

**Abstract.**—Reproductive data from 95 mature female shortfin mako sharks, *Isurus oxyrinchus* Rafinesque, 1810, including 35 pregnant females, together with data on 450 postnatal fish were collected from around the world. Size at birth was approximately 70 cm total length (TL) and litter size varied from 4 to 25, increasing with maternal size. Embryo length-at-capture data predicted a gestation period of 15–18 months and late winter to midspring parturition in both hemispheres. A temporal analysis of uterus width index and gonadosomatic index of pregnant and postpartum females indicated that the reproductive cycle is three years. The median TL-at-maturity of females from the western North Atlantic (2.98 m) was greater than that of females from the Southern Hemisphere (2.73 m) and they were 16–19% heavier in the TL range of 2.5–3.5 m.

Recently ovulated females and a litter with 2.6–3.3 cm TL embryos having external gills, a large yolk sac, and still inside their egg cases, are described. We describe a litter of embryos (52.0 cm TL) with huge yolk-filled stomachs. Litters of 59.9- and 68.8-cm-TL embryos showed a decline in the mass of the yolk-filled stomach from 29.1% to 10.9% of total mass and an increase in hepatosomatic indices from 3.7% to 7.0% as gestation advances. When the mass of the yolk-filled stomach was excluded, the mass-length relationship of shortfin mako embryos could be fitted with a power regression similar to that for postnatal fish. The condition factor of lamnid embryos (including yolk-stomach mass) reaches a maximum between 20 and 35 kg/m<sup>3</sup> when the embryos are midterm and have the largest yolk stomachs. The condition factor of alopiid embryos remains constant, indicating that no large yolk-filled stomach develops.

## Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids

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The shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, is a pelagic species with a circumglobal distribution in tropical and temperate seas (Garrick, 1967). It is frequently taken by commercial fisheries, mainly as bycatch of tuna and swordfish longlining, and is an important recreational species (e.g. Casey and Kohler, 1992; Pepperell, 1992). It is one of five species in the family Lamnidae comprising the genera *Isurus*, *Carcharodon*, and *Lamna* (Compagno, 1984). All lamnids are large, active pelagic sharks that regulate their body temperature (Carey et al., 1985; Goldman, 1997). Reproduction in lamnids is oophagous (Swenander, 1907; Lohberger, 1910; Bass et al., 1975; Gilmore, 1993; Francis, 1996).

Our knowledge of shortfin mako biology and reproductive parameters has increased considerably in the last 30 years. Garrick (1967)

showed that the 12 nominal species of *Isurus* represent a single world-wide species, *I. oxyrinchus*; these findings were confirmed by Heist et al. (1996). Both males and females were thought to mature at around 1.8 m TL (Bigelow and Schroeder, 1948; Gubanov, 1978; Cailliet et al., 1983). With the collection of more extensive data it has become apparent that females mature at a much larger size than males (2.7–2.8 m; Pratt and Casey, 1983; Stevens, 1983; Cliff et al., 1990).

Our review of available reproductive data showed that female shortfin makos have similar reproductive characteristics in all regions. Based on a small number of mostly near-term litters, litter size is 4–16 in Australia (Stevens, 1983) and 9–14 in South Africa (Cliff et al., 1990). Litter sizes from other parts of the world are reported to be between 6 and 18, with the exception of a

litter of 25–30 from the Mediterranean Sea (Sanzo, 1912; Mollet et al.<sup>1</sup>). Pratt and Casey (1983) reported April parturition at a size of 65–75 cm TL in the western North Atlantic. Stevens (1983) and Cliff et al. (1990) suggested November parturition at about 70 cm TL in New South Wales and KwaZulu-Natal, respectively. The data presented by Gilmore (1993) showed no clear time of parturition, but investigation during the course of our study revealed several data errors (see Table 1). Cliff et al. (1990) proposed a 6- or 18-month gestation but indicated that 18 months appeared more feasible, based on a gestation of a little over 1 year postulated by Pratt and Casey (1983). Pratt and Casey (1983) reported first year growth rates of about 50 cm per year in the western North Atlantic, whereas Cailliet et al. (1983) suggested growth rates half as fast off California. Recent tagging results from California<sup>2</sup> and New Zealand (Saul and Holdsworth, 1992; Saul<sup>3</sup>) have shown that growth rates in the Pacific are similar to those reported for the Atlantic.<sup>4</sup> The size-frequency modes reported by Hanan et al. (1993) and O'Brian and Sunada (1994) confirmed high juvenile growth rates for California sharks.<sup>4</sup>

Currently there is growing concern over the extent of pelagic shark catches worldwide, both as targeted fishing and, particularly, as bycatch of high-seas longlining. Further attempts to manage resources of shortfin makos will require, among other demographic data,<sup>4</sup> information on reproductive parameters. Although this species is commonly caught in a variety of fisheries (Bonfil, 1994), few pregnant females have been documented and extensive biological data from a single location do not exist. Given all these factors and assuming reproductive synchronism of mating and gestation, spring parturition, and consistency in growth and size at birth of sharks from several widely spaced regions, we decided to combine all available information, adjusting for seasonal shifts between hemispheres. Our study documents the reproductive biology of female shortfin mako sharks from around the world.

## Materials and methods

### Materials examined

Reproductive and morphometric data from 95 mature females, including 35 pregnant individuals (Table 1), together with data on 450 postnatal fish, including almost 200 age-0+ fish, were collected from around the world. Much of the data came from the western North Atlantic (largely unpublished, with the exception of data on three pregnant females), from eastern Australia (all unpublished, except four pregnant females reported by Stevens [1983]), and from KwaZulu-Natal, South Africa (either unpublished or providing substantially more detailed information than that reported by Cliff et al. [1990]). For methods of collection, measurement, and assessment of maturity see Pratt and Casey (1983); Stevens (1983); Cliff et al. (1990); and Stevens and McLoughlin (1991).

### Morphometrics

We used total length (TL, expressed in meters or cm) for our length measurement following Stevens (1983) and calculated TL of western North Atlantic and some South African sharks from the relationship with fork length (FL) (Casey and Kohler, 1992) or precaudal length (PCL) (Cliff et al., 1990), respectively. Total length of embryos, if not measured, was estimated from TL-FL ratios (1.156 at TL 60 cm; 1.203 at TL 35 cm) and the TL-PCL ratio (1.294 at TL 60 cm) of similar-size specimens.

We defined power regression as a linear  $y$ -on- $x$  regression of log-transformed data. We used Student residuals and leverage, an index of the leverage of each observation on the size of the mean square error, to carry out linear regression residual analyses (Wilkinson, 1986). We fitted power regressions to our mass-length data of females weighing more than 55 kg (TL= $\sim$ 2 m) from the western North Atlantic and the Southern Hemisphere (no maternal data were available from Brazilian litters) and reported back-transformed equations in the form  $M$  (kg)= $a$   $TL^b$  (m). The prepower coefficient " $a$ " predicts the mass of a 1-m-TL shortfin mako because we used meters as the unit of length in all such calculations (Mollet and Cailliet, 1996). We were interested only in possible mass differences of adolescent and mature females from different regions and chose 55 kg as the suitable minimum. A geometrical mean (GM) regression gives the correct functional relationship (Mollet and Cailliet, 1996), but we wanted to compare our results with previously reported back-transformed  $y$ -on- $x$  power regressions. An  $F$ -test and the linear interaction model were used to check for statisti-

<sup>1</sup> Mollet, H. F., A. D. Testi, L. J. V. Compagno, and M. P. Francis. 1999. Re-identification of a lamnid shark embryo. In review.

<sup>2</sup> Laughlin, L. 1997. California Department of Fish and Game, 330 Golden Shore, Long Beach, CA 90802. Personal commun.

<sup>3</sup> Saul, P. 1997. Blue Water Marine Research, RD 3, Whangarei New Zealand. Personal commun.

<sup>4</sup> Mollet, H. F., and G. M. Cailliet. 1997. Preliminary demographic analysis of the shortfin mako shark, *Isurus oxyrinchus*. Program and Abstract of the American Society of Ichthyologists and Herpetologists (ASIH) and American Elasmobranch Society (AES) Annual Meeting, University of Washington, Seattle WA, June 26–July 1, 1997, 336 p.

**Table 1**

Summary of *Isurus oxyrinchus* litter data. SST = sea surface temperature. ECS = eggcases with single egg; NIA = not included in analysis; WY = without yolk (yolk-stomach punctured).

No.	TL embryo <sup>l</sup> (cm)	Mass embryo <sup>l</sup> (kg)	Litter size	TL female (m)	Mass female (kg)	Capture date	Capture location	SST (°C)	References and comments
1	0 (ECS)		11	2.92	236	19 Mar 87	KwaZulu-Natal	23.0	This study; Cliff et al. (1990)
2	0 (ECS)		14	2.88	217	10 Jun 86	KwaZulu-Natal	21.1	This study; Cliff et al. (1990)
3	2.6–3.3 (5)		9	3.09 <sup>2</sup>	270 <sup>3</sup>	9 Jan 93	W. North Atlantic		This study
4	25–31		18	~3.05	334	22 Aug 78	DeSoto Canyon, FL		Branstetter (1981); Gilmore (1993)
5	29.5–39.5		15	3.37 <sup>3</sup>	363	5 Dec 92	Daytona Beach, FL		Putz <sup>6</sup> ; Colket <sup>7</sup> ; this study
6	36.1(1)	0.80(1)	25–30	3.85 <sup>3</sup>	~500	~Aug 1903	Strait of Messina, Italy		Sanzo (1912); Gilmore (1993); Mollet et al. <sup>8</sup> ; this study
7	34.8 mean		13	2.88 <sup>2</sup>	217 <sup>3</sup>	late Jun 93	Gulf of Guinea (1.5N, 1W)	28.5	Castro and Mejuto (1995)
8	39.4 mean	1.456 mean	16(11F)	3.37	380	15 Nov 84	Okinawa Japan		Uchida et al. (1987); Gilmore (1993, embryo TL range reported were means of L and R uterus)
9	~41 NIA		6	3.15 <sup>3</sup>	~270	~Apr 79	New South Wales, Au	18–21	Stevens (1983)
10	42.3–49.2		18	~3.66(12)	547	2 Mar 90	Kona, HI	27.8	This study; Rizzuto <sup>9</sup> , Hodson <sup>10</sup>
11	45.0–48.5	0.60–0.90(WY)	12(6F)	2.97 <sup>2</sup>	224 <sup>3</sup>	1 Apr 85	Florida Straits		Gilmore (1993), Putz <sup>6</sup>
12	~50(1)		9	2.84 <sup>4</sup>	195 <sup>3</sup>	18 Sep 92	S. Pacific (24S, 155E)	~20	This study
13	49.5–53.0(2)	1.63–2.30(2)	12(8F)	3.04 <sup>2</sup>	271	10 Aug 81	Port Edward, SA	19.5	Cliff et al. (1990)
14	50.4–54.0	1.435–2.370	15(5F,9M)	3.25	313	pre-1832	Marseille, Med. Sea		Vaillant (1889)
15	53.0–60.8		12(6F)	3.04 <sup>2</sup>	271	17 Aug 92	S. Pacific (30S, 156E)	~20	This study
16	53.0–59.0		12	3.31	337 <sup>3</sup>	15 Jan 92	Puerto Rico	26.3	This study; Gilmore (1993, incorrect TL for mother and embryos)
17	59.0(1)	3.53(1)	5	2.69 <sup>2</sup>	165 <sup>3</sup>	10 Jul 84	KwaZulu-Natal	21.0	Cliff et al. (1990)
18	56.8–62.0	2.100–2.800	9(5F)	3.34	284	13 Feb 94	WNA, 20.4N, 73.5 W		This study; Castro <sup>11</sup>
19	~60		4	3.11 <sup>3</sup>	259	24 Aug 92	S. Pacific (30S, 160E)	~20	This study
20	~60		14	3.39 <sup>3</sup>	340	27 Aug 97	KwaZulu-Natal	19.3	This study
21	60	fully developed	6	2.63	153 <sup>3</sup>	Sep 79	New South Wales, Au	18–21	Stevens (1983); Gilmore (1993)
22						4 Oct 80	New South Wales, Au	18–21	Stevens (1983); Gilmore (1993)
23							Red Sea		Gohar and Mazhar (1964)

Continued

Table 1 (continued)

