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# BIOLOGICAL OBSERVATIONS ON *SPHYRNA LEWINI* AND *S. TUDES* (CHONDRICHTHYES, SPHYRNIDAE) FROM NORTHERN BRAZIL

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CHONDRICHTHYES
*SPHYRNA LEWINI*
*SPHYRNA TUDES*
REPRODUCTION
SHARK BIOLOGY
EQUATORIAL ATLANTIC

ABSTRACT. – We analyse aspects of the reproductive biology of *Sphyrna lewini* and *S. tudes* occurring in coastal waters (6-35 m depth) with a wide salinity range (20 to 34‰). Specimens were captured with gillnets by an artisanal fishery. Captures of *S. lewini,* which exhibit a high degree of sexual segregation, were composed mainly by juvenile specimens from 45 to 173 cm TL, including new born specimens. All females and 94.2 % of males were immature. *S. lewini* matures in Maranhao waters at smaller sizes than in other areas. *S. tudes* was obtained in near all stages of the sexual cycle. Total length as well as size and number of embryos are larger than in other areas. Pregnancy was observed practically throughout the year. Comparison of abundance patterns of *Sphyrna* species and other sharks in Maranhao waters with those from other areas points to a similar organization of coastal shark communities in different spots of the tropics.

CHONDRICHTIENS
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RÉSUMÉ. – Quelques aspects de la reproduction de *Sphyrna lewini* et *Sphyrna tudes* des eaux cotières entre 6 et 35 m de profondeur où le taux de salinité varie de 20 à 34‰, sont présentés. Les spécimens ont été capturés par pêche artisanale au moyen de filets maillants dérivants. L'analyse des captures de *S. lewini* montre un degré élevé de ségrégation sexuelle et une gamme de longueur totale variant de 45 à 173 cm LT, y compris celle des jeunes à la naissance. Toutes les femelles et 94,2 % des mâles sont immatures. Sur la côte du Maranhao, *S. lewini* atteint la maturité sexuelle à une taille inférieure à celle qui est observée dans les autres sites. En ce qui concerne *S. tudes,* tous les stades de maturité sexuelle ont été observés. La longueur totale, la taille et le nombre d'embryons sont plus importants que dans les autres régions. Des femelles gravides ont été observées presque toute l'année. Si l'on compare les taux d'abondance des espèces du genre *Sphyrna* et des autres Requins de la côte du Maranhao avec ceux qui ont été calculés pour d'autres zones tropicales, on observe une organisation semblable des communautés.

## INTRODUCTION

From 1986 to 1992 several papers were published on the reproductive biology of shallow water sharks occurring off Maranhao, in northern Brazil, aiming at a contribution to the knowledge of parameters important to the dynamics of these species (Lessa 1987; Lessa & Silva 1992; Silva & Lessa 1991). Other research in the area was directed to the management of fisheries (Stride 1992; Stride *et al.* 1992) or related to community ecology (Lessa 1986, Lessa & Menni 1994, Menni & Lessa in press). The assessment carried out by the SUDENE (1983), pointed out an available biomass of sharks around 23,000 mt/year in coastal waters from 25 to 100 m depth. This was atributed to the littoral morphology, with a complex littoral line and several rivers which promote complex trophic webs.

Sharks of the family Sphyrnidae are rather common along the Brazilian coast, where six out of the eight known species are recorded (Sadowsky 1965). Lessa (1986) states that in Maranhao waters four species occur, namely *S. tiburo* (Linné, 1758), *S. lewini* (Griffith & Smith, 1834), *S. tudes* (Valenciennes, 1822) and *S. mokarran* (Rüppel, 1837), being 18 % of sharks landings.

Half of this figure corresponds to *S. tiburo*. Although this is the most abundant species of the genus in the area, *S. lewini* and *S. tudes* are the fifth and eighth species respectively in the abundance range among 22 chondrichthyans. These species were obtained in a Maranhao shallow water artisanal fishery directed to the capture of the carite, *Scomberomorus brasiliensis*. Stride *et al.* (1992), using three different nets, obtained captures where the daggernose shark *Isogomphodon oxyrhynchus* (Müller & Henle, 1839) was the first and *S. tudes* the second most abundant species.

Gadig *et al.* (1991) stated that between June 1987 and December 1990, off from Amapá coast to Rio Grande do Norte, northward of our study area, 3,844 sharks were collected 546 of them (14 %) were hammerheads : *S. media* (7 specimens), *S. lewini* (11 specimens), *S. mokarran* (44 specimens), *S. tudes* (79 specimens) and *S. tiburo* (450 specimens). The latter is the most abundant hammerhead in Maranhao waters as in the rest of the Brazilian coast.

Although *Sphyrna* species sympatrycally occur off Maranhao, some degree of exclusion is evidenced in feeding differences (Lessa and Menni 1994). Moreover, while *S. tiburo* spent its entire cycle within the studied area (Silva and Lessa 1991 ; Lessa & Silva 1992), the other three species do not.

