

New data on the reproductive biology of the Atlantic weasel shark, *Paragaleus pectoralis* (Chondrichthyes: Hemigaleidae) from the coast of Senegal (eastern tropical Atlantic)

by

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ABSTRACT. - The Atlantic weasel shark, *Paragaleus pectoralis* (Garman, 1906), is the only species of the genus *Paragaleus* to be recorded off the western coast of Africa. It is commonly landed at the fishing sites along the Senegalese coast. Adult males and females are mostly captured in spring and summer. The smallest male and female adults were 810 mm and 900 mm total length (TL), respectively. The largest male and the largest female adults were 1.32 m and 1.38 m TL, respectively, and weighed 7.55 kg and 11 kg, respectively. There was no significant difference for total mass and TL relationship between males and females. Mating occurred from March to May, and parturition in May and June. Gestation lasted approximately one year. Females had biennial or triennial reproductive cycle. Vitellogenesis did not occur while females were pregnant. Diameter of the largest yolky oocytes ranged from 25 to 31 mm (mean: 28.6 ± 2.6) and their mass from 8.8 to 9.9 g (mean: 9.4 ± 0.5). Both uteri were compartmentalized into chambers, with a single embryo in each chamber. Size and mass at birth, based on near-term embryos were between 390-500 mm TL and 214-407 g, respectively. A chemical balance of development based on mean dry masses of the largest yolky oocytes and the fully developed embryos was 14.8. Ovarian fecundity was slightly higher than uterine fecundity. There was a slight positive correlation between uterine fecundity and female TL, not between ovarian fecundity and female TL. Litter sizes ranged from two to seven (mean: 4.6 ± 1.6) with males outnumbering females.

RÉSUMÉ. - Nouvelles données sur la biologie de la reproduction du milandre jaune, *Paragaleus pectoralis* (Chondrichthyes: Hemigaleidae) de la côte du Sénégal (Atlantique oriental tropical).

Le milandre jaune, *Paragaleus pectoralis* (Garman, 1906), est l'unique espèce du genre *Paragaleus* signalée au large de la côte ouest de l'Afrique. Elle est communément débarquée sur les sites de pêche situés au long du littoral sénégalais, et les captures concernent surtout des mâles et femelles adultes rapportés au printemps et en été. Les plus petits adultes mâle et femelle mesuraient respectivement 810 mm et 900 mm de longueur totale (LT). Les plus grands adultes mâle et femelle mesuraient respectivement 1,32 m et 1,38 m LT et pesaient respectivement 7,55 kg et 11 kg. Il n'y a pas de relation significative taille-masse entre mâles et femelles. L'accouplement a lieu de mars à mai, et la parturition en mai et juin. La gestation dure approximativement une année. Les femelles ont un cycle de reproduction bisannuel ou trisannuel. La vitellogenèse ne se déroule pas en même temps que la gestation. Le diamètre des plus grands ovocytes riches en vitellus est compris entre 25 et 31 mm (moyenne : $28,6 \pm 2,6$) et leur masse entre 8,8 et 9,9 g (moyenne : $9,4 \pm 0,5$). Les deux utérus sont compartimentés en chambres et dans chacune d'elles un unique embryon se développe. La taille et la masse à la naissance, fondées sur les embryons à terme, se situent entre 390-500 mm et 214-407 g. Une balance chimique de développement fondée sur les masses sèches moyennes des plus grands ovocytes et des embryons à terme est égale à 14,8. Il y a une faible relation positive entre la fécondité et la LT des femelles. En revanche, il n'y a pas de relation entre la fécondité utérine et la LT des femelles. Les portées varient de deux à sept (moyenne : $4,6 \pm 1,6$). Parmi les deux catégories d'embryons, les mâles sont significativement plus nombreux que les femelles.

Key words. - Chondrichthyes - Hemigaleidae - *Paragaleus pectoralis* - ASE - Senegal - Reproductive Biology.

The genus *Paragaleus* comprises four species (Compagno, 1999), of which only the Atlantic weasel shark, *Paragaleus pectoralis* (Garman, 1906), occurs off the African western coast (Fischer *et al.*, 1981; Compagno, 1984). The species is reported off Madeira and Canary Islands (Branstetter, 1984) but not off Morocco (Lloris and Rucabado, 1998). *P. pectoralis* was recorded by Maurin and Bonnet (1970) and Maigret and Ly (1986) off Mauritania. The species is commonly caught off Senegal (Budker, 1935; Cadenat, 1950;

Cadenat and Blache, 1981; Capapé *et al.*, 1994). It is also reported off Guinea-Bissau (Sanchès, 1991), in the Gulf of Guinea (Blache *et al.*, 1970) and probably off Angola. Southward, off South Africa, it is replaced by its close congeneric species, the whitetip weasel shark *Paragaleus leucomatus* Compagno & Smale, 1985.

