Validating blueline tilefish *Caulolatilus microps* ages in the U.S. South Atlantic using bomb radiocarbon (F14C)

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Validating blueline tilefish *Caulolatilus microps* ages in the U.S. South Atlantic using bomb radiocarbon ($F^{14}C$)

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Abstract

Age validation is a critical component of an age-based stock assessment and subsequent species management. Our study used bomb radiocarbon analysis to validate age estimates of Blueline Tilefish *Caulolatilus microps*, a species for which regional stock assessment scientists have identified age validation as a high priority. We compared a *C. microps* $F^{14}C$ chronology to $F^{14}C$ chronologies for finfish of the U.S. South Atlantic Bight (SAB) and the north-west Atlantic. The high degree of correspondence in the chronologies exhibited for *C. microps* and other species of the SAB suggests a differential ^{14}C uptake pattern in the SAB slope waters that is likely the result of local hydrological processes that delay ^{14}C reaching the environments inhabited by these species. Our study was able to validate *C. microps* ages up to 25 years in the SAB, with strong evidence suggesting they are living to at least 50 years old.

KEYWORDS
age validation, blueline tilefish, bomb radiocarbon, *Caulolatilus microps*

1 | INTRODUCTION

Age estimates are critical for population demographics calculations and age-based life-history parameters (e.g., growth, mortality, stock productivity), and are required for age-structured population dynamics models. As such, age validation is a critical component of an age-based stock assessment and subsequent species management. The primary goal of any age validation study is to determine whether the age estimates produced are, on average, correct for the species in question, with any associated error randomly distributed and no systematic bias (Francis et al., 2010). The focus of age validation is therefore to examine the bias of age determinations, not the precision of independent reads (Francis et al., 2010).

Validating age estimates can be a difficult and time-consuming task. However, there are a multitude of age validation methods available, including marginal increment analysis, radiometric dating, tag and re-capture, chemical tagging, and bomb radiocarbon analysis (Campana, 2001). Bomb radiocarbon analysis is an accurate age validation method that has been successfully applied to studies of fishes around the world (Andrews et al., 2015; Campana et al., 2008, 2016; Horn et al., 2010), including the south-eastern coast of the United States (Filer & Sedberry, 2008; Friess & Sedberry, 2011; Lytton et al., 2016).

Two pieces of information are necessary to use bomb radiocarbon analysis to validate an age: (1) a test data set that includes estimated ages and the associated radiocarbon values and (2) an accepted reference data set of ages and radiocarbon values for another species with a similar life history to the region and environment of interest (Francis et al., 2010). An implicit assumption of age validation using bomb radiocarbon analysis is that the test and reference species occupy the same, or similar, environments with respect to ^{14}C availability, so that the carbon incorporated into the carbonate structures of the two species in the same year will contain the same proportion of ^{14}C (Francis et al., 2010). In previous work, the test and reference data sets showed a similar rapid increase in bomb radiocarbon (^{14}C) levels beginning in the same year, with the timing at a specific locale being a function of local hydrographic processes (Francis et al., 2010). The timing of the ^{14}C rise in oceanic waters relative to the peak observed in the atmosphere is later because of the time required for ^{14}C to migrate from the atmosphere to the specific marine region of interest (Francis et al., 2010). Due to the mixing rates of oceanic surface and deep waters, deeper oceanic waters have been shown to experience further delays in the timing of the ^{14}C rise (see Campana et al., 2016; Grammer et al., 2015; Horn et al., 2010).

Blueline tilefish (*Caulolatilus microps*, Goode & Bean, 1878) are a long-lived, commercially important, deepwater demersal species for which a recent stock assessment identified validation of an ageing methodology as a high priority (SEDAR, 2017). *C. microps* are patchily distributed at depths of 48–236 m over irregular bottom conditions characterized by ledges, boulders, or rubble piles along the outer continental shelf, shelf break, and upper north-west Atlantic slope (Dooley, 1978; Parker & Mays, 1998; Ross & Huntsman, 1982). A commercial fishery for *C. microps* along the south-eastern U.S. coast began developing in the mid-1980s (Harris et al., 2004; Parker & Mays, 1998). From 1993 to 2005, total annual landings of *C. microps* averaged 64.7 mt (range 32.6–115 metric tons), before steeply increasing to a peak of 333 mt in 2008[a]. *C. microps* landings moderated to a degree between 2009 and 2014, averaging 137 mt (range 63–214 mt), and have declined to an average of 38 mt (range 32–50 mt) between 2015 and 2021 due to significant management action in the U.S. South Atlantic resulting from the stock status determined as overfished and undergoing overfishing (SEDAR, 2013; SEDAR, 2017).

Deepwater species, including *C. microps* (Harris et al., 2004; SEDAR, 2013), are some of the most difficult species to age (Fenton et al., 1991; Friess & Sedberry, 2011; Lytton et al., 2016; Peres & Haimovici, 2004). Ageing difficulties affect stock assessment accuracy and uncertainty, and can lead to problems when managing a stock to prevent overfishing. Reducing assessment uncertainty for *C. microps* is important since deepwater species are notoriously susceptible to overfishing and slow rates of recovery because of general species longevity, slow growth, and slow maturation rates (Clark, 2001; Clarke et al., 2003).

