

Abstract.— Age and growth of the school shark *Galeorhinus galeus* was studied from rings in the vertebra and length-frequency data. Samples were collected by trawling off the southern Brazilian coast from June 1980 to September 1986. Histological studies were also conducted on the characteristics of the vertebra. Standard histological techniques and microradiography were used to determine the pattern of vertebral calcification. The vertebrae of *G. galeus* are composed of calcified cartilage. Chondrocytes in calcified zones remain alive, probably nourished through vascular channels extending from the perichondrium into the cartilage matrix. A narrow zone of uncalcified matrix at the outer edge of the centrum indicates that calcification is preceded by initial development of hyaline cartilage. The vertebra presents a pattern of alternating heavily and less heavily mineralized zones, narrow and wide, respectively. The narrow zones were named rings, which are translucent under transmitted light and white to the microradiograph. These rings are probably laid down yearly in a slow-growing phase extending throughout the four winter months of June to September. Lengths at age were back-calculated and the von Bertalanffy growth parameters are: males— $K = 0.092$, $L_{\infty} = 152$ cm, and $t_0 = -2.69$; females— $K = 0.075$, $L_{\infty} = 163$ cm, and $t_0 = -3.00$. ELEFAN software was used to determine the growth curve best fitted to length-frequency data, but results overestimated the growth rate due to the slow growth and modal overlap.

Age, Growth, and Structure of Vertebra in the School Shark *Galeorhinus galeus* (Linnaeus, 1758) from Southern Brazil

Beatrice Padovani Ferreira

Fundacao Universidade do Rio Grande, Rio Grande, RS, 96200, Brazil

Present address: Marine Biology Department

James Cook University of North Queensland, Townsville Q4811, Australia

Carolus Maria Vooren

Departamento de Oceanografia, Fundacao Universidade do Rio Grande
Rio Grande, RS, 96200, Brazil

The elasmobranch skeleton consists of calcified cartilage. In most elasmobranchs, vertebrae are the only available structure that display periodic rings, which are useful for determining age. These rings result from different ratios of organic matrix/mineral, making the zones optically distinct (Casselman 1974). Since the description by Ridewood (1921), several techniques have been developed for enhancing the visibility of these rings thus making the counts easier and more accurate. However, information about the histology of elasmobranch vertebral rings is limited, and statements about their chemical composition and optical properties are contradictory (Casselman 1983).

The school shark *Galeorhinus galeus* is one of the principal species in the shark fishery in southern Brazil (Vooren and Betito In press). With the purpose of providing information for management decisions, age and growth of the Brazilian school shark were determined from rings in the vertebrae and length-frequency data. A histological study was conducted to investigate the structure of the vertebrae and to determine variations in their composition.

Materials and methods

The study area was the continental

shelf and upper slope off southern Brazil, between latitudes 34° and 30°S, at depths between 10 and 500 m. Data used for size-frequency analysis were obtained during trawl fisheries of this area from June 1980 to September 1986 (Table 1). All fishes were sexed and their total length (TL, cm) was measured from the tip of the snout to the extremity of the upper lobe of the tail, which was stretched back to be aligned with the body axis. Vertebrae were collected during the cruises listed in Table 1, and samples were chosen to include both sexes and the full size-range available. Sexual maturity and reproductive stage (Table 2) were determined according to size criteria established for this species by Peres (1989).

The data were processed on the Statistical Package for the Social Sciences, SPSS (Nie 1975). Length-frequency distributions for both sexes were plotted by cruise, by month, and also by a selected combination of the two largest samples. The ELEFAN (Electronic Length Frequency Analysis) software (Pauly and David 1981) was used to determine growth parameters (k and L_{∞}) from length-frequency data. The goodness of fit was given by the index R_n .

Vertebrae for age determination were dissected in the field from the

region under the first dorsal fin. The vertebrae were cleaned, frozen, and preserved in 70% ethanol. Several techniques were tried to aid enhancement and interpretation of the vertebral rings. Vertebrae of 10 sharks were sectioned into two halves, through transverse or sagittal planes, and the exposed faces were polished on wet 600-grit sandpaper. They were decalcified in 1% formic acid for 1 hour, rinsed in running water for 24 hours, dried and stained with graphite powder. The material was observed with a dissection microscope at 10× magnification using reflected light.

Vertebrae from 82 individuals (35 males, 45 females, and 2 embryos) were dehydrated in ethanol, cleared in styrene, embedded in polyester resin, sectioned with a jeweller's saw in transverse and sagittal planes, and polished on wet 400-grit sandpaper to obtain slices of 50–250 microns. Radiographs of all sections were taken with Soft X-ray equipment by Moureuil (France), at settings of 10–30 kV, 5–15 mA, and exposure times of 3–5 minutes. Kodak Industrex M radiography film was used. The radiographs were mounted on glass slides as were vertebra sections, either directly or after staining with Harris's haematoxylin or basic fuchsin. Vertebrae from five sharks were prepared and sectioned by standard histological techniques for calcified material. Sections were stained with Sudan 4 for observation of the lipid contents of cells.

A dissecting microscope at 10× magnification was used for measuring and counting growth rings, and a compound microscope at 100× magnification for observation of cell structure and details of the margin of the vertebra. The criteria to define a ring requires that it must occupy a distinct translucent zone relative to adjacent opaque zones and that the ring traverse the corpus calcareum and intermedialia (modified from Casey et al. 1985).

Measurements of growth increments were made with an ocular micrometer positioned to measure distances from the focus (notochordal remnant) to successive growth bands. The radius of each centrum was measured from the focus to the distal margin of the corpus calcareum (Fig. 1). The widths of individual translucent and opaque zones were measured in the microradiographs of 10 individuals. The periodicity of the formation of the rings was studied by examining the margins of the vertebrae collected from June to September. The

Table 1

Catch data of *Galeorhinus galeus* during cruises conducted by the NOC Atlantic Sul. Asterisks indicate vertebrae collected.

Cruise code/year (month)	Sites	Latitudes (min.-max.)	Depth (m)	Male ----- (n) -----	Female ----- (n) -----
3/80 (June)	1	— —	120	19	370
4/80 (July)	1	— —	—	65	94
7/80 (Sep.)	7	30°44'–35°52'S	120	108	114
*7/81 (Sep.)	5	— —	—	55	161
9/81 (Sep.)	8	30°36'–34°24'S	120	184	276
3/82 (July)	10	— —	—	491	160
10/83 (Aug.)	7	30°42'–34°22'S	100	—	30
3/83 (Nov.)	14	30°44'–34°16'S	160	43	36
*4/84 (June)	15	— —	—	301	230
2/85 (June)	7	— —	—	72	104
*3/85 (July)	23	— —	—	76	101
*4/86 (July)	12	32°00'–34°00'S	500	65	414

