

Bomb dating and age validation using the spines of spiny dogfish (*Squalus acanthias*)

Steven E. Campana · Cynthia Jones ·
Gordon A. McFarlane · Sigmund Myklevoll

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Abstract Bomb radiocarbon has previously been used to validate the age of large pelagic sharks based on incorporation into vertebrae. However, not all sharks produce interpretable vertebral growth bands. Here we report the first application of bomb radiocarbon as an age validation method based on date-specific incorporation into spine enamel. Our results indicate that the dorsal spines of spiny dogfish, *Squalus acanthias*, recorded and preserved a bomb radiocarbon pulse in growth bands formed during the 1960s with a timing which was very similar to that of marine carbonates. Using radiocarbon assays of spine growth bands known to have formed in the 1960s and 1970s as a dated marker, we confirm the validity of spine enamel growth band

counts as accurate annual age indicators to an age of at least 45 year. Radiocarbon incorporation into northeast Atlantic dogfish spines occurred in similar years as those in the northwest Atlantic and northeast Pacific, although the amount of radiocarbon differed in keeping with the radiocarbon content of the different water masses. Published reports suggesting that Pacific dogfish are longer lived and slower growing than their Atlantic counterparts appear to be correct, and are not due to errors in interpreting the spine growth bands. Radiocarbon assays of fin spine enamel appears to be well suited to the age validation of sharks with fin spines which inhabit the upper 200 m of the ocean.

Keywords Age determination · Shark · Longevity · Growth rate

S. E. Campana (✉)
Bedford Institute of Oceanography, P.O. Box 1006,
Dartmouth, Nova Scotia, Canada B2Y 4A2
e-mail: campanas@mar.dfo-mpo.gc.ca

C. Jones
Center for Quantitative Fisheries Ecology, Old
Dominion University, Norfolk, Virginia 23508, USA

G. A. McFarlane
Pacific Biological Station, Nanaimo, British
Columbia, Canada V9R 5K6

S. Myklevoll
Institute of Marine Research, P.O. Box 1870 Nordnes,
N-5817 Bergen, Norway

Introduction

Spiny dogfish, *Squalus acanthias*, are small squaloid sharks common in the surface mixed layer of coastal temperate oceans around the world. Studies to date suggest that they are both long-lived and slow-growing, making them among the least productive of the shark species (Smith et al. 1998; Cortés 2000). Most of these productivity calculations have been based on the dogfish population in the northeast Pacific Ocean, which

appears to grow much more slowly and reach a much greater longevity than does the population in the northwest Atlantic (Ketchen 1975; Nammack et al. 1985; Saunders and McFarlane 1993). While it is possible that the reported differences are real and reflect true differences in growth rate, it is also possible that the differences are due to errors in age determination associated with the interpretation of the growth bands on the fin spines, a process which is subjective and whose accuracy is difficult to confirm. Based on recaptures of oxytetracycline-tagged individuals, the spine growth bands have been demonstrated to form annually in dogfish of the northeast Pacific (Beamish and McFarlane 1985; McFarlane and Beamish 1987). However, age validation studies are not available for the northwest Atlantic spiny dogfish population, nor have any studies been done which demonstrate that the interpretation of the growth bands was comparable between the two populations.

Dogfish lack the otoliths, which are typically used to age teleost fish. Whereas otoliths grow concentrically in all dimensions around a central core, with no subsequent resorption or reworking of deposited material (Campana and Thorrold 2001), dogfish spines grow both from the base of the spine, and internally along the length of the vascularized pulp cavity (Holden and Meadows 1962; Beamish and McFarlane 1985). A non-mineralized dentine layer separates the pulp cavity from the outer, mineralized enamel layer. Although there is some evidence of annual markings in the dentine layer, their presence can be difficult to detect and it is not clear that the entire growth sequence can be observed (McFarlane and Beamish 1987). Only the growth bands in the enamel layer are both readily observed and believed to be metabolically static. However, the composition of the spine enamel (which is unknown, but may be hydroxyapatite) is very different than that of otoliths (calcium carbonate). The carbon source also differs: whereas the primary source is dissolved inorganic carbon in the case of otoliths (Schwarcz et al. 1998), it is likely to be metabolic carbon in the case of spines. These differences make the growth and content characteristics of the spine somewhat more difficult to predict than in the otolith.

