LIFE HISTORY AND DIET OF TWO SOUTHERN AFRICAN SMOOTHHOUND SHARKS, *MUSTELUS MUSTELUS* (LINNAEUS, 1758) AND *MUSTELUS PALUMBES* SMITH, 1957 (PISCES: TRIAKIDAE)

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Aspects of the life history and biology of two sympatric coastal shark species (*Mustelus mustelus* and *M. palumbes*) off southern Africa are described and compared. Free-swimming male *M. mustelus* measured 390–1 450 mm total length (*TL*), whereas females were recorded up to 1 650 mm *TL*. Most specimens of both sexes were found at depths shallower than 100 m. Males mature at 950–1 300 mm *TL* and females at 1 250–1 400 mm *TL*. Reproduction is seasonal, and each cycle may take one year or longer, if there is a resting period between pregnancies. Litter size was correlated with female size and varied between 2 and 23. The largest embryo measured 425 mm *TL*. The hepatosomatic indices were negatively correlated to embryo length in both species. Prey was dominated by crustaceans, although cephalopods became important in larger *M. mustelus*. There was a good relationship between prey size and fish size. Free swimming male *M. palumbes* measured 275–1 008 mm *TL*, whereas females were recorded up to 1 126 mm *TL*. *M. palumbes* males were most often taken from 100–180 m deep and females from 60–140 m. Males mature at 750–850 mm *TL* and females at 800–100 mm *TL*. Reproduction appears to be aseasonal in *M. palumbes* and litters of 3–15 young were recorded, with larger females having larger litters. The largest embryo recorded measured 340 mm *TL*. The timing of reproductive cycles could not be established, but a high proportion of non-pregnant females suggests that there may be a resting period following pregnancy. Crustaceans were the dominant prey type recorded, although larger predators ate a wider variety of prey types than smaller individuals. Although there was overlap in the prey taken by the two shark species, the composition of the diet was strongly influenced by the prey available in different habitats.

The genus *Mustelus* Linck, 1790 (Family Triakidae, Order Carcharhiniformes) is a wide-ranging group of at least 20 species of demersal sharks found on the shelves and uppermost slopes of temperate and tropical continental seas. The distribution and biology of these sharks, termed smoothhounds or gummy sharks, is summarized in Compagno (1984). Compagno (1988) details anatomical characters of the family and provides distinguishing features of the genera. Three species of smoothhounds are found off southern Africa, according to Heemstra (1973, pers. comm.), Compagno (1984), Bass *et al.* (1986), and Compagno *et al.* (1989). The hardnose smoothhound *Mustelus mosis* Hemprich and Ehrenberg, 1899 is a Western Indian Ocean species, which is found as far south as KwaZulu-Natal. The other two species overlap in distribution more with each other than either does with *M. mosis*, but all three co-occur in the waters of KwaZulu-Natal. The smoothhound *M. mustelus* (Linnaeus 1758) is found in the eastern Atlantic and south-west Indian Ocean. The whitespotted smoothhound *M. palumbes* Smith 1957 is endemic to southern Africa and is found from Namibia to northern KwaZulu-Natal. Until Heemstra's (1973) world revision of the genus *Mustelus,* the three southern African smoothhounds were readily confused with one another, and with *Triakis mega-lopterus* (Smith, 1849), because of their close morphological similarity. Bass *et al.* (1975) omitted work on *Mustelus* from their comprehensive survey of the sharks of the east coast of southern Africa because of the confused taxonomic situation in the genus at that time.

Smoothhounds are active, strong-swimming epibenthic sharks that feed mostly on invertebrates. Crustaceans are their most important prey, although a variety of other invertebrates and a number of species of small teleost fish are also taken. Smoothhounds also scavenge on fisheries offal. They are fairly slender with flattened ventral surfaces on the head and body as an apparent adaptation to benthic feeding. They have small teeth in multiserial rows, with low cusps or rounded crowns in most species (Compagno 1984, 1988).

