Spatial variability in the fecundity of Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) in the northern Gulf of Mexico

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Abstract—Spatial variability in life history characteristics, including age at maturity, growth rates, and reproductive periodicity, has been documented for a number of shark species. Among causative factors hypothesized to induce dissimilarities, clinal variation is most often linked to temperature. However, if spatial differences in prey abundance were the causative factor, it could be masked by clinal variation. If prey abundance is the actual driver, intraspecific differences should be evident over a broad longitudinal range (i.e., constant water temperature) characterized by a demarcation of low and high productivity. In this study, Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) were collected for 1 year throughout the northern Gulf of Mexico (GOM) by using standardized bottom longline gear. Reproductive data were collected from 253 gravid females, and mean (4.2 versus 3.4 embryos) and median (4 versus 3 embryos) brood sizes were higher west of longitude 88°W than to the east. Based on fisheries survey data, spatial trends in abundance of Atlantic croaker (*Micropogonias undulatus*), a common prey item, coincided with that of Atlantic sharpnose sharks, and both were more abundant west of 88°W. Although differences in brood sizes appear minor, potential lifetime reproductive output for females was calculated to be over 2 times greater in the western versus the eastern GOM.

An essential component for appropriately assessing and effectively managing populations of elasmobranchs (sharks, skates, and rays) is accurate species-specific information pertaining to reproductive biology (Walker, 2005). However, intraspecific differences in important reproductive characteristics, such as size at maturity, size at birth, and reproductive periodicity, have been shown to occur within some shark species (e.g., Lombardi-Carlson et al., 2003; Sulikowski et al., 2007; Driggers and Hoffmayer, 2009), complicating the management process. For example, Yamaguchi et al. (2000) examined the reproductive biology of starspotted smooth-hounds (*Mustelus manazo*) at 5 locations in the eastern Pacific Ocean and found that individuals at the northernmost sampling location had a higher age and size at maturity and longer reproductive cycle than conspecifics at

lower latitudes. Because of the importance of reproductive data as inputs into demographic and population models (Cortés, 2002), it is imperative to describe the life history of a species at various locations throughout its range and to not assume that these variables are spatially constant.

Intraspecific variability in reproductive traits for sharks has largely been documented along latitudinal clines (e.g., Taniuchi et al., 1993; Horie and Tanaka, 2002; Lombardi-Carlson et al., 2003). For example, Parsons (1993) examined several reproductive characteristics for bonnetheads (*Sphyrna tiburo*) off the west coast of Florida in the western North Atlantic Ocean and reported, among other differences, that females at a higher latitude had a longer gestation period, had a larger size at maturity, and gave birth to larger offspring than females at a lower latitude.

Similarly, Colonello et al. (2007) found that female angular angel sharks (*Squatina guggenheim*) off the coast of South America mature at larger sizes at higher latitudes than conspecifics at lower latitudes.

Among studies that have documented spatial disparities in reproductive traits, several hypotheses focusing on regional differences in prey availability, temperature, mortality, and energetics related to migrations have been formulated (e.g., Parsons, 1993; Yamaguchi et al., 2000; Sulikowski et al., 2007; Walker, 2007). Most studies that have examined geographic variability in reproductive traits for sharks have in total (e.g., Yamaguchi et al., 2000; Colonello et al., 2007) or in part (e.g., Lombardi-Carlson et al., 2003; Walker, 2007) attributed observed disparities to differences in water temperatures associated with changes in latitude. Cope (2006) suggested that, in addition to latitudinal variability as a cause for different reproductive traits, regional differences in fishing pressure could result in varying intraspecific life histories. This hypothesis was later supported by Walker (2007), who suggested that length-selective fishing mortality resulted in differences in sizes at maturity and maternity for gummy sharks (*Mustelus antarcticus*) at 2 locations off southern Australia. Walker (2007) also stated that another possible explanation was differences in environmental conditions between sampling locations. Parsons (1993) considered variability in prey abundance along the west coast of Florida as a cause of the reproductive differences found in bonnetheads; however, he concluded differences were related to seasonal variation in water temperature and photoperiod.

If spatial differences in prey availability could result in variability in important life history characteristics, one would expect to see differences within a shark species inhabiting a broad longitudinal range (i.e., constant water temperature) characterized by a strong demarcation of relatively low and high productivity. Therefore, the objective of this study was to compare the fecundity of Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) between the eastern and western areas of the northern Gulf of Mexico (GOM), with the former region characterized by low productivity and the latter by high productivity (e.g., Riley, 1937).

Materials and methods

Atlantic sharpnose sharks were collected throughout the northern GOM from April through October 2011 by using standardized bottom longline gear. The gear consisted of 1.8 km of 4.0-mm diameter monofilament mainline with 100 gangions constructed with a size 148 snap, 3.7 m of 3.0-mm diameter monofilament leader, and a 15/0 circle hook (model no. 39960D, O. Mustad & Son A.S.[1], Gjovik, Norway) and was set at depths of 7–459 m (mean: 99.8 m

[standard deviation (SD) 100.0]). Four bottom longline vessels sampled throughout U.S. waters of the northern GOM for 20 days in each month. Biologists on each vessel were requested to retain and freeze a maximum of 10 female sharks greater than 650 mm fork length (FL) during each 20-d period. This size was selected because it approximately coincided with estimates of size at 50% maturity for female Atlantic sharpnose sharks (e.g., Driggers et al.[2]). All collected sharks were subsequently transported to the National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories for reproductive data collection.

Hoffmayer et al. (2013) proved that there is significant seasonal variability in the timing of ovulation, mating, and parturition among Atlantic sharpnose sharks in the northern GOM. Because reproductive asynchrony could obfuscate potential differences in the reproductive biology of this species when comparing the eastern and western GOM, we chose to focus solely on fecundity. To assess fecundity, each specimen was thawed and an incision was made from the cloaca to the pectoral girdle. An incision was then made in each uterus, and contents were removed. The number of embryos in the uteri was then counted, and the sex of all individuals within each brood was recorded. Unfertilized eggs and embryos in very early stages of development were not included in counts because of the uncertainty of correctly identifying a blastodisc in frozen and subsequently thawed specimens. Therefore, as development of embryos within a single brood is synchronous and thus negates potential bias associated with omitting all uterine eggs in the blastodisc stage of development, only macroscopically visible embryos were included in counts.

To determine the longitude that would be used to separate the northern GOM into eastern and western areas, a map of catch per unit of effort (CPUE, defined as number of Atlantic sharpnose sharks caught per 100 hook hours) for all longline sets was generated with the mapping software Surfer (vers. 11.5.1069; Golden Software, Golden, CO), by using a point kriging function and semi-variogram model with a linear component, anisotropy angle of 0, and anisotropy ratio and variogram slope of 1. Using the same methods, we mapped the distribution of Atlantic croaker (*Micropogonias undulatus*), a primary prey species of Atlantic sharpnose sharks in the northern GOM (Bethea et al., 2006; Higgs et al., 2012), to examine similarities in the spatial abundance of predator and prey. Data on catch of Atlantic croaker (defined as kilograms per trawl hour) were retrieved from the Southeast Area Monitoring and Assessment Program (SEAMAP) Trawl Survey database (available from website, accessed May 2017). Trawl survey data, which were collected yearly during June–July and October–November, were

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[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2] Driggers, W. B., III, E. R. Hoffmayer, J. K. Carlson, and J. Loefer. 2013. Reproductive parameters for Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) from the western North Atlantic Ocean. Southeast Data, Assessment, and Review SEDAR34-WP-30, 5 p. [Available from website.]

limited to the years 2009–2014 and collected by using the methods described by Rester[3].

