Reproductive Biology of the Silky Shark *Carcharhinus falciformis* (Chondrichthyes: Carcharhinidae) off the west coast of Baja California Sur, Mexico

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Abstract

The silky shark *Carcharhinus falciformis* population has declined drastically in the last few years, due to extensive by-catch in tuna purse-seine and longline fisheries in the eastern Pacific Ocean. No information exists on the reproductive biology of this species in the eastern Pacific Ocean to support fishery or conservation management. A total of 295 silky sharks were analyzed, with 179 females captured, ranging between 88 and 316 cm TL and 116 males, ranging between 142 and 260 cm TL. The sex ratio of females to males was 1: 0.6. The increase in of oocytes instead of ovarian egg and oviducal gland diameters as well as the presence of uterine eggs or developing embryos indicated that female maturation occurred at about 180 cm TL; while clasper development and the presence of sperm clumps indicated that males matured at about 182 cm TL. The short-term sperm storage found in females could be an advantage for species that present sexual segregation and live in open waters, increasing reproductive efficiency. In the 20 gravid females examined, the average number of embryos per female was five, with a range of 2-9 embryos. Females with embryos 6-8 cm TL were observed in July and September; whereas embryos 20-30 cm TL were found from September to November. One female with full term embryos (80 cm) was captured at the end of June suggesting an 11-12 month gestation period.

Zusammenfassung

Die Bestände des Glatthais *Carcharhinus falciformis* sind in den letzten Jahren drastisch zurückgegangen, verursacht durch die Tunfischerei mit Ringwadennetzen und Langleinen im östlichen Pazifischen Ozean, bei der Glatthaie als Beifang in die Netze geraten. Über die Fortpflanzungsbiologie dieser Art im östlichen Pazifik gibt es bisher keine Informationen, mit denen Fischereimanagement oder Schutzmaßnahmen unterstützt werden könnten. Insgesamt wurden 295 Glatthaie analysiert; 179 der gefangenen Tiere waren Weibchen zwischen 88 und 316 cm Gesamtlänge (TL), 116 Männchen zwischen 142 und 260 cm TL. Das Geschlechterverhältnis zwischen Weibchen und Männchen betrug 1:0,6. Nimmt man die Zunahme des Durchmessers der Eier in den Eierstöcken und der Eileiterdrüsen sowie das Vorhandensein von Eiern im Uterus oder die Entwicklung von Embryos zum Maßstab, muss man zu dem Schluss kommen, dass die Geschlechtsreife der Weibchen bei einer Länge von 180 cm TL eintritt; Männchen werden bei 182 cm TL geschlechtsreif, gemessen an der Entwicklung des Klammerorgans und der Anwesenheit von Samenklumpen. Die kurzzeitige Speicherung von Samen, wie man sie bei Weibchen feststellen konnte, dürfte bei Arten, bei denen die Geschlechter getrennt und im freien Wasser leben, von Vorteil sein, sie steigert den Fortpflanzungserfolg. Bei den 20 untersuchten trächtigen Weibchen fanden sich zwei bis neun, durchschnittlich fünf Embryos. Weibchen mit 6-8 cm TL großen Embryos konnten im Juli und September festgestellt werden, während 20-30 cm TL lange Embryos zwischen September und November vorkamen. Ein Weibchen mit voll entwickelten Embryos (80 cm) konnte Ende Juni gefangen werden, was auf eine Trächtigkeitsdauer von 11-12 Monaten schließen lässt.

Résumé

La population du *Carcharinus falciformis* a drastiquement diminué ces dernières années à cause de la capture involontaire en sennes à thons et de la pêche à longue ligne dans le Pacifique est. On ne dispose pas d'informations sur la biologie reproductive de cette espèce dans le Pacifique est pour assister la pêche oula préservation. Un total de 295 individus ont été examinés : 179 femelles, de 88 à 316 cm de LT, et 116 mâles, de 142 à 260 cm de LT. Le sex ratio des femelles par rapport aux mâles était de 1:0,6. L'augmentation du diamètre de l'œuf ovarien et de la glande de l'oviducte, ainsi que la présence d'œufs utérins ou d'embryons en développement ont indiqué que la maturité de la femelle se produisait à environ 180 cm de LT ; d'autre part, le développement du ptérygopode et la présence de paquets de sperme montrent que les mâles sont mûrs à près de 182 cm de LT. Le stockage de courte durée de sperme trouvé chez des femelles pourrait être un avantage pour des

espèces qui pratiquent une ségrégation sexuelle et vivent en eau libre, en augmentant l'efficacité reproductive. Pour les 20 femelles pleines examinées, le nombre moyen d'embryons par femelle était de cinq, dans une fourchette de 2-9 embryons. Des femelles avec de embryons de 20-30 cm de LT on été trouvées de septembre à novembre. Une femelles porteuse d'embryons arrivés à terme (80 cm) a été capturée fin juin, ce qui suppose une gestation de 11-12 mois.

Sommario

Negli ultimi anni le popolazioni di squalo seta *Carcharhinus falciformis* del Pacifico orientale si sono ridotte drasticamente a causa delle numerose catture accidentali con reti a circuizione e con palamito. Non esistono dati sulla biologia riproduttiva di questo squalo nell'oceano Pacifico orientale tali da sostenere politiche di controllo della pesca o di conservazione della specie. Complessivamente sono stati analizzati 295 esemplari di squalo seta, 179 femmine di taglia compresa tra gli 88 e i 316 cm TL e 116 maschi di taglia compresa tra i 142 e i 260 cm TL. Il rapporto femmine: maschi era di 1: 0.6. L'incremento del diametro delle uova e delle ghiandole dell'ovidotto e la presenza di uova uterine o embrioni in fase di sviluppo indicano che la femmina raggiunge la maturazione a circa 180 cm TL; lo sviluppo dello pterigopodio e la presenza di masse di sperma indicano che il maschio matura a circa 182 cm TL. Il mantenimento dello sperma solo per brevi periodi nella femmina potrebbe essere un vantaggio per la specie che mostra segregazione dei sessi e abita acque aperte, incrementando l'efficienza riproduttiva. Nelle 20 femmine gravide esaminate il numero medio di embrioni per femmina era pari a cinque, con un intervallo di 2-9 embrioni. Femmine con embrioni di 6-8 cm TL erano osservate in luglio e settembre, mentre embrioni di 20-30 cm TL erano rinvenuti da settembre a novembre. Una femmina con embrioni allo stadio finale (80 cm) è stata catturata alla fine di giugno suggerendo un periodo di gestazione di 11-12 mesi.

