

## Comparison of deterministic growth models fitted to length-at-age data of the piked spurdog (*Squalus megalops*) in south-eastern Australia

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**Abstract.** Age and growth estimates of *Squalus megalops* were derived from the first dorsal fin spine of 452 sharks, ranging from 274 to 622 mm total length. Age bias plots and indices of precision indicated that the ageing method was precise and unbiased. Edge analysis of the enameled surface of whole spines and similarities in the banding pattern deposited in the enameled surface of spines and in spine sections supported the hypothesis of annual band formation. Multiple versions of two growth models were fitted to length-at-age data, from which a two-phase von Bertalanffy model produced the best fit. For males, the change in growth rate corresponded with size-at-maturity, whereas for females, the change was slightly before size-at-maturity. Regardless of the growth model used, growth rate of females ( $0.034$  to  $0.098$  years<sup>-1</sup>) was very low, making *S. megalops* highly susceptible to overexploitation by fisheries.

**Additional keywords:** age, AIC, Gompertz, Squalidae, von Bertalanffy.

### Introduction

The von Bertalanffy function (von Bertalanffy 1938) has been the most commonly used model to describe growth of sharks, despite criticism (Knight 1968; Roff 1980). As indicated by Carlson and Baremore (2005), few studies on shark growth have examined alternative models (but see Carlson and Baremore 2005; Bishop *et al.* 2006), and most studies simply fitted the von Bertalanffy function to the data. Hence, a range of growth models should be compared to determine the function that provides the best description of the growth process (Haddon 2001).

Age and growth rates have been mainly studied for commercially important sharks, such as spiny dogfish *Squalus acanthias*, gummy sharks *Mustelus antarcticus* and school sharks *Galeorhinus galeus*; however, little is known about the age and growth of non-commercial squalid sharks (Squalidae). Although dogfish are among the most abundant demersal sharks of temperate seas (Compagno 1984), most of the ageing studies on this family have focused on *S. acanthias* (e.g. Holden and Meadows 1962; Ketchen 1975; Beamish and McFarlane 1985). For this species, maximum age was reported to vary widely, with a reported maximum age of up to 80 years (McFarlane and Beamish 1987). For other species of *Squalus*, age and growth rate have been estimated for the shortspine spurdog *S. mitsukurii* in the North Pacific Ocean (Wilson and Seki 1994; Taniuchi and Tachikawa 1999) and the longnose spurdog *S. blainvillei* in the Mediterranean Sea (Cannizzaro *et al.* 1995). Age and growth rate information of the piked spurdog *S. megalops* was estimated for sharks from South African waters (Watson and Smale 1999).

Growth rates and maximum ages differed between males and females: the largest male was 572 mm total length (TL) and 29 years old, whereas the largest female was 782 mm TL and 32 years old.

*Squalus megalops* (Macleay, 1881) is a demersal species that is distributed off southern and eastern Australia, from Carnarvon (Western Australia) to Townsville (Queensland), including Tasmania (Last and Stevens 1994). However, the distribution of this species requires further revision because it has also been reported off the coasts of Brazil (Vooren 1992) and South Africa (Bass *et al.* 1976), and there are unconfirmed reports off Indo China, New Caledonia and New Hebrides (Last and Stevens 1994). This species inhabits the continental shelf and upper continental slope (depths <510 m) in warm, temperate and tropical areas (Last and Stevens 1994). *Squalus megalops* has a high natural abundance in southern Australia (Bulman *et al.* 2001; Graham *et al.* 2001) and, even though it is one of the major by-catch shark species in the area (Walker *et al.* 2005), its abundance has remained stable off New South Wales (south-east coast of Australia) since it was first surveyed in 1976–77 (Graham *et al.* 2001). At present, a lack of biological data hampers a classification of the conservation status of this species (Cavanagh *et al.* 2003).

Until the present study, the age and growth rate of the Australian population(s) of *S. megalops* remained unknown. Given that age and growth parameters can vary among regions (e.g. Parsons 1993; Taniuchi and Tachikawa 1999), age and growth information for *S. megalops* from Australian waters is required for population assessment of this species in this region. The

purpose of the present study was to estimate the age of *S. megalops* captured in south-eastern Australia and compare different growth models to determine which model provides the best fit to growth data.

## Materials and methods

### Sampling

Specimens of *Squalus megalops* were obtained from the by-catch of demersal trawl and shark gill-net vessels operating in the Southern and Eastern Scalefish and Shark Fishery in waters off south-eastern Australia. Samples were collected monthly between October 2002 and April 2004, with the exception of the August–September period, when *S. megalops* appeared to move off the fishing grounds and weather conditions restricted sampling. Specimens were sexed and measured (total length, TL,  $\pm 1$  mm).

