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Age validation of the northern stock of black sea bass (*Centropristis striata*) in the Atlantic Ocean

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Abstract—Inaccurate age determinations can have serious effects on age-structured stock assessments that are used to manage fish populations. A recent push toward using an age-based model for the northern stock of black sea bass (*Centropristis striata*) led to an increase in direct aging effort in the northeastern United States. Yet, no large-scale otolith age validation study for this stock exists. We examined the annual periodicity of otolith growth in this species through marginal increment analysis with otoliths of fish from 3 age groups (fish of ages 1–2, ages 3–4, and ages 5+) and from 2 regions, north and south of the Hudson Canyon. Additionally, we validated the assignment of the first annulus through modal length–frequency analysis of young-of-the-year fish. The marginal increment ratio differed between age groups throughout the year, supporting the separation of these samples for age validation purposes. Higher ratios were observed in black sea bass from the region south of the Hudson Canyon throughout most of the year; however, fish from north of the canyon appear to accrete more otolith material during winter. Annual growth increments were deposited once per year, in spring or early summer, for all fish. In addition, absolute age was validated for the first time for this stock.

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The range of the northern stock of black sea bass (*Centropristis striata*) off the coast of the northeastern United States extends from Cape Hatteras, North Carolina, to the Gulf of Maine (Mercer, 1978). This species can live to 15 years of age and reach approximately 60 cm in total length (TL) (Shepherd and Lambert, 1996). Black sea bass support an important commercial fishery and a valued recreational fishery that is worth over half the total annual landings (Musick and Mercer, 1977; NEFSC, 2017). This stock experienced a recent range expansion, linked to warming ocean trends (Bell et al., 2015; McBride et al., 2018), into coastal Maine waters—an area where this species had been rarely seen historically (Bigelow and Schroeder, 1953). The importance of this fishery, and the gaps in data on growth, age, migration patterns, and stock structure of black sea bass, led to a push for additional research on this species.

The accuracy of age data is crucial to stock assessments; errors in these estimates can undermine fisheries management and lead to overexploitation (Campana, 2001). A catch-at-age stock assessment model for the northern Atlantic stock of black sea bass was rejected in 2012, because of insufficient age data (NEFSC, 2012; ASMFC[1]). In response, agencies along the Atlantic coast of the United States began to collect and age samples of black sea bass, and a statistical catch-at-age model was accepted in 2016 (NEFSC, 2017). However, despite the increase in direct aging, there has been little effort to complete a large-scale age validation study for this stock.

Age estimates for black sea bass are primarily done by using otoliths, which are often the most accurate aging structure (Casselman, 1983). Calcium carbonate layers are accreted onto otoliths daily, and a seasonal banding pattern is formed, with bands differentiated as opaque or translucent (Campana and Thorrold, 2001). Age is determined

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[1] ASMFC (Atlantic States Marine Fisheries Commission). 2013. Proceedings of the 2013 black sea bass ageing workshop, 17 p. ASMFC, Arlington, VA. [Available from website.]

by counting band pairs (one opaque and one translucent band) from the otolith core (birth) to the otolith edge (age at capture), making the assumption that one band pair equals 1 year in a fish's life (Beamish and McFarlane, 1983). Errors occur when growth layers identified as annuli (yearly growth bands) do not truly correspond to 1 year of growth (McBride, 2015). Validation of an aging method is a process that verifies that putative annuli occur once per year. Although there have been attempts to validate otolith aging methods for the northern stock of black sea bass, these studies were limited by small ranges, few age classes, or modest sample sizes (Mercer, 1978; Robillard et al.[2]). Thus far, no large-scale age validation study has been done for the northern stock of black sea bass with samples representative of those included in the stock assessment process (i.e., samples caught with a variety of gear types and from a variety of locations, sources, and age classes). Furthermore, no work has yet been published that validates the first annulus on otoliths for black sea bass in the northern stock, an imperative step to validating absolute age (Campana, 2001).

Verifying the location of the first annulus is a necessary step in validating aging methods; otherwise, age estimates could be biased in either direction (Campana, 2001). Additionally, the identification of the first annulus is often a primary source of error in aging practices (Campana, 2001) and is a known issue in reading otoliths of black sea bass (Dery and Mayo, 1988; ASMFC[1]). Reported discrepancies between identification of age-0 versus age-1 fish contributed to the exclusion of fall indices in the latest stock assessment (NEFSC, 2017).

The goal of this study was to identify the timing of annulus deposition and validate the current otolith aging method for the entire geographic range and observed age classes of the northern stock of black sea bass in the Atlantic Ocean, by using marginal increment analysis (MIA) and first annulus validation for young of the year (YOY).

Materials and methods

Sample collection and selection

The most common method of age validation is MIA, which measures growth from the last fully completed annulus to the edge of the aging structure (i.e., measures the marginal increment) at different times throughout the year (Campana, 2001). Marginal increment analysis requires samples to be collected across an entire year, preferably monthly, as well as across the observed age range of the selected species (Beamish and McFarlane, 1983; Campana, 2001). Constraints related to obtaining adequate sample sizes for individual ages led to the creation of 3 age bins, ages 1–2 (AB1), ages 3–4 (AB2), and ages 5 and older (AB3), which also account for growth differences among the age groups (Pilling et al., 2000; Winner et al., 2017). Age determinations supplied by collaborating institutions were used to classify samples to begin processing. Otoliths without an age estimate were assigned to classes on the basis of an age–length key created from samples previously aged by staff of the Massachusetts Division of Marine Fisheries (MA-DMF) (senior author, unpubl. data).

To capture potential growth variability between regions, a goal of 40 samples per age bin was chosen for MIA. Sagittal otoliths from samples of black sea bass were provided by collaborators across the northeastern United States who acquired them from both fishery-dependent and fishery-independent sources (Table 1, Fig. 1). A total of 1440 otoliths from black sea bass were initially subsampled for this study; however, 49 of those otoliths were excluded because they were broken or poorly sectioned and could not be reliably aged or measured. Additionally, marginal increment ratios (MIRs) could not be calculated for fish that were age 1 prior to annulus formation as a result of the use of 1 January as the year-class advancement date (Dery and Mayo, 1988) and were removed from analysis (number of samples [*n*]=23). Samples of black sea bass used for MIA (*n*=1335) were collected every month of the year, and they ranged in size from 100 to 605 mm TL and in age from 1 to 12 years (Table 2, Fig. 2). Sex data was available for 854 samples: 490 females (110–500 mm TL) and 364 males (130–546 mm TL).

Assessment of the first annulus can be completed 1) by measuring the completed first annulus of YOY in the season of annulus formation and 2) by tracking the modal length frequency of the smallest fish in the population to confirm that measured samples are YOY (Campana, 2001; Carvalho et al., 2017). Age-0 samples for first annulus validation were collected in the fall during the MA-DMF resource assessment survey (September 2017, *n*=30) and during the Northeast Fisheries Science Center (NEFSC) bottom-trawl survey (October 2016, archive, *n*=3). Age-1 samples caught in the summer and used in MIA were also used for comparison. These samples were collected during the MA-DMF ventless-trap survey (July and August 2015–2017, otolith archive, *n*=36). Total lengths ranged from 35 to 120 mm for age-0 fish and from 110 to 207 mm for age-1 fish.

A reference collection (*n*=100) with ages spanning from 0 to 10 years was created by using otoliths archived by the MA-DMF. These samples were used to assess reader error before and after otolith aging was completed for this project and were independent of the samples used in MIA.

Sample preparation

Age estimates made by using whole otoliths tend to underestimate fish age and use of otolith sections has resulted in higher accuracy (Hyndes et al., 1992; Fowler and Short, 1998). Therefore, sectioned otoliths were used in this study. Additionally, completing marginal increment measurements

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[2] Robillard, E., J. W. Gregg, J. Dayton, and J. Gartland. 2016. Validation of black sea bass, *Centropristis striata*, ages using oxytetracycline marking and scale margin increments, 17 p. Stock Assess. Rev. Comm., SARC 62 working paper. [Available from Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 166 Water St., Woods Hole, MA.]

