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Reproduction and Embryonic Development of the Shortfin Mako, *Isurus oxyrinchus* Rafinesque, 1810, in the Northwestern Pacific

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Shoou-Jeng Joung and Hua-Hsun Hsu (2005) Reproduction and embryonic development of the shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, in the northwestern Pacific. *Zoological Studies* **44**(4): 487-496. The reproductive biology of the shortfin mako shark, *Isurus oxyrinchus* Rafinesque, 1810 is described based on 750 females and 498 males (including 24 pregnant females) collected from Oct. 2001 to Mar. 2004 at Nanfangao fish market, northeastern Taiwan. The size at maturity was 210 and 278 cm total length (TL) for males and females, respectively. Size at birth was approximately 74 cm TL, and litter size ranged from 4 to 15, with a mean of 11.1; there was no increase in litter size with maternal size. The mating period is from Jan. to June, and pupping occurs between Dec. and July. We estimated the gestation period to be 23-25 mo and the corresponding reproductive cycle to be 3 yr. Embryos are nourished by oophagy, and develop a grossly distended abdomen as their “yolk stomach” fills with ova. Small embryos, 15-22 cm in TL, are able to swallow egg capsules, but do not yet have teeth. Teeth form in embryos at about 26 cm TL, and they begin shedding at 42 cm TL. A subsequent set of teeth are formed at 61 cm TL. Uterine cannibalism (adelphophagy) occurs occasionally, most likely due to unequal embryonic growth. http://zoolstud.sinica.edu.tw/Journals/44.4/487.pdf

Key words: Shortfin mako, *Isurus oxyrinchus*, Reproduction, Uterine cannibalism.

The shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, is a pelagic species with a circum-global distribution in tropical and temperate seas (Compagno 2001). This shark is common in the waters off northeastern Taiwan (Fig. 1) and according to catch statistics from the Nanfangao fish market near Suao City, they comprise more than 420 tons or 22% of the total annual shark catch in the region. Most are caught by drift longlines in Taiwanese waters.

Isurus oxyrinchus is a member of the family Lamnidae which includes 3 genera: *Carcharodon*, *Lamna*, and *Isurus* (Compagno 2001). Reproduction within the lamnoids is poorly understood. Our knowledge of shortfin mako biology and reproductive parameters has increased considerably in the last 30 yr (Mollet et al. 2000). Stevens (1983) recorded 4 pregnant females and their embryos, and confirmed that this species, like other lamnoids, is oophagous. In this unusual form of embryonic development, the pregnant female ovulates an enormous number of ova that are consumed by the embryos within the uterus. The embryos develop grossly swollen abdomens as they store large quantities of yolk for later growth (Gilmore 1993, Francis and Stevens 1999, Mollet et al. 2000).

Maturity in males has been reported to occur at 180-195 cm TL (Cailliet et al. 1983, Stevens 1983). Females mature at a much larger size than males (Pratt and Casey 1983, Stevens 1983). Mollet et al. (2000) reviewed available reproductive data and showed the sizes at 50% maturity for western North Atlantic and Southern Hemisphere female shortfin mako are 298 and 273 cm TL, respectively.

Mollet et al. (2000) showed that the litter size for a female shortfin mako ranges from 4 to 18

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embryos and possibly reaches 25-30 embryos per litter. They also suggested late-winter to mid-spring parturition in both hemispheres. In addition, Mollet et al. (2000) reported a 15-18 mo gestation, and a 3 yr reproductive cycle. Duffy and Francis (2001) observed a pregnant shortfin mako with 8 near-term embryos in the summer off Hawke Bay, New Zealand, and suggested that they have an extended parturition period, possibly even year-round. Most of the data used in the analysis of the reproductive parameters of the shortfin mako were collected from the Atlantic Ocean and Southern Hemisphere. There are few reports about the biology of this species in the northwestern Pacific. This study provides the first detailed information concerning reproduction and embryonic development of the shortfin mako shark populations in the northwestern Pacific.

MATERIALS AND METHODS

Most of the reproductive data from the 498 male and 726 female shortfin makos were collected between Oct. 2001 and Dec. 2002. The 24 pregnant individuals were observed between Jan. 2000 and Mar. 2004 (Table 1). All data were collected from landings by the commercial longline and harpoon fishery off northeastern Taiwan at the Nanfangao fish market (Fig. 1). All sharks were caught between the surface (harpoon) and 200 m in depth.

Body weight in kilograms (BW, kg), precaudal length (PCL, cm), fork length (FL, cm), total length (TL, cm), and clasper length (in cm) were measured following Branstetter and McEachran (1986). Total lengths are reported for all sharks in this study. The relationship between body weight (BW) and total length (TL) for males, females, and embryos is provided and fits the equation BW =