INTRODUCTION

The silky shark, *Carcharhinus falciformis*, is a cosmopolitan species found throughout tropical and subtropical waters. In the eastern Pacific it ranges from southern Baja California to Peru. It is an abundant offshore oceanic and epipelagic tropical shark. It occasionally occurs inshore where the water is as shallow as 18 m; in the open ocean it occurs from the surface down to at least 500 m depth. Water temperatures of 23° to 24° C have been recorded where it occurs (Compagno 1984). In the eastern Pacific Ocean the silky shark is captured by longline and occasionally with gillnets (Au 1991), and makes up to 30% of all captured sharks; however, this species has declined drastically in recent years, due to by-catch from tuna purse-seiners in the eastern Pacific Ocean (Watson 2008). This species is common in the pelagic longline fisheries, but is also taken in gill nets off the west coast of Mexico, representing one of the ten most important shark species in captures from Mexican Pacific waters (Castillo-Geniz et al. 2010). Despite its high abundance abundance in the region, there are few data concerning *C. falciformis*' biology and studies focused on its reproductive biology are necessary to design and implement strategies for the regulation of its fishery.

Some published information exists on reproduction of this species, limited to the studies of Gilbert & Schlernitzauer (1965, 1966), Branstetter (1987) and Bonfil et al. (1993). The only study done on *C. falciformis* in Mexican waters is that of Bonfil et al. (1993); however, the information is from the Mexican Atlantic Ocean. Silky shark biology from this area has been briefly discussed in a bachelor's thesis (Cadena 2001). The aim of the present study is to determine the reproductive parameters and morphology of the reproductive tract and sperm storage of both sexes in *C. falciformis* from the eastern Pacific Ocean. These data would allow the stock assessment of species harvested by fisheries and the ecological risk assessment of species caught as bycatch (Walker 2004).

MATERIALS AND METHODS

From 2000 to 2002, silky sharks were obtained from commercial catches off Punta Lobos and Punta Belcher (Fig. 1), the two major shark fishing camps in Baja California Sur, Mexico. Specimens from Punta Lobos were caught by longlines while in Punta Belcher they were caught with gill nets. Total length was measured (Compagno 1984). Clasper length was measured from the insertion of the inner corner of the pelvic fin to its distal tip. The meager information available for shark species and critical examination of recently acquired specimens demonstrates that, even though there are shared reproductive characters throughout the orders, there are also differences in the reproductive biology between the various genera and species (Castro 1996). Males were considered mature when claspers were completely calcified and the riphiodon could be spread open (Springer 1960; Clark & von Schmidt 1965). Females were considered mature when they had at least one of the following characteristics: gravidity, ripe ovarian eggs, oviducal gland width over 20 mm in diameter, or a well-developed uterus. Most of the time checking for uterine scars in the uterus was undertaken for most of the females, to avoid taking into account

aborted females; sometimes fishermen allowed us to take samples just while they are preparing the sharks for transportation, so in a few cases it was impossible to be sure of the presence of these scars. Additionally, maturity was corroborated in males by the presence of sperm clumps in the seminal vesicle (Pratt & Tanaka 1994); whereas in females it was corroborated by the presence of sperm in the oviducal gland. The reproductive system was removed and fixed in buffered 10% formalin. Sections 5-6 μm thick were prepared using the conventional histological process with haematoxylin-eosin stain (Castro & Wourms 1993) to analyze the gonads under the microscope.

RESULTS

Seasonal abundance, sex ratio and size

Silky sharks are seasonal in commercial catches of the west coast of Baja California Sur from June to November (summer and autumn), with a maximum frequency in September. A total of 179 females and 116 males were examined. The sex ratio was 1F:0.6M. The range in total length for females was 88-316 cm (average 180 cm TL), and for males the range was 142-260 cm TL (average 182 cm TL). Specimens 176 to 225 cm TL comprised 76% of the total captures.

Morphological and histological analysis: males

The testes in the silky shark are almost totally surrounded by the epigonal organ except in the distal region. They are paired, elongated and dorsoventrally flattened organs (Fig. 2), which are attached to the dorsal wall of the abdominal cavity by a mesorchium. Depending on the size of the adult, the testes range from 17 to 33.5 cm in length. Seminiferous follicle development spreads from a germinal zone across the diameter of the testicles to the opposite wall, where the efferent ductules form a manifold collection system to receive spermatozoa (Fig. 3). The efferent ductules continue in a series of fine tubules and communicate with the head of the epididymis.

The epididymides are convoluted, unpigmented and digitiform (Fig. 2). In adults, each epididymis

