

Abstract. – The school shark *Galeorhinus galeus* was sampled by otter trawl on the continental shelf of southern Brazil from 1980 to 1986 between latitudes 32°S and 34°40'S, at depths between 10 and 500 m. The species is a winter migrant, present in the study area from April to November. A total of 1548 specimens were examined. Sexual maturity occurred at total length of 107–117 cm in males, and 118–128 cm in females. The reproductive cycle was annual in the male and three years in the female, with uterine rest and slow vitellogenesis during the first year, maturation of oocytes and copulation during the second year, and gestation during the third year. In November, the diameter of mature follicle was 4.6–5.5 cm, ovulation occurred, and full-term embryos occurred with average total length of 30.3 cm. Uterine fecundity varied between 4 and 41 with a mean of 23.1, of which 94.2% were normal embryos, 5.2% were non-developing eggs, and 0.6% were abnormal embryos. Copulation took place up to 5 months before ovulation, with passive transport of spermatophores through the uterus. Liver weight as a percent of gutted body weight averaged 8% in immature animals of both sexes, 7% in gravid females, 11% in adult males and nongravid females in the first year of the reproductive cycle, and 17% in non-gravid females in the second year of the cycle, and it decreased during winter.

Sexual Development, Reproductive Cycle, and Fecundity of the School Shark *Galeorhinus galeus* off Southern Brazil

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Annual landings of demersal sharks at the port of Rio Grande, Brazil, increased from 1414 tons in 1973 to 3217 tons in 1986 and then decreased to 2023 tons in 1989 (SUDEPE 1990). This raises the question of the impact of increasing fishing effort on the stocks. The school shark *Galeorhinus galeus* comprises the major part of the landings (Wahrlich and Peres 1990). Accounts of fisheries for this species in other areas are classic examples of the rule that sharks are unable to maintain their abundance under heavy fishing. This is due to their live-bearing mode of reproduction, which implies that fecundity is low and recruitment is proportional to the abundance of the adults (Holden 1977). Management of the fishery requires estimates of reproductive parameters.

The reproductive cycle of female *G. galeus* has been described as annual off California and Tunisia, and biannual off Australia (Ripley 1946, Olsen 1984, Capapé and Mellinger 1988). However, the simultaneous occurrence of three distinct reproductive stages of adult females off southern Brazil led to the hypothesis of a triannual reproductive cycle (Vooren and Guzinski 1982). This hypothesis was tested in the present study.

This paper describes sexual maturation and the reproductive cycle for both sexes, and uterine and ovarian fecundity of female school shark off southern Brazil.

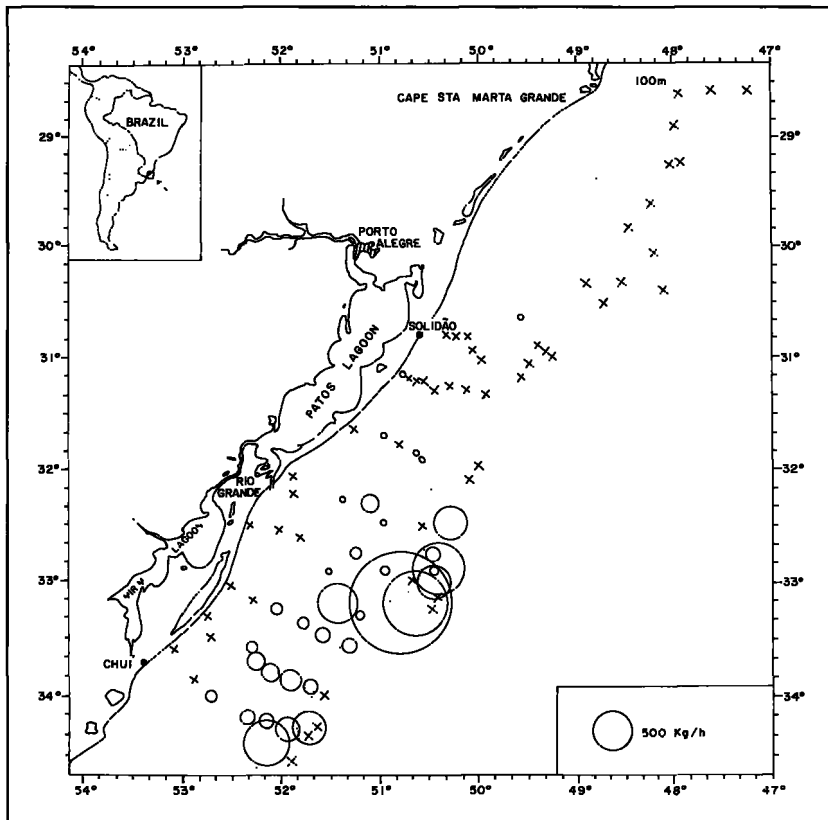
Materials and methods

The study area was the continental shelf of Rio Grande do Sul, between Cape Santa Marta Grande (lat. 28°40'S) and Chuí (lat. 33°44'S), Brazil. From June 1980 to September 1986, the area was surveyed during 12 cruises by the RV *Atlântico Sul*, at depths between 10 and 500 m, using an otter trawl with groundrope of 50 m and codend mesh of 45 mm between opposed knots (see Fig. 1 for location of stations). Tows lasted 60 minutes, and towing speed was 5.5 km/hour. Samples were also obtained with similar nets during five commercial trawling trips. The data series includes all months of the year except December and March. One specimen found on 13 December 1985 on the beach near Rio Grande, and nine specimens obtained on 24 June 1986 from commercial landings at Montevideo, were also examined.

In each haul, the weight of the catch (in g) and the body length (in cm) and sex of all specimens were recorded. Total length (TL) was measured with the tail aligned with the long axis of the body. Biological data were taken from random samples of the catches, totaling 904 females of 43.0–154.5 cm TL and 644 males of 43.5–148.0 cm TL. Weights (in g) of the whole body, liver, and gonads were recorded. Total body weight was measured until November 1983. Thereafter, the eviscerated body

Figure 1

The study area with sampling grid for the school shark *Galeorhinus galeus*, during 9–30 August 1983 (depths <100m) and 17 July–17 September 1986 (depths of 100–500m) off Brazil. Surface area of circles indicates catch rates in kg/hour bottom trawling, and crosses indicate zero catches.



weight was measured, as recommended by Mellinger (1966), for study of certain aspects of reproduction. The gonad weight included that of the epigonal organ cut in front of the rectal gland. Epigonal organ weights were also measured in 43 specimens. In males, the length of the clasper was measured from the posterior origin of the pelvic fin. For females, the following data were recorded: diameter and color of the largest ovarian follicle, width of the nidamentary gland, presence or absence of embryos and uterine eggs, weight of the full gravid uterus, and greatest width of the non-gravid uterus. Embryos were measured, sexed, and weighed with and without the yolk sac. Fecundity was determined by counting maturing ovarian follicles (“ovarian fecundity”) and uterine eggs and embryos (“uterine fecundity”). Hepatosomatic and gonadosomatic indices were calculated, using the weight of the organs as a percent of the eviscerated body weight. The latter indices were obtained using the linear regression equation of eviscerated weight as a function of total length. Separate equations were used for sexually immature sharks of both sexes, adult males, and adult females (Table 1).

Histological smears of the reproductive organs were obtained from 7 males and 17 females, ranging from 124 to 148cm TL. Testes smears were made from cross-section surfaces on glass slides. The nidamentary gland was opened lengthwise and smears were made of the surface of its lumen on glass slides. Smears were also made of the contents of the epididymis and the seminal vesicle. Smears were

fixed in a solution of equal proportions of ethanol and ethyl ether and stained with haematoxylin-eosin.

