

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

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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 witnessed in the wild and difficult to infer from freshly caught wild specimens. Reproductive behavior often results in conspecific and interspecific conflicts. Conspecific sexual conflict may be consensual as well as intersexual. Although specific reproductive behaviors have

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 aquariums, 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 the following: 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 aquariums. 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 to 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 behavioral 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 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

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

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 aquariums, 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 - yolk sac; VA2 = Viviparous - aplacental - with uterine villi or trophomemata; 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
<i>Haplolepharus pictus</i>	dark shy shark	O	
<i>Hemiscyllium hallstromi</i>	Papuan epaulette shark	O	
<i>Hemiscyllium ocellatum</i>	epaulette shark	O	West and Carter, 1990; Schmid and Murru, 1991
<i>Heterodontus francisci</i>	horn shark	O	Dempster and Herald, 1961
<i>Heterodontus galeatus</i>	crested bullhead shark	O	Last and Stevens, 1994
<i>Heterodontus japonicus</i>	Japanese bullhead shark	O	Uchida et al., 1989; Hagiwara, 1990
<i>Heterodontus mexicanus</i>	Mexican horn shark	O	
<i>Heterodontus portusjacksoni</i>	Port Jackson shark	O	
<i>Heteroscyllium colcloughi</i>	blue-gray carpet shark	O	Horton, pers. com.
<i>Hydrolagus collieri</i>	spotted ratfish	O	Sathyanesan, 1966; Van Dykhuizen et al., 1997
<i>Leucoraja erinacea</i>	little skate	O	
<i>Leucoraja ocellata</i>	winter skate	O	
<i>Mustelus californicus</i>	gray smooth-hound	VP	
<i>Mustelus canis</i>	dusky smooth-hound	VP	
<i>Mustelus manazo</i>	star-spotted smooth-hound	VA1	
<i>Mustelus norrisi</i>	Florida smooth-hound	VP	
<i>Myliobatis californicus</i>	bat eagle ray	VA2	
<i>Negaprion brevirostris</i>	lemon shark	VP	
<i>Okamejei kenojei</i>	spiny rasp skate	O	
<i>Orectolobus japonicus</i>	Japanese wobbegong	VA1	Whitley, 1940 in Demski, 1990b; Hagiwara, 1990; Uchida et al., 1997)
<i>Orectolobus maculatus</i>	spotted wobbegong	VA1	Whitley, 1940 in Demski, 1990b
<i>Orectolobus ornatus</i>	ornate wobbegong	VA1	
<i>Parmaturus xanthurus</i>	filetail cat shark	O	
<i>Poroderma africanum</i>	striped cat shark	O	
<i>Poroderma pantherinum</i>	leopard cat shark	O	
<i>Potamotrygon histrix</i>	porcupine river stingray	VA2	
<i>Potamotrygon magdalenae</i>	Magdalena river stingray	VA2	
<i>Potamotrygon motoro</i>	ocellate river stingray	VA2	Thorson et al., 1983
<i>Potamotrygon ocellata</i>	red-blotched river stingray	VA2	
<i>Potamotrygon orbignyi</i>	smooth back river stingray	VA2	
<i>Potamotrygon schroederi</i>	rosette river stingray	VA2	
<i>Pristis pectinata</i>	smalltooth sawfish	VA1	Liu, pers. com.
<i>Pteroplatytrygon violacea</i>	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 aquariums, 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 - yolk sac; 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
<i>Raja binoculata</i>	big skate	O	
<i>Raja clavata</i>	thornback ray	O	
<i>Raja eglanteria</i>	clearnose skate	O	Luer and Gilbert, 1985
<i>Raja microocellata</i>	small-eyed skate	O	
<i>Raja montagui</i>	spotted skate	O	
<i>Raja rhina</i>	longnose skate	O	
<i>Raja texana</i>	roundel skate	O	
<i>Raja undulata</i>	undulate ray	O	
<i>Rhina ancylostoma</i>	bowmouth guitarfish	VA1	Uchida et al., 1990
<i>Rhinobatos hymniciphalus</i>	ringstraked guitarfish	VA1	
<i>Rhinobatos lentiginosus</i>	Atlantic guitarfish	VA1	
<i>Rhinobatos productus</i>	shovelnose guitarfish	VA1	
<i>Rhinoptera bonasus</i>	cornnose ray	VA2	Davis, pers. com.; Henningsen, personal observation
<i>Rhinoptera javanica</i>	Javanese cornnose ray	VA2	Uchida, 1982; Uchida et al., 1990; Uchida et al., 1997
<i>Rhynchobatus djiddensis</i>	giant guitarfish	VA1	Bok, pers. com.
<i>Scyliorhinus canicula</i>	smallspotted cat shark	O	Bolau, 1881; Schensky, 1941, in Pratt and Carrier, 2001)
<i>Scyliorhinus retifer</i>	chain dogfish	O	Castro et al., 1988
<i>Scyliorhinus stellaris</i>	nursehound	O	
<i>Scyliorhinus tokubee</i>	Izu cat shark	O	
<i>Scyliorhinus torazame</i>	cloudy cat shark	O	
<i>Sphyrna tiburo</i>	bonnethead shark	VP	Uchida, 1982, Hagiwara, 1990
<i>Squalus acanthias</i>	spiny dogfish	VA1	
<i>Squatina japonica</i>	Japanese angel shark	VA1	
<i>Stegostoma fasciatum</i>	zebra shark	O	Uchida et al., 1990; Uchida et al., 1997
<i>Taeniura lymma</i>	bluespotted ribbontail stingray	VA2	Riggles, pers. com.
<i>Taeniura meyeni</i>	blotched fantail ray	VA2	Gamer and Mackness, 1998b
<i>Torpedo marmorata</i>	marbled electric ray	VA2	
<i>Triacnodon obesus</i>	whitetip reef shark	VP	Uchida, 1982; Garner and Mackness, 1998a
<i>Triakis scyllium</i>	banded houndshark	VA1	Ankley, pers. com.
<i>Triakis semifasciata</i>	leopard shark	VA1	
<i>Trygonorrhina</i> sp. A (undescribed)	eastern fiddler ray	VA1	
<i>Urobatis halleri</i>	round stingray	VA2	
<i>Urobatis jamaicensis</i>	yellow stingray	VA2	
<i>Urolophus aurantiacus</i>	sepia stingray	VA2	Hagiwara, 1990; Uchida et al., 1990

