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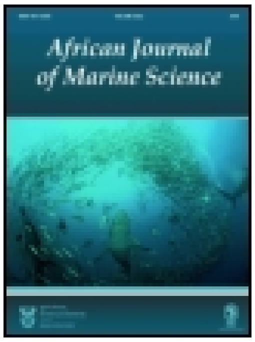

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Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 11. The scalloped hammerhead shark *Sphyrna lewini* (Griffith and Smith)

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Between 1978 and 1998, a total of 3 385 scalloped hammerhead sharks *Sphyrna lewini* was caught in the protective nets off KwaZulu-Natal. The mean annual catch was 166 sharks (range 60–279). There was a significant decrease in catch rate with time, but the relationship with the population size in KwaZulu-Natal waters is unknown. Size and sex segregation is indicated. Sizes-at-50% maturity were 161.5cm (males) and 183.1cm (females). Most of the catch (91%) was immature, but neonates are poorly sampled by the 51-cm meshed nets. In small animals (<160cm precaudal length, PCL), males significantly outnumbered females by 2.2:1, and in large animals by 3.6:1. The length-mass relationship differed between sexes. Catches of both small and large animals were highest in summer. Most of the large males were caught in November and December, consistent with an inshore movement of mature animals to breed in summer, but no evidence of recent mating was observed in either sex. Females pregnant with term embryos (median embryo length per litter 30.4–36.2cm) were caught between October and March. These females tended to have maximum ovarian follicle diameters of ≥30mm, indicating that mating would occur shortly after parturition. The median size of 11 litters was 10 embryos. The Tugela Bank to the north of the netted region appears to be a nursery ground. Teleosts, comprising 42 families and 60 identified species, dominated the diet in terms of frequency of occurrence (77%), followed by cephalopods (25%).

Keywords: cpue, distribution, embryos, gill nets, length frequency, length-weight relationships, maturity, nursery grounds, reproduction, seasonality, stomach contents

Introduction

Hammerhead sharks are found in all tropical and warm temperate oceans (Gilbert 1967). Early references to *Sphyrna* species in the South-West Indian Ocean are doubtful with regard to the specific identification (Bass 1972), although modern reports are accurate to species level (Compagno 1984). The scalloped hammerhead shark *Sphyrna lewini* (Griffith and Smith) is essentially circumglobal in coastal warm temperate and tropical seas. It occurs over continental and insular shelves and in the deep water adjacent to them (Compagno 1984). Off the east coast of southern Africa, *S. lewini* has been recorded from northern Moçambique to the south coast of KwaZulu-Natal (KZN, Bass *et al.* 1975). It is also apparently fairly common off Madagascar (Fourmanoir 1961). *S. lewini* coexists with the smooth hammerhead *S. zygaena* and the great hammerhead *S. mokarran* in the coastal waters of KZN (Cliff 1995).

S. lewini is the third most numerous shark caught in the gill nets that are routinely set and hauled to reduce the risk of shark attack at the beaches of KZN (Wallett 1983). The National Sharks Board (NSB) maintains nets, known locally as shark nets. *S. lewini* has been studied in several localities worldwide, although there are few comparative studies locally. This paper is the eleventh in a series describing the general biology and catch statistics of each of the 14 species of shark commonly caught in the nets.

Material and Methods

The shark nets, which have a stretched mesh of 51cm, are set parallel to the shore, 300–500m offshore, in water 10–14m deep (Cliff *et al.* 1988). The total length of the gill nets set on the KZN coast changed from 43km in 1988 to 39.4km in 1998. The distribution of the nets is shown in Figure 1.

The catch and life-history data presented in this study were recorded between 1978 and 1998. Shark nets have been in place off the KZN coast since 1952, but until 1978 data were considered unreliable, primarily in terms of differentiation between the three sphyrnid species. Units of effort are expressed as kilometres of net per year (km-net year^{-1}). Shark length is expressed as precaudal length (PCL), the straight-line distance between perpendiculars to the snout

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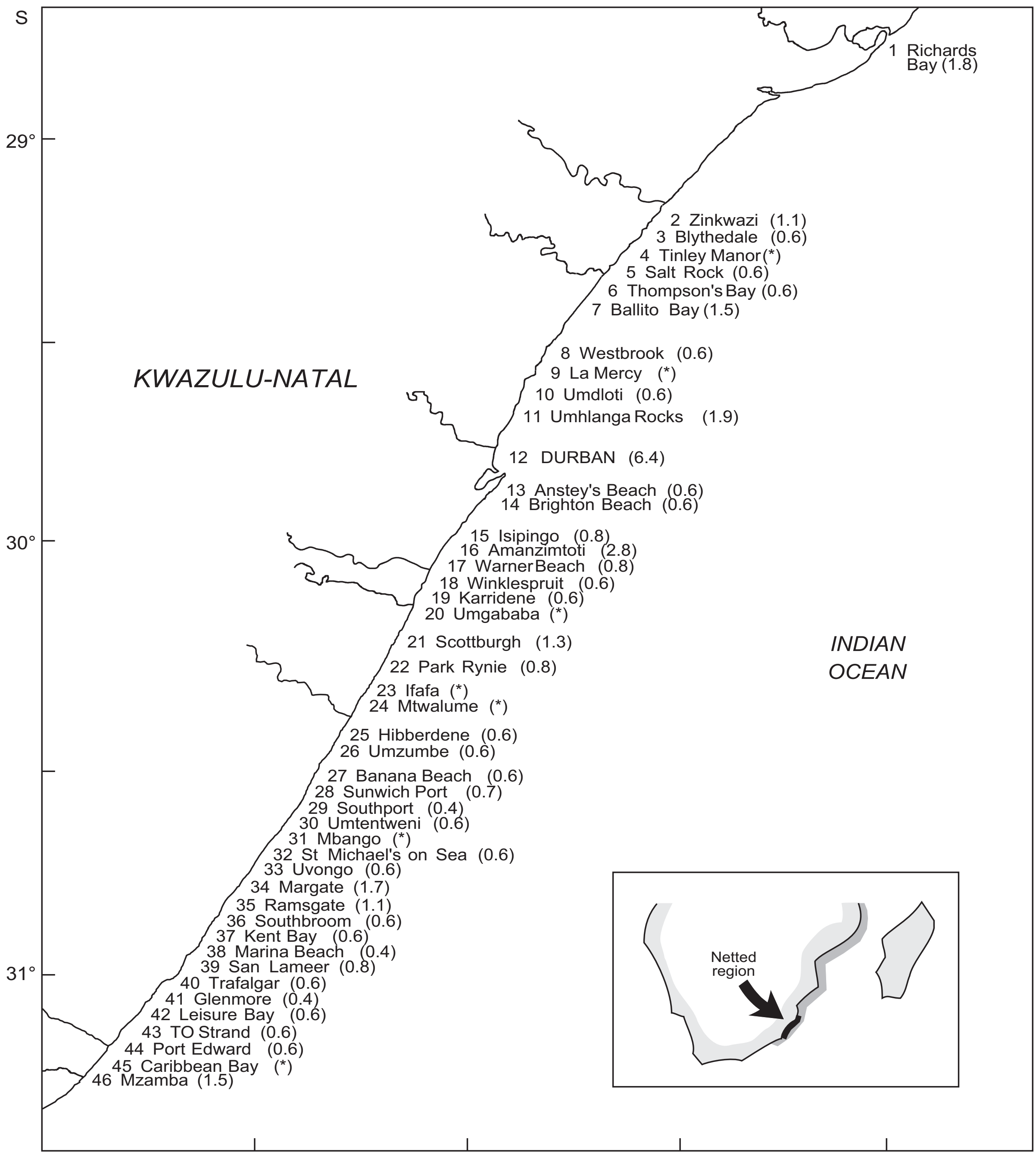

