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ARTICLE

Age, Growth, Natural Mortality, and Reproductive Seasonality of Knobbed Porgy from Southeastern United States Waters

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Abstract
The Knobbed Porgy *Calamus nodosus*, an important secondary species in reef fish catches of the southeastern United States, was recently the subject of a fishery closure due to the porgy complex quota being exceeded. Knobbed Porgy (n = 448) were aged using sectioned sagittal otoliths. Opaque zones on otolith sections were annular, forming in March–July (peaking in May). Knobbed Porgy ranged from 1 to 21 years, and the largest fish measured 507 mm TL. Body size relationships relating TL, FL, and total body weight (W) for Knobbed Porgy were TL = 1.07·FL + 22.93 (n = 3,173; r^2 = 0.97), FL = 0.91·TL − 12.54 (n = 3,173; r^2 = 0.97), $W = (1.38 \times 10^{-5})\text{TL}^{3.03}$ (n = 12,732; r^2 = 0.92), and $W = (7.99 \times 10^{-5})\text{FL}^{2.79}$ (n = 3,199; r^2 = 0.90). Mean length at age was significantly different between Knobbed Porgy collected in North Carolina through southeast Florida (northern region) and those collected in the Florida Keys (southern region). The von Bertalanffy growth equations for Knobbed Porgy were $L_t = 412[1 - e^{-0.20(t + 1.97)}]$ (n = 448) for all regions combined, $L_t = 403[1 - e^{-0.38(t + 0.0001)}]$ (n = 117) for northern region fish, and $L_t = 326[1 - e^{-0.42(t + 1.61)}]$ (n = 331) for southern region fish. Age-varying estimates of natural mortality were 0.36–0.79 year^{-1} (ages 2–21) for the northern region and 0.42–0.67 year^{-1} (ages 1–12) for fish from the Florida Keys. Hydrated oocytes were present during February–April in macroscopically staged ovaries (n = 148) for fish from the Florida Keys, and gonadosomatic index data indicated that the month of peak spawning in females was April. The updated life history information should be useful to fishery managers in formulating effective management strategies.

The Knobbed Porgy *Calamus nodosus* is a moderate-sized porgy (family Sparidae) capable of attaining sizes in excess of 500 mm TL. The species is distributed throughout the southeastern United States (SEUS) seaboard (from North Carolina to the Florida Keys, including the Dry Tortugas) and throughout the Gulf of Mexico to the Yucatan Peninsula of Mexico (Randall and Caldwell 1966). Adult Knobbed Porgy associate with wrecks and hardbottom structure along the continental shelf of the SEUS. Randall and Caldwell (1966) collected juvenile and subadult Knobbed Porgy from seagrass habitats in the U.S. Virgin Islands, although juvenile habitats in the SEUS have not been described in the literature. Horvath et al. (1990) concluded that Knobbed Porgy were protogynous hermaphrodites.

Although not a primary target species of SEUS reef fisheries, the Knobbed Porgy is abundant enough in the catches to be considered an important secondary species in the snapper–grouper complex. Estimated SEUS annual landings from headboats during 1981–2015 averaged 14,456 fish at an average total weight of 9,269 kg (Kelly Fitzpatrick, National Marine Fisheries Service [NMFS],

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Southeast Fisheries Science Center, Beaufort Laboratory, unpublished data), while recreational landings from private anglers and charter boats averaged 13,345 fish at an average total weight of 7,043 kg (data from the NMFS Marine Recreational Information Program [MRIP]; https://www.st.nmfs.noaa.gov/recreational-fisheries/data-and-documentation/queries/index). Recreationally caught Knobbed Porgy are predominantly landed from the Florida Keys (53%), while the east coast of Florida (excluding the Florida Keys) accounts for 10% and the Carolinas and Georgia account for 37% on an annual basis (Figure 1A). Commercial fishermen from North Carolina and South Carolina landed an average of 8,695 and 6,757 kg, respectively, during 1985–2014, while commercial landings from the Florida east coast (Figure 1B) in 2000–2014 averaged only 87 kg (https://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html). With the exception of an unusually large amount of landings in 1988 attributable to the Florida Keys recreational fishery as well as the South Carolina commercial fishery, landings were variable, with no consistent directional trends.

The Knobbed Porgy is currently included in the South Atlantic Fishery Management Council's Snapper–Grouper Fishery Management Plan (SAFMC 2017). The species is included in a complex of reef fishes managed with a recreational 20-fish daily aggregate bag limit and annual catch

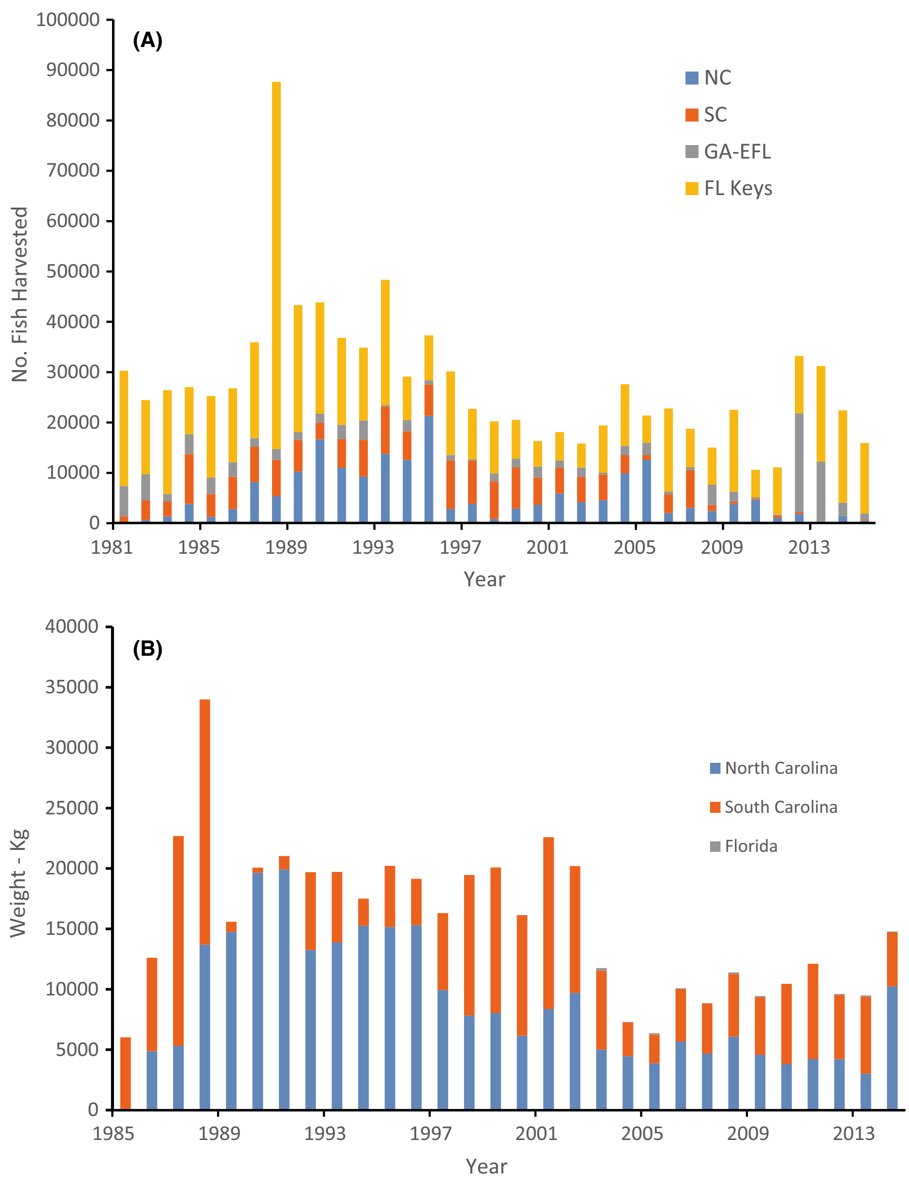

FIGURE 1. Annual landings of Knobbed Porgy from (**A**) the recreational headboat fishery (1981–2015) and (**B**) the commercial fishery (1985–2015) in the southeastern United States (NC = North Carolina; SC = South Carolina; GA–EFL = Georgia–eastern Florida; FL Keys = Florida Keys).

limits (ACLs), or quotas, applied to a multispecies porgy complex (Burton et al. 2017). The 2017 recreational and commercial ACLs for the porgy complex are 48,495 and 16,487 kg, respectively (SAFMC 2017). Due to its larger size, the Knobbed Porgy is one of the more desired species in this porgy complex, and the average annual landings reported above equate to 34% and 41% of the combined recreational and commercial ACLs, respectively, for this single species.

