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Determination of limited histotrophy as the reproductive mode in *Mustelus schmitti* Springer, 1939 (Chondrichthyes: Triakidae): analysis of intrauterine growth of embryos

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This work analyzed length-mass relationship, growth in length, mass variations and dynamic of yolk sac depletion of *Mustelus schmitti* embryos, extracted from females catched by the artisanal fishery acting off La Paloma (34°39'S, 54°10´W, Uruguay) during 2006 and 2007. Differences in total length and total mass between sexes were not significant. Embryos showed a negative allometric growth for both years with a slope change near the day 170 of the year, likely to be associated with the depletion of the external yolk sac. Gompertz and Von Bertalanffy curves were adjusted for each year. Parturition date was determined around the day 300 of the year. Yolk depletion followed a logistic dynamic $Yt=1/(1+e^{(-13.749 + 0.072*t)})$ for 2006 and $Yt=1/(1+e^{(-10.472 + 0.054*t)})$ for 2007. Embryos showed a mean increase in total dry mass of 5.4g in 187 days which, together with yolk depletion dynamics, indicates additional energetic supply, suggesting that *M. schmitti* presents limited histotrophy.

Este trabajo analizó las relaciones largo-masa, crecimiento en talla, variaciones en masa y dinámica de consumo del saco vitelino de embriones de *Mustelus schmitti* extraídos de hembras capturadas por la flota pesquera artesanal del puerto de La Paloma (34°39'S, 54°10´W, Uruguay) durante 2006 y 2007. Las diferencias en largo total y masa total entre sexos no fueron significativas. Los embriones mostraron crecimiento alométrico negativo en ambos años, con un cambio de pendiente cercano al día 170, probablemente asociado con el agotamiento del saco vitelino externo. Se ajustaron curvas de crecimiento de Gompertz y VonBertalanffy para cada año. La fecha de parición se determinó cerca del día 300 del año. El consumo de vitelo siguió una dinámica logística $Yt=1/(1+e^{(-13.749 + 0.072*t)})$ en 2006 y $Yt=1/(1+e^{(-10.472 + 0.054*t)})$ en 2007. Los embriones mostraron un aumento promedio de masa seca de 5.4g en 187 días, esto, junto con la dinámica de consumo de vitelo, indicó una provisión adicional de energía, sugiriendo que *M. schmitti* presenta histotrofía limitada.

Keywords: Embryo growth, Matrotrophy, Narrownose smoothhound, Reproductive mode, Southwestern Atlantic.

Introduction

Chondrichthyans exhibit all major vertebrate reproductive modes (Dulvy & Reynolds, 1997), which can be broadly categorized in oviparity and viviparity. Viviparous strategies can be further categorized into lecithotrophy and matrotrophy, based on the magnitude and way nutrients are transferred from the mother to the embryos throughout their development (Wourms, 1981; Musick & Ellis, 2005). In strictly lecithotrophic species the mother does not provide additional supply to the embryos apart from the oocyte yolk (Musick & Ellis, 2005). The nourishment of developing embryos by a source other than yolk is known as matrotrophy (Wourms, 1981). This process can occur

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through a variety of strategies such as uterine secretions (histotrophy), placental transfer (placentatrophy), or through the consumption of unfertilized eggs (ovatrophy) or even sibling embryos (adelphotrophy) (Dulvy & Reynolds, 1997). The gain or loss of mass between fertilized eggs and full-term embryos has been used to establish the maternal-embryonic nutritional relationship of chondrichthyan species (Ranzi, 1934; Frazer *et al*., 2012). Postnatal growth of sharks has received considerable attention as a life history parameter, mainly because of its fishing and conservation implications. However, less information is available for the embryonic period (Lucifora *et al*., 2004). The known relevance of embryonic life history traits is increasing, as links between the length of gestation period and the neonate mass have been established on several taxa (Ricklefs, 2010).

