

The Elasmobranch Husbandry Manual: Captive Care of Sharks, Rays and their Relatives

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Chapter 16

Reproduction, Embryonic Development, and Reproductive Physiology of Elasmobranchs

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Abstract: Chondrichthyan reproduction is characterized by internal fertilization, diverse reproductive modes, complex reproductive cycles, late sexual maturity, iteroparity (several litters per lifetime), and small brood size. Embryonic development in elasmobranchs ranges from two months to at least two years, and generally proceeds uninterrupted, with the exception of those species in which embryonic diapause has been confirmed. Relatively little information on reproduction in captive elasmobranchs has been published. Information on reproduction from wild conspecifics is therefore useful in assessing reproductive potential in captive elasmobranchs. Reproduction in captive animals may provide insights into hormonal fluctuations, behavior, and maternal-brood relationships. Differences from wild conspecifics may result from constraints associated with the captive environment. Detailed, accurate information relating to reproductive biology and physiology should be collected from captive specimens, and disseminated via peer-reviewed publications.

REPRODUCTION AND DEVELOPMENT

Reproduction in chondrichthyans is variable in terms of the functional morphology of the reproductive tract, biology and behavior,

embryonic development, and modes of embryonic nutrition. In general, the reproductive biology of elasmobranchs is characterized by: delayed sexual maturity, diverse modes of embryonic nutrition, different reproductive cycles, and low

fecundity. Several excellent summaries provide extensive detail on reproduction in elasmobranchs and holocephalans (e.g., Wourms 1977; Wourms 1981; Dodd, 1983; Wourms et al., 1988). The intent of this chapter is to summarize the general properties of reproductive biology in chondrichthyans, focusing on elasmobranchs, and apply them to captivity. Compared to wild conspecifics, relatively little has been published on the reproductive biology of captive elasmobranchs in aquariums.

REPRODUCTIVE ANATOMY

Reproductive anatomy is the same for each sex across elasmobranch taxa, although there are some specializations in each sex and asymmetries, particularly with respect to the female reproductive tract. The principal components of the reproductive tract in male elasmobranchs include the: testes; epidymis; Leydig's gland; vas deferens; seminal vesicle; siphon sac, clasper gland, or alkaline gland; and the clasper. The principal components of the reproductive tract in female elasmobranchs include the: ovaries; ostia (ostium); oviduct; shell gland; uterus; and cervix.

There are numerous photographs and drawings available in the literature depicting the reproductive tracts in general, and for several species (e.g., Castro, 1983; Maruska et al., 1996), as well as those for the commonly depicted spiny dogfish (*Squalus acanthias*). The gonads, testes in males and ovaries in females, are located in a dorsal retroperitoneal position, supported by mesenteries, mesorchia, and mesovaria, respectively. Gonad structure varies across taxon groups within the subclass (Pratt, 1988). Primarily, morphological differences occur in the gonad type (Pratt, 1988), claspers in males (Compagno, 1988), and nidamental, oviducal, or shell gland in females (Hamlett et al., 1998). Both testes are active in all species studied to date, and the zonate pattern of the mature elasmobranch testis lends itself well to physiological and histological studies (Dodd, 1983; Callard, 1988; Callard and Klosterman, 1988; Parsons and Grier, 1992). The siphon sac in male sharks is replaced by the clasper gland and alkaline gland in batoids.

Both left and right ovaries and oviducts are functional in some groups (e.g., skates). The right ovary and both oviducts are functional in other groups (e.g., lamniform and carcharhiniform sharks), whereas only the left ovary and oviduct

are functional in others (e.g., many myliobatiform rays). The main specializations in the female reproductive tract occur in the shell gland and the uteri. The shell gland is reduced in viviparous forms. Uterine specializations include infoldings, uterine villi or trophonemata (in myliobatiform rays), and compartmentalization (in placental viviparous sharks). Additional specializations have occurred in the reproductive tracts for the storage and packaging of sperm in the seminal vesicles, prior to copulation, in some males (Pratt and Tanaka, 1994), and prior to ovulation and fertilization, in the shell gland, in some females (Pratt, 1993), in those species that have been investigated.

