

Gulf and Caribbean Research

Volume 33 | Issue 1

2022

Distribution, Maturity, Age and Growth of Gray Snapper (*Lutjanus griseus*) in the Northwestern Gulf of Mexico

Joel Anderson

Texas Parks and Wildlife, joel.anderson@tpwd.texas.gov

Dusty McDonald

Texas Parks and Wildlife, Dusty.McDonald@tpwd.texas.gov

Ethan Getz

Texas Parks and Wildlife, ethan.getz@tpwd.texas.gov

Roberta Weixelman

Texas Parks and Wildlife, Roberta.Weixelman@tpwd.texas.gov

See next page for additional authors

Follow this and additional works at: <https://aquila.usm.edu/gcr>



Part of the [Marine Biology Commons](#)

To access the supplemental data associated with this article, [CLICK HERE](#).

Recommended Citation

Anderson, J., D. McDonald, E. Getz, R. Weixelman, F. Grubbs and J. Ferguson. 2022. Distribution, Maturity, Age and Growth of Gray Snapper (*Lutjanus griseus*) in the Northwestern Gulf of Mexico. *Gulf and Caribbean Research* 33 (1): 14-27.

Retrieved from <https://aquila.usm.edu/gcr/vol33/iss1/2>

DOI: <https://doi.org/10.18785/gcr.3301.02>

This Article is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in *Gulf and Caribbean Research* by an authorized editor of The Aquila Digital Community. For more information, please contact aquilastaff@usm.edu.

Distribution, Maturity, Age and Growth of Gray Snapper (*Lutjanus griseus*) in the Northwestern Gulf of Mexico

Authors

Joel Anderson, *Texas Parks and Wildlife*; Dusty McDonald, *Texas Parks and Wildlife*; Ethan Getz, *Texas Parks and Wildlife*; Roberta Weixelman, *Texas Parks and Wildlife*; Faye Grubbs, *Texas Parks and Wildlife*; and Jason Ferguson, *Texas Parks and Wildlife*

GULF AND CARIBBEAN

R E S E A R C H

Volume 33
2022
ISSN: 2572-1410



Published by

**THE UNIVERSITY OF
SOUTHERN MISSISSIPPI**

GULF COAST RESEARCH LABORATORY

Ocean Springs, Mississippi

DISTRIBUTION, MATURITY, AGE, AND GROWTH OF GRAY SNAPPER (*LUTJANUS GRISEUS*) IN THE NORTHWESTERN GULF OF MEXICO

Joel Anderson¹, Dusty McDonald², Ethan Getz³, Roberta Weixelman¹, Faye Grubbs³, and Jason Ferguson⁴

¹ Perry R. Bass Marine Fisheries Research Station, Texas Parks and Wildlife, 3864 FM 3280, Palacios, TX, 77465 USA; ² Corpus Christi Fisheries Management District, Inland Fisheries Division, Texas Parks and Wildlife, P.O. Box 116, Mathis, TX 78368, USA; ³ Upper Laguna Madre Field Office, Coastal Fisheries Division, Texas Parks and Wildlife, 1409 Waldon Road, Corpus Christi, TX 78418, USA; ⁴ Lower Laguna Madre Field Office, Coastal Fisheries Division, Texas Parks and Wildlife, 95 Fish Hatchery Road, Brownsville, TX, 78250, USA; * Corresponding author email: joel.anderson@tpwd.texas.gov

ABSTRACT: Recent population expansion of Gray Snapper, *Lutjanus griseus*, in the northern Gulf of Mexico is driving increasing catch in the recreational fishery in Texas. We assessed long-term trends in distribution and abundance of Gray Snapper in Texas using fishery-dependent and fishery-independent data collected by the Texas Parks and Wildlife Department in the years 1980–2019. Boosted regression trees (BRT) were used to evaluate factors (water quality, season, depth, bay and inlet distance) driving Gray Snapper presence in fishery-independent samples of juveniles (seines) and subadults (gill nets) found in estuaries. Estuarine Gray Snapper were subsequently sampled from gill nets, and otolith age and gonad development were evaluated microscopically to assess patterns of age, growth, and maturity. Increasing Gray Snapper abundance in Texas was coupled with expansion of the population age structure in comparisons before and after 1993. Gray Snapper juveniles and subadults encountered in Texas estuaries are generally associated with lower bays and offshore passes, and are more common in the late summer/early fall. Comparison of size (total length in mm) of recreational catch inshore versus offshore suggests that mature adults recruit to offshore habitats around 409 mm TL, or around 3 years old, which is approximately coincident with the onset of sexual maturity. Increasing abundance coupled with an expanding age structure of Gray Snapper in Texas have co-occurred with increasing winter temperatures over time. Population expansion could be facilitated by management measures that improve overwinter survival of juveniles and subadults in estuaries prior to offshore recruitment.

KEY WORDS: population growth, recruitment, population dynamics, age structure, otoliths

INTRODUCTION

Gray Snapper, *Lutjanus griseus*, also known as mangrove snapper, are found in the western Atlantic and Gulf of Mexico (GOM) from North Carolina to Brazil, and infrequently as far north as Massachusetts (Hoese and Moore 1998). Gray Snapper are increasing in abundance relative to historical inshore and offshore angler catches in Texas waters and the US Exclusive Economic Zone in the western GOM, and this increase in abundance is likely driven by increased wintertime minimum temperatures over the last 40 years (Tolan and Fisher 2009). Gray Snapper is a semi-tropical species having a relatively high lower lethal temperature relative to other Texas estuarine fishes (11–14 °C; Starck and Schroeder 1971) and have been reported to be a common casualty during cold temperature events in Texas (Gunter 1941, 1951, McEachron et al. 1994). Although their abundance has been increasing in Texas, the range of the Gray Snapper population might be constrained by overwinter survival of juveniles and subadults within estuaries, which can be subject to thermal extremes (Wuenschel et al. 2012). Continued expansion of the Gray Snapper population in the northern GOM is therefore difficult to predict, and such projections would benefit from data pertaining to spatial and temporal trends.

The presence of multiple independent stocks of Gray Snapper in the northern GOM has been previously detected using genetic methods (Gold et al. 2009), and therefore it would be worthwhile to explore whether reproductive biology and growth in the western GOM is similar to what has already been reported elsewhere in the range of the species. Data per-

taining to the reproductive biology of Gray Snapper would be advantageous for developing management goals that are tied directly to specific life history events, such as age and/or size at maturity, and the timing of recruitment to offshore habitats. Starck and Schroeder (1971) provided the most extensive study of reproductive biology in Gray Snapper based on observations in Florida, and found females to be reproductively mature as small as 200 mm SL, and males as small as 190 mm SL. With regard to spawning location, Croker (1962) noted a difference in maturity stages observed in inshore versus offshore locations, leading Starck and Schroeder (1971) to conclude that spawning occurs offshore. Domeier et al. (1996) observed offshore movement consistent with adult migration for spawning in the Florida GOM, and found size-at-maturity for both males and females to be consistent with Starck and Schroeder (1971). Most of what we know about the reproductive biology of Gray Snapper therefore comes from studies in the eastern GOM and Atlantic coast of Florida. Data from the western GOM are limited and would improve the ability of fishery managers in this area to link management priorities to stock-specific reproductive benchmarks.

Growth data from Gray Snapper have also been reported in multiple previous studies (Johnson et al. 1994, Burton 2001, Allman and Grimes 2002, Fischer et al. 2005, Allman and Goetz 2009). The similarity of growth parameters observed in the northern GOM (Louisiana; Fischer et al. 2005) versus the southeast Atlantic coast (Florida; Burton 2001) suggests that growth might be a relatively consistent process across much

of the range of the species (i.e., similar growth curve parameters). However, a previous study on the Atlantic coast of North America noted differences in growth of juveniles driven by latitude (Denit and Sponaugle 2004), and Andrade and Santos (2019) implied that at the edge of the species' range, variation in growth might be driven by phenotypic plasticity in the face of water temperature extremes. In this context, an age and growth function generated from known-aged individuals in the western GOM would more reliably allow for estimates of age projected backwards onto fishery data sets (e.g., estimates of age based on observed fish lengths) such as the extensive fishery-dependent and fishery-independent data possessed by the Texas Parks and Wildlife Department (TPWD).

Currently, there are no size or bag restrictions for Gray Snapper in Texas, owing mainly to the historical rarity of this species. However, the Gray Snapper is becoming a recreationally popular species in Texas, particularly in southern estuaries where they are more commonly found, and the potential exists for the expansion of this fishery in the face of recently observed increases in species abundance in the area. In this study, we used data from long-running fishery-independent sampling by TPWD as well as angler (creel) surveys, coupled with dissections of reproductive tissues and otolith analysis, to elicit information related to basic biological parameters associated with Gray Snapper distribution, maturity, age, growth and recruitment in Texas. We used abundance and age structure data to examine the expansion of the Gray Snapper population in the western GOM first reported by Tolan and Fisher (2009). In that study, increases in abundance of Gray Snapper were shown to be related to increases in water temperature in Texas approximately before and after 1993. The temperature trend observed by Tolan and Fisher (2009) has continued into the present (Supplemental Figure S1), and it would be worthwhile to determine whether increasing temperature has accelerated abundance trends and/or has been coupled with chang-

es in population age structure. Increases in abundance, body size and age structure of Gray Snapper throughout the GOM, and in Texas specifically, may result in increased opportunities for recreational anglers. Thus, the objective of this work was to improve the biological data upon which future management of the Gray Snapper recreational fishery in Texas can be based.

MATERIALS AND METHODS

Fishery-independent sampling

Collections of juvenile and subadult/adult Gray Snapper were carried out via fishery independent sampling in the years 1980 - 2019 by the TPWD using bag seines and gill nets (annual sample sizes can be found for each gear in Supplemental Tables S1 and S2). The TPWD fishery independent monitoring program has sampled finfishes in Texas estuaries using the same general methodology throughout the entire length of this study, and therefore year-to-year changes in abundance and distribution can be reliably assessed with these data. Gray Snapper were sampled from all major bays in Texas (Figure 1) through the duration of the study, with 3 exceptions. In East Matagorda Bay, bag seine sampling was initiated in 1983. In Sabine Lake, gill nets and bag seines were both initiated in 1986. In Cedar Lakes, bag seines and gill nets were initiated in 1996.

