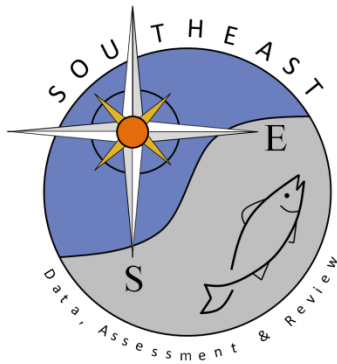


Bomb radiocarbon and tag-recapture dating of sandbar shark
(*Carcharhinus plumbeus*)

Andrews, Allen H.; Natanson, Lisa J.; Kerr, Lisa A.; Burgess,
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Abstract—The sandbar shark (*Carcharhinus plumbeus*) was the cornerstone species of western North Atlantic and Gulf of Mexico large coastal shark fisheries until 2008 when they were allocated to a research-only fishery. Despite decades of fishing on this species, important life history parameters, such as age and growth, have not been well known. Some validated age and growth information exists for sandbar shark, but more comprehensive life history information is needed. The complementary application of bomb radiocarbon and tag-recapture dating was used in this study to determine valid age-estimation criteria and longevity estimates for this species. These two methods indicated that current age interpretations based on counts of growth bands in vertebrae are accurate to 10 or 12 years. Beyond these years, we could not determine with certainty when such an underestimation of age begins; however, bomb radiocarbon and tag-recapture data indicated that large adult sharks were considerably older than the estimates derived from counts of growth bands. Three adult sandbar sharks were 20 to 26 years old based on bomb radiocarbon results and were a 5- to 11-year increase over the previous age estimates for these sharks. In support of these findings, the tag-recapture data provided results that were consistent with bomb radiocarbon dating and further supported a longevity that exceeds 30 years for this species.

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Bomb radiocarbon and tag-recapture dating of sandbar shark (*Carcharhinus plumbeus*)

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Bomb radiocarbon dating has evolved as a useful method for validating the age of fishes. The validation of age relies on a preserved record of the rapid increase in radiocarbon (¹⁴C) that occurred in the world's oceans as a result of atmospheric testing of thermonuclear devices in the 1950s and 1960s (Broecker and Peng, 1982). The uptake of bomb-produced ¹⁴C by the marine environment, reported as $\Delta^{14}\text{C}$ in reference to an established pre-nuclear ¹⁴C record (Stuiver and Pollach, 1977), was virtually synchronous in the mixed layer of mid-latitude oceans and was first recorded from marine carbonates in hermatypic corals (Druffel and Linick, 1978). Application for the dating of fishes began with an innovative comparison of $\Delta^{14}\text{C}$ values recorded in otolith carbonate in relation to regional $\Delta^{14}\text{C}$ records from hermatypic corals (Kalish, 1993). The temporal specificity of otolith $\Delta^{14}\text{C}$ provided an independent determination of age and corroborated age estimates determined from counting growth zones in otoliths (Campana,

2001). Bomb radiocarbon dating has since been successfully applied to validate age estimates of numerous teleost fishes (e.g., Andrews et al., 2007; Ewing et al., 2007; Neilson and Campana, 2008), elasmobranchs (e.g., Campana et al., 2002, 2006; Kneebone et al., 2008), and other marine organisms (e.g., Frantz et al., 2005; Roark et al., 2006; Stewart et al., 2006; Kilada et al., 2007).

The first application of bomb radiocarbon dating to validate ages in long-lived sharks addressed the porbeagle (*Lamna nasus*) and, preliminarily, the shortfin mako (*Isurus oxyrinchus*; Campana et al., 2002). Unlike the otoliths of bony fishes, in which the source of ¹⁴C is inorganic and uptake is mostly synchronous with the marine environment, the vertebrae of porbeagle provided evidence for a phase lag of approximately three years in the timing of the rise in $\Delta^{14}\text{C}$. This lag was attributed to a trophic-level delay in the propagation of ¹⁴C or to depth-related dilution of carbon sources, or to both, in relation to the

formation of vertebrae from organic carbon sources. Use of measurements from known-age individuals, in relation to measurements made in adult vertebrae, ruled out the possibility of reworked vertebral carbon throughout the life of the shark. This procedure enabled age validation for porbeagle and shortfin mako (Campana et al., 2002; Ardizzone et al., 2006). By contrast, a study of the white sharks (*Carcharodon carcharias*) of the eastern North Pacific Ocean indicated that aspects of life history, such as large-scale movements and feeding below the ocean mixed layer, can lead to mixed $\Delta^{14}\text{C}$ results that confound attempts to validate age (Kerr et al., 2006).

The sandbar shark (*Carcharhinus plumbeus*) is a cosmopolitan species of subtropical and tropical seas and was the cornerstone large coastal shark taken in the western North Atlantic (WNA) and Gulf of Mexico (GOM) bottom longline shark fisheries from the early 1980s until 2008 when they were allotted to a research-only fishery (NMFS, 2008). Modeling regional population dynamics has led to conclusions that the population is in need of rebuilding (Brewster-Geisz and Miller, 1999; Cortes, 1999). The most recent stock assessment of the large coastal shark complex of this region revealed that sandbar sharks are currently overfished, and overfishing is occurring (NMFS, 2006). Because fishing authorities set management measures using stock assessment models that increasingly and necessarily rely on age data (Cailliet and Andrews, 2008), even greater importance must be placed on age validation as a requirement for stock assessments (Payne, 2006). Validated age data enable stock assessment scientists 1) to understand and monitor long-term changes in population age-structure; 2) to determine the timing of important life history events (e.g., age at first maturity); 3) to measure vital rates (e.g., growth and natural mortality); and 4) to monitor fishing mortality rates and their long-term effects on the population.