The smoothhounds genus *Mustelus* Linck, 1790 (Triakidae) comprises 27 species of small demersal sharks that inhabit temperate and tropical waters of the continental shelves of all oceans (Musick, 2004; Ebert *et al*., 2013). The Narrownose smooth-hound *Mustelus schmitti* Springer, 1939, is a benthopelagic species, endemic of the coastal waters of the south-western Atlantic Ocean (Compagno, 2005; Cousseau & Perrotta, 2004). It has an annual reproductive cycle with an 11-12 months long gestation period, with parturition occurring towards December, at the beginning of the austral summer (Oddone *et al*., 2005; Colautti *et al*., 2010). This species migrates seasonally within its distribution range, being found in Uruguayan and Argentinean waters during the summer and in south Brazilian continental shelf during winter (Vooren, 1997). As a result this species is caught by several artisanal and industrial fisheries in Argentina, Uruguay and Brazil, which affect different parts of the stock during its life cycle (Vooren, 1992; Oddone *et al*., 2007; Pereyra *et al*., 2008). Mark recapture studies have begun to be performed on this species (Perez *et al*., 2014), however no results on migration patterns have been reported by this mean. Genetic evidence is congruent with regional migration, especially when tested in adult females (Pereyra *et al*., 2010).

Mustelus schmitti, classified as endangered (Massa *et al*., 2006), was previously considered in the literature as a yolk-sac viviparous species (Menni *et al*., 1986; Sidders *et al*., 2005). Nevertheless, Menni *et al.* (1986) suggested that the uterine fluid could play a role in the nutrition of the embryos since the yolk sac is reabsorbed in early stages of gestation. Histological studies have confirmed the presence of mucous secretions from the uterine walls, which contribute to embryonic nourishment once yolk reserves are exhausted, suggesting some degree of matrotrophism (Souto, 1986; Vooren, 1992; Hamlett, 2005; Galíndez *et al*., 2010). However, according to Frazer *et al.* (2012) evidence on the mass variation of embryos through the intrauterine growth process is necessary to complement the morphological findings and properly assess and describe any species reproductive mode.

This study aims to characterize the intrauterine growth cycle of *M. schmitti* embryos. The importance of maternal contribution is evaluated through the analysis of the temporal variation in embryo mass, which in time allows a proper determination of the species reproduction mode.

Material and Methods

Biological data was obtained through the artisanal fishing fleet acting off La Paloma (34°39'S, 54°10′W), Uruguay, South western Atlantic, during 2006 and 2007. The boats operated at depths between 18 and 38 m and used 11 cm mesh size stretched mesh bottom gill nets. At each sampling event, individuals were randomly selected after landings. Pregnant females were collected dead from the nets, their reproductive tracts, including uteri content, were removed and frozen for later analysis in the laboratory. After unfrozen, embryos were removed from the individual uterine compartment. They were sexed and measured for total length (TL) to the nearest cm below *sensu* Compagno (1984). The "embryonic system" was defined as the embryo plus its external yolk sac. Total wet mass of the embryonic system (TM) was obtained. Afterwards, the external yolk sac was removed as near the embryo's belly as possible, and embryo wet mass (EM) was registered. Finally the external yolk sac wet mass (YM) was obtained as YM=TM-EM.

Parametric or non-parametric tests were chosen after normality and homogeneity of variance had been tested by Shapiro-Wilk and Levene's tests, respectively (Zar, 2010). The differences in TL and TM distribution between sexes and years, were analysed using two independent Kruskal-Wallis test (Zar, 2010). To describe the relationship between length and weight of the embryos, the data was log-transformed and, continuous and segmented, linear curves were adjusted (Muggeo, 2003). Regressions were made between TM and TL, and in order to evaluate the possible effect of the yolk sac over this relationship, EM and TL regressions were also fitted.

The relationship between TL and time was analysed in order to infer the size and time of parturition. To describe the embryonic growth pattern three different models were fitted by near least square procedure for each year: Linear, Von Bertalanffy and Gompertz (Lucifora *et al*., 2004; Braccini *et al*., 2006; Ricklefs, 2010). The Akaike information criterion was applied to compare these models (Akaike, 1974).

