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Age, Growth, and Natural Mortality of Whitebone Porgy, *Calamus Leucosteus*, From the Southeastern United States

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Abstract

Ages of whitebone porgy (*Calamus leucosteus*) (n = 559) from southeastern U. S. commercial and recreational fisheries from 1975 – 2017 were determined using sectioned otoliths. Opaque zones were annular, forming April – July (peaking in June). Ages ranged from 2 – 19 years, and the largest fish measured 513 mm TL (total length, mm). Body size relationships were: TL = 1.09 FL + 16.07 (n = 469, r^2 = 0.97), FL = 0.89 TL – 6.39 (n= 469, r^2 = 0.97), $W = 2.8 \times 10^{-5}$ TL$^{2.91}$ (n = 462), and $W = 6.8 \times 10^{-5}$ FL$^{2.82}$ (n = 417) where W is total weight (grams, g) and FL is fork length (mm). The von Bertalanffy growth equations were $L_t = 365\ (1 - e^{-0.35\ (t\ +\ 1.37)})$ (n = 559) for all areas combined, $L_t = 365\ (1 - e^{-0.55(t\ +\ 0.00)})$ (n = 185) for fish from North Carolina through Cape Canaveral, Florida, and $L_t = 368\ (1 - e^{-0.25\ (t\ +\ 2.51)})$ (n = 374) for fish from southeast Florida. Mean size-at-age was significantly different between regions for ages 4 – 9, (92% of total samples). Point estimates of natural mortality were M = 0.22 and M = 0.30 for northern- and southern-region fish, respectively, while age-specific estimates of M were 0.85 – 0.55 y^{-1} for ages 2– 19 for the northern region and 0.41 – 0.26 (ages 2-14) for southern region fish. This study presents updated life history parameters for whitebone porgy from the Atlantic waters off the southeastern United States.

Keywords: Age-Growth, Natural Mortality, Whitebone Porgy, Sparidae

1. Introduction

Whitebone porgy (*Calamus leucosteus* Jordan and Gilbert 1885) is a moderate sized porgy (Family Sparidae) found in the western Atlantic. The species is distributed in coastal waters of the United States from North Carolina through the Florida Keys and into the Gulf of Mexico to the Yucatan Peninsula of Mexico (Randall & Caldwell, 1966). Adult whitebone porgy are frequently encountered near sponge-coral hardbottom habitat at depths of 10 – 100 m (Powles & Barans, 1980), and the species also associates with soft-bottom habitat (McEachran & Fechhelm, 2005), a characteristic which made it important to trawl fishermen (Waltz, Roumillat & Wenner, 1982) prior to the 1989 trawl ban in federal waters of the U.S. South Atlantic (SAFMC, 1988).

Whitebone porgy is an important secondary species in the snapper-grouper fishery of the southeastern U. S. (SEUS – Cape Hatteras NC through the Dry Tortugas FL) reef fishery. Estimated SEUS annual landings from recreational fisheries (combined headboat and private recreational/charterboat sources) from 1981 – 2015 averaged 22,305 fish at a total weight of 13,439 kg. Recreationally-caught whitebone porgy are predominantly landed from the Georgia-central Florida area (61%), while North Carolina accounted for 17%, South Carolina for 19% and the south Florida-Florida Keys area accounted for only 2% of total landings on an annual basis (Fig. 1). Commercial fisheries landings from the SEUS were low, totaling 5,000 kg from 1981 – 2015, with 99% of this being attributed to South Carolina.

Whitebone porgy is currently included in the South Atlantic Fishery Management Council's Snapper-Grouper Fishery Management Plan (SAFMC, 2017). The species is managed by inclusion in the 20-fish aggregate bag limit for recreational fisheries. Recreational catches are further regulated by a porgy complex (jolthead porgy *Calamus bajonado* Schneider 1801;

knobbed porgy *Calamus nodosus* Randall and Caldwell 1966; whitebone porgy; saucereye porgy *Calamus calamus* Valenciennes 1830; and scup *Stenotomus chrysops* Linnaeus 1766) aggregate annual catch limit (ACL), or quota, of 48,495 kg (SAFMC, 2017). The commercial fishery is managed with an ACL of 16,487 kg for the porgy complex. The recreational quota for the porgy complex was reached on September 17, 2014, triggering the first closure of the recreational fishery for those five species. The fishery closed again two years later, on September 3, 2016, when monitoring determined that 131% of the quota had been harvested.

Published studies on whitebone porgy in SEUS waters are limited to studies describing habitat associations (Powles & Barans, 1980; Grimes, Manooch & Huntsman, 1982) and life history studies describing feeding ecology (Sedberry, 1989) and age, growth and reproduction (Waltz, Roumillat & Wenner, 1982) of fish from the South Atlantic Bight, the area between Cape Hatteras, NC and Cape Canaveral, FL. We used sagittal otoliths collected through dockside sampling programs of the fisheries operating in the southeastern U.S., thus expanding the geographic range and the overall size of fish sampled compared to the previous study. These samples were used to provide updated estimates of growth parameters and natural mortality, both of which are important inputs into stock assessments that contribute to the computation of annual catch quotas or overfishing limits.

2. Materials and Methods

2.1 Sampling

Whitebone porgy (n = 573) were sampled from fisheries landings by NMFS and state agencies' port agents sampling the recreational and commercial fisheries along the SEUS coast from 1975 – 2017 following sampling designs by the Southeast Region Headboat Survey (Fitzpatrick et al., 2017) and the National Marine Fisheries Service Trip Interview Program. The majority of samples were collected from fish caught by headboat anglers (n = 552), with the commercial fisheries sector (n = 15) and the private recreational sector (n = 6) accounting for the rest. All specimens were captured by conventional vertical hook and line gear. Total lengths (TL) and/or fork lengths (FL) of specimens were recorded in millimeters (mm). Whole weight (W) in grams was recorded for fish landed in the recreational headboat fishery. The commercial fishing operations tend to gut the fish at sea to preserve the optimum quality of the meat intended for market, and whole weights were not available. Sagittal otoliths were removed during dockside sampling and stored dry in coin envelopes.

2.2 Age Determination and Timing of Opaque Zone Formation

The sagittal otoliths of whitebone porgy were small and too dense to obtain an age reading from the whole structure; therefore, transverse sections were taken from each sample using the methods of Potts & Manooch (1995). The otoliths were affixed to glass slides and mounted on a low-speed saw equipped with a thin wafering blade. A series of three, 0.5 mm sections were taken from each sample ensuring the core area was included in at least one of the sections. The sections were then adhered to a glass slide and covered with a mounting medium, which improved the refractive nature of the section when viewed through the microscope at 12.5X magnification using transmitted light.

