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Age, Growth, and Mortality of Atlantic Tripletail in the North-Central Gulf of Mexico

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Abstract

In the southeastern USA and the Gulf of Mexico (GOM), Atlantic Tripletail *Lobotes surinamensis* are increasingly targeted by recreational anglers, indicating that stock status should be assessed. A critical need for such assessments is age-specific data; however, previous studies have drawn conflicting conclusions regarding the most appropriate structure for aging. Moreover, growth parameters and mortality rates for GOM Atlantic Tripletail are unknown. Therefore, the goals of this study were to (1) evaluate sagittal otoliths and first dorsal spines as aging structures; (2) model combined and sex-specific growth; and (3) estimate mortality rates for GOM Atlantic Tripletail. From 2012 to 2019, Atlantic Tripletail ($N = 230$, including a near-record-size specimen) were collected from the north-central GOM via hook and line and were aged using otoliths and first dorsal spines. Total length ranged from 212 to 940 mm, and age ranged from 0.07 to 5.27 years. Otoliths produced higher percent agreement (95.0%) and lower average percent error (3.0%) between readers compared to spines (82.9% and 6.5%, respectively). The von Bertalanffy growth parameters differed slightly between the otolith-based data (mean asymptotic length [L_{∞}] = 762.42 mm, Brody growth rate coefficient [k] = 0.69 year⁻¹, and hypothetical age at which length equals zero [t_0] = -0.58 year) and spine-based data (L_{∞} = 718.83 mm, k = 0.79 year⁻¹, and t_0 = -0.56 year). For both otolith- and spine-based sex-specific data, the best-fitting version of the von Bertalanffy growth function permitted L_{∞} to vary by sex. Chapman–Robson estimates of instantaneous total mortality rate and total annual mortality rate were 1.15 and 68.66%,

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respectively. Based on empirical, life history-based methods, the instantaneous natural mortality rate was estimated at 0.75–0.97 and the instantaneous fishing mortality rate was estimated at 0.18–0.45, suggesting low levels of exploitation. These growth parameters and mortality estimates will provide information for future stock assessments, thereby ensuring sustainability of the GOM stock of Atlantic Tripletail.

The Atlantic Tripletail *Lobotes surinamensis* is a deep-bodied marine fish in the order Lobotiformes; its generic name is derived from the unique tri-lobed appearance produced by its rounded dorsal, anal, and caudal fins (Gudger 1931; Carpenter 2002; Betancur-R et al. 2017). Color patterns vary by individual; juveniles are often bright yellow and darken to a brown, bronze, or black color with age (Baughman 1941; Carpenter 2002). Atlantic Tripletail are coastal migratory pelagic fish (Merriner and Foster 1974; Streich et al. 2013) that inhabit warm seas, including southeastern U.S. Atlantic waters and the Gulf of Mexico (GOM; Gudger 1931; Baughman 1943). Adults and juveniles have been reported to occur in shallow bays and nearshore areas (Baughman 1941) as well as surface waters of deep offshore areas (Caldwell 1955). In U.S. Atlantic and GOM waters, seasonal migrations appear to be driven by temperature, with Atlantic Tripletail entering U.S. Atlantic coast estuaries in the spring and leaving in the fall (Merriner and Foster 1974; Streich et al. 2013). Similarly, GOM Atlantic Tripletail occur along the northern GOM coast in the summer (April–October) and are found in particularly high abundance in Alabama and Mississippi waters during those months (Baughman 1941).

Previous studies have investigated the biology and ecology of Atlantic Tripletail along the southeastern U.S. Atlantic and GOM coasts. Diet studies suggest that Atlantic Tripletail are opportunistic predators, consuming a variety of fishes along with shrimp, crabs, and the occasional squid (Merriner and Foster 1974; Franks et al. 2003; Strelcheck et al. 2004). Atlantic Tripletail are batch spawners and reproduce during the summer in U.S. Atlantic waters and the GOM (Merriner and Foster 1974; Brown-Peterson and Franks 2001; Parr et al. 2016). The species is thought to spawn offshore based on collections of larvae above the outer continental shelf (Ditty and Shaw 1994); however, direct evidence of spawning (e.g., identification of specific spawning locations) is nonexistent (Strelcheck et al. 2004) and whether or when adults leave estuaries to spawn is unknown. Juvenile Atlantic Tripletail grow quickly (Armstrong et al. 1996; Franks et al. 2001), experience a wide range of growth during their first year (up to 600 mm TL; Strelcheck et al. 2004), and mature by age 1 (Merriner and Foster 1974; Brown-Peterson and Franks 2001; Parr et al. 2016). Although Merriner and Foster (1974) hypothesized that Atlantic Tripletail could reach a maximum age of 10 years based on an assumed maximum weight of 20.41 kg (45 lb), the maximum reported age is only 7 years from the U.S. Atlantic coast

(Armstrong et al. 1996) and 4.09 years from the GOM (Strelcheck et al. 2004). Armstrong et al. (1996) estimated the total instantaneous mortality rate (Z) at 0.84 for Atlantic Tripletail from Florida's Atlantic coast; however, no mortality estimates exist for GOM Atlantic Tripletail.

Juvenile Atlantic Tripletail associate with *Sargassum* (Baughman 1941; Dooley 1972; Wells and Rooker 2004; Hoffmayer et al. 2005), whereas adults tend to congregate around shallow-water structure, such as wrecks (Kelly 1923), buoys (Hughes 1937), pilings (Gudger 1931), and various flotsam (Baughman 1941). In the shadows of these structures, they often float on their sides, possibly seeking to imitate other floating items (Gudger 1931; Breder 1949). Recreational anglers capitalize on the unique habitat associations of Atlantic Tripletail by sight-casting for them (Hughes 1937; Baughman 1941). They are not only easy to spot but also put up a thrilling fight once hooked, making them a popular target among sport fishers over the past century (Kelly 1923; Gudger 1931; Baughman 1941). A recent analysis of recreational fishing trends revealed an increase in public interest in this species since 1990 (VanderKooy 2016). Furthermore, GOM Atlantic Tripletail recreational catch data substantiate this observation. Average total catch of Atlantic Tripletail from 2015 to 2019 was more than four times greater than that from 1982 to 2014 (241,025 versus 54,815 fish); in fact, catch in 2019 was more than twice that of any previous year on record (510,907 fish in 2019 versus 208,146 fish in 2006, the second-highest year; National Marine Fisheries Service, Fisheries Statistics Division, personal communication). In 2000, Alabama initiated state management by enacting a minimum size limit of 407 mm (16 in) TL and a commercial and recreational bag limit of three fish per person. In 2012, the minimum size limit was increased to 458 mm (18 in) TL. Mississippi began managing Atlantic Tripletail in 2014 and immediately matched Alabama's present regulations (VanderKooy 2016). Save for an assessment of Florida Atlantic Tripletail (Armstrong et al. 1996), no regional stock assessments exist and the species is not regulated or assessed by the National Marine Fisheries Service in any region (VanderKooy 2016).

Given the increasing interest in the recreational harvest of Atlantic Tripletail (VanderKooy 2016), accurate and up-to-date age and growth information is needed to inform management. Since the 1970s, scales, otoliths, fin spines, and fin rays have been used to estimate Atlantic Tripletail age, yet an appraisal of these studies reveals inconsistencies among the methodologies and findings

(Table 1; Merriner and Foster 1974; Armstrong et al. 1996; Franks et al. 1998; Strelcheck et al. 2004; Parr et al. 2018). For example, studies from the GOM concluded that otoliths were illegible and that spines were the best structure for aging Atlantic Tripletail (Franks et al. 1998; Strelcheck et al. 2004), whereas a study from southeastern U.S. Atlantic waters concluded that otoliths and spines were equally suitable for aging (Parr et al. 2018). Additionally, the most recent age study from the GOM (Strelcheck et al. 2004) used samples collected 20 years ago and consequently may not capture the dynamics of the current recreational fishery. Moreover, growth parameters and mortality estimates are undocumented for GOM Atlantic Tripletail, and sex-specific growth parameters are nonexistent for the species. Therefore, the goals of our study were to (1) evaluate the use of otoliths and first dorsal spines as aging structures; (2) model combined and sex-specific growth; and (3) estimate mortality rates for north-central GOM Atlantic Tripletail.

METHODS

Sampling.—Atlantic Tripletail were sampled from recreational harvest on Dauphin Island, Alabama, during May–September in 2012–2019 (except 2013). Specifically, Atlantic Tripletail data and samples were collected during annual Roy Martin Young Anglers Tournaments and Alabama Deep Sea Fishing Rodeos as well as from carcasses donated by local charter captains and recreational anglers. All fish were caught via hook and line in Mississippi or Alabama waters (primarily in Mobile Bay or Mississippi Sound; Figure 1) and were landed in Alabama. Exact catch locations (GPS coordinates) were undocumented for most fish. This sampling generally yielded legal-size Atlantic Tripletail. To augment the size distribution available for age and growth analyses, a small number of sublegal-size Atlantic Tripletail was collected via hook and line from inshore waters near Dauphin Island

and offshore waters south of Orange Beach, Alabama (Figure 1), during July–September 2019. Additionally, in October 2019, the fourth-largest Atlantic Tripletail on record worldwide (17.8 kg; International Game Fish Association) was landed by recreational angler J. Jorgensen off Venice, Louisiana (Figure 1). Fortunately, the angler kept the fish for preservation purposes and agreed to provide its length, weight, sex, and sagittal otoliths for use in this study. This particular specimen will henceforth be referred to as “Jorgensen’s fish.”

