Preliminary age estimation of New Zealand white shark (Carcharodon carcharias)

Prepared for Department of Conservation

August 2022

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Revision	Description	Date
Version 1.0		03/08/2022

Quality Assurance Statement		
signature	Reviewed by:	Darren Stevens
signature	Formatting checked by:	Jess Moffat
signature	Approved for release by:	Richard O'Driscoll

Finucci, B., Ó Maolagáin, C. (2022). Preliminary age estimation of New Zealand white shark (*Carcharodon carcharias*). NIWA Client Report 2022230WN. 50 p.

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Executive summary

White shark (*Carcharodon carchariasI,* Māori: mangō-taniwha, ururoa, and tuatini) is a wide-ranging coastal and pelagic shark, occurring throughout most of New Zealand's waters, from the Kermadec Islands to Campbell Island/Motu Ihupuku and the northern Macquarie Ridge. White sharks are susceptible to population reduction because of their low productivity and naturally low population size. Understanding age and growth is vital for the conservation and management of white sharks and can be used to estimate population growth rates and other important demographic parameters, and to inform developing technologies such as close-kin mark recapture.

Here, vertebral banding patterns and microCT imaging were used to estimate age and growth for New Zealand white sharks for the first time. Vertebrae were obtained from white sharks reported dead from sources including commercial and recreational fishing vessels, and beach cast specimens over a 30-year period (1991 to 2021). Most white shark samples were collected around the North Island and were sampled throughout the year. The final sample (n = 38) included 20 females (1.52 to 5.36 m total length, TL), 12 males (1.87 to 4.85 m TL), and six unsexed sharks (2.26 to 3.0 m TL).

Vertebrae were difficult to read, particularly when counting the narrow increments near the margin of the vertebrae from old sharks. There was strong agreement between readers for age estimates of young New Zealand white sharks, but large disagreement for older sharks. Growth was modelled for both readers separately. Nearly half of the individuals were young (1–2 years old) and only six sharks were estimated to be older than 10 years of age. One shark (1.53 m TL) had no fully formed growth bands or distinct birth band, and was likely captured shortly after birth. Maximum age estimates from the band counts for Reader 1 and Reader 2, respectively, were 30 and 45 years for males (4.85 m TL) and 19 and 44 years for females (5.36 m TL).

The preliminary work here suggests New Zealand white sharks are relatively fast growing initially, and possibly long-lived. The relationship between length and growth was found to be nearly linear for young New Zealand white sharks. White sharks are born at approximately 1.5 m TL during the summer months (January, February) and deposition of opaque banding likely occurs in the winter months (May to August). White sharks were estimated to double their birth length to 3 m TL within five years, equating to an annual growth rate of approximately 30 cm per year. This rate of growth is similar to estimates from previous studies from Australia, South Africa, and California. Growth appeared to slow at approximately 3 m in length, which may be indicative of changes in diet, movement or habitat, or a reallocation of energy from somatic growth to reproductive development (i.e., maturity). Age-at-maturity could not be assessed here because of the small sample size, particularly for large individuals. However, based on known length-at-maturity estimates, age-at-maturity may occur at 7–10 years for males and 14+ to 22+ years for females. Additional samples of large sharks will be needed to comprehensively understand age and growth of white sharks that inhabit New Zealand waters.

Age estimates could not be validated and bomb radiocarbon dating is unlikely to provide any useful insight here because samples are unlikely to be old enough for this validation technique. New Zealand white sharks should continue to be sampled when accidentally captured, or when found dead (e.g., beach cast specimens) to increase the sample size, particularly for larger sharks. A combined New Zealand-Australia study should be carried out to characterise the life history parameters of the South Pacific white shark population.

1   Introduction

White shark (*Carcharodon carcharias*, Māori: mangō-taniwha, ururoa, and tuatini) is a wide-ranging coastal and pelagic shark, occurring throughout most temperate and tropical oceans. In New Zealand, white sharks are widespread, occurring from the Kermadec Islands in the north to Campbell Island/Motu Ihupuku and the northern Macquarie Ridge in the south (Roberts et al. 2015). They are reported from shallow coastal waters including estuaries and the open ocean, at depths from the surface to over 1200 m (Francis et al. 2012). Movement studies have shown that white sharks are highly migratory, with juveniles and adults moving from temperate New Zealand waters to subtropical and tropical waters of Australia, the Coral Sea, and southwestern Pacific Islands during the austral autumn, winter, and spring (Duffy et al. 2012).

White shark have been protected in New Zealand waters under Schedule 7A of the Wildlife Act since 2007, but the species continues to be caught as bycatch in commercial and recreational fisheries (Finucci et al., in review). Both juvenile and adult sharks are taken in set net, trawl, and demersal longline fisheries, with some reports of entanglements in commercial rock lobster and cod pot float lines (Ford et al. 2015; Ford et al. 2018). The effect of fishing on New Zealand's white shark population is unknown. However, the true rate of white shark interactions with fisheries is likely to be underestimated due to underreporting and low observer coverage, particularly in inshore fisheries (Francis 2017; Finucci et al., in review).

White sharks are susceptible to population reduction because of their low productivity and naturally low population size. The species is estimated to reach lengths of over 7 m total length (TL), with confirmed maximum size records of 5.5 m TL (males) and 6.4 m TL (females) (Rigby et al. 2019). Growth rates vary regionally, with males reaching maturity between 3.1–4.1 m TL and females generally reaching maturity between 4.0–5.0 m TL (Francis 1996; Pratt 1996; Tanaka et al. 2011). Reports of gravid white sharks are rare, but female white sharks are estimated to give birth to 2 to 17 pups every two to three years (Francis 1996; Domeier 2012). The only documented gravid female from New Zealand was a 5.36 m total length (TL) female with seven full-term embryos measuring 143 to 145 cm TL (Francis 1996). Genetic mark-recapture analyses of the eastern Australian-New Zealand population estimated the regional adult abundance to be between 280 and 650 individuals, with a total population size between 2500 and 6750 individuals (Hillary et al. 2018). The mean adult population trend is estimated to have remained stable since the early–mid 2000s (Bruce et al. 2018). The species is globally assessed as Vulnerable by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Rigby et al. 2019), and within New Zealand, it is classified as Nationally Endangered due to the estimated small population size (Duffy et al. 2018).

Knowledge of age and growth parameters is vital for the conservation and management of white sharks. This information can be used to estimate population growth rates and other important demographic parameters such as maximum age, age at maturity, and productivity (e.g., r_{max}, Pardo et al. (2016)). Age and growth parameters are also essential inputs for developing technologies. For example, the genetic mark-recapture analyses of the eastern Australian-New Zealand population used sex-specific parameters estimated from genetic identification of half-sibling pairs (Hillary et al. 2018). The detection of these pairs required knowledge of the year of sampling and age or estimated age (from length) at sampling. However, none of the New Zealand samples came from sharks of known age. Life history parameters for New Zealand white sharks are poorly defined due to their relative rarity and operational difficulties associated with sampling large individuals aboard

commercial fishing vessels. Thus, the aim of this study was to provide the first comprehensive estimates of age and growth for New Zealand white sharks.

2   Methods

Vertebrae were obtained from white sharks reported dead from sources including commercial and recreational fishing vessels (bottom setnet, longline, cray pot, bottom trawl, rod and line), and beach cast specimens from 1991 to 2021.

2.1   Vertebrae preparation

The location along the vertebrae column where vertebrae were sampled was not known for most samples. Given that sampling was consistently taken based on advice by two individuals (C.A.J. Duffy, Department of Conservation and M.P. Francis, NIWA), it was assumed samples were taken from beneath the first dorsal fin unless otherwise stated. Three duplicates were identified between NIWA and DOC-supplied samples and two individual sharks had additional cranial vertebrae samples. For consistency, these cranial samples were not included in further analysis.

Previously processed microscopy slides were available for three individuals collected in 1991 and 1996. These slides were in poor condition, but two were included here because they included some of the largest available samples (ururoa_40, 4.85 m TL, and ururoa_45, 5.36 m TL). The remaining slide included vertebra from one fully formed embryo (ururoa_39) but was not included in any analysis.

Vertebrae were trimmed of excess muscle and connective tissue, and then frozen. Genetic material was retained from each sample for future use and stored in ethanol. Biological details for most sharks were reported, including total length (TL), sex and for some, fork length (FL), weight, and maturity stage. Vertebral blocks were defrosted, individual vertebra were dissected, neural and haemal arches removed and trimmed of connective tissue and stored frozen until further processing.

The following measurements were taken from the largest visible vertebrae (post-defrosting, in mm): vertebral radius (VR, the midpoint of the notochordal remnant to the distal margin of the intermedialia along the same diagonal as the band pair measurements (Natanson et al. 2002), dorsal ventral length, medial-lateral length, and anterior-posterior length. The relationship between TL and VR was used to assess the allometric relationship between vertebral and body growth. This relationship has been shown to be linear for the shortfin mako and white sharks, with good correspondence ($R^2 = 0.98$) (Natanson & Skomal 2015). Regressions were fit to all data (combined-sex, including unsexed sharks), as well as the male and female data separately, and an Analysis of Covariance (ANCOVA) was used to test for statistically significant differences between the regressions of each sex.

A selection of individual vertebra from each sample were separated and briefly bleached in 42 g.l–1 sodium hypochlorite (for about 15 min), soaked in freshwater, air dried for 48 hrs, and glued to small wooden blocks with epoxy resin (Figure 1). The wooden blocks were then placed in a Secotom-60 saw's chuck for sectioning (Figure 1). Vertebrae were sectioned in the frontal plane(medio-laterally) by making two cuts with a single diamond-edged blade to produce sections ranging 0.6–0.9 mm thick, producing 'bowtie' sections (Wilson et al. 1987) (Figure 1). No grinding, polishing or staining was performed. This preparation technique is the same as that used in previous age and growth studies of New Zealand sharks (Bishop et al. 2006; Francis 2016). The half centra remaining after thin sectioning were further sectioned to reveal two faces for analysis.

A sub-sample of whole vertebrae were stained with a standard solution of alizarin red to trial improving visibility of external centrum face growth bands, after bleaching and drying.

Preliminary age estimation of New Zealand white shark *(Carcharodon carcharias)*
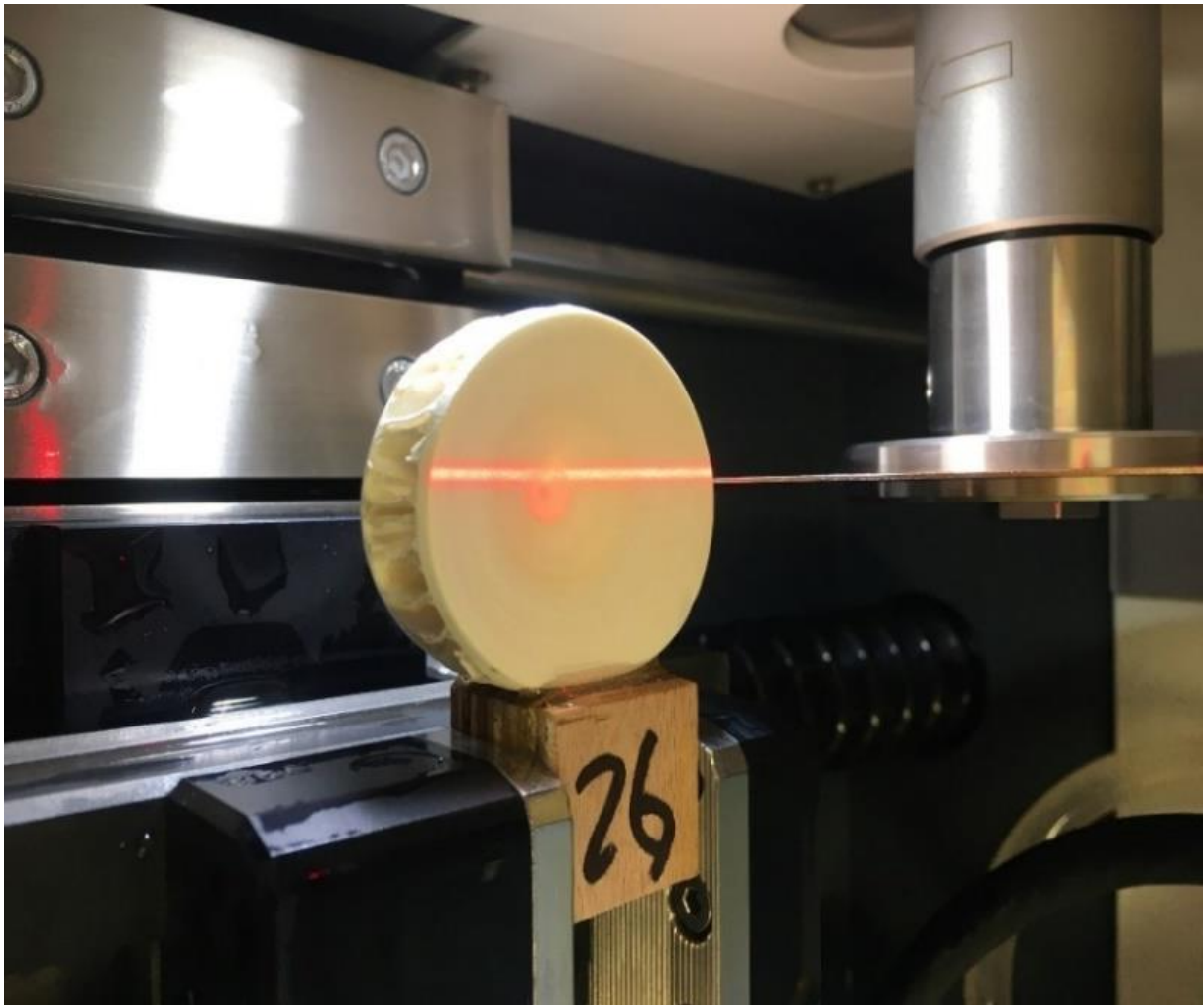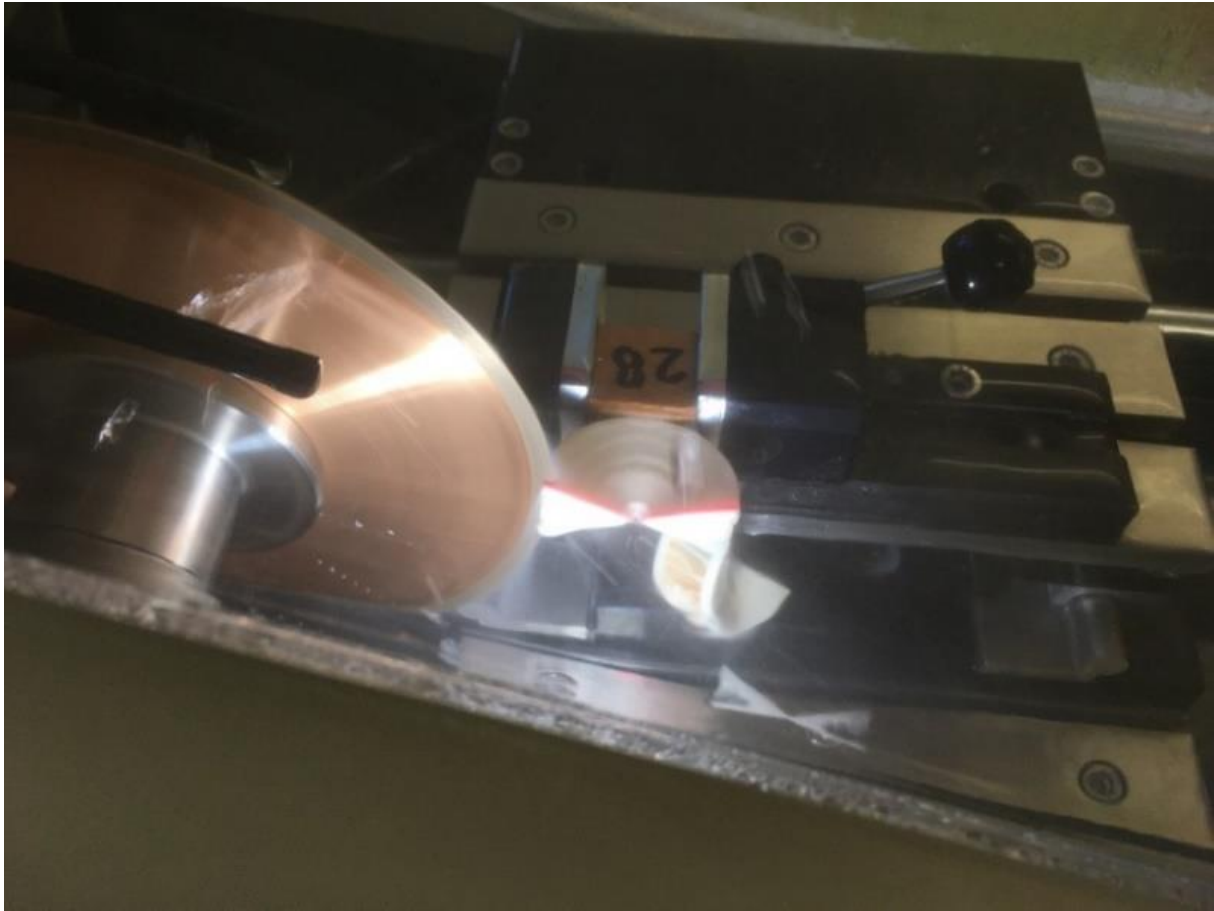
Figure 1: Cleaned vertebrae adhered to wooden stubs with epoxy resin (top panel); vertebra prior to sectioning showing laser guided sectioning transect (middle panel); classic "bowtie" sections being completed (bottom panel).

2.2   Vertebrae interpretation

Each thin section was digitally photographed at a variety of magnifications using both reflected and transmitted light under a Nikon SMZ25 stereomicroscope with attached DS-Ri2 camera (with a resolution of 4908x3264 pixels). Half centra and all thin sections were x-rayed onto Industrex M100 x-ray film using a Philips source operating at 50kV and 5mA. X-ray films were developed and fixed for standard times and resultant images were digitally captured using a Nikon stereomicroscope SMZ25 with attached DS-Ri2 camera (Figure 2).
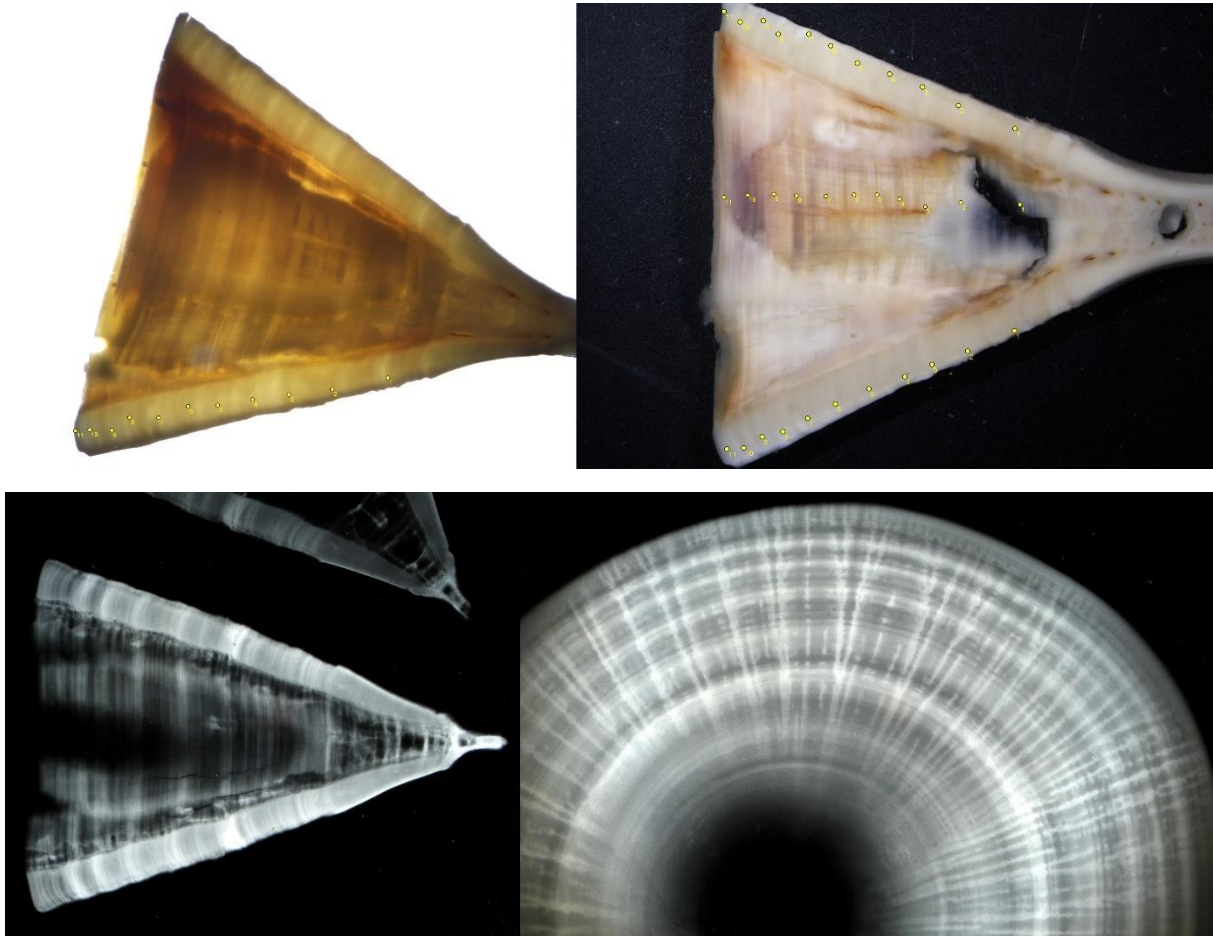
Figure 2: **Example of annotated thin section images under transmitted light (top left panel) and reflected light (top right panel), and an example of digitally captured images from x-rays for both thin section (bottom left panel) and the correlate whole centrum face (bottom right panel).**

Shark species often display a 'birth band', which is a prominent contrasting band in the centrum deposited about or soon after birth. Identification of this band is important to determine where subsequent band counts should begin. A slight angle change in the corpus calcareum (the highly calcified outer surface of the centrum, see Figure 3) coincided with this band. The birth band in white sharks was defined as the first prominent translucent (light under transmitted light) band (Figure 3). For white sharks, the appearance of the birth band has been estimated to occur at approximately 9.4 mm from the focus (Natanson et al. 2015). This measurement cue was used as a guide here, especially if the location of the birth band was uncertain in our preparations. The location of the birth band varies naturally among sharks (through variation in size or time of birth), and with the position along the vertebral column from which vertebrae were collected (vertebral size varies with position, Bishop et al. 2006), but a range between 9.2 and 9.8 mm was expected.