*S. lewini* is a placental viviparous species with a circumtropical distribution in tropical and warm temperate areas. Off the Atlantic coast of South America, it occurs from Colombia to Uruguay (Menni 1976; Compagno 1984). It is a coastal pelagic or semi – oceanic shark ranging from the coast to about 275 m depth entering estuaries and bays (Compagno 1984). Off Rio Grande do Sul, juveniles remain during their first year of life in the inshore area (Lessa and Vooren 1982).

Sadowky (1965) reported it from Cananeia, off the Sao Paulo state, and Carneiro & Vooren (1986) found it among 19 sharks and rays commercially captured at Rio Grande do Sul, in both cases from coastal areas. *S. lewini* is also listed among the pelagic sharks captured in the longline fisheries in the South Atlantic between 20-40°S and 39-57°W, together with *Prionace glauca*, *Isurus oxyrhynchus*, *Lamna nasus*, *Carcharhinus longimanus*, *C. signatus*, *Alopias superciliosus* and *S. zygaena* (Mora *et al.* 1991). It is also captured in pelagic samples obtained with longline under 200 m depth, between 20 and 23°S together with 25 shark species and the pelagic stingray *Dasyatis violacea* (Sadowsky *et al.* 1986; Menni *et al.* 1995).

With a somewhat different acompanying fauna, *S. lewini* is hand-line captured in the pink– shrimp fishery off Sao Paulo (Tomás *et al.* 1991). These captures included species of *Carcharhinus* (mainly *C. plumbeus*) (see Menni & Lessa 1995) and *Galeocerdo cuvieri* (62.2 % in weight), *S. lewini*, *S. zygaena* and *S. mokarran* (21 %), *C. brevipinna* and *C. limbatus* (13.2 %) and *I. oxyrhynchus* (2.6 %). Sphyrnid captures are larger in summer.

*S. lewini* has been reported from the coast of Pernambuco and neighbour states (Guedes 1989). Also from the wide area, including Maranhao, from Amapa to Rio Grande do Norte (Bezerra *et al.* 1991) and from the estuarine complex of Paranagua Bay (Barletta & Correa 1989). Off Maranhao the species is obtained between Ilha de Santana and Barra de Lencois, where it is captured with gillnets in shallow water bays. Sampling in the same area with "igarape" nets (closing a mangrove bay) also provides *S. lewini* (with *S. tiburo* and *S. tudes*) within a grand total of 132 species including both chondrichthyans and osteichthyans (Garrido Martins-Juras *et al.* 1987).

*S. tudes* is a small species inhabiting coastal waters in South America from Venezuela to Uruguay (Cervigon 1966; Compagno 1984; Menni *et al.* 1984). Sadowsky (1965) reported it as an abundant species in littoral waters off Cananeia. It is captured with gillnets during summer from Cabo de Maguari off Marajó Bay, where specimens measured between 57 and 120 cm and pregnant females were observed (Barthem 1985). There stomach contents was restricted to catfish (Ariidae); ariid eggs were also reported as a major food item (Castro 1989).

The aim of this paper is to describe some biological traits of *S. lewini* and *S. tudes*, based on captures obtained by the artisanal fishery along the western coast of Maranhao.

## MATERIAL AND METHODS

Samples from the area between Lencois and Tubarao Bays (Fig. 1) were obtained in intervals of about 15 days from June 1984 to december 1986 and on March 1988. A gillnet ("cacœira") 900 m long and 7.2 m high, with an 8 cm mesh between opposed knots, was used by the small sailing boat fleet at depths varying from 6 to 35 m. Salinity ranges from 20 to 34.41 ‰ (mean 27.52, N = 18) (Lessa 1986; Menni & Lessa in press). Samples included 101 specimens of *S. lewini* captured in 24 hauls and 79 specimens of *S. tudes* captured in 16 hauls.

The following data were obtained for each specimen : sex, total length (TL) in cm, total weight (TW) in g, gutted weight (GW) in g, and liver weight (LW) in g. For males the testes weight in g, epididymides width in cm, clasper condition (calcified or uncalcified) and presence or absence of liquid in the seminal vesicle were noted. Ovary condition (presence or absence of vitellogenic oocytes), presence of eggs or embryos in uteri, ovary weight and nidamental gland width were obtained for females. Grams (g) and cm were used in

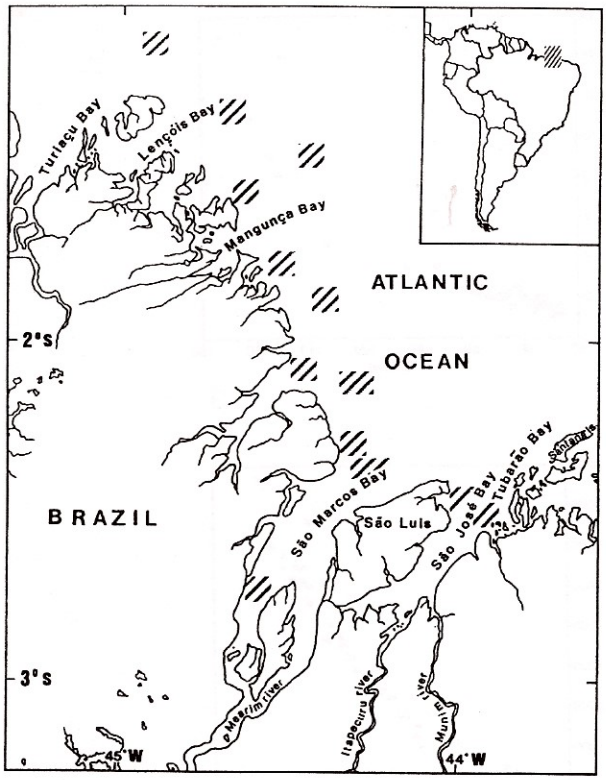


Fig. 1. – The studied area in the coast off Maranhao, Brazil. Fishing areas indicated by short diagonal lines.

