CHAPTER

15

Observations on a Pregnant White Shark with a Review of Reproductive Biology

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Introduction

Lamnoid sharks (order Lamniformes) are typically large and uncommon, making them difficult to study. White sharks *Carcharodon carcharias* are no exception, and they pose the additional problem of being potentially dangerous to researchers. As a result, little is known about their biology, ecology, and behavior. In particular, our knowledge of reproduction in white sharks is rudimentary and is based partly on inferences drawn from other lamnoids. The reproductive mode is thought to be aplacental viviparity, with embryos being nourished by oophagy (Compagno, 1984b; Uchida *et al.*, 1987; Bruce, 1992; Gilmore, 1993).

Review of the Literature

Few reports exist describing pregnant female or embryonic white sharks. Most were based on limited secondhand observations and many of the accounts are inaccurate. The reports are discussed briefly below (Table I).

In a paper describing the anatomy of white sharks, Parker (1887) provided diagrams of parts of the skeleton and brain of a 55-cm embryo that came from the Australian Museum, Sydney. However, L. J. V. Compagno of the South African Museum (personal communication) has determined from the shape of the chondrocranium that the embryo came from a species of *Carcharhinus*, not *Carcharodon*.

Sanzo (1912) described and illustrated a 36-cm lamnid embryo from a shark caught between Italy and Sicily. By a process of elimination, he concluded that the embryo was from a white shark. Sanzo's embryo, which is in the Museum of Zoology in Florence, Italy, has recently been reexamined in detail and identified as *Isurus oxyrinchus* (A. D. Testi, H. F. Mollet, L. J. V. Compagno, and G. Bernardi, unpublished data).

A white shark caught in Egypt contained nine embryos, each 61 cm long (Norman and Fraser, 1937). Each embryo was reported to weigh 49 kg (108 lb), which is obviously erroneous (see also Bigelow and Schroeder, 1948; Randall, 1973). Tricas and McCosker (1984) suggested that the reported weight referred to all of the embryos combined, indicating a mean weight of 5.4 kg per embryo. This seems plausible, although *I. oxyrinchus* embryos 58–60 cm long weigh only 1.4–1.7 kg each (Stevens, 1983).

Bigelow and Schroeder (1948) noted reports of embryos measuring 20–61.6 cm, but gave no details or sources. Their figure of 61.6 cm may refer to the embryos from Norman and Fraser's Egyptian shark. Bigelow and Schroeder (1948, p. 138, footnote 14) also cited a report by Doderlein (1881, p. 69) of a 63-cm specimen and suggested that it may have been an embryo. However, inspection of Doderlein's original

TABLE I **Pregnant Female and Embryonic White Sharks**

No.	Date	Location	Female TL (m)	Embryo Observed (N)	Embryo TL (cm)	Reference
1	Summer 1934	Alexandria, Egypt	4.30	9	61	Norman and Fraser (1937)
2					20–61.6	Bigelow and Schroeder (1948)
3	November 17, 1981 November 26, 1982 November 26, 1982	Queensland, Australia	3.20 4.00 4.20	4 11 14 7		Paterson (1986); J. D. Stevens (personal communication)
4	February 16, 1985 April 2, 1986	Kin, Okinawa, Japan Taiji, Wakayama, Japan	5.55 ≈4.70	0[a] 7	≈100–110	Uchida *et al.* (1987); Ellis and McCosker (1991)
5	February–March 1988	Taiwan		3	≈100	D. A. Ebert (personal communication)
6	October–November	South Australia	≈4.20 ≈4.70 ≈5.20	11 13 6–7	≈60 ≈5 ≈30	Bruce (1992)
7	November 13, 1991	North Cape, New Zealand	≈5.36	7	143–145	This study
8	May 14, 1992 May 22, 1992	Uchinoura, Japan Toyo-cho, Kochi, Japan	4.80 5.15	5 10	130 135–151	Uchida *et al.* (Chapter 14)
9	September 1992	Cape Bon, Tunisia	≈5.30	2		Fergusson (Chapter 30)
10	March 1994	South Australia		2[b]	127	J. D. Stevens (personal communication)

TL, Total length; ≈, estimated length.
[a]Numerous ova were present in the uteri, but no embryos were visible.
[b]Two aborted embryos were taken from a litter of unknown size.

account (written in Italian) revealed that a mistake had been made in the translation: the 63-cm measurement referred to the width of a set of jaws in the Palermo Museum.

In an account of the beach-meshing program in Queensland, Australia, Paterson (1986) recorded four pregnant females of a total of 480 white sharks caught. J. D. Stevens (personal communication) investigated this report and obtained copies of the fishing contractor's log entries for three of the pregnant sharks. The smallest of the three was reportedly 3.2 m total length (TL), but it is unlikely that a shark of this length would be mature (see Discussion). In fact, the three Queensland white sharks for which measurements are available are the smallest mature females on record. It is hard to imagine that these sharks were misidentified by an experienced meshing contractor. Perhaps they were incorrectly measured, or perhaps the measurements were not TLs. Unfortunately, the uncertainty over the lengths also casts doubt on the accuracy of the litter size information (Table I). The embryos were not measured.

Uchida *et al.* (1987) briefly described two pregnant white sharks from Japanese waters. One contained a large number of uterine eggs (192 were counted in the left uterus) but no embryos. The uteri were enlarged, suggesting that embryos had recently been aborted or born (S. Uchida, personal communication). The uterine eggs were thought to have been remnants of ova produced as food for the embryos. The second Japanese shark was not examined, but from photographs and interviews with people involved, Uchida *et al.* (1987) deduced that she contained seven embryos about 100–110 cm long. Their abdomens were distended by large volumes of yolk, seen spilling from their slashed bellies in the photograph provided by Ellis and McCosker (1991, p. 89). The illustration caption incorrectly states that the pools of yolk were embryonic membranes (S. Uchida, personal communication).

D. A. Ebert (personal communication) was shown photographs of three white shark embryos during a visit to Taiwan in 1988. The embryos came from a large female caught in February or March of that year. Neither the mother nor the embryos were measured, but Ebert estimated the embryos to be 100 cm TL. The abdomens of the embryos were distended.

Bruce (1992) reported a fisherman's account of three pregnant white sharks caught off South Australia in October and November (years not given). The lengths of the sharks and their embryos were apparently estimated rather than measured. Litter sizes were 6–13, and embryo sizes were 5–60 cm.

Two pregnant white sharks carrying large embryos were caught in Japan in 1992, and embryos from one of these were examined in detail (see Chapter 14, by Uchida *et al.*). Fergusson (Chapter 30) discusses the capture of a pregnant female white shark off Tunisia in 1992. She contained two embryos when hauled ashore, but no measurements were taken on the mother or the embryos.

In March 1994, a South Australian fisherman caught two small white sharks in a set net. The net also had a large hole in it, suggesting that the small sharks were embryos aborted by the mother while she struggled to escape (J. D. Stevens, personal communication). One of the embryos was examined in a decayed state, several weeks after capture. It measured 127 cm TL and weighed 14.5 kg, although the capture weight was thought to have been about 18–20 kg (J. D. Stevens, personal communication).

The capture of a pregnant female white shark carrying seven full-term embryos in New Zealand in November 1991 provided an opportunity to improve our knowledge of reproduction in the species. The female was butchered before she could be examined, but two of her embryos, and the jaws from a third, were obtained for study, along with two videotapes and a number of photographs of the mother and the embryos. In this chapter, I report observations made on the female and her embryos.

The new observations presented here and those by Uchida *et al.* (Chapter 14) bring the number of reported pregnant female white sharks or litters to 15 (Table I). I review here the available data on reproductive mode, parturition, litter size, size at birth, female length at maturity, and mating. However, crucial reproductive parameters such as the length of the gestation period and the average annual fecundity remain unknown. Until such data are available, it will be impossible to estimate population replacement rates and to determine the status of white shark populations.

Materials and Methods

Capture, Landing, and Disposal

A female white shark was caught by C. Garrett on the afternoon of November 13, 1991, at North Cape, New Zealand (34°25′ S, 173°03′ E). She was caught in a 140-mm mesh set net in 8 m of water, and towed by Garrett and another fisherman to Houhora Harbour, a distance of 48 km. The shark was dragged ashore on November 14 and winched onto the tray of a tow truck. During this process, five embryos were aborted through the combined effects of gravity, compression of the abdomen, and direct human assistance. The female and her embryos remained on the truck overnight and were weighed on a log-weighing machine in Kaitaia on November 15. That afternoon, the female was cut up for bait at Awanui Wharf, and two more embryos were discovered inside her. The jaws were removed from an embryo of unknown length and sex by G. Kinnear, and the offal and the seven embryos were discarded over the edge of the wharf.

