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Reproduction and Development of the Pacific Angel Shark, *Squatina californica*, off Santa Barbara, California

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Specimens of *Squatina californica* were collected from commercial gill-net boats off Santa Barbara, California, from Jan.–Nov. 1983 for studies of reproduction. Sexual maturity in both males and females began between 900 and 1000 mm TL. Fecundity estimates from egg and embryo numbers ranged between 1 and 11. The number of young did not increase with increasing size of the female after maturity. Reproduction in the angel shark appears to follow an annual cycle. Embryo size from samples of pregnant females taken in eight months increased gradually for the 12 months between Aug. and July. Pupping occurred in spring and each female had an average of six pups. Growth rates ranged from 45 mm TL per month in very young embryos to 10 mm TL per month in those approaching the size at birth and the overall mean growth rate was 23 mm TL per month. Individual developmental morphology is described for five embryos ranging in size from 35.4–175 mm TL.

THE Pacific angel shark, *Squatina californica*, is a temperate water species that is found primarily in depths between 3–46 m (Miller and Lea, 1972; Eschmeyer et al., 1983; Compagno, 1984). The species ranges from southeastern Alaska to Baja and the Gulf of California and perhaps also from Peru to south Chile (Kato et al., 1967; Eschmeyer et al., 1983; Compagno, 1984). A fishery for the angel shark was initiated in 1976 off Santa Barbara, California. It has since expanded rapidly and the angel shark dressed weight landings have ranged from 329 lbs in 1977 to 328,513 lbs in 1983 and 610,281 lbs in 1984 (John Richards, California Sea Grant Program and John Sunada, California Department of Fish and Game, pers. com.).

Holden (1974, 1977) hypothesized that elasmobranchs have a late age at first reproduction, low fecundities, a long gestation period and slow growth rates. These factors should combine to make elasmobranchs highly susceptible to overfishing. Due to the recent increase in fishing pressure on the angel shark, it has become important to learn more about the biology of this species to determine if its life-history characteristics follow Holden's (1974, 1977) generalizations.

The Pacific angel shark reportedly attains a maximum total length (TL) of 1524 mm and a weight of 27 kg (Beebe and Tee Van, 1941; Miller and Lea, 1972; Compagno, 1984). Reproduction is ovoviviparous (Bigelow and Schroeder, 1948; Compagno, 1984), but little other information on the reproduction and development of the Pacific angel shark is available.

The purpose of this study was to obtain information on the reproduction and development of the Pacific angel shark by examining periodic samples of reproductively mature individuals over a one year period.

MATERIALS AND METHODS

Specimens of angel sharks were collected off Santa Barbara, California between Gaviota and Ventura from Jan.–Nov. 1983. Samples were collected monthly except for the months of April, June and Sept. when it was impossible to sample. Additional information on maturity of 46 males collected between 1979 and 1982 was also used. Most specimens were collected from commercial halibut gill or trammel nets operating at depths of 6–37 m. The primary capture method involved 20.32 cm mesh trammel nets. Numbers and lengths of nets varied with the fishermen, who usually set nets during the morning and retrieved them one or two mornings later. Samples were also obtained from fishermen who fished with otter trawls at depths of 58–77 m.

Reproductive information was taken on 71 males and 76 females, which ranged in size from a 35.4 mm TL embryo to a 1180 mm TL adult. Large specimens were dissected on board and small specimens were frozen for dissection at a later date. Measurements taken on most specimens were total length (mm), alternate length (mm) (the distance from the origin of the first dorsal fin to the origin of the second dorsal fin) and inner and outer clasper lengths (mm) of

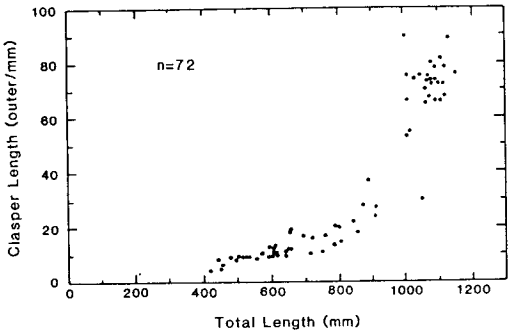

Fig. 1. The relationship of outer clasper lengths (mm) and total length (mm) of 72 male angel sharks.