The TL of each fish was measured to the nearest millimeter. Weight was recorded to the nearest kilogram for fish that were sampled prior to being filleted. Both sagittal otoliths were extracted from each fish for aging purposes. Beginning in 2014, the first dorsal spine was also extracted from each fish (except Jorgensen’s fish) based on the methods of Franks et al. (1998). Pairs of otoliths were rinsed, dried, and placed into 1.5-mL centrifuge tubes for storage. Spines were placed directly into 1.5-mL centrifuge tubes for storage. All fish were sexed macroscopically. Two-sample Kolmogorov–Smirnov tests were used to examine differences in length and weight distributions between sexes ($\alpha = 0.05$). Length–weight regressions were used to model the relationship between TL and weight, both overall and by sex, for Atlantic Tripletail (Ogle et al. 2018). The length–weight regressions were generated in R (R Core Team 2018) using the add-on package FSA (Ogle et al. 2018).

Otolith and spine processing.—The left sagittal otolith from each individual was embedded in epoxy (100 parts EpoThin 2 Resin to 45 parts EpoThin 2 Hardener by weight; Buehler, Lake Bluff, Illinois) and allowed to cure for at least 24 h. If the left otolith was missing or broken through the core, the right otolith was used. Each embedded otolith was attached to a slide with Crystalbond (Aremco Products, Valley Cottage, New York) and sectioned using an Isomet low-speed saw (Buehler). According to the Gulf States Marine Fisheries Commission, a

TABLE 1. Summary of Atlantic Tripletail age and growth studies from the southeastern USA and Gulf of Mexico (growth parameters are reported in Table 3; NC = North Carolina; FL = Florida; MS = Mississippi; AL = Alabama; GA = Georgia; F = female; M = male).

Study attribute	Merriner and Foster (1974)	Armstrong et al. (1996)	Franks et al. (1998)	Strelcheck et al. (2004)	Parr et al. (2018)	This study
Study region	NC	FL east coast	MS	AL	GA	MS, AL
<i>N</i>	14	260	58	119	243	230
Sex ratio (F:M)	4:10	126:120	24:26	61:49	105:126	131:88
Primary aging structure(s)	Scales	Sagittal otoliths	First dorsal spines	First dorsal spines	Sagittal otoliths, first dorsal spines	Sagittal otoliths, first dorsal spines
TL range (mm)	190–706	307–805	116–725	293–763	Not specified	212–940
Age range (all)	0–3+	0–7	0–4	0.87–4.09	1–5	0.07–5.27
Maximum age (F)	2+	7	4	4.09	5	5.27
Maximum age (M)	3+	6	4	3.15	4	4.06

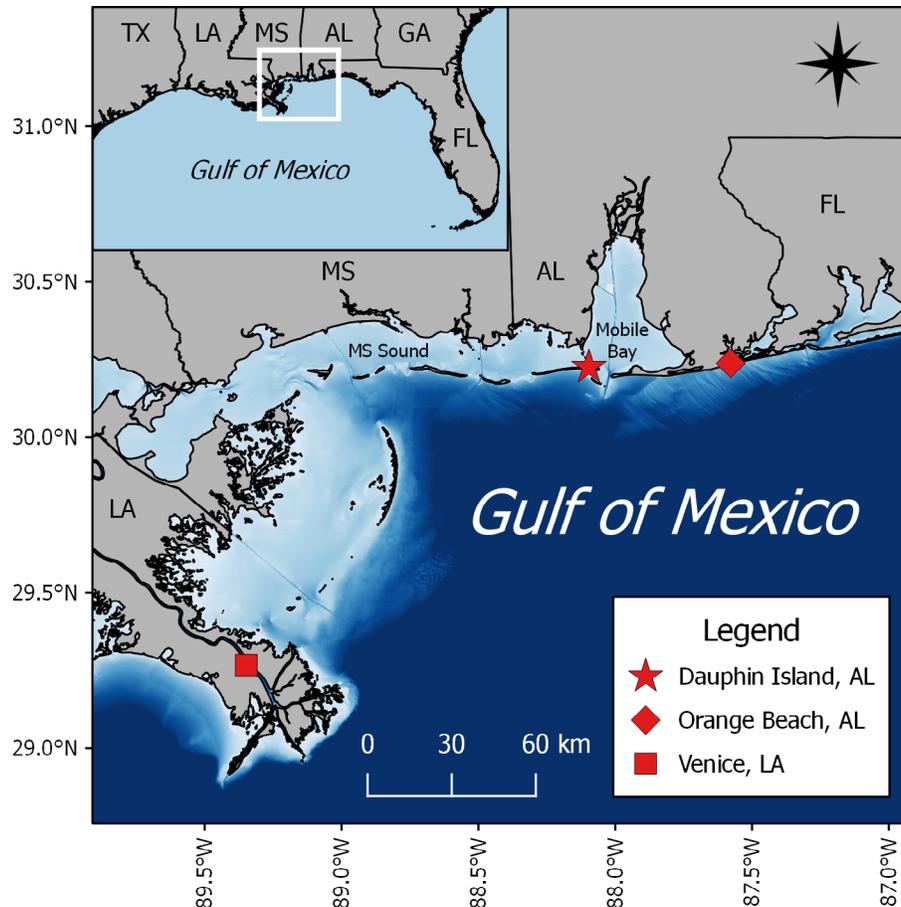


FIGURE 1. Map of the present study's sampling region in the Gulf of Mexico (TX = Texas; LA = Louisiana; MS = Mississippi; AL = Alabama; GA = Georgia; FL = Florida). The map was generated using Quantum GIS (Quantum GIS Development Team 2019).

thickness of 0.5 mm is optimal for interpreting opaque zones in the otoliths of many GOM fishes (VanderKooy 2009). Therefore, three consecutive, 0.5-mm transverse sections were cut simultaneously with four 10-cm, diamond-coated blades (Norton Saint-Gobain, Worcester, Massachusetts). The sections were affixed to a slide using Cytoseal 60 mounting medium (Thermo Scientific, Waltham, Massachusetts) and allowed to air-dry for at least 24 h. Each spine was placed in boiling water for 1 min to loosen tissue around the spine and then was brushed with a toothbrush to remove the tissue. The spine was then attached to an index card with hot glue and sectioned using the same blades and low-speed saw. Based on Franks et al. (1998), a thickness of 0.25 mm is optimal for interpreting translucent zones in first dorsal spines from Atlantic Tripletail. Therefore, three consecutive, 0.25-mm transverse sections were cut simultaneously beginning at the condyle base. The sections were affixed to a slide using Cytoseal 60 and allowed to air-dry for at least 24 h.

Aging.—Otolith and spine sections were aged using an Olympus SZX16 stereomicroscope (Olympus Corporation,

Tokyo) with transmitted light (brightfield illumination). The best section from each otolith and the best section from each spine were aged by two readers. Aging was conducted independently (without consulting the other reader) and blindly (without knowledge of fish capture date, fish size, or the age already assigned to each fish's other structure). For measurement purposes, a photograph of each otolith and spine section was generated at 16 \times and 20 \times magnification, respectively, using an Excelis 16 MP microscopy camera with CaptaVision version 5.1 (Accu-Scope and UNITRON, Commack, New York). Given their size, the otolith sections from Jorgensen's fish were photographed at 12.5 \times magnification. The distance along the sulcus from the core to the first opaque zone was measured in all otoliths; for age-0 fish, the distance from the core to the edge of the otolith was measured instead. Photographs were analyzed using Image-Pro 10 (Media Cybernetics, Rockville, Maryland).

The Gulf States Marine Fisheries Commission does not currently provide aging protocols for Atlantic Tripletail (VanderKooy 2009); therefore, aging protocols were established cooperatively by the readers prior to aging.

Although age has not been validated in Atlantic Tripletail, the number of opaque zones (in otoliths) or translucent zones (in spines) was assumed to represent the age of the fish in years. General aging guidelines followed VanderKooy (2009); details are as follows. The best otolith section was defined as the section that was cut closest to the otolith core and at the most perpendicular angle. The number of thin opaque zones was counted along the ventral edge of the sulcal groove. Margin codes (1–4) were assigned to otolith margins according to VanderKooy (2009). A code of 1 was assigned when an opaque zone was present on the edge; a code of 2 indicated that a translucent zone was forming to one-third complete on the edge; a code of 3 was assigned when the translucent zone was one-third to two-thirds complete on the edge; and a code of 4 indicated that the translucent zone was two-thirds to fully complete on the edge. Age-class was then determined following protocols for other species that deposit opaque zones during early spring (VanderKooy 2009). Specifically, age-class was equal to the number of opaque zones, except when a fish was collected between January 1 and June 30 and the margin code was 3 or 4, in which case the age-class was equal to the number of opaque zones plus 1. Otoliths that were deemed unreadable (due to a lack of discernable opaque and translucent zones) were assigned a code of “U” and omitted from further analyses.

The best spine section was defined as the section with the clearest succession of opaque and translucent zones and the lowest amount of core erosion (significant core erosion was defined by the readers as erosion extending out to or beyond the first counted translucent zone). The number of thin translucent zones present around the entire circumference of the section was counted and recorded as the age-class (years) of the fish. If a spine section contained doublets or multiples, these were each counted as one translucent zone (Franks et al. 1998; Parr et al. 2018). If a spine section contained a translucent zone, doublet, or multiple that was located very near to the core of the section and did not completely encircle the core, it was skipped (not counted). For each spine, readers documented whether the first translucent zone, doublet, or multiple was skipped as well as whether significant core erosion was present. Spines deemed unreadable (due to a lack of discernable opaque and translucent zones or excessive core erosion) were assigned a code of “U” and omitted from further analyses.