calculation of equations in all cases, but large weights are given in kilograms (k) in the text. Measurements under 10 cm and weights under 100 g are given with a precision of 0.1. Calculation of the nutritive dependency index ([embryo weight/(egg diameter)$^3$] × 1000) follows Otake (1990).

## RESULTS

### *S. lewini*

Fifty three males and 48 females were considered, the sexual ratio being 1.1. Total length ranged from 46 to 173 cm (W = 400 g to 1.3 k) for males and from 45 to 149 cm (W = 400 g to 13.0 k) for females. A high degree of sexual segregation was observed, 66.7 % of the samples being composed of one sex.

The equation

$$GW = 4.78 \times 10^{-3} \times TL^{2.97},$$

with r = 0.99 and N = 100 describes the gutted weight-length regression for both sexes together. Within the examined size range differences among sexes were not significant (Fig. 2).

Captures were mainly composed by juveniles. Newborn individuals, juveniles of both sexes and mature males were observed, but no mature females. Specimens from 45 to 58 cm TL composed 50.5 % of the capture. Two males and 3 females showed umbilical scars. Only 3 mature males 94, 150 and 173 cm TL were obtained, being 2.9 % of the total capture.

Twenty seven males showed uncalcified claspers. Size of the clasper increases in a linear form until 135 cm TL (Fig. 3). After this size the slope changed with total length increase. Instead the epididymides width shows a constant slope (Fig. 4), and they appear meandered since 151 cm TL. Content in the seminal vesicle was observed since 93 cm TL, but it may be present or not over this size. In only one case (173 cm TL) it was found plenty.

One specimen 94 cm TL (TW = 3.7 k) with a well calcified clasper, testes weighting 18.4 g, epididymides 1.2 cm width and with liquid in the seminal vesicle was considered mature. Some larger specimens were not. The next mature male measured 150 cm TL (TW $\geqslant$ 17.1 k), had a well calcified clasper, testes weighting 54.0 g and epidydimides width of 1.6 cm. Specimens 151 and 155 cm TL had testes with 15.0 and 29.5 g respectively but uncalcified claspers. The following mature male measured 173 cm, with 51.4 g testes, scrolled epidydimides 2.1 cm width and seminal vesicle full.

The equation

$$LW = 1.1189 \times 10^{-3} \times TL^{2.5204},$$

with r = 0.80 for N = 45 describes the liver weight increase with length in males.

Forty six females have ovaries without noticeable oocytes. A granular ovary (W= 3.0 g) appeared in a female 89 cm TL. First evidence of ovarian development was found in the largest female (149 cm TL), with white oocytes < 1 mm (ovary weight without epigonal organ = 4.0 g). Nidamental glands (which in this species constitute a true seminal receptacle, Pratt 1993), showed a marked width variation related to immaturity of specimens.

The equation

$$LW = 1.2887 \times 10^{-2} \times TL^{1.9015},$$

with r = 0.76 for N = 40 describes the liver weight – total length relationship in females.

### *Sphyrna tudes*

Samples were composed by 50 males ranging from 44 to 117 cm TL (W= 400 g to 8.3 k) and 28 females ranging from 38 to 129 cm TL (W 240 g to 7.2 k). Sexual ratio was 1.7 :1 significantly sided to males. Relationships between TL and gutted weight were different for each sex. For males the equation was