Atmospheric testing of atomic bombs in the 1950s and 1960s resulted in a rapid and well-documented increase in radiocarbon (^{14}C) in the world's oceans (Druffel and Linick 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. A similar pattern of increase, lagged by several years due to the incorporation of dietary carbon, has been documented in shark vertebrae (Campana et al. 2002). Here we report the first radiocarbon assays of the fin spines of spiny dogfish, demonstrating that they too recorded and preserved a bomb radiocarbon pulse in growth bands formed during the 1960s. Through comparison of radiocarbon assays in recently formed spine material collected between 1960 and 2002 with growth bands of older dogfish matched for year of formation, we confirm that growth bands form annually on the dogfish spine. Based on the age-validated spines, we then test for differences in the growth rate and longevity of spiny dogfish between the northwest Atlantic and the northeast Pacific.

Methods

Second dorsal spines were collected from 32 spiny dogfish caught in the northwest Atlantic ($n = 8$), northeast Atlantic ($n = 11$) and northeast Pacific ($n = 13$) between 1959 and 2002 (Table 1). Samples from the northeast Atlantic (which occasionally consisted of first dorsal spines rather than second dorsal) were obtained as part of a tag-recapture program carried out by the Institute of Marine Research in Bergen, Norway between 1958 and 1980, while those from the northwest Atlantic were obtained from the commercial dogfish fishery off of Nova Scotia in 2002. Northeast Pacific dogfish samples were obtained on research vessel cruises carried out by the Pacific Biological Station in 1980–1981, and again in 2003. The total length of samples from all regions ranged from 69 cm to 99 cm. All spines had been stored dry in paper envelopes after removal from the dogfish.

Table 1 Summary of $\delta^{13}\text{C}$ (‰) and $\Delta^{14}\text{C}$ assay results for annual growth bands microsampled from dogfish spines from three populations. Growth bands sampled are shown

as the range of bands sampled, counting distally from the spine base. Mean year of growth band formation is that based on the mean number of growth bands

