Reproduction of the angular angel shark (*Squatina guggenheim*): geographic differences, reproductive cycle, and sexual dimorphism

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The reproductive ecology of *Squatina guggenheim* from two coastal areas in South America is analysed. In both sexes, individuals from ER (El Rincón coastal system, the more southern area) attained a larger maximum total length (L_T) and a heavier weight at a given length than those from LP (La Plata River estuary). Females from ER mature at a significantly larger L_T than females from LP. These patterns could be explained by an advantage of larger body size at higher latitudes in providing more reserves for winter, because individuals from ER have a larger liver than those from LP. Spines in the outer part of the pectoral fins were observed only in adult males. Fecundity increased with female total length. Females have a 3-y reproductive cycle, consisting of 10–12 months of gestation and 2 y of oocyte maturation. The embryonic growth fits the Gompertz model. Birth is in November or December, as inferred from embryo size and the presence of neonates and young of the year. Densities of *S. guggenheim* in LP peaked in spring and summer along the Uruguayan coast, suggesting a seasonal movement perpendicular to the shore. The reproductive pattern found suggests a population with low productivity.

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Introduction

Angel sharks (Squatiniformes) are benthic elasmobranchs that inhabit shelf and upper slope environments in temperate and tropical regions of the world (Compagno, 1984). Like other benthic elasmobranchs, they tend to have low dispersal capability (Standora and Nelson, 1977), which usually results in specimens from nearby areas having almost no mixing (Gaida, 1997). As this restricted mixing may produce different life history parameters, it is of value to study possible life history differences within angel shark species, even at small geographic scales.

Four species of angel shark occur along the Atlantic coast of South America: *Squatina dumeril* (Gadig *et al.*, 1999), *S. argentina*, *S. guggenheim*, and *S. occulta* (Vooren and da Silva, 1991; Cousseau and Figueroa, 2001; Milessi *et al.*, 2001). The angular angel shark *S. guggenheim* has a wide geographic distribution from Espírito Santo (~23°S, Brazil) to central Patagonia (~45°S, Argentina; Vooren and da Silva, 1991; Sunyé and Vooren, 1997), in waters 10–80 m deep (Cousseau and Figueroa, 2001). There is some information on the reproductive biology of *S. guggenheim*. Both sexes attain sexual maturity at ~700–800 mm total length (L_T; Cousseau, 1973; Sunyé and Vooren, 1997), and females attain larger size than males (Cousseau, 1973). Only the left ovary is functional, birth size is about 250 mm L_T, and gestation lasts 10–12 months (Cousseau, 1973; Sunyé and Vooren, 1997), with uterine and cloacal phases (Sunyé and Vooren, 1997). However,

other important reproductive parameters that may potentially influence the population dynamics, such as reproductive cycle duration, litter size variation, and spatio-temporal location of nursery areas, are mostly unknown.

Here we analyse the reproductive ecology of *S. guggenheim* in two nearby coastal ecosystems off temperate South America. We quantify fecundity and the duration of the reproductive cycle, describe sexual dimorphism and embryonic growth, and determine the birth season and the distribution of newborn pups.

Material and methods
Taxonomic nomenclature

The taxonomic nomenclature of Vooren and da Silva (1991) is followed throughout. However, it should be noted that Soto (2001) correctly stated that the name *S. guggenheim* Marini, 1936 is a senior synonym of *S. occulta* Vooren and da Silva, 1991. Therefore, Soto (2001) suggested that the name for the species here and elsewhere referred to as *S. guggenheim* should be *S. punctata* Marini, 1936. However, Marini (1936) gives only a picture of an angel shark named *S. punctata* and does not include any description of the species, which makes *S. punctata* a *nomen nudum*. Pending clarification and in order to avoid further confusion, we follow Vooren and da Silva (1991) in their classification of the angel sharks of the southwest Atlantic.

Sampling and study area

Sharks were collected from ten bottom-trawl research cruises conducted between March 2000 and December 2003. Two coastal areas off eastern South America, whose core areas are separated by $\sim$750 km, were sampled: the La Plata River estuary and adjacent marine waters (LP), and the coastal system of El Rincón (ER; Figure 1).

The LP area is characterized by vertical stratification in salinity, which can vary from 15 to 30 depending on wind force and freshwater discharge (Jaureguizar et al., 2003). Mean bottom water temperature is 20°C during the period December–March (spring and summer) and 10–12°C during the months June–September (winter). In each period, estuarine waters are almost fully thermally homogeneous both vertically and horizontally (Guerrero et al., 1997).

The ER coastal system is influenced by the discharges of the Colorado and Negro Rivers. The system is vertically homogeneous owing to tidal stirring and wind mixing (Guerrero, 1998). Low salinities ($<$30–33) are restricted to a narrow strip near the coast between the mouth of the Negro River and Blanca Bay (Guerrero, 1998). Water temperatures are lower than in LP. Bottom temperatures are 13–15°C during the months November–March (Guerrero, 1998), and $<$10°C from July to September (Jaureguizar, 2004).

Trawls lasted 15 min at a speed of 4 knots. The net had a stretched mesh size of 120 mm. The month and number of angular angel sharks collected during each research cruise for each area was LP: March 2000 (4), July 2001 (15), November 2001 (28), February 2002 (7), August 2002 (33), April 2003 (36), May 2003 (80); ER: November 2000 (14), March 2002 (47); LP/ER: December 2003 (85).

In all, 352 specimens (157 males and 195 females) were collected and examined, 233 (105 males and 128 females) from LP, and 119 (52 males and 67 females) from ER.

Size, size at maturity, and secondary sexual characters

All animals caught were frozen and subsequently thawed for analysis in the laboratory. The specimens were measured to the
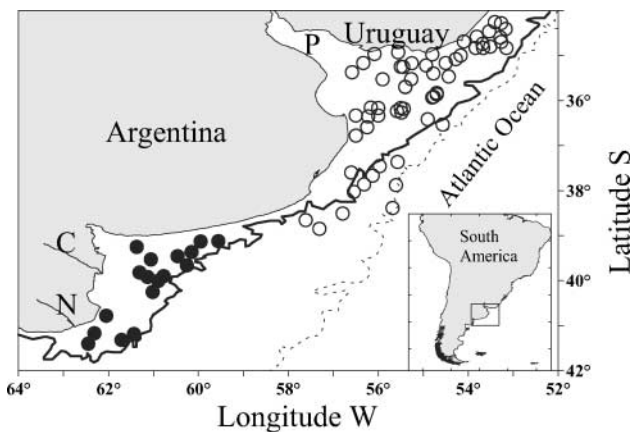

Figure 1. Map of the study area showing the two areas considered. The circles mark the localities where samples of angular angel sharks, *Squatina guggenheim*, were taken (empty circles: LP and Uruguayan coast; filled circles: ER). P, C, and N are the La Plata, Colorado, and Negro rivers, respectively. The solid and dashed lines are the 50 and 200 m isobaths, respectively. The inset shows the location of the study area in South America.

nearest millimetre for total length (L_T). Total weight (W_T), liver weight (W_L) and gonad weight (W_G) were recorded to the nearest gramme. For each geographic area, the relationship between L_T and W_T was calculated separately for each sex. Also, comparisons between the L_T–W_T relationships for the same sex from different areas were performed. The null hypothesis of no differences between slopes was tested using ANCOVA on ln-transformed variables. Comparisons of length (L_T) frequency distributions of adult (i.e. $>$700 mm L_T) angel sharks between areas were performed with the Kolmogorov-Smirnov test. The comparisons were carried out separately for each sex.