Figure 1: Netted beaches on the KZN coast and, in parenthesis, the length of nets in kilometres in January 1998. Several net installations (*) were removed permanently during the study period, 1978–1998. Inset shows the locality of the netted region and the distribution of *S. lewini* in the southern African region (after Compagno 1984, Compagno *et al.* 1989)

and the precaudal notch. This is considered to be the most precise measure of a shark with a precaudal notch (Cliff 1995). Lengths cited from the literature were converted to PCL for ease of comparison. The following relationship was found between PCL and fork length (FL):

$$FL = 1.07PCL + 2.27 \text{ (n = 722, r = 0.97, range 53.7–243cm PCL)} \quad (1)$$

Upper caudal length (UCL) was measured in centimetres as a straight line from the tip of the upper caudal fin to the precaudal notch. The relationship between UCL and PCL is linear (Gilbert 1967, Bass *et al.* 1975) and is represented by

$$UCL = 0.393PCL + 4.77 \text{ (n = 1 681, r = 0.923, range 53.7–243cm PCL)} \quad (2)$$

Total length (TL) was not recorded for this species prior to 1990, hence the following equation was adopted:

$$TL = PCL + 0.8UCL \text{ (Bass et al. 1975)} \quad (3)$$

By substituting UCL from Equation 2 into Equation 3,

$$TL = 1.314PCL + 3.816 \quad (4)$$

The relationship used for small specimens (embryos and neonates), however, was

$$PCL = 0.731TL \text{ (Bass et al. 1975)} \quad (5)$$

The following relationship was used to relate TL to FL

$$TL = 1.30FL + 1.28 \text{ (Stevens and Lyle 1989)} \quad (6)$$

A simple linear regression was applied to the log-transformed length and mass data to determine the body mass to PCL relationship. The relationships for males and females were compared using Student's t-test (Zar 1974).

Measurements of reproductive structures are given by Cliff *et al.* (1988) and criteria for visual assessment of maturity follow Bass *et al.* (1975). Measurements included gonad mass (both sexes), uterus width and the diameter of the largest ovarian follicle (females) and the inner length of the right clasper (males). Males were considered to be mature when the claspers were fully calcified. Maturity in females was indicated by the presence of distinct ovarian follicles and uteri that had expanded from a thin, tube-like condition to form loose sacs. The presence of a ruptured hymen was sometimes used for confirmation. Size at maturity was determined following Welch and Foucher (1988), cited by Mollet *et al.* (2000). A logistic model of the form $Y = [1 + e^{-(a + bX)}]^{-1}$ was fitted to the binomial maturity data (immature = 0, mature = 1) of females and males respectively, using SPSS Regression Models™ Version 12.0. Median length-at-maturity was calculated using the expression MPCL = –a/b.

Stomach content data are reported for the period 1983–1998. Depending on extent of digestion, each prey item was identified and classified to the lowest possible taxon and each taxon was quantified as percentage frequency of occurrence (%F), percentage by number (%N) and percentage by mass (%M) according to the definitions of Hyslop (1980). Stomachs containing only hard prey items such as teleost otoliths and cephalopod beaks were considered empty because these digestion-resistant items may have been in the stomach for a long time, hence biasing the analysis. Otoliths and beaks found in the stomachs were identified using archived reference material stored at the Port Elizabeth Museum. A cumulative prey curve, as described by Ferry *et al.* (1997) in Gelsleichter *et al.* (1999), was used to determine whether sufficient *S. lewini* stomachs had been sampled to fully describe the diet. The order in which the stomachs were analysed was randomised and the mean number of new prey species found consecutively in the stomachs was plotted against the number of stomachs examined. Contingency table analysis was used to test for differences in diet between small and large *S. lewini* (after Cortés 1997). The dietary diversity of these two size-classes was compared in terms of prey numbers using the Shannon-Weiner Index (H') and Margalef's Species Richness Index (d'). Their dietary overlap was assessed, without data transformation, by means of the Bray-Curtis Measure of Similarity (S), using PRIMER™ Version 5.

Net Catches

Annual variation

Between 1978 and 1998, 3 385 scalloped hammerhead sharks were caught in the nets at an average of 166.19 sharks per year (range 60–279). Catch rate ranged from 1.47 to 7.39 sharks km-net^{-1} year^{-1} over the study period. Catch more than doubled between 1983 and 1985 but this cannot be explained by any operational changes. Overall, the linear regression of catch rate against time yielded a significant negative slope ($p < 0.05$, Figure 2). The relationship between the population size of *S. lewini* in KZN waters and catch rate in the shark nets is unknown, but declining catch rate may indicate a declining population size. *S. lewini* is captured in a number of local fisheries. It is the most abundant elasmobranch species taken as bycatch in the commercial prawn fishery operating on the Tugela Bank off central KZN (Fennessy 1994). The bycatch consists primarily of newborn individuals. In addition, *S. lewini* is taken as bycatch by commercial and recreational skiboat fishers (P Pradervand, Oceanographic Research Institute, pers. comm.). Sphyrnids, including *S. lewini*, are also caught by artisanal and commercial fishing operations in neighbouring Moçambique (Sousa *et al.* 1997), but it is unknown whether stocks are shared with KZN.

Length distribution and sex ratio

Males significantly outnumbered females overall (2.3:1 M:F, χ^2 test, $p < 0.0001$, $n = 3\,182$). This is consistent with previous studies in coastal waters, which concluded that females tend to be found farther offshore than males (e.g. Branstetter 1987, Klimley 1987, Stevens and Lyle 1989).

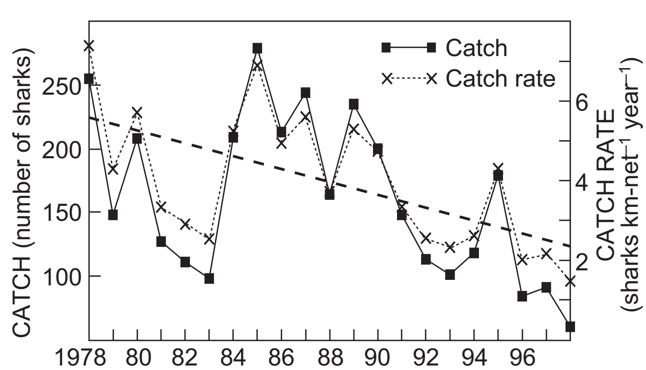

Figure 2: Catch and catch rate of *S. lewini* in the KZN shark nets, 1978–1998

Most *S. lewini* caught in the nets were <160cm PCL (Figure 3). Newborn animals, however, although present in the region (Fennessy 1994), are poorly sampled by the nets, probably because of their small size. Applying sizes at maturity calculated in this study (see below), the sex ratio of immature animals was 2.2:1 ($p < 0.0001$, $n = 2\ 827$) and of mature animals 6.7:1 ($p < 0.0001$, $n = 240$). A small proportion of mature animals in the total catch has also been recorded in other studies of *S. lewini* populations conducted in inshore waters, such as those off Hawaii (Clarke 1971), eastern Australia (Simpfendorfer and Milward 1993) and northern Brazil (Lessa *et al.* 1998).

Males ranged from 53.7cm (2.2kg) to 230.1cm (124kg) and females from 66cm (4.1kg) to 243cm (268kg, Figure 4). Compagno (1984) gives a maximum size of between 279cm and 317cm for this species. There was a significant difference in the length-mass relationships of males and females ($p < 0.05$). Females were heavier than males at lengths >100cm. The largest female was only 30cm longer than the largest male but was more than twice the mass. This was also found to be the case in Taiwan for *S. lewini* (Chen *et al.* 1990). The reason may be a difference in diet. The reported tendency for female *S. lewini* to move offshore at a younger age than males results in a change in diet (Klimley 1987). They appear to have increased predatory success offshore compared with the inshore males and hence accumulate more bulk (Klimley 1987). Differences between male and female length-body mass relationships are common among sharks and other chondrichthyans (e.g. Cliff *et al.* 1988, Cliff and Dudley 1991, 1992).

