

## AGE AND GROWTH OF THE SHORTRNOSE SPINY DOGFISH *SQUALUS MEGALOPS* FROM THE AGULHAS BANK, SOUTH AFRICA

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Lengths-at-age and growth rates of dogfish *Squalus megalops* collected from the Agulhas Bank, South Africa, were estimated by counting the pigment bands on the enameled surface of the second dorsal fin spine. Dogfish are relatively slow-growing and long-lived. The maximum ages observed were 29 years for males and 32 years for females. Growth was best described by the Von Bertalanffy growth model and a significant difference in the growth rates for each gender was demonstrated. Females attained larger sizes (largest aged was 782 mm TL;  $L_{\infty} = 932.145$  mm,  $K = 0.0328$ ) than the males (largest aged was 572 mm TL;  $L_{\infty} = 525.878$ ,  $K = 0.0893$ ). Males attained 50% maturity at about 9 years of age (400 mm TL) and females at approximately 15 years (490 mm TL). Estimates suggest a high biomass of *S. megalops* on the Agulhas Bank, possibly making it appropriate for exploitation. However, its life-history characteristics necessitate a cautious management approach should it become a target species, particularly because it is already taken as a bycatch of the trawlfishery. A feasibility study of age validation showed that oxytetracycline was absorbed by the dorsal fin spine of captive specimens, although laboratory conditions were inadequate to maintain this species over a prolonged period.

Dogfish (genus *Squalus*) are some of the most commonly caught chondrichthyans in commercial trawl catches (down to 600 m) off southern Africa. Species caught are the shortnose spiny dogfish *Squalus megalops*, the longnose spiny dogfish *S. mitsukurii* and the spotted spiny dogfish, *S. acanthias* and the roughskin spiny dogfish *S. asper*. (Compagno *et al.* 1989a).

There is confusion in the classification of the genus *Squalus*, because of the similarity in morphological and biological characteristics of fish from different regions (Myagkov and Kondyurin 1986). Last and Stevens (1994) have suggested that *S. megalops* is an Australian endemic and have described its distribution off southern Australia and Tasmania, but as unconfirmed off southern Africa, Indo China, New Caledonia and New Hebrides. To rectify the confusion, members of the *S. megalops* group from southern Africa need to be critically compared with those from the western Pacific and from the eastern north Atlantic (Compagno *et al.* 1991). For the present, the group from southern Africa is referred to as *S. megalops* (Compagno 1990a, Compagno *et al.* 1991), pending a revision of its status.

Dogfish have been described as the smallest and most abundant demersal shark of temperate and tropical seas (Compagno 1984). Sharks represent a substantial bycatch of the demersal trawlfishery targeting hake off the Western and South-Eastern Cape and in Namibian waters (Compagno 1990b). Analysis of the routine South Coast demersal research trawl catches on the Agulhas Bank has shown that *S. megalops* form a substantial component of the shelf fish community (Smale *et al.* 1993). It has been estimated to have the

fifth largest biomass of species caught on the surveys (Japp *et al.* 1994). They are presently considered "trash" and are usually discarded dead at sea (Compagno *et al.* 1989b).

The life-history characteristics of most elasmobranchs (slow growth, late maturation and low fecundity) make them vulnerable to fishing pressure (Nammack *et al.* 1985, Hanchet 1988, Pratt and Casey 1990). A shift in the status of *S. megalops* from trash to target species would probably result in increased fishing pressure. At present, the development of a management plan is difficult, because of a lack of adequate biological data, especially accurate information on age and growth. Bass *et al.* (1976) provided information on the status of the species in a summary of the biology of *S. megalops* from the east coast of southern Africa, and Ebert *et al.* (1992) presented preliminary findings on the feeding of this species from the west coast of southern Africa.

In elasmobranchs, age estimates are based on growth bands, which appear as alternating opaque and translucent zones on calcified structures such as the vertebrae and fin spines (Ketchen 1975, Beamish and McFarlane 1985, Nammack *et al.* 1985, Tucker 1985, Branstetter 1987, Cailliet 1987, 1990, Freer and Griffiths 1993, Branstetter and Musick 1994). Several researchers have used the spine for age determination purposes in the commercially important spotted spiny dogfish *Squalus acanthias* (Ketchen 1975, Beamish and McFarlane 1985, Nammack *et al.* 1985). The enumeration of growth bands in spines offers a quick and reliable method of age determination for the two shark families (Squalidae and Heterodontidae) that possess dorsal fin

