

Reproductive Biology of the Cuban Dogfish in the Northern Gulf of Mexico

Authors: Jones, Lisa M., Driggers, William B., Hoffmayer, Eric R., and Hannan, Kristin M.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 5(5) : 152-158

Published By: American Fisheries Society

URL: <https://doi.org/10.1080/19425120.2013.768572>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

SPECIAL SECTION: ELASMOBRANCH LIFE HISTORY

Reproductive Biology of the Cuban Dogfish in the Northern Gulf of Mexico

Lisa M. Jones, William B. Driggers III,* Eric R. Hoffmayer,
and Kristin M. Hannan

National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories,
Post Office Drawer 1207, Pascagoula, Mississippi 39567, USA

Alyssa N. Mathers

National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory,
3500 Delwood Beach Road, Panama City, Florida 32408, USA

Abstract

Within the northern Gulf of Mexico, the Cuban Dogfish *Squalus cubensis* is the most frequently encountered squalid in continental shelf and slope waters. Despite the relatively high abundance of Cuban Dogfish in the region, there is a dearth of information regarding even the most basic aspects of the species' biology. Furthermore, what has been reported is conflicting and of questionable utility. From 2005 to 2012, 139 male and 252 female Cuban Dogfish were collected opportunistically. The analyses indicated that male Cuban Dogfish reach 50% maturity at 379 mm stretch total length (STL) and are capable of reproducing throughout the year. Females reach 50% maturity at 466 mm STL and 50% maternity at 478 mm STL. Brood size ranges from one to four, and vitellogenesis and gestation are concurrent. Although samples were not collected during all months of the year, the presence of ova in the blastodisc stage of development during the summer and fall, coupled with the relatively high variability of embryo size within fall months, suggest that Cuban Dogfish reproduce asynchronously.

In the past two decades, knowledge of the life histories of many chondrichthyan fishes has increased significantly (Caillet and Goldman 2004). However, most of this knowledge is limited to species that are commercially important or inhabit waters that are relatively easy to sample, such as coastal habitats. Chondrichthyans occurring within deepwater habitats represent almost half of all known species within this class, yet information about the basic biology of most species remains limited due to a number of factors, including the difficulties associated with sampling the deepwater environment and taxonomic uncertainty (Kyne and Simpfendorfer 2010). While historically the depths occupied by deepwater sharks were not heavily influenced by anthropogenic forces, human activity is escalating within deepwater habitats. For example, within the northern Gulf of Mexico,

fisheries and petroleum industry activities are operating at increasingly greater depths (Powell et al. 2003). As conservation and management efforts will likely begin focusing on deepwater organisms in the near future, it is imperative to gain an understanding of their life histories, particularly for *k*-selected species such as squalid sharks.

Within the northern Gulf of Mexico, the Cuban Dogfish *Squalus cubensis* is the most frequently encountered squalid (National Marine Fisheries Service, unpublished data). This species is endemic to the western Atlantic Ocean, is reported to occur at depths between 60 and 380 m, and reaches a maximum size of approximately 110 cm TL (McEachran and Fechhelm 1998). Despite the relatively high abundance of the species, information about its reproduction is scarce and disparate. For

Subject editor: Kenneth Goldman, Alaska Department of Fish and Game, Homer

*Corresponding author: william.driggers@noaa.gov
Received October 29, 2012; accepted January 9, 2013

example, Cruz-Pacheco (1997) reported brood size to range from 1 to 26, while Compagno (1984) reported “about 10” offspring per brood. There are similar discrepancies in the estimates for size at maturity, with Compagno (1984) and Castro (2011) reporting it to be approximately 50 cm TL and McEachran and Fechhelm (1998) providing estimates up to 75 cm TL. Because of the importance of vital rates in understanding the population dynamics of the species, the objective of this study was to describe the reproductive biology of Cuban Dogfish.

METHODS

Cuban Dogfish were collected throughout the northern Gulf of Mexico from 2005 to 2012 during National Marine Fisheries Service, Mississippi Laboratories longline and trawl surveys (see Driggers et al. 2008, 2010 for gear specifics) and opportunistically aboard commercial fishing vessels utilizing similar gear. After collection, all specimens were frozen whole prior to being processed (no later than 2 months after capture). Once thawed, the precaudal length (from the tip of the snout to the origin of the caudal fin), FL (from the tip of the snout to the posterior notch of the caudal fin), TL (from the tip of the snout to the posterior tip of the caudal fin while in a natural position), and stretch total length (STL; from the tip of the snout to the posterior tip of the caudal fin while fully extended along the axis of its body) were recorded. All lengths were measured to the nearest millimeter and taken on a straight line along the axis of the body. Weight was measured to the nearest 0.1 kg prior to evisceration. To test for differences in the length–length and length–weight relationships between males and females, data were compared using analysis of covariance (ANCOVA). As weight did not increase linearly with length, those data were log transformed prior to analysis.

