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Age, growth, and mortality of threatened Warsaw grouper, *Hyporthodus nigritus*, in the Gulf of Mexico

Running head: Demographics of Warsaw grouper

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Abstract

Warsaw grouper (*Hyporthodus nigritus)* in the Gulf of Mexico (GoM) are currently managed as a single-stock; however, patchy distribution of suitable habitat may promote the development of discrete populations with different life history characteristics thereby complicating conservation policy. We estimated ages and age-length relationships of Warsaw grouper from different geographic regions in the GoM and applied von Bertalanffy growth functions (VBGF) to estimate growth parameters (L_∞ and K) for each region. Otolith-based ages ranged from 1 to 91 years and estimated L_∞ and growth coefficient (K) derived from the VBGF for all Warsaw grouper combined were 188.8 cm total length (TL) and 0.034 respectively. Region-specific growth parameters were similar for most of the GoM when VBGFs were limited to Warsaw grouper $\leq$ 25 years old, though growth was considerably faster from the southeast GoM. When our age-length key was applied to fisheries-dependent length data from the GoM in 2001-2006 and 2011-2016, this fishery was comprised primarily of Warsaw grouper < age-1, but the mean age increased between catches from 2001-2006 (4.7 ± 8.3) and 2011-2016 (7.6 ± 6.4). Instantaneous mortality rates (Z) based on the decline of log abundance on age indicated relatively low Z rates across the four regions (range: 0.09-0.18), with a significantly higher mortality rate in the western GoM (0.17) than the eastern GoM (0.08). In this study we also observed a greater longevity (91 years) for the species than previously documented, greater than double the longevity used to develop current management policy.

Keywords: von Bertalanffy, growth function, natural mortality, subpopulation, fisheries, longevity

1. Introduction

Warsaw grouper, *Hyporthodus nigritus*, (F. Epinephelidae) are found throughout the western Atlantic Ocean, ranging from northern United States (U.S.) to south of Rio de Janeiro, Brazil, including throughout the GoM and Caribbean Sea basins (Manooch and Mason, 1987; Farmer and Karnauskas, 2013; Aguilar-Perera et al., 2019). Because they exhibit periodic life history traits (e.g., slow growth, late maturity, episodic recruitment), Warsaw grouper are considered highly vulnerable to exploitation pressure due to their low naturality mortality and long generation interval (Winemiller and Rose, 1992; Coleman et al., 2000). Perceived vulnerability combined with a population assessment indicating the population was overfished has led to strict regulations to avoid overexploitation of Warsaw grouper in all U.S. territorial waters (GMFMC, 1999). Even with strict species-specific fishing regulations in place, Warsaw grouper habitat overlaps with commonly targeted congeners and release mortality is very high (Shertzer et al., 2018; Runde et al., 2020; Paxton et al., 2021), thereby highlighting the need for increased information on the demographics of this data-deficient species (Aguilar-Perera et al., 2019).

In U.S. territorial waters, Warsaw grouper are currently managed as two separate populations, one along the eastern seaboard where a year-round catch moratorium is in place and one in the GoM. However, the patchy and limited distribution of suitable habitat within these large geographic areas may support the development of spatially discrete populations (Hanski, 1998; Koenig and Coleman, 2013). A recent population structure assessment using chemical markers in otoliths suggests that individual movement of this species is limited across the GoM, suggesting that subpopulations may exist within this region (Sanchez et al., 2020). Under the assumption of a single well-mixed population in the GoM, previous stock assessments have not attempted to develop region-specific population demographics (e.g., growth, mortality, etc.). If population demographics differ among geographic regions, then a basin-wide total allowable catch may lead to extirpation of discrete subpopulations unable to sustain exploitation pressures (Kritzer and Sale, 2004; Ying et al., 2011). This can be especially true if subpopulations exhibit limited connectivity (Holland and Herrera, 2012). For a metapopulation sustained through episodic recruitment, extirpation of subpopulations can decrease the frequency of successful year-classes, further compounding deleterious effects of age truncation that often results from the overexploitation of a slow life history species (Longhurst, 2002; Smedbol and Wroblewski, 2002; Beamish et al., 2006)

To address the potential for dissimilar population demographics among potentially discrete subpopulations in the GoM, we developed and compared regional age-length relationships and associated population parameters of Warsaw grouper for the northwest GoM (nwGoM), northcentral GoM (ncGoM), northeast GoM (neGoM), and the southeast GoM (seGoM). GoM-wide and regional age-length data were fitted to a von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938; Pardo et al., 2013) to model fish growth and determine if regional differences exist in growth parameters (L_∞, K). In addition, declines in the log abundance on age were used to estimate total mortality (Z) of Warsaw grouper in the GoM. Using region-specific VBGF, age composition of the commercial catch of Warsaw grouper was assessed from 2001-2006 and 2011-2016 to expose any potential changes in the fishery between the two decades.

2. Methods

Archived otoliths from Warsaw grouper were provided by the Panama City Laboratory of the National Oceanic and Atmospheric Administration (NOAA) Southeast Fisheries Science

Center. Otoliths were collected by NOAA Fisheries' observers from fishery dependent and fishery independent surveys in the GoM from 2011-2016. Collected otoliths were initially rinsed, dried, and archived in paper envelopes at the Panama City Lab, Florida. Additional otoliths were provided by the Louisiana Department of Wildlife and Fisheries, Texas A&M University-Corpus Christi, and Texas A&M University at Galveston (TAMUG). Otoliths were weighed (mg), embedded in Struers epoxy resin, and sectioned at 1.0 mm thickness with a Buehler ISOMET saw in the Fisheries Ecology Laboratory at TAMUG. Otolith cross-sections were mounted onto petrographic slides with Crystalbond 509 thermoplastic glue and polished using a series of 320-, 600-, and 800-grit sand paper to a thickness between approximately 0.5-0.8 mm until the core and growth increments were clearly visible. Age was determined for each otolith by enumerating growth increments using a previously validated method (Sanchez et al., 2019).