No.	TL embryo/ <sup>1</sup> (cm)	Mass embryo/ <sup>1</sup> (kg)	Litter size	TL female (m)	Mass female (kg)	Capture date	Capture location	SST (°C)	References and comments
24	60.5(1)	~1.134(10)	10	2.93 <sup>3</sup>	229	20 Feb 52	Cat Cay, Bahamas		Depperman <sup>2</sup> ; Garrick (1967); Gilmore (1993, incorrect embryo TL); this study
25	60.5(1)					26 Mar 09	Nagasaki, Japan		Garrick (1967)
26	58.2-64.0(5)	1.42-1.72(5)	16	2.80 <sup>3</sup>	186	28 Sep 80	New South Wales, Au	18-21	Stevens (1983); Gilmore (1993)
27	65.0(1)					1971-73	Atlantic (off NW Cuba)		Guitart-Manday (1975)
28	63.5-69.8		10(5F)						IGFA <sup>13</sup> ; this study
NIA			10						Gubanov (1978)
29	64.5-70.4	1.84-2.49(13 <sup>5</sup> )	10(6F)			Oct 92	S/SW Brazil		Costa et al. <sup>14</sup> ; this study
30	64.6-70.7	2.300-3.125	13(6F)	3.14 <sup>2</sup>	266 <sup>3</sup>	15 Aug 97	S. Pacific 24.5S, 156.5E	21.2	This study
31	66-70		10				S. W. Indian Ocean		Bass et al. (1975)
32	65.5-73.8(15)	2.30-2.84(15)	16(9F, 6M)			Sep 94	S/SW Brazil		Costa et al. <sup>15</sup> ; this study
33	66.1-69.3(2)		14			Oct 92	S/SW Brazil		Costa et al. <sup>14</sup> ; this study
34	71.2(1)					Oct 92	S/SW Brazil		Costa et al. <sup>14</sup> ; this study
35	~75 NIA	fully developed	11			late Jan 83?	Green Canyon, LA		Branstetter <sup>16</sup> ; this study

<sup>1</sup> Number in parentheses gives number of embryos of litter investigated if not all were available;

<sup>2</sup> Estimated from  $FL = 0.9286 TL - 0.0171$  (Casey and Kohler, 1992);

<sup>3</sup> Estimated from  $M = 7.658 TL^{3.1}$  (Stevens, 1983), Southern Hemisphere,  $M = 9.933 FL^{3.1546}$  (Casey and Kohler, 1992), northern hemisphere;

<sup>4</sup> Used data given in Cliff et al. (1990) to calculate TL from PCL;

<sup>5</sup> Mass range of 3 litters with 10, 2, and 1 embryo (stored in same bag and weighed later).

<sup>6</sup> Putz, O. 1995. Grolmanstrasse 48, 10623 Berlin, Germany. Personal commun.

<sup>7</sup> Colket, T. 1996. 2020 Cordova Ave., Vero Beach, FL 32960. Personal commun.

<sup>8</sup> Mollet, H. F., A. D. Testl., L. J. V. Compagno, and M. P. Francis. 1999. Re-identification of a lamnid shark embryo. In review.

<sup>9</sup> Rizzuto, J. 1996. Kona mako the world's biggest? New Zealand Fishing News 19(7):22, 102.

<sup>10</sup> Hodson, G. 1996. Hustler Sportfishing, P.O. Box 4976, Kailua-Kona, HI 96755.

<sup>11</sup> Castro, J. 1998. NOAA/NMFS, SEFC, 75 Virginia Beach Dr., Miami, FL 33149. Personal commun.

<sup>12</sup> Depperman, B. 1953. Maternity mako model. Sports Afield, March 1953:86-7.

<sup>13</sup> International Game Fish Association (IGFA). 1979. Game Fish Yearbook, p. 138. 300 Gulf Stream Way, Dania Beach, FL 33004.

<sup>14</sup> Costa, F. E. S., F. M. S. Braga, A. F. Amorim, C. A. Arfelli. 1994. Analysis of mako sharks, *Isurus oxyrinchus*, from Santos longliners off South and Southeast Brazil. Program and Abstracts ASIH and AES Annual Meeting. USC Los Angeles, California, June 1994, 217 p. Dates from A. F. Amorim 1995. CPPM Santos, São Paulo-Brazil. Personal commun.

<sup>15</sup> Costa, F. E. S., F. M. S. Braga, A. F. Amorim, C. A. Arfelli. 1995. Reproductive biology of shortfin mako, *Isurus oxyrinchus*. Resumos VII Reunião do Grupo de Trabalho sobre Pesca e Pesquisa de Tubarões e Raias do Brasil, Rio Grande, November 20-24, 1995.

<sup>16</sup> Branstetter, S. 1996. NMFS Southeast Regional Office, 9721 Executive Center Dr. N., St. Petersburg, FL 33702. Personal commun.

cally significant differences between hemispheres (Neter and Wassermann, 1974). The condition factor ( $CF = \text{total mass}/TL^3$ , in units of  $\text{kg}/\text{m}^3$ ) was used as a qualitative estimate of the size of the yolk-filled stomach in lamnid and alopiid embryos.

The calculation of gonadosomatic index (GSI) (ovary mass as percentage of total mass) and hematomatic index (HSI) (liver mass as percentage of total mass) required a mass estimate if the shark was not weighed. For a few sharks only the mass was available and a TL estimate was required. We estimated mass or TL (from FL) of western North Atlantic and Southern Hemisphere sharks from the equations of Casey and Kohler (1992) and Stevens (1983), respectively. Only two dimensions (length and width) were available for the ovaries of western North Atlantic sharks and the mass had to be estimated. The estimates were calibrated with an ovary of dimensions  $19.6 \times 8.7$  cm and mass of 0.630 kg (Fig. 2C in Stevens, 1983). The resulting GSI values proved to be comparable with those obtained from weighed ovaries of mature Southern Hemisphere sharks.

### Size at maturity

In the absence of embryos or egg cases, the maturity of nonpregnant females was determined from GSI, maximum ova diameter (MOD), oviducal gland diameter (measured in western North Atlantic specimens only), uterus width, and absence of a hymen. We fitted a logistical model  $Y = [1 + e^{-(a+bX)}]^{-1}$  to our binomial maturity data (immature=0, mature=1) of female specimens with TL > 2.0 m (Wilkinson, 1986; Welch and Foucher, 1988). Two meaningful parameters to characterize maturation, namely median TL-at-maturity ( $MTL = -a/b$ ) and slope at MTL ( $S = b/4$ ), can be expressed in terms of  $a$  and  $b$  as given. An  $F$ -test was used to check for statistically significant differences between hemispheres (Neter and Wassermann, 1974).

### Litters, gestation, and parturition

Data collected on litters included number of embryos, length and mass of embryos, maternal length and mass, capture date and location, and sea surface temperature (Table 1). Data for 21 litters, either not previously published or published with errors, are presented. We fitted a power regression to the litter size and maternal length data. For two recently fertilized South African fish, the number of uterine egg cases containing a single blastodisc ovum was assumed to be the litter size. The gestation period was estimated from seven litters from the western North Atlantic, one from the Gulf of Guinea, one

from the Mediterranean Sea, two from Japan, seven from Australia, four from South Africa, and four from Brazil ( $n=26$ ). The litters from Hawaii (no. 10 in Table 1) and the Gulf of Mexico (no. 35) were not included because of uncertain length data. We defined early-, mid-, and near-term litters as having embryo size between 0 to 20, 20 to 45, and 45 to 70 cm TL, respectively. Embryos of a term litter had TLs between 65–75 cm. Capture dates and TL estimates of 188 age-0+ fish from the western North Atlantic (extrapolations based on Fig. 3 in Pratt and Casey [1983] [ $n=45$ ]), from California (Cailliet et al., 1983; Cailliet<sup>5</sup>) ( $n=16$ ), and from New South Wales, Australia (Pepperell, 1992; Pepperell<sup>6</sup>) ( $n=119$ ), and South Africa ( $n=8$ ), were also considered in the estimation of size at birth and time of parturition.

Capture dates from Northern and Southern Hemisphere fish were combined on a single time scale based on seasons. For example, spring was defined as 21 March to 21 June in the north and from 23 September to 23 December in the south. Seasons were further divided into three periods of equal length to define the terms early, mid, and late (e.g. early spring in the north lasts from 21 March to 20 April).

To support the combination of Northern and Southern Hemisphere data for the shortfin mako, we examined sandtiger shark (*Carcharias taurus*) data from South Africa (Bass et al., 1975) and the eastern United States (Gilmore et al., 1983). These data were also used to support our use of a linear regression to estimate gestation and parturition from the slope of the embryo TL versus seasonal time regression, as well as size at birth. Bass et al. (1975) reported that 100-cm neonate sandtiger sharks were born from June through August after a gestation of 8–9 months. Gilmore et al. (1983) reported that 100-cm neonates were born from December through March after 9–12 months of gestation. We analyzed reported length-at-capture data by using a linear regression which yielded similar estimates for time of parturition and gestation period from intercept and slope:

South Africa: Jul.–Aug. parturition, 10 months gestation,  $n=27$ ,  $r^2=0.93$ ;

Eastern United States: Jan.–Feb. parturition, 8 months gestation,  $n=14$ ,  $r^2=0.83$ ;

Combined data: midwinter parturition, 9 months parturition,  $n=41$ ,  $r^2=0.93$ .

<sup>5</sup> Cailliet, G. M. 1997. Moss Landing Marine Laboratory, PO Box 530, Moss Landing, CA 95039. Personal commun.

<sup>6</sup> Pepperell, J. G. 1997. Pepperell Research and Consulting Pty, PO Box 818, Caringbah, NSW 2229, Australia. Personal commun.

These results justified combining shortfin mako data from different regions and the use of a linear regression. Embryonic development may, however, deviate from a straight line and be more S-shaped; therefore a straight line may underestimate time of fertilization and overestimate parturition. These deviations cancel each other and a straight line still provides a good estimate of gestation.

### Reproductive cycle

We lacked sufficient numbers of females in all reproductive stages to determine the reproductive cycle from a stage-frequency distribution. For many litters, little or no maternal data were available, which precluded the use of a more rigorous multivariate statistical analysis in determining the reproductive cycle. We used temporal uterus width index data (UWI, uterus width as % of TL) of pregnant and postpartum females with a graphical comparison of 2- and 3-year reproductive cycles. The uterus of postpartum shortfin mako sharks shrinks after parturition. We chose the reproductive cycle compatible with this, given that our results suggested an extended gestation period of 15–18 months. For easier graphic interpretation, we plotted the 19 March (1988) Southern Hemisphere specimen a few days later. This procedure assured that the specimen appeared at the beginning of the gestation period (fall) on the far left-hand side of the temporal graphs. The use of polar coordinates did not provide a better presentation.

## Results

### Pregnant females and details of selected litters

There were 35 pregnant females on record (Table 1), with mean length of 3.1 m (range 2.63–3.85 m,  $n=24$ ) and mass range of 153–547 kg. Capture dates ranged from pre-1832 (Vaillant, 1889; no. 14, Table 1) to 27 August 1997 (no. 20, Table 1). Capture locations were distributed worldwide and corresponding sea surface temperatures, where available, ranged from 18° to 28.5°C. Detailed information was available for six females, three in very early pregnancy and three with well-developed embryos (Table 2).

Two recently fertilized South African sharks of 2.92 and 2.88 m were caught in late summer and late fall of 1987 and 1986 (nos. 1 and 2 in Tables 1 and 2, respectively). A 3.09-m female was caught near Puerto Rico in January (early winter) with a litter of nine early-term embryos (no. 3 in Tables 1 and 2). The 2.6–3.3 cm embryos, each still inside an egg case, had external gills and a large yolk sac (Fig.

1A). The size of the yolk sac was estimated from Fig. 1A to be  $0.9 \times 0.6$  cm, assuming the embryo in the center of the figure was 3.0 cm. There were over 40 nutritive egg cases in each uterus (Fig. 1B).

A 3.25-m female with a near-term litter was caught in the same month and location (January and Puerto Rico, respectively) by a commercial swordfish longliner (no. 16 in Table 1, no. 4 in Table 2). This female carried 15 embryos of around 52 cm, each with a similarly large yolk-filled stomach (Fig. 1C). No uterine compartments were observed and no egg cases remained in the uterus. A 3.34-m female shark stranded on the beach at Umhlanga, South Africa, in late winter (no. 20 in Table 1; no. 5 in Table 2). This female carried a litter comprising nine embryos of about 60 cm. Emerging adultlike teeth were present in both jaws of the embryo examined. The stomachs of four embryos that were cut open had no shed teeth but had large amounts of yolk (Fig. 1D). No uterine compartments were observed and no egg cases remained in the uterus. About one liter of clear, viscous fluid (not seawater) was found in each uterus but was not analyzed. A Japanese longliner caught a 3.14-m female in the southern Pacific in midwinter (no. 30 in Table 1, no. 6 in Table 2). The 13 full-term embryos had a length of about 69 cm and a total mass of 36.8 kg, 14% of the estimated maternal mass of 266 kg. The embryo stomachs were slightly distended and contained small but variable amounts of yolk.

