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

Crystal LouAllen Hightower[1,2], J. Marcus Drymon[3,4], Amanda E. Jefferson[3,4], Matthew B. Jargowsky[3,4], Emily A. Seubert[3], Simon Dedman[5], John F. Mareska[6], Sean P. Powers[1,2, *]

1. University of South Alabama
Department of Marine Sciences
5871 USA Drive North
Mobile, AL 36688, United States

2. Dauphin Island Sea Lab
101 Bienville Boulevard
Dauphin Island, AL 36528, United States

3. Mississippi State University
Coastal Research and Extension Center
1815 Popps Ferry Road,
Biloxi, MS 39532, United States

4. Mississippi-Alabama Sea Grant Consortium
703 East Beach Drive
Ocean Springs, MS 39564, United States

5. Stanford University
Hopkins Marine Station
120 Oceanview Blvd
Pacific Grove, CA 93950, United States

6. Alabama Department of Conservation and Natural Resources
Marine Resources Division
PO Box 189
Dauphin Island, AL 36528, United States

* Corresponding author
spowers@disl.edu

1   **Abstract**

2   Gulf of Mexico red drum (*Sciaenops ocellatus*) is an immensely popular sportfish, yet is

3   currently managed as a data-limited stock in federal waters. Despite advances in data-limited

4   assessments, the most recent federal stock assessment for Gulf of Mexico red drum was not

5   recommended for providing management advice. Consequently, we sought to address data gaps

6   highlighted in the assessment by i) producing up-to-date overall and sex-specific growth models,

7   ii) updating estimates of natural mortality, iii) generating standardized indices of relative

8   abundance, and iv) providing predictions of habitat suitability. Using a data series from 2006 –

9   2018, ages ranging from 0 – 36 years were assigned to 1,178 red drum. A negative binomial

10   generalized linear model including the variables year, depth, surface temperature, dissolved

11   oxygen, and bottom salinity was used to standardize an index of relative abundance.

12   Examination of catch per unit effort revealed that adult red drum were significantly more

13   abundant in state waters relative to federal waters. These findings were well explained by habitat

14   suitability models, which identified surface velocity, surface temperature, and depth as the

15   strongest predictors of relative abundance. Collectively, our investigation reveals that the adult

16   spawning stock is not fully protected by the harvest moratorium in federal waters.

17

Introduction

18 **Introduction**

19   Advances in data collection approaches and stock assessment techniques have ushered in

20 the next generation of United States stock assessments (Lynch et al. 2018). For data-rich stocks,

21 traditional catch and catch per unit effort (CPUE) are increasingly augmented with robust

22 fishery-independent data sources and ecosystem-based inputs (Lynch et al. 2018), often using

23 spatially-explicit approaches (e.g., Goethel et al. 2011, Berger et al. 2017). Despite these

24 advances, more than half of US stocks remain data-limited (Newman et al. 2015). Improving

25 basic data inputs for data-limited stocks is imperative for increasing the quality of assessments

26 for these species. For stocks under aggressive rebuilding schedules, where catch data may not

27 reflect population trends or where harvest is completely restricted, the need for reliable time

28 series that track abundance is even more critical.

29   Gulf of Mexico (GoM) red drum (*Sciaenops ocellatus*) are a highly prized species

30 supporting valuable recreational fisheries. Recreational harvest of red drum is permitted in all

31 GoM state waters (out to 3 nautical miles (nmi) in Louisiana, Mississippi, and Alabama and out

32 to 9 nmi in Texas and Florida), but a harvest moratorium in federal waters has been in place

33 since 1987. In addition, commercial harvest is prohibited in all GoM states except Mississippi.

34 Consequently, the data sources that would be useful for assessing GoM red drum (e.g.,

35 commercial landings) are lacking (Powers et al. 2012). Thus, despite a wealth of knowledge on

36 population connectivity (e.g., Rooker et al. 2010), movement and recruitment (e.g., Burnsed et

37 al. 2020), and spawning (e.g., Lowerre-Barbieri et al. 2019), GoM red drum are classified by

38 NOAA Fisheries as a "data-limited species" (SEDAR 2016).

39   The 2006 amendment to the Magnuson-Stevens Fishery Conservation and Management

40 Act required annual catch limits for all federally managed stocks, a mandate that spurred

41   significant advances in the development of data-limited assessment methods (Newman et al.

42   2015). One of these data-limited methods (DLMtool, Carruthers and Hordyk 2018) was recently

43   used to assess a suite of data-limited species in the GoM, including lane snapper (*Lutjanus*

44   *synagris*), wenchman (*Pristipomoides aquilonaris*), yellowmouth grouper (*Mycteroperca*

45   *interstitialis*), speckled hind (*Epinephalus drummondhayi*), snowy grouper (*E. niveatus*), almaco

46   jack (*Seriola rivoliana*), lesser amberjack (*S. fasciata*), and red drum (SEDAR 2016). During this

47   assessment, at least one data-limited method was identified as having preferable performance

48   compared to the status quo for every species examined, with the notable exception of red drum

49   (SEDAR 2016). Thus, despite new tools tailored to the assessment of data-limited species,

50   coupled with a wealth of information about red drum population biology and ecology, the

51   outputs from this assessment were not recommended for providing management advice for red

52   drum (SEDAR 2016).

53   While many stocks will inevitably remain data-limited (Newman et al. 2015), careful

54   examination of existing data deficiencies can improve our ability to assess stocks like GoM red

55   drum. Specific data recommendations from the most recent red drum assessment included i)

56   expand efforts to collect age and length samples at varying sizes, seasons, months, and locations,

57   particularly for offshore fish, ii) identify or optimize fishery-independent surveys to characterize

58   relative abundance in federal waters, and iii) explore ways to increase data collection from

59   existing fishery-independent surveys (SEDAR 2016). To that end, the goals of this study were to

60   combine data from fishery-independent surveys operating throughout the year and across the

61   continental shelf to i) produce up-to-date overall and sex-specific growth models, ii) update

62   estimates of natural mortality, iii) generate standardized indices of relative abundance, and iv)

4

63   provide predictions of habitat suitability for red drum in the north central GoM, which can then

64   be used to optimize future fishery-independent surveys.

65

66   **Materials and Methods**

67   *Data collection*

68   Catch data for adult red drum were collected as part of fishery-independent bottom

69   longline surveys conducted during spring, summer, autumn, and winter in the north central GoM

70   from 2006 – 2018 (Figure 1). Bottom longline locations were selected using a stratified-random

71   sampling design and sampled following standardized methods described in Drymon et al. (2013,

72   2020). Briefly, the main line consisted of 1.85 km (1 nmi) of 4 mm monofilament (545 kg test)

73   that was set with 100 gangions. Gangions consisted of a longline snap and a 15/0 circle hook

74   baited with Atlantic mackerel (*Scomber scombrus*). Each gangion was made of 3.66 m of 3 mm

75   monofilament (320 kg test). All sets were soaked for 1 hour and mid-set measurements of

76   surface and bottom temperature (°C), salinity (psu), and bottom dissolved oxygen (mg l^{-1}), as

77   well as start and end set-depth (m), were recorded. During the bottom longline retrieval, all red

78   drum encountered were measured to the nearest mm (maximum total length), weighed, and

79   retained red drum were sexed. Sagittal otoliths were extracted for age and growth analyses.

80   Catch data were converted to CPUE, expressed as the number of individuals 100 hooks^{-1} hour^{-1}.

81   To augment the collection of adult red drum from the bottom longline survey, smaller red

82   drum were collected and aged from the Alabama Department of Conservation and Natural

83   Resources, Marine Resources Division (AMRD) monthly gillnet survey from 2006 – 2018. This

84   survey included areas of Coastal Alabama from eastern Mississippi Sound to western Perdido

85   Bay and Mobile Bay (Figure 1; Livernois et al. 2020). The AMRD gillnet survey involves two

86 different nets: a small mesh gillnet and a large mesh gillnet. The small mesh gillnet consists of 5

87 panels that are 45.0 m long by 2.4 m deep, each containing stretch meshes ranging in size from

88 5.1 – 10.2 cm. The large mesh gillnet consists of 4 panels that are also 45.0 m long by 2.4 m

89 deep, with stretch meshes ranging in size from 11.4 – 15.2 cm. Red drum caught in either gillnet

90 were measured to the nearest mm (maximum total length), weighed, and sexed. Sagittal otoliths

91 were extracted for age and growth analyses.

92   For all ages combined (longline and gillnet), two-sample Kolmogorov-Smirnov tests

93 were used to examine differences in length and weight distributions between sexes. Some

94 longline-collected red drum lacked total length measurements. For longline-collected red drum

95 that had both maximum total and fork length measurements, maximum total length was

96 regressed on fork length, resulting in the equation:

$$Total\ Length = 1.04(Fork\ Length) + 23.53 \qquad (1)$$

98 where total and fork lengths are expressed in millimeters ($n = 346$, $R^2 = 0.96$). This regression

99 was used to estimate lengths of longline-collected red drum that were lacking a maximum total

100 length measurement ($n = 238$).

101

102 *Otolith processing and aging*

103   All otoliths were processed following procedures detailed in Powers et al. (2012) and

104 VanderKooy et al. (2020). A portion of the fish aged in Powers et al. (2012) were also included

105 in the present study; however, these fish were re-aged during the present study for consistency.

106 Once otoliths were processed, aging was conducted independently (without consulting the other

107 reader) and blindly (without knowledge of fish capture date or size) by two readers. Each otolith

108 section was viewed using a stereomicroscope with transmitted light (brightfield illumination).

109   The number of opaque zones was counted along the ventral edge of the sulcus acusticus. A

110   margin code (1 − 4) was assigned to the otolith margin according to the Gulf of Mexico Marine

111   Fisheries Commission (GSMFC) otolith manual (VanderKooy et al. 2020).

112   Whole age, in years, was calculated for each fish according to GSMFC guidelines. If the

113   collection month was January – June and the margin code was 3 or 4, then the whole age equaled

114   the number of opaque zones, plus 1. If the collection month was October – December and the

115   margin code was 1 or 2, then the whole age equaled the number of opaque zones, minus 1. For

116   all other combinations of capture month and margin code, the whole age equaled the number of

117   opaque zones. Next, the number of days between the capture date and October 1 (the assumed

118   birthdate of red drum; Ditty 1986) of the previous year were calculated. This number was then

119   divided by the total number of days in the capture year, and the result was added to the whole

120   age to yield the fractional age.

