

# Bomb dating and age determination of large pelagic sharks

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**Abstract:** Despite their notoriety and role as apex predators, the longevity of large pelagic sharks such as the porbeagle (*Lamna nasus*) and shortfin mako (*Isurus oxyrinchus*) is unknown. Vertebral growth bands provide an accurate indicator of age in young porbeagle, but age validation has never been reported for any large shark species past the age of sexual maturity. Here, we report the first application of bomb radiocarbon as an age validation method for long-lived sharks based on date-specific incorporation of radiocarbon into vertebral growth bands. Our results indicate that porbeagle vertebrae recorded and preserved a bomb radiocarbon pulse in growth bands formed during the 1960s. Through comparison of radiocarbon assays in young, known-age porbeagle collected in the 1960s with the corresponding growth bands in old porbeagle collected later, we confirm the validity of porbeagle vertebral growth band counts as accurate annual age indicators to an age of at least 26 years. The radiocarbon signatures of porbeagle vertebral growth bands appear to be temporally and metabolically stable and derived mainly from the radiocarbon content of their prey. Preliminary radiocarbon assays of shortfin mako vertebrae suggest that current methods for determining shortfin mako age are incorrect.

**Résumé :** Malgré leur notoriété et leur rôle de prédateurs supérieurs, les grands requins pélagiques, tels que les requins taupes communs (*Lamna nasus*) et les requins taupes bleus (*Isurus oxyrinchus*), ont une durée de vie encore inconnue. Les bandes de croissance des vertèbres sont des indicateurs précis de l'âge chez de jeunes requins taupes communs, mais aucune validation de l'âge n'a été faite chez les grands requins au delà de l'âge de la maturité sexuelle. On trouvera ici une première utilisation du carbone radioactif produit par les essais nucléaires pour valider l'âge des requins à grande longévité, par l'analyse de l'incorporation du carbone radioactif dans les bandes de croissance de leurs vertèbres à des dates précises. Les vertèbres des requins taupes communs ont enregistré et conservé une signature de carbone radioactif provenant des essais nucléaires faits dans les années 1960. La comparaison des analyses de carbone radioactif faites chez de jeunes requins taupes communs d'âge connu et récoltés dans les années 1960 avec celles des bandes de croissance chez de vieux requins capturés plus tard confirme la validité de l'utilisation des bandes de croissance des vertèbres pour déterminer avec précision l'âge au moins jusqu'à 26 ans. Les signatures de carbone radioactif dans les bandes de croissance des vertèbres des requins taupes communs semblent être stables dans le temps et peu affectées par le métabolisme; elles sont dérivées en majeure partie du contenu en carbone radioactif de leurs proies. Les analyses préliminaires de carbone radioactif dans les vertèbres des requins taupes bleus semblent indiquer que les méthodes courantes de détermination de l'âge chez ce poisson sont erronées.

[Traduit par la Rédaction]

## Introduction

Porbeagle (*Lamna nasus*) and shortfin mako (*Isurus oxyrinchus*) sharks have been reported to grow at very different rates and achieve very different longevities (Cailliet et al. 1983; Pratt and Casey 1983; Natanson et al. 2002), despite their common family membership (Lamnidae) and similar

life history characteristics. The most likely explanation for such differences is errors in age determination associated with the interpretation of the vertebral growth bands, a process that is subjective and whose accuracy has seldom been confirmed (Cailliet 1990). Based on recaptures of known-age and oxytetracycline-tagged individuals, the vertebral bands have been demonstrated to form annually in sexually immature porbeagle up to an age of 11 years (Natanson et al. 2002). However, the interpretation of growth bands in sexually mature porbeagle has not been validated and is complicated by the extreme narrowness of the bands and the potential for resorption along the growing edge. Vertebrae are one of the few structures known to produce periodic growth bands in sharks, given that elasmobranchs lack the otoliths that form the basis for accurate age determinations in bony fishes (Secor et al. 1995). Therefore, vertebrae are usually the best structures upon which to base estimates of shark age, longevity, growth, and mortality rate.