Table 1

States of the northeastern United States in whose waters off the Atlantic coast black sea bass (*Centropristis striata*) were captured during 2013–2017, number of samples (*n*), sampling years, range of final age estimates for samples, and fishery type in which and gear type by which fish were captured. Otoliths from sampled fish were used in marginal increment analysis and first annulus validation. Gear types include bottom trawl, ventless trap, gill net, and hook and line. The following collaborators were the sources of samples: Massachusetts Division of Marine Fisheries (MA-DMF), North Carolina Department of Environment and Natural Resources (NC-DENR), NOAA Northeast Fisheries Science Center (NEFSC), Northeastern University, Rhode Island Department of Environmental Management (RI-DEM) in collaboration with the Commercial Fisheries Research Foundation (CFRF) and Virginia Institute of Marine Science (VIMS), and Rutgers University.

Capture location	*n*	Sampling years	Final age range (years)	Fishery type	Gear type	Source
Massachusetts	538	2013–2017	0–8	Independent	Trawl, trap	MA-DMF
Massachusetts–North Carolina	201	2013–2016	2–11	Dependent	Trawl	NC-DENR
Massachusetts–North Carolina	377	2015–2017	0–6	Independent; Dependent	Trawl	NEFSC
Maine and Massachusetts	90	2013–2016	1–5	Independent; Dependent	Trap, hook and line	Northeastern University
Rhode Island	69	2017	2–7	Dependent	Trawl, trap, gill net	RI-DEM, CFRF, VIMS
New Jersey	93	2017	1–12	Independent	Trap, hook and line	Rutgers University

on whole otoliths is difficult because of their curvature and the presence of broad, diffuse bands; whereas, sectioned otoliths have a crisp line at the distal edge of an annulus from which to measure. Left-sided otoliths were selected preferentially for consistency. Otoliths were embedded with epoxy resin and hardener (West System[3], Gougeon Brothers Inc., Bay City, MI) in silicone molds. Transverse sections (0.5 mm thick) were cut along the dorsoventral plane, containing the otolith core (Fig. 3A), by using an IsoMet Low Speed Saw with a diamond blade (Buehler, Lake Bluff, IL). All otolith preparation used these methods, including preparation of samples for MIA, first annulus analysis, and the reference collection.

Otolith aging and measurements

In black sea bass, the outside edge of the opaque growth zone formed in winter is considered the annulus (Dery and Mayo, 1988). A date of 1 January was used for year-class advancement. Age determinations were made under a compound microscope (100× magnification) by placing sectioned otoliths on a glass slide with mineral oil. Each otolith was aged independently by 2 experienced readers without knowledge of fish size, capture location, or any previous age interpretations. If ages differed between readers, a consensus reading was required for final age determination. These ages were used to group samples into the 3 age bins for analysis, replacing the initial determination used to bin samples during the sample selection. Final ages for the reference collection were made following these same methods. To assess precision and bias, each person read otoliths in the reference collection (with samples randomized prior to each reading) before and after MIA samples were read.

Annulus measurements were made by using Image-Pro Premier, vers. 9.1 (Media Cybernetics Inc., Rockville, MD), a compound microscope-camera system (Axiostar Plus microscope, ZEISS Microscopy, Jena, Germany, and QImaging MicroPublisher camera, Teledyne Photometrics, Tucson, AZ). A straight line was drawn along the dorsal side of the sulcal groove, from the otolith core to otolith edge (radius), and the distal edge of each opaque band was marked (Fig. 3B). Measurements (in millimeters) from otolith core to each marked annulus were generated by the software on the basis of a coordinate plane.

Statistical analysis

All analyses and visualizations for this project were run by using statistical software R, vers. 3.6.1 (R Core Team, 2019). Paired ages from readings of black sea bass otoliths were evaluated for precision and aging bias by using Chang's coefficient of variation (CV) (Chang, 1982) and a modification of the Bland–Altman bias plot (McBride, 2015). Additionally, the precision of the age estimates of each reader was assessed by comparing each reader's reference collection session and the reference collection final ages. A CV below 5% is recommended for precision among readers for aging studies (Campana, 2001; McBride, 2015). Coefficients of variation were produced by using the FSA package, vers. 0.8.25 (Ogle et al., 2019), in R.

Marginal increments are expressed as a proportion of the previous year's growth (Hood et al., 1994; Winner

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[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

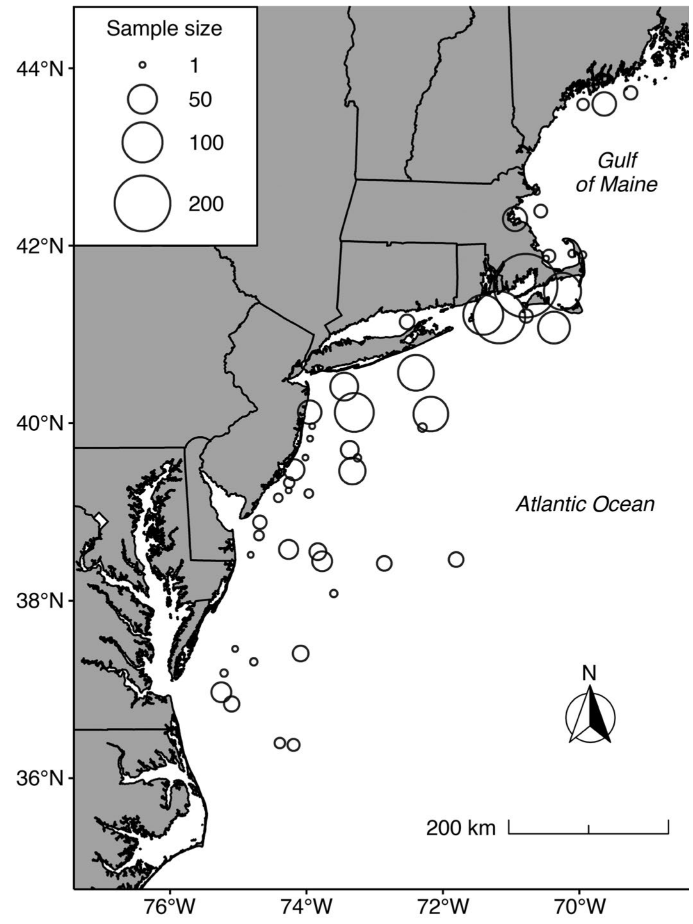

Figure 1

Map of locations where black sea bass (*Centropristis striata*) were caught in the Atlantic Ocean off the northeastern United States during 2013–2017. Sagittal otoliths were removed from sampled fish and used for marginal increment analysis and first annulus validation. Size of circles indicates the number of samples collected at each location.

et al., 2017), as the MIR (Vilizzi and Walker, 1999; Zlokovitz et al., 2003). If annuli are formed once per year, monthly MIR should indicate a sinusoidal pattern with only one minimum per year, when annulus formation is complete and new growth begins (Wenner et al., 1986; Pilling et al., 2000). Marginal increment ratios were calculated following Condini et al. (2014) by dividing the marginal increment (completed edge growth) by the measurement of the presumed previous year's growth (full band pair, one translucent band and one opaque band) (Fig. 3B):

$$MIR = (R_t - R_{t-1}) / (R_{t-1} - R_{t-2}),$$

where R_t = the otolith radius (core to edge);
R_{t-1} = the measurement from otolith core to the distal edge of the last opaque band; and
R_{t-2} = the measurement from otolith core to the distal edge of the penultimate opaque band.

