

Aspects of reproductive biology of the scalloped hammerhead shark, *Sphyrna lewini*, off northeastern Brazil

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Synopsis

Ninety four scalloped hammerhead sharks, *Sphyrna lewini* (53 females and 41 males) ranging in size from 121 to 321 cm total length (TL), were collected from surface gillnetters operating off northeastern Brazil and throughout the southwestern equatorial Atlantic Ocean between January and December 1996. A common regression for TL and eviscerated weight (EW) was calculated as, $\log EW = -11.786 + 2.889 \log TL$. Females and males were categorised into reproductive stages (4 and 2, respectively) according to morphological changes in their gonads. Size at sexual maturity for females was estimated to be 240 cm, while males appeared to mature at between 180 and 200 cm. Gravid females had between 2 and 21 embryos or pups, varying in TL from 3 to 38 cm. There was no relationship between maternal length and size of litter. Copulation and parturition appear to occur outside the sampled area and possibly closer to the coast. With the exception of slightly lower uterine and ovarian fecundities, the results support the few existing data on the reproductive cycle of *S. lewini* in other areas.

Introduction

The scalloped hammerhead shark, *Sphyrna lewini*, is a semi-oceanic species globally distributed throughout tropical and temperate oceans (Compagno 1984). Characterised by a range of habitats, the young typically occur in shallow bays and estuaries, while adults tend to frequent continental shelves and adjacent waters to depths of 275 m (Clarke 1971, Compagno 1984, Klimley 1987). The abundance and accessibility of *S. lewini* in these areas means that it often comprises a large proportion of elasmobranch catches from commercial fishing activities, such as shrimp trawling (e.g. Castro 1993), longlining (e.g. Branstetter 1987, Chen et al. 1988) and gillnetting (e.g. Stevens & Lyle 1989).

Owing to availability and commercial importance, aspects of their reproductive biology have been described at various locations including, Hawaii

(Clarke 1971), Southern Africa (Bass et al. 1975), the Gulf of Mexico (Branstetter 1981, 1987), Taiwan (Chen et al. 1988), northern Australia (Stevens & Lyle 1989), northern Brazil (Lessa et al. 1998) and Senegal (Capapé et al. 1998). Despite this research, with the exception of the work done by Chen et al. (1988) off Taiwan, there is little information available on females and particularly gravid individuals throughout their distribution. This is attributed to sexual segregation of adults and the preference of females for deeper areas away from inshore fishing grounds (Branstetter 1987, Stevens & Lyle 1989).

Until recently, such disequilibrium in catch compositions of *S. lewini* precluded descriptions of the reproductive biology of females off northeastern Brazil. Artisanal gillnetters working in and around estuaries along the north coast frequently catch juveniles and some information was presented on their biology in

a previous study (Lessa et al. 1998). While adjacent oceanic areas, including various sea mounts and offshore islands, have been extensively fished by a pelagic longline fleet for the past 20 years (see Hazin et al. 1998 for details) catches of *S. lewini* have always been very low (less than 0.05% of total shark catch – Hazin et al. 1990). In 1996, however, several vessels in this fleet employed monofilament gillnets (for a period of 12 months) and caught relatively greater numbers of adult *S. lewini* (approx. 13% of total catch) in the same areas fished with longlines. Given the absence of information on reproductive biology of adults in the southwestern Atlantic Ocean and the paucity of data on females from most areas throughout the world, our aim in the present study was to examine some of the specimens caught to supplement the existing literature.

Material and methods

This work was based on 94 sharks (53 females and 41 males) collected from the catches of commercial fishing vessels using drifting gillnets in the southwestern equatorial Atlantic (>150 km from the coast of northeastern Brazil, Figure 1) between January and December 1996. The gillnets used were up to 12 m in depth, had a buoyed headline of between 1 and 7 km in length, and consisted of monofilament mesh with a size between the knots (stretched mesh) of 17 to 30 cm. Nets were set by hand at the surface each day at approx. 18:00 h and hauled the following morning at approx. 5:00 h.

