Environmental Biology of Fishes **38**: 139–149, 1993.

The storage of spermatozoa in the oviducal glands of western North Atlantic sharks

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Received 28.10.1991 Accepted 23.12.1992

Key words: Insemination, Elasmobranchs, Sperm, Nidamental or shell glands, Lamniformes, Carcharhiniformes

Synopsis

Spermatozoa stored in oviducal glands of sharks sampled off the North American east coast were revealed by viewing stained tissue sections using light microscopy. Of eleven species surveyed, sperm were found in nine: *Alopias vulpinus, Lamna nasus, Carcharhinus obscurus, Carcharhinus plumbeus, Galeocerdo cuvieri, Prionace glauca, Rhizoprionodon terraenovae, Sphyrna lewini,* and *Sphyrna tiburo.* Three insemination patterns are proposed to account for differences noted in these findings: (1) non-storage/immediate insemination for sharks such as *Lamna nasus;* (2) short-term storage/delayed insemination as found in sharks in which ovulation is prolonged over weeks or months such as *Rhizoprionodon terraenovae,* and (3) long-term storage/repeated insemination, a characteristic of nomadic sharks such as *Prionace glauca* and *Carcharhinus obscurus* which can store sperm in specialized tubules for months to years.

Introduction

Sperm storage has evolved independently in every vertebrate class except the lampreys (class Agnatha) (Howarth 1974). The presence of an elasmobranch seminal receptacle was first suggested by researchers who noticed that female skates of the genus *Raja* continued to lay fertile eggs while segregated from males in aquaria (Lo Bianco 1909, Raj 1914, Clark 1922). Metten (1941) first described sperm storage in the shell secreting nidamental or oviducal gland of *Scyliorhinus canicula.* Prasad (1944, 1945) found spermatozoa in the oviducal glands of five species of elasmobranchs from the Indian Ocean. Matthews (1950) searched unsuccessfully for spermatozoa in female *Cetorhinus maximus;* and Stevens (1974) could not locate stored sperm in oviducal glands of *Prionace glauca* in British waters. An understanding of sperm storage will help elucidate the poorly known reproductive dynamics of elasmobranch populations.

Materials and methods

Sharks were sampled from landings at sportfishing tournaments and from research and commercial catches using longline fishing gear in the region extending from the Gulf of Mexico along the northeast coast to the waters south of Sable Island, Canada. Collections were made as specimens became available between March and November of the 7-year period. For this analysis, histological sections of mature or nearly mature females captured from 1982 to 1987 were studied.