Average percent error (APE) was calculated to evaluate between-reader precision for otoliths and spines (Beamish and Fournier 1981; Campana 2001). If a given structure was assigned different ages, the readers consulted with each other to reach an agreement. Once every structure was assigned one agreed-upon final age (or designated as

unreadable), APE was calculated using the otolith final age-classes and spine final age-classes to estimate precision between otolith- and spine-based ages. Fractional age (years) was then calculated using a July 1 birthdate, a date that was defined by Strelcheck et al. (2004) in accordance with Brown-Peterson and Franks (2001). More specifically, the birthdate was subtracted from the date of capture, the resulting number was divided by the number of days in the year of capture, and then that number was added to the age-class. Two-sample Kolmogorov–Smirnov tests were used to examine differences in otolith- and spine-based fractional age distributions between sexes ($\alpha = 0.05$).

Modeling growth.—To model growth of all specimens, the von Bertalanffy growth function (VBGF; von Bertalanffy 1938) was fitted to all otolith-based fractional age data and then to all spine-based fractional age data:

$$l_t = L_\infty [1 - e^{-k(t-t_0)}], \quad (1)$$

where l_t is predicted TL (mm), L_∞ is mean asymptotic length (mm), k is the Brody growth rate coefficient (year^{-1}), t is time (i.e., age; years), and t_0 is the hypothetical age (years) at which length equals zero. Female, male, and unknown-sex observations were included; the fish of unknown sex consisted primarily of age-0 individuals (young of the year), which were critical for anchoring the growth curve.

Sex-specific growth was also modeled using the VBGF for both otolith- and spine-based fractional age data. Eight candidate versions of the VBGF were fitted to the sex-specific data: a general version, which allowed all three parameters (L_∞ , k , and t_0) to vary between sexes; three versions that allowed two of the three parameters to vary between sexes; three versions that allowed only one parameter to vary between sexes; and a common version, which held all three parameters constant between sexes (Ogle 2016; Nelson et al. 2018; Jefferson et al. 2019). Akaike’s information criterion was used to rank the model versions based on fit and to identify the best-fitting version (Akaike 1998; Katsanevakis and Maravelias 2008; Ogle 2016). All growth parameters were modeled in R (R Core Team 2018) using the add-on packages FSA (Ogle et al. 2018) and nlstools (Baty et al. 2015).

Estimating mortality.—All mortality estimates were generated using otolith-based age data to enable comparisons with other otolith-based mortality estimates. The otolith-based age-class data were used in an age-based catch curve (Chapman and Robson 1960) to estimate Z , total annual survival rate (S), and total annual mortality rate (A). A weighted regression model (Maceina and Bettoli 1998; Miranda and Bettoli 2007) was also fitted to the otolith-based age-class data for comparison purposes. Although some age-0 fish were captured via hook and line, only fully recruited ages (age 1 and older) were used in these analyses.

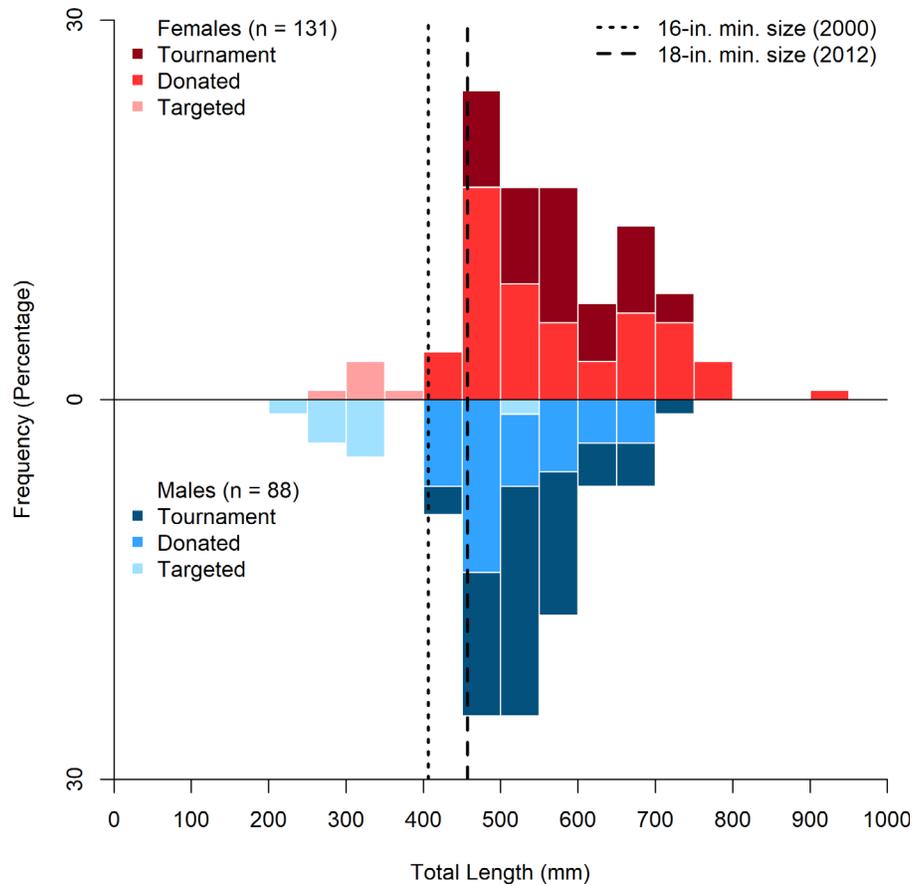


FIGURE 2. Length frequency distributions, by sampling method, for female and male Atlantic Tripletail sampled for age and growth analyses. Vertical lines indicate minimum size limits implemented in Alabama in 2000 (dotted line; 407 mm [16 in]) and 2012 (dashed line; 458 mm [18 in]).

Instantaneous natural mortality rate (M) was estimated using three empirical methods (Then et al. 2015; Ogle 2016). The first method was Hoenig's (1983) log-transformed linear regression for fishes (Hoenig_{fishes}):

$$M = e^{1.46 - 1.01 \cdot \log_e(t_{\max})}, \quad (2)$$

where t_{\max} is the maximum fractional age of the animal in years. The second method was Hoenig's nonlinear least-squares estimator (Hoenig_{nls}; Then et al. 2015):

$$M = 4.899 t_{\max}^{-0.916}, \quad (3)$$

where t_{\max} is maximum fractional age as defined above. Finally, Pauly's (1980) nonlinear least-squares estimator was used, omitting temperature (Pauly_{nls-T}; Then et al. 2015):

$$M = 4.118 k^{0.73} L_{\infty}^{-0.333}, \quad (4)$$

where k and L_{∞} are the parameters from the otolith-based VBGF. A range of values representing instantaneous

fishing mortality rate (F) was calculated from estimates of Z and M ($F = Z - M$; Ogle 2016). Many of the Atlantic Tripletail sampled during the present study were collected from fishing tournaments. Since these fish could have been biased toward larger sizes and ages (thus artificially decreasing the Z - and F -estimates), differences in average length and fractional age were examined between tournament and donated fish. All mortality analyses were conducted in R (R Core Team 2018) using FSA (Ogle et al. 2018).

RESULTS

Morphometrics

In total, 230 Atlantic Tripletail were sampled during the study. Of those, 24 were sampled during the Roy Martin Young Anglers Tournament, 78 were sampled during the Alabama Deep Sea Fishing Rodeo, and 112 were donated by local charter captains and recreational anglers. Finally, 15 sublegal-size Atlantic Tripletail, along with Jorgensen's fish, were collected during 2019

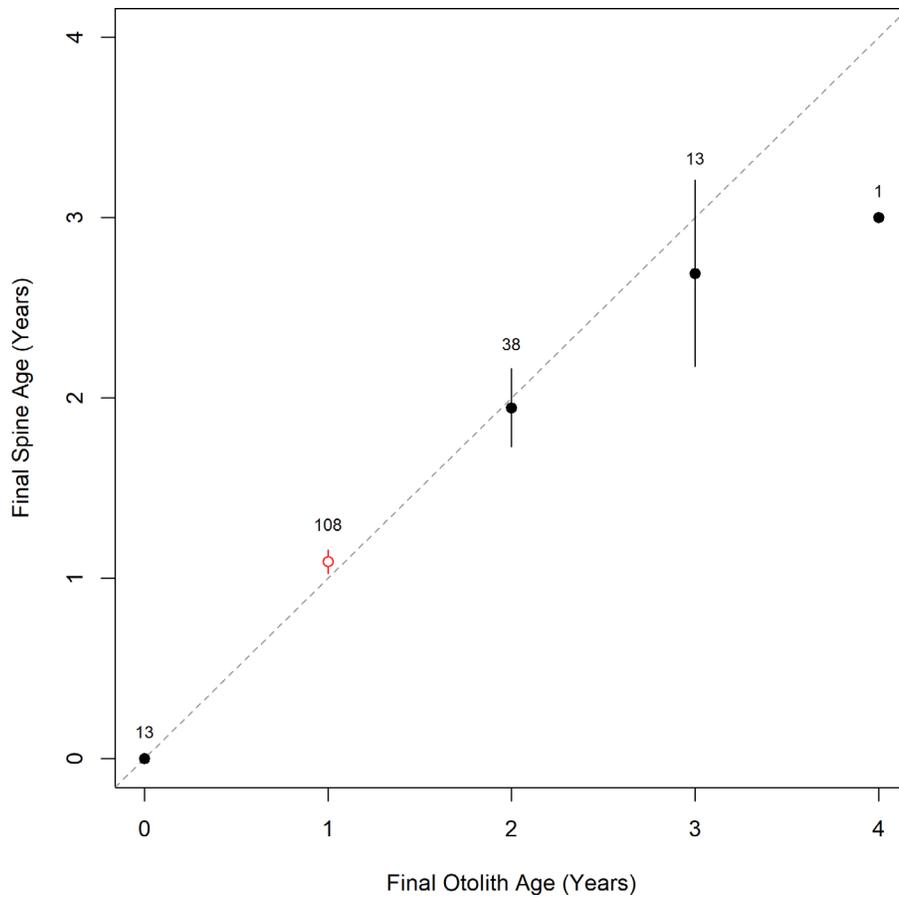


FIGURE 3. Age bias plot of final spine age-classes versus final otolith age-classes for Atlantic Tripletail sampled in the Gulf of Mexico. Open, red points with red confidence intervals represent mean final spine age estimates that differ significantly from the corresponding mean final otolith age estimates. Sample sizes, as per the number of otolith-based ages, are indicated for each age.