Smoothhounds are often abundant in enclosed bays with soft bottoms, where they may have a major impact on the invertebrates and small, bottom fish. They can be important for artisanal and commercial fisheries, owing to their abundance, moderate size, and ease of capture by gear that can be used on small fishing vessels or from the shore (Smale 1996a). Not only can the sharks be readily handled without hazard to their captors, but the teeth of smoothhounds have a

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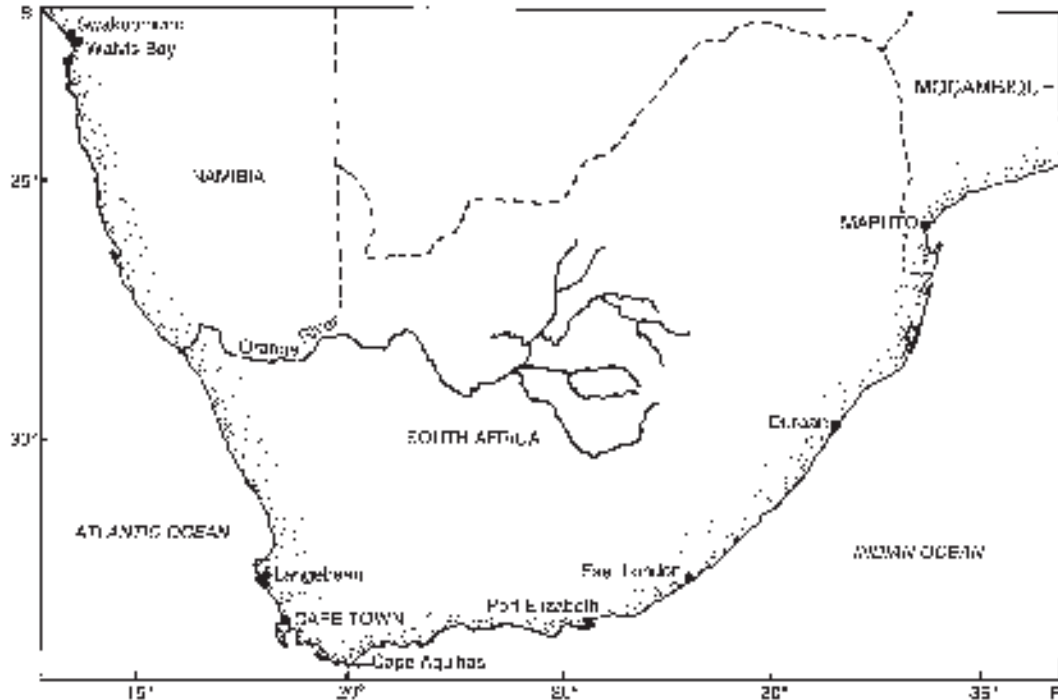
Fig. 1: Map of southern Africa showing places mentioned in the text

minimal impact on fishing gear, which allows them to be readily caught with light, monofilament gillnets or longlines.

Off southern Africa, smoothhounds are commonly caught by commercial trawlers, linefishing boats and shore-based anglers. They have generally not been used for human consumption, despite the fact that they are highly esteemed food fish elsewhere and are subject to commercial fisheries. This attitude has changed since the late 1980s and they are now targeted in the Western Cape, particularly when prime teleost targets are absent. Areas of intensive fishing include Struis Bay, Saldanha Bay and St Helena Bay. The flesh is dried and utilized locally or exported to Australia, Europe and Africa, and the fins of larger specimens are exported to the oriental market (Smale 1996a). Commercial trawlers generally discard most cartilaginous fish in favour of more commercially valuable bony fish, except for some landings of skates (family Rajidae) and St Joseph *Callorhinchus capensis*, (family Callorhinchidae). However, smooth-hounds and other chondrichthyans that are caught in commercial trawls are generally dead when boated and so are subjected to fisheries pressure from the large southern African trawl fleet, even though they may not be utilized. Cartilaginous fish are commonly

returned alive to sea at many amateur angling com-petitions, particularly those featuring tag-and-release contests, although this practice was only started in the Cape in about 1986. Problems remaining to be resolved include accurate identification of the family Triakidae by anglers, and the unknown survival rate of captured and released chondrichthyans. Light-tackle boat competition anglers have often caught large quantities of smoothhounds. Since the 1990s such anglers have usually released their catch unless an exceptionally large fish is hooked.