Atmospheric testing of atomic bombs in the 1950s and 1960s resulted in a rapid and well-documented increase in radiocarbon ( $^{14}\text{C}$ ) in the world's oceans (Druffel and Linick

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1978). The period of radiocarbon increase was almost synchronous in marine carbonates such as corals, bivalves, and fish otoliths around the world (Kalish 1993; Weidman and Jones 1993; Campana 1997), allowing the period of increase to be used as a dated marker in calcified structures exhibiting growth bands. Here, we report the first radiocarbon assays of growth bands in pelagic shark vertebrae, demonstrating that they too recorded and preserved a bomb radiocarbon pulse in growth bands formed during the 1960s. Through comparison of radiocarbon assays in young, known-age porbeagle with growth bands of old porbeagle matched for year of formation, we confirm the validity of porbeagle vertebral growth band counts as accurate age indicators. Finally, we use the porbeagle radiocarbon chronology to question the validity of accepted methods for determining age in shortfin mako.

## Methods

Cervical vertebrae were collected from 15 porbeagle caught in the northwest Atlantic between 1962 and 2000, ranging in length from 72 to 264 cm fork length. Ages were presumed to be 0–26 years based on band counts visible in transverse sections using the interpretation criteria of Natanson et al. (2002). Vertebrae were stored in 70% ethanol or frozen prior to sectioning; the samples collected in the 1960s were preserved in formalin.

Multiple samples from each of the 15 vertebral sections ( $N = 35$  samples, 12–37 mg each) were extracted from individual growth bands visible in the corpus calcareum region while working at 16 $\times$  magnification under a binocular microscope. In all cases, the first-formed growth band (corresponding to the first year of growth) was extracted from each vertebra; additional growth bands corresponding to later growth were extracted from some, but not all, vertebrae. Extracted samples were isolated as solid pieces using a Gesswein high-speed hand tool fitted with steel bits <1 mm in diameter. To minimize surface contamination, the external surface of each sample was removed and discarded using the hand tool, and then the remaining sample was sonified in Super Q water. After drying, the sample was weighed to the nearest 0.1 mg in preparation for assay with accelerator mass spectrometry. All samples were assayed for  $\delta^{13}\text{C}$  (to determine the carbon source) and  $\Delta^{14}\text{C}$  (measure of radiocarbon), with  $\Delta^{14}\text{C}$  calculated as per Stuiver and Polach (1977).

The onset of nuclear testing in the late 1950s resulted in a marked and widespread increase in  $\Delta^{14}\text{C}$  in marine dissolved inorganic carbon (DIC) that is easily detected in all marine carbonates growing in surface waters during the 1960s (Druffel 1989; Campana and Jones 1998). To assign dates of formation to an unknown 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). In the case of carbonates, the years corresponding to the onset of radiocarbon increase are synchronous in reference chronologies based on corals, bivalves, and otoliths and are thus interchangeable (Campana 1999). In the case of vertebral material, however, synchrony with carbonates could not be assumed. Therefore, we used vertebrae from young porbeagle (age  $\leq 6$  and fork length <188 cm) as our known-age, or reference, chronology ( $N = 5$  sharks, 8 samples).

Fork length and growth band numbers are accurate indicators of age in young porbeagle (Natanson et al. 2002), with a maximum ageing error of no more than  $\pm 2$  years. Therefore, the age of the young porbeagle was known with enough certainty to be considered known age.

A single shortfin mako vertebra from a 328-cm female captured in the northwest Atlantic in 1977 was sectioned, aged, and microsampled using the same protocol described above for the porbeagle. A total of four growth bands, including the first and last formed, were removed from this vertebra for assay.

The reference  $\Delta^{14}\text{C}$  carbonate chronology for the northwest Atlantic was derived from assays of known-age fish otoliths formed between 1949 and 1982. The collection and radiocarbon assay of 39 age 1–3 haddock (*Melanogrammus aeglefinus*) otoliths have been described elsewhere (Campana 1997); the chronology was supplemented by 17 age-1 redfish (*Sebastes* spp.) otoliths collected between 1957 and 1969 and prepared in a similar manner. There was no detectable difference between the haddock and redfish chronologies; therefore, they were pooled and used as the reference carbonate chronology. The  $\Delta^{14}\text{C}$  chronology of aragonitic fish otoliths parallels that of North Atlantic corals and bivalves (Campana 1997) and thus is a good proxy for the  $\Delta^{14}\text{C}$  DIC history of the porbeagle environment.

