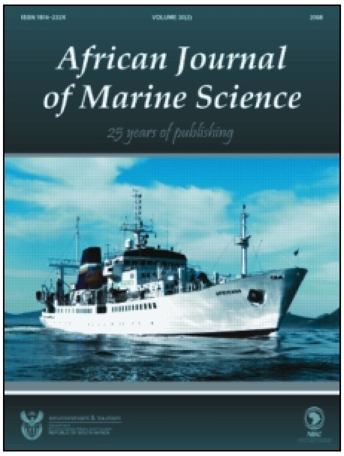

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Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 10. The dusky shark *Carcharhinus obscurus* (Lesueur 1818)

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Between 1978 and 1999, a total of 5 626 dusky sharks *Carcharhinus obscurus*, constituting 20% of the total shark catch, was caught in the protective nets off KwaZulu-Natal, South Africa. The mean annual catch was 256 sharks (SD = 107.5, range 129–571). There was no significant linear trend in catch rate with time. Of the total *C. obscurus* catch, 677 (12%) were found alive and 217 of these (3.8%) were tagged and released. Only three tagged animals were recaptured. The size frequency distribution of the catch was trimodal, the modes of each sex consisting of small (mostly neonate), medium (adolescent) and large (mostly mature) sharks respectively. Geographical and seasonal distributions were characteristic for each of these size categories. Females significantly outnumbered males in all size categories, the greatest disparity (2.72:1) being in large animals. This probably reflects the movement inshore of near-term pregnant females to drop their pups. On 128 occasions, groups of five or more sharks were found together in a net installation, the largest group consisting of 113 animals. Group catches tended to coincide with the annual 'sardine run', a seasonal influx of *Sardinops sagax*. The sardine run affects the distribution of medium and large sharks. Few animals were sampled in mating condition and there were few newly pregnant or mid-term females, but there are indications that the gestation period may be as much as two years. Teleosts dominated the diet in terms of frequency of occurrence (63%) and elasmobranchs in terms of mass (51.4%).

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

Introduction

The dusky shark *Carcharhinus obscurus* (LeSueur 1818) is a common coastal pelagic species with a patchy distribution in tropical and warm temperate seas. It is found on continental and insular shelves from the surf zone to adjacent oceanic waters and to a depth of 400m (Compagno 1984, Last and Stevens 1994). In an analysis of life history traits of 230 shark populations, comprising 164 species, Cortés (2000) characterised *C. obscurus* as being of large size and with slow growth, high longevity and few offspring, the large size of which reduces vulnerability to predation. O'Gower (1995) grouped *C. obscurus* with a number of carcharhinid and lamnid species characterised by being pelagic, having open-water nurseries, migrating long distances and probably segregating by sex and/or size. Smith *et al.* (1998) ranked *C. obscurus* second lowest in a list of 26 shark species ordered according to estimated productivity. Declining catch rates in the North-West Atlantic Ocean (NWA), coupled with the life history characteristics of the species, have led to concerns about its ability to sustain fishing mortality (Musick *et al.* 1993). Similarly, Govender and Birnie (1997) have expressed concerns about the high rate of instantaneous fishing mortality in a primarily recreational fishery for juveniles in the South-West Indian Ocean (SWI). By contrast, there is a managed demersal gillnet fishery targeting neonates and small juveniles off south-western Australia (Simpfendorfer 1999, 2000). Simpfendorfer (1999) suggests that the fishery is sustainable because only a small proportion of age-classes is targeted.

C. obscurus occurs in the western Indian Ocean from the Red Sea to the southern tip of South Africa, as well as off Madagascar (Bass *et al.* 1973, Garrick 1982, Compagno 1984). Off KwaZulu-Natal, South Africa, adults are common in water 200–400m deep, but they come inshore seasonally (Bass *et al.* 1973). Juveniles are common in the surf zone of KwaZulu-Natal (KZN) and seasonally in the Eastern and Southern Cape (Bass *et al.* 1973). *C. obscurus* is the species most frequently captured in the protective shark nets off KwaZulu-Natal, which are maintained by the Natal Sharks Board (NSB) to minimise risk of shark attack. This paper is the tenth 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 distribution of shark nets along the KwaZulu-Natal coast is shown in Figure 1. The nets, with a stretched mesh of 51cm, are set in water 10–14m deep, parallel to the shore

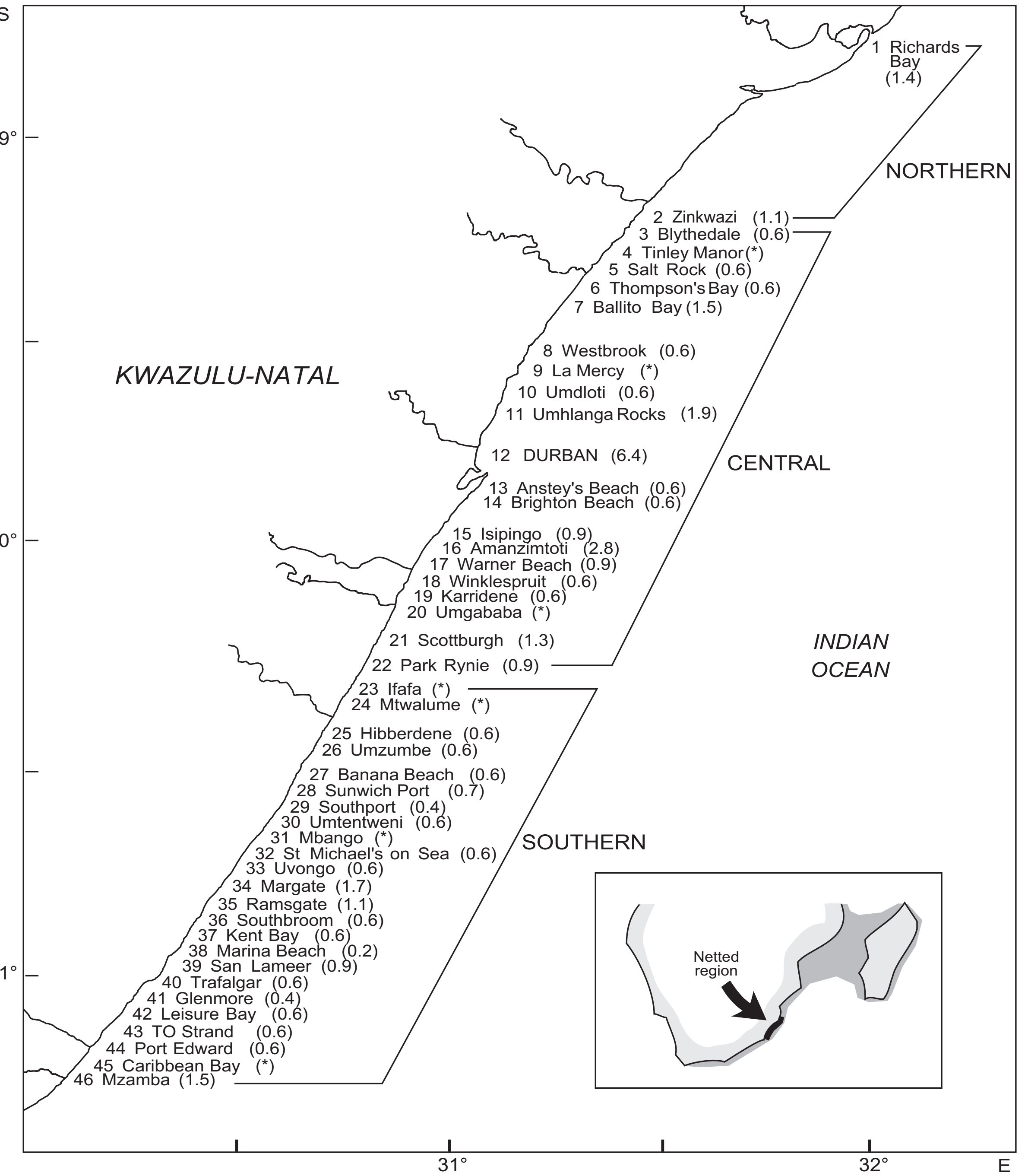

Figure 1: Netted beaches on the KwaZulu-Natal coast and, in parenthesis, the length of nets in kilometres in January 1999. Several net installations (*) were removed permanently during the study period 1978–1999. Northern, Central and Southern regions are defined for use in Figure 6. Inset shows the locality of the netted region and the distribution of *C. obscurus* in the southern African region (after Compagno 1984, Compagno *et al.* 1989)

and 300–500m offshore. Details of the netting operation are given by Cliff *et al.* (1988) and Dudley (1997). In January 1999, the total length of netting was 39km. Units of effort are standardised as kilometres of net per year (km-net year^{-1}).

Shark nets were installed at Durban in 1952 and installation at other localities began in the early 1960s. Catch and biological records, however, are regarded as having been reliable only since 1978. Prior to then, *C. obscurus* was frequently confused with other carcharhinids taken in the nets, particularly the sandbar shark *Carcharhinus plumbeus* (through the presence of an interdorsal ridge) and the copper shark *Carcharhinus brachyurus* (through colouration and body shape). Hence the period 1978–1999 is regarded formally as the study period, although catch and catch-rate data are presented here for the period 1966–1999.

All shark lengths used in this report, including those cited from the literature, are precaudal lengths (PCL), because this is considered to be a more precise measurement than total length (TL). Precaudal length and fork length (FL) were measured as straight lines, parallel to the body (i.e. connecting perpendiculars to the reference points), from the tip of the snout to the precaudal notch and the fork of the caudal fin respectively. Upper caudal length (UCL) was measured as a straight line from the precaudal notch to the tip of the upper caudal fin. Definitions of total length (TL) vary in the literature. TL is usually taken to be the distance, parallel to the body, from the snout tip to the tip of the upper caudal lobe with the caudal fin in the 'natural' position. The precision of this method depends, however, on the definition of natural position, i.e. on the angle at which the caudal fin is positioned relative to the long axis of the shark. Bass *et al.* (1973) proposed the formula

$$TL = PCL + 0.8UCL \qquad (1)$$

based on an angle of 37°, whereas Dodrill (1977) modified the angle to 32° to obtain

$$TL = PCL + 0.85UCL \qquad (2)$$

Some authors do not define TL, but probably visually estimate the angle at which to place the caudal fin and then take the direct measurement. A different method used by Compagno (1984) and Stevens (1984) involves depressing the upper caudal lobe from the natural position to lie parallel to the body axis. This method was also used by Dodrill (1977) for embryos, which have non-rigid caudal lobes. To facilitate comparison of the current findings with those reported in the literature, three equations are calculated for converting between TL and PCL:

For TL with the upper caudal fin in its (visually estimated) natural position,

$$TL = 1.312PCL + 4.552 \ (n = 554,\ p < 0.001,\ \text{range } 60.5\text{–}284.0\text{cm PCL}) \qquad (3)$$

For TL with the upper caudal fin depressed into line with the body axis,

$$TL = 1.326PCL + 6.551 \ (n = 543,\ p < 0.001,\ \text{range } 60.5\text{–}284.0\text{cm PCL}) \qquad (4)$$

If a linear relationship is assumed between PCL and UCL, the following equation facilitates conversion of PCL to TL by means of Equations 1 and 2:

$$UCL = 0.339PCL + 3.894 \ (n = 2\,591,\ p < 0.001,\ \text{range } 57.0\text{–}284.0\text{cm PCL}) \qquad (5)$$

In this report, total lengths cited in the literature have been converted to PCL by means of the method considered most appropriate to the authors concerned.

The equation relating fork length (FL) to PCL is

$$FL = 1.074PCL + 2.053 \ (n = 1\,098,\ p < 0.001,\ \text{range } 60.5\text{–}284.0\text{cm PCL}) \qquad (6)$$

Mouth width (MW), the straight line distance between the corners of the mouth, can be expressed as

$$MW = 0.130PCL - 2.111 \ (n = 640,\ p < 0.001,\ \text{range } 61.0\text{–}284.0\text{cm PCL}) \qquad (7)$$

and girth (GIR), measured at the third gill slit, as

$$GIR = 0.525PCL - 4.507 \ (n = 146,\ p < 0.001,\ \text{range } 72.2\text{–}284.0\text{cm PCL}) \qquad (8)$$

Measurements of reproductive structures are as defined by Cliff *et al.* (1988) and criteria for visual assessment of maturity follow Bass *et al.* (1973). Size-at-50% maturity was determined using a logistic function in combination with maximum-likelihood estimation.

Stomach contents were sorted to the lowest possible taxon and expressed as frequency of occurrence (%F). Stomachs containing only otoliths, cephalopod beaks or elasmobranch egg cases were regarded as empty. From 1983, the items in each group were counted and a wet mass obtained, making it possible to express stomach contents in terms of percentage by mass (%M) and by number (%N) — Hyslop (1980). Otoliths and cephalopod beaks were kept and identified against reference material in the collection of the Port Elizabeth Museum. In analysing the diet, pregnant females were separated from the other adults and contingency table analysis was used, after Cortés (1997), to test for differences in diet across predator size-related categories.

