Age and growth of the whiskery shark, Furgaleus macki, from southwestern Australia

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Synopsis

Age and growth of the whiskery shark, *Furgaleus macki*, from southwestern Australia were examined using vertebral ageing and tag-recapture data. The readability of bands on the vertebral centra varied markedly between individuals. Four readers were used to make band counts, with the most experienced reader having the lowest 'index of average percent error' and the highest level of agreement with final counts. Marginal increment analysis indicated that opaque bands form in January. With parturition occurring from August to October, size data suggests that the first band is probably formed 15–17 months after birth. The age at maturity was estimated to be 4.5 years for males, and 6.5 years for females. The oldest male was 10.5 years, and oldest female was 11.5 years. Von Bertalanffy growth parameters for males were $L_{\infty}=121.5\,\mathrm{cm}$ fork length, $K=0.423\,\mathrm{year}^{-1}$, $t_0=-0.472\,\mathrm{years}$, were $L_{\infty}=120.7\,\mathrm{cm}$ fork length, $K=0.369\,\mathrm{year}^{-1}$, $t_0=-0.544\,\mathrm{years}$ for females, and were $L_{\infty}=118.1\,\mathrm{cm}$ fork length, $K=0.420\,\mathrm{year}^{-1}$, $t_0=-0.491\,\mathrm{years}$ for combined sexes. Data from a tag recapture study were analysed using a maximum likelihood method to verify the estimates of growth parameters from vertebral ageing. Von Bertalanffy growth parameters from the tag recapture study were $L_{\infty}=128.2\,\mathrm{cm}$ fork length, $K=0.288\,\mathrm{year}^{-1}$, $t_0=-0.654\,\mathrm{years}$. The two methods of estimating growth parameters produced similar results, with rapid growth until approximately 5 years of age, after which there was little increase in length.

Introduction

The whiskery shark, *Furgaleus macki* (Whitley, 1943), is a triakid shark endemic to the continental shelf waters of southern Australia between North-West Cape and eastern Victoria (Last & Stevens 1994). They are born at approximately 22 cm fork length (FL), males mature at 107 cm FL, females mature at 112 cm FL, and reach a maximum size of approximately 130 cm FL (Simpfendorfer & Unsworth 1998a).

A demersal gillnet and longline fleet operating in the region between the mid-west coast of Western Australia and the Great Australian Bight target F. macki, as well as dusky, Carcharhinus obscurus, sandbar, Carcharhinus plumbeus, gummy, Mustelus antarcticus and school, Galeorhinus galeus sharks (Lenanton et al. 1989, Simpfendorfer & Donohue 1998). This fishery began in the early 1940s, but significant catches of *F. macki* were not made until the 1970s¹. Annual catches of 400–600 tonnes (live weight) were made during the 1980s. Reductions in abundance, restrictions on the level of effort allowed in the fishery, and changing targeting practices, resulted in significant decreases in catch during the 1990s, with current annual catches of between 200 and 250 tonnes (Simpfendorfer & Donohue 1998).

¹ Heald, D.I. 1987. The commercial shark fishery in temperate waters of Western Australia. Fisheries Department Western Australia Report (75). 71 pp.

Falling catch rates in the 1980s prompted the Western Australian Government, through its agency Fisheries Western Australia, to introduce a management plan which created a limited entry, input controlled, fishery (Lenanton et al. 1989). A research program was established in 1994 to collect biological data on the key commercial shark species caught by the fishery, and improve stock assessments to provide information to resource managers. This paper reports the results of research aimed at determining the age and growth of *F. macki* in south-western Western Australia based on vertebral ageing and tag-recapture data.

Materials and methods

Vertebral analysis

Furgaleus macki were sampled onboard commercial gillnet vessels operating in south-western Western Australia and from fish markets, where the catch was sold, between April 1993 and October 1997. Commercial vessels used 16.5 cm or 17.8 cm stretched mesh gillnets with a height of approximately 2 m and lengths from 3.5 to 7.2 km. Nets were demersal and set for periods from 4 to 24 h. The majority of specimens were obtained from the commercial nets during normal fishing operations. Samples of smaller F. macki were obtained using gillnets with a mesh size of 10 cm which were deployed from commercial fishing vessels. These nets were constructed to specifically target smaller F. macki (<90 cm FL) that were not caught by the larger mesh sizes used by the commercial fishery.