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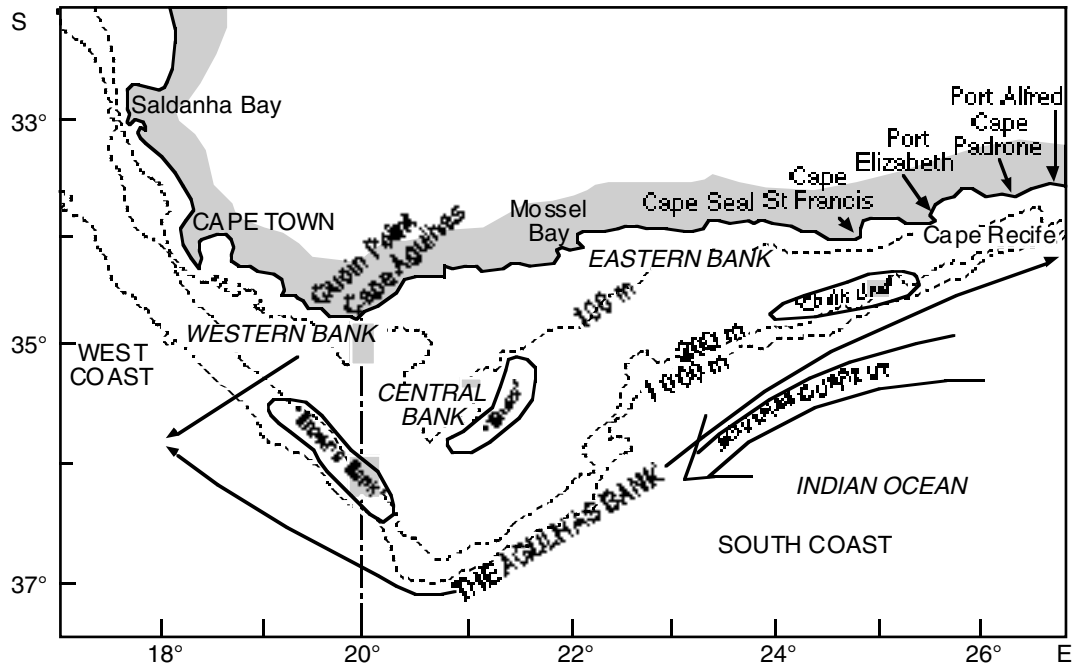


Fig. 1: Map illustrating the oceanographic features of the Agulhas Bank. The popular commercial fishing grounds (Browns Bank, the Blues and the Chalk Line grounds) are shown

spines (Ketchen 1975, Beamish and McFarlane 1985). Furthermore, the use of this method allows direct comparison with previous work on other dogfish.

The focus of this study was an examination of the pigment bands on the enameled surface of the second (or posterior) dorsal fin spine for an age and growth study, and to estimate age at maturity and longevity of *S. megalops* on the Agulhas Bank. The potential of this species for exploitation and its susceptibility to overexploitation is briefly discussed.

## MATERIAL AND METHODS

Specimens were collected from the research survey trawls of the F.R.S. *Africana* during May and September/October 1995. The area surveyed extended from Cape Agulhas (20°E) to Port Alfred (26°54' E), and included all depths to 500 m (Fig. 1). Details of the survey area and methods used are described by Badenhorst and Smale (1991). Additional monthly samples were taken from catches from depths of 150–250 m by commercial trawlers between May 1995 and April 1996 off Cape St Francis (24°52' E) and

Port Alfred.

The removal of the second dorsal spine followed the method described by Chilton and Beamish (1982). The skin, tissue and cartilage were carefully removed from the spine without boiling or immersion in any chemical. The cleaned spine was rubbed briskly with a cloth to clean, polish and highlight the pigment bands on the enameled surface and was then left to air-dry.

The total length (*TL*) of each fish was taken from the tip of the snout to the tip of the upper lobe of the caudal fin, depressed in a line horizontal with the body (Compagno 1984). Sexual maturity was determined following dissection (Watson and Smale 1998) and the sexes were treated separately.