$$GW = 3.23 \times 10^{-3} \times TL^{3.05},$$

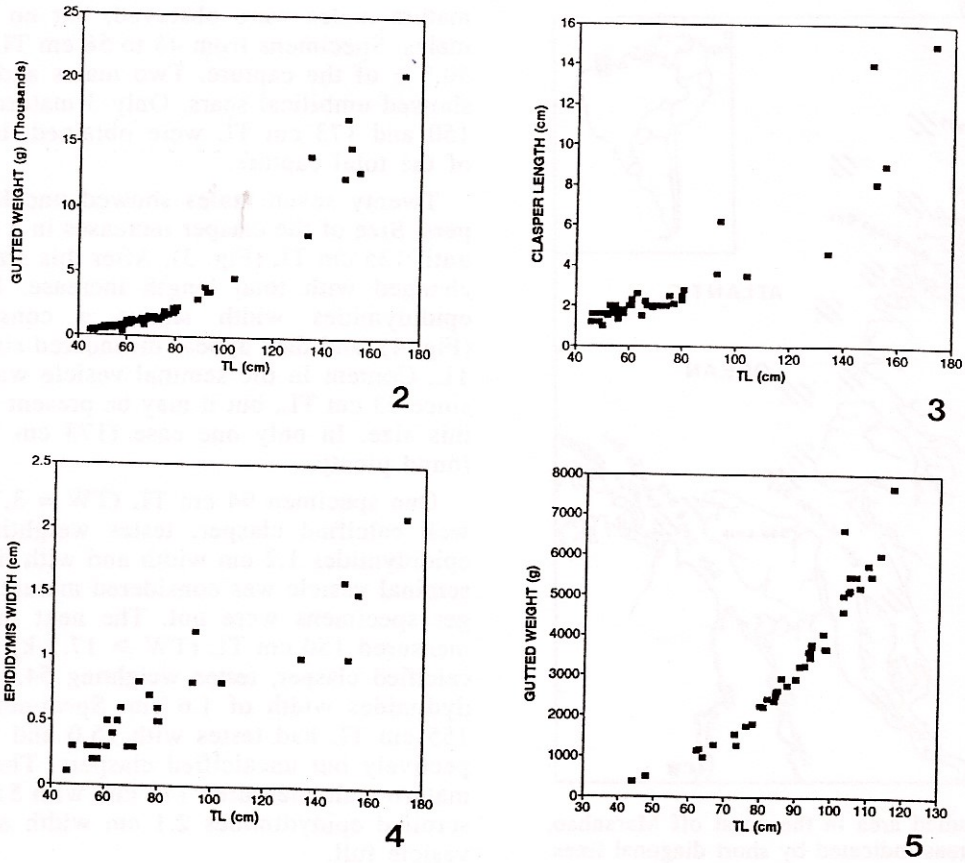


Fig. 2-5. – *S. lewini,* relationships between total length and gutted weight (2), clasper length (3), and epididymis width (4). *S. tudes*, Relationship between total length and gutted weight in males (5).

with r = 0.99 for N = 44 (Fig. 5).

For females the equation was $GW = 3.59 \times 10^{-3} \times TL^{3.058}$, with r = 0.99 for N = 28 (Fig. 6).

Until 90 cm TL (N = 19) most of males (N = 16, 84.2 %) have uncalcified claspers and empty seminal vesicles. Over 90 cm TL, all specimens (N = 25) showed calcified claspers. The 3 stages in clasper development demonstrated by Stride *et al.* (1992) were observed here in spite of the lower number of specimens (Table I).

Testes weight ranged between 1.0 g (at 63 cm TL) and 67.0 g (at 117 cm TL) (Table II). Claspers measuring between 1.0 and 5.9 cm were always uncalcified; between 6.0 and 9.9 cm they were calcified or not (about 1.5 to 1 proportion), and from 10.0 to 13.4 cm they were always well calcified.

Width of epididymides is rather variable, though it increases regularly as specimens grows (Fig. 7). Until 90 cm TL width of epididymides ranged from 0.1 to 0.9 cm (N = 18, mean = 0.5 cm). Specimens with well calcified claspers since over 90 cm TL have epididymides ranging from 0.6 to 1.6 cm width (N = 23, mean 1.0 cm). All specimens larger than 109 cm TL have epididymides over 1.0 cm width.

Presence of clear liquid in the seminal vesicle was observed at 80, 84 and 87 cm TL, but the characteristics of liquid changed since 90 cm TL, becoming opaque with white granulations and thick in some cases, agreeing with clasper development. Testes weight ranges from 1.0 to 67.0 g (Table II) being

$$\text{Testes weight} = 1.2678 \times 10^{-2} \times e0.^{0750 \times TL}$$

with r = 0.87 for N = 40. If mean values of testes weight by length classes (N = 10) are utilized, the value of r increased to 0.93, being

$$\text{Testes weight} = 2.0692 \times 10^{-2} \times e^{0.0715 \times TL}$$

Total length – liver weight relationship is given by the equation

$$LW = 1.8809 \times e^{0.0433 \times TL}$$

with r = 0.88 for N = 49. The relatively low value of r is due to large variation of liver weight in mature specimens, already observed in *Carcharhinus porosus* and *S. tiburo* (Lessa 1986/87; Silva & Lessa 1991).

No macroscopic evidence of ovarian development was observed from 38 to 91 cm TL. Over

Table I. – *S. tudes*. Total length and clasper condition (N = 44).

| Length classes (cm) | Clasper condition % flexible | % rigid | Number of specimens |
|---|---|---|---|
| 40 - 44 | 100 | 0 | 1 |
| 45 - 49 | 100 | 0 | 1 |
| 50 - 54 | - | - | - |
| 55 - 59 | - | - | - |
| 60 - 64 | 100 | 0 | 2 |
| 65 - 69 | 100 | 0 | 1 |
| 70 - 74 | 50 | 50 | 2 |
| 75 - 79 | 100 | 0 | 1 |
| 80 - 84 | 71 | 29 | 7 |
| 85 - 89 | 100 | 0 | 3 |
| 90 - 94 | 12 | 87 | 8 |
| 95 - 99 | 0 | 100 | 5 |
| 100 - 104 | 0 | 100 | 6 |
| 105 - 109 | 0 | 100 | 3 |
| 110 - 114 | 0 | 100 | 3 |
| 115 - 119 | 0 | 100 | 1 |