Burton et al. (2017) documented the initial porgy complex closure on September 17, 2014, due to the quota being reached. The fishery closed again on September 3, 2016, when 131% of the recreational ACL was estimated to have been landed. Previous Knobbed Porgy life history studies were of limited geographic and fishery sector coverage (Horvath et al. 1990; Borden 2001) and hindered managers from determining appropriate ACLs. The purpose of this study was to examine sagittal otoliths and gonad samples in order to provide updated estimates of growth parameters, examine growth for differences by geographic region, and derive information about natural mortality and reproductive seasonality, all of which are valuable data inputs into stock assessments and the formulation of ACLs (Carruthers et al. 2017).

METHODS

Study area.— Our study area encompassed a broad latitudinal range extending from Cape Hatteras, North Carolina, to the Dry Tortugas, 112.65 km (70 mi) west of Key West, Florida (24–35°N; Figure 2). The SEUS continental shelf ranges from 0- to 100-m depth and consists of sand and mud substrates, with patchily distributed areas of natural hardbottom ledges and temperate reefs throughout the region (Bacheler and Ballenger 2018). These hardbottom habitats range from flat pavement to high-relief ledges covered in sponges, algae, and octocorals (Schobernd and Sedberry 2009). The habitat in the southern portion of the area (i.e., in the Florida Keys and Dry Tortugas) is predominantly a coral reef environment that is dominated by hard corals as well as octocorals and sponges. The entire SEUS continental shelf habitat is greatly influenced by the presence of the Gulf Stream, a northward-flowing, warmwater current originating in southern Florida that keeps the temperature of the SEUS continental shelf waters relatively warm (mean annual bottom temperature from 1990 to 2015 was approximately 26°C; Bacheler et al. 2018), allowing the presence of temperate and subtropical species as far north as North Carolina.

Sampling.— Recreational and commercial fisheries landings from the SEUS coast were sampled for Knobbed Porgy by NMFS and state fisheries port agents during 2015 and 2016; sampling occurred year round. Additionally, 77 archived otolith samples collected by the Southeast Region Headboat Survey (SRHS) during 2003–2014 were used to augment samples from North Carolina through southeast Florida. All specimens used in this study were taken on hook-and-line gear. Data were collected as previously described by Burton et al. (2017). Specimens were measured for TL and/or FL (mm), and whole weight (W; g) was recorded for fish landed in the recreational headboat fishery. Fish landed by commercial fisheries were eviscerated at sea and were excluded from the W–TL regression analysis. Sagittal otoliths were removed during dockside sampling and were stored dry in coin envelopes.

Age determination and timing of opaque zone formation.— Otoliths were processed and analyzed using the methods described by Burton et al. (2017). The sections were viewed under a dissecting microscope at 12.5× using transmitted light, and age was determined by recording an opaque zone count and edge type code by a reader (M.L.B.) with extensive experience in interpreting otolith sections (Burton 2001; Burton et al. 2017). Age determinations were made with no knowledge of the date of capture or fish size for each sample. The edge 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 edge. The codes used (Harris et al. 2007) are as follows: 1 = opaque zone forming on the edge of the otolith section; 2 = narrow translucent zone on the edge, generally less than 30% of the width of the previous translucent zone; 3 = moderate translucent zone on the edge, generally 30–60% of the width of the previous translucent zone; and 4 = wide translucent zone on the edge, generally greater than 60% of the width of the previous translucent zone.

We plotted edge types by month of capture to determine the timing of opaque zone formation. Using edge frequency analysis, we assigned a calendar age to all samples by increasing the opaque zone count by 1 if the fish was caught before that year's opaque zone was formed and had an edge with a moderate to wide translucent zone (type 3 or 4). Fish with edge type 1 or 2 that were caught during the time of year when opaque zones were forming were assigned a calendar age equivalent to the opaque zone count, as were fish caught during months after opaque zone formation.

A random subset of the otolith sections (n = 352; 79%) was read by a second reader (J.P.), and an index of between-reader average percent error (APE) was calculated (Beamish and Fournier 1981). This was done to ensure accuracy in interpretation of the growth zones on the otolith. When readers were not in agreement for a specimen, the sections were viewed again together. The sample was retained in the study if agreement was reached; otherwise, it was excluded from further analysis.

Growth.— Growth of Knobbed Porgy was estimated as previously described by Burton et al. (2017). Specifically,

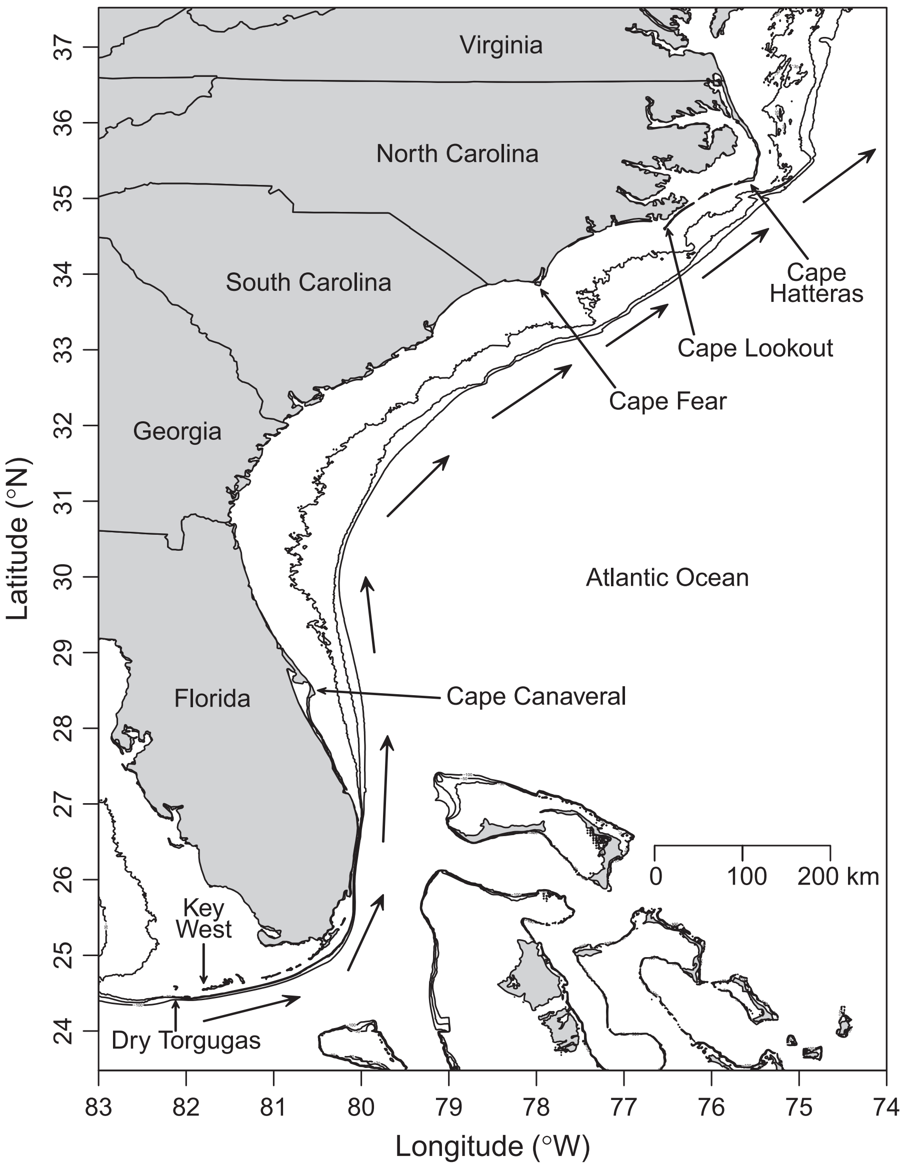

FIGURE 2. The southeastern United States (SEUS; from North Carolina to the Dry Tortugas, Florida) study area. Black contour lines show the 30-, 50-, and 100-m depth isobaths; arrows indicate the flow of the warmwater Gulf Stream. (Figure created by N. Bacheler, National Oceanic and Atmospheric Administration).

we used the von Bertalanffy (1938) growth model,

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

where L_∞ = the theoretical maximum length, k = the Brody growth coefficient (rate at which maximum size is attained), and t_0 = the theoretical age at a length of zero.