Bag seines, used to assess the juvenile Gray Snapper population, were 18.3 m long and 1.8 m deep, with 19 mm nylon mesh in the wings and 13 mm nylon mesh in the bag (1.8 m wide bag). Bag seines were pulled parallel to shorelines for 15.2 m and were deployed in each major bay in Texas throughout each month and year of the study, in grids selected by stratified random sampling design (stratified by bay). All individuals were enumerated and measured to the nearest mm total length (TL) and released. The normal size range of individuals captured in TPWD bag seines is < 120 mm TL, although occasionally much larger individuals are sampled. In order to focus analyses only on juveniles, individuals > 120 mm TL were

excluded from bag seine data analysis. Given that all seines were pulled over a predetermined distance, catch-per-unit-area (CPUE) was calculated as total catch divided by total area sampled (0.03 hectares; units = catch/ha).

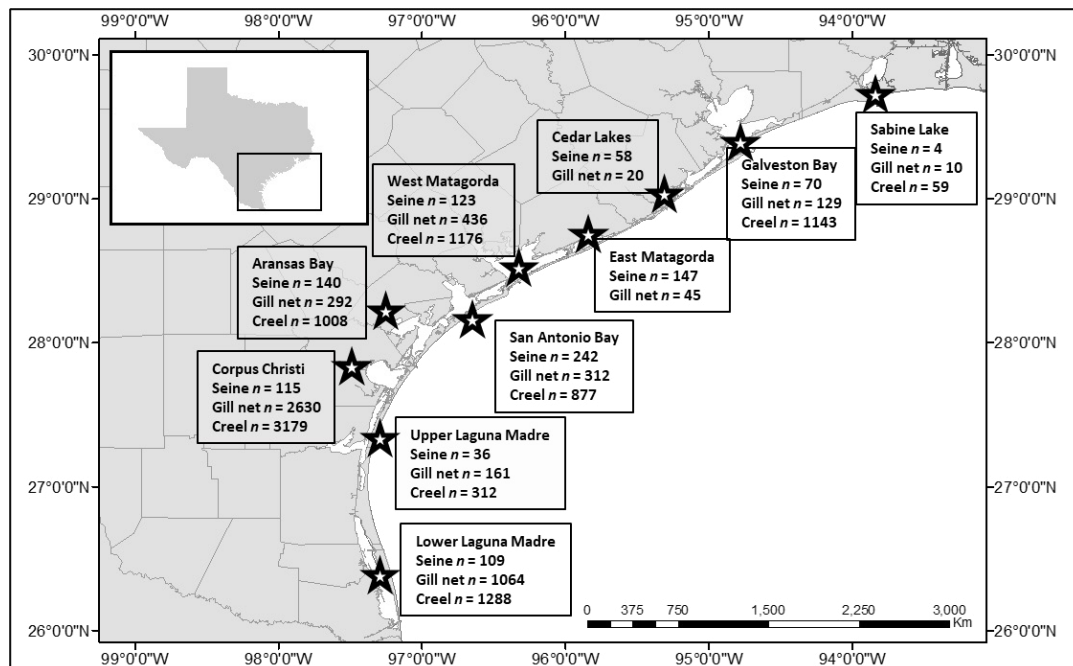


FIGURE 1. Map of Gray Snapper sample sites in Texas. Sample sizes (number of individuals captured) for seines, gill nets, and angler surveys (creels) appear below each major bay. The creel sample size for West Matagorda bay also includes creels conducted at boat ramps that are technically in East Matagorda.

Gill nets were used to assess the subadult and adult Gray Snapper population. For the purposes of this study, “subadult” will be used to refer to Gray Snapper ≥ 1 year of age, but prior to sexual maturity, whereas “adult” refers to sexually mature fish. Gill nets were deployed overnight perpendicular to shorelines, had a total length of 182.9 m, and were divided evenly into 4 panels of 45.7 m each, with mesh sizes of 152 mm, 127 mm, 102 mm and 76 mm (listed relative to distance from shoreline, with 76 mm being adjacent to the shoreline). Gill nets were deployed within 1 hour of sunset and retrieved the next day immediately after sunrise. Gill net deployments were confined to two, 10-week “seasons” in spring (April – June) and fall (Sept – Nov). Individual fish were enumerated and measured to the nearest mm TL. While most individuals were released, subsets of fish from gill net observations were retained for maturity stage and otolith microstructure analysis (described below). For gill net gear, CPUE was estimated as the total catch divided by the elapsed time of deployment (units = catch/hour).

In the case of both gear types, latitude, longitude, and water parameters at each sample point were also recorded (temperature [°C], salinity, dissolved oxygen [DO, mg/mL], and depth [0.1 m]). Depth was measured at the deepest point in both gear deployments. Inlet distance was calculated in ArcMap 10.8 (ESRI, Redlands, California) as the distance (km) between the centroid of each 1 minute x 1 minute sample grid to the nearest Gulf/bay pass. For a more detailed description of sampling methods, see Martinez–Andrade (2015).

Fishery–dependent sampling

The TPWD has not historically deployed a fishery–independent gear that reliably catches adult Gray Snapper populations offshore in the greater GOM. In order to improve sampling distribution of larger (and presumably older) individuals, we used TL data acquired from angler creel surveys collected during the course of the TPWD marine sport–harvest monitoring program, where recreationally caught Gray Snapper were encountered both inshore and offshore. Angler survey data were collected for the same time period that fishery–independent data collection took place (1980 – 2019). The target population for angler surveys was sport–boat, guided, and tournament angling parties with trip lengths of < 12 hours, who ended their trips between 1000 to 1800 hours at conventional marine boat access sites. Surveys were focused on ramps with heavy usage, and selection of high–use sites was based in part on historical trailer rove surveys (TPWD, unpublished data). Survey data were binned by inshore (estuaries bounded by barrier islands, inclusive of GOM passes) and offshore (extending offshore from barrier islands) trips based on angler responses. For each angler survey, all Gray Snapper were measured to the nearest mm TL (contingent upon approval of the angler). This sampling universe resulted in observations of 7,454 Gray Snapper caught by the recreational fishery in inshore areas, and 1,588 caught offshore. A more detailed description of the angler survey methodology employed can be found in Green and Campbell (2005).

Catch and distribution statistical analysis

Annual trends in CPUE were qualitatively assessed in both bag seines and gill nets using bar plots of year versus CPUE. For bag seine data, length–frequency plots were used to track cohort growth through months. Because a majority of bag seine catches occurred between July and December (98%, see results), length–frequency plots were confined to these months.

To evaluate spatial patterns associated with catch location, bag seine and gill net samples were interpolated and mapped using the Spatial Analyst tool in ArcMap 10.6.1 (ESRI, Redlands, CA). Bag seine and gill net catches were interpolated separately to assess the distribution of juvenile and subadult/adult Gray Snapper respectively. Geospatial kriging (e.g., Oliver 1990) was used to interpolate Gray Snapper catch throughout all bays based on catch abundance and location (spatial units were 1 minute x 1 minute grids). Heatmaps were then generated from kriging data to identify single or multiple adjacent grids with concentrated Gray Snapper catch.

Due to a high number of zero catch observations of Gray Snapper in fishery–independent samples, we converted total catch data (abundance) to presence/absence (per gear deployment). We used a boosted regression tree approach (BRT) to determine whether there were specific conditions that were commonly associated with catch in both juveniles (bag seine) and subadults/adults (gill net). The BRT framework was selected over traditional statistical approaches because (1) the BRT approach is particularly well suited for eliciting non–linear relationships between predictor and response variables, (2) the BRT approach can easily deal with complex suites of variable types (e.g., combinations of continuous and nominal variables) and (3) the BRT approach is intrinsically robust to multicollinearity between predictors, and as such constrictive a priori assumptions surrounding correlation between explanatory variables can be relaxed.

For each gear, the optimal number of boosting trees was determined using a cross–validation procedure (Hastie et al. 2001) assuming a Bernoulli error distribution, with default tree complexity of 5 nodes, a learning rate of 0.01, and a bag fraction of 0.5 (see Elith et al. 2008 for a more detailed description of these parameters). The cross–validated model was simplified by exploring the impact of removing variables systematically on the predictive deviance of the simplified model relative to the full model (with all variables included). Variables were removed via qualitative examination of the plot of the change in deviance explained as a function of systematic variable removal. A final simplified model was constructed with the lowest contributing variables excluded. The impact of each variable on Gray Snapper presence/absence in the final model was assessed using partial dependence plots, which were generated by fitting a generalized additive model (GAM) spline to the plots of explanatory variables against fitted values of catch probability from the BRT. For bag seines, explanatory variables included in the initial cross–validation included bay, inlet distance, salinity, temperature, oxygen, depth and month. Initial review of dissolved oxygen values suggested that instrumentation error might have resulted in

abnormally high estimates of dissolved oxygen in a small number of bag seine deployments. For this reason, observations in the top 2.5% tail of the distribution of this variable were coded as missing data. For gill nets, the initial model included the variables bay, inlet distance, salinity, temperature, oxygen, depth, and season (spring/fall; since gill nets are not set in every month, season was chosen as a temporal predictor). The BRT analysis was performed in R version 3.6.1 (R Core Team 2019) using the package *gbm* v 2.1.8 (Ridgeway 2013), with additional modified code described in the supplementary files of Elith et al. (2008), and GAMs were fit to the BRT plots using the package *mgcv* (Wood 2017).

Analysis of size and sexual maturity

A sample of individuals observed in TPWD fishery-independent gill nets were retained for analysis of weight (gonad weight and body weight) and maturity. Individuals of both sexes sampled between 2006–2010 were supplemented with samples obtained by hook-and-line angling (by the authors) throughout the sample area during the same time period (final $n = 686$). Samples for this analysis were obtained from March – November, after which Gray Snapper generally disappeared from inshore areas.

The relationship between TL (mm) and body weight (BW, g) was examined using plotting and ANCOVA analysis. The TL and BW for each individual were log-transformed and plotted by sex in order to qualitatively look for differences in TL/BW ratio. ANCOVA was used to quantitatively determine if the relationship between TL and BW was significantly different between sexes. For this analysis, log (BW) was modeled as a dependent variable and log (TL) was modeled as a covariate, with sex as a categorical treatment variable. An additional interactive term (logTL * sex) was included in order to test the underlying assumption of homogeneity of slopes between sexes.

