



The biology of *Mustelus schmitti* in southern Patagonia, Argentina

G. E. CHIARAMONTE*‡ AND A. D. PETTOVELLO†

**División Ictiología y Estación Hidrobiológica de Puerto Quequén, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina* and †*Centro de Investigaciones de Puerto Deseado, Alte. Brown y Colón, 9050 Puerto Deseado, Argentina*

(Received 3 September 1999, Accepted 16 May 2000)

The relationship of body weight and total length (L_T) of *Mustelus schmitti* in southern Patagonia was different between sexes. Changes in maturity stages in males appear at larger sizes in Ría Deseado specimens than in the Mar del Plata area. Mature females ranged from 795 to 913 mm while all male specimens >759 mm L_T were mature. The data suggest that mating occurs before parturition, with simultaneous ovulation. The diet of adult *M. schmitti* was mainly carcinophage and the diet of young-of-the-year and adults differed. The young-of-the-year use the Ría Deseado as a pupping area. © 2000 The Fisheries Society of the British Isles

Key words: pupping area; reproduction; stocks; feeding; South-west Atlantic.

INTRODUCTION

The smoothhound *Mustelus schmitti* Springer, 1939, called gatuzo, is an abundant, economically important and endemic shark from the coastal waters of south-western South America. The distribution of this small triakid extends from north of Rio de Janeiro, Brazil (Figueiredo, 1977) to southern Patagonia, Argentina (47°45'S) (Fig. 1) where temperatures range from 8 to 11.7° C at the surface and from 5.5 to 11° C at the bottom (Menni, 1985, 1986). This species is caught commonly by commercial trawlers and with gillnets from Rio Grande do Sul, Brazil to northern Patagonia, Argentina (Chiaramonte, 1998). It is poorly known in southern Patagonia, and its reproductive process has been studied mainly in Buenos Aires province and northern Patagonia (Menni, 1985, 1986; Menni *et al.*, 1986; Cousseau *et al.*, 1998). It is a non-placental ovoviviparous species with uterine compartments (Menni *et al.*, 1986). They suggested that the reproductive cycle is annual, with 11 months of gestation period and immediate ovulation, and gave a brief outline of embryonic development, size at maturity and reproductive cycle. Diaz de Astarloa *et al.* (1997) found differences in the total length at maturity between 1978 and 1993 in the samples collected in the North Argentine coast. Cousseau (1986) noted an increasing mean total length with latitude in the area of the Buenos Aires province, but data on the biology of the stocks of the different fishing areas has not been reported.

Springer (1967) stated that sharks migrate to rather specific places where the females lay eggs or give birth to young. With two exceptions, the species

‡Author to whom correspondence should be addressed. Tel.: 54 11 982 9410; fax: 54 11 982 5243 or 4494; e-mail: gchiarom@mail.retina.ar

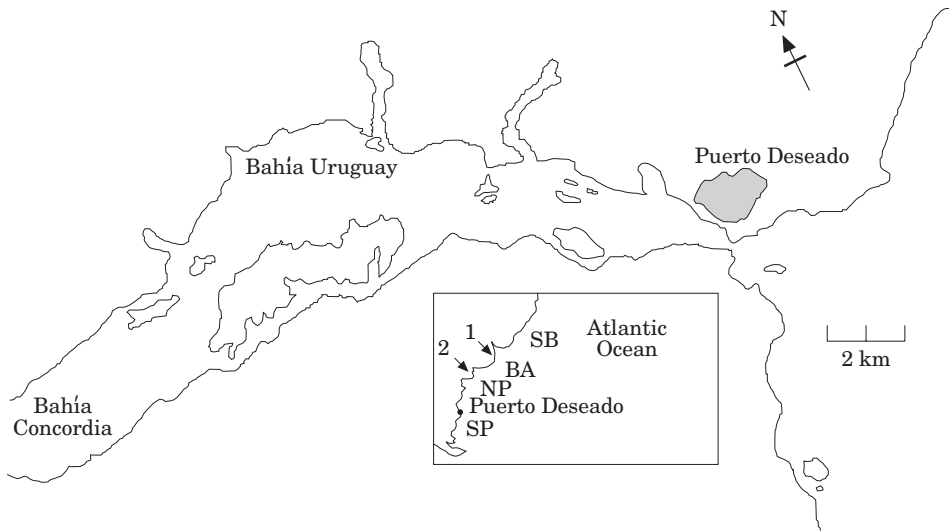


FIG. 1. Sampling location, Ría Deseado. Areas of South West Atlantic where *Mustelus schmitti* was studied: SB, South Brazil; BA, Buenos Aires province; NP, North Patagonia; SP, South Patagonia. Other pupping areas: 1, Bahía Samborombón; 2, El Rincón.

requirements for nursery areas may be limited by water depth and habitat type. The young of shallow-water sharks tend to concentrate in the shallower parts of the population range which typically represent nursery areas. Bass (1978) divided nursery areas into primary and secondary types: primary nurseries are those in which parturition occurs and where the young live for a short time, while secondary nurseries are those in which juveniles are present after having left the primary nursery and before reaching maturity. Castro (1987) stated that most species have a geographically discrete nursery, and that nurseries are located usually in highly productive shallow waters, such as coastal marshes and estuaries, where the young can find abundant food. Cousseau (1982, 1986) observed large mature specimens in two coastal areas (Bahía Samborombón and El Rincón, Fig. 1) in the province of Buenos Aires during the spring (October 1981). In northern Patagonia, the Bahía Engaño area ($43^{\circ}30'S$) was identified as a pupping area for this and other shark species (Van der Molen *et al.*, 1998).

