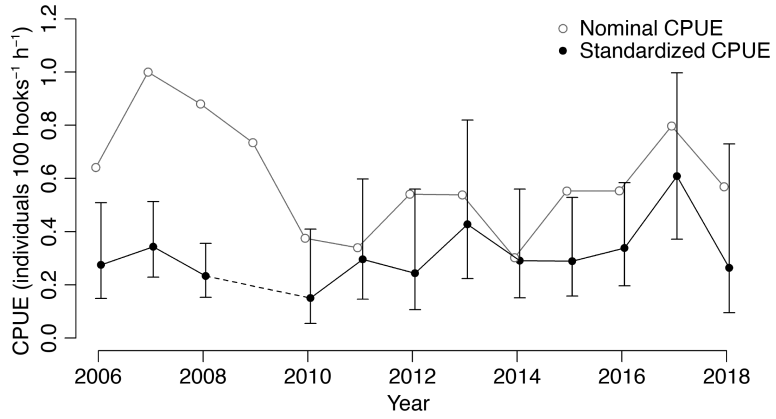

Figure 5

Nominal and standardized catch per unit of effort (CPUE) of red drum (*Sciaenops ocellatus*) from bottom longline surveys conducted in the north-central Gulf of Mexico during 2006–2018. A mean of 100 stations (standard deviation 22) were sampled per year (range: 80–143 stations). Median values are shown in the index standardized by fitting a negative binomial generalized linear model to the CPUE data. For 2009, there is no standardized CPUE estimate because of a lack of positive catch data with corresponding data for abiotic variables from that year. Error bars indicate 95% confidence intervals of standardized CPUE.

versus 31 years), a difference that illustrates the importance of sampling enough large, presumably old individuals. Specifically, we collected more than 4 times more individuals larger than 1000 mm TL than Bennetts et al. (2019); 2 of these fish, 1 male and 1 female, were assigned ages of 36 years. Although fish older than 36 years are likely rare off Mississippi and Alabama, future efforts to model age and growth for red drum should consider collections that span the entirety of the range of the species. Future research also should account for the effects of gear selectivity, temporal or spatial changes in age structure, variable recruitment, and unexplained variance arising from individuals of undetermined sex, all of which are potential sources of bias in growth model parameters in this study.

Despite the large sample size and broad size distribution of red drum captured by using 2 fishery-independent gear types, individuals between 600 and 800 mm TL (ages 3–6) were notably rare in our study. Interestingly, it is in this size range that red drum in this region undergo maturation, according to mean estimates of size and age at maturity from Bennetts et al. (2019). Specifically, mean age at 50% maturity for males and females is approximately 3 years, with fully mature individuals (spawning capable and elevated gonadosomatic index) undetected until ages 5 and 6 (Bennetts et al., 2019). Therefore, although a multi-panel gill net can adequately sample fish of ages 0–2 and the bottom longline can adequately sample fish of age 7 and older, fish between the ages of 3 and 6 years are not selected by either gear type. Similar size selectivity has been reported for red drum off the West Florida Shelf. Using 3 fishery-independent gear types (haul seine, trammel net, and purse seine), Winner et al. (2014) demonstrated that red drum that were 600–800 mm TL were not well represented in the catch in either haul seines or purse seines, yet they were dominant in trammel-net surveys. These examples illustrate that population dynamics are difficult to assess for red drum and that multiple gear types are needed to describe population dynamics across all life stages of this species.

Surprisingly, a comprehensive review of life history studies of red drum revealed that recent age-based estimates of M are not available for this species (SEDAR, 2016). During the most recent stock assessment, it was concluded that the updated Hoenig equation using longevity (Then et al., 2015) was the most robust approach for red drum. Our estimate of annual M based on the Then et al. (2015) approach was 0.14 year^{-1}, a rate that is similar to the range of values used in

Table 2

Percentage of contribution of the 3 variables identified through analysis with boosted regression trees as the most influential on relative abundance of red drum (*Sciaenops ocellatus*) in the north-central Gulf of Mexico between 2006 and 2018. The area under receiver-operator-curve (AUC) and cross-validated (CV) AUC scores, with standard errors (SEs), were used to assess the model's ability to discriminate between species presence and absence.