Little is known about the reproductive biology of the Atlantic weasel shark. Some information is provided by Budker (1935), Cadenat (1950), Cadenat and Blache (1981)

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and Capapé *et al.* (1994) for specimens from the Senegalese waters, or summarized by Branstetter (1984) and Compagno (1984). New records of specimens enable us to expand the previous data and to improve our current knowledge of the species. Aspects of the reproduction of *P. galeus* are given in this article, with emphasis on size at sexual maturity, reproductive cycle, fecundity, and sex-ratio.

MATERIAL AND METHODS

A total of 126 *Paragaleus pectoralis*, 66 males and 60 females, was examined; the monthly collection is presented in table I. All the specimens were caught by demersal gill-nets off the Senegalese coast between 1994 and 2002, at depths between 20 and 100 m, generally on sandy bottoms, occasionally on muddy or detritic bottoms (Fig. 1). In addition, 43 developing embryos and 54 near-term embryos were examined.

The total length (TL) of specimens was measured to the nearest millimetre following Bass *et al.* (1973) and weighed to the nearest gram. Clasper length (CL, mm) was measured according to Collenot (1969), as was the diameter of yolky oocytes. Oocytes and embryos were removed from the ovaries and then measured and weighed.

The onset of sexual maturity was determined in males from the condition and length of claspers following Bass *et al.* (1973), Stevens and Mc Loughlin (1991) and Watson and Smale (1998). The claspers of juveniles are shorter than pelvic fin length, flexible and not calcified, those of sub-adults are greater than pelvic fin length, flexible but slightly calcified. In adults, claspers are elongated, longer than pelvic fins length, rigid and calcified. Some aspects of the testes and other reproductive organs are given following Capapé *et al.* (1990, 2002) and Bridge *et al.* (1998). Size at sexual maturity was determined in females from the condition of ovaries and the morphology of the reproductive tract (Capapé *et al.*, 1990). In both males and females, specimens were divided in three categories: juveniles, sub-adults and adults.

To investigate the embryonic development and the role of the mother during gestation, a chemical balance of development (CBD) was considered. CBD is based on the mean dry mass of fertilized eggs and fully developed embryos. CBD can be computed as the mean dry mass of fully devel-

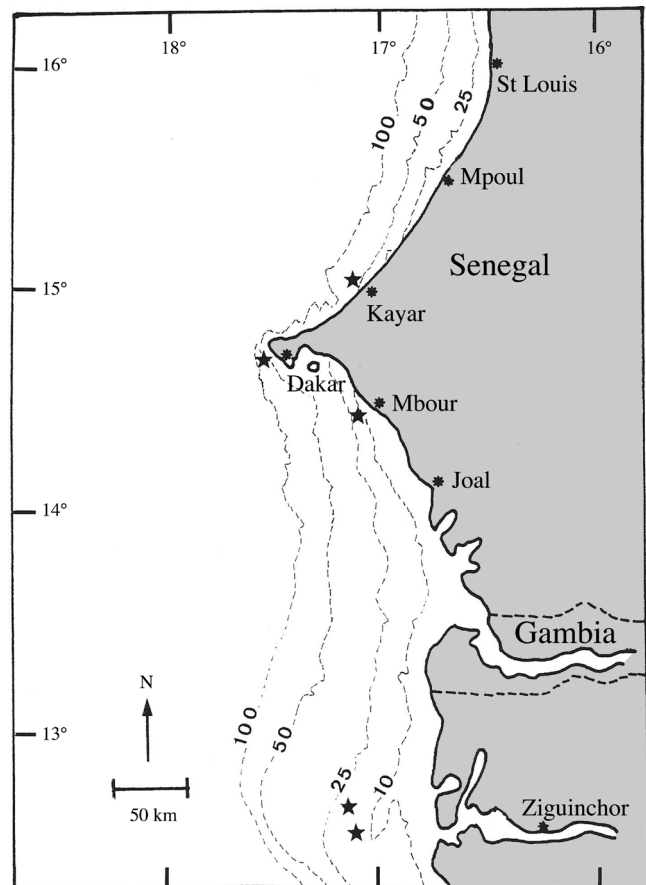


Figure 1. - Map of Senegal showing the landing sites and capture sites (black stars) of *Paragaleus pectoralis* (redrawn from Kébé and Le Reste, 1993). Depth contours in metres. [Carte du Sénégal montrant les sites de débarquement et les sites de capture (étoiles noires) de *Paragaleus pectoralis* (redessiné d'après Kébé et Le Reste, 1993). Contours des lignes de profondeur en mètres.]

