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Sexual development, size at maturity, size at maternity and fecundity of the blue shark *Prionace glauca* (Linnaeus, 1758) in the Southwest Atlantic

Santiago Montealegre-Quijano[a,*,1], Andrei T.C. Cardoso[a], Renato Z. Silva[b], Paul G. Kinas[c], Carolus M. Vooren[a]

[a] Universidade Federal do Rio Grande (FURG), Instituto de Oceanografía, Laboratório de Elasmobrânquios e Aves Marinhas, Caixa Postal 474, Rio Grande, RS CEP 96201-900, Brazil

[b] FURG, Instituto de Ciências Biológicas, Laboratório de Biologia de Parasitos de Organismos Aquáticos, Caixa Postal 474, Rio Grande, RS CEP 96201-900, Brazil

[c] FURG, Instituto de Matemática, Estatística e Física, Laboratório de Estatística Ambiental, Caixa Postal 474, Rio Grande, RS CEP 96201-900, Brazil

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ABSTRACT

Size at maternity and size at maturity of the blue shark *Prionace glauca* were studied from samples collected during ten commercial longline fishing cruises off southern Brazil and in adjacent international waters. The sharp increase of the amplitude of the values of reproductive variables at a given fork length (FL) was evidence that from that FL reproduction occurred. Thus, we calculated the proportion of mature sharks in FL classes to estimate the median size at maturity. The accelerated growth of the claspers started before the beginning of the testis maturation and semen production, whereas the accelerated development of the ovary and the oviducal glands started simultaneously. Although most females with mating marks were mature, few had sperm stored in the oviducal glands. The population parameter of size at 50% of maturity was estimated at 171.2 cm FL for females and 180.2 cm FL for males. The median size at maternity was estimated in 193.9 cm FL and half of the females with five to six years old were recruited for reproductive phase of life. As most shark species, *P. glauca* in the Southwest Atlantic reach maturity at about three-fourths of its maximum size and half of its maximum age. Median litter size was 33 embryos. A positive not significant linear relationship between the uterine fecundity and the size of the pregnant female was observed.

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1. Introduction

The blue shark *Prionace glauca* (Linnaeus, 1758) is an oceanic species with worldwide distribution in temperate and tropical waters (Compagno et al., 2005). Taken mainly as bycatch, *P. glauca* is the most common species of shark in longline and gill net fisheries in all oceans (Castro et al., 1999), with an estimated 6.5–11 million individuals caught per year (Bonfil, 1994; Clarke et al., 2006). In the Atlantic Ocean, population assessments carried out to date do not indicate major impacts on populations (Anonymous, 2008). The comparatively high reproductive rate of *P. glauca* (Nakano and Seki, 2003), which implies in high natural mortality and comparatively high biological productivity (Smith et al., 2008; Walker, 2005a,b), it most likely explains why stocks of *P. glauca* throughout the world have withstood prolonged high fishing mortality without apparent stock collapse. However, significant decreases of catch rates of *P. glauca* in the Atlantic over the past three decades have been documented (Simpfendorfer et al., 2002; Baum et al., 2003; Campana et al., 2006; Aires-da-Silva et al., 2008; Cortés, 2008; Pons and Domingo, 2009; Baum and Blanchard, 2010). Thus, the divergences between the published assessments of the state of the stocks of *P. glauca* and the growing concern about the conservation status

Abbreviations: FL, fork length; RCL, relative clasper length; LFD, largest folicle diameter; OW, ovary weight; OGD, oviducal gland diameter; OGW, oviducal gland weight.

* Corresponding author. Tel.: +55 13 3828 3066.
E-mail addresses: smquijano@registro.unesp.br, smquijano@gmail.com (S. Montealegre-Quijano).
[1] Universidade Estadual Paulista "Júlio de Mesquita Filho" – UNESP, Campus de Registro, Engenharia de Pesca, Rua Nelson Brihi Badur, 430 Vila Tupy, CEP 11900-000, Registro, SP, Brazil.

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of this key species for the oceanic ecosystem (Camhi et al., 2009; Stevens, 2005) justify the necessity for further studies on its population biology.

The knowledge of the reproductive aspects of exploited species is essential for the sustainable management of the fishery. Therefore, given the abundance, distribution range and commercial importance of the blue shark, aspects of its reproductive biology have been studied extensively over much of its distribution in the Pacific ocean (Carrera-Fernández et al., 2010; Cruz-Ramírez et al., 2012; Francis and Duffy, 2005; Nakano, 1994; Stevens, 1984; Strasburg, 1958; Suda, 1953 in Nakano and Seki, 2003), Indian ocean (Gubanov and Grigor'yev, 1975; Gubanov, 1978) and Atlantic ocean (Amorim et al., 1998; Bornatowski and Schwingel, 2008; Castro and Mejuto, 1995; Hazin et al., 1994a, 2000; Jolly et al., 2013; Legat and Vooren, 2008; Mazzoleni and Schwingel, 2002; Megalofonou et al., 2009; Mejuto and García-Cortés, 2005; Pratt, 1979; Stevens, 1974). In the South Atlantic, most studies were conducted in tropical and subtropical waters off Brazil, the Gulf of Guinea, and adjacent international waters. Although vast literature has been produced, the key population parameters expressing maternity as a function of length (or age) and number of offspring produced per pregnancy as a function of maternal length (or maternal age), required for input to demographic or synthetic-fishery models are presently scarce. Given the ecological and fishery significance of this species, estimates of these parameters would valuably contribute and aid future stock assessment and ecological risk assessment from effects of fishing. Thus, the aim of the present study was to estimate the size at maturity, size at maternity and fecundity of *P. glauca* in the Southwest Atlantic through sampling of commercial catches at sea.

2. Methodology

2.1. Sampling and data collection

Samples of *P. glauca* were collected aboard two Brazilian longline vessels, from 2004 to 2009, during ten commercial fishing cruises in the southwest Atlantic (Lat. 24°20′ to 37°41′S, Long. 25°32′ to 51°02′W). Four cruises were in summer (February/2004, March/2005, February/2008 and January/09), one was in autumn (June/2004), three were in winter (September/2004, July/2005, August/2006) and two were in spring (December/2005 and October/08) (Fig. 1). Details on the oceanographic conditions during fishing trips and on technical aspects of the fishing operations are given in Montealegre-Quijano and Vooren (2010).

In the catch of each longline set, all blue sharks were sexed and the fork length (FL) was measured in the total catch or in a random sample of it, depending on the working conditions. FL was measured rounded down to the nearest centimeter below the actual length, as the distance between the tip of the snout and the fork of the tail along a line parallel to the body axis, using a wooden caliper 3.0 m long. The presence or absence of pregnancy was recorded for each female caught. Pregnancy was confirmed by the presence of embryos or eggs in the *uteri*, but also by the presence of distended *uteri* containing *placentae* or umbilical cords in post-partum females.

Sharks sampled for measurements of their reproductive organs were mostly chosen at random in each longline set. The number of sharks sampled for each reproductive variable depended on the working conditions on deck. However, given the scarcity of females from all life stages and small juveniles of both sexes, priority was given to these categories. Testes and ovaries without epigonal organ and oviducal glands were preserved in 10% buffered formalin for measurements ashore of length and weight of each testis, weight of ovary, diameter of largest ovarian follicle, and weight and diameter (maximum width) of the oviducal glands. At times, not all reproductive variables could be recorded for each sampled shark.

2.2. Maturity assessment in males

Maturity of the males was determined from *in situ* observations of the sexual products and from the relative developmental stage of reproductive organs. Five reproductive variables were considered for the analysis of their relation to body growth: the presence or absence of semen in the *ampullae* of the *ductus deferens*, the length and wet weight of testes, and the size and rigidity degree of claspers. Presence of semen was defined as the presence of a white liquid extruded from a cross-sectional cut through the thick caudal portion of the kidney, where the *ampullae* are situated (Pratt, 1979). It should be advised that the presence of semen is not necessarily indicative of the presence of spermatozeugmata, and thus males with semen may not be functionally mature (Pratt, 1979).

Immature male elasmobranchs have small flexible claspers and mature male elasmobranchs have large rigid claspers (Stehmann, 2002). Thus, the outer length of one clasper of 1083 blue sharks was measured to the nearest millimeter along the lateral clasper surface, from the insertion of the clasper in the pelvic fin base to the clasper tip (Compagno et al., 2005). Through manual assessment of the resistance of the clasper to deformation, 666 specimens were classified as having flexible or rigid claspers. Points at which abrupt transitions occur in the relationship between the clasper length and FL are related to sexual development (Conrath, 2005). To identify these points and thus obtain estimates of the FL and clasper length at which the clasper development starts and ends, the method described by Francis and Duffy (2005) was applied. Clasper length was expressed as a percentage of the FL, thus defining the relative clasper length (RCL). A split linear regression was fitted to RCL and FL data. Split linear regression consists of two simple linear regressions fitted to no overlapping data ranges that meet at a FL = p called the break point, at which RCL = h. The split linear regression has the form:

$$\mathrm{RCL} = f(\mathrm{FL} - p) + h \quad \text{for FL} < p$$

$$\mathrm{RCL} = g(\mathrm{FL} - p) + h \quad \text{for FL} = p$$

where f and g are slope parameters for the two limbs of the regression, and h and p are the y-axis and x-axis coordinates of the break points (Francis and Duffy, 2005). The parameters f, g, h and p were estimated through least squares method (Zar, 1999).

2.3. Maturity assessment in females

We recorded one or more of five reproductive variables: the classificatory variable "pregnant" (PR) or "non-pregnant" (NPR), and four continuous quantitative variables that reflected the relative developmental stage of reproductive organs. Thus, maturity of the females was determined from observations of current or recent pregnancy (*i.e.* presence of embryos, uterine eggs, placenta or umbilical cords in the uterus), or by measuring the ovary and the oviducal glands. The quantitative variables were: ovary weight (OW), diameter of the largest ovarian follicle (LFD), and diameter (maximum width) and the weight of the oviducal glands (OGD and OGW, respectively). For each of these four quantitative variables, non-pregnant females were classified as mature or immature, according to the respective minimum values to classify the non-pregnant female as mature. This minimum value is denominated as the "critical value" of the variable. For each one of the four quantitative reproductive variables, the non-pregnant females which had values of the reproductive variables lower than the respective critical value, were classified as immature. To choose and adjust

