Reproductive biology and seasonal distribution of *Mustelus schmitti* (Elasmobranchii: Triakidae) in the Rio de la Plata oceanic front, south-western Atlantic

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The population structure and reproductive biology of *Mustelus schmitti* was analysed during autumn (1994, 1995) and spring (1994) in the Rio de la Plata oceanic front. The samples consisted mainly of adult males and immature females, indicating that nursery areas are situated elsewhere. In autumn, the highest female densities occurred between 36°S and 35°S, with densities decreasing further south, and high male densities occurred over all latitudes of the study area. In spring, both sexes occurred north of latitude 36°30′S. Males attained maturity at 59 cm total length (TL), and females at 72 cm TL. Litter size varied from one to ten in spring and two to nine in autumn, with embryos ranging from 9 to 26 cm and 7 to 26 cm TL respectively. The mean TL of embryos was significantly higher in spring (22 cm), suggesting that parturition occurs in late spring and summer. Litter size was found to increase with female TL.

INTRODUCTION

The Patagonian smoothhound *Mustelus schmitti* Springer 1939, (Chondrichthyes: Elasmobranchii: Triakidae) locally known as 'gatuzo', is an endemic shark in the coastal waters of the south-western Atlantic, occurring from southern Patagonia (47°45′S) (Chiaramonte & Pettovello, 2000) to Rio de Janeiro, Brazil (22°27′S) (Figueiredo, 1977), and inhabiting coastal waters and down to 140 m depth (Figueiredo, 1977; Vooren, 1997). Three species of *Mustelus* occur in the area, *Mustelus canis*, *M. fasciatus* and *M. schmitti*, the latter being exploited extensively in industrial and artisanal fisheries off Argentina, Uruguay and southern Brazil (Cousseau, 1986; Vooren, 1997; Chiaramonte, 1998; Miranda & Vooren, 2003; Paesch & Domingo, 2003).

In spite of its commercial importance, our knowledge of its life history and population structure is limited (Cousseau, 1986; Chiaramonte & Pettovello, 2000), except with regard to reproduction (Menni, 1986; Souto, 1986). The length distribution in coastal waters (depth < 50 m) indicates that larger specimens are found in deeper waters and that mean length increases southward (Cousseau, 1986). A major concentration of *M. schmitti* off southern Patagonia, with a particular population structure, was described by Chiaramonte & Pettovello (2000).

Managing shark resources requires a good knowledge of spatial distribution and population structure, including the reproductive season and the size-at-first-maturity as basic parameters, to support management measures (Mollet et al., 2000). In southern Brazil the catches occur principally in winter (Vooren, 1997; Miranda & Vooren, 2003), while in Uruguayan waters the highest catches take place in summer and autumn (Paesch & Domingo, 2003). These differences in the seasonal catches in the region are likely a consequence of the migratory behaviour of *M. schmitti*.

In this work we analysed the spatial population structure in autumn and spring with regard to depth and latitude in the Rio de la Plata oceanic front (south-western Atlantic). Various aspects of the reproductive biology of *M. schmitti* are presented and the hypothesis about seasonal migrations of the species between Argentinean, Uruguayan and Brazilian waters is discussed.

MATERIALS AND METHODS

Data for assessing the population structure and spatial distribution of *Mustelus schmitti* were obtained during three bottom trawl research cruises carried out in autumn 1994 and 1995 and spring 1994 on board the RV 'Aldebarán' (operated by DINARA, Uruguay). These surveys are designed for the assessment of demersal fisheries resources in the ZCPAU (Argentinean–Uruguayan Common Fishing Zone, Figure 1, Table 1). At each sampling location, a 30 min tow was conducted at a towing speed of approximately 3 knots during daylight. A high-opening 'Engel' type net of 80 mm (stretched mesh) cod end was used. Trawl stations were selected using a stratified random sample design, which was defined by depth and latitude (Ehrhardt et al., 1977). Bottom temperature was recorded at each fishing station using a conductivity–temperature–depth (CTD) profiler (Seabird 19). Fresh specimens of *M. schmitti* were sampled on board immediately after each trawling station. Sex and total length (TL) to the nearest cm below the actual length aligned with body axis, was recorded and the relative frequency of TL (pooled