Onboard commercial vessels specimens were sexed, fork length measured to the nearest centimetre, and a section of the vertebral column from the anterior of the neck region removed. Specimens obtained from fish markets had been partially processed when examined and the only length measure available was partial length (origin of first dorsal fin to dorsal origin of caudal fin). The relationship between partial length (PL) and fork length (FL), with measurements in centimetres, is:

$$FL = 18.2 + 1.408PL$$
 $(n = 327, r^2 = 0.832).$

The removal of viscera, pelvic fins and claspers by fishers made it impossible to determine the sex of specimens from markets.

Vertebrae were stored frozen until processed. After defrosting, excess tissue was excised and individual centra separated before immersion in 5% sodium hypochlorite solution to remove any remaining flesh. Immersion times in hypochlorite varied with the size of the vertebrae and the age of the solution. Cleaned centra were dried in an oven at 50°C. Clean, dry centra were embedded in fibreglass resin and sectioned longitudinally using a diamond tipped blade. Sections were ground on wet and dry paper until approximately 300 microns thick. Micro-radiographs were made by placing sections on top of a light-proof bag containing Structrix D4 FW scientific grade film (Agfa) and exposing them in a soft X-ray machine (Hewlett-Packard Faxitron 43805) at 25 kV and 2 ma for 90 s. Films were developed using standard developing procedures.

Micro-radiographs were prepared of three separate centra from each individual. Micro-radiographs were examined under a dissecting microscope with transmitted light. The radius of vertebrae were measured using an optical micrometer. The relationship between vertebral radius (*S*) and shark fork length (FL) was determined by fitting a power curve:

$$FL = uS^v$$
,

where u and v are constants. When the value of v equals one, the relationship is linear. Comparison of FL-S relationships between males and females were undertaken using analysis of covariance (ANCOVA).

Counts of the growth bands (defined as a transparent band, which was dark on the micro-radiographs, and the adjacent opaque band, which was white on the micro-radiographs) were made for each of the three micro-radiographs from each individual. Counts were made without knowledge of the size, sex, or previous results for the individual. Four readers were used to make counts, reading each of the three microradiographs from each specimen. Reader A was a biologist with experience in shark ageing, readers B and C were biologists without experience in shark ageing, and reader D was a laboratory technician with experience in ageing teleost fishes using otolithes and scales. The birth mark was identified by a change in angle, often with an associated opaque band, on each microradiograph, and the number of growth bands formed beyond this were counted. Each micro-radiograph was assigned a qualitative readability on a scale: 0, unreadable; 1, banding pattern visible but impossible to interpret accurately; 2, bands observable, but several difficult to interpret; 3, bands observable, but 1 or 2 difficult to interpret; 4, banding pattern unambiguous. The consensus count for each individual for each reader was determined by taking the count that matched in at least two of the three micro-radiographs. If the counts for each of the three micro-radiographs were all different that individual was excluded from analysis for that reader. The same approach was used to determine the final number of bands in each specimen, with a consensus reached between the final counts for each reader.

The index of average percentage error (IAPE), was calculated for the band counts of each reader using the method described by Beamish & Fournier (1981):

IAPE =
$$\frac{1}{N} \sum_{j=1}^{N} \left(\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \right) \times 100,$$

where N is the number of animals aged, R is the number of readings done, X_{ij} is the age of the jth animal at the ith reading, and X_j is the mean age of the jth fish from i readings.

The periodicity of band formation was evaluated using marginal increment analysis (e.g. Branstetter & Stiles 1987, Cailliet et al. 1990). The distance of the final opaque band, and the penultimate opaque band, from the edge of the centrum were measured using an optical micrometer for micro-radiographs that had clear band patterns and undamaged centrum edges. The marginal increment was taken as the distance from the last band to the edge of the centrum as a proportion of the distance between the last and the penultimate bands. Marginal increments were compared between months of capture using a Kruskal-Wallis one way analysis of variance on ranks.

A modified form of the von Bertalanffy equation was fitted to the length-at-age data to ensure that the curve passed through the known size at birth:

$$L_T = L_0 + (L_\infty - L_0)(1 - e^{-KT}),$$

where L_0 is the length at time zero (size at birth = $22 \,\mathrm{cm} \,\mathrm{FL}$), L_T is the length at time T, L_∞ is the asymptotic length, and K is the Brody growth coefficient. The time at length zero (t_0) was calculated by substituting $L_T = 0$ and solving for T. Only specimens which had a readability of two or higher were used in the length at age analysis. This approach is similar to that used by Goosen & Smale (1997).