The goal of our study was to validate age estimates of *C. microps* (i.e., confirm assumed annual increment counts) from the U.S. South Atlantic Bight (SAB) by comparing the onset of bomb-produced radiocarbon ($F^{14}C$) (Campana et al., 2008). We compared a *C. microps* bomb radiocarbon chronology to reference chronologies for finfish of the SAB and the north-west Atlantic (NWA). The findings of our study demonstrate the importance of appropriate reference chronology selection for bomb radiocarbon analysis and will have impacts on the methods used to age *C. microps* for stock assessments in the U.S. South Atlantic.

2 | MATERIALS AND METHODS

The Marine Resource Monitoring, Assessment and Prediction program (MARMAP) of the South Carolina Department of Natural Resources (SCDNR) collects *C. microps* otoliths annually via routine fishery-independent sampling. The MARMAP program used a variety of sampling gears to collect *C. microps* including short bottom longlines, kali poles, experimental traps, and commercial bandit reels baited with either squid or clupeids. All otoliths in our study were collected by MARMAP between 1983 and 1997 from waters offshore of South Carolina (between 32.1 and 32.8°N latitude) in depths ranging from 57 to 210 m ($\bar{X} \pm SD = 180 \pm 6.9$ m).

Prior to the selection of otoliths for use in age validation, two readers independently examined sectioned left otoliths to provide age estimates using a Leica M125 dissecting microscope under transmitted light at a magnification of 40–100×, without knowledge of fish size, capture date, or age estimated by the other reader. If two sections were available, readers used the section containing the core unless there was an obvious reason not to utilize that section, such as damage to the otolith. Increment counts were determined based on the counts of all opaque growth increments along the medial surface of the transverse otolith section dorsal to the sulcus (Figure 1). SCDNR age readers identified the first increment as the first opaque zone with a clear translucent zone separating it from the core; often this increment would appear as a doublet. If a doublet was not present, readers considered the first increment to be the first opaque zone with a clear translucent zone separating it from the core. We often encountered the groups of tightly compacted increments described by Harris et al. (2004), which typically occurred within the first few increments. The inner increments (up to ~6) were considered broad and diffuse, with outer (>6) increments becoming more regularly spaced, but tightly grouped. The inner increments were more clearly defined at 40–60× magnification, while outer increments were best read at 60–100× magnification. In many of the otolith sections, readability decreased at various points along the chosen reading axis, forcing readers to shift to a new reading axis by following a growth increment out along a lateral plane.

After initial increment counts, we selected 20 specimens for bomb radiocarbon age validation based on birth year as determined from increment count and year of capture (Table 1). We embedded the right sagittal otolith of each selected specimen in resin and obtained a single 1-mm thick transverse section through the core using a low-speed Isomet® saw. We washed the resultant section with deionized water and allowed it to dry overnight, then removed the extraneous otolith material surrounding the core using a Dremel® model 732 tool with a carbide-cutting wheel. To prevent cross-contamination we used a new carbide-cutting wheel for each otolith and performed core removal under a ventilation system. We removed additional surface contaminants by sonicating the extracted otolith cores for two 30-s time intervals in deionized water, followed by acid leaching in 10% HNO_3 for 30 s and rinsing with deionized water. After drying overnight, each otolith core was then measured to the nearest 0.01 mg to ensure enough material had been obtained for bomb radiocarbon analysis (>5 mg).

We shipped the resulting otolith cores in new sterile plastic 5-mL vials to the National Ocean Services Accelerator Mass Spectrometry (NOSAMS) facility at the Woods Hole Oceanographic Institution. Otolith core samples were then analyzed for $\Delta^{14}C$ using accelerator mass spectrometry (AMS) following standard methods (additional information can be found online: www.whoi.edu/nosams/radiocarbon-data-calculations). NOSAMS staff then calculated the fraction modern