Oviducal glands (called variously nidamental

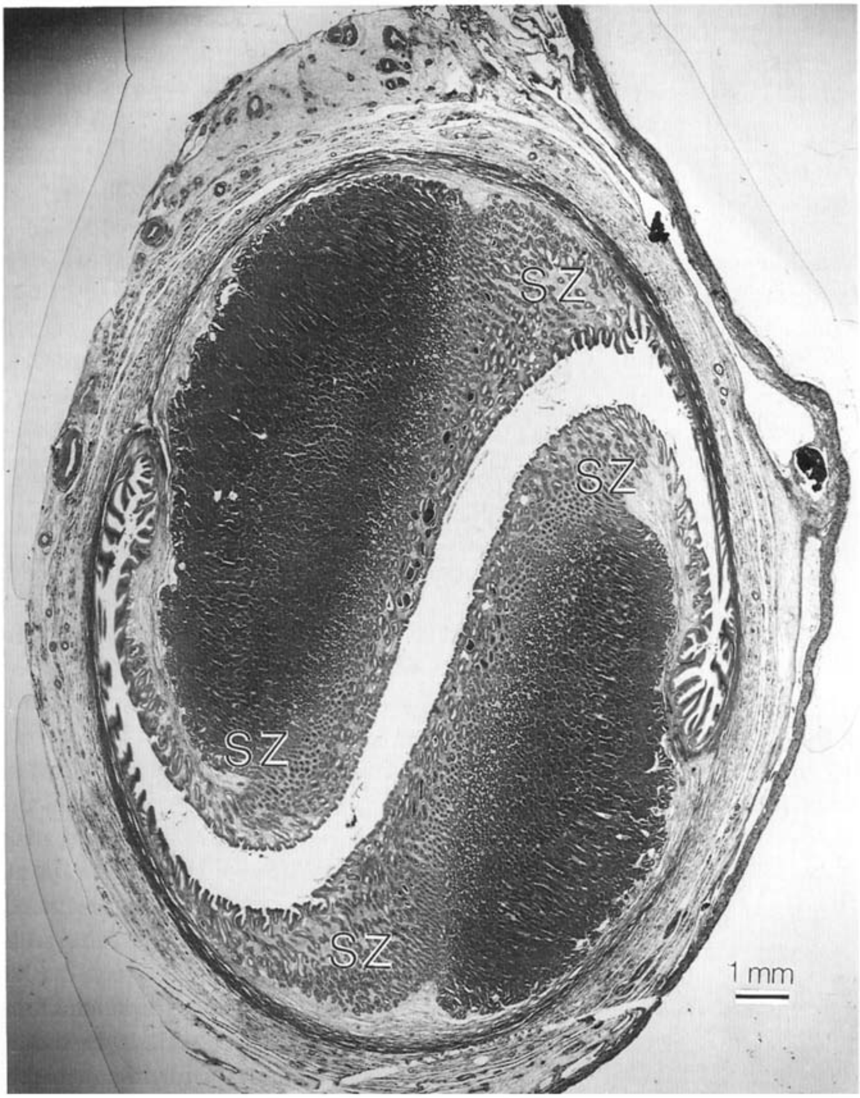

Fig. 1. Oviducal gland of the blue shark, *Prionace glauca.* Transverse section of lower gland. Recently inseminated sperm appear as dark masses in shell secreting tubules surrounding the 'S' shaped central lumen (from Pratt 1979), SZ= sperm storage zone.

and shell glands by other workers) were removed with as little disturbance to the tissue as possible and preserved in Bouin solution because of its rapid penetration and mordant qualities. Each gland was excised gently with a new blade to prevent dislocation of possible stored sperm and cross contamination from other specimens. The posterior third of each collected oviducal gland was subdivided in the field and sectioned in the laboratory. Other higher and lower oviducal cuts were made if circumstances permitted. Smears from blue sharks, *Prionace glauca,* and a few other species were prepared by expressing fluid from the cut posterior third of the gland (Pratt 1979). Mallory's triple stain highlighted spermatozoan heads, making them easier to locate in large tissue sections (Fig. 1). Paraffin cross-sections were examined using light microscopy at 40 times magnification to locate likely tubules and tissue masses. Using the above technique, stored sperm could usually be recognized at a magnification of 160× and confirmed at 720× (Fig. 2).

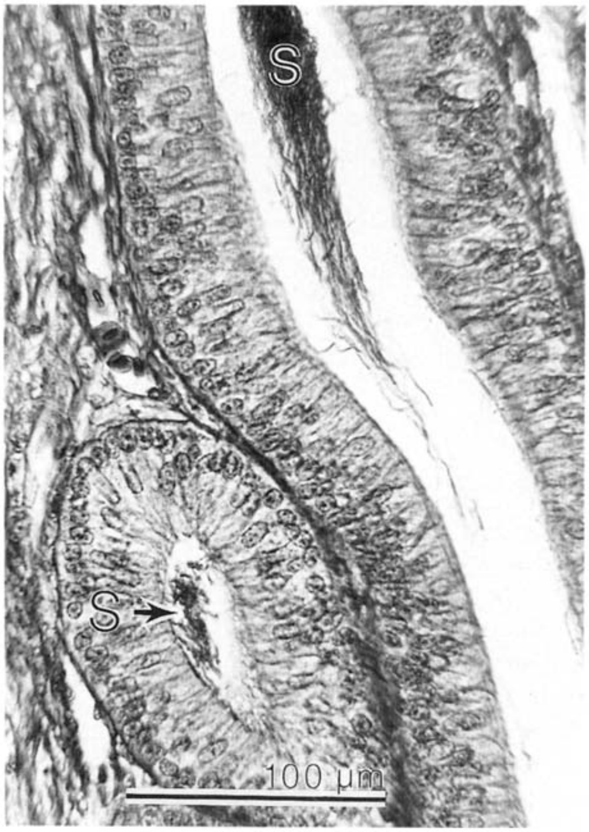

Fig. 2. Sperm stored in oviducal tubule of *Prionace glauca;* Mallory's triple stain. Original magnification 720x, S= sperm.