Tag-recapture data

Furgaleus macki were tagged and released in southwestern Australia between March 1994 and March 1998. Specimens were obtained onboard commercial fishing vessels as described for vertebral analysis. Sharks were measured, sexed and tagged using Jumbo Rototags (Dalton Supplies) inserted into the first dorsal fin. Information on tag recaptures, including date, location and length were reported by commercial fishers operating in the demersal gillnet and demersal longline fishery. Fishers operating in the fishery were provided with tape measures and trained how to measure fork length in an attempt to improve accuracy of recapture details.

Length data from tag-recaptures were analysed using the method of Francis (1988) that fits a modified form of the von Bertalanffy growth curve using a maximum likelihood technique. This model estimates six parameters – growth rates (g_{α} and g_{β}) at two sizes (α and β), standard deviation of the growth increment (ν), mean measurement error (m), standard deviation of the measurement error (s) and contamination probability(p_c). The change in length (ΔL) for a shark of length L_1 at liberty for a given period (ΔT) is given by:

$$\Delta L = \left[\frac{\beta \cdot g_{\alpha} - \alpha \cdot g_{\beta}}{g_{\alpha} - g_{\beta}} - L_{1} \right] \times \left[1 - \left(1 + \frac{g_{\alpha} - g_{\beta}}{\alpha - \beta} \right)^{\Delta T} \right].$$

The likelihood function is:

$$\lambda = \sum_{i} \log[(1-p)\lambda_i + p/R],$$

where

$$\lambda_i = \frac{\exp(-0.5(\Delta L_i - \mu_i - m)^2/(\sigma_i^2 + s^2))}{[2\pi(\sigma_i^2 + s^2)]^{0.5}}.$$

In this study the standard deviation of the growth increment was assumed to be proportional to the time at liberty. The two growth rate parameters can be used to estimate the von Bertalanffy K and L_{∞} values:

$$K = -\ln(1 + ((g_{\alpha} - g_{\beta})/(\alpha - \beta))),$$

$$L_{\infty} = (\beta g_{\alpha} - \alpha g_{\beta})/(g_{\alpha} - g_{\beta}).$$

The value of t_0 was estimated by positioning the von Bertalanffy curve such that $L_0 = 22 \,\mathrm{cm}$ FL. Only recaptures for animals that had been at liberty for 60 days or more were used in the analysis.

Results

Vertebral analysis

Vertebrae from 598 *F. macki* were processed and microradiographs produced. The length of specimens varied

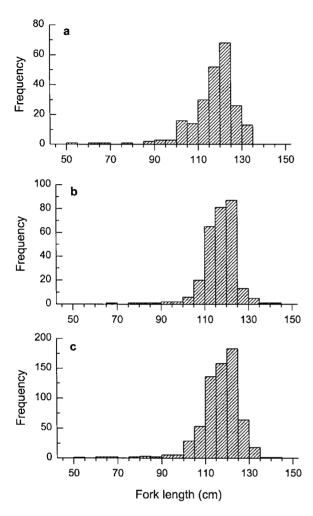


Figure 1. Length frequency distributions of (a) male, (b) female, and (c) combined sexes (including individuals for which sex could not be determined) Furgaleus macki from which vertebrae were used in age determination.

in size from 50 to 140 cm FL, with the majority between 100 and 130 cm FL (Figure 1).

The radius of centra ranged from 3.4 to 8.1 mm, with the majority between 5.0 and 7.3 mm (Figure 2). There was no significant differences in the relationship between radius and fork length for males and females (ANCOVA, F=0.065, p=0.799), and so the data were combined. The relationship between radius and fork length for 534 individuals was allometric ($r^2=0.488$), with the 95% confidence interval of v being 0.53–0.63.

The clarity of bands on centra varied considerably between individuals. The readability of microradiographs from 102 (17%) individuals was less than

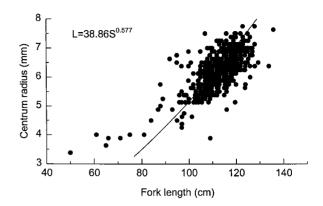


Figure 2. Relationship between centrum radius and fork length of 534 Furgaleus macki from south-western Australia.

two, and these were excluded from the analysis of age. Of the remaining 496 vertebrae 308 (62%) had a readability of 2, 184 (37%) had a readability of 3, and 2 (1%) had a readability of 4.