Between spring 1995 and summer 1998 a survey of the ichthyofauna was conducted in the Ría Deseado area (Fig. 1). Specimens of *M. schmitti* were captured from this estuary during each spring–summer season. In this study the life history of *M. schmitti* is investigated in southern Patagonia, with particular interest in the life cycle and the role of this estuary for the smoothhound life cycle.

MATERIALS AND METHODS

PHYSICAL SETTING

The Patagonian coastline extends from the Colorado River ($42^{\circ}S$) to the Strait of Magellan ($52^{\circ}S$). The Ría Deseado (Fig. 1; $47^{\circ}45'S$; $65^{\circ}55'W$) is a 40 km penetration of

the South Atlantic Ocean inside the coast. The Deseado River flows into the bottom of the Ria, and has a very low water supply. Salinity along the Ria fluctuates between 3.3 and 3.4‰. The tidal range has amplitudes of near 6 m and the tidal currents are very strong. The following abbreviations will be used in the text: RS, Río Grande do Sul, Brazil; BA, Buenos Aires; NP, northern Patagonia; SP, Ria Deseado area in southern Patagonia.

SOURCE OF SAMPLES

The smoothhounds were sampled with hook and line, beach seines and from recreational fishermen. Because the tidal currents in the area are very strong, gillnets used in 1995 were discarded in the 1996–1997 surveys. Specimens were taken from November 1994 to February 1998. All samples were frozen until processing.

GENERAL BIOLOGICAL MEASUREMENTS

Whenever possible, each shark was sexed, measured, weighed, and examined for reproductive conditions. Precaudal length (L_{PC}) and total length (L_T) were measured to the nearest mm on a horizontal line between perpendiculars, from the tip of the snout to the insertion of the upper caudal lobe and to the tip of the upper lobe of the caudal peduncle at its maximum extension. Total weight (W) and gutted weight (W_G) were registered to the nearest g. To test differences of the length–weight relationship between sexes Student's t -test was used (Zar, 1996). Differences of L_T v. L_{PC} between sexes were tested by means of ANCOVA.

REPRODUCTIVE ANALYSES

Complete reproductive tracts were dissected from both male and female sharks and processed in the laboratory. For each male reproductive tract, the testes were excised from the surrounding epigonal gland and weighed to the nearest 0.1 g. Then gonadosomatic index was calculated for mature mass by using the following formula:

$$I_G = 100G B^{-1}$$

where I_G is gonadosomatic index, G is fresh gonad weight and B is somatic body weight (stomach empty, gonads removed).

Clasper length (L_C) was measured from the point of insertion at the cloaca to the tip of claspers. The degree of calcification of claspers was measured and recorded as one of the following categories: immature I (non calcified); immature II (adolescent, partially calcified, with developing testis); mature III (fully calcified, and the base of the clasper could be rotated, directed the clasper anteriorly; Clark & von Schmidt, 1965).

For each female reproductive tract the posterior section of the oviduct and the ovary was classified as follows: 1, thin tubular structure and undeveloped ovary; 2, thin tubular structure and developed ovary with white ova; 3, tubular structure enlarged with yolked ova in ovary; 4, tubular structure distended with yolked eggs or visible embryos in oviduct. The embryos were measured for L_T and sexed. The maximum diameter of the ova was measured with calipers to the nearest 0.01 mm and the minimum diameter of the ova with a calibrated binocular microscope. Since large ova were never spherical, only the greatest diameters were measured. Females with ovaries that contained yolked ova were considered to be maturing. Once the oviduct condition had advanced to condition 4, they were considered mature. Sharks were considered to be young-of-the-year (YOY) when they had unhealed yolk sac scars (Castro, 1993; Simpfendorfer & Milward, 1993).

FEEDING

Stomach contents were processed and analysed in the laboratory. All components were identified to the lowest possible taxonomic level and counted. Whenever possible, for the crab *Cyrtograpsus angulatus*, the weight of each specimen was recorded. To determine the proportion of the total diet corresponding to a food item, the frequency–occurrence method was applied (Hyslop, 1980). For YOY and adults and between