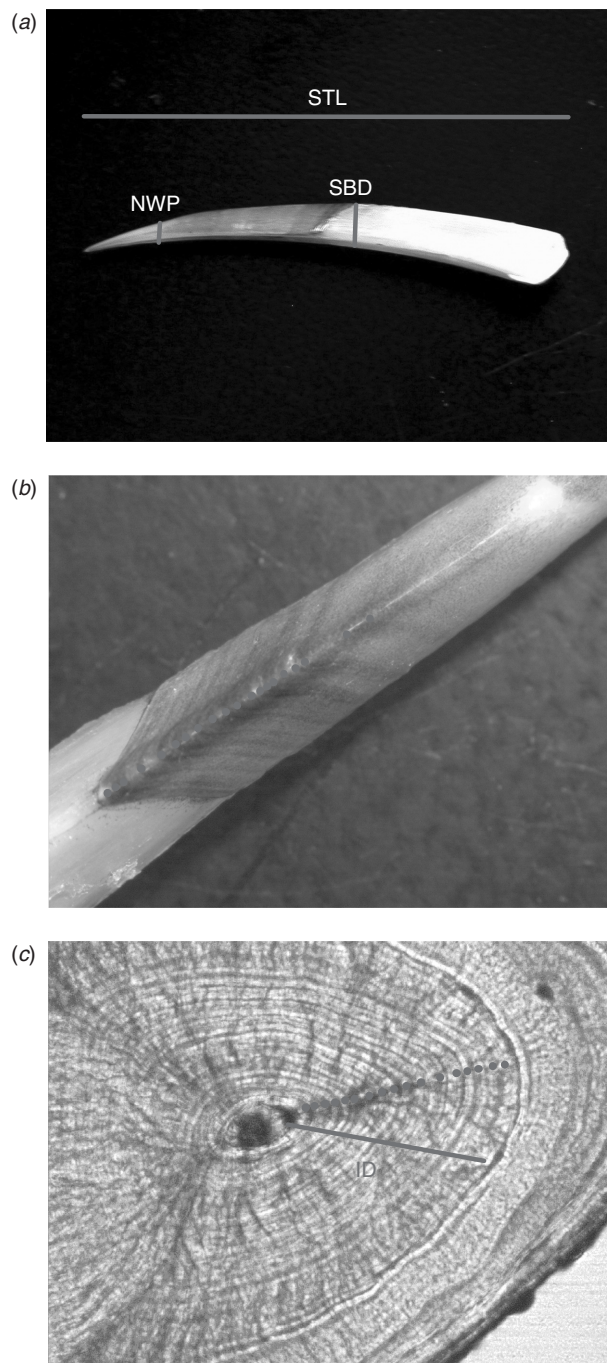
### Spine and vertebrae preparation

Two portions of the vertebral column (post cranial and thoracic vertebrae) and the first and second dorsal fin spines (DFS) were removed and stored frozen for age estimation. Spines were extracted by cutting horizontally just above the vertebral column to ensure that the spine base and stem were intact (Beamish and McFarlane 1985). Soft tissue was removed by immersing vertebrae and spines in hot water (55°C) for 0.5 to 1 min and trimming off the skin, flesh, and cartilage with a scalpel. Cleaned spines were then rubbed with a cloth to highlight the bands on the enameled surface. For vertebrae, the remaining tissue was removed by soaking them in 4% sodium hypochlorite solution. Soaking time varied with the size of the vertebrae (between 10 and 20 min) to avoid ‘over-bleaching’. Spines were air-dried and stored in paper envelopes, whereas vertebrae were stored in a freezer. Measurements of spines were recorded to the nearest 0.01 mm using electronic calipers, following Ketchen (1975) (Fig. 1a).

### Age estimation

A pilot study was conducted to determine which of the two structures – vertebrae or spines – was more appropriate for age estimation. Whole and cross-sectioned vertebrae ( $\sim 300$   $\mu$ m) were used. Sections were obtained by embedding vertebrae in epoxy resin and sectioning with a lapidary saw (Gemmasa, Adelaide) with a diamond-impregnated blade. Sections were cleaned using ethanol and water, air-dried and mounted on glass slides using epoxy resin. Sections were examined under transmitted light using a Leica IM 4.0 digital image system (Leica, Wetzlar, Germany) on a Leica DMLB compound microscope. Vertebrae of *S. megalops* are poorly calcified, with very fragile *inter-medialia*; therefore, from sectioned vertebrae, only the *corpus calcareum* was used. No clear banding pattern was observed on whole or sections of vertebrae; hence, different stains (alizarin red S, silver nitrate, cobalt nitrate, ninhydrin) were used to enhance readability. However, no improvement in readability was observed, and subsequently only spines were used for further age estimation.

Bands deposited on the external enameled surface of spines were counted using a dissecting microscope (10 $\times$ ) and reflected light (Fig. 1b). A band was defined as an alternating opaque and translucent zone or ridge present on the enameled surface



**Fig. 1.** Dorsal fin spine (DFS) of *Squalus megalops*. (a) Lateral view of worn second DFS showing the different measurements recorded following Ketchen (1975); STL, spine total length; SBD, spine-base diameter; NWP, no-wear point. (b) Anterior view of the first DFS of a 495 mm TL female showing 20 bands on the enameled surface (6 $\times$ ). (c) Section of the first DFS of a 456 mm TL female showing 17 bands on the inner dentine (ID) layer (100 $\times$ ).

(McFarlane and Beamish 1987; Watson and Smale 1999). Solid bands on the leading edge of the spine that were split on the trailing edge were counted as a single band (Watson and Smale 1999). Bands visible only as a dark mark on the leading edge,

**Table 1. Readability scores assigned to readings of spines**  
(modified from Officer *et al.* 1996)

Readability score	Description
1	Band count unambiguous with clear bands
2	Band count unambiguous but bands of diminished clarity
3	Two band counts possible but indicated count is most likely
4	More than two interpretations possible; count is best estimate
5	No band count possible; unreadable

**Table 2. Definition of edge type of whole spines for edge analysis**  
(following Holden and Meadows 1962)

Edge type	Description
Dark	Dark band observed at edge of enamel
Light	Dark band just formed and a light band of a width less than half the width of the light band between the last two dark bands observed at edge of enamel
Wide light	Light band observed at edge of enamel, equal to or more than half the width of the light band between the last two dark bands

but similar in thickness to neighbouring bands that did continue to the trailing edge, were also counted as single bands (Watson and Smale 1999). A subjective readability score was assigned to each spine following Officer *et al.* (1996) (Table 1). After three readings, spines with a readability score of 4 (ambiguous band counts) or 5 (no band counts possible) were not used for further analysis.

The spines of ten full-term embryos were examined to determine pre-birth bands. No bands were observed, and it was assumed that the first band was deposited just prior to or after birth (birthmark; e.g. Holden and Meadows 1962; Moulton *et al.* 1992). Thus, the final band count was calculated as the total number of bands counted minus one.

