Reproduction of the sawback angelshark *Squatina aculeata* (Chondrichthyes: Squatinidae) off Senegal and Tunisia

by

Christian CAPAPÉ (1), Youssouph DIATTA (2), Amadou Abdoulaye SECK (3), Olivier GUÉLORGET (1), Jamila BEN SOUISSI (4) & Jeanne ZAOUALI (4)

ABSTRACT. - Reproduction of the sawback angelshark *Squatina aculeata* is presented with specimens captured off Tunisia (central Mediterranean) and off Senegal (eastern tropical Atlantic). The smallest adult male and adult female were 120 and 137 cm total length (TL), respectively, and weighed 12.7 and 22.0 kg, respectively. Above 122 cm TL for males and 143 cm TL for females, all the observed specimens were adult. The largest male and the largest female were 152 and 175 cm TL and weighed 24.0 kg and 32.0 kg, respectively. Males and females presented similar total length versus total mass relationships, although the latter were considerably heavier than the former. Size at birth was between 30.3 and 35.0 cm TL and mass at birth between 276 and 325 g. The two ovaries and the two uteri were functional. Ripe ovarian follicles ready to be ovulated ranged between 76 and 85 mm in diameter and weighed between 200 and 237.6 g. Gestation lasted one year approximately, but ovarian follicles growth blocked at the beginning of gestation. However, ovarian follicles growth started again before embryos were at mid-term gestation. This is a new case of semi-delayed vitellogenesis typical of *Squatina* spp. A biannual reproductive cycle remains a suitable hypothesis. A calculated chemical balance of development based on dry masses of ripe follicles and full-term embryos was # 0.66 and showed that *S. aculeata* is a purely lecithotrophic species as other studied squatinid species. Ovarian fecundity ranged from 12 to 22 and is higher than uterine fecundity, which ranged from 8 to 12. Both categories of fecundity were slightly related with females size. The sex-ratio was 1: 1 in embryos. The subadult males significantly outnumbered the female ones. This was not the case for juveniles, adults and for the total sample.

RÉSUMÉ. - Reproduction de l'ange de mer épineux *Squatina aculeata* (Chondrichthyes: Squatinidae) au large du Sénégal et de la Tunisie.

La reproduction de l'ange de mer épineux *Squatina aculeata* est décrite à partir de spécimens capturés au large du Sénégal (Atlantique oriental tropical) et de la Tunisie (Méditerranée centrale). Le plus petit mâle adulte et la plus petite femelle adulte mesuraient 120 et 137 cm de longueur totale (LT) et pesaient 12,7 et 22,0 kg, respectivement, tous les individus observés étaient adultes, au-dessus de 122 cm LT pour les mâles et de 143 cm LT pour les femelles. Dans notre échantillon, le plus grand mâle et la plus grande femelle avaient une LT de 152 et 175 cm et pesaient respectivement 24 kg et 32 kg. Les relations taille-masse sont semblables chez les mâles et les femelles, bien que ces dernières soient plus lourdes. La taille à la naissance se situait entre 30,3 et 35,0 cm LT et la masse entre 276 et 345 g. Les deux ovaires et les deux utérus sont fonctionnels. Les follicules ovariens mûrs, prêts à être pondus, avaient un diamètre compris entre 76 et 85 mm et une masse comprise entre 200 et 237,6 g (79,7 ± 1,9). La gestation durerait approximativement une année, mais il apparaît un blocage de la vitellogenèse au début de la gestation, et une incapacité à ovuler aussitôt après la gestation. Toutefois la croissance des follicules augmente à nouveau avant que les embryons ne soient à mi-développement. C'est un nouveau cas de vitellogenèse “semi-bloquée”. Un cycle de reproduction bisannuel resterait une hypothèse plausible. Une balance chimique de développement fondée sur les masses sèches des ovocytes mûrs et des embryons à terme était # 0,66 et montrait que *S. aculeata* est une vraie espèce “lécithotrophique”, comme le sont les autres squatinidés. La fécondité ovarienne variait de 12 à 22 et elle était plus élevée que la fécondité utérine qui variait de 8 à 12. Les deux catégories de fécondité sont légèrement corrélées avec la taille des femelles. La sex-ratio des embryons était de 1:1 pour les embryons. Les mâles subadultes étaient significativement plus nombreux que les femelles, ce qui n'était pas le cas pour les juvéniles et pour les adultes.

Key words. - Chondrichthyes - Squatinidae - *Squatina aculeata* - ATE - MED - Senegal - Tunisia - Reproduction.

Three species of the genus *Squatina* Risso, 1810 are reported from the FNAM area (Roux, 1977, 1984) and the eastern tropical Atlantic (Springer, 1990): the sawback angelshark *Squatina aculeata* Cuvier, 1829, the smoothback angelshark *S. oculata* (Bonaparte, 1840) and the common angelshark *S. squatina* (Linnaeus, 1758). The former seems to be the less abundantly reported whatever the area (Compagno, 1984).

(1) Laboratoire d'Ichtyologie, Université Montpellier II, Sciences et Techniques du Languedoc, 34095 Montpellier CEDEX 5, FRANCE. [capape@univ-montp2.fr]

(2) Département de Biologie animale, Faculté des Sciences et Techniques, Université Cheikh Anta Diop de Dakar, BP 5005 Dakar, SÉNÉGAL.

(3) Musée de la Mer, Institut fondamental d'Afrique noire Cheikh Anta Diop, Gorée, SÉNÉGAL.

(4) Département des Ressources animales, halieutiques et des Technologies alimentaires, Institut national agronomique de Tunisie, 43 avenue Charles-Nicolle, Cité Mahrajène, 1082 Tunis, TUNISIE.