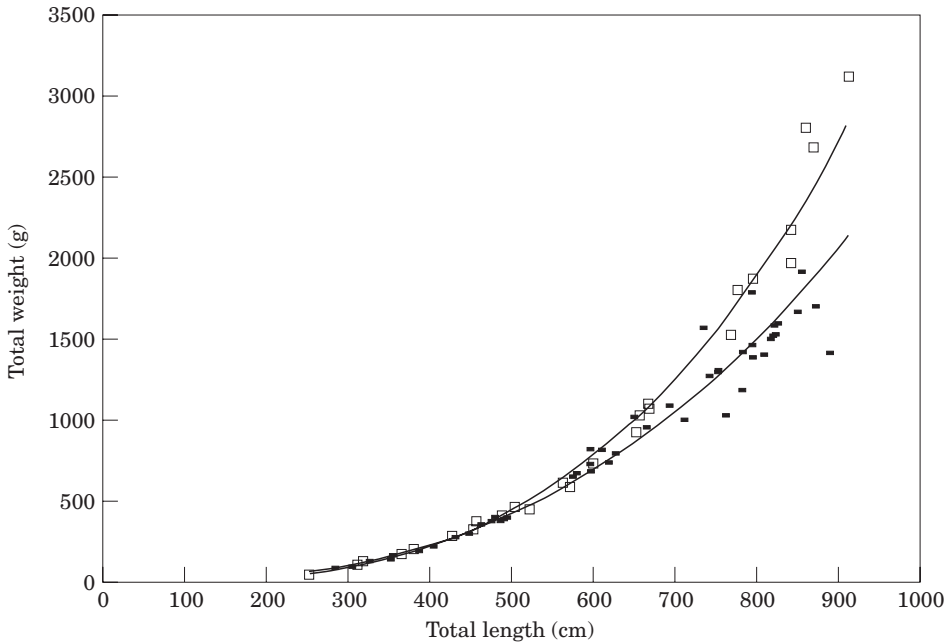


Fig. 2. Relationship between total weight and total length. —, Males: $W=1.69 \times 10E-04 \times L_T^{2.389}$; $r^2=0.98$. □, Females: $W=2.92 \times 10E-07 \times L_T^{3.384}$; $r^2=0.99$.

different sexes, diet overlaps (α) were estimated using Schoener's index (α) (Wallace, 1981):

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |p_{ji} - p_{ij}| \right)$$

where p_{ji} is the proportion of the i th resource used by YOY (or males), and p_{ij} is the proportion of the i th resource used by the adults (or females, according to the analysis carried out). Diets were considered different when overlap values were <0.5 (Keast, 1985).

RESULTS

SIZE RANGE

Of a total of 88 free-swimming individual *M. schmitti* sampled, 11 were YOY (with yolk sac scars) and 77 were adolescents (immature) and adults (mature), ranging from 252 to 913 mm L_T . Males ($n=56$) were 281–887 mm (90–2054 g) and females ($n=32$) 252–913 mm (48–3121 g).

MORPHOMETRICS

Females attained a greater length and mass than males (Fig. 2). Differences of slopes of the logarithmic relationship between L_T and W for males and females were significant (Student's t -test: $t > 1.993$, $P < 0.001$). W v. W_G (Fig. 3) gave a proportion of 82% of gutted weight for males, and 79% for females. Because the slopes of the lines of the relationship between L_T and L_{PC} were not significantly

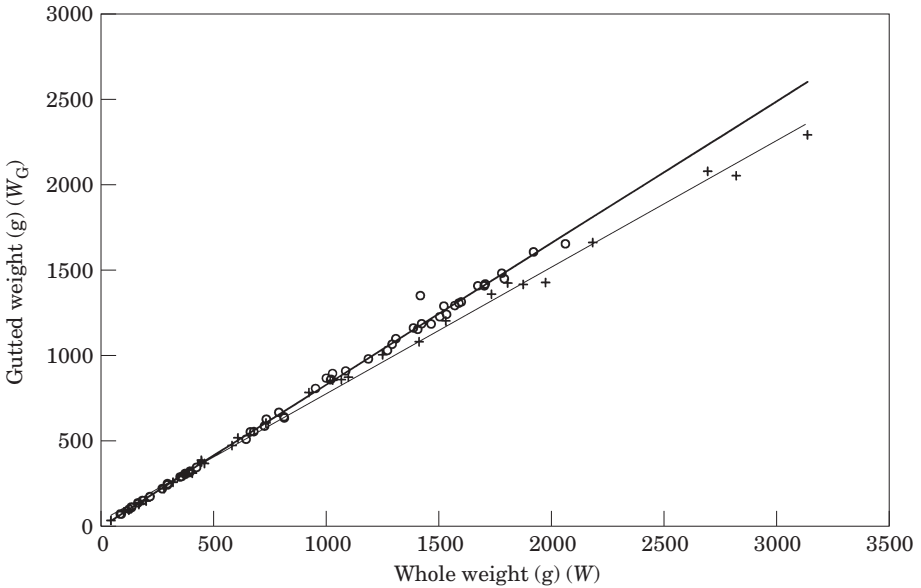


FIG. 3. Relationship between gutted weight and total weight. \circ , Males: $W_G=0.8384W-5.726$; $r^2=0.9961$. $+$, Females: $W_G=0.794W+31.477$; $r^2=0.9968$.

different between sexes (ANCOVA: $P=0.615$, d.f.=76), the following relationship was given for both genders:

$$L_{PC}=0.832 L_T - 10.618 \quad (r^2=0.99, n=79)$$

SIZE AT MATURITY

The size at maturity of *M. schmitti* varied in connection with gender. In males, the development of the testis was gradual [Fig. 4(a)], while clasper length increased abruptly [Fig. 4(b)]. Claspers began to elongate at *c.* 620 mm L_T [Fig. 4(b)] and became calcified by 759 mm L_T (Table I). All specimens <690 mm L_T had uncalcified claspers and were considered immature. Specimens of 708–750 mm L_T were in a transitional adolescent stage, characterized by elongated claspers that were uncalcified, or when calcified, they would barely fold. The smallest mature male measured 708 mm L_T . All male specimens >759 mm L_T were mature.