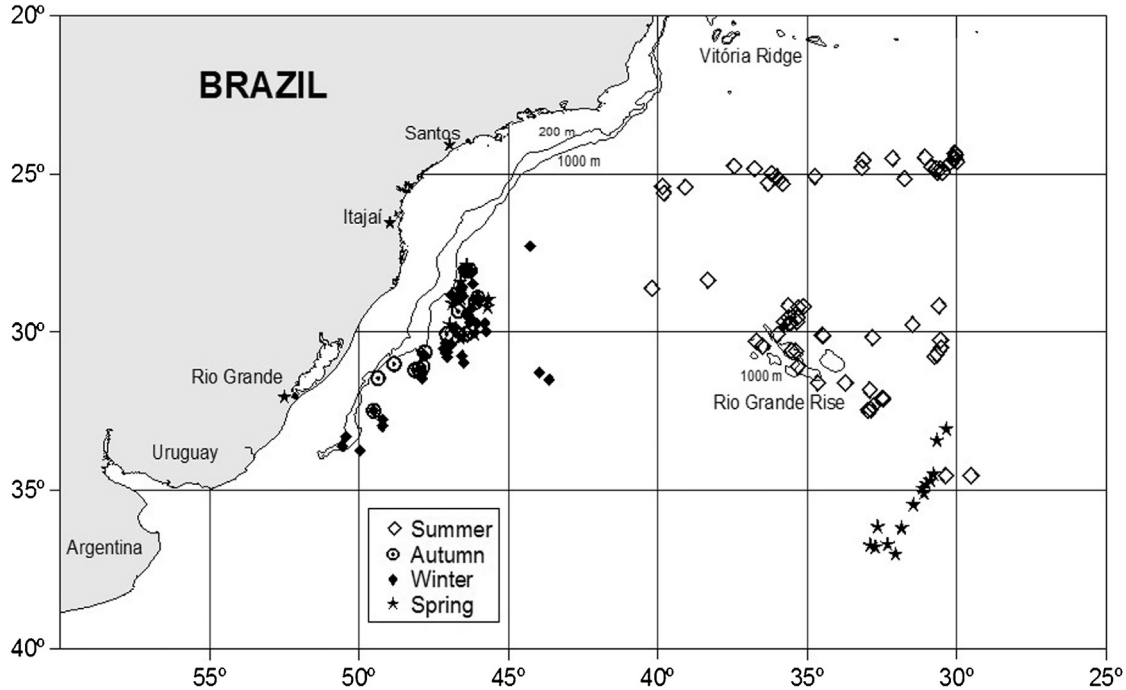

Fig. 1. The sampling area in the Southwest Atlantic. The initial position of the longline set is plotted by seasons of the year.

the critical value of each variable, we analyzed the scatter pattern in the graphs of the relationship between FL and the respective reproductive variable.

2.4. Mating marks and their relationship with the onset of maturity in females

Fresh wounds or scars are often observed on the female's flanks or fins and appear in the form of a series of small incisions arranged in a semicircle. This type of injury has been interpreted as the result of non-food bites made by males during courtship and mating, and are therefore called "mating marks" (Pratt, 1979; Pratt and Carrier, 2005; Stevens, 1974). A premise for mating is that the mature female that is able and willing to mate emits specific signals which are perceived by the mature male thus releasing its reproductive behavior. If mating marks could be used to infer on the female's maturity, then it is expected that the oviducal glands of sharks with mating marks have stored sperm (Hamlett et al., 2005; Pratt, 1993). To test this hypothesis for *P. glauca* in the Southwest Atlantic, histological sections were made of oviducal glands of 41 females with mating marks that were caught in October/08 and January/09. After fixation in a buffered solution of formaldehyde 4%, oviducal glands were transferred to Bouin's solution. After dehydration in a graded ethanol series, the glands were embedded in paraffin and sagitally sliced at 7 μm thickness. The histological sections were stained with Hematoxylin–Eosin *sensu* Behmer et al. (1976). Then, the proportion of females with mating marks that had sperm stored was calculated.

2.5. Estimating size at maturity

Maturity occurs at the smallest FL at which the individual is classified as sexually mature according to the criteria adopted for our definition of maturity. The corresponding population parameter L_{50} is the FL at which a model fitted to the proportions of maturity of the FL classes predicts the maturity proportion of 0.50. Such a model implies that the magnitude of L_{50} is the median FL at maturity, briefly referred to as "size at maturity".

To the randomly sampled sharks for measurement of reproductive organs, the proportion of mature specimens in 5.0 cm FL classes, calculated as the ratio between the number of mature sharks (y_i) and the total number of sharks (n_i) in the ith FL class, was analyzed to estimate the median FL at maturity (L_{50}) by sex. If p_i denotes the probability of a shark in the ith FL class being mature, then y_i can be described by a Binomial model $Bin(n_i,p_i)$. The premise of larger sharks having a greater probability of being mature is the fundamental concept that drives this analysis. The logit transformation of p_i, and thus, the resulting logistic model to the probabilities p_i was applied to fit the data:

$$\ln\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1(\mathrm{FL}_i - \mathrm{FL}_{\mathrm{mn}})$$

where β_0 and β_1 are parameters, FL_i is the midpoint in each ith FL class, and $\mathrm{FL}_{\mathrm{mn}}$ is the mean fork length, included to centralize the logistic regression, making it easier to interpret the parameters β_0 and β_1. The parameter β_0 is the transformed logit of the probability of a shark with a size equal to $\mathrm{FL}_{\mathrm{mn}}$ being mature. The parameter β_1 is the mean increment in the logit of p_i for each centimeter added to the fork length. If the FL has influence on the likelihood of being mature, then β_1 should have a positive value. Moreover, $\beta_1 = 0$ would indicate that variations in the length of sharks do not change the probabilities of maturity (Kinas and Andrade, 2010). From the above equation it follows that L_{50} is obtained from:

$$L_{50} = -\frac{\beta_0}{\beta_1} + \mathrm{FL}_{\mathrm{mn}}$$

Estimates of the model parameters were obtained through a Bayesian approach (Kinas and Andrade, 2010). Non-informative prior distributions were used for all parameters. Posterior distributions, mean values and credibility interval (CRI 95%) of all parameters and for L_{50} were estimated through Markov Chain Monte Carlo methods using R2OpenBUGS library within R software (R Core Team, 2012).

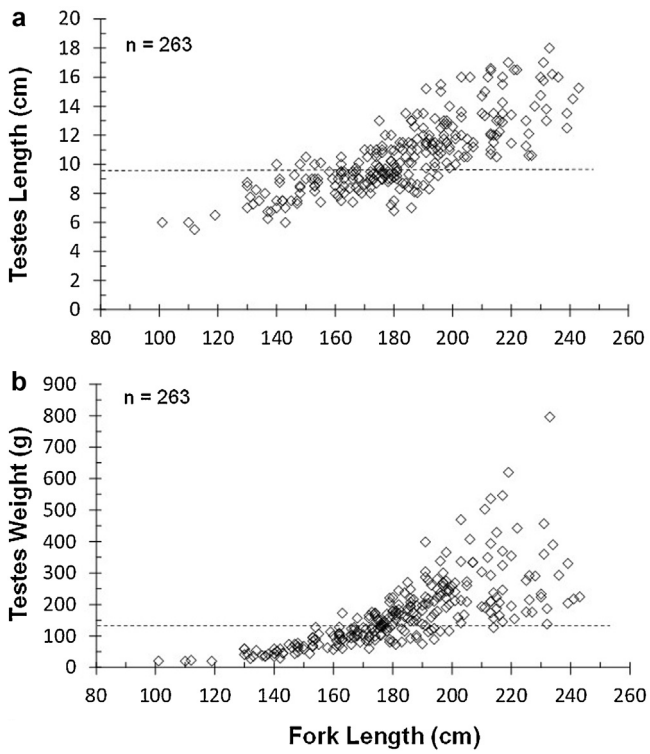

Fig. 2. Relationship of the length of one randomly chosen testis (a), and of the cumulative weight of both testes (b), with the fork length of the blue shark *P. glauca* in the Southwest Atlantic. Dotted lines represent the position of the critical values for maturity.

2.6. Estimating size at pregnancy

The females recruited to maternity are those females that give birth during a given year and thus produce the new cohort of that year. The maternity ogive is the curve that describes the relationship between the proportion of maternity and FL (Walker, 2005a,b). The gestation period and the litter developmental stage of blue sharks in the Southwest Atlantic are synchronized at population level, with the onset of gestation in late summer (March), and birth the following spring (December) (Montealegre-Quijano, 2007). Thus, pregnant females at any time in the year are recruited for maternity.

The proportion of maternity as a function of FL displayed a sigmoidal pattern. The logistic function was fitted to these data, and the L_{50} thus obtained was the estimate of the population median FL at maternity, briefly referred to as "size at maternity". Data used in this analysis were the records of presence or absence of pregnancy, for the pooled females of all cruises except those in spring and early summer (October–January) because during that period most mature females were in the interval between birth and next pregnancy.

2.7. Fecundity

Ovarian fecundity was estimated by counting the number of ovarian follicles ≥ 5.0 mm, in 55 mature non-pregnant sharks randomly chosen in spring and early summer. The uterine fecundity was estimated by counting the number of eggs or embryos in the utero of 87 females caught at all seasons of the year. Relationships of ovarian and uterine fecundity with FL were analyzed.

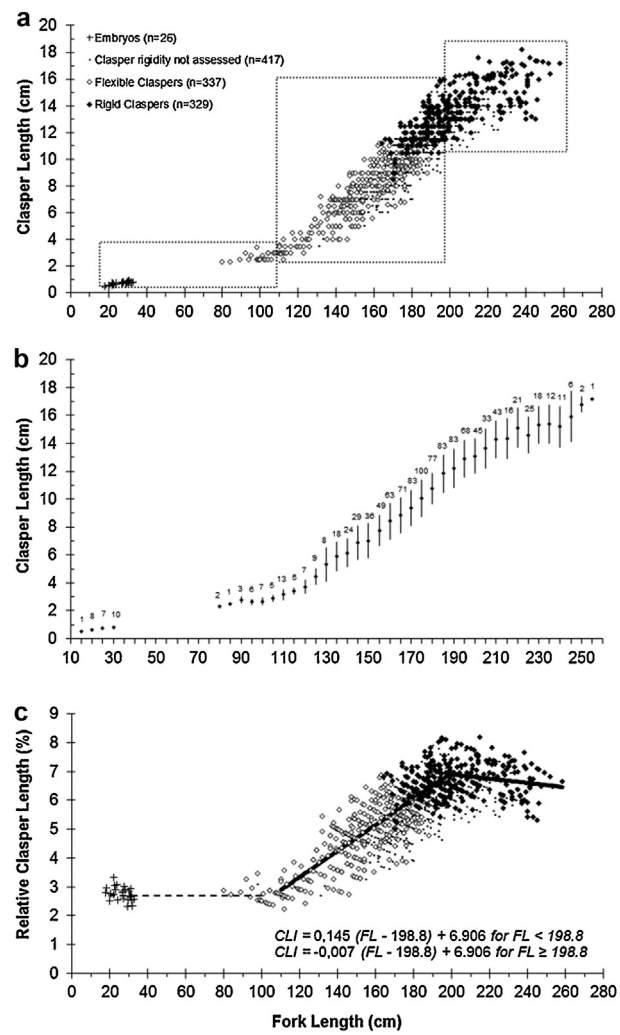

Fig. 3. Clasper size as a function of the FL of the blue shark *P. glauca* in the Southwest Atlantic. (a) Clasper outer length in relation to FL; (b) clasper mean length and standard deviation by FL classes of 5.0 cm FL; and (c) relative clasper length and split regression fit.