Immediately after being landed, sharks were measured (total length – TL and fork length – FL, see Garrick 1982 for details), dissected and weighted (eviscerated weight – EW). Reproductive organs were removed and stored in a solution of 10% formalin in sea water prior to being transported to the laboratory. Data collected from females included weight of the functional right ovary, maximum ovarian follicle diameter (MOFD), width of the oviducal gland and largest uterus and if present, the number of eggs or embryos and the length and sex of pups. Using the methods described by Pratt (1993), the oviducal glands of 36 females were examined for the presence of spermatozoa. The weight of testes, length and calcification state of claspers and the presence of seminal fluid in ampulla ductus deferens were recorded from males. Reproductive organs were measured to the nearest 0.1 mm using vernier calipers. A gonosomatic index (GSI) for mature males was calculated by dividing weight of testes by

eviscerated weight $\times 1000$. Insufficient data precluded the analysis of GSI per month and data were pooled across seasons throughout the year. There were insufficient mature females caught across seasons to provide meaningful analysis of temporal changes in their GSI.

Inferences on stages of maturation were made according to definitions provided in previous studies (e.g. Springer 1960, Pratt 1979, Branstetter 1981). Depending on the development of the oviducal gland, uteri, MOFD and ovary, females were separated into 4 stages. Specimens were considered juvenile if they had undeveloped sexual organs, filiform uteri, and no vitellogenic activity in their ovaries. Maturing females had enlarged oviducal glands and showed evidence of vitellogenesis. Ovulating females had uterine eggs and mature oocytes in their ovaries, while in gravid specimens ovulation was complete. Male maturation was evaluated according to development of the testes and calcification of claspers. Individuals with relatively short, flexible claspers and filiform ampullae ductus deferens were considered juvenile. Adults were characterised by elongated and calcified claspers.

Statistical analyses

Linear regressions of EW and TL were calculated separately for males and females and then compared using appropriate analysis of co-variance (ANCOVA). Size-frequency distributions of males and females were compared using a two-sample Kolmogorov–Smirnov test ($p = 0.05$). Regression analysis was used to examine the relationships between litter size and TL for mature females. Data describing seasonal changes in GSI for mature males were tested for heteroscedasticity using Bartlett's test, and then analysed in an unbalanced one-factor analysis of variance (ANOVA). Chi-squared goodness-of-fit tests were used to examine the hypothesis of an equal sex ratio among numbers of *S. lewini* sampled and pups from gravid females.

Results

Although there was some temporal variability between sexes caught during the period examined (Table 1), the pooled sex ratio of males to females (1:1.29) was not significantly different from 1:1 ($\chi^2 = 1.53$, $p > 0.05$). The majority of specimens were sampled in the latter half of the year and mostly between July and November. The Kolmogorov–Smirnov test detected