Males.—The length of the right clasper was measured from the pelvic fin insertion to the tip of the apophysis. Males with calcified claspers that could be rotated 180°, freely opening rhipidions, and a functional siphon sac were classified as mature. The presence of sperm was not used as a criterion of maturity due to the flocculent condition of the semen that resulted from freezing. Additionally, testis condition was not considered a criterion for maturity, as spermatogenesis has been shown to occur in immature males of other elasmobranch species (Pratt 1993). To conduct gross examinations of internal reproductive tissues, an incision was made from the cloacal origin to the pectoral girdle. The condition of the epididymides, ductus deferentes, and seminal vesicles was noted as turgid or regressed. If turgid, pressure was applied along the length of the reproductive tracts to determine whether semen was present. The right testis was removed and its length and weight measured. Gonadosomatic index (GSI) values for mature individuals, defined as

$$\text{GSI} = [\text{gonad weight}/(\text{weight of shark} - \text{gonad weight})] \times 100,$$

were compared among months using analysis of variance (ANOVA) to determine whether there was a peak period for spermatogenesis.

Females.—After thawing and making an incision from the cloacal origin to the pectoral girdle, we removed the ovaries and recorded the total number of developing follicles and the width of the largest follicle. Follicles were classified as undeveloped, selected, vitellogenic, or atretic. Additionally, the maximum widths of the right oviducal gland and the uterus were measured. Uterus widths were only obtained for nongravid females and measured at the widest point. Individuals that were gravid or had vitellogenic follicles, enlarged oviducal glands, and developed uteri were considered mature. Both uteri were inspected for the presence of ova and developing embryos. When embryos were present, STL and weight were measured and sex was recorded when externally visible. A chi-square test with Yates' correction was utilized to determine whether the male : female embryo ratio was different than the expected 1:1. Because monthly embryo length data did not meet the assumption of parametric statistics (i.e., were nonnormally distributed and heteroscedastic), the Kruskal–Wallis test was used to compare the median STLs of the embryos by month. Gonadosomatic index values for mature individuals, defined as

$$\text{GSI} = \{[\text{gonad weight}/(\text{weight of shark} - (\text{gonad weight} + \text{total weight of embryos}))] \times 100,$$

were compared among months using (ANOVA) to determine the time of ovulation.

To determine the sizes at which 50% of the males and females were mature, the logistic model

$$Y = [1 + e^{-(a+bx)}]^{-1},$$

where Y is the proportion mature and x is STL, was fitted to binomial maturity data using least-squares nonlinear regression. The median STL at maturity was determined as $-a/b$ (Mollet et al. 2000). The same methodology was used to determine size at first maternity using binomial pregnancy data. Analysis of variance and Tukey's honestly significant difference multiple-range test were utilized to determine whether there was a significant difference in the mean depth of capture for immature and mature individuals of both sexes. All statistical tests were conducted following the methods of Zar (1999) using Statgraphics Plus version 5.1 and were considered significant at $\alpha = 0.05$.

RESULTS

Over the course of this study, 139 male and 252 female Cuban Dogfish were collected throughout the northern Gulf of Mexico (Figure 1). Males ranged from 204 to 466 mm STL and females from 212 to 564 mm (Figure 2). The relationships among the four length measures and between STL and weight are reported in Table 1. There was no significant difference among

TABLE 1. Length–length and length–weight relationships for Cuban Dogfish specimens collected in the northern Gulf of Mexico, used to convert from one measure of length to another or from stretch total length to weight. All lengths are in millimeters and all weights in kilograms. Abbreviations are as follows: PCL = precaudal length, STL = stretch total length, and WT = weight.

Conversion	<i>n</i>	Equation	<i>r</i> ²
STL to PCL	384	$PCL = -6.23 + 0.80 STL$	0.99
STL to FL	391	$FL = -1.94 + 0.88 STL$	0.99
STL to TL	389	$TL = 1.50 + 0.96 STL$	0.99
STL to WT	138	$WT = \exp[-5.28 + (9.79 \times 10^{-3}) STL]$	0.95
STL to WT	247	$WT = \exp[-4.88 + (8.68 \times 10^{-3}) STL]$	0.96
STL to WT	385	$WT = \exp[-4.92 + (8.78 \times 10^{-3}) STL]$	0.97
(males)			
(females)			
(sexes combined)			

length–length relationships between the sexes ($F = 1.08$, $df = 380$, $P = 0.30$); however, there was a significant difference in the length–weight relationship between males and females ($F = 15.63$, $df = 375$, $P < 0.01$).

