Reproductive and population parameters of spiny dogfish *Squalus acanthias* in the south-western Atlantic Ocean

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The objective of this study was to estimate reproductive and population parameters of the spiny dogfish *Squalus acanthias* for the south-western Atlantic Ocean. In total, 2714 specimens (1616 males and 1098 females) were collected from surveys carried out using research vessels. Males ranged from 225 to 861 mm total length (L_T) and females from 235 to 925 mm L_T. The size at maturity of females (651 mm) was significantly greater than that of males (565 mm). The maximum proportion of mature individuals (P_{max}) of the gestation ogive was <1, which indicates that a proportion of mature females was not in gestation. This inactivity may be explained by the occurrence of resting periods between cycles or by the asynchrony of the reproductive cycle. The estimated P_{max} for the maternity ogive suggested that about one third of mature females were in the maternity stage (*i.e.* with embryos >156 mm). The temporal and spatial co-occurrence of non-gravid adult females at different stages of ovarian development, as well as gravid females at all embryonic development stages would indicate that the female reproductive cycle in the south-western Atlantic Ocean is asynchronous. The results indicate that *S. acanthias* is susceptible to fishing pressure on account of its length at maturity, extended reproductive cycles and low fecundity.

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Key words: elasmobranch; maternity; maturity; reproductive asynchrony; shark.

INTRODUCTION

The spiny dogfish *Squalus acanthias* L. 1758 is a relatively small shark that occurs in temperate waters of the world oceans (Compagno, 1984; Nelson, 2006). This shark shows regional population trends characterized by extensive and complex seasonal migrations. Despite its wide distribution, panmixia has been dismissed due to the heterogeneity of populations (Veríssimo *et al.*, 2011). In South American waters, *S. acanthias* is distributed from 33° S in the Atlantic Ocean (Menni, 1985; García de la Rosa, 1998; Massa *et al.*, 2007; Domingo *et al.*, 2008; Di Giacomo *et al.*, 2009) to South Pacific waters (Compagno, 1984; Reyes & Torres-Florez, 2009). Recent studies suggest low genetic divergence between collections from the Atlantic and South Pacific basins (Veríssimo *et al.*, 2011).

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The reproduction of *S. acanthias* has been studied throughout the world. There is considerable variation in population parameters, but in general, *S. acanthias* is lecithotrophic with slow growth (Campana *et al.*, 2009; Tribuzio *et al.*, 2009; Bubley *et al.*, 2013), a late age of sexual maturity (Campana *et al.*, 2009; Bubley *et al.*, 2013), widespread low fertility and a complex reproductive cycle (Compagno, 1984; Hanchet, 1988; Jones & Ugland, 2001; Demirhan & Seyhan, 2007; Capapé & Reynaud, 2011). These features are common to many species of sharks and suggest a low reproductive potential and low intrinsic growth rate. These life-history characteristics make the species highly vulnerable to exploitation and in need of special attention.

Populations of *S. acanthias* have been affected by fishing for almost a century, with different intensity depending on the fishery. In the North Atlantic, for example, on the coast of the U.S.A. and Canada, this shark has been drastically impacted due to the continued removal of large numbers since the early 20th century (Rago *et al.*, 1998; Wallace *et al.*, 2009). Throughout its range in the south-western Atlantic Ocean, *S. acanthias* is taken as by-catch by major industrial fisheries, but is typically discarded at sea (Massa *et al.*, 2004; Seco Pon & Gandini, 2007; Domingo *et al.*, 2008; Massa, 2009; Cedrola *et al.*, 2012).

Knowledge of the biology of *S. acanthias* in the south-western Atlantic Ocean is fragmentary. Studies investigating sexual maturity (Menni, 1985; Gosztonyi & Kuba, 1998; Di Giacomo *et al.*, 2009; Oddone *et al.*, 2015) and diet composition (Menni, 1985; Kohen Alonso *et al.*, 2002; Belleggia *et al.*, 2012) are covered in the literature. Less well documented are maternal condition and fecundity, which has important implications for demographic studies because of the complex and multi-annual reproductive cycle.

The objectives of the present study were to estimate reproductive and population parameters of *S. acanthias* for the south-western Atlantic Ocean. This study is part of the guidelines of the National Plan of Action for the Conservation and Management of Sharks in Argentina, for the generation of information on those species for which there is international concern.

MATERIALS AND METHODS

In total, 2714 specimens of *S. acanthias* (1616 males and 1098 females) were collected from surveys carried out using the R.V. *Dr Eduardo L. Holmberg* and *Cap. Oca Balda* of the Instituto Nacional de Investigación y Desarrollo Pesquero (National Institute for Fisheries Research and Development, Argentina) (Table I and Fig. 1). Fishing was conducted using a standard bottom trawl (Engel type net, 200 mm inner mesh size with a vertical height of 5 m and a horizontal opening of 20 m) at 7·4 km h^{-1} (4 knots) for 30 min in each sampling location.

For each specimen, total length (L_T, mm), total body mass (M_{TB}, g) and liver mass (M_L, g) were recorded. In two research surveys (EH-0110 and EH-0412), the number of specimens caught and measured on board was considerably higher than those analysed in the laboratory. Size distributions of the specimens collected on board were representative of the total capture. The morphometric relationship between L_T and M_{TB} was calculated for each sex. The data were ln transformed for regressions and the null hypothesis of no difference between the slopes was tested using ANCOVA (Zar, 1984).

According to the literature, all specimens of *S. acanthias* from the south-western Atlantic belong to the same genetic group (Veríssimo *et al.*, 2011). Therefore, specimens taken in all research surveys were considered as a single population in order to estimate reproductive parameters. The provenance (research surveys) of the specimens was considered only for the analysis of reproductive seasonality.

TABLE I. Specimens of the *Squalus acanthias* analysed by reproductive stage. The research surveys code and date are indicated

Code	Year	Date	Males			Females				
			S1	S2	S3	S1	S2	S3	S4	S5
EH-0110	2010	16 January to 14 February	44	20	105	74	10	13	10	4
OB-0111	2011	18 January to 9 February	84	23	97	98	8	2	2	5
EH-0111	2011	12 April to 8 May	12	9	35	48	15	26	7	22
EH-0311a	2011	7 August to 28 August	33	0	395	25	0	9	3	5
EH-0311b	2011	13 September to 3 December	152	33	356	147	41	18	21	22
EH-0411	2011	19 December to 12 November	39	32	92	104	32	48	61	78
EH-0412	2012	16 May to 2 June	3	6	46	16	5	39	22	58
Total			1616			1098				
			2714							

S1, juvenile; S2, sub-adult; S3 (males), adult; S3 (females), adult non-gravid; S4, ovulatory; S5, gravid.

