

Abstract.—The spotted gully shark, *Triakis megalopterus*, was sampled opportunistically over a 12-year period from catches of shore and ski-boat fishermen using hooks and lines. Most specimens (89.6%) were taken from rocky reefs less than 10 m deep, 8% were caught at 11–20 m, and only 2.4% were recorded from waters more than 20 m deep. The reproductive biology of 35 males and 87 females was examined. The spotted gully shark exhibits aplacental viviparity. Size at 50% maturity for males is ca. 1320 mm total length (TL) and for females ca. 1450 mm TL. Maximum sizes recorded here were 1520 mm TL for males and 2075 mm TL for females. Gestation appears to last 19–21 months. The female reproductive cycle may be 2–3 years, depending on the time between pregnancies. The sex ratio of embryos was found to be 1:1 but the postpartum male:female ratio was 1:2.5. Size at birth was estimated to be 420–450 mm TL. The smallest free-swimming individual recorded was 576 mm TL. Number of embryos per pregnancy ranged between 5 and 15, with a mean of 9.7. A total of 110 stomachs were examined in the feeding study. Diet changed with increase in shark size. Small sharks (<1 m) preyed mainly on Cape rock crabs, *Plagusia chabrus* (78% of mass), whereas sharks of 1–1.4 m preyed largely on Cape rock crabs (48%) and cephalopods (33%). Teleosts were more important for sharks larger than 1.4 m (54%); most of these prey were associated with rocky reefs.

Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa

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The genus *Triakis* Müller and Henle, 1838, commonly called leopard shark, comprises small to moderately large, harmless, stocky sharks that feed on invertebrates and fish. *Triakis* is currently restricted to five species: *Triakis acutipinna* Kato, 1968 (sharpfin houndshark); *T. maculata* Kner and Steindachner, 1867 (spotted houndshark); *T. scyllium* Müller and Henle, 1839 (banded houndshark); *T. semifasciata* Girard, 1854 (leopard shark); and *T. megalopterus* (Smith, 1849) (sharptooth houndshark or spotted gully shark; Compagno, 1988).

Triakis megalopterus is a stout houndshark with a broadly rounded snout and a large mouth with small, pointed teeth. The head and body are gray or bronze above, usually with numerous small black spots, and white underneath (Bass et al., 1975). It is endemic to southern Africa (Compagno et al., 1989), where it occurs from northern Namibia, at about 21°45'S, 13°57'E, to Coffee Bay in Eastern Cape, South Africa, at 31°59'S, 29°09'E. The species is a common inshore bottom-dwelling shark of temperate continental waters, where it is caught by anglers in shallow subtidal waters. It prefers rocks and crevices in the shal-

lows and is confined to water shallower than 50 m along the Cape coast (Bass et al., 1975; Compagno et al., 1989, 1991).

Very little has been published on the biology of this species (Bass et al., 1975). Although all five species of *Triakis* are viviparous, they lack yolksac placentas and the embryos obtain nourishment from their yolksacs (Bass et al., 1975; Castro, 1983; Compagno, 1984; Kusher et al., 1992). Bass et al. (1975) and Compagno (1984) provided some information on the food habits of *T. megalopterus*, noting the presence of crabs (*Plagusia chabrus*), teleost fishes, and one small shark (*Scyliorhinus capensis*) in stomach contents.

At present, there is no scientific information that could guide management decisions on *T. megalopterus*, with the possibility of a small population size and limited range distribution (Compagno et al. 1989; Goosen, 1997), this species could be vulnerable to overexploitation in inshore multispecies shark fisheries. Off California, *T. semifasciata* has declined in abundance and consequently management measures have been proposed there (Smith and Abramson, 1990; Cailliet, 1992).

The aim of this study was to investigate the reproductive and feeding biology of *T. megalopterus*. Investigations of age and growth will be documented elsewhere. Improved knowledge of this species could underpin management strategies for this component of the multi-species shark fisheries off South Africa, which are known to be expanding (Smale, 1997).

Materials and methods

Specimens were collected over a 12-year period, between February 1984 and October 1996, from catches made with hooks and lines by rock, surf, and ski-boat fishermen. All specimens used in this study were collected along the Eastern Cape coastline between Cape St. Francis (34°12'S; 24°52'E) and Coffee Bay (31°59'S; 29°09'E), South Africa (Fig. 1). Specimens collected for biological sampling were examined as soon as possible after capture, or were frozen for later study. Sharks were measured to the nearest millimeter and, where possible, weighed with a spring scale accurate to 100 g. Measurements of total length (TL) can vary considerably depending on the placement of the caudal fin during measurement (Branstetter et al., 1987); in this study TL was measured on a horizontal line between perpendiculars, from the tip of the nose to the tip of the tail, with the tail at its maximum extension (Compagno, 1984). Total length is used throughout this paper, unless otherwise noted.

Reproductive information was collected for 35 males and 87 females. Maturity stages largely followed Bass et al. (1975), with minor modifications (Goosen, 1997). Each specimen was assigned to one of the reproductive stages: embryo, immature, adolescent, mature, and, in females, pregnant. The clasper was measured in length from the point of outside insertion in the pelvic fin to the tip of the clasper (CLO); from the point of insertion at the cloaca to the tip of the clasper (CLI); and in width at its thickest point (CBW) (Compagno, 1984). For females, the following data were collected: diameter of the two largest ovarian eggs, width of the oviducal gland, greatest width of the uterus, absence or presence of embryos and uterine eggs, and numbers of embryos and eggs if present.

