

**The reproductive biology of the sandbar shark,
Carcharhinus plumbeus (Chondrichthyes: Carcharhinidae),
from the Gulf of Gabès
(southern Tunisia, central Mediterranean)**

Bécher SAÏDI¹, Mohamed Nejmeddine BRADAÏ¹, Abderrahman BOUAÏN²,
Olivier GUÉLORGET³ and Christian CAPAPÉ³

¹ *Institut national des Sciences et Technologies de la Mer, Centre de Sfax, B.P. 1035,
3018 Sfax, Tunisia*

² *Faculté des Sciences de Sfax, 3018 Sfax, Tunisia*

³ *Laboratoire d'Ichtyologie, Université Montpellier II, Sciences et Techniques du
Languedoc, 34095 Montpellier, Cedex 05, France*

*The sandbar shark, *Carcharhinus plumbeus*, is commonly captured in the Gulf of Gabès (southern Tunisia). Of 932 specimens collected from January 2001 to May 2004, the smallest mature male was 1545 mm total length and the largest male was 1935 mm. All males above 1600 mm were mature. Adult females ranged 1660-2815 mm, while all females above 1720 mm were mature. The pupping season occurred in spring and early summer, with parturition in July. Gestation was estimated at twelve months, with females appearing to reproduce in alternate years. The diameter of the largest yellow-yolked oocytes ranged 29-32 mm (mean 30.3±1.2) with the mass ranging 9.1-13.3 g (mean 11.9±1.3). Both uteri were compartmentalized into chambers and a single embryo developed in each chamber. Length and weight at birth, based on near-term embryos, were estimated at 450-650 mm and 532-1458 g. The chemical balance of development, based on the mean dry masses of the largest yellow-yolked oocytes and near-term embryos, was 40.3, showing that *C. plumbeus* is a matrotrophic species. Ovarian fecundity was slightly higher than uterine fecundity. There was a positive relationship between uterine fecundity and total length of females. Litter sizes ranged 4-10 (mean 6.9±1.1). Embryos and free-swimming juvenile and adult females significantly outnumbered males.*

Key words: Chondrichthyes, Carcharhinidae, *Carcharhinus plumbeus*, reproductive biology, Gulf of Gabès, southern Tunisia, central Mediterranean

INTRODUCTION

Six species of the genus *Carcharhinus* are reported in the Tunisian waters. The sandbar shark, *C. plumbeus*, is the most commonly landed, especially at fishing sites in the Gulf of Gabès, southern Tunisia (BRADAÏ *et al.*, 2002,2004).

Data on the reproductive biology of the sandbar shark have been reported for specimens from the western Atlantic (BIGELOW & SCHROEDER, 1948; SPRINGER, 1960; CLARK & VON SCHMIDT, 1965; BRANSTETTER, 1981; CASEY *et al.*, 1985; MUSICK *et al.*, 1993; CASTRO *et al.*, 1999), Gulf of Mexico (CASTILLO-GÉNIZ *et al.*, 1998), Brazil (AMORIM *et al.*, 1998), eastern Atlantic (CADENAT & BLACHE, 1981; CAPAPÉ *et al.*, 1994), South Africa (BASS *et al.*, 1973), China Sea (TANIUCHI, 1971), off Australia (STEVENS & MC LOUGHLIN, 1991), Indian Ocean (WHEELER, 1962), and Red Sea (BARANES & BEN-TUVIA, 1978; BARANES & WENDLING, 1981) but information on the species in the Mediterranean is scarce and from Italian waters (LO BIANCO, 1909; RANZI, 1932, 1934; TORTONESE, 1956; BINI, 1967). Recently, COSTANTINI & AFFRONTE (2003) described a pregnant female caught in the northern Adriatic Sea. CAPAPÉ (1984) gave morphological data and preliminary observations on the reproductive biology of specimens from the Tunisian coast. New records of *C. plumbeus* from the Gulf of Gabès (southern Tunisia) provide additional data, increasing our knowledge of the species in this area and in the Mediterranean, and allowing us to evaluate whether there are significant differences in traits such as size, reproductive cycle, and fecundity between the local population and those of other areas.

MATERIAL AND METHODS

A total of 932 sandbar sharks, 336 males and 596 females, were collected in the Gulf of Gabès from January 2001 to May 2004 (Figs. 1, 2).

Samples were collected by commercial trawlers, gill-netters, and bottom and pelagic long line vessels (Table 1).

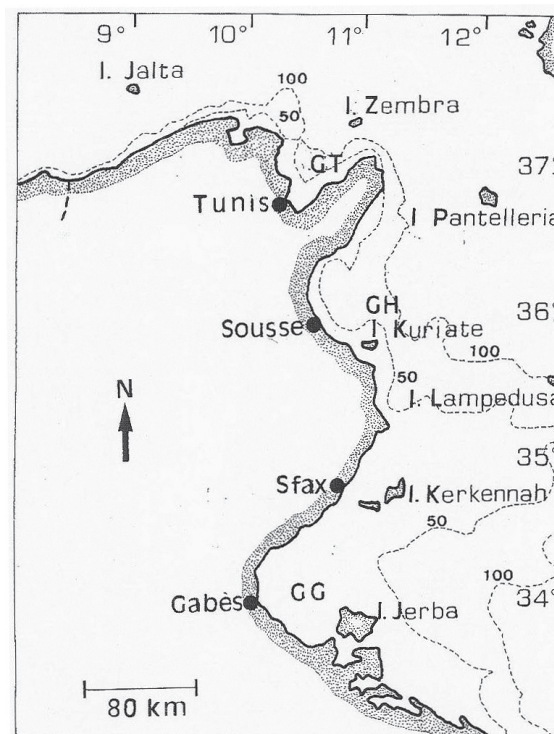


Fig. 1. Map of Tunisia. GG: Gulf of Gabès. GH: Gulf of Hammamet. GT: Gulf of Tunis

Table 1. Gears used to capture *Carcharhinus plumbeus* in the Gulf of Gabès

Gear	Males	Females	Total
Trawl	136	165	301
Gill-net	80	254	334
Longline	120	177	297
Total	336	596	932

The bottom trawl nets, with a cod end of 20 mm stretched mesh, were used to capture shrimps and demersal fishes at depths of 30-100 m. Sharks were by-catch species. Sandbar sharks were targeted March-July between Jerba Island and Zarzis by gill-nets constructed of polyamide monofilament netting with a stretched mesh size of 300-400 mm. Gill-nets were 1000-3000 m long, set on the sea floor at depths of 10-25 m, and checked and cleared of catch, or pulled and reset, daily. These special gill-nets, used