Maturity was assessed macroscopically following the criteria of Walker (2005) and Colonello *et al.* (2011). Males were classified as juvenile, sub-adult or adult, based on the development of claspers and testes. Depending on the development of the oviducal gland, uteri and ovary, females were separated into one of five maturity stages: (1) juvenile: small ovaries lacking differentiation of follicles, oviducal glands undifferentiated from uteri, which were slender and straight; (2) sub-adult: small ovaries with some ovarian follicle differentiation lacking mature ova, uteri narrow and constricted; (3) adult non-gravid: large ovaries and vitellogenic mature ova, developed but empty uteri; (4) ovulatory: small ovaries and fertilized ova in uteri, but non-differentiated embryos; (5) gravid: small or large ovaries and small or large embryos in the uteri.

The inner claspers length (L_C, mm), as measured from the end of the cloaca to the tip of the claspers, and the testis mass (M_T, g) were recorded for each male. The oviducal gland width (W_{OG}, mm), uterus width (W_U, mm) number and diameter of the largest ovarian follicles (D_{LOF}, mm) and ovary mass (M_O, g) were recorded for females. The embryos L_T and yolk sac width were also recorded in gravid females.

A logistic model was fitted to the maturity data (maturity ogive) using a maximum likelihood approach in order to estimate size at 50% maturity (L_{T50}):

$$P_i = P_{max} \left[1 + e^{-\ln 19 (L_{Ti} - L_{T95})(L_{T95} - L_{T50})^{-1}} \right]^{-1}, \tag{1}$$

where P_i is the proportion of mature individuals at the *i*th L_T (L_{Ti}), P_{max} is the maximum proportion of mature individuals (defined as 1) and L_{T50} and L_{T95} are the L_T at which individuals attain the 50 and 95% of P_{max}.

The timing of the male reproductive cycle was determined macroscopically through the variation in the gonado-somatic index I_G ($I_G = 100 M_T M_{TB}^{-1}$) and the presence of sperm in the vas deferens. In females, the hepato-somatic index ($I_H = 100 M_L M_{TB}^{-1}$), gonado-somatic index ($I_G = 100 M_O M_{TB}^{-1}$), diameter of the largest ovarian follicle and embryos L_T were compared between research surveys.

In order to identify and define stages of embryonic development, the relationship between the diameter of the yolk sac and embryos L_T was analysed by fitting a piece-wise linear regression with one break point following Toms & Lesperance (2003):

$$y_i = \begin{cases} \beta_0 + \beta_1 x_i + \varepsilon_i & \text{for } x_i \leq \alpha \\ \beta_0 + \beta_1 x_i + \beta_2 (x_i - \alpha) + \varepsilon_i & \text{for } x_i > \alpha \end{cases} \tag{2}$$
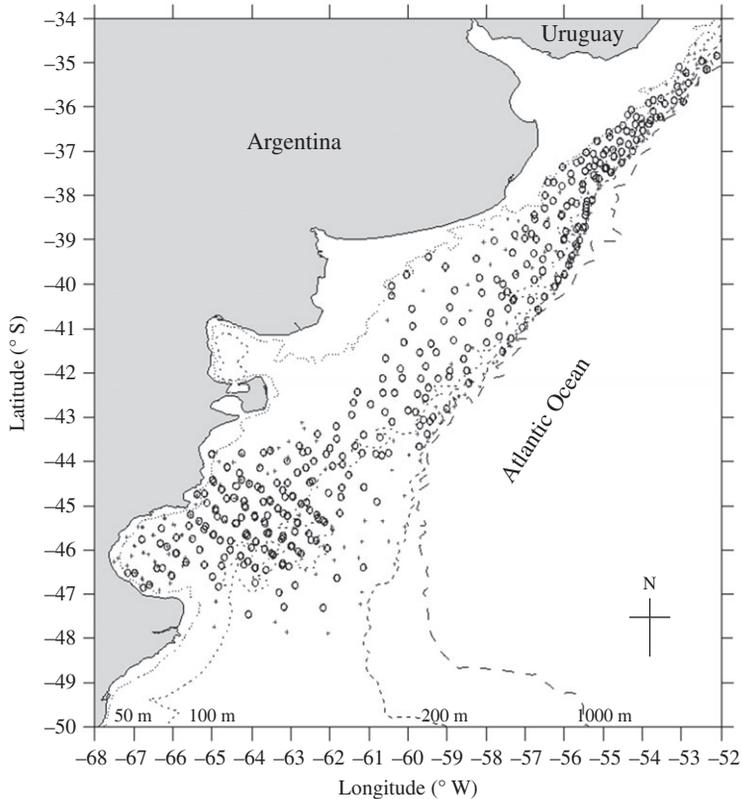
FIG. 1. Map of study area showing trawl stations with capture (○) and without (+) capture of *Squalus acanthias*.

where y_i is the diameter of the yolk sac for the ith embryo and x_i is the corresponding embryo L_T. The β_0 is the intercept, β_1 and $\beta_1 + \beta_2$ are the slopes of the two lines and α is the breakpoint. The errors (ε_i) were defined to be independent and additive, with a mean of zero and constant variance. The classic methodology used to analyse embryonic growth and development requires monthly sampling of gravid animals (Braccini *et al.*, 2006). Due to the impossibility of having a monthly sample covering the entire study region (*c.* 855 000 km^2), this investigation considered that stages of pregnancy can be inferred from the differential consumption of the yolk by embryos. For this analysis, two stages of gestation were defined using the breakpoint estimated from piece-wise linear regression. Stage 5.1 was identified as females bearing embryos with $L_T < \alpha$; stage 5.2 was identified as females bearing embryos with $L_T > \alpha$.

Equation (1) was also used to determine the relationship between L_T and (1) the proportion of females in gestation condition (gestation ogive; females with fertilized oocytes or embryos in the uterus, stages 4, 5.1 and 5.2) and (2) the proportion of females in the maternal condition (maternal ogive; females with embryos in the second step of development, stage 5.2). To estimate the gestation and maternal ogives, the P_{max} was estimated as a parameter, indicating the maximum proportion of females in the gestation and maternal conditions (L_{T95m}). To examine whether gestation is synchronous without resting or displays some degree of asynchrony and resting period, a logistic model that defines $P_{max} = 1$ (synchronous without resting gestation) was compared with a logistic model in which P_{max} is estimated (asynchronous or with resting period gestation). For this purpose, the Akaike information criterion (AIC) was used (Burnham & Anderson, 2002). The uncertainty of the logistic ogive parameters was estimated from 1000 Monte-Carlo simulations using the Cholesky factorization of the covariance matrix (Aubone, 2010).