samples) by sex was calculated. As TL data were not normally distributed and did not have homogeneous variance, the differences between the length composition by sex for each cruise and between cruises were tested using Mann–Whitney and Kruskal–Wallis tests respectively (Sokal & Rohlf, 1998). The relationship between TL and depth by cruises was tested for significance. Using χ^2 (chi-square) tests (Sokal & Rohlf, 1998), we analysed whether the proportion of males:females (sex ratio) and immature:mature of sharks by trawl station were equal. According to the results of the test, the spatial distribution and abundance (density, expressed as individuals per n.m.^{2}) of females/males and immature/mature sharks by sex was plotted. Density was calculated as C/A where, C=capture of individuals by hauls and A=swept area (velocity* time* horizontal opening* 1852 m^{-1}).

A random sub-sample of 170 males and 151 females from all cruises was collected for analysis of sexual development and reproduction. For males, clasper length (to the nearest cm below the actual clasper length) was measured *sensu* Compagno (1984), from the point of insertion to the distal end. Females were considered mature when large, yellow oocytes were present and/or embryos where present *in uteri*, following the methodology by Peres & Vooren (1991) for viviparous elasmobranchs. To calculate length at 50% maturity (TLM50), a logistic model was fitted to binomial maturity data (immature=0, mature=1): $Y=(1+e^{-(a+bX)})^{-1}$, where Y is the proportion of mature individuals and X the TL class. Median TL-at-maturity is given by $-a/b$ (Mollet et al., 2000). As no data on rigidity of the clasper to assess calcification were available, then TLM50 in males was inferred by analysing the claspers size and development. From this relationship, a criterion for classifying the males as mature ('adult')/immature ('juvenile') was developed. Specimens with TL similar or greater than TLM50 are referred to as 'adult'. In addition to the former maturity estimation, the logistic model was fitted to the TL–clasper length data. Data collected on litters included number and length (to the nearest cm) of the embryos. A linear regression was fitted to the litter size and embryo total length (ETL) in relation to maternal total length (MTL). The time of parturition was inferred by analysing the TL frequency distribution of the embryos, and comparing them between seasons by a Student *t*-test (Sokal & Rohlf, 1998). The same test was used for comparing litter size (LS) between seasons. An estimation of the reproductive potential defined as the proportion of population potentially able to take part in reproduction, i.e. above TLM50 (Walker, 1999) is given.

RESULTS

A total of 2255 (1657 male and 598 female) *Mustelus schmitti* was caught. The species occurred over the whole latitudinal range of the survey area (Figure 1), and between 51–134 m depth and 6.8–20.4°C bottom temperature (Table 1). Total length composition of the population between the sexes did not differ significantly among cruises ($P>0.05$, Table 1, Figure 2). The Kruskal–Wallis test detected that the lowest median TL values occurred in spring for both sexes (males: K=72.46, $P<0.05$; females: K=34.05, $P<0.05$, Table 1) with a high proportion of individuals ranging from 35 to 58 cm TL (Figure 2).
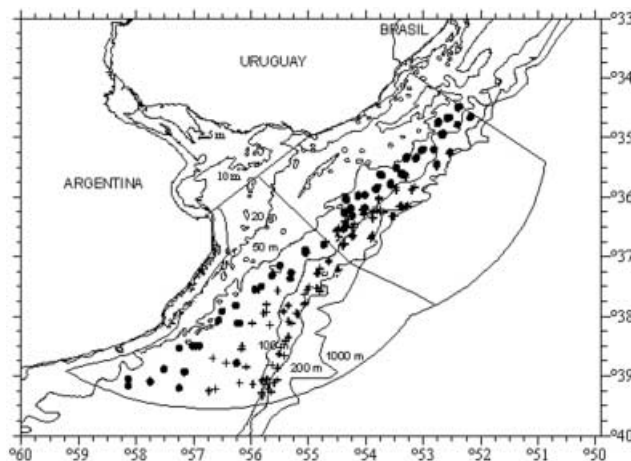

Figure 1. Map of the study area, the Argentinean–Uruguayan Common Fishing Zone (ZCPAU), where the cruises were carried out. Each single fishing station is represented by a cross. Stations where *Mustelus schmitti* occurred are represented by solid black dots.