To estimate these parameters, we fitted the observed length-at-age data to the von Bertalanffy model by minimizing the negative log-likelihood function using AD Model Builder (http://www.admb-project.org). The calendar age of the fish (Age_c) was adjusted for the time of year in which the fish was caught (Mo_c) compared to month of peak spawning, or "birthdate" (Mo_b; determined from the reproductive data collected in this study), so that growth of the fish throughout the year before or after its "birthday" was accounted for. This procedure resulted in a fractional or monthly biological age (Age_f):

$$\text{Age}_f = \text{Age}_c + [\text{Mo}_c - \text{Mo}_b/12].$$

Body size relationships.— For weight–length relationships, we regressed W on TL (n = 12,372) or on FL (n = 3,177) using all fish sampled for lengths and whole weights by the SRHS from 1972 to 2016. We examined a nonlinear fit ($W = a\mathrm{TL}^b$) using nonlinear least-squares estimation (SAS version 9.4; SAS Institute 1987), as well as a linearized fit of the log-transformed data, $\log_e(W) = a + b \cdot \log_e(\mathrm{TL})$, examining residuals to determine which regression model best fit the data. For length–length relationships, we regressed TL on FL or FL on TL (n = 3,173) using linear regression.

Natural mortality.— Following the procedures outlined by Burton et al. (2016), we estimated the instantaneous rate of natural mortality (M) of Knobbed Porgy by using two methods (Hewitt and Hoenig 2005; Charnov et al. 2013). Hewitt and Hoenig's (2005) longevity mortality relationship is

$$M = 4.22/t_{max},$$

where t_{max} is the maximum age of the fish in the sample. The Charnov et al. (2013) method uses 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 and Hoenig (2005) uses longevity to generate a static, or age-invariant, estimate applied to all ages in the population. The Charnov et al. (2013) method is based upon evidence suggesting that M is inversely related to body size. This method generates age-varying rates of M and is currently used in Southeast Data, Assessment, and Review stock assessments (SEDAR 2017).

We calculated survivorship to the oldest observed age in the population by applying the M to the fully recruited ages in the fishery (modal age + 1) using the following equation:

$$\text{Survivorship (\%)} = 100 \times \{\exp[-\textstyle\sum(M\text{age}_f - M\text{age}_o)]\},$$

where $M\text{age}_f$ = natural mortality at the first age of full recruitment; and $M\text{age}_o$ = natural mortality at the oldest age in the population.

Reproductive seasonality.— Gonads were collected from fish caught on headboats. Port agents assigned sex after visual examination of the gonads (rounded cross section: females; triangular cross section: males). As time permitted, whole gonads were dissected out of the fish and preserved on ice for transport back to the laboratory. Gonads were weighed to the nearest 0.01 g and were staged using the gonad macroscopic classification scheme of Brown-Peterson et al. (2011). For this study, we visually assigned sex and stage only to mature fish that we could confidently identify to sex. We did not include immature fish or transitioning fish due to possible inaccuracies involved with trying to visually sex or stage these fish, respectively, without the aid of histological analyses. We assessed reproductive seasonality using monthly plots of (1) mean gonadosomatic index (GSI),

$$\text{GSI} = (\text{gonad wight/whole weight} \times 100),$$

and (2) the relative proportion of female gonadal development stages (mature females only).

RESULTS

Age Determination and Timing of Opaque Zone Formation

In total, 450 Knobbed Porgy sagittae were sectioned. We counted opaque zones on 448 (99.6%) of them; two samples were illegible and dropped from the study. The Florida Keys–Dry Tortugas region accounted for 74% of the samples (n = 331), while 26% of the samples (n = 117) came from areas north of the Florida Keys (Table 1). Ninety-one percent (n = 410) of fish used were sampled from headboats, while the remainder (n = 38) came from the commercial sector.

An edge type was assigned to 100% of samples (n = 448) for analysis of opaque zone formation timing. Knobbed Porgy otoliths exhibited opaque edges during March–July, peaking in May (Figure 3). Opaque edges were not seen from August through February. Edge types were predominantly narrow translucent during July–October, followed by moderate to wide translucent from October through February. Wide translucent edges were found during March–June, coinciding with the peak occurrence of opaque edges in May. This progression of edge types provided conclusive evidence that opaque zones on Knobbed Porgy otoliths were annular marks.

We assigned calendar ages by increasing the annulus count by 1 for fish caught during January–July and having an edge type of 3 or 4. For fish caught in January–July

TABLE 1. Number of sagittal otolith samples used in the Knobbed Porgy age and growth study. Samples were collected from commercial and recreational fisheries landings along the coast of the southeastern United States in 2003–2016 (GA–SEFL = Georgia–southeast Florida).

State or area	Commercial	Recreational	Total
North Carolina	31	16	47
South Carolina		54	54
GA–SEFL	7	9	16
Florida Keys		331	331
Total	38	410	448

with an edge type of 1 or 2 or for fish of any edge type caught during August–December, calendar age was equivalent to the annulus count.

Opaque zones on Knobbed Porgy otoliths were not difficult to interpret (Figure 4), and edge types were assigned consistently between readers. The most consistent zone counts were made on the ventral side of the section, and zones were readily traceable from the sulcal groove out into the lateral plane. Between-reader APE was 6.07% (n = 352), close to the benchmark acceptable APE value of 5% (Campana 2001). Direct agreement between readers was 64%, and agreement within ±1 year was 94%. After a second reading, no samples were excluded from analysis due to reader disagreement. Ages determined by the second reader slightly overestimated 6 of the 15 ages (Figure 5).

Growth

Growth of Knobbed Porgy (n = 448) was modeled using fractional ages based on the birth month of April determined from the reproductive samples collected during this study. Knobbed Porgy ranged from 197 to 507 mm TL and from age 1 to 21, but only 23 fish were older than age 12. Growth, estimated from all samples in the study, was described by the following equation:

$$L_t = 461\left[1 - e^{-0.10(t+6.38)}\right].$$

Examination of our data indicated that Knobbed Porgy had two distinct growth patterns. The majority of our samples used in the aging analyses were from the Florida Keys (n = 331), and these fish ranged in age from 1 to 12 years and in size from 197 to 365 mm TL (Table 2). Fish from a combined area encompassing North Carolina through southeast Florida (n = 117; northern region) ranged in age from 2 to 21 years and in size from 262 to 507 mm TL (Table 3). Mean age of fish from the Florida Keys was 4.36 years (n = 331; SE = 0.09), while the mean age of northern region fish was 8.96 years (n = 117; SE = 0.40). Average size differed between regions as well; mean TL of Knobbed Porgy from the Florida Keys was 294 mm (n = 331; SE = 1.41), while the mean TL of northern region fish was 373 mm (n = 117; SE = 4.91). An ANOVA of length at age revealed significant differences ($P \leq 0.05$) by region for 8 of the 11 ages for which there were enough samples to compare regions (Table 4; Figure 6). Based on these analyses, we determined that it was not appropriate to pool the data for estimation of growth parameters, and we re-estimated the von Bertalanffy growth models for each region, resulting in the following equations:

$$\text{Northern region } (n = 117)\text{: } L_t = 408\left[1 - e^{-0.29(t+1.38)}\right]$$

and

$$\text{Florida Keys } (n = 331)\text{: } L_t = 323\left[1 - e^{-0.38(t+2.29)}\right].$$