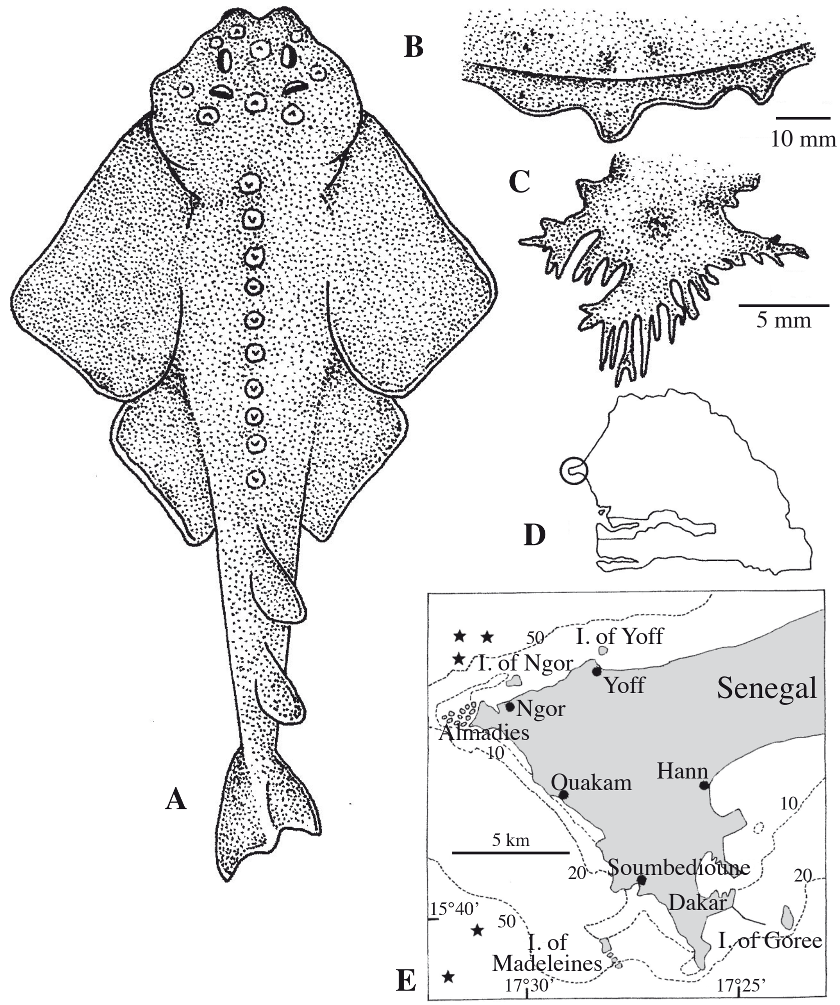

Figure 1. - *Squatina aculeata* Cuvier, 1829. **A**: General morphology. Dorsal surface; **B**: Frontal cephalic lobe; **C**: External nasal flap; **D**: Map of Senegal pointing out the Cape Verde Peninsula (circle); **E**: Western part of the Cape Verde Peninsula (redrawn from Sourie, 1954) showing the landing sites and captures sites (black stars) of *S. aculeata*. A, B, C, redrawn and adapted from Capapé and Roux (1980). *[Squatina aculeata Cuvier, 1829. **A** : Morphologie générale. Face dorsale ; **B** : Lobe céphalique frontal ; **C** : Valvule nasale externe ; **D** : Carte du Sénégal mettant en évidence la presqu'île du cap Vert (cercle). **E** : Partie occidentale de la presqu'île du cap Vert (redessinée d'après Sourie, 1954) montrant les sites de débarquements et les lieux de capture de* S. aculeata. *A, B, C redessinés et adaptés à partir de Capapé et Roux (1980).]*

In the Mediterranean Sea, *S. aculeata* is recorded in restricted areas and its capture remains rather rare. In western Mediterranean, Moreno (1995) and Barrull and Mate (2002) considered its occurrence doubtful off the Spanish coast. Capapé *et al*. (2000) did not reported it off France. Tortonese (1956) and Bini (1967) cited the species in Italian waters, but records are based on specimens deposited in ichthyological collections. De Maddalena (pers. com., 2004) considers its occurrence doubtful in these areas. Soljan (1975) reported it in the Adriatic Sea, but Lipej, Jardas and Soldo (pers. com., 2004) have never recorded the species in this sea and added that this also the case for the two other Mediterranean squatinids.

Along the Maghrebin shore, *S. aculeata* was formerly reported off Algeria (Dieuzeide *et al*., 1953). However, Hemida (pers. com., 2004) has never recorded the species although thorough investigations targeting sharks have been conducted in the area since 1996 (Hemida, 1998; Hemida and Capapé, 2003; Hemida *et al*., 2002), whilst it was also reported off Tunisia, especially in the Gulf of Tunis (Quignard and Capapé, 1971a; Capapé, 1989) until to date.

In the eastern Mediterranean, *S. aculeata* is reported off Greece (Economidis, 1973) and off Turkey (Kabasakal, 2002), where it is very rare (Kabasakal, pers. com., 2004) and it is not recorded in the Sea of Marmara (Kabasakal, 2003). Golani (1996) reported *S. aculeata* off the coast of Israel but at present the sawback angelshark is no more recorded in the area (Golani, pers. com., 2004).

S. aculeata was never recorded north of the Strait of Gibraltar, but was reported southward off Morocco (Collignon and Aloncle, 1972), Mauritania (Maurin and Bonnet, 1970; Maigret and Ly, 1986), Senegal (Cadenat, 1950; Séret and Opic, 1990; Capapé *et al*., 1994), Guinea-Bissau (Sanchès, 1991) and the Gulf of Guinea (Blache *et al*., 1970). Its occurrence seems probable off Angola until Namibia (Poll, 1951; Fischer *et al*., 1981; Compagno, 1984).

Aspects of the reproductive biology of both *S. oculata* and *S. squatina* from the Tunisian waters were studied by Capapé *et al*. (1990), and of *S. oculata* from the coast of Senegal by Capapé *et al*. (1999, 2002). By contrast, little information is dealt by ichthyological literature on *S. aculeata*. Compagno (1984) noted: "Maximum total length about 188 cm, becoming adult at 124 cm". Moreno (1995) and Barrull and Mate (2002) added that birth occured at a total length between 25 and 30 cm. Moreover, scarce information is provided by Capapé (1974) for specimens from off Tunisian and by Capapé *et al*. (1994) for those from the coast of Senegal. Further observations carried out in these two areas allow to collect further data in order to expand and improve our current knowledge about the reproductive biology of the sawback angelshark.

MATERIAL AND METHODS

A collection of 116 *S. aculeata* was examined, including 63 males and 53 females. Eighty-nine, 48 males and 41 females, were captured by commercial gill-net, at a depth less than 80 m, off Senegal, mainly off the Cape Verde Peninsula, and landed at the fishing site of Ouakam, 5 km north of Dakar (Fig. 1). Twenty-seven specimens, 15 males and 12 females were caught at 50-100 m depth, between 1970 and 2002, in the Tunisian waters by trawling, especially in the Gulf of Tunis (24) and occasionnaly (3) southward, in the Gulf of Gabès (Fig. 2).

Morphological and reproductive data were similar for the specimens of both areas, so we have decided to include them in a single sample. The monthly collection of the observed specimens is summarized in table I.

In addition, 34 developing embryos and 33 near term embryos were examined.

The specimens were measured to the nearest millimetre for total length (TL) following Bass *et al*. (1973) and weighed to the nearest gramme, when possible. Measurements comprised clasper length (CL, mm) according to Collenot (1969), and the diameter of yellow yolked or ripe follicles and developing follicles. All the developing and fully yolked follicles and the embryos were removed from the ovaries and the uteri and then measured and weighed to the nearest decigramme.

The onset of sexual maturity was determined in males from the condition and the length of claspers (CL). Bass *et al*. (1973) and Stevens and Mc Loughlin (1991) noted that claspers of juveniles are short and flexible and males are adult when claspers are rigid, elongated and calcified. Some aspects of the testes and the genital organs are provided. The size of females at sexual maturity was determined from the condition of ovaries and the morphology of the reproductive tract following Natanson and Cailliet (1986), Capapé *et al*. (1990, 2002) and Bridge *et al*. (1998). Three categories of specimens were distinguished for both males and females: juveniles, subadults 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 developed embryos divided by the mean dry mass of yellow yolked follicles 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 Wrisez (1989). CBD is a tentative estimate.

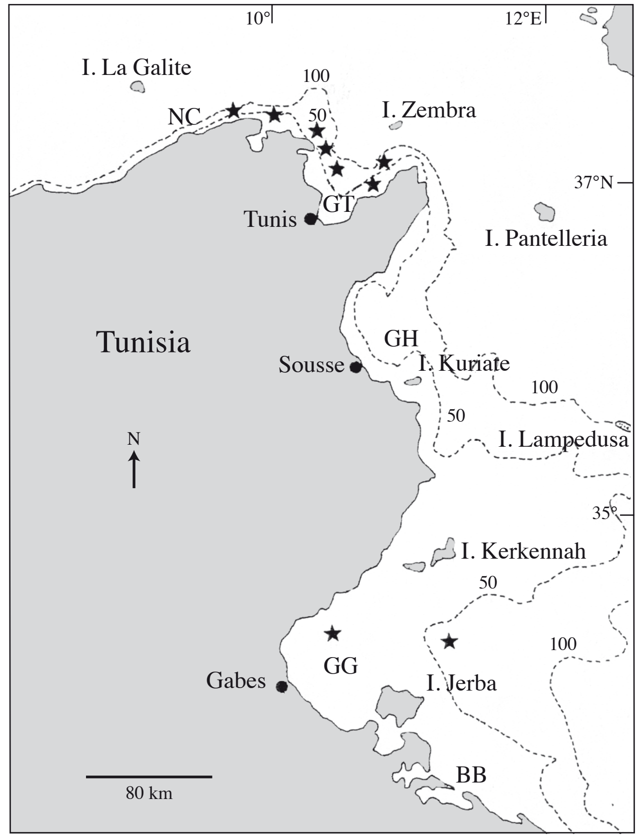

Figure 2. - Map of Tunisia showing the captures sites (black stars) of *Squatina aculeata* in the area. BB: Bahiret El Biban; GG: Gulf of Gabès; GH: Gulf of Hammamet; GT: Gulf of Tunis; NC: Northern Coast. *[Carte de Tunisie montrant les lieux de captures (étoiles noires) de* Squatina aculeata *dans la région. BB : Bahiret El Biban. GG : Golfe de Gabès. GH : Golfe de Hammamet ; GT : Golfe de Tunis ; NC : Côte septentrionale.]*