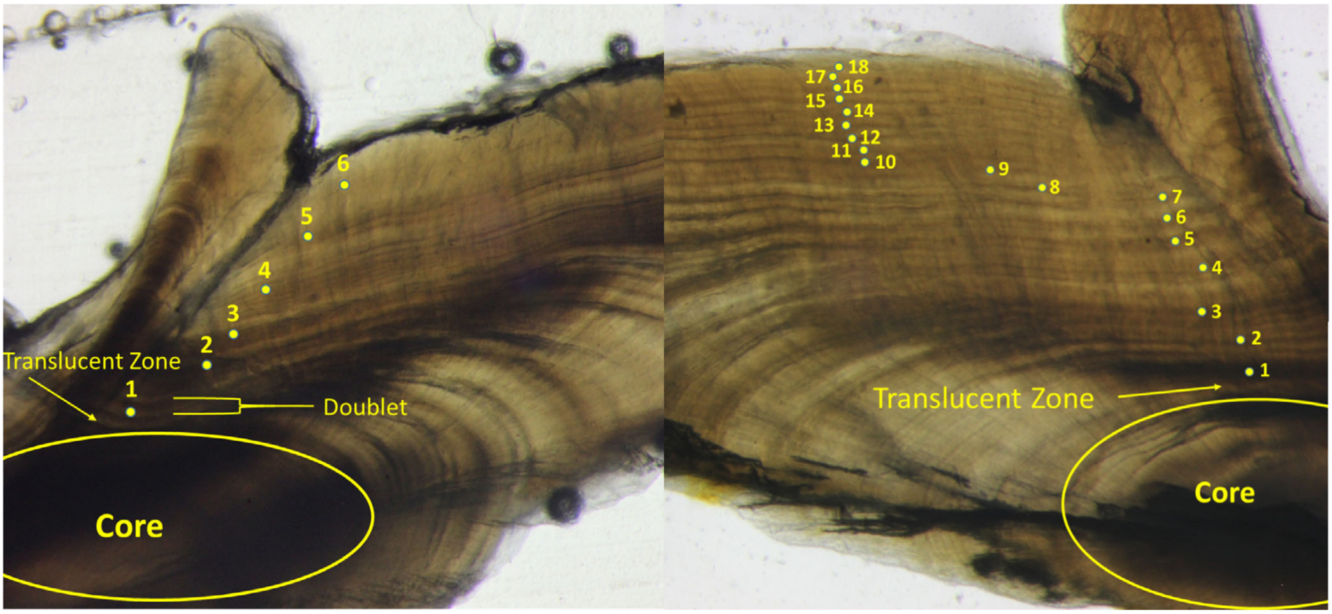

FIGURE 1 Blueline tilefish otolith transverse section. Left panel, otolith thin section depicting a doublet that serves as the first increment as aged via the South Carolina Department of Natural Resources; the outer increments appear as broad diffuse fields and were grouped. Right panel, otolith thin section lacking a clear doublet at the first increment. The first increment was considered the first opaque zone with a clear translucent zone separating it from the core along its entire length; subsequent increments appear as broad diffuse bands out to ~7 and then become more tightly compact and regularly spaced. Each dot represents an increment with its respective count.

($F^{14}C$), which is a measurement of the deviation of a sample's radiocarbon content from that of the "modern" standard (Donahue et al., 1990; Reimer et al., 2004). "Modern" is defined as 95% of the radiocarbon concentration (in AD 1950) of NBS Oxalic Acid I, normalized to $\delta^{13}C_{VPDB}$ ($\delta^{13}C_{VPDB} = -19‰$; Karlen et al., 1964; Olsson, 1970). A correction to $F^{14}C$ is made to normalize the sample result to a $\delta^{13}C_{VPDB}$ value of −25‰, assuming a quadratic mass fractionation dependency using simultaneously measured $^{13}C/^{12}C$ ratios on the AMS system. An advantage of using $F^{14}C$, in contrast to $\Delta^{14}C$ as generally reported in fish bomb radiocarbon age validation studies, is that $F^{14}C$ does not change with time (i.e., does not depend on the year of measurement; Stenstrom et al., 2011). The resultant statistic, $F^{14}C$, when plotted against birth year, provides a measure of the increase in ^{14}C due to uptake of ^{14}C from nuclear bomb testing in the 1950s through the early 1970s compared to ^{14}C levels found in 19th century wood.

In addition to the 20 samples selected for our study, 20 historical samples were included in our analysis from an unpublished bomb radiocarbon study performed in the early 2000s at the SCDNR (Table 1) that were also processed at the NOSAMS facility. We excluded one of these historical samples from further analysis due to a lack of consensus among age readers (Table 1). We did not rely exclusively on the historical samples for the current age validation study because most of the estimated birth years fell between 1970 and 1986. When performing an age validation study using bomb radiocarbon it is best to use samples with presumed birth years that fall primarily during the period of drastic increase in atmospheric and surface water ^{14}C concentrations due to nuclear testing, which occurred between 1958 and 1970 (Kalish, 1993).

A well-established ^{14}C reference set of known age fish, coral, or other carbonate structures is not currently available for the U.S. South Atlantic region. However, there are three independent bomb radiocarbon studies of deepwater U.S. South Atlantic finfish species (wreckfish [*Polyprion americanus*], red bream [*Beryx decadactylus*] and barrelfish [*Hyperoglyphe perciformes*]) that have been conducted using fish collected from the Charleston Bump area of the SAB (Filer & Sedberry, 2008; Friess & Sedberry, 2011; Lytton et al., 2016). Considering the similar uptake pattern of ^{14}C observed in these three independent studies and the proximity to our study area, we chose to combine the radiocarbon data for wreckfish, red bream and barrelfish, and use it as a SAB radiocarbon reference chronology (Table S1).

We also used a traditional finfish radiocarbon reference chronology from the NWA for comparison due to its proximity to the study area in the same ocean basin and because it is influenced by the same water mass and was used as a reference chronology in the studies that generated the SAB chronology. The NWA reference chronology comprises bomb radiocarbon data from haddock (*Melanogrammus aeglefinus*), red fish (*Sebastes* spp.), yellowtail flounder (*Limanda ferruginea*), and bivalves collected in the NWA (Table S2; Campana et al., 2008).