## Measurements of the spine

Spine measurements were recorded using digital calipers (accurate to 0.01 mm) following Ketchen (1975) – see Figure 2:

- (i) total length of enamel from spine tip to edge of enamel on anterior edge of spine;

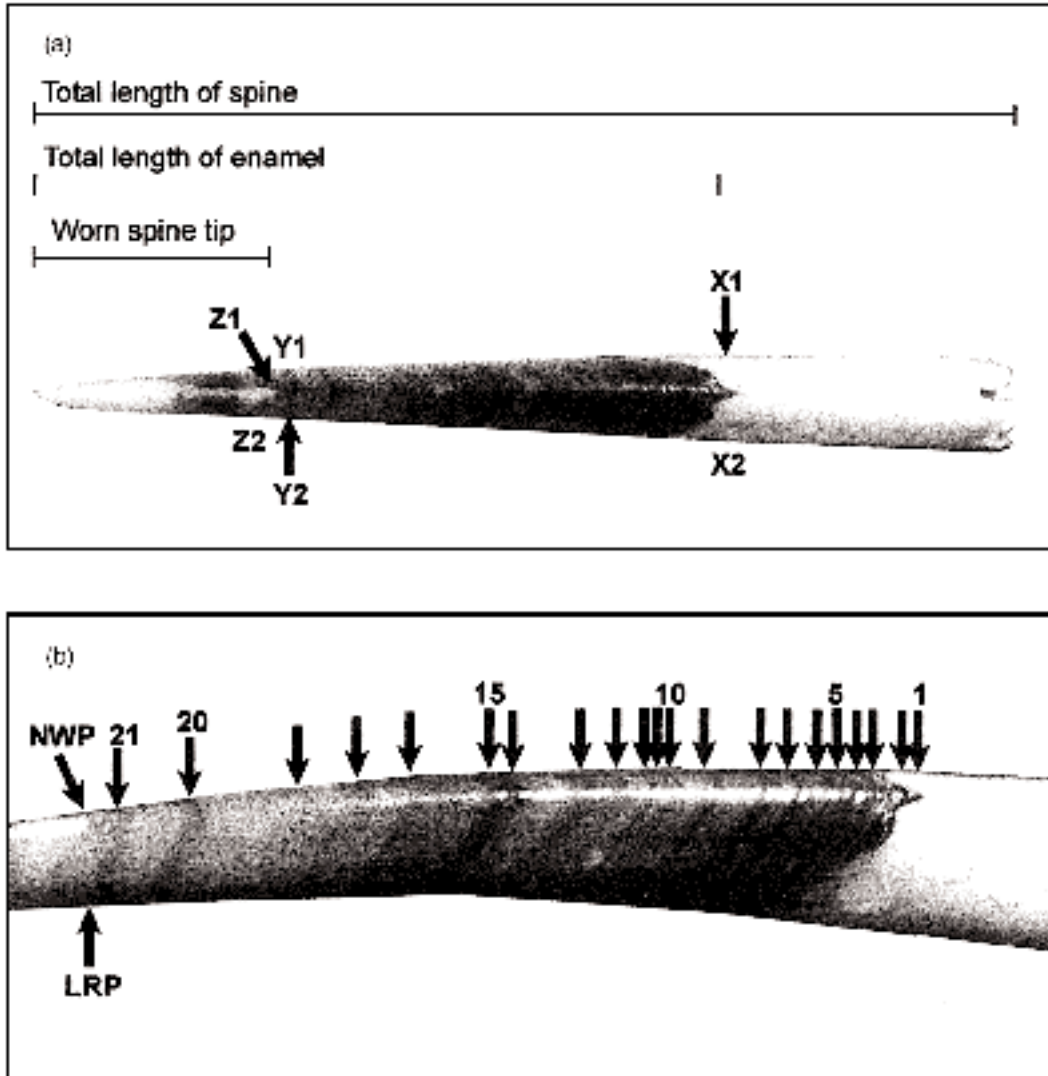


Fig. 2: (a) Anterior view of a cleaned second dorsal fin spine of *S. megalops*, illustrating the position of the measurement of spine base diameter (X1–X2), last readable point (LRP, Y1–Y2) and no-wear point (NWP, Z1–Z2) (modified from Ketchen 1975); (b) antero-lateral view of the fin spine, illustrating 21 band counts

- (ii) spine base diameter at the basal edge of the enamel, X1 – X2;
- (iii) spine base diameter at last readable point (LRP), Y1 – Y2; or
- (iv) spine base diameter at no-wear point (NWP), Z1 – Z2.

The terms NWP and LRP are explained fully below.

#### Interpreting and counting the bands

Bands were identified following the method of McFarlane and Beamish (1987a). They appeared as alternating opaque and translucent zones on the spine. All distinct, darkened bands and/or ridges along the surface of the spine were counted using a stereoscopic light microscope (using a 10× eyepiece with a magni-

fication of 0.8×) with reflected light. It was sometimes easier to read the more faint and narrow bands with the naked eye, or using a magnifying glass (4×), while rotating and tilting the spine.

