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Reproductive biology of lamnoid sharks

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Synopsis

The capture of recently inseminated or pregnant specimens of *Carcharias taurus, Isurus paucus, I. oxyrinchus, Alopias superciliosus* and *A. vulpinus* has allowed new information to be obtained on the reproductive biology of these species. Oophagy and embryonic cannibalism (adelphophagy) have been documented in *C. taurus*, but only oophagy in other lamnoid species. The occurrence of up to nine embryos of similar size per uterus in *Isurus* and no indication of functional erect teeth in embryos leaves considerable doubt that embryophagy occurs in this genus. Considerable data has been collected on *Carcharias taurus* which allows a lamnoid reproductive model to be developed and tested, in spite of the obvious differences between the reproductive biology of this species and other lamnoids. Gonad structure, ovarian development, fertilization, early embryonic differentiation, embryonic nutrition and parturition, in *C. taurus* and other lamnoids differs significantly from other elasmobranchs.

Introduction

Five to seven families have been placed in the order lamniformes (Compagno 1977, 1984, Eschmeyer 1990). In addition to a variety of anatomical characters, the order is unified by a common reproductive style: embryos examined from nine of the sixteen species within the order have been found to be oophagous (Table 1). The first detailed description of lamnoid embryos and documentation of oophagy was made by Swenander (1907) for the porbeagle shark, *Lamna nasus* (as *L. cornubica*). Lohberger (1910) followed Swenander with the most detailed anatomical study of a lamnoid embryo yet published. Shann (1911) published a description of *Lamna nasus* embryos without knowledge of the studies of Swenander (1907) or Lohberger (1910) and misidentified the yolk stomach, describing it as a yolk sac. Shann later corrected his error commenting

further on oophagy in *L. nasus* (Shann 1923). During this period oophagy was described for the great white shark, *Carcharodon carcharias* (as *C. rondoletii* Müller & Henle), by Sanzo (1912), for embryos taken from a female captured in the Straits of Messina 31 March 1905. Documentation of oophagy in other species has only occurred during the past few decades (Table 1).

Most lamniform species are inhabitants of deep oceanic waters and are typically pelagic or mesopelagic. However, the sand tiger shark, *Carcharias taurus*[1] and *C. tricuspidatus*[1] commonly inhabit shallow neritic waters. The accessibility of *C. taurus* has allowed its capture and study on a routine basis, thus giving us most of our present information on the reproductive biology of lamnoids. For this rea-

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[1] Taxonomic nomenclature follows Compagno 1984, and Eschmeyer 1990.

Table 1. Summary of lamnoid shark reproductive information.

Species/Reference	Parturition size, TL (cm)	Parturition period	Smallest free swimming, TL (cm)	Female mat. size, TL (cm)	Total no. embryos	Oophagy documented
Carcharias taurus						
Springer (1948)	97	winter	91	239	2	X
Bass et al. (1975)	100–105	winter	95	220	2 (3)[1]	X
Gilmore et al. (1983)	91–105	winter		237	2 (9)[1]	X
Sadowsky (1970)				228	2	X
Cadenat (1956a)	120					
Taniuchi (1970)			95–96			
Cetorhinus maximus						
Sund (1943)	150	summer			6	
Matthews (1950)						
Bigelow & Schroeder (1948)			165	457–610		
Pseudocarcharias kamoharai						
Bass et al. (1975)					4	X
Fujita (1981)	40–43	variable		98.2–98.5	4	X
Abe et al. (1969)			59	99		
Carcaharodon carcharias						
Klimley (1985)		summer/fall	122			
Smith (1951)			140			
Bass et al. (1975)			140	427–445		
Scattergood (1962)			91			
Fitch (1949)				137–154		
Randall (1973)			137			
Bigelow & Schroeder (1948)			145	427	9	
Casey & Pratt (1985)		summer	122	406		
Sanzo (1912)					25–30	X
Uchida et al. (1987)	110+	spring/summer			7	X
Norman & Fraser (1948)				427	9	
Cailliet et al. (1985)	~125	spring/summer	129	366–427		
Isurus oxyrinchus						
Cadenat (1950)						X
Gilmore (data)	70	spring/summer	76.5		12	X
Bigelow & Schroeder (1948)						
Stevens (1983)	70	winter/spring	76.7	280	4–16	X
Garrick (1967)			68–71			
Bass et al. (1975)	60–70		71	280–291		
Vaillant (1889)					7	
Guitart-Manday (1966)				205		
Uchida et al. (1987)		spring		337	16	X
Branstetter (1981)		winter/spring		300	18	
Gubanov (1978)	110			180		
Depperman (1953)					10	
Gohar & Mazhar (1964)				263	6	
Pratt, Casey, Castro, Gilmore (data) (1992)		winter		220	14+	X
Isurus paucus						
Guitart-Manday (1966)	92			245	2	

Table 1. Continued.

Species/Reference	Parturition size, TL (cm)	Parturition period	Smallest free swimming, TL (cm)	Female mat. size, TL (cm)	Total no. embryos	Oophagy documented
Garrick (1967)			123			
Gilmore (1983)	97	winter			2	X
Casey & Pratt (pers. comm.)	122*	winter			4	
Lamna nasus						
Bigelow & Schroeder (1948)	61	summer	74	152	1–4	X
Bass et al. (1975)			70–75		2–4	
Aasen (1966)		spring	85–87			
Shann (1911, 1923)	75	spring	82.5		4	
Templeman (1963)	61–76			232	4	
Dunlop (1892)		spring/summer			2	
Swenander (1907)		spring/summer			2	X
Nakaya (1971)				219	4	X
Lamna ditropis						
Otake (pers. comm. 1985)	79.5+			194–250	3	
Alopias superciliosus						
Osipov (1968)	60–62					
Gruber & Compagno (1981)	100–130	variable		350	2	
Bigelow & Schroeder (1948)			130			
Cadenat (1956b)					2	X
Nakamura (1935)				332–366	2	
Fourmanoir (1961)			180			
Bass et al. (1975)	100–103		161			
Gilmore (1983)	105				2	X
Springer (1943)				300	2	
Gubanov (1978)	100		180			
Stillwell & Casey (1976)				315	2	
Alopias vulpinus						
Hixon (1979)	139–142	summer				
Bigelow & Schroeder (1948)			117	487	2–(4?)	
Vaillant (1885)	150–155					
Gubanov (1972, 1978)	149	spring/summer	153	260–330	2	
Leim & Scott (1966)	152			426	2–(4?)	
Strasburg (1958)		summer		315	2	
Alopias pelagicus						
Nakamura (1935)				270–330	2	
Otake & Mizue (1981)				264–282	2	X
Strasburg (1958)					2	

[1] Prior to or during adelphophagy; * = FL.

son, it has been used as a model species for reproductive styles in lamniform sharks. However, more thorough analyses of the meager information available for other lamniform species and critical examination of recently acquired specimens demonstrates that, even though there are shared reproductive characters throughout the order, there are also differences in the reproductive biology between the various genera and species.

More pregnant specimens of *Carcharias taurus* have been captured on a world wide basis than any other lamnoid. In every case, only a single embryo

Fig. 1. Photo of one of two uteri with six oviphagous embryos 43.0–49.2 cm TL per uterus from *Isurus oxyrinchus* (HBOM 103:00250–00253).

has been found in each uterus at parturition (Bass et al. 1975, Gilmore et al. 1983). Intra-uterine cannibalism (embryophagy or adelphophagy) has been documented in this species by the same authors. Recent captures of pregnant thresher sharks, *Alopias vulpinus* (Gubanov 1972), pelagic thresher, *A. pelagicus* (Otake & Mizue 1981) and bigeye thresher shark, *A. superciliosus* (Gruber & Compagno 1981, Gilmore 1983) have also documented no more than a single embryo per uterus. However, although oophagy has been documented in all alopiid species, embryophagy has not. Multiple embryos per uterus at parturition, or near term, have been documented in isurid sharks: *Lamna nasus* (maximum of two/uterus, Bass et al. 1975); salmon shark, *Lamna ditropis* (two/uterus, Tsuguo Otake, personal communication, June 1985); mako, *Isurus oxyrinchus* (Fig. 1) (max. of nine/uterus, Bass et al. 1975, Branstetter 1981, Stevens 1983); longfin mako, *Isurus paucus* (max. of two/uterus, Harold Pratt & Jack Casey NMFS, personal communication, 1988) and crocodile shark, *Pseudocarcharias kamoharai* (max. of two/uterus, Fujita 1981). Though definitive documentation is lacking, multiple embryos (7–30) have been recorded for *Carcharodon carcharias*

(Fig. 2) (Sanzo 1912, Uchida et al. 1987). Information on embryonic development is rudimentary or totally lacking for the Indian sand tiger shark, *Carcharias tricuspidatus,* smalltooth sand tiger, *Odontaspis ferox,* bigeye sand tiger shark, *C. noronhai* (Odontaspididae), basking shark, *Cetorhinus maximus* (Cetorhinidae), goblin shark, *Mitsukurina owstoni* (Mitsukurinidae) and megamouth shark, *Megachasma pelagios* (Cetorhinidae [Maisey 1985]).

