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Reproductive biology of the school shark, *Galeorhinus galeus*, off Argentina: support for a single south western Atlantic population with synchronized migratory movements

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Synopsis

We sampled school sharks, *Galeorhinus galeus*, in Anegada Bay, Argentina, to investigate reproductive ecology. Males dominated the catches in October and April, while females were more abundant than males from November to March. Males were estimated to mature at a smaller size (108–119 cm total length) than females (mean 125 mm total length). Differences between fecundity and fertility were not dependent on mother size. The largest embryos were found in late October and November, coinciding with ovulation. This indicates that gestation lasts about 12 months. Embryonic growth was best described by a Gompertz model. Four groups of females were recognized: (1) juveniles up to 129 cm TL, with translucent-to-white ovarian follicles; (2) mature, non-pregnant, pre-ovulatory females with yellow ovarian follicles and low gonadosomatic index (GSI); (3) mature non-pregnant ovulating females with large yellow ovarian follicles, high GSI; and (4) pregnant females carrying near term embryos, with minute ovarian follicles. These observations support a 3-year female reproductive cycle. The patterns of occurrence, reproductive condition, and embryonic growth of school sharks in northern Argentina are complementary to those from southern Brazil, supporting the hypothesis that there is a single large population of school sharks in the south western Atlantic.

Introduction

The school shark, *Galeorhinus galeus* (Carcharhiniformes: Triakidae), is a medium-sized shark that occurs in coastal and shelf temperate waters in the northeast and southeast Pacific, northeast and south Atlantic, Mediterranean Sea, southern Australia and New Zealand (Compagno 1984, Last & Stevens 1994). Its life history is characterized by slow growth, high longevity (up to 50 years, Olsen 1984), late age at maturity (Stevens 1999), low fecundity (Peres & Vooren 1991, Stevens 1999), and low mortality (Stevens 1999), and the species is highly vulnerable to over fishing (Stevens 1999).

In the south western Atlantic it is presumably a migratory species travelling seasonally between southern Brazil and northern Patagonian waters (Vooren 1997). Off southern Brazil, school sharks occur only in winter months (June–September) mainly at depths around 100 m. The species leaves the area by October and is absent during spring and summer months (Peres & Vooren 1991). On this basis, Vooren (1997) hypothesized that in the south west Atlantic school sharks spend the winter in the northern part of its range off southern Brazil (30–34°30′S), and then migrate southwards off northern Argentina (35–45°S) in summer. This migration would be related to giving birth in nursery areas that putatively occur off northern Argentina (Tricas et al. 1997, Vooren 1997, Walker 1999).

Until now these statements could not be verified due to the lack of life history information on school sharks from Argentinean waters (Menni 1986). Available data on the reproductive biology of school sharks off Argentina are scant and were not taken over prolonged time periods (Menni 1985, Menni et al. 1986, Chiaramonte 2000), which preclude inferences on possible migratory movements.

In this paper, we present data on reproduction of school sharks from Anegada Bay throughout the time of residence of school sharks off Argentina. We estimated size at maturity, female reproductive cycle, birth season, gestation, embryonic growth parameters, and monthly relative abundance.

Methods

Source of samples and study area

We obtained samples from the recreational shark fishery that operates in Anegada Bay, Argentina. All sharks caught in this fishery are landed in the town of Bahía San Blas, where we sampled school sharks from October 1999 to April 2000 and from October 2000 to March 2001. These sampling periods correspond to the shark-fishing season, which coincides with the time of occurrence of large sharks in Anegada Bay (Lucifora et al. 2002).

Anegada Bay (40°30′S, 62°00′W, Figure 1) is a shallow area with many banks and small islands.

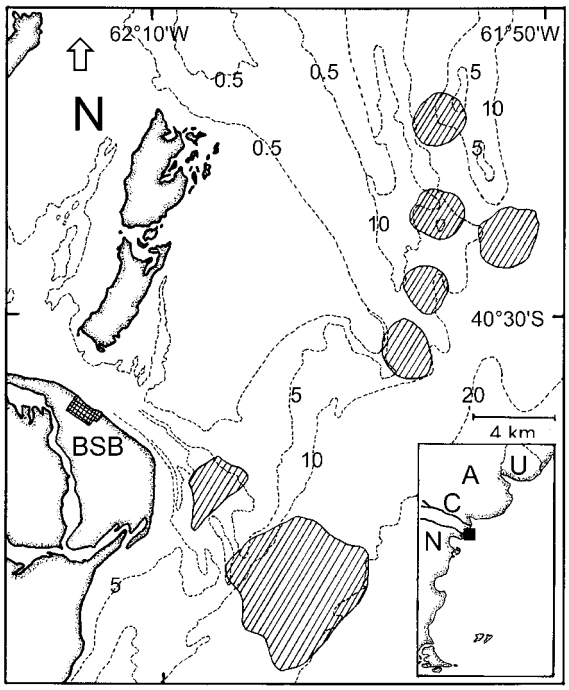

Figure 1. Map of Anegada Bay, Argentina, showing the recreational shark fishery fishing grounds (striped areas) from where samples were obtained. The inset shows the location of Anegada Bay (square) on the eastern shore of South America. A: Argentina, U: Uruguay, C: Colorado River, N: Negro River, BSB: Bahía San Blas. Isobaths in meters.