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Annuli were assumed to consist of pairs of wide translucent zones followed by narrow opaque zones starting after the dense, opaque core area. The opaque zones, representing one year's complete growth, were enumerated. Age determination was based on recording an opaque zone count and margin type code by an experienced reader (MLB) with extensive experience interpreting otolith sections (Burton, 2001; Burton, Potts & Carr, 2016) with no knowledge of date of capture or fish size for each sample. The margin codes refer to the type of zone, opaque or translucent, and in the case of translucent zones the amount of that zone between the last opaque zone formed and the otolith section margin. The codes used are outlined below:

1 = opaque zone forming on the margin of the otolith section;

2 = narrow translucent zone on the margin, generally < 30% of the width of the previous translucent zone;

3 = moderate translucent zone on the margin, generally 30% - 60% of the width of the previous translucent zone;

4 = wide translucent zone on the margin, generally > 60% of the width of the previous translucent zone (Harris et al., 2007).

To ensure consistency in interpretation of the growth zones on the otolith, a subset of the otolith sections (n = 410; 73 %) were then read by a second reader (JP), and an index of between-reader average percent error (IAPE) was calculated, following the methodology of Beamish & Fournier (1981). Where readings for a specimen disagreed, the sections were viewed again together. If consensus was reached the sample was retained; otherwise, it was excluded from further analysis.

Marginal increment analysis was used to assess the timing of opaque zone formation and to verify that they were annually formed. The margin types were plotted by month of capture to determine if the opaque zones were deposited primarily in one season or month. Based upon margin frequency analysis, all samples were assigned a calendar age, obtained by increasing the opaque zone count by one if the fish was caught before that year's opaque zone was formed and had a margin which was a moderate to wide translucent zone (type 3 or 4). Fish caught during the time of year of opaque zone formation with a margin type of 1 or 2, as well as fish caught after the time of opaque zone formation, were assigned a calendar age equivalent to the opaque zone count.

2.3 Growth

Growth of whitebone porgy was estimated using the von Bertalanffy (1938) growth model:

$L_t = L_\infty (1 - e^{(-K(t - t_0))})$ where L_∞ = theoretical maximum length, K = Brody growth coefficient (rate at which maximum size is attained), and t_0 = theoretical age at size 0.

Parameters were estimated from observed length at age data using PROC NLIN, a nonlinear regression procedure using least squares estimation and the Marquardt iterative algorithm option, in SAS statistical software (version 9.4; SAS Institute Inc., 1987) [Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA]. Initial model runs were unweighted. If the residuals of these runs appeared skewed at the tails of the sample distribution, we inverse-weighted the model by $1/n$ of each calendar age. To account for growth of the fish throughout the year before or after its "birthday", the calendar age of the fish (A_c) was adjusted for the time of year (month) caught (M_c) compared to month of peak spawning, or "birthdate", (M_b), determined from previous studies on reproduction, thus creating a fractional, or monthly biological age, (A_f):

$$A_f = A_c + ((M_c – M_b)/12).$$

2.4 Body-Size Relationships

Because different biological fish surveys may record one length measurement type preferred over another, or the caudal fin of the fish may be damaged, and generally fish are assessed and managed based on whole weight, we provide the meristic conversion equations for whitebone porgy. For weight – length relationships we regressed W on TL (n = 462) and W on FL (n = 417) using whitebone porgy measured for this study, examining both a non-linear fit using nonlinear least squares estimation (vers. 9.4; SAS Institute, Inc., 1987) and a linearized fit of the log-transformed data. Residuals were examined to determine which regression was the appropriate one. For length-length relationships, we used a linear regression model for TL on FL and FL on TL (n = 469).

2.5 Natural Mortality

We estimated the instantaneous rate of natural mortality (M) of whitebone porgy using two methods:

(1) Hewitt & Hoenig (2005) longevity mortality relationship

$$M = 4.22/t_{max}{}^{-}$$

where t_{max} is the maximum age of the fish in the sample; and

(2) Charnov, Gislason & Pope's (2013) method using life history parameters

$$M = (L/L_\infty)^{-1.5} K$$

where L_∞ and K are the von Bertalanffy growth equation parameters and L is fish length at age;

The equation of Hewitt & Hoenig (2005) uses longevity to generate a single point estimate. The Charnov, Gislason & Pope (2013) method, which incorporates life history information via the growth parameters, is based upon evidence suggesting that M decreases as a power function of body size. This method generates age-specific rates of M.

As a test of the efficacy of the value of M at age and the probability of the species living to the oldest age in the population, cumulative survival (ϕ) to each age 2+ was calculated with the estimate natural mortality rates:

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$$\phi(a) = 100 \times \exp\left(-\sum_{a=1}^{A-1} M_a\right)$$

where M_a is the natural mortality rate at age a, and A is the age of interest.

3. Results

3.1 Age Determination and Timing of Opaque Zone Formation

A total of 573 whitebone porgy sagittae were sectioned. We were able to count opaque zones on 559 (97.6%) whitebone porgy sections, as 14 samples were determined to be illegible and excluded from the analyses. Geographic and fishery sector distribution of our aging samples are shown in Table 1. The North Carolina region accounted for 11% (n = 59), South Carolina contributed 5% (n = 30), the Georgia-central Florida area accounted for 17% (n = 96), and southeast Florida samples totaled n = 373 (67%). Only one fish was sampled from the Florida Keys. The majority of samples were collected from fish caught by headboat anglers (n = 541), with the commercial fisheries sector (n = 12) and the private recreational/charter boat fishery (n = 6) accounting for the rest.

We were able to assign a margin type to 100% of our samples (n = 559) for our analysis of opaque zone formation timing. Whitebone porgy otoliths exhibited opaque zones on the margin April - July, with a peak in June (Fig. 2). Formation of opaque and translucent zones exhibited a clear oscillating pattern of the opaque zones forming April – July, to a narrow translucent zone June – October, to moderate translucent zone October – March, and to the widest translucent zone March – May. Opaque zones on the margin were absent from August through March. We assumed that opaque zones on whitebone porgy otoliths were annuli.