Gonads were removed from both male and female specimens and the wet weight of gonads (GW, 0.01 g) was recorded. The ratio of gonad weight to body weight was used to develop gonadosomatic indices (GSI), or the ratio of the contribution of mass to reproductive and somatic tissues, respectively (gonad weight/whole body weight). We observed fat deposits associated with the gonads of both males and females (similar to what was described in Starck and Schroeder 1971). We did not include the weight of these fat deposits in estimation of either BW or GW when calculating GSI, because the range of weights of fat deposits was often an order of magnitude greater than actual reproductive tissues.

We classified ovarian maturity of females ($n = 285$) using ovary dissections and following the maturity class designations described in Brown–Peterson et al. (1988). An ovarian tissue sample was placed in clearing solution consisting of 6 parts ethanol, 3 parts formalin and 1 part acetic acid (Brown–Peterson et al. 1988) and oocytes were assigned to one of five maturation stages based on size and appearance in microscopic examination (0 = juvenile or no visible oocytes, 1 = primary growth oocytes present or “immature”, 2 = cortical alveoli, 3 = advancing, or early vitellogenic, 4 = late vitellogenic). In the event that any female had oocytes representing a mix of stages,

they were coded with the more advanced stage. Females were considered sexually mature at stage 2 with the appearance of cortical alveoli and were assumed to be capable of spawning in the upcoming reproductive season (i.e., “developing”, Brown–Peterson et al. 2011).

We tracked mean GSI by month (with years grouped) to determine whether there was evidence for spawning seasonality in months typically reported from other Gray Snapper studies (June – August; Starck and Schroeder 1971; Domeier et al. 1996; Tzeng et al. 2003; Denit and Sponaugle 2004). An ANOVA was used to determine if there was significant variability in mean GSI among months, and the significance of parameter estimates (individual months) was assessed to determine whether there were months with higher than mean GSI, indicating initiation of the spawning season. Based on summer and early fall spawning reported in previous studies (Starck and Schroeder 1971; Domeier et al. 1996; Tzeng et al. 2003; Denit and Sponaugle 2004), and an elevated GSI observed in June (see results) we examined oocyte stages in May – September ($n = 215$) to look for evidence of impending spawning (i.e., oocyte stages > 2).

Age and growth

Otolith-based age was obtained for 650 individuals collected between 2006 – 2010 and included all but 36 females from the maturity analysis that had missing or damaged otoliths. Both sagittal otoliths were removed, cleaned, and stored for otolith age analysis. The left sagittal otolith was used for most specimens; in the case of damage, the right sagittal otolith was used for analysis. Otoliths were set in epoxy resin and sequential 0.3 mm sections were made until the otolith core was sectioned. The core section was mounted on a slide and imaged using a Nikon light dissecting microscope with Nikon Elements software (Nikon Corp., Tokyo, Japan).

For assignment to age, all individuals were assumed to have a 1 July birth date, based on 2 previous studies (Domeier et al. 1996, Allman and Grimes 2002). A 1 July birth date was also supported in the current study by the fact that young-of-the-year Gray Snapper begin appearing in bag seines in July with a mean size indicative of recent hatch (~43 mm TL, see results). Biological age was estimated as the number of annuli present, plus an adjustment for the number of months advancing from the 1 July birth date at the time of capture; biological age was rounded to the nearest 1/10th year. Detailed age class estimation methods for Gray Snapper are generally standardized throughout state resource agencies in the GOM and southern US Atlantic and can be found in VanderKooy et al. (2020).

A growth curve was fit to the relationship between fractional biological age and individual TL of captured fish. First, we tested whether there were differences in growth parameters between sexes. Starting parameters for a von Bertalanffy growth curve were generated using the combined data, and then these parameters were improved with Monte Carlo simulations in known male ($n = 208$) and female ($n = 286$) parsed data sets. Initial runs suggested instability in the L_{inf} parameter (asymptotic length), so we estimated the growth parameter (k) and the length at time zero (t_0) while holding L_{inf} constant in each sex

at 696 mm TL. We feel that constrained parameter estimation was justified, because: (1) the constrained L_{inf} was informed by a consensus mean from multiple previous studies (Johnson et al. 1994, Burton 2001, Fischer et al. 2005, Allman and Goetz 2009), (2) parameter estimation for k and t_0 were relatively robust to the chosen fixed value of L_{inf} (data not shown), and (3) the growth function performed relatively well across all ages based on comparisons with observed ages. Then we compared the standard errors for both unconstrained parameters (k and t_0) to determine whether there were significant differences between sexes. This preliminary analysis demonstrated no difference in growth trajectories between males and females (see results), a finding that was supported by previous studies (Fischer et al. 2005, Allman and Goetz 2009). As such, sexes were combined along with additional unknown sex individuals ($n = 156$) to improve the final sample size for curve fitting. Size-at-age was modeled using a final von Bertalanffy growth function, with L_{inf} again constrained to 696 mm TL. All steps of growth modeling were carried out using the R package FSA (Ogle et al. 2021). Mean size-at-age estimates (rounded to age in years) were generated from the fitted mean value of the growth function for each age class, and these were compared to mean TL observed in the field to assess reliability of the growth function.

To test the hypothesis that increasing abundance in Texas has been coupled with an expanding age structure, we estimated age structure distributions using TL of Gray Snapper from fishery-independent gill nets and fishery-dependent creel surveys in years up to and including 1993, and again in years after 1993. Age structure was estimated by solving the growth function for age and applying this function to all observed lengths throughout each period. Age estimates were rounded to the nearest whole age value, and age distribution bins were estimated as the % of total catch in each bin for each era. Chi-square (X^2) tests were used to determine whether age distributions were significantly different between eras. Separate tests were conducted for fish sampled in gill nets and creel surveys (since gill nets did not include offshore fish). Since only individuals < 7 years old were used to generate the growth function, all ages ≥ 6 were grouped into a single "6+" bin for these analyses.

Offshore migration related to maturity and spawning has been documented for Gray Snapper (Croker 1962; Starck and Schroeder 1971; Domeier et al. 1996; Claro and Lindeman 2003); as such, fish observed during angler creel surveys were sorted into inshore and offshore bins to investigate the size and age at which recruitment to offshore habitats occurs. Logistic regression was used to model the mean size at which individuals were more likely to be encountered offshore (50% recruitment to offshore habitats). The mean TL at 50% recruitment (the inflection point from logistic regression) was then used to estimate mean age at offshore recruitment based on the growth function constructed in this study.

RESULTS

Catch, distribution, and habitat association analysis

During the course of 40 y of sampling, we observed 1,044

Gray Snapper juveniles in Texas bag seines. After excluding larger (> 120 mm TL) individuals, the size range of juveniles observed in bag seines followed a normal distribution, centered at 57 mm TL (range 18 – 118 mm TL). A majority of the bag seine catches occurred between the months of July and December (1,022 individuals, roughly 98% of all captures), peaking in September (380 individuals observed). Gray Snapper were rarely observed in bag seines; only 543 out of 72,904 deployments, or less than 1% of all seine samples, caught at least one individual. The CPUE of Gray Snapper appeared to increase through the duration of the study when plotted

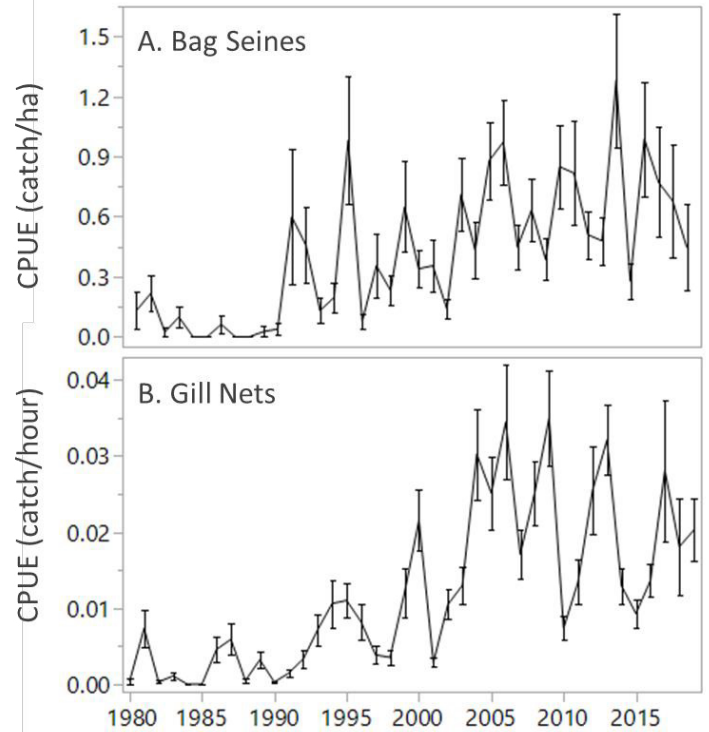


FIGURE 2. Annual mean (\pm se) catch per unit effort (CPUE) of Gray Snapper in fishery independent samples in Texas. A. Bag seines (catch/hectare). B. Gill nets (catch/hour). CPUE is combined across all sample locations in this study.

against year (Figure 2A). Juvenile Gray Snapper begin appearing in bag seine samples in July at a mean size of 43 mm TL, and mean size increased through the fall into October (58 mm TL) at which point catch declined precipitously in November and December (Figure 3). Heatmaps yielded clear patterns in juvenile distribution with catches primarily associated with GOM passes (Figure 4).