This area is highly influenced by discharges of nutrient-rich continental waters from the Colorado and, mainly, Negro rivers (Guerrero 1998) and it is an important spawning and nursery area for a number of bony (Macchi & Acha 1998) and cartilaginous fishes (Cousseau 1986).

Abundance

We estimated monthly abundance of school sharks in Anegada Bay from October to April through catch per unit effort (CPUE) during three fishing seasons (1998–1999, 1999–2000, and 2000–2001). We calculated CPUE as the number of sharks caught per boat per fishing trip per day. We assessed monthly differences in mean CPUE by means of one-way ANOVA. We used the Tukey test for unequal sample size to locate significant differences (Zar 1984).

We analysed monthly variations in relative abundance of each sex and reproductive stage (i.e.

males, adult females with eggs in the uteri, adult females with empty uteri, and adult females with embryos) by calculating the proportion of each group as percent of the total number of school sharks examined in each month.

We constructed size frequency distributions and sex ratios by month. Also, we constructed a size frequency distribution with data obtained from trawls in two research cruises (n = 260 sharks in 6 trawls). These cruises occurred in November 1998 (n = 20 trawls) and November 1999 (n = 26 trawls) off Anegada Bay in waters deeper (mean depth = 32.5 ± 7.5 m) than those in which the recreational fishery operated (usually 5–10 m, maximum depth approximately 20 m). Each trawl lasted 15 min, trawl speed was four knots, and stretched mesh size between opposed knots was 120 mm.

Reproduction

We determined sex, measured (precaudal length, PCL; total length in natural position, TL and total length with the tail stretched, TL_s), and dissected sharks at fish processing plants. We recorded the presence of seminal fluid, and clasper inner length (i.e. the length from the base to the tip of the clasper along its mesial side) (Compagno 1984) and degree of calcification in males, and uteri and oviducal gland width in females.

We calculated the relationship between PCL and TL to estimate TL for six specimens with the caudal fin removed prior to being measured. We also calculated the relationship between TL_s and TL to make comparisons with published data with lengths reported as TL_s. We use TL throughout this paper.

We regarded males as mature when they had calcified claspers longer than their pelvic fins that could be rotated anteriorly and their epididymides were highly convoluted. Females were considered mature when they had uteri widened along their entire lengths, heart-shaped oviducal glands and yellow ovarian follicles or were pregnant (Peres & Vooren 1991). We estimated size at maturity by calculating the proportion of mature individuals in 5-cm size intervals and fitting a logistic ogive ($p = 1/(1 + \exp(\alpha + (\beta \times TL)))$), where p is the estimated proportion of mature individuals at a given length, and α and β are model parameters) through a maximum likelihood procedure (Roa et al. 1999). Then we estimated the length at which 50% individuals were mature from the ogive.

We recorded liver and gonad mass with a precision of 5 g. As we could not record total mass, we calculated hepatosomatic and gonadosomatic indices (HSI and GSI, respectively) as liver or gonad mass divided by TL^3 (Taniuchi 1988, Yamaguchi et al. 1997).

We recorded the number of ripe ovarian follicles, number of embryos in the uteri, number of non-viable eggs in the uteri, number of atretic follicles in the ovary and measured the maximum diameter of ovarian follicles. We considered flaccid follicles with granulated yolk invaded by narrow blood vessels to be atretic. We considered the number of ovarian follicles to be the maximum potential fecundity at any given size. We considered the number of viable embryos to be the fertility (Helfman et al. 1997). We constructed regression lines for fecundity and fertility against TL and assessed them by testing the significance of correlation coefficients. We tested the null hypothesis of no difference in slopes and intercepts between both lines with the Student's t test (Zar 1984).

We plotted embryo length against date from October 1999 to March 2001. This allows us to make inferences on the time of parturition and the length of gestation. Once we estimated the gestation period, we plotted the mean length of litters against gestation time in days for calculating embryonic growth parameters. We took mean lengths of litters in winter months (May, June, July, August, and September) from Peres & Vooren (1991). We tested three growth models for describing the embryonic growth; namely the linear, von Bertalanffy, and Gompertz models.

We analysed changes in maximum diameter of ovarian follicles (precision ± 0.5 mm), GSI, and HSI relative to total length for identifying reproductive stages of mature non-pregnant females.