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 Javanese cownose 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*), whitespotted 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 to Chapter 16 of this manual) appears to be the case at least in females (Cliff, 1989; Branstetter and Musick, 1994; Castro et al., 1999; Goldman, 2002). Reproductive behaviors for sand tigers in aquariums 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, when 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. [Author's note (September, 2004): Revised estimates of age and growth in sand tiger sharks in the Northwest Atlantic indicate that it grows more slowly than previously thought and that annual bands, verified by validation, are laid down in the vertebral centra (Goldman, 2002). Consequently, ages at maturity are considered to be 6-7 years and 9-10 years for males and females, respectively, in this population, rather than four years for males and five years for females (Branstetter and Musick, 1994; Goldman, 2002). This result may be indicative of the species or yet another example of differences between populations. A further observation in this species in the southwestern Atlantic by Lucifora et al. (2002) was that males appeared lighter in color coincident with the mating period, an observation made in captive males (Gordon, 1993; Henningsen, in prep.)]

Nurse shark

A mating group of nurse sharks has been the subject of an ongoing 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 aquariums 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 m³ 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 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 aquariums. 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.

Whitespotted bamboo shark

The whitespotted 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 aquariums. 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 whitespotted 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 whitespotted 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 whitespotted 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 horn and nurse sharks (Castro, 2000; Michael, 2001).

