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A PRELIMINARY STUDY OF AGE AND GROWTH OF THE SMOOTH-HOUND SHARK *MUSTELUS MUSTELUS* (TRIAKIDAE)

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Age and growth of the smoothhound shark *Mustelus mustelus* was investigated from banding patterns in sectioned vertebral centra of 136 specimens, using a modified Alizarin red S technique to stain bands on the centra. Fabens' method ($L_t = L_\infty - (L_\infty - L_0)e^{-Kt}$) was statistically more robust than the Von Bertalanffy method, and provided growth models of $L_t = 2\ 041.8 - (2\ 041.8 - 390)e^{-0.06t}$ for females and $L_t = 1\ 530.1 - (1\ 530.1 - 390)e^{-0.1t}$ for males. The Von Bertalanffy growth model was, however, used because of insignificant differences between the two methods. Parameters obtained were: $L_t = 2\ 049.6\ (1-e^{-0.06(t+3.55)})$ for females and $L_t = 1\ 451\ (1e^{-0.12(t+2.14)})$ for males. The predicted age at maturity was 6–9 years for males and 12–15 years for females. The oldest female in the samplewas estimated to be 24 years and measured 1 640 mm total length (*TL*); the oldest male was estimated to be 17 years and measured 1 280 mm *TL*. Results are considered preliminary, because the assumptions with regard to timing of bands formation could not be validated.

The genus *Mustelus* (Family Triakidae, Order Carcharhiniformes), commonly called smoothhounds, has at least 20 species distributed worldwide, which are abundant in both temperate and tropical nearshore waters (Compagno 1984). Off southern Africa, one of the most common species is *Mustelus mustelus* (Linnaeus, 1758), which is a large, plain grey or black-spotted smoothhound. It is also widespread in the Eastern Atlantic Ocean and the Mediterranean Sea (Compagno *et al*. 1989). Smoothhounds are commonly caught by commercial trawlers, linefishing boats and shore-based anglers in southern African waters. Traditionally, they have not used for human consumption, but this attitude is beginning to change and these sharks are now targeted along the South African coast.

Growth is of fundamental importance to an understanding of the life history of a fish species. More importantly, in conjunction with length and mass data, it provides the fisheries biologist with information necessary for stock assessment of populations. Growth bands deposited in vertebral centra have been used for age determination of sharks. The growth pattern in a centrum consists of a series of incremental zones concentric about the centre. Cailliet *et al*. (1983) found that the zones are the result of two kinds of concentric marks. They defined a "ring" as the narrowest kind of concentric mark observed, and used the term "band" to refer to wider concentric marks that may be composed of groups of rings. Bands formed during summer are usually opaque and calcified, whereas those formed during winter are translucent and less calcified (Cailliet *et al*. 1983, Cailliet and Radtke 1987, Martin and Cailliet 1988).

Various authors have postulated that these growth zones are deposited annually, but few critical tests of this hypothesis, such as age validation, have been accomplished, especially for elasmobranchs (Beamish and McFarlane 1983, Smith 1984, McFarlane and Beamish 1987, Brown and Gruber 1988, Kusher *et al*. 1992). Inaccurate estimates of age can result in very serious errors in the understanding and management of fish populations (Beamish and McFarlane 1983). The objectives of this study were to estimate the age and growth of *M. mustelus* from vertebral growth bands and to construct growth curves for males and females. Vertebral bands have been used for estimating growth and longevity of five other species of *Mustelus* (Francis and Francis 1992).

MATERIAL AND METHODS

Specimens of *M. mustelus* were collected between Mossel Bay and Port Elizabeth, South Africa, over the period December 1983 to July 1991. All sharks were sexed and total length (*TL*) was measured to the nearest millimetre (Compagno 1984). For age determination, approximately five centra were excised from the vertebral column under the first dorsal fin. The vertebrae in this position are the largest in the vertebral column. Excess tissue was removed by gently scrubbing it off the vertebrae after boiling the material in water for a few minutes. The centra were then stored in 50% alcohol until processed. They were not preserved in formalin because of the decalcifying action of formic acid (LaMarca 1966).

