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Author: Hendon, Jill M.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 5(5) : 174-180

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2013.799618

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Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 5:174–180, 2013
© American Fisheries Society 2013
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2013.799618

SPECIAL SECTION: ELASMOBRANCH LIFE HISTORY

Occurrence of an Intersexual Blacktip Shark in the Northern Gulf of Mexico, with Notes on the Standardization of Classifications for This Condition in Elasmobranchs

Jill M. Hendon*
Gulf Coast Research Laboratory, Center for Fisheries Research and Development, University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, Mississippi 39564, USA

David M. Koester
Department of Biology, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005, USA

Eric R. Hoffmayer and William B. Driggers III
National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, 3209 Frederic Street, Pascagoula, Mississippi 39567, USA

Angela M. Cicia[1]
Department of Marine Biology, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005, USA

Abstract

An intersexual Blacktip Shark *Carcharhinus limbatus* with a testis, immature female reproductive tracts (embedded), and claspers was caught in the Gulf of Mexico. Histology of the single gonad revealed that all stages of spermatogenesis were occurring; however, the absence of ovaries and a male duct system suggests that neither sex would have been functional in this individual. Intersexuality has been reported in 17 families and 36 species of elasmobranchs. The degree to which the different sexes are present in a given individual is often difficult to categorize by normal hermaphroditic standards, as this is typically an anomalous presentation in elasmobranchs. Therefore, this report provides three categories for classification (basic, incomplete, and complete intersexuality) to standardize terminology and allow for more precise comparisons to be made among elasmobranch examples. Basic intersexuals have gonadal tissue of only one sex and a combination of other male and female characters with neither or only one sex being complete. Incomplete intersexuals have gonadal tissue of both sexes and a combination of other male and female characters; however, neither or only one sex is complete. Complete intersexuals have claspers as well as gonadal tissue and tracts for both sexes. The majority of the reported intersexual elasmobranchs, including the shark described here, are basic intersexuals.

Subject editor: John Mandelman, New England Aquarium, Boston, Massachusetts

*Corresponding author: jill.hendon@usm.edu
[1]Present address: Department of Molecular, Cellular, and Biomedical Sciences, University of New Hampshire, 129 Main Street, Durham, New Hampshire 03824, USA.
Received September 30, 2012; accepted April 17, 2013

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Intersexuality, or the presence of both male and female sex characters (including primary and secondary features) in an individual, has been reported in a wide range of taxa (Armstrong and Marshall 1964). Many intersexual vertebrates are also considered hermaphroditic because they possess the gonads of both sexes, implying that there could be functionality of both at some point during the individual's lifetime. Among vertebrates, teleost fishes have a relatively high occurrence of normal hermaphroditism, which is thought to have evolved as an adaptation to increase reproductive yield (Devlin and Nagahama 2002). However, intersexuality has rarely been reported in elasmobranch fishes. As sex designation for elasmobranchs is a genetically determined gonochoristic expression, the presence of both sexes in an individual is typically considered abnormal and an "unadaptive characteristic" (Atz 1964).

Many of the terms traditionally used to describe intersexuals are defined by normal hermaphroditic functionality (e.g., simultaneous and sequential; Sadovy and Shapiro 1987). Therefore, it is not possible to classify the typically gonochoristic elasmobranch examples by these means. The term pseudohermaphrodite, which describes a case in which the externally apparent sex is different from the internal anatomical designation, has been used (e.g., Irvine et al. 2002), and while this term does apply to known elasmobranch examples it does not fully capture the variation in intersexual expression that has been found in this group.

The Blacktip Shark *Carcharhinus limbatus* is one of the most abundant shark species in the western North Atlantic Ocean and an important commercial species in the southeastern United States (Castro 1996). As this shark is relatively abundant, well studied, and frequently encountered, we would expect that any normal hermaphroditic tendencies for this species would be well documented; however, only one case of intersexuality has been reported from a specimen caught in the Atlantic Ocean off the southeastern United States (Castro 1996). In this article we describe a second example of an intersexual Blacktip Shark that was collected during routine shark sampling in Mississippi waters. The literature on intersexual elasmobranchs was also compiled to put this Blacktip Shark into context with other reported specimens. As there were no existing terms for classifying the full range of expression of intersexuality found in elasmobranchs, three new terms are defined.