We estimated the year of initial $F^{14}C$ increase using:

$$C_T = C_p - 0.9(C_P - C_L)$$

TABLE 1 Summary of radiocarbon ($F^{14}C$) results from blueline tilefish (*Caulolatilus microps*) otoliths collected off the south-east coast of the United States via fishery-independent research of the MARMAP program

NOSAMS accession	SCDNR ID	Gear	Coll. year	Latitude (°N)	Depth (m)	TL (mm)	$F^{14}C$	σ	$\delta^{13}C$	Age	Age SE	Sample age	Birth year	Sample year
136,730	821608-1	Kali	1982	32.73	210	597	0.9388	0.0025	−2.12	21	2.9059	0.5	1961	1961.5
136,731	821601-3	Kali	1982	32.73	210	655	0.9395	0.0027	−2.34	30	2.5899	0.5	1952	1952.5
136,738	821612-5	Kali	1982	32.73	198	778	0.9422	0.0019	−2.94	22	1.9726	0.5	1960	1960.5
136,731	821608-3	Kali	1982	32.73	210	589	0.9429	0.0024	−3.30	13	0.9689	0.5	1969	1969.5
136,746	861436-4	Kali	1986	32.72	210	649	0.9476	0.0027	−2.10	25	0.9966	0.5	1961	1961.5
134,740	834005-6	Bandit	1983	32.73	185	628	0.9509	0.0020	−2.30	18	1.2150	0.5	1965	1965.5
136,744	851646-4	Kali	1985	32.63	177	588	0.9535	0.0022	−2.39	20	0.9184	0.5	1965	1965.5
136,737	821612-4	Kali	1982	32.73	198	580	0.9580	0.0021	−1.88	22	1.2857	0.5	1960	1960.5
136,748	861447-1	Kali	1986	32.63	185	550	0.9647	0.0019	−3.46	18	1.2000	0.5	1968	1968.5
136,745	851919-1	Kali	1985	32.62	190	600	0.9669	0.0026	−2.74	24	0.9619	0.5	1961	1961.5
136,733	821609-1	LBLL	1982	32.73	196	714	0.9697	0.0028	−1.95	21	2.2887	0.5	1961	1961.5
45054[a]	834047-1	Kali	1983	32.73	198	584	0.9718	0.0042	−2.05					
136,743	840690-2	Kali	1984	32.73	201	526	0.9721	0.0021	−1.97	20	1.1429	0.5	1964	1964.5
136,739	821631-2	Kali	1982	32.73	209	596	0.9814	0.0021	−2.45	19	1.1429	0.5	1963	1963.5
136,734	821609-2	Kali	1982	32.73	196	595	0.9894	0.0025	−3.68	16	2.0777	0.5	1966	1966.5
136,741	834053-4	LBLL	1983	32.73	207	722	1.0128	0.0022	−2.34	21	1.2509	0.5	1962	1962.5
136,735	821610-2	LBLL	1982	32.73	194	597	1.0190	0.0024	−2.63	9	1.3171	0.5	1973	1973.5
136,742	834061-1	Kali	1983	32.72	198	583	1.0240	0.0021	−2.56	16	1.0627	0.5	1967	1967.5
136,747	861437-5	Kali	1986	32.73	194	567	1.0332	0.0021	−2.78	18	0.8921	0.5	1968	1968.5
136,732	821609-1	Kali	1982	32.73	196	778	1.0374	0.0030	−3.33	30	4.3716	0.5	1952	1952.5
45,063	861426-1	Kali	1986	32.74	190	574	1.0415	0.0041	−1.88	14	0.9368	0.5	1972	1972.5
45,059	851911-1	Kali	1985	32.54	201	478	1.0422	0.004	−2.83	13	0.5654	0.5	1972	1972.5
45,056	834062-1	LBLL	1983	32.73	207	494	1.0471	0.0052	−2.84	13	0.8081	0.5	1970	1970.5
136,736	821612-2	LBLL	1982	32.73	198	682	1.0509	0.0020	−3.22	15	0.7377	0.5	1967	1967.5
45,060	851918-5	Kali	1985	32.63	188	496	1.0548	0.0033	−3.10	10	0.7377	0.5	1975	1975.5
45,057	840704-7	Kali	1984	32.74	199	528	1.0550	0.0037	−2.52	12	0.7825	0.5	1972	1972.5
45,062	861423-1	Kali	1986	32.73	201	640	1.0552	0.004	−3.53	9	1.3638	0.5	1977	1977.5
45,064	861432-5	Kali	1986	32.71	198	410	1.0583	0.005	−2.77	14	1.5000	0.5	1972	1972.5
45,055	834053-5	LBLL	1983	32.73	207	531	1.0595	0.0037	−3.50	10	0.6901	0.5	1973	1973.5
45,061	851921-1	Kali	1985	32.63	181	532	1.0608	0.0037	−3.30	16	0.7190	0.5	1969	1969.5
45,068	981284-1	Trap	1998	32.84	174	609	1.0616	0.0036	−1.49	30	1.3801	0.5	1968	1968.5
45,069	971688-2	Trap	1997	32.75	183	563	1.0661	0.0039	−2.83	10	0.3401	0.5	1987	1987.5
45,066	971707-2	SBLL	1997	32.64	185	523	1.0686	0.0042	−3.10	12	0.4206	0.5	1985	1985.5