Table 1. *Dates of the three cruises from where data for this study were taken.*

	Cruise 1	Cruise 2	Cruise 3
	autumn 1994	spring 1994	autumn 1995
Date	10 June–9 July	9 September–6 October	24 May–16 June
No. ts	76	80	81
L	34.30–39.17	34.31–39.20	34.29–39.17
D, m	51–398	51–334	50–324
T	5.3–15.9	5.08–9.61	4.9–20.4
O *M. schmitti*	13	10	21
Latitudinal range	34.30–39.06	34.40–36.16	34.29–39.02
D *M. schmitti*	54–134	51–130	53–129
T *M. schmitti*	9.1–15.9	8.5–9.6	6.8–20.4
TNo. *M. schmitti*	740	611	904
No. (%) I ♂	24 (3.24)	70 (11.45)	20 (2.21)
No. (%) I ♀	102 (13.78)	215 (35.18)	103 (11.39)
No. (%) M ♂	554 (74.86)	276 (45.17)	713 (78.87)
No. (%) M ♀	60 (8.11)	50 (8.18)	68 (7.52)
TL range ♂	38–80	36–81	44–82
TL range ♀	34–85	35–84	39–86
Mean TL (±SD) ♂	65.12 ±7.41	60.57 ±10.43	66.6 ±6.47
Mean TL (±SD) ♀	63.16 ±10.7	59.2 ±12.41	65.97 ±9.89
Median TL ♂	66	63	68
Median TL ♀	64	61	68

No. ts, number of trawling stations; L, latitudinal; D, m, depth, metres; T, range of temperature °C of hauls carried out; O *M. schmitti*, number of fishing stations where *Mustelus schmitti* occurred; D *M. schmitti*, depth and temperature (T *M. schmitti*) range where *M. schmitti* occurred; TNo. *M. schmitti*, total number of fish analysed; No. %, number and percentage of I, immature, M, mature males and females; TL, total length ranges and mean (SD, standard deviation) and median for males and females, r^2=determination coefficient for the total length–depth relationship.
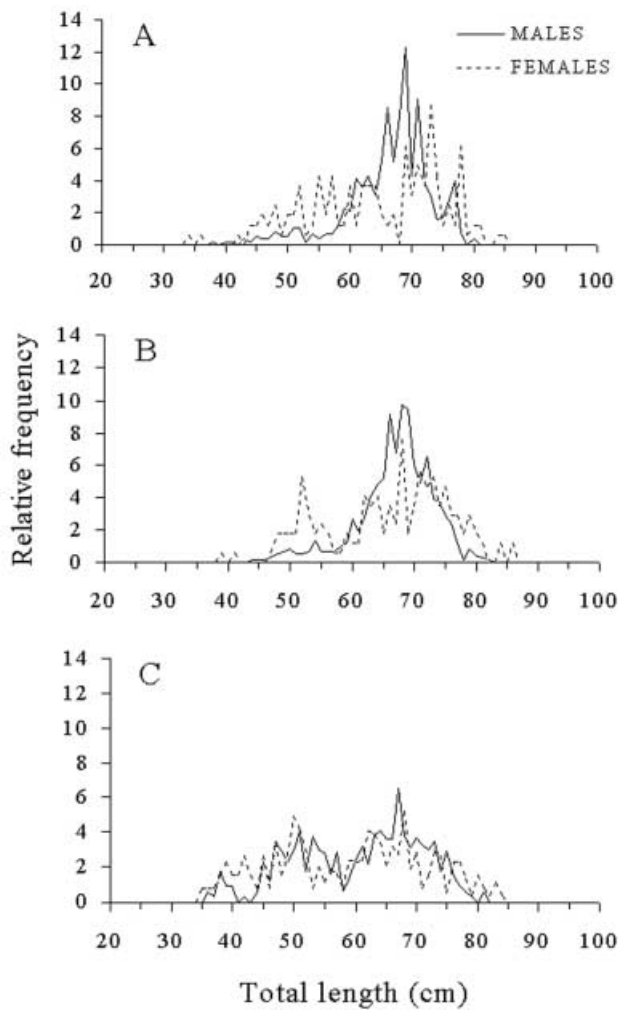
Figure 2. Population structure of *Mustelus schmitti* represented by the relative frequencies (%) of total length (cm) by sexes in (A) the 1994 autumn cruise; (B) the 1994 spring cruise; and (C) the 1995 autumn cruise.
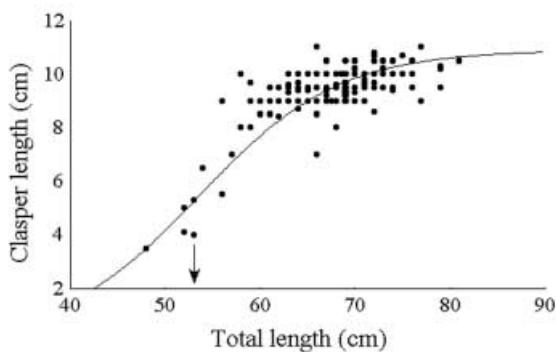