Some validated age and growth information exists for sandbar shark, but more comprehensive information on its biological development is needed. Age has been validated for juvenile sandbar sharks in Hawaii by using marginal increment analysis and oxytetracycline (OTC) marking (Romine et al., 2006), and for adults up to approximately 17 years in Australia with the use of tag-recapture data (McAuley et al., 2006). However, studies geographically removed from the WNA are of limited use for that region. In the WNA–GOM region, one laboratory study validated growth up to 112 cm (Branstetter, 1987). Estimates of age, growth, and longevity were primarily “unvalidated” by using vertebral centra and observations of growth in tag-recapture programs (Casey et al., 1985; Casey and Natanson, 1992; Sminkey and Musick, 1995; Merson and Pratt, 2001). Use of tag-recapture data to determine growth characteristics can be complicated because revisions may be needed as additional recaptures continue to provide new data over time (*cf.* growth parameters presented in Casey and Natanson [1992] with those in Casey et al. [1985]). In addition, maximum size (L_{max}) is typically underestimated in tag-recapture studies, although

the tag-recapture method offers several advantages, including a useful verification of younger age classes, estimates of longevity, and valid measures of age and growth when used in concert with OTC-marked growth bands. Therefore, use of both bomb radiocarbon and tag-recapture dating methods can produce a series of age and growth determinations that can facilitate accurate growth modeling throughout ontogeny of a species. The sandbar shark is not known to move into deep water; thus it is a good candidate for bomb radiocarbon dating because complications from greatly depleted ^{14}C sources with depth are unlikely (i.e., Kerr et al., 2006). It was hypothesized that an application of bomb radiocarbon dating would 1) provide independent estimates of age that either corroborate or refute age estimates from counting growth band-pairs; and 2) provide a minimum longevity for sandbar shark. It was further hypothesized that additional tag-recapture age and growth data from OTC-injected sandbar sharks would be in agreement with the bomb radiocarbon age data.

Materials and methods

Bomb radiocarbon dating

Sandbar shark vertebrae, collected from the WNA and stored frozen, with capture years ranging from 1965 to 1985 were obtained from 1) the Apex Predators Program of the National Marine Fisheries Service (NMFS; $n=4$); and 2) the Florida Program for Shark Research ($n=1$) for bomb radiocarbon analyses (Table 1). Successful application of bomb radiocarbon dating requires that structures used to determine age come from sharks that were alive during some portion, or all, of the period of rapid increase in $\Delta^{14}\text{C}$ from atmospheric bomb testing (~1955 to 1970 for the marine environment). Five sharks collected between 1965 and 1981 were selected for analysis on the basis of estimated age from sex specific growth curves (Casey et al., 1985) and collection dates, to estimate birth year (Table 1). Age estimates from growth band counts for four of these sharks were made before our study by using histological techniques described elsewhere (Casey et al., 1985). Contiguous vertebrae were used for the ^{14}C analyses.

Vertebrae from the five individual sharks were sampled for ^{14}C analysis by using accelerator mass spectrometry (AMS). A section of the vertebral centrum was removed from the corpus calcareum of each vertebra along the sagittal plane. Sections were cut thicker than typically used for age estimates (2–3 mm) to ensure that there was adequate material to meet minimum sample size requirements. Sections were mounted on glass microscope slides with fine-meshed, double-stick nylon tape. A New Wave® (Electro Scientific Industries, Fremont, CA) micromilling machine with a 0.3-mm diameter bit (Brassler®, Savannah, GA) was used to drill a series of overlapping holes around the circumference of the targeted growth band pair (one opaque and one translucent band; *sensu*

Table 1
Size, year of capture, estimated age, and sex of sandbar shark (*Carcharhinus plumbeus*) sampled in this study.

Specimen number	Fish fork length (cm)	Year of capture	Estimated age (yr)	Estimated birth year	Sex
SB 43	136.5	1965	10.3	1955	F
SB 47970	160.0	1985	14.2	1971	F
SB 745	167.0	1976	16.4	1960	M
SB 118	167.5	1966	15.6	1950	F
SB 749	170.0	1981	16.1	1965	F

Cailliet et al., 2006). The location of the series of drill holes was carefully chosen to extract the targeted growth-band pair within the corpus calcareum and to minimize the possibility of including external vertebral material not formed during that year of growth. The intermedialia of the vertebral centrum was avoided because banding is poorly defined near the corpus calcareum. The width of growth-band pairs was used as the target size for extraction therefore, the amount of material extracted decreased as the width of growth band pairs decreased. Drilling depth was just short of the depth required to pass completely through the section to provide a secure mount for the extracted block of vertebral material. Final removal of the sample was made with a razor blade, firmly pressed to the slide.

A total of thirteen growth-band pairs were extracted from the corpus calcareum of the five sandbar shark vertebrae. The first growth-band pair after the birth band (estimated to be the first year of growth after birth) and one to four subsequent growth band pairs farther toward the outer edge of the corpus calcareum were extracted from each vertebra. The last band pair, corresponding to the last year of growth, was targeted to provide a sample where time of formation was constrained by the collection date. The location for extraction of the most recent vertebral sample was usually proximal to the distal tip of the corpus calcareum because of reduced band width and poor edge condition at the tip. The extracted samples weighed approximately 10 mg; the specific values were not specifically recorded owing to an oversight.

Demineralization of vertebral samples was performed to isolate the organic portion (collagen) by dissolving the inorganic component that can increase carbon yield from the accelerator mass spectrometry (AMS) graphitization process (Brown et al., 1988). Samples were soaked in 0.25 N HCl for 24 hours at refrigerator temperatures to reduce reaction rate. Treated samples were dried in an oven at 60°F (16°C) and placed in clean quartz tubes. Copper oxide (CuO, oxidizing agent) and silver (Ag, for impurity removal: SOx and NOx) were added to the treated organic samples at levels specified for AMS (Center for Accelerator Mass Spectrometry [CAMS], Lawrence Livermore National Laboratory).

