Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic

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This study analyses the sexual activity and segregation of sand tiger sharks, *Carcharias taurus*, from Anegada Bay (Argentina). Reproduction-linked movements along the South American Atlantic coast were inferred from data from several SW Atlantic localities. Male sand tigers (n=162) matured at 193 cm total length (L_T). Females (n=77) matured between 218 and 235 cm L_T. These figures are similar to those from other populations, although size-at-maturity of males was slightly different from South African and Australian populations. In females, the size of ovarian follicles was positively correlated with gonadosomatic index and negatively correlated with hepatosomatic index, while the liver was significantly larger than in males. Sand tiger sharks were present in Anegada Bay from December to April. Males were significantly more abundant than females (2:1). Significant differences in reproductive condition through time were observed in males. During January and February males had seminal vesicles full of spermatozeugmata but by March and April the vesicles were empty. As the proportion of males with a lighter colouration peaked from January to March, it is very likely that mating takes place during January and February. The skewed sex-ratio during the mating season indicates a possible strong competition for mates among males, as observed in captivity. Males, females and some juveniles occur in Argentinean and Uruguayan waters, where mating takes place. Pregnant females occur in subtropical waters of southern Brazil, where they give birth. Given that pregnant and non-pregnant females occur at the same time in different zones, we suggest that the female reproductive cycle is biennial. Striking differences among migratory patterns of sand tiger sharks from the SW and NW Atlantic and South Africa were observed.

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Introduction

The sand tiger shark, *Carcharias taurus* Rafinesque, 1810 (Lamniformes: Odontaspididae), is a large coastal predator occurring in the NW Atlantic, Mediterranean and NW coast of Africa, SW Atlantic, and the coasts around southern Africa, Australia, and SE Asia (Compagno, 1984; Last and Stevens, 1994). *C. taurus* is a viviparous species. After eclosion from the egg envelope, the largest embryo feeds on the smaller ones (intra-uterine cannibalism or adelphophagy), and then grows to birth size by feeding on unfertilized oocytes supplied by the mother (oophagy). As a result of this reproductive mode only one embryo per uterus is born (Gilmore *et al.*, 1983; Compagno, 1984). Ecological aspects of reproduction, including the timing and location of reproductive events, gestation and nursery grounds are unknown through most of the range of

C. taurus. Information on some aspects of the reproductive ecology is available for NW Atlantic (Gilmore et al., 1983; Gilmore, 1993) and South African populations (Bass et al., 1975). These reproductive characteristics may show variability among populations and are important for management.

Reproduction-linked movements of sand tiger sharks from the NW Atlantic (Gilmore, 1993) and southern Africa (Bass et al., 1975) have been documented. In SE Australia migratory movements are thought to occur, although evidence is not conclusive (Krogh, 1994; Pollard et al., 1996). These movements have been inferred from the occurrence of individuals of different sex or at different reproductive stages in different areas (Gilmore, 1993) and subsequently confirmed by tagging-and-recapture studies (Kohler et al., 1998). However, the migratory pattern seems to be differ between regions and cannot be generalized.

Like many other galeoid sharks, *C. taurus* is very susceptible to overfishing by several methods (e.g. netting of beaches, spearfishing, commercial and recreational fishing). Sand tiger shark populations have been severely depleted in several parts of the world including SE Australia (Krogh, 1994; Pollard et al., 1996; Smith and Pollard, 1999; Environment Australia, 2000) and the NW Atlantic (Castro et al., 1999).

In the SW Atlantic, *C. taurus* ranges from Rio de Janeiro (23°S, Brazil; Bigelow and Schroeder, 1948) southwards to San Matías Gulf (41°30′S, Argentina; Menni, 1986a). Most previous research on *C. taurus* in the region has focused on taxonomy (e.g. Lahille, 1928; Sadowsky, 1970) or is limited to miscellaneous observations from comparatively few specimens (Cervigón and Bastida, 1974; Menni et al., 1986). Until now, the general biology of *C. taurus* in the region has remained unknown (Menni, 1986b) despite the species being harvested throughout its regional range (Charvet, 1995; Chiaramonte, 1998; Nion, 1999; Lucifora, 2001).

In this paper, we describe the reproductive biology of *C. taurus* from the SW Atlantic and provide a hypothesis on reproduction-linked migratory movements in the region.