Calendar ages were assigned as follows: for fish caught January through July and having an margin type of 3 or 4, the annuli count was increased by one; for fish caught in that same time period with an margin type of 1 or 2, calendar age was equivalent to annuli count; for fish caught from August to December, the calendar age was equivalent also to the annuli count.

Opaque zones on whitebone porgy otoliths were moderately easy to interpret (Fig. 3) and margin types were assigned consistently between readers. Between-reader IAPE on a subset of the samples was 4.89% (n = 410), which falls within Campana's (2001) acceptable value of 5% APE for species of moderate longevity and reading complexity. Direct agreement between readers was 68%, and agreement within ± 1 year was 98%. Consensus on between-reader counts was reached on all samples, and no samples were excluded from further analyses. An age-bias plot (Fig. 4) indicated that there was no bias in age readings by one reader or the other, and the average difference in readings between readers was 0.17 years. The opaque zones were easy to trace from the sulcal groove out into the lateral plane on the dorsal side of the sections, where the most consistent counts were made.

3.2 Growth

Growth of whitebone porgy was modeled using fractional ages based on the birth month, or month of peak spawning, of May determined from a reproductive study of fish collected from the SEUS (Waltz, Roumillat & Wenner, 1982). Whitebone porgy in this study ranged from 222 – 513 mm TL and ages 2 – 19, but only 17 fish were older than age-12. Growth is described by the following equation:

$L_t = 365\ (1 - e^{-0.35\ (t\ +\ 1.37)})$ (n = 559, Fig. 5).

Closer examination of our data indicated differences in mean size and age by area. The majority of our samples were from southeast Florida (n = 374) and these fish ranged from ages 2 – 14 and 227 – 435 mm TL (Table 2). Fish from the combined area encompassing North Carolina through central Florida (n = 185) ranged from 2 – 19 years and 222 – 513 mm TL (Table 3). Modal ages of whitebone porgy were 4 years for southeast Florida and 5 years for the northern region. Mean age of fish from southeast Florida was 4.68 years (n = 374, SE = 0.09), while mean age of northern area fish was 7.18 (n = 185, SE = 0.25). Modal lengths were 275 mm TL for southeast Florida and 350 mm TL for the northern region. Average size differed between areas as well; mean TL of whitebone porgy from southeast Florida was 305 mm (n = 374, SE = 1.78) while mean size of northern area fish was 350 mm TL (n = 185, SE = 3.61). Both size and age were significantly different between areas based on t-tests: t = 9.17, P < 0.0001 for age and t = 11.08, P < 0.0001 for length. An analysis of variance (ANOVA) of length-at-age by region revealed significant differences in size-at-age for ages 4 – 9 for which there were adequate samples for a comparison (Table 4). Based on these differences in size-at-age of whitebone porgy between the two regions, we re-estimated the von Bertalanffy growth models by region, resulting in the following equations:

NC-central FL – $L_t = 364\ (1 - e^{-0.62\ (t\ +\ 0.15)})$, n = 185; and

SEFL – $L_t = 372\ (1 - e^{-0.19\ (t\ +\ 4.28)})$, n = 374 (Fig. 5).

Our growth model was not able to estimate size at the youngest ages accurately due to lack of smaller, younger fish in our samples. We had only six age-2 fish from southeast Florida and seven age-2 fish from the northern region. This lack of younger fish is likely attributable to the fact that the majority of our samples were from fishery-dependent sources. Selectivity imposed by either gear (hook-size) or anglers (culling for larger sizes) likely led to lack of smaller fish in our samples, leading to the large negative value for t_0 for southeast Florida fish. With no age-0 or age-1 fish and very few age-2 fish available to help describe the growth curve at the earliest ages, we used the method of McGarvey & Fowler (2002) to re-estimate the growth models. This procedure adjusts for the bias imposed by minimum size limits or some other selectivity imposed by the fishery by using a left-truncated normal probability density function of length. The procedure assumes a zero probability of capture below a specified minimum size limit. We assumed a minimum size limit of 222 mm TL for our northern region fish and 227 mm TL for our southeast Florida fish (smallest sizes caught) and re-computed the growth models by minimizing the negative sum of log-likelihoods using AD Model Builder estimation software (http://www.admb-project.org). The resulting equations are:

NC-central Florida – $L_t = 365\ (1 - e^{-0.55\ (t + 0.00)})$, $n = 185$; and

SEFL – $L_t = 368\ (1 - e^{-0.25\ (t + 2.51)})$, $n = 374$.

3.3 Body-Size Relationships

Statistical analyses revealed an additive error term (variance not increasing with size) in the residuals of the *W* – TL and *W* – FL relationships for whitebone porgy, indicating that a direct non-linear fit of the data was appropriate. The relationships are described by the following equations:

$W = 2.8 \times 10^{-5}\ \mathrm{TL}^{2.91}$ ($n = 462$, SE (a) = 6.01×10^{-6}; SE (b) = 0.037, and

$W = 6.8 \times 10^{-5}\ \mathrm{FL}^{2.82}$ ($n = 417$, SE (a) = 1.3×10^{-5}; SE (b) = 0.035

The relationships between TL and FL are described by the equations

TL = 1.09 FL + 16.07 ($n = 469$; $r^2 = 0.97$; $P < 0.0001$) and

FL = 0.89 TL – 6.39 ($n = 469$; $r^2 = 0.97$; $P < 0.0001$).

3.4 Natural Mortality

Natural mortality (*M*) was estimated to be 0.30 y^{-1} and 0.22 y^{-1} for whitebone porgy from the southeast FL and the NC-central FL regions, respectively, using Hewitt & Hoenig's (2005) method integrating all ages into a single point estimate. Age-specific estimates of *M* using Charnov, Gislason & Pope (2013) and derived from the bias-corrected parameter estimates are presented in Tables 2 and 3. We used the midpoint of each age (e.g., 0.5, 1.5, 2.5, etc.) to calculate age-specific *M*, because the Charnov, Gislason & Pope (2013) method cannot mathematically calculate *M* for age-0. Also, for stock assessment purposes where the integer age is used to describe the entire year of the fish's life, the mid-point gives the median value of *M* for that age.