The potential fecundity was defined by the number of ovarian follicles and fertility was given by the number of embryos in the uterus. Finally, the number of ovarian follicles and the number of embryos were related to female L_T using linear regression.

RESULTS

Males ranged from 225 to 861 mm L_T and females from 235 to 925 mm L_T (Fig. 2). North of 41° S, the proportion of females >700 mm L_T increased and specimens <350 mm L_T were not found (Fig. 2), whereas between 44° and 47° S, the largest proportion of individuals were males >560 mm L_T (Fig. 2). Specimens <350 mm L_T (neonates) were captured in trawls carried out in the Gulf between 65° and 68° W (EH-0110, OB-0111 and EH-0311a) (Fig. 2).

The morphometric relationship between L_T and M_{TB} was different between sexes (males: $M_{TB} = 2E\text{-}06 \times L_T^{3.0675}$; females: $M_{TB} = 3E\text{-}07 \times L_T^{3.3906}$) ($F_{2,508} = 49.093$, $P < 0.001$). Female mass was greater than males at any given L_T. These morphometric differences were observed for juveniles and adults.

The inner clasper length, according to L_T, was the best parameter to describe maturation in males [Fig. 3(a)], while the development of the testes (estimated from the mass) of adults presented a wide range of variation for each L_T [Fig. 3(b)]. Size at maturity in males was observed between 518 and 665 mm L_T and the maturity ogive showed a value of 565 mm for the L_T at which 50% of the population was mature [Fig. 3(c)]. This value was equivalent to 65% of the maximum L_T recorded for males. Significant differences were observed in I_G between the research surveys ($F_{6,887} = 9.24$, $P < 0.01$); however, the magnitude of these differences was low [Fig. 3(d)].

The uterus and oviducal gland width were the variables that best represented the onset of sexual maturation in females [Fig. 4(a), (b)]. The largest juvenile specimen measured was 760 mm L_T and the smallest adult specimen was 609 mm L_T (Fig. 4). The L_{T50} was estimated at 651 mm L_T [Fig. 4(d)], representing the 70% of the maximum L_T observed for females. Moreover, the size at maturity of females was larger than that of males. This difference can be considered significant due to non-overlapping 95% c.i. (Payton *et al.*, 2003). For the gestation ogive, the model including three parameters was best supported by the data (ΔAIC = 25.9). This model showed that the maximum proportion of gestational females was 0.88 and was attained at *c.* 766.2 mm L_T [Table II and Fig. 4(d)].

The largest embryo was 247 mm L_T, whereas the smallest measurable embryo was 37 mm L_T. The size of the yolk sac decreased as the size of embryos increased, showing two phases of decline with a break point at an embryo L_T of 156 mm [Fig. 5(a)]. During the second phase, the decrease in vesicle width was significantly higher than in the previous phase. All embryos >230 mm exhibited an empty external vitelline sac [Fig. 5(a)]. The diameter of the ovarian follicles increased during embryonic development, reaching the presumptive pre-ovulatory condition when embryos were near birth (*i.e.* without a yolk sac) [Fig. 5(b)].