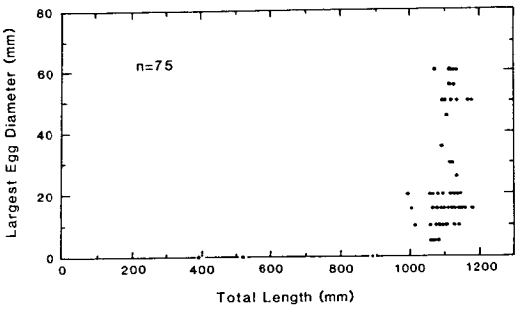

Fig. 2. The relationship between total length (mm) and largest egg diameter (mm) for 75 female angel sharks. The three smallest females had no eggs at all.

males. For many specimens, weight was taken with a spring scale accurate to ±0.2 kg.

After obtaining measurements, the abdominal cavity was opened with an incision from the cloaca to the pectoral girdle and the gonads were removed. The gonads, either ovaries and oviducts or epididymides, were frozen and later transferred to 10% formalin and then to 40% isopropyl alcohol.

Maturity in males was determined using three methods: 1) clasper length vs total length graphs, where maturity is indicated when clasper length suddenly increases relative to total length (Holden and Raitt, 1974); 2) coiling of the epididymis; and 3) sperm smears taken from the epididymis, stained using the Harleco Diff-Quik stain set (Pratt, 1979) and examined for viable sperm under a compound microscope.

Sexual maturity in females was determined by the number and size of eggs and embryos and the condition of the ovaries and oviducts. Once several females were examined, stages of maturity were defined based on the following criteria (Holden and Raitt, 1974). Immature sharks had small, flaccid and undeveloped ovaries and oviducts with no discernable eggs. Maturing sharks had ovaries and oviducts which were enlarging and ovaries which contained visible eggs 5–10 mm in diameter. Mature sharks had ovaries containing large, heavily yolked eggs 50–60 mm in diameter. Mature or reproductively active sharks had fertilized eggs and/or embryos in the oviducts. Recent post-partum sharks had flaccid and stretched oviducts and vagina.

All eggs and embryos were counted and measured to the nearest 1 mm while either fresh or after having been thawed. The average number of maturing eggs per individual and/or number of embryos per individual were calculated to provide two independent estimates of average fecundity. A frequency histogram was produced to show the range in number of embryos in both oviducts and the number of maturing eggs (>35 mm in diameter) in both ovaries. The largest egg diameter was plotted against total length of females to indicate where the onset of maturity occurred. The mean embryo size per month was calculated and plotted to obtain information on seasonality of mating, gestation period and pupping season.

Preserved embryos at five arbitrarily chosen developmental stages were examined for initial development of adult characteristics such as teeth, mouth position, coloration, body proportions and eye position. Yolk sac and gill filament characteristics were also noted.

Results

Male characteristics.—Males matured at 900–1000 mm TL. Of the 20 males greater than 1000 mm TL, all were considered mature by at least two of the three maturity criteria. Clasper length increased rapidly between 900 and 1000 mm TL (Fig. 1). Viable sperm were found in 15 of the 20 sperm smears taken on individuals which were between 690 and 1150 mm TL. Totally coiled epididymides were found in 19 of the 20 fish examined which were larger than 1000 mm TL. The epididymis was slightly coiled in one 690 mm TL individual and coiling was complete in one 865 mm TL individual.

Female characteristics.—Females also matured at approximately 900–1000 mm TL (Fig. 2). Egg diameter increased noticeably in the 74 specimens larger than 900 mm TL examined from

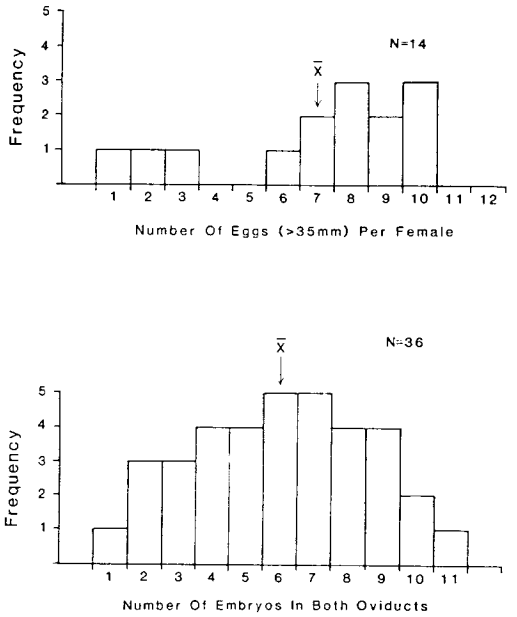

Fig. 3. Frequency histograms of: a) the number of eggs (>35 mm in diameter) in both ovaries; and b) the number of embryos in both oviducts. Arrows indicate the mean for each graph.