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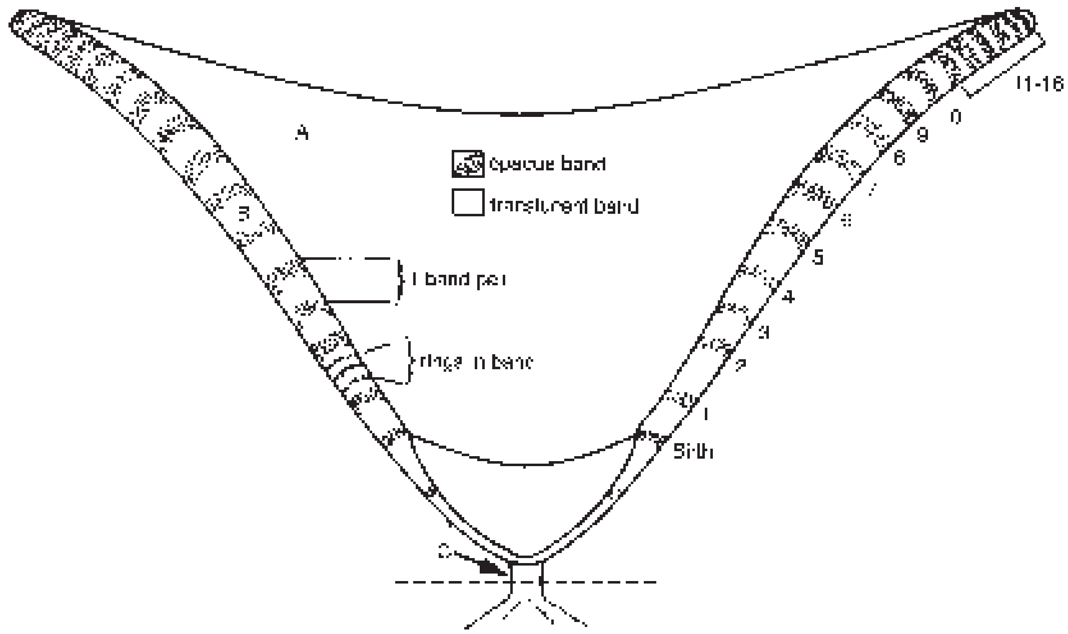

Fig. 1: Diagrammatic representation of a longitudinal vertebral section of *M. mustelus* used for age determination. 1,2,3, etc. = year marks; A = intermedialia; B = corpus calcareum; C = notochordal remnant (focus)

A resin-embedding and sectioning method was used to prepare the vertebral centra for reading, so that growth zones closely spaced near the margin of a centrum would be clearly distinguishable. Vertebrae were embedded in clear polyester casting resin. To ensure adequate penetration of the resin, the smaller centra were first soaked for 12 h in uncatalysed resin diluted 1:10 with acetone. Different size troughs were used to mould the individual samples. When thoroughly hardened (after approximately 48 h) and removed from the moulds, the embedded centra were sectioned about 0.2 mm thick along the central longitudinal axis using a jewellers' saw. Three sections along the widest diameter of each centrum were made. Several techniques were tried to improve the definition of the vertebral bands: silver nitrate (Stevens 1975), alizarin red S (LaMarca 1966, Cailliet *et al*. 1983, Gruber and Stout 1983), ninhydrin (Davenport and Stevens 1988) and Harris hematoxylin (Casey *et al*. 1985). X-radiography was also tested and found to be the least successful technique for elucidating bands.

Alizarin red S was selected because of its ease of use and consistent results, but the original method was slightly modified to adapt it to the sectioned vertebrae. The stain was prepared by mixing the supernatant of a saturated aqueous solution of alizarin red S with 0.2% NaOH in a 1:9 ratio. Only two of the most clearly defined sections from each centrum were used for staining. The first section was stained for one minute in the solution and then washed in tap water for 10 minutes. The second section was stained for two minutes in the solution, washed for 10 minutes in tap water and then soaked in 3% H_2O_2 for one hour to improve differentiation. Finally, the sections were rinsed in tap water to remove excess H_2O_2. The sections were then attached to a glass microscope slide with clear enamel nail polish.

