ISSN: 0001-5113 AADRAY	ACTA ADRIAT., 47 (2): 111 - 126, 2006	UDC:597.33:591.16](261-15)

Reproduction in the milk shark, *Rhizoprionodon acutus* (Rüppell, 1837) (Chondrichthyes: Carcharhinidae), from the coast of Senegal (eastern tropical Atlantic)

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The milk shark, Rhizoprionodon acutus *(Rüppel, 1837), is the shark species most abundantly landed at fishing sites along the Senegalese coast in the eastern tropical Atlantic. Adult males and females were mainly captured from March to September. The smallest adult male was 840 mm total length (TL) and weighed 2650 g; all males above 950 mm TL were adult. The smallest adult female was 890 mm TL and 4800 g; all females above 1000 mm were adult. The largest male and female were 1215 mm and 1260 mm TL and 6700 g and 6830 g, respectively. There was a significant difference in the total mass vs. TL relationship between males and females. Parturition and mating occurred in May and June. Gestation lasted approximately one year. Females had an annual reproductive cycle although some reproduced in alternate years. The diameter and mass of the largest yolked oocytes ranged 20-23 mm (mean 21.2±0.9) and 4.1-5.6 g (mean 4.8±0.5). Both uteri were compartmentalized into chambers with a single embryo in each chamber. Size and mass at birth, based on term embryos and neonates, ranged 325-500 mm TL (mean 391.4±24.4) and 127-350 g (mean 220.7±37.9). A chemical balance of development based on mean dry mass of the largest yolked oocytes and term embryos was 23. Ovarian fecundity was slightly higher than uterine fecundity. There was a slight positive relationship between uterine fecundity and female TL, but not between ovarian fecundity and female TL. Litter sizes ranged from one to eight (mean 3.5±1.3) with males and females equally distributed. In free-swimming specimens, females significantly outnumbered males, especially among sub-adult and adult specimens.*

Key words: Chondrichthyes, Carcharhinidae, *Rhizoprionodon acutus*, reproductive biology, Senegal, eastern tropical Atlantic

INTRODUCTION

Ten carcharhinid species occur off the coast of Senegal (BLACHE *et al.*, 1970; CADENAT & BLACHE, 1981; SÉRET & OPIC, 1990). The milk shark, *Rhizoprionodon acutus* (Rüppell, 1837), is the most commonly and regularly landed at fishing sites (CAPAPÉ *et al.*, 1994). Its flesh, fresh or dried as "Sali", is locally appreciated for human consumption and fins are collected and prepared under the vernacular "laâf". COMPAGNO (1984) noted that the species is one of the most abundant shark species in the inshore waters where it occurs and pointed out its commercial interest to local fisheries.

Of the seven species of *Rhizoprionodon* reported by COMPAGNO (1984), *R. acutus* has the widest geographic distribution. Scarce information was provided by BUDKER (1935), SETNA & SARANDGHAR (1949) from Bombay (India), and BASS *et al.* (1975) from southern Africa. General data from various areas were summarized by BRANSTETTER (1984) and COMPAGNO (1984). Thorough studies were published on *R. acutus* from Indian waters by KRISHNAMOORTHI AND JAGADIS (1986) and KASIM (1991) and the coastal waters of Oman by HENDERSON *et al.* (2006). CADENAT & BLACHE (1981) and CAPAPÉ *et al.* (1994) provided information on *R. acutus* from off the coast of Senegal.

Recent investigations carried out in the area allow earlier data to be expanded and our knowledge on the species to be improved. Aspects of the reproduction of *R. acutus* are given in this article, including size at sexual maturity, reproductive cycle, fecundity, and sex ratio.

MATERIALS AND METHODS

A total of 520 specimens, 174 males and 346 females, were collected (Table 1). The specimens were caught by demersal gill-nets, generally on sandy bottoms at depths of 20-100 m but occasionally on muddy or detritic bottoms, off the Senegalese coast in 1993-2004 (Fig. 1). *Rhizoprionodon acutus* is caught together with the Atlantic weasel shark, *Paragaleus pectoralis* (Garman, 1906) and, less often, with the dusky shark, *Carcharhinus limbatus* (Valenciennes, 1841). In addition, 78 developing embryos and 295 near-term embryos were examined.

The specimens were measured for total length (TL) to the nearest mm following BASS *et al.* (1975) and to the nearest gram. Clasper length (CL, mm) was measured according to COLLENOT (1969), from the forward rim of pelvic girdle to the tip of clasper. Oocytes and embryos were removed from the ovaries, measured, and weighed, as was the diameter of yolked oocytes.