Area	Dogfish ID	Year collected	Age	Growth bands sampled	Mean year of band formation	$\delta^{13}\text{C}$ of band	$\Delta^{14}\text{C}$ of band
NE Atlantic	H265	1959	22	13–22	1942.0	-14.1	-69.4
				1–2	1958.0	-13.8	-71.9
	H401	1960	15	7–15	1949.5	-14.1	-81.1
				1–2	1959.0	-13.6	-67.6
	H661	1963	25	17–25	1942.5	-13.7	-61.0
				1–2	1962.0	-14.3	-50.0
	H2257	1964	19	16–19	1947.0	-13.5	-81.7
				1–2	1963.0	-15.1	-23.4
	H1719	1965	14	11–14	1953.0	-13.8	-80.4
				1–2	1964.0	-14.0	-44.8
	H6136	1966	15	12–15	1953.0	-14.2	-72.4
				1–2	1965.0	-14.2	1.5
	HB1294	1976	16	18	1958.5	-13.7	-21.3
				1–6	1973.0	-13.6	98.2
	HB1201	1977	19	18–19	1959.0	-13.6	-40.3
1–8				1973.0	-14.3	101.7	
HB1170	1978	16	14–16	1963.5	-13.7	61.7	
			1–6	1975.0	-15.2	85.3	
HB1263	1978	22	20–22	1957.5	-13.9	-11.8	
			1–7	1974.5	-14.2	109.5	
NOR11529	1979	15	12–15	1966.0	-13.7	92.9	
			1–8	1975.0	-14.7	89.5	
NW Atlantic	85D	1996	10	3–4	1993.0	-14.4	30.5
	1416	2002	21	18–21	1983.0	-15.0	50.8
	1834	2002	21	17–21	1983.5	-14.1	62.7
	254	2002	21	17–21	1983.5	-14.3	50.3
	260	2002	25	22–25	1979.0	-14.2	54.3
	904	2002	21	18–21	1983.0	-14.0	27.8
	1412	2002	17	3–4	1999.0	-15.0	1.8
				14–17	1987.0	-13.1	54.6
NE Pacific	2238	2002	20	18–19	1984.0	-14.0	62.3
	10	1980	39	30–39	1946.0	-13.9	-113.0
				25–28	1954.0	-12.6	-106.0
				8–11	1971.0	-12.8	-12.1
				1–6	1977.0	-12.4	49.7
	17	1980	9	1–6	1977.0	-13.9	-49.2
				28–30	1951.5	-13.0	-108.0
	2	1980	31	8–11	1971.0	-13.2	19.5
				1–6	1977.0	-13.5	3.2
	5	1980	52	44–52	1932.5	-14.0	-133.0
				28–32	1950.5	-12.7	-104.0
				8–11	1971.0	-12.3	29.7
				1–6	1977.0	-11.7	59.6
				10–13	1969.0	-13.2	36.0
	DF22220	1980	13	1–4	1978.0	-14.5	0.8
11–12				1969.0	-13.8	-11.8	
DF22170	1980	12	1–8	1976.0	-13.8	-4.8	
			9	1971.5	-13.1	-8.7	
DF19979	1980	9	9	1971.5	-13.1	-8.7	
DF23042	1981	11	10–11	1971.0	-12.2	-1.2	
			1–8	1977.0	-14.4	18.5	
12	1981	7	1–4	1979.0	-14.0	0.5	

Table 1 continued

Area	Dogfish ID	Year collected	Age	Growth bands sampled	Mean year of band formation	$\delta^{13}\text{C}$ of band	$\Delta^{14}\text{C}$ of band
	DF43719	1989	11	9–11	1979.5	-12.8	-8.4
				1–7	1985.5	-14.4	24.1
	DF100	2003	52	26–34	1973.5	-14.0	2.8
				16–24	1983.5	-13.1	11.6
				1–10	1998.0	-13.7	-2.2
	DF15	2003	52	46–52	1954.5	-13.8	-121.8
				27–34	1973.0	-14.0	3.4
				16–25	1983.0	-13.7	16.2
				1–10	1998.0	-13.4	5.7
	DF94	2003	51	40–51	1958.0	-13.8	-6.0
				27–35	1972.5	-13.8	10.8
				16–24	1983.5	-12.9	8.6
				1–10	1998.0	-13.4	4.0

All ages were based on counts of presumed annual growth increments (growth bands) that were visible on the external spine surface after light polishing. The strong white band near the spine base was assumed to represent a check rather than a growth band. Age interpretation was carried out while working at 6 \times magnification under reflected light with a binocular microscope. Spine growth bands were also digitally photographed at a minimum resolution of 1,280 \times 1,024 then enhanced. Transverse and longitudinal sections of the spine did not reveal interpretable growth bands, nor were complete growth sequences visible in whole or sectioned vertebrae.

To insure comparability in age interpretation among regions, all age interpretations used to guide micromilled samples were made by the same experienced age reader of Atlantic dogfish spines, and replicated by a second experienced age reader (SC). To insure that these age interpretations were also consistent with the original interpretations of the region, a subsample of Pacific spines were aged by both the above-mentioned age reader and the primary reader of dogfish spines in the Pacific (GM). Age comparisons were restricted to the no-wear region of the spine, so as to remove all error associated with worn growth bands. Bias between age readers was evaluated with age bias plots, whereas precision was quantified using the coefficient of variation (CV) (Campana 2001).