Each time the nets were checked, sea surface temperature was measured and vertical water clarity was estimated at each net installation. Although the clarity estimate does not approximate a Secchi-disk measurement, thereby limiting its value in comparative studies, it serves as an index useful in relating shark capture to prevailing turbidity.

Net Catches

Annual variation

Catch and catch-rate data are shown for the period 1966–1999 (Figure 2a), but prior to 1978 misidentification undoubtedly occurred. Between 1978 and 1999, a total of 5 626 *C. obscurus* was caught (annual mean 256, SD = 107.5, range 129–571), constituting 20.0% of the total shark catch for that period. Mean catch rate was 6.31 sharks km-net^{-1} year^{-1}, and there was no significant linear trend in catch or catch rate with time (n = 22 years, p = 0.381 and 0.198 respectively, Figure 2a). The occurrence of adult and sub-adult sharks in the netted region in winter is influenced by the influx of sardine *Sardinops sagax*, a phenomenon known locally as the 'sardine run' (Armstrong *et al.* 1991). The NSB attempts to remove the nets in advance of the arrival of the sardine shoals in order to minimise catches of accompanying marine predators. Varying success in these efforts, particularly prior to the 1990s, has contributed to high annual variation in catch and, in order to limit this source of variability, catch and catch rate were replotted after excluding catches taken during the months of June and July (Figure 2b). Again there was no significant trend

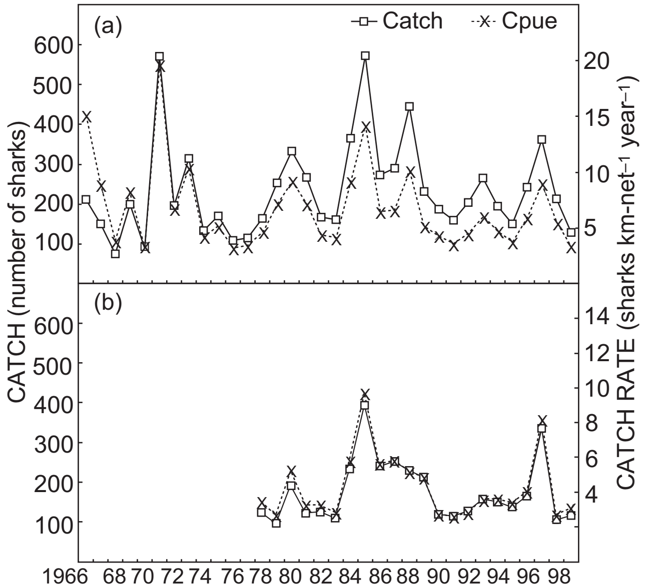

Figure 2: Catch and catch rate of *C. obscurus* in the KwaZulu-Natal shark nets; (a) 1966–1999 (species identification poor pre-1978) and (b) 1978–1999 (excluding data from June and July, the months of the sardine run)

in catch or catch rate (n = 22 years, p = 0.993 and 0.780 respectively).

The catch of each sex was sub-divided into three major size categories, which consisted primarily of small, medium and large sharks, as well as a fourth intermediate category that was caught in low numbers (see below). Annual catch rates of each were regressed against time. There were no significant trends in catch rate of any of the three major categories of either sex.

The above results indicate that current levels of exploitation of *C. obscurus* by the shark nets are sustainable. The concerns expressed by Govender and Birnie (1997), however, pertaining to a recreational fishery that is exploiting the juvenile component of the same stock as the nets, provide a warning that catches should continue to be monitored closely. In the NWA, where the stock was exploited by both recreational and commercial fisheries, Musick *et al.* (1993) found declines in catch per unit effort (cpue) of all three maturity categories — juvenile, adolescent and adult.

Length distribution

The length frequency distribution was trimodal (Figure 3), the modes of each sex consisting of small, medium and large sharks. These size categories approximated reproductive stage in that they consisted primarily of juvenile (reproductive organs undeveloped), adolescent (reproductive organs developing) and adult (sexually mature) sharks respectively. A fourth, intermediate, size category of animals that was seldom captured fell between the small and medium categories. The length-mass relationships for the two sexes did not differ (Student's t-test, p > 0.05) and therefore sexes were combined (Figure 4). Free-swimming males ranged from 61cm (4.90kg) to 258cm (252kg), and females from 57cm (1.90kg) to 284cm (450kg). In a previous study in the SWI, free-swimming females ranged from 54cm to 278cm and males from 52cm to 252cm (Bass *et al*. 1973). Maximum sizes in the NWA appear to be 273cm (female, read from Springer 1960, Figure 3) and 237cm (male, Clark and von Schmidt 1965). Off New South Wales, Australia, a female of 256cm and a male of 243cm were recorded (Stevens 1984). Therefore, the 284cm specimen (377cm TL using Equation 3) from the present study may be the largest on record.

Geographical and seasonal distribution by size and sex

Segregation by size and/or sex has been recorded frequently in this species (Springer 1940, Clark and von Schmidt 1965, Bass *et al.* 1973, Dodrill 1977, Gubanov 1988, Smale 1991, Bonfil 1997, Simpfendorfer and Donohue 1998). In the present study, the catch was divided by sex and size category and the geographical and seasonal distribution of each category was examined.

Small *C. obscurus* (<100cm PCL) of both sexes were caught throughout the year, but most commonly between November and February (Figure 5). A December peak concurs with the findings of Bass *et al*. (1973) and van der Elst (1979). Catch rates were highest in the central region between Blythedale and Park Rynie (Figures 1, 6). The intermediate size-class (100–139cm), caught in relatively low numbers (Figure 3), tended to occur between November and April and was found primarily in the northern (Richards Bay–Zinkwazi) and southern (Ifafa–Mzamba) regions (not shown). Medium animals (140–209cm) of both sexes peaked in winter (June–July) in the southern region and in summer (November–January) in the north (Figures 5, 6). Captures of large (≥210) females peaked in the northern region between March and August and in the southern region between May and July (Figure 6a). Large males exhibited a narrow peak in June and July in the southern region (Figure 6b). Medium and large sharks were caught relatively infrequently in the central region.

There is therefore a degree of spatial and temporal separation of small from medium and large sharks. The presence of large females from late summer onwards, and primarily in the northern region, is probably related to parturition (see below), the neonates subsequently recruiting to the shark nets primarily in the central region several months later. The winter peak in the south of medium and large sharks of both sexes is related to the seasonal abundance of food in the form of the sardine run (see below). However, the summer peak of medium sharks in the north is unexplained.

Females significantly outnumbered males in all size categories (χ^2 test, p < 0.0001): <100cm PCL 1:1.43 M:F; 100–139cm 1:1.73; 140–209cm 1:1.40; and ≥210cm 1:2.72. The greatest disparity was in the large animals, probably reflecting the movement inshore of near-term pregnant females to drop their pups. Bass *et al*. (1973) found that adult females outnumbered males by about 8:1 on the outer shelf as well as inshore. Also, they recorded sex ratios in small sharks ≤92cm of 1:1.7 M:F on the KZN coast, although Smale (1991) reported no significant difference in a sample

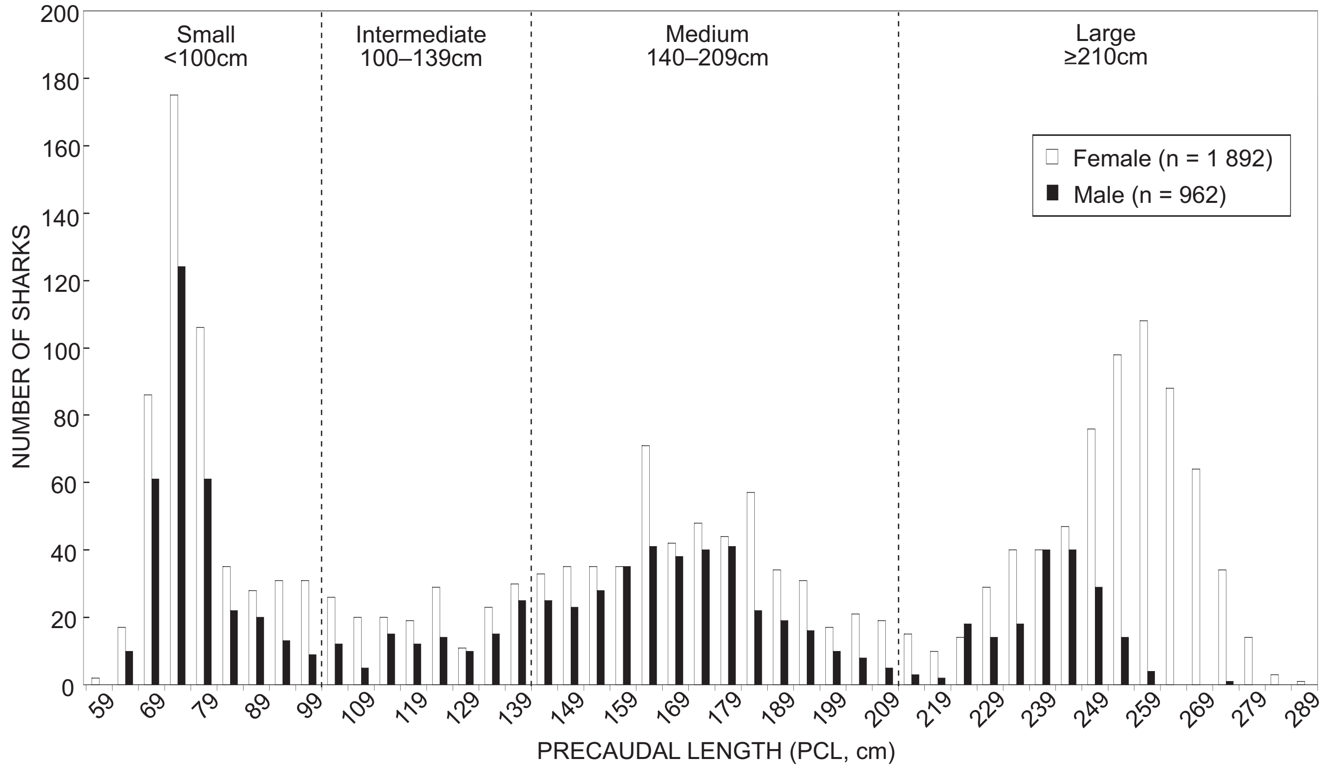

Figure 3: Length frequency distribution of *C. obscurus* caught in the KwaZulu-Natal shark nets, 1978–1999, depicting the size categories used in the text

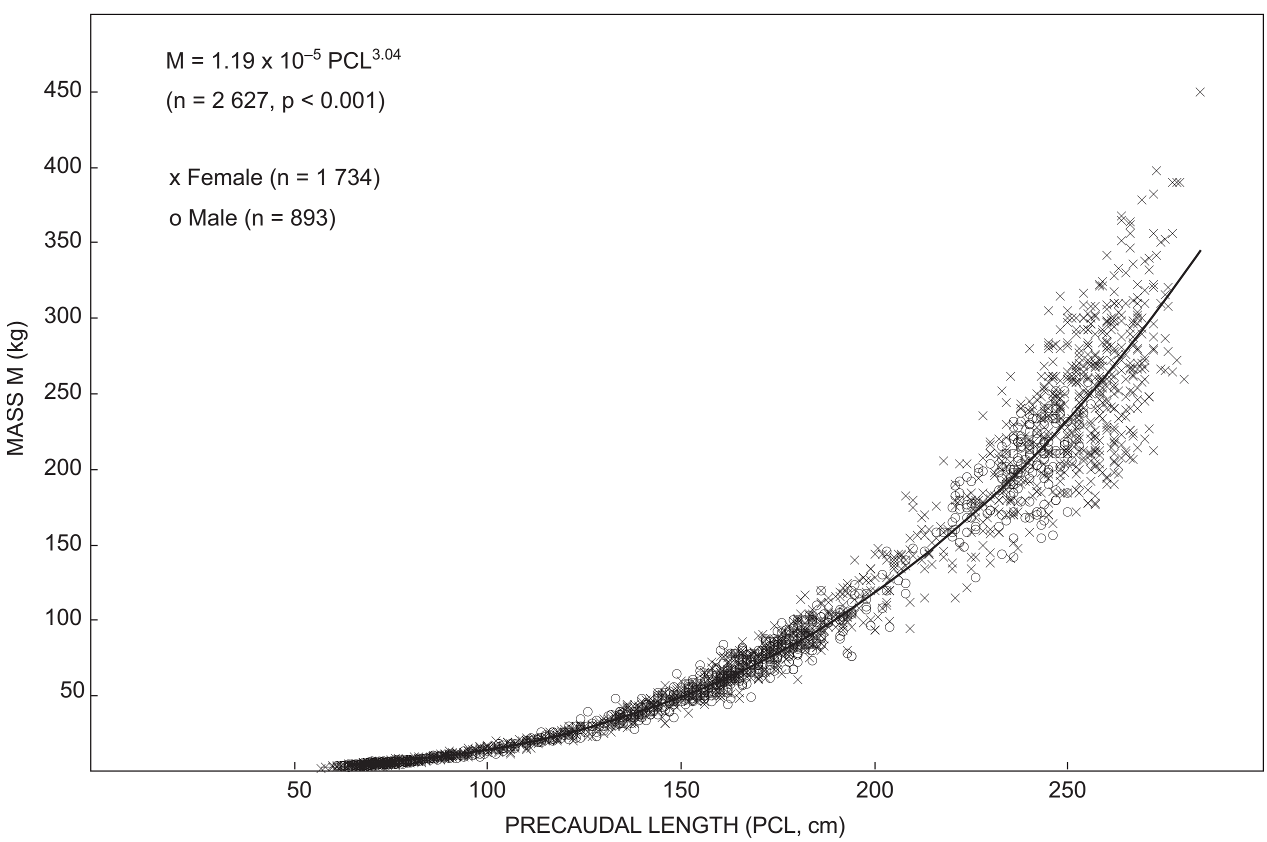

Figure 4: Length-mass relationship of *C. obscurus*, sexes combined (excluding embryos)

