Descriptions of age, growth, and natural mortality of Mutton Snapper, *Lutjanus analis*, collected from fisheries-independent and -dependent sources in the southeastern United States from 1977 – 2022

Christopher E. Swanson, Shanae D. Allen, and Jessica L. Carroll

SEDAR79-DW-22

31 August 2023



This information is distributed solely for the purpose of pre-dissemination peer review. It does not represent and should not be construed to represent any agency determination or policy.

Please cite this document as:

Swanson, Christopher E., Shanae D. Allen, and Jessica L. Carroll. 2023. Descriptions of age, growth, and natural mortality of Mutton Snapper, *Lutjanus analis*, collected from fisheries-independent and -dependent sources in the southeastern United States from 1977 – 2022. SEDAR79-DW-22. SEDAR, North Charleston, SC. 34 pp.

Descriptions of age, growth, and natural mortality of Mutton Snapper, *Lutjanus analis*, collected from fisheries-independent and -dependent sources in the southeastern United States from 1977 – 2022.

Christopher E. Swanson¹, Shanae D. Allen¹, and Jessica L. Carroll¹ ¹Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, Florida

Overview

Mutton Snapper, *Lutjanus analis*, is one of several reef-dwelling snapper (Family *Lutjanidae*) targeted by commercial and recreational fisherman and considered a valuable resource in nearshore Florida waters. They are also found to obtain larger sizes compared to other nearshore *Lutjanus* species (e.g., Gray Snapper [*Lutjanus griseus*] and Lane Snapper [*Lutjanus synagris*]). Mutton Snapper have been assessed through the Southeast Data Assessment and Review (SEDAR) process twice and the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWC-FWRI) has been the lead for both assessments; a benchmark assessment was conducted in 2008 (SEDAR 15A 2008) and an update to that assessment was performed in 2015 (SEDAR 15AU 2015).

Here, life history information available from 1977 – 2022 is characterized pertaining to the age, growth, and natural mortality of Mutton Snapper in the southeastern United States. Appropriate models are provided to describe growth and natural mortality as well as morphometric conversion factors and equations. The objective is to provide adequate information concerning these aspects of Mutton Snapper life history to help facilitate discussions and recommendations in the upcoming SEDAR 79 Southeastern U.S. Mutton Snapper Data Workshop.

Methods

Morphometrics and Conversion Factors

Morphometrics characterize the size and shape of an organism and reduce the idea of physical form to a series of measured variables (Ihssen et al. 1981). These include multiple types of length (standard [SL], fork [FL], and total [TL]) or weight (total [TW] or gutted [GW]) measurements. Morphometric data for Mutton Snapper are collected by various fishery-dependent and -independent data collection programs (e.g. Trip Interview Program [TIP], Marine Recreational Information Program [MRIP], Southeast Region Headboat Survey [SRHS], and FWRI's Fisheries Dependent Monitoring [FWRI-FDM] program) and help facilitate comparisons between the length and weight measurement data from other studies.

Ideally, the length type used within a stock assessment is consistent with the management regulations of that species. For Mutton Snapper, the current management regulations on minimum legal size specifies an 18" maximum total length ("max") where the fish is measured by compressing the tail to its maximum length. However, methods of measuring total length were found to differ between data sources which necessitated a conversion to maximum TL. For example, the SRHS measures Mutton Snapper using a natural TL ("relaxed") where the fish is measured with the tail flat in its normal shape instead of compressed to its maximum length. Therefore, included here is the relationship between natural TL and maximum TL as was also provided by the two prior stock assessments for this species (SEDAR 15A 2008, SEDAR 15AU 2015).

Morphometric data from fishery-dependent and -independent sources were combined to estimate morphometric equations and conversion factors. Linear (for length-length conversion) and non-linear (for length-weight conversion) regressions were conducted in R (R Core Team 2020) and outliers were removed if they fell outside of the 99.9th percentile prediction interval. Linear regressions are in the form

Y = a + bX and non-linear regressions are in the form $W = aL^b$. Non-linear length-weight models in real space demonstrated less prediction error compared to linear length-weight models in lognormal space. Reported here is also the gutted weight to total (whole) weight conversion of 1.11 (SEDAR 15A 2008).

Available Age Data

Age data available for Mutton Snapper in the southeastern U.S. were supplied by the National Marine Fisheries Service's Southeast Fisheries Science Center (NMFS-SEFSC) laboratories (Miami, Panama City, and Beaufort), FWRI, and the Gulf States Marine Fisheries Commission (GSMFC). Data were collected by federal and state biologists involved in fishery-dependent (e.g., TIP, SRHS, and MRIP) and fishery-independent (e.g., FWRI's Fisheries Independent Monitoring and Fish Biology) biological data collection programs from 1977 – 2022 on both Atlantic and Gulf of Mexico coasts.

Data were spatially delineated into 5 regions within Florida waters and based on where the sampled fish was landed: Northeast Florida (Nassau County south to Brevard County), Southeast Florida (Indian River County south to Miami-Dade County), Florida Keys (Monroe County), Southwest Florida (Levy County south to Collier County), and Northwest Florida (Escambia County south to Dixie County). Areas outside of Florida are defined as either "West of Florida" for states west of Florida through Texas along the Gulf of Mexico or "North of Florida" for states north of Florida through North Carolina along the southeastern US Atlantic. The Dry Tortugas region (Monroe County west of longitude -82.7 and south of latitude 25) is also described here because it was an area sampled by both fishery-dependent and -independent sources. However, only fishery-independent data were regular in reporting Mutton Snapper sampled there. Fishery-dependent sources were inconsistent in their reporting of coordinates from the Dry Tortugas region as an area fished; therefore, spatial delineation for the purposes of these analyses was defined by where Mutton Snapper were landed. The gears defined here are grouped into hook and line (encompassing hook and line, bandit rigs, and electric or hydraulic reels), long line, other (comprised largely of spear, seine, as well as pots and traps), and unknown.

Otolith Processing and Age Determination

Sectioned otoliths are the preferred structures for ageing Mutton Snapper (Mason and Manooch 1985, Burton 2002) and the left sagittal otolith was processed for age determination. Otoliths were attached directly to cardstock using hot glue, then cut using a Buehler Isomet low-speed saw with a multiblade configuration to create three thin transverse sections (VanderKooy et al. 2020). Sections were then adhered to glass slides using a clear mounting medium. Otoliths were examined using stereo microscopes with objectives ranging from 0.63X–2.0X magnification and either transmitted or reflected light. Each otolith was read at least twice, either by an individual reader two times, or by two different readers. reads by staff A third read was conducted to resolve any discrepancies between the two age estimates. All ages were determined without reader knowledge of fish length or sex (VanderKooy et al. 2020 , Carroll and Lowerre-Barbieri 2019).

Marginal increment analyses (Burton 2002) have indirectly validated that Mutton Snapper form an opaque annulus in the spring (typically March – May) and deposition is assumed to be completed by July 1. Calendar ages were calculated using annulus count (number of opaque zones), degree of marginal completion, average date of otolith increment deposition, and date of capture. Using these criteria, age was assigned by readers to advance by one year if a large translucent zone (more than 2/3 translucence) was visible on the margin and the capture date was between January 1 and June 30. For fish collected after June 30, age was typically assigned to be annulus count. Calendar ages were converted to biological (i.e., fractional) ages based on a June 1 hatch date and month of capture for fitting growth curves.

Precision Calculations

Precision measurements are valuable for evaluating the structure's ease of age determination, the reproducibility of an individual's age, and the skill level of each reader in a laboratory (Campana 2001). Average percent error (APE) and coefficient of variation (CV) are the two most widely used precision calculations (Campana 2001) and are considered "age independent" methods for determining precision (Kimura & Lyons 1991). APE is calculated as:

$$APE_j = 100\% \times \frac{1}{R} \sum_{i=1}^{R} \frac{|x_{ij} - x_j|}{X_j}$$

for otoliths with multiple age determinations (*R*), X_{ij} is the *i*th age estimate for the *j*th fish. Disagreement by one year between readers on a 2-year-old fish is weighted more heavily than a one year discrepancy of a 20-year-old fish (Kimura and Anderl 2005). When individual errors are averaged across all samples, the outcome is the average percent error for the data set (Beamish and Fournier 1981, Campana 2001).