Figure 3. The relationship between clasper length (cm) and total length (cm) for *Mustelus schmitti*.

No relationship between depth and TL for all cruises was found (Table 1). The resulting overall and seasonal sex ratio was not significantly different from 1:1 ($P > 0.05$). Males predominated in many hauls, except above latitude 36°00′S, where females predominated (χ^2 test by hauls not shown).

Because of the absence of neonates and scarce incidence of juvenile males, the relationship between TL and clasper
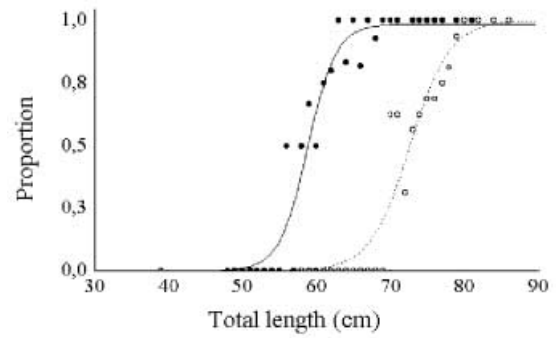
Figure 4. The logistic model fitted for the relationship between total length (cm) and fraction of mature females (empty circles) and males (filled circles) of *Mustelus schmitti*.
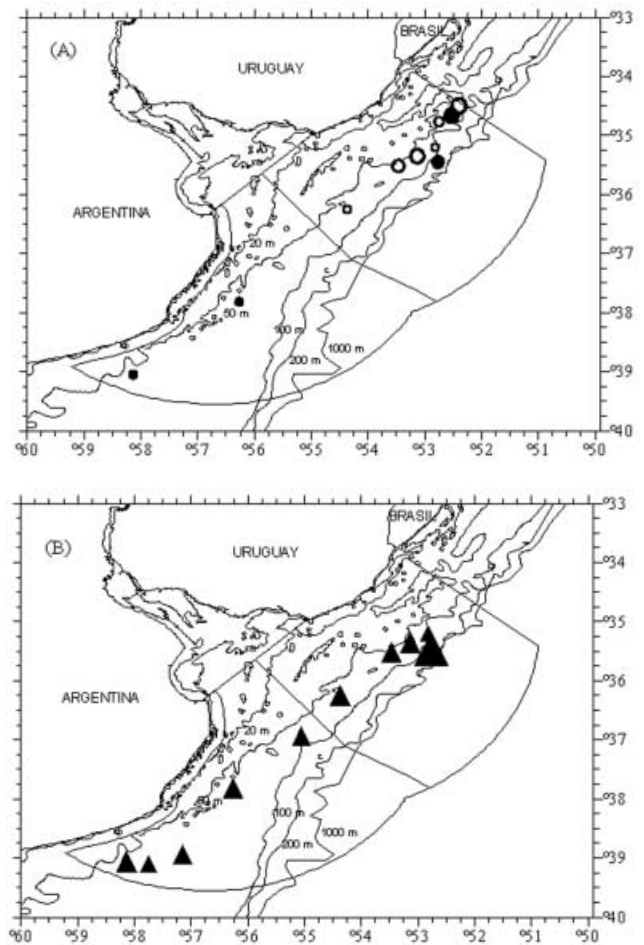

Figure 5. Distribution and density of immature and mature *Mustelus schmitti* in the Argentinean–Uruguayan Common Fishing in autumn 1994 for (A) females (circles); and (B) males (triangles). Symbol sizes correspond to densities of up to 500, up to 3000 and more than 3000 specimens. Immature and mature specimens are represented by empty and solid symbols respectively.