To assess the dynamic of yolk depletion along the year, YM data were categorized into a binary format, where 1 represented the presence of external yolk sac (YM>0) and 0 the absence of it. In order to estimate the probability of occurrence of external yolk sac at a given time, a logistic function was adjusted by maximum likelihood (Hosmer *et al*., 2013) for each year.

The presence of an additional matrotrophic nourishing source and its magnitude were studied through the comparison of the embryonic system mass (TM) along both years. In order to eliminate the noise caused by different amounts of water on each tissue, the embryonic system total dry mass (TDM) was calculated. The Gummy shark (*Mustelu*s *antarcticus* Günther, 1870) conversion rates were applied, the rate for yolk eggs was applied on the external yolk sac (dry mass= 0.521*wet mass), while for embryos the corresponding coefficient was applied (dry mass= 0.160*wet mass) (Frazer *et al*., 2012). This species was chosen because of being very close to *M. schmitti*, both taxonomically and due to its reproductive characteristics. The two species develop uterine compartments, and the embryos are not yolk reliant for the entire gestation period (Menni *et al*., 1986; Storrie *et al*., 2009; Galíndez *et al*., 2010; Sidders *et al*., 2005). Moreover Galíndez *et al*. (2010) have observed the occurrence of mucous secretions of the uterine mucosa as noted previously in *M. antarcticus* (Storrie *et al*., 2009). The mean mass variation of the embryo system along each year was calculated using TDM values. All statistical analysis and graphical representations were performed using the open statistical software R, version 3.0.2 (R Development Core Team, 2012).

Results

A total of 459 embryos of *Mustelus schmitti* were collected, 219 of them during 2006 and 240 during 2007 (Table 1). Total length ranged from 6.5 to 32.7 cm with a mean of 19.7 cm. The TM varied between 0.95 g and 50.86 g with a mean of 19.5 g. There were significant differences between years in TM (KW, Hc=8.312, p<0.01) as well as in TL distribution (KW test, Hc=8.493, p=0.03). In both cases 2007 showed slightly higher values than 2006. Differences between sexes, within each year, were not significant for the TL distribution (2006 KW, $Hc=1.17x10^{-6}$, p=0.99; 2007 KW, Hc=0.8374, p=0.36) or TM distribution (2006 KW, Hc=0.091, p=0.9; 2007 KW, Hc=0.169, p=0.68). Regressions between mass and length of embryos (Table 2) showed a higher slope in all EM regressions compared to TM regressions. In segmented linear regressions, very similar breakpoints were found, for TM and EM, in both years.

Table 1. Overview of the data set used for this study detailing: Date of sampling, number of embryos per sampling event and the proportion of female embryos of *Mustelus schmitti* in the catch (*indicates significant differences from the ratio 1:1 on a chi-square test).

Date	Embryos (n)	% Females
30/05/06	91	52
06/07/06	25	56
04/08/06	62	54
15/09/06	13	54
08/10/06	17	38*
29/11/06	11	45
18/05/07	66	44
26/06/07	54	43
31/07/07	20	45
23/10/07	70	46
26/11/07	30	31*

Table 2. Continuous and segmented linear regressions applied to length and mass data for *Mustelus schmitti* embryos. The "Variables" column show the independent and dependent variables and its transformation, Total mass includes the internal and external yolk sac and the embryo, while Embryo mass includes the embryo without the external yolk sac. When a segmented linear regression was applied a Slope 2 and a breakpoint value with its error are shown.

Variables		Year	Intercept	Slope 1	Slope 2	Break Point	r^2
log(Total Mass)	log(Total Length)	2006	-3.15	2.00	3.43	2.79 +- 0.015	0.97
log(Total Mass)	log(Total Length)	2006	-5.19	2.77	---	---	0.95
log(Embryo Mass)	log(Total Length)	2006	-4.39	2.45	3.45	2.80 +- 0.022	0.98
log(Embryo Mass)	log(Total Length)	2006	-5.77	2.97	---	---	0.97
log(Total Mass)	log(Total Length)	2007	-2.20	1.66	2.96	2.68 +- 0.022	0.97
log(Total Mass)	log(Total Length)	2007	-4.96	2.72	---	---	0.97
log(Embryo Mass)	log(Total Length)	2007	-4.04	2.34	3.00	2.69 +- 0.044	0.98
log(Embryo Mass)	log(Total Length)	2007	-5.42	2.87	---	---	0.98