Sexual maturity in males was estimated from the size and condition of the clasper (elongation and calcification) and the development of testes and reproductive ducts. Males were divided into three reproductive stages: immature (short and non-calcified clasper, with testes not lobated and efferent ducts straight), maturing (long, calcifying claspers, gonads and ducts starting to lobate and coil, respectively), and mature (long fully calcified claspers with fully lobated testes and highly coiled ducts; Capapé et al., 2002). Clasper length was measured from the origin of the clasper at the cloaca to its tip.

Following Capapé et al. (1990), females were classified into three reproductive stages according to ovarian follicle size, and ovary and oviduct condition: juvenile, whitish ovaries, ovarian follicles $<$1 mm wide, membrane-like oviducts with inconspicuous oviducal glands; sub-adult, well-differentiated oviducts and primarily white, translucent ovarian follicles, but some beginning to accumulate yolk; adult, either gravid or with ovaries containing maturing ovarian follicles. Female size at maturity was estimated from the relationship between uteri width and L_T. In each geographic area, the proportion of mature fish in 20-mm intervals of L_T was calculated for both sexes.

A logistic ogive was fitted to the data using a maximum likelihood approach in order to estimate size at 50% maturity (L_{T50}) for both sexes. Differences in L_{T50} between both sexes in the same area and between the same sex in both areas were evaluated through a log-likelihood ratio test.

All animals were examined for secondary sexual characters associated with sexual maturation.

Reproductive condition and female reproductive cycle

To assess seasonal changes in body and reproductive condition, hepatosomatic (I_H) and gonadosomatic (I_G) indices were calculated as $I_H = W_L/W_T\ 100$, and $I_G = W_G/W_T\ 100$, respectively. Possible seasonal changes in I_H and I_G of females from LP were assessed through correlation analyses between those indices and month. In males from LP, seasonal differences in I_H and I_G were tested with ANOVA. The I_H of adult sharks of the same sex was compared between both areas using a Student's t-test. To avoid the effect of seasonal variation in I_H, comparisons were made only among fish caught during the same month, so only males caught during April and May (autumn) and females caught during December (late spring) were compared.

Different stages of the female reproductive cycle were identified on the basis of the size of ovarian follicles and the value of I_G in different months. The stages identified were tested with a canonical correlation analysis based on the Bray–Curtis distance (Anderson and Robinson, 2003). This analysis was performed on the variables L_T, W_T, W_G, maximum diameter of ovarian follicle, and number of embryos. All variables were fourth-root transformed. A permutation test (Anderson and Robinson, 2003) was

carried out to test the null hypothesis of no differences among the different stages identified.

Litter size, embryonic growth, birth season, and abundance

The number and the sex of the embryos in each litter were recorded. It was possible to estimate embryonic growth from LP. Three different models were fitted: the von Bertalanffy $[L_t = L_\infty (1 - \exp(-K (t - t_0)))]$, the Gompertz model $[L_t = L_\infty \exp(-K (t - t_0))]$, and the logistic model $[L_t = L_\infty/(1 + \exp(-K (t - t_0)))]$; where L_t is the total length (mm) at age t (in days) and L_∞, K, and t_0 are model parameters (reported $\pm$ s.e.). The model with the lowest Akaike's information criterion (AIC) was chosen as the best at describing the data (Maindonald and Braun, 2003).

Seasonal occurrence of neonates and young of the year in LP was investigated by mapping the presence of angular angel sharks <300 mm L_T in spring and summer (February 2000 and December 2003; 45 and 89 tows, respectively), autumn (May 2003; 27 tows), and winter (August 2002; 58 tows).

Densities of *S. guggenheim* (kg km^{-2}) were estimated separately for spring (November–December) and winter (July–August) in LP. Data from three research cruises carried out during November and December 1999 (100 tows), December 2003 (89 tows), and July and August 2002 (58 tows) were used. Densities were calculated by dividing the catch in a tow by the swept area. Swept area was calculated as the horizontal aperture of the net (measured with a Doppler sensor) multiplied by the swept distance, which was trawl speed (4 knots, corrected for current speed) multiplied by trawl duration (15 min).

Results

Size, size at maturity, and secondary sexual characters

The relationship between L_T and W_T was sexually dimorphic in LP (ANCOVA, $t = 3.22$, d.f. $= 240$, $p = 0.001$; Figure 2a) but not in ER ($t = 0.79$, d.f. $= 97$, $p = 0.429$; Figure 2b). Males from ER were significantly heavier at a given L_T than males from LP ($t = 2.17$, d.f. $= 148$, $p = 0.032$), but the L_T–W_T relationship of females did not differ significantly between areas ($t = 0.09$, d.f. $= 189$, $p = 0.926$).

Angular angel sharks of both sexes from ER attained a larger L_T than those from LP (Kolmogorov–Smirnov test for males, $D = 22.57$, $n = 81$, $p < 0.01$; for females, $D = 8.67$, $n = 57$, $p < 0.01$; Figure 3a and b, respectively).

In LP, the smallest adult female was 675 mm and the largest juvenile was 730 mm L_T (Figure 4a), whereas L_{T50} was calculated as 713.4 mm L_T (Figure 5a). Most adult females in LP had uterus widths ranging from 12 to 55 mm, and uterus width of gravid females ranged from 37.9 to 98 mm (Figure 4a).

In ER, the range between the smallest adult and the largest juvenile female was 720–794 mm L_T (Figure 4b), and L_{T50} was 770.1 mm L_T (Figure 5a). The uterus width of adult females from ER ranged from 6 to 47.5 mm, and was wider (68–86 mm) in gravid females (Figure 4b). The L_{T50} was significantly different between areas ($G = 5.397$, d.f. $= 1$, $p = 0.020$).

