

Mating in the reef white-tip shark *Triaenodon obesus*

T. C. Tricas¹ and E. M. Le Feuvre²

¹ Department of Zoology, University of Hawaii at Manoa; Honolulu, Hawaii 96822, USA

² 2240 Cambridge; Cardiff, California 92007, USA

Abstract

Mating reef white-tip sharks, *Triaenodon obesus*, were observed and photographed in shallow waters of the Hawaiian Islands. The sharks copulated in a stationary parallel orientation with their heads on the bottom and bodies angled upwards approximately 45° into the water column. Pair contact during copulation was maintained by the male's left clasper anchored in the female's vent and by his tight oral grasp of the female's left pectoral fin. Results show that reposed sedentary modes of copulation are not limited to small species. In a reproductive context, biting behavior by male sharks functions as a premating releaser for female cooperation and for pair-contact maintenance during copulation.

Introduction

Although internal fertilization is relatively uncommon among fishes, it is the sole mode of reproduction for all extant elasmobranchs. In sharks and batoids, copulation occurs by means of specialized male intromittent organs known as claspers. Because most species are wide ranging and difficult to observe, field documentation of their mating behavior is extremely rare, generally fortuitous, and particularly inconclusive. In most cases, published studies consist of verbal descriptions and drawings of courtship, pair formation, copulation (e.g. Bolau, 1881; Gudger, 1912; Matthews, 1950; Clark, 1963, 1975; Price, 1967; Johnson and Nelson, 1978; Klimley, 1980; McCourt and Kerstitch, 1980; Tricas, 1980), or mating scars (Springer, 1960, 1967; Stevens, 1974).

The most complete and detailed accounts of shark copulation exist for species held in aquaria (Dempster and Herald, 1961; Taylor, 1971; Uchida, 1982). Prior photographic documentation exists only for two small captive species, the cat shark *Scyliorhinus canicula* [Schensky,

1914 (same photo also published in Kyle, 1926); Hardy, 1959], and the horn shark *Heterodontus francisci* (Taylor, 1971), and none have been previously published for larger species or individuals mating in the wild.

The reef white-tip shark *Triaenodon obesus* is widely distributed on shallow tropical and subtropical reefs of the Indo-Pacific. Although *T. obesus* is sometimes diurnally active, it is considered a nocturnal predator that forages over the reef for small fish, octopods, and large crustaceans. More detailed studies exist on its general biology (Randall, 1977; Nelson and Johnson, 1980) and feeding behavior (Hobson, 1963). Taxonomists presently include *T. obesus* in the family Carcharhinidae (Compagno, 1973; Compagno and Garrick, 1983).

This paper describes mating in *Triaenodon obesus* and presents the first published photographic documentation of shark copulation in the field. Herein, we amend previous hypotheses on the behavior and functional morphology of sharks during courtship and copulation.

Materials and methods

Two copulating *Triaenodon obesus* (approximately 1.75 m total length, TL) were observed and photographed by one of us (E.M.L.) while diving in waters 7 m deep at Molokini, on 12 June 1982 at 11.46 hrs. Molokini is a small island approximately 4 km off the southwest shore of Maui, Hawaii, with a shallow sheltered reef that consists of living hard coral with scattered basalt boulders and sand patches. The fish community is similar to other inshore areas of Hawaii (see Hobson, 1974), except for a concentrated and apparently resident population of approximately 10 reef white-tip sharks. Scars and pigment-spots made it possible to recognize individuals at Molokini over the last three years.

The sharks were photographed using a Nikonos III camera, 15 mm lens, underwater strobe, and Kodachrome 64 color film. Divers were in contact with the sharks for