3. Results

3.1. Sexual development and maturity criteria of the male

3.1.1. The testes

Males of *P. glauca* had two similarly developed testes. No significant differences were found in the mean size ($t = 1.651$; $p = 0.192$; d.f. = 280) or in the mean weight ($t = 1.648$; $p = 0.158$; d.f. = 472) between the right and left testes. Testis length and total pooled weight of both testes increased with FL, varying from 5.5 to 18.0 cm and from 19.6 to 796.0 g (Fig. 2). The range of variation of the total pooled weight of both testes by FL class increased abruptly from 170 cm FL onwards, at average testes weight of 125.0 g. This abrupt increase in the testes weight reflected the onset of maturity. At about 200 cm FL virtually all sharks had testes length and weight greater than these critical values (Table 1).

3.1.2. The claspers

Clasper size of 1083 blue sharks with FL of 80–258 cm, ranged from 2.3 to 18.2 cm. Clasper growth occurred in three phases delimited by two break points: the first at 110 cm FL and 2.5% relative clasper length (RCL), and the second at 198.8 cm FL and 6.9% RCL

Table 1
Relative frequencies (%) of mature males of the blue shark *P. glauca* in the FL classes for each reproductive variable in the southwest Atlantic. *n* = total number of sharks within the FL class. 251658240.

FL (cm)	Testis length ≥ 9.5 cm		Testes weight ≥ 125 g		Rigid clasper		Clasper length ≥ 12 cm		Rigid clasper ≥ 12 cm		Semen in the ductus	
	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
80	–	–	–	–	0	2	0	2	0	2	–	–
85	–	–	–	–	0	1	0	1	0	1	–	–
90	–	–	–	–	0	2	0	2	0	2	–	–
95	–	–	–	–	0	6	0	6	0	6	–	–
100	0	1	0	1	0	8	0	8	0	8	–	–
105	–	–	–	–	0	5	0	5	0	5	–	–
110	0	2	0	2	0	13	0	13	0	13	–	–
115	0	1	0	1	0	5	0	5	0	5	–	–
120	–	–	–	–	0	7	0	7	0	7	–	–
125	–	–	–	–	0	9	0	9	0	9	–	–
130	0	7	0	7	0	8	0	8	0	8	0	6
135	0	4	0	4	0	18	0	18	0	18	0	3
140	11.1	9	0	9	0	29	0	24	0	29	0	8
145	12.5	8	0	8	0	36	0	29	0	36	0	8
150	20.0	10	10.0	10	0	40	0	36	0	40	0	10
155	50.0	4	0	4	0	18	0	49	0	18	0	4
160	33.3	15	13.3	15	3.7	27	0	63	0	27	0	15
165	30.8	13	15.4	13	12.1	33	0	71	0	33	15.4	13
170	45.0	20	45.0	20	30.3	33	2.4	83	6.1	33	20.0	20
175	60.9	23	78.3	23	40.4	47	11.0	100	17.0	47	13.0	23
180	57.1	21	76.2	21	58.1	43	16.9	77	20.9	43	30.0	20
185	63.2	19	82.2	19	87.0	46	49.4	83	71.7	46	52.9	17
190	85.7	21	76.2	21	100	39	61.4	83	71.8	39	61.1	18
195	95.0	20	90.0	20	100	43	79.4	68	88.4	43	94.4	18
200	100	10	100	10	100	26	86.7	45	92.3	26	90.0	10
205	100	6	100	6	100	18	90.9	33	100	18	100	6
210	100	14	100	14	100	28	97.7	43	100	28	100	14
215	100	11	100	11	100	7	100	16	100	7	100	11
220	100	4	100	4	100	13	100	21	100	13	100	4
225	100	6	100	6	100	13	100	25	100	13	100	6
230	100	8	100	8	100	11	100	18	100	11	100	8
235	100	3	100	3	100	12	100	12	100	12	100	3
240	100	2	100	2	100	11	100	11	100	11	100	1
245	–	–	–	–	100	6	100	6	100	6	–	–
250	–	–	–	–	100	2	100	2	100	2	–	–
255	–	–	–	–	100	1	100	1	100	1	–	–
260	100	1	100	1	–	–	–	–	–	–	–	–

(Fig. 3). The three phases of clasper growth were characterized as follows:

(1) First stage composed by embryos ranging in size from 18 to 33 cm FL and small juveniles from 80 to 109 cm FL. The clasper length increased with small standard deviation from 0.5 to 3.4 cm, but the RCL remains constant at about 2.5% (Fig. 3). In this stage, the clasper grew proportionally to the body growth as a whole.
(2) Second stage composed of sharks ranging in size from 110 to 198 cm FL with clasper length ranging from 2.3 to 16.0 cm. The mean clasper length by FL classes increased with high standard deviation from 3.2 to 12.5 cm. The RCL increased from 2.8 to 6.9% (Fig. 3). In this stage the clasper growth was faster than body growth.
(3) Third stage composed of sharks ranging in size from 199 to 258 cm FL with clasper length ranging from 11.5 to 18.2 cm. In this stage, although the mean clasper length increased from 13.3 to 16.9 with high standard deviation, the RCL decreased slowly from 6.9 to 6.4% (Fig. 3). In this stage the clasper grew slightly slower than the body as a whole.

Clasper rigidity was assessed in 666 individuals, of which 49.4% had rigid claspers (Table 1). The largest shark with flexible clasper had 189 cm FL, whereas the smallest shark with rigid clasper had 164 cm FL (Fig. 3c). The proportion of sharks with flexible claspers decreased with increasing clasper length, whereas the proportion of sharks with rigid claspers increased with increasing clasper length (Fig. 4a and b). Clasper length in the transition stage, from flexible to rigid, ranged from 8.0 to 11.9 cm. An abrupt transition in the proportion of sharks with flexible to rigid claspers occurs at 10–11 cm clasper length (Figs. 3a and 4b). Claspers with length <12 cm were mostly flexible (83.5%), whereas almost all claspers ≥12 cm were rigid (99.6%) (Fig. 4a and b). Rigid claspers with length ≥12.0 cm predominated in sharks with FL ≥ 180 cm, and for sharks with rigid claspers, 100% had claspers lengths ≥12 cm at 205 cm FL (Table 1).

3.1.3. The contents of the ductus deferens

The presence or absence of semen in the ductus deferens was assessed in 246 blue sharks caught in summer. The FL of those sharks ranged from 130 to 241 cm. The smallest shark with semen had 166 cm FL, whereas the largest without semen was 202 cm FL. A total of 114 sharks (46.3%) had semen reserve and rigid claspers. However, 25.5% of the sharks with rigid claspers had no semen reserves. From 185 cm FL onwards, most sharks within each FL class had semen, but it was from 205 cm FL onwards that 100% of sharks had semen stored (Table 1; Fig. 4c and d).

3.1.4. Maturity criteria

The criterion of maturity for the males was obtained through the analyses of FL range of sharks with semen stored in the *ductus deferens*, and of the relationship between FL and the variables measured in the testes and claspers. The FL class at which 100% of

Table 2
Relative frequencies (%) of mature females of the blue shark *P. glauca* in the FL classes for each reproductive variable in the southwest Atlantic. *n* = total number of sharks within the FL class. Only non-pregnant females were included in the quantitative reproductive variables.

FL (cm)	Pregnancy (all months together)		Ovary weight ≥ 35 g		Largest folic. diameter ≥ 7.5 mm		Ovid. gland weight ≥ 6 g		Ovid. gland diameter ≥ 25 mm		Mature	
	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
70	0	1	–	–	–	–	–	–	–	–	–	–
75	0	2	–	–	–	–	–	–	–	–	–	–
80	0	3	–	–	–	–	–	–	–	–	–	–
85	0	4	0	1	0	1	–	–	–	–	0	1
90	0	8	0	1	0	1	–	–	–	–	0	1
95	0	5	0	3	0	3	0	2	0	2	0	3
100	0	4	–	–	–	–	–	–	–	–	–	–
105	0	12	0	1	0	1	0	1	0	1	0	1
110	0	10	0	2	0	2	0	2	0	2	0	2
115	0	6	0	2	0	2	0	1	0	1	0	2
120	0	4	0	2	0	1	0	1	0	1	0	2
125	0	7	0	2	0	1	0	1	0	1	0	2
130	0	4	0	2	0	2	0	2	0	2	0	2
135	0	6	0	4	0	4	0	3	0	3	0	4
140	0	4	0	3	0	2	33.3	3	0	3	0	3
145	0	4	0	2	0	2	0	2	0	2	0	2
150	0	4	0	3	0	3	0	2	0	2	0	3
155	0	11	16.7	6	16.7	6	14.3	7	0	7	16.7	6
160	8.3	12	22.2	9	33.3	9	22.2	9	33.3	9	18.2	11
165	9.5	21	25.0	8	25.0	8	50.0	8	37.5	8	33.3	12
170	12.5	32	55.6	18	65.0	20	58.8	17	66.7	18	68.2	22
175	20.5	44	65.4	26	60.7	28	70.8	24	53.8	26	71.8	39
180	25.0	72	70.0	30	58.3	36	68.8	32	50.0	38	82.5	57
185	18.8	69	80.0	25	87.1	31	80.0	20	90.0	30	89.6	48
190	28.3	46	73.7	19	87.5	24	88.9	18	86.9	23	97.4	38
195	55.6	45	80.0	5	77.8	9	71.4	7	80.0	10	100	37
200	51.2	41	100	8	100	13	100	8	75.0	12	100	34
205	48.1	27	100	2	100	7	100	3	100	8	100	21
210	48.4	31	100	3	100	6	100	3	100	7	100	22
215	62.5	8	100	2	100	3	100	2	100	3	100	8
220	25.0	8	100	3	100	3	100	3	100	3	100	5
225	100	4	–	–	–	–	–	–	–	–	100	4
230	100	2	–	–	–	–	–	–	–	–	100	2
235	100	1	–	–	–	–	–	–	–	–	100	1
240	100	1	–	–	–	–	–	–	–	–	100	1
245	50.0	2	100	1	100	1	100	1	100	1	100	2

sharks had rigid claspers was smaller than the FL classes at which 100% of sharks had semen in the *ductus* deferens or met the critical values of the testes (10.5 cm and 125 g) (Table 1). However, by combining the variables "rigid claspers" and "clasper length ≥ 12.0 cm", it was observed that the FL class at which 100% of sharks fulfilled both these requirements, matched with the FL class at which 100% of sharks had semen reserves and met the critical values of the testes (Table 1). Thus, for the male we defined as the single criterion for maturity the simultaneous presence of rigid claspers and ≥12.0 cm.

3.2. Sexual development and maturity criteria of the female

3.2.1. The gonads and the oviducal glands

Females of *P. glauca* had a single ovary on the right side of the body cavity. The largest visible follicles were whitish in sharks with FL < 150 cm and yellow or orange in larger sharks. The largest follicle diameter (LFD) and ovary weight (OW) for sharks with FL < 155 cm varied respectively from 2.0 to 7.0 mm and from 1.4 to 30.0 g, whereas for sharks with FL ≥ 155 cm the LFD diameter ranged from >2.0 to 22.0 mm, in ovaries weighing from 9.1 to 331.6 g (Fig. 5a and b). In the individual female the two oviducal glands were always at the same stage of development. No significant differences between the right and left oviducal glands were found in the mean diameter ($t = 1.651$; $p = 0.473$; d.f. = 290) and in the mean weight ($t = 1.651$; $p = 0.354$; d.f. = 266). In ventral view, oviducal glands with diameter and weight respectively greater than 24.0 mm and 6.0 g were markedly heart-shaped with the acute end pointing caudally.