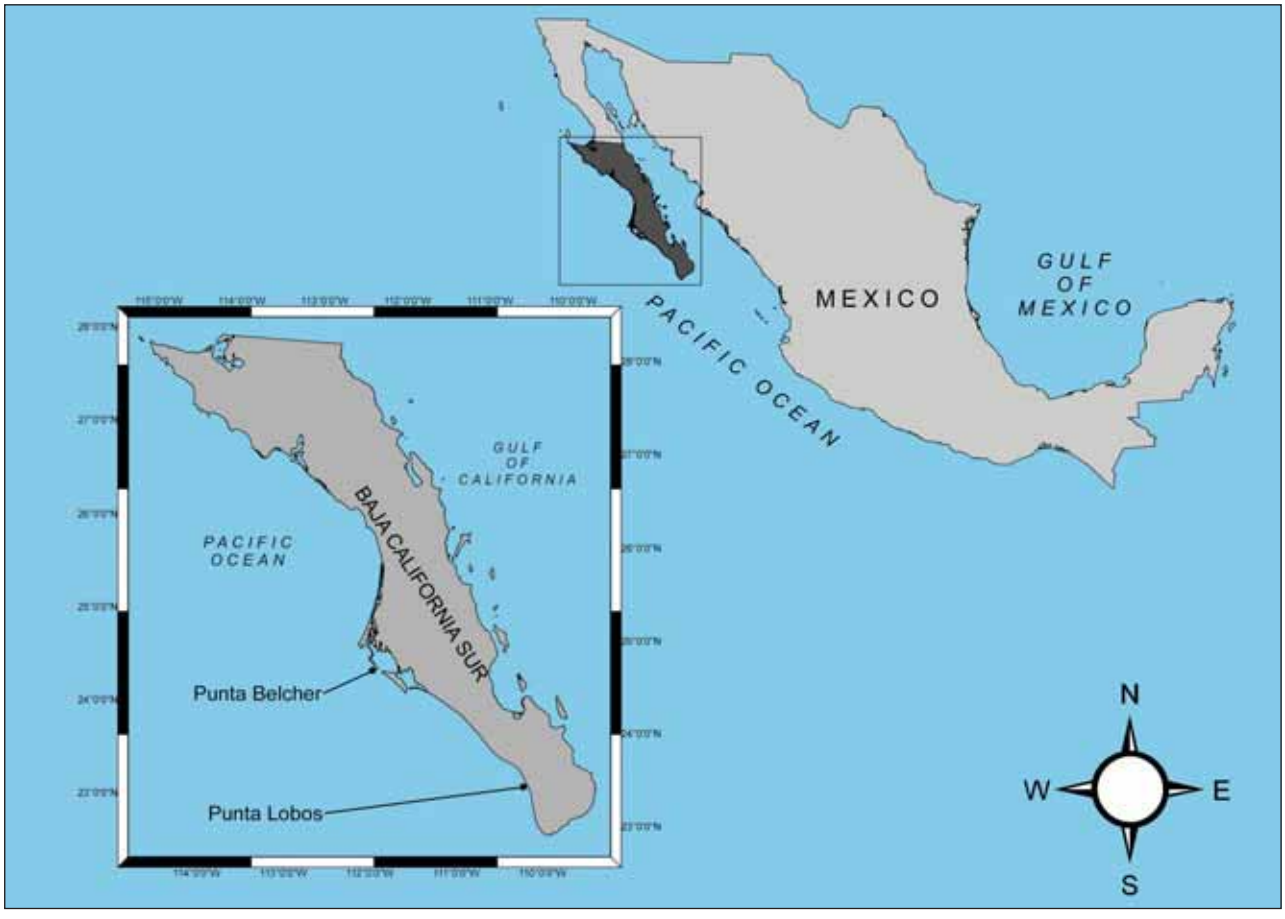

Fig. 1. Location of the fishing camps Punta Belcher and Punta Lobos in the west coast of Baja California Sur, Mexico.

is approximately 25 cm long and 2 cm wide. The tubules of this organ are divided in two types: Leydig glands and epididymis tubules. The epithelium

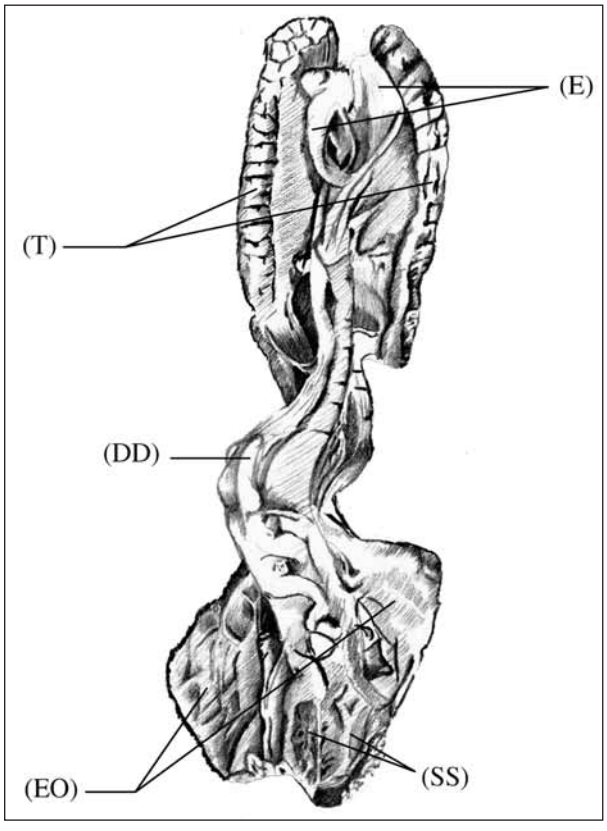

Fig. 2. Male reproductive system. Epididymis (E), testis (T), deferens ducts (DD), epigonal organ (EO) and sperm sacs (SS).

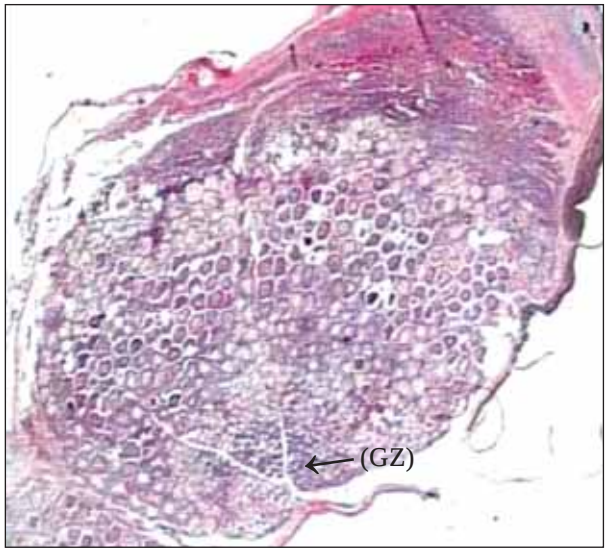

Fig. 3. Cross section of the testis showing the diametric development of follicles. Germinal zone (GZ).

of the Leydig gland has two kinds of cells: ciliated and secretory (Fig. 4a). The epididymis tubule has a pseudostratified columnar epithelium with cilia and individual spermatozoa scattered in the lumen (Fig. 4b). In addition to sperm, three types of particulate matter occur in the lumen of the ducts: Sertoli cell bodies, Sertoli cytoplasts, and Leydig gland bodies. The role of these components in sperm aggregation or maintenance is unknown (Hamlett 1999). Towards the terminal end of the epididymis the ductus deferens are formed (Fig. 2). In *C. falciformis*, organized masses of naked sperm bound with a cohesive matrix forming ovoid to sub-spherical masses were found in the seminal vesicle (Fig. 2). These ovoid sperm aggregates (96 to 310 μm) were found as a single layer of radially aligned sperm clumps organized around a core of eosinophilic material (Fig. 5) known as single layer spermatozeugmata (Pratt & Tanaka 1994).