length resulted in an incomplete sigmoid curve, where the portion below the inflexion point was missing (Figure 3). The pattern of rapid clasper growth occurred at 53–59 cm TL, with little further growth between 59–80 cm TL. Males with claspers ⩾90 mm were then defined as adults and this criterion was used for the classification of the
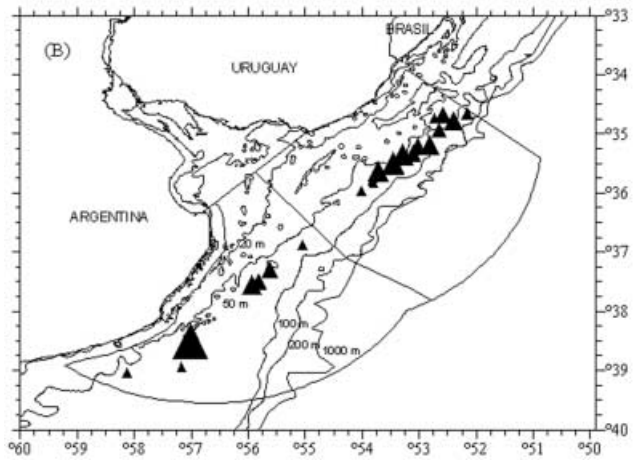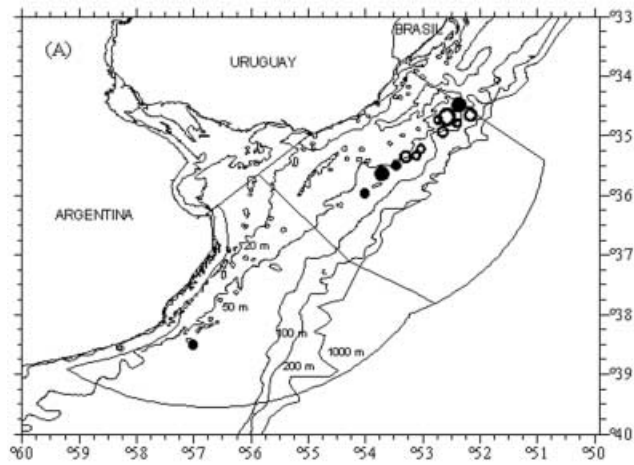
Figure 6. Distribution and density of immature and mature *Mustelus schmitti* in the Argentinean–Uruguayan Common Fishing in autumn 1995 for (A) females (circles); and (B) males (triangles). Symbol sizes correspond to densities of up to 500, up to 3000 and more than 3000 specimens. Immature and mature specimens are represented by empty and solid symbols respectively.

Figure 7. Distribution and density of immature and mature *Mustelus schmitti* in the Argentinean–Uruguayan Common Fishing in spring 1994 for (A) females (circles); and (B) males (triangles). Symbol sizes correspond to densities of up to 500, up to 3000 and more than 3000 specimens. Immature and mature specimens are represented by empty and solid symbols respectively.
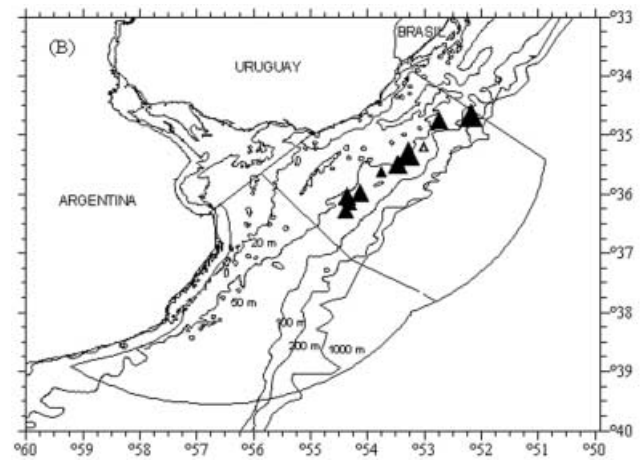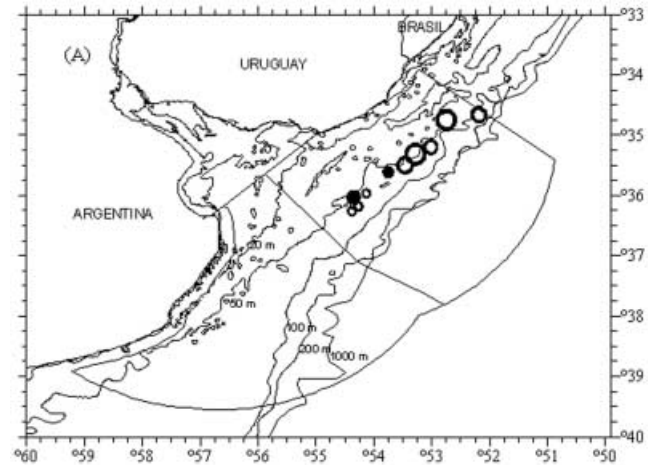
specimens. The estimated TLM50 for males was 59 cm (r=0.97, Figure 4).

