Age under-estimation in New Zealand porbeagle sharks (*Lamna nasus*): is there an upper limit to ages that can be determined from shark vertebrae?

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Abstract.   Annual deposition of growth bands in vertebrae has been validated for many shark species, and is now widely regarded as the norm. However, vertebrae are part of the shark's axial skeleton, and band deposition may stop in old sharks when somatic growth ceases. We aged vertebral sections from New Zealand porbeagle sharks (*Lamna nasus*) under reflected white light and using X-radiographs. Bomb radiocarbon assays supported vertebral age estimates up to ∼20 years, but not at older ages. The results suggest that older porbeagles were under-aged by as much as 50% from vertebral band counts, presumably because band width declined to a point where it became unresolvable. This has important implications for growth studies on other long-lived sharks. Estimated ages at sexual maturity were 8–11 years for males and 15–18 years for females, and longevity may be ∼65 years. New Zealand and North Atlantic porbeagles differ in these parameters, and in length at maturity and maximum length, suggesting genetic isolation of the two populations.

Additional keywords: bomb radiocarbon, longevity, maturity, validation.

Introduction

Sharks are cartilaginous fishes, and they lack the large, calcareous otoliths that are typically used to estimate the age and growth of teleosts. Consequently, scientists have had to use other hard parts, usually the vertebrae, for studies of shark growth. Deposition of vertebral growth bands has been validated as annual in many shark species (Cailliet and Goldman 2004), and there is only one well documented exception to this rule – the Pacific angel shark (*Squatina californica*), which appears to have aperiodic deposition (Natanson and Cailliet 1990). The shortfin mako shark (*Isurus oxyrinchus*) was for a long time regarded as having biannual band deposition, but recent studies have confirmed annual deposition (Campana *et al*. 2002*a*; Ardizzone *et al*. 2006; Natanson *et al*. 2006).

Vertebrae form part of the axial skeleton of a shark so, in theory, if the shark's somatic growth ceases, then deposition of material on the outer margin of the vertebrae should also cease. By contrast, teleost otoliths are suspended in a fluid-filled chamber that permits continued deposition of new material after somatic growth has ceased. It seems surprising then, that shark vertebrae appear to be such good recorders of age. It may be that validation studies have not detected cessation of band deposition because too few older sharks were aged, somatic growth had not ceased, or vertebrae are capable of growing radially after axial (anterio-posterior) growth has ceased.

In the present study, we investigate the deposition of vertebral growth bands in porbeagle sharks (*Lamna nasus* (Bonnaterre,

1788)), from New Zealand. This species has already received considerable attention. Aasen (1963) developed a growth curve for north-west Atlantic porbeagles from length–frequency data, and counted bands on a vertebral section from a single shark, in one of the first studies to use vertebral bands to age a shark. He concluded that porbeagles live at least 20 years and probably up to 30 years. Francis and Stevens (2000) analysed length–frequency data to produce growth curves for juvenile New Zealand and Australian porbeagles. Natanson *et al*. (2002) conducted a comprehensive study of age and growth in north-west Atlantic porbeagles using a large sample of vertebral sections. They validated their ageing technique up to an age of 11 years using recapture of oxytetracycline-injected and known-age juveniles, and corroborated their vertebra-based growth curves using independent length–frequency and tag–recapture data. Campana *et al*. (2002*a*) extended the validation of north-west Atlantic age estimates to 26 years using bomb radiocarbon analysis (Kalish 1993; Kalish *et al*. 1997; Campana and Jones 1998). Here, we use the same vertebral ageing protocol used in the north-west Atlantic, and also apply bomb radiocarbon analysis to validate our ageing technique for New Zealand porbeagles. We present evidence that band deposition ceases in older New Zealand porbeagles, and suggest that age under-estimation may be a consequence of cessation of somatic growth in this and other long-lived shark species.

Porbeagle sharks have a circumglobal distribution in temperate and subantarctic waters in the southern hemisphere, mainly

in latitudes 30–55°S (Last and Stevens 1994; Yatsu 1995*a*; Compagno 2001). They are common in oceanic waters around New Zealand, where they are caught incidentally in tuna long-line and midwater trawl fisheries. Reported catches are small (100–300 t per year (Sullivan *et al.* 2005)), but they probably under-estimate actual catches because of discarding at sea and inaccurate conversion factors for processed shark fins. Most por-beagles caught by the tuna longline fishery are juveniles, though mature males make up a significant part of the catch around northern New Zealand (Francis *et al.* 2001; Ayers *et al.* 2004). The size composition of the catch by trawl fisheries is unknown.

Porbeagle sharks have proven highly sensitive to over-fishing in the North Atlantic Ocean (Campana *et al.* 2002*b*), and are listed as 'Vulnerable' on the World Conservation Union (IUCN) redlist (http://www.iucnredlist.org/, verified December 2006), prompting fears that catches in the southern hemisphere may not be sustainable. Management responsibility for porbeagles in the western and central Pacific Ocean lies with the newly formed Western and Central Pacific Fisheries Commission, but regional management is unlikely to be implemented for some time (Sullivan *et al.* 2005). In the meantime, the New Zealand Ministry of Fisheries aims to regulate catches in New Zealand waters: porbeagles were introduced into the Quota Management System in October 2004 with a total allowable catch of 249 t (Sullivan *et al.* 2005). Basic population information on stock range, size and status, and biological productivity is not avail-able, and must be determined to underpin current and future management. Our aim in undertaking the present study was to estimate growth rate, longevity, and age at maturity for use in stock assessment and management.

Materials and methods

Vertebral ageing

Vertebrae used for ageing porbeagles were mostly collected from tuna longline vessels by Ministry of Fisheries observers, but a few specimens came from other sources, including research ves-sels and inshore set net fishers (Fig. 1). Vertebrae were collected between 1995 and 2003, but most (97%) were collected in 2002 and 2003. The tuna longline fishery has traditionally operated in three main regions: north, south-west and south-east New Zealand (Fig. 1). Most of our samples came from the South-west New Zealand fishery, which targets southern bluefin tuna (*Thunnus maccoyii*) in autumn–winter (April–July) (90% of the vertebrae were collected in April–June).

A block of 4–6 vertebrae was removed from beneath the first dorsal fin of each shark, trimmed of neural and haemal arches, muscle and connective tissue and then frozen. Sex and fork length (*FL*, measured in a straight line from the tip of the snout to the fork in the tail, to the nearest centimetre below actual length) were recorded. Vertebrae for sectioning were selected from a subsample of sharks to represent the full-length range of both sexes (67–205 cm), although males outnumbered females. Vertebrae were sectioned frontally by making two cuts with a single diamond-edged saw blade to produce a section ~0.6-mm thick. Because of the large size of the vertebrae relative to our sectioning saw, we were only able to cut half 'bowtie' sections, and they frequently snapped off between the birth band and the
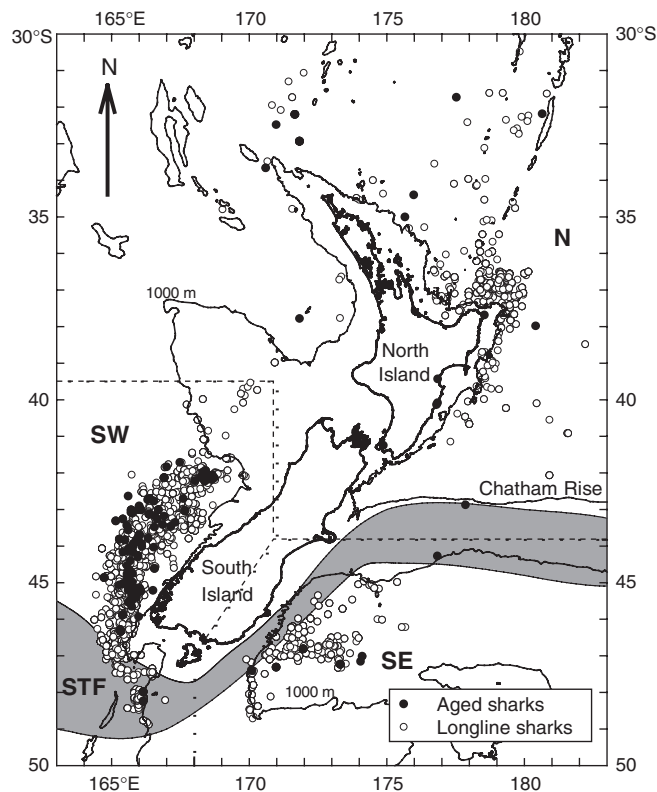

Fig. 1. Map of the New Zealand region showing start-of-set locations for observed tuna longline sets that caught porbeagles, and capture loca-tions of porbeagles that were aged in this study. Three subregions (N, north; SW, south-west; SE, south-east) used for length–frequency analysis are also shown. The grey shaded zone shows the approximate mean position of the Subtropical Front (STF), which separates subtropical waters in the north from subantarctic waters in the south.

focus. Sections were stored in 70% isopropyl alcohol until they were read.