Morphological and histological analysis: females

In *C. falciformis*, only the right ovary is functional, as in most carcharhinids (Pratt 1988). It is located at the distal surface of the epigonal organ, at the forward end of the abdominal cavity (Fig. 6), and attaches to the dorsal wall of the abdominal cavity by a mesovarium. The ovary in adults ranged from 9 to 25 cm long and from 2.6 cm to 9.6 cm wide. Ovulating females carried 8-11 oocytes 30-35 mm in diameter. The silky shark ovary contained corpora atretica in various stages of development. In 86 ovaries, we found these structures to range from 4-34 mm in diameter. Post-ovulatory follicles (corpora lutea) from 6 to 33 mm were found in the ovaries of pregnant females. The relative development of the corpora lutea and corpora atretica and their function remains unknown (Dodd 1983). The paired oviducts are slender segments, which emerge from the peritoneal cavity by an ostium in the falciform ligament (Fig. 6). The upper portion of each oviduct is narrow and short, and leads into the oviducal gland. This gland is heart-shaped, from 13 to 50 mm in diameter. Externally, each gland resembles a symmetrical white organ with two horns on the lateral anterior surface (Fig. 6). Sperm storage was found in only one of 50 glands of analyzed mature females. The spermatozoa were located in the thin-walled tubules of the oviducal gland around the curves of the lumen. The tubules are formed by two different types of cells, secretory and ciliated. The sperm was loosely packed in tubules with well-stained heads up current (Fig.7).

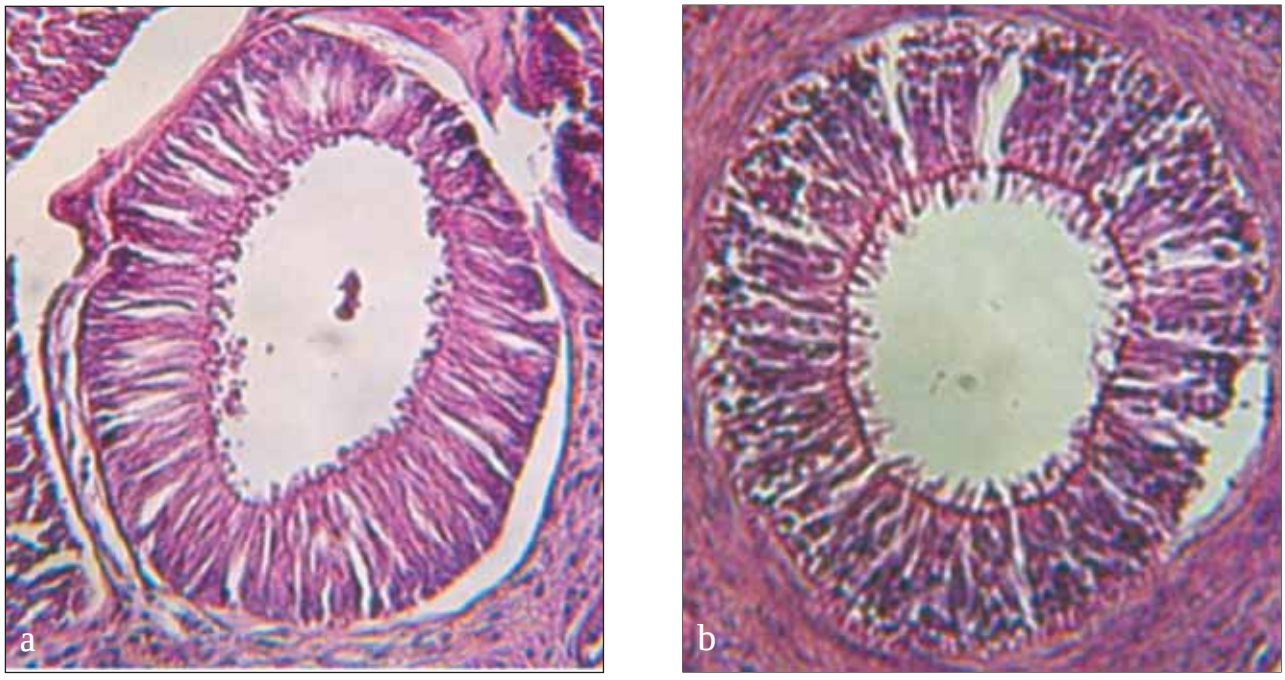

Figure 4a-b. Micrographs of Leydig gland (a) and epididymis tubule (b).

The uterus is divided in two parts, one of which is designated as the third membrane store chamber. In the oviducal gland, the fertilized egg is enclosed in a membrane; it then passes through the third membrane store chamber and enters the uterus. The third membrane remains around the embryo until it reaches birth size. The uterus size increases with the size of the developing embryo. In females with uterine eggs, the uterus is 20-22 cm long; in females with small embryos (6-8 cm TL), the uterus is 33-34 cm long; and in term females (80 cm embryos), the uterus reaches almost 50 cm long and a width of about 15 cm.