121   If any otolith was assigned different whole ages, the readers consulted with each other or

122   a third reader aged the otolith. If the two initial readers did not reach an agreement, or if the third

123   reader did not agree with one of the two initial readers, the otolith was excluded from further

124   analysis. Average percent error (APE) was calculated for all whole ages to evaluate between-

125   reader precision (Beamish and Fournier 1981, Campana 2001). Two-sample Kolmogorov-

126   Smirnov tests were used to examine differences in fractional age distributions between sexes.

127

128   *Modeling growth*

129   To estimate growth parameters for red drum in this study, the von Bertalanffy growth

130   function (VBGF) was fit to female, male, and unknown sexed red drum for the complete data set,

131 fishery-independent AMRD gillnet data set, and bottom longline data set using the following

132 equation:

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

134 where L_t = predicted total length in millimeters, L_∞ = mean asymptotic length in millimeters, K =

135 Brody growth rate coefficient in years^{-1}, t = time (fractional age) in years, and t_0 = hypothetical

136 age at which length equals 0 in years (von Bertalanffy 1938).

137   The VBGF was used to model sex-specific growth. Eight candidate versions of the

138 VBGF were fit to the sex-specific fractional age data: a general version, where all three

139 parameters ($L\infty$, K, and t_0) could vary between sexes; three versions where two of the three

140 parameters could vary between sexes; three versions where only one parameter could vary

141 between sexes; and a common version where all three parameters were held constant between

142 sexes (Ogle 2016, Nelson et al. 2018, Jefferson et al. 2019). Akaike's Information Criterion

143 (AIC) was used to rank these models based on fit and to identify the best-fitting version (Akaike

144 1998, Katsanevakis and Maravelias 2008, Ogle 2016). All growth parameters were modeled in

145 the R v3.6.3 language and software environment (R Core Team 2020) using the add-on packages

146 *FSA* (Ogle et al. 2020) and *nlstools* (Baty et al. 2015).

147

148 *Estimating mortality*

149   Using whole ages of bottom longline specimens, an age-based catch curve (Chapman and

150 Robson 1960) was created for calculating total mortality; however, graphical examination of the

151 catch curve revealed that critical assumptions necessary for estimating instantaneous total

152 mortality had been violated (Tuckey et al. 2007, Smith et al. 2012). Specifically, red drum did

153 not appear to fully recruit to the gear until age 20, so any mortality estimates generated from this

154   catch curve would not be representative of the stock. Although total mortality estimates were

155   unattainable, instantaneous natural mortality rate (*M*) was calculated using three empirical

156   methods (Then et al. 2015, Ogle 2016):

157   1. Hoenig$_{fishes}$, Hoenig's (1983) log-transformed linear regression for fishes:

158
$$M = e^{1.46 - 1.01 log_e(t_{max})}, \tag{3}$$

159   where *t$_{max}$* is the maximum age of the animal in years;

160   2. The Hoenig$_{nls}$ (non-linear least squares) estimator (Then et al. 2015):

161
$$M = 4.899 t_{max}^{-0.916}, \tag{4}$$

162   where *t$_{max}$* is the maximum age of the animal in years; and

163   3. The Pauly$_{nls-T}$ (non-linear least squares, omitting temperature) estimator (Pauly 1980,

164   Then et al. 2015):

165
$$M = 4.118 K^{0.73} L_\infty^{-0.333}, \tag{5}$$

166   where *K* and *L$_\infty$* are parameters from the combined VBGF. All mortality analyses were

167   conducted in R using *FSA*.

168

169   *Relative abundance*

170   Yearly changes in CPUE for red drum sampled during the bottom longline survey were

171   examined by generating a nominal index of relative abundance. To standardize the index of

172   relative abundance, a negative binomial generalized linear model (nbGLM) (Hardin and Hilbe

173   2007) was fit to the CPUE data using the *glmmTMB* package (Brooks et al. 2017) in R. Abiotic

174   variables thought to influence CPUE were added to the model using forward step-wise model

175   selection. Akaike's Information Criterion was used to identify the best-fitting model. Model fit

176   was examined by using the *DHARMa* package (Hartig 2017) in R to check for uniformity,

177 outliers, dispersion, and zero-inflation. Multicollinearity was tested using the *performance*

178 package (Lüdecke et al. 2019) in R, with variance inflation factors (VIFs) less than 10 signifying

179 low correlation (Dormann et al. 2013). To create a standardized yearly index, the abiotic

180 variables thoughts to influence CPUE were set to their median values.

181

182 *Spatial analysis*

183   The index of relative abundance generated above was used to examine trends in red drum

184 relative abundance. First, minimum distance from shore (km) was calculated in QGIS (Quantum

185 GIS Development Team 2019). Then, nominal CPUE was calculated for four discrete areas: less

186 than 3 nmi from shore (i.e., state waters), 3 – 6 nmi from shore, 6 – 9 nmi from shore, and

187 greater than 9 nmi from shore. Finally, a one-way ANOVA, followed by a Tukey multiple

188 pairwise-comparisons test, was used to test for differences in nominal CPUE between these four

189 areas. Age and length versus distance from shore were also examined to identify the composition

190 of red drum vulnerable to recreational fishermen in state waters versus those protected in federal

191 waters.

192

193 *Habitat modeling*

194   Boosted regression trees (BRTs) were used to describe the relationships between the

195 CPUE of red drum from the bottom longline survey and environmental variables potentially

196 influencing distribution and abundance. Specifically, BRTs were fit for three seasons

197 (meteorological spring, summer, and autumn); winter data were not included in BRT analyses

198 given few red drum captured (n = 35) and relatively low effort (n = 70 stations). Boosted

199 regression trees use machine learning to fit complex, non-linear relationships and offer predictive

200 advantages over generalized linear or additive models (GLMs and GAMs). For a complete

201 description of BRTs and the methods used in this study, see Drymon et al. (2020).

202   Preliminary analyses indicated a high proportion of zero values (i.e., zero-inflated data).

203 To account for the preponderance of zeros, a two-step (i.e., delta or hurdle) process was chosen

204 to model catch data. Presence/absence probability was modeled using a BRT with a binary

205 distribution and continuous non-zero (i.e., abundance) probability was modeled using a BRT

206 with a Gaussian distribution. Because the catch data also contained some instances of

207 anomalously high catch (i.e., long-tailed data), non-zero data were natural log-transformed.

208 Predictions were reverse log-transformed so that the final model is a product of the binary and

209 Gaussian BRTs (Lo et al. 1992).

210   Sixteen variables from multiple sources were considered for the BRT models

211 (Supplemental Table 1). While some variables (e.g., temperature, salinity and dissolved oxygen)

212 were collected on-site during bottom longline sampling, all predictor data were obtained

213 following methods outlined in Drymon et al. (2020) to facilitate comparisons with previous

214 habitat modeling in the same region. Surface and bottom temperature (°C), salinity (psu), and

215 three-dimensional surface and bottom current velocity (surface, northward, upward; m/s), as well

216 as sea surface height (m), were obtained from the Hybrid Coordinate Ocean Model (HYCOM)

217 data server (4 km resolution). Bottom dissolved oxygen (mg l^{-1}) was obtained from the National

218 Oceanic and Atmospheric Administration (NOAA)[1] and interpolated across $\sim100-250$ survey

219 stations (number varied by year). Depth (m) and substrate grain size (mm) were obtained from

220 the United States Geological Survey (USGS)[2], 0.33 arc seconds, (~10 m resolution). Daylength

---

[1] https://www.ncddc.noaa.gov/hypoxia/products/2010
[2] http://pubs.usgs.gov/ds/2006/146/basemaps/gmx_grd/gmx_grd.zip

221 (min) was calculated in R using code by Simon Dedman[3]. Given the quantity of potential

222 predictor data considered within the BRT models, some degree of spatial autocorrelation was

223 anticipated (e.g., between distance from shore and depth, between surface and bottom

224 temperature, etc.); however, BRTs are robust to autocorrelation among independent variables

225 (Abeare 2009). All BRT models were fit using the package *gbm.auto* (Dedman et al. 2017) in R.

226 Learning rate (lr), bag fraction (bf), and tree contribution (tc) are parameters that are used in

227 concert to achieve minimum predictive error (Elith et al. 2008). These were optimized using

228 *gbm.auto* for each season model run.

229

230 *Model performance and interpretation*

231   The BRT modeling approach automatically partitioned the data into training and testing

232 sets, a ratio dictated by the bag fraction. Ten-fold cross-validation (CV) was then performed,

233 with the members of the training/testing sets randomized each time. Performance metrics

234 included training/testing correlation, CV deviance (and standard error (SE)) and correlation (and

235 SE), as well as Area Under Receiver-Operator-Curve (AUC) and its CV and CV SE for the

236 binary models (Parisien and Moritz 2009). The final Gaussian fitted functions from the BRT

237 were visualized using marginal effect plots to indicate the effect of a particular variable on the

238 response after accounting for the average effects of other model variables (Elith et al. 2008).

239

240 *Habitat suitability*

241   The distribution of suitable habitat was predicted via the BRTs described above.

242 Environmental data for model predictions were obtained as detailed above, except that HYCOM

---

[3] www.github.com/SimonDedman/daylength

12

243   data were extracted for one representative date per season (monthly groupings per each season,

244   i.e., MAM/JJA/SON) at a resolution of 4 km. Representative dates for environmental data were

245   selected by ranking the absolute value of the differences of all sites' values for all variables

246   against the mean for those variables, then identifying the date within each season that most

247   closely matched those values. The BRT models then generated predictive CPUE values for each

248   2 km × 2 km cell. These values were then then mapped in QGIS using the heatmap setting to

249   produce color points weighted by the predicted abundances generated from the BRT. Using

250   *gbm.auto*, the coefficient of variance was calculated for the predicted abundance values at each 2

251   km x 2 km cell to represent model variance.