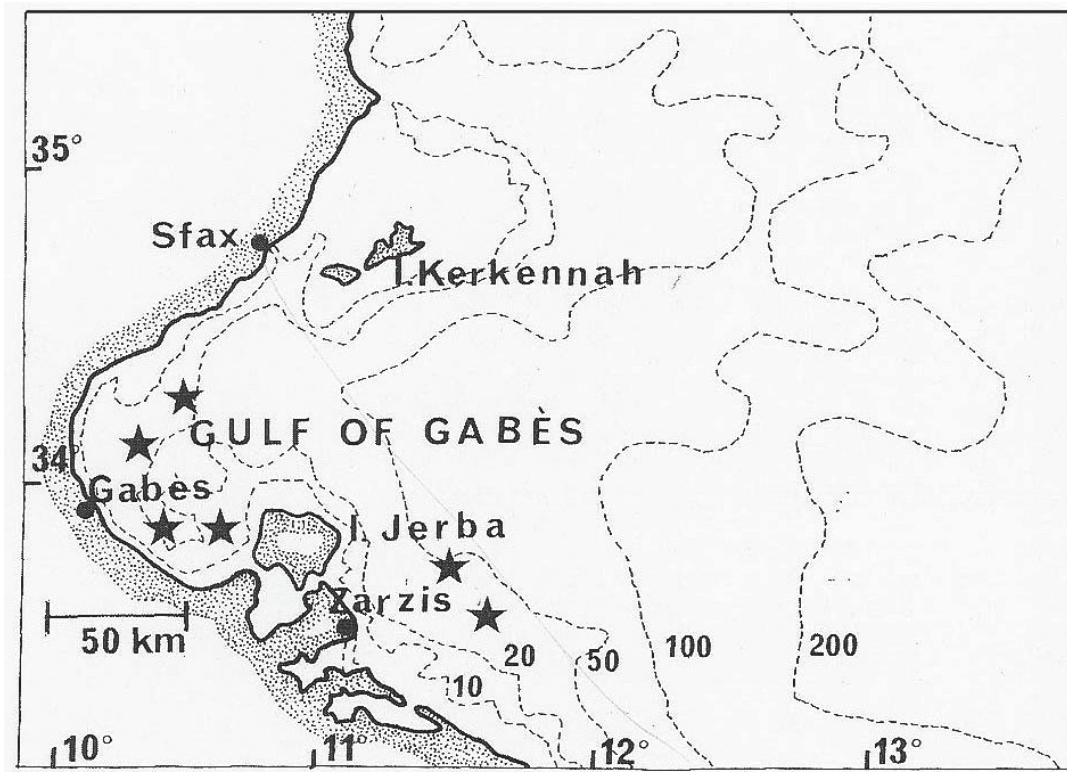


Fig. 2. *Carcharhinus plumbeus* capture sites (black stars)

only to capture sharks, are locally known as “kallabia” from “kalb’ bhar” (literally sea dog) which means shark in Arabic. *C. plumbeus* were also captured by pelagic and bottom long lines. Pelagic lines, used June-August, consist of a heavy nylon monofilament mainline, 7-28 km long, connected to buoys by a 10 m buoy line. Twenty-five large hooks (hook size: 00-01) are suspended every, approximately, kilometer, at depths of 30-100 m. Bottom long lines, used August-October, consist of a heavy nylon monofilament (1.5-3 km long) with small hooks, generally 200 (hook size: 04-05) suspended every kilometer and a single hook per light stick. For both types of long lines, the hooks were baited with pieces of teleosts such as pilchard and mackerel or cephalopods such as cuttlefish.

Total length (TL) of the specimens was measured to the nearest millimeter following BASS *et al.* (1973) and CASTRO (1996) and weight was measured to the nearest gram, when possible. Clasper length (CL, mm) was measured from the forward rim of the pelvic girdle to the

tip of the clasper, following COLLENOT (1969). The diameters of yellow-yolked and developing oocytes from the ovaries and total lengths of embryos from uteri were measured to the nearest millimeter. Both categories of oocytes and embryos were weighed to the nearest gram. Embryos were sexed when possible.

In males, the onset of sexual maturity was determined by the condition and length of the claspers. BASS *et al.* (1973) and STEVENS & MC LOUGHLIN (1991) noted that claspers of juveniles are short and flexible and that males are mature when claspers are rigid, elongated, and calcified. Aspects of the testes and genital organs were recorded. In females, sexual maturity was determined from the condition of the ovaries and the morphology of the reproductive tract following NATANSON and CAILLIET (1986), CAPAPÉ *et al.* (1990, 2002), and BRIDGE *et al.* (1998).

Ovarian fecundity was estimated by counting the ripe oocytes in the females while uterine fecundity was determined by counting the litters in pregnant females.

A chemical balance of development (CBD) was used to evaluate embryonic development and the role of the female during gestation. The CBD was calculated as the mean dry mass of fully developed embryos divided by the mean dry mass of yellow-yolked oocytes or eggs. Standard water content values were 50% for ripe oocytes and 75% for fully developed embryos, based on chemical analyses of the small spotted cat shark, *Scyliorhinus canicula*, by MELLINGER & WRISEZ (1989). The CBD is a tentative estimate

Tests for significance ($p < 0.05$) were performed by using ANOVA, STUDENT'S t test, and the chi-square test. Linear regression was performed following log transformation of data. Correlations were assessed by least-squares regression. In the relationship between mass and total length, comparisons of curves were carried out by ANCOVA.

RESULTS

Size of males

Three life stages of male development were investigated, juvenile, sub-adult and adult (Fig. 3).

During the juvenile stage, the males had short flexible claspers. Testes and genital ducts were membranous and inconspicuously developed. The 307 juvenile males ranged 450-1380 mm TL. Fifty-eight were small free-swimming specimens with an unhealed scar on the ventral surface, probably neonates, ranging 450-650 mm TL (mean 600.0 ± 13.2 mm) and 400-1740 g (mean 1237.1 ± 157.2 g).

During the sub-adult stage, the claspers were slightly calcified and elongated. The testes were developed, but had no externally visible spermatocysts and there were no sperm in the seminal vesicles. The genital ducts were developed and the *ductus deferens* (*sensu* HAMLETT *et al.*, 1999) was slightly convoluted. Seventeen sub-adults were observed. The smallest specimen was 1340 mm TL and its eviscerated mass was 12 041 g; the largest specimen was 1595 mm TL and its eviscerated mass was 18 500 g.

During the adult stage, the claspers were rigid, elongated, and calcified. Testes and genital ducts were well-developed. Spermatocysts were externally visible and there was sperm in the seminal vesicles. The *ductus deferens* was clearly twisted. Twelve adults were collected.