Garrett asked a taxidermist, K. Flutey, to preserve and mount the jaws of the female. Flutey also requested some of the embryos so that he could make casts from them. On November 16, 3 days after the female had been caught, Garrett retrieved two of the embryos from beneath Awanui Wharf at low tide. The embryos were then frozen and delivered to Flutey.

I eventually obtained from Flutey one intact embryo and one embryo from which the jaws and the pectoral and pelvic fins had been removed. In January 1994, I examined the embryo jaws in the possession of Kinnear. Photographs were obtained from the *Northern Advocate* newspaper, as were videotapes from two private citizens. One of the tapes spanned the period from the landing of the shark at Houhora Harbour to its butchering at Awanui Wharf. This tape also covered the abortion of five embryos and the measuring and weighing of the female.

Total Length Measurements

TL measurements made from the snout to a perpendicular dropped from the posterior tip of the upper caudal lobe while the latter is in its natural position (Bigelow and Schroeder, 1948) are referred to as TL_{nat}. TL measured with the upper caudal lobe flexed down to lie parallel with the body midline (Compagno, 1984b) are referred to as TL_{flex}. For small white sharks, TL_{nat} may be converted to TL_{flex} by multiplying by 1.025. This conversion factor is based on a free-living New Zealand white shark that measured 1521 mm TL_{nat} and 1559 mm TL_{flex}. When the measurement method is uncertain, TL is not subscripted. Other morphometric measurements were taken using the methods of Compagno (1984b).

Results

Observations on the Pregnant Female

The length of the shark cannot be determined precisely. One of the videotapes showed it being measured in a straight line with a measuring tape. The posterior reference point was probably the caudal fork, but this is not certain, because of the angle of the camera and the movement of people around the shark. One of the measurers called out the length as "5 m," but this must be regarded as approximate. A fork length (FL) of 5 m equates to a TL of 5.36 m using the linear geometrical mean regression of Mollet and Cailliet (Chapter 9). Photos taken of the shark lying on the truck showed that its FL was longer than the length of the tray (4.42 m), confirming a TL >4.75 m. The half-girth, measured just behind the pectoral fins, was reported on a videotape as 1.8 m, giving a girth of about 3.6 m.

The first upper right tooth had an enamel height of 51 mm, and the perimeter of the upper jaw measured 115 cm after freezing [both measurements were made by me using the method of Randall (1973)]. These dimensions are greater than any presented by Randall (1973). Furthermore, Randall did not give regression equations for his plots of enamel height and jaw perimeter versus TL, so mathematical extrapolation is impossible. Extrapolations by eye from both plots suggest a TL of 5.5–6 m.

The shark plus her seven embryos weighed 1360 kg. This is an underestimate of weight at capture, because she had lost significant quantities of uterine fluid, as well as other body fluids through dehydration, during the 18 hours she had spent out of the water before weighing. The intact embryo weighed 26.1 kg, indicating a litter weight of about 180 kg.

Four of the five aborted embryos emerged headfirst. The fifth was dragged out tailfirst, after considerable pulling and sideways rocking, by a man who reached into the dilated cloaca. These observations suggest that birth normally occurs headfirst in white sharks. Each embryo was accompanied by a gush of uterine fluid as it emerged from the cloaca. The uterine fluid released by the female during the abortion of her embryos was mostly clear, but during the abortion of one embryo, it was stained yellow–brown, suggesting that some of that embryo's intestinal contents (see below) had been released *in utero*. This presumably resulted from compression of the embryo before or during the abortion.

On December 31, 1991, 46 days after the disposal of the offal and the embryos, I dived under Awanui Wharf to search for vertebrae from the female shark. The wharf is situated on a muddy tidal river, and underwater visibility was zero. Searching was further hampered by rubbish dumped from the wharf and mounds of Pacific oysters *Crassostrea gigas*. In 1 hour of searching, I found a single vertebra that still had a plug of cartilage protruding from the ventral edge. The vertebra had clear black and white bands (Fig. 1), presumably as a result of a sulfide reaction with the anaerobic mud. [A technique developed by Hoenig and Brown (1988) for aging sharks from their vertebrae uses ammonium sulfide to stain annual bands.] The vertebra had 22 (±1) black bands and was 63 mm in diameter. The black bands disappeared after 2 days of air-drying and exposure to daylight.

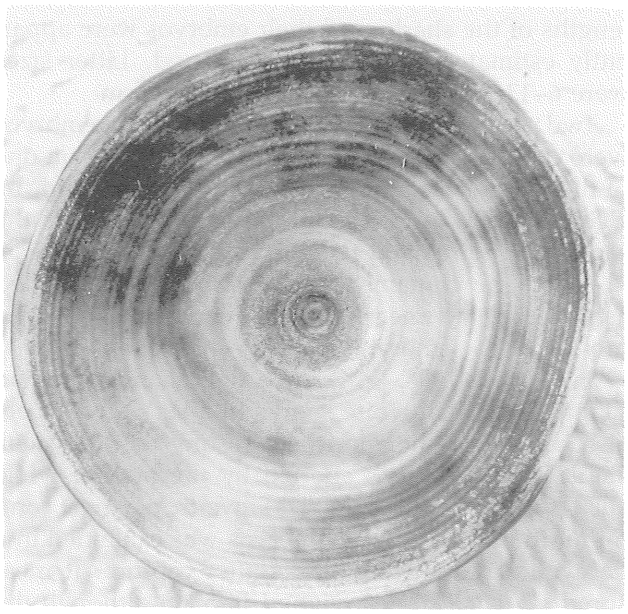

FIGURE 1 Vertebra from an approximately 5.36-m pregnant female white shark caught at North Cape, New Zealand.

Measurements of the Embryos

Despite the long period between capture and freezing, the two retrieved embryos were in excellent condition. The intact embryo (NMNZ P.27570; see Fig. 2A) measured 1449 mm TL_{nat} and weighed 26.1 kg (Table II). The embryo from which the jaws and fins had been removed measured 1430 mm TL_{nat} and weighed 23.5 kg, suggesting a whole mass similar to that of the intact embryo. The embryos were externally similar to a 1521 mm TL_{nat} free-living female white shark caught in Kaipara Harbour, New Zealand (36°23′ S, 174°15′ E), on January 19, 1993 (Fig. 2B and Table II). Visible differences include a larger abdomen and girth and a more lunate caudal fin in the embryos than in the free-living shark.

Other External Characters of the Embryos

An umbilical cord was not visible in videotapes of the five aborted embryos, nor were there any umbilical cord remnants in the two embryos examined.