Vertebral radius is usually measured between the focus of the 'bowtie' section and the vertebral margin along the corpus calcareum, but this was impossible in most of our sections. The only routinely available vertebral size measurement was cen-trum length (*CL*) measured as the maximum distance between the outer edges of the corpus calcareum in the anterio-posterior direction (Fig. 2).

Sections were drained and read wet using a Wild M400 binoc-ular microscope (Wild, Heerbrugg, Switzerland) under reflected white light at 6.3× magnification. X-radiographs were taken of sections laid flat on X-ray film using a Philips 140 kV beryl-lium industrial machine (Philips Elektronik Industrie GmbH, Hamburg, Germany) at 45 kV and 5 mA. Counts were made of opaque bands following the method of Natanson *et al.* (2002) for north-west Atlantic porbeagles.

Reader 1 (MPF) counted all vertebrae under reflected white light, and from X-radiographs. Readability was scored using a five-point scale ranging from 1 for excellent to 5 for unreadable. Reader 2 (SEC) aged a subset of 61 vertebrae under reflected white light. Ages were estimated by subtracting the birth band (identified after Natanson *et al.* (2002)) from the opaque band
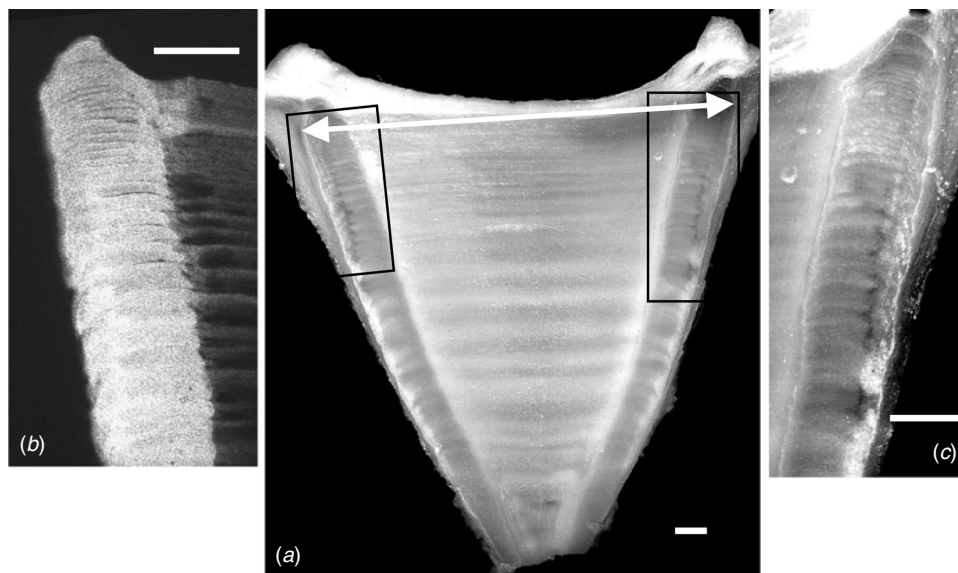
Fig. 2. (*a*) Reflected white light micrograph of a half-centrum vertebral section from a 200-cm fork length (FL) male porbeagle shark (POS197). Black rectangles indicate areas enlarged in (*b*) and (*c*). White arrow shows centrum length (CL) measurement. (*b*) X-radiograph enlargement of part of (*a*). (*c*) Reflected white light enlargement of part of (*a*). Opaque band counts for this shark were 35 (Reader 1, reflected white light), 38 (Reader 1, X-radiograph), and 37 (Reader 2, reflected white light). Scale bars = 1 mm.

count of Reader 1. We did not attempt to assess the marginal increment width or state because most vertebrae were collected during a 3-month period. The timing of opaque-zone formation is unknown, so no correction could be made for time of capture in relation to time of band formation.

Age-determination bias between band counts made under white light and X-radiography was explored using an age-bias plot (Campana *et al.* 1995). To estimate ageing precision, we calculated average percentage error (APE) and the mean coefficient of variation (CV) (Campana *et al.* 1995; Campana 2001). CV is numerically $\sqrt{2}$ ($= 1.414$) times greater than APE.

Growth curves were fitted to the length-at-age data from white light band counts using the von Bertalanffy growth model:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad (1)$$

where L_t is the expected length at age t years, L_∞ is the asymptotic maximum length, K is the Brody growth coefficient, t is the fish age in years and t_0 is the theoretical age at zero length. To test for significant differences between male and female growth curves, we applied an age-standardised randomisation test (Cox and Hinkley 1974). A randomisation test may be more reliable than the more commonly used likelihood-ratio test (Kimura 1980) because the latter assumes that the residuals from fitting the von Bertalanffy growth model are normally distributed with constant variance (A. Dunn, National Institute of Water and Atmospheric Research, Wellington, New Zealand, personal communication). For each of 1000 simulated datasets, selected randomly with replacement from the original data, fish were allocated randomly to each subgroup (i.e. the two sexes). The null distribution was generated by calculating, for each dataset, the difference between the residual sum of squares obtained from fitting the full data and that obtained by fitting the subgroups

(A. Dunn, NIWA, New Zealand, personal communication). The probability that growth curves fitted separately to the two subgroups represented an improvement over fitting a single growth curve to the pooled data was determined by comparing the actual difference in residual sum of squares with the simulated null distribution. In conducting the randomisation test, we randomly selected fish within each age class. This preserved the age structure of the different subgroups and allowed a more accurate comparison.

Radiocarbon assays

Vertebrae were selected from 11 porbeagles 163–200-cm *FL* for radiocarbon assays. These samples were chosen to represent middle-aged and old sharks with birth dates that spanned the period from the mid 1960s to the mid 1980s. Vertebrae were sectioned as described above, and aged by Reader 2 while working at 6× magnification under reflected light with a binocular microscope. Vertebral sections were digitally photographed at a minimum resolution of 1280 × 1024 and then enhanced.

Three or four samples of vertebral material weighing 4.3–15.4 mg each were extracted by Reader 2 from groups of 1–3 growth bands visible in the corpus calcareum while working at 16× magnification under a binocular microscope. Extracted samples were isolated as solid pieces using a Gesswein high-speed hand tool (Gesswein, Bridgeport, Connecticut, USA) fitted with steel bits less than 1 mm in diameter. In all cases, the birth band or the second growth band (corresponding to the first year of growth after birth) was extracted from each vertebra; additional growth bands corresponding to later growth were also extracted. The presumed date of sample formation was calculated as the year of porbeagle collection minus the number of bands counted between the mid-point of the sample and the

outer edge of the section. After sonification in water that had been distilled, millipore-filtered and put through reverse osmosis, the sample was dried and weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided δ^{13}C (‰) values, which were used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as Δ^{14}C, which is the per mille (‰) 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).

The onset of nuclear testing in the late 1950s resulted in a marked and widespread increase in Δ^{14}C in marine dissolved inorganic carbon (DIC), which is detectable in all biogenic 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 to compare the Δ^{14}C of the unknown sample with a Δ^{14}C chronology based on known-age material (a reference chronology). For carbonates, the years corresponding with the onset of radiocarbon increase are synchronous in reference chronologies based on corals, bivalves and teleost otoliths, and are thus interchangeable (Campana 1999). We used a combined reference chronology from three species of south-west Pacific fishes (Kalish 1993, 1995; Kalish *et al*. 1997). However, the bomb radiocarbon chronology recorded in shark vertebrae slightly lags that of carbonates by several years, since the carbon source for vertebrae is dietary (metabolic) rather than DIC (Campana *et al*. 2002*a*). Therefore, we also used a reference chronology developed from known-age porbeagles from the north-west Atlantic (Campana *et al*. 2002*a*). The period of increase in this chronology should be similar to that of Pacific porbeagles, although the latter might reflect the more depleted radiocarbon values of the Pacific.