In LP, the smallest adult male was 683 mm L_T, and the largest juvenile was 750 mm (Figure 6a). Adolescent males with calcifying claspers were between 695 and 757 mm L_T (Figure 6a). Juvenile males had claspers up to 170 mm long, but most had claspers of <130 mm (Figure 7a). Adolescent male clasper lengths ranged
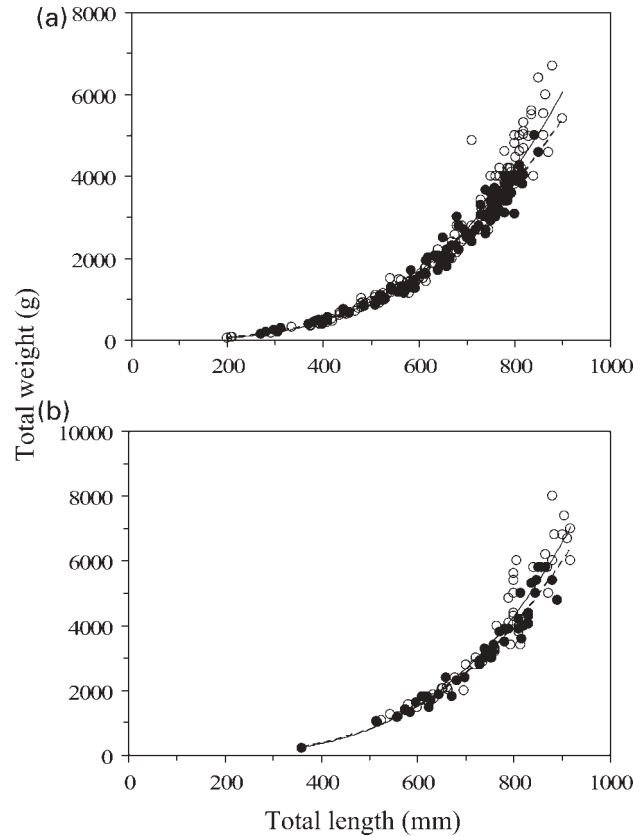

Figure 2. Relationship between total weight (g) and total length (mm) of angular angel sharks from (a) the LP and north Argentine and Uruguayan coast and (b) ER, Argentina. Empty circles and solid line, females; filled circles and dashed line, males.
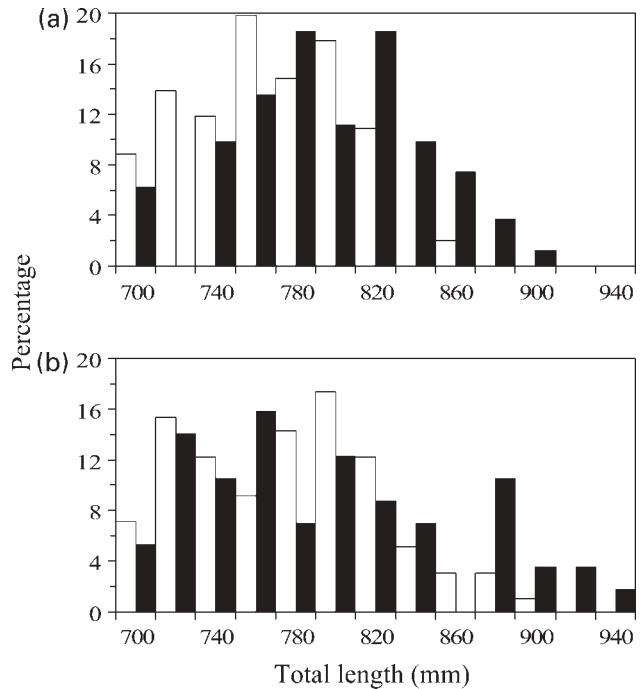

Figure 3. Length frequency distributions of (a) male ($n = 182$) and (b) female ($n = 155$) adult angular angel sharks. Empty bars, LP and north Argentine and Uruguayan coast; filled bars, ER, Argentina.
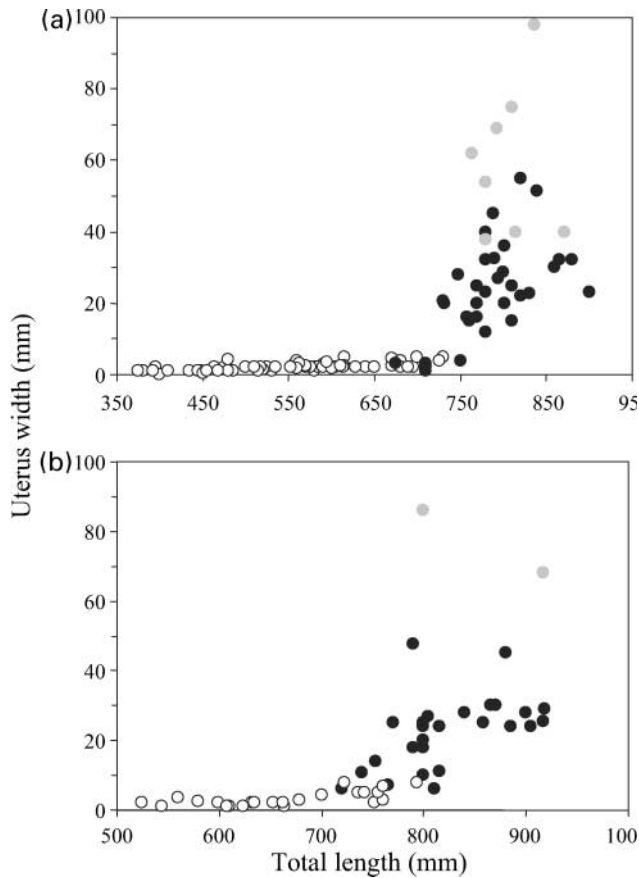
Figure 4. Relationship between uterus width (mm) and total length (mm) of female angular angel sharks from (a) the LP and north Argentine and Uruguayan coast and (b) ER, Argentina. Empty and black circles are juvenile and adult females, respectively; grey circles are pregnant females.

Figure 5. Proportion of mature individuals per 20 mm total length intervals of (a) female and (b) male angular angel sharks from the LP and north Argentine and Uruguayan coast (empty circles, thin line), and ER, Argentina (filled circles, bold line). Dashed lines mark the total length at which 50% of the animals are mature.

between 116 and 156 mm (Figure 6a). Most adult males had claspers longer than 140 mm and up to 260 mm (Figure 6a). All males with calcified claspers had developed efferent ducts and well developed testes. L_{T50} for males from LP was 724.5 mm L_T (Figure 5b), not significantly different from the L_{T50} of females from LP ($G = 0.399$, d.f. $= 1$, $p = 0.527$).

In ER, the smallest adult male was 758 mm, and the largest juvenile was 820 mm L_T (Figure 6b). Accordingly, two adolescent males with calcifying claspers measured 752 and 757 mm L_T (Figure 6b). Juvenile clasper lengths were up to 168 mm, and adult from 150 to 200 mm (Figure 6b). Claspers of adolescent males were 144 and 152 mm long (Figure 6b). The L_{T50} for males from ER was 750.0 mm L_T (Figure 5b), not significantly different either from males from LP ($G = 0.824$, d.f. $= 1$, $p = 0.364$) or from females from ER ($G = 0.638$, d.f. $= 1$, $p = 0.425$).