Results

Abundance

We found significant differences in monthly CPUE of school sharks in the three fishing seasons

studied (1998–1999: $F = 5.44$, df = 4, $p = 0.002$; 1999–2000: $F = 12.62$, df = 6, $p < 0.001$; 2000–2001: $F = 36.55$, df = 5, $p < 0.001$; Figure 2). In general, CPUE was highest in October and November, medium to high in December, lowest in January through March, and intermediate in April (Figure 2).

Males dominated the catches in October and April (63–71% of examined specimens), reaching their lowest abundance from November to March (Figure 3). On the other hand, females were more abundant than males from November to March (67–100%), and were less abundant in October and April (28–36%; Figure 3). Mature non-pregnant females peaked in October and November (16–31%), mature females with recently ovulated eggs peaked in December and January (50–100%), and females carrying embryos in various stages of development peaked in March (75–100%) (Figure 3). Females with near term embryos occurred only in October and November. Size frequency distributions obtained from the recreational fishery showed that the size range of males did not vary substantially among October, November and April. In contrast, size frequency distributions of females were different among months, with the smallest females being present in October and April (Figure 4). Size frequency distributions from school sharks obtained by trawling showed that juveniles around 110 cm TL were present off Anegada Bay in November (Figure 5).

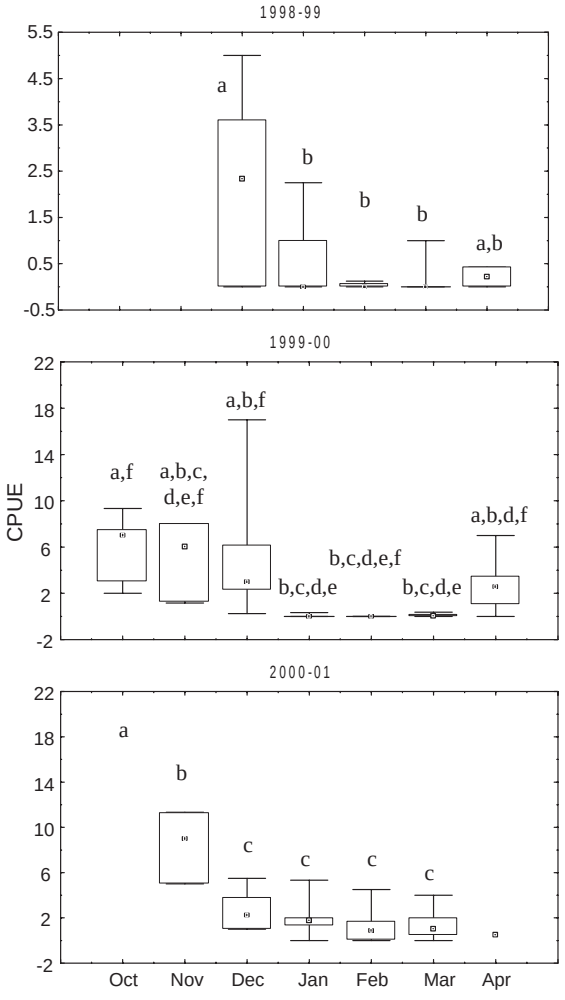

Figure 2. Monthly CPUE as number of sharks caught per fishing boat per day of school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina, during three fishing seasons (1998–1999, 1999–2000, 2000–2001). The square is the median, the box encloses values between the 25th and the 75th percentile, and the whiskers are minimum and maximum values. Distributions with the same letter are not significantly different (Tukey test for unequal sample size, p level = 0.05).

Reproduction

We examined 411 school sharks (123 males and 288 females).

The linear relationships between PCL and TL, and TL_s and TL were described by the following equations:

$$TL(cm) = 1.119 \times PCL(cm) + 13.738$$
$$(r = 0.967, n = 364, range = 92–153.2 \text{ cm TL})$$
$$TL(cm) = 0.995 \times TL_s(cm) - 2.353$$
$$(r = 0.983, n = 234, range = 97–152.8 \text{ cm TL})$$

The smallest male examined measured 49.2 cm TL and the largest one 152.8 cm TL. The smallest mature male was 119 cm TL and the largest juvenile male 108.8 cm TL (Figure 6). We could not estimate size at 50% maturity in males due to the lack of data in the range of 108–120 cm TL. Females ranged from 48.3 to 153.2 cm TL. The smallest mature female measured 118 cm TL and the largest juvenile 129 cm TL (Figure 7). Maximum uterus width of juvenile females was 27 mm, but most juvenile females had uteri less than 19 mm wide. Minimum uterus width of mature females was 10.5 mm, but most had uteri wider than 17 mm and up to 155 mm in pregnant