to broaden the size distribution available for analyses. Of the 230 sampled fish, 131 were identified as female, 88 were identified as male, and 11 were classified as unknown sex. The female-to-male ratio was 1.49:1.00 and significantly differed from a 1:1 ratio ($\chi^2 = 8.44$, $df = 1$, $P < 0.01$). Total length ranged from 212 to 940 mm (Figure 2). Weight was recorded for 158 Atlantic Tripletail and ranged from 0.34 to 17.8 kg. Kolmogorov-Smirnov tests revealed that females were significantly longer ($D = 0.21$, $P = 0.02$) and heavier ($D = 0.30$, $P < 0.01$) than males. The overall length-weight regression indicated a strong relationship between TL and weight:

$$\log_{10}(\text{weight}) = -19.80 + 3.36 \cdot \log_{10}(\text{TL}) (R^2 = 0.96). \quad (5)$$

According to the sex-specific length-weight regression, neither the slope ($P = 0.40$) nor the intercept ($P = 0.40$) of the sex-specific parameters was significant.

Age

Overall, 229 pairs of otoliths and 202 first dorsal spines were collected for aging purposes. However, 19 otoliths (8.3%) and 14 spines (6.9%) were deemed unreadable and were omitted from further analyses. The between-reader percent agreement estimates for otoliths and spines were 95.0% and 82.9%, respectively. The between-reader APE estimates for otoliths and spines were 3.0% and 6.5%, respectively. The percent agreement between otolith and spine final ages was 79.8%, and the APE was 6.1% (Figure 3). After consulting with each other, reader 1 and reader 2 were able to agree on final ages for all readable otoliths and spines. Otolith ages ranged from 0.07 to 5.27 years, while spine ages ranged from 0.07 to 4.05 years (Figure 4). Jorgensen's fish represented the only age-5 specimen in this study. The median and mean ages were 1.0 and 1.4 years, respectively, for otoliths and spines. The maximum age of females in the sample was 5.27 and 4.05 years according to otolith- and spine-based data,

respectively. The maximum age of males in the sample was 4.06 and 3.20 years according to otolith- and spine-based data, respectively. Kolmogorov–Smirnov tests showed that female and male fractional age distributions differed significantly for both otolith-based data ($D=0.22$, $P=0.02$) and spine-based data ($D=0.25$, $P<0.01$). Otolith margin codes ranged from 1 to 3, with the vast majority ($N=179$; 97.3%) of otoliths that were assigned a margin code ($N=184$) receiving a 1 or 2. Average otolith margin code was lowest in May, increased from May to July, and remained approximately the same from July to September (Figure 5). No fish collected between January 1 and June 30 were assigned a margin code of 3 or 4. For all otoliths assigned an age of at least 1 year ($N=196$), the average measurement from the core to the first opaque zone was 0.82 mm. Core-to-margin measurements for the otoliths from age-0 fish ranged from 0.35 to 0.63 mm. Only five otoliths had a core-to-first-opaque-zone measurement less than 0.63 mm. Readers noted significant core erosion in 16.1% of spines. Readers skipped the first translucent zone in 67.4% of spines, and there was no discernable pattern for skipping by spine age-class (Table 2).

Growth

The VBGF equations for otolith- and spine-based age data (including females, males, and unknown sex), respectively, were

$$l_{t(O)} = 762.42 \left\{ 1 - e^{-0.69[t - (-0.58)]} \right\} \quad (6)$$

and

$$l_{t(S)} = 718.83 \left\{ 1 - e^{-0.79[t - (-0.56)]} \right\} \quad (7)$$

(Figure 6). For the sex-specific otolith data, the model version that allowed L_{∞} to vary by sex (fit2L) provided the best fit to the data (Table 3; Figure 7A). Based on fit2L, the VBGF equations for female and male otolith data, respectively, were

$$l_{t(F,O)} = 766.97 \left\{ 1 - e^{-0.71[t - (-0.59)]} \right\} \quad (8)$$

and

$$l_{t(M,O)} = 726.44 \left\{ 1 - e^{-0.71[t - (-0.59)]} \right\}. \quad (9)$$

Similarly, for the sex-specific spine data, the model version that allowed L_{∞} to vary by sex (fit2L) provided the best fit to the data (Table 3; Figure 7B). Based on fit2L, the VBGF equations for female and male spine data, respectively, were

$$l_{t(F,S)} = 724.32 \left\{ 1 - e^{-0.81[t - (-0.58)]} \right\} \quad (10)$$

and

$$l_{t(M,S)} = 691.43 \left\{ 1 - e^{-0.81[t - (-0.58)]} \right\}. \quad (11)$$

All VBGF parameters from the present study, as well as from Parr et al. (2018) for comparison, are listed in Table 4.

Mortality

Chapman–Robson estimates of Z , S , and A were 1.15, 31.34%, and 68.66%, respectively (Table 5). The weighted regression produced similar results: Z was 1.20, S was 30.15%, and A was 69.85%. Estimates of M obtained from the three estimators were as follows: 0.80 from $Hoenig_{fishes}$, 0.97 from $Hoenig_{nls}$, and 0.75 from $Pauly_{nls-T}$. Based on estimates of Z and M from this study, the F of Atlantic Tripletail in the north-central GOM is approximately 0.18–0.45. Tournament fish were, on average, just 15.5 mm larger and 0.03 years older than donated fish (excluding Jorgensen’s fish), indicating a lack of bias from the tournament samples with respect to the mortality estimates (Figure 2).

DISCUSSION

Atlantic Tripletail in the GOM experience rapid growth and appear to be relatively short lived. Future studies examining growth in this species should use sagittal otoliths for several reasons. First, our otolith-based ages produced higher between-reader agreement and lower between-reader APE compared to our spine-based ages. Second, the otoliths were consistently shaped and in turn yielded consistently shaped sections (Figure 4); this facilitated identification of opaque zones and enabled measurement-based analysis. Third, the otoliths (as is typical) lacked evidence of core erosion or resorption, meaning that early opaque zones were not obscured or lost (VanderKooy 2009). Lastly and importantly, the first opaque zone was easier to locate in otoliths and was always included in the assigned age according to basic otolith aging protocol (VanderKooy 2009). Unfortunately, an inherent drawback to using otoliths for aging is that fish must be sacrificed to enable otolith extraction, while spines may provide a nonlethal aging method (although the postrelease survival of fish with excised spines is unknown; Parr et al. 2018). Another disadvantage associated with otoliths is the presence of heavy, dark hash marks in the sections (Figure 4I). In addition, the otoliths sometimes lacked alternating opaque and translucent zones or had excessive numbers of opaque and translucent

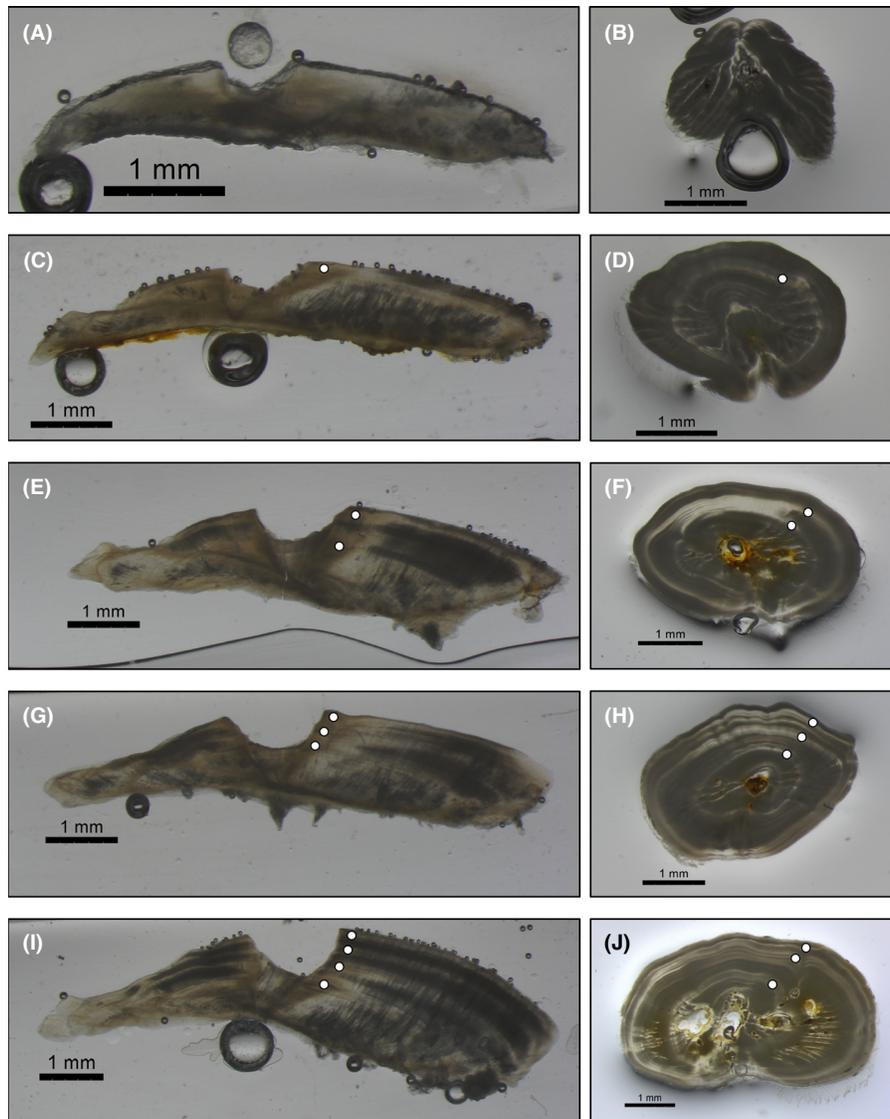


FIGURE 4. Cross-sections of otoliths (left panels) and spines (right panels) for individual Atlantic Tripletail aged as (A–B) 0 years; (C–D) 1 year; (E–F) 2 years; and (G–H) 3 years. Panels (I) and (J) represent an individual assigned an age of 4 years based on the otolith but 3 years based on the spine. Substantial core erosion in the spine section likely resulted in underestimation of age. The scale bar on each image represents 1 mm.