To determine whether the first or the second DFS was more appropriate for age estimation, a random sub-sample of first and second DFS from 61 individuals was read on two occasions (separated by a minimum of one month) without knowledge of the length of the specimens. The readability scores of the first and second DFS were compared. The coefficient of variation (CV; Chang 1982) and the index of average percentage error (APE; Beamish and Fournier 1981) were calculated to evaluate precision between readings (first v. second reading) and between structures (first v. second DFS). Age-bias plots (Campana *et al.* 1995) were used to detect count differences between the two structures. The first DFS showed better readability scores and higher precision between readings (see 'Results'); hence, this spine was used for age estimation.

All first DFS were read three times by a single reader (first reader), with a time period of at least one month separating the readings. A second reader read a random sub-sample of 50 spines for evaluation of between-reader variability and between-reader bias. To evaluate within- and between-reader precision, the CV and APE index were calculated. Age bias plots were used to detect systematic count differences between the first and second reader. To accept a count for age estimation, the counts of at least two of three readings had to be identical. If counts differed,

spines were recounted a fourth time and the same procedure was applied. If the difference persisted, the spine was discarded (< 9% of readings).

For worn spines, Ketchen's (1975) correction method was adopted to ensure that bands were not missing. The relationship between band counts and spine-base diameter (SBD) was estimated for unworn spines from males ( $n = 45$ ) and females ( $n = 46$ ). For worn spines, the diameter of the spine at the most distal point of no wear (NWP) was then measured (Fig. 1a). From the relationship between band counts and SBD, the number of bands corresponding to the diameter at the NWP of worn spines was calculated and added to the original count of bands (Ketchen 1975).

### Verification

A random sub-sample of spines from 10 female and 10 male sharks was sent to G. A. McFarlane from the Pacific Biological Station, and to G. Watson and M. J. Smale from Port Elizabeth Museum at Bayworld, who agreed that the spines were appropriate to estimate the age of *S. megalops*. The annual periodicity of band deposition on whole spines was investigated by analysing the edge of their enameled surface (Holden and Meadows 1962; Nammack *et al.* 1985; Taniuchi and Tachikawa 1999). The edge of spines collected throughout the year was classified as dark, light or wide light following Holden and Meadows (1962) (Table 2).

Counts on spine sections were compared with counts on the external enameled surface for a sub-sample of sharks ( $n = 89$ ) as a second form of verification. Serial sections ( $\sim 300 \mu\text{m}$ ) were taken from the tip of each first DFS to determine the optimal position of sectioning. The same method for sectioning vertebrae was used to obtain spine sections. The inner dentine layer exhibited the clearest banding pattern and was hence used for counting (Fig. 1c) (Maisey 1979; Clarke *et al.* 2002a). Maximum count of bands in the inner layer was found at the apex

**Table 3.** Summary of growth models fitted to length-at-age data

Model	Equation
VBGM	$L_t = L_\infty (1 - e^{-k(t-t_0)})$
2VBGM	$L_t = L_\infty (1 - be^{-kt})$ , $b = (L_\infty - L_0/L_\infty)$
TPVBGM	$L_t = L_\infty (1 - e^{-kA_t(t-t_0)})$ , $A_t = 1 - h/((t - t_h)^2 + 1)$
Gompertz	$L_t = L_\infty e^{-e^{-(k(t-t_0))}}$
2Gompertz	$L_t = L_0 e^{G(1-e^{-kt})}$ , $G = \ln(L_\infty/L_0)$

VBGM, von Bertalanffy growth model; 2VBGM, two-parameter modified VBGM; TPVBGM, two-phase VBGM; 2Gompertz, two-parameter modified form of the Gompertz growth model;  $L_t$ , mean length at time  $t$ ;  $L_\infty$ , theoretical asymptotic length;  $k$ , growth coefficient;  $t_0$ , theoretical age at zero length;  $h$ , magnitude of the maximum differences between VBGM and TPVBGM;  $t_h$ , age at which transition between the two growth phases occurs;  $L_0$ , mean length at birth (214 mm for males and females).

of the pulp cavity, representing the optimal position of sectioning. The sections were examined under transmitted light using a Leica IM 4.0 digital image system on a Leica DMLB compound microscope. Within the internal dentine layer, a band was defined as a pair of dark (opaque) and light (translucent) concentric rings (Irvine 2004). Counting started at the pulp cavity (centre) and continued outwards to the junction between inner and outer dentine layers (Irvine 2004). Age-bias plots (Campana *et al.* 1995) were used to detect count differences between external (enameled surface) and internal (sections) counts.

#### Growth estimation

Several alternative growth models were fitted to length-at-age data for each sex: the traditional von Bertalanffy growth model (VBGM; von Bertalanffy 1938), a two-parameter modified form of VBGM (2VBGM; Fabens 1965), a two-phase von Bertalanffy growth model (TPVBGM; Soriano *et al.* 1992), the Gompertz growth model (Ricker 1975), and a two-parameter modified form of the Gompertz growth model (2Gompertz; Mollet *et al.* 2002) (Table 3). Model parameters were estimated by least-squares non-linear regression. Akaike's Information Criterion (AIC) was used to determine the model that provided the best fit to the length-at-age data (Buckland *et al.* 1997; Burnham and Anderson 2002)