Growth band counts varied between readers. The average band counts were similar for readers A, B, and D, but were at least 1.5 bands higher for reader C (Table 1). The IAPE of band counts for each reader did not differ greatly, and was lowest for reader A and highest for reader D. The number of specimens for which consensus counts could be reached were highest for reader A and lowest for reader C. Final band counts across all readers were obtained for a total of 277 individual F. macki, 258 of which were from specimens with readability values of 2 or greater. Individual readers contributed differentially to the final counts. Reader A had the highest level of agreement between consensus and final counts, readers B and D had similar levels of agreement, and reader C had a low level of agreement.

Marginal increments were measured from 146 individual F. macki. Lowest monthly mean marginal increments were recorded in January, with an increasing trend throughout the year (Figure 3). This indicated that a single opaque band may be formed each year in F. macki. However, marginal increments did not vary significantly between months (Kruskal-Wallis one way analysis of variance on ranks, H=15.1, d.f. =10, p=0.128). Assuming that opaque bands formed in January the first band would have been formed either at an age of 3 to 5 months, or 15 to 17 months, since parturition occurs from August to October (Simpfendorfer & Unsworth 1998a). Given the size of individuals that had a single band (50–61 cm FL) it was assumed that the band was formed after 15–17 months as growth to

Reader	Average count	IAPE	Number of consensus counts	% agreement with all final counts (n = 277)	% agreement with final counts for vertebrae with readability ≥ 2 (n = 258)
A	6.33	8.46	452	70.4	75.2
В	6.01	9.60	412	57.0	61.2
C	7.95	9.39	413	29.6	29.2
D	6.44	10.20	317	62.4	67.0
Final	6.57	_	277	_	_

Table 1. Assessment of band counts for Furgaleus macki from south-western Australia by individual readers.

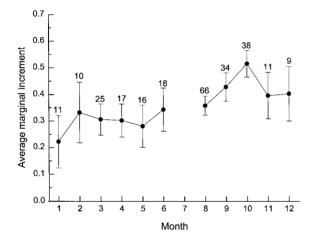


Figure 3. Mean monthly marginal increments of opaque bands for Furgaleus macki from south-western Australia. Error bars represent \pm one standard error. Numbers above each month indicate sample sizes.

these sizes within 3–6 months was not consistent with the growth rates of other species of triakid sharks (e.g. Yudin & Cailliet 1990, Kusher et al. 1992, Moulton et al. 1992, Rountree & Able 1996, Goosen & Smale 1997).

The majority of specimens that had consensus counts were aged between 4.5 years and 10.5 years. The maximum age of an individual from final counts (consensus between readers) was 10.5 years from males, and 11.5 years for females. The maximum age based on the consensus for a single reader (but not between readers) was 12.5 year, with the highest individual band count by any reader being 16 (=16.5 years).

Von Bertalanffy growth curves were fitted to the length-at-age data assuming that bands were formed annually after the first band was completely formed after 18 months (Figure 4). Growth of males and females appeared to be rapid over the first three or four years, but subsequently slowed. There appeared to be little or no increase in length after four or six years of age for males and females, respectively. The von Bertalanffy growth parameters for males, females and combined sexes were similar (Table 2), with *K* values higher for males and combined sexes, than for females.

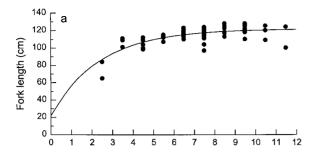
Tag recapture data

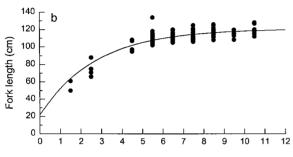
A total of 512 *F. macki* ranging from 81 to 135 cm FL, with most between 95 and 120 cm FL, were tagged and released in south-western Australia (Figure 5). Fifty tagged *F. macki* were recaptured after periods at liberty between 1 and 1226 days (3.4 years), and ranged in size from 98 to 134 cm FL. Growth analysis was conducted on 29 individuals that had sufficient recapture data, and had been at liberty at least 60 days (25 were at liberty greater than 300 days).

The von Bertalanffy growth parameters derived from the Francis (1988) method were $K=0.288~{\rm year^{-1}}$ and $L_{\infty}=128.2~{\rm cm}$ FL. By fixing the size at birth at 22 cm FL the t_0 value was estimated to be -0.654 years. The growth curve described by these parameters is similar to that of the combined sexes growth curve derived from the vertebral ageing data (Figure 4c, Table 3).