A total of 31 immature and 108 mature males were collected during the months of January, March, July, October, November, and December. Clasper length slightly increased with body length and then abruptly increased at approximately 350 mm STL (Figure 3). Testis length and width also increased at approximately 350 mm STL, suggesting the onset of puberty at this size. In all cases, once claspers were fully calcified, the rhipidions freely opened, the claspers could be rotated, and the siphon sac was functional, indicating that these changes in requisite sexual characteristics occur concurrently. The smallest mature male was 375 mm STL while the largest immature male was 411 mm STL, with the size at 50% maturity for males being 379 mm STL (Figure 4; $a = -77.4106$, $b = 0.204116$). There was a significant difference among mean monthly GSI values ($F = 9.38$, $df = 105$, $P < 0.01$), with these values being greatest in January (mean = 0.66, SE = 0.09) and lowest in October (mean = 0.38, SE = 0.03) (Figure 5). However, semen was present in all mature males with the exception of one individual

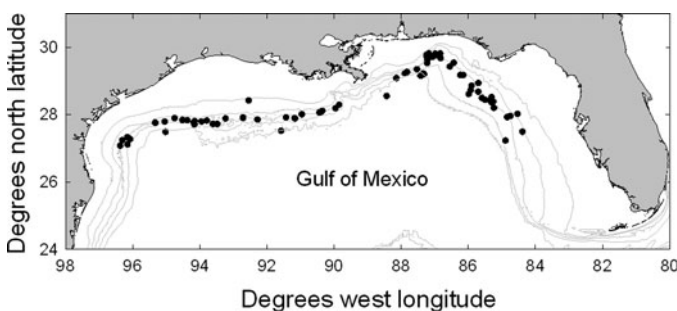


FIGURE 1. Locations where Cuban Dogfish specimens were collected in the northern Gulf of Mexico. Note that multiple specimens were collected at most locations. The 50-, 100-, 200-, 500- and 1,000-m isobaths are indicated.

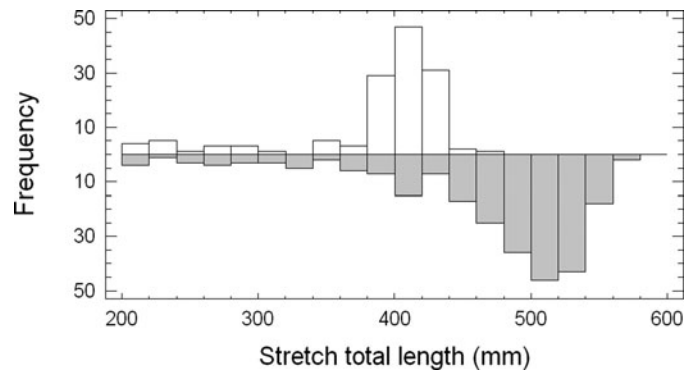


FIGURE 2. Length frequency distribution of male (white bars; $n = 139$) and female (gray bars; $n = 252$) Cuban Dogfish collected in the northern Gulf of Mexico during this study.

in October and eight in November, suggesting that males are capable of reproducing during all of the months sampled.

A total of 87 immature and 165 mature females were collected during the months of January, March, July, September, October, November, and December. During the maturation process, development of the oviducal glands begins at approximately 420 mm STL, followed by development of the uteri at approximately 460 mm STL (Figure 6). The largest immature female was 520 mm STL, and the smallest mature female was 446 mm. The size at 50% maturity for females was 466 mm STL (Figure 4; $a = -55.2516$, $b = 0.118477$). The total number of vitellogenic follicles in both ovaries ranged from 1 to 11 (mean = 3.92, SD = 2.20). There was no significant statistical difference in the number of vitellogenic follicles in the left (mean = 2.29, SD = 1.37) and right (mean = 2.01, SD = 1.56) ovaries of mature females ($t = -1.02$, $df = 75$, $P = 0.31$). Within the right ovary, the number of selected follicles ranged from 1 to 42 (mean = 8.25, SD = 6.85); however, the number of vitellogenic follicles only ranged from 1 to 9, demonstrating that not all selected follicles complete development. When present, the number of atretic follicles ranged from 1 to 20 (mean = 4.96, SD = 4.59). The maximum vitellogenic follicle diameter was significantly different among months ($F = 7.65$, $df = 123$, $P < 0.01$). The

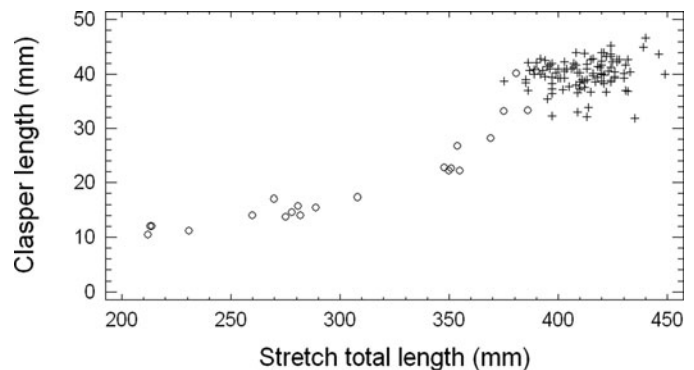


FIGURE 3. Relationships between right clasper length and stretch total length for immature (circles) and mature (plus signs) male Cuban Dogfish.