CV is the ratio of standard deviation over the mean (Chang 1982) and is written as:

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R - 1}}}{X_j}$$

Precision estimates between readers were calculated using a random subsample from recreational and commercial collections. This quality control subsample of 240 fish included samples from 2018–2020 that were aged by the three primary Mutton Snapper readers. Standard protocol for quality control ageing typically calls for a larger subsample. However, Mutton Snapper ageing was conducted primarily during the COVID pandemic so overlapping ageing reads (especially resolution of disagreements) were difficult to ascertain. APE and CV precision estimates were calculated on the entire age dataset (from individual first and second reads of all fish), as well as the quality control subsample. Age bias plots assessing reader precision of the quality control subsample were generated using FSA: fisheries stock analysis R Package (Ogle 2020).

Growth

Length-at-age data were filtered to eliminate observations that included a known size or effort bias or if lengths were collected using a known non-random sampling method or were selected by quota sampling. Data were further restricted to records containing complete information on year, month, and state (or were assigned a state based on area fished or sample location if the area fished was unknown or unassigned). Finally, total length observations were grouped by calendar age and iteratively Z-scored; outliers were removed using threshold values of ± 8 in the first iteration and values of ± 4 in the second iteration.

Length-at-age data based on biological (i.e., fractional) ages and maximum total length data were modeled using a size-truncated von Bertalanffy growth model (Diaz et al. 2004) executed in ADMB (Auto Differentiate Model Builder). This growth model accounts for minimum size restrictions (using a truncated normal distribution) which influence non-random sampling across ages (e.g., smaller fish not available to sample); however, it does not account for dome-shaped selectivity (e.g., larger fish not available to sample). It also allows for the exploration of alternative variance structures. Model options for variance structure used here were constant standard deviation (sigma) with age, constant CV with age, CV increasing linearly with age, and CV increasing linearly with size at age. Growth models were applied to both unweighted data and data weighted by using the inverse (1/n) of the count of each calendar age (Burton et al. 2015). Size truncation for the fishery-dependent data was set using the minimum size limits of 12" TL first implemented by the SAFMC Snapper-Grouper FMP amendment on 1/1/92, then 16" TL implemented on 1/23/95, and 18" TL implemented on 2/10/18. Model selection criteria was based on model convergence (maximum gradient < 0.0001), model objective function (minimized negative loglikelihood), Akaike Information Criteria (AIC), and model standardized-residual diagnostic plots.

Natural Mortality

Natural mortality, M, characterizes all causes of natural (i.e, non-fishing) mortality such as predation, starvation, disease, and senescence (Gulland 1983, Hilborn and Walters 1992) but may also include some forms of human-induced mortality not due to fishing (Maunder et al. 2023). While it is one of the most influential parameters within fisheries stock assessment, it is rarely observed or measured in fish populations; consequently, it is difficult to estimate and remains a large source of uncertainty within most stock assessment models (Vetter 1988, Hampton 2000, Maunder et al. 2023). M is commonly treated as a constant within stock assessment processes and textbooks (e.g., Hilborn and Walters 1992, Quinn and Deriso 1999, Haddon 2011), but application as a size-dependent or equivalent age-dependent function using a stock-specific growth function with constant M scaled to a fully selected age or range of ages (e.g., the 'Lorenzen M' model) is becoming more commonly practiced in stock assessments conducted in the southeastern United States (Lorenzen 2022, Lorenzen et al. 2022).

Constant as well as size- and age-dependent estimates of natural mortality of Mutton Snapper were explored using the approaches and recommendations presented in the recent review of natural mortality estimation methods by Maunder et al. (2023) and the 'generalized length-inverse mortality (GLIM)' paradigm presented by Lorenzen (2022). Where relevant, all natural mortality models assumed von Bertalanffy growth. Constant *M* estimates were calculated based on the longevity and empirical *K* models updated by Hamel and Cope (2022) and the revised Pauly_{nls-T} model described in Then et al (2015). These estimates of constant *M* were then converted to mortality-at-length and -age by applying the survival equations described in Lorenzen (2000, 2005) and using age-3 as the reference age for the constant *M* estimate. A similar method was performed in SEDAR 15AU (2015), but the cumulative mortality rate was predicted for ages 3 and greater and scaled so that it agreed with the constant *M* estimate based on the Hoenig (1983) model. Therefore, this was also explored by applying that scaling to all three constant *M* estimates presented here.

In addition, allometric scaling models for mortality at length or weight were explored using the mortalityweight model described in Lorenzen (1996), the length-inverse model described in Lorenzen (2022; see equation 1a therein), and the empirically based length-inverse model described in Lorenzen (2022; see Table 1 therein). For the length-inverse model, the Hamel and Cope (2022) longevity-based estimate of constant *M* was used as the mortality at reference length scale parameter and the length associated with age-3 as the reference length. Scaling the cumulative mortality rate predicted for ages 3 and greater so that it agreed with the constant *M* estimate was also explored. In the empirically based length-inverse model, the mortality at asymptotic length parameter, $M_{L\infty}$, was calculated using the parameters described by the best fit regression (model 6) located in Table 3 of Lorenzen et al. (2022) where a = 0.42, c = 0.93, and *K* is the von Bertalanffy growth coefficient. The $M_{L\infty}$ parameter is described by Lorenzen et al. (2022) as "closely related to constant adult *M* traditionally used in fisheries assessments". Longevity estimates were based on the observed maximum age for Mutton Snapper and the mortality-weight model utilized the parameters of the non-linear length-weight model converting maximum total length (mm) to total weight (g).

Results

Morphometrics and Conversion Factors

Updated length-length (linear regression) and length-weight (non-linear regression) conversion equations were developed for southeastern U.S. Mutton Snapper and are presented in Table 1.

Available Age Data

A total of 25,586 otoliths were assigned ages for Mutton Snapper from years 1977 - 2022 (Table 2). The majority of otoliths were found to be ages 3 to 5 (53.2%) and ages 2 - 9 comprised 86.1% of the data (Table 2).

Ages sampled from the recreational fishery (n = 12,549 otoliths, Table 3, Figure 1) constituted a total of 49.0%, predominantly from the headboat survey (n = 10,106 otoliths, Table 4, Figure 1b), while ages sampled from the commercial fishery (n = 11,827 otoliths, Tables 3 and 4, Figure 1) made up 46.2%. Age data from fishery-independent sources totaled 1,210 otoliths (4.7%) from Mutton Snapper (Tables 3 and 4, Figure 1). The total number of ages sampled annually from fishery-dependent and -independent sources was very low throughout the 1980s and otoliths during this time were only sampled from the headboat fishery (Figures 1b). Beginning in 1992, otoliths started to be sampled from multiple fishery modes and the number of samples continually increased until a peak in 2010 (n = 1,926 otolith samples, Figure 1). Afterwards, the total number of age samples began decreasing to an annual average ~1,000 samples through 2022 (Figure 1). Sampling during years 2019 - 2021 were below average and were likely impacted by COVID-19 during years 2020 - 2021. Hook and line gear contained 75.3% of samples (n = 19,258 otoliths, Table 5) followed by long line gear (n = 4,346 otoliths, Table 5, Figure 2).

Age data for Mutton Snapper are predominantly (97.4%) from the state of Florida (n = 24,890 otoliths). Within Florida, 40.3% (n = 10,303 otoliths) of samples came from the southeast Florida region (Indian River County south to Miami-Dade County and 32.4% (n = 8,293 otoliths) came from the Florida Keys region (Monroe County, Table 6, Figure 3). The number of samples from the southwest Florida region totaled 4,463 otoliths (17.4%) and was lowest west of Florida (n = 11 otoliths, Table 6, Figure 3).

The distribution of ages among fishery-dependent sources was generally similar with modes occurring at ages 3 and 4 (Figure 4); however, samples from the commercial fishery contained a higher proportion of older fish (Figure 4) and were primarily from the long line gear (Figure 5). Samples of older Mutton Snapper (i.e., > 8 years) were sparse from fishery-independent surveys (Figure 4). In the southeast region, the distribution of Mutton Snapper ages was noticeably younger (mean = 3.87 years, median = 4 years) compared to the Florida Keys region (mean = 6.78 years, median = 6 years) and all the other regions (Figure 6). The southwest region contained the highest proportions of older ages (mean = 9.11 years, median = 7 years, Figure 6) within Florida waters and is where the long line commercial fishery for Mutton Snapper is concentrated. Outside of Florida waters where fishing pressure for Mutton Snapper significantly decreases, sampled ages were oldest north of Florida (mean = 11.87 years, median = 8 years, Figure 6). Figure 7 shows the age distribution by year with evidence of strong year classes in 2008, 2014, and 2017. Another stronger year classes may also have occurred in 1984, however, samples sizes during this earlier period were very low.