Growth bands were defined as a band pair consisting of one translucent and one opaque band as described by Cailliet & Goldman (2004) and assumed to signify one year of growth. Band pair counts were made of translucent bands beyond the birth band on high resolution photo-micrographs (Figure 3). Distinct bands usually traversed the corpus calcareum, while bands within the intermedialia were usually less distinct (see Figure 3). Indistinct bands could often not be traced across both structures, but the full width of the section was examined where possible. In larger sharks, band pairs (one translucent and one opaque band) near the margin became much narrower and difficult to resolve. Increased magnification and adjustment of lighting angle was sometimes necessary to visualise and count these finer bands. In porbeagle sharks, Francis et al. (2007) showed using radiocarbon dating that at least some of these narrow bands become unresolvable beyond an age of about 20 years, leading to substantial age underestimation of older sharks.

Reference ages were not available for this study. Two readers counted vertebral bands: Reader 1 (Alastair V. Harry, Fisheries Western Australia) and Reader 2 (Caoimhghin Ó Maolagáin, NIWA). Readers 1 and 2, experienced in reading shark vertebrae, carried out a single count of all sections. Reader 2 also counted bands from the whole vertebra. Counts were annotated on the captured images using ImageJ software (Abramoff et al. 2004).

No age estimates were removed from the final dataset, regardless of age consensus, due to the small sample size and poor condition of microscopy slides for the largest samples. Counts from Reader 1 and Reader 2 were included in the final analysis. Between-reader age-estimation bias and precision were explored with a frequency distribution of the age differences, an age-bias plot (Campana et al. 1995), and plots of the average percent error (APE) and the mean coefficient of variation (CV) (Campana et al. 1995; Campana et al. 2001). The precision for reading shark vertebrae in other studies was expected to be low, with CVs usually exceeding 10% (Campana 2001).
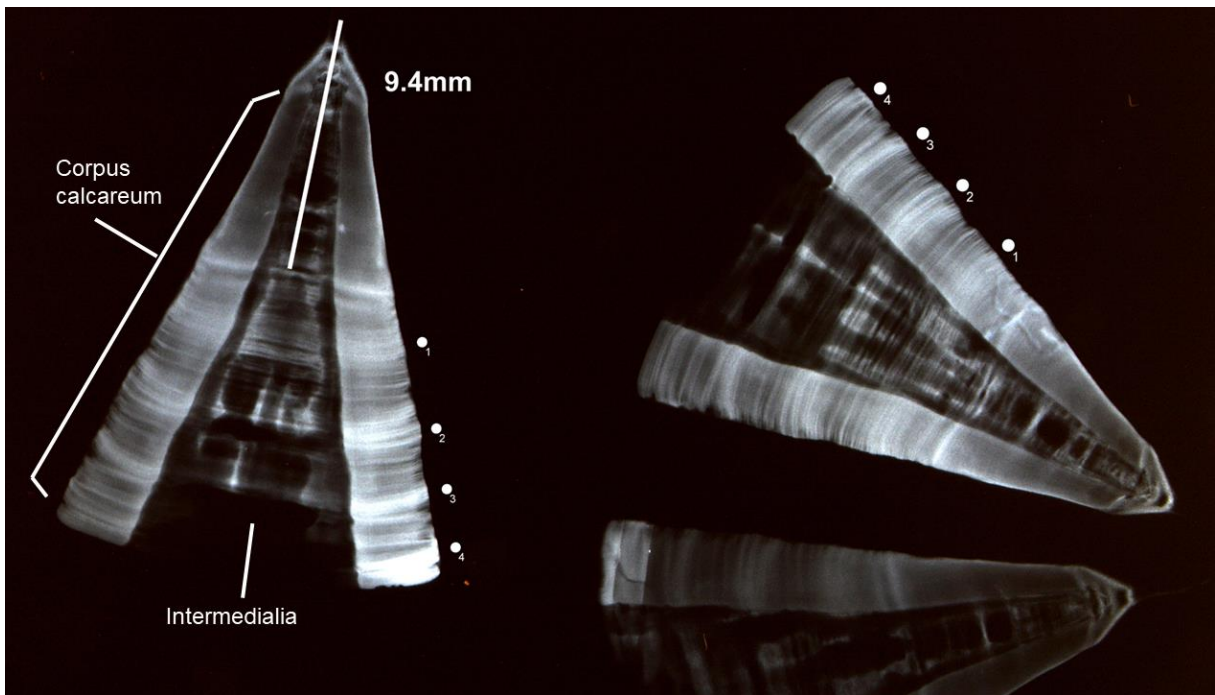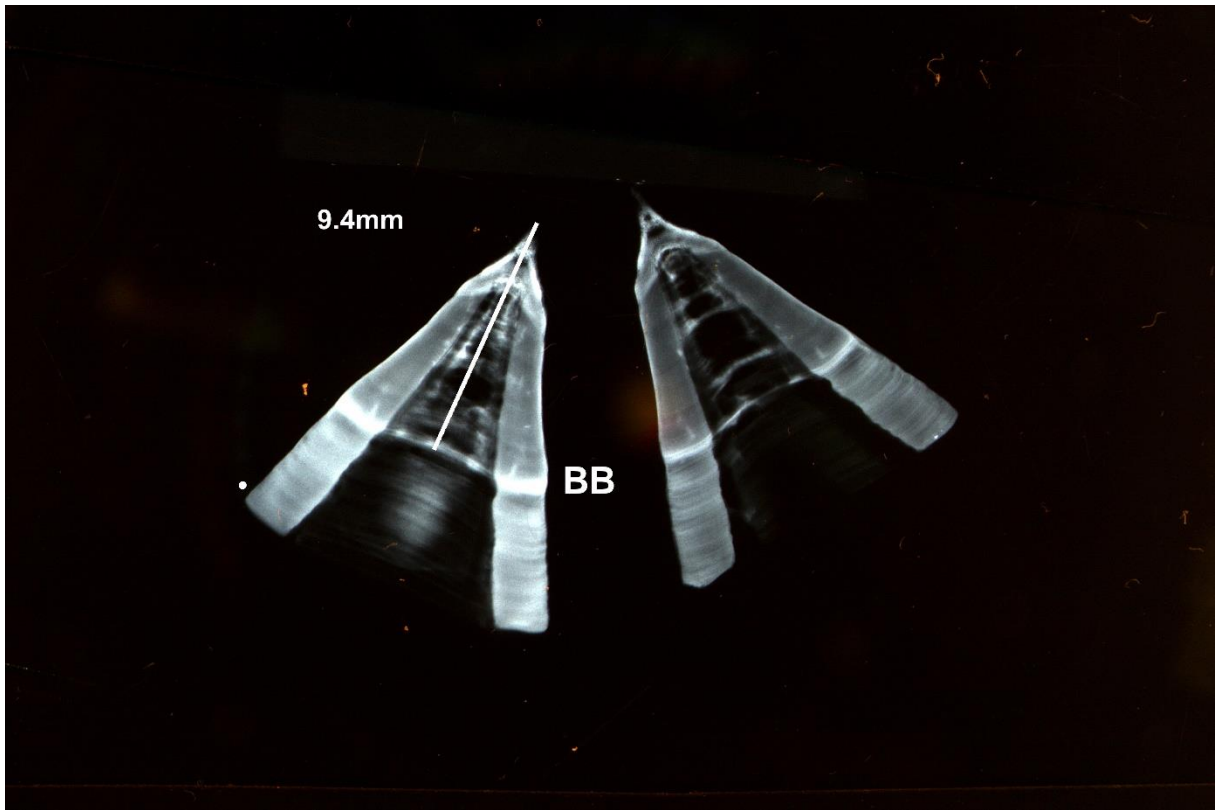
Figure 3: Thin section with a clearly defined birth band (BB) and reference length of 9.4 mm based on Natanson & Skomal (2015) (top panel) and annotated band pair counts beyond the birth band (bottom panel).

2.3　Estimation of growth

Growth curves were fitted to the length-at-age data using the R package *FSA* which fits non-linear curves using the R package *nlstools*. To make direct comparisons with other white shark growth analysis from the Pacific and Indian Oceans (e.g., O'Connor 2011, see Table 1), data were fitted with the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938).

The VGBF growth curves were compared with visual length observations of individual white sharks at Stewart Island that were resighted at least once between 2007 and 2014 (C.A.J Duffy, unpublished data). Shark age at initial sighting was determined using the outputs of each growth curve and the visual length estimation. Where more than one length estimate was available, an average length between the two observations was used.

2.4　Marginal increment ratios

Marginal increment ratios (MIRs) can be used as a validation technique to determine the periodicity of band formation (Cailliet et al. 2006). MIRs are calculated by comparing the widths of the ultimate and penultimate band pairs (Conrath et al. 2002). The mean values of these ratios are then generally plotted by month or season of capture. It is also recommended that MIR analysis should be restricted to individual age classes (Campana 2001), and individuals estimated to be age 0 should also not be included because they lack fully formed band pairs (Cailliet et al. 2006). A preliminary MIR analysis was conducted here and included all samples with fully formed band pairs, excluding ururoa_40 and ururoa_45 for the poor readability of the available slides. Ratios were plotted by month. Mean ratio values were not calculated due to small sample sizes.

2.5　Reference collection

The recommended size for a reference collection for a species of medium longevity is 500 vertebral sections, with 200 being randomly drawn for reading prior to ageing a new sample (Francis 2016). The present study aged only 39 white shark vertebral sections, so all sections have been placed in the reference collection, and the collection will be augmented by new sections following any future studies. The reference sections and band counts will be archived in the NIWA Age database. Genetic samples will be archived at the Auckland War Memorial Museum.

2.6　Micro-CT scans

Selected and cleaned whole vertebrae (one small, medium, and large vertebral sample) were imaged with micro-computed tomography (micro-CT) equipment. The two smaller vertebrae were imaged using a Skyscan 1172 machine at the Bioengineering Institute of the University of Auckland by Dane Gerneke. The larger specimen was examined using a large volume X-ray micro-CT system (Nikon XT H 225 ST) by Egon Perilli and Sophie Rapagna at Flinders University, Australia. Micro-CT uses X-ray technology to produce digital image slices through objects, which can be reconstructed into virtual, 3-dimensional images that can be rotated and viewed in any orientation (Geraghty et al. 2012). Micro-CT imaging has utility in revealing the structure of hard parts and the presence or absence of growth bands (Francis et al. 2018). The machine settings used for our study were optimised after initial viewing but gave eventual pixel resolutions ranging from 19 μm to 38 μm for the two machines, and dependent on whether downscaled data was used. Data files were post-processed with Bruker CTVox and Dataviewer software packages, with various 3D routines that provided both serial sections and video animations for further analysis.

2.7   Vertebrae interpretation with density profiles

To further assist in the interpretation of band formation, line scans to generate grey level density profiles were created using lines overlaid on x-ray images in ImageJ. This method was used on a subset of prepared vertebral thin section x-rays by creating a line profile down adjacent arms of the corpus calcareum in transverse view to produce a graph showing peaks where grey level intensity of the image signal (i.e., a proxy for ring or band density) was higher. Peaks observed in the graph were inferred to corelate to band patterns in the corpus calcareum and were compared with interpretations of thin sections from transmitted light images, as well as whole vertebral estimates.

3 Results

3.1 Sample size

The final ageing dataset included vertebrae of 38 individual white sharks (Appendix A). One sample (ururoa_15) was double labelled as both white shark and mako (*Isurus oxyrinchus*). To confirm species identification, a cytochrome oxidase I COI sequence was analysed. Both GenBank and BoLD confirmed the sample as a 100% match to *Carcharodon carcharias*, without any other near species matches. The reference COI sequence is reported in Appendix B.

Most white shark samples were collected around the North Island (Figure 4, Appendix A). White sharks were sampled during a 30-year period (1991–2021). Samples were taken in 21 of the 30 years, with no more than four samples reported from a single year (2005). Sharks were sampled throughout the year, in every month except April, and were sampled mostly in spring (September to November, 13 samples) and summer (December to February, 11 samples) (Figure 5). Depth of capture was recorded for 12 individuals, from the surface to 146 m depth.
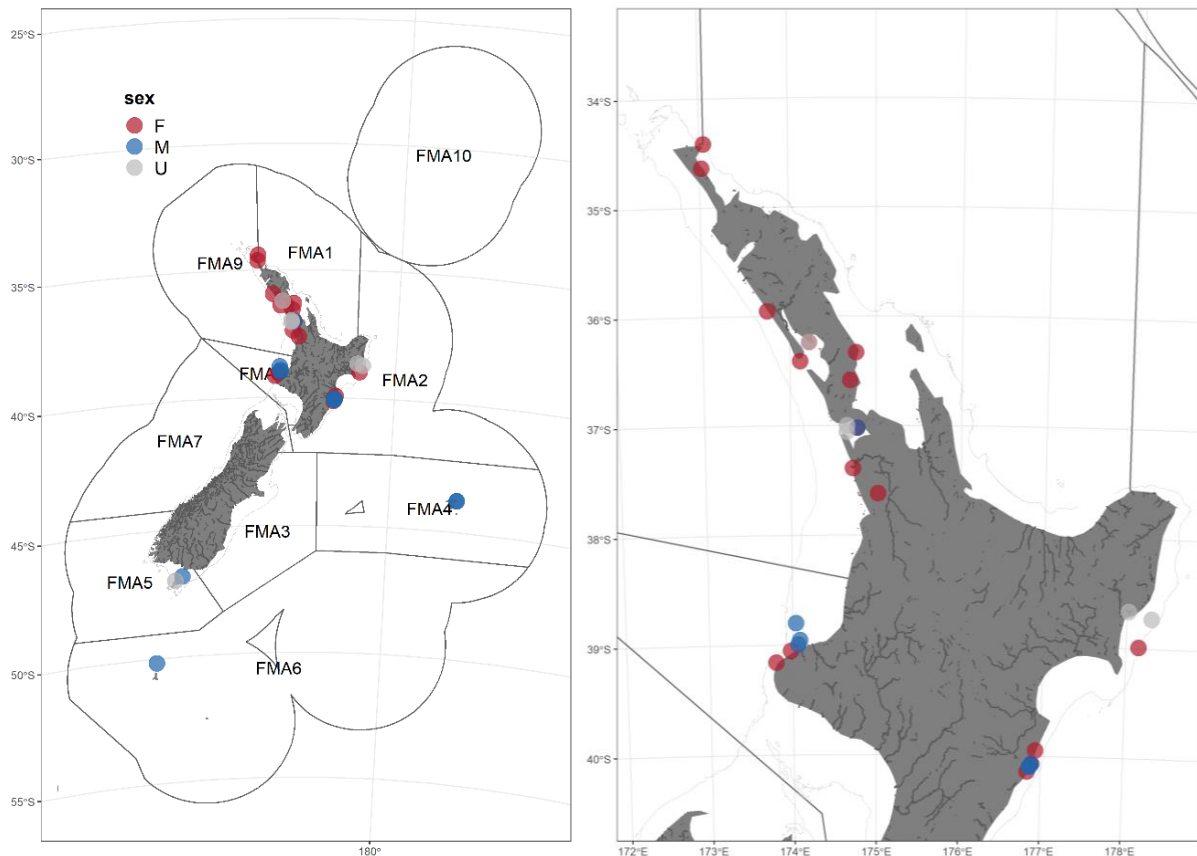
Figure 4: Location where white sharks were sampled by sex.