The BRT model for bag seines (1,500 trees in the final model) indicated that inlet distance explained the highest amount of deviance in Gray Snapper presence (33.1%), followed by month (24.0%), DO (21.8%), and bay (21.2%; Figure 5). Juveniles were more frequently observed near GOM inlets, and probability declined as distance to the inlet increased. Catch probability was highest in the months July – November, and was highly variable among bays (no directional spatial trend was apparent from partial dependence plots). Finally, the relationship between Gray Snapper juvenile presence and oxygen

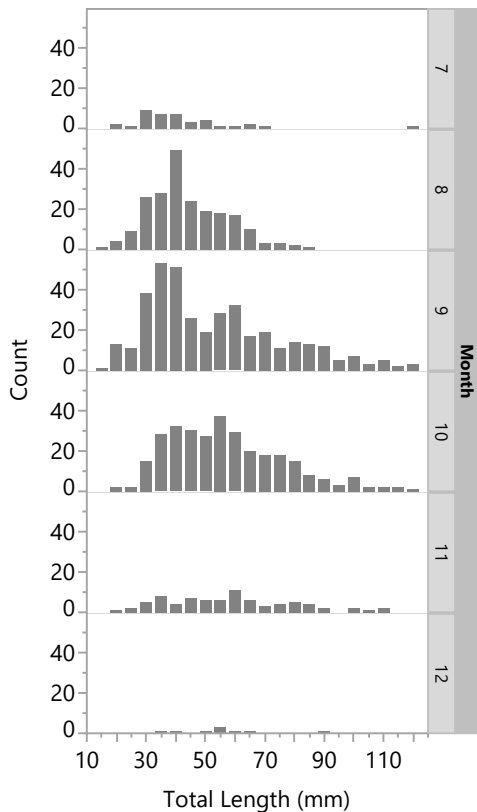
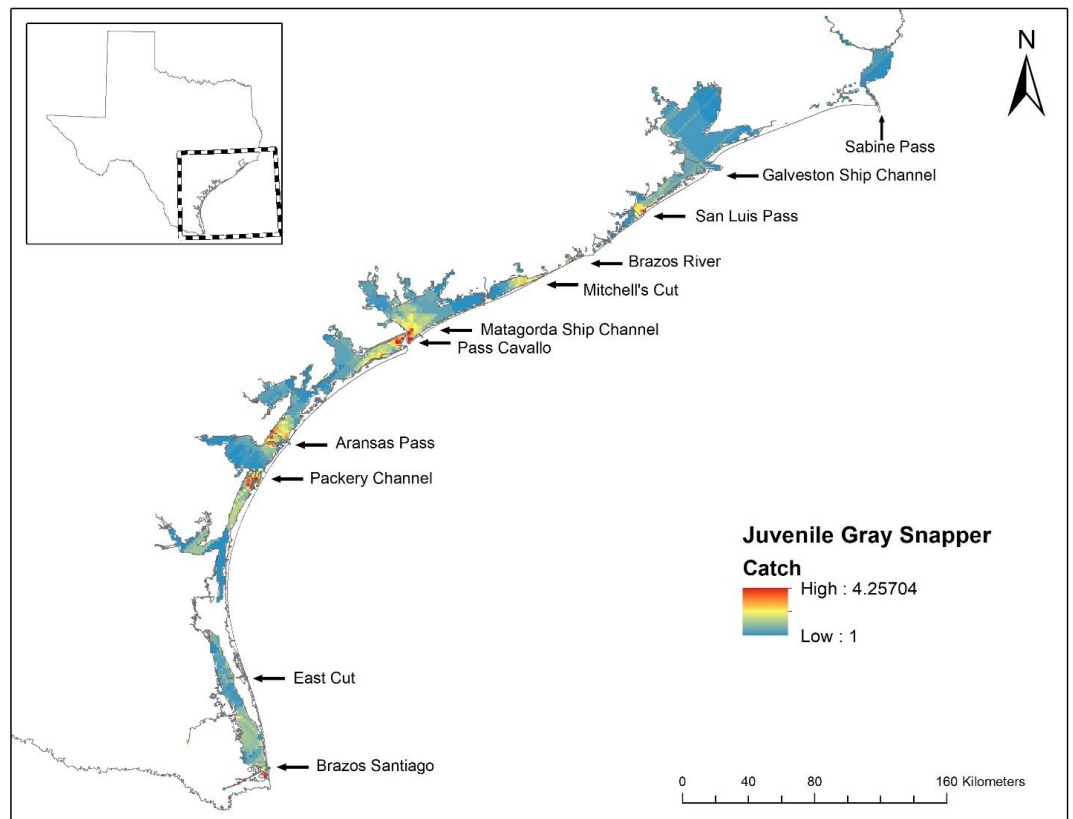


FIGURE 3. Length-frequency of Gray Snapper (< 120 mm TL) captured in Texas Parks and Wildlife bag seines for the months of July - December, 1980 - 2019. All years and geographic sample locations are combined. The months of January - June are not included because very few individuals were captured in those months.

was not easily characterized, but in general presence seemed to be associated with DO levels > 5 mg/L. Temperature, salinity and depth were dropped from the BRT during the model simplification step, indicating that these variables were poor predictors of juvenile Gray Snapper catch in the presence of other variables.

In gill net samples, 5,099 Gray Snapper were observed through the duration of the study. The mean TL observed was 307 mm (range 124–593 mm TL); the distribution of catch size might be biased (Figure 6, top), likely due to gear bias (gill nets are unlikely to catch Gray Snapper < 200 mm TL at the same rate as larger individuals due to large mesh sizes). Gray Snapper

FIGURE 4. The inshore distribution of juvenile Gray Snapper in Texas predicted based on spatial interpolation (kriging) of observed catch from 1980 - 2019. High abundance associated with labeled Gulf of Mexico passes was implied based on increased probability of catch in these areas.



were most often caught in fall gill nets (Sept–Nov, $n = 4,474$ observed) compared to spring gill nets (Apr–June, $n = 625$ observed), although CPUE dropped precipitously between October and November. Observations of Gray Snapper in gill nets were more common than in bag seines, with 1,761 of 29,607 gill net deployments catching at least one individual (~6%). As with bag seine samples, CPUE generally increased through the duration of the study when plotted against year (Figure 2B), although there was high inter-annual variability in CPUE. Spatial patterns in gill net catches were also similar to bag seines with heatmaps revealing high concentrations of Gray Snapper near GOM passes (Figure 7).

The BRT model for gill nets (4,800 trees in the final model) indicated that, again, inlet distance explained the highest amount of deviance (25.5%; Figure 8), with Gray Snapper presence declining with increased distance. Bay explained 22.8% of the deviance, with a general latitudinal trend (southern bays tended to have higher presence than northern ones), although Corpus Christi bay was associated with exceptionally high presence compared to all others. Salinity (17.1%), season (12.1%), temperature (11.5%) and depth (11.0%) were all included in the final model. Catch was more common in the fall, and in grids with salinity between 30–40, relatively high temperature, and relatively high depth. Dissolved oxygen was dropped from the BRT during the model simplification step.

Throughout the study period, 9,042 Gray Snapper were measured at angler creel surveys. Landings were observed from 3,654 trips with an average of 2.5 fish per boat. Length

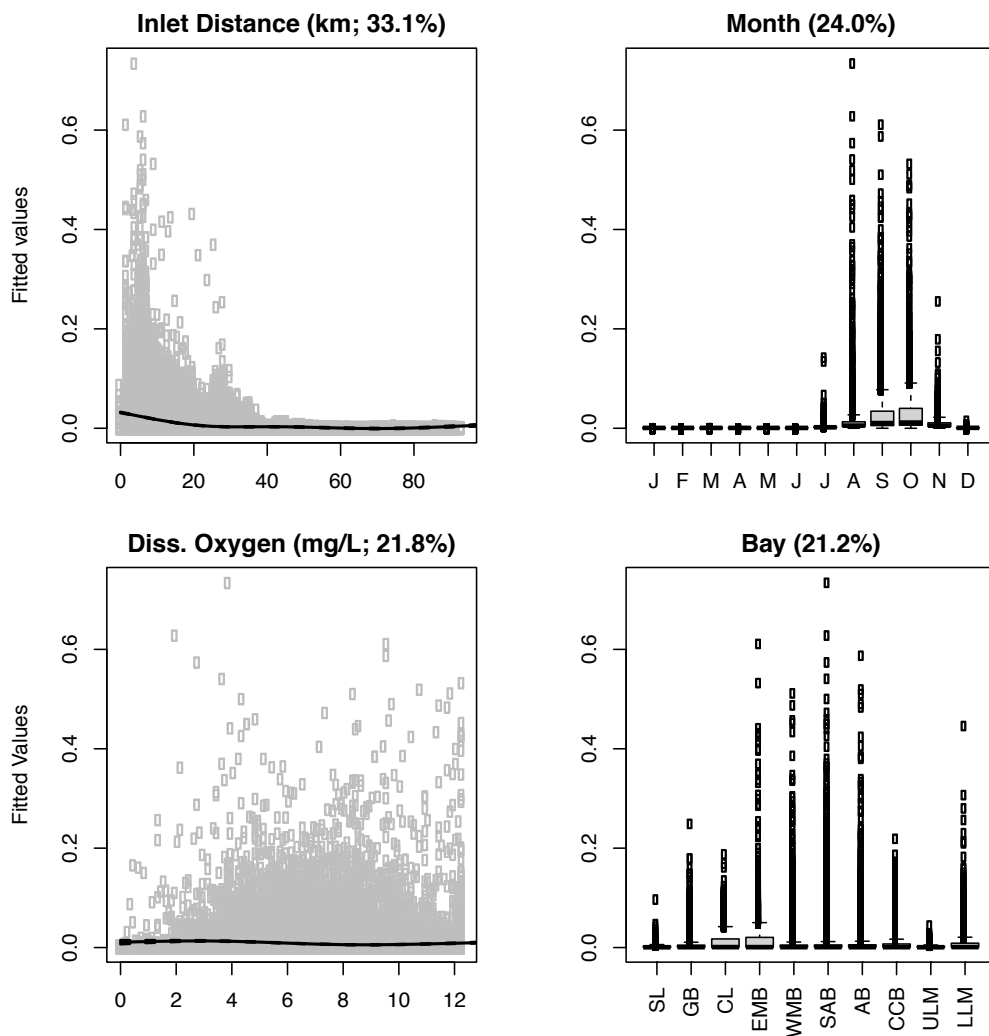


FIGURE 5. Fitted values of probability of catch based on boosted regression tree (BRT) analysis of juvenile Gray Snapper in fishery-independent bag seines. For continuous variables (distance, dissolved oxygen), gray circles are fitted values and black splines were fit to the data using a generalized additive model. The number in parentheses is the relative variable importance from BRT.

ing a TL/BW ratio that was consistent between the sexes at all sizes examined. The interactive term (TL * sex) was also not significant ($F_1 = 0.273, p = 0.602$).