The present study follows Compagno (1988) with respect to nomenclature.

Table 1

Biometric variables (Y) as a function of total body length (TL) in *Galeorhinus galeus* from Rio Grande do Sul, Brazil. TL* indicates body length of the mother, N indicates sample size, R is correlation coefficient. Weights in g, lengths in cm.

Variable	Equation	N	R
Eviscerated weight, adult male	$Y = 3.95 \times 10^{-3} \times TL^{2.97}$	124	0.91
Eviscerated weight, adult female	$Y = 5.38 \times 10^{-4} \times TL^{3.39}$	128	0.93
Eviscerated weight, immatures	$Y = 2.15 \times 10^{-3} \times TL^{3.10}$	138	0.99
Weight of testis	$Y = -5.20 TL^{3.32}$	131	0.74
Weight of epigonal organ, male	$Y = -4.67 TL^{2.89}$	13	0.94
Ovarian fecundity	$Y = 0.49 TL - 43.15$	57	0.68
Uterine fecundity	$Y = 0.53 TL - 49.44$	137	0.66
Mean length of embryo per litter, June–July	$Y = 0.025 TL^* + 18.78$	39	0.13
Mean length of embryo per litter, Aug–Sep	$Y = 0.14 TL^* + 7.24$	46	0.44

Results

Spatial and temporal distribution

School sharks were seasonally abundant at depths of 40–350 m, between latitudes 32°S and 34°30'S. In this area, mean catch rates per cruise were high from June to September, attaining values up to 376 kg/hour at depths between 40 and 100 m, and 620 kg/hour between 100 and 350 m. Figure 1 shows the sampling grid and catches for August 1983 and 17 July–17 September 1986. Within the study area, the entire area of distribution was covered by the sampling grid.

The species was scarce in April, May, October, and November, and absent in January and February. The school shark is characterized as a seasonal migrant, entering the study area in autumn, attaining peak abundance during winter, and leaving in spring.

Sexual development and organization of gametes in the male

Sexual maturation of the male was inferred from the length of the clasper. The relationship between clasper length and total length was sigmoid (Fig. 2). The curve rose steeply between 85 and 117 cm TL, and dispersion was greatest in this range. The curve flattened out for clasper lengths greater than 10.5 cm. This latter value was taken as the lower limit for sexual maturity. On the basis of this criterion, sexual maturation began at 85 cm TL. The smallest mature male measured was 107 cm TL, 50% maturity occurred at 111 cm, and all males greater than 117 cm were mature. The clasper of the adult measured, on average, 12.0 cm, ranging from 10.5 to 14.0 cm.

Potential equations described adequately the relationship of gonad and epigonal organ weight to total length (Fig. 3, Table 1). At total lengths less than 85

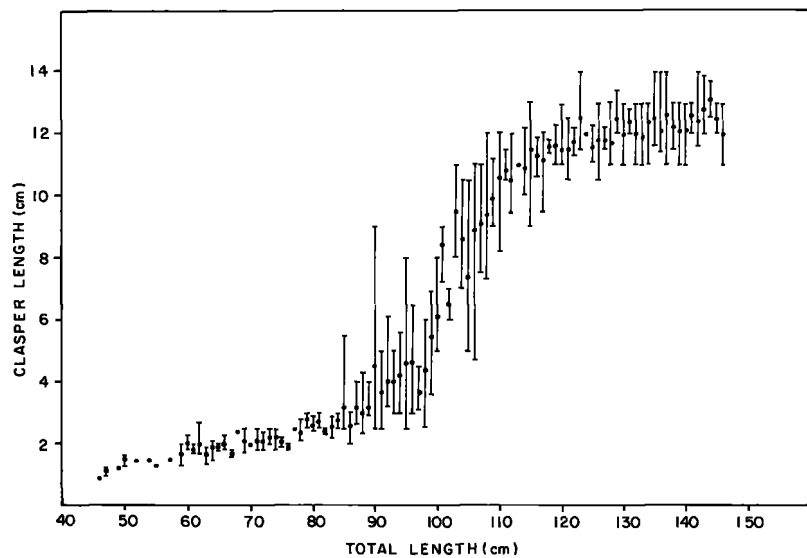


Figure 2

Relationship between total body length and length of clasper in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil. Points indicate the mean, and vertical lines the range for length-class intervals of 1 cm.

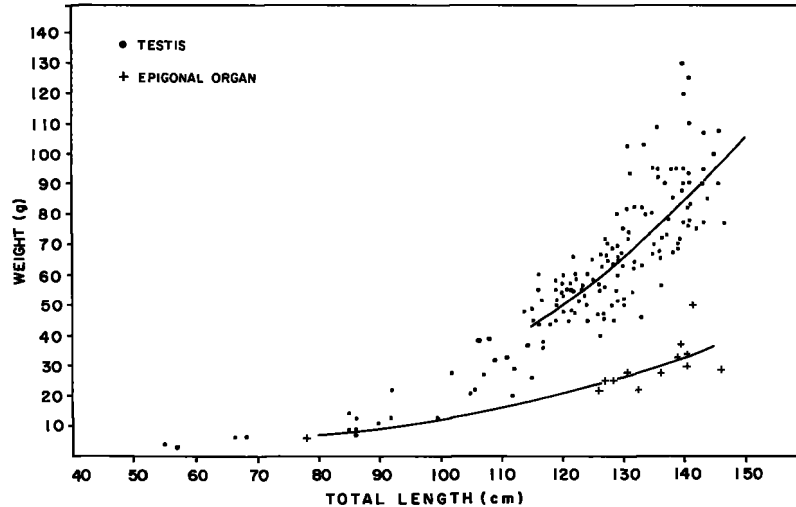
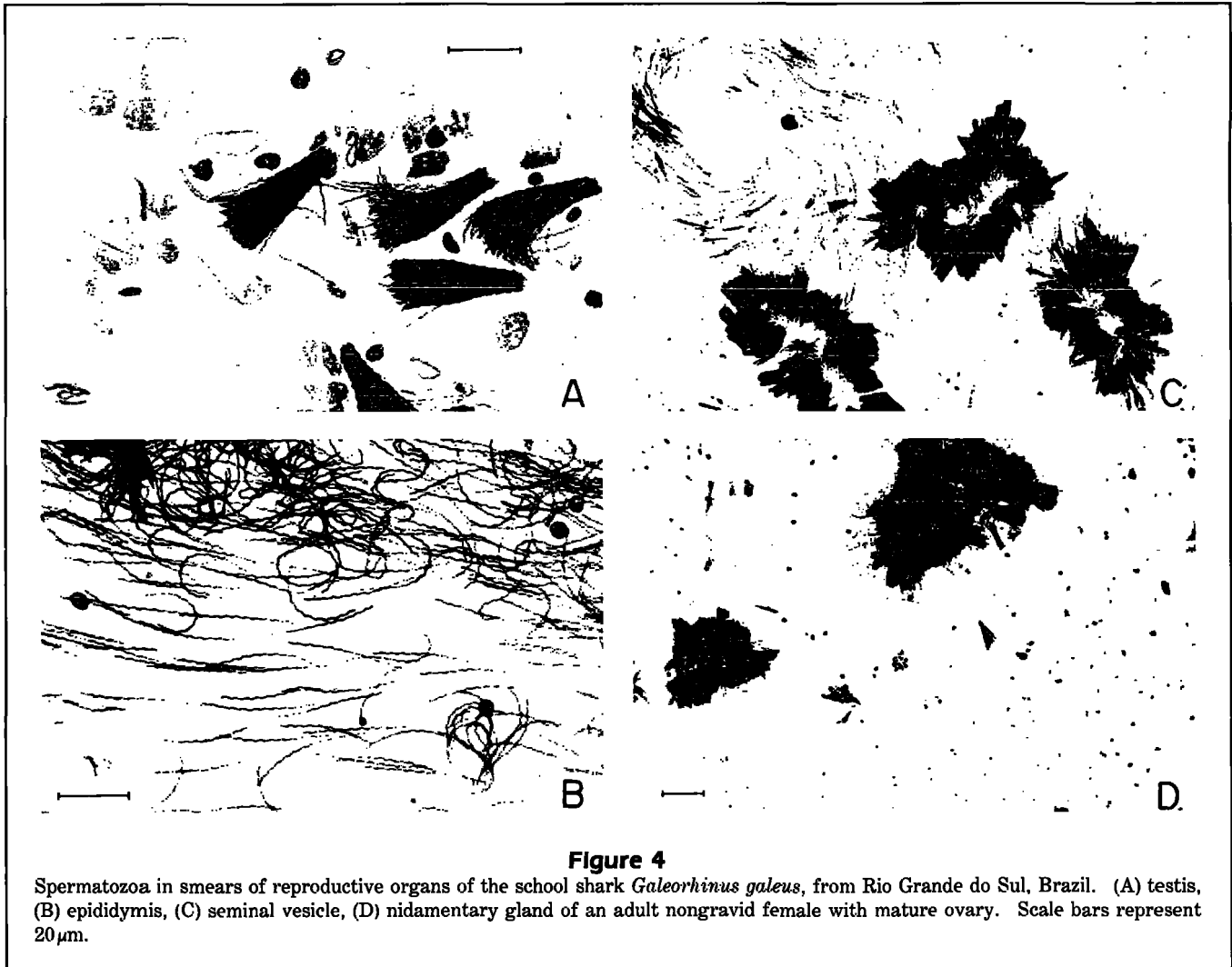