Spermatozoa may be stored in the female reproductive tract from the short-term to periods exceeding two years, in some species (Dodd, 1983; Castro et al., 1988; Pratt, 1993). In other species, such as the Atlantic stingray (*Dasyatis sabina*), there was no evidence for sperm storage by females in a distinct study area (Maruska et al., 1996; Tricas et al., 2000). Mollet et al. (2002) suggested sperm storage for a year in the pelagic stingray (*Dasyatis* [= *Pteroplatytrygon*] *violacea*) based on captive specimens.

Oviducal sperm storage, beyond a few days to weeks, is unlikely in oophagous sharks, due to the volume of ova that passes through the oviducal gland, and long-term sperm storage has not been observed in lamniform species studied to date (Pratt, 1993). The examples provided above illustrate the variability that occurs with regard to sperm storage. For many species, however, it is not known whether or not sperm storage occurs. In addition, it is not known whether captivity may alter (shorten or lengthen) the period of sperm storage in those species in which it has been documented. Sperm storage might have to be taken into account, therefore, when estimating the length of gestation.

The source of specimens is an important consideration as reproductive parameters for a given species may vary depending upon the geographical position within its range (e.g., Parsons, 1993; Lucifora et al., 1999). Parsons (1993) documented differences in mean size at birth and size at maturity in the bonnethead shark (*Sphyrna tiburo*) in two geographically separated populations. The sandbar shark (*Carcharhinus plumbeus*) is another example of a species in which the litter size, mean size at birth, and size at maturity may vary according to the geographical area within its distribution (Springer, 1960; Wass, 1973; Taniuchi, 1971; Joung and Chen, 1995).

MATURITY STATUS

Maturity status in males can be determined from the size and degree of calcification of the claspers, and the ease of opening of the clasper rhipidion, as well as the degree of rotation. Clasper rotation is not a definitive character of maturity in all species, however, as claspers rotate in all size classes of the porbeagle shark (*Lamna nasus*), for example (Jensen et al., 2002). In living specimens, maturity is more difficult to assess with certainty (Pratt and Tanaka, 1994), but external characters related to the claspers usually allow relatively easy assessment. The progression from immaturity to maturity in males can be determined from the rapid increase in clasper length relative to total length (disc width in rays). The presence of viable sperm is a positive indicator of maturity (Pratt, 1979). Upon dissection in males, the progression to maturity can be determined from the vas deferens, as it becomes coiled in adults. In females, maturity is difficult to assess based upon external characters and dissection allows assessment of the status of ovarian recrudescence, oviduct, nidamental gland, and uteri. Furthermore, pregnancy and the degree of development of embryos or fetuses may be determined. The transition to maturity in females is assessed by examining the width of the shell gland, the transition from threadlike undifferentiated uteri to ribbon-like well-differentiated uteri, and ovarian development. In live captive females, diagnostic *in vivo* imaging (refer Chapter 22 of this manual) is helpful in determining ovarian activity, diameter of the shell gland, oviducts and uteri, and size of embryos or fetuses. These imaging techniques afford a more subjective assessment than when working with dissected specimens.

REPRODUCTIVE CYCLES

Reproductive cycles have been classified by several authors (Wourms, 1977; Dodd and Sumpter, 1984; Koob and Callard, 1999; Hamlett and Koob, 1999). The cycles as defined by Koob and Callard (1999) are:

1. continuous for those species that reproduce throughout the year,
2. seasonal for those species that are reproductively active for only a part of the year, and
3. punctuated for those species that are pregnant for about a year and the next pregnancy is at least a year later.

The stages of the reproductive cycle exhibit certain characteristics. While there is some variation for males, the greatest number of stage-specific characters is displayed by females. In males, the main general stages correspond to mating, the stages of spermatogenesis, and testicular development (Maruska et al., 1996). The stages of the reproductive cycle in females can vary for each type of reproductive cycle. As an example of a seasonal cycle, the placental viviparous bonnethead shark has nine stages: mating, pre-ovulation, ovulation, post-ovulation, early pregnancy, implantation, late pregnancy, parturition, and post-partum. (Manire et al., 1995).