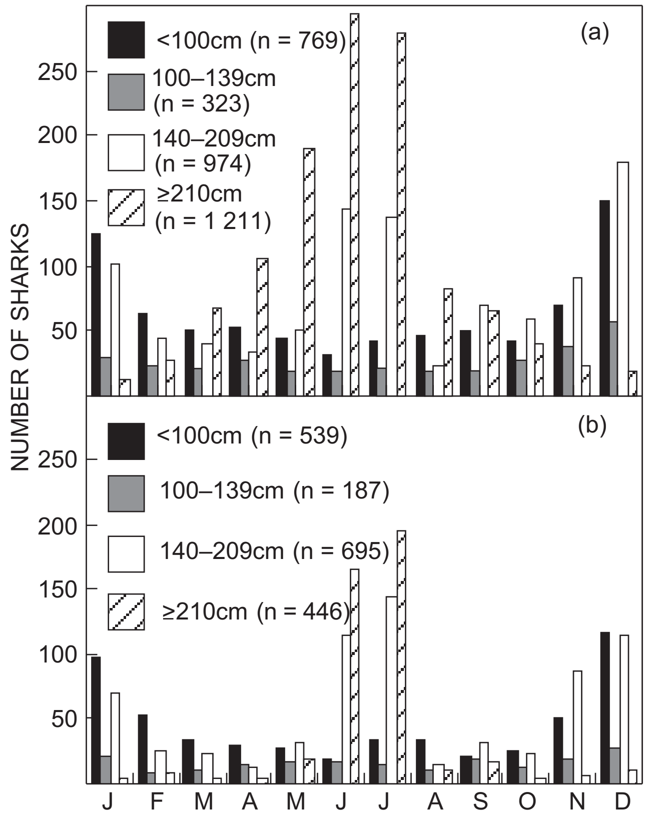

Figure 5: Seasonal distribution (catch) by size category (cm) of (a) female and (b) male *C. obscurus* caught in the KwaZulu-Natal shark nets, 1978–1999

of only 48 small sharks caught in the coastal waters of the Eastern Cape. Gubanov (1988) sampled a number of widespread localities in the Indian Ocean and usually found that females outnumbered males. Elsewhere, in a sample of only 15 adolescent and adult sharks in the South-West Pacific, 67% were female (Stevens 1984), in the western Gulf of Mexico two studies reported adult samples that were exclusively female (Springer 1940, Clark and von Schmidt 1965), and off the east coast of Florida a sample of 30 adolescent and adult specimens included 29 females (Dodrill 1977).

Tagging and movements

There have been several tagging studies focused primarily on small *C. obscurus* on the KZN coast (Davies and Joubert 1967, Bass *et al.* 1973, Govender and Birnie 1997). In the current study, of the 5 626 sharks caught 677 (12%) were found alive, of which 217 (3.8%) were tagged and released. The numbers tagged per size-class were: <100cm PCL, 20 sharks (25% of those found alive); 100–139cm, 30 sharks (45%); 140–209cm, 115 sharks (41%); and ≥210cm, 52 sharks (24%). From 1987, all tags applied by NSB staff to *C. obscurus* were dart tags with stainless steel heads, prior to which plastic fin tags were used. From 1993, 34 tagged animals were injected with oxytetracycline (OTC, dosage 25mg kg^{-1}) as part of an ongoing age and growth study. In addition to animals caught in the conventional net installations, NSB staff dart-tagged 40 specimens, encompassing all four size categories, of which 21 were injected. Some of these additional animals, which were captured using various gear types, were tagged off the Eastern and Western Cape Provinces. A final category of tagged animal consists of small sharks tagged by shore- or boat-anglers with fin tags and recaptured in the nets.

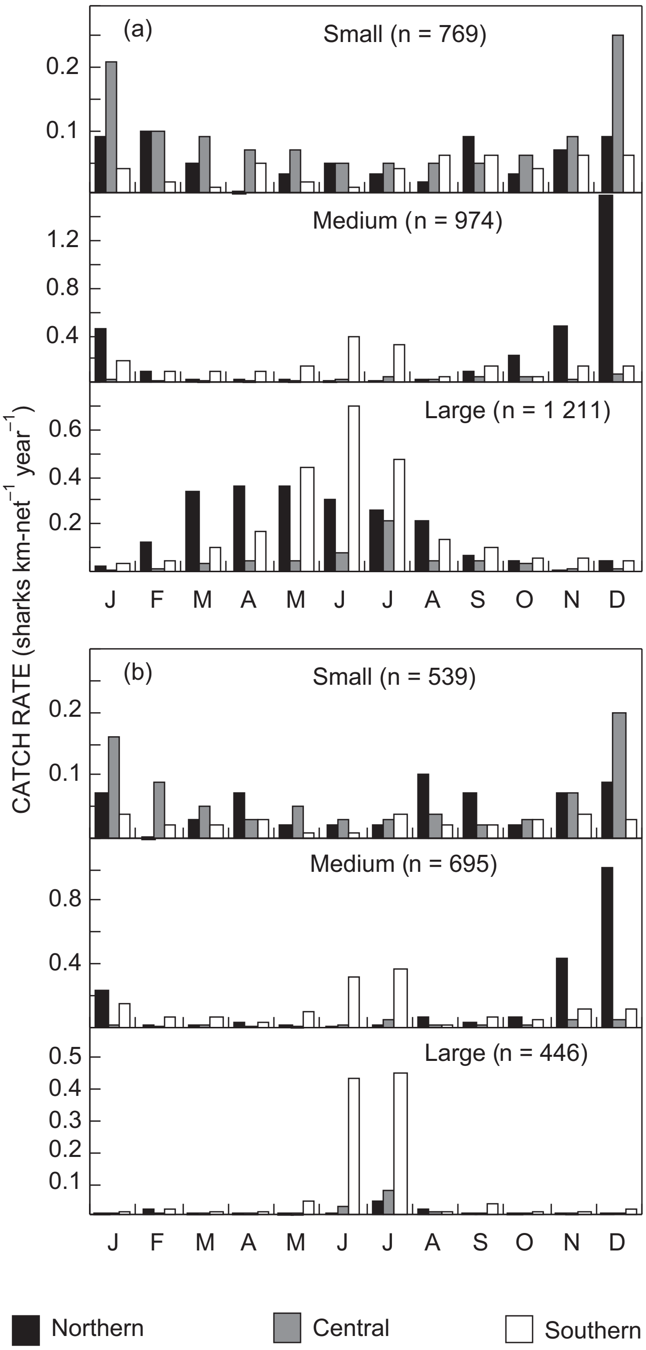

Figure 6: Geographic and seasonal distribution (catch rate) of small, medium and large (a) female and (b) male *C. obscurus* in the KwaZulu-Natal shark nets, 1978–1999 (Northern, Central and Southern regions are defined in Figure 1)

Of the 217 netted animals tagged, only three were recaptured (1.4%), and an additional tag was found washed up on the beach 54km from the tagging locality. Two of the three recaptures were of animals <100cm, with times at liberty of 22 days and 23 days and distances travelled of 6km and 8km respectively. The third animal, a female, measured 150cm when released at San Lameer (Figure 1) in March 1984, and had grown to 189cm when recaptured 1 742 days later at Salt Rock (Figure 1) in December 1988, having travelled a distance of 192km. The growth curve of Natanson and Kohler (1996) yields an age at tagging of 9.1 years, which, when added to a time at liberty of 4.8 years, yields an age at recapture of 13.9 years. The predicted age of a shark of 189cm is 15.1 years, the difference of 1.2 years being well within the 95% confidence limits of the growth curve.

Of the 40 additional animals tagged, six were recaptured, all on hook and line. All six were animals of <100cm and five demonstrated no movement, albeit that one of these was at liberty for 222 days and grew from 82cm to 88cm. The sixth specimen (65cm) was tagged and injected at Umhlanga (Figure 1) and recaptured 37 days later 17km away at Westbrook (Figure 1). The OTC had been incorporated into various hard parts, but the time at liberty was too short to be useful for ageing purposes.

A total of 33 angler-tagged animals was recaptured by NSB staff, mostly in the shark nets, and a further 55 shed tags were recovered. The animals were mostly <100cm and most demonstrated short-distance, short-duration movements on the KZN coast.

Higher recapture rates than that obtained for netted animals were reported in the previous tagging studies in KZN waters; for example, 4.2% (Bass *et al*. 1973) and 7.7% (Govender and Birnie 1997). In their analysis of tagging data obtained primarily from recreational angling, Govender and Birnie (1997) expressed concern that fishing mortality greatly exceeds natural mortality. Whereas many of the recoveries in both these studies were from localities on the KZN coast, some of the tagged small sharks were recovered as much as 1 200km away in Cape waters. Three recoveries recorded more recently indicate movements of small sharks over distances of 1 227–1 374km (B Mann, Oceanographic Research Institute, Durban, pers. comm.). One of these animals measured 80cm at the time it was tagged at Macassar off the South-West Cape and it was recovered at Port St Johns, 1 374km to the north-east and about 100km from the KZN border. If this animal, which was probably a year old at the time of tagging, was born in KZN waters, it undertook two long migrations in its first year. Simpfendorfer (2000) estimated growth rates up to Age 5 of 8–11cm year^{-1} in a tagging study conducted off south-western Australia. In the NWA, times at liberty of up to 15.8 years (Natanson *et al.* 1995) and distances travelled of up to 3 300km (Casey *et al.* 1987) have been recorded, the latter pertaining to adult and sub-adult sharks moving between the north-eastern USA and the south-western Gulf of Mexico (Bonfil 1997). Musick *et al.* (1993) pointed out that highly migratory species may be subjected to wide-scale fishing pressure on populations. In the SWI, movements of adults and sub-adults are not well understood and may not cover distances of this magnitude. Also unknown is the extent to which exploitation may occur elsewhere within the species' range.

Group occurrence

On 128 occasions, groups of five or more *C. obscurus* were found together in a net installation. Mean group size was 12 animals (SD 13.4). The largest group consisted of 113 animals, found in the Mzamba installation (1.49km of netting) on 30 May 1997. This was the date of the highest single-day capture of *C. obscurus* taken in all net installations — 163 animals. Most (79%) of the 1 523 sharks caught in groups were either medium (36%) or large (43%). Within these groups females outnumbered males by 1.3:1 overall.

In all, 81 of the groups (63% of the total number of groups) were caught in the winter months of May–July and these were taken primarily south of Durban, i.e. the region and period corresponding with the sardine run. Exclusively female and female dominant groups together outnumbered exclusively male and male dominant groups by 2.25:1, but there were relatively few groups consisting exclusively of either sex (14 groups, or 17% of the total; Table 1). The size composition of over half (57%) of all groups was exclusively large or large dominant.

The composition and geographical distribution of group catches taken in the summer months of November–January (Table 2) differed considerably from those of winter. In all, 14 (67%) of the groups were taken north of Durban and all of these consisted of medium sharks only. Again, however, exclusively female and female dominant groups together outnumbered (by 2.6:1) exclusively male and male dominant groups. Not reflected in Table 2 are two unusual group catches taken at Mzamba on consecutive days in November 1985. A total of 71 animals of unrecorded sex were caught and 63 of these were large sharks.

Environmental conditions at the nets

Nearshore sea surface temperatures associated with catches of *C. obscurus* ranged from 16.4°C in October to 27.2°C in March. The months with the lowest and highest mean prevailing temperatures are August and February respectively (Cliff *et al.* 1989). Seasonal peaks in *C. obscurus* in both summer and winter, albeit of different size-classes, suggest that temperature does not directly determine the seasonal distribution of the species within the study area. Bass *et al.* (1973) suggested that juveniles have an optimum temperature range of between 19°C and 23°C, with few caught in KZN waters between February and April, a period when the water is warmer than 23°C. In the present study, however, the highest catches of small sharks were in December and January, months when water temperatures are close to or >23°C. South of the study area, juveniles are scarce in winter in the waters of Algoa Bay in the Eastern Cape, when the temperature is <19°C (Bass *et al*. 1973). Off eastern Florida, Dodrill (1977) sampled adolescent and adult *C. obscurus* over a temperature range of 15.5–30.0°C.