$$AIC = n \ln(\hat{\sigma}^2) + 2p$$

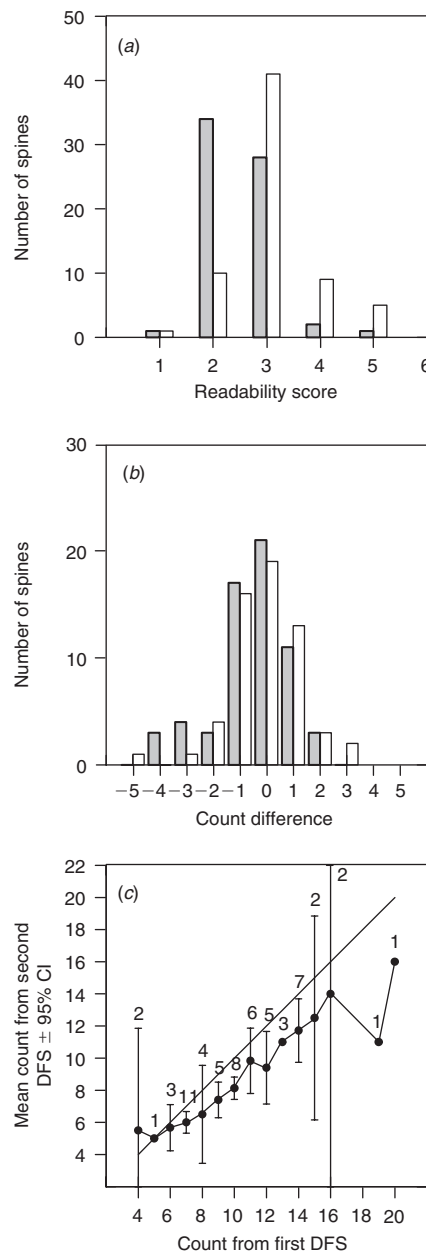
where  $n$  is sample size;  $\hat{\sigma}^2$  is residual sum of squares divided by  $n$ ; and  $p$  is number of parameters.

Comparisons among the AIC values of different growth models enabled the best model for each sex to be selected, i.e. those models with the lowest AIC values. For model comparisons, the  $\Delta AIC$  and Akaike weights ( $w_i$ ) were calculated. The  $\Delta AIC$  is a measure of each model relative to the best model and is calculated as

$$\Delta AIC = AIC_i - \min AIC \quad (1)$$

where  $AIC_i$  = AIC value of model  $i$ ; and  $\min AIC$  = AIC value of the best model.

Akaike weights ( $w_i$ ) represent the probability of choosing the correct model from the set of candidate models and are



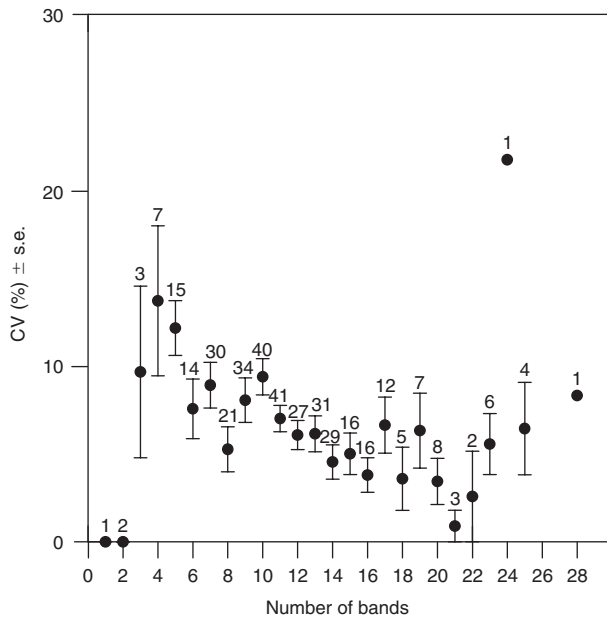
**Fig. 2.** Comparison between first (grey) and second (white) dorsal fin spines (DFS) for 61 sharks. (a) Distribution of readability scores assigned to readings of each spine. (b) Distribution of differences between two readings on first and second DFS. (c) Age bias plots. The solid line is the 1:1 relationship. Sample sizes are given above each corresponding count.

calculated as

$$w_i = \frac{\exp(-\Delta AIC/2)}{\sum_{r=1}^R \exp(-\Delta AIC/2)}$$

where  $R$  is the number of candidate models.

Once the best model was determined, the growth curves of males and females were compared by a  $\chi^2$  test on likelihood ratios (Kimura 1980; Cerrato 1990).



**Fig. 3.** Mean ( $\pm$  s.e.) values of coefficient of variation (CV) for each band class read by the principal reader. Sample sizes are given for each corresponding band class.