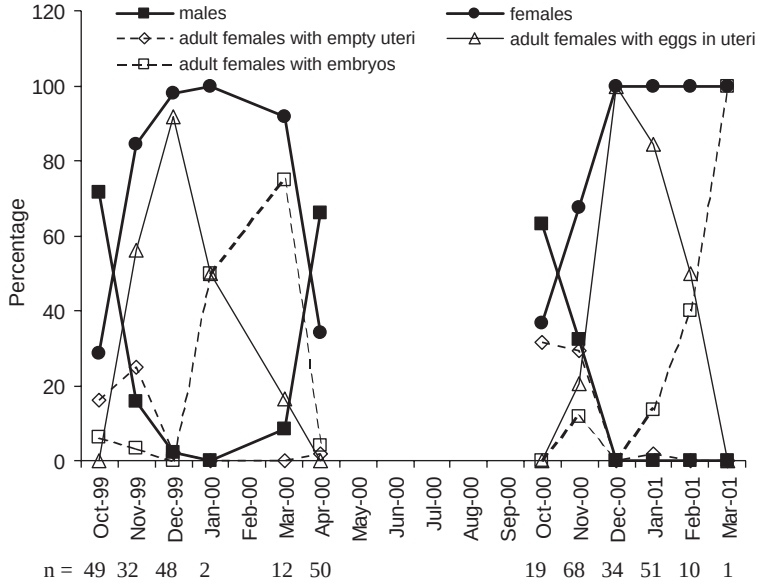

Figure 3. Variation in the proportional abundances of different stages of school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina, during spring to autumn. Sample size (n) for each month is shown.

females with term embryos (Figure 7a). Oviducal gland was as wide as 25 mm in juvenile females. In mature females oviducal gland was always larger than 19 mm with a maximum at 45 mm in ovulating females (Figure 7b). The estimated parameters of the logistical ogive were $\alpha = 57.32$ and $\beta = -0.46$. Size at 50% maturity in females was 124.72 mm TL (Figure 8).

Mean fecundity was 24.92 (±4.39 SD), and mean fertility was 24.19 (±4.26 SD) pups per female. The correlation coefficients of fecundity ($r = 0.57$, $t = 9.18$, $n = 174$, $p < 0.001$) and fertility ($r = 0.60$, $t = 9.90$, $n = 174$, $p < 0.001$) with TL were significantly different from 0, indicating that fecundity and fertility increased with female TL. The regression parameters of the linear relationships were: slope = 0.376 and intercept = −26.264 for TL vs. fecundity, slope = 0.384 and intercept = −28.030 for TL vs. fertility. The slopes were not significantly different ($t = 1.803$, $df = 344$, $p = 0.072$), but the intercept of fecundity was significantly higher than that of fertility ($t = 1.805$, $df = 345$, $p = 0.036$). On average, fertility was 1.77 pups smaller than fecundity. This difference was constant throughout the size range investigated, which indicates that differences between fecundity and fertility are not dependent on mother size (Figure 9).

The largest embryos were consistently found in late October and November coincident with ovulation (Figure 10a). This indicates that gestation lasts about 12 months. Embryonic growth showed a sigmoidal pattern that was best described by a Gompertz growth curve (i.e. $L_t = L_\infty \exp(-k^{-1}\exp[a - kt])$; $R^2 = 0.989$), where t is age in days of gestation, L_t is length at age t, and L_∞, k and a are parameters of the model with values 29.770, 0.021, and −1.171, respectively, Figure 10b). The other two models tested did not copy the sigmoidal pattern of the school shark embryonic growth and had a poorer fit than the Gompertz model (linear $R^2 = 0.916$, von Bertalanffy $R^2 = 0.915$).

There were two stages of mature non-pregnant females, clearly separable by GSI (Mann–Whitney U test, $U = 427$, $n_1 = 14$, $n_2 = 25$, $p < 0.001$, Figure 11a) and maximum diameter of ovarian follicles ($t = 22.35$, $df = 37$, $p < 0.001$, Figure 11b). One group had GSI values between 0.027 and 0.07 (mean = 0.040 ± 0.0099), and ovarian follicles of 42–57.5 mm (mean = 49.38 ± 4.11) and were pre-ovulatory. The second group had

