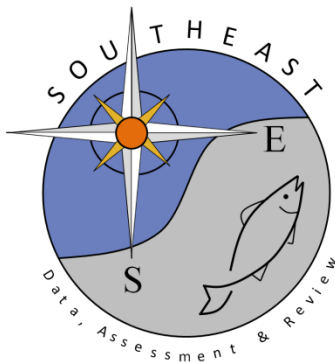


Age validation of great hammerhead shark (*Sphyrna mokarran*),
determined by bomb radiocarbon analysis

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Abstract—Preliminary validation of annual growth band deposition in vertebrae of great hammerhead shark (*Sphyrna mokarran*) was conducted by using bomb radiocarbon analysis. Adult specimens ($n=2$) were collected and thin sections of vertebral centra were removed for visual aging and use in radiocarbon assays. Vertebral band counts were used to estimate age, and year of formation was assigned to each growth band by subtracting estimated age from the year of capture. A total of 10 samples were extracted from growth bands and analyzed for $\Delta^{14}\text{C}$. Calculated $\Delta^{14}\text{C}$ values from dated bands were compared to known-age reference chronologies, and the resulting patterns indicated annual periodicity of growth bands up to a minimum age of 42 years. Trends in $\Delta^{14}\text{C}$ across time in individual specimens indicated that vertebral radiocarbon is conserved through time but that habitat and diet may influence $\Delta^{14}\text{C}$ levels in elasmobranchs. Although the age validation reported here must be considered preliminary because of the small sample size and narrow age range of individuals sampled, it represents the first confirmation of age in *S. mokarran*, further illustrating the usefulness of bomb radiocarbon analysis as a tool for life history studies in elasmobranchs.

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Age validation of great hammerhead shark (*Sphyrna mokarran*), determined by bomb radiocarbon analysis

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Validation of the periodicity of vertebral growth band deposition over the entire life span of a species is an important aspect of age estimation and growth determination in elasmobranch fishes (Caillet and Goldman, 2004; Francis et al., 2007). Accurate age estimation is critical because it forms the basis for calculating growth and mortality rates, age at maturity, and estimates of longevity, all of which are essential for population assessment. The need for accurate age and growth estimates is especially great for many elasmobranch species, which tend to be data poor and highly vulnerable to fishing pressure (Musick, 1999). Bomb radiocarbon dating has been successfully used to validate age estimates for several elasmobranch species (e.g., Campana et al., 2002; Kneebone et al., 2008; McPhie and Campana, 2009). The peak in atmospheric radiocarbon (^{14}C) from testing nuclear bombs in the 1950s and 1960s is used as a marker that can be dated in the calcified structures of marine organisms. Bomb testing yielded synchronous known-age reference chronologies in corals, bivalves, and fish otoliths worldwide (Campana,

1997; Druffel, 1989), which can be used to confirm the accuracy of age estimates for various marine species (Campana et al., 2002). The presence of a tracer over such a protracted time span makes bomb radiocarbon analysis highly suitable for age validation, especially for typically long-lived elasmobranchs.

The great hammerhead shark (*Sphyrna mokarran*) is a large (maximum size of 550–610 cm total length [TL]) cosmopolitan species found circumtropically in both inshore and oceanic habitats to depths of over 80 meters (Compagno, 1984). Great hammerhead sharks tend to be reef-associated, but some populations undertake seasonal offshore migrations (Compagno, 1984). Life history information for the great hammerhead shark is very limited; reports consist mostly of notes on their reproduction (Stevens and Lyle, 1989). There are no published age validations for *S. mokarran*.

The vulnerability of great hammerhead sharks to fishing pressure is potentially high given the tendency of elasmobranchs to exhibit slow growth, late age at maturity, and

low fecundity (Musick, 1999). Although not generally targeted in fisheries, *S. mokarran* are favored among incidentally caught species because their fins are highly valued due to their size and the density of their fin rays. In an assessment of the Hong Kong shark fin market, it was found that fins from hammerhead shark species were among the most valuable fin types in the market (Clarke et al., 2004; Abercrombie et al., 2005). Recently, concern has arisen in regard to populations of *S. mokarran* worldwide because the International Union for Conservation of Nature (IUCN) assessed the species as endangered.¹ These circumstances illustrate the need for validated age estimates of *S. mokarran*. Here, we present the preliminary results of bomb radiocarbon analysis as a novel and accurate method of age validation for this species.