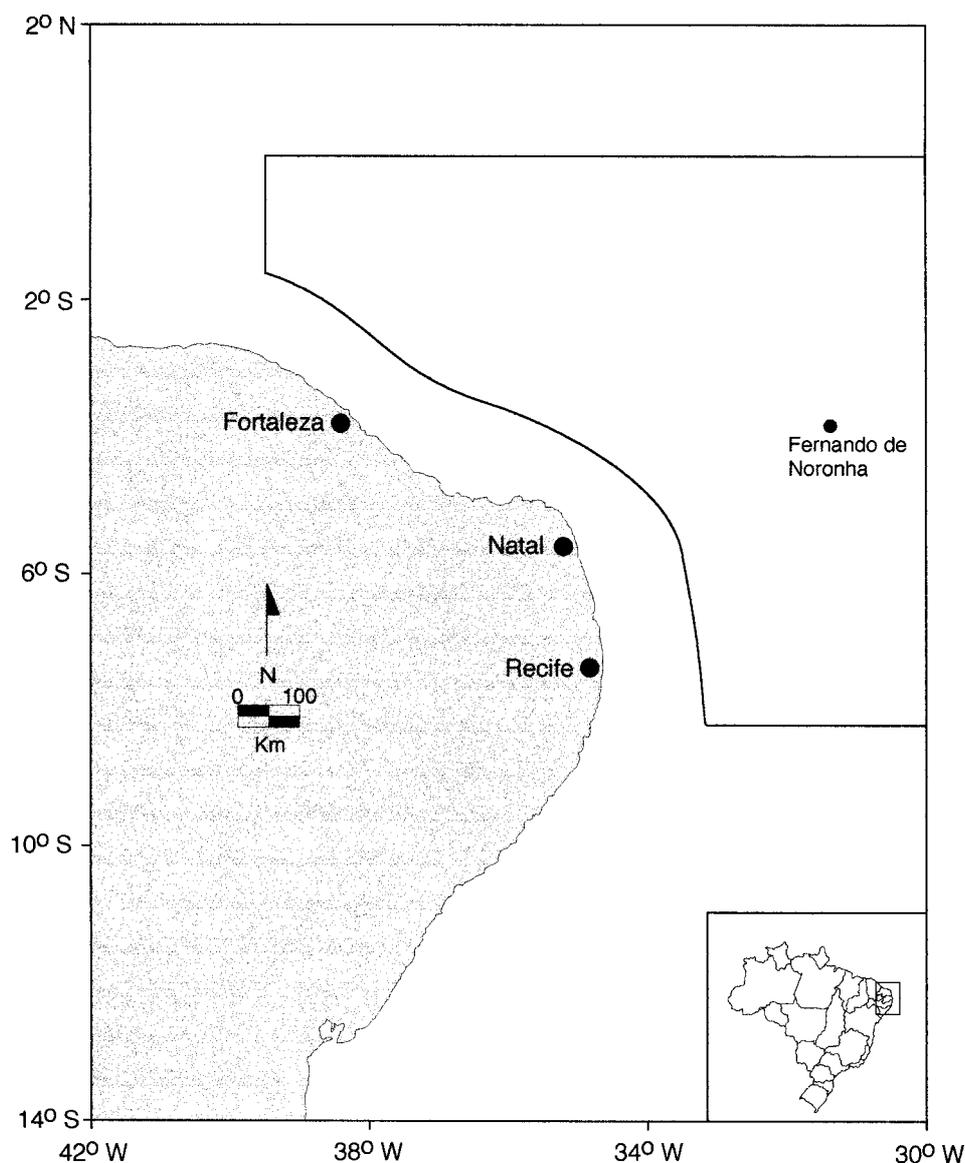


Figure 1. Location of fishing area.

significant differences in size-frequency compositions between males (ranging from 123 to 321 cm TL) and females (ranging from 121 to 273 cm TL), with proportionally more females between 201 and 279 cm TL captured. One male, 321 cm TL, represents the largest measured specimen to date. ANCOVA failed to detect significant differences in regression coefficients ($F = 0.017$, $p > 0.05$) or elevations ($F = 0.3707$, $p > 0.05$) between the regressions of $\log EW$ and $\log TL$ for males ($\log EW = -11.883 + 2.908 \log TL$, $r^2 = 0.962$,

$n = 36$) and females ($\log EW = -12.032 + 2.935 \log TL$, $r^2 = 0.933$, $n = 50$). A common regression was calculated as $\log EW = -11.786 + 2.889 \log TL$.

Females

Nine of the specimens sampled were juveniles, ranging in size from 121 to 220 cm TL. They had light ovaries, narrow oviducal glands and uteri and undeveloped ovarian follicles (Table 2, Figures 2a–c).

Table 1. Numbers of *S. lewini* sampled during each month in 1996.

Month of capture	Males		Females		Total
	Juveniles	Adults	Juveniles	Adults	
January	1	4	5	0	10
February	0	0	0	0	0
March	0	3	1	0	4
April	0	1	0	0	1
May	0	0	0	0	0
June	2	6	0	0	8
July	1	13	3	2	19
August	0	3	12	3	18
September	0	1	0	0	1
October	1	2	8	8	19
November	0	3	3	6	12
December	0	0	1	1	2

Table 2. Characteristics of female *S. lewini* in each maturation stage and the length range and number of specimens. All lengths and widths are in centimeters and weights in grams.