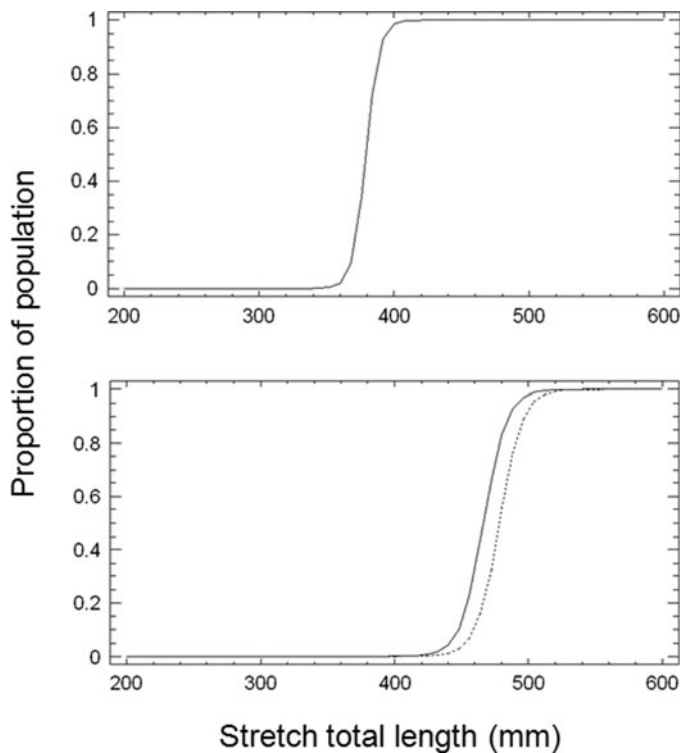


FIGURE 4. Size-at-maturity ogives (solid lines) for male (upper panel) and female (lower panel) Cuban Dogfish. The size-at-maturity ogive for females (dashed line) is also included in the lower panel.

multiple-range test indicated that vitellogenesis commences during the summer months and culminates in January; however, there was a considerable amount of variability in maximum vitellogenic follicle diameters within months, suggesting a degree of asynchrony within the population sampled (Figure 7).

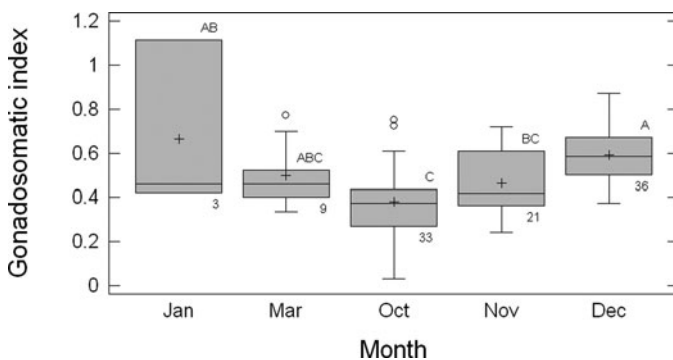


FIGURE 5. Box-and-whisker diagrams of the monthly gonadosomatic index values (see text for definition) for mature male Cuban Dogfish collected in the northern Gulf of Mexico. The height of each box extends from the 25th to the 75th percentile; the black line within each box represents the median and the plus sign the mean. The thin vertical lines indicate the maximum and minimum values except for data points that are more than 1.5 times the interquartile range, which are represented by circles. The number below each box is the sample size for that month. Boxes with common letters are not significantly different based on Tukey's multiple-range test.

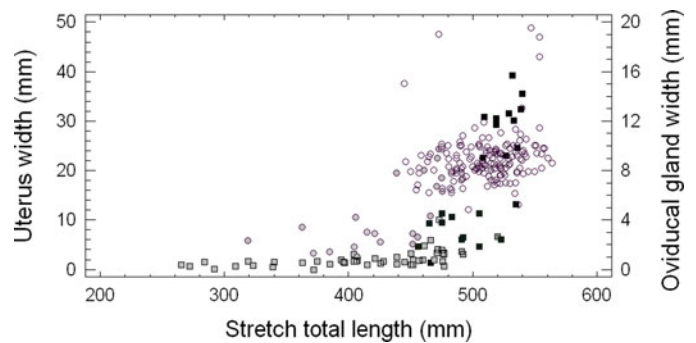


FIGURE 6. Relationships between stretch total length and (1) right uterus width (squares) and (2) right oviducal gland width (circles) for Cuban Dogfish. Data points in gray represent immature individuals, those in white and black represent mature individuals.

Furthermore, there was no significant difference in GSI values among the months ($F = 0.02$, $df = 79$, $P = 0.99$). The largest vitellogenic follicle observed in January had a diameter of 30.50 mm. We could not determine whether this size corresponded with the follicle size immediately preceding ovulation due to the lack of samples from late winter and early spring.