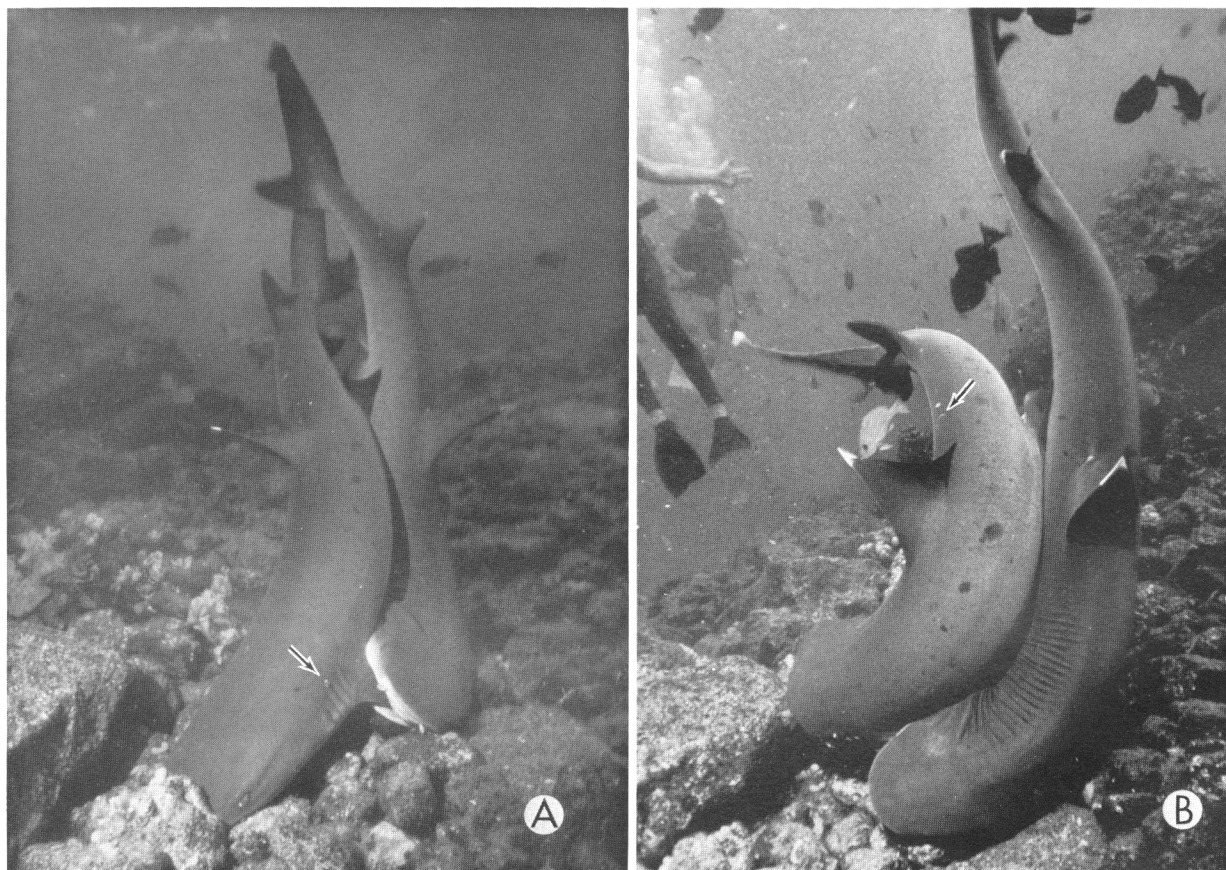


Fig. 1. *Triaenodon obesus*. A pair of copulating reef white-tip sharks approximately 1.75 m TL at Molokini Island, Hawaii on 12 June 1982. (A) Sharks parallel with heads on reef bottom and bodies angled upward; male (at right) with female's left pectoral fin in his mouth. (B) Rolling of female (at left) onto male and initiation of clockwise rotation of pair around female's snout that is lodged between some small boulders. Arrows indicate tooth cuts on female

approximately 2 min and a series of 8 photographs were taken within a 1 min period.

Results

The two *Triaenodon obesus* were initially observed in a parallel orientation, with heads on the bottom and bodies angled upwards into the water column at about 45° (Figs. 1 A and 2 B). The left clasper of the male was bent medially approximately 90° and inserted one-third into the female's cloaca (Fig. 2 B). The right clasper also was medially directed, but at a lesser angle of approximately 30°. It was not possible to determine whether the latter angle was due to active clasper flexion or to passive bending. The male also held the female's left pectoral fin entirely within his mouth. The pair remained in this immobile parallel orientation throughout the observation period. The lateral-inferior position of the male however, created an imbalance of the pair and a tendency to roll to their left (Fig. 1 B). The pair remained upright by subtle, often synchronized undulations of their bodies and tails. The only noticeable spatial displacement observed was a slow pivoting of the pair centered about the female's

snout. The siphon sacs of the male appeared as two ventral bilateral bulges that extended from his pelvic region anterior to the pectoral girdle (Fig. 2 B). The left sac was narrower in width than the right and appeared to be more laterally constricted. Neither shark appeared disturbed by the diver's presence or close approaches for photography.