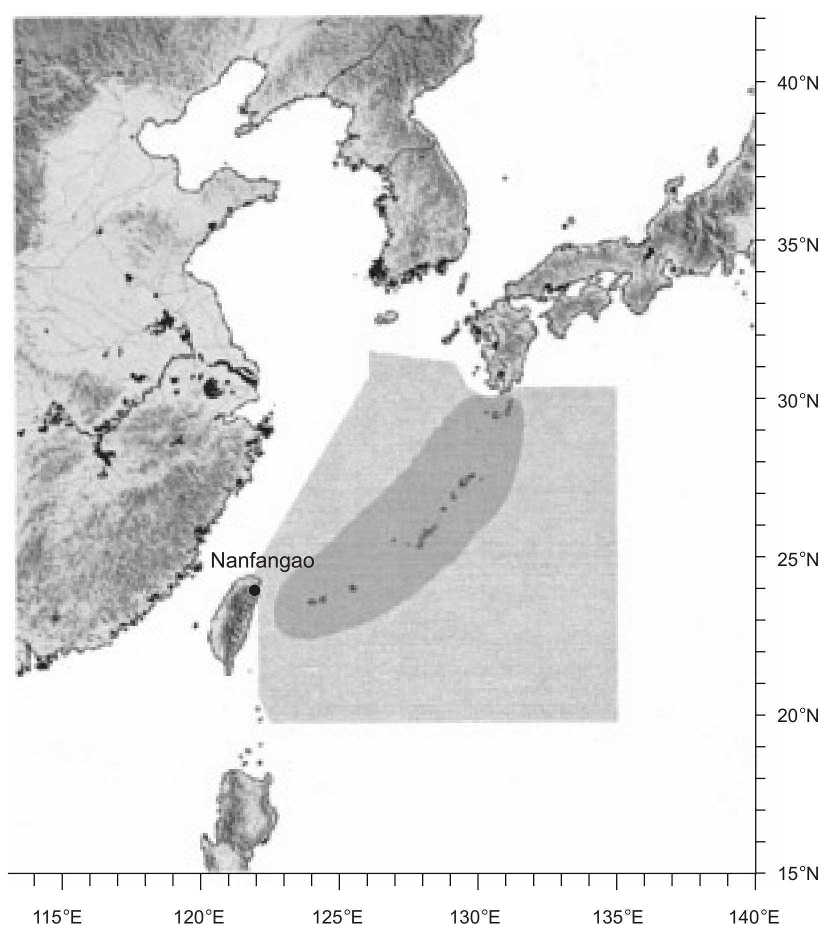

Fig. 1. Sampling area for *Isurus oxyrinchus* off eastern and northeastern Taiwan. The shaded region represents the longline fishing area. The dark region represents the main sampling area.

aTL^b. The model was fit to the data using the PROC NLIN method of SAS (ref). Differences between the sexes were tested using Chi-square tests of likelihood ratios (Kimura 1980) implemented using SAS (ref).

Reproductive organs were removed from each specimen. In males, testes were weighed to the nearest gram (g), clasper length was taken, and its calcification stage noted. In females, ovaries were weighed to the nearest gram, the condition of fertile eggs or embryos in the uterus was recorded, and measurements were taken of the uterus and shell gland widths when possible. Several embryonic developmental stages are recognized in embryos, based on gill filaments, stomach contents, and teeth (Gilmore 1983).

Sexual maturity of males was determined from clasper length and calcification, and testes weight (Tanaka et al. 1990). In the absence of embryos or egg cases, the maturity of females was determined from the gonadosomatic index (GSI) (ovary weight as a percentage of total weight), uterus width, and shell gland width (Chen et al. 1997, Mollet et al. 2000). The size at 50% maturity for male and female sharks was determined by fitting a logistic model, $Y = [1 + e^{-(a + bX)}]^{-1}$, where Y is the binomial maturity data (immature = 0, mature = 1; Carlson et al. 2003) and X is total length (cm).

The mating period was estimated from mating scars and the appearance of fertile eggs in females, and from the GSI (testes weight as a percentage of total weight) of mature males. The gestation and parturition period were estimated from data on the monthly growth of embryos and capture dates of the smallest free-swimming juveniles.

To compare our results with other studies, spring in this study was defined from 21 Mar. to 21 June (Mollet et al. 2000).

RESULTS

Length-weight relationship

All length-to-weight relationships for the northwestern Pacific shortfin mako were linear and are described by the following regressions:

Table 1. Summary of *Isurus oxyrinchus* litter data. Figures in parentheses give the number of embryos investigated if all the litter were not available. #Embryonic stomach contents not examined. WY, without yolk; [x]fangs absent; [x+]fangs in some parts of jaws present; [+]fangs complete