Female whitespotted 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 whitespotted 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 (Henningesen, 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 (Henningesen, 2002). Multiple males have been observed to mate with a single female, as is the case for the Javanese cownose 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. [Author's note (September, 2004): The mating behavior of southern stingrays in the wild was reported by Chapman et al. (2003) to be similar to that described in the manta ray, *Manta birostris* (Yano et al. 1999) and consisted of a sequence five distinct steps. As described here, multiple males mating with a single female, and copulation occurring within minutes to hours following parturition, was observed. Observations on captive animals may therefore reflect behavior in the wild.]

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 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 SeaWorld 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 aquariums that are not included in the 100 species listed in Table 17.1. Of the species not bred in captivity, several populations of wild

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.	●	●	

conspecifics have declined severely, locally as well as globally. Vulnerable and depleted species, especially those that are frequently in demand for display in aquariums (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 large-tooth sawfish (*Pristis perotteti*) to estimate population recovery rates for both species. It is 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-Ferguson, 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 aquariums 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.

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REFERENCES

- Atkinson, S., T. J. Ragen, W. G. Gilmartin, B. L. Becker, and T. C. Johanos. 1998. Use of a GnRH agonist to suppress testosterone in wild male Hawaiian monk seals (*Monachus schauinslandi*). *General and Comparative Endocrinology* 112: 178-182.
- Bigelow, H. B. and W. C. Schroeder. 1953. Fishes of the western North Atlantic. No. 1, Part 2. Sawfishes, Guitarfishes, Skates, Rays, and Chimaeroids. Sears Foundation for Marine Research, Yale University, New Haven, Connecticut, USA. 588 p.
- Birkhead, T. R. and G. A. Parker. 1997. Sperm competition and mating systems. *In: Behavioural Ecology: An Evolutionary Approach*, 4th edition, p. 121-145. J. R. Krebs and N. B. Davies (eds.). Blackwell Science, Ltd., London, England.
- Branstetter, S. and J. A. Musick. 1994. Age and growth estimates for the sand tiger in the northwestern Atlantic Ocean. *Transactions of the American Fisheries Society* 123: 242-254.
- Bres, M. 1993. The behavior of sharks. *Reviews in Fish Biology and Fisheries* 3: 133-159.
- Carrier, J. C., H. L. Pratt, Jr., and L. K. Martin. 1994. Group reproductive behavior in free-living nurse sharks, *Ginglymostoma cirratum*. *Copeia* 1994: 646-656.
- Castro, J. I., P. M. Bubucis, and N. A. Overstrom. 1988. The reproductive biology of the chain dogfish, *Scyliorhinus retifer*. *Copeia* 3: 740-746.
- Castro, J. I., C. M. Woodley, and R. L. Brudek. 1999. A preliminary evaluation of the status of shark species. *FAO Fisheries Technical Paper* 380. Food and Agriculture Organization of the United Nations, Rome, Italy. 72 p.
- Castro, J. I. 2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. *Environmental Biology of Fishes* 58: 1-22.
- Chapman, D. D., M. J. Corcoran, G. M. Harvey, S. Malan, and M. Shivji. 2003. Mating behavior of southern stingrays, *Dasyatis americana* (Dasyatidae). *Environmental Biology of Fishes* 68: 241-245.
- Clark, E. 1963. The maintenance of sharks in captivity, with a report on their instrumental conditioning. *In: Sharks and Survival*, p. 115-149. P. W. Gilbert (ed.). D. C. Heath and Co., Boston, Massachusetts, USA.
- Cliff, G. 1989. Breeding migration of the sand tiger shark, *Carcharias taurus*, in southern African waters. 68th Annual Meeting of the American Society of Ichthyologists and Herpetologists, 5th Annual Meeting of the American Elasmobranch Society, San Francisco State University, San Francisco, CA, USA, 57-23 June, 1989, Abstract, p. 76.
- Compagno, L. J. V. 1984. Sharks of the World. *FAO Species catalogue*, *FAO Fisheries Synopsis* 125, Vol. 4, Part 1. Food and Agriculture Organization of the United Nations, Rome, Italy. 655 p.