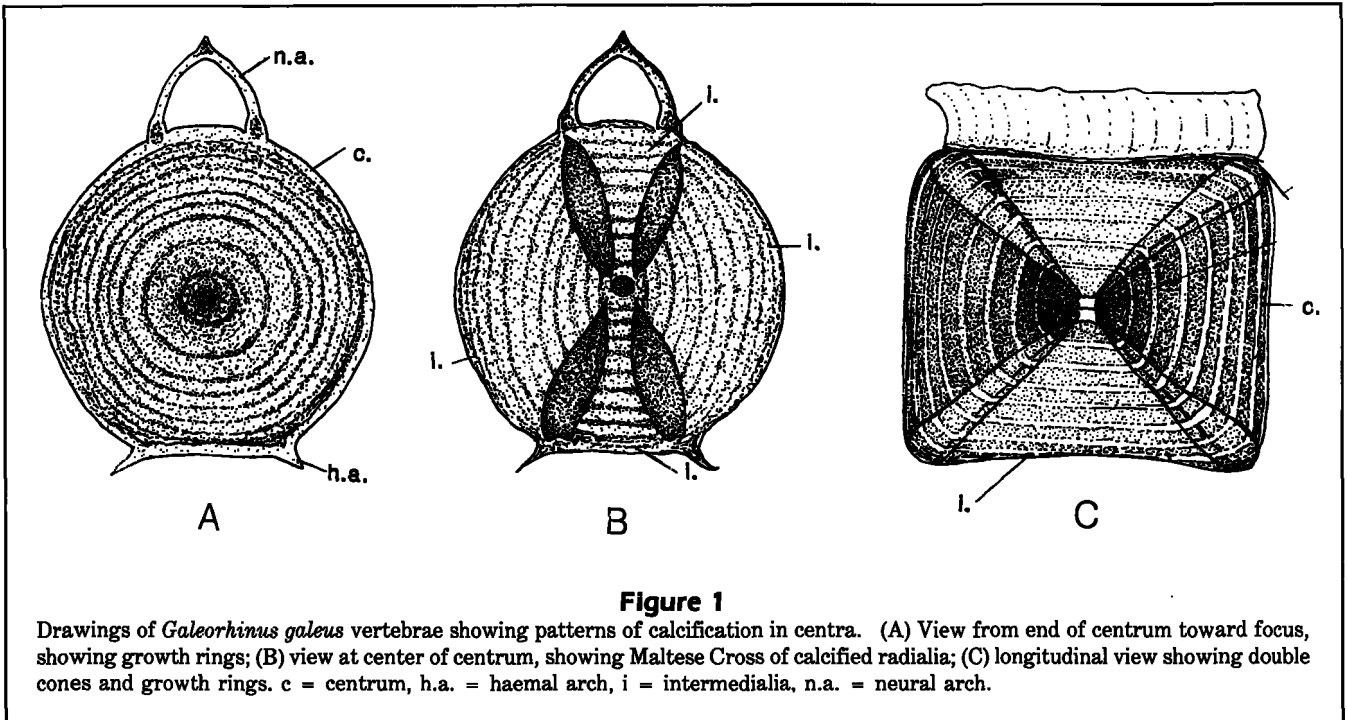
Table 2

Sexual maturity of *Galeorhinus galeus* determined by size class. Data from Peres (1989).

	Total length (cm)	
	Males	Females
Juveniles	43–88	43–103
Adolescents	93–108	108–123
Adults	113–143	128–153

marginal zone was classified into three types: pre-ring, consisting of a wide, less calcified zone; ring, consisting of a more calcified zone; and post-ring, consisting of a narrow, less calcified zone. Measurements of marginal increments were considered to be ineffective because the widths of zones varied greatly between size classes.

A linear regression of TL as a function of centrum radius was fitted to the data for juveniles and adults (sexes combined and separate) and the equality of



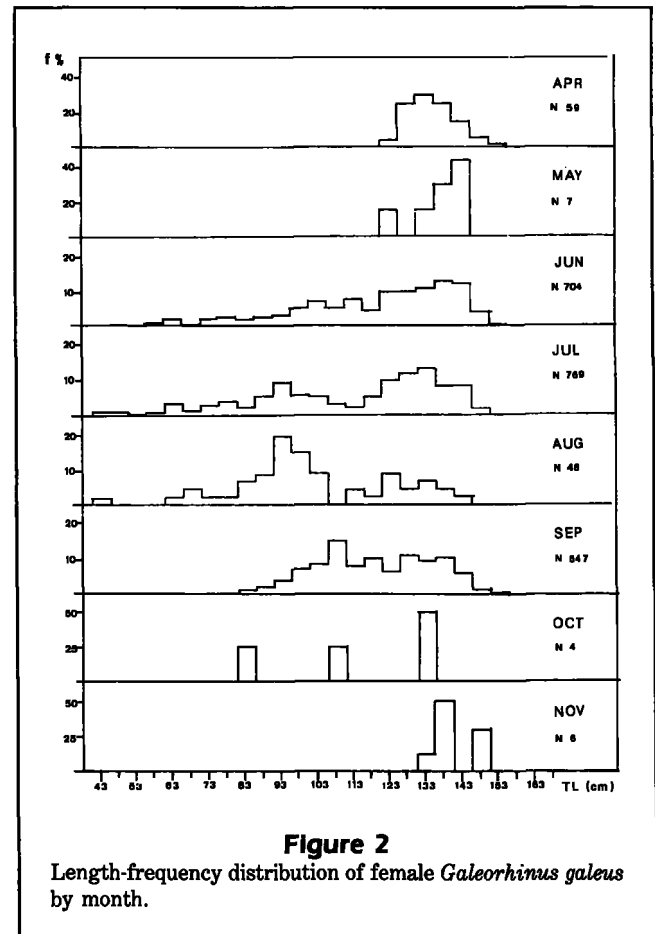
slopes of the regression lines tested (Sokal and Rohlf 1981). As they were found to be different, a power relationship was fitted to $TL \times$ centrum radius for each sex. Each ring was measured and these values inserted into the power equation to back-calculate the length of each shark at formation of the respective ring. The von Bertalanffy growth model was fitted to the mean lengths-at-age, using the methods of Ford and Beverton as cited by Gulland (1977).

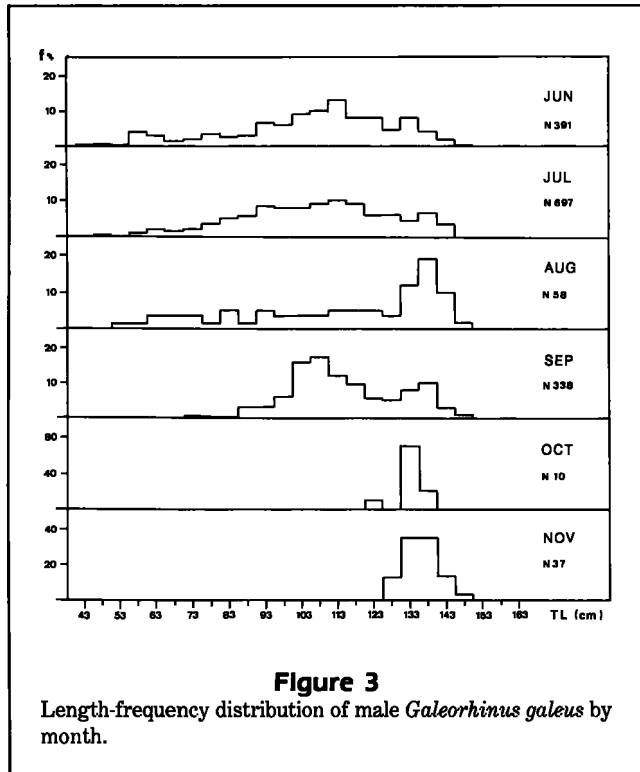
Results

Size composition

School sharks were present in the study area from April to November. During April and May all captured individuals were adolescent or adult gravid females (Fig. 2). From June to September the largest captures were registered (Table 1) and individuals from both sexes and all sizes (43–148 cm) were present (Figs. 2, 3). Larger juveniles were still captured during September, but individuals smaller than 70 cm TL were caught only from June to August.

A size variation within the sample size composition was also observed when analyzing the length frequencies plotted by cruise (Figs. 4, 5). Some size classes were better sampled during certain cruises. For instance, the sample was mainly composed of adults during cruises 3/80, 7/80, and 4/86, and of juveniles



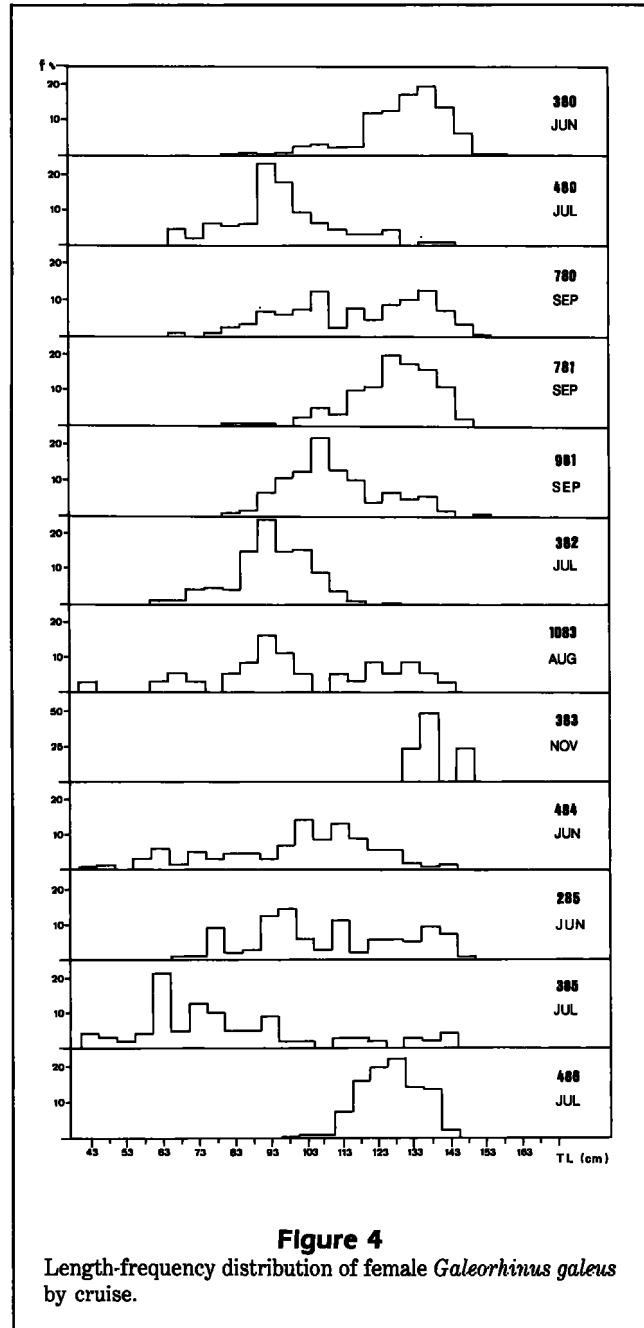


during cruises 4/80, 9/81, and 3/82. Smaller length classes were more frequently caught during cruises 4/84 and 3/85, but did not form a marked mode in the length-frequency distribution.