Results

Sperm storage areas

Spermatozoa are usually located in the thin-walled tubules of the lower oviducal gland around the curves of the 'S'-shaped lumen. Sperm is almost never found in the thick-walled secretory tubules of the central gland. The blue shark oviducal cross-section in Figure 1 has sperm in all of these locations as well as in the central tubules bordering the lumen and in the lumen itself. This is a characteristic of only recently inseminated sharks. There is considerable variation among species, some have sperm stored in tubules that course posteriorly/anteriorly along the peripheral edge of the shell secreting zone. In *Sphyrna lewini,* the shell secreting tubules seem to have invested the connective tissue tunic surrounding the gland. *Carcharhinus obscurus* and others have a few large diameter, thin-walled tubules among the secretory tubules.

Lamniformes

Alopiidae

Alopias superciliosus. Four mature big eye threshers, caught in May, were examined (Table 1). The sampled females were not pregnant or in early or late stages of pregnancy. Spermatozoa were not observed in any *A. superciliosus* females after a thorough search of all levels of the four oviducal glands.

Alopias vulpinus. A broad size range of female common threshers was sampled in June and July of various years (Table 2). No stored spermatozoa were found in gravid or post-partum females and most adults. One 220cm fork length (FL) adult female had a moderate amount of spermatozoa, with brightly stained heads, in a loose arrangement in the shallow tubules and lumen of the shell gland. This is the most posterior location for sperm storage that I have observed in any species. Hematose bruises on the vaginal walls of this female suggest recent copulation. Bite marks were not noted however.

Lamnidae

Isurus oxyrinchus. Summer samples of ten large juvenile and adult female shortfin makos revealed a complete absence of stored spermatozoa in all sizes (Table 3). No evidence of recent copulation was apparent in this seasonal sample. Marks that were obviously fresh and older healed tooth cuts, probably from other large makos, were noted around the

Table 1. Lamniformes, *Alopias superciliosus.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
200	May	gravid	near term	No	–
217	May	adult	–	No	–
227	May	gravid	early	No	–
220	May	gravid	early	No	–

head and gills of all specimens over 300cm. In the absence of other supporting evidence, these cuts are probably the result of agonistic behavior, perhaps related to intraspecific feeding competition.

Lamna nasus. A 227cm mature female porbeagle shark with moderate amounts of spermatozoa in the oviducal tubules (Fig. 3a, b) and free sperm in the lumen of the oviducal gland was examined in October of 1985 (Table 4). The presence of fresh vaginal abrasions and the capture of a 216cm mature male with hematose claspers on the same long line set suggested a very recent copulation.

Carcharhiniformes

Carcharhinidae

Carcharhinus obscurus. Samples of eleven adult post-partum and near-term dusky sharks from 255 to 292cm all contained small masses of stored spermatozoa (Fig. 4), usually deep in the oviducal tubules (Table 5). In contrast to spermatozoa found in freshly inseminated sharks of other species (Fig. 2), the heads may be aligned with neighboring sperm, but the entire mass is interwoven with groups of densely-packed sperm which are not aligned with the supporting tubule. The sperm heads in these post-partum sharks also stain faintly when compared to sharks that have copulated recently.

Carcharhinus plumbeus. Sandbar sharks were sampled from May through September in a wide variety of sizes and reproductive conditions (Table 6). Very small amounts of sperm were found in two sharks; a near-term pregnant female and a post-partum female.

Galeocerdo cuvieri. Examination of eight tiger sharks, juvenile to adult, revealed one 280cm adult with oviducal sperm (Table 7), detected in a smear preparation. The small amount is consistent with long-term tubule storage.

Prionace glauca. Blue sharks exhibited a variety of conditions of sperm storage (Table 8). Copious amounts of sperm were in the lumens and tubules of oviducal glands of freshly mated females with internal and external mating scars (Fig. 1, 2). Moderate amounts were found in non-gravid adults with healed mating marks and small amounts of tangled sperm with poorly stained heads were present in

Table 2. Lamniformes, *Alopias vulpinus.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
194	Jun	juvenile	–	No	–
195	Jun	juvenile	–	No	–
195	Jun	juvenile	–	No	–
197	Jul	sub-adult	–	No	–
217	Jun	post partum	–	No	–
219	Jun	adult	–	No	–
219	Jun	adult	–	No	–
220	Jun	adult	–	++	L, T
223	Jun	adult	–	No	–
224	Jun	post partum	–	No	–
224	Jun	adult	–	No	–
228	Jun	gravid	near term	No	–
229	Jun	adult	–	No	–
229	Jun	adult	–	No	–
237	Jun	adult	–	No	–
240	Jun	post partum	–	No	–
241	Jun	gravid	near term	No	–
262	Jul	adult	–	No	–

Note: ++= moderate; T= tubule; L= lumen.

