

Size Structure, Abundance and Preliminary Information on the Reproductive Parameters of the Shortspine Spurdog (*Squalus mitsukurii*) in the Argentinean-Uruguayan Common Fishing Zone from the mid-1990s

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Abstract

A total of 1 893 males and 1 124 females of *Squalus mitsukurii* were collected from latitudes 34° 30' S and 37° 00' S, in the south-western Atlantic Ocean, during early autumn, late autumn and spring 1995, early autumn 1996 and early autumn 1998. Length-frequency distributions significantly varied between sexes for all seasons ($P < 0.05$). Mature males predominated in all seasons throughout the analyzed area, according to their presence in the catches. In all periods sampled, immature females predominated except for late autumn 1995 where mature females were dominant. Significant differences in density among seasons were recorded for immature and mature females and mature males ($P < 0.05$). Density of immature females and mature males were significantly different ($P < 0.05$) for late autumn 1995 and early autumn 1996. Size-at-maturity was 43.1 cm and 55.9 cm total length for males ($n = 1\ 181$) and females ($n = 862$) receptively. The percentage of pregnant females ranged from 21.4% in spring 1995 to 49.8% in late autumn 1995. Ovarian fecundity varied significantly between early autumn 1995 and late autumn 1995 from 1–15 and uterine fecundity from 1–10, respectively. Embryo total length varied from 0.5–22.0 cm, attaining the highest values in autumn months. Size-at-birth was estimated to be 22–24 cm total length.

Keywords: Chondrichthyes, length distribution, reproduction, size-at-maturity, *Squalus mitsukurii*, SW Atlantic

Introduction

The shortspine or greeneye spurdog (*Squalus mitsukurii* Jordan and Snyder 1903) is a bathyal and benthopelagic elasmobranch species (Musick *et al.*, 2004). It is found in cold-temperate to tropical seas of the continental and insular shelves, upper slopes, submarine ridges and seamounts. It is observed primarily between 100 and 700 m, though it has been recorded as deep as 954 m and as shallow as 4 m depth (Carpenter, 2003; Compagno *et al.*, 2005; Cavanagh *et al.*, 2007). The geographic distribution is extensive and patchy and includes the northwest, southwest and central Pacific Ocean and the south Atlantic Ocean (Compagno, 1984, 2005). However, the distributional status of *S. mitsukurii* may change when thorough systematic studies are carried out on a regional or global basis, as there are actually

taxonomic problems related to *S. mitsukurii* in the Indo-Pacific and Atlantic populations. However, the review of these taxonomical issues for *S. mitsukurii* is taking place in the present (Stevens, 2004; Kyne and Simpfendorfer, 2007).

S. mitsukurii exhibit yolk-sac viviparity, with four to nine pups per litter, most births occurring in the autumn³ off the east coast of South Africa. The gestation period could take up to two years and sexual segregation of females would also occur in this species (Compagno, 1984). Within our study area, Lucifora *et al.* (1999) provided maturity estimations for around the Rio de la Plata River mouth (36° 05' S to 36° 39' S and 53° 23' W to 53° 48' W), of 51–55 cm and 52–60 cm total length for males and females, respectively. The species feeds mainly on bony fishes but also on cephalopods and crustaceans (Wilson and Seki, 1994; Compagno *et al.*, 2005).

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³The following seasons occur in the southern hemisphere: summer (Jan–Mar), autumn (Apr–Jun), winter (Jul–Sep) and spring (Oct–Dec)

In the southwest Atlantic, *S. mitsukurii* occurs off the Rio de la Plata and its oceanic front (Meneses and Paesch, 2003), moving to the southern Brazilian shelf in winter, where it is an important component of the local commercial fisheries (Vooren, 1997). Off Uruguay, the species is incidentally caught by the commercial offshore bottom trawl fishery (Paesch and Domingo, 2003), landed by vessels targeting the Argentine hake (*Merluccius hubbsi*) and piked dogfish (*Squalus acanthias*). However, the quantification of these landings is very difficult because they are not reported in the fishing statistics (Paesch, pers. obs.).

The lack of information on landings for this species in Uruguay is a matter of concern. For the period 1995–1998, the RV *Aldebarán* (from the Dirección Nacional de Recursos Acuáticos, Uruguay) carried out several research cruises in the Argentinean-Uruguayan Common Fishing Zone and collected specimens of *S. mitsukurii*, but the data gathered had not been analysed. Although almost one decade has passed since collection of the samples, we believe that the analysis of this information would make a valuable contribution to the understanding the population of this species. Dramatic declines of the catches of *S. mitsukurii* have been reported in other areas, suggesting extreme vulnerability (Wilson and Seki, 1994; Graham *et al.*, 2001). However, in spite of the fact that Kyne and Simpfendorfer (2007) consider that *S. mitsukurii* is one of the *Squalus* species with more considerable biological data available, the conservation status of the species is considered as “data deficient” by the IUCN Red List of Threatened Species (Cavanagh *et al.*, 2007). This fact reinforces the need to analyse and present available data. The management of shark species requires a good knowledge of spatial distribution, population structure and reproductive parameters, to support management measures (Mollet *et al.*, 2000). In this way, the aim of this work is to analyze the spatial size structure, preliminary information on the reproductive parameters and abundance of *S. mitsukurii*, during summer, autumn and spring along the Uruguayan continental shelf of the south-western Atlantic Ocean for the period 1995–1998.

Materials and Methods

Sampling methods

Samples of *S. mitsukurii* were obtained during five bottom trawl research cruises carried out in early autumn 1995, late autumn 1995, spring 1995, and early autumn 1996 and 1998 on board of the RV *Aldebarán*. These surveys were designed for the assessment of demersal fisheries targeting the Argentine hake (*Merluccius hubbsi*) resources in the Argentinean-Uruguayan Common Fishing Zone (ZCPAU, 34° 30'–37° 00' S, between 50 and 250 m) (Fig. 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 with an 80 mm (stretched mesh) codend was used. Trawl stations were selected using a stratified random sampling design, which was defined by depth and latitude (Ehrhardt *et al.*, 1977).

Distribution and abundance analysis

Fresh specimens of *S. mitsukurii* were sampled on board immediately after each trawling station. The specimens were sexed and measured to total length (TL) to the nearest cm *sensu* Compagno (1984), and the relative frequency of TL (pooled samples) by sex was calculated. For detecting differences in the length distributions by sex and season a Kolmogorov-Smirnov test was performed. For comparing total length distributions by sex among seasons, a Kruskal-Wallis *H*-test (given by “*Hc*”) was used. Post-hoc Mann-Whitney *U*-test Bonferroni corrected was performed when differences among seasons were detected (Sokal and Rohlf, 1998). The non-parametric correlation Spearman coefficient was used to analyse the relationships between size and depth (Sokal and Rohlf, 1998).

