Elasmobranch Husbandry Manual: Proceedings of the First International Elasmobranch Husbandry Symposium, 2001, pages 239-250.

Chapter 17
Captive Breeding and Sexual Conflict in Elasmobranchs

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Abstract: Successful reproduction has been recorded in many different species of cartilaginous fish held in captivity; representing the various reproductive modes recorded in chondrichthyans. Documentation of behaviors of captive chondrichthyans has provided a foundation to our knowledge of reproductive behavior, as these interactions are rarely been reported for many species, mating systems remain poorly understood. Captive breeding may reduce pressure on wild populations, particularly for those species where severe declines have been documented. Such efforts may be opportunistic, directed, or undertaken in collaboration with other institutions. Detailed behavioral records relevant to reproduction should be collected and maintained for all captive elasmobranchs and shared through peer-review publication.

Reproductive behaviors in chondrichthyans are often complex and until recently few qualitative studies of reproductive behaviors in elasmobranchs have been published (Pratt and Carrier, 2001). Several reviews of reproductive behavior have been presented in the last decade (Bres, 1993; Demski, 1990a; Demski, 1990b; Pratt and Carrier, 2001). The majority of reproductive behaviors reported in the literature have been observed in captive elasmobranchs, as it is difficult to closely monitor wild conspecifics. One hundred species of chondrichthyans are known to have exhibited reproductive behaviors or reproduced in captivity: in aquaria, semi-natural confinements, and laboratories. These species include one holocephalan and 99 elasmobranchs; oviparous and viviparous species comprise 40% and 60%, respectively (Table 17.1).

As noted by Parker (1979), Davies (1992, in Birkhead and Parker 1997), and Reynolds (1996), all mating systems may be the result of intrasexual and intersexual conflict. Mating systems in elasmobranchs have resulted in adaptations in both sexes, such as sexual dimorphism in skin thickness (Pratt, 1979; Kajiura et al., 2000) and sexually dimorphic dentition (McCourt and Kerstitch, 1980; Kajiura and Tricas, 1996). The intent of this chapter is to provide a brief summary of: chondrichthyans bred in captivity (including a closer examination of five sample species), the range of observed sexual conflicts, methods of controlling reproduction, and suggestions for the future.

SEXUAL CONFLICT

Intra- and intersexual behaviors evolved in environments very different from those in aquaria. Captive animals are confined to the limited space provided by the aquarium system, and the full spectra of behaviors are almost always modified or attenuated. Consequently, captive sharks, skates, or rays may be subject to persistent chasing and biting by members of the same or opposite sex, from which they may have limited ability to escape. In addition, wounds inflicted during pre-copulatory or copulatory behaviors in captive elasmobranchs may act as entry sites for pathogens such as bacteria and fungi (refer Chapter 26 of this manual), particularly if they are aggravated by teleost cohabitants.

Several behaviors relating to reproduction have been documented in semi-natural and captive settings. Intersexual interactions may range from one or more males following a female, to nosing the female, to grasping and copulation (Johnson and Nelson, 1978; Uchida et al., 1990; Gordon, 1993). Nosing, as observed in sand tiger sharks, *Carcharias taurus* (Gordon, 1993) and blacktip reef sharks, *Carcharhinus melanopterus* (Gordon, 1993; Riggles, pers. com.), consists of the male positioning its snout just under the cloaca of the female. In other animal taxa, some behaviors, and specifically reproductive behaviors, are often induced via biochemical compounds. Pheromones have been identified in several invertebrate and vertebrate groups, including teleosts (Sorensen et al., 1995; Sorensen et al., 2000). Although no pheromones have been identified in elasmobranchs to date, behavioral observations during reproduction (i.e., Springer, 1967; Johnson and Nelson, 1978; Castro et al., 1988; Gordon, 1993) suggest that pheromones may be released by the female and may induce part of the male behavior repertoire. Ongoing but unpublished investigations on reproductively active clearnose skates, *Raja eglanteria*, strongly suggest that male skates respond to secretions released by reproductively active females (Rasmussen, pers. com.). In some skates and rays, many social and reproductive behaviors are mediated via electroreception using the ampullary system (New, 1994; Tricas et al., 1995; Sisneros et al., 1998; Sisneros and Tricas, 2002). It is likely therefore that reproductive behavior is mediated via visual, biochemical, and electroreceptive cues in elasmobranchs; the importance of each cue may differ across species or groups.