Table I. - Monthly collection of *Squatina aculeata* observed in the sample. *[Récolte mensuelle des* Squatina aculeata *observés dans l'échantillon.]*

Sex	Category	Months												
		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Males	Juvenile	-	-	1	-	2	2	4	3	1	2	2	1	18
	Subadult	3	6	2	2	7	2	1	2	1	-	1	-	27
	Adult	2	1	3	2	1	5	-	-	-	2	1	1	18
	Total	5	7	6	4	10	9	5	5	2	4	4	2	63
Females	Juvenile	2	1	3	1	-	3	3	3	-	-	-	-	16
	Subadult	3	1	-	2	2	2	-	-	3	1	1	2	17
	Adult	2	2	3	3	3	-	2	2	-	1	1	1	20
	Total	7	4	6	6	5	5	5	5	3	2	2	3	53
Grand total		12	11	12	10	15	14	10	10	5	6	6	5	116

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

Three stages of male development were considered: juvenile, subadult and adult (Fig. 3). During the juvenile stage, the males had short and flexible claspers and both testes and genital duct were membranous and inconspicuously developed. Juvenile stage included 18 males between 32 and 122 cm TL. Among the juveniles, four small free-swimming specimens exhibited an unhealed scar on their ventral surface and were probably neonates, ranging between 32 and 34 cm TL.

During the subadult stage, the claspers presented a slight calcification and elongation. The testes were developed, but without externally visible spermatocysts and no sperm in the seminal vesicles. The genital duct was developed and the *ductus deferens* (*sensu* Hamlett *et al*., 1999) slightly convoluted. Twenty seven subadults were observed. The smallest specimen was 91 cm TL and weighed 6.8 kg, the largest specimen was 121 cm TL and weighed 14 kg.

During the adult stage, the claspers were rigid, elongated and calcified. Both testes and genital duct were well-developed. Spermatocysts were externally visible and sperm occurred in seminal vesicles. The *ductus deferens* was clearly twisted. Eighteen adults were collected. The smallest adult was 120 cm TL and weighed 12.7 kg, but above 122 cm TL, all the observed males were adult. The largest males reached 151 and 152 cm TL, and both weighed 24 kg.

Females

Similar to males, three categories of females were considered: juvenile, subadult and adult.

During the juvenile stage, the females, ranging between 30.5 and 102 cm TL, had whitish ovaries, follicles of only microscopic size, membrane-like oviducts and inconspicuous nidamentary glands. Of the 16 juveniles collected, four were neonates (see males, above); they ranged between 30.5 and 34 cm TL and weighed between 275 and 298 g.

Seventeen subadult females were collected, ranging between 102 and 140 cm TL and weighing between 14 and 22 kg. They had primarily white, translucent follicles, a well-differentiated genital duct and nidamentary glands visible and slightly rounded.

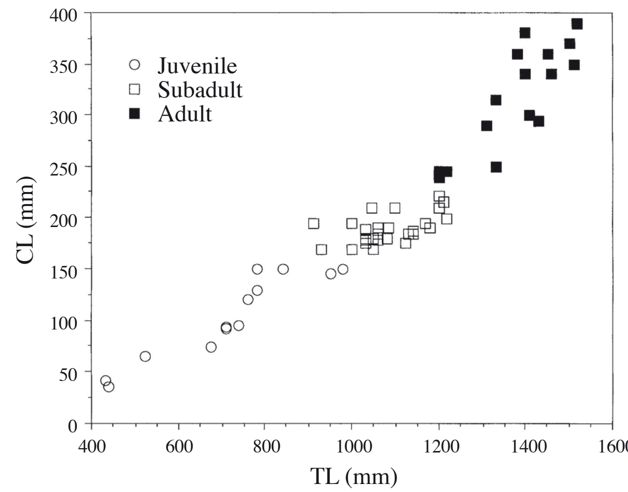

Figure 3. - Clasper Length (CL) *vs* Total Length (TL) in male *Squatina aculeata*. *[Longueur des ptérygopodes (CL) en fonction de la longueur totale (LT) chez les mâles de* Squatina aculeata.*]*

The 20 adults TL ranged from 137 to 175 cm TL. The functional ovary exhibited batches of developing and fully yolked follicles. Developing follicles observed in non-gravid females were mostly over 25 mm in diameter. The genital tract was fully developed and in some specimens both uteri contained eggs or embryos at different stages of development.

The smallest adult female with ovaries containing fully yolked follicles ready to be ovulated, was 137 cm TL and weighed 22 kg (Tab. II, record 10), and above 143 cm TL, all the females were adult. The smallest gravid female was 152 cm TL, weighed 27 kg and carried full term embryos (Tab. II, record 13). The largest female was 175 cm TL and also the heaviest female, its mass reached 32 kg (Tab. II, record 18). Of the 20 adult females examined, eight were pregnant.

Reproductive cycle

As all squatinids previously studied, the sawback angelshark is an aplacental viviparous elasmobranch species, with two ovaries and two uteri, both functional. The ovaries produced follicles batches similar in diameter and in mass. However, a single batch only developed into fully yolked follicles or ripe follicles which are ovulated. Forty ripe ovarian follicles removed from three females (Tab. II, records 7, 8 and 9), ranged between 76 and 85 mm (79.7 ± 1.9) in diameter and weighed between 200 and 237.6 g (221.3 ± 10.4). Most of observed females exhibited maturing or ripe follicles equally distributed in each ovary. However, in some females, they were slightly more abundant in the left ovary than in the right one but in a single female, it was the reverse (Tab. II, record 18).

Table II shows that follicles reached maturity in March-

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

Record	Month of catch	Female size (TL, cm)	Female mass (kg)	Ovarian activity	Follicle number	Follicle diameter (mm)	Follicle mass (g)	Uterine content	Number	Embryo size (TL, cm)	Embryo mass (g)	Embryo + yolk sac mass (g)
1	Jan.	150	23	Vitellogenesis	7+7	36-39	27.5-32.2	-			-	
2	Jan.	165	30	Resting (?)	-	-	-	Embryos	6+6	9.2-11.0	12-13	200-210
3	Feb.	152	27	Vitellogenesis	10+9	45-47	44.6-49.7	-			-	-
4	Feb.	152	27	Vitellogenesis	9+9	52-59	76-82.6	-			-	-
5	Mar.	146	23	Vitellogenesis	9+8	27-28	8.5-8.9	-			-	-
6	Mar.	143	26	Vitellogenesis	10+10	7-déc	?	Embryos	5+5	16.0-17.3	65.5-68	215-225
7	Mar.	148	29	Vitellogenesis	7+5	78-85	205-235	-			-	-
8	Apr.	156	25	Vitellogenesis	8+8	78-81	200-237.6	-			-	-
9	Apr.	155	29	Vitellogenesis	6+6	78-83	200-233.5	-			-	-
10	Apr.	137	22	Resting	-	-	-	Eggs	6+6	-	-	-
11	May	163	29	Vitellogenesis	8+8	24-25	6.3-6.6	Fetuses	6+6	32.0-34.5	-	270-298.5
12	May	163	29	Vitellogenesis	6+6	23-25	5.9-6.2	Fetuses	6+6	33.0-34.0	-	290-300.3
13	May	152	?	Vitellogenesis	8+8	25-26	6-6.2	Fetuses	4+4	32.0-34.0	-	276.5-302
14	Jul.	175	32	Vitellogenesis	8+8	25-28	?	-	-	-	-	-
15	Jul.	167	29	Vitellogenesis	8+8	?	?	Fetuses	(?) aborted	33.3	-	
16	Aug.	148	24	Vitellogenesis	8+7	25-27	8.3-8.5	-	-	-	-	
17	Aug	148	25	Vitellogenesis	8+6	25-28	8.5-8.8	-	-	-	-	-
18	Oct.	167	28	Vitellogenesis	7+8	29-30	18-22	-	-	-	-	-
19	Nov.	167	?	Resting	-	-	-	Embryos	6+6	< 0.5	?	< 210
20	Dec.	163	26	Vitellogenesis	6+6	35-36	28.5-33.2	-	-	-	-	-

