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Age and Growth Studies of Gummy Shark, *Mustelus antarcticus* Günther, and School Shark, *Galeorhinus galeus* (Linnaeus), from Southern Australian Waters

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Abstract

Age–length data were derived from counting stained bands on whole vertebral centra obtained from gummy shark, *Mustelus antarcticus*, captured by gill-nets during 1973–76 in Bass Strait and from gummy shark and school shark, *Galeorhinus galeus*, captured during 1986–87 in Bass Strait and waters off South Australia. The data were fitted to the von Bertalanffy growth equation after adopting the Francis reparametrization and correcting for sampling bias caused by the selectivity effects of the gill-nets of various mesh sizes used to capture the sharks.

The von Bertalanffy growth curves of male and female gummy shark were significantly different, but the growth curves of male and female school shark were not. The growth curves suggest that growth rates of male and female gummy shark in Bass Strait were lower during 1986–87 than during 1973–76 and that the growth rates of male and female gummy shark and school shark in Bass Strait during 1986–87 were lower than those in South Australia at the same time. These apparent temporal and spatial differences in growth patterns of gummy shark are explained by the 'Phenomenon of Apparent Change in Growth Rate'. It is concluded that the growth curves determined for 1986–87 are distorted by the effects of a long history of high and length-selective fishing mortality and that actual growth patterns of gummy shark are better represented by the von Bertalanffy growth equation determined for shark caught in Bass Strait during 1973–76, when fishing mortality was much lower.

Verification of age estimates was attempted by comparing von Bertalanffy growth curves derived from age–length data with those derived from tag release–recapture length-increment data, but these comparisons highlight the limitations of using tag data for this purpose. Although reasonable agreement was found between such growth curves for gummy shark, it appears that school shark older than 11 years cannot be aged accurately from stained whole or sectioned vertebrae. Sectioned vertebrae from a school shark recaptured 35·7 years after being tagged and released and calculated as having an age exceeding 45 years gave estimates of only 18–20 years of age.

Introduction

Gummy shark, *Mustelus antarcticus* Günther, and school shark, *Galeorhinus galeus* (Linnaeus), landed in about equal quantities, provide most of the catch in the shark fishery of southern Australia. The fishery began in the mid-1920s and, until recent licensing restrictions were imposed, produced more than 5000 t (live weight) annually (Walker 1988, in press), valued at $15 million to fishers in Victoria, Tasmania and South Australia (Campbell *et al.* 1991). Initially, fishers targeted school shark and used several hundred baited hooks attached to a sinking main-line up to 10 km long. In 1964 bottom-set gill-nets were introduced into the fishery, and by the early 1970s most of the catch was being taken by this method. After the fishers adopted gill-nets, for several years, gummy shark replaced

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school shark as the predominant species in the catch. Increased targeting for gummy shark was partly caused by a ban in Victoria on the sale of large school shark during 1972–85 because of their mercury content (Walker 1976, 1988, in press). When first introduced, most of the gill-nets used in Bass Strait had a mesh size of 7 inches (178 mm), whereas most of those used in waters off South Australia and Tasmania had a mesh size of 8 inches (203 mm). By 1975, when a legal minimum mesh size of 6 inches (152 mm) was proclaimed, most nets used in Bass Strait had a mesh size of 6 inches and most of those used off South Australia had a mesh size of 7 inches.

Development of the fishery and subsequent concerns about overfishing stimulated interest in collecting life-history information and producing reliable stock assessments for gummy shark and school shark. During the 1940s and 1950s, tagging and biological studies on school shark (Olsen 1953, 1954, 1959, 1984; Grant *et al.* 1979; Stanley 1988; Moulton *et al.* 1989) and tagging studies on gummy shark (Stanley 1988; Walker 1989) were undertaken by the CSIRO. During the mid-1970s, the Fisheries and Wildlife Division of Victoria (now the Fisheries Branch) undertook similar studies on gummy shark (Walker 1984, 1989; Kirkwood and Walker 1986) and on school shark. During 1986–87 the Fisheries Branch undertook further field studies on the two species (MacDonald 1988; Walker 1988, in press; Walker and Moulton 1992), and during 1985–86 the Western Australian Department of Fisheries undertook studies on the gummy shark (Lenanton *et al.* 1990). In the studies by the Victorian Fisheries Branch, the selectivity effects of gill-nets and the ageing of sharks were given special attention.

Sharks of different sizes are not equally vulnerable to capture by gill-nets. Small sharks swim through gill-nets but become progressively more vulnerable to capture as they grow. After reaching the length of maximum vulnerability, they then become progressively less vulnerable because their heads cannot so readily penetrate the meshes of the nets (Kirkwood and Walker 1986). In a fishery susceptible to gill-net selectivity, the probability of a slow-growing shark being caught in a gill-net with a particular mesh size is higher than that of a fast-growing one. A slow-growing shark is vulnerable to capture for a longer period than a fast-growing shark. Consequently, the von Bertalanffy growth (VBG) parameters K, L_∞ and t_0 (von Bertalanffy 1938) estimated by using length-increment data from recapture of tagged sharks are biased because a disproportionately smaller number of fast-growing tagged sharks are recaptured. In addition, as pointed out by Ricker (1969, 1975) for fish, VBG parameters estimated by using age–length data from vertebral ageing are biased by the tendency of gill-nets to select more of the larger members of the young age classes and smaller members of the older age classes. Such an unrepresentative sample from the population produces a growth rate less than the rate derived from a representative sample (Ricker 1975). For the VBG model, sampling bias tends to decrease the magnitude of estimates of K and increase the magnitude of estimates of L_∞ and t_0. Under-representation of larger members of the older age classes in the sample, caused by the use of gill-nets with bigger mesh sizes, tends to decrease estimates of the magnitude of L_∞.

To correct for the effects of sampling bias, caused by length-specific gill-net selectivity, on estimates of VBG parameters, we used gill-nets of various mesh sizes to sample the shark populations and applied the mathematical corrections developed by Dow (1992). During 1973–76, samples for ageing gummy shark were collected from Bass Strait, where the gummy shark fishery was mainly based. Subsequently, as the number of gummy sharks caught commercially outside Bass Strait increased and as the need for more information for management of the school shark stocks increased, samples of both species were collected in Bass Strait and in waters off South Australia during 1986–87.

In this paper, we present the results of these ageing studies and test statistically for the effects of sex and sampling region of gummy shark and school shark on VBG curves derived from results of vertebral ageing. We also test for the effect of sampling period in Bass Strait to determine whether growth patterns of gummy shark had changed in response to rapidly increasing fishing effort between 1973–76 and 1986–87. These VBG curves are compared with VBG curves determined from length-increment data for school sharks tagged and released during 1942–56 (Grant *et al.* 1979) and for gummy sharks and school sharks tagged and released during 1973–76 (Walker 1984, 1989).

The usual methods of age determination for bony fishes of examining increment lines in skeletal structures, such as otoliths, scales or bones, are not applicable to sharks. Most skeletal structures of sharks and other chondrichthyans consist of nonmineralized cartilage, but some cartilaginous tissues contain calcium phosphate deposited in two principal patterns: the tesserae pattern found in the mineralized tissues, such as the jaws, and the more complex internalized pattern found in the centra and their accessory cartilages (Clement 1986, 1992). The pattern in a centrum is a series of incremental lines concentric about the centre (Ridewood 1921). This pattern indicates that growth is on the edge of the centrum, where the diameter and length of the centrum, and therefore the length of the shark, can increase.

Distinct concentric walls of mineralized cartilage enclosing seams of unmineralized hyaline cartilage consisting of concentrically deposited fibres of collagen were found by Clement (1986) by applying photomicrographic, microradiographic and scanning electron micrographic techniques to *Squatina squatina* (Linnaeus). He concluded that incremental lines visible on the articular surfaces of the centra are external manifestations of variations in internal deposition. As such, methods for estimating the age of sharks and other chondrichthyans have focused on analysis of translucent and opaque 'bands' in whole and sectioned calcified vertebral centra (Martin and Cailliet 1988). Bands formed during summer are usually opaque (calcified) and bands formed during winter are translucent (less calcified) (Cailliet *et al.* 1983*b*; Cailliet and Radtke 1987; Martin and Cailliet 1988). We counted bands stained with alizarin red on the surface of whole vertebral centra and, as have most authors ageing sharks (Cailliet *et al.* 1986), assumed they are deposited annually to estimate the ages of gummy shark and school shark.

Cailliet *et al.* (1986) emphasized the need to test the assumption of annual periodicity and prescribed procedures of 'vertification' and 'validation'. They defined 'verification' as the process of evaluation of an assumption and 'age verification' as the process of confirming an age estimate by comparison with age estimates from other indeterminate methods, which can only be validated when that process is complete. They defined 'age validation' as the conclusion, after sufficiently testing hypotheses about the temporal periodicity of band deposition, that bands counted are deposited predictably. Validation therefore requires proving the accuracy of an age estimate by comparison with a determinate method, and this procedure must be completed for all age classes available.

On the basis of these definitions and verification procedures for elasmobranchs listed by Cailliet *et al.* (1986), Cailliet (1990) and Cailliet and Tanaka (1990), by comparing our VBG curves determined from age–length data with VBG curves determined from length-increment data available from field tagging studies, we attempted to verify, but not validate, our age estimates. More direct methods of age verification and age validation for gummy shark and school shark are the focus of current research by the Victorian Fisheries Branch in collaboration with the University of Melbourne.