Figure 3

Relationship between total body length and weight of epigonal organs and testis in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

cm, gonad weight was similar to the weight of the epigonal organ, and testes were not visually evident. Between 85 and 140 cm TL, epigonal organ increased from 10 to 30 g, and gonad weight increased to an



average of 90 g. Thus, the increase of gonad weight with body size reflects mostly growth of the testes, and can be interpreted in terms of sexual development. The gonadosomatic index varied about the mean of 0.6 at total lengths less than 117 cm, and 0.9 at greater body lengths. The attainment of sexual maturity, as indicated by the clasper, was accompanied by a marked increase in relative weight of the testes. Growth of the testes continued after the attainment of sexual maturity, as indicated by gonad weights of 35–60 g at 115 cm TL, and 75–130 g at 145 cm TL.

Smears of the testes showed that sperm occurred in bundles within the testicular ampullae (Fig. 4A). In the epididymis, sperm occurred singly (Fig. 4B). The head of the spermatozoon measured, on average, 47 μm and the tail about 100 μm (n 62). In all smears of the seminal vesicle, sperm occurred in circular or oblong

agglomerations, with their heads towards the center (Fig. 4C). Such structures were called spermatophores. The shortest and longest axes of the spermatophores measured, on average, 142 and 201 μm , respectively (n 64).

Sexual development of the female

The female has one functional ovary, situated on the right. Ovarian follicles were visible to the naked eye at total lengths greater than 80 cm. Follicle color varied with its diameter: transparent and colorless, up to 0.6 cm; opaque white, 0.4–1.2 cm; pale to sulphur yellow, 1.0–2.5 cm; and golden yellow, 3.5–5.5 cm. Follicles of ovulating females ranged from 4.6 to 5.5 cm, which is therefore the size range of the mature follicle. The weight of 58 mature ovaries increased with body size

and varied from 400 to 1600g, including the epigonal organ of 25–60g. Maturing ovaries contained 12 to 34 follicles of uniform size, with diameter greater than 3.5cm. Such ovaries occurred in females larger than 122cm TL (Fig. 5).

The smallest pregnant female was 118cm TL. Incidence of pregnancy increased to about 50% at body sizes greater than 130cm (Table 2). The developing uterus appeared as a strip of white tissue with diameters up to 0.3cm in females of less than 110cm. The uterus widened first at its posterior end, becoming bottle-shaped at lengths of 110–125cm TL, with a diameter of 1.0–2.3cm at its widest part. Fully-formed uteri, uniform in width, measured 2.0–4.0cm in diameter and occurred in females larger than 121cm TL. All non-gravid females with total lengths greater than 128cm possessed such uteri.

The width of the nidamentary gland varied about 0.4cm in females of less than 112cm, and increased to values between 1.8 and 4.6cm in females larger than 125cm TL (Fig. 6).

Based on color and size of the ovarian follicle, width of the nidamentary gland and uterus, and the incidence of pregnancy, it is concluded that sexual maturity first occurred at 118cm TL, 50% maturity at 123cm TL, and full maturity at 128cm TL. In the nongravid adult female, the uterus had a diameter of 2.0–4.0cm, the nidamentary gland was 1.8–3.5cm in width, and the ovary contained yellow follicles of diameters 1.4–5.5cm.

In one nongravid female of 154.5cm TL, the ovary was reduced to four atretic follicles with diameters less than 0.4cm, and the nidamentary glands were reduced in width (Fig. 6). The dorsal coloration of the body of this female was light grey with dark blotches. This 41-year-old female (Ferreira and Vooren 1991) was considered senile, the only such specimen encountered.

Reproductive cycle of the female

If the reproductive cycle of the female is synchronous at the population level, fertilization and birth should occur at definite seasons, and at any given time all gravid females should contain embryos in the same stage of development. If, in addition, the reproductive cycle lasts three years, three distinct categories of adult females are expected to simultaneously exist. A time-series of measurements of embryos and ovarian follicles, histological smears of the nidamentary gland, and seasonal records of ovulation showed that this was the case.

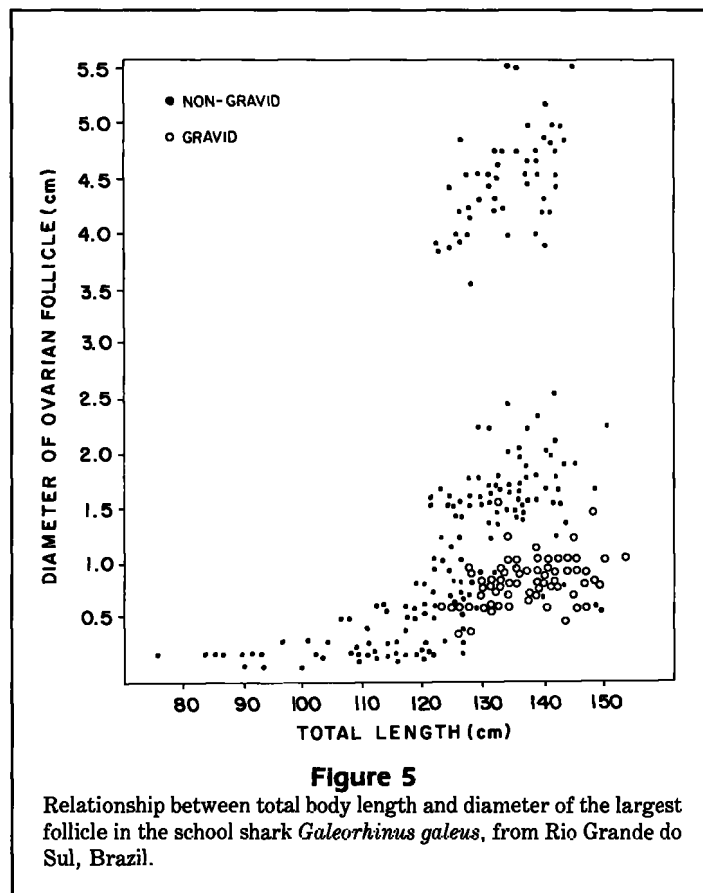


Figure 5

Relationship between total body length and diameter of the largest follicle in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Table 2

Incidence of pregnancy in *Galeorhinus galeus* from Rio Grande do Sul, Brazil, as a percent of the sample (n), by classes of total length (TL) in cm.