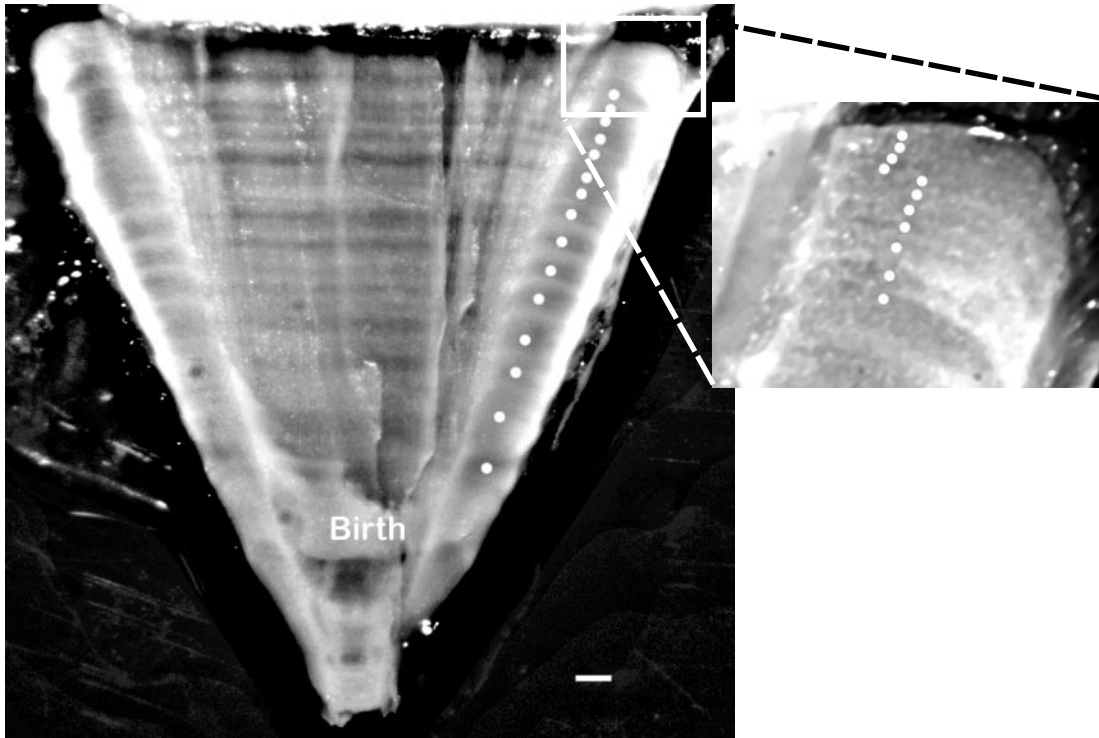
## Results and discussion

Growth bands visible in porbeagle vertebral sections tended to be broad and diffuse in sharks <4 years old, increasing in clarity but decreasing in width with age (Fig. 1). In sharks >12–15 years of age, growth bands narrowed to the point where greater magnification and digital enhancement was required to resolve bands near the growing margin. Nevertheless, growth band counts were consistent and reproducible between independent age readers and sections, giving us confidence that we were not missing a portion of the vertebral growth history.

Porbeagle  $\delta^{13}\text{C}$  was relatively constant across all samples, averaging  $-14.27$  (SE = 0.09) (Table 1). Depleted values such as these are characteristic of metabolic and dietary carbon and are markedly different from the values of  $-1$  to  $-3$  typically found in otoliths (Fry 1988; Kalish 1993; Campana 1997). Although the  $\delta^{13}\text{C}$  values did not vary with the date of formation,  $\Delta^{14}\text{C}$  values increased sharply from about  $-100$  in vertebral material formed before 1960 to about  $+50$  after 1970, declining slowly thereafter to about  $+25$  in the year 2000 (Fig. 2a). Although the period of increasing  $\Delta^{14}\text{C}$  differed, the sigmoidal shape of the porbeagle  $\Delta^{14}\text{C}$  curve was very similar to the bomb signal expected of  $\Delta^{14}\text{C}$  in the marine environment (Druffel 1989).