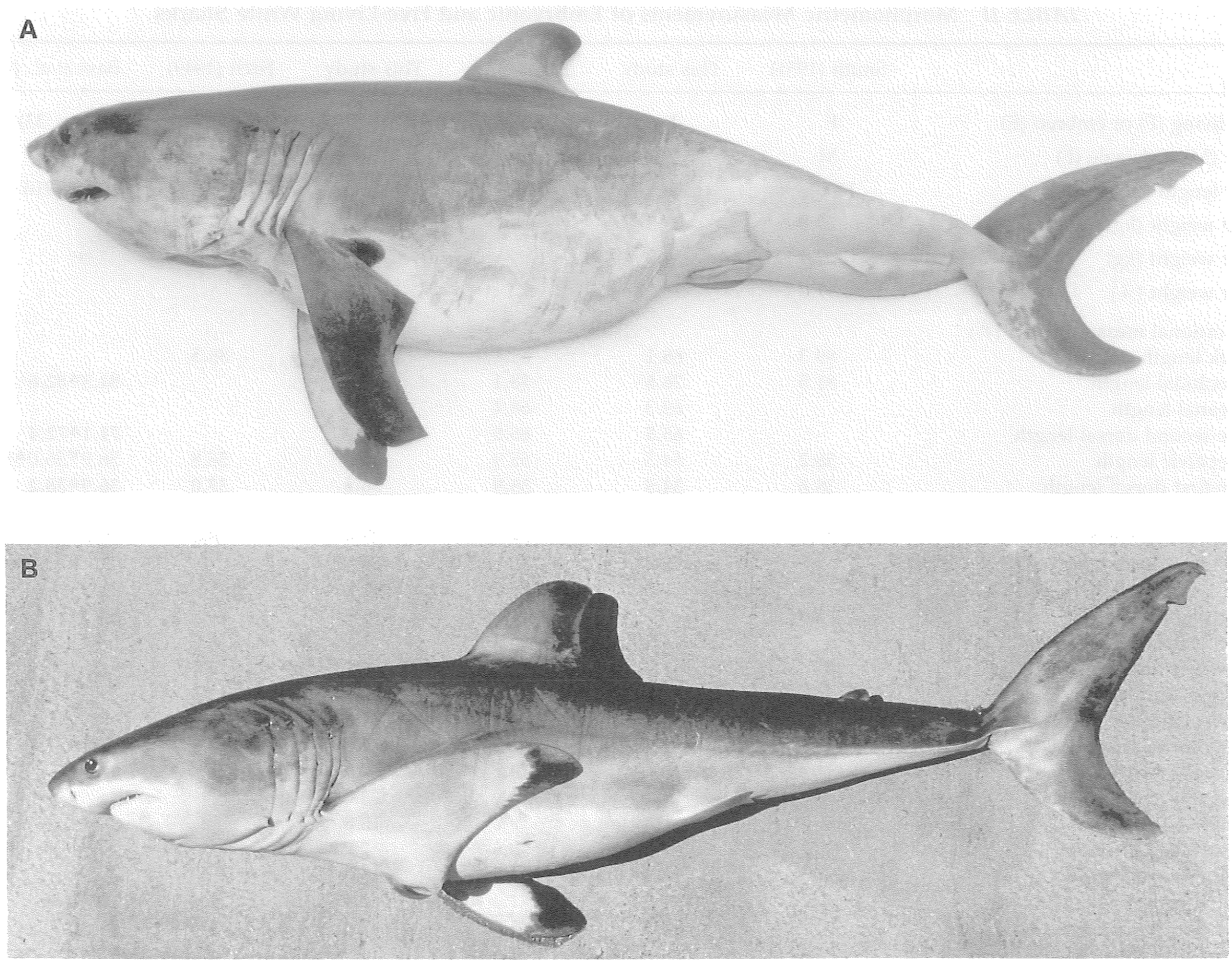

FIGURE 2 (A) A 1449-mm female embryo (NMNZ P.27570) from an approximately 5.36-m pregnant female white shark caught at North Cape, New Zealand. (B) A 1521-mm female free-living white shark caught in Kaipara Harbour, New Zealand.

Both embryos and the Kaipara shark had small (about 2–5 mm long), faint, healed scars on the throat between the bases of the second gill slits.

The embryos and the Kaipara shark all had color patterns resembling those of larger juveniles and adults (Fig. 2), including a black blotch in the pectoral axil of all three animals. Minute spiracles were found in the 1449-mm embryo and the Kaipara shark, but not in the 1430-mm embryo. The first dorsal fins of both embryos and the Kaipara shark were rounded at the apex (Fig. 2).

Teeth of the Embryos

The jaws of the 1449-mm embryo were examined *in situ*. The upper teeth were not erect, being oriented posteriorly or obliquely upward (toward the roof of the mouth). The medial margins of left and right teeth 1–5 (counted from the symphysis) of the first (outermost) series had basal cusps, as did the lateral margins of teeth 1–10. The first upper right tooth (Fig. 3) had an enamel height of 11.0 mm, and the width at the enamel base was 8.4 mm. In the lower jaw, some of the small posterior teeth were covered by a denticle-covered layer of skin. The remainder were oriented upward and posteromedially, and most were presumably functional. On the left side, the first nine teeth were uncovered, apart from the fifth, which was not erect and was held by a small sliver of skin. On the right side, the first four teeth were uncovered, teeth 5 and 6 had their points protruding through the skin, and the remainder were completely covered by skin. All visible bottom teeth had two basal cusps. In both jaws, there were tooth scars outside most of the upper and lower teeth, indicating that an earlier series of teeth had been shed.

TABLE II **Morphometric Measurements of Embryonic and Free-Living White Sharks**

	Smith (1951)	This study	This study	This study	Fitch (1949)	Bass *et al.* (1975)
Free-living (F) or embryo (E)	F	E	E[a]	F	F	F (N = 33)
Male (M) or female (F)	M	F	F	F		M and F
Total length (mm)	1400	1430	1449	1521	1543	1700–3910
Body weight (kg)	20.0	>23.5	26.1	24.8		
Liver weight (kg)	3.4	4.3		4.0		
Liver weight (%)	17.0	*16.5*[b]		16.1		
Proportional measurements (%)						
Fork length	89.3	88.1	88.1	88.4	88.5	
Precaudal length	81.5	**76.6**[b]	**78.1**	**78.4**		**81.3▲82.6**[b]
Preanal length		69.3	68.4	68.4		
Pre-second dorsal length		**65.5**	**66.8**	**67.0**		**71.1▲72.4**
Prepelvic length	56.2	*54.5*	55.9	54.4	56.8	56.9▼56.0▲59.3
Pre-first dorsal length	38.6	**34.5**	**35.9**	**36.6**	**37.0**	**36.9▲38.2**
Head length		***24.8***	**26.6**	**27.0**		
Prepectoral length	26.4	*24.5*	24.2	25.4	28.2	26.2
Prebranchial length		19.7	20.6	20.4		22.4▼21.4▲21.9
Prespiracular length			11.3	11.8		11.8
Preoral length	5.9		6.3	6.2		8.2▼7.2▲8.2
Preorbital length		4.5	4.2	4.2	6.2	5.7▼5.3▲5.7
Prenarial length		**3.6**	**3.7**	**4.1**	**4.3**	**4.3**
Snout–vent length		*55.9*	57.0	55.9		
Vent–caudal length		*43.4*	43.3	44.7		
Interdorsal space	21.3	21.3	22.1	22.2	21.8	23.7▲24.8
Dorsal–caudal space		10.6	10.8	10.3		
Pectoral–pelvic space			25.9	23.0		
Pelvic–anal space			9.0	10.8		
Anal–caudal space		7.8	8.6	7.7		
Pelvic–caudal space		***18.5***	**19.0**	**19.8**		
Eye length		1.5	1.4	1.4	1.6	1.4▼1.0
Eye height		1.5	1.6	1.4	1.5	
Mouth length	5.4		*4.8*	5.3		4.8
Mouth width	9.8		*10.7*	*8.2*	8.2	9.6▼8.8▲10.4
Nostril width		1.5	1.5	1.4	1.4	1.7▼1.5▲1.6
Internarial space	4.0	4.0	4.1	3.9		4.0▼3.8▲4.0
Interorbital space			7.7	6.9		
Eye–spiracle space			6.1	5.8		
Intergill length		**6.2**	**6.3**	**6.4**		**7.2▲8.2**
First gill slit height	8.5			8.5	9.1	9.4▼8.3▲10.3
Fifth gill slit height	8.8			8.2	10.0	9.9▼9.5▲10.2
First dorsal length		11.7	12.4	11.6		
First dorsal anterior margin		13.6	13.6	13.5	13.0	
First dorsal base	9.3	9.6	9.9	9.7	9.7	9.8
First dorsal height	9.3	9.2	8.8	*9.4*		10.5
First dorsal inner margin		2.7	2.5	2.4		2.7
First dorsal posterior margin		*7.7*	8.6	*7.8*		
Second dorsal length		3.5	3.2	3.6		
Second dorsal anterior margin		2.9	2.6	3.0		
Second dorsal base		1.5	1.6	1.6	1.3	1.5
Second dorsal height		1.3	1.5	*1.9*		1.5
Second dorsal inner margin		*1.4*	2.1	1.9		2.0
Pectoral anterior margin	20.7		22.2	21.4	21.4	
Pectoral base			7.5	6.2	7.0	6.9
Pectoral inner margin			*4.1*	*5.0*		5.5
Pectoral posterior margin			*19.0*	*17.0*		
Pectoral height			19.7	19.5		
Pelvic length			8.1	8.7		

(continues)

TABLE II (*Continued*)

	Smith (1951)	This study	This study	This study	Fitch (1949)	Bass *et al.* (1975)
Pelvic anterior margin			5.9	6.6		
Pelvic base			5.9	5.6	5.8	
Pelvic height			5.1	*5.1*		
Pelvic inner margin			3.7	3.1		
Pelvic posterior margin			5.8	*5.8*		
Anal length		3.1	3.4	3.3		
Anal anterior margin		3.0	2.9	2.9		
Anal base		1.4	1.4	1.6	1.3	1.5
Anal height		1.4	1.5	*1.4*		1.6
Anal inner margin		1.9	2.0	2.1		1.9
Anal posterior margin		*1.3*	1.1	*1.1*		
Dorsal caudal margin		**25.8**	**24.3**	**23.4**		**23.5▼21.8**
Preventral caudal margin		19.2	19.0	*15.6*		18.3
Upper postventral caudal margin		12.8	11.9	13.0		
Lower postventral caudal margin		9.7	10.4	9.9		
Caudal fork width		7.9	8.2	8.2		
Caudal fork length		10.9	10.8	10.1		
Subterminal caudal margin		1.3	1.4	1.4		
Subterminal caudal width		2.7	2.8	2.6		
Terminal caudal margin		4.1	4.2	3.6		
Terminal caudal lobe		4.7	5.1	4.4		5.2▼4.1
Trunk height		*19.2*	*22.8*	*17.4*		
Abdomen height		*16.8*	*21.7*	*16.4*		
Tail height		*9.8*	*10.7*	*9.2*		
Caudal peduncle height		2.9	2.8	2.8		
Caudal peduncle width			6.2	5.8		
Girth	**60.0**	***50.3***	***51.1***	***44.0***		
Teeth	13 + 13 / 12 + 12	14 + 12 / 12 + 12	12 + 13 / 12 + 12	12 + 13 / 12 + 12		13 + 13[c] / 12 + 12

[a]Specimen NMNZ P.27570.