(Continues)

TABLE 1 (Continued)

NOSAMS accession	SCDNR ID	Gear	Coll. year	Latitude (°N)	Depth (m)	TL (mm)	$F^{14}C$	σ	$\delta^{13}C$	Age	Age SE	Sample age	Birth year	Sample year
45,065	971676-1	SBLL	1997	32.74	181	595	1.0703	0.0042	−4.22	10	0.4286	0.5	1987	1987.5
45,067	971708-3	Trap	1997	32.63	190	515	1.0750	0.0042	−2.78	11	0.5084	0.5	1986	1986.5
45,050	831690-9	Bandit	1983	32.09	73	341	1.0795	0.0044	−4.48	3	0.4041	0.5	1980	1980.5
45,051	831690-5	Bandit	1983	32.09	73	594	1.0828	0.0038	−3.49	9	0.5714	0.5	1974	1974.5
45,052	831691-1	Trap[b]	1983	32.07	71	576	1.0874	0.0043	−3.66	3	1.2037	0.5	1980	1980.5
45,053	831691-10	Trap[b]	1983	32.07	71	433	1.0901	0.0043	−4.79	4	0.6801	0.5	1979	1979.5
45,058	851580-1	Bandit	1985	32.36	57	438	1.0992	0.0037	−4.10	12	0.8650	0.5	1973	1973.5

Note: NOSAMS accession, identification number assigned by the Woods Hole National Ocean Sciences Accelerator Mass Spectrometry Facility (13XXXX, contemporary sample; 4XXXX, historical sample); SCDNR-ID, collection and specimen number for individual fish (project code is P05 for all); Kali, Kali Pole; Bandit, Bandit Reel; LBLL, MARMAP long bottom longline gear; SBLL, MARMAP short bottom longline gear; Trap, MARMAP experimental fish trap; σ, $F^{14}C$-sigma value provided by NOSAMS; Age SE, the estimated age estimate standard error based on independent reads of the same fish by different individuals experienced in ageing blueline tilefish; Sample age, estimated age of the bomb radiocarbon sample, which is assumed to be 0.5 for all fish as we are using the core material from the otolith; Sample year, birth year (determined from increment count and year of capture) corrected for the "sample age" of the sample (e.g., birth year + sample age).

[a]A consensus age for this specimen could not be determined, thus it was excluded from all further bomb radiocarbon analyzes.

[b]MARMAP Florida trap used to capture specimen.

where C_T is the value corresponding to the 10% threshold contribution of $F^{14}C$ (Campana et al., 2008). C_P and C_L represent the peak and lowest values found within a chronology. The year of initial increase (Y_T) is then estimated as the first year the chronology exceeds C_T. Deviations in estimates of Y_T from test and reference data sets indicate potential biases in age estimates of the test data. All analyses were performed using the R Statistical Program version 3.3.1. Because all authors of reference data sets reported results in $\Delta^{14}C$, we used the R function "AbsoluteFractionModern_from_Delta14C" available in the *SoilR* package (Sierra et al., 2012) to convert these to $F^{14}C$ measures.

2.1 | Ethics statement

C. microps were collected under a Letter of Acknowledgement from the National Oceanographic and Atmospheric Administration National Marine Fisheries Service and biological samples were obtained using methods of euthanasia consistent with recommendations from the American Fisheries Society. (https://doi.org/10.47886/9781934874394.ch8).

3 | RESULTS

The *C. microps* otoliths used in the current bomb radiocarbon analysis ($n = 39$) had increment counts ranging from 3 to 30, and estimated birth years (assuming one increment formed per year) ranged from 1952 to 1987 (Table 1). The average percentage error between SCDNR age readers for these otoliths was 6.94% with an average CV (coefficient of variation) of 9.82%, and there was no apparent ageing bias. Otolith core values of $F^{14}C$ ranged from 0.939 ($\Delta^{14}C = -62.49‰$) for a fish with an estimated birth year of 1961 to 1.099 ($\Delta^{14}C = 92.10‰$) for a fish with an estimated birth year of 1973 (Table 1). All values were well within the range of previously published $F^{14}C$ levels reported for finfish reference chronologies of the SAB (Table S1) and the NWA (Table S2).

Levels of $F^{14}C$ in otolith cores from *C. microps* increased prominently beginning in the early 1960s, peaked in the mid- to late-1970s, and declined toward the end of the time series. The $F^{14}C$ chronology of *C. microps* was similar to the SAB $F^{14}C$ chronology (Figure 2a). Compared to the NWA chronology (Figure 2b), there is a clear difference in uptake patterns, with an apparent delay in both peak $F^{14}C$ values and the onset of $F^{14}C$ increase for *C. microps*.

The onset of $F^{14}C$ increase for *C. microps* in our study was estimated to occur in 1960 (Table 2). Similarly, the estimated onset of $F^{14}C$ for the SAB reference chronology was 1959 (Table 2). For the NWA reference chronology, however, the onset of $F^{14}C$ increase was estimated to occur several years earlier, in 1956 (Table 2).