The  $\Delta^{14}\text{C}$  chronology prepared using only the young, known-age porbeagle is considered a reference chronology, since the year of formation of each micromilled sample is known with certainty. Since the date of growth band formation of an unknown sample can then be determined from its  $\Delta^{14}\text{C}$  value (at least if the date falls in the critical period of rapid increase in the 1960s), this date can subsequently be compared with the date estimated from a count of the growth bands; congruence indicates age validation, since incorrectly interpreted annuli would result in an incorrect age

**Fig. 1.** Thin section of a vertebra from a 264-cm fork length porbeagle collected in 1999. White circles indicate growth bands presumed to be formed annually; the photographic inset indicates the very narrow growth bands seen near the growing edge. The age of the shark was 26 years based on the number of growth bands and no more than 31 years based on radiocarbon values. Scale bar = 1 mm.



and hence an incorrect estimate of date of formation. In this study, the reference chronology of the known-age porbeagle was indistinguishable from that based on older porbeagle through the critical period of rapid increase in the 1960s (Fig. 2a). Since any errors in the age interpretation of the older sharks would have been evident in  $\Delta^{14}\text{C}$  values that lay off the curve defined by the known-age sharks, the sharks aged 9–26 years must have been aged correctly (on average) based on the vertebral growth bands. In light of the relative stability in  $\Delta^{14}\text{C}$  after 1970, it would have been very difficult to detect any underageing in sharks born after 1970. However, overageing would have been easily detected, since a  $\Delta^{14}\text{C}$  value of more than 0 would have been completely incompatible with a date of formation before about 1963. Thus, the  $\Delta^{14}\text{C}$  value of 55 in the first-formed growth band of a 26-year-old porbeagle collected in 2000 cannot have formed prior to 1970, indicating an age of no more than 31. Similarly, underageing of any sharks born between 1959 and 1962 would be easily detected based on depleted  $\Delta^{14}\text{C}$  values. With the exception of a 24-year-old shark, which appears to have been underaged by about 3 years, vertebral band counts provided accurate ages for porbeagle up to age 26.

Shark vertebrae have been considered to be metabolically unstable ever since Welden et al. (1987) reported that Pb:Ra dating failed to produce the expected gradient between inner and outer growth zones. However, our results indicate that any metabolic reworking must be minimal. Of the nine sharks from which multiple growth bands were sampled, all showed the same within-shark bomb signal across year of formation as that demonstrated by the across-shark analysis (Fig. 2b). Ontogenetic effects were not evident, indicating that the bomb signal was not diluted by subsequent growth

over a period of up to 23 years. Comparison of  $\Delta^{14}\text{C}$  values in vertebral growth bands formed at different ages, matched by year of formation, showed no consistent differences, indicating that the bomb signal was not transported across growth bands through time. There was a visible but non-significant tendency for the recently formed growth bands in some of the older sharks to be slightly depleted in  $\Delta^{14}\text{C}$  compared with younger sharks growing at the same time (median depletion <20). As discussed in the next paragraph, the most likely explanation for this minor depletion is that of diet switching to larger, and hence older (more depleted), prey by the larger sharks. Since the  $\Delta^{14}\text{C}$  signal was incorporated into the noncalcified component of the vertebrae, and since the previously reported Pb:Ra assays were based on elemental analogs of calcium that were not clearly part of the growth band (Welden et al. 1987), it seems likely that the organic fraction of the shark vertebral growth band analyzed in our study was more stable physiologically than any calcified components. This finding has important implications for future bomb-dating studies of sharks, since it satisfies an important assumption of this age validation method: that the carbon in the vertebral material is metabolically and temporally stable.

The shark  $\Delta^{14}\text{C}$  chronology was phase shifted about 3 years towards more recent dates compared with a reference carbonate  $\Delta^{14}\text{C}$  chronology characteristic of bivalves, corals, and fish otoliths in the northwest Atlantic (Fig. 3). This phase shift appears to have been due to the source of carbon used for vertebral growth. No detectable  $\text{CO}_2$  was generated by acid dissolution of the vertebral material sampled for  $^{14}\text{C}$  assay, indicating that calcium carbonate was not present. Therefore, the  $^{14}\text{C}$  must have been incorporated into pro-

**Table 1.** Summary of  $\delta^{13}\text{C}$  and  $\Delta^{14}\text{C}$  assay results for individual growth zones microsampled from shark vertebrae.