When considering the cumulative estimate of survivorship on the fully recruited age to the oldest age, the Hewitt & Hoenig (2005) method estimates 5% survivorship for both the southern and northern areas, while the Charnov, Gislason & Pope (2013) estimate is 6% for whitebone porgy from southeast Florida and 0.04% for the northern region. Since estimating survivorship using only the fully recruited ages disregards a large amount of mortality occurring on younger fish, we estimated survivorship using all ages as well. Survivorship for fish from southeast Florida (ages 0 – 14) and northern region fish (ages 0 – 19) was identical in both regions, 1%, using Hewitt & Hoenig's (2005) constant *M*, while the age-specific method of Charnov, Gislason & Pope (2013) resulted in survivorship of 0.7% in southeast Florida and 0.00006% for the northern region.

4. Discussion

Otolith margin analysis demonstrated that whitebone porgy deposited one annulus per year from March-July, with peak annulus formation occurring in June. This timing is similar to that found by Waltz, Roumillat & Wenner (1982) of annulus deposition in June and July for fish from the South Atlantic Bight. Additionally, other members of the family Sparidae in the SEUS have similar timing of increment formation. Horvath, Grimes & Huntsman (1990) concluded from indirect evidence that knobbed porgy from North Carolina and South Carolina initiated annulus deposition in June and July, while Burton et al. (2019) found annulus deposition in knobbed porgy occurred from April through July, with a peak in June. Red porgy (*Pagrus pagrus* Linnaeus 1758) were found to deposit annuli from March through May, with peak in April for fish from North Carolina through southeast Florida (Potts & Manooch, 2001a). Littlehead porgy (*Calamus proridens* Jordan and Gilbert 1884) formed opaque zones from April – July in the eastern Gulf of Mexico (Tyler-Jedlund & Torres 2015).

Initially, growth of whitebone porgy was comparable in both regions, but by age-4 fish from the northern region were significantly larger than those from the southern region (Tables 2 and 3). This trend continued through age-9, when sample sizes became too small to statistically test. Whitebone porgy growth reached 80% of L_∞ by age-4 for southeast Florida fish, while northern region fish attained 90% of L_∞ by age-4. Our study contained only eight fish older than age-9 from the southern region and only 17 fish older than age-11 from the northern region. Longevity of whitebone porgy from both regions of our study exceeded the maximum age of 12 years found by Waltz, Roumillat & Wenner (1982), while maximum age from northern region fish in our study was substantially greater than from southern region fish, 19 years vs. 14 years. Northern-region whitebone porgy from our study had a longevity similar to that found by Horvath, Grimes & Huntsman (1990) for knobbed porgy from North Carolina and South Carolina, (17 years).

In that study the southern region fish came exclusively from the recreational fishery. If fish exhibit a general ontogenetic shift from shallow water to deeper water as they grow and mature, we would expect older and larger fish to be collected from deeper waters. Waltz, Roumillat & Wenner (1982) and Tyler-Jedlund & Torres (2015) collected the majority of their specimens from shallow-water fishery-independent trawl surveys, but then supplemented their collections with hook-and-line fishing on offshore hard-bottom reef habitats for larger fish. Both of these studies concluded that the average size of the fish increased with fishing depth. The SEUS commercial fishery tends to fish in deeper water and thus would have a greater chance of capturing the older and larger fish. Since recreationally caught fish dominated samples from both regions in our study (only 12 of the 559 fish aged in this study were from the commercial fishery), we do not believe the difference in size-at-age or in longevity between regions in this study can be explained by the fishery of origin of the samples.

Whitebone porgy from this study attained larger sizes and older ages in the northern region than in southeast Florida. These results showing differences in a species' growth over a range of latitudes are part of a trend being observed in age and growth studies of other reef fish species in the SEUS. Burton (2001) concluded that gray snapper (*Lutjanus griseus* Linneaus 1758) exhibited differences in maximum size and age between the northeast and southeast coast of Florida, Potts & Manooch (2001b) found that white grunt (*Haemulon plumieri* Lacepede 1801) from North Carolina and South Carolina achieved a maximum size that was

150 mm TL larger than white grunt from southeast Florida, and Murie & Parkyn (2005) found that white grunt from the northwest Florida coast were larger at age than fish from the southwest coast. Within the family Sparidae. Tyler-Jedlund & Torres (2015) found that littlehead porgy grew larger in the northern portion of their study area in the Gulf of Mexico than did fish in the southern region (Tampa Bay vs. Charlotte Harbor, FL), and Burton et al. (2019) found that knobbed porgy attained larger sizes and older ages in the northern portion of their study area than did fish from the southern portion.

Estimating fish growth for a population can be problematic when age samples come from one source, such as fishery-independent survey or fishery-dependent port sampling, or even one gear type. Each variable has its own selectivity. All fish used in this aging study were collected from fishery-dependent sources. The lack of smaller, younger fish that might have been obtained from fishery-independent sampling resulted in an inability to accurately estimate growth at the earliest ages. Our samples contained no age-1 fish in either region, and we had only six age-2 fish from southeast Florida and seven from the northern region. The smallest age-2 fish were 227 mm TL and 222 mm TL in the southern and northern regions, respectively. The growth curves modeled on the samples available for this study should only be used to characterize the fish retained in the fishery. To estimate the growth parameters for the population, a statistical correction for the left truncated distribution of length-at-age for the ages affected by the fishery selectivity was used. This procedure had a very slight effect on the growth parameters from the northern region, because the uncorrected model had already estimated a low t_0 value. The procedure had a greater effect on the southern regions, where the left side truncation in the distribution in length-at-age was most evident on ages 3-5. Though the starting point of the southern region growth curve was smaller when using the bias-corrected estimated parameters, the size at age-0 was not biologically reasonable for the population. By age-2, the fish from the southern region had already reached the inflection of the growth curve, causing the model to have nothing to direct the rate of attaining the inflection. This growth model should be used to estimate size of fish vulnerable only to the fishery.

It is interesting to note that the theoretical maximum length of whitebone porgy from the northern and southern regions were similar. Because we did not have specific locations of fishing for each sample, there could be an area of transition from one growth morph to another. Initially, the fish from the entire area appeared to grow at a comparable rate. Then by age-4 the fish from the northern area were significantly larger than those from SEFL and FL Keys. Clearly, the observed length-at-age from the northern area shows the largest fish in the population.