Multiple samples ($n = 64$), usually representing groups of 1–3 growth bands (up to 10 bands, in areas of slow growth), were micromilled from the enamel layer of each spine. In most cases, attempts were made to isolate samples from near the base (representing the period just prior to collection), the unworn region nearest the tip (representing the oldest portion of the spine), and the mid-region of each spine. Enamel samples were isolated as solid pieces with a Merchantek computer-controlled micromilling machine using steel cutting bits and burrs. Any dentine which remained attached to the enamel sample after micromilling was removed using a Gesswein high-speed hand tool fitted with a steel burr. The date of sample formation was calculated as the year of dogfish collection minus the growth band count from spine base to the midpoint of the range of growth bands comprising the sample, to which was added 0.5 to adjust for the fact that the spine base was counted as the first growth band. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). Since the carbon content of the spine enamel was about 10%, the minimum sample weight which could be assayed was about 3 mg. AMS assays also provided $\delta^{13}\text{C}$ (‰) values, which were used to correct for isotopic fractionation effects and provide information on the source of the carbon. 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 prior to 1950 according to methods outlined by 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) which 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 spine material however, synchrony with carbonates could not be assumed. Therefore, we used newly formed dogfish spine enamel (within two growth bands of the spine base) for our known-age, or reference, chronology. Dogfish spines are known to grow outward from the base of the spine, with the newest material being found at the base (Holden and Meadows 1962; Beamish and McFarlane 1985). Since the date of collection was known for all dogfish, and making the reasonable assumption that 1–2 growth bands from the base represents 1–2 years before the date of collection with a maximum error of no more than ± 2 year, the dates of formation of the basal growth bands were considered to be of known age.

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 2000. The collection and radiocarbon assay of 56 age 1–3 haddock, *Melanogrammus aeglefinus*, and redfish, *Sebastes* spp., otoliths has been described elsewhere (Campana 1997; Campana et al. 2002); the chronology was supplemented by 17 age 1–2 haddock and yellowtail flounder, *Limanda ferruginea*, otoliths collected between 1980 and 2000 and prepared in a similar manner. There was no detectable difference between the haddock, redfish and yellowtail chronologies; therefore they were pooled and used as the reference carbonate chronology. The $\Delta^{14}\text{C}$ chronology of aragonitic fish otoliths in the NW Atlantic 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 spiny dogfish environment. The reference chronologies for the northeast Pacific Ocean were drawn from known-age assays of Pacific halibut and rockfish otoliths (Kerr et al. 2004; Piner and Wischniowski 2004).

Results

Growth band sequences were clearly visible along fin spines, although it was often difficult to distinguish between a broad diffuse band and two or more closely packed growth bands in spines from the Atlantic (Fig. 1). In such cases, similarity in appearance and spacing to adjacent growth bands was used as a guide to interpretation. Spines from the Pacific tended to be more clear, and characterized by narrower growth increments, than were those from the Atlantic (Fig. 1). In most cases, the most medial growth mark appeared as a white check, which we interpreted as approximating the region of current enamel formation. The distal tips of larger dogfish (>60 cm fork length) were

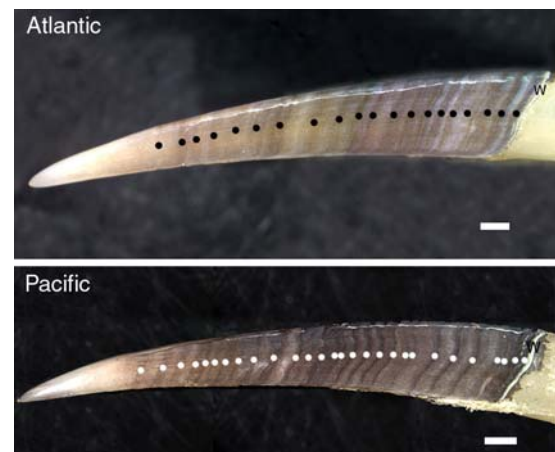


Fig. 1 Second dorsal spine of spiny dogfish collected in the northwest Atlantic (Top) and northeast Pacific (Bottom) annotated to show annual growth bands. The ages of the Atlantic (fork length 74 cm) and Pacific (total length 95 cm) dogfishes were interpreted as 20 and 28 years, respectively, before adjustment for growth bands formed before birth and the expected number of unobserved bands in the worn tip. The white check (W) was assumed to represent the region of active enamel formation. Scale bar is 2 mm

often worn to the extent that enamel was no longer visible. Since the tip of the spine corresponded to the region formed at or around birth, the oldest enamel of the spine (corresponding to the age of the dogfish) was often not available for assay.