### Litter size

The majority of the litters examined for this study were near-term. The mean number of embryos per litter (litter size) was 12.5 (range: 4 to 27.5,  $n=30$ ). The largest litter comprised 25–30 embryos (we used 27.5 in our calculations) in a female caught in the Mediterranean Sea in about August of 1903 (Sanzo, 1912). The capture date was inferred from the observation that it occurred during a long holiday period (summer) at the University of Messina.<sup>7</sup> A summer date agrees with the dates of the traditional swordfish fishery, in which this shark was probably caught.<sup>8</sup> One of these embryos was described by Sanzo (1912) as being a great white shark, *Carcharodon carcharias*, but a recent re-examination has shown it to be a shortfin mako shark.<sup>1</sup> The male to female ratio of 10 litters was 57:68 and is not significantly different from 1:1 (pooled  $\chi^2=0.80$ , Yates corrected,  $P=0.37$ ).

<sup>7</sup> Notarbartolo di Sciarra, G. 1997. Istituto Centrale per la Ricerca Applicata al Mare (ICRAM), via di Casalotti 300, 00166 Rome, Italy. Personal commun.

<sup>8</sup> Fergusson, I. 1998. The Shark Trust, 36 Kingfisher Court, Hambridge Road, Newbury, UK RG14 5SJ. Personal commun.

**Table 2**

Details for pregnant *Isurus oxyrinchus*. (1–3) Females in very early pregnancy with blastodisc and nutritive egg cases. Observations appear in proposed chronological order. (4–6) Females with well-developed embryos. (L=left; R=right.) GSI = gonadosomatic index; HSI = hematosomatic index.

No.	TL (m)	Date	Location	Observations
1	2.92	19 Mar. 1987	KwaZulu-Natal	6(L)+5(R) egg cases with single egg; no blastodisc observed; 4(L)+8(R) nutritive egg cases with numerous burst eggs; capsule being formed in left oviducal gland; GSI = 1.13%, HSI = 10.6%; mating bites.
2	2.88	10 June 1986	KwaZulu-Natal	7(L)+7(R) egg cases with single egg (some blastodisc); 12(L+R) nutritive egg cases with up to 14 eggs of 4 mm diameter; several ova being encapsulated in right oviducal gland; GSI = 1.21%, HSI = 10.3%; mating bites.
3	3.09	9 Jan. 1993	Puerto Rico	7(L) empty egg cases; 4(L) blastodisc egg cases at least, with one embryo each (~3.0 cm TL, badly disintegrated when measured); 5(R) blastodisc egg cases (3×10 cm) with one embryo each (2.6, 2.9, 3.0, 3.0, & 3.3 cm TL); 43(L) + 42(R) nutritive egg cases (3×5 cm) with 16–20 eggs per capsule, 7–9 g each capsule, 334 g total (R); 2(L) egg cases in lower oviduct; GSI ~5% (estimate from ovary dimensions 44×27 cm).
4	3.25	15 Jan. 1992	Puerto Rico	7(L) embryos (1 female, 5 males, and 1 lost), 51.0–54.0 cm, 1.660–2.300 kg; 8(R) embryos (4 females), 50.5–53.8 cm, 1.435–2.370 kg; mean length and mass of 14 embryos 52.0 cm (SE 0.4) and 2.000 kg (SE 0.071); uteri dimensions 103×22 cm (L), 111×22 cm (R); GSI ~0.3% (estimate from ovary dimensions 27×9 cm), spent ovary.
5	3.34	27 Aug. 1997	KwaZulu-Natal	9(L+R) embryos (5 females), 56.8–62.0 cm (mean 59.9 cm, SE 0.6), 2.100–2.800 kg (mean 2.416 kg, SE 0.094); embryo stomachs with 551–846 g yolk, 26.2–32.0% of total embryo mass (n=4); embryo livers 75–110 g, HSI range 3.4–4.1% (n=4); GSI = 0.185% (spent ovary), HSI = 2.465%.
6	3.14	15 Aug. 1997	South Pacific	13 (L+R) embryos (6 females), 64.6–70.7 cm (mean 68.8 cm, SE 0.5); 2.300–3.125 kg (mean 2.830 kg, SD 0.062); embryo stomachs with 73–478 g yolk, 2.6–15.3% of embryo mass; embryo spiral valve with 68–88 g yolk, 2.4–3.3% of embryo mass (mean 2.9%); embryo livers 146–234 g, HSI range 5.2–8.0% (mean 7.0%, SE 0.2); GSI and HSI of female not available.

Litter size (LS) increased with maternal TL according to

$$LS=0.810 TL^{2.346} \quad (n=24, P=0.013, r^2=0.25)$$

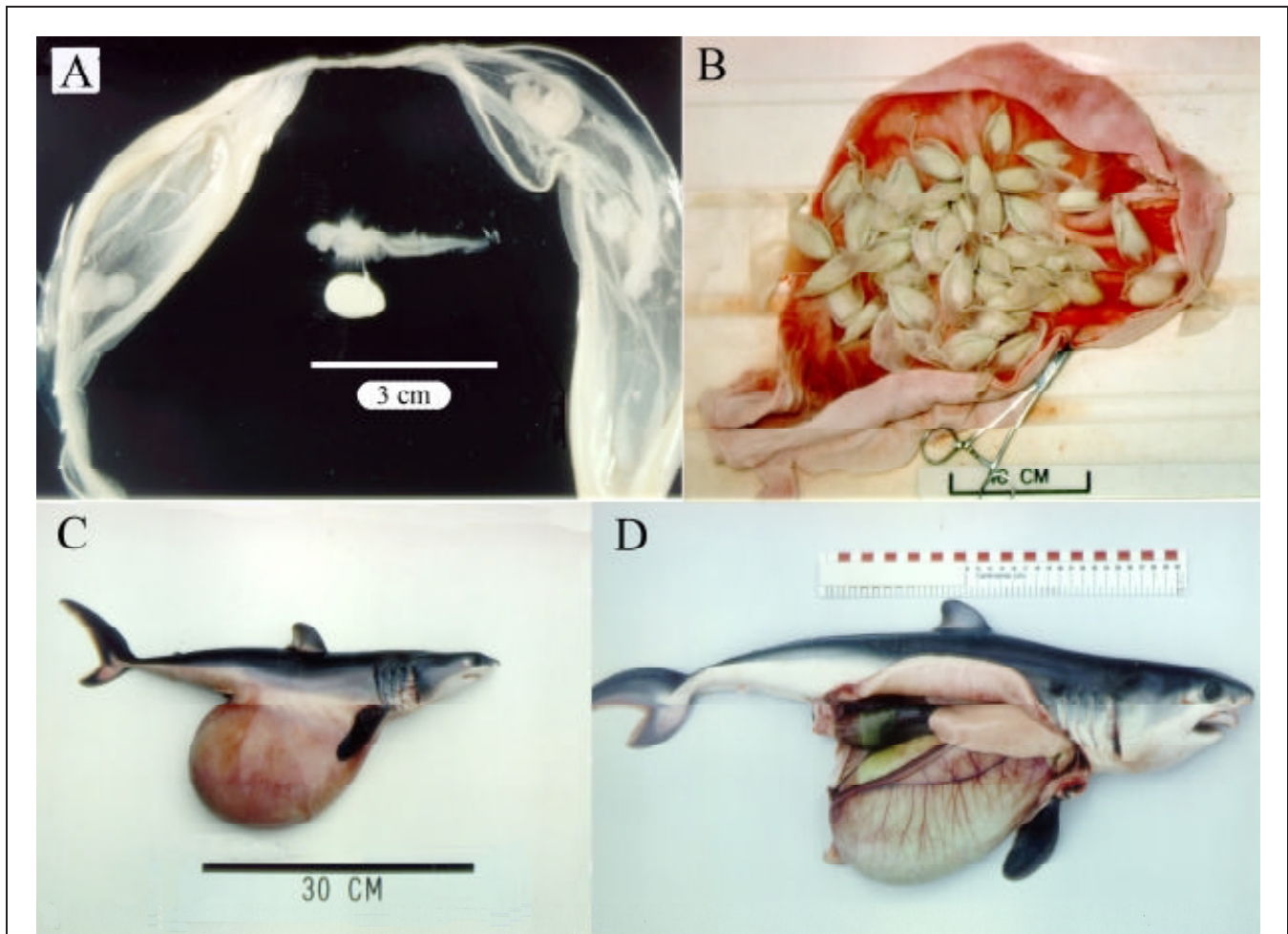
and fell within the band of a model calculation ( $LS=(0.26 \text{ to } 0.46) TL^{3.10}$ ). The model was derived from the maternal mass-length relationship ( $M=7.658 TL^{3.10}$ ; Stevens, 1983) by postulating that the litter mass is a constant fraction of the pregnant female mass (10–15%, based on available data) and by using an estimate of the embryo mass at birth (2.5–3.0 kg, based on available data). The power regression was still significant ( $P=0.029$ ) if the smallest litter of four (an outlier) and the largest litter of 27.5 were excluded.

There were no significant differences between the mean litter size of Northern (14.0,  $n=13$ ) and Southern Hemisphere females (11.1,  $n=17$ , ANOVA,  $P=0.09$ ) or between western North Atlantic (12.8,  $n=8$ ) and Southern Hemisphere females (ANOVA,  $P=0.28$ ).

### Indicators of sexual maturity

The size of reproductive organs increased as the shortfin mako approached maturity (Fig. 2). A logarithmic scale was necessary to present the large GSI range between 0.00044% and ~5.0% (Fig. 2A), reflecting ovaries weighing less than 10 g in immature sharks smaller than 2.4 m, up to an estimated 11.3–13.5 kg in a female in early pregnancy (no. 3 in Table 2). There was considerable overlap in the GSI of adolescent females (range: 0.005–0.28%,  $n=28$ ) and that of mature, nonpregnant females with inactive ovaries (range: 0.08–0.81%,  $n=38$ ) or pregnant females with near-term embryos and spent ovaries (GSI=0.185% and ~0.3%,  $n=2$ ). The GSI (1.1%) of recently fertilized females with egg cases and the GSI (~5%) of the female with the 3-cm embryos were the largest observed (Fig. 2A).

Oocytes of noticeable size (1 mm) appeared in maturing females larger than 2.4 m (Fig. 2B). The MOD of immature fish ranged from 1.0 to 4.0 mm



**Figure 1**

*Iserurus oxyrinchus* embryos and egg cases. (A) 3-cm-TL embryos with external gills, large yolk sac, and still within the egg cases from right uterus of pregnant female (no. 3 in Tables 1 and 2). Embryo in the center was removed from egg case. (B) Right uterus containing 42 nutritive egg cases from female with embryos shown in A. Scale bar, 10 cm (C) Embryo from a litter of 15 with mean TL=52.0 cm and mean mass=2.000 kg with large yolk stomach of estimated dimensions 19 × 12 cm (no. 16 in Table 1). (D) Embryo from a litter of 9 (mean TL=59.9 cm, mean mass=2.426 kg, mean yolk mass=29.1%, mean HSI=3.7%) dissected to show yolk stomach, spiral valve, and right liver lobe. Upper jaw cartilage is visible and emerging adultlike teeth are present in both jaws (no. 20 in Table 1). Scale bar, 30 cm.

( $n=17$ ) and overlapped considerably with that in mature sharks which had a range of 1–8 mm ( $n=26$ ). The blastodisc ova appeared to be 6–8 mm in diameter, given the MOD of 8 mm and the estimated spherical diameter of 7 mm of the yolk sac of a 3-cm embryo (Fig. 2B). Nutritive eggs appeared to have a slightly smaller diameter at 4–6 mm. This diameter was based on a MOD of 6 mm for the female in early pregnancy (Fig. 2B) and on the 4-mm ova found in the uteri of two fertilized South African females (Table 2). A spent ovary in a female with large embryos also contained 6-mm ova (Fig. 2B).

The oviducal gland remained undeveloped until the onset of maturity and then increased rapidly in

diameter in females of 2.7–3.0 m, as they matured (Fig. 2C, western North Atlantic specimens only). The range in immature fish was from 0.1 to 1.1 cm ( $n=32$ ). There was considerable overlap in the diameter of the adolescent oviducal gland, ranging from 2.5 to 4.7 cm ( $n=11$ ) and in the diameter of mature females, ranging from 2.3 to 5.1 cm ( $n=19$ ). The oviducal gland diameter of two pregnant females, one with early-term, the other with near-term embryos, were similar (4.9 and 4.2 mm, respectively) to that of nonpregnant mature females.

Uterus width provided the best indication of maturity. There was little overlap between immature females in the range of 0.3–6.5 cm (mean 1.6, SE=0.2,



$n=58$ ) and mature females in the range of 5.0–22.7 cm (mean 10.7, SE 0.7,  $n=44$ ) (Fig. 2D). The uterus widths of pregnant (with egg cases or embryos) and nonpregnant females overlapped.