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug	Sep.	Oct.	Nov	Dec.	Total
Males													
Juveniles	-	-	-	-	-	-	-	-	6	1	-	-	7
Sub-adults	-	2	4	-	1	-	-	4	1	1	-	-	13
Adults	3	4	9	8	12	-	-	6	3	1	-	-	46
Total	3	6	13	8	13	-	-	10	10	3	-	-	66
Females													
Juveniles	-	-	1	-	-	-	5	-	-	-	-	-	6
Sub-adults	-	-	4	1	-	-	-	5	2	-	-	-	12
Adults	-	4	5	6	10	5	8	0	4	-	-	-	42
Total	-	4	10	7	10	5	13	5	6	-	-	-	60
Grand total	3	10	23	15	23	5	13	15	16	3	-	-	126

Table I. - Monthly collection of *Paragaleus pectoralis* observed in the sample. [Récolte mensuelle de *Paragaleus pectoralis* observée dans l'échantillon.]

oped embryos divided by the mean dry mass of yolky oocytes or eggs. Water content of 50% in ripe oocytes and 75% in fully developed embryos were standard values, based on chemical analyses of the small spotted catshark, *Scyliorhinus canicula*, by Mellinger and Wrisetz (1989). CBD is a tentative estimate.

Tests for significance ($p < 0.05$) were performed by using ANOVA, Student t-test and the chi-square test. The linear regression was expressed in decimal logarithmic coordinates. Correlations were assessed by least-squares regression. In the relationship mass versus total length, comparisons of curves were carried out by ANCOVA.

RESULTS

Size at sexual maturity

Males

During the juvenile stage, the claspers were short and flexible and both testes and genital ducts were membranous and inconspicuously developed. The juvenile stage comprised seven specimens ranging in size between 450 and 520 mm TL and weighing between 280 and 490 g. Among them, six juveniles exhibited an unhealed scar on their ventral surface and were probably neonates, ranging between 450 and 490 mm TL and weighing between 280 and 345 g.

During the sub-adult stage, the claspers were slightly calcified and elongated. The testes were developed, but no spermatocysts were externally visible and no sperm occurred in the seminal vesicles. The genital ducts were developed and the ductus deferens (sensu Hamlett *et al.*, 1999) was slightly convoluted. Thirteen sub-adults specimens were examined. The smallest specimen was 630 mm TL and weighed 1050 g, the largest 890 mm TL and weighed 2100 g.

During the adult stage, the claspers were rigid, elongated and calcified. Both testes and genital ducts were obviously developed. Spermatocysts were externally visible and seminal vesicles contained sperm. The ductus deferens was clearly twisted. Forty-six adults were collected. The smallest specimen was 810 mm TL and weighed 1950 g, and the largest 1320 mm TL and weighed 7550 g. However, the heaviest male was 1300 mm TL and weighed 8650 g.

The relationship between CL (mm) and TL (mm) is: $CL (mm) = 0.14 TL (mm) - 18.03$; $n = 66$; $r = 0.95$ (Fig. 2).

Females

During the juvenile stage, the females ranging between 460 and 570 mm and weighing between 285 and 900 g had membranous ovaries, membrane-like oviducts, and inconspicuous oviducal glands. Of the six juveniles collected, five were neonates (see males above), between 460 and 490 mm TL and the heaviest weighed 490 g.

Twelve sub-adult females were collected, ranging between 650 and 1000 mm TL and weighing between 1100 and 6700 g. They presented ovaries with translucent oocytes, well-differentiated genital ducts and visible and slightly rounded oviducal glands.

Forty-two females were collected; they ranged from 900 to 1380 mm TL and weighed from 5150 to 11000 g, however, the heaviest specimen was 1370 mm TL. Developing oocytes were observed in non-gravid females and mostly were greater than 12 mm diameter. The genital ducts and the oviducal glands were fully developed. The smallest pregnant female was 900 mm TL (Tab. II, record 1). Of the 42 adult females collected, two had yolky oocytes in their ovaries and their uteri were in a resting phase (Tab. II, records 6 and 17), 25 were pregnant with developing or near-term embryos, and 15 had both ovaries and genital tracts in a resting phase, but they were well developed (see above adult stage).