Of the 23 mature nongravid females, 9 specimens (473–535 mm STL) possessed enlarged uteri and fully developed follicles (20.3–23.0 mm), indicating recent parturition and imminent ovulation. Ten specimens (490–522 mm) also had expanded uteri but smaller developing follicles (6.6–19.5 mm), suggesting an extended period between pregnancies for some females. Four smaller specimens (443–473 mm) with mature uteri and developing follicles (9.1–18.8 mm) were most likely entering their first reproductive cycle.

Size at first maternity was estimated to be 478 mm STL (Figure 4; $a = -56.4405$, $b = 0.118038$). The total number of embryos per brood ranged from one to four (mean = 2.22, $SD = 0.69$). Among the 142 gravid females examined, there was a significantly greater number of embryos in the right uterus (mean = 1.38, $SD = 0.88$) than in the left uterus (mean = 0.88,

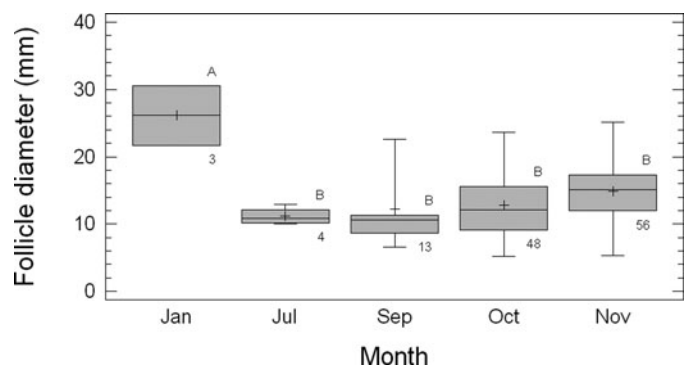


FIGURE 7. Box-and-whisker diagrams of the maximum vitellogenic follicle diameter for Cuban Dogfish, by month. The thin vertical lines indicate the maximum and minimum values; otherwise the diagrams are as described in Figure 5.

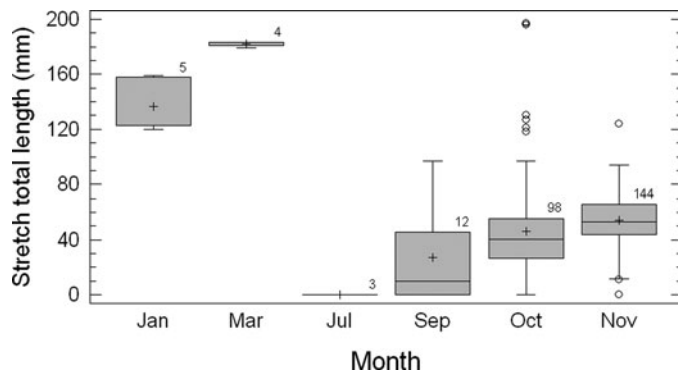


FIGURE 8. Box-and-whisker diagrams of embryo size for Cuban Dogfish, by month. See Figure 5 for more information.

SD = 0.48) ($t = 8.10$, $df = 141$, $P < 0.01$). There was a weak but significant relationship between maternal body length and brood size ($F = 18.92$, $df = 135$, $P < 0.01$, $r^2 = 0.11$; brood size = $-2.69 + [9.58 \times 10^{-3}]$ STL) with a general trend of larger females having larger broods; however, the maximum brood size of four was only observed in individuals of intermediate sizes (490–519 mm STL). Embryos in the blastodisc phase of development were observed from September through October and in July. Median embryo STL was significantly different among months, with smallest lengths occurring from September to October and the largest in March (Kruskal–Wallis test; $H = 57.10$, $P < 0.01$; Figure 8). The ratio of male to female embryos was not significantly different than 1:1 ($\chi^2 = 0.24$, $P > 0.50$). The largest embryo observed measured 197 mm STL and the smallest free-swimming individual was 204 mm STL, with both specimens being captured in October. These data suggest that the size at birth for Cuban Dogfish is approximately 200 mm STL.

Sharks were collected at depths ranging from 50 to 459 m (mean = 251.73, SD = 76.18). There was a significant difference in the mean depth of capture among mature and immature males and females ($F = 162.93$, $df = 336$, $P < 0.01$). The multiple-range test indicated that mature females were caught at a significantly shallower mean depth (198.11, SD = 44.93) than immature females (299.03, SD = 51.87) and males of both life stages. The mean depth of capture for immature and mature males was 340.77 m (SD = 47.74) and 327.87 m (SD = 56.62), respectively.