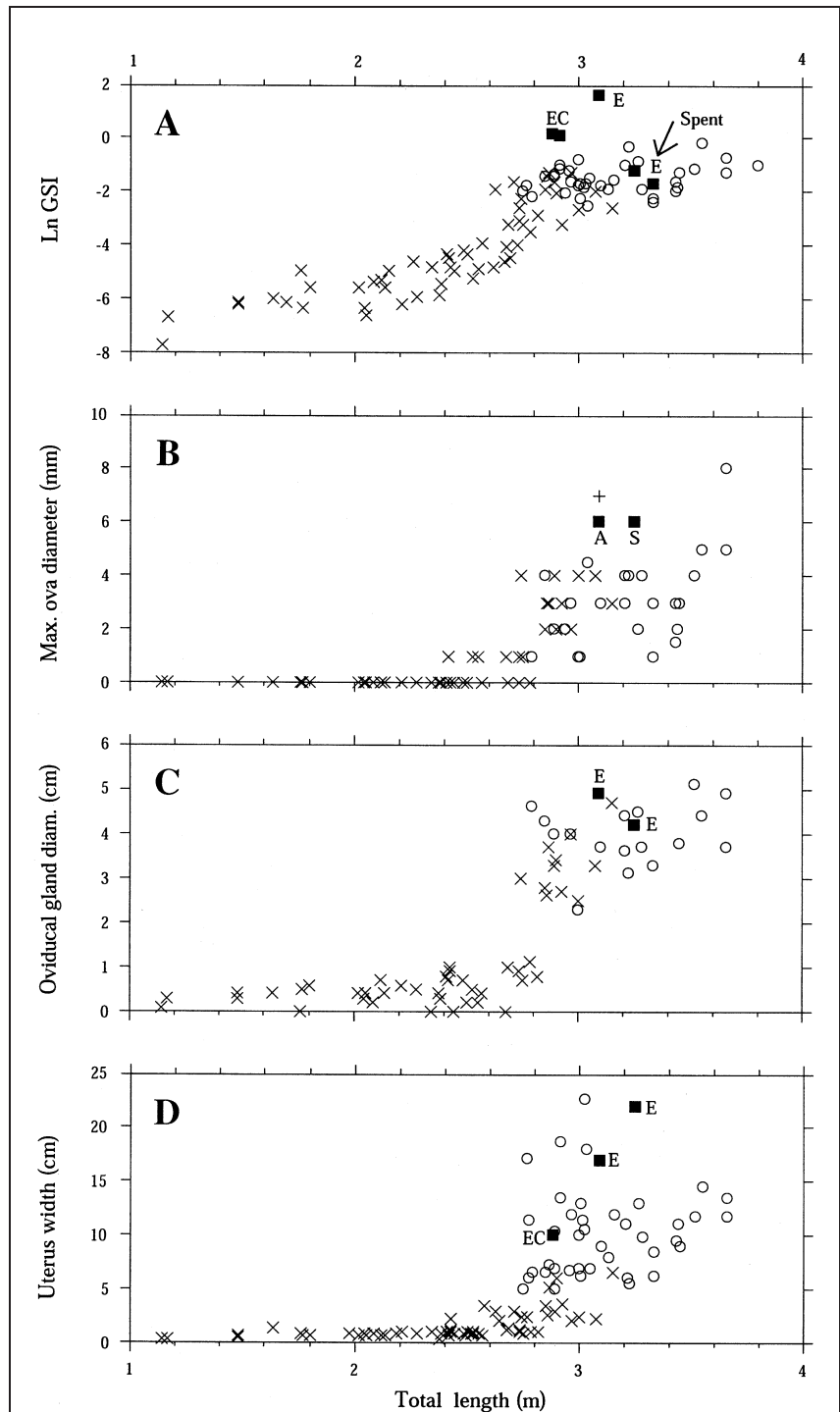
The HSI of immature and mature females in the TL range of 0.73–3.66 m varied from 1.2 to 17.9% and the overall mean HSI of 6.7% (SE=0.25%,  $n=161$ ) was a little lower than the HSI of near-term embryos (see below). The large HSI range of immature females (1.2–17.6%,  $n=125$ ) was almost the same as that of mature females (2.5–17.9%,  $n=36$ ).

### Gestation and parturition

The capture of two females with litters containing 3.0- and 52-cm embryos (Table 2, nos. 3 and 4) in the same month (January) and location (Puerto Rico) suggested that gestation is longer than one year. Assuming a gestation in excess of 12 months, the mean embryo length for 26 litters and the length for 188 age-0+ fish from both the Northern and Southern Hemisphere were graphed against season of capture (Fig. 3A). Based on the three females caught in early pregnancy (Table 2), ovulation takes place in fall. Parturition occurs in late winter to mid-spring at ca. 70 cm. The length-at-capture data of the age-0+ fish indicated a smooth continuation of the growth rate evident *in utero*.

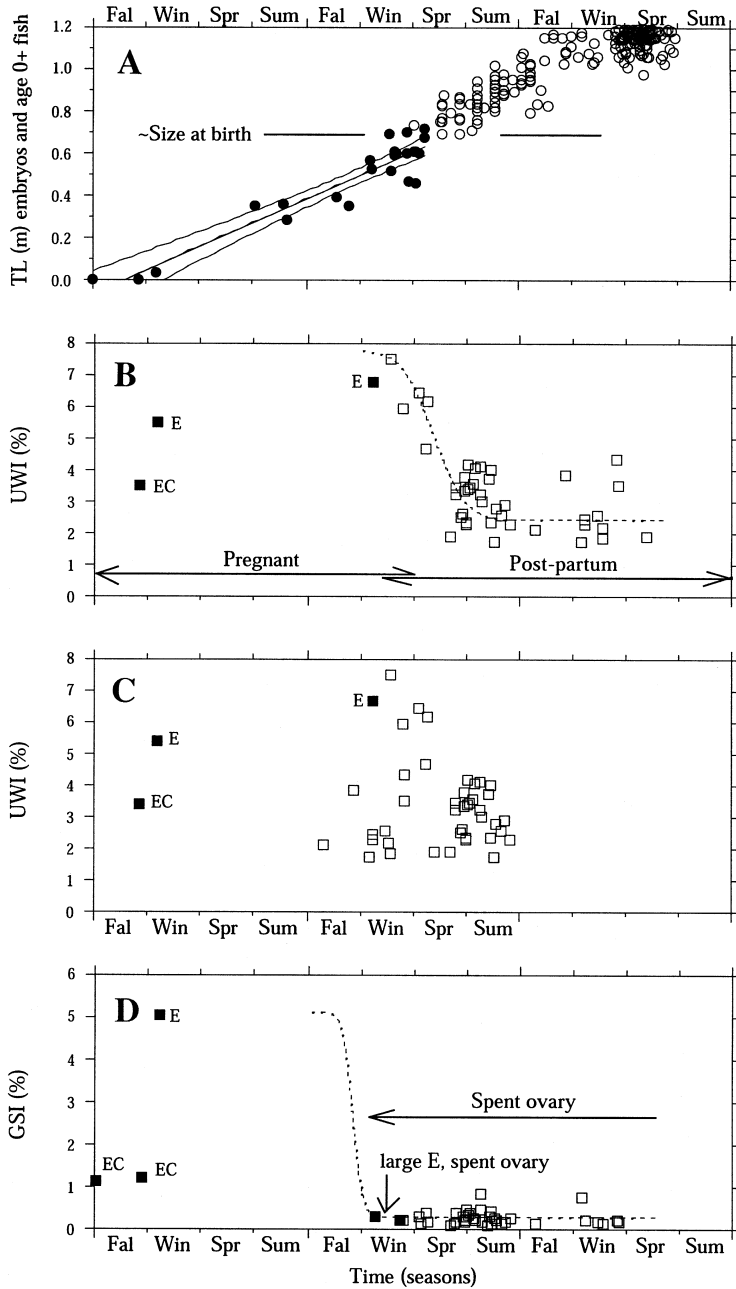
The relationship between embryo length and time of capture of all western North Atlantic litters ( $n=7$ , slope=3.7 cm/month, SE=0.6 cm/mo.,  $P=0.002$ ,  $r^2=0.87$ ) predicted a gestation of 19 months. The combined Northern Hemisphere data, which include five mid-term litters, yielded a gestation of 20 months ( $n=11$ , slope=3.4 cm/month, SE=0.05 cm/mo.,  $P<0.001$ ,  $r^2=0.84$ ).

There were no mid-term litters from the Southern Hemisphere. If the two females with recently fertilized



**Figure 2**

The relationships between four reproductive parameters and length of female *Isurus oxyrinchus*. (A) Natural logarithm (Ln) of gonadosomatic index (GSI) was used. (B) Maximum ova diameter. Lack of, or very small oocytes, are indicated by 0 diameter. A = female with active ovary and 3-cm-TL embryos; + = diameter of yolk sac of 3-cm-TL embryo; S = female with spent ovary and 52-cm-TL embryos. (C) Oviducal gland diameter of western North Atlantic specimens. (D) Uterus width. (■) = pregnant; (○) = mature, not pregnant; (×) = immature and adolescent; (●) = embryos present; (●) = egg cases with single ovum present.)



**Figure 3**

Gestation, parturition, and reproductive cycle of *Isurus oxyrinchus*. (A) The relationships between length of embryos and age-0+ fish, and time of capture. Regression with 95% confidence band for the line of combined embryo data from Northern and Southern Hemispheres is shown. ●=embryos; ○=age-0+ fish. (B) Temporal uterus width index (UWI) of mature females based on a 3-year reproductive cycle. The dotted line was fitted to the data by eye. (C) Temporal UWI of mature females based on a 2-year reproductive cycle. (D) Temporal gonadosomatic index (GSI) based on a 3-year reproductive cycle. The dotted line shows suggested decrease of GSI during last third of gestation. (■=pregnant; □=mature, not pregnant; E=embryos present; EC=egg cases with single ovum present).

ova (Table 2, nos. 1 and 2) are more than one year apart from the near-term litters (on the basis of the Northern Hemisphere data), the regression predicted a 19-mo. gestation period ( $n=15$ , slope=3.7 cm/mo., SE=0.3 cm/mo.,  $P<0.001$ ,  $r^2=0.92$ ). It is also possible to fit these data with a regression that predicts a 6.7-mo. gestation period ( $n=15$ , slope=10.4 cm/mo., SE=1.8 cm/mo.,  $P<0.001$ ,  $n=15$ ,  $r^2=0.73$ ).

The intercept and slope of Northern and Southern Hemisphere regressions, assuming a gestation longer than 12 months, were not significantly different ( $P=0.8$  and  $0.7$ , respectively) and the combined regression was

$$\text{Embryo TL (cm)} = 3.71 (\text{SE} = 0.27)T, \\ (P < 0.001, r^2 = 0.89, n = 26)$$

where  $T$  = the number of months since midfall.

It predicted a gestation period of 15–24 months (19 for the line) with 70 cm for the size-at-birth (Fig. 3A). However, we suggest the shorter estimate is more realistic because parturition appears to be a little earlier than what was indicated by the regression. The GM regression line (not shown) was slightly steeper than the  $y$ -on- $x$  regression and predicted a gestation of 17.8 months. The GM regression reflects the functional relationship better because of the uncertainties of several dates. Therefore, we concluded that the best estimate for the gestation is 15–18 months. When the three early-term litters with fairly high leverage ( $L=0.2$ – $0.35$ ) were excluded, the gestation was still around 18 months based on a significant regression ( $P=0.001$ ) with a slope of 3.8 cm/month (SE= 0.6,  $n=23$ ).