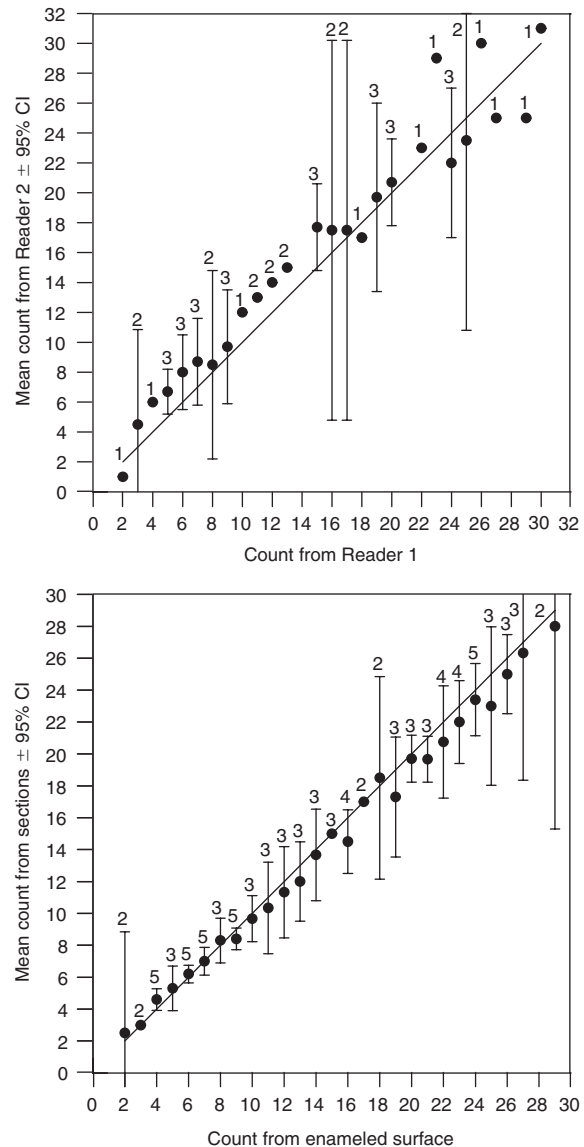
## Results

### Age estimation

The first dorsal fin spines (DFS) provided better readability scores and more precise readings than the second DFS. Most first DFS had a readability score of 2 (51.5%) or 3 (42.4%), whereas most of the second DFS had a readability score of 3 (62.1%) or greater (Fig. 2a). Differences between readings for first and second DFS varied by up to five bands, but differences were mostly  $\pm 1$  count (Fig. 2b). Mean coefficient of variation (CV) and index of average percentage error (APE) among readings were 7.53 and 5.33%, respectively, for the first DFS and 9.03 and 6.39%, respectively, for the second DFS, indicating that more precise counts were obtained when the first DFS was used. Mean CV and APE between the first and second DFS were 14.04 and 9.93% respectively. Agreement between first and second DFS decreased with the number of bands counted (Fig. 2c). The first DFS was used for age estimation because it showed a clearer readability pattern, higher precision between readings, and an overall higher number of bands.

The relationship between the first DFS length and total length was linear (DFS length =  $0.086$  total length [TL] -  $2.739$ ,  $r^2 = 0.9$ ) and there was no significant difference between males and females (Student's  $t$ -test,  $t = 1.77$ , d.f. = 98,  $P > 0.05$  for comparison of slopes, and  $t = 1.07$ , d.f. = 98,  $P > 0.05$  for comparison of elevations). The increase in DFS length with total length shows that spines grow throughout life, indicating that this structure is useful for age estimation.

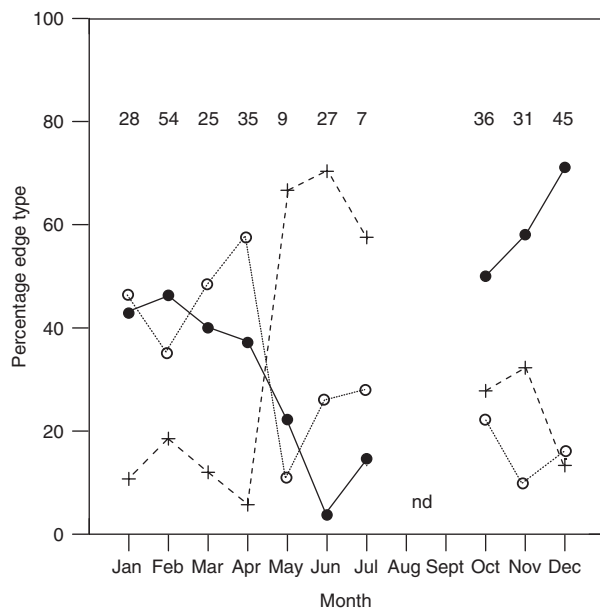
A total of 493 first DFS were examined, of which 41 (8.3%) were rejected because they did not conform to the selection criteria (i.e. readability score  $\leq 3$  and identical counts from at least two of three or four readings). Band counts from 163 males (274 to 470 mm TL) and 289 females (287 to 622 mm TL)



**Fig. 4.** Age-bias plot for the comparison of band counts between readers and band counts on spine sections and on the external enameled surface. The solid line is the 1:1 relationship. Sample sizes are given above each corresponding count.

were used for age estimation. Within-reader precision among readings (sexes combined) was high: mean CV and APE were 6.99 and 4.94% respectively. Overall, for each band class, CV was low, exhibiting the lowest values for mid-band classes (14 to 23 band class) (Fig. 3). Mean CV and APE between readers (sexes combined) were 11.35 and 8.03% respectively. There were no systematic differences between readers (Fig. 4). Worn spines (4.9% for males and 15.9% for females) were corrected for missing bands using the equations derived from the relationship between the number of bands and spine-base diameter (SBD) of unworn spines ( $\text{Counts}_{\text{male}} = 0.394\text{SBD}^{3.064}$ ,  $r^2 = 0.83$ ;  $\text{Counts}_{\text{female}} = 0.965\text{SBD}^{2.083}$ ,  $r^2 = 0.94$ ).





**Fig. 5.** Monthly variation in the type of enamel edge. White circle: wide light edge (WL); black circle: light edge (L); +: dark edge (D); nd, no data. Sample sizes are given for each corresponding month.

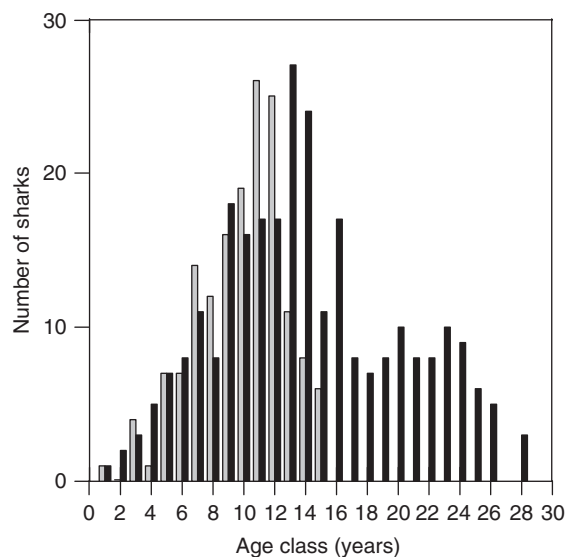
#### Verification

The nature of the enamel edge varied with month (Fig. 5). At no time of the year were the spines entirely of one edge type. Most sharks collected between May and July (autumn-winter) had dark edges, whereas the highest percentage of light edges occurred in sharks collected between October and December (spring-early summer). For spines with wide light edges, the highest percentage was found in sharks collected between January and April (summer-autumn). This annual edge pattern suggests that dark rings form during the cold period of the year. In addition, there was good agreement between counts on spine sections and counts on the external enameled surface (Fig. 4).