It is the objective of this paper to review some of the recent discoveries illuminating embryonic reproductive development in lamnoid sharks, comment on inaccuracies presently in the literature, and present a variety of hypotheses on the function and evolution of lamnoid reproductive systems. The need for further cooperative studies on a worldwide basis is stressed, particularly for cosmopolitan pelagic and mesopelagic species often captured in oceanic longline fisheries. Not only should specimens be obtained, but there should be careful documentation of basic environmental information taken at the time and place where the shark was captured.
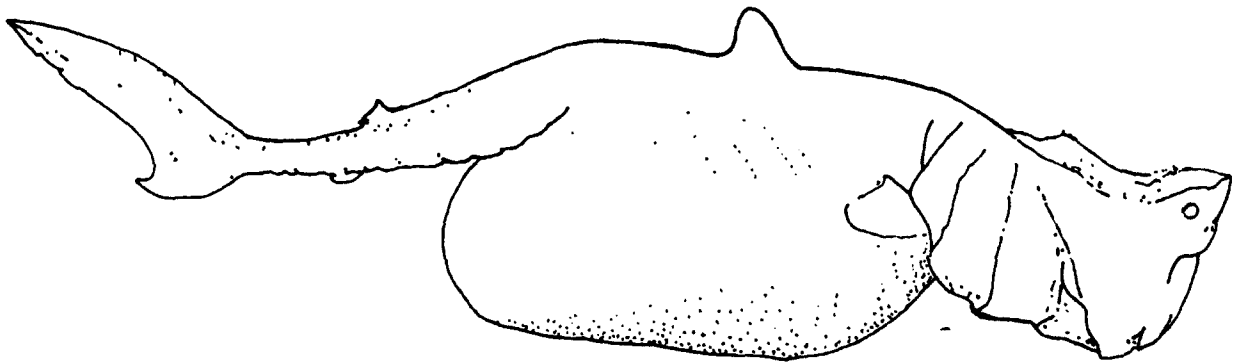
Fig. 2. Sketch of a *Carcharodon carcharias* embryo. Redrawn from Sanzo (1912).

Study material

All study material is curated in the Harbor Branch Oceanographic Museum (HBOM). The following material was examined: *Isurus oxyrinchus,* HBOM 103:00079, 00111, 00118, 00154, 00185, 00190, 00202, 00219, 00250–00253, 00310; *Isurus paucus,* HBOM 103:00078, 00080, 00109, 00121, 00177, 00191, 00192, 00208, 00213, 00291; *Alopias vulpinus,* HBOM 103:00303, 00320; *Alopias superciliosus,* HBOM 103:00108, 00147, 00156, 00157, 00163, 00171, 00176, 00187, 00203–00206, 00211, 00218, 00223, 00226–00232, 00240, 00319; *Carcharias taurus* (as *Odontaspis taurus*) HBOM 103:00065, 00069, 00101–00104, 00133–00139, 00141–00145, 00162, 00170, 00179, 00183, 00199, 00220, 00221, 00225, 00227, 00242, 00244–00249, 00254–00257, 00260–00265, 00267–00290, 00292–00302, 00304–00309; *Carcharodon carcharias,* HBOM 103:00200–00214.

Comparative reproductive anatomy

Male anatomy. – *Cetorhinus maximus* is the only lamniform species whose male reproductive anatomy has received comprehensive detailed descriptive treatment (Matthews 1950), although Pratt (1988) has recently described testicular structure for various lamnoid species in a review of elasmobranch gonad structure. Specimens were examined from the Harbor Branch Oceanographic Museum collections and from material collected from the Florida Straits, donated by commercial fishermen.

These specimens included male *Alopias superciliosus, Isurus oxyrinchus, I. paucus* and *Carcharias taurus,* immature and in reproductive condition. Their reproductive anatomy was very similar to that of *Cetorhinus maximus,* though differing in the relative size of various organs. Paired testes were always associated with the epigonal organ and are of the radial type described by Pratt (1988). The germinal zone is located at the center of each of several lobes, from which radiate seminiferous follicles ending in the surrounding efferent ductules (Pratt 1988). This testis type described for the lamnoids is unique among the sharks and is only seen elsewhere in the batoid order, Myliobatiformes. The relative position, size and development of the epididymus, ductus deferens and seminal vesicle were similar in all species. The seminal vesicle structure in *Carcharias taurus* resembles that described for *C. maximus* in that it is divided into several chambers which are then subdivided by smaller membranous septa. These chambers are turgid with spermatophores in individuals in mating condition.

The spermatophore structure differs significantly between *Isurus oxyrinchus* and *C. taurus.* The spermatophores of *C. taurus* are nearly identical to those described for *Cetorhinus maximus* by Matthews (1950). No discrete form was observed as the sperm were immersed in a semitransparent hyaline matrix. As the sperm laden matrix extrudes through the urogenital papilla, the 'spermatophores' break into cylindrical bodies of various lengths (Fig. 3a). These bodies gradually dissolve in sea water, releasing the sperm which then undergo rapid swimming

movements. In *Isurus oxyrinchus* the seminal vesicle contained white opaque spermatophores with discrete form and size, resembling 1× 2.5 mm rice grains (Fig. 3b). The sperm were closely packed in a matrix with little hyaline material relative to the spermatophores in *C. taurus* (Fig. 3c–d). These spermatophores did not dissolve as readily in sea water and sperm release could only be elicited by mechanically opening the spermatophore within sea water. The urogenital papillae and clasper structure in *C. taurus, A. supercilliosus* and *I. paucus* were as described for L. nasus (= *L. cornubica*, Jungerson 1899) and *C. maximus* (Matthews 1950).

Female anatomy. – Female lamniform sharks have a single functional right ovary situated at the anterior end of the epigonal organ and suspended from the dorsal abdominal cavity by a mesovarium (Fig. 4a–d). Specimens examined revealed this general anatomical pattern in *A. superciliosus, Isurus paucus, I. oxyrinchus, C. taurus* and *C. carcharias*. The same general lamnoid reproductive morphology has been documented in *L. nasus, A. vulpinus, A. pelagicus, C. maximus* and *P. kamoharii* by other authors (Shann 1911, 1923, Nakamura 1935, Matthews 1950, Gubanov 1972, Fujita 1981, Otake & Mizue 1981). A smooth fibrous coat from the anterior epigonal organ covers the ovarian follicles thus creating an ovary of the 'internal type' described by Pratt (1988). As Pratt (1988) states, 'this ovary type presents a 3-dimensional surface area' associated with the ellipsoidal interior lumen surrounding the oocyte mass, therefore, giving 'much more available surface area to generate yolked oocytes than the relatively planar ovary found in other [elasmobranch] orders'. A pocket, or efferent ovarian pore (Fig. 4c), opens to the abdominal cavity and allows ovulated ova to escape to the ostium. This pocket, situated anterior and dorsally on the right side of the ovary, enlarges as the ovary matures and reaches maximum size when ovulation peaks. The ovary reaches maximum size and ovulation rate during the oophagous interval of embryonic development in *C. taurus* (Fig. 4a). During gestation the ovary in *C. taurus* may reach a maximum size of 36.0 to 45.5 cm in length and weight of 8.5 kg, containing over 22 000 ova, 1.3 to 10.0 mm in diameter (Fig. 4b) (Gilmore et al. 1983). Hamlett (1983) estimates that embryos of *C. taurus* may ingest 17 000 ova during gestation. The maximum ovarian weight presented for *C. maximus* by Matthews (1950) was 12.2 kg with an estimated six million ova having diameters ranging from 0.5 to 5.0 mm. As this latter specimen was not in gestation, the ovary may not have reached maximum size. However, the maximum ova diameters observed by Matthews could represent the largest diameters attained for *C. maximus* as there was evidence of recent copulation, and therefore ovulation was proximate. Maximum ovarian weights and ova diameters at ovulation are not known for *I. paucus* or *I. oxyrinchus* as pregnant specimens examined were near parturition, a period when ovulation has ceased and the ovary begins to atrophy (Fig. 4c) (Gilmore 1983, Gilmore et al. 1983). Maximum ova diameters are around 5.0 mm in *Alopius superciliosus* (Gruber & Compagno 1981, Gilmore 1983).

After ovulation, the ova pass through the efferent ovarian pore, over the mesovarium, and enter the ostium situated near the central confluence of the paired lobes of the liver and the paired oviducts. The ova are apparently alternately shuttled to either oviduct as they pass through the anterior oviduct from the ostium, pass through a bifurcation in the oviduct (Fig. 4d) and then to either right or left oviducal glands. The oviduct bifurcation point anterior to the oviducal glands must have a gating mechanism which allows alternate movement of ova to either oviduct. Evidence for the alternate movement of ova to each oviduct is the synchronous formation of egg capsules containing a similar number of ova in each oviducal gland.