Maximum Age

The current maximum observed age of Mutton Snapper based on sectional otoliths is 42 years; the fish (n = 1 otolith) was collected in the Florida Keys in 2015 and represents the maximum age for the entire southeastern U.S. stock. This is an update to the previous assessment (SEDAR 15AU 2015) which had a

terminal year of 2013 and an observed maximum age at 40 years from samples (n = 6 otoliths) collected in Florida, South Carolina, and North Carolina.

Precision Calculations

Campana (2001) suggests an APE of 5% or less as an acceptable benchmark for precision, which corresponds to approximately a 7.6% CV calculation. The APE and CV of the Mutton Snapper age dataset at the time of this precision evaluation (n=24,738 otoliths) was 1.2% and 1.7%, while the quality control subsample (n=240) was 1.7% and 2.2%, respectively. These values are well below the benchmark for acceptable precision standards indicating that Mutton Snapper reads were highly precise. Age bias plots of the quality control subsample of the primary FWRI readers reveals overall high precision and low bias (Figure 8). The quality control subsample consisted of fish ages 2–30, which is representative of the larger fishery-dependent life history dataset. No single age class was determined to be significantly different from the consensus age for any readers. Ageing precision was highest amongst the youngest and most numerous age classes. Variability was generally higher for older age classes, which is to be expected, but differing reads were consistently within one year of the consensus age.

Growth

Mutton Snapper length-at-age displayed a size truncated profile (Figure 9a) and the number of sampled lengths was highest between 400 - 500 mm TL (Figure 9b). The truncated pattern due to the enacted minimum size limits was seen in the commercial and recreational length-at-age data which contained similar profiles (Figure 10). Analogous to the pattern seen in the age data, the commercial fishery contained a higher proportion of larger fish (>~800 mm TL) sampled largely from the long line gear (Figure 11). The fishery-independent length-at-age data contained smaller and younger fish not present in fishery-dependent data, but also showed a paucity of older and larger individuals (Figure 10). Lack of larger and older individuals will likely result in poor model estimation of L_{∞} ; therefore, the fishery-independent for use in modeling growth. Length-at-age by region is shown in Figure 12 and profiles display patterns similar to those described in the age data above.

From the available age data, a total of 24,234 length-at-age observations were retained (94.7%) for sizetruncated modeling of growth. The fit statistics for the size-truncated von Bertalanffy growth models indicated that models fit to the inverse-weighted data were significantly better than those fit to the unweighted data (Table 7). The model whose variance was estimated with CV was a linear function of age contained the lowest AIC value (Table 7, Figure 13) with equation:

$$L_t = 847 (1 - e^{(-0.163 (t + 1.115))})$$

The residuals for this model indicate overall goodness of fit (Figure 14a – b) and by fishery (Figure 14c), by region (Figure 14d), and by calendar age (Figure 14e). Residuals by year indicate some inconsistency in fitting to the earlier and data-poorer period before year 1991 (Figure 14f). This model estimated the average asymptotic maximum length to be 14 mm smaller than when previously assessed ($L_{\infty} = 861$ mm, SEDAR 15AU 2015; which was smaller still compared to the initial assessment where $L_{\infty} = 874$ mm, SEDAR 15A 2008).

The models whose variances were estimated with a constant sigma or with CV as a linear function of size at age had nearly the same AIC values and differed from the best fit model by less than 2 AIC units. These models estimated smaller L_{∞} parameters (837.6 mm and 841.7 mm, respectively) and similar *K* parameters (0.175 and 0.164, respectively, Table 7).

Natural Mortality

The estimation methods of natural mortality along with their respective equations are presented in Table 8. Longevity estimates were based on the observed maximum age for Mutton Snapper (t_{max} = 42 years) and the von Bertalanffy growth parameter values were based on the final growth model above (L_{inf} = 847 mm, K = 0.163, t0 = -1.115). Length-weight model parameters of Mutton Snapper used within the mortality-weight model were obtained from the non-linear length-weight model converting maximum total length (mm) to total weight (g) where a = 4.59E-6 and b = 3.160.

Constant mortality estimates based on the longevity and empirical *K* models were found to be M = 0.129 yr⁻¹ and 0.253 yr⁻¹, respectively. The revised Pauly_{nls-T} model also estimated M = 0.253 yr⁻¹. The mortality at asymptotic length parameter was estimated to be $M_{L\infty} = 0.282$. Thus, estimates of constant *M* correlated with growth were nearly double those based on longevity and maximum age would need to be about half (~age 21 years) for the longevity model to equal the empirical *K* model estimates of *M*.

Converted mortality-at-age estimates ranged from 0.302 - 0.068 yr⁻¹ for the longevity model, from 0.514 - 0.116 yr⁻¹ for the longevity (scaled) model, from 0.593 - 0.133 yr⁻¹ for the empirical *K* model, and from 0.594 - 0.134 yr⁻¹ for the revised Pauly_{nls-T} model (Table 9, Figure 15). Cumulative survival to the oldest age class for these models is 2.7%, 0.2%, 0.1%, and 0.1%, respectively. Estimates of mortality-at-age for empirical *K* (scaled) and Pauly_{nls-T} (scaled) models are not reported here because cumulative survival to the oldest age class in both models was less than 0.001%.

Estimated mortality-at-age from the mortality-weight model ranged from $1.146 - 0.224 \text{ yr}^{-1}$, from $0.378 - 0.063 \text{ yr}^{-1}$ for the length-inverse model, from $0.691 - 0.115 \text{ yr}^{-1}$ for the length-inverse (scaled) model and from $1.695 - 0.282 \text{ yr}^{-1}$ for the length-inverse (empirical) model (Table 10, Figure 15). Both the mortality-weight and the length-inverse (empirical) models estimated high natural mortality-at-age where cumulative survival to the oldest age class was also less than 0.001%. For the length-inverse and length-inverse (scaled) models, cumulative survival to the oldest age class for these models is 2.9% and 0.2%, respectively.

In SEDAR 15AU (2015), constant natural mortality was calculated using methods from Hoenig (1983) and Hewitt and Hoenig (2005) where M = 0.11 yr⁻¹ for a maximum age of 40 years and scaled across ages 3 - 40. Mortality-at-age was estimated to range from 0.406 - 0.099 yr⁻¹. During that update assessment, Then et al. (2015) was published and the Hoenig_{nls} equation, which calculated M = 0.17 yr⁻¹, was also used and explored as a sensitivity run. While these methods may no longer be recommended (e.g., older data or lack of adequate transformation; see Maunder et al. 2023), the estimates are similar in magnitude to the more recent longevity-based estimates provided here.

In addition to these methods being developed independently, Maunder et al. (2023) recommends allowing M to be estimated within the integrated assessment model where estimation of a greater range of sampling processes (e.g., selectivity, effective sample size) may reduce bias and result in improved precision of estimated quantities. Internal estimation will also allow for data conflicts to be evaluated through processes such as likelihood component profiling on M. Longevity-based estimators of M are considered more informative (Then et al. 2015, Cope and Hamel 2022) and should be accompanied by measures of uncertainty (e.g., see the Natural Mortality Tool developed by Cope and Hamel [2022] and the standard deviations in lognormal space developed by Hamel and Cope [2022]).

Literature Cited

- Beamish, R.J., and Fournier, D.A. 1981. A method for comparing the precision of a set of agedeterminations. Canadian Journal of Fisheries and Aquatic Sciences 38:982-983.
- Burton, M.L. 2002. Age, growth and mortality of mutton snapper, *Lutjanus analis*, from the east coast of Florida, with a brief discussion of management implications. Fishery Research 59:31-41.
- Burton, M.L., Potts, J.C., and Carr, D.R. 2015. Age, growth, and natural mortality of yellowfin grouper (*Mycteroperca venenosa*) from the southeastern United States. PeerJ 3:e1099.
- Carroll, J., and Lowerre-Barbieri, S.K. 2019. Interactions of dimorphic growth, reproductive behavior, and a size-regulated fishery: a case study using spotted seatrout *Cynoscion nebulosus*. Mar Ecol-Prog Ser 608:233-245.
- Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age-determination. Canadian Journal of Fisheries and Aquatic Sciences 39:1208-1210.
- Cope, J.M., and Hamel, O.S., 2022. Upgrading from M version 0.2: An application-based method for practical estimation, evaluation and uncertainty characterization of natural mortality. Fish. Res. https://doi.org/10.1016/j.fishres.2022.106493.
- Diaz, G., Porch, C., and Ortiz, M. 2004. Growth models for red snapper in the US Gulf of Mexico waters estimated from landings with minimum size restrictions. Contribution SFD-2004038. Sustainable Fisheries Division, NOAA Fisheries.13p.
- Gulland, J.A. 1983. Fish Stock Assessment. A Manual of Basic Method. FAO/Wiley Series on Food and Agriculture, Rome, 241 p.
- Haddon, M. 2011. Modelling and Quantitative Methods in Fisheries, second ed. CRC Press, Boca Raton.
- Hamel, O.S., and Cope, J.M. 2022. Development and considerations for application of a longevity-based prior for the natural mortality rate. Fish. Res. 256. 106477
- Hampton, J. 2000. Natural mortality rates in tropical tunas: size really does matter. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(5), 1002-1010.
- Hewitt, D.A., and Hoenig, J.M. 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fishery Bulletin 103:433437.
- Hilborn, R., and Walters, C.J. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman & Hall, London, UK, p. 570.
- Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 81:898903.
- Ihssen, P.E., Booke, H.E., Casselman, J.M., McGlade, J.M., Payne, N.R. and Utter, F.M. 1981. Stock identification: materials and methods. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 1838–1855.
- Kimura, D.K., and Anderl, D.M. 2005. Quality control of age data at the Alaska Fisheries Science Center. Mar Freshw Res 56:783-789.