- Compagno, L. J. V. 2001. Sharks of the World. FAO Species Catalogue for Fishery Purposes, No. 1, Vol. 2. Food and Agriculture Organization of the United Nations, Rome, Italy. 269 p.
- Davies, N. B. 1992. Dunnock behavior and social evolution. Oxford University Press, Oxford, England.
- Dempster, R. P. and E. S. Herald. 1961. Notes on the hornshark, *Heterodontus francisci*, with observations of mating activities. Occasional Papers of the California Academy of Sciences 33: 17.
- Demski, L. S. 1990a. Neuroendocrine mechanism controlling sexual development and behavior of sharks and rays. Journal of Aquaculture and Aquatic Sciences 5: 53-67.
- Demski, L. S. 1990b. Elasmobranch reproductive biology: implications for captive breeding. Journal of Aquaculture and Aquatic Sciences 5: 84-95.
- Dral, A. J. 1980. Reproduction en aquarium du requin du fond tropical, *Chiloscyllium griseum* Müll. et Henle (Orectolobidés). Reviews in French Aquariology 7: 99-104.
- Felberbaum, R. E., M. Ludwig, and K. Diedrich. 2000. Clinical applications of GnRH-antagonists. Molecular and Cellular Endocrinology 166: 9-14.
- Garner, R. 1997. Shark breeding success. Australasian Regional Association of Zoological Parks and Aquaria Newsletter 35: 11.
- Garner, R. 1998. Preliminary report regarding captive breeding observations of the brown-banded bamboo shark, *Chiloscyllium punctatum* Muller and Henle, 1838. Thylacinus 22(1): 31-32.
- Garner, R. and B. Mackness. 1998a. Captive breeding of the whitetip reef shark, *Triaenodon obesus*. Thylacinus 22(2): 16-17.
- Garner, R. and B. Mackness 1998b. First captive breeding of the blotched fantail ray *Taeniura meyeni* (Müller and Henle, 1841) in Australia. Thylacinus 22(2): 22-24.
- Gilmore, R. G., J. W. Dodrill, and P. A. Linley. 1983. Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque). Fishery Bulletin 81(2): 201-225.
- Gilmore, R. G. 1993. Reproductive biology of lamnoid sharks. Environmental Biology of Fishes 38: 95-114.
- Goldman, K. J. 2002. Aspects of age, growth, demographics and thermal biology of two lamniform shark species. Ph.D. dissertation. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. 220 p.
- Gordon, I. 1993. Pre-copulatory behavior of captive sand tiger sharks, *Carcharias taurus*. Environmental Biology of Fishes 38: 159-164.
- Hagiwara, S. 1990. Reproduction of chondrichthyans in captivity at Shimoda Floating Aquarium. Journal of Aquaculture and Aquatic Sciences 5(4): 119 (abstract).
- Hamlett, W. C. and T. J. Koob. 1999. Female reproductive system. In: Sharks, Skates, and Rays, p. 398-443. W. C. Hamlett (ed.). Johns Hopkins Press, Baltimore, Maryland, USA.
- Henningsen, A. D. 1999. Levels of recirculating reproductively-related steroid hormones in female elasmobranchs. Implications for reproduction in a captive environment. Aquarium Sciences and Conservation 2: 97-116.
- Henningsen, A. D. 2000. Notes on reproduction in the southern stingray, *Dasyatis americana* (Chondrichthyes: Dasyatidae) in a captive environment. Copeia 2000(3): 826-828.
- Henningsen, A. D. 2002. Age and growth in captive southern stingrays, *Dasyatis americana*. 18th Annual Meeting of the American Elasmobranch Society, 82nd Annual Meeting of the American Society of Ichthyologists and Herpetologists. University of Kansas, Westin Crown Center Hotel, Kansas City, MO, USA, July 3-8, 2002, Abstract, p. 167.
- Heupel, M. R., J. M. Whittier, and M. B. Bennett. 1999. Plasma steroid hormone profiles and reproductive biology of the epaulette shark, *Hemiscyllium ocellatum*. Journal of Experimental Zoology 284: 586-594.