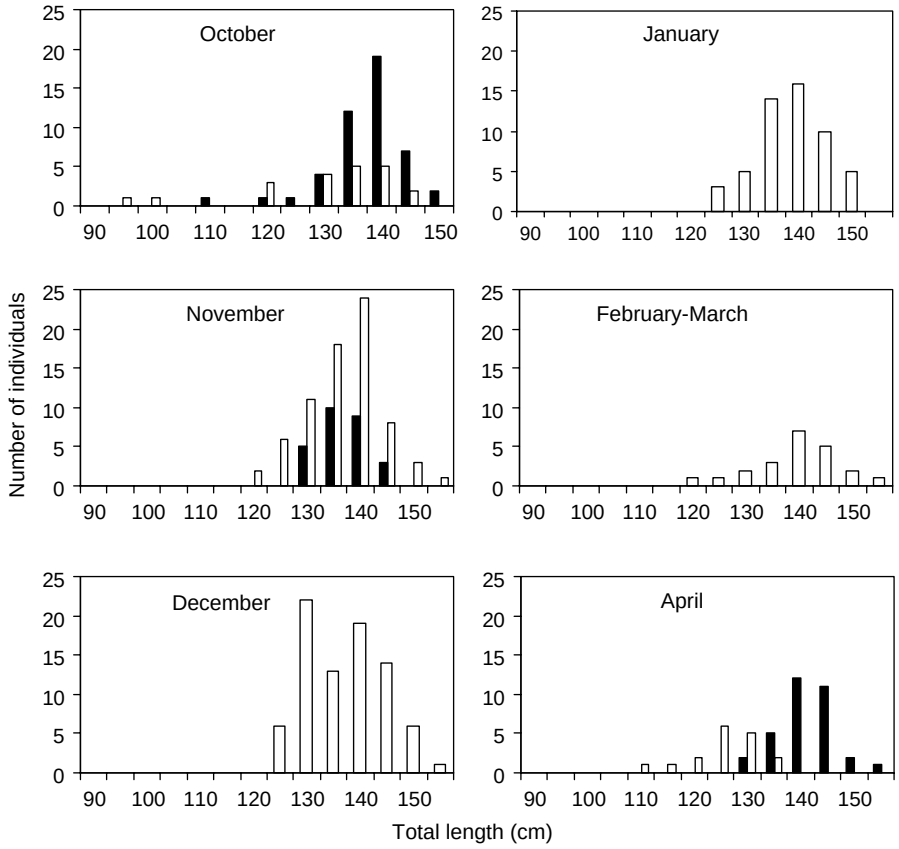

Figure 4. Monthly size frequency distribution of school sharks, *Galeorhinus galeus*, in Anegada Bay, Argentina, during spring to autumn. Filled bars are males and empty bars are females. Data for February and March were combined due to small sample size.

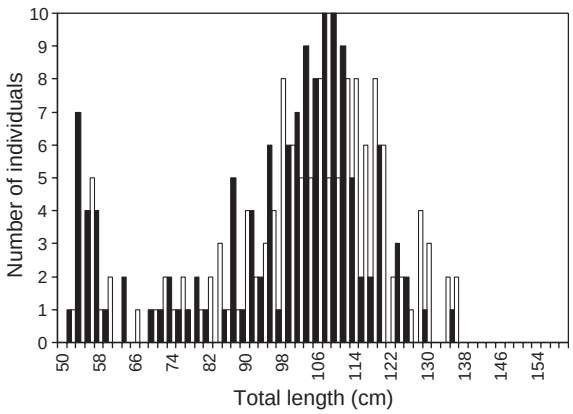

Figure 5. Size frequency distribution of school sharks, *Galeorhinus galeus*, caught off Anegada Bay, Argentina, by trawling (n = 6 trawls). Filled bars are males and empty bars are females.

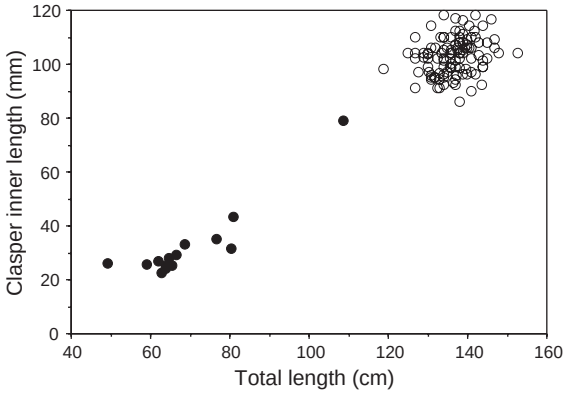

Figure 6. Relationship between total length and clasper inner length for school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina. Filled circles are juvenile males with uncalcified claspers, and empty circles are adult males with fully calcified claspers (n = 123).