A comparison between Atlantic and Pacific age readers indicated that the spines from the two oceans were interpreted consistently. Age bias plots indicated no bias between Atlantic and Pacific age readers interpreting Pacific spines, and no bias between multiple Atlantic age readers interpreting Atlantic spines. Ageing precision was similar in both populations: the CV was 7.2% between Atlantic and Pacific agers of Pacific spines, and 8.0% between multiple Atlantic age readers of NW Atlantic spines.

Although spine $\delta^{13}\text{C}$ would not be expected to change very much through the period of bomb testing, it can be a reflection of the carbon source. Spine $\delta^{13}\text{C}$ ranged between -11.7‰ and -15.2‰ with an overall mean of -13.7‰ (SE = 0.09) (Table 1). Differences in $\delta^{13}\text{C}$ among areas were significant (ANOVA, $P < 0.05$), with the Pacific spines (mean = -13.3‰) significantly less depleted than those from the northeast Atlantic (mean = -14.0‰) and northwest Atlantic (mean = -14.2‰). $\delta^{13}\text{C}$ declined weakly but significantly with both year of formation ($P < 0.05$, $r^2 = 0.20$) and age at formation ($P < 0.05$, $r^2 = 0.21$) in the northeast Atlantic, but not in the other areas.

Although the magnitudes differed among areas, the increase in the spine $\Delta^{14}\text{C}$ through the 1960s was very similar to the bomb signal expected of $\Delta^{14}\text{C}$ in the marine environment (Fig. 2). In the Atlantic, spine $\Delta^{14}\text{C}$ increased sharply from about -80 in spine enamel formed before 1958, to values of about 100 after 1970, declining slowly thereafter to just above 0 in 1998 (Fig. 2A). Both the northeast and northwest Atlantic spine samples resembled the reference chronology for the northwest Atlantic (based on known-age otoliths), suggesting that the uptake of ^{14}C into the spine enamel mirrored that of marine DIC. In the northeast Pacific, spine $\Delta^{14}\text{C}$ also reflected the otolith-based reference chronologies for the region, albeit with more variance for the post-bomb (1970–1998) section of the curve

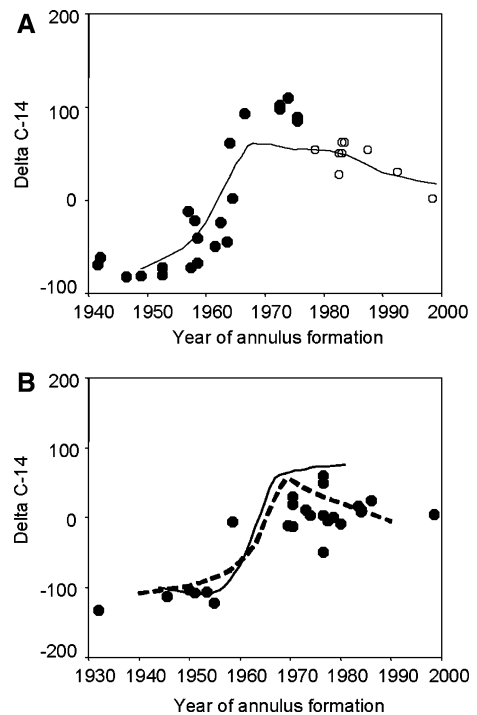


Fig. 2 $\Delta^{14}\text{C}$ in individual growth bands of dogfish spines versus year of formation inferred from counts of the growth bands. The $\Delta^{14}\text{C}$ chronology of the spines (symbols) was similar to that of a reference carbonate chronology (lines smoothed with a loess curve) from the same area, with the crucial feature being the period of rapid increase. (Top) Fish from the northeast Atlantic (\bullet) and northwest Atlantic (\circ) have been plotted with the reference chronology from the Atlantic (solid line); (Bottom) Fish from the northeast Pacific (\blacktriangle) have been plotted with the Pacific reference chronologies from Piner and Wischniowski (2004) (solid line) and Kerr et al. (2004) (dashed line)