Table II. – *S. tudes*. Mean values of testes weight (N = 40) by total length classes.

| Length classes (cm) | Testes weight (g) | Number of specimens |
|---|---|---|
| 60 - 64 | 1.0 | 1 |
| 65 - 69 | 1.0 | 1 |
| 70 - 74 | 1.2 | 1 |
| 75 - 79 | 5.0 | 1 |
| 80 - 84 | 12.3 | 5 |
| 85 - 89 | 10.3 | 3 |
| 90 - 94 | 17.8 | 9 |
| 95 - 99 | 21.9 | 5 |
| 100 - 104 | 29.7 | 6 |
| 105 - 109 | 32.1 | 4 |
| 110 - 114 | 40.3 | 3 |
| 115 - 119 | 67.0 | 1 |

80 cm TL (W = 2.2 k) the ovary appears as a well defined organ (W = 2.2 g) with no vitellogenic oocytes. The nidamental gland is 0.4 cm width and the uteri threadlike. At 120 cm TL ovary weighted 46.0 g (Fig. 8). Larger ovary weights were noted in pregnant females.

Only one yellow oocyte (0.2 cm width) was observed at 85 cm TL (W = 3.5 k), with 60 whites (ovary weight 0.5 g, width 2.0 cm). Three vitellogenic oocytes (0.5 to 0.7 cm) were observed in a 91 cm TL female (W = 3.5 k), with ovary weighting 3.2 g, the nidamental width 0.9 cm and the uterus undeveloped weighting less than 1.0 g.

At 95 cm TL (TW = 4.0 k) the ovary weight was 5.4 g, with 3 vitellogenic oocytes 0.6 to 0.9 cm diameter, plus many no vitellogenic ones. The nidamental gland width was 1.7 cm, and the uterus was still threadlike.

A female measuring 96 cm TL (W = 4.4 k) had an ovary 5.9 g with 8 vitellogenic oocytes from 0.5 to 0.8 cm width. At this size the uterus shows indications of development, being tubular but still slightly vascularized.

Relationships between total length and the nidamental width (Fig. 9) show two stages, a first one without increased width until about 85 cm TL, and a second one, from about 90 cm TL, with variable widths between 0.3 and 2.5 cm (Stride *et al.* 1992).

The smaller pregnant female, captured in December, was 115 cm TL. She carried 6 embryos (3 each sex) in the left uterus and 5 (3 males, 2 females) in the rigth one (Table III). The largest embryo in this female measured 17 cm TL. The largest embryos observed were carried by a female 120 cm TL captured on July. The ovary was 6.0 cm width, with 60 small no vitellogenic oocytes 0.3 cm width and 6 vitellogenic ones 1.1 cm width. Each uterus weighted 128 g with a width of 11 cm. The right uterus contained 2 failed eggs weighing 7.0 and 6.3 g, plus 3 female and 1 male embryos. The left one contained an aborted egg 10.1 g and 3 male and 2 female embryos (Table III).

The largest pregnant female measuring 120 cm TL was captured in March. The uterus contained developing eggs with a mean size 4.4 cm and weights of 125 g (left uterus) and 150 g (right uterus) (Table III). Ovary of this specimen weighted 46.0 g with around 20 vitellogenic oocytes 0.2 cm width, 2 with 3.1 cm diameter and numerous smaller ones.

Assuming that uterine eggs must be of a similar size to ripe ovaric eggs, we obtained the nutritive dependency index as $[44.2*/(4.37**)^3] \times 1000 = 529.66$ (* Mean of 9 embryos from a 120 cm TL female; ** mean of uterine eggs of a 120 cm TL female).

Females with ova or embryos in uteri as well as maturing ovaries were captured in December