#### Growth estimation

Males ranged from 1 to 15 years in age, whereas females reached a maximum age of 28 years. Most males were 11 to 12 years old, whereas most females were 13 to 14 years (Fig. 6). Growth parameters of *Squalus megalops* were estimated separately from five models fitted to length-at-age data (Table 4). Growth models fitted the data well, with females showing higher coefficients of determination ( $r^2 \geq 0.88$ ) than males ( $r^2 \geq 0.72$ ).

For males, the two-phase von Bertalanffy growth model (TPVBGM) was the best of the growth models fitted with an Akaike weight ( $w_i$ ) of 0.54 (Table 4). However, the von Bertalanffy (VBGM) and Gompertz growth model followed rather closely ( $w_i = 0.24$  and  $0.19$  respectively), revealing a degree of uncertainty regarding the best model for fitting length-at-age data of males. The TPVBGM predicted values (and 95% confidence intervals) of asymptotic lengths ( $L_\infty$ ) and growth coefficients ( $k$ ) of 455 (19) mm TL and  $0.158$  ( $0.05$ )  $\text{years}^{-1}$  respectively.



**Fig. 6.** Age distribution for male (grey) and female (black) *Squalus megalops*.

For females, the best fitting model was the TPVBGM with a  $w_i$  of 0.95 (Table 4); other models gave lower values of  $w_i$ , indicating that they do not fit the length-at-age data as well. The TPVBGM predicted values (and 95% confidence intervals) of  $L_\infty$  and  $k$  of 756 (88) mm TL and  $0.042$  ( $0.01$ )  $\text{years}^{-1}$  respectively.

The TPVBGM provided the best fit for females and a better fit than other models for males; therefore, this function was used to construct the growth curves for both sexes (Fig. 7). Likelihood ratio tests indicated significant differences between the growth curves of the two sexes ( $P < 0.001$ ). Males grew faster than females (Table 4). Predicted length-at-age of males was initially higher, but after they attained eight years of age, growth of males and females was similar up to ~10 years when transition between growth phases occurred (Fig. 7; Table 4). After age 10, growth of males slowed down whereas growth of females continued with length, increasing steadily throughout their lifespan.

#### Discussion

The first dorsal fin spines (DFS) of *Squalus megalops* showed clearer readability, higher precision between readings and an overall higher number of bands than the second DFS. Most ageing studies on squalid sharks use whole second DFS because it is larger and the tip of the first DFS tends to be worn down (Cailliet and Goldman 2004). Although some studies have used the first DFS as a check (e.g. Nammack *et al.* 1985), few have compared the suitability of the first and second DFS for ageing (but see Holden and Meadows 1962; Irvine 2004). Given that the structure of the first and second DFS is similar (e.g. Holden and Meadows 1962; Clarke *et al.* 2002a), preference for first or second DFS for age estimation should be a question of readability. Sections of the first DFS of the birdbeak dogfish *Deania calcea* (Clarke *et al.* 2002a) and the gulper shark *Centrophorus squamosus* (Clarke *et al.* 2002b) provided better readability than sections from the second DFS. For *S. megalops*

**Table 4. Growth estimates (with 95% confidence intervals) and model selection criterion for male and female *Squalus megalops***  
Refer to Table 3 for meaning of parameters

Model	Parameter	Estimate	Males ( <i>n</i> = 157)				Estimate	Females ( <i>n</i> = 274)			
			<i>r</i> <sup>2</sup>	AIC	ΔAIC	<i>w<sub>i</sub></i>		<i>r</i> <sup>2</sup>	AIC	ΔAIC	<i>w<sub>i</sub></i>
VBGM	<i>L</i> <sub>∞</sub> (mm)	455 (21)	0.74	851.85	1.68	0.24	829 (126)	0.89	1774.94	9.50	0.01
	<i>k</i> (years <sup>-1</sup> )	0.144 (0.05)					0.034 (0.01)				
	<i>t</i> <sub>0</sub> (years)	-5.72 (2.50)					-10.83 (2.82)				
2VBGM	<i>L</i> <sub>∞</sub> (mm)	440 (9)	0.73	856.19	6.02	0.03	699 (33)	0.88	1791.11	25.68	<0.01
	<i>k</i> (years <sup>-1</sup> )	0.198 (0.02)					0.056 (0.01)				
TPVBGM	<i>L</i> <sub>∞</sub> (mm)	455 (19)	0.75	850.17	0	0.54	756 (88)	0.89	1765.43	0	0.95
	<i>k</i> (years <sup>-1</sup> )	0.158 (0.05)					0.042 (0.01)				
	<i>t</i> <sub>0</sub> (years)	-4.86 (2.10)					-9.77 (2.60)				
	<i>h</i>	0.094 (0.08)					0.087 (0.05)				
	<i>t<sub>h</sub></i> (years)	10.5 (0.60)					10.2 (0.60)				
Gompertz	<i>L</i> <sub>∞</sub> (mm)	449 (17)	0.74	852.27	2.10	0.19	717 (59)	0.89	1771.92	6.49	0.04
	<i>k</i> (years <sup>-1</sup> )	0.172 (0.05)					0.063 (0.01)				
	<i>t</i> <sub>0</sub> (years)	-3.54 (1.68)					0.026 (0.81)				
2Gompertz	<i>L</i> <sub>∞</sub> (mm)	433 (7)	0.72	861.11	10.94	<0.01	632 (18)	0.88	1804.37	38.90	<0.01
	<i>k</i> (years <sup>-1</sup> )	0.252 (0.02)					0.098 (0.01)				

AIC, Akaike's information criterion; ΔAIC, AIC differences between models; *w<sub>i</sub>*, Akaike weights; *n*, sample size.

off South Africa, Watson and Smale (1999) only used the second DFS, rejecting after several readings 12% of spines for age estimation; in contrast, in the present study only 8% of the spines used were rejected, probably as a result of the better readability of first DFS. Therefore, for *S. megalops*, the clearer pattern of bands observed in the first DFS made this structure easier to read and hence more suitable for age analyses than the second DFS.