Reproductive cycle

The weasel shark is a placental viviparous elasmobranch. In juvenile females, two ovaries were observed, they were membranous, slender and of similar size and weight. However, some morphological differences develop as the specimens grew and reached maturity. In most specimens, the right ovary continued to increase in length and mass and then became functional. In two specimens, only the left one was functional (Tab. II, records 7 and 11), and in four specimens, both ovaries were functional (Tab. II, records 5, 10, 19 and 20). In each specimen, the non-functional ovary was rudimentary. By contrast, both uteri were generally functional. Nevertheless, in two females (Tab. II, records 3 and 9), only the right uterus was functional and in

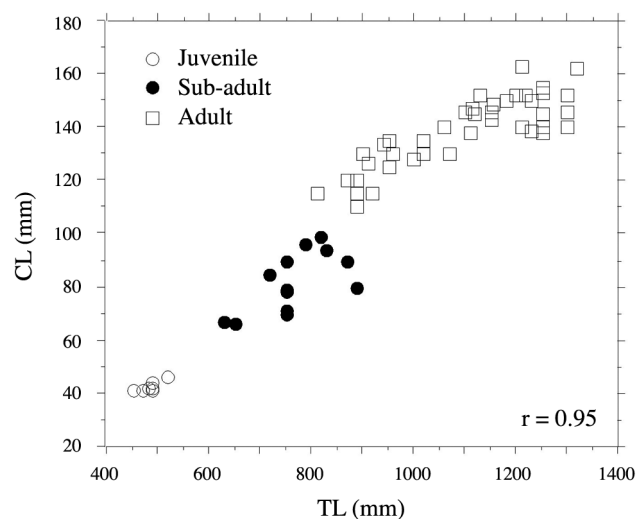


Figure 2. - Clasper length (CL) vs total length (TL) in male *Paragaleus pectoralis*. [Relation entre la longueur des claspers (CL) et la longueur totale (TL) chez les mâles de *Paragaleus pectoralis*.]

Table II. - Reproductive cycle of female *Paragaleus pectoralis*. Condition of ovary and uteri during gestation. [Cycle de reproduction des femelles de *Paragaleus pectoralis*. État de l'ovaire et des utérus pendant la gestation.]

Record number	Month of catch	Size of female (TL, mm)	Mass of female (g)	Ovarian activity	Oocyte diameter (mm)	Oocyte number	Uterine content	Embryo size (TL, mm)	Embryo mass (g)	Embryo number (left+right)
1	Feb.	900	5150	Resting	-	-	Embryos	300-310	78.3-82.5	3+2
2	Feb.	1125	7600	Resting	-	-	Embryos	302-330	80.5-84.6	2+2
3	Feb.	1250	7600	Resting	-	-	Embryos	330-332	83-86.5	0+2
4	Feb.	1330	9400	Resting	-	-	Embryos	325-335	83.5-85.5	3+3
5	Mar.	1110	6300	Vitellogenesis	22-25	4+6	-	-	-	-
6	Mar.	1250	8200	Vitellogenesis	25-28	8	-	-	-	-
7	Mar.	1000	6700	Vitellogenesis	14-15	8	Embryos	350-362	113-137	3+2
8	Apr.	1070	5500	Resting	-	-	Embryos	405-410	156-162	3+2
9	Apr.	1115	6800	Resting	-	-	Embryos	396-420	144-178	0+2
10	Apr.	1200	6400	Vitellogenesis	14-16	4+5	Embryos	385-400	151-172	2+1
11	May	1070	7600	Vitellogenesis	14-15	6	Embryos	410-430	165-185	5+2
12	May	1110	7900	Vitellogenesis	12-14	?	Embryos	430-442	237-280	3+3
13	May	1130	8500	Resting	-	-	Embryos	390-405	167-195	2+2
14	May	1140	6400	Vitellogenesis	13-15	8	Embryos	430-470	251-326	3+3
15	May	1170	6700	Resting	-	-	Embryos	436-490	261-340	3+3
16	May	1210	9000	Resting	-	-	Embryos	420-440	214-241	3+3
17	May	1210	8900	Vitellogenesis	25-31	8	-	-	-	-
18	May	1260	8900	Vitellogenesis	23-25	8	-	-	-	-
19	May	1270	11000	Vitellogenesis	11-12	14	Embryos	465-500	317-407	3+3
20	May	1280	10000	Vitellogenesis	15	10	Embryos	390-460	219.5-261.5	5+2
21	Jun.	1070	5200	Resting	-	-	Embryos	430-450	265-290	2+2
22	Jun.	1160	6800	Resting	-	-	Embryos	425-455	265-295	2+2
23	Jun.	1180	6500	Resting	-	-	Embryos	460	262-290	1+1
24	Jun.	1200	7000	Vitellogenesis	15-18	8	Embryos	420-460	246-285	1+3
25	Jun.	1230	7500	Vitellogenesis	13-14	8	Embryos	470-480	260-316	3+0
26	Jul.	1150	6800	Vitellogenesis	13-15	6	-	-	-	-
27	Jul.	1210	6900	Vitellogenesis	14-15	8	-	-	-	-