Discussion

Micro-radiographs have been used to aid the ageing of a variety of triakid sharks, including *Galeorhinus galeus* (Ferreira & Vooren 1991), *Mustelus antarcticus* (Officer et al. 1996), *Mustelus californicus* (Yudin & Cailliet 1990), *Mustelus henlei* (Yudin & Cailliet 1990),





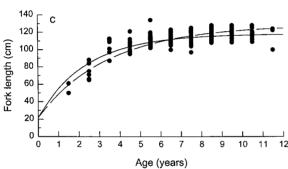


Figure 4. Von Bertalanffy growth curves for (a) male, (b) female, and (c) combined sexes (including individuals for which sex could not be determined) Furgaleus macki from south-western Australia. Dashed line on (c) represents the von Bertalanffy growth curve estimated from tag-recapture data using the Francis (1988) model.

and *Mustelus manazo* (Cailliet et al. 1990, Yamaguchi et al. 1996). However, as Officer et al. (1996) reported, micro-radiographs can at times produce band patterns that are difficult to interpret due to what were termed 'major' and 'minor' marks. 'Major' marks represented annual bands, while 'minor' marks were formed interannually with no regular periodicity. The occurrence of 'minor' marks on micro-radiographs of *F. macki* centra may account for the relatively high degree of variability between readers, with only 52% of readable vertebrae producing final counts. The use of consensus counts within and between readers to produce final

Table 2. Von Bertalanffy growth parameters for Furgaleus macki from south-western Australia estimated using length-at-age data.

Parameter	Male	Female	Combined sexes
$\overline{L_{\infty} \text{ (cm FL)}}$	121.5	120.7	118.1
K (year ⁻¹)	0.423	0.369	0.420
t_0 (years)	-0.472	-0.544	-0.491
n	67	112	258

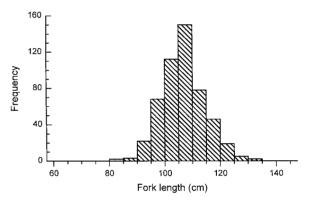


Figure 5. Length frequency distribution of 512 tagged Furgaleus macki released in south-western Australia.

Table 3. Estimates of parameters from the Francis (1988) growth model for 29 tagged and recaptured *Furgaleus macki* from south-western Australia.

Parameter	Estimated value		
g _α	7.05 cm FL year ⁻¹		
g_{β}	2.04 cm FL year ⁻¹		
v	0.13 cm FL year ⁻¹		
m	0.14 cm FL		
S	1.18 cm FL		
p_c	0.20		

counts, and a prior knowledge of Officer et al.'s (1996), conclusions is assumed to have reduced the potential misinterpretation in the counting of bands for *F. macki*.

The results of this study indicate that previous experience may be an important factor in the ageing of elasmobranchs when using counts of bands on vertebral centra. The reader with greatest experience in shark ageing produced the lowest IAPE, the highest level of consensus between readings, and had the largest number of consensus counts used to calculate final

counts. The reader with previous experience in ageing teleosts also had a high level of consensus counts used to calculate final counts, but had a low level of agreement between counts. The two readers without previous experience had similar IAPE's and consensus between counts, but had very different input to the final counts. Reader C produced counts that were much greater on average than all other readers, suggesting that they may have had difficulty distinguishing between the 'major' and 'minor' marks as described by Officer et al. (1996).

The cycle in marginal increments for *F. macki* suggest that like many other species of triakid shark, bands on the vertebral centra are formed annually (e.g. Smith 1984, Cailliet et al. 1990, Yudin & Cailliet 1990, Ferreira & Vooren 1991, Kusher et al. 1992, Yamaguchi et al. 1996). This conclusion is further supported by the close agreement between von Bertalanffy growth parameters derived from the vertebral ageing and tagrecapture data. Further work to validate the periodicity of band formation for *F. macki* would be useful in confirming the annual nature of the bands.