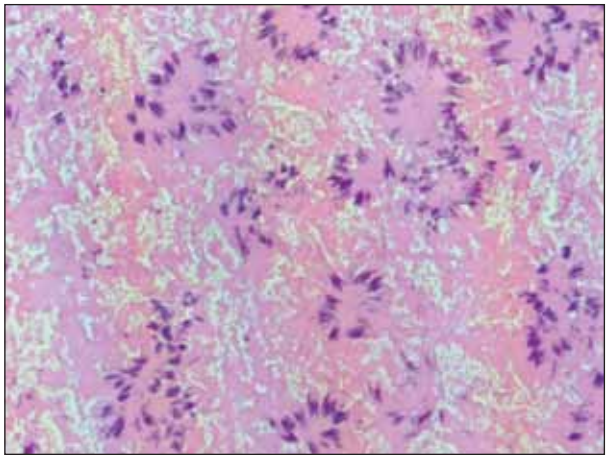

Fig. 5. Micrographs showing the sperm clump in males.

Size at maturity

Males: Development of the testis is gradual; at about 180 cm TL it can reach a length of 25 cm (Fig. 8). Sharks with uncalcified claspers had testes in early stages of spermatogenesis and a small amount of sperm present in the lower epididymis. The claspers begin to elongate at about 160 cm TL and become calcified at 179 cm TL. All specimens larger than 181 cm TL were mature, with sperm aggregates present in the seminal vesicle (Fig. 9). The size at maturity L_{50} (with 95% CI) in males occurred at 182 (180-182) cm TL.

Females: The size of the oviducal gland started to increase when females reached 180 cm TL (Fig. 10). In juveniles under 170 cm TL the gland measured 5-10 mm in width; whereas in females 180 cm TL it measured 20-40 mm in width. Immature females had undeveloped oocytes 6-10 mm in maximum diameter. The oocytes did not start growing until the females reached 180 cm TL (Fig. 11). The size at maturity L_{50} (with 95% CI) in females occurred at 180 (179-180) cm TL. Larger females were also seen to be carrying ripe oocytes 20-43 mm in diameter. The presence of ovulatory females with mating bites on their bodies or with sperm in their uteri was very sporadic. Only two recently inseminated females were caught during our study, on 31 August 2001 and 31 July 2002. One of them had oocytes 32 mm in diameter.

Another female caught on 24 November 2000 bore mating scars and oocytes 35 mm in diameter. In our sample of 20 gravid females, the average number of embryos per female was five, with a range of 2-9 embryos. Ovulating females with uterine eggs and embryos 6-8 cm TL were observed in July and September, whereas embryos 20-30 cm TL were found from September to November. Only one female with full term embryos (80 cm) was captured at the end of June.

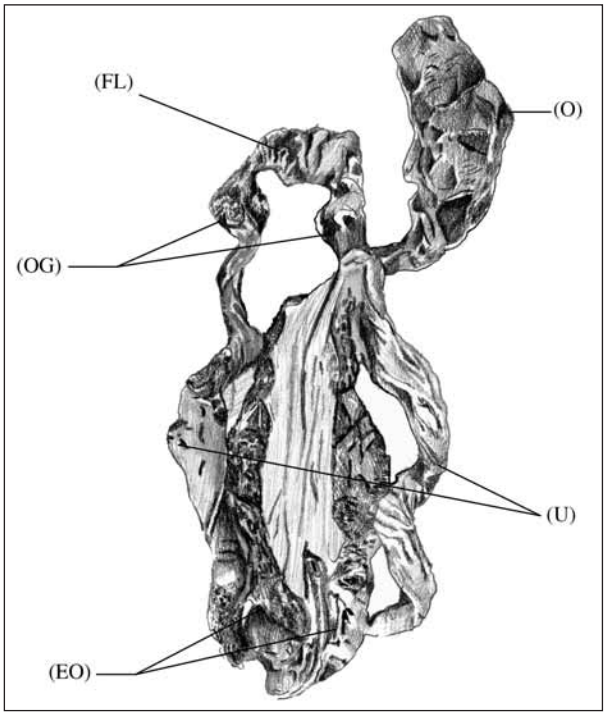

Fig. 6. Female reproductive system. Ovary (O), oviducal gland (OG), uterus (U), and epigonal organ (EO).

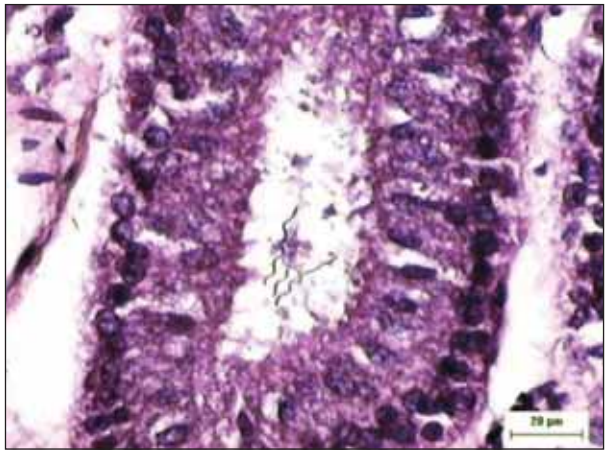

Fig. 7. Micrographs showing the sperm storage in the oviducal gland.

DISCUSSION

Carcharhinus falciformis begins its northward migration in June. The schools stay off the west coast of Baja California Sur from June to October, arriving off Punta Belcher and Punta Lobos in August, although most of the adults arrive in September and October (Fig. 12). The timing of the *C. falciformis* captures was consistent with changes in the surface water temperature. Gómez & Vélez (1982) recorded that the water temperature of the California current increases to 20°C to 25°C in summer. *Carcharhinus falciformis* leave the west coast of Baja California Sur in early fall and migrate southward when the sea surface water temperature decreases below 20°C. It is known that the increase in water temperature influences the migrations of other carcharhinids such as *C. isodon* and *C. limbatus* off the east coast of the U.S.A. (Castro 1993, 1996). Most of the *C. falciformis* examined along the west coast of Baja California Sur were large specimens (176-225 cm TL). Cadena (2001) found similar sized sharks (170-220 cm TL) in the Gulf of California. Juveniles of *C. falciformis* have been recorded in coastal waters of south-west Mexico. Chong-Robles (2003) found gravid females carrying term embryos and neonates (50-83 cm TL) in March and May off the Oaxaca, Mexico, coast; whereas Ronquillo (1999) found gravid females in Chiapas, Mexico, during June. It appears that *C. falciformis* use the coastal waters of south-west Mexico as nursery grounds and migrate to the north in the summer to feed and possibly to copulate. Villatorio & Rivera (1994) reported a 1F:1M sex ratio. Del Rosario (1998) and Ronquillo (1999) reported the same ratio for Guatemala and Chiapas respectively. Bonfil et al. (1993) suggested a 1F:1M ratio for *C. falciformis* in nature. Their results differ from our findings (1F:0.6M), although those studies correspond to annual samplings and the presence of *C. falciformis* off the western coast of Baja California Sur is seasonal, occurring from July to October.