Our samples were from 20 female sharks ranging in lengths from 1.52 to 5.36 m TL (mean = 2.77 m TL), 12 male sharks ranging in lengths from 1.87 to 4.85 m TL (mean = 2.68 m TL), and six unsexed sharks ranging in lengths from 2.26 to 3.0 m TL (mean = 2.84 m TL, Figure 6). Weight was available for 13 individuals: seven females (24.9–265 kg) and six males (64–835 kg). Nearly all sharks were immature. Only three sharks were mature: one female (5.36 m TL) from North Cape and two males (3.60 m TL and 4.85 TL), one from Stewart Island (Bunker Islets) and one from the Chatham Islands.
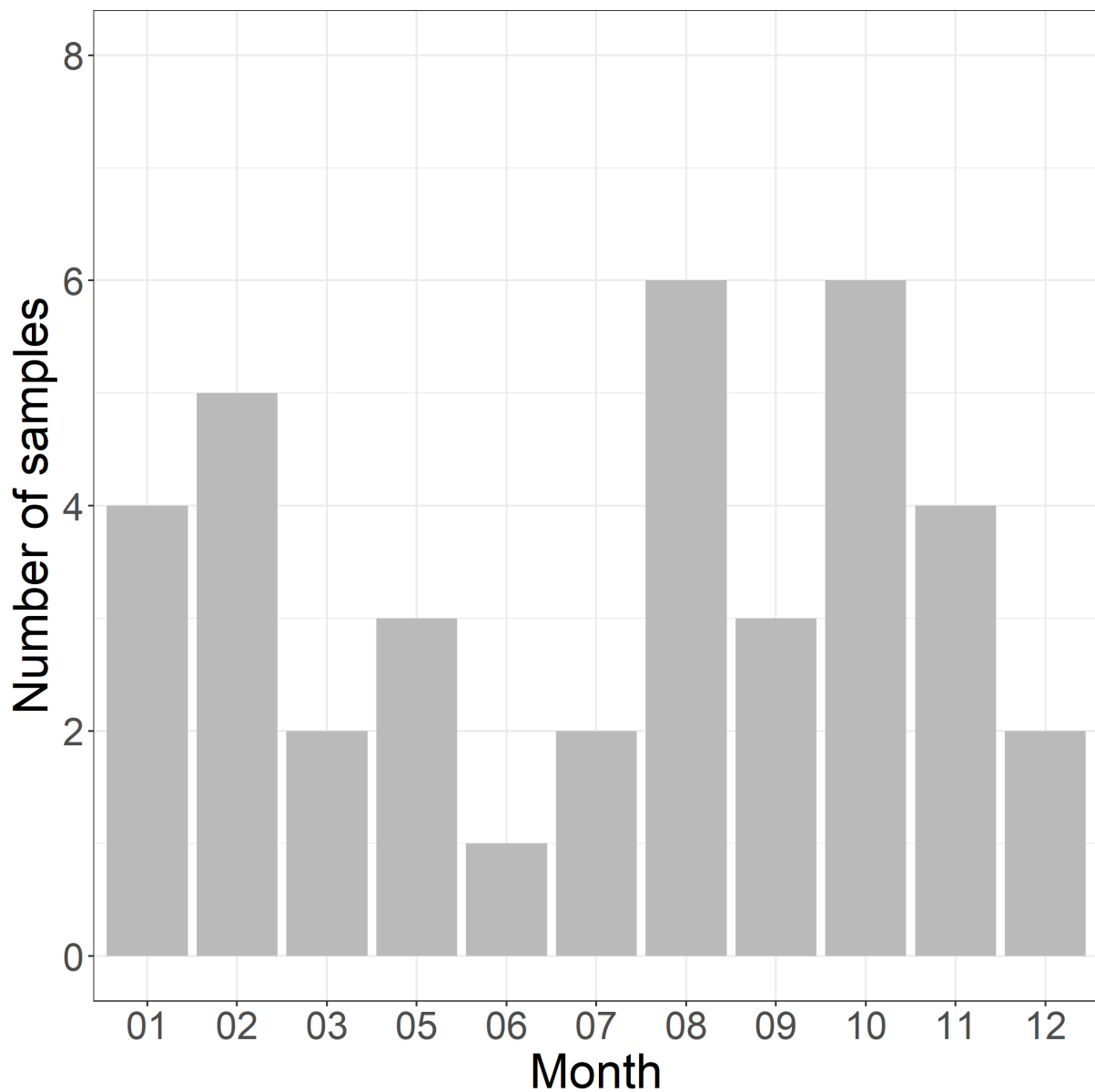
Figure 5:   **White shark sampling by calendar month.**
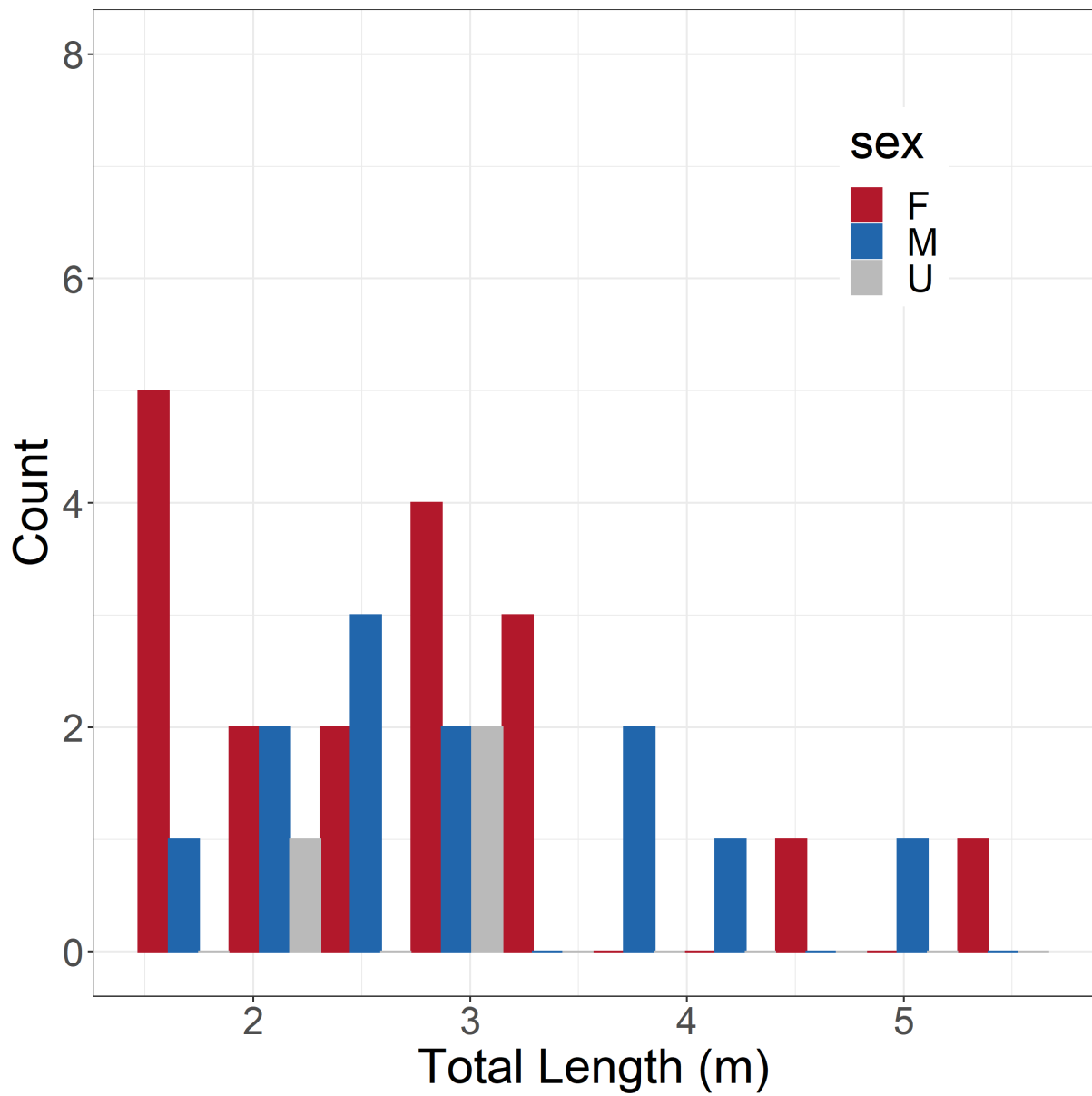
Figure 6: **Length frequency of sampled sharks by sex.** M= male; F= female; U = unsexed.

3.2 Relationship between total length and vertebral radius

The relationship between total length and vertebral radius is shown in Figure 7. This relationship was significant for males (n = 11, $R^2 = 0.976$, $p < 0.001$) and females (n = 17, $R^2 = 0.847$, $p < 0.001$), although there was no significant difference between the regressions ($F_{1,25} = 3.291$, $p = 0.081$). Thus, the data was combined to give the following regression based on 31 samples (11 males, 17 females, 3 samples of unknown sex):

$$TL = 8.093VR + 0.191 \ (R^2 = 0.85)$$

This regression was used to estimate the length for two female sharks and three unsexed sharks. The five samples with no known length data were estimated to range in length from 1.8 m to 4.6 m.
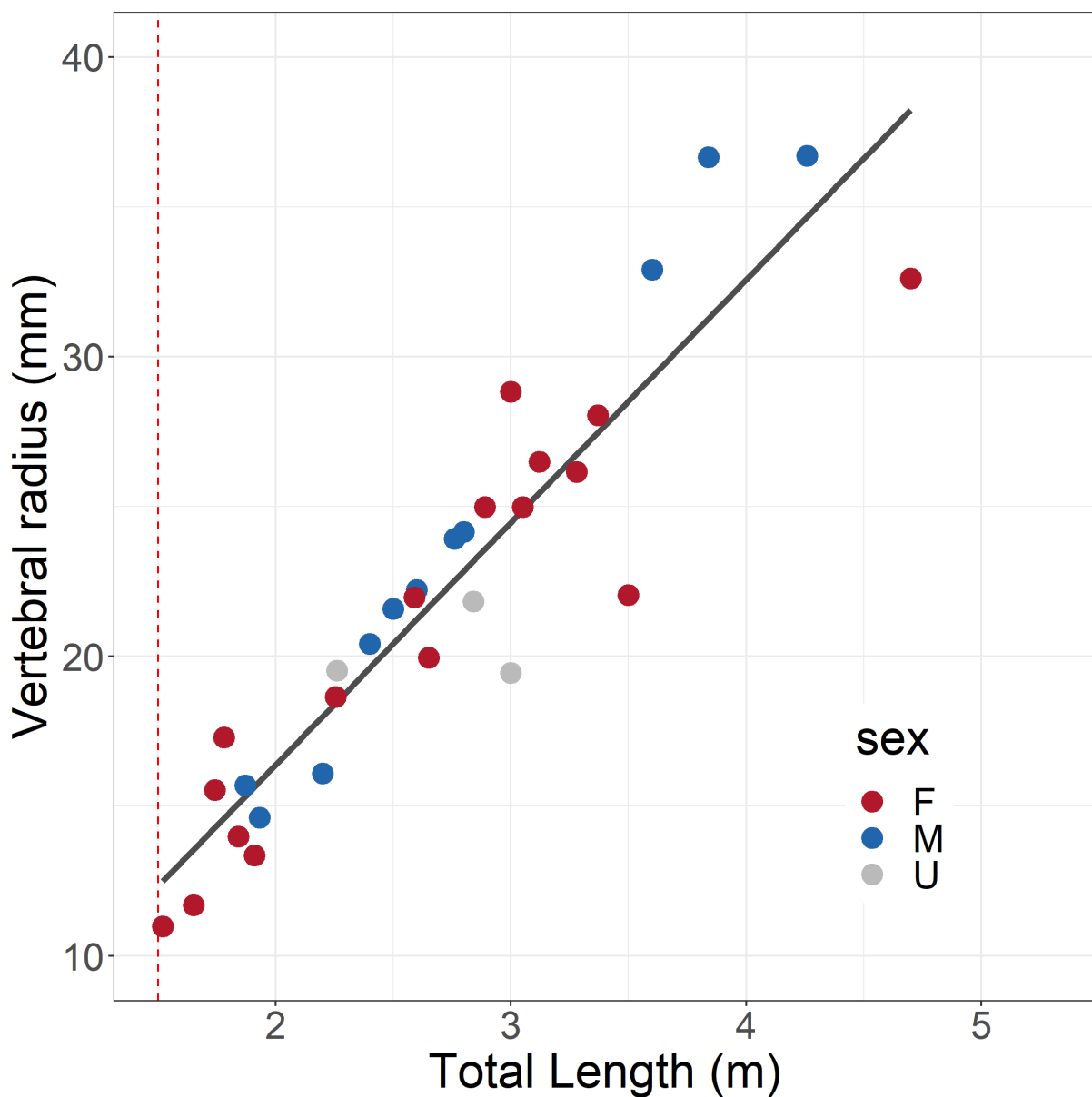
Figure 7: **Relationship between total length (m) and vertebral radius (mm).** Linear regression is shown for the combined-sex vertebral samples. Estimated size at birth (1.5 m, Francis (1996) indicated by the vertical dashed line.

3.3   Age readings

Vertebrae were difficult to read, particularly when counting the narrow increments near the margin of vertebrae from old sharks. Additional fine growth rings were present in most vertebrae and the distinction between these rings and bands was not always obvious. These finer growth increments may be associated with finer increments of time, such as lunar or monthly pattern (Brown & Gruber 1988). Readings were highly variable between readers, with an overall CV of 20.77% and APE of 14.69%, and absolute differences (Reader 1 minus Reader 2) ranging from −1 years to 25 years (mean 2.39) (Figure 8). Readings of 76% of the vertebrae agreed within ±2 years. Reader 1 showed a tendency to count more bands than Reader 2, but this was non-significant (paired t-test, $p > 0.05$) (Figure 8A, B). Age bias occurred in larger sharks, and the slope of the age-bias regression was significantly different from 1 (slope = 0.532, $p = 0.016$; Figure 8C).

Agreement (±2 years) for age estimates was improved to 91% when only considering sharks up to 10 years of age (age estimates defined by the more conservative reader, Reader 2, n = 32). Readings were similar between readers; there was some improvement with the overall CV (17.51%) and APE (12.38%), and absolute differences (Reader 1 minus Reader 2) ranging from −1 years to 4 years (mean 0.562). There was no agreement (±2 years) between readers for sharks greater than 10 years of age (n = 6).

Most (74%, n = 28) sharks were estimated to be under the age of 5 and a quarter (n = 10) of sampled sharks were estimated to be 1 year of age (Figure 9). One shark (ururoa_1, 1.53 m TL) had no fully formed growth bands or distinct birth band, and was likely a neonate (Figure 10). Maximum age estimates from the band counts for Reader 1 and Reader 2, respectively, were 30 and 45 years for males (4.85 m TL) and 19 and 44 years for females (5.36 m TL).
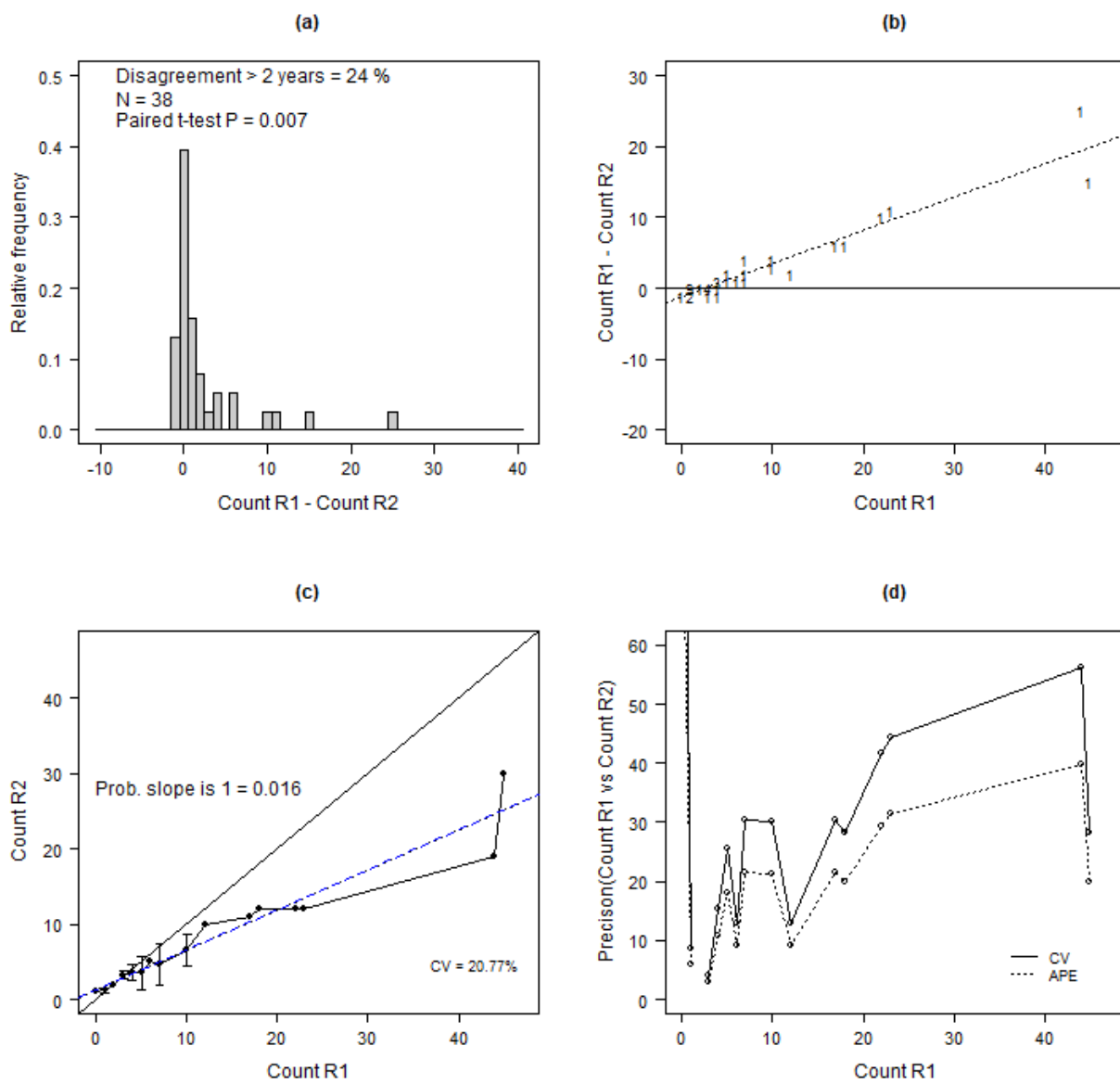
Figure 8: **Analysis of vertebral band count differences between Reader 1 and Reader 2.** Dotted and dashed lines are fitted linear regressions. CV, coefficient of variation; APE, average percentage error.
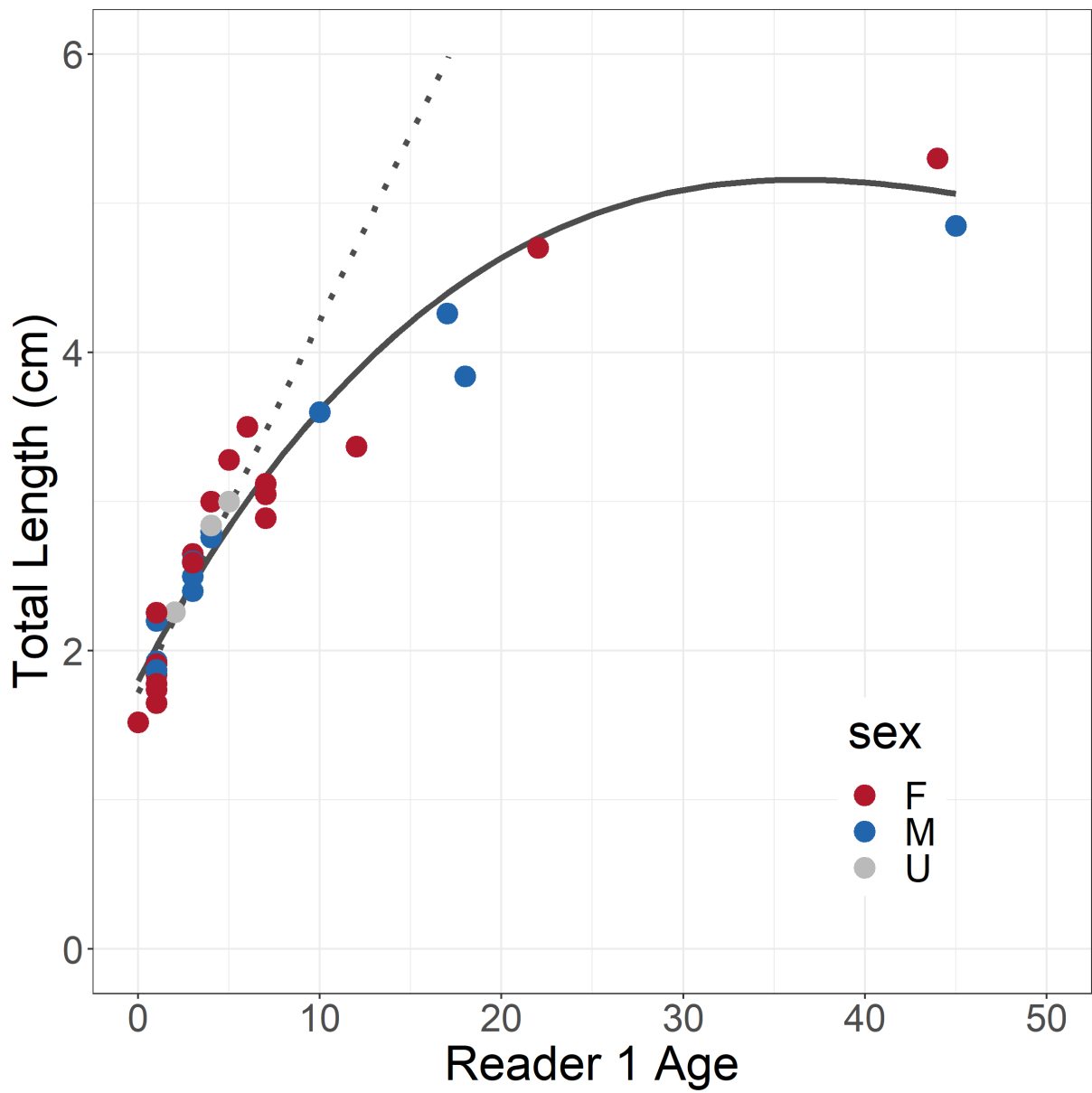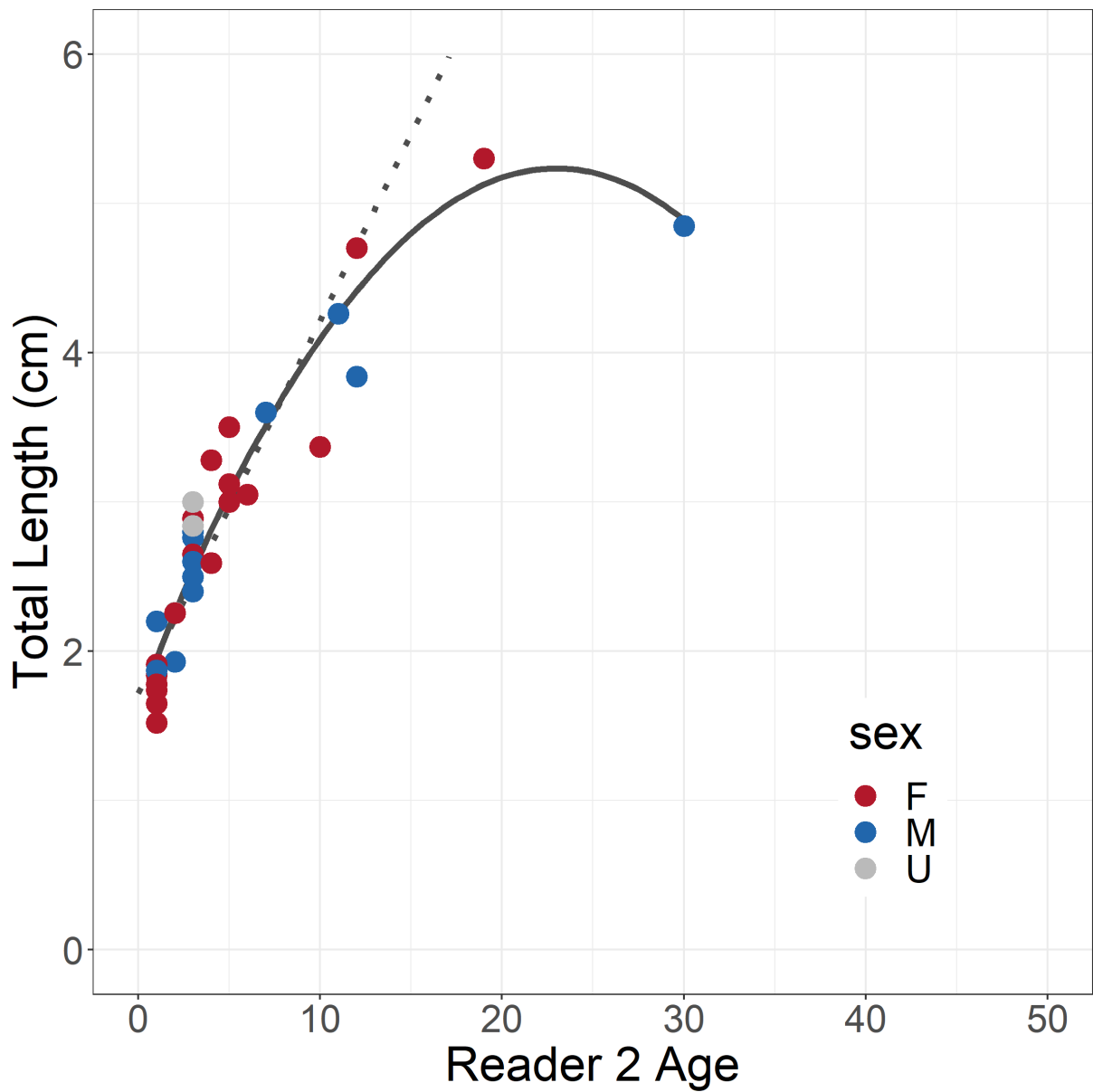
Figure 9:   **Age-at-length estimates for Reader 1 (top panel) and Reader 2 (bottom panel).**   Data were fitted with a moving regression (LOESS, solid line) and a linear model for sharks 5 years of age and younger (dashed line).
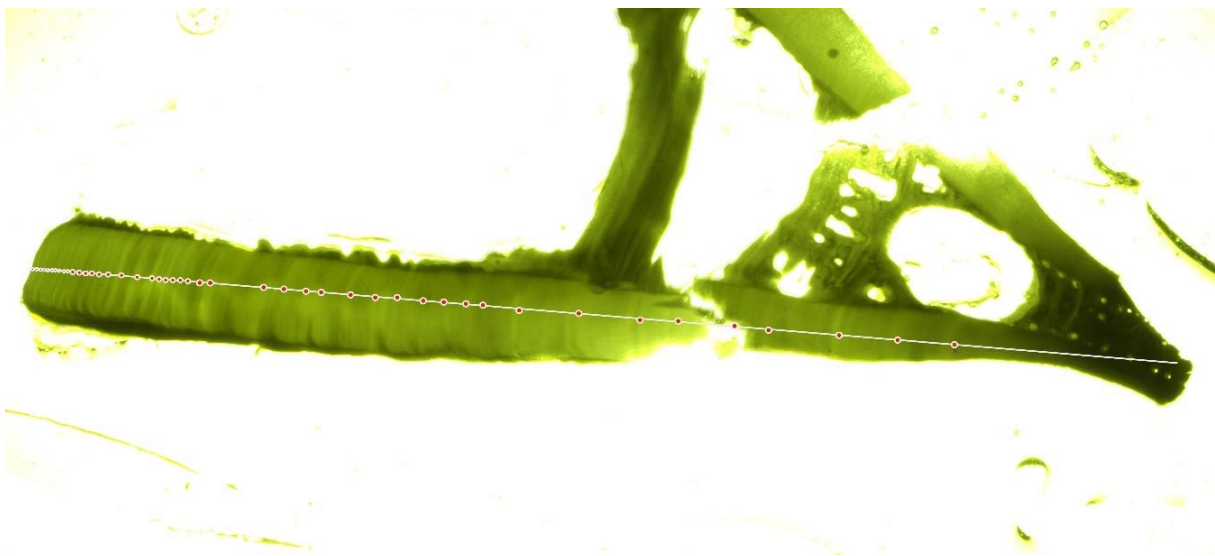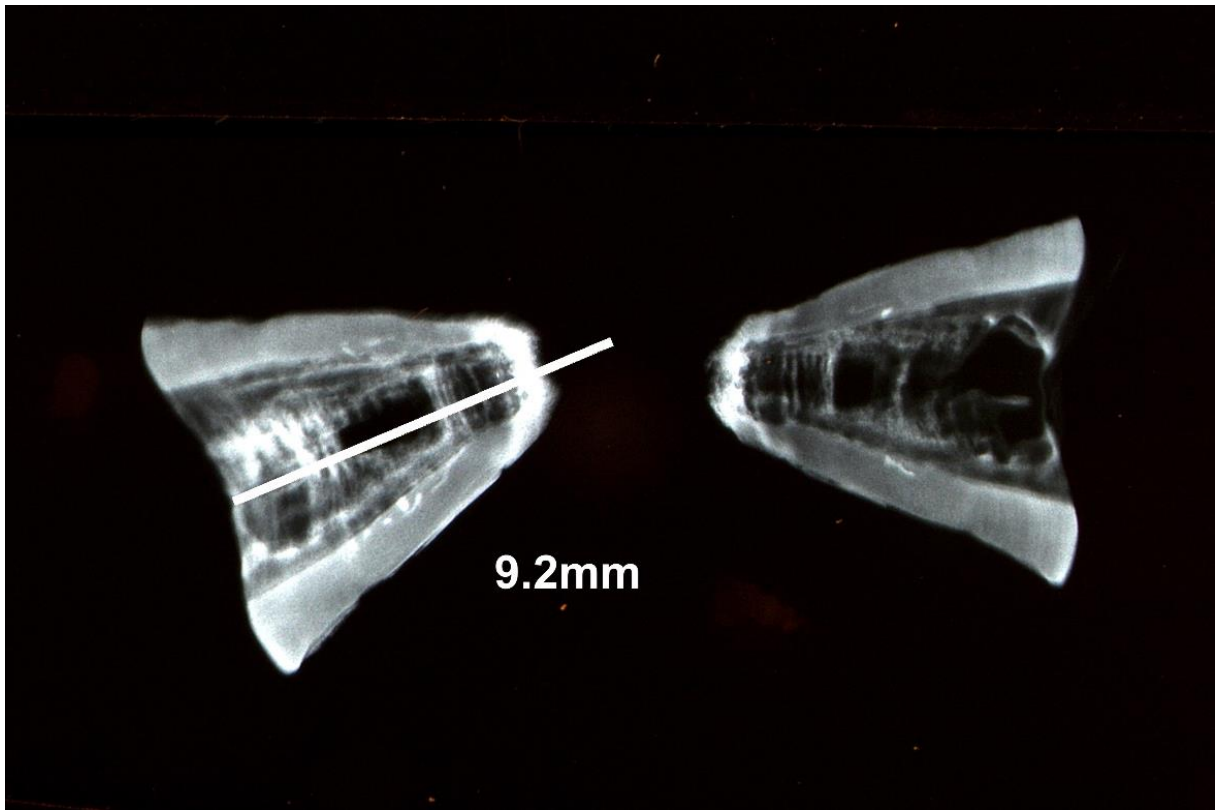
Figure 10: Thin section for vertebrae for ururoa_1 (top panel) and ururoa_45 with annotated counts by Reader 1 (bottom panel).