No.	Embryo TL (cm)	Mean embryo TL (cm)	Embryo weight (g)	Litter size	Yolk weight (g)	Female TL (cm)	Female weight (kg)	Capture date	Fangs
1#	0	0	-	-	-	284	224	2002/2/28	x
2	14.8-22.0	19.8	30-140 (9)	10 (2F)	40 (1)	337	356	2001/11/14	x
3	26.0-37.4 (12)	32.3	280-2100 (12)	13 (2F)	20-1340 (12)	-	287	2003/10/8	x+
4#	36.0 (1)	36.0	220 (1,WY)	-	-	341	336	2001/12/12	+
5#	36.0-39.0	37.4	-	15 (7F6M)	520 (1)	296	315	2001/11/6	+
6	38.0-41.0	39.4	1220-1820	14 (6F)	820-1420	326	284	2002/11/11	+
7	39.0-41.5	40.3	1390-1650 (5)	10 (4F)	840-1120 (5)	296	253	2002/10/21	+
8#	43.0	43.0	-	6 (3F)	-	-	-	2000/1/10	x
9	42.4-49.8	44.6	960-1374 (2)	13 (4F)	510-778 (2)	295	232	2002/12/19	x
10#	44.9-48.0	46.1	1300 mean	10 (6F)	605-820 (2)	286	218	2001/11/14	x
11	53.0-58.0 (10)	55.9	1600-2300 (11)	12 (8F)	660-1100 (11)	304	304	2001/12/19	x
12	56.5-62.0	59.4	1300-2340	12 (5F)	100-840	-	274	2002/12/25	x
13	61.0-70.5	64.7	1670-3120	9 (3F)	220-810	272	184	2001/12/12	x+
14	62.5-68.0	65.0	2040-2980	12 (9F)	380-780	-	345	2002/12/25	x+
15#	61.0-69.0	65.1	-	11 (6F)	-	310	268	2004/3/3	+
16#	63.0-70.0	66.7	-	11 (7F)	-	292	228	2003/3/18	x+
17	63.5-72.0 (6)	66.7	1860-2490 (6)	10 (6F)	60-230 (6)	-	233	2003/12/24	x+
18	65.0-70.0	67.4	2860-4100 (3)	4 (2F)	860-1800 (3)	-	375	2003/1/23	x+
19	65.0-71.5	68.5	2100-2740 (10)	11 (6F)	120-280 (10)	-	267	2003/1/23	+
20#	61.0-74.5	68.6	-	12 (5F)	-	296	284	2003/1/16	+
21	64.5-74.0	69.6	2120-3320	11 (5F)	-	306	259	2003/1/15	+
22	50.0-79.0	69.9	700-4100 (11)	12 (6F)	58-520 (11)	302	352	2001/12/11	+
23	70.0-79.0 (13)	72.4	2160-3800 (13)	15 (4F9M)	20-450 (12)	340	407	2002/12/24	+
24	68.0-77.5	74.0	1910-3400	11 (8F)	30-160	285	237	2003/1/24	+

PCL = 0.784 + 0.816 TL, (n = 1240, r^2 = 0.986, range 80-375 cm TL, 65-301 cm PCL); and

FL = 0.952 + 0.890 TL, (n = 1236, r^2 = 0.986, range 80-375 cm TL, 72-332 cm FL).

The relationship of BW vs. TL did not significantly differ between sexes (X^2 = 0.20, P > 0.05). The relationship for the sexes combined was best described by the following exponential curve:

$BW = 1.1 \times 10^{-5}\ TL^{2.95}$, ($n$ = 612, r^2 = 0.98, range 80-345 cm TL, 3.4-407 kg BW).

Size at maturity

Male

Claspers began to rapidly extend at about 162 cm TL. Individuals of < 184 cm TL generally had uncalcified claspers, while those over 213 cm TL had calcified claspers (Fig. 2a). Testes weight rapidly increased at 186 cm TL (Fig. 2b).

Fifty percent maturity in males was estimated to occur at 210 cm TL based primarily on clasper condition. Percent maturity was related to TL by the following equation: $Y = [1 + e^{-(20.036 - 0.095X)}]^{-1}$ (Fig. 3).

Female

Shell gland width rapidly increased in females of between 260 and 296 cm TL (Fig. 4a). The increase in uterus width was similar to that of the shell gland in females of between 264 and 294 cm TL (Fig. 4b). The GSI rose noticeably between 275 and 283 cm TL (Fig. 4c). The smallest pregnant female observed was 272 cm TL, and the largest immature individual observed was 283 cm TL.

Fifty percent of female shortfin makos were mature at 278 cm TL. The percent maturity was related to TL using the following equation: $Y = [1 + e^{-(92.837 - 0.335X)}]^{-1}$. Due to a lack of maturing females, this relationship may vary slightly in future studies.

Mating, parturition, gestation period, and reproductive cycle

Our data suggest that the shortfin mako has an extended mating period ranging from Jan. to June. A female with fertilized eggs was caught at the end of Feb. (Table 1). Since lamnoid females do not appear to store sperm after mating (Pratt 1993), this indicates that this female had mated sometime in Jan. or Feb. Fresh mating scars on females were also observed in Jan., Mar., Apr., and June. In addition, the GSI of mature males increased in Jan. and decreased after May, although no data are available for Nov. and Dec. (Fig. 5).