Quartz tubes were evacuated, sealed, and heated for 2 hours at 900°C to convert the organic carbon to CO₂. Sample CO₂ was converted to graphite (Vogel et al., 1984, 1987) and measured for ¹⁴C content with AMS at the CAMS. The ¹⁴C values were reported as Δ¹⁴C (Stuiver and Polach, 1977) and age corrected by using the estimated year of formation in relation to 1950. The ¹⁴C values were then adjusted for fractionation by using an assumed δ¹³C value of -15‰ based on a previous study (Campana et al., 2002) and other standards (Stuiver and Polach, 1977).

Sandbar shark Δ¹⁴C data were compared with existing hermatypic coral Δ¹⁴C records for the WNA for a temporal alignment. Because this species is known to cover great distances along the Atlantic seaboard seasonally and ontogenetically (Grubbs et al., 2007), the Δ¹⁴C records from hermatypic coral off the Florida Keys and Bermuda (Druffel and Linick, 1978; Druffel, 1989) and validated shark vertebrae (porbeagle from western North Atlantic; Campana et al., 2002) were used as reference chronologies for comparison to the measured values from aged sandbar shark vertebrae. Fish otolith Δ¹⁴C records were also considered for calibration purposes (i.e., Campana et al., 2008) but were not used in our analysis because the Δ¹⁴C record was intermediate in time and magnitude to the coral and shark Δ¹⁴C records and did not provide additional temporal clarity. Age of sandbar sharks was calibrated by aligning measured Δ¹⁴C values with the Δ¹⁴C reference chronologies, and estimated age was adjusted for some sharks according to the temporal alignment of these data.

OTC tag-recapture dating

Tag-recapture data were obtained and analyzed by using the methods of Casey et al. (1985) and by using only recaptures obtained since the publication by Casey and Natanson (1992). In addition, vertebrae were processed from OTC-injected and recaptured specimens. Two adjacent vertebrae were sectioned and examined concurrently to align band pairs with the OTC mark. One section was removed for histological examination (Casey et al., 1985) and the other, a thicker section, was made to preserve the OTC mark. The thicker section was made by using a gem saw (Raytech, Middleton, CT)

Table 2

Summary of results from radiocarbon analyses. Estimated shark age from growth band counts with calculated birth year, year of growth-band formation, and ages for each sandbar shark (*Carcharhinus plumbeus*) vertebra. Resultant $\Delta^{14}\text{C}$ values and the adjusted year of growth-band (GB) formation for each sample are given along with bomb radiocarbon age of the shark, where applicable. SD=standard deviation

Sample number	Age determined from growth bands			$\Delta^{14}\text{C}$ (SD) (%)	Age determined from radiocarbon data	
	Shark age (yr)	Year of GB formation	Age sampled		Adjusted year	Shark age (yr)
SB 43	10.3	1955			N.C. ¹	
		1957	2	-67.6 (4.2)	N.C. ¹	
		1963	8	-21.2 (3.6)	N.C. ¹	
		1965				10.3
SB 47970	14.2	1971			1960	
		1972	1	-79.8 (4.1)	1962	
		1977	6	125.3 (5.9)	1967	
		1985				25 (23–27)
SB 745	16.4	1960			1955	
		1961	1	-64.3 (4.0)	1956	
		1967	7	-78.6 (3.9)	1962	
		1976				≥20
SB 118	15.6	1950			N.C. ²	
		1951	1	-53.3 (4.2)	N.C. ²	
		1965	15	N.M. ³		
		1966				N.C. ²
SB 749	16.1	1965			1954	
		1966	1	-7.8 (4.4)	1955	
		1967	2	-110.9 (3.9)	1956	
		1970	5	-70.6 (3.9)	1959	
		1974	9	-61.7 (4.0)	1963	
		1980	15	16.6 (4.6)	1980	
		1981				≥26

¹ No change: Values in alignment with calibration curves.

² No change: Not enough information to assess an adjustment (with prebomb reference)

³ Not measured: Sample was lost during preparations for accelerator mass spectrometry.