Embryos were measured, sexed, and weighed. The mean length of embryos in each litter was calculated after abnormally developed individuals were excluded. Seasonality of mating, gestation period, and

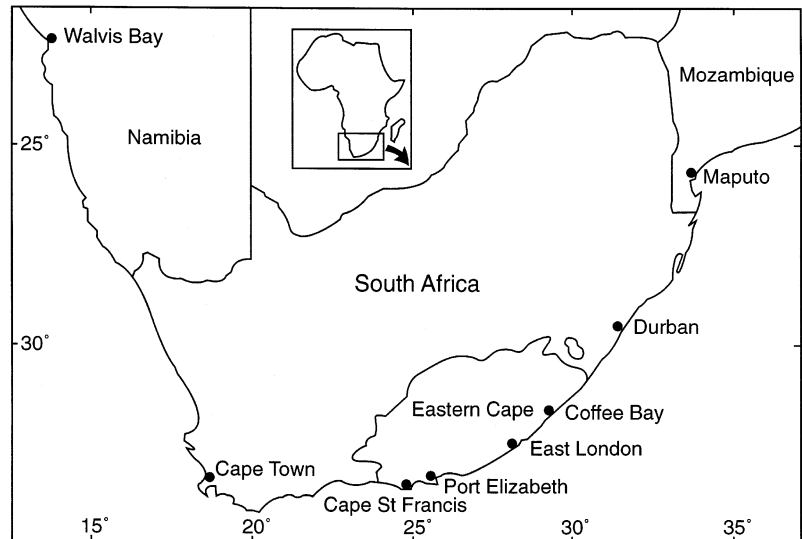


Figure 1

Southern Africa showing places mentioned in the text.

pupping season were examined by comparing embryo sizes in different months. Hepatosomatic indices (HSI) were calculated from the formula

$$HSI = (LW/BW) \times 100,$$

where *LW* = liver weight in grams; and
BW = total body weight in grams.

Stomach contents were examined as soon as possible after capture, or frozen for later analysis. Prey were identified to the lowest possible taxon. Excess liquid was drained off and the mass of the remains determined to the nearest 0.1 g on a top-loading pan balance. Bait used to capture the sharks was excluded from analyses.

Size measurements used for prey were carapace width (CW) in crabs, mantle length (ML) in cephalopods, and total length (TL) in teleosts and all other prey. After whole fish prey were measured, otoliths were removed to verify identification and paired, counted, and measured. Otoliths were used to identify well-digested prey and to estimate their length. Similarly, cephalopod beaks were collected, counted, and measured. Neither formalin nor alcohol was used to store stomach contents, because otoliths exposed to such preservatives become etched or brittle (Smale et al., 1995). Lengths of well-digested cephalopods and teleosts were determined from regressions relating beak and otolith lengths to body length (Smale, 1983; Smale et al., 1993, 1995). Digested otoliths had a chalky eroded appearance and were not measured for use in prey size estimates.

Diet was quantified by 1) frequency of occurrence (%F), the ratio of stomachs containing a particular prey to stomachs containing any prey, expressed as a percentage; 2) numerical importance (%N), the number of each prey expressed as a percentage of the total number of prey items; and 3) gravimetric importance (%M), the wet mass of a prey category as a percentage of the total weight of the stomach contents (Hyslop, 1980). By using all three methods of analysis, we avoided bias associated with the use of any one method (Hynes, 1950; Windell, 1968; Hyslop, 1980). No combination of methods was used because this may have resulted in combining sources of error (Berg, 1979). Reconstituted prey weights were not used because bias may have been introduced as a result of the different digestion and accumulation rates of fish otoliths and cephalopod beaks (Smale, 1983). Consequently, the actual wet mass of each item in stomachs was used to investigate prey composition in this study (Smale, 1991).

Preliminary analyses revealed considerable differences in prey between sharks of different sizes, and samples were subsequently divided into three arbitrary size classes: less than ≤ 999 mm, 1000–1399 mm, and ≥ 1400 mm TL. To investigate the relation between sizes of predator and prey, reconstructed prey lengths and masses were calculated with otolith and beak measurements. Recorded wet masses and carapace widths and lengths had to be used for crustaceans, and only intact crustaceans were included in the predator–prey size analysis. Common names used for crustaceans are after Holthuis (1991).

Results

Depth range

Material collected in this study was derived from fishermen exploiting a wide range of depths. Both shore-based and boat-based catches were sampled, although the proportion of effort in different depth ranges was not quantifiable. Nevertheless, *T. megalopterus* was taken mainly from shallow water. Of 125 specimens where collection depth was known, 89.6% were taken in shallow waters of 10 m and less. Only 8% were collected at 11–20 m and 2.4% at >20 m. The greatest capture depth recorded in this study was approximately 30 m, at an offshore bank. No obvious size-based habitat segregation was evident in this relatively small sample.

Size range and maturation

The overall male-to-female ratio in sharks sampled was 1:2.5. The smallest male and female sharks cap-

tured were 576 mm and 725 mm, respectively. Females attain larger sizes than males; the largest male sampled was 1520 mm, compared with the largest female of 2075 mm. The clasper length (CLI) of the smallest male was 43 mm and that of the largest (a male of 1402 mm TL) was 239 mm (Fig. 2A). Based on clasper size, degree of calcification, and presence of sperm in the seminal vesicle, maturation in these sharks begins at about 1210 mm and is complete at about 1369 mm (Fig. 2A). Claspers of one specimen of 1345 mm were not quite rigid but sperm presence was noted. The smallest mature male was 1250 mm and the largest immature male was 1196 mm. The claspers of adults measured, on average, 225 mm (range 205–239 mm, $n=16$).

Increase in the diameter of ovarian eggs indicates the beginning of maturation. Small eggs (<4 mm diameter) could be seen in the ovaries of females of 977 mm and larger. Egg diameter increased noticeably in specimens larger than 1460 mm (Fig. 2B). Mature females had yellow yolk-filled ova larger than 4 mm in diameter. The developing uteri appear as thin strips of translucent tissue with diameters of up to 2.5 mm in females smaller than 1365 mm. As maturation proceeds, the uterus widens first at its posterior end, becoming bottle-shaped at lengths of 1391–1405 mm, with a diameter of 4–16 mm at its widest part (Fig. 2C). One female of 1490 mm TL had a uterus width of 16 mm. All females over 1460 mm, except the previously mentioned individual, had uterus widths wider than 20 mm, and all adult females had uterus widths measuring 20–140 mm ($\bar{x}=82.81$, $n=27$). The oviducal gland was difficult to distinguish in the smallest females but usually measured between 3 and 7 mm ($\bar{x}=5.64$, $n=14$) in females of less than 1365 mm, and grows little until females reach 1460 mm (Fig. 2D). All females over 1460 mm had oviducal glands wider than 20 mm and all adult females, both pregnant and non-pregnant (resting), had oviducal glands measuring 20–51 mm ($\bar{x}=31.7$, $n=29$). The smallest pregnant female measured 1465 mm TL.