[b]Measurements showing a consistent trend are in boldface; approximate values are in italics; arrowheads (▼ and ▲) indicate decreasing and increasing trends, respectively, with increasing total length; both symbols designate minimum at intermediate shark lengths.

[c]Usual tooth formula for South African white sharks (Bass *et al.*, 1975); actual total tooth counts ranged from 23 to 28 for upper teeth and from 21 to 25 for lower teeth of 32 specimens (Bass *et al.*, 1975: Table 7).

The jaws of the 1430-mm embryo were not examined in detail, but a number of photographs taken after their removal from the embryo, but before cleaning and drying, were available for study. In the right upper jaw, none of the teeth was erect. Only the third tooth of the first series remained, and it pointed posteriorly (Fig. 4A). Most of the second series of teeth had erupted from the lining of the mouth, but they were not yet functional (Fig. 4A and B). In the lower jaw, most teeth were erect and functional (Fig. 4C). Tooth scars in both jaws indicated that an earlier series of teeth had been shed (Fig. 4C).

The jaws removed by Kinnear were in a dried state, so it was impossible to determine how many teeth had originally been uncovered. The first upper left tooth had an enamel height of 12 mm. In the upper right jaw, the medial margins of teeth 1–8 had basal cusps. In the upper left jaw, only the first five teeth were uncovered, and all had medial cusps. In both the left and right sides of the upper jaw, teeth 1–10 had lateral cusps. In the lower jaw, on both the left and right sides, the first eight teeth had medial cusps, and the first nine teeth had lateral cusps.

Internal Organs of the 1430-mm Embryo

The visceral cavity of the 1430-mm embryo was dissected. Much of the distended abdomen was occupied by a liver weighing 4.3 kg. Assuming that this embryo weighed about the same as the 1449-mm embryo (i.e., 26.1 kg), the liver would have represented 16.5% of its total body weight.

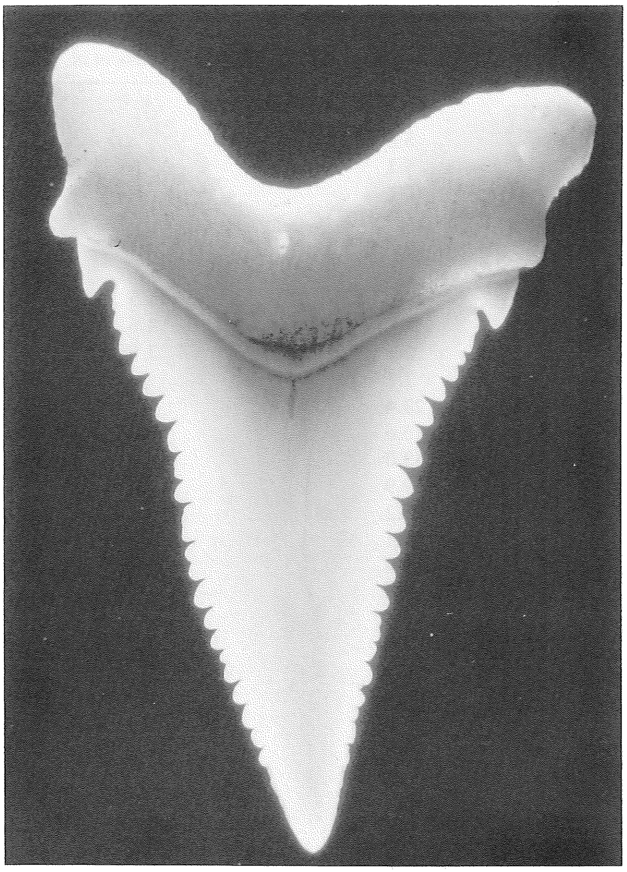

FIGURE 3 First upper right tooth from a 1449-mm female embryo white shark (NMNZ P.27570). (Photo courtesy of A. Blacklock.)

The complete digestive tract weighed 1.2 kg (4.6% of the estimated total weight), but the gut contents weighed only 0.4 kg (1.5%). No yolk or egg membranes were found in the gut, although the intestine (including the spiral valve) was packed with a viscous brown–green material that may have been a waste product of yolk digestion. Similar material was described by Springer (1948) from the spiral valve of embryonic *Carcharias taurus*.

The stomach contained a small quantity of bloody fluid, 81 teeth, and numerous denticles. The teeth were white and displayed no effects of digestion. The largest tooth had an enamel height of 10.5 mm. Using the jaws of the Kaipara shark as a model, I attempted to reconstruct tooth series from the upper teeth removed from the stomach. Most of the teeth appear to have come from a single series, with the addition of a few teeth from an earlier series and one tooth from the next series (Fig. 5). The absence of the third upper right tooth from the main tooth series is consistent with the observation that the third upper right tooth was the only tooth that remained in the first series of the embryo's jaw (Fig. 4A). The fourth upper left tooth was also missing from the stomach series, but unfortunately, no photos of the upper left jaw were available to determine whether that tooth was still present in the jaw. In a plot of enamel height versus tooth width at the enamel base, most of the upper teeth in Fig. 5 fell on a straight line (Fig. 6). The exceptions were the two teeth from either side of the symphysis; they were markedly more slender than the others.

The intestine contained at least 110 teeth and numerous denticles. Most of the teeth were partly eroded and stained brown. They were smaller than those found in the stomach; the largest had an enamel height of 4 mm, but most had enamel heights <2 mm.

Since a single tooth series in a white shark's jaws comprises about 50 teeth (Table II), the 191 teeth found in the stomach and intestine of the embryo represent almost four full series.

Discussion

Observations on the Pregnant Female

The size of the vertebra found under Awanui Wharf and the number of visible bands (22 ± 1) agree closely with a 65-mm diplospondylous precaudal vertebra having 21 bands that was removed from a 6-m white shark caught at Gans Bay, South Africa (L. J. V. Compagno, personal communication). An age of 21–23 years for white sharks 5–6 m TL is consistent with an extrapolation of the growth curve for eastern North Pacific white sharks given by Cailliet *et al.* (1985).

Measurements of the Embryos

Smith's (1951) proportional measurements of FL, precaudal length, prepelvic length, pre-first dorsal length, and prepectoral length for a 1400 mm TL free-living white shark are all greater than those for the other small white sharks shown in Table II. The reason is unknown, but may relate to the use of a different method for measuring TL. The girth measurement given by Smith (60%) is also considerably larger than that of the two North Cape embryos, but it appears that he reported maximum girth (at the level of the first dorsal fin) rather than the girth behind the pectoral fins, as was used for the embryos and the Kaipara shark.