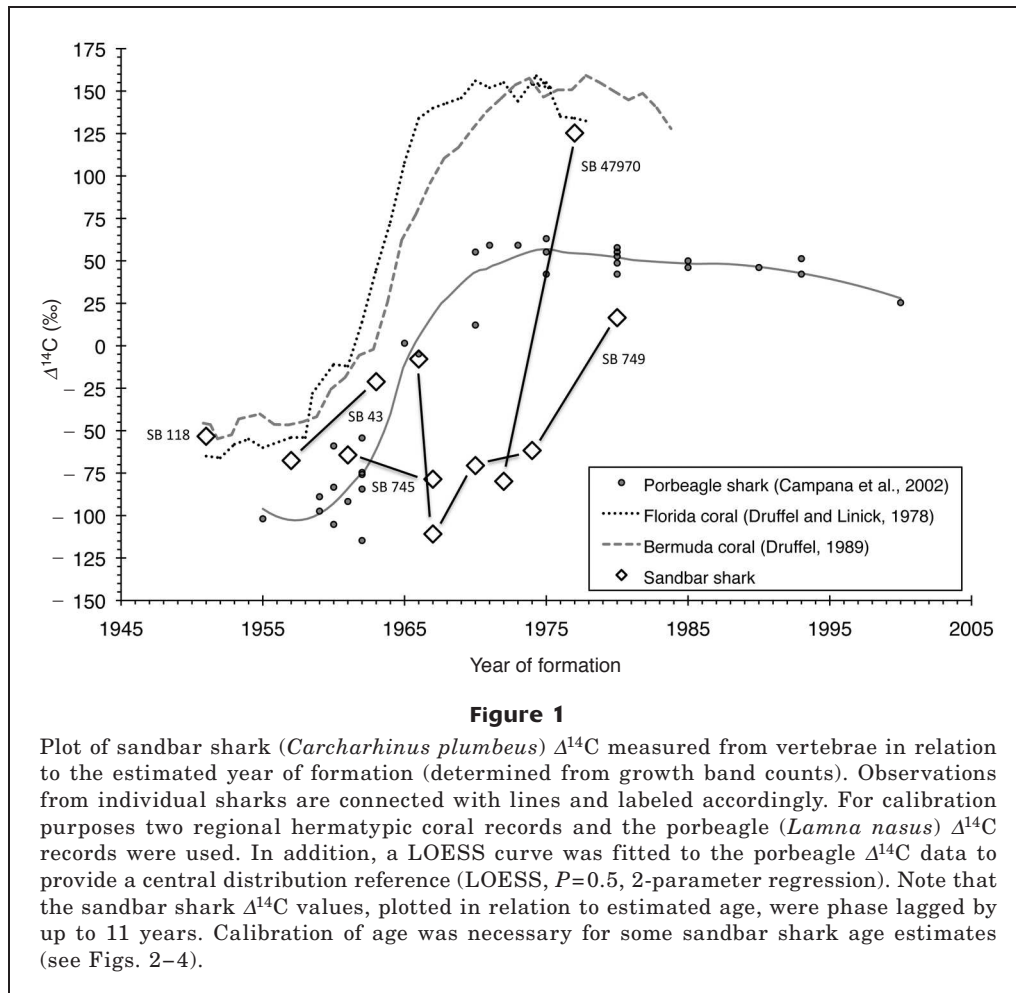
with two diamond blades separated by a 0.6-mm spacer. Photographs of both sections were taken—the thicker sections under UV light and the thinner histological sections under reflected lighting. Resulting photographs were superimposed to determine the location of the OTC mark on the histological section and counts and measurements were determined from the combined images.

Results

Bomb radiocarbon dating

Values of $\Delta^{14}\text{C}$ measured in sandbar shark vertebrae, provided in parts per million (‰) ± 1 standard deviation

[SD]), ranged from prebomb to peak and postbomb levels (Table 2). Prebomb levels were similar to those in the porbeagle record, with values as low as -110.9‰ (SD=3.9). The peak $\Delta^{14}\text{C}$ value exceeded expectations and was similar in magnitude to hermatypic coral $\Delta^{14}\text{C}$ records (125.3‰, SD=5.9). Despite the strong indication of bomb-produced radiocarbon in several vertebrae, the growth-band derived years of formation for many of the samples were not in agreement with the bomb radiocarbon dating $\Delta^{14}\text{C}$ references (Fig. 1). One sample was lost from specimen SB 118; therefore, the vertebra was useful only as a prebomb $\Delta^{14}\text{C}$ reference value. The age of the youngest specimen (SB 43), estimated at 10.3 years, was supported by the $\Delta^{14}\text{C}$ results; yet the estimated ages of the other three adult



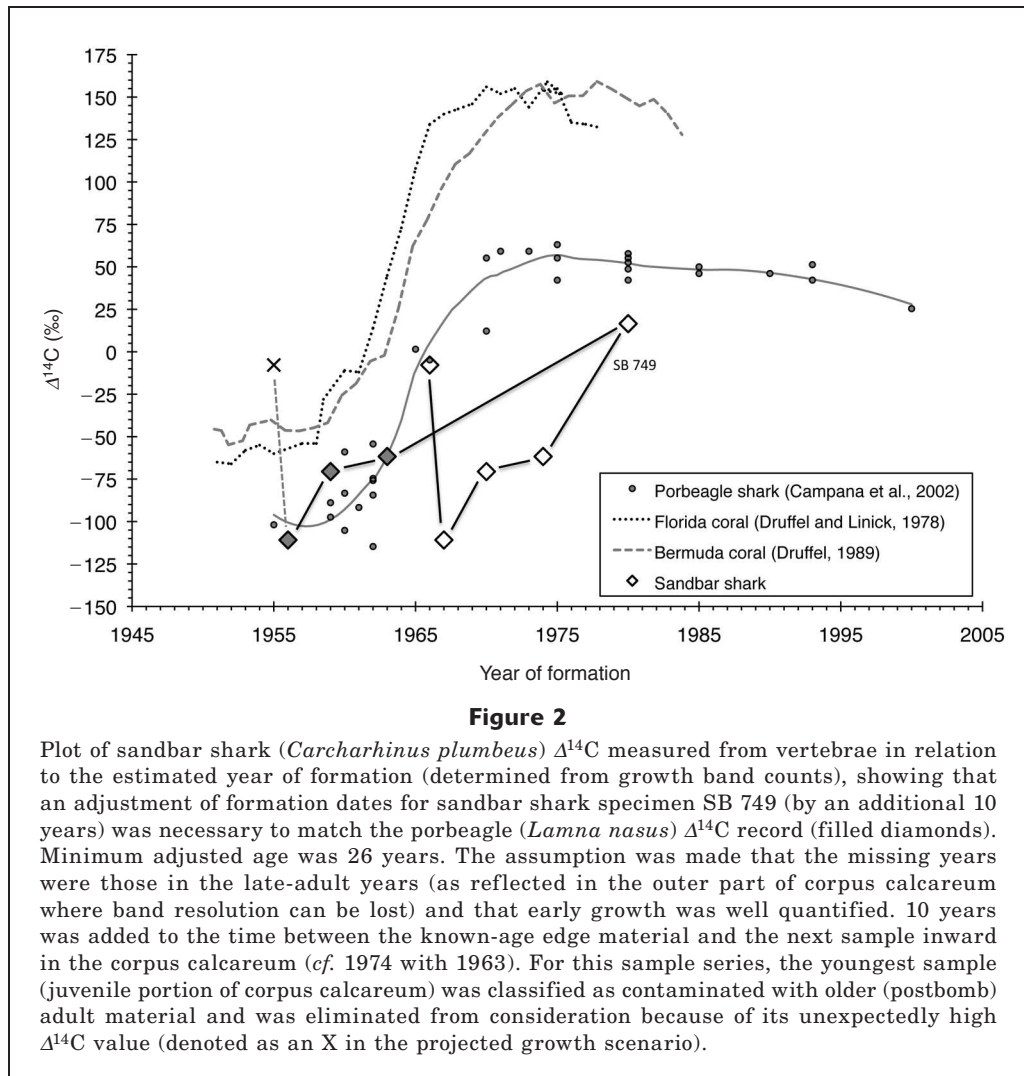
sharks were not in agreement with the reference $\Delta^{14}\text{C}$ chronologies.