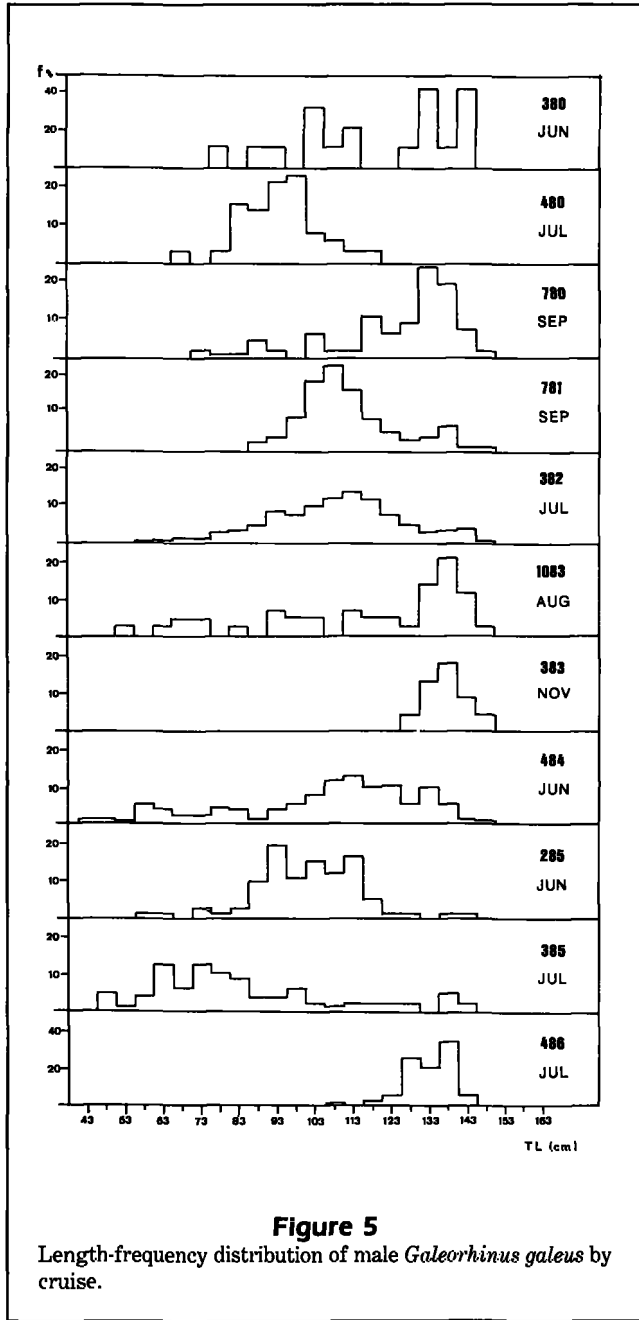
Techniques for enhancing vertebral rings

Rings were visible in all the attempted methods, but because of the large number of rings and marginal crowding in the centra of older sharks, only detailed microscopic observations were successful in providing comprehensive readings and measurements. The graphite method was an easy and simple technique that provided good results in enhancing rings of vertebrae of younger sharks. However, the large number of rings near the margin of vertebrae of older sharks was difficult to determine using this technique, and the number of rings was always underestimated compared with results by other techniques.

Stained sections of vertebrae provided good results in enhancing rings both in calcified and decalcified material. In the latter, no measurements were taken because of shrinkage and distortions observed after the decalcification procedure. The matrix shrank in the space formerly occupied by the mineral, and this zone became narrower than in the calcified state.



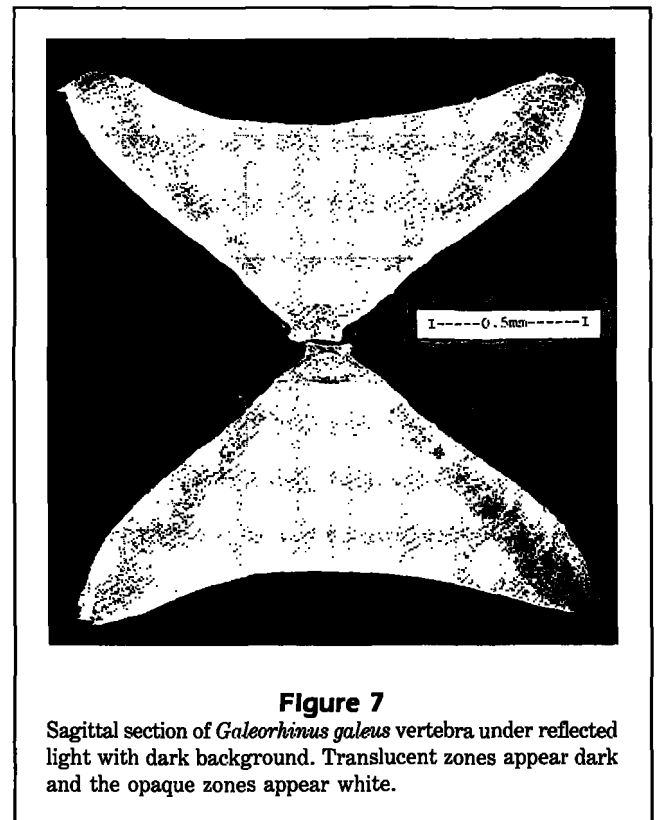
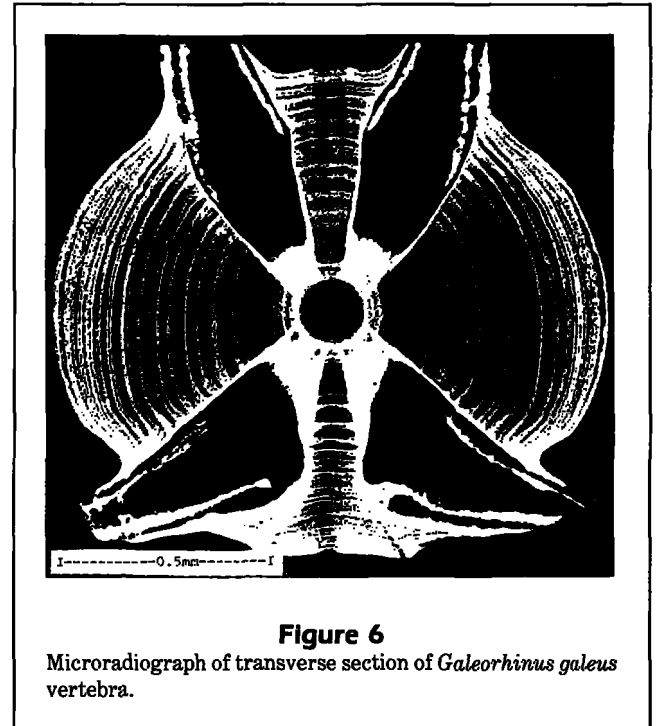
The most satisfactory technique for enhancing and counting rings was microradiography. With this method, the more calcified zones appeared white while the less calcified appeared dark (Figs. 6, 8). Direct observations of the sections showed that the former more mineralized zones were translucent and the latter less-mineralized zones were opaque when observed under transmitted light (Figs. 7, 8). Sections of various thickness were examined. The best contrast between zones was obtained from sections between 250 and



750 μ for readings of interior rings and from 50 to 100 μ thick for readings on the margins.