METHODS

On 12 June 2009, a Blacktip Shark was caught off Cat Island, Mississippi (30°09.223′N, 89°06.443′W) during routine monthly longline sampling. The shark, which was identified in the field as a male due to the presence of claspers, was dead upon capture and therefore was measured, weighed, and placed on ice for further analysis. In the laboratory, an incision was made into the peritoneal cavity and the reproductive tissues were examined. A thin cross-section of tissue was taken from multiple sections of the right gonad, preserved in 10% formalin, and shipped to the University of New England for histological analysis. The tissue was processed according to routine paraffin procedures and stained with hematoxylin and eosin (Sulikowski et al. 2004); its spermatogenic development was classified based on Maruska et al. (1996).

A thorough literature search was conducted and all published records of intersexual elasmobranchs found were compiled. These reports were then grouped based on the degree to which the examples expressed male and female characters, and new classifications (basic, incomplete, and complete intersexuality) were defined.

Intersexuality classifications.—The three new classifications of elasmobranch intersexuals cover the range of male/female expression reported in the literature. Basic intersexuals have gonadal tissue of only one sex (nonhermaphroditic) and a combination of other male and female reproductive characters (primary and secondary); however, neither or only one sex is present completely. Incomplete intersexuals are hermaphroditic elasmobranchs that possess gonadal tissue of both sexes and a combination of other male and female reproductive characters (primary and secondary); however, neither or only one sex is present completely. Both basic and incomplete intersexuals have the potential to function as only one sex. Complete intersexuals are hermaphroditic elasmobranchs that exhibit claspers, gonadal tissue of both sexes, and both male and female reproductive tracts. These elasmobranchs have the potential to be functional as either sex.

RESULTS

The intersexual Blacktip Shark from Mississippi waters had a FL of 83.8 cm, weighed 6.25 kg, and exhibited small, uncalcified claspers measuring 66 mm from the anterior cloacal opening to the tip of the clasper, which did not extend past the posterior edge of the pelvic fin. Externally, the shark appeared to be a normal juvenile male. When the peritoneal cavity was opened, both male and female reproductive structures were observed (Figures 1, 2A). Even though left and right gonads develop in normal males, only the right gonad was developing, while the left appeared undeveloped. The right gonad was 90 mm long (11 mm at the widest point), weighed 7 g, and exhibited patchy areas of development that were lobular in appearance, similar to that of maturing testicular tissue. Embedded in the dorsal wall on both the left and right sides were immature anterior and posterior oviducts with enlarging oviducal glands (left, 7.2 mm wide; right, 9.0 mm). Two undeveloped uteri were present, and the posterior portions, which were united at the cervix, were beginning to emerge from the dorsal wall. Epididymides, ductus deferentes, and seminal vesicles were not present. Histological analysis of the gonadal cross-sections revealed that the right gonad consisted exclusively of seminiferous tubules with all stages of spermatogenesis (germinal zone, early spermatocysts, spermatocytes, spermatids, immature sperm, mature spermatocyst, and a degenerate zone; Maruska et al.

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FIGURE 1. Body cavity of the basic intersexual Blacktip Shark from Mississippi waters. Although a vertebral sample was removed prior to taking the photo, the immature female reproductive tract, including oviducal glands (Og) and uteri (U), as well as immature claspers (C) are apparent.

1996) being present, indicating a maturing testis (Figure 2B). As this specimen did not have gonadal tissue from both sexes, it was considered a basic intersexual.

Among the three types of intersexual elasmobranchs, basic intersexuality has been found in the most species, 17 (12 sharks, 2 rays, and 3 skates), from the families Squalidae, Centrophoridae, Etmopteridae, Somniosidae, Scyliorhinidae, Triakidae, Carcharhinidae, Torpedinidae, Rhinobatidae, Arhynchobatidae, Rajidae, and Dasyatidae (Table 1). Incomplete intersexuality has been identified in 15 species (11 sharks, 1 ray, and 3 skates) from the families Hexanchidae, Squalidae, Etmopteridae, Somniosidae, Squatinidae, Scyliorhinidae, Carcharhinidae, Arhynchobatidae, Rajidae, and Myliobatidae (Table 1). Complete intersexuality is the most integrated form and has been identified in 11 species (7 sharks, 3 rays, and 1 skate) from the families Squalidae, Etmopteridae, Heterodontidae, Scyliorhinidae, Carcharhinidae, Torpedinidae, Narcinidae, Rajidae, and Dasyatidae (Table 1).