Evaluating differences between VBG curves determined for populations of *Mustelus manazo* Bleeker from two separate localities in waters off Japan, Cailliet *et al.* (1990) identified several sources of variance: *(a)* preparation technique (e.g. viewing specimens of whole vertebrae or sectioned vertebrae, chemical treatment of specimens, and image enhancement method), *(b)* intra-reader and inter-reader accuracy and precision, *(c)* sample size and sample bias, *(d)* individual fish variation, and *(e)* reliability of the VBG model to mathematically describe growth. Tanaka *et al.* (1990) investigated some of these sources to explain seemingly different VBG curves published for male and female blue shark, *Prionace glauca* (Linnaeus), from several widely separated regions of the Pacific and Atlantic Oceans. They concluded that population and environmental effects could not be used confidently to account for the suggested differences in VBG curves among these populations. Real differences, if they exist, are obscured by variability due to methods, interpretation and statistical fit.

In our study, we were interested in variation between individual sharks and variation due to sex of the sharks and to sampling region and sampling period. To minimize other variation, we standardized, firstly, the mesh sizes of the gill-nets used to catch the sharks for collection of vertebra samples, secondly, the methods of sample preparation and staining, and thirdly, the reader, so that all centra were stained and the bands were counted by the one person. Problems associated with the VBG parameters to adequately describe growth in length of fish were also addressed.

Francis (1988*a*, 1988*b*) describes several inadequacies of the VBG model: *(a)* parameters K and L_∞ have different meanings depending on whether they are estimated from age–length data or tag length-increment data (see also Sainsbury 1980), *(b)* parameter t_0 is always estimated by extrapolation beyond the range of the data, and *(c)* parameter L_∞ is often outside the range of the data. Knight (1968) showed the inadequacy of L_∞ when age–length data are not extensive enough to demonstrate asymptotic growth. In addition, there is inevitably a high inverse correlation between estimates of K and L_∞ (Knight 1968); consequently, comparison of these parameters between populations of a species, between sexes, or between species can be meaningless. Similar VBG curves can have very different parameter combinations.

To avoid some of these problems, and because of the lack of young sharks and old sharks in our data, we used the Francis parameters with standard errors (Francis 1988*a*, 1988*b*) to compare lengths at selected ages between different populations. The VBG parameters were subsequently determined to describe the shape of the growth curves.

Materials and Methods

Field Sampling

Between 8 June 1973 and 29 November 1976, the FRV *Sarda* and four different commercial fishing vessels were used to catch 2769 gummy sharks and 1201 school sharks from 162 sites mainly in Bass Strait. Most of the sharks were either disssected or tagged and released. The fishing gear consisted of 12 gill-nets and 400 hooks attached to two long-lines. Each gill-net was 250 m long and 1·7 m deep. The hooks (of various sizes) were clipped 5–20 m apart to sinking synthetic rope ('Super Saran') main-line by way of 1-m snoods with wire traces. Eight of the gill-nets had a hanging coefficient of 0·60 and mesh sizes ranging from 2 to 9 inches (51 to 229 mm), in steps of 1 inch (25 mm); two had a hanging coefficient of 0·53 and mesh sizes of 6 inches (152 mm) and 7 inches (178 mm); and two had a hanging coefficient of 0·67 and mesh sizes of 6 inches and 7 inches. The thickness of webbing filaments and the breaking strain for each mesh size varied, respectively, from 0·47 mm and 101 N for the 2-inch mesh size to 1·05 mm and 467 N for the 9-inch mesh size (Kirkwood and Walker 1986). The fishing gear, or some components of it, were set on the seabed usually between 0400 and 0600 hours at depths ranging from 5 to 79 m. Mean fishing times were 5·8 h for the gill-nets and 3·9 h for the long-lines.

Between 28 February 1986 and 9 December 1987, 11 different commercial vessels were used to catch 1620 gummy sharks and 912 school sharks from 144 sites in Bass Strait (BS) and waters off South Australia (SA). The fishing gear consisted of four gill-nets, each 500 m long and 1·7 m deep. The gill-nets had a hanging coefficient of 0·60 and mesh sizes ranging from 5 to 8 inches (127 to 203 mm), in steps of 1 inch. The thickness of webbing filaments and the breaking strain for all mesh sizes were 0·90 mm and 359 N, respectively. The fishing gear was set on the seabed, usually twice a day, at various times throughout the day and night (depending on the stage of the tidal cycle) at depths ranging from 9 to 201 m. Mean fishing time for the gill-nets was 4·8 h.

Sharks were measured to the nearest millimetre as total length; the tail of each shark was first allowed to take a natural position and the top caudal lobe was then placed parallel to the body axis. Four to six anterior vertebrae from each shark, placed in a labelled vial, were stored aboard the vessels at about −15°C during 1973–76 and at about −4°C during 1986–87. Vertebrae were collected from 327 gummy sharks during 1973–76 and from 1268 gummy sharks and 655 school sharks during 1986–87. Vertebrae were also collected from embryos in various stages of development and from newborn and young sharks.

Tagging

In an attempt to verify our age estimates, results from two separate tagging studies were used for comparison with our results from analysis of age–length data. During 1942–56, 6495 school sharks captured by hooks were tagged and released, with 2590 being double-tagged with internal (without protruding streamers attached) and external Peterson disc tags and the remainder being tagged with only external tags (Stanley 1988). Results from analysis of length-increment data for 103 recaptured sharks presented by Grant *et al.* (1979) are reproduced. During 1973–76, 1525 gummy sharks and 631 school sharks captured by gill-nets and hooks were tagged with internal tags (with protruding streamers attached) and released (Walker 1989). In the present paper, additional results from analysis of length-increment data for 213 recaptured gummy sharks and 52 recaptured school sharks are presented.

Laboratory Processing

In the laboratory, the vertebrae were stored at −22°C. For analysis, the vertebrae were thawed, separated, trimmed of connective tissue, including the neural and haemal arches, and soaked in a 2·5% sodium hypochlorite solution until the fascial material could be removed effectively. Small vertebrae (3–5 mm diameter) could be cleaned effectively in 30–40 min; larger vertebrae (>15 mm diameter) often required soaking for 1–2 h. Overexposure to sodium hypochlorite produced chalky or partly decalcified vertebrae, which adversely affected the subsequent uptake of the stain. As a safeguard against mistreatment of samples, one or two vertebrae were set aside and not chemically treated. When clean, the treated vertebrae were placed under a flow of tap water for about 30 min to remove traces of bleach and then left to air-dry.

During the study, vertebrae from several sharks of various lengths and from a tagged school shark recaptured after 35·7 years were also sectioned. These vertebrae were embedded in a general purpose GP5A polyester resin and oriented so that a thin section about 1 mm thick would include the central embryonic region, both or either of the two centrum faces, and a section of the longitudinal vertebral support column. A food blender with a 15-cm-diameter blade of 0·5-mm thickness was used to cut the section.

Several staining techniques were tested to improve the definition of the vertebral bands: silver nitrate (Stevens 1975), alizarin red (Galtsoff 1952; LaMarca 1966; Cailliet *et al.* 1983*a*, 1983*b*; Gruber and Stout 1983), and ninhydrin (Schneppenheim and Freytag 1980; Davenport and Stevens 1988). Alizarin red was selected because of its ease of use and consistent results.

Before undertaking routine age estimation, the number of bands counted on the centra of vertebrae was compared with the number counted on sectioned vertebrae from the same sharks. Although these preliminary comparisons indicated that there was good agreeement for small sharks and sharks of medium length, for large school sharks the degree of agreement was more variable. We rcognize that some authors favour sectioning vertebrae because, as we found for large sharks, the number of bands counted on sectioned vertebrae sometimes exceeds the number counted on whole vertebrae. However, in a male school shark tagged and released when it was 1350 mm long and recaptured after 35·7 years at liberty and estimated to have attained an age of more than 45 years (Moulton *et al.* 1989), we counted only 14 vertebral bands visible on the surfaces of the centra and 18–20 bands on the sectioned vertebrae. Given evidence that counting bands on both sectioned and whole vertebrae can underestimate the age of older sharks, we chose to avoid the time-consuming task of embedding and sectioning vertebrae.

For routine processing, each whole vertebra was immersed in a freshly prepared dilute alkaline solution of alizarin red prepared from a concentrated solution of alizarin red and 0·1% potassium hydroxide solution in the ratio of 1:9 (after Gruber and Stout 1983). The duration of immersion (2–30 min) depended on the size of the vertebra. When stained, the vertebra was washed in tap water for 1 min and the vertebral bands were counted immediately by viewing the surface of one centrum on each vertebra under a stereomicroscope at appropriate magnification, using incident light (×7–×14).

For embryos and newborn sharks, a darkly stained 'core' of about 2 mm diameter was always present at the centre, but no clear band was visible outside the centrum core. A band, usually faintly stained, was usually present in the centra of sharks judged to be several months old. We assumed, therefore, that the first band is laid down at about the time of birth or shortly afterwards. This first band is referred to as the 'birth band'.

All stained vertebrae from each sample were examined and the bands on the most evenly and clearly stained centra were counted. A small proportion of bands either were incompletely stained or appeared as closely paired rings. With increasing shark size, bands near the outer perimeter become compacted and often lacked definition. This was compounded by the characteristic curvature of the outer perimeter and the difficulty of delineating the point where new growth material was deposited. Therefore, any staining beyond the outermost discernible vertebral band was recorded as present or absent.