Pattern of vertebral calcification

The vertebra of *Galeorhinus galeus* is composed of calcified cartilage. Its centrum consists of a corpus calcareum of two obtuse, hollow cones with their apices joined and opposed. The space around the two cones is organized into four oblique basalia and four calcified



intermedialia: dorsal, ventral and lateral (Fig. 1) (Goodrich 1958, Ridewood 1921). In transverse section through the center of the centrum (focus), these radial

calcifications within the basalia have the shape of a Maltese Cross (White 1937) (Figs. 1B, 6). This "carcharoid" pattern is characteristic of the families Triakidae, Sphyrnidae, and Carcharhinidae (Applegate 1967). Above the centrum is a neural arch. In the center of the centrum is a hole, marking the position of the

primitive notochord, which we adopted as the focus of the vertebra. Within each cone, the focus is surrounded by a series of concentric rings which are read through techniques using the whole centra.

The inside of each cone is lined by a perichondrium, which consists of a fibrous layer covering a germinative layer of chondroblast cells (Fig. 9). During growth phases, the chondroblasts differentiate into chondrocytes to form the mature cartilage, a densely cellular tissue consisting of rounded cells embedded in their secreted organic matrix. The body of the vertebra forming the intermedialia is also invested by a perichondrium. In sagittal section the differences between the two regions can be observed: the cells of the cone are smaller and embedded in a more abundant matrix than those of the intermedialia (Fig. 10). Mineralization occurs throughout the matrix and both regions present an alternate pattern of more and less mineralized zones, corresponding to the concentric rings that can be seen inside the cone.

The properties of the narrow and wide zones, which occur in an alternating sequence, were defined by comparing microradiographs and direct observations with transmitted and reflected light of sections of the same vertebra. In this species the narrow zone, which we define as a ring, is optically translucent and appears white on the radiograph, being opaque to the X-ray beam, and therefore more calcified. The wide zone, defined here as a growth zone, is optically opaque and appears dark on the radiograph, being semi-transparent to the X-ray beam, and therefore less calcified (Figs. 7, 8).

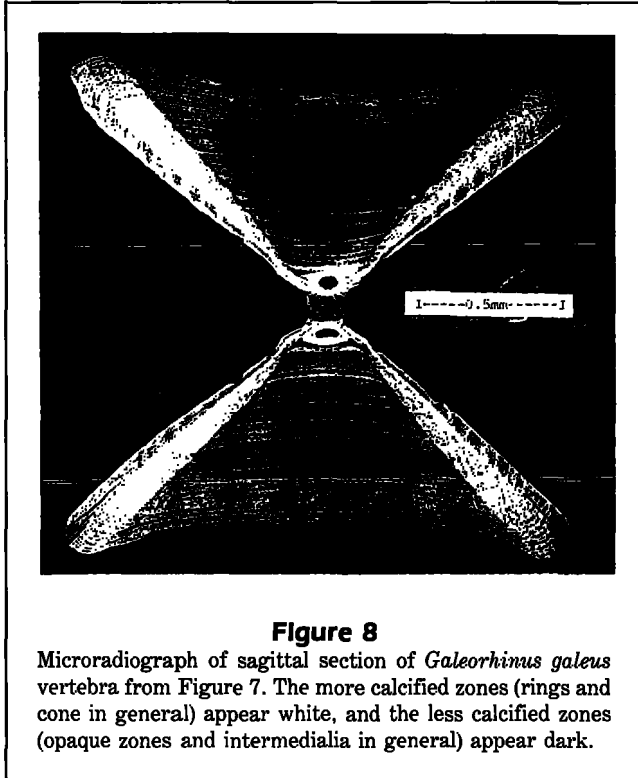


Figure 8

Microradiograph of sagittal section of *Galeorhinus galeus* vertebra from Figure 7. The more calcified zones (rings and cone in general) appear white, and the less calcified zones (opaque zones and intermedialia in general) appear dark.

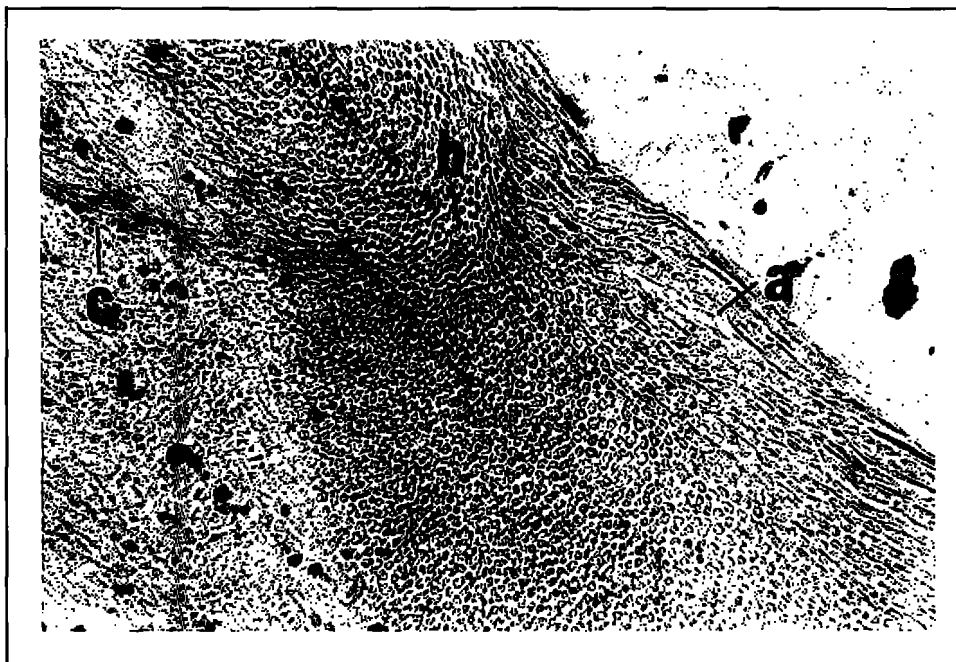


Figure 9

Sagittal section of *Galeorhinus galeus* vertebra showing part of the cone and intermedialia. Starting from external side: a = perichondrium; b = ring crossing cone; c = ring crossing intermedialia. (Harris's haematoxylin, 100x)

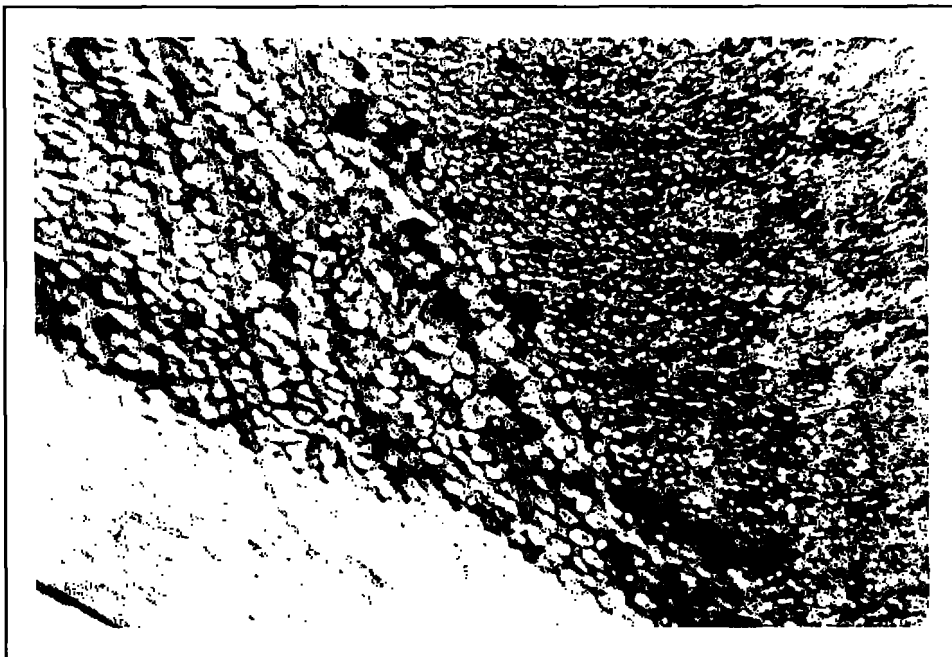


Figure 10
Sagittal section of *Galeorhinus galeus* vertebra showing contrasting tissue of cone and intermedialia. (Harris's haematoxylin, 100×)