Mean water clarity associated with *C. obscurus* capture was 2.79m (SE 0.034m, range 0–15m, n = 4 591). This differed (one-sample t-test, $p < 0.001$) from the prevailing

Table 1: Sex and size composition of *C. obscurus* shark groups caught in the winter (May–July); medium and large animals only. Sex or size dominance was defined by one sex or size category outnumbering the other by a factor of 2 or more. If there was no dominance, the category was defined as mixed

	Number of shark groups ($n \geq 5$ sharks group^{-1})					
Size category	Male only	Male dominant	Female only	Female dominant	Sexes mixed	Total
Medium only				1	1	2
Medium dominant		4		3	3	10
Large only		3	4	8	4	19
Large dominant	2	4	4	3	14	27
Size mixed		3	4	9	7	23
Total	2	14	12	24	29	81

Table 2: Sex and size composition of *C. obscurus* shark groups caught in the summer (November–January); medium and large animals only

	Number of shark groups ($n \geq 5$ sharks group^{-1})					
Size category	Male only	Male dominant	Female only	Female dominant	Sexes mixed	Total
Medium only		4	3	7	3	17
Medium dominant				1		1
Large only			1			1
Large dominant						
Size mixed		1		1		2
Total		5	4	9	3	21

annual mean for the study area, which was 3.22m. At Mzamba, the beach with the highest catch, the respective values were 2.17m (capture associated) and 2.69m (prevailing), which also differed significantly. As with the blacktip shark (Dudley and Cliff 1993), there is a tendency for captures to be associated with conditions slightly more turbid than average, possibly a consequence of reduced visibility of the nets. Also sampling in nearshore waters, Dodrill (1977) caught *C. obscurus* primarily in clean water and in daytime, factors he suggested were consistent with a pelagic habit.

Biology

Reproduction

Males

Size-at-50% maturity is 210cm, with the attainment of maturity indicated by rapid lengthening and calcification of the claspers (Figure 7). This equates to an age of 19.2 years, using the growth curve of Natanson and Kohler (1996). Bass *et al.* (1973) suggested a size at maturity of approximately 218cm. Elsewhere, length-at-maturity was reported as being 213cm (NWA, Springer 1960), and smallest mature males as measuring 224cm (northern Gulf of Mexico, Branstetter 1981) and 233cm (New South Wales, Stevens 1984). Of a sample of 667 males from which maturity data were obtained, 513 (77%) were immature and 154 mature. The mature males were caught almost exclusively in June and July (134 animals, 87%). Only two appeared to be approaching mating condition (ampullae of ducti epididymides full of seminal fluid) and none was considered to have recently mated (bleeding claspers). A total of 69 animals (45% of the mature specimens) had regressed testes, indicating that they were in a post-active condition, and 77 animals (50%) were inactive. The macroscopic distinction between post-active and inactive testes was not always clear. Data on seasonal variation in mean gonad index (GI: gonad mass/shark mass × 100) in mature males were few, but monthly variation was significant (Kruskal-Wallis, $p < 0.01$). Values ranged from 0.35% in January to 0.05% in September (Figure 8). In the NWA, Clark and von Schmidt (1965) sampled a mature male in April with much semen in the right ampulla and speculated that this may indicate spring mating. Branstetter (1981) sampled a male in this condition in the Gulf of Mexico in July. *C. obscurus* is capable, however, of storing sperm in the ampullae, probably for weeks, and therefore its presence alone does not indicate mating activity (Pratt and Tanaka 1994); those authors sampled three such males in July in the NWA but the claspers showed no evidence of mating activity. There are insufficient male reproductive data from either hemisphere to determine when mating of *C. obscurus* takes place.

Monthly variation in hepatosomatic index (HSI, liver mass/shark mass x 100) of mature males was non-significant (Kruskal-Wallis, $p > 0.05$), but there were indications of an increase in winter (June–August, Figure 8), with values ranging from 8.8% in January to 14.7% in August. The absence of samples during spring prevents the resolution of HSI seasonality and the investigation of a possible link between HSI and GI in mature males. Variation in HSI was significant ($p < 0.001$) in immature animals, both sexes combined, with a peak in June and July (Figure 9). Values ranged from 6.7% in April to 12.7% in June. The winter peak probably reflects the abundance of food provided by the sardine run.

Females

Size-at-50% maturity is 214cm; applying the growth curve of Natanson and Kohler (1996) this would equate to an age of

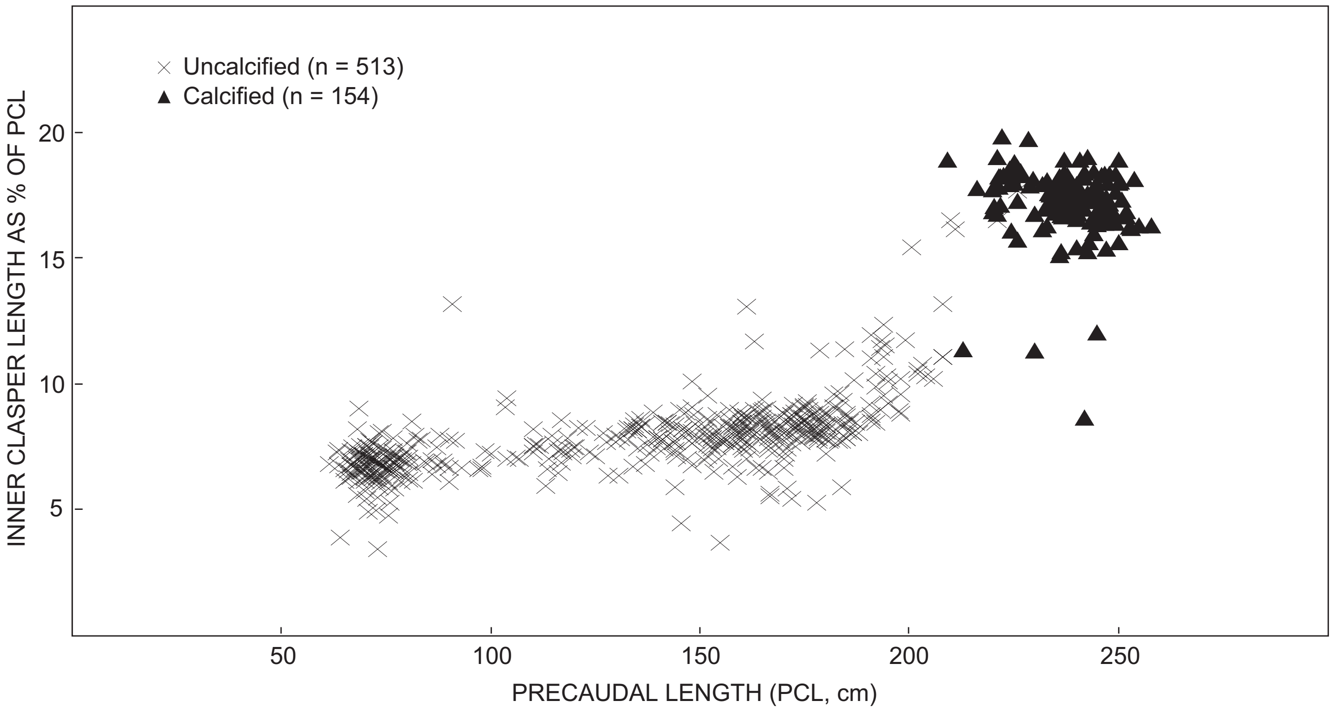

Figure 7: Relationship between inner clasper length and precaudal length (PCL) in male *C. obscurus*

20.0 years. The smallest mature female measured 202cm and the smallest pregnant female 221cm. Bass *et al.* (1973) reported a size range at maturity of 202–234cm and their smallest pregnant female was 241cm. Elsewhere, smallest mature females were reported as measuring 229cm (northern Gulf of Mexico, Branstetter 1981) and 211cm (New South Wales, Stevens 1984). Uterus widths tended to be <5cm in immature animals, but began to increase markedly in animals between 200cm and 220cm (Figure 10), with the predicted width for an animal of 211cm being 4.4cm, increasing to 11.5cm in an animal of 272cm PCL. Post-partum animals had very variable uterus widths, some as wide as 29cm.

Mature females were assessed as being either inactive, recently mated, pregnant or post-partum, although there is likely to be overlap between late post-partum and inactive individuals. Individual maximum ovum diameter (MOD) values were plotted against month of capture in an assumed three-year reproductive cycle (Figure 11), after the suggestion of Musick *et al.* (1993) that the cycle may require at least three years (see discussion of gestation period below). Most inactive animals were allocated to Year 3, but those with large ova and assumed to be approaching mating condition were allocated to Year 1. Pregnant animals with near-term embryos and post-partum animals were allocated

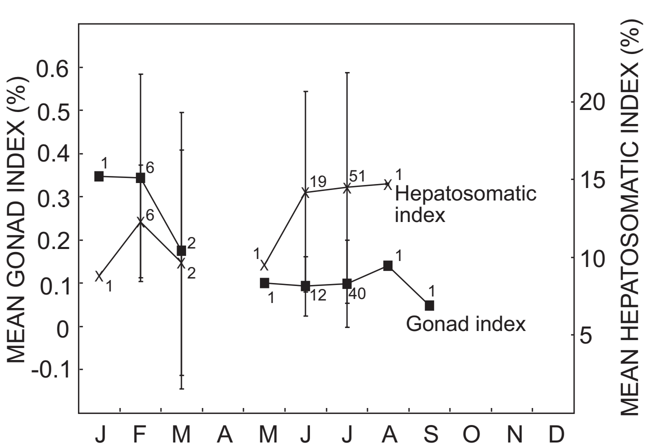

Figure 8: Mean monthly gonad indices and hepatosomatic indices of mature male *C. obscurus*. Bars represent 95% confidence limits on the means, data labels represent sample size. No data were obtained in April or between October and December

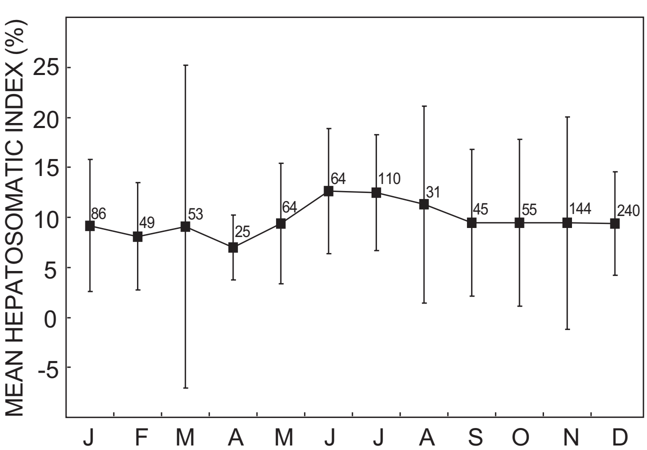

Figure 9: Mean monthly hepatosomatic indices of immature *C. obscurus* of both sexes. Bars represent 95% confidence limits on the means, data labels represent sample size

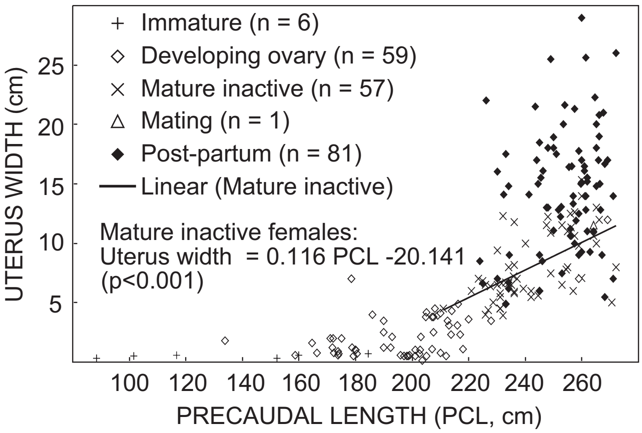

Figure 10: Relationship between uterus width and precaudal length (PCL) of non-pregnant female *C. obscurus*

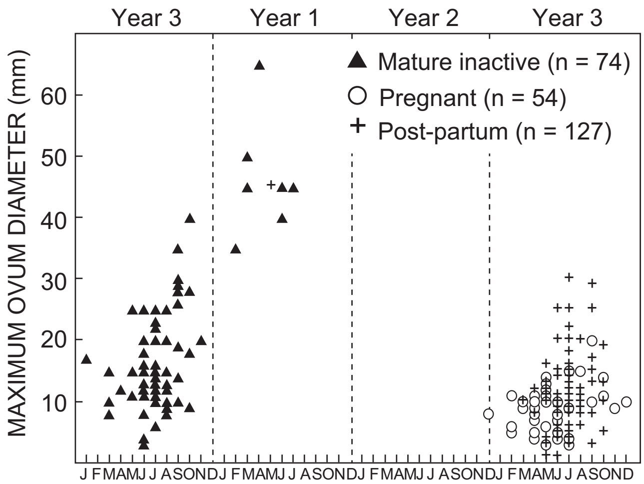

Figure 11: Reproductive cycle of mature female *C. obscurus* illustrated by changes in maximum ovum diameter