Discrepancies between actual and expected Δ^{14}C levels suggested age under-estimation from vertebral band counts. To simulate the possible magnitude of any under-ageing, we increased the age estimates for each shark older than 20 years (as aged by Reader 2) by eye until its radiocarbon trajectory aligned with that of the north-west Atlantic porbeagle reference chronology (see Results). Importantly, the adjustment phase-shifted all growth bands within a shark's vertebra by the same amount, thus maintaining the same relative year of formation. Because radiocarbon assays were performed on only a few sharks, we could not calculate adjusted ages for all sharks older than 20 years. In order to predict the adjusted age of any shark older than 20 years, we fitted an asymptotic curve to the data (adjusted *v*. estimated ages) and forced it through the point (20 : 20). An asymptotic curve was used based on the hypothesis that the age estimate obtained under white light will tend towards a maximum as increment width near the margin declines and becomes unresolvable. The fitted curve had a form analogous to a von Bertalanffy curve forced through the length at birth (Simpfendorfer *et al*. 2002):

$$A = A_0 + (A_\infty - A_0)(1 - e^{-k(A' - A'_0)}) \qquad (2)$$

where A is the age estimate from Reader 2, A_0 is the origin on the age-estimate axis (= 20 years), A' and A'_0 (= 20 years) are the corresponding adjusted age values, A_∞ is the asymptotic age and k is a rate constant that determines how quickly the curve converges to the asymptote. (It would have been statistically

more correct to rearrange Eqn (2) so that A' was the dependent variable, and minimise the sum of squares in the y-direction rather than the x-direction; however, when this was attempted the function would not converge, probably because of the very small sample size.) Adjusted growth curves were then derived by combining the von Bertalanffy growth curve based on estimated ages up to 20 years with the length-at-adjusted age for ages greater than 20 years.

The width of the marginal growth increment is an index of recent growth rate. For each of the 11 sharks used for radiocarbon dating, we measured the width of the last visible increment on the outer edge of the corpus calcareum under a microscope using reflected light.

Habitat and food

Information on the spatial and depth distribution of porbeagles, and their prey, was sought to help interpret vertebral radiocarbon patterns. Although radiocarbon levels in DIC decline with depth below the surface mixed layer, the radiocarbon source for shark vertebrae is the shark's prey (Campana *et al*. 2002*a*). Therefore the radiocarbon taken up by the shark will depend on the trophic level, age and vertical distribution of its prey. In particular, prey that inhabit or migrate vertically to depths below the mixed layer may expose the sharks to radiocarbon levels different from the depth at which the shark is captured.

The operating depth of the tuna longlines used to sample most porbeagles in our study was not known. Experiments with time–depth recorders show that pelagic longlines are affected by currents and can be quite mobile with the lines rising and/or falling during sets (Boggs 1992; Yano and Abe 1998). For tuna longliners operating in New Zealand waters between 1993 and 2004, we analysed the vessel master's best estimate of minimum and maximum depth of their gear, as recorded by observers.

Observers also recorded the stomach contents of 3654 porbeagles caught around New Zealand between 1994 and 2004. They estimated by eye the volumetric percentage (usually to the nearest 10%) of fish, squid, crustaceans, salps, bait and 'other' in each stomach. Where possible, the main prey items were identified to species, but because all work was done at sea, and stomach content analysis of by-catch species was not a high priority, such information was not often available. We calculated the mean percentage composition of the stomach contents after grouping sharks by 25-cm length class and by sex. Empty stomachs and stomachs containing only bait were ignored for this purpose.

Length–frequency distributions were compiled for porbeagles measured by observers on tuna longline vessels in each of the three main fishing regions during the period 1993–2005. Most south-east, south-west and north region sharks were measured in April, May–June and June–July respectively.

Length conversions

The measurement standard for porbeagles in the north-west Atlantic is fork length measured over the curve of the body (FL_{OTB}) (Campana *et al*. 2002*a*; Natanson *et al*. 2002). To compare our results with those from the north-west Atlantic, we converted FL_{OTB} lengths reported in the literature to straight line FL as follows (lengths in centimetres): $FL = 0.90 + 0.95\ FL_{OTB}$ (SEC, unpubl. data; $n = 172$, $R^2 = 0.997$).
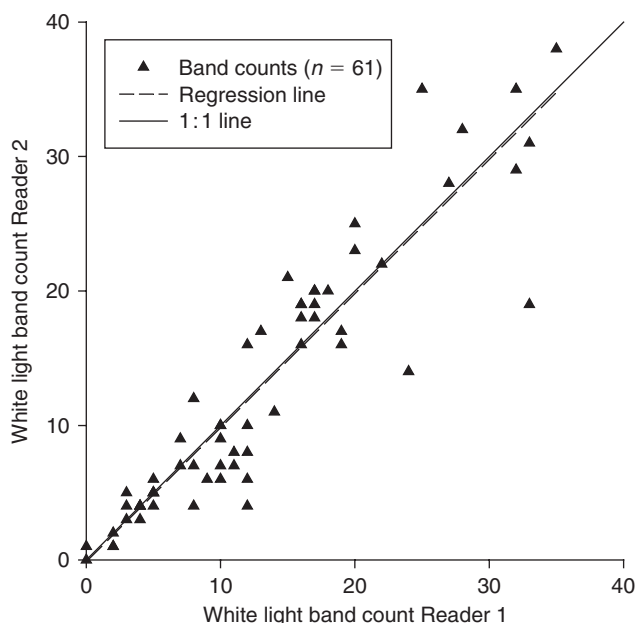
Results

Vertebral age and growth

There was a linear relationship between CL and FL: $CL = -0.082 + 0.069\,FL$ ($n = 125$, $R^2 = 0.76$). There was a considerable amount of variability in the data, presumably because vertebrae were not always collected from the same part of the vertebral column, but there was no evidence of non-linearity. A non-linearity would indicate uncoupling of vertebral and somatic growth, and that material was either being deposited anterioposteriorly on the vertebrae after somatic growth stopped, or that somatic growth continued after anterio-posterior vertebral growth ceased.

A high proportion of the vertebrae were difficult to read: 84% of white light sections and 88% of X-radiographs were scored as readability 3 or 4 (moderate or poor respectively), but only 3% of each were scored as 5 (unreadable). The greatest difficulty was experienced in counting the narrow increments near the margin of the vertebrae from old sharks. A comparison of reflected white light and X-radiograph images from the same shark (the oldest in our sample) is shown in Fig. 2.

Readers 1 and 2 showed no systematic variation in their age estimates for sections viewed under white light – a linear regression line through the data was practically indistinguishable from the 1 : 1 line (Fig. 3). However, there was a large amount of variability for individual readings. This confirms that age was difficult to estimate in these sharks, but provides confidence that both readers were, on average, reading the vertebrae in the same way.

Band counts made by Reader 1 from sections viewed under reflected white light and from X-radiographs also showed considerable variability, with some paired readings differing by a factor of two or more (Fig. 4). However, on average the white light and X-radiograph readings were consistent for sharks aged

up to ∼20 years. In older sharks, the variability increased, and X-radiograph counts tended to be greater than white light counts, though sample sizes were small and sometimes the converse was true. The APE for the comparison between white light and X-radiograph counts was 12.2% and the CV was 17.2%.