**Reproductive cycle**

A three-year reproductive cycle provided the best fit to the temporal UWI data. UWI increased in early-term females and reached a maximum of 7–8% at parturition (Fig. 3B). The pregnant female with the 52-cm embryos and UWI of 6.8% would be expected to give birth

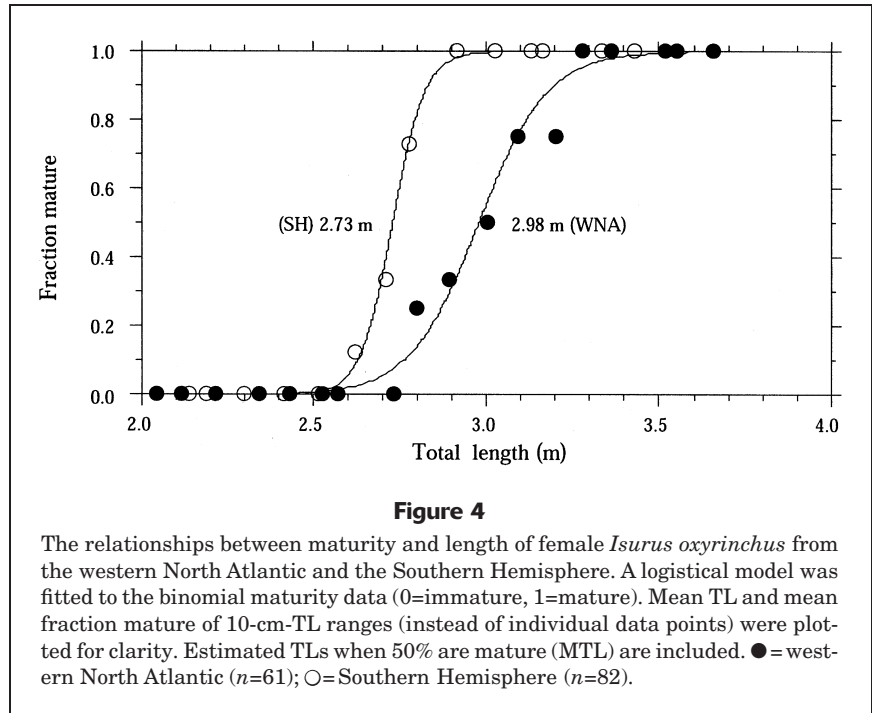
about 3–4 months later and have a UWI around 7% at that time. The UWI decreased in postpartum females over a 6 month period to values around 2–4% (Fig. 3B, curve fitted by eye). With a 2-year cycle, UWI showed no decreasing pattern for postpartum females and low UWI values between 2% and 4% extended over almost the entire second year of the reproductive cycle (Fig. 3C). This result would suggest aseasonal parturition; however, this conclusion is in conflict with the observed seasonal parturition indicated by Figure 3A.

The GSI was not as useful in determining the length of the reproductive cycle because it decreased during pregnancy. Recently ovulated females had a GSI of 1.1% and an early-term female had an estimated GSI of about 5% (Fig. 3D). We suggest that the GSI remains high until the embryos are about 40–50 cm long, and then decreases (Fig. 3D, curve fitted by eye). Two females with large embryos (mean: 52.0 and 59.9 cm) had low GSIs of ~0.3% and 0.185%, respectively, indicating that ovulation had ceased (spent ovary). The GSI during at least the last quarter of gestation (i.e.  $\geq 4$  months) was similar to that of postpartum females (mean: 0.26%, SE=0.03%,  $n=38$ ). When we tried to fit the GSI data with a 2-year cycle, we found that data for six postpartum females caught in winter (five from South Africa) overlapped with those for the two pregnant females with large embryos. This would extend parturition into fall and would conflict with convincing seasonal parturition data (Fig. 3A).

The remaining reproductive parameters were not helpful in determining the reproductive cycle. No temporal pattern was evident for MOD. Oviducal gland diameters were available mostly for summer captures only and possible temporal changes could not be investigated. There was no clear temporal pattern in the HSI because we had few data for pre-ovulating and early-term pregnant females.

### Regional differences

The scarcity of data precluded a meaningful statistical comparison of many reproductive parameters for female shortfin makos from different regions. However, we were able to substantiate differences for mass and length-at-maturity for females from



the western North Atlantic and the Southern Hemisphere (South Africa and Australia; no data were available from Brazil).

Western North Atlantic females were significantly heavier by 19–66 kg or 16–19% than Southern Hemisphere females ( $P<0.001$  in TL range 2.5–3.5 m). The latter data were combined because the power regressions for South African ( $n=47$ ) and Australian females ( $n=22$ ) were not statistically different ( $P=0.164$ ,  $F^*<F(0.95,2,65)$ ). The back-transformed M-TL relationships were

$$M=7.299 TL^{3.224} \quad (n=63, r^2=0.94, \text{ western North Atlantic females } 2.0\text{--}3.7 \text{ m TL});$$

$$M=6.824 TL^{3.137} \quad (n=69, r^2=0.90, \text{ Southern Hemisphere females } 2.0\text{--}3.4 \text{ m TL}).$$

The median TL-at-maturity (MTL) of 61 western North Atlantic females (2.98 m, SE=0.045) was significantly larger by 25 cm ( $P<0.001$ ,  $F^*>>F(0.95,2,147)$ ), than that of 82 Southern Hemisphere females (2.73 m, SE=0.02 m) (Fig. 4). The data from South Africa and Australia were combined because MTL in South Africa was only 11 cm smaller than MTL in Australia and the length of these fish was not measured consistently. The maturation size of western North Atlantic sharks extended from 2.76 m, when 10% were mature, to 3.20 m when 90% were mature and was 16–35 cm larger than that in the Southern Hemisphere, where the range was 2.60–2.85 m. The largest immature female from the western

North Atlantic (3.15 m) was a virgin. The smallest mature female from the Southern Hemisphere of 2.63 m was pregnant (no. 23 in Table 1).

### Liver-, yolk-, and total mass of embryos

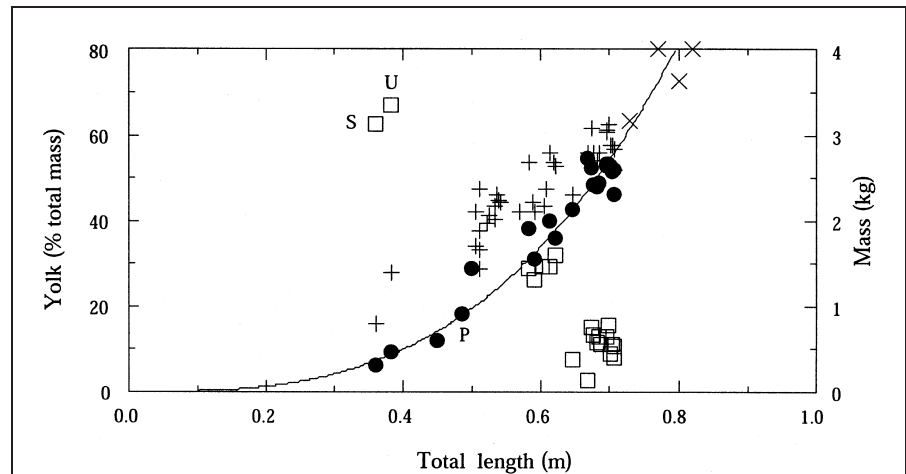
There was a significant positive relation between the HSI and the length of near-term embryos, rising from 3.8% in a litter with a mean length size of 59.9 cm to 7.0% in a litter with a mean length size of 68.8 cm. The slope was 0.34%/cm (SE=0.04%/cm,  $P < 0.001$ ,  $r^2=0.83$ ,  $n=17$ ). The TL range of the embryos in these two litters was small (12.5 cm) but they covered almost 50% of the HSI range. The increasing HSI was accompanied by a corresponding decrease in the amount of yolk in the stomach from 29.1% to 10.9% of total mass. The yolk percentage versus TL regression was significant with slope  $-1.64\%/cm$  (SE= 0.33%/cm,  $P < 0.001$ ,  $r^2=0.62$ ,  $n=17$ ).

The mass-length relationship of embryos is complicated owing to the highly variable mass of the yolk-filled stomach. The scarce data indicated that the yolk mass amounts to 60–70% of total mass for mid-term litters and then decreases to around 10% in a full-term litter (Fig. 5, y-axis on left). When the mass of the yolk-filled stomach was subtracted from the total mass, a power regression could be fitted to net embryo mass ( $M_{net}$ ) (Fig. 5, y-axis on right). The back-transformed equation was

$$M_{net} = 8.198 TL^{3.117}$$

( $n=21$ ,  $r^2=0.98$ , TL range= 0.36–0.71 m).

The mass of the smallest free-swimming fish agreed with the predicted mass based on the extrapolated curve beyond the upper limit of the embryo data (Fig. 5). The corresponding condition factors of shortfin mako embryos ( $CF_{net} = M_{net}/TL^3$ ) were between 7.3 and 7.9 kg/m<sup>3</sup> and were similar to postnatal values. If the mass of the yolk-filled stomach was included, the condition factor ( $CF = M/TL^3$ ) reached values as large as 26 kg/m<sup>3</sup> when the embryos were mid-term and had the largest yolk stomachs (Fig. 6, *I. oxyrinchus* data).



**Figure 5**

The relationships between 1) yolk % (left y-axis), 2) embryo mass with and without yolk (right y-axis), and length of *Isurus oxyrinchus* embryos. A power regression was fitted to embryo mass without yolk data. □ = yolk %; ● = embryo mass without yolk; + = embryo mass with yolk; × = mass of free swimmers; S = Sanzo (1912); U = Uchida et al. (1987); remaining data from this study including P = upper and lower limit of mass range of litter with punctured yolk-stomachs.

## Discussion

### Embryonic development

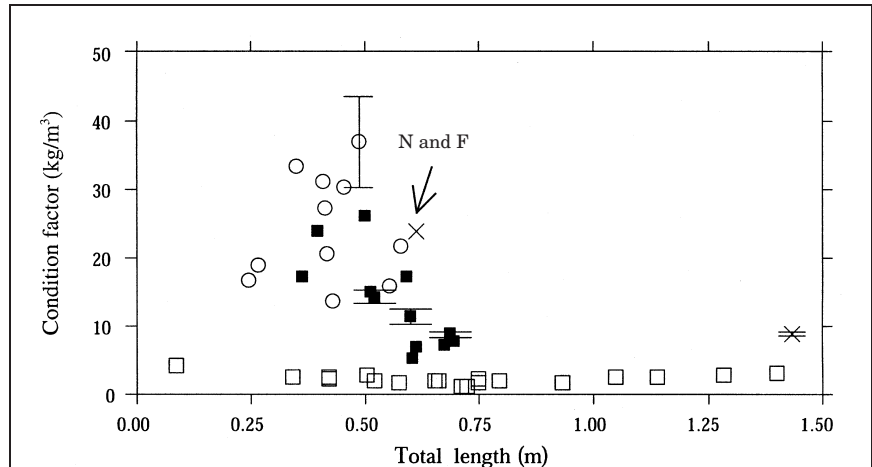
Our data documented early and late embryonic development of the shortfin mako. As expected, it was similar to that reported for other lamnids (Swenander, 1907; Lohberger, 1910; Otake, 1990; Gilmore, 1993; Francis and Stevens, 2000) in which the embryos hatch at about 6 cm TL and then feed on nutritive eggs (oophagy) until the beginning of the last third of the gestation period. Embryonic nutrition may also include egg jelly absorbed through the external gill filaments in the prehatching phase and uterine milk in the posthatching phase (Hamlett, et al. 1985; Gilmore, 1993; Koob and Straus, 1998).

After mating, the largest of the relatively small ova are ovulated, fertilized, and packaged into egg cases (one blastodisc ovum per egg case) as evident in three cases in our study (Table 2). The diameter of these blastodisc ova appears to be slightly larger (~7 mm) than the nutritive ova (4–6 mm) and the ova remaining in the ovary (4–6 mm); this larger diameter may also apply to other lamnids and lamnoids. Mating may stimulate the enlargement of the largest ova in the ovary and trigger subsequent ovulation. The capsules with nutritive ova are formed after the blastodisc ova have been encapsulated. Blastodisc egg cases with only one fairly large ovum were observed in the bigeye thresher shark, *Alopias superciliosus* (Moreno and Morón, 1992). In

the sandtiger shark, the blastodisc capsules contain up to 14 blastodisc ova, but only one egg develops and absorbed material and other encapsulated ova contribute more to initial development than does the yolk sac (Gilmore et al., 1983). A possible early-term great white shark had a total of 192 egg cases of three types of different size and mass in the left uterus, but the size and number of the ova were not reported (Uchida et al., 1987).

We observed 3-cm-TL shortfin mako embryos still attached to a relatively large yolk sac and inside egg cases (Fig. 1A). It is not clear at what size the embryos hatch from the egg cases, possibly 5–6 cm, the size at which porbeagle (*Lamna nasus*) and sandtiger sharks hatch (Swenander, 1907; Gilmore et al., 1983). This estimate agrees with an estimate of the embryo TL calculated from the diameter of the blastodisc ovum (Mollet, unpubl. data). Bigeye thresher embryos hatch at a slightly larger size (7–8 cm FL) because their yolk sac diameter (11 mm) is greater than that of porbeagle and sandtiger sharks (Chen et al., 1997).