For plotting the spatial distribution and abundance (density, expressed as individuals per squared nautical miles) of females/males and immature/mature sharks by sex, density was calculated as C/A where, C = number of individuals captured per haul, and A = swept area (= velocity×time×horizontal opening/1852, km²). Horizontal opening was estimated through net sounders. Analysis of Variance (ANOVA) (Sokal and Rohlf, 1998) was used to compare the density of immature males and females and mature males and females among seasons respectively. In these cases, data were transformed using $\ln(x+1)$. Normality and homogeneity were tested with Shapiro-Wilk test and Levene’s test. Multiple comparison Tukey test was performed when means differed significantly among seasons. In all cases a significant level of $P<0.05$ was used.

Reproductive parameters analysis

The proportion of males:females (sex ratio) and immature:mature sharks by trawl station was analysed using a chi-square χ^2 -test (Sokal and Rohlf, 1998). A random sub-sample of males and females from all seasons was collected for analysis of sexual development and reproduction. For males, clasper length (to the nearest cm below the actual clasper length) was measured from the point of insertion to the distal end, *sensu* Compagno (1984). As no data on rigidity of the clasper to assess calcification were available, then TL_{50} (size at which 50% of the specimens were mature) in males was inferred

Table 1. Data on the five cruises carried out. Number of trawling stations (Nts), number of fishing stations where *Squalus mitsukurii* occurred (N *S. mitsukurii*), total number of specimens analysed (TN *S. mitsukurii*), number and percentage (N) of immature (I) and mature (M) males and females, total length (TL, cm) ranges and mean (SD = standard deviation) and median for males, females and maximum distance (K-S *Dmax*) of the Kolmogorov Smirnov test for length-frequency distributions between sexes (*= significant differences) and Spearman coefficient values for the relationship between total length and depth (TL-depth r_s).

Measurement	Early autumn 1995 (Cruise 1)	Late autumn 1995 (Cruise 2)	Spring 1995 (Cruise 3)	Early autumn 1996 (Cruise 4)	Early autumn 1998 (Cruise 5)
Nts	44	44	42	39	38
N <i>S. mitsukurii</i>	35	40	33	34	25
TN <i>S. mitsukurii</i>	503	603	451	1 048	412
N (%) I ♂	29 (8.3)	35 (15.4)	79 (28.0)	68 (8.6)	50 (19.3)
N (%) I ♀	119 (76.8)	244 (65.1)	146 (86.4)	206 (75.7)	88 (57.5)
N (%) M ♂	319 (91.7)	193 (84.6)	203 (72.0)	708 (91.2)	209 (80.7)
N (%) M ♀	36 (23.2)	131 (34.9)	23 (13.6)	66 (24.3)	65 (42.5)
TL range ♂	27–79	25–76	27–69	33–68	26–66
TL range ♀	30–74	29–82	25–78	31–77	24–73
Mean TL (±SD) ♂	49.9 ± 8.6	53.6 ± 10.0	50.4 ± 10.5	55.1 ± 8.3	53.2 ± 11.3
Mean TL (±SD) ♀	49.4 ± 9.5	52.4 ± 9.7	46.0 ± 8.5	47.7 ± 10.1	50.3 ± 8.8
Median TL ♂	46.0	56.0	52.0	57.5	58.0
Median TL ♀	49.0	50.0	46.0	46.0	53.0
K-S <i>Dmax</i>	0.195*	0.258*	0.353*	0.450*	0.486*
TL-depth r_s	0.241	0.103	0.192	0.08	-0.21

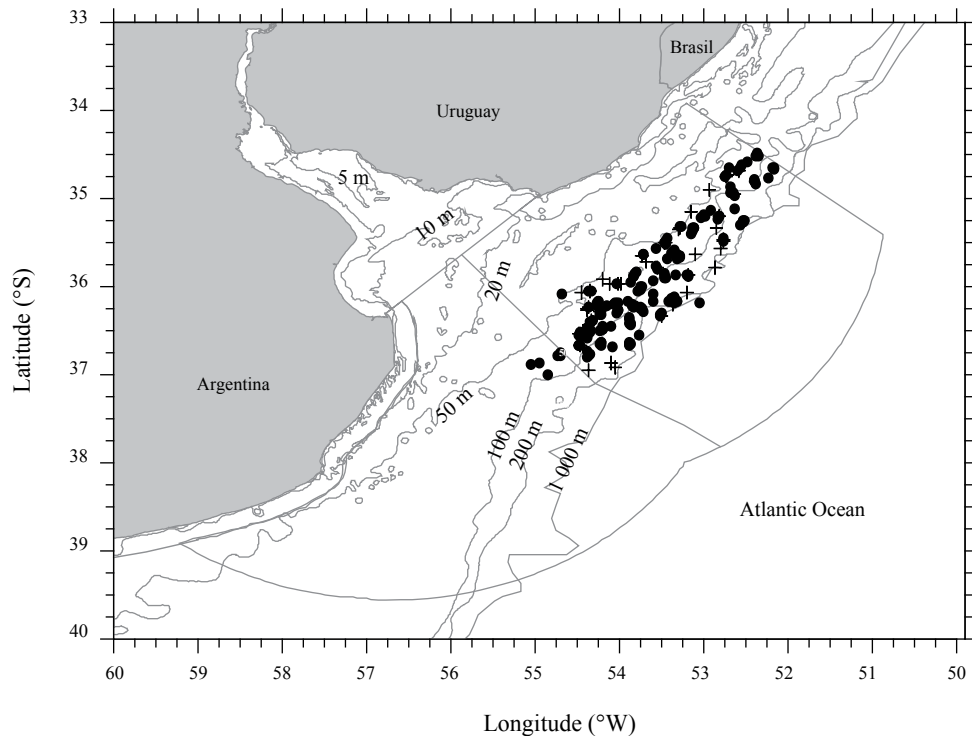


Fig. 1. Map of the study area showing the Argentinean-Uruguayan Common Fishing Zone (ZCPAU), where the cruises were carried out. Symbols represent single fishing stations. Presence (solid black dots ●) and absence (crosses +) of *S. mitsukurii*.

by analyzing the clasper size and development, by plotting clasper length against total length. The logistic model (presented below for the females) was fitted to the TL clasper length data. The inflection point of the logistic curve was calculated by the ratio of the equation parameters $-a/b$. Females were considered mature when large, yellow oocytes were present in the ovary and/or embryos were present in oviducts, following the methodology by Peres and Vooren (1991) for lecithotrophic viviparous elasmobranchs. Presence of yolk in the oviduct was recorded and assumed as an ovulation sign. Length at 50% maturity (TL_{50}) was calculated by a logistic model fitted to the maturity data as follows:

$$Y = 1/(1 + e^{-(a+bX)})$$

where Y is the proportion of mature individuals, X is the TL (by 2.0 cm classes), and TL at 50% maturity is given by $-a/b$ (Mollet *et al.*, 2000). Similarly, for females, TL at 50% maternity (MTL_{50}) was inferred by calculating the proportion of females in maternal condition (gravid) by TL class and fitting the logistic model (Restrepo and Watson, 1991).