3.2.2. Maturity criteria

The females that were pregnant were *ipso facto* classified as sexually mature. The FL of the smallest pregnant female was 163 cm. In Fig. 5 it is seen that among the non-pregnant females the amplitude of the variation of the ovary and the oviducal gland increased abruptly as FL increased to ≥160 cm. This reflects the periodical changes that are known to occur in the ovary and the oviducal gland during the reproductive cycle of the mature female elasmobranch. Ovary weight ≥ 35 g, largest follicle diameter ≥ 7.5 mm, oviducal gland diameter ≥ 25 mm and oviducal gland weight ≥ 6 g were almost absent at FL < 160 cm but were numerous from 160 cm FL onward. Therefore the non-pregnant female was classified as sexually mature when she met at least two of the following four criteria: ovary weight ≥ 35 g, ovarian follicle diameter ≥ 7.5 mm, oviducal gland diameter ≥ 25 mm, or oviducal gland weight ≥ 6 g. The use of the critical values of at least two reproductive variables as the criterion of maturity of the non-pregnant female was meant to have the effect that the borderline cases of the non-pregnant females that met only one of the four critical values of reproductive variables were classified as immature. In Table 2 it is seen that such borderline cases were likely to occur mostly in the FL range from 155 to 200 cm. In that table it is also seen that at FL = 155 cm the critical value of each of the four quantitative variables began to classify females as mature, and that from FL ≥ 205 cm onwards

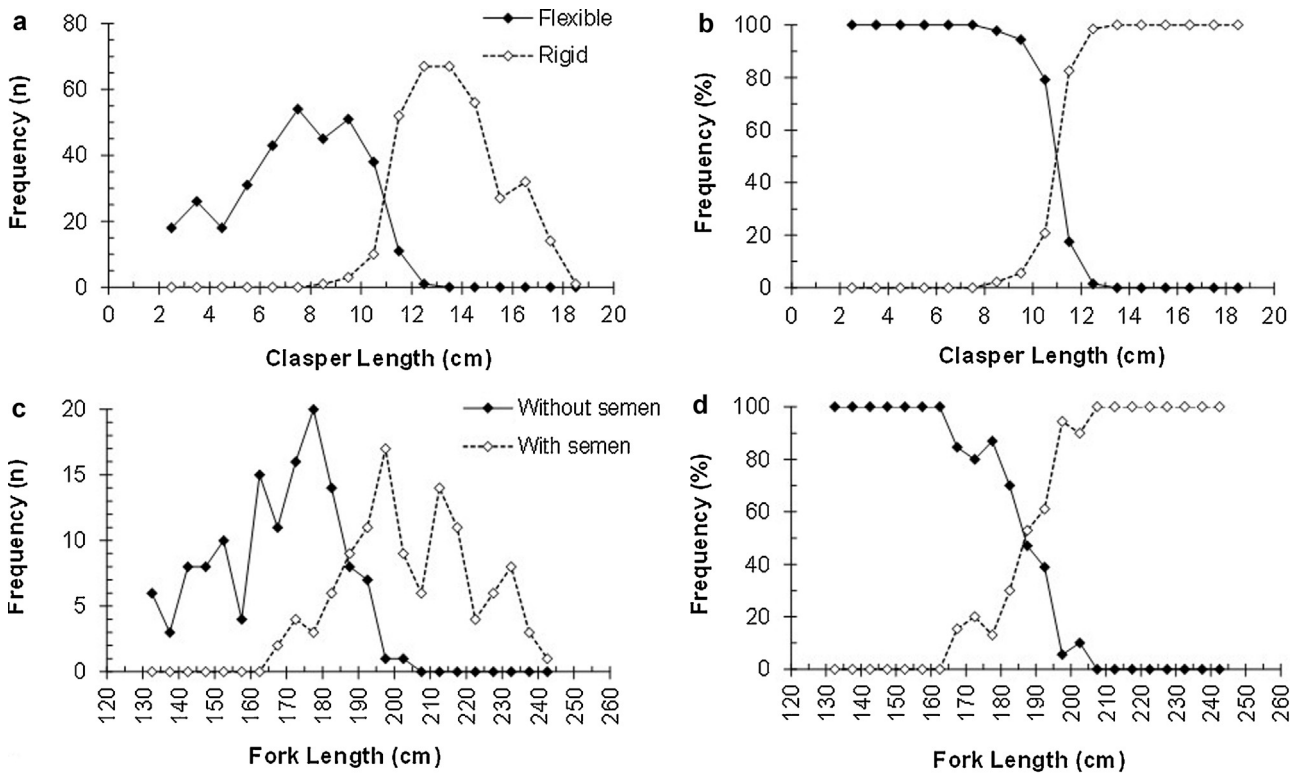

Fig. 4. Clasper length frequency distribution for flexible and rigid claspers (a and b), and fork length frequency distribution of sharks with and without semen in the ampullae of the ductus deferens (c and d).

the critical values of all four variables classified all the females as sexually mature.

3.2.3. Mating marks and their relationship with maturity of the female

In the total sample of 5363 blue sharks of both sexes, mating marks occurred only in the females, with frequency of 27.2% and at FL from 141 to 248 cm (Fig. 6a). Almost all the females with mating marks were mature (96.4%). Most of the females with mating marks were non-pregnant, whereas most of the pregnant females had no mating marks (Table 3). In the histological sections of the oviducal glands of 41 females with mating marks, 36.6% of such females had stored sperm (Table 4), which was observed in copious amounts in the lumen and the tubules of 40% of the oviducal glands, and in small amounts only in the tubules of 60% of the glands (Fig. 7). Of the females without mating marks and with sperm stored, 93.3% were non-pregnant (Table 4). Thus, the small proportions of pregnant females with mating marks and of pregnant females with sperm stored are evidence that the males of *P. glauca* court mainly non-pregnant mature females. Only 36.6% of the females with mating marks had sperm stored in the oviducal glands (Table 4). This is evidence that about two-thirds of the mating attempts had not resulted in sperm transference.

Table 3
Absolute frequency (n) of the mature females for all combinations of their categories: pregnant (PR), non-pregnant (NPR), mating marks present (MMP) and mating marks absent (MMA).

Category	PR	NPR	n
MMP	24	109	133
MMA	129	70	199
n	153	179	332

3.3. Size at maturity and size at maternity

According to the maturity criteria herein defined, the smallest mature female and male blue sharks had 157 and 163 cm FL, respectively. All females with FL ≥ 195 cm and all males with FL ≥ 205 cm were mature (Tables 1 and 2). Through fitting the logistic curve to the proportions of maturity in the FL classes, the L_{50} for maturity of the females of *P. glauca* from the Southwest Atlantic was estimated at 171.2 cm FL, and the L_{50} for maturity of the males was estimated at 180.2 cm FL (Table 5; Fig. 8). Pregnant females occurred in the FL classes of 160–245 cm (Fig. 6b). The L_{50} for maternity of *P. glauca* from the Southwest Atlantic was estimated in 193.9 cm FL (Table 5; Fig. 8).

3.4. Ovarian and uterine fecundity

Ovarian fecundity was estimated from 55 mature females with FL range of from 157 to 248 cm. Developed follicles in the ovaries of these females were identified by their similar LFD ≥ 6.0 mm and the typical bright orange color. Numerous tiny whitish follicles were considered immature, and therefore not developed for the current reproductive event. The average number of developed follicles was

Table 4
Numbers (n) and fork length (FL) range of the pregnant (PR) and non-pregnant (NPR) females, respectively with and without sperm stored in the oviducal gland, from a sample of 41 mature females of *P. glauca* with mating marks, collected in October 2008 and January 2009 in the Southwest Atlantic.

		With sperm	Without sperm	Total
PR	n	1	3	4
	FL (cm)	182	182, 186, 205	
NPR	n	14	23	37
	FL (cm)	157–206	172–248	
Total		15	26	41

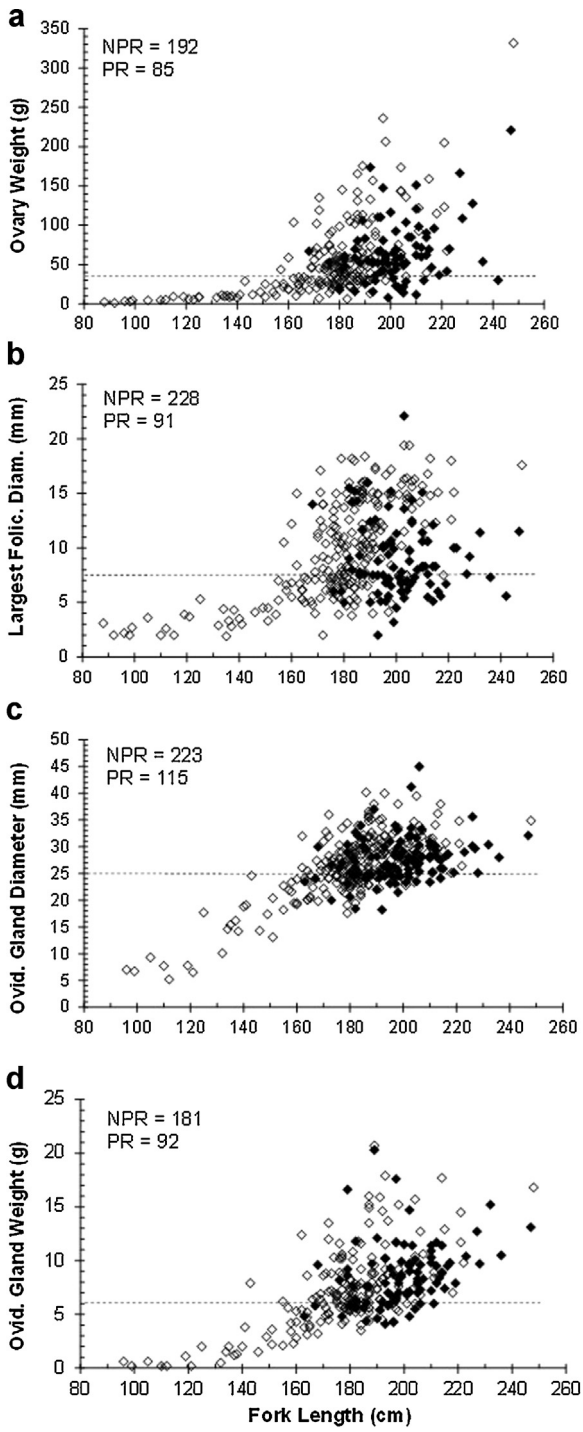

Fig. 5. Development of the reproductive organs of the female of *P. glauca* in the Southwest Atlantic. Variation of the ovary weight (a), of the maximum follicle diameter (b), and of the diameter and weight of the oviducal glands (c and d) in relation with fork length. White diamonds are non-pregnant females, and black diamonds are pregnant females. Dotted lines represent the position of the critical values for maturity.

60 (S.D. 18.6) with a range of from 23 to 112 follicles. There was no trend in the relationship between the ovarian fecundity and the FL (Fig. 9).