The $F^{14}C$ chronologies for each of the deepwater finfish studies within the SAB reference were similar to that of *C. microps* in the current study, as evidenced by high overlap of the 95% confidence intervals for each species based on generalized additive model smoothers

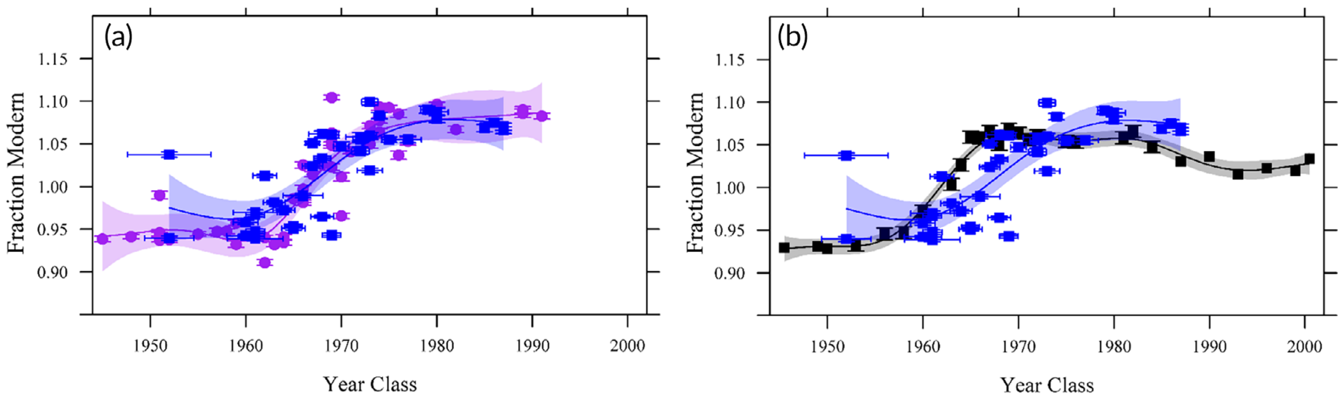

FIGURE 2 Comparing the blueline tilefish bomb-produced radiocarbon ($F^{14}C$) (blue) chronology to the (a) South Atlantic Bight (purple) and (b) north-west Atlantic (black) reference chronologies. Horizontal and vertical error bars represent the standard error estimate for age estimates and the $F^{14}C$ σ from the bomb radiocarbon analysis, respectively. Shaded polygons represent 95% confidence intervals of $F^{14}C$ estimates based on generalized additive model smoothers.

TABLE 2 Estimation of the onset of $F^{14}C$ increase using the methodology of Campana et al. (2008) for blueline tilefish and for each of the finfish reference chronologies considered

Set	C_P	C_L	C_T	Y_T[a]
Blueline tilefish	1.0992	0.9388	0.9548	1960
SAB	1.1044	0.9322[b]	0.9494	1959, 1965[c]
NWA	1.0680	0.9282	0.9422	1956

Note: C_P and C_L represent the peak and lowest values found within a chronology. C_T is the value corresponding to the 10% threshold contribution of $F^{14}C$. The year of initial increase (Y_T) is then estimated as the first year the chronology exceeds C_T.

Abbreviation: NWA, north-west Atlantic; SAB, South Atlantic Bight.

[a]We did not consider any estimate of Y_T that was earlier than 1955; the onset of the $F^{14}C$ increase did not begin prior to 1955.

[b]We excluded an outlier value of $F^{14}C$ of 0.9109 (see Table S1) measured for barrelfish from the calculation.

[c]The first year that $F^{14}C$ exceeded C_T was 1959; despite samples from other years between 1959 and 1965, $F^{14}C$ did not exceed C_T again until 1965.

(Figure 3a). The updated SAB bomb radiocarbon reference chronology including the new data from the current study is shown in Figure 3b.

4 | DISCUSSION

The uptake pattern of $F^{14}C$ in *C. microps* in our study was comparable with chronologies reported in studies of other species and areas (e.g., Campana et al., 2008; Filer & Sedberry, 2008; Friess & Sedberry, 2011; Lytton et al., 2016) and supports interpreted increment counts as annual growth indicators in our *C. microps* otoliths. If the ageing methodology had not been successful at identifying consistent structures, there would have been no observable uptake pattern or coherent time series for *C. microps* in our study (Campana, 1997). The outlier with an estimated birth year of 1952 and $F^{14}C$ value of 1.03 may be due to a processing error where not all of the otolith material was removed to the core, or an ageing error attributed to the difficulty in agsing deepwater species. However, it is not unreasonable to expect a level of stochasticity in the mechanisms by which different fish encounter different $F^{14}C$ levels due to the complex process in which atmospheric bomb $F^{14}C$ enters the marine environment and mixes to depth (Kalish, 1995).