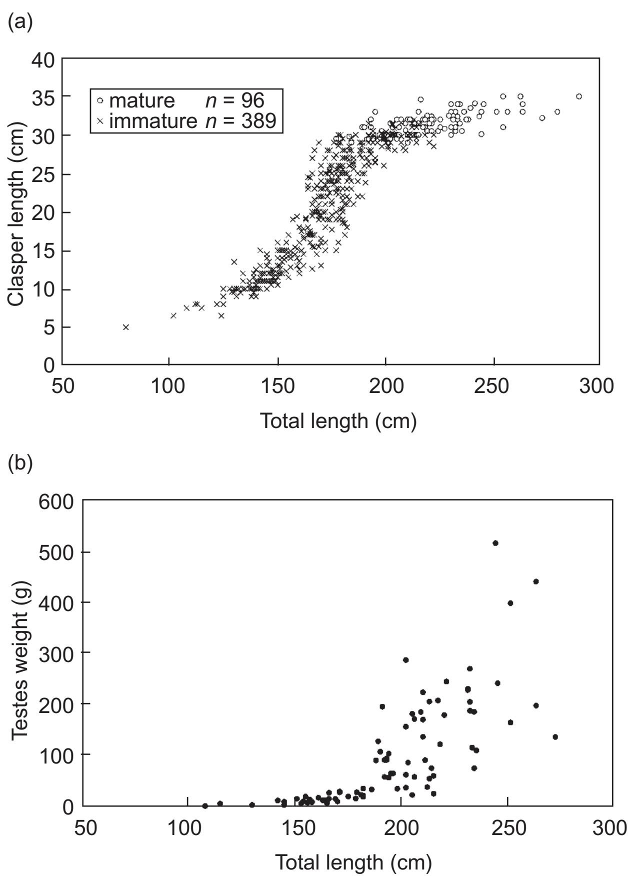

Fig. 2. (a) Relationship between clasper length and total length of the male shortfin mako. (b) Relationship between testis weight and total length of male shortfin makos. (n = 85).

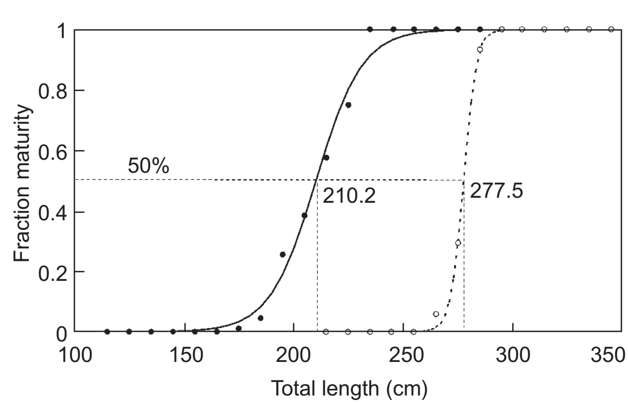

Fig. 3. Maturity ogive for male and female shortfin makos. Size class intervals are 10 cm TL.

A litter of 15 full-term embryos (range, 70-79 cm TL; mean, 74.0 cm, Table 1) was observed in Dec. These embryos were fully developed and indistinguishable from juveniles, except for a slight distension of the abdomen, suggesting they would be born that month. Two 80 cm TL postnatal pups were caught in Aug., suggesting birth in June to July. The parturition period appears to extend from Dec. to July.

Fertilization is followed almost immediately by ovulation. A 337 cm TL female with a litter containing embryos averaging 19.8 cm TL was caught in Nov. (Table 1). If she had been fertilized in June (the postulated end of the mating season), the average growth rate would be 3.9 cm/mo. At this growth rate, birth size (74 cm, see below) would not be reached for over 1 yr, suggesting a gestation period closer to 2 yr.

For the purpose of reproductive cycle estimation, all adult females were reviewed, but the data from mating and parturition periods were excluded. Some pre-mated or recently postpartum females without embryos which were sampled in those periods appeared to have been resting that year, but in fact, they should have been counted as pregnant individuals. In addition, sharks exceeding 200 kg were always gutted by the long-line fishermen at sea, thus data on reproductive organs of adult female shortfin makos were difficult to obtain. Two of the 11 females had healed mating scars, although they had been gutted, and their condition could not actually be determined. Another 5 females had embryos, and the remaining 4 were in a resting condition. The ratio of pregnant females to females that were resting was 7:4, which is close to 2:1. This suggests that the northwestern Pacific shortfin mako has a 3 yr reproductive cycle. However this needs to be confirmed with more data.