Geographical and seasonal distribution

To investigate differences in distribution (geographical and seasonal) between large and small scalloped hammerhead sharks, the catch was divided into specimens >160cm ($n = 287$) and those ≤160cm ($n = 2\ 899$). The catch rate of small animals was generally higher from Winklespruit (Beach 18) southwards than to the north, where there was an isolated peak at Westbrook (Beach 8) (Figure 5a).

The catch rates for large *S. lewini* were highest at the northernmost installations, Richards Bay (Beach 1) and Zinkwazi (Beach 2) — 1.51 and 1.41 sharks km-net^{-1} year^{-1} respectively — and at two installations in the centre of the netted region, Brighton Beach (Beach 14) and Umzumbe (Beach 26) — 1.24 and 1.52 sharks km-net^{-1} year^{-1} respectively (Figure 5b).

Figure 6a shows that small *S. lewini* exhibited strong seasonality, with catch peaking in summer (November–January). Highest catches were in January (512) and lowest in June (94). Therefore, small animals within the size range sampled by the nets tend to move out of the region in winter, possibly offshore (Bass 1970). Simpfendorfer and Milward (1993) suggest that once juveniles leave the shallow inshore waters for deeper oceanic water, they return only for seasonal reproductive purposes. In the present study, however, small animals appeared to return to inshore waters in summer. Whether the poorly sampled smaller size-classes (≤80cm) remain inshore throughout the year is unknown.

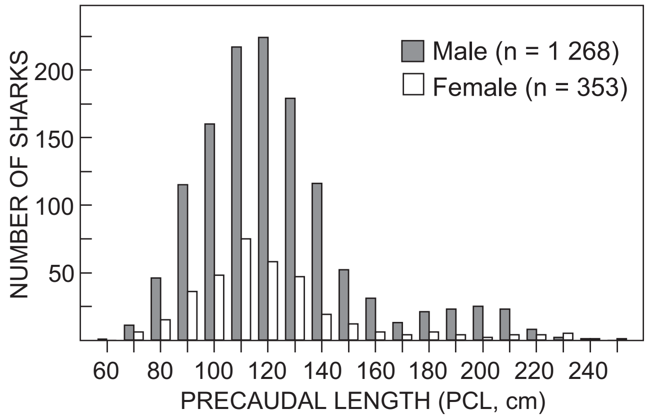

Figure 3: Length frequency distribution of *S. lewini* caught in the KZN shark nets, 1978–1998

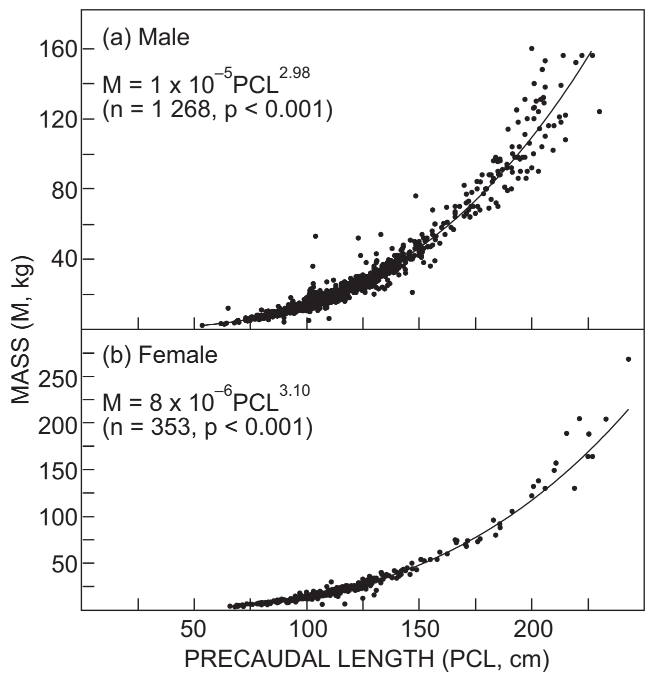

Figure 4: Length-mass relationship of (a) male and (b) female *S. lewini* (excluding embryos)

Seasonality in large *S. lewini* was less pronounced than in small animals, but catches did peak briefly in early summer (November and December) and were lowest in winter (July and August, Figure 6b). Movement of adults into inshore waters in summer may be for reproductive purposes (Clarke 1971). It would appear that the social organisation of *S. lewini* is such that small animals are protected from being eaten by large ones. Adult males and females live in segregated schools, away from the young, except during parturition (Bass 1970). This would explain the relative rarity of large specimens taken in the same study area as the more abundant small animals. Size segregation may also minimise competition for food.

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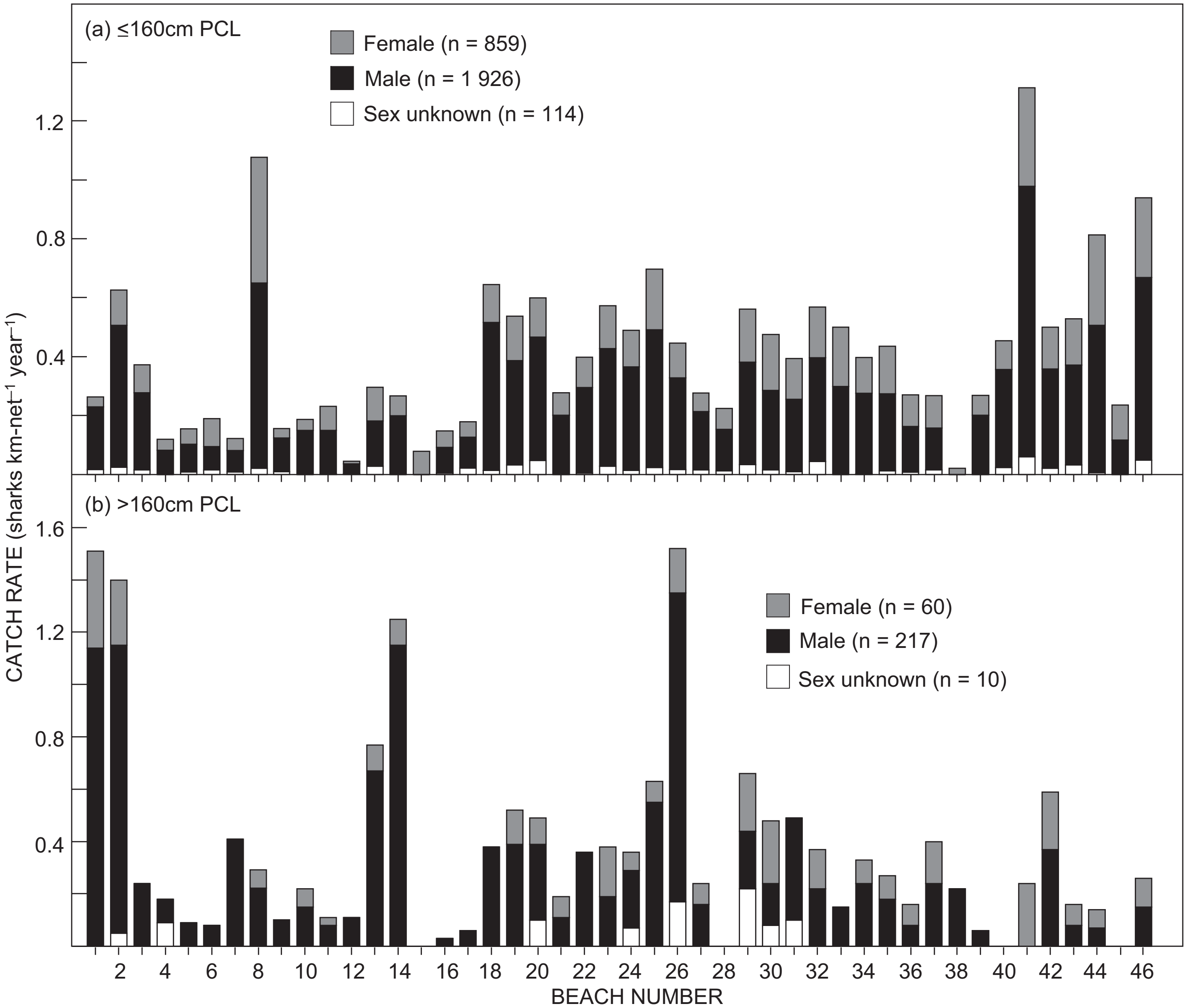