Reproduction

Of 48 sexually mature females sampled, 81% were pregnant. The number of embryos per litter ranged from 5 to 15 ($\bar{x}=9.7$, $n=38$). One female had 16 egg cases, but of these only 13 had normal embryos, one was empty, and two contained retarded embryos (length 6.5% of the next smallest embryo length). Considering the size of the female (1650 mm TL), it is possible that litters of up to 16 pups may be recorded. There is no significant difference in the number of embryos between left and the right uteri

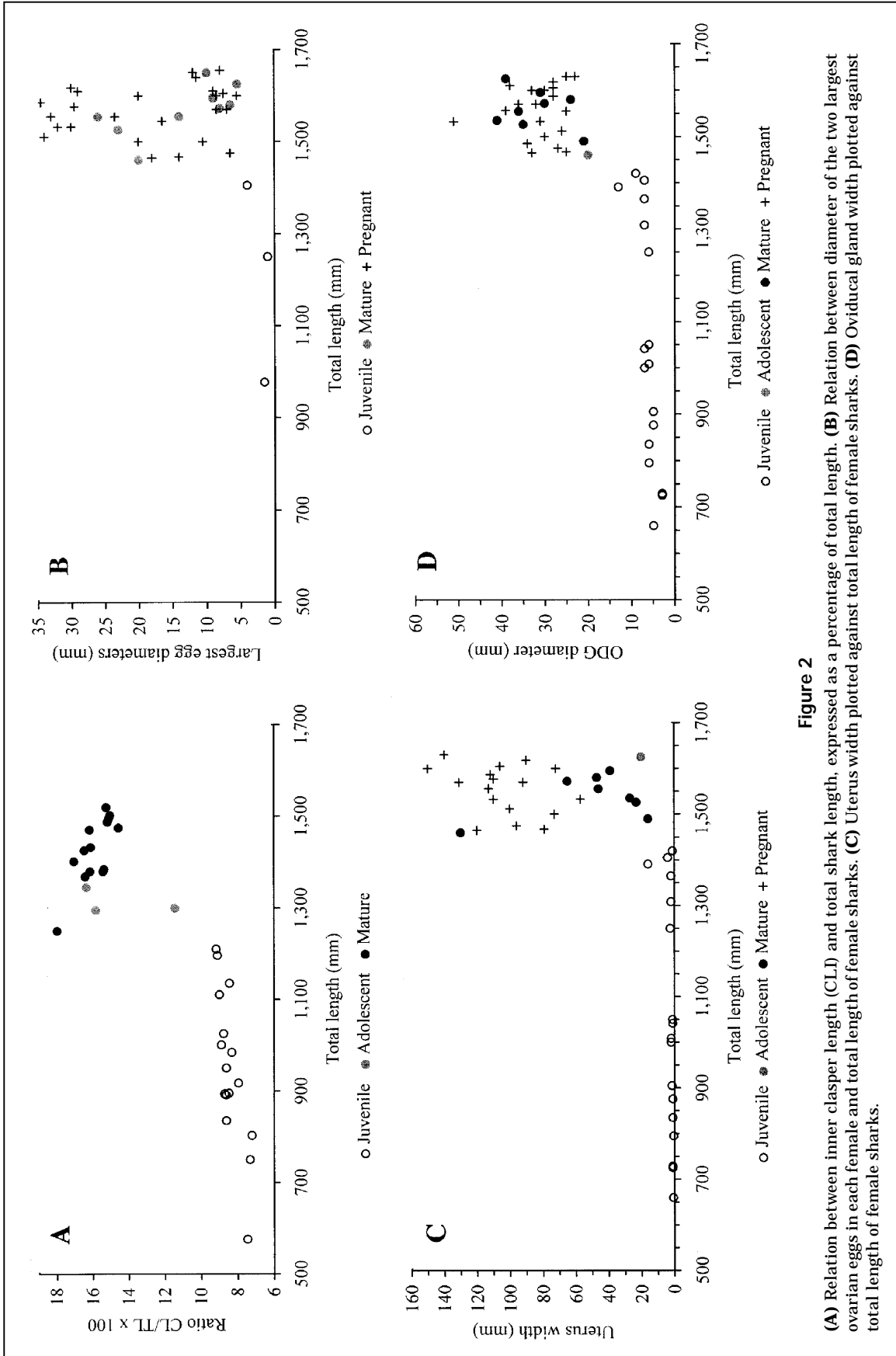
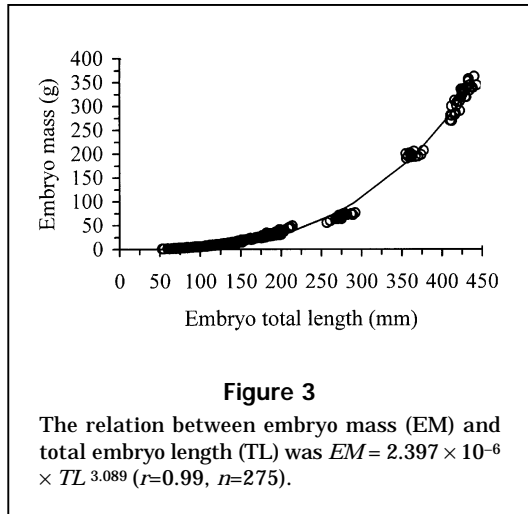


Figure 2

(A) Relation between inner clasper length (CLI) and total shark length, expressed as a percentage of total length. (B) Relation between diameter of the two largest ovarian eggs in each female and total length of female sharks. (C) Uterus width plotted against total length of female sharks. (D) Oviducal gland width plotted against total length of female sharks.