Characteristic	Juvenile	Maturing	Ovulating	Gravid
Width of oviducal gland	<1.9	2.4–3.9	3.7–5.2	3–4
Width of uteri	<1.5	1.5–5.5	9.2–12.5	11–22
MOFD	<0.6	0.8–1.9	3.4–5	0.9–2.6
Weight of ovary	<13	14.5–60	82–134.5	24.5–90
Total length of specimens	121–220	213.5–255	240–254	244–273
Number of specimens	9	22	6	10

Maturing females comprised the majority of the sample and ranged in size from 213.5 to 255 cm TL. Their functional right ovary had increased in weight to between 14.5 and 60 g (Figure 2d) and was fully differentiated from the epigonal organ. Their uteri were thick and MOFD was generally greater than 1 mm (Figures 2b,c). Although all specimens longer than 220 cm had enlarged and clearly discernible oviducal glands (Figure 2a), sexual maturity appeared to occur only in individuals greater than 240 cm TL – the size of the smallest ovulating female. Compared to maturing individuals, these females had much wider uteri (e.g. 9.2–12.5 cm) and heavier ovaries (82–134.5 g) that were characterised by thick yellow follicles (Figures 2b,d). Gravid females ranged in size from 244 to 273 cm TL and had relatively heavy ovaries (24.5–90 g) and large MOFD (0.9–2.6 cm), providing

some evidence to suggest that they were ready for ovulation shortly after parturition. Spermatozoa were detected in only one of the females examined: a 246 cm TL gravid individual. None of the females showed any evidence of mating scars.

The uterine contents of the 10 gravid females captured during the study are summarised in Table 3. Litter size ranged from 2 to 21 embryos and pups with a mean (SE) of 14.3 (2.31). All embryos from individual gravid females showed a similar state of development. They were longitudinally oriented in individual chambers and in the same direction as the mother. The sex ratios of embryos in individual females showed considerable variation, although the total pooled ratio (1:1.74) was significantly biased towards females ($\chi^2 = 8.67$, $p < 0.01$). No significant linear relationship was detected between size of gravid female and number of embryos ($F = 0.034$, $p > 0.05$).

Males

Of the 41 males examined, 5 were considered juveniles with thin epididymis and filiform ampulla ductus deferens without seminal fluid. Their claspers were flexible, varying in length from 5.5 to 16 cm, while their testes were light (less than 25.5 g) and not fully differentiated from the epigonal organ (Figures 3a,b). Adult specimens ranged in size from 202 to 321 cm TL. All had thick epididymis, seminal fluid in the ampulla ductus deferens and calcified and rigid claspers (17 to 24 cm in length). Weight of testes varied from 7.5 to 238.5 g. ANOVA failed to detect significant differences in seasonal variation of GSI for mature males ($F = 1.67$, $p > 0.05$) (Figure 4).

Discussion

Males have tended to dominate catches of *S. lewini* in the majority of studies (e.g. Clark & von Schmidt 1965, Clarke 1971, Branstetter 1981, 1997, Stevens & Lyle 1989, but see Chen et al. 1988). This has been attributed to the inshore location of sampled areas and sexual segregation of females, which tend to move offshore at a smaller size than do males (Klimley 1987, Stevens & Lyle 1989). The few studies done in oceanic areas have shown that aggregations are often comprised of various-sized sharks of both sexes, although females frequently are more common (Wakabayashi &