Table 3. Lamniformes, *Isurus oxyrinchus.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
253	Jun	juvenile	–	No	–
264	Jul	juvenile	–	No	–
277	Aug	juvenile	–	No	–
277	Jul	juvenile	–	No	–
284	Jul	juvenile	–	No	–
286	Aug	adult	–	No	–
296	Jun	adult	–	No	–
323	Aug	adult	–	No	–
338	Aug	adult	–	No	–
339	Jul	adult	–	No	–

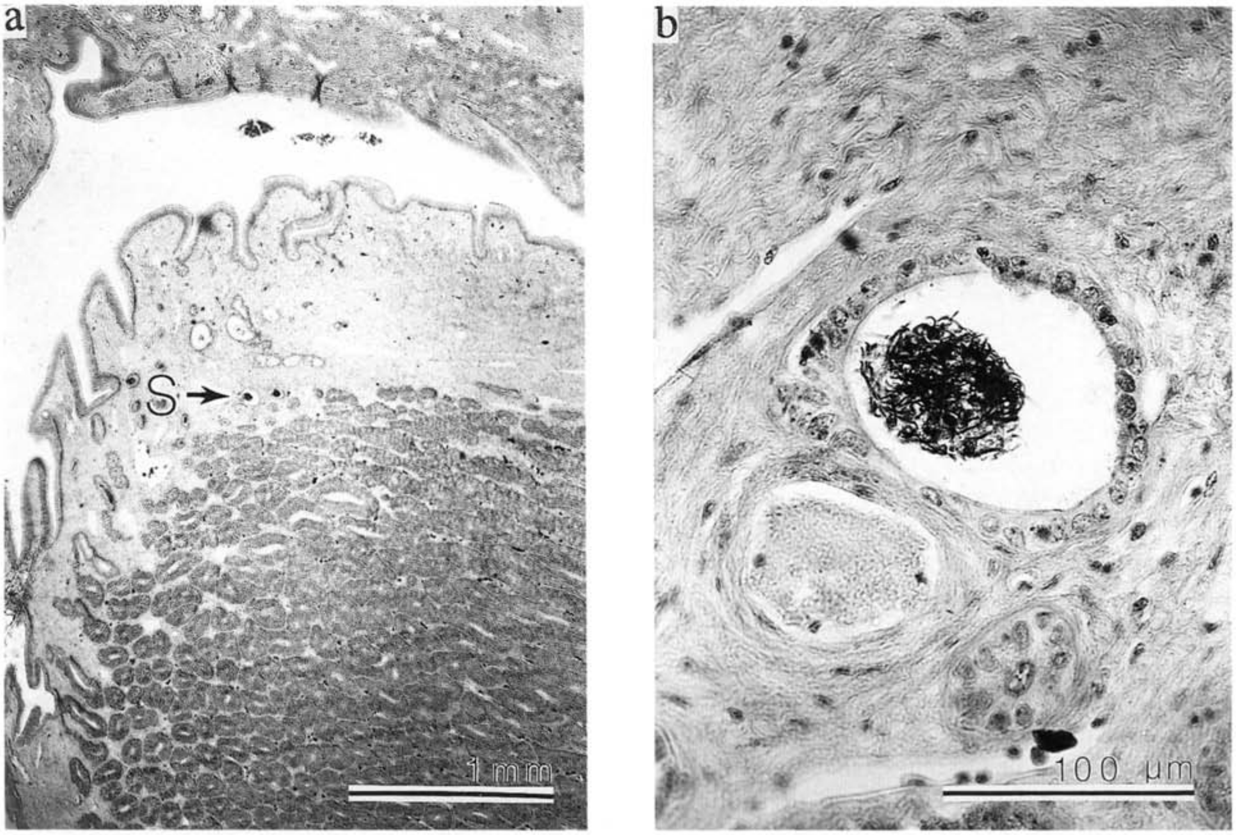

Fig. 3. a – Lower oviducal section of 227 cm FL porbeagle, *Lamna nasus,* with fresh mating scars. b – Magnification of center of a with the darkly stained sperm heads characteristic of fresh or short-term storage in tubule lined with cuboidal, ciliated epithelium.

near-term, gravid females, including the one blue shark reported here [see Pratt (1979) for a review of blue shark sperm storage].

Rhizoprionodon terraenovae. Examination of 13 adult non-gravid and gravid female Atlantic sharpnose sharks captured from May to September revealed many females to be in the early stages of pregnancy and still in possession of oviducal sperm (Table 9). The single, late-gestation female lacked sperm; a recently post-partum female, with fresh uterine placental scars, and external tooth cuts had a large quantity of sperm in the oviducal lumen. This suggests that mating can closely follow parturition in this species.