The smallest female with white ova in the ovary measured 457 mm L_T with largest ova 2.91 mm in diameter. The minimum length at maturity was 795 mm L_T . The L_T of the smallest gravid female was 842 mm, while that of the smallest female with uterine eggs was 795 mm. The largest egg diameter measured was 12.20 mm. A 776 mm L_T female caught on 23 February 1997 had developing uteri and no oocytes in the ovary. Presumably this female would have ovulated the following spring for the first time. Another specimen caught on 4 January 1998 measuring 791 mm L_T with thin uteri and no oocytes in the ovary was the largest immature female seen.

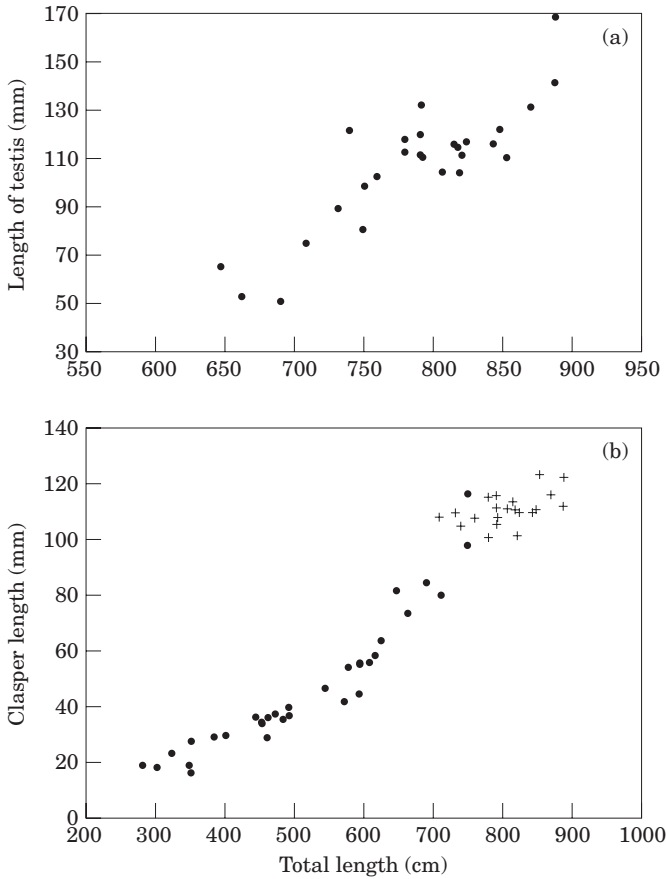


FIG. 4. (a) Relationship between testis length and total length. (b) Relationship between clasper length and total length. +, Mature; ●, immature.

REPRODUCTION

The mean monthly values for the gonadosomatic index (I_G) for adult males [Fig. 5(a)] increased sharply from November to February (spring to summer). For females, the I_G ranged from a maximum of 1.35 in March from a single specimen to a minimum of 0.85 in November. The average maximum ova diameter [Fig. 5(b)] was higher in spring than in summer. No evidence of mating scars was observed.

Two gravid females were caught in spring 1994 and 1995. One female caught in the first week of November 1994 carried six embryos 208–224 mm L_T , while another caught on 12 December 1995 carried embryos 254–281 mm L_T . Between January and March YOY were caught in Ría Deseado waters. The smallest free swimming neonate captured in this study measured 252 mm L_T and was a female caught on 22 February 1998. The smallest free swimming male was caught on 15 February 1998, measuring 281 mm L_T (Fig. 6).

TABLE I. Clasper condition

Date	L_T	L_{Te}	L_C	I/M
23 Feb. 1997	594	69.3	54.6	I
18 Feb. 1996	624	76.6	63.45	I
18 Feb. 1995	647	65	81.6	I
23 Feb. 1995	662	52.6	73.2	I
18 Feb. 1995	690	50.7	84.6	I
5 Feb. 1995	708	74.6	108.2	M
18 Feb. 1995	731	88.7	109.8	M
25 Feb. 1996	739	121	105	M
23 Feb. 1997	749	80.1	98	I
23 Feb. 1997	750	98	116.4	I
5 Feb. 1995	759	102	107.8	M
19 Nov. 1995	779	112.25	100.9	M
19 Nov. 1995	779	117.45	115.5	M

Date, Date of the capture; L_T , total length (mm); L_{Te} , testis length (mm); L_C , clasper length (mm); I/M, immature/mature.

FEEDING

Of the 77 stomachs examined, 10 (15.1%) were empty, all from adults and none from YOY. Feeding data revealed 64.9% overlap among diets by sex ($\alpha=0.649$). The diet of YOY differed significantly from that of the adults ($\alpha=0.413$), with only 41.3% overlap. The main prey item in adults' stomachs was the crab *C. angulatus* (50.4%), followed by other fishes (excluding Zoarcidae, *Austroatherina incisa* and *Sprattus fuegensis*) with 11.2% Serolidae (9.3%) and Polychaeta (9.3%) (Table II). In YOY, the main prey item was Euphausiacea (27.2%), followed by *C. angulatus* (22.7%) and Serolidae (18.1%). Decapoda amounted to 51.9% of total items, fishes were 11.81% and polychaete worms were 7.87%.