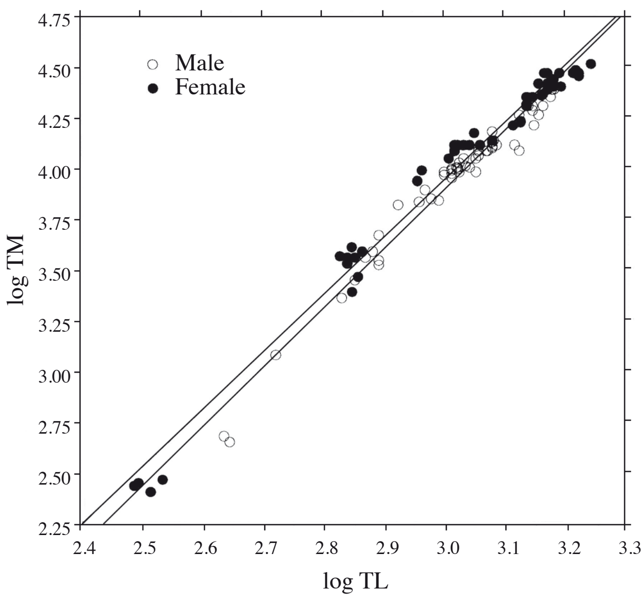

Figure 4. - Relationships Total Mass (TM) vs Total Length (TL) expressed in logarithmic co-ordinates for male and female *Squatina aculeata*. TL was measured to the nearest mm and TM to the nearest g. *[Relations entre la masse totale (TM) et la longueur totale (TL) exprimées en coordonnées logarithmiques pour les mâles et les femelles de* Squatina aculeata. *TL est mesurée au mm près et TM au g près.]*

April since ripe follicles ready to be ovulated were found in three females (see above), and eggs in the uteri of a female caught in April (Tab. II, record 10). Females containing embryos at different stages of development were caught between January and March (Tab. II, records 2 and 6). The pregnant female caught in October (Tab. II, record 19) contained embryos at the beginning of the development, which exhibited external gill filaments and a large yolk sac, they were not pigmented and cannot be sexed. Its ovaries were in a resting phase. The second female caught in January (Tab. II, record 2) also carried embryos with external gill filaments but slightly pigmented and which could be sexed; while in the ovaries translucent follicles began to accumulate yolk. This suggests that both ovaries were at the end of the resting phase. Vitellogenesis became evident in a pregnant female with embryos at mid-term of development (Tab. II, record 6), well formed, pigmented and without external gill filaments. The external yolk sac considerably decreased and was transferred *pro parte* into an internal yolk sac externally visible on the dorsal surface. Females carrying near term embryos were captured in May (Tab. II, records 11, 12 and 13) and in July, unfortunately this female (Tab. II, record 15) aborted when handled and a single embryo was recovered by fishermen. In full-term embryos, the external yolk sac was totally reabsorbed into the internal yolk sac, used as nutrients by neonates. Parturition probably occurred between May and July.

At the end of gestation, the maturing follicles were only between 24 and 26 mm in diameter and weighed less than 8 g (Tab. II, records 11, 12 and 13). After parturition vitellogenesis went on and follicles developed regularly from May to the end of the gestation, they weighed 6 g (Tab. II, records 7, 8 and 9) to March-April (Tab. II, records 11, 12 and 13) and were ready to be ovulated and reached about 210 g.

As for *S oculata* (see Capapé *et al*., 1999, 2002), an egg-capsule was not clearly observed around the recently ovulated eggs. However, remains of capsular structures were found in one female which carried early stage embryos (Tab. II, record 2).

The developing embryos carried by females captured in January (Tab. II, record 2) and in March (Tab. II, record 6) were in closed uteri without communication with cloaca. However, near term embryos (Tab. II, records 11, 12, 13) were surrounded by uteri slightly distended at distal end which communicate with cloacal chamber, consequently some embryos were located in cloaca and close to mothers vent which was slightly distended.

Size and mass

Thirty-three full-term embryos were examined, ranging between 30.3 and 35.0 cm TL (32.4 ± 1.2) and weighing between 276 and 325 g (295.9 ± 57.7). Moreover, seven smallest free-swimmimg specimens, four males and three females, were collected by fishermen and ranged from 30.5 to 34.5 cm TL and from 260 to 305 g. They exhibited an unhealed scar on the ventral surface and a conspicuous internal yolk sac. They were neonates, or at least, youngs of the year.

The relationships of total mass vs total length were not significantly different between males and females (Fig. 4). For males: log TM = 2.89 log TL -4.78 ($r = 0.98$; $n = 54$) and for females: log TM = 2.80 log TL - 4.47 ($r = 0.99$; $n = 50$).

Fresh masses of the 28 largest ripe oocytes ranged from 200 and 237.6 g (221.3 ± 10.4). and 33 full-term embryos ranged in mass from 276 and 325 g (295.9 ± 57.7). CBD based on mean dry masses calculated for *S. aculeata* was # 0.66.

Fecundity

Ovarian fecundity was based on the number of oocytes counted in each adult female. We counted the full yolked follicles ready for ovulation in females and the largest follicles in other pregnant females (in all 17 females, see table II). Ovarian fecundity ranged from 12 to 22 (mean: 15.4 ± 2.7). There was a slight positive relation between ovarian fecundity and female size. Uterine fecundity was based on the number of eggs, developing and/or fully term embryos (in all 7 females, see table II). It ranged from 8 to 12 (11.1 ± 1.5). Similar to ovarian fecundity, uterine fecundity is slightly related to female size.

Sex-ratio

Among the two categories of embryos we have distinguished, developing and full-term, males and females were equally distributed for the total sample but not in each female. The subadult males significantly outnumbered the female ones. This was not the case for juveniles and adults (Tab. III).

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

	Category	Males	Females	Males: Females
Uterine content	Developing embryos	11	11	1/1
	Full term embryos	17	16	1.06/1
Total uterine content		28	27	1.03/1
Free-swimming specimens	Juveniles	18	16	1.12/1
	Subadults	27	17	1.58/1
	Adults	18	20	1.11/1
Total free-swimming specimens		63	53	1.43/1
Grand total		91	70	1.30/1

DISCUSSION

The occurrence of the sawback angelshark in some Mediterranean areas remains questionable and the records reported in the literature probably are only occasional captures.

At present, *S. aculeata* is not commonly caught off the Tunisian coast where it is less abundant than its two sympatric species, *S. squatina* and *S. oculata* according to Bradaï (2000), so further observations and demographic analyzes are needed, prior to confirmation that a sustainable sawback angelshark population has been established in the area.

By contrast, *S. aculeata* is relatively abundant in the eastern tropical Atlantic, especially off the coast of Senegal where it is landed throughout the year, but a bit less than its sympatric species, the smoothback angelshark. For both species, the fins are collected and prepared under the vernacular name of "laaf", flesh is appreciated and used for local consumption, fresh or dry, salted by handicraft, under the vernacular name of "sali" (Gueye-Ndiaye, 1993; Gueye-Ndiaye *et al.*, 1996). This economical usefulness could explain as this was the case for *S. oculata* and other large sharks, as carcharhinid species, why in sample both subadults and adults outnumbered the juveniles.