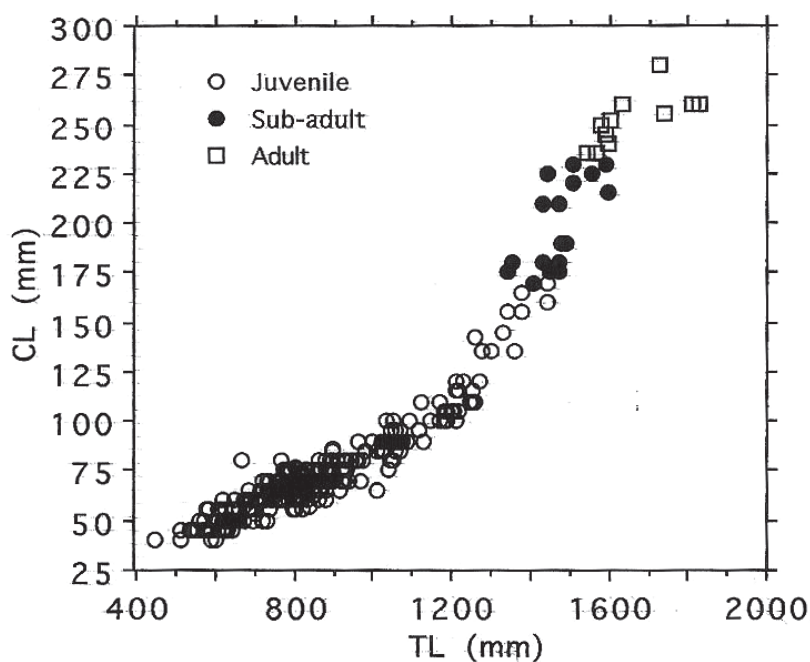


Fig. 3. Clasper length (CL) vs total length (TL) in male *Carcharhinus plumbeus*

The smallest was 1545 mm TL and 17 542 g. All males above 1600 mm TL were adult. The largest was 1935 mm TL with an eviscerated mass of 36 000 g.

Size of females

Similar to males, there were three categories of females: juvenile, sub-adults and adults.

Juvenile females, ranging between 500-1640 mm TL, had whitish ovaries, follicles of microscopic size, membrane-like oviducts and inconspicuous oviducal glands. Of the 418 juveniles collected, 62 were neonates (see males, above) ranging between 500-650 mm TL (mean 590.44±10.5 mm) and 851-1651 g (mean 1264±115.7 g).

Ten sub-adult females were collected, ranging 1640-1715 mm TL and 19 750-26 000 g. They had primarily white, translucent follicles and a well-differentiated genital duct. The oviducal glands were visible and slightly rounded.

The 168 adults ranged from 1660 to 2815 mm TL. They had functional ovaries containing

batches of developing and fully-yolked oocytes, and fully-developed genital ducts. The smallest adult with ovaries containing fully-yolked oocytes ready to be ovulated was 1660 mm TL and 22 700 g. All females above 1720 mm TL were mature. The smallest gravid female was 1720 mm TL and 25 500 g and carried five full-term embryos. The largest female was 2815 mm TL and 44 000 g. Of the 168 adult females, 14 were pregnant with fully-developed embryos.

The monthly collection for each category of males and females is presented in Table 2.

Reproductive cycle of females

Carcharhinus plumbeus is a placental viviparous elasmobranch species. Two ovaries were observed in juvenile females. Morphological differences between the ovaries developed as the specimens grew and reached maturity. The right ovary continued to increase in length and mass and became functional, whereas the left ovary became rudimentary and non-functional. The right ovary produced oocyte batches similar

Table 2. Monthly collection of *Carcharhinus plumbeus* observed in the sample

Sex	Category	Months												Total
		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	
Males														
	Juvenile	-	2	10	32	34	57	50	42	25	46	4	5	307
	Sub-adult	-	-	-	2	12	2	1	-	-	-	-	-	17
	Adult	-	-	-	1	4	2	2	2	-	1	-	-	12
	Total	-	2	10	35	50	61	53	44	25	47	4	5	336
Females														
	Juvenile	3	1	19	43	68	70	75	59	26	47	6	1	418
	Sub-adult	-	-	-	1	4	1	2	-	2	-	-	-	10
	Adult	-	-	5	34	99	20	7	1	-	2	-	-	168
	Total	3	1	24	78	171	91	84	60	28	49	6	1	596
	General total	6	3	34	113	219	221	137	104	53	96	10	6	932

Table 3. Reproductive cycle of female *Carcharhinus plumbeus*, as indicated by condition of ovaries and uteri

Number of record	Month of catch	Size of female (TL, mm)	Ovarian activity	Oocytes diameter (mm)	Oocytes number	Uterine content	Embryos size (TL, mm)	Embryos mass (gramme)
1	Mar.	1910	Resting	2-4	numerous	Embryos	450-560	500-695
2	Mar.	1970	Resting	2-4	numerous	Embryos	492-580	530-840
3	Mar.	1990	Resting	2-4	numerous	Embryos	480-575	520-750
4	Apr.	1930	Vitellogenesis	22-26	16	-	-	-
5	Apr.	2030	Vitellogenesis	29.5-32	11	-	-	-
6	Apr.	1795	Resting	2-4	numerous	Embryos	440-495	490-580
7	May	1720	Resting	2-4	numerous	Embryos	425-480	400-485
8	May	1775	Resting	2-4	numerous	Embryos	350-362	480-485
9	May	1895	Resting	2-4	numerous	Embryos	535-605	810-985
10	May	1790	Resting	2-4	numerous	Embryos	455-520	545-835
11	May	1980	Resting	2-4	numerous	Embryos	535-605	810-985
12	May	2000	Resting	2-4	numerous	Embryos	525-595	790-1025
13	May	2100	Resting	2-4	numerous	Embryos	510-555	760-790
14	May	1995	Vitellogenesis	29-32	12	-	-	-
15	Jun.	1770	Resting	1-3	numerous	Embryos	455-480	540-790
16	Jun.	1800	Resting	3-4	numerous	Embryos	535-565	810-1050
17	Jul.	1890	Resting	3-4	numerous	Embryos	570-625	990-1290
18	Aug.	2040	Resting	3-5	numerous	-	-	-

in size and mass, but only one of the batches developed into fully-yolked or ripe oocytes, the other entered atresia. By contrast, both uteri were functional.

Two categories of reproducing females were observed. The first comprised females with conspicuous vitellogenetic activity. Their ovaries contained developing (Table 3, record 4) or fully-yolked (Table 3, record 5 and 14) oocytes. Sixteen of the 23 fully-yolked oocytes found in records 5 and 14 were measured; they ranged 29-32 mm (mean 30.3 ± 1.2 mm) in diameter and weighed 9.1-13.3 g (mean 11.9 ± 1.3 g). The uteri in these three females, caught in April-May, were neither

distended nor in the rest phase. The second category comprised females carrying near-term pups. Ninety-six fully developed embryos (36 male and 60 female) ranged 430-610 mm TL (mean 530.2 ± 11.1 mm) and 391-1458 g (mean 881.7 ± 111.5 g). Thirty-two near-term embryos weighed 532-1458 g (mean 962.9 ± 240.7 g). The ovaries of near-term females were in a rest phase and no vitellogenetic activity was noticed. Near-term females were collected in May-July (Table 3, records 9, 16 and 17) and a post-partum female was collected in August (Table 3, record 18). The uteri of pregnant females were compartmentalized into chambers and a

single embryo developed in each chamber. Each embryo was connected to the uterine wall by an unadorned umbilical stalk. The uterine folds were developed and very convoluted at the distal ends of both uteri. In August and September, 120 free-swimming neonates or young of the year (58 male and 62 female) were observed.