Age-length data for Warsaw grouper from the GoM were fitted to a VBGF (Eq.1) using the non-linear least squares method with 10,000 Monte Carlo simulations designed for data-limited stocks (Sparre and Venema, 1998) to estimate growth parameters L_∞ (cm) and K with confidence intervals (RStudio, package "TropFishR"). Relationships between otolith mass and fish age were tested using a linear regression (RStudio, package "nlme").

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

Age-length data were then organized into the four geographic regions to estimate region-specific growth rates: nwGoM (Texas continental shelf), ncGoM (Louisiana to Mobile Bay, AL), neGoM (Mobile Bay, AL to Tampa Bay, FL), and the seGoM (Tampa Bay, FL through the Florida Keys) (Figure 1). Region-specific VBGFs were based on Warsaw grouper less than age-25 because fish with older than 25 years were rare or deficient in certain regions (RStudio, package "FSA"). Samples were also pooled into two larger regions—western GoM (nwGoM + ncGoM) and eastern GoM (neGoM + seGoM)—to further evaluate the influence of the entire age range on growth parameters. In addition to the traditional three parameter VBGF, two parameter models (with a fixed t0 = 0) were run to address large negative t0 values and their influence on L_∞ and K.

Region-specific and overall GoM total instantaneous mortality rates (Z) were estimated with a traditional regression catch-curve analyses on age frequency data. For each catch-curve model, age-composition of the catch was binned by year (age) and the frequency (f) of each age was natural log transformed [ln(f)]. Natural log transformed frequency was then plotted by age and a linear regression was run through points beginning with the age with the highest catch frequency under the assumption that after this point gear selectivity and natural mortality are constant. Differences in regression slopes (Z) from the nwGoM, ncGoM, neGoM, and seGoM were analyzed using an ANCOVA (RStudio, package "stats").

Length-frequency data of the 2001-2006 and 2011-2016 commercial fisheries were compared to assess changes in the fishery over the last two decades. Data were separated into catches from the wGoM and eGoM based on either the documented state that fish were landed (2001-2006) or shrimp zone of the catch (2011-2016) and converted to age by rearranging VBGFs; shrimp zone of catch was not available for a large proportion of the 2001-2006 catch data. Age-frequencies were developed for each region using region-specific (wGoM or eGoM) growth parameters. Age composition of the catch was compared between the two fishery periods using Kolmogorov-Smirnov tests, both for each region individually and with data for both regions pooled (RStudio, package "FSA").

3. Results

Ages were determined for a total of 497 otoliths from Warsaw grouper collected between 2011 and 2018. Mean age was 9.2 ± 6.9 years with a range from age-1 to age-91 (Table 1). No difference in mean age was detected among the 4 regions (ANOVA, $F_{3,493} = 1.9$, $p < 0.05$); however, region-specific differences in length were detected with Warsaw grouper in our sample larger in the nwGoM and seGoM (101.8 cm and 104.8 cm TL) than the ncGoM and neGoM (94.5 cm and 90.6 cm TL) (ANOVA, $F_{3,493} = 9.1$, $p < 0.05$). The linear relationship between otolith mass and fish age was significant ($F_{1,301} = 1303$, $p < 0.001$) and resulted in linear model *Age (years) = 33.4 x Otolith Mass (g) - 3.2* (Figure 2).

Growth parameters for the VBGF for the whole GoM were L_∞ = 188.8 cm (CI: 168-217) and K = 0.034 (CI: 0.02-0.05) (Figure 3). When the sample was split into the eastern GoM and western GoM, L_∞ and K were not statistically different between the eastern GoM [L_∞ = 176.3 cm (149-230 cm), K = 0.049 (0.02-0.08)] and western GoM [L_∞ = 192.3 cm (167-229 cm), K = 0.031 (0.04-0.12)] (Figure 4A). Regional-specific growth parameters from the VBGF for fish less than age-25 varied among the four regions, with L_∞ highest and K lowest for Warsaw grouper from the seGoM (L_∞ = 153.3 cm, K = 0.077), however statistical comparison with this region was not possible due to an inability to develop confidence intervals due to linearity in the growth function. Growth parameters were relatively similar for individuals collected from the other three regions in the northern GoM: nwGoM (L_∞ = 123.1 cm, K = 0.188), ncGoM (L_∞ = 117.5 cm, K = 0.121), neGoM (L_∞ = 113.2 cm, K = 0.156) (Figure 5). In the two-parameter model (t0 = 0), growth parameters L_∞ and K estimates were considered biologically unrealistic and are therefore not addressed further .

Total instantaneous mortality (*Z*) estimated from catch-curve analysis for Warsaw grouper from the GoM was 0.12 y^{-1} (Table 2), with *Z* in the western GoM (0.17 y^{-1}; Figure 4B) significantly higher than in the eastern GoM (0.08 y^{-1}; Figure 4C) (ANCOVA, $F_1 = 10.5$, $p < 0.01$). Regional-specific catch-curve slopes and therefore total instantaneous mortality rates were significantly different (ANCOVA, $F_3 = 6.7$, $p < 0.01$) with *Z* higher in the ncGoM (0.18 y^{-1}; Figure 6B), than the nwGoM (0.09 y^{-1}; Figure 6A), neGoM (0.12 y^{-1}; Figure 6C), and seGoM (0.06 y^{-1}; Figure 6D) (Tukey HSD, $p < 0.05$).