Comparison of GSI by TL suggested that acceleration of investment in reproductive tissues begins between 200–250 mm TL for females, and between 250–300 mm TL in males. As expected, GSI was higher in females for a given size than males, and this difference was significant ($t_2 = 14.95, p < 0.0001$). The majority of females examined were either juveniles or had primary growth oocytes ($n = 235$), or had cortical alveoli oocytes ($n = 45$). Only 5 females were found to have early ($n = 2$) or late ($n = 3$) vitello-

ranged from 109–858 mm TL with a mean of 310 mm TL (Figure 6, bottom). Offshore landings accounted for only 18% of observed Gray Snapper, most likely due to higher fishing pressure inshore. While Gray Snapper landings were recorded in every major bay system, Corpus Christi Bay contributed the most with 35% of the coastwide landings ($n = 3,179$ individuals observed). Gray Snapper were mainly caught incidentally; 68% of landings were by anglers who indicated that they were seeking other species such as Red Snapper, *Lutjanus campechanus*, with 8% of those specifically fishing for Red Snapper.

Analysis of sexual maturity

The relationship comparing TL to BW in both male and female Gray Snapper was log–linear and suggested a consistent allometric pattern between length and weight throughout the inshore residency period (Supplemental Figure S2). The ANCOVA suggested a highly significant relationship between log–transformed TL and BW ($F_1 = 24,036, p < 0.001$), but the variable sex was not significant ($F_1 = 0.37, P = 0.540$), suggest-

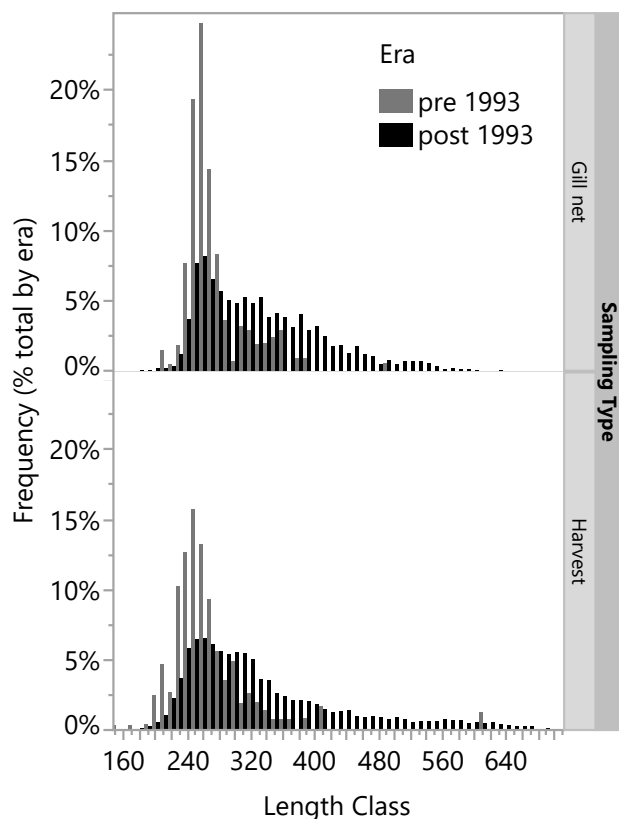


FIGURE 6. Length distribution of Gray Snapper captured in Texas from 1980–2019. Samples were parsed by era (pre- and post-1993) in order to compare distributions before and after the period of significant increases in winter temperatures and Gray Snapper abundance noted by Tolan and Fisher (2009). Top panel—data from fishery independent gill nets; bottom panel—data from fishery-dependent angler creel surveys.

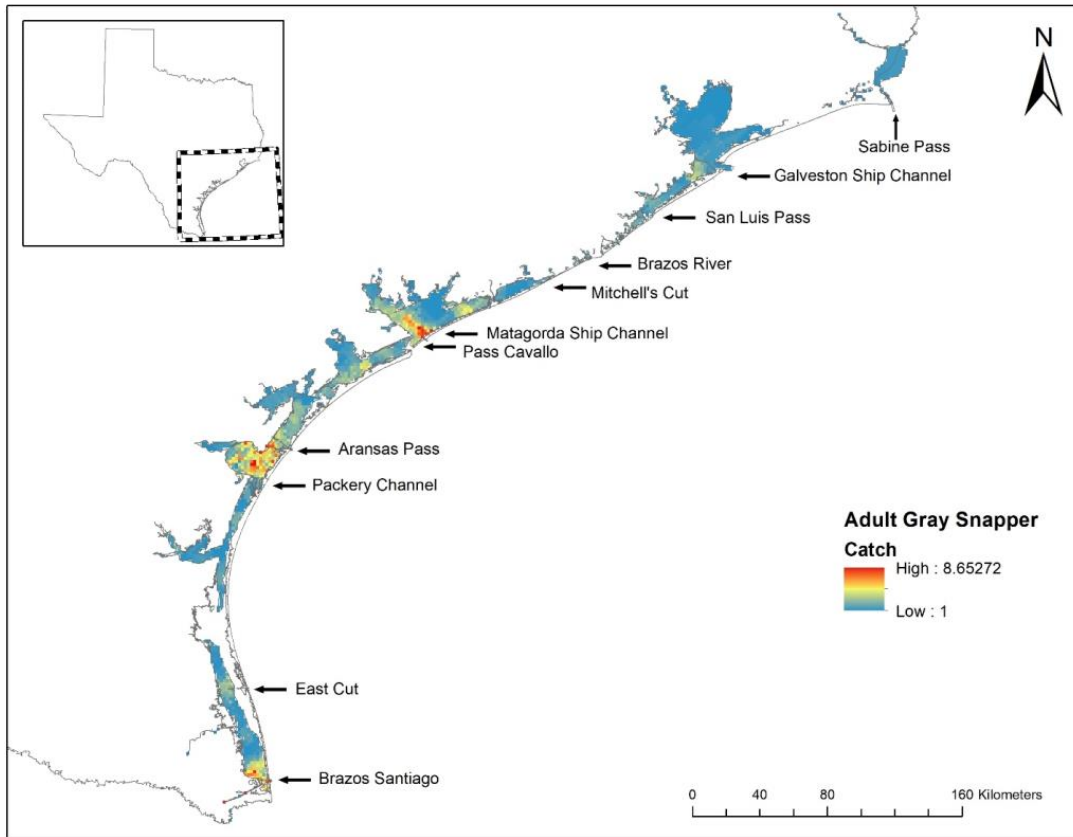


FIGURE 7. The inshore distribution of subadult and adult Gray Snapper in Texas predicted based on spatial interpolation of observed catch from 1980 - 2019. High abundance associated with labeled Gulf of Mexico passes was implied based on increased probability of catch in these areas.

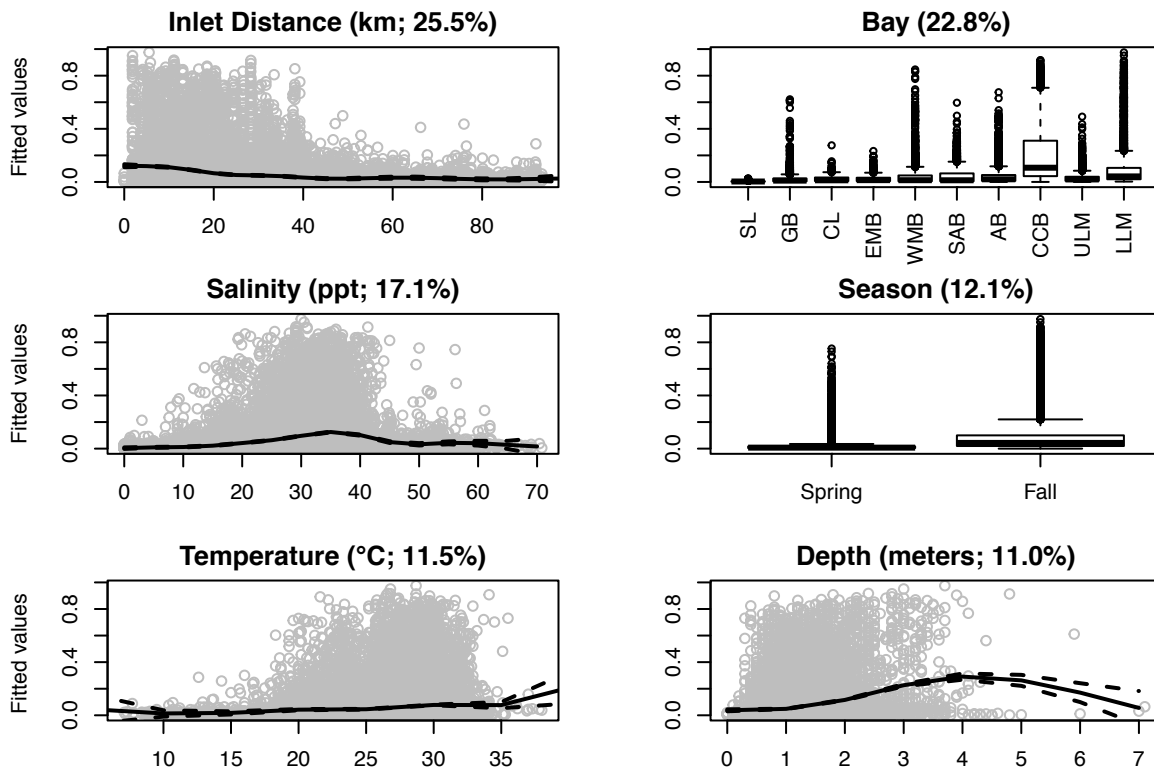


FIGURE 8. Fitted values of probability of catch based on boosted regression tree (BRT) analysis of subadult and adult Gray Snapper catch in fishery-independent gill nets. For continuous variables (inlet distance, salinity, temperature, depth) gray circles are fitted values and black splines were fit to the data using a generalized additive model. The number in parentheses is the relative variable importance from BRT.