252

253   **Results**

254   *Catch data*

255   Between May 2006 and November 2018, 1,296 bottom longline sets were conducted and

256   815 red drum were caught (Figure 2), 741 of which were measured and 472 of which were kept

257   for otolith collection. Approximately 100 stations were sampled each year (mean = 100, SD =

258   22, range 80-143), and survey effort (number of sets) was relatively well distributed across the

259   three seasons examined in the BRTs: spring (n = 460), summer (n = 405), and autumn (n = 361).

260   Red drum caught on the bottom longline were primarily encountered in state waters across all

261   seasons (Figure 2) and were exclusively larger than size at 50% maturity according to Bennetts

262   et al. (2019) (Figure 3A).

263   To supplement the 472 red drum retained from the bottom longline, otoliths from an

264   additional 709 gillnet-captured red drum were analyzed, thus providing a total of 1,181 red drum

265   for age and growth analyses. Of these fish, 392 were female, 369 were male, and 420 were

266 unknown sex. The female-to-male ratio was 1.06:1 and did not differ significantly from a 1:1

267 ratio ($X^2 = 0.70$, DF = 1, $P = 0.40$). Total length ranged from 80 – 1102 mm (Figure 3B). The

268 average (± SE) total length of all specimens (bottom longline and gillnet combined) was 619.13

269 ± 8.22 mm. Kolmogorov-Smirnov tests revealed that females were significantly longer (D =

270 0.20, $P < 0.01$) and heavier (D = 0.18, $P < 0.01$) than males.

271

272 *Age*

273   Ages were assigned to 1,178 red drum. Otoliths from the remaining 3 fish (0.25% of all

274 specimens) were deemed unreadable and were omitted from further analysis. Four fish had no

275 length measurements and were also omitted from further analysis. The between-reader percent

276 agreement was 93.46% and the between-reader APE was 4.52%; these estimates were largely

277 driven by differences in the margin codes assigned to age-0 fish. Whole age ranged from 0 – 36

278 years and fractional age ranged from 0.37 – 36.53 years. The maximum age of both sexes was 36

279 years; however, Kolmogorov-Smirnov tests showed that fractional age distributions differed

280 significantly by sex (D = 0.15, $P < 0.01$). The mean ages of females and males were 11.72 and

281 9.90 years, respectively.

282

283 *Growth and mortality*

284   The VBGF equation for all age data combined (including females, males, and unknown

285 sex) is

286 $$l_t = 950.45(1 - e^{-0.31(t-(-0.26))}) \quad \text{(Figure 4A).} \quad (6)$$

287 For the sex-specific data, the model version which allowed L_∞ and t_0 to vary by sex ("fit2L2T")

288 best fit the data. "Fit2L2T" was followed closely by "fit2L2K" (L_∞ and K vary; ΔAIC = 1.7) and

289 "fitGeneral" (all parameters vary; ΔAIC = 1.7). Based on "fit2L2T," females have a higher L_∞

290 value compared to males. The VBGF equations for female and male red drum, respectively, are

$$l_{t(F)} = 969.63(1 - e^{-0.30(t-(-0.35))}) \qquad (7)$$

292 and

$$l_{t(M)} = 932.71(1 - e^{-0.30(t-(-0.45))}) \text{ (Figure 4B).} \qquad (8)$$

294 All VBGF parameters from the present study are listed in Table 1. Estimates of M were as

295 follows: Hoenig$_{fishes}$ = 0.12, Hoenig$_{nls}$ = 0.14, and Pauly$_{nls\text{-}T}$ = 0.39.

296

297 *Relative abundance*

298   The final version of the nbGLM included the variables year, depth, surface temperature,

299 dissolved oxygen, and bottom salinity. The variables latitude, longitude, bottom temperature,

300 surface salinity, and daylength were also tested but were excluded from the final version of the

301 model. Model fit was deemed appropriate as the model did not suffer from deviations from

302 uniformity, outliers (Supplemental Figure 1), dispersion ($P = 0.92$), or zero-inflation ($P = 0.87$).

303 The VIF analysis indicated a lack of multicollinearity, as all VIFs were less than 2. Year was not

304 significant ($P = 0.13$) and there were no trends within the standardized index (Figure 5),

305 indicating that the declines in the nominal CPUE data from 2007 – 2010 reflect increases in

306 offshore sampling effort beginning in 2010 rather than changes in red drum relative abundance.

307

308 *Spatial analysis*

309   From 2006 – 2018, bottom longline sets were distributed fairly evenly between state

310 (46%) and federal (54%) waters. Nominal CPUE ($\pm$ SE, number of stations) was highest less

311   than 3 nmi from shore (1.13 ± 0.10, n = 602), followed by 3 – 6 nmi from shore (0.72 ± 0.18, n =

312   103), 6 – 9 nmi from shore (0.35 ± 0.19, n = 58), and greater than 9 nmi from shore (0.08 ± 0.03,

313   n = 533). The one-way ANOVA found that distance from shore was significant ($P < 0.01$). The

314   Tukey multiple pairwise-comparisons test indicated that nominal CPUE was significantly higher

315   less than 3 nmi from shore compared to 6 – 9 nmi from shore ($P < 0.01$) and greater than 9 nmi

316   from shore ($P < 0.01$). Nominal CPUE was also significantly higher 3 – 6 nmi from shore

317   compared to greater than 9 nmi from shore ($P < 0.01$). Both age (D = 0.414, $P < 0.01$) and length

318   distributions (D = 0.422, $P < 0.01$) were significantly different for red drum caught in state

319   versus federal waters. Notably, fish were older and larger in state waters (average age of 18 years

320   and average length of 938 mm) compared to federal waters (average age of 12 years and average

321   length of 887 mm). Further examination revealed a negative correlation between age and

322   distance from shore (r = -0.239, $P < 0.01$) and size and distance from shore (r = -0.274, $P <$

323   0.01).

324

325   *Model performance and interpretation*

326   Model performance was assessed for all red drum across the three sampling seasons:

327   spring, summer, and autumn. Training data AUC scores were high across all seasons (0.90),

328   indicating very good model performance according to criteria defined in Lane et al. (2009)

329   (Table 2). Cross-validated AUC scores (± SE) were 0.85 – 0.86 (± 0.01), indicating that model

330   overfitting was negligible (Hijmans and Elith 2013).

331

332   *Habitat suitability*

16

333 Across all seasons, surface northward velocity, surface temperature, and depth were the

334 three most influential predictors of red drum abundance (Table 2). In particular, red drum

335 showed a preference for surface northward velocities greater than 0 m/s, with high preferences

336 for velocities greater than 0.1 m/s (Figure 6A, D, G). Preferences for surface temperatures less

337 than 22°C (Figure 6B, E, H) and depths between 5 and 17 m (Figure 6C, F, I) were also

338 apparent. These predictors were consistent across seasons. In general, the most suitable habitat

339 for red drum was predominately within state waters. A seasonal shift in predicted habitat

340 suitability was detected, suggesting red drum prefer shallower habitats in the spring and autumn

341 as opposed to deeper waters during the summer (Figure 7). Coefficients of variance of the

342 predicted relative abundance were low, but were highest in deeper waters (Supplemental Figure

343 2). Since all fish in the BRT analysis were larger than size at 50% maturity (Figure 3A), we are

344 confident that these results do not confound localized spatial preferences with life-history shifts

345 in habitat use.

346

347 **Discussion**

348 Our findings, based on a large sample size and broad size distribution, support previous

349 studies indicating that GoM red drum are a relatively long-lived, slow-growing species. Perhaps

350 not surprisingly, our findings are most similar to those of Bennetts et al. (2019); both studies

351 used three-parameter VBGFs to model sex-specific growth from a similar number and size range

352 of fish in Mississippi and Alabama. However, the maximum age reported in the present study is

353 notably older than the maximum age reported by Bennetts et al. (2019) (36 vs. 31 years), a

354 difference that illustrates the importance of sampling enough large, presumably old individuals.

355 Specifically, we collected more than 4 times more individuals larger than 1000 mm TL than

356   Bennetts et al. (2019); two of these fish, one male and one female, were assigned ages of 36

357   years. While fish older than 36 are likely rare off Mississippi and Alabama, future efforts to

358   model age and growth for red drum should consider collections that span the entirety of the

359   species' range, as well as account for the effects of gear selectivity, temporal or spatial changes

360   in age structure, variable recruitment, and unexplained variance arising from unsexed

361   individuals, all of which are potential sources of growth model parameter bias in the current

362   study.

363   Despite the large sample size and broad size distribution captured using two fishery-

364   independent gear types, individuals between 600 and 800 mm TL (ages 3 – 6) were notably rare

365   in our study. Interestingly, this is precisely when red drum in this region undergo maturation,

366   according to mean size- and age-at-maturity estimates from Bennetts et al. (2019). Specifically,

367   mean age at 50% maturity for males and females is approximately 3 years, with fully mature

368   individuals (spawning capable and elevated GSI) undetected until ages 5 and 6 (Bennetts et al.

369   2019). Thus, while a multi-panel gillnet adequately samples ages 0 – 2, and the bottom longline

370   adequately samples fish aged 7 and older, fish between the ages of 3 and 6 aren't selected for by

371   either gear type. Similar size selectivity been shown for red drum off the west Florida shelf.

372   Using three fishery-independent gear types (haul seine, trammel net, and purse seine), Winner et

373   al. (2014) demonstrated that 600 – 800 mm red drum were not well represented in either haul

374   seines or purse seines, yet were dominant in trammel net surveys. These examples illustrate the

375   difficulty in assessing red drum and suggest that multiple gear types are needed to describe

376   population dynamics across all life stages of this species.

377   Surprisingly, a comprehensive review of red drum life history studies revealed that recent

378   age-based natural mortality estimates are lacking for this species (SEDAR 2016). During the

18

379   assessment, it was concluded that the updated Hoenig equation using longevity (Then et al.