Additional interactions include but are not limited to pectoral fin biting in sharks and rays and male gouging of the dorsal surface of the female in

Table 17.1. Chondrichthyan reproduction in captivity showing species that have completed the reproductive cycle in a captive environment, as well as those that have exhibited mating behavior in captivity. The list includes species from aquaria, laboratories, and semi-natural environments. It does not refer to species that were known to be gravid when retained in captivity. Reproductive modes, as per Hamlett and Koob (1999), include the following: O = Oviparous; VA1 = Viviparous - aplacental - yolksac; VA2 = Viviparous - aplacental - with uterine villi or trophonemata; VA3 = Viviparous - aplacental - with oophagy and (with or without) intrauterine cannibalism; and VP = Viviparous - placental. Unless otherwise specified, source references were the International Zoo Yearbook, 1971-1997, Vols. 11-35, Zoological Society of London.

Species name	Common name	Mode	Reference
Aetobatus narinari	spotted eagle ray	VA2	Uchida, 1982; Uchida et al., 1990; Uchida et al., 1997
Apristurus brunneus	brown cat shark	O	
Atelomycterus macleayi	Australian marbled cat shark	O	
Atelomycterus marmoratus	coral cat shark	O	
Brachaelurus waddi	blind shark	O	
Carcharhinus acronotus	blacknose shark	VP	Kaiser, pers. com.
Carcharhinus leucas	bull shark	VP	Uchida et al., 1997
Carcharhinus melanopterus	blacktip reef shark	VP	Riggles, pers. com.
Carcharhinus perezi	Caribbean reef shark	VP	Kaiser, pers. com.
Carcharhinus plumbeus	sandbar shark	VP	Engelbrecht, pers. com.
Carcharias taurus	sandtiger shark	VA3	Gordon, 1993; Garner, 1997
Cephaloscyllium umbratile	Japanese swell shark	O	Hagiwara, 1990
Cephaloscyllium ventriosum	swell shark	O	
Chiloscyllium arabicum	Arabian carpet shark	O	
Chiloscyllium griseum	gray bamboo shark	O	Dral, 1980
Chiloscyllium indicum	slender bambooshark	O	
Chiloscyllium plagiosum	white-spotted bamboo shark	O	
Chiloscyllium punctatum	brown-banded bamboo shark	O	Schmid and Murru, 1991; Garner, 1998
Dasyatis akajei	red stingray	VA2	
Dasyatis americana	southern stingray	VA2	Henningsen, 2000
Dasyatis brevicaudata	shortail stingray	VA2	
Dasyatis chrysonata	blue stingray	VA2	
Dasyatis fluviorum	estuary stingray	VA2	
Dasyatis izuensis	Izu stingray	VA2	
Dasyatis matsubarai	pitted stingray	VA2	
Dasyatis pastinaca	common stingray	VA2	
Dasyatis sabina	Atlantic stingray	VA2	
Etmopterus lucifer	blackbelly lantern shark	VA1	Uchida et al., 1990
Ginglymostoma cirratum	nurse shark	VA1	Klimley, 1980; Kuenen, 2000; Marin-Osorno, personal observation
Gymnura altavela	spiny butterfly ray	VA2	
Gymnura japonica	Japanese butterfly ray	VA2	
Gymnura micrura	smooth butterfly ray	VA2	