In adult males from both areas, there were small spines near the outermost tip of the pectoral fin dorsal surface. These spines were thin, erect, low, and inclined towards the shark's midline (Figure 7), and were absent in juvenile males, and in juvenile and adult females. In adolescent males, spines were present only on the fin edges, and there were fewer spines than in adult males. The spines formed a triangular patch, widening from the anterior to the posterior corner of the pectoral fins, but they were not arranged in rows.
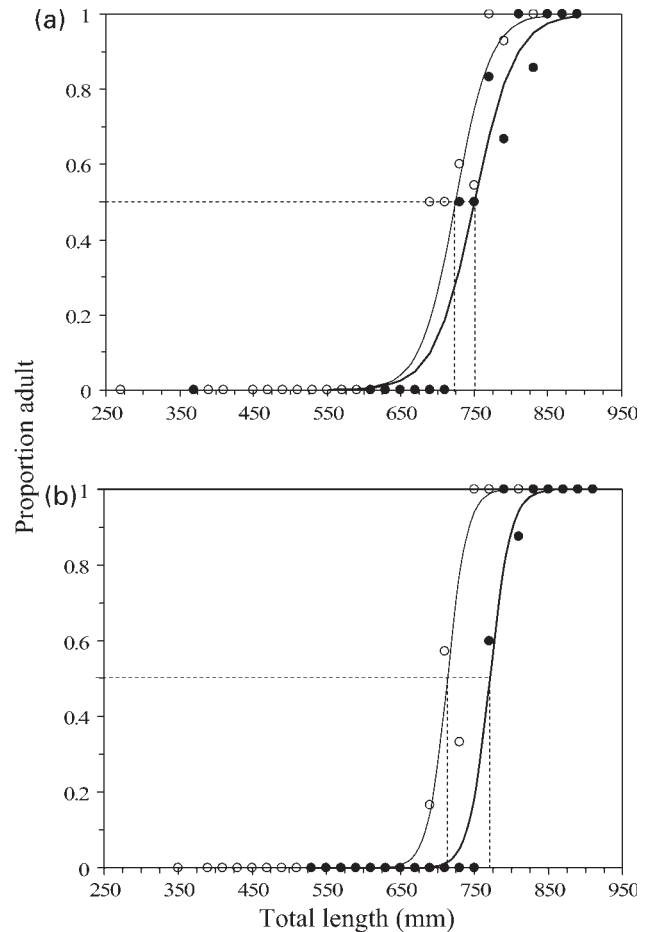
Reproductive condition and female reproductive cycle

In males from LP, both I_H ($F_{6,34} = 3.50$, $p = 0.008$; Figure 8a) and I_G ($F_{5,22} = 11.6$, $p = 1.4 \times 10^{-5}$; Figure 8b) showed similar significant changes through the year. In general, both indices peaked during summer (December, February, March) and were lowest during winter and spring (May–November).

Adult males and females from ER had significantly higher I_H than the same sex from LP ($I_H \pm$ s.d.: males$_{LP} = 2.74 \pm 0.68$, males$_{ER} = 3.89 \pm 0.71$, $t = 2.84$, d.f. $= 10$, $p = 0.018$; females$_{LP} = 3.24 \pm 0.75$, females$_{ER} = 4.32 \pm 0.66$, $t = 3.15$, d.f. $= 15$, $p = 0.007$).

Throughout the year, two types of adult non-pregnant females could be distinguished on the basis of I_G and the maximum diameter of ovarian follicles in LP (Figure 9). Of note is that the intercepts of both I_G ($t = 1.81$, d.f. $= 30$, $p = 0.04$) and the maximum diameter of ovarian follicles ($t = 4.12$, d.f. $= 40$, $p = 0.0001$) were significantly higher in one group than in the other. These two groups of adult non-pregnant females were correctly identified in the canonical correlation analysis conducted on L_T, W_G, I_G, maximum diameter of ovarian follicles and number of embryos, with the Bray–Curtis dissimilarity distance (Figure 10). The permutation test indicated that the two stages of
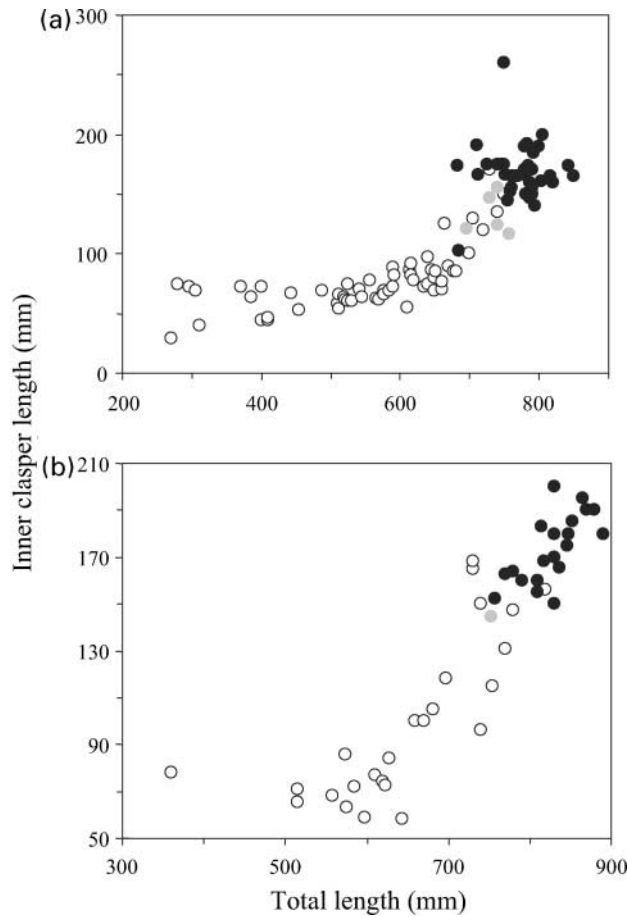
Figure 6. Relationship between clasper length (mm) and total length (mm) of male angular angel sharks from (a) the LP and north Argentine and Uruguayan coast and (b) ER, Argentina. Empty, grey, and black circles are juvenile, adolescent, and adult males, respectively.
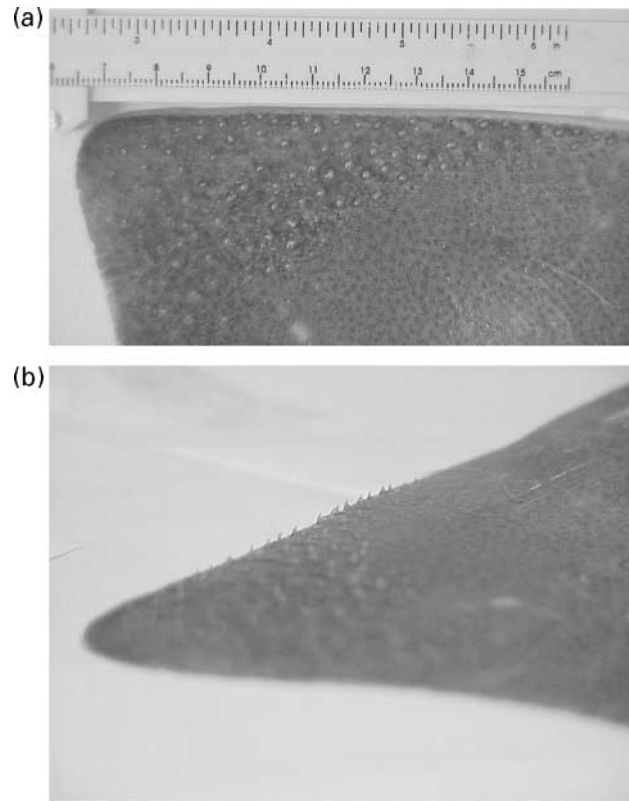