For the estimation of uterine fecundity, the embryos in the litters of 87 pregnant females with FL from 165 to 247 were counted. Litter size varied from 9 to 74 embryos about the median of 33 (mean 33.5; S.D. 12.5). The embryo sex ratio was assessed in 37

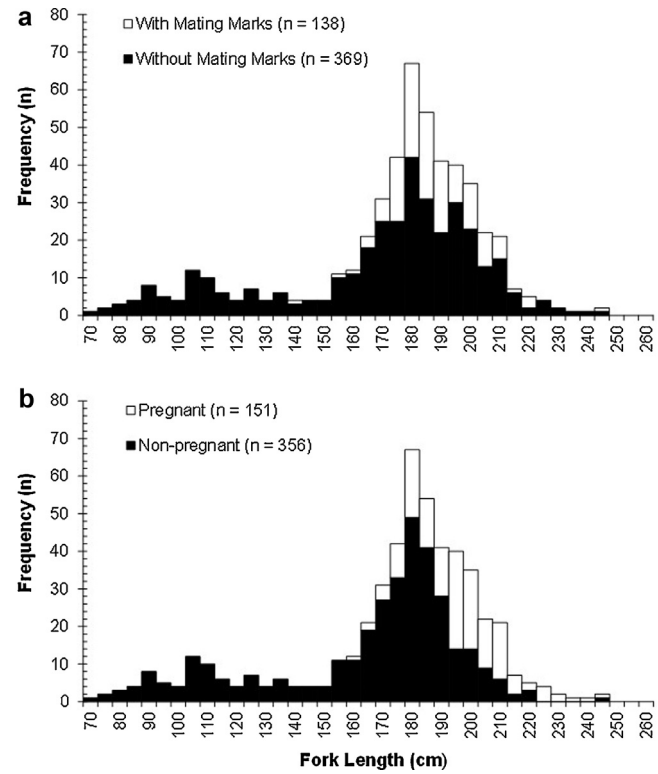

Fig. 6. Size frequency distribution of female blue sharks with and without mating scars (a), and pregnant and non-pregnant (b), caught in ten longline fishing cruises carried out in the Southwest Atlantic between 2004 and 2009.

pregnant females, and no evidence of a significant difference from 1:1 was found ($X^2 = 198.6$; $p > 0.05$; $n = 1269$). Grouping the 37 pregnant females, the overall litter sex ratio (males to females) was 1.08:1. Although not significant, a trend toward an increase in uterine fecundity (UF) with the body size of the pregnant female was observed (UF = 0.4334 FL−54.547; $r = 0.521$) (Fig. 9). The linear model was chosen because the better correlation index.

4. Discussion

4.1. Sexual development and maturity criteria

The criteria to classify blue sharks as mature or immature were based on the relative developmental stage of the reproductive organs. In the relationship between the size or weight of the reproductive organs and the FL it is seen that, as the FL increases, an abrupt change in the scatter pattern occurs around 160 cm FL. The

Table 5
Descriptive statistics of the MCMC posterior distribution for each logistic model parameter. Columns 2.5%, 50% and 97.5% are the first second and third quantiles.

	Mean	S.D.	2.5%	50%	97.5%
Males					
β_0	−3.5	0.4	−4.2	−3.4	−2.7
β_1	0.2	0	0.2	0.2	0.3
L_{50} (cm)	180.2	0.73	178.8	180.2	181.7
Females					
β_0	−1.8	0.4	−2.5	−1.8	1
β_1	0.2	0	0.1	0.2	0.2
L_{50} (cm)	171.1	1.4	167.9	171.2	173.6
Maternity					
β_0	−2.8	0.4	−3.5	−2.8	−2.2
β_1	0.1	0.0	0.1	0.1	0.1
L_{50} (cm)	194.0	1.9	190.3	193.9	197.9

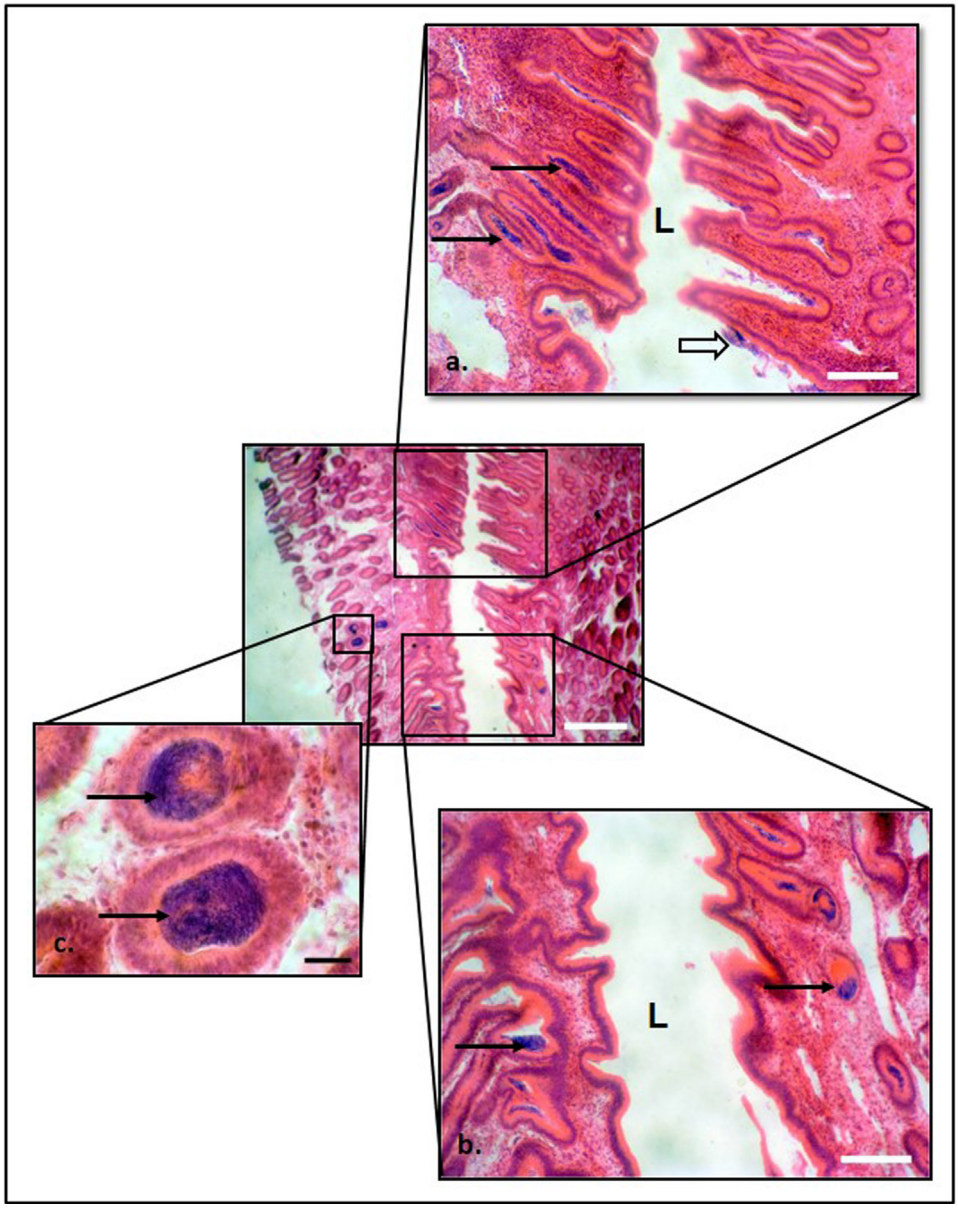

Fig. 7. Microphotographs of the lower portion of the oviducal gland of *Prinonace glauca* in sagittal orientation. (a and b) Details of the sperm storage (solid black arrows) within the tubular portion of the simple tubular convoluted glands that reach the lumen (L) of the oviducal gland. Sperm presence within the lumen (L) of the oviducal gland (opened black arrow). Scale bar: 170 μm and 125 μm, respectively. (c) Sperm storage (black arrows) within the convoluted portion of the simple tubular glands of the oviducal gland. Scale bar: 25 μm. Stain for all microphotographs: Haematoxilin–Eosin.

range of values of the reproductive variable increases sharply, and values greater than those at FL < 160 cm begin to appear higher than in the previous section. In the reproductive cycle of mature elasmobranchs, cyclical changes occur in the size and weight of the reproductive organs (Castro, 2000; Lucifora et al., 2004; Peres and Vooren, 1991; Walker, 2005a,b), which also had been observed for *P. glauca* in the northern hemisphere (Henderson et al., 2001; Nakano, 1994; Pratt, 1979). Thus, the sharp increase in the amplitude of the values of reproductive variables of *P. glauca* from 160 cm FL onwards is evidence that maturity occurs from that FL.

Given that our data are a pooled sample of all the months of the year, the range of values of reproductive variables in the sample masks seasonal variation in the size and weight of these reproductive organs. Therefore, to define the critical values of the reproductive quantitative variables, we chose values by which, at any time of the reproductive cycle, a mature shark will be classified as such. Hence, we defined critical values slightly above the lower limit of the seasonal variation of reproductive variables.

The calcification stage of claspers, herein referred as degree of rigidity, is the most common criterion used to classify male elasmobranchs as mature (Conrath, 2005). Despite subjectivity and inaccuracy of the method (Conrath, 2005; Walker, 2005a,b), authors studying the reproductive biology of *P. glauca* have used the clasper size and rigidity as criteria of maturity (Aasen, 1966; Carrera-Fernández et al., 2010; Cruz-Ramírez et al., 2012; Hazin et al., 1994a, 2000; Henderson et al., 2001; Nakano et al., 1985; Nakano, 1994; Pratt, 1979; Stevens, 1984). Using a wide range of sizes, from juveniles to adults, the general pattern of the relationship between clasper length and body length in most of these studies is that the clasper grows continuously, without reaching a maximum. We also observed this general pattern for the absolute clasper length (Fig. 3a). In other species of elasmobranchs this methodology demonstrates an S-shaped scattergram (Lucifora