Off the Senegalese coast, males matured at a smaller size (120-122 cm TL) than females (137-143 cm TL) while the latter reached a larger TL than the former, 152 and 175 cm, respectively. This difference in size between sexes was reported in other squatinid species such as *S. squatina* and *S. oculata* from the Tunisian coast (Capapé *et al.*, 1990), and also for *S. oculata* from the Senegalese coast (Capapé *et al.*, 2002). A similar sexual dimorphism is found in the ornate angelshark, *S. tergocellata*, from the Great Australian Bight according to Bridge *et al.* (1998), who noted that "this form of sexual dimorphism is not universal in elasmobranch species but it is common". Many similar instances were described in the literature, except in scyliorhinid species according to Mellinger (1989, 2002).

Size at birth was between 30.3 and 35 cm TL and mass at birth between 276 and 325 g. This confirms previous literature data (e.g., Moreno, 1995; Barrull and Mate, 2002).

Both ovaries were functional in all the observed females, in agreement with Bridge *et al.* (1998) for *S. tergocellata* and Capapé *et al.* (1990, 2002) for *S. squatina* and *S. oculata*. Follicles are symetrically distributed in the ovaries of *S. tergocellata* (Bridge *et al.*, 1998) and *S. oculata* from both Tunisian and Senegalese coasts, however; the left ovary tends to be more productive in *S. aculeata*. These observations contrasted with the assymetry observed by Cousseau (1973) in *S. argentina* where the right ovary is atretic, and non-fonctional in other squatinids such as *S. dumeril*, *S. californica* (Natanson and Cailliet, 1986), *S. guggenheim* and *S. occulta* (Sunye and Vooren, 1997). By contrast, more oocytes are produced by the right ovary in *S. squatina* from the Tunisian coast (Capapé *et al.*, 1990).

As noted for squatinids from the Tunisian coast (Capapé *et al.*, 1990), in *S. oculata* caught off Senegal (Capapé *et al.*, 2002) and *S. tergocellata* from the Great Australian Bight (Bridge *et al.*, 1998) an entire egg case was not clearly observed in *S. aculeata*. However, Sunye and Vooren (1997) described a single egg capsule surrounding all uterine ova in both *S. guggenheim* and *S. tergocellata* from Brazilian waters. Nevertheless, remains of capsular structure found in *S. oculata* (see Capapé *et al.*, 2002) and in *S. aculaeta* suggest that an egg capsule probably occurs in every squatinid species but is very fragile and Capapé *et al.* (2002) noted that "from capture to handling, the specimens were not the object of adequate handling in order to preserve the integrity of the capsule".

Females having yellow yolked follicles in ovaries were caught in April and other females bearing ova or full-term embryos in uteri in May. All these records suggest that gestation period lasted one year, at least. This was also the case for *S. oculata* from off Senegal (Capapé *et al.*, 2002). Moreover, a one-year gestation period seems to be corroborated by records 19, 1 and 6 (Tab. II) which pointed out a regular increase in size and growth of embryos. Natanson and Cailliet (1986) determined that *S. californica* gestation period approximately lasted 10 months. Capapé *et al*. (1990) noted that "it was difficult to delineate an annual cycle" for both *S. squatina* and *S. oculata* from off Tunisia. Bridge *et al*. (1998) estimated "that *S. tergocellata* has a gestation period of 6-12 months". In angelsharks from southern Brazil, Sunye and Vooren (1997) described a ten-months gestation which ended by a cloacal gestation, lasting six months. Bridge *et al*. (1998) noted that the possibility of uterine-cloacal gestation in all squatinid species needs further observations. By contrast an uterine-cloacal gestation *sensu* Sunye and Vooren (1997) cannot be excluded in *S. aculaeta* with regard to our observations, but it could last three months approximately from March to May. Sunye and Vooren (1997) added that during the second phase "the embryos develops in sea water and must be autonomous with respect to osmoregulation, a condition similar to oviparous embryos after pre-eclosion" and "the quality of the uterine-cloacal environment is expected to be controlled by the flow of sea water through the vent into and out the chamber". Similar patterns were described by Kormanik and Evans (1986) and Kormanik (1988) in *Squalus acanthias* during the second year of gestation. This phenomenon could partially explain the embryos growth at the end of the gestation (Tab. II, records 2 and 6 compared with records 8, 9 and 10). With special regard to *S. aculeata*, we think that an inadequate handling during capture induced the presence of near term embryos in cloaca, so in agreement with Sunye and Vooren's opinion (1997) a thorough histological study is needed prior to state on the exact role of cloaca during gestation in squatinids.

A semi-delayed vitellogenesis (see Capapé *et al*., 1990; Capapé *et al*., 2002) was observed in *S. aculeata*. However, the block of vitellogenesis did not last until mid-term gestation as this was reported in previously studied squatinids (Capapé *et al*., 1990; Capapé *et al*., 2002). Similar patterns were suspected in other squatinid species (Cousseau, 1973; Natanson and Cailliet, 1986) and described without comments by Bass *et al*. (1975) in *S. africana* who recorded two females with "embryos averaged 27 cm in length and ranged from 26 to 28 cm", closed to be expelled, size at birth being between 27 and 35 cm (Fowler, 1925; Bass *et al*., 1975). Moreover, they noted that "the ovaries of these two females contained developing ova of about 17 mm diameter" and added that diameter of ripe oocytes ranged from 50 to 60 mm.

Translucent follicles started to accumulate yolk at an early stage of embryonic development (Tab. I, record 2). Then, we observed a regular increase of follicles until ovulation, which lasted probably one year, from May to March-April. Consequently, a biannual reproductive cycle remains a probable hypothesis and agrees with previous observations carried out on other squatinid species (Capapé *et al*., 1990., 2002).

The CBD of # 0.66 obtained for *S. aculeata* is closed to the CBD of # 0.50 obtained for both *S. squatina* and *S. oculata* from the Tunisian coasts and the CBD of # 0.73 for *S. oculata* from the Senegalese waters. They are very low values and typical of purely lecithotrophic species producing heavier eggs. In lecithotrophic species, the mother only protected the embryonic development and provided inorganic nutrients to the embryos (Mellinger, 1989, 2002; Hamlett *et al*., 1998a, 1998b). This was also observed in centrophorids (Ranzi, 1932; Guallart and Vicent, 2001).

By contrast, in matrotrophic elasmobranchs, the contribution of mother-derived organic and inorganic molecules is very important (Wourms, 1977, 1981; Hamlett and Wourms, 1984; Hamlett *et al.,* 1985a-e; Hamlett, 1987, 1989; Hamlett *et al.,* 1993a, 1993b; Fishelson and Baranes, 1998; Hamlett *et al*., 2002). These species produce an egg mass that is clearly less than the mass of fully developed embryos. Matrotrophy is characteristic of dasyatids, rhinopterids and gymnurids (Wourms, 1977, 1981; Wourms *et al*., 1988; Mellinger, 1989; Capapé *et al*., 1992; Seck *et al*., 2002). For instance CBD of # 65.8 was calculated for *Carcharinus brevipinna* (Capapé *et al*., 2003), # 69 for *C. limbatus* (Capapé *et al*., 2004) and # 47 for Mediterranean *Dasybatus violacea* (Hemida *et al*., 2003), # 30.6, for the butterfly ray *Gymnura altavela* from Tunisian waters (Capapé *et al*., 1992), and # 31.12 for the bull ray *Pteromylaeus bovinus* from the coast of Senegal (Seck *et al*., 2002).

