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

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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 (TANICHI, 1971), off Australia (STEVENS & MCLoughlin, 1991), Indian Ocean (WHEELER, 1962), and Red Sea (BARANES & BEN-TUWIA, 1978; BARANES & WENDELING, 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).

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

<table>
<thead>
<tr>
<th>Gear</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trawl</td>
<td>136</td>
<td>165</td>
<td>301</td>
</tr>
<tr>
<td>Gill-net</td>
<td>80</td>
<td>254</td>
<td>334</td>
</tr>
<tr>
<td>Longline</td>
<td>120</td>
<td>177</td>
<td>297</td>
</tr>
<tr>
<td>Total</td>
<td>336</td>
<td>596</td>
<td>932</td>
</tr>
</tbody>
</table>

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
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 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 & WRIZEZ (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](image-url)
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 to...
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 vitellogenic 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 vitellogenic activity was noticed. Near-term females were collected in May-July (Table 3, records 9, 16 and 17) and a postpartum female was collected in August (Table 3, record 18). The uteri of pregnant females were compartmentalized into chambers and a

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

<table>
<thead>
<tr>
<th>Number of record</th>
<th>Month of catch</th>
<th>Size of female (TL, mm)</th>
<th>Ovarian activity</th>
<th>Oocytes diameter (mm)</th>
<th>Oocytes number</th>
<th>Uterine content</th>
<th>Embryos size (TL, mm)</th>
<th>Embryos mass (gramme)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Mar. 1910</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>450-560</td>
<td>500-695</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Mar. 1970</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>492-580</td>
<td>530-840</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Mar. 1990</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>480-575</td>
<td>520-750</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Apr. 1930</td>
<td>Vitellogenesis</td>
<td>22-26</td>
<td>16</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Apr. 2030</td>
<td>Vitellogenesis</td>
<td>29.5-32</td>
<td>11</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Apr. 1795</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>440-495</td>
<td>490-580</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>May 1720</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>425-480</td>
<td>400-485</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>May 1775</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>350-362</td>
<td>480-485</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>May 1895</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>535-605</td>
<td>810-985</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>May 1790</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>455-520</td>
<td>545-835</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>May 1980</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>535-605</td>
<td>810-985</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>May 2000</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>525-595</td>
<td>790-1025</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>May 2100</td>
<td>Resting</td>
<td>2-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>510-555</td>
<td>760-790</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>May 1995</td>
<td>Vitellogenesis</td>
<td>29-32</td>
<td>12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Jun. 1770</td>
<td>Resting</td>
<td>1-3</td>
<td>numerous</td>
<td>Embryos</td>
<td>455-480</td>
<td>540-790</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>Jun. 1800</td>
<td>Resting</td>
<td>3-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>535-565</td>
<td>810-1050</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>Jul. 1890</td>
<td>Resting</td>
<td>3-4</td>
<td>numerous</td>
<td>Embryos</td>
<td>570-625</td>
<td>990-1290</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>Aug. 2040</td>
<td>Resting</td>
<td>3-5</td>
<td>numerous</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
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 ± 11.1) and their mass between 391 and 1458 g (mean: 881.7 ± 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 ± 10.5), their mass between 851 and 1660 g (mean: 1264 g ± 115.7). The males TL ranged between 450 and 650 mm (mean: 600.0 mm ± 13.2) and their mass between 400 and 1740 mm (mean: 1237.1 g ± 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±3.8) in four females ranging 1700-2030 mm TL. Uterine fecundity (4-10; mean 6.9±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).

![Image](image_url)

*Fig. 4. Total mass (TM) vs total length (TL) expressed in logarithmic co-ordinates for male and female Carcharhinus plumbeus*
### 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 & AFFRONTE, 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-CHAPULÍ, 1984).

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

<table>
<thead>
<tr>
<th>Category</th>
<th>Males</th>
<th>Females</th>
<th>Females: Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uterine content</td>
<td>Embryos</td>
<td>36</td>
<td>60</td>
</tr>
<tr>
<td>Free-swimming specimens</td>
<td>Juveniles</td>
<td>307</td>
<td>418</td>
</tr>
<tr>
<td></td>
<td>Sub-adults</td>
<td>17</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>12</td>
<td>168</td>
</tr>
<tr>
<td>Total free-swimming</td>
<td></td>
<td>336</td>
<td>596</td>
</tr>
<tr>
<td>specimens</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>General total</td>
<td></td>
<td>374</td>
<td>656</td>
</tr>
</tbody>
</table>

**Fig. 5. Relationship between litter size and total length (TL) in Carcharhinus plumbeus**
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>
<thead>
<tr>
<th>Size at sexual maturity (mm)</th>
<th>Maximal size (mm)</th>
<th>Area</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males Females</td>
<td>Males Females</td>
<td>Western Atlantic</td>
<td>BIGELOW and SCHROEDER (1948)</td>
</tr>
<tr>
<td>1800</td>
<td>2500</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1830</td>
<td>1830</td>
<td>2260</td>
<td>2300</td>
</tr>
<tr>
<td>1800</td>
<td>1770</td>
<td>2130</td>
<td>2200</td>
</tr>
<tr>
<td>1920</td>
<td>1850</td>
<td>2040</td>
<td>2340</td>
</tr>
<tr>
<td>1900</td>
<td>1900</td>
<td>1900</td>
<td>Italian waters</td>
</tr>
<tr>
<td>1630</td>
<td>1900</td>
<td>2260</td>
<td>2470</td>
</tr>
<tr>
<td>1760</td>
<td>1760</td>
<td>1760</td>
<td>Red Sea</td>
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<tr>
<td>1840</td>
<td>1890</td>
<td>1900</td>
<td>2030</td>
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<tr>
<td>1800</td>
<td>1850</td>
<td>2230</td>
<td>2290</td>
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<tr>
<td>1660</td>
<td>1700</td>
<td>2250</td>
<td>2480</td>
</tr>
<tr>
<td>1560</td>
<td>1580</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1545-1600</td>
<td>1660-1720</td>
<td>1935</td>
<td>2185</td>
</tr>
</tbody>
</table>
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 &

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

Table 6. Size at birth of Carcharhinus plumbeus reported from different areas
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; HAMLET 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 Gabés.

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

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**SAŽETAK**

Pas trupan šiljokrilac, *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 šiljokrilac, *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