During the oophagous embryonic phase, lamnids develop huge yolk-filled stomachs, sandtiger sharks develop large yolk-filled stomachs, and alopiids develop only slightly extended yolk-filled stomachs according to photographs and our calculated condition factors (Nakamura, 1935; Gilmore et al., 1983; Moreno and Morón, 1992; our Fig. 6 for lamnids and alopiids). The condition factors of the shortfin mako (our data and references in Table 1), the porbeagle (Templeman, 1963; Francis<sup>9</sup>), the salmon shark, *Lamna ditropis* (Lohberger, 1910; Otake, 1990), and the great white shark (Norman and Fraser, 1938) reach a maximum between 20 and 35 kg/m<sup>3</sup> when the embryos are midterm. The condition factor decreases in the last third of gestation and approaches values similar to those of postnatal lamnids (our data for the shortfin mako; Francis and Stevens (2000) for the porbeagle; Uchida et al., 1996; Francis, 1996 for the great white shark). The yolk-stomach in the sandtiger shark reaches its largest size between 33.4



**Figure 6**

The relationship between condition factor ( $M/TL^3$ ) and TL of lamnid and alopiid embryos. Error bars give  $\pm 2$  SE of mean, if available. ■ = *Isurus oxyrinchus*; ○ = *Lamna* spp.; × = *Carcharodon carcharias*; □ = *Alopias* spp. See Table 1 for sources of *I. oxyrinchus* data. *Lamna* spp. data from Lohberger (1910); Templeman (1963); Otake (1990); Francis;<sup>9</sup> Otake<sup>10</sup>. *Carcharodon carcharias* data from Norman and Fraser (1938, NandF); combined Francis (1996) and Uchida et al. (1996). *Alopias* spp. data from Joseph (1954); Cadenat (1956); Gubanov (1972); Hixon (1979); Gilmore (1983); Moreno and Morón (1992); Otake (1990).

and 80 cm TL, but no embryo masses were reported by Gilmore et al. (1983) and therefore the condition factor could not be calculated. The condition factors of thresher shark embryos are much smaller if TL rather than PCL is used as the length parameter. However, if the alopiids were to develop a large yolk-filled stomach, then the condition factor of mid-term embryos would be considerably larger compared with that of early- and near-term embryos, which is not the case (Fig. 6). The embryonic development of alopiids proceeds at a steady rate without development of a large yolk-filled stomach and we expect ovulation of nutritive ova right up to parturition. Francis and Stevens (2000) have suggested that the puzzling gross abdominal distention observed in porbeagle embryos (and other lamnids) is energetically inefficient for the pregnant female.

The HSIs of shortfin mako embryos from a full-term litter were between 5% and 8% and the yolk-stomach constituted 3–15% of body mass. These combined nutrient reserves may provide neonates with nutrition while they improve their hunting ability. From the metabolic rate of a shortfin mako pup reported by Graham et al. (1990) (1.5% of body mass/d), we estimated that a 20% reserve would enable pups to survive for about 20–30 days. This

<sup>9</sup> Francis, M. P. 1997. National Institute of Water and Atmospheric Research (NIWA), P.O. Box 14-901, Wellington, New Zealand. Personal commun.

<sup>10</sup> Otake, T. 1998. Mie University, 1515 Kamihama, Tsu, Mie 514, Japan. Personal commun.

estimate agrees with the observation that a sandtiger pup born in captivity at Sea World of Orlando did not eat until 25 d after birth (Gilmore et al., 1983). By comparison, HSI values of 13–19% were recorded in three great white shark full-term embryos with stomach yolk mass between 0% and 4% (Francis, 1996; Uchida et al., 1996). A near-term 97-cm-TL longfin mako, *Isurus paucus*, embryo had a large liver but surprisingly small amounts of yolk in the cardiac stomach (0.54%) (Gilmore, 1983).

There is no convincing evidence<sup>11</sup> to confirm that older shortfin mako embryos eat smaller ones while in the uterus, as claimed by Tricas et al. (1997). They possibly inferred this conclusion from a misleading statement in Compagno (1988, p. 83).<sup>12</sup> Costa et al.<sup>13</sup> suggested that uterine cannibalism occurs on the basis of a piece of lower jaw found in the stomach of a term embryo. This behavior is difficult to explain, and Francis (1996) observed only shed teeth in the stomach of a great white shark full-term embryo. We expected to but did not find any shed teeth in the stomach of near-term embryos. Embryonic cannibalism has only been documented in the sandtiger shark (Gilmore et al., 1983) and seems unlikely in the shortfin mako with a litter size as high as 25–30.

### Litter size

Data on litter size of shortfin makos were scarce and possibly biased by low values due to abortion during capture and the reported large value of 25–30 in Sanzo (1912). The lowest values of 4–6 were for near-term litters (TL~60 cm) reported anecdotally by game fishermen. Although we are sure they are reliable, they should be taken as minimum estimates because such low values suggest abortion during capture, especially for near-term litters. Abortion is unlikely for mid-term embryos with their huge yolk stomachs.<sup>11</sup> A means model test was not conclusive because litter size also depends on maternal size, which was not available for five near-term litters. The number of embryos in the Sanzo (1912) litter was also based on information from a fisherman; however, a study of the original Italian text has sug-

gested that the value of 25–30 is reliable.<sup>7</sup> Although western North Atlantic females are slightly heavier than females of similar size from South Africa and Australia, there were no regional differences in litter size between the two regions.

The mean litter size of 12.5 is larger than that for other lamnids, although data for some species are scarce. The longfin mako has a mean litter size of four (range 2–8,  $n=3$ , Compagno, 1984; Killam and Parsons, 1986; Casey<sup>14</sup>). The mean litter size of the great white shark is 8.9 (range: 4–14,  $n=11$ ; Francis, 1996; Uchida et al., 1996). A single litter of four was reported for the salmon shark (Otake, 1990). The litter size of the porbeagle is 2–5, mostly 4 (e.g. Swenander, 1907; Templeman, 1963; Francis and Stevens, 2000). A weak relationship between litter size and maternal length in the shortfin mako also exists for the great white shark (based on data in Francis, 1996). A positive relation between litter size and maternal size has been observed for many carcharhinids (Compagno, 1988).

### Indicators of sexual maturity

The GSI was not conclusive in determining sexual maturity in lamnids because near-term and post-partum females both have low values. In oophagous sharks the ovary continues production to nourish the embryos well into gestation, thus producing high GSIs. The large variations in ovary size in mature shortfin makos (0.2–12 kg; GSI ~0.1–5.0%) were as expected. Data from other lamnids are scarce. A longfin mako with near-term embryos had a spent ovary with GSI=0.46% (Gilmore, 1983). Active ovaries in mid-term porbeagles weighed 2.75 kg (GSI 2.35%) and 6.3 kg (GSI 3.6%) (Francis and Stevens, 2000; Swenander, 1907). Arfelli and de Amorim<sup>15</sup> observed a 12-kg ovary (GSI 0.48%) in a nonpregnant 5.3-m-TL great white shark.

We found that MOD was not useful for determining maturity in shortfin makos, whereas it is in sharks without oophagy (e.g. Pratt, 1979; Peres and Vooren, 1991; Parsons, 1993). The values near the upper limit of the observed range (1–8 mm, Fig. 2B) were similar to values (5–11 mm) reported for other lamnids (Swenander, 1907; Gilmore, 1983; Bruce,

<sup>11</sup> Gilmore, R. G. 1999. Dynamic Corp., Kennedy Space Center, FL 32899. Personal commun.

<sup>12</sup> Compagno, L. V. C. 1998 and 1999. Shark Research Centre, P.O. Box 61, 8000 Cape Town, South Africa. Personal commun.

<sup>13</sup> Costa, F. E. S., F. M. S. Braga, A. F. Amorim, and C. A. Arfelli. 1995. Reproductive biology of shortfin mako, *Isurus oxyrinchus*, Rafinesque 1809. Resumos VII Reunião do Grupo de Trabalho sobre Pesca e Pesquisa de Tubarões e Raias do Brasil<sup>1</sup>. Rio Grande, November 20–24, 1995. Fundacao Universidade do Rio Grance, FURG Rio Grande, RS Brasil.

<sup>14</sup> Casey, J. 1986. Distribution of the longfin mako (*Isurus paucus*) in the northwest Atlantic. Program and Abstracts ASIH and AES Annual Meeting, Victoria BC, Canada, 15–21 June 1986, no page numbers.

<sup>15</sup> Arfelli, C. A., and A. F. de Amorim. 1993. Notes on the white shark (*Carcharodon carcharias*) caught off Cananéia, São Paulo-Brazil. Program and Abstracts ASIH and AES Annual Meeting. The University of Texas at Austin, 27 May–2 June 1993, 348 p.

1992; Francis and Stevens, 2000) and lamnoids (Matthews, 1950; Gilmore et al., 1983; Chen et al., 1997; Yano et al., 1999). The report of a 50-mm diameter egg in the ovary of a 3.37-m-TL shortfin mako with an empty uterus (Applegate, 1966) is inexplicable.

Uterus width was the most suitable reproductive parameter for distinguishing between immature and mature female shortfin makos and also between different reproductive stages of mature females. Our data indicated that immature shortfin mako have UWIs between 0.17% and 2.1%, whereas mature shortfin makos have UWIs between 1.7% and 7.5%, with the largest values occurring at parturition and in early postpartum females (Fig. 3B). Little comparative data for other lamnids were available. Two immature great white sharks of 4.8 m and 4.9 m had a UWI of 2.1% and 1.6%, respectively.<sup>12, 16</sup> A 5.2-m-TL great white shark had a UWI of 7.7%; this fish may have recently given birth (Stevens, unpubl. data). However, a 5.2-m, 1520 kg female reported by Bruce (1992) to be mature, and bearing possible mating scars had UWIs of only 0.88–1.0% (left) and 0.44–0.56% (right); these values appear to be far too small for a mature shark of this size.

Our study failed to confirm the potential of HSI as a good indicator of reproductive status. Our sample size was large (immature,  $n=125$ ; mature,  $n=35$ ); however, we had few data for pregnant fish. Cliff et al. (1990) observed the highest HSIs in two recently fertilized females, which also had high GSIs. Their observations suggested that HSI might be useful as an indicator of reproductive status; however, their sample size was small ( $n=12$ ). They also noted that the HSIs of males were just as variable and covered about the same range (2.9–13.7%). For sharks with long gestation period, the HSI may not be tied closely to the reproductive cycle. Because the shortfin mako has a high metabolic rate (Graham et al., 1990), reserves in the liver cannot be expected to last longer than a few weeks.

### Gestation period

A small number of early and mid-term litters from the western North Atlantic and the Northern Hemisphere supported a gestation period in excess of 12 months. By contrast, the absence of measured mid-term litters from the Southern Hemisphere made it possible also to fit the data with a 6–7 month gestation period. It is highly unlikely that a regional difference of this magnitude could exist in a widely distributed species such as the shortfin mako. It is

therefore most probable that the duration of gestation is 15–18 months in both hemispheres.

Is a 6–7 month gestation possible for the Northern Hemisphere? Reproductive asynchrony (where individuals in an accessory population are out of phase with the principal population) is a possibility for wide-ranging oceanic sharks, and was suggested for the great white shark (Lineaweaver and Backus, 1970). For our shortfin mako data, we would have to propose that the early-term (no. 3 in Table 1) and all five mid-term litters (nos. 4–8) belong to the accessory population(s). However, the gestation period becomes indeterminate when these litters are excluded from the calculations. It is far more probable that these pregnant females belong to the principal populations, should this theory apply to the shortfin mako, and that the gestation period is 15–18 months. Additional data would be needed to test the hypothesis of reproductive asynchrony for elasmobranchs.

No embryo length data were available for an early fall litter from the Southern Hemisphere (no. 9 in Table 1). If the gestation period were 6–7 months, this litter would have been at the blastodisc stage (as were litters no. 1 and no. 2 in Table 2) and might have been overlooked without detailed examination of the uterus. If the gestation period was 18 months, the embryos of this litter would have been 35–45 cm long and would have been observed (as they were) during gutting of the pregnant fish on the boat.

Body temperature may account for some of the difference in the gestation between the shortfin mako (15–18 months) and the porbeagle (9 months in both hemispheres; Francis and Stevens, 2000). The porbeagle and the salmon shark possess a sizable kidney rete, which is not found in the shortfin mako, and body temperatures are in general higher in *Lamna* than in *Isurus*.<sup>17</sup> Cloacal temperature measurements from 21 salmon sharks had a mean of 23.3°C (SD=1.1°) which is probably most representative of the uterus area.<sup>17</sup> This temperature could be 5°C higher than the temperature of the uterus in the shortfin mako, which prefers water temperatures around 18°C and is known for vertical movements into colder water (Casey and Kohler, 1992; Carey and Scharold 1990; Holts and Bedford, 1993).

Our litter of 3.0-cm-TL embryos confirmed slow shortfin mako embryonic development, at least during the early stage. These very early-term embryos were found next to more than 40 nutritive egg cases in each uterus (Fig. 1B, Table 2). Gilmore (1993) reported that

<sup>16</sup> Bruce, B. 1998. CSIRO Marine Research, P.O. Box 1538, Hobart, Tasmania 7001. Personal commun.