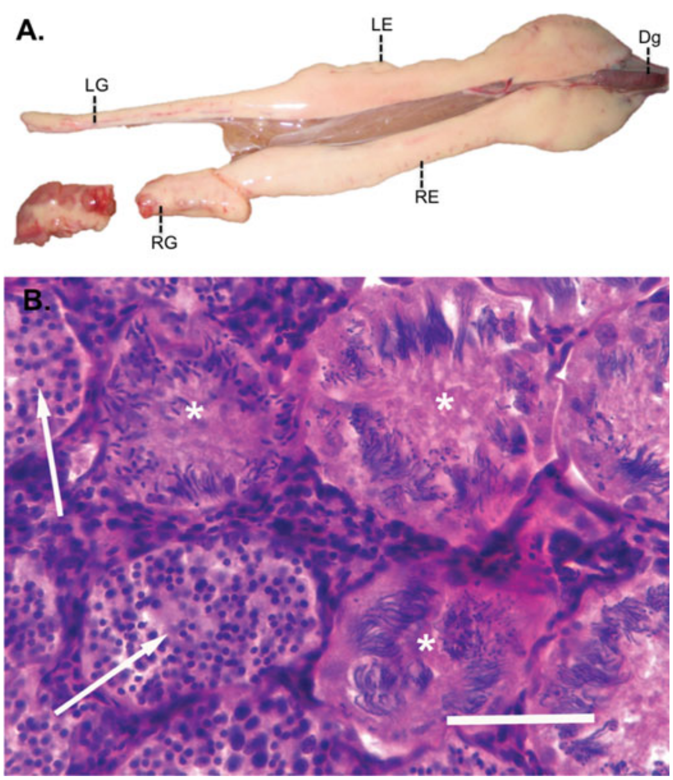

FIGURE 2. Gonads of the basic intersexual Blacktip Shark from Mississippi waters. Panel **(A)** shows the left (LG) and right gonads (RG) and epigonal organs (LE and RE) as well as the digitiform gland (Dg). Panel **(B)** is a photomicrograph of a histological cross section through the right gonad (taken from the area of the break in [A]) stained with hematoxylin and eosin. It shows spermatocysts representative of two stages of spermatogenesis: stage IV, which is characterized by early spermatids (arrows); and stage V, which is characterized by spermatids undergoing spermiogenesis (asterisks). Stages based on Maruska et al. (1996); bar = 200 μm.

DISCUSSION

The basic intersexual Blacktip Shark described here represents the first reported occurrence of intersexuality in an elasmobranch in the Gulf of Mexico and only the second report of this condition in the species. The length and noncalcified state of the claspers initially suggested that this specimen was an immature male developing in line with normal, similarly sized males for this species (see Castro 1996). An internal examination, however, provided different insight. Only the right gonad was developing, as is consistent with most female carcharhinids, but the histology of the tissue revealed it to be testicular. The length of the gonad was slightly larger than what Castro (1996) reported for similarly sized, normal males. Although spermatogenesis was occurring in the testis, the specimen was still likely a juvenile, as spermatogenesis is known to precede clasper maturation (Clark and von Schmidt 1965). The oviducal glands were still embedded in the dorsal wall of the peritoneal cavity and were of similar size to those of juvenile females as reported by Castro (1996). The absence of ovaries and a male duct system suggests that neither sex would have been functional in this individual.

The majority (>50%) of reported basic intersexuals exhibited claspers externally and a female reproductive tract and gonad internally (e.g., Yano and Tanaka 1989; Gianeti

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TABLE 1. Reported intersexual elasmobranchs. Species are categorized by degree of intersexuality as follows: B = basic intersexuality, I = incomplete intersexuality, and C = complete intersexuality (see text for more details). This nomenclature follows Compagno (2005).