The age of three adult sandbar sharks (SB 745, SB 749, SB 47970) was underestimated by approximately five to 11 years in relation to the reference $\Delta^{14}\text{C}$ chronologies and resulted in an increase in age to at least 20 to 26 years. The age of specimen SB 749 was underestimated by at least 11 years after alignment with the porbeagle $\Delta^{14}\text{C}$ reference record for a revised age of at least 26 years. To make the alignment, we had to assume that the innermost sample (year-1) of the vertebra was an inaccurate extraction that included more recent (postbomb) material (Fig. 2). This conclusion was supported by the measured postbomb $\Delta^{14}\text{C}$ level from the innermost sample of the corpus calcareum (-7.8‰ , $\text{SD}=4.4$) when compared to more recently formed samples that were clearly prebomb and further into the life of the shark (Table 2). The age of specimen SB 47970 was underestimated, requiring adjustment of 10 to 12 years based on a simultaneous alignment of the measured $\Delta^{14}\text{C}$ values in relation to the coral and porbeagle shark $\Delta^{14}\text{C}$ reference chronologies. The near peak $\Delta^{14}\text{C}$ value could not have been formed earlier than 1965 (based on the maximum

rise in $\Delta^{14}\text{C}$ from the Florida coral record), yet the measured prebomb $\Delta^{14}\text{C}$ value could be no later than 1962 (based on the rise in $\Delta^{14}\text{C}$ from the porbeagle record; Fig. 3). With these alignment constraints, and with the assumption that there was no problem with interpreting age from the early growth between the two samples (five years), a median age of 25 ± 2 years was determined for this shark. The age for specimen SB 745 was underestimated by at least five years to align with the porbeagle $\Delta^{14}\text{C}$ record, but this shark could have been older because prebomb values alone are not diagnostic (Fig. 4).

OTC tag-recapture dating

Since 1992, 173 tagged sandbar sharks have been recaptured as part of the NMFS Apex Predators Program. Ten of these sharks were estimated to have lived more than 20 years (20.1–31.1 years) based on time-at-liberty (TAL) and the estimated age at time of release determined from the sex-specific growth curves of Casey et al. (1985). These sharks were tagged at 80–183 cm fork length (FL) and had a TAL of 2.6–26.9 years (Table 3). In addition, 22 sharks with estimated lengths at tagging