<sup>17</sup> Goldman, K. 1998. Virginia Institute of Marine Science (VIMS), P.O. Box 1346, Gloucester Pt., VA 23062. Personal commun.

production of empty and blastodisc egg cases preceded that of nutritive egg cases in the sandtiger shark and that each oviducal gland produced one egg case per day. We observed that blastodisc egg cases preceded the nutritive egg cases in the shortfin mako (no. 2 in Table 2). Therefore, the 2.7–3.3 cm TL embryos would be about 40–50 days old. They were at a very early stage of development because the yolk sac was almost intact, and oophagy may not begin until the embryos are about 3–4 months old and 5–6 cm long.

The gestation period of the shortfin mako is about twice as long as that of the sandtiger shark (9 months; Cliff, unpubl. data), which has a term litter mass (13 kg), about half that of the shortfin mako (25–40 kg). Scant ovary data for the shortfin mako and extensive ovary data for the sandtiger shark (Gilmore et al., 1983; Cliff, unpubl. data) suggested that the masses of ovulating ovaries are similar in the two species. The shortfin mako would therefore require about twice as long to nourish a litter double the weight of that of the sandtiger shark.

Our interpretation of reported great white shark data suggested that the gestation is longer than one year and probably similar to that of the shortfin mako. Parturition is in late spring (Klimley, 1985; Francis, 1996; Uchida et al., 1996). Uchida et al. (1987; 1996) suggested that a 5.55-m-TL, 1970-kg female captured in mid-February had aborted an entire litter of near-term embryos. However, the presence of almost 200 egg cases in the left uterus (weighing 9 kg) and the robust appearance of the specimen, probably due to a large liver, suggest that this great white shark was at an early stage of gestation. Further support for our gestation estimate of about 18 months was the capture of a great white shark with a midterm litter of nine embryos in the summer of 1934 (Norman and Fraser, 1938). Length and mass of these embryos (61 cm TL, 5.4 kg as suggested by Ellis and McCosker, 1991) were as expected for midterm embryos with a large yolk-filled stomach ( $M/TL^3=23.8 \text{ kg/m}^3$ , Fig. 6) and birth was expected 9 months later in spring.

Gestation periods longer than 12 months were reported for the whitetip reef shark, *Triaenodon obesus* (13.5 mo.), the tiger shark, *Galeocerdo cuvier* (13–16 and 15–16 mo.), the dusky shark, *Carcharhinus obscurus* (22 mo.), and the spiny dogfish, *Squalus acanthias* (18–24 mo.) (Compagno, 1984; Uchida et al., 1990; Randall, 1992; Musick et al., 1993; Crow<sup>18</sup>). The basking shark, *Cetorhinus maxi-*

*mus*, probably has a gestation period longer than 12 months, but we agree with Pauly<sup>19</sup> that the reported gestation period of 3.5 years by Parker and Stott (1965) was based on fallacious reasoning.

### Parturition in Northern and Southern Hemispheres

Based on a few full-term litters and a large number of neonates, parturition occurred mainly in late winter to midspring in both hemispheres (Fig. 3A). Pratt and Casey (1983) reported “late spring parturition” in the western North Atlantic, but April should be called early spring; and the data in their Figure 3 suggest that parturition begins as early as late February (late winter). Other large pelagic and near-shore sharks have seasonal parturition in late spring to early summer in both hemispheres (e.g. Bass et al., 1973; Pratt, 1979; Klimley, 1985; Randall, 1992; Musick et al., 1993; Francis, 1996; Crow<sup>18</sup>). Parturition of the porbeagle peaks in June–July in both hemispheres which Francis and Stevens (2000) found puzzling.

### Reproductive cycle and resting period

Given a gestation period of about 18 months and a distinct seasonal spring parturition, the reproductive cycle for shortfin makos is either 2 or 3 years. There were insufficient data to determine its duration conclusively, but a 2-year cycle would only allow a recovery period of some 6 months, which would appear to be insufficient. Our temporal UWI data (Fig. 3B) support a 3-year reproductive cycle, which would mean an 18-month resting period.

There is conflicting evidence about the need for a resting period after parturition in elasmobranchs. For many medium to large sharks a resting period has been documented. Peres and Vooren (1991) reported a 3-year reproductive cycle for the soupfin shark, *Galeorhinus galeus*, off southern Brazil with a gestation of 12 months. The gestation for the whitetip reef shark is 13.5 months and the reproductive cycle is 2 or 3 years (Uchida et al., 1990). Musick et al. (1993) suggested that the sandbar shark, *Carcharhinus plumbeus* (with one-year gestation), must have a resting period of at least one year, requiring a 2-year reproductive cycle. The 2-year reproductive cycle for the sandtiger shark with 8–9 mo. gestation period is well documented (Branstetter and Musick, 1994; Cliff, unpubl. data). Tagging and cap-

<sup>18</sup> Crow, G. L. 1995. The reproductive biology of the tiger shark, *Galeocerdo cuvier*, in Hawaii: a compilation of historical and contemporary data. Program and Abstract ASIH and AES Annual Meeting, University of Alberta, Edmonton, Alberta, Canada, June 15–19 1995, 229 p.

<sup>19</sup> Pauly, D. 1978. A critique of some literature data on the growth, reproduction and mortalities of the lamnid shark *Cetorhinus maximus* (Gunnerus). Report to the Pelagic Fisheries Commission, International Council for the Exploration of the Seas, CM 1978/H17, Copenhagen.



tive grow-out studies indicated that the nurse shark *Ginglymostoma cirratum* has a 2-year reproductive cycle with a 3.5–4.5 months gestation and a ~20 months resting period.<sup>20</sup> A 3-yr reproductive cycle was proposed for the dusky shark and the tiger shark with 22-mo. and 15–16 mo. gestation periods, respectively (Musicke et al., 1993; Crow<sup>18</sup>). Francis and Stevens (2000) reported that gestation in the porbeagle lasts 9 months, which would allow for only a very short resting period if they have pups every year. Francis (1996) suggested that the great white shark might have little or no resting period because mating was observed immediately after parturition.

In the 3-year cycle of the shortfin mako, mating could occur either after parturition, which would require sperm storage, or after the resting period and before ovulation. Two recently fertilized shortfin makos from South Africa caught in March and June had fresh mating scars, suggesting mating takes place in late summer–fall before ovulation. It may be selectively advantageous for mating to occur in summer–fall prior to ovulation when the females appear to be in a different geographical area, rather than after parturition in spring of the previous year near the pupping grounds, because both sexes may be feeding actively at that time.

There was an uneven distribution of reproductive stages in our shortfin mako data. Pre-ovulating and early to mid-term pregnant females were poorly represented. Casey and Kohler (1992) suggested that adult females remain far offshore in more tropical waters. We propose that this suggestion applies particularly to pre-ovulating females ready to be mated and early to midterm females. Because the shortfin mako prefers 18°C water (Casey and Kohler, 1992), these females are likely to be found in deeper water and are less likely to be caught.

### Regional differences

The studies of Garrick (1967) and Heist et al. (1996) have suggested that there is only one circumglobal species of shortfin mako, *Isurus oxyrinchus*. Despite this conclusion, we found that there were significant differences in the median TL-at-maturity of females and in their mass-length relationship between the Northern and Southern Hemispheres. Small regional differences in size at maturity have been reported for a number of other elasmobranch species, including widely distributed species such as the sandbar shark (Last and Stevens, 1994), scalloped hammer-

head shark, *Sphyrna lewini* (Branstetter, 1987; Chen et al., 1990), soupfin shark (Peres and Vooren, 1991), and dusky shark, *Carcharhinus obscurus* (Natanson and Kohler, 1996). Our estimates of the duration of gestation and reproductive cycle are unlikely to be greatly affected by these differences.

Determining reproductive parameters for the large, wide-ranging and oceanic shortfin mako proved difficult. A dedicated sampling program conducted throughout the year within a particular region may still not provide the necessary data. We believe our approach of combining scarce data from widely spaced localities was justified.

### Acknowledgments

The data collected by Abner Kingman as an observer on a swordfish longliner proved to be very useful. We are most grateful to Malcolm P. Francis and Ken J. Goldman for many suggestions and for data on porbeagles and salmon sharks. We thank Fabio E. S. Costa and Alberto F. Amorim for litter data from Brazil, David W. Welch for help with the statistical analysis, Nancy E. Kohler for providing HSI data, Dave B. Holts for the California drift gillnet fishery data, and Gregor M. Cailliet for reviewing the manuscript. A large number of people provided data and useful suggestions, and we acknowledge Shelton P. Applegate, Steven Branstetter, Barry D. Bruce, José I. Castro, Tris Colket; Leonard J. V. Compagno; Gerald L. Crow; David A. Ebert, Ian K. Fergusson, R. Grant Gilmore and Oliver Putz, William C. Hamlett, Glen Hodson, Leanne Laughlin, Robert N. Lea, Jean R. C. de Marignac, Sanford A. and Barbara Moss, John A. Musick, Gavin J. P. Naylor, Giuseppe Notarbartolo di Sciarra, Tsuguo Otake, Daniel Pauly, Julian G. Pepperell, John E. Randall, Peter Saul, Jeffrey A. Seigel, Colin A. Simpfendorfer, Antonio D. Testi, and Senzo Uchida. GC wishes to thank his colleagues at the Natal Sharks Board for assistance in providing and examining specimens. HFM wishes to thank Cherilyn Chin, Juan E. Ezcurra, Scott R. Greenwald, John B. O'Sullivan, and Gilbert Van Dykhuizen at the Monterey Bay Aquarium for help and support. Anne L. Mollet proofread the manuscript. Comments by four anonymous and two NMFS reviewers helped us to focus and strengthen our findings.

### Literature cited

#### Applegate, S. P.

1966. A possible record-sized bonito shark, *Isurus oxyrinchus* Rafinesque, from Southern California. Calif. Fish Game 52:204–207.

<sup>20</sup> Carrier, J. C., and H. L. Pratt. 1998. Albion College, 4705 Kellogg Ctr., Albion, MI 49224. Unpubl. data.