Jan.–Nov. 1983. Small (<5 mm in diameter) eggs began to appear in the ovaries of females over 800 mm TL. The smallest female found with eggs was 810 mm TL. All females over 1000 mm TL had eggs that ranged from less than 5 mm in diameter to 70 mm in diameter. Most females with developing embryos had eggs 20 mm or less in diameter. Those without embryos had a wide range of egg sizes between 10 and 60 mm in diameter. The smallest female found with young was 1079 mm TL.

In most specimens, only the left ovary was functional. In 21 of the 29 (72%) samples with two ovaries, the right ovary had not developed. In one specimen, the left ovary had not developed. The development of the second ovary did not seem to be correlated with size, as both large and small females were found with and without two functional ovaries.

Fecundity estimates for the 36 pregnant females examined in detail ranged between 1 and 11 (Fig. 3). The number of large, maturing eggs (>35 mm in diameter) seen in the combined ovaries of female individuals ranged from 1–10, with a mean of 7 (Fig. 3a). The number of embryos observed per female ranged from 1–11, with a mean of 6 (Fig. 3b). The number of

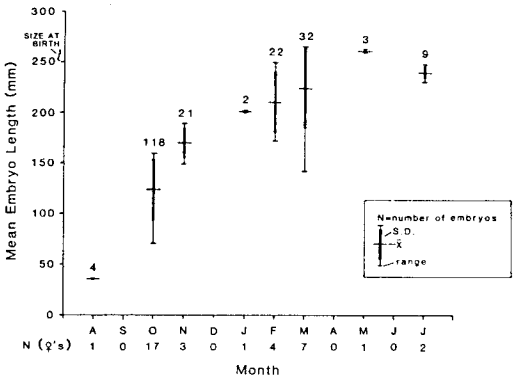

Fig. 4. The relationship between mean embryo length (mm) in pregnant females and month for samples taken in 1983.

young varied a great deal among individuals and did not appear to increase with increasing size of the female. The size range of mature females was quite narrow (1000–1200 mm TL; Fig. 2).

The oviducts were filled with solid yolk in 13 (19%) of the mature females. No membranes divided the yolk in these specimens. These oviducts were vascularized and often appeared orange. The ducts were filled but not overextended.

Mean embryo sizes, from samples of pregnant females taken in consecutive months, increased gradually during a 10 month period from Aug. through July (Fig. 4). Growth rates ranged from 45 mm TL per month in the very young embryos to 10 mm TL per month in those approaching the size at birth. Overall mean growth rate was 23 mm TL per month. Females with embryos were found in all of the months sampled. The embryos were found in various stages within each month. Young began to reach the average size at birth, which is approximately 250–260 mm TL based on the largest embryos and the smallest free-living individuals encountered (Natanson et al., 1984), in March.

Development.—Descriptions of individual developmental morphology for five preserved embryos of increasing sizes (35.4 mm TL, 71 mm TL, 112 mm TL, 151 mm TL and 175 mm TL) are as follows.

Embryo, 35.4 mm TL.—This embryo was one of four from the right oviduct of a 1130 mm TL specimen caught in Aug. 1983 (Fig. 5). At this stage in development, the skin was transparent

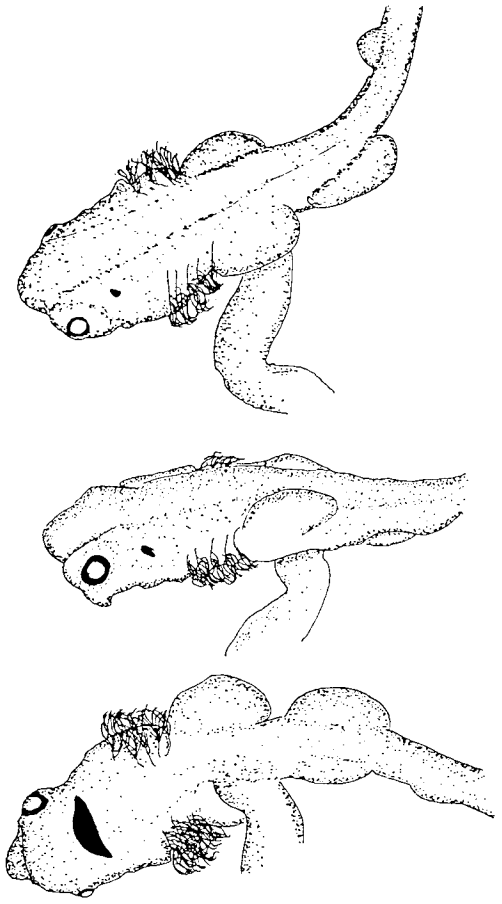

Fig. 5. Three views of a 35.40 mm TL embryo. The top view is dorsal, the middle is lateral from the left side and the lower is ventral. Note the subterminal mouth, protruding eyes and external gill filaments. Picture was drawn using a Wilde camera lucida at ×60.