Figure 5: Geographic distribution of (a) ≤160cm and (b) >160cm *S. lewini* caught in the KZN shark nets, 1978–1998

Biology

Reproduction

Males

The length at maturity based on the calcification of the claspers (Figure 7) was calculated to be 161.51cm (Figure 8a), which is larger than all but one of the lengths reported from other localities for *S. lewini*: North-West Atlantic (180cm, Bigelow and Schroeder 1948); Gulf of Mexico (136.4cm, Branstetter 1987), south-west equatorial Atlantic (134–149cm, Hazin *et al.* 2001), Gulf of California (121.4cm, Klimley 1987); and Taiwan (148cm, Chen *et al.* 1988). The largest immature individual was 206cm and the length of the claspers was 14.6% of PCL. The smallest mature specimen was 136cm, with a clasper length of 12.5% of PCL. Only 15% (n = 136) of the males studied were considered mature. Most of the mature males were caught in November (29) and December (27), consistent with an inshore movement of mature specimens to breed in summer (Compagno 1984, Stevens and Lyle 1989). Most mature males were caught in the northern installations of Richards Bay (Beach 1) and Zinkwazi (Beach 2) and relatively few were caught in the southern installations (Figure 9). Only 11 males had full sperm sacs and no seasonal or geographic patterns of occurrence were apparent either in these or in post-active males.

Mean gonad index (GI: gonad mass / shark mass x 100) was low for males caught between late spring and early autumn, with a minimum of 0.12% in February and an increase towards winter (Figure 10a). Levels continued increasing until September, the end of winter, when a high of 0.48% was recorded for a single individual, then decreased again to December. In males off Australia, GI peaked from

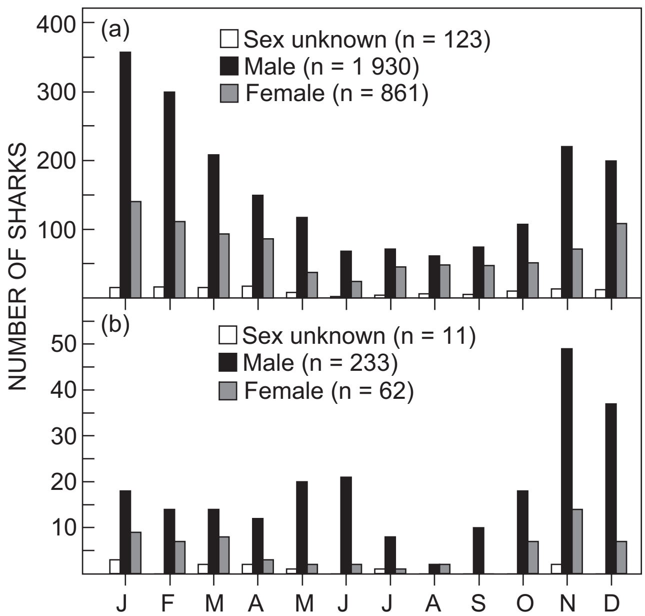

Figure 6: Seasonal distribution of (a) ≤160cm and (b) >160cm *S. lewini* caught in the KZN shark nets, 1978–1998

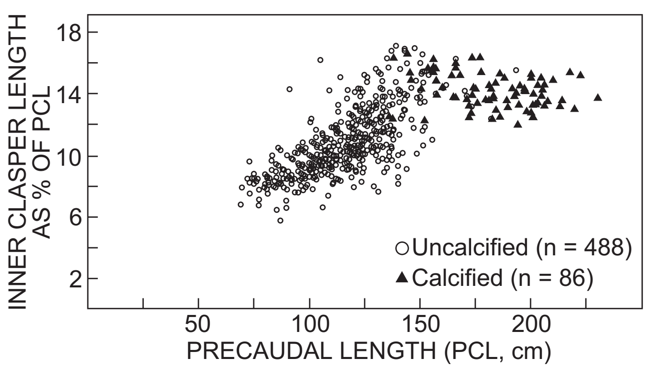

Figure 7: Relationship between inner clasper length and precaudal length in male *S. lewini*

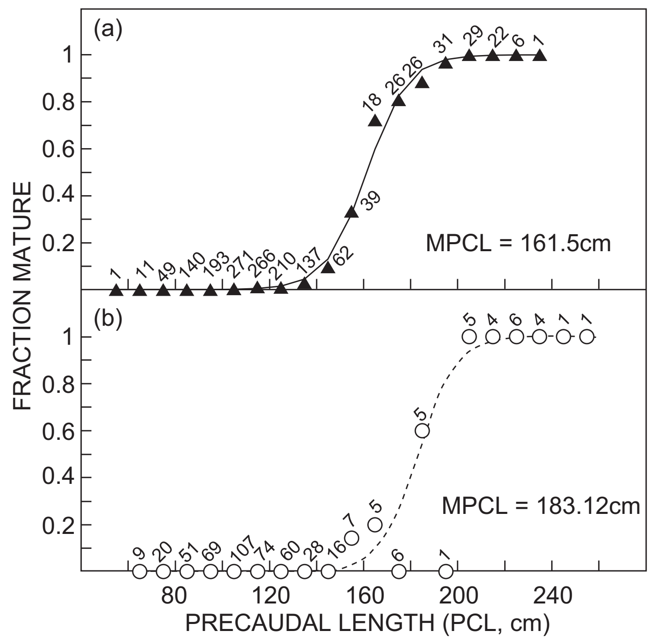

Figure 8: Relationship between maturity and length of (a) male and (b) female *S. lewini*. Mean fraction mature per 10-cm PCL interval was plotted for simplicity, with sample sizes shown. Estimated sizes-at-50% maturity (MPCL) are included. (Logistic model parameters — male: a = 18.574 (SE = 1.303), b = 0.115 (SE = 0.009), n = 1 539; female: a = 22.890 (SE = 5.233), b = 0.125 (SE = 0.029), n = 479)

September through to December and this was interpreted as an indication of mating (Stevens and Lyle 1989). Small sample size renders the present analysis inconclusive, a problem also encountered by Hazin *et al.* (2001).

Mean hepatosomatic index values (HSI: liver mass / shark mass x 100) were low for *S. lewini* caught in February (3.02%), then increased to a maximum of 10.53% in June (autumn/winter) before decreasing again slowly towards the beginning of summer (Figure 10b). The peak in HSI appears to occur about three months prior to the peak in GI. Rossouw (1987) linked fluctuations in HSI with reproductive cycles in female lesser sand sharks *Rhinobatos annulatus*, stating that liver reserves are depleted during reproductive activity. The author did not investigate the contribution of liver lipids to reproduction in males, but Dudley and Cliff (1993) suggest a possible link in male blacktip sharks *Carcharhinus limbatus*, with the peak in GI lagging that in HSI by two months.

In an effort to distinguish between reproductive and non-reproductive effects, mean monthly HSI values were calculated for immature females and males combined. Non-reproductive seasonal effects are apparent in that HSI again peaks in winter, reaching a maximum of 6.21% in July, but the peak is much narrower than in adult males (data not shown). This suggests that non-reproductive effects do not fully explain seasonality in mature animals.