This paper concentrates on the life history of *M. mustelus* and *M. palumbes* in waters of the Eastern and Western Cape. It represents the first detailed study on *M. palumbes* and the first on *M. mustelus* in the southern hemisphere. The geographic and bathy-metric distribution of these species on the Cape west coast are detailed in Compagno *et al.* (1991).

MATERIAL AND METHODS

Material was collected from four sources. These included amateur shore-based fishing competitions between East London and Langabaan Lagoon (Fig. 1),
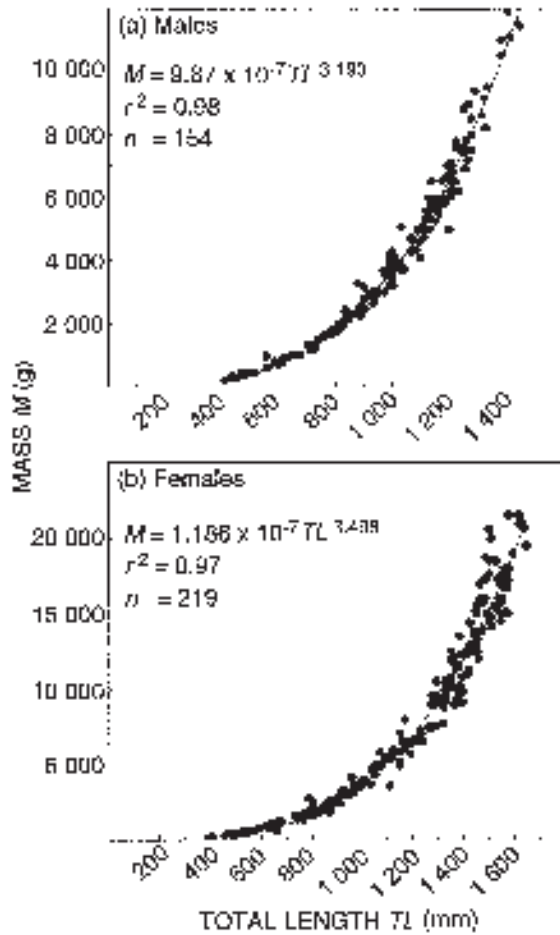
Fig. 2: Relationship between total length and mass for (a) male and b) female *M. mustelus*

line-boats and commercial trawlers on the Agulhas Bank between December 1984 and January 1990, and research cruises onboard F. R. S. *Africana* during demersal trawling surveys of commercial fish stocks off the Eastern and Western Cape. The research cruises provided large numbers of specimens with precise information on depth and locality, which was not available from the other sources. The trawling methodology for these cruises is given in Payne *et al.* (1984) and Badenhorst and Smale (1991).

On capture, the sampling locality and fishing depth were noted and all specimens were measured. The total length (Compagno 1984 – i.e. with the tail extended in a straight line to provide maximum length, rather than "natural position" length), precaudal length, mass and sex of the animals were recorded.

The animals were staged into three groupings of either immature, adolescent or mature, using the criteria of Bass *et al.* (1975). Other observations on the animals' condition, including pregnancy, were made. Total length (*TL*) is used throughout this paper, unless specifically noted otherwise. Claspers were measured on males and the nidamental glands and uteri of females were also examined. The development of these organs in the females and the degree of coiling of the seminiferous tubules and the presence of sperm in the seminal vesicle of males provided additional information on the degree of sexual development.

Livers of all individuals were weighed, as well as the gonads of sexually mature individuals. The uterus width and oviducal gland and largest ovarian eggs were measured. Uterine eggs, embryos and empty egg cases were removed and counted, and the embryos were sexed when large enough. Embryos and their yolk sacs were measured and weighed, and subsamples of these were preserved.