Fertilization is assumed to occur in the anterior oviduct in the vicinity of the ostium. This is based on the capture of recently mated *C. taurus* females on 8 and 12 May 1986 (off Daytona Beach, FL) which contained active sperm throughout the oviduct up to the ostium. The 12 May specimen contained sperm throughout the oviduct and within the first capsule formed. This capsule did not contain ova, only ovalbumin and sperm (Type I capsule of Gilmore et al. 1983) indicating oviducal gland activity and capsule formation prior to the arrival of ova. Serial sections of the oviducal gland of pregnant *C. taurus* have not demonstrated sperm storage in this
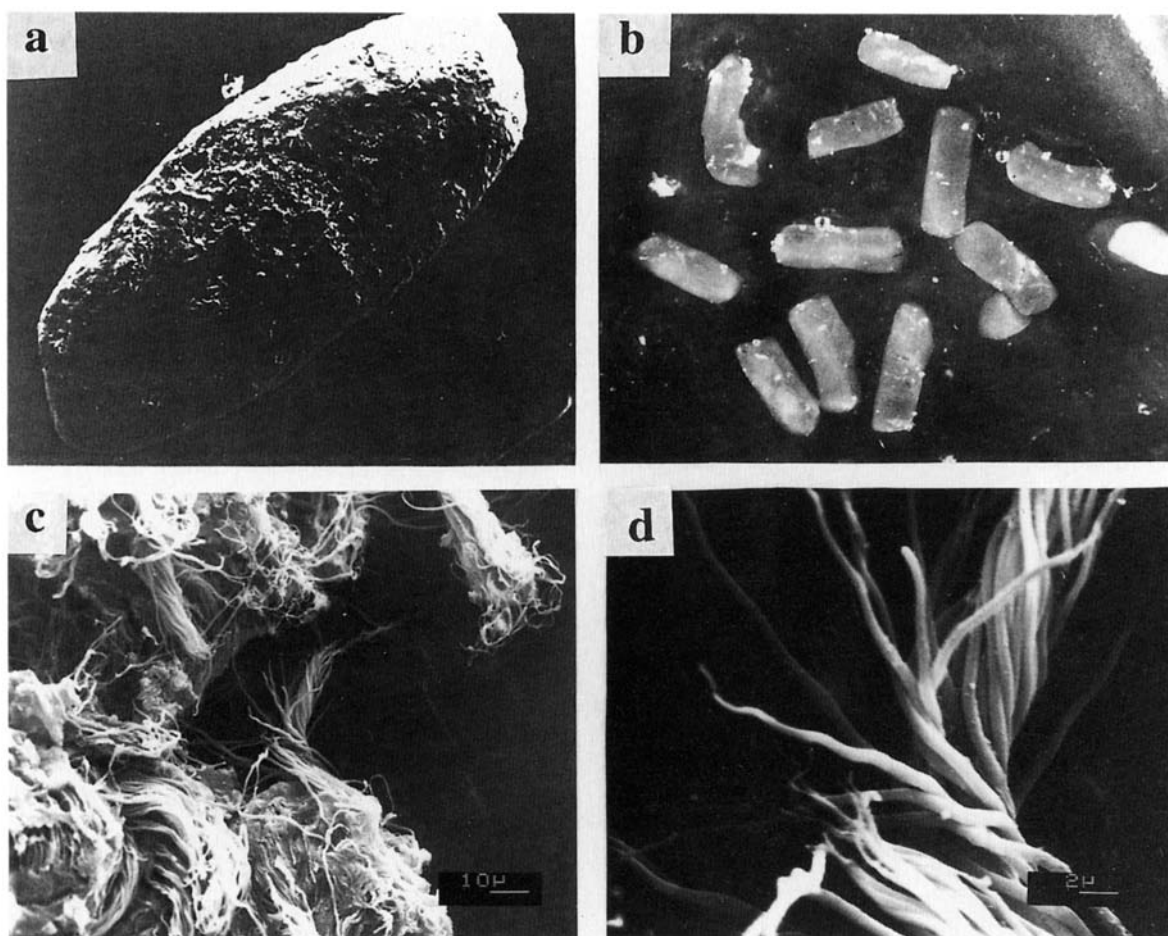
Fig. 3. a – Spermatophores of *Carcharias taurus.* b – SEM of spermatophore of *Isurus oxyrinchus.* c – SEM of internal exposure of spermatophore of *I. oxyrinchus* showing sperm aggregations. d – SEM detail of (c).

species (our observations and Pratt 1993). The first capsule to contain ova, only contains a single ovum. Multiple ova occur in increasing numbers in successive capsules. Initial observations indicated that although multiple blastodiscs may be seen on several ova in a single egg capsule, only one embryo developed per capsule (Gilmore et al. 1983). However, recent observations reveal that up to three embryos may develop within a single capsule in *C. taurus.* A pregnant *C. taurus* captured in mid June 1985 (off Daytona Beach, FL) contained capsules with two and three embryos in each of two capsules, respectively.

As egg capsules leave the oviducal gland, a membranous (collagen) tail forms behind the capsule head which contains ova and/or ovalbumin. In *C. taurus,* six basic capsule types have been identified ranging from those containing no ova and only a gelatinous ovalbumin/mucoid material, to those containing numerous fertilized or unfertilized ova (up to 23 ova per capsule, Gilmore et al. 1983). Egg capsules leave the oviducal gland and pass through the isthmus and enter the uterus typically in synchrony in both oviducts. The capture of a series of pregnant *C. taurus* in succession reveals a temporal pattern in the number and position of capsules in each oviduct over a 24 h period. This pattern reveals that ova encapsulation occurs on a 24 h interval with newly formed capsules typically occurring within
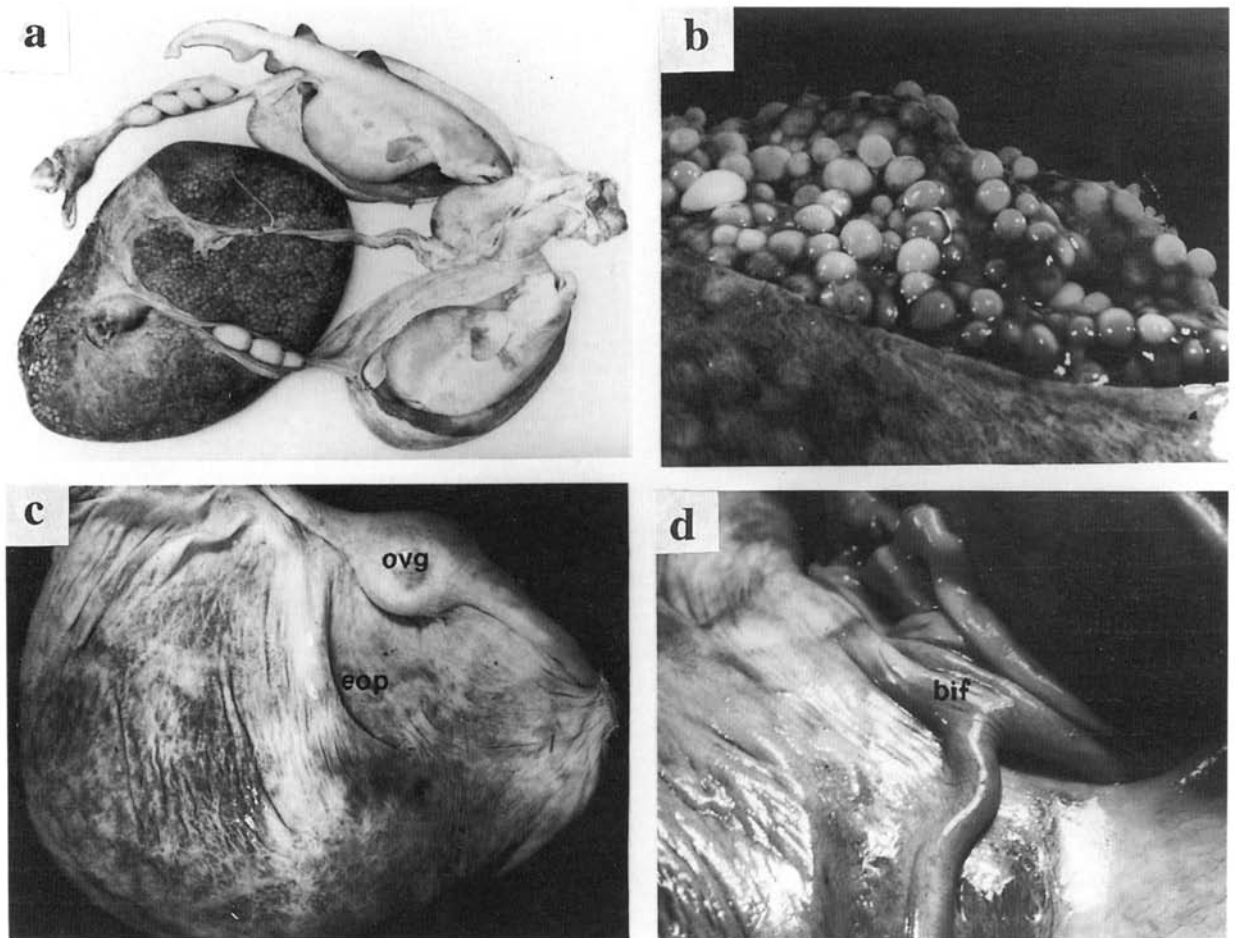
Fig. 4. a – Ovary, paired oviducts with egg capsules and oviphagous embryos of *Carcharias taurus* captured off Stuart, Florida, September 1989. Note nearly identical position and number of capsules in each oviduct. Photo courtesy of José Castro. b – Ova up to 10 mm in diameter in ovary with membrane excized for exposure, *C. taurus*. c – Ovary of pregnant *Isurus oxyrinchus* (HBOM 103:00253) showing efferent ovarian pore (eop) and oviduct including the oviducal gland (ovg). d – Anterior oviduct of *Carcharodon carcharias* showing bifurcation (bif) of oviduct a few centimeters posterior to the ostium (to the right) at the liver.

the oviducal gland in specimens captured near dawn.