Specimens of 50–57 cm TL were in a transitional stage, characterized by elongated, uncalcified claspers, ranging from 4.0 to 9.0 cm (mean=5.8; SD=1.6; N=8). The transition between juvenile and adults occurs in the later stages of this length range. By fitting the logistic model to the TL–clasper length relationship, TLM50 was estimated at 53 cm (r=0.92). From 57 cm TL onwards, the claspers grew slower in relation to TL, varying from 7.0 to 11.0 cm (mean=9.6; SD=0.6; N=162). This TL range consisted of adult males with fully developed, calcified claspers.

The smallest mature female was 66 cm TL and contained ripe vitellogenic oocytes. The largest immature female was 78 cm TL and presented no sign of sexual activity or development. The estimated TLM50 was 72 cm (r=0.97) (Figure 4).

Embryos ranged from 9 to 26 cm TL (mean=15; SD=3.6; N=107) in autumn and from 7 to 26 cm in spring (mean=22; SD=3.5; N=129), with larger embryos in the spring (Student's t-test: t=9.17; df=210; P<0.05).

From 126 females sampled in autumn, 16 gravid females were recorded. In spring, 22 females were gravid from a total of 25 sampled females. The TL range of gravid females was 70–82 cm in autumn and 66–82 cm in spring. The percentage of gravid females was 13% and 88% in autumn and spring respectively. In autumn, litter size ranged from 2 to 9 (mean=6.1; SD=2.5; N=16). In spring, litter size ranged from 1 to 10 (mean=5.3; SD=2.3; N=22). There was no significant difference in litter size between these seasons (Student's t-test: t=1.07; df=36; P>0.05). Litter size was found to increase significantly with MTL according to the equation: LS=0.393*MLF−22.961 (r=0.61; P<0.05). There was no significant correlation between ETL and MTL (r=0.08; P>0.05).

In autumn, the highest immature and mature female densities occurred north of latitude 36°00′S, and were less abundant further south (Figures 5A & 6A). In contrast, high densities of mature males were observed in all latitudes of the study area, though densities were highest between 36°00 and 37°00′S latitude (Figures 5B & 6B).

In spring, both males (mature) and females (immature and mature) occurred exclusively above latitude 36°30′S (Figure 7A,B). In all seasons and most hauls, both sexes occurred down to 134 m depth.

Samples collected during the survey consisted mainly of adult specimens. The reproductive potential varied between 82.97 and 86.39% in autumn and 53.35% in spring. For males, 74.86–78.87% were mature in autumn, while 45.17% were mature in spring. For mature females the percentage varied between 7.52 and 8.18% for all seasons (Table 1).

DISCUSSION

Although only two seasons (spring/autumn) were available for this study, a major concentration of adult *Mustelus schmitti* occurred in the north of the study area during spring. This can be related to the fact that this species is a winter immigrant off southern Brazil, where it is taken in commercial fisheries (Vooren, 1997). In Uruguayan waters, the highest catches occurred during the summer and autumn (December and April) (L. Paesch, unpublished data), before they return to the Brazilian continental shelf in the winter. In these circumstances, the concentration of individuals during spring may represent the immigrants that reside in Uruguayan and Argentinean waters during the summer for reproduction.

Unlike the observations by Cousseau (1986), the size of *M. schmitti* did not appear to increase with depth, though data for neonates and inshore waters were lacking in the current study. The size differences between sharks captured in the autumn and spring cruises can be explained by seasonal movements of small, immature *M. schmitti* during spring. Adult males predominated in most hauls, except above latitude 35°00′S where females predominated. Sexual segregation has been previously observed for this species by Cousseau (1986). That no neonatal specimens occurred in our samples suggests that nursery areas are situated outside the survey area. Indeed, coastal nursery areas have been identified in Bahia de Samborombón, Bahia Blanca and Bahia Engaño, (Argentinean waters) (Cousseau, 1986; Van der Molen et al., 1998), where individuals are approximately 30 cm long. The fact that young *M. schmitti* are not caught in the survey has implications for the application of this survey to assess recruitment of this species.