- Kimura, D.K., and Lyons, J.J. 1991. Between-reader bias and variability in the age-determination process. Fishery Bulletin 89:53-60.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in fish: a comparison of natural ecosystems and aquaculture. J. Fish. Biol. 49, 627–647.
- Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish stocking programmes. Can. J. Fish. Aquat. Sci. 57, 2374–2381.
- Lorenzen, K. 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philos Trans R Soc B-Biol Sci 360:171-189.
- Lorenzen, K. 2022. Size- and age-dependent natural mortality in fish populations: Biology, models, implications, and a generalized length-inverse mortality paradigm. Fish. Res. 255, 106454.
- Lorenzen, K., Camp, E.V., and Garlock, T.M. 2022. Natural mortality and body size in fish populations. Fish. Res. 252, 106327.
- Mason D.L., and Manooch, C.S. 1985. Age and growth of mutton snapper along the east coast of Florida. Fisheries Research 3: 93-104.
- Maunder, M.N., Hamel, O.S., Lee, H., Piner, K.R., Cope, J.M., Punt, A.E., Ianelli, J.N., Castillo-Jordan, C., Kapur, M.S., and Methot, R.D. 2023. A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment. Fish. Res. 257, 106489.
- Ogle, D.H., Wheeler, P., and Dinno, A. 2020. FSA: Fisheries Stock Analysis. R package version 0.8.31, https://github.com/droglenc/FSA.
- Quinn, T.J., and Deriso, R.B. 1999. Quantitative Fish Dynamics. Oxford University Press.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
- SEDAR. 2008. SEDAR 15A Stock Assessment Report 3 (SAR 3). South Atlantic and Gulf of Mexico Mutton Snapper. South Atlantic Fishery Management Council. Charleston, SC. 410 pp.
- SEDAR. 2015. SEDAR 15A Update. South Atlantic and Gulf of Mexico Mutton Snapper. South Atlantic Fishery Management Council. Charleston, SC. 144 pp.
- Then, A.Y., Hoenig, J.M., Hall, N.G., and Hewitt, D.A. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. 72, 82–92.
- VanderKooy, S., Carroll, J., Elzey, S., Gilmore, J., and Kipp, J. 2020. A practical handbook for determining the ages of Gulf of Mexico and Atlantic Coast fishes, Gulf States Mar. Fish Comm Publ: 300.
- Vetter, E.F. 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. US 86, 25–43.

Tables

Table 1. Length-length and length-weight relationships developed for southeastern U.S. Mutton Snapper. Linear length-length regressions are in the form Y = a + bX and non-linear length-weight regressions are in the form $W = aL^b$. SL: standard length; FL: fork length; TL: total length; TW: total weight.

	LENGTH- LENGTH														
					Min	Max	Avg.		Adj.						
Y (mm)	а	b	X (mm)	n	X (mm)	X (mm)	X (mm)	MSE	r2						
FL	17.5033	1.1301	SL	2,019	196	723	410.3	79.109	0.994						
$TL_{relaxed^{\ast}}$	18.5711	1.2244	SL	2,462	75	723	370.4	173.197	0.990						
$TL_{max^{**}}$	35.6926	1.2057	SL	1,855	121	723	408.2	122.244	0.991						
TL _{max}	15.5177	1.0710	FL	2,886	195	819	491.4	35.412	0.998						
FL	-9.8710	0.9282	TL _{relaxed}	16,967	125	882	509.5	53.741	0.994						
TL _{max}	10.3668	1.0057	TL _{relaxed}	1,407	261	863	500.7	45.505	0.996						
	LENGTH-WEIGHT														
	Min Max Avg. Adj.														
Y (g)	а	b	X (mm)	n	X (mm)	X (mm)	X (mm)	MSE	r2						
Y (g) TW	a 4.05E-05	b 2.9425	X (mm) SL	n 1,764	X (mm) 75	X (mm) 723	X (mm) 370.9	MSE 66724.564	r2 0.995						
Y (g) TW TW	a 4.05E-05 1.31E-05	b 2.9425 3.0490	X (mm) SL FL	n 1,764 22,880	X (mm) 75 118	X (mm) 723 850	X (mm) 370.9 466.3	MSE 66724.564 48012.329	r2 0.995 0.985						
Y (g) TW TW TW	a 4.05E-05 1.31E-05 7.11E-06	b 2.9425 3.0490 3.1004	X (mm) SL FL TL _{relaxed}	n 1,764 22,880 28,395	X (mm) 75 118 99	X (mm) 723 850 895	X (mm) 370.9 466.3 507.7	MSE 66724.564 48012.329 50856.330	r2 0.995 0.985 0.980						
Y (g) TW TW TW TW	a 4.05E-05 1.31E-05 7.11E-06 3.99E-06	b 2.9425 3.0490 3.1004 3.1904	X (mm) SL FL TL _{relaxed} TL _{max}	n 1,764 22,880 28,395 1,370	X (mm) 75 118 99 156	X (mm) 723 850 895 885	X (mm) 370.9 466.3 507.7 540.2	MSE 66724.564 48012.329 50856.330 56813.658	r2 0.995 0.985 0.980 0.989						
Y (g) TW TW TW TW TW	a 4.05E-05 1.31E-05 7.11E-06 3.99E-06 4.59E-06	b 2.9425 3.0490 3.1004 3.1904 3.1601	X (mm) SL FL TL _{relaxed} TL _{max} TL _{max_final***}	n 1,764 22,880 28,395 1,370 36,369	X (mm) 75 118 99 156 110	X (mm) 723 850 895 885 926	X (mm) 370.9 466.3 507.7 540.2 521	MSE 66724.564 48012.329 50856.330 56813.658 61558.950	r2 0.995 0.985 0.980 0.989 0.979						
Y (g) TW TW TW TW TW	a 4.05E-05 1.31E-05 7.11E-06 3.99E-06 4.59E-06	b 2.9425 3.0490 3.1004 3.1904 3.1601	X (mm) SL FL TL _{relaxed} TL _{max} TL _{max_final****}	n 1,764 22,880 28,395 1,370 36,369	X (mm) 75 118 99 156 110	X (mm) 723 850 895 885 926	X (mm) 370.9 466.3 507.7 540.2 521	MSE 66724.564 48012.329 50856.330 56813.658 61558.950	r2 0.995 0.985 0.980 0.989 0.979						
Y (g) TW TW TW TW TW	a 4.05E-05 1.31E-05 7.11E-06 3.99E-06 4.59E-06	b 2.9425 3.0490 3.1004 3.1904 3.1601	X (mm) SL FL TL _{relaxed} TL _{max} TL _{max_final***}	n 1,764 22,880 28,395 1,370 36,369 ENGTH-V	X (mm) 75 118 99 156 110 VEIGHT	X (mm) 723 850 895 885 926	X (mm) 370.9 466.3 507.7 540.2 521	MSE 66724.564 48012.329 50856.330 56813.658 61558.950	r2 0.995 0.985 0.980 0.989 0.979						
Y (g) TW TW TW TW TW	a 4.05E-05 1.31E-05 7.11E-06 3.99E-06 4.59E-06	b 2.9425 3.0490 3.1004 3.1904 3.1601	X (mm) SL FL TL _{relaxed} TL _{max} TL _{max_final***}	n 1,764 22,880 28,395 1,370 36,369 ENGTH-V	X (mm) 75 118 99 156 110 <u>VEIGHT</u> Min	X (mm) 723 850 895 885 926 Max	X (mm) 370.9 466.3 507.7 540.2 521 Avg.	MSE 66724.564 48012.329 50856.330 56813.658 61558.950	r2 0.995 0.985 0.980 0.989 0.979 Adj.						
Y (g) TW TW TW TW TW Y (kg)	a 4.05E-05 1.31E-05 7.11E-06 3.99E-06 4.59E-06	b 2.9425 3.0490 3.1004 3.1904 3.1601 b	X (mm) SL FL TL _{relaxed} TL _{max} TL _{max_final***} LH	n 1,764 22,880 28,395 1,370 36,369 ENGTH-V	X (mm) 75 118 99 156 110 <u>VEIGHT</u> Min X (cm)	X (mm) 723 850 895 885 926 Max X (cm)	X (mm) 370.9 466.3 507.7 540.2 521 Avg. X (cm)	MSE 66724.564 48012.329 50856.330 56813.658 61558.950 MSE	r2 0.995 0.985 0.980 0.989 0.979 Adj. r2						
Y (g) TW TW TW TW Y (kg) TW	a 4.05E-05 1.31E-05 7.11E-06 3.99E-06 4.59E-06 a 6.63E-06	b 2.9425 3.0490 3.1004 3.1904 3.1601 b 3.1601	X (mm) SL FL TLrelaxed TLmax TLmax_final*** LH X (cm) TLmax_final***	n 1,764 22,880 28,395 1,370 36,369 ENGTH-V n 36,369	X (mm) 75 118 99 156 110 VEIGHT Min X (cm) 11.0	X (mm) 723 850 895 885 926 Max X (cm) 92.6	X (mm) 370.9 466.3 507.7 540.2 521 Avg. X (cm) 52.1	MSE 66724.564 48012.329 50856.330 56813.658 61558.950 MSE 61558.950	r2 0.995 0.985 0.980 0.989 0.979 Adj. r2 0.979						