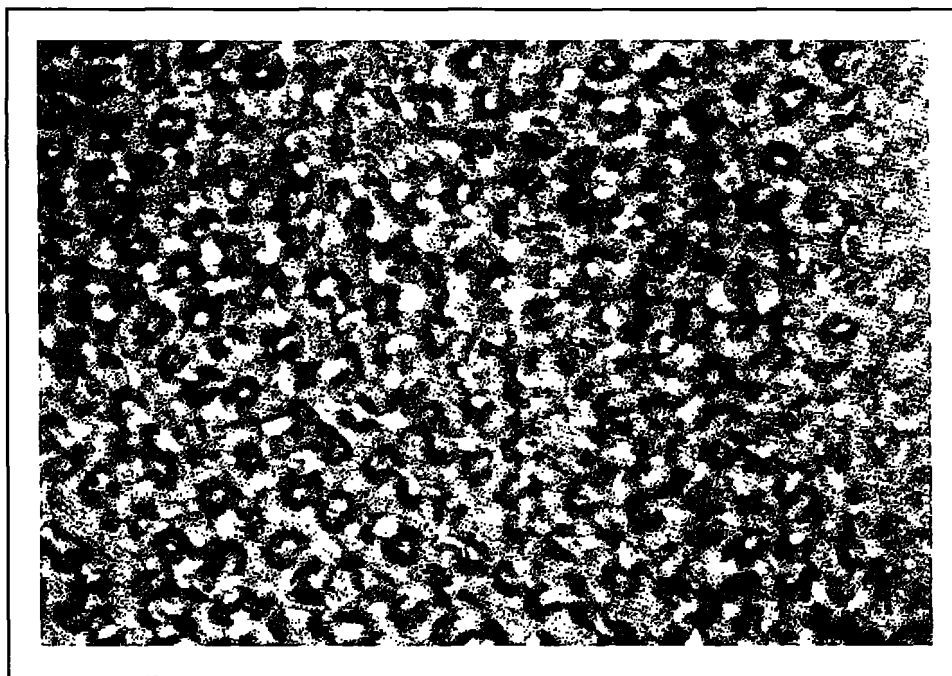
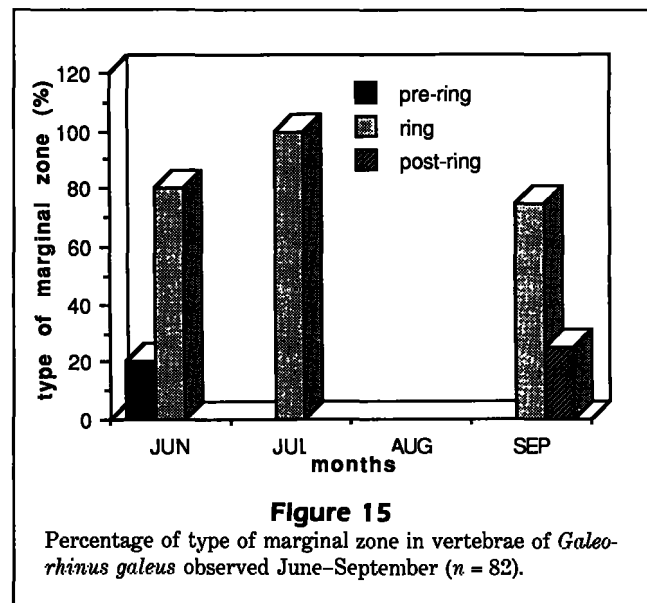
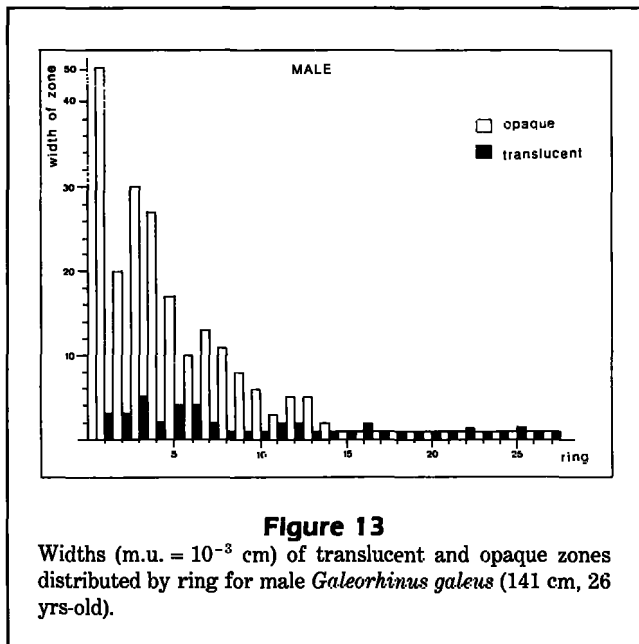
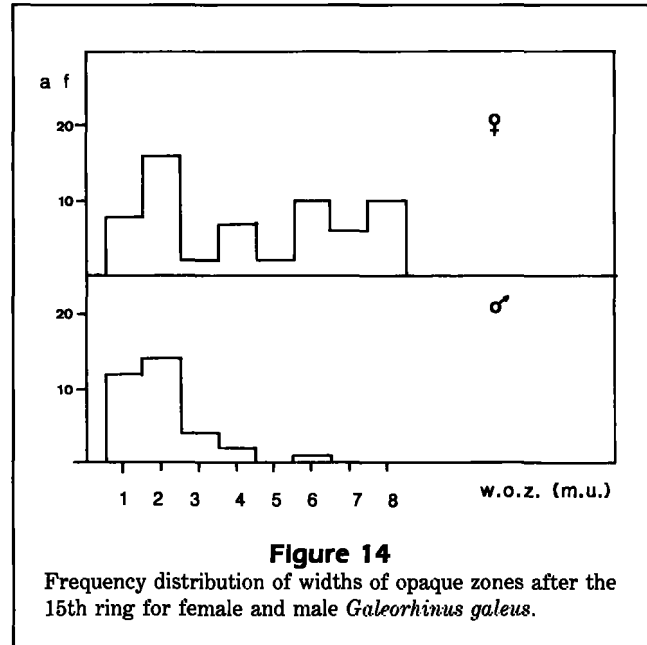
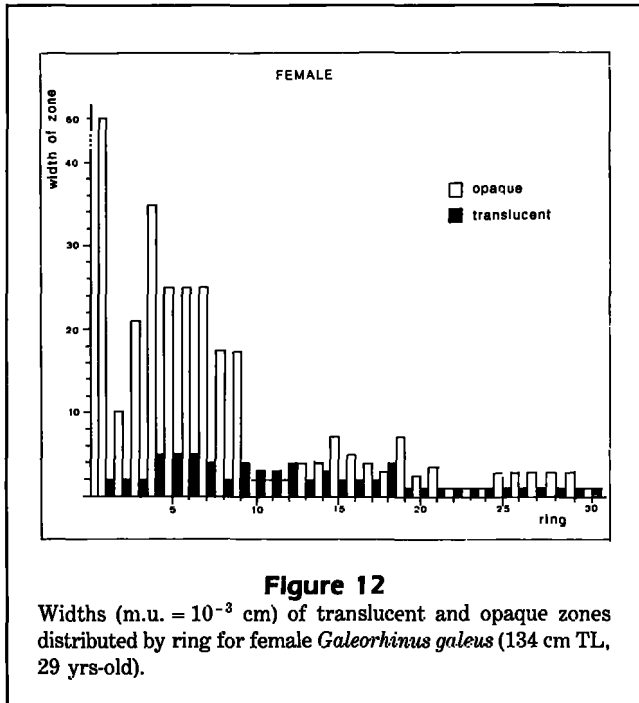


Figure 11
Section of vertebral tissue of *Galeorhinus galeus* showing the thin channels linking the cells. (Harris's haematoxylin, 400×)

Thin vascular channels connecting the cartilage cells were observed in haematoxylin-stained sections of resin-embedded vertebrae. These canaliculi form a network in the matrix between cells providing an opportunity for fluids and nutrients to reach the interior from the external medium (Fig. 11). Absence of lipid inclusions in the chondrocytes is interpreted as evidence of a healthy and active cellular metabolism. The presence

of isogenic groups of cells suggests that cells divide interstitially and thus effect interstitial growth.

The widths of translucent and opaque zones varied in individuals. Rings were usually narrower than adjacent opaque zones, but with increased body size (TL), both attained the same average size (Figs. 12, 13). Width of a male's opaque zones decreases gradually, and after about the 15th ring the two zones are equal



in width. Females have the same general pattern, but some variation in width still can be detected after the 15th ring has been formed (Fig. 14).