Figure 7. (a) Dorsal and (b) postero-dorsal view of the outer tip of the left pectoral fin of an adult male angular angel shark showing the patch of alar spines. Note the inward inclination of the spines in (b). The scale bar is in centimetres.

adult non-pregnant females plus the pregnant females are significantly different ($t_2 = 1.22$; 9999 permutations; $p = 0.0001$), and 60 out of 67 (89.6%) of the fish were correctly classified to stage. This pattern indicates that maturation of ovarian follicles lasts about 2 y, before ovulation and the beginning of gestation.

The I_H of both types of adult non-pregnant females and juvenile females increases significantly from February to December (adults with small ovarian follicles: Spearman's $r = 0.596$, $n = 19$, $t = 3.06$, $p = 0.007$; adults with large ovarian follicles: $r = 0.644$, $n = 12$, $t = 2.66$, $p = 0.024$; juveniles: Spearman's $r = 0.522$, $n = 79$, $t = 5.38$, $p < 0.001$; Figure 11). In contrast, the I_H of pregnant females did not show any significant seasonal trend ($r = 0.295$, $n = 13$, $t = 1.025$, $p = 0.327$; Figure 11). Adult non-pregnant females with large ovarian follicles and high I_G also had the highest I_H (Figure 11). The slope and the intercept of the regression line for this group were significantly higher than those of adult non-pregnant females with small ovarian follicles and low I_G (slope: $t = 4.68$, d.f. = 27, $p < 0.001$; intercept: $t = 3.51$, d.f. = 28, $p = 0.001$), and the slope was significantly steeper than that of juveniles ($t = 5.70$, d.f. = 87, $p < 0.001$). In contrast, adult non-pregnant females with small ovarian follicles and low I_G had I_H indistinguishable from those of juvenile females (slope: $t = 1.20$, d.f. = 94, $p = 0.233$; intercept: $t = 0.918$, d.f. = 95, $p = 0.361$).

Litter size, embryonic growth, birth season, and abundance

Fecundity ranged from two to eight embryos per female (mean = 4.07) and was significantly and positively correlated with L_T (slope = 0.046, intercept = −32.6, $r = 0.804$, $n = 12$, $t = 4.29$, $p = 0.001$; Figure 12a). Five females (L_T 730, 770, 790, 840, and 820 mm, caught on 4, 11, 19, 3, and 1 December, respectively) had a single capsule in each uterus containing three eggs. The maximum size of embryos within the uteri was 265 mm L_T, and the minimum size of free-living pups was 270 mm L_T.

The embryonic growth was best described by the Gompertz model, because it had the lowest AIC and the closest estimate of size at birth ($L_\infty = 257.4 \pm 11.7$, $K = 0.015 \pm 0.0016$, $t_0 = -11.6 \pm 4.5$, AIC = 158.5; Figure 12b). The logistic model had a poorer fit and underestimated the size at birth ($L_\infty = 245.4 \pm 10.7$, $K = 0.025 \pm 0.0023$, $t_0 = 135.2 \pm 5.7$, AIC = 164.5). The von Bertalanffy model had the worst fit and overestimated size at birth ($L_\infty = 437.0 \pm 118.8$, $K = 0.003 \pm 0.001$, $t_0 = -13.6 \pm 6.6$, AIC = 183.8). Given that ovulating females were found in December and that the largest embryos and the smallest free-swimming pups were found also in December, gestation lasts about 12 months.

The time of occurrence of the largest embryos coincides with the first appearance of fish <300 mm L_T in LP (Figure 13a), indicating that the birth season is in spring or early summer. Some neonates and young of the year were recorded in autumn, but they were absent in winter (Figure 13b and c). The
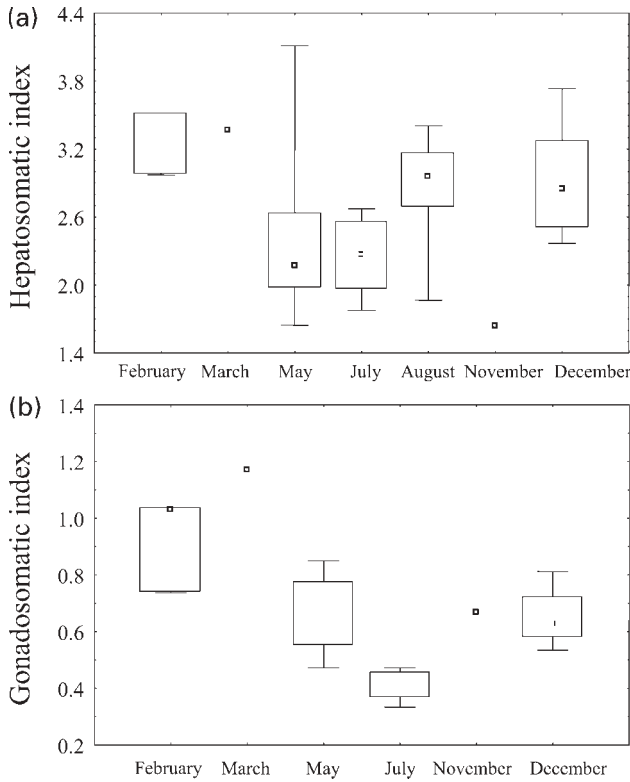
Figure 8. Monthly variation in the (a) hepatosomatic and (b) gonadosomatic indices of male angular angel sharks. For each month, the dot represents the median, the box marks the 25th and 75th percentiles, and the whiskers mark the minimum and maximum values. Sample sizes were: (a) February (3), March (1), May (15), July (7), August (10), November (1), December (4); (b) February (3), March (1), May (15), July (7), November (1), December (4).

abundance of *S. guggenheim* in LP was higher during spring and summer than during winter (Figure 14), suggesting some seasonal bathymetric displacements possibly associated with parturition.