Bands on the vertebrae of each sample were counted by a single reader who classed each vertebrae as 'readable' or 'unreadable', based on either or both the degree of differentiation effected by the stain and the difficulty in interpreting the arrangement of the vertebral bands. By assuming that vertebral bands were formed annually, and by selecting 1 January as an arbitrary birth date based on the growth of embryos *in utero* (Olsen 1954; Walker 1984; Lenanton *et al.* 1990), ages from band counts were calculated from the formula,

age = number of vertebral bands
− 1 for birth band
+ 1 only if outer perimeter was stained
+ proportion of year from 1 January to capture date.

The reproducibility of age estimates by this method was assessed by a 'double-blind' test whereby two readers independently aged a sample of 569 gummy sharks and 580 school sharks collected during 1986–87. Each reader was presented with one whole vertebrae from each shark, and where either reader classified a vertebra as 'unreadable' the shark was rejected from the sample. The age estimates from the two readers were compared by a t-test for comparison of means of paired observations.

Determination of growth curves

The age–length data and the tag length-increment data were fitted to two separate models developed by Francis (1988*a*, 1988*b*) and adapted by Dow (1992) to correct for sampling bias caused by length-specific gill-net selectivity. Both models involved reparametrization of the VBG equation,

$$l_t = L_\infty[1 - e^{-K(t-t_0)}] ,$$

where K, L_∞ and t_0 are the VBG parameters and l_t is the length of a shark at age t. For age–length data, these parameters are replaced by l_ϕ, l_χ and l_ψ, the mean lengths of fish estimated by the model at the arbitrary ages of ϕ, χ and ψ, respectively, where $\chi = (\phi + \psi)/2$ and ϕ and ψ are chosen to represent the range of the data. For tag length-increment data, the VBG parameters are replaced by g_a and g_b, the mean annual growth increments of fish estimated by the model at the arbitrary lengths of a and b, respectively, which are also chosen to represent the range of the data.

For both models, the selectivity of the gill-nets used for sampling the shark population for age–length data and used by fishers for recapture of tagged sharks to provide length-increment data is assumed to be described by the gamma function, where maximum selectivity is set equal to 1. Selectivity is expressed as a function of length of shark and the selectivity parameters α and β, where α and β are in turn expressed as functions of mesh size and the parameters θ_1 and θ_2 (see Kirkwood and Walker 1986). Dow (1992) assumes that the length–frequency distribution of sharks in the population of each age class and the length-increment frequency distribution at each length for the population of tagged sharks are described by gamma probability density functions (pdfs) (i.e. 'prior distributions') rather than normal pdfs, as usually assumed (e.g. Fabens 1965; Francis 1988*a*, 1988*b*). Dow (1992) then shows that the length–frequency distribution for each age class of sharks in the sample captured by the gill-nets and the length-increment frequency distribution at each length of tagged sharks recaptured by the fishers' gill-nets are also described by gamma pdfs ('posterior distributions'). This is because the product of a gamma pdf (adopted for describing the 'prior distribution' of the shark population or tagged sharks) by a gamma function (adopted for describing the selectivity of the gill-nets used to collect the sample or to recapture tagged sharks) gives a gamma pdf (adopted for describing the 'posterior distribution' of the sample or recaptured tagged sharks). Dow (1992) then derives the likelihood for the 'posterior distribution' of each model from the product of the selectivity function of gill-nets derived by Kirkwood and Walker (1986) and the likelihood for the 'prior distribution' derived by Dow (1992) from the likelihood developed by Francis (1988*a*, 1988*b*). For hooks that are non-selective (Walker 1984), the likelihood for the 'posterior distribution' equals the likelihood for the 'prior distribution' (Dow 1992).

The Francis growth parameters (with standard errors) for each model were estimated by maximizing log-likelihood functions ('posterior distributions'), using the Nelder–Mead simplex algorithm (Nelder and Mead 1965). The selectivity parameters θ_1 and θ_2 used in these statistical analyses were estimated for gummy shark and school shark separately for each of 1973–76 and 1986–87 from the length–frequency distribution of sharks caught in the experimental gill-nets of 5-, 6-, 7- and 8-inch mesh sizes ($\theta_1 = 186$ and $\theta_2 = 35\,477$ for gummy shark during 1973–76, $\theta_1 = 186$ and $\theta_2 = 36\,695$ for gummy shark during 1986–87, $\theta_1 = 192$ and $\theta_2 = 67\,595$ for school shark during 1986–87) (Victorian Fisheries Branch, unpublished data).

Not all data available were used in these analyses. Only age–length data from stained vertebrae designated as 'readable' were included in these statistical analyses. Length-increment data from tagged sharks released during 1973–76 and recaptured by gill-nets were included only when mesh size was known.

χ^2-tests on likelihood ratios (Rao 1973; Silvey 1975) were used to determine whether growth varied with sex of the sharks and with sampling region and sampling period. This approach, advocated by Kimura (1980) for comparison of VBG curves, was shown by Cerrato (1990) to be more reliable than comparison of individual VBG parameters based on the t-test or χ^2-test (Gallucci and Quinn 1979; Kingsley 1979; Misra 1980, 1986) or simultaneous comparisons of two or three VBG parameters based on the Hotelling T^2 test (Kingsley 1979; Bernard 1981).

By using the transformation equations presented by Francis (1988*b*), values for the three VBG parameters of K, L_∞ and t_0 were derived from l_ϕ, l_χ and l_ψ, but only K and L_∞ could be derived from g_a and g_b. From tag length-increment data, t_0 can be estimated only if values of t and l_t are known for one point on the curve. We used two methods. One method was to calculate t_0 by substituting in the tagging VBG equation l_0 = mean length at birth when $t = 0$ years. The other method was to calculate t_0 by substituting l_χ when $t = \chi$ years determined from age–length data. Any age could be used, but $t = \chi$ years was selected because it is an age near the centre of the data range, where the determined VBG curve is well defined.

Results

Gummy Shark

The largest female gummy shark captured during field operations (1750 mm total length) was much longer than the largest male shark captured (1451 mm). Of the male sharks captured by gill-nets of 5-, 6-, 7- or 8-inch mesh size and subsequently aged, 53% were captured by 5-inch, 29% by 6-inch, 15% by 7-inch, and 3% by 8-inch mesh size. For the female sharks, 43% were captured by 5-inch, 29% by 6-inch, 18% by 7-inch, and 10% by 8-inch mesh size. The mean length of sharks caught in these mesh sizes increased with increasing mesh size. For 5-, 6-, 7- and 8-inch mesh sizes, respectively, mean lengths in BS were 932, 1103, 1204 and 1390 mm during 1973–76 and 853, 979, 1101 and 1255 mm during 1986–87, and mean lengths in SA were 1032, 1096, 1210 and 1304 mm during 1986–87. These data show, for each mesh size, that sharks caught in BS were longer during 1973–76 than during 1986–87 and that sharks caught during 1986–87 were longer in SA than in BS. When catches by the 5-, 6-, 7- and 8-inch mesh sizes were corrected for the two extra gill-nets of 6-inch mesh size and two extra gill-nets of 7-inch mesh size used during 1973–76, the proportion of sharks caught by the 5-inch mesh size, 1 inch less than the legal minimum mesh size of 6 inches, increased from 26% during 1973–76 to 61% during 1986–87, thus indicating a major change in the length–frequency composition of the shark population in BS.

Results of the 'double-blind' test for reproducibility of age estimates indicated that the estimates from the two readers were not significantly different ($n = 569$, mean difference = $0\cdot040$ years, standard error = $0\cdot048$ years, $t = 0\cdot835$, and $P > 0\cdot05$). Percentage agreement between the two readers in age assigned within 0 years was 49%, within ± 1 year was 88%, and within ± 2 years was 96%.

Table 1. Age–length data from vertebral ageing of gummy shark and school shark captured by experimental gill-nets of 5-, 6-, 7- and 8-inch mesh size

Region and period	Length (mm)	Number at age (years) 0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	Total
									Male gummy shark										
BS 1973–76	<700	1																	1
	700–799			1	1														2
	800–899			4	4	3													11
	900–999			3	8	3	2												16
	1000–1099				6	14	2				1								23
	1100–1199				2	11	10	1	2										26
	1200–1299					3	3	4	1	1		1							13
	1300–1399								2			1							3
	Total	1		8	21	34	17	5	5	1	1	2							95
BS 1986–87	<700		4	7		1													12
	700–799		9	28	18	2													57
	800–899		4	31	57	15	2		1										110
	900–999			15	36	31	12	4											98
	1000–1099			1	12	17	16	10	3	1									60
	1100–1199					6	13	6	1	1		1							28
	1200–1299					1	3	1	4		1		1						11
	1300–1399						1			1									2
	⩾1400														1				1
	Total		17	82	123	73	47	21	9	3	1	1	1		1				379
SA 1986–87	700–799			1															1
	800–899			1	4	5	2												12
	900–999			2	7	6	3	2	1		1								22
	1000–1099			1	3	7	5	9	5			1							31
	1100–1199				1	6	5	10	2	8	2								34
	1200–1299					2	4	2	5	5	2	1	2	1					24
	1300–1399						1		3	3	2	1	1						11
	⩾1400								1		1								2
	Total			5	15	26	20	23	17	16	8	3	3	1					137