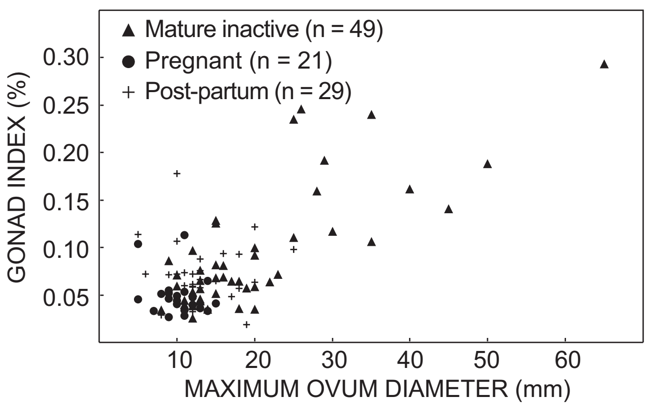

Figure 12: Relationship between maximum ovum diameter and gonad index in mature female *C. obscurus*

to Year 3, with the exception of a specimen with embryos of mean length 57cm that was caught in December and was allocated to the end of Year 2. No MOD values were available from pregnant females with mid-term embryos (30–40cm), which would be assumed to have fallen within Year 2. The presence of near-term pregnant animals in most months of the year suggests a prolonged pupping season, and consequently a prolonged period when fertilisation may occur. One animal with an MOD of 45mm was classed as post-partum, but may have been inactive and approaching mating. From Figure 11 it could be assumed that MOD ≥40mm denotes an animal approaching mating condition. If so, then only eight, or 3% of the 255 mature females sampled, were in this condition. Elevated GI values (approximately 0.15% or greater) tended to be evident in animals with MOD ≥25mm (Figure 12), but the potential for ova to grow considerably larger than this suggests that GI is a less reliable indicator of mating condition. Similarly, HSI also appears to be a less reliable indicator in this species. Whereas animals with large ova tended to have relatively high HSI values, numerous other animals with high HSI values did not have large ova (Figure 13).

Only two animals exhibited signs of having mated recently. One animal, caught in July, was documented as having plentiful sperm in both uteri, a GI of 0.14%, an MOD of 26mm and an HSI of 12.3%. The GI and MOD values are lower than might be expected to indicate mating. The second animal was caught in February and had mating bites on both flanks and pectoral fins, in the region of the cloaca and on the belly posterior to the pectoral fins. No sperm was found. GI was 0.11%, MOD 35mm and HSI 12.3%. Bass *et al.* (1973) sampled no females with ripe eggs off KZN and suggested that mating and early pregnancy probably occur to the north.

In the western Gulf of Mexico, Clark and von Schmidt (1965) recorded MOD values of 14–20mm in November, 20mm in December and 25mm in January. They speculated that full size (undefined) would be reached in spring. Off eastern Florida, Dodrill (1977) reported that ovarian eggs develop from 17mm in early October to 31–42mm in March and suggested that the animals then move offshore to mate in April–May. A specimen caught in July with an MOD of 40mm indicated a prolonged mating season (Dodrill 1977). Observers on shark fishing vessels off the south-eastern USA have recorded nine sharks between January and July with MOD values of between 30mm and 50mm (G Burgess and C Knickle, Florida Museum of Natural History, Gainesville, USA, unpublished data). One of these sharks, caught in January and with an MOD of 38mm, was newly pregnant.

Within pregnant females, most embryos were at or near full term, which limits the potential to assess changes in MOD, GI and HSI during gestation. In 52 pregnant females with mean embryo lengths ranging from 57.2cm to 75.9cm, there was a significant linear relationship between MOD and embryo length ($p < 0.03$), with predicted MOD increasing from 6.2mm to 11.6mm. There was a non-significant increase in GI with increasing embryo length (embryo range 35.5–75.9cm, $p = 0.89$, $n = 81$ females) and a non-significant decrease in HSI (embryo range 29.6–76.7cm, $p = 0.29$, $n = 187$ females), the bulk of embryos in both samples

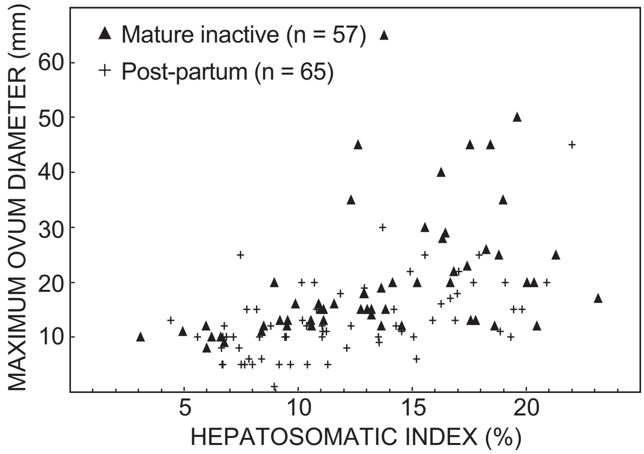

Figure 13: Relationship between maximum ovum diameter and hepatosomatic index in mature, non-pregnant female *C. obscurus*

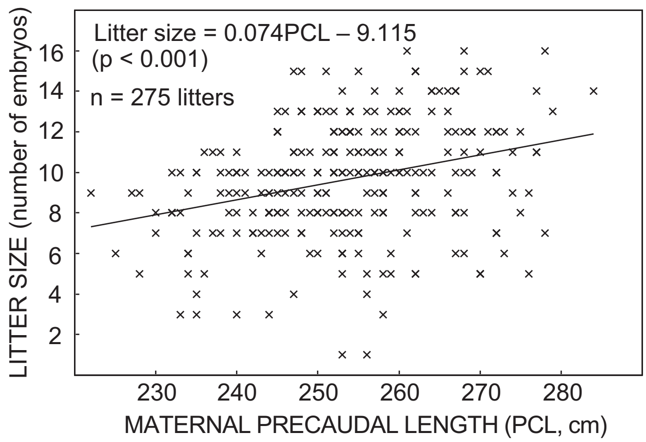

Figure 14: Relationship between maternal precaudal length (PCL) and litter size in *C. obscurus*

measuring 55cm or more. The increase in MOD during gestation indicates the onset of vitellogenesis in preparation for the subsequent mating event. A total of 8 post-partum animals had MOD ≥25mm. Most of these were caught in the second half of the year and the ova may have been due to reach full development during the first half of the following year. There are insufficient data to determine the interval between parturition and subsequent mating, but it may be approximately one year (Figure 11).

Stevens (1984) reported two post-partum females caught off New South Wales in December and February (summer) with MOD values of 12mm and GI values of 0.02% and 0.03%, indicating that these animals were not close to mating condition. Off south-eastern USA, pregnant females with term or near-term embryos tended to be caught between January and April (G Burgess and C Knickle, unpubl. data). Most (n = 14 sharks) had MOD values of ≤20mm, but three had values of 25–30mm. Post-partum animals (n = 10 sharks) were caught between January and July and six of these had MOD values <20mm. Four post-partum animals, however, two caught in January and two in July, had MOD values of 30–40mm and therefore appeared to have been ready to mate. Dodrill (1977) reported post-partum females with small ovarian eggs in July. As in the SWI, therefore, the norm appears to be a delay between parturition and mating, with some possible exceptions, and the duration of the interval may be about one year.

Pratt (1993) found long-term stored spermatozoa in the nidamental glands of each of a sample of 11 near-term and post-partum *C. obscurus*. He pointed out that the viability of the sperm was unknown but observed that, if females are capable of delaying fertilisation until physiologically prepared, this would increase population fecundity in a highly migratory species of low density.

Embryos, gestation and nursery grounds

The median litter size of 285 litters was 10 embryos, and the largest litters, of which three were found, consisted of 16 embryos. Partially aborted litters, presumably resulting from capture stress, were frequently observed, which may have caused an underestimate of median litter size. Litter size increased with maternal length ($p < 0.001$, n = 275 litters, Figure 14). Total numbers of male and female embryos were equal (χ^2, $p > 0.9$, n = 2 676 embryos), as was the number of embryos found in left and right uteri (χ^2, $p > 0.8$, n = 2 602 embryos). Previously, Bass *et al.* (1973) reported a mean litter size of 10 (n = 14 litters) and, in the NWA, Clark and von Schmidt (1965) reported a mean of eight (n = 16 litters).

The average range of embryo lengths within a litter was 7.5% (SE = 0.23%) of the mean length (n = 280 litters, runts and litters with single embryos excluded). Embryo mass within a litter was more variable, with an average range of 22.1% of the mean mass (n = 274 litters, SE = 0.76%). A number of litters consisting of well-developed embryos also contained one or more undeveloped eggs. The length-mass relationship for embryos (excluding runts) was $M = 8 \times 10^{-6}$ $PCL^{3.15}$ (n = 2 554, $p < 0.001$, range 33.0–79.1cm PCL).

Only four litters with mean lengths <50cm were sampled, being caught in February (34.6cm), April (44.1cm), July (35.5cm) and September (45.9cm) respectively (Figure 15). This temporal distribution is consistent with a prolonged breeding season and the small sample indicates that mating and most of the gestation period occurs away from the netted region, in agreement with the conclusions of Bass *et al.* (1973). Also indicative of a long season is the fact that females with large embryos were caught in most months, from early February to late December, although 82% (213 litters) were caught between early March and early July (Figures 15, 16). Captures of post-partum females peak in July and August (Figure 16), indicating that most pregnant females have dropped their young by that time. Most litters were at or near term irrespective of month of sampling, with 34% (96 litters) having a mean length in the size range 61–65cm, 48% (133 litters) in the range 66–70cm and 11% (30 litters) >70cm (Figure 15). There is, however, within embryos >60cm, a significant linear relationship between mean embryo length per litter and week of capture ($p < 0.001$, n = 259 litters, NSB data only), with the litter of largest embryos, sampled in August, having a mean length of 76.7cm. The predicted length of term embryos increased from 64cm in the first week of February to 72cm in the penultimate week of December. Therefore, whereas it appears that size at birth is usually 61–70cm and that most embryos are born in the first half of the year, embryos conceived later in the year may be born at a larger size. The competitive advantage conferred by a larger size at birth must be outweighed by other factors (i.e. seasonal abundance of food in winter), which select for pupping earlier in the year at a smaller size.

In litters with a mean embryo length >60cm there is a significant increase in embryo length with maternal length ($p < 0.001$, $n = 247$ litters, maternal length range 222–284cm, predicted mean embryo length range 64.1–69.5cm).

Bass *et al.* (1973) reported a range of size at birth of 52–76cm, but noted that most neonates with open or newly closed umbilical slits measured 61–68cm. Elsewhere, the reported size range at birth in the NWA is 61–70cm (Bigelow and Schroeder 1948, cited by Clark and von Schmidt 1965) and the mean size at birth off Western Australia is 68cm (Simpfendorfer 2000). Size at birth in the NWA predicted from a von Bertalanffy growth curve is 73.5cm (Natanson *et al.* 1995).

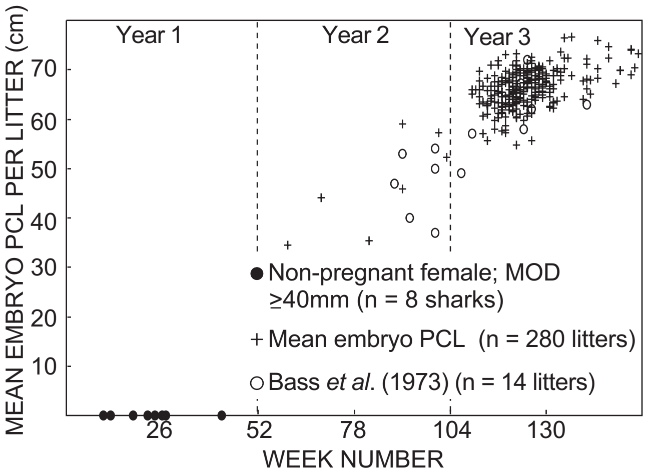

Figure 15: Relationship between time of year and either occurrence of large ova (MOD) or precaudal length (PCL) of *C. obscurus* embryos

It appears likely that the gestation period is of the order of two years (Figure 15). Mating appears to occur generally during the second quarter of Year 1 and parturition during the second quarter of Year 3. Although a one-year gestation cannot be ruled out, embryonic growth rate would be extremely high given the large size at birth.