380   2015) was the most robust approach for red drum. Our estimate of instantaneous annual natural

381   mortality based on the Then et al. (2015) approach was 0.14 y^{-1}, which is similar to the range of

382   values used in the assessment (0.16 y^{-1} – 0.18 y^{-1}). Unfortunately, the current assessment

383   approach (DLMtool, Carruthers and Hordyk 2018) does not allow for age-dependent estimates of

384   M. This is potentially problematic for red drum, as fishing pressure is higher for juveniles, which

385   likely experience different natural mortality rates relative to older individuals. As red drum

386   become less data-limited, developing the ability to account for age-based differences in natural

387   mortality should be prioritized.

388   The development of a gulf-wide index of relative abundance generated from fishery-

389   independent bottom longline surveys is critical for future assessments of red drum. During the

390   last assessment, six potential methods were considered for generating catch advice. The only

391   method to meet the performance criteria was Islope, which is solely based on an index of relative

392   abundance (Carruthers and Hordyk 2018). For GoM red drum, the index of relative abundance

393   deemed most representative of the adult spawning stock was the index based upon our bottom

394   longline survey. Thus, the index of relative abundance generated in this study is an important

395   step toward producing catch advice for this data-limited species. This index suggests that the

396   relative abundance of red drum has varied little over the past thirteen years. However, given the

397   long lifespan of red drum, changes in relative abundance for this species are likely to be delayed

398   and gradual. Consequently, continued fishery-independent monitoring is essential, both for

399   characterizing changes in the population and for increasing the stability of catch advice

400   generated from future assessments that apply the Islope approach (Sagarese et al. 2018).

401   Current management of red drum in the GoM relies on each GoM state meeting an

402   escapement goal (30%) of 4-year-old red drum. The premise of this management scheme is that

403   most of these fish would enter the offshore adult population where the federal moratorium on

404   GoM red drum protects the adult spawning stock. However, CPUE for adult red drum was

405   substantially higher in state waters than in federal waters. This has been shown in other areas of

406   the GoM (e.g., Winner et al. 2014) and along the east coast of Florida (Reyier et al. 2011),

407   particularly from August to November when adults return to state waters to spawn (Lowerre-

408   Barbieri et al. 2016 and 2018). These individuals travel to localized natal areas where they are

409   targeted within spawning aggregations (Burnsed et al. 2020). Although state-level management

410   for red drum is primarily focused on regulating the harvest of juveniles using slot limits, the

411   current management plans for four out of five GoM states (i.e., except Florida) also afford

412   opportunities to keep a red drum larger than the slot limit. For example, landings data from the

413   Marine Recreational Information Program (MRIP 2021) demonstrate that nearly 20% of redfish

414   taken from Mississippi and Alabama state waters are greater than 30 inches fork length, whereas

415   no fish this size are landed in Florida (Figure 8). Our findings clearly demonstrate that off the

416   coast of Alabama, the federal moratorium does not protect the larger, older age classes of red

417   drum from harvest. Adequately protecting these fish will require state management measures that

418   either completely prohibit the harvest of large individuals (e.g., Florida) or impose a tag system

419   that allows a single over-slot fish per year (e.g., Texas).

420   The catch data support the outputs from the BRTs, which indicate that adult red drum

421   prefer inshore, state waters. It is long established that red drum spawning schools aggregate near

422   tidal passes (Lowerre-Barbieri et al. 2008, Reyier et al. 2011); our analysis provides a

423   mechanistic explanation for this observation, confirming the importance of surface current

424 velocity when defining suitable habitat for red drum. Temperature is also well known as a strong

425 predictor of red drum habitat use. Previous work from this region documented bimodal peaks in

426 relative abundance in the spring and autumn and noted that these peaks corresponded to

427 temperatures of 21 and 20 degrees, respectively (Powers et al. 2012), which are consistent with

428 the preferred temperature values identified in this study. Based on the habitat suitability

429 predictions from the BRTs, we speculate that during the summer, adult red drum may be using

430 deeper, cooler waters as a thermal refuge.

431 **Conclusions**

432 Clearly, assessing a stock under a complete harvest moratorium presents distinct

433 challenges. Nonetheless, when the data typically used to assess stock status (e.g., commercial

434 catch data) are lacking, an opportunity exists to consider alternative data sources, which can

435 sometimes provide new information about stock dynamics (Olney and Hoenig 2001). Such is the

436 case for GoM red drum. In addition to updated ages, growth models, and natural mortality

437 estimates, our investigation reveals that the adult spawning stock is not fully protected by the

438 federal harvest moratorium. Moreover, our habitat suitability models identify factors that may

439 predict suitable habitat for red drum in other regions of the GoM. Collectively, the findings from

440 this study, in concert with future efforts to combine nearshore indices of relative abundance from

441 standardized bottom longline surveys throughout the region (e.g., SEAMAP), will be critical for

442 advancing GoM red drum from its status as a data-limited stock.

443

444 **Acknowledgments**

448   the Alabama Marine Resources Division for collecting and sharing red drum gillnet data. This

449   work was conducted in accordance with IACUC protocol #1562086 and was funded in part by

450   the Gulf of Mexico Fishery Management Council.

451 **Literature Cited**

452 Abeare, S.
453   2009. Comparisons of Boosted Regression Tree, GLM and GAM Performance in the
454   Standardization ofYellowfin Tuna Catch-Rate Data from the GulfofMexico Lonline
455   (sic) Fishery. Master's thesis, Louisiana State University, Baton Rouge, LA.
456
457 Akaike, H.
458   1998. Information theory and an extension of the maximum likelihood principle. Pages 199–
459   213 in E. Parzen, K. Tanabe, and G. Kitagawa, editors. Selected papers of Hirotugu
460   Akaike. Springer, New York.
461
462 Baty, F., C. Ritz, S. Charles, M. Brutsche, J.-P. Flandrois, and M.-L. Delignette-Muller.
463   2015. A toolbox for nonlinear regression in R: the package nlstools. Journal of Statistical
464   Software 66:1–21.
465
466 Beamish, R. J., and D. A. Fournier.
467   1981. A method for comparing the precision of a set of age determinations. Can. J. Fish.
468   Aquat. Sci. 38:982–983.
469
470 Bennetts, C. F., R. L. Leaf, and N. J. Brown-Peterson.
471   2019. Sex-specific growth and reproductive dynamics of Red Drum in the northern Gulf of
472   Mexico. Mar. Coast. Fish. 11:213–230.
473
474 Berger, A. M., Goethel, D. R. and Lynch, P. D.
475   2017. Introduction to "space oddity: recent advances incorporating spatial processes in the
476   fishery stock assessment and management interface". Can. J. Fish. Aquat. Sci.
477   74(11), pp.1693-1697.
478
479 Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H. J.
480 Skaug, M. Machler, and B. M. Bolker.
481   2017. glmmTMB balances speed and flexibility among packages for zero-inflated
482   generalized linear mixed modeling. The R Journal 9(2):378–400.
483
484 Burnsed, S. W., Lowerre-Barbieri, S., Bickford, J. and Leone, E. H.
485   2020. Recruitment and movement ecology of red drum *Sciaenops ocellatus* differs by natal
486   estuary. Mar. Ecol. Prog. Ser. 633, pp.181-196.
487
488 Campana, S. E.
489   2001. Accuracy, precision and quality control in age determination, including a review of
490   the use and abuse of age validation methods. J. Fish. Biol. 59:197–242.
491
492 Carruthers, T. R. and Hordyk, A. R.
493   2018. The Data-Limited Methods Toolkit (DLM tool): An R package for informing
494   management of data-limited populations. Methods Ecol. Evol. 9(12), pp.2388-2395.
495

23

496 Chapman, D. G., and D. S. Robson.
497　　　1960. The analysis of a catch curve. Biometrics 16:354–368.
498
499 Dedman, S., R. Officer, M. Clarke, D. G. Reid, and D. Brophy.
500　　　2017. Gbm.auto: a software tool to simplify spatial modelling and Marine Protected Area
501　　　　　planning. PLoS One 12:e0188955. doi: 10.1371/journal.pone.0188955
502
503 Ditty, J. G.
504　　　1986. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana:
505　　　　　composition, relative abundance, and seasonality. Fish. Bull. 84:935–946.
506
507 Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, et al.
508　　　2013. Collinearity: a review of methods to deal with it and a simulation study evaluating
509　　　　　their performance. Ecography 36:27–46. doi: 10.1111/j.1600-0587.2012.07348.x
510
511 Drymon, J. M., L. Carassou, S. P. Powers, M. Grace, J. Dindo, and B. Dzwonkowski.
512　　　2013. Multiscale analysis of factors that affect the distribution of sharks throughout the
513　　　　　northern Gulf of Mexico. Fish. Bull. 111:370–380. doi: 10.7755/fb.111.4.6
514
515 Drymon, J. M., S. Dedman, J. T. Froeschke, E. A. Seubert, A. E. Jefferson, A. M. Kroetz, J. F.
516 Mareska, and S. P. Powers.
517　　　2020. Defining sex-specific suitability for a northern Gulf of Mexico shark assemblage.
518　　　　　Front. Mar. Sci. 7(35). doi: 10.3389/fmars.2020.00035.
519
520 Elith, J., J. R. Leathwick, and T. Hastie.
521　　　2008. A working guide to boosted regression trees. J. Anim. Ecol. 77:802–813. doi:
522　　　　　10.1111/j.1365-2656.2008.01390.x
523
524 Goethel, D. R., Quinn, T. J. and Cadrin, S. X.
525　　　2011. Incorporating spatial structure in stock assessment: movement modeling in marine
526　　　　　fish population dynamics. Rev. Fish. Sci. 19(2), pp.119-136.
527
528 Hanley, J. A., and B. J. McNeil.
529　　　1982. The meaning and use of the area under a Receiver Operating Characteristic (ROC)
530　　　　　curve. Radiology 143: 29-36.
531
532 Hardin, J. W., and J. Hilbe.
533　　　2007. Generalized linear models and extensions. Stata Press.
534
535 Hartig, F.
536　　　2017. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression
537　　　　　models. R package version 0.1, 5.
538
539 Hijmans, R. J., and J. Elith.
540　　　2013. Species Distribution Modeling with R. R CRAN Project. Vienna: R Foundation for
541　　　　　Statistical Computing.