Prior to conducting analyses, data related to the lengths of all females captured, to the lengths of all gravid females, and to brood size were investigated to identify outliers on a regional basis. Outliers were defined as those points that were 3 times above or below the upper and lower quartiles. We employed *t*-tests to compare region-specific lengths of female sharks for all captured individuals, length of gravid females, and brood sizes. If data did not adhere to the assumptions of normality and homoscedasticity, as indicated by skewness, kurtosis, and *F*-tests, data were log-transformed. If the assumptions of parametric statistics were still not met after transformation, Mann–Whitney *W* (length) and Kolmogorov–Smirnov (distributions) tests were used to compare data between regions. Regression analyses were used to examine the relationship between maternal body length and brood size for each region and for both areas combined. Length and brood-size data were log-transformed, and analysis of covariance (ANCOVA) was used to determine if there was a difference in regression lines between the eastern and western GOM. To describe the relationship for combined areas, 21 regression models were fitted, and the one selected to best represent the relationship was chosen on the basis of the highest coefficient of determination (r^2). Further, to examine if there was a latitudinal effect on brood size, a linear regression was conducted on latitude of capture of gravid females and the associated brood sizes. All statistical tests were considered significant at an α of 0.05.

To examine the potential lifetime reproductive output (PLRO) of 2 hypothetical female Atlantic sharpnose sharks with disparate mean brood sizes, the total number of offspring attributable to these females over their lifetimes was calculated. On the basis of the results of Driggers et al.[2] and Hoffmayer et al. (2013), it was assumed that in the northern GOM, female Atlantic sharpnose sharks mature at an age of 1.3 years, have a maximum longevity of 17.2 years, reproduce annually, and gestate for approximately 1 year and that the sex ratio of embryos is 1:1. Although mating occurs over a protracted period, the earliest stages of gestation are generally observed in July (Hoffmayer et al., 2013). Therefore, we assumed that the age at first maternity for Atlantic sharpnose sharks in the northern GOM was 3 years. We made a simplifying assumption that the mortality rate of the female, her offspring, and subsequent generations was zero throughout each hypothetical female's lifetime. Additionally, we did not account for the relationship between length and brood size because growth models specific to the eastern and western regions of the northern GOM were not available to back-transform size at age.

To test if prey availability affects the fecundity of female Atlantic sharpnose sharks in the eastern and western GOM, we examined condition factor between the 2 regions. Because body weight of females can vary widely depending on reproductive condition (e.g., state of maturity, degree of embryo development, and brood size) and female Atlantic sharpnose sharks are not completely reproductively synchronous in the northern GOM, we examined the condition factor of males as a proxy. Males were better suited for this analysis because their body weight is less affected by reproductive state. Although testis weight does vary throughout the year, the resolution of scales used in the field was 0.25 kg; therefore, seasonal change in testis weight was considered undetectable. Furthermore, because weights were obtained at sea, vessel motion could have increased measurement error. As a result, regression analyses were applied to length and weight data from all males, with the exception of specimens that were damaged because of depredation, and the model best describing the relationship was fit to the data. The best fit model was considered that with the highest r^2. Those data points that had Studentized residuals greater than 2 in absolute value were considered outliers and were removed from the data set.
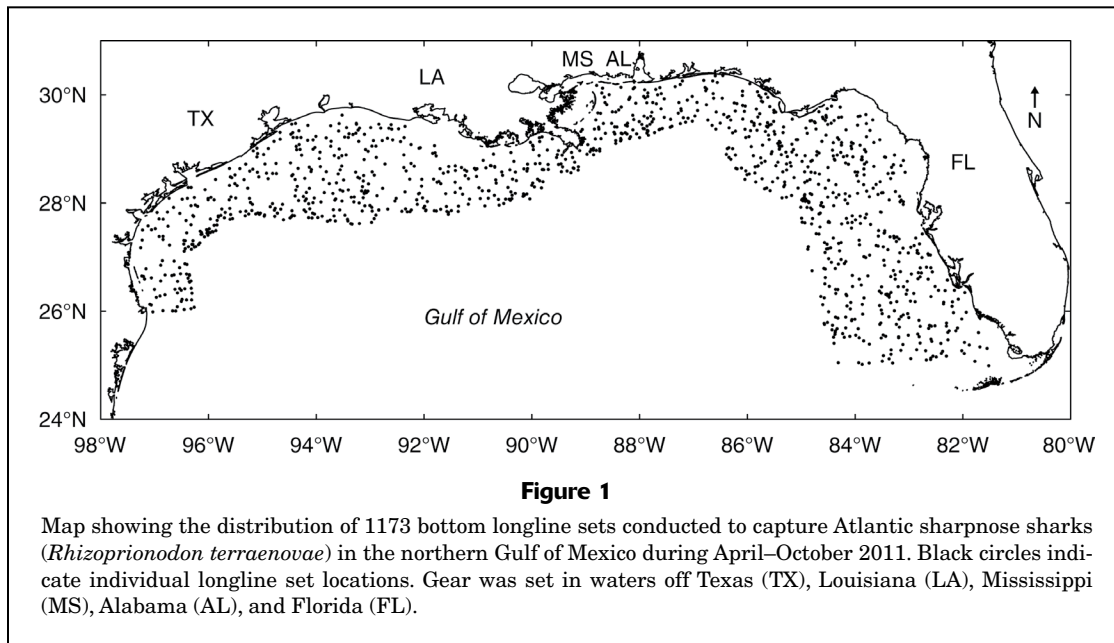
Region-specific length–weight regressions were then analyzed by using ANCOVA after parameters were log-transformed. Additionally, non-transformed length and weight data were used to calculate Fulton's condition factor (*K*), as outlined in Froese (2006). Prior to calculating *K*, all length and weight data, which were originally recorded in millimeters and kilograms, were converted into centimeters and grams, respectively. Despite trying multiple transformations (e.g., cube root, log, and square), these data did not conform to the assumptions of parametric statistics. As a result, Mann–Whitney *W* (length) and Kolmogorov–Smirnov (distributions) tests were used to compare *K* values between regions.

Data from males collected on the West Florida Shelf were also used to examine latitudinal effects on body length and weight. Data were limited to males for the reasons outlined previously and were truncated to include only mature sharks captured east of 85°W. Males were considered mature if they had calcified claspers that freely rotated 180° and had a functional rhipidion. The spatial limit was applied so that males outside of the latitudinal cline were excluded (i.e., shelf axis runs north–south and excludes an expansive east–west component). Regression analyses were performed with latitude and body size (i.e., length and weight) as the independent and dependent variables, respectively.