a single female, the left one (Tab. II, record 25). However, in these three females, the non-functional uterus was normally developed, but was not distended. Two categories of adult females were observed: non-pregnant and pregnant. The non-pregnant females (see Tab. II, records 5, 6, 17, 18, 26 and 27) had yolky oocytes in the ovaries, which were between 23 and 31 mm in diameter. The largest oocytes were found in a female caught in May (Tab. II, record 17), their diameter was between 25 and 31 mm (28.6 ± 2.6) and their mass ranged between 8.8 and 9.9 g (9.4 ± 0.5). The ovaries of the non-pregnant females were in a resting phase and their uteri were not distended.

Among the pregnant females, those with developing embryos were caught between February and May (Tab. II, records 1 to 4, records 7 to 11 and 13) and those with near-term embryos in May (Tab. II, records 12, 14, 15, 16, 19 and

20) and June (Tab. II, records 21 to 25). All these records show a regular increase of embryos in size and mass, until gestation end. The embryos were completely formed and connected to the placenta by an adorned umbilical cord. The umbilical cord exhibited short and numerous appendiculae (*sensu* Hamlett *et al.*, 1993a). The placenta was rounded, lobulated and implanted in a slight depression of the uterine wall. All placenta were located at the distal end of both uteri which were convoluted and exhibited obvious folds. The uteri were compartmentalized and a single embryo developed in each chamber. All the embryos, we have examined, were sexed, 56 males and 41 females were found.

Size and mass

Fifty-four near-term embryos were removed from 11 pregnant females (Tab. II, records 12, 14, 15, 16, and 19 to

25), ranging between 390 and 500 mm (449.2 ± 24.3) and weighing between 214 and 407 g (278.8 ± 45.9). There was a relationship between total length (TL) and total mass (TM) in near-term embryos, as follows: $TM \text{ embryos} = 1.60 \text{ TL embryos} - 439.68$; $n = 54$; $r = 0.85$ (Fig. 3). The total length of the umbilical cord was between 175 and 290 mm (214.4 ± 41.4) and its mass between 15.5 and 24 g (15.8 ± 1.8). No relationship exists between length and mass of embryos and length and mass of umbilical cord.

Eleven small free-swimming specimens, six males and five females were collected by fishermen. They exhibited an unhealed scar on the ventral surface, and probably were neonates. They ranged from 450 to 490 mm TL (475.9 ± 13.9) and weighed from 280 to 335 g (310.4 ± 27.6).

The relationship between total mass and total length did not show significant differences between males and females (Fig. 4). The relationships are for males: $\log TM = 3.12 \log TL - 5.80$; $r = 0.98$; $n = 66$ and for females: $\log TM = 3.24 \log TL - 6.09$; $r = 0.98$; $n = 60$; with $F = 1.15$ and $p = 0.28$.

Mean fresh masses of eight yolky oocytes and of 54 near-term embryos were 9.4 g and 278.8 g, respectively. CBD based on mean dry masses calculated for *P. pectoralis* was 14.8.

Fecundity

Ovarian fecundity based on the number of both developing and yellow yolked oocytes counted in 14 adult females (Tab. II) ranged from 6 to 14 (8.5 ± 1.9). There was a slight positive correlation between ovarian fecundity and female size. Uterine fecundity, based on the number of both developing and near-term embryos found in 21 pregnant females (Tab. II), ranged between two and seven (4.6 ± 1.6). Uterine fecundity was not related to female size.

Sex-ratio

Males outnumbered females in the two categories of embryos we have distinguished. In the three categories of free-swimming specimens, males slightly outnumbered females, as well as in the total sample. However, numbers of males and females are not significantly different whatever the categories of embryos and free-swimming specimens (χ^2 test; $p > 0.05$) (Tab. III).