The embryo TL distribution by day (Fig. 1), confirms a clear annual reproductive cycle as previously reported for *M. schmitti* (Menni *et al*., 1986; Souto, 1986; Oddone *et al*., 2005; Sidders *et al*., 2005). The relationship between embryonic TL and time was best described by the Gompertz growth curve (Table 3). The Gompertz and Von Bertalanffy growth curves presented similar r^2 and AIC scores. However, in the Von Bertalanffy 2006 model the goodness of fit of the t_0 estimation was below the standard (p>0.05). The linear model did not follow the general growth pattern of *M. schmitti* embryos and had a slightly poorer fit, particularly in the AIC score, than the other models. According to the embryo TL distribution for both years, and the known size at birth of *M. schmitti* (26 cm, Oddone *et al*., 2005) it can be inferred that parturition may occurs around the day 300 of the year, corresponding to beginning of November.

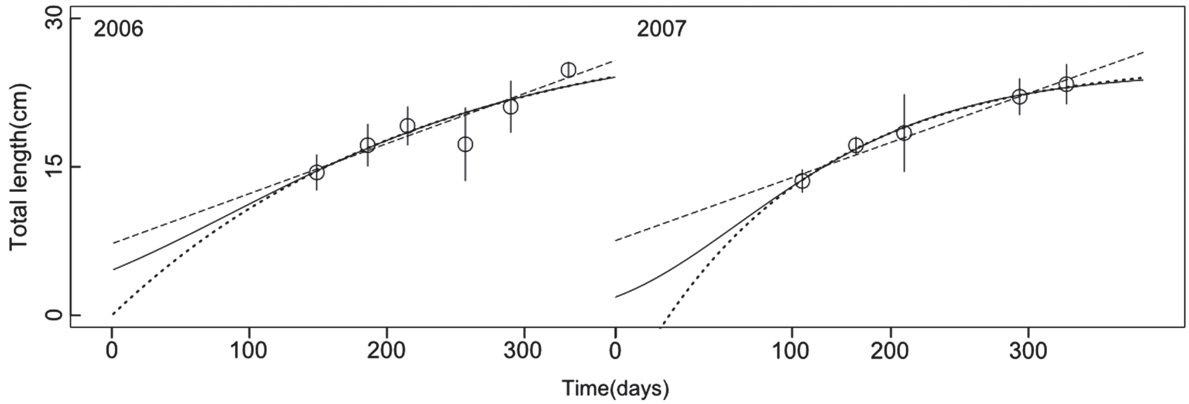

Fig 1. Mean embryo total length and standard deviation as a function of the ordinal day of the year considering the two consecutive years (2006 and 2007) for *Mustelus schmitti* embryos. Dashed line represents the linear model adjusted to the individual data, continuous line is for the Gompertz model and the pointed line represents the Von Bertalanffy growth curve.

Table 3. Growth curves adjusted to total length data (TL) of *Mustelus schmitti* for each year of the study. In "Equation" t is the ordinal day of the year. Within years "Parameters" show the estimations made by least square, the asterisks denote the level of confidence of such estimations: *** p<0.001, ** p<0.01, no asterisks means p>0.05. "r2" is the quasi-r squared score, and "AIC" is Akaike´s information criteria.

Model	Equation	2006			2007		
		Parameters	r2	AIC	Parameters	r2	AIC
Linear	TL= a + b*t	a = 7.243***	0,6	991,0	a = 7.492***	0.78	999,0
		b = 0.051***			b = 0.050***		
Von bertalanffy	TL= Linf(1-e(k* (t-t0)))	Linf = 29.986***	0,6	989.6	Linf = 25.729***	0.80	979.7
		k = 0.004**			k = 0.008***		
		t0 = -0.064			t0 = 40.277**		
Gompertz	TL= Linf(-b(-k*t))	Linf = 27.735***	0,6	990.7	Linf = 24.742***	0.80	980.9
		b = 1.807**			b = 2.628***		
		k = 0.007***			k = 0.011***		