3.4 Growth analysis

VGBF growth curves were fitted to the combined-sex age estimates for Reader 1 and Reader 2 separately (Figure 11). VGBM model parameters for Reader 1 were L_∞ = 5.035 m TL, k = 0.083 year^{-1}, t_0 = -5.055 years, L_0 = 1.441 m TL and model parameters for Reader 2 were L_∞ = 5.141, k = 0.125 year^{-1}, t_0 = -2.635 years, and L_0 = 1.734 m TL (see Table 1). Assuming annual deposition of band pairs, white sharks showed fast growth during their first 23 years. For age estimates for both readers, growth appears to be almost linear in the first few years of age. For Reader 1, white sharks were estimated to reach 2.5 m by 3 years, 2.8 m by five years, and 3.6 m by 10 years. For Reader 2, white sharks were estimated reached 2.6 m by 3 years, 3.2 m by 5 years, and 4.08 m by 10 years. In either case, sharks nearly doubled their birth length of approximately 150 cm (Francis 1996) within five years. Growth appeared to slow by years 5–6.

The VGBF growth curves were compared with visual length observations of individual white sharks (n = 30) (Figure 12). Most (n = 21) sharks were resighted on one occasion, eight sharks were resighted twice, and one shark was resighted three times. The longest time period between resights was four years (n = 3). When compared to the VGBF growth curves, age estimates and projected growth of the resighted sharks appeared more similar to the growth curves from Reader 2 up to approximately 10 years of age. Sharks estimated to be between the ages of 10 and 20 years were more similar to the age estimates of Reader 1 (but did not correspond to the growth curve). The largest sharks (based on visual observation) and their estimated age and growth did not correspond to either growth curve.
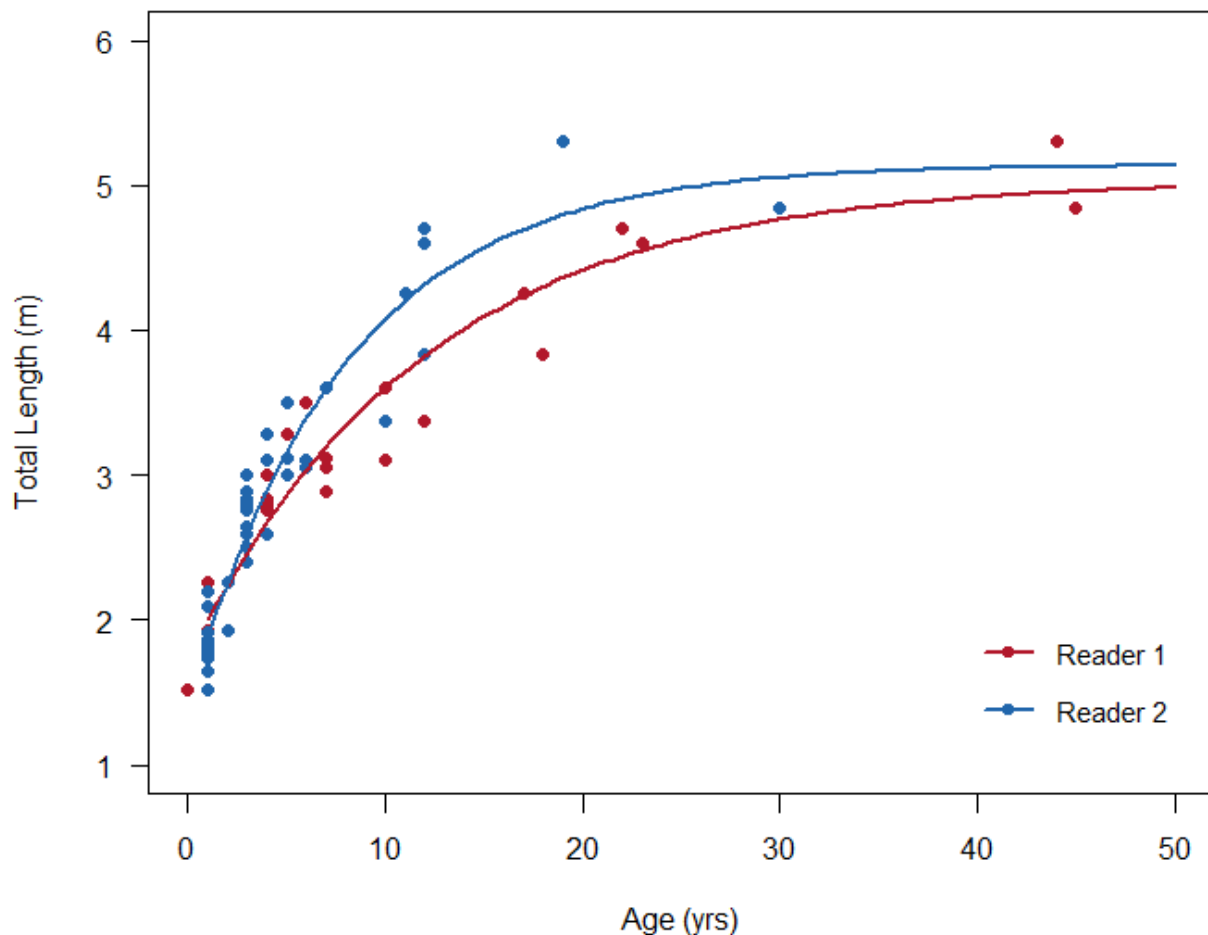
Figure 11: **VGBF curves for white sharks (combined-sex) based on the age estimates of Reader 1 and Reader 2.**
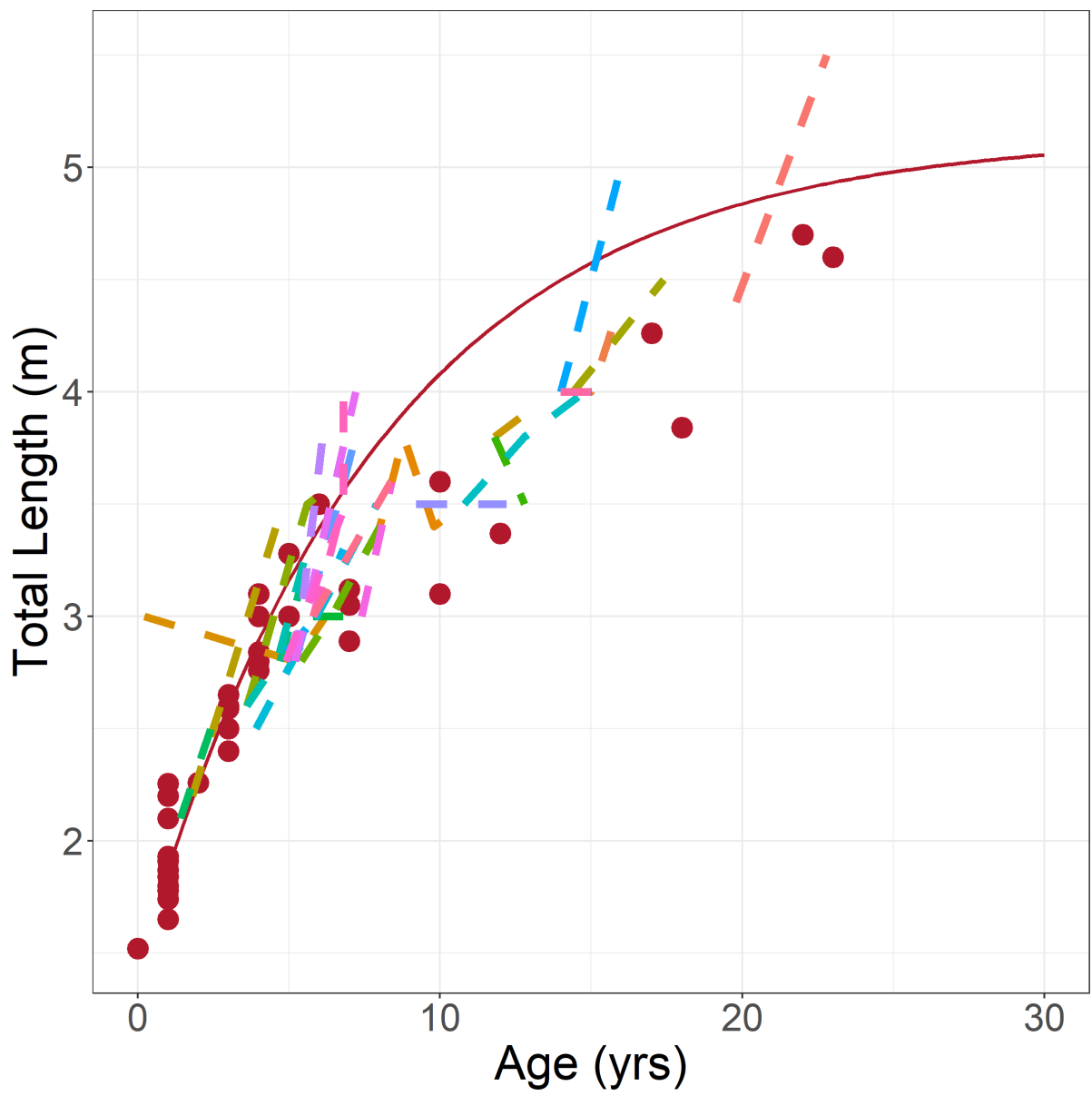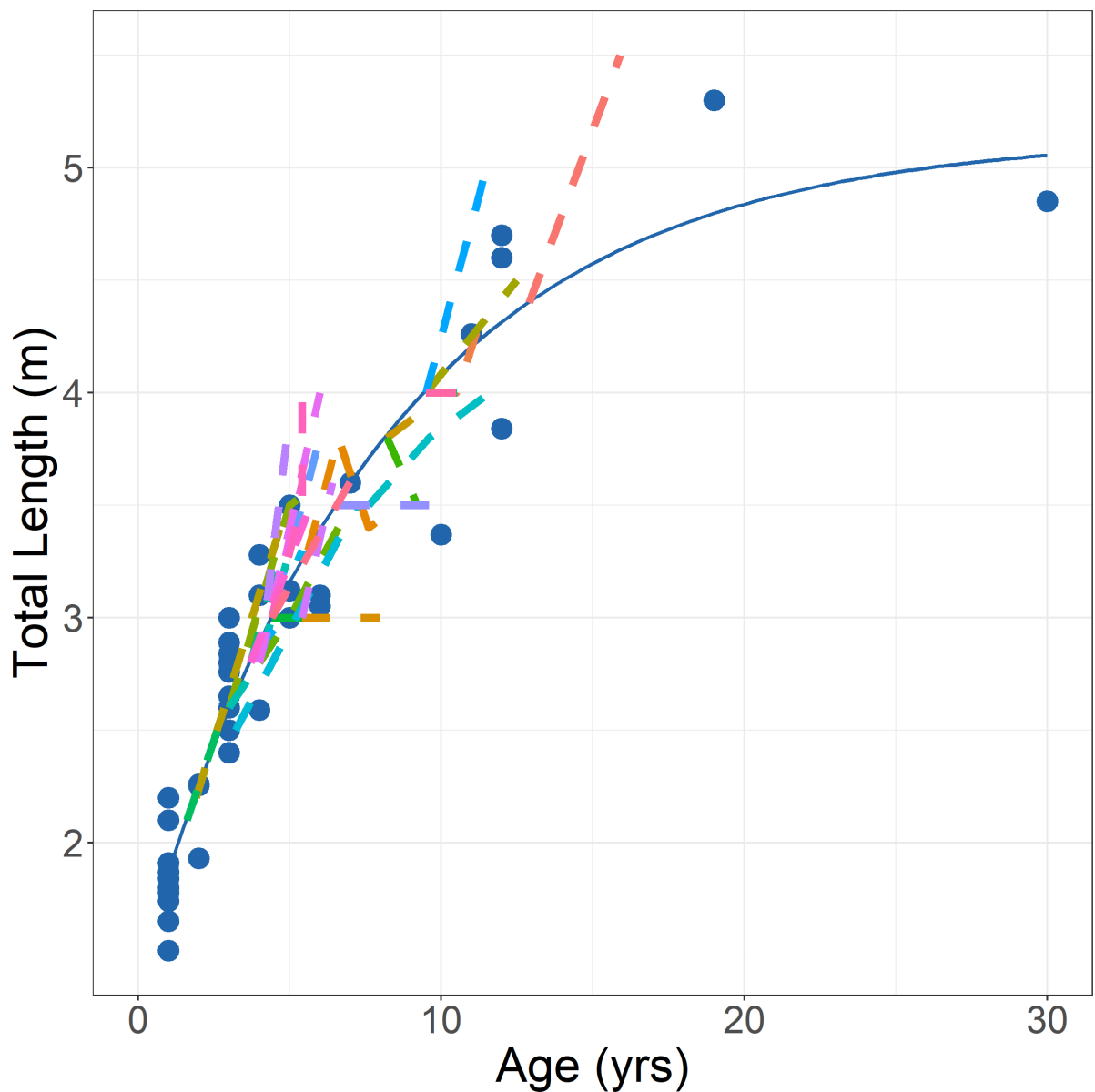
Figure 12: VGBF curves for white sharks (combined-sex, solid line) based on the age estimates of Reader 1 (top panel) and Reader 2 (bottom panel) overlayed with visual length observations of individual white sharks and their estimated age and projected growth based on the VGBF analysis for each reader (dashed lines). Each colour represents a unique white shark.