Female gummy shark

BS 1973–76	700–799			1	1														2
	800–899		2	5	1														8
	900–999			4	13	1													18
	1000–1099		1		9	6	3	1											20
	1100–1199				4	8	6	2	2										22
	1200–1299					2	6	6	2	3									19
	1300–1399						4	3	6	4									17
	1400–1499							1	3	7	2	1	1						15
	1500–1599							1	1	1	1	1	1	1	1				8
	1600–1699										1				2				3
	⩾1700											1			1				2
	Total		3	10	28	17	19	14	14	15	4	3	2	1	4				134
BS 1986–87	<700	3	4	7	1														15
	700–799		16	35	17	2													70
	800–899		9	50	57	20	1												137
	900–999		1	9	33	37	1	3	2										86
	1000–1099			3	7	20	11	7	1		1								50
	1100–1199				2	9	10	5	3										29
	1200–1299						3	7		2	1								13
	1300–1399						1		2	4	2								9
	1400–1499									2	1								3
	1500–1599									1					1	1			3
	1600–1699							1						1				1	3
	Total	3	30	104	117	88	27	23	8	9	5			1	1	1		1	418
SA 1986–87	700–799		1	1	1		1												4
	800–899			13	4	8	1	3											29
	900–999			6	21	19	4	2	1										53
	1000–1099			1	19	17	19	14	6	2									78
	1100–1199				2	15	14	7	8	2	6								54
	1200–1299				1	6	12	15	11	11	4	3	1						64
	1300–1399						1	5	7	5	3	2	1						24
	1400–1499								2	3	4	3	2	1			1		16
	1500–1599								1	2	1	2	1		1				8
	1600–1699											1	1	1		1			4
	Total		1	21	48	65	52	46	36	25	18	11	6	2	1	1	1		334

Table 1 (*continued*)

Region and period	Length (mm)	Number at age (years) 0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	17+	18+	19+	20+	Total
											Male school shark												
BS 1986–87	<700		1	8																			9
	700–799			13	5	1																	19
	800–899			2	18	10	3																33
	900–999				4	10	4	1		1													20
	1000–1099					2		3	1														6
	1100–1199						3	2	2														7
	1200–1299						1	2	2		1												6
	1300–1399							1	3		3												7
	1400–1499											1	1										2
	1500–1599										1	1		1	2	1		1					7
	1600–1699													1									1
	Total		1	23	27	23	11	9	8	1	5	2	1	2	2	1		1					117
SA 1986–87	700–799			1	1	1																	3
	800–899			2	8	3																	13
	900–999				5	9	7	2	1		1												25
	1000–1099				1	4	10	5	1														21
	1100–1199					1	7	5	5	4		1											23
	1200–1299					1	1	3	9	1	2	1	1										19
	1300–1399								2	9	3	5	2	1									22
	1400–1499								2	2	5	1	2	4	2		2						20
	1500–1599										1								1				2
	Total			3	15	19	25	15	20	16	12	8	5	5	2		2		1				148

Female school shark

BS 1986–87	<700	2	3	1																		6
	700–799	1	23	4	1		1															30
	800–899	1	2	20	9	1																33
	900–999			6	12	6	1															25
	1000–1099			1	5	7	1															14
	1100–1199					2	2	1														5
	1200–1299					1		1	1	1												4
	1300–1399						1	2			1	1										5
	1400–1499							1	1	2	2	1										7
	1500–1599												4			1		1				6
	1600–1699												1			2						3
	⩾1700											1										1
	Total	4	28	32	27	17	6	5	2	3	3	3	5			3		1				139
SA 1986–87	700–799		1	3	1																	5
	800–899		1	6	2	2																11
	900–999			3	7	8	4	1														23
	1000–1099			1	8	15	5	1														30
	1100–1199				3	2	10	7	2													24
	1200–1299					3	7	11	14	3	2											40
	1300–1399				1		1	6	7	7	3	6	1	2								34
	1400–1499							2	2	10	10	6	5	4	2						1	42
	1500–1599								1	5	7	6	9	1	2	1				1		33
	1600–1699								1		1	1					1		1			5
	Total		2	13	22	30	27	28	27	25	23	19	15	7	4	1	1		1	1	1	247

Of the vertebrae from gummy sharks processed for age determination, 97% were designated 'readable'. These provided age estimates for a total of 95 male and 134 female sharks caught in BS during 1973–76, 379 male and 418 female sharks caught in BS during 1986–87, and 137 male and 334 female sharks caught in SA during 1986–87 by experimental gill-nets of 5-, 6-, 7- and 8-inch mesh size. The age range 3–11 years, covering the range of the ages selected for the Francis parameters (i.e. $\phi = 3$, $\psi = 11$ and $\chi = 7$ years), includes 96% of the data for aged male sharks and 94% for female sharks (Table 1). The highest age estimate was 13+ years for a male shark and 16+ years for a female shark. The mean age of sharks caught in BS during 1973–76 (mean = 5·5 years, standard deviation = 2·4 years) was more than the mean age of sharks caught in BS during 1986–87 (mean = 4·0, s.d. = 1·8 years) but less than the mean age of sharks caught in SA during 1986–87 (mean = 6·3, s.d. = 2·2 years).

Table 2. χ^2 log-likelihood ratio tests for effects of sex of shark, sampling period and sampling region on VBG curves determined from age–length data for gummy shark and school shark captured by gill-nets of 5-, 6-, 7- and 8-inch mesh size

Values are log-likelihood ratios (i.e. $ML_{(1+2)} - ML_1 - ML_2$, where ML is the maximum log-likelihood and 1 and 2 represent the two sexes, the two sampling periods or the two sampling regions, depending on the test). *$P<0·05$; **$P<0·01$; ***$P<0·001$; $^{\mathrm{n.s.}}$ not significant; 4 degrees of freedom. n.d., No data

Test for sex

To determine whether VBG curves for male and female sharks differed for BS during 1973–76, 1986–87 and the periods combined; for SA during 1986–87; and for BS and SA combined during 1986–87

	BS 1973–76	BS 1986–87	BS Combined	SA 1986–87	BS and SA combined 1986–87
Gummy shark	11·3*	15·3**	26·6***	13·4**	30·5***
School shark	n.d.	1·3$^{\mathrm{n.s.}}$	n.d.	4·6$^{\mathrm{n.s.}}$	3·9$^{\mathrm{n.s.}}$

Test for sampling period

To determine whether VBG curves for sharks during the periods 1973–76 and 1986–87 differed in BS for each sex separately and for the sexes combined

	♂	♀	♂ + ♀
Gummy shark	32·7***	42·8***	75·5***
School shark	n.d.	n.d.	n.d.

Test for sampling region

To determine whether VBG curves in BS and SA differed for each sex separately and for the sexes combined during 1986–87

	♂	♀	♂ + ♀
Gummy shark	23·6***	18·8***	44·2***
School shark	5·6$^{\mathrm{n.s.}}$	6·4$^{\mathrm{n.s.}}$	10·0*

Likelihood ratio tests on age–length data (Table 2) and on length-increment data from recapture of sharks tagged and released during 1973–76 (log-likelihood ratio = 17·2; $P<0·01$) indicated significant differences between the VBG curves of male and female gummy sharks. Because of these differences, the results from male and female sharks are spearated for the Francis parameters (Table 3) and the von Bertalanffy parameters (Table 4). Comparison of the Francis parameters and inspection of their standard errors indicates that in BS mean lengths at ages 3, 7 and 11 years estimated from age–length data were significantly higher during 1973–76 than during 1986–87 (Table 3, Fig. 1). Similarly, during 1986–87 mean lengths at ages 3 and 7 years, but not at age 11 years, were significantly higher in SA than in BS (Table 3, Fig. 2).

Table 3. Francis parameter estimates (l_3, l_7 and l_{11}) (with standard errors) determined from age–length data, mean length of shark at ages 3, 7 and 11 years predicted by the 1973–76 tagging VBG equations based on various estimates of t_0, and sample size (n) for male and female gummy shark separately and for male and female school shark combined

Species	Sex	Region	Period	n	Length (mm) l_3	(s.e.)	l_7	(s.e.)	l_{11}	(s.e.)
Age–length data from sharks caught by experimental gill-nets of 5-, 6-, 7- and 8-inch mesh size										
Gummy shark	♂	BS	1973–76	95	870	(23)	1200	(23)	1319	(52)
			1986–87	379	819	(7)	1083	(12)	1244	(41)
		SA	1986–87	137	882	(44)	1159	(15)	1241	(33)
		Total	1986–87	516	820	(8)	1114	(8)	1263	(23)
	♀	BS	1973–76	134	862	(28)	1310	(15)	1584	(24)
			1986–87	418	808	(7)	1146	(11)	1427	(23)
		SA	1986–87	334	874	(21)	1170	(11)	1399	(20)
		Total	1986–87	752	813	(8)	1163	(7)	1412	(15)
School shark	♂ + ♀	BS	1986–87	257	760	(9)	1159	(10)	1444	(13)
		SA	1986–87	398	749	(22)	1181	(7)	1425	(8)
		Total	1986–87	655	753	(9)	1173	(6)	1429	(7)
Age–length data from sharks caught by experimental gill-nets of 2-, 3-, 4-, 5-, 6-, 7-, 8- and 9-inch mesh size										
Gummy shark	♂	BS	1973–76	137	853	(15)	1187	(21)	1363	(55)
	♀			190	845	(15)	1281	(14)	1581	(22)
Tag length-increment data from sharks caught by commercial gill-nets of 6-, 7- and 8-inch mesh size and by hooks										
t_0 estimated by substituting $t=0$ and $l_0=$ mean length at birth[A]										
Gummy shark	♂	BS	1973–76	124	733		1063		1254	
	♀		1973–76	89	665		1035		1340	
School shark	♂ + ♀	BS	1973–76	52	825		1217		1417	
			1942–56	103	805		1187		1386	
t_0 estimated by substituting $t=7$ and $l=l_7$ from 1973–76 BS ageing VBG curve										
Gummy shark	♂	BS	1973–76	124	969		1200		1337	
	♀		1973–76	89	1020		1310		1580	
t_0 estimated by substituting $t=7$ and $l=l_7$ from 1986–87 BS ageing VBG curve										
Gummy shark	♂	BS	1973–76	124	769		1083		1260	
	♀		1973–76	89	800		1146		1431	

[A] 335 mm for gummy shark (Walker 1984) and 300 mm for school shark (Grant *et al.* 1979).