Reader 1's white light band counts were used to generate growth curves, because Reader 2 aged only a subset of the sections. Length-at-age estimates for male and female porbeagles with fitted von Bertalanffy growth curves are shown in Fig. 5,
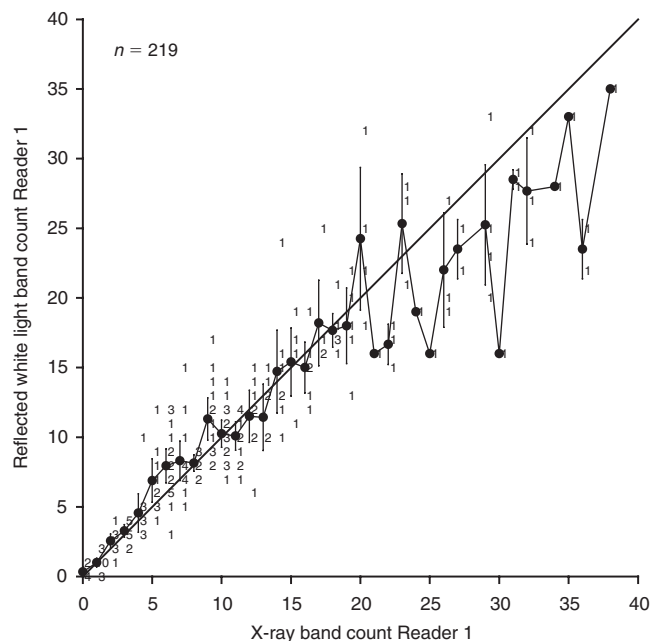
Fig. 4. Comparison of white light and X-radiograph opaque band counts made by Reader 1. Numerals (displaced right for clarity) indicate sample sizes and solid circles with error bars indicate the mean and twice the standard error. The diagonal line is the expected 1 : 1 relationship.

Fig. 3. Comparison of white light band counts between Readers 1 and 2. The diagonal line is the expected 1 : 1 relationship.
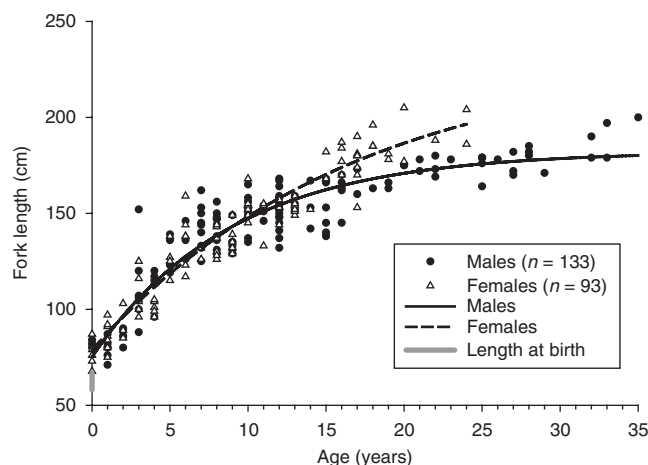
Fig. 5. Relationship between fork length and estimated age (Reader 1, white light) for male and female porbeagles, with fitted von Bertalanffy growth curves. The length at birth range reported by Francis and Stevens (2000) is also shown.

Table 1.   Growth model parameter estimates and standard errors (s.e.) for male and female porbeagle sharks, based on white light age estimates by Reader 1

L_∞, asymptotic maximum length; K, Brody growth coefficient; t_0, theoretical age at zero length

Sex	Sample size	$L_\infty \pm$ s.e. (cm)	$K \pm$ s.e. (year^{-1})	$t_0 \pm$ s.e. (years)
Males	133	182.2 ± 3.2	0.112 ± 0.010	-4.75 ± 0.57
Females	93	233.0 ± 16.9	0.060 ± 0.011	-6.86 ± 0.95

and the von Bertalanffy growth parameters are given in Table 1. The growth curves showed rapid, near-linear growth up to an age of ~5 years, followed by reduced growth, and divergence of male and female curves at ~11 years. A randomisation test showed that male and female growth curves were significantly different ($P < 0.0001$), with females being larger at a given age than males. The oldest sharks in our sample were males, but this may reflect the larger male sample size, and the paucity of mature females caught in the tuna longline fishery (Ayers *et al*. 2004). The oldest male was estimated to be 35 years old from vertebral band counts, and the oldest female was 24 years old. The growth curves intersected the length axis at 75.2 cm for males and 78.6 cm for females, which are both greater than the reported length at birth of 58–67 cm *FL* (Francis and Stevens 2000). This discrepancy is at least partly due to use of integral ages rather than fractional ages corrected for the date of capture, but may also result from size selectivity of the longline hooks or an absence of new-born young from the fishing grounds.

The maximum ages estimated from X-radiographed sections were 38 and 32 years for males and females respectively.

Radiocarbon assays

The δ^{13}C levels recorded in porbeagle vertebrae (Table 2; mean $\pm$ s.e. $= -14.03 \pm 0.10‰$) were not significantly different from those found in north-west Atlantic porbeagles ($-14.27 \pm 0.09‰$ (Campana *et al*. 2002*a*)) and are consistent with levels expected to result from dietary (metabolic) uptake of carbon (Campana *et al*. 2002*a*).

Reference chronologies derived from the south-west Pacific teleosts *Pagrus auratus*, *Centroberyx affinis* and *Macruronus novaezelandiae* all showed coincident rapid increases in Δ^{14}C during the 1960s, and variable values greater than 50‰ after 1970 (Fig. 6*a*). The reference chronology for north-west Atlantic porbeagles showed a similar pattern but with a slight lag and lower plateau after 1970. Since the post-bomb Δ^{14}C is merely a reflection of water mixing rates, it is the year corresponding to the initial increase in Δ^{14}C that serves as the dated reference point. The initial radiocarbon increase first became apparent in 1959 in the otolith-based reference chronologies and ~1960 in the vertebral chronology.

A total of 37 samples were removed from the vertebrae of 11 New Zealand porbeagle sharks for radiocarbon analysis, but one was lost in processing, leaving us with results for 36 samples (Table 2). Reader 2's age estimates were used for the radiocarbon analyses for consistency, because Reader 2 also located and sampled the individual growth bands for radiocarbon assay. The counting accuracy of the radiocarbon assays was reasonably

good, with a mean standard deviation of 5‰ for any individual assay. Four porbeagles that were aged as 16–20 years by Reader 2 (POS060, 062, 085, 087), and thus believed to have been born after 1980, had high Δ^{14}C levels (mean 38.5‰, range 15–55‰) in each band sampled, consistent with the level expected in radiocarbon-enriched waters post-1970 (Table 2, Fig. 6*b*). A fifth shark (POS045) aged as 35 years had positive radiocarbon values for the 10th and 20th bands, but its birth band sample was lost in processing. Similarly, all but two of the older sharks showed an increase in Δ^{14}C in the more recently formed growth bands, as would be expected. However, the timing of the increase was substantially different from that of the reference chronologies: most of the growth bands believed to have formed after 1970 (based on band counts) in these older sharks had Δ^{14}C levels more consistent with pre-bomb levels (Fig. 6*b*). For two sharks (POS165 and POS203), there was no detectable Δ^{14}C enrichment in the first 20 vertebral bands (subsequent bands were not analysed in those sharks, which had estimated ages of 31 and 32 years respectively).

Discrepancies between actual and expected Δ^{14}C levels might be caused by age under-estimation. To simulate the possible magnitude of any under-ageing, we increased the age estimates for each shark older than 20 years (as aged by Reader 2) by eye until its radiocarbon trajectory aligned with the north-west Atlantic porbeagle reference chronology (Fig. 6*b*; adjusted ages and corresponding year of growth are given in Table 2). Importantly, the adjustment phase-shifted all growth bands within a shark's vertebra by the same amount, thus maintaining the same relative year of formation. In all cases, the adjusted chronologies showed an increase in Δ^{14}C of the expected magnitude over the appropriate time period. Adjustments required to align the curves ranged from 4 to 34 years, with the required adjustment increasing with estimated age (Fig. 7). There was a significant negative correlation ($r = -0.62$, $n = 11$, $P < 0.05$) between the width of the last increment visible near the margin of the vertebra and the adjustment required to align the curves, i.e. larger adjustments were required for sharks having narrow marginal increments.