Species	Type(s)	References
Hexanchidae		
Bluntnose Sixgill Shark *Hexanchus griseus*	I	Semper (1875)
Broadnose Sevengill Shark *Notorynchus cepedianus*	I	Daniel (1934)
Squalidae		
Spiny Dogfish *Squalus acanthias*	B I	Rowan (1929); J. Gelsleichter, R. D. Grubbs, and J. A. Musick (abstract from American Society of Ichthyologists and Herpetologists/American Elasmobranch Society meeting, 1997).
Longnose Spurdog *Squalus blainvillei*	B I	Kousteni and Megalofonou (2010)
Shortnose Spurdog *Squalus megalops*	C	Braccini (2009)
Centrophoridae		
Lowfin Gulper *Centrophorus lusitanicus*	B	Cadenat (1960)
Etmopteridae		
Black Dogfish *Centroscyllium fabricii*	I	Yano (1995)
Southern Lantern Shark *Etmopterus granulosus*	B C	Wetherbee (1996); Irvine et al. (2002)
Brown Lantern Shark *Etmopterus unicolor*	B	Yano and Tanaka (1989)
Somniosidae		
Portuguese Dogfish *Centroscymnus coelolepis*	I	Veríssimo et al. (2003)
Rough Dogfish *Centryoscymnus owstoni*	B	Yano (1985)
Squatinidae		
Atlantic Angel Shark *Squatina dumeril*	I	Merriman and Olsen (1949)
Heterodontidae		
Port Jackson Shark *Heterodontus portusjacksoni*	C	Jones et al. (2005)
Scyliorhinidae		
Longhead Catshark *Apristurus longicephalus*	B I C	Iglésias et al. (2005)
New Zealand Catshark *Halaelurus dawsoni*	I	Francis (2006)
Spotted Dogfish *Scyliorhinus canicula*	B I C	Bamber (1917); Murray and Baker (1924); Arthur (1950); Chapman (1951); Fuller and Zacharov (1960); King (1966); Capapé and Zahnd (1974); Ellis and Shackley 1997
Nursehound *Scyliorhinus stellaris*	C	Vayssière and Quintaret (1914); Capapé et al. (1979)
Triakidae		
Bigeye Hound Shark *Iago omanensis*	B	Compagno and Springer (1971)
Brown Smoothhound *Mustelus henlei*	B	Pérez-Jiménez and Sosa-Nishizaki (2008)
Smalleye Smoothhound *Mustelus higmani*	B	Springer and Lowe (1963)
Carcharhinidae		
Blacktip Shark *Carcharhinus limbatus*	B I	Castro (1996); this study
Blue Shark *Prionace glauca*	C	Pratt (1979)
Rhinobatidae		
Brazilian Guitarfish *Rhinobatos horkelii*	B	Gianeti and Vooren (2007)
Narcinidae		
Black-Spotted Electric Ray *Narcine timlei* (also known as Spotted Numbfish)	C	Nair and Soundararajan (1973)
Torpedinidae		
Marbled Electric Ray *Torpedo marmorata*	C	Capapé (1974)
Ocellated Torpedo *Torpedo torpedo*	B	Dalù et al. (2003)

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TABLE 1. Continued.

Species	Type(s)	References
Arhynchobatidae		
Alaska Skate *Bathyraja parmifera*	I	Matta (2006)
Bering Skate *Rhinoraja interrupta*	B	Haas and Ebert (2008)
Multispine Skate *Rhinoraja multispinis*	I	Scenna et al. (2007)
Rajidae		
Thorny Skate *Amblyraja radiata*	I	Templeman (1987)
Atlantic Starry Skate *Raja asterias* (also known as Mediterranean Starry Ray)	B	Quignard and Negla (1971)
Thornback Skate *Raja clavata*	B	Matthews (1885); Hoek (1894)
Twineye Skate *Raja miraletus*	C	Quignard and Capapé (1972)
Dasyatidae		
Tortonese's Stingray *Dasyatis tortonesei*	C	Capapé et al. (2012)
Pelagic Stingray *Pteroplatytrygon violacea*	B	Ribeiro-Prado et al. (2009)
Myliobatidae		
Banded Eagle Ray *Aetomylaeus nichofii*	I	Capapé and Desoutter (1979)

and Vooren 2007; Haas and Ebert 2008; Pérez-Jiménez and Sosa-Nishizaki 2008). This is the most minor form of intersexuality, as the primary gonad and tract was typically unaffected. Although the basic intersexual shark from Mississippi waters did have the external claspers and internal female tract, the gonad was testicular. A Longnose Spurdog (Kousteni and Megalofonou 2010) and Smalleye Smoothhound (Springer and Lowe 1963) are examples of the reverse formation, with male gonads internally and no claspers externally.