3.5   Marginal increment ratios

Marginal increment ratios were calculated for 30 of the sampled sharks. The MIR was highest in the summer months (December to February) and the trend indicated a general decline in growth formation leading into the austral autumn and winter months, and an increasing trend leading into spring (October onwards) (Figure 13). October showed the biggest spread in ratio measurements, which could be divided into young sharks (3–4 years old) with lower ratios and older sharks (6+ years) with higher ratios.
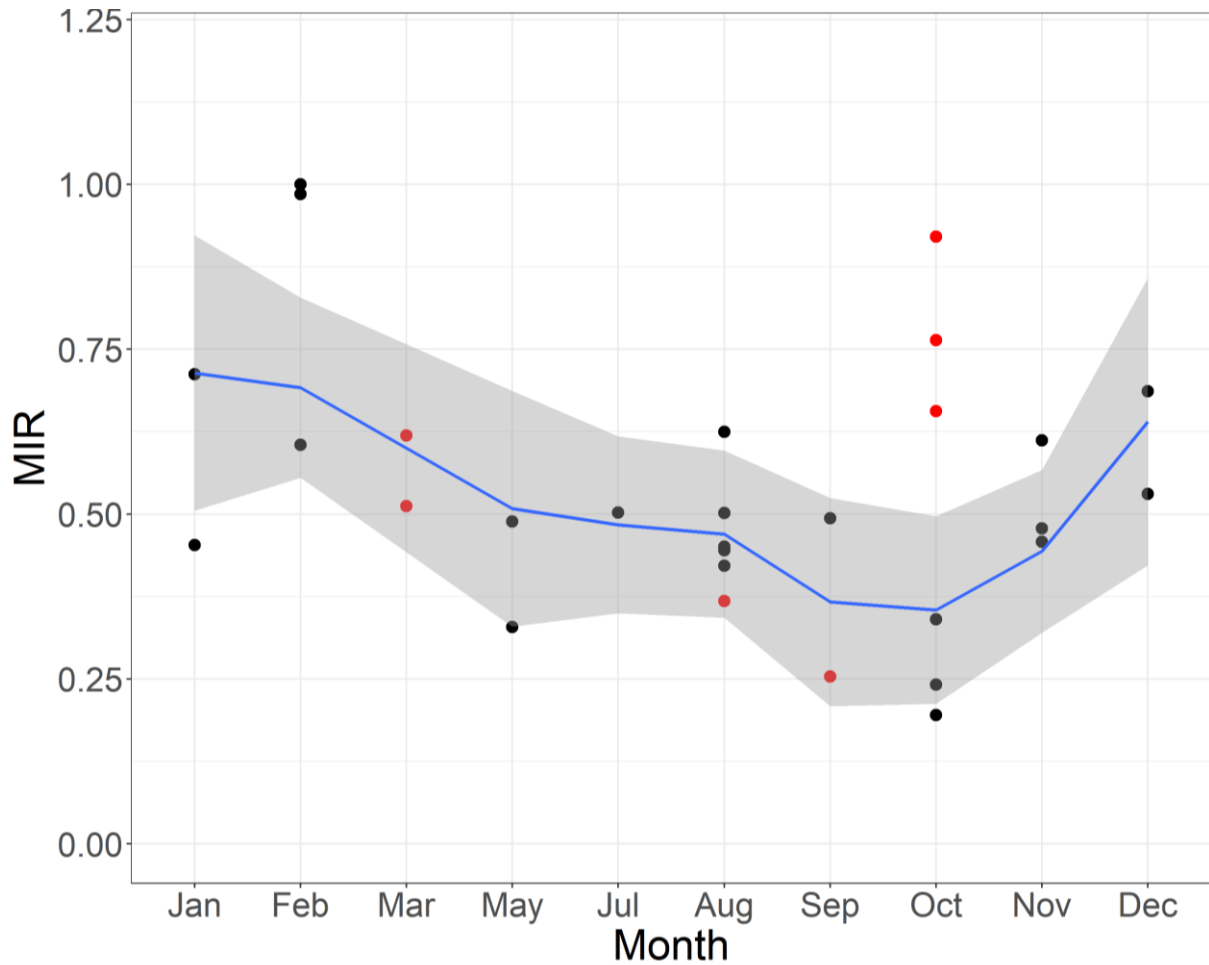
Figure 13:   **Marginal increment ratio (MIR) by month of capture.**   Black dots indicate sharks aged 5 years or less and red dots indicate sharks aged older than 5 years. Data for sharks aged 5 or less were fitted with a moving regression (LOESS).

3.6   Micro-CT scans and density profiles

Micro-CT scans and their density profiles are shown in Figures 14–19. Micro-CT scans of vertebrae from three sharks (ururoa_10, _15, and _30) are shown in Figures 14, 16, and 18. Growth bands were clearly visible for all three samples and were useful in assisting growth band reads. The density profiles for micro-CT scans showed some differentiation across the thin section of the vertebrae (Figure 16 vs Figure 17), but these density profiles generally agreed with the initial read counts. When applied to the vertebrae thin sections under high contrast (Figures 15, 17, and 19), the density profiles were more pronounced, and provided good correspondence to age estimates (compared to