24

542
543 Hoenig, J. M.
544   1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82:898–903.
545
546 Jefferson, A. E., R. J. Allman, A. E. Pacicco, J. S. Franks, F. J. Hernandez, M. A. Albins, S. P.
547 Powers, R. L. Shipp, and J. M. Drymon.
548   2019. Age and growth of gray triggerfish (*Balistes capriscus*) from a north-central Gulf of
549   Mexico artificial reef zone. Bull. Mar. Sci. 95:177–195.
550
551 Katsanevakis, S., and C. D. Maravelias.
552   2008. Modelling fish growth: multi-model inference as a better alternative to a priori using
553   von Bertalanffy equation. Fish. Fish. 9:178–187.
554
555 Lane, J. Q., P. T. Raimondi, and R. M. Kudela.
556   2009. Development of a logistic regression model for the prediction of toxigenic *Pseudo-*
557   *nitzschia* blooms in Monterey Bay. Calif. Mar. Ecol. Prog. Ser. 383:37–51.
558
559 Livernois, M. C., Powers, S. P., Albins, M. A. and Mareska, J. F.
560   2020. Habitat associations and co-occurrence patterns of two estuarine-dependent predatory
561   fishes. Mar. Coast. Fish 12(1), pp.64-77.
562
563 Lo, N. C. H., L. D. Jacobson, and J. L. Squire.
564   1992. Indices of relative abundance from fish spotter data based on delta-lognormal
565   models. Can. J. Fish. Aquat. Sci. 49, 2515–2526. doi: 10.1139/f92-278.
566
567 Lowerre-Barbieri, S. K., Barbieri, L. R., Flanders, J. R., Woodward, A. G., Cotton, C. F. and
568 Knowlton, M. K.,
569   2008. Use of passive acoustics to determine red drum spawning in Georgia waters. Trans.
570   Am. Fish. 137(2), pp.562-575.
571
572 Lowerre-Barbieri, S. K., Walters Burnsed, S. L. and Bickford, J. W.
573   2016. Assessing reproductive behavior important to fisheries management: a case study with
574   red drum, *Sciaenops ocellatus*. Ecol. Appl. 26(4), pp.979-995.
575
576 Lowerre-Barbieri, S. K., Tringali, M. D., Shea, C. P., Walters Burnsed, S., Bickford, J., Murphy,
577 M. and Porch, C.
578   2019. Assessing red drum spawning aggregations and abundance in the Eastern Gulf of
579   Mexico: a multidisciplinary approach. ICES J. Mar. Sci. 76(2), pp.516-529.
580
581 Lüdecke, D., D. Makowski, and P. Waggoner.
582   2019. performance: Assessment of regression models performance. CRAN.
583
584 Lynch, P.D., Methot, R. D. and Link, J. S.
585   2018. Implementing a Next Generation Stock Assessment Enterprise: An Update to the
586   NOAA Fisheries Stock Assessment Improvement Plan.
587

588 MRIP (Marine Recreational Information Program).
589   2021. Recreational fishing data and statistics queries. National Oceanic and Atmospheric
590   Administration Fisheries, Silver Spring, Maryland.
591

592 Nelson, T. R., A. E. Jefferson, P. T. Cooper, C. A. Buckley, K. L. Heck, and J. Mattila.
593   2018. Eurasian perch *Perca fluviatilis* growth and fish community structure, inside and
594   outside a marine-protected area in the Baltic Sea. Fish. Manag. Ecol. 25:172–185.
595

596 Newman, D., Berkson, J. and Suatoni, L.
597   2015. Current methods for setting catch limits for data-limited fish stocks in the United
598   States. Fish. Res. 164, pp.86-93.
599

600 Ogle, D. H.
601   2016. Introductory fisheries analyses with R. CRC Press, Boca Raton, FL.
602

603 Ogle, D. H., P. Wheeler, and A. Dinno.
604   2020. FSA: Fisheries Stock Analysis. R package version 0.8.27. Available:
605   https://github.com/droglenc/FSA.
606

607 Olney, J. E. and Hoenig, J. M.
608   2001. Managing a fishery under moratorium: assessment opportunities for Virginia's stocks
609   of American shad. Fisheries, *26*(2), pp.6-12.
610

611 Parisien, M. A., and M. A. Moritz.
612   2009. Environmental controls on the distribution of wildfire at multiple spatial scales. Ecol.
613   Monogr. 79:127–154. doi: 10.1890/07-1289.1
614

615 Pauly, D.
616   1980. On the interrelationships between natural mortality, growth parameters, and mean
617   environmental temperature in 175 fish stocks. ICES J. Mar. Sci. 39:175–192.
618

619 Powers, S. P., C. L. Hightower, J. M. Drymon, and M. W. Johnson.
620   2012. Age composition and distribution of Red Drum (*Sciaenops ocellatus*) in offshore
621   waters of the north central Gulf of Mexico: an evaluation of a stock under a federal
622   harvest moratorium. Fish. Bull. 110(3):283–292.
623

624 Quantum GIS Development Team
625   2019. Quantum GIS Geographic Information System, v3.8.1.
626

627 R Core Team.
628   2020. R: A language and environment for statistical computing. R Foundation for Statistical
629   Computing, Vienna, Austria.
630

631 Reyier, E. A., Lowers, R. H., Scheidt, D. M. and Adams, D. H.

632   2011. Movement patterns of adult red drum, *Sciaenops ocellatus*, in shallow Florida lagoons
633   as inferred through autonomous acoustic telemetry. Environ. Biol. Fishes. 90(4),
634   pp.343-360.
635
636 Rooker, J. R., G. W. Stunz, S. A. Holt, and T. J. Minello.
637   2010. Population connectivity of red drum in the northern Gulf of Mexico. Mar. Ecol. Prog.
638   Ser. 407:187-196.
639
640 Sagarese, S. R., Harford, W. J., Walter, J. F., Bryan, M. D., Isely, J. J., Smith, M. W., Goethel,
641 D. R., Rios, A. B., Cass-Calay, S. L., Porch, C. E. and Carruthers, T. R.
642   2019. Lessons learned from data-limited evaluations of data-rich reef fish species in the Gulf
643   of Mexico: implications for providing fisheries management advice for data-poor
644   stocks. Can. J. Fish. Aquat. Sci. 76(9), pp.1624-1639.
645
646 SEDAR.
647   2016. SEDAR49: Gulf of Mexico Data-limited Species Stock Assessment Report [online].
648   SEDAR, North Charleston, South Carolina. Available from sedarweb.org [accessed
649   September 2021].
650
651 Smith, M. W., A. Y. Then, C. Wor, G. Ralph, K. H. Pollock, and J. M. Hoenig.
652   2012. Recommendations for catch-curve analysis. N. Am. J. Fish. Manag. 32(5):956–967.
653
654 Then, A. Y., J. M. Hoenig, N. G. Hall, and D. A. Hewitt.
655   2015. Evaluating the predictive performance of empirical estimators of natural mortality rate
656   using information on over 200 fish species. ICES J. Mar. Sci. 72:82–92.
657
658 Tuckey, T., N. Yochum, J. Hoenig, J. Lucy, and J. Cimino.
659   2007. Evaluating localized vs. large-scale management: the example of tautog in Virginia.
660   Fisheries 32(1):21–28.
661
662 VanderKooy, S., J. S. Elzey, J. Gilmore, and J. Kipp, editors.
663   2020. A practical handbook for determining the age of Gulf of Mexico and Atlantic Coast
664   fishes, 3rd edition. Gulf States Marine Fisheries Commission, Ocean Springs, MS.
665
666 von Bertalanffy, L.
667   1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol.
668   10:181–213.
669
670 Winner, B. L., Flaherty-Walia, K. E., Switzer, T. S. and Vecchio, J. L.
671   2014. Multidecadal evidence of recovery of nearshore red drum stocks off west-central
672   Florida and connectivity with inshore nurseries. N. Am. J. Fish. Manag. 34(4),
673   pp.780-794.

674 **Tables**

675 **Table 1** – von Bertalanffy growth parameters for combined (sexes pooled, including unknown

676 sex) and sex-specific red drum age data. L_∞ = mean asymptotic length in millimeters, K = Brody

677 growth rate coefficient in years^{-1}, t_0 = hypothetical age at which length equals 0 in years, and SE

678 = standard error.

	L_{inf} ± SE	K ± SE	t_0 ± SE
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

679

680

681 **Table 2** – Seasonal percent contribution of the three most influential factors identified by the boosted regression trees. The AUC score

682 assesses model ability to discriminate species presence and absence (Hanley and McNeil 1982), with a value of 0.9 considered a 'very

683 good score' (Lane et al. 2009).

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

684

29

Figures

Figure 1 – Bottom longline (black shaded) and gillnet (blue shaded) study regions. The red dashed line indicates the boundary between state and federal waters.

Figure 2 – Catch per unit effort (CPUE, red drum, hooks^{-1} hour^{-1}) for red drum from the bottom longline survey during spring, summer, and autumn of 2006 – 2018. Shaded circles increase with CPUE, and X indicates effort with no red drum catch.

Figure 3 – A) Length frequency distributions for red drum (sexes combined) encountered on the bottom longline. B) Length frequency distributions for female and male red drum examined for age and growth analyses from bottom longline and gillnet data sets. The dashed line represents size at 50% maturity according to Bennetts et al. (2019).

Figure 4 – Combined (A) and sex-specific (B) von Bertalanffy growth curves for red drum sampled during the present study.

Figure 5 – Nominal (individuals 100 hooks^{-1} hour^{-1}, open circles) and standardized (filled circles) CPUE of red drum from the bottom longline survey, 2006 – 2018. Approximately 100 stations per year (mean = 100, SD = 22, range 80 – 143) were sampled. Median values are shown in the standardized index. For 2009, there is no standardized CPUE estimate due to a lack of positive catch data with corresponding abiotic measurements from that year.

Figure 6 – Marginal effect plots for the variables identified by the BRTs as the most influential in predicting red drum relative abundance in spring (A–C), summer (D–F), and autumn (G–I).