It is important to note that the reproductive cycle in captive animals may differ from that observed in wild conspecifics. Several species have been observed to mate immediately following parturition in captive animals, whereas a longer gap is observed in the wild, in the order of days to weeks in some cases. The Javanese cownose ray (*Rhinoptera javanica*) and the cownose ray (*Rhinoptera bonasus*) are two examples of this phenomenon (Smith and Merriner, 1986; Uchida et al., 1990; Henningsen, personal observation). In addition, parturition and mating may occur at a different time of year than in wild conspecifics. Other aspects of reproductive biology such as maternal-brood relationships may differ between wild and captive conspecifics as has been reported in the southern stingray (*Dasyatis americana*) (Henningsen, 2000). The opportunities provided by aquariums, however, can offer conditions for studies that may otherwise be extremely difficult or expensive. Gestation, for example, can often be estimated as the period between copulation and parturition in captive specimens. Care must be taken to ensure that estimates are placed in the context of a captive setting (i.e., results may be different in wild conspecifics).

DEVELOPMENT

The period from fertilization to hatching in oviparous species, or parturition in viviparous species, is referred to as incubation and gestation, respectively, in this chapter. Similar to other poikilotherms, temperature may have a profound effect on development time, decreasing with an increase in temperature. Some of the best available information on the effects of temperature upon incubation has been obtained for hemiscyllids, as they are commonly maintained and readily reproduce in captivity. For example,

Garner (2003) noted a 12% decrease in incubation from 115 to 101 days with an increase in temperature from 24 to 27°C in the brownbanded bamboo shark (*Chiloscyllium punctatum*). Michael (2001) observed a 27% decrease for the same temperature increase.

REPRODUCTIVE MODES

While reproductive modes have been classified in several ways (see: Breder and Rosen, 1966; Wourms, 1977; Wourms, 1981; Wourms et al., 1988; Compagno, 1990; Hamlett et al., 1992; Hamlett and Koob, 1999), two basic forms of parity, oviparity and viviparity, occur in chondrichthyans. There are variations, however, as some oviparous species deposit eggs at an early stage of development (e.g., skates and some scyliorhinids), while others deposit eggs at an advanced stage of development (e.g., some scyliorhinids) (Wourms et al., 1988). These forms correspond to Compagno's (1990) extended and retained forms of oviparity, respectively. For this chapter, the modes of reproduction will be discussed as described in Hamlett and Koob (1999):

1. oviparity;
2. aplacental yolk sac viviparity;
3. aplacental viviparity with uterine villi or trophonemata;
4. aplacental viviparity with oophagy and (with or without) intrauterine cannibalism; and
5. placental viviparity.

Although reproductive modes of chondrichthyans are not strongly correlated to their phylogeny (Compagno, 1990), there are some trends. As in other vertebrates, oviparity is thought to be the primitive condition and viviparity more derived (Callard et al., 1995; Luer and Gilbert, 1991; Dulvy and Reynolds, 1997). All extant holocephalans and rajoids are oviparous, and although oviparity also occurs in certain shark taxa, approximately two-thirds of the sharks and all other batoids are viviparous (Wourms, 1977; Wourms, 1981; Compagno, 1990). In some families, reproductive mode is consistent, but variations have been documented at both the family and generic level. The genus *Mustelus*, for example, contains species that exhibit aplacental yolk-sac viviparity, while others use placental viviparity. Oophagy is predominant in lamniform sharks; however, the orectolobiform tawny nurse shark (*Nebrius ferrugineus*) and the carcharhiniform false cat shark (*Pseudotriakis*

microdon) are both reported to be oophagous (Yano, 1992; Teshima et al., 1995). It is in females, particularly in the uterus, where several specializations have occurred to accommodate developing embryos and fetuses (Hamlett and Hysell, 1998). Furthermore, the frequently observed larger size of females compared to conspecific males has often been attributed to increasing the space available to developing embryos.