Sphyrnidae
Sphyrna lewini. Four scalloped hammerheads comprised of one non-gravid adult, one post-partum, and two gravid females (Table 10) revealed several storage conditions. A nulliparous adult had not yet been successfully inseminated. The two nearly full-term gravid females both contained spermatozoa and a recently post-partum female had fresh mating scars on the right flank and copious amounts of sperm in the tubules of the shell gland. The post-partum female possessed spermatozoa-laden tu-

Table 4. Lamniformes, *Lamna nasus.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
227	Oct	adult	–	++	T

Note: ++ = moderate; T = tubule.

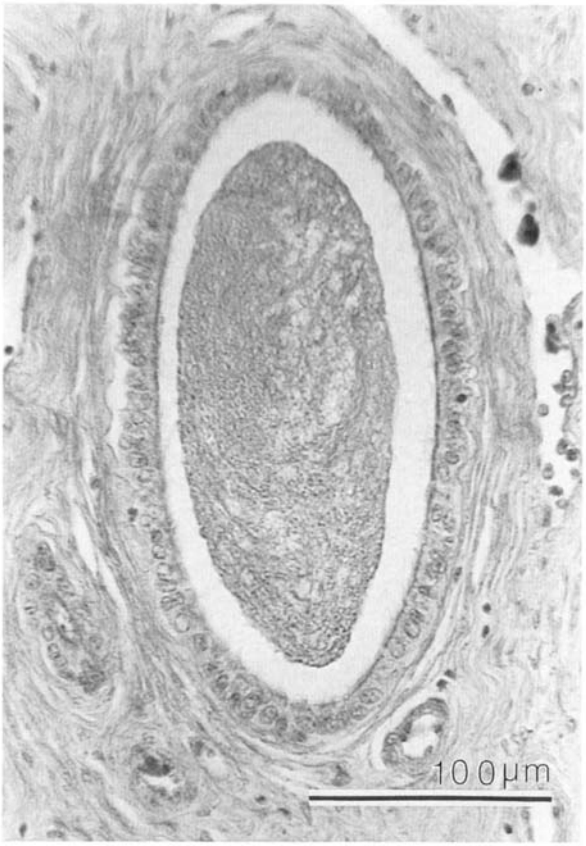

Fig. 4. Long-term stored sperm of the dusky shark, *Carcharhinus obscurus*, full-term gravid female, 257 cm FL.

bules in the connective tissue surrounding the posterior shell-secreting tubules. In contrast to other

Table 5. Carcharhiniformes, *Carcharhinus obscurus.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
255	Jun	post partum	–	+	T
255	Jun	post partum	–	+	T
257	Jun	gravid	near term	+	T
269	Jul	gravid	near term	+	T
269	Jun	adult	–	+	T
270	Jun	post partum	–	+	T
273	Jun	post partum	–	+	T
278	Jun	post partum	–	+	T
279	Jun	post partum	–	+	T
280	Jun	post partum	–	+	T
292	Jun	post partum	–	+	T

Note: + = sparse; T = tubule.

Table 6. Carcharhiniformes, *Carcharhinus plumbeus.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
158	Jul	gravid	near term	+	T
160	May	gravid	near term	No	–
160	Jun	post partum	–	No	–
161	Jul	post partum	–	No	–
162	Sep	gravid	mid term	No	–
164	Jun	adult	–	No	–
166	Aug	gravid	early	No	–
167	May	adult	–	No	–
170	Jun	adult	–	No	–
171	Aug	post partum	–	No	–
174	Jul	post partum	–	No	–
174	Jun	adult	–	No	–
175	Sep	gravid	–	No	–
175	Jun	adult	–	No	–
179	Jun	post partum	–	No	–
179	Jul	adult	–	No	–
183	Jun	post partum	–	+	T

Note: + = sparse; T = tubule.

species, sperm in the scalloped hammerhead can be stored in separate tubules located in the heavy connective tissue tunic surrounding the oviducal gland (Fig. 5), as well as in tubules which course anteriorly/posteriorly among the shell-secreting tubules throughout most of the gland.

Sphyrna tiburo. The oviducal gland of a gravid 93 cm female bonnethead shark in the process of transmitting eggs to the uterus was replete with

Table 7. Carcharhiniformes, *Galeocerdo cuvieri.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
258	Aug	juvenile	–	No	–
258	Jun	juvenile	–	No	–
267	Jul	juvenile	–	No	–
270	Jun	adult	–	No	–
272	Jul	adult	–	No	–
280	Jul	adult	–	+	SMR
298	Jul	post partum	–	No	–
313	May adult	–	No	–	

Note: + = sparse; SMR = smear.