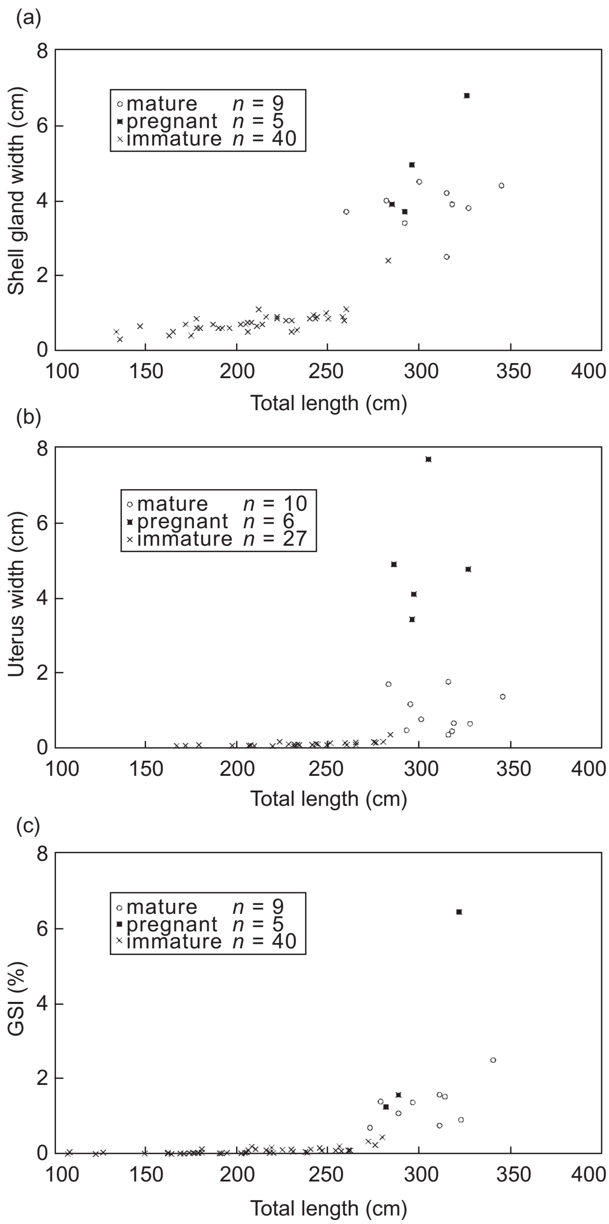

Fig. 4. (a) Relationship between shell gland width and total length of female shortfin makos. (b) Relationship between uterus width and total length of female shortfin makos. (c) Relationship between GSI and total length of female shortfin makos.

Litter size and size at birth

The average number of embryos per litter was 11.1 (range, 4-15; *n* = 22). Litter size did not increase with maternal size. The female-to-male

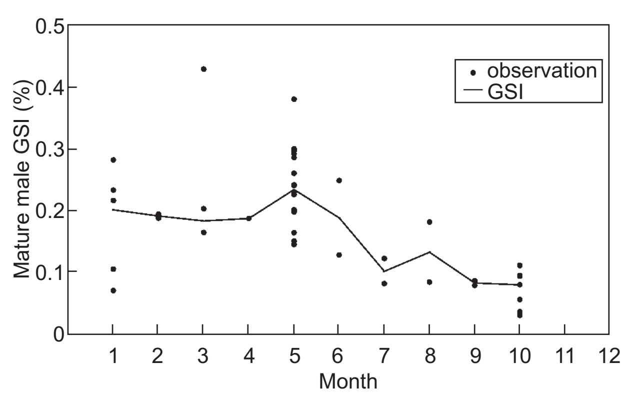

Fig. 5. Monthly changes in GSI for mature males. (*n* = 45).

ratio of embryos was 103: 111 (2: 8 - 8: 4, n = 20 litters), and this did not significantly differ from 1 (chi-square test, X^2 = 0.48, P > 0.05).

The largest embryo measured was 79 cm TL, and the maximum mean length of near-term embryos in an entire litter was 74.0 cm TL (Table 1, no. 24). The smallest free-swimming individual collected during the parturition period (Jan., Fig. 6) was 74 cm TL. Therefore, size at birth of shortfin mako was estimated to be about 74 cm TL.

Embryonic development

Embryos were classified into 5 stages based on observations of 24 litters.

Stage 0

Just after mating, the largest ova (6-8 mm) were ovulated, fertilized, and packaged into an egg case which contained 1 blastodisc ovum per egg case. Although no embryos were observed in the egg cases, we presumed that small embryos would hatch when the egg cases were about 4-5 cm TL based on the measurement of a 5.5 cm long fertilized egg capsule. Pregnant females kept ovulating smaller ova (5-6 mm) which were packaged into egg capsules (several ova per egg case) and became nutritive egg capsules which embryos consumed after hatching.

Stage 1

In this stage, embryos are visible. We presumed that embryos absorb uterine milk after hatching and up to a length of 10-14 cm TL. In the stomachs of several embryos, 1 or 2 broken nutritive egg capsules were found although the embryos had no teeth. We speculated that the embryos crushed the egg capsules with their jaws prior to consuming them. Embryos in this stage had obvious external gill filaments, the caudal fin was notably curved with the upper lobe much longer than the lower lobe, the abdomen was slightly bulged out, and no pigmentation was found on the body (Fig. 7a).

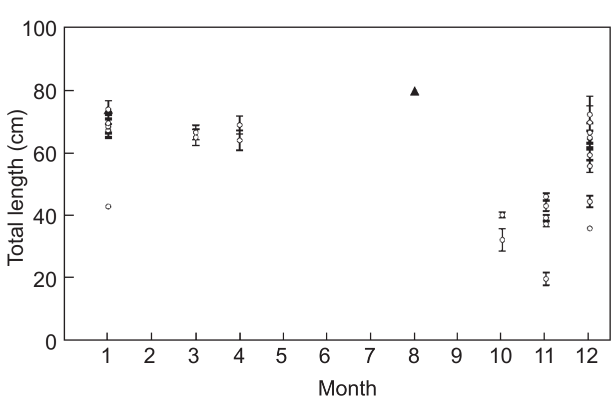

Fig. 6. Mean embryo length-month relationship for shortfin makos. ▲: free-swimmers; ○: embryos. The number of litters was 24. Vertical bars indicate ± 1 SD.

Stage 2

In this stage, embryonic TL ranged from 26 to 42 cm. Peg-like and recurved fangs were present in both jaws. One 40 cm TL embryo from a litter of 14 (mean TL, 39.4 cm; mean BW, 1.496 kg; mean yolk mass, 1110 g) had a greatly distended yolk-filled stomach (Fig. 7b). A dense covering of blood vessels was present on the abdomen, and pigmentation was present on the tip of the caudal fin. At the end of this stage, pregnant females stopped ovulating ova, and the bulging yolk stomach of the embryos reached their maximum size.