able 17.1 (continued). Chondrichthyan reproduction in captivity showing species that have completed the reproductive cycle in a captive environment, a vell as those that have exhibited mating behavior in captivity. The list includes species from aquaria, laboratories, and semi-natural environments. It does nc efer to species that were known to be gravid when retained in captivity. Reproductive modes, as per Hamlett and Koob (1999), include the following: O)viparous; VA1 = Viviparous - aplacental - yolksac; VA2 = Viviparous - aplacental - with uterine villi or trophonemata; VA3 = Viviparous - aplacental - wit ophagy and (with or without) intrauterine cannibalism; and VP = Viviparous - placental. Unless otherwise specified, source references were the Internationa oo Yearbook, 1971-1997, Vols. 11-35, Zoological Society of London.

Species name	Common name	Mode	Reference
Haploblepharus edwardsii	puff-adder shy shark	O	
Haploblepharus pictus	dark shy shark	O	
Hemiscyllium hallstromi	Papauan epaulette shark	O	
Hemiscyllium ocellatum	epaulette shark	O	West and Carter, 1990; Schmid and Murru, 1991
Heterodontus francisci	horn shark	O	Dempster and Herald, 1961
Heterodontus galeatus	crested bullhead shark	O	Last and Stevens, 1994
Heterodontus japonicus	Japanese bullhead shark	O	Uchida et al., 1989; Hagiwara, 1990
Heterodontus mexicanus	Mexican horn shark	O	
Heterodontus portusjacksoni	Port Jackson shark	O	
Heteroscyllium colcloughi	blue-gray carpet shark	O	Horton, pers. com.
Hydrolagus colliei	spotted ratfish	O	Sathyanesan, 1966; Van Dykhuizen et al., 1997
Leucoraja erinacea	little skate	O	
Leucoraja ocellata	winter skate	O	
Mustelus californicus	gray smooth hound	VP	
Mustelus canis	dusky smooth hound	VP	
Mustelus manazo	star-spotted smooth hound	VA1	
Mustelus norrisi	Florida smooth hound	VP	
Myliobatis californicus	bat ray	VA2	
Negaprion brevirostris	lemon shark	VP	
Okamejei kenojei	spiny rasp skate	O	
Orectlobus japonicus	Japanese wobbegong	VA1	Whitley, 1940 in Demski, 1990b; Hagiwara, 1990; Uchida et al., 1997)
Orectolobus maculatus	spotted wobbegong	VA1	Whitley, 1940 in Demski, 1990b
Orectolobus ornatus	ornate wobbegong	VA1	
Parmaturus xaniurus	filetail cat shark	O	
Poroderma africanum	striped cat shark	O	
Poroderma pantherinum	leopard cat shark	O	
Potamotrygon histrix	porcupine river stingray	VA2	
Potamotrygon magdalenae	Magdalena river stingray	VA2	
Potamotrygon motoro	occelate river stingray	VA2	Thorson et al., 1983
Potamotrygon ocellata	red-blotched river stingray	VA2	
Potamotrygon orbignyi	smooth back river stingray	VA2	
Potamotrygon schroederi	rosette river stingray	VA2	
Pristis pectinata	smalltooth sawfish	VA1	Liu, pers. com.
Pteroplatytrygon violacea	pelagic stingray	VA2	Mollet et al., 2002; Morales, pers. com.

Table 17.1 (continued). Chondrichthyan reproduction in captivity showing species that have completed the reproductive cycle in a captive environment, as well as those that have exhibited mating behavior in captivity. The list includes species from aquaria, laboratories, and semi-natural environments. It does not refer to species that were known to be gravid when retained in captivity. Reproductive modes, as per Hamlett and Koob (1999), include the following: O = Oviparous; VA1 = Viviparous - aplacental - yolksac; VA2 = Viviparous - aplacental - with uterine villi or trophonemata; VA3 = Viviparous - aplacental - with ophagy and (with or without) intrauterine cannibalism; and VP = Viviparous - placental. Unless otherwise specified, source references were the International Zoo Yearbook, 1971-1997, Vols. 11-35, Zoological Society of London.