Adjusted ages were as high as 65 years (two sharks) (Table 2, Fig. 7). The predicted curve relating adjusted ages to estimated ages is shown in Fig. 7, and its estimated parameters were $A_\infty = 31.9$ years and $k = 0.076$ year^{-1}. Rearranging Eqn (2) and substituting the parameter estimates gives:

$$A' = \frac{\ln\left(1 - \frac{A-20}{31.9-20}\right)}{-0.076} + 20 \qquad (3)$$

Adjusted von Bertalanffy growth curves were produced by using Eqn (3) to convert the predicted length-at-age estimates for sharks older than 20 years to predicted length-at-adjusted-age (Fig. 8). For females, the adjusted growth curve differed little from the original von Bertalanffy growth curve because few females were aged greater than 20 years. For males, the adjusted growth curve was very similar to the von Bertalanffy growth curve over the full range of the latter, but extended well to the right of it because of the much greater adjusted ages. Mature females are relatively rare in the tuna longline catch (Francis *et al*. 2001; Ayers *et al*. 2004) and the big difference between the

Table 2. Results of radiocarbon analyses carried out on 11 porbeagle sharks

Three or four vertebral bands per shark were sampled and assayed for radiocarbon (mean standard deviation = 5‰). The estimated age of the shark, and the 'mean band age' of each band sampled were recorded by Reader 2 (0 represents the birth band, 1 is the first band outside the birth band, etc.), allowing the calculation of the year of growth. The adjusted age and adjusted year of growth are theoretical values required to align the measured Δ^{14}C levels with a reference chronology (see text for details). *FL*, Fork length

Specimen	Date	*FL* (cm)	Sex	Age	Adjusted age	Mean band age	δ^{13}C (‰)	Δ^{14}C (‰)	Year of growth	Adjusted year of growth
POS045	8 May 2002	179	M	35	39	0	–	–	1967.0	1963.0
						10	−14.4	17.8	1977.0	1973.0
						20	−14.0	43.3	1987.0	1983.0
POS060	15 June 2002	180	F	20	20	1	−14.1	33.4	1983.0	1983.0
						5	−13.6	47.9	1987.0	1987.0
						10.5	−14.6	38.7	1992.5	1992.5
						19.5	−14.4	24.7	2001.5	2001.5
POS062	17 June 2002	190	F	20	20	1	−13.9	47.6	1983.0	1983.0
						5	−13.5	54.7	1987.0	1987.0
						10.5	−14.8	33.7	1992.5	1992.5
						19.5	−13.8	34.2	2001.5	2001.5
POS085	7 June 2002	163	M	19	19	1	−14.1	49.1	1984.0	1984.0
						5	−13.5	43.6	1988.0	1988.0
						10.5	−13.6	23.8	1993.5	1993.5
POS087	8 June 2002	170	F	16	16	1	−14.3	49.8	1987.0	1987.0
						5	−13.6	42.0	1991.0	1991.0
						10.5	−14.3	15.2	1996.5	1996.5
POS165	18 April 2003	179	M	31	65	1	−13.5	−57.1	1973.0	1939.0
						10.5	−13.0	−57.7	1982.5	1948.5
						20	−13.4	−62.8	1992.0	1958.0
POS176	8 May 2003	179	M	29	57	1	−13.7	−58.2	1975.0	1947.0
						10.5	−14.0	−66.0	1984.5	1956.5
						20	−14.6	−29.8	1994.0	1966.0
POS193	20 June 2003	172	M	28	46	0	−14.5	−58.0	1975.0	1957.0
						5.5	−14.1	−42.8	1980.5	1962.5
						10.5	−14.6	−24.2	1985.5	1967.5
						20	−15.3	37.2	1995.0	1977.0
POS197	18 April 2003	200	M	38	55	0	−14.1	−48.4	1965.0	1948.0
						10.5	−13.0	−65.8	1975.5	1958.5
						20	−15.1	−22.3	1985.0	1968.0
POS199	18 April 2003	173	M	22	45	1	−14.3	−49.7	1982.0	1959.0
						5.5	−13.3	−35.3	1986.5	1963.5
						9.5	−13.2	−22.9	1990.5	1967.5
						20	−14.1	55.2	2001.0	1978.0
POS203	17 May 2003	185	M	32	65	0	−14.3	−74.4	1971.0	1938.0
						8.5	−13.4	−69.7	1979.5	1946.5
						20	−15.0	−80.5	1991.0	1958.0

two sexes in the age range of the adjusted curves is probably a result of unrepresentative female sampling.

Habitat and food

Porbeagles occur throughout New Zealand waters (Fig. 1), but there are regional variations in the size composition of sharks taken by the tuna longline fishery (Fig. 9). Juveniles smaller than 100 cm were rare in the south-east region, but they made up a significant proportion of the catch in the south-west region, and dominated the length distribution in the north region. Juveniles smaller than 100 cm probably comprise five year classes (see Fig. 5), so the observed distribution pattern is not simply due

to an influx of new-born recruits into the south-west and north regions. It therefore appears that juveniles shorter than 100 cm are more abundant north of the Subtropical Front (STF) than south of it.

For 13 071 observed tuna longline sets, the minimum estimated depth was usually 40–60 m (77% of sets) and the maximum depth was 80–180 m (77% of sets). Nearly all sets (99%) had estimated maximum depths of 200 m or less. We conclude that longlines fish the upper 200 m of the water column.

Of 3654 shark stomachs examined by observers on tuna longliners, 2426 (66.4%) were empty or contained only bait. Of the remaining 1228 sharks, most (1113 sharks) contained only fish
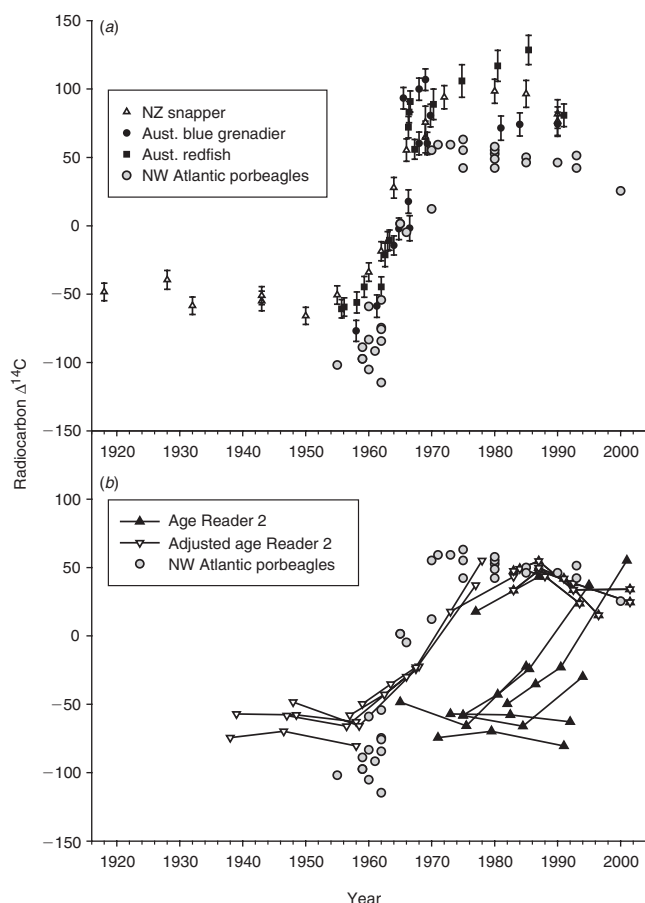
Fig. 6. (*a*) Reference radiocarbon chronologies derived from south-west Pacific Ocean teleosts (New Zealand snapper *Pagrus auratus* (Kalish 1993), Australian blue grenadier *Macruronus novaezelandiae* (Kalish *et al.* 1997) and Australian redfish *Centroberyx affinis* (Kalish 1995)) and north-west Atlantic Ocean porbeagle sharks (Campana *et al.* 2002*a*). Error bars are ±1 standard deviation. (*b*) Variation in radiocarbon concentration in New Zealand porbeagle shark vertebral growth bands relative to their year of formation (based on age estimates of Reader 2) (mean standard deviation = 5‰). Also shown are the same radiocarbon data plotted for adjusted ages, which are theoretical values required to align the measured radiocarbon levels with the north-west Atlantic porbeagle reference chronology (see text and Table 2 for details). Solid lines link radiocarbon measurements from different growth bands on the same shark.

or squid. There appeared to be a major ontogenetic change in diet among size classes (Fig. 10). The smallest size class (50–74 cm) ate mainly squid (mean volume ± s.e. = 70.5 ± 10.1%) followed by fish (24.2 ± 9.7%), whereas all larger size classes ate mainly fish (65.6 ± 1.4%) followed by squid (26.2 ± 0.8%). However, the sample size of small sharks was small (*n* = 19) and may have been unrepresentative of small porbeagles.