There were very few fish younger than age 2 available to us, and we had a single fish smaller than 200 mm TL. A paucity of smaller, younger fish is often due to gear selectivity. All fish in our study were from fishery-dependent sources, and the smallest fish were probably excluded by

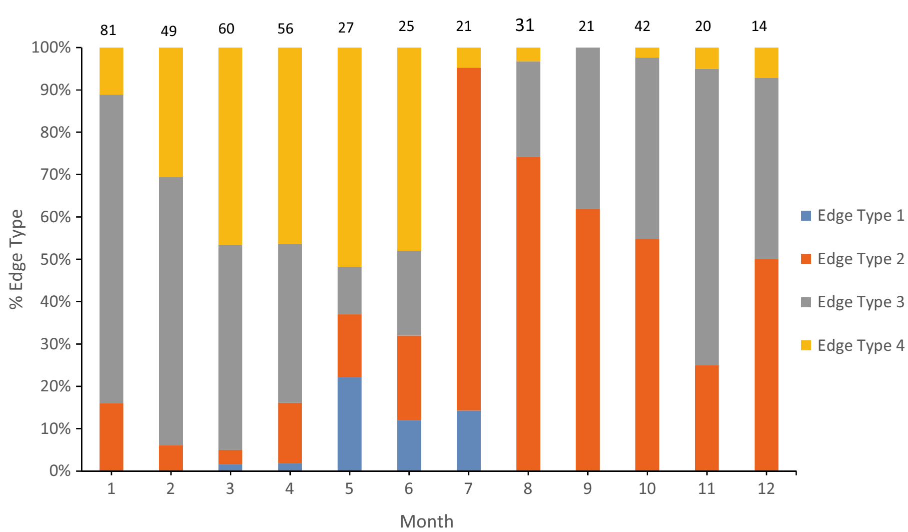

FIGURE 3. Monthly percentage of all otolith edge types for Knobbed Porgy collected from the southeastern United States, 2003–2016. Edge codes are as follows: 1 = opaque zone on edge, indicating annulus formation; 2 = small translucent zone, <30% of previous translucent zone; 3 = moderate translucent zone, 30–60% of previous translucent zone; and 4 = wide translucent zone, >60% of previous translucent zone. Sample sizes are shown above the columns.

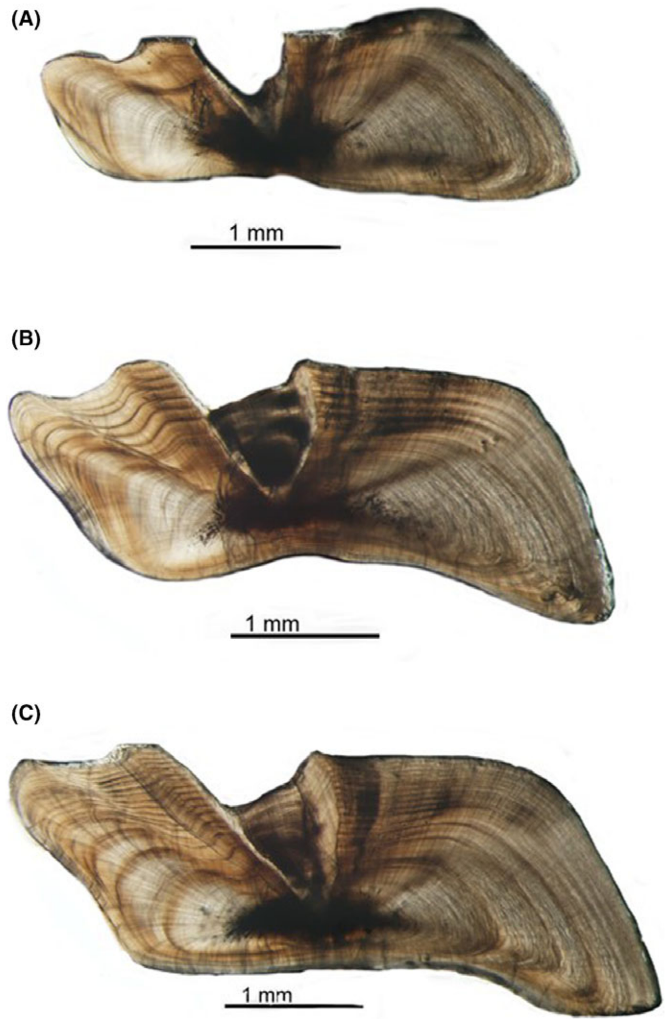

FIGURE 4. Sections of otoliths from Knobbed Porgy: (**A**) 282-mm TL, 2-year-old fish; (**B**) 315-mm TL, 8-year-old fish; and (**C**) 475-mm TL, 15-year-old fish. Age was determined by counting opaque zones along the dorsal axis and sulcal groove using transmitted light at 12.5× magnification.

the hook size used by fishers. Additionally, fishers likely select for larger fish, and existing aggregate-species bag limits might lead to the culling of smaller fish if they are caught. Thus, the model was not able to accurately estimate size at the earliest ages, resulting in the large negative estimates of t_0. We therefore re-estimated the growth models with McGarvey and Fowler's (2002) bias-correction method, which adjusts for the bias imposed by minimum size limits or other selectivity factors imposed by the fishery using a left-truncated normal probability density function of length and assuming a zero probability of capture below the minimum size limit. We re-estimated the growth models with t_0 freely estimated and assuming an effective minimum size limit of 230 mm TL for the coastwide and Florida Keys models and 260 mm TL for the northern region model. We applied the full, untruncated normal likelihood to specimens not subject to the minimum size limit. Parameters were then estimated by minimizing the negative sum of log-likelihoods using AD Model Builder. The resulting equations are (Figure 7)

$$\text{Coastwide } (n = 448)\text{: } L_t = 412\left[1 - e^{-0.20(t+1.97)}\right];$$

$$\text{Northern region } (n = 117)\text{: } L_t = 403\left[1 - e^{-0.38(t+0.0001)}\right];$$

and

$$\text{Florida Keys } (n = 331)\text{: } L_t = 326\left[1 - e^{-0.42(t+1.61)}\right]$$

(associated parameter SEs: coastwide, $L_\infty = 22.5$, $K = 0.08$, $t_0 = 2.07$; northern region, $L_\infty = 11.99$, $K = 0.09$, $t_0 = 0.003$; Florida Keys, $L_\infty = 12.09$, $K = 0.23$, $t_0 = 1.83$).

Body Size Relationships

Visual examination of a scatter plot of the residuals from the nonlinear model fits of the *W*–TL and *W*–FL relationships for Knobbed Porgy exhibited multiplicative error (variance increasing with size). We concluded that a linearized $\log_e$ transform fit of the data was appropriate, resulting in the following equations:

$$W = 3.03 \cdot \log_e(\text{TL}) - 11.20$$

and

$$W = 2.79 \cdot \log_e(\text{FL}) - 9.44$$

(for the *W*–TL equation: $n = 12{,}732$, $r^2 = 0.92$, $P < 0.0001$, $\text{SE}_a = 0.05$, $\text{SE}_b = 0.01$; for the *W*–FL equation: $n = 3{,}119$, $r^2 = 0.90$, $P < 0.0001$, $\text{SE}_a = 0.09$, $\text{SE}_b = 0.02$). These equations were transformed back to the form $W = aL^b$ after adjusting the intercepts for log-transformation bias (Beauchamp and Olson 1973). The resulting equations are

$$W = (1.38 \times 10^{-5})\text{TL}^{3.03}$$

and

$$W = (7.99 \times 10^{-5})\text{FL}^{2.79}$$

(for the *W*–TL equation: $n = 12{,}732$, mean square error [MSE] = 0.023; for the *W*–FL equation: $n = 3{,}119$, MSE = 0.016). Length–length relationships are described by the equations

$$\text{TL} = 1.07 \cdot \text{FL} + 22.93$$

and

$$\text{FL} = 0.91 \cdot \text{TL} - 12.54$$

(for the FL to TL [top] equation: $n = 3{,}173$, $r^2 = 0.97$, $P < 0.0001$; for the TL to FL [bottom] equation: $n = 3{,}173$, $r^2 = 0.97$, $P < 0.0001$).