The L_{T95m} (gravid females with embryos >156 mm L_T) was estimated at 763 mm L_T with a P_{max} of 0.29 L_T [Table II and Fig. 4(d)]. Non-gravid adult females (stage 3), post-ovulatory females (stage 4) and gravid females (stage 5) at different stages of gestation (stage 5), were captured across all surveys (Fig. 6). Adult females (gravid and non-gravid) showed ovarian follicles at different stages of development, from 10
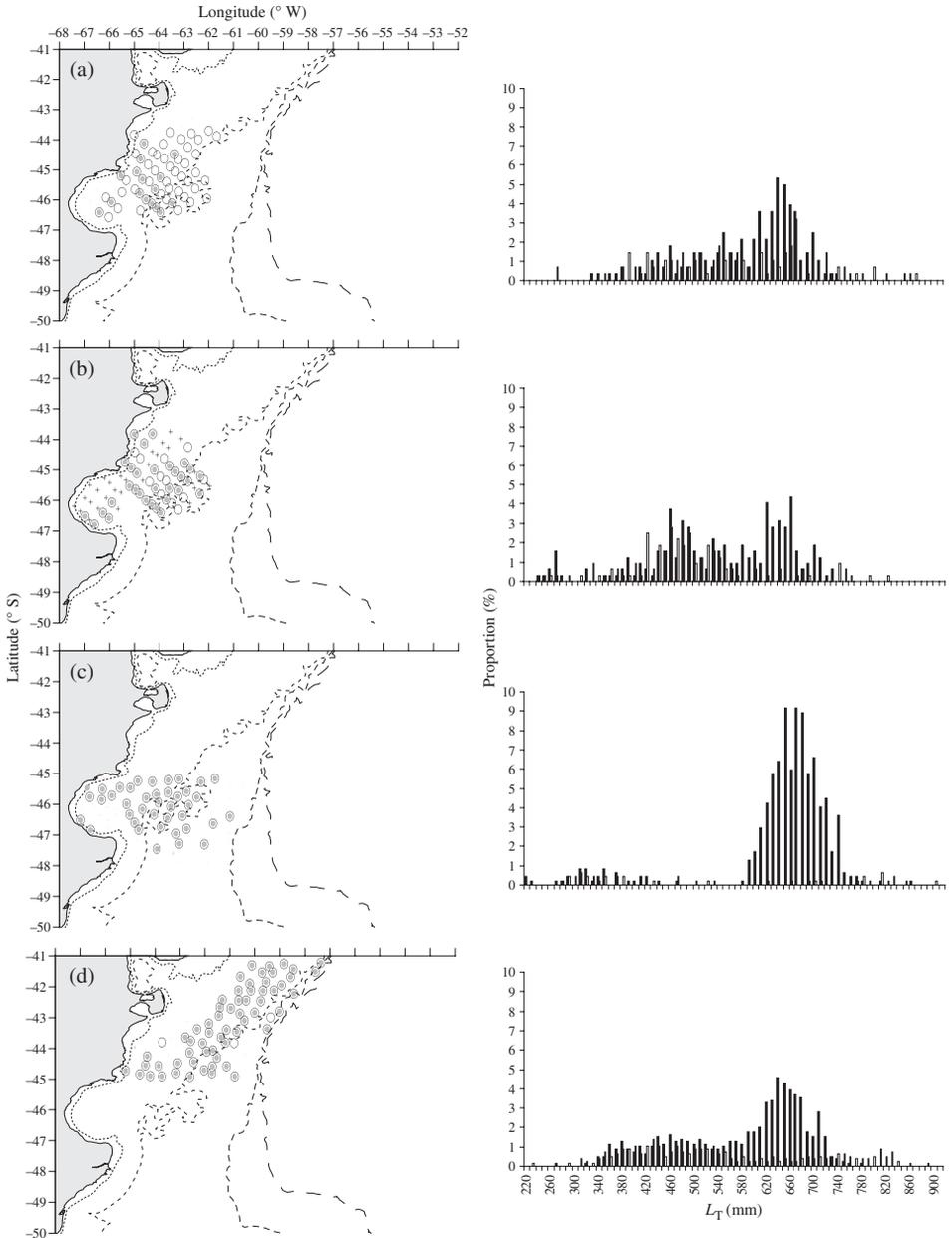
FIG. 2. Map of study area showing stations without capture (+), with capture (○) and with sampling (●) of *Squalus acanthias* and total length (L_T) frequency distribution of females (□) and males (■) analysed from research cruises (a) EH0410, (b) OB0111, (c) EH0111a, (d) EH0111b, (e) EH0411, (f) EH0412 and (g) EH0411.
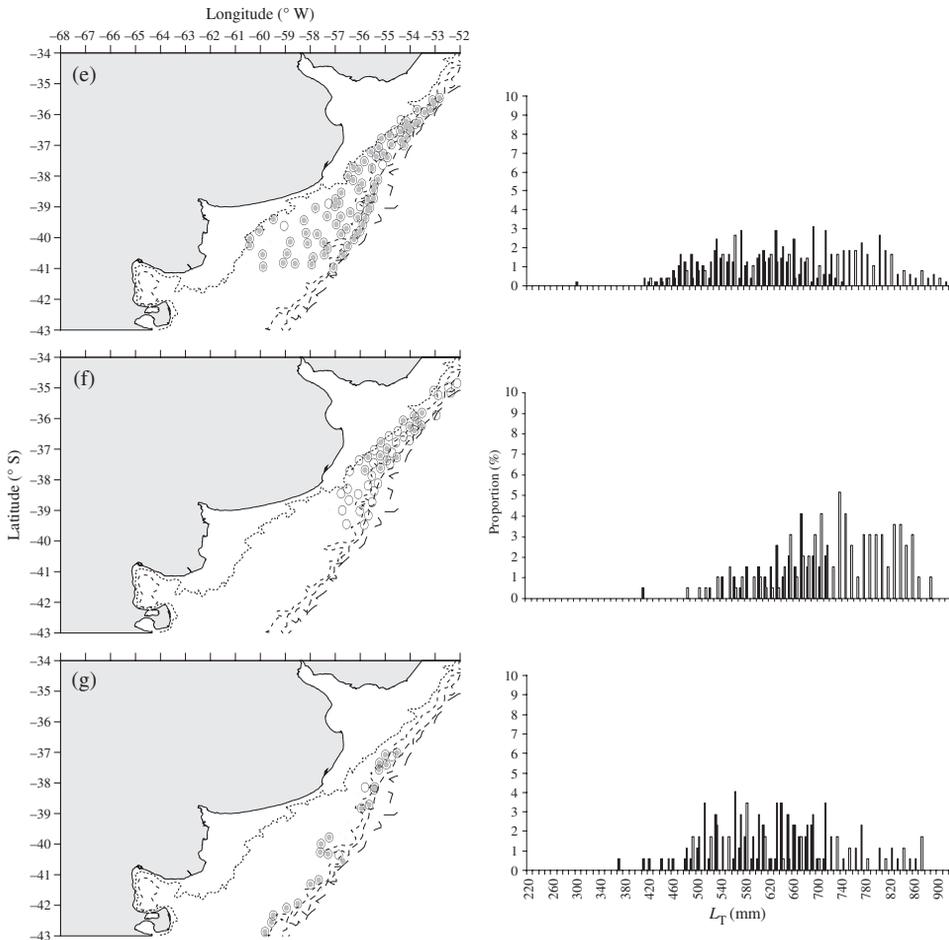
FIG. 2. Continued

to >35 mm; the latter presumably correspond to pre-ovulatory follicles [Fig. 6(a)]. Moreover, I_G variation was observed [Fig. 6(b)]. Gravid females at different stages of gestation, possessing newly differentiated to near-term embryos were captured during all surveys [Fig. 6(c)]. According to the range in the size of the largest embryo and the smallest specimen (*i.e.* a presumptive neonate) captured on research surveys, the L_T at birth was estimated between 230 and 266 mm.