All vertebrae were prepared and read by one reader, using predetermined objective criteria for band definition. This technique may minimize any bias introduced by multiple readers (Sminkey and Musick 1995). Three independent blind readings were made of the number of bands present, and of the edge characteristics of each centrum. Sections were read using a stereo or dissecting microscope at 10× magnification with transmitted light from below. The criterion used to define an annual growth band was that the band must occupy a distinct narrow opaque zone relative to a wider adjacent translucent zone in the corpus calcareum (Fig. 1). Other faint marks were considered to be rings within bands. The birth mark was defined as the first distinct mark distal to the focus that coincided with a slight change in the angle of the corpus

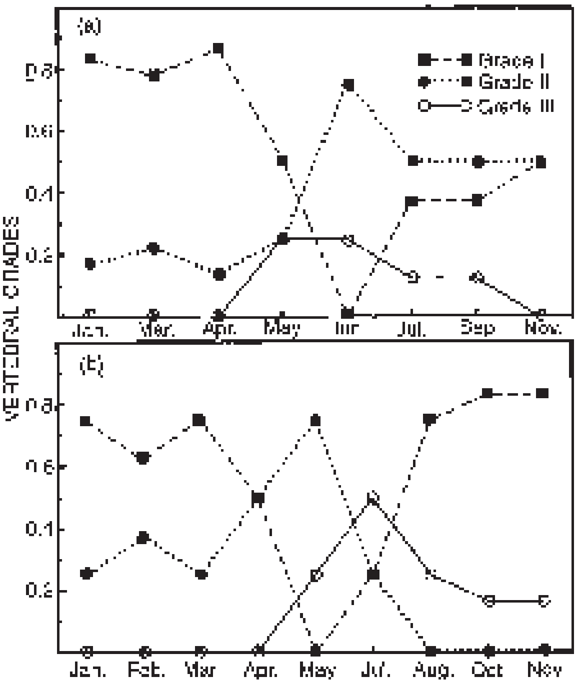

Fig. 2: Monthly variation in the proportions of (a) female and (b) male *M. mustelus* having each three vertebral grades of centrum edges

calcareum. The next mark was designated "1" and interpreted to be the first year mark and marks 2, 3, 4, etc. as succeeding year marks (Fig. 1).

The clarity of bands was classed into three types: Type I, high band clarity; Type II, medium band clarity; Type III, low band clarity. Only centra of Types I and II were considered for age determination, and then only if at least two counts were equal and the third count did not vary by more than one band. The average percent error index (APEI, Beamish and Fournier 1981) was used to calculate band count precision. Powers (1983) suggested that APEI needs to be <10% for the ageing method to be accepted. Band periodicity was evaluated by comparing date of capture with the state of the peripheral band developing on the centrum edge. The centrum edge was categorized using the grading described by Tanaka and Mizue (1979): Grade I, opaque band forming at the marginal edge; Grade II, narrow translucent band beginning to form on the marginal edge; Grade III, broad translucent band well formed on the marginal edge. Again, only centra of Types I and II centra were considered for edge characterization, but only if all three readings of edge characteristics were the same.

Three different growth models were tested against observed lengths-at-age, using the computer program PC-Yield 2.2 (Punt and Hughes 1989). They were Von Bertalanffy (1957, 3-parameter model), generalized Von Bertalanffy (4-parameter model) and Schnute (1981) growth model. Models were applied to females, males and the combined data set. They were fitted using an iterative, non-linear minimization procedure (Butterworth *et al*. 1989, Punt and Hughes 1989). Minimization of the sum-of-squared absolute (as opposed to relative) differences was used, because the residuals for these models were homoscedastic. Likelihood ratio tests (Draper and Smith 1966) revealed that the 3-parameter Von Bertalanffy model fitted the data better than the generalized Von Bertalanffy and Schnute growth models.