Reader 2), particularly for older individuals where banding delineation at the centrum edge becomes more difficult to interpret (Figures 17, 18, Appendix C).
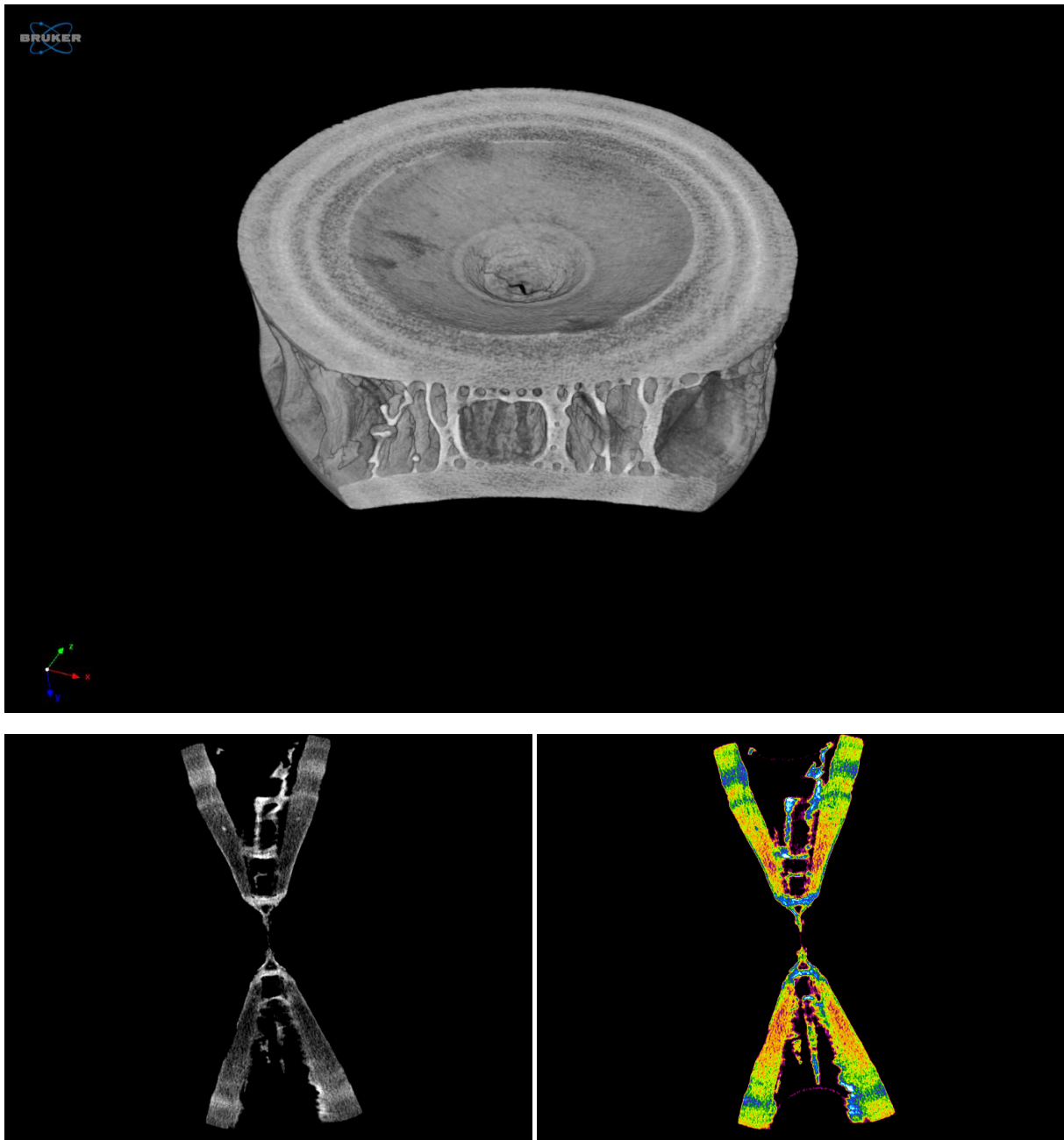
Figure 14: **Examples of microCT images, including the whole vertebrae (top panel) and vertebral centra in black and white and colourised (bottom panels) for ururoa_10 (age estimate of 1).**
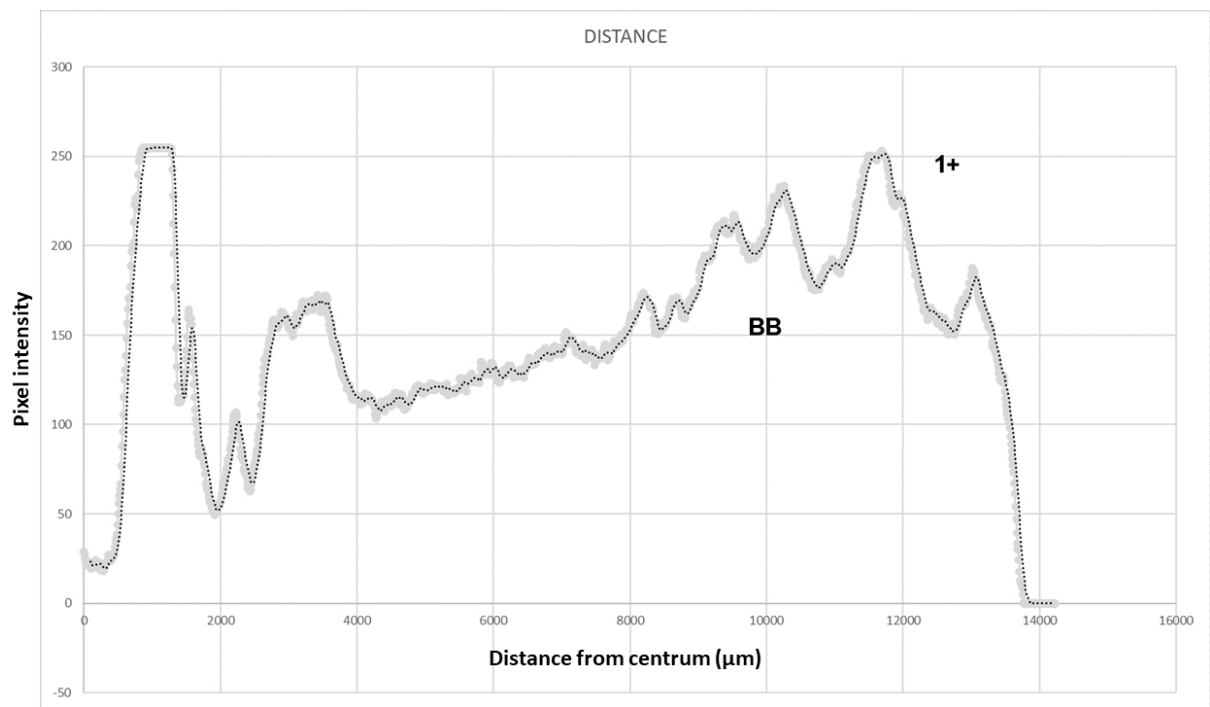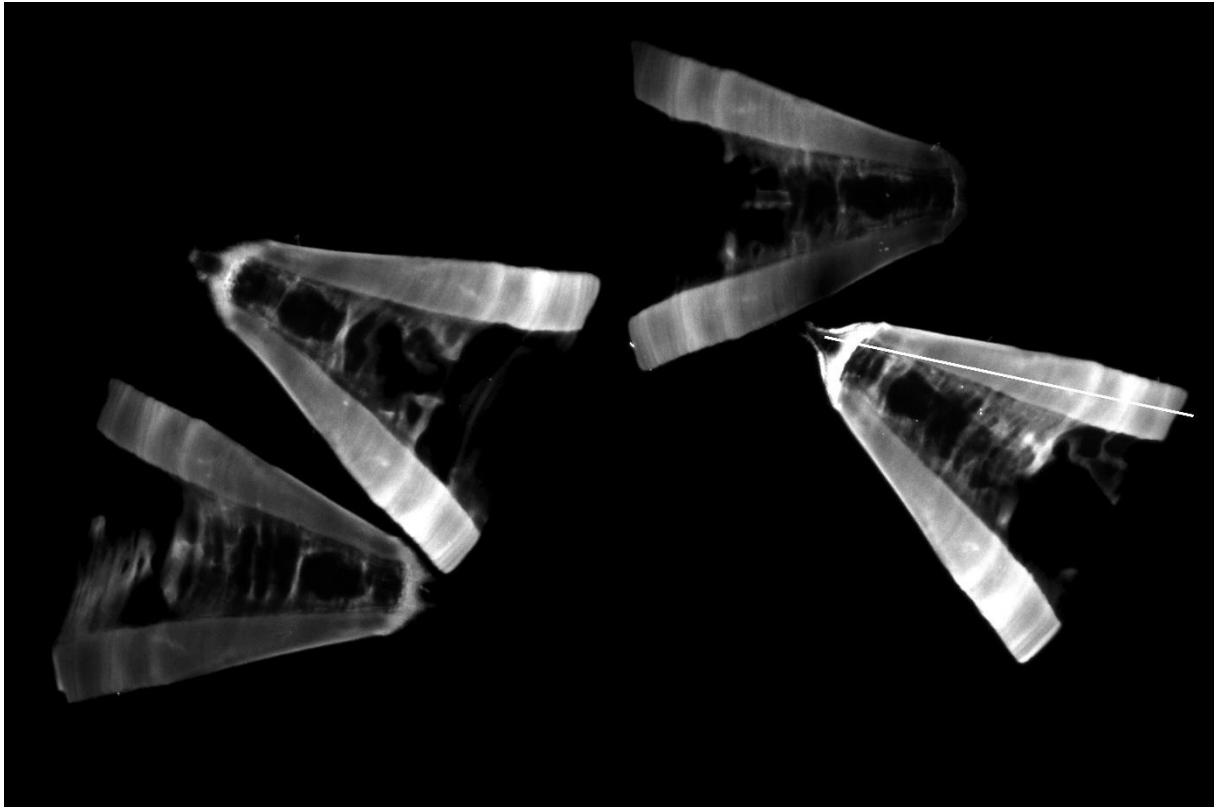
Figure 15: **Vertebrae thin section x-ray of ururoa_10 and its density profile (taken along the white line) indicating the number of band patterns.** BB = birth band.
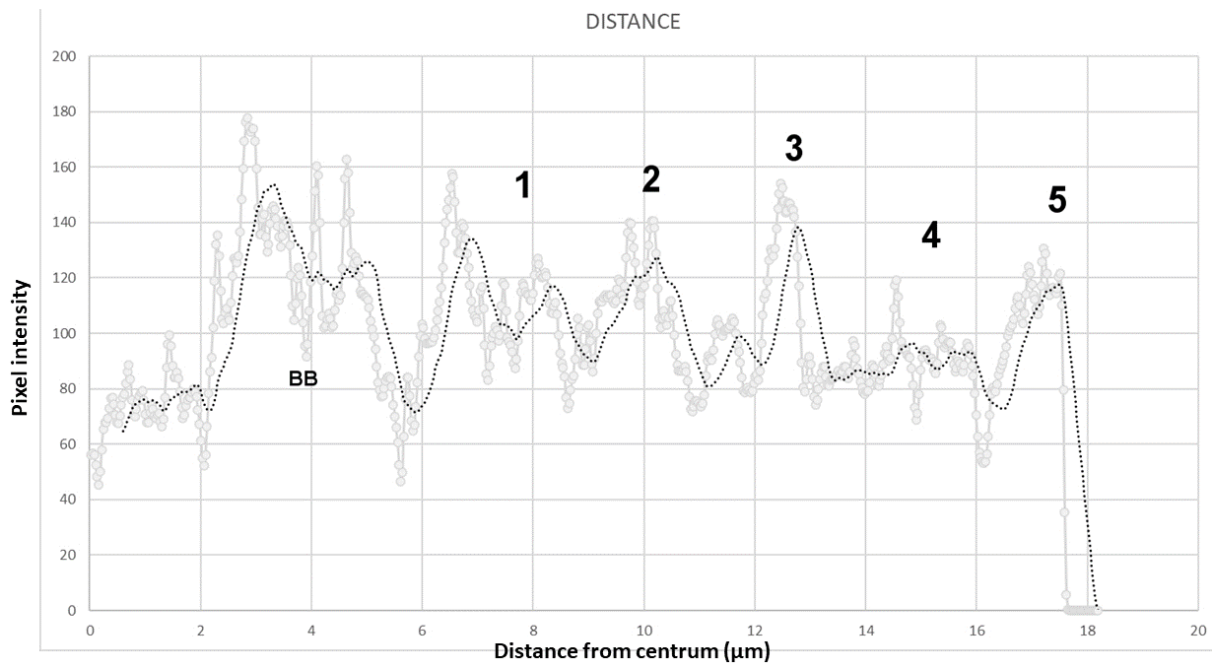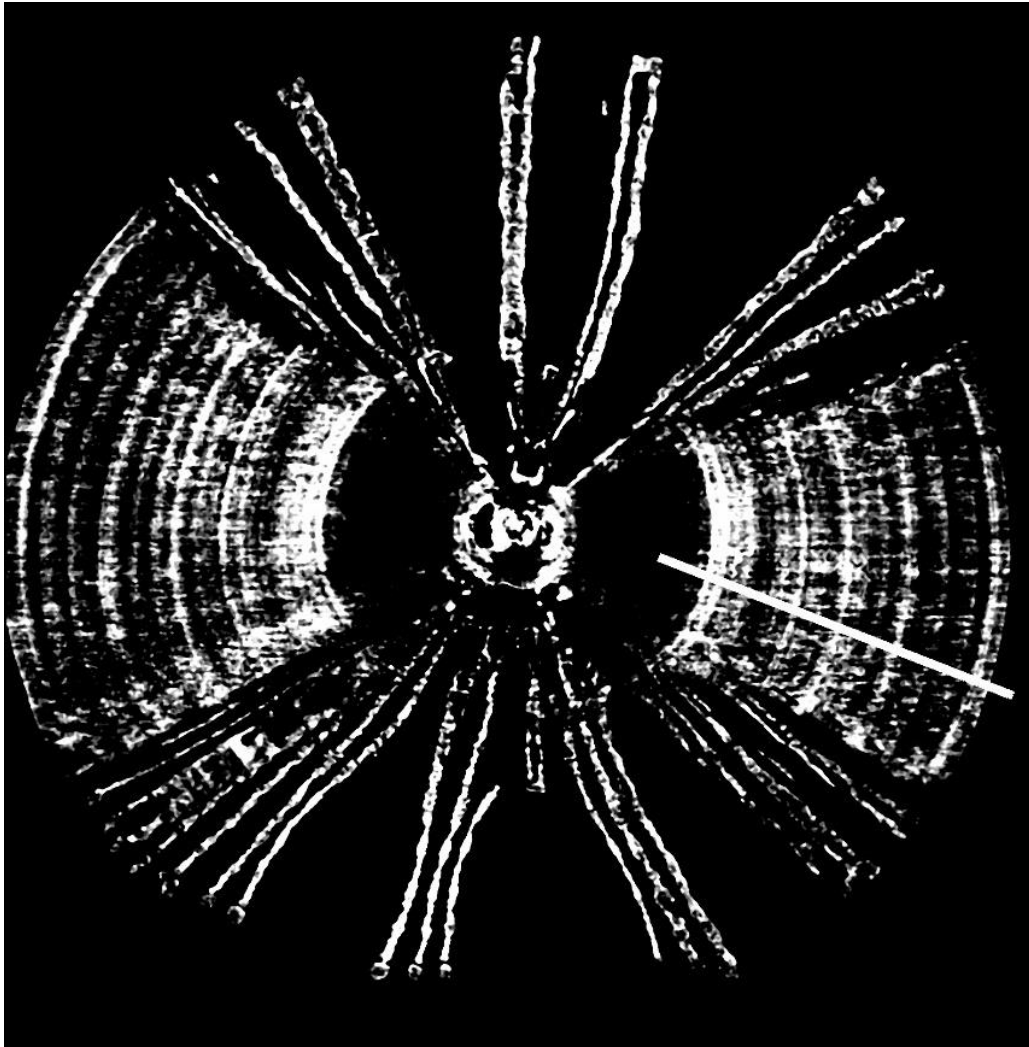
Figure 16: **MicroCT image of ururoa_30 and its density profile (taken along the white line) indicating the number of band patterns.** BB = birth band.
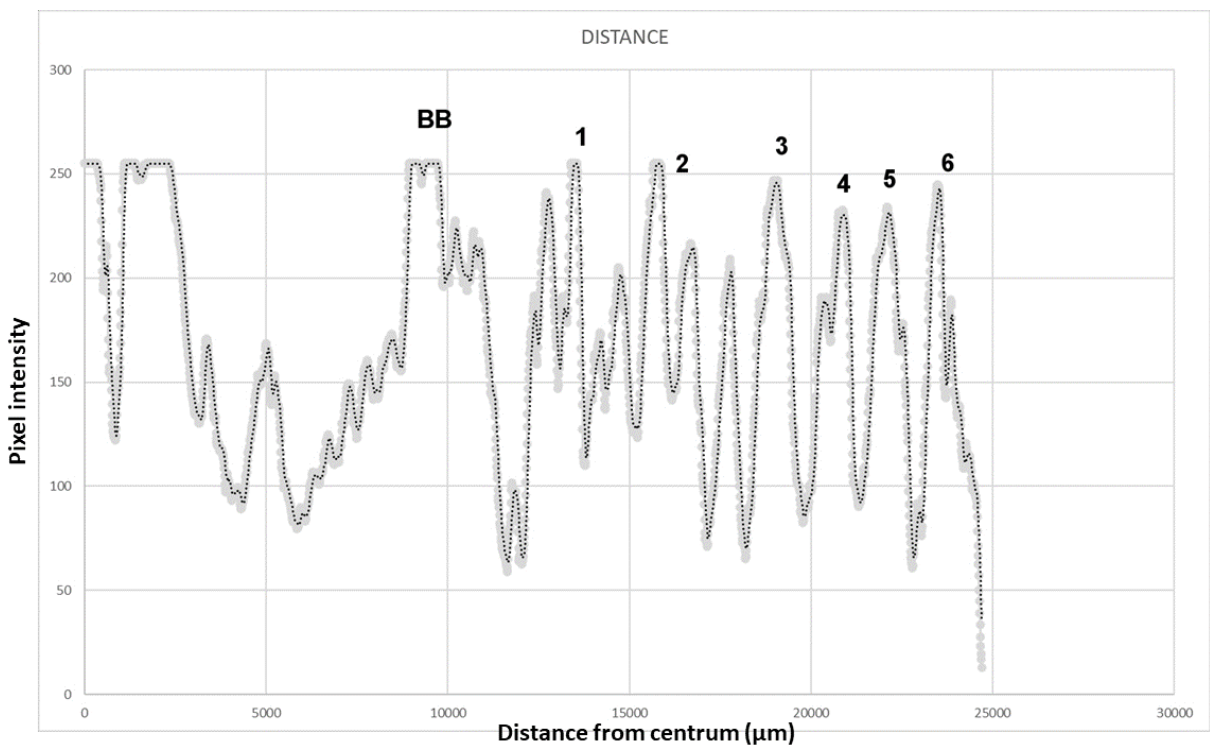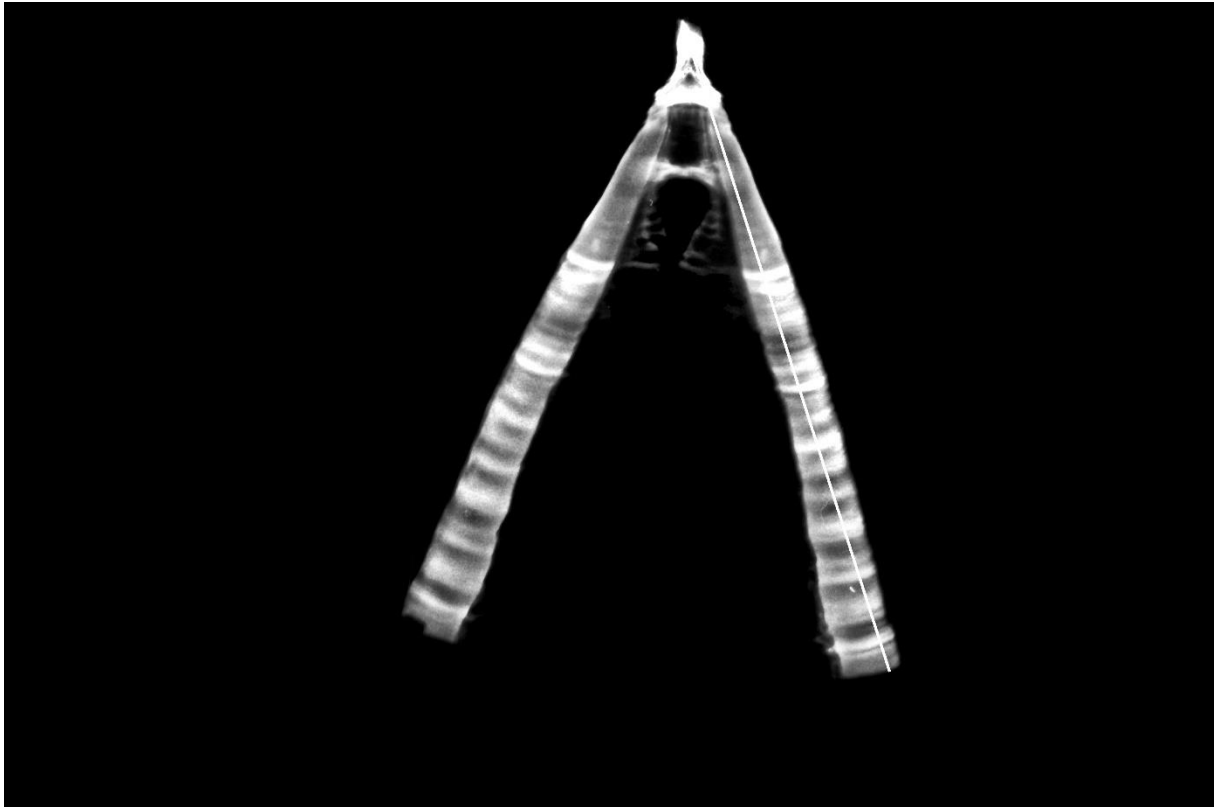
Figure 17: Vertebrae thin section x-ray of ururoa_30 and its density profile (taken along the white line) indicating the number of band patterns. BB = birth band.
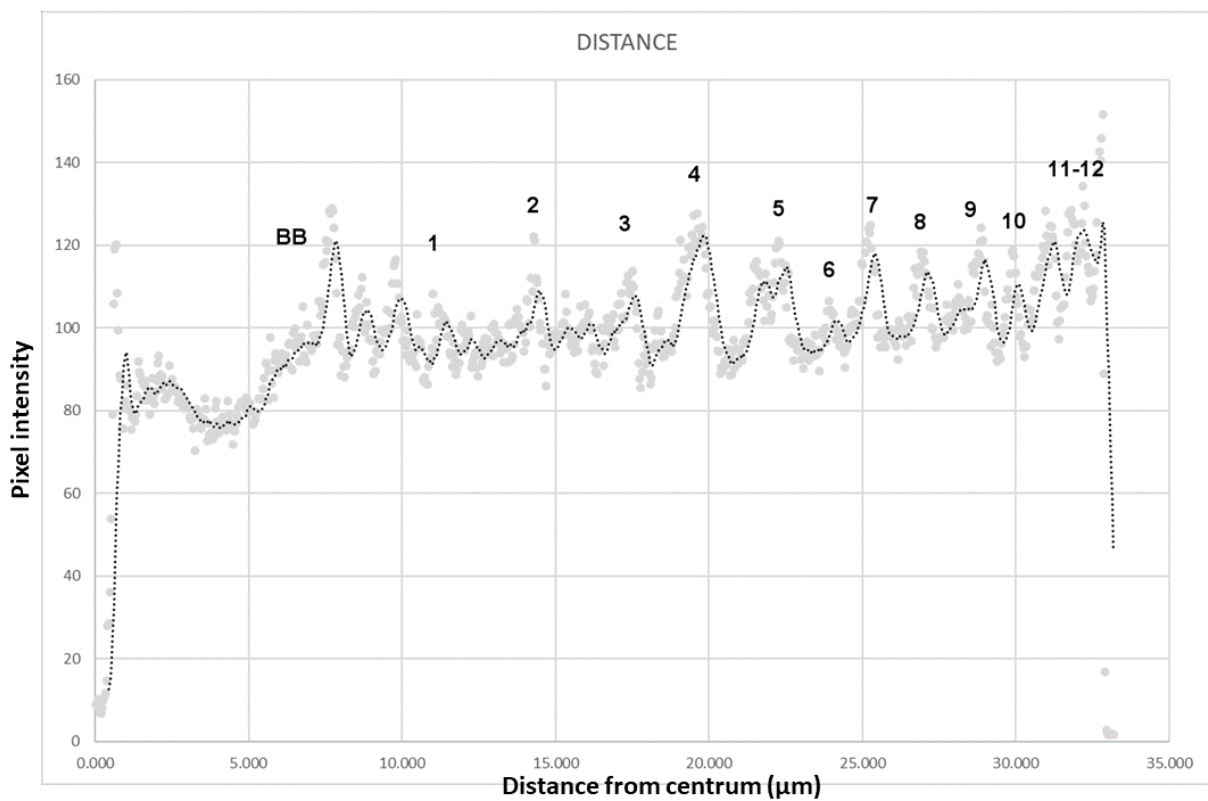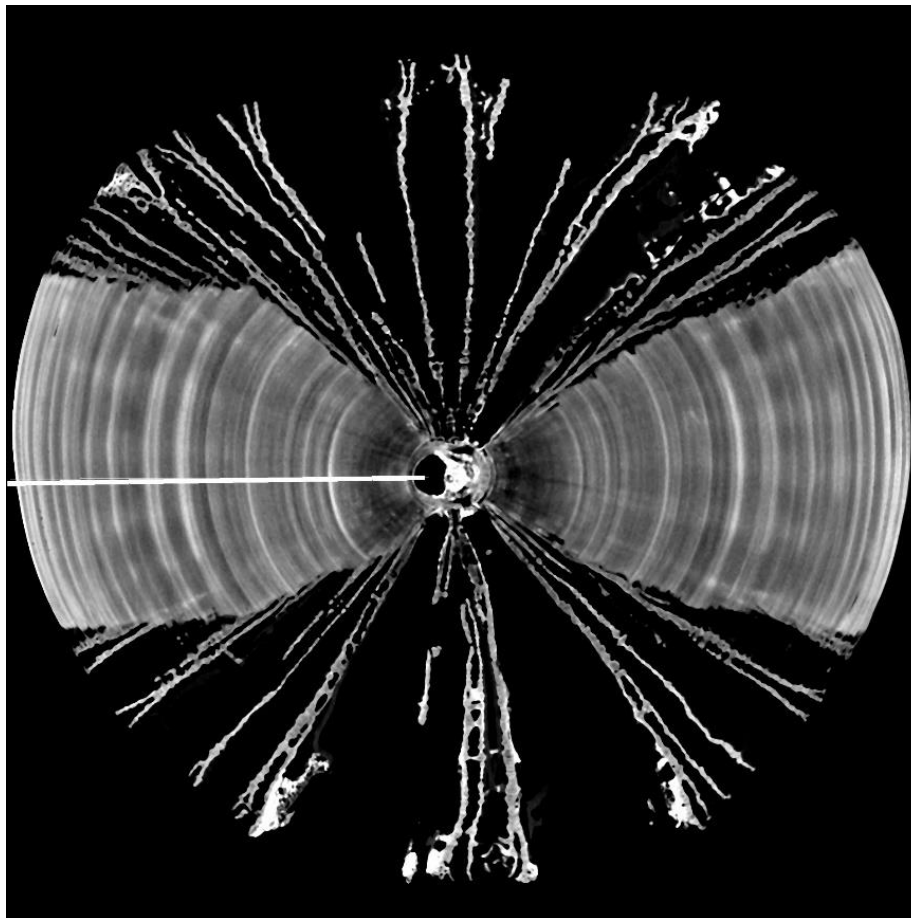
Figure 18: **MicroCT image of ururoa_15 and its density profile (taken along the white line) indicating the number of band patterns.** BB = birth band.
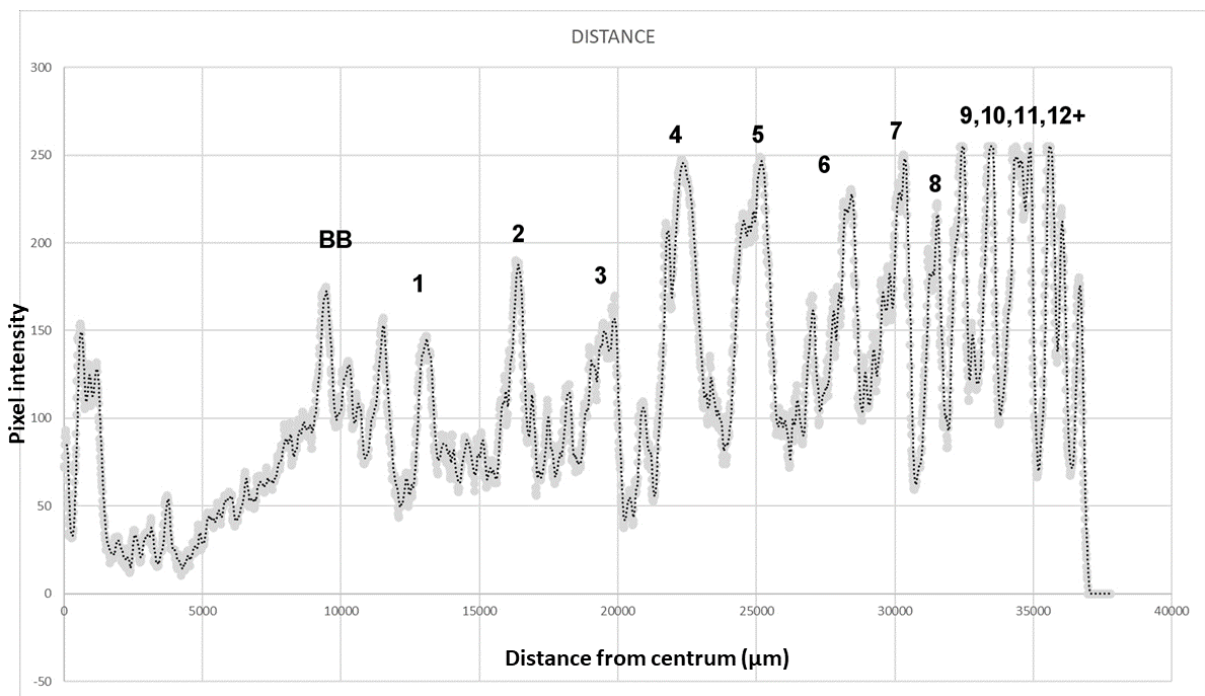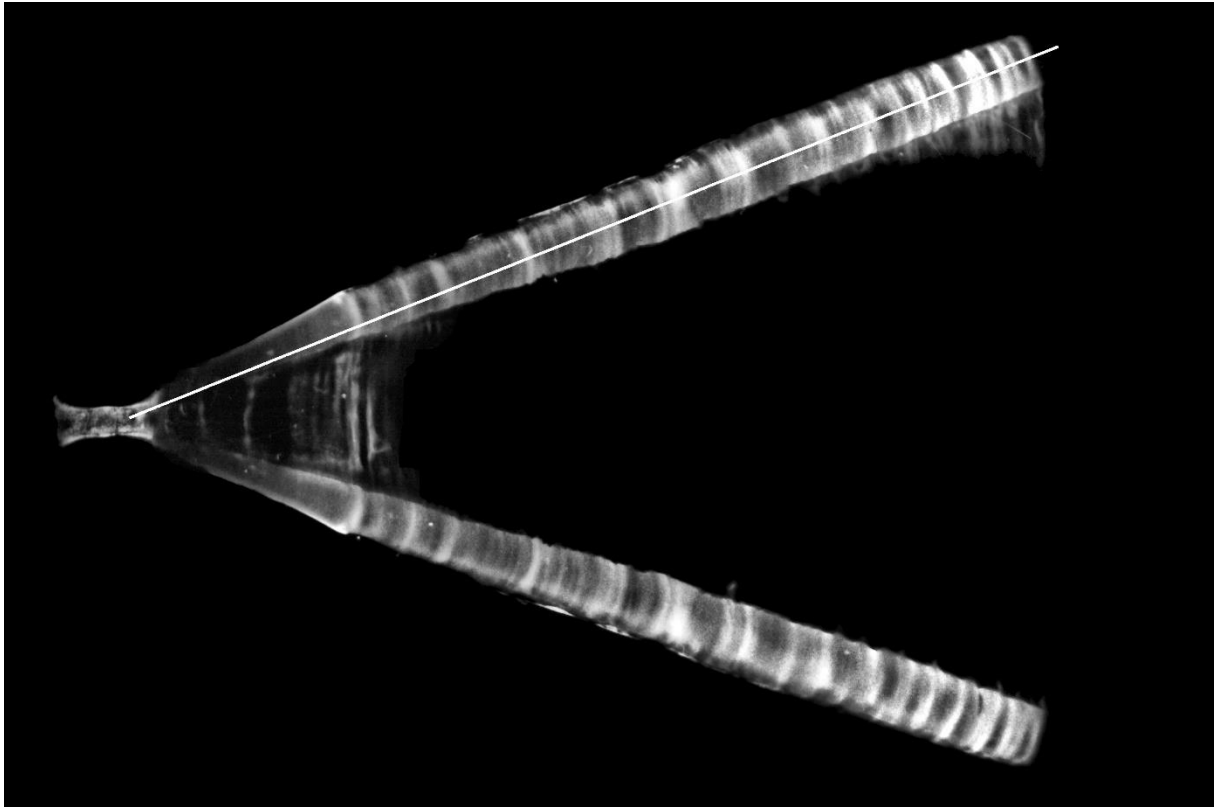
Figure 19: Vertebra thin section x-ray of ururoa_15 and its density profile (taken along the white line) indicating the number of band patterns. BB = birth band.

4 Discussion

Vertebral banding patterns were used to estimate age and growth for New Zealand white sharks for the first time. Information on New Zealand white shark life history (e.g., size- and age-at-maturity, fecundity, and longevity) is poorly defined because of their relative rarity and operational difficulties associated with sampling such large sharks aboard commercial fishing vessels. The samples used here were collected over a period of 30 years; nearly half of the individuals were young (1–2 years old) and only six sharks were estimated to be older than 10 years of age. Vertebrae were not easy to age visually, particularly for older individuals. There was strong agreement between readers for age estimates of young New Zealand white sharks, but large disagreement for older sharks. Age estimates could not be validated. Additional samples of large sharks will be needed to comprehensively understand age and growth of white sharks that inhabit New Zealand waters.