A band that was solid on the leading edge of the spine and split on the trailing edge was counted as a single band. If visible only as a dark mark on the leading edge of the spine, the band was counted if it was similar in thickness to neighbouring bands that did continue to the trailing edge of the spine. Bands that appeared to be broad and very dark to the naked eye were usually multiple bands, and were counted individually, because there was no reason to group the bands (Beamish and McFarlane 1985). Faint, fine, hair-like lines lying parallel to distinct bands (often close to the spine tip), as well as white lines on the leading edge of the spine, were not counted, because they were not considered to be distinct bands (McFarlane and Beamish 1987b). The bands towards the spine tip were usually lighter in colour and less distinct than those nearer the base.

The spine base diameter of free-swimming early juveniles, with a yolk sac scar, was termed the "birth diameter". This diameter (taken as an average of all those measured) was marked with permanent ink on the distal portion of all spines not worn below this point. Any rings distal from this mark resulted from growth of the spine before the first band had been laid down and were not included in the count.

The spine tip showed increased wear as a result of abrasion as the fish aged. The bands in this region became faint and difficult to count as the enamel eroded or chipped off. Furthermore, the enamel at the basal end of the spine may also become so eroded that it no longer wraps around the spine, but remains as a tapering piece of enamel on the anterior edge. Enamel wearing may result in a significant loss of bands and this has to be considered when aging *S. megalops* using this method.

### Estimation of age

Three alternative methods of estimating age from the bands were used, depending on the condition of the spine (Ketchen 1975).

- (i) The bands on the spines of young fish that showed no wear were counted up to the marked birth diameter. This would be the total band count for the spine, because no correction would be needed.
- (ii) In spines where the enamel showed wear, bands were counted up to the point (usually close to the spine tip) at which the enamel showed no wear – the no wear point (*NWP*). The bands closer to the spine tip are not discernible if the spine is colourless as a result of enamel wear.
- (iii) If the bands along most of the spine were very faint, the count was taken to the last clearly discernible band. This is termed the last readable point (*LRP*), following the advice of G. A. McFarlane (Pacific Biological Station, Canada, pers. comm.).

Each of these three methods gives the observed band count (*O*). In spines read to the *NWP* or *LRP*, the position of the last band counted falls short of the birth diameter. Correction for missing bands was made using the method described by Ketchen (1975). The number of bands read from unworn spines (those with no enamel wear) was regressed against spine-base diameter. A regression equation was obtained for both males and females. For worn spines (showing enamel wear), the spine diameter at the *NWP* or *LRP* was measured and the number of bands corresponding to this measurement was calculated from the regression equation. This is the correction estimate (*C*). The age of the fish was then estimated using the formula:

$$\begin{aligned} \text{Observed (O) + correction estimate (C)} \\ &= \text{total number of bands} \\ &= \text{estimate of age (Ketchen 1975, Fahy and Gleeson 1990).} \end{aligned}$$

This method markedly reduces the number of spines that would otherwise have been rejected as unreadable (Ketchen 1975).

### Band counts and verification

It was decided to follow a procedure for counting bands similar to that used for the spines of *S. acanthias* by Holden and Meadows (1962) and Ketchen (1975). Initially, the bands on a random subsample of 12 female and 12 male spines were counted by the two authors independently of knowledge of each others interpretation. As validation for this species has not yet been achieved, this subsample was sent to G. A. McFarlane and his colleagues from the Pacific Biological Station for band verification. They agreed that it was appropriate to age *S. megalops* using the criteria presented in McFarlane and Beamish (1987a). Because the counts made by both laboratories were comparable in most cases, age was estimated by counting the bands on the spine using their criteria for *LRP*.

For the rest of the material, only the first author counted the bands on all the spines. A band count for each spine was done at least twice, each after a time-

lapse of at least two months. In order to prevent bias, these counts were made without reference to previous counts, length or sex of the fish. When the counts differed by one, half the spines were assigned to the lower count value and half to the higher value; if the counts differed by two, the mean count value was taken, and if the band count differed by three, the middle count value was taken. If the count differed by more than three, the spines were read again, and another time if necessary. After this, a count difference of greater than three bands resulted in rejection of the spine for age estimation.

### Growth estimation

Three different growth models were tested against the observed length-at-age data, using the program PC-Yield 2.2 (Punt and Hughes 1989). They were the Schnute (4 parameters), the Gompertz, and Von Bertalanffy (3 parameters) for females and males. Models were fitted using an iterative, non-linear minimization procedure (Butterworth *et al.* 1989, Punt and Hughes 1989). Minimization of the sum-of-squared absolute (as opposed to relative) differences was used, even though the residuals for this method were heteroscedastic. Likelihood ratio tests revealed that the Gompertz and Von Bertalanffy models fitted the data best. Because there was little difference between the models, and because Von Bertalanffy growth parameters have often been used in comparing aspects of the life history of the *Squalus* species (Ketchen 1975, Nammack *et al.* 1985, Saunders and McFarlane 1993), this model was used.