- Bass, A. J., J. D. D'Aubrey, and N. Kistnasamy.**  
**1973.** Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). *Oceanogr. Res. Inst. Invest. Rep.* 33:1–168.  
**1975.** Sharks of the east coast of southern Africa. IV. The families Odontaspidae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. *Oceanogr. Res. Inst. Invest. Rep.* 39:1–102.
- Bigelow, H. B., and W. C. Schroeder.**  
**1948.** Part 1: sharks. In *Fishes of the western North Atlantic*, p. 59–546. Sears Foundation for Marine Research, Yale Univ.
- Bonfil, R.**  
**1994.** Overview of world elasmobranch fisheries. *FAO Fisheries Technical Paper* 341:1–119.
- Branstetter, S.**  
**1981.** Biological notes on the sharks of the north central Gulf of Mexico. *Contribb. Mar. Sci.* 24:13–34.  
**1987.** Age, growth and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. *Env. Biol. Fish.* 19:161–173.
- Branstetter, S., and J. A. Musick.**  
**1994.** Age and growth estimates for the sandtiger in the northwestern Atlantic Ocean. *Trans. Am. Fish. Soc.* 123:242–254.
- Bruce, B. D.**  
**1992.** Preliminary observation on the biology of the white shark, *Carcharodon carcharias*, in South Australian waters. In *Sharks: biology and fisheries* (J. G. Pepperell, ed.), p. 1–11. *Aust. J. Mar. Freshwater Res.* 43.
- Cadenat, J.**  
**1956.** Note d'ichthyologie ouest-africaine. Vol. XV: Sur un requin-renard nouveau pour la faune d'Afrique occidentale française *Alopius superciliosus* (Lowe) 1840? *Bull. Inst. Fr. Afr. Noire* 18A:1257–1266.
- Cailliet, G. M., L. K. Martin, J. T. Harvey, D. Kusher, and B. A. Weldon.**  
**1983.** Preliminary studies on the age and growth of the blue shark, *Prionace glauca*, common thresher, *Alopius vulpinus*, and shortfin mako, *Isurus oxyrinchus*, from California waters. In *Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks* (E. D. Prince and L. M. Pulos, eds.), p. 179–188. U. S. Dep. Commer., NOAA Tech. Rep. NMFS 8.
- Carey, F. G., J. G. Casey, H. L. Pratt, D. Urquhart, and J. E. McCosker.**  
**1985.** Temperature, heat production and heat exchange in the lamnid sharks. *Memo. S. Cal. Acad. Sci.* 9:92–108.
- Carey, F. G., and J. V. Scharold.**  
**1990.** Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* 106:329–342.
- Casey, J. G., and N. E. Kohler.**  
**1992.** Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the western North Atlantic. In *Sharks: biology and fisheries* (J. G. Pepperell, ed.), p. 45–60. *Aust. J. Mar. Freshwater Res.* 43.
- Castro, J. A., and J. Mejuto.**  
**1995.** Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. *Mar. Freshwater Res.* 46:967–73.
- Chen, C. T., T. C. Leu, S. J. Joung, and N. C. H. Lo.**  
**1990.** Age and growth of the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. *Pac. Sci.* 44:156–170.
- Chen C. T., K. M. Liu, and Y. C. Chang.**  
**1997.** Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839) (Chondrichthyes: Alopiidae), in the northwestern Pacific. *Ichthyological Research* 44:227–235.
- Cliff, G., S. F. J. Dudley, and B. Davis.**  
**1990.** Sharks caught in the protective gill nets off Natal, South Africa. 3. The shortfin mako, *Isurus oxyrinchus* (Rafinesque). *S. Afr. J. Mar. Sci.* 9:115–126.
- Compagno, L. J. V.**  
**1984.** *FAO species catalogue: sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis (125), vol. 4, part 1: Hexanchiformes to Lamniformes*, 249 p. FAO, Rome.  
**1988.** *Sharks of the order Carcharhiniformes*. Princeton Univ. Press, Princeton, NJ, 467 p.
- Ellis, R., and J. E. McCosker.**  
**1991.** *Great white shark*. Harper Collins Publishers, New York NY, 270 p.
- Francis, M. P.**  
**1996.** Observations on a pregnant white shark with a review of reproductive biology. In *Great white sharks: the biology of *Carcharodon carcharias** (A. P. Klimley and D. G. Ainley, eds.), p. 157–172. Academic Press, San Diego CA.
- Francis, M. P., and J. D. Stevens.**  
**2000.** Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus*, in the Southwest Pacific Ocean. *Fish. Bull.* 98(1):41–63.
- Garrick, J. A. F.**  
**1967.** Revision of sharks of genus *Isurus* with description of a new species (Galeoidea, Lamnidae). *Proc. U. S. Nat. Mus.* 118:663–694.
- Gilmore, R. G.**  
**1983.** Observation on the embryos of the longfin mako, *Isurus paucus*, and the bigeye thresher, *Alopias superciliosus*. *Copeia* 1983:375–382.  
**1993.** Reproductive biology of lamnid sharks. *Env. Biol. Fish.* 38:95–114.
- Gilmore, R. G., J. W. Dodrill, and P. A. Linley.**  
**1983.** Reproduction and embryonic development of the sandtiger shark, *Odontaspis taurus* (Rafinesque). *Fish. Bull.* 81:201–225.
- Gohar, H. A. F., and F. M. Mazhar.**  
**1964.** The elasmobranchs of the north-western Red Sea. *Publ. Mar. Biol. Stat. Al-Ghardaqa (Red Sea) No.* 13:1–144.
- Goldman, K. J.**  
**1997.** Regulation of body temperature in the white shark, *Carcharodon carcharias*. *J. Comp. Physiol. B* 167:423–429.
- Graham, J. B., H. Dewar, N. C. Lai, W. R. Lowell, and S. M. Arce.**  
**1990.** Aspects of shark swimming performance determined using a large water tunnel. *J. Exp. Biol.* 151:175–192.
- Gubanov, Ye. P.**  
**1972.** On the biology of thresher shark (*Alopius vulpinus*) in the North-west Indian Ocean. *J. Ichthyol.* 12:591–600.  
**1978.** The reproduction of some species of pelagic sharks from the equatorial zone of the Indian ocean. *J. Ichthyol.* 18:781–792.
- Guitart-Manday, D.**  
**1975.** Las pesquerías pelágico-oceánicas de corte radio de acción en la región noroccidental de Cuba [Short-range marine pelagic fishing of northeast Cuba]. *Seria Oceanologica, Oceanographic Institute Academy of Sciences of*

- Cuba 31, p. 3–26. [Translated for the National Science Foundation and the US Department of Commerce, NOAA, NMFS by the Agence Tunisiennes de Public-Relations, Tunis.]
- Hamlett, W. C., D. J. Allen, M. D. Stribling, F. J. Schwartz, and L. J. A. DiDio.**  
**1985.** Permeability of external gill filaments in the embryonic shark. Electron microscopic observations using horseradish peroxidase as a macromolecular tracer. *J. Submicrosc. Cytol.* 17:31–40.
- Hanan, D. A., D. B. Holts, and A. L. Coan Jr.**  
**1993.** The California drift gill net fishery for shark and swordfish 1981–82 through 1990–91. *Fish. Bull.* 175: 1–93.
- Heist, E. J., J. A. Musick, and J. E. Graves.**  
**1996.** Genetic population structure of the shortfin mako (*Isurus oxyrinchus*) inferred from restriction fragment length polymorphism analysis of mitochondrial DNA. *Can. J. Fish. Aquat. Sci.* 53:583–538.
- Hixon, M. A.**  
**1979.** Term fetuses from a large common thresher shark, *Alopias vulpinus*. *Calif. Fish Game* 65:191–2.
- Holts, D. B., and D. W. Bedford.**  
**1993.** Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the Southern California Bight. *Aust. J. Mar. Freshwater Res.* 44:501–509.
- Joseph, D. C.**  
**1954.** A record-size thresher from Southern California. *Calif. Fish Game* 40:433–435.
- Killam, K., and G. Parsons.**  
**1986.** First record off the longfin mako, *Isurus paucus*, in the Gulf of Mexico. *Fish. Bull.* 84:748–749.
- Klimley, A. P.**  
**1985.** The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. *Mem. S. Cal. Acad. Sci.* 9:15–40.
- Koob, T. J., and J. W. Straus.**  
**1998.** On the role of egg jelly in *Raja erinacea* egg capsule. *Bull. Mt. Desert Island Biol. Lab.* 37:117–119.
- Last, P. R., and J. D. Stevens.**  
**1994.** Sharks and rays of Australia. Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia, 513 p. + 84 color plates.
- Lineaweaver, T. H., and R. H. Backus.**  
**1970.** The natural history of sharks. 1984 reprint, Nick Lyons Books/Schocken Books, New York, NY, 256 p.
- Lohberger, J.**  
**1910.** Über zwei riesige Embryonen von *Lamna*. *Abh. K. Bayer. Akad. Wiss. IV. Suppl. Bd.* 2:1–45.
- Matthews, L. H.**  
**1950.** Reproduction in the basking shark, *Cetorhinus maximus*, (Gunnerus). *Phil. Trans. B. Royal Soc. Lond.* 234: 247–316.
- Mollet, H. F., and G. M. Cailliet.**  
**1996.** Using allometry to predict body mass from linear measurements of the white shark. *In* Great white sharks: the biology of *Carcharodon carcharias* (A. P. Klimley and D. G. Ainley, eds.), p. 81–89. Academic Press, San Diego CA.
- Moreno, J. A., and J. Morón.**  
**1992.** Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839). *In* Sharks: biology and fisheries (J. G. Pepperell, ed.), p. 77–86. *Aust. J. Mar. Freshwater Res.* 43.
- Musick, J. A., S. Branstetter, and J. A. Colvocoresses.**  
**1993.** Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. mid-Atlantic coast. *In* Conservation biology of elasmobranchs (S. Branstetter, ed.), p. 1–19. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 115.
- Nakamura, H.**  
**1935.** On the two species of the thresher shark from Formosan waters. *Mem. Fac. Sci. Agric. Taihoku Imp. Univ.* 14:1–6.
- Natanson, L. J., and N. E. Kohler.**  
**1996.** A preliminary estimate of age and growth of the dusky shark *Carcharhinus obscurus* from the south-west Indian Ocean, with comparison to the western North Atlantic population. *S. Afr. J. Mar. Sci.* 17:217–224.
- Neter, J., and W. Wassermann.**  
**1974.** Applied linear statistical models. Richard D. Irwin Inc., Homewood, IL, 842 p.
- Norman, J. R., and F. C. Fraser.**  
**1938.** Giant fishes, whales and dolphins. W. W. Norton and Company Inc., New York, NY, 361 p.
- O'Brian, J. W., and J. S. Sunada.**  
**1994.** A review of the southern California experimental drift longline fishery for sharks, 1988–1991. *CalCOFI Rep.* 35: 222–229.
- Otake, T.**  
**1990.** Classification of reproductive modes in sharks with comments on female reproductive tissues and structures. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics and the status of fisheries (H. L. Pratt, S. H. Gruber, T. Taniuchi, eds.), p. 113–130. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 90.
- Parker, H. W., and F. C. Stott.**  
**1965.** Age, size, and vertebral calcification in the basking shark *Cetorhinus maximus* (Gunnerus). *Zool. Meded. (Leiden)* 40:305–319.
- Parsons, G. R.**  
**1993.** Geographic variation in the reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. *Env. Biol. Fish.* 38:25–35.
- Pepperell, J. G.**  
**1992.** Trends in the distribution, species composition and size of sharks caught by gamefish anglers off South-eastern Australia, 1961–90. *In* Sharks: biology and fisheries (J. G. Pepperell, ed.), p. 213–225. *Aust. J. Mar. Freshwater Res.* 43.
- Peres, M. B., and C. M. Vooren.**  
**1991.** Sexual development, reproductive cycle, and fecundity of the school shark *Galeorhinus galeus* off southern Brazil. *Fish. Bull.* 89:655–667.
- Pratt, H. L., Jr.**  
**1979.** Reproduction in the blue shark, *Prionace glauca*. *Fish. Bull.* 77:445–70.
- Pratt, H. L., Jr., and J. G. Casey.**  
**1983.** Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. *Can. J. Fish. Aquat. Sci.* 40:1944–1957.
- Randall, J. E.**  
**1992.** Review of the biology of the tiger shark (*Galeocerdo cuvier*). *In* Sharks: biology and fisheries (J. G. Pepperell, ed.), p. 21–31. *Aust. J. Mar. Freshwater Res.* 43.
- Sanzo, L.**  
**1912.** Embrione di *Carcharodon Rondeletii* M. Hle. (?) con particolare disposizione del sacco vitellino. *Regio Comitato Talassografico Italiano, Memoria* XI:1–12.
- Saul, P., and J. Holdsworth.**  
**1992.** Cooperative gamefish tagging in New Zealand waters 1975–90. *New Zealand Fisheries Technical Report* No. 33, 24 p.

**Stevens, J. D.**

1983. Observations on reproduction in the shortfin mako *Isurus oxyrinchus*. *Copeia* 1983:126–130.

**Stevens, J. D., and K. J. McLoughlin.**

1991. Distribution, size and sex composition, reproductive biology, and diet of sharks from Northern Australia. *Aust. J. Mar. Freshwater Res.* 42:151–199.

**Swenander, G.**

1907. Über die Ernährung des Embryos der *Lamna cornubica*. *Zoologische Studier Tollagnade Tullberg Uppsala* 1907:283–289.

**Templeman, W.**

1963. Distribution of sharks in the Canadian Atlantic (with special reference to Newfoundland waters). *Bull. Fish. Res. Board Can.* 140:1–77.

**Tricas, T. C., K. Deacon, P. Last, J. E. McCosker,****T. I. Walker, and L. Taylor.**

1997. The Nature Company guides. Sharks and rays (L. Taylor, consultant ed.). Time-Life Books, Time Life Inc. San Francisco, CA, 288 p.

**Uchida S., M. Toda, and Y. Kamei.**

1990. Reproduction of elasmobranchs in captivity. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries* (H. L. Pratt, S. H. Gruber, T. Taniuchi, eds.), p. 211–237. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 90.

**Uchida, S., M. Toda, K. Teshima, and K. Yano.**

1996. Pregnant white sharks with near-term fetuses from

Japan. In *Great white sharks. The biology of *Carcharodon carcharias** (A. P. Klimley and D. G. Ainley, eds.). Academic Press, San Diego, CA, p. 139–155.

**Uchida, S., F. Yasuzumi, M. Toda, and N. Okura.**

1987. On the observation of reproduction in *Carcharodon carcharias* and *Isurus oxyrinchus*. *Rep. of Japanese Group for Elasmobranch Studies* 24:5–6.

**Vaillant, L.**

1889. Note sur un foetus gigantesque d'*Oxyrhina spallanzani* Bonap. *Bull. Soc. Philom. Paris* 1:38–39.

**Welch, D. W., and R. P. Foucher.**

1988. A maximum likelihood methodology for estimating length-at-maturity with application to Pacific cod (*Gadus macrocephalus*) population dynamics. *Can. J. Fish. Aquat. Sci.* 45:333–343.

**Wilkinson, L.**

1986. SYSTAT: The system for statistics. SYSTAT Inc., Evanston IL, 18 chapters and 4 appendices without continuous page numbers.

**Yano K., Y. Yabumoyo, S. Tanaka, O. Tsukada, and****M. Furuta.**

1999. Capture of a mature female megamouth shark, *Megachasma pelagios*, from Mie, Japan. In *Proc. 5th Indo-Pac. Fish Conf., Noumea 3–8 November 1997* (B. Seret and J. Y. Sire, eds.), p. 351–365. Société Française d'Ichtyologie and Institut de Recherche pour le Développement, Paris.