Tail flat, in its natural state $TL_{relaxed^*}$ - Tail flat, in its natural state $TL_{max^{**}}$ - Tail compressed to its maximum length

TLmax_final*** - Contains both observed and converted length measurements

																					Age (yea	ars)																					
Year	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	42	Total
1977	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
1979	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
1980	0	0	7	8	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
1981	0	0	11	84	29	4	6	3	5	1	2	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	149
1982	0	0	2	27	72	20	4	15	6	9	3	4	0	0	0	0	2	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	169
1983	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
1984	0	0	17	5	0	2	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32
1985	0	0	6	41	21	1	6	10	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	88
1986	0	0	3	3	21	2	0	1	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33
1987	0	2	3	2	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
1988	0	0	8	12	8	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	55
1990	0	0	1	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	· 11
1991	0	2	6	3	16	2	2	2	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52
1992	0	2	15	24	16	16	10	10	1	4	2	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	101
1995	0	0	2	24	33	8	10	10	3	4	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	02
1994	0	0	12	58	48	27	7	3	5	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	162
1996	0	0	11	30	58	34	17	6	5	4	1	2	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	170
1997	0	2	25	29	48	39	44	28	15	6	2	3	2	0	1	0	1	0	ő	0	1	0	ő	2	1	2	ő	0	1	0	0	1	0	ő	0	ő	0	ő	0	ő	ő	0	253
1998	56	13	38	132	60	50	25	22	10	1	3	2	0	Ő	0	Ő	0	0	Ő	Ő	0	0	Ő	0	0	0	Ő	ő	0	ő	0	0	õ	Ő	Ő	Ő	ő	ő	0	Ő	Ő	Ő	412
1999	19	22	54	125	70	50	18	15	13	5	1	1	2	1	0	Ő	Ő	1	0	Ő	Ő	Ő	0	1	0	1	0	Ő	Ő	õ	Ő	õ	0	0	0	0	0	Ő	Ő	0	0	0	399
2000	21	12	107	169	101	28	22	6	5	5	5	0	0	1	0	Ő	Ő	0	0	1	0	1	0	0	Ő	0	0	Ő	Ő	õ	õ	õ	0	0	0	0	0	0	Ő	0	0	0	484
2001	12	9	59	225	108	66	20	15	5	9	3	3	0	2	6	5	2	2	2	0	2	2	0	0	1	0	1	1	0	0	0	2	0	2	0	0	0	0	0	1	0	0	565
2002	0	3	36	173	176	113	49	24	10	6	3	8	4	3	4	3	5	1	2	1	3	1	2	1	0	0	1	2	2	1	2	0	1	1	2	1	0	0	0	0	0	0	644
2003	0	4	43	172	251	86	43	20	13	8	3	17	10	5	7	6	5	5	3	6	7	4	5	0	4	2	1	2	1	0	0	3	1	0	1	1	1	1	1	0	1	0	743
2004	1	1	46	101	123	106	54	32	27	13	8	6	5	2	5	2	1	6	7	3	1	1	4	1	2	3	2	1	2	3	1	1	0	2	1	0	0	1	0	1	1	0	577
2005	0	2	56	331	152	92	54	55	26	17	5	3	5	5	5	3	2	6	2	6	4	4	1	0	1	0	3	3	2	1	0	0	0	1	1	1	0	0	0	0	0	0	849
2006	0	0	20	211	113	76	98	92	62	20	23	21	16	15	6	11	14	5	7	4	5	7	3	1	3	4	3	1	1	1	0	2	3	1	3	0	2	0	0	0	1	0	855
2007	0	3	95	222	280	91	61	37	43	24	12	18	7	11	7	3	6	7	4	6	8	4	2	2	4	2	1	0	2	4	1	0	1	2	0	3	0	0	0	0	0	0	973
2008	0	0	79	477	149	224	120	78	61	53	33	24	18	7	5	2	3	6	4	7	3	3	9	7	5	0	1	0	1	2	1	0	2	0	0	0	0	0	0	0	0	0	1,384
2009	0	0	43	267	526	97	227	86	64	43	40	27	16	16	8	5	5	7	6	6	2	4	2	1	3	2	1	0	0	4	3	1	0	1	1	0	0	0	0	0	0	0	1,514
2010	0	0	24	298	485	491	113	201	79	49	40	29	15	19	19	9	10	5	2	3	3	5	7	6	5	3	0	1	1	0	1	2	0	0	0	0	0	0	0	0	1	0	1,926
2011	0	0	10	114	343	321	330	68	135	37	24	18	19	13	11	11	4	5	3	9	8	0	2	4	1	5	3	2	0	0	2	0	2	2	0	0	1	0	0	0	1	0	1,508
2012	0	0	33	18	114	192	165	216	73	131	56	31	30	28	14	20	18	14	9	6	6	7	2	3	4	5	2	3	4	1	2	1	1	0	0	1	1	1	0	0	1	0	1,213
2013	1	1	45	128	33	104	137	159	151	48	44	30	22	12	8	13	10	10	7	4	4	4	5	1	3	2	1	2	0	1	1	0	0	2	0	0	0	0	0	0	0	0	993
2014	0	4	78	360	111	22	75	106	116	115	42	26	10	9	15	12	6	6	9	8	7	6	5	5	3	0	4	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1,163
2015	1	3	74	212	244	96	15	59	65	79	48	12	13	13	8	9	12	12	5	6	2	4	3	4	6	2	2	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1,008
2016	1	2	52	246	250	326	78	15	33	49	72	59	21	19	11	9	8	13	2	6	2	6	2	3	1	3	2	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1,296
2017	0	1	19	1/2	214	165	207	44		27	32	58	42	24	9	10	5	8	8	8	11	3	5	5	5	1	1	2	2	1	0	0	0	1	0	0	0	0	0	0	0	0	1,075
2018	1	1	9	113	238	227	1/8	190	44	12	16	42	49	50	20	21	10	9	9	0	8	/	9	3	5	3	5	1	4	4	1	2	0	0	0	0	0	0	1	0	0	0	1,282
2019		1	3	14	233 56	107	90	60 64	55	13	1	6	10	10	20	10	7	5	13	2	5	4	2	4	1	0	2	3	3	1	4	3	1	1	1	0	0	0	0	0	0	0	602
2020	0	1	2	14	82	140	243	04	12	40	1 28	3	0	5	11	13	10	0	15	2	2	3	4	4	1	2	2 0	5	1	2	3	5	1	1	1	1	0	0	0	0	0	0	745
2022	1	1	13	+2 62	122	172	243	303	134	33	20	25	3	3	4	7	17	13	8	4	1	5	2	7	4	8	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0	0	1 131
Total Number	116	90	1.175	4.812	5.034	3.769	2.792	2.176	1.366	906	579	466	339	296	222	191	169	157	118	114	102	88	84	68	62	53	36	29	29	29	23	20	15	17	12	10	7	3	3	2	6	1	25.586
Percent	0.453	0.352	4.592	18.807	19.675	14.731	10.912	8.505	5.339	3.541	2.263	1.821	1.325	1.157	0.868	0.747	0.661	0.614	0.461	0.446	0.399	0.344	0.328	0.266	0.242	0.207	0.141	0.113	0.113	0.113	0.090	0.078	0.059	0.066	0.047	0.039	0.027	0.012	0.012	0.008	0.023	0.004	

Table 2. Number of ages of Mutton Snapper sampled by year from the southeastern U.S. from 1977 – 2022.