DISCUSSION

Paragaleus pectoralis is only recorded off the African western coast and could be considered as an endemic species of the area. In Senegalese waters, the species is mainly caught during spring and summer and captures especially concern adults of both sexes. Most of the adult females observed were pregnant, generally carrying well-developed

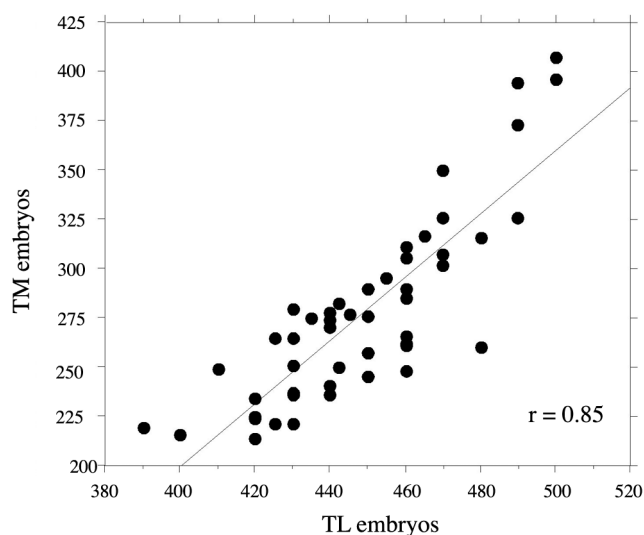


Figure 3. - Total mass (TM) versus total length (TL) in embryos of *Paragaleus pectoralis* (logarithmic coordinates). [Relation entre la masse totale (TM) et la longueur totale (TL) chez les embryons de *Paragaleus pectoralis* (coordonnées logarithmiques).]

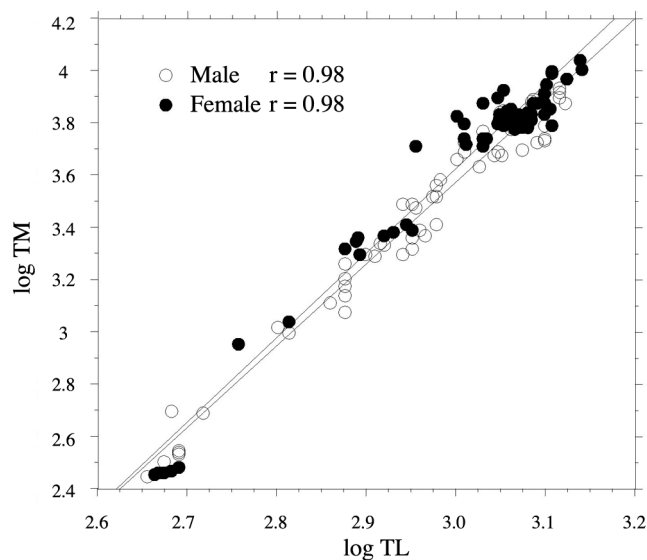


Figure 4. - Total mass (TM) versus total length (TL) expressed in logarithmic coordinates for male and female of *Paragaleus pectoralis*. [Relation entre la masse totale (TM) et la longueur totale (TL) exprimée en coordonnées logarithmiques pour les mâles et les femelles de *Paragaleus pectoralis*.]

or near-term embryos. They approached the coast when the inshore waters become warmer to find nursery areas where they expelled their brood. The Atlantic weasel shark and the sharpnose shark, *Rhizoprionodon acutus*, are concomitantly landed in the fishing sites of the Cape Verde Peninsula, the former a bit less than the latter. The flesh, fresh or dry, as 'sali', is locally appreciated for human consumption and fins are collected and prepared under the vernacular name of 'laâf' (Gueye-Ndiaye, 1993; Gueye-Ndiaye *et al.*, 1996).

This usefulness pro parte explains why large-sized specimens outnumbered small-sized ones in the sample.

In *P. galeus*, males matured at a smaller size than females and reached a smaller maximal size in agreement with Cadenat and Blache (1981). In our sample, females were generally heavier than males; moreover specimens of both sexes normally grew in mass. As other elasmobranch species they found sufficient resources in Senegalese waters to develop and reproduce (Diatta *et al.*, 2001, 2002).

The near-term embryos and the neonates reported in the present study suggest that size at birth ranged between 390 and 500 mm TL and between 214 and 407 g in mass.