The Von Bertalanffy growth model is

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

where  $L_\infty$  is the asymptotic length,  $K$  is the rate at which  $L_t$  approaches the asymptote,  $L_t$  is the total length at time  $t$ , and  $t_0$  is the hypothetical age at zero length.

Standard errors (*SE*) and 95% confidence intervals (*CI*) for each parameter were calculated using a non-parametric bootstrap technique (500 bootstraps) and the percentile method respectively (Punt and Hughes 1989). The likelihood ratio test for significant differences in the fit of the model for males and females was also conducted (Punt and Hughes 1989).

### Age validation

An attempt was made to mark the spines of captive *S. megalops* with oxytetracycline (OTC) in order to

validate the periodicity of band deposition and to determine growth rate.

Eight dogfish were caught using hooks and handlines from a skiboat in Algoa Bay. They were sexed, weighed and *TL* was measured. An intraperitoneal injection of OTC was administered, using a dosage of 25 mg per kilogramme body mass (McFarlane and Beamish 1987b), and an internal identifying tag (Trovan® Passive Transponder System) was injected under the skin next to the first dorsal fin. The fish were kept together in a circular, indoor wire-frame pool, 60 cm deep with a diameter of 3 m. The pool was supplied with a constant flow of natural seawater, which was filtered using a biological filter and foam fractionator. There was no method of temperature control in the room or in the water, and the diurnal light rhythm was natural. The fish were offered a diet of small pieces of squid, octopus and fish approximately twice per week.

Upon natural death, the dorsal fin spine was removed and viewed under reflected ultraviolet light in order to locate the fluorescent deposition of OTC. An Olympus BX 50 microscope with camera attachment was used to view and photograph the spine. The OTC mark was located under reflected normal light and the distance from the base of the enamel (on the anterior edge of the spine) to the OTC mark was measured using digital calipers. The number of bands between the mark and the enamel edge was counted.

## RESULTS

Although some preliminary difficulties in band identification were experienced, the verification exercise lent confidence to band counting. In a preliminary estimate of precision, 230 spines were counted, two or more times. Of these counts, 20% were the same, 25.7% were within one year of each other, 22.6% were within two years of each other and 11.7% were within three years of each other. Only 20% were greater than three years difference from each other. With practice, band counting improved and only 12% of the spines from the final sample were rejected as a result of band count differences greater than three years with repeat readings.

Of the 978 specimens collected, 110 spines were too damaged to attempt a band count. Band counts of 764 spines (88% of the processed material) were used in the age estimation; 255 males (232–572 mm *TL*) and 509 females (235–782 mm *TL*). The regression to correct for missing bands, using the method devised by Ketchen (1975), was calculated from 86 unworn

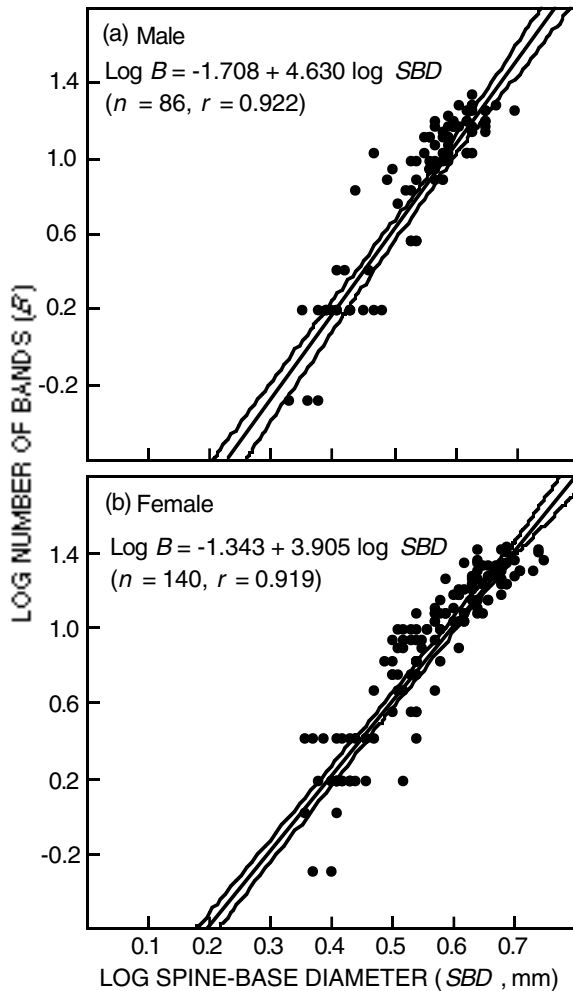


Fig. 3: Relationship between diameter of unworn spines and number of bands (equivalent to years) counted for (a) male and (b) female *S. megalops*

spines from males and from 140 unworn spines from females (Fig. 3). The spine diameter at birth, taken as a mean of 15 spine-base diameters of early juveniles (<1 year old), measured  $1.61 \pm 0.22$  mm.