DISCUSSION

The presence of ova in the blastodisc stage of development during the summer and fall, coupled with the relatively high variability of embryo size in fall months (Figures 7, 8), suggests that Cuban Dogfish reproduce asynchronously, as is thought to be the norm for deepwater chondrichthyans (Kyne and Simpfendorfer 2010). For example, based in part on the year-round presence of large embryos, Watson and Smale (1998) determined that Shortnose Spurdogs *S. megalops* reproduce asynchronously and

attributed this to the temporally stable environment occupied by these sharks. However, Watson and Smale (1998) went on to report that size segregation of the species within their sampling area could have biased their results due to inadequate sampling of all areas. Similarly, our results could be biased due to the preponderance of samples being collected during the late summer and fall. Based on mean monthly follicle diameters and the observation of the progression in mean embryo size from July forward, there is the possibility that a portion of the population is synchronous, with ovulation occurring in late spring and early summer. However, samples will need to be collected equally throughout the year to determine whether a degree of synchrony is present.

Based on the rate of embryonic development and concurrent vitellogenesis, our data indicate that female Cuban Dogfish reproduce biennially. Recently fertilized ova were primarily observed during the summer; however, as previously mentioned, our data are based on specimens collected during 6 months of the year and are variable within the months sampled. Therefore, these data do not have the resolution necessary to definitively determine gestation period. The data indicated a mainly continuous reproductive cycle, although a small portion of mature females (6.0%) appeared to have a resting period after parturition and before ovulation, while ovarian follicles matured. Evidence for a resting period was also found in 10–20% of Shortnose Spurdogs and 18% of mature female Shortspine Spurdogs *S. cf. mitsukurii* examined in Australian waters (Graham 2005) and 10% of mature female Spiny Dogfish *S. acanthias* examined off New Zealand (Hanchet 1988).

The lack of significant bias in the sex ratio of the embryos, combined with the preponderance of females in the study (64% of all specimens), especially in specimens larger than 440 mm STL (Figure 2), suggests that sexual segregation is occurring in this species. There did not appear to be a regional effect, as immature and mature males and females were collected throughout the continental shelf edge and slope water of the northern Gulf of Mexico. However, there was segregation by depth, as males were collected in deeper water than females and mature females were found to occur in significantly shallower waters than immature females and males. Even young-of-the-year Cuban Dogfish primarily occurred in water depths >350 m. Sexual segregation with depth and area is relatively common among squalids (e.g., Yano and Tanaka 1988; Yano 1995; Clarke et al. 2001; Bañón et al. 2006; Hazin et al. 2006).

The results of this study are consistent with past reports on the reproductive biology of Cuban Dogfish in that they confirm the aplacentally viviparous reproductive mode typical of sharks within the order Squaliformes; however, our findings differ from those of other studies with regard to vital rates, such as fecundity and size at maturity. This is of particular importance for stock assessments, as such assessments rely on accurate information about the reproductive biology of given species (Walker 2005), and current knowledge of the basic biology of the Cuban Dogfish is not extensive enough to allow for stock assessment

(IUCN 2012). Size at maturity estimates for Cuban Dogfish have been reported by a number of authors (e.g., Compagno and Vergara 1978; Compagno 1984; McEachran and Fechhelm 1998); however, in each case it appears that these works simply report the estimate provided by Bigelow and Schroeder (1948) without specific citation. For example, Compagno and Vergara (1978) state that Cuban Dogfish mature at 50 cm or less without providing sex-specific information, specific measures of TL (i.e., natural versus stretch), or supporting documentation. Compagno (1984) cites the same size at maturity but also references Bigelow and Schroeder (1948) and Compagno and Vergara (1978). Bigelow and Schroeder (1948) state that their estimate of maturity was based on a single mature male of 524 mm TL (544 mm STL using the conversion formula in Table 1) and that “maturity is reached at a length not much greater than 500 mm TL” (519 mm STL). The results of our study suggest that Cuban Dogfish mature at smaller sizes than those reported by Bigelow and Schroeder (1948) and thus subsequent authors.

Similarly, the results of our analyses indicate that past works have overestimated the fecundity of Cuban Dogfish. Most sources give the brood size for Cuban Dogfish as 10 (e.g., Castro 1983; Compagno 1984; McEachran and Fechhelm 1998), though one gives the exceptional estimate of up to 26 (Cruz-Pacheco 1997), which is almost 6.5 times greater than the maximum brood size that we observed (4). Furthermore, the maximum number of preovulatory vitellogenic follicles that we observed was less than the brood size reported by all other sources. As regional variability in important life history parameters has been shown to occur in numerous species (Cope 2006), it is possible that the variability in maximum brood size is associated with spatial differences in the reproductive biology of Cuban Dogfish. However, the large degree of disparity between the observed maximum brood size of 4 reported herein and the 26 reported by Cruz-Pacheco (1997) is of concern. While no estimates of maximum longevity or age at maturity are available for Cuban Dogfish, if they have a life history similar to that of a congener that reaches approximately the same maximum adult size, such as the Shortnose Spurdog, and we use the female-specific estimates of 32 years as the maximum age and 15 years as the age at 50% maturity (Watson and Smale 1999), the importance of this disparity in brood sizes becomes apparent. For example, if a female Cuban Dogfish reaches maturity at 15 years, lives to age 32, has a biennial reproductive cycle, and carries the maximum brood size of 4 found in this study, its total lifetime fecundity would be 32; by contrast, with a brood size of 26 its total lifetime fecundity would be 208.