One possible scenario to explain the discrepancy in estimating onset of $F^{14}C$ increase for *C. microps* between the two reference chronologies is that the ageing methodology employed in the current study for *C. microps* results in biased age estimates, with age estimates representing under-ages relative to true age. Under this scenario, the obvious explanation for ageing bias in *C. microps* derives from the difficulty of ageing deepwater species (see Andrews et al., 2015; Campana et al., 2016; Fenton et al., 1991; Peres & Haimovici, 2004), with the difficulty of increment identification in *C. microps* being reviewed in previous work (Harris et al., 2004; Ross & Huntsman, 1982). General species longevity, slow growth, and slow maturation rates of deepwater species (Clark, 2001; Clarke et al., 2003) lead to the formation of tightly compacted increments in older individuals. In addition, deepwater environments are characterized by a lack of seasonality of the physical features of the environment (e.g., water temperature), necessitating that the formation of growth increments be driven by other factors (Swan & Gordon, 2001). Ross and Huntsman (1982) suggested that water temperature was not the primary driver for increment formation in *C. microps*, as the annual range of bottom temperatures along the shelf-edge zone was just equivalent to the minimum range that could induce decreased growth in fish. They suggested that increments in *C. microps* otoliths instead arise from a physiological rhythm or annual feeding cycle correlated with photoperiod. Alternatively, growth increments observed in deepwater finfish may reflect seasonal changes in prey availability derived from the surface environment (Swan & Gordon, 2001). If underageing is occurring, misinterpreted annuli are likely within the first several broad and diffuse increments that were grouped and

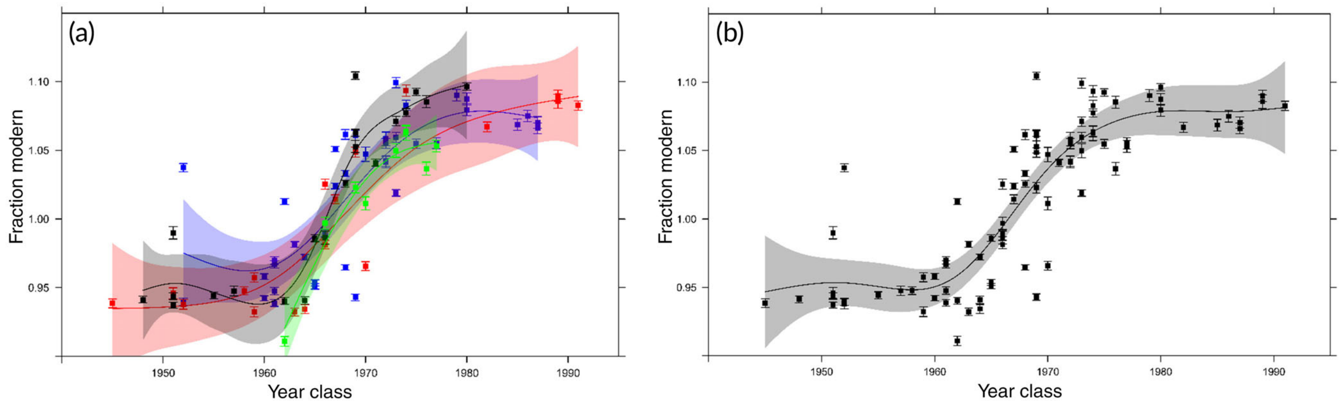

FIGURE 3 (a) Individual South Atlantic Bight (SAB) species $F^{14}C$ chronologies for wreckfish (black), red bream (red), barrelfish (green), and blueline tilefish (blue) and (b) updated SAB reference chronology including data from the current study. Horizontal and vertical error bars represent the standard error estimate for age estimates and the $F^{14}C$ σ from the bomb radiocarbon analysis, respectively. Shaded polygons represent 95% confidence intervals of $F^{14}C$ estimates based on generalized additive model smoothers.

interpreted as a single annulus by the SCDNR age readers in the current study.