Results

A total of 1173 longline sets were conducted (Fig. 1), resulting in the capture of 4082 Atlantic sharpnose sharks. Females (number of specimens [*n*]=1943) and males (*n*=1910) ranged in size from 278 to 992 mm FL (mean: 726.6 mm FL [SD 104.3]) and from 296 to 915 mm FL (mean: 726.9 mm FL [SD 86.7]), respectively (sex and lengths were not recorded for 229 individuals because of

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[3] Rester, J. K. (ed.). 2011. SEAMAP environmental and biological atlas of the Gulf of Mexico, 2009. Gulf States Mar. Fish. Comm., no. 198, 74 p. [Available from website.]

Figure 1

Map showing the distribution of 1173 bottom longline sets conducted to capture Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) in the northern Gulf of Mexico during April–October 2011. Black circles indicate individual longline set locations. Gear was set in waters off Texas (TX), Louisiana (LA), Mississippi (MS), Alabama (AL), and Florida (FL).

damage inflicted by other sharks). In the western GOM, females ranged in size from 278 to 992 mm FL (n=1590; mean: 735.1 mm FL [SD 102.7]), and in the eastern GOM, they ranged from 390 to 884 mm FL (n=353; mean: 687.8 mm FL [SD 102.6]). Males ranged in size from 296 to 915 mm FL in the western GOM (n=1697; mean: 731.8 mm FL [SD 86.0]) and from 384 to 860 mm FL in the eastern GOM (n=213; mean: 684.1 mm FL [SD 84.5]). Visual inspection of the interpolated distribution map based on CPUE of Atlantic sharpnose sharks throughout the northern GOM revealed a distinct discontinuity in the abundance of the species at approximately 88°W (Fig. 2). Therefore, for the purposes of subsequent analyses, the western GOM was defined as that region west of 88°W, and the eastern GOM was defined as the area east of 88°W.

Outliers omitted from the data sets were limited to one 278-mm-FL female collected in the western GOM and 3 broods of 8 embryos observed in the eastern GOM. Mean sizes of females captured in the eastern and western GOM were 687.9 mm FL (SD 102.6) and 735.1 mm FL (SD 102.1), respectively, and there was a significant difference in the median sizes of females captured in the 2 regions: 695 mm FL in the east and 760 mm FL in the west (W=356,870, P<0.01) (Fig. 3). Similarly, among gravid female specimens examined (n=253), there was a significant difference in the mean FL among individuals in the eastern (752.2 mm FL [SD 64.5]) and western (779.5 mm FL [SD 54.2]) GOM (t=−2.89, P<0.01) (Fig. 4). There was no significant relationship between latitude and body length (F=1.26, P=0.27) or weight (F=2.27, P=0.14) for mature males on the West Florida Shelf.
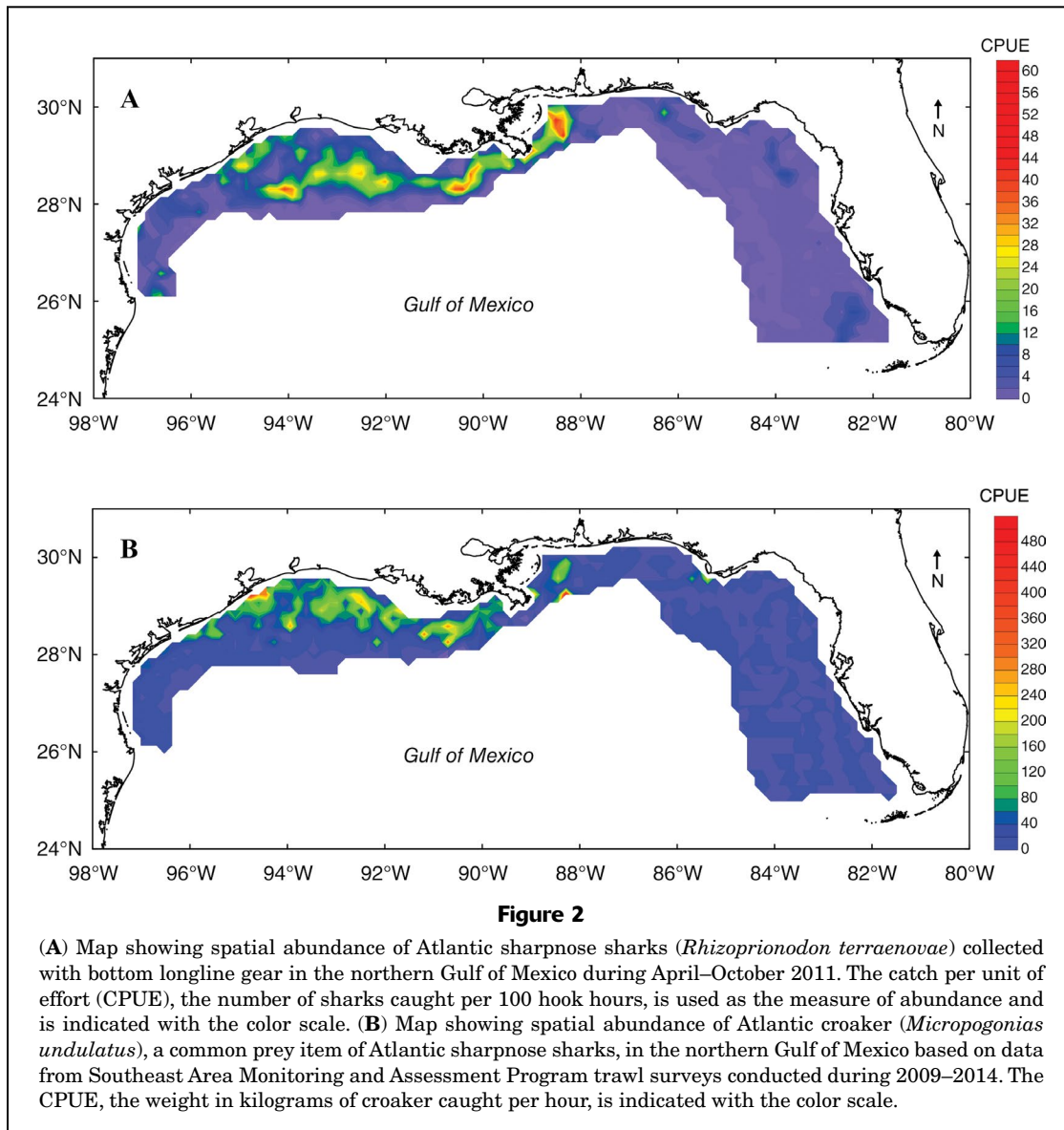
During this study, brood-size data were collected from 253 gravid females (eastern GOM: n=42; western GOM: n=211),

ranging in size from 647 to 935 mm FL (mean: 775.0 mm FL [SD 56.8]) (Fig. 5). There was no significant difference between the slopes (F=2.12, P=0.15) or intercepts (F=0.27, P=0.61) for the relationship between maternal FL and brood size when comparing specimens collected in the eastern and western GOM. There was a significant positive relationship between maternal FL and brood size (F=305.88, P<0.01, r^2=0.55) for data collected from the combined areas (Fig. 6); this relationship was described by the following equation:

$$brood\ size = \sqrt{-58.1084 + 0.000129332 \times FL^2}.$$

However, there was no significant relationship between latitude and brood size (F=2.48, P=0.12, r^2=0.58) (Fig. 7). There was a significant difference in the mean brood size between the 2 regions (t=−3.03, P<0.01) with mean brood sizes of 3.4 embryos (SD 1.4) and 4.2 embryos (SD 1.7) in the eastern and western GOM, respectively. When including those values considered outliers (i.e., 3 broods of 8 embryos from the eastern GOM), data were not normally distributed and could not be made so through transformation. However, median brood size was significantly lower (W=5398.5, P=0.02) among gravid females in the eastern GOM (median: 3 embryos; mean: 3.7 embryos [SD 1.8]) than in the western GOM (median: 4 embryos; mean: 4.2 embryos [SD 1.7]) (Fig. 5).