Of the 31 female stomachs studied, 4 (12.9%) had no prey, 10 (32.2%) had only one item, 11 (35.4%) had two items, 4 (12.9%) had three items, and 2 (6.4%) had four items. In stomachs of 56 males, 6 (10.7%) had no prey, 25 (44.6%) had one item, 16 (28.5%) had two items, 8 (14.2%) had three items, and 1 (1.7%) had four items.

The weight of one prey item increased with fish size. The weight of crabs *C. angulatus* in the stomach varied with length of *M. schmitti* (Fig. 7), but the relationship was not significant.

DISCUSSION

The southern limit of occurrence of *M. schmitti* is a protected area, the Ría Deseado. During late spring, schools of *M. schmitti* arrive in Ría Deseado from the open sea. Breeding adults, newborn and juveniles spend the summer in the waters of the Ría and leave it late in summer. In spite of the effort carried out during the study, the number of specimens caught was lower than expected. This low abundance might be explained by a border effect. Another factor that could

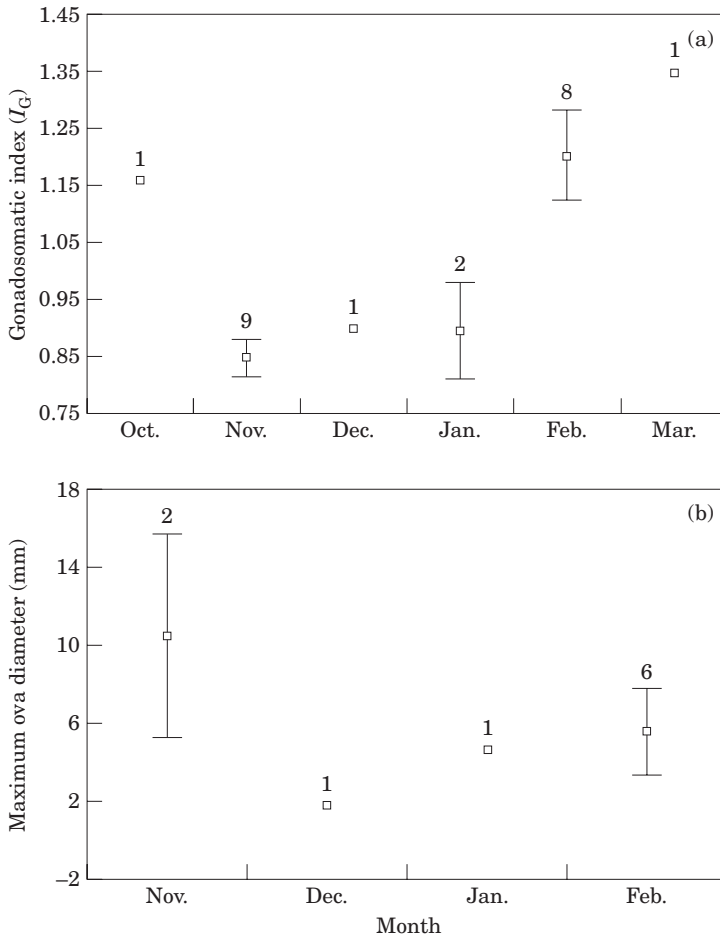


FIG. 5. (a) Mean gonadosomatic index plotted by month. (b) Maximum ova diameter plotted by month. □, Mean \pm S.E.

have affected the low yield was the exclusive use of passive gears (line and hooks), because of the difficulty of trawling over irregular bottoms. Moreover, the use of beach seines was not effective.

In *M. schmitti* of SP, the weight of the testis increased from February, after the mating season. This fact was coincident with the development of the new ova in females during summer, along with parturition. The minimum average value of male I_G occurred in November, along with the maximum average value of ova diameter. The gestation period could conclude around the end of spring during December. In November a female was found with embryos, small oocytes (0.29–5.30 mm diameter) and uterine eggs (5.70–15.40 mm), and another one in December with embryos and uterine eggs (1.30–18.20 mm). Present data suggest that mating occurs before parturition, with immediate ovulation. This evidence implies that mature females in the region become pregnant each year. Taking into account these factors, it is concluded that the gestation period for *M. schmitti* in the area is at least 12 months. Similar results were obtained by

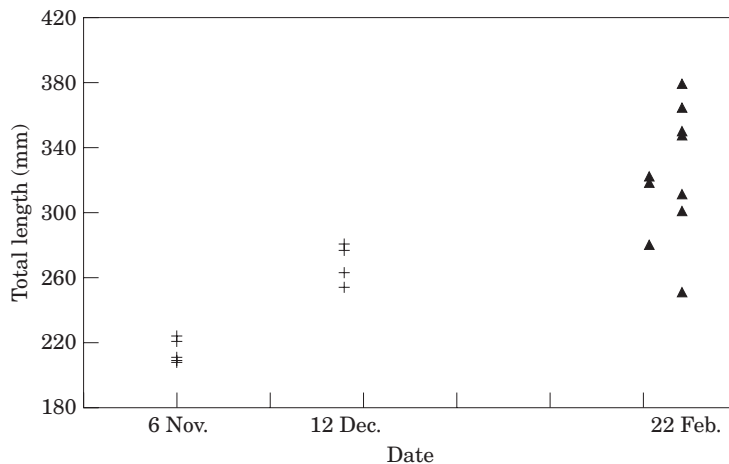


Fig. 6. Total length of embryos (+) and free swimming young (▲), plotted by date.