The female had fresh tooth cuts on her back just posterior to the first dorsal fin, and one large crescent-shaped bite mark over her left gill slits (Fig. 1, arrows). The male had no visible fresh cuts.

Discussion and conclusions

In spite of the incomplete accounts of shark mating behavior, certain trends within and between species are apparent. For example, most studies show that sharks mate while reposed on the bottom, exhibit little intra-specific variability in mating posture, and use insertion of a single clasper by the male. In this report and from aquarium observations of Uchida (1982), reef white-tip sharks, *Triaenodon obesus*, orient parallel, with the male grasping the female by her pectoral fin. Relative individual positions may differ however, as Uchida illustrated a

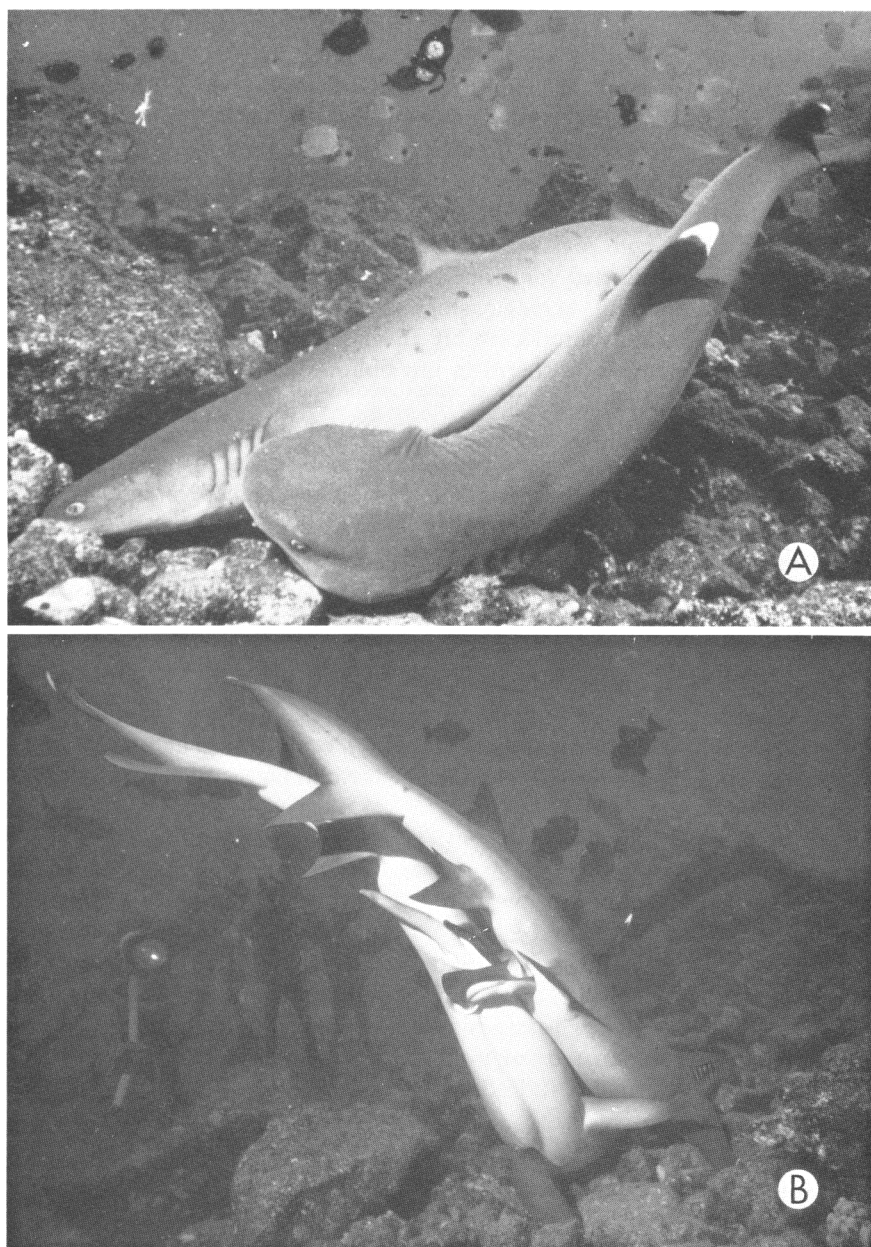


Fig. 2. *Triaenodon obesus* in copulation. (A) Sharks in stationary parallel orientation on bottom. (B) Ventral view showing intromission. Clasper of male (at left) is bent medially and inserted into cloaca of female. Siphon sacs of male distended. Photographs taken within approximately 30 s after Fig. 1

lateral position of the male above (rather than below) and on the right (rather than left) side of the female. In that account, the male used his right clasper which was medially directed and held the tip of the female's left pectoral fin in his mouth. A very similar posture was observed during mating in the small demersal horn shark *Heterodontus francisci* (Dempster and Herald, 1961; Taylor, 1971). In the cat shark *Scyliorhinus canicula*, the male encircled the female with his body around her pelvic region and showed no grasping of the female's pectoral fin during copulation (Bolau, 1881; Schensky, 1914; Hardy, 1959). However, in the related *S. torazame*, Uchida (1982) reported that the male bit the side of the female while encircling her body during intromission. During copulation in the nurse shark *Ginglymostoma cirratum*, the male rested on his back parallel to the female (Klimley, 1980).

The blackfin reef shark *Carcharhinus melanopterus* mated on the bottom in a non-swimming posture with single clasper insertion (Johnson and Nelson, 1978). Lemon sharks, *Negaprion brevirostris*, provided an exception for inshore species, where a pair swam in a parallel orientation while in (presumed) copulation. A pair was observed for one-half hour swimming in a shark pen "... side by side, heads slightly apart but the posterior half of their bodies in such close contact and the swimming movements so perfectly synchronized that they gave the appearance of a single individual with two heads, ..." (Clark, 1963). The female in that observation also had evidence of tooth marks on one side of her body and on top of her head. This latter species differs from most other inshore sharks for which mating has been observed by its larger size and more wide-ranging habits.