- Johnson, R. H. and D. R. Nelson. 1978. Copulation and possible olfaction-mediated pair formation in two species of carcharhinid sharks. Copeia 1978: 539-542.
- Kajiura, S. M. and T. C. Tricas. 1996. Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray, *Dasyatis sabina*. Journal of Experimental Biology 199: 2297-2306.
- Kajiura, S. M., A. P. Sebastian, and T. C. Tricas. 2000. Dermal bite wounds as indicators of reproductive seasonality and behavior in the Atlantic stingray, *Dasyatis sabina*. Environmental Biology of Fishes 58: 23-31.
- Klimley, A. P. 1980. Observations of courtship and copulation in the nurse shark, *Ginglymostoma cirratum*. Copeia 1980: 878-882.
- Kuennen, M. 2000. A log of captive births by an Atlantic nurse shark, "Sarah". Drum and Croaker 31: 22-24.
- Last, P. R. and J. D. Stevens. 1994. Sharks and Rays of Australia. CSIRO Press, Collingwood, Victoria, Australia. 513 p.
- Lucifora, L. O., R. C. Menni, and A. H. Escalante. 2002. Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. ICES Journal of Marine Science 59: 553-561.
- Luer, C. A. and P. W. Gilbert. 1985. Mating behavior, egg deposition, incubation period and hatching in the clearnose skate, *Raja eglanteria*. Environmental Biology of Fishes 13: 161-171.
- Luer, C. A. 1989. Elasmobranchs (sharks, skates, and rays) as animal models for biomedical Research. In: Nonmammalian Animal Models for Biomedical Research, p. 121-147. A. D. Woodhead and K. Vivrito (eds.). CRC Press, Boca Raton, Florida, USA.
- McCourt, R. M. and A. N. Kerstitch. 1980. Mating behavior and sexual dimorphism in dentition in the stingray, *Urolophus concentricus* from the Gulf of California. Copeia 1980: 900-901.
- Michael, S. W. 1993. Reef Sharks and Rays of the World. Sea Challengers, Monterey, California, USA. 107 p.
- Michael, S. W. 2001. Aquarium Sharks and Rays. Tropical Fish Hobbyist Publications, Neptune City, New Jersey, USA. 254 p.
- Mollet, H. F., J. M. Ezcurra, and J. B. O'Sullivan. 2002. Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832). Marine and Freshwater Research 53: 531-541.
- New, J. G. 1994. Electric organ discharge and electrosensory reafference in skates. Biological Bulletin 187: 64-75.
- Parker, G. A. 1979. Sexual selection and sexual conflict. In: Sexual Selection and Reproductive Competition in Insects, p. 123-166. M. S. Blum and N. A. Blum (eds.). Academic Press, New York, USA.
- Parker, P. and D. J. Bucher. 2000. Seasonal variation in abundance and sex ratio of grey nurse (sand tiger) sharks, *Carcharias taurus*, in northern New South Wales, Australia: A survey based on observations of recreational scuba divers. Pacific Conservation Biology 5 (4): 336-346.
- Pepperell, J. G. 1992. Trends in the distribution, species composition and size of sharks caught by gamefish anglers off South-eastern Australia, 1961-1990. Australian Journal of Marine and Freshwater Research 43: 213-225.
- Pollard, D. A., M. P. Lincoln Smith, and A. K. Smith. 1996. The biology and conservation status of the grey nurse shark (*Carcharias taurus* Rafinesque 1810) in New South Wales, Australia. Aquatic Conservation: Marine and Freshwater Ecosystems 6: 1-20.
- Pratt, H. L., Jr. 1979. Reproduction in the blue shark, *Prionace glauca*. Fishery Bulletin 77: 445-470.
- Pratt, H. L., Jr. and J. C. Carrier. 2001. A review of elasmobranch reproductive behavior with a case study of the nurse shark, *Ginglymostoma cirratum*. Environmental Biology of Fishes 60: 157-188.