Given that Cuban Dogfish concurrently undergo vitellogenesis and gestation and that they are a small-bodied species with relatively large young, it does not seem possible that they could carry the reproductive products (i.e., fully developed follicles and embryos) suggested by Cruz-Pacheco (1997) due to space limitations within the coelom. Given this, the lack of detail provided by Cruz-Pacheco (1997), and the fact that we observed a

maximum brood size of 4 among the 142 pregnant females we examined, we believe the Cruz-Pacheco (1997) estimate to be questionable, perhaps the result of a typographical error or the inclusion of data from a more fecund congener. For example, Cruz-Pacheco (1997) included individuals up to 1,100 mm TL in his analysis. We did not observe any individuals greater than 564 mm STL in our study and therefore speculate that Cruz-Pacheco (1997) included data from another squalid inhabiting the Gulf of Mexico, most likely Shortspine Spurdogs, that were erroneously identified as Cuban Dogfish.

The mean brood size of 2.2 for Cuban Dogfish is one of the smallest among species within the genus. For example, mean brood size estimates for congeners include 7.1 for Spiny Dogfish (Jones and Geen 1977), 5.6 for Edmund's Spurdogs *S. edmundsi*, 6.7 for Indonesian Spurdogs *S. hemipinnis*, 8.5 for Philippines Spurdogs *S. montalbani* (White and Dharmadi 2010), 4.1 for Shortnose Spurdogs (Hazin et al. 2006), and 7.3 for Shortspine Spurdogs (Fischer et al. 2006). While we have no knowledge of the age at maturity or longevity of Cuban Dogfish, its relatively low mean brood size is of particular concern in itself, as dogfishes in general have among the lowest known potential for population increase (Frisk et al. 2001). Furthermore, chondrichthyan fishes occupying deepwater habitats have significantly lower rebound potential than those inhabiting shallower waters (Simpfendorfer and Kyne 2009), and several coastal and pelagic species are reported to have declined significantly due to fishing pressure (e.g., Myers and Worm 2005). As fishing pressure increases in deepwater habitats, it will be imperative to consider the susceptibility of Cuban Dogfish to levels of exploitation beyond those that are sustainable.

ACKNOWLEDGMENTS

We thank M. Grace, S. Gulak, C. Jones, and the crews of the NOAA Ships *Oregon II*, *Gordon Gunter*, and *Pisces* for assistance in collecting specimens.

REFERENCES

- Bañón, R., C. Piñero, and M. Casas. 2006. Biological aspects of deep-water shark *Centroscyrmnus coelolepis* and *Centrophorus squamosus* in Galician waters (north-western Spain). *Journal of the Marine Biological Association of the United Kingdom* 86:843–846.
- Bigelow, H. B., and W. C. Schroeder. 1948. Sharks. Pages 59–546 in J. Tee-Van, editor. *Fishes of the western North Atlantic, part one, lancelets, cyclostomes, sharks*. Sears Foundation for Marine Research, New Haven, Connecticut.
- Cailliet, G. M., and K. J. Goldman. 2004. Age determination and validation in chondrichthyan fishes. Pages 399–447 in J. C. Carrier, J. A. Musick and M. R. Heithaus, editors. *Biology of sharks and their relatives*. CRC Press, Boca Raton, Florida.
- Castro, J. I. 1983. *The sharks of North American waters*. Texas A&M University Press, College Station.
- Castro, J. I. 2011. *The sharks of North America*. Oxford University Press, New York.
- Clarke, M. W., P. L. Connelly, and J. J. Bracken. 2001. Aspects of reproduction of the deep water sharks *Centroscyrmnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. *Journal of the Marine Biological Association of the United Kingdom* 810:1019–1029.