Under the previously stated assumptions, the total number of offspring the hypothetical females would give birth to in the eastern and western GOM during each mother's lifetime (first generation of each mother's 15 broods [B1–15, G1]) would be 51 and 63, respectively. During the 17-year lifespans of the 2 hypothetical females, the 5 generations associated with each female's first brood (i.e., B1, G1–5) would produce 64.1 young in the eastern

Figure 2

(**A**) Map showing spatial abundance of Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) collected with bottom longline gear in the northern Gulf of Mexico during April–October 2011. The catch per unit of effort (CPUE), the number of sharks caught per 100 hook hours, is used as the measure of abundance and is indicated with the color scale. (**B**) Map showing spatial abundance of Atlantic croaker (*Micropogonias undulatus*), a common prey item of Atlantic sharpnose sharks, in the northern Gulf of Mexico based on data from Southeast Area Monitoring and Assessment Program trawl surveys conducted during 2009–2014. The CPUE, the weight in kilograms of croaker caught per hour, is indicated with the color scale.
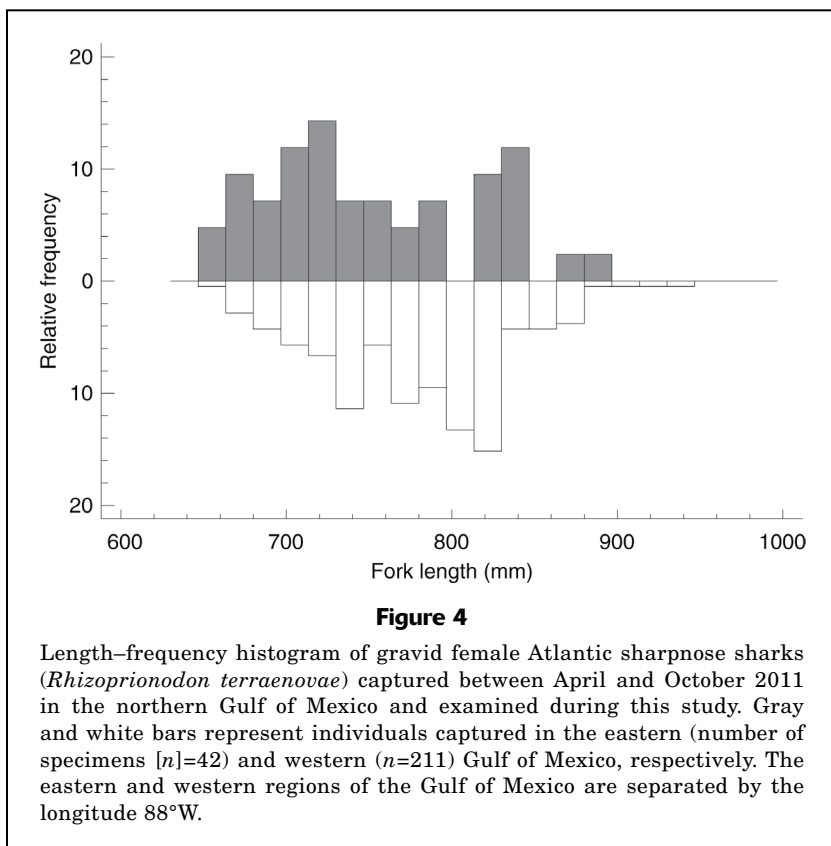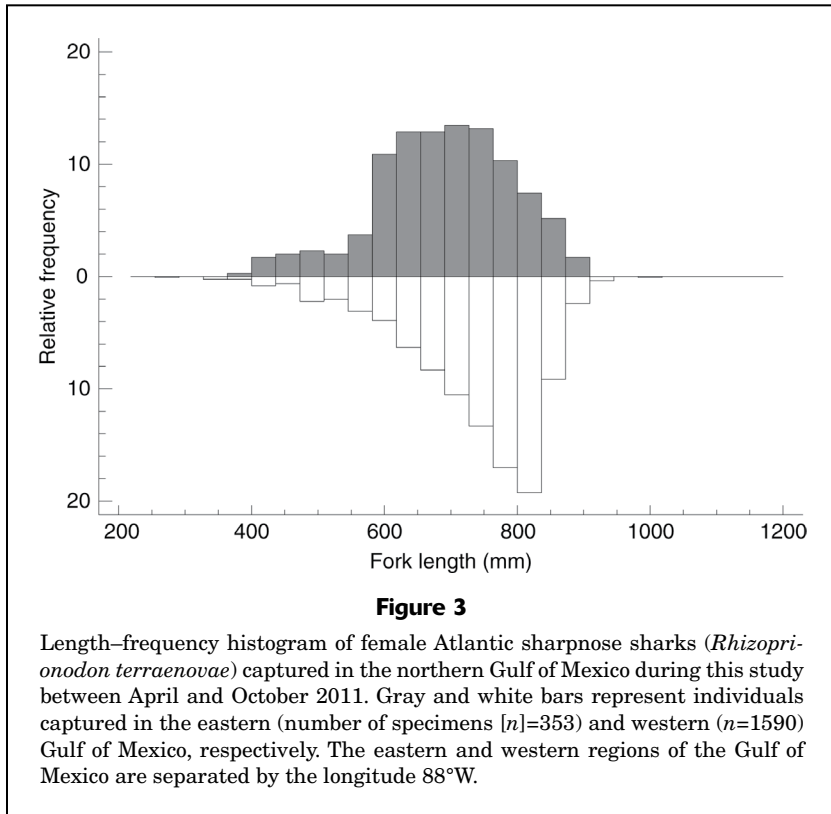
GOM and 152.1 young in the western GOM. Further, over each mother's lifetime, all broods (B1–15) and generations (G1–5) would result in a PLRO of 394.2 and 814.0 pups in the eastern and western GOM, respectively (Table 1).

A total of 1910 males were collected throughout the study area. For 1884 of those specimens, length and weight data were available. Data collected from 97 individuals were determined to be outliers (i.e., Studentized residuals >2) and were removed from subsequent analyses. Of the retained data, male body sizes were 296–915 mm FL and 0.2–5.6 kg in the western GOM (n=1587) and 384–860 mm FL and 0.5–4.2 kg in the eastern GOM (n=200). Neither length nor weight data met the assumptions of parametric statistics; however, the median length (755 versus 691 mm FL; W=219,880; P<0.01) and weight (3.3 versus 2.4 kg; W=235,136; P<0.01) of males were greater in the

western GOM than in the eastern GOM. There was no significant difference in the slope of regression lines between log FL and log weight for male Atlantic sharpnose sharks in the 2 regions (F=0.62, P=0.43); however, the intercepts were significantly different (F=123.78, P<0.01), indicating that, at a given FL, the mean weight of a male Atlantic sharpnose shark is greater in the western GOM than in the eastern GOM.