704   **Figure 7** – Predicted relative abundance from BRT models for red drum in spring (A), summer

705   (B), and autumn (C). Light shades indicate areas of low predicted abundance and dark shades
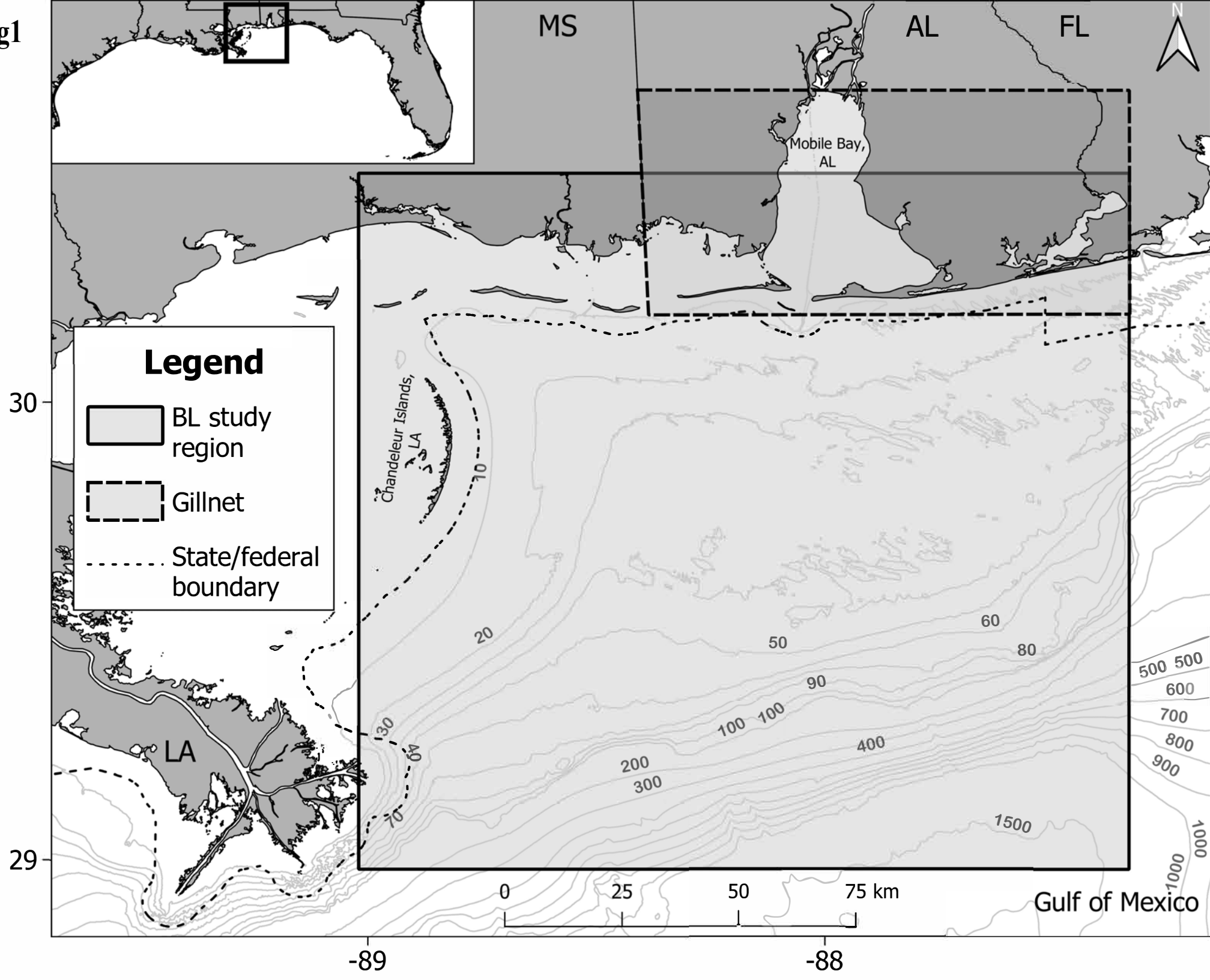
706   indicate areas of high predicted abundance.
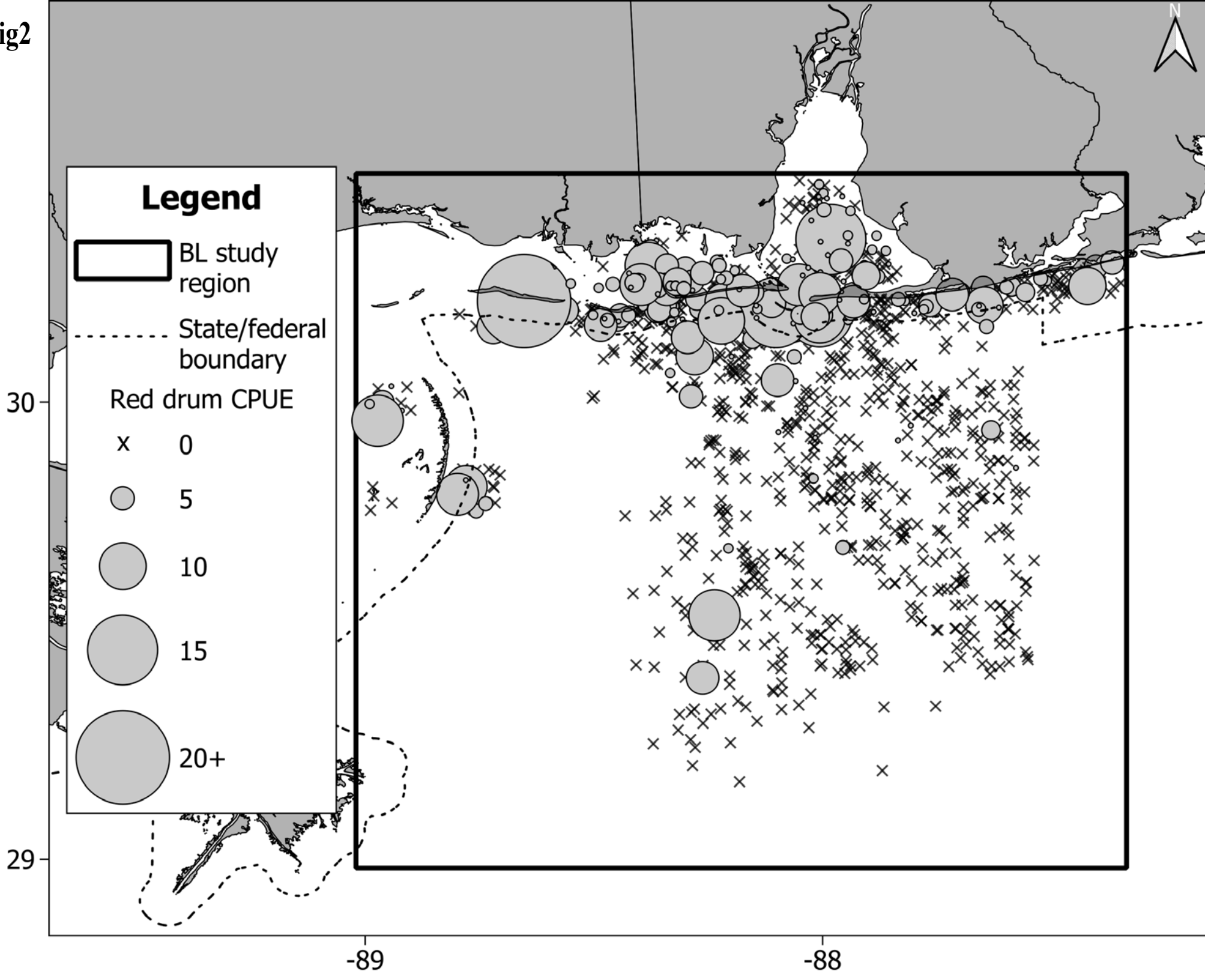
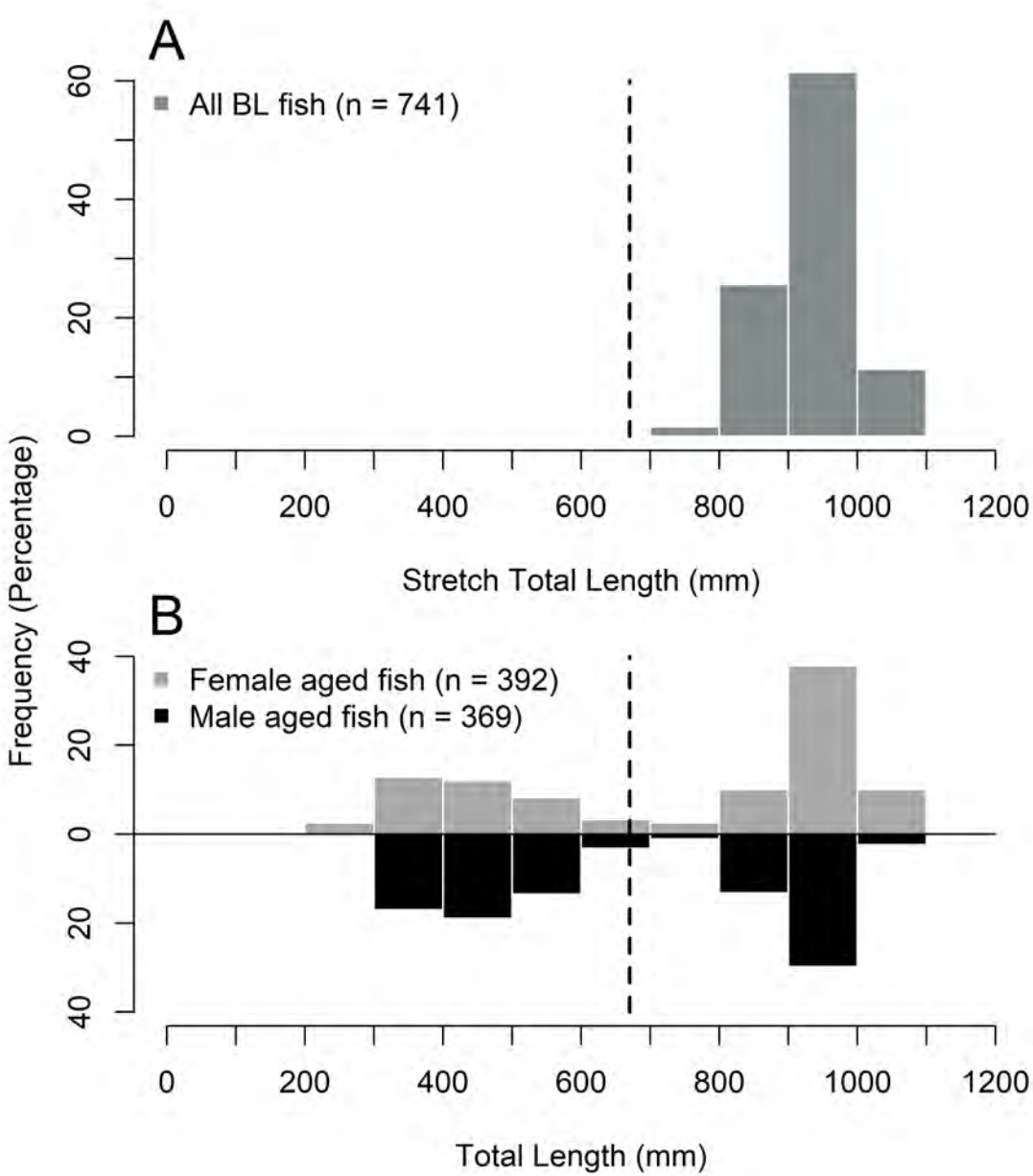707   **Figure 8** –Red drum harvest data for Mississippi/Alabama (A) and Florida (B), 2006-2018. The