Size and mass relationships

Ninety six fully developed embryos, 36 males and 60 females were examined. Their TL ranged between 430 and 610 mm TL (mean: 530.2 mm \pm 11.1) and their mass between 391 and 1458 g (mean: 881.7 \pm 111.5). Moreover, between August and September, 120 free-swimming specimens, 62 females and 58 males were observed, they exhibited an unhealed umbilical scar on the ventral surface, they were neonates or at least, young of the year. The females TL ranged between 500 and 650 mm (mean: 590.44 \pm 10.5), their mass between 851 and 1660 g (mean: 1264 g \pm 115.7). The males TL ranged

between 450 and 650 mm (mean: 600.0 mm \pm 13.2) and their mass between 400 and 1740 mm (mean: 1237.1 g \pm 157.2).

The relationship between TL and total mass (TM) significantly differed between males and females ($F = 18.0$; $p = 0.001$). The relationships were $\log_{TM} = 2.81 \log_{TL} - 4.71$; $r = 0.98$; $n = 68$, for males, and $\log_{TM} = 3.27 \log_{TL} - 6.06$; $r = 0.97$; $n = 87$, for females (Fig.4). The CBD for the 16 measured fully-yolked oocytes and 32 near-term embryos was 40.3.

Fecundity and sex ratio

Ovarian fecundity was based on the number of fully-yolked oocytes (9-16; mean 12 \pm 3.8) in four females ranging 1700-2030 mm TL. Uterine fecundity (4-10; mean 6.9 \pm 1.1) was estimated from 14 females ranging 1720-2100 mm TL. The relationship between litter size and total length was litter size = $-15.95 + 0.12 TL$ (mm), $r = 0.85$ (Fig. 5). Females significantly outnumbered males in all categories (Table 4).

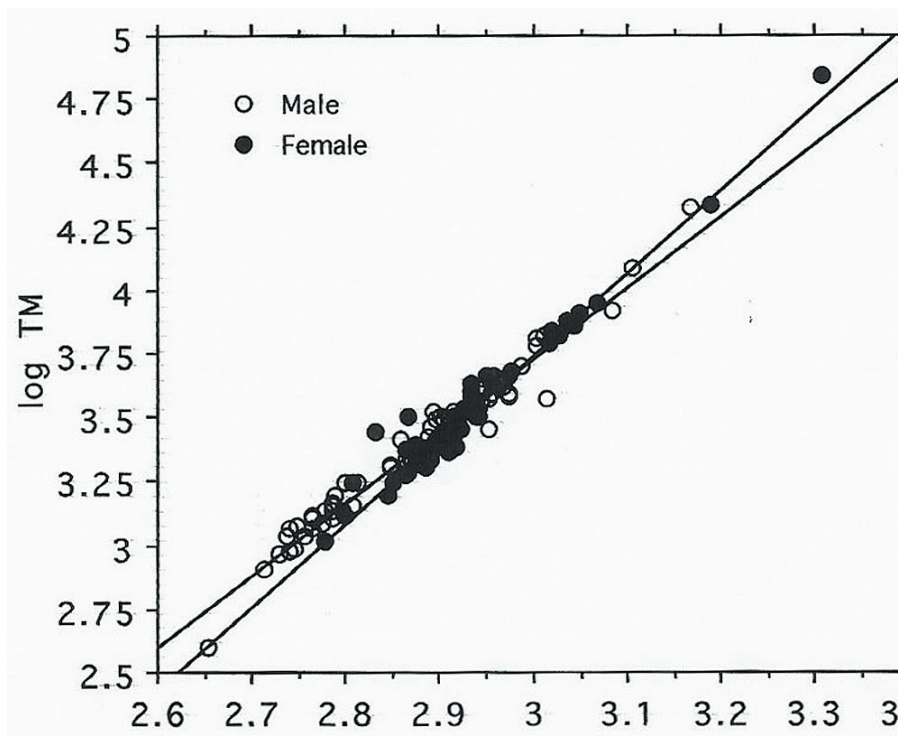


Fig. 4. Total mass (TM) vs total length (TL) expressed in logarithmic co-ordinates for male and female *Carcharhinus plumbeus*

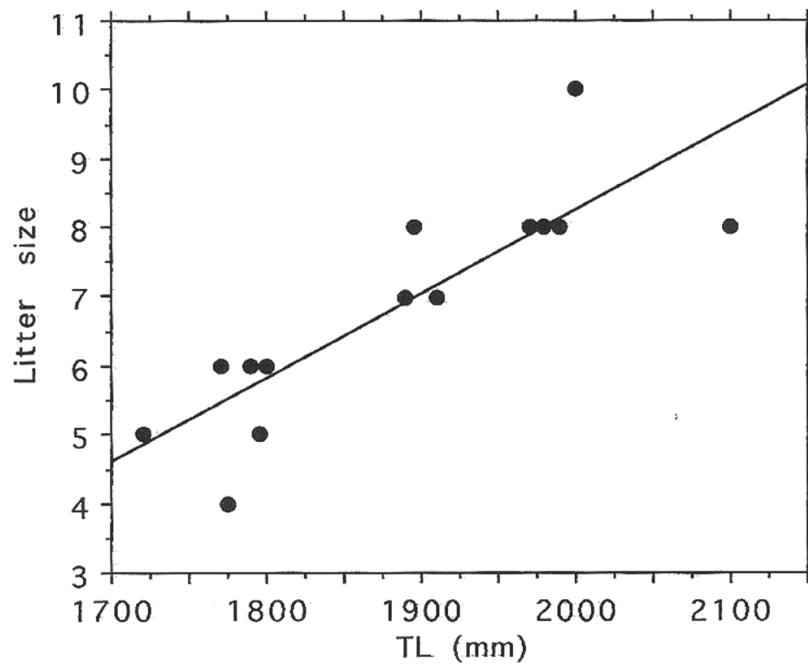


Fig. 5. Relationship between litter size and total length (TL) in *Carcharhinus plumbeus*

Table 4. *Carcharhinus plumbeus* sex ratio for each category of specimens and for the total sample

Category		Males	Females	Females: Males
Uterine content	Embryos	36	60	1.2: 1
Free-swimming specimens	Juveniles	307	418	1.4: 1
	Sub-adults	17	10	1: 1.7
	Adults	12	168	8.4:1
Total free-swimming specimens		336	596	1.8: 1
General total		374	656	1.7:1

DISCUSSION

Carcharhinus plumbeus is widely distributed and undertakes large migrations (GARRICK, 1982; COMPAGNO, 1984). Records of sandbar sharks are reported throughout the Mediterranean (CAPAPÉ, 1989), but the species seems to be more abundant in the Adriatic Sea (COSTANTINI & AFFRONTI, 2003), the Levantine Basin (BARANES & BEN-TUVIA, 1978; BARANES & WENDLING, 1981; GOLANI, 1996), and off the Maghrebin shore

(BRADAÏ, 2000; HEMIDA *et al.*, 2002; BRADAÏ *et al.*, 2002,2004).