The onset of sexual maturity in males was determined from the length and condition of the claspers following BASS *et al.* (1975), STEVENS & MC LOUGHLIN (1991), and WATSON & SMALE (1998). Claspers of juveniles are shorter than the

Table 1. Monthly collection of Rhizoprionodon acutus captured off the coast of Senegal

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Males	Juveniles	8	2	2	-	1	39	4	11	3	2	-	6	78
	Sub-adults	-	-	4	5	19	4	3	1	2	3	3	5	49
	Adult	3	4	1	3	14	8	3	-	4	1	3	3	47
	Total	11	6	7	8	34	51	10	12	9	6	6	14	174
Females	Juveniles	5	4	-	-	11	30	7	5	1	1	2	10	76
	Sub-adults	4	5	3	1	50	40	30	1	-	-	3	1	138
	Adults	-	1	4	4	76	36	7	-	4	-	-	-	132
	Total	9	10	7	5	137	106	44	6	5	1	5	11	346
Grand total		20	16	14	13	171	157	54	18	14	7	11	25	520

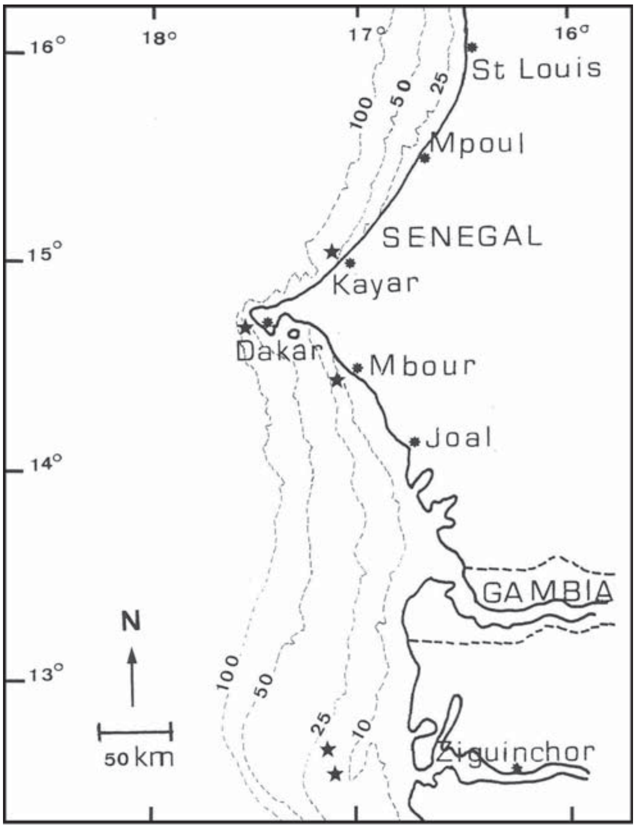

Fig. 1. Map of Senegal showing the landing and capture sites (★) of Rhizoprionodon acutus *(redrawn from Kébé and Le Reste, 1993). Depth contour in meters*

pelvic fin, flexible, and not calcified; those of sub-adults are longer than the pelvic fin, flexible, and slightly calcified; and adult claspers are longer than the pelvic fins, rigid, and calcified. Aspects of the testes and other reproductive organs in this study follow CAPAPÉ *et al.* (1990, 2002) and HENDERSON *et al.* (2006). Size at sexual maturity in females was determined from the condition of the 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 embryonic development and the role of the female during gestation, a chemical balance of development (CBD) was determined as the mean dry mass of fully-developed embryos divided by the mean dry mass of yolked oocytes or eggs. A water content of 50% in ripe oocytes and 75% in fully-developed embryos were used as standard values, based on chemical analyses of the small spotted catshark, *Scyliorhinus canicula*, by MELLINGER & WRISEZ (1989). The CBD is an estimate of the degree of nutritional support provided by the female, not counting yolk reserves.

ANOVA, student's *t*, and chi square tests were used to determine for significance ($p<0.05$). Linear regression was expressed in decimal logarithmic coordinates. Correlations were assessed by least-squares regression. In the relationship of mass to total length, ANCOVA was used to compare curves.

RESULTS

Size at sexual maturity in males

In all, 78 male juveniles ranged 430-780 mm TL (Fig. 2). They weighed 320-1500 g. Claspers were short and flexible, and testes and genital ducts were slightly developed and thread-like.

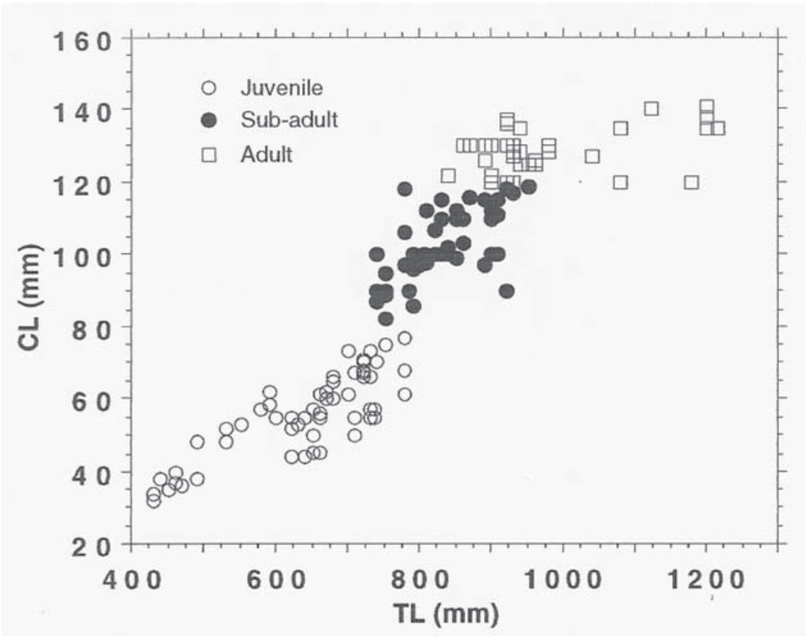

Fig. 2. Clasper length (CL) vs total length (TL) in male Rhizoprionodon acutus

Fifteen specimens (430-490 mm TL, 320-350 g) had an unhealed scar on the ventral surface and were probably neonates. Juveniles were mostly caught in June, but also in August.