A 2-way analysis of variance (ANOVA) was used to assess average MIRs between different times of year and among age bins, as recommended by Campana (2001). The Akaike information criterion (AIC) was used to identify the best model for analysis, varying predictors (*Month Bin*, *Age Bin*, and *Region*), additivity, and interactions. Month bins (e.g., January–February and March–April) were used instead of individual months because missing data would have precluded interactive models from running. Missing data were also the reason that region (i.e., capture location) could be included only as an additive predictor and not as an interactive one. The regions designated for this analysis were north and south of the Hudson Canyon, as described in the report for the latest stock assessment (NEFSC, 2017). This canyon begins 100 km from the mouth of the Hudson River and extends approximately 600 km to the southeast (NEFSC, 2017). Additionally, monthly average MIRs were used to visually assess the timing of annulus formation for each age bin.

The possibility of differences in growth of black sea bass between regions (Dery and Mayo, 1988), as well as the recent separation of the northern stock into 2 subunits north and south of the Hudson Canyon, motivated an analysis that included *Region* as an interactive predictor. In a 3-way ANOVA, seasons were used instead of month bins because of missing data. Seasons, chosen on the basis of information available about migration of black sea bass (they arrive inshore by April and leave by October or November; Drohan et al., 2007), were as follows: January, February, and March (winter); April, May, and June (spring); July, August, and September (summer); and October, November, and December (fall). Regions were designated as described previously, although a difference in sample sizes should be noted (north: n=970; south: n=365). Methods used to account for this unbalanced design are described at the end of this section. The AIC was used to identify the best model for analysis, varying predictors (*Season*, *Age Bin*, and *Region*), additivity, and interactions.

Because an ANOVA does not account for the cyclical nature of MIRs and because this lack of adjustment is a noted source of concern for MIA studies based solely on this statistical test (Okamura et al., 2013), a circular-linear model (see Okamura et al., 2013) was fit to the data from this study to analyze how many cycles (i.e., annuli) exist in a time span of 1 year. This method was used to assess AIC values for 3 models: models with no cycle (model N), 1 cycle (model A), and 2 cycles (model B) in the MIR data. This method was used separately for each age bin as well as for each region (with age bins combined). This analysis was completed in R, by using

Table 2

Number of samples of black sea bass (*Centropristis striata*), by month of capture and age estimate, from which sagittal otoliths were removed and used for marginal increment analysis. Ages in this table represent the final age assignments used in this study. Age bin 1 (AB1), age bin 2 (AB2), and age bin 3 (AB3) are provided to indicate which ages are included in each bin. Samples were collected in the Atlantic Ocean off the northeastern United States during 2013–2017. Blank cells indicate no otolith samples were available for that age bin and month combination.

Age bin	Age (years)	Month												
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
AB1	1				1		2	15	21	17	21	7		84
	2		13	22	24	42	43	29	23	29	32	18	6	281
AB2	3	15	17	20	7	24	13	21	20	22	15	10	16	200
	4	25	32	25	12	16	36	32	27	22	20	30	25	302
AB3	5	42	46	39	41	27	27	27	28	27	7	2	19	332
	6	1	4	9	5	16	15	12	11	10	1		4	88
	7		2	4	1	6		4	1	2			7	27
	8	1			2	1	1	1	1	1			5	13
	9	3	1		2									6
	11												1	1
	12			1										1
Total		87	115	120	95	132	137	141	132	130	96	67	83	1335

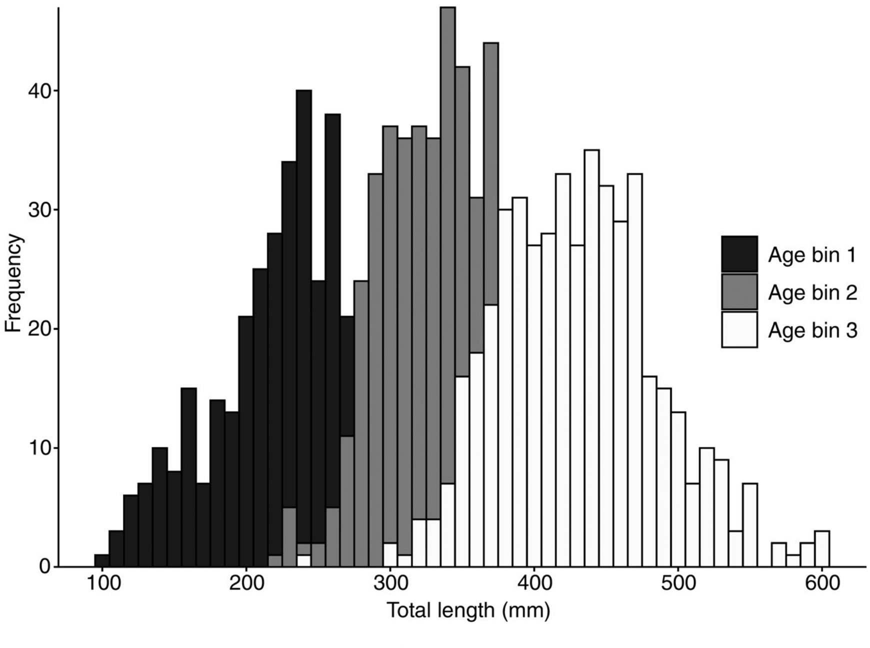

Figure 2

Length–frequency histograms for each age bin of black sea bass (*Centropristis striata*) from which sagittal otoliths were removed and used in marginal increment analysis. Samples were captured in the Atlantic Ocean off the northeastern United States between 2013 and 2017. Age bin 1 includes ages 1–2, age bin 2 comprises ages 3–4, and age bin 3 includes ages 5+.

code included in the supplemental material (SIII) of Okamura et al. (2013).

Measurements of otoliths from samples of age-0 black sea bass collected in the fall and age-1 black sea bass collected in summer were compared by using Welch's 2-sample *t*-test for first annulus validation. For age-1 fish sampled in summer, measurements were also compared with the first annulus measurements of all samples used

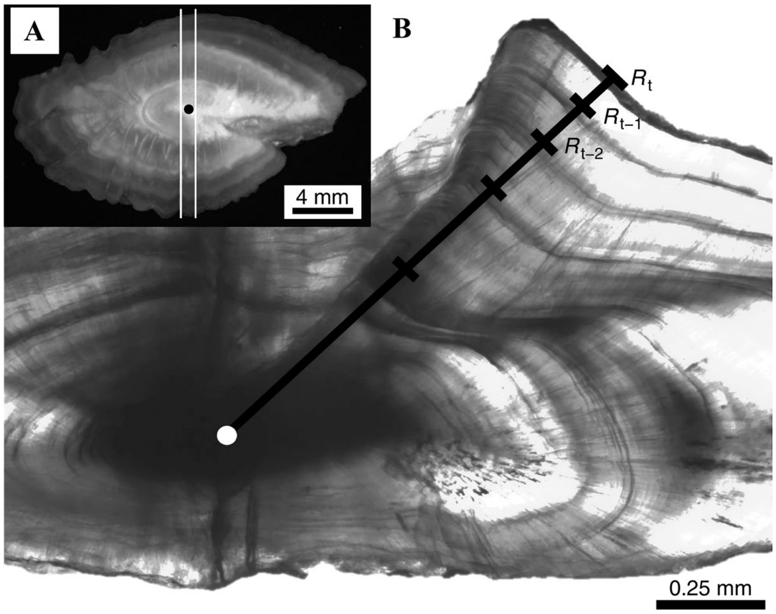

Figure 3

(**A**) Position of the transverse dorsoventral section (0.5 mm thick) taken through the core (black dot) of a whole sagittal otolith from a black sea bass (*Centropristis striata*) collected from Massachusetts in May 2015. (**B**) Measurements for marginal increment analysis on a sectioned otolith taken from the core (white dot) to the distal edge of each annulus (black bars); the black sea bass from which this otolith was removed was captured from Massachusetts in May 2014. The measurements are R_t, which depicts the otolith radius (core to edge); R_{t-1}, the distance to the final annulus (core to the last opaque band); and R_{t-2}, the distance to the penultimate annulus (core to the penultimate opaque band). The equation used to determine the marginal increment ratio (MIR) is $MIR=(R_t-R_{t-1})/(R_{t-1}-R_{t-2})$.

in MIA to confirm proper identification of the samples collected for this study. Length–frequency plots of the smallest fish (first 2 length modes) captured during the fall resource assessment survey (September 2016–2017) and the summer ventless trap survey (July–August 2016–2017) were evaluated to confirm identification of the fall age-0 and summer age-1 samples as YOY. Differences in first annulus measurements between otoliths from fish collected in the regions north and south of the Hudson Canyon were also compared with Welch's 2-sample *t*-test.