Age and mortality estimates derived for Warsaw grouper from the commercial fishery in the GoM indicated that the majority of fish were less than 10 years of age. For the 2001-2006 sample, mean age was 4.7 ± 8.3 years with a range from 0 to 100 years. For 2011-2016, mean fish age was 7.6 ± 6.4 years with a range from 0 to 58 years. Mean age of Warsaw grouper collected from the commercial fishery in 2011-2016 was higher across the entire GoM (KS Test, $D = 0.33$, $p < 0.001$) and for both the eastern GoM (KS Test, $D = 0.31$, $p < 0.001$) and western GoM (KS Test, $D = 0.35$, $p < 0.001$) independently. Age-based catch curves led to identical instantaneous total mortality rates ($Z = 0.23$ y^{-1}) between the 2001-2006 collection period and the 2011-2016 collection period (Figure 7).

4. Discussion

The age-length relationship developed here for Warsaw grouper indicates that the population(s) in the GoM are long-lived, have low growth coefficients (*K*), and large asymptotic lengths (L_∞) relative to other exploited species in the western Atlantic Ocean (Wilson and Nieland, 2001; Harris et al., 2011), including shallow water groupers (Hood and Schleider, 1992; Crabtree and Bullock, 1998; Lombardi-Carlson et al., 2008). The low *K* value for Warsaw grouper reveals that growth to asymptotic length is slow regardless of geographic location in the GoM, with estimates of L_∞ and K similar to Warsaw grouper in the western Atlantic Ocean along the U.S. eastern seaboard (Manooch and Mason, 1987). These K and L_∞ estimates in the current study are lower and higher, respectively, than a recent estimate for Warsaw grouper in the GoM that estimated K and L_∞ to be 0.14 and 153.3 cm using a Bayesian parameter estimation method and simulated age-length data which appeared to decouple, at least visually, from the non-simulated data (Barnett et al., 2020). Interestingly, initial parameter estimates for Barnett et al., (2020) were much closer to those in the current study, however, they were dismissed as the authors showed a preference for the results of the simulated data. Large individuals were rare in both studies, a potential result of size truncation from overexploitation and preferential selection of large individuals, which can lead to correspondingly low L_∞ estimates when the parameter estimation method accounts for overexploitation (Taylor et al., 2005; Cooper et al., 2013). However, the occurrence of large individuals in the recreational fishery (>180 cm TL) and the typical slow-growth of deepwater species suggest the lower K and larger L_∞ estimates are reasonable for the population in a more virgin state (Cailliet et al., 2001; King & McFarlane, 2003; Clark, 2009). In addition, the lower K estimate is comparable to estimates on deepwater congeners in both the western Atlantic Ocean, *Hyporthodus niveatus*, and Pacific Ocean, *Hyporthodus octofasciatus* and *Hyporthodus quernus* (Costa et al., 2011; Wakefield et al., 2015; Andrews et al., 2019), which all have K estimates <0.08.

The oldest Warsaw Grouper in this study (age-91) is 28 years older than current maximum age estimates (Barnett et al., 2020), greatly increasing the longevity estimate for the species. While this marked increase in maximum age may seem surprising, this individual was 34.2 cm TL larger and had an otolith mass nearly 60% heavier than an age-59 fish previously validated with a bomb-radiocarbon analysis (Sanchez et al., 2019). In fact, the otolith mass-age relationship developed using bomb radiocarbon validated ages lead to an age-96 estimate for the individual (2.51-g otolith), again similar to results from *H. octofasciatus* and *H. quernus* in the Hawaiian Islands where otolith-mass relationships were used to estimate ages of prebomb fish (Andrews et al., 2011; Andrews et al. 2019). Furthermore, longevity approaching 100 years is not uncommon for deepwater species (Cailliet et al., 2001, Munk, 2001, Horn et al., 2012) and longevity of 80 or more years has been reported for other species in the deepwater grouper complex in the GoM using bomb radiocarbon validation techniques (Cook et al., 2008; Andrews et al., 2013; Sanchez et al., 2019). Such an increase in longevity would substantially decrease current SEDAR (Southeast, Data, and Assessment Review) natural mortality estimates for the species which use the Hoenig and Hewitt (1993) estimate, from 0.10 y^{-1} (SEDAR, 2004) to 0.05 y^{-1} (our data) and emphasizes the importance of validating age estimates for the development of effective management policy (Cailliet and Andrews, 2008).

Instantaneous natural mortality estimates (M) using the modified $Hoenig_{nls}$ (0.079 y^{-1}) and modified $Pauly_{nls}$ (0.062 y^{-1}) equations (Then et al., 2014) indicate high vulnerability of Warsaw grouper to exploitation pressure and were below the basin-wide instantaneous total mortality estimate (0.12 y^{-1}). Similarities between the longevity based and growth parameter based *M* estimates add support to parameter estimation, and are comparable to those from *H. quernus* that were estimated to range between 0.058 and 0.094 by Andrews et al., (2019). When VBGFs were run on eastern (neGoM, seGoM) and western (ncGoM, nwGoM) regions independently, the natural mortality rate was lower in the western GoM (0.058 y^{-1}) than eastern GoM (0.083 y^{-1}), potentially indicating decreased resilience to exploitation (Pauly, 1980; Gislason et al., 2010). The lower *M* estimate derived from the western GoM using the VBGF growth parameters method corresponds to the region that catch curves indicated higher total mortality (Z) and that has contributed most to the commercial fishery since the deepwater grouper fishery was changed to an Individual Fishing Quota Fishery Management Program in 2010 (Figure 8; Courtesy: NOAA Fisheries). Of additional concern, catch totals from the western GoM have decreased substantially since peaking in 2013, even while the total allowable catch has remained constant. It should be noted, however, that this decrease in catch does not necessarily indicate a decrease in catch per unit effort which was not calculated.