Discussion

Geographic variation in size and size at maturity

Our results show that both sexes attain a larger maximum size, and that female angular angel sharks mature at a larger size in ER than in LP. Additionally, for a particular L_T, they are heavier in ER than in LP. This latitudinal increase in body size has been reported for other sharks (e.g. Leloup and Olivereau, 1951; Taniuchi *et al.*, 1993; Horie and Tanaka, 2002). One of the hypotheses that may explain this pattern in ectotherms is that a larger body size in higher latitudes might allow an individual to have more energy stored for the season of low resource availability (Blackburn *et al.*, 1999). Cartilaginous fish store energy as lipids in the liver (Craik, 1978). In *S. guggenheim*, both sexes have a larger I_H in ER than in LP, suggesting an advantage in the storage of energy for fish from ER. This is one of the most common explanations of latitudinal variation in body size, and has been found to be true for several animal groups (Blackburn *et al.*, 1999). More variation in body size is expected given that *S. guggenheim* ranges farther north and south than LP and ER, respectively. This is supported by the latitudinal increase in size at maturity from 720 mm L_T (Vooren and
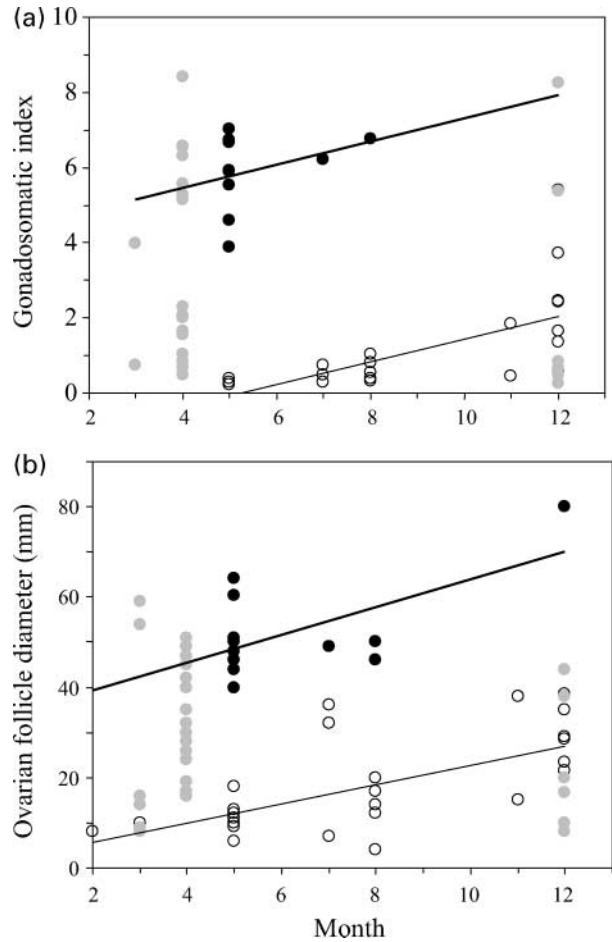

Figure 9. Monthly variation in (a) gonadosomatic index and (b) maximum diameter of ovarian follicle (mm) in adult non-pregnant female angular angel sharks. The empty circles and thin line are females in the first year of the ovarian cycle, the black circles and bold line are females in the second year of the ovarian cycle. Grey circles are females from the ER Argentina.
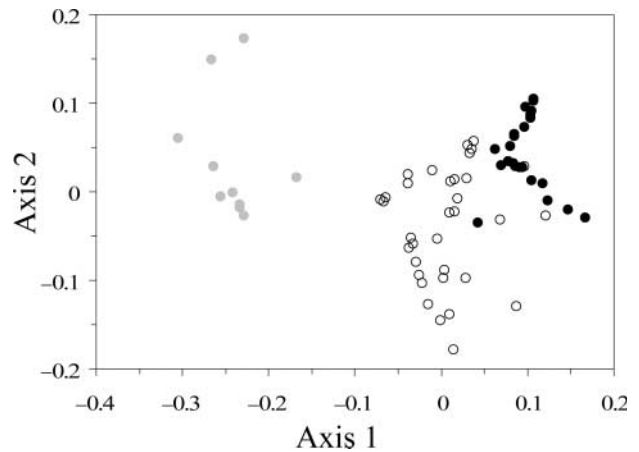

Figure 10. Plot of the first two canonical axes of a canonical correlation analysis based on the Bray–Curtis dissimilarity measure on four variables for three reproductive stages of the angular angel shark. Empty circles, adult females in the first year of oocyte maturation; black circles, adult females in the second year of oocyte maturation; grey circles, pregnant females.
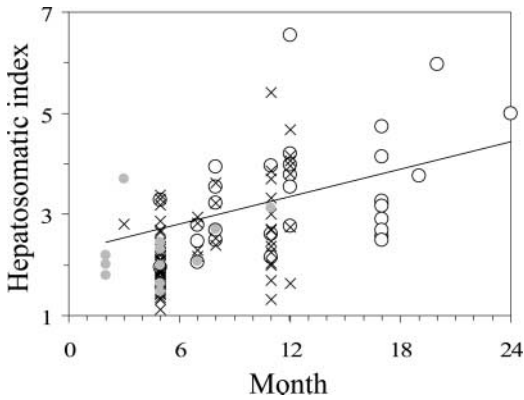
Figure 11. Monthly variation in hepatosomatic index in adult female angular angel sharks. The empty circles and line are adult non-pregnant females, grey circles are pregnant females, and crosses are juvenile females.
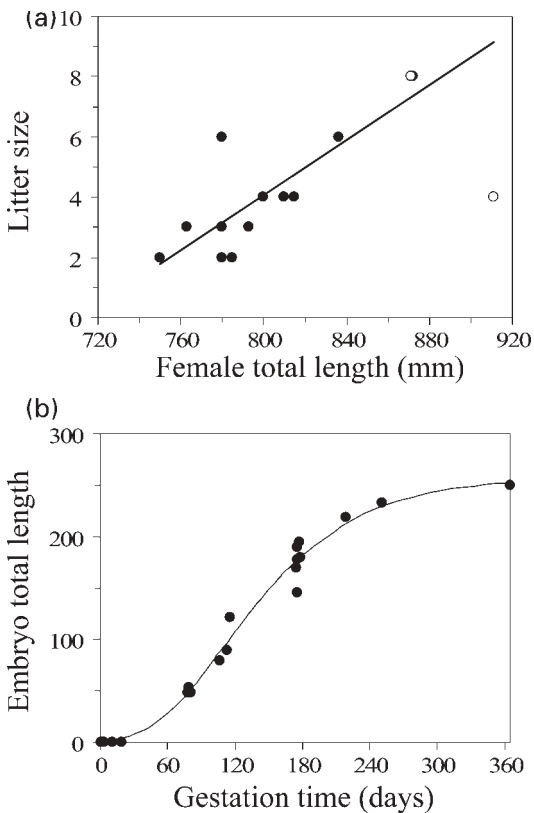

Figure 12. (a) Relationship between litter size and female total length (mm) of angular angel sharks from the LP and north Argentine and Uruguayan coast (filled circles and line). The empty circles are fish from the ER, Argentina. (b) Embryonic growth (in mm) of *S. guggenheim* from the LP and north Argentine and Uruguayan coast. The line is a Gompertz growth model fitted to the data.