Although fewer specimens of *Alopias* spp., *Isurus* spp., *Pseudocarcharias kamoharii* and *Lamna nasus* have been examined, capsule formation and variation in capsule morphology resembles that found in *C. taurus* (Gubanov 1972, Fujita 1981, Gruber & Compagno 1981, Gilmore 1983, Gilmore et al. 1983). Capsules produced early in the ovulation cycle do not contain ova, whereas capsules produced during the major oophagous interval in embryonic development contain the largest number of ova.

Embryonic development in *C. taurus* has been well documented from early development to parturition (Gilmore et al. 1983). Embryos of this species pass through at least six nutritive phases during gestation. The first two occur while the embryo is encapsulated. During early cellular differentiation, encapsulated 13 mm embryos utilize endocoelomic yolk within the cardiac stomach, valvular intestine, pericardial and coelomic cavities and do not consume yolksac yolk supplies. This phase resembles the early development in amphibian embryos.

Encapsulated embryos larger than 13 mm TL (=

total length) appear to consume or absorb materials such as albumin, mucous or other ova within the capsule after their oral cavities, jaws and alimentary tracts have developed sufficiently. The yolksac declines in size in embryos near hatching (= embryo emergence from the capsule), approximating 60 mm TL.

The uterine epithelium is highly vascularized and folded, particularly at the isthmus, and villiform structures can be observed throughout the remainder of the uterus (Fig. 5, 6). This large surface area and proximity of maternal blood supplies apparently insures oxygenation of the uterine fluid and may enhance fluid secretion. Oxygenation of uterine fluid, which is undoubtedly a major source of respiratory oxygen, is necessary as lamnoids produce very large embryos without placentation.

A functional embryonic dentition (embryonic teeth = emb), not resembling adult dentition (adult teeth = adl), develops between 40 and 60 mm TL, and apparently aids the embryo to escape from the capsule in addition to puncturing other capsule membranes after hatching (Fig. 7, 8) (Gilmore et al. 1983, Hamlett 1983). After hatching at lengths approximating 60 mm TL, the embryo obviously consumes yolksac yolk supplies and possibly uterine fluid. At lengths of 100 to 334 mm, hatched embryos actively search for and attack egg capsules containing other embryos to the exclusion of capsules containing only unfertilized ova. Smaller encapsulated embryos are either killed during capsular attacks by the larger hatched embryo, or are ripped from their capsules into the uterine cavity. Adult females captured during July and August have contained dead, mangled embryos within the uterine cavity along with a single living larger embryo (100–334 mm TL), which may have within its mouth and digestive tract up to four embryos (Gilmore et al. 1983). This cannibalistic phase has only been documented in *C. taurus*.

After the *C. taurus* embryo reaches a total length over 330 mm and has consumed all siblings, it begins to consume the large number (60–90) of turgid egg capsules within the uterus that contain unfertilized ova. These capsules can contain up to 23 unfertilized ova/capsule and are produced daily throughout this period of gestation. It is during this period

that the ovary reaches its maximum size, ovulation rates are high, embryonic growth rates are maximal and the distention of the cardiac stomach ('the yolk stomach', Shann 1911) occurs. Embryos in this latter phase have been documented in *Lamna nasus* (Swenander 1907, Shann 1911, Lohberger 1910), *Isurus oxyrinchus* (Stevens 1983, Uchida et al. 1987, Fig. 1), and *Carcharodon carcharias* (Sanzo 1912). Extensive abdominal cavity distention, due to yolk consumption, has not been observed in alopiid embryos to date (Otake & Mizue 1981, Gruber & Compagno 1981, Gilmore 1983). However, oophagy has been documented in *A. vulpinus* (Gubanov 1972), *A. pelagicus* (Otake & Mizue 1981), *A. superciliosus* (Gilmore 1983), *Isurus oxyrinchus* (Stevens 1983), *I. paucus* (Gilmore 1983) and *Pseudocarcharias kamoharii* (Fujita 1981). It is likely that all lamnoid sharks are oophagous yet not necessarily embryophagous.

Development of functional dentition, emb teeth, in lamnoid embryos may give some indication of the capacity to hunt and consume other embryos in utero (Fig. 7, 8). Erect functional teeth have been well documented in *C. taurus* embryos starting at a TL of 40 mm (Gilmore et al. 1983, Hamlett 1983). The embryonic dentition of *A. pelagicus, A. superciliosus, C. carcharias, I. oxyrinchus, I. paucus* and *P. kamohari* have been found to be variously non-functional, consisting of folded, not erect, soft or covered (with a membrane) adult teeth or microscopic emb teeth (Sanzo 1912, Nakamura 1935, Fujita 1981, Kiyoshi Fujita personal communication 1985, Gilmore 1983, Gilmore et al. 1983, Tsuguo Otake personal communication 1985, Uchida et al. 1987). However, Gruber & Compagno (1981) describe 'functional' teeth in a 20.6 cm TL embryo of *A. superciliosus*. Two 59.0–61.5 cm TL embryos of *A. vulpinus* taken from a female captured off Daytona Beach, Florida on 19 January 1989 were found to have small emb teeth along the edge of the mouth. These teeth do not resemble the adult teeth which were forming under a membranous sheath in the mouth of the same embryos. Several egg capsules found with these embryos were sliced open indicating that these teeth were capable of opening capsules and possibly killing and consuming other embryos. However, no smaller dead or consumed em-
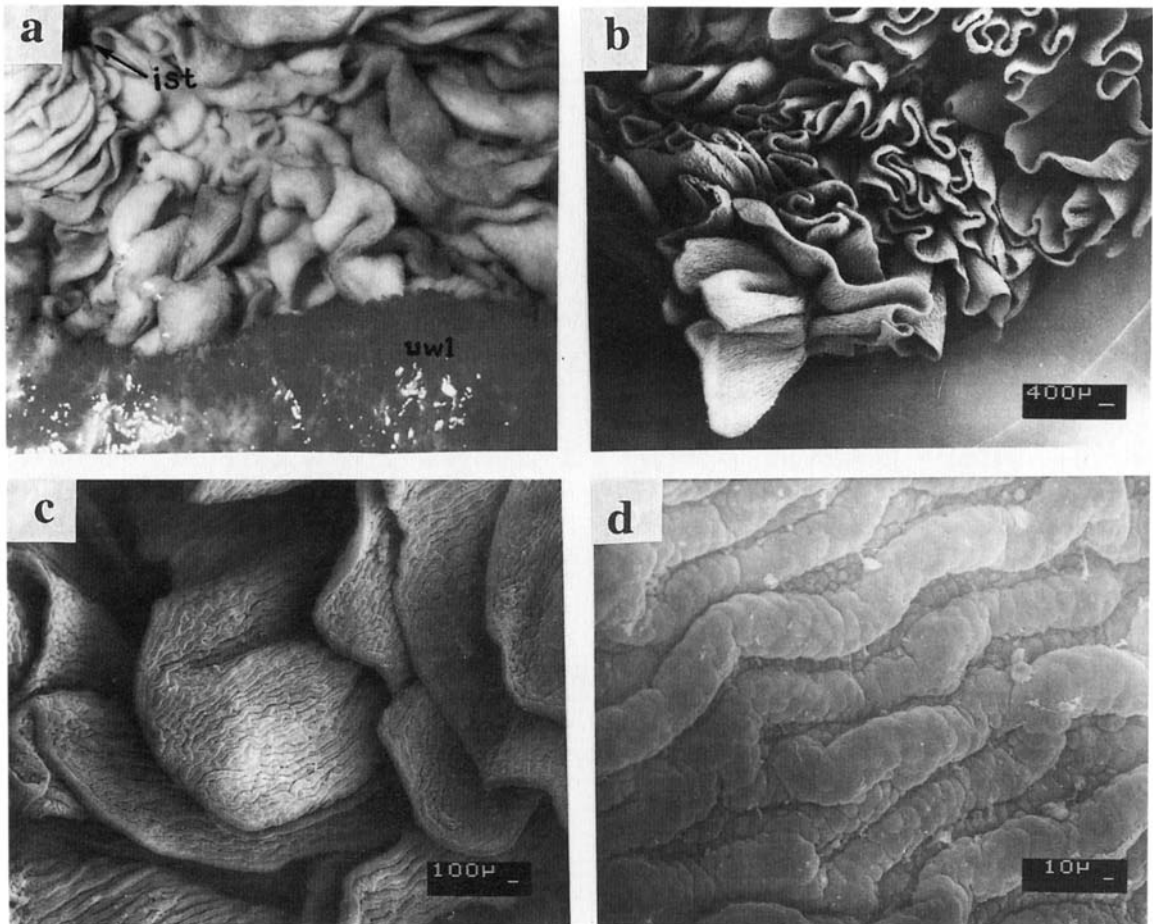
Fig. 5. a – Uterine membrane at isthmus (ist) with isthmian folds readily differentiated from remainder of uterine wall (uwl) with tropho-nemata in pregnant *Isurus oxyrinchus* (HBOM 103:00250). b – Scanning electron micrograph (SEM) enlargement of microfolds located on the isthmian folds photographed in (a). c – SEM enlargement of (b) showing ridges on microfolds. d – SEM enlargement of (c) showing detail of microfold ridges.