Table 8. Carcharhiniformes, *Prionace glauca.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
195	Jun	adult	–	+++	T
223	Apr	adult	–	++	SMR
234	Apr	adult	–	++	SMR
234	Jun	post-partum	–	+++	T
265	May	adult	–	++	T
273	Jun	gravid	near term	+	T

Note: + = sparse; ++ = moderate; +++ = abundant; SMR = smear; T = tubule.

well-stained sperm, packed densely in tubules adjacent to the shell secretory tubules (Table 11, Fig. 6). Sperm also occurred in small amounts in the lumen entrained in a blue staining material that originates in the shell secretory zone. Since the uteri contained developing eggs, recent copulation is unlikely.

Discussion

The elasmobranchs that develop sperm storage capabilities and the styles for their employment are quite varied. As in other animals which internally inseminate numerous ova from a single copulation, sperm must be retained for at least the duration of ovulation to permit insemination. This necessitates the development of a seminal receptacle in close enough proximity to the passing ovum to permit insemination but far enough out of the main stream of

Table 9. Carcharhiniformes, *Rhizoprionodon terraenovae.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
70	Aug	adult	–	+	T
80	Aug	gravid	early	No	–
80	Aug	gravid	early	No	–
81	Aug	gravid	early	++	T
81	Aug	gravid	early	+	T
82	Aug	gravid	early	No	–
82	May	gravid	near term	No	–
84	Aug	gravid	early	++	T
85	Aug	gravid	early	No	–
86	Aug	gravid	early	No	–
87	Sep	gravid	early	No	–
87	Aug	gravid	early	+	T
89	May	post partum	–	+++	L

Note: + = sparse; ++ = moderate; +++ = abundant; T = tubule; L = lumen.

Table 10. Carcharhiniformes, *Sphyrna lewini.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
173	May	adult	–	No	–
204	May	gravid	near term	+	T
214	Jul	gravid	near term	++	T
219	Jul	post partum	–	+++	T

Note: + = sparse; ++ = moderate; +++ = abundant; T = tubule.

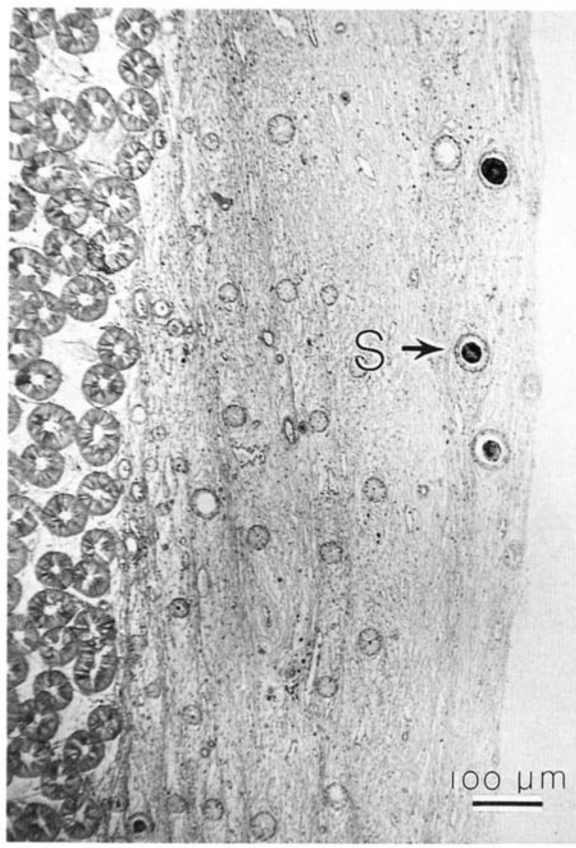

Fig. 5. Sperm stored in connective tissue tunic of the oviducal gland of a mature scalloped hammerhead, *Sphyrna lewini.* S = sperm.