Ovarian fecundity is higher than uterine fecundity. This is due to fact that some fully yolked follicles were subjected to atresia. Moreover, some pregnant females may have been aborted during capture or handling, and may have partially lost their brood. Moreover, in squatinids according to Sunye and Vooren (1997) "the uterine-cloacal chamber communicates with the external environment", this "explains why *Squatina* aborts so easily". This patterns was observed in squatinid species by Cousseau (1973), Bass *et al*. (1975), Rahn and Yesaki (1976, *in* Sunye and Vooren, 1997), Capapé *et al*. (2002) and in the present article. However, Natanson and Cailliet (1986) and Capapé *et al*. (1990) noted "that capture and transportation of the angelsharks did not cause any loss of uterine contents". Both fecundities are slightly related with females size.

S. aculeata litter-sizes ranged from 8 to 12 with an average of 11.1. They were between 7 and 18 in *S. squatina*, 5 and 8 in *S oculata* from the Tunisian coast (Capapé *et al*., 1990) and 3 and 8 in *S. oculata* from off Senegal. This low fecundity points out that, as other elasmobranchs species, the sawback angelshark is not prolific, and its biannual reproductive cycle furthermore involves poor recruitment. Moreover, tagging experiments made in the Tunisian waters showed that *Squatina* spp. are not prone to large movements in the area (Quignard and Capapé, 1971b; Capapé *et al*., 1990). As this was probably the case for other shark species (Hemida *et al*., 2002), migrations of *S. aculeata* from the eastern tropical Atlantic through the Strait of Gibraltar remains doubtful.

The sex-ratio of the embryos shows that the sexes are approximately in equal numbers. Similar data were reported by Bridge *et al*. (1998) on *S. tergocellata* and on *S. oculata* from off Senegal (Capapé *et al*., 2002). This was also the case for different species of sharks from the Australian waters (Stevens and Mc Loughlin, 1991), the Red Sea (Waller and Baranes, 1994), the Mediterranean (Capapé *et al*., 2003, 2004) and throughout the world (Bridge *et al*., 1998). By contrast, among post-partum specimens changes in sex-ratio appeared. For instance, the subadult males significantly outnumbered the female ones, but among the adults, females were slightly more numerous than the males, probably because the pregnant specimens approached inshore waters in order to find accurate areas and expell their near term embryos, this agrees with Capapé *et al*. (2002) for Senegalese *S. oculata*. Bridge *et al*. (1998) observed "changes in sex-ratio for *S. tergocellata* in the commercial catch throughout the year on a montly basis". Moreover, sex-ratios for the other studied angelsharks species were not reported (Cousseau, 1973; Natanson and Cailliet, 1986; Capapé *et al*., 1990; Sunye and Vooren, 1997).

According to Bridge *et al*. (1998), these changes may be explained by sampling bias, "species targeting at the time of capture", but also by sexual segregation, which could be considered as a rule in elasmobranch species with regard to numerous literature data (see Muñoz-Chapuli, 1984), and "may reduce intra and interspecific competition".

Acknowledgments. - Jeanne Zaouali is indebted to her late husband and Christian Capapé to his late friend, Mr Mohamed Zaouali, past-president of the Office National des Pêches de Tunisie, for his interest and his assistance throughout the period of their investigations along the Tunisian coast. All the authors are grateful to the fishermen from the Tunisian coast who provided them material and they particularly thank the fishermen of Ouakam fishing site in Senegal and especially Mr Abdoulaye Diop and Mr Alioune Ndoye for providing information and material. We are grateful to Dr Alessandro De Maddalena, Dr Daniel Golani, Dr Farid Hemida, Pr Ivan Jardas, Dr Hakan Kabasakal, Dr Lovrenc Lipej and Dr Alen Soldo for providing information on the occurrence of *Squatina aculeata* in different Mediterranean areas. We also thank Dr Bernard Séret from MNHN (Paris) for sending important papers and constructive comments, which allowed us to improve the manuscript. Thanks are also due to two anonymous referees for their useful and helpful comments on the manuscript.

REFERENCES

BARRULL J. & I. MATE, 2002. - Tiburones del Mediterràneo. 291 p. Arenys del Mar (Spain): Els llibres del Set-Ciènces.

BASS A.J., D'AUBREY J.D. & N. KISTNASAMY, 1973. - Sharks of the East coast of Southern Africa. III. The genus *Carcharhinus* (Carcharhinidae). *Invest. Rep. Oceanogr. Res. Inst*., 33: 1-168.

BASS A.J., D'AUBREY J.D. & N. KISTNASAMY, 1975. - Sharks of the east coast of southern Africa. III. The families Hexanchidae, Chlamydoselachidae, Heterodontidae, Pristiophoridae and Squatinidae. *Invest. Rep. Oceanogr. Res. Inst*., 43: 1-50.

BINI G., 1967. - Atlante dei Pesci delle Coste italiane. 1, Leptocardi, Ciclostomi, Selaci. 106 p. Milano: Mondo Sommerso.

BLACHE J., CADENAT J. & A. STAUCH, 1970. - Clé de détermination des poissons de mer signalés dans l'Atlantique oriental (entre le 20^e^ parallèle N et le 15^e^ parallèle S). *Faune Trop*., 18: 1-479.

BRADAÏ N.M., 2000. - Diversité du peuplement ichtyque et contribution à la connaissance des sparidés du golfe de Gabès. Thèse Doct. Fac. Sciences, 600 p. Univ. Sfax (Tunisie).

BRIDGE N.F., Mc KAY D. & G. NEWTON, 1998. - Biology of the ornate angelshark (*Squatina tergocellata*) from the Great Australian Bight. *Mar. Freshw. Res*., 49: 679-686.

CADENAT J., 1950. - Poissons de mer du Sénégal. *Init. Afr*., 3: 1-345.

CAPAPÉ C., 1974. - Observations sur la sexualité, la reproduction et la fécondité de 16 Sélaciens vivipares placentaires des côtes tunisiennes. *Arch. Inst. Pasteur Tunis*, 51: 229-256.

CAPAPÉ C., 1989. - Les Sélaciens des côtes méditerranéennes : aspects généraux de leur écologie et exemples de peuplements. *Océanis*, 15: 309-331.

CAPAPÉ C. & C. ROUX, 1980. - Étude anatomique des ptérygiopodes des Squatinidæ (Pisces, Pleurotremata) des côtes tunisiennes. *Bull. Mus. Natl. Hist. Nat., Paris*, 4^e^ sér., 2^e^ section A, 4: 1161-1180.

CAPAPÉ C., QUIGNARD J.-P. & J. MELLINGER, 1990. - Reproduction and development of two angelsharks, *Squatina squatina* and *S. oculata* (Pisces: Squatinidæ), off Tunisian coasts: Semi-delayed vitellogenesis, lack of egg capsule and lecithotrophy. *J. Fish Biol*., 37: 347-356.

CAPAPÉ C., ZAOUALI J., TOMASINI J.-P. & J.-L. BOUCHEREAU, 1992. - Reproductive biology of the spiny butterfly ray, *Gymnura altavela* (Linnaeus, 1758) (Pisces: Gymnuridae) from off the Tunisian coasts. *Sci. Mar*., 56: 347-55.

CAPAPÉ C., DIOP M. & M. N'DAO, 1994. - Observations sur la biologie de la reproduction de dix-sept espèces de Sélaciens d'intérêt économique capturés dans la région marine de Dakar-Ouakam (Sénégal, Atlantique oriental tropical). *Bull. Inst. Fondam. Afr. Noire Cheikh Anta Diop, Dakar*, sér. A, 47: 87-102.

CAPAPÉ C., ZORZI G. & A.A. SECK, 1999. - New data on the eggs of the angelshark *Squatina oculata* Bonaparte, 1840 (Pisces: Squatinidae). *Oebalia*, 25: 53-60.