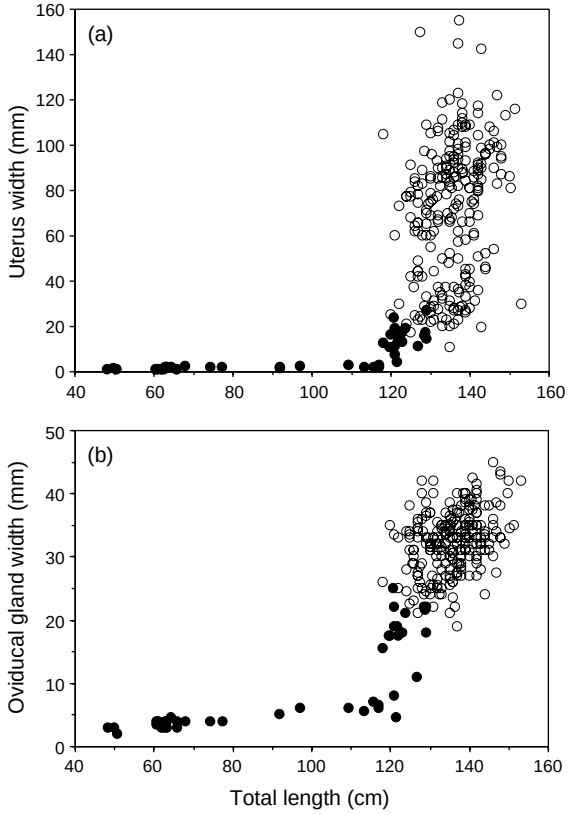

Figure 7. Relationship between total length and a – uterus width and b – oviducal gland width in female school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina. Filled circles are juvenile females and empty circles are adult females (n = 288).

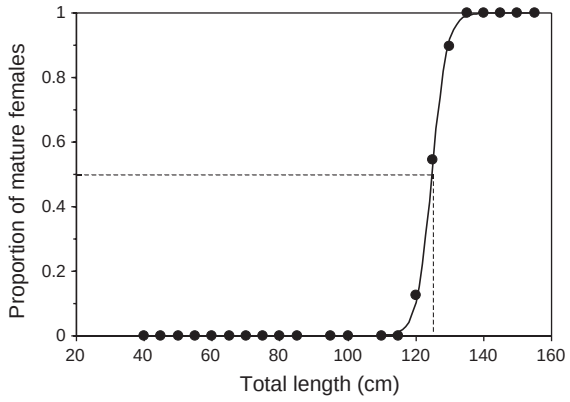

Figure 8. Proportion of adult females per 5-cm size intervals for female school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina. Dashed lines mark the size at which 50% of individuals are adult (n = 287).

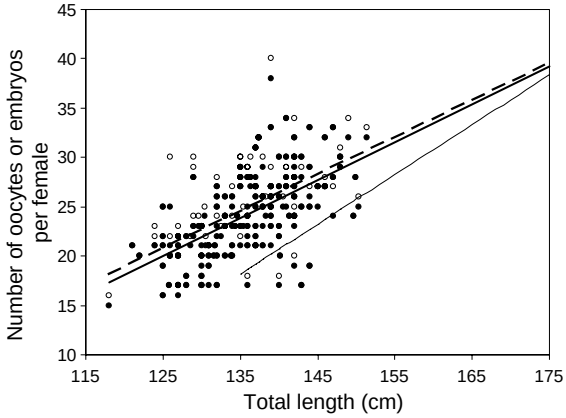

Figure 9. Relationship between female total length and the number of oocytes (fecundity) and the number of viable embryos in the uteri (fertility) for female school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina. The bold line is the linear regression for fertility, the bold dashed line is the linear regression for fecundity, and the entire non-bold line is the fertility of school sharks from southern Australia (taken from Olsen 1984) (n = 174).

GSI values between 0.0037 and 0.008 (mean = 0.0056 ± 0.0014), and ovarian follicles of 17.5–27.5 mm (mean = 22.43 ± 2.45). Therefore, four groups of females were present in Anegada Bay: (1) juveniles up to 129 cm TL, with translucent-to-white ovarian follicles smaller than 19 mm wide; (2) mature pre-ovulatory females with yellow ovarian follicles and GSI as previously described and empty uteri; (3) mature ovulating females with larger yellow ovarian follicles and GSI as described above and uteri empty or partially filled with recently ovulated eggs; and (4) pregnant females carrying near term embryos, with gonads and ovarian follicles comparable to those observed in juvenile females.

Discussion

The seasonal fluctuation of CPUE complements the pattern observed off southern Brazil. The highest CPUEs in Anegada Bay are from October to December. At this time, school sharks disappear from south Brazilian waters (Peres & Vooren 1991). In early October and April, CPUEs in Anegada Bay are low and catches are composed mainly of males. Pregnant and ovulating females arrive in Anegada Bay by mid October and leave