If Smith's (1951) measurements are ignored, some

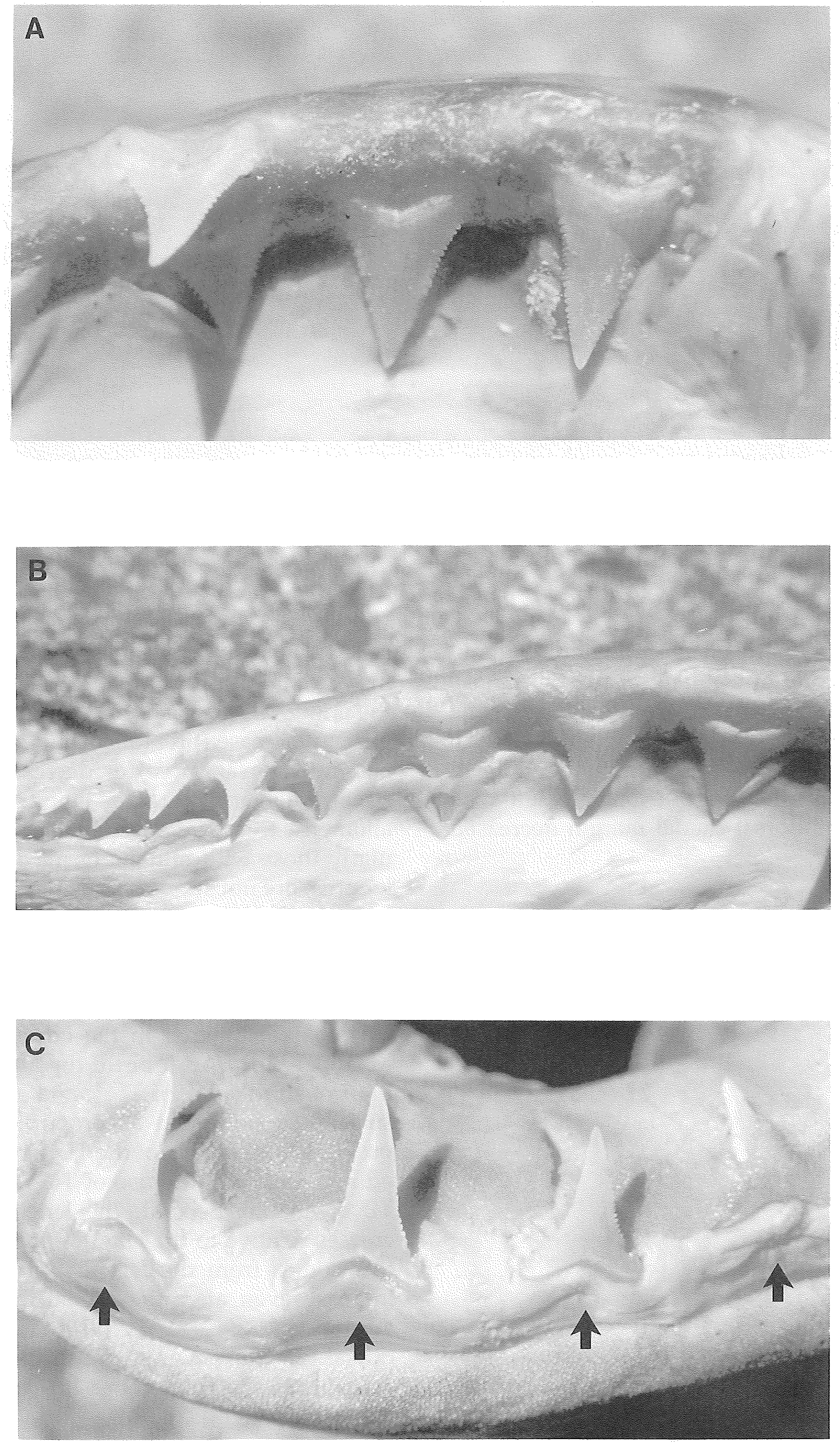

FIGURE 4 (A) First three upper right teeth from a 1430-mm female embryo white shark (viewed from inside the jaw; symphysis to the right). (B) Teeth 4–11 from the upper right jaw of a 1430-mm female embryo white shark (viewed from inside the jaw). (C) First four lower left teeth from a 1430-mm female embryo white shark (symphysis on the left). Arrows indicate scars from a previous series of teeth.

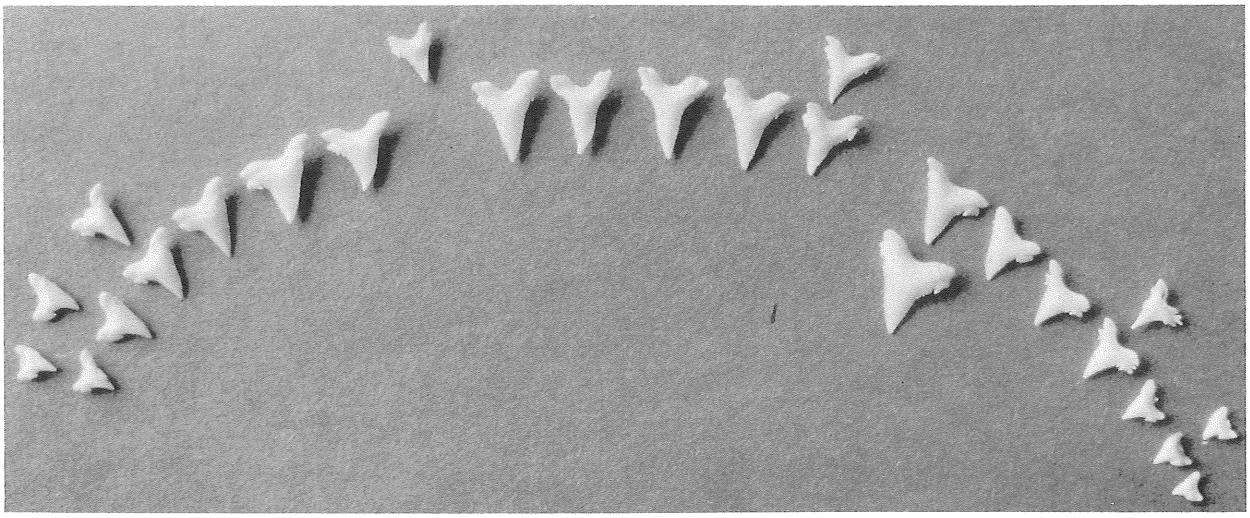

FIGURE 5 Upper jaw tooth series reconstructed from teeth found in the stomach of a 1430-mm female embryo white shark. The teeth are arranged with their anterior faces visible (teeth on the left of the photo are from the right half of the jaw, and vice versa).

consistent allometric patterns are apparent. Precaudal length, pre-second dorsal length, pre-first dorsal length, head length, prenarial length, and intergill length all increased (as a proportion of TL) as TL increased. For the two embryos and the Kaipara shark, the pelvic–caudal space also increased with TL. Conversely, the dorsal caudal margin decreased proportionally with increased TL. A number of other measurements showed no consistent trends among the embryos and small free-living sharks, but did appear to increase (prebranchial length, preoral length, and interdorsal space) or decrease (eye length) between small and large free-living sharks. Some of the allometric trends reported by Bass *et al.* (1975), particularly those with minima or maxima at intermediate lengths, are not supported by the new data presented in Table II.

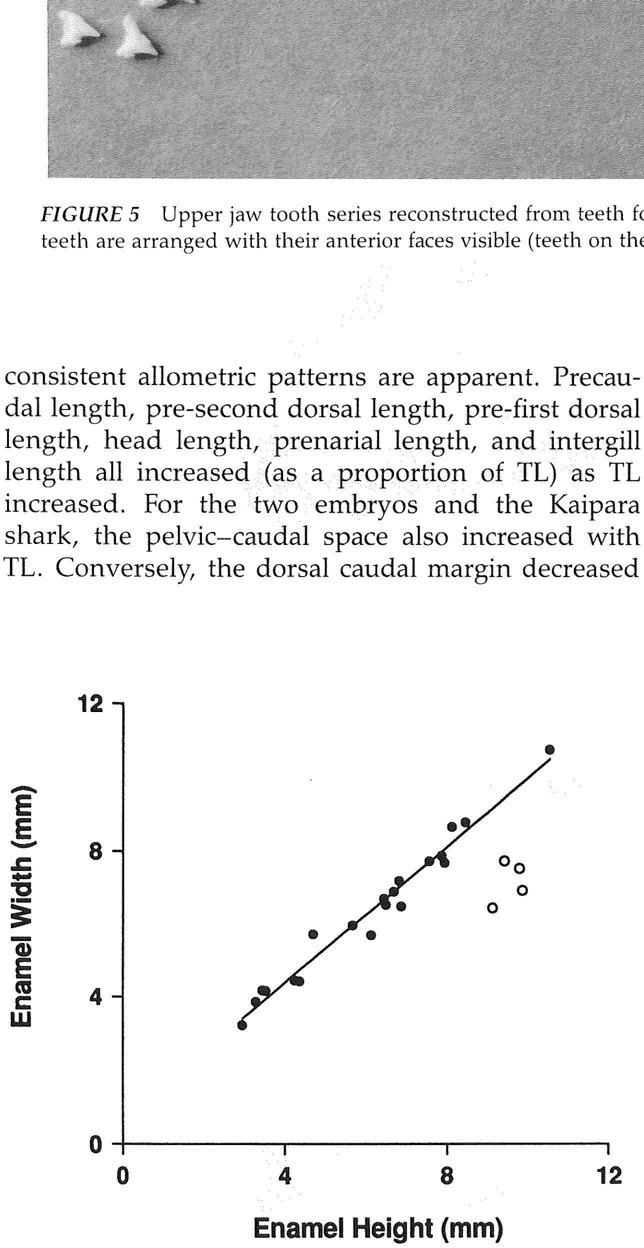

FIGURE 6 Relationship between enamel height and enamel width for the upper jaw teeth shown in Fig. 5. The first two teeth from both the left and right sides of the jaw are indicated by open circles and were omitted when fitting the regression line (enamel width = 0.645 + 0.935 enamel height; N = 20, r = 0.985).