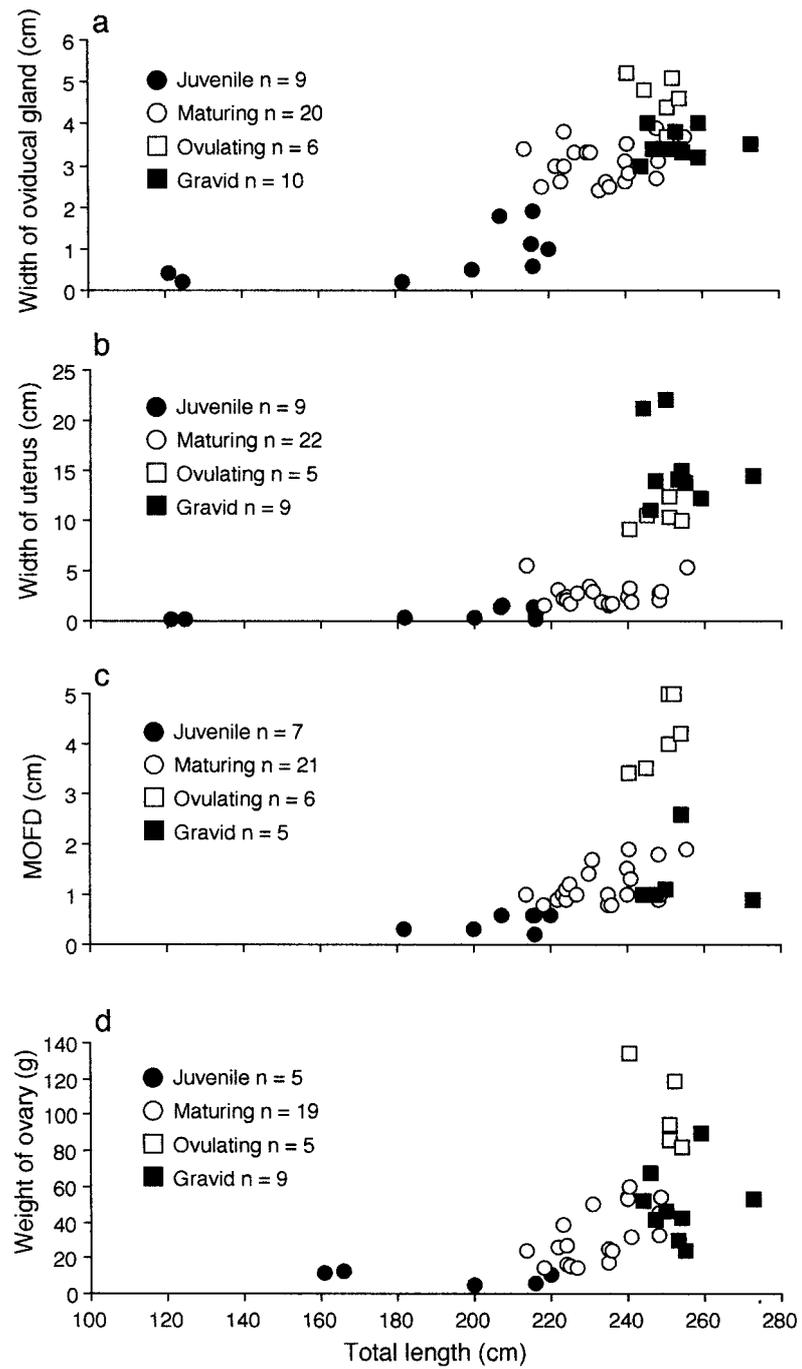


Figure 2. Relationships between total length and: a – width of oviducal gland, b – width of uterus, c – MOFD, and d – weight of ovary across the various stages of maturation for females.

Iwamoto 1981, Chen et al. 1988. The available data support these trends off northern Brazil, since Lessa et al. (1998) recorded larger and more juveniles males (46 to 173 cm TL) than females (45 to 149 cm TL) in shallow coastal areas. Although not significant, slightly

Table 3. Summaries of the month of capture, total length (TL), and number and sex of embryos found in the 10 gravid *S. lewini* (TL in cm, * = not sexed).

Month of capture	TL of gravid specimen	TL range of embryos	Number of embryos		
			Male	Female	Total
July	258.9	3–5.5	*	*	14
August	246	3–4	*	*	11
August	254	17–20	9	11	20
October	253.3	10.5–13	6	12	18
October	247.2	11.5–13.5	0	2	2
October	272.8	13–15.5	4	10	14
October	255.1	14–17	2	0	2
October	249.9	29.9–33.7	11	10	21
November	259	32.5–35.5	9	12	21
November	244	32–38	2	18	20

greater numbers of females (i.e. ratio of 1 : 1.29) were sampled in the present study.

Evaluation of the maturation stages of female *S. lewini* showed considerable overlap between cohorts (Table 2, Figure 2), however, the minimum sizes at each stage are comparable to observations by Stevens & Lyle (1987) who noted TLs of 228, 229 and 238 cm for mature non-virgin, pre-ovulatory, and pregnant females, respectively. Because many of the individuals greater than 240 cm in the present study had enlarged oviducal glands, thick uteri and heavy ovaries (Figure 2), it is likely sexual maturity was approached at this length. This estimate is larger than the sizes of 210 and 200 cm TL proposed by Chen et al. (1988) and Stevens & Lyle (1989) for specimens captured in the western Pacific Ocean, but similar to that (i.e. 250 cm TL) provided by Branstetter (1987) for individuals from the Gulf of Mexico (Table 4).