bryos have been found to date in this species or any other lamnoid except *C. taurus*. A more detailed study of the ontogeny of embryonic dentition may demonstrate two distinct types of dentition, an embryonic set and a set similar to the adult form. The predicted level of consumption of egg capsules in *C. taurus* during a single pregnancy (1000–1700 capsules containing 17 000 ova, Hamlett 1983), may require continual embryonic tooth loss and replacement while within the uterus. Associated with this loss would be an ontogenetic transition in tooth morphology and function.

Although embryophagy has only been documented in *C. taurus*, it may also occur in other lam-noids, particularly those that consistently produce single large embryos per uterus (e.g. alopiids). Embryophagy occurs in *C. taurus* embryos when they are between 10 and 30 cm TL. Although other lamnoid embryos have been captured in the same interval of development, the only ones which have been examined for cannibalism and oophagy are the alopiids. All three alopiid species have been examined: *A. pelagicus* (42.1–52.1 cm TL, Otake & Mizue 1981), *A. superciliosus* (20.6 cm TL, Gruber & Compagno 1981, Gilmore 1983), and *A. vulpinus* (8.9–114.0 cm TL, Gubanov 1972, Gilmore examination). Only yolk has been found, demonstrating oophagy, not embryophagy. Late embryos of *A. su-*
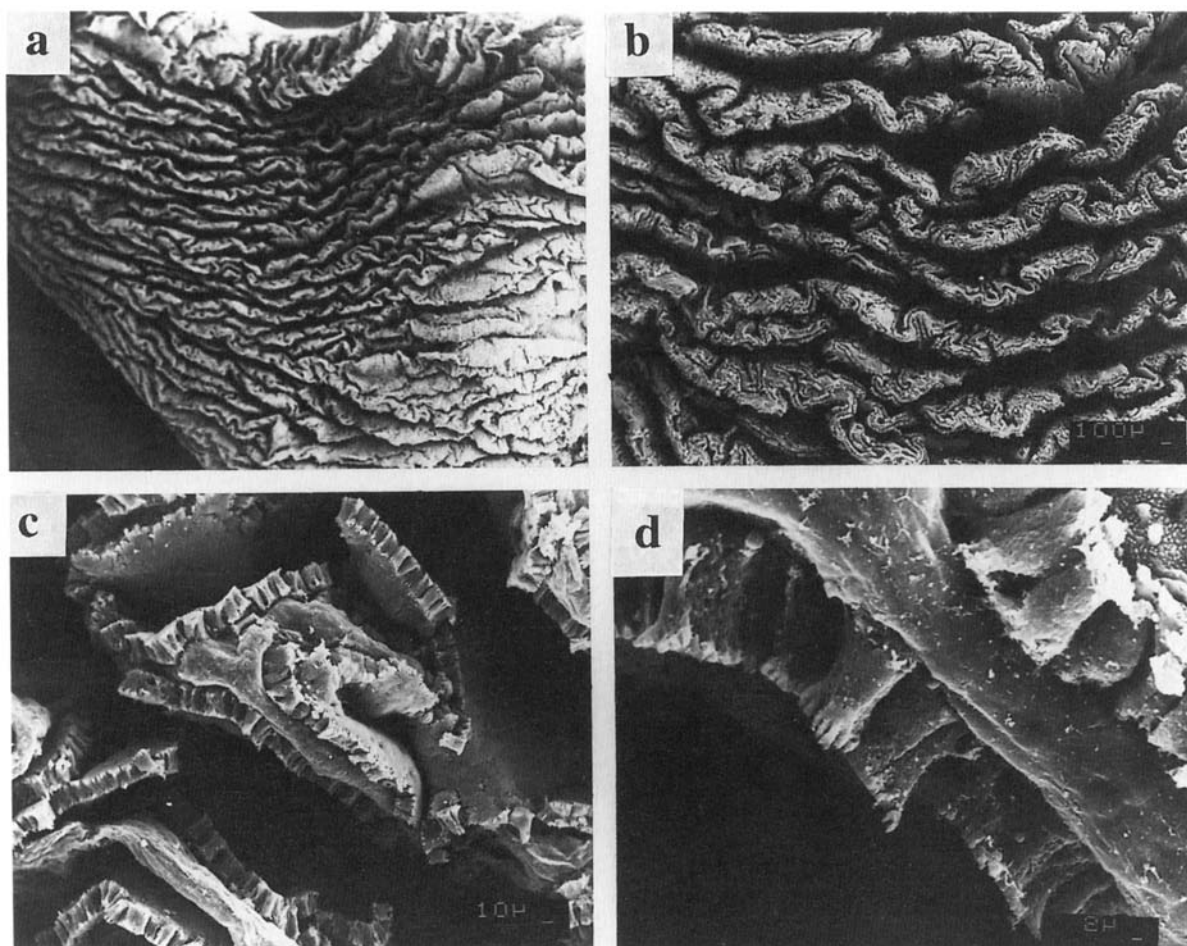
Fig. 6. a – SEM of trophonemata of uterine wall in a pregnant *Isurus oxyrinchus* (HBOM 103:00253). b – SEM enlargement of (a). c – SEM enlargement of (b) showing epithelium of trophonemata. d – SEM enlargement of (c) showing terminal microvilli on epithelium of trophonemata of uterine wall.

perciliosus, near 105 cm TL, have been found to consume egg capsules intact, swallowing them whole (Gilmore 1983). Larger embryos are undoubtedly capable of swallowing egg capsules whereas smaller embryos may find it necessary to mutilate the capsule prior to consumption. Embryonic teeth in *Alopias* spp. may be an adaptation for capsule consumption and oophagy, not embryophagy. However, the lack of specimens and data means that embryophagy cannot be entirely ruled out in other lamnoid species.

Embryophagy is also questioned in *Isurus* and *Lamna* due to the common occurrence of multiple embryos at term in each uterus. These embryos lack

erect teeth when approaching parturition (Gilmore 1983, Fig. 7, 8).

Embryos of all species typically have metabolized all intrauterine yolk supplies during the last two months of gestation. These late term embryos do not have distended cardiac stomachs, and as a percentage of body weight, may have considerably enlarged livers or livers with similar proportions as adult livers. During this period, ovulation has ceased and the maternal ovary atrophies. At parturition, the embryos are large, and may function as active predators soon after birth (Table 1).
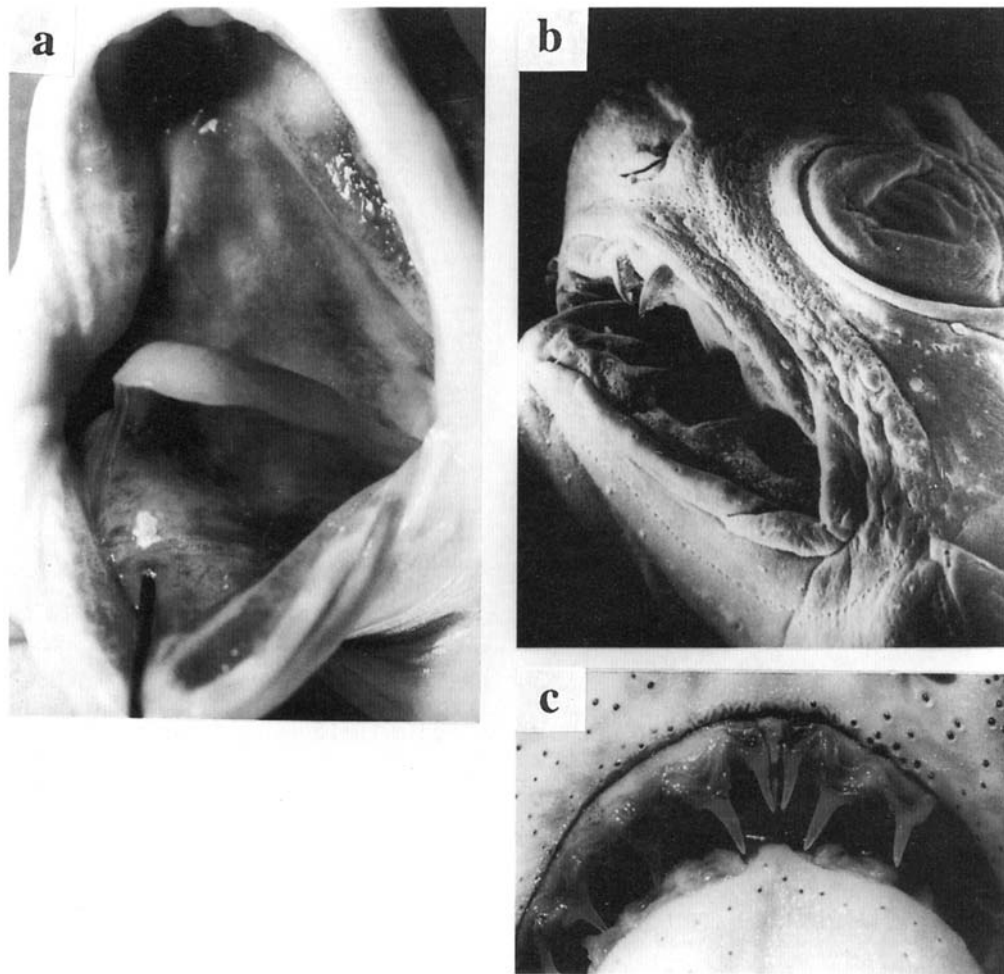
Fig. 7. a – Mouth of 48 cm TL embryo of *Isurus oxyrinchus* (HBOM 103:00250) showing lack of erect dentition. b – SEM of lateral view of 50 cm embryo of *Carcharias taurus* showing embryonic (emb) teeth which do not resemble the adult dentition. c – Frontal view of dentition of a 91 cm TL embryo of *Carcharias taurus* (HBOM 103:00182) which died at birth showing adult dentition type with well developed lateral denticles (lad) on either side of the major cusp.