Year	COM	REC	FI	Total
1977	0	2	0	2
1979	0	1	0	1
1980	0	17	0	17
1981	0	149	0	149
1982	0	169	0	169
1983	0	4	0	4
1984	0	32	0	32
1985	0	88	0	88
1986	0	33	0	33
1987	0	14	0	14
1988	0	33	0	33
1990	0	6	Õ	6
1991	0	11	Õ	11
1992	47	5	Õ	52
1993	47	54	Ő	101
1994	63	29	Ő	92
1995	36	126	Ő	162
1996	146	24	Ő	170
1997	233	20	Ő	253
1998	208	0	204	412
1999	236	Ő	163	399
2000	215	4	265	484
2000	310	41	214	565
2002	415	120	109	644
2003	407	336	0	743
2003	314	263	Ő	577
2005	344	505	0	849
2005	537	318	Ő	855
2007	293	676	4	973
2008	573	804	7	1 384
2000	414	1 094	6	1,501
2010	881	1,039	6	1,926
2010	770	735	3	1,508
2012	571	633	9	1,200
2012	515	474	4	993
2013	540	620	3	1 163
2015	335	670	3	1,105
2015	286	999	11	1,000
2017	366	703	6	1,220
2018	543	720	19	1,075
2010	<u> </u>	402	20	856
2017	537	50	15	602
2020	505	180	60	745
2021	706	346	79	1 1 2 1
Total	11 827	12 549	1 210	25 586

Table 3. Number of Mutton Snapper age samples by commercial (COM), recreational (REC), and fishery independent (FI) sectors collected from the southeastern U.S. from 1977 – 2022.

Table 4. Number of Mutton Snapper age samples by Commercial (Com), Headboat (HB), Charter, Private, fishery independent scientific surveys (SS), and tournament (Tour) fishing modes collected from the southeastern U.S. from 1977 – 2022.

Year	Com	HB	Charter	Private	SS	Tour	Total
1977	0	2	0	0	0	0	2
1979	0	1	0	0	0	0	1
1980	0	17	0	0	0	0	17
1981	0	149	0	0	0	0	149
1982	0	169	0	0	0	0	169
1983	0	4	0	0	0	0	4
1984	0	32	0	0	0	0	32
1985	0	88	0	0	0	0	88
1986	0	33	0	0	0	0	33
1987	0	14	0	0	0	0	14
1988	0	33	0	0	0	0	33
1990	0	6	0	0	0	0	6
1991	0	11	0	0	0	0	11
1992	47	5	0	0	0	0	52
1993	47	53	0	0	0	1	101
1994	63	29	0	0	0	0	92
1995	36	126	0	0	0	0	162
1996	146	24	0	0	0	0	170
1997	233	20	0	0	0	0	253
1998	208	0	0	0	204	0	412
1999	236	0	0	0	163	0	399
2000	215	3	1	0	265	0	484
2001	310	12	20	7	214	2	565
2002	415	2	113	4	109	1	644
2003	407	118	208	7	0	3	743
2004	314	137	122	4	0	0	577
2005	344	241	261	3	0	0	849
2006	537	234	74	3	0	7	855
2007	293	580	81	15	4	0	973
2008	573	742	54	8	7	0	1.384
2009	414	993	83	18	6	0	1.514
2010	881	945	75	19	6	0	1.926
2011	770	533	192	10	3	0	1,508
2012	571	587	46	0	9	0	1.213
2013	515	431	43	0	4	0	993
2014	540	539	77	4	3	0	1.163
2015	335	587	83	0	3	0	1.008
2016	286	954	45	0	11	0	1.296
2017	366	549	137	17	6	0	1.075
2018	543	485	215	20	19	Ő	1.282
2019	434	293	89	19	20	1	856
2020	537	15	30	5	15	0	602
2021	505	70	50	60	60	Ő	745
2022	706	240	30	76	79	Ő	1.131
Total	11,827	10,106	2,129	299	1,210	15	25,586

Year	H&L	LL	OTHER	UNK	Total
1977	2	0	0	0	2
1979	1	0	0	0	1
1980	17	0	0	0	17
1981	149	0	0	0	149
1982	169	0	0	0	169
1983	4	0	0	0	4
1984	32	0	0	0	32
1985	88	0	0	0	88
1986	33	0	0	0	33
1987	14	0	0	0	14
1988	33	0	0	0	33
1990	6	0	0	0	6
1991	11	0	0	0	11
1992	42	1	0	9	52
1993	55	11	0	35	101
1994	50	5	0	37	92
1995	127	3	0	32	162
1996	132	0	0	38	170
1997	226	24	3	0	253
1998	342	3	67	0	412
1999	335	5	59	0	399
2000	266	9	177	32	484
2001	342	52	171	0	565
2002	476	94	73	1	644
2003	592	147	4	0	743
2004	286	147	3	141	577
2005	560	166	0	123	849
2006	390	402	20	43	855
2007	649	232	2	90	973
2008	1,168	208	6	2	1,384
2009	1,349	136	24	5	1,514
2010	1,526	365	34	1	1,926
2011	1,261	229	18	0	1,508
2012	897	246	24	46	1,213
2013	632	255	45	61	993
2014	792	287	70	14	1,163
2015	779	162	49	18	1,008
2016	1,133	121	36	6	1,296
2017	790	236	49	0	1,075
2018	893	338	49	2	1,282
2019	676	89	85	6	856
2020	528	32	42	0	602
2021	577	70	76	22	745
2022	828	271	31	1	1,131
Total	19,258	4,346	1,217	765	25,586

Table 5. Number of Mutton Snapper age samples by hook and line (H&L), long line (LL), other, and unknown fishing gears collected from the southeastern U.S. from 1977 – 2022.

Table 6. Number of Mutton Snapper age samples collected by region within the southeastern U.S. from 1977 – 2022. Regions are defined as North of Florida (North of FL), Northeast Florida (NE FL), Southeast Florida (SE FL), the Florida Keys (FL Keys), the Dry Tortugas (Dry Tortugas), Southwest Florida (SW FL), Northwest Florida (NW FL), and West of Florida (West of FL).

Year	North of FL	NE FL	SE FL	FL Keys	Dry Tortugas	SW FL	NW FL	West of FL	Total
1977	0	2	0	0	0	0	0	0	2
1979	0	0	1	0	0	0	0	0	1
1980	0	0	16	1	0	0	0	0	17
1981	0	6	80	63	0	0	0	0	149
1982	0	0	65	104	0	0	0	0	169
1983	0	0	4	0	0	0	0	0	4
1984	0	0	32	0	0	0	0	0	32
1985	0	6	81	1	0	0	0	0	88
1986	0	8	25	0	0	0	0	0	33
1987	0	4	10	0	0	0	0	0	14
1988	0	8	25	0	0	0	0	0	33
1990	0	6	0	0	0	0	0	0	6
1991	0	7	0	4	0	0	0	0	11
1992	0	5	46	0	0	1	0	0	52
1993	0	5	52	32	0	12	0	0	101
1994	0	7	61	19	0	5	0	0	92
1995	0	22	117	22	0	1	0	0	162
1996	4	2	150	14	0	0	0	0	170
1997	7	1	189	32	0	24	0	0	253
1998	0	5	388	16	0	3	0	0	412
1999	0	1	359	31	1	7	0	0	399
2000	0	4	328	142	0	10	0	0	484
2001	0	10	342	154	0	58	1	0	565
2002	0	37	420	83	0	104	0	0	644
2003	2	28	550	11	0	152	0	0	743
2004	10	10	369	29	0	157	2	0	577
2005	25	12	578	58	0	173	2	1	849
2006	37	8	276	89	0	445	0	0	855
2007	30	16	603	95	0	228	1	0	973
2008	28	13	671	458	7	207	0	0	1,384
2009	22	33	685	631	6	137	0	0	1.514
2010	17	26	948	549	6	379	0	1	1.926
2011	37	35	661	530	1	242	0	2	1,508
2012	42	7	196	794	1	173	0	0	1.213
2013	7	27	148	536	1	259	15	0	993
2014	7	26	353	479	0	262	36	0	1.163
2015	6	9	303	508	Õ	182	0	Õ	1.008
2016	12	89	328	718	Õ	140	9	Õ	1.296
2017	18	55	174	568	3	253	4	Õ	1.075
2018	27	49	200	646	0	313	40	7	1.282
2019	34	155	143	352	õ	170	2	Ó	856
2020	8	386	25	132	õ	51	0	Õ	602
2021	102	281	111	176	$\tilde{2}$	52	21	õ	745
2022	81	381	190	216	0	263	0	õ	1.131
Total	563	1,792	10.303	8.293	28	4,463	133	11	25.586

Table 7. Parameter estimates from the size-truncated von Bertalanffy growth models used to predict length ('maximum total length mm)-at-age (fractional, yr) for southeastern U.S. Mutton Snapper. Variance parameter(s) were modeled with constant standard deviation (sigma) with age, constant coefficient of variation (CV) with age, CV increasing linearly with age, and CV increasing linearly with size at age. Growth models were applied to both unweighted (--) data and data weighted by using the inverse (1/n) of the count of each calendar age. The final model selected was the size-truncated model applied to the inverse-weighted data where CV was a linear function of age.

