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SQUALIOLUS LATICAUDUS IN THE WESTERN NORTH ATLANTIC OCEAN: DISTRIBUTIONAL AND LIFE HISTORY OBSERVATIONS

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ABSTRACT

The spined pygmy shark (*Squaliolus laticaudus* Smith and Radcliffe, 1912) is among the smallest known species of sharks and despite its wide distribution, fewer than 100 specimens have been reported globally. On 28 October 2007, 24 spined pygmy sharks, with total lengths ranging from 120 to 210 mm, were collected in a single deepwater trawl in the northern Gulf of Mexico. All specimens, with the exception of two females, were immature. Follicle conditions in the two mature females indicated that vitellogenesis and gestation are consecutive. The stomachs of six specimens contained single cephalopod or teleost prey. Our catch and examinations of museum accessed specimens confirm the questioned presence of spined pygmy sharks in the Gulf of Mexico and demonstrate that it is more widely distributed in the western North Atlantic Ocean than previously known.

In the northern Gulf of Mexico, at least 30 shark species occupy deepwater habitats (McEachran and Fechhelm, 1998; Compagno, 2002); however, our understanding of species diversity and distributions is rudimentary. For example, within the past decade the occurrence of two species of large (> 3 m total length; TL) deepwater sharks in the northern Gulf of Mexico, the goblin (*Mitsukurina owstonii* Jordan, 1898) and sleeper (*Somniosus* sp.) sharks, has been documented (Parsons et al., 2002: Benz et al., 2007) and the capture of yet a third, the bramble shark [*Echinorhinus brucus* (Bonaterre, 1788)] awaits formal reporting (G. Burgess and J. Neer, unpubl. data). Other deepwater sharks such as the spined pygmy shark (*Squaliolus laticaudus* Smith and Radcliffe, 1912) are thought to inhabit the northern Gulf of Mexico (Compagno, 2002) but captures have yet to be reported.

Squaliolus laticaudus occurs in the Atlantic, Indian, and western Pacific Oceans and inhabits mesopelagic waters between 200–500 m (Seigel, 1978). It is a small squalid that reaches a maximum total length (TL) of approximately 25 cm, placing *S. laticaudus* among the smallest known living species of sharks (Compagno, 1984). Although the species has been recognized for almost a century, *S. laticaudus* remains one of the rarest sharks in collections (Castro, in press). The paucity of *S. laticaudus* specimens has resulted in extremely limited knowledge on the biology and distribution of the species. For example, until 2006, *S. laticaudus* was assumed to be aplacentally viviparous, based solely on its taxonomic position within the Squaliformes. This reproductive mode was finally verified by Cunha and Gonzalez (2006) from a single female caught off Brazil. Herein we document the presence of *S. laticaudus* in the northern Gulf of Mexico and provide new information on the behavior, diet, distribution, morphometrics, and reproductive biology of this poorly understood species.

Material and Methods

Squaliolus laticaudus specimens were collected on 28 October 2007 while conducting a deepwater trawl in the northern Gulf of Mexico (28°36′39″N, 89°57′42″W) aboard the U.S. National Oceanic and Atmospheric Administration ship R/V Gordon Gunter. The otter trawl was a two-seamed net with a 27.43 m head rope. The webbing used was primarily braided polyethylene, with 20.3, 10.2, and 7.0 cm stretched mesh in the wings, belly, and lead, respectively. The cod end was constructed of heavy double 14 cm stretched mesh webbing with a 0.06 cm heavy delta knotless liner. The net was fished on the bottom for 33.3 min, covering a linear distance of approximately 3.59 km.

All measurements and dissections were conducted on fresh specimens prior to being frozen. Straight line measurements (in mm) taken on the long the axis of the bodies of all specimens included: precaudal length (tip of rostrum to origin of upper lobe of caudal fin), fork length (tip of rostrum to posterior notch of caudal fin), TL (tip of rostrum to posterior tip of caudal fin while in its natural position), and stretch TL (tip of rostrum to posterior tip of caudal fin while fully extended). Additional selected morphological measurements (Table 1) were taken following Compagno (1984) to facilitate future comparisons between this and other studies as well as to provide measurements of fresh specimens prior to freezing and/or fixation. All specimens were weighed to the nearest 0.1 g.

An incision was made from the cloaca to the pectoral girdle in order to examine reproductive tracts and stomach contents. Prey items were removed from the cardiac stomach, enumerated, and identified to the lowest possible taxon. Reproductive tissues were inspected and measured under a stereo zoom dissecting microscope using dial calipers.