Migration and reproduction

The only lamnoid species which has been studied consistently in all life history stages is *C. taurus*. The location of mating, gestation, parturition and juvenile development can now be documented with some degree of certainty. Figure 9 depicts the movements of *C. taurus* in the Western Atlantic off the east coast of North America. Historically, adult males and juveniles 1 to 2 m TL have typically dominated the catch of *C. taurus* in shallow nearshore waters of the mid-Atlantic bight during the summer months (Bigelow & Schroeder 1948, Jack Casey

NMFS, personal communication 1987, Steve Branstetter personal communication 1990). From Spring to September adult females with embryos 13 to 600 mm TL have been recorded primarily from south of Cape Hatteras to Jupiter Island, Florida, or in the northern Gulf of Mexico. Females carrying embryos over 800 mm TL, or that have recently given birth, have been captured consistently during the cooler months from November to February off Florida (Springer 1948, Clark & Von Schmidt 1965, Gilmore et al. 1983). Recently spent females and females nearing first maturation have been caught on the same shark longline from January to March
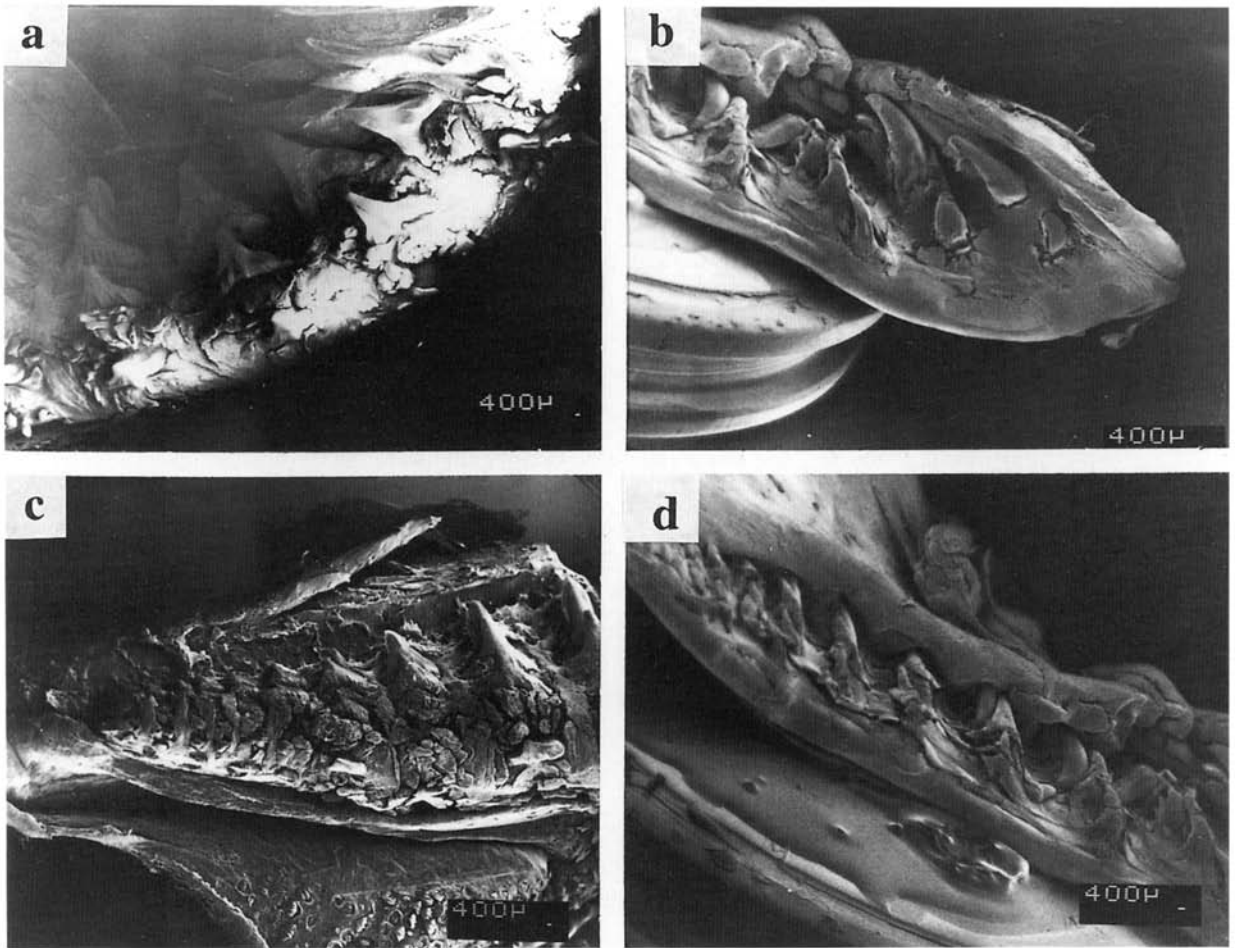
Fig. 8. a – SEM of dentition of 53.6 cm TL embryo of *C. taurus* (HBOM 103:00264) revealing multiple tooth rows of anterior-most teeth (symphysis to upper right) and change in tooth morphology between rows. b – SEM of dentition of 48 cm TL *I. oxyrinchus* embryo (HBOM 103:00250) showing multiple rows of anterior teeth (symphyseal teeth to right) and membranous sheath over teeth partially exposed by SEM preparation. c – SEM of (a) showing posterior lateral tooth rows. d – SEM of (b) showing posterior lateral tooth rows.

(Springer 1948, Gilmore unpublished data). Males caught during this period were all mature and with seminal vesicles full of spermatophores. Mating scars were apparent on one February male captured off Ft. Pierce, Florida (Gilmore et al. 1983) and on several males observed in mixed sex aggregations off the coast of North Carolina during May 1988 (Gilmore unpublished data). Major scarring around the nape and pectorals in males and females has been commonly observed in mating aggregations of sand tigers off North Carolina and Florida. Recent observations of mating behavior in captive Australian *C. taurus* have documented female bites

on courting males and a hierarchal social status in courting males (Gordon 1993). Mating activity occurs in relatively shallow water, at depths less than 30 m off the Florida east coast (from 29°00' to 27°00'N) in late February to April, just after parturition. In North Carolina, mating apparently occurs in late April and early May. Females in early gestation typically occur inshore while males virtually disappear from the inshore catch during the late spring and summer in Florida waters (Gilmore et al. 1983). Off North Carolina the males remain on the mating grounds until July. Male migration out of the mating and gestation grounds is probably both off-

shore and northward as mature males are often caught north of Cape Hatteras.

The characteristic seasonal developmental pattern for *C. taurus* has been observed through specimens collected for 37 years (Gilmore et al. 1983, personal observations and capture notes). The developmental stages of the embryos within a gravid female can now be predicted within a few weeks. Embryonic development is synchronous for all individuals captured in one region of the species range. The synchronous development observed in Florida embryos over many years indicates that a very predictable environmental cue governs mating activity and gonadal condition. Males and females rendezvous at the same location at the same time each year, both off Florida and North Carolina. There appears to be a delay of two weeks to a month in development between *C. taurus* specimens from the Carolinas and Florida (based on capture records maintained by José Castro and R.G. Gilmore).