Materials and methods

Study area

Sampling was carried out in the small town of Bahía San Blas (Argentina, Figure 1) during the shark fishing seasons (October to April) of 1998–1999, 1999–2000 and 2000–2001. All sharks caught in Anegada Bay are landed in Bahía San Blas. Anegada Bay is a shallow area with numerous small islands and banks influenced by the discharges of Colorado and Negro rivers (Figure 1). During the time of residence of sand tiger sharks in the

region (late spring to autumn), water temperature ranges from 12 to 16°C (Martos and Piccolo, 1988). A coastal front results from the confluence of continental waters (mainly discharge of the Negro River) with shelf water masses (Guerrero, 1998). This coastal front makes the region an important nursery area for several coastal species including striped weakfish, *Cynoscion guatucupa* (Cuvier, 1830), whitemouth croaker, *Micropogonias furnieri* (Desmarest, 1823) (Macchi and Acha, 1998), and narrownose smoothhound shark, *Mustelus schmitti* Springer, 1939 (Cousseau et al., 1998). Rod-and-reel recreational fisheries for sharks [*C. taurus*; *M. schmitti*; broadnose sevengill, *Notorynchus cepedianus* (Péron, 1807); school shark, *Galeorhinus galeus* (Linnaeus, 1758); and copper shark, *Carcharhinus brachyurus* (Günther, 1870)] and bony fishes [*M. furnieri*; *C. guatucupa*; silversides, *Odonthestes argentinensis* (Valenciennes, 1835)] exist in the region. Shark fishing is carried out by small boats (up to 7 m long). Depth at shark fishing grounds is usually 5–20 m (Figure 1).

Reproduction

Most specimens were obtained from the recreational shark fishery from southern Anegada Bay, and three additional specimens were obtained from research cruises conducted in coastal waters of Uruguay and northern Argentina. Once the sharks are landed, a shark-processing service for obtaining meat and jaws is offered to fishermen. As a result all sharks are transferred to fish-processing plants.

All specimens were examined fresh. Changes in colouration, considered indicators of pre-copulatory behaviour (Gordon, 1993), were noted immediately after landing. Total length with the caudal fin in natural position (L_T), precaudal length (L_{PC}), sex, uteri and oviducal gland width, and inner clasper length were recorded at fish-processing plants within 2–4 h of capture. The caudal fin of some sharks was cut off before we could record L_T, and L_T was estimated from L_{PC} using the equation:

$$L_T(cm) = 1.239 \times L_{PC}(cm) + 18.129$$

(r = 0.986; n = 182; range = 89–267 cm L_T)