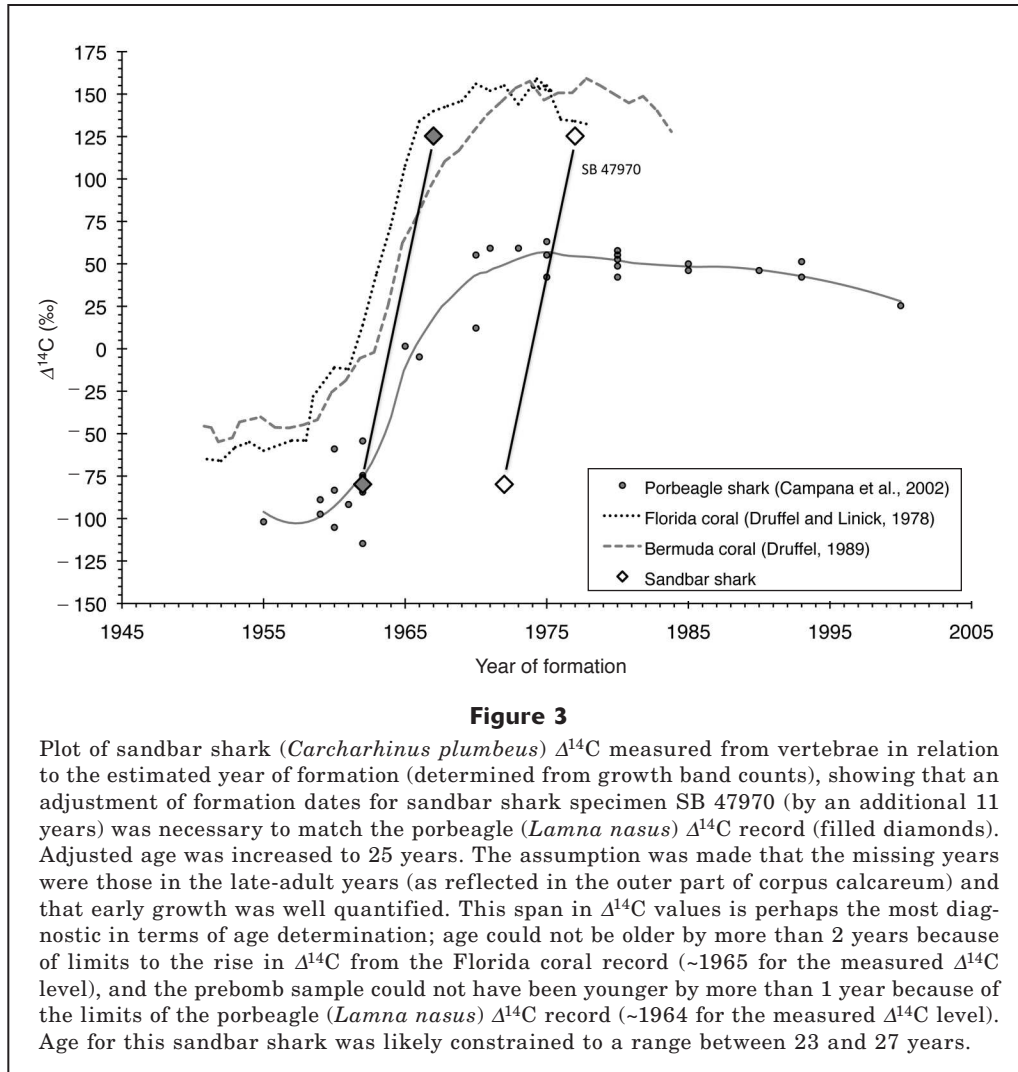


of 73–140 cm FL were recaptured after a minimum of 10 years at liberty (TAL 10.0–27.7 years). Ages for these sharks ranged from 13.1 to 36.0 years (Table 3). The tag of the shark at liberty 27.7 years was compromised over time: the last of 3 digits on the tab was worn off by the time of recapture. This shark was one of ten sandbar sharks measured and tagged on the same day within this number series. These sharks ranged in size from 99 to 122 cm FL at recapture and longevity was estimated at 33 to 36 years for these sharks for this longest period before recapture.

One OTC-tagged recaptured shark was examined that measured 68 cm at tagging and 150.4 cm FL at recapture. Time at liberty was 11.8 years and the estimated age at tagging was 1.6 years. Twelve band pairs were visible after the OTC mark as determined by the criteria of Casey et al. (1985) and the total estimated age was 13.6 years. This estimate was one year more than the growth curve estimate (12.6 years), but was within the margin of uncertainty of the growth function.

Re-examination of vertebrae

Because the bomb radiocarbon analyses revealed discrepancies in age, four of the original histological sections were re-examined to determine whether banding existed in the sections that would correspond with the bomb radiocarbon ages. Many additional band pairs were visible in the vertebrae of these specimens and support the ages indicated by the bomb radiocarbon analyses. These band pairs were not considered to represent annual growth in the early study because they did not fit the criteria defined in the study and were not counted. If an approach were used to count all band pairs, this would also indicate that the age-validated specimen SB 43 was more than 10 years old (maximum addition of three years in relation to coral $\Delta^{14}\text{C}$ records). In addition, the recently collected OTC-marked specimen would necessarily have an age greater than the known TAL and lead to the conclusion that early growth was not underestimated. These findings indicate that the band pair counts with the Casey et al. (1985) criteria



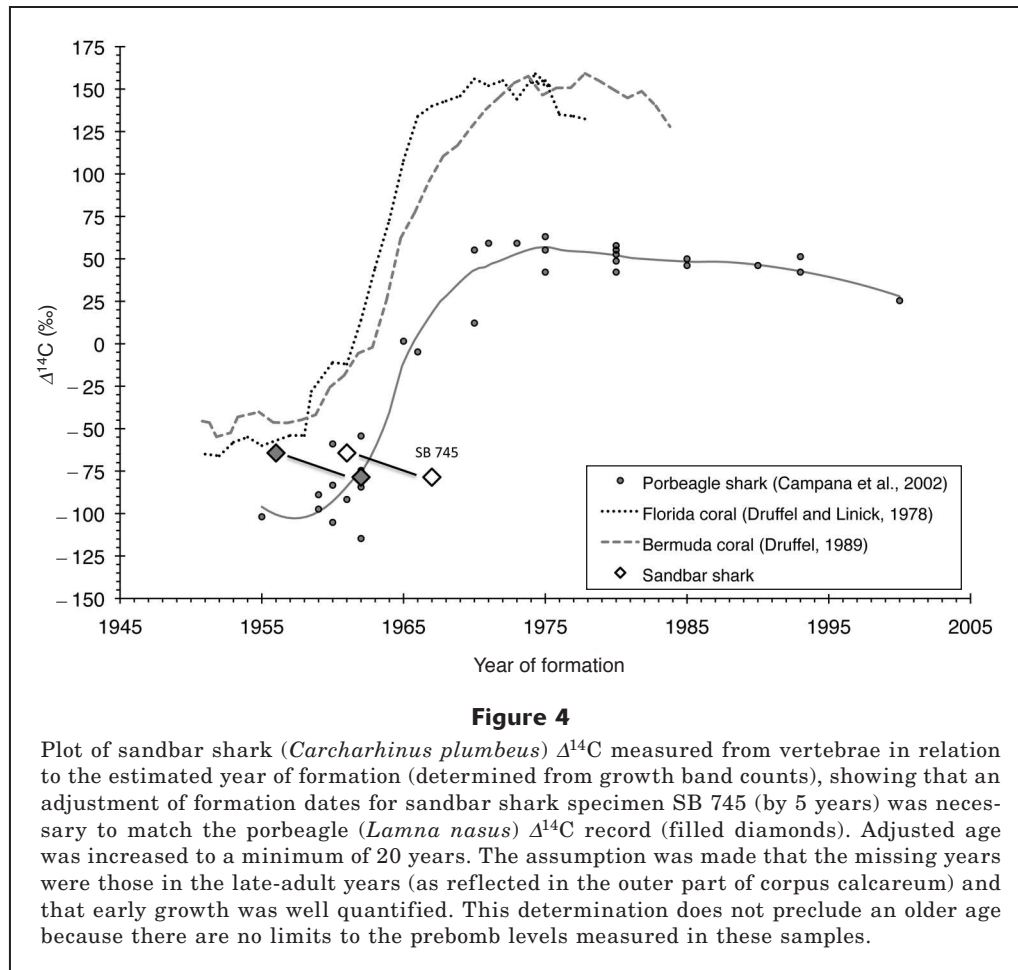
were reliable as a measure of annual growth to at least 12 years (10 and 12 years validated in this study with bomb radiocarbon and OTC marking, respectively). After this time of band formation in the vertebrae, either growth-band pairs do not provide an accurate measure of annual growth or the criteria for counting must be changed to incorporate a finer growth band structure. Until all sizes and ages can be validated, it would not be possible to determine how the growth-band counting criteria need to change.