TL	% pregnant	n	TL	% pregnant	n
115	0	5	135	52	21
116	0	3	136	50	14
117	0	7	137	50	16
118	13	8	138	46	22
119	0	8	139	73	26
120	11	9	140	75	16
121	0	7	141	62	21
122	0	9	142	50	18
123	13	16	143	50	14
124	10	10	144	57	14
125	36	11	145	75	8
126	14	22	146	100	8
127	32	19	147	100	3
128	42	19	148	67	3
129	30	20	149	71	7
130	42	12	150	0	1
131	56	25	151	100	2
132	50	12	152	100	1
133	38	16	153	0	2
134	62	21	154	50	2

Within the study area, gravid females occurred from April to December and nongravid adult females from June to November. Ovulating females, females which had recently completed ovulation, and the largest mature ovarian follicles occurred in November and December. Full-term embryos without the yolk sac were observed in November, as was also noted by De Buen (1952) off Uruguay. The monthly-length frequency distributions of embryos were unimodal, and modal embryonic total length increased from 13 cm in April to 31 cm in November (Fig. 7). Ovulation and birth both occurred in November–December, therefore gestation lasts 12 months.

In gravid females (GR), ovarian follicles were opaque white and did not grow (Fig. 8). Two distinct types of nongravid females occurred during the same time-periods each year. First-year nongravid females (NGR-1) occurred from June to September and had light-yellow ovarian follicles 0.5–2.5 cm in diameter. Second-year nongravid females (NGR-2) were present July to November and had golden-yellow follicles of 3.5–5.5 cm diameter.

From June to September, follicle diameter of NGR-1 females remained about 1.5 cm (Fig. 9), while ovary weights ranged from 70 to 130 g. Thus, vitellogenesis was slow. Females over the full size range of adults were classified as NGR-1 (Fig. 5). This category included the maturing, virgin phase but consisted mainly of resting females.

In NGR-2 females, the modal diameter of the largest follicle increased from 4.2 cm in July to 5.5 cm in November (Fig. 9). Accelerated vitellogenesis and ovarian maturation occurred in this phase. In November, these females had dilated nidametary glands (the four greatest values in Fig. 6) and uteri containing a transparent viscous material resembling egg white.

The reproductive cycle of the female lasts three years. During the first 12 months after parturition, the oviduct remains in a resting stage and vitellogenesis is slow (NGR-1 stage). During the following 12 months, large mature follicles are produced, and the nidametary gland and uteri are prepared for ovulation, which occurs in November–December (NGR-2 stage). Gestation lasts 12 months, during which there is no vitellogenesis, and parturition takes place in November–December (GR stage).

Nidametary gland smears from one of eight NGR-2 females, collected in July 1986, had a large number of whole spermatophores, similar to those observed in the seminal vesicle of the male (Fig. 4). Thus, mating

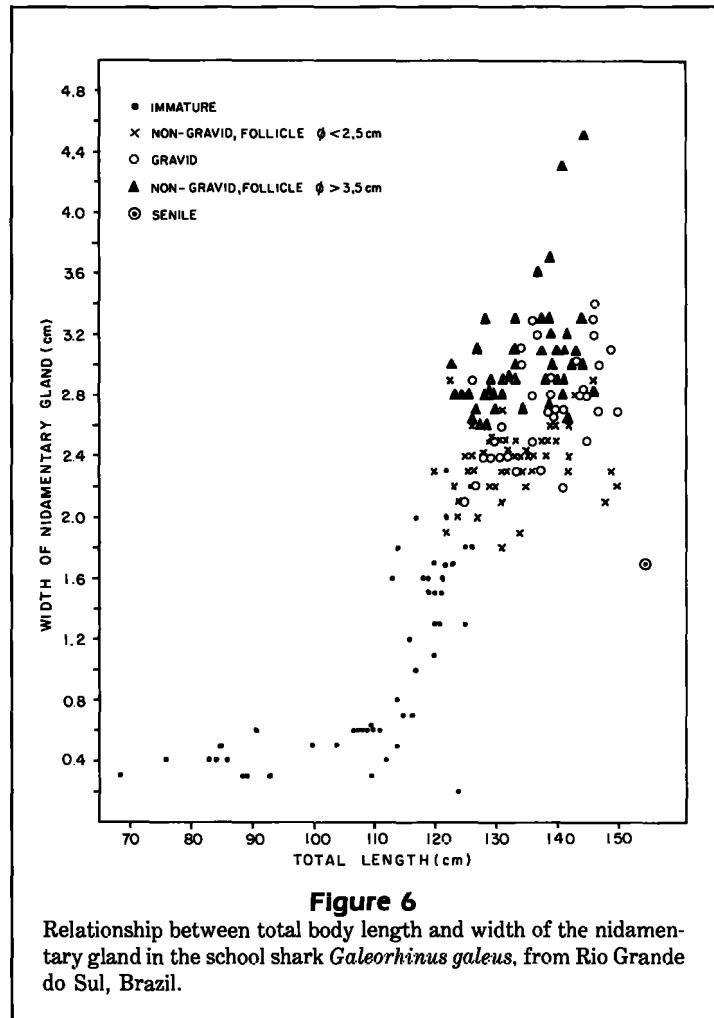


Figure 6

Relationship between total body length and width of the nidametary gland in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

apparently begins during the NGR-2 phase as early as July, at least five months before ovulation, and the sperm is carried to the nidametary gland by passive transport.

Fecundity

Fecundity increased linearly with body size of the female (Table 1, Fig. 10). In 58 NGR-2 females of 123–146 cm TL, ovarian fecundity ranged from 12 to 34 with a mean of 22.7 per female. In 140 females of 123–154 cm TL, uterine fecundity ranged from 4 to 41 with a mean of 23.1. Of the items in the uteri, 94.2% were normal embryos, 5.2% were nondeveloping eggs, and 0.6% were dead or abnormal embryos. In 79% of the gravid females, there were at least one or two nondeveloping eggs, but the total number of these eggs per female, ranged up to 34.