CAPAPÉ, C., TOMASINI J.A. & J.P. QUIGNARD, 2000. - Les elasmobranches pleurotrêmes de la côte du Languedoc (France méridionale) : observations biologiques et démographiques. *Vie Milieu*, 50: 123-133.

CAPAPÉ C., SECK A.A., GUEYE-NDIAYE A., DIATTA Y. & M. DIOP, 2002. - Reproductive biology of the smoothback angelshark, *Squatina oculata* (Elasmobranchii: Squatinidae), from the coast of Senegal (eastern tropical Atlantic). *J. Mar. Biol. Ass. U.K*., 82: 635-640.

CAPAPÉ C., HEMIDA F., SECK A.A., DIATTA Y., GUÉLORGET O. & J. ZAOUALI, 2003. - Distribution and reproductive biology of the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1841) (Chondrichthyes: Carcharhinidae). *Isr. J. Zool*., 49(3): 269-286.

CAPAPÉ C., SECK A.A., DIATTA Y., REYNAUD C., HEMIDA F. & J. ZAOUALI, 2004. - Reproductive biology of the blacktip shark, *Carcharhinus limbatus* (Chondrichthyes: Carcharhinidae) off west and north African coasts. *Cybium*, 28(4): 275-284.

COLLENOT G., 1969. - Étude biométrique de la croissance relative des ptérygopodes chez la roussette *Scyliorhinus canicula* L. *Cah. Biol. Mar.*, 10: 309-329.

COLLIGNON J. & J. ALONCLE, 1972. - Catalogue raisonné des poissons des mers marocaines, I: Cyclostomes, Sélaciens, Holocéphales. *Bull. Inst. Pêch. Maroc*, 19: 1-164.

COMPAGNO L.V.J., 1984. - FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1: Hexanchiformes to Lamniformes. *FAO Fish. Synop.* (125), 4(2): 1-249.

COUSSEAU M.B., 1973. - Taxonomia y biologia del pez angel, *Squatina argentina* (Pisces, Squatinidae). *Physis, A*, 32: 175-195.

DIEUZEIDE R., NOVELLA M. & J. ROLAND, 1953. - Catalogue des poissons des côtes algériennes. *Bull. Stn. Aquic. Pêch. Castiglione* (n.s.), 4, 1952[1953]: 1-135.

ECONOMIDIS P.S., 1973. - Catalogue des poissons de la Grèce. *Hell. Oceanol. Limnol.*, 11: 421-600.

FISCHER W., BIANCHI G. & W.B. SCOTT, 1981. - Fiches FAO d'Identification des Espèces pour les Besoins de la Pêche. Atlantique centre-est ; Zones de Pêche 34, 47 (en partie). Canada Fond de Dépôt. Ottawa, Ministère des Pêcheries et Océans Canada, en accord avec l'organisation des Nations-Unies pour l'Alimentation et l'Agriculture, Vol. 165, pag. var.

FISHELSON L. & A. BARANES, 1998. - Observations on the Oman shark, *Iago omanensis* (Triakidae) with emphasis on the morphological and cytological changes of the oviduct and yolk sac during gestation. *J. Morphol.*, 263: 151-165.

FOWLER H.W., 1925. - Fishes from Natal, Zululand, and Portuguese East Africa. *Proc. Acad. Nat. Sci. Phila.*, 77: 187-268.

GOLANI D., 1996. - The marine ichthyofauna of the Eastern Levant. History, inventory and characterization. *Isr. J. Zool.*, 42: 15-55.

GUALLART J. & J.J. VICENT, 2001. - Changes in composition during embryo development of the gulper shark, *Centrophorus granulosus* (Elasmobranchii, Centrophoridae): An assessment of maternal-embryonic nutritional relationships. *Environ. Biol. Fish.*, 61: 135-150.

GUEYE-NDIAYE A., 1993. - La transformation artisanale des produits halieutiques sur le littoral et son impact sur l'environnement. *In*: Gestion des Ressources côtières et littorales du Sénégal. Actes de l'Atelier de Gorée (Sénégal), juillet 1992 (Diaw A.T., Bâ A., Bouland P., Diouf P.S., Lake L.-A., Mbow M.-A., Ndiaye P. & M.D. Thiam, eds), pp. 323-334. Gland (Suisse): UICN.

GUEYE-NDIAYE A., DIOP M., N'DAO M. & C. CAPAPÉ, 1996. - Note sur une exploitation artisanale de poissons fermentés-séchés à Ouakam (Sénégal, Atlantique oriental tropical. *Ichthyophysiol. Acta*, 21: 201-206.

HAMLETT W.C., 1987. - Comparative morphology of the elasmobranch placental barrier. *Arch. Biol.* (Bruxelles), 98: 135-162.

HAMLETT W.C., 1989. - Evolution and morphogenesis of the placenta in sharks. *J. Exp. Zool.* (suppl.), 2: 35-52.

HAMLETT W.C. & J.P. WOURMS, 1984. - Ultrastructure of the pre-implantation shark yolk sac placenta. *Tissue Cell*, 16: 613-625.

HAMLETT W.C., ALLEN D.J., STRIBLING M.D., SCHWARTZ F.J. & L.J.A. DIDIO, 1985a. - Permeability of external gill filaments in the embryonic shark. Electron microscopic observations using horseradish peroxydase as a macromolecular tracer. *J. Submicrosc. Cytol.*, 17: 31-40.

HAMLETT W.C., WOURMS J.P. & J.A. HUDSON, 1985b. - Ultrastructure of the full-term yolk sac placenta. I. Morphology and cellular transport at the fetal attachment site. *J. Ultrastruct. Res.*, 91: 192-206.

HAMLETT W.C., WOURMS J.P. & J.A. HUDSON, 1985c. - Ultrastructure of the full-term yolk sac placenta. II. The smooth proximal segment. *J. Ultrastruct. Res.*, 91: 207-220.

HAMLETT W.C., WOURMS J.P. & J.A. HUDSON, 1985d. - Ultrastructure of the full-term yolk sac placenta. III. The maternal attachment site. *J. Ultrastruct. Res.*, 91: 221-231.

HAMLETT W.C., WOURMS J.P. & J.P. SMITH, 1985e. - Stingray placental analogues: Structure of trophonemata in *Rhinoptera bonasus*. *J. Submicrosc. Cytol.*, 17: 541-550.

HAMLETT W.C., EULITT A.M., JARELL J.R. & M.A. KELLY, 1993a. - Uterogestation and placentation in elasmobranchs. *J. Exp. Zool.*, 266: 347-367.

HAMLETT W.C., MIGLINO M.A. & L.J.A. DIDIO, 1993b. - Subcellular organization of the placenta in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *J. Submicrosc. Cytol. Pathol.*, 25: 535-545.

HAMLETT W.C., HYSELL M.K., GALVIN J. & R. SPIELER, 1998a. - Reproductive accomodations for gestation in the Atlantic guitarfish, *Rhinobatos lengitinosus*, Rhinobatidae. *J. Elisha Mitchell Sci. Soc.*, 144: 199-208.

HAMLETT W.C., KNIGHT D.P., KOOB T.J., JEZIOR M., LUONG T., ROZYCKI T., BRUNETTE N. & H.K. HYSELL, 1998b. - Survey of oviducal gland structure and function in elasmobranchs. *J. Exp. Zool.*, 282: 399-420.

HAMLETT W.C., HYSELL M.K., ROZYCKI T., BRUNETTE N., TUMILTY K., HENDERSON. A. & J. DUNNE, 1999. - Sperm aggregation and spermatozeugma formation in the male genital ducts in the clearnose skate, *Raja eglanteria*. *In*: Proc. 5th Indo-Pac. Fish Conf. Nouméa, Nov. 1997 (Séret B. & J.-Y. Sire, eds), pp. 281-291. Paris: Soc. Fr. Ichtyol. & ORSTOM.