We provide the first estimates of natural mortality of whitebone porgy in the literature. We believe that the region-specific estimates of M derived from the maximum-age-based method of Hewitt & Hoenig (2005) obtained in this study, M = 0.22 and M = 0.30 for the northern and southern regions, respectively, were reasonable estimates for the fully recruited ages in our study. The estimate for the southeast Florida region compared favorably with the estimate of M = 0.32 for the congeneric jolthead porgy, a species with a similar longevity, 13 years (Burton et al., 2017). Since the longevity of fish in the northern region was larger, we expect the natural mortality to be smaller. We do not believe either of these estimates are suitable values of *M* for all ages, because younger fish are more vulnerable to predation, and thus likely have higher mortality rates. Charnov, Gislason & Pope's (2013) age-specific estimates of *M* are a more appropriate estimator for the younger ages. The Charnov, Gislason & Pope (2013) estimates of *M* for the youngest ages in our samples were almost four times the value of the Hewitt & Hoenig (2005) point estimate for the northern fish and are one-third larger for southern fish. Age-specific estimates of *M* for the age at full recruitment to the fishery was equal to the estimate of constant *M* for the southern fish but was almost three times as large as the value of constant *M* for the northern fish. The age-specific estimates of *M* for the older ages continue to decrease slowly until stabilizing at 0.26 at age-11 for southern fish and 0.55 at age-9 for northern fish (Tables 2 and 3).

When deciding which estimator to use, the reliability of the input to the estimator should be considered. Generally, we do not believe that purely size-based estimates, are appropriate. Because of the tightly, inversely-correlated relationship of L_∞ to K, and the effect t_0 has on those parameters, the age-varying estimates of *M* from Charnov, Gislason & Pope's (2013) equation can be greatly influenced. For the case with whitebone porgy and the separate growth morphs, the estimates of *M* detail these issues (Tables 2 and 3). The fish from the northern area live longer and grow larger, yet the estimates of *M* are more than two times higher on the fully-recruited ages than for the fish from the southern area. We have confidence in the maximum ages found in this study because they are similar to what was found for this species and other porgy species in previous studies (Waltz, Roumillat & Wenner, 1982, SEDAR, 2012, Burton et al., 2017) conducted in the SEUS. Also, generally accepted estimates of *M* in the U.S. Southeastern region have been based on longevity for the fully recruited fish to the fisheries (e.g., SEDAR 2012). It seems intuitive to scale the Charnov, Gislason & Pope (2013) estimates of *M* to the Hewitt & Hoenig (2005) point estimate. The calculation of survivability to the oldest ages also seems more reasonable after scaling. These fish have been subjected to decades of fishing pressure, yet our study still found fish of moderately long life. It seems reasonable to expect four to five percent of the population to live to the oldest ages, or maybe longer.

5. Conclusions

This updated study of whitebone porgy age and growth incorporates samples from a broader geographic area than previously utilized. We have shown that whitebone porgy from the northern extent of its distribution achieves greater size and longevity than southern fish, something that should be considered by fishery managers. We concluded that size-at-age was significantly different between regions for enough ages that growth should be estimated separately for the regions. We have shown that otolith sections of whitebone porgy contain easily identifiable annuli and that otolith sections are reliable structures for aging. We provide the first reported estimates of natural mortality and survivorship for the species. These results begin to fill an information gap for this data poor species and may allow fishery regulators to set future ACLs that are based on better scientific data such as life history parameters, versus less than optimum data that have been used in the past for data-limited species (e.g., catch histories), as pointed out by Carruthers *et al*., 2017.

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Appendix

Table 1. Number of samples of sagittal otoliths that were used for age and growth study of whitebone porgy (*Calamus leucosteus*) collected from 1975–2017 from fisheries landings along the coast of the southeastern United States. Samples were collected in the following regions: North Carolina (NC), South Carolina (SC), Georgia-central east Florida (GA-CFL), southeast Florida (SEFL), and the Florida Keys (FL Keys)

State	Commercial	Recreational	Total
NC	2	57	59
SC	—	30	30
GA-CFL	10	86	96
SEFL		373	373
FL Keys	—	1	1
Total	12	547	559

Table 2. Observed and predicted mean total length (TL) from the inverse-weighted von Bertalanffy growth model, measured in millimeters, and natural mortality at age (*M*, Charnov, Gislason & Pope 2013) data for whitebone porgy (*Calamus leucosteus*) collected from 1975 – 2017 from southeast Florida. Mortality estimates are presented both unscaled and scaled to the Hewitt & Hoenig (2005) estimate of constant *M* for all ages. Standard errors of the means (SE) are provided in parentheses

Age	*n*	Mean TL (± SE)	TL range	Predicted TL	Charnov $M\text{-}y^{-1}$	Scaled Charnov
2	7	273 (12)	235 - 332	249	0.41	0.46
3	104	289 (3)	227 - 385	275	0.36	0.40
4	108	300 (3)	243 - 390	300	0.33	0.36
5	59	310 (4)	261 - 387	312	0.31	0.34
6	42	317 (6)	232- 410	324	0.30	0.32
7	20	326 (8)	271 – 410	334	0.28	0.31
8	17	327 (7)	287 – 386	341	0.28	0.30
9	9	348 (13)	291 – 400	347	0.27	0.30
10	2	334 (48)	286 – 382	352	0.27	0.29
11	3	364 (32)	301 – 396	355	0.26	0.29
12	2	424 (12)	412 - 435	358	0.26	0.28
14	1	327	–	362	0.26	0.28

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Table 3. Observed and predicted mean total length (TL) from the inverse-weighted von Bertalanffy growth model, measured in millimeters, and natural mortality at age (*M*, Charnov, Gislason & Pope 2013) data for whitebone porgy (*Calamus leucosteus*) collected from 2003–2016 from North Carolina through central Florida. Mortality estimates are presented both unscaled and scaled to the Hewitt and Hoenig (2005) estimate of constant *M* for all ages. Standard errors of the means (SE) are provided in parentheses

Age	*n*	Mean TL (± SE)	TL range	Predicted TL	Charnov M-y^{-1}	Scaled Charnov
2	6	260 (10)	231 - 286	244	0.85	0.34
3	16	294 (13)	222 - 407	295	0.70	0.28
4	18	331(10)	247 - 390	325	0.63	0.25
5	31	354 (6)	282 - 425	342	0.59	0.24
6	24	356 (9)	280- 430	352	0.57	0.23
7	17	370 (10)	295 - 444	357	0.56	0.22
8	18	365 (10)	300 - 438	361	0.56	0.22
9	15	377 (15)	291- 510	362	0.55	0.22
10	4	368 (20)	328 - 417	364	0.55	0.22
11	19	357 (7)	306 - 395	364	0.55	0.22
12	1	356	-	365	0.55	0.22
13	4	390 (45)	305 - 513	365	0.55	0.22
14	4	364 (13)	335 - 395	365	0.55	0.22
15	3	350 (6)	340 - 362	365	0.55	0.22
16	2	351 (29)	322 - 380	365	0.55	0.22
17	2	348 (7)	342 - 355	365	0.55	0.22
19	1	360	–	365	0.55	0.22