Forty-nine sub-adults were observed, ranging 740-920 mm TL and 1650-2680 g. The testes were developed, but no spermatocysts were externally visible and there was no sperm in the seminal vesicles. The genital ducts were conspicuously visible and the *ductus deferens* (HAMLETT *et al*., 1999; CALLARD *et al*., 2005) was slightly convoluted. The claspers were slightly calcified and elongated. They grew fastest during this stage (see Fig. 2). Sub-adults were generally caught during March-July with a peak in May.

Forty-seven adults ranged 840-1215 mm TL and 2650-6700 g. All males greater than 950 mm TL were adult. The claspers were rigid, calcified, and elongated. Spermatocysts were externally visible and seminal vesicles contained sperm. The *ductus deferens* was notably twisted. Adults were mostly landed in May and June.

Size at sexual maturity in females

Juvenile females ranged 430-810 mm TL and 300-1800 g. They had membranous ovaries, thread-like oviducts, and inconspicuous oviducal glands. Six were neonates, unhealed scars on the ventral surface, ranging 430-480 mm TL and weighing up to 380 g. Juveniles were mostly caught in June, but also in May.

The 138 sub-adult females ranged 780-960 mm TL and 1870-4500 g. Sub-adult females had ovaries with translucent oocytes, well-differentiated genital ducts, and slightly rounded oviducal glands. The uteri walls were thickened. They were collected mostly in May and June.

The 133 adult females ranged 890-1260 mm TL and 4800-6830 g. Two were pregnant females carrying term embryos. Above 1000 mm, all females were adult. They were collected in March-September, with peaks in May (76 specimens) and June (36 specimens).

Reproductive status of females

The milk shark is a placental viviparous elasmobranch. Juvenile females had two ovaries that were membranous, slender, and similar in size and mass. As the females grew, only the left ovary developed and became functional, the right being rudimentary or absent. However, in one adult female caught in March (1010 TL; 5850 g), both ovaries were functional. Both uteri were functional in adult females. Of 110 pregnant

Table 2. Reproductive status adult female Rhizoprionodon acutus, *by month*

		Jan	Feb	Marr	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Pregnant	Carrying encapsuled eggs	-	-	-	-	4	-	2	-	-	-	-	-	6
	Carrying developing embryos	-	1	2	3	11	2	3	-	4	-	-	-	26
	Carrying near-term embryos	-	-	1	2	45	30	-	-	-	-	-	-	78
	Total	-	1	3	5	60	32	5	-	4	-	-	-	110
Non-pregnant	Post-partum	-	-	-	-	5	2	-	-	-	-	-	-	7
	With vitellogenic activity	-	-	1	-	3	-	-	-	-	-	-	-	4
	In complete break phase	-	-		-	6	3	2	-	-	-	-	-	11
	Total	-	-	4	-	14	5	2	-	-	-	-	-	22
Grand total		-	1	4	5	74	37	7	-	4	-	-	-	132

females, six had encapsulated eggs in the uteri, 26 had developing embryos, and 78 had near-term embryos (Table 2). Most pregnant females concomitantly exhibited vitellogenic activity and embryonic development; as embryos grew in both uteri, a cohort of oocytes matured and accumulated yolk for the next ovulation and fertilization.

In contrast, the ovary of 19 specimens was in a resting phase: three females with developing embryos (Table 3, records 9, 33, 34) and 16 near-term females. One near-term female was captured in March (record 2), two in April (records 7 and 9), 45 in May, 30 in June, and none the rest of the year (Table 4). Five post-partum specimens were captured in May and two in June, with ovaries containing yolked oocytes and placental attachment sites in the uteri. Four non-virgin non-pregnant females had ovaries containing yolked oocytes and well-developed uteri without placental attachment sites. Eleven other specimens, non-virgin, were in the complete resting phase.

Table 3. Reproductive cycle of female Rhizoprionodon acutus: *condition of ovary and uteri during gestation*

No.	Month of catch	TL of female (mm)	Mass of female (g)	Ovarian activity	Oocyte diameter (mm)	No. of oocytes	Uterine content	TL of embryo (mm)	Embryo mass (g)	No. of embryos (left+right)
1	Feb	1010	4200	Vitellogenesis	14-15	3	Embryos	260-263	50-58	2+1
2	Mar	980	4750	Vitellogenesis	20-22	6	Embryos	380-390	201-234	2+2
3	Mar	990	5000	Vitellogenesis	11	8	Embryos	130-134	9-10	3+0
4	Mar	1060	6200	Vitellogenesis	13	8	Embryos	250-280	51-70	2+3
5	Apr	920	4600	Vitellogenesis	6	5	Embryos	133-135	9.3-12	2+2
6	Apr	950	3900	Resting	-	-	Embryos	295-310	95-106	2+1
7	Apr	980	3500	Vitellogenesis	20-21	4	Embryos	325-360	127-188	2+3
8	Apr	1040	5000	Vitellogenesis	12	5	Embryos	200	25-27	1+1
9	Apr	1040	5500	Resting	-	-	Embyos	370-395	204-249	2+3
10	May	980	4600	-	-	-	Eggs	-	-	1+1
11	May	1020	4200	-	-	-	Eggs	-	-	2+2
12	May	1050	4500	-	-	-	Eggs	-	-	3+3
13	May	930	3980	Vitellogenesis	16-17	4	Embryos	330-347	117-152	2+1