Region-specific (4-regions) comparisons for Warsaw grouper <age-25 indicated that age-length relationships were potentially distinct in the seGoM while similar through the northern GoM regions (nwGoM, ncGoM, neGoM). While a statistical comparison was not possible with the seGoM using the least squares method, this only occurred because the relationship with the age-length relationship was too linear to develop confidence intervals, thereby suggesting growth rates remained high for individuals in the seGoM through age-25. Visual inspection of VBGFs from all four regions indicates that growth rates appear to slow down for the regions in the nwGoM, ncGoM, and neGoM well before age-25. Furthermore, fish from the seGoM experience unique chemical histories when compared to the other regions in the (Sanchez et al., 2020). This combination of dissimilar otolith chemistry and increased growth rates highlight the region as a potential subpopulation with discrete population demographics.

The predicted age-composition of the Warsaw grouper from the commercial fishery changed substantially over the last two decades based on length-based converted ages. From 2001-2006 the fishery was comprised primarily of Warsaw grouper less than age-5 (mean: 4.7 years) while fish were significantly older (mean: 7.8 year) in the 2011-2016 fishery. The observed increase in age between the assessment time frames may be due to a reduction in fishery pressure as a result of regulation changes in 1999 that limited the recreational catch of Warsaw grouper to one fish per boat per day (GFMFC, 1999) and is a more likely cause than exploitation induced shifts in growth rates between the two periods (Hilborn and Minte-Vera, 2008). It is also possible that changes in fishing methods may contribute to a shift in age-distribution of the catch between the two time periods. Average depth of gear deployment increased from 100 m from 2001-2006 to 110 m from 2011-2016. The shift to deeper sets could result in the targeting of larger individuals since Warsaw grouper may undergo an ontogenetic shift to deeper depths with age (Barnett et al., 2020) or could represent a move to new fishing grounds with more virgin stocks. Regardless, the 2011-2016 fishery was mostly composed of fish less than age-10 (75%) and almost exclusively of fish less than age-20 (96%), an indication that past catch rates could have led to age-truncation of the population (Secor et al., 2015). For a species that relies on episodic recruitment success during years with favorable conditions, reestablishment of the full age-structure is critical and could take decades for such a long-lived species (Berkeley et al., 2004; Russ and Alcala, 2004; van Gemert and Anderson, 2018).

Here, we demonstrate that Warsaw grouper are longer-lived than previously considered but that the population in the GoM may be in a rebuilding state following changes in conservation policy (Manooch and Mason, 1987; Hewitt and Hoenig, 2005; Barnett et al., 2020). While average size of fish in the commercial fishery has increased significantly over the last two decades, past overexploitation has led to size and age truncation in the population and likely decreased resilience to stochastic events (Anderson et al., 2008; Cooper et al., 2013; Rouyer et al., 2013; Secor et al., 2015), which are expected to have an increased influence on fish stocks in a changing climate (Brander, 2007; Griffith at al., 2018). While increased size-composition of the commercial catch may be linked to changes in fish methods, our analysis does not exclude the possibility that changes in management policy could have increased survivorship. However, the small proportion of larger, older Warsaw grouper in the sample and commercial catch composition supports the need for continued strict management to allow the virgin age-structure to be reestablished (Berkeley et al., 2014).

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Table 1. Summary statistics of age data for the entire basin (GoM) and individual regions, including estimated total mortality rates (Z) from age-based catch-curves. Group_L and Group_A show statistically significant groupings of regions for lengths and ages, respectively, (Tukey HSD, $p < 0.05$).

Region	n	Length (mm)	Group_L	Age	Group_A
GoM	497	970 ± 192	--	9.2 ± 6.9	--
nwGoM	102	1018 ± 233	A	10.2 ± 8.0	A
ncGoM	295	945 ± 149	B	8.8 ± 6.1	A
neGoM	38	906 ± 222	B	8.3 ± 8.9	A
seGoM	62	1048 ± 238	A	10.4 ± 6.9	A

Table 2. Growth parameters from the von Bertalanffy Growth Function (L_∞, K, t_0) and associated natural mortality (M) rates calculated for the different regional groupings of age data in the Gulf of Mexico (GoM). The $Hoenig_{nls}$ M was estimated using a t_{max} = age-91. All M estimates from 2-region groups were calculated with the $Pauly_{nls}$ equation. For the 4-region grouping, samples only included data from fish estimated <age-25. w = west, e = east, nw = northwest, nc = northcentral, ne = northeast, se = southeast

Grouping	Region	L_∞	K	t_0	Z	M
GoM	$Hoenig_{nls}$	188.8	0.034	-12.6	0.12	0.079
	$Pauly_{nls}$					0.062
2-Region	wGoM	192.3	0.031	-14.1	0.17	0.058
	eGoM	176.3	0.049	-8.8	0.08	0.083
4-Region	nwGoM	123.1	0.188	-1.4	0.09	
	ncGoM	117.5	0.121	-5.5	0.18	
	neGoM	113.2	0.156	-3.9	0.12	
	seGoM	153.3	0.077	-5.9	0.06	