Data collected on litters included number of pups per female in each oviduct, sex and TL (cm) of the embryos. The sex ratio of embryos was calculated for spring 1995 and early autumn 1998, as embryo sex was only recorded in that cruises. Differences from the expected 1:1 were analysed using χ^2 -test (Sokal and Rohlf, 1998). However, data on the embryos sex was only recorded in spring 1995 and autumn 1998. Ovarian (number of vitellogenic follicles in the ovaries, OF) and uterine fecundity (number of macroscopically visible embryos, UF) were assessed and compared among cruises by Kruskal-Wallis H -test.

The relationship between both variables and maternal total length (MTL) was also assessed by linear regression. The time of parturition was inferred by analyzing the TL frequency distribution of the embryos, and an ANOVA test was used to compare the mean embryo TL among season (Sokal and Rohlf, 1998).

Results

Population structure and seasonal distribution

Total lengths ranged from 24–82 cm for females ($n = 1\,124$) and from 25–79 cm for males ($n = 1\,893$) (Fig. 2). Significant differences in the length-frequency distributions between sexes were found ($P < 0.05$) (Table 1). For males and females, the length composition varied significantly among seasons ($H_c = 92.40$ for males and $H_c = 84.17$ for females). Post-hoc pair-wise comparison for males were not significant ($P > 0.05$) between early autumn, and spring 1995; between late autumn 1995 and early autumn 1996 and 1998 and between early autumn 1996–1998 (Table 2). Post-hoc pair-wise comparison for females were not significant ($P > 0.05$) between late autumn 1995–early autumn 1998 and spring 1995–early autumn 1996 (Table 2). A positive and significant relationship ($P < 0.05$) were found between depth and TL, except for autumn 1998 (Table 1).

Abundance

Mature males predominated in all seasons throughout the study area (Fig. 3b, d, f, h, j), whereas the highest densities of immature males were found in spring 1995 were recorded in two hauls at depths of 136 and 70 m. Immature females predominated in all seasons (Fig. 3a, c,

Table 2. Results of pairwise comparisons for Mann-Whitney test Bonferroni corrected for males and females among seasons.

	Early autumn 1995	Late autumn 1995	Spring 1995	Early autumn 1996	Early autumn 1998
Males					
Early autumn 1995	-				
Late autumn 1995	7.42 E-10*	-			
Spring 1995	1	0.002*	-		
Early autumn 1996	1.77 E-17*	1	7.42 E-10*	-	
Early autumn 1998	8.57 E-06*	1	0.001*	1	-
Females					
Early autumn 1995	-				
Late autumn 1995	0.030*	-			
Spring 1995	0.006*	1.26 E-11*	-		
Early autumn 1996	0.033*	1.12 E-11*	1	-	
Early autumn 1998	0.020*	1	1.62 E-07*	3.65 E-05*	-

* = significant difference

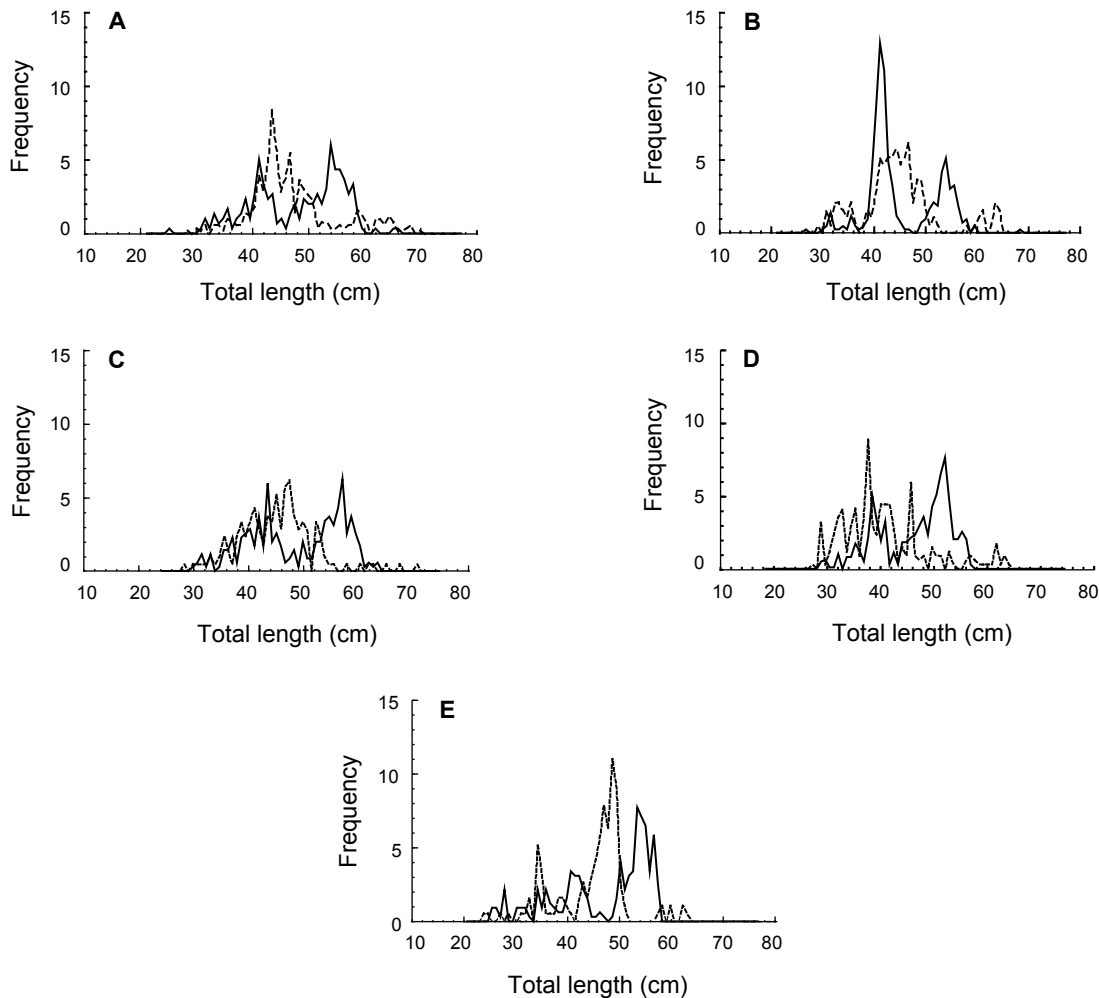


Fig. 2 Total length-distribution of *S. mitsukurii* represented by the relative frequencies (%) of total length (cm) by sex and season; (A) early autumn 1995; (B) late autumn 1995; (C) spring 1995; (D) early autumn 1996; and (E) early autumn 1998. (continuous line = males; dotted line = females).

e, g, i), except for late autumn 1995 when mature females were dominant (Fig. 3c).