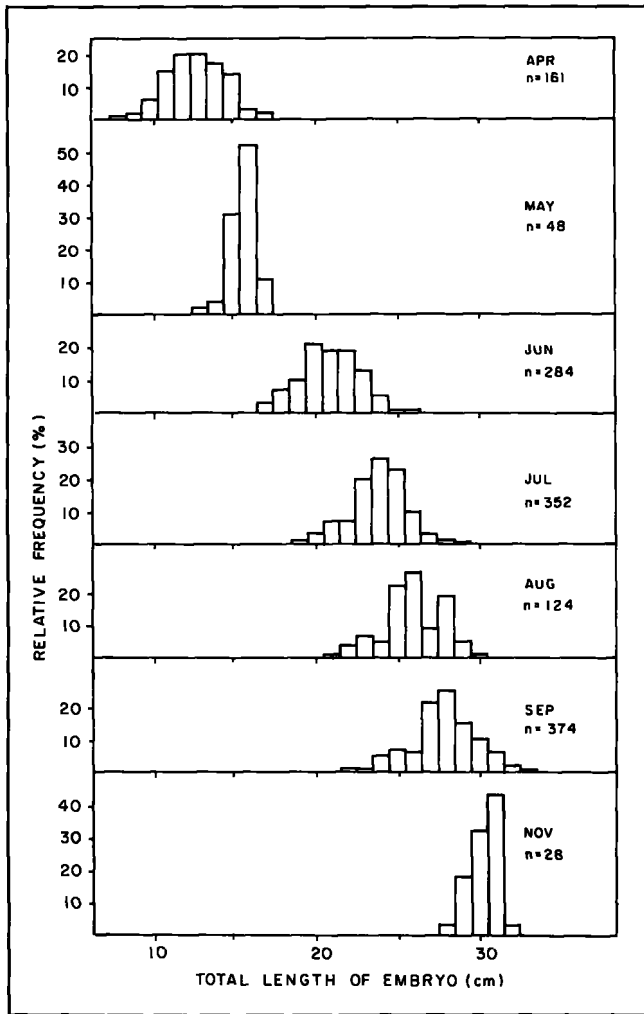


Figure 7 (above)

Monthly distributions of relative frequencies of total length of embryos of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

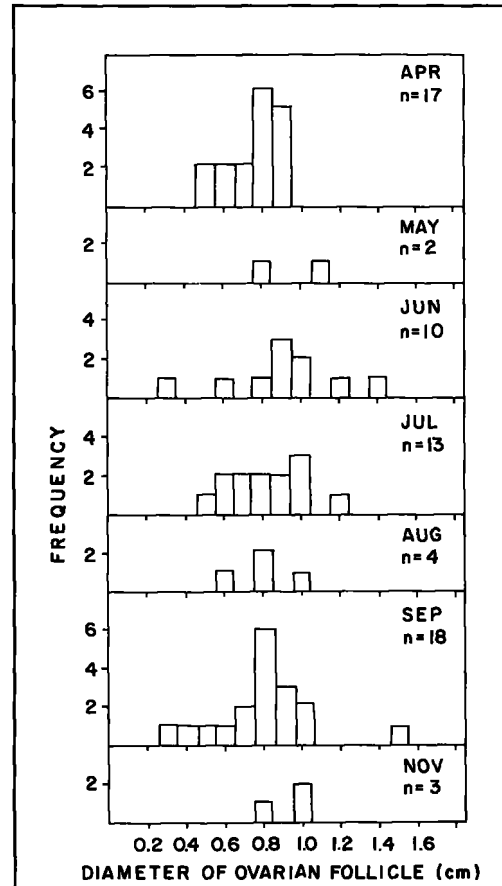


Figure 8

Monthly distributions of width frequencies of the largest ovarian follicle in gravid females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

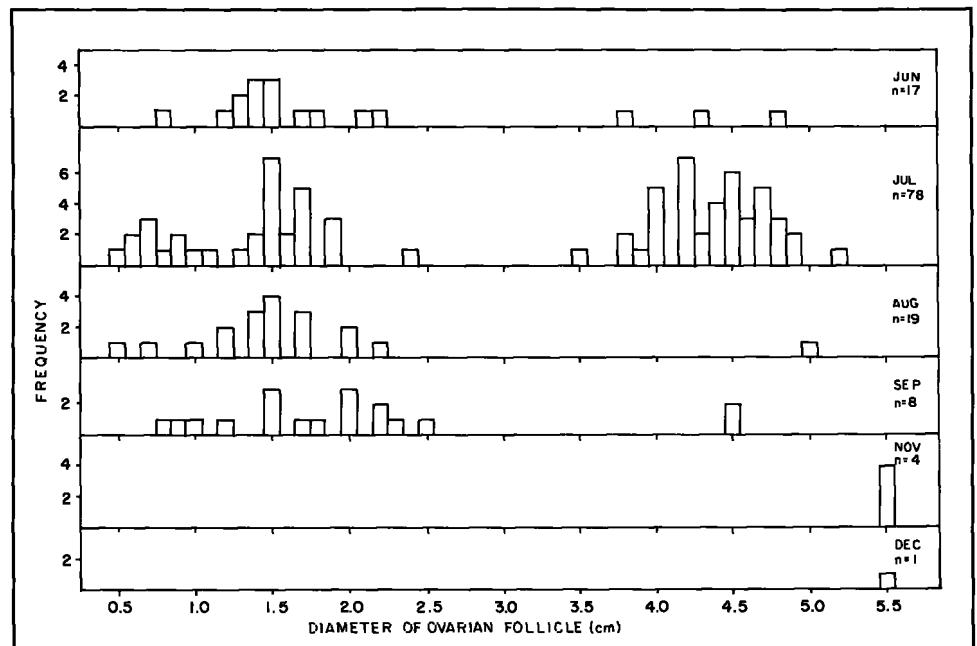


Figure 9 (right)

Monthly distributions of width frequencies of the largest ovarian follicle in non-gravid adult females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

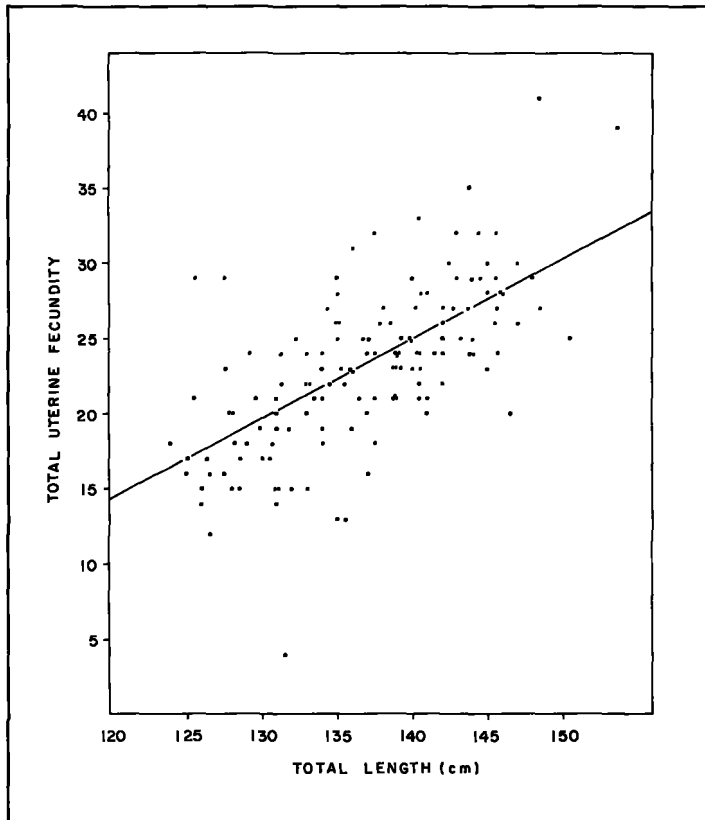


Figure 10
Relationship between total body length and uterine fecundity in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Gestation

Outgrowths of the uterine wall divided the uterus into separate gestation chambers for each embryo. The quantity of liquid in the chambers of the two uteri increased from about 200 g in April to 500–900 g in July, constituting respectively 8.3 and 28.0% of the weight of the full uteri in those months. Uteri were swollen and turgid due to the increasing mass of the litter and liquid, and in July attained weights between 1230 and 5520 g.

Embryos situated near the cloaca were about 2–4 cm larger than those situated near the nidamental gland. In August and September, but not in April, mean total length per litter increased linearly with total length of the mother (Table 1, Fig. 11). This indicates that embryos grow faster in the larger females.