(Fig. 2b). Pre-bomb $\Delta^{14}\text{C}$ (between 1932 and 1958) measured in Pacific spines averaged about -110 , while post-bomb spine $\Delta^{14}\text{C}$ tended to be above 0.

Bomb radiocarbon can only serve as a reliable dated marker if its position relative to the growth bands remains static through the subsequent life of the animal. There was little evidence of metabolic reworking of the radiocarbon signal in the spine enamel. Of the 22 dogfish from which multiple growth bands were sampled, all showed the same within-spine bomb signal across year of formation as that demonstrated by the across-spine analysis (Fig. 3). Ontogenetic effects were not evident, indicating that the bomb signal was

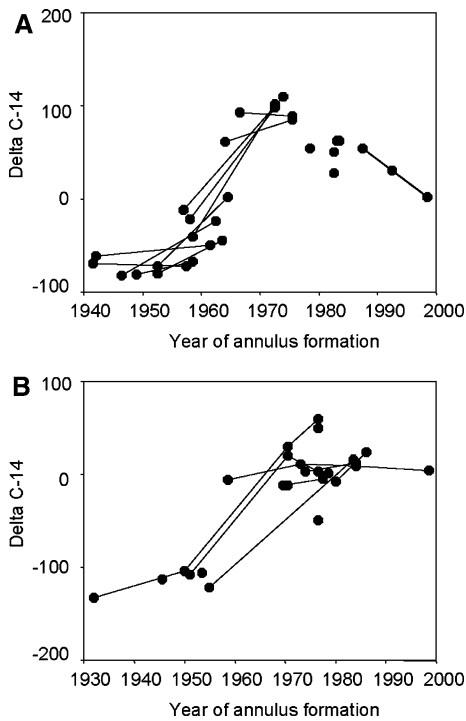


Fig. 3 $\Delta^{14}\text{C}$ in individual growth bands of dogfish spines versus year of formation inferred from counts of the growth bands. The $\Delta^{14}\text{C}$ chronology within each dogfish spine (each line corresponds to an individual spine) paralleled the across-spine chronology, indicating that the bomb signal of a single growth band remained stable as the dogfish grew older. (Top) Atlantic Ocean; (Bottom) Pacific Ocean

not diluted by subsequent growth over a period of up to 44 year.

It is safe to assume that samples milled from near the base represent enamel formed within 1–2 years of capture; hence, a year of formation can be assigned to these samples with considerable certainty. The $\Delta^{14}\text{C}$ chronology prepared using these known-date samples was very similar to that based on earlier-formed growth bands nearer to the spine tip (Fig. 4). Since any errors in the age interpretation of the older spines would have been evident in $\Delta^{14}\text{C}$ values that lay-off the curve defined by the known-date spines, the dogfish aged 7–52 years must have been aged correctly (on average) based on the number of growth bands. No known-date samples from pre-bomb growth bands were available for the Pacific dogfish, which limited the comparisons, which were