(paired t test; $P>0.5$). Of the 244 embryos that were sexed, 122 were male and 122 were female.

The relation between wet body mass and total length of embryos was described by a power curve (Fig. 3):

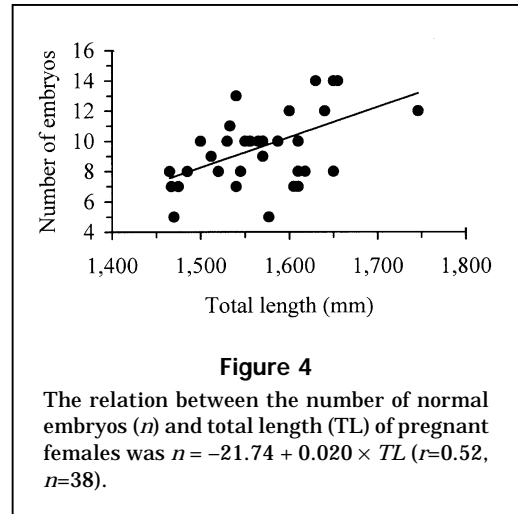
$$W = 2.397 \times 10^{-6} \times TL^{3.089}, \quad [r^2=0.994; n=275]$$

where W = embryo weight; and
 TL = embryo total length.

Weight of near-term embryos ranged from 300 to 362 g ($\bar{x}=331.4$ g; $n=23$).

During all stages of development, the embryos within a uterus often differed in size; the largest embryos were as much as 30% longer than the smallest. Greater differences were found in early stages of embryonic development. Larger embryos usually occupy a more posterior position, suggesting that they are older than litter mates in more anterior positions. The embryos in both uteri were at equivalent developmental stages in all the samples. Embryo orientation within the uteri was normally head forward. Only two embryos from one batch lay head backward. Description of the developmental morphology of embryos was given by Goosen (1997).

Average observed embryo length in females between 19 May and 25 August was 425 mm ($n=30$). A female caught on 19 May had an embryo length range of 416–443 mm ($\bar{x}=431$ mm; $n=15$), whereas another female, caught on 25 August, had embryos in the length range of 412–440 mm ($\bar{x}=425$ mm; $n=8$). Yolk sacs were barely visible in the smaller of these embryos, and the largest had closed umbilical scars between the pectoral fins. Denticles and teeth of larger ones had erupted from the skin; one or two black spots were noted on some embryos. Their large size



and eruption of teeth and denticles suggested that they had developed approximately to term. No embryo examined during this study showed any sign of a placental attachment between embryonic and maternal tissue. Embryos were readily removed from the uterus at all stages of development. Embryos are separated from each other in the uterus by enveloping uterine membranes, from which they apparently emerge shortly before birth. The largest embryo measured 443 mm and weighed 341 g. Based on available information, size at birth is estimated at 420–450 mm; birth probably occurs between May and August. The smallest free swimming individual, 576 mm in length, was taken in August.

Careful examination of embryos and uterine eggs showed that some of the uterine eggs failed to develop. Of 39 pregnant females, 11 (28%) had some nondeveloping uterine eggs. The greatest number of nondeveloping uterine eggs carried by a single female was 4 out of a total of 11, but most had only one or two. Of these pregnant females, 10 (26%) contained empty egg cases (no yolk). The largest number of empty egg cases carried by a single female was 12 (out of a total of 12). Occasionally, one embryo in a litter was deformed or retarded in growth. Because of the nondevelopment of a small proportion of uterine eggs, the number of developing, apparently normal embryos is a better measure of reproductive output than the number of uterine eggs. The relation between number of normal embryos and total length of the mother may be described by a linear regression (Fig. 4):

$$n = -21.74 + 0.02 TL, \quad [n = 38]$$

where n = litter size; and
 TL = the total length of the mother in mm.

Litter size was found to be significantly correlated with total length of the mother ($P < 0.01$, $r = 0.52$, $n = 38$).

The relation between shark length and liver mass was very variable but approximated a power relation (Fig. 5). The maximum recorded weight of females was about three times that of males; variation was higher in mature and pregnant individuals than in immature individuals.

To investigate the possible function of the liver as an energy source during pregnancy, female HSI was plotted against mean embryo TL (Fig. 6). Although the trend appeared negative, there was no significant correlation between mean embryo length and HSI ($r = 0.242$, $P > 0.05$; $n = 31$).

Plotting mean embryo size against month of the year resulted in a scatterplot with two clusters of

points but with no clear trend (Fig. 7). Extending the time axis to 24 months and shifting the larger embryos 12 months along the time axis yielded a clear trend. This finding would suggest that there is a gestation period of 19–21 mo and that the entire cycle spans approximately two years, excluding any resting period. Of a subsample of 11 mature females taken between May and August, four (36%) were resting (they showed no sign of recent pregnancy and had only small ova in the ovary) and the rest were pregnant, five (46%) with pups of intermediate size and two (18%) with large, near-term pups.

Feeding

A total of 110 stomachs were examined, consisting of 34 males (576–1520 mm TL) and 76 females (660–1746 mm TL). Females had a higher percentage of empty stomachs (20.5%) than males (12.1%). Preliminary analysis indicated a change in diet with predator size. This was investigated by grouping the data into three arbitrary size classes: smaller than ≥ 999 mm TL, 1000–1399 mm TL, and ≥ 1400 mm TL and longer. Prey taken clearly changes with increasing size (Fig. 8). Although invertebrates were important initially, larger sharks took more vertebrates (Table 1).