Discussion

The comparisons of measured $\Delta^{14}\text{C}$ values from sandbar shark vertebrae with regional reference chronologies provided age determinations that exceeded age estimates from visual growth-band counts for three of the largest sharks in this study. Levels of $\Delta^{14}\text{C}$ recorded in sandbar shark vertebrae during the rise in marine $\Delta^{14}\text{C}$ and postbomb periods were unexpectedly low based on

their estimated year of band formation determined from growth-band counts. This finding led us to conclude that ages had been underestimated for these adult sandbar sharks by 5 to 11 years, thereby providing explanation for the temporal offset and providing evidence that these individuals were considerably older.

Considerable evidence shows that diet is the primary source of carbon in the skeletal structure of sharks and that collagen retains its time specificity in respect to its deposition in vertebrae (Fry, 1988; Campana et al., 2002, 2006); hence, an alternative explanation for the unexpectedly attenuated $\Delta^{14}\text{C}$ values measured in sandbar shark vertebrae could be a shift or mix in dietary carbon sources. To address this potential explanation for sandbar sharks, we turned to the well-documented study of white sharks from the eastern North Pacific Ocean (Kerr et al., 2006). For white sharks, the unexpectedly low $\Delta^{14}\text{C}$ values in the vertebrae could not be explained as problems with age estimation; collection year and known-age juvenile samples provided temporal constraints that eliminated



age-related discrepancies. Instead, feeding habits of these sharks in deep offshore waters appear to explain the observations.

For the sandbar shark, a scenario similar to that of the white shark would be possible if the single sample from year-1 of specimen SB 749 was considered uncontaminated. This $\Delta^{14}\text{C}$ value was clearly postbomb value at -7.8‰ (SD=4.4). Including this sample would preclude an increase in age for this sandbar shark, as well as the other sharks in our study and explain the unexpectedly low $\Delta^{14}\text{C}$ values. Based on the growth band age estimates alone, the temporal distribution of the $\Delta^{14}\text{C}$ data for sandbar shark would be similar to that of the white shark (*cf.* Fig. 1 of this study with Fig. 1 of Kerr et al. [2006]). However, the well-documented feeding behavior and depth-related life history of sandbar shark do not support this hypothesis (Springer, 1960; Stillwell and Kohler, 1993; Conrath and Musick, 2007). In addition, although it is certain there was some non-surface-derived ^{14}C included in the sandbar shark diet based on the lowest measured $\Delta^{14}\text{C}$ values (-78.6‰ to -110.9‰ *cf.* -40.2‰ to -66‰ for corals), the levels were similar to the lowest $\Delta^{14}\text{C}$ values measured in the porbeagle $\Delta^{14}\text{C}$ reference chronology (-74.6‰ to -114.7‰). Because of important life history considerations, it was

concluded that the innermost sample (year-1) from the vertebra from specimen SB 749 was inaccurately extracted and included more recently formed vertebral material. In support of this conclusion is the series of three additional samples that would have formed after this sample, all of which were clearly classified as pre-bomb material.

The most plausible explanations for underestimated ages of sandbar sharks in this study are either a lack of band pair formation at the oldest adult ages or a problem with the interpretation of growth bands. The validated age of the youngest specimen (SB 43) provides some evidence that age can be determined visually with growth-band counts in the earliest years of growth. A validated age of ten years for this shark provides evidence that the missing years for the larger shark were most likely those from the latter years of life. This argument was well documented for porbeagle shark off New Zealand, for which age estimation was accurate to approximately 20 years but was underestimated by several decades for older sharks (Francis et al., 2007). Estimation of age from band pair counts was not possible for older sharks because as somatic growth of the shark slowed or ended, vertebral growth ceased. A similar scenario was described for school shark or

Table 3

Tag and recapture data for sandbar shark (*Carcharhinus plumbeus*) over a period of several decades. Specimen IDs 1–10 revealed life spans exceeding 20 years and the remaining specimens had time at liberty (TAL) exceeding 10 years. Age at tagging was estimated from the Casey et al. (1985) growth function. Age at recapture was the sum of estimated age at capture and time at liberty. Italicized lengths were estimated. NR=not reported. U=unidentified.