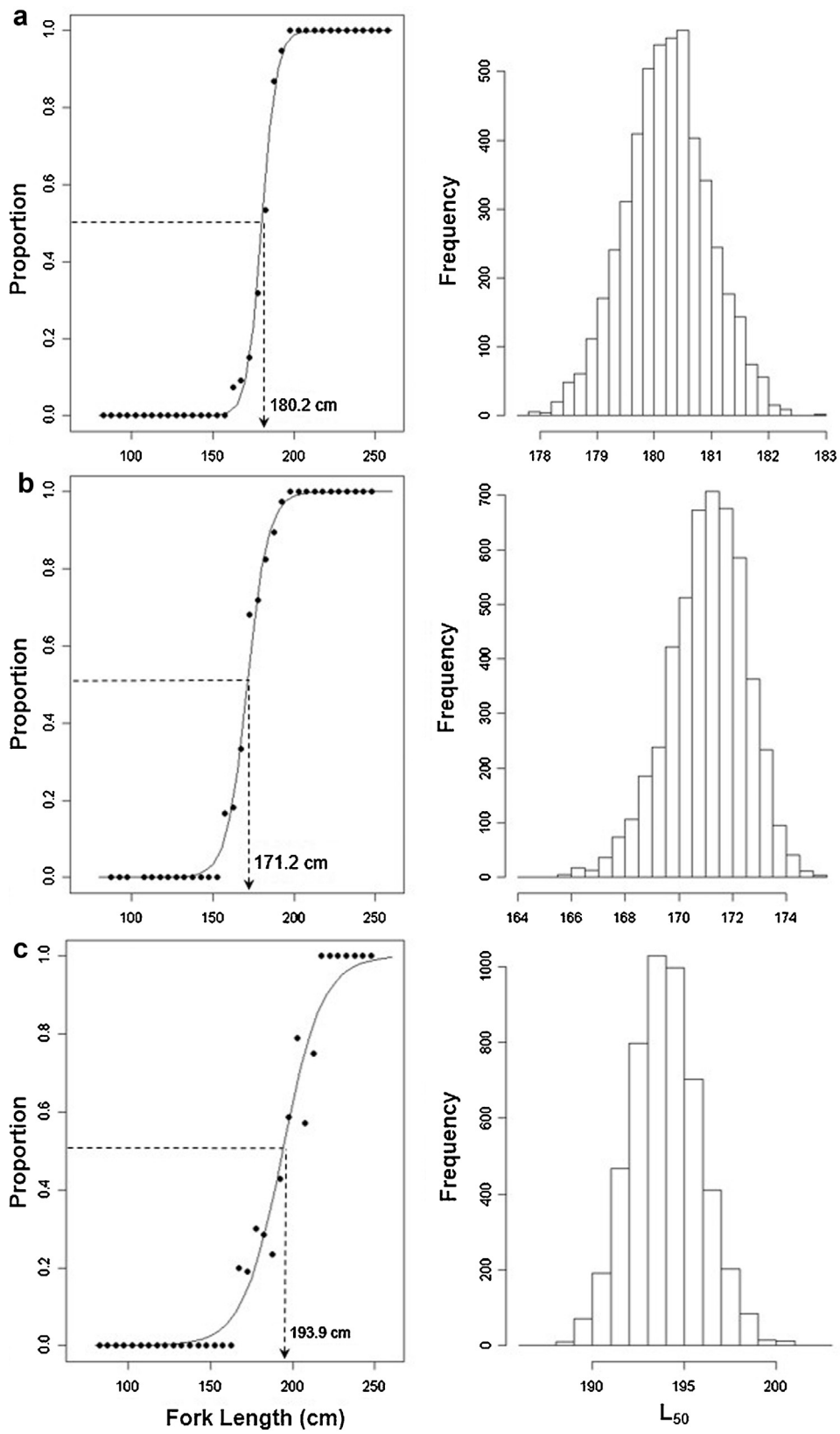

Fig. 8. Maturity and maternity ogives. Logistic model fit to the proportion of mature males (a), mature females (b) and pregnant females (c) in FL classes of 5.0 cm, and the respective L_{50} posterior distributions representing the 95% Bayesian credibility interval.

et al., 2005; Motta et al., 2007; Peres and Vooren, 1991; Yokota and Lessa, 2007).

However, a clear pattern appears when the clasper length is expressed as a proportion of the FL. In that way, using the outer clasper length (Compagno et al., 2005), we identified two inflection points that define the lower and upper limits of the body and clasper size ranges at which the clasper growth is fastest. This feature has previously been observed in other elasmobranch species

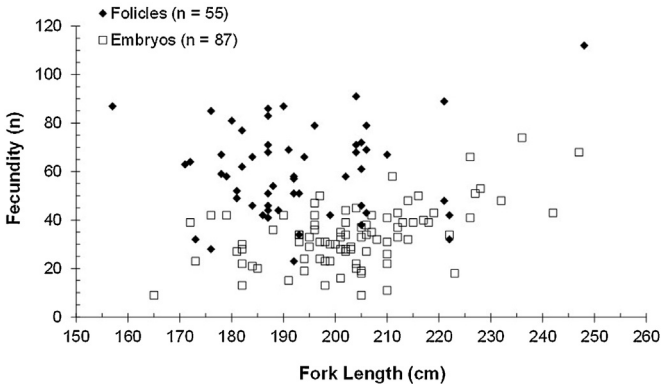

Fig. 9. Relationship between the litter size (black diamonds) and of the number of developed ovarian follicles (white diamonds) with the maternal fork length of the blue shark *P. glauca* in the southwest Atlantic.

but not in *P. glauca* (Francis and Duffy, 2005; Stevens, 1984; Stevens and McLoughlin, 1991). Due to the absence of small sharks from the samples, Stevens (1984) found in the clasper size – FL relationship of *P. glauca* from Australia a pattern with only the upper inflection point. However, Francis and Duffy (2005), analyzing absolute and relative clasper lengths in samples of a wide range of FL, as was done in the present study, found the pattern without inflection points, and considered this pattern to be a characteristic of *P. glauca*. A wide range of FL and relative clasper length were analyzed in both studies, from embryos and small juveniles to large adults. However, the relative clasper lengths in the study by Francis and Duffy (2005) were larger than in the present study, and increased continuously from the embryonic stage onwards, with a slight tendency to stability at the top. The only methodological difference between the two studies is the type of clasper measurement. We used the outer clasper length, measured between the clasper insertion in the pelvic fin and the posterior tip, whereas Francis and Duffy (2005) used the inner clasper length, measured between the anterior margin of the cloaca and the posterior clasper tip (Compagno et al., 2005). Thus, the clasper measurement used by Francis and Duffy (2005) includes a portion of body length, situated between the front edge of the cloacal vent and the base of clasper. Assuming that there is no population difference, it is likely that this methodological difference explains the smaller relative clasper lengths (RCL) in our present study, and thus the difference between the two studies in the pattern of the RCL–FL relationship.

The claspers begins to grow at an accelerated rate from 120 cm FL, whereas the testis begins to grow at an accelerated rate from 170 cm FL (Figs. 2 and 3) which is the same size class at which the frequency of occurrence of semen in the ampullae of the ductus deferens abruptly increases (Fig. 4). Thus, as pointed out by Pratt (1979), the degree of rigidity of the clasper is not a good criterion for maturity, since a small proportion of sharks with rigid claspers still do not have fully developed gonads. However, we demonstrated that 100% of sharks with fully developed testes or with sperm stored, had rigid claspers $\geq$ 12 cm, and therefore could be satisfactorily classified as mature by the combination of the variables clasper length and rigidity. From about 200 cm FL onwards, 100% of sharks had rigid claspers, fully developed gonads and semen stored (Table 1), virtually the same FL and clasper length at the upper break point of the relationship between clasper size and FL. Thus, this is evidence that fully developed claspers with minimum size of 12 cm is a good criterion for maturity.

In the females, the accelerated development of the ovary and the oviducal glands starts at 160 cm FL, and most females with fully developed reproductive organs had FL $\geq$ 170 cm (Fig. 5; Table 2). Therefore it is evident that the development of those organs is rapid. This same pattern has been observed for *P. glauca* in other regions (Carrera-Fernández et al., 2010; Cruz-Ramírez et al., 2012; Francis and Duffy, 2005; Hazin et al., 2000; Henderson et al., 2001; Nakano, 1994; Pratt, 1979).

The proportion of females with mating marks by FL evidenced that females start to be courted by males from 160 cm onwards, and the highest proportion occurs in FL classes from 170 to 190 cm. Therefore, the synchrony in the FL range between the sexual development of the females, and courted females, is evidence that males recognize mature females in reproductive condition, and that females from 170 cm FL onwards are apt to breed.

4.2. Size at maturity

Estimates of size at maturity for *P. glauca* at the Southwest Atlantic obtained in this study match fairly well within the general global pattern (Table 6). Given that *P. glauca* is caught by gillnets in addition to longlines, regional differences in maturity may be due to the possibility of length-selective fishing mortality from gillnets creating distortions to maturity ogives as it was demonstrated for *Mustelus antarticus* (Walker, 2007). Likewise, the possibility of geographic variation in the periodicity of the reproductive cycle, or in age at maturity may also be correlated with these geographical variations in the size at maturity, as has been shown for *Mustelus manazo* (Yamaguchi et al., 2000) and *M. antarcticus* (Walker, 2007). However, it is most likely that methodological issues are of great influence for these differences. There is no consensus on the definition of 'maturity' and although most authors had analyzed reproductive variables to classify mature sharks, rarely the respective critical values or maturity criteria have been defined. This is an important source of variation, because depending on the critical values used to define the maturity criteria, the proportion of mature animals by size class changes, and thus also the estimated median size at maturity.

The distribution and abundance of the life stages of *P. glauca* in the southwest Atlantic provides support to the hypothesis of a single blue shark population in the southern half of the Atlantic Ocean (Amorim et al., 1998; Carvalho et al., 2010; Castro and Mejuto, 1995; Hazin et al., 1994b; Mejuto and García-Cortés, 2005; Montealegre-Quijano and Vooren, 2010). The recapture of a South African-tagged juvenile blue shark off Uruguay lends support to this hypothesis (da Silva et al., 2010). However, size at maturity estimates in the equatorial region (Hazin, 1991 in Lessa et al., 2004) are larger than our estimates for the southwest Atlantic, mainly for females (Table 6). Given that the critical values were similar between both studies, it is possible that distortion is due to the absence of young sharks in equatorial waters (Castro and Mejuto, 1995; Hazin et al., 1994a,b, 2000; Mejuto and García-Cortés, 2005). However, it should also be considered the fact that the estimates of Hazin (1991 in Lessa et al., 2004) are almost from 25 years ago, and therefore difference in the sizes at maturity may also be an effect of fishing on the population (Hilborn and Hilborn, 2012).

The largest male and female blue sharks recorded in our commercial longline cruises were 262 and 247 cm FL, respectively (Montealegre-Quijano and Vooren, 2010). Most of the size distributions reported for the South Atlantic also found larger sizes for males than for females (Amorim et al., 1998; Castro and Mejuto, 1995; Hazin et al., 1994a,b, 2000; Kotas et al., 2010; Lessa et al., 2004; Legat and Vooren, 2008; Mazzoleni and Schwingel, 2002; Mejuto and García-Cortés, 2005). However, Carvalho et al. (2011) found no difference between sexes in maximum lengths of 11,932 blue sharks caught over a broad fishing area in the Southwest Atlantic. Therefore, it is likely that the small difference in maximum observed sizes between sexes is not significant, and thus this

Table 6
Global estimates of size at maturity and size at maternity of the blue shark *P. glauca*, and their respective calculated ages. Original data in total length (TL) were converted to fork length (FL) through the Kohler et al. (1995). FL–TL relationship (FL = 1.3908 + 0.8313TL). Age estimates were calculated through the von Bertalanffy growth function obtained by Lessa et al. (2004). 'Maturity Definition' refers to the way as mature sharks were recognized. Method estimation is the way as the population parameter was estimated.