#### Determination of age

Even though band deposition for *S. megalops* has not been validated, based on studies of *S. acanthias* (Beamish and McFarlane 1985), it has been assumed

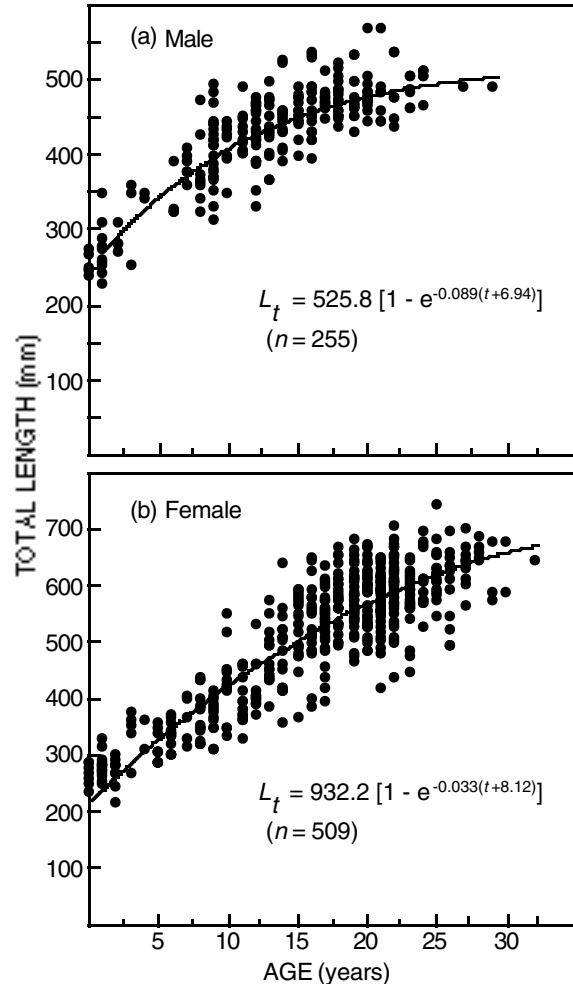


Fig. 4: Calculated Von Bertalanffy growth curve and observed length-at-age for (a) male and (b) female *S. megalops*

here that the bands counted were deposited annually. Hence, the number of bands equates to age (years). The observed band count ( $O$ ) plus correction estimate ( $C$ ), using the procedure devised by Ketchen (1975) for worn spines, determined the age of the fish. The maximum estimated age for the females was 32 years (639 mm  $TL$ ), whereas that for the males was 29 years (489 mm  $TL$ ). The maximum  $O$  value for a female was 30 years for an individual of 639 mm  $TL$ , whereas a count of 29 bands ( $O$ ) was the highest observed for a male of 489 mm  $TL$ . The maximum calculated  $C$  value was 18, which was added to an  $O$  value of 10

Table I: Von Bertalanffy growth parameters and the standard errors (SE) and 95% confidence intervals (CI) for male and female *S. megalops*

Parameters	Estimate	SE	95% CI
Males ( $n = 255$ )			
$L_{\infty}$ (mm)	525.9	14.9	502.2 – 559.9
K	0.09	0.01	0.07 – 0.11
$t_0$ (years)	-6.9	0.9	-5.5 – -9.1
Females ( $n = 509$ )			
$L_{\infty}$ (mm)	932.2	102.4	815.0 – 1 206.8
K	0.03	0.01	0.02 – 0.04
$t_0$ (years)	-8.1	1.1	-6.5 – -10.7

to give an age estimate of 28 years for a female of 647 mm TL. In males, the maximum  $C$  value calculated was 7, which was added to an  $O$  value of 17 to provide an estimated age of 24 years for a specimen of 510 mm TL.

## Growth

The relationship of length to estimated age of males and females is exemplified by the Von Bertalanffy growth curve in Figure 4. No outliers were rejected from this dataset. The three parameters ( $K$ ,  $L_{\infty}$  and  $t_0$ ) for males and females are given in Table I. A likelihood ratio test showed that the differences between male and female growth were highly significant ( $p < 0.001$ ).