			Marginal Effect 1		Marginal Effect 2		Marginal Effect 3	
Season	Training data AUC score	CV AUC score (SE)	Variable	%	Variable	%	Variable	%
Spring	0.90	0.86 (0.01)	Northward velocity of surface current	26.2	Surface temperature	20.7	Depth	14.7
Summer	0.90	0.85 (0.01)	Northward velocity of surface current	25.8	Surface temperature	20.4	Depth	14.6
Autumn	0.90	0.86 (0.01)	Northward velocity of surface current	25.8	Surface temperature	20.4	Depth	14.4

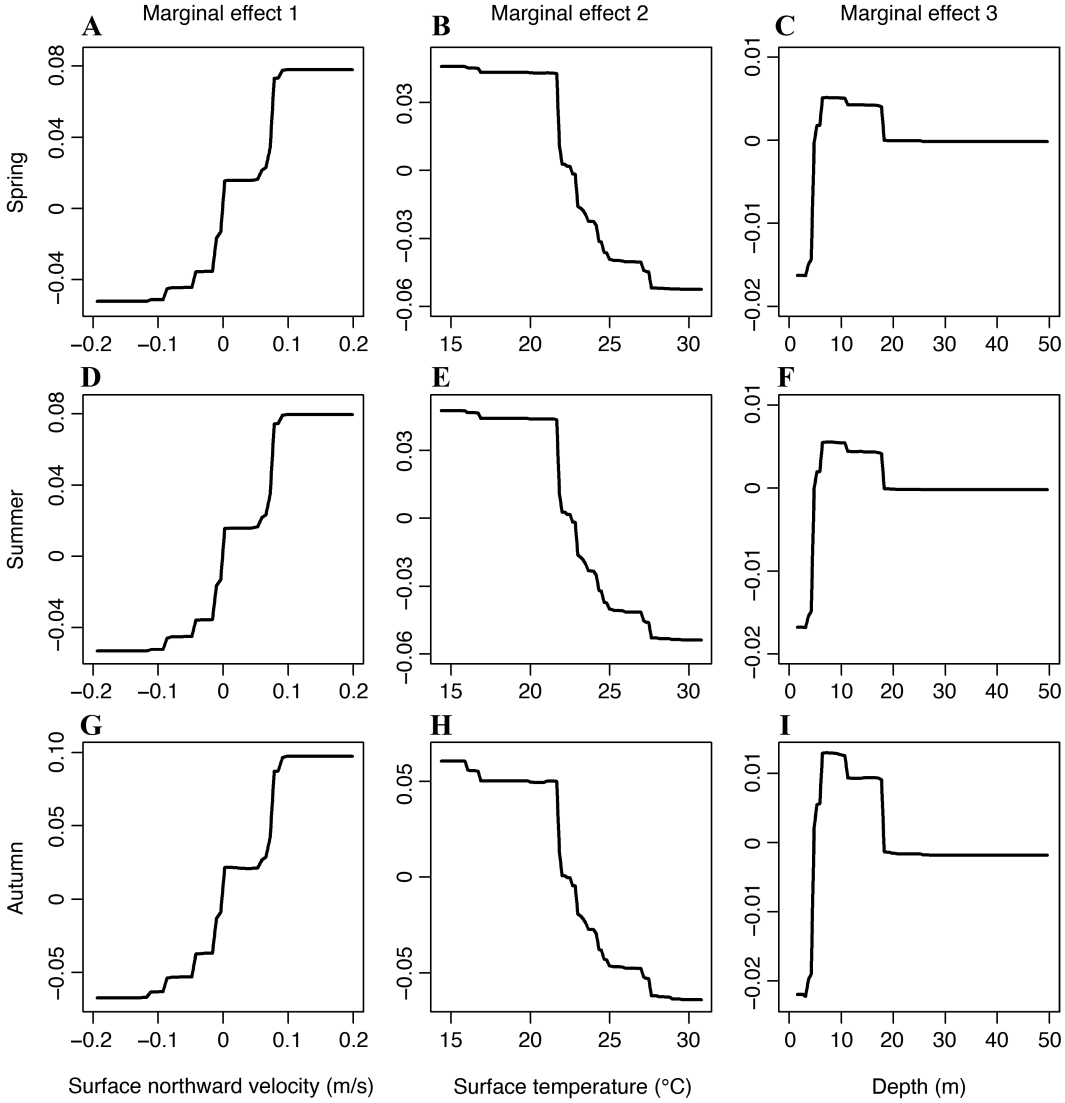

Figure 6

Marginal effect plots for the 3 variables identified through analysis with boosted regression trees (BRTs) as the most influential in predicting relative abundance of red drum (*Sciaenops ocellatus*) in (**A**–**C**) spring, (**D**–**F**) summer, and (**G**–**I**) autumn in the north-central Gulf of Mexico: northward velocity of the surface current, surface temperature, and depth. Data used in the BRT analysis were from surveys conducted in 2006–2018.

the assessment (0.16–0.18 year^{-1}). Unfortunately, the current approach for stock assessments (DLMtool; Carruthers and Hordyk, 2018) does not allow for age-dependent estimates of *M*. The inability to model age-dependent mortality is potentially problematic for red drum because fishing pressure is higher for juveniles, which likely experience different *M* than that experienced by older individuals. As the red drum becomes less data-limited, development of the ability to account for age-based differences in *M* should be prioritized.

The development of a Gulf-wide index of relative abundance generated from fishery-independent bottom longline surveys is critical for future assessments of red drum. During the last stock assessment, 6 potential methods were considered for generating catch advice. The only method to meet the performance criteria was Islope, which is solely based on an index of relative abundance (Carruthers and Hordyk, 2018). For GOM red drum, the index of relative abundance deemed most representative of the adult spawning stock was the index based on data from our bottom longline survey. Therefore, the index of relative abundance generated in this study is an important step toward producing catch advice for this data-limited species. This index indicates that the relative abundance of red drum has varied little over the past 13 years. However, given the long life span of red drum,