In contrast to females, males appeared to mature at a shorter TL, although the few small specimens captured mean it is difficult to provide an accurate estimate of the size range. Three of the 5 males classed

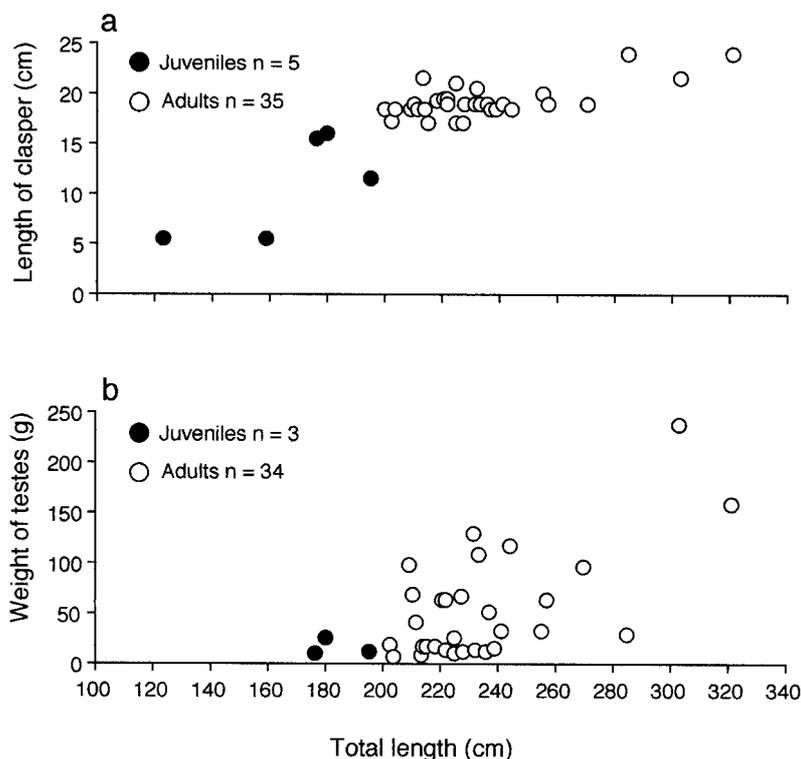


Figure 3. Relationships between total length and: a – length of clasper, and b – weight of testes for juvenile and adult males.

as juveniles (176, 180 and 195 cm TL), had calcifying claspers (i.e. semi-rigid) that were considerably longer than those in the remaining two juveniles (123 and 159 cm TL – Figure 3a). Given these observations and that all specimens longer than 200 cm TL were adults, males probably approached maturity at between 180 and 200 cm. In the only other relevant study off northern Brazil, Lessa et al. (1998) observed 53 males (46 to 173 cm TL) and found three (94, 150 and 173 cm TL) with evidence of calcified claspers (although the length of the clasper in the shortest specimen was less than 7 cm). Other studies have shown considerable

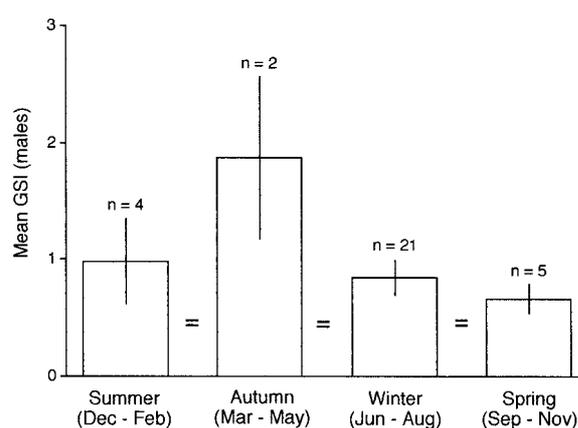


Figure 4. Differences in mean GSI (\pm se) of mature males between seasons.

variability among estimates of size at maturity, ranging from 140 to 198 cm TL (Table 4).