Age–length data from an additional 42 male and 56 female gummy sharks captured by experimental gill-nets of 2-, 3-, 4- and 9-inch mesh size and by hooks during 1973–76 were added to the 95 male and 134 female gummy sharks captured by experimental gill-nets of 5-, 6-, 7- and 8-inch mesh size during 1973–76 and included in separate analyses (Tables 3 and 4). About half of these additional data points were in the otherwise poorly represented

Table 4. VBG parameters (K, L_∞ and t_0) determined by transformation of Francis parameters estimated from age-length data and tag length-increment data, maximum log-likelihood (ML), and sample size (n) for male and female gummy shark separately and for male and female school shark combined

Species	Sex	Region	Period	n	K (year^{-1})	L_∞ (mm)	t_0 (years)	ML
Age-length data from sharks caught by experimental gill-nets of 5-, 6-, 7- and 8-inch mesh size								
Gummy shark	♂	BS	1973–76	95	0·253	1387	−0·90	−568·9
			1986–87	379	0·124	1495	−3·41	−2202·4
		SA	1986–87	137	0·304	1275	−0·86	−841·8
		Total	1986–87	516	0·170	1417	−2·08	−3067·8
	♀	BS	1973–76	134	0·123	2019	−1·55	−798·9
			1986–87	418	0·047	2778	−4·29	−2458·4
		SA	1986–87	334	0·064	2188	−4·99	−2039·7
		Total	1986–87	752	0·086	2019	−3·01	−4516·9
School shark	♂ + ♀	BS	1986–87	257	0·084	2158	−2·17	−1526·3
		SA	1986–87	398	0·144	1737	−0·92	−2400·3
		Total	1986–87	655	0·124	1829	−1·29	−3936·6
Age-length data from sharks caught by experimental gill-nets of 2-, 3-, 4-, 5-, 6-, 7-, 8- and 9-inch mesh size								
Gummy shark	♂	BS	1973–76	137	0·160	1559	−1·94	−821·6
	♀			190	0·094	2236	−2·05	−1145·0
Tag length-increment data from sharks caught by commercial gill-nets of 6-, 7- and 8-inch mesh size and by hooks								
t_0 estimated by substituting $t=0$ and l_0 = mean length at birth[A]								
Gummy shark	♂	BS	1973–76	124	0·137	1516	−1·82	−674·3
	♀		1973–76	89	0·049	2746	−2·65	−503·5
School shark	♂ + ♀	BS	1973–76	52	0·168	1626	−1·21	−279·5
			1942–56[B]	103	0·164	1600	−1·27	–[C]

[A] (Walker 1984); (Grant *et al.* 1979). [B] After Grant *et al.* (1979). [C] No data.

age classes of 0+, 1+ and 2+ years. This inclusion in the analyses, for each of male and female gummy sharks, altered only slightly the VBG curves where the magnitude of the VBG parameter K decreased and the magnitudes of the VBG parameters L_∞ and t_0 increased.

Mean lengths at ages 3, 7 and 11 years predicted by the 1973–76 tagging VBG equation, where t_0 was derived from mean length at birth by substituting $l_0 = 335$ mm (Walker 1984) when $t = 0$ years, agree poorly with the mean lengths at these ages predicted by the 1973–76 BS, 1986–87 BS and 1986–87 SA ageing VBG equations (Table 3). Similarly, mean lengths at the three ages predicted by the 1973–76 tagging VBG equation, where t_0 was derived from length at age 7 determined as Francis parameters from the 1973–76 BS age-length data, also agree poorly with the three mean lengths predicted by the 1973–76 BS ageing VBG equation (Table 3). However, mean lengths at the three ages predicted by the 1973–76 tagging VBG equation, where t_0 was derived from length at age 7 determined as Francis parameters from the 1986–87 BS age-length data, agree well with the three mean lengths predicted by the 1986–87 BS ageing VBG equation (Table 3, Fig. 3).

School Shark

The largest female school shark captured during field operations (1745 mm total length) was of similar length to the largest male shark captured (1714 mm). Of the male sharks,

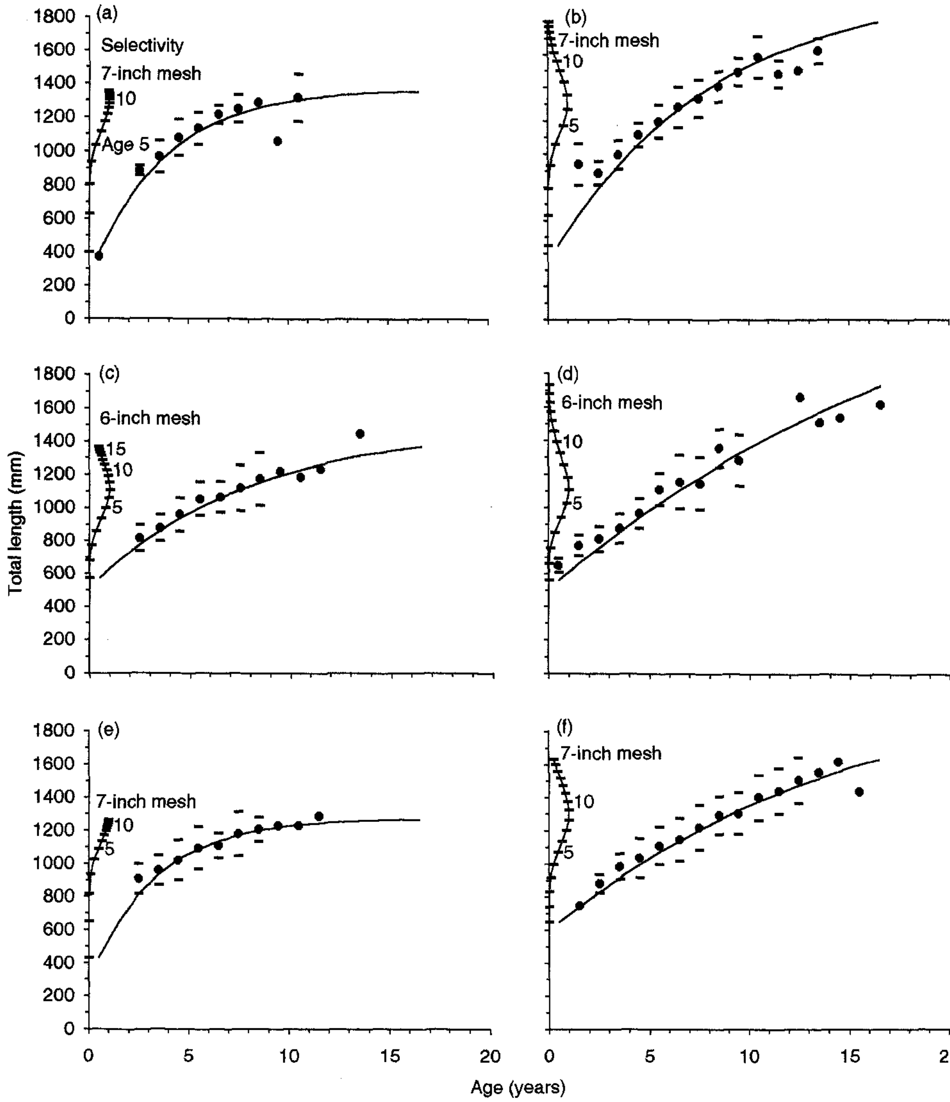

Fig. 1. VBG curves for (*a*) male and (*b*) female gummy shark in BS during 1973–76, for (*c*) male and (*d*) female shark in BS during 1986–87, and for (*e*) male and (*f*) female shark in SA during 1973–76, determined from age–length data. (Gill-net selectivity curves are inserted for the predominant mesh sizes of 7 inches used by commercial fishers in BS during 1973–76 and SA during 1986–87 and of 6 inches used in BS during 1986–87. The mean length of each age class in the sample is represented by ●, and one standard deviation about the mean is represented by —.)

37% were captured by 5-inch, 31% by 6-inch, 21% by 7-inch, and 11% by 8-inch gill-nets. For female sharks, 34% were captured by 5-inch, 25% by 6-inch, 23% by 7-inch, and 18% by 8-inch gill-nets. The mean length of sharks caught in these mesh sizes increased with increasing mesh size. For 5-, 6-, 7- and 8-inch mesh sizes, respectively, during 1986–87, mean lengths were 842, 975, 1267 and 1210 mm in BS and 1070, 1167, 1292 and 1383 mm in SA. These data show, for each mesh size, that sharks caught were longer in SA than in BS.