In the Gulf of Gabès, landings of sandbar sharks occurred year round, especially from March to October, with a peak in May-July. The landings consisted of juveniles of both sexes and adult females, usually near-term pregnant females that apparently approached the coast to give birth in a nursery area with advantageous environmental conditions (MUÑOZ-CHAPULI, 1984).

Size at sexual maturity and maximum size vary with location (Table 5), in agreement with the MORENO's findings (1995). Similar patterns were more evident for the closely related spinner (*C. brevipinna*) and blacktip (*C. limbatus*) sharks, according to STEVENS & MC LOUGHLIN (1991) and CAPAPÉ *et al.* (2003, 2004). Males mature at a shorter length than females, corroborating previous observations for carcharhinid species (BRANSTETTER, 1981; GARRICK, 1982; MELLINGER, 1989). Females were heavier than males. Specimens of both sexes grew and reproduced in the Gulf of Gabès, showing that a sustainable *C. plumbeus* population is definitively established in the area, in agreement with CAPAPÉ (1984, 1989).

The fully-developed embryos and neonates reported in the present study suggest that size at birth is 450-650 mm in the Gulf of Gabès

(Table 6), confirming findings of GARRICK (1982) who noted that in carcharhinid species “a considerable variation in size of young at birth is largely geographic”, and observations carried out on *Carcharhinus* spp from the Tunisian coast (see CAPAPÉ *et al.*, 2003, 2004).

Females with fully-yolked oocytes ready to be ovulated were observed in April and May and near-term females were observed from April to July, suggesting that ovulation occurs at the end of spring/early summer with parturition in summer. Embryonic development appeared to last at least one year, in agreement with data from the Tunisian coast and other areas (CAPAPÉ, 1984). Generally, parturition occurs from the end of winter throughout the summer. SPRINGER (1960) reported that females expel their brood off Florida in spring while TANIUCHI (1971) reported parturition during early summer in the

Table 5. Sizes at sexual maturity and maximal sizes of *Carcharhinus plumbeus* reported from different areas

Size at sexual maturity (mm)		Maximal size (mm)		Area	Authors
Males	Females	Males	Females		
	1800		2500	Western Atlantic	BIGELOW and SCHROEDER (1948)
1830	1830	2260	2300	Western Atlantic	SPRINGER (1960)
1800	1770	2130	2200	Mauritian	WHEELER (1962)
1920	1850	2040	2340	Western Atlantic	CLARK and VON SCHMIDT (1965)
	1900		1900	Italian waters	BINI (1967)
1630	1900	2260	2470	South Africa	BASS <i>et al.</i> (1973)
	1760		1760	Red Sea	BARANES and BEN-TUVIA (1978)
1840	1890	1900	2030	Gulf of Mexico	BRANSTETTER (1981)
1800	1850	2230	2290	Coast of Senegal	CADENAT and BLACHE (1981)
1660	1700	2250	2480	Coast of Tunisia	CAPAPÉ (1984)
1560	1580	-	-	Northern Australia	STEVENS and MC LOUGHLIN (1991)
1545-1600	1660-1720	1935	2185	Gulf of Gabès	Present study

Table 6. Size at birth of *Carcharhinus plumbeus* reported from different areas

Size at birth (mm)	Area	Authors
> 440	Italian waters	TORTONESE (1956)
# 510	Western Atlantic	SPRINGER (1960)
600-750	China Sea	TANIUCHI (1971)
600-750	South Africa	BASS <i>et al.</i> (1973)
546-605	Coast of Senegal	CADENAT and BLACHE (1981)
580-650	Coast of Tunisia	CAPAPÉ (1984)
530-660	Southern Australia	STEVENS and MC LOUGHLIN (1991)
# 597	Brazil	AMORIM <i>et al.</i> (1998)
450-650	Gulf of Gabès	Present study

China Sea. By contrast, parturition occurred earlier off South Africa, in February and early March, according to BASS *et al.* (1973). CADENAT & BLACHE (1981) noted that, off the western African coast, there appeared to be a relationship between season and embryo size.

In our sample, the occurrence of developing or fully-yolked oocytes in the ovaries of non-pregnant females and the lack of vitellogenesis in gravid females, especially near-term ones, are evidence of a biennial reproductive cycle, in agreement with SPRINGER (1960), BASS *et al.* (1973), and STEVENS & MC LOUGHLIN (1991). By contrast, other studies found an annual cycle in female reproduction (HAMLETT *et al.*, 1993a,b). CAPAPÉ (1984) also suggested an annual cycle, based on pregnant females with vitellogenic activity off the Tunisian coast. BRANSTETTER (1981) and SCHWARTZ (1984) collected near-term blacknose (*C. acronotus*) females carrying large developing ovarian eggs. HAZIN *et al.* (2002) and DRIGGERS *et al.* (2004) reported that vitellogenesis and embryonic development occurred consecutively in *C. acronotus*. STEVENS & MC LOUGHLIN (1991) suggested an annual cycle in *C. brevipinna*,

while CAPAPÉ *et al.* (2003) suspected both annual and biennial cycles. CAPAPÉ *et al.* (2004) clearly described similar patterns in *C. limbatus*, however, BRANSTETTER (1981) and CASTRO (1996) suggested that this species reproduces in alternate years. With regard to observations carried out by LYLE (1987) on the creek waller (*C. fitzroyensis*) and blacktip reef (*C. melanopterus*) sharks and by SIMPFENDORFER & UNSWORTH (1998) on a placental elasmobranch (the whiskery shark, *Furgaleus macki*), CAPAPÉ *et al.* (2004) suggested that the length of the reproductive cycle depends on whether the female is energetically capable of producing both a litter and yellow-yolked oocytes within a twelve month period. As noted by DRIGGERS *et al.* (2004), it is important to understand the variability in life-history strategy when developing population dynamics models.