Table 3. Cont'd

No.	Month of catch	TL of female (mm)	Mass of female (g)	Ovarian activity	Oocyte diameter (mm)	No. of oocytes	Uterine content	TL of embryo (mm)	Embryo mass (g)	No. of embryos (left+right)
14	May	980	4800	Vitellogenesis	14-15	4	Embryos	290-310	102-106	2+1
15	May	990	4000	Vitellogenesis	16-17	4	Embryos	310-315	100-102	1+1
16	May	990	4000	Vitellogenesis	16	2	Embryos	310-312	100-105	1+1
17	May	1000	4200	Vitellogenesis	16	2	Embryos	335-342	101	2+0
18	May	1020	4200	Vitellogenesis	14-16	4	Embryos	260-290	200-210	3+0
19	May	1020	5600	Vitellogenesis	6-8	5	Embryos	40-45	3.5-4.1	1+1
20	May	1022	4500	Vitellogenesis	13-15	5	Embryos	315-345	100-105	2+2
21	May	1030	4300	Vitellogenesis	16-17	5	Embryos	310-325	108-145	2+2
22	May	1030	6200	Vitellogenesis	14-15	5	Embryos	275-295	100-106	2+2
23	May	1040	4600	Vitellogenesis	13-15	5	Embryos	320-330	114-121	2+2
24	Jun	900	3500	Vitellogenesis	17	2	Embryos	335	100	1+0
25	Jun	900	3550	Vitellogenesis	7	5	Embryos	63-65	4-5.1	1+1
26	Jun	1070	5500	Resting	-	-	Embryos	81-104	4.4-5.5	2+3
27	Jul	990	3500	-	-	-	Eggs	-	-	3+1
28	Jul	1010	5850	-	-	-	Eggs	-	-	1+1
29	Jul	1010	5850	-	-	-	Eggs	-	-	1+1
30	Jul	980	4750	Vitellogenesis	14-15	5	Embryos	235-240	43-45	1+1
31	Jul	1000	4200	Vitellogenesis	11-12	7	Embryos	250	51-55	2+2
32	Sep	1040	4550	Vitellogenesis	5	7	Embryos	200-205	25-29	2+0
33	Sep	1060	5200	Resting	-	-	Embryos	178-190	68-78	2+2
34	Sep	1060	5230	Resting	-	-	Embryos	170-181	20-21	2+0

Table 4. Sizes of females and their near-term embryos

	Females					Embryos							
		Total length (mm)		Mass (g)		Total length (mm)		Mass (g)		In left uterus	In right uterus	Male	Fem.
	n	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	n	n	n	n
Mar	1	980	-	4750	-	380-390	385.5±4.2	201-234	218.2±13.9	2	2	2	2
Apr	2	980-1040	1010±42.4	3500-5500	4500±1414	325-395	363.3±19.9	127-249	192.6±35.5	4	6	6	4
May	45	890-1260	1026±62	3500-6830	5226±224	320-500	392±31.7	135-350	221.8±42	83	77	74	86
Jun	30	890-1170	1049±47	4500-6800	5858±585	332-435	393.5±18.5	129-310	219.2±34.7	64	57	61	60
Total	78	890-1260	1034±57	3500-6830	5444±876	325-500	391.4±24.4	127-350	220.7±37.9	153	142	143	152

The ovaries of pregnant females produced oocyte crops similar in size and mass. Thirty-nine yolky oocytes were removed from near-term females, with diameters ranging 20-23 mm (mean 21.2±0.9) and masses 4.1-5.6 g (mean 4.8±0.5). All developing oocytes in females with developing embryos were less than 18 mm diameter. Fertilized eggs in females at the beginning of gestation were enveloped in a diaphanous brownish capsule with a large twisted filament at each ends. Twelve capsules and fertilized eggs were removed from three females (records 27, 28, 29). Masses of oocytes and encapsulated eggs did not significantly differ (Table 5).

Table 5. Size of encapsulated eggs removed from adult female Rhizoprionodon acutus

		Total length (mm)		Width (mm)		Mass (g)	
	n	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
Capsule	12	330	324±18	-	-	1.2-1.7	1.4±0.2
Fertilized egg	12	41-45	43.7±1.5	20-23	21.2±1.4	4.1-5.6	4.8±0.6

Pregnant females with developing embryos were caught in April-September while near-term females were caught in March-July, mostly in May-June, showing that parturition occurs during this period. Females with encapsulated eggs were captured in May-July (records 9-12, 26-28), suggesting that gestation lasts 11-14 months, with twelve the most probable. This hypothesis is corroborated by the regular increase in size and mass of the embryos (records 3, 8-12, 19, 25). Embryos were not equally distributed in each uterus, they were more abundant in the left but not significantly different from the number in the right.

Embryonic development

Prior to ovulation, the uterine walls were smooth. After the encapsulated eggs entered the uteri, they were surrounded by folds of the uterine wall and each embryo developed in a separate chamber. The smallest embryos were 40 mm and 45 mm TL, weighing 3.5 g and 4.1 g, one in each uterus of record 19. They were non-pigmented, free in the uteri; the umbilical cord was 50 mm long and 0.5 g. The yolk stalk was well developed, slightly vascularized and contained a large quantity of yolk, 2.5 g and 3.1 g for each embryo, respectively. The embryos were partially dependent on their yolk reserves. External gill filaments were well developed. They could not be sexed.