Assumptions for all statistical tests were evaluated by using visual diagnostic plots and were found to conform to assumptions of normality and homogeneity of variance. Type III sums of squares were used for both ANOVAs because of the unbalanced data. Post hoc multiple comparison analyses were conducted by using estimated marginal means, because sample sizes were not balanced among factor levels (Lenth, 2019), and Tukey's honestly significant difference test. A significance level of 0.05 was used in all statistical tests in this study. Model selection, ANOVAs, post hoc analyses, and visualizations were done by using R and the following packages in R: car, vers. 3.0-3 (Fox and Weisberg, 2019), emmeans, vers. 1.4.1 (Lenth, 2019), multcomp, vers. 1.4-10 (Hothorn et al., 2008), and ggplot2, vers. 3.2.1 (Wickham, 2016).

Results

Marginal increment analysis

Initial independent age determinations agreed for 1222 otoliths (89%); a consensus reading was required for the remaining samples. Precision was high and bias was low between readers in this study (CV=2.2%) (Fig. 4). Additionally, the precision of each reader was high (CVs <2%) for both individuals from the reference collection, before and after samples collected for this study were examined. For samples that had been aged previously, final age estimates from this study were compared with previous estimates from collaborators, and age determinations differed for 107 fish (11%) and had a CV of 2.5%. There was no bias.

The interactive model with the predictors of *Month Bin* and *Age Bin* had the lowest AIC value and was selected for further analysis. An interaction between *Month Bin* and *Age Bin* for MIR (F=13.795, df=10, P<0.0001) revealed the lowest mean MIR occurred for AB1, followed by AB2 and AB3 (P<0.01) for the month bins January–February, March–April, and May–June; however, the remaining month bins had slightly different patterns. The MIRs for AB1 and AB2 were similar in July–August (P=0.3143) and November–December (P=0.3178) but were smaller than those for AB3 (P<0.001). Also, MIRs for AB2 and AB3 were similar in September–October (P=0.8206) but were larger than those for AB1 (P<0.001).

Campana (2001) noted that a minimum in the MIR should occur once per year and be significantly different from the MIR in other times of the year. Figure 5, A–C, shows that the minimum MIR in each age bin (indicated with the letter *a* above boxes for month bins) occurred once per year and was different from that of other month bins (P<0.0001). The only exception was for AB3, which appeared to have a minimum that extended from July–August through September–October (P=0.9849); whereas the minimums for AB1 and AB2 were both in July–August only. Plots of raw data show the monthly MIR for AB3 declined in July prior to reaching a minimum in August (Fig. 6C). Similarly, a depression in MIR occurred in May–June for AB1 (Figs. 5A and 6A). For all age bins, MIR gradually increased throughout the year after the minimum occurred.

The model with 2-way interactions between *Age Bin*, *Season*, and *Region* had the lowest AIC value and was

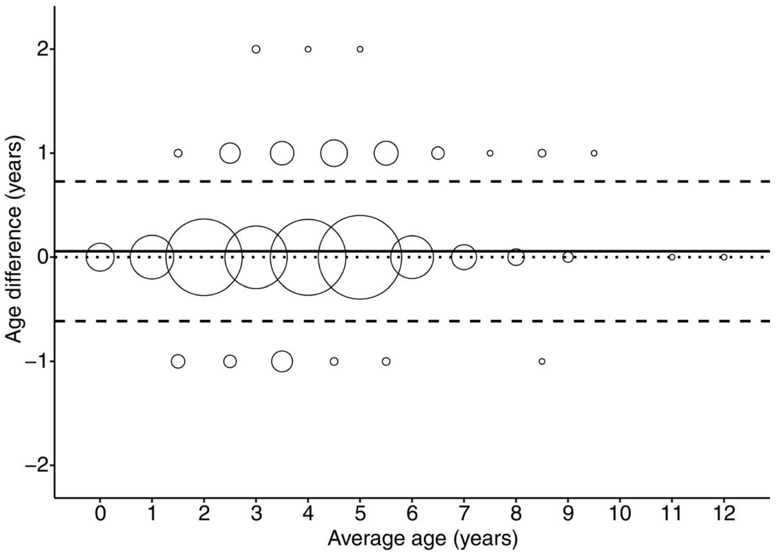

Figure 4

Bland–Altman bias plot of differences in age determinations between readers (reader 2–reader 1) of sagittal otoliths from black sea bass (*Centropristis striata*) caught in the Atlantic Ocean off the northeastern United States during 2013–2017. The dotted black line (located at 0) represents no bias in age estimates, the solid black line indicates the degree and direction of bias in age estimates for samples used in this study, and the dashed black lines indicate 95% confidence limits. Size of circles indicates the number of samples.

selected for further analysis. No interaction between *Age Bin* and *Region* was observed (F=1.717, df=2, P=0.1800); however, there was an interaction between *Season* and *Region* (F=3.593, df=3, P=0.0132). Marginal increment ratios were higher in the winter, spring, and fall for otoliths from fish sampled south of the Hudson Canyon than those for otoliths from fish collected north (P<0.010, P<0.05, and P<0.0001, for each season respectively), but MIRs for regions were similar in summer (P=0.4486). Figure 7, A and B, shows that there was one minimum MIR per year for each region and that it occurred in summer and was different from the MIRs for all other seasons (P<0.0001). This minimum occurred once per year for each region and was verified by plotting monthly means (Fig. 6, D and E). An interaction was also detected between *Season* and *Age Bin* (F=16.602, df=6, P<0.0001), corroborating results from the previous model, meaning there were differences in MIR between age bins in each season (P<0.0100). The only variant was that MIRs for AB1 and AB2 in summer were similar (P=0.4830), an outcome that was also observed in the model with the predictor *Month Bin*.

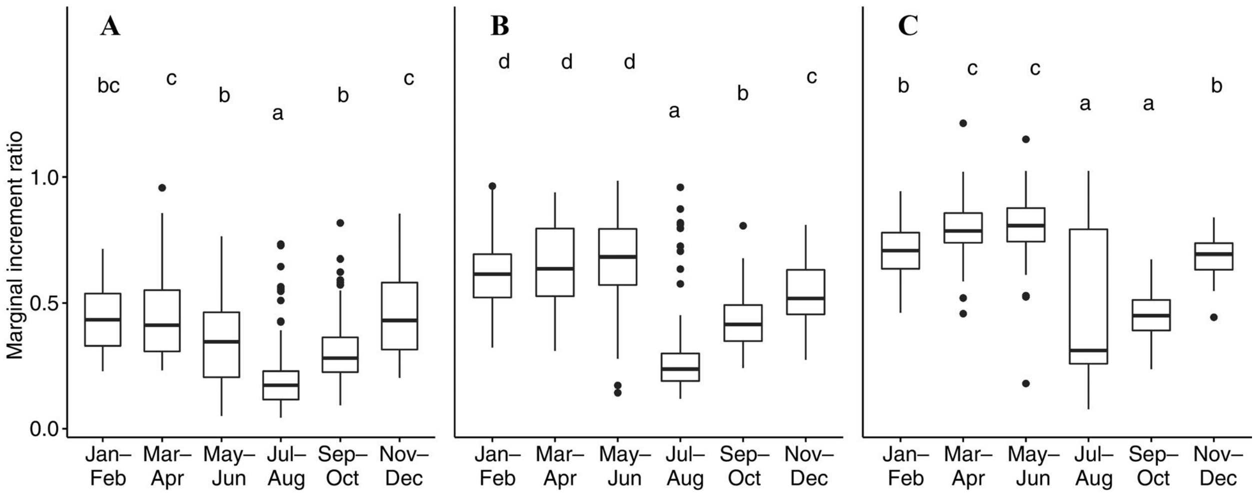

Figure 5

Box plots of marginal increment ratios for sagittal otoliths from black sea bass (*Centropristis striata*) captured in the Atlantic Ocean off the northeastern United States during 2013–2017, by month bin for (**A**) age bin 1 (ages 1–2), (**B**) age bin 2 (ages 3–4), and (**C**) age bin 3 (ages 5+). Letters above the boxes denote significant differences (significance level=0.05; tested with Tukey's honestly significant difference by using estimated marginal means). In each box plot, the thick horizontal line indicates the median, the areas above and below the median represent the 25th and 75th percentiles, the thin vertical lines indicate the 95% confidence limits, and the points indicate outliers.