From June to September, 91% of the vertebrae examined showed more calcified zones forming at the margins (Fig. 15). During June this percentage was 80%, rising to 100% during July and falling to 75% in September. The vertebrae observed with less calcified

zones at margins during June (20%) were of the pre-ring type (wide less-calcified zone), and the ones observed during September (25%) were of the post-ring type (narrow less-calcified zone). These results indicated that the ring formation probably occurred during the winter months (June to September). One mark per year seems to be the most likely case for the school shark, and results here reflect this assumption.

In vertebrae of embryos at 8 months of intrauterine age, only the cartilage of cones was mineralized and no rings were visible (Fig. 16). Their intermedialia was

formed by a hyalin, unmineralized cartilage (Fig. 17). A 45 cm TL juvenile shark's vertebra showed some mineralization of the intermedialia, but unmineralized areas were still present. Two rings were observed (Fig. 18). The first ring was probably formed during the first winter after the birth in November (Peres 1989). The most recent one was just forming on the margin. In adult individuals the largest number of rings was 41, observed in a female of 155 cm TL.

Histological observations revealed the presence of a thin uncalcified layer at the very edge of the vertebrae, peripheral to the outermost narrow or wide calcified

zones at the margin (Fig. 18). This indicates that the marginal growth of the vertebra starts with the formation of an unmineralized layer of cartilage which is subsequently mineralized. This layer is probably present throughout the year and does not by itself indicate periodicity of ring formation.

Back-calculation

All linear regressions of total length on vertebral radius were significant ($p < 0.05$). The regression slopes were significantly different between juveniles and adults ($p < 0.05$) and between adult males and females ($p < 0.05$). Therefore, a power relationship was found to be more adequate to fit the pooled data for juveniles and adults of each sex. The following equations were obtained: Females ($N = 26$), $TL = 32.59 \times R^{0.827}$ and males ($N = 33$), $TL = 25.07 \times R^{0.897}$, where N indicates sample size and R radius of vertebra, with TL in cm and R in micrometric units ($1 \text{ m.u.} = 10^{-3} \text{ cm}$) (Fig. 19).

Lengths were back-calculated by age class and did not reveal the occurrence of Rosa Lee phenomenon (Gulland 1977), so the lengths at age were averaged (Table 3). The von Bertalanffy growth parameters were: females, $k = 0.075$, $L_{\infty} = 163 \text{ cm}$, and $t_0 = -3.00$; males, $k = 0.092$, $L_{\infty} = 152 \text{ cm}$, and $t_0 = -2.69$. The growth curves calculated from these parameters are shown in Fig. 20.

Using the ELEFAN software, several attempts were made to find the growth curve best fitted to the length-frequency data. In order to obtain a data set contain-

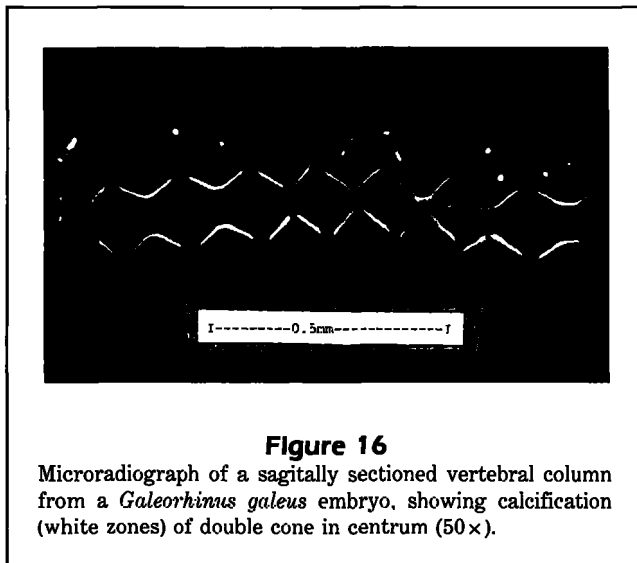


Figure 16

Microradiograph of a sagittally sectioned vertebral column from a *Galeorhinus galeus* embryo, showing calcification (white zones) of double cone in centrum ($50\times$).

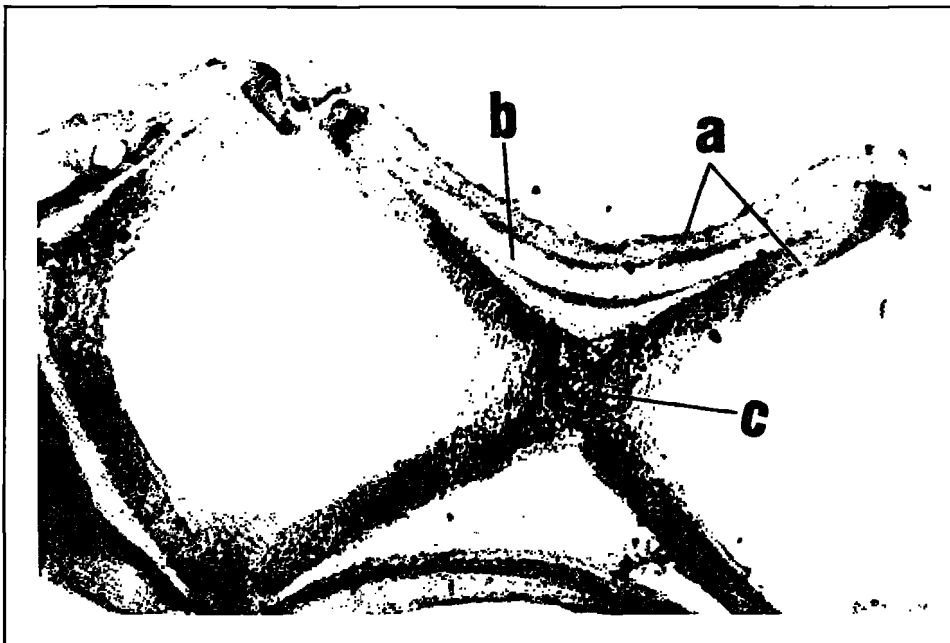


Figure 17

Sagittal section of vertebra from a *Galeorhinus galeus* embryo, showing (a) perichondrium, (b) hyaline cartilage in intermedialia, and (c) calcified cartilage of cones. (Haematoxylin, $100\times$)

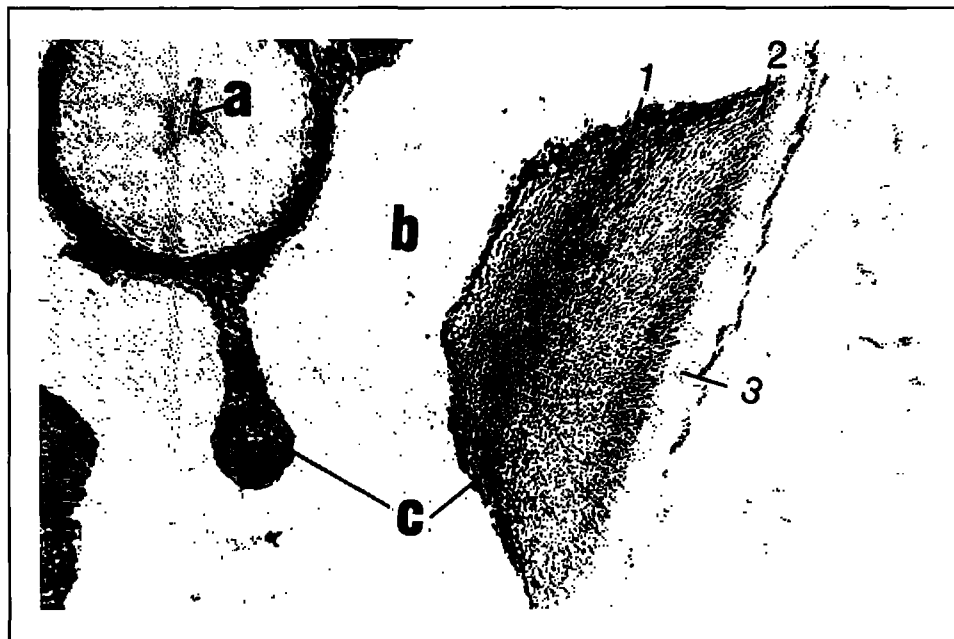


Figure 18
 Portion of a transverse section of a vertebral centrum from a 2d-year *Galeorhinus galeus* juvenile, showing (a) focus, (b) hyaline cartilage, and (c) calcified cartilage of intermedialia. (1) 1st ring, (2) 2d ring, and (3) uncalcified margin. (Haematoxylin, 50x)