Klippel, 2005) in southern Brazil ($\sim$31°S) to 750 mm L_T (Awruch, 2000) in the San Matías Gulf ($\sim$42°S).

The L_T–W_T relationship of *S. guggenheim* is sexually dimorphic in LP, but not in ER. Angel sharks appear to be variable in this respect, because species with (smoothback angel shark *S. oculata*; Capapé *et al.*, 2002) and without (ornate angel shark
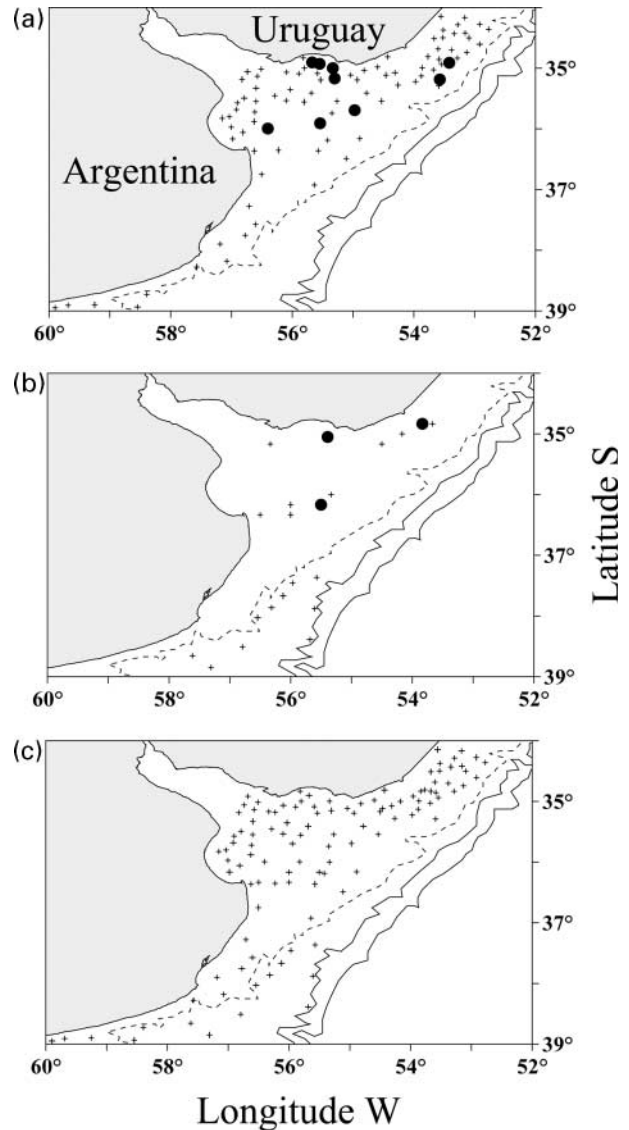

Figure 13. Distribution of neonates and young-of-the-year (fish <300 mm total length) angular angel sharks (*S. guggenheim*) from the LP and north Argentine and Uruguayan coast during (a) spring and summer (December and February), (b) autumn (May), and (c) winter (August). Crosses are positions where samples were taken but no neonates or young of the year were obtained, dots indicate presence of neonates and/or young of the year. The 50, 100, and 200 m isobaths are shown.

S. tergocellata, Bridge *et al.*, 1998; sawback angel shark *S. aculeata*, Capapé *et al.*, 2005) sexually dimorphic L_T–W_T relationships have been reported. Body size is more sexually dimorphic in LP, suggesting that a selective pressure common to both sexes is selecting for large body size in both sexes in ER.

Spines as a secondary sexual character

Adult males are characterized by the presence of a patch of small spines near the tip of the pectoral fins (Figure 7). This is clearly a sexually dimorphic trait, because neither juvenile males nor juvenile and adult females have such spines. This pattern is strikingly similar to the alar thorns of skates (Rajidae). Alar thorns are a
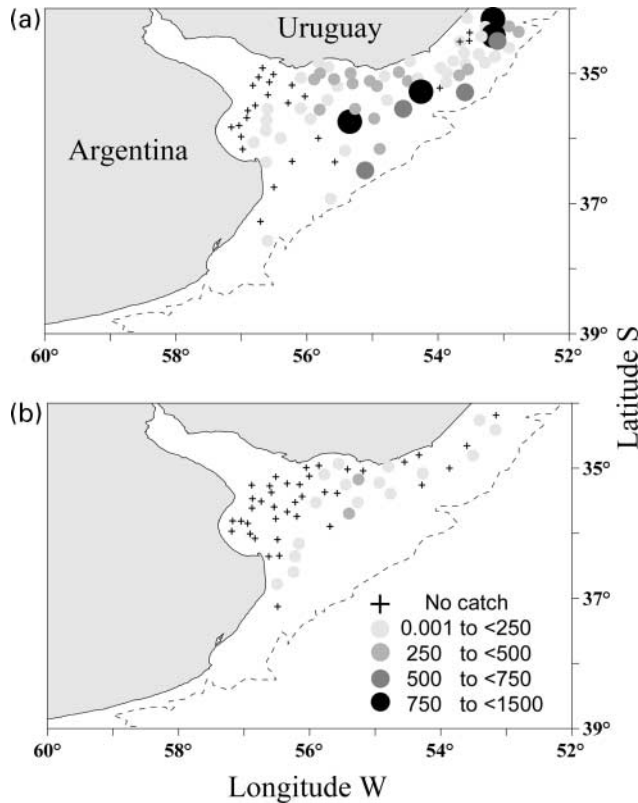
Figure 14. Density (kg km^{-2}) of angular angel sharks during (a) spring (November and December) and (b) winter (July and August). The dashed line is the 50 m isobath.

synapomorphy of the family Rajidae (McEachran and Dunn, 1998), and are employed by the male to retain its position during copulation (Luer and Gilbert, 1985). The copulatory behaviour of angel sharks is unknown, but given that the thorns of males are similar in appearance, size, and location to the alar thorns of skates, they may well play a role in reproduction/copulation of angel sharks. The occurrence of these spines has been mentioned as present in the sand devil *S. dumeril* (Bigelow and Schroeder, 1948) and in an undescribed species of angel shark from the Gulf of California (Michael, 1993). Vooren and Klippel (2005) state that they are present in males, being a general characteristic of angel sharks. This suggests that spine occurrence might be widespread within the order Squatiniformes.