- Reid, D. D. and M. Krogh. 1992. Assessment of catches from protective shark meshing off New South Wales beaches between 1950 and 1990. *Australian Journal of Marine and Freshwater Research* 43: 283-296.
- Reynolds, J. D. 1996. Animal breeding systems. *Trends in Ecological Evolution* 11: 68-72.
- Sathyanesan, A. G. 1966. Egg-laying of the chimaeroid fish *Hydrolagus colliciei*. *Copeia* 1966: 132-134.
- Schmid, T. H., L. M. Ehrhart, and F. F. Snelson, Jr. 1988. Notes on the occurrence of rays (Elasmobranchii, Batoidea) in the Indian River Lagoon system, Florida. *Florida Scientist* 51: 121-128.
- Schmid, T. H. and F. L. Murru. 1991. Observations on the reproductive biology of bamboo sharks (Hemiscylliidae) maintained in captivity. 71st Annual Meeting of the American Society of Ichthyologists and Herpetologists, 7th Annual Meeting of the American Elasmobranch Society. American Museum of Natural History, New York, USA, June 15-20, 1991, Abstract, p. 33
- Simpfendorfer, C. A. 2000. Predicting population recovery rates for endangered western Atlantic sawfishes using demographic analysis. *Environmental Biology of Fishes* 58: 371-377.
- Sisneros, J. A., T. C. Tricas, and C. A. Luer. 1998. Response properties and biological function of the skate electrosensory system during ontogeny. *Journal of Comparative Physiology A*, 183: 87-99.
- Sisneros, J. A. and T. C. Tricas. 2002. Ontogenetic changes in the response properties of the peripheral electrosensory system in the Atlantic stingray (*Dasyatis sabina*). *Brain, Behavior and Evolution* 59: 130-140.
- Sorensen, P. W., A. R. Brash, F. W. Goetz, R. G. Kellner, L. Bowdin, and L. A. Vrieze. 1995. Origins and functions of F prostaglandins as hormones and pheromones in the goldfish. *In: Proceedings of the Fifth International Symposium on the Reproductive Physiology of Fish*, p. 252-254. F. W. Goetz and P. Thomas (eds.). The University of Texas, Austin, USA.
- Sorensen, P. W., A. P. Scott, and R. L. Kihlsinger. 2000. How common hormonal metabolites function as relatively specific pheromonal signals in the goldfish. *In: Proceedings of the Sixth International Symposium on the Reproductive Physiology of Fish*, p. 125-128. B. Norberg, O. S. Kjesbu, G. L. Taranger, E. Anderson, and S. O. Stefansson (eds.). University of Bergen, Bergen, Norway.
- Springer, S. 1967. Social organization of shark populations. *In: Sharks, Skates, and Rays*, p. 149-174. P. W. Gilbert, R. F. Mathewson, and D. P. Rall (eds.). Johns Hopkins Press, Baltimore, Maryland, USA.
- Thorson, T. B., J. K. Langhammer, and M. I. Oetinger. 1983. Reproduction and development of the South American freshwater stingrays, *Potamotrygon circularis* and *P. motoro*. *Environmental Biology of Fishes* 9(1): 3-24.
- Tricas, T. C., S. W. Michael, and J. A. Sisneros. 1995. Electro-sensory optimization to conspecific phasic signals for mating. *Neuroscience Letters* 202: 129-131.
- Tullis, A., G. M. Peterson, and C. Hull. 1997. Developmental changes in the metabolism and morphology of embryonic white spotted bamboo sharks, *Chiloscyllium plagiosum*. 77th Annual Meeting of the American Society of Ichthyologists and Herpetologists, 13th Annual Meeting of the American Elasmobranch Society. University of Washington, Seattle, USA, June 26-July 2, 1997, Abstract, p. 295
- Uchida, S. 1982. Elasmobranch fishes around Ryukyu Island and their cultural status in the big water tank of aquarium. Report of Japanese Group for Elasmobranch Studies, Ocean Research Institute, University of Tokyo, 14: 1-8.
- Uchida, S., M. Toda, and Y. Kamei. 1990. Reproduction of elasmobranchs in captivity. *In: Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and Status of the Fisheries*, p. 211-237., H. L. Pratt, Jr., S. H. Gruber, and T. Taniuchi (eds.). U. S. Department of Commerce, NOAA Technical Report NMFS 90.
- Uchida, S., M. Toda, N. Tanaka, and Y. Kamei. 1997. Reproduction of elasmobranchs in captivity (II). *In: Proceedings of the Fourth International Aquarium Congress*, June 23-27, 1996, Tokyo. p. 99-107. Tokyo, Japan, by the Congress Central Office of IAC '96, Tokyo Sea Life Park.
- Van Dykhuizen, G., K. Light, D. Wrobel, and D. Powell. 1997. Ratfish romance at the Monterey Bay Aquarium. 77th Annual Meeting of the American Society of Ichthyologists and Herpetologists, 13th Annual Meeting of the American Elasmobranch Society. University of Washington, Seattle, USA, June 26-July 2, 1997, Abstract, p. 298
- Voss, J., L. Berti, and C. Michel. 2001. *Chiloscyllium plagiosum* (Anon., 1830) born in captivity: Hypothesis for gynogenesis. *Bulletin of the Institute of Oceanography, Monaco* 20(1): 351-353.
- West, J. G. and S. Carter. 1990. Observations on the development and growth of the epaulette shark *Hemiscyllium ocellatum* (Bonnaterre) in captivity. *Journal of Aquaculture and Aquatic Sciences* 5(4): 11-117.
- Whitley, G. P. 1940. The fishes of Australia. Part 1. The sharks, rays and devilfish, and other primitive fishes of Australia and New Zealand. Royal Zoological Society of New South Wales, Mosman. 280 p.
- Yano, K., F. Sato, and T. Takahashi. 1999. Observations of the mating behavior of the manta ray, *Manta birostris*, at the Ogasawara Islands, Japan. *Japanese Ichthyological Research* 46: 289-296.