Condition factors for male Atlantic sharpnose sharks in the western GOM ranged from 0.56 to 1.03 (mean: 0.78 [SD 0.08]) and from 0.62 to 0.88 in the eastern GOM (mean: 0.73 [SD 0.06]). The median K values were significantly different between the 2 regions (W=228636, P<0.01), with the median K being higher in the western GOM (0.72) than in the eastern GOM (0.78). Similarly, the distribution of K values in the 2 regions were

Figure 3

Length–frequency histogram of female Atlantic sharpnose sharks (*Rhizopri-onodon terraenovae*) captured in the northern Gulf of Mexico during this study between April and October 2011. Gray and white bars represent individuals captured in the eastern (number of specimens [*n*]=353) and western (*n*=1590) Gulf of Mexico, respectively. The eastern and western regions of the Gulf of Mexico are separated by the longitude 88°W.

Figure 4

Length–frequency histogram of gravid female Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) captured between April and October 2011 in the northern Gulf of Mexico and examined during this study. Gray and white bars represent individuals captured in the eastern (number of specimens [*n*]=42) and western (*n*=211) Gulf of Mexico, respectively. The eastern and western regions of the Gulf of Mexico are separated by the longitude 88°W.
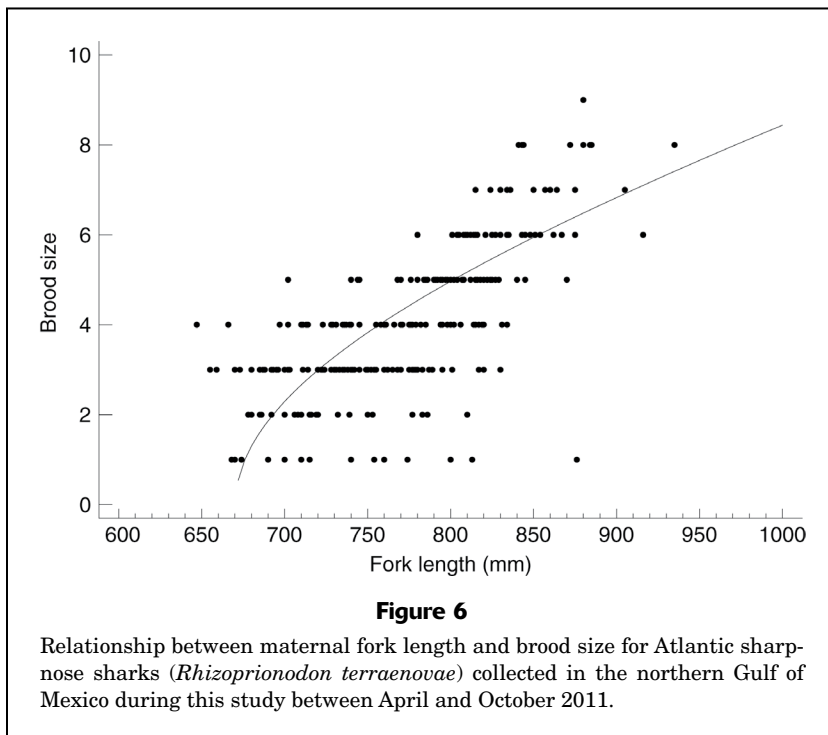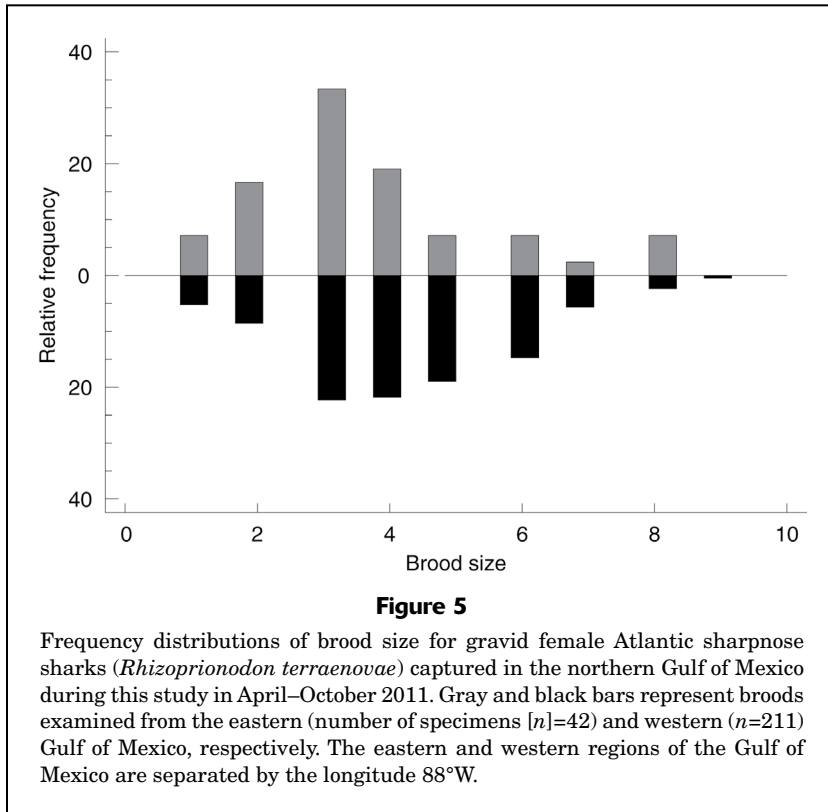
significantly different (Kolmogorov–Smirnov statistic: 4.84, $P<0.01$) (Fig. 8). Visual inspection of the interpolated distribution map based on CPUE of Atlantic croaker throughout the region revealed a distinct discontinuity in the abundance of the species at approximately 88°W; the same spatial discontinuity was observed for CPUE of Atlantic sharpnose sharks (Fig. 2).

Discussion

The phenomenon of spatial variation in the reproductive biology of elasmobranchs has been demonstrated by a number of studies, with many authors hypothesizing that this variability is primarily related to temperature and is therefore often associated with latitudinal gradients (e.g., Menni and Lessa, 1998; Yamaguchi et al., 2000; Tovar-Ávila et al., 2007). To our knowledge, the first evidence for temperature-based spatial variability among elasmobranch conspecifics is attributable to Olsen (1954), who demonstrated that, among other differences, female topes (*Galeorhinus galeus*) ovulated 3 months earlier off Australia and gave birth 1 month earlier off Tasmania, in warmer areas compared with cooler areas. Similarly, Springer (1960) stated that female sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean likely have smaller pups and give birth at a later date in cooler versus warmer waters. Conversely, Lombardi-Carlson et al. (2003) found that bonnetheads within the GOM have larger sizes at birth in cooler waters. However, Lombardi-Carlson et al. (2003) also reported that bonnetheads inhabiting higher latitudes gave birth at a later date, similar to what Springer (1960) suggested for sandbar sharks.