Small sharks fed almost entirely on crabs (Fig. 8). The Cape rock crab, *Plagusia chabrus*, dominated in the smaller two size classes of shark, in terms of mass (78.3% and 48.5%, respectively; Table 1). Larger crustacean taxa appeared in the diet of larger sharks. Cape slipper lobster, *Scyllarides elisabethae*, appeared in the second size class and Cape rock lobster, *Jasus lalandii*, and scalloped spiny lobster, *Pan-*

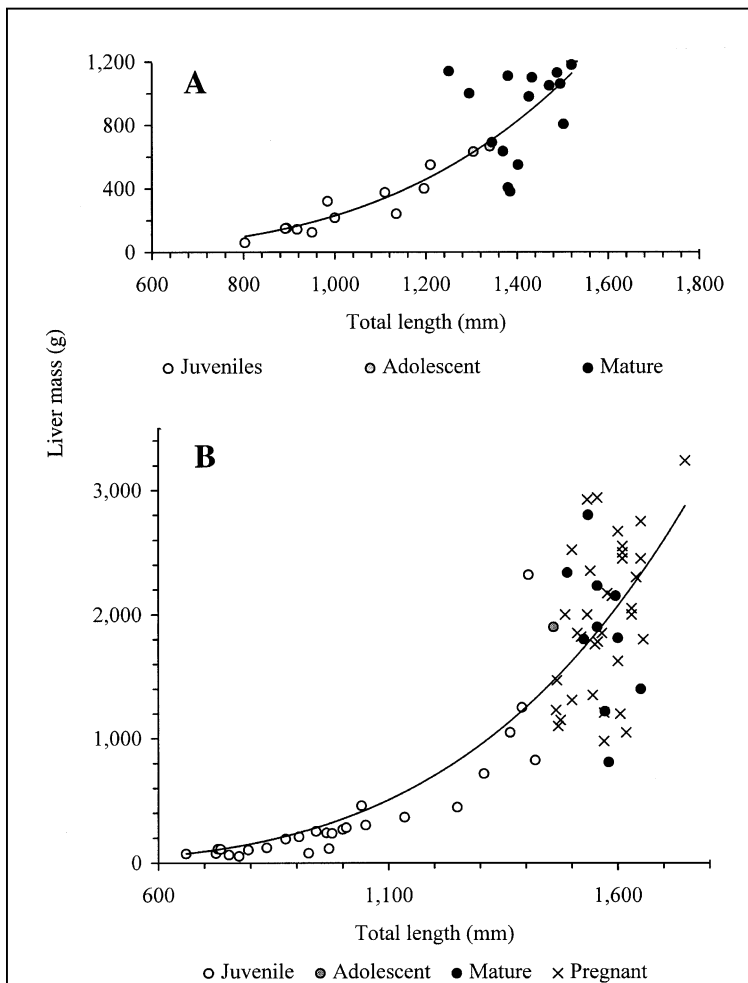


Figure 5

(A) The relation between liver mass (LM) and total length of male *T. megalopterus* was $LM = 9.517 \times 10^{-10} \times TL^{3.794}$ ($r = 0.83$, $n = 28$).
 (B) The relation between liver mass (LM) and total length of female *T. megalopterus* was $LM = 1.964 \times 10^{-9} \times TL^{3.752}$ ($r = 0.86$, $n = 73$).

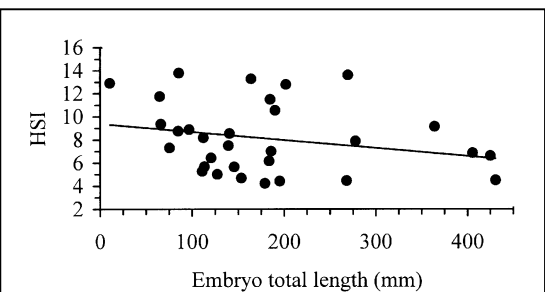


Figure 6

The relation between hepatosomatic index (HSI) of pregnant females and the mean length (TL) of normally formed embryos in the litter was $HSI = 9.376 - 0.0068 TL$ ($r = 0.242$, $n = 31$).

ulirus homarus, appeared in the largest size class. Although crustaceans were important prey of the large sharks, they were less dominant in the diet.

Teleosts became more important prey for larger sharks. They included representatives from at least 10 families and 14 species (Table 1). They dominated the prey of large sharks by mass (53.9%) and by number (47%), whereas they contributed only 10.3% and 14.2% by mass for the medium and small-size classes, respectively (Fig. 8). Only three species of fish were eaten by the smallest sharks, of which barred fingerfin, *Cheilodactylus pixi*, was the most important. Six species were taken by the medium-size class, and twotone fingerfin (*Chirodactylus brachydactylus*) was the most important. The diet of the large-size class was dominated by several species, viz. seacatfish (*Galeichthys* sp.), cob (*Argyrosomus inodorus*), red tjo-tjo (*Pagellus bellottii natalensis*), and blue hottentot (*Pachymetopon aeneum*). The two largest teleost species ingested, based on recalculated total length, were a 336-mm sand steenbras (*Lithognathus mormyrus*) and a 334-mm seacatfish (*Galeichthys* sp.). Both were taken by sharks longer than 1500 mm TL.

Cephalopods were the second most important forage category for medium-size sharks (Fig. 8). The common octopus (*Octopus vulgaris*) and the squid *Loligo vulgaris reynaudii* were the most important species, making up 25.5% and 7.8% by mass, respectively. Cephalopods were minor prey for the largest class of sharks (4.6% by mass).

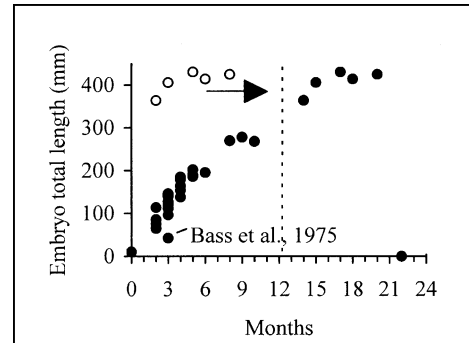


Figure 7

Mean size of normal embryos in each litter plotted against month of the year. The arrow indicates a shift of large litters (empty circles) to the same months one year later.

Elasmobranchs were relatively unimportant prey of spotted gully sharks. One stomach had the remains of a lesser sandshark (*Rhinobatos* sp.), another contained remains of a brown catshark (*Haploblepharus fuscus*), and two contained catshark eggs. The occurrence of anomalous food items was very rare. Inedible remains included a bryophyte (one stomach) and an unidentified mussel (one stomach).