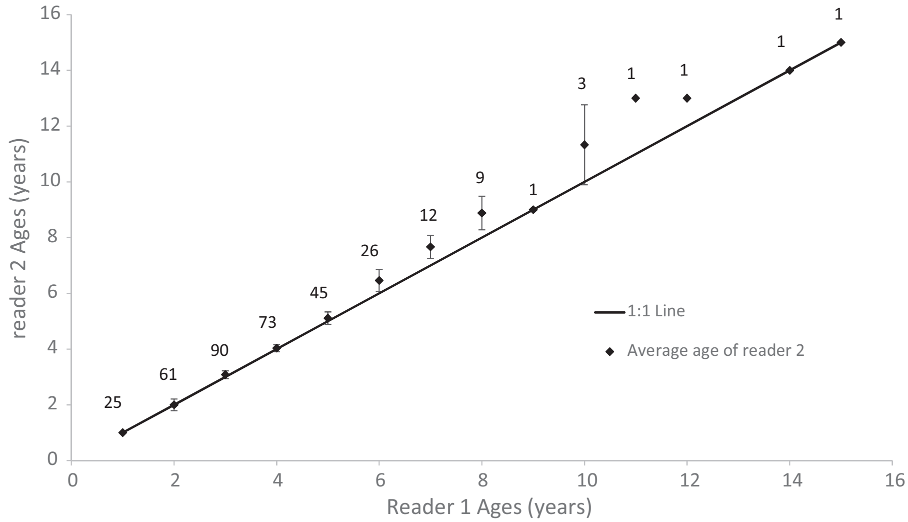

FIGURE 5. Age bias plot for 352 Knobbed Porgy sampled from the southeastern United States (2003–2016) and aged by two primary readers. The first reader's age estimates (*x*-axis) are plotted against the second reader's mean age estimates for the same-aged fish (*y*-axis). Error bars are 95% confidence intervals. Sample sizes for each age are given above the data points.

TABLE 2. Observed mean TL (mm; SE in parentheses) at age, predicted mean TL at age from the von Bertalanffy growth model, and estimated natural mortality (*M*) at age (Charnov et al. 2013) for Knobbed Porgy collected from the Florida Keys in 2015–2016. Mortality estimates from the Charnov et al. (2013) method are presented both unscaled and scaled to the Hewitt and Hoenig (2005) *M* estimate.

Age	*n*	Mean (SE) observed TL	TL range	Predicted TL	Unscaled *M* (year^{-1})	Scaled *M* (year^{-1})
1	6	238 (9)	197–255	221	0.67	0.55
2	34	266 (2)	235–292	256	0.56	0.46
3	70	282 (2)	230–320	279	0.51	0.41
4	89	295 (2)	250–347	294	0.47	0.38
5	62	303 (3)	247–345	303	0.45	0.37
6	34	308 (4)	272–355	309	0.44	0.36
7	19	315 (6)	270–365	313	0.43	0.35
8	8	318 (6)	292–347	316	0.43	0.35
9	4	315 (6)	302–330	318	0.43	0.35
10	2	331 (6)	325–337	319	0.42	0.34
11	2	325 (20)	305–345	320	0.42	0.34
12	1	327		320	0.42	0.34

Natural Mortality

Estimates of *M* were 0.35 and 0.20 year^{-1} for Knobbed Porgy from the Florida Keys and the North Carolina–southeast Florida region, respectively, using Hewitt and Hoenig's (2005) age-invariant method. Age-varying *M* estimates obtained by the Charnov et al. (2013) method 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 midpoint better represents the average annual size and gives the median value of *M* for that age. Another reason for using the midpoint was that the Charnov et al. (2013) method cannot mathematically calculate *M* for age 0. We present age-specific *M* estimates both scaled and unscaled to the Hewitt and Hoenig (2005) static estimate.

For Knobbed Porgy from the Florida Keys, the Hewitt and Hoenig (2005) method estimated 6% cumulative survivorship to the oldest age for the fully recruited ages, and the Charnov et al. (2013) method estimated 3% cumulative survivorship. For northern region fish, survivorship was estimated to be 9% using the Hewitt and Hoenig (2005) method and 1% using the Charnov et al. (2013) method. Use of all ages in the survivorship estimates would include high mortality that likely occurs in younger

TABLE 3. Observed mean TL (mm; SE in parentheses) at age, predicted mean TL at age from the von Bertalanffy growth model, and estimated natural mortality (M) at age (Charnov et al. 2013) for Knobbed Porgy collected from North Carolina–southeast Florida (i.e., northern region) in 2003–2016. Mortality estimates from the Charnov et al. (2013) method are presented both unscaled and scaled to the Hewitt and Hoenig (2005) M estimate.

Age	n	Mean (SE) observed TL	TL range	Predicted TL	Unscaled M (year^{-1})	Scaled M (year^{-1})
2	3	281 (13)	262–307	208	0.79	0.42
3	12	296 (7)	264–345	268	0.59	0.32
4	7	313 (14)	264–360	310	0.50	0.27
5	5	369 (11)	343–390	339	0.45	0.24
6	8	383 (613)	327–432	359	0.42	0.23
7	8	365 (15)	310–434	373	0.40	0.22
8	20	385 (12)	343–445	383	0.39	0.21
9	11	382 (7)	328–441	390	0.38	0.21
10	11	401 (18)	297–507	395	0.37	0.21
11	4	407 (12)	391–441	398	0.37	0.20
12	6	410 (19)	357–482	401	0.37	0.20
13	2	395 (38)	357–433	402	0.36	0.20
14	5	377 (11)	352–402	403	0.36	0.20
15	3	428 (40)	372–505	404	0.36	0.20
16	6	424 (20)	342–475	405	0.36	0.20
17	4	391 (14)	355–425	405	0.36	0.20
18	1	362		405	0.36	0.20
19				406	0.36	0.20
20	1	425		406	0.36	0.20
21	1	398		406	0.36	0.20

TABLE 4. Analysis of variance (ANOVA) results comparing length at age by geographic region (North Carolina–southeast Florida versus the Florida Keys) for individual ages of Knobbed Porgy sampled in 2003–2016. A double asterisk (**) indicates a high probability of significant difference between regions.

Age	n	ANOVA results
2	37	$F = 0.9$, $P = 0.34$
3	82	$F = 2.97$, $P = 0.08$
4	96	$F = 2.95$, $P = 0.09$
5	67	$F = 29.95$, $P = 0.0001$**
6	42	$F = 52.85$, $P = 0.0001$**
7	27	$F = 20.76$, $P = 0.0001$**
8	18	$F = 28.60$, $P = 0.0001$**
9	24	$F = 21.62$, $P = 0.0001$**
10	13	$F = 12.04$, $P = 0.0006$**
11	6	$F = 12.99$, $P = 0.0004$**
12	7	$F = 8.51$, $P = 0.0037$**

age-classes and is not accounted for when using only fully recruited ages. When we used all ages, survivorship was similar between fish from the Florida Keys (ages 0–12) and fish from the northern region (ages 0–21): 1% using Hewitt and Hoenig's (2005) constant M and 0% using the Charnov et al. (2013) age-specific M estimates.