The chemical balance of development of 40.3 indicates that *C. plumbeus* is a matrotrophic species (WOURMS, 1977, 1981) in which the contribution of mother-derived organic molecules is very important (HAMLETT & WOURMS, 1984; HAMLETT *et al.*, 1985a,b,c,d,e, 1993a,b, 2002; HAMLETT, 1987, 1989; FISHELSON &

BARANES, 1998). Such species produce an egg mass that is clearly less than the mass of near-term embryos. Matrotrophy is characteristic of carcharhinids, dasyatids, gymnurids, and rhinopterids (MELLINGER, 1989; CAPAPÉ *et al.*, 1992; HAMLETT *et al.*, 1998a,b; SECK *et al.*, 2002). However, the CBD value of *C. plumbeus* is lower than those calculated for the sympatric species, *C. brevipinna* and *C. limbatus* (65.8 and 69, respectively). This phenomenon could be due to sampling, but also to the fact that eggs are slightly heavier in *C. plumbeus*, probably because the species reproduces in alternate years in the Gulf of Gabès.

Ovarian fecundity was higher than uterine fecundity as a consequence of fully-yolked oocytes that were not ovulated and entered atresia. Pregnant females probably aborted during capture and handling and may have partially lost their brood. This phenomenon is less frequent in placental viviparous than in aplacental viviparous species. In the former, embryos are protected by uterine chambers and linked by an umbilical stalk to the uterine wall. Embryos in the latter species are free in the uteri, with some species, such as squatinids (see SUNYE & VOOREN, 1997), being submitted to an utero-cloacal gestation at the end of embryonic development. Both categories of fecundity and especially uterine fecundity were related to the size of the female, in agreement with BRANSTETTER (1981), CAPAPÉ (1984), COMPAGNO (1984), and STEVENS & MC LOUGHLIN (1991).

Litter sizes ranged 4-10 (mean 6.9) in pregnant females, not significantly different from reports on other sandbar sharks elsewhere. Off the Tunisian coast, CAPAPÉ (1984) noted that females carried 3-14 embryos. In the western Atlantic (off the eastern coast of America), SPRINGER (1960) reported a litter size of 1-14 (mean 9), CLARK & VON SCHMIDT (1965) 4-11 (mean 9), and BRANSTETTER (1981) 6-11. Off Brazil, AMORIM *et al.* (1998) recorded 7-10 embryos in fifteen pregnant females. Off the eastern tropical Atlantic, CADENAT & BLACHE (1981) noted litter sizes of 5-12. Off southern Africa, BASS *et al.* (1973) found eight embryos in

two females. In the Indian Ocean, WHEELER (1962) found litters of 6-11 (mean 8.3) for *C. plumbeus* caught off the Mauritius and Seychelles Islands. In the Red Sea, BARANES & BEN-TUVIA (1978) found six embryos in one female. In the Pacific Ocean, off Hawaii, TESTER (1969) recorded litter sizes of 1-8 (mean 5.5). In the China Sea, TANIUCHI (1971) found litter sizes of 2-10 (mean 5.6) and, off northern Australia, STEVENS & MC LOUGHLIN (1991) reported sizes of 3-8 (mean 6). In the Mediterranean, LO BIANCO (1909) reported on the largest litter recorded in *C. plumbeus*, 18 embryos in one female caught off Naples.

In embryos in our sample, females significantly outnumbered males. STEVENS & MC LOUGHLIN (1991) noted that the sex ratio in embryos was 1:1 in all areas for which information is available (SPRINGER, 1960; TANIUCHI, 1971; BASS *et al.*, 1973; WASS, 1973; BARANES & WENDLING, 1981). However, off Brazil, of 60 embryos found in fifteen pregnant females, 35 were female and 25 were male (AMORIM *et al.*, 1998). In other carcharhinid species, female and male embryos occur in approximately equal numbers (STEVENS & MC LOUGHLIN, 1991; CAPAPÉ *et al.*, 2004). Among the *post partum* population in our study, females significantly outnumbered males, except for sub-adults, in agreement with CAPAPÉ (1984) and reports from other areas (STEVENS & MC LOUGHLIN, 1991). SPRINGER (1960) suggested that the skewed sex ratio in *C. plumbeus* off Florida was the result of a high mortality rate in males. STEVENS & MC LOUGHLIN (1991) suggested that the sex ratio observed for *C. plumbeus* resulted from both sexual segregation and gear selectivity. Sexual segregation is common in many shark species (MUÑOZ-CHAPULI, 1984). CASTRO (1993) stated that carcharhinid species give birth in nursery areas, probably the reason why adult females were particularly abundant in our sample (more fishing is conducted close to sandbar shark nursery areas). Further, gear selectivity cannot be ignored; in the Gulf of Gabès, shark species of economic importance are targeted during some periods of the year by special gill-nets, e.g. *kallabia* (see above)

REFERENCES

- AMORIM, A.F., A. ARFELLI & L. FAGUNDES. 1998. Pelagic elasmobranchs caught by long liners off southern Brazil during 1974-97: an overview. *Mar. Freshwater Res.*, 49(7): 621-632.
- BARANES, A. & A. BEN-TUVIA. 1978. Occurrence of the sandbar shark *Carcharhinus plumbeus* in the northern Red Sea. *Isr. J. Zool.*, 27: 45-51.
- BARANES, A. & J. WENDLING. 1981. The early stages of development in *Carcharhinus plumbeus*. *J. Fish Biol.*, 18: 159-175.
- BASS, A.J., J.D. D'AUBREY & N. KISTNASAMY. 1973. Sharks of the east coast of southern Africa. III. The genus *Carcharhinus* (Carcharhinidae). *Invest. Rep. Ocean. Res. Inst.*, 33: 1-168.
- BIGELOW, H.B. & W.C. SCHROEDER. 1948. Sharks. In: *Fishes of the Western North Atlantic Mem. Sears Fdn. Mar. Res.* 1(1) : 59-576.
- BINI, G. 1967. *Atlante dei pesci delle coste italiane*. 1, Leptocardi, Ciclostomi, Selaci. Mondo Sommerso, Milano, 106 pp.
- BRADAĬ, M.N. 2000. Diversité du peuplement ichtyque et contribution à la connaissance des sparidés du golfe de Gabès. Ph.D. thesis, University of Sfax, Tunisia, 600 pp.
- BRADAĬ, M.N., B. SAĬDI, M. GHORBEL, A. BOUAĬN, O. GUÉLORGET & C. CAPAPÉ. 2002. Observations sur les requins du golfe de Gabès (Tunisie méridionale, Méditerranée centrale). *Mésogée*, 60:61-77
- BRADAĬ, M.N., J.P. QUIGNARD, A. BOUAĬN, O. JARBOUI, A. OUANNES-GHORBEL, L. BEN ABDALLAH, J. ZAQUALI & S. BEN SALEM. 2004. Ichtyofaune autochtone et exotique des côtes tunisiennes: recensement et biogéographie. *Cybiurn*, 28 (4):315-328.
- BRANSTETTER, S. 1981. Biological notes on the sharks of the north central Gulf of Mexico. *Contrib. Mar. Sci.*, 24: 13-34.
- BRIDGE, N.F., D. MC KAY & G. NEWTON. 1998. Biology of the ornate angel shark (*Squatina tergocellata*) from the Great Australian Bight. *Mar. Freshwater Res.*, 49: 679-686.
- CADENAT, J. & J. BLACHE. 1981. Requins de Méditerranée et d'Atlantique (plus particulièrement de la côte occidentale d'Afrique). *Faune trop.*, ORSTOM, 21: 1-330.
- CAPAPÉ, C. 1984. Nouvelles données sur la morphologie et la biologie de la reproduction de *Carcharhinus plumbeus* (Nardo, 1827) (Pisces, Carcharhinidae) des côtes tunisiennes. *Inv. Pesq.*, 48: 115-137.
- CAPAPÉ, C. 1989. Les Sélaciens des côtes méditerranéennes: aspects généraux de leur écologie et exemples de peuplements. *Océanis*, 15: 309-331.
- CAPAPÉ, C., J.P. QUIGNARD & J. MELLINGER. 1990. Reproduction and development of two angel sharks, *Squatina squatina* and *S. oculata* (Pisces: Squatinidae), off Tunisian coasts: semi-delayed vitellogenesis, lack of egg capsule and lecithotrophy. *J. Fish Biol.*, 37: 347-356.
- CAPAPÉ, C., J. ZAOUALI, J.P. TOMASINI & 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., M. DIOP & 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 orientale tropicale). *Bull. Inst. Fond. Afr. Noire Cheikh Anta Diop, Dakar, sér. A*, 47: 87-102.
- CAPAPÉ, C., A.A. SECK, A. GUEYE-NDIAYE, Y. DIATTA & M. DIOP. 2002. Reproductive biology of the smoothback angel shark, *Squatina oculata* (Elasmobranchii: Squatinidae), from the coast of Senegal (eastern tropical Atlantic). *J. Mar. Biol. Ass. U.K.*, 82: 635-640.
- CAPAPÉ, C., F. HEMIDA, A.A. SECK, Y. DIATTA, O. GUÉLORGET & 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., A.A. SECK, Y. DIATTA, C. REYNAUD, F. HEMIDA & J. ZAOUALI. 2004. Reproductive