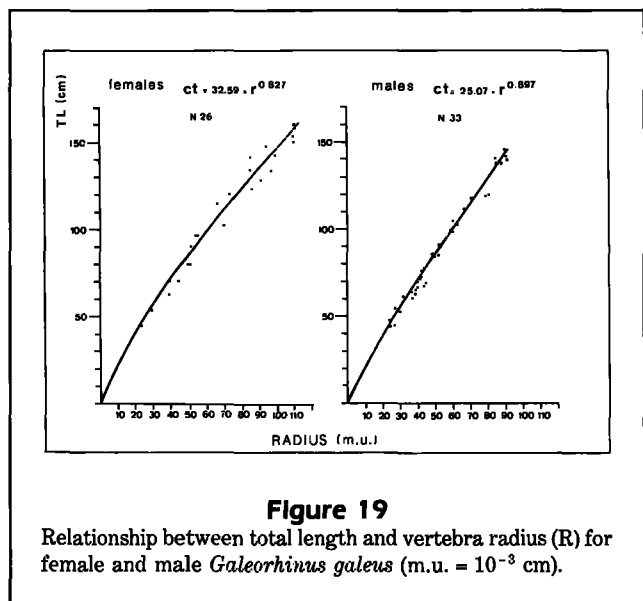


Figure 19
 Relationship between total length and vertebra radius (R) for female and male *Galeorhinus galeus* (m.u. = 10⁻³ cm).

ing the widest possible range of TL at a given time of the year, the data for June and July 1985 were pooled. Von Bertalanffy growth parameters were obtained as follows: females, $k = 0.2$ and $L_{\infty} = 157$ cm ($R_n = 612$); and males, $k = 0.2$ and $L_{\infty} = 157$ cm ($R_n = 429$).

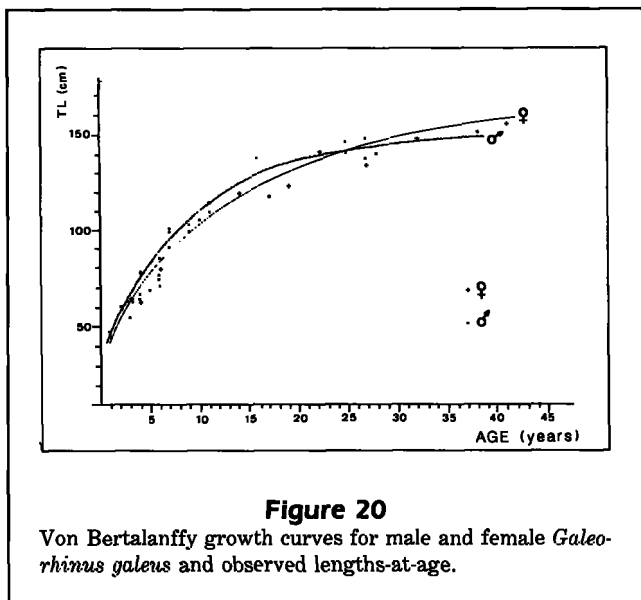
Discussion

The area of greatest uncertainty for interpreting and measuring growth zones in shark centra is near the

Table 3
 Back-calculated lengths (TL, mm) at age for male and female *Galeorhinus galeus*.

Age (years)	Ring	Male		Female	
		(n)	TL	(n)	TL
0	1	18	343	18	323
1	2	17	464	18	424
2	3	16	545	17	496
3	4	16	616	15	579
4	5	12	693	13	668
5	6	12	762	11	747
6	7	8	818	10	818
7	8	5	893	9	890
8	9	4	947	9	946
9	10	4	998	9	992
10	11	4	1027	8	1037
11	12	4	1070	6	1048
12	13	3	1137	4	1091
13	14			4	1123
14	15			4	1152
15	16			2	1196
16	17			2	1215
17	18			1	1259
18	19			1	1309
19	20			1	1334
20	21			1	1347
21	22			1	1371

margin (Casey et al. 1985). Distinguishing the presence of the last ring is a common problem (Casey et al. 1985, Stevens 1975, Walker 1986). Using microradiography, the margin can be easily observed in school shark



vertebrae and the ring formation identified. This technique is not subject to problems derived from the presence of marginal connective tissue (Stevens 1975), and a large number of thin rings near the margin can be counted.

From observation of margins of vertebrae, we can conclude that ring formation probably occurred during the period June–September. The high percentages of ring formation observed in the sample indicated that the process probably extends over a larger period than observed in the current study, covering perhaps half of the year. The growth band would be formed during the remaining period, and the rings would thus be annual marks. However, as vertebrae were examined only for four-month periods (June–September), the need for a proper validation remains, as emphasized by Beamish and McFarlane (1983). The hypothesis that two rings could be formed during a year was disregarded, due mainly to the results of Grant et al. (1979). These authors estimated a longevity of 40 years for *Galeorhinus australis* (= *Galeorhinus galeus*, Compagno 1984) in South Australia, from mark-recapture data. Several individuals were recaptured after periods of more than 25 years at large, and 10% of the recaptures occurred 15 years after release. This evidence supported the hypothesis of one ring per year, which also led to the conclusion that individuals can attain up to 40 years of age.

Casey et al. (1985), observing a large number of rings near the margin, suggested that if these could be interpreted as annual marks, the ages determined for several species of sharks may have been underestimated. The present results agree with this hypothesis,

and provide evidence that the school shark is a long-lived, slow-growing species.

The conclusion that the rings are translucent and strongly calcified, while the growth bands are optically opaque and less calcified is in agreement with the fact that the rings are stained dark by the silver nitrate technique (Stevens 1975, Cailliet et al. 1983). Casselman (1974, 1983) concluded that the translucent zone in calcified tissue of fish is more heavily mineralized than adjacent opaque zones and that calcium content is directly related to translucency.

In reference to the mode of calcification of cartilage, Moss (1977) wrote that "something radically different occurs in shark cartilage, making it certain that there can be no unitary description of vertebrate cartilaginous calcification." Hoenig and Walsh (1982) described the occurrence of vascularized cartilage canals in calcified vertebrae of several species of sharks. Many canals were found to contain blood cells, and they suggested a nutritive role for these canals. However, diffusion through the matrix is impossible after mineralization and in mammals; for instance, calcification of endochondral bone causes cellular degeneration and death of chondrocytes, because the isolated cells cannot maintain a normal metabolism (Robbins 1975). In the school shark, however, chondrocytes remain alive after calcification, as is evident from their normal, lipid-free appearance in calcified zones. Interchange between cells and vascular elements is probably sustained after mineralization by the canaliculi that were observed permeating the intercellular matrix.

The growth of crystals within a preformed organic structure is the basic mode of skeletal formation (Weiner 1984). Narrow uncalcified matrix areas observed at the edge of school shark vertebrae show that development of hyaline cartilage precedes the process of calcification. In addition, evidence of interstitial growth indicates that the tissue still remains uncalcified for a while after the appositional growth. In the vertebrae of embryos only the cone area was calcified. Among juveniles some uncalcified zones occurred also in the intermedialia. During the adult phase, the cone and intermedialia display the same mineralization pattern, with corresponding opaque and translucent alternate zones. This is evidence that the calcification, even when occurring at different times, follows the same pre-established rules. Weiner (1984) suggests that the organic matrix performs active, specific roles in this process. Growth of hydroxyapatite crystallites occurs in the space between collagen fibrils and perhaps within them (Glimcher in Kemp 1984). Therefore, regions of organic matrix formed during slow-growth phases would offer more space for crystal growth when exposed to the calcium and phosphate ions which form the mineral crystallites. Such regions, e.g., the rings,

would be characterized by relatively heavier calcification compared with the more rapidly growing, less calcified zones. In addition, the formation of the ring takes at least 4 months, but during the first 10 years of life the width of a ring is much less, in comparison with adjacent growth bands, than it would be if the growth rate were constant throughout the year. It is concluded that in *G. galeus* the ring represents a period of slow growth, and that mineralization is more intense during this period.