4.1 New Zealand white shark age and growth

The preliminary work here suggests New Zealand white sharks are relatively fast growing initially, and possibly long-lived. White shark growth parameters can vary by region, and previous studies using similar analysis (x-rays of vertebral centra and assumed annual deposition of band pairs) have investigated age and growth of white sharks from southern Australia (Malcolm et al. 2001; O'Connor 2011), the northeast Pacific Ocean (Cailliet et al. 1985), the southwest Indian Ocean (Wintner & Cliff 1999), and off the coast of Japan (Tanaka et al. 2011) (Table 1). The relationship between length and growth was found to be nearly linear for young New Zealand white sharks. White sharks were estimated to double their birth length from approximately 1.5 m TL to 3 m TL within five years, equating to an annual growth rate of approximately 30 cm per year (k parameter estimate of 0.083 or 0.125 year^{-1}). This rate of growth is similar to estimates from the Northeast Pacific (California, k = 0.058 year^{-1}) and South Africa (k = 0.065 year^{-1}) (Cailliet et al. 1985; Wintner et al. 1999) and slower than the Northwest Pacific (Japan, k = 0.196/0.159 year^{-1} for males and females, respectively) (Tanaka et al. 2011). An initial study from Australian white sharks (Western Australia to New South Wales, including Tasmania) suggested two possible growth scenarios using "high" and "low" band count models (high band count including those rings that were similar to bands and a low band count excluding ambiguous rings) (Malcolm et al. 2001). The "low" band count method provided similar results to our study, with Australian white sharks estimated to reach lengths of 3 m by 6 years of age (k = 0.071 year^{-1}). Sharks reached the same length by 8 years of age under the "high" band count method (k = 0.042 year^{-1}) (Malcolm et al. 2001). A more recent Australian study, which also used microCT analysis to assist with age estimates, determined a more moderate growth rate (k = 0.053 year^{-1}) (O'Connor 2011). O'Connor (2011) included a prior length-at-birth of 1.40 m TL in the growth model, based on length estimates of full-term New Zealand white shark embryos (Francis 1996). Length-at-birth was not included *a prior* in the models here because both models had similar starting lengths; size-at-birth was estimated in this study at 1.73 m TL (Reader 1) and 1.44 m TL (Reader 2). The smallest free-swimming shark in this study was 1.52 m TL. This individual did not have any vertebral growth beyond its birth band, indicating it was likely to have been captured shortly after birth.

Growth in New Zealand white sharks appeared to slow at approximately 3 m in length. Changes in growth can be indicative of changes in diet, movement or habitat, or a reallocation of energy from somatic growth to reproductive development (i.e., maturity) (Roff 1983; Dahlgren & Eggleston 2000). Such aspects of New Zealand white sharks are poorly defined. Long-distance movements and regional connectivity of sub-adult (>3 m) and adult males, and sub-adult females tagged at aggregation sites in central and southern New Zealand are well known (Duffy et al. 2012; Francis et

al. 2015), but fine scale habitat use in coastal waters, and movements of juveniles are unknown. White sharks engage in ontogenetic shifts in habitat type, with juvenile white sharks (<3 m) generally confined to coastal, shelf-based waters and large individuals engaging in long, offshore movements in pelagic habitat (Skomal et al. 2017; Bruce et al. 2019). Changes in habitat use are also likely to correspond to ontogenetic shifts in diet; Australian white sharks begin to consume marine mammals at lengths >2.7 m (Malcolm et al. 2001), and New Zealand white sharks 2.5 m+ TL are observed around pinniped colonies near Stewart Island (Francis et al. 2015). These behavioural changes may influence the shifts in growth observed in this study, but cannot be confirmed without additional ecological and movement studies of young New Zealand white sharks.

Age-at-maturity could not be assessed here because of the lack of maturity data and small sample size, particularly for large individuals. Length-at-maturity for New Zealand white sharks is estimated to occur at 3.6 m TL for males and 4.5–5 m TL for females (Francis 1996). Using these length-at-maturity estimates and the growth curves calculated here, age-at-maturity may occur at approximately 7 and 14+ years for males and females, respectively, under the interpretation of Reader 2 or at 10 and 22+ years under the interpretation of Reader 1. The largest difference in age interpretations (25 years, 19 vs 44 years) was for the largest shark (ururoa_40, 5.36 TL), which only had previously processed microscopy slides in poor condition to assess. This shark was female and mature, and was gravid with seven late-term embryos (1.43–1.45 m TL) when captured. When first collected, the whole vertebra of ururoa_40 was visually assessed to have 22 (+/-1) visible banding pairs (Francis 1996), which is most similar to the age estimate for Reader 2 (19 years). If the vertebrae interpretation of Reader 2 is indeed an accurate representation of age, this would make this female white shark a relatively young mature individual based on validated ages. While sexual maturity for female white sharks has been previously estimated at 13–18 years (Cailliet et al. 1985; Wintner et al. 1999; Malcolm et al. 2001), bomb radiocarbon validated ages for North Atlantic and Indian Ocean white sharks have reassessed female age-at-maturity of 30–33 years (Hamady et al. 2014; Andrews & Kerr 2015; Natanson et al. 2015; Christiansen et al. 2016). It is possible that South Pacific white sharks reached maturity at a smaller size; unvalidated Australian white shark age-at-maturity has been estimated at 10–13 years in males and 18–23 years in females (Malcolm et al. 2001). Validated growth estimates for other lamnid sharks (e.g., porbeagle) have shown New Zealand sharks grow noticeably slower than their counterparts in the North Atlantic, although New Zealand porbeagle are rarely reported to reach the same lengths (Francis et al. 2007). Given that New Zealand (and Australian) sharks reached similar lengths (5 m+) to those reported in other studies, it seems more likely that age-at-maturity estimates would be similar to those confirmed overseas.

Longevity for white sharks has been debated for some time. Here, the oldest individual was estimated to be at least 30 years of age (4.85 m TL, male), and possibly as old as 45. Initial studies suggested a maximum age of 12–15 years for white sharks (Cailliet et al. 1985). In more recent years, bomb radiocarbon (14C) dating has been employed to validate banding pairs. Bomb radiocarbon analysis has proven to be a useful technique to remove subjectivity in age estimates and confirm annual band pair formation in the vertebrae of several shark species (Campana et al. 2002; Francis et al. 2007). It is particularly useful for larger sharks, where reduced clarity of outer growth bands has resulted in gross underestimation of age. For example, bomb radiocarbon dating of New Zealand porbeagle (*Lamna nasus*) confirmed annual band pair deposition to approximately 20 years, but beyond this age, ages could be underestimated by up to 50% (20 years) (Francis et al. 2007). This indicated that vertebral growth had slowed or ceased over time, and it has since been shown that band counts alone systematically underestimates shark age (Harry 2018). When accounting for a slowing or cessation of band pair deposition in the outer portion of the vertebral centra, bomb

radiocarbon analysis for white sharks from the Northwest Atlantic Ocean confirmed annual band pair formations up to 44 years, with a suggested longevity of ~73 years (Hamady et al. 2014; Natanson et al. 2015). Elsewhere, bomb radiocarbon analysis has confirmed longevity of >30 years in the Northeast Pacific Ocean (Andrews et al. 2015), and >38 years in the Southwest Indian Ocean (Christiansen et al. 2016). Bomb radiocarbon dating is unlikely to provide any useful age validation for the samples available in this study. For bomb radiocarbon dating to be successful, samples would need to have been collected from sharks alive during the 1980s, at a minimum (Francis et al. 2007). The earliest collected samples with available genetic samples are from 1993, and these were relatively small (1.52–3.5 m TL), and likely young, individuals (no more than six years of age).

Table 1: **White shark growth parameter estimates from studies conducted in the Pacific and Indian Oceans.** Standard errors for estimates from this study are provided in brackets.

Region	n	Sex	L_∞ (m, TL)	k (year^{-1})	t_0 (years)	L_0 (m, TL)	Reference
New Zealand (Reader 1)	38	Combined	5.035 (4.461–6.897)	0.083 (0.066, 0.184)	-5.05 (-4.78, -1.70)	1.734	This study
New Zealand (Reader 2)	38	Combined	5.141 (4.414–6.847)	0.125 (0.060, 0.183)	-2.63 (-4.50, -1.63)	1.441	This study
Southern Australia	51	Combined	732.3 (high) 659.8 (low)	0.042 (high) 0.071 (low)	4.173 (high) -2.330 (low)	NA	Malcolm et al. (2001)
Southern Australia	79	Combined	7.466	0.053	-3.80	1.400	O'Connor (2011)
East Pacific Ocean (California)	21	Combined	7.637	0.058	-3.53	1.250	Cailliet et al. (1985)
Northwest Pacific Ocean (Japan)	21	Male and Female	4.550 (M), 6.067 (F)	0.196 (M), 0.159 (F)	-1.92/-1.63	1.425 (M) 1.507 (F)	Tanaka et al. (2011)
Southwest Indian Ocean (South Africa)	11 2	Combined	6.860	0.065	-4.40	NA	Wintner & Cliff (1999)

4.2 Marginal increment ratios

Marginal increment ratios were highest in summer months (December to February) and lowest in the autumn and winter months. While the MIR analysis calculated here was non-significant and based on a small sample size, this general trend was similar to that reported from Australian sharks (O'Connor 2011). The MIR analysis conducted by O'Connor (2011) was also not statically significant, but a substantial MIR reduction reported during the winter months and a constant ratio trend over spring and summer months suggested that the opaque banding may be formed annually in winter. Opaque bandings for New Zealand white sharks became particularly obvious for sharks captured in between the months of May and August. O'Connor (2011) speculated that Australian white sharks were born in summer months, and this observation can be confirmed here. The smallest free-swimming shark in this study (1.52 m TL, mentioned above) was captured shortly after birth in January. The capture of the gravid female shark (ururoa_40) with late-term pups in November also indicates pupping occurs around New Zealand in the summer months (Francis 1996). White shark pupping grounds have long been suspected around the west and east coast of the top half of the North Island, where many of the samples used here were collected.

There appeared to be two clusters of MIR measurements observed from samples collected in October. The clusters could be classified generally into two subgroups: young sharks (3–4 years old) with lower MIR ratios and older sharks (6+ years) with higher MIR ratios. The difference in MIR measurements may simply be reflective of a small sample size (n = 6), although given that the clustering of ages occurred around the same time when changes in growth were observed (5 years, approximately 3 m TL), these ratios may also be indicative of a change in growth and/or maturity and the deposition of banding pairs on the vertebrae. MIRs are expected to increase as sharks mature due to a marked reduction in growth and reduced width between band margins (Conrath et al. 2002). However, sufficient sampling (both by month and size class) will be needed to confirm this observation here.

4.3   MicroCT imaging

MicroCT imaging was found to be useful for assisting with the ageing process. It provides a non-destructive, high-quality image with the flexibility to explore the best means of reading the whole vertebrae through image enhancement and rotation. MicroCT imaging can have an extremely high readability success rate, with previous studies reporting a 97% success rate in sample readability (O'Connor 2011). The downside of microCT imaging is that the scanning process is expensive, and could only be employed on a small sub-sample here. This technique is also not a validation tool so age estimates are still subjective. The creation of density profiles was also useful in separating and distinguishing opaque banding (presumed to be an annual year of growth here) from finer growth rings. The age estimates from the combined use of the microCT imaging and density profiling corresponded well to Reader 2 age estimates, which would suggest New Zealand white sharks are relatively fast growing and mature at ages younger than estimates overseas.

4.4   Recommendations

4.4.1   Continued collection of biological sampling, particularly of larger sharks

The New Zealand white shark collection for ageing is relatively small, and is mostly comprised of young (1–2 year) individuals. Sampling of larger sharks is needed to provide more robust growth estimates, allow for growth estimates by sex, and to estimate age-at-maturity. The collection of shark vertebrae is a lethal sampling method and should only occur when sharks are accidentally caught as bycatch and reported dead upon capture, or when found dead (e.g., beach cast specimens). White sharks do interact with commercial and recreational fisheries in New Zealand (Finucci et al., in review), and sampling protocols should continue through the Ministry for Primary Industries Observer Programme. All efforts should be made to fully utilise sharks (e.g., vertebrae, tissue, stomach sampling) when lethal interactions occur, and regardless of life status, all encountered sharks should be measured for size, sex, and where possible, maturity stage. Tissue samples of live sharks may be useful for future non-lethal ageing techniques (See Section 4.4.2).

4.4.2   Investigate alterative non-lethal means of ageing

The use of vertebrae to age sharks is a lethal process and is not ideal for white shark, a protected species in New Zealand. Emerging technologies, such as DNA methylation, have been successful in estimating fish age via tissue samples (Mayne et al. 2021). Further models are being explored for fish (A. Budd, University of Western Australia, pers. comm.) and may prove to be useful for white shark ageing in the future. DNA methylation, however, does require validated ageing data (See Section 4.4.3).

4.4.3   Complete a New Zealand-Australia white shark growth study

New Zealand and Australia share the South Pacific population of white sharks (Hillary et al. 2018). There have been at least two studies estimating growth parameters for Australian white sharks (Malcolm et al. 2001; O'Connor 2011), and there is current interest in revisiting and improving these previous analyses (J. O'Connor, United Nations University, pers. comms.). Additional samples are also available for use at Australian institutes (e.g., Flinders University, C. Huveneers, pers. comm.). A joint study combining all available samples from New Zealand and Australia should be carried out to characterise the life history parameters of the South Pacific white shark population. Historic Australian white shark samples may also be suitable for bomb radiocarbon dating validation as samples from these studies date back to 1987 (O'Connor 2011).

4.4.4   Assessment of vertebrae elemental composition

Vertebral chemistry (elemental composition, e.g., barium, lithium, magnesium) can be a used as natural tag to reconstruct movement and environmental histories of sharks. For example, elemental signatures have been used to determine natal origins of highly dispersive species, and can be used to correlate temporal and spatial movements patterns from coastal to oceanic habitats (Smith et al. 2016; Mohan et al. 2018). Vertebral chemistry can also influence band pair deposition (Mohan et al. 2018). The measurement of elemental signatures of the vertebral collection via laser ablation inductively coupled plasma mass spectrometry may provide insight into movement patterns, particularly for juvenile individuals, for which there is currently no data available.

5   Acknowledgements

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Appendix A   White shark samples and associated data

Table A1:   **White shark samples and associated data.**

niwa_prep_no	date	region	location	latitude	longitude	lgth_TL	sex	maturity	largest visible vertebra measurements (defrosted-mm)				comments
									vertebral radius	dorsal-ventral	medial-lateral	anterior-posterior	
ururoa_1	19-01-1993	Kaipara Harbour	North Channel, inside bar	36.41	174.12	1.52	F	immature	10.99	20.24	21.07	8.73	
ururoa_2	21-02-1993	Manukau Harbour	Near airport	37.02	174.78	3.50	F	immature	22.04	39.28	38.86	15.53	
ururoa_3	23-02-1993	Manukau Harbour	Near airport	37.02	174.78	1.93	M	immature	14.61	27.77	27.78	12.82	
ururoa_4	08-10-1995	New Plymouth	NW of city	38.95	174.09	2.40	M	immature	20.41	37.74	37.37	14.80	
ururoa_5	03-03-2000	Hawkes Bay	Kairakau Beach	39.95	176.94	3.37	F	immature	28.05	50.57	51.59	22.41	duplicate sample available
ururoa_6	18-09-2005	Chatham Islands	Okawa, Hanson Bay	43.78	176.23	4.26	M	immature	36.71	65.53	67.77	27.37	
ururoa_7	20-03-2008	Auckland Islands	N Auckland Is	50.19	166.28	3.84	M	immature	36.66	63.90	63.82	30.50	
ururoa_8	19-08-1997	Hawkes Bay	Pourerere Beach	40.10	176.86	NA	F	likely immature	25.84	46.88	46.04	22.60	estimated TL = 3.10
ururoa_9	19-10-2006	Stewart Island	Thuk Bay (?), Stewart Island	NA	NA	NA	U	likely immature	26.22	45.37	45.16	21.08	estimated TL = 3.10
ururoa_10A	28-05-1998	Hawkes Bay	Paoanui Point	40.07	176.89	1.91	F	immature	13.35	25.13	24.77	12.22	
ururoa_11	31-08-2004	Gisbourne	Ariel Reef	38.73	178.30	NA	U	likely immature	14.02	24.79	24.99	10.35	estimated TL = 1.80
ururoa_12	19-10-2005	Waikato	Waikato	37.62	175.02	NA	F	likely immature	40.08	71.56	76.42	33.18	estimated TL = 4.60
ururoa_13	07-11-1997	Hawkes Bay	Paoanui Point	40.07	176.89	2.76	M	immature	23.93	42.68	42.69	18.70	
ururoa_14	07-08-1998	Hawkes Bay	Pourerere Beach	40.10	176.86	2.89	F	immature	24.98	44.76	45.80	19.79	additional cranial sample
ururoa_15	01-10-2005	Waikato	Port Waikato	37.39	174.73	4.70	F	immature (maturing)	32.62	52.40	60.90	26.00	
ururoa_16	01-02-2009	Stewart Island	Bunker Islets	46.86	168.25	3.60	M	mature	32.90	58.90	56.20	24.95	
ururoa_17	17-09-2017	Northland	Great Exhibition Bay, c. 12.5 km se of the entrance to Parengarenga Harbour	34.64	173.02	1.84	F	immature	13.99	25.56	25.36	11.18	
ururoa_18	25-08-1998	Hawkes Bay	Pourerere Beach	40.10	176.86	2.20	M	immature	16.09	27.19	27.30	13.40	
ururoa_20	01-05-1999	Hawkes Bay	Pourerere Beach	40.10	176.86	1.87	M	immature	15.70	28.70	28.40	12.69	
ururoa_21	16-11-2015	Taranaki	2 nautical miles off Tapuwae, south of New Plymouth	39.05	173.98	2.65	F	immature	19.96	36.88	35.22	16.21	
ururoa_22	22-07-2019	Hawkes Bay	Mahia Peninsula, off Table Cape	38.99	178.15	1.65	F	immature	11.69	22.26	22.29	10.28	
ururoa_23	01-08-2005	Taranaki	Stoney River, Cape Egmont	39.16	173.80	3.00	F	immature	28.83	51.75	50.48	23.60	additional cranial sample
ururoa_24	18-08-2014	Taranaki	New Plymouth	38.99	174.07	2.50	M	immature	21.58	38.94	39.15	17.40	duplicate sample available
ururoa_25	28-05-2021	Northland	Baylys Beach	35.95	173.75	1.78	F	immature	17.29	30.35	30.20	14.26	
ururoa_26	06-07-2020	Taranaki	Taranaki	38.80	174.04	2.80	M	immature	24.15	43.11	43.33	19.89	
ururoa_27	29-12-2008	Kaipara Harbour	Tinopai	36.24	174.23	3.28	F	immature	26.15	48.90	48.92	22.85	
ururoa_28	29-01-2006	Manukau Harbour	Oru Bay (?)	NA	NA	2.84	U	immature	21.83	39.56	39.53	18.70	
ururoa_29	05-02-2006	Hawkes Bay	Paoanui Point	40.07	176.89	3.12	F	immature	26.50	47.86	47.84	21.83	

niwa_prep_no	date	region	location	latitude	longitude	lgth_TL	sex	maturity	largest visible vertebra measurements (defrosted-mm)				comments
									vertebral radius	dorsal-ventral	medial-lateral	anterior-posterior	
ururoa_30	03-10-1997	Hawkes Bay	Ouepoto Beach Domain	40.14	176.84	3.05	F	immature	24.99	46.81	47.88	19.77	
ururoa_31	20-12-1999	Hawkes Bay	Pourerere Beach	40.10	176.86	2.60	M	immature	22.22	37.94	38.06	17.10	
ururoa_32	09-02-2007	Manukau Harbour	Grahams Beach	37.06	174.66	2.26	U	immature	19.53	34.11	34.31	16.14	
ururoa_33	25-11-2021	Northland	Omaha Beach	36.33	174.77	2.25	F	immature	18.65	33.44	32.87	14.29	
ururoa_34	03-10-2000	Kaipara Harbour	Tinopai	36.24	174.23	3.00	U	immature	19.45	36.16	35.33	18.01	
ururoa_35	02-01-2020	Hauraki Gulf	Orewa Beach	36.59	174.70	2.59	F	immature	21.97	38.72	39.21	16.98	
ururoa_37	28-09-2004	Gisbourne	Gisbourne	38.66	178.02	NA	U	likely immature	17.55	31.73	30.87	13.69	estimated TL = 2.10
ururoa_38	15-01-1992	Manukau Harbour	Manukau Harbour	37.02	174.78	1.74	F	immature	15.54	NA	27.99	13.91	only one vertebra available, partially cut; duplicate sample available
ururoa_39	13-11-1991	North Cape	North Cape	34.42	173.05	1.43	F	immature	NA	NA	NA	NA	historic prepped slides held at NIWA; fully formed embryo, not included in analysis
ururoa_40	13-11-1991	North Cape	North Cape	34.42	173.05	5.36	F	mature	NA	NA	NA	NA	historic prepped slides held at NIWA
ururoa_45	1996	Chatham Islands	Chatham Islands	NA	NA	4.85	M	mature	NA	NA	NA	NA	historic prepped slides held at NIWA