Species name	Common name	Mode	Reference
Raja binoculata	big skate	O	
Raja clavata	thornback skate	O	
Raja eglanteria	clearnose skate	O	Luer and Gilbert, 1985
Raja microocellata	smalleyed skate	O	
Raja montagui	spotted skate	O	
Raja rhina	longnose skate	O	
Raja texana	roundel skate	O	
Raja undulata	undulate skate	O	
Rhina ancyclostoma	bowmouth guitarfish	VA1	Uchida et al., 1990
Rhinobatos hynnicephalus	ringstraked guitarfish	VA1	
Rhinobatos lentiginosus	Atlantic guitarfish	VA1	
Rhinobatos productus	shovelnose guitarfish	VA1	
Rhinoptera bonasus	cownose ray	VA2	Davis, pers. com.; Henningsen, personal observation
Rhinoptera javanica	flapnose ray	VA2	Uchida, 1982; Uchida et al., 1990; Uchida et al., 1997
Rhynchobatus djiddensis	giant guitarfish	VA1	Bok, pers. com.
Scyliorhinus canicula	small-spotted cat shark	O	Bolau, 1881; Schensky, 1941, in Pratt and Carrier, 2001)
Scyliorhinus retifer	chain cat shark	O	Castro et al., 1988
Scyliorhinus stellaris	nursehound	O	
Scyliorhinus tokubee	Izu cat shark	O	
Scyliorhinus torazame	cloudy cat shark	O	Uchida, 1982, Hagiwara, 1990
Sphyrna tiburo	bonnethead shark	VP	
Squalus acanthias	piked dogfish	VA1	
Squatina japonica	Japanese angel shark	VA1	
Stegostoma fasciatum	zebra shark	O	Uchida et al., 1990; Uchida et al., 1997
Taeniura lymma	blue-spotted ribbontail stingray	VA2	Riggles, pers. com.
Taeniura meyeni	speckled stingray	VA2	Garner and Mackness, 1998b
Torpedo marmorata	marbled torpedo	VA2	
Triaenodon obesus	whitetip reef shark	VP	Uchida, 1982; Garner and Mackness, 1998a
Triakis scyllium	banded houndshark	VA1	
Triakis semifasciata	leopard shark	VA1	Ankley, pers. com.
Trygonnorhina sp. A (undescribed)	eastern fiddler ray	VA1	
Urobatis halleri	round stingray	VA2	
Urobatis jamaicensis	yellow stingray	VA2	
Urolophus aurantiacus	sepia stingray	VA2	Hagiwara, 1990; Uchida et al., 1990

myliobatiform rays. The occurrence and type of male-induced bites on female pectoral fins in dasyatids can be used to determine reproductive behavior as well as seasonality (Kajiura et al., 2000). Although Kajiura et al. (2000) observed these behaviors in wild Atlantic stingrays, *Dasyatis sabina*, similar observations can readily be made in captive elasmobranchs. As many as five or more males may chase a captive female cownose ray, *Rhinoptera bonasus*, during mating behaviors, something also observed in the field (Pratt, pers. com.; Henningsen, personal observation). This behavior has also been observed in the flapnose ray, *Rhinoptera javanica* (Uchida et al., 1990). Sexual conflict in captive rhinopterids may be so profound as to cause severe lacerations on the trailing edges of the pectoral fins of females and even mortality (Uchida et al., 1990; Henningsen, personal observation).

EXAMPLE SPECIES

Captive breeding and sexual conflict and has been observed in many species of elasmobranchs. We present brief summaries for five species: sand tiger sharks, sandbar sharks (*Carcharhinus plumbeus*), white spotted bamboo sharks (*Chiloscyllium plagiosum*), nurse sharks (*Ginglymostoma cirratum*), and southern stingrays (*Dasyatis americana*) to point out the importance of recording and clearly defining reproductive behaviors and reproductive events in captive elasmobranchs. These examples serve as models only and a complete coverage of all species is beyond the scope of this chapter.