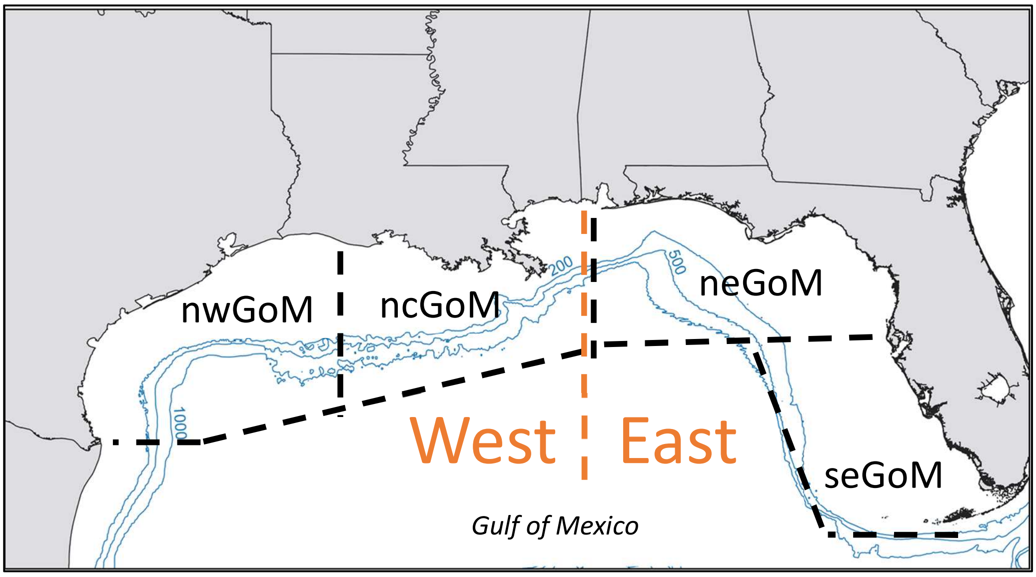

Figure 1. Map of analysis regions both the sub-region (black dashed lines) and eastern/western (orange dashed lines) Gulf of Mexico (GoM) von Bertalanffy growth functions. nw = northwest, nc = northcentral, ne = northeast, se = southeast.

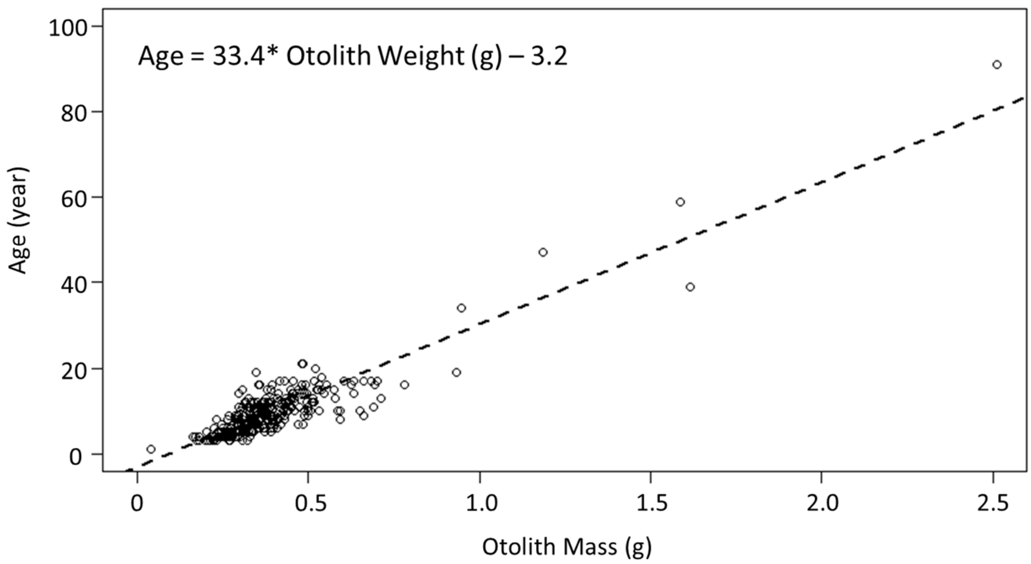

Figure 2. Linear regression between otolith mass (g) and age (years) for Warsaw grouper in the Gulf of Mexico. Linear model was significant (RSE = 3.2, df = 301, $p < 0.001$) and explained a large proportion of variability ($R^2 = 0.81$).