zones in close proximity; both of these conditions resulted in a designation of “unreadable.” Interestingly, Franks et al. (1998) and Strelcheck et al. (2004) reported that otolith sections from Mississippi and Alabama Atlantic Tripletail were indecipherable, whereas Parr et al. (2018) found the opposite among Georgia Atlantic Tripletail. Parr et al. (2018) attributed these contrasting conclusions to geographic and climatic differences between the Atlantic Ocean and GOM, but we hypothesize that the contrasting conclusions may be due to differences in microscopy. For example, Strelcheck et al. (2004) used a compound microscope with reflected light to view otolith sections, whereas we, like Parr et al. (2018), used

stereomicroscopes with transmitted light. Furthermore, potential differences in available illumination options (e.g., brightfield, oblique, and darkfield) among studies, along with increases in the quality of microscopy cameras and image analysis software since the late 1990s, may explain our success and that of Parr et al. (2018) in aging Atlantic Tripletail otoliths.

First dorsal spines of Atlantic Tripletail appear to be inferior aging structures for several reasons. First, spine-based ages generated lower agreement and higher APE compared to otolith-based ages. Second, the translucent zones within spine sections were often inconsistent within the section (e.g., appearing wide and bright in one area of

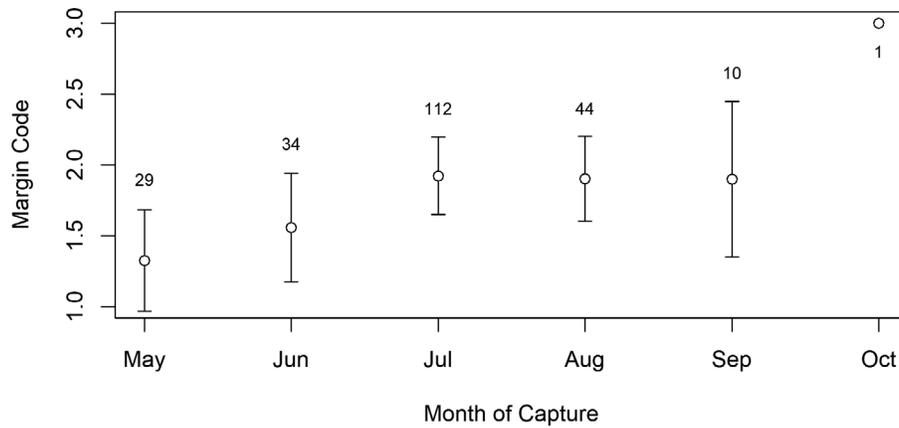


FIGURE 5. Mean margin code (\pm SD) assigned to Atlantic Tripletail otoliths by month of capture in the Gulf of Mexico. Sample sizes are indicated for each month. Margin codes are defined in Methods.

TABLE 2. Percentage of Atlantic Tripletail spines, by age, for which readers skipped the first translucent zone, doublet, or multiple based on its incompleteness and proximity to the spine core.

Spine age (years)	Number of spines examined	% Skipped first translucent zone
0	14	21.4
1	119	74.8
2	39	53.9
3	15	86.7
4	2	100.0
All	189	67.4

the section yet thin and muted in another; Figure 4), which hindered identification and enumeration of the translucent zones by the readers. Third, although the spines were unaffected by hash marks, approximately one-sixth of the spines exhibited significant core erosion (Figure 4J). A common issue in spine aging studies, erosion signifies that early translucent zones may have been resorbed into the core, resulting in loss of those zones and potential underestimation of age (Casselman 1983; Franks et al. 1998; Parr et al. 2018). Fourth, the spines (and, consequently, the spine sections) were inconsistent in shape, which made measurement-based aging guidelines impractical. Fifth and lastly, the most problematic issue with spines is the lack of an established protocol for including versus skipping the first translucent zone (or doublet or multiple, as the case may be) in the age assignment. Three previous studies have aged Atlantic Tripletail based on the examination of first dorsal spines. Franks et al. (1998) always skipped the first translucent zone (i.e., never counted it toward the assigned age), whereas Strelcheck et al. (2004) and Parr et al. (2018) included it. After completion of their study, Parr et al. (2018) suggested that the

criteria of Franks et al. (1998) should be followed only for age-2 and younger fish; in other words, the first multiple should not be skipped in age-3 or older fish. Unfortunately, this approach illustrates a circular logic. When the goal is to assign an age to a fish of unknown age, it is impossible for the reader to choose from different protocols developed for fish of different ages because age is, in fact, unknown. Due to the lack of an established protocol and the inconsistency in the presence or absence of a translucent zone close to the core, we decided to simply skip the first zone if it appeared too close to or did not completely encircle the spine's core. In this way, our decision to skip or count the first zone was unrelated to the age of the fish. For each spine, we noted whether we had or had not skipped the first zone in hopes that we could provide guidance for future studies. Our results indicated that we skipped the first zone in 67.4% of spines (Table 2). To test the precision of our spine aging method, we compared otolith-based age-classes to spine-based age-classes from our method and the methods of Franks et al. (1998) and Strelcheck et al. (2004). Results indicated that our spine aging method produced the highest percent agreement between otolith- and spine-based ages (79.8% versus 58.4% for Franks et al. 1998 and 32.4% for Strelcheck et al. [2004]). Even though our method was more precise, since we neither skipped all of the first zones nor counted all of the first zones, and the irregularity of spine sections made core-to-first-translucent-zone measurements impractical, we discourage the use of first dorsal spines for aging Atlantic Tripletail unless nonlethal aging methods are required.

The inclusion of Jorgensen's fish in the present study represents an invaluable addition to our knowledge of Atlantic Tripletail longevity. At 17.8 kg, Jorgensen's fish weighed only 1.4 kg less than the world-record Atlantic Tripletail, which was landed in Zululand, South Africa, in

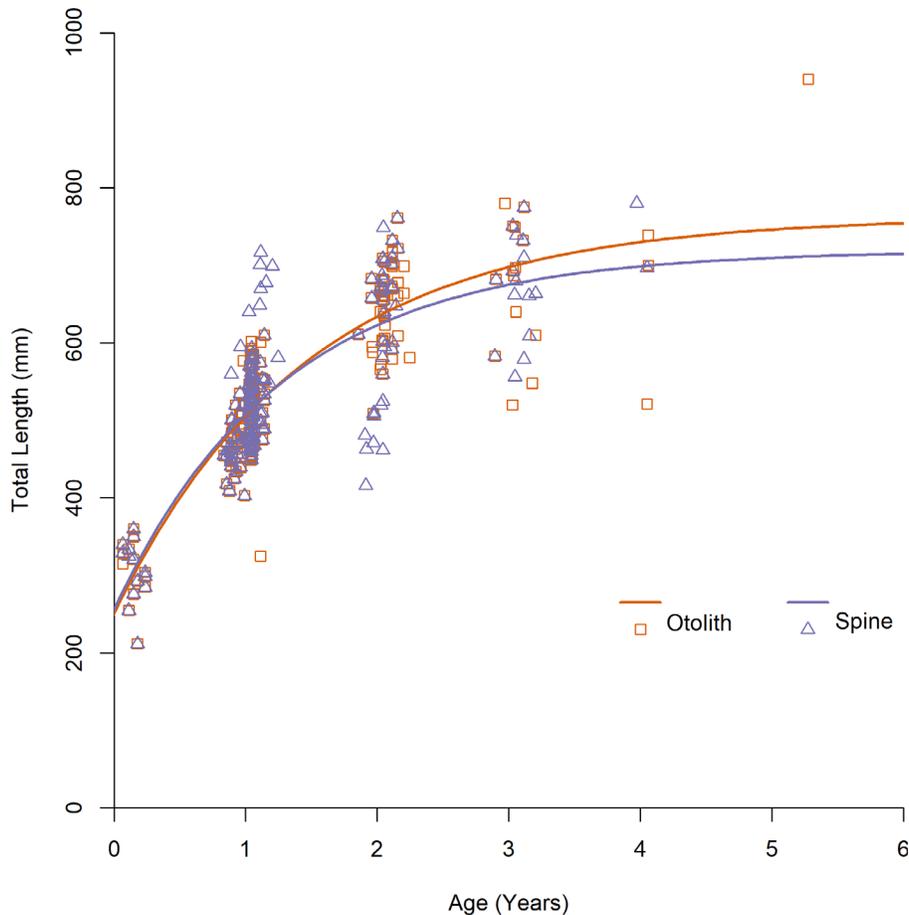


FIGURE 6. von Bertalanffy growth curves for otolith- and spine-based fractional ages of Atlantic Tripletail sampled in the Gulf of Mexico.