Table 11. Carcharhiniformes, *Sphyrna tiburo.*

Fork length (cm)	Month of capture	Maturity	Stage of pregnancy	Sperm present	Location
93	May	gravid	early	+++	L, T

Note: +++ = abundant; T = tubule; L = lumen.

egg movement to ensure retention of most of the sperm. The oviducal gland, with its long, narrow tubules, provides this capability in elasmobranchs thus far investigated. Some tubules appear to be specialized for sperm retention and, in some species, such as *Sphyrna lewini,* may constitute a true seminal receptacle. As selective pressure over time favored sperm retention in the oviducal gland, sperm storage was a logical consequence. Its development probably facilitated the adoption of a nomadic lifestyle by many pelagic species, such as the tiger and scalloped hammerhead, as well as the delayed fertilization in the far-ranging blue shark.

This overview of 11 species suggests three different fates for oviducal spermatozoa (Table 12). In some species of the order Lamniformes, but not restricted to them, sperm is received by the oviducal gland and held briefly, probably a matter of days, until ovulation is complete. The high productivity of this gland and the thousands of eggs passed to feed the uterine young (oophagy) (see Gilmore 1983, this volume, Gilmore et al. 1983, and Wourms 1977, for a review) would probably 'flush' stored sperm out of the gland. Sperm held for immediate insemination are characterized by their location in the lu-

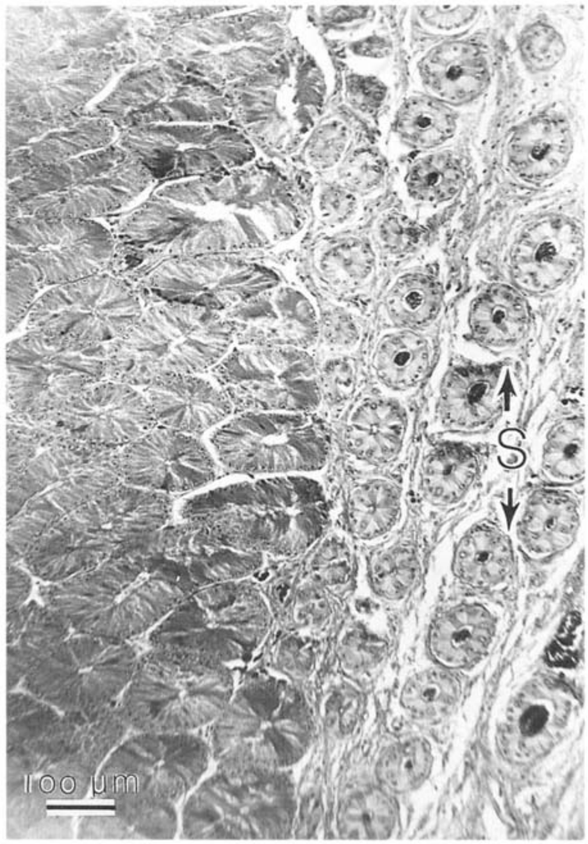

Fig. 6. Sperm stored in secreting tubules of the bonnethead, *Sphyrna tiburo.* S = sperm.

Table 12. Fate of spermatozoa in the oviducal glands of sharks.

Condition	Probable residence time	Typical characteristics	Species examples
Non-storage			
Immediate insemination	Days	Sperm densely packed in lumen or shallow tubes in a random direction, heads stain well	*Alopias vulpinus* *Lamna nasus*
Short-term storage			
Delayed insemination	Weeks to months	Sperm loosely packed in tubules with heads 'upcurrent' away from lumen, heads stain well	*Prionace glauca* *Rhizoprionodon terraenovae*
Long-term storage			
Repeated insemination possible	Months to years	Sperm densely packed in unaligned masses in tubules deep in gland, sperm heads stain faintly	*Carcharhinus obscurus* *Sphyrna lewini*

men, shallow tubules and pockets in the gland. Sperm held for current use have a random orientation. Their heads take stain very well. Examples in this data set include *Alopias vulpinus* and *Lamna nasus.*

Short-term storage for delayed insemination or as a precursor to long-term storage is characterized by sperm that are loosely packed in longer tubules and which penetrate more deeply into the oviducal gland. Sperm tend to polarize with their heads pointing 'upcurrent' into the gland. Metten (1941) noted that in *Scyliorhinus canicula,* all ciliary current in the oviducal gland swept toward the lumen and uterus. The sperm are possibly swimming actively to stay in place for weeks and perhaps months in species such as *S. canicula* as well as in non-pregnant *Prionace glauca* and *Rhizoprionodon terraenovae.*