The weight of 38 large follicles of ovulating females varied from 42 to 56 g. The weight of 59 newly ovulated eggs varied between 40 and 100 g with a mean of 59.4 g, which is the magnitude of the yolk reserve in the egg. From April to September, mean total length and yolkless weight of the embryos increased from 13.3 to 28.0 cm and from 10.0 to 65.0 g, while the weight of the full yolk sac decreased from 45 to 17 g. There was no yolk sac in a litter of 28 embryos in November. These embryos averaged 30.3 cm TL and 92.9 g total weight. The sex ratio of embryos did not differ significantly from unity: 599 were males and 625 were females.

Cycle of the liver

In sexually immature sharks, the hepatosomatic index (HSI) did not change with body size but varied about the mean of 7.9 throughout the range of total lengths. The HSI of males increased at sexual maturity to a mean of 11.4 (Fig. 12).

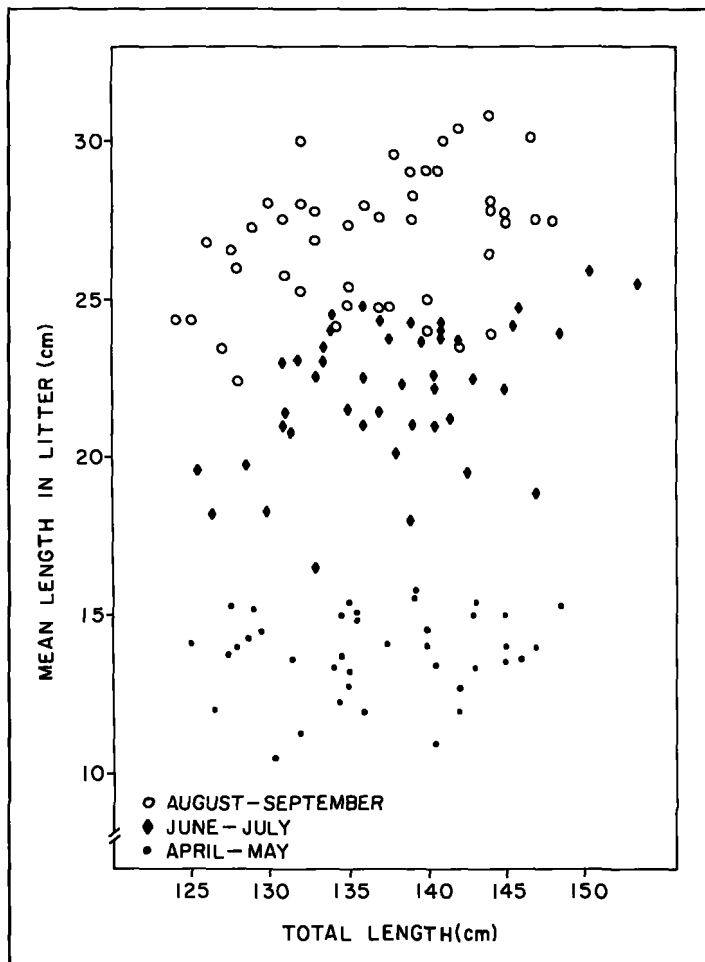


Figure 11
Relationship between total body length of the mother and mean length in litter of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

The HSI of adult females varied during the reproductive cycle; the mean was 7.2 in GR females, 10.8 in NGR-1, and 17.2 in NGR-2 females (Fig. 13). In all categories, the mean monthly HSI decreased from a maximum in early winter to a minimum in spring (Fig. 14).

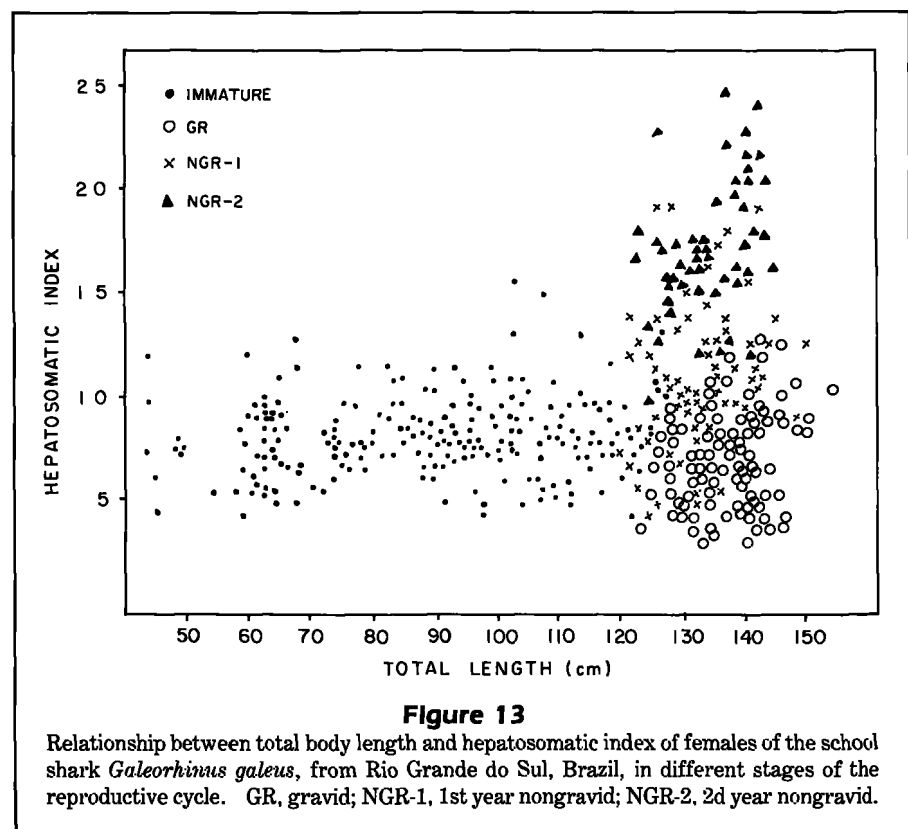
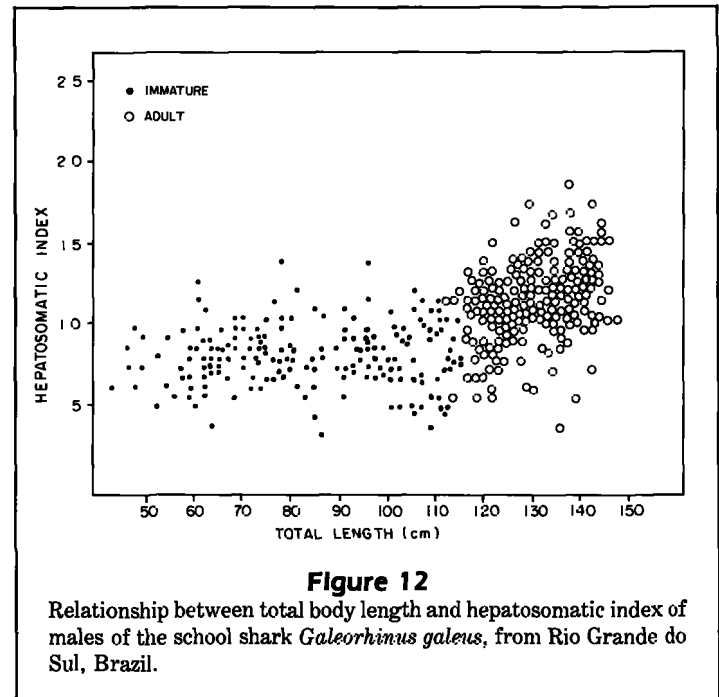
Discussion

Body size at attainment of sexual maturity, as a percent of maximum size, and the slope of the linear regression of fecundity on total length are similar in the western South Atlantic, Australian, and eastern North Pacific populations of the school shark (Table 3, Fig. 15). It is concluded that these parameters of reproduction are characters at the species level.