1989. As such, Jorgensen's fish is the largest Atlantic Tripletail ever aged (by over 100 mm) and the oldest Atlantic Tripletail (5.27 years) aged from the GOM. Excluding Jorgensen's fish, the maximum age among our other samples (otoliths and spines) was 4.06 years. Previous studies from Mississippi (Franks et al. 1998) and Alabama (Strelcheck et al. 2004) found maximum ages of 4.0 and 4.09 years, respectively. Parr et al. (2018) reported a maximum age of 5 years for a single Atlantic Tripletail from Georgia. Only one study has described a maximum age of 6 years or older: Armstrong et al. (1996) assigned an age of 6 years to three Atlantic Tripletail and 7 years to one Atlantic Tripletail, all of which were collected from Florida's east coast and aged using otoliths. Armstrong et al. (1996) assigned these ages to specimens measuring no greater than 805 mm. By contrast, Jorgensen's fish measured 940 mm and was assigned an age of just 5.27 years. Our ability to assess whether these discrepancies represent true differences in growth or simply differences in aging protocols is limited. Given the important management implications of assigning a greater maximum age to Atlantic Tripletail, we recommend additional sampling

and aging of specimens collected from the east coast of Florida.

The growth parameters estimated from our study are different from those reported by the only other study to model Atlantic Tripletail growth (Table 4; Figure 8; Parr et al. 2018). Parr et al. (2018) fit the VBGF to otolith- and spine-based age data for fish sampled in Georgia. Compared to our results, Parr et al. (2018) reported larger L_{∞} estimates for otolith- and spine-based ages by about 68 and 96 mm, respectively (Table 4). This suggests that GOM Atlantic Tripletail may reach a smaller average maximum size than Georgia Atlantic Tripletail. Conversely, our k -estimates are greater than those from Parr et al. (2018) by about 0.27 and 0.33 year^{-1} for otolith- and spine-based ages, respectively, suggesting that GOM Atlantic Tripletail may reach their maximum size faster than Georgia Atlantic Tripletail. Alternatively, the difference in k -estimates may be due to the lack of age-0 fish sampled by Parr et al. (2018). The inclusion of age-0 fish in the present study likely helped to produce more accurate k -estimates by anchoring the growth curves; furthermore, if smaller fish (<200 mm) had been included, the k -

TABLE 3. Comparison of all candidate versions of the von Bertalanffy growth function that were fitted to otolith- and spine-based sex-specific Atlantic Tripletail age data. The parameters that were allowed to vary (L_∞ = mean asymptotic length [mm]; k = Brody growth rate coefficient [year^{-1}]; t_0 = hypothetical age at which length equals zero [years]), number of model parameters (K), log-likelihood, Akaike's information criterion (AIC), AIC difference (ΔAIC), and AIC weight are given for each model version.

Aging structure	Model version	Parameter(s) allowed to vary	K	Log-likelihood	AIC	ΔAIC	AIC weight
Otolith	fit2L	L_∞	5	-1,075.1	2,160.2	0.0	0.31
	fit2L2K	L_∞, k	6	-1,074.3	2,160.6	0.3	0.26
	fitGeneralVB	L_∞, k, t_0	7	-1,073.5	2,161.0	0.7	0.21
	fit2L2T	L_∞, t_0	6	-1,074.9	2,161.9	1.6	0.14
	fit2K	k	5	-1,076.9	2,163.8	3.6	0.05
	fit2K2T	k, t_0	6	-1,076.9	2,165.8	5.6	0.02
	fit2T	t_0	5	-1,078.3	2,166.5	6.3	0.01
	fitCommonVB	None	4	-1,082.4	2,172.8	12.5	0.00
Spine	fit2L	L_∞	5	-993.1	1,996.2	0.0	0.32
	fit2K	k	5	-993.8	1,997.7	1.5	0.16
	fit2L2K	L_∞, k	6	-992.9	1,997.7	1.5	0.15
	fit2L2T	L_∞, t_0	6	-993.1	1,998.1	1.9	0.12
	fit2T	t_0	5	-994.4	1,998.9	2.7	0.09
	fitGeneralVB	L_∞, k, t_0	7	-992.6	1,999.2	3.0	0.07
	fit2K2T	k, t_0	6	-993.8	1,999.7	3.5	0.06
	fitCommonVB	None	4	-996.4	2,000.7	4.5	0.03

estimates might have been even higher. Notably, a truncated size distribution could have impacted the terminal portions of the growth curves presented by Parr et al. (2018). Specifically, none of the fish collected by Parr et al. (2018) was larger than the otolith-based L_∞ estimate and only one fish was larger than the spine-based L_∞ estimate. Consequently, the VBGFs reported by Parr et al. (2018) failed to approach asymptotes until ages greater than the reported maximum age of 5 years. The models presented in the Parr et al. (2018) study align more closely with the mean size at age reported by Franks et al. (1998) and Strelcheck et al. (2004) for ages 2 and 3 than do ours (Figure 8). However, the Parr et al. (2018) models underestimate the sizes of fish less than age 2 and overestimate the sizes of fish older than age 3. Although our otolith curves overestimate the size at age of Atlantic Tripletail compared to Franks et al. (1998) and Strelcheck et al. (2004), this is probably because those size-at-age estimates were based on spine ages, which we found produced greater variability in size at age among young fish (specifically, ages 1 and 2) compared to otoliths (Figure 6).

Our study is the first to model Atlantic Tripletail growth in a sex-specific framework. The results of the otolith- and spine-based sex-specific modeling procedures suggest sexual dimorphism, with females growing to larger maximum sizes than males (Table 4). These results agree with our Kolmogorov–Smirnov tests for mean size at age between females and males. Other studies have reported a variety of conclusions. Based on length–weight regression

and mean size-at-age analysis, Armstrong et al. (1996) concluded that females were significantly heavier at length and slightly larger at age compared to males. Strelcheck et al. (2004) also reported that females were significantly longer and heavier than males. The results of Franks et al. (1998) disagreed in that weight at length did not differ between males and females. Lastly, Parr et al. (2018) found that females were significantly heavier than—but not longer than—males. Sexual dimorphism in Atlantic Tripletail could have implications for stock health if the largest fish harvested are disproportionately female.

Our mortality estimates represent the first reported mortality estimates for GOM Atlantic Tripletail. The only previous mortality estimates were reported for Atlantic Tripletail from the east coast of Florida by Armstrong et al. (1996), who also used the Chapman–Robson method to calculate Z and S . Our Z -estimate was greater than the previous estimate (0.84) and our S -estimate was lower than the previous estimate (43.0%; Table 5). These differences between studies stem from dissimilarities in the age range (0–5 years versus 0–7 years) and the quantity of fish in each age-class. Unfortunately, no prior estimates of Atlantic Tripletail M exist. Armstrong et al. (1996) predicted Atlantic Tripletail M to be 0.3–0.6 based on similar (though unspecified) species, but since the Atlantic Tripletail is one of only two species in the family Lobotidae and has unique biological and ecological characteristics (e.g., seasonal migrations), we question the validity of this prediction. Although our M -estimates

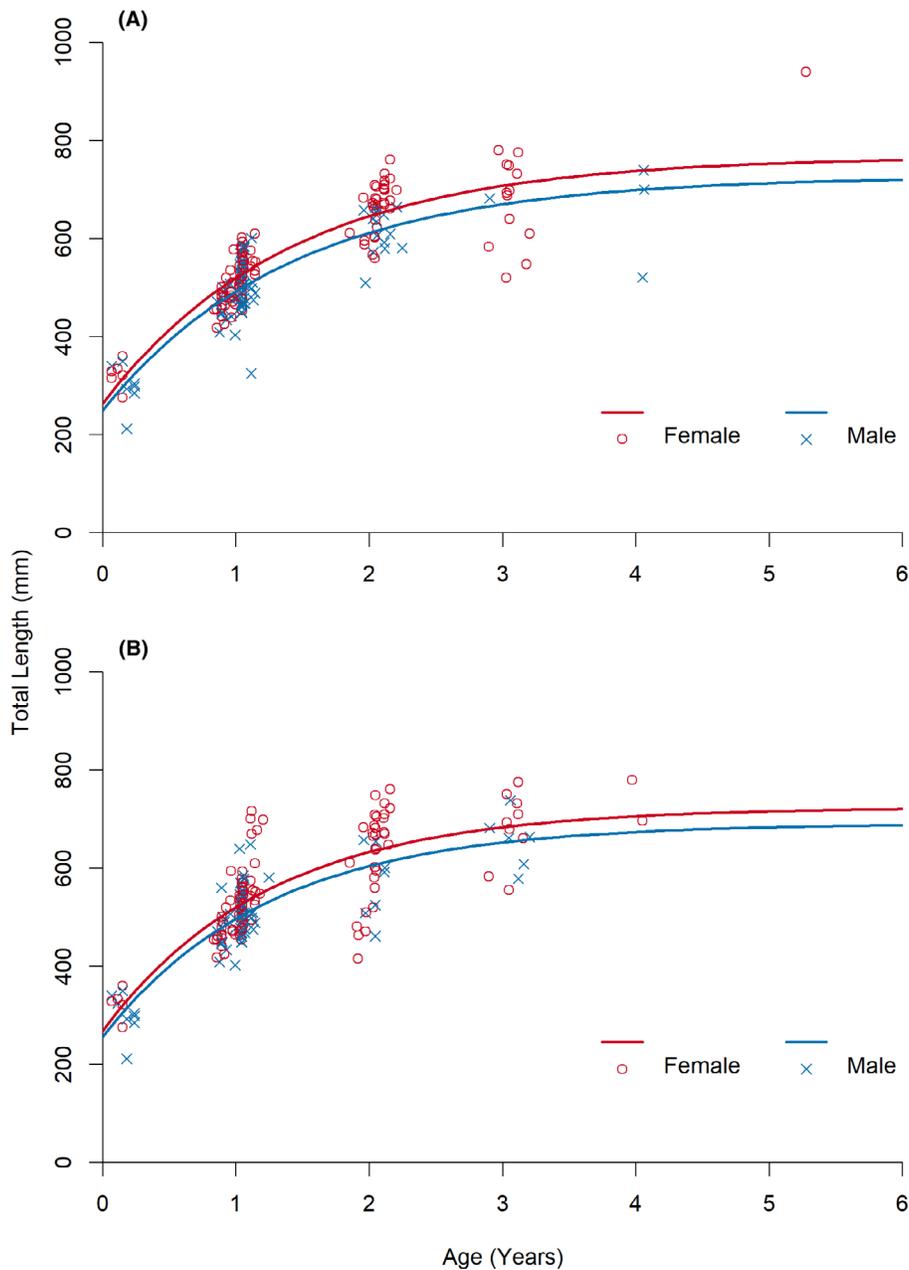


FIGURE 7. Sex-specific von Bertalanffy growth curves for Gulf of Mexico Atlantic Tripletail based on (A) otolith-based fractional ages and (B) spine-based fractional ages.