Geographical region	Females		Male		*n*		Maturity definition	Method of estimation	Reference
	FL (cm)	Age (year)	FL (cm)	Age (year)	Females	Males			
Sexual maturity									
North Pacific	156.0–177.6	3.8–4.9	170.2	4.5	230	977	PR-TY & MC-RVA	P50-CFD	Nakano (1985, 1994)
Northeast Pacific	154.4	3.7	164.3	4.2	402	626	MC-RVA	OGV-L50	Carrera-Fernández et al. (2010)
Northeast Pacific	146.9	3.4	146.9	3.4	93	68	MC-RVA	OGV-L50	Cruz-Ramírez et al. (2012)
Southwest Pacific	170.0–190.0	4.5–5.6	194.0	5.8	26	58	MC-RVA	OGV-AVR	Francis and Duffy (2005)
Equatorial Indian Ocean	151.0	3.6	151.0	3.6	125	175	PR-TY/MC-RVA	–	Gubanov and Grigor'yev (1975)
Southwest Indian	163.0	4.1	168.8	4.4	85	120	MC-RVA	OGV-L50	Jolly et al. (2013)
North Atlantic	–	–	197.6	6.1	–	268	CLP	P50-CFD	Aasen (1966)
Northwest Atlantic	185.0	5.3	183.0	5.1	210	114	MC-RVA	P50	Pratt (1979)
Northwest Atlantic	–	–	201.0	6.3	1025	1212	MC-RVA	P50	Campana et al. (2004)
Northeast Atlantic	151.0	3.6	–	–	353	–	MMP	SML	Stevens (1974)
Mediterranean	179.9	5.0	170.1	4.5	178	323	MC-RVA	OGV-L50	Megalofonou et al. (2009)
Equatorial Southwest Atlantic	190.9	5.6	188.4	5.5	88	82	MC-RVA	–	Hazin (1991) in Lessa et al. (2004)
Southwest Atlantic	171.2	4.5	180.2	5.0	398	666	MC-RVA	OGV-L50	This study
Maternity									
North Pacific	172.3	4.6			668		PR-TY	P50-CFD	Nakano et al. (1985)
Northwest Pacific	166.8	4.3					PR-TY	SML	Suda (1953) in Nakano and Seki (2003)
Southwest Pacific	218.0	7.6			33		PR-TY	AVR	Stevens (1974)
Southwest Pacific	202.0	6.4			40		PR-TY	AVR	Francis and Duffy (2005)
Equatorial Indian Ocean	209.2	6.9			235		PR-TY	SML	Gubanov (1978)
North Atlantic	178.5–204.2	4.9–6.5			–		–	–	Bigelow and Shroeder (1948) in Nakano and Seki (2003)
Equatorial Southeast Atlantic	180.0	5.2			548		PR-BS	P50-NLF	Castro and Mejuto (1995)
Southwest Atlantic	193.9	5.8			313		PR-BS	OGV-L50	This study

AVR, Average length; CLP, clasper length and rigidity; L_{50}, logistic model applied to the proportion of maturity or maternity by length class; MC-RVA, maturity criteria derived from reproductive variables analyses; MMP, mating marks present; OGV, maturity ogive fitted; P50-CFD, 50th percentile of cumulative frequency distribution; P50-NLF, 50th percentile non-linear function; PR-BS, pregnancy during breeding season; PR-TY, pregnancy throughout the year; PROBIT, probit analyses; SML, smallest mature sharky.

explains why the ratio between the size at maturity and the largest observed length was virtually the same in both sexes (68.8% for males and 69.3% for females). *P. glauca* seems to be different from most shark species, because most commonly the maximum size of males is about 10% smaller than in females (Cortés, 2000).

If the sizes at maturity and the maximum observed FLs are expressed in ages through the von Bertalanffy growth function estimated for the Southwest Atlantic (Lessa et al., 2004), males mature at 5.0 years old and attain maximum age of 13.1 years, whereas females mature at 4.5 years old and attain maximum age of 10.6 years. Thus, our results for *P. glauca* in the Southwest Atlantic agree with the general pattern for sharks in which both males and females reach maturity at about three-quarters of their maximum size and half of their maximum age (Cortés, 2000).

4.3. Size at maternity

For the assessment of populations of viviparous elasmobranches through demographic analysis, the median body size at maternity is a relevant parameter because only at her gestation the female is effectively recruited to the reproductive phase of life (Walker, 2005a,b). However, the proportion of pregnant females by size varies depending on the timing of the reproductive cycle, and therefore it is necessary, for the size at maternity analysis, to restrict the data to the months in which all the females that are apt to breed, are expected to be pregnant. In the South Atlantic, the timetable of the reproductive cycle of *P. glauca* is still not fully known, but some evidences allowed us to define the pregnancy period as being from late summer (March) to late winter (September) (Amorim et al., 1998; Bornatowski and Schwingel, 2008; Hazin et al., 1994a, 2000; Kotas et al., 2010; Legat and Vooren, 2008; Mazzoleni and Schwingel, 2002; Mejuto and García-Cortés, 2005; Montealegre-Quijano, 2007).

The size at first maternity was 22.7 cm greater than the estimated size at maturity of the female. Translating into ages (Lessa et al., 2004), maternity occurs at 5.8 years old, roughly one year later than onset of maturity. This matches well with the required period for the development of the reproductive organs and for gestation, which has been estimated that lasts 9–12 months in the Atlantic Ocean (Montealegre-Quijano, 2007; Pratt, 1979). Therefore, based on the principle of the ogive of maternity, half of the females of *P. glauca* with ages from five to six years old are already effectively recruited to the reproductive phase. Given that maternity criterion is the presence of embryos or eggs in uterus, regional differences in the size at maternity may be due to the estimation method used, or to the selectivity of the fishing gear, or even to the regional life stage composition.

4.4. Ovarian and uterine fecundity

The maximum litter sizes observed in this study confirms for the Southwest Atlantic the high fertility of the species recorded in other parts of the world (Aasen, 1966; Castro and Mejuto, 1995; Mejuto and García-Cortés, 2005; Nakano, 1994; Pratt, 1979; Strasburg, 1958). In some species, reproductive failure occurs during gestation and the number of pups actually surviving to gestation may be considerably smaller than the initial number of ovulated eggs present in the uterus (Conrath, 2005). Our data are evidence that around 50% of mature follicles are fertilized and survive until the fetal stage. However, the minimum values of litter size should be looked at with caution because some pregnant females in the terminal phase of pregnancy were seen aborting when brought on board. This corroborates the potential difficulty with simply counting uterine eggs or embryos mentioned by Conrath (2005) about abort during the stress of capture. Since we did not count placental scars in the uterus to determine if embryos were aborted, therefore our estimates of fecundity should be considered as the lower limit of fecundity.

5. Conclusion

Blue sharks have been exploited for six decades in the Southwest Atlantic, but began to be landed just at the end of 1970s (Amorim et al., 1998). Since then its meat has been sold in domestic markets of Brazil and Uruguay, whereas their fins have been exported to Asia (Clarke et al., 2006). In spite of this, no consensus exists about the population status. The presence of males and females of all life stages during any time of the year in the study area (Amorim et al., 1998; Montealegre-Quijano and Vooren, 2010), allows us to conclude that samples from this area are representative of the entire harvested stock. Therefore, estimates of the reproductive parameters herein presented are useful for stock assessment of *P. glauca* in the Southwest Atlantic. Size at maturity and size at maternity are population parameters that must show signs of overfishing. Thus, the first estimates we provided here for this ocean are reference points for future studies, and could be used for management proposes.

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References

Aasen, O., 1966. Blåhaien *Prionace glauca* (Linnaeus, 1758). Fisken Havet 1, 1–17.

Aires-da-Silva, A.M., Hoey, J.J., Gallucci, V.F., 2008. A historical index of abundance for the blue shark (*Prionace glauca*) in the western North Atlantic. Fish. Res. 92, 41–52.

Amorim, A.F., Arfelli, C.A., Fagundes, L., 1998. Pelagic elasmobranches caught by longliners off southern Brazil during 1974–97: an overview. Mar. Freshwater Res. 49 (7), 621–632.

Anonymous, 2008. Report of the 2008 Shark Stock Assessments Meeting. ICCAT/SCRS/2008/017.

Baum, J.K., Blanchard, W., 2010. Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. Fish. Res. 102, 229–239.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299, 389–392.

Behmer, O.A., Tolosa, E.M.C., Neto, A.G.F., 1976. Manual de técnicas para histologia normal e patológica. Editora da Universidade de São Paulo, São Paulo.

Bonfil, R., 1994. Overview of world elasmobranch fisheries. In: FAO Fish. Tech. Pap. 341.

Bornatowski, H., Schwingel, P.R., 2008. Alimentação e reprodução do tubarão-azul *Prionace glauca* (Linnaeus, 1758), capturado na costa sudeste e sul do Brasil. Arq. Ciên. Mar. 41, 98–103.

Camhi, M.D., Valenti, S.V., Fordham, S.V., Fowler, S.L., Gibson, C., 2009. The Conservation Status of Pelagic Sharks and Rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop. IUCN Species Survival Commission Shark Specialist Group, Newbury, UK.

Campana, S.E., Marks, L., Joyce, W., Kohler, N.E., 2004. Effects of recreational and commercial fishing on the blue shark (*Prionace glauca*) population in Atlantic Canada, waters. Canadian Stock Assessment Secretariat (CSAS) Res. Doc. No. 2004/069.

Campana, S.E., Marks, L., Joyce, W., Kohler, N.E., 2006. Effects of recreational and commercial fishing on the blue sharks (*Prionace glauca*) in Atlantic Canada, with inferences on the North Atlantic population. Can. J. Fish. Aquat. Sci. 63, 670–682.

Carrera-Fernández, M., Galván-Magaña, F., Ceballos-Vásquez, B.P., 2010. Reproductive biology of the blue shark *Prionace glauca* (Chondrichthyes: Carcharhinidae) off Baja California Sur, México. Aqua 16 (3), 101–110.

Carvalho, F.C., Murie, D.J., Hazin, F.H.V., Hazin, H.G., Leite-Mourato, B., Travassos, P., Burgess, G.H., 2010. Catch rates and size composition of blue sharks (*Prionace glauca*) caught by the Brazilian pelagic longline fleet in the southwestern Atlantic Ocean. Aquat. Living Resour. 23, 373–385.

Carvalho, F.C., Murie, D.J., Hazin, F.H.V., Hazin, H.G., Leite-Mourato, B., Burgess, G.H., 2011. Spatial predictions of blue shark (*Prionace glauca*) catch rate and catch probability of juveniles in the Southwest Atlantic. ICES J. Mar. Sci. 68 (5), 890–900.

Castro, J.A., 2000. The biology of the nurse shark *Ginglimostoma cirratum* off the Florida east coast and the Bahamas Islands. Environ. Biol. Fish. 58, 1–22.

Castro, J.A., Mejuto, J., 1995. Reproductive parameters of blue shark *Prionace glauca*, and other sharks in the Gulf of Guinea. Mar. Freshwater Res. 46, 967–973.

Castro, J.I., Woodley, C.M., Brudek, R.L., 1999. A preliminary evaluation of the status of shark species. In: FAO Fish. Tech. Paper No. 380. Rome.

Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H., Shivji, M.S., 2006. Global estimates of sharks using trade records from commercial markets. Ecol. Lett. 9, 1115–1126.

Compagno, L., Dando, M., Fowler, S., 2005. Sharks of the World, 1st ed. Princeton University Press, Oxford.