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Table 4. Results of analysis of variance (ANOVA) of length-at-age by geographic region (North Carolina –central Florida versus southeast Florida-Florida Keys) for individual ages of whitebone porgy (*Calamus leucosteus*) aging samples collected from the southeastern United States in 1975–2017. An asterisk (*) indicates a significant probability value. An en dash indicates that the sample distribution did not allow for a test of significance

Age	*n*	Region
2	13	*F*=0.43, *P*=0.511
3	120	*F*=0.31, *P*=0.579
4	126	*F*=12.01, *P*=0.001*
5	90	*F*=33.44, *P*=0.0001*
6	66	*F*=19.68, *P*=0.0001*
7	37	*F*=15.38, *P*=0.0001*
8	35	*F*=10.57, *P*=0.0001*
9	24	*F*=3.96, *P*=0.047*
10	6	*F*=1.27, *P*=0.261
11	22	*F*=0.1, *P*=0.756
12	3	*F*=2.57, *P*=0.109
13	4	–
14	5	*F*=1.64, *P*=0.200
15	3	–
16	2	–
17	2	–
19	1	–

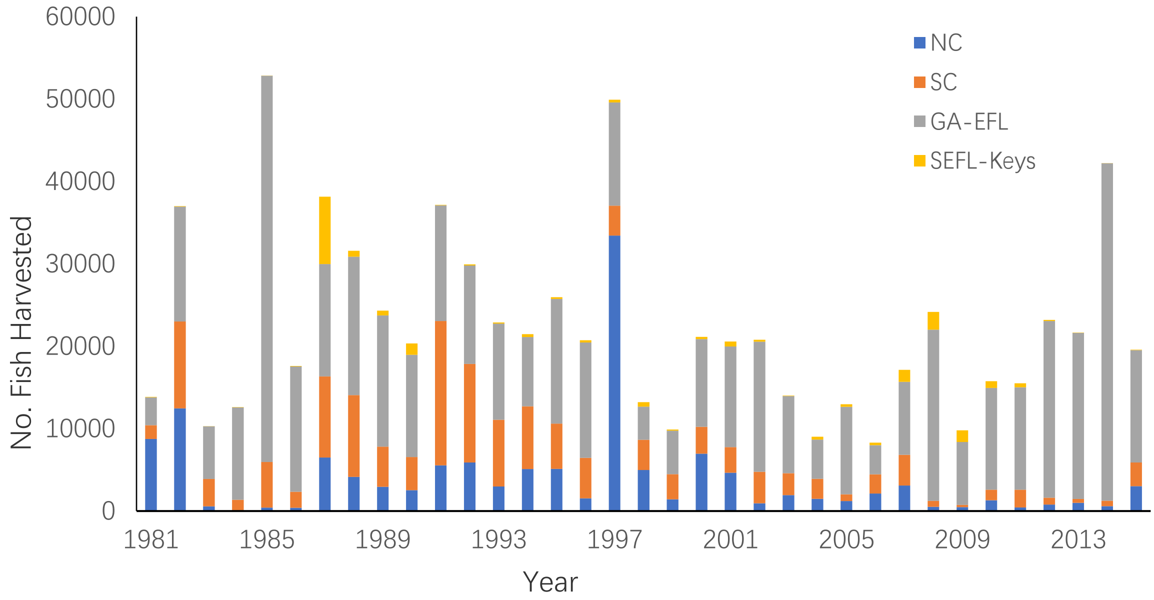

Figure 1. Annual landings in numbers of fish of whitebone porgy (*Calamus leucosteus*) harvested from the combined recreational (headboat and private boat-charterboat) fishery, 1981 – 2015, from the southeast United States

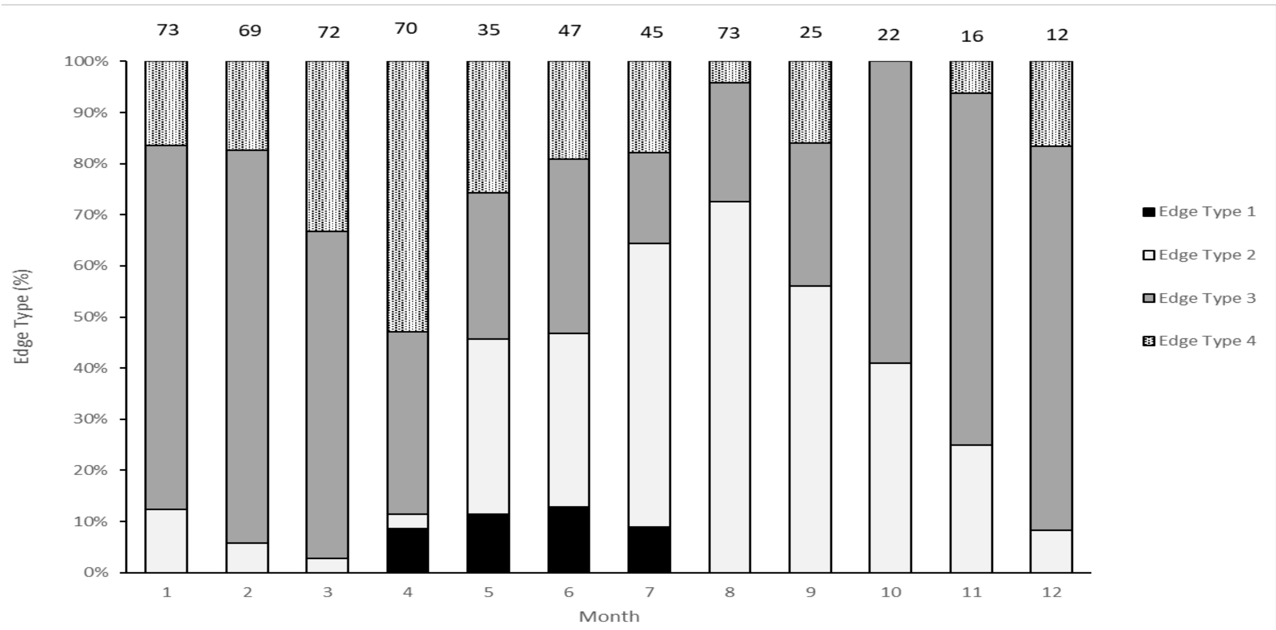

Figure 2. Monthly percentage of all margin types for whitebone porgy (*Calamus leucosteus*) collected from the southeastern United States from 1975 – 2017

Margin codes: 1, opaque zone on margin, indicating annulus formation; 2, small translucent zone, <30% of previous translucent zone; 3, moderate translucent zone, 30 – 60% of previous translucent zone; 4, wide translucent zone, > 60% of previous translucent zone. Sample sizes are shown above columns.