The dense groups of spermatozoa in the seminal vesicles of adult males of the school shark were designated spermatophores, in analogy with structures described in the basking shark *Cetorhinus maximus* and the blue shark *Prionace glauca* (Matthews 1950, Pratt 1979). During the present study, spermatophores were also found in the seminal vesicle of the smooth dogfish *Mustelus canis* and the sand shark *Eugomphodus taurus*. It seems that the grouping of spermatozoa in dense agglomerations is a common feature in elasmobranchs.

There is no discontinuity in the gonadosomatic index of school shark adult males, such as would indicate the simultaneous existence of different reproductive stages, as was observed in females. All smears of the seminal vesicle of adult males in July contained spermatophores. It is concluded that all adult males present in the area during winter are in the mating stage.

In the western South Atlantic population, copulation occurs up to at least 5 months before ovulation. Gestation is highly synchronized, with all phases from ovulation to birth being timed at the population level. This requires that at a particular period each year, all NGR-2 females will have mated and will be ready to ovulate.



The extended mating period ensures this. The same is observed in the blue shark, where the female mates up to 12 months before ovulation (Pratt 1979).

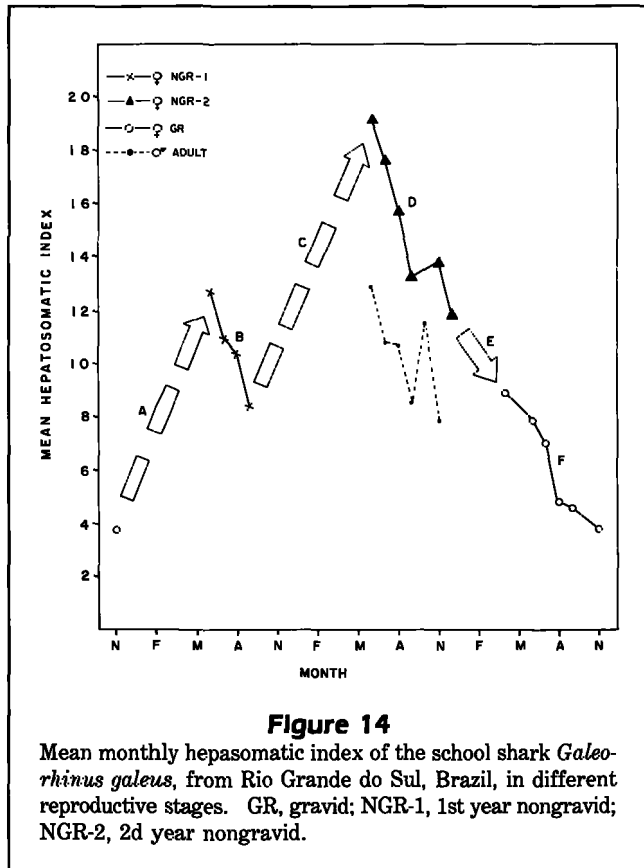


Figure 14

Mean monthly hepatosomatic index of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil, in different reproductive stages. GR, gravid; NGR-1, 1st year nongravid; NGR-2, 2d year nongravid.

Ripley (1946) concluded that in eastern North Pacific animals, gestation lasts 12 months during which there is no vitellogenesis and that parturition occurs in summer. Data on the female cycle in this population were obtained from a single sampling area where, in a sample of 3747 females, 88% were gravid, 11% had large ovarian follicles, and 1% were resting. The percentages reflect the situation at a certain point of the migration route of the gravid females, but the data indicate the simultaneous presence of three categories of adult females. In winter, Olsen (1954) observed two types of nongravid Australian females: one with the largest ovarian follicles ranging from 4.0 to 5.0 cm in diameter, and the other with maximum follicle diameters of 1.0–2.0 cm. These two categories occurred simultaneously and in similar numbers. Parturition took place in November–December, and size at birth was about 31 cm TL. Olsen (1954) assumed that gestation starts immediately after mating in winter and lasts 6 months. The presence of the two nongravid categories was explained by a period of 18 months for the production of the mature follicle, giving a cycle of 2 years. However, in view of the data on gestation in western South Atlantic and eastern North Pacific animals, it is unlikely that this phase lasts only 6 months in Australian animals.

Therefore, we conclude that the duration and timing of the reproductive cycle are similar in these three populations of school shark.

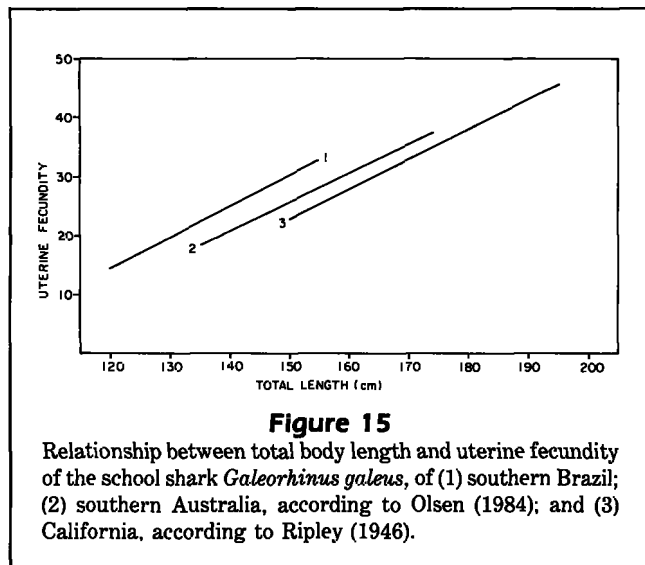
The observed increase in body size of embryos from the anterior to the posterior end of the uterus has also been noted in eastern North Pacific and Australian animals. This may partly reflect duration of the ovulation process, during which eggs enter the oviducts in pairs at intervals of 24–48 hours in the smooth dogfish, in the skates, *Raja brachyura* and *Raja erinacea*, and in the sand shark (TeWinkel 1950, Holden 1974, Gilmore et al. 1983). Assuming an interval of 36 hours in the school shark, the duration of ovulation for all eggs would range between 10 and 40 days, depending on fecundity. The size difference between the first and the last embryo in the uterus would then reflect the growth of the first embryo during the ovulation period, although the possibility of a corresponding difference in yolk reserve remains to be investigated.

In spring, liver weight as a proportion of total body weight (HSI) of the eastern North Pacific adult female NGR-2 was 14%, and about 4% in GR females. In the

Table 3

Total length (TL, in cm) and age (years) at stages of sexual development in geographical populations of *Galeorhinus galeus*. Data on the Australian population after Olsen (1984) and on the eastern North Pacific population after Ripley (1946). Age in the western South Atlantic population after growth curve by Ferreira and Vooren (1991). Length ratio expresses TL at first maturity, as a percent of observed maximum values.

	SW Atlantic	Australia	NE Pacific
Male			
TL 1st maturity	107.0	120	135
Age 1st maturity	10.5	8	—
TL 50% maturity	111.0	—	142
Age 50% maturity	11.4	—	—
TL full maturity	117.0	132	175
Age full maturity	13.2	10	—
TL maximum	148.0	155	185
Age maximum	36.1	41	—
Length ratio	72.3	77.4	73.0
Female			
TL 1st maturity	118.0	135	150
Age 1st maturity	14.1	12	—
TL 50% maturity	123.0	—	158
Age 50% maturity	15.7	—	—
TL full maturity	128.0	—	180
Age full maturity	17.5	—	—
TL maximum	154.5	174	195
Age maximum	36.2	53	—
Length ratio	76.1	77.6	76.9



Australian animals, the HSI ranged from 6.0 to 11.0 in GR females, and from 15.0 to 24.0 in NGR-2 females (Olsen 1954). Since these values are similar to those of comparable eastern South Atlantic females, it is concluded that the liver cycle of adult females observed in the present study is characteristic of the species.