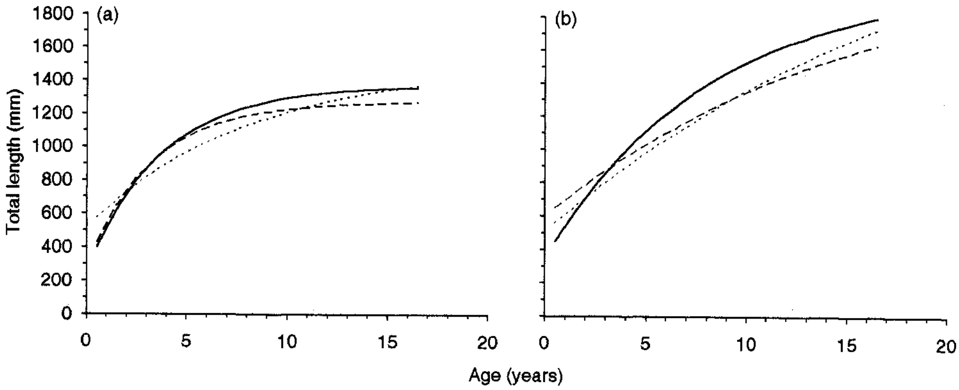

Fig. 2. VBG curves for (*a*) male and (*b*) female gummy shark, derived from age–length data for sharks captured during 1973–76 in BS (———) and during 1986–87 in BS (·········) and SA (– – –).

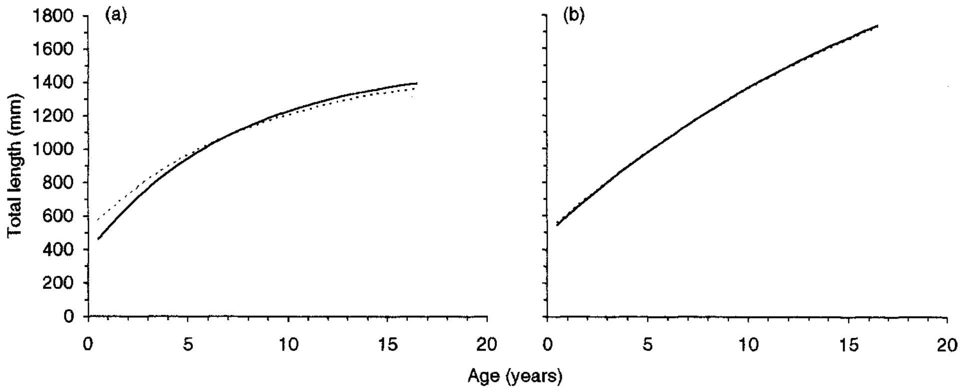

Fig. 3. VBG curves for (*a*) male and (*b*) female gummy shark, derived from age–length data for sharks captured in BS during 1986–87 (———) and from tag length-increment data available from BS and SA by recapture of sharks tagged and released during 1973–76 (·········).

Results of the 'double-blind' test for reproducibility of age estimates indicated that the estimates from the two readers were significantly different ($n = 580$, mean difference = 0·112 years, standard error = 0·048 years, $t = 2{\cdot}328$, and $P < 0{\cdot}05$). Percentage agreement between the two readers in age assigned within 0 years was 47%, within ±1 year was 84%, and within ±2 years was 96%.

Of the vertebrae from school sharks processed for age determination, 91% were designated 'readable'. These provided age estimates for a total of 117 male and 139 female sharks caught in BS and 148 male and 247 female sharks caught in SA during 1986–87. The age range 3–11 years, covering the range of the ages selected for the Francis parameters (i.e. $\phi = 3$, $\psi = 11$ and $\chi = 7$ years), includes 84% of the data for male sharks and 82% for female sharks (Table 1). The highest age estimate was 17+ years for a male shark and 20+ years for a female shark. The mean age of sharks caught in BS (mean = 5·1, s.d. = 3·1 years) was less than the mean age of sharks caught in SA (mean = 8·0, s.d. = 3·1 years).

Likelihood ratio tests on age–length data from vertebral ageing (Table 2) and on length-increment data from recapture of sharks tagged and released during 1973–76 (log-likelihood ratio = 1·4; $P>0{\cdot}05$) indicated no significant differences between the VBG curves of male and female school sharks. Consequently, the results from male and female sharks are combined for the Francis parameters (Table 3) and the von Bertalanffy parameters (Table 4).

There were no age–length data available from 1973–76 to test whether VBG curves changed between 1973–76 and 1986–87; however, the VBG curve determined from length-increment data from recapture of sharks tagged and released during 1942–56 (Grant *et al.* 1979) and the VBG curve determined from length-increment data from recapture of sharks tagged and released during 1973–76 were similar. Estimates of t_0 for the VBG curves determined from the two tagging studies were obtained by using a mean length at birth of 300 mm (Grant *et al.* 1979) (see Table 4). Estimates of t_0 calculated on the basis of mean length at age 7 years determined from age–length data are not presented because they are almost identical to those determined from mean length at birth. There was good agreement between the 1986–87 ageing VBG curve (BS and SA combined) and both tagging VBG curves over the age range 0–11 years, but mean lengths predicted for ages exceeding 11 years exceeded those predicted by the tagging VBG equations (Fig. 4).

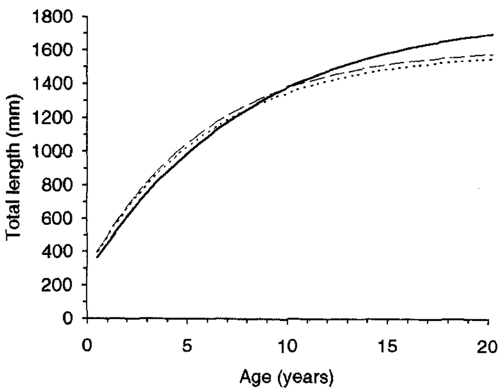

Fig. 4. VBG curves for male and female school shark combined, derived from age–length data for sharks captured during 1986–87 in BS and SA (———) and from tag length-increment data available from these regions by recapture of sharks tagged and released during 1942–56 (– – –) and 1973–76 (·········).

Likelihood ratio tests indicated a significant difference ($P<0{\cdot}05$) between the BS and SA ageing VBG curves (Table 2), although comparison of the Francis parameters indicates only marginal differences in mean lengths of sharks at ages 3, 7 and 11 years (Table 3). Differences become large only when predicted mean length is extrapolated to ages exceeding 11 years of age, which are outside the age range of 3–11 years covering 83% of the age-length data (Fig. 5).

Discussion

Gummy Shark

Six conclusions can be drawn from our results for gummy shark: *(1)* At any age over 3 years, the mean length of female gummy sharks is larger than the mean length of male sharks. *(2)* Gummy sharks have a maximum life span of about 16 years. *(3)* The mean length of male or female gummy sharks in BS, at any age, was shorter during 1986–87 than during 1973–76. *(4)* During 1986–87, the mean length of male or female gummy sharks, at any age in the range from 3 to about 7 years, was longer in SA than in BS. *(5)* For male and female sharks, the 1986–87 ageing VBG curve agrees much better than the 1973–76 ageing VBG curve with the 1973–76 tagging VBG curve. *(6)* The 1973–76 ageing VBG curves are likely to give a better representation of mean growth of gummy sharks than are the 1986–87 ageing VBG curves.

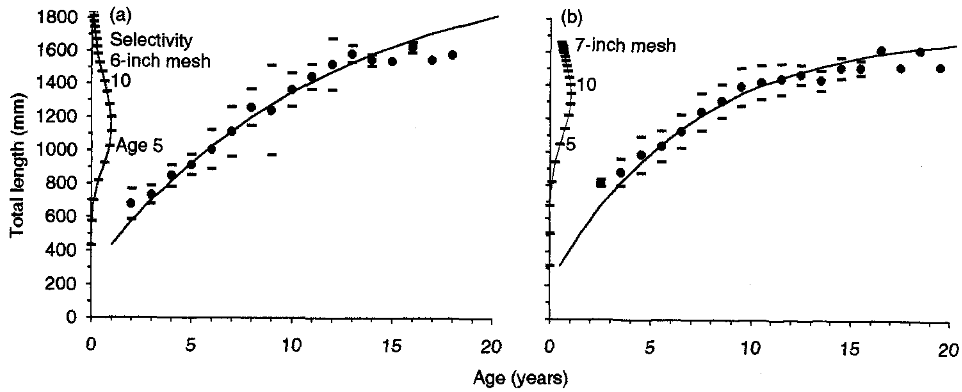

Fig. 5. VBG curves for male and female school shark combined, derived from vertebral age–length data for sharks captured during 1986–87 in (*a*) BS and (*b*) SA. (Gill-net selectivity curves are inserted for the predominant mesh sizes of 6 inches used by commercial fishers in BS and of 7 inches used in SA during 1986–87. The mean length of each age class in the sample is represented by ●, and one standard deviation about the mean is represented by —.)

Maximum ages of 13+ years for male and 16+ years for female gummy sharks suggest a life span longer than maximum ages reported for other species of the genus *Mustelus*, e.g. 0–9+ years for *M. manazo* from waters off Japan (Tanaka and Mizue 1979; Cailliet *et al.* 1990) and 0–9+ years for *M. californicus* Gill and 0–13+ years for *M. henlei* (Gill) from waters off central California (Yudin and Cailliet 1990). A larger maximum length and a faster growth rate for female than male sharks are common among species of the genus *Mustelus* as well as among species of other genera. Examples in the genus *Mustelus* include *M. manazo* (Taniuchi *et al.* 1983; Cailliet *et al.* 1990) and *M. californicus* (Yudin and Cailliet 1990); the difference for *M. henlei*, however, is not so marked (Yudin and Cailliet 1990). Examples in other genera include *Carcharhinus tilstoni* (Whitley) and *C. sorrah* (Valenciennes) from waters off northern Australia (Davenport and Stevens 1988) and *C. limbatus* (Valenciennes) from waters off Florida (Killam and Parsons 1989).