Females

Few mature female specimens (n = 22) were captured in the nets. Similarly, few mature female *S. lewini* have been sampled in most studies elsewhere (Clark and Von Schmidt 1965, Branstetter 1981, 1987, Stevens and Lyle 1989, Capapé *et al.* 1998), an exception being the study by Chen *et al.* (1988). The largest immature specimen in the present study measured 192cm and the smallest mature specimen 155.2cm. The estimated length at maturity was 183.12cm (Figure 8b). Female *S. lewini* in the Gulf of Mexico matured at about 187cm (Branstetter 1987), in the south-west equatorial Atlantic at 180cm (Hazin *et al.* 2001), in the Gulf of California at 162cm (Klimley 1987) and in the central Indo-Pacific at 149–157cm (Chen *et al.* 1988, Stevens and Lyle 1989). In the current study, uterus width increased slightly with increasing length in immature animals. There was very little overlap in uterus width between immature (≤30mm) and mature specimens (28–140mm).

Most mature females were caught between October and March. Mean maximum ovarian follicle diameter (MOD) and

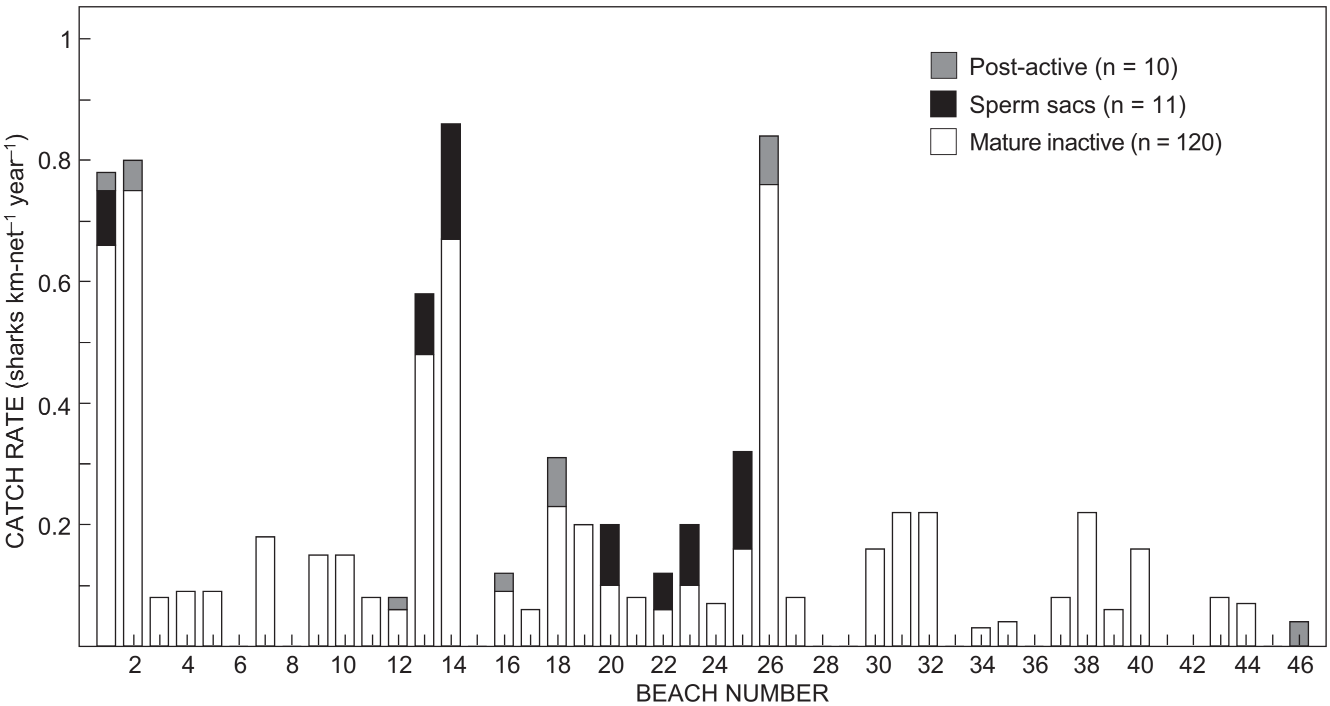

Figure 9: Geographic distribution of mature male *S. lewini* caught in the KZN shark nets, 1978–1998

GI values were calculated for mature females (including pregnant individuals), but the sample sizes were small (n = 14 and 19 respectively). Mean monthly MOD values exhibited maxima in November (31mm, n = 6) and December (41mm, n = 2), and GI in November (0.37%, n = 7), December (0.45%, n = 2) and April (0.38%, n = 2). Chen *et al.* (1988) regarded ovarian follicles >30mm as being near ovulation.

All pregnant females had term or near-term embryos and were captured between October and March. They tended to have MOD values ≥30mm (Table 1), indicating that fertilisation would occur shortly after parturition. Castro (1993) and Chen *et al.* (1988) suggest that females reproduce annually. Long-term storage of spermatozoa has been described in *S. lewini*, potentially enabling fertilisation to occur in post-partum females without fresh insemination (Pratt 1993).

Embryos and nursery grounds

Median litter size was 10 embryos (range 2–19, n = 11 litters, Table 1). This is at the lower end of the range 2–38 reported in the literature (see summary by Hazin *et al.* 2001). In the South-West Indian Ocean, Bass *et al.* (1975) recorded a single litter of 30 embryos. Observation of aborted embryos during capture in the KZN shark nets may partly explain the small litter sizes recorded in the present study.

The relationship between embryo mass (M) and PCL was $M = 0.00543PCL^{3.92}$ ($p < 0.05$, n = 85). The overall ratio of male to female embryos was unity (χ^2 test, $p > 0.05$, n = 101), as was the distribution of sexes, and of numbers of embryos, between left and right uteri ($p > 0.05$, n = 101 in both cases).

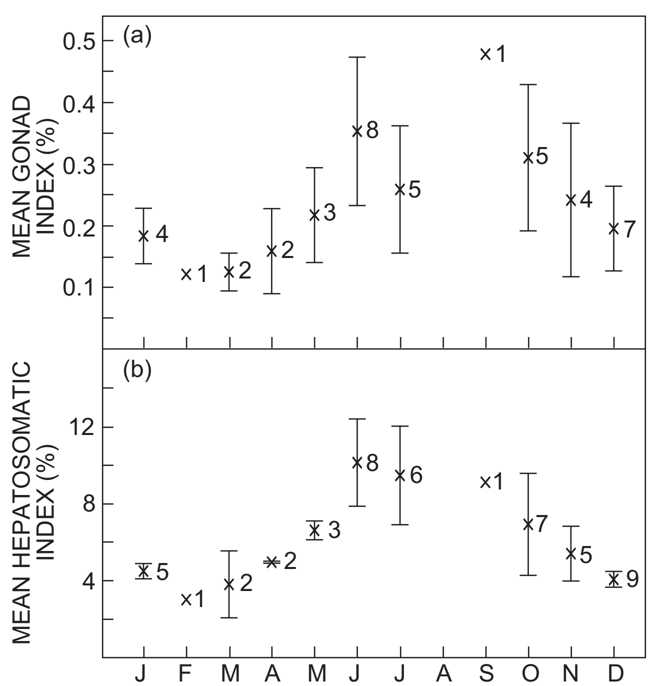

Figure 10: Mean monthly of (a) gonad indices and (b) hepatosomatic indices of mature male *S. lewini*. Error bars represent 95% confidence limits on the means; data labels represent sample size

All litters were sampled between October and March (spring–summer), but there was no increase in size of embryo during that period, suggesting a prolonged pupping

Table 1: Summary of litter data for pregnant female *S. lewini* caught in the KZN shark nets, 1978–1998