The internal organs were transported to the laboratory and immediately examined. The weights of the liver, testes, and right ovary were recorded to the nearest g, and maximum diameter of ovarian follicles was recorded. Females with wide, ribbon-like uteri and enlarged oviducal glands were considered mature. Males were considered mature when having a highly coiled epididymis, long calcified claspers that could be rotated towards the head. Size at maturity was inferred from the allometric growth patterns (against L_T) of uteri and
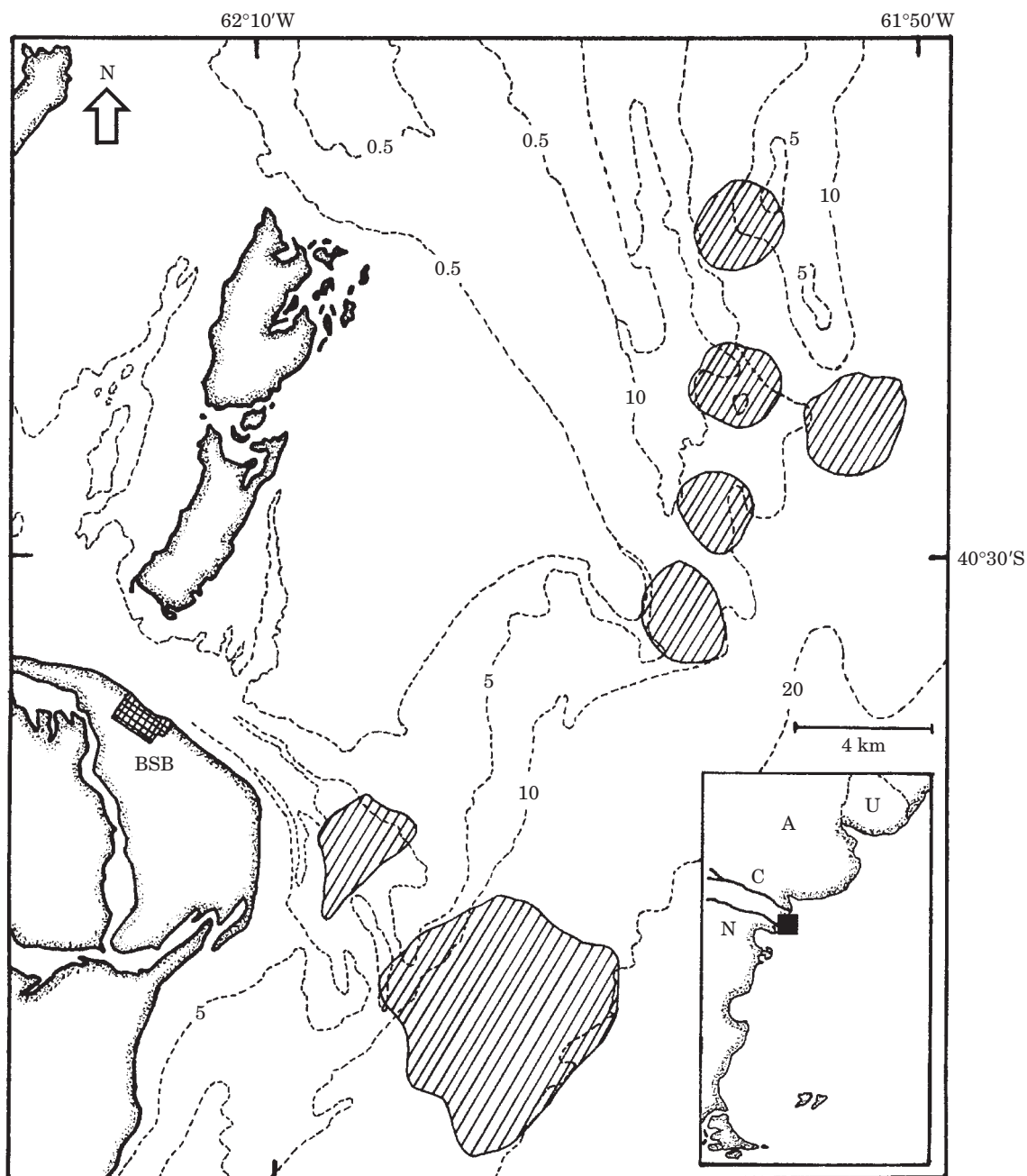
Figure 1. Location of fishing grounds (striped areas) for sand tiger sharks, *Carcharias taurus*, in Anegada Bay, Argentina. Dashed lines are isobaths (in metres). The inset shows the location of Anegada Bay (black square) in southern South America. Colorado (C) and Negro (N) rivers are also shown. BSB: Bahía San Blas, A: Argentina, U: Uruguay.

oviducal glands in females, and from allometric clasper growth and calcification in males.

As a measurement of sexual activity, the monthly proportion of males with sperm aggregations (spermatozeugmata, Hamlett, 1999) in the seminal vesicles was calculated from January to April. Monthly differences in mean proportions were evaluated with one-way ANOVA. When significant differences were detected, a Tukey test was used to locate the differences (Zar, 1984).

As total weight could not be recorded, we calculated both gonadosomatic and hepatosomatic indices (I_G and I_H, respectively) following Taniuchi (1988) as:

$$I_G \text{ (or } I_H) = \text{Gonad (or liver) weight}/L_T^3 \times 100$$
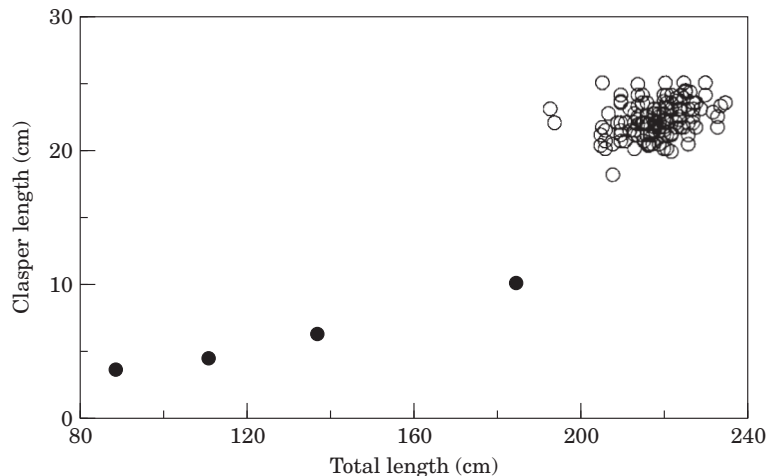
Figure 2. Total length–inner clasper length relationship in sand tiger sharks, *Carcharias taurus*, from the SW Atlantic. Solid circles depict juvenile males. Empty circles represent adult males with calcified claspers.