For females, the number and diameter of each vitellogenic follicle from both ovaries were recorded. If a female was gravid, embryos or uterine eggs were removed and measured when possible. Females were considered mature if they were gravid or had vitellogenic follicles and well developed uteri.

The outer (pelvic fin insertion to tip of apopyle) and inner (anterior most point of cloaca to tip of apopyle) lengths of the right clasper, as well as the length and width of the right testis were measured for each male. Males were considered mature if their claspers were calcified, rotated 180° relative to their natural position and had a freely opening rhipidion (Clark and von Schmidt, 1965). Testes condition was not considered a criterion for maturity as spermatogenesis has been shown to occur in immature males of other elasmobranch species (Pratt, 1996). All specimens were frozen after examination and deposited in the Florida Museum of Natural History (accession number UF 176375).

To examine the geographic distribution of *S. laticaudus* in the western North Atlantic Ocean, our capture data were combined with previously reported accounts and data associated with specimens obtained from museum collections (acronyms follow Leviton et al. (1985) and Leviton and Gibbs (1988)). Additionally, identifications of museum specimens were verified due to the close resemblance between *S. laticaudus* and *Squaliolus aliae* Teng, 1959; a species not reported from the western North Atlantic.

Material Examined.—*Gulf of Mexico:* USNM 187941, R/V Oregon sta. 2396, 28°59′N, 88°37′W, 265–290 fm, 31 Jan 1959 (1: 140 mm TL female); USNM 365693, R/V Oregon sta. 3437, 27°11′N, 87°55′W, 380–600 fm, 21 Nov 1961 (4: 215 mm TL adult female with 3 embryos, an 86 mm TL male and 86 and 91 mm TL females); LACM 55942-1, 29°26′00″N, 87°17′00″W, 70–130 m, 1973? (1: 175 mm TL mature male); LACM uncat., Mexico, Veracruz; UF 174635, R/V Oregon II sta. 42555, 29°21′46.8″N, 87°29′31.2″W, 210 fm, 26 Mar 1985 (1: 98 mm TL female); UF 176528, R/V Gordon Gunter Cruise 630605, Station 053. 27°53.39′N, 91°09.97′W, 274 m, 26 Oct 2006 (1: 108 mm TL female); UF 176375, R/V Gordon Gunter Cruise 0706, Station 72, 28°36′39″N, 89°57′42″W, 274.0–278.6 m, 28 Oct 2007 (24: 10 females 123–210 mm TL and 14 males 120–172 mm TL). *Northwest Atlantic:* UF 80088, R/V Needler Cr. N057 set 28, Scotian Shelf, 41°16′0.12″N, 57°28′0.12″W, over 4800 m, 15 Feb

Figure 1. Lateral view of a live female *Squaliolus laticaudus* (210 mm total length) captured in the northern Gulf of Mexico on 28 October 2007.

1986 (1: 155 mm TL female); ARC 8705227, Scotian Shelf, 41.0167°N, 56.8°W, 5 Apr 1979, (1: 228 mm TL female); ARC 8705397, R/V Belogorsk, Scotian Shelf, 39.7333°N, 56.9667°W, 1 Apr 1979 (1: 123 mm TL female); ARC 8703938, R/V Needler Cr. No 57 set 31, Scotian Shelf, 41.3°N, 60.5°W, 17 Feb 1986 (1: 100 mm TL female); MCZ 135325, Grand Banks, 43°50N, 45°40W, taken over 1000+ fm, 19 Aug 1992 (1: 148 mm TL); MCZ 82828, RV Oceanus Cr 121, Gulf Stream ring 82B over Norfolk Canyon, 36°54′36″N, 73°36′00″W, 400–600 m, 20 June 1982 (1: 118 mm TL female); LACM 55940-1, Acre 12-69, Bermuda, 32°14′00″N, 64°02′00″W, 0–100 m, 22 Aug 1971 (1: 240 mm TL female).

Results

Life History Observations.—Twenty-four *S. laticaudus* were collected with females (n = 10) ranging from 123 to 210 mm TL and 1.1–6.7 g and males (n = 14) ranging from 120 to 172 mm TL and 1.0–3.3 g (Fig. 1; Table 1). Conversions among the four length measures taken and the TL-weight relationship are presented in Table 2. Bottom depth at the capture location ranged from 274.0 to 278.6 m and temperature ranged from 11.2 to 26.3 °C in the water column (mean = 19.4 °C, S.D. = 4.4). It is uncertain if the sharks were caught on the bottom or while the net was ascending during haul back; however, that all the sharks were in a single group in the front of the net indicated they were captured near the end of the trawl period, suggesting that they were captured in the water column.