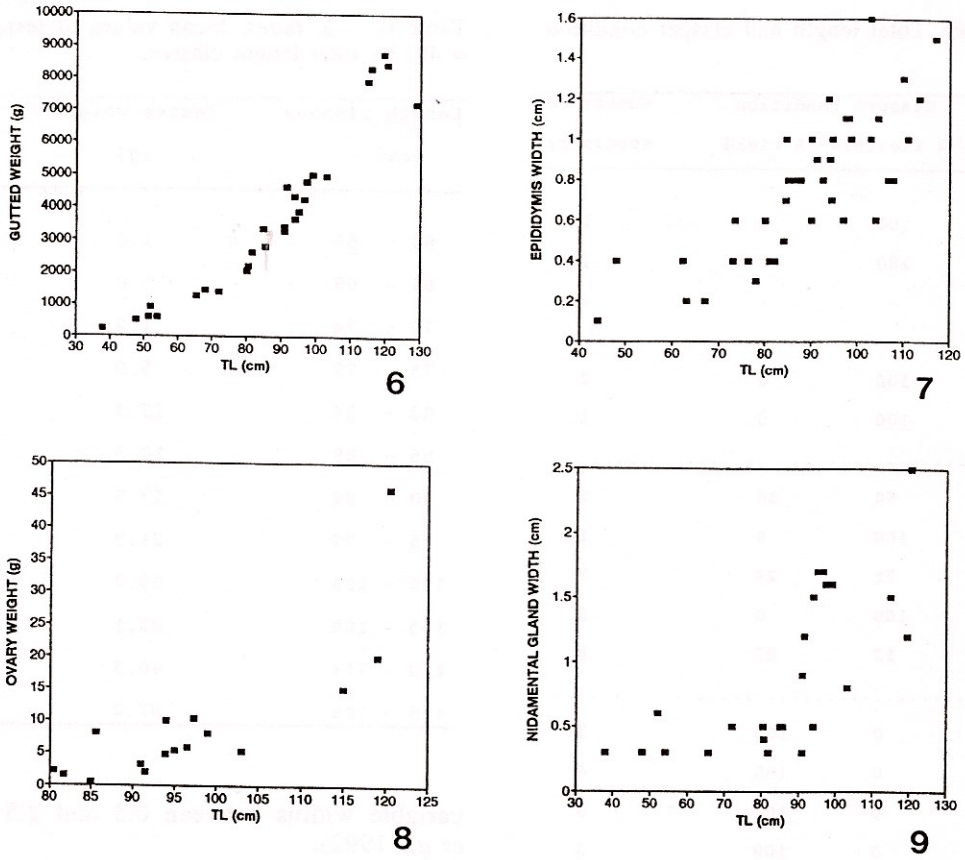


Fig. 6-9. – *S. tudes,* relationships between total length and gutted weight in females (6), epididymis width, N = 41 (7), ovary weight (8) and oviducal gland width, N = 24 (9).

1984 and April and July 1985, the former two dates within the rainy season.

Total length-liver weigth relationship is given by the equation $LW = 0.8873 \times e^{0.05291}$, with r = 0.96 for N = 25.

In both species the increase in liver weight involves two stages; the former with a slight increase, and a rapid growth after maturity onset.

## DISCUSSION

Four hammerhead sharks make 18 % of the total capture of the artisanal fishery at Maranhao (Lessa 1986). Most abundant is *S. tiburo*, which represents 10 % (Silva & Lessa 1991; Lessa & Silva 1992).

The limited size range of *S. lewini* in the area (45-173 cm) is accompanied by a high degree of sexual segregation. Percentage of captures with only one sex is twice that observed in *Squalus acanthias* and *Schroedereicthys bivius* in the South Atlantic (Menni *et al.* 1979; Menni 1985, 1986). It appears from Stride *et al.* (1992) and the present data (see also Lessa & Menni 1994 and Menni & Lessa in press), that only a small part of a *S. lewini* population reaches the Maranhao coast. Klimley (1987) suggested that one of the causes of segregation in *S. lewini* would be feeding differences between sexes. Samples of the second half of 1984 showed a drastic sexual segregation not observed the following year. This agrees with the lack of a strong seasonality in the chondrichthyan community as a whole, though some aspects as presence of rare species and feeding seasonality are apparently loosely related to the rainy season. Community composition changes in different moments, as result of considerable in and outgoing of species. Permanent species changed in abundance, but appear organized in assemblages (clusters) with some temporal consistency. Particular combination of species (recurrent groups *sensu* Fager 1967; associations *sensu* Margalef 1977) consistently appear at different dates, but the replacing do not coincide with alternation of dry and rainy periods or other observable environmental regularity (Lessa & Menni 1994).

Table III. – *S. tudes*. feature of embryos (M : male, F : female).

| Sex | TL (cm) | TW (g) | W without vitellus (g) |
|---|---|---|---|
| Female 115 cm TL, W= 8,500 g | | | |
| | | LEFT UTERUS | |
| M | 14.2 | 16 | 15 |
| M | 14.5 | 16 | 15 |
| M | 15.2 | 15 | 14 |
| F | 13.6 | 20 | 15 |
| F | 14.6 | 18 | 15 |
| F | 15.0 | 17 | 15 |
| | | RIGHT UTERUS | |
| M | 14.3 | 16 | 15 |
| M | 14.4 | 17 | 15 |
| M | 15.5 | 18 | 17 |
| Female 119.5 cm TL, TW= 9,200 g | | | |
| | | LEFT UTERUS | |
| M | 22.0 | 41.0 | 39.2 |
| F | 22.0 | 42.8 | 40.0 |
| F | 22.0 | 41.2 | 36.8 |
| F | 23.0 | 46.0 | 43.0 |
| | | RIGHT UTERUS | |
| M | 22.0 | 44.0 | 41.0 |
| M | 22.3 | 47.0 | 45.0 |
| M | 22.5 | 44.0 | 41.0 |
| F | 21.3 | 45.0 | 42.8 |
| F | 22.0 | 47.0 | 43.0 |

Stride *et al.* (1992) also observed low similarity between year occurrences and were unable to find seasonality patterns.