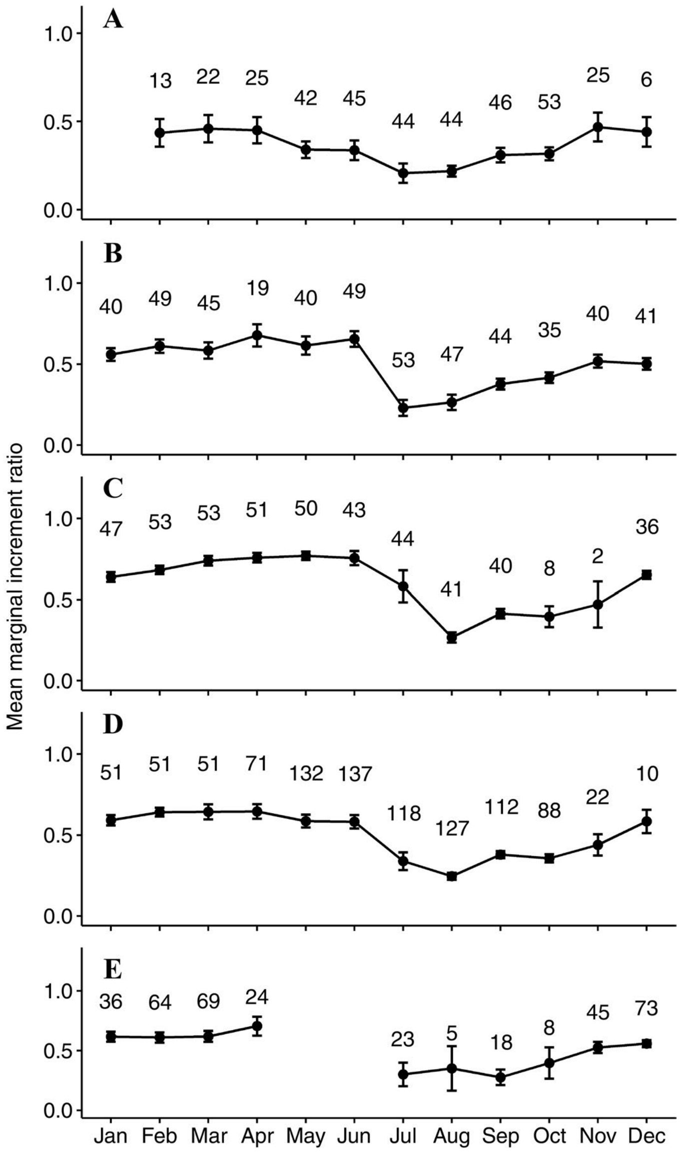

Figure 6

Monthly mean marginal increment ratios for black sea bass (*Centropristis striata*) caught in the Atlantic Ocean off the northeastern United States during 2013–2017, for (**A**) age bin 1 (ages 1–2), (**B**) age bin 2 (ages 3–4), and (**C**) age bin 3 (ages 5+) and for the regions (**D**) north and (**E**) south of the Hudson Canyon. Numerals above data points denote the number of samples for each month. Error bars indicate 2 standard errors of the mean.

Results of assessment with AIC values for the Okamura et al. (2013) circular-linear models (hereafter referred to as *the Okamura analysis*) indicate that 1 cycle was completed within a time span of 1 year for each age bin and both regions (i.e., model A had the lowest AIC values for all iterations). This finding confirms results from the interactive models and mean MIR visualizations, which indicate that the MIR reaches one minimum per year (Figs. 5, 6, and 7).

Young of the year: measurements and length–frequency analysis

Radius measurements of otoliths from age-0 samples collected in the fall were smaller than the first annulus measurements of age-1 samples (t =−11.92, df=67, P≤0.0001). The mean radius of otoliths from age-0 fish was 0.36 mm, compared with a mean annulus measurement of 0.60 mm for otoliths from age-1 samples. The first annulus measurements of otoliths from age-1 samples collected in summer were similar to the first annulus measurements of otoliths from all MIA samples (t=1.01, df=37, P=0.3205). Measurements of the first annulus (for all samples used in MIA, n=1299) range from 0.41 mm to 0.92 mm with a mean of 0.61 mm. Mean first annulus measurements were similar between regions (t=−1.19, df=629, P=0.2365), at 0.61 mm for otoliths of samples from the region north of the Hudson Canyon and 0.62 mm for otoliths of fish from the region to the south.

Results of modal length–frequency analysis done with data from the resource assessment and ventless trap surveys confirm that samples used for first annulus validation were YOY (Fig. 8). A distinct modal separation between ages was apparent in the samples used for MIA, and length modes of the smallest fish overlapped in each survey. Measured lengths of age-0 fish collected in the fall and used in this study were from 35 to 120 mm TL, comparable to the length range for the first mode of fish captured in the fall during the resource assessment survey, from 20 mm TL to approximately 125 mm TL (Fig. 8A). Age-1 fish caught in summer and used in this study had lengths of 110–207 mm TL; whereas, lengths of the smallest mode of black sea bass collected in summer during the ventless trap survey were 60 mm TL to approximately 180 mm TL (Fig. 8B).

Discussion

Annulus periodicity and timing

The results of this study verify that one opaque band and one translucent band were deposited per year in otoliths of black sea bass. One clear minimum MIR was observed, and otolith growth continued throughout the year for samples in each age bin and from both regions. This sinusoidal pattern is consistent with results of other MIA studies that have confirmed that one annulus is deposited per year (Wenner et al., 1986; Vilizzi and Walker, 1999; Pilling et al., 2000). Additionally, the Okamura analysis confirmed these results, also indicating that 1 cycle occurred per year in each age group and in each region.

Annulus deposition is considered finished when new translucent growth is observed at the otolith edge. In other

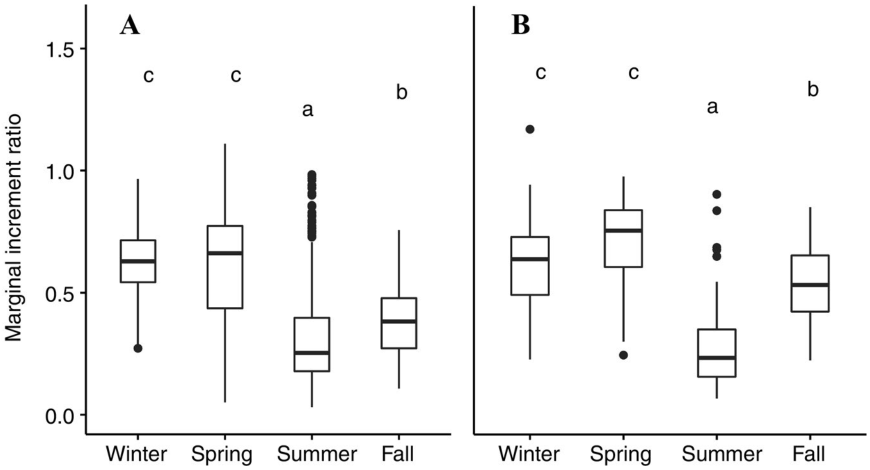

Figure 7

Box plots of marginal increment ratios for sagittal otoliths from black sea bass (*Centropristis striata*) captured in the Atlantic Ocean off the northeastern United States during 2013–2017, by season for the regions (**A**) north and (**B**) south of the Hudson Canyon. Letters above the boxes denote significant differences (significance level=0.05; tested with Tukey's honestly significant difference by using estimated marginal means). In each box plot, the thick horizontal line indicates the median, the areas above and below the median represent the 25th and 75th percentiles, the thin vertical lines indicate the 95% confidence limits, and the points indicate outliers.