- biology of the blacktip shark, *Carcharhinus limbatus* (Chondrichthyes: Carcharhinidae) off west and north African coasts. *Cybium*, 28(4): 275-284.
- CASEY, J.G., H.L. PRATT & C.E. STILLWELL. 1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Can. J. Fish. Aquat. Sci.*, 42: 963-975.
- CASTILLO-GÉNIZ, J.L., J.F. MARQUÈS-FARIA, M.C. RODRIGUEZ DE LA CRUZ, E. CORTES & A. CID DEL PRADO. 1998. The Mexican artisan fishery in the Gulf of Mexico: towards a regulated fishery. *Mar. Freshwater Res.*, 49: 611-620.
- CASTRO, J.I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the sharks nurseries of the south eastern coast of the United States. *Env. Biol. Fish.*, 38: 37-48.
- CASTRO, J.I. 1996. Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. *Bull. Mar. Sci.*, 59(3): 508-522.
- CASTRO, J.I., C.M. WOODLEY & R.L. BRUDEK. 1999. A preliminary evaluation of the status of shark species. *FAO Fisheries Technical Paper*, N° 380. Rome, FAO, 72 pp.
- CLARK, E. & K. VON SCHMIDT. 1965. Sharks of the central Gulf of Florida. *Bull. Mar. Sci.*, 15: 13-83.
- COLLENOT, G. 1969. Etude biométrique de la croissance relative des ptérygopodes chez la roussette *Scyliorhinus canicula* L. *Cah. Biol. Mar.*, 10: 309-329.
- 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 2. Carcharhiniformes. *FAO Fish. Syn.* (125), Part 2: 251-655.
- COSTANTINI, M & M. AFFRONTE. 2003. Neonatal and juvenile sandbar sharks in the northern Adriatic Sea. *J. Fish. Biol.*, 62(3): 740-744.
- DRIGGERS, W.B., D.A. OAKLEYS, G. ULRICH, J.K. CARLSON, B.J. CULLUM & J.M. DEAN. 2004. Reproductive biology of *Carcharhinus acronotus* in the coastal waters of South Carolina. *J. Fish Biol.*, 64(6): 1540-1551.
- 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.
- GARRICK, J.A.F. 1982. Sharks of the genus *Carcharhinus*. NOAA Technical Report, NMFS Circular N° 34: 1-194.
- GOLANI, D. 1996. The marine ichthyofauna of the eastern Levant. History, inventory and characterization. *Isr. J. Zool.* 42: 15-55.
- 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., D.J. ALLEN, M.D. STRIBLING, F.J. SCHWARTZ & L.J.A. DIDIO. 1985a. Permeability of external gill filaments in the embryonic shark. Electron microscopic observations using horseradish peroxidase as a macromolecular tracer. *J. Submicrosc. Cytol.*, 17: 31-40.
- HAMLETT, W.C., J.P. WOURMS & 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., J.P. WOURMS & 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., J.P. WOURMS & 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., J.P. WOURMS & J.P. SMITH. 1985e. Stingray placental analogues: structure of trophoblasts in *Rhinoptera bonasus*. *J. Submicro. Cytol. Pathol.*, 17: 541-550.
- HAMLETT, W.C., A.M. EULITT, R.J. JARRELL & M.A. KELLY. 1993a. Uterogestation and placentation in elasmobranchs. *J. Exp. Zool.*, 266: 347-367.