Month of capture	Maternal PCL (cm)	Litter size	Embryo size range (cm)	Median embryo size (cm)	Sex ratio F:M	Maternal MOD (mm)
October	210	12	31.0–35.6	33.5	1:2	26
October	243	16	32.4–36.0	34.9	5:11	34
November	203	19	30.0–34.0	32.8	8:11	32
November	227	9	26.6–32.1	30.4	2:1	32
November	238	8	34.8–37.5	36.2	3:1	30
November	201	10	31.0–34.4	33.7	3:2	32
November	233	10	–	–	–	33
December	227	14	28.0–32.0	31.0	1:1	–
January	187	2	–	–	–	–
February	184	3	34.0–38.5	35.6	1:2	30
March	216	8	24.7–36.2	33.1	1:7	8

season (Table 1). Clarke (1971) reported that parturition occurs throughout the year off Hawaii, but with a summer increase, and a number of other authors report summer parturition (e.g. Bass *et al.* 1975, Chen *et al.* 1988, Stevens and Lyle 1989, Capapé *et al.* 1998, Hazin *et al.* 2001). The absence in the present study of newly pregnant females or females with mid-term embryos precludes the determination of gestation period. For *S. lewini* off north-eastern Taiwan (Chen *et al.* 1988) and in the south-west equatorial Atlantic (Hazin *et al.* 2001), the period is estimated to last about 10 months. The largest embryo measured 38.5cm, which is larger than the previously estimated size at birth of 33–36cm for the region (Bass *et al.* 1975). Fennessy (1994), however, measured free-swimming *S. lewini* of 29cm captured by prawn trawlers fishing on the Tugela Bank. The smallest free-swimming male and female specimens caught in the shark nets was 50cm.

Size at birth of *S. lewini* in the North-West Atlantic was reported as being 28–33cm (Castro 1983), in the central Indo-Pacific as 33–36cm (Chen *et al.* 1988, Stevens and Lyle 1989) and in the south-west equatorial Atlantic as >28cm (Hazin *et al.* 2001). In the north-east tropical Atlantic, Capapé *et al.* (1998) recorded embryos of up to 38cm and free-swimming individuals as small as 32cm.

Some 64% of the pregnant females were caught at Richards Bay, the northernmost installation (Figure 11), and also the site where the largest number of mature males were captured. This concentration of mature and pregnant specimens may indicate the proximity of a breeding ground and a nursery area. Studies carried out by Fennessy (1994) on the Tugela Bank, about 50km south-west of Richards Bay, revealed large numbers of *S. lewini* ranging from 28cm to 111cm, with a mean size of 43cm. That site, which has waters shallower than 50m, a muddy sea floor and permanently turbid water, may constitute a local nursery area. Other nursery grounds for this species tend to be in sheltered waters (Clarke 1971, Castro 1993, Simpfendorfer and Milward 1993), whereas the Tugela Bank is exposed.

Feeding

Of the 1 373 stomachs examined, four were everted and 537 (39.2% of non-everted stomachs) were empty. The mean food mass in 832 non-empty stomachs was 142g (SE = 10), which represented 0.53% of the mean predator mass. An average of 2.5 prey items (SE = 0.1) was found per stomach. A total of 63 families and 80 species were identified. A summary of the stomach contents is provided in Table 2.

The cumulative prey curve derived from the 832 stomachs with food did not reach an asymptote (Figure 12), indicating that the sample size was insufficient to adequately describe the diet. A possible explanation for this is the small number (40) of stomachs from large sharks (≥170cm).

Elasmobranchs

Elasmobranchs occurred in 11.8% of stomachs containing food and constituted 17.5% by mass and 5.4% by number. Representatives from eight families (five shark and three batoid) and seven species (four shark) were identified (Table 2). Sharks were slightly more common than batoids. The dominant family was Scyliorhinidae (5.2%F).

Teleosts

S. lewini fed mainly on teleosts, which were found in 76.7% of stomachs containing food and constituted 62.5% by mass and 55.6% by number. Representatives from 42 families and 60 species were identified (Table 2). No species dominated, with the most common being *Trichiurus lepturus* (7.8%F), *Pomadasys olivaceum* (5.8%F), *Pagellus natalensis* (4.0%F), *Diplodus sargus* (3.5%F) and *Sarpa salpa* (3.0%F).

Cephalopods

Cephalopods were the second most common prey group, occurring in 24.8% of stomachs with food and constituting 19.9% by mass and 37.4% by number. The most common groups were the families Octopodidae (8.3%F) and Sepiidae (7.8%F) and the suborder Teuthoidea (6.8%F). Smale and Cliff (1998) provided a detailed analysis of the cephalopod prey of *S. lewini*. Unlike the present study they used all the beaks found, not only those with accompanying soft tissue. They calculated reconstituted prey mass from beak measurements and found oceanic squid of the families Octopoteuthidae (22.8%M) and Ancistrocheiridae (50.3%M) to be more important than the neritic families of Octopodidae (7.7%M) and Sepiidae (11.2%M). Because the shark nets are situated within 1km of the shore, the soft

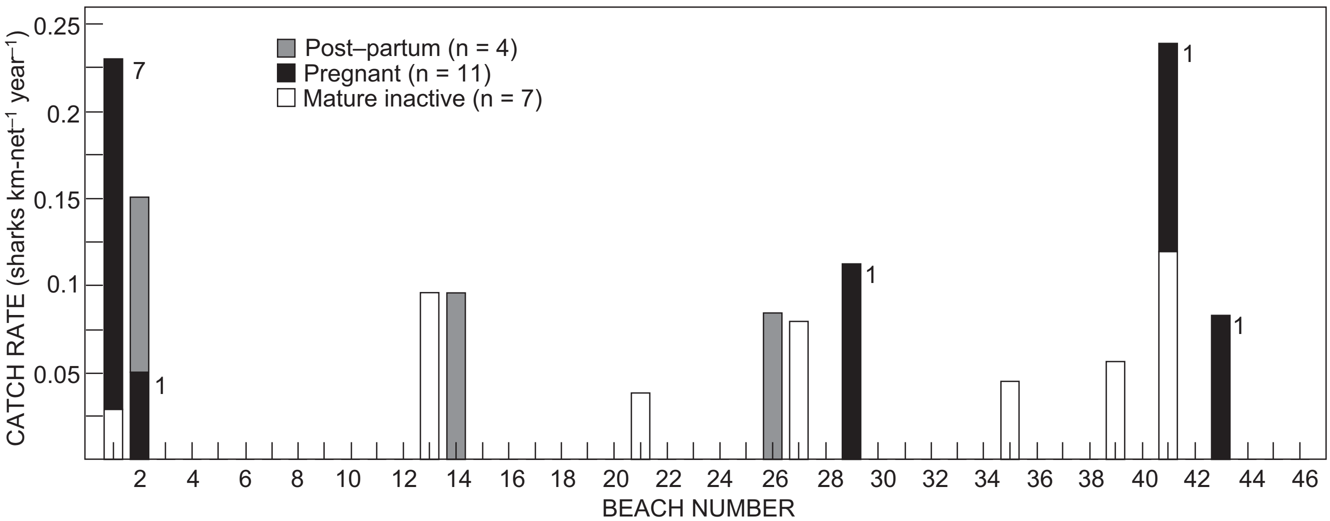

Figure 11: Geographic distribution of mature female *S. lewini* caught in the KZN shark nets, 1978–1998. Data labels represent numbers of pregnant females