Density distributions for all the seasons were not normal ($P < 0.05$) while homogeneity was found for all cruises. Significant differences in density among seasons were recorded for immature and mature females and mature males. Non significant differences ($P > 0.05$) between seasons were found for immature males (Table 3). Significant differences with regard to density were detected between immature females and mature males ($P < 0.05$) for late autumn 1995 and early autumn 1996 respectively being the density of mature males lower than the density of immature females. The opposite pattern was observed in early autumn 1996. Density of mature females significantly varied ($P < 0.05$) for the pair early autumn 1995 and late autumn 1995–early autumn 1996 and for the pair late autumn 1995 and early autumn 1998, with the highest density values recorded in the latter (Tables 3 and 4).

Maturity estimations

Males. Males collected for reproductive analysis ranged from 25.0 to 75.0 cm TL ($n = 1\,181$, Table 1). The clasper length was highly variable throughout the size range, but clasper growth became faster as the sharks approached maturity, which corresponded to the range 40.0–55.0 cm TL. Total length at 50% maturity was inferred from the clasper length-TL relationship by calculating the point of inflection of the logistic curve, which was located at 43.1 cm of TL ($r = 0.913$, $n = 1\,181$, Fig. 4a). From ~60.0 cm TL onwards, claspers grew slower in relation to TL, varying from 5.0 to 8.0 cm of length. This TL range consisted of adult males with fully developed claspers.

Females. Females collected for reproductive analysis ranged from 24.0 to 82.0 cm TL ($n = 862$, Table 5). The smallest mature female was 48.0 cm TL. The largest

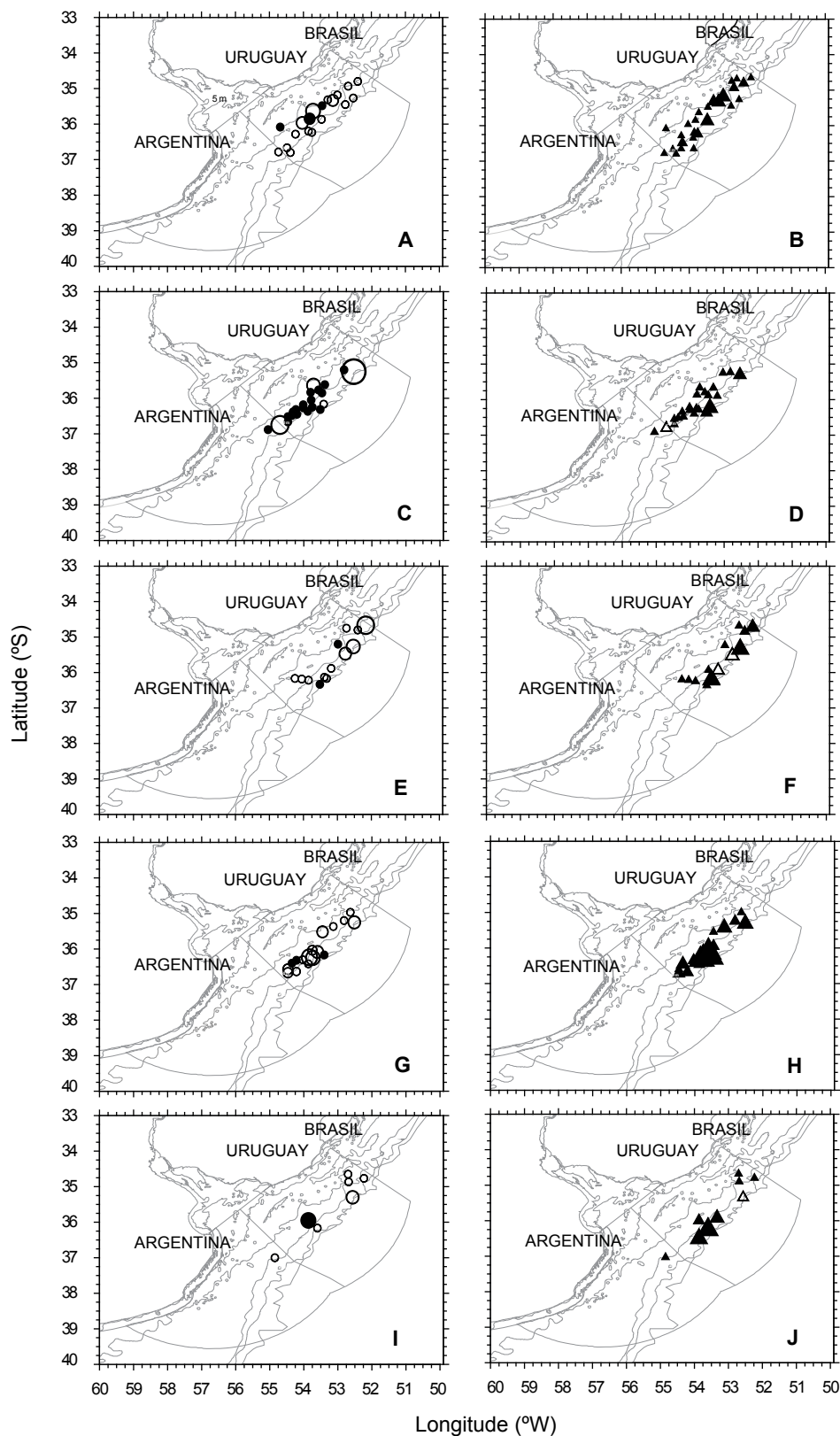


Fig. 3. Distribution and density of immature and mature *Squalus mitsukurii* in the Argentinean-Uruguayan Common Fishing in early autumn 1995 for females (A) and males (B); late autumn 1995 for females (C) and males (D); spring 1995 for females (E) and males (F); early autumn 1996 for females (G) and males (H); early autumn 1998 for females (I) and males (J). Symbols (females, circles; males, triangles) size corresponds with three density categories; of up to 500 (•, ▲), up to 3000 (●, ▲) and more than 3000 specimens (●, ▲). Immature and mature specimens are represented by empty and solid symbols respectively.