Despite the resemblance of the pectoral fin spines to skate alar thorns in location and sexual dimorphism, they are different in form and arrangement from skate's alar thorns (e.g. they are not arranged in parallel rows or in grooves; McEachran and Konstantinou, 1996).

Reproductive condition and female reproductive cycle

Males have the highest I_G and I_H in summer, suggesting that energy stored in the liver is not used for production of sperm, given that both indices peak at the same time. The mating season could not be established, but the increase in male I_G during summer may be indicative of the mating season. In contrast, Cousseau (1973) suggested that males might produce sperm continuously. Natanson and Cailliet (1986) also suggested that male Pacific angel sharks *S. californica* might be able to mate

throughout the year. Further research using more reliable indicators of mating activity is required to define the mating season of *S. guggenheim*.

Three reproductive stages were observed in adult females: (1) adult, not pregnant females, with low I_G and small ovarian follicles; (2) adult, not pregnant females, with high I_G and large ovarian follicles; and (3) pregnant females. The simultaneous occurrence of females in stages 1 and 2 indicates that the maturation of the oocytes takes 2 y (Figure 9), and implies that the female reproductive cycle is triennial, as suggested by Vooren and Klippel (2005). Other angel sharks have reproductive cycles of 2 y (*S. oculata*, *S. squatina*, *S. aculeate*, Capapé *et al.*, 1990, 2002, 2005, respectively; *S. tergocellata*, Bridge *et al.*, 1998) and possibly 4 or 5 y (*S. occulta*, Vooren and Klippel, 2005). *S. californica* is thought to have an annual reproductive cycle (Natanson and Cailliet, 1986; Cailliet *et al.*, 1992), but great variation in ovarian follicle diameter is apparent in adult females (Figure 2 of Natanson and Cailliet, 1986), which may be indicative of a longer reproductive cycle.

Multiannual reproductive cycles are common among elasmobranchs. Cycles three years long have been observed in just four other sharks: the school shark *Galeorhinus galeus* from the southwest Atlantic (Peres and Vooren, 1991; Lucifora *et al.*, 2004), the blacktip shark *Carcharhinus limbatus* from South Africa (Dudley and Cliff, 1993), the shortfin mako *Isurus oxyrinchus* (Mollet *et al.*, 2000), and the dusky shark *C. obscurus* (Dudley *et al.*, 2005). *S. guggenheim* shares the same pattern with *G. galeus* and *C. limbatus*: 2 y of oocyte maturation plus about 1 y of gestation. However, these species are neither closely related nor similar in reproductive mode, which indicates that the pattern must have evolved several times independently and is not dependent on reproductive mode. All sharks with 3-y reproductive cycles appear to be long-lived, so long reproductive cycles may be selected through extended iteroparity. The longevity of *S. guggenheim* (and other angel sharks) is unknown, but the only angel shark whose longevity has been estimated, *S. californica*, lives to at least 35 years (Cailliet *et al.*, 1992), suggesting that as a taxon, they may be long-lived. In the case of non-placental species (i.e. *S. guggenheim*, *G. galeus*, and *I. oxyrinchus*), the long period of oocyte maturation may allow production of larger or richer oocytes that will nourish larger or stronger offspring.

Adult females at stage 2 have the largest liver of females of the species, indicating that the liver has its maximum size at ovulation and, as indicated by the low I_H of pregnant females, that it decreases in size as pregnancy proceeds. This cannot be explained by embryonic nourishment by the mother, because angel shark embryos are thought to be exclusively lecithotrophic (Capapé *et al.*, 1990, 2002, 2005). On the other hand, the peak in I_H is concurrent with vitellogenesis, and is most likely due to the production of large amounts of vitellogenin by the liver.

Litter size, embryonic growth, birth season, and abundance

The increase in fecundity with size explains the larger maximum size of females. Such an increase in fecundity with female size is common in elasmobranchs, but among angel sharks, it has previously been observed in just one species (Capapé *et al.*, 2005). However, female angel sharks commonly attain larger size than males (Capapé *et al.*, 1990, 2002; Bridge *et al.*, 1998), suggesting that females gain some advantage from being larger.

The estimate of the gestation time (10–12 months) is consistent with previous estimates (Cousseau, 1973; Sunyé and Vooren, 1997). The embryonic growth of elasmobranchs has been described as linear (blue shark *Prionace glauca*; Pratt, 1979), von Bertalanffy-like (Atlantic sharpnose shark *Rhizoprionodon terraenovae*; Parsons, 1983, and Castro and Wourms, 1993; blacktip shark *C. limbatus*, Castro, 1996), and sigmoid Gompertz-like (finetooth shark *C. isodon*; Castro, 1993; *G. galeus*; Lucifora et al., 2004). The embryonic growth of *S. guggenheim* fits a Gompertz model. The birth size estimated by the Gompertz model was consistent with the observed smallest sizes and with previous estimates of birth size (∼250 mm L_T; Cousseau, 1973; Sunyé and Vooren, 1997). The poor fit of the von Bertalanffy model was due to the non-sigmoid pattern of that model. We suggest that, as in other animals (Robbins and Robbins, 1979), the embryonic growth of elasmobranchs generally fits a sigmoid pattern, best described by the Gompertz or logistic models. It is likely that the non-sigmoid patterns found in some species are a result of the scarcity of embryos caught at very early stages of development.

The presence of term embryos as well as neonates supports a parturition season in spring and early summer. This is consistent with information on this and other angel sharks in which neonates are found during spring and summer (Natanson and Cailliet, 1986; Sunyé and Vooren, 1997; Bridge et al., 1998; Capapé et al., 2002).

In coastal LP waters, angel sharks are more abundant in spring and especially along the Uruguayan coast (Figure 14). In winter, abundance is much lower. High spring densities along the Uruguayan coast may be related to the presence of water of higher salinity there than in other parts of the LP during that season, as the flow of the La Plata River changes seasonally discharging freshwater along the Uruguayan coast during winter and along the Argentine coast in spring and summer (Guerrero et al., 1997). This hypothesis is supported by the absence of *S. guggenheim* in low salinity areas of the La Plata River (Jaureguizar et al., 2004).

A reproductive cycle of 3 y translates into a mean annual fecundity of only 0.67–2.33. This extremely low fecundity may result in a population with low productivity (Cousseau, 1973), and could be the cause of the steep decline (85% in 12 y) in abundance of *S. guggenheim* caused by fisheries of the southwest Atlantic (Miranda and Vooren, 2003). The pattern might be common to other angel sharks, because other species have suffered great declines in many regions (Rogers and Ellis, 2000; Vacchi et al., 2000; Graham et al., 2001).

It is clear that populations of *S. guggenheim* and other angel sharks must be monitored closely, and that the level of human-induced mortality needs to be kept very low in order to avoid further decline and to conserve the species.

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