Similar patterns were observed in two embryos of record 25 (63-65 mm TL, 4.5-5.1 g). The umbilical cord increased in size and mass (80 mm, 0.8 g). Rudimentary claspers appeared in the male embryo. Implantation occurred when embryos were 81-104 mm TL and 4.4-5.5 g. There were two females in the left uterus and one female and two males in the right uterus in record 26. The yolk sac and implantation site on the uterine wall were conspicuously vascularized. The uterine wall was folded at the implantation site and remains of the yolk (weighing 1.5-2.1 g) were still visible. The umbilical cord was 80-110 mm TL and 0.9-1.5 g. Appendiculae (CASTRO & WOURMS, 1993; HAMLETT, 1993; HAMLETT *et al*., 1993abc) were apparent on the umbilical cord. They were less than 2 mm in length. External gill filaments were considerably smaller but visible until they completely disappeared in embryos of 112-115 mm TL and 6.5-7.1 g. The umbilical cord was 15.3-16 mm and 2.3-2.6 g. The residual yolk was still visible and remained throughout the embryonic development. The embryo was completely formed except the spiracle. The skin was pink and unpigmented. The appendiculae of the umbilical cord grew to 5 mm and were branched. Placentation was complete.

Similar patterns were found in embryos of 130-135 mm TL and 9-12 g in records 3 and 5, however the spiracle was inconspicuously visible. Embryos of 170-280 mm TL and 20-70 g were completely formed and pigmented in records 1, 4, 8, 29-34. The umbilical cords were 160-200 mm TL and 2.2-2.5 g. Villi were abundant, reaching 45-50 mm, and branched. Placental attachment was robust and strongly implanted in the uterine wall obviously folded at its distal end. Midterm embryos were 260-315 mm, 100-110 g, and well pigmented in records 6, 14, 18, 20-23. The umbilical cords were 200-220 mm TL and from 2.5 g to just under 3 g. Appendiculae were considerably lengthened and reached 10 mm TL. They decreased as the embryos grew in size and mass until reaching full term (CASTRO & WOURMS, 1993). Term embryos were more robust and heavier than in earlier stages, reaching 325-500 mm TL and 127-350 g. Term embryos were similar in pigmentation to neonates. The lengths and abundance of appendiculae dropped. Appendiculae extended from the umbilical cord to the proximal portion of the yolk sac where vascular channels were visible and the distal portion had a lobulated surface. Maternal and fetal tissues were separated by a space and continuous egg capsule. The uterus was strongly convoluted and folded throughout the surface, particularly at the distal end. The lengths of the umbilical cord in 45 term embryos was 200-280 mm (mean 235.5±27.5) and the mass was 3.6-6.6 g (mean 4.3±0.9).

Size and mass

The size of term embryos ranged 325-500 mm TL (mean 391.4±24.4) and 127-350 g (mean 220.7±37.9). Of 21 neonates, 13 were captured in June, two in July, and six in September. Among them, 15 were male and six female. Neonates ranged 430-470 mm TL (mean 457.7±23.2) and 320-450 g (mean 351.3±34.1). There were significant biometrical differences in mean size and mean mass between term embryos and neonates.

There were significant differences in relationship between total mass (TM) and total length (TL) between males and females ($F = 3.42$; $p = 0.04$). For males, log TM = 3.192 log TL - 5.973; $r = 0.97$; n = 174, and for females, log TM = 3.338 log TL - 6.376; $r = 0.97$; n = 346 (Fig. 3). The fresh mass of thirty-nine yolky oocytes ranged 4.1-5.6 g (mean 4.8±0.5), and of 78 term embryos 127-350 g (mean 220.7). CBD was 23.

Fecundity

Ovarian fecundity was based on the number of yolked oocytes in near-term females, showing vitellogenic activity concomitant to embryonic development. Ovarian fecundity ranged 2-8 (mean 4.5±1.9). Twelve fully-yolked oocytes were counted in an adult female with two functional ovaries; this specimen was not included in our statistics. There was no relationship between ovarian fecundity and female size. Uterine fecundity, based on the number of encapsulated eggs, developing embryos, and term embryos in the female's uteri, ranged 1-8 (mean 3.5±1.3). Litter size slightly rose with female TL and was 0.014 mm TL - 11.03; $r = 0.6$; for 78 specimens.

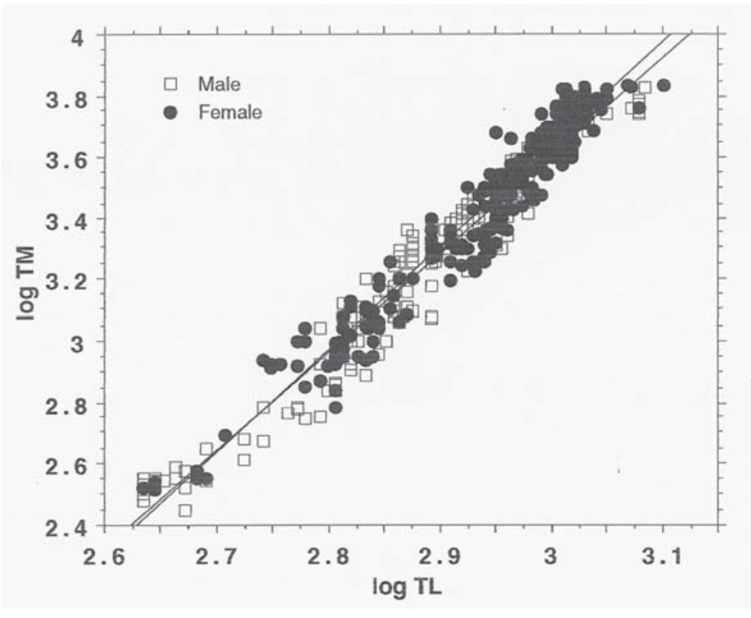

Fig. 3. Total mass (TM) versus total length (TL) expressed in logarithmic co-ordinates for male and female Rhizoprionodon acutus