The number of ovarian follicles (potential fecundity) varied between 1 and 18 (mean ± S.D. = 7·5 ± 3·0) and was correlated with L_T ($r^2 = 0.76$, $F_{1,250} = 318$, $P < 0.01$). The litter size varied from 2 to 12 (mean ± S.D. = 6·2 ± 2·9) and was correlated with the L_T. The slope of the regression was greater in the second stage of gestation (embryos >156 mm L_T). During the first stage of gestation (stage 5.1), fertility varied between 2 and 14 with a mean ± S.D. of 6·2 ± 3·0 and mode of 5, while in the second stage (stage 5.2) it ranged from 1 to 12 with a mean ± S.D of 6·1 ± 2·6 and mode of 5. The litter sex ratio was 1·19:1 and did not differ from 1:1 ($\chi^2 = 5.49$, d.f. = 1, $P < 0.05$).
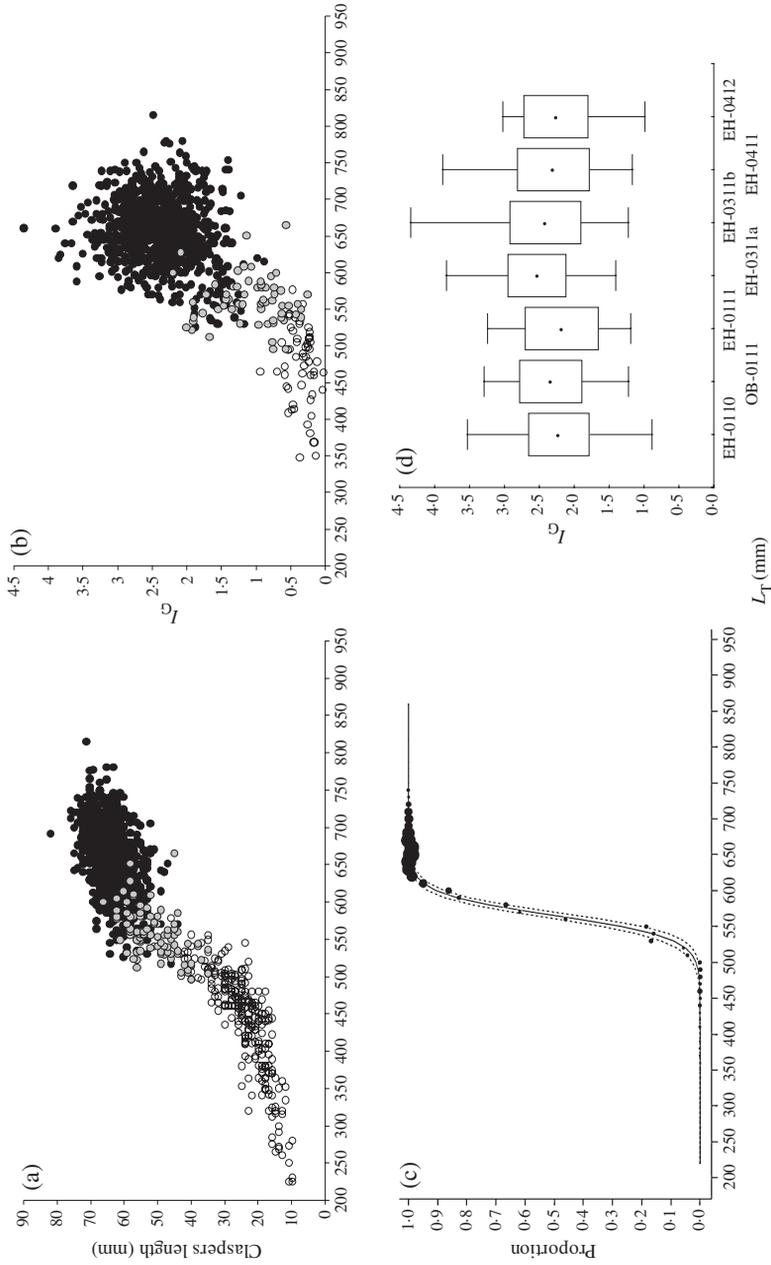
FIG. 3. Relationship between total length (L_T) of *Squalus acanthias* and (a) inner clasper length and (b) gonado-somatic index (I_G) (○, stage 1, juveniles; ◒, stage 2, juveniles; ●, stage 3, mature), (c) proportion of mature males; the maturity ogive was fitted by $y = \left\{ 1 + e^{\left[-\ln 19(x-610)(610-565)^{-1} \right]} \right\}^{-1}$ (——, maturity ogive; ······, 95% C.I.; size of symbols is related to number of specimens by L_T class) and (d) monthly variation of I_G of mature males in research surveys (●, mean; box, S.D.; whiskers, minimum and maximum).
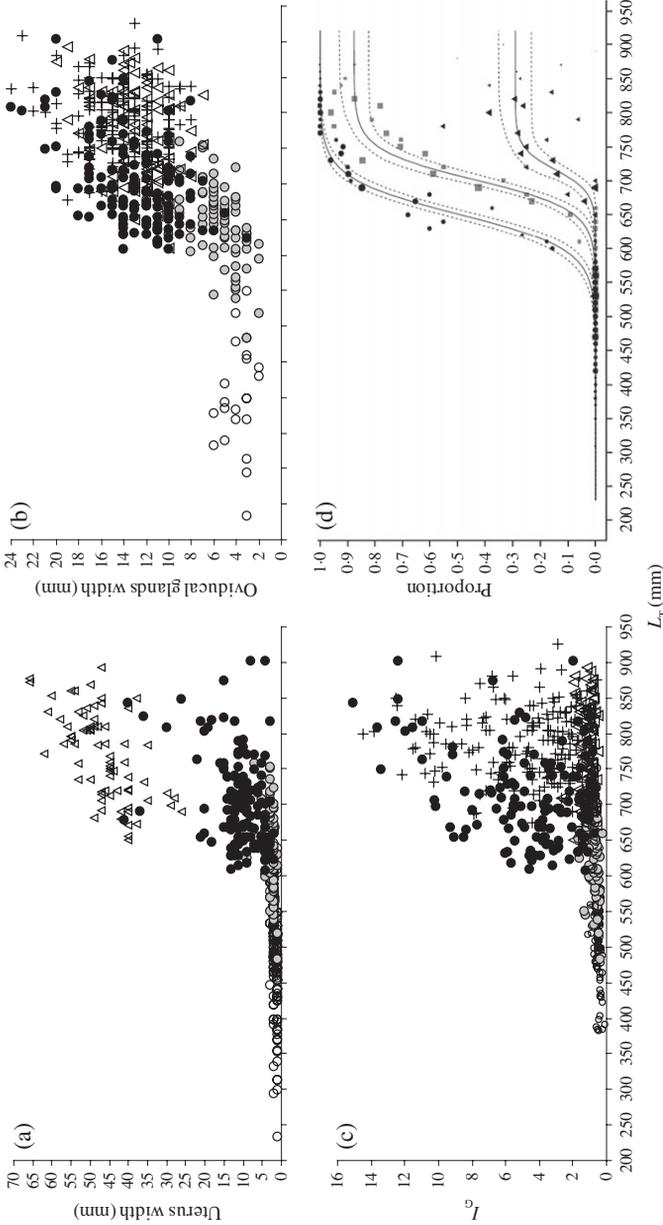
FIG. 4. Relationship between total length (L_T) of *Squalus acanthias* and (a) uterus width, (b) oviducal gland width and (c) gonado-somatic index (I_G) ○, stage 1 juveniles; ●, stage 2 juveniles; ⬤, stage 3 adults; △, stage 4 post-ovulatory; ●, stage 5 gravid) and (d) proportion of mature females (●, gestational females (▲, , stages 4 and 5) and maternity females (——— stage 5 with embryos >156 mm L_T) with their ogives (.....) and 95% C.I. (); the maturity ogive was fitted by $y = \left\{ 1 + e^{\left[-\ln 19(x - 728)(728 - 651)^{-1} \right]} \right\}^{-1}$, the gestational ogive was fitted by $y = 0 \cdot 88 \left\{ 1 + e^{\left[-\ln 19(x - 766)(766 - 701)^{-1} \right]} \right\}^{-1}$ and the maternity ogive was fitted by $y = 0 \cdot 29 \left\{ 1 + e^{\left[-\ln 19(x - 763)(763 - 716)^{-1} \right]} \right\}^{-1}$; the size of symbols is related to the number of specimens by L_T class.

TABLE II. Summary of reproductive variables estimated for *Squalus acanthias*

Sex	Stage	Parameter	Mean	C.I.$_{95lower}$	Median	C.I.$_{95upper}$
Males	Maturity	L_{T95}	610	603	610	616
		L_{T50}	565	561	565	569
Females	Maturity	L_{T95}	728	716	729	740
		L_{T50}	651	644	651	658
	Gestation	L_{T95}	766	742	765	789
		L_{T50}	701	692	701	711
		P_{max}	0·88	0·82	0·88	0·93
	Maternity	L_{T95}	763	725	763	803
		L_{T50}	716	699	716	733
		P_{max}	0·29	0·23	0·29	0·35

P_{max}, maximum proportion of mature individuals; L_{T95}, total length at which individuals attain 95% of P_{max}; L_{T50}, total length at which individuals attain 50% of P_{max}.