The growth in males is initially rapid, but it then slows down in subsequent years (Fig. 4a). Using the example of a 29 year-old fish, 68% of the growth occurred in the first five years, 80% within nine years and 90% of the growth had occurred by the time the fish was 15 years old. There was an increase in length of only about 100 mm over the 20 years from age 9 to age 29 years. The curve for females illustrated no such period of rapid initial growth, but rather that length increase was steady (Fig. 4b). Less than half (46%) of the growth of a 30 year-old female had occurred by the age of five years, 57% within nine years and after 15 years the fish was 70% of its full size. The difference in growth rates between males and females is clearly illustrated in Figure 5.

Male *S. megalops* in the population sampled reached 50% maturity at around 400 mm TL, at an age of about 9 years, and 100% maturity was achieved only at 450 mm TL and an age of 15 years. The youngest mature male sampled was 7 years old (288 mm TL). The size estimated for 50% maturity of female *S. megalops* was ~500 mm TL, which was achieved at an age

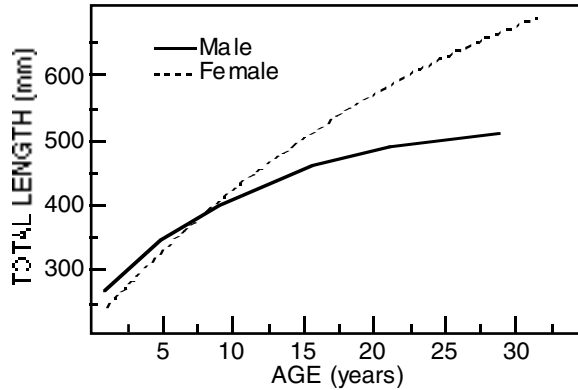


Fig. 5: Comparison of growth curves for male and female *S. megalops*

of 15 years, but all would be mature at 22 years of age (580 mm TL). The youngest mature female sampled was 14 years old (472 mm TL). Pregnancy followed maturity closely, and 50% of the population were pregnant at 510 mm TL and at an age of 16 years. All were pregnant at an age of 24 years (610 mm TL). Both sexes attained a similar maximum age (29 years for males and 32 years for females).

## Validation

Six female and two male dogfish were injected with OTC. The sharks survived in the laboratory aquarium for periods of 5–133 days (see Table II). During that time, all the fish showed negative growth. When viewed under reflected ultraviolet light, a slight diffuse fluorescence was visible only on the spines of fish that had survived for longer than 53 days after administration of the OTC. The fluorescence was apparent only on the very edge of the enamel of the spines of survivors up to 103 days. After a period of between 103 and 130 days, the OTC was incorporated into the band beginning to form at the basal end of the enamel. In the spines of the fish that survived more than 130 days, the fluorescence showed throughout the band being formed.

Validation of annual band periodicity for *S. megalops* was not achieved because of laboratory limitations. The sharks showed signs of agitation when approached and would swim around rapidly and bump the edges of the pool. In some cases they even swam over the edge of the pool. The fish did not feed well in captivity, even though they were regularly offered a variety of food. Furthermore, the temperature regime in the

Table II: Initial total length (TL) and mass of captive *S. megalops*, and changes in their length and mass during captivity. The presence or absence of fluorescence in the bands formed on the dorsal fin spine after administration of oxytetracycline (OTC) are shown

TL (mm)	Mass (g)	Change in length (mm)	Change in mass (g)	Sex	Days survived in captivity	OTC mark	New band forming after OTC mark
594	1 030	-36	-480	F	5	No	None
570	800	-09	-250	F	38	No	None
580	1 000	-25	-230	F	47	No	None
675	1 430	-22	-100	F	53	Yes	None
580	750	-17	-150	F	93	Yes	None
585	1 000	-39	-550	F	103	Yes	Yes
525	550	-23	-400	M	130	Yes	Yes
492	400	-29	-200	M	133	Yes	Yes

aquarium (16–24°C) rose above their preferred temperature of about 11°C (Smale *et al.* 1993). Despite these problems, the results indicate that OTC is incorporated into the growing spine and that it can therefore be used for studies of age validation in this species.