Table 3. Results of the analysis of variance (mean squares) tests performed for comparing the density of immature and mature male and female *Squalus mitsukurii* among seasons.

	Immature males	Immature females	Mature males	Mature females
Between seasons	13 727	21 731	11 840	35 272
Within	6 013	6 613	3 366	4 835
<i>Fc</i>	2 283	3 225	3 517	6 736
<i>P</i>	0.066	0.015	0.010	<0.001

Table 4. Results of the Tukey test performed for comparing the significant differences in the density of immature female, mature male and mature female *Squalus mitsukurii* among seasons. Numbers below and above the zeros diagonal represent the *Q* and the *p* values respectively.

	Early autumn 1995	Late autumn 1995	Spring 1995	Early autumn 1996	Early autumn 1998
Immature females					
Early autumn 1995	–	0.793	0.944	0.398	0.853
Late autumn 1995	1 591	–	0.337	0.037*	0.217
Spring 1995	1 064	2 655	–	0.847	0.999
Early autumn 1996	2 502	4 093	1 438	–	0.940
Early autumn 1998	1 421	3 012	0.357	1 081	–
Mature males					
Early autumn 1995	–	0.313	0.998	0.775	1
Late autumn 1995	2 719	–	0.504	0.022*	0.305
Spring 1995	0.463	2 256	–	0.575	0.997
Early autumn 1996	1 637	4 356	2 100	–	0.784
Early autumn 1998	0.022	2 742	0.485	1 615	–
Mature females					
Early autumn 1995	–	0.006	0.753	0.032*	1 000
Late autumn 1995	4 974	–	0.148	0.979	0.011*
Spring 1995	1 693	3 281	–	0.409	0.855
Early autumn 1996	4 169	0.805	2 476	–	0.054
Early autumn 1998	0.279	4 695	1 414	3 889	–

* = significant difference

immature female was 51.0 cm TL, presenting no sign of sexual activity or development. The smallest gravid female was 49.0 cm of TL and bore two embryos. The estimated TL_{50} was 51.9 cm ($r = 0.94$, $n = 32$, Fig. 4b). Size at 50% maternity was estimated at 55.9 cm ($r = 0.97$, $n = 32$, Fig. 4b) and the percentage of gravid females varied from 21.4% in spring 1995 to 49.8% in late autumn 1995.

Fecundity and observations on the reproductive seasonality

The Ovarian Fecundity (*OF*) was positively correlated with the *MTL* and so was the Uterine Fecundity (*UF*) ($r^2 = 0.37$, $P < 0.05$ and $r^2 = 0.38$; $P < 0.05$, respectively, sample sizes in Table 5). The predictive regressions

for these relationships are: $OF = -3.89 + 0.13MTL$ and $UF = -3.35 + 0.12MTL$ (Fig. 5a, b). Ovarian fecundity varied significantly among seasons ($Hc = 15.84$, $P < 0.05$) from one (early autumn 1995) to 15 (late autumn 1995). Uterine fecundity varied from one (early autumn 1995) to 10 (late autumn 1995) being significantly different among seasons ($Hc = 15.47$, $P < 0.05$).

In the spring of 1995, a total of 36 mature females were observed, with two females possessing four and five recently ovulated and fertilized ova in the oviduct. In the early autumn 1995, recently ovulated and fertilized ova were also observed in three females from a total of 65 mature females, in numbers of three, three and four per female (Table 5).

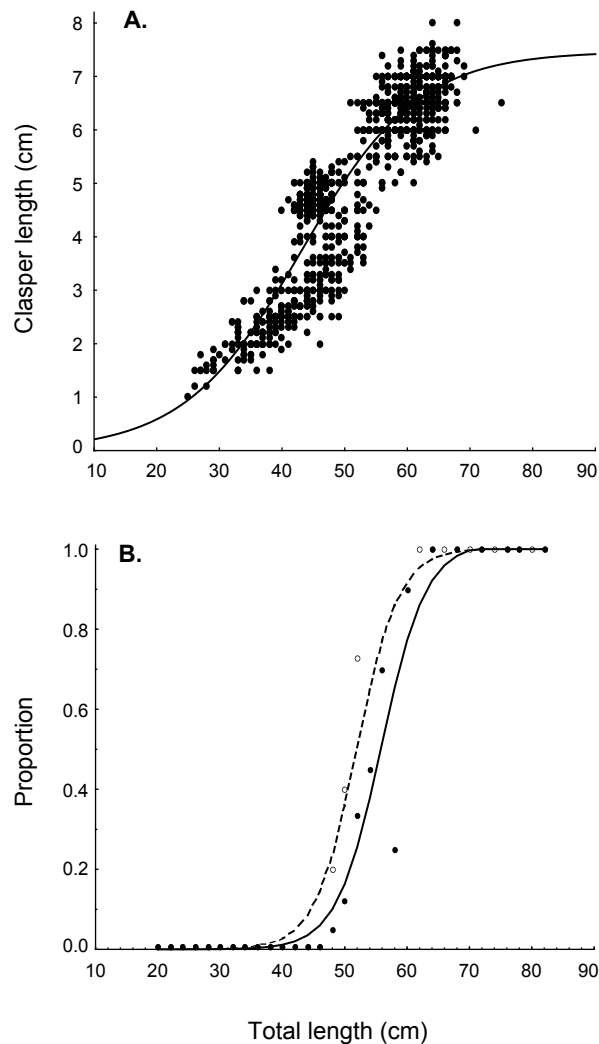


Fig. 4. The relationship between (A) clasper length (cm) and total length (cm) along with the fitted logistic model for the males ($n = 1\ 181$) and (B) the proportion of mature females (empty circles) and females in maternal condition (full circles) in relation with total length (cm) for the females ($n = 862$), for *Squalus mitsukurii*.

Embryo TL varied from 0.5 cm (late autumn 1995) to 22.0 cm (early autumn 1995 and early autumn 1996, Table 5). Embryo TL varied significantly among seasons ($F_{4,358} = 22.88, P < 0.05$) attaining the highest values in early autumn 1996 and 1998 (Fig. 5c). The highest relative frequency of 22.0 cm TL was recorded in early autumn 1996. Embryo TL frequency distributions by seasons are showed in Fig. 6. Sex ratio showed no significant difference from the expected 1:1 ($\chi^2 = 2.8, d.f. = 1, P > 0.05$; Table 5).