In addition to ontogenetic variation in prey, prey size increased with growth (Fig. 9). Cape rock crab (*Plagusia chabrus*) was an important prey for sharks

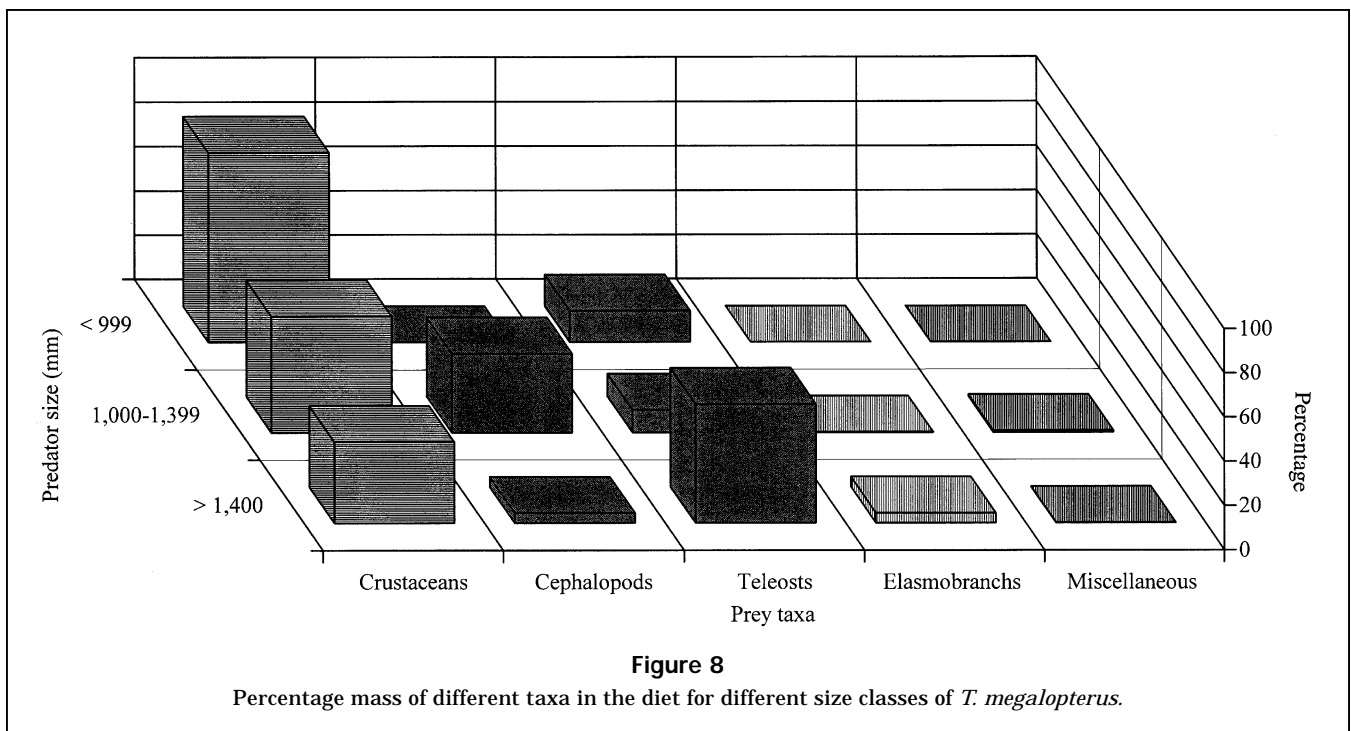


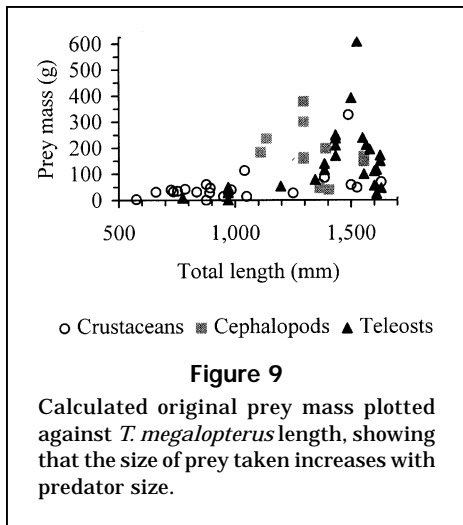
Figure 8

Percentage mass of different taxa in the diet for different size classes of *T. megalopterus*.

Table 1
Prey composition of three size groups of *T. megalopterus* from the Eastern Cape.