Embryonic development in cartilaginous fishes has been reported to range from two months in the pelagic stingray, to at least 3½ years in the frilled shark (*Chlamydoselachus anguineus*) (Ranzi, 1932; Tanaka et al., 1990), although two years has also been suggested for the latter (Gudger, 1940). Generally, development proceeds uninterrupted; exceptions are those species with embryonic diapause such as: the Australian sharpnose shark (*Rhizoprionodon taylori*) (Simpfendorfer, 1992), the bluntnose stingray (*Dasyatis say*) (Snelson et al., 1989), the Brazilian guitarfish (*Rhinobatos horkeli*) (Lessa et al., 1986 in Simpferdorfer, 1992), the shovelnose guitarfish (*Rhinobatos productus*) (Villavicencio-Garayzar, 1993a; Villavicencio-Garayzar et al., 2001), the common guitarfish, (*Rhinobatos rhinobatos*) (Abdel-Aziz et al., 1993), the giant electric ray (*Narcine entemedor*) (Villavicencio-Garayzar et al., 2001), the Brazilian electric ray (*Narcine brasiliensis*) (Villavicencio-Garayzar, 1993b), and the whiptail stingray (*Dasyatis brevis=diptera*) (Villavicencio-Garayzar et al., 2001). The reader is referred to Wourms (1977) and the references therein for summaries of development. Details of embryonic development have been given for oviparous (Luer and Gilbert, 1985), aplacental yolk-sac viviparous (Natanson and Cailliet, 1986;), aplacental viviparous with uterine villi or trophonemata (Lewis, 1982; Thorson et al., 1983; Amesbury, 1997), aplacental viviparous with oophagy with or without intrauterine cannibalism (Gilmore et al., 1983, Gilmore 1993; Francis and Stevens, 2000), and placental viviparous (e.g., Hamlett, 1993; Wourms, 1993) species. Excellent photographs and drawings that depict the stages of embryonic/fetal development are available in the literature (i.e., Gilmore et al., 1983; Castro, 2000).

REPRODUCTIVE ABNORMALITIES IN CAPTIVITY

Reproductive abnormalities occur in elasmobranchs as well as in other animals. It is difficult to ascertain the occurrence of certain reproductive

abnormalities in wild conspecifics, but in some captive elasmobranch species broods can include both term live fetuses as well as incompletely developed stillborn fetuses. This phenomenon has been observed in the sand tiger shark (*Carcharias taurus*) (Gordon, pers. com.), the southern stingray (Henningsen, personal observation), and the leopard shark (*Triakis semifasciata*) (Ankley, pers. com.). Deformed or “stunted” or “runt of the litter” embryos do occur in nature (Smale and Goosen, 1999). Females have retained encapsulated ova, and there are observations of mortalities associated with “egg-bound” female spotted wobbegongs (*Orectolobus maculatus*) (Gordon, pers. com.). Whether it is unique to captive sharks is unknown, but it is not uncommon for female sand tiger sharks to release infertile ova (Henningsen, personal observation; Gordon, pers. com.) or female nurse sharks (*Ginglymostoma cirratum*) to shed “wind” eggs (fully-formed egg capsules devoid of yolk or embryos).

Another observed abnormality is retention of term fetuses in utero beyond the expected time of parturition in both wild and captive specimens. This “over-gestation” has been noted in some batoids such as the cownose ray (Henningsen, 1999) and the yellow stingray (*Urobatis jamaicensis*). In the former, term fetuses have remained live in utero up to two months past the normal suggested gestation of 11 months (Smith and Merriner, 1986; Henningsen, 1999), and in the latter, up to four months (Stamper, pers. com.) past the normal 3-5 month gestation (Spieler, pers. com.; Hamlett, pers. com.). The two examples cited here correspond to a range of 20-100% over-gestation time. Retention in utero has also been observed in pelagic stingrays (Mollet et al., 2002). In contrast, gravid female elasmobranchs may readily abort when faced with stress, both environmental and physiological (Smith, 1980; Snelson et al., 1988).