Of 364 prey items identified to species, 55.8% were dealfish (*Trachipterus trachypterus*), 24.5% were Ray's bream (*Brama* sp., probably *B. australis*), and 6.3% were hoki (*Macruronus novaezelandiae*). These three species are common in the by-catch of tuna longlines (Ayers *et al.* 2004) and some of the prey may have been scavenged from the longlines. Only two mesopelagic fishes were recorded – both were
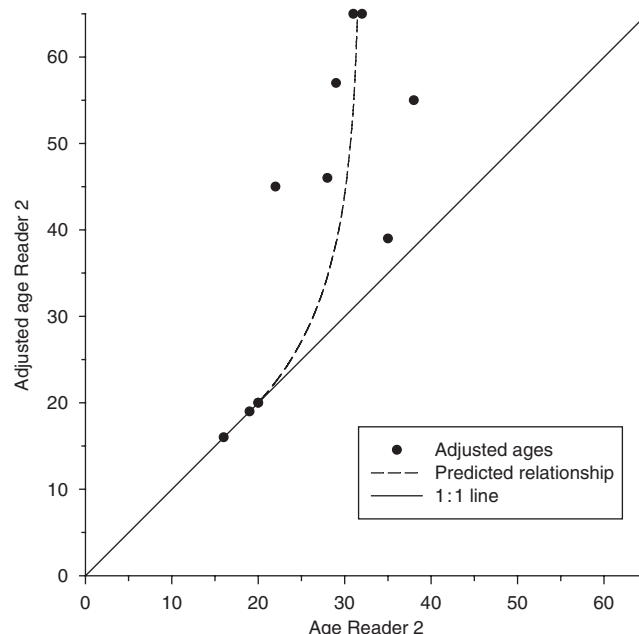

Fig. 7. Comparison of porbeagle shark age estimates of Reader 2 and their adjusted ages. The adjusted ages are theoretical values required to align the measured radiocarbon levels with the north-west Atlantic porbeagle reference chronology (see text and Table 2 for details). The three points lying on the diagonal 1 : 1 line represent four sharks (including two aged 20 years) whose ages were not adjusted. The dashed line is an asymptotic curve (Eqn (2)) fitted to sharks with estimated ages older than 20 years in order to predict adjusted ages.
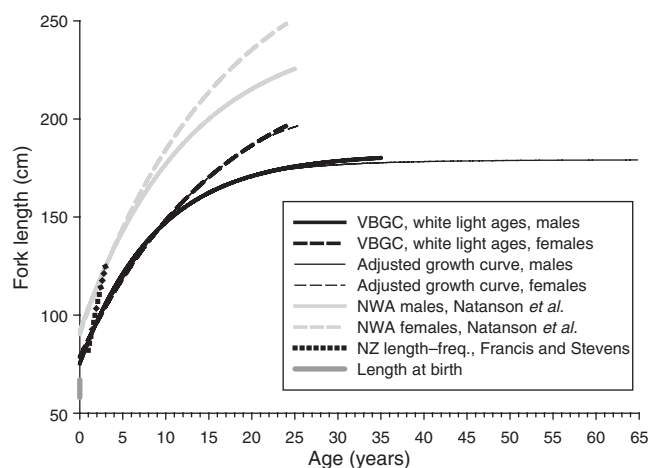

Fig. 8. Von Bertalanffy growth curves (VBGC) and adjusted growth curves (see text for details) for male and female porbeagle sharks from the present study. Also shown are growth curves for New Zealand porbeagles derived from length–frequency data (Francis and Stevens 2000) and north-west Atlantic Ocean porbeagles derived from vertebral bands (Natanson *et al.* 2002).

lighthouse fish (*Photichthys argenteus*), a species that is relatively common over seabed depths of 500–1200 m around central New Zealand. Other items recorded occasionally included unidentified octopus, salps and crustaceans.
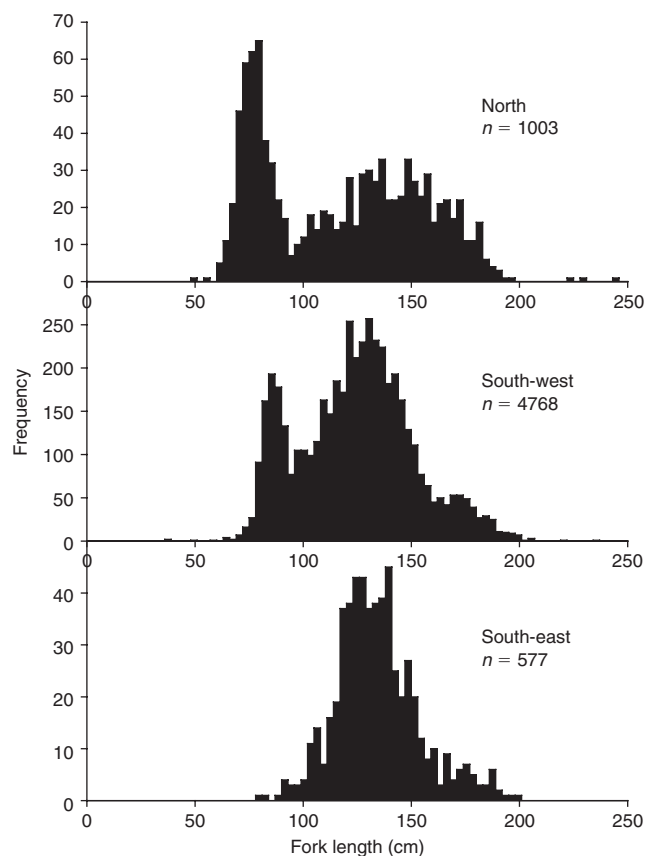
Fig. 9. Length–frequency distributions for porbeagle sharks measured by observers on tuna longline vessels in three subregions (see Fig. 1) during April–July 1993–2005.
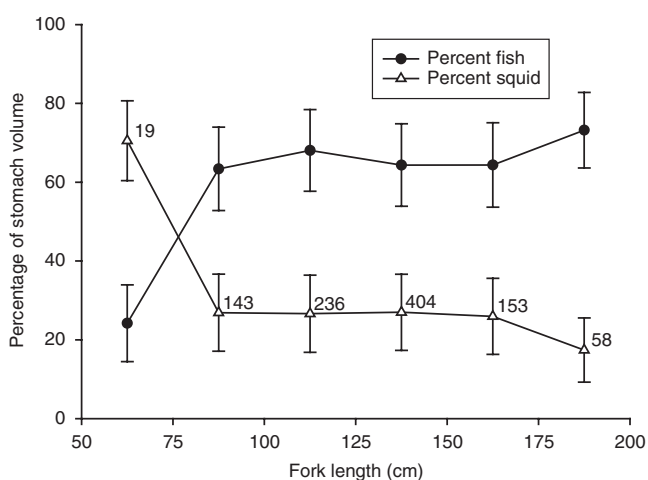
Fig. 10. Variation with fork length (25 cm length classes) in the volume of fish and squid in the stomachs of porbeagles (mean percentage ± s.e.). Sample sizes are shown above the squid data points. The right hand data point in each series includes four sharks longer than 200 cm.

Discussion

Bomb radiocarbon assays failed to validate the ages of New Zealand porbeagle sharks estimated from vertebral band

counts. The ages of the younger porbeagles were interpreted reasonably precisely by both readers, and those ages were consistent with the radiocarbon results; however, substantial discrepancies were apparent for sharks older than ~20 years. This was surprising, because the ageing method used in this study was previously validated for north-west Atlantic porbeagles, using a variety of methods including bomb radiocarbon, oxytetracycline injection and recaptures of known age animals (Campana *et al.* 2002*a*; Natanson *et al.* 2002).

Given that the carbon pathway in fish tissues is reasonably well understood (Schoeninger and DeNiro 1984; Hesslein *et al.* 1993), there are relatively few possible explanations for our observations: (1) the ages of the younger sharks were interpreted correctly, but those of the older sharks were under-estimated; (2) $\Delta^{14}C$ in the environment of New Zealand porbeagles does not show the abrupt increase around 1960 that has been observed elsewhere; and (3) the extent and timing of the uptake of $\Delta^{14}C$ varied dramatically among porbeagles, with some never having been exposed to high $\Delta^{14}C$ levels. Below, we explore these hypotheses in more detail.