words, the opaque annulus is being completed when MIRs are at a maximum before dropping to a minimum, which indicates new growth. The timing of annulus completion in this study was dependent on age bin. Maximum MIR for AB1 was observed in March–April (Fig. 6A); however, the decline in May–June (prior to the minimum in July) indicates that some fish were completing the annulus in these months. Therefore, annulus completion occurred between April and June for AB1. This variability was not surprising given the extensive spatial range from which these samples were collected (from Maine to Virginia). Miller et al. (2016) reported that overwintering adult black sea bass gathered along a defined shelf contour but that juveniles were scattered across the shelf and were exposed to a wider range of temperatures and salinities. Variation between individuals in this youngest age group, therefore, may be magnified by the environmental conditions experienced while overwintering.

The maximum MIR for AB2 was observed in June, followed by a stark decline to a minimum in July and August and a continuation of growth thereafter (Fig. 6B). Annulus completion largely occurred in June for this age bin, and new, translucent material began to be deposited on otoliths in July. Reduced variability in the timing of annulus deposition in this age group, compared with that in AB1, was likely a result of a more consistent growth rate between ages and regions.

Maximum and minimum MIRs for AB3 occurred in June and August, respectively (Fig. 6C). The mean MIR in July fell between these extremes, similar to the pattern observed in May–June in AB1. This finding indicates that some otoliths had new, translucent growth in July (a small amount of growth at the otolith margin); whereas, for others the opaque annulus was still being deposited (a large amount of growth at the otolith margin). The delay in annulus deposition for some samples in AB3 (with the minimum MIR occurring in August, as compared with in July for AB1 and AB2) could be related to energy allocated to spawning rather than to growth during this period. Morales-Nin and Ralston (1990) observed a decline in otolith growth as spawning season progressed and stated, "during the maturity period the metabolic energy seems to be diverted from growth, causing the formation of thin increments [as] seasonal growth rings." The northern stock of black sea bass typically spawns between April and October, with spawning peaking in June–July (Mercer, 1978; Wuenschel et al., 2013; McBride et al., 2018). Of the 44 black sea bass in AB3 that were measured in July, 25 samples were classified as fish in spawning condition (i.e., maturity data associated with otolith samples indicated the fish were ripe or ripe and running).

In other studies of black sea bass in the northern stock, annulus formation appears to have been associated with spawning period (Mercer, 1978; Alexander, 1981; Caruso, 1995); however, this connection may be coincidental (Beckman and Wilson, 1995). Instead, annulus deposition timing is likely the result of a combination of environmental and physiological processes (Fowler and Short, 1998). Additionally, black sea bass have a variety of reproductive strategies, including maturation as young, small males

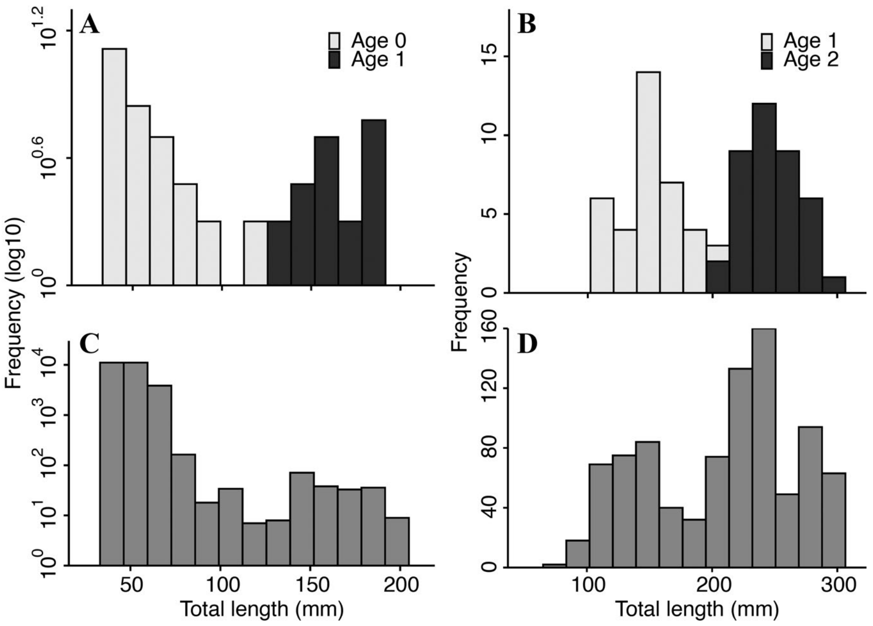

Figure 8

Length–frequency distributions of black sea bass (*Centropristis striata*) from the Atlantic Ocean off the northeastern United States whose sagittal otoliths were used in marginal increment analysis and first annulus validation: (**A**) age-0 and age-1 fish captured in the fall (September and October 2016–2017) and (**B**) age-1 and age-2 fish captured in summer (July and August 2015–2017). Length–frequency distributions are also presented for (**C**) black sea bass ≤220 mm in total length (TL) captured in the fall (September 2016–2017) during the Massachusetts Division of Marine Fisheries (MA-DMF) resource assessment survey and (**D**) black sea bass ≤310 mm TL captured in summer (July and August 2015–2017) during the MA-DMF ventless trap survey.

(Provost et al., 2017), that could also affect otolith growth in young age groups (<3 years) as well. Instead, the variability in annulus deposition for AB3 in this study could be due to the difficulty of accurately measuring growth at the otolith edge of older fish. The decline in otolith growth with increasing age made it challenging to discern the start of translucent edge growth; therefore, an apparent delay in annulus deposition could be an artifact of the measurement method. Mercer (1978) noted a delay in annulus deposition in age-5 black sea bass captured off the mid-Atlantic coast; however, sample sizes were low, and whole otoliths were used. As discussed previously, measurements on whole otoliths are less precise because of diffuse banding patterns and otolith curvature.

Otolith annulus deposition for black sea bass in the northern stock has been reported to occur in a range of months, from May and June (Dery and Mayo, 1988; Robillard et al.[2]) to August (Alexander, 1981). Mercer (1978) concluded that opaque deposition occurred in April and May, but the results from that study were highly variable; the drop in mean marginal increment in that study occurred from March through July in the ages examined (ages 1–5). Wenner et al. (1986) conducted marginal increment analysis on otoliths from black sea bass in the southern Atlantic stock and found that annual deposition of growth bands occurred in April and May for ages 0–10 combined. The timing of annulus deposition on otoliths from black sea bass in our study appears to generally agree with these previous reports (spring or early summer); however, detailed comparisons were difficult because of limitations in sampling locations, gear types, age range representation, or sample sizes in these studies.

First annulus validation

None of the previously mentioned published works on aging of black sea bass in the northern stock include validation of the first annulus. Hales and Able (1995) and McBride et al. (2018) conducted studies to validate the otolith daily aging method; however, in both studies fish less than 1 year old were used. Marginal increment analysis can be used to verify annual banding deposition patterns in an aging structure; however, if the first annulus had not been validated, values produced by using that aging method could have been incorrect by a consistent amount. In this study, the location of the first annulus was validated by measuring annuli on otoliths from YOY: the mean measurement for the first annulus in age-1 samples was larger than the expected total radius of an age-0 fish caught in the previous fall. Additionally, the first annulus measurements from age-1 fish and the first annulus measured on all samples used in MIA were similar, indicating that it was identified correctly in the MIA.