Aspects of the reproductive cycle of *S. lewini* have been proposed by Chen et al. (1988) and collaborated by data collected on individual females in other studies (Table 4). Vitellogenesis and gestation each appear to take about 10 months with ovulation and parturition mostly occurring between July and October (autumn) and May and July (summer), respectively, in the northern hemisphere. The data recorded from the 10 pregnant females examined in the present study also support this cycle. For example, the smallest embryos recorded were between 3 and 5.5 cm TL from a gravid female caught in July, while the largest (32 to 38 cm TL) were recorded from two females in November (Table 3). Gestation probably starts in autumn, and given that the largest observed embryos were shorter than the 45 to 50 cm size at birth postulated in most studies (Table 4) parturition likely occurs during mid to late summer. The lack of near-term females in the sample, combined with the observation by Lessa et al. (1998) of several neonates (>45 cm TL) in estuarine areas off northern Brazil provides some evidence to indicate that parturition occurs outside the examined area, and probably closer to the coast.

Some evidence of the simultaneous development of ovarian follicles and embryos, along with the presence of spermatozoa in one gravid female, suggests that females may be capable of giving birth annually (see

Table 4. Summary of studies describing some aspects of the reproductive biology of *S. lewini*. TL in cm (Na = not available).

Sampled location	TL at maturity		Gestation period	Parturition	Litter size	TL at birth	Reference
	Males	Females					
Hawaii	Na	Na	Na	Year round (peak in summer)	15–31	40–50	Clarke (1971)
Southern Mozambique	140–165	212	Na	Summer	30	50	Bass et al. (1975)
Gulf of Mexico	180	250	12 months	Na	> 30	49	Branstetter (1987)
Northeastern Taiwan	198	210	10 months	Summer	12–38	>47	Chen et al. (1988)
Northern Australia	140–160	200	9–10 months	Summer	13–23	45–50	Stevens & Lyle (1989)
Senegal	Na	Na	Na	Summer	18–22	37–52	Capapé et al. (1998)
Northern Brazil	<150	Na	Na	Na	Na	40–50	Lessa et al. (1998)
Northeastern Brazil	180–200	240	10 months	Summer	2–21	>38	Present study

also Chen et al. 1988, Capapé et al. 1998). In partial support of this, adult males showed large variation in their weight of testes (Figure 3b) which typically is associated with a seasonal fluctuation in sperm production (e.g. Hazin et al. 2000). Further, there was some evidence of a peak in mean GSI of mature males during autumn (Figure 4) which may coincide with a mating season, however ANOVA failed to detect any significant temporal differences in mean GSI. A smaller standard error, achieved through greater replication (e.g. only two males were caught during autumn) would be required to detect clear patterns of difference. The absence of additional data precludes any accurate determination of the time or location of copulation, although because none of the sampled females showed evidence of fresh mating scars (normally associated with this species – Wakabayashi & Iwamoto 1981) this probably occurs outside the sampled area.

Unlike the results from Chen et al. (1988), we failed to detect any relationship between maternal length and size of litter for the 10 females examined. Further, the uterine fecundity (between 2 and 21 pups – Table 3) of these females was considerably lower than that (e.g. between 12 and 38 pups) recorded in previous work (Table 4). This later result may be biased by abortion during capture in the gillnets (owing to trauma incurred as sharks struggle to free themselves – e.g. Clarke 1971), however, ovarian fecundity in maturing specimens was also generally lower (i.e. between 7 to 40 oocytes) than previous observations (e.g. 37 to 46 oocytes – Capapé et al. 1988). It is difficult to postulate reasons for such relatively low fecundity, other than that it may be an inherent characteristic of the stock off northeastern Brazil. More detailed analysis, involving a greater sample size, would be required to validate this observation. The significantly greater number of female pups in litters is similar to observations made by Capapé et al. (1998), but differs from the equal proportions recorded by Chen et al. (1988) and Stevens & Lyle (1987).

With the exception of some anomalies concerning fecundity, the results presented here concur with much of the existing information available on the reproductive biology of *S. lewini*. Further fishery-independent research is still required off northeastern Brazil, however, to locate areas of copulation and parturition and provide some analysis of other stock-specific life history parameters, as well as abundances and distributions.

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