No contents were found in 18 of the stomachs examined. The stomach contents of six specimens contained single cephalopod or teleost prey item. Three squid were identified as *Abralia redfieldii* Voss, 1955. Two cephalopods and one teleost were in an advanced state of digestion thus preventing identification to a lower taxonomic level.

All males examined were immature as determined by the absence of completely calcified claspers and siphon sacs separated from the abdominal musculature. There was a significant positive linear relationship between TL and outer clasper length ($F = 8.38$, $P < 0.01$; $r^2 = 0.43$) and inner clasper length ($F = 24.96$, $P = 0.02$; $r^2 = 0.69$). Testes width increased with body length ($F = 11.47$, $P < 0.01$; $r^2 = 0.56$); however, there was no significant relationship between body length and testes length ($F = 2.41$, $P = 0.16$, $r^2 = 0.23$). No development of the germinal zone, epididymides, ductus deferentes, or seminal vesicles was observed in individuals smaller than 152 mm TL. One specimen, measuring 172 mm TL, had partially calcified claspers and a functional rhipidion.

Table 1. Proportional morphometrics of *Squaliolus laticaudus* expressed as percentage of total length (TL). Mean and range of values are reported for each morphometric by sex. Morphometric values for sexes combined are reported as mean and standard deviation.

Morphometric	Female	Male	Sexes combined
Size range (mm TL)	123–210	120–172	120–210
n	10	14	24
Preorbital length	8.3 (6.2–10.2)	7.9 (2.3–9.2)	8.1 (1.49)
Preoral length	15.0 (13.6–16.0)	14.5 (7.7–16.1)	14.7 (1.68)
Prespiracular length	17.0 (14.8–19.6)	17.0 (15.6–19.1)	17.0 (1.19)
Prepectoral fin length	29.9 (27.2–32.3)	30.4 (28.7–33.6)	30.2 (1.52)
Head length	33.3 (27.8–39.5)	29.7 (27.8–31.7)	31.3 (3.91)
Pre-first dorsal fin length	38.2 (35.7–40.2)	38.4 (36.6–40.3)	38.3 (1.35)
Prepelvic fin length	63.8 (61.2–65.2)	63.1 (60.7–65.1)	63.4 (1.36)
Pre-second dorsal fin length	67.6 (65.8–70.9)	67.2 (65.0–70.4)	67.4 (1.55)
Internarial space	2.5 (2.2–3.0)	2.5 (2.2–2.9)	2.5 (0.2)
Eye length	6.3 (5.3–8.1)	6.4 (5.5–7.9)	6.4 (0.77)
Mouth length	6.6 (5.7–7.4)	6.8 (6.0–8.0)	6.7 (0.59)
Pectoral fin pelvic fin space	32.3 (29.9–35.3)	31.1 (28.2–33.6)	31.6 (1.61)
Interdorsal space	23.5 (19.7–27.4)	23.9 (24.9–27.3)	23.7 (2.07)
Dorsal caudal fin space	7.3 (5.7–9.0)	8.7 (6.8–10.3)	8.1 (1.25)
Pelvic fin caudal fin space	19.6 (17.7–25.1)	20.5 (17.6–22.8)	20.1 (1.68)

Eight immature females ranged in size between 123–148 mm TL and had right uterus widths of 0.5–1.3 mm. The ovaries of seven immature females appeared smooth and showed no sign of follicular development. Both the right and left ovaries of the 134 mm TL immature specimen showed obvious signs of vitellogenesis. The left ovary had 12 developing follicles, ranging in diameter from 0.2 to 0.3 mm; the right ovary had six developing follicles ranging in size from 0.2 to 0.5 mm. All follicles were developing on the periphery of each ovary distal to the vertebral column.

Two mature females were captured; one postpartum and one gravid. The postpartum specimen (209 mm TL) had distended uteri that were flaccid, and its left and right ovaries each contained two vitellogenic follicles that ranged in diameter from 6.2 to 7.1 mm. There was no sign of vitellogenic activity in the pregnant specimen (210 mm TL). The left and right uteri of the gravid specimen contained two and three eggs, respectively. The maximum observed egg diameter was 20.9 mm; however, three eggs were ruptured during removal from the egg membranes and thus no measurements were taken. Both intact uterine eggs were in the blastodisc stage of development. The oviducal glands of all females, regardless of maturity stage, were not visible at a magnification of 50×. A 215 mm TL museum archived female (USNM 365693) collected in the Gulf of Mexico on 21 November 1961 contained three em-

Table 2. Length-length and length-weight conversions for *Squaliolus laticaudus,* based on 24 specimens collected in the northern Gulf of Mexico. TL = total length (mm), PCL = precaudal length (mm), FL = fork length (mm), STL = stretch total length (mm), WT = weight (g).