The 3-parameter Von Bertalanffy growth model is described as:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \quad ,$$

where L_t is the total length at age t, L_∞ is the asymptotic length, K is the rate at which L_t approaches the asymptote, and t_0 is the hypothetical age at zero length. Standard errors (*SE*) and 95% confidence intervals (*CI*) for each parameter of the model were calculated using a (conditioned) parametric bootstrap technique (Efron 1981) and the percentile method (500 bootstraps).

An alternative method was also used, with the 3-parameter Von Bertalanffy growth equation being expressed in the form (Fabens 1965):

$$L_t = L_\infty (1 - b e^{-Kt}) = L_\infty - (L_\infty - L_0) e^{-Kt} \quad ,$$

$$b = (L_\infty - L_0)/L_\infty = e^{Kt_0} \quad ,$$

where L_0 is the length at birth. L_0 was taken as 390 mm, which approximates the average length of term embryos and it was the same length as the smallest free swimming individual found (Smale and Compagno 1997). The two unknown parameters were simultaneously estimated by using a non-linear estimation routine with "Solver" in Microsoft® Excel 97. Cailliet *et al*. (1992) and Van Dykhuizen and Mollet (1992) proposed that use of L_0 rather than t_0 would be more suitable for sharks with a well-defined length-at-birth (L_0). This eliminates the questionable assumption that growth *in utero* can serve as a model for *post-partum* growth (Pratt and Casey 1990).

RESULTS

Of the 253 smoothhounds examined, 117 (46 %) had Type III centra and were therefore not considered for further analysis. The remaining 136 centra, 68 fe-

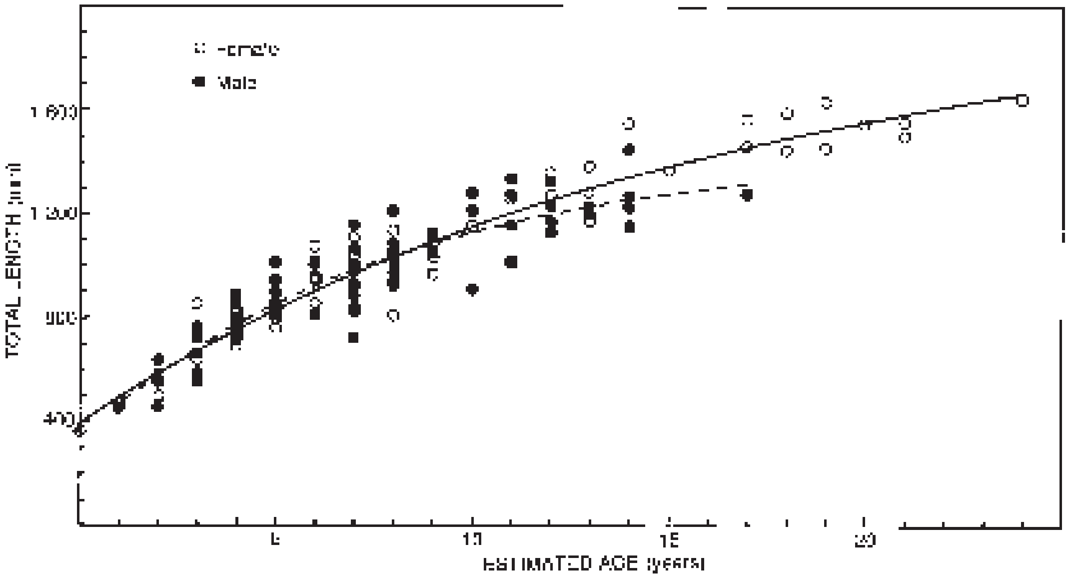

Fig. 3: Calculated Von Bertalanffy (3-parameter) growth curves and observed length-at-age for male and female *M. mustelus*

males (360–1 640 mm) and 68 males (457–1 450 mm), were used for age determination. Whereas bands were noticeable in the intermedialia, they were more clearly distinguished in the corpus calcareum. Vertebrae of younger specimens had a distinct banding pattern, with very little ring formation within bands in the corpus calcareum. As size increased, ring formation became more evident near the edge of the vertebrae. Monthly variation of the centrum edge grade frequency by sex is shown in Figure 2. Because the frequency of Grade I had one large seasonal mode, it was assumed that the bands were laid down annually. The mode in Grade I formed from January to April for females, and from August to March for males.