Reproductive Seasonality

Gonads from 257 individuals (109 males and 148 females) were assessed for reproductive development. Since the majority of fish used in the reproductive portion of this study came from the Florida Keys ($n = 248$), we removed the nine northern fish from the reproductive analyses. Knobbed Porgy ovaries began developing in December, followed by the formation of yolked oocytes in January and mostly hydrated oocytes from February to April, and a majority of fish were in a regressing or resting gonad stage from May to November (Figure 8A). A plot of mean monthly GSI (Figure 8B) indicated that gonads made up the highest percentage of body weight in March for male Knobbed Porgy and in April for females. Two fish were visually identified as transitional, and 140 fish were identified as unknown sex or immature; these fish were not used in the analyses due to uncertainty in accurately identifying transitioning protogynous fish or in discerning immature fish from a resting/regressing stage without histology. Mean length and age data for Knobbed Porgy from our samples showed the pattern expected in a protogynous species. Mean sizes of fish sampled were 279 mm TL ($n = 182$; SE = 1.68) for females and 313 mm TL ($n = 124$; SE = 1.85) for males. Mean ages were 3.5 years ($n = 182$; SE = 0.1) for females and 5.5 years ($n = 124$; SE = 0.17) for males. Females comprised the

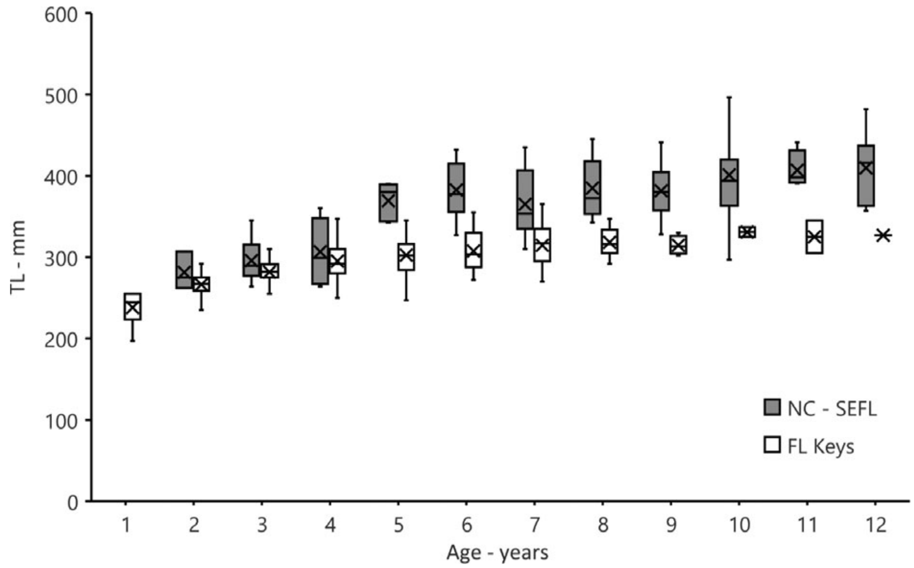

FIGURE 6. Paired mean observed TLs at age of Knobbed Porgy caught from North Carolina–southeast Florida (NC–SEFL) compared to fish caught from the Florida Keys (FL Keys). The box-and-whisker plots indicate the mean (×), the median (horizontal bar), the second through third quartiles (column), and the first and fourth quartiles (whiskers).

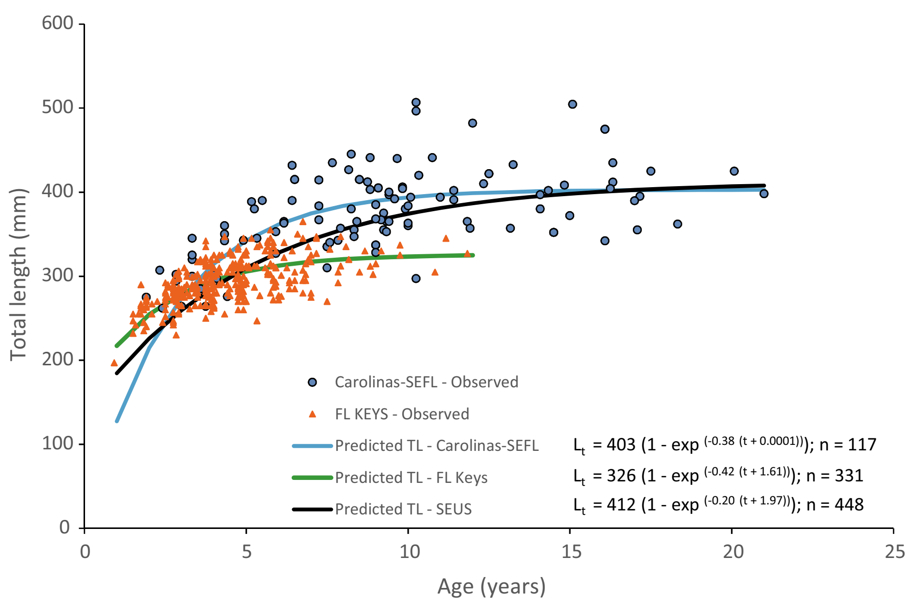

FIGURE 7. Comparison of observed fractional TL at age of Knobbed Porgy to von Bertalanffy growth curve predicted TLs for the Florida Keys (FL Keys), North Carolina–southeast Florida region (Carolinas–SEFL), and coastwide southeastern U.S. (SEUS) region. All curves are size limit bias-corrected model runs (following the method of McGarvey and Fowler 2002).

smaller size-classes and younger ages in the samples (Figure 9), with the older and larger fish being primarily males, a pattern expected for protogynous fish.

DISCUSSION

Otolith edge analysis demonstrated that Knobbed Porgy deposited one annulus per year from March to July, with peak annulus formation occurring in May. Using measurements from the focus to each annulus on scales, Horvath et al. (1990) concluded that Knobbed Porgy from North Carolina and South Carolina initiated annulus deposition in June and July. Other members of the family Sparidae in the SEUS have similar timing of increment formation (see the review by Burton et al. 2017).

Initially, Knobbed Porgy grew rapidly in both geographic regions through age 4, but the fish from the northern area continued to grow at a faster rate compared to fish from the southern area, attaining larger sizes at age. Average observed sizes of Knobbed Porgy from the Florida Keys were 266, 303, and 331 mm TL for ages 2, 5, and 10, respectively, whereas fish in the northern region attained average sizes of 281, 369, and 401 mm TL at the same respective ages (Table 2). Our study contained only five fish older than age 9 (1.5%) from the southern region compared to 44 fish older than age 9 (37%) from the northern region. Knobbed Porgy from the southern region exhibited a longevity similar to that found in a previous study of Knobbed Porgy (Borden 2001) and in a study of Whitebone Porgy *Calamus leucosteus* (Waltz et al. 1982)—a maximum age of 12 years in each case—and these studies each had few fish older than age 8. Knobbed Porgy from our northern region, dominated by samples from North Carolina and South Carolina, had a longevity similar to values reported by Horvath et al. (1990) for fish from these states: 21 and 17 years, respectively. One possible contributing factor to this difference in maximum size and age attained between regions might be the substantially higher level of population and fishing pressure that is found in the southern portion of the range. Recreational fishing effort data from MRIP show that 69% of total SEUS recreational effort comes from south Florida (https://www.st.nmfs.noaa.gov/recreational-fisheries/data-and-documentation/queries/index). South Florida is densely populated, and excessive fishing pressure may be cropping the population before these fish have a chance to achieve their potential maximum growth. Another possible