In the NWA, Springer (1940) found no seasonality in embryo size, but Clark and von Schmidt (1965) sampled embryos in winter in two size-groups, 29–52cm and 61–73cm. Musick *et al.* (1993) combined data from a number of NWA studies (Clark and von Schmidt 1965, Dodrill 1977, Branstetter 1981) and postulated that gestation could last about 22 months. Musick *et al.* (1993) also noted that the large size at birth corresponds with an extended gestation period. Branstetter (National Marine Fisheries Service, St Petersburg, USA, pers. comm.) added to all available published information from the NWA unpublished data from the Virginia Institute of Marine Science longline programme for sharks and suggested that mating could occur in about June of Year 1 and parturition in April–May of Year 3. Similarly, unpublished observer data from the shark fishery off south-eastern USA (G Burgess and C Knickle, pers. comm.) form a pattern in which newly pregnant females or females with large ova occur between January and July of Year 1, females with embryos of 48–63cm between March and September of Year 2 and females with embryos of 56–80cm between January and April of Year 3. Three litters of embryos measuring 56–58cm sampled in January and February of Year 3 would presumably have reached term later in the year, suggesting that the pupping season extends beyond April. Seasonal reproductive patterns in sharks caught in this fishery are incompletely sampled, the semi-annual fishing season being primarily January–March and July–August (C Knickle, pers. comm.). Despite the SWI and NWA being in opposite hemispheres, the reproductive cycles of the dusky shark in the two regions are not six months out of phase. A feature common to both the current study and the data of G Burgess and C Knickle (pers. comm.) is

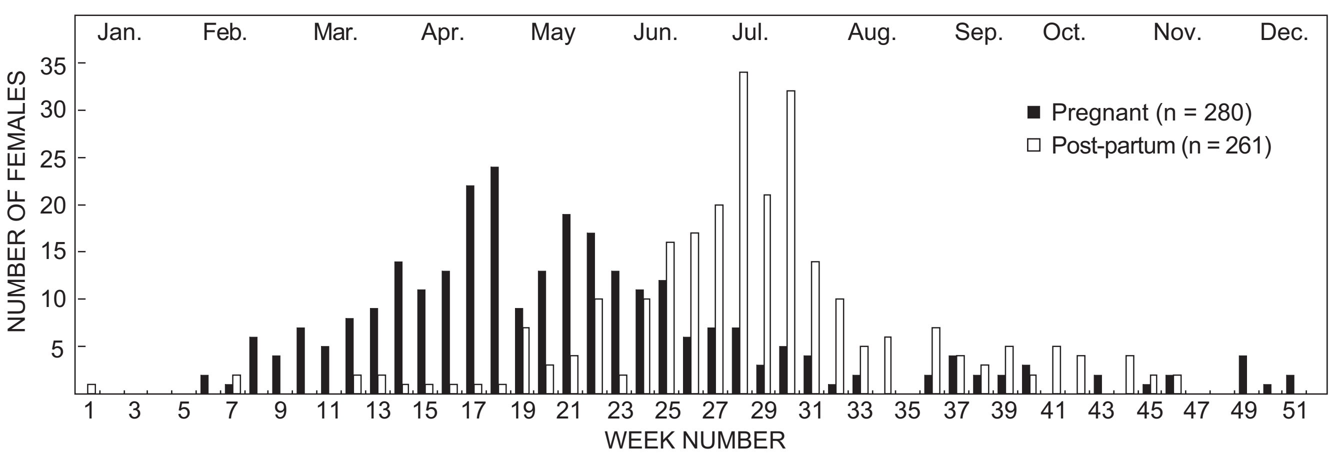

Figure 16: Seasonal distribution of catch of pregnant and post-partum *C. obscurus*

the relative scarcity of pregnant females other than those with embryos at or near term. Off KZN, this raises the question: why do neither newly pregnant nor, if gestation lasts two years, mid-term females come inshore in winter to take advantage of the abundant food provided by the sardine run, whereas adolescents of both sexes, post-partum females and adult males do so? The whereabouts of such females are unknown, but could be investigated through the use of pop-up tags that transmit archived geolocation data to satellite (Voegeli *et al.* 2001).

Highest annual catches of pregnant sharks were taken at Zinkwazi and Richards Bay, the two northernmost localities (Figures 1, 17a) and mean annual catch rate was highest, by a factor of 2.3, at Zinkwazi (Figure 17b). Therefore, although pupping probably occurs throughout the netted region, the northern area, flanking the productive Tugela Bank (Fennessy 1994), may be a preferred pupping ground. Competition shore-anglers historically travelled to this area in August and September to target neonate *C. obscurus* (B Wareham, Natal Coast Anglers Union, pers. comm.). The occurrence of small *C. obscurus* in nearshore waters, including the surf zone, from Richards Bay to the southern border of KZN indicates, however, that the entire area constitutes a nursery ground. In general, small *C. obscurus* are caught in the shark nets in summer, with catches peaking in December and January and being highest in the central region (Figure 6). Modal size-classes were 66–70cm and 71–75cm (Figure 3), i.e. representing about 5cm growth in the 6–8 months since birth in April–June. This is consistent with an estimate of growth in the SWI of 11.2cm in the first year, derived from the growth curve of Natanson and Kohler (1996). Farther south, Smale (1991) recorded small *C. obscurus* in Eastern Cape waters, with partially open umbilical scars and measuring an average of 72cm. This concurs with the tagging work of Bass *et al.* (1973), who showed that the primary movement of neonates tagged in the Durban region was to the south-west. Elsewhere in the Indian Ocean, Gubanov (1988, p. 69) reported the coastal waters of the island of Socotra in the Arabian Sea as 'places of reproduction', and Last and Stevens (1994) reported inshore nursery grounds off Western Australia.

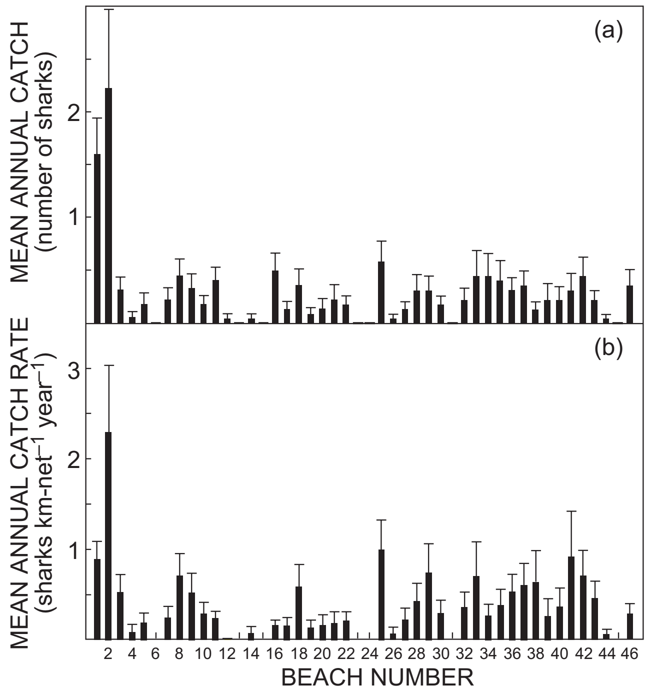

Figure 17: Geographical distribution of pregnant *C. obscurus* in the KwaZulu-Natal shark nets, 1978–1999, expressed as (a) mean annual catch and (b) mean annual catch rate per net installation. Error bars denote 1 SE. Beach numbers refer to Figure 1

Feeding

Of the 1 971 stomachs examined, 147 (7.4%) were everted and 1 099 (60.2% of non-everted stomachs) were empty. The mean mass of the contents from the 725 stomachs containing food was 1 131g (SE = 139g) and the mean number of prey items was 11.9 (SE = 2.3). Details of the prey are presented by frequency of occurrence (%F), by mass (%M) and by number (%N) for five size categories of predator (Table 3).

Elasmobranchs
Elasmobranchs occurred in 24.7% of stomachs and constituted 51.4% by mass, but only 2.1% by number. Representatives from 10 elasmobranch families (five shark and five batoid) and 17 species (12 shark) were identified (Table 3). Sharks were more common than batoids in all five predator categories presented below. The dominant family was the Carcharhinidae (3.4%F) and the most common species was *C. obscurus* (1.9%F). The heaviest single prey item was the remains of a large shark, which constituted 13.7% of the body mass of the adult female in which it was found.

Teleosts
C. obscurus fed mainly on teleosts, which were found in 63.0% of stomachs containing food and constituted 41.6% by mass and 95.1% by number. Representatives from 30 families and 42 species were identified (Table 3). Sardine was the most common prey species (17.3%F, 32.7%M and 72.1%N). The highest number of sardine found in a single stomach was 483; they constituted 12.3% of the body mass of an adult male. Unidentified engraulids were also present in high numbers (20.1%N). Other well-represented teleost families were Sparidae (4.1%F) and Scombridae (3.7%F). The otoliths of 67 teleosts were found without associated soft tissue in 53 stomachs, the most common species being piggy *Pomadasys olivaceum* (seven in six stomachs) and snapper kob *Otolithes ruber* (five in two stomachs).

Cephalopods
Cephalopods were found in 15.3% of stomachs and constituted 1.3% by mass and 1.5% by number. Cuttlefish (Sepiidae) were the most common (7.9%F). The beaks of 111 cephalopods were found without associated soft tissue in 98 stomachs. They included 46 *Octopus* spp. (39 stomachs), 27 Sepiidae (26 stomachs), 36 squids (32 stomachs) and two *Argonauta* spp. (one stomach). The

Table 3: Stomach contents of *C. obscurus* caught in the shark nets, 1983–1999. Details of the prey are presented by frequency of occurrence (%F), by mass (%M) and by number (N%) for five size categories of predators. Totals represent number of non-empty stomachs (F) and mass prey items (M, kg)

	Predator category														
	Small			Intermediate			Medium			Large (excl. pregnant)			Pregnant		
Prey category	%F	%M	N%	%F	%M	N%	%F	%M	N%	%F	%M	N%	%F	%M	N%
Elasmobranchs	19.0	29.8	13.0	43.8	62.5	30.0	21.9	45.4	1.4	24.3	52.2	1.0	46.4	77.7	41.2
Carcharhinidae															
Unidentified carcharhinid							0.9	2.6	0.0	1.5	9.3				
Carcharhinus brachyurus (copper shark)										0.7	0.8	0.0			
C. brevipinna (spinner shark)							0.5	1.8	0.2						
C. limbatus (blacktip shark)							0.5	0.1	0.0						
C. obscurus (dusky shark)	0.4	2.6	0.3	2.5	2.9	1.7	2.7	3.3	0.2	2.9	5.5	0.1	6.7	11.8	5.9
C. plumbeus (sandbar shark)										0.7	1.4	0.0			
Mustelus mustelus (smooth-hound)													3.3	8.6	2.9
Rhizoprionodon acutus (milkshark)	0.4	0.8	0.3	1.3	1.1	0.8									
Scyliorhinidae															
Halaelurus lineatus (banded catshark)							0.9	0.2	0.0						
Sphyrnidae															
Sphyrna sp. (hammerhead)				1.3	4.9	0.8				2.9	7.1	0.1			
Sphyrna lewini (scalloped hammerhead)							0.9	6.8	0.0						
S. zygaena (smooth hammerhead)							0.9	9.4	0.0	0.7	0.8	0.0			
Odontaspididae															
Carcharias taurus (spotted ragged-tooth)										1.5	6.0	0.1			
Squatinidae															
Squatina africana (African angelshark)							0.5	0.5	0.0						
Rajidae															
Unidentified rajid (skate)										0.7	0.0	0.0			
Rhinobatidae															
Rhinobatos sp. (guitarfish)	0.4	0.4	0.3				0.5	1.9	0.0	0.7	0.3	0.1	3.3	2.3	2.9
Rhynchobatus djiddensis (giant guitarfish)													3.3	30.6	2.9
Myliobatidae															
Unidentified myliobatid	0.4	1.2	0.3	1.3	0.9	0.8									
Pteromylaeus bovinus (bullray)				1.3	9.0	0.8							3.3	5.6	2.9
Rhinoptera javanica (flapnose ray)	0.4	1.4	0.3							1.5	2.8	0.1			
Mobulidae															
Mobula sp. (devilray)	0.4	0.1	0.3	1.3	1.5	0.8									
Dasyatidae															
Unidentified dasyatid (stingray)	0.4	0.7	0.3	1.3	2.9	0.8									
Gymnuridae															
Gymnura natalensis (backwater butterflyray)				1.3	3.0	0.8									
Unidentified shark	0.8	1.8	0.5	5.0	4.5	3.3	0.9	1.9	0.0	0.7	0.0	0.0	3.3	0.0	2.9
Unidentified small shark	8.7	14.1	6.0	16.3	10.6	10.8	5.4	3.0	0.3	1.5	0.1	0.1			
Unidentified large shark	0.4	0.5	0.3	1.3	10.1	0.8	2.7	6.3	0.2	8.8	17.1	0.3	13.3	16.6	11.8
Unidentified batoid	1.6	0.3	1.1	1.3	0.4	0.8							3.3		
Unidentified ray	4.0	5.5	3.0	8.8	10.7	5.8	4.0	6.2	0.2	1.5	1.0	0.1	3.3		
Unidentified elasmobranch	1.6	0.5	1.4	1.3	0.0	0.8	2.2	1.4	0.1	0.7	0.0	0.0	3.3		
Teleosts	65.1	57.4	59.6	55.0	32.5	52.5	62.9	47.2	96.1	72.1	40.9	98.6	26.6	16.4	23.5
Elopidae															
Elops machnata (ladyfish)													3.3	9.7	2.9
Anguilliformes															
Unidentified anguilliform (eel)	0.4	0.6	0.3				0.5	0.2	0.0						
Muraenidae															
Unidentified moray	0.4	0.4	0.3												
Clupeidae															
Unidentified clupeid	0.4	0.6	2.5				0.5	0.1	0.3						
Etrumeus sp. (round herring)				1.3	0.1	0.8				0.7	0.0	0.1			2.9
Sardinops sagax (sardine)	0.8	1.3	3.3	5.0	2.1	5.0	24.1	34.9	50.0	48.2	38.8	96.4	3.3	0.3	2.0

Table 3 cont.