Sixteen hauls (66.7 %) were composed by one sex against 8 with both sexes, with the same number of individuals of each sex; in the Gulf of Mexico, instead, males greatly outnumbered females (Branstetter 1981).

Maximum size of this species has been reported about 370-420 cm TL (Compagno 1984), 295 cm TL (male, Bass *et al.* 1975) 316 cm TL (female, Stevens & Lyle 1989) and 300 cm TL (Branstetter 1990). Our smaller specimen was a 45 cm TL female, slightly under the minimum (46.8 cm TL) reported by Stevens & Lyle (1989). It is also smaller than the smallest free swimming individuals recorded (Wakabashi & Iwamoto 1981) but agreeing with the known size at birth about 40-50 cm TL (Clarke 1971; Bass *et al.* 1975). In our samples, specimens between 47.6 and 55.6 cm TL still have umbilical scars.

Samples gathered at Maranhao are mainly composed by juveniles. This situation is also reported by Stride *et al.* (1992), in spite of the use of gillnets with larger mesh size (180-300 mm) (90 specimens, mean size 115.2 cm). This does not appear to be a sampling artifact; Hoff & Musick (1990) stated that as an adult, *S. lewini* occupies offshore waters more commonly than coastal waters (Clarke 1971, Klimley 1981, Branstetter 1987). Ninety one percent of the specimens examined by Stevens and Lyle (1989) were smaller than 150 cm TL and immature. All our females were in this stage as well as 94.3 % of males.

No mature females were captured. Three mature males measured 94 cm TL (W = 3.7 k), 150 cm TL (W = 17 k) and 173 cm TL (W = 21.3 k). The largest immature male measured 155 cm TL (W = 3.6 k). Reported sizes of male first maturity are 145 to 165 cm TL (Bass *et al.* 1975) and 140 to 160 cm TL (Stevens & Lyle 1989). These authors cited the smallest mature specimen measuring 135 cm and the largest immature measuring 165 cm TL. Although mature specimens are few, it appears that maturity size of males at Maranhao are smaller than in other areas. Data for males (Stride *et al.* 1992) agree with current information, but data concerning females show different results. Available data do not allow the identification of the three steps in clasper development as observed for example in *Isogomphodon oxyrhynchus*, *Carcharhinus porosus* (Lessa 1986; 1986/87) and *S. tiburo* (Silva & Lessa 1991).

Stride *et al.* (1992) examined *S. lewini* off the coast of Maranhao finding gravid females measuring 140 cm TL (6 embryos) and 190 cm TL (5 embryos). This is a considerable smaller size than reported by Compagno (1984, 212 cm TL) and Branstetter (1987, 250 cm TL). Litter sizes were also smaller at Maranhao, with 5 and 6 embryos, against 15 to 31 reported by Compagno (1984).

The available information shows that *S. lewini* reaches maturity at smaller sizes in Maranhao than in other areas, pointing to population differences in development along the distribution range. Lack of data about trophic condition of the environment at the time of fishing renders adventurous to advance an hypothesis based on local productivity (which is presumed high), or on food availability. In the latter case, it should be noted that both *S. tiburo* and *S. lewini* restricted themself to a small part of the large number of apparently available preys.

Interpopulation size-reproductive differences are well known in *Squalus acanthias* (Ketchen

Table IV. – Reproductive stages in *S. tudes* from Maranhao and Trinidad. Measurements in cm, weights in K.

| | Maranhao | | Trinidad |
|---|---|---|---|
| | This paper | Stride et al. (1992) | Castro 1989 |
| Total range males | 44-117 | 43-122 | [108][1] |
| Total range females | 37-129 | 45-132 | – |
| > immature male | 85 | 90 | 79 |
| < mature male | ~90 | 82 | 80 |
| > immature female | 91 | ~90[2] | 92 |
| First ovaric eggs at | 80.5 | – | 86 |
| Vitellogenic eggs appear at | 85 | 104 | 98 |
| > female without eggs | 91 | – | 92 |
| < gravid female | 115 | 101 | 98.7 |
| Maximum size nid. gland | 2.5 | 2.3 | 3.0 |
| Embryos size | 13.6-23 | 8-34 | 23/30 |
| Litter size | 8-9 | 5-19[3] | 5/12 |
| Mother size | 115-119 | 101-132 | – |
| Pregnacy observed | March-July-Dec. | June-July/Oct-Nov./ Jan.-April | – |
| > free swimming juvenil | 48[4] | 32 - 33 | 32-33[5] |
| > male length/weight | 117/8.2 | – | 121/8.7 |
| > female length/weight | 129/7.2 | – | 120/9.0 |

[1] Average size of adults. [2] First maturity calculated at 92 cm (males) and 115 cm (females). [3] Significantly correlated with mother size. [4] With umbilical scars. [5] Size at birth 30 cm.