The spatial distribution of mature/immature individuals indicates that they occur in areas of commercial trawling activity, and could be caught when still immature. This fact has consequences for the stock, as the females affected by fishing mortality cannot mature and reproduce. However, the immature female part of the population may be favoured as a large part of the area between 34° and 37°30′S corresponds to an area where trawling is forbidden for most of the year, in order to protect the nursery area of the hake *Merluccius hubbsi* (Rey et al., 1996). A major proportion of mature males also occurred in this area.

The litter size of this species, combined with the duration of the reproductive cycle, result in a low fecundity. Gestation requires 10–11 months and the sexual cycle is annual, lasting 12 months, with copulation occurring

shortly after parturition (Souto, 1986). Parturition would take place in spring or early summer in this area (Cousseau, 1986; Menni, 1986; Souto, 1986; Puig, 1987). We considered the maximum TL recorded for the embryos (26 cm) as the size-at-birth for *M. schmitti* in this area. Similar values (24–28 cm) were recorded by Figueiredo (1977), Menni (1986), Souto (1986) and Chiaramonte & Pettovello (2000).

According to the available data and methods used, two values of size at maturity for males were calculated: 53 and 59 cm. However we considered 59 cm TL as the more appropriate TLM50, as this estimate corresponds to adult males with calcified claspers ready for copulation. The value of TL=53 cm corresponds to males with an elongating but uncalcified clasper. Souto (1986) and Puig (1987) found values of 56 cm and 58 cm respectively. In Argentinean waters, the phase of clasper elongation occurred at 62 cm and TLM50 was estimated at 76 cm TL (Chiaramonte & Pettovello, 2000). We estimated TLM50 for the females as 72 cm. Souto (1986) estimated this parameter at 59 cm TL, but our estimation is closer to the 79 cm TL reported by Chiaramonte & Pettovello (2000). The size of *M. schmitti* increased southward (Cousseau, 1986) and the same could happen with TLM50. Therefore, we can draw the hypothesis that maturation in Argentinean waters occurs at a higher TL than in Uruguayan waters. This can be confirmed by comparing the size of the smallest gravid females we observed (66 cm TL) and the value recorded by Puig (1987) of 58 cm TL, for the same area, with the smallest gravid female observed by Chiaramonte & Pettovello (2000) of 82 cm TL. We found that litter size varied from 1 to 10, in contrast with Souto (1986) who observed 1 to 19 embryos.

Fisheries critically affect elasmobranch stocks, and may even push them to the level of commercial (and even biological) extinction. Over the past 20 years, south-western Atlantic fisheries have critically affected several coastal demersal elasmobranch species whose distribution ranges include the continental shelves of Uruguay, Argentina and Brazil, including *Galeorhinus galeus*, *M. schmitti*, angel sharks and various 'skates and rays' (Chiaramonte, 1998; Van der Molen et al., 1998; Miranda & Vooren, 2003; Paesch & Domingo, 2003). Overfishing of elasmobranchs is also widely reported in the North Atlantic (e.g. Dulvy & Reynolds, 2002; Baum et al., 2003). Major problems for managing elasmobranch stocks include the lack of precise, species-specific landings data, and paucity of biological knowledge, which hampers stock assessment. Because of the low fecundity and slow growth rates of sharks, it is crucial to have reliable estimates of the annual catches (Van der Molen et al., 1998). For these reasons, sharks should be given management attention equal to that given to other threatened marine predators (Baum et al., 2003).

Due to its migratory habits, *M. schmitti* is caught by different fishing fleets that affect different parts of the stock during its life cycle. Low annual fecundity (1 to 10 embryos, with a 12 months interval between successive litters) (Souto, 1986) is a matter of concern for a species subjected to high fishing mortality. Unfortunately, stock assessments for elasmobranchs are rarely undertaken and population dynamics and

sustainable yields are unknown for nearly all sharks in the region. Hence more biologically-integrated studies are necessary to facilitate appropriate and effective management.

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