Maturation in males is reached at about 182 cm TL and it involves the gradual development of the testes, the calcification of the claspers and the presence of sperm aggregates in the seminal vesicle. The testes development (diametric) and spermatogenesis in *C. falciformis* are similar to those found in the catshark *Scyliorhinus canicula* (Dodd 1983). According to Hamlett (1999), in all elasmobranchs thus far examined the fundamental details of seminiferous follicle development and spermatogenesis are similar. The sperm clumps found in *C. falci-*

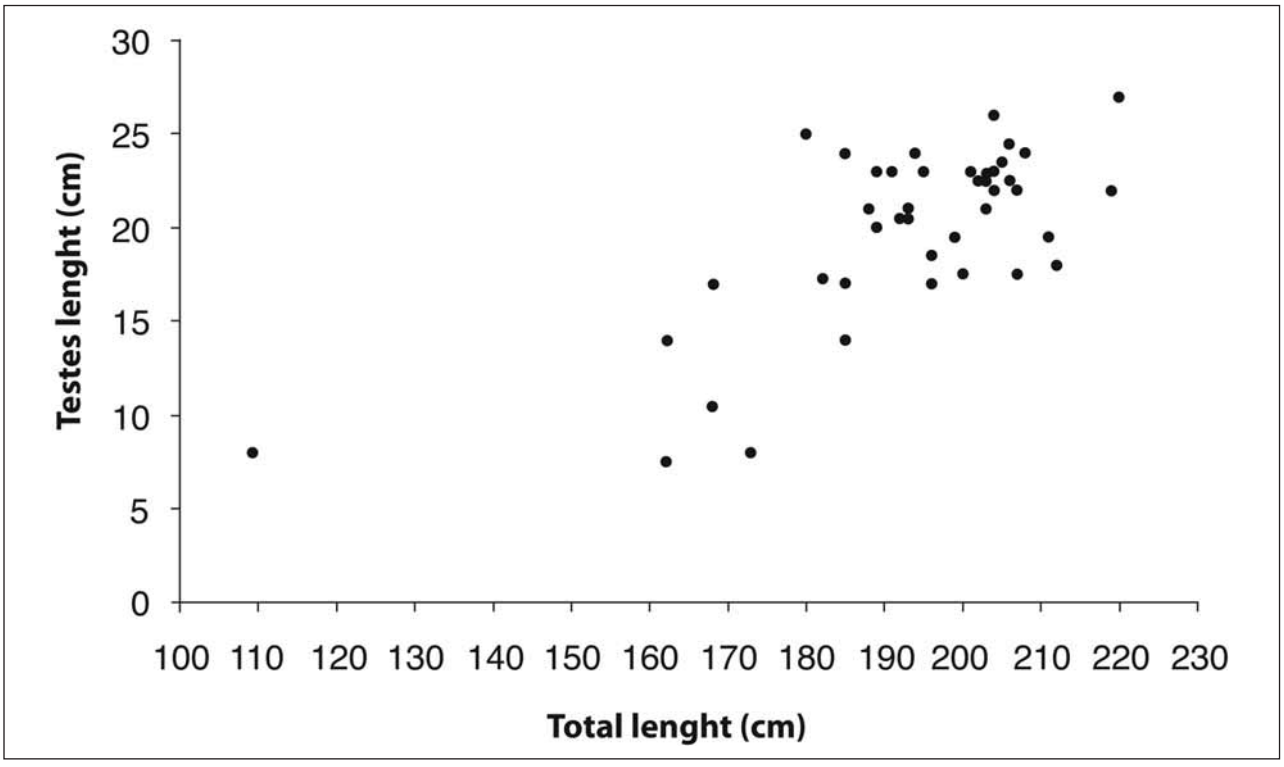

Fig. 8. Total length versus testes length.