## DISCUSSION

The calculated value of  $L_{\infty} = 932.2$  mm for female *S. megalops* is much greater than the largest observed TL of 782 mm from this study and of 710 mm noted by Compagno (1984) for the species. Such a “discrepancy” in maximum size may be attributable either to an underestimation of the ages of the older fish sampled (because of the amount of wear of the spine or unintentional grouping of bands – see McFarlane and Beamish 1987a) or to a poor representation of larger fish in the sample used to estimate growth. Estimating the ages of the older fish involved the enumeration of often very faint bands visible on the unworn portion of the spine and then adding these to the estimated number of bands that were lost as a result of erosion of the spine tip (following Ketchen 1975). Both counts may have added error to the age estimation (Beamish and McFarlane 1985). However, the inclusion of the worn spines to estimate band number in the eroded portion of the spine would have produced better results than the rejection of all the worn spines, which would have introduced serious bias (Nammack *et al.* 1985). The spread of the data obtained in this study suggests that individual growth rates may be inherently variable. This variability would make the banding on spines more difficult to interpret. For the males, the estimated  $L_{\infty}$  value of 525.9 mm was close to the observed maximum TL of 572 mm. Estimating the age of males from spines would have resulted from errors similar to those encountered in females.

Segregation by size and sex is known for *S. megalops* populations (Watson 1996). Therefore, trawling may have introduced a sampling bias. Mature females predominate in shallow water and at the east of the Agulhas Bank (Watson 1996), and both these areas were less frequently sampled than the central Bank. Mature and immature males are trawled over much of the Agulhas Bank, so their sampling was probably more representative.

Female *S. megalops* take (on average) 22 years to reach maturity, whereas males take only 15 years. These estimated ages are similar to the results obtained from the retrieval of tagged *S. acanthias* from the Strait of Georgia (McFarlane and Beamish 1987a), where *S. acanthias* females take (on average) 23 years to reach maturity and males take 14 years. The values of  $t_0$  and K for males and females in this study are comparable to those found for *S. acanthias* (Saunders and McFarlane 1993), as a result of slow growth in both species. However, as Moulton *et al.* (1992) discuss, a comparison of these parameters may be meaningless, because of factors such as the high inverse correlation between K and  $L_{\infty}$  (Knight 1968), and because  $t_0$  is estimated by extrapolation beyond the range of the data (Francis 1988a, b). Furthermore,  $L_{\infty}$  is inadequately described when age-length data are not extensive enough to demonstrate asymptotic growth (Knight 1968).

Although the annual deposition of bands in vertebrae and spines has been validated in some sharks (Beamish and McFarlane 1985, Branstetter 1987, Cailliet 1990), it has not been examined in *S. megalops*. In the study conducted here, it was proposed to collect a range of sizes of dogfish in different seasons of the year and to keep fish of both sexes alive for at least one year. However, keeping the sharks in captivity proved to be of limited success. Injection of OTC seems to be a useful technique for validation work in this species, but a long-term field study of OTC-injected



sharks using tag-and-recapture techniques was beyond the scope of the present work. Validation is clearly necessary to test the assumption that the bands are deposited annually.

*S. megalops* exhibit reproductive and growth characteristics typical of sharks. They have low fecundity and produce only 2–4 pups per litter (born at 232–277 mm *TL*, Watson and Smale 1998). Characteristics such as slow growth, dimorphism with respect to size (females attain a maximum of 782 mm and males 572 mm *TL*), late maturation and longevity are also life-history characteristics found in other shark species (Pratt and Casey 1990). The maximum estimated age was 29 and 32 years for males and females respectively. Although *S. acanthias* matures at a similar age to *S. megalops* (McFarlane and Beamish 1987a), it appears to attain a greater maximum age of at least 70 years (Beamish and McFarlane 1985). *S. acanthias* attains greater size and has litters of up to 32 young, although this number varies geographically (Hanchet 1988). Although validation has yet to be undertaken in *S. megalops*, it is possible that maximum ages may be greater than those estimated to date.

This is the first study to estimate the age and growth of *S. megalops* from the Agulhas Bank. In view of the life-history characteristics of this species, it would appear that its potential to withstand a targeted fishery is limited, particularly as it is already taken as a bycatch of the demersal trawl fishery (Japp *et al.* 1994). Although the biomass of this species appears to be high on the Agulhas Bank (Japp *et al.* 1994), the potential yield of the fishery would be expected to be low, if the aim was to avoid severely reducing the stock size. Furthermore, the capacity of the stock to rebuild, should it be overexploited, would be low, because of slow growth, late maturity and small litter sizes. Although such effects have long been postulated (Holden 1974), and are supported by investigations on similar species (e.g. Nammack *et al.* 1985, Compagno 1990a), modelling has not been attempted. This study provides information that may be used in stock assessment models, which could contribute towards management of the resource.

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