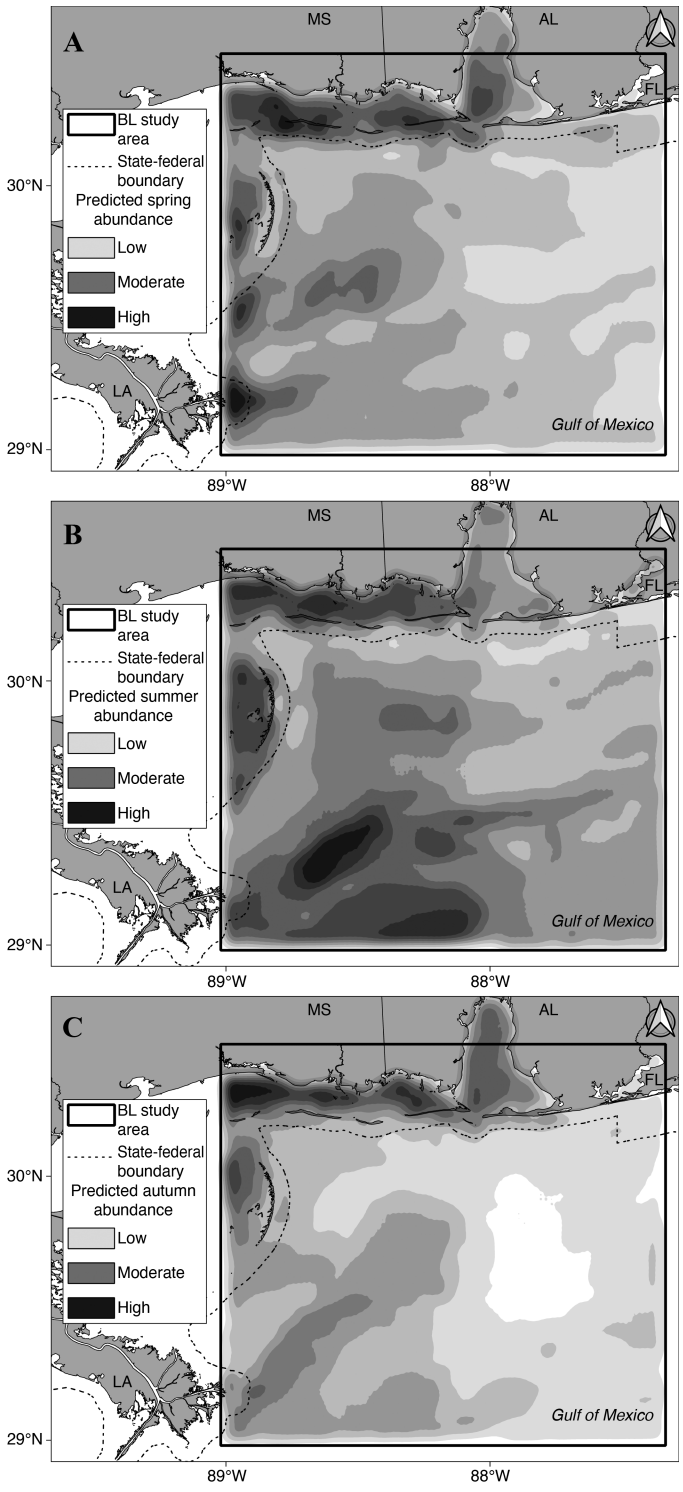

Figure 7

Maps of the study area showing predicted relative abundance from boosted regression trees (BRTs) for red drum (*Sciaenops ocellatus*) collected in (**A**) spring, (**B**) summer, and (**C**) autumn during bottom longline (BL) surveys in the north-central Gulf of Mexico. Light shades indicate areas of low predicted abundance, and dark shades indicate areas of high predicted abundance. The dashed line that follows the coastline indicates the boundary between state and federal waters. Data used in the BRT analysis were from surveys conducted in 2006–2018.

changes in relative abundance for this species are likely to be delayed and gradual. Consequently, continued fishery-independent monitoring is essential, both for characterizing changes in the population and for increasing the stability of catch advice generated from future stock assessments that apply the Islope approach (Sagarese et al., 2019).

Management of red drum in the GOM currently relies on each GOM state meeting an escapement goal (30%) of 4-year-old red drum (SEDAR, 2016). The premise of this management scheme is that most of these fish would enter the offshore adult population where the federal moratorium on GOM red drum protects the adult spawning stock. However, CPUE for adult red drum in the north-central GOM has been substantially higher in state waters than in federal waters (Powers et al., 2012). Similar differences in CPUE between jurisdictions has been observed in other areas of the GOM (e.g., Winner et al., 2014) and along the east coast of Florida (Reyier et al., 2011), particularly from August through November when adults return to state waters to spawn (Lowerre-Barbieri et al., 2016, 2019). These individuals travel to natal areas where they are targeted within spawning aggregations (Burnsed et al., 2020).

Although state-level management of red drum is primarily focused on regulating the catch of juveniles by using slot limits, the current management plans for 4 out of 5 GOM states (i.e., all GOM states except Florida) also afford opportunities to keep a red drum larger than the slot limit. For example, landings data from the NOAA Marine Recreational Information Program (recreational fisheries statistics, available from website, accessed September 2021) indicate that nearly 20% of red drum taken from Mississippi and Alabama state waters have been greater than 762 mm FL (30 in FL), whereas no fish larger than this size have been landed in Florida (Fig. 8). Our findings clearly indicate that off the coast of Alabama, the federal moratorium does not protect the larger, older age classes of red drum from exploitation. Adequately protecting these fish will require state management measures that either completely prohibit the catch of large individuals (e.g., as is done in Florida) or impose a tag system that allows a single over-slot fish per year (e.g., as is done in Texas).