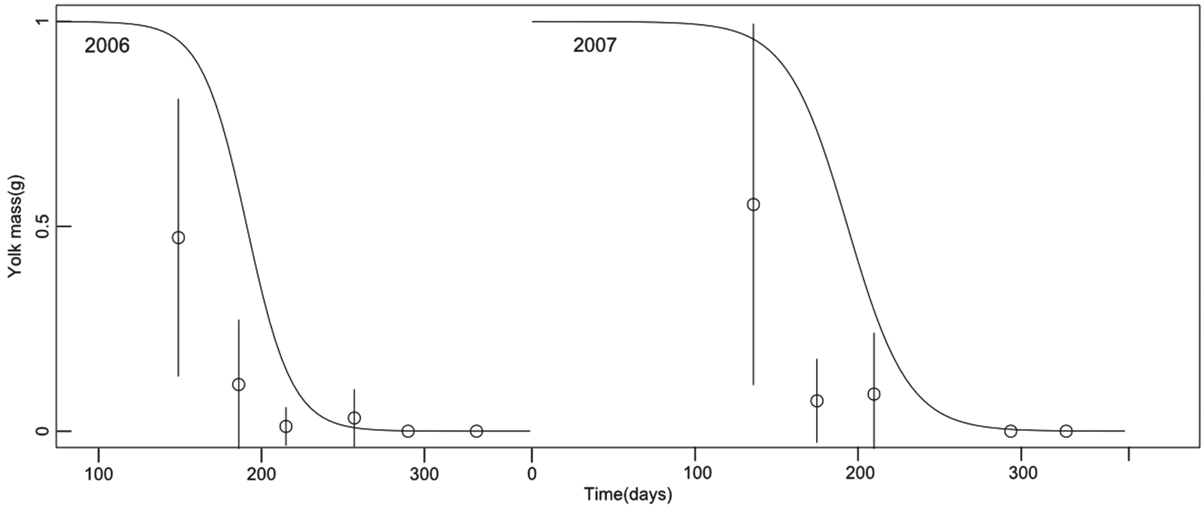

Fig 2. Mean yolk mass and standard deviation as a function of the ordinal day of the year considering the two consecutive years (2006 and 2007) for *Mustelus schmitti* embryos. Using the same y axis values the continuous line represents the logistic curve adjusted for presence/absence of yolk sac, the probability of an embryo having external yolk sac is given by $Yt=1/(1+e^{(-13.749 + 0.072*t)})$ for 2006 and $Yt=1/(1+e^{(-10.472 + 0.054*t)})$ for 2007.

The YM variation along both years showed a clear pattern of consumption by the embryos (Fig. 2). The yolk depletion logistic curve for 2006 was described by: $Y_t=1/(1+e^{(-13.749+0.0720*t)})$ ($p<0.01$, $R^2=0.60$), according to this function, 50% of embryos depleted their yolk sacs by the ordinal day 191 and 75% of the embryos by the 206th day. For the year 2007 the logistic curve was: $Y_t=1/(1+e^{(-10.472+0.054*t)})$ ($p<0.01$, $R^2=0.65$), 50% of embryos depleted their yolk sac by the day 195 and 75% by the day 215.

The variations found in TDM showed a steady increase reaching a mean total gain from May to November of 6.02g in 183 days and 4.71g in 192 days during 2006 and 2007 respectively (Fig. 3). The percent of change was 298% increase in 2006 and 238% in 2007.