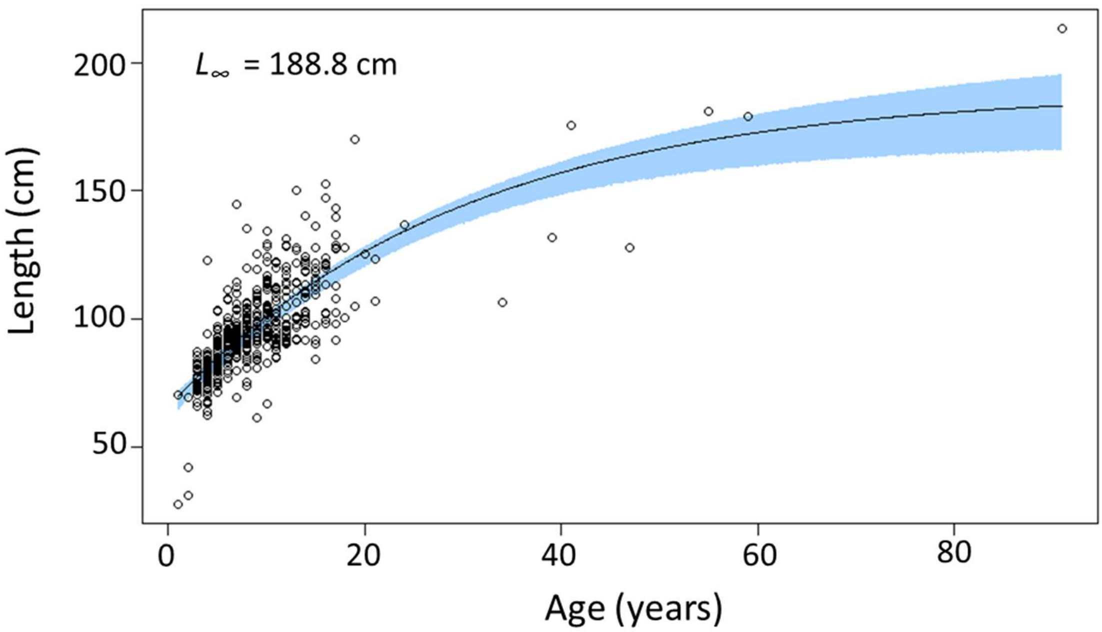

Figure 3. von Bertalanffy growth function and confidence interval (blue area) for the entire Gulf of Mexico population plotted using growth parameters developed with the non-linear least-squares method with 10,000 Monte Carlo simulations (L_∞ = 188.8 cm, K = 0.034, t_0 = -12.6).

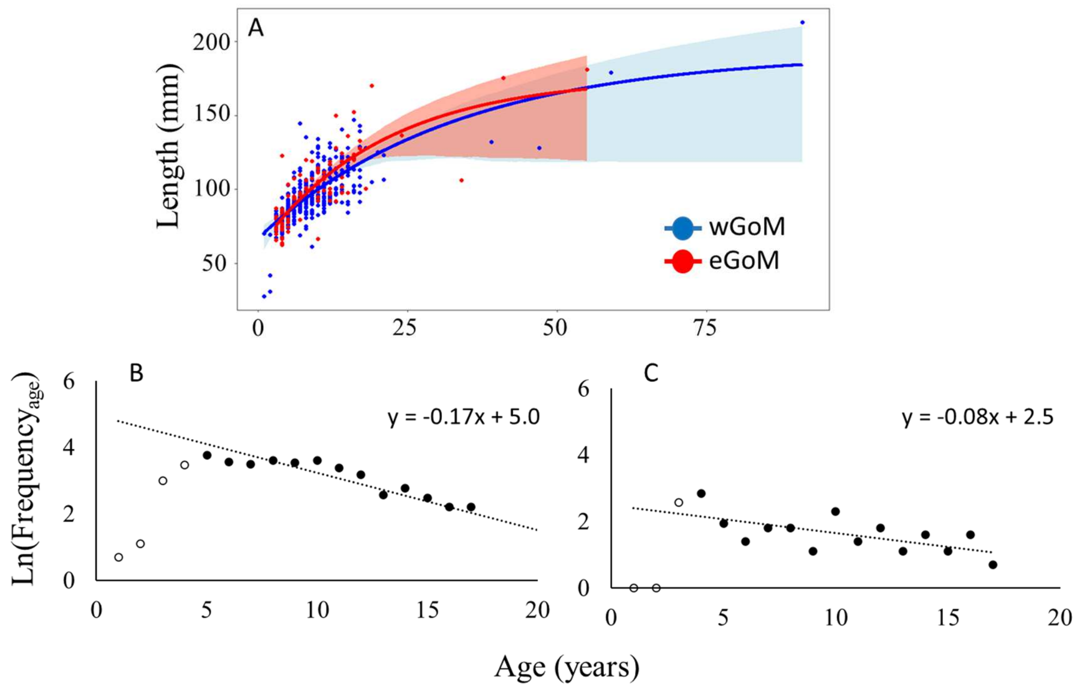

Figure 4. A) von Bertalanffy growth functions and age-based catch curves for age-length samples from the B) western Gulf of Mexico (wGoM) (L_∞ = 192.3 cm, K = 0.031, t_0 = -14.1) and (C) and eastern Gulf of Mexico (eGoM) (L_∞ = 176.3 cm, K = 0.049, t_0 = -8.8). Slope of the catch curve represents total instantaneous mortality estimate (Z).