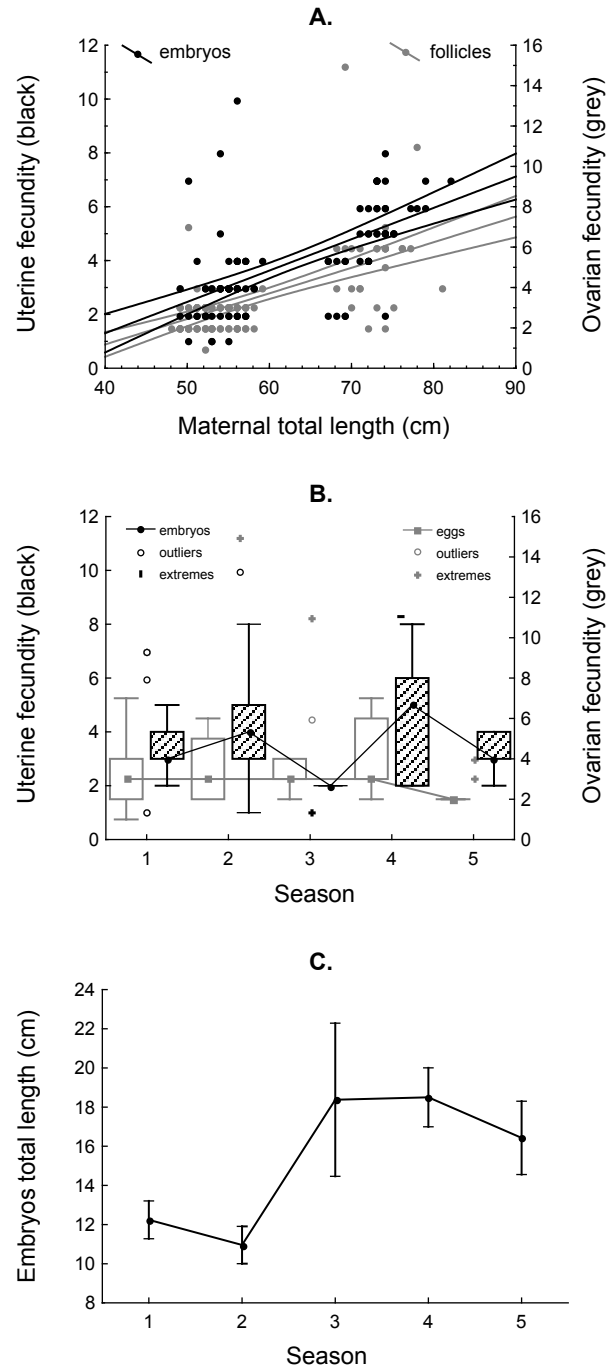


Fig. 5. Ovarian ($n = 53$) and uterine ($n = 93$) fecundity versus (A) maternal total length (cm) and (B) season; (C) mean embryos total length (cm) ($n = 359$) for (1) early autumn 1995; (2) late autumn 1995; (3) spring 1995; (4) early autumn 1996; and (5) early autumn 1998, by season for *Squalus mitsukurii*. Vertical bars denote 95% confidence intervals.

Table 5. Total number of females; mature females (total length range, cm); ovarian fecundity (range of vitellogenic follicles); number of gravid females (total length range, cm); uterine fecundity (range of embryo count); embryos total length (range, cm), sexual ratio of the litter and ovulation signs for female *Squalus mitsukurii* by season.

	Early Autumn 1995				Late Autumn 1995				Spring 1995			
	range	mean	SD	<i>n</i>	range	mean	SD	<i>n</i>	range	mean	SD	<i>n</i>
Females	30–79	50.9	10.6	171	29–82	53.8	11.2	287	25–78	46	8.5	168
Mature females	52–79	61	8.8	65	52–82	62.5	8.4	143	52–78	57.3	6.6	36
Ovarian fecundity	1–7	3.2	1.2	56	2–14	4.1	3.3	16	2–11	3.7	2	19
Gravid females	52–79	61	8.8	65	52–82	62.5	8.4	143	52–78	57.3	6.6	36
Uterine fecundity	1–7	3.6	1.7	34	1–10	4.4	1.9	37	1–2	1.8	.4	5
Embryos TL	1–21	12.2	5.4	131	.5–22	10.9	7	136	10–20	18.4	3.4	8
Litter sexual ratio		1:1				—				—		
Ovulation signs		x				—				—		

	Early Autumn 1996				Early Autumn 1998			
	range	mean	SD	<i>n</i>	range	mean	SD	<i>n</i>
Females	31–77	49.4	11	149	24–73	48.5	9.8	87
Mature females	52–77	61.8	8.2	51	52–73	56.2	5.2	43
Ovarian fecundity	2–7	4.1	1.7	19	2–4	2.2	0.6	12
Gravid females	52–77	60.8	8.2	51	52–73	56.2	5.2	43
Uterine fecundity	2–8	4.7	2.1	14	2–4	3.3	0.7	14
Embryos TL	12–22	18.5	3.8	54	13–20	16.4	2.1	35
Litter sexual ratio		—				1.7:1		
Ovulation signs		—				x		

(–) no data (x) presence

Discussion

Vooren (1997) considered *Squalus mitsukurii* as a winter migrant, reproducing in Uruguayan and Argentine waters in the summer, and migrating in the winter back to the continental shelf of southern Brazil. As our samples were obtained in autumn and spring, predominance of adults was expected. Our observations in fact showed that male *S. mitsukurii* adults dominated during most sampling periods, while for females, juveniles were more common. However, there was no relationship between fish size and depth for both sexes. Segregation by size and sex is commonly observed among *Squalus* species, though the population structure may vary by species and location. Litvinov (1990) observed that *S. mitsukurii* on the Nazca and Sala y Gomez seamounts was in the form of two schools consisting of individuals of similar size and sex. The same author noted habitat segregation by sex for this species. Comparison of different seamounts in the southeastern Pacific Ocean revealed significant differences in the size distribution for both sexes. Other *Squalus*

species, such as *S. megalops* show complex population structures, with segregation by sex and size (with small females and males segregated from large females). Female *S. megalops* exhibited segregation by breeding condition, as large females in the first year of pregnancy were separated from those in the second year (Braccini *et al.*, 2006a). The same may occur with *S. mitsukurii*, the reason why mostly immature females were recorded in our samples. Sion *et al.* (2003) noted significant differences between length-frequency distributions for males and females *S. blainvillei* with the sex ratio being 1:1 in both analyzed periods (September–October 1999 and April 2000). Graham (2005) recorded heavily dissimilar sex ratios for *S. megalops*. For *S. mitsukurii* Fischer *et al.* (2006) noted significant deviation towards females and Litvinov (1990) also found a sex ratio different from 1:1. However, Sion *et al.* (2003) recorded sex ratios of 1:1 for *S. blainvillei*.