Our knowledge of mating in pelagic sharks is virtually non-existent. Commercial fishermen off Santa Catalina Island, California have seen large (5 m TL) white sharks, *Carcharodon carcharias*, swimming slowly at the surface side-by-side in very close contact at their posterior regions (Tricas, unpublished data). Stevens (1974) inferred mating behaviors for the pelagic blue shark *Prionace glauca* from the location and patterns of tooth cuts on females. He found little evidence of jaw impressions on the pectoral fins of females, and suggested that blue sharks may swim during intromission, similar to the lemon shark *N. brevirostris*, as described by Clark (1963). While the lack of substrates in pelagic habitats may account for swimming activity in some species during mating, it is possible that some pelagic sharks copulate in a non-swimming, vertically descending mode. This latter scenario may include oral grasping of the female by the male.

In feeding contexts, biting behavior by sharks can function either to immobilize or consume prey (Tricas and McCosker, 1984), while in social situations biting can also express aggression under various conditions (e.g. Limbaugh, 1963; Baldrige and Williams, 1969; Johnson and Nelson, 1973). In reproductive contexts, male biting behavior also serves multiple functions. Springer (1960) first suggested that biting by male sandbar sharks, *Carcharhinus plumbeus* (= *Eulamia milberti*), may serve as a premating releaser for females [depicted later by Ellis (1976, his Plate 16)]. He hypothesized "... the male persistently follows and occasionally bites the female on the back until she swims upside down (for clasper insertion by the male)". This precopulatory releasing function is supported by reports of biting behavior in the horn shark *Heterodontus francisci* (Dempster and Herald, 1961; Taylor, 1971), nurse sharks *Ginglymostoma cirratum* (Gudger, 1912; Klimley, 1980), *Carcharhinus* sp. (Clark, 1975), and other species during mating-related activities. Tooth-cut patterns on the bodies of female blue sharks, *Prionace glauca*, also support the premating releaser hypothesis, but not the fin-grasping function during copulation (Stevens, 1974). It is clear, however, that in large and medium-sized sharks such as *Triaenodon obesus*, pectoral biting by males functions to maintain parallel orientation of the individuals during copulation. Pectoral grasping (or biting) by the male would impede normal swimming for a copulating pair of sharks, and therefore might be restricted to non-swimming modes of copulation. It is probable that the tooth cuts on the dorsal ridge and gill region of the female in this study were inflicted by males (and perhaps the same copulating male) during prior courtship. This indicates that male biting behavior functions in reproduction as (1) a precopulatory releaser, and (2) a bond-maintenance mechanism during copulation.