Unlike in other studies, the differences in brood sizes observed in our study could not be explained by temperature. To examine if temperature was responsible for differences in brood size, we took 2 approaches: 1) direct comparison of the relationship between brood size and latitude and 2) comparison of mature male body size along the West Florida Shelf as a proxy to determine if there was an increase in body size along

Figure 5

Frequency distributions of brood size for gravid female Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) captured in the northern Gulf of Mexico during this study in April–October 2011. Gray and black bars represent broods examined from the eastern (number of specimens [*n*]=42) and western (*n*=211) Gulf of Mexico, respectively. The eastern and western regions of the Gulf of Mexico are separated by the longitude 88°W.

Figure 6

Relationship between maternal fork length and brood size for Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) collected in the northern Gulf of Mexico during this study between April and October 2011.

use mature males as a proxy for females to remove spatial variability in the number of young of the year and juveniles that could potentially obfuscate trends we were examining. By using only mature individuals, we limited this analysis to individuals that were approaching the growth asymptote. Although it would have been ideal to examine females, we were able to assign maturity status to males on the basis of non-lethal, external examinations, eliminating the need to sacrifice females and rely on subjective maturity assignments that could have resulted in inclusion of nulliparous individuals or those that were entering their first reproductive cycle as mature individuals.

In the case of the relationship between brood size and latitude of capture, there was no significant relationship between the 2 variables. Similarly, there was no significant difference in the length and weight of mature males along the West Florida Shelf over latitudes ranging from approximately 25°N to 30°N. Furthermore, although a significant relationship existed between size and fecundity for Atlantic sharpnose sharks in the combined areas, the results of the ANCOVA indicate no significant difference in the brood size of similarly sized females in the eastern and western GOM. However, the mean and median sizes of females were larger in the western GOM.

The homogeneity in body length of Atlantic sharpnose sharks across the West Florida Shelf is not consistent with what has been observed for bonnetheads, which are reported to be larger with increasing latitude off the west coast of Florida (Parsons, 1993; Lombardi-Carslon et al., 2003). The disparity between our results and those of Parsons (1993) and Lombardi-Carslon et al. (2003) is likely related to the migratory habits between the 2 species. For example, on the basis of acoustic monitoring, Heupel et al. (2006) reported that bonnetheads in Charlotte Harbor, Florida, are resident within estuaries proximal to the monitoring site and rarely make long-distance seasonal migrations. This finding is supported by tag-recapture data and genetic analyses indicating that bonnetheads have a fine-scale population structure in the eastern GOM and that, when migrating from a specific estuary, they move into
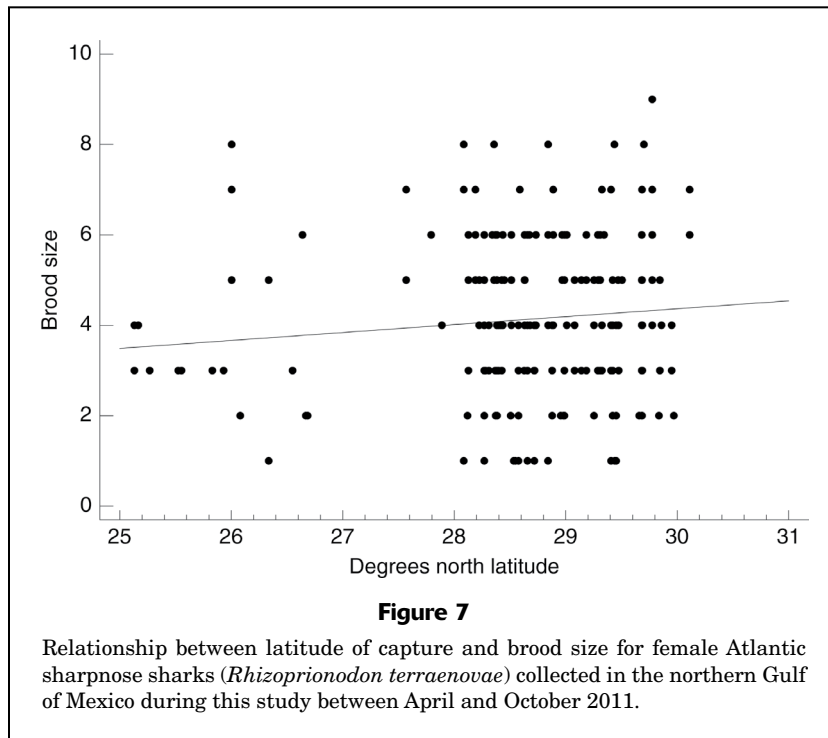
the latitudinal cline. Recall that males were analyzed to avoid the confounding issues of female body weight changing throughout the reproductive cycle (e.g., embryos in varying states of development). In addition, we chose to

Figure 7

Relationship between latitude of capture and brood size for female Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) collected in the northern Gulf of Mexico during this study between April and October 2011.

approximately 125–930 km. Conversely, Yamaguchi et al. (2000) found that the brood size of starspotted smooth-hounds decreased with latitude in similarly sized females over a latitudinal cline of approximately 1800 km. However, Yamaguchi et al. (2000) also noted a significant positive relationship between maternal length and brood size, a relationship that has been established for numerous shark species (e.g., Ford, 1921), and reported that females at higher latitudes attained longer lengths than conspecifics at lower latitudes. We found neither a difference in size-specific fecundity of Atlantic sharpnose sharks along the West Florida Shelf nor a difference in body size along a latitudinal cline of approximately 600 km. However, we did find significant differences in these characteristics between the eastern and western GOM, indicating a factor other than latitude or temperature is responsible for the observed differences.

Although our sampling occurred over a period of only 1 year, it is possible that the higher fecundity of Atlantic sharpnose sharks in the western GOM versus the eastern GOM is a density-dependent response to a past reduction in population size within that region. Rose et al. (2001) reviewed density dependence among fish species, defined compensatory changes as those that increase or decrease population growth when density is low and high, respectively, and stated that depensatory changes slow population growth rates at low densities. Studies of density-dependent change in shark populations have largely focused on temporal differences in growth rates, size and age at maturity, and fecundity for affected populations (e.g., da Silva and Ross[6]; Sminkey and Musick, 1995; Sosebee, 2005). For example, Taylor and Gallucci (2009) determined that, for spiny dogfish (*Squalus acanthias*) in the northeast Pacific Ocean, age at maturity decreased while fecundity increased over a 60-year period. Carlson and Baremore (2003) compared data on the life history of Atlantic sharpnose sharks published between 1979 and 1984 with direct estimates obtained from necropsies and vertebral analysis from 1998 to 2001 and found that, although size and age at maturity decreased and growth rates increased between the 2 periods, no change was evident in size at parturition or fecundity.

If the differences we observed in fecundity between the eastern and western GOM were related to a change in population density, fecundity should have been highest in the area of lowest adult abundance or of highest adult mortality. However, results of our study indicate that

neighboring systems (Tyminski et al.[4]; Portnoy et al., 2015; Fields et al., 2016). Unlike for bonnetheads, no fine-scale population structure has been observed for Atlantic sharpnose sharks in the northern GOM (Heist et al., 1996; Davis et al., 2019) and tag-recapture data show relatively larger scale movements in the region compared with those of bonnetheads (Tyminski et al.[4]; Deacy[5]). If brood size is affected by temperature, the phenomenon would be expected to be most evident in a species, such as bonnetheads, that has been shown to make limited movements outside of spatially discrete areas along a latitudinal cline.