Wilson and Seki (1994) noted that for January 1985–November 1988, *S. mitsukurii* was the most abundant

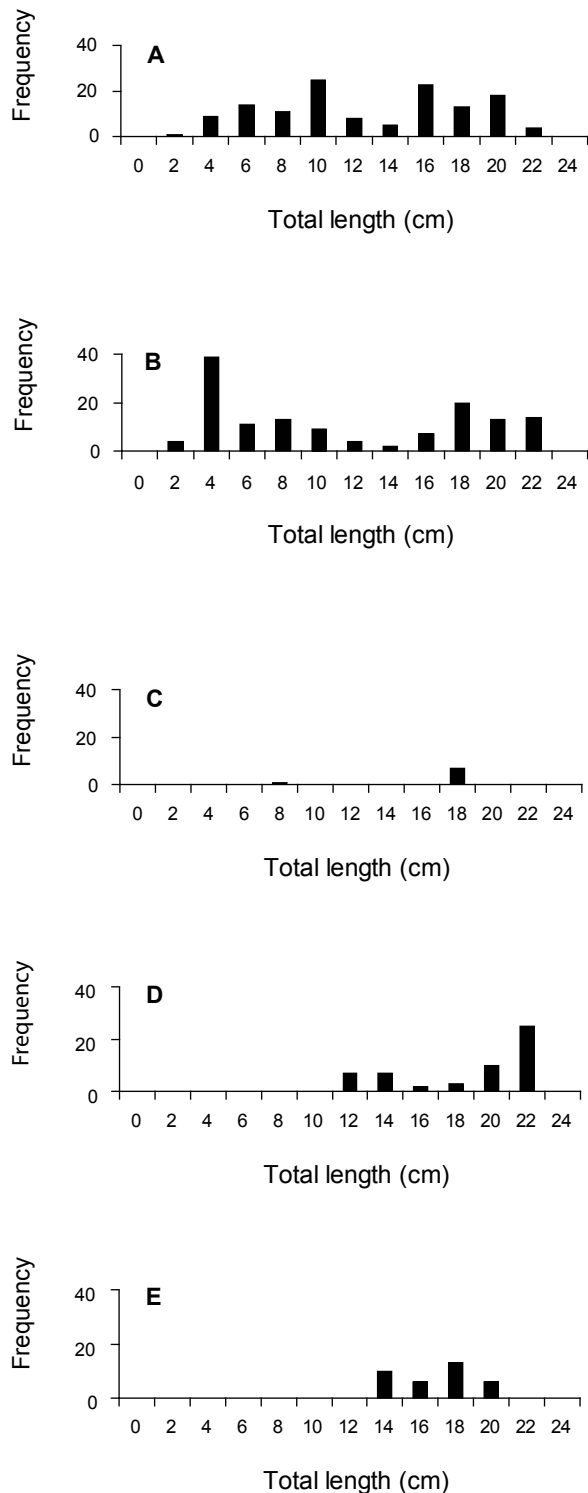


Fig. 6. Relative frequency of total length (cm) for embryos of *Squalus mitsukurii* for (A) early autumn 1995; (B) late autumn 1995; (C) spring 1995; (D) early autumn 1996 and (E) early autumn 1998.

fish species captured as by-catch in the Southeast Hancock Seamount (Pacific Ocean). However, the dramatic decline in the catch of *S. mitsukurii* during that period could indicate the sensitivity of the species to overfishing. The same authors argued that the limited habitat area could be another risk of overexploitation for the seamount populations of *S. mitsukurii*. Fischer *et al.* (2006) raised the question of the selectivity of some gears, as traps and longlines used in their survey, which are also typical of other Brazilian fisheries, as responsible of the depletion of juvenile *S. mitsukurii*, recommending gear restrictions to avoid young fishing mortality. Graham (2005) noted that in spite of the fact that stocks of some *Squalus* species inhabit large areas seemingly subject to light exploitation, they were already greatly depleted on the main trawling ground. The assessment of elasmobranch populations is often limited by the lack of biological information (Cortés, 1998). This fact is especially valid for non-targeted species (Braccini *et al.*, 2006b, c) such as *S. mitsukurii*. Therefore, it is expected that the reproductive parameters calculated in this study may aid in the adequate management of the species, namely with special regard to the presence of a large number of juveniles in the samples, which reflects the vulnerability of these specimens to the fishing gear.

Female *S. mitsukurii* attain a larger total length than males, also observed for the same species by Wilson and Seki (1994) and Fischer *et al.* (2006) and commonly reported in sharks (Cortés, 2000) and batoids (Capapé *et al.*, 2000; Capapé *et al.*, 2008; Mnasri *et al.*, 2009). However, in *S. mitsukurii*, Litvinov (1990) observed maximum sizes virtually equal in both sexes. The maximum total length recorded in the present study for *S. mitsukurii* in both sexes is within the range reported by other authors in other areas (Table 6). For males, this value varied from the range 48.0–51.9 cm (Central North Pacific) to 110.0 cm (SE Atlantic) whereas the females from 68.0–71.9 cm (Central North Pacific) to 110.0 cm (SE Atlantic). Size at maturity along with size at 50% maturity (when available) reported for *S. mitsukurii* in this study and elsewhere are presented in Table 6. This parameter varied from 40.0–45.0 cm TL (this study) to 65.0 cm TL (SE Atlantic) in the males and 49.0–51.0 TL (this study) cm to 89.0 cm TL (Central North Pacific). Taniuchi *et al.* (1993) already reported the variability in reproductive parameters of *S. mitsukurii* by examining specimens from four NW Pacific localities, demonstrating later that age at maturity also varied between areas (Taniuchi *et al.*, 1999). Litvinov (1990) raised the possibility for the existence of reproductively isolated subpopulations. Lucifora *et al.* (1999) argued on the plasticity of the size at maturity for this species. For Fischer *et al.* (2006) the considerable differences in sizes at maturity between populations from the northern Pacific

Table 6. Reproductive parameters estimated for *Squalus mitsukurini* in the present study and by other authors in different regions (Locality); as male and female maximum size observed (total length, cm) (MMS, FMS respectively); male and female size (total length) at first maturity (MSm, FSsm, respectively); male and female size at 50% maturity (MS50%cm, cm; FS50%cm, cm); ovarian fecundity (OF); uterine fecundity (UF); parturition season and size at birth (cm).