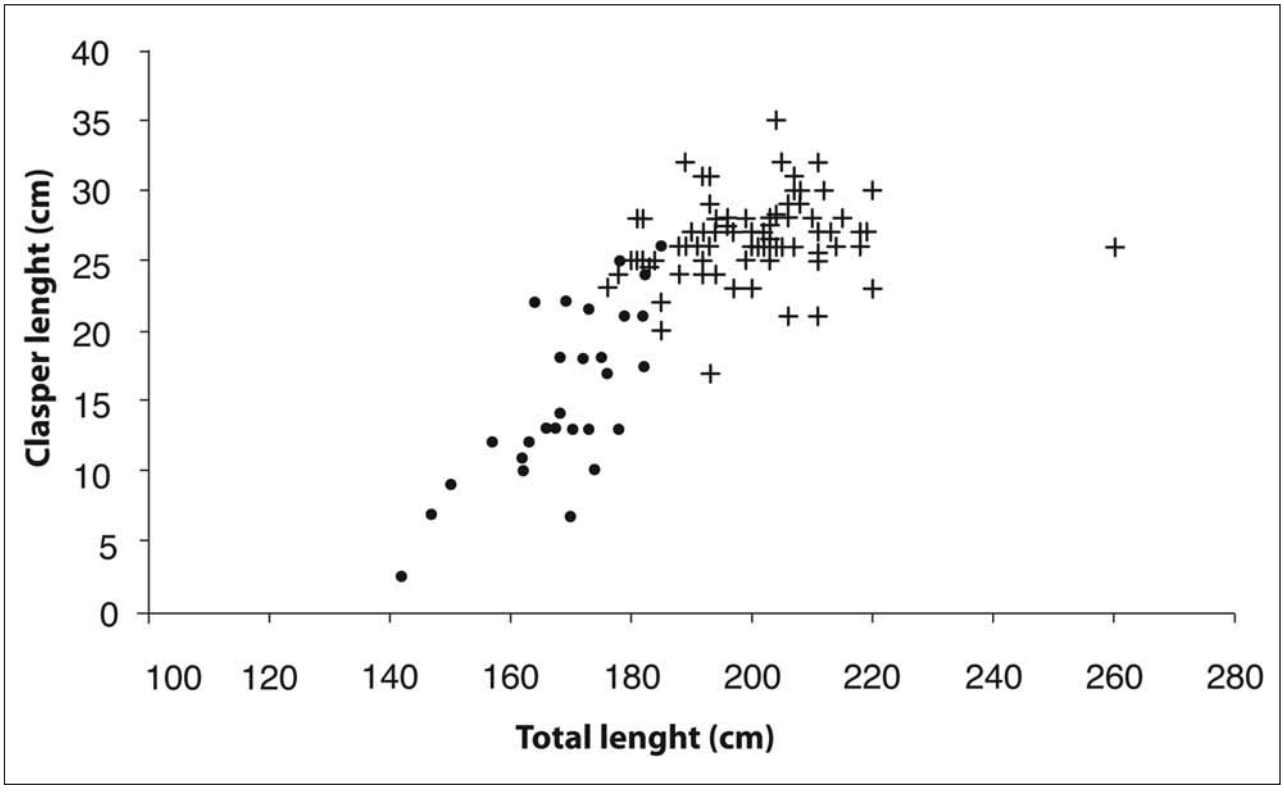

Fig. 9. Total length versus clasper length and degree of calcification. The cross corresponds to the males with fully calcified claspers and spermatozeugmata in the seminal vesicle.

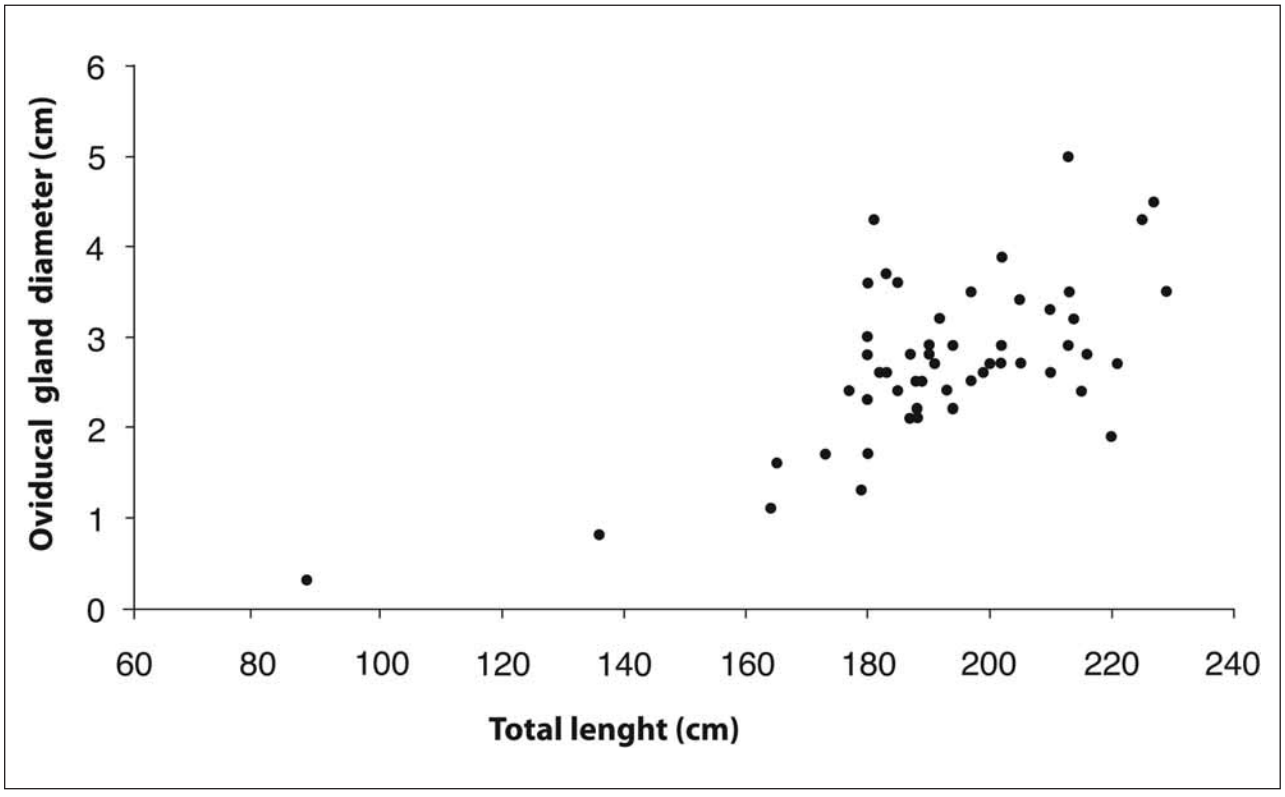

Fig. 10. Total length versus oviducal gland length.