Hypothesis 1: the ages of older porbeagles are under-estimated

Our age estimates appear to be valid for sharks up to ~20 years old. Evidence in support of this consists of: (1) radiocarbon levels in the first-formed vertebral bands that demonstrate that these individuals were born post-1970, and so the sharks must have been younger than 32 years (= capture date 2002 minus 1970); (2) similarity (albeit with individual variability) of white light age estimates by both readers, one of whom was experienced in ageing north-west Atlantic porbeagles using a validated technique; and (3) agreement (on average) between white light and X-radiograph age estimates by Reader 1.

Under this hypothesis, age estimates for older sharks were increasingly under-estimated. At the extreme, we may have under-estimated the ages of some sharks by ~50% (two sharks aged 31 and 32 years from vertebral band counts had radiocarbon-adjusted ages of 65 years) (Table 2, Fig. 7). Evidence for the age under-estimation hypothesis lies in the shapes of the within-shark radiocarbon chronologies, which are similar to the shape of surface marine bomb radiocarbon curves. If the vertebral growth increments were being misinterpreted consistently along the growth sequence, the slope of the increasing bomb signal would be flattened relative to the Atlantic porbeagle reference chronology. However, this was not evident, suggesting that the visible growth bands were formed annually, with no gaps, for the first 20 years of life. Rather, the whole bomb signal sequence appeared to be phase-shifted (delayed), which would occur if growth at the vertebral margin had ceased. In the absence of a precisely dated vertebral marker, there is no irrefutable indicator of a stoppage in growth. However, it is reasonable to expect that vertebral growth would slow appreciably before stopping altogether. Reduced vertebral growth was indeed observed in association with the apparently under-aged sharks, since the width of the outermost vertebral increment decreased in concert with the extent of age under-estimation.

In many shark species, plots of body length against vertebral radius are linear over most of their range. But in some sharks,

including north-west Atlantic porbeagles, there is clear non-linearity in the larger sharks (Natanson *et al*. 2002, 2006; Skomal and Natanson 2003), indicating that radial vertebral growth continues after somatic growth slows or ceases. This offers some hope that old, slow-growing sharks continue to record annual increments in their vertebrae. Our data on porbeagle centrum length showed no evidence of uncoupling of somatic growth and axial (anterio-posterior) vertebral growth, but this is not surprising as axial skeletal growth is presumably essential for there to be an increase in fork length. Also, *CL* may not be a good proxy for growth band deposition because *CL* is measured almost at right angles to the direction of band deposition. However, there is also evidence to the contrary, suggesting that vertebral band deposition may cease in some old sharks. For example, the school shark *Galeorhinus galeus* is known to live a minimum of ∼54 years in Australian waters (estimated from the maximum period at liberty of 41.75 years for a tagged shark plus its estimated age at tagging of 12 years) (Coutin 1992), yet the maximum age estimate from counts of stained bands on whole vertebrae was only 20 years (Moulton *et al*. 1992). Maximum ages estimated for the same species from X-radiographs of vertebral sections were higher (25 and 41 years from studies in New Zealand and Brazil respectively (Ferreira and Vooren 1991; Francis and Mulligan 1998)), but still well short of the tag-based estimate of longevity. Furthermore, radiocarbon levels in Australian school sharks were phase-shifted to the right in the same way as our porbeagle values were, suggesting significant age under-estimation in this species as well (Kalish and Johnston 2001).

Hypothesis 2: radiocarbon in the environment of New Zealand porbeagles did not increase abruptly around 1960

The depleted δ^{13}C levels in porbeagle vertebrae (mean approximately -14) indicated that the radiocarbon must have been metabolically derived from the prey, since the δ^{13}C of DIC is close to zero (Schwarcz *et al*. 1998). Given that the prey are the primary source of radiocarbon in porbeagle vertebrae, there are only two possible explanations for radiocarbon levels in the prey being depleted relative to that expected of DIC in surface marine waters: (1) porbeagles feed primarily on prey that came from water masses depleted in bomb radiocarbon. Although there are no direct measurements of radiocarbon in porbeagle prey around New Zealand, our dietary observations indicate that porbeagle feed primarily on short-lived species feeding in surface marine waters. Thus it is reasonable to expect that the radiocarbon content of the prey will reflect that of the DIC, and therefore this explanation is rejected; or (2) there has been a time lag in the increase of DIC bomb radiocarbon in New Zealand waters compared with that observed elsewhere in the world oceans, leading to delayed uptake of bomb radiocarbon by prey. This possibility is explored further below.

There is little direct evidence of the timing of the bomb radiocarbon increase in New Zealand waters, as few vertical or horizontal DIC radiocarbon sections are available. Nevertheless, the limited data indicate that there was significant Δ^{14}C enrichment of DIC to depths of 600 m or greater by at least the late 1980s (Lassey *et al*. 1990; Sparks *et al*. 1992; Sabine *et al*. 2002; Orsi and Whitworth 2005; World Ocean Circulation Experiment

2005). If data from the southern Indian Ocean (Kalish *et al*. 1997) are also applicable to the south-western Pacific, significant enhancement to considerable depths would have occurred no later than the late 1970s.

DIC Δ^{14}C levels are low in subantarctic waters south of New Zealand ($>54°$S) (Sabine *et al*. 2002; Orsi and Whitworth 2005; World Ocean Circulation Experiment 2005). If porbeagles consumed prey from farther south than ∼58°S and deeper than ∼150 m, they might encounter radiocarbon levels lower than 0‰, but they would probably not encounter pre-bomb levels at the surface no matter how far south they went. Porbeagles are known from at least 58°S in the central South Pacific, but their greatest abundance is further north (48–54°S in summer, further north in winter) (Yatsu 1995*a*). Thus it appears unlikely that the distribution of porbeagle resulted in exposure to pre-bomb radiocarbon levels.

Direct evidence of the timing of the bomb radiocarbon increase also comes from the reference chronologies based on Δ^{14}C in the cores of otoliths from three New Zealand and Australian teleosts (*Pagrus auratus*, *Centroberyx affinis* and *Macruronus novaezelandiae*) (Kalish 1993, 1995; Kalish *et al*. 1997). The first two species inhabit inshore waters shallower than ∼150 m as juveniles, whereas juvenile *M. novaezelandiae* inhabits depths of 100–400 m (Hurst *et al*. 2000). These chronologies provide strong evidence that surface Δ^{14}C levels in DIC in the New Zealand region increased in concert with radiocarbon levels elsewhere in the world. Thus it appears unlikely that Hypothesis 2 is valid.

Hypothesis 3: the extent and timing of the uptake of radiocarbon varied dramatically among porbeagles

This hypothesis arises directly from Hypothesis 2. It proposes that porbeagles vary in the extent to which they feed on prey originating from radiocarbon-enriched waters. Specifically, it invokes behavioural mechanisms, in terms of the depth range or spatial distribution of the prey consumed, to explain variations in radiocarbon levels among sharks. Behavioural differences among sharks would need to be dramatic for this hypothesis to be realistic; for example some porbeagles must never have encountered radiocarbon-enriched prey, some must have fed on enriched prey all of their lives, and some must have switched from depleted to enriched prey part-way through their lives.

In the north Atlantic Ocean, porbeagles feed mainly on fishes followed by lesser amounts of squid (Gauld 1989; Ellis and Shackley 1995; Joyce *et al*. 2002). At Kerguelen Island in the southern Indian Ocean, porbeagles take both squid and pelagic fishes (Cherel and Duhamel 2004). Pelagic fish prey predominated in our more qualitative New Zealand data, and in other reports from the South Pacific Ocean (Stevens *et al*. 1983; Yatsu 1995*b*). There was no evidence that New Zealand porbeagles eat significant amounts of vertically migrating prey. However, nearly all of the feeding data for South Pacific porbeagles come from sharks caught on surface longlines or in surface drift gill-nets, so the results may be biased towards prey occurring in surface oceanic waters.

Evidence in support of porbeagles feeding on prey that inhabit radiocarbon-enriched waters consists of: (1) predominance of juveniles shorter than 100 cm FL north of the STF and their

paucity south of the STF; (2) predominance of pelagic fishes and squid in the diet, and paucity of deepwater or vertically migrating species; (3) capture of large numbers of porbeagles as by-catch on tuna longlines that predominantly fish depths shallower than 200 m; (4) the presence of enriched radiocarbon levels across the entire vertebrae of sharks aged 16–20 years caught in 2002; (5) capture of substantial numbers of mature male porbeagles north of the STF (Ayers *et al*. 2004).