Sand tiger shark

The sand tiger is widely distributed in warm temperate waters (Compagno, 1984; Castro et al. 1999), and undergoes coastal seasonal migrations that are coupled with the reproductive cycle (Gilmore et al., 1983; Cliff, 1989; Gilmore, 1993; Pollard et al. 1996) and governed by water temperature (Compagno, 1984; Parker and Bucher, 2000).

In Australia, males are predominant in southern Queensland during July to October, while a high proportion (77.4%) of the catch from beach meshing off central New South Wales (NSW) at the same time of year is composed of females (Reid and Krogh, 1992). The sex ratio of the sand tiger population shifts from a majority of females in spring (September-November) to a majority of males in autumn/winter (March-August) at the northern sites, indicating that the movements of the sexes may differ (Parker & Bucher, 2000). Migrations of sand tigers in South African waters appear to follow a similar seasonal pattern to those described by Reid and Krogh (1992), Pepperell (1992), and Pollard et al. (1996) for conspecifics in Australian waters.

Although the reproductive cycle of the sand tiger has been reported to be annual (Gilmore et al., 1983, Gilmore, 1993), a biennial cycle (punctuated cycle: refer Chapter 16 of this manual) appears to be the case, at least in females (Cliff, 1989; Branstetter and Musick, 1994; Castro et al., 1999). Reproductive behaviors for sand tigers in aquaria have occurred in South Africa, Australia, and the USA. To date, successful captive reproduction from copulation to parturition has occurred only in Australia and South Africa. Pre-copulatory as well as copulatory behavior in sand tigers was described by Gordon (1993) from captive specimens at Manly Oceanworld, Sydney, NSW, Australia. The most recent sequence of reproduction in the existing captive population of three mature males and four mature females occurred from September to November 2000 and lasted approximately 53 days (Kinnunen, personal observation). Gordon (1993) reported pre-copulatory and copulatory behavior occurring 14 months apart, of just over a month in duration, and suggested that captive sharks may mate annually. Information from Seaworld Durban and the National Aquarium in Baltimore corroborate this suggestion as annual pre-copulatory behavior has been observed (Bok, pers. com.; Henningsen, personal observation). Annual copulation was witnessed by one of the authors (Garner) at Underwater World, Mooloolaba, Queensland, Australia. It is possible that the reproductive cycles are annual and biennial for males and females, respectively, but further work is required to confirm this suggestion.

One of the authors (Garner) and Fischer (pers. com.) have documented reproduction in sand tiger sharks at Underwater World, Mooloolaba, from 1993 to 2001. Three successful parturitions by one female, “Big Mamma”, in 1992 (wild-copulation), 1997 (captive copulation), and 1999 (captive copulation) were observed. Further, two pre-term stillborn pups (~70-80 cm TL), born in 2000, were attributed to a female shark born of “Big Mamma” in 1992. The age of the latter female corroborates the estimate of the age at maturity given by Branstetter and Musick (1994).

It is worthwhile noting that although most of the sexual conflicts in sand tiger sharks, at several institutions, conform to Gordon's (1993) basic descriptions, duration and seasonality vary (Bok, pers. com.; Choromanski, pers. com.; Zoller, pers. com.). Temperature, in addition to social structure of the captive population, has been suggested by one of the authors (Garner) to be a critical factor for successful captive reproduction in sand tigers. It was noted, however, on one occasion, where pre-copulatory behaviors extended for several months, that salinity appeared to play a role in cessation of the behaviors (Zoller, pers. com.). Despite these suggestions, critical cues have not been positively identified, as captive sand tigers maintained at different institutions under similar temperature, photoperiod, and social structures may or may not be reproductively active. It has been suggested that the disruption of a stable, reproducing captive colony can severely delay if not extinguish reproductive success in sand tigers, which may of course be illustrative of several other species of elasmobranchs. It should be noted that annual intrasexual conflicts have been observed in male sharks in the absence of females. The conflicts between males may be severe and previously undescribed behaviors have been observed between male sharks (Henningsen, personal observation). These observations highlight the need for ongoing detailed behavioral studies in this species.