708   dashed line represents size at 50% maturity according to Bennetts et al. (2019). Data are from the

709   NOAA Marine Recreational Information Program web site (MRIP 2021).

710   **Supplemental Figure 1** – Residual diagnostic plots for examining model fit were created using

711   the DHARMa package (Hartig 2017), which calculates quantile regression to compare the

712   empirical 0.25, 0.50 and 0.75 quantiles with the theoretical 0.25, 0.50 and 0.75 quantiles. Any

713   significant deviation from the expected quantile would be indicated in red.

714   **Supplemental Figure 2** – Coefficient of variation of predicted relative abundance from BRT

715   models for red drum in spring (A), summer (B), and autumn (C). Light shades indicate areas of

716   low predicted abundance and dark shades indicate areas of high predicted abundance.
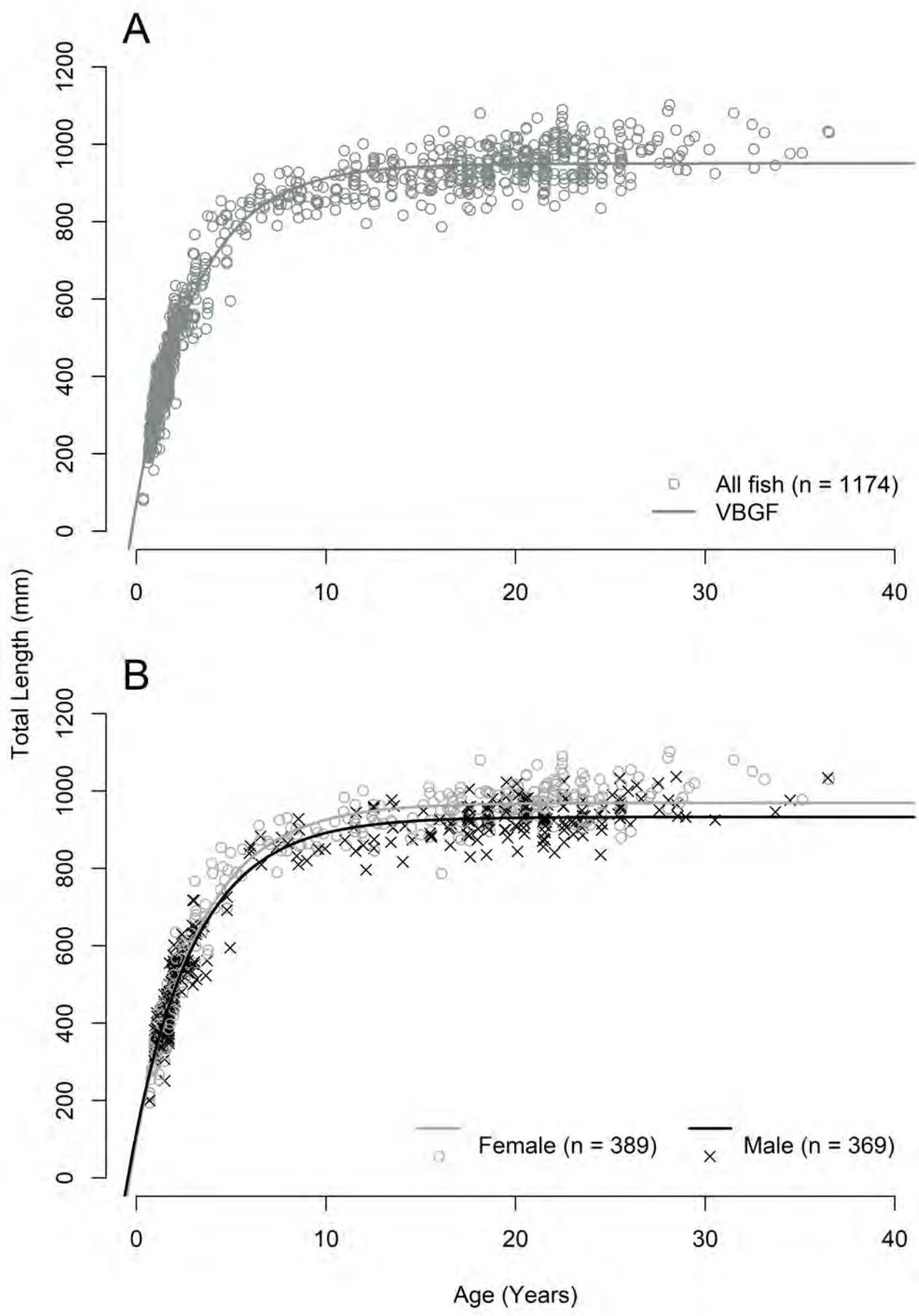
Fig1