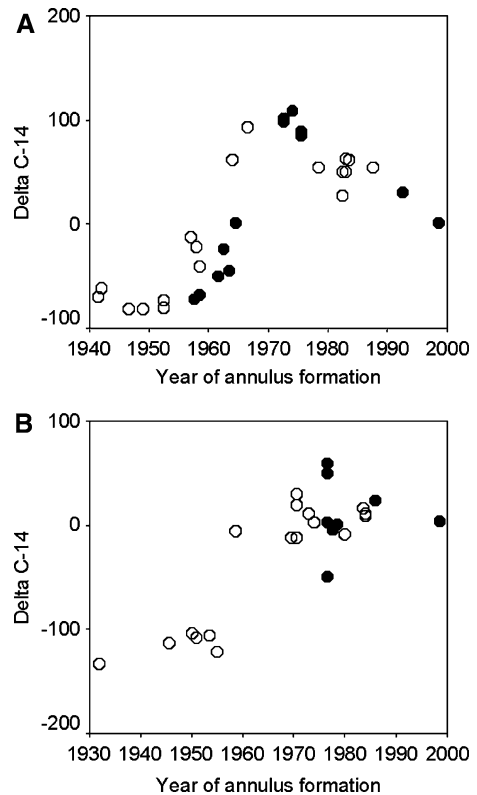


Fig. 4 $\Delta^{14}\text{C}$ in individual growth bands of dogfish spines versus year of formation inferred from counts of the growth bands. The radiocarbon chronology apparent in growth bands formed shortly before collection of the dogfish (implying that the date of band formation was known to within 1–2 year) (\bullet) was similar to that of growth bands formed earlier in life (nearer the spine tip) (\circ). This indicated that the age of the growth bands was relatively accurately interpreted in the older dogfish. (Top) Atlantic Ocean; (Bottom) Pacific Ocean

possible. However, in the case of the Atlantic dogfish, both the known-date and the test samples extended through the period of rapid increase in bomb radiocarbon through the 1960s. In light of the relative stability in $\Delta^{14}\text{C}$ after 1970, it would have been difficult to detect any under-ageing in dogfish born after 1970. However, over-ageing 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 $\Delta^{14}\text{C}$ values between 60 and 95 in the growth bands of dogfish collected in 1978 and 1979, and presumed to have formed 14 years before collection based on growth band counts from the spine base, cannot have been

aged with an error of more than ± 1 –2 year or the assay values would have been totally inconsistent with both the known-date assay curve and the reference chronology. Similarly, under-ageing of any sharks born before 1958 would have been easily detected based upon the presence of depleted $\Delta^{14}\text{C}$ values in apparently post-bomb samples. None of the spines with pre-bomb $\Delta^{14}\text{C}$ values were underaged to an extent that would place them into the period of radiocarbon increase. Nevertheless, there were three samples with presumed dates of formation in the late 1950s whose $\Delta^{14}\text{C}$ was slightly higher than expected based on the known-date samples. These samples, micromilled 18–21 growth bands from the spine base, may either have been overaged by a few years or may have inadvertently included underlying dentine representing later years of formation.

Discussion

Our results indicated that the amount and timing of bomb radiocarbon incorporated into dogfish spine enamel was very similar to that of DIC in the surrounding water. Comparison of $\Delta^{14}\text{C}$ values in spine growth bands formed at different ages within a spine indicated that the bomb signal was not transported across growth bands through time. Similar stability in deposited radiocarbon was reported for vertebral growth bands in large pelagic sharks (Campana et al. 2002). Since the period of increase in radiocarbon in the water is both known and predictable throughout the surface marine waters of the world (Druffel and Linick 1978; Campana 2001), and given the metabolic stability of the radiocarbon once deposited in the spines, radiocarbon in spiny dogfish spines appears to be well suited as a dated marker for age validation. Since ageing errors would have shifted the presumed date of growth band formation, the annual correspondence between spine and DIC radiocarbon chronologies supported the conclusion that our interpretation of spine growth bands as age indicators must have been accurate, at least on average, to an age of 52 year.

Spine $\delta^{13}\text{C}$ averaged -13.7 , which is markedly different than the values of -1 to -3 typically found in otoliths (Kalish 1993; Campana 1997). Whereas the carbon source for otoliths is largely DIC with a $\delta^{13}\text{C}$ close to zero (Schwarcz et al. 1998), strongly depleted values such as those observed in the dogfish spines are more characteristic of metabolic and dietary carbon (Fry 1988). As such, it seems likely that the carbon source for the spine enamel is of dietary origin, similar to that of shark vertebrae (Campana et al. 2002). Campana et al. (2002) documented a phase-shifting between the vertebral radiocarbon of porbeagle sharks and the reference carbonate chronology due to the presence of deepwater, ^{14}C -depleted prey in the diet. The absence of this phase-shifting in dogfish spines is also consistent with a dietary source for spine carbon, since most of the dogfish diet would be expected to be found with the dogfish in shallow coastal waters (< 200 m) (Jones and Geen 1977; Alonso et al. 2002), and thus reflect the radiocarbon content of the surface mixed layer DIC.