Females aged between 0 years (embryo) and 24 years corresponded to the smallest (360 mm) and the largest (1 640 mm) specimens sampled. Males of 457 and 1 280 mm were aged as one and 17 years old respectively (Fig. 3). The APEI was calculated at 5.7% for the entire sample and was therefore within the acceptable limits for use of ageing results for population analysis (Powers 1983).

A significant difference between modelled length-at-age for males and females was found using a likelihood ratio test ($F = 2.95$, $df = 3.130$, $p < 0.05$, Punt and Hughes 1989). The fitted Von Bertalanffy models for both sexes are shown in Figure 3 and parameter estimates are given in Table I. Fabens' method also showed a significant difference between modelled length-at-age for males and females, using a likelihood ratio test ($F = 4.55$, $df = 2.132$, $p < 0.025$, Punt and Hughes 1989). Parameter estimates of Fabens' method are given in Table I. No significant differences exist between Fabens' and the Von Bertalanffy method using a likelihood ratio test for male ($F = 0.65$, $df = 1.66$, $p > 0.5$) and female ($F = 0.17$, $df = 1.66$, $p > 0.5$) model fits. Fabens' method is statistically more robust than the Von Bertalanffy model because it has fewer parameters. However, because of insignificant differences between the two methods and the general use of the Von Bertalanffy model, it was decided to present only the Von Bertalanffy model graphically.

DISCUSSION

Analysis of the peripheral edge of the centra indicated an onset of opaque band deposition in late winter or early spring, followed by the development of a translucent band in autumn. A significant difference between opaque (Grade I) and thick translucent (Grade III) band deposition exists (ANOVA; $p < 0.025$ for female, $p < 0.01$ for male), supporting the hypothesis of annual band pair formation. Analysis of the centrum edges of three species of *Mustelus*, one pair

Table I: Parameter estimates using Fabens' method and standard errors (*SE*) and 95% confidence intervals (*CI*) for the Von Bertalanffy growth model fitted to length-at-age data for *M. mustelus*

Parameter	Fabens' method	Von Bertalanffy		
	Estimate	Estimate	*SE*	95% *CI*
		Female (n = 68)		
L_∞	2 041.8 mm, *TL*	2 049.6 mm, *TL*	253.9	1 727.9, 2 644.5
K	0.06	0.06	0.03	0.04, 0.09
t_0	–	–3.55	0.96	–5.31, –1.9
		Male (n = 68)		
L_∞	1 530.1 mm, *TL*	1 451 mm, *TL*	35 190.1	1 270.3, 2 513.8
K	0.1	0.12	0.04	0.06, 0.2
t_0	–	–2.14	1.69	–4.75, –0.7
		Both sexes (n = 136)		
L_∞	1 926.7 mm, *TL*	1 989.4 mm, *TL*	201.8	1 745.1, 2 513.8
K	0.07	0.06	0.01	0.04, 0.08
t_0	–	–3.82	0.7	–5.34, –2.74

of translucent and opaque bands was discerned for each year by (Yudin and Cailliet 1990), supporting annual deposition in this group of sharks.

Casey *et al*. (1985) found that age of older sandbar sharks was usually more difficult to ascertain than that of younger ones, because the centrum bands of the older individuals were difficult to interpret. In the present study, this was also true in older smoothhound sharks, even on vertebral sections that had particularly distinct band definition. The three sections taken from each larger shark often showed variability in band numbers. Only those specimens with close agreement between band numbers were used. However, it was difficult to adhere rigidly to criteria (one year mark = an opaque band + a translucent band), because of the large number of rings near the margin that could alternatively be interpreted as year marks. If future studies prove these rings to be annual depositions, then the maximum age estimates of 17 years for males and 24 years for females obtained in this study are underestimates.