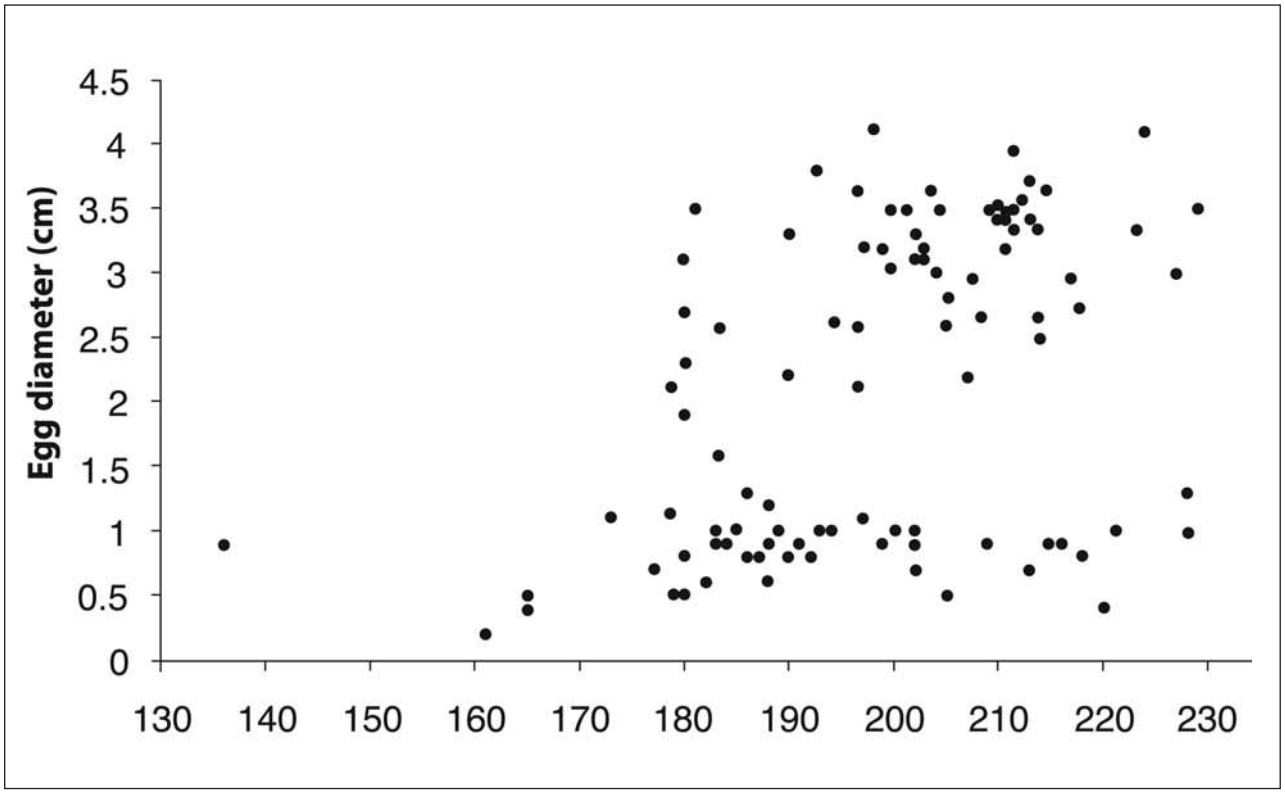

Fig. 11. Total length versus egg diameter.

Table I. Size at maturity of silky shark *Carcharhinus falciformis* in different parts of the world.

Author and year	Region	Size at maturity TL (cm)
Strasburg (1958)	Central Pacific	♀213-216
	INDIAN OCEAN	
Fourmanoir (1961)	Madagascar	♀248-269 ♂240
Stevens (1984)	Aldabra Atoll	♀216 ♂239
	SOUTH PACIFIC	
Stevens (1984)	Tasman Sea	♀202-208 ♂214
	EAST PACIFIC	
Bonfil et al. (1993)	Campeche Bank	♀232-246 ♂225
Del Rosario (1998)	Pacific coast of Guatemala	♀176 ♂178
Ronquillo (1999)	Gulf of Tehuantepec, Mexico	♀180
Cadena (2001)	Gulf of California, Mexico	♀180 ♂180
Present study	West Coast of Baja California Sur, Mexico	♀180 ♂182

formis (single layered spermatozeugmata), have been found in other carcharhinids like the black tip shark *Carcharhinus limbatus* and the sandbar shark *Carcharhinus plumbeus* (Pratt & Tanaka 1994). We confirmed that the presence of sperm aggregates is a more reliable indicator of maturity than clasper condition because the presence of sperm aggregates ensures that if the shark copulates there is a better probability of fecundation. We acknowledge that the use of the clasper calcification criterion instead of the presence of sperm aggregates is more practical and economical (but the sperm aggregation method is more accurate by far).

Maturation in females is reached at about 180 cm TL and is marked by the growth of the oviducal gland, enlargement of the uteri and the ripening of the oocytes. This size at maturity corresponds with the sizes recorded for *C. falciformis* in the Mexican Pacific and Guatemala (Del Rosario 1998; Ronquillo 1999; Cadena 2001). Although *C. falciformis* is considered a circumtropical species (Castro 1983), the size at maturity is different in different areas (Table I). Fourmanoir (1961) found for Madagascar that males mature at about 240 cm TL and females at about 248-269 cm TL. At Aldabra Atoll, Indian Ocean, Stevens (1984) found that males mature at about 239 cm TL and females at about 216 cm TL. In the Pacific Ocean, Strasburg (1958) recorded 12 pregnant females of 213-236 cm TL and Stevens (1984) recorded mature males at 214 cm TL and females at 202-208 cm TL for the Tasman Sea. A possible explanation in relation to differences in the maturity size is that individuals from the eastern Pacific Ocean are smaller than those from the Indian Ocean. This has been recorded for other carcharhinids like the black tip shark, *C. limbatus*. Castro (1996) stated that *C. limbatus* in the western North Atlantic differs significantly in numerous traits such as size, markings, age at maturity, brood size and other characters from the Pacific specimens.

We observed the absence of a defined seasonality for *C. falciformis* reproduction off the west coast of Baja California Sur. The sperm found inside one oviducal gland belonged to a pregnant female with intrauterine eggs. The arrangement of the sperm inside the tubules coincides with the "short-term sperm storage" classification defined by Pratt (1993) and is found in sharks in which ovulation is prolonged over several weeks. Sperm storage is an advantage for species that presents sexual segregation and lives in open waters, increasing the efficiency in reproduction. Strasburg (1958) stated that the brood size of *C. falciformis* was two to eleven embryos. Gilbert & Schlenitzauer (1966) report one female with nine embryos in the Atlantic Ocean. Cadena (2001) gave a range of 1-12 young for specimens seen off the Gulf of California. In the 20 gravid females recorded in our study, the average number of embryos per female was five, with a range of 2-9 embryos. Unfortunately characteristics such as low fecundity and a late age of sexual maturation, leave species like *C. falciformis* vulnerable to overexploitation.

Fig. 12. Silky shark, caught by artisanal fishermen, Punta Lobos, Baja California Sur, México. Photo by M. Carrera.

ACKNOWLEDGEMENTS

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