Incomplete intersexuals have the greatest combinations of male and female characters. For example, Veríssimo et al. (2003) found a Portuguese Dogfish with no claspers but an ovary and oviduct on the right as well as a testis with no male or female tract on the left, while Templeman (1987) documented a Thorny Skate, with ovaries and oviducts as well as testes and claspers. Castro's (1996) report of an intersexual Blacktip Shark described a gravid female that also possessed a clasper and possibly a testis. An "ovotestis," a gonad with both male and female tissue, was also commonly found in this type of intersexuality (e.g., Yano 1995; Dalù et al. 2003). Two hexanchids have shown another variation of incomplete intersexuality in which the females routinely present a rudimentary testis within the mesovarium (Semper 1875; Daniel 1934).

Complete intersexuals exhibited the most development of both sexes within one individual. The most common presentation was of a male and female tract on both the left and right sides of the peritoneal cavity (e.g., King 1966; Capapé et al. 1979; Pratt 1979; Jones et al. 2005). Bilateral gynandromorphic-like arrangements were also found, as was the case in the Shortnose Spurdog, which had a male gonad and tract on the right side of the peritoneal cavity and a female gonad and tract on the left side (Braccini et al. 2009). As in the incomplete intersex group, ovotestes were common in this type of intersexuality (e.g., Vayssiere and Quintaret 1914; Capapé and Zahnd 1974). Although the structures for both sexes are present in this type of intersexuality, improper development or maturation was often reported, rendering one or both sexes nonfunctional.

All three types of intersexuality have similar numbers of elasmobranch families represented. The majority of the documented species are from the Squalidae, Etmopteridae, Scyliorhinidae, Triakidae, Arhynchobatidae, and Rajidae families. In most species only one type of intersexuality was identified; however, this number is heavily dependant on the low numbers of reported individuals, with most studies reporting only a single specimen. The Spotted Dogfish and the Longhead Catshark were the only elasmobranchs in which all three types of intersexuality were found (Table 1). Interestingly, the Longhead Catshark was also the species with the greatest number of identified intersexual specimens. Iglésias et al. (2005) reported that 85% of the 82 individuals sampled from the Indian and Pacific oceans were intersexual and suggested that this was a case of normal hermaphroditism. The incidence rate was also higher in a discrete population of Lantern Sharks in Sugura Bay, Japan, in which 21% of the 70 specimens were basic intersexuals (Yano and Tanaka 1989); however, the authors believe that this is a result of environmental contamination.

Although only one intersexual Blacktip Shark was found in all the years of routine sampling in the waters in and around Mississippi, the lack of knowledge about the occurrence of intersexuality in elasmobranchs and the rarity of the condition within the family make documentation of this information valuable for those studying the development, life history patterns, and population dynamics of elasmobranchs. It is not surprising that the majority of the reported cases are from species commonly encountered in classroom dissections (e.g., Spotted Dogfish and Spiny Dogfish) or fisheries sampling (e.g., rajids). The aqueous environment and lack of many highly visible, sexually distinguishing characters in elasmobranchs often allow

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such anomalies to be acknowledged only when close or internal examinations are conducted. Although the introduced classifications of basic, incomplete, and complete intersexuality clarify whether the structures necessary for reproduction are present, it is important to note that developmental and histological analysis of the structures is still necessary to determine actual functionality. It is hoped that these classifications will provide researchers with a more accurate and standardized means for assessing intersexuality in elasmobranchs.

ACKNOWLEDGMENTS

We thank R. M. Simmons and B. Gregory of the Research Vessel *Tom McIlwain*; A. Karels and T. Holland for assistance in the collection of the Mississippi Blacktip Shark specimen; N. Brown-Peterson for histological review; J. Shaw for obtaining many of the sources; G. Poulakis, J. Mandelman, and an anonymous reviewer for their thorough evaluation of the manuscript; and J. Sulikowski for collaborative assistance. The shark discussed in this paper was collected while sampling for a NOAA-funded cooperative Southeast Area Monitoring and Assessment Program (NA06NMF4250011). All sampling protocols were approved by University of Southern Mississippi's Institutional Animal Care and Use Committee (09031202 and 09031203).

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