Few other lamnoids have been studied in enough detail to determine migratory patterns relative to reproduction. However, extant data from certain locations around the world allow some predictions to be made. Pregnant *I. oxyrinchus* have only been captured between 20° and 30° N or S latitude in the Pacific, Atlantic, Gulf of Mexico and northeastern Red Sea (Vaillant 1889, Depperman 1953, Gohar & Mazhar 1964, Guitart-Manday 1975, Branstetter 1981, Stevens 1983, Uchida et al. 1987). Data are limited, but parturition in *I. oxyrinchus* appears to occur either during the spring, or summer, at most locations (Table 2). Its congener, *I. Paucus*, is equally lacking in reproductive information as only four pregnant specimens have been captured, two with multiple embryos (Casey & Pratt NMFS personal communication 1986, John Randall personal communication 1985) and two with two or fewer embryos (Guitart-Manday 1975, Gilmore 1983). Three pregnant *I. paucus* specimens were taken in the Florida Straits and north of Puerto Rico (Guitart-Manday 1975, Gilmore 1983, Casey & Pratt NMFS personal communication 1986) and one off Hawaii (John Randall personal communication 1985). Since all of the pregnant makos, short or longfin, from the Atlantic Ocean have come from the sub-
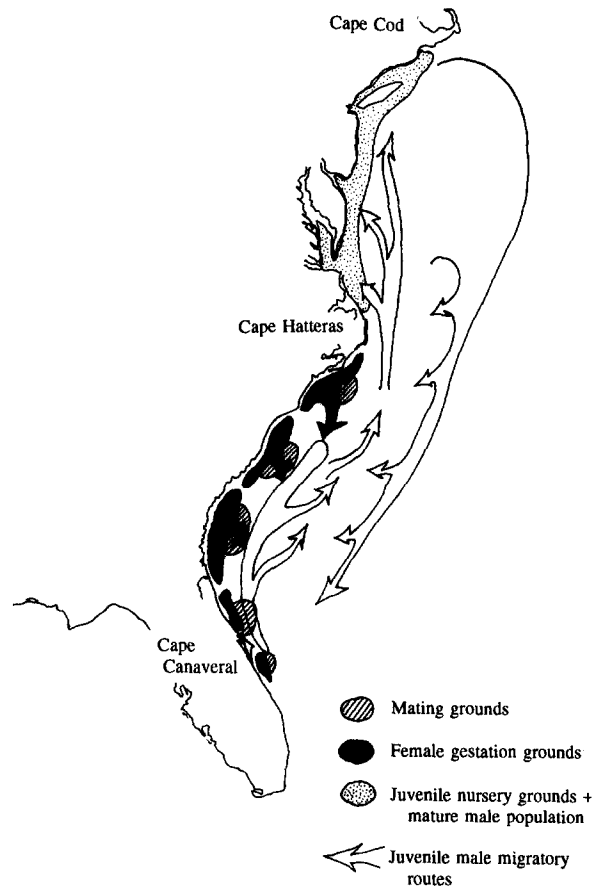

Fig. 9. Map of eastern seaboard of United States showing gestation grounds (black: spring-winter), parturition sites (white: winter), neonate/juvenile migration (arrows: spring/summer), nursery grounds (stipple: several years), mating sites (black: spring) and southward migration of males and recently mature females (winter).

tropical/tropical western Atlantic between 20° and 30° N in the Gulf of Mexico, or in the vicinity of the Florida Straits, it is likely that this region is a location for parturition in makos or at least a maternity site. The capture of three ripe males *I. paucus* in the northern Gulf of Mexico on 16 April 1985 on the same set line (27°35′N, 89°55′W, Steve Branstetter personal communication 1990, Killam & Parsons 1986) and a single large mature female (342 cm FL) on 1 April also in the northern Gulf of Mexico (28°55′N, 85°35′W, Killam & Parsons 1986) may indicate male/female syntopy within weeks and possible mating activity in the northern Gulf.

Extensive collections of the white shark, *Carcha-*

rodon carcharias, made in North American waters have failed to yield pregnant females. However, sexual syntopy and free swimming young of the year have been documented both off the west coast and the northeast (Casey & Pratt 1985, Klimley 1985). Female *C. carcharias* apparently give birth off the California coast south of Point Conception during the summer (smallest specimen 122 cm TL in July, Klimley 1985). Most adult male-female syntopy occurs north of Pt. Conception, indicating mating most likely occurs in the vicinity of the principal adult feeding grounds off the coast of northern or central California, possibly during the fall. In the northeastern U.S. mating apparently also occurs in the feeding grounds in the Mid-Atlantic Bight with most records of syntopy in large adults coming from late summer (Casey & Pratt 1985). The smallest free swimming specimens were taken during the summer (to 122 cm TL, Casey & Pratt 1985). The Mid-Atlantic Bight apparently acts as a nursery ground and adult mating ground. However, the location of parturition may be further south based on winter/spring occurrence of juvenile and adult white sharks in the Florida Straits over the past few years (Gilmore unpublished data). The routine occurrence of juvenile *C. carcharias* off Daytona Beach, Florida, during the winter suggests that the nursery ground for this species is broadly the western North Atlantic continental shelf with the distribution of the species influenced by water temperatures (around the 15° C isotherm range 11–24° C, Casey & Pratt 1985). A similar occurrence of juveniles inshore in the warm latitudes of South Africa during the winter and adult male-female syntopy at cooler latitudes during the summer (Bass et al. 1975) indicates that the seasonal distribution observed off the North American coast may be a generalized pattern for *C. carcharias*.

Little is known of migration relative to reproduction in *Lamna* spp. though they appear to be con-

Table 2. Reproductive seasonality and pregnancy in *Isurus* spp. Authors are: 1= Depperman (1953); 2= Gilmore data; 3= Branstetter (1981); 4= Uchida et al. (1987); 5= Stevens (1983); 6= Gilmore (1983); 7= Casey & Pratt personal communication; 8= Pratt, Casey, Castro, Gilmore personal observation (1992).

Isurus oxyrinchus (size at birth: 60–70cm TL; free swimming 64–77cm TL)				
Date	Author	Location	Embryo number (size in cm TL)	Estimated parturition period
Embryos				
Northern hemisphere				
Jan.	8	Puerto Rico	14+(65–67)	winter
Feb.	1	Florida Straits	10(28–29)	spring/summer
April	2	Florida Straits	12(40–43)	summer
Aug.	3	N. Gulf of Mexico	18(25–31)	winter/spring
Nov.	4	Okinawa, Japan	16(39–40)	spring
Southern hemisphere				
Sept.	5	New S. Wales, Aust.	4(60)	winter/spring
Sept.	5	New S. Wales, Aust.	16(58–64)	winter/spring
Oct.	5	New S. Wales, Aust.	14(60)	winter/spring
Juveniles				
June	3	N. Gulf of Mexico	1(77)	spring*
June	2	Florida Straits	1(105)	summer**
August	2	Florida Straits	1(91)	summer*
Isurus paucus (size at birth: 122cm TL; free swimming 123cm TL)				
Dec.	6	Florida Straits	1(97)	winter
Jan.	7	Puerto Rico	4(113–122)	winter

*Based on 70cm parturition size (Stevens 1983).
**Based on 27.9cm yr^{-1} growth for 81–198cm makos (Casey et al. 1986).

fined to cool temperate waters with parturition occuring during the spring (Aasen 1966, Templeman 1963).

Pregnant alopiids have been captured from a variety of locations throughout the world (Table 3). *Alopias vulpinus* embryos have been taken from specimens captured off New York and Florida and embryo length data indicates spring or summer parturition at most locations and spring mating in the northwestern Red Sea. Gubanov (1972) presents capture data which indicate a spatial and temporal separation of *A. vulpinus* based on ontogeny and sex with most pregnant females and juveniles occuring in the northwestern portion of the Indian Ocean from February to May (93% females were pregnant), while sexual syntopy was greatest in the Maldives and Chagos islands during summer and fall. Most pregnant *A. superciliosus* have been captured in the Florida Straits and both winter and summer parturition periods are indicated in this

species.[2] Captures of pregnant *Alopias pelagicus* also indicate a variable mating period.

Although accounts and fisheries of *Cetorhinus maximus* date back to the last century, little life history data exist. Basking sharks are most apparent in the British Isles during the summer. They are easily observed at the surface during this period. Mating behavior and direct evidence of recent mating (sperm in oviducts, Matthews 1950) demonstrates that *C. maximus* mates off the British Isles during the summer. However, the location of parturition, which apparently occurs during the winter or spring remains a mystery.

Nothing has been published on the periodicity of reproduction in *Pseudocarcharias*.

[2] Recent captures of *A. superciliosus* embryos are from the western Atlantic (Moreno & Morón 1992).

Table 3. Reproductive seasonality and pregnancy in *Alopias* spp. Authors are: 1 = Gilmore data; 2 = Gubanov (1972); 3 = Gohar & Mazhar (1964); 4 = Stillwell & Casey (1976) or Strasburg (1958); 5 = Hixon (1979); 6 = Gruber & Compagno (1981); 7 = Nakamura (1935); 8 = Guitart-Manday (1975); 9 = Otake & Mizue (1981).