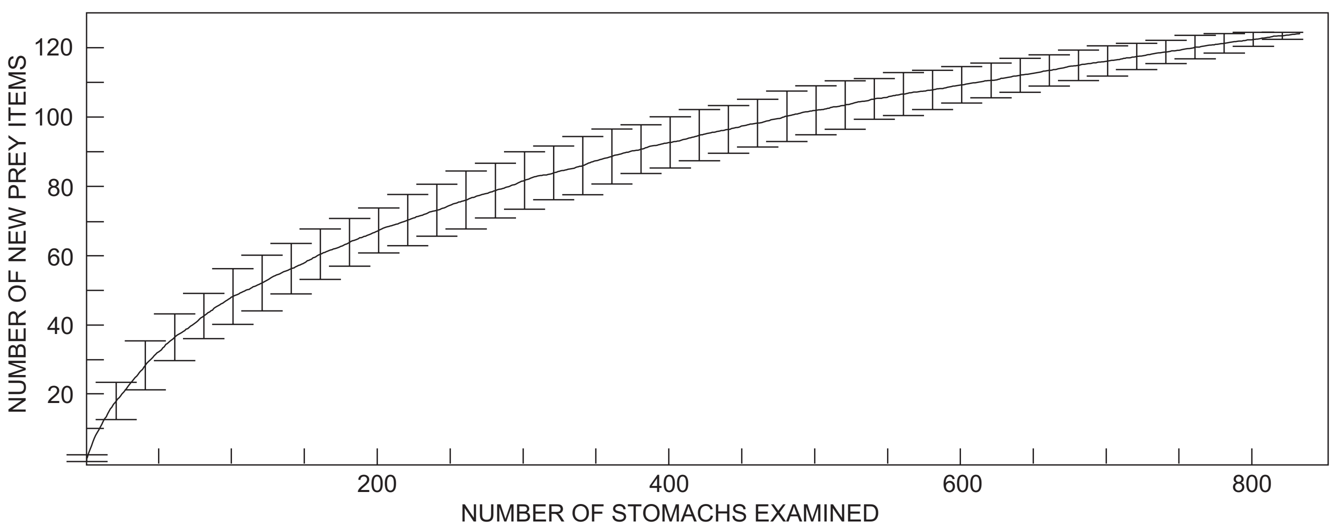

Figure 12: Randomised cumulative prey curve derived from the contents of 832 *S. lewini* stomachs with food. Mean values are plotted and error bars represent 95% confidence limits on the means

tissues of oceanic cephalopods are far more likely than those of neritic species to have been completely digested, leaving only the digestion-resistant beaks.

Other prey

The incidence of other prey categories was low, comprising crustaceans (2.6%F), birds (0.2%F) and gastropods (0.1%F). Fishermen's bait was also found (0.1%F). Inedible items not shown in Table 2 included seaweed (six stomachs), riverine and terrestrial vegetation (three stomachs), stones (two stomachs) and plastic (one stomach).

Vertical distribution of prey

Most of the common prey species were either benthic or demersal, with the exception of *T. lepturus* which is regarded as benthopelagic (Smith and Heemstra 1991). The incidence of pelagic shoaling fish of the family Clupeidae and the genera *Decapturus* and *Trachurus* was extremely low. It would appear that *S. lewini* in coastal KZN waters feed mainly on or near the seabed.

Size of prey

There was no relationship between predator and prey lengths for prey items that could be measured. Of the measured prey, 40% were 10–20cm long, with the largest prey item being a geelbek *Atractoscion aequidens* of 95cm fork length. This was one of eight prey items longer than 70cm, all found in sharks of ≥109cm. Three of the eight were cutlass fish *Trichiurus lepturus*, an extremely slender fish. *S. lewini* generally ingest small prey items because prey size is restricted by the narrow mouth and the small non-serrated teeth.

Table 2: Stomach contents of *S. lewini* caught in the KZN shark nets, 1983–1998, expressed as percentage frequency of occurrence (%F), percentage by mass (%M) and percentage by number (%N). Totals represent number of stomachs (F), mass of prey items (M, kg) and number of prey items (N) respectively

Prey category	%F	%M	%N
ELASMOBRANCHS	11.8	17.5	5.4
Squalidae (dogfish)	0.1	0.1	0.0
Carcharhinidae (requiem sharks)			
Rhizoprionodon acutus (milk shark)	0.1	0.0	0.0
Scyliorhinidae (catsharks)			
Halaelurus lineatus (banded catshark)	0.6	1.1	0.3
Haploblepharus edwardsii (puffadder shyshark)	0.1	0.2	0.0
Unidentified catshark	4.5	4.2	2.2
Pseudocharchariidae (crocodile sharks)	0.1	0.0	0.0
Squatinidae (angelsharks)			
Squatina africana (African angelshark)	0.1	1.6	0.0
Rajidae (skates)	0.3	0.3	0.1
Rhinobatidae (guitarfish)			
Rhinobatos annulatus (lesser guitarfish)	0.2	0.6	0.1
Rhinobatos leucospilus (greyspot guitarfish)	0.1	1.6	0.0
Unidentified guitarfish	1.2	3.0	0.5
Dasyatidae (stingrays)			
Gymnura natalensis (backwater butterflyray)	0.3	1.3	0.1
Unidentified stingray	0.1	0.5	0.0
Unidentified elasmobranch	0.7	0.1	0.3
Unidentified batoid	0.5	0.2	0.2
Unidentified ray	0.1	0.1	0.0
Unidentified small shark (<1m PCL)	2.4	2.6	1.1
TELEOSTS	76.7	62.5	55.6
Anguilliformes (eels)			
Unidentified eel	1.4	1.2	0.7
Congridae (conger eels)			
Conger wilsoni (Cape conger eel)	0.1	0.0	0.0
Muraenesocidae (pike congers)			
Muraenesox bagio (pike conger)	0.1	0.2	0.0
Clupeidae (herrings)			
Etrumeus teres (East Coast roundherring)	0.1	0.0	0.0
Sardinops sagax (South African sardine)	0.7	0.7	0.8
Etrumeus whiteheadi (redeye roundherring)	0.2	0.0	0.1
Hilsa kelee (kelee shad)	0.1	0.1	0.0
Engraulidae (anchovy)			
Thryssa vitrirostris (orangemouth glassnose)	0.1	0.0	0.1
Ariidae (seacatfish)			
Galeichthys feliceps (white seacatfish)	1.1	0.5	0.5
Unidentified seacatfish	1.1	1.5	0.5
Plotosidae (eel-catfish)			
Plotosus nkunga (eel-catfish)	0.1	0.0	0.1
Unidentified eel-catfish	0.8	2.6	0.3
Synodontidae (lizardfish)			
Saurida undosquamis (largescale lizardfish)	0.3	0.4	0.1
Unidentified lizardfish	1.4	1.3	0.6
Merlucciidae (hakes)			
Merluccius capensis (shallow-water hake)	0.2	0.0	0.1
Belonidae (needlefish)			
Ablennes hians (barred needlefish)	0.1	0.0	0.0
Exocetidae (flyingfish)	0.4	0.2	0.2
Syngnathidae (pipefish & seahorses)	0.2	0.0	0.1
Platycephalidae (flatheads)			
Cociella crocodile (crocodile flathead)	0.7	0.3	0.4
Unidentified flathead	0.2	0.9	0.1
Triglidae (gurnard)			
Chelidonichthys kumu (blue fin gurnard)	0.1	0.0	0.0
Peristediidae (armoured gurnard)	0.1	0.1	0.0
Dactylopteridae (helmet gurnard)	0.1	0.1	0.0
Serranidae (rockcod)			
Epinephelus andersoni (catface rockcod)	0.1	0.1	0.0
Serranus cabrilla (comber)	0.2	0.1	0.1
Unidentified rockcod	0.4	0.2	0.1
Teraponidae (thornfish)	0.1	0.3	0.1
Priacanthidae (bigeyes)	0.1	0.2	0.0
Pomatomidae (elf)			
Pomatomus saltatrix (elf)	2.9	2.3	1.3
Haemulidae (rubberlips & grunters)			
Diagramma pictum (sailfin rubberlip)	0.2	0.2	0.1
Pomadasys commersonnii (spotted grunter)	1.0	3.8	0.5
Pomadasys maculatum (saddle grunter)	0.4	0.2	0.3
Pomadasys olivaceum (piggy)	5.8	1.5	3.9
Pomadasys striatum (striped grunter)	0.1	0.0	0.0
Sparidae (sea bream)			
Chrysoblephus puniceus (slinger)	0.2	0.4	0.1
Diplodus cervinus (zebra)	0.4	0.6	0.1
Diplodus sargus (blacktail)	3.5	1.8	1.7
Pachymetopon aeneum (blue hottentot)	0.1	0.0	0.0
Pachymetopon grande (bronze bream)	0.2	0.8	0.1
Pagellus natalensis (red tjor-tjor)	4.0	1.3	2.4
Polysteganus coeruleopunctatus (blueskin)	0.1	0.2	0.0
Rhabdosargus spp. (stumpnose)	0.6	0.2	0.2
Rhabdosargus holubi (Cape stumpnose)	0.1	0.0	0.0
Rhabdosargus sarba (Natal stumpnose)	0.1	0.1	0.0
Rhabdosargus thorpei (bigeye stumpnose)	0.4	0.2	0.1
Sarpa salpa (strepie)	3.0	1.4	1.5
Unidentified sea bream	0.2	0.1	0.1
Scorpididae (stonebream)			
Neoscorpis lithophilus (stonebream)	0.5	1.3	0.2
Mullidae (goatfish)			
Parupeneus cyclostomus (gold-saddled goatfish)	0.1	0.1	0.0
Unidentified goatfish	0.2	0.3	0.3
Sciaenidae (kob)			
Argyrosomus japonicus (dusky kob)	0.2	0.7	0.1
Argyrosomus thorpei (squaretail kob)	0.5	0.0	0.2
Atractoscion aequidens (geelbek)	0.1	1.1	0.0
Atrobucca nibe (longfin kob)	0.2	0.0	0.1
Johnius amblycephalus (bellfish)	0.2	0.2	0.1
Johnius dussumieri (small kob)	2.8	1.0	1.7
Otolithes ruber (snapper kob)	1.6	1.2	0.7
Umbrina ronchus (slender baardman)	0.4	0.1	0.1
Unidentified kob	0.6	0.3	0.4
Leiognathidae (soapies)			
Secutor insidiator (slender soapy)	0.5	0.1	0.9
Unidentified soapy	0.6	0.2	0.2
Oplegnathidae (knifejaws)			
Oplegnathus conwayi (Cape knifejaw)	0.5	0.1	0.2
Unidentified knifejaw	0.1	0.5	0.0
Carangidae (kingfish)			
Decapturus spp. (scads)	0.1	0.0	0.0
Parastromateus niger (black promfret)	0.1	1.0	0.0
Trachurus delagoa (African horse mackerel)	1.4	0.3	0.6
Trachurus trachurus (horse mackerel)	0.1	0.0	0.1
Unidentified kingfish	0.1	0.1	0.0
Cheilodactyleidae (fingerfins)	0.2	0.6	0.1
Pomacentridae (damselfish)	0.1	0.0	0.0
Mugilidae (mullets)			
Liza tricuspidens (striped mullet)	0.2	0.1	0.1
Unidentified mullet	0.1	0.1	0.1
Sphyraenidae (barracuda)			
Sphyraena qenie (sharpfin barracuda)	0.6	0.2	0.3
Sphyraena jello (pickhandle barracuda)	0.1	0.0	0.0