Off the Senegalese coast, *P. pectoralis* mating probably occurred from March to May, when both male and female adults are the most encountered and equally distributed. Parturition occurred in May and June, in agreement with Budker (1935) and Cadenat and Blache (1981). The largest yolky

oocytes were carried by two females caught in May. Their size and mass suggested that they were probably close to being ovulated and that the gestation period lasted one year minimum. This opinion agrees with the regular growth of developing embryos from February to May-June. Cadenat (1950) found fertilized eggs in females caught in July and August, but he did not provide more information on them such as morphology, size, and mass.

Furthermore, in our sample, the occurrence of developing or yolky oocytes in the ovaries of non-pregnant females and the lack of important vitellogenic activity in gravid females, especially the near-term ones support a priori a biennial reproductive cycle. However, among the latter, two categories of specimens must be considered. A first category comprised near-term females with ovaries in a complete resting phase; a second category included near-term females with ovaries at the beginning of vitellogenesis. The ovary contained batches of translucent oocytes less than 0.5 mm in diameter and other batches of developing oocytes not exceeding 18 mm in diameter and weighing 1 g maximum. In the first category of females, whether or not vitellogenic activity started again soon after parturition remains questionable and no complete break phase, nor sign of vitellogenic activity, nor embryonic development, was observed in 15 females. This could extend the reproductive cycle to more or less three years in some individ-

Table III. - Sex-ratio in *Paragaleus pectoralis* for each category of specimens and for the total sample. [Sex-ratio chez *Paragaleus pectoralis* pour chaque catégorie de spécimens et pour l'ensemble de l'échantillon.]

Category		Males	Females	Males: Females
Uterine content	Developing embryos	24	19	1.26: 1
	Near-term embryos	32	22	1.45: 1
Total uterine content		56	41	1.36: 1
Free-swimming specimens	Juveniles	7	6	1.16: 1
	Sub-adults	13	12	1.08: 1
	Adults	46	42	1.09: 1
Total free-swimming specimens		66	60	1.10: 1
Grand total		122	101	1.21: 1

Table IV. - Comparison of chemical balance of development (CBD) calculated in *Paragaleus pectoralis* and other viviparous elasmobranch species. [Comparaison de la balance chimique de développement (CBD) calculée chez *Paragaleus pectoralis* et d'autres espèces d'élasmobranches vivipares.]

Species	CBD	Category	Area	Authors
<i>Hexanchus griseus</i>	3.70	Semi-lecithotrophe	Mediterranean coasts	Capapé <i>et al.</i> (2004a)
<i>Carcharhinus brevipinna</i>	65.80	Matrotrophe	Coast of Tunisia	Capapé <i>et al.</i> (2003)
<i>C. limbatus</i>	69.00	Matrotrophe	Coast of Senegal	Capapé <i>et al.</i> (2004b)
<i>Oxynotus centrina</i>	1.36	Lecithotrophe	Mediterranean	Capapé <i>et al.</i> (1999)
<i>Etmopterus spinax</i>	0.83	Lecithotrophe	Coast of Tunisia	Capapé <i>et al.</i> (2001a)
<i>Rhinobatos cemiculus</i>	1.00	Lecithotrophe	Gulf of Gabès	Capapé & Zaouali (1994)
<i>Squatina aculeata</i>	0.66	Lecithotrophe	Coast of Senegal	Capapé <i>et al.</i> (2005)
<i>S. oculata</i>	0.50	Lecithotrophe	Gulf of Tunis	Capapé <i>et al.</i> (1990)
<i>S. oculata</i>	0.73	Lecithotrophe	Coast of Senegal	Capapé <i>et al.</i> (2002)
<i>Torpedo mackayana</i>	1.20	Lecithotrophe	Coast of Senegal	Capapé <i>et al.</i> (2001b)
<i>Dasyatis centroura</i>	15.00	Matrotrophe	Coast of Tunisia	Capapé (1993)
<i>D. chrysonota</i>	25.60	Matrotrophe	Gulf of Gabès	Capapé & Zaouali (1995)
<i>D. violacea</i>	47.00	Matrotrophe	Mediterranean coasts	Hemida <i>et al.</i> (2003)
<i>Gymnura altavela</i>	30.60	Matrotrophe	Coast of Tunisia	Capapé <i>et al.</i> (1992)
<i>Pteromylaeus bovinus</i>	31.10	Matrotrophe	Coast of Senegal	Seck <i>et al.</i> (2002)
<i>Paragaleus pectoralis</i>	14.80	Matrotrophe	Coast of Senegal	This study

uals. Similar patterns were described in the spotted gully shark, *Triakis megalopterus*, from South Africa (Smale and Goosen, 1999). So, a reproductive cycle greater than two years could be a suitable hypothesis. In the second category of females, a reproductive cycle in alternate years remains the most probable hypothesis. This pattern could pro parte explain why, in the area, landings of *P. pectoralis* are frequent but not abundant (Budker, 1935; Cadenat and Blache, 1981; Fischer *et al.*, 1981; Capapé *et al.*, 1994 and furthermore, Séret and Opic, 1990 did not mention its occurrence in the area), a bit less than those of other shark species, such as *Mustelus mustelus*, *Rhizoprionodon acutus* and *Sphyrna lewini*, which reproduce annually (Capapé *et al.*, 1994, 1998) or *Carcharhinus limbatus*, which reproduces annually or biennially (Capapé *et al.*, 2004b).