Locality	MMS	FMS	MSm	FSsm	MS50%cm	FS50%cm	OF	UF	Size at birth	Parturition	Reference
E coast of S Africa - S Atlantic	110	110	65	72	-	-	-	4-9	22-26	most births in autumn	Compagno (1984)
Sala y Gómez - SE Pacific	104	104	-	85	-	-	-	-	-	-	Litvinov (1990)
Off Argentina - SW Atlantic	no data	78.5	-	-	-	-	-	4-6	23 ¹	-	Gostonyi and Kuba (1998)
Rio de la Plata Mouth - SW Atlantic	66	86	51-55	52-60	-	-	-	-	-	-	Lucifora <i>et al.</i> (1999)
SE Hancock Seamount - Central North Pacific	-	-	-	89	48	69	1-6	1-6	21-26	not well-defined	Wilson and Seki (1994)
NE Brazil - SW equatorial Atlantic Ocean	73	94.3	-	-	65	77.8	3-27	3-11	22.5	probably summer	Fischer <i>et al.</i> (2006)
Choshi - Central N Pacific	68.0-71.9	96.0-99.9	-	-	-	-	4-15	4-15	-	-	Taniuchi <i>et al.</i> (1993) ²
Ogasawara - Central N Pacific	-	72.0-75.9	-	-	-	-	2-9	2-9	-	-	Taniuchi <i>et al.</i> (1993) ²
Hancock Seamount - Central N Pacific	48.0-51.9	68.0-71.9	-	-	-	-	-	-	-	-	Taniuchi <i>et al.</i> (1993) ²
Masseiba - Central N Pacific	no data	92.0-95.9	-	-	-	-	5-10	6-9	-	-	Taniuchi <i>et al.</i> (1993) ²
Off the east coast of S Africa - S Atlantic	81.0	95.0	58-60	69	-	-	5-9	4-9	22-26	probably April	Bass <i>et al.</i> (1976)
S Brazil - SW Atlantic	64.0	81.0	53	65	54	65	1-9	2-9	23-24	-	Calderón (1994)
Uruguayan continental shelf, SW Atlantic	79	82	40-55	49-51	43.1	51.9	1-15	1-10	22-24	autumn-winter	Present study

¹maximum total length observed; ²Total length was in all cases estimated from the analysis of the of specimens occurrence by maturity stage at 4 cm intervals; - no data

and Atlantic (as those shown in Table 6) could mask the presence of two species: *S. mitsukurii* for the Pacific and *S. blainvillei* for the Atlantic. For the NW Pacific Ocean, Taniuchi *et al.* (1993) observed that both sexes matured at smaller sizes and that the fecundity and size ranges of pregnant females were lower at latitudes closer to the equator. Fischer *et al.* (2006) however reported the opposite pattern for the southwestern Atlantic, the result of several abiotic and biotic factors including the effect of fisheries. Populations of *S. mitsukurii* have been intensively fished in the southwestern Atlantic for the past 30 years (see Vooren *et al.* (1990) for the South Brazilian area). However, stocks from off northeastern Brazil would have not been exploited yet, according to Fischer *et al.* (2006). However, more research is needed to assume so. Similarly to Wilson and Seki (1994), the currently study observed a positive correlation between ovarian fecundity and maternal size. This relationship was expected and has been observed in several other *Squalus* species (Avsar, 2001). We noted that ovarian fecundity varied from 1 to 15 vitellogenic follicles and uterine fecundity varied from 1 to 10 embryos in *S. mitsukurii*. Both values are within the range recorded by other authors elsewhere (Table 6). Large ovarian and uterine fecundity ranges for *S. mitsukurii* were recorded by Fischer *et al.* (2006) (3–27 and 3–11, respectively) and by Taniuchi *et al.* (1993) (4–15 and 4–15, respectively), comparing with authors from other areas (Table 5). Fischer *et al.* (2006) observed that the fecundity-female size positive correlation in *S. mitsukurii* would be the reason why southern Brazilian *S. mitsukurii* females have a lower number of vitellogenic follicles and embryos, when compared with specimens from other areas that attain larger sizes. Our results are consistent with those of Calderón (MS 1994), for southern Brazil, who recorded similar female maximum and maturity sizes as well as similar fecundity values (Table 6). Capapé *et al.* (2002) and Conrath (2004) argued that the difference between ovarian and uterine fecundity indicates that a certain number of oocytes undergo atresy. However, some authors recorded the same maximum number of ovarian follicles and embryos in *S. mitsukurii* (Table 6). For other squaloid sharks, mean biennial fecundity was calculated in eight pups by female in *S. acanthias*, with positive relationships between size and fecundity (Avsar, 2001). In the roughskin spurdog *Cirrhigaleus asper* uterine fecundity was found to be 12–19 (Fischer *et al.*, 2006).

In the present study, the analysis of the relative frequency of embryos TL demonstrated that the largest embryos (full term litters) occurred in early autumn 1996. Also high embryos TL classes were observed in late autumn 1995. Parturition could therefore occur in autumn-winter off Uruguay. The presence of ovulating females and candled uterine embryos in early spring 1995

would indicate that ovulation may occur immediately after birth. However, we are aware that the present data are not sufficient to assess the length and timing of the events compounding the reproductive cycle (*i.e.*, ovulation, mating, gestation, birth) and the possible synchronicity to the population level. Graham (2005) observed that in three *Squalus* species reproduction was continuous, with no evidence of seasonality. Bass *et al.* (1976), Wilson and Seki (1994) and Fischer *et al.* (2006) assumed (despite the fragmentary data) a biennial cycle for *S. mitsukurii*, consistent with those described for *S. acanthias*, where females undergo a 22-month long cycle (Wourms, 1977; Compagno, 1984). However, complex asynchronous cycles have been reported for squalid sharks (Yano and Tanaka, 1988; Yano, 1995; Watson and Smale, 1998). The hypothesis of parturition occurring in the period July–August off Uruguay, is reinforced by the fact that in early autumn 1995 the lowest percentage of gravid females was recorded, which could indicate that to the population level, most females had already given birth. So a reproductive cycle for *S. mitsukurii* off Uruguay on a biennial basis is rather speculative, as a longer cycle for the species would be also possible. Wilson and Seki (1994) reported evidences of a not well defined parturition period in *S. mitsukurii*. However, they observed the presence of the smallest uterine embryos in autumn and winter, that at the same time, were absent in spring and summer, indicating a well-defined seasonal production cycle for young. Concomitant development of vitellogenesis and gestation had already been noted for *S. mitsukurii* by Litvinov (1990) and Fischer *et al.* (2006). As specimens of 24 cm TL recorded in our samples were free-swimming and the maximum size of an intrauterine embryo was 22 cm TL we inferred that size at birth may be situated in the TL range of 22–24 (Table 5).

In the present study, maternity and maturity ogives were presented, with MTL_{50} exceeding TL_{50} by 4.0 cm. Braccini *et al.* (2006b) argued that for species with complex reproductive cycles longer than one year, maternity ogives must be considered, apart from maturity ogives, otherwise population models would overestimate recruitment rates and bias assessment. Further age and growth studies are necessary and recommended in order to understand these processes temporally altogether with the reproductive parameters determined in this study.

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