The null hypothesis of no correlation was tested for the relationships between maximum diameter of ovarian follicles and I_G and I_H.

The null hypothesis of no sexual differences in I_H was tested with a Mann–Whitney U test (Zar, 1984). Length frequency distributions were estimated for each sex and compared by using the Kolmogorov-Smirnov test (Zar, 1984). Trends in reproductive condition through time were investigated by analysing monthly variations in I_G and I_H with one-way ANOVA.

The sex ratio was calculated, and compared with the expected ratio 1:1 (no sexual segregation) by means of the chi-square test with the Yates' correction (Zar, 1984).

Abundance

Abundance in Anegada Bay was quantified calculating catch per unit effort (CPUE) in two ways: one as sharks caught per hook per day ($CPUE_h$), and the other as sharks caught per fishing trip per day ($CPUE_t$). Trends in $CPUE_h$ and $CPUE_t$ were analysed separately for each year. Differences in mean monthly $CPUE_h$ and $CPUE_t$ were assessed with the Kruskal–Wallis test; non-parametric multiple comparisons tests were carried out when significant differences were found (Conover, 1980).

Results

Reproduction

We examined 239 specimens of *C. taurus*, 162 males and 77 females. The smallest specimen was a presumably young-of-the-year male 89 cm L_T from coastal Uruguayan waters, and the largest was a 267 cm L_T female from southern Anegada Bay. The largest male measured 236 cm L_T and the smallest female 136 cm L_T.

The smallest mature male measured 193 cm L_T and the largest immature one was 185 cm L_T (Figure 2). All males from Anegada Bay were mature. Testis weight was between 5 (89 cm T_L) and 125 g (215 cm T_L). The presence of spermatozeugmata in the seminal vesicles was not evenly distributed from January to April (one-way ANOVA, F=44.977, n=56, d.f.=3, p<1×10^{-6}). All males caught in January and February had full seminal vesicles, and by March and April most males lacked spermatozeugmata (Tukey test for unequal sample size; January–February: p=0.138; January–March: p=0.00016; January–April: p=0.00016; February–March: p=0.00016; February–April: p=0.00016; March–April: p=0.999). Light-coloured males were most common in January, February and March (20%, 14.28% and 19.23% of all examined males; n=75, 35 and 26, respectively). No light-coloured males were observed in December (n=2) or April (n=21). Both I_G (one-way ANOVA, F=6.068, n=157, d.f.=4, p=0.0001) and I_H (one-way ANOVA, F=10.024, n=161, d.f.=4, p<1×10^{-6}) of males showed significant monthly differences. I_G was highest in April while I_H was at a minimum in January (Table 1).

Females matured between 218 and 235 cm L_T (Figure 3). Ovary weight ranged from 12.7 (136 cm L_T) to 555 g (247 cm L_T). No pregnant females were caught.

Maximum diameter of ovarian follicles was significantly and positively correlated with I_G (r=0.426, n=59, t=3.552, p=0.00078; Figure 4a). The correlation between the maximum diameter of ovarian follicles and I_H was significant and negative (r=-0.522, n=59, t=4.616, p=0.00002; Figure 4b).

Mean I_H differed significantly between sexes with females having larger livers relative to L_T than

Table 1. Mean monthly values of gonadosomatic and hepatosomatic indices of sand tiger sharks, *Carcharias taurus* from the SW Atlantic. Standard deviation and sample size (between parentheses) are also given. Means sharing the same letter are not significantly different at p<0.05 (Tukey test for unequal sample size).