Compagno and Smale (1985) observed in pregnant female *P. leucolomatus* caught in May off Nosy Bay (South Africa): a right ovary "with poorly differentiated ova", one embryo in each uterus with placenta attached to the uterine wall in "posteriormost fourth of uterus". The developing embryos were 215 mm and 219 mm respectively, and weighed 28 g and 26 g. A biennial reproductive cycle in *P. leucolomatus* such as in *P. pectoralis* remains a suitable hypothesis that needs further confirmation.

Generally viviparous shark species displaying pregnancies develop compartments or chambers that enclose a single embryo. Capapé *et al.* (2003, 2004b) listed several species belonging to different families such as carcharhinids, triakids, sphyrnids and in the present case a hemigaleid species, *P. pectoralis*. Unfortunately, the weather conditions during landings did not enable us to preserve placental analogues (*sensu* Hamlett, 1987, 1989; Hamlett *et al.*, 1985a-e) in order to carry out a thorough histological study. However, a preliminary observation under a binocular microscope suggested that the placental disk is less complex than that of *R. terraenovae* (Hamlett *et al.*, 1993a, 1993b) in agreement with Cadenat and Blache (1981). This feature could partially explain why the CBD of c. 14.8 calculated for *P. pectoralis* is lower than those previously reported for other placental viviparous species such as carcharhinids. Furthermore, the *P. pectoralis* CBD is also lower than those estimated in aplacental viviparous species such as gymnurids, dasyatids or myliobatids. This phenomenon could be partially explained by the role of trophonemata in embryonic development in the latter species (Hamlett *et al.*, 1985a-e). However, *P. pectoralis* is strictly a matrotrophic species (*sensu* Wourms, 1977, 1981; Wourms *et al.*, 1988). By contrast, in lecithotrophic species, CBD had very low values, due to the fact that in these species, the mother only protected the embryonic development and provided inorganic nutrients to the embryos (Mellinger, 1989; Hamlett and Hysell, 1998; Hamlett *et al.*, 1998). Furthermore, in some shark species, such as the bluntnose sixgill shark, *Hexanchus griseus* (Capapé *et*

al., 2004a), the eggs were heavy but the mother's role during gestation could not be totally neglected: they are defined as semi-lecithotrophic species (see Tab. IV).

As in other viviparous elasmobranch species previously studied, ovarian fecundity is higher than uterine fecundity, mainly due to fact that some yolked oocytes did not ovulate and entered atresia. Abortions, especially during handling, cannot be excluded. Ovarian fecundity was slightly related to size; this was not observed for uterine fecundity and could explain why litter sizes were the object of intraspecific variations as this is also the case for size at birth. Similar patterns were observed in other placental viviparous sharks (Capapé *et al.*, 2005).

The sex ratio of both developing and near-term embryos shows that males outnumbered females. By contrast, in several placental viviparous species from different areas sexes are rather in equal numbers (Stevens and Mc Loughlin, 1991). For instance, it is 1: 1 in *Iago omanensis* from the northern Red Sea (Waller and Baranes, 1994), *C. limbatus* from the Gulf of Mexico (Castillo *et al.*, 1998) and for *C. brevipinna* from Tunisian waters (Capapé *et al.*, 2003), and also in an aplacental viviparous species, *T. megalopterus* (Smale and Goosen, 1999). In the post partum population, males slightly outnumbered females and adults of both sexes were distributed in about equal numbers. Springer (1960) suggested a high rate of mortality in males. According to a literature review, Stevens and Mc Loughlin (1991) considered that it was the consequence of sexual segregation in adults (Muñoz-Chapuli, 1984). Pregnant females entered inshore waters to expel their embryos in the best environmental conditions. A similar phenomenon was previously described for *S. lewini* and *C. limbatus* and causes to suggest us that Senegalese waters could be a shark nursery area (*sensu* Castro, 1993).

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