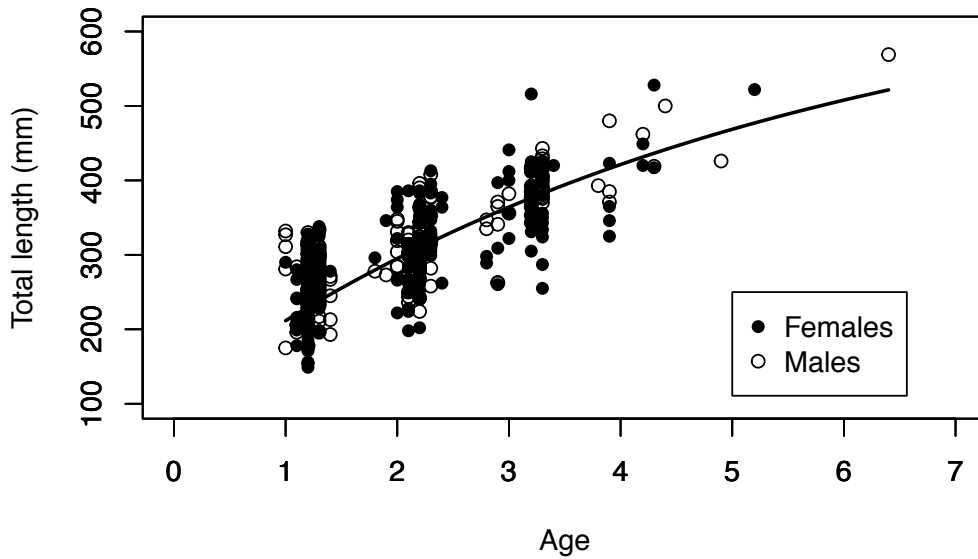


FIGURE 9. A von Bertalanffy growth function showing the relationship between age and total length (mm) for 650 Gray Snapper sampled in Texas from 2006 - 2010. Age was estimated using annulus counts from otoliths extracted from each individual, with a fractional correction for capture date. Sexes were combined for age/growth analysis after preliminary analysis yielded no evidence of sexual dimorphism.

TABLE 1. Age and growth of Gray Snapper ($n = 650$) sampled in Texas from 2006-2010. Age-based total length (TL, mm) estimates from a von Bertalanffy growth function (VBF) fit to the data are compared to mean values observed in samples (obs).

Age	n (obs)	TL (mm, VBF)	TL (mm, obs)
1	379	229	231
2	180	312	307
3	81	382	382
4	8	439	453
5	1	477	522
6	1	522	569

genic oocytes. Hydrated oocytes were not observed. Mean TL of juvenile females was 229 mm TL, compared to those with primary growth oocytes (293 mm TL) or cortical alveolar oocytes (338 mm TL). There was significant variability in GSI when examined by month ($X^2_7 = 75.15, p < 0.0001$), which was driven primarily by exceptionally high GSI for both males and females in June. Additionally, the weight of fat deposits associ-

ated with gonads was correlated with gonad weight, suggesting a reproductive function, although the correlation was relatively poor ($r^2 = 0.27, p < 0.001$). All 5 individuals with vitellogenic oocytes were observed within the expected May - September spawning season.

Age and growth

Based on otolith age, individuals retained for age analysis (all caught inshore) ranged from 1-6 years, but the majority (99%) were age 4 or younger. The growth function fit to age and total length performed well for all age classes ≤ 4 , based on qualitative examination of mean estimated TL versus actual sampled lengths (Table 1, Figure 9). The fit was also adequate for ages 5 and 6, but the sample sizes for these age classes was exceedingly low ($n = 1$, age underestimated in each case). The growth function parameters were $L_{inf} = 696$ mm, $k = 0.164$, and $t_0 = -1.741$.

When the growth function was applied to lengths observed in TPWD gill nets and creel surveys throughout the entire length of the study, there was clear increase in the distribution of older age classes (ages 3-6+) in the modern era (1994-2019) as compared to the historical era (1980-1993, Table 2), and this change in the distribution of ages was significant in both gill

TABLE 2. Distribution of ages of Gray Snapper observed in Texas in early (1980-1993) and late (1994-2019) samples. These ages were based on the distribution of observed total lengths in Texas Parks and Wildlife Department gill nets and angler harvest surveys, with age estimated using a von Bertalanffy growth function solved for age at capture. Ages 6+ were grouped to account for the limitations of the growth function (age 6 was the oldest individual observed).

Age	Gill Net				Angler Harvest			
	n, 1980-1993	% of total, early	n, 1994-2019	% of total, late	n, 1980-1993	% of total, early	n, 1994-2019	% of total, late
0	4	1.2	26	0.6	16	8.4	252	2.8
1	275	84.4	2050	46.9	150	78.5	4583	51.8
2	42	12.9	1325	30.3	20	10.5	2349	26.5
3	4	1.2	597	13.6	4	2.1	733	8.3
4	0	0.0	223	5.1	0	0.0	328	3.7
5	1	0.3	68	1.6	0	0.0	189	2.1
6+	0	0.0	85	1.9	1	0.5	417	4.7

TABLE 3. Distribution of estimated ages of Gray Snapper observed in inshore versus offshore samples in Texas, based on angler catch survey data. Age was estimated using a von Bertalanffy growth function solved for age at capture, for individuals observed in Texas creel surveys in the years 1980–2019. Ages 6+ were grouped to account for the limitations of the growth function (age 6 was the oldest individual observed in the otolith data set).

Age	n (Inshore)	% (Inshore)	n (Offshore)	% (Offshore)
0	258	3.5	10	0.6
1	4540	60.9	193	12.2
2	2091	28.1	278	17.5
3	430	5.8	307	19.3
4	96	1.3	232	14.6
5	29	0.4	160	10.1
6+	10	0.1	408	25.7

net samples ($X^2_6 = 221.13$, $p < 0.0001$) and creel survey samples ($X^2_6 = 104.95$, $p < 0.0001$). While the most common age class during both eras was age 1, age classes > 1 year have been more commonly encountered after 1993 compared to years up to and including 1993.

Larger Gray Snapper were much more common offshore compared to inshore based on creel survey landings, implying an older age structure in offshore fish (Table 3). When age was estimated from TL in individuals sampled from angler surveys, the majority of fish observed inshore (98%) were $<$ age 4 while 50% of offshore landings were age 4 or older. The lack of older age classes inshore contributed to the significant difference between age distributions ($X^2_6 = 3337.7$, $p < 0.0001$). Logistic regression analysis suggested that 50% recruitment of Gray Snapper to offshore areas occurred at 409 mm TL (about age 3, based on age estimates from TL).

DISCUSSION

The spatial and temporal distribution of Gray Snapper catch in Texas appears to be driven by multiple factors. In the case of both juveniles and older individuals, distance to the nearest inlet was the best predictor of Gray Snapper presence (Gray Snapper were proximally associated with GOM passes). Subadults/adults from gill nets were primarily found in estuaries south of West Matagorda Bay in relatively high salinity, temperature and depth, and primarily in the fall. Juveniles were associated with late summer/fall months (July – October), and DO and bay also were good predictors of presence, although bay demonstrated no clear geographical trend. The relatively high presence of juvenile Gray Snapper in summer and early fall occurred during the warmest months of the year, similar to what was previously reported in Florida (Lindeman et al. 2001, Flaherty et al. 2014). In Texas, water quality characteristics (temperature, salinity, DO) associated with high catch frequency are likely to be merely coincidental to season, resulting in demotion of the explanatory power of these variables in the bag seine BRT model (only DO was not dropped during variable selection). Similarly, while the correlation of high temperature

and salinity with subadult/adult Gray Snapper presence itself might imply habitat preference, it might also be driven in part by annual inshore/offshore movement in and out of estuaries, resulting in a seasonality of catch. A vast majority (88%) of gill net catches in this study were collected during the fall season. Seasonal migration of Gray Snapper in and out of estuaries has been reported previously (Starck and Schroeder 1971, Luo et al. 2009) and seems to be the case in the western GOM as well. The concentration in and around GOM passes of both juvenile and subadult/adult Gray Snapper suggests that inshore/offshore movements might be periodic and frequent, and that Gray Snapper use lower bays extensively, relative to other estuarine habitats. An alternative interpretation is that Gray Snapper might be more common in pass areas because many (although not all) of the GOM passes in Texas include improved structures, such as rock jetties. Whether or not similar mid-bay structures (such as pilings or reefs) are used extensively by Gray Snapper could not be reliably assessed with these data, because TPWD gill nets are only deployed along shorelines. It is worth noting that this interplay (GOM access vs. underwater structure) represents an avenue for future study of Gray Snapper habitat use in Texas. In any case, the association of Gray Snapper with GOM passes may be equally driven by their preference for marine, rather than estuarine water conditions, as well as the general ontological shift from estuarine to marine habitats that seems to occur with age in this species.

Interestingly, bay was a significant predictor of both subadult/adult and juvenile catch; however, while there was a clear latitudinal pattern with larger individuals (southern latitudes had higher gill net presence), there was no clear latitudinal pattern associated with juveniles. In fact, the BRT model fit for juvenile presence was highest in Cedar Lakes and East Matagorda Bay, the 3rd and 4th most northern estuaries sampled in the study. While this finding might be an artifact of low statistical power due to small numbers of observed juveniles, differences in geographical occurrence of juvenile versus subadult/adult Gray Snapper might also imply that populations in northern estuaries are impacted by high juvenile and subadult mortality. Juvenile Gray Snapper begin entering estuaries in July when temperature is near its annual peak (Texas coastwide mean 30.6°C). However, temperature in more northern estuaries can become intolerable for overwintering juveniles and subadults, resulting in high mortality in these areas, and ultimately in a disparity between juvenile and adult abundance in northern versus southern areas. Wuenschel et al. (2012) used thermal tolerance laboratory challenges in concert with field observations to demonstrate that the distribution of Gray Snapper on the Atlantic coast is indeed limited by chronic exposure to temperatures near the lower lethal limit in the northern extreme of the species range. Historically, the northern part of the Texas coast has probably been near the extent of the range of tolerable winter temperatures for Gray Snapper (Tolan and Fisher 2009), which has constrained the abundance of this species.

Despite seasonal temperature constraints on the historical distribution of Gray Snapper, both the abundance and

age structure of Gray Snapper populations in Texas have expanded over the past 40 years. Since 1993, the adult population has become larger on average, a finding that implies that a broader range of annual cohorts are now being encountered in both fishery-dependent and fishery-independent data sets. A broader, more stable age distribution might imply that winter minimum temperatures are now more conducive to population expansion than they were historically. This hypothesis is supported by increased minimum winter temperatures throughout the western GOM since about 1993 (Tolan and Fisher 2009). In this context, it is possible that the range and abundance of this species can be expected to expand throughout the GOM, assuming continuation of this climate trend. Poleward expansion of tropical and subtropical species has been observed worldwide (Figueira and Booth 2010, Nakamura et al. 2013, Verges et al. 2014) and specifically in the northern GOM (Tolan and Fisher 2009, Heck et al. 2015, Anderson et al. 2019, Purtlebaugh et al. 2020). Coincidental expansion of semi-tropical mangrove habitat into Texas (Armitage et al. 2015) might also be augmenting expansion of Gray Snapper populations since juveniles utilize these habitats extensively (Thayer et al. 1987, Luo et al. 2009).