DISCUSSION

The size ranges of the specimens captured in this study are consistent with the observed ranges from research surveys previously conducted in the south-western Atlantic Ocean shelf during 1978 (Menni, 1985), between 1994 and 1998 (García de la Rosa, 1998) and between 1995 and 2010 (Oddone *et al.*, 2015). As observed in many species of sharks and batoids, females of *S. acanthias* attained a greater maximum L_T and L_{T50} compared to males. This kind of sexual dimorphism is frequent in species where larger females produce more and larger offspring (Lombardi, 1998). This suggests that, if fertility is positively correlated with body size, females become sexually mature later and larger than males (Stearns, 1992). The observed correlations between L_T females with fecundity and fertility would support this hypothesis for *S. acanthias*.

The maximum L_T and sexual maturity estimated for *S. acanthias* in the study area were smaller than those estimated in the North Pacific and North Atlantic Oceans (Campana *et al.*, 2009; Tribuzio *et al.*, 2009; Veríssimo *et al.*, 2011). In the North Pacific Ocean, maximum L_T varied between 1200 (females) and 1000 mm (males) and the L_{T50} between 751 (males) and 899 mm (females) (Tribuzio *et al.*, 2009). On the Scotian shelf, the maximum L_T varied between 1121 (females) and 957 mm (males) and the L_{T50} between 821 (females) and 635 mm (males) (Campana *et al.*, 2009). In the Gulf of Maine (Bubley *et al.*, 2013), sizes at maturity were larger than those estimated in this study. On the other hand, female sexual maturity was attained at a similar size (760–880 mm) in the north-east Atlantic Ocean (Jones & Ugland, 2001).

The sizes at maturity estimated for males and females of *S. acanthias* in this study were lower than those estimated by Oddone *et al.* (2015) for the south-western Atlantic Ocean between 34° and 40° S. Maturity ranges were also different from those observed by Oddone *et al.* (2015) for males (55–62 mm L_T) and females (58–85 mm L_T). It is likely that these differences are related to methodological procedures (*i.e.* number of samples, maturity criteria and study area). Moreover, the maturity range observed in females of *S. acanthias* was wider compared to the observations of research surveys conducted during 1978 in the study region (Menni, 1985). The values estimated by Menni (1985) represent the range of gestation rather than maturity, because females
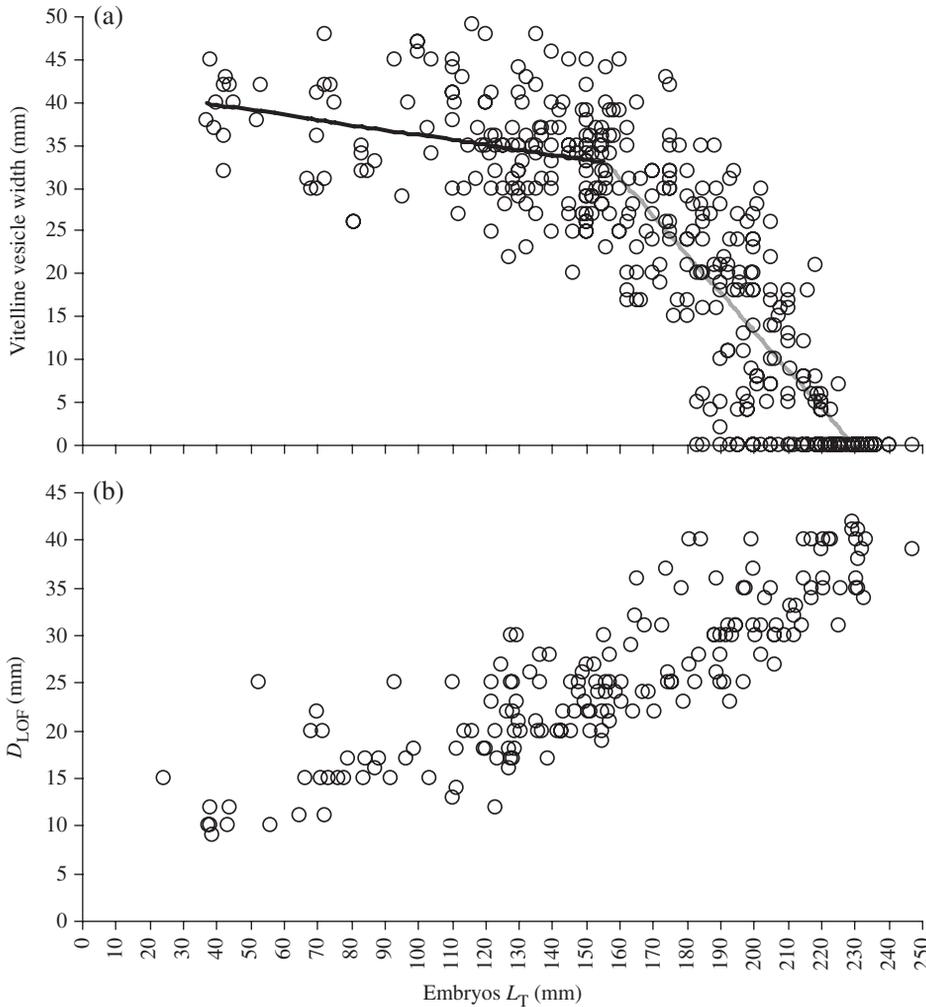
Fig. 5. Relationships between embryo total length (L_T) and (a) vitelline vesicle width and (b) the diameter of the largest ovarian follicles (D_{LOF}) in gravid females of *Squalus acanthias*. (a) Linear regressions have been adjusted to the data considering one break point: intercept (β_0) (95% c.i.) = 42·01 (37·90 to 45·22), break point (α) = 155·89 (143·14 to 163·35), first slope (β_1) = −0·05 (−0·08 to −0·01) and second slope ($\beta_1 + \beta_2$) = −0·45 (−0·48 to −0·41).

were considered mature when eggs or embryos were observed in the uterus. *Squalus acanthias* is the largest squaloid of the south-western Atlantic Ocean. Both sexes attain larger maximum size and maturity than *Squalus mitsukurii* Jordan & Snyder 1903 and *Squalus cubensis* Howell Rivero 1936 (Lucifora *et al.*, 1999).