The stomach contents were removed, sorted and identified to the lowest possible taxon. Watery fluid was allowed to drain from the contents for about two minutes before weighing. Carapace widths of crabs and the total length of bony fish and stomatopods were recorded whenever possible. Teleost fish remains were identified from otoliths (Smale *et al.* 1995), and cephalopods were usually identified using their mandibles or "beaks" (Clarke 1986) and compared with the collections held in the Port Elizabeth Museum. Recalculated lengths for fish and cephalopods were obtained using the otolith length/total length (fish) and beak length/mantle length (cephalopod) regressions from Smale (1983) and from unpublished data (Port Elizabeth Museum). The wet mass of prey remains (as opposed to back-calculated estimates) are reported in the diet analyses in this paper.

RESULTS

Mustelus mustelus

SIZE RANGE

The 937 free-swimming individuals sampled ranged from 390 to 1 650 mm *TL*. Males (*n* = 430) were 391–1 450 mm (206–11 900 g) and females (*n* = 507) 390–1 650 mm (192–21 500 g).

MORPHOMETRICS

Females attained a larger length and mass than males (Fig. 2). Because the slopes of the lines of the relationship between total length and precaudal length
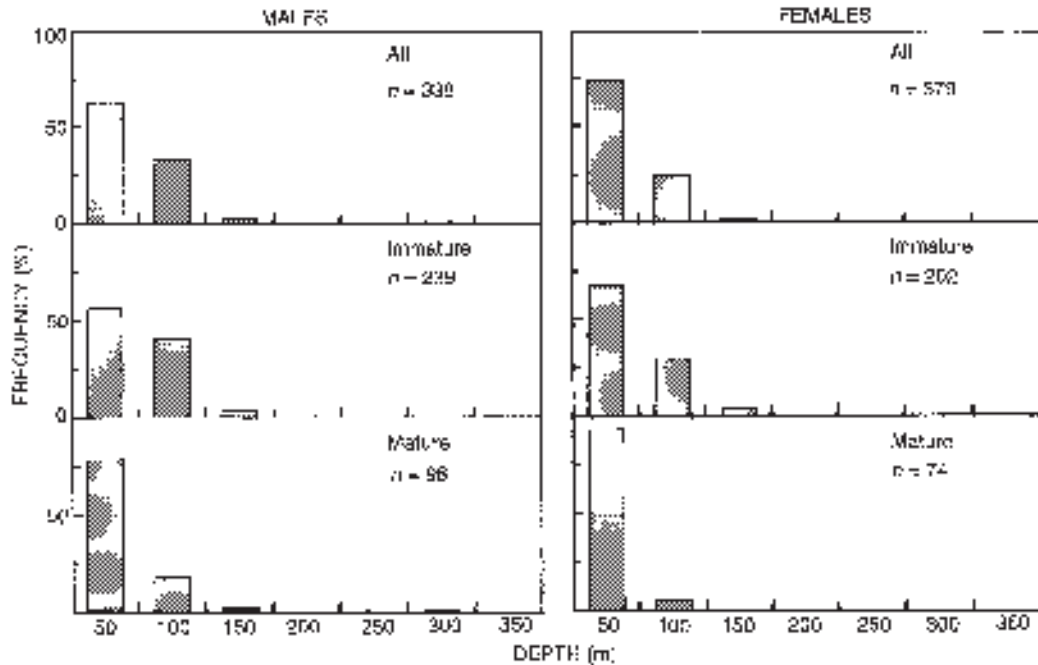
Fig. 3: Depth distribution of different maturity stages of *M. mustelus* sampled in this study, where depth was known

(*PCL*) were not significantly different between sexes (ANCOVA *, p* = 0.777, *df* = 263), the following relationship is given for both genders:

$$PCL = 0.821\ TL - 21.472\ (r^2 = 0.99, n = 265).$$

DISTRIBUTION

The data presented here reveal that *M. mustelus* is a shallow-water, coastal species. Most specimens of both sexes were caught in water shallower than 100 m, although they were occasionally taken from water as deep as 280 m. By comparison with males, a greater proportion of females was taken in water <50 m deep, and this was especially marked in mature individuals. Mature and pregnant females in particular were caught more frequently in shallow water (Fig. 3), although there was a considerable overlap in the depth of capture of all stages. Males and immature females were frequently taken deeper and often together in the same net. Because a variety of capture methods was used to collect *M. mustelus,* it is not possible to quantify the sampling effort in the different areas and depth zones. Trawl records suggest that the species is commonly found over sand or shale plains, although they may also be caught by hook and line near rocky reefs.