Materials and methods

Vertebrae for bomb radiocarbon age validation were taken from two *S. mokarran* specimens (SM-112 and SM-114) caught from commercial longline vessels off the Georgia coast in the U.S. south Atlantic between 2003 and 2004. Specimens were both male, measuring 300 cm and 276 cm fork length (FL), respectively. Although *S. mokarran* are frequently caught as bycatch in several commercial and recreational fisheries, it is difficult to obtain vertebral samples from individuals of sufficient age for the purposes of this study. Ideally, specimens would have vertebral tissue formed between 1955 and 1965, the years encompassing the period of initial increase in ¹⁴C (Campana et al., 2002; Piner et al., 2005). However, individuals living during this time period would at present be quite large (>300 cm FL) and the occurrence of specimens of this size are infrequent in catches available for sampling. The two specimens used in this study provided the only vertebral samples of appropriate age available to the authors at the time of this study.

Vertebrae were collected either from the area under the dorsal fin or above the branchial chamber, stored on ice, and later frozen upon arrival at the laboratory. Excess tissue was manually removed from thawed vertebrae, which were then soaked in varying concentrations of sodium hypochlorite solution for 5–30 minutes to remove remaining tissue. Cleaned vertebrae were rinsed in tap water and stored in 70% ethanol. Vertebral sections (1 mm thick) were prepared by a single longitudinal cut with paired blades separated by a spacer on an IsoMet low-speed diamond-bladed saw (Buehler, Lake Bluff, IL). Sections were immersed in ethanol and digitally photographed under a binocular microscope at 16–40× magnification with reflected light.

Age interpretation was based on visual counts of paired growth increments (growth bands) from images enhanced for contrast with Adobe Photoshop CS2 (Adobe Systems, Inc., Burlington, NJ), and interpretation was based on the criteria of Natanson et al. (2002).

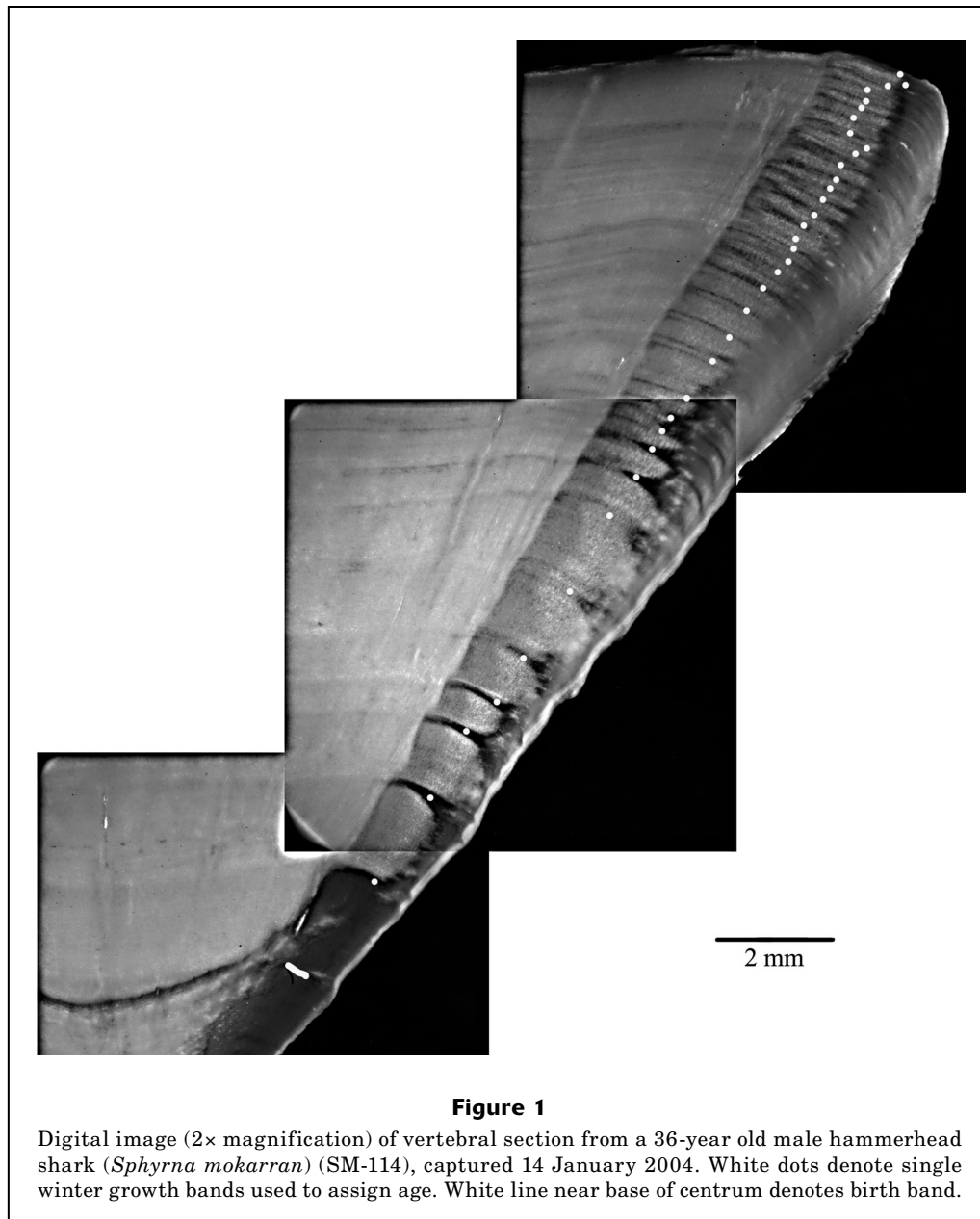
Vertebral tissue samples ($n=10$ samples; 4–9 mg each) were extracted from multiple growth bands in the corpus calcareum region of each vertebral section. Extractions were performed under the binocular microscope with 16× magnification. Extracted samples were isolated as solid pieces by using a Gesswein high-speed hand tool (Gesswein, Bridgeport, CT) fitted with steel bits <1 mm in diameter. The first-formed growth band (corresponding to the first year of growth) was extracted from each vertebra; individual growth bands corresponding to later years were also extracted. The samples from both specimens corresponding to the most recent growth (where growth bands were very narrow) consisted of 6–10 pooled growth bands. The presumed date of sample formation (i.e. growth band formation) was calculated as the year the shark was collected minus the growth band count from the birth band to the mid-point of the sample. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ¹⁴C assay with accelerator mass spectrometry (AMS). AMS assays also provided $\Delta^{13}\text{C}$ (‰) values, which were used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as $\Delta^{14}\text{C}$, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay before 1950 according to methods outlined by Stuiver and Polach (1977).