The estimated fertility is consistent with the ranges proposed for this region (Menni, 1985; García de la Rosa, 1998; Gosztonyi & Kuba, 1998; Di Giacomo *et al.*, 2009; L. N. Chavez, unpubl. data). The average fertility estimated (6) and the 2 year reproductive cycle may provide an annual fertility of three embryos. This value is slightly higher than other squaloid sharks with a 2 year reproductive cycle such as piked spurdog *Squalus*
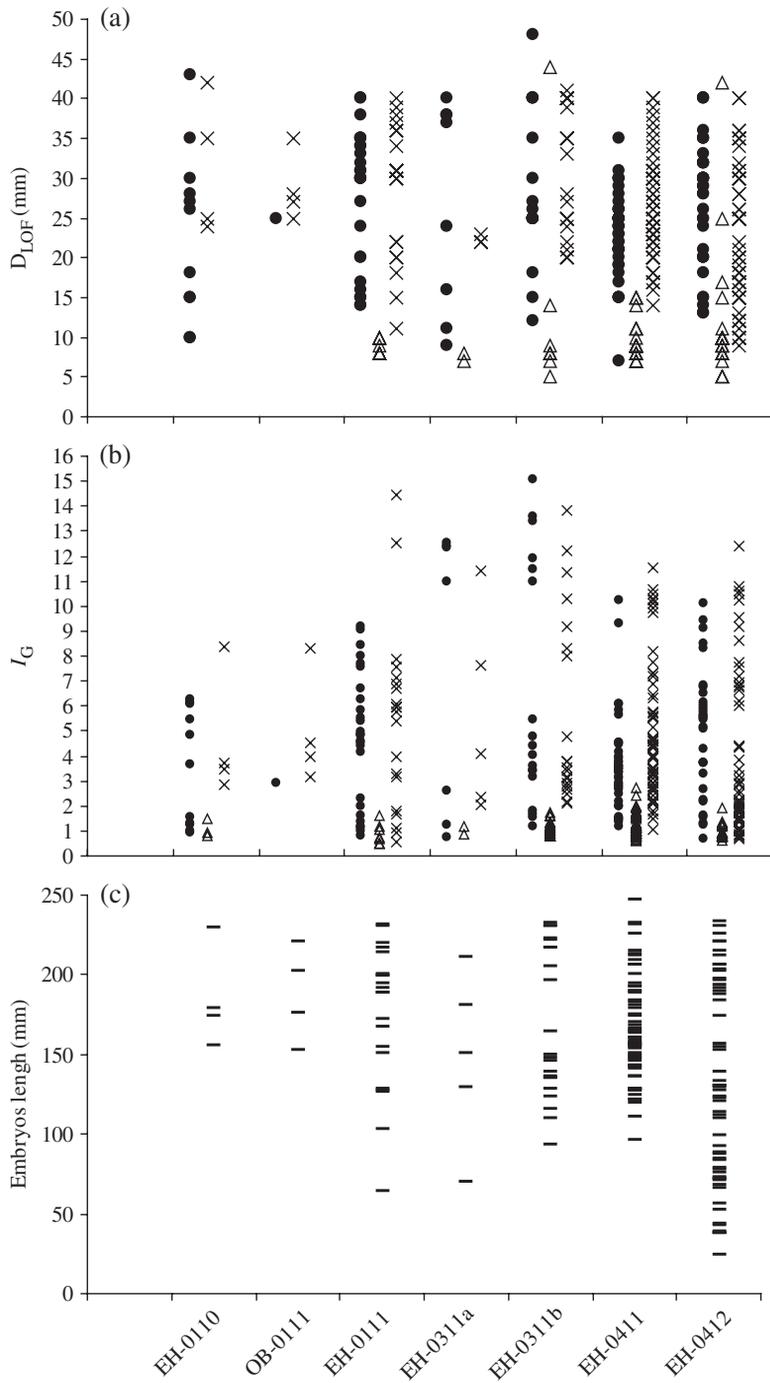
FIG. 6. Variation between research surveys in values of (a) the diameter of the largest ovarian follicles (D_{LOF}), (b) gonado-somatic index (I_G) and (c) embryo total length of *Squalus acanthias* (●, mature non-gravid females; △, post-ovulatory females; ×, gravid females; ▬, embryo size).

megalops (Macleay 1881) (Braccini *et al.*, 2006). The differences in fertility between the stages of gestation could be a consequence of the increased frequency of spontaneous abortions during the second stage of gestation. The stress generated by the operation of fishing and handling prior to sampling result in the release of embryos. As was mentioned by Braccini *et al.* (2006) for *S. megalops*, this result is supported by the presence of embryos on the deck of the vessel (J. H. Colonello, pers. obs.). During the first stage of gestation, embryos have a large yolk sac and show little movement, characteristics that may decrease the frequency of spontaneous abortions.

The P_{max} of the gestation ogive was smaller than 1 (0·88), which indicates that some mature females (beyond their first reproductive cycle) were not in the gestation process. This inactivity may be explained by the occurrence of resting periods between cycles or in asynchrony of the reproductive cycle. The temporal and spatial co-occurrence of non-gravid adult females at different stages of ovarian development, as well as gravid females at all embryonic development stages would indicate that the female reproductive cycle of *S. acanthias* in the south-western Atlantic Ocean is asynchronous. Most reproductive cycles are synchronous in sharks, but species have also been recorded with asynchronous cycles, such as *S. megalops* (Braccini *et al.*, 2006). In synchronous species, reproductive events (birth and mating) are spatially and temporally bounded, while in asynchronous species reproductive events overlap. For synchronous sharks with multi-year reproductive cycles, it is feasible to differentiate a cohort of embryos throughout the year that correspond to the steps of gestation. Furthermore, gravid females with near-term embryos are commonly observed in a determined area and time of year. Studies of *S. acanthias* in other regions argue the possibility that the female reproductive cycle is synchronous (Hanchet, 1988; Jones & Ugland, 2001; Demirhan & Seyhan, 2007) or asynchronous (Capapé & Reynaud, 2011). It is noteworthy that in the research survey carried out during June between 34° and 41° S, gravid females were found with embryos of <50 mm L_T. This stage was not observed in other surveys. Although the available information suggests reproductive asynchrony of *S. acanthias* in the south-western Atlantic Ocean, reproductive synchrony cannot be dismissed completely. The implications associated with potential reproductive asynchrony as a temporal delimitation of reproductive events and essential areas should be analysed in future work.

The P_{max} for maternity is usually fixed at 0·5 for a biennial reproductive cycle. The estimated P_{max} for the maternity ogive of *S. acanthias* suggests that approximately one third of mature females are in the maternity stage (*i.e.* with embryos >156 mm L_T) and are contributing to the annual recruitment. Each stage of embryo development (stages 5.1 and 5.2) defined in this study, however, did not exactly represent years. The last stage of gestation (stage 5.2) could be shorter than 1 year, whereas the period between ovulation (stage 4) and the end of the first stage of gestation (stage 5.1) could take >1 year. Therefore, annual recruitment could be underestimated because a proportion of gestating females in the first stage are also contributing to this event.