The maximum duration of long-term storage is difficult to determine. Large, densely packed, unaligned masses of sperm are stored in thin-walled tubules usually deep in the shell gland. The heads do not stain as vividly or as distinctly as the loosely packed, aligned sperm masses of species exhibiting short-term storage. This condition is repeatedly present in near-term, gravid *Carcharhinus obscurus, Sphyrna lewini,* and *Prionace glauca.* The minimum storage interval would be the gestation period, as successful insemination could probably not occur through a uterus containing embryos and their supporting tissues. Gestation time must be added to any seasonal, maturational delay such as subadult female blue sharks experience (Pratt 1979). Storage to the time of observation could be from 10 to 11 months to 14 or 15 months. Whether such long-stored sperm masses contain sufficient quantities of capacitized sperm to be capable of fertilizing a subsequent generation of eggs is unknown at this time. Repeated fresh inseminations are probably the rule in these females; but in a highly migratory species of low density, fecundity of the population would certainly be increased if fertilization could be affected in the absence of male contact.

Species account

Based on comparisons made in this study, phylogeny and the effectiveness of sperm storage are related. Examination of the more plesiomorphic sharks suggests that they employ simpler insemination styles. Lamniform sharks examined thus far do not show evidence of sperm storage. Perhaps the high volume of eggs and shell material characteristic of this order prohibits this secondary use of the oviducal gland. Of the thirty-four lamnoids investigated the only two that contained spermatozoa, a 220 cm *Alopias vulpinus* and a 227 cm *Lamna nasus,* had both obviously recently mated.

The Carcharhiniformes display much more variety. Post-partum and gravid dusky sharks, *Carcharhinus obscurus,* almost always contained masses of stored sperm. Dusky sharks are more nomadic and less abundant than many other carcharhinids and the development of stored sperm may be a necessity for their perpetuation.

The alternate year sexual cycle of the sandbar sharks probably makes the storage of spermatozoa unnecessary, and possibly temporally unfeasible. Sperm would have to be stored for a minimum of two years to fertilize the next litter. This may be beyond the upper limit for elasmobranch seminal storage. The summer sample of tiger sharks reported here is outside the geographic range of sexually active individuals. Prasad (1944) demonstrated sperm storage in Indian Ocean tiger sharks. Due to their nomadic nature, sperm could be present in any mature female (270 cm and larger). The blue sharks, *Prionace glauca,* surveyed in Table 8 were chosen to represent the range of blue shark oviducal conditions; for more information see Pratt (1979). Part of the success and abundance of the Atlantic sharpnose, *Rhizoprionodon terraenovae,* must result from its efficient reproductive styles. Yearly mating and short-term storage are used to ensure that nearly every adult female is pregnant most of the year. The scalloped hammerhead, *Sphyrna lewini,* has well-developed, long-term sperm storage capabilities, yet is capable of mating in a post-partum condition. The tubules found in the surrounding connective tissue may be the first step in formation of a separate seminal receptacle for this species.

The 93 cm bonnethead shark, *Sphyrna tiburo*, is of interest because it reveals the probable sequence of insemination. A small amount of the stored sperm is released from the nearby shell secreting zone and flows out into the lumen to surround the egg. While the shell material is still liquid, the entrained sperm contact and inseminate the egg. One egg was present in each uterus of this specimen. Bonnetheads typically give birth to 8 to 12 pups in late summer (Castro 1983). The process was just beginning for this specimen.

Conclusion

The storage of spermatozoa in the oviducal glands of female elasmobranchs increases the chances of successful insemination, particularly for species that are nomadic or of relatively low population densities. After a single mating, or a series of copulations, the females of some species can delay and physiologically control the time of fertilization and subsequent parturition. This ability enhances reproductive success. Poorly understood factors such as sperm storage may make the critical difference whether a species flourishes or not. The large populations of blue sharks and scalloped hammerheads in the world ocean could be a consequence of these species' ability to utilize stored sperm and may prove to be a positive factor in the possible limited resilience of the few species of elasmobranchs, such as some skates, that can endure modest fishing pressure. Sperm storage also provides flexibility and survival advantage for females and the population by uncoupling mating activities and the time of fertilization which can occur after a long migration. It may ensue that females self-inseminate when each individual is physiologically prepared and bears mature ovarian eggs, healed mating wounds and replete energy reserves.

Phylogeny and the complexity and probable efficiency of sperm storage may also be related. The more plesiomorphic species in this study show less complex storage styles. A survey of the large squaliform order and other ancient groups may confirm this conclusion.

Acknowledgements

I am grateful to J. Casey, N. Kohler, C. Stillwell and the members of the Apex Predator Investigation who made this research possible; to the members of the American Elasmobranch Society who made this symposium a reality, and to the sport and commercial fishers, tournament organizers and dealers who made these sharks available.

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