To assign dates of formation to an unknown tissue sample, it is necessary that the $\Delta^{14}\text{C}$ of the unknown sample be compared with a $\Delta^{14}\text{C}$ chronology based on known-age material (a reference chronology). To match the water mass characteristics of *S. mokarran* habitat, we used a reference chronology for Florida corals developed by Druffel (1989). This chronology would be expected to show $\Delta^{14}\text{C}$ values comparable to those of the great hammerhead shark because of similarity of habitat. However, the carbon source for vertebrae is metabolic in origin unlike the dissolved inorganic carbon (DIC) source for coral (Campana et al., 2002). Therefore, we also used a reference chronology developed from known-age porbeagle (*Lamna nasus*) in the northwest Atlantic (Campana et al., 2002). The period of increase in ¹⁴C in this chronology would be expected to be very similar to that of great hammerhead sharks inhabiting the U.S. south Atlantic, although with very different absolute values owing to the different water mixing characteristics of the two regions.

Results

Based on annual growth band counts, the age estimate for each vertebra was 42 years for SM-112 and 36 years for SM-114, yielding birth years of 1961

¹ Camhi, M. D., S. V. Valenti, S. V. Fordham, S. L. Fowler, and C. Gibson. 2009. The conservation status of pelagic sharks and rays: report of the IUCN shark specialist group pelagic shark Red List workshop, 78 p. IUCN Species Survival Commission Shark Specialist Group, Newbury, UK.



and 1967, respectively (Fig. 1). These estimates fall within the range of dates useful for bomb radiocarbon analysis and indicate that the specimens were both born during the initial rise in ^{14}C . Bomb radiocarbon analysis yielded results for seven samples from SM-112 and three from SM-114 (Table 1). Values of $\delta^{13}\text{C}$ were relatively stable over the range of samples (mean = -11.0 , standard deviation [SD] = 0.1) and were similar to those from other elasmobranch species, verifying a dietary (metabolic) carbon source (Fry, 1988; Campana, 1997; Campana et al., 2006). The mean standard deviation of the individual radiocarbon assays was about 5%.

Values of $\Delta^{14}\text{C}$ in *S. mokarran* ranged from 18.6 to 148.3 units, reaching a maximum in the early 1970s

(Fig. 2). The birth dates of the two sharks were not quite old enough for us to document the initial year of radiocarbon increase, which likely occurred before 1961. Given the available data, the trend in timing and magnitude of the $\Delta^{14}\text{C}$ chronology for all of the *S. mokarran* samples most closely resembled that of Florida coral. Timing of the period of increase and peak in $\Delta^{14}\text{C}$ was also similar between *S. mokarran* and porbeagle chronologies, but there were large differences in absolute values.