In oviparous species, oviposition usually occurs in pairs, several days apart (Luer and Gilbert, 1985; Koob and Callard, 1999; Castro et al., 1988). In placental viviparous species, parturition normally occurs within minutes to hours (Parsons, 1991; Parsons, 1993). However, normal full-term fetuses have been born days to weeks apart in some captive placental viviparous specimens, including the bull shark (*Carcharhinus leucas*) (Uchida et al., 1997) and blacktip reef shark (*Carcharhinus melanopterus*) (Riggles, pers. com.). It is unclear whether this protracted parturition is due to environmentally-driven

endocrine factors. Another plausible explanation is that successive parturitions, as well as stillbirths and abortions, originated in a separate uterus. Protracted parturition is normal in some species. In some lecithotrophic, aplacental species, such as the nurse shark, parturition is normally spread out over several days. Ovulation is a prolonged process spread over 2-3 weeks in this species, and embryos may be found at different stages of development in the uterus (Castro, 2000). This “conveyor belt” method occurs in the retained oviparous species, referred to in Wourms et al. (1988) and Compagno (1990).

Conditions in aquariums are suitable for describing other abnormalities. Hermaphroditism has been observed in elasmobranchs, but not as yet in captivity. A case of gynogenesis has been reported in an aquarium (Voss et al., 2001).

REPRODUCTIVE PHYSIOLOGY

The physiological control of reproduction should be considered when attempting to promote or inhibit reproduction in captive animals. Reproductive physiology has been reviewed by several authors (for example see Dodd, 1983; Callard et al., 1988; Hamlett, 1999; Hamlett and Koob, 1999). Demski (1990a; 1990b) provides a focused discussion for reproduction in captive elasmobranchs.

As in other key components of life history, environmental parameters have profound effects upon reproduction. Environmental cues, primarily temperature and photoperiod, are relayed via the central nervous system to target organs such as the gonads, thyroid, and interrenal gland. The effects, both positive and negative, are mediated through the neuroendocrine system (Demski, 1990a; Demski, 1990b; Redding and Patiño, 1993; Henningsen, 1999). Gonadotropin releasing hormone (GnRH) is important in vertebrates in regulating gonadotropin release, and hence reproductive physiology, through the hypothalamus-pituitary-gonadal axis (Demski, 1990a; Pierantoni et al., 1993; Forlano et al., 2000). Unique to chondrichthyans, however, GnRH reaches the gonadotropes, in the ventral lobe of the pituitary in elasmobranchs and in the buccal lobe of the pituitary in holocephalans, via the systemic circulation (Pierantoni et al., 1993; Sherwood and Lovejoy, 1993; Wright and Demski, 1993). It is important to note the effect that environmental parameters have on reproductive physiology in captive elasmobranchs, because

factors such as temperature and photoperiod can readily be altered in aquarium systems.