Nurse shark

A mating group of nurse sharks has been the subject of an on-going investigation in the Dry Tortugas National Park, Dry Tortugas (Carrier et al., 1994; Pratt and Carrier, 2001). This investigation has provided detailed observations on social structure and mating behavior, and provides documented cases of polygyny and polyandry (Pratt and Carrier, 2001). Nurse sharks have been commonly maintained in aquaria for extended periods of time (Clark, 1963; Castro, 2000), yet their reproductive biology has only recently been detailed by Castro (2000). Mating behavior and copulation in captivity has been previously described for this species (Klimley, 1980).

During 1997 one of the authors (Marin-Osorno) observed reproductive behaviors, including copulation, in a captive population of nurse sharks (consisting of five males and four females) at the Aquario de Veracruz. Only two of the nine nurse sharks in the 1,250 m^3 multi-species exhibit were mature, a 267 cm TL male and a 250 cm TL female. Behavioral observations included the presence of a "blocking male", as described by Carrier et al. (1994). Other behaviors were more in accord with field observations described by Carrier et al. (1994), rather than Klimley's (1980) observations of captive nurse sharks.

In captive nurse sharks there have been instances of conflict, involving adult males, directed towards immature conspecifics, and also involving immature animals, directed towards mature consexual conspecifics. Interspecific conflicts by mature and immature nurse sharks have been directed toward tiger (*Galeocerdo cuvier*), sandbar, and sand tiger sharks (Marin-Osorno, personal observation; Henningsen; personal observation; Martel-Bourbon, pers. com.). Such conspecific and interspecific interactions have been observed in several facilities. The reason for these presumably non-reproductively mediated behaviors is not known.

Sandbar shark

The sandbar shark is a widely distributed species that is commonly maintained in public aquaria. Reproduction in this species has been described for captive specimens (Uchida et al., 1990). Although the authors did not observe mating, mating scars were noted and subsequent parturition described. Other instances of reproduction in sandbar sharks have occurred at several institutions (Areitio, pers. com.; Engelbrecht, pers. com.). For the purpose of illustration, a summary of three successive pregnancies, in the same adult female sandbar shark, at the Madrid Zoo Aquarium, is given below. The sharks, four males and one female, were obtained in May of 1985, each ~170 cm TL. The sharks were maintained in a multi-species display using a combination of natural and artificial lighting, with temperature ranging annually from 21-26°C. The first mating was observed in May of 1997, with subsequent parturition in May of 1998. The second and third mating occurred in May of 1999 and May 2001, with parturition occurring in May 2000 and May 2002, respectively (Areitio, pers. com.). These observations agree with the biennial cycle of wild female conspecifics. Observations indicate a shorter, more direct, pre-copulatory period (as short as 1-3 days, preceding copulation) than that observed in sand tiger sharks.

White spotted bamboo shark

The white spotted bamboo shark is a commonly maintained hemiscyllid that is often available in the hobbyist trade. Its biology is poorly known despite its abundance within public aquaria. Like several other similar hemiscyllids it reproduces readily in captivity, given the proper conditions. Males mature at 50-65 cm TL and females mature at ~80 cm TL (Michael, 1993; Compagno, 2001; Michael, 2001). Captive white spotted bamboo sharks are often maintained at a constant temperature and photoperiod. The lack of a temperature change may allow continuous breeding rather than a restricted annual cycle. Similar observations have been reported for the epaulette shark, *Hemiscyllium ocellatum* (Heupel et al., 1999).