The age-0 and age-1 samples in this study were confirmed to be YOY by comparing their modal length frequencies to the length frequencies of the smallest black sea bass caught in the fall during the resource assessment survey and in the summer during the ventless trap survey (Fig. 8). The similarities between the length frequencies are clear, and the designation of the samples in this study as YOY was appropriate. It should be noted that the samples measured for first annulus validation in this study were all from waters of Massachusetts. The similarity in first annulus measurement between these samples and all the samples used in MIA, as well as the previously mentioned similarity in mean first annulus measurements between regions, north and south of the Hudson Canyon, indicates that the first annulus validation completed in this study is applicable to the whole northern stock.

Age-bin separation

Results of this study confirm that separating samples into age bins was necessary for accurate age validation for this species. As a fish ages, somatic growth slows and otolith growth bands become closer together (Beamish and McFarlane, 1983). Otolith growth in a fish's first year is expected to be greater than growth in its second year, which will be greater than growth in its third year, and so on until, at a certain size or age, growth becomes more consistent. Differences in mean MIR between age bins throughout the year indicate that otolith deposition varies with age. For example, otoliths from fish in AB1 had a lower mean MIR than those from the other 2 age bins throughout most of the year. Additionally, the peak MIR for this age bin was less than 0.5. Marginal increment ratios that approach 1.0 would indicate that the completed edge growth on an otolith equals the growth of the penultimate annulus. The low peak MIR for AB1 signifies that there was rapid growth in the penultimate annulus followed by a decline in growth in the following year, as expected for this age group.

Conversely, AB3 had the highest MIRs throughout the year and came closer to approaching 1.0 at the time of annulus completion (mean MIR: 0.76, in May–June). Otoliths in this age bin have a higher proportion of edge growth compared with that of the penultimate annulus because growth has slowed, and annuli measurements were more consistent. This pattern is supported by the observed somatic growth of black sea bass with age, where the rapid growth experienced by younger fish slows considerably by ages 5–6 (NEFSC, 2017; McMahan et al., 2020). As expected, MIRs for AB2 fall between the values for AB1 and AB3 throughout most of the year. The effect of the interaction between *Age Bin* and *Month Bin* in the first model did not affect annulus validation, but it does further indicate the varied growth patterns throughout the year for otoliths from black sea bass in these age bins.

Regional differences within the northern stock

The documented variability of otolith growth for black sea bass by location (Dery and Mayo, 1988), as well as the recent separation of the northern stock into 2 subunits, motivated an analysis of possible differences in otolith growth between the regions north and south of the Hudson Canyon. The interaction between *Age Bin* and *Season* corroborated findings from the model with the predictor *Month Bin* discussed previously. No interaction between *Age Bin* and *Region* indicates that there was no regional difference in otolith edge growth within each age bin. The interaction between *Season* and *Region*, however, indicates that there was variability in otolith edge growth between regions throughout the year.

Higher MIRs were observed for otoliths from fish caught in the region south of the Hudson Canyon in the winter, spring, and fall, but there was no difference in MIRs between regions in summer. The similarity of MIRs in summer is not surprising because the absolute amount of growth following annulus deposition is small (Mercer 1978; Robillard et al.[2]). Differences throughout the rest of the year indicate that fish from south of the Hudson Canyon completed a higher proportion of the previous year's growth at these times than fish from the north, indicating that overall annual otolith growth may be lower for fish from the region south of the Hudson Canyon. Additionally, fish from the south had an 81% increase in edge growth from summer to fall, compared with a 23% increase achieved by fish from the north in the same period. Instead, fish from north of the Hudson Canyon had a 60% increase in growth from fall to winter; whereas, the increase in growth for the region south was 14%.

These findings are in line with those of previous research, but additional work is needed. In several studies, black sea bass were larger and had faster growth rates throughout the year at higher latitudes (Alexander, 1981; Dery and Mayo, 1988; Kolek[4]; Caruso, 1995; McMahan et al., 2020). McMahan et al. (2020) postulated that black sea bass from northern regions (e.g., north of Cape Cod) may either have adapted to grow in lower temperatures or have countergradient variation, with more growth achieved in the shorter growing season (i.e., winter). The differences in migration patterns between the 2 populations (i.e., east–west for fish south of the Hudson Canyon and north–south for fish in the north region) likely result in exposure to different temperatures throughout the year. This temperature variability could explain the differences in otolith growth between the 2 groups of fish in this study; however, a closer look at growth is needed to address this topic and should be considered for future research.

Although there were differences in otolith deposition between fish from the 2 regions, the otolith aging method

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[4] Kolek, D. 1990. Homing of black sea bass, *Centropristis striata*, in Nantucket Sound, with comments on seasonal distribution, growth rates, and fisheries of the species. MADMF Black Sea Bass Investig. Intern. Rep., 9 p. [Available from Mass. Div. Mar. Fish., 251 Causeway St., Boston, MA 02114.]

was validated for each region (one minimum MIR in summer, with 1 cycle present in the Okamura analysis). Annulus deposition was completed in June for black sea bass from the region north of the Hudson Canyon, with otolith growth for some fish lagging into July (Fig. 6D). Annulus deposition for otoliths from fish caught south of the Hudson Canyon was completed on or after April but before July, indicating a similar timing of late spring or early summer for fish in this region.

Conclusions

Results from this study indicate that one opaque annulus per year is deposited on otoliths of black sea bass in late spring or early summer. Younger fish (ages 1–4) completed annulus formation earlier in the season than older fish, although this finding is likely an artifact of measurement difficulty for the older age groups. For fish in all age groups, annulus formation was completed and new translucent material had begun by July or August. Although there were slight differences in material deposition between regions, the otolith aging method was validated for samples captured from both regions. Additionally, the first annulus was confirmed in this study, validating, in conjunction with MIA, the absolute age of black sea bass in the northern stock.

The results of this study help ensure the accuracy and precision of aging practices for black sea bass by validating the otolith aging method used by agencies and organizations across the Atlantic coast of the northeastern United States. In this study, we included samples that reflect age data used in black sea bass stock assessments (i.e., samples captured from the entire spatial range of the northern stock, with a variety of methods, in various types of fisheries, and from multiple age groups). Age data produced by using a validated age determination method will reduce uncertainty in the stock assessment. Several agencies from the northeastern United States supply age estimates for the assessment of the northern stock of black sea bass. Scales have largely been phased out because of the preference for otoliths; however, variation exists between the use of whole otoliths, sectioned otoliths, or a combination of both (ASMFC[5]). Sectioned otoliths—which were used for age validation in this study—tend to be clearer, easier to interpret, and provide more accurate age determinations (Hyndes et al., 1992; Fowler and Short, 1998). We therefore recommend abiding by the results presented here for aging of black sea bass in the future.

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Literature cited

Alexander, M. S.
1981. Population response of the sequential hermaphrodite black sea bass, *Centropristis striata*, to fishing. M.S. thesis, 104 p. State Univ. NY Stony Brook, Stony Brook, NY.

Beamish, R. J., and G. A. McFarlane.
1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743. Crossref

Beckman, D. W., and C. A. Wilson.
1995. Seasonal timing of opaque zone formation in fish otoliths. *In* Recent developments in fish otolith research. Belle W. Baruch Lib. Mar. Sci. 19 (D. H. Secor, J. M. Dean, and S. E. Campana, eds.). p. 27–43. Univ. South Carolina Press, Columbia, SC.

Bell, R. J., D. E. Richardson, J. A. Hare, P. D. Lynch, and P. S. Fratantoni.
2015. Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. ICES J. Mar. Sci. 72:1311–1322. Crossref

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. Fish. Bull. 53:1–577.