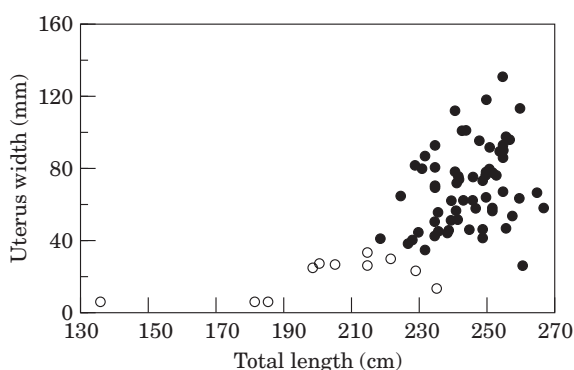|	Gonadosomatic index		Hepatosomatic index	
	Mean	Standard deviation (n)	Mean	Standard deviation (n)
December	7.17×10^{-6}	2.49×10^{-6} (3)[a]	3.19×10^{-4}	2.06×10^{-5} (3)[a]
January	7.13×10^{-6}	1.13×10^{-6} (72)[b]	3.43×10^{-4}	7.66×10^{-5} (75)[b]
February	7.18×10^{-6}	1.40×10^{-6} (34)[b]	4.05×10^{-4}	1.16×10^{-4} (35)[a]
March	7.28×10^{-6}	1.19×10^{-6} (27)[b]	4.23×10^{-4}	9.88×10^{-5} (27)[a]
April	8.64×10^{-6}	1.51×10^{-6} (21)[a]	4.66×10^{-4}	9.14×10^{-5} (21)[a]

Figure 3. Total length–uterus width relationship in sand tiger sharks, *Carcharias taurus*, from the SW Atlantic. Empty and solid circles are immature and mature females, respectively.

males (females' mean $I_H = 0.060 \pm 0.022$, males' mean $I_H = 0.039 \pm 0.010$, U=2317, $n_{males}=162$, $n_{females}=77$, $p = 4.35 \times 10^{-15}$).

Length–frequency distributions were significantly different between sexes, females (mean $L_T = 238.97$ cm) being larger than males (mean $L_T = 216.11$ cm) (Kolmogorov–Smirnov, $d_{max} = 0.79$, $n_{males}=148$, $n_{females}=77$, p<0.001; Figure 5).

The reproductive condition of females did not significantly vary through time, as indicated by monthly comparisons of both I_G (one-way ANOVA, F=0.971, n=74, d.f.=4, p=0.429) and I_H (one-way ANOVA, F=1.804, n=77, d.f.=4, p=0.137).

The sex ratio was significantly biased towards males (2.06:1, $\chi^2 = 27.801$, d.f.=1, $p = 9.41 \times 10^{-8}$). This sex ratio was not different to a ratio of 2 males per female ($\chi^2 = 0.026$; d.f.=1; p=0.818).

Abundance

Sand tiger sharks were present in Anegada Bay from December to late April (summer–autumn of the Southern Hemisphere). During the 3 years of study no sand tiger sharks were caught in October or November. Low
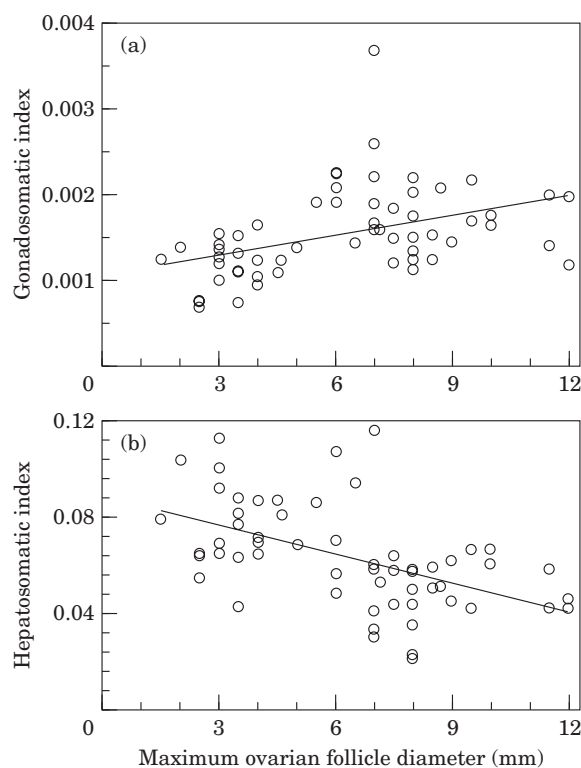

Figure 4. Relationships between maximum diameter of ovarian follicles and gonadosomatic (a) and hepatosomatic (b) indices in sand tiger sharks, *Carcharias taurus*, from the SW Atlantic.