Stage 3

At this stage, the female decreased production of nutritive capsules, thus the bulging yolk stomachs decreased to between 42 and 62 cm as the yolks were absorbed. The gill filaments had begun to shrink back on one 44 cm TL embryo at this stage, and pigmentation was deposited on its body, however, the skin was still smooth, lacking dermal denticles (Fig. 7c). Embryos shed and swallowed their fangs at about 40 cm TL (Fig. 8). The fangs were shed in a distinct order, from the upper jaw to the lower jaw and from the center to the angle of the jaw.

Stage 4

The final stage of embryonic development was from 62 cm to birth. One 74 cm TL near-term embryo had a lunate caudal fin, complete pigmentation, and reabsorbed external gills (Fig. 7d). New adult-like teeth were present. The only difference from postnatal individuals was a slightly bulging abdomen. The liver weight increased rapidly as the yolk stomach decreased starting at about 65 cm TL (Fig. 9). Surplus yolk stored in the stomach and the large liver provide postnatal juveniles with an energy store that increases their survival chances.

The body weight of embryos rapidly increased between 20 and 40 cm TL (stage 2) due to the consumption of large numbers of nutritive egg capsules. Embryonic weight (minus yolk weight) steadily increased throughout the gestation period (Fig. 10). The weights of two 80 cm free-swimming juveniles were similar to the yolk-free weights of the largest embryos. The relationship between weight (in g) and total length (in cm) of shortfin mako embryos is as follows:

Embryo total weight = 4.52 $TL^{1.51}$ (n = 132, r^2 = 0.97); and

Embryo weight minus yolk = 0.0046 $TL^{3.09}$ (n = 131, r^2 = 0.99).

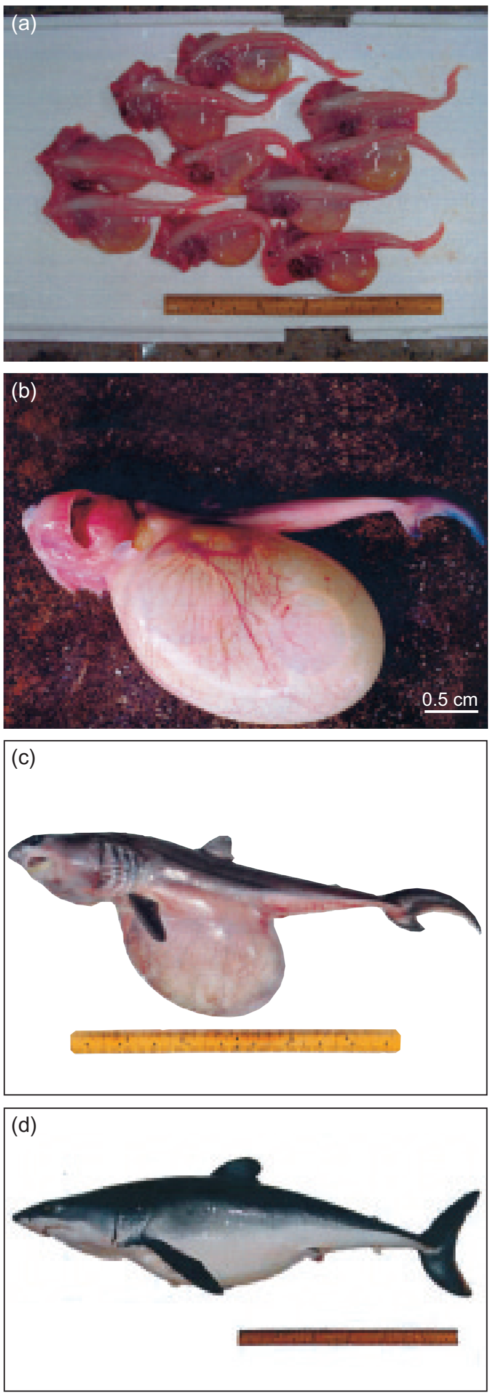

Fig. 7. Changes in shortfin mako embryo external shape with increasing size (not to the same scale). (a) Ten embryos from a litter (14.8-22.0 cm TL); (b) a 40 cm TL embryo with huge yolk-filled stomach; (c) a 43.6 cm TL embryo showing its decreasing stomach; (d) a 74 cm TL near-term female.

Intrauterine cannibalism

Stomach contents of the embryos were examined in 16 of the 24 litters. Two complete embryos (a 33 cm male and a 28 cm female) were observed in the stomach of a 71 cm near-term embryo (Table 1, no. 22; Fig. 11a). Additionally, a 68 cm embryo (Table 1, no. 15) contained a partially digested 20 cm male embryo (Fig. 11b). These observations indicate that uterine cannibalism may occur in the shortfin mako.

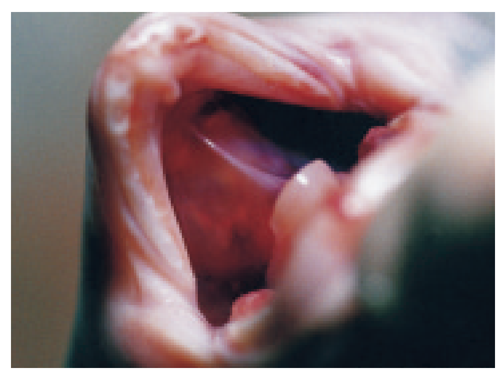

Fig. 8. Embryos having swallowed their fangs at a size of 40 cm TL.