The formation of the first opaque band at periods other than one year after birth occurs when parturition and opaque band formation occur at different times of the year. For example, Branstetter et al. (1987) reported that the tiger shark, Galeocerdo cuvier, was born in summer and the first band was formed in winter six months after birth. Bands were subsequently formed annually in winter. Branstetter & Stiles (1987) reported a similar occurrence in the bull shark, Carcharhinus leucas. In contrast to G. cuvier and C. leucas, F. macki is born in the period from August to October with band formation complete in January. In this situation the first band would be expected to form after three to five months. However, to achieve the sizes observed for F. macki with a single band, individuals would have to more than double their length in this time. Rountree & Able (1996) reported that Mustelus canis grew to double the size at birth within six months while feeding in highly productive estuarine nurseries. While it is possible that F. macki achieves very high growth rates it is more likely, based on data from other triakid species, that they reach two to three times the size at birth after 15 to 17 months. Growth rates such as these are also supported from the tag-recapture data. However, the lack of small individuals in the tag-recapture data makes the estimation of early growth rates uncertain. Further ageing and tagging of F. macki smaller than 80 cm FL will provide useful data on the growth of juveniles.

Simpfendorfer & Unsworth (1998a) reported that the size at maturity for F. macki in south-western Australia was 107 cm FL for males and 112 cm FL for females. These sizes correspond to ages of approximately 4.5 years for males, and 6.5 years for females, based on the von Bertalanffy growth curves derived from vertebral analysis. The maximum observed ages of F. macki (10.5 years for males and 11.5 years for females) were of a similar magnitude to several other species of triakid sharks. For example, Yamaguchi et al. (1996) reported that Mustelus manazo has a maximum age of 8 years for males and 10 years for females. Yudin & Cailliet (1990) reported the maximum age of Mustelus californicus as 9 years, and for M. henlei as 13 years. Kusher et al. (1992) aged male Triakis semifasciata to a maximum of 24 years. On the basis of the age distribution from the commercial catches of F. macki it appears that this species is recruited to the gillnet fishery at an age of approximately 5 years. This is probably a result of the size selectivity of the gillnets used in the fishery. However, there also appears to be a difference in the distribution of animals above and below approximately 90 cm FL which may influence the age at which they are recruited to the fishery. Extensive experimental netting within the area of the fishery (10-100 m depth) using small mesh gillnets (5-10 cm mesh) caught only a small number of juvenile F. macki (Simpfendorfer unpublished data). This suggests that the main nursery areas may be in deeper water or habitats not fished by the commercial fishery.

The Body growth coefficient (K) estimated for F. macki from vertebral analysis were higher than those previously reported for other species of the family Triakidae. Most values of K have been less than 0.3 year⁻¹ (e.g. Yudin & Cailliet 1990, Cailliet et al. 1990, Ferreira & Vooren 1991, Moulton et al. 1992, Yamaguchi et al. 1996). The small differences in K between vertebral ageing and tag-recapture methods may have been the result of gillnet selectivity in the commercial fishery from which the vertebral samples were obtained. Simpfendorfer & Unsworth (1998b) estimated the peak selectivity of the commercial gillnets (16.5 and $17.8\,\mathrm{cm}$ mesh) to be 110 to $120\,\mathrm{cm}$ FL. Individuals over this size would have been underrepresented in the catch and the upper size of animals in the catch constrained. As a result the value of L_{∞} may have been under-estimated and K over-estimated. If this was the case, growth parameters estimated from the tag-recapture data may be more representative of the growth of *F. macki* than those from the vertebral analysis.

The use of the Francis (1988) model for the analysis of the tag-recapture data allowed for measurement error to be estimated. The low value of m and s from the F. macki data suggest that fork length measurements were made relatively accurately at the time of release, and also by commercial fishers at the time of recapture. The Francis model does not allow for release and recapture measurement error to be estimated separately so it is not possible to determine the accuracy of these two measurements on the basis of these data. Although a small level of measurement error at the time of release would not be unexpected, the provision of tape measures and training to commercial fishers probably assisted in keeping the overall measurement error low. Results of the Francis model also indicate that the contamination probability was relatively high (20%). This indicates that about one fifth of the data used were outliers, possibly because of errors such as incorrect length measurement (e.g. measures other than fork length) or mis-reporting (e.g. wrong tag number, wrong recapture date).

The growth of F. macki can be separated into two distinct phases. The first phase occurs from birth to an age of approximately four and a half years. Growth during this phase is rapid with individuals increasing from approximately 22 cm FL at birth to over 100 cm FL. At the end of this phase, individuals are near to maturity. The rapid growth of F. macki observed during this phase is similar to that reported for Mustelus canis (Rountree & Able 1996) and M. henlei (Yudin & Cailliet 1990). The second phase of growth, from approximately five years onwards, is characterised by a limited increase in length. The plateau in the growth during this phase resulted in a relatively low value of L_{∞} . The change in growth rates of F. macki at around five years of age is possibly the result of sacrificing somatic growth for reproductive investment.

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