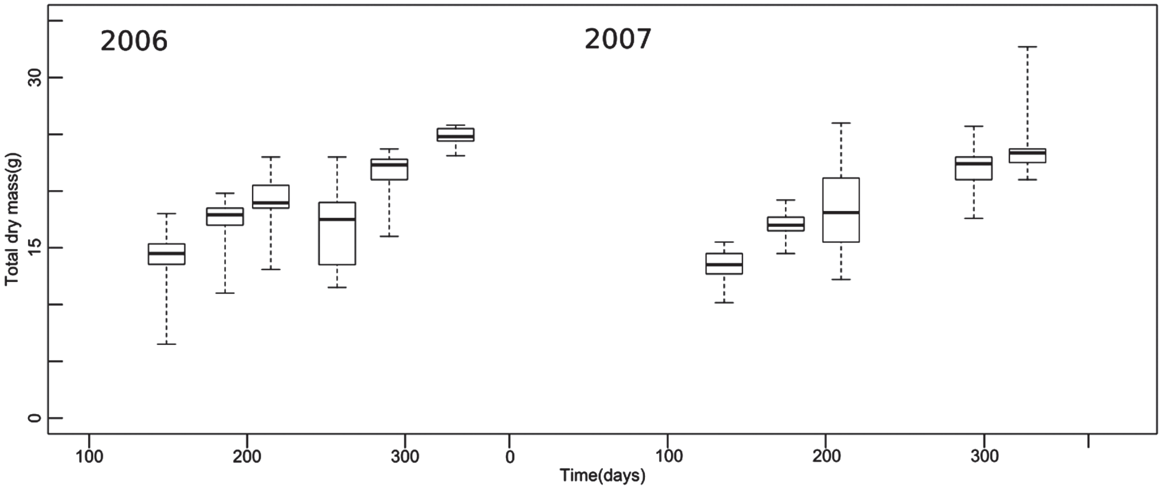

Fig 3. Relationship between total dry weight (g) (*Mustelus schmitti* embryos and its yolk sac) and time (ordinal days), along 2006 and 2007. The bottom and top of the box are the first and third quartiles, and the band inside is the median, the ends of the whiskers represent the range of the distribution. This graphic shows a clear increase in mass that has been associated with matrotrophy.

Discussion

The statistical differences found in TL and TM distribution between 2006 and 2007 could be related to environmental factors of each year that may produce different, but similar, embryonic characteristics. The slope of the TL *vs*. TM continuous linear regression was coincident with previous studies in the area (Segura & Milessi, 2009) showing a negative allometric growth, indicating that embryos grow slim towards the end of gestation. No previous studies on TL *vs*. EM in the area are available. The segmented linear regressions mean break point corresponded to ordinal day 170 on both years. At this time, the yolk depletion curve has started its decrease, so it is logical to think that variations in the continuity of the length-mass relationship are influenced by the external the yolk sac.

Previous studies in this area have suggested that parturition takes place in late spring or early summer (Oddone *et al*., 2005). This result indicates that the parturition period could start at mid spring, and continue until early summer. A better understanding of the parturition date of this heavily exploited species (Pereyra *et al*., 2008), could allow to adapt the fishing season, in order to diminish the presence of pregnant females in the catch.

The yolk depletion curve fitted in this work indicates that nearly 75% of the embryos continue their development for almost 100 days after the external yolk sac is depleted. A similar pattern of yolk depletion for *M. schmitti* was found by Sidders *et al.* (2005) at a southern location (38°S). They observed that during fall (about mid pregnancy) the external yolk sac was absent in embryos that have attained only 57.2% of their final size, corresponding to a TL of 151 mm. This pattern of consumption of the external yolk sac towards mid-gestation has also been found for other non-placental species of the *Mustelus* genus (*e.g. M. antarcticus*, *M. manazo*) (Yamaguchi *et al*., 2000; Storrie *et al*., 2009). The yolk depletion curve could constitute a useful tool to assess the differences, between years, in the condition and development of embryos. Also, fast comparisons with data obtained at any time of the year could be made.