CPUEs were obtained in December, which reflects the arrival of sand tiger sharks to the study area in that month (Figure 6). No significant differences in CPUE were found from January to April (Figure 6). This pattern indicates that sand tiger sharks arrived to Anegada Bay in December and that they remained in that area throughout summer and autumn. According to fishermen sand tiger sharks can be caught up to mid May and are then absent from Anegada Bay until December.
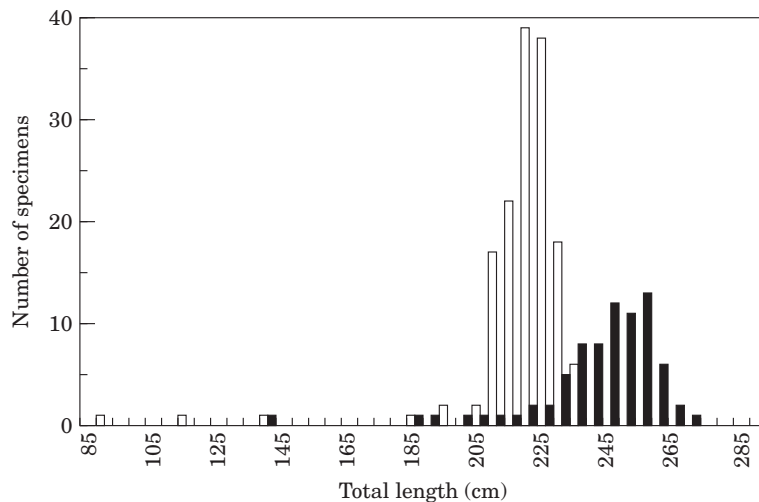
Figure 5. Length–frequency distribution for sand tiger sharks, *Carcharias taurus*, from Uruguay and Argentina. Solid bars: females; empty bars: males; numbers under the x-axis are upper values of 5-cm length intervals.

Discussion

Off the east coast of the USA, male sand tiger sharks mature at 190–195 cm L_T (Gilmore *et al.*, 1983; Branstetter and Musick, 1994), and females at 220–229 cm L_T (Branstetter and Musick, 1994; Castro *et al.*, 1999). In South African waters males mature between 202 and 220 cm L_T and females at 220 cm L_T (Bass *et al.*, 1975). Both sexes from Australian waters mature at about 220 cm L_T (Last and Stevens, 1994). Our figures are close to these, excepting the large size at maturity of males from Australia. Sadowsky (1970) observed pregnant females as small as 225 cm L_T in south Brazil, agreeing with our estimate of female size at maturity (218–235 cm L_T) for the SW Atlantic population.

Liver is larger in females than in males as indicated by differences in I_H. This may be related to the increased energy expenditure that females face during vitellogenesis, oocyte maturation, and gestation. The liver is a key organ in female reproduction because it is involved in yolk production through production of vitellogenin, the yolk precursor (Koob and Callard, 1999). Females store large quantities of lipids in the liver during the pre-vitellogenic phase of the reproductive cycle, and these reserves are depleted during vitellogenesis and gestation. The negative correlation between I_H and maximum diameter of ovarian follicles found in females reinforces this hypothesis. The lipid reserves of the liver may also be used for female metabolism if gestating sand tiger females do not eat during pregnancy (Michael, 1993). Sexual dimorphism in liver size is often noted in elasmobranchs (Rossouw, 1987; Silva and Lessa, 1991).

Assuming that the occurrence of aggregated spermatozoa in the seminal vesicles of male elasmobranchs is an accurate indicator of mating activity (Hamlett, 1999), our results suggest that mating takes place in January and February (summer) and that mating activity is almost complete by March and April (late summer-autumn). Gordon (1993) reported that captive male specimens of *C. taurus* acquire a lighter colouration during pre-copulatory behaviour. In our samples, light-coloured males occurred from January to March, reinforcing the hypothesis that mating takes place during summer months in Anegada Bay. In South Africa, Bass *et al.* (1975) found females with fresh mating scars from October through December (spring). On the US Atlantic coast, the mating season extends from late winter to early spring off Florida, and during autumn off North Carolina (Gilmore, 1993). From this evidence, it appears that the timing of reproductive events differs among populations of *C. taurus*, possibly in response to local ecological conditions.