A significant upward shift of the Gray Snapper age distribution in Texas indicates that future expansion of this species in the western GOM may benefit from an additive effect of decreased mortality at the juvenile stage, as well as increased reproductive output due to the persistence of older age classes. Previous work on long-lived fishes in both the Atlantic and Pacific demonstrated that an old-growth age structure is as important as overall spawning biomass in maintaining stable populations (Berkeley et al. 2004), and age structure has been directly linked to the ability of fish populations to respond to variability in recruitment (Durant and Hjermmann 2017). The reproductive output of older, larger individuals is generally greater than that of smaller, younger individuals, and this disparity might be compounded as individuals age (Barneche et al. 2018). Thus, the expanding age structure of Gray Snapper in Texas implies the potential for a disproportionate increase in spawning productivity, and the increased presence of older, larger individuals may imply a more robust capability of reproductive response to future catastrophic population-scale events such as winter freezes. One caveat to the interpretation of age data is that we used estimated lengths from fishery-independent samples, rather than otolith microstructure data itself, to characterize the changing age structure of Gray Snapper. These ages were based on a growth curve that was derived using mainly subadult (\leq age 4) inshore fish. Based on the trajectory of the growth curve from inshore samples, biases in estimates of ages might have occurred in larger offshore fish which were not represented in the growth model. Additionally, one of the underlying assumptions of our analysis is that growth rate has not changed appreciably over time, such that a growth function derived from fish sampled recently (2006–2010) could be applied across the entire time series. While these biases may have had some impact on backwards-projection of age through time, the relative consistency of pattern between fishery-independent

and fishery-independent data sets, as well as the observation of increased presence of multiple older age classes simultaneously, seems to support a broadening age structure across the time series. Significant differences in the distribution of total length in Gray Snapper sampled between 1980–1993, versus those from 1994–2019, indicates that the average age of Gray Snapper in Texas has indeed increased over time.

Size and age at sexual maturity in Gray Snapper from Texas are similar to what was reported by Domeier et al. (1996) on the Atlantic coast as well as Starck and Schroeder (1971) in southern Florida. In those studies, sexual maturity was observed in individuals as small as 182 mm SL and 198 mm SL for males and females, respectively, and a majority of individuals were sexually mature by 240 mm SL (Domeier et al. 1996). Evidence of sexual maturity from our data was constrained by the fact that no fully mature females were observed in our samples, even in the known spawning season for the species. However, we estimated most individuals were capable of spawning between ages 2 (299 mm TL) and 3 (371 mm TL), based on increased presence of cortical alveoli oocytes, which are generally absent outside of the spawning season (Starck and Schroeder 1971, Domeier et al. 1996). Increased investment in reproductive tissues (as evidenced by increase in GSI) occurred between 200–300 mm TL, and the weight of fat deposits associated with ovary tissues increased rapidly between age 2 (2.5 g) and age 3 (3.7 g; data not shown) and these were correlated with gonad weight. Starck and Schroeder (1971) noted the appearance and growth of fat deposits associated with reproductive tissues as a sign of advancing maturity.

A majority of Gray Snapper (99%) observed inshore were \leq age 4 based on annulus counts, suggesting that inshore habitats are primarily used by juveniles and subadults. Significant differences in the estimated age distributions of Gray Snapper inshore and offshore support the idea that migration related to ontogeny and/or attainment of sexual maturity occurs in Texas, the majority of which occurs between age 3 and 4. This is consistent with a previous study that also reported that Gray Snapper recruit to targeted fisheries at age 4 (Fischer et al. 2005), and another that reported large aggregations of adults on offshore reef habitats (Bacheler et al. 2020). While others have documented periodic inshore/offshore migrations related to spawning activity (Starck and Schroeder 1971, Luo et al. 2009), our results suggest that permanent emigration from inshore habitats in Texas occurs for most individuals by age 4. Combined with data that indicates the potential 50% sexual maturity by age 3, it is likely that permanent offshore migration occurs after or coincident with attainment of sexual maturity for most individuals. One caveat to this finding is the possibility of gear bias associated with inshore versus offshore sport harvest by anglers. The majority of Gray Snapper catches in Texas occur when anglers are targeting other species, and it could be expected that the typical size of offshore tackle could be selecting for larger individuals. However, even if gear selection has biased the results here, the large mean size of Gray Snapper reported offshore in another study in Texas ($>$ 350 mm TL, Shipley et al. 2020) compared to the mean size of inshore individuals observed here (\sim 300 mm

TL) seems to validate the size difference between the 2 areas.

The high percentage of larger Gray Snapper observed offshore most likely constitutes the bulk of the spawning stock biomass in Texas. The fact that only 5 females were observed inshore with vitellogenic oocytes reinforces this conclusion, and offshore spawning is also supported by the literature from other areas (Croker 1962, Starck and Schroeder 1971, Domeier et al. 1996, Claro and Lindeman 2003). Croker (1962) reported no ripe fish (females with fully mature eggs) among 790 individuals collected inshore in Florida Bay, and Rutherford et al. (1989) speculated that Gray Snapper recruiting to nursery areas of the Florida Everglades National Park were most likely spawned outside of the park offshore of the Florida Keys. At offshore artificial reefs, Gray Snapper have been documented as the fourth–most abundant species in Texas with an average length > 350 mm TL (Shiple et al. 2020). This latter finding validates the size disparity observed in the current study, and further supports the interpretation that the offshore segment of Gray Snapper populations is made up primarily of older, reproductive individuals.

There are currently no targeted management regulations for Gray Snapper in Texas state waters. Catch has historically been sporadic, and there is not an organized recreational fishery for this species; a majority (68%) of the recreational catch is incidental based on TPWD creel data. However, the findings of this study suggest increasing recreational opportunity via expansion of the Gray Snapper population, and this expansion may be driven not only by more favorable winter temperatures, but also the increased availability of offshore structural habitat. The state of Texas has actively expanded offshore habitat since the mid–1970s via deployment of underwater artificial reefs sites. These activities have accelerated since 1990 with the creation of the Artificial Reef Program, embedded within TPWD, which has made 261 deployments of decommissioned oil and gas platforms, ships, and other smaller reefing materials such as pyramids and culverts (Shiple et al. 2020). Further research should seek to understand the significance of these

structures to Gray Snapper, and how the expansion of artificial reefs in Texas may be contributing to the proliferation of the stock in recent years. For instance, it is unclear whether these structures represent important spawning areas or serve some other function (Bacheler et al. 2020), but it is clear that they are used extensively by Gray Snapper in Texas (Shiple et al. 2020). In any event, continued expansion of Gray Snapper in Texas might be coupled with increased angler interest, and there may be benefits to future regulation of catch for this species.

Multiple findings from this study can inform future management. First, it seems clear that there are 2 primary components to the Texas Gray Snapper population: inshore (juvenile and subadult) and offshore (adult). Future management of recreational catch should be cognizant of how size–based regulations might impact each component. Second, our data suggest that while Gray Snapper may mature prior to offshore recruitment, a majority of individuals recruit to the offshore component by age 4. While some reproductive individuals might occasionally return to estuaries, the bulk of the spawning stock in Texas are probably permanent offshore residents. Third, Gray Snapper are most commonly associated with warmer water and southern estuaries in Texas, but the increasing winter minimum temperatures in Texas noted by Tolan and Fisher (2009) have resulted in a more robust population with a broader age structure coastwide. Although winter temperatures have been more favorable since about 1993, it is likely that extreme winter weather (such as the February 2021 hard freeze throughout coastal Texas) will continue to be a persistent constraint on the expansion of Gray Snapper in the western GOM. Future management measures might include a minimum size limit in the recreational fishery that protects vulnerable life stages that are impacted most heavily by wintertime estuarine extremes (e.g. Wuenschel et al. 2012). Such measures would have the added benefit of protecting most individuals up to attainment of sexual maturity, and subsequently recruitment to offshore habitats, and would potentially increase the available spawning stock biomass coastwide.

ACKNOWLEDGMENTS

The authors thank field personnel from throughout the TPWD Coastal Fisheries Division for providing 40 years of data from field sampling that was used for statistical analyses. Clint Hurley, E. Young and K. Willis (TPWD) assisted with laboratory examinations and data entry. Zachary Olsen (TPWD) provided helpful R code for plotting and interpreting BRT results. Mark Fisher (TPWD) coordinated an internal review of this work consisting of comments from 3 anonymous reviewers. Britt Bumguardner (TPWD, retired) assisted with project conceptualization.

LITERATURE CITED

- Allman, R.J., and L.A. Goetz. 2009. Regional variation in the population structure of Gray Snapper, *Lutjanus griseus*, along the west Florida shelf. *Bulletin of Marine Science* 84:315–330. <https://www.ingentaconnect.com/content/umrsmas/bullmar/2009/00000084/00000003/art00006#>
- Allman, R.J., and C.B. Grimes. 2002. Temporal and spatial dynamics of spawning, settlement, and growth of Gray Snapper from the West Florida shelf as determined from otolith microstructures. *Fishery Bulletin* 100:391–403. <https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/2002/1003/allman.pdf>
- Anderson, J.D., D. Williford, A. Gonzalez, C. Chapa, F. Martinez–Andrade, and R.D. Overath. 2019. Demographic, taxonomic and genetic characterization of the snook species complex (*Centropomus* sp.) along the leading edge of its range in the northwestern Gulf of Mexico. *North American Journal of*