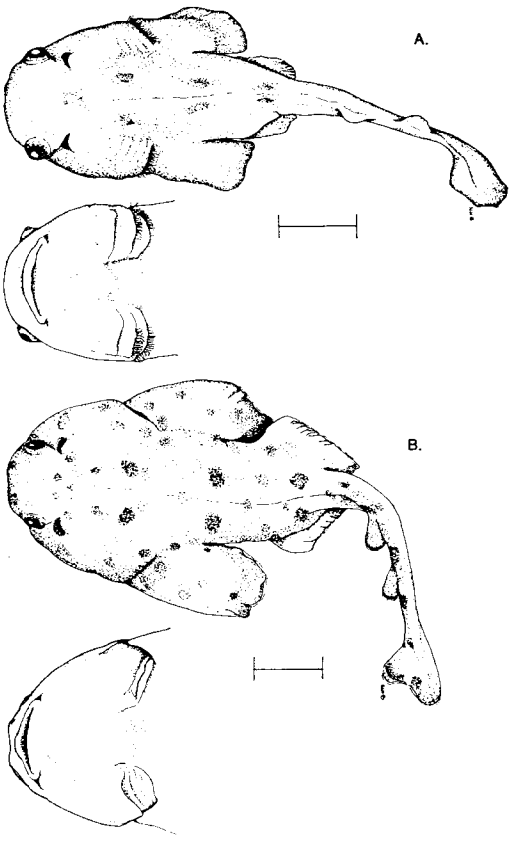

Fig. 6. A) Drawing of a 71 mm TL embryo. B) Drawing of a 112 mm TL embryo. The scale bar is 1 cm long.

with a yellowish tint. All fins were evident but not well developed. Gill filaments were visible and extended approx. 2 mm past the gills. Barbels were present around the subterminal mouth. A broad ridge extended over the dorsal surface of the embryo. Unlike in the adult, the eyes protruded. No teeth or secondary sexual characteristics had developed. Nutrition was from an external yolk supply.

Embryo, 71 mm TL (Fig. 6A).—This embryo was from a 1138 mm TL shark caught in Oct. 1983. The skin was less transparent than in the 35.4 mm TL embryo although the brain and internal organs were visible. Six brown pigment spots were located dorsally. All fins were developing but pectoral fins were small relative to the head. Gill filaments were present but barely extended past the gill openings. The mouth was in a subterminal position and the eyes protruded. A remnant of the dorsal ridge found in the 35.4 mm TL specimen was now located over the cranial area. Claspers appeared to be forming but were in a very early stage of development. No teeth had developed. Nutrition was by external yolk supply.

Embryo, 112 mm TL (Fig. 6B).—This specimen was from a 1100 mm TL female caught in Oct. 1983. There was still some transparency of the skin, as the brain and some muscle could still be seen. More brown pigment spots were visible dorsally along the tail and onto the fins than in the previous specimen. The background skin was yellowish. The head was slightly larger rel-