TABLE II. Diet of adults and young of the year of *M. schmitti* in Ría Deseado, Patagonia, Argentina

Prey item	Adults		YOY	
<i>n</i>	66		11	
Full stomach	56		11	
Empty stomach	10		0	
	F	%	F	%
<i>Cyrtograpsus angulatus</i>	54	50.4	5	22.7
<i>Peltarion spinosulum</i>	3	2.8	0	0.0
Majidae	4	3.7	0	0.0
Amphipoda	2	1.8	3	13.6
Serolidae	10	9.3	4	18.1
Alpheidae	1	0.9	0	0.0
Euphausiacea	0	0.0	6	27.2
Polychaeta	10	9.3	0	0.0
Polyplacophora	1	0.9	0	0.0
<i>Loligo gahi</i>	6	5.6	3	13.6
<i>Sprattus fueguensis</i>	1	0.9	0	0.0
<i>Austroatherina incisa</i>	0	0.0	1	4.5
Zoarcidae	1	0.9	0	0.0
Other Osteichthyies	12	11.2	0	0.0
Algae	2	1.8	0	0.0

Souto (1986) for RS while Menni *et al.* (1986) found that in BA this period was 11 months with immediate ovulation. Even when Pratt & Casey (1990) denote that gestation in warmer seas is shorter than in more temperate seas for some species, this pattern is not clear for *M. schmitti*. No evidence of mating scars was

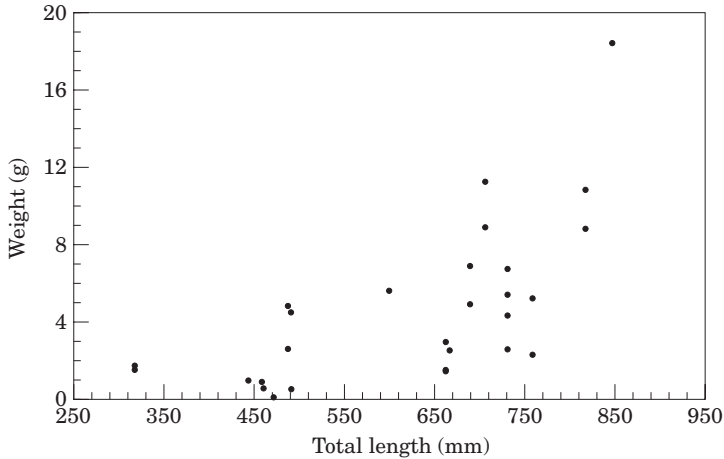


FIG. 7. Relationship between weight of crabs (*Cyrtograpsus angulatus*) found in the stomach contents and the total length of sharks.

observed in *M. schmitti*. Smale & Compagno (1997) made the same observation in *Mustelus mustelus* (L.) and explained it in view of the crushing dentition of the species.

The manner in which shark reproduction varies geographically has been the aim of a few studies. Springer (1960) showed some latitudinal reproductive differences in the western North Atlantic population of *Carcharhinus plumbeus* (Nardo). Parsons (1993) found latitudinal differences in two populations of *Sphyrna tiburo* (L.) in the timing of reproductive events, growth parameters, and male and female maturation and size distribution. Lenanton *et al.* (1990) found differences in the maximum frequency of pregnancy and fecundity between south-western and south-eastern Australian stocks of *Mustelus antarcticus* Günther. Although Menni *et al.* (1986) found that females of *M. schmitti* were heavier than males, and there was no difference in the relationship of body weight and total length for males and females in BA specimens: in the present sample this relationship differed between sexes (Fig. 2). Differences in length increased from maturity stage I to maturity stage III between BA (Menni *et al.*, 1986) and SP areas (Fig. 1). Size at maturity in males was greater in SP than in BA and NP areas (Fig. 1; 38° S; Menni *et al.*, 1986; between 34° and 42° S, Díaz de Astarloa *et al.*, 1997; Cousseau *et al.*, 1998) in Argentina and RS area (30°40' and 33°44'S; Souto, 1986) in Brazil. Mature males ranged from 708 to 887 mm L_T in SP, 510 to 660 mm L_T in RS (Souto, 1986), 517 to 780 mm in BA (Menni *et al.*, 1986) and 525 to 870 mm in NP (Menni, 1985). Immature females ranged from 252 to 791 mm L_T in SP, and 260 to 742 mm L_T in BA (Menni *et al.*, 1986). Mature females ranged from 795 to 913 mm L_T in SP, 590 to 780 mm L_T in RS (Souto, 1986), 590 to 895 mm L_T in BA (Menni *et al.*, 1986) and 615 to 1085 mm L_T in NP (Menni, 1985).