Reproductive endocrinology is a major component of reproductive physiology and has been described in numerous articles (e.g., Koob et al., 1986; Rasmussen et al., 1992; Manire et al., 1995; Manire et al., 1999a; Snelson et al., 1997). The principal hormones associated with reproduction in elasmobranchs are steroid and peptide hormones similar to other vertebrates. Although about 19 different reproductively-related steroid hormones have been identified in elasmobranchs, detailed investigations conducted throughout the reproductive cycle have, until recently, focused on four of these: 17- β estradiol, progesterone, testosterone, and 5 α -dihydrotestosterone (Manire et al., 1999a). Recent work has shown that other steroids, principally other androgens and progestins as well as glucocorticoids, may play important roles at key points during reproduction (Garnier et al., 1999; Manire et al., 1999a; Manire et al., 1999b). It is beyond the scope of this manual to present a review of elasmobranch reproductive endocrinology, but a summary of the hormones associated with reproduction is presented below. Serum steroid titers have been published for oviparous (e.g., Sumpter and Dodd, 1979; Koob et al., 1986; Heupel et al., 1999; Rasmussen et al., 1999), aplacental yolk sac (Lupo di Prisco et al., 1967; Tsang and Callard, 1987; Fasano et al., 1992), aplacental with trophonemata (Snelson et al., 1997; Tricas et al., 2000), oophagous with embryophagy (Rasmussen and Murru, 1992) and placental viviparous species (i.e. Rasmussen and Gruber, 1993; Manire et al., 1995; Manire et al., 1999a; Manire and Rasmussen, 1997). Putative as well as definitive roles for steroids during reproduction in elasmobranchs have been identified; these include regulation of the reproductive tract and modulating behavior (Callard and Koob, 1993; Callard et al., 1993; Sisneros and Tricas, 2000). In addition to steroid hormones, peptide hormones, such as relaxin and the oxytocin-like peptides, have been determined to play key roles during reproduction (Koob et al., 1984; Callard and Koob, 1993; Sorbera and Callard, 1995).

The levels of specific steroids not only play key roles in reproduction, but clearly can be associated with stages of the reproductive cycle in some cases. In addition, the levels of the steroids rise in accordance with maturational status (Rasmussen and Gruber, 1993). Most studies of the endocrine cycle in elasmobranchs have focused on females, and few studies have examined the steroid levels over the entire

reproductive cycle in male elasmobranchs (Manire and Rasmussen, 1997). In general, the levels of androgens in males peak prior to the period of maximum sperm production and mating. The patterns for estradiol and progesterone vary in those species that have been investigated. The levels of steroids in females over the entire reproductive cycle show some variations, but some trends are consistent. The levels of estradiol, for example, increase prior to and during vitellogenesis, when yolk products are stored in the developing oocytes (follicular phase). Progesterone peaks in the peri-ovulatory and post-ovulatory periods, with some differences observed in the timing of this peak. The duration of the post-ovulatory peak in progesterone, when it occurs, is correlated to the functional life of the corpora lutea (post-ovulatory cycle), the source of the progesterone. Despite these similarities, the steroid levels and the timing of peaks vary considerably in those species examined.

To date, the sole published values of reproductively-related hormones in elasmobranchs in a public aquarium were by Rasmussen and Murru (1992). The titers obtained from carcharhinids were comparable to those in non-stressed, wild sharks. In two captive populations of sand tiger sharks, one of the authors (Henningesen) observed reproductively-related hormone differences between the groups, particularly in males. In addition, monthly sampling of one of these captive populations revealed significant individual variation with respect to the levels of steroids as well as the timing of steroid peaks. Similar studies would be valuable for determining reproductive status in captive elasmobranchs.

SUGGESTIONS FOR THE FUTURE

Acquisition of many species of elasmobranchs, for display in aquariums, is becoming increasingly restricted (refer to Chapter 3 of this manual). Captive specimens must be viewed as a resource, both for captive breeding programs (refer to Chapter 17 of this manual) and for obtaining data relevant to the biology and conservation of wild populations. Valuable, detailed information relating to reproduction can be obtained with relatively little effort from existing captive specimens. Such information should be obtained from all available specimens. Focus should be placed on documenting this information and publishing it in peer-reviewed outlets. Examples of such studies include investigations into the reproductive biology of nurse sharks (Castro,

2000) and reproductive parameters for Southern stingrays (Henningsen, 2000).

Imaging techniques can be used to collect details on reproductive tract development in live specimens (refer to Chapter 22 of this manual). Measurements taken (oocyte diameter, etc.), however, should be validated. The directive is to collect more quantitative data on reproductive biology and physiology from captive elasmobranchs. Serum hormone titers, coupled with morphological and behavioral correlates should be monitored.

By collecting and publishing information on reproduction of elasmobranchs in aquariums, the gap between what is known and published for wild conspecifics and what is known for captive specimens will be closed. In addition, more differences or similarities between wild and captive conspecifics can be documented.

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