A second possible scenario to explain the discrepancy in estimating the onset of the $F^{14}C$ increase for *C. microps* between the two reference chronologies is that currently employed ageing methodology for *C. microps* results in unbiased age estimates. In this scenario, the lack of correspondence in the $F^{14}C$ chronology for *C. microps* and reference chronologies from the NWA is the result of regional differences in hydrological processes with respect to ^{14}C. The apparent ageing bias exhibited by *C. microps* relative to a geographically disparate reference chronology is not an uncommon occurrence for radiocarbon studies performed on deepwater fishes from the SAB region. Filer and Sedberry (2008), Friess and Sedberry (2011), and Lytton et al. (2016) all hypothesized that the apparent underageing relative to a Haddock reference chronology (Campana, 1997) in their respective studies may have resulted from differences in oceanographic conditions derived from localized upwelling events, regional differences in onset of ^{14}C increases in surface waters, and differential surface-to-depth mixing rates of water masses experienced in the two regions. A growing body of research is documenting the period of delay one would expect for the bomb signal to penetrate from the surface to increasingly deeper waters. In the south-west Pacific Ocean, Grammer et al. (2015) suggested 5–10 years for radiocarbon to reach depths ~400–500 m, with initial increase not beginning until 1963 and not peaking until the early 1980s. In the north-east Atlantic, Nydal (1993) suggested a period of 18 years for $F^{14}C$ penetration to a depth of 1000 m; assuming a linear increase in depth through time, signal penetration to 200 m depth would take 3.6 years. Similarly, the bomb signal took 14 years to penetrate to a depth of 800 m in the Indian Ocean (Rubin & Key, 2002); given the same calculations presented above, 3.5 years would be required to penetrate to a depth of 200 m. Finally, within the north-west Atlantic, Campana et al. (2016) suggested a 9-year delay for the $F^{14}C$ signal to reach a depth of 390–450 m, relative to the same NWA reference chronology used in the current study. Friess and Sedberry (2011) could not attribute the observed phase-shift to this phenomenon because juvenile red bream have a long pelagic stage and therefore the $F^{14}C$ signal from the core in these otoliths would be expected to be similar to surface levels. While it is known that juveniles of *Caulolatilus* sp. inhabit demersal adult burrows as a means for predator avoidance (Able et al., 1987), habitat use by larval and age 0 *C. microps* is not precisely understood. Captive reared juveniles of the closely related tilefish species *Lopholatilus chamaeleonticeps* have been observed settling to the bottom and beginning to dig by 1.5-cm standard length (Fahay, 1983), and analysis of $\delta^{13}C$ values and $\delta^{15}N$ values of eye lens protein suggests long single location residency throughout the lifespan (Vecchio et al., 2021).

The consistent offset between the NWA reference chronology and radiocarbon data from SAB deepwater species *C. microps* (the current study), red bream (Friess & Sedberry, 2011), barrelfish (Filer & Sedberry, 2008), and wreckfish (Lytton et al., 2016) suggests unique environmental or oceanographic conditions in the study region. It is improbable that growth increment counts in each of these studies led to underageing by the same proportional amount relative to the NWA reference chronology. A more likely explanation is that the NWA chronology was inappropriate for use as a reference curve for these species. Thus, we agree with the assessment of Campana et al. (2016) that it appears inevitable that the bomb signal would be delayed in reaching the depth of *C. microps* in the present study, with the delay resulting in the appearance of an apparent underageing bias relative to the reference chronology from shallower waters in the NWA. This phenomenon is further supported by the appearance of slight overageing (~1 year) of the *C. microps* in our study compared to the red bream, barrelfish, and wreckfish included in the SAB reference chronology, which all generally inhabit slightly deeper waters (375–700 m).

A strength of age validation using the bomb radiocarbon technique is that it allows for the validation of a maximum age because one can validate the age of individual fish up to the year of onset of increases in ^{14}C to the fish's environment. Inspection of the ages of fish with estimated birth years in the early 1960s ($F^{14}C$ onset suggested introduction of ^{14}C into the environment due to nuclear testing in 1960) in the current study indicates that *C. microps* ages are validated up to 25 years in the SAB. There were many specimens that we estimated to be 40–50 years old, but we did not select for bomb radiocarbon sampling because their presumed birth years did not fall within the period of drastic increase in atmospheric and surface water ^{14}C concentrations due to nuclear testing. Because we validated annual increment formation, have consistency with our age estimates both between and within readers, and due to the prevalence of *C. microps* with ages of 40–50 years old in MARMAP samples, we feel confident that *C. microps* live to at least 50 years, which is 10 years older than the maximum age of 40 years used in the most recent stock assessment (SEDAR 50).

In conclusion, the SAB reference chronology presented here provides reasonable evidence of a differential ^{14}C uptake pattern in SAB deeper waters (~200–700 m deep) that is likely the result of local hydrological processes causing a delay of ^{14}C reaching the local environments inhabited by these species. The results from *C. microps* in our study both agree with the properties of this unique regional chronology and contribute additional data that can be added to a SAB reference curve. We have provided methodology to accurately interpret annual growth increments of *C. microps* otoliths that will lead to more consistency in ageing this deepwater species. We provide evidence that *C. microps* live to at least 50 years old (even older with underageing error plausible), which would be a new benchmark maximum age for stock assessments in the region. The conflicting results of the ageing methodology validation, depending on the reference chronology used for comparison, highlight the importance of using a reference chronology from the same, or similar, environments with respect to ^{14}C availability. Cross-basin (Kastelle et al., 2016) and even within-basin (Wischniowski et al., 2015) comparisons have revealed chronologies with distinctly different properties between a validation and a reference data set, demonstrating how misapplication may lead to ageing error. While our study provides a more appropriate bomb radiocarbon reference chronology for use within deeper waters of the SAB, the development of a true region-specific chronology in the SAB consisting of known-age specimens remains necessary to unequivocally distinguish between ageing error and effects of oceanographic processes (Piner & Wischniowski, 2004), and should be a future research goal. This chronology, along with additional information on the early life history of *C. microps* and other deepwater species, would provide invaluable resources to confirm the results of the current study and further aid in the precision and accuracy of ageing deepwater species in the region.

AUTHOR CONTRIBUTIONS

Joseph C. Ballenger performed the majority of the data analysis. Kevin R. Spanik was highly involved in the research and contributed to data generation, data analysis, and manuscript preparation.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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