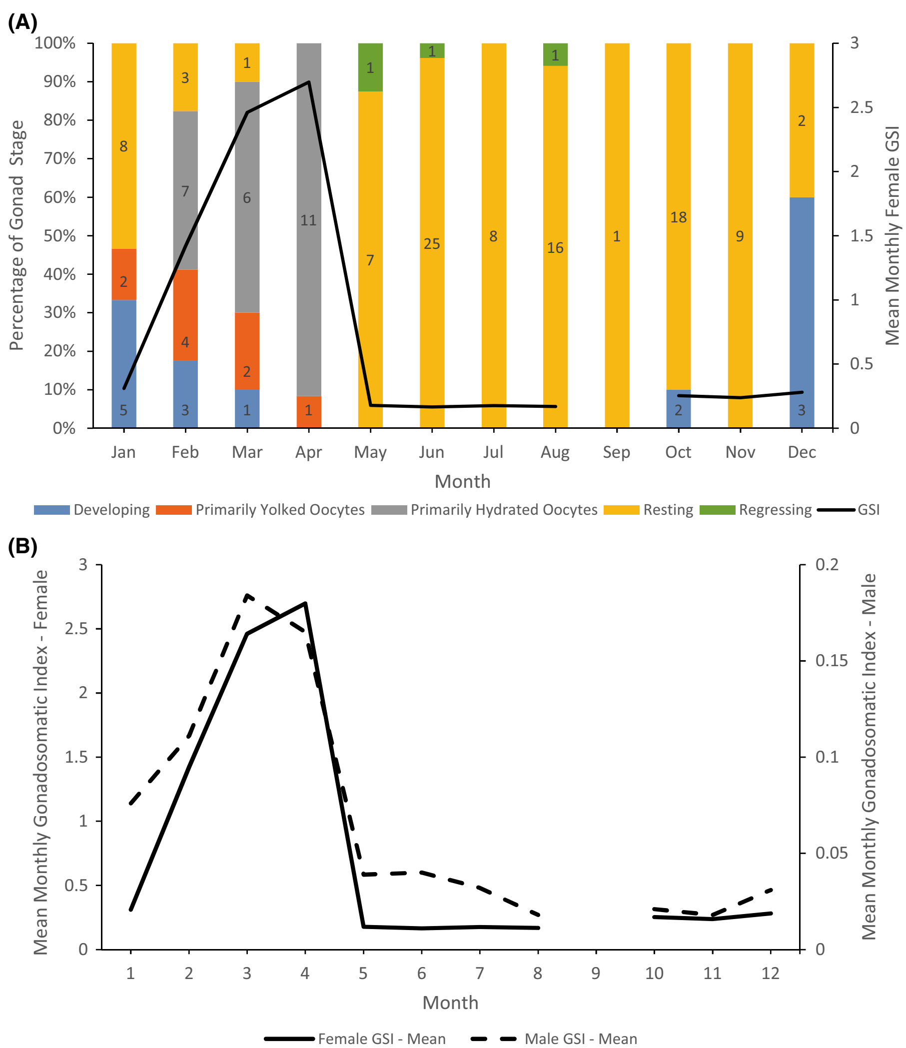

FIGURE 8. Reproductive seasonality of Knobbed Porgy collected from the Florida Keys in 2015–2016, as determined by (**A**) relative proportion of female gonadal development by month, determined macroscopically, presented with mean monthly gonadosomatic index (GSI) for females; and (**B**) mean monthly GSI for males and females. Sample sizes for each month or reproductive stage are shown on the columns in panel A.

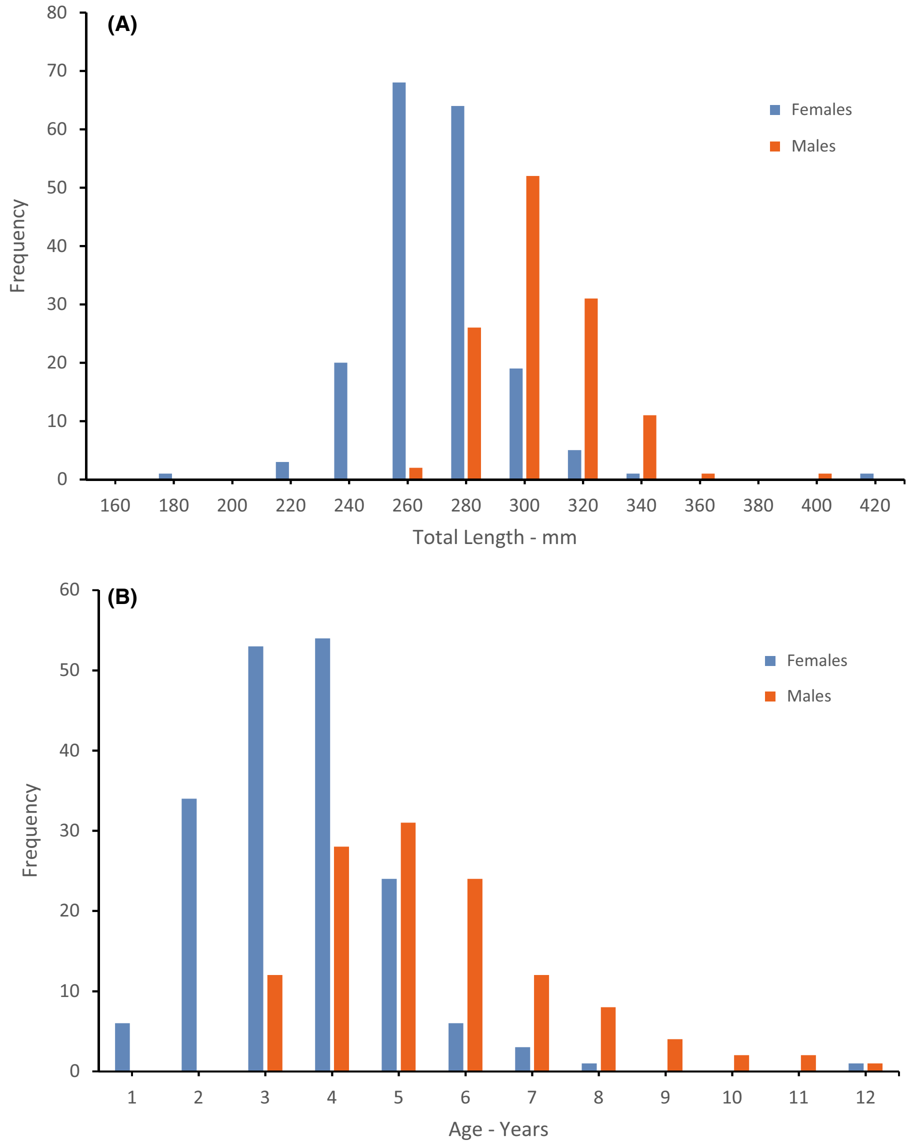

FIGURE 9. (**A**) Length frequency and (**B**) age frequency distributions of male and female Knobbed Porgy collected from the Florida Keys in 2015–2016.

explanation may be the origin of the samples themselves. Northern region fish were a mix of samples from the commercial fishery (32%) and recreational fishery (68%), while the Florida Keys fish were exclusively caught by recreational anglers. The SEUS commercial fishery and the recreational fishery off the Carolinas tend to fish at greater depths, and if Knobbed Porgy 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 et al. (1982) and Tyler-Jedlund and Torres (2015) used fishery-independent trawl gear to collect the preponderance of their specimens (Whitebone Porgy and the congeneric Littlehead Porgy *Calamus proridens*, respectively) from shallow water, but they augmented their samples with hook-and-line fishing on deeper reefs. These studies found that the average size of the fish increased with fishing depth.

Differences in mean size or age of snapper–grouper species by geographic region are well documented in the literature. Tyler-Jedlund and Torres (2015) found that Littlehead Porgy in the Gulf of Mexico grew larger in the northern portion of their study area than in the southern portion (i.e., Tampa Bay versus Charlotte Harbor, Florida). Gray Snapper *Lutjanus griseus* exhibited differences in maximum size and age between the northeast and southeast coast of Florida (Burton 2001). Potts and Manooch (2001) observed that White Grunts *Haemulon plumieri* from North Carolina and South Carolina achieved a maximum TL that was 150 mm larger than White Grunts from southeast Florida, although age ranges were similar between the two regions. Murie and Parkyn (2005) found a similar result for White Grunts along Florida's west coast: fish from a northern study area (Crystal River to Steinhatchee) were larger at age than fish from the southern study area (St. Petersburg to Port Richey), even though these two areas were separated by a distance of only 80.47 km (50 mi).