In a gill-net fishery where the length of maximum vulnerability of the sharks for the mesh size used is less than the maximum length reached by sharks, the probability of capture of a slow-growing shark is higher than that of a fast-growing one. The probability of a particular shark being caught at any instant depends, however, on its length and the total fishing effort for each mesh size. Hence the length–frequency distribution of sharks in a particular age class of the population at any time depends on the history of varying levels of fishing effort and mesh sizes of the gill-nets used in the fishery. Within a young cohort, where most sharks are shorter than the length of maximum selectivity for the gill-nets, the small sharks, which are slow-growing, will experience lower fishing mortality than will the larger ones, which are fast-growing. Conversely, amongst older cohorts, where most sharks are longer than the length of maximum selectivity, the slow-growing sharks will experinece higher fishing mortality than will the fast-growing ones. Hence, in a fishery with rising fishing mortality where cohorts vulnerable to the fishing gear are markedly reduced, the proportions of young and slow-growing sharks in the total population increase. Actual growth rates do not necessarily change, but VBG curves determined from ageing or tagging studies can give the appearance of changed growth rates.

The 'Phenomenon of Apparent Change in Growth Rate' was first described by Lee (1912) from back-calculation of lengths of fish at earlier ages from growth zones on fish scales. Similar observations from 'back-calculation', first by Sund (1911), have been made for numerous species and are usually referred to as 'Rosa Lee's Phenomenon' (Ricker 1969).

We did not use the method of 'back-calculation'; hence, to describe the hypothesis adopted for explaining our results, we avoid the term 'Rosa Lee's Phenomenon' and adopt the term originally applied by Lee (1912), which is the 'Phenomenon of Apparent Change in Growth Rate' (PACGR).

We were able to detect the PACGR in the gummy shark population because a large change in fishing effort and changes in mesh size of gill-nets used in the fishery occurred between our two sampling periods. From 1973–76 to 1986–87, annual fishing effort targeted at gummy shark tripled in BS, whereas in SA it increased from a negligible intensity to one nearly as high as that in BS. In BS, mesh size changed from predominantly 7 inches in 1973 to mainly 6 inches in 1976, where it remained until 1986–87. In other regions, mesh size was mainly 7 inches (Walker, in press). This reduction of mesh size in BS, from 7 inches, which has a maximum selectivity of 1290 mm shark length, to 6 inches, which has a maximum selectivity of 1106 mm shark length (Kirkwood and Walker 1986), increased fishing mortality for smaller and younger sharks.

The 1973–76 BS ageing VBG curves determined from age–length data for sharks captured by gill-nets of 5-, 6-, 7- and 8-inch mesh size, when extrapolated over the age range 0–3 years, where there are few data, predict mean length-at-birth values of 282 mm for male and 350 mm for female sharks, which compare well with the estimate of 335 mm for both sexes made from studies of growth of embryos by Walker (1984). The BS 1973–76 ageing VBG curves recalculated to include age–length data for sharks captured by gill-nets of 2-, 3-, 4- and 9-inch mesh size and by hooks predict mean length-at-birth values of 416 mm for male and 392 mm for female sharks, which also compare well with the estimate of 335 mm. The BS 1986–87 ageing VBG curves, on the other hand, predict mean length-at-birth values of 515 mm for male and 507 mm for female sharks, which do not compare so well with the estimate of 335 mm. It is concluded that the 1973–76 ageing VBG curves represent the mean growth of gummy sharks better than do the 1986–87 ageing VBG curves because they were affected less by length-specific fishing mortality.

Differences detected between the ageing VBG curves for BS and SA during 1986–87 are also consistent with the hypothesis of PACGR caused by length-selective fishing mortality. The effects of culling fast-growing sharks in several young classes would occur among older age classes in SA than in BS because the mesh size of most gill-nets used in SA was 1 inch larger than that in BS. Furthermore, because male sharks grow more slowly than do female sharks and therefore take longer to reach an age for full recruitment, it is to be expected that the effects of length-selective fishing mortality on PACGR will differ between male and female sharks in BS and SA. In addition to this effect, because female sharks reach a longer maximum length than do male sharks, the countereffect of fast-growing sharks escaping the gill-nets is likely to be stronger for female than for male sharks. These effects help to explain why there is close agreement between the ageing VBG curves for male sharks aged 0–5 years during 1986–87 in SA and those during 1973–76 in BS (Figs 1 and 2) and why there are differences in the shape of the ageing VBG curves between male and female sharks in BS and SA during 1986–87 (Fig. 2).

Another factor that might have contributed to the difference in the VBG curves between BS and SA during 1986–87 is the difference in age composition between the populations in the two regions. In BS 6% of the sharks had estimated ages of 0–2+ years, 89% had ages of 3–7+ years, and 5% had ages of 8–16+ years, whereas in SA no sharks were 0–2+ years old, 68% had ages of 3–7+ years, and 32% were 8–16+ years old (Table 1). Such differences may be a result of one or more of the following: length-dependent (or age-dependent segregation of the population; length-dependent migration, where the faster-growing sharks move from BS to SA before the slower-growing sharks; or a reduction in the number of larger gummy sharks in BS, where commercial fishing for gummy sharks has been more intensive for a longer period than in SA. Tagging studies indicate that rates of movement between these regions vary with sex and length of shark but that there is a definite movement of part of the population from BS to SA. Of 881 male sharks tagged and released mainly in BS during 1973–76, none were recaptured in SA, whereas of 644 tagged female sharks, seven were recaptured in SA and one was recaptured off Western Australia. On average, recaptured female sharks shorter than 1100 mm when tagged and released moved similar distances as male sharks shorter than this length. However, although larger male sharks moved shorter distances, larger female sharks moved much longer distances (Walker 1984). Although minimal rates of movement indicated by tagging studies provide some support for the hypothesis that the differences in the VBG curves between BS and SA might be explained by separate substocks, results of genetic studies provide no evidence that gummy sharks in these two regions form separate breeding stocks (MacDonald 1988).

More difficult to explain is the anomaly of why the 1973–76 tagging VBG curves, particularly the one for female sharks, where t_0 is derived from mean length at age 7 years, agree well with the 1986–87 ageing VBG curves (Table 3, Fig. 3) but agree poorly with the 1973–76 ageing VBG curves (Table 3). The more expected result was that the 1973–76 tagging VBG curve would agree with the 1973–76 BS ageing VBG curve. The hypothesis that the sharks tagged were taken from a population affected by length-selective fishing mortality appears to be unlikely because fishing effort was relatively low during the entire 1973–76 period when the sharks were tagged and released. Furthermore, because tagging was undertaken concurrently with capture of sharks for ageing, the tag length-increment data should be no more affected by length-selective fishing mortality than were the 1973–76 age–length data. Length-selective fishing mortality occurring after 1973–76 during the period when many of the tagged sharks were recaptured should not have caused PACGR. Errors in ageing are an alternative hypothesis that might explain this anomaly.

The anomaly creates a dilemma in deciding which VBG curves to compare for the purpose of age verification. Comparison of the 1986–87 BS ageing VBG curves with the 1973–76 tagging VBG curves, where t_0 is derived from mean length at age 7 years, suggests that there are no biases in ageing. Alternatively, comparison of the 1973–76 BS ageing VBG curves with the 1973–76 tagging VBG curves suggests significant ageing biases depending on the method selected for determining t_0. Given the apparent change in growth rates between 1973–76 and 1986–87 determined from age–length data, it would seem to be more appropriate to compare the 1973–76 ageing VBG curves with the 1973–76 tagging VBG curves than to compare the 1986–87 ageing VBG curves with the 1973–76 tagging VBG curves.

Verification by this approach also depends on selecting a method for calculating t_0 for the 1973–76 tagging VBG curves. The three mean lengths predicted by the 1973–76 ageing VBG curves for the ages of 3, 7 and 11 years, respectively, are 733, 1063 and 1254 mm for male sharks and 665, 1037 and 1340 mm for female sharks (Table 3). When t_0 is calculated on the basis of mean length at birth, the ages predicted by the tagging curves to give these mean lengths, respectively, are 2·1, 4·8 and 8·4 years for male sharks and 1·7, 4·3 and 7·3 years for female sharks, indicating biases in the three age estimates of −0·9, −2·2 and −2·6 years for male sharks and −1·3, −2·7 and −3·7 years for female sharks. When the alternative approach of calculating t_0 on the basis of mean length at age 7 years is adopted, the ages predicted by the tagging curves to give the three mean lengths of 969, 1200 and 1337 mm for male sharks and 1020, 1310 and 1580 mm for female sharks are 3·8, 7·0 and 12·2 years for male sharks and 4·1, 7·0 and 10·9 years for female sharks, indicating biases of +0·8, 0·0 and +1·2 years for male sharks and +1·1, 0·0 and −0·1 years for female sharks.

Calculating t_0 on the basis of mean length at any other age would indicate a different bias. Other than rejecting mean length at birth because it assumes that embryos grow according to the same VBG curve as sharks after birth, and rejecting mean length at birth and length at ages 1·0 and 2·0 years because they are outside the range of most tag length-increment and age–length data, there is no objective basis for deciding on the most appropriate age. If t_0 is calculated on the basis of mean length at age 3 years, then the estimated ages at the three mean lengths (3·0, 6·0 and 10·0 years for male sharks and 3·0, 5·8 and 9·1 years for female sharks) are biased by 0·0, −1·0 and −1·0 years for male sharks and 0·0, −1·2 and −1·9 years for female sharks. Hence, on the basis of these comparisons, age estimates cannot be verified other than to conclude that age biases, if present, increase with increasing age, with the range being about −1 to +1 years for sharks aged 3 years and about −2 to +1 years for sharks aged 11 years.