(0.75–0.97) are higher than the estimates of Armstrong et al. (1996), we suggest that ours are more accurate since they were calculated based upon biological parameters specific to Atlantic Tripletail. Our resulting estimates of F (0.18–0.45) overlap with those from Armstrong et al. (1996; 0.24–0.54) and indicate a low level of exploitation, yet the nature of our data set warrants further consideration, particularly with respect to the assumptions of catch curve analysis. The assumption of constant vulnerability was likely met because our

tournament samples did not appear to be biased toward older fish and most of our fish appeared to be fully recruited to the gear by age 1. However, due to an increase in fishing pressure over the course of the study, the assumption of constant mortality was likely not met. Lastly, the assumption of a closed population is difficult to evaluate given the lack of knowledge concerning Atlantic Tripletail migration patterns and spawning activity. Future tagging studies (e.g., telemetry) could provide additional insight into the fulfillment of these assumptions

TABLE 4. All von Bertalanffy growth parameters reported to date for combined (sexes pooled, including unknown sex) and sex-specific Atlantic Tripletail age data (L_∞ = mean asymptotic length [mm]; k = Brody growth rate coefficient [year^{-1}]; t_0 = hypothetical age at which length equals zero [years]).

Data set	Structure	Parr et al. (2018)			Present study		
		L_∞	k	t_0	L_∞ (SE)	k (SE)	t_0 (SE)
Combined	Otolith	830	0.42	-0.63	762.42 (23.14)	0.69 (0.08)	-0.58 (0.09)
	Spine	815	0.46	-0.54	718.83 (24.94)	0.79 (0.11)	-0.56 (0.11)
Female	Otolith				766.97 (22.41)	0.71 (0.08)	-0.59 (0.10)
	Spine				724.32 (24.60)	0.81 (0.11)	-0.58 (0.12)
Male	Otolith				726.44 (23.25)	0.71 (0.08)	-0.59 (0.10)
	Spine				691.43 (25.94)	0.81 (0.11)	-0.58 (0.12)

TABLE 5. Estimated instantaneous total mortality rate (Z), total annual survival rate (S), total annual mortality rate (A), and instantaneous natural mortality rate (M) listed by estimation method for Atlantic Tripletail. Three methods were used to estimate M (Hoenig_{fishes} = Hoenig's [1983] log-transformed linear regression for fishes; Hoenig_{nls} = Hoenig's nonlinear least-squares estimator; Pauly_{nls-T} = Pauly's [1980] nonlinear least-squares estimator, omitting temperature).

Metric	Estimation method				
	Chapman–Robson	Weighted regression	Hoenig _{fishes}	Hoenig _{nls}	Pauly _{nls-T}
Z	1.15	1.20			
S (%)	31.34	30.15			
A (%)	68.66	69.85			
M			0.80	0.97	0.75

and could thereby contribute to our understanding of Atlantic Tripletail mortality.

Since all Atlantic Tripletail sampled for this study were collected during May–September, we were unable to verify increment periodicity in otoliths and spines via marginal increment analysis. However, an increase in assigned otolith margin code by month of capture, coupled with a lack of assigned margin codes greater than 2 during the first half of the calendar year, suggests that GOM Atlantic Tripletail likely deposit opaque zones in otoliths during early spring (Figure 5). This is consistent with many other GOM species (e.g., Red Drum *Sciaenops ocellatus*, Spotted Seatrout *Cynoscion nebulosus*, Southern Flounder *Paralichthys lethostigma*, Sheepshead *Archosargus probatocephalus*, and Red Snapper *Lutjanus campechanus*; VanderKooy 2009). Franks et al. (1998) also concluded that translucent zones in Atlantic Tripletail spines were recently deposited among fish collected from May to September, and those authors specifically noted the highest percentage of marginal zones in the spines of fish collected during July. Interestingly, our study indicates that opaque zones in otoliths are deposited just prior to the seasonal (i.e., summertime) occurrence of GOM Atlantic Tripletail in coastal estuarine areas. For GOM Atlantic

Tripletail, warming water temperatures may simultaneously cue migration into coastal areas (Streich et al. 2013) and opaque zone deposition in otoliths.

We assigned an age-class of 0 years to several specimens ($N = 13$ fish for which the corresponding otolith and spine were both assigned an age of 0) ranging from 212 to 360 mm TL and collected during July–September 2019. If we assume that GOM Atlantic Tripletail spawn from June to August (Ditty and Shaw 1994; Brown-Peterson and Franks 2001), then these fish grew to considerable lengths in just 1–3 months. Several observations support our designation of these fish as age 0. First, our otolith margin code analysis (Figure 5) indicates that all fish spawned in 2018 should have deposited their first opaque zone during the spring of 2019. We did not observe any opaque or translucent zones designated as annual growth increments in the fish we classified as age 0, which signifies that they were spawned after spring 2019. Second, our core-to-margin measurements for the otoliths from the 13 age-0 fish ranged from 0.35 to 0.63 mm, whereas only five otoliths from fish assigned an age-class of at least 1 year had a core-to-first-opaque-zone measurement less than 0.63 mm. Clearly, it is atypical for the first opaque zone to be located less than 0.63 mm from the core. Third and most

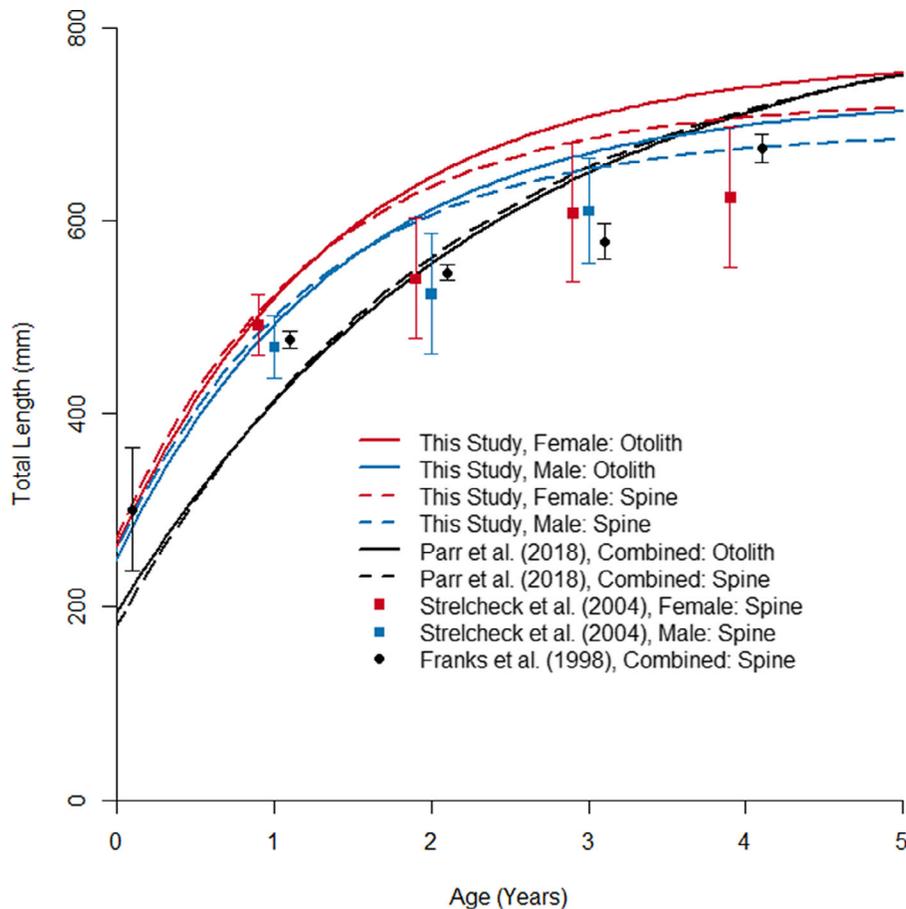


FIGURE 8. Comparison of existing growth models and mean size-at-age estimates (\pm SE) for Atlantic Tripletail to date.

simply, Atlantic Tripletail grow rapidly (Franks et al. 2001). Studies have noted that Atlantic Tripletail can grow up to 500 mm TL (Franks et al. 1998) or even 600 mm TL (Strelcheck et al. 2004) in their first year of life. For example, Franks et al. (1998) assigned an age of 0 years to fish as large as 255 mm TL. Additionally, Armstrong et al. (1996) assigned an age of 0 years to fish of approximately 300–600 mm TL. Like us, these authors noted that the length estimates were high for age-0 fish. We thus conclude that the most reasonable explanation for these observations is the remarkably fast growth of Atlantic Tripletail during their first year of life.