Prey category	Small %F	Small %M	Small %N	Intermediate %F	Intermediate %M	Intermediate %N	Medium %F	Medium %M	Medium %N	Large (excl. pregnant) %F	Large (excl. pregnant) %M	Large (excl. pregnant) %N	Pregnant %F	Pregnant %M	Pregnant % N
Hilsa kelee (kelee shad)	0.4	0.2	0.3	1.3	0.5	3.3									
Pellona ditchela (Indian pellona)	0.4	0.0	0.3												
Engraulidae															
Unidentified engraulid (anchovy)	0.4	0.0	0.3				1.8	1.7	41.1						
Thryssa vitrirostris (orangemouth glassnose)				1.3	0.0	0.8									
Chirocentridae															
Chirocentrus dorab (wolfherring)	0.4	0.0	0.3												
Ariidae															
Unidentified ariid (sea catfish)	0.4	0.5	0.3	1.3	0.5	0.8	0.5	0.1	0.0						
Galeichthys feliceps (white seacatfish)	0.4	0.0	0.3	1.3	0.5	0.8	0.5	0.1	0.0						
Plotosidae															
Plotosus sp. (eel-catfish)	0.4	0.7	0.3							0.7	0.3	0.0			
Chloropthalmidae															
Chlorophthalmus punctatus	0.4	0.2	0.3												
Synodontidae															
Unidentified synodontid (lizardfish)	0.4	0.0	0.3												
Macrouridae															
Unidentified macrourid (grenadier)	0.4	0.2	0.3												
Exocoetidae															
Unidentified exocoetid (flyingfish)								0.5	0.4	0.0					
Serranidae															
Undentified serranid (rockcod)											0.7	0.0	0.0		
Pomatomidae															
Pomatomus saltatrix (elf)	1.6	1.3	1.4				0.5	0.1	0.0	0.7	0.1	0.0	3.3	0.0	2.9
Haemulidae															
Pomadasys commersonnii (spotted grunter)				2.5	0.4	1.7				0.7	0.7	0.0			
Pomadasys olivaceum (piggy)	5.2	0.7	3.5	1.3	0.2	0.8	1.3	0.0	0.1						
Pomadasys striatum (striped grunter)	0.4	0.1	0.3				1.3	0.1	0.1						
Sparidae															
Unidentified sparid	0.4	0.1	0.3												
Chrysoblephus puniceus (slinger)	1.2	0.4	0.8				0.5	0.0	0.0	0.7	0.0	0.0			
Diplodus sargus (blacktail)	2.8	2.3	2.2												
Pachymetopon grande (bronze bream)							0.5	0.0	0.0						
Pagellus bellottii natalensis (red tjor-tjor)	1.2	0.1	0.8				0.5	0.0	0.0	0.7	0.0	0.0			
Rhabdosargus sarba (Natal stump-nose)	0.4	0.1	0.3				0.5	0.0	0.0						
Sarpa salpa (strepie)	2.0	1.8	1.4	1.3	0.0	0.8	0.5	0.0	0.0						
Rhabdosargus sp. (stumpnose)										0.7	0.1	0.0			
Cheimerius nufar (santer)							0.5	0.2	0.0						
Scorpididae															
Neoscorpis lithophilus (stonebream)	0.4	0.1	0.3												
Gerreidae															
Unidentified gerreid (pursemouth)	0.8	0.5	1.1												
Mullidae															
Unidentified mullid (goatfish)							0.5	0.2	0.0						
Sciaenidae															
Unidentified sciaenid (kob)	0.8	2.5	2.4												
Argyrosomus thorpei (squaretail kob)	0.4	0.0	0.5												
Atractoscion aequidens (geelbek)										0.7	0.2	0.0			
Atrobucca nibe (longfin kob)										0.7	0.0	0.1			
Johnius dussumieri (small kob)	1.2	0.2	0.8				0.5	0.0	0.0						
Otolithes ruber (snapper kob)	0.4	0.5	0.3				0.5	0.1	0.2						
Umbrina ronchus (slender baardman)	0.4	1.0	0.3	1.3	0.3	0.8									

Table 3 cont.

Prey category	Predator category														
	Small			Intermediate			Medium			Large (excl. pregnant)			Pregnant		
	%F	%M	%N	%F	%M	%N	%F	%M	%N	%F	%M	%N	%F	%M	%N
Leiognathidae															
Unidentified leiognathid (soapy)	0.4	2.0	0.3												
Leiognathus equula (slimy)	0.8	0.5	0.8												
Secutor insidiator (slender soapy)													3.3	0.0	2.9
Oplegnathidae															
Oplegnathus conwayi (Cape knifejaw)					1.3	0.1	0.8	0.5	0.6	0.0					
Carangidae															
Unidentified carangid				1.3	5.4	0.8									
Decapturus sp. (scad)	0.4	0.0	1.4												
Decapterus russelli (Indian scad)	0.4	0.1	0.3												
Lichia amia (garrick)										0.7	0.2	0.0			
Trachinotus botla (largespotted pompano)							0.5	0.7	0.0						
Trachurus delagoa (African maas-banker)	0.8	0.1	0.5							0.7	0.0	0.0			
Cheilodactyleidae															
Unidentified cheilodactylid (fingerfin)							0.5	0.0	0.0						
Chirodactylus brachydactylus (twotone fingerfin)							0.5	0.2	0.0						
C. jessicalenorum (Natal fingerfin)								0.5	0.3	0.0					
Cichlidae															
Unidentified cichlid							0.9	0.3	0.0						
Mugilidae															
Unidentified mugilid (mullet)	0.8	0.8	0.5	1.3	1.3	0.8									
Liza macrolepis (large-scale mullet)	0.8	0.4	1.9												
Sphyraenidae															
Sphyraena sp. (barracuda)				1.3	0.5	0.8									
Gempylidae															
Thyrsites atun (snoek)	0.4	0.8	0.3												
Scombridae															
Unidentified scombrid	3.2	7.5	2.2	1.3	3.6	0.8	0.5	0.1	0.0	0.7	0.0	0.0			
Scomber japonicus (mackerel)	0.4	0.4	0.3	2.5	0.2	3.3	2.2	1.9	0.4	0.7	0.1	0.1			
Scomberomorus plurilineatus (queen mackerel)	0.4	1.2	0.3												
Thunnus albacares (yellowfin tuna)	0.4	2.0	0.3				0.5	1.0	0.0				3.3	4.2	2.9
Auxis sp. (tuna)				1.3	2.9	0.8									
Euthynnus affinis (Eastern little tuna)	0.4	1.5	0.3												
Katsuwonus pelamis (skipjack tuna)					1.3	4.8	0.8								
Pleuronectiformes															
Unidentified flatfish	0.4	0.1	0.3	1.3	0.1	0.8									
Unidentified cynoglossid (tonguefish)	0.4	0.0	0.3												
Balistidae															
Unidentified triggerfish	0.4	0.1	0.3	1.3	0.3	0.8	0.5	0.4	0.0						
Ostraciidae															
Unidentified boxfish							0.5	0.0	0.0						
Unidentified teleost	39.3	24.5	32.1	33.8	9.0	25.8	22.8	3.6	3.6	21.2	0.4	1.8	10.0	1.8	8.8
MAMMALS	2.0	2.5	1.3	2.5	2.0	1.7	4.5	4.0	0.2	4.3	6.3	0.1	7.1	3.7	5.9
Unidentified cetacean (dolphins, whales)							0.5	0.0	0.0						
Unidentified dolphin	2.0	2.5	1.4	1.3	0.0	0.8	3.6	1.7	0.2	1.5	0.6	0.1	3.3	3.4	2.9
Tursiops aduncus (bottlenose dolphin)										0.7	0.4	0.0			
Unidentified whale										2.2	5.3	0.1			
Unidentified mammal				1.3	0.5	0.8	0.9	2.5	0.0				3.3	0.3	2.9
CEPHALOPODS	16.7	6.4	14.0	12.5	2.0	11.7	17.9	2.3	1.1	8.6	0.5	0.3	25.0	1.9	26.5
Octopodidae (octopi)															
Octopus spp.	3.2	1.5	3.8	5.0	1.1	3.3	4.0	1.7	0.4	1.5	0.5	0.1	3.3	1.3	2.9

Table 3 cont.

	Predator category														
	Small			Intermediate			Medium			Large (excl. pregnant)			Pregnant		
Prey category	%F	%M	%N	%F	%M	%N	%F	%M	%N	%F	%M	%N	%F	%M	%N
Teuthoidea (squids)	2.4	0.3	1.6	1.3	0.3	3.3	1.3	0.1	0.1						
Loligo spp.	0.8	0.0	0.5												
Ommastrephidae	0.4	0.0	0.8												
Sepiidae (cuttlefish)	6.0	2.0	5.4	6.3	0.6	5.0	12.1	0.6	0.7	7.3	0.1	0.2	15.6	0.7	20.6
Unidentified cephalopod	3.8	2.7	3.0	1.3	0.0	0.8	1.3	0.1	0.1				3.3	0.0	2.9
CRUSTACEANS	4.0	0.6	2.6	5.0	0.9	3.3	10.7	1.2	1.3	0.7	0.0	0.0	3.6	0.1	2.9
Decapoda															
Brachyura (crabs)	0.8	0.0	0.5	2.5	0.5	1.7	6.3	1.0	1.3	0.7	0.0	0.0	3.3	0.1	2.9
Macrura (rock lobsters)															
Panulirus homarus (East Coast spiny lobster)	1.6	0.4	1.1	2.5	0.4	1.7	2.7	0.1	0.1						
Unidentified prawn	0.8	0.1	0.5				0.5	0.0	0.0						
Anomura (hermit crabs)							0.5	0.0	0.0						
Unidentified crustacean	0.8	0.0	0.5				1.3	0.1	0.1						
MISCELLANEOUS ITEMS															
Unidentified fish remains				1.3	0.1										
Gastropods	0.4	0.0	0.3			0.8	1.3	0.0	0.1						
Fisherman's bait	6.4	3.3	5.2	1.3	0.2	0.8									
Totals	252	31	386	80	32.3	120	223	177.2	4 636	140	457.8	4 328	30	36.3	34

squids included *Loligo* spp. (eight in eight stomachs), *Todarodes* spp. (three in two stomachs), *Ancistrocheirus lesueuri* (three in three stomachs) and one *Octopoteuthis* sp. All these cephalopods and those listed in Table 3 are neritic, except *Argonauta* and the seven individuals belonging to the last three genera of squids listed above, which are oceanic.

Other prey

Other prey categories were crustaceans (5.5%F), comprising mainly brachyuran crabs, and mammals (3.4%F), mainly dolphins. Of the 65 crabs from 20 stomachs, 75% were found in four stomachs and identified as *Charybdis* sp. No bird or sea turtle remains were found. Inedible items not shown in Table 3 included seaweed (31 stomachs), riverine and terrestrial vegetation (nine stomachs), sand (four stomachs), stones (six stomachs), tin (one stomach) and plastic (three stomachs).

Size-related variation in diet

Small (<100cm) — A total of 647 stomachs was examined, of which 17 (2.6%) were everted and 378 (60.0% of non-everted stomachs) were empty. The mean mass of the contents of the 252 stomachs containing food was 124g (SE = 11g) and the mean number of prey items was 1.2 (SE = 0.06). The prey was dominated by teleosts (Figure 18), followed by elasmobranchs and cephalopods (Table 3). The most common teleost families as listed in Table 3 were two demersal groups, Haemulidae and Sparidae, and the pelagic Scombridae. There was a high incidence of piggy (5.2%F) and cuttlefish (6.0%F). The incidence of sardine was the lowest within the five size categories.