Table 6. Sex ratio of specimens of Rhizoprionodon acutus

		Males	Females	Male:Female
Uterine content	Developing embryos	35	43	1:1.2
	Term embryos	143	152	1:1.1
	Total	178	195	1:1.1
Free-swimming specimens	Juveniles	78	76	1.02:1
	Sub-adults	49	138	1:2.8
	Adults	47	132	1:2.8
	Total	174	346	1:2
Grand total		352	541	1:1.54

Sex-ratio

Females slightly outnumbered males in developing and term embryos collected from pregnant females (Table 6). Among free-swimming juveniles, males and females were equally distributed. Females significantly outnumbered males among sub-adults and adults (chi square test, $p<0.05$).

DISCUSSION

The milk shark, *Rhizoprionodon acutus*, is widely distributed and prone to large migrations (COMPAGNO, 1984). Off the coast of Senegal, the milk shark is captured throughout the year, especially April-August. During this period, adults are particularly landed at fishing sites along the Senegalese coast. From March to September, large specimens are targeted by fishermen for their economical usefulness, as are other shark species (CAPAPÉ *et al*., 2003, 2004, 2005). Pregnant females were relatively abundant in the sample as they probably approach the coast when inshore waters warm up to find prey and give birth.

The occurrence of juveniles, sub-adults, and adults among specimens from both sexes and the abundance of pregnant females and neonates suggest that the *R. acutus* population is established in the area. CADENAT & BLACHE (1981), SÉRET & OPIC (1990), and CAPAPÉ *et al.* (1994) previously suspected that *R. acutus* is the most abundant and regularly caught shark species in Senegalese waters; this was confirmed by CAPAPÉ *et al*. (1998a), CAPAPÉ *et al*. (2003, 2004, 2005), and the present article.

In *R. acutus* from the coast of Senegal, males matured at a smaller size than females and reached a smaller maximum size, in agreement with CADENAT & BLACHE (1981). Females are generally heavier than males, as in other shark species caught in this area where there are sufficient resources to them to develop and reproduce (DIATTA *et al*., 2001, 2002). However, off the western coast of Africa, CADENAT & BLACHE (1981) noted that the largest male was 1780 mm and 22 kg and largest female 1650 mm and17 kg; measurements that should be considered exceptional (COMPAGNO, 1984). Off the east coast of southern Africa, BASS *et al.* (1975) noted that males mature at 680-720 mm TL and females at 700-800 mm, that the smallest pregnant female measured 710 mm TL, and that the largest male and female were 890 mm TL and 1020 mm TL, respectively. SETNA & SARANDGHAR (1949) noted that the species did not grow beyond 940 mm TL and the smallest adult was approximately 740 mm TL off Bombay (Indian Ocean). In the same area, KRISHNAMOORTHI & JAGADIS (1986) found adult females as small as 650 mm TL. Off Oman, HENDERSON *et al.* (2006) noted that females matured between 620 and 740 mm TL. Specimens from these areas are smaller than those off Senegal. In agreement with SPRINGER (1960) and BASS *et al.* (1975), we admit that different populations of *R. acutus* may differ with regard to size. According to COMPAGNO (1984), *R. acutus* is the largest species of the genus *Rhizoprionodon*. For example, SIMPFENDORFER (1992) noted that male and female *R. taylori* from Cleveland Bay in north Queensland (Australia) matured at 560 mm and 575 mm TL, respectively, consequently their maximum sizes are also smaller.

The term embryos and neonates in the present study suggest that size at birth ranges 325-500 mm TL and 127-350 g, in agreement with earlier observations CADENAT & BLACHE (1981) made on specimens from the western coast of Africa. Off South Africa, BASS *et al.* (1975) reported 300-350 mm as the size at birth, with term embryos reaching up to 340 mm and free-swimming specimens 290-350 mm TL. Off Bombay, SETNA & SARANDGHAR (1949) recorded a female carrying near-term embryos of 237 mm TL, an unusual report indicating that the embryo appeared fully developed long before gestation was complete and that a significant portion of the pregnancy was spent on increasing size. Off Oman, HENDERSON *et al.* (2006) noted that size at birth was 370 mm TL. However, geographic intraspecific differences, generally relating to female size (HENDERSON *et al*., 2006), cannot be neglected in size at birth. With regard to *R. taylori*, SIMPFENDORFER (1992) noted that the size at birth appears to range 220-260 mm TL. STEVENS & MC LOUGHLIN (1991) observed similar patterns in shark species from northern Australia.