	< 999 mm TL			1,000–1,399 mm TL			> 1,400 mm TL		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
Crustaceans									
<i>Atergatis roseus</i>							2.38	1	1.63
<i>Ovalipes trimaculatus</i>	4	1.89	0.27	4	1.39	0.02	9.52	5	1.83
<i>Plagusia chabrus</i>	76	69.81	78.29	60	50	48.48	30.95	16	16.26
<i>Jasus lalandii</i>							2.38	1	6.65
<i>Panulirus homarus</i>							4.76	2	4.78
<i>Scyllarides elisabethae</i>				8	2.78	1.72	11.90	6	4.65
Caridea	8	3.77	0.06				2.38	1	0.11
Unidentified crab spp.	20	13.21	7.18	16	8.33	2.45	9.52	5	0.86
Molluscs									
Cephalopods									
<i>Loligo vulgaris reynaudii</i>				8	2.78	7.83	2.38	1	0.96
<i>Octopus vulgaris</i>				24	13.89	25.48	7.14	3	1.72
<i>Sepia</i> sp.							2.38	1	0.01
Gastropods									
<i>Haliotis midae</i>				4	1.39	2.51	2.38	1	1.90
Teleosts									
Ariidae									
<i>Galeichthys</i> sp.							11.90	6	13.10
Carangidae									
<i>Trachurus trachurus capensis</i>				4	1.39	2.32			
Cheilodactylidae									
<i>Cheilodactylus pixi</i>	8	5.66	13	4	1.39	0.07	2.38	1	0.45
<i>Chirodactylus brachydactylus</i>				4	1.39	3.98			
Gobiesocidae									
<i>Chorisochismus dentex</i>							2.38	1	1
Haemulidae									
<i>Pomadasyd olivaceum</i>	4	3.77	0.79						
Mugilidae									
<i>Liza richardsonii</i>							2.38	1	0.94
Platycephalidae							2.38	1	0.01
Pomatomidae									
<i>Pomatomus saltatrix</i>							7.14	2	0.70
Sciaenidae									
<i>Argyrosomus inodorus</i>				4	1.39	0.93	4.76	4	8.50
Sparidae							4.76	2	0.01
<i>Diplodus sargus capensis</i>	4	1.89	0.40	4	1.39	0.50	2.38	1	0.10
<i>Lithognathus mormyrus</i>							2.38	1	3.37
<i>Pachymetapon aeneum</i>							4.76	6	4.65
<i>Pagellus bellottii natalensis</i>				4	1.39	1.92	4.76	5	5.25
<i>Sarpa salpa</i>							2.38	2	2.76
Unidentified teleost remains				16	5.56	0.61	30.95	14	13.02
Elasmobranchs							2.38	1	0.18
Scyliorhinidae							2.38	1	0.16
<i>Haploblepharus fuscus</i>							2.38	1	0.94
<i>H. fuscus</i> (egg cases)				4	2.78	0.28	2.38	2	0.31
Rhinidae									
<i>Rhinobatos</i> sp.							2.38	1	2.65
Skate sp. (egg case)							2.38	1	0.31
Miscellaneous									
Bryophyte							4.76	2	0.02
Unidentified mussel				4	1.39	0.86			
Tapeworm				4	1.39	0.03			
Unidentified material							2.38	1	0.20
Total¹	25	53	1092.64	25	72	3,014.90	42	100	4,898.95

¹ Totals are numbers of stomachs with prey, number of prey items, and prey wet mass (g).



of a wide range of sizes, and there was a significant linear relation between crab carapace width and total length of sharks ($r=0.37$, $P<0.05$, $n=39$; Fig. 10A). Limited numbers of teleosts made analysis difficult. Combined data for two species (*Cheilodactylus pixi* and *Diplodus sargus*) showed a significant relation between the lengths of prey and sharks ($r=0.97$, $P<0.01$; $n=7$; Fig. 10B). The sample size of other prey species was too small to make similar analyses.

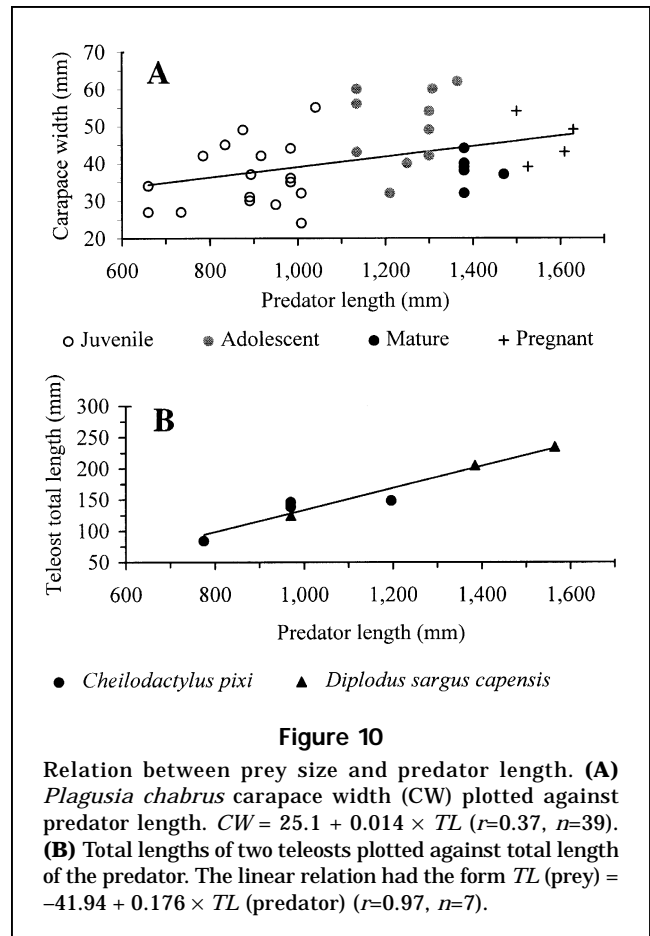
Discussion

Depth range

This study confirmed earlier reports that *T. megalopterus* prefers shallow rocky reefs (Bass et al., 1975; Compagno et al., 1989, 1991). They were found very rarely in deep waters, despite extensive sampling in deep waters for a variety of other sharks, including the closely related *Mustelus* species (Smale, 1991; Smale and Compagno, 1997). The nature of the samples precluded precise determination of intraspecific habitat choice, but there were no obvious differences in habitat choice by sharks of different sizes. The skewed sex ratio, which needs further investigation, may be due to sampling bias or social factors.

Reproduction

In *T. megalopterus*, eggs produced by the single functional ovary pass through the oviducal gland, where they are probably fertilized before they are enclosed in the membranous egg case. Embryonic development is ovoviviparous, embryos receiving nourishment from the yolk sac. However, some egg cases were slightly adherent and others intimately connected



to the uterus wall. There was no evidence of the yolk sac forming a placental attachment at later stages of development, supporting Compagno's (1984) summary of the genus.

The size at which 50% of male sharks are mature is equivalent to mean size at maturity (Lenanton et al., 1990). Data from the present study indicated that males mature at approximately 1320 mm. Compagno (1984) estimated that males mature at 1300–1400 mm. On the basis of width of the oviducal gland and the diameter of the uterus and eggs, females begin to mature at about 1391 mm, and 50% maturity is achieved at about 1450 mm; all females larger than 1500 mm are mature. Compagno (1984) estimated that females mature between 1400 and 1500 mm and reported mature females of 1400–1740 mm. In this study, 50% maturity of female sharks is attained at about 1450 mm, which represents 70% of the maximum size observed, 2075 mm. This size falls within the range of 60%–90% noted by Holden and Raitt (1974). The smallest pregnant female measured 1465 mm.