When trends in $\Delta^{14}\text{C}$ for the two specimens were examined individually, a difference in trajectories was apparent between SM-112 and SM-114. Values from both specimens fell mostly along the curve of the coral chronology, with one exception. The sample

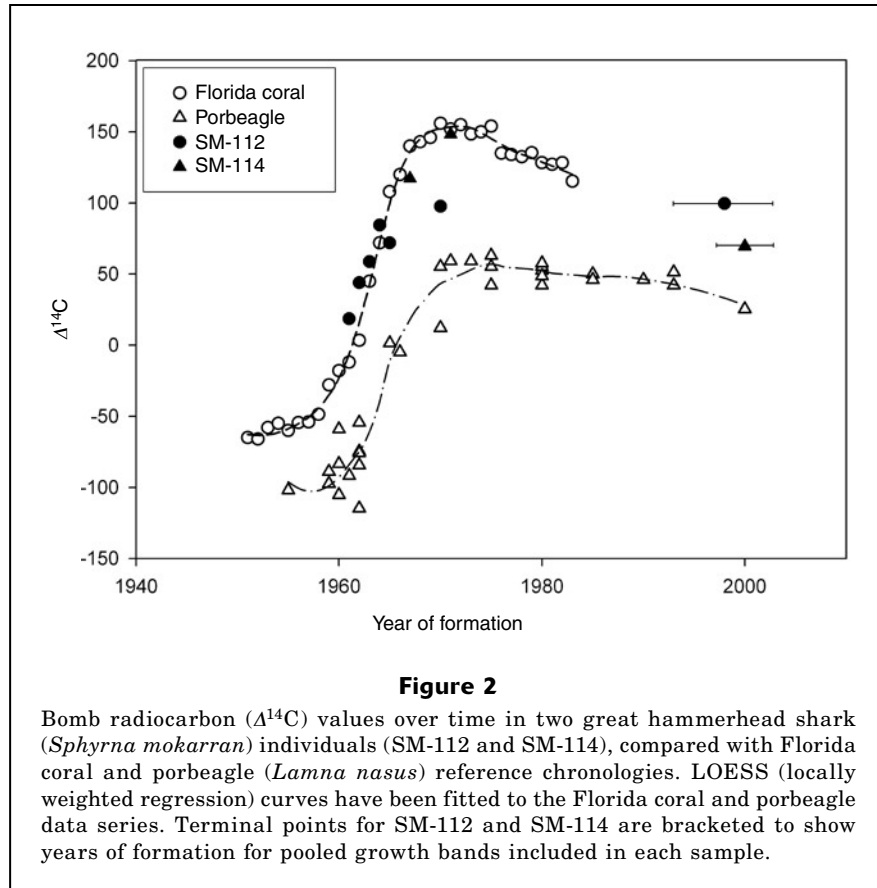


Table 1

Summary of age data and bomb radiocarbon analysis for vertebral samples taken from great hammerhead sharks (*Sphyrna mokarran*). Sample SM-112 was male, fork length=300 cm, aged at 42 years, and captured on 23 July 2003. Sample SM-114 was male, fork length=276 cm, aged at 36 years, and captured on 14 January 2004. Year of formation=year of growth-band formation.

Sample	Year of formation	Median year of formation	Estimated age	$\delta^{13}\text{C}$	$\Delta^{14}\text{C}$
SM-112	1961	1961	0	-11.4	18.6
	1962	1962	1	-11.4	43.9
	1963	1963	2	-11.0	58.7
	1964	1964	3	-10.5	84.4
	1965	1965	4	-9.9	71.9
	1970	1970	9	-9.2	97.7
	1993–2003	1998	37	-10.7	99.7
SM-114	1967	1967	0	-12.0	117.2
	1971	1971	4	-12.0	148.3
	1997–2003	2000	32	-12.2	69.8

dated 1970 from SM-112 fell well below the curve of the coral chronology, whereas the most recent (pooled) sample from SM-112 fell more closely to the expected downward trajectory for Florida coral. Samples from SM-114 were nearly synchronous with the coral chro-

nology extrapolated to the year 2000. Within-shark patterns in $\Delta^{14}\text{C}$ accumulation were similar to those of the reference chronologies, confirming that carbon recorded in the vertebrae is conserved through time.