Off the coast of Senegal, mating probably occurs in May and June when both male and female adults are most recorded in the area, or in June and July according to CADENAT & BLACHE (1981). The abundance of near-term females caught in May and June and the occurrence of neonates from May to July suggest that parturition occurs in spring and early summer off Senegal, in agreement with CADENAT & BLACHE (1981). Females carrying term embryos were captured in March-June and females with encapsulated eggs in May-July, suggesting that *R. acutus* from the Senegalese coast have a gestation period of at least one year. This hypothesis is corroborated by the regular growth of embryos throughout the year. In addition, as embryos developed in the uteri, a crop of oocytes was enlarging and receiving yolk in the ovary; apparently, soon after parturition, the females mated, ovulated, and conceived again. Hence, an annual cycle remains the most probable in *R. acutus*, as it is in the congeneric species *R. terraenovae* (CASTRO & WOURMS, 1993; HAMLETT *et al*., 1993b) and probably *R. taylori* (SIMPFENDORFER, 1992).

In contrast, the occurrence of yolked oocytes in the ovaries of some non-pregnant females and the lack of important vitellogenetic activity in gravid females, especially near-term ones, support a hypothetical biennial cycle. Some adult females had a complete resting phase in both the ovary and uteri, as in the spotted gully shark, *Triakis megalopterus*, from South Africa (SMALE & GOOSEN, 1999). This could extend the reproductive cycle to more or less than two years in some females. However, an annual cycle was the most observed in *R. acutus* while a biennial or triennial cycle remained occasional, in agreement with DEVADOSS (1988) for *R. acutus* off India. On the other hand, HENDERSON *et al.* (2006) observed the lack of an annual cycle in *R. acutus* off Oman and suggested a gestation period of over one year or a more complex reproductive cycle including a diapause in embryonic development, as in *R. taylori* (SIMPFENDORFER, 1992), meaning that females may not reproduce every season. According to CAPAPÉ *et al.* (2004), the length of the reproductive cycle in placental viviparous sharks is related to whether or not the females are energetically capable of producing both a litter and yolky oocytes in a twelve-month period or more, as suggested by SIMPFERDORFER & UNSWORTH (1998) for the whiskery shark, *Furgaleus macki*. An annual cycle in *R. acutus* could partially explain why it is the most abundant species in the area, more abundant than other carcharhinid species such as the sympatric species, the Atlantic weasel shark, *P. pectoralis*, which reproduces in alternate years (CAPAPÉ *et al*., 2005).

As in other viviparous sharks, female *R. acutus* develop compartments or chambers that enclose a single embryo (CAPAPÉ *et al*., 2003, 2004). Embryonic development observed in *R. acutus* in this study is similar to that described for the closely related species, *R. terraenovae* (HAMLETT *et al.*, 1985b; CASTRO & WOURMS, 1993), and other carcharhinid species such the spinner shark, *Carcharhinus plumbeus* (BARANES & WENDLING, 1981), and *C. brevipinna* (CAPAPÉ *et al.*, 2003). Three phases of embryonic development were identified. During the first phase, the embryos were free in the uteri, lecithotrophic, and nourished by yolk stored in the yolk sac and gas exchange possibly through the yolk sac and the integument (CASTRO & WOURMS, 1993). This phase lasted approximately two months and embryos reached 63-65 mm TL at the end. The second phase involved the concomitant development of the mother's uterine folds and embryo gill-filaments for gas exchange (HAMLETT *et al.*, 1985 a), the resorption of yolk that increases the role of mother during gestation, and the nourishment of embryos by the histotroph produced by the maternal uterus (HAMLETT *et al.*, 2005). This phase lasted two months or a bit more and ended with implantation when the embryos were 81-104 mm. During the third phase, nutrition required for embryonic development was exclusively supplied by the mother until parturition. During this phase of 6-8 months, the embryos were strictly matrotrophic and gas exchange occurred through the placenta and the appendiculae (HAMLETT *et al.*, 1993a,b,c; CASTRO & WOURMS, 1993).

An embryonic diapause was not observed in *R. acutus* as it was in *R. taylori* (SIMPFENDORFER, 1992) and *R. terranovae* (LOEFER & SEDBERRY, 2003). Ovulation occurs when Senegalese waters are rather warm (REBERT, 1983) and embryonic development soon after. This phenomenon was suspected in rhinobatids from Senegal (CAPAPÉ *et al.*, 1998b; SECK *et al.*, 2004), probably due to the fact that they are a sedentary species that inhabits restricted areas which undergo environmental changes. By contrast, *R. acutus* is a rather migratory species that lives in open waters.

The high CBD value (23) corroborates the mother's role during embryonic development and allows us to state that *R. actus* is a matrotrophic species (WOURMS, 1977, 1981; WOURMS *et al.*, 1988; HAMLETT *et al.*, 2005), such as other carcharhinid species (CAPAPÉ *et al.*, 2003, 2004, 2005; SAÏDI *et al.*, 2005). In gymnurid (CAPAPÉ *et al.*, 1992) and dasyatid species (CAPAPÉ, 1993; CAPAPÉ & ZAOUALI, 1995), the trophonemata plays an important role during gestation, so they are considered histotrophic species (HAMLETT *et al.*, 2005).