Although few observations on reproduction in white spotted bamboo sharks have been published (e.g., Michael, 2001), its mating behavior is similar to that described in other hemiscyllids, notably the gray bamboo shark, *Chiloscyllium griseum* (Dral, 1980 in Pratt and Carrier, 2001), and the epaulette shark (West and Carter, 1990). In addition to the male initiating mating behavior, West and Carter (1990) observed instances of the female initiating mating in the epaulette shark, although this has not yet been observed in white spotted bamboo sharks. In wild epaulette sharks, mating was focused from July to November on Heron Island Reef, Heron Island, Australia (Heupel et al., 1999). The end of the mating season was coincident with an increase in water temperature, but it was not determined whether water temperature was a critical cue (Heupel et al., 1999). Similar to other hemiscyllids, female epaulettes may store sperm, allowing sperm to fertilize ova for a period of at least several months. In addition, females will occasionally produce “wind eggs”, or empty egg cases without yolk or embryo, as reported in sharks such as horn and nurse sharks (Castro, 2000; Michael, 2001).

Female white spotted bamboo sharks produce pairs of eggs every 7-10 days, over the course of the egg-laying season. It is advisable to separate egg cases from adults, particularly adult males, as they may prey upon the egg cases (Michael, 2001). Incubation time and embryonic development vary with temperature, but eggs hatch after about 125-128 days at 25°C (Tullis et al., 1997; Michael, 2001). Although not verified, a possible case of gynogenesis was reported in the white spotted bamboo shark (Voss et al., 2001).

Southern stingray

The southern stingray is common in coastal subtropical and tropical waters of the western Atlantic, including the Gulf of Mexico and the Caribbean (Bigelow and Schroeder, 1953). Maturity has been reported to occur at 51 cm DW (disc width) and 75-80 cm DW, for males and females, respectively (Bigelow and Schroeder, 1953; Schmid et al., 1988). It is a hardy species that has been successfully maintained long-term in captivity. Many details on the life history of this species are lacking in the literature. It is noteworthy that average size at parturition, and litter size, reported for one captive population, differs from that reported for wild conspecifics (Henningsen, 2000). A positive relation between maternal DW and litter size, and an inverse relation between litter size and mean DW of neonates, has been observed. Age at sexual maturity has been recorded as 3-4 years and 5-6 years, for males and females, respectively. Size at maturity was found to be similar to that reported for wild conspecifics (Henningsen, 2002). Multiple males have been observed to mate with a single female, as is the case for the flapnose ray (Uchida et al., 1990). Mating occurred immediately, to within hours, after parturition and was always venter to venter. Intersexual interactions have been observed between mating and subsequent copulation, and male-inflicted bites on females are similar to those described by Kajiura et al. (2000) in Atlantic stingrays.

PROMOTION AND INHIBITION OF REPRODUCTION

Reproduction in captive elasmobranchs can be promoted or inhibited by several means. Demski (1990b) and Henningsen (1999) describe physiological as well as environmental methods of promoting reproduction. Important biological cues such as temperature and photoperiod can be manipulated, as can social structure (e.g., mature males:mature females), which may be essential to successful captive reproduction. An application of the use of environmental factors to control reproduction is given in Luer and Gilbert (1985) and Luer (1989) for the clearnose skate, with temperature being the critical factor. The temperature during captive breeding in the clearnose skate mimics the conditions during the reproductive cycle in wild conspecifics (Luer, 1989).

Both reproduction and sexual conflicts among captive elasmobranchs can be controlled through a judicious approach to husbandry. The easiest method of eliminating reproduction is by maintaining a single sex within a collection. Reproduction occurs throughout the year in both southern stingrays and cownose rays at the National Aquarium in Baltimore, Baltimore, Maryland, USA, where both sexes are maintained continuously within the same aquarium system (Henningsen, 2000). At Sea World, Orlando, Florida, USA, male elasmobranchs are kept separated from females until reproductive activity is desired (Davis, pers. com.).

Other important physiological processes that can have negative or positive impacts on reproduction include stress, thyroid status, and metabolism (Henningsen, 1999). Although not yet investigated in elasmobranchs, future studies may show that gonadotropin releasing hormone (GnRH) agonists and antagonists are useful for controlling reproduction, as they are in some other vertebrates (e.g., Atkinson et al., 1998, Felberbaum et al., 2000).