- Fisheries Management 40:190–208. <https://doi.org/10.1002/nafm.10394>
- Andrade, H., and J. Santos. 2019. Life history of the Gray Snapper at the warm edge of its distribution range in the Caribbean. *Marine and Coastal Fisheries* 11:315–327. <https://doi.org/10.1002/mcf2.10087>
- Armitage, A.R., W. Highfield, P. Louchouart, and S. Brody. 2015. The contribution of mangrove expansion to salt marsh loss on the Texas Gulf coast. *PloS ONE* 10:e0125404. <https://doi.org/10.1371/journal.pone.0125404>
- Bacheler, N.M., Z.D. Gillum, K.C. Gregalis, C.M. Schobernd, Z.H. Schobernd, and B.Z. Teer. 2020. Spatial patterns in relative abundance and habitat use of adult Gray Snapper off the southeastern coast of the United States. *Marine and Coastal Fisheries* 12:205–219. <https://doi.org/10.1002/mcf2.10118>
- Barnache, D.R., D.R. Robertson, C.R. White, and D.J. Marshall. 2018. Fish reproductive–energy output increases disproportionately with body size. *Science* 360:642–645. <https://doi.org/10.1126/science.aao6868>
- Berkeley, S.A., M.A. Hixon, R.J. Larson, and M.S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29:23–32. [https://doi.org/10.1577/1548-8446\(2004\)29\[23:FSVPOA\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2)
- Brown–Peterson, N.J., P. Thomas, and C.R. Arnold. 1988. Reproductive biology of the Spotted Seatrout, *Cynoscion nebulosus*, in south Texas. *Fishery Bulletin* 86:373–388. <https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/1988/862/brown.pdf>
- Brown–Peterson, N.J., D.M. Wyanski, F. Saborido–Rey, B.J. Macewicz, and S.K. Lowerre–Barbieri. 2011. A standard terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries* 3:52–70. <https://doi.org/10.1080/19425120.2011.555724>
- Burton, M.L. 2001. Age, growth, and mortality of Gray Snapper, *Lutjanus griseus*, from the east coast of Florida. *Fishery Bulletin* 99:254–265. <https://spo.nmfs.noaa.gov/content/age-growth-and-mortality-gray-snapper-lutjanus-griseus-east-coast-florida>
- Claro, R., and K.C. Lindeman. 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. *Gulf and Caribbean Research* 14:91–106. <http://doi.org/10.18785/gcr.1402.07>
- Croker, R.A. 1962. Growth and food of the Gray Snapper, *Lutjanus griseus*, in Everglades National Park. *Transactions of the American Fisheries Society* 91:379–383.
- Denit, K., and S. Sponaugle. 2004. Growth variation, settlement and spawning of Gray Snapper across a latitudinal gradient. *Transactions of the American Fisheries Society* 133:1339–1355. <http://doi.org/10.1577/T03-156.1>
- Domeier, M.L., C.C. Koenig, and F.C. Coleman. 1996. Reproductive biology of the Gray Snapper with notes on spawning for other Western Atlantic snappers (Lutjanidae). In: F. Arreguin–Sanchez, J.L. Munro, M.C. Balgos, and D. Pauly, eds. *Biology and Culture of Tropical Groupers and Snappers*. ICLARM Conference Proceedings 48, Makati City, Philippines, p. 189–201.
- Durant, J.M., and D.Ø. Hjermmann. 2017. Age–structure, harvesting and climate effects on population growth of Arcto–boreal fish stocks. *Marine Ecology Progress Series* 577:177–188. <http://doi.org/10.3354/meps12210>
- Elith, J., J.R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77:802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Figueira, W.F. and D.J. Booth. 2010. Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology* 16:506–516. <https://doi.org/10.1111/j.1365-2486.2009.01934.x>
- Fischer, A.J., M.S. Baker, Jr., C.A. Wilson, and D.L. Nieland. 2005. Age, growth, mortality, and radiometric age validation of Gray Snapper from Louisiana. *Fishery Bulletin* 103:307–319. <https://spo.nmfs.noaa.gov/content/age-growth-mortality-and-radiometric-age-validation-gray-snapper-lutjanus-griseus-louisiana>
- Flaherty, K.E., T.S. Switzer, B.L. Winner, and S.F. Keenan. 2014. Regional correspondence in habitat occupancy by Gray Snapper (*Lutjanus griseus*) in estuaries of the southeastern United States. *Estuaries and Coasts* 37:206–228. <https://doi.org/10.1007/s12237-013-9652-x>
- Gold, J.R., E. Saillant, N.D. Ebel, and S. Lem. 2009. Conservation genetics of Gray Snapper (*Lutjanus griseus*) in U.S. waters of the northern Gulf of Mexico and western Atlantic Ocean. *Copeia* 2009:277–286. <https://doi.org/10.1643/CI-08-071>
- Green, L.M. and R.P. Campbell. 2005. Trends in finfish landings of sport–boat anglers in Texas Marine Waters, May 1974 – May 2003. Management Data Series No. 234, Texas Parks and Wildlife Department, Coastal Fisheries Division, Austin, TX, USA, 556 p. https://tpwd.texas.gov/publications/pwdpubs/media/mds_coastal/Series%202_MDS234.pdf
- Gunter, G. 1941. Death of fishes due to cold on the Texas coast, January, 1940. *Ecology* 22:203–208.
- Gunter, G. 1951. Destruction of fishes and other organisms on the south Texas coast by the cold wave of January 28–February 3, 1951. *Ecology* 32:731–736.
- Hastie T., R. Tibshirani, and J.H. Friedman. 2001. *The Elements of Statistical Learning: Data Mining, Inference, and Prediction*. Springer–Verlag, New York, NY, USA, 745 p.
- Heck, K.L., Jr., F.J. Frodrige, S. Madsen, C.J. Baillie, and D.A. Byron. 2015. Seagrass consumption by native and a tropically associated fish species: Potential impacts of the tropicalization of the northern Gulf of Mexico. *Marine Ecology Progress Series* 520:165–173. <http://doi.org/10.3354/meps11104>
- Hoese, H.D. and R.H. Moore. 1998. *Fishes of the Gulf of Mexico*, 2nd edition. Texas A&M University Press, College Station, TX, USA, 422 p.
- Johnson, A.G., L.A. Collins, and C.P. Keim. 1994. Age–size structure of Gray Snapper from the southeastern United States: A comparison of two methods of back–calculating size at age from otolith data. *Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies* 48:592–600.

- Lindeman, K.C., T.N. Lee, W.D. Wilson, R. Claro, and J.S. Ault. 2001. Transport of larvae originating in southwest Cuba and the Dry Tortugas: Evidence for partial retention in grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:732–747.
- Luo, J., J. Serafy, S. Sponaugle, P. Teare, and D. Kieckbusch. 2009. Movement of Gray Snapper *Lutjanus griseus* among subtropical seagrass, mangrove, and coral reef habitats. *Marine Ecology Progress Series* 380:255–269. <http://doi.org/10.3354/meps07911>
- Martinez–Andrade, F. 2015. Marine Resource Monitoring Operations Manual. Texas Parks and Wildlife, Coastal Fisheries Division, Austin, TX, USA, 131 p.
- McEachron, L.W., G.C. Matlock, C.E. Bryan, P. Unger, T.J. Cody, and J.H. Martin. 1994. Winter mass mortality of animals in Texas Bays. *Northeast Gulf Science* 13:121–138. <http://doi.org/10.18785/negs.1302.06>
- Nakamura, Y., D.A. Feary, M. Kanda, and K. Yamaoka. 2013. Tropical fishes dominate temperate reef fish communities within western Japan. *PLoS ONE* 8:e81107. <https://doi.org/10.1371/journal.pone.0081107>
- Ogle, D.H., P. Wheeler, and A. Dinno. 2021. FSA: Fisheries Stock Analysis. R package version 0.8.32.9000. <https://github.com/droglenc/FSA>. (viewed on 3/23/2021).
- Oliver, M.A. 1990. Kriging: A method of interpolation for Geographical Information Systems. *International Journal of Geographic Information Systems* 4:313–332.
- Purtlebaugh, C.H., C.W. Martin, and M.S. Allen. 2020. Poleward expansion of common snook *Centropomus undecimalis* in the northeastern Gulf of Mexico and future research needs. *PLoS ONE* 5:e0234083. <https://doi.org/10.1371/journal.pone.0234083>
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>. (viewed on 7/20/2021).
- Ridgeway, G. 2013. gbm: generalized boosting regression models. R package version 2.1. R Foundation for Statistical Computing, Vienna, Austria. <https://cran.r-project.org/web/packages/gbm/index.html>
- Rutherford, E.S., J.T. Tilmant, E.B. Thue, and T.W. Schmidt. 1989. Fishery harvest and population dynamics of Gray Snapper, *Lutjanus griseus*, in Florida Bay and adjacent waters. *Bulletin of Marine Science*. 44:139–154.
- Shiple, B.J., K.A. O’Shaughnessy, A. Baldwin, and D.J. Shively. 2020. The Texas Artificial Reef Program: Fish Composition and Monitoring. Texas Parks and Wildlife, Coastal Fisheries Division Management Data Series number 201, Austin, TX, USA, 56 p.
- Starck, W.A. II, and R.E. Schroeder. 1971. Studies in Tropical Oceanography No. 10: Investigations on the Gray Snapper. University of Miami Press, Coral Gables, FL, USA, 226 p.
- Thayer, G.W., D.R., Cloby, and W.F. Hettler, Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. *Marine Ecology Progress Series* 35:25–38.
- Tolan, J.M. and M. Fisher. 2009. Biological response to changes in climate patterns: Population increases of Gray Snapper (*Lutjanus griseus*) in Texas bays and estuaries. *Fishery Bulletin* 107:36–44. <https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/2009/1071/tolan.pdf>
- Tzeng, M.W., J.A. Hare, and D.G. Lingquist. 2003. Ingress of transformation stage Gray Snapper, *Lutjanus griseus* (Pisces: Lutjanidae) through Beaufort Inlet, North Carolina. *Bulletin of Marine Science* 72:891–908.
- 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 edition. Publication Number 300, National Oceanic and Atmospheric Association, Gulf States Marine Fisheries Commission and Atlantic States Marine Fisheries Commission, Ocean Springs, MS, USA, 294 p. http://www.asmf.org/files/Science/GOM_AtlanticCoast_FishAgeingHandbook_2020web.pdf
- Verges, A., F. Tomas, E. Cebrian, E. Ballesteros, Z. Kizilkaya, P. Dendrinis, A.A. Karamanlidis, D. Spiege, and E. Sala. 2014. Tropical Rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology* 2014:1518–1527. <https://doi.org/10.1111/1365-2745.12324>
- Wood, S. 2017. Generalized Additive Models: An Introduction with R, 2nd edition. Chapman and Hall/CRC, Boca Raton, FL, USA, 496 p.
- Wuenschel, M.J., J.A. Hare, M.E. Kimball, and K.W. Able. 2012. Evaluating juvenile thermal tolerance as a constraint on adult range of Gray Snapper (*Lutjanus griseus*): A combined laboratory, field and modeling approach. *Journal of Experimental Marine Biology and Ecology* 436:19–27. <http://doi.org/10.1016/j.jembe.2012.08.012>