The proportional decrease in the dorsal caudal margin appears to be due to two processes. First, the two lobes of the caudal fin of embryos are presumably folded together in the uterus and are strongly lunate at birth. After birth, the lobes diverge, resulting in "shrinkage" of TL_{nat} and an increase in measurements expressed as proportions of TL_{nat}. This problem is an artifact of the TL_{nat} measurement method and supports the use of TL_{flex} for measuring the TL of sharks. Second, the length of the body increases relative to the length of the tail. Evidence for this comes from the fact that (1) body proportions increase even after the caudal fin has attained the adult shape (Bass *et al.*, 1975) (Table II), and (2) the dorsal caudal margin decreases proportionally throughout life from about 26% to 22% of TL (Table II).

Other External Characters of the Embryos

When referring to black axillary blotches, Bass *et al.* (1975) stated that "we have not seen such marks on specimens from [South Africa]." However, axillary blotches have been found by other South African researchers (Smith, 1951; L. J. V. Compagno, personal communication). The occurrence of axillary blotches is also variable in the Mediterranean (see Chapter 30, by Fergusson).

Smith (1951) did not find spiracles in a 1400 mm TL South African white shark, and Bass *et al.* (1975) reported that spiracles were not always present in white sharks >1700 mm TL. A rounded first dorsal fin was also reported for a 1400-mm South African white shark (Smith, 1951).

Teeth of the Embryos

The teeth found in the jaws of the three North Cape embryos closely resembled those of small free-living white sharks (Smith, 1951; my unpublished observation by comparison with the 1521-mm Kaipara shark). The lower jaw teeth were mainly functional, but the upper jaw teeth were not. Several species of lamnoid sharks have embryonic dentitions that differ from those of postpartum individuals (Moreno *et al.*, 1989; Moreno and Morón, 1992b; Gilmore, 1993). Distinct embryonic dentitions may be an adaptation for oophagy (Gilmore, 1993). However, egg capsules may be swallowed whole in *Alopias superciliosus* (Moreno and Morón, 1992b), indicating that functional teeth are not a prerequisite for oophagy. More detailed analysis of the morphology of the smaller teeth taken from the guts of white shark embryos might elucidate the ontogeny of tooth structure in this species.

Internal Organs of the 1430-mm Embryo

The proportional liver weight of about 16.5% is slightly lower than that reported for a 1500 mm TL white shark embryo from Japan (18.56%; see Chapter 14, by Uchida *et al.*). These values for embryonic liver weight are at the upper end of the range for free-swimming juvenile white sharks: comparative liver weights include 17.0% for a 1400-mm shark (Smith, 1951), 16.1% for the 1521-mm Kaipara shark (Table II), and 5–22% for juveniles <2 m TL (Cliff *et al.*, 1989). Adults may have a liver weight as high as 24% (Uchida, 1983, personal communication; Cliff *et al.*, 1989). The lack of yolk in the stomach of the 1430-mm embryo, and the large liver, are consistent with suggestions that lamnoid embryos consume all intrauterine yolk supplies and store the energy in an enlarged liver before birth (Gilmore, 1993).

The presence of teeth in the guts of white shark embryos may be a general phenomenon. Teeth were also found recently in embryos from Japan and South Australia (Uchida *et al.*, Chapter 14; J. D. Stevens, personal communication). The South Australian embryo had 69 teeth in its stomach, the largest of which were 10.3 and 10.4 mm enamel height. The intestine was not examined.

There are three possible explanations for the presence of teeth and denticles in the gut of white shark embryos. First, and most likely, is that the embryo had swallowed its own shed teeth and denticles. This explanation is supported, for the teeth at least, by (1) the presence of most of a single series of teeth in the stomach, (2) the absence in the stomach of the third upper right tooth and the presence of a matching tooth in the jaw of the embryo, and (3) the presence of tooth scars in the jaws. Second, embryos may shed their teeth and denticles into the uterus, from which they are ingested incidentally during feeding. Although this is possible, such behavior would probably lead to a more random assortment of upper jaw teeth in the gut than was actually found. Third, the embryo had eaten one (or more) of its siblings. The teeth in the stomachs of the 1430-mm North Cape embryo and the 1270-mm South Australian embryo were large, and must have come from embryos of similar size. It is difficult to imagine embryos devouring similar-sized siblings.

Teeth have also been found in the guts of two embryos of *C. taurus* from South Africa (G. Cliff, personal communication) and in a New Zealand free-living 1280 mm TL specimen of *Mitsukurina owstoni* (C. Duffy, personal communication). Teeth were not found in the guts of embryonic *A. superciliosus* by Moreno and Morón (1992b). The ingestion of teeth may not be restricted to lamnoid sharks, and may simply have been overlooked by previous workers.

Reproductive Mode

Intermediate-stage white shark embryos exhibit the enormously distended abdomens that are characteristic of oophagous species (Uchida *et al.*, 1987; Ellis and McCosker, 1991). The 1430-mm late-stage embryo in this study had no yolk in its gut, possibly because it was near birth. However, Uchida *et al.* (Chapter 14) found yolk and egg membranes in the stomachs of similar-sized embryos removed from the Toyo-cho shark. White sharks are therefore clearly oophagous, but are they also embryophagous? If *embryophagy* is defined as the consumption of one's siblings, then any embryo that consumes fertilized eggs is technically practicing embryophagy. However, the consumption of well-developed embryos has been documented only in *C. taurus* (Gilmore *et al.*, 1983;

Gilmore, 1993). It therefore seems sensible to restrict the term *embryophagy* to those embryos that eat other well-developed embryos.

Evidence is lacking to indicate that white shark embryos are embryophagic. In the embryophagous *C. taurus*, only one embryo survives in each uterus, so litter size is never more than two embryos (Bass *et al.*, 1975; Gilmore *et al.*, 1983; Gilmore, 1993). In white sharks, maximum litter size is at least 10 (see Chapter 14, by Uchida *et al.*), and perhaps as high as 14 (Table I). The possession of relatively large litters provides strong evidence that embryophagy does not occur in white sharks (see also Gilmore, 1993).

Maximum litter sizes in lamnoid sharks vary from 2 to 18 embryos, with most species at the lower end of the range (Table III). Only *I. oxyrinchus*, with up to 18 embryos, has a litter size comparable to that of white sharks. Why is litter size typically 4 or fewer embryos in most lamnoids, when embryophagy is known only in *C. taurus*? Pregnant females of most species are seldom caught, and the causes of differential fecundity are unknown, although Gilmore (1993) discussed several hypotheses.

Placental attachments do not form between white shark embryos and their mother. Uchida *et al.* (1987) found no evidence of umbilical cords in photos taken of intermediate-stage embryos. Late-stage embryos in this study and intermediate- and late-stage embryos reported by Uchida *et al.* (1987; see also Chapter 14) had small well-healed scars on their throats. These scars persist for an unknown period after birth (Ellis, 1975; Stevens, 1983; Klimley, 1985b), but they are not the site of umbilical attachments; they may represent the site of absorption of the yolk sac and its stalk (see also Pratt and Casey, 1990).

The available evidence indicates that the reproductive mode in white sharks is aplacental viviparity, with embryos being nourished by oophagy.

Parturition

Embryos >100 cm TL have been caught from late winter to summer (Table I). Embryos ≥127 cm were almost certainly near birth, indicating that parturition occurs in spring or summer (Table I). Further support for this timing is provided by a 5.2-m female caught off Tasmania, Australia, on January 30, 1993. She had large (40 cm wide), flaccid, empty uteri, indicating that she had recently given birth (B. D. Bruce and J. D. Stevens, personal communication). Another 5.2-m female caught off South Australia in April 1990 had a large ovary and large but empty uteri (Bruce, 1992) and may also have been postpartum. Most neonate white sharks (<155 cm TL) have also been caught in spring–summer (Casey and Pratt, 1985; Klimley, 1985b; Fergusson, Chapter 30) (Table IV).