Given the energy assigned to tissues, organs and systemic differentiation during embryonic development (Lucifora *et al*., 2004). Unless additional nutrients, other than the yolk contained in the external sac, are provided by the mother, the mass of an embryonic system is expected to decrease throughout development (Frazer *et al*., 2012). There is a continuum from strict yolk sac viviparity to matrotrophic histotrophy attributed to the variation in the quantity and quality of uterine secretions exhibited by histotrophic species (Hamlett *et al*., 2005; Frazer *et al*., 2012). For this reason, it can be very difficult to discern between the different reproductive modes, mainly at the lower end of matrotrophy. The change in organic mass throughout embryonic development provides information on the existence and quantity of additional maternal nutrient sources (Guallart & Vicent, 2001). Any organic mass gain of embryos during development, and any mass loss lower than approximately 20%, were established as thresholds to classify matrotrophic species (Hamlett *et al.*, 2005). However, Frazer *et al.* (2012) suggested that this value is unsuitable for discerning between lecithotrophic and incipient histotrophy species. Furthermore, because there is a wide inter-species variation in the conversion efficiency from yolk to embryo growth, separating reproductive modes with slight differences based on a single threshold value, is not recommended (Frazer *et al*., 2012). The present study covers the last 188 days of a gestation period of 300-365 days approximately (Menni *et al*., 1986; Chiaramonte & Pettovello, 2000). During this time we reported a mean increase of 5.4 g in TDM (Fig. 3). These results confirm that the mother continues providing energy until the last stages of development. Histological studies conducted for this species observed a high production of uterine fluids (Souto, 1986; Galindez *et al*., 2010). Souto (1986) found high concentrations of glycosaminoglycans in these fluids, which are an important source of nutrition for embryos. In addition, these substances were also found in the digestive tract of at term *M. schmitti* embryos, demonstrating its use as an energy source for embryonic growth (Souto, 1986). Growth rate of shark embryos has been verified to be proportional to the concentration of organic substances in the uterine secretions (Ranzi, 1934), explaining the growth of embryos once the external yolk sac is exhausted.

If we consider the reported wet mass of the freshly laid eggs, for southern Brazilian waters (2g, Vooren, 1992) the mean TDM increase for the full gestation period would be 5.94g, nearly 570% of initial dry mass. Storrie *et al.* (2009) were the first to perform a complete description of minimal histotrophy in a shark species, *M. antarcticus*, finding a gain in dry mass of approximately 800%. Although higher than the one found here, it must be considered that this work does not cover the entire period of gestation. And that the calculation of the percentual mass increase was estimated from egg mass data obtained by another study (Vooren, 1992). It would be advisable to make these estimates with data covering the entire period of gestation from uterine eggs to term embryos, and thus obtain a more accurate value for comparison with other species. Given the morphological similarities between these two species, it is likely that *M. schmitti* exhibit the same reproductive mode that *M. antarcticus*. Furthermore, the positive variation in TDM of *M. schmitti* embryonic system, together with reproductive tract histological studies (Souto, 1986; Galindez *et al*., 2010), indicate minimal histotrophy as the reproductive mode for this species.

Maternal-embryonic nutritional relationship of species has been found to give great insight into the species risk of extinction when exposed to fishing pressure (García *et al*., 2007). Oviparous species are considered to have the highest resilience, followed by lecitotrophic and then histotrophic species, with placental viviparity having the lowest resilience to exploitation. The accurate classification of *M. schmitti* reproduction mode modifies the estimations of its resilience to fishing pressure and may provide advice on the conservation measures to be taken in order to protect this endangered species.

In order to improve this work, it would be important to determinat*e M. schmitti* dry/wet mass conversion ratio. Similarly, it is advisable to properly dry and then incinerate the samples, in order to determine water and inorganic matter content, to establish change in organic content (Guallart & Vicent, 2001; Hamlett *et al*., 2005). A combination of methods, *e.g.* mass changes (Guallart & Vicent, 2001; Huveneers *et al*., 2011), histology and electron microscopy of the uterus (Storrie *et al*., 2009), radio-tracer assay (Riesch *et al*., 2010) and uterine fluid analysis (Kormanik, 1988) throughout gestation, are crucial to discern between reproductive modes. The information blanks, corresponding to the periods when the directed artisanal fishery targeted other species (Ligrone *et al*., 2014), did not mask the reproductive cycle or the importance of maternal energetic contribution. To date there is no complete reproductive analysis based on females for this area, this information is important and complementary to the presented here. Also there is little information on nursery areas on the Uruguayan coast and no recruitment calculations have been made for this species in the area. All of which are valuable knowledge in order to achieve a sustainable use of the resource.

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