Conversion	Equation	r^2
TL → PCL	PCL = –2.7612 + (0.8853 * TL)	0.96
TL → FL	FL = –3.4830 + (0.9876 * TL)	0.99
TL → STL	STL = –2.3819 + (1.0352 * TL)	0.99
TL → WT	WT = e (–2.1728 + (0.0186 * TL))	0.95

bryos, an 86 mm TL male and 86 and 91 mm TL females, representing the second known gravid specimen of the species.

Distribution.—In the western North Atlantic Ocean, *S. laticaudus* has been previously reported from Suriname (Uyeno and Sasaki, 1983), Bermuda (Seigel et al., 1977), the eastern Sargasso Sea (Vinnichenko, 1997), Virginia, and the Grand Banks (Moore et al., 2003), the Scotian Shelf of Canada, and northwestern Atlantic seamounts (Kukuyev, 1982); however, it has not previously been reported from the Gulf of Mexico. In addition to the 24 specimens reported herein, five unreported specimens collected in the northern Gulf of Mexico were located in museum collections. The report of these captures establishes the presence of *S. laticaudus* in the Gulf of Mexico and represents the largest number of free-swimming individuals of this species collected anywhere.

Discussion

Squaliolus laticaudus was described by Smith and Radcliffe in 1912, based on specimens collected in the western Pacific Ocean (Seigel, 1978). Subsequent captures expanded its range throughout much of the world's tropical and subtropical oceans. Although McEachran and Fechhelm (1998) included *S. laticaudus* among the fishes occurring in the northern Gulf of Mexico, Compagno (2002) considered the presence of this shark in the region uncertain. The Gulf of Mexico collections documented herein—plus additional captures from Suriname, Bermuda, Norfolk Canyon, the Scotian Shelf, the Grand Banks, and northwestern Atlantic seamounts—indicate that *S. laticaudus* is widely distributed in the western North Atlantic (Fig. 2).

In his revision of the genus *Squaliolus*, Seigel (1978) examined 17 *S. laticaudus* specimens collected in a commercial fishing net off the coast of Japan. Sadowsky et al. (1985) reported on the discovery of more than 45 *S. laticaudus* in the stomach of a single bigeye tuna (*Thunnus obesus* Lowe, 1839) captured off Brazil. Comparing our data with that of Seigel (1978) and Sadowsky et al. (1985), it is apparent that *S. laticaudus* occasionally aggregates; however, the frequency with which this occurs is unknown. The related *S. aliae* apparently also aggregates as large numbers have been observed in hauls associated with sergestid shrimp (G. Burgess, unpubl. data). Sharks are thought to aggregate for a number of reasons, including foraging, predator avoidance, and mating (Heupel and Simpfendorfer, 2005). While predator avoidance cannot be discounted, it is probable that the aggregation observed during this study was associated with feeding as mesopelgic cephalopods and teleosts were present in both the trawl catch and the stomachs of six *S. laticaudus* specimens. It is unlikely that the group of sharks represented a mating aggregation as all males were immature and only two females with vitellogenic follicles were observed.

Seigel (1978) determined that male *S. laticaudus* reach maturity between 152 and 223 mm TL, however, the one mature male he examined was 223 mm TL. In the current study, five males between 152 and 179 mm TL were in early stages of maturation. Although the right testis of all males in our sample > 149 mm TL had a visible germinal zone, the ductus deferens and seminal vesicles were not developed in any individual, including the 172 mm TL male with partially calcified claspers. These data indicate that male *S. laticaudus* mature at a size larger than, or at least at the higher end of the range, suggested by Seigel (1978).