Variance Parameter	Parameters	Weighting	Ν	NegLL	AIC	L_{∞}	K	t_0	Varpar[1]	Varpar[2]	Gradient
Constant sigma	4		24,234	129,945	259,898	823.8	0.2042	-0.294	62.8212		4.98E-05
Constant CV	4		24,234	129,867	259,741	839.0	0.1771	-0.945	0.1094		1.05E-04
CV as linear function of age	5		24,234	129,637	259,283	838.5	0.1779	-0.899	0.1250	0.0297	1.59E-03
CV as linear function of size at age	5		24,234	129,693	259,395	839.5	0.1793	-0.846	0.1479	0.0874	3.39E-05
Constant sigma	4	Inverse	24,234	227.548	463.097	837.6	0.1747	-0.975	56.6350		1.42E-07
Constant CV	4	Inverse	24,234	233.331	474.662	831.7	0.1821	-0.993	0.0915		2.16E-08
CV as linear function of age	5	Inverse	24,234	225.684	461.369	847.3	0.1633	-1.115	0.1391	0.0279	7.13E-07
CV as linear function of size at age	5	Inverse	24,234	226.590	463.180	841.7	0.1643	-1.046	0.2567	0.0578	3.88E-07

Table 8. Constant and size- or age-dependent natural mortality models (assuming von Bertalanffy growth where relevant). L_{∞} is the von Bertalanffy asymptotic length; *K* is the von Bertalanffy growth coefficient; M(w) is the natural mortality rate at weight W; M(a) and M(L) is the natural mortality rate-at-age and - length, respectively; t_{max} is the observed maximum age; $M_{L\infty}$ is the natural mortality rate at asymptotic length (c = -1).

Approach	Equation	Reference	Notes
Constant			
Longevity	$M = 5.4/t_{max}$	Hamel and Cope (2022)	Standard deviation in log space = 0.31
Empirical K	<i>M</i> = 1.55 <i>K</i>	Hamel and Cope (2022)	Standard deviation in log space = 0.85
Pauly _{nls-T} revised	$M = 4.118 \ K^{0.73} L_{\infty}^{-0.33}$	Then et al. (2015)	L_{∞} in units of cm
Allometric			
Weight	$M(w) = 3 W^{-0.288}$	Lorenzen (1996)	Uses the non-linear model converting maximum total length (mm) to weight (g)
Length-inverse	$M(L) = M_{Lr}(L/L_r)^c$	Lorenzen (2022)	A constant <i>M</i> estimate used as M_{Lr} ; length associated with age-3 as reference length (L_r)
Length-inverse (empirical)	$M(a) = M_{L\infty} (1 - e^{-K(a - a0)})^{c}$	Lorenzen (2022), Lorenzen et al. (2022)	$ln(M_{L\infty}) = 0.42 + 0.93 ln(K);$ see Model 6, Table 3 in Lorenzen et al. (2022)

Table 9. Natural mortality-at-age, M(a), or -weight, M(w), of Mutton Snapper with an observed maximum age of 42 years. 'Longevity', 'Empirical K', and the 'Pauly_{nls-T} revised' estimates of M(a) are derived following Lorenzen (2000, 2005) using their respective constant M estimates (0.129, 0.253, 0.253) as the reference M scaled to age 3 and the von Bertalanffy growth model parameters ($L_{inf} = 847$; K = 0.163; t0 = -1.115). The 'Longevity (scaled)' model scaled the cumulative mortality rate predicted for ages 3 – 42 to the longevity-based constant M estimate.

			Longevity	Longevity (scaled)	Empirical K	Pauly _{nls-T} revised
Age (yr)	Length (mm)	Weight (g)	M(a)	M(a)	M(a)	M(a)
0	141	28.3	0.302	0.514	0.593	0.594
1	247	167.0	0.197	0.336	0.388	0.388
2	337	446.8	0.153	0.261	0.301	0.301
3	414	853.7	0.129	0.219	0.253	0.253
4	479	1354.9	0.113	0.193	0.223	0.223
5	534	1914.0	0.103	0.175	0.202	0.203
6	581	2498.5	0.095	0.163	0.188	0.188
7	621	3082.2	0.090	0.153	0.177	0.177
8	655	3646.3	0.086	0.146	0.168	0.169
9	684	4177.8	0.082	0.141	0.162	0.162
10	709	4669.1	0.080	0.136	0.157	0.157
11	729	5116.4	0.078	0.133	0.153	0.153
12	747	5518.6	0.076	0.130	0.149	0.150
13	762	5877.0	0.075	0.127	0.147	0.147
14	775	6193.6	0.074	0.125	0.145	0.145
15	786	6471.7	0.073	0.124	0.143	0.143
16	795	6714.5	0.072	0.123	0.141	0.141
17	803	6925.6	0.071	0.121	0.140	0.140
18	809	7108.6	0.071	0.121	0.139	0.139
19	815	7266.5	0.070	0.120	0.138	0.138
20	820	7402.6	0.070	0.119	0.137	0.138
21	824	7519.6	0.070	0.119	0.137	0.137
22	827	7619.9	0.069	0.118	0.136	0.136
23	830	7705.9	0.069	0.118	0.136	0.136
24	833	7779.5	0.069	0.117	0.135	0.136
25	835	7842.4	0.069	0.117	0.135	0.135
26	837	7896.1	0.069	0.117	0.135	0.135
27	838	7941.9	0.068	0.117	0.134	0.135
28	840	7981.0	0.068	0.117	0.134	0.135
29	841	8014.3	0.068	0.116	0.134	0.134
30	842	8042.6	0.068	0.116	0.134	0.134
31	842	8066.8	0.068	0.116	0.134	0.134
32	843	8087.3	0.068	0.116	0.134	0.134
33	844	8104.8	0.068	0.116	0.134	0.134
34	844	8119.7	0.068	0.116	0.134	0.134
35	845	8132.4	0.068	0.116	0.134	0.134
36	845	8143.1	0.068	0.116	0.133	0.134
37	845	8152.3	0.068	0.116	0.133	0.134
38	846	8160.1	0.068	0.116	0.133	0.134
39	846	8166.7	0.068	0.116	0.133	0.134
40	846	8172.3	0.068	0.116	0.133	0.134
41	846	8177.1	0.068	0.116	0.133	0.134
42	846	8181.1	0.068	0.116	0.133	0.134

Table 10. Natural mortality-at-age, M(a), or -weight, M(w), of Mutton Snapper with an observed maximum age of 42 years. The 'Mortality-weight' model followed Lorenzen (1996) and used length-weight parameters a = 4.59E-6 and b = 3.160. The 'Length-inverse' and 'Length-inverse (scaled)' estimates of M(a) follow Lorenzen (2022) using the Hamel and Cope (2022) constant M estimate (0.129) as the mortality at reference length scale parameter, the von Bertalanffy growth model parameters ($L_{inf} = 847$; K = 0.163; t0 = -1.115), and the exponent c = -1. The 'Length-inverse (scaled)' model scaled the cumulative mortality rate predicted for ages 3 - 42 to the longevity-based constant M estimate. The 'Length-inverse (empirical)' model used $M_{L\infty}$ (0.282), the von Bertalanffy growth coefficient, and the exponent c = -1.