Pregnant white sharks reputedly carrying small embryos have been caught in spring or summer (Norman and Fraser, 1937; Bruce, 1992) (Table I). The embryo lengths of 5–60 cm reported by Bruce (1992) for spring-caught white sharks were estimated by a fisherman, and are thus almost certainly imprecise and inaccurate. Nevertheless, the embryos were clearly at an early or intermediate developmental stage, rather than being close to birth. The Kin white shark reported by Uchida *et al.* (1987) had large empty uteri, suggestive of recent birth, in winter (February). There are several possible explanations for these observations: (1) the reported embryo lengths and/or capture dates were incorrect; (2) the reproductive cycle is non-

TABLE III **Maximum Litter Sizes Reported for Lamnoid Sharks**

Family	Common name	Species	Litter size (max)	Reference
Odontaspididae	Sand tiger shark	*Carcharias taurus* (=*Eugomphodus*)	2[a]	Bass *et al.* (1975); Gilmore *et al.* (1983)
Pseudocarchariidae	Crocodile shark	*Pseudocarcharias kamoharai*	4	Bass *et al.* (1975); Fujita (1981)
Alopiidae	Pelagic thresher	*Alopias pelagicus*	2	Otake and Mizue (1981)
	Bigeye thresher	*Alopias superciliosus*	4	Guitart Manday (1975); Moreno and Morón (1992b)
	Thresher	*Alopias vulpinus*	7	Moreno *et al.* (1989)
Lamnidae	White shark	*Carcharodon carcharias*	14	This study (Table II)
	Shortfin mako	*Isurus oxyrinchus*	18	Branstetter (1981)
	Longfin mako	*Isurus paucus*	4	Gilmore (1993)
	Salmon shark	*Lamna ditropis*	4	Paust and Smith (1986)
	Porbeagle	*Lamna nasus*	5[b]	Bigelow and Schroeder (1948); Templeman (1963); Gauld (1989)

[a]Litter sizes often exceed 2 in early gestation, but only two embryos survive to birth (Gilmore, 1993).
[b]The number is rarely greater than 4.

TABLE IV **Small Free-Living White Sharks from the Southern Hemisphere**

No.	Date	Location	TL (cm)	Sex (M/F)	Mass (kg)	Reference
1	March 1967	Eden, New South Wales, Australia	139			Kemp (1991)
2	1950	Algoa Bay, South Africa	140	M	20	Smith (1951), L. J. V. Compagno (personal communication)
3	December 1984	Cronulla, New South Wales, Australia	146	M	31	J. D. Stevens (personal communication)
4	January 18, 1992	Adelaide, South Australia, Australia	147		27	B. D. Bruce (personal communication)
5	May 1, 1986	Ciskei, South Africa	151	M	30	L. J. V. Compagno (personal communication)
6		Durban, South Africa	152		25	Randall (1973)
7		Durban, South Africa	152		25	Randall (1973)
8	January 19, 1993	Kaipara Harbour, New Zealand	152	F	25	This study
9	March 1, 1981	Port Stephens, New South Wales, Australia	153	F	31	J. D. Stevens (personal communication)
10	September 14, 1991	Bayly's Beach, New Zealand	≈155	M	37	This study
11	January 1985	Bird Island, South Africa	159	M	31	L. J. V. Compagno (personal communication)
12	December 15, 1989	Bird Island, South Africa	160	M	40	D. A. Ebert (personal communication)
13	September 27, 1964	Natal, South Africa	170	F	47	Bass *et al.* (1975), L. J. V. Compagno (personal communication)
14	January 15, 1992	Manukau Harbor, New Zealand	174	F	74	This study

synchronous, with females carrying embryos at different stages of development during spring–summer; or (3) the gestation period is longer than 1 year, resulting in two (or more) cohorts of embryos being present in the population at any given time. The second and third explanations seem more likely than the first.

Birth in white sharks is probably headfirst. In most viviparous shark species, young are born tailfirst (Uchida *et al.*, 1990; Pratt and Castro, 1991), but headfirst birth occurs in *C. taurus* (Gilmore *et al.*, 1983).

Embryos and pregnant or postpartum white sharks have been reported from New Zealand, Australia, Taiwan, Japan, and the Mediterranean Sea (Table I). Newborn and 0+ young [i.e., <176 cm TL, based on the growth curve provided by Cailliet *et al.* (1985)] have been reported from New Zealand, Australia, South Africa, the eastern North Pacific, the western North Atlantic, and the Mediterranean (Casey and Pratt, 1985; Klimley, 1985b; Fergusson, Chapter 30) (Table IV). Therefore, parturition probably occurs in many distinct, mostly temperate, locations worldwide.

Size at Birth

Estimation of the length of white sharks at birth has been hampered by the rarity of pregnant females and small free-living young. Unfortunately, the lengths of the three "smallest" free-living white sharks reported in the literature are erroneous. Bigelow and Schroeder (1953) reported a 91-cm (3-ft) white shark, but later corrected this to 145 cm (Bigelow and Schroeder, 1958). Ellis and McCosker (1991, p. 65) illustrated a small white shark with a caption stating that it was 104 cm (41 in.) long. However, the photograph is of a specimen measured and dissected by H. L. Pratt, who informed me (personal communication) that it was actually 122 cm long. Klimley (1985b: Appendix 1, No. 39) cited a record of a 1085-mm white shark provided by C. Swift. The specimen is in the collection of the Scripps Institution of Oceanography, La Jolla, California, and the catalogue entry states that it was 2000 mm long. R. H. Rosenblatt (personal communication) has examined the specimen and confirmed that it is much larger than 1 m. He suggested that the data sheet measurement of 1085 mm was a transcription error for 1850 mm.

The smallest reliably measured free-living white sharks appear to be three 122-cm North American specimens (Casey and Pratt, 1985; Klimley, 1985b). There have been unconfirmed reports of free-living white sharks <122 cm (Casey and Pratt, 1985; L. J. V. Compagno, personal communication), but to my knowledge, none has been accurately measured.

A number of sharks in the size range 125–140 cm have also been caught (Smith, 1951; Casey and Pratt, 1985; Klimley, 1985b; Ellis and McCosker, 1991; Fergusson, Chapter 30). The smallest Southern Hemisphere white shark reported so far was 139 cm (Table IV), but this may simply reflect the fact that fewer juvenile white sharks have been caught there than in the Northern Hemisphere.

Length at birth is therefore about 120–150 cm. This range will probably be extended at both ends as further information is obtained. Data are insufficient to determine whether length at birth varies regionally. A wide range in length at birth is typical of many shark species, but the range in *weight* at birth in white sharks is remarkable: the 122-cm free-living sharks weighed only 12–16 kg (Casey and Pratt, 1985), whereas large embryos weighed 26–32 kg (Uchida *et al.*, Chapter 14; this study). However, newborn white sharks may lose weight initially while they are learning to feed, so the real difference in weight at birth may be less than this.

Female Length at Maturity

For the purposes of this chapter, female white sharks were judged to be mature if they were pregnant or if either the ovary **or** the uteri were large and well developed (Fig. 7). The largest immature females were 4.72 m (Springer, 1939) and about 5 m (Parker, 1887). [Parker reported the length of this shark as 17 ft (5.18 m), but it was probably measured over the curve of the body, as was another larger white shark discussed in the same paper. From measurements given by Parker for the latter shark, the straight-line length is 95.7% of the length measured over the curve. Applying this conversion factor to a length of 5.18 m gives an estimated 4.96 m TL for the immature shark.] In both of these sharks, the ovaries were small and the oviducts were not well developed.

The three smallest mature females reported (3.2-, 4-, and 4.2-m pregnant sharks) were all caught and measured by the same Queensland beach-meshing contractor (Paterson, 1986; J. D. Stevens, personal communication). Maturity at 3.2 m seems highly unlikely, given the size range of other immature and mature females (Fig. 7). This also raises concern about the accuracy of the other two Queensland measurements. A pregnant female of about 4.2 m, reported by Bruce (1992), was apparently not measured. The next smallest mature female was the 4.27 m (14 foot) pregnant Egyptian shark (Norman and Fraser, 1937), but this measurement is suspect because of other errors in the account. The 4.45 m mature female reported by Bass *et al.* (1975) was probably slightly longer than this, because their computational method underestimates TL.