The reproductive parameters reported in the present paper suggest differences in life history between the SP stock of *M. schmitti* and the RS, BA and NP stocks. At least two sources for these variations should be focused. First, the increasing mean total length with latitude reported by Cousseau (1986) sustains

the hypothesis of a latitudinal cline derived from adaptations to small variations in oceanographic conditions. The second hypothesis implies that the fishing pressure could force a density-dependent response of the shark stocks, e.g. the decrease in the size at maturity for *M. schmitti* in BA area from 1978 to 1993 (males: 600–549 mm; females: 626–605) reported by Diaz de Astarloa *et al.* (1997). This decrease adds more distance in the differences of size at maturity between BA and SP stock. However, this hypothesis of change in size at maturity as a density-dependent response in *M. schmitti* needs more thorough studies, since Walker (1998) assigned the density-dependent response to natural mortality rate rather than to reproductive rate or growth rate in *M. antarcticus* stocks.

The diet of adult *M. schmitti*, like the majority of *Mustelus* species, was mainly carcinophage (Heemstra, 1973; Compagno, 1984), and present results agree mostly with those of Olivier *et al.* (1968), Menni (1985, 1986), Menni *et al.* (1986) and Capitoli *et al.* (1995). However, there were differences in the diets of the YOY and of adults. Smale & Compagno (1997) concluded that the trend for larger prey organisms to be eaten by larger sharks is partly related to the type and strength of the exoskeleton in crustaceans. Smaller sharks may be unable to handle and crush larger crustaceans. Then, the dominance of Euphausiacea in YOY stomach contents would be explained by the small size of the specimens, more than by a pelagic or planktonic diet. For the item *C. angulatus*, YOY consumed small crabs (Fig. 6), while adults ate both small and large crabs.

Springer (1967) suggested that the only important predators of sharks are other sharks, and that the nursery areas may be chosen based on the absence of large sharks. However, both Springer (1967) and Branstetter (1990) noted that the degree of protection from predation afforded by nursery areas varied among species. Other shark species occur in the Ría and would be using it as a nursery area (Gosztonyi, 1973). In the course of this study, anglers in the same area and during four sport tournaments caught 41 sevengill sharks *Notorynchus cepedianus* (Peron). Eighteen stomach contents were examined, but only three had food, other than *M. schmitti*; the others were empty or everted. Sport fishermen noted that a big fish (presumably *N. cepedianus*) ate the body of a hooked smoothhound, leaving only its head. This could indicate that the Ría Deseado is both a nursery and a predatory area for some sharks.

The authors thank L. Asseo de Choch, O. Juanola, L. Policastro, N. Renaudeau d'Arc, L. Tamini and M. Tanuz for field assistance; the Area Pasantías, Facultad de Ciencias Exáctas y Naturales—Universidad de Buenos Aires; S. M. Bonaventura for her helpful comments; and M. B. Cousseau and R. Menni for their critical review of the manuscript. GC's field work was partly financed by the National Science and Technology Secretariat (SECyT).

References

- Bass, A. J. (1978). Problems in studies of sharks in the southwest Indian Ocean. In *Sensory Biology of Sharks, Skates and Rays* (Hodgson, E. S. & Mathewson, R. F., eds), pp. 545–594. Arlington: Office of Naval Research, Department of the Navy.
- Branstetter, S. (1990). Early life-history implications of selected carcharhinoid and lamnoid sharks of the Northwest Atlantic. In *Elasmobranchs as Living Resourcesources:*