MANAGEMENT OF A CAPTIVE BREEDING PROGRAM

The implementation of a captive breeding program requires proper management. Once the target species is selected, all necessary details need to be worked out, including initial and on-going requirements for the species and its offspring. Suggested requirements vary from those that must be met before the program can begin, to those that are more of a program management type. Even in its simplest form, several steps are involved in a well-designed captive breeding program and these have been summarized in Table 17.2.

RECOMMENDATIONS

There are many species of chondrichthyans maintained in aquaria that are not included in the 100 species listed in Table 17.1. Of the species not bred in captivity, several populations of wild conspecifics have declined severely, locally as well as globally. Vulnerable and depleted species, especially those that are frequently in demand for display in aquaria (e.g., pristids, sand tiger sharks, sandbar sharks, etc.), should be the target of research and captive breeding programs.

The smalltooth sawfish (*Pristis pectinata*), for example, is listed as critically endangered in the western North Atlantic and has been extirpated from much of its range (Simpfendorfer, 2000). Due to a paucity of biological information on the smalltooth sawfish, Simpfendorfer's (2000) demographic analysis used information from the largetooth sawfish (*Pristis perotteti*) to estimate population recovery rates for both species. It is

Table 17.2

Steps involved in a well-designed captive breeding program for elasmobranchs, showing those steps that should be considered before and during the program, and those steps that should be considered on a continuous basis.

Tasks	Before	During	Continued
1. Select species.	?		
2. Gather information from other institutions and the literature.	?	?	?
3. Determine environmental requirements.	?	?	
4. Determine spatial requirements.	?		
5. Determine social structure.	?	?	
6. Determine methods (i.e., natural, hormonally induced, etc.).	?	?	?
7. Develop alternative methods.	?	?	?
8. Plan for surplus, broodstock, and progeny.	?		?
9. Ensure adequate holding space for all life stages.	?	?	?
10. Develop plan to inhibit reproduction if desired.	?		?
11. Maintain complete and accurate records.	?	?	?
12. Disseminate information: publish in peer-reviewed outlets.		?	?

only recently, during the revision of this chapter, that promising news of reproductive behavior has been recorded for captive smalltooth sawfish. Pre-copulatory behavior was observed in a captive population of smalltooth sawfish (one male and four females) at the Atlantis Paradise Resort and Casino, New Providence Island, Bahamas. The male sawfish showed great interest in some of the females, notably in the late summer to fall, although attempted or successful copulation was not observed (Kelley, pers. com.). During March of 2003, one of the female sawfish gave birth to, or aborted, young. Unfortunately, the remains of only two pups/fetuses were found, the others probably preyed on by sharks (Liu, pers. com.). This event was quite significant because it was the first known case of captive reproduction in smalltooth sawfish or any other pristid.

A cooperative effort between institutions may aid greatly in breeding species such as the smalltooth sawfish, sand tiger sharks, sandbar sharks, etc. The principal objective of such programs would be to reduce the number of animals taken from the wild, not necessarily to restock wild populations. Although the latter is certainly possible, it is beyond the scope of this chapter to consider all of the benefits and risks associated with introducing captive-born animals into wild populations.

With few exceptions, mating systems of elasmobranchs are not well known and specimens in aquaria represent a valuable source of information for many species. However, the effects of captivity must be taken into consideration when interpreting results and drawing conclusions about wild conspecifics. We urge the collection and publication of detailed observations relating to reproduction and reproductive behaviors, particularly for those species or behaviors not described in the literature.

ACKNOWLEDGEMENTS

The authors thank their respective institutions. In particular, the senior author expresses his thanks for support to the Biological Programs Department of the National Aquarium in Baltimore. Appreciation is extended to Wes Pratt for graciously providing extremely helpful comments on an earlier draft.

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