Stages of the reproductive cycle were difficult to define with the samples available from this study. It is feasible to suggest, however, that most of the gestation period is comprised of the stages between undifferentiated embryos (stage 4) and embryos <155 mm L_T (stage 5.1). The second stage of gestation with embryos >156 mm L_T (stage 5.2) appears to be shorter, due to faster consumption of the vitelline sac for metabolic requirements and the absence of additional nutrients. Environmental factors (*i.e.* temperature) may influence pregnancy duration (Jones & Ugland, 2001).

The stability of the I_G of adult males suggests that males do not have a marked reproductive seasonality. This result would be consistent with histological studies in the north-western Atlantic Ocean that confirm the ability of males to produce sperm throughout the year (McClusky, 2005). The potential female asynchrony and continuous sperm production indicate that mating can occur throughout the year. In the Gulf of San Matías (41°–42° S; 64°–65° W, Argentina), higher concentrations of adult females compared to males have been found in November, although no dominance of a particular reproductive stage was observed (Di Giacomo *et al.*, 2009). A similar trend has been observed in the coastal waters of Buenos Aires (36°–39° S, Argentina) where adult females in all reproductive stages arrive in July (winter) until they reach their highest concentrations in November (spring) (Cortés & Jaureguizar, 2012; L. N. Chavez, unpubl. data). The occurrence of adult females in all reproductive stages without adult males indicates that this migration to coastal waters is not related to birth or mating. In the north-western Atlantic Ocean, sexual segregation of *S. acanthias* occurs both spatially and temporally (Shepherd *et al.*, 2002; Dell'Apa *et al.*, 2014), although the exact combination of factors that drive these behaviours has not been specified (Dell'Apa *et al.*, 2014). On the east coast of the North Atlantic Ocean, the migratory patterns of *S. acanthias* are also complex and while there would be a flow of specimens depending on the latitude, satellite marker studies indicate that the prevailing movements are in relation to depth (Sulikowski *et al.*, 2010).

Aggregations of mature females were recorded at the northern of the study area (a region with warmer waters). Spatial segregation by sex in adult stages of sharks has been associated with sex differences in energy requirements; females are often found in more productive habitats (Klimley, 1987) or warmer areas during pregnancy as a way to accelerate embryonic growth and optimize the reproductive cycle (Economakis & Lobel, 1998; Jones & Ugland, 2001; Dell'Apa *et al.*, 2014). Furthermore, adult females may avoid males to circumvent energy demanding copulation, while males may move into habitats commonly occupied by females for mating and/or feeding (Dell'Apa *et al.*, 2014). Similar spatial segregation was observed for *S. acanthias* in the north-western Atlantic Ocean, with mature females most commonly reported at significantly shallower depths (Shepherd *et al.*, 2002; Dell'Apa *et al.*, 2014; Sagarese *et al.*, 2014).

The capture of juvenile specimens of <350 mm L_T in the Gulf between 65° and 68° S could indicate that this region is a breeding area for *S. acanthias*. Although this result is affected by lack of seasonal sampling, aggregations of juveniles and adult males have also been observed between October and March in this area (Cedrola *et al.*, 2012). The confirmation of these breeding and nursery areas must be assessed in future works using seasonal and systematic sampling.

Vooren (1997) and Oddone *et al.* (2015) mentioned that *S. acanthias* reproduce during the summer in Uruguayan and Argentinean waters between 34° and 39° S, and migrate to the continental shelf of Brazil in the winter. *Squalus acanthias* is not a dominant demersal elasmobranch species over the continental shelf and upper slope of Brazil and Uruguay between 28° 40′ and 34° 34′ S (Vooren, 1997; Vooren *et al.*, 2005). Sexual segregation and the relative abundances (expressed as t and individuals by nautical mile) observed on the south-western Atlantic shelf between 34° and 54° S (García de la Rosa, 1998; Massa, 2009; this study) suggest that the main distribution of *S. acanthias* in the south-western Atlantic Ocean occurs south of 33° S and the presence of this shark on the south Brazil shelf is occasional and with low abundance.

Comparing the results of this study with those obtained during surveys carried out three decades ago (Menni, 1985; García de la Rosa, 1998), stability is observed in the estimations of fertility and L_T, birth, maturity, maternity and fertility. This stability is consistent with the relative stability of the abundance indices in the study region (Massa, 2009). It should be noted that the available evaluation surveys do not allow for a comprehensive assessment of the abundance of this shark, because of the wide distribution area in the south-western Atlantic Ocean (Massa, 2009). On the other hand, a decrease in the trophic level of *S. acanthias* has been detected (Kohen Alonso *et al.*, 2002; Belleggia *et al.*, 2012), suggesting that there has been an indirect effect of fishing pressure on this shark at the ecosystem level during the 1990s through fishing down the food web (Kohen Alonso *et al.*, 2002; Belleggia *et al.*, 2012).

Squalus acanthias is taken as by-catch in most trawl fisheries of Argentina, but is typically discarded at sea. Data from on-board observers shows that (no official statistics) 94 to 97% of captured *S. acanthias* are discarded (A. M. Massa, unpubl. data). Argentinean landings of *S. acanthias* may be recorded specifically or into the category unidentified sharks. Between 2006 and 2012 average annual landings of this shark were 185 t (unidentified sharks = 961 t), and between 2013 and 2014 this diminished to 44 t (unidentified sharks = 1022 t) (Minagri, 2015).

Management measures for best practice of capture and discard or areas closed to trawling are applied in Argentina. For instance, closed areas are implemented south of 34° S. The largest management marine area in Patagonian waters is a permanent closed region covering 184 200 km^2; this area was established in 1997 in order to protect the Argentine hake *Merluccius hubbsi* Marini 1933, and trawlers are not allowed to fish (Bertolotti *et al.*, 2001; Bezzi *et al.*, 2004). During the spring and summer months (December to March), when all closed areas are effective, *c.* 26% of the continental shelf south of 34° S is closed to commercial fishing; it is expected that several chondrichthyan populations benefit from the establishment of these closed areas (Colonello *et al.*, 2014). The annual closed areas established at depths >50 m represent *c.* 23–25% of the habitat range of *S. acanthias* in the shelf between 34° and 55° S. Although there is no direct management measures, closed areas can result in an indirect benefit for the conservation of this shark.

The present results indicate that *S. acanthias* is susceptible to fishing pressure on account of its large length at maturity, extensive reproductive cycles and low fecundity. Therefore, it is necessary to continue to assess the direct and indirect effects of pressure on this shark.

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