- Compagno, L. J. V. 1984. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Hexanchiformes to Lamniformes. FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis 125:116–117.
- Compagno L. J. V., and R. Vergara. 1978. Squalidae. In W. Fischer, editor. FAO species identification sheets for fishery purposes: western central Atlantic Fishing Area 31, volume V. Food and Agriculture Organization of the United Nations, Rome.
- Cope, J. M. 2006. Exploring intraspecific life history patterns in sharks. U.S. National Marine Fisheries Service Fishery Bulletin 104:311–320.
- Cruz-Pacheco, M. J. 1997. La biología y pesquería del cazón espinoso *Squalus cubensis* (Howell-Rivero, 1936) en las aguas del estado de Veracruz. [The biology of and fishery for the Cuban Dogfish *Squalus cubensis* (Howell-Rivero, 1936) in the waters of the state of Veracruz.] Master's thesis. Universidad Nacional Autónoma México, Mexico City, Mexico.
- Driggers, W. B. III, G. H. Burgess, A. N. Hamilton Jr., N. M. Hopkins, and C. M. Schobernd. 2010. *Squaliolus laticaudus* in the western North Atlantic Ocean: distributional and life history observations. Bulletin of Marine Science 86:831–838.
- Driggers, W. B. III, G. W. Ingram Jr., M. A. Grace, C. T. Gledhill, T. A. Henwood, C. N. Horton, and C. M. Jones. 2008. Popping areas and mortality rates of young Tiger Sharks *Galeocerdo cuvier* in the western North Atlantic Ocean. Aquatic Science 2:161–170.
- Fischer, A. F., D. P. Veras, F. H. V. Hazin, M. K. Broadhurst, G. H. Burgess, and P. G. V. Oliveira. 2006. Maturation of *Squalus mitsukurii* and *Cirrhigaleus asper* (Squalidae, Squaliformes) in the southwestern equatorial Atlantic Ocean. Journal of Applied Ichthyology 22:495–501.
- Frisk, M. G., T. J. Miller, and M. J. Fogarty. 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. Canadian Journal of Fisheries and Aquatic Sciences 58:969–981.
- Graham, K. J. 2005. Distribution, population structure and biological aspects of *Squalus* spp. (Chondrichthyes: Squaliformes) from New South Wales and adjacent Australian waters. Marine and Freshwater Research 56:405–416.
- Hanchet, S. 1988. Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 55:537–549.
- Hazin, F. H. V., A. F. Fischer, M. K. Broadhurst, D. Veras, P. G. Oliveira, and G. H. Burgess. 2006. Notes on the reproduction of *Squalus megalops* off northeastern Brazil. Fisheries Research 79:251–257.
- IUCN (International Union for Conservation of Nature). 2012. The IUCN red list of threatened species: *Squalus cubensis*. Available: <http://www.iucnredlist.org/details/61416/0>. (October 2012).
- Jones, B. C., and G. H. Geen. 1977. Reproduction and embryonic development of Spiny Dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia. Journal of the Fisheries Research Board of Canada 34:1286–1292.
- Kyne, P. M., and C. A. Simpfendorfer. 2010. Deepwater Chondrichthyan. Pages 37–113 in J. C. Carrier, J. A. Musick, and M. R. Heithaus, editors. Sharks and their relatives, II: biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, Florida.
- McEachran, J. D., and J. D. Fechhelm. 1998. Fishes of the Gulf of Mexico, volume 1: Myxiniiformes to Gasterosteiformes. University of Texas Press, Austin.
- Mollet, H. F., G. Cliff, H. L. Pratt Jr., and J. D. Stevens. 2000. Reproductive biology of the female Shortfin Mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. U.S. National Marine Fisheries Service Fishery Bulletin 98:299–318.
- Myers, R. A., and B. Worm. 2005. Extinction, survival or recovery of large predatory fishes. Philosophical Transactions of the Royal Society of London B (Biological Sciences) 360:13–20.
- Powell, S. M., R. L. Haedrich, and J. D. McEachran. 2003. The deep-sea demersal fish fauna of the northern Gulf of Mexico. Journal of Northwest Atlantic Fishery Science 31:19–33.
- Pratt, H. L. Jr. 1993. The storage of spermatozoa in the oviducal of western North Atlantic sharks. Environmental Biology of Fishes 38:139–149.
- Simpfendorfer, C. A., and P. M. Kyne. 2009. Limited potential to recover from overfishing raises concerns for deep-sea sharks, rays and chimaeras. Environmental Conservation 36:97–103.
- Walker, T. I. 2005. Reproduction in fisheries science. Pages 81–127 in W. C. Hamlett, editor. Reproductive biology and phylogeny of Chondrichthyes: sharks, batoids, and chimaeras. Science Publishers, Enfield, New Hampshire.
- Watson, G., and M. J. Smale. 1998. Reproductive biology of shortnose spiny dogfish, *Squalus megalops*, from the Agulhas Bank, South Africa. Marine and Freshwater Research 49:695–703.
- Watson, G., and M. J. Smale. 1999. Age and growth of the Shortnose Spiny Dogfish *Squalus megalops* from the Agulhas Bank, South Africa. South African Journal of Marine Science 21:9–18.
- White, W. T., and Dharmadi. 2010. Aspects of maturation and reproduction in hexanchiform and squaliform sharks. Journal of Fish Biology 76:1362–1378.
- Yano, K. 1995. Reproductive biology of the Black Dogfish, *Centroscyllium fabricii*, collected from waters off western Greenland. Journal of the Marine Biological Association of the United Kingdom 75:285–310.
- Yano, K., and S. Tanaka. 1988. Size at maturity, reproductive cycle, fecundity, and depth segregation of the deep sea squaloid sharks *Centroscymnus owstoni* and *C. coeleolepis* in Suruga Bay, Japan. Nippon Suisan Gakkai 54: 167–174.
- Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice Hall, Upper Saddle River, New Jersey.