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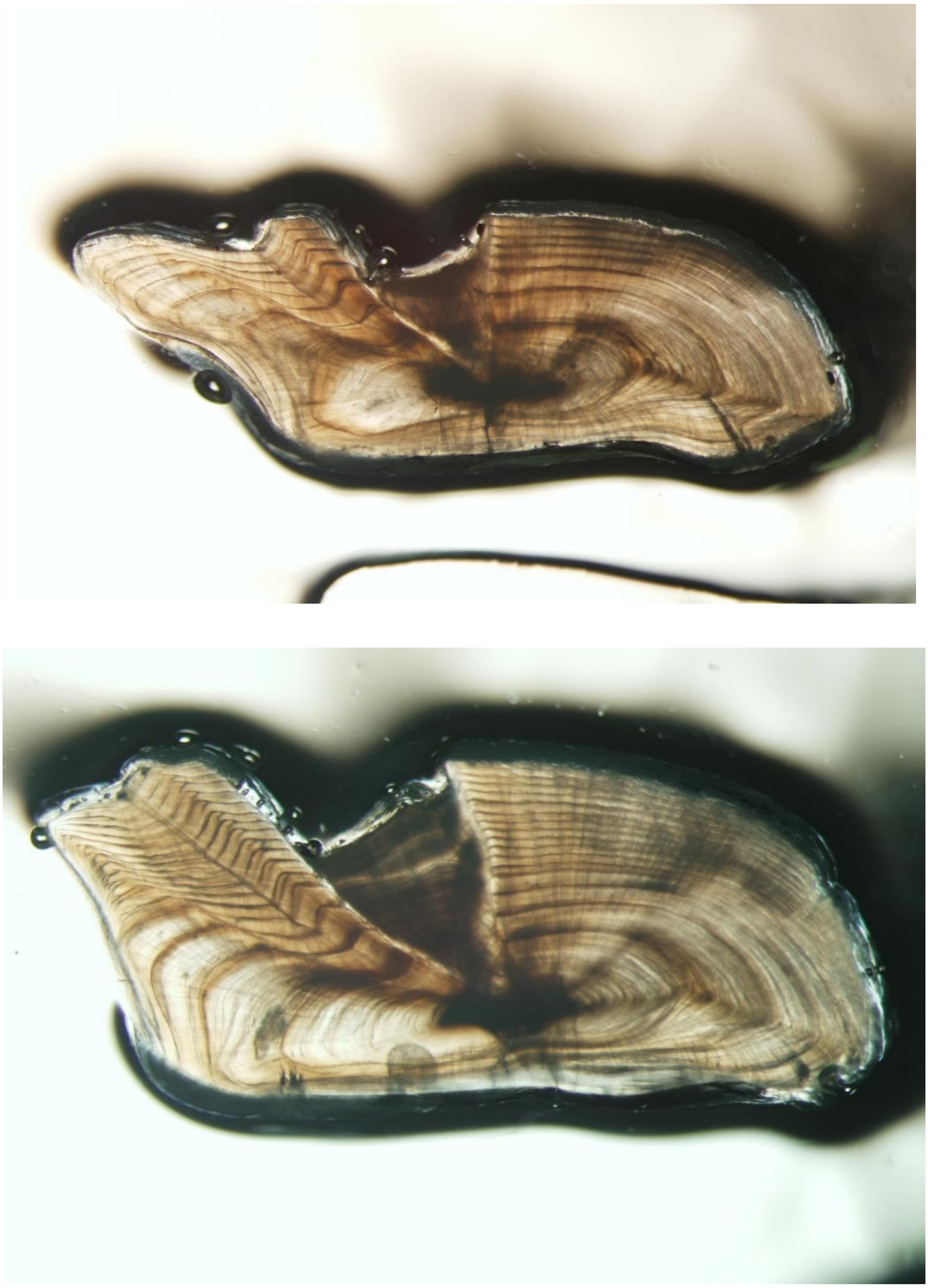

Figure 3. Sections of otoliths from whitebone porgy (*Calamus leucosteus*): (A) 372 mm TL 7-yr old; (B) 380 mm TL 16-yr old

Note: Age was determined by counting opaque zones along the ventral axis and sulcal groove using transmitted light at 12.5 x magnification.