As in other viviparous elasmobranch species, ovarian fecundity is slightly higher than uterine fecundity, mainly due to the fact that some yolky oocytes do not ovulate and enter atresia. Abortions, especially during capture and handling, cannot be excluded. Ovarian fecundity is not related to size. In contrast, uterine fecundity is related to size (as in *R. taylori*; SIMPFENDORFER, 1992). The litter size in *R. acutus* off Bombay is usually two, one embryo in each uterus (SETNA & SARANDGHAR, 1949). The size in *R. acutus* from South African waters was 2-8 in 27 litters, usually 3-6, with an average of 4.7 (BASS *et al.*, 1975). A litter size of 1-6 occurred in specimens off Madras (KRISHNAMOORTHI & JAGADIS, 1986) and Oman (HENDERSON *et al.*, 2006). These data agree with our observations and those of CADENAT & BLACHE (1981) for specimens from western Africa.

Females slightly outnumbered males in developing and term embryos, in agreement with KRISHNAMOORTHI & JAGADIS (1988) and STEVENS & MC LOUGHLIN (1991), who noted that sexes occurred in equal numbers in several placental viviparous species from different areas. In contrast, HENDERSON *et al.* (2006) noted twice as many female embryos as male in *R. acutus* off Oman. The sex ratio was reported as 1:1 in litters of *R. terranovae* from the southeastern United States. The reason for such large differences is unclear (HENDERSON *et al.*, 2006). A ratio of 1:1 was found in *Iago omanensis* from the northern Red Sea (WALLER & BARANES, 1994), *Carcharhinus limbatus* from the Gulf of Mexico (CASTILLO *et al.*, 1998), and *C. brevipinna* from Tunisian waters (CAPAPÉ *et al.*, 2003), as well as in the aplacental viviparous *Triakis megalopterus* (SMALE & GOOSEN, 1999). In our study, male juveniles slightly outnumbered females in the *post partum* population, while females significantly outnumbered males in the sub-adult and adult stages. SPRINGER (1960) suggested a high rate of mortality in *C. plumbeus* males while KASIM (1991) noted that male *R. acutus* are exposed to moderately higher fishing pressure than females. According to a literature review, STEVENS & MC LOUGHLIN (1991) considered it a consequence of sexual segregation in adults (see also MUÑOZ-CHAPULI, 1984) as pregnant females enter inshore waters to expel their embryos in the best environmental conditions. A similar phenomenon was described for *Sphyrna lewini*, *C. brevipinna*, *C. limbatus*, and *Paragaleus pectoralis*, suggesting that Senegalese waters could be shark nursery areas (CASTRO, 1993).

ACKNOWLEDGEMENTS

The authors are grateful to two anonymous referees for helpful comments on the manuscript. We also wish to thank fishermen from the Senegalese coast who provided several specimens, especially Mr. Abdoulaye DIOUF and Mr. Alioune NDOYE from the fishing site of Ouakam.

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Received: 15 February 2006
Accepted: 21 September 2006

Biologija reprodukcije *Rhizoprionodon acutus* (Rüppell, 1837) (Chondrichthyes: Carcharhinidae) u obalnom području Senegala (istočni dio tropskog Atlantika)

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SAŽETAK

Morski pas, *Rhizoprionodon acutus* (Rüppel, 1837), je najviše rasprostranjen na ribarskim postajama duž senegalske obale istočnog dijela tropskog Atlantika. Odrasli mužjaci i ženke su pretežito lovljeni od ožujka do rujna. Ukupna duljina (TL) najmanjeg primjerka mužjaka iznosila je 840 mm, a težina 2650 g, dok su svi odrasli mužjaci bili duži od 950 mm TL. Najmanja odrasla ženka bila je duga 890 mm TL i teška 4800 g, a sve odrasle ženke bile su duže od 1000 mm. Najveći primjerak mužjaka bio je dug 1215 mm i težak 6700 g, a najveći primjerak ženke bio je 1260 mm dug i 6830 g težak. Ustanovljena je statistički značajna razlika između odnosa mase i ukupne duljine (TL) kod mužjaka i ženki. Parenje i porod se odvijaju u svibnju i lipnju. Trudnoća je trajala oko godinu dana. Ženke su imale godišnji reproduktivni ciklus iako su se neke razmnožavale u naizmjeničnim godinama. Promjer najveće oocite sa žumanjcem iznosio je 20-23 mm (prosjek 21.2±0.9), a težina je kolebala između 4.1-5.6 g (prosjek 4.8±0.5). Oba uterusa bila su podijeljena u komorice i u svakoj od komorica razvijao se po jedan embrij. Dužina i težina kod rođenja, mjerena na embrijima i novorođenim primjercima procijenjene su na 325-500 mm TL (prosjek 391.4±24.4) i 127-350 g (prosjek 220.7±37.9). Kemijska ravnoteža razvoja, temeljena na prosječnoj suhoj težini najvećih oocita sa žumanjcem i embrijima bliskog vremenskog razdoblja, bila je 23. Ovarijska plodnost bila je veća od uterine plodnosti. Ustanovljen je pozitivni odnos između uterine plodnosti i ukupne duljine ženki, ali takav odnos nije ustanovljen kod ovarijske plodnosti i ukupne duljine (TL). Veličine izlegnutih mladih kolebale su od 1 do 8 (prosjek 3.5±1.3) podjednako kod mužjaka i ženki.

Općenito je bilo više ženki nego mužjaka, naročito među slobodno plivajućim odraslim primjercima.

Ključne riječi: Chondrichthyes, Carcharhinidae, *Rhizoprionodon acutus*, biologija reprodukcije, Senegal, istočni dio tropskog Atlantika