The catch data support the outputs from the BRTs, and the results of BRT analysis indicate that adult red drum prefer inshore, state waters. It has been long established that schools of spawning red drum aggregate near tidal passes (Lowerre-Barbieri et al., 2008; Reyier et al., 2011); the results of our analysis indicate a mechanistic explanation for this observation, confirming the

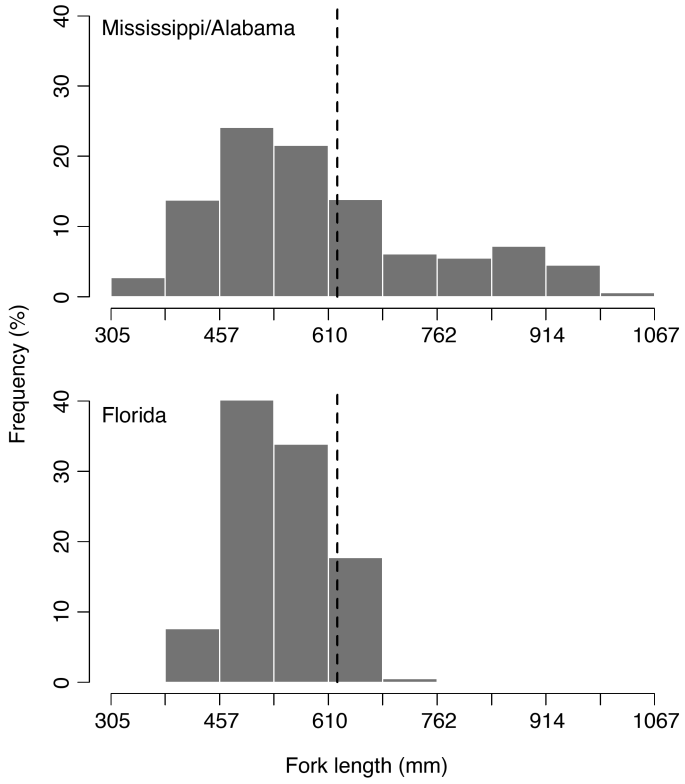

Figure 8

Length–frequency distributions for red drum (*Sciaenops ocellatus*) caught in waters off Mississippi and Alabama and off Florida between 2006 and 2018. Data are from the NOAA Marine Recreational Information Program. The vertical dashed line represents size at 50% maturity, reported by Bennetts et al. (2019).

importance of surface current velocity when defining suitable habitat for red drum. Temperature is also a well known and strong predictor of habitat use of red drum. In previous work in this region, bimodal peaks in relative abundance in the spring and autumn were documented as was the correspondence of these seasonal peaks to temperatures of 21°C and 20°C, respectively (Powers et al., 2012), which are consistent with the temperatures identified in this study as those preferred by red drum. On the basis of habitat suitability predictions from the BRTs, we speculate that during the summer, adult red drum may be using deep (>30 m), cool (~20°C) waters as a thermal refuge.

Conclusions

Clearly, assessing a stock under a complete catch moratorium presents distinct challenges. Nonetheless, when the data typically used to assess the status of a stock (e.g., commercial catch data) are lacking, an opportunity exists to consider alternative data sources, which can sometimes provide new information about stock dynamics (Olney and Hoenig, 2001). Such is the case for GOM red drum. In addition to updated ages, growth models, and *M* estimates, the results of our investigation reveal that the adult spawning stock is not fully protected by the federal catch moratorium. Moreover, through use of our habitat suitability models, we identified factors that may predict suitable habitat for red drum in other regions of the GOM. Collectively, the findings from this study, in concert with those from future efforts to combine nearshore indices of relative abundance from standardized bottom longline surveys throughout the region (e.g., the surveys of the Southeast Area Monitoring and Assessment Program), will be critical for advancing the stock of red drum in the GOM from its status as data-limited.

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