The function of siphon sacs in sharks was suggested as pre-ejaculatory sperm-storage organs (Agassiz, 1871), clasper lubricant glands (Bolau, 1881), serotonin production sites to induce oviducal contractions after insemination and facilitate sperm transport (Mann, 1960), and storage reservoirs for sea water used to flush sperm out of the

clasper and into the female's reproductive tract (Leigh-Sharpe, 1920; Gilbert and Heath, 1972). While we are unable to comment conclusively on their function from our observations, it appeared that the sac on the same side (left) as the inserted clasper was being constricted, possibly to force fluid (probably sea water or other substances) into the left clasper and out into the female. Since both sacs were clearly distended but only one clasper was inserted (and one sac used), it seems unlikely that they would serve to store sperm prior to mating due to the apparent variability in clasper use. In fact, no evidence exists of sperm in the siphon sacs of sharks (Gilbert and Heath, 1972).

In conclusion, distinct differences exist in patterns of courtship and copulation among shark species. In spite of these general differences however, there are many similarities in the orientation, posture, and behavioral components of these patterns between taxonomic and ecologically dissimilar species. For the reef white-tip shark, male biting behavior during reproduction functions as both a precopulatory releaser for females and bond-maintenance during copulation. It is likely that the evolution of specific mating patterns are guided largely by morphology (size, shape, dentition, flexibility), ecology (e.g. habitat, presence of substrate), and the behavioral plasticity of each species.

Acknowledgements. The field observations and eight photographs were taken by the junior author. The manuscript was written by the senior author. We thank N. Harris and E. Reese for their help in bringing us together. L. Taylor, J. Randall, the Seattle Hui, and anonymous reviewers provided helpful comments on the manuscript. An English translation of Uchida's (1982) paper is available upon request from the senior author. This paper is dedicated to R. Radtke.

Literature cited

- Agassiz, L.: On the method of copulation among selachians. Proc. Boston Soc. nat. Hist. 14, 339–341 (1871)
- Baldrige, H. D. and J. Williams: Shark attack: feeding or fighting? Milit. Med. 134, 130–133 (1969)
- Bolau, H.: Über die Paarung und Fortpflanzung der *Scyllium*-Arten. Z. wiss. Zool. 35, 321–325 (1881)
- Clark, E.: Maintenance of sharks in captivity, with a report on their instrumental conditioning. In: Sharks and survival, pp 115–149. Ed. by P. W. Gilbert. Boston: D.C. Heath & Co. 1963
- Clark, E.: The strangest sea. Natn. geogr. Mag. 148, 338–343 (1975)
- Compagno, L. J. V.: *Gogolia filewoodi*, a new genus and species of shark from New Guinea (Carcharhiniformes: Triakidae), with a redefinition of the family Triakidae and a key to the triakid genera. Proc. Calif. Acad. Sci. 39, 383–410 (1973)
- Compagno, L. J. V. and J. A. F. Garrick: *Nasolamia*, new genus, for the shark *Carcharhinus velox* Gilbert, 1898 (Elasmobranchii: Carcharhinidae). Zoology Publs. Univ. Wellington 76, 1–16 (1983)
- Dempster, R. P. and E. S. Herald: Notes on the hornshark, *Heterodontus francisci*, with observations on mating activities. Occ. Pap. Calif. Acad. Sci. 33, 1–7 (1961)