Changes in male I_G and I_H are expected since the reproductive status of males changes through the season. The increasing trend in I_G indicates incipient gonad enlargement possibly as a result of gamete production during winter for the following summer. The minimum of I_H of males in January coincides with peaks of indicators of mating activity. Most sand tiger females occurring in the study area were adult. No significant trend in their reproductive condition was observed during their period of residence in Argentinean waters. Sand tiger sharks are present from October to May and females strongly outnumbered males. Aggregations of pregnant females carrying embryos 501–800 mm L_T are present in southern Brazil in April and May (Sadowsky, 1970). On the basis that mature females at different reproductive stages (pregnant in Brazil and mature but non-pregnant in Argentina) occur at the same time in
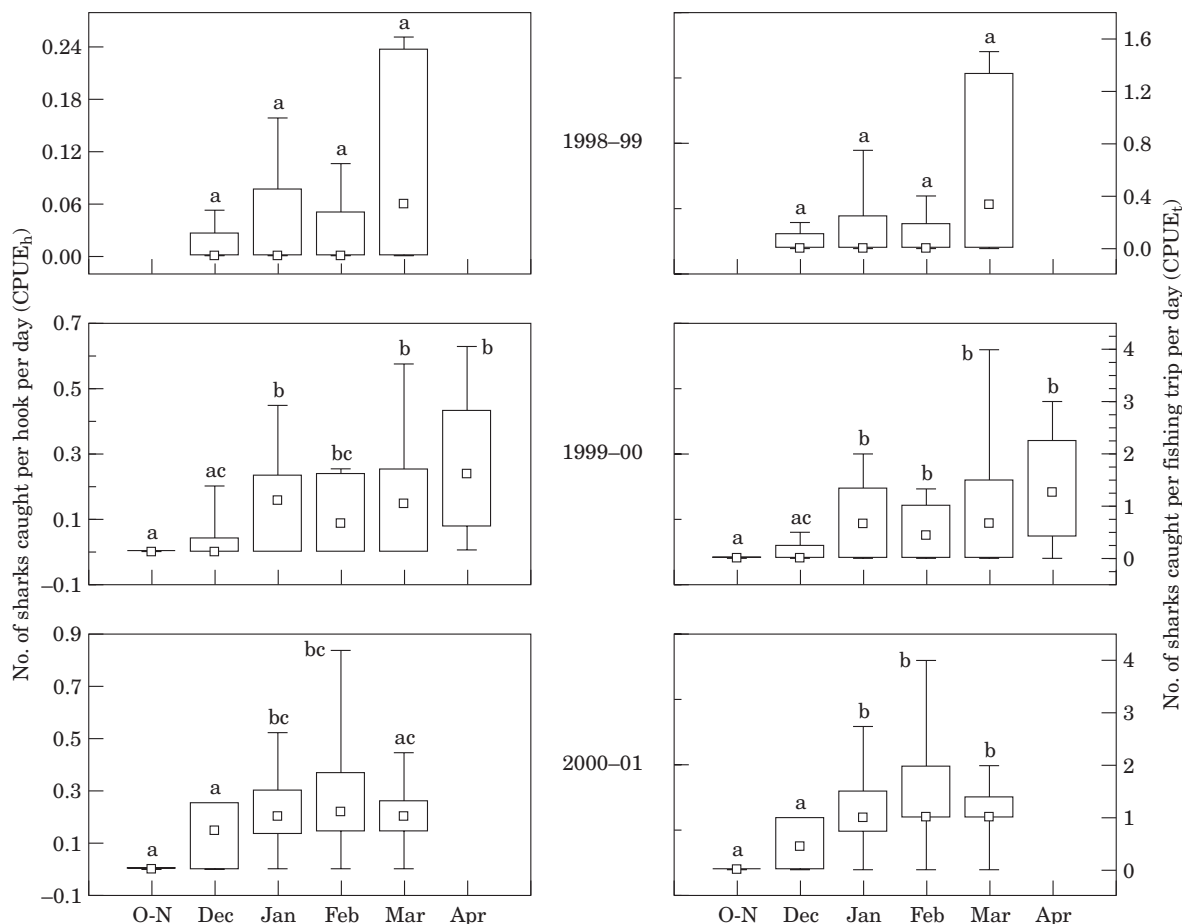
Figure 6. Occurrence of sand tiger sharks, *Carcharias taurus*, in Anegada Bay (Argentina) as indicated by the number of sharks caught per hook per day ($CPUE_h$) and the number of sharks caught per fishing trip per day ($CPUE_t$) in three fishing seasons (1998–1999, 1999–2000 and 2000–2001). Squares are median values; lower and upper box limits are the 25 and 75 percentile, respectively; and whiskers show the range between minimum and maximum observations. Distributions with different letters are significantly different (non-parametric multiple comparisons test). O–N: October–November, Dec: December, Jan: January, Feb: February, Mar: March, Apr: April.