Species	Sample	Fork length (cm)	Year collected	Age (years)	Year of annulus formation	$\delta^{13}\text{C}$ of annulus	$\Delta^{14}\text{C}$ of annulus
Porbeagle	762-14	127	1962	2	1962	-15.0	-74.6
					1961	-14.4	-91.7
	762-31	187	1962	12	1960	-14.2	-105.2
					1962	-14.3	-114.7
	862-10	166	1962	9	1962	-14.3	-114.7
					1960	-14.3	-83.3
					1962	-14.4	-75.8
					1959	-14.6	-97.4
					1962	-14.5	-97.4
	862-5	188	1962	6	1959	-14.5	-97.4
					1959	-14.4	-88.9
					1962	-14.7	-84.4
	862-6	181	1962	7	1962	-14.7	-84.4
					1955	-14.6	-101.9
	862-8	174	1962	9	1955	-14.6	-101.9
					1985	-13.3	50.0
	LN19	227	1985	16	1980	-14.0	52.6
					1975	-14.8	42.2
					1970	-14.9	55.2
					1985	-13.9	46.1
					1980	-14.2	55.2
					1975	-14.7	63.1
					1971	-15.3	59.2
LN3	72	1965	0	1965	-13.5	1.5	
				1993	-14.7	42.2	
LN37	236	1993	24	1980	-14.2	42.2	
				1970	-13.9	12.2	
				1965	-12.6	1.5	
LN4	70	1965	0	1965	-12.6	1.5	
				1966	-14.2	-4.8	
LN6	146	1966	7	1966	-14.2	-4.8	
				1962	-14.1	-54.3	
				1960	-13.8	-59.0	
				1993	-14.0	51.3	
				1980	-14.1	57.8	
LN85	239	1993	21	1973	-14.9	59.2	
				1993	-14.0	51.3	
				1980	-14.1	57.8	
P99	264	2000	26	2000	-13.8	25.4	
				1990	-13.9	46.1	
				1980	-14.1	48.7	
				1975	-14.9	55.2	
				1977	-12.7	52.6	
Shortfin mako	M151	328	1977	1977	-12.7	52.6	
				1974	-12.4	38.8	
				1970	-12.3	-90.1	
				1967	-13.9	-100.2	

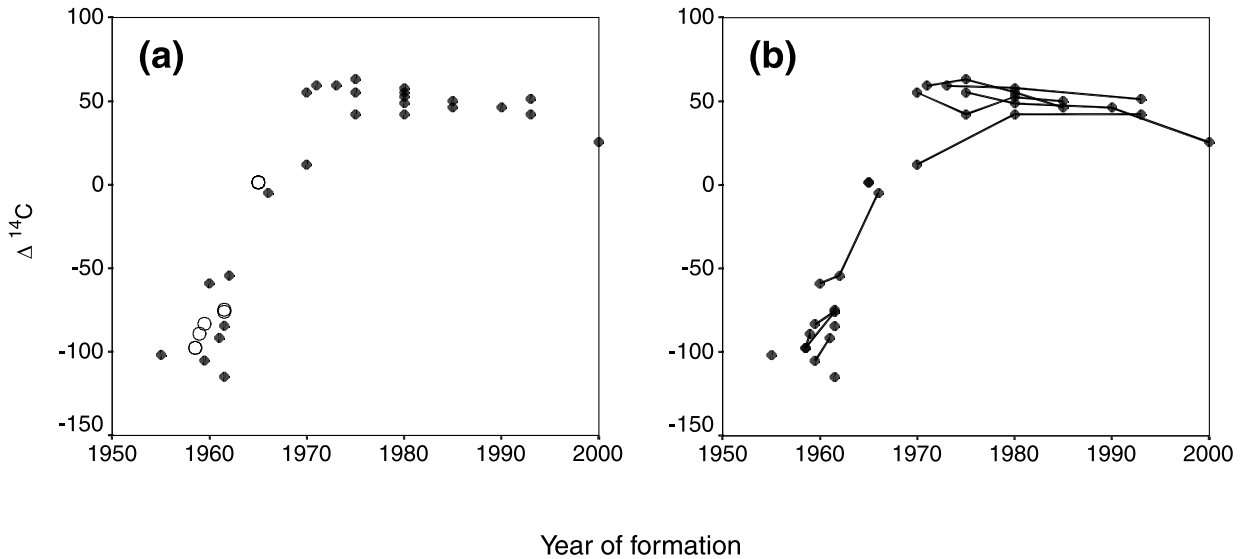
teinaceous or cartilaginous material rather than the calcium carbonate characteristic of other bomb-dated taxa (Kalish 1993). Since dietary sources are the primary source of carbon into noncalcified fish tissues (Fry 1988), the  $^{14}\text{C}$  content of the porbeagle prey would be expected to have a major influence on the  $^{14}\text{C}$  content of the porbeagle itself. Stomach content analyses of 533 porbeagle collected throughout the year demonstrated that the diet of porbeagle was dominated by fish (91% by weight), primarily alepisaurids, gadids, pleuronectids, and clupeids (S.E. Campana, unpublished data). On the basis of the length frequencies of the major prey taxa and published age-length keys, the mean weighted age of the prey was estimated to be 3.3 years. Reasonable errors in assigning ages to the prey taxa do not appreciably change this result. Since fish growth (in weight) is exponential, the weighted mean age of the prey tissue was 1.8 years, thus accounting for most of the phase differential between the porbeagle and reference  $\Delta^{14}\text{C}$  chronology. The remaining