Intermediate (100–139cm) — A total of 172 stomachs was examined, of which four (2.3%) were everted and 88 (52.3%) were empty. The mean mass of the contents of the 80 stomachs containing food was 449g (SE = 50 g) and the mean number of prey items was 1.1 (SE = 0.1). Like the small *C. obscurus*, the prey was dominated by teleosts (Figure 18), followed by elasmobranchs, which were more important by mass, and cephalopods (Table 3). There was a high incidence of sardine (5.0%F) and cuttlefish (6.3%F; Table 3).

Medium (140–209cm) — A total of 613 stomachs was examined, of which 16 (2.6%) were everted and 374 (62.6% of non-everted stomachs) were empty. The mean mass of the contents of the 223 stomachs containing food was 734g (SE = 49g) and the mean number of prey items was 19.3 (SE = 1.3). The prey was dominated by teleosts (Figure 18), followed by elasmobranchs and cephalopods (Table 3). There was a high incidence of sardine (24.1%F) and cuttlefish (12.1%F). Table 3). The other important teleost groups were Scombridae and Sparidae. The incidence of crustaceans (10.7%F), mainly brachyuran swimming crabs, was the highest of all the size categories. Sardine and unidentified engraulids comprised 50.0% and 41.1% by number respectively.

Large (≥210cm) excluding pregnant females — A total of 337 stomachs, excluding those of pregnant females, was examined, of which 46 (13.6%) were everted and 151 (51.9% of non-everted stomachs) were empty. The mean mass of the contents of the 140 stomachs containing food was 3 890g (SE = 632g) and the mean number of prey items was 26.9 (SE = 7.5). The prey was dominated by teleosts,

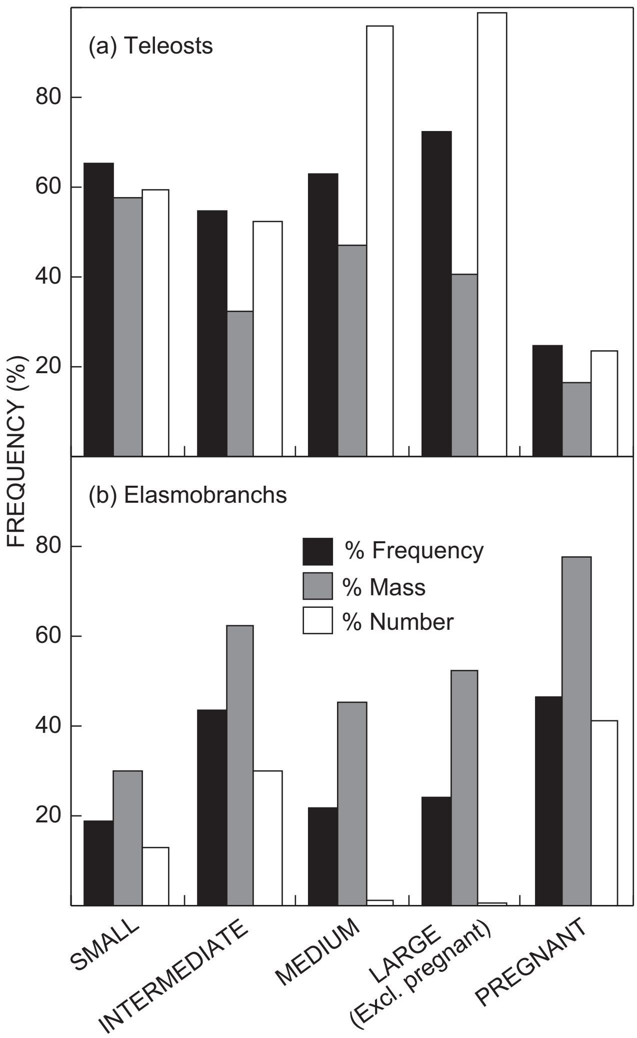

Figure 18: Teleost and elasmobranch contribution to the diet of five size categories of *C. obscurus*

although elasmobranchs were more important by mass (Figure 18). The incidence of cephalopods was the lowest within the five size categories (Table 3). Sardine were the most important prey item (48.2%F) and constituted 96.4% by number. There was a high incidence of cuttlefish (7.3%F).

Pregnant females — A total of 200 stomachs was examined, of which 62 (31.0%) were everted and 108 (78.3% of non-everted stomachs) were empty. The mean mass of the contents of the 30 stomachs containing food was 1 939g (SE = 565 g) and each stomach only contained a single prey item. This was the only group in which elasmobranchs were more important than teleosts (Figure 18). This group also had the highest incidence of cephalopods (Table 3). The incidence of sardine was very low (3.3%F) and the single stomach contained only one sardine. This group had the highest incidence of both cuttlefish (15.6%F) and *C. obscurus* (6.7%F).

Contingency table analysis — There were significant differences in the incidence of the major prey groups among the size categories (χ^2 test, $p < 0.001$, Table 4). Pregnant females provided the greatest source of variability, with more elasmobranchs and fewer teleosts than expected. There was no significant difference between the observed and expected values of prey categories in small *C. obscurus*. Elasmobranchs, followed by crustaceans, accounted for the greatest variability in the prey groups. The incidence of cephalopods and mammals was not different from that expected.

Scavenging

A total of 79 stomachs contained prey that was scavenged from the shark nets. An example was the presence of freshly ingested remains of a single stingray *Dasyatis* sp. in the stomachs of three small *C. obscurus* that were caught next to the ray. Scavenging was recorded in *C. obscurus* of all size categories. The highest incidence was among the intermediate size-class, at 20% of those with stomach contents, and the lowest (6%) was among the medium *C. obscurus*. Of the scavenged prey, 19% were teleosts, 60% of which were Scombridae (tunas and mackerels), 78% were elasmobranchs and 3% marine mammals (dolphins). The most common sharks scavenged were hammerheads *Sphyrna* spp. (19%F) and *C. obscurus* (11%F).

Despite constituting 19% of the animals scavenged, teleosts comprised only 5% by number of the total catch in the shark nets (NSB, unpublished data). Sharks comprised 66% of the catch and 67% of the animals scavenged and batoids 19% and 11% respectively. Small *C. obscurus* were responsible for most of the scavenging on teleosts and rays. The medium and large *C. obscurus* scavenged almost exclusively on sharks. Both recorded cases of scavenging on dolphins were by large *C. obscurus*. Two large sharks were caught with whale remains in their stomachs, after a dead whale was sighted close inshore.

Comparison with other feeding studies

This is the sixth detailed feeding study of *C. obscurus*. In all six studies about 60% of stomachs examined were empty and teleosts were the dominant prey category by frequency, with values ranging from 58–78%. Two of the other three South African studies, one in KZN (van der Elst 1979) and another in the Eastern Cape (Smale 1991), were of sharks caught largely by recreational shore-anglers. In Western Australia, most of the sharks were caught in small mesh gillnets, although some larger specimens were taken on set lines (Simpfendorfer *et al.* 2001). Longlines were used by Gelsleichter *et al.* (1999) in their study in the NWA. In these four studies, >90% of the sharks sampled were small. The fifth study, also conducted in KZN (Bass *et al.* 1973), sampled sharks of all sizes and in a variety of ways, with no indication of the proportion of small sharks. The current study provides the first large sample of stomach contents of large *C. obscurus*.

In KZN, the diet of small *C. obscurus* comprised a wide variety of demersal and pelagic teleosts, although with a virtual absence of sardine, which were found in nearly 10% of individuals from the Eastern Cape (Smale 1991) and Western Australia (Simpfendorfer *et al.* 2001). In small *C. obscurus*, the incidence of cephalopods varied considerably, ranging from 1%F in the NWA (Gelsleichter *et al.* 1999) through 17%F in the present study to just over 50%F in the Eastern Cape

Table 4: Contingency table analysis of the variations in the five major prey categories found in the stomachs of five size categories groups of *C. obscurus*. Values shown are the observed number of stomachs containing the given prey category; expected values are in parenthesis. The overall χ^2 statistic* is highly significant ($p < 0.001$)

Prey category	Small	Intermediate	Medium	Large (excl. pregnant)	Pregnant	n_i	χ^2_i
Teleost	164 (151)	44 (53)	141 (149)	101 (87)	7 (17)	457	11.27
Elasmobranch	48 (59)	35 (21)	49 (58)	34 (34)	13 (7)	179	19.21
Cephalopod	42 (37)	10 (13)	40 (36)	12 (21)	7 (4)	111	7.80
Crustacean	10 (13)	4 (5)	24 (13)	1 (8)	1 (1)	40	16.06
Mammal	5 (8)	2 (3)	10 (8)	6 (5)	2 (1)	25	3.61
n_j	269	95	264	154	30	812	
χ^2_j	6.04	12.19	11.99	12.31	15.41		57.98*

(Smale 1991) and Western Australia (Simpfendorfer *et al.* 2001). Of the cephalopods, cuttlefish were far more common than squids; van der Elst (1979) reported the opposite. Smale (1991) found the squid *Loligo vulgaris reynaudii* in 49% of stomachs of *C. obscurus*, reflecting its abundance in coastal Eastern Cape waters. In the present study, crustaceans, mainly brachyuran swimming crabs, were found in only 4% of stomachs of small sharks, compared with nearly 20% in the NWA (Gelsleichter *et al.* 1999).

Catches of small *C. obscurus* peaked in the summer when no sardine were present in the warm waters of KZN. In winter, occurrence of medium and large *C. obscurus*, other than pregnant females, overlapped with the presence of sardine. The incidence of sardine in pregnant females was very low in comparison to other large *C. obscurus*. Although their catches peaked from late April to early June, prior to the arrival of the sardine shoals, a total of nine pregnant females was caught on the South Coast during the sardine run. Because only one of these sharks had ingested sardines, in this case a single fish, it would appear that pregnant females do not select sardine. Instead, they appear to concentrate on elasmobranchs, whose larger size provides not only a greater return on energy expended but possibly renders them easier to catch. There was a very low incidence of other shoaling fish, including three clupeid genera, in all size categories.

The most common elasmobranch prey species was *C. obscurus* itself, with the highest incidence in pregnant females and the lowest in small *C. obscurus*. These results support the observations of Simpfendorfer *et al.* (2001) that larger specimens may be an important predator of the neonates, thereby possibly regulating population size at high levels of abundance. This is in contrast to findings for the spinner shark *Carcharhinus brevipinna*, which also has a nursery ground in the netted region. There was no evidence of large individuals of that species, particularly pregnant females, feeding on its neonates (Allen and Cliff 2000). Sharks were found more frequently than batoids in the stomachs of *C. obscurus*, a result that was also reported by Simpfendorfer *et al.* (2001) and Bass *et al.* (1973). Conversely, batoids were the only elasmobranch prey in the Eastern Cape (Smale 1991) and NWA (Gelsleichter *et al.* 1999).

The number of confirmed cases of scavenging on net-caught prey represented some 10% of non-empty stomachs. This figure appears to be high, indicating that scavenging may be an important source of food for *C. obscurus.* In bull sharks *Carcharhinus leucas*, only 3% of non-empty stomachs contained prey scavenged from the nets (Cliff and Dudley 1991). Bass *et al.* (1973) reported that large *C. obscurus* often follow trawlers working off the KZN and Moçambican coasts, inflicting considerable damage to the nets. Despite the high incidence in the present study of scavenging by *C. obscurus*, there were no cases of scavenging on land animals and birds or on food items discarded by humans, such as butcher's bones, which are often found in the stomachs of tiger sharks *Galeocerdo cuvier* (NSB, unpublished data).

The incidence of stomach eversion increased from <3% in small to medium *C. obscurus* to 14% in large *C. obscurus*, excluding pregnant females, and peaked at 31% in term pregnant females. It is not apparent why more large *C. obscurus* evert their stomachs upon capture than younger sharks, although the presence of a large volume of embryos (about 10×5kg) could increase the tendency for stomach eversion in pregnant females. Stomach eversion is not mentioned in the other feeding studies referred to above, suggesting that its incidence in small *C. obscurus* is generally very low.

Pregnant females showed a low incidence of stomachs with food (22.5%), as opposed to 47.6% for other large *C. obscurus* and 37–48% for small to medium *C. obscurus*. These females were almost all close to parturition, which would lend support to the hypothesis that feeding may be suppressed at this time to avoid predation on the shark's own young. Springer (1960) found that female sandbar sharks *Carcharhinus plumbeus* of the NWA population do not feed while in the principal nursery areas.

In summary, *C. obscurus* is a generalised predator, feeding throughout the water column on a variety of prey, mainly teleosts. The high incidence of cuttlefish and representatives of the teleost families, Sparidae and Haemulidae, indicates that this species often feeds close to the bottom on both rocky and sandy substrates. The differences in diet among the five size categories reflect, in part, the seasonal and geographical variations in the distribution of both predators and prey. Medium and large *C. obscurus*, other than pregnant females, take advantage of the large abundance of sardine in winter in the southern and central regions of the KZN coast. Other small shoaling teleosts found in KZN nearshore waters are eaten but in very low numbers. Pregnant females appear to shift their prey selection from teleosts to elasmobranchs.

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