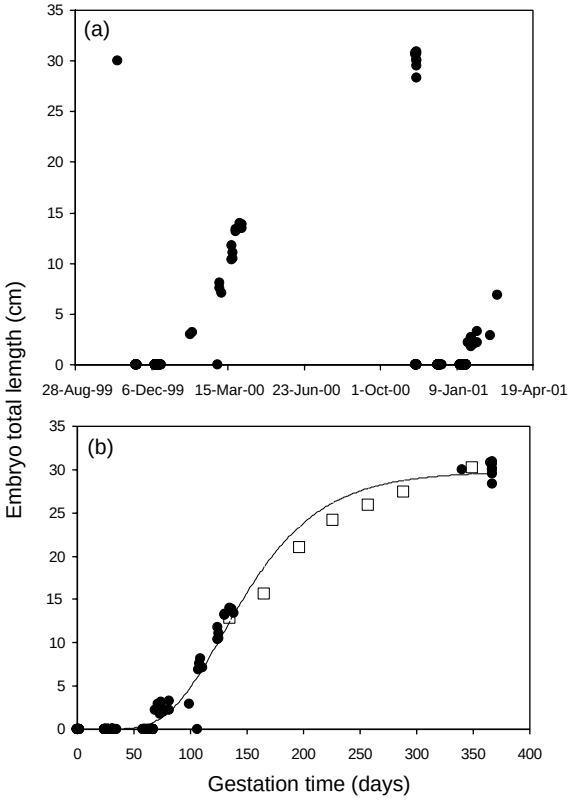

Figure 10. Embryonic growth of school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina. a – Embryo size as a function of date. b – Growth of embryos. The squares are data from southern Brazil (n = 7, taken from Peres & Vooren 1991). The line is a Gompertz curve fitted by maximum likelihood procedures (n = 188).

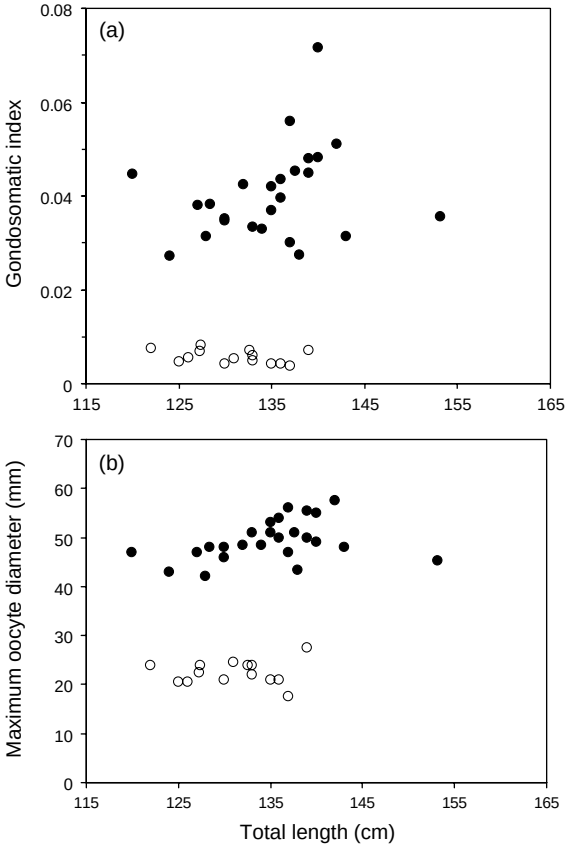

Figure 11. Relationships of total length with a – gonadosomatic index and b – maximum oocyte diameter for adult non-pregnant female school sharks, *Galeorhinus galeus*, from Anegada Bay, Argentina. Filled circles are pre-ovulatory females, and empty circles are females with oocytes at midterm (n = 39).

the area by late March. Pregnant females are found from March to September in southern Brazilian waters (Ferreira & Vooren 1991, Peres & Vooren 1991). This concordance in temporal patterns between Brazilian and Argentinean waters argues for seasonal movements between both areas. Previous studies are in accord with this proposed temporal pattern. In August and September both juvenile males and juvenile females (though not pregnant females) were present on the inner shelf between 39° and 42°S (Menni 1985). Off Mar del Plata (38°S, Argentina) juvenile males occurred from January to April and juvenile females occurred from January to June (Menni et al. 1986). Also, only males were present in coastal Uruguayan waters during winter months (De Buen 1950). This suggests that females spend the coldest months offshore (Ferreira & Vooren 1991, Peres & Vooren 1991), while males and juveniles stay in coastal waters (De Buen 1950, Menni 1985, Menni et al. 1986, this study). This migratory pattern with females arriving in coastal nursery areas in the summer and spending the winter in deeper shelf waters, and males and juveniles spending the winter in coastal waters appears to be generalized among the different populations of school sharks around the globe (Walker 1999).

The school shark is sensitive to temperature fluctuations. West & Stevens (2001) showed that school sharks from southern Australia move within a temperature range of about 5°C. Highest water temperatures off Anegada Bay (16–17°C) are recorded from January to March, whereas in October and November water temperature is

12–13 °C (Martos & Piccolo 1988). The low numbers of school sharks caught from January to March in Anegada Bay could be a result of movements to slightly offshore waters as coastal waters warm. Our samples were mostly taken in waters 5–10 m depth and thus high temperature could explain the low CPUE from January through March.