When estrogen was administered to the female of the spotted catfish *Scyliorhinus canicula*, the liver increased in size and produced vitellogenin and released it into the blood (Craik 1978). Estrogen is produced by the granulosa of the maturing ovarian follicle of the spiny dogfish *Squalus acanthias*, and by the mature testis of *Torpedo marmorata*, *Scyliorhinus canicula*, *Squalus acanthias*, and *Raja clavata* (Lance and Callard 1969, Craik 1978, Dodd 1983). This explains why in the western South Atlantic school shark the HSI increases in both sexes after sexual maturation and varies with the cycle of the adult ovary, reaching a maximum during the NGR-2 stage. Ripley and Bolomey (1946) show that in spring the proportion of oil in the liver of the eastern North Pacific adult is about 60% in males and NGR-1 females, 40% in GR and post-partum females, and 70% in NGR-2 females and those with uterine eggs. Thus, the changes in HSI of the adult female reflect a major variation in the quantity of lipids in the liver during the reproductive cycle.

The submerged weight (SW_i) in seawater of an object i can be determined by the model

$$SW_i = m_i (1 - d_s / d_i),$$

where m_i is the mass of the object in g, and d_s and d_i are the specific densities of seawater and of the

object, respectively, in g/cm^3 . A negative submerged weight indicates buoyancy. Using this model, submerged weight for the eviscerated body and the oil reserve in the liver was calculated for males and females of 130 cm TL in all three reproductive stages. For submerged weight of the body, m_i was calculated from the regressions in Table 1, and d_i was estimated at $1.065 g/cm^3$, which is the mean of the liver-free body density of 13 species of sharks (Baldrige 1970). For submerged weight of the oil reserve, the liver mass calculated from the HSI in the present study was multiplied by the percentage of oil in the liver in the eastern North Pacific school shark. For the specific density of the liver oil in the different reproductive stages, values from Bone and Marshal (1982) were used: GR females, non-metabolizable lipids, $0.860 g/cm^3$; NGR-2 females, metabolizable lipids, $0.930 g/cm^3$; NGR-1 and males, the median of these values, $0.895 g/cm^3$. To calculate the submerged weights of the mature ovaries of NGR-2 females 130 cm TL, the regression of ovarian fecundity on total length was combined with data on mass and volume of 14 follicles (4.0 cm in diameter). This resulted in an ovary mass of 665.00g and a specific density of $1.108 g/cm^3$. The specific density of seawater was taken as $1.024 g/cm^3$, according to Baldrige (1970).

The results are summarized in Table 4. In males and NGR-1 females, the buoyancy of the liver is about one-fourth the submerged weight of the eviscerated body. In NGR-2 females, the increased liver buoyancy compensates for 60% of the submerged weight of the yolk mass in the ovary. Through the production of estrogen, the maturing ovary also controls, simultaneously, the vitellogenic and hydrostatic functions of the liver. Besides providing buoyancy when this is most needed, the metabolic reserve of the NGR-2 female guarantees resources for vitellogenesis and maturation of the follicle, thus ensuring the timing of reproduction.

The specific density of embryos, for example, $1.035 g/cm^3$ in the sandbar shark *Carcharhinus milberti* (Baldrige 1970), is much less than that of yolk. During gestation of aplacentary sharks, some organic matter in the yolk reserve is lost but water is absorbed, and the full-term embryo weighs twice as much as the yolk (Ranzi 1932). The specific density of the uterus decreases during gestation because of the increase of intrauterine liquid and embryos and the decrease of egg yolk. This enables the gestating female to metabolize her lipid reserves without loss of buoyancy, and explains the low liver buoyancy in this stage. The reduction in liver volume also provides space for the gravid uteri. Such a trade-off between lipids and water without change in overall buoyancy also occurs during the winter fasting of *Clupea harengus* (Iles 1984).

Table 4

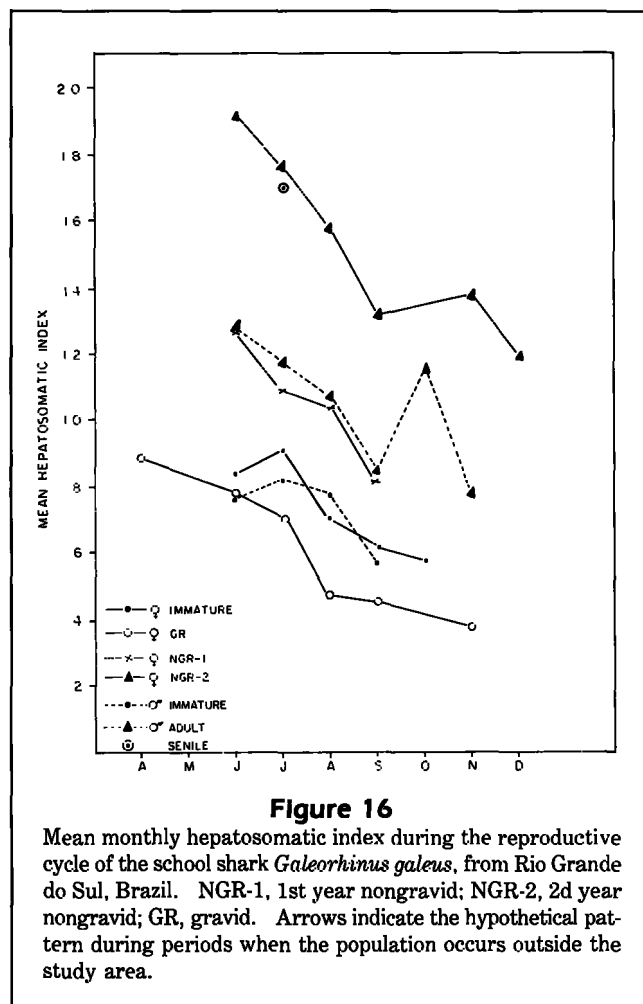
Submerged weight of parts of the body in *Galeorhinus galeus* from Rio Grande do Sul, Brazil. NGR-1, 1st year nongravid; NGR-2, 2d year nongravid; GR, gravid.

Item	Submerged weight (g)
Adult male, liver oil	-73.9
NGR-1 female, liver oil	-71.9
NGR-2 female, liver oil	-100.4
GR female, liver oil	-42.3
Adult male, eviscerated body	+288.7
Adult female, eviscerated body	+296.4
NGR-2 female, mature ovary	+50.4

The gradual decrease of the HSI in both sexes during winter suggests that at that time, the population invests little effort in feeding and lives mostly off its lipid reserves. From interpolation in the observed HSI pattern, it is concluded that during the first two summers after parturition, the female accumulates lipids. During the third year of the cycle, HSI decreases constantly from ovulation to parturition (Fig. 16). In coastal waters of Uruguay, the species is caught by bottom gillnets during winter and by bottom longlines during summer (De Buen 1952). This is consistent with the hypothesis of the endogenous periodicity of feeding under hormonal control, as in *Clupea harengus* (Iles 1984). It is suggested that in the school shark, feeding during winter is reduced to the intake of proteins necessary for the continuous production of urea. In the liver of the female, a seasonal and a three-year cycle are timed to store and metabolize lipid reserves, to synthesize and transfer vitellogenin, and to control buoyancy, in a sequence which corresponds with the varying physiological needs during the reproductive cycle.

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