Discussion

Although a larger sample size would have been preferable in this study, the results of the bomb radiocarbon assays support the hypothesis of annual growth band deposition in *S. mokarran* vertebrae. Additionally, the similarity in the timing of increase and peak in $\Delta^{14}\text{C}$ between the great hammerhead shark samples and both reference chronologies indicates that the aging techniques employed in this study produce ages accurate to within a few years. It is generally accepted that the timing of the initial increase in $\Delta^{14}\text{C}$ in relation to prebomb values is the most accurate dated marker for age validation (Campana et al., 2008). Although there were no prebomb samples in our study (all $\Delta^{14}\text{C}$ values were above zero), the close alignment of values between *S. mokarran* samples and those from the coral chronology during the period of increase indicates that our ages were assigned correctly. If the specimens analyzed in this study had been under-aged, the entire great hammerhead shark chronology would have been shifted to the right in relation to the coral chronology, and over-aging would have caused the reverse to be true. No such shifting was apparent.

Differences in both the magnitude and timing of radiocarbon chronologies between vertebral samples and those from carbonate sources have been noted in previous age studies of elasmobranchs. The difference in the magnitude of $\Delta^{14}\text{C}$ values is largely attributable to the different carbon sources in carbonate (DIC uptake) compared to cartilaginous (dietary uptake) systems (Fry, 1988), but also to environmental factors such as habitat depth and the mixing rates of waters (Williams et al., 1987). This difference has been demonstrated in porbeagle (Campana et al., 2002), shortfin mako (*Isurus oxyrinchus*) (Ardizzone et al., 2006), and white sharks (*Carcharodon carcharias*) (Kerr et al., 2006), as well as in two species of skates (McPhie and Campana, 2009), and can also be caused by the age of the carbon in prey items found at different depths, which can produce a delay in the radiocarbon chronology. In the case of *S. mokarran*, however, overall values of $\Delta^{14}\text{C}$ followed those of Florida coral very closely, indicating little difference in timing of uptake between coral and vertebrae. The similarity in values of $\Delta^{14}\text{C}$ is likely due to similarity in habitat for both the coral and the shark; *S. mokarran* are reef-associated for much of their lives (Compagno, 1984) and feed on reef-associated prey (Stevens and Lyle, 1989), which may assimilate carbon more quickly because of the well-mixed shallow habitat. Kneebone et al. (2008) found that young tiger sharks (*Galeocerdo cuvieri*) exhibit similar patterns in $\Delta^{14}\text{C}$ uptake, attributing the pattern to a diet of small teleosts during the time that these sharks inhabit shallow nursery grounds. Campana et al. (2006) also found similar results in spines of spiny dogfish (*Squalus acanthias*), in which carbon uptake into fin spines mirrored that of DIC uptake in otolith chronologies from the same region.

Despite the apparent similarities between values of $\Delta^{14}\text{C}$ in *S. mokarran* and Florida coral, there were some

differences, such as the slight left shift in the first two samples from SM-112 and the depletion of $\Delta^{14}\text{C}$ in the penultimate (1970) sample from SM-112, in relation to the rest of the chronology. The first two samples from SM-112, corresponding to formative years of 1961 and 1962, respectively, fell slightly left of the coral curve. Although a phase-shift to the right can be explained as a diet- or habitat-induced delay in carbon uptake, a shift to the left could indicate a slight over-aging of SM-112 of only 1–2 years, or the shift could be the result of inclusion of material from more recently formed bands in the sample. In addition, the $\Delta^{14}\text{C}$ in the 1970 sample from SM-112 was depleted in comparison to the rest of the chronology and approached values more like those of porbeagle as opposed to coral. This singular deviation could again be the result of an error in micromilling or could be the start of a more depleted trajectory for SM-112, reflecting an ontogenetic shift in habitat and diet. Although reef-associated for much of their lives, *S. mokarran* also undertake oceanic migrations through deeper water habitats (Compagno, 1984) that tend to be depleted in $\Delta^{14}\text{C}$. Consumption of prey from these habitats would result in depleted values of $\Delta^{14}\text{C}$ in the vertebrae, as demonstrated in porbeagle and other deepwater sharks (Campana et al., 2002). Another possibility for this depletion in $\Delta^{14}\text{C}$ is a shift in age of prey taken by SM-112; owing to its size this shark may have taken larger (and possibly older) prey. Obtaining additional $\Delta^{14}\text{C}$ samples from both sharks would certainly clarify these results.

This study confirms the longevity of great hammerhead sharks to an age of at least 42 years, although maximum reported lengths indicate that they may live well beyond this age. Further study on the life history of *S. mokarran* is needed to identify factors affecting individual patterns in $\Delta^{14}\text{C}$ assimilation.

Acknowledgments

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