Alopias vulpinus (size at birth: 111–149 cm TL; free swimming 115–153 cm TL)				
Date	Author	Location	Embryo number (size in cm TL)	Estimated parturition period
19 Jan.	1	Florida Straits	2(59–61)	spring/summer
19 Feb.	2	N.W. Indian Ocean	2(8.9)	summer
April	2	N.W. Indian Ocean	2(114)	spring/summer
23 April	3	N.W. Red Sea	4–5 capsules	? mating in April
4 June	4	Christmas Island	2(114)	summer
3 June	5	Ventura, California	4*(139–142)	summer
Alopias superciliosus (size at birth: 100–105 cm TL; free swimming 130 cm TL)				
Mar.	7	Suo, Taiwan	2(37)	summer/fall
9 May	1	Florida Straits	2(55–60)	summer
18 June	1	Florida Straits	2(105–106)	summer
29 June	6	Florida Straits	2(21–21)	winter
Sept.	1	Florida Straits	2( )	
most Aug. thru-Sept.	8	Florida Straits/Cuba	2(near term)	summer/fall
Alopias pelagicus				
March	7	Suo, Taiwan	2(44)	summer
April	4	Fanning Is., Pac.	2(unknown)	
9–12 Sept.	9	E.Indian Ocean	2/2(42–45/50–52)	winter/spring

*Unverified number of embryos, lengths are for two embryos examined.

Discussion

The mechanisms of viviparity differ significantly between the lamniform and the galeiform sharks. However, both groups produce relatively large embryos at parturition which have been nourished throughout gestation by various maternal nutritive sources, including ovulation, uterine fluids or placentation. If the various mechanisms of viviparity evolved independently in several taxa of chondrichtyan fishes, then similar evolutionary pressures may be acting on all of these groups. Since both the lamnoids and galeoids are typically large aggressive apical predators, the rapid growth of embryos and the production of a large neonate at parturition would allow a decided predatory advantage with very low progeny mortalities relative to oviparous species, particularly teleostean fishes. The production of a large embryo is particularly important if growth rates after parturition are not as fast as sympatric teleostean predators. Large teleostean predators such as the mackerals, tunas (Scombridae) and the billfishes (Istiophoridae and Xiphiidae) have fecundities ranging from several hundred thousand to 16 million eggs, typically spawn several times within one year, grow rapidly (maturation in less than four years for many species) and have relatively short life spans (i.e. generally less than 10 years) relative to the lamnoids and galeoids which may take two decades to mature (Manooch & Raver 1984, Branstetter & McEachran 1986, Branstetter 1990).

Consistent differences in embryo size and fecundity in lamnoid sharks appear to have some association with the neonatal environment. Parallel reproductive patterns in embryo size and fecundity observed in galeoid sharks further demonstrates the potential impact of neonatal environments on reproductive biology. Evolutionary pressure from environmental sources impact reproductive mechanisms which may then vary with the organisms' habitat and niche preference, in addition to its' phyletic history. Selection for the number and size of embryos differs between pelagic and nearshore habitats in both lamnoids and galeoid sharks. High energy, environmentally unstable and heterogenous estuarine or nearshore continental shelf ecosystems would present a different challenge to survival (i.e.,

more food, abundant predators in a variety of size ranges, more physiological stress) than deep water ecosystems (i.e. patchy food availability, low predator density, little environmental instability, and therefore less physiological stress). Given these differing environmental scenarios, large precocious embryos with few siblings may be selected for in highly productive and competitive shallow nearshore environments. The smallest embryos and largest litters in both lamnoids (18 embryos, 60–70 cm TL in *Isurus oxyrhinchus,* Table 2) and carcharhinids (up to 135 embryos, 35–44 cm TL in *Prionace glauca,* Pratt 1979) have been recorded from pelagic species. The largest embryos have been recorded from estuarine and coastal species (2 embryos, 100 cm TL in the lamnoid species *Carcharias taurus* or 7 embryos, 140 cm TL in *Carcharodon carcharias,* Uchida et al. 1987) and the galeoid species (7–12 embryos, 70 cm in *Carcharhinus leucas* or 5–12 embryos, 85–100 cm TL in *C. obscurus,* Dodrill 1977). There may be exceptions with pelagic species that give birth at location or during periods in which food availability is high. The abundance of juvenile and pregnant *A. vulpinus* (typically two embryos, 11–149 cm TL) in the northwestern Indian Ocean during the upwelling season, a period of increased aquatic productivity (Gubanov 1972), insures resource availability for both embryos and immature threshers.

The higher incidence of young *C. taurus* in estuaries of the Mid-Atlantic Bight and *C. carcharias* inshore on the east and west coast of North America are undoubtedly responses to both food availability and predatory pressures. Sand tiger sharks mate synchronously each year in the late winter and spring after parturition, which allows the juveniles to utilize estuaries of the Mid-Atlantic Bight during a period of optimum food availability, the summer and early fall. Abundant food resources insure rapid growth to a size that will eliminate most predatory mortality.

Abundant food resources allow rapid neonate and juvenile growth. Lamnoid growth rates and time to maturation appear to be shorter than for carcharhinid sharks of similar adult body size (Branstetter 1990). It is estimated that male *C. taurus* may mature within four or five years, females

112

within eight years (190–220 cm TL, Gilmore et al. 1983), while *C. carcharias* may mature within 9–10 years (366–427 cm TL, Cailliet et al. 1985), *Alopias superciliosus* in 3.5 to 4.5 years (300–350 cm TL, Gruber & Compagno 1981).

Oophagy has been documented in nine of the sixteen species of lamniform sharks. This reveals complementary reproductive styles within the order Lamniformes. Several authors have stated that embryophagy apparently occurs in lamnoid species other than *C. taurus* (Compagno 1984). However, universal occurrence of embryophagy in the order is questioned, based on the occurrence of multiple embryos within a single uterus at parturition in six of the same nine species (Table 1). Several hypotheses have been proposed to explain this differential fecundity, but the paucity of early embryonic stages in lamnoid collections worldwide has not allowed these hypotheses to be tested.

The mechanism for differential fecundity in lamnoids may be explained by the following hypothetical reproductive scenarios: (1) Lamnoids with multiple embryos per uterus release multiple ova throughout pregnancy, therefore, insuring fertilization of multiple embryos. *C. taurus* initially releases a single fertilized ova which is followed by a gradual increase in number of ova encapsulated, ranging from 1 to eventually 23 ova per capsule, though capsules produced after two weeks are not fertilized. (2) In lamnoids with multiple term embryos, several embryos may occur in the first capsule produced. These embryos then hatch synchronously and consume other embryos which either remain in their capsules, or have only recently hatched, all of which are smaller than the first group to hatch. Those first to hatch synchronously refrain from consuming one another due to size similarity. (3) Differential sperm viability allows for extended (2 weeks) fertilization of ova in *C. taurus*, while short term sperm viability in species with multiple embryos per uterus only permits fertilization of the first group of ova to arrive in the anterior oviduct. (4) Multiple matings with short sperm viability account for extended fertilization of ova in *C. taurus*, while single short term encounters in pelagic species allow a single transfer of sperm which fertilize multiple ova released during mating. All of these representative scenarios

may play some role in explaining the observations made to date. Detailed analysis of these hypotheses will have to wait until sufficient study material is available with the isolation of reproductive locations and capture of pregnant females.

Another important area of study is the functional significance of embryophagy and oophagy in the development of lamnoids. Why do lamnoids, particularly *C. taurus*, have a low fecundity rate and embryonic cannibalism while carcharhinids which produce young of similar size to lamnoids have higher fecundity without cannibalism? The only lamnoid we know in detail, *C. taurus*, reproduces annually and mature females are pregnant through at least 75% of their adult life, whereas carcharhinids often skip a year between pregnancies. However, the production of two pups a year does not match a fecundity rate of 10–15 pups every other year in many of the carcharhinids within the same adult size range. Is the fitness of the lamnoid embryo greater than the carcharhinid in regard to prey capture or energetics as a result of oophagy and embryophagy? Do lamnoids have better success in prey acquisition and capture immediately after parturition due to prior hunting experience in utero? Or does embryonic cannibalism in *C. taurus* eliminate embryonic competition for food resources in order to produce a larger embryo in the shortest period of time on an annual basis? Stribling et al. (1980) demonstrated that *C. taurus* embryonic growth rates supersede that recorded for all other elasmobranch species examined with a 1.2×10^6 increase in dry weight during gestation.

These questions need to be treated in a serious study of the life histories, behavior and ecology of both lamnoids and carcharhinids in the field and in captive systems through careful descriptive studies and well designed experiments.

of critical literature. José Castro allowed use of his photo of *C. taurus* embryos. I thank Tris Colket, Eric Sander, Kenneth Cheatham and John Krall for furnishing invaluable specimens of various lamnoid species. Patricia Linley prepared EM specimens. This constitutes contribution number 852 to the Harbor Branch Oceanographic Institution.

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114

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