In discussing rings in skeletal structures, Beamish and McFarlane (1983, p. 741) concluded ". . . when growth is reduced . . . it is possible, even probable, that there would be a change in the appearance of an annulus and that the method of age determination will have to be modified. Only by validating the method can it be proven that fish are not older than estimated". The outer rings for the larger specimens are at best difficult to read and at worst may not be annual in adult smoothhound sharks. It is possible that the outer rings reflect changes in the life history patterns, e.g. migrations in males, or alternate-year pupping in females. In captive spotted gully sharks *Triakis megalopterus* injected with oxytetracycline (OTC), Goosen (1997) found that rings within bands are often misinterpreted as annual bands. Such errors in age determination will make a substantial difference in calculating the theoretical maximum reproductive output, which is a major consideration in managing shark fisheries (Casey and Natanson 1992).

The maximum ages of 17 years for males and 24 years for females determined in this study suggest a lifespan much longer than maximum ages reported for other species of the genus *Mustelus*. For example, maximum ages of 16 years for *M. antarcticus* (Moulton *et al*. 1992), 13 years for *M. henlei* (Yudin and Cailliet 1990), 12 years for *M. lenticulatus* (Francis and Francis 1992), and nine years for both *M. californicus* (Yudin and Cailliet 1990) and *M. manazo* (Tanaka and Mizue 1979, Cailliet *et al*. 1990) are given in the literature. No age validation studies were done on any of those species. The term "age validation" used here is *sensu* Beamish and McFarlane (1983), who suggested that the only true validation is OTC marking, coupled with tag-recapture data from the field or laboratory. This procedure must be undertaken for all age-classes to avoid misinterpretation of bands, as was experienced by Goosen (1997).

The largest female obtained during this study was 1 640 mm (20.7 kg), although a specimen of 1 732 mm (25 kg) has been recorded from the Western Cape (unpublished data). This indicates that female *M. mustelus* grow at least 92 mm larger than was previously reported. Distinct size differences seem to exist between areas. Larger specimens (>1 600 mm) are more commonly caught in the Western than in the Eastern Cape (pers. obs.). Factors such as diet composition and environmental conditions may contribute to these differences and need further investigation. Female *M. mustelus* grow to a larger size than males and are apparently longer-lived. For the present study, the difference between the maximum ages obtained for females and males was seven years. The same trend is also apparent in other *Mustelus* species (Francis 1981, Cailliet *et al*. 1990, Yudin and Cailliet 1990).

Smale and Compagno (1997) showed that size at maturity of *M. mustelus* varies with sex, occurring between 950 and 1 100 and between 1 250 and 1 400 mm in males and females respectively. These values are relatively high compared to a maximum value of 900 mm for males and 1 000 mm for females reported for other *Mustelus* species (Francis and Francis 1992). Using sex-specific growth parameters estimated in this study, predicted ages at maturity are 6 – 9 years for males and 12 – 15 years for females. These are older than estimates obtained for other *Mustelus* species (Francis and Francis 1992).

High L_∞ for females and large t_0 values for both sexes were obtained from the Von Bertalanffy growth equation. Whereas t_0 can theoretically be related to the gestation period (Holden 1974), in practice it is an artificial value, because the Von Bertalanffy equation does not necessarily describe growth *in utero* accurately. The use of L_0 rather than t_0 is therefore more robust and it cannot be ignored as in the case of an artificial t_0. Fabens' method provided an acceptable alternative to the Von Bertalanffy model in this study, and needs to be considered in future ageing studies of elasmobranchs. The large variance associated with the Von Bertalanffy parameters (Table I) can be attributed to the small sample size. Cailliet and Tanaka (1990) and Francis and Francis (1992) suggested that parameters of the Von Bertalanffy growth equation will be poorly estimated if inadequate samples of large and/or small individuals were available.

Although preliminary, the analysis of growth bands in this study indicates that the smoothhound shark is a relatively late-maturing, long-lived and slow-growing species. This combination of *K*-selected characteristics will render the species susceptible to overexploitation under increased commercial fishing pressure. However, validation of the ageing method is necessary.

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