Despite no evidence of latitudinal variability in the fecundity of Atlantic sharpnose sharks being found in our study and for bonnetheads by Lombardi-Carlson et al. (2003), such a trend has been identified for other species. For example, Chen et al. (1981) found higher brood sizes of Japanese spurdogs (*Squalus japonicus*) with increasing latitude between 2 sampling locations in the Indo-Pacific along a latitudinal cline of approximately 350 km. Other species for which similar trends of larger broods associated with increasing latitude have been observed include the shortspine dogfish (*S. mitsukurii*) and gummy shark (Lenanton et al., 1990; Taniuchi et al., 1993), along latitudinal clines of

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[4] Tyminski, J. P., R. E. Hueter, and J. Morris. 2013. Tag-recapture results of bonnethead (*Sphyrna tiburo*) and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks in the Gulf of Mexico and Florida coastal waters. Southeast Data, Assessment, and Review SEDAR34-WP-31, 13 p. [Available from website.]

[5] Deacy, B. 2018. Personal commun. Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., 3500 Delwood Beach Rd., Panama City, FL 32408-7403.

[6] da Silva, H. M., and M. R. Ross. 1993. Reproductive strategies of spiny dogfish, *Squalus acanthias*, in the NW Atlantic. ICES CM 1993/G:51, 18 p. [Available from website.]

Table 1

Potential lifetime reproductive output (PLRO) of 2 hypothetical female Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) in the eastern and western regions of the northern Gulf of Mexico. The numbers of pups in the columns on either side of the age column represent the brood size (B1–15) attributable to each female (first generation, G1) and her female offspring (subsequent 4 generations, G2–G5) throughout the 17-year lifespan of the original 2 hypothetical females. The eastern and western regions of the Gulf of Mexico are separated by the longitude 88°W.

Western region					Age (years)	Eastern region				
					0					
					1					
					2					
				$4.2_{B1,G1}$	3	$3.4_{B1,G1}$				
				$4.2_{B2,G1}$	4	$3.4_{B2,G1}$				
				$4.2_{B3,G1}$	5	$3.4_{B3,G1}$				
			$8.8_{B1,G2}$	$4.2_{B4,G1}$	6	$3.4_{B4,G1}$	$5.8_{B1,G2}$			
			$8.8_{B2,G2}$	$4.2_{B5,G1}$	7	$3.4_{B5,G1}$	$5.8_{B2,G2}$			
			$8.8_{B3,G2}$	$4.2_{B6,G1}$	8	$3.4_{B6,G1}$	$5.8_{B3,G2}$			
		$18.5_{B1,G3}$	$8.8_{B4,G2}$	$4.2_{B7,G1}$	9	$3.4_{B7,G1}$	$5.8_{B4,G2}$	$9.8_{B1,G3}$		
		$18.5_{B2,G3}$	$8.8_{B5,G2}$	$4.2_{B8,G1}$	10	$3.4_{B8,G1}$	$5.8_{B5,G2}$	$9.8_{B2,G3}$		
		$18.5_{B3,G3}$	$8.8_{B6,G2}$	$4.2_{B9,G1}$	11	$3.4_{B9,G1}$	$5.8_{B6,G2}$	$9.8_{B3,G3}$		
	$38.9_{B1,G4}$	$18.5_{B4,G3}$	$8.8_{B7,G2}$	$4.2_{B10,G1}$	12	$3.4_{B10,G1}$	$5.8_{B7,G2}$	$9.8_{B4,G3}$	$16.7_{B1,G4}$	
	$38.9_{B2,G4}$	$18.5_{B5,G3}$	$8.8_{B8,G2}$	$4.2_{B11,G1}$	13	$3.4_{B11,G1}$	$5.8_{B8,G2}$	$9.8_{B5,G3}$	$16.7_{B2,G4}$	
	$38.9_{B3,G4}$	$18.5_{B6,G3}$	$8.8_{B9,G2}$	$4.2_{B12,G1}$	14	$3.4_{B12,G1}$	$5.8_{B9,G2}$	$9.8_{B6,G3}$	$16.7_{B3,G4}$	
$81.7_{B1,G5}$	$38.9_{B4,G4}$	$18.5_{B7,G3}$	$8.8_{B10,G2}$	$4.2_{B13,G1}$	15	$3.4_{B13,G1}$	$5.8_{B10,G2}$	$9.8_{B7,G3}$	$16.7_{B4,G4}$	$28.4_{B1,G5}$
$81.7_{B2,G5}$	$38.9_{B5,G4}$	$18.5_{B8,G3}$	$8.8_{B11,G2}$	$4.2_{B14,G1}$	16	$3.4_{B14,G1}$	$5.8_{B11,G2}$	$9.8_{B8,G3}$	$16.7_{B5,G4}$	$28.4_{B2,G5}$
$81.7_{B3,G5}$	$38.9_{B6,G4}$	$18.5_{B9,G3}$	$8.8_{B12,G2}$	$4.2_{B15,G1}$	17	$3.4_{B15,G1}$	$5.8_{B12,G2}$	$9.8_{B9,G3}$	$16.7_{B6,G4}$	$28.4_{B3,G5}$
		Total PLRO=814.0 pups						Total PLRO=394.2 pups		

Atlantic sharpnose sharks are most abundant in the western GOM, where fecundity is the highest.
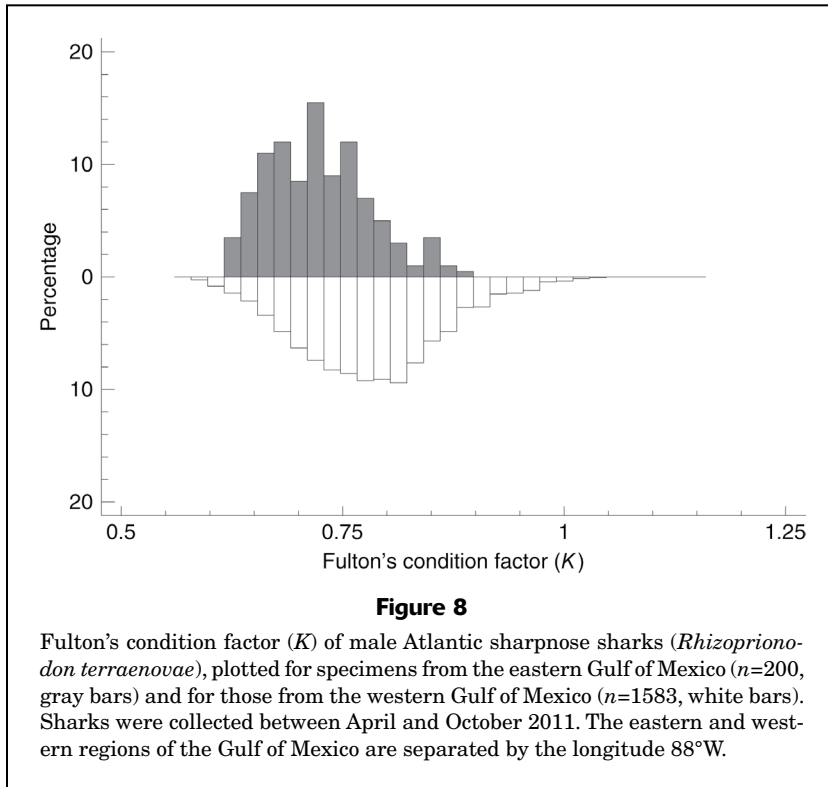
Spatial differences in the abundance of Atlantic sharpnose sharks were evident with greater abundance west than east of 88°W. The clear demarcation in abundance is similar to that reported for nurse sharks (*Ginglymostoma cirratum*) by Hannan et al. (2012), who found that nurse sharks were most abundant east of 88°W and largely absent to the west of that longitude. The authors hypothesized that the distribution of nurse sharks was driven primarily by the presence of hard-bottom substrate. Similarly, Portnoy et al. (2014), using genetic analyses of nuclear encoded microsatellites and mitochondrial DNA, described the population structure of blacknose sharks (*Carcharhinus acronotus*) in the western North Atlantic Ocean and reported a barrier to gene flow in the northern GOM corresponding with the Mississippi River Delta, in close proximity to 88°W. Portnoy et al. (2014) went on to speculate that the outflow of freshwater from the Mississippi River created a barrier to movement across the GOM for the stenohaline blacknose shark. Results of genetic analyses of Atlantic sharpnose sharks indicates that there is one genetic stock of the Atlantic sharpnose shark throughout the northern GOM (Heist et al., 1996; Todd et al., 2004; Davis et al., 2019). However, of the 118 tagged Atlantic sharpnose sharks for which recapture data were available from previous studies, only 3 individuals moved between the eastern and western GOM (Kohler et al., 1998; Bethea and Grace[7]; Hendon et al.[8]). Therefore, demarking the eastern and western GOM at 88°W is well supported and coincided with a discontinuity in the distribution of the predominant prey of Atlantic sharpnose sharks.