$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	
3 414 853.7 0.429 0.129 0.235 0.576 4 479 1354.9 0.376 0.111 0.203 0.498 5 534 1914.0 0.340 0.100 0.182 0.446 6 581 2498.5 0.315 0.092 0.167 0.410 7 621 3082.2 0.297 0.086 0.157 0.384 8 655 3646.3 0.283 0.081 0.148 0.364	
44791354.90.3760.1110.2030.49855341914.00.3400.1000.1820.44665812498.50.3150.0920.1670.41076213082.20.2970.0860.1570.38486553646.30.2830.0810.1480.364	
5 534 1914.0 0.340 0.100 0.182 0.446 6 581 2498.5 0.315 0.092 0.167 0.410 7 621 3082.2 0.297 0.086 0.157 0.384 8 655 3646.3 0.283 0.081 0.148 0.364	
6 581 2498.5 0.315 0.092 0.167 0.410 7 621 3082.2 0.297 0.086 0.157 0.384 8 655 3646.3 0.283 0.081 0.148 0.364	
7 621 3082.2 0.297 0.086 0.157 0.384 8 655 3646.3 0.283 0.081 0.148 0.364	
8 655 3646.3 0.283 0.081 0.148 0.364	
9 684 4177.8 0.272 0.078 0.142 0.349	
10 709 4669.1 0.263 0.075 0.137 0.337	
11 729 5116.4 0.256 0.073 0.133 0.327	
12 747 5518.6 0.251 0.071 0.130 0.319	
13 762 5877.0 0.246 0.070 0.128 0.313	
14 775 6193.6 0.243 0.069 0.126 0.308	
15 786 6471.7 0.240 0.068 0.124 0.304	
16 795 6714.5 0.237 0.067 0.122 0.300	
17 803 6925.6 0.235 0.066 0.121 0.297	
18 809 7108.6 0.233 0.066 0.120 0.295	
19 815 7266.5 0.232 0.065 0.119 0.293	
20 820 7402.6 0.231 0.065 0.119 0.291	
21 824 7519.6 0.229 0.065 0.118 0.290	
22 827 7619.9 0.229 0.064 0.118 0.288	
23 830 7705.9 0.228 0.064 0.117 0.287	
24 833 7779.5 0.227 0.064 0.117 0.286	
25 835 7842.4 0.227 0.064 0.116 0.286	
26 837 7896.1 0.226 0.064 0.116 0.285	
27 838 7941.9 0.226 0.063 0.116 0.285	
28 840 7981.0 0.226 0.063 0.116 0.284	
29 841 8014.3 0.225 0.063 0.116 0.284	
30 842 8042.6 0.225 0.063 0.116 0.283	
31 842 8066.8 0.225 0.063 0.115 0.283	
32 843 8087.3 0.225 0.063 0.115 0.283	
33 844 8104.8 0.225 0.063 0.115 0.283	
34 844 8119.7 0.224 0.063 0.115 0.283	
35 845 8132.4 0.224 0.063 0.115 0.282	
36 845 8143.1 0.224 0.063 0.115 0.282	
37 845 8152.3 0.224 0.063 0.115 0.282	
38 846 8160.1 0.224 0.063 0.115 0.282	
39 846 8166.7 0.224 0.063 0.115 0.282	
40 846 8172.3 0.224 0.063 0.115 0.282	
41 846 8177.1 0.224 0.063 0.115 0.282	
42 846 8181.1 0.224 0.063 0.115 0.282	

Figures



Figure 1. Number of Mutton Snapper age samples collected per year from the southeastern U.S. from 1977 – 2022. (a) Bar plots by commercial (Com), recreational (Rec), and fishery independent (FI) sectors and (b) by commercial (Com), recreational (Headboat [HB], Charter, Private, tournament [Tour]), and fishery-independent (scientific surveys [SS]) fishing modes.



Figure 2. Number of Mutton Snapper age samples by hook and line (H&L), long line (LL), other, and unknown fishing gears collected from the southeastern U.S. from 1977 - 2022.



Figure 3. Number of Mutton Snapper age samples collected by region within the southeastern U.S. from 1977 – 2022.Regions are defined as North of Florida (North of FL), Northeast Florida (NE FL), Southeast Florida (SE FL), the Florida Keys (FL Keys), the Dry Tortugas (Dry Tortugas), Southwest Florida (SW FL), Northwest Florida (NW FL), and West of Florida (West of FL).



Figure 4. Histograms of Mutton Snapper age samples collected by commercial (COM), recreational (REC), and fishery independent (FI) sectors within the southeastern U.S. Bin increments are equal to 1 year.



Figure 5. Histograms of southeastern U.S. Mutton Snapper age samples collected by gear from fisherydependent and -independent data sources between 1977 - 2022. Bin increments are equal to 1 year.



Figure 6. Histograms of Mutton Snapper age samples collected by region within the southeastern U.S. Regions are defined as North of Florida (North of FL), Northeast Florida (NE FL), Southeast Florida (SE FL), the Florida Keys (FL Keys), the Dry Tortugas (Dry Tortugas), Southwest Florida (SW FL), Northwest Florida (NW FL), and West of Florida (West of FL). Bin increments are equal to 1 year.



Figure 7. Histograms of Mutton Snapper age samples for calendar age (0 to 20 years) collected from the southeastern U.S. from 1980 – 2022. Bin increments are equal to 1 year.



Figure 8. Age bias plots for the three primary FWRI ageing staff from quality control subsample (n=240). X-axis is consensus age, y-axis is agreement between reader and consensus age. The gray vertical lines of each point demonstrate the age estimation range by each reader, and the black vertical lines indicate the confidence interval of the individual age classes. Open points indicate that a significant difference was detected between the individual reader and the consensus age. The histogram to the right denotes distribution of age agreement for each reader and the upper histogram illustrates the age distribution of the entire sample.



Figure 9. Southeastern U.S. Mutton Snapper collected from fishery-dependent and -independent data sources between 1977 – 2022. (a) Scatterplot of the length ('maximum' total length mm)-at-age (fractional, yr) and (b) histogram of the number of length samples in 20 mm bin increments.



Figure 10. Southeastern U.S. Mutton Snapper length ('maximum' total length mm)-at-age (fractional, yr) by commercial (COM), recreational (REC), and fishery independent (FI) sectors between 1977 – 2022.



Figure 11. Southeastern U.S. Mutton Snapper length ('maximum' total length mm)-at-age (fractional, yr) by gear from fishery-dependent and -independent data sources between 1977 – 2022.



Figure 12. Southeastern U.S. Mutton Snapper length ('maximum' total length mm)-at-age (fractional, yr) by region between 1977 – 2022. Regions are defined as North of Florida (North of FL), Northeast Florida (NE FL), Southeast Florida (SE FL), the Florida Keys (FL Keys), the Dry Tortugas (Dry Tortugas), Southwest Florida (SW FL), Northwest Florida (NW FL), and West of Florida (West of FL).



Figure 13. Size-truncated southeastern U.S. Mutton Snapper length ('maximum' total length mm)-at-age (fractional, yr) collected from fishery-dependent and -independent data sources between 1977 - 2022 (n = 24,234 otoliths). The dark orange line is the predicted length-at-age from the best fit size-truncated von Bertalanffy growth model applied to inverse-weighted data where CV was a linear function of age.



Figure 14. Standardized residual diagnostic plots for the size-truncated von Bertalanffy growth model applied to inverse-weighted data where CV was a linear function of age: a) density distribution, b) normal probability plot (quantiles vs standardized residuals), c) standardized residuals by fishery, d) standardized residuals by region, e) standardized residuals by age, and f) standardized residuals by year. Boxplots include the median, upper and lower quartiles, and outliers (open circles).



Figure 15. Natural mortality-at-age, M(a), of Mutton Snapper with an observed maximum age of 42 years. 'Longevity', 'Empirical K', and the 'Pauly_{nls-T} revised' estimates of M(a) are derived following Lorenzen (2000, 2005) using their respective constant M estimates (0.129, 0.253, 0.253) as the reference M scaled to age 3 and the von Bertalanffy growth model parameters ($L_{inf} = 847$; K = 0.163; t0 = -1.115). The 'Longevity (scaled)' model scaled the cumulative mortality rate predicted for ages 3 - 42 to the longevity-based constant M estimate. The 'Mortality-weight' model followed Lorenzen (1996) and used length-weight parameters a = 4.59E-6 and b = 3.160. The 'Length-inverse' and 'Length-inverse (scaled)' estimates of M(a) follow Lorenzen (2022) using the longevity-based constant M estimate as the mortality at reference length scale parameter, the von Bertalanffy growth model parameters, and the exponent c = -1. The 'Length-inverse (scaled)' model scaled the cumulative mortality rate predicted for ages 3 - 42 to the longevity-based constant M estimate. The 'Length-inverse (empirical') model used $M_{L\infty}$ (0.282), the von Bertalanffy growth coefficient, and the exponent c = -1.