Gestation in sharks is usually 10–12 mo and prolonged gestation periods are apparently rare, although *Squalus acanthias* has a gestation period of

22–24 mo (Wourms, 1977; Nammack et al., 1985; Hanchet, 1988; Wourms and Demski, 1993; Wourms, 1994). The gestation of frilled sharks, *Chlamydoselachus anguineus*, may be as long as three and a half years (Tanaka et al., 1990). The proposed gestation of about 20 mo in *T. megalopterus* is longer than the estimated 12 mo in *Triakis semifasciata* (Castro, 1983; Talent, 1985; Smith and Abramson, 1990). If the 20-mo estimate is correct, any females that mate shortly after parturition would have a resting period of two to three months. Some mature but nonpregnant females, however, show no sign of ovarian egg growth and development at the same time that others have large ovarian eggs or uterine eggs (or both) and small fetuses. These resting females represented 36% of the sample of 11 mature females taken between May and August. These females probably skip a year and have an extended reproductive break of at least 12–15 mo, which would prolong the cycle to at least 3 years for some individuals. On the other hand, some pregnant females about to undergo parturition have large ovarian eggs, and these individuals may mate within a few months and apparently forego the extended resting period.

On the basis of embryo growth rates presented above, mating and fertilization probably occur from about October to early December. Females carry term embryos of 422–440 mm (largest embryos) between the last week of May and the last week of August, which would approximate the time of parturition. Compagno's (1984) estimate of size at birth was much smaller (300–320 mm) than that of our findings. From observations of embryonic development, it was noted that during the late stages of embryo development (from ca. 400 mm), both external and internal yolks were absent. The small amount of yellow substance in the spiral valve was thought not to be an internal yolk reserve, but the area of absorption. It was also noted that each embryo was contained in a soft egg case with ca. 500 mL of fluid (Goosen, 1997). Wourms and Demski (1993) noted that in *Squalus acanthias*, several months into the 22-mo gestation period, embryos can ionoregulate and osmoregulate in a uterine solution resembling seawater. This might be the case for *T. megalopterus* and could contribute to near-term embryo nourishment until parturition occurs.

The liver mass of a shark is a good index of the shark's condition (Springer, 1960). In our study it was found to fluctuate widely, particularly after maturation. Seasonal variation in HSI of the lesser sandshark (*Rhinobatos annulatus*) has been attributed to fluctuations in lipid content of the liver, which has been correlated with reproductive condition in females (Rossouw, 1987). Similar changes in HSI have been recorded in pregnant females of three

Mustelus species (King, 1984; Smale and Compagno, 1997). Although low HSI values were found in pregnant females with near-term embryos in this study, the relation was not statistically significant, possibly suggesting that HSI fluctuates with other physiological factors. These observations were based on a small sample size and need further investigation.

Feeding

This study showed that *T. megalopterus* changes diet with growth, which suggests that it selects prey of suitable size. Because there is no evidence to date of marked habitat change with growth, and all sizes of shark do not have the same prey, it is unlikely that they are feeding opportunistically, even if they favor abundant species. Opportunistic feeding *sensu* Wetherbee et al. (1990) implies that stomach contents are varied but of composition and abundance similar to those of prey in the environment. Smale (1996) noted that the term "opportunistic" should be used with caution because it is difficult to distinguish between abundance and availability. Ontogenetic variation in feeding of *T. megalopterus* appears to be attributable to broadening the diet to include more energetically rewarding species (e.g. teleosts), although benthic prey are still taken.

Spotted gully sharks fed primarily on the crab *Plagusia chabrus*; as sharks grew, larger individuals were taken. This finding conforms with those where large crabs were taken by larger leopard sharks (*T. semifasciata*; Talent 1976). Although spotted gully sharks are most abundant near reefs, they may also hunt over sandy areas to exploit the crab *Ovalipes trimaculatus*, which prefers sandy substrates. Spotted gully sharks preyed largely on nocturnally active lobsters (Paterson, 1969; Smale, 1978; Zoutendyk, 1988) and crabs (Brown, 1961; Warner, 1977), suggesting that they are nocturnal hunters that take crustaceans as they emerge. Such activity may explain why anglers catch them more frequently at night.

As the sharks increase in size, they use a much wider variety of prey groups, including teleosts. Therefore, with growth the spotted gully shark is able to attack and ingest larger prey species. Nocturnally hunting sharks may be able to take some teleosts when they are less active or resting at night. Elasmobranchs became increasingly important prey with growth, a finding that supports previous observations of congeners taking elasmobranchs (Bass et al., 1975; Russo, 1975; Talent, 1976; Compagno, 1984).

Octopus vulgaris was the most common cephalopod prey. It inhabits reefs (Smale and Buchan, 1981; Roper et al., 1984) and emerges from its den to hunt

between dusk and dawn (Smale and Buchan, 1981), making it vulnerable to nocturnal predators. Squid (*Loligo vulgaris reynaudii*) is common throughout the Agulhas Bank (the continental shelf between Cape Town and Port Elizabeth) but become concentrated inshore in spring and early summer, when it spawns (Sauer and Smale, 1991; Augustyn et al., 1992). Egg laying is concentrated on the bottom during the day in waters 10–50 m deep (Augustyn, 1990; Sauer et al., 1997). Squid are thought to be especially vulnerable to predation during mating and spawning (Smale, 1991; 1996). Sauer and Smale (1991) recorded *T. megalopterus* as one of the squid predators in the vicinity of spawning aggregations, which illustrates its ability to exploit a superabundant prey resource by day, even though it normally appears to hunt at night.

In conclusion, it is evident that the habitat preferences of gully sharks make them vulnerable to exploitation by inshore fishermen. Their life history traits—large size at maturity, prolonged gestation period, and relatively small litter size—suggest that this species is unsuitable for sustained harvesting by either recreational or commercial fishing.

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