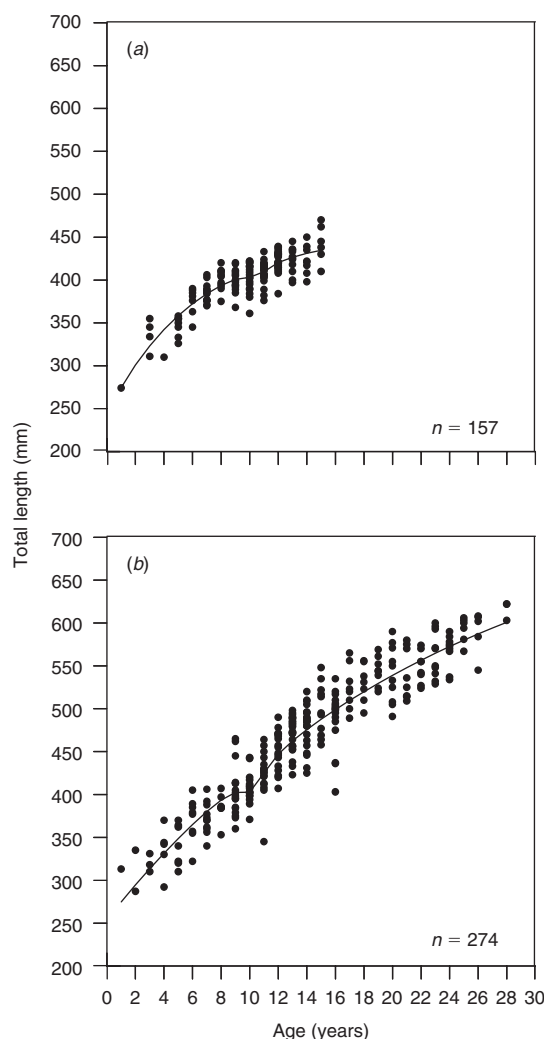
The low values of the coefficient of variation (CV) and the average percentage error (APE) index for the within- and between-reader analyses suggested high precision for the age assessment of *S. megalops*. These two indices assume that variability among observations of individual fish can be averaged over all age classes, obscuring differences in precision (Hoenig *et al.* 1995). However, when calculations were made for each age class (within-reader only), between-age class variability was low. A trend of increasing within-reader precision was observed for the mid-range age classes, suggesting that these classes are easier to read. The age bias plot indicated no bias in the age estimation of Reader 1 (principal reader). Few studies on the age and growth of squalid sharks provide estimates of precision and bias, despite their importance for any ageing studies (Campana 2001). However, when such estimates are produced (Holden and Meadows 1962; Ketchen 1975; Nammack *et al.* 1985; Clarke *et al.* 2002a, 2002b; Irvine 2004), most studies report high reproducibility of age estimates, further supporting the use of spines as a precise approach for ageing squalid sharks.

Analysis of the enamel edge of whole spines supports the hypothesis of annual band formation in *S. megalops*. The peak in dark bands observed during late autumn-winter (May to July), followed by the peak in light bands during spring-early summer (October to December), and by the peak in wide light bands during early autumn (March to April), was the expected pattern for annual band deposition. A similar pattern was reported for *Squalus acanthias* off north and west Scotland (Holden and Meadows 1962) and off the north-eastern USA (Nammack *et al.* 1985). For *S. acanthias*, the timing of light and dark band

formation on the enamel edge of spines was validated using mark-recapture oxytetracycline (OTC)-tagged sharks (Tucker 1985).

Band counts of the inner dentine layer (spine sections) of first DFS of *S. megalops* were in good agreement with counts of the enameled surface, verifying the age estimates obtained from counts of the enameled surface of spines. Counts of bands of the inner dentine have been used for age estimation of other squalid sharks (e.g. Clarke *et al.* 2002a, 2002b; Irvine 2004). For *S. acanthias*, comparisons of internal (sections) and external (enameled surface) counts agreed within ±2 bands (Holden and Meadows 1962). However, for the deepwater velvet dogfish *Centroscyrmnus crepidater*, Portuguese dogfish *C. coelolepis* and New Zealand lantern shark *Etmopterus baxteri*, the number of external bands exceeded the number of internal bands in sharks older than 3 to 5 years (Irvine 2004).