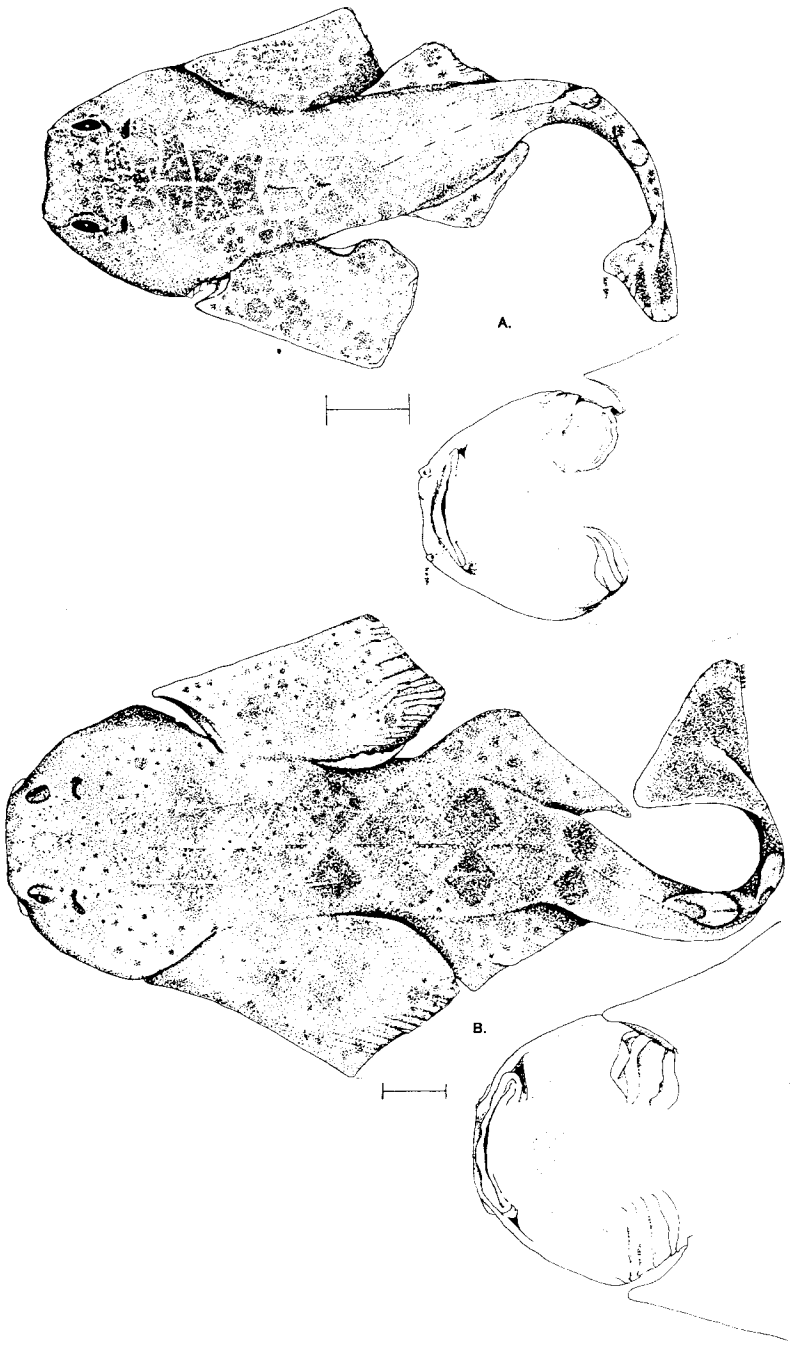

Fig. 7. A) Drawing of a 151 mm TL embryo. B) Drawing of a 175 mm TL embryo. The scale bar is 1 cm long.

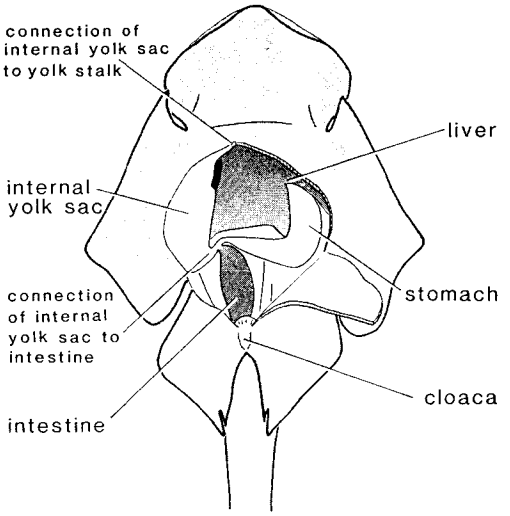

Fig. 8. Ventral view of the internal organs of an embryonic angel shark.

ative to the fins than in the adult. External gill filaments were no longer present. The eyes protruded somewhat, but not as much as in smaller specimens and the mouth had moved farther towards the terminal position. The bulge on the head was reduced. A single row of small teeth, each tooth being approx. 0.124 mm long, was present in both jaws. Claspers were visible. Nutrition was from an external yolk supply.

Embryo, 151 mm TL (Fig. 7A).—This specimen was taken from a 1137 mm TL female caught in Nov. 1983. There was no longer any transparency associated with the skin. Spots covered the skin and came together in a somewhat reticulated pattern with yellowish lines in between. Fins were completely developed and in the same proportion to the body as in the adult. Teeth were present in rows. The eyes did not protrude and the mouth was in the terminal position. The external yolk was still present; however, an internal yolk sac was beginning to bud at the site where the external yolk joins the anterior portion of the stomach (Fig. 8).