phase discrepancy was presumably due to the >100 m depth occupied by porbeagle and its prey, a depth range at which the appearance of the bomb  $^{14}\text{C}$  signal is delayed relative to shallower waters (Williams et al. 1987).

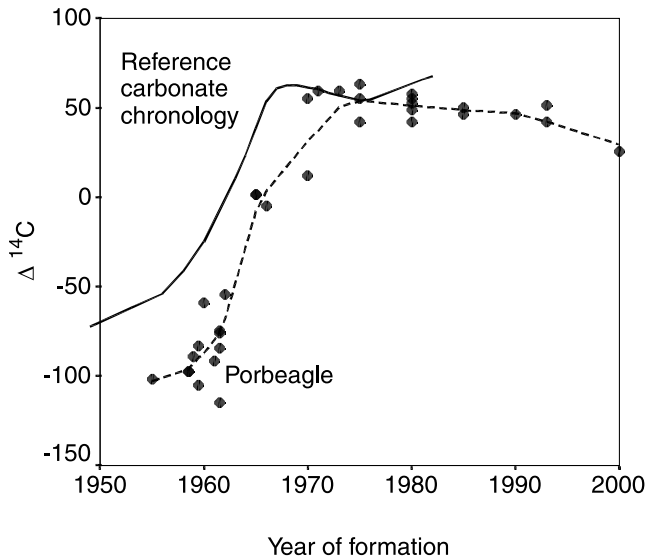
The prebomb vertebral  $\Delta^{14}\text{C}$  was depleted by about 30 relative to otolith carbonate chronologies from the same waters (Fig. 3), presumably reflecting the reduced  $\Delta^{14}\text{C}$  levels in DIC and prey at depths >100 m. Although the postbomb vertebral  $\Delta^{14}\text{C}$  of 50 was similar to that of the otolith carbonate chronology, the correspondence may have been fortuitous; the absolute value of postbomb  $\Delta^{14}\text{C}$  in the water column is highly variable and can vary between 0 and 200 across depths and locations depending on water mass mixing rates and residence times (Druffel 1989; Weidman and Jones 1993).

Radiocarbon assays of a single shortfin mako vertebra suggested that the shark was considerably older than first suspected. Samples of the first, last, and two intermediate growth bands from a large female caught in 1977 contained