- HAMLETT, W.C., A.M. MIGLINO & L.J.A. DIDIO. 1993b. Subcellular organization of the placenta in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. J. Submicro. Cytol. Pathol., 25: 535-545.
- HAMLETT, W.C., M.K. HYSELL, J. GALVIN and R. SPIELER. 1998a. Reproductive accommodations for gestation in the Atlantic guitarfish, *Rhinobatos lengitinosus*, Rhinobatidae. J. El Mitchell Sci. Soc., 144: 199-208.
- HAMLETT, W.C., D.P. KNIGHT, T.J. KOOB, M. JEZIOR, T. LUONG, T. ROZYCKI, N. BRUNETTE & H.K. HYSELL. 1998b. Survey of oviducal gland structure and function in elasmobranchs. J. Exp. Zool., 282: 399-420.
- HAMLETT, W.C., M.K. HYSELL, T. ROZYCKI, N. BRUNETTE, K. TUMILTY, A. HENDERSON & 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, 3-8 Nov. 1997, Paris, Soc. Fr. Ichthyol. & ORSTOM, pp. 281-291.
- HAMLETT, W.C., J.A. MUSICK, C.K. HYSELL & D.M. SEVER. 2002. Uterine epithelial-sperm interaction, endometrial cycle and sperm storage in the terminal zone of the oviducal gland of the placental smoothhound, *Mustelus canis*. J. Exp. Zool., 292: 129-144.
- HAZIN, F.B.H., P.G. OLIVEIRA & M.K. BRADHURST. 2002. Reproduction of the blacknose shark (*Carcharhinus acronotus*) in coastal waters off northeastern Brazil. Fish. Bull., 100: 143-148.
- HEMIDA, F., R. SERIDJI, N. LABIDI, J. BENSACI & C. CAPAPÉ. 2002. New data on *Carcharhinus* spp (Chondrichthyes: Carcharhinidae) from off the Algerian coast (southern Mediterranean). Acta Adriat., 43(2): 83-93.
- LO BIANCO, S. 1909. Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. Mitt. Zool. Stn., Neapel, 19(4): 513-761.
- LYLE, J.M. 1987. Observations on the biology of *Carcharhinus cautus* (Whitley), *C. melanopterus* (Quoy & Gaimard) and *C. fitzroyensis* (Whitley) from northern Australia. Aust. J. Mar. Freshw. Res., 38: 701-710.
- MELLINGER, J. 1989. Reproduction et développement des Chondrichthyens. Océanis, 15: 283-303.
- MELLINGER, J. & J. WRISEZ. 1989. Biologie et physiologie comparée de deux sélaciens ovipares, les roussettes *Scyliorhinus canicula* et *Scyliorhinus stellaris*. Evolution 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. France, 114: 51-62.
- MORENO, J.M. 1995. Guia de los tiburones de aguas ibéricas, Atlántico Nororiental y Mediterráneo. (Editor). Piramide, Madrid, Spain, 310 pp.
- MUÑOZ-CHAPULI, R. 1984. Ethologie de la reproduction chez quelques requins de l'Atlantique-Nord. Cybium, 8(4): 1-14.
- MUSICK, J.A., S. BRANSTETTER & J.A. COLVOCORESSES. 1993. Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the US mid-Atlantic coast. In: S. Branstetter (Editor). Conservation Biology of Elasmobranchs. NOAA Technical Report, NMFS, pp. 1-18.
- 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.
- RANZI, S. 1932. Le basi fisio-morfologiche dello sviluppo embrionale dei Selaci. I. Pubbl. Staz. Zool. Napoli, 12(2): 256-60.
- RANZI, S. 1934. Le basi fisio-morfologiche dello sviluppo embrionale dei Selaci. II. Pubbl. Staz. Zool. Napoli, 14(3): 331-437.
- SCHWARTZ, F.J. 1984. Occurrence, abundance, and biology of the blacknose shark, *Carcharhinus acronotus* in north Carolina. Northeast Gulf Sci., 7 (1): 29-47.
- SECK, A.A., Y. DIATTA, A. GUEYE-NDIAYE & 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(1): 87-96.
- SIMPFENDORFER, C.A. & P. UNSWORTH. 1998.
Reproductive biology of the whiskery shark,
Furgaleus macki, off south-western Australia.
Mar. Freshwater Res., 49: 687-693.
- SPRINGER, S. 1960. Natural history of the sandbar
shark *Eulamia milberti*. *Fish. Bull., Fish
Wildl. Ser. US*, 178: 1-38.
- STEVENS, J.D. & K.J. MC LOUGHLIN. 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 angel sharks from southern
Brazil. *J. Fish Biol.*, 50: 86-94.
- TANIUCHI, T. 1971. Reproduction of the sandbar
shark, *Carcharhinus milberti*, in the east
China Sea. *Jpn. J. Ichthyol.*, 18(2): 94-98.
- TESTER, A.L. 1969. Cooperative Shark Research
and Control Program. Final Report 1967-69.
Hawaii, University of Hawaii, 47 pp.
- TORTONESE, E. 1956. Leptocardia, Ciclostoma,
Selaci. In: *Fauna d'Italia*. Bologna: Calderini
(Editor). Bologna, 334 pp.
- WHEELER, J.F.G. 1962. Notes on the three common
species of sharks in the Mauritius-Seychelles
area. *Proc. R. Soc. Arts Sci. Mauritius*, 2(2):
146-160.
- 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.

Received: 23 July 2004

Accepted: 11 February 2005

**Biologija reprodukcije morskog psa, *Carcharhinus plumbeus*
(Chondrichthyes: Carcharhinidae),
u Gabeškom zaljevu (južni Tunis, centralni Mediteran)**

Bécher SAÏDI ¹, Mohamed Nejmeddine BRADAÏ ¹, Abderrahman BOUAÏN ²,
Olivier GUÉLORGET ³ i Christian CAPAPÉ ³

¹ Nacionalni institut znanosti i tehnologije mora, Centar Sfax, P.P. 1035, 3018 Sfax, Tunis

² Fakultet znanosti u Sfaxu, 3018 Sfax, Tunis

³ Laboratorij za ihtiologiju, Sveučilište u Montpellier-u II, Znanosti i tehnika Languedoc-a,
34095 Montpellier, Cedex 05, Francuska

SAŽETAK

Pas trupan šljokrilac, *Carcharhinus plumbeus*, redovito se lovi u Gabeškom zaljevu (južni Tunis). Od 932 primjerka, sabrana od siječnja 2001 do svibnja 2004, najmanji zreli mužjak bio je dug 1545 mm, a najveći 1935 mm. Svi muški primjerci, duži od 1600 mm, bili su spolno zreli. Odrasle ženke bile su duge od 1660 do 2815 mm, od kojih su one preko 1720 mm dužine, bile spolno zrele. Sazrijevanje se odvijalo u proljeće i rano ljeto, s okotom u srpnju. Vrijeme nošenja je procijenjeno na 12 mjeseci. Ženke su se razmnožavale u izmjeničnim godinama. Promjer najvećih oocita (sa žumanjcem) iznosio je 29-32 mm (prosječno 30,3 ±1,2) i mase 9,1-13,3 g (prosječno 11,9 ±1,3). Uterusi su bili pregrađeni u komorice. U svakoj komorici razvijao se samo po jedan embrij. Dužina i težina kod rođenja, bazirane na embrijima približno iste starosti, procijenjene su na 450-650 mm i 532-1458 g. Kemijska ravnoteža razvoja, bazirana na srednjim suhim težinama zrelih oocita i embrijima približno iste starosti, iznosila je 40,3 što znači da je pas trupan šljokrilac, *Carcharhinus plumbeus*, matrotrofna vrsta. Plodnost ovarija bila je nešto veća od fekunditeta uterusa. Dobiven je pozitivan odnos između fekunditeta uterusa i totalne dužine ženki. Broj izleglih mladih bio je 4-10 (srednjak 6,9±1,1). Embriji i slobodno plivajuće odrasle ženke znatno su nadmašivale mužjake.

Ključne riječi: Chondrichthyes, Carcharhinidae, *Carcharhinus plumbeus*, Gabeški zaljev, južni Tunis, centralni Mediteran