Appendix B COI sequence for ururoa_15

TAAAGATATTGGTACCCTTTATTTAATTTTTGGTGCATGAGCAGGAATAGTGGGAACAGCCCTAAGCCTTTTAA
TCCGTGCCGAGCTGGGTCAACCAGGTTCCCTCCTCGGAGATGACCAGATTTATAATGTTATTGTGACCGCCCAT
GCCTTCGTAATAATCTTCTTCATGGTAATGCCCATCATAATTGGGGGTTTTGGGAATTGACTAATCCCATTAATA
ATTGGTGCCCCGGACATAGCCTTCCCCCGAATAAATAACATAAGCTTCTGACTCCTTCCCCCTTCCTTTTTACTAC
TCCTAGCTTCAGCCGGAGTTGAAGCAGGAGCCGGCACTGGTTGAACAGTCTACCCTCCCCTGGCCGGTAATTT
AGCACACGCAGGAGCATCCGTTGACCTGGCTATCTTCTCCCTTCACCTAGCAGGTATTTCCTCAATCTTGGCCTC
AATTAACTTTATTACAACTATCATCAATATGAAACCCCCAGCAATCTCCCAATACCAAACACCCCTGTTCGTATG
ATCCATCTTAGTAACAACCATCCTTCTTCTCCTAGCCCTTCCAGTGCTCGCAGCCGGCATCACAATGTTACTTACT
GACCGAAATCTAAACACAACATTCTTTGATCCAGCAGGAGGAGGAGACCCTATTCTCTACCAACATCTTTTCTG
ATTTTTTGGTC

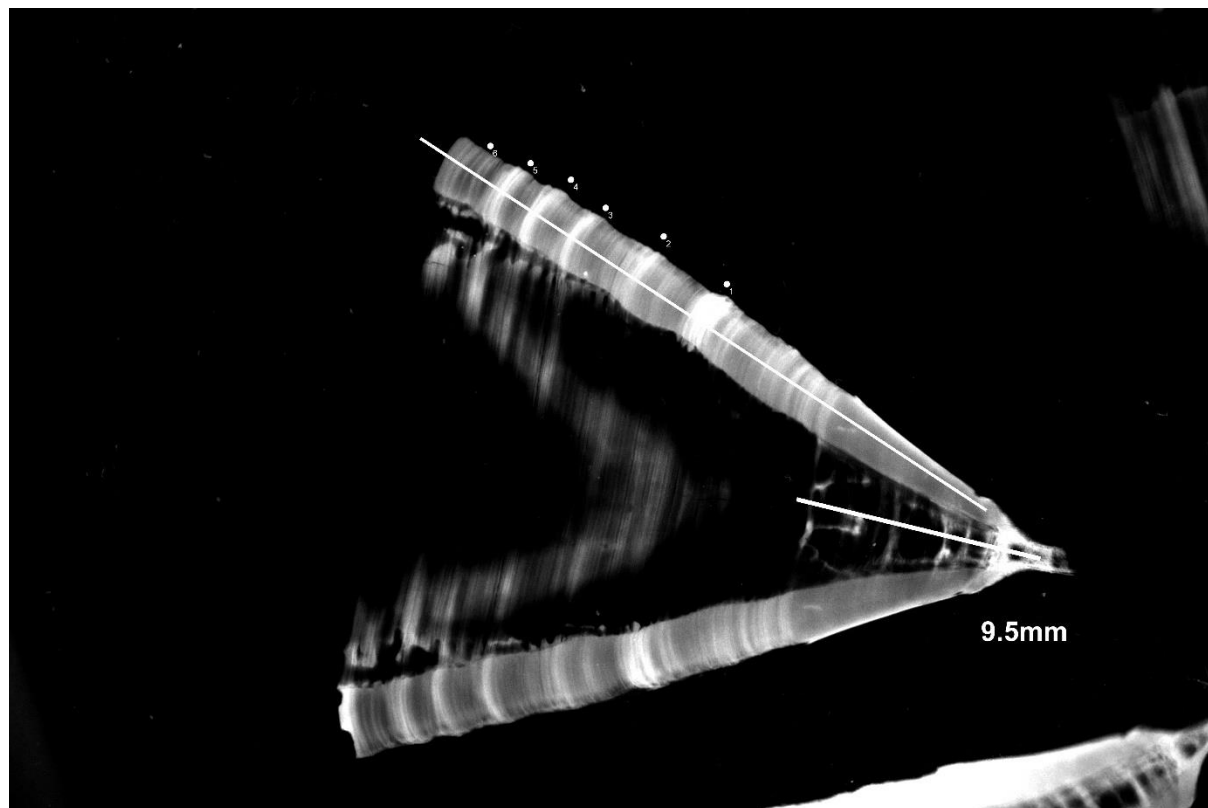# Appendix C   Additional density profiles
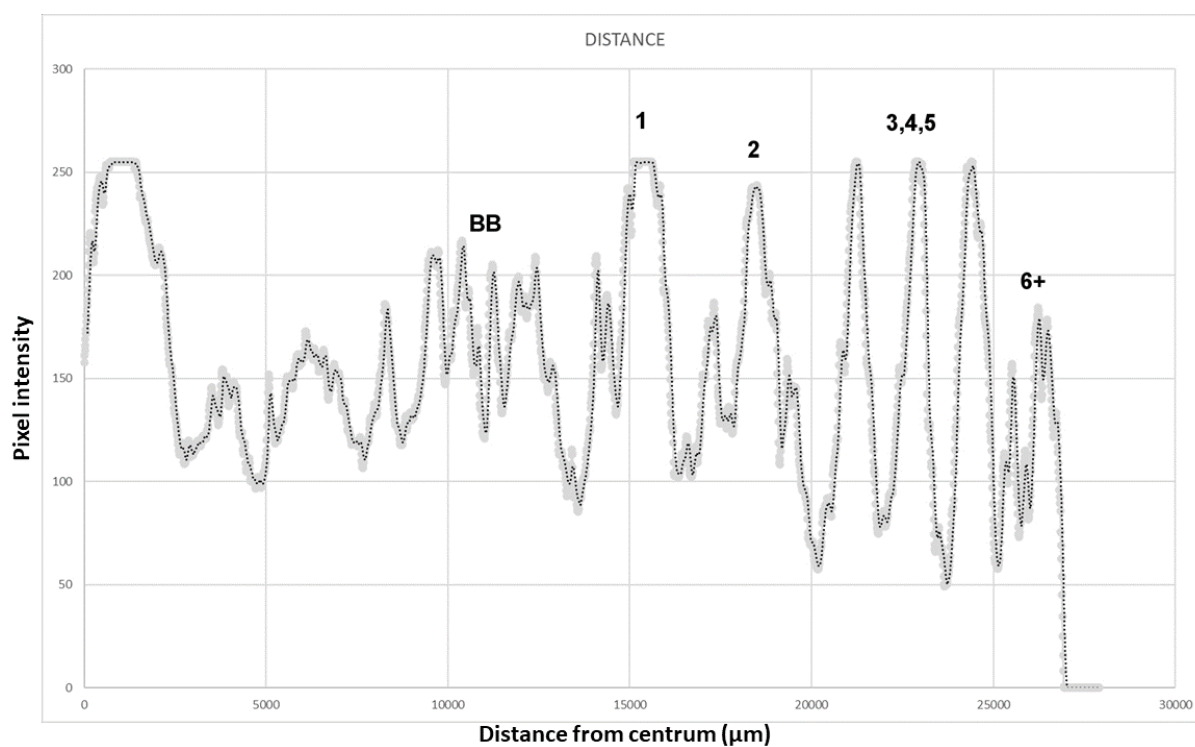
Figure A1:   Thin section x-ray of ururoa_16 and its density profile (taken along the white line) indicating the number of band patterns.   BB = birth band.
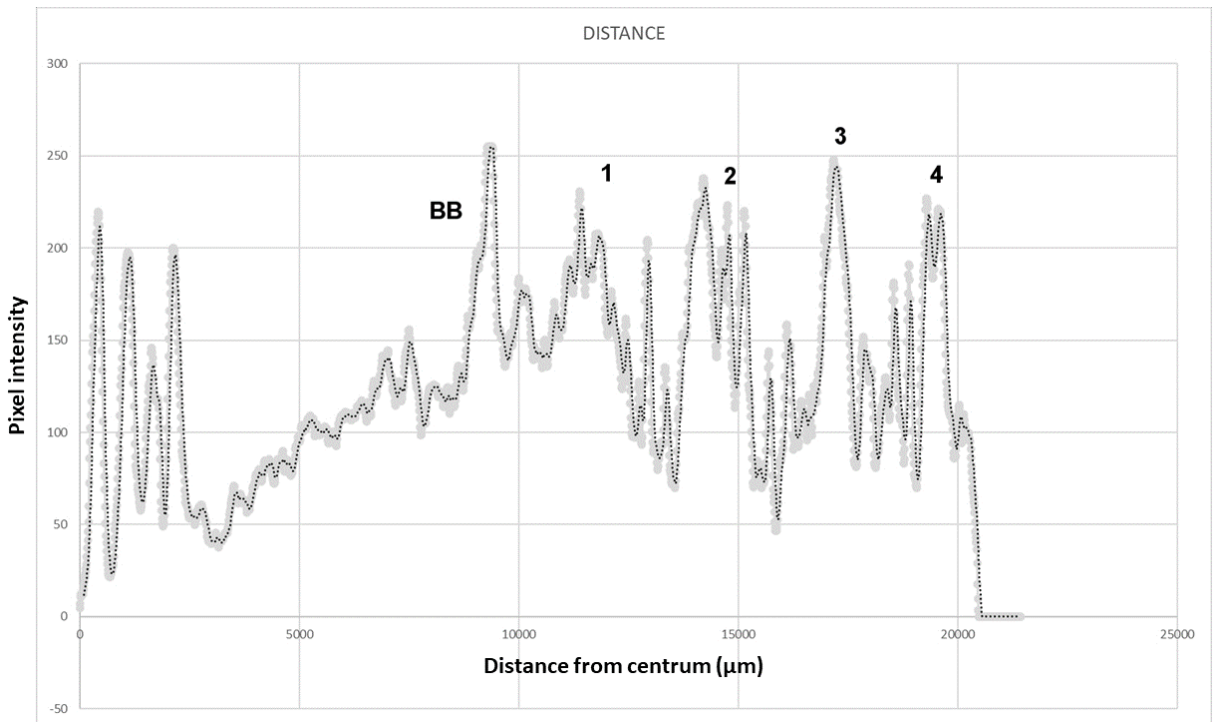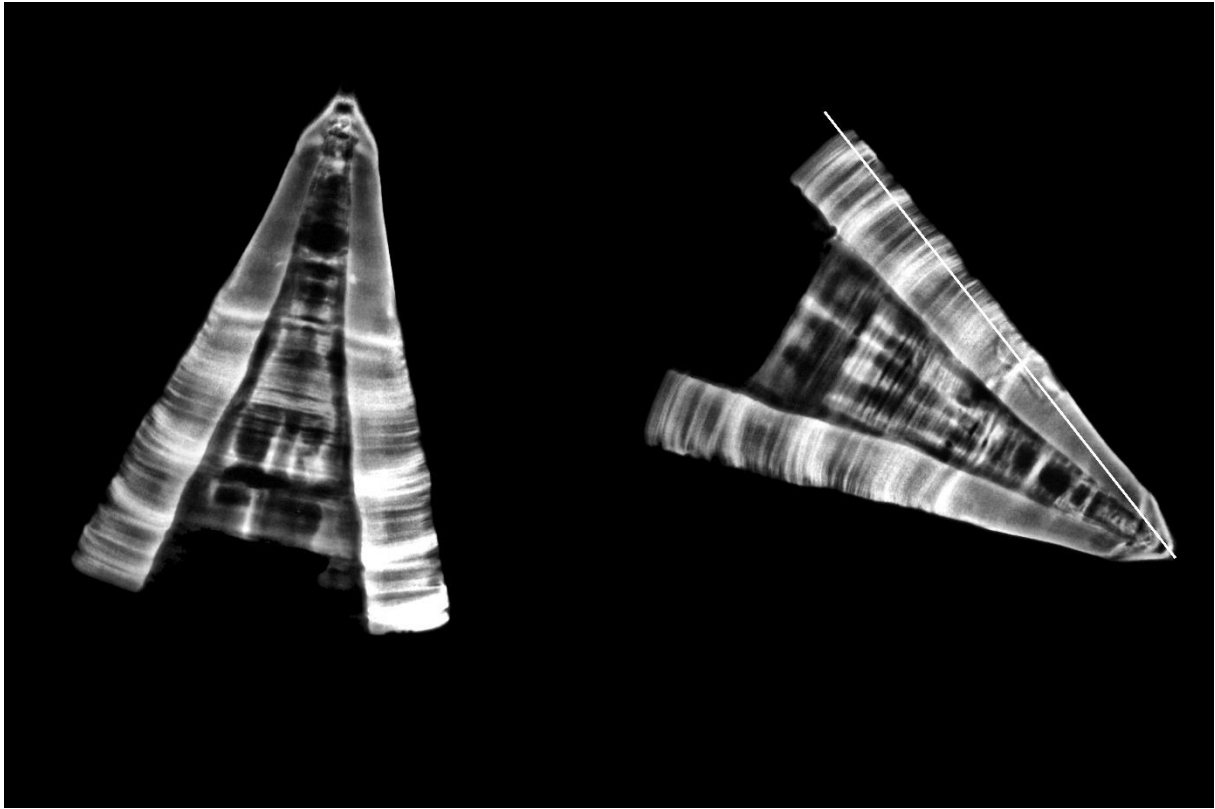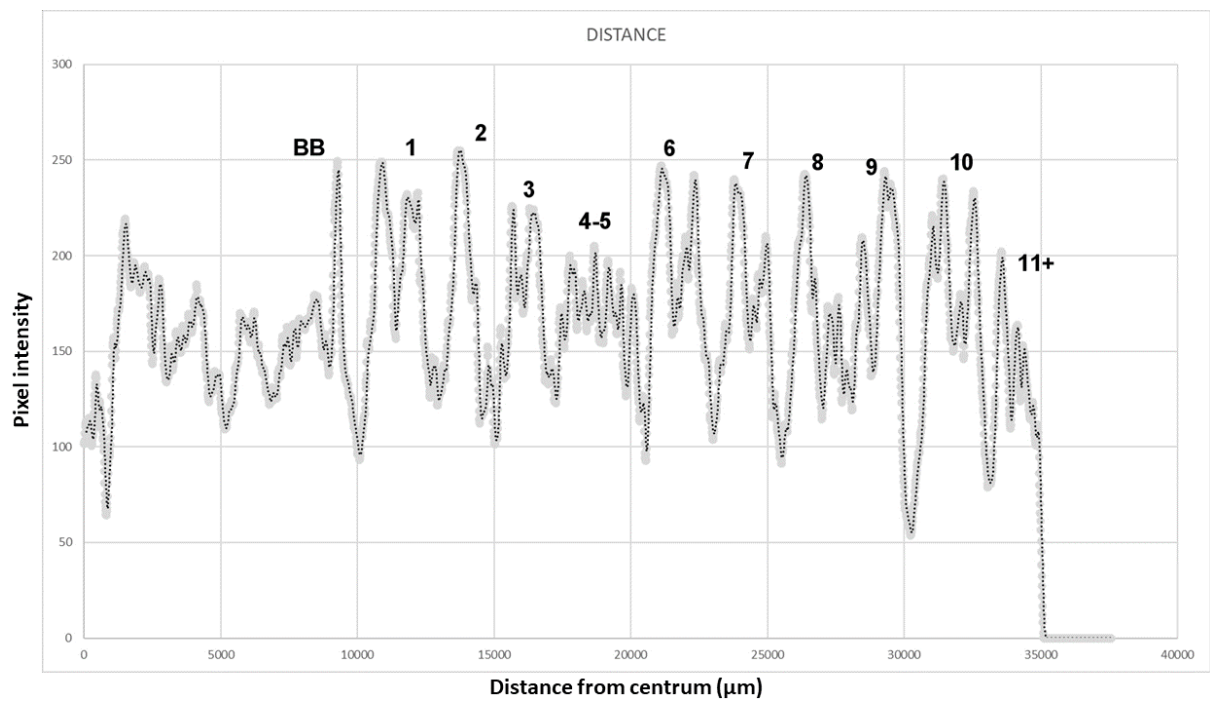
Figure A2: **Thin section x-ray of ururoa_2 and its density profile (taken along the white line) indicating the number of band patterns.** BB = birth band.

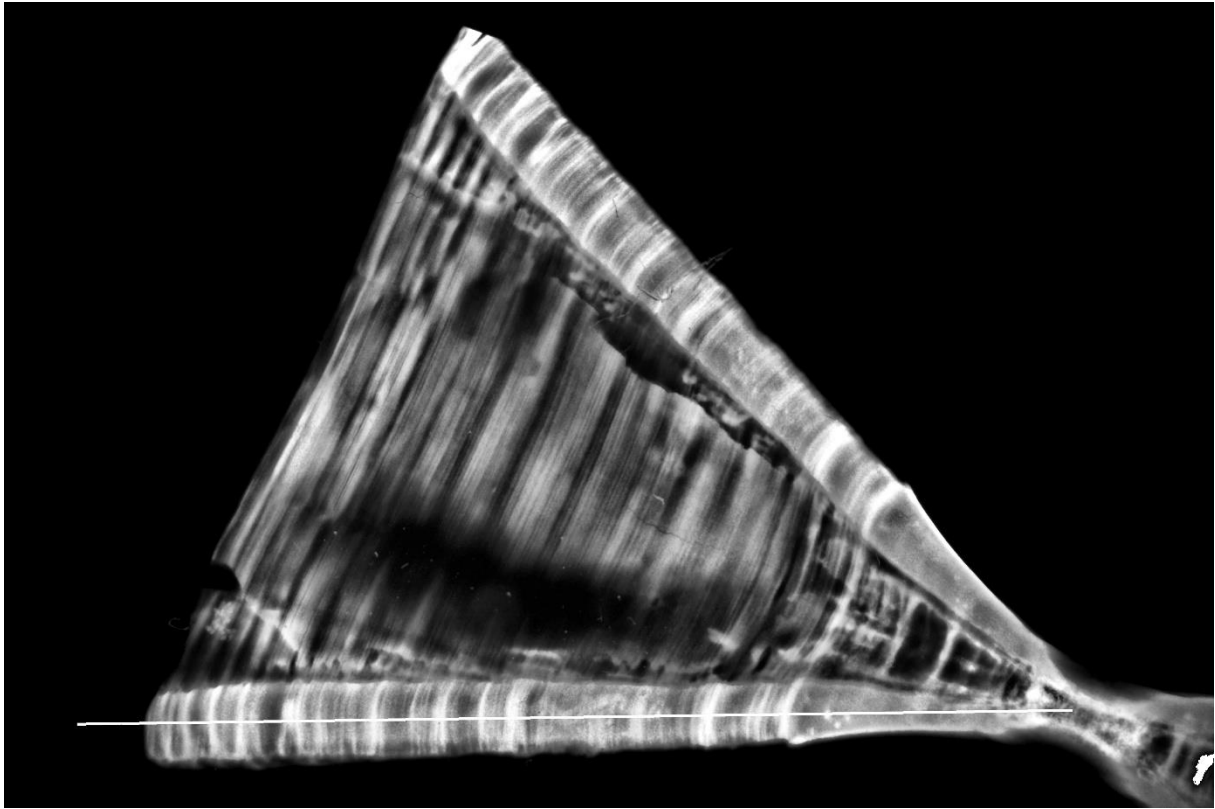**Figure A3:** **Thin section x-ray of ururoa_7 and its density profile (taken along the white line) indicating the number of band patterns.** BB = birth band.