Specimen ID	Sex	Fork length (cm)			TAL (yr)	Estimated age (years)	
		Tagging	Recapture	Growth		Tagging	Recapture
1	F	183	160	-23	2.6	19	21.4
2	F	152	170	18	7.6	13	20.5
3	M	139	140	1	9.0	11	20.1
4	F	152	145	-7	10.2	13	23.0
5	F	156.6	169	12	12.1	14	25.7
6	M	154	NR		12.1	14	25.9
7	M	127	203	76	12.7	9	21.8
8	M	80	141	61	24.9	3	27.8
9	M	106	136	30	24.9	6	31.1
10	F	87	166	79	26.9	4	30.6
11	M	137	152	15	11.0	11	21.7
12	F	73	202	129	11.0	2	13.1
13	M	82	154	72	11.0	3	14.2
14	M	90	127	37	11.0	4	15.1
15	F	131	127	-4	11.1	10	20.6
16	U	102	131	29	11.1	6	16.7
17	F	127	162	35	11.5	9	20.4
18	U	115	178	63	11.5	7	18.9
19	M	137	148	11	11.7	11	22.4
20	F	102	202	100	12.1	6	17.7
21	M	115	156	41	12.8	7	20.2
22	F	91	140	49	13.2	4	17.4
23	M	140	155	15	13.4	11	24.6
24	F	127	169	42	13.5	9	22.4
25	F	90	152	62	13.6	4	17.7
26	F	102	152	50	14.5	6	20.1
27	F	123	165	42	15.6	8	24.0
28	F	122	160	38	16.8	8	25.0
29	F	102	167	65	17.5	6	23.1
30	U	115	183	68	18.0	7	25.4
31	F	91	168	77	18.4	4	22.6
32	U	99–122	146	47–24	27.8	5–8	33–36

tope shark (*Galeorhinus galeus*) in Australia (Kalish and Johnston, 2001).

There is evidence to support a similar conclusion in terms of reduced or ceased somatic growth of the vertebrae. Two of the sandbar sharks in this study could be older because once prebomb $\Delta^{14}\text{C}$ levels were attained there was no limit to maximum age. In contrast, the age of specimen SB 47970 was well constrained by the upper and lower limits of the $\Delta^{14}\text{C}$ reference chronologies for an age of 25 ± 2 years. The five years estimated from band pair counts between the measured values for SB 47970 is consistent with the validated early growth from SB 43 (10 years old). Therefore, the addition of 11 years, as part of the age estimate that was not quantified for late adult life, was chosen to shift the observed

five-year early growth period to match the $\Delta^{14}\text{C}$ reference records.

In general, bomb radiocarbon dating of sharks must be qualified with empirical evidence to support a temporal correlation with a regional $\Delta^{14}\text{C}$ reference chronology. Complexities tied to ontogenetic changes in feeding were recently observed to varying degrees in bomb radiocarbon dating studies of other sharks. Bomb radiocarbon dating of tiger shark (*Galeocerdo cuvier*) not only validated age estimates up to 20 years, but also provided information about carbon sources from the measured levels of $\Delta^{14}\text{C}$ (Kneebone et al., 2008). The interesting finding with tiger shark in terms of ^{14}C uptake was in the differences and similarities of values between juveniles and an adult shark. Measured $\Delta^{14}\text{C}$ values from

juvenile tiger sharks were in agreement over time with a hermatypic coral record from Florida, indicating there was no phase lag in terms of the timing of the $\Delta^{14}\text{C}$ signal for the early growth of vertebrae. In contrast, the older adult, one that lived through the period of bomb testing to nearly the end of the marine $\Delta^{14}\text{C}$ record, was mostly in phase with the porbeagle record as an adult, and deviated to match the coral record in what would have been the juvenile portion of the adult vertebrae. These findings can be logically attributed to tiger shark juveniles feeding on short-lived and near-surface food sources and adults shifting to older food sources, represented as a phase lag that can be attributed to trophic-level changes (Kneebone et al., 2008). A similar scenario was observed for the great hammerhead (*Sphyrna mokarran*), where there was close agreement with a coral $\Delta^{14}\text{C}$ record in some years and attenuation of the $\Delta^{14}\text{C}$ signal in others (Passerotti et al., 2010). For the sandbar shark, carbon is derived from mixed sources throughout ontogeny and $\Delta^{14}\text{C}$ values range from agreement with the attenuated and phase-lagged porbeagle record to agreement with the elevated and timely coral records. In general, no time-specific correlation was observed with either record, and this finding is consistent with the wide-range of sandbar shark feeding habits.

The use of vertebrae as an exclusive tool to age sandbar shark has well-documented limitations. Casey et al. (1985) used strict age-estimation criteria and noted that ages may be underestimated owing to a large number of uncounted growth bands at the margin. The uncounted banding pattern did not fit the criteria formulated from observed early growth; therefore, the bands were not counted at the time. A subsequent tag-recapture study provided support for the notion that age was underestimated and evidence was presented for much slower growth and greater longevity (Casey and Natanson, 1992). Tag-recapture data generated since Casey and Natanson's publication and presented herein provides an indication of an even greater longevity (33–36 years). These data were further supported by the bomb radiocarbon results that indicated ages were underestimated late in adult life.

For age determination of smaller sharks, Casey and Natanson (1992) suggested that the band counts may have an annual periodicity until a threshold size and age, at which the deposition rate changes. At the time of the Casey and Natanson's study, the only age validation was from a laboratory OTC study for sharks no larger than 112 cm (Branstetter, 1988), and the conclusion was that periodicity of band-pair deposition changed after 5–6 years. Branstetter (1988) argued that the Casey et al. (1985) criteria were limited to early growth and this view is supported by the bomb radiocarbon and OTC findings of the present study.

Conclusion

In light of these results, it is important to emphasize the need for age validation across all size (and age) classes

for the sandbar shark. Given the potential for changes in the periodicity of band pair formation throughout ontogeny, the application of complementary age validation methods is preferred in order to provide a verifiable and defensible position for the determination of important life history parameters for sharks and other fishes.

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