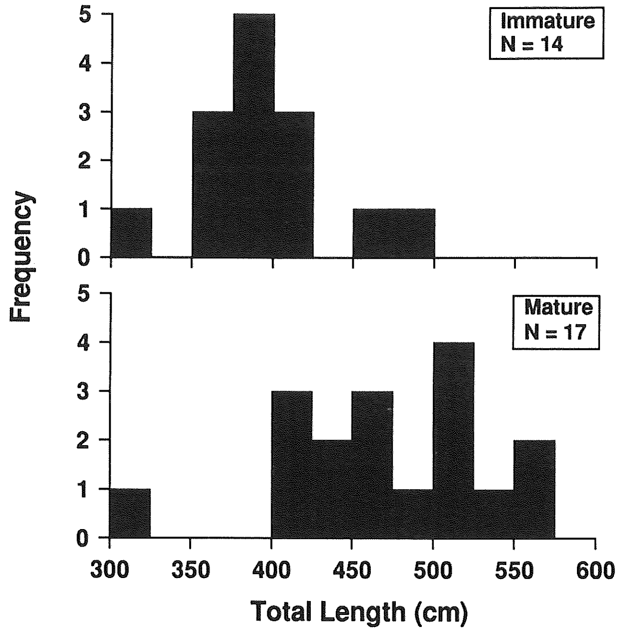

FIGURE 7 Length–frequency distributions of immature and mature female white sharks (N = sample size). Sources were Parker (1887), Norman and Fraser (1937), Springer (1939), Bigelow and Schroeder (1948), Scattergood *et al.* (1951), Bass *et al.* (1975), Casey and Pratt (1985), Paterson (1986; length data provided by J. D. Stevens, personal communication), Uchida *et al.* (1987; see also Chapter 14), Cliff *et al.* (1989), Bruce (1992, personal communication), Nakaya (1994), P. Coutin (personal communication), J. D. Stevens (personal communication), and this study.

I conclude that most female white sharks mature within the size range 4.5–5 m (Fig. 7). Some females may mature at <4.5 m, but this remains to be confirmed. Male white sharks mature at about 3.6 m (Nakaya, 1994; Pratt, Chapter 13), but the number of males examined over the critical size range is small.

Female white sharks grow larger than males. No male is known to exceed 5.5 m TL (Compagno, 1984b), whereas females may exceed 7 m (see Chapter 10, by Mollet *et al.*). The morphometric database compiled by Mollet *et al.* contained 20 females >5 m but no males in this range.

Mating

Mating has rarely been observed in wild sharks of any species, so it is not surprising that there are no published accounts of mating in white sharks. In other shark species, a number of physical signs have been used to infer recent mating, including semen or spermatophores flowing from the claspers, swollen siphon sacs, chafed claspers, and bite marks on females (Clark and von Schmidt, 1965; Springer, 1967; Pratt, 1979; Gilmore *et al.*, 1983). Published and un-

TABLE V **Evidence of Mating by White Sharks in Australia and New Zealand**

Date	Location	Evidence	Reference
November 9, 1969	Westernport, Victoria, Australia	Seminal fluid in the claspers of a 3.75-m male	R. M. Warneke (personal communication)
February 1981	New South Wales, Australia	Spermatophores oozing from the genital papilla of a 4.5-m male	Stevens (1984)
April 26, 1990	Streaky Bay, South Australia, Australia	Semicircular series of healed tooth marks on the left flank below the first dorsal fin of a 5.2-m female	Bruce (1992)
November 1990	Port Welshpool, Victoria, Australia	Bite marks on the pectoral fin of a 3.5-m immature female	P. Coutin (personal communication)
ca. November 1991	Nugget Point, Otago, New Zealand	Observation of mating between two individuals	A. Strachan (personal communication)
January 30, 1993	Southern Tasmania, Australia	Numerous bite marks on the left pectoral fin of a 5.2-m mature female	B. D. Bruce and J. D. Stevens (personal communication)

published accounts of such mating "indicators," and one observation of mating in white sharks of Australia and New Zealand, are summarized in Table V.

In November 1969, R. M. Warneke (personal communication) caught and examined a 3.75-m male white shark and observed the following:

Claspers chafed at base, at angle with outer flange of pelvic fin, indicating recent sexual activity? Several times, when the carcass was on its side and being maneuvered for measuring, the uppermost clasper momentarily rotated 90°. Adjacent to the base of each clasper was a swollen chambered sac filled with a fluid containing semi-transparent oblong–ovoid capsules (from memory about 7–8 mm long), which looked remarkably like over-cooked, boiled rice. This semen was running from the groove in each clasper.

Similarly, Stevens (1984) found spermatophores oozing from the genital papilla of a 4.5-m male caught in February.

Fresh bite marks were found on an immature female caught in November (P. Coutin, personal communication) and a mature female caught in January (B. D. Bruce and J. D. Stevens, personal communication). Healed bite marks were found on a mature female in April (Bruce, 1992). Because bite marks have been found in immature females and mature white sharks of both sexes, some bites may result from nonsexual intraspecific aggression rather than mating activity (Pratt *et al.*, 1982; Casey and Pratt, 1985; Bruce, 1992). Bite marks on immature females might be explained by premature mating, as has been documented in subadult female *Prionace glauca* (Pratt, 1979). However, Pratt (1993) argued that female lamnoids are incapable of long-term sperm storage, raising doubts that premature mating is effective in white sharks.

An account of two white sharks mating in southern New Zealand is contained in a letter written to the New Zealand Department of Conservation by a temporary employee. A. Strachan was employed to count and monitor New Zealand fur seals *Arctocephalus forsteri*, at a colony at Nugget Point, Otago (46°27′ S, 169°49′ E). White sharks were frequently seen from the clifftop vantage point, and at an unspecified date before December 22, 1991 (probably in November), she made the following observation:

I have unwittingly been fortunate to witness a mating [between two white sharks]. I had thought at the beginning they were fighting as one animal appeared to be attempting to grasp the other with its great mouth, making great gouges in its side. However, they had eventually become motionless, one under the other, turning over from time to time belly to belly. This obvious copulation lasted some forty minutes before the animals finally parted and glided off in opposite directions.

This account sounds highly plausible, based on what is known about mating behavior in other sharks, but I have been unable to contact Strachan to confirm her observations or to obtain further details.

Despite reservations about whether all of the above observations indicate mating activity, it is probably significant that all were made during the austral spring–summer, except for the observation by Bruce (1992). The latter occurred in autumn (April) and involved *healed* bite marks. Because parturition is also thought to occur in spring–summer, mating may occur soon after parturition, and females may carry successive litters of embryos with little or no resting period in between. This, however, remains to be demonstrated.

Summary

A 5.36-m pregnant female white shark *C. carcharias* was caught at North Cape, New Zealand, on Novem-

ber 13, 1991. Her first upper right tooth had an enamel height of 51 mm, and vertebral bands indicated an age of about 22 years. She was carrying seven full-term embryos. Two of these were obtained for study, along with the jaws of a third. The two embryos measured 143 and 145 cm TL, and the larger one weighed 26.1 kg. Morphometric data from the embryos were compared with data from free-living white sharks. One embryo was dissected and found to have a large liver (16.5% of body weight). There was no yolk or egg membranes in the gut, but the stomach and intestine contained 191 teeth. It is thought that the embryo had ingested its own shed teeth.

A review of the reproductive biology of white sharks revealed their reproductive mode to be aplacental viviparity, with embryos nourished by oophagy. No evidence of embryophagy was found. Maximum litter size is at least 10, and perhaps as high as 14. Parturition probably occurs in temperate locations worldwide during spring–summer. The gestation period is unknown. Length at birth is 120–150 cm, and female length at maturity is about 4.5–5 m. Mating probably occurs in spring–summer. A mating event observed in New Zealand was described.

Acknowledgments

This chapter would not have been possible without the foresight and help of C. Garrett, who expended much time and energy in bringing the North Cape shark ashore, and K. Flutey, who was responsible for saving the two embryos. Valuable information was also obtained from videotapes taken by J. Bradley and R. Grange and photographs provided by the *Northern Advocate* newspaper and R. Grange. G. McGregor provided the Kaipara Harbour white shark. For permission to use their unpublished data, I am indebted to B. D. Bruce, G. Cliff, L. J. V. Compagno, P. Coutin, D. A. Ebert, H. L. Pratt, J. D. Stevens, and S. Uchida. For other information, assistance, advice, and comments on the manuscript, I thank the above as well as D. G. Ainley, S. Ballara, C. Bradley, G. Cuthbert, R. Ellis, I. K. Fergusson, R. Forlong, M. A. Fraser, R. G. Gilmore, I. Gordon, M. Johnson, A. P. Klimley, J. E. McCosker, M. McGrouther, H. F. Mollet, J. Pepperell, R. H. Rosenblatt, P. Saul, C. Sherman, P. Stipa, A. Strachan, C. Thorburn, and R. M. Warneke.