There was a visible but small tendency for the recently formed growth bands in some of the spines growing during the 1960s to be slightly depleted in $\Delta^{14}\text{C}$ compared to growth bands formed earlier in life. A similar phenomenon in porbeagle vertebrae was attributed to diet switching to larger, older prey by bigger sharks (Campana et al. 2002). It is possible that a similar explanation applies to dogfish. The tendency for spine $\Delta^{14}\text{C}$ to decrease with dogfish age would be consistent with this view, since larger, older prey would provide more depleted $\Delta^{14}\text{C}$ if tissue accumulated during the period of bomb ^{14}C increase. Alternatively, some of the spines may have been over-aged, or underlying dentine may not have been completely removed from the enamel samples.

The pre-bomb spine $\Delta^{14}\text{C}$ was very similar to the otolith carbonate chronologies from the same waters, as would be expected given the surface mixed layer depths occupied by dogfish and their diet. The post-bomb spine $\Delta^{14}\text{C}$ was also similar to that of the otolith carbonate chronology in each region, but the correspondence in the northeast Pacific was much more variable than in the Atlantic; since the absolute

value of post-bomb $\Delta^{14}\text{C}$ in the water column is sensitive to water mass mixing rates and residence times (Druffel 1989; Weidman and Jones 1993), the area- and time-specific upwelling of the eastern Pacific would be expected to introduce more variability into radiocarbon levels. This variability in water-borne Pacific $\Delta^{14}\text{C}$ was also evident in the difference between the two North Pacific reference chronologies shown in Fig. 2. Of more importance to age validation is the timing of the initial post-bomb increase in spine radiocarbon relative to that in the DIC, since it is the year of initial increase that is most invariant throughout the world, and thus serves as the most reliable dated marker (Piner and Wischniowski 2004). The correspondence between the Atlantic spine chronology and the reference chronology was quite precise, both appearing to increase around 1958. With the data available, it was more difficult to pinpoint the initial increase in the Pacific spine chronology. However, with the Pacific spine $\Delta^{14}\text{C}$ showing peak values around 1970 and minima around 1954, the period of increase must have been within a couple of years of that evident in the reference chronologies.

Do Pacific dogfish grow more slowly and live longer than northwest Atlantic dogfish? This study indicates that our interpretation of the growth bands on the spines is accurate in both oceans. Moreover, our age comparisons in which spines from both oceans were aged by the same primary age reader indicates that our age interpretations for both populations are consistent with those that have been published. Therefore, the published work suggesting that Pacific spiny dogfish are both longer lived and slower growing than their northwest Atlantic counterparts appears to be accurate, and is not due to interpretational errors in one or both populations (Ketchen 1975; Nammack et al. 1985; Saunders and McFarlane 1993). The cause of the difference in growth rates between the two oceans remains unknown, but may be linked to population-level differences in reproductive output (Campana, unpublished).

The use of spine enamel bomb radiocarbon to determine age and confirm the periodicity of growth bands should be appropriate for all

surface mixed layer shark species with fin spines where at least some of the growth bands were formed prior to 1965. If fin spines in teleost fishes form similarly to those in sharks, the method should also be appropriate for age validation in teleost fishes with fin spines. It is unlikely that deepwater shark species could be used, due to the delayed arrival of the bomb radiocarbon signal at depth. 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 spine 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 vertebrae is sometimes required depending on location and depth; although this was not an issue with spiny dogfish, phase shifting due to diet might be expected in the case of other shark species.

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