The diet of Atlantic sharpnose sharks is primarily composed of teleosts, which have made up approximately 66% of the identifiable remains in examinations of stomach contents (Cortés, 1999). Bethea et al. (2006) examined ontogenetic differences in the diet of Atlantic sharpnose sharks in the eastern GOM and reported that the Atlantic croaker was the most commonly identified prey within adult stomachs (6.5% index of relative importance [IRI]; all other identified species had an IRI ≤2.4%) despite their absence among the 7 most abundant prey species that were present in the study area. Higgs et al. (2012) examined the diet of

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[7] Bethea, D. M., and M. A. Grace. 2013. Tag and recapture data for Atlantic sharpnose, *Rhizoprionodon terraenovae*, and bonnethead shark, *Sphyrna tiburo*, in the Gulf of Mexico and US South Atlantic: 1998–2011. Southeast Data, Assessment, and Review SEDAR34-WP-04, 19 p. [Available from website.]

[8] Hendon, J. M., E. R. Hoffmayer, and G. R. Parsons. 2013. Tag and recapture data for Atlantic sharpnose, *Rhizoprionodon terraenovae*, and bonnethead, *Sphyrna tiburo*, sharks caught in the northern Gulf of Mexico from 1998–2011. Southeast Data, Assessment, and Review SEDAR34-WP-33, 8 p [Available from website.]

Figure 8

Fulton's condition factor (*K*) of male Atlantic sharpnose sharks (*Rhizopriono-don terraenovae*), plotted for specimens from the eastern Gulf of Mexico (*n*=200, gray bars) and for those from the western Gulf of Mexico (*n*=1583, white bars). Sharks were collected between April and October 2011. The eastern and western regions of the Gulf of Mexico are separated by the longitude 88°W.

that region. Although there was a significant relationship between maternal length and brood size, this relationship was not significantly different between regions; therefore, there was no statistical difference in the brood size of similarly sized females between areas. This finding indicates that the larger brood sizes observed in the western GOM were related to the larger maximum size of females, and we postulate that larger female and brood sizes are a direct effect of prey availability. Future research should examine potential differences in embryonic growth between regions to determine if excess energy is directed to developing larger embryos rather than larger broods within similarly sized females, perhaps through a common-garden experimental design. However, because of the protracted and asynchronous reproductive cycles of female Atlantic sharpnose sharks in the northern GOM (Hoffmayer et al., 2013), we were not able to compare size at birth between the eastern and western GOM.

The difference of 0.6 pups per brood in the mean brood size of females between the eastern and western GOM, superficially, appears minor. Discussion of reproductive value (e.g., Fisher, 1930) and net reproductive rate are hampered by the lack of region-specific growth models necessary to back-transform age at size as would be required to calculate age-specific fecundity, age-specific mortality rates, and intrinsic rates of increase. However, the PLRO calculated in this study for 2 hypothetical females indicates the significance of the disparity. In both scenarios, which include multiple generations, the hypothetical female in the western GOM would be responsible for the production of more than 2 times the number of sharks than the hypothetical female in the eastern GOM. Therefore, even small changes in reproductive value, which may be statistically insignificant, can have large effects on population size.

The higher reproductive potential of Atlantic sharpnose sharks in the western versus the eastern GOM has numerous implications, such as variable population recovery rates, spatial variability in forage base for predators of Atlantic sharpnose sharks, possible effects on distributions of larger sharks, and potential region-specific mesopredator release and trophic cascades if populations of predators of Atlantic sharpnose sharks decline in the GOM. Future research should model the effects of varying abundance levels of Atlantic sharpnose sharks on the ecology of the 2 areas. Further, the results of this study underline the need to examine the life history of wide-ranging species throughout their range rather than assuming that traits of individuals from a discrete location are applicable to individuals over broad expanses, particularly those for which individuals show limited

Atlantic sharpnose sharks in the western GOM and, like Bethea et al. (2006), found the Atlantic croaker to be the dominant prey species (reported to have the highest IRI of all species, but no value was given). Results of these studies indicate that the Atlantic croaker is a preferred prey species of Atlantic sharpnose sharks and, as such, the similarity in the distributions of predator and prey reported herein are not unexpected.

In terms of CPUE during SEAMAP trawl surveys, among species that are potential prey for Atlantic sharpnose sharks, the Atlantic croaker ranks 16th in the eastern GOM (1.82 kg/h) and 1st in the western GOM (91.60 kg/h). Further, among the 15 most frequently caught potential prey species during SEAMAP trawl surveys in the 2 regions, the CPUE of prey was almost 3 times greater in the western GOM (174.62 kg/h) than in the eastern GOM (64.66 kg/h) (Pollack and Hanisko[9]). Given the strong spatial relationship between Atlantic sharpnose sharks and Atlantic croaker, prey availability appears to be a more plausible explanation of the observed differences in brood size between regions.

The higher abundance of prey in the western GOM had 2 noticeable effects on Atlantic sharpnose sharks in that region: the condition factor of male Atlantic sharpnose sharks (and females by proxy) was higher in the western GOM and both sexes attained larger sizes in

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[9] Pollack, A., and D. Hanisko. 2017. Unpubl. data. Miss. Lab., Southeast Fish. Sci., Cent., Natl. Mar. Fish. Serv., 3209 Frederic St., Pascagoula, MS 39567-4112.

movement (e.g., small coastal sharks). Seemingly small differences in important life history characteristics, such as fecundity, could have significant effects on rebound potential for species adversely impacted by recreational and commercial fisheries.

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