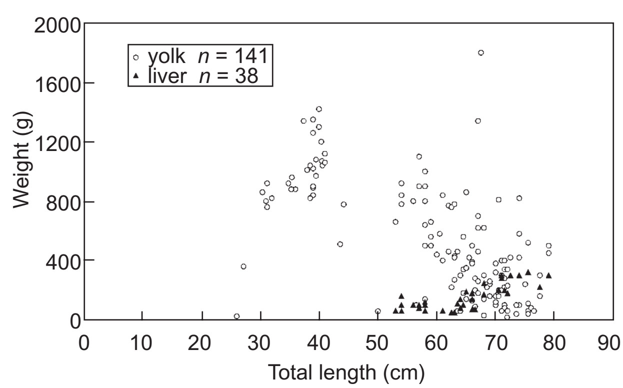

Fig. 9. Relationship of yolk and liver weights with the total length of shortfin mako embryos.

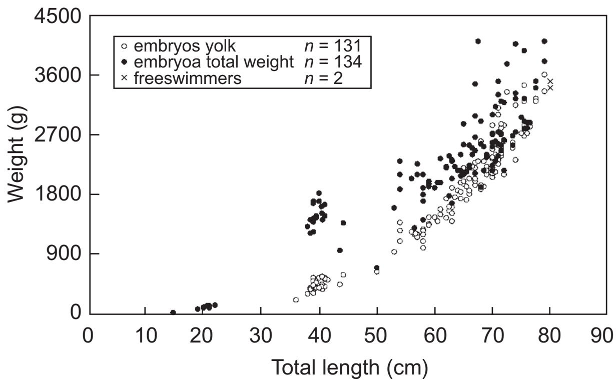

Fig. 10. Relationship between the weight and total length of shortfin mako embryos.

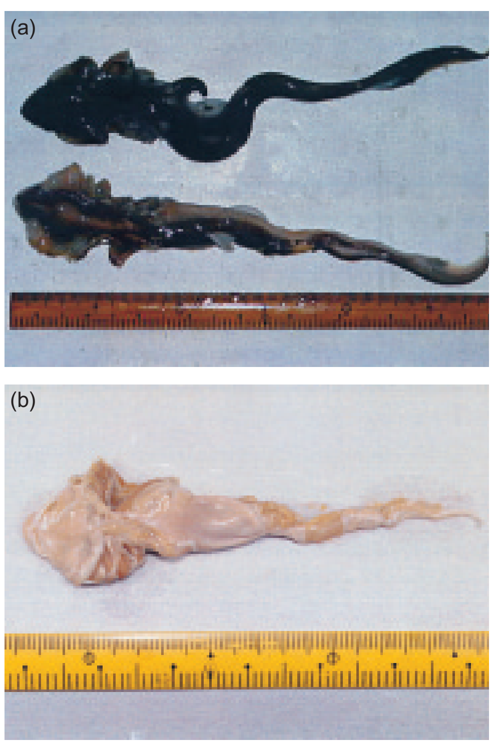

Fig. 11. Embryos (from 2 litters) swallowed in utero by larger individuals (not to the same scale). (a) A 32.5 cm TL male (top) and a 28.0 cm TL female (bottom); (b) a 20.0 cm TL male.

DISCUSSION

Previous information on the size at maturity for male shortfin makos was limited. Stevens (1983) noted that males mature at 195 cm TL based on 42 specimens from the Atlantic Ocean. In the northwestern Pacific, male shortfin makos mature at between 184 and 213 cm TL based on 498 individuals, and 50% maturity was at 210 cm TL.

In the current study, females were found to mature at between 260 and 296 cm TL, and 50% maturity was at 278 cm TL. This is similar to that in the Southern Hemisphere (273 cm), but much smaller than that in the western North Atlantic (295 cm) (Mollet et al. 2000) suggesting that regional differences may exist in size at maturity. Regional reproductive differences have been documented for *Squalus japonicus* and *Sphyrna tiburo* (Chen et al. 1981, Parsons 1993). Size at maturity might also change in different eras such as in *Galeus eastmani* and *G. nipponensis* (Horie and Tanaka 2000).

In the northwestern Pacific, parturition takes place between Dec. and July. Mollet et al. (2000) suggested that parturition occurs in late-winter to mid-spring worldwide. Duffy and Francis (2001) observed a pregnant female, which had 8 near-term embryos, in summer off New Zealand. Their observation extends Mollet's et al. (2000) parturition period and corresponds with the results of our study. However, Duffy and Francis (2001) also speculated that shortfin makos may breed throughout the year. A much-lower GSI of adult males after July (Fig. 5) indicates a restricted mating period which should correspond with a restricted parturition period.

Although we did not have data on litters from Apr. to Sept., we estimated a 23-25 mo gestation period for northwestern Pacific shortfin mako sharks. This is longer than the 15-18 mo proposed by Mollet et al. (2000) but is similar to that reported in the Southern Hemisphere by Duffy and Francis (2001). Other lamnoids such as the sand tiger, *Carcharias taurus*, and porbeagle, *Lamna nasus*, have gestation periods of only 9 and 8-9 mo, respectively (Gilmore et al. 1983, Francis and Stevens 2000, Jensen et al. 2002).