Vooren and Betito (In press) have shown that individuals of *Galeorhinus galeus* migrate northwards into the study area starting in April, until their peak abundance in September. At this time the school shark is abundant on the shelf south of lat. 32°S and scarce or absent further north. After September, the fish migrate southward from the study area, are scarce there in November, and absent in January and February. At the onset of winter, a marked change in temperature preference occurs, with most fishes occurring at 18–20°C from April to June and at 11–15°C in August and September, although water masses of higher temperatures are available during the latter months. The present data show that gravid females arrive first, making up all the April and May catches. From June onwards, other groups (adult males, non-gravid adult females and juveniles of both sexes) migrate into the area. The whole population experiences the decrease in temperature from June to August (Vooren and Betito In press). Thus, the period of slow growth and ring formation in vertebral centra coincides with this change in temperature preference of the population at the onset of winter. Similar results have been reported for other species (Stevens 1975, Jones and Geen 1977), confirming the general view that ring formation is associated with low temperature and slow vertebral growth (Longhurst and Pauly 1987).

As for the process involved, Casselman (1974) has suggested that during slow-growth phases, the amount of protein available for appositional growth might be reduced although minerals would still be available. In the shark vertebra, slow growth is evidently associated with a reduced rate of deposition of matrix components, which include both collagen fibrils and polysaccharides. Digestion and depletion of the carbohydrate moiety of the matrix during the slow-growth phase would facilitate interaction between collagen fibrils and mineral ions, thus promoting calcification. Mugiya (1987) has shown that in fish otoliths both calcium uptake and protein synthesis vary in an endogenous process controlled by hormones. In the school shark vertebrae, a matrix less dense in protein formed during slow-growth phases could be the cue to a higher calcium uptake to fill the space available for mineralization. Jones and Geen (1974) related wider rings with

warmer years in spines of *Squalus acanthias*, and this relationship may explain the variation in the width of the rings which is observed in vertebrae of adult female school sharks (Fig. 15). Gravid females which migrate into the study area during March to May show preference for higher temperatures, and it is possible that they remain in the warmer part of the species' temperature range during the winter. If so, their rings might grow faster than in fishes that remain at lower temperatures. The distribution of the different components of the population in the study area during the winter should be investigated in detail to test this hypothesis.

Reading vertebrae is the most important tool for age determination in many elasmobranchs. Length-frequency analysis is most suitable for fast-growing species because of the assumption that all fishes in the sample have the same age at the same length (Longhurst and Pauly 1987). In slow-growing, long-lived species, however, a given size class contains several different age groups (Gruber and Stout 1983). The Von Bertalanffy growth parameters estimated by ELEFAN software (Pauly and David 1981), using length-frequency data, overestimated the growth rate determined by vertebral readings. These values were approximately the same as those found by Olsen (1954) when analyzing length-frequency data for the Australian school shark. Later, Grant et al. (1979), using tag-recapture methods, estimated lower values of growth rates and concluded that length-frequency analysis was impracticable in this species.

Acknowledgments

Special thanks are due to Dr. Daoiz Mendoza for all his help and assistance with the histological aspects of this work. We thank Monica B. Peres for the valuable information and Mauro Maida, Dr. Garry R. Russ, Marcus V.S. Ferreira, and Annadel Cabanban for their constructive criticisms of the manuscript. We also thank the people from Projeto Talude and RV *Atlantico Sul* who helped with the field work. The research was sponsored by the Brazilian Ministry of Science and Technology (CNPq).

Citations

- Applegate, S.P.
1967 A survey of shark hard parts. In Gilbert, P.W., R.F. Mathewson, and D.P. Rall (eds.), *Sharks, skates and rays*, p. 37–67. John Hopkins Press, Baltimore.
- Beamish, R.J., and G.A. McFarlane
1983 The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* 112:735–743.

- Cailliet, G.M., L.K. Martin, D. Kusher, P. Wolf, and B.A. Welden**
 1983 Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes and sharks, p. 157-165. NOAA Tech. Rep. NMFS 8.
- Casey, J.G., H.L. Pratt Jr., and C.E. Stillwell**
 1985 Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. *Can. J. Fish. Aquat. Sci.* 42:963-975.
- Casselmann, J.M.**
 1974 Analysis of hard tissue of pike *Esox lucius* L. with special reference to age and growth. *In* Bagenal, T.B. (ed.), Ageing of fish, p. 13-27. Unwin Bros., Surrey, England.
 1983 Age and growth assessment of fishes from their calcified structures — Techniques and tools. *In* Proceedings of international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes and sharks, p. 1-17. NOAA Tech. Rep. NMFS 8.
- Compagno, L.J.V.**
 1984 Sharks of the world. FAO species catalogue. FAO Fish. Synop. 4 (125), pt. 2:386-389.
- Goodrich, E.S.**
 1958 Studies on the structure and development of vertebrates, Vol I. Dover Publ. Inc., NY, 485 p.
- Grant, C.J., R.L. Sandland, and A.M. Olsen**
 1979 Estimation of growth, mortality and yield per recruit of the Australian school shark, *Galeorhinus australis*, from tag recoveries. *Aust. J. Mar. Freshwater Res.* 30:625-637.
- Gruber, S.H., and R.G. Stout**
 1983 Biological materials for the study of age and growth in a tropical marine elasmobranch the lemon shark, *Negaprion brevirostris* (Poey). *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes and sharks, p. 193-205. NOAA Tech. Rep. NMFS 8.
- Gulland, J.A. (editor)**
 1977 Fish population dynamics. John Wiley, NY, 372 p.
- Hoenig, J.M., and A.H. Walsh**
 1982 The occurrence of cartilage canals in shark vertebrae. *Can. J. Zool.* 62:483-485.
- Jones, B.C., and G.H. Geen**
 1977 Age determination of an elasmobranch (*Squalus acanthias*) by X-ray spectrometry. *J. Fish. Res. Board Can.* 34:44-48.
- Kemp, N.E.**
 1984. Organic matrices and mineral crystallites in vertebrate scales, teeth and skeletons. *Am. Zool.* 24:965-976.
- Longhurst, A.R., and D. Pauly**
 1987 Ecology of tropical oceans. Acad. Press, San Diego, 407 p.
- Moss, M.L.**
 1977 Skeletal tissue in sharks. *Am. Zool.* 17:335-342.
- Mugiya, Y.**
 1987 Phase difference between calcification and organic matrix formation in the diurnal growth of otoliths in the rainbow trout *Salmo gairdneri*. *Fish. Bull., U.S.* 85:395-401.
- Nie, N.H., C.H. Hull, J.C. Jenkins, K. Steinbrenner, and D.H. Bent**
 1975 Statistical package for the social sciences, 2d ed. McGraw-Hill, Boston, 675 p.
- Olsen, A.M.**
 1954 The biology, migration and growth rate of the school shark, *Galeorhinus australis* (MacLeay) in south-eastern Australian waters. *Aust. J. Mar. Freshwater Res.* 5:353-410.
- Pauly, D., and N. David**
 1980 An objective method for determining fish growth from length-frequency data. ICLARM (Int. Cent. Living Aquat. Resourc. Manage.) Contrib., Newsl. 3(3):13-15.
 1981 ELEFAN 1, a BASIC program for the objective extraction of growth parameters from length frequency data. *Meeresforschung/Rep. Mar. Res.* 28(4):205-211.
- Peres, M.B.**
 1989 Desenvolvimento, ciclo reprodutivo e fecundidade do cacao bico-de-cristal *Galeorhinus galeus* L. no Rio Grande do Sul. MSc. thesis, Fundacao Universidade do Rio Grande, RS, Brasil, 76 p. [in Portuguese, Engl. abstr.].
- Ridewood, W.G.**
 1921 On the calcification of the vertebral centra in sharks and rays. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 210:311-407.
- Robbins, S.L.**
 1975 Patologia estrutural e funcional. Interamericana, Mexico, 1516 p.
- Sokal, R.R., and F.J. Rohlf**
 1981 Biometry, 2d ed. W.H. Freeman, NY, 859 p.
- Stevens, J.D.**
 1975 Vertebral rings as a means of age determination in the blue shark *Prionace glauca*. *J. Mar. Biol. Assoc. U.K.* 55: 657-665.
- Vooren, C.M., and R. Betito**
 In press. Distribution and abundance of demersal elasmobranch fishes on the continental shelf of Rio Grande do Sul, Brazil. *Bull. Mar. Sci.*
- Walker, T.I.**
 1986 Southern shark assessment project. 2d Review, October 1986. *Mar. Sci. Lab. Prog. Rev.* 66, Queenscliff, Victoria, Australia, 48 p.
- Weiner, S.**
 1984 Organization of organic matrix components in mineralized tissues. *Am. Zool.* 24:945-951.
- White, E.G.**
 1937 Interrelationships of the elasmobranchs with a key to the order Galea. *Bull. Am. Mus. Nat. Hist.* 74:25-138.