- Ellis, R.: The book of sharks, 320 pp. New York: Grosset & Dunlap 1976
- Gilbert, P. W. and G. W. Heath: The clasper-siphon sac mechanism in *Squalus acanthias* and *Mustelus canis*. Comp. Biochem. Physiol. 42 A, 97–119 (1972)
- Gudger, E. W.: Summary of work done on the fishes of Tortugas. Yb. Carnegie Instn Wash. 11, 148–150 (1912)
- Hardy, A.: The open sea: its natural history. Part 2. Fish and fisheries, 322 pp. Boston: Houghton Mifflin Co. 1959
- Hobson, E. S.: Feeding behavior in three species of sharks. Pacif. Sci. 17, 171–194 (1963)
- Hobson, E. S.: Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish Bull. U.S. 72, 915–1031 (1974)
- Johnson, R. H. and D. R. Nelson: Agonistic display in the gray reef shark, *Carcharhinus menisorrhah*, and its relationship to attacks on man. Copeia 1973, 76–84 (1973)
- Johnson, R. H. and D. R. Nelson: Copulation and possible olfaction-mediated pair formation in two species of carcharhinid sharks. Copeia 1978, 539–542 (1978)
- Klimley, A. P.: Observations of courtship and copulation in the nurse shark, *Ginglymostoma cirratum*. Copeia 1980, 878–882 (1980)
- Kyle, H. M.: The biology of fishes, 396 pp. London: Clowes & Sons, Ltd. 1926
- Leigh-Sharpe, W. H.: The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoir I. J. Morph. 34, 245–265 (1920)
- Limbaugh, C.: Field notes on sharks. In: Sharks and survival, pp 63–94. Ed. by P. W. Gilbert. Boston: D.C. Heath & Co. 1963
- Mann, T.: Serotonin (5-hydroxytryptamine) in the male reproductive tract of the spiny dogfish. Nature, Lond. 188, 941–942 (1960)
- Matthews, L. H.: Reproduction in the basking shark, *Cetorhinus maximus* (Gunner). Phil. Trans. R. Soc. (Ser. B) 234, 247–316 (1950)
- McCourt, R. M. and A. N. Kerstitch: Mating behavior and sexual dimorphism in dentition in the stingray *Urolophus concentricus* from the Gulf of California. Copeia 1980, 900–901 (1980)
- Nelson, D. R. and R. H. Johnson: Behavior of the reef sharks of Rangiroa, French Polynesia. Res. Rep. natn. geogr. Soc., Wash. 12, 479–499 (1980)
- Price, K. S.: Copulatory behavior of the clearnose skate, *Raja eglanteria*, in Lower Chesapeake Bay. Copeia 1967, 854–855 (1967)
- Randall, J. E.: Contribution to the biology of the whitetip reef shark (*Triaenodon obesus*). Pacif. Sci. 31, 143–164 (1977)
- Schensky, F.: Tier- und Pflanzleben der Nordsee, Leipzig: Werner Klinkhardt 1914. (Cited by Matthews, 1950)
- Springer, S.: Natural history of the sandbar shark, *Eulamia milberti*. Fishery Bull. Fish Wildl. Serv. U.S. 61, 1–38 (1960)
- Springer, S.: Social organization of shark populations. In: Sharks, skates, and rays, pp 149–174. Ed. by P. W. Gilbert, R. F. Mathewson and D. P. Rall. Baltimore: John Hopkins Press 1967
- Stevens, J. D.: The occurrence and significance of tooth cuts on the blue shark (*Prionace glauca* L.) from British waters. J. mar. biol. Ass. U.K. 54, 373–378 (1974)
- Taylor, L. R.: Shark sex. Fishlife Mag. 2, 17–22 (1971)
- Tricas, T. C.: Courtship and mating-related behaviors in myliobatid rays. Copeia 1980, 553–556 (1980)
- Tricas, T. C. and J. E. McCosker: Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. Proc. Calif. Acad. Sci. 43 (14), 221–238 (1984)
- Uchida, S.: Elasmobranch fishes around Ryukyu Islands and their cultural status in the big water tank of aquarium. Rep. Jap. Grp Elasmobranch Stud., Ocean Res. Inst., Univ. Tokyo 14, 1–8 (1982)

Date of final manuscript acceptance: October 5, 1984.
Communicated by N. D. Holland, La Jolla