The estimate of size at 50% maturity for females agrees with previous estimates for southwest Atlantic school sharks (Peres & Vooren 1991, Chiaramonte 2000). The maximum length we observed was less than maximum lengths reported for school sharks from the northeast Pacific (Roedel & Ripley 1950, Hart 1988), the southern Mediterranean (Capapé & Mellinger 1988), and southern Australia (Last & Stevens 1994). These observations confirm observations from the literature reviewed by Walker (1999) who observed the same pattern. Geographic variation in size at maturity and maximum size is common in sharks (Menni 1985, Bonfil et al. 1993, Taniuchi et al. 1993, Lucifora et al. 1998), which reflects the plasticity of these traits.

It is common that shark fecundity varies depending on female size (Olsen 1984, Capapé & Mellinger 1988, Peres & Vooren 1991, Chiaramonte 2000). On average, southwest Atlantic females have higher fertilities than Australian females. Beyond the maximum size attained by southwest Atlantic school sharks (>155 cm TL), females from southern Australia have fertilities similar to maximum fertilities of southwest Atlantic females. Despite differences in maximum size, average maximum fertilities are approximately equal in southern Australia and the southwest Atlantic, as a result of a lower average fecundity of Australian school sharks.

Although fertility was lower than fecundity, the difference was constant throughout the size range of adult females. This implies that larger females lose a smaller proportion of their fecundity than do smaller females. For example, a precocious 120 cm TL female will lose, on average, 4.6% of its litter whereas a 140 cm TL female will lose only 2.7%. This could be a factor selecting for a delayed maturity in addition to the increase of litter size in absolute numbers.

If the female reproductive cycle were asynchronous among individuals, a gradient in ovarian follicle size should be observed at any time. However, mature non-pregnant females are clearly divided into two groups and a gradient is not observed in ovarian follicle size and gonadosomatic index (Figure 11). This supports the proposed 3-year long reproductive cycle for female school sharks from southern Brazil (Peres & Vooren 1991). In contrast, Capapé & Mellinger (1988) reported an annual reproductive cycle for female school sharks from the southern Mediterranean, and Olsen (1984) reported a 2-year cycle for females from southern Australia. This variation could be due to population differences. However, Peres & Vooren (1991) suggested that gestation in southern Australian school sharks could last 12 months instead of 6 months, which would result in a 3-year long reproductive cycle, like in southwest Atlantic school sharks.

The occurrence of females carrying near term embryos in Anegada Bay suggests that parturition occurs in Argentinean waters during late spring-summer. However, no neonate school sharks are caught in Anegada Bay. In October and November a gill-net fishery for narrownose smoothhound sharks, *Mustelus schmitti*, where neonate school sharks might be caught, occurs in the study area. However, no neonate school sharks have been caught in this fishery (L.O. Lucifora, personal observations). In addition, the monitoring of catches of boats that target small species (e.g., *M. schmitti*) has not detected the presence of school shark neonates. Large numbers of school sharks congregate in northern Patagonian closed gulfs and bays during summer and, perhaps, nursery grounds are located there.

Post-natal growth in elasmobranchs is usually best described by the von Bertalanffy growth model (Hoenig & Gruber 1990). Indeed, all growth studies of school sharks have fit a von Bertalanffy model (Olsen 1984, Ferreira & Vooren 1991, Moulton et al. 1992, Francis & Mulligan 1998). In contrast, the pattern of embryonic development appears to be more variable. Linear growth was suggested for embryos of the blue shark, *Prionace glauca* (Pratt 1979); a von Bertalanffy-like growth pattern for embryos of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Parsons 1983, Castro & Wourms 1993) and the blacktip shark, *Carcharhinus limbatus* (Castro 1996); and a sigmoidal Gompertz-like pattern for embryos of the

finetooth shark, *Carcharhinus isodon* (Castro 1993). The data on school shark embryonic growth presented here fit a Gompertz curve (Figure 10b). A substantial part of the embryonic development is allocated to tissue, organ and systemic differentiation, while most post-natal development is somatic growth and reproductive activity. Clearly, these differences may account for the differences between embryonic and post-natal growth of the school and other sharks.

The pattern of embryonic growth is characterized by a phase of fast growth until reaching an inflexion point, and a slow growth phase after the inflexion point. In summer and autumn (December–May) surface water temperature off Anegada Bay is 16–17°C (Martos & Piccolo 1988). Remarkably, the inflexion point is located at about 140–150 days of gestation (April), when autumn begins, water temperature decreases, and pregnant females move to south Brazilian shelf waters. Furthermore, once off Brazil school sharks spend the coldest months in waters of the outer shelf at 11–15°C (Ferreira & Vooren 1991). This change in temperature could explain, at least in part, the decrease in embryonic growth rate.

Results presented here suggest that school sharks from Argentina migrate seasonally possibly comprising a single population with individuals from Brazil and Uruguay. Then, we recommend common management policies among Brazil, Uruguay and Argentina. Experimental tagging, age and growth studies off Argentina, and population dynamics studies should be carried out in the near future for validating the hypotheses presented here and improving the knowledge and management of this school shark population.

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