Table 2: (cont.)

Prey category	%F	%M	%N	Prey category	%F	%M	%N
Unidentified barracuda	0.6	0.1	0.2	CEPHALOPODS	24.8	19.9	37.4
Mugiloididae (sandsmelts)				Octopodidae (octopi)			
Parapercis robinsoni (smallscale sandsmelt)	0.1	0.1	0.0	*Octopus* spp. (octopus)	8.3	4.3	12.7
Acanthuridae (surgeonfish)	0.1	0.0	0.0	Teuthoidea (squid)			
Trichiuridae (frostfish)				Loliginidae (loligo squid)	1.4	0.4	2.0
Trichiurus lepturus (cutlass fish)	7.8	3.9	5.4	Lycoteuthidae (lycoteuthid squid)	0.1	0.0	0.0
Unidentified frostfish	5.7	4.9	3.5	Enoploteuthidae (enope squid)	0.8	1.8	2.1
Scombridae (tuna)				Octopoteuthidae (octopus squid)	1.1	2.2	2.0
Scomber japonicus (mackerel)	2.2	2.4	1.2	Unidentified squid	5.2	7.6	13.9
Scomberomorus commerson (king mackerel)	0.1	2.4	0.0	Sepiidae (cuttlefish)	7.8	3.4	4.5
Unidentified tuna	0.2	0.4	0.1	Unidentified cephalopod	0.2	0.1	0.1
Pleuronectiformes (flatfish)	1.4	0.2	0.9	CRUSTACEANS	3.5	0.4	1.5
Bothidae (lefteye flounders)	0.6	0.0	0.6	Brachyura (crabs)	1.0	0.1	0.4
Pleuronectidae (righteye flounders)	0.1	0.2	0.1	Macrura (crayfish)	0.5	0.1	0.1
Cynoglossidae (tongue fish)	0.4	0.0	0.1	Caridea (prawns)	1.3	0.1	0.5
Ostraciidae (boxfish)	0.4	0.1	0.1	Unidentified crustacean	0.7	0.1	0.4
Unidentified teleost	26.7	10.9	17.4	GASTROPODS			
BIRDS				Unidentified gastropod	0.1	0.0	0.0
Unidentified bird	0.2	0.0	0.0	MISCELLANEOUS			
				Fishermen's bait	0.1	0.0	0.1
TOTAL					832	118.1	2 116

Table 3: Contingency table analysis of the variations in the four major prey groups found in small (<130cm) and large (≥130cm) *S. lewini*. Values shown are the observed number of stomachs containing the prey; expected values are in parentheses. The overall χ^2 statistic* is significant (p < 0.025)

Prey group	Small sharks	Large sharks	n_i	χ^2_i
Elasmobranch	66 (78)	33 (21)	99	8.63
Teleost	509 (503)	130 (136)	639	0.31
Cephalopod	170 (163)	37 (44)	207	1.41
Crustacean	22 (23)	7 (6)	29	0.14
n_j	767	207	974	
χ^2_j	2.23	8.27		10.50*

Size-related variation in diet

The sample of *S. lewini* was divided into two size categories, split at 130cm in order to increase the sample of large animals. The ranking by frequency of occurrence of the major prey groups was the same for both predator size groups, but contingency table analysis revealed significant differences in the incidence of the prey groups (χ^2 test, $p < 0.025$, Table 3). Of the prey groups, elasmobranchs provided most of the variability in that their occurrence was considerably higher than expected in the larger sharks and lower in the smaller sharks. An increase in elasmobranch prey with shark size has been reported in other shark species, for example the great hammerhead shark *Sphyrna mokarran* (Cliff 1995) and the bull shark *Carcharhinus leucas* (Cliff and Dudley 1991). The smaller sharks had a slightly more diverse diet (H' = 2.6; d' = 20.4) than the larger sharks (H' = 2.1; d' = 15.0), although there was a high level of overlap (S = 0.64).

Comparison with other feeding studies

Bass *et al.* (1975) found a slightly higher incidence of empty stomachs (47%) in 186 *S. lewini* from KZN and southern Moçambique. The incidence of teleosts in stomachs containing food was similar (80%F), but that of elasmobranchs was very low (1%F), possibly because only about 8% of the stomachs were from sharks of 130cm or larger, compared with 21% in the present study. Off northern Australia, only 21% of *S. lewini* sampled had empty stomachs and fish were found in 87% of stomachs with food, cephalopods in 31% and crustaceans in 5% (Stevens and Lyle 1989). Of those fish, only four of the listed prey were elasmobranchs. Neonates sampled in Hawaii fed only on teleosts (68%F) and crustaceans (53%F), whereas the adults fed mainly on pelagic squid (Clarke 1971). There were no incidents in the present study of *S. lewini* scavenging on animals already caught in the shark nets, whereas 11% of dusky sharks *Carcharhinus obscurus* stomachs contained remains scavenged in this manner (Dudley *et al.* 2005).

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