Campana, S. E.
2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59:197–242. Crossref

Campana, S. E., and S. R. Thorrold.
2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Can. J. Fish. Aquat. Sci. 58:30–38. Crossref

Caruso, P. G.
1995. The biology and fisheries of black sea bass (*Centropristis striata*) in Massachusetts waters. M.S. thesis, 118 p. Univ. Rhode Island, Kingston, RI.

Carvalho, M. G., C. Moreira, H. Queiroga, P. T. Santos, and A. T. Correia.
2017. Age, growth and sex of the shanny, *Lipophrys pholis* (Linnaeus, 1758) (Teleostei, Blenniidae), from the NW coast of Portugal. J. Appl. Ichthyol. 33:242–251. Crossref

Casselman, J. M.
1983. Age and growth assessment of fish from their calcified structures—techniques and tools. *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks; Miami, 15–18 February 1982 (E. D. Prince and L. M. Pulos, eds.), p. 1–17. NOAA Tech. Rep. NMFS 8.

Chang, W. Y. B.
1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39:1208–1210. Crossref

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[5] ASMFC (Atlantic States Marine Fisheries Commission). 2018. Report of the quality assurance/quality control fish ageing workshop, 50 p. ASMFC, Washington, D.C. [Available from website.]

Condini, M. V., C. Q. Albuquerque, and A. M. Garcia.
2014. Age and growth of dusky grouper (*Epinephelus marginatus*) (Perciformes: Epinephelidae) in the southwestern Atlantic, with a size comparison of offshore and littoral habitats. Fish. Bull. 112:311–321. Crossref

Dery, L. M., and J. P. Mayo.
1988. Black sea bass, *Centropristis striata*. *In* Age determination methods for northwest Atlantic species (J. Pentilla and L. M. Dery, eds.), p. 59–69. NOAA Tech. Rep. NMFS 72.

Drohan, A. F., J. P. Manderson, and D. B. Packer.
2007. Essential fish habitat source document: black sea bass, *Centropristis striata*, life history and habitat characteristics, 2nd ed. NOAA Tech. Memo. NMFS-NE-200, 68 p.

Fowler, A. J., and D. A. Short.
1998. Validation of age determination from otoliths of the King George whiting *Sillaginodes punctata* (Perciformes). Mar. Biol. 130:577–587. Crossref

Fox, J., and S. Weisberg.
2019. An R companion to applied regression, 3rd ed., 608 p. Sage Publ., Thousand Oaks, CA.

Hales, L. S., Jr., and K. W. Able.
1995. Effects of oxygen concentration on somatic and otolith growth rates of juvenile black sea bass, *Centropristis striata*. *In* Recent developments in fish otolith research. Belle W. Baruch Lib. Mar. Sci. 19 (D. H. Secor, J. M. Dean, and S. E. Campana, eds.), p. 135–153. Univ. South Carolina Press, Columbia, SC.

Hood, P. B., M. F. Godcharles, and R. S. Barco.
1994. Age, growth, reproduction, and the feeding ecology of black sea bass, *Centropristis striata* (Pisces: Serranidae), in the eastern Gulf of Mexico. Bull. Mar. Sci. 54:24–37.

Hothorn, T., F. Bretz, and P. Westfall.
2008. Simultaneous inference in general parametric models. Biom. J. 50:346–363. Crossref

Hyndes, G. A., N. R. Loneragan, and I. C. Potter.
1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. Fish. Bull. 90:276–284.

Lenth, R.
2019. Emmeans: estimated marginal means, aka least-squares means. R package, vers. 1.4.1. [Available from website, accessed July 2019.]

McBride, R. S.
2015. Diagnosis of paired age agreement: a simulation of accuracy and precision effects. ICES J. Mar. Sci. 72:2149–2167. Crossref

McBride, R. S., M. K. Tweedie, and K. Oliveira.
2018. Reproduction, first-year growth, and expansion of spawning and nursery grounds of black sea bass (*Centropristis striata*) into a warming Gulf of Maine. Fish. Bull. 116:323–336. Crossref

McMahan, M. D., G. D. Sherwood, and J. H. Grabowski.
2020. Geographic variation in life-history traits of black sea bass (*Centropristis striata*) during a rapid range expansion. Front. Mar. Sci. 7:567758. Crossref

Mercer, L. P.
1978. The reproductive biology and population dynamics of black sea bass, *Centropristis striata*. Ph.D. diss., 196 p. Coll. William Mary, Williamsburg, VA. [Available from website.]

Miller, A. S., G. R. Shepherd, and P. S. Fratantoni.
2016. Offshore habitat preference of overwintering juvenile and adult black sea bass, *Centropristis striata*, and the relationship to year-class success. PLoS ONE 11(1):e0147627. Crossref

Morales-Nin, B., and S. Ralston.
1990. Age and growth of *Lutjanus kasmira* (Forskål) in Hawaiian waters. J. Fish Biol. 36:191–203. Crossref

Musick, J. A., and L. P. Mercer.
1977. Seasonal distribution of black sea bass, *Centropristis striata*, in the Mid-Atlantic Bight with comments on the ecology and fisheries of the species. Trans. Am. Fish. Soc. 106:12–25. Crossref

NEFSC (Northeast Fisheries Science Center).
2012. 53rd Northeast Regional Stock Assessment Workshop (53rd SAW) assessment summary report. Northeast Fish. Sci. Cent. Ref. Doc. 12-03, 33 p. [Available at website.]
2017. 62nd Northeast Regional Stock Assessment Workshop (62nd SAW) assessment report. Northeast Fish. Sci. Cent. Ref. Doc. 17-03, 261 p. [Available at website.]

Ogle, D. H., P. Wheeler, and A. Dinno.
2019. FSA: fisheries stock analysis. R package, vers. 0.8.25. [Available from website, accessed September 2019.]

Okamura, H., A. E. Punt, Y. Semba, and M. Ichinokawa.
2013. Marginal increment analysis: a new statistical approach of testing for temporal periodicity in fish age verification. J. Fish Biol. 82:1239–1249. Crossref

Pilling, G. M., R. S. Millner, M. W. Easey, C. C. Mees, S. Rathacharen, and R. Azemia.
2000. Validation of annual growth increments in the otoliths of the lethrinid *Lethrinus mahsena* and the lutjanid *Aprion virescens* from sites in the tropical Indian Ocean, with notes on the nature of growth increments in *Pristipomoides filamentosus*. Fish. Bull. 98:600–611.

Provost, M. M., O. P. Jensen, and D. L. Berlinsky.
2017. Influence of size, age, and spawning season on sex change in black sea bass. Mar. Coast. Fish. 9:126–138. Crossref

R Core Team.
2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed July 2019.]

Shepherd, G. R., and M. C. Lambert.
1996. Assessment of black sea bass north of Cape Hatteras, North Carolina. Northeast Fish. Sci. Cent. Ref. Doc. 95-17, 57 p. [Available from website.]

Vilizzi, L., and K. F. Walker.
1999. Age and growth of the common carp, *Cyprinus carpio*, in the River Murray, Australia: validation, consistency of age interpretation, and growth models. Environ. Biol. Fishes 54:77–106. Crossref

Wenner, C. A., W. A. Roumillat, and C. W. Waltz.
1986. Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. Fish. Bull. 84:723–741.

Wickham, H.
2016. ggplot2: elegant graphics for data analysis, 2nd ed., 260 p. Springer-Verlag, New York.

Winner, B. L., T. C. MacDonald, and K. B. Amendola.
2017. Age and growth of sheepshead (*Archosargus probatocephalus*) in Tampa Bay, Florida. Fish. Bull. 115:155–166. Crossref

Wuenschel, M. J., R. S. McBride, and G. R. Fitzhugh.
2013. Relations between total gonad energy and physiological measures of condition in the period leading up to spawning: results of a laboratory experiment on black sea bass (*Centropristis striata*). Fish. Res. 138:110–119. Crossref

Zlokovitz, E. R., D. H. Secor, and P. M. Piccoli.
2003. Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. Fish. Res. 63:245–259. Crossref