SIZE AT MATURITY

The size at maturity of *M. mustelus* varied with gender, being 950–1 300 mm in males and 1 250–1 400 mm in females (Fig. 4). Males and females were all mature by 1 350 and 1450 mm respectively. The smallest pregnant female measured was 1 263 mm.

Concomitant with maturity, clasper length increased rapidly in males of 950–1 050 mm *TL.* Calcification usually occurred from a length of about 1 000 mm (Fig. 5a). In immature males, the vas deferens was nearly straight, but it started to coil at adolescence. Where the male was mature, the duct was tightly coiled and at least some sperm was found in the seminal vesicle throughout the year.

Maturation of females was characterized by a gradual enlargement of the nidamental gland and a widening and thickening of the uterus. During adolescence, uterine widening was initiated at the posterior end, and expansion progressed anteriorly with maturity. During its expansion phase, the expanded uterus was at least two or three times the width of the unwidened section. Expansion of the oviducal gland and uterus began from a length of about 1 200 mm and continued to 1400 mm, although the uterus also
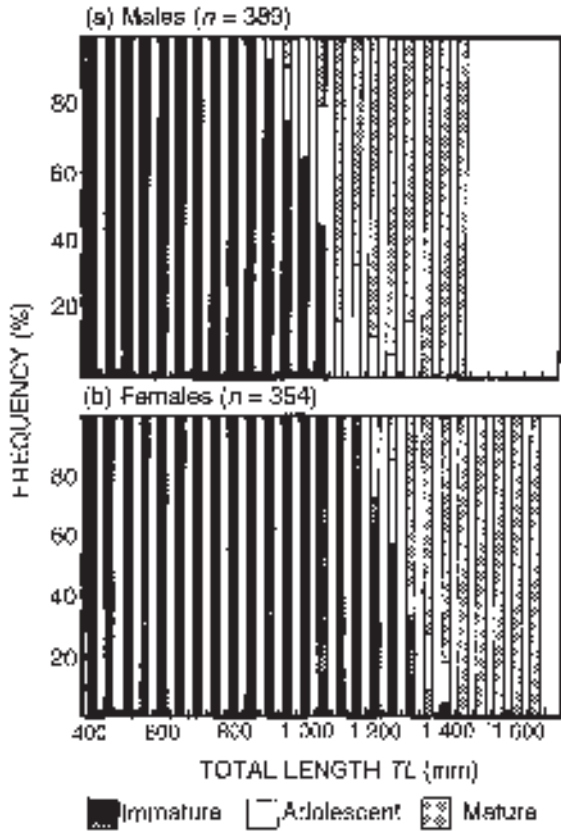
Fig 4: Percentage of immature, adolescent and mature (a) male and (b) female *M. mustelus* in 50-mm length-classes

Fig. 5: Relationship between (a) clasper length and total length of *M. mustelus,* expressed as a percentage of total length, and (b) uterus width, oviducal gland length and width, and total length of *M. mustelus,* including pregnant females

expanded considerably with reproductive activity (Fig. 5b). With maturity, ovarian eggs also increased in size and became more yolky and yellow in colour after they had attained a diameter of about 5 mm.

REPRODUCTION

From the gonadosomatic indices (Fig. 6a), it would appear that testes were largest in the first half of the year, whereas ovaries were largest in the second half of the year (Fig. 6b). Largest eggs were recorded in the first quarter and smallest eggs were found in midyear. Egg diameters increased from about July through to March. Mating was at the beginning of the year before eggs were passed into the uterus, giving rise to the low ovary masses. Examination of the ovaries revealed that the few remaining, large yolked eggs appeared to be resorbed in the ovary after ovulation