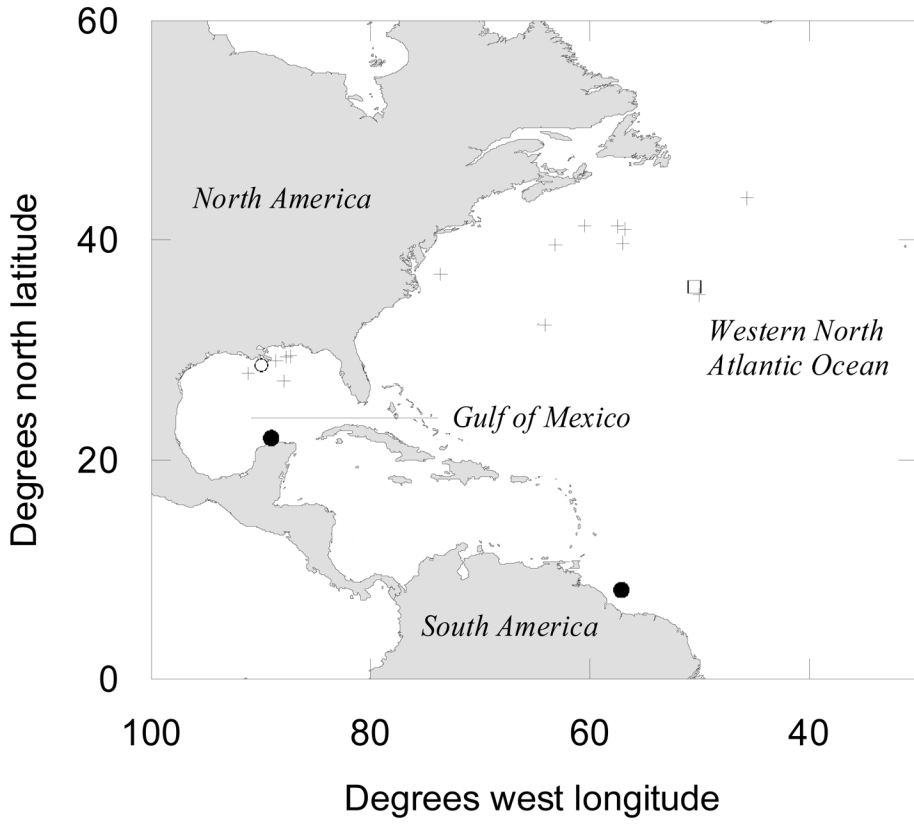

Figure 2. Capture locations of *Squaliolus laticaudus* in the western North Atlantic Ocean. + = 1 individual, □ = 2 individuals, and O = 24 individuals. ● = approximate locations of single specimens.

The reproductive tract of all females was similar to other squaliform sharks except for the absence of visible oviducal glands. The oviducts of all female specimens were thoroughly examined and, despite magnification, no discernible oviducal glands were observed. It is possible that the oviducal glands do not develop until the onset of maturity; however, unless abrupt recrudescence and regression of these glands occurs around the time of ovulation, they are much smaller, relative to the size of the oviducts, than is observed in other elasmobranchs.

Two of the females examined had developing follicles present. Seigel (1978) suggested that each ovary of mature females can contain up to 12 developing follicles. One immature female captured during this study verified that an ovary can have 12 developing follicles; however, the postpartum female we examined had only two vitellogenic follicles in each ovary, the pregnant female we collected had only five ovarian eggs, and the maximum brood size of four reported by Cunha and Gonzales (2006) all indicate that all developing follicles do not complete development and undergo atresia. The number (three) and size of the embryos (86, 86, and 91 mm TL) taken from the 215 mm TL museum-housed (USNM 365693) female differ from the only other recorded pregnant female, a 260 mm TL Brazilian specimen which had four embryos (90, 94, 97, and 97 mm TL; Cunha and Gonzalez, 2006).

The largest immature female collected during this study was 148 mm TL while the smallest mature specimen was 209 mm TL. These data agree with the estimated range in size at maturity between 169–197 mm TL reported by Seigel (1978). However, for some elasmobranch species, it has been demonstrated that there is regionally based intraspecific variability in important life history characteristics, such as size-at-maturity and fecundity (Parsons, 1993; Carlson et al., 2003; Driggers et al., 2004). Since *S. laticaudus* has an almost circumglobal distribution, it is possible that there is spatial variability in life history traits, such as size at maturity, resulting from genetic differentiation. The absence of *S. laticaudus* in the eastern Pacific Ocean suggests that the distribution of this species may be limited by reduced water temperature. Furthermore, as *S. laticaudus* primarily inhabits waters associated with islands and continental slopes (Seigel, 1978), dispersal could be limited. The potential for both latitudinal and longitudinal barriers to gene dispersal suggests that the life history of *S. laticaudus* should be examined in multiple localities throughout its range.

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