- Advances in the Biology, Ecology, Systematics and the Status of the Fisheries* (Pratt, H. L. Jr, Gruber, S. H. & Taniuchi, T., eds). Washington, D.C.: NOAA Technical Report, NMFS 90.
- Capitoli, R. R., Ruffino, M. L. & Vooren, C. M. (1995). Alimentação do tubarão *Mustelus schmitti* Springer na plataforma costeira do estado do Rio Grande do Sul, Brasil. *Atlântica, Rio Grande* **17**, 109–122.
- Castro, J. I. (1987). The position of sharks in marine biological communities. In *Sharks, an Inquiry into Biology, Behavior, Fisheries and Use* (Cook, S., ed.), pp. 11–17. Corvallis: Oregon State University Extension Service.
- Castro, J. I. (1993). The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes* **38**, 37–48.
- Clark, E. & von Schmidt, K. (1965). Sharks of the Central Gulf Coast of Florida. *Bulletin of Marine Science* **15**, 13–83.
- Chiaromonte, G. E. (1998). Shark fisheries in Argentina. *Marine and Freshwater Research* **49**, 601–609.
- Compagno, L. J. V. (1984). FAO species catalogue 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Parts 1 and 2. *F.A.O. Fisheries Synopsis* **125**, 655 pp.
- Cousseau, M. B. (1982). Investigaciones sobre el gatuzo. In *Informe del Primer Año de Investigaciones del Proceso Pesquero de los Recursos Costeros*. Mar del Plata: Archivo INIDEP.
- Cousseau, M. B. (1986). Estudios biológicos sobre peces costeros con datos de dos campañas de investigación realizadas en 1981. V. El gatuzo (*Mustelus schmitti*). *Publicaciones de la Comisión Técnica Mixta del Frente Marítimo* **1**, 60–66.
- Cousseau, M. B., Carozza, C. R. & Macchi, G. J. (1998). Abundancia, reproducción y distribución de tallas del gatuzo (*Mustelus schmitti*) en la zona común de pesca Argentino-Uruguaya y en El Rincón. Noviembre, 1994. In *Resultados de una Campaña de Evaluación de Recursos Demersales Costeros de la Provincia de Buenos Aires y del Litoral Uruguayo, Noviembre, 1994* (Lasta, C. A., ed.). *Mar del Plata: Informe Técnico* **21**, INIDEP, pp. 103–115.
- Diaz de Astarloa, J. M., Carozza, C. R., Guerrero, R. A., Baldoni, A. G. & Cousseau, M. B. (1997). Algunas características biológicas de peces capturados en una campaña costera invernal en 1993, en el área comprendida entre 34° y 42° S (Atlántico Sudooccidental) y su relación con las condiciones ambientales. *Mar del Plata: Informe Técnico* **14**, INIDEP, 35 pp.
- Figueiredo, J. L. (1977). *Manual de Peixes Marinhos do Sudeste do Brasil. I.—Introdução, Cações, Raias e Quimeras*. São Paulo: Ed. Museu de Zoologia, Universidade São Paulo.
- Gosztanyi, A. (1973). Sobre el dimorfismo sexual secundario en *Halaehurus bivius* (Müller y Henle 1841) Garman 1913 (Elasmobranchii, Scyliorhinidae) en aguas patagónico-fueguinas. *Physis (A)* **32**, 317–323.
- Heemstra, P. C. (1973). A revision of the shark genus *Mustelus* (Squaliformes Carcharhinidae). Ph.D. Thesis, University of Miami.
- Hyslop, E. J. (1980). Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology* **17**, 411–429.
- Keast, A. (1985). Development of dietary specializations in a summer community of juvenile fishes. *Environmental Biology of Fishes* **13**, 211–224.
- Lenanton, R. C. J., Heald, D. I., Platell, M., Cliff, M. & Shaw, J. (1990). Aspects of the reproductive biology of the gummy shark, *Mustelus antarcticus* Günther, from waters off the south coast of Western Australia. *Australian Journal of Marine and Freshwater Research* **41**, 807–822.
- Menni, R. C. (1985). Distribución y biología de *Squalus acanthias*, *Mustelus schmitti* y *Galeorhinus vitaminicus* en el Mar Argentino en agosto-setiembre de 1978 (Chondrichthyes). *Revista del Museo de La Plata (nueva serie) sección zoología* **xiii** **138**, 151–182.

- Menni, R. C. (1986). Shark biology in Argentina: a Review. In *Indo-Pacific Fish Biology: Proceedings Second International Conference Indo-Pacific Fishes* (Uyeno, T., Arai, R., Taniuchi, T. & Matsuura, K., eds), pp. 425–436. Tokyo: Ichthyological Society of Japan.
- Menni, R. C., Cousseau, M. B. & Gosztonyi, A. R. (1986). Sobre la biología de los tiburones costeros de la Provincia de Buenos Aires. *Anales de la Sociedad Científica Argentina* **ccxiii**, 3–27.
- Olivier, S. R., Bastida, R. & Torti, M. R. (1968). Ecosistema de las aguas litorales. *Publicaciones del Servicio de Hidrografía Naval*, H **1025**, 5–45.
- Parsons, G. R. (1993). Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. *Environmental Biology of Fishes* **38**, 25–35.
- Pratt, H. L. Jr & Casey, J. G. (1990). Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries* (Pratt, H. L. Jr, Gruber, S. H. & Taniuchi, T., eds). Washington, D.C.: NOAA Technical Report, NMFS 90.
- Simpfendorfer, C. A. & Milward, N. E. (1993). Utilization of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes* **37**, 337–345.
- Smale, M. J. & Compagno, L. J. V. (1997). Life history and diet of the two southern African smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* Smith, 1957 (Pisces: Triakidae). *South African Journal of Marine Science* **18**, 229–248.
- Souto, C. F. M. (1986). Estudo comparativo da reprodução nos cações *Mustelus schmitti*, Springer 1939 e *M. canis*, Mitchill 1815 (Pisces: Squaliformes), na plataforma continental do Rio Grande do Sul—Brasil. Ms.Sc. Thesis, Universidade do Rio Grande.
- Springer, S. (1960). Natural history of the sandbar shark, *Eulamia milberti*. *U.S. Fishery Bulletin* **61**, 1–38.
- Springer, S. (1967). Social organization of shark populations. In *Sharks, Skates and Rays* (Gilbert, P. W., Mathewson, R. F. & Rall, D. P., eds), pp. 149–174. Baltimore: Johns Hopkins Press.
- Van Der Molen, S., Caille, G. & González, R. (1998). Incidental capture of shark in Patagonian coastal trawl fisheries. *Marine and Freshwater Research* **49**, 641–644.
- Walker, T. I. (1998). Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* **49**, 553–572.
- Wallace, R. K. (1981). An assessment of diet-overlap indices. *Transactions of the American Fisheries Society* **110**, 72–76.
- Zar, J. H. (1996). *Biostatistical Analysis*. New Jersey: Prentice Hall.