Although previous studies have documented rapid growth during the first year of life for Atlantic Tripletail, a mechanism to explain such a wide range in lengths at age has yet to be proposed. In 1999, Atlantic Tripletail of very small sizes (45–115 mm TL), which were surely age 0, were collected from the north-central GOM on July 30 (Franks et al. 2001). Remarkably, in July, August, and September 2019, we collected much larger Atlantic Tripletail (212–360 mm TL) from the north-central GOM that also appeared to be age 0. If all of these fish are, indeed,

very close in age (all spawned in early summer), perhaps the substantial difference in length at age is due to variation in the quality of the juveniles' *Sargassum* habitat (e.g., higher or lower food availability), the duration of their stay, or whether they even inhabit *Sargassum* at all. Alternatively, the unknown movement and migration patterns of Atlantic Tripletail could impact otolith periodicity in some way. Other potential explanations relate to spawning. Although the spawning season is reportedly June–August in the GOM (Brown-Peterson and Franks 2001), direct evidence of spawning is presently undocumented. If spawning occurs outside of the proposed spawning season or if the spawning season is protracted, then our large age-0 fish could be months older than the small age-0 fish collected by Franks et al. (2001). Alternatively, our large age-0 fish may have been spawned at more southerly latitudes and dispersed northward, via the Loop Current, to the north-central GOM.

Our study provides new information about GOM Atlantic Tripletail, including an evaluation of aging structures, updated ages and growth parameters, and mortality estimates; nonetheless, much of the species' biology and

ecology remains unknown. Until validation of age estimates is accomplished, all assigned ages must be considered assumed rather than known. Additionally, little is understood about the seasonal migration patterns of the species, and spawning locations are unidentified. Studies that employ electronic or high-dollar reward tags or that collect biological samples such as gonads should be prioritized to address these respective research needs. As the popularity of Atlantic Tripletail increases among recreational anglers, researchers must address these and other knowledge gaps to inform management and ensure future sustainability of the species.

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REFERENCES

- Akaike, H. 1998. Information theory and an extension of the maximum likelihood principle. Pages 199–213 in E. Parzen, K. Tanabe, and G. Kitagawa, editors. Selected papers of Hirotugu Akaike. Springer, New York.
- Armstrong, M. P., R. E. Crabtree, M. D. Murphy, and R. G. Muller. 1996. A stock assessment of Tripletail, *Lobotes surinamensis*, in Florida waters. Florida Department of Environmental Protection, Florida Marine Research Institute, St. Petersburg.
- Baty, F., C. Ritz, S. Charles, M. Brutsche, J.-P. Flandrois, and M.-L. Delignette-Muller. 2015. A toolbox for nonlinear regression in R: the package nlstools. Journal of Statistical Software [online serial] 66(5).
- Baughman, J. L. 1941. On the occurrence in the Gulf coast waters of the United States of the Triple Tail, *Lobotes surinamensis*, with notes on its natural history. American Naturalist 75:569–579.
- Baughman, J. L. 1943. Additional notes on the occurrence and natural history of the Triple Tail, *Lobotes surinamensis*. American Midland Naturalist 29:365–370.
- Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences 38:982–983.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181–213.
- Betancur-R, R., E. O. Wiley, G. Arratia, A. Acero, N. Bailly, M. Miya, G. Lecointre, and G. Orti. 2017. Phylogenetic classification of bony fishes. BMC Evolutionary Biology 17:article 162.
- Breder, C. M. 1949. On the behavior of young *Lobotes surinamensis*. Copeia 1949:237–242.
- Brown-Peterson, N. J., and J. S. Franks. 2001. Aspects of the reproductive biology of Tripletail, *Lobotes surinamensis*, in the northern Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute 52:586–597.
- Caldwell, D. K. 1955. Offshore records of the Tripletail, *Lobotes surinamensis*, in the Gulf of Mexico. Copeia 1955:152–153.
- Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.
- Carpenter, K. E. 2002. Lobotidae: tripletails. Page 1505 in K. E. Carpenter, editor. The living marine resources of the western central Atlantic. Food and Agriculture Organization of the United Nations, Rome.
- Casselman, J. 1983. Age and growth assessment of fish from their calcified structures—techniques and tools. NOAA Technical Report NFMS 8:1–17.
- Chapman, D. G., and D. S. Robson. 1960. The analysis of a catch curve. Biometrics 16:354–368.
- Ditty, J. G., and R. F. Shaw. 1994. Larval development of Tripletail, *Lobotes surinamensis* (Pisces: Lobotidae), and their spatial and temporal distribution in the northern Gulf of Mexico. U.S. National Marine Fisheries Service Fishery Bulletin 92:33–45.
- Dooley, J. K. 1972. Fishes associated with the pelagic *Sargassum* complex, with a discussion of the *Sargassum* community. Contributions in Marine Science 16:1–32.
- Franks, J. S., J. T. Ogle, J. R. Hendon, D. N. Barnes, and L. C. Nicholson. 2001. Growth of captive juvenile Tripletail *Lobotes surinamensis*. Gulf and Caribbean Research 13:75–78.
- Franks, J. S., K. E. VanderKooy, and N. M. Garber. 2003. Diet of Tripletail, *Lobotes surinamensis*, from Mississippi coastal waters. Gulf and Caribbean Research 15:27–32.
- Franks, J. S., J. R. Warren, D. P. Wilson, N. M. Garber, and K. M. Larsen. 1998. Potential of fin spines and fin rays for estimating the age of Tripletail, *Lobotes surinamensis*, from the northern Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute 50:1022–1037.
- Gudger, E. W. 1931. The Triple-Tail, *Lobotes surinamensis*, its names, occurrence on our coasts and its natural history. American Naturalist 65:49–69.
- Hoening, J. M. 1983. Empirical use of longevity data to estimate mortality rates. U.S. National Marine Fisheries Service Fishery Bulletin 82:898–903.
- Hoffmayer, E. R., J. S. Franks, B. H. Comyns, J. R. Hendon, and R. S. Waller. 2005. Larval and juvenile fishes associated with pelagic *Sargassum* in the northcentral Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute 56:259–269.

- Hughes, K. F. 1937. Notes on the habits of the Triple-Tail, *Lobotes surinamensis*. American Naturalist 71:431–432.
- Jefferson, A. E., R. J. Allman, A. E. Pacocco, J. S. Franks, F. J. Hernandez, M. A. Albins, S. P. Powers, R. L. Shipp, and J. M. Drymon. 2019. Age and growth of Gray Triggerfish (*Balistes capricus*) from a north-central Gulf of Mexico artificial reef zone. Bulletin of Marine Science 95:177–195.
- Katsanevakis, S., and C. D. Maravelias. 2008. Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. Fish and Fisheries 9:178–187.
- Kelly, H. A. 1923. Triple-tail numerous in North Carolina. Copeia 1923:109–111.
- Maceina, M. J., and P. W. Bettoli. 1998. Variation in Largemouth Bass recruitment in four mainstream impoundments on the Tennessee River. North American Journal of Fisheries Management 18:998–1003.
- Merriner, J. V., and W. A. Foster. 1974. Life history aspects of the Tripletail, *Lobotes surinamensis* (Chordata-Pisces-Lobotidae), in North Carolina waters. Journal of the Elisha Mitchell Scientific Society 90:121–124.
- Miranda, L. E., and P. W. Bettoli. 2007. Mortality. Pages 229–277 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.
- Nelson, T. R., A. E. Jefferson, P. T. Cooper, C. A. Buckley, K. L. Heck, and J. Mattila. 2018. Eurasian Perch *Perca fluviatilis* growth and fish community structure, inside and outside a marine-protected area in the Baltic Sea. Fisheries Management and Ecology 25:172–185.
- Ogle, D. H. 2016. Introductory fisheries analyses with R. CRC Press, Boca Raton, Florida.
- Ogle, D. H., P. Wheeler, and A. Dinno. 2018. FSA: fisheries stock analysis. R package version 0.8.22. Available: <https://github.com/droglenc/FSA>. (November 2020).
- Parr, R. T., R. B. Bringolf, and C. A. Jennings. 2018. Efficacy of otoliths and first dorsal spines for preliminary age and growth determination in Atlantic Tripletails. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 10:71–79.
- Parr, R. T., C. A. Jennings, N. D. Denslow, K. J. Kroll, and R. B. Bringolf. 2016. Evaluation of reproductive status in Atlantic Tripletail by traditional and nonlethal approaches. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 8:16–22.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Science 39:175–192.
- Quantum GIS Development Team. 2019. Quantum GIS geographic information system. Open Source Geospatial Foundation Project. Available: <https://www.qgis.org/en/site/index.html>. (March 2021).
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Streich, M. K., C. A. Calinowsky, and D. L. Peterson. 2013. Residence, movement patterns, and habitat use of Atlantic Tripletail in Ossabaw Sound estuary, Georgia. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 5:291–302.
- Strelcheck, A. J., J. B. Jackson, J. H. Cowan Jr., and R. L. Shipp. 2004. Age, growth, diet, and reproductive biology of the Tripletail, *Lobotes surinamensis*, from the north-central Gulf of Mexico. Gulf of Mexico Science 22:45–53.
- Then, A. Y., J. M. Hoening, N. G. Hall, and D. A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES Journal of Marine Science 72:82–92.
- VanderKooy, S. J., editor. 2009. A practical handbook for determining the age of Gulf of Mexico fishes. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.
- VanderKooy, S. J., editor. 2016. Biological profile for Tripletail in the Gulf of Mexico and the western central Atlantic. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.
- Wells, R. J., and J. R. Rooker. 2004. Spatial and temporal patterns of habitat use by fishes associated with *Sargassum* mats in the northwestern Gulf of Mexico. Bulletin of Marine Science 74:81–99.