Conrath, C.L., 2005. Reproductive biology. In: Musick, J.A., Bonfil, R. (Eds.), Management Techniques for Elasmobranchs Fisheries. FAO Fish. Tech. Paper No. 474. Rome. , pp. 103–126.

Cortés, E., 2000. Life history patterns and correlations in sharks. Rev. Fish. Sci. 8 (4), 299–344.

Cortés, E., 2008. Standardized catch rates for blue and mako sharks from the U.S. pelagic longline logbook and observer programs. ICCAT Col. Vol. Sci. Pap. 62 (5), 1447–1466.

Cruz-Ramírez, A., Soriano-Velásquez, S.R., Santana-Hernández, H., Ramírez-Santiago, C.E., Acal-Sánchez, D.E., 2012. Aspectos reproductivos del tiburón azul *Prionace glauca* capturado por la flota palangrera de mediana altura del Puerto de Manzanillo. Colima. Ciencia Pesq. 20, 39–48.

da Silva, C., Kerwath, S.E., Wilke, C.G., Meyer, M., Lamberth, S.J., 2010. First documented southern transatlantic migration of a blue shark *Prionace glauca* tagged off South Africa. Afr. J. Mar. Sci. 32 (3), 639–642.

Francis, M.P., Duffy, C., 2005. Length and maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus* and *Prionace glauca*) from New Zealand. Fish. Bull. 103, 489–500.

Gubanov, Y.P., 1978. The reproduction of some species of pelagic sharks from the equatorial zone of the Indian Ocean. J. Ichthyol. 18 (5), 781–792.

Gubanov, Y.P., Grigor'yev, V.N., 1975. Observations on the distribution and biology of the blue shark *Prionace glauca* (Carcharhinidae) of the Indian Ocean. J. Ichthyol. 15, 37–43.

Hamlett, W.C., Knight, D.P., Pereira, F.T.V., 2005. Oviducal glands in Chondrichthyans. In: Hamlett, W.C. (Ed.), Reproductive Biology and Phylogeny of Chondrichthyes. Sharks, Batoids and Chimaeras. Science Publisher Inc., Plymoth.

Hazin, F.H.V., Kihara, K., Otsuka, K., Boeckman, C.E., Leal, E.C., 1994a. Reproduction of the blue shark *Prionace glauca* in South-Western Equatorial Atlantic Ocean. Fish. Sci. 60 (5), 487–491.

Hazin, F.H.V., Boeckman, C.E., Leal, E.C., Lessa, R., Kihara, K., Otsuka, K., 1994b. Distribution and relative abundance of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean. Fish. Bull. 92, 474–480.

Hazin, F.H., Pinheiro, P.B., Broadhurst, M.K., 2000. Further notes on the reproduction of the blue shark and a postulated migratory pattern in the South Atlantic Ocean. Ciência Cultura 52, 114–120.

Henderson, A.C., Flannery, K., Dunne, J., 2001. Observations on the biology and ecology of the blue shark in the North-east Atlantic. J. Fish. Biol. 58, 1347–1358.

Hilborn, R., Hilborn, U., 2012. Overfishing: What Everyone Needs to Know. Oxford University Press, New York, pp. 141.

Jolly, K.A., da Silva, C., Attwood, C.G., 2013. Age, growth and reproductive biology of the blue shark *Prionace glauca* in South African waters. Afr. J. Mar. Sci. 35 (1), 99–109.

Kinas, P.G., Andrade, H.A., 2010. Introdução à análise bayesiana (com R). MaisQnada Editora, Porto Alegre.

Kohler, N.E., Casey, J.G., Turner, P.A., 1995. Length-weight relationships for 13 species of sharks from the western North Atlantic. Fish. Bull. 93 (2), 412–418.

Kotas, J.E., Lin, C.F., Albanez, F.F., Santos, S., Pazeto, F.D., 2010. Observações biológicas do tubarão-azul, *Prionace glauca* (Linnaeus, 1758), em cruzeiros de prospecção pesqueira na zona econômica exclusive do Sudeste-Sul do Brasil. Rev. CEPSUL 1, 43–60.

Legat, J.F.A., Vooren, C.M., 2008. Caracterização da morfologia uterina e das fases de desenvolvimento embrionário do tubarão-azul *Prionace glauca* (Linnaeus, 1758). Arq. Ciên. Mar. 41 (2), 14–20.

Lessa, R., Santana, F.M., Hazin, F.H., 2004. Age and growth of the blue shark of the northeastern Brazil. Fish. Res. 66, 19–30.

Lucifora, L.O., Menni, R.C., Escalante, A.H., 2004. Reproductive biology of the school shark, *Galeorhinus galeus*, off Argentina: support for a single south western Atlantic population with synchronized migratory movements. Environ. Biol. Fish. 71, 199–209.

Lucifora, L.O., Menni, R.C., Escalante, A.H., 2005. Reproduction and seasonal occurrence of the copper shark, *Carcharhinus brachyurus*, from Patagonia, Argentina ICES. J. Mar. Sci. 62, 107–115.

Mazzoleni, R.C., Schwingel, P.R., 2002. Aspectos da biologia das espécies capturadas por espinhel pelágico na região sul das ilhas de Trindade e Martín Vaz no verão de 2001. Notas Téc. FACIMAR 6, 51–57.

Megalofonou, P., Damalas, D., De Metrio, G., 2009. Biological characteristics of blue shark, *Prionace glauca*, in the Mediterranean Sea. J. Mar. Biol. Ass. U.K. 89, 1233–1242.

Mejuto, J., García-Cortés, B., 2005. Reproductive and distribution parameters of the blue shark *Prionace glauca*, on the basis of on-board observations at sea in the in the Atlantic, Indian and Pacific Oceans. ICCAT Col. Vol. Sci. Pap. 58 (5), 951–973.

Montealegre-Quijano, S., (Doctoral thesis) 2007. Biologia populacional do tubarão-azul, *Prionace glauca* (Linnaeus, 1758). na região sudoeste do Oceano Atlântico. Federal University of Rio Grande, Brazil (in Portuguese, with English abstract).

Montealegre-Quijano, S., Vooren, C.M., 2010. Distribution and abundance of the life stages of the blue shark *Prionace glauca* in the Southwest Atlantic. Fish. Res. 101, 168–179.

Motta, F.S., Namora, R.C., Gadig, O.B.F., Braga, F.M.S., 2007. Reproductive biology of the Brazilian sharpnose shark (*Rhizoprionodon lalandii*) from southeastern Brazil. ICES J. Mar. Sci. 64, 1829–1835.

Nakano, H., 1994. Age, reproduction and migration of blue shark in the North Pacific Ocean. Bull. Natl. Res. Inst. Far Seas Fish. 31, 141–255.

Nakano, H., Seki, M.P., 2003. Synopsis of biological data on the blue shark, *Prionace glauca*. Bull. Fish. Res. Agency 6, 18–55.

Nakano, H., Makihara, M., Shimazaki, K., 1985. Distribution and biological characteristics of blue shark in the central North Pacific. Bull. Fac. Fish. Hokkaido Univ. 36 (3), 99–113.

Peres, M.B., Vooren, C.M., 1991. Sexual development, reproductive cycle, and fecundity of the school shark *Galeorhinus galeus* off southern Brazil. Fish. Bull. 89, 655–667.

Pons, M., Domingo, A., 2009. Actualización de la estandarización de la CPUE del tiburón azul (*Prionace glauca*) capturado por la flota palangrera pelágico de Uruguay (1992–2007). ICCAT Col. Vol. Sci. Pap. 64 (5), 1614–1622.

Pratt Jr., H.L., 1979. Reproduction in the blue shark. Fish. Bull. 77 (2), 445–470.

Pratt Jr., H.L., 1993. The storage of spermatozoa in the oviducal glands of western North Atlantic sharks. Environ. Biol. Fish. 38, 139–149.

Pratt Jr., H.L., Carrier, J.C., 2005. Elasmobranch courtship and mating behavior. In: Hamlett, W.C. (Ed.), Reproductive Biology and Phylogeny of Chondrichthyes. Sharks, Batoids and Chimaeras. Science Publisher Inc., Plymoth, pp. 129–170.

R Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0 http://www.R-project.org/

Simpfendorfer, C.A., Hueter, R.E., Bergman, U., Connett, S.M.H., 2002. Results of a fishery-independent survey for pelagic sharks in the western North Atlantic 1977–1994. Fish. Res. 55, 175–192.

Smith, S.E., Au, D.W., Show, C., 2008. Shark productivity and reproductive protection and a comparison with teleosts. In: Camhi, M.D., Pikitch, E.K., Babcock, E.A. (Eds.), Sharks of the Open Ocean: Biology, Fisheries and Conservation. Blackwell Publishing, Oxford, pp. 298–308.

Stehmann, M.F.W., 2002. A proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces Chondrichthyes). Arch. Fish. Mar. Res. 50, 23–48.

Stevens, J.D., 1974. The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L.) from British waters. J. Mar. Biol. Ass. 54, 373–378.

Stevens, J.D., 1984. Biological observations on sharks caught by sport fishermen off New South Wales. Aust. J. Mar. Freshwater Res. 35, 573–590.

Stevens, J.D., 2005. Blue shark *Prionace glauca* (Linnaeus, 1758). In: Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A., Musick, J.A. (Eds.), Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes. Status Survey. IUCN/SSC Shark Specialist Group, Gland, Switzerland/Cambridge, pp. 309–311.

Stevens, J.D., McLoughlin, K.J., 1991. Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. Aust. J. Mar. Freshwater Res. 42, 151–199.

Strasburg, D.W., 1958. Distribution, abundance and habitats of pelagic sharks in the central Pacific Ocean. Fish. Bull. U. S. Fish. Wildlife Serv. 58, 335–361.

Walker, T.I., 2005a. Reproduction in fisheries science. In: Hamlett, W.C. (Ed.), Reproductive Biology and Phylogeny of Chondrichthyes. Sharks, Batoids and Chimaeras. Science Publisher Inc., Plymoth, pp. 81–128.

Walker, T.I., 2005b. Management measures. In: Musick, J.A., Bonfil, R. (Eds.), Management Techniques for Elasmobranchs Fisheries. FAO Fish. Tech. Paper No. 474. Rome. , pp. 216–242.

Walker, T.I., 2007. Spatial and temporal variation in the reproductive biology of gummy shark *Mustelus antarcticus* (Chondrichthyes: Triakidae) harvested off southern Australia. Mar. Freshwater Res. 58, 67–97.

Yamaguchi, A., Taniuchi, T., Shimizu, M., 2000. Geographical variations in reproductive parameters of the starspotted dogfish. *Mutelus manazo*, from five localities in Japan and Taiwan. Environ. Biol. Fish. 57, 221–233.

Yokota, L., Lessa, R.P., 2007. Reproductive biology of three ray species: *Gymnura micrura* (Bloch & Schneider, 1801). *Dasyatis guttata* (Bloch & Schneider, 1801) and *Dasyatis marianae* Gomes, Rosa & Gadig, 2000, caught by artisanal fisheries in Northeastern Brazil. Cah. Biol. Mar. 48, 249–257.

Zar, J.H., 1999. Biostatistical Analysis, 4th ed. Prentice-Hall, New Jersey.