these two regions, we suggest that the female reproductive cycle is biennial. A biennial reproductive cycle has been suggested for the NW Atlantic population (Branstetter and Musick, 1994) and is common in most large galeoid sharks (Castro *et al.*, 1999). Furthermore, the weight of the right functional ovary of females from Anegada Bay (up to 555 g) is much less than from pregnant females from Florida waters (3700–8500 g; Gilmore *et al.*, 1983). This suggests that females from Anegada Bay are in the resting phase of the reproductive cycle. A resting phase with low I_G values prior to ovulation and gestation has been observed in another lamnoid shark, the shortfin mako *Isurus oxyrinchus* Rafinesque, 1810 (Mollet *et al.*, 2000). The analysis of sex ratios also supports a biennial reproductive cycle. The number of mature females in Anegada Bay is half that of males, while 95% of catches in the same season in

southern Brazil are pregnant females (Sadowsky, 1970). This indicates that the female population is split into two groups, gravid females in the north (Brazil) and non-pregnant females engaged in mating activities in the south (Anegada Bay, Argentina).

The predominance of males (sex ratio 2:1) during the mating season suggests that male competition for mates may occur. Gordon (1993) observed that captive male sand tigers interact agonistically during precopulatory behaviours and a hierarchy is formed, until the dominant male copulates with the courted female. Multiple copulations of female sand tigers in captivity have also been suggested (Gordon, 1993). Our results on sex ratio and mating indicators are highly reconcilable with direct observations of mating activities in captive specimens, suggesting a mating system with high levels of male competition. A polygamous mating system with possible

strong male competition has been observed in the lemon shark *Negaprion brevirostris* (Poey, 1868) (Feldheim *et al.*, 2001).

Detailed descriptions of reproduction-linked migrations of *C. taurus* are available for the NW Atlantic and South African populations. In the NW Atlantic, mature males and juveniles occur between Cape Cod and Cape Hatteras while mature and pregnant females inhabit the more southern waters between Cape Hatteras and Florida (Gilmore, 1993). Mating takes place in southern waters where pregnant females give birth (Gilmore, 1993). In southern Africa pregnant females migrate from KwaZulu-Natal southwards to the Cape region where they give birth during winter and early spring (Bass *et al.*, 1975). It has been suggested that the migratory movements of sand tiger sharks from SE Australia are opposite to those from South Africa (Pollard *et al.*, 1996). Our results, combined with data from other SW Atlantic localities, show that mature males, females and some juveniles occur in Argentinean and Uruguayan waters during late spring, summer and autumn. Mating occurs in Argentinean waters, with pregnant females occurring in the warmer waters off southern Brazil, where parturition takes place. Some newborns and juveniles disperse southwards, since several small specimens have been reported from Argentinean and Uruguayan waters (Cervigón and Bastida, 1974; Menni *et al.*, 1986; this study). During winter, males may migrate offshore to continental shelf waters since they are not found in significant numbers either in coastal Argentinean/Uruguayan waters (Meneses, 1999; Nion, 1999; this study) or in southern Brazil (Sadowsky, 1970). This migratory pattern is more similar to the NW Atlantic pattern than to the South African one. Major differences include the region where parturition takes place and the direction of female movements. In South Africa, birth takes place in temperate waters (off the Cape coast) while in the NW and SW Atlantic it occurs in subtropical waters (off the Carolinas and Florida, and off Brazil, respectively). Females move poleward in South Africa to give birth, whereas the migration towards gestation grounds is equatorial in the SW Atlantic. NW Atlantic females do not appear to move (Gilmore, 1993).

Regional differences in both the timing and location of reproductive events among different populations of *C. taurus* might be related to differences in environmental and/or biological regimes. It has been suggested that some differences in life-history traits in the bonnethead shark, *Sphyrna tiburo* (Linnaeus, 1758), and the Brazilian sharpnose shark, *Rhizoprionodon lalandii* (Valenciennes, 1839), may be related to temperature (Parsons, 1993; Menni and Lessa, 1998). Unfortunately, the ecological factors influencing the reproductive cycles of elasmobranchs are mostly unknown (Hamlett and Koob, 1999).

SW Atlantic sand tiger sharks are difficult to manage effectively because they move between countries and high localized fishing pressure will affect the whole population. The situation is complex because different reproductive stages and events occur under different jurisdictions (pregnancy in Brazil and mating in Argentina) and because sexes are not equally distributed throughout the species' range. Thus, a management strategy involving Brazil, Uruguay and Argentina is required to manage effectively the SW Atlantic population of *C. taurus*.

Acknowledgements

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