Several authors (e.g. Beamish and McFarlane 1983; Cailliet 1990; Campana 2001) have stressed the need for validation of the temporal periodicity of band deposition and of the absolute age for accurate age estimation. Captive rearing of OTC-tagged *S. megalops* was attempted in order to validate the periodicity of band deposition. However, as with a similar study in South Africa (Watson and Smale 1999), maintenance of sharks in captivity was met with limited success. More rigorous methods of age validation, such as the bomb radiocarbon method (Druffel and Linick 1978), is not applicable to *S. megalops* because samples of sharks born during the period of <sup>14</sup>C increase (1955 to 1970) are not available. Annual deposition of bands on spines of squalid sharks has been validated for *S. acanthias* on both sections and the enameled surface of whole spines (Beamish and McFarlane 1985; Tucker 1985; McFarlane and Beamish 1987). Although it does not necessarily follow that these bands are annual in other squalid sharks (Clarke *et al.* 2002b), for *S. megalops*, the most parsimonious interpretation of available evidence (edge analysis and comparisons of internal and external bands) points to annual formation of bands. However, further research



**Fig. 7.** Two-phase von Bertalanffy growth model (TPVBGM) fitted to length-at-age data derived from counts on the first dorsal fin spine (DFS) of (a) male and (b) female *Squalus megalops*. Estimates of model parameters are given in Table 4.

is needed to confirm annual band deposition and absolute age of *S. megalops*. A pilot tagging study gave promising results (9 recaptured sharks out of 617 tagged; Brown *et al.* 2000); hence, a large-scale release-recapture program of known-age and marked sharks or OTC-tagged sharks (Beamish and McFarlane 1985; Campana 2001) would provide information on periodicity of band deposition.

Growth model selection is not a straightforward process. Based on the goodness-of-fit criterion used (Akaike's Information Criterion, AIC), the best model for both sexes was the two-phase von Bertalanffy growth model (TPVBGM). The use of a TPVBGM allows growth to be divided into two phases, such as changes in habitat (e.g. from coastal to off-shore waters), feeding habits (e.g. from a planktivorous to a piscivorous diet) or energy allocation (e.g. from energy allocated to growth, as in juveniles, to energy allocated to growth and reproduction, as in adults). For male *S. megalops* the change in growth rate

corresponded with size at maturity, whereas for females, the change was slightly before the size females began to mature (Braccini *et al.* 2006a). This would support the energy allocation hypothesis as an explanation of two-phase growth. However, the other two hypotheses cannot be discarded, because *S. megalops* exhibits a strong pattern of size segregation (Graham 2005; Braccini *et al.* 2006b) where juveniles and adults may occur in different habitats, and large and small individuals have different feeding habits (Braccini *et al.* 2005).

The quality of data used in the fitting process and the shape of the growth curve are of similar importance in the description of the growth process, particularly when samples are collected from commercial fishing operations. When growth models are fitted to these types of data, the resulting parameters may be different from those obtained from a more representative sample (Haddon 2001). Most studies on age and growth of elasmobranchs obtain samples from commercial fisheries and assume that data are unbiased. However, the length-age scattergram and the growth curve of *S. megalops*, particularly of females (see Fig. 7 of the present study; Watson and Smale 1999), and other shark species (e.g. Moulton *et al.* 1992; Cannizzaro *et al.* 1995) does not asymptote, suggesting that either samples are not representative of the entire population and further sampling of large individuals is required, or that those species do not exhibit an asymptotic maximum length and hence asymptotic models are not adequate to describe growth. Linear growth of long-lived species such as sharks has only been reported for juveniles (e.g. Simpfendorfer 2000) or when sampling is not representative of all size classes (e.g. Wintner 2000). Hence, it is more likely that the observed scattergram and the subsequent growth curve derived are products of unrepresentative data, owing to a combination of several factors. Length-selective sampling bias and length-selective fishing mortality of gill-nets can cause distortions to growth curves (Moulton *et al.* 1992; Walker *et al.* 1998). In the present study, most samples were collected from demersal otter trawl and Danish seine vessels. Although the selectivity of the mesh of the trawl cod-end is not adequately understood, length-selective sampling bias and fishing mortality might partially account for the shape of the growth curve and the scatter of data points for *S. megalops*.

The movement pattern of *S. megalops* may affect the size classes encountered by the trawl fishery. Parturition is likely to occur outside the fishing grounds (Graham 2005). Because *S. megalops* is an opportunistic predator that consumes a wide range of prey items, larger neonates and juveniles are thought to move to the fishing areas to feed on trawl discards or prey exposed by trawl operations that disturb sediments (Braccini *et al.* 2005). Hence, the larger neonates and juveniles would then become available to sampling by the trawl gear and thereby create a bias in the size distribution of neonates and juveniles sampled, owing to a higher probability of collecting large, fast-growing individuals rather than small, slow-growing individuals. For intermediate-aged sharks, the large, fast-growing individuals of an age class may have been selectively removed from the population by fishing (Walker *et al.* 1998; Haddon 2001). This length-selective removal of the largest sharks of the available age classes by fishing has a biasing effect when sampling these age classes. Also, fishing mortality might have removed the older individuals from the population, making these age classes not available



to sampling. Alternatively, due to the strong size segregation exhibited by *S. megalops* (Graham 2005; Braccini et al. 2006b), if certain size class or size classes (e.g. the largest females of each age class) occurred outside the trawling areas, only the smallest individuals would be available for sampling and the size-at-age frequency distribution of the age classes would be biased. The biasing factors listed above might have distorted the size-frequency distribution of males and females, which might have led to the two-phase growth pattern observed. Therefore, alternative growth models such as VBGM and Gompertz should also be considered when modelling the growth dynamics of *S. megalops*.

Precision estimates, the relationship between spine total length and TL, edge analysis, and agreement between counts on the inner dentine layer and the enameled surface support the use of the first DFS for the age estimation of *S. megalops*. Based on goodness-of-fit criterion, the best growth model for males and females was the TPVBGM. However, model selection cannot only be based on quality of statistical fit and, given that length-at-age data might not be representative of real growth, results should be interpreted with caution. Regardless of the model used, the growth rate of *S. megalops* (particularly of females) is very low, even within the range of growth rates reported for shark species (0.03 to 1.337 years<sup>-1</sup>) (Cailliet and Goldman 2004). The reproductive output of this species is also low: litter size is at most four and the reproductive cycle is almost two years (Braccini et al. 2006a). These characteristics indicate that *S. megalops* has low biological productivity and is therefore at higher risk to the effects of fishing than species with greater biological productivity.

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