HAMLETT W.C., MUSICK J.A., HYSELL C.K. & D.M. SEVER, 2002. - Uterine epithelial-sperm interaction, endometrial cycle and sperm storage in the terminal zone of the oviductal gland of the placental smoothound, *Mustelus canis*. *J. Exp. Zool.*, 292: 129-144.

HEMIDA F., 1998. - The shark and skate fishery in the Algerian basin: Biological and technological aspect. *Shark News*, 12: 14.

HEMIDA F. & C. CAPAPÉ, 2003. - Observations on blue sharks, *Prionace glauca* (L., 1758) (Chondrichthyes: Carcharhinidae), from the Algerian coast (southern Mediterranean). *J. Mar. Biol. Ass. U.K.*, 83(4): 873-874.

HEMIDA F., SERIDJI R., LABIDI N., BENSACI J. & C. CAPAPÉ, 2002. - New data on *Carcharhinus* spp (Chondrichthyes: Carcharhinidae) from off the Algerian coast (southern Mediterranean). *Acta Adriat.*, 43(2): 83-93.

HEMIDA F., SERIDJI R., ENNAJAR S., BRADAÏ M.N., COLLIER E., GUÉLORGET O. & C. CAPAPÉ, 2003. - New observations on the reproductive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832) (Chondrichthyes: Dasyatidae) from the Mediterranean Sea. *Acta. Adriat.*, 44(2): 193-204.

KABASAKAL H., 2002. - Elasmobranch species of the seas of Turkey. *Annales, Ser. Hist. Nat.*, 12(1): 15-22.

KABASAKAL H., 2003. - Historical and contemporary records of sharks from the Sea of Marmara, Turkey. *Annales, Ser. Hist. Nat.*, 13(1): 4-18.

KORMANIK G.A., 1988. - Time course of the establishment of uterine seawater conditions in late-term pregnant spiny dogfish (*Squalus acanthias*). *J. Exp. Biol.*, 125: 173-180.

KORMANIK G.A. & D.H. EVANS, 1986. - The acid-base status of prenatal pups of the dogfish *Squalus acanthias* in the uterine environment. *J. Exp. Biol.*, 114: 303-324.

MAIGRET J. & B. LY, 1986. - Les Poissons de Mer de Mauritanie. 213 p. Nouadhibou - Compiègne: CNROP - Sciences naturelles publications.

MAURIN C. & M. BONNET. - 1970. Poissons des côtes nord-ouest africaines (campagnes de la Thalassa), (1962 et 1968). *Rev. Trav. Inst. Sci. Tech. Pêch. Marit.*, 34: 125-170.

MELLINGER J., 1989. - Reproduction et développement des Chondrichthyens. *Océanis*, 15: 283-303.

MELLINGER J., 2002. - Sexualité et Reproduction des Poissons. 349 p. Paris: CNRS éditions.

MELLINGER J. & J. WRISEZ, 1989. - Biologie et physiologie comparée de deux sélaciens ovipares, les roussettes *Scyliorhinus canicula* et *Scyliorhinus stellaris*. Évolution de la matière sèche, de l'eau et des ions (Cl^-, Na^+, K^+) dans le vitellus de *S. canicula* au cours du développement. *Bull. Soc. Zool. Fr.*, 114: 51-62.

MORENO J.M., 1995. - Guia de los Tiburones de Aguas ibèricas, Atlantico Nororiental y Mediterràneo. 310 p. Madrid: Piramide edit.

MUÑOZ-CHAPULI R., 1984. - Éthologie de la reproduction chez quelques requins de l'Atlantique-Nord. *Cybium*, 8(4): 1-14.

NATANSON L.J. & J.M. CAILLIET, 1986. - Reproduction and development of the Pacific angelshark, *Squatina californica*, off Santa Barbara, California. *Copeia* (1990), 4: 987-994.

POLL M., 1951. - Poissons. I. Généralités. II. Sélaciens et Chimères. *Rés. Sci. Expéd. Océanogr. Belg. Eaux Côt. Afr. Atl. Sud* (1948-1949), 4(1): 1-154.

QUIGNARD J.-P. & C. CAPAPÉ, 1971a. - Liste commentée des Sélaciens de Tunisie. *Bull. Inst. Natl. Sci. Tech. Oceanogr. Pêche Salammbô*, 2(2): 131-141.

QUIGNARD J.-P. & C. CAPAPÉ, 1971b. - Note préliminaire sur le marquage des Sélaciens des côtes de Tunisie. *Bull. Inst. Natl. Sci. Tech. Oceanogr. Pêche Salammbô*, 2(2): 143-155.

RANZI S., 1932. - Le basi fisio-morfologiche dello sviluppo embrionale dei selaci. I. *Pùbbl. Stn. Zool. Napoli*, 12: 209-290.

ROUX C., 1977. - Les anges de mer (Squatinidae) de l'Atlantique et de la Méditerranée. *Bull. Off. Natl. Pêches Tunisie*, 1(2): 159-167.

ROUX C., 1984. - Squatinidae. *In*: Fishes of the North-Eastern Atlantic and Mediterranean/ Poissons de l'Atlantique du Nord-Est et de la Méditerranée, Vol. 1 (Whitehead P.J.P., Tortonese E., Bauchot M.-L., Hureau J.-C. & J. Nielsen, eds), pp.148-151. Paris: UNESCO.

SANCHÈS J.G., 1991. - Catàlogo dos principais Peixes marinhos da Republica da Guiné-Bissau. 429 p. Lisboa: INIP Publications.

SECK A.A., DIATTA Y., GUEYE-NDIAYE A. & C. CAPAPÉ, 2002. - Observations on the reproductive biology of the bull ray, *Pteromylaeus bovinus* (E. Geoffroy Saint-Hilaire, 1817) (Chondrichthyes: Myliobatidae) from the coast of Senegal (Eastern tropical Atlantic). *Acta Adriat.*, 43: 87-96.

SÉRET B. & P. OPIC, 1990. - Poissons de Mer de l'Ouest africain tropical. 416 p. Init.-Doc., 49. Paris: ORSTOM.

SOLJAN T., 1975. - I Pesci dell'Adriatico. 522 p. Verona: Mondadori.

SOURIE R., 1954. - Contribution à l'étude écologique des côtes rocheuses du Sénégal. *Mém. Inst. Afr. Noire*, 38: 1-342.

SPRINGER S., 1990. - Squatinidae. *In*: Check-List of the Fishes of the eastern tropical Atlantic (CLOFETA), Vol. 1 (Quéro J.-C., Hureau J.-C., Karrer C., Post A. & L. Saldanha, eds), pp. 77-78. Paris: UNESCO.

STEVENS J.D. & K.J. MCLOUGHLIN, 1991. - Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. *Aust. J. Mar. Freshw. Res.*, 42: 151-199.

SUNYE P.S. & C.M. VOOREN, 1997. - On cloacal gestation in angelsharks from southern Brazil. *J. Fish Biol.*, 50: 86-94.

TORTONESE E., 1956. - Leptocardia, Ciclostomata, Selachii. *In*: Fauna Italiana, 2. 332 p. Bologna: Calderini.

WALLER G.N.H & A. BARANES, 1994. - Food of *Iago omanensis*, a deep water shark from the northern Red Sea. *J. Fish Biol.*, 45: 37-45.

WOURMS J.P., 1977. - Reproduction and gestation in Chondrichthyan fishes. *Am. Zool.*, 17: 379-410.

WOURMS J.P., 1981. - Viviparity: The maternal-fetal relationship in fishes. *Am. Zool.*, 21: 473-515.

WOURMS J.P., GROOVE J.P. & J. LOMBARDI, 1988. - The maternal-embryonic relationship in viviparous fishes. *In*: Fish Physiology (Hoar W.S., Randall D.J. & E.M. Donaldson, eds), Vol. 1, pp. 1-134. New-York: Academic Press.

Reçu le 23 février 2004.
Accepté pour publication le 1er septembre 2004.