Fig2

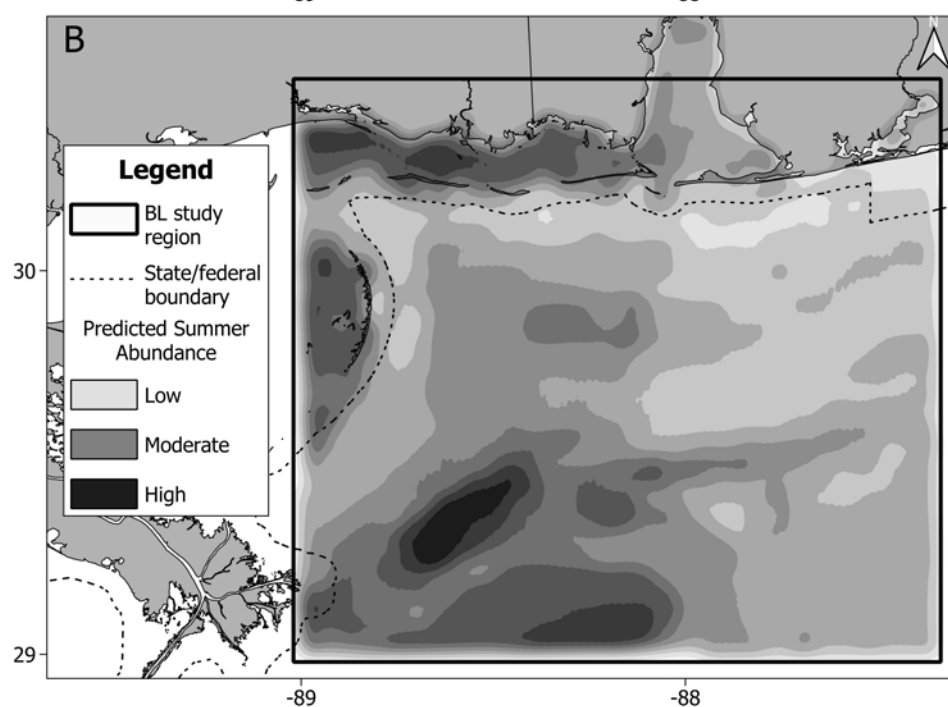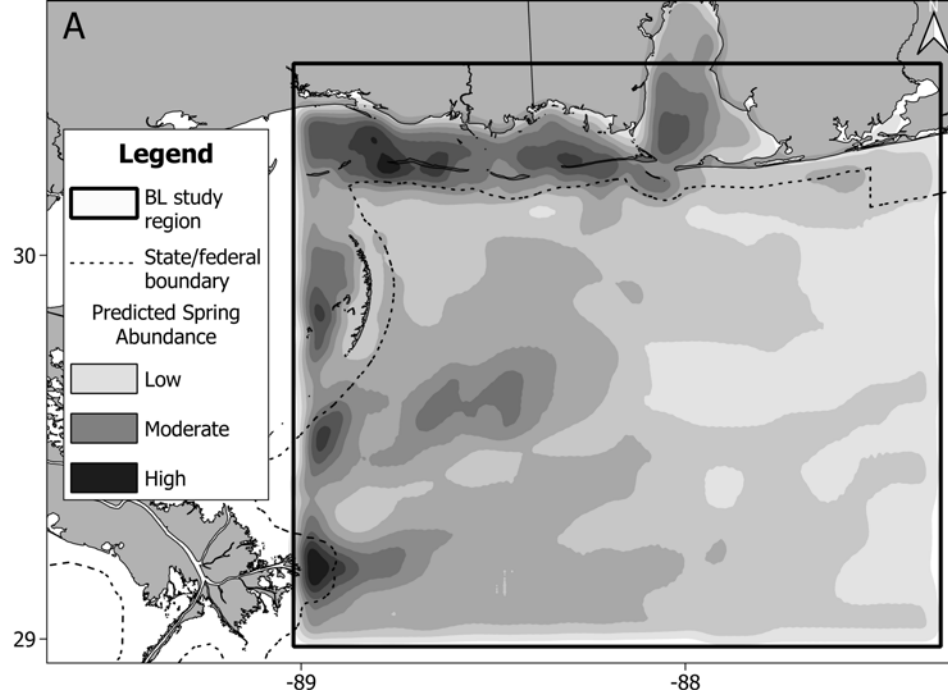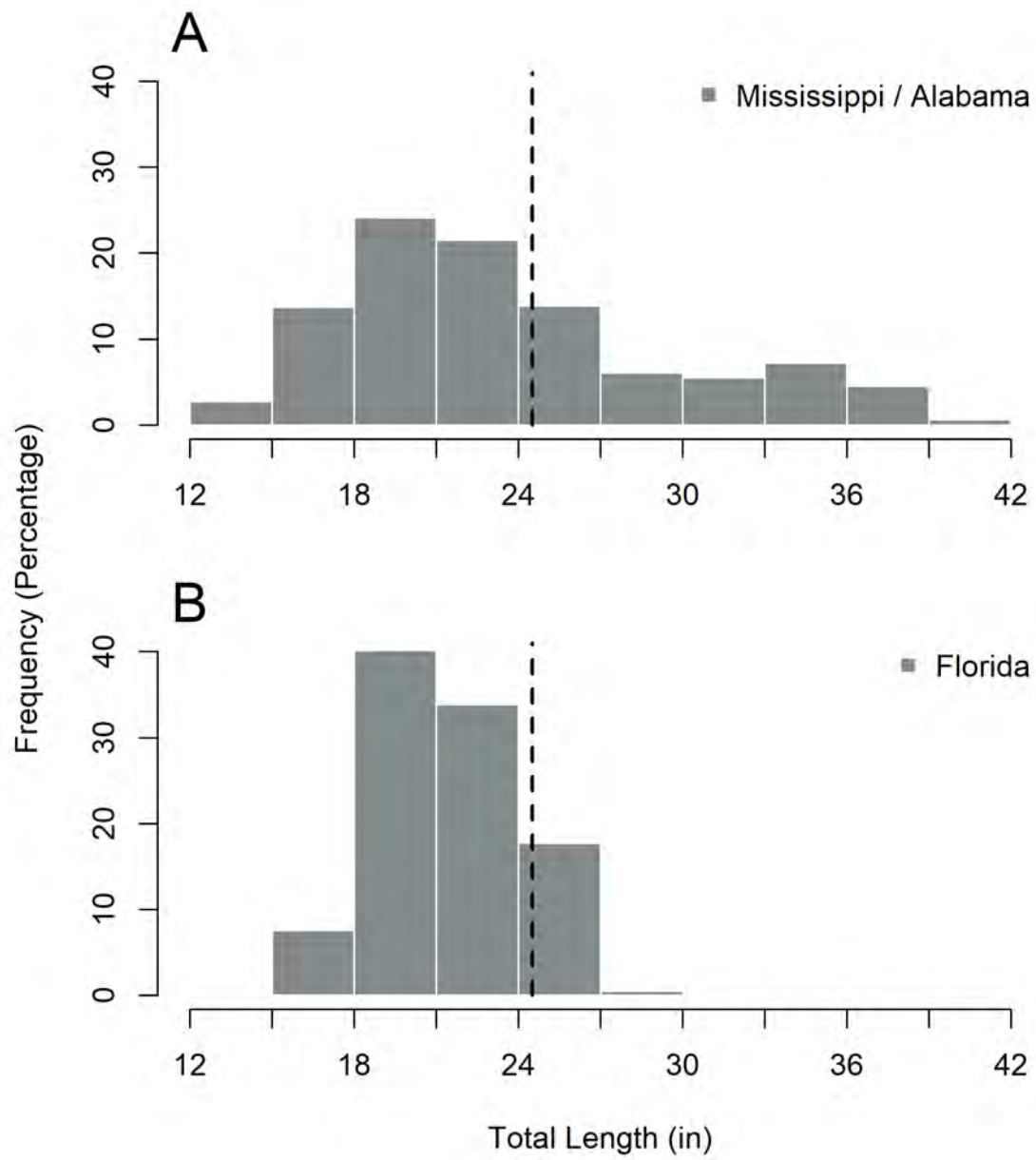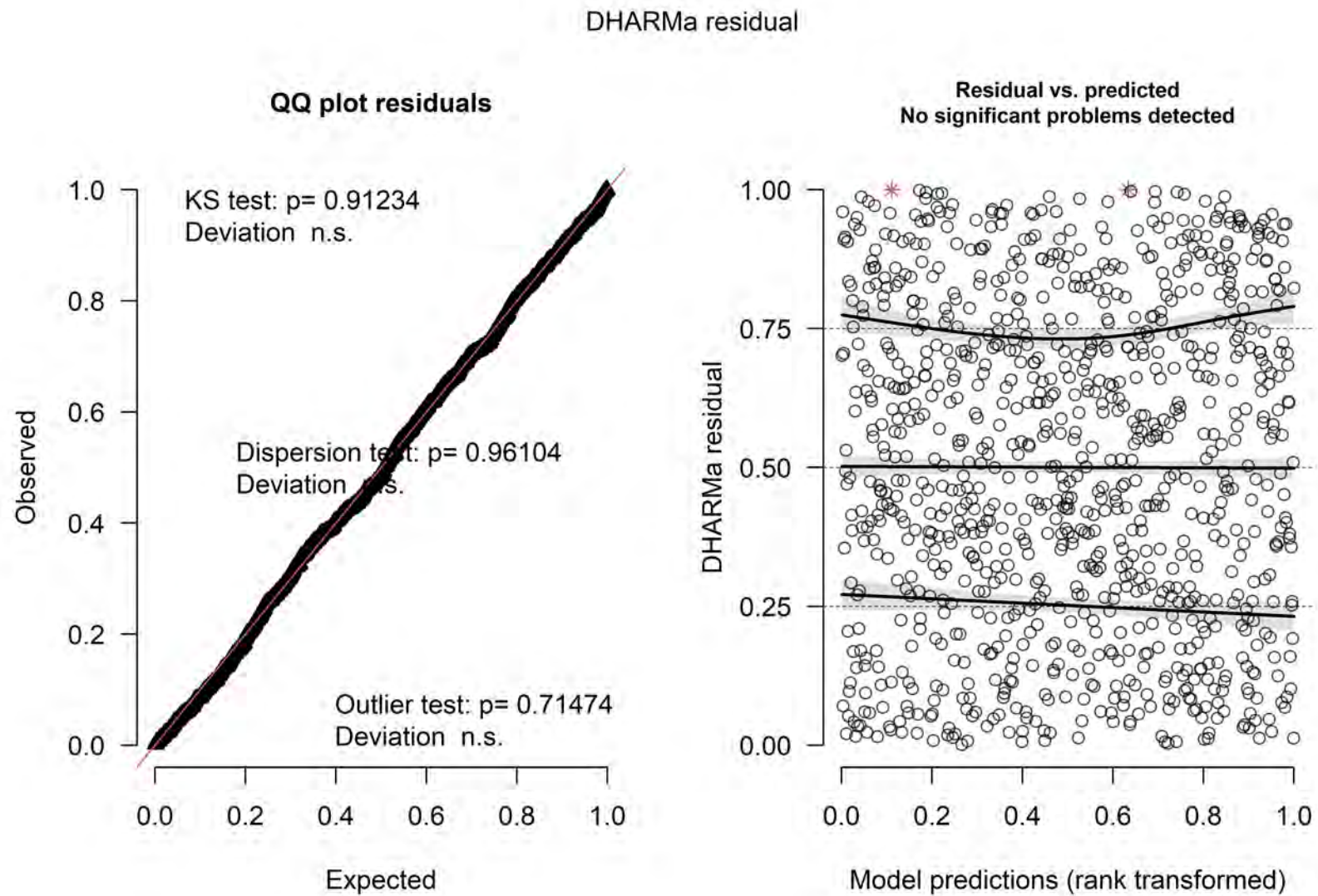**Fig3**

Fig4

Fig5

Fig6

Fig7

Fig8

Supplemental Table 1: Mean values and range for potential predictor variables included in the boosted regression trees (Table from Drymon et al. 2020)

Predictor	Source	Mean ± SE	Range
Surface temperature (°C)	HYCOM	25.788 ± 0.110	15.090 to 33.500
Bottom temperature (°C)	HYCOM	24.202 ± 0.109	14.280 to 31.970
Surface salinity (psu)	HYCOM	30.666 ± 0.139	0.004 to 36.013
Bottom salinity (psu)	HYCOM	31.935 ± 0.152	0.004 to 38.349
Surface eastward velocity, u (m/s)	HYCOM	0.027 ± 0.004	-0.465 to 0.538
Bottom eastward velocity, u (m/s)	HYCOM	0.020 ± 0.002	-0.239 to 0.219
Surface northward velocity, v (m/s)	HYCOM	-0.001 ± 0.003	-0.505 to 0.432
Bottom northward velocity, v (m/s)	HYCOM	0.003 ± 0.001	-0.353 to 0.232
Surface upward velocity, w (m/s)	HYCOM	$-2.513e^{-8} \pm 9.374e^{-8}$	$-1.710e^{-5}$ to $1.790e^{-5}$
Bottom upward velocity, w (m/s)	HYCOM	$1.410e^{-6} \pm 8.354e^{-7}$	$-4.005e^{-4}$ to $3.023e^{-4}$
Sea surface height (m)	HYCOM	-0.005 ± 0.003	-0.312 to 0.329
Bottom DO (mg/l)	NOAA	5.604 ± 0.048	0.224 to 12.161
Depth (m)	USGS	22.518 ± 0.813	1.500 to 635.00
Substrate grain size (mm)	USGS	0.097 ± 0.006	0.001 to 7.172
Daylength (min)	Calculated	772.557 ± 1.637	622.083 to 846.800
Distance from shore (km)	Calculated	20.798 ± 0.712	0.002 to 101.715

SFig1

DHARMa residual

QQ plot residuals

KS test: p= 0.91234
Deviation n.s.

Dispersion test: p= 0.96104
Deviation n.s.

Outlier test: p= 0.71474
Deviation n.s.

Observed

Expected

Residual vs. predicted
No significant problems detected

DHARMa residual

Model predictions (rank transformed)

SFig2