PERSONAL COMMUNICATIONS

- Ankley, M. 2000. Long Beach Aquarium of the Pacific, Long Beach, CA 90802, USA.
- Areitio, P. 2000. L'Oceanographic, Inc., Grupo Parques Reunidos, s/n. 46013, Valencia, Spain.
- Bok, A. 2000. Sea World Aquarium, Durban, South Africa.
- Choromanski, J. 1998. Ripley Aquariums, Inc., Orlando, FL 32819, USA.
- Davis, R. 2002. SeaWorld Florida, Orlando, FL 32821, USA.
- Engelbrecht, M. P. O. 2000. Dillon Beach, CA 94929, USA.
- Fischer, A. 2000. Underwater World, Mooloolaba, Queensland, 4557, Australia.
- Horton, M. 2000. Sea World Australia, Queensland 4217, Australia.
- Kaiser, S. 2000. Atlantis Paradise Island Resort and Casino, New Providence Island, Bahamas.
- Kelley, G. 2000. Atlantis Paradise Island Resort and Casino, New Providence Island, Bahamas.
- Liu-Ferguson, M. 2000. Atlantis Paradise Island Resort and Casino, New Providence Island, Bahamas.
- Martel-Bourbon, H. 2000. New England Aquarium. Central Wharf. Boston, MA 02110, USA.
- Pratt, H. L., Jr. 2000. Apex Predators Investigation. Narragansett Laboratory. Narragansett, RI 02882, USA.
- Rasmussen, L. E. L. 2000. Department of Biochemistry and Molecular Biology. Oregon Graduate Institute. Beaverton, OR 97006, USA.
- Riggles, G. 2000. Indianapolis Zoo, Indianapolis, IN 46222, USA.
- Zoller, C. 2000. Moody Gardens. One Hope Boulevard, Galveston, TX 77554, USA.