Embryo, 175 mm TL (Fig. 7B).—This specimen was taken from a 1146 mm TL female caught in Nov. 1983. This embryo resembled the adult except for the presence of both internal and external yolk sacs. During the final stages of development, more yolk was stored in the internal sac which increased in size; the external sac was eventually resorbed and the connection became sealed. No free-living young were found to contain internal yolk sacs, which presumably are resorbed before parturition. Captive young taken from the female prematurely did not feed until the internal yolk sac was completely resorbed.

Discussion

Based on indicators used in this study (clasper length increase, sperm smears, epididymis coiling), the male angel shark begins to mature at 900–1000 mm TL. All the males in this study over 1030 mm TL were mature. Males may mature fully before this point, but there was a paucity of specimens between 865 and 1030 mm TL. Males appear to follow documented reproductive development in clasper length growth (Holden and Raitt, 1974) and epididymis coiling (Pratt, 1979). Sperm smears collected at various times of the year were all viable, indicating that males may be physically capable of mating all year long. However, there may be other factors controlling the seasonality of mating.

The female angel shark begins maturing between 900 and 1000 mm TL. Because of a lack of specimens between 800 and 1000 mm TL, it was difficult to determine an accurate size at which the ovary first begins to develop and when embryos first appear. Fifty percent of the females have matured by 1070 mm TL and this is 0.7 of the maximum reported length. This fits Holden's (1974) generalization that maturity in female elasmobranchs is between 0.6 and 0.9 of their asymptotic length. By the time the females have reached 1120 mm TL, 100% of them are mature.

The angel shark appears to have an approximately 10 month gestation period. Parturition seems to take place between March and June and mating probably occurs soon after. However, because females with embryos were found during all months, even the non-pupping season, and some elasmobranchs rest a period of time between litters (Springer, 1960), this contention needs further study. Indeed, Couch (1862) thought that *S. squatina* might have young twice a year, based on qualitative observations that "some of them are found in a fertile condition at opposite seasons." Our results, however, are similar to the seasonal cycle and growth of embryos reported for *S. squatina* by Lo Bianco (1899). *S. squatina* is reported to have pups in July in England (Couch, 1862; Breder and Ro-

sen, 1966) and in Dec.–Feb. in the Mediterranean (Lo Bianco, 1888, 1899; Breder and Rosen, 1966). One other species, *S. dumeril,* from the Atlantic, has been reported to pup in June or July (Gordon, 1956).

A maximum of 11 pups was seen in one individual and egg numbers indicated that 10 eggs could become ripe at one time. The number of young in the Pacific angel shark has been observed to range from 8–13 (P. Beguhl, commercial fisherman, Santa Barbara, California, pers. com.). The number of embryos seen in this study may have been low due to trauma-induced pupping in the nets. *S. dumeril* has been reported to have up to 25 embryos in one individual (Bigelow and Schroeder, 1948; Gordon, 1956); this is high compared to the data on *S. californica.* Compagno (1984) cited 7–11 pups per litter for *S. africana* and 9–20 pups per litter for *S. squatina* and Couch (1862) stated that *S. squatina* had up to 20 pups.

In most elasmobranch species with only one functional ovary, the left ovary is reduced (Dodd et al., 1983). Observations on specimens of *S. dumeril* have shown that only the left ovary is functional (Backus, 1957; Merriman and Olsen, 1949; Hoese, 1962). Our observations on *S. californica* indicated that in most cases only the left ovary is functional but in some cases both ovaries are functional.

Hoese (1962) observed that the oviducts in two female *S. dumeril* were filled with a "cheesy" yellowish fluid. This was also observed in the Pacific angel shark and appeared to be yolk. The reason for these yolk-filled oviducts is unknown; however, they may represent resorption of unfertilized ovulated eggs.

During the approximately 10 month gestation period, the embryo receives nutrition from an external yolk supply as evidenced by the gradual shrinkage of this yolk supply over time. There is a gradual shifting of yolk into an internal sac, which occurs after the embryo reaches approximately 150 mm TL. The internal sac, which is also found in *Squalus acanthias,* is used as a storage area from which yolk is slowly transferred to the intestine for final digestion and absorption (Te Winkel, 1943; Wourms, 1977).

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