Yatsu (1995*a*) showed that mean porbeagle bodyweight in the South Pacific Ocean increased as sea surface temperature decreased. Catch per unit effort data were also suggestive of seasonal migration of porbeagle sharks (northward in winter and southward in summer), as has been shown for north-west Atlantic porbeagles (Campana and Joyce 2004). These results imply that larger sharks are able to penetrate further south and inhabit colder waters than smaller sharks, presumably because the former have a greater endothermic capacity. Such migrations would carry larger sharks south of the STF and possibly into subantarctic waters that are depleted in radiocarbon. Notwithstanding, it seems likely that these same sharks would have spent most or all of their juvenile stage north of the STF in waters shallower than 200 m, and therefore would have consumed prey species exposed to surface marine radiocarbon during the vertebral growth period analysed for radiocarbon. Consequently, this hypothesis is not consistent with our current understanding of the habitat and diet of porbeagles in the New Zealand region.

Assessment of hypotheses

Hypotheses 2 and 3 seem implausible. Although limited, the evidence on the timing and extent of penetration of atmospheric bomb radiocarbon suggest that DIC in the surface waters around New Zealand became enriched over a similar timeframe to that in other parts of the world. Enrichment had reached depths of 600 m or more by at least the late 1980s and probably earlier. Furthermore, a recent study in the Gulf of Alaska found Δ^{14}C levels in live corals collected at 720-m depth that were far greater than ambient Δ^{14}C, and comparable to surface levels (Roark *et al*. 2005). This suggests that penetration of bomb radiocarbon into deep water may be accelerated by settlement of particulate organic matter, thus potentially enriching the prey of porbeagles inhabiting depths well below those enriched by DIC Δ^{14}C. We cannot rule out the possibility of latitudinal migrations carrying porbeagles into or out of depleted subantarctic waters, but it appears that juveniles and adult males spend much of their lives north of the STF in waters that have been enriched since the 1960s. Although hypotheses 2 and 3 cannot be completely rejected with the available evidence, we believe it is highly unlikely that, even if applicable, these mechanisms could generate time lags in the uptake of Δ^{14}C of the magnitude observed, i.e. 34 years.

Hypothesis 1 appears the most plausible of the three hypotheses. It implies that the ages of the older porbeagles were under-estimated by as much as 50%, despite using the protocol that had been validated for north-west Atlantic porbeagles. A simple explanation for such age under-estimation is that the growth increments deposited in vertebrae become increasingly narrow as the growth of the porbeagle slows, eventually reaching a point where vertebral growth either stops or becomes

visually indistinguishable from neighbouring increments. This explanation is supported by the observation that the greatest age adjustments were required for vertebrae having the narrowest marginal growth increments, and the higher age estimates obtained from X-radiographs than white light. An apparently similar age under-estimation by 50% or more has been reported for Australian school shark (Kalish and Johnston 2001).

In a recent investigation of white sharks (*Carcharodon carcharias*) from the north-east Pacific, Kerr *et al*. (2006) found good correspondence between vertebral band age estimates and bomb radiocarbon levels for known-age (1–2 year old) sharks, but for older sharks, radiocarbon levels were depleted relative to levels expected from the age estimates. This depletion was not a result of age under-estimation because it was found in marginal growth bands of known deposition date. Kerr *et al*. attributed their findings to feeding by large white sharks on deepwater prey that contained depleted bomb radiocarbon levels. Their findings indicate that there may be various explanations for mismatches between measured and expected radiocarbon levels in shark vertebral bands, but this would not explain the apparently-delayed radiocarbon chronology in the age 1 porbeagle vertebral bands.

Annual band deposition has been 'validated', with varying degrees of confidence, in the vertebrae of many shark species (Cailliet and Goldman 2004). Thus annual band deposition is becoming regarded as a general phenomenon in sharks (with the exception of *Squatina californica*, or studies with little empirical support (Parker and Stott 1965)). However, bomb radiocarbon assays carried out on porbeagle sharks in this study, and on school sharks by Kalish and Johnston (2001), strongly suggest that the vertebrae of some old, long-lived shark species either deposit vanishingly-narrow increments, or cease to grow altogether, after a certain age. To our knowledge, these are the only two studies with sufficient information to investigate the periodicity of vertebral band formation in sharks older than 26 years. As such, it is possible that abbreviated vertebral growth is a common characteristic of sharks that have neared their maximum longevity or size. Either way, our conclusions underline the often-stated point that validation studies must encompass the full age range of a species (Beamish and McFarlane 1983; Campana 2001; Cailliet and Goldman 2004): validation of an ageing technique that encompasses only the younger ages does not constitute full validation.

Population growth differences

If the von Bertalanffy growth curves in Fig. 5 are reliable up to around 20 years of age, New Zealand porbeagles appear to grow more slowly than indicated by previous MULTIFAN analysis of length–frequency data (Fig. 8) (Francis and Stevens 2000). However, MULTIFAN analyses tend to be driven by modal progression of the first few age classes, and these age classes may have been represented only by larger individuals in our samples used for vertebral age estimation (because of size-selectivity of tuna longline hooks). Length–frequency data for another lamnid shark, the shortfin mako, indicated that first-year growth is very rapid, and that vertebral growth studies based on samples from size-selective fisheries failed to detect this, and the subsequent slowing of growth (Pratt and Casey 1983; Bishop *et al*. 2006; Natanson *et al*. 2006). A good sign of this bias in vertebral growth

curves is that they cross the *y*-axis well above the known length at birth. Bishop *et al.* (2006) converted length–frequency data for 0+ shortfin makos to length-at-age, and included them in a growth curve otherwise based on vertebral ages; they then used a Schnute generalised growth function to successfully model the growth trajectory. Such an approach might also be fruitful for New Zealand porbeagles, and explain the apparent discrepancy between MULTIFAN- and vertebra-based growth curves.

Comparison of our vertebra-based curves with similar curves for north-west Atlantic porbeagles (Natanson *et al.* 2002) is difficult because the latter show poor agreement between the *y*-axis intercepts and the length at birth (which is similar in both hemispheres (Francis and Stevens 2000; Jensen *et al.* 2002)) (Fig. 8). But it appears that New Zealand and north-west Atlantic porbeagles may grow at similar rates up to an age of about four years, after which New Zealand porbeagles grow noticeably slower. Furthermore, north-west Atlantic porbeagles grow much larger than their southern hemisphere counterparts. Although maximum lengths are difficult to determine, sharks longer than 200 cm are common in the North Atlantic (Gauld 1989; Campana *et al.* 2001), whereas around New Zealand and Australia they are very rare (Stevens and Wayte 1999; Francis *et al.* 2001; Ayers *et al.* 2004).

Differences in the length at sexual maturity also exist between hemispheres. Median lengths at maturity for New Zealand porbeagles are 140–150 cm for males and 170–180 cm for females (Francis and Duffy 2005), compared with 166 cm and 208 cm respectively for north-west Atlantic porbeagles (Jensen *et al.* 2002). Based on these lengths at maturity, and the von Bertalanffy growth curves in Fig. 5, the estimated ages at maturity for New Zealand porbeagles are 8–11 years for males and 15–18 years for females. By comparison, north-west Atlantic porbeagles mature slightly younger at ~8 and 13 years for males and females respectively (Jensen *et al.* 2002).

The longevity of New Zealand porbeagles is uncertain. For males, the greatest white light age estimate was 35 years, and the greatest X-radiograph age estimate was 38 years. Few large females were available for analysis, but the oldest X-radiograph age of 32 years approached that for males. When age estimates were adjusted for the observed bomb radiocarbon lag, a longevity of ~65 years was indicated. The oldest porbeagle aged in the north-west Atlantic was 26 years (Natanson *et al.* 2002), but that may also under-estimate longevity because the long history of heavy fishing of that population may have removed a high proportion of old sharks.

Thus porbeagle populations in the North Atlantic and around New Zealand differ substantially in their biological characteristics: New Zealand porbeagles reach a smaller maximum size, mature at a smaller size and greater age, and probably live considerably longer than northern porbeagles.

Acknowledgements

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