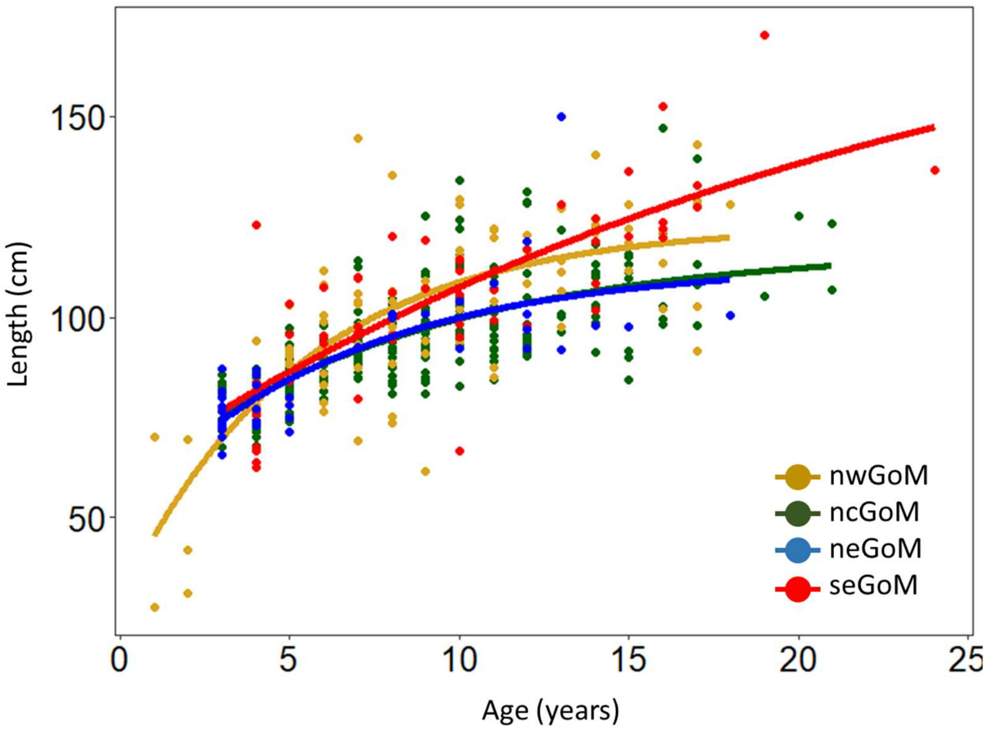

Figure 5. Region-specific von Bertalanffy growth functions and growth parameters A) northwest Gulf of Mexico (L_∞ = 123.1 cm, K = 0.188, t_0 = -1.4), B) northcentral Gulf of Mexico (L_∞ = 117.5 cm, K = 0.121, t_0 = -5.5), C) northeast Gulf of Mexico (L_∞ = 113.2, K = 0.156, t_0 = -3.9), and D) southeast Gulf of Mexico (L_∞ = 153.3, K = 0.077, t_0 = -5.9).

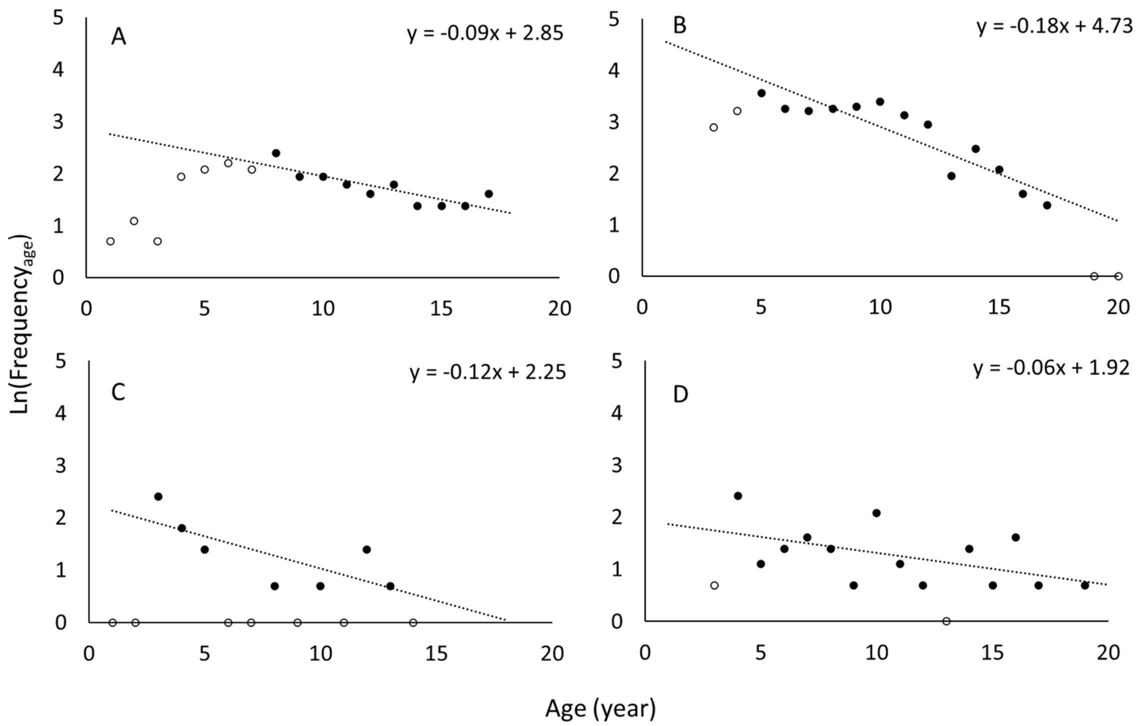

Figure 6. Age-based catch curves for age-length samples from the A) northwest Gulf of Mexico, B) northcentral Gulf of Mexico, C) northeast Gulf of Mexico, and D) southeast Gulf of Mexico. Slope of the catch curve represents total instantaneous mortality estimate (*Z*).