Data on litter size of shortfin mako sharks are scarce; in addition, estimates of litter size are often biased by low values due to abortion during capture (Mollet et al. 2000). In this study, the mean litter size was 11.1 (range, 4-15); this is close to the 12.5 reported by Mollet et al. (2000). Our smallest litter size (4) is the same as that reported by Stevens (1983). The largest litter size in this study (15) is smaller than the previously reported maximum litter sizes of 16 (Stevens 1983), 18 (Branstetter 1981), and questionably 25-30 (Mollet et al. 2000 2002). Litter sizes in other lamnoid species were found to be lower: sand tiger, bigeye thresher, *Alopias superciliosus*, and pelagic thresher, *A. pelagicus*, sharks generally have 2 pups (Gilmore et al. 1983, Chen et al. 1997, Liu et al. 1999), the longfin mako, *I. paucus*, has 2-8, salmon shark, *Lamna ditropis*, has 2-5, porbeagle shark has 4 (Francis and Stevens 2000, Compagno 2001, Jensen et al. 2002), and the great white shark, *Carcharodon carcharias*, has 2-14 (Compagno 2001, Mollet et al. 2002).

Size at birth of the shortfin mako is smaller than that of most other large lamnoids. The porbeagle shark is the only species with a smaller size at birth (59-72 cm TL, Jensen et al. 2002). Size at birth of the bigeye and pelagic thresher sharks is > 130 cm (Chen et al. 1997, Liu et al. 1999), that of the sand tiger and great white sharks is 120-165 cm TL (Gilmore et al. 1983, Compagno 2001, Mollet et al. 2002), and that of longfin mako sharks is 97 cm TL, much longer than that of the shortfin mako (Gilmore 1983, Compagno 2001). There seems to be no direct and obvious relationship between gestation period, litter size, and size at birth in lamnoid sharks. Litter weight and ovary weight may determine the gestation periods of oophagous sharks (Mollet et al. 2000).

The embryonic sex ratio of most shark species is 1: 1, except in a few species such as *Centroscymnus coelolepis* (Yano and Tanaka 1988). However, the sex ratio of adult northwestern Pacific shortfin makos sampled from the fishery from Oct. 2001 to Oct. 2002 was 1: 2.5 (1242 females and 503 males) showing that the sexes are segregated. Larger porbeagle sharks (> 150 cm FL) also segregate by sex (Francis and Stevens 2000). However, the sex ratio of captured specimens from Jan. to June (during the mating period) in this study was 1: 1.3 suggesting that Taiwanese and Japanese waters (dark area in Fig. 1) may be the mating ground of the northwestern Pacific shortfin mako.

Embryonic development in oophagous sharks is not easily observed. Early-term embryos of sand tiger and porbeagle sharks have teeth which they use to tear open nutritive egg capsules. Chen et al. (1997) also noted that early-stage bigeye thresher shark embryos open egg capsules using their teeth. However, shortfin mako embryos between 15 and 22 cm eat nutritive egg capsules but have no teeth. Teeth may help embryos eat egg capsules, but they may not be essential if the embryos can crush or swallow the capsules.

Lamnoid shark embryos have different "embryonic" and "adult" dentition. The embryonic-adult dental transition occurs at around 30-60 cm TL (Gilmore 1993, Shimada 2002). In this study, fangs of the shortfin mako embryos were shed at 39.5 cm TL, and had disappeared completely by 42 cm TL. Adult-like teeth had appeared by 61 cm TL. Fangs of the porbeagle embryos are shed at 41-45 cm TL (Francis and Stevens 2000). Teeth of the bigeye and pelagic thresher sharks disappear at around 60 cm TL (Chen et al. 1997, Liu et al. 1999).

Oophagy and embryonic cannibalism (adelphophagy) have been documented in the sand tiger shark, but only oophagy has been noted in other lamnoid species (Gilmore 1993). However, Gilmore (1983) suspected that adelphophagy may occur in the bigeye thresher shark. Uterine cannibalism observed in the shortfin mako is recorded for the first time in this study. Adelphophagy was observed in 2 cases out of 16 litters. No scars or bites were observed on the bodies of the 3 embryos that were eaten. The situation differs from that in *Carcharias taurus* as smaller shortfin mako embryos were "swallowed" not "attacked" by larger embryos. Unequal food may cause this phenomenon to occur. There are 5 or 6 embryos in each uterus, and the embryos are always orientated with their head towards the anterior end of the uterus. An embryo which is closest to the cloaca might get fewer egg capsules due to keen sibling competition. If this condition continues throughout the gestation period, the weak embryo would be much smaller than others and might then be swallowed by a larger embryo. Different embryonic orientation in utero also causes unequal development in porbeagle sharks (Francis and Stevens 2000). Francis and Stevens (2000) observed 1 porbeagle embryo that had abdominal lacerations, although there was no more-definite evidence of adelphophagy. Therefore, embryonic cannibalism may occur in some lamnoid sharks which have more than 2 pups per litter. Uterine cannibalism occurred in 12.5% of the litters examined in this study indicating that it occasionally occurs in the shortfin mako.

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