1972). Comparison of vital statistics of this species in the southwestern Atlantic (Menni 1985) shows that : – number of embryos by litter (3-14), is similar to the northeastern Pacific (2-13) and norteastern Atlantic (2-15), but the mean (7.03) is closer to the eastern Pacific (7.3 ; 6.2) than to the northeastern Atlantic (5.4). – Females minimum maturity length (70 cm, based on eggs or embryos presence) is smaller in this population than in other reported by Ketchen (1972 ; 74 to > 95 cm). – Maximum length of immature females is also smaller (74 against 80 to 114 cm). – Largest female (95 cm) was smaller than in other areas (108 to < 135 cm).

Along the Brazilian coast, differences in biological traits have been observed in several species. In *Rhizoprionodon lalandi*, while females mature at 49 cm off Maranhao, Ferreira (pers. comm.) mentioned 50-60 cm for Rio de Janeiro, and Compagno (1984) 54 cm. Moreover, 27 cm size embryos from Maranhao were developed enough to suggest a birth size about 30 cm. Compagno (1984) stated 33-34 cm for sizes at this stage and the figure for Rio de Janeiro is 34 cm. It must be noted that water temperatures off Rio de Janeiro are between 15 and 18 °C against 27-30 °C at Maranhao (Menni & Lessa in press).

The largest male of *C. acronotus* obtained off Maranhao was smaller than that reported by Schwartz (1984) from North Carolina but the largest female (170 cm TL) was larger than that observed there (154 cm TL). Both male and female seem to mature at smaller sizes in Maranhao, where male maturity was observed at 78 cm TL against 110 cm TL off North Carolina, and the smaller pregnant female measured 110 cm TL against 120 cm TL.

Geographic variation in reproductive traits is known in populations of *S. tiburo* only separated by 3 latitudinal degrees (Parsons 1993). Differences were observed in size and age at maturation, time of fertilization, rate of embryonic development, size at birth, gestation period, incidence of infertility, and energetic investment in offspring. Differences in timing of reproductive events are related to latitudinal differences in seasonal temperature and photoperiod (Parson 1993). This au-

thor stated that variation in reproductive styles are not easily explained, and examined food limitation (see above), selective predation and temperature as possible factors, without reaching a conclusion. Answer to these questions surely will result from a detailed ecological analysis of zonal productivity related to fish populations and genetic approaches.

Previous work on *S. tudes* in Maranhao based in larger samples shows size ranges rather similar to those observed here, with a sexual ratio also sided to the males (2.44 :1). Calculated sizes of first maturity were 92 cm TL for males and 115 cm TL for females. The number of embryos were 5-19 for mother sizes between 101-132 cm TL) with an $r = 0.76$, $P < 0.05$) (Stride *et al.* 1992).

The most particular aspect of the biology of *S. tudes* in the Maranhao area is that, in spite of the low number of specimens, both sexes occur in near all stages of the sexual cycle. Instead, Castro (1989) reported that in spite of hundreds of golden hammerheads seen, gravid females were seldom collected during this surveys, or seen in the market. Reproductive stages of *S. tudes* from Maranhao show similar traits to those described for the same area (Stride *et al.* 1992) and for the Trinidad population (Castro 1989) (Table IV). Anyway, females in Maranhao are somewhat larger than in Trinidad (132 against 122 cm). Larger females were also observed in southern Brazil (Sadowsky 1965). Male sizes are quite similar. Slightly larger embryos were also observed (34 against 30 cm) and the number of embryos, which is correlated with mother size, is also largest (19 against 12) (Stride *et al.* 1992).

Stages of nidamental gland development are very similar in both our and Trinidad samples (Fig. 9; and Castro 1989, Fig. 4). Also, clasper development is rather similar, though full calcification is reached at larger sizes in Maranhao. While 98 % of well calcified clasper in Trinidad were seen in males from 80 cm TL, that percentage is reached since 90 cm TL in Maranhao.

Pregnancy in Maranhao has been observed during almost the whole year, including January to April, June and July, and October, November and December (Stride *et al.* 1992, and original data). The nutritive dependency index has a value not far from the mean reported by Otake (1990) for a few placental species.

Off the Orinoco Delta, *S. tudes* and *C. porosus* are the most common sharks in coastal waters less than 40 m depth. Also common are *S. media* and *S. tiburo,* which are captured together. *S. lewini* and *S. mokarran* were caught ocassionally (Castro 1989). Within the Maranhao chondrichthyan community, at similar depths, *C. porosus* and *S. tiburo* are the dominant sharks. Besides, *S. lewini* is occasional and *S. mokarran* is rare (Lessa & Menni 1994; Menni & Lessa in press).

Sharks have been rarely studied from the scope of community ecology (Lessa & Menni 1994; Menni & Gosztonyi 1982; Muñoz Chápuli 1985a 1985b; Stride *et al.* 1992). A fossil chondrichthyan assemblage in tropical conditions from the Miocene of France (Bessedick 1984), is similar to the Maranhao community in the presence of Aetobatus, *Dasyatis*, and particularly the restricted distributed *Isogomphodon* (Lessa & Menni 1994). In the Marannhao community *Isogomphodon oxyrhynchus*, though not closely associated with the other species, has a constant presence and is an important part of the community in terms of weight. These aspects point to the possibility of a similar organization of shark communities in shallow coastal environments in the tropics.

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