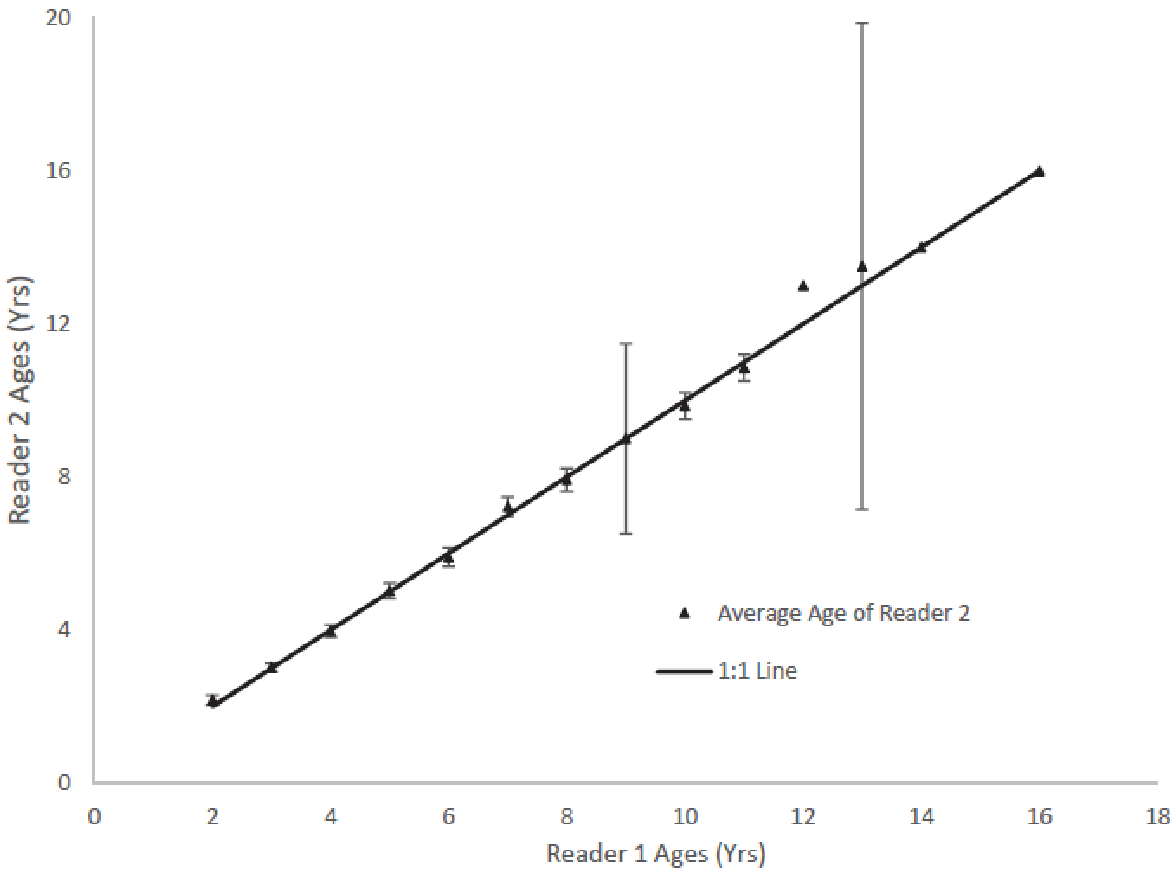

Figure 4. Age bias plot for 410 whitebone porgy (*Calamus leucosteus*) sampled from the southeastern United States from 1975 – 2017 and aged by two primary readers

Note: The first reader's age estimates (X-axis) are plotted against the second readers mean age estimates for the same-aged fish (Y-axis). Error bars are 95% confidence intervals.

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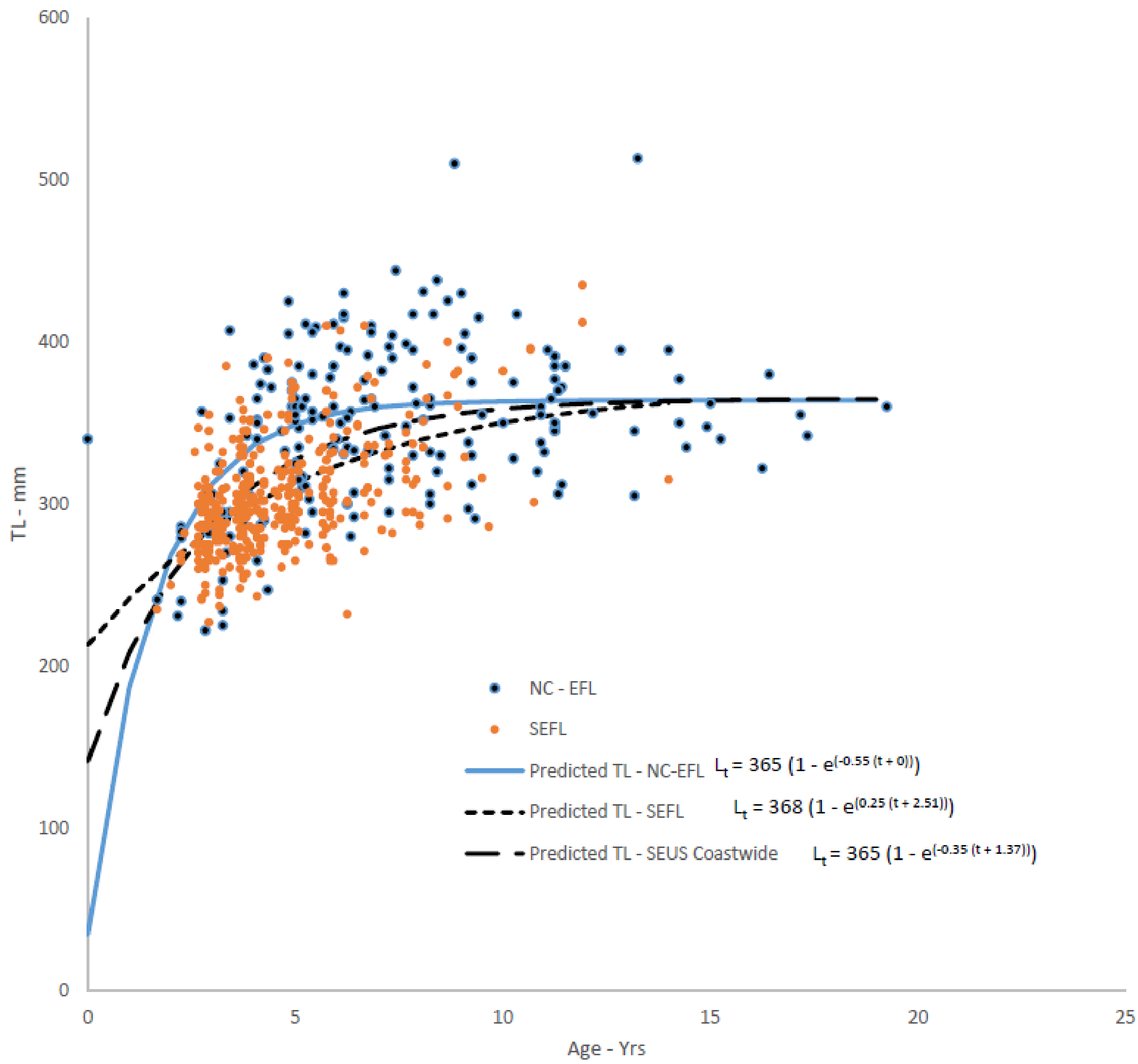

Figure 5. Comparison of observed fractional size-at-age of whitebone porgy (*Calamus leucosteus*) to von Bertalanffy growth curves for southeast Florida, North Carolina-central Florida, and coast-wide SEUS regions. All curves are inverse-weighted model runs.