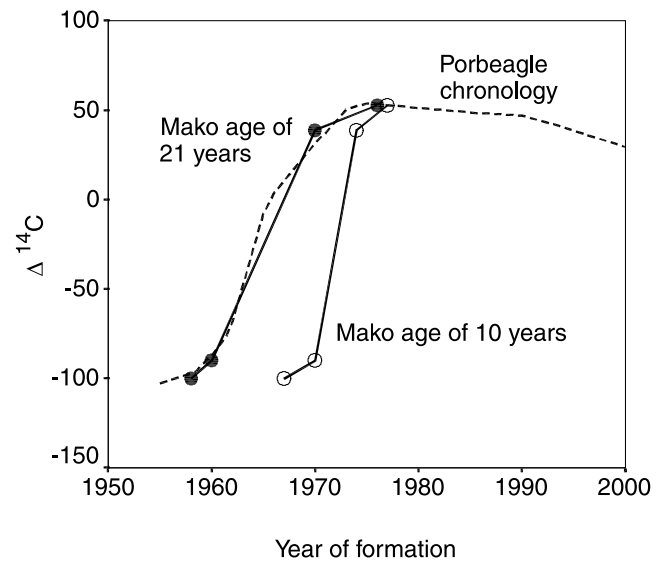
**Fig. 2.**  $\Delta^{14}\text{C}$  in individual growth bands of porbeagle vertebrae versus year of formation inferred from counts of the growth bands. (a) The period of bomb-induced increase apparent in growth bands of young, known-age porbeagle (open circles) was indistinguishable from that based on older porbeagle (solid circles), indicating that the growth bands were accurately interpreted in the older porbeagle. (b) The  $\Delta^{14}\text{C}$  chronology within individual sharks (each line corresponds to a shark) was similar to the across-shark chronology, indicating that the bomb signal of a single growth band remained stable as the shark grew older.



**Fig. 3.**  $\Delta^{14}\text{C}$  in individual growth bands of porbeagle vertebrae versus year of formation inferred from counts of the growth bands. The  $\Delta^{14}\text{C}$  chronology of porbeagle vertebrae (circles, fitted with a Loess curve) was similar to that of a reference carbonate chronology from the northwest Atlantic (solid line, smoothed with a Loess curve) but lagged because of the depleted  $\Delta^{14}\text{C}$  of the diet. While not evident from the figure, the unsmoothed reference chronology is relatively constant prior to 1956.



**Fig. 4.**  $\Delta^{14}\text{C}$  in individual growth bands of a large shortfin mako vertebra versus year of formation inferred from two alternative interpretations of the growth bands.  $\Delta^{14}\text{C}$  values would be expected to fall on the curve defined by the porbeagle (Loess fit shown by dashed line) if the age interpretation of the growth bands in the mako were correct. An age of 10 years (open circles) was based on published criteria (Pratt and Casey 1983), while an age of 21 years (solid circles) was based on criteria used to age porbeagle (Natanson et al. 2002).



a  $\Delta^{14}\text{C}$  signal that would be expected of a porbeagle between the ages of 19 and 23 years (Fig. 4). Interpretation of the vertebral growth bands using published criteria for shortfin mako (Pratt and Casey 1983) yielded an age of 10 years; the ageing protocol of Pratt and Casey (1983) assumed that two band pairs form each year. An age of 21–22 years was ob-

tained by the authors using criteria used to age porbeagle (Natanson et al. 2002) and Pacific shortfin mako (Cailliet et al. 1983), which assumes a single band pair formed each year. Assuming that the porbeagle bomb signal is also applicable to the shortfin mako, the depleted  $\Delta^{14}\text{C}$  values of the

first and fourth growth bands were completely inconsistent with an age of <19 years and most consistent with an age of 21 years. Furthermore, there is no obvious reason why the shortfin mako vertebra would fail to record the bomb  $\Delta^{14}\text{C}$  signal in a manner similar to that of porbeagle; the differences in distributional range, diet, temperature, and preferred depth between the species (at young ages) are insufficient to produce anything other than minor differences in the vertebral bomb chronology. Clearly, a definitive growth rate cannot be based on a single shark. Nevertheless, these results clearly indicate that only the older of the two age interpretations is possible for the shortfin mako analyzed. Further radiocarbon assays of shortfin mako vertebrae should provide a definitive resolution of this age determination question.

The use of vertebral bomb radiocarbon to determine age and confirm the periodicity of growth bands should be appropriate for all shark species where at least some of the growth bands were formed prior to 1965. Whereas bomb signals in fish otoliths are limited by the small amounts of material available for assay (Campana 1999), sequential sampling of multiple growth bands from a single vertebra can be used to prepare a complete  $\Delta^{14}\text{C}$  chronology and thus confirm the age of a single shark. Adjustments for phase shifting of the bomb signal in otoliths are sometimes required depending on location and depth; phase shifting due to diet would also be expected in the case of sharks.

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