Apart from difficulties identified by Francis (1988*a*, 1988*b*) of comparing a VBG curve determined from age–length data with one determined from tag length-increment data, we have identified the additional potential problem of PACGR when comparing such VBG curves determined from data collected during different time periods. These difficulties raise the need for caution when adopting the suggestion by Cailliet *et al.* (1990) of comparing such curves as a method for age verification for sharks.

PACGR caused by length-selective fishing mortality might also partly explain some of the concern expressed by Cailliet *et al.* (1990) that the VBG equation is not always the most appropriate mathematical equation to describe the growth of a shark species. Just as PACGR resulting from length-selective fishing mortality on the predominantly young cohorts in the population appears to have caused the magnitude of K to decrease and the magnitudes of t_0 and L_∞ to increase for male and female gummy shark in BS and female gummy shark in SA, PACGR resulting from length-selective fishing mortality might also explain the pattern commonly reported by other authors where the value of t_0 exceeds the period of gestation and the value of L_∞ exceeds the length of the largest sharks observed in the population. This pattern was found by Davenport and Stevens (1988) for *Carcharhinus tilstoni* from northern Australia, by Casey *et al.* (1985) for *C. plumbeus* (Nardo) from the western North Atlantic, by Branstetter and Stiles (1987) for *C. leucas* from the northern Gulf of Mexico, and by Branstetter (1987) for *C. falciformis* (Bibron) from the north-western Gulf of Mexico. Overestimation of age and, as explained earlier, sampling bias can also produce this pattern. On the other hand, as we found for male gummy shark in SA, PACGR resulting from length-selective fishing mortality on older cohorts appears to have caused the magnitude of K to increase and the magnitude of L_∞ to decrease without affecting the magnitude of t_0.

While age overestimation, sampling bias, and length-selective fishing mortality can give reductions in apparent growth rates, high fishing mortality can cause increases in actual growth rates through density-dependent responses to reductions in stock abundance and cause increases or decreases in actual growth rates through evolutionary adaptation in response to artificial selection by the fishing gear. Environmental effects and fluctuations in recruitment can affect estimates of actual growth rates of teleosts and invertebrates, but these effects are likely to be minimal in our study because gummy shark are relatively long-lived, they are well developed at birth and hence are likely to have a fairly stable survival rate, and the number of births each year depends closely on the size of the parental stock (Walker 1992). Any subtle increase in actual growth rate of gummy shark due to these effects between 1973–76 and 1986–87 could not be detected by our study because they would have been masked by the effects of length-selective fishing mortality causing apparent reduction in growth rates.

Artificial selection by the gill-nets is unlikely to have had a measurable effect on growth rates through evolutionary adaptation, given the short period between 1973–76 and 1986–87 and the mean generation period of about 8 years for gummy shark. Such an effect is, however, possible in the long term (Law 1991). Gummy sharks are caught by gill-nets of 6-inch mesh size at ages much younger than the age at first sexual maturity (Walker 1992); hence, the fast-growing sharks that minimize the period of high vulnerability to capture before they reproduce have a higher probability of surviving to produce progeny. Predominant use of gill-nets of larger mesh size (7 inches or more) would, however, increase fishing mortality on a wider range of age classes and perhaps cause artificial selection towards slower growth rates.

The higher mean lengths predicted for ages of 0+ and 1+ years by the 1986–87 BS ageing VBG equation than by the 1973–76 BS ageing VBG equation should not be interpreted as increased growth rates in response to the reduction in stock density between these two periods. The two age classes are outside the age range of 3–11 years that includes most of the data, and the 1986–87 BS ageing VBG equations do not describe the growth of these two age classes accurately because, as discussed earlier, they poorly predict mean length at birth.

The phenomenon of density-dependent growth rates is well documented for bony fishes (Hile 1936; Beckman 1948; Le Cren 1958; Parsons 1967; Shepherd and Grimes 1983; Ross and Almeida 1986) but is not well known for sharks. Given the marked changes in size and structure of the gummy shark population between 1973–76 and 1986–87 changes in growth rates in response to changes in population density would not be unexpected. Holden (1973) speculated about possible mechanisms for density-dependent regulation in dogfish populations: perhaps compensatory decreases in natural mortality occur when predation, cannibalism, competition or disease decrease; compensatory increases in fecundity occur when food is more readily available or when foetal mortality decreases; and compensatory increases in growth rate occur when more abundant food induces earlier maturity and greater fecundity for each age class (assuming that fecundity and maturity are related to size rather than age). Holden (1973) suggested that a change in fecundity was the mechanism regulating populations of the Scottish–Norwegian dogfish, *Squalus acanthias* Smith and Radcliffe, but Wood *et al.* (1979) suggested natural mortality as the principal mechanism for density-dependent regulation of abundance for the population of *S. acanthias* in waters off British Columbia. Wood *et al.* (1979), in reaching their conclusions, had evaluated the theoretical effectiveness of the possible mechanisms and each mechanism's ability to simulate historical patterns of catch rates in the fishery. Adopting a similar approach, Walker (1992) argues in favour of variable natural mortality of pre-recruits as the principle mechanism for density-dependent regulation of the gummy shark population.

School Shark

Four conclusions can be drawn for school shark: *(1)* Male and female school sharks reach similar maximum lengths and have similar VBG curves. *(2)* VBG curves determined from 1942–56 and 1973–76 tag length-increment data for all ages and from 1986–87 age-length data for ages 0–11 years are similar. *(3)* During 1986–87, the mean lengths of sharks, at any age in the range 0–11 years, in BS and SA were similar. *(4)* The method of staining whole or sectioned vertebrae with alizarin red is unreliable for ageing school sharks longer than about 1300 mm total length.

Grant *et al.* (1979) detected a statistically significant difference between the VBG curves of male and female school sharks when using length-increment data from recapture of sharks tagged and released during 1942–56. The difference was small, and our failure to detect a difference might be explained by the use of fewer data in the analysis of the length-increment data from the 1973–76 tag releases (52 recaptured sharks) than from the 1942–56 releases (103 recaptured sharks) and by the additional complexity of correcting for bias caused by length-selective gill-nets. Ageing error and correction for sampling bias might explain why a significant difference was not detected between VBG curves for male and female sharks determined from the 1986–87 age–length data. Examples of other species exhibiting similar VBG curves between male and female sharks include *C. plumbeus* (Casey *et al.* 1985) and *Isurus oxyrinchus* Rafinesque (Pratt and Casey 1983).

There is close agreement between the 1942–56 and 1973–76 tagging VBG curves for all ages and the 1986–87 BS and SA ageing VBG curves for ages of 0–11 years. Despite a long history of rising fishing mortality and declining stock abundance (Walker, in press), there is no evidence of density-dependent changes in growth rates or of PACGR, although mutually cancelling effects are possible. Broader gill-net selectivity curves (θ_2 has a value of

67 595 for school shark, which is much larger than the value of 36 695 for gummy shark during 1986–87), a longer life span (Grant *et al.* 1979), greater mobility (Olsen 1954), and a respite from high fishing mortality from 1973 to the end of the 1970s because of the ban on the sale of large school sharks in Victoria are some differences between school shark and gummy shark that might explain why PACGR was evident for gummy shark but not for school shark.

The same arguments raised during discussion on the differences in VBG curves of gummy shark from BS and SA during 1986–87 can be applied to school shark (Fig. 5). Of the school sharks from BS, 34% were estimated to be 0–2+ years old, 53% were 3–7+ years old, and 13% were 8–17+ years old, and of the school sharks from SA, 8% were 0–2+ years old, 58% were 3–7+ years old, and 34% were 8–20+ years old. Results of tagging studies indicate a much higher exchange of sharks between BS and SA for school shark (Olsen 1954) than for gummy shark (Walker 1984).

The tagging VBG curves indicate relatively little growth after about 11 years of age. For sharks approaching and older than 11 years, it is likely that the ages have been underestimated because of compaction of the vertebral bands near the outer edge of the vertebrae. In contrast to the VBG curves of short-lived sharks such as the gummy shark (Figs 1 and 2), VBG curves of the long-lived school shark exhibit long plateaus of little growth after about age 11 years (Grant *et al.* 1979). If growth in overall length is negligible, it follows that growth of the vertebrae will be negligible and therefore the growth bands will be more difficult to detect. A maximum age estimate of 20 years for a recaptured tagged shark calculated to have an age exceeding 45 years indicates that the ages of the oldest sharks in the population are likely to be severely underestimated by the alizarin-red staining method. Among our samples, 9% of the school sharks were estimated to be more than 11 years of age. Hence, although the majority of the sharks captured in the southern shark fishery can be aged by this method, the method is unreliable for sharks longer than 1300 mm. Ageing of these large sharks requires alternative methods such as the microradiographic method used by Ferreira and Vooren (1991), who have produced age estimates up to 41 years for *Galeorhinus galeus* from waters off southern Brazil.

The VBG curves for *G. galeus* produced by Ferreira and Vooren (1991) are, however, very different from any of those produced from southern Australia. The absence of Rosa Lee's Phenomenon in their data provides evidence that the lower estimates of K and the larger estimates of t_0 produced for the sharks from southern Brazil were not caused by sampling bias or length-selective fishing mortality. Alternative hypotheses that might explain the differences in the VBG curves between the two countries are that *(a)* there were real differences in the growth rates and *(b)* the microradiographic method overestimated the age of sharks from southern Brazil.

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