Since our study lacked any samples from fishery-independent sources, we lacked the smallest and youngest fish necessary to accurately estimate growth at the earliest ages, specifically 0–2 years, which is likely due to selectivity of the fishery-dependent gear. Our samples contained only six age-1 fish (the smallest was 197 mm TL, but the other five were 230 mm TL or larger). All age-1 fish were from the Florida Keys. The northern region samples contained no age-1 fish and only three age-2 fish, the smallest of which was 262 mm TL. The paucity of the youngest fish dictates caution in interpreting growth curves generated from these data. To account for this bias imposed by fishery selectivity, we re-estimated growth parameters using a bias-correction procedure, which reduced the initial starting point of the coastwide and northern region growth curves (Figure 7). There was little difference in the predicted sizes at youngest ages between estimation methods for fish from the Florida Keys.

The predicted maximum size of Knobbed Porgy from the Florida Keys (326 mm TL) was slightly larger than that of Littlehead Porgy from southwest Florida (306 mm TL; Tyler-Jedlund and Torres 2015). The age ranges were similar for these two species, with a maximum age of 12 years for Florida Keys Knobbed Porgy versus 10 years for Littlehead Porgy. Knobbed Porgy were larger in the northern region than in the Florida Keys, and the maximum observed size of 507 mm TL for northern fish in our study was basically equal to the maximum size of Knobbed Porgy (512 mm TL) reported by Horvath et al. (1990) in a study consisting of primarily fishery-dependent samples from North Carolina and South Carolina. The k-value for fish from the Horvath et al. (1990) study ($k = 0.17$) was about half of the value we calculated for our northern region fish. One possible reason for this is that our study included more intermediate size-at-age fish than the previous study. A larger number of intermediate sizes at age could result in a higher calculated k-value despite the presence of larger-sized fish. Maximum ages were similar, 21 versus 17 years, for the current study versus the Horvath et al. (1990) study. The oldest fish in the population are rarer; thus, the chance to encounter the maximum age might be explained by the difference in sample size between studies or the source of samples. Both studies relied on fishery-dependent sources; the only difference is that our study included some commercially caught fish, whereas the fishery-dependent samples in the Horvath et al. (1990) study were caught exclusively by recreational anglers on headboats. Since commercial fishing likely takes place in deeper waters, it is possible that the inclusion of commercial samples in the current study increased our chances of encountering the maximum age in the population.

Natural mortality of fish is an important life history input into stock assessments. We herein provide the first literature estimates of M for Knobbed Porgy. The region-specific estimates of M (southern region: $M = 0.35$; northern region: $M = 0.20$) generated from the longevity-based equation of Hewitt and Hoenig (2005) were reasonable for the fully recruited ages in our study. The estimate for the Florida Keys was similar to the M estimate of 0.32 for the Jolthead Porgy *Calamus bajonado*, a species with a similar longevity (13 years: Burton et al. 2017). Since the longevity of fish in the northern region was higher, we expected M to be smaller. We do not believe that either of these M estimates is suitable to apply to younger ages, as younger fish will have significantly higher natural mortality due to predation. Age-specific M values from the Charnov et al. (2013) method are more appropriate estimates for the ages younger than the age at full recruitment to the fishery. The Charnov et al. (2013) estimates of M for the youngest ages were twice the value of the Hewitt and Hoenig (2005) estimate for Florida Keys fish and four times that for the northern region fish. Age-specific estimates of M for the age at full recruitment to the fishery (age 5 for southern region fish; age 10 for northern region fish) were slightly higher than the estimate of constant M for the southern region fish and twice the value of constant M for the northern region fish. The value of M for the older ages decreased until stabilizing at 0.42 (age 10) for southern region fish and 0.36 (age 13) for northern region fish (Tables 2, 3).

Consideration should be given to the reliability of the life history parameters used in the estimation of M. In this study, emphasis on size-based estimators may not be appropriate. Estimates of L_∞ are closely, inversely correlated with k. The lack of the younger, smaller fish that are needed to accurately describe early fish growth will affect the trajectory of the growth curve and the value of L_∞. This will in turn influence the value of M. In this case, we have more confidence in the maximum age as the primary input into the estimate of M because it is similar to what was found for this species in a previous study (Horvath et al. 1990). Although the possibility exists that the maximum age of Knobbed Porgy is greater than 21 years, to date we have found no evidence to support this.

Natural mortality on the youngest fish in a population is always high, but once the fish approach the asymptote of their maximum size, M levels out (Lorenzen 1996). Survivability to the maximum age offered a sense of the reliability of M estimates because it was calculated on the fully recruited ages in the population (when fish were at or near the asymptote of their growth). The fish from the Florida Keys approached L_{∞} by age 4 and fully recruited to the fishery by age 5. Based on an M value of 0.35, survivability to the oldest age was 6%. Using the Charnov et al. (2013) age-specific M, the chance of surviving to the oldest age was 3%. Given that Knobbed Porgy have the potential to live longer than was suggested by data from the Florida Keys, a lower value of M seems reasonable. Thus, we recommend that the age-specific vector of M (Charnov et al. 2013) be scaled so that its cumulative M over the range of fully recruited ages equals the cumulative M over these ages for the Hewitt and Hoenig (2005) estimate. Likewise, Knobbed Porgy from the northern region reached the asymptote of growth by age 9 and fully recruited to the fishery by age 10. It is interesting to note the late age of full recruitment, which may suggest that the younger and smaller fish were not in the areas where the fishery was operating or that they were not retained in the catch. Age-10 and older fish represented 38% of our northern sample set. For the fully recruited ages, survivorship to the oldest age based on the Hewitt and Hoenig (2005) estimate of M was 9%. Using the Charnov et al. (2013) age-specific estimates of M, the chance of surviving to the oldest age was 1%. Because our sample size for Knobbed Porgy from the northern region was small and porgy species have been shown to live in excess of 20 years, we believe it is feasible that close to 9% of the population will live to the oldest age found in this study. As with the Florida Keys fish, we recommend scaling the age-specific vector of M for the fully recruited ages to the Hewitt and Hoenig (2005) estimate.

Our findings of peak reproductive activity from February through April are similar to findings by Horvath et al. (1990) and Borden (2001), who determined based on GSIs that peak spawning occurred during May and June for fish primarily from North Carolina and South Carolina. It is highly plausible that the inclusion of a large percentage of fish from a more southerly region (the Florida Keys) in our samples had an effect on our findings, as fish from a warmer temperature regime may spawn earlier in the year than northern fish. Horvath et al. (1990) postulated from their data that Knobbed Porgy underwent sexual transition between 300 and 500 mm TL. They did not speculate on size or age at maturity, and we would be hesitant to do that as well, given that we did not employ histological analysis for this study. Although fully developed gonads can be staged macroscopically with some accuracy, we are not certain that we could correctly differentiate immature specimens from regressing or resting specimens, and this might lead to a flawed estimate of age or size at first maturity.

Conclusions

This updated study of Knobbed Porgy provides life history information from geographic regions previously unstudied. We have shown that Knobbed Porgy from the northern region of their distribution achieve greater size and longevity than southern individuals, a conclusion that has relevance to fishery management. Given the magnitude of overall landings of Knobbed Porgy by the various fisheries when compared to other high-profile species, it is unlikely that this species will be the subject of a stock assessment by federal fisheries scientists in the near future. However, the differences in longevity and size at age highlighted here could affect yield calculations and thus have an influence on the setting of ACLs. Fishery managers may consider whether Knobbed Porgy from the two regions need to be managed under different ACLs. There is no evidence from the literature that fish from these two areas are genetically distinct, but this could be an area for future research. We provide the first published data on Knobbed Porgy reproduction in Florida waters, confirming a discrete late-winter reproductive season. We have shown that otolith sections from Knobbed Porgy are reliable aging structures containing easily enumerable annuli. We also provide the first reported estimates of M for Knobbed Porgy in any geographic area. For fishery managers responsible for setting annual catch quotas, our results offer the most current scientific data and eliminate the need for reliance on the suboptimal data streams that are more common in data-limited management scenarios, such as catch histories (Carruthers et al. 2017).

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