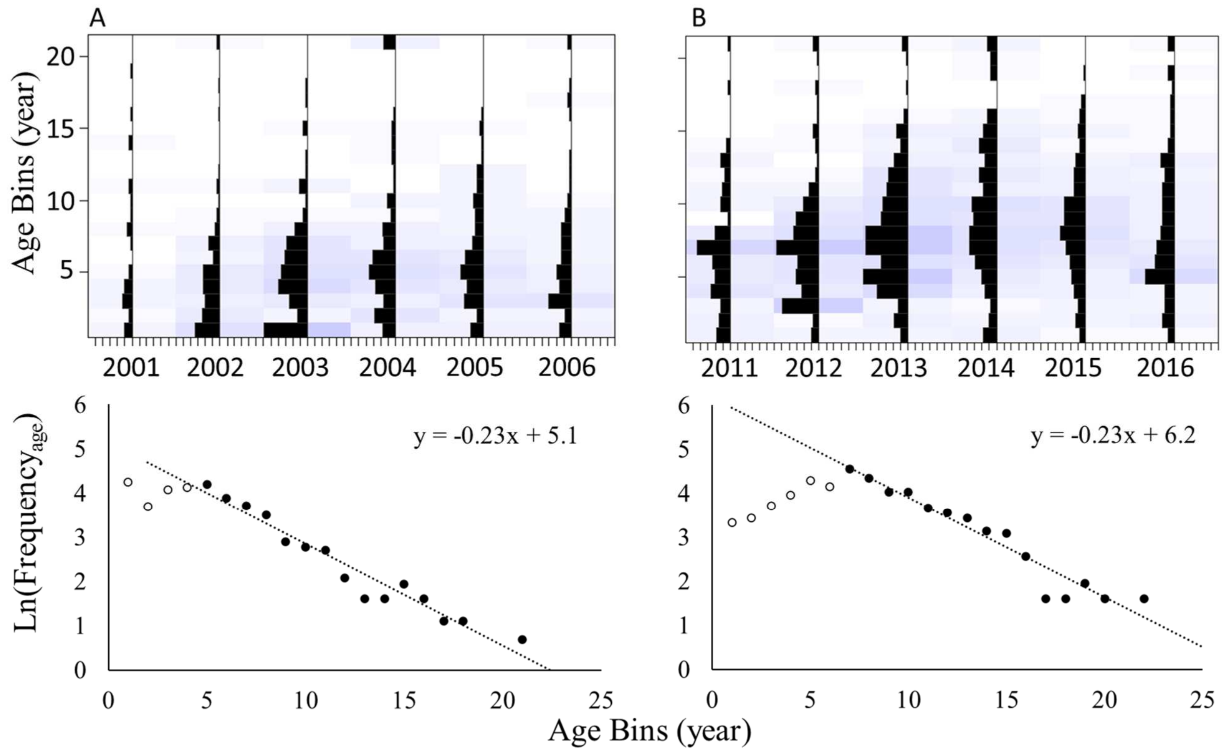

Figure 7. Annual age composition and catch curves from all years pooled from 2001-06 (A) and 2011-16 (B) in NOAA samples for the Warsaw grouper commercial fishery. Age was estimated from length data using rearranged von Bertalanffy Growth Functions developed for the eastern Gulf of Mexico and western Gulf of Mexico in this study. Slope of the catch curve represents total instantaneous mortality estimate (*Z*).

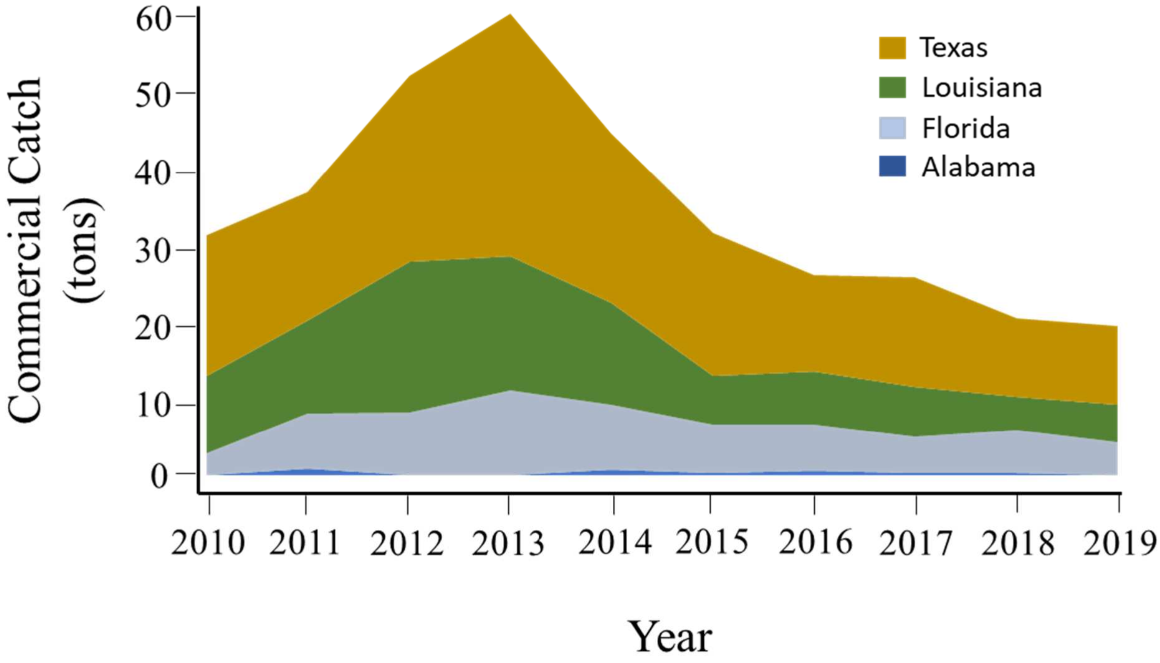

Figure 8. Commercial catch totals (tons) of Warsaw grouper by state landed since the Deepwater Grouper – Tilefish Individual Fishing Quota Fishery Management Program was implemented in 2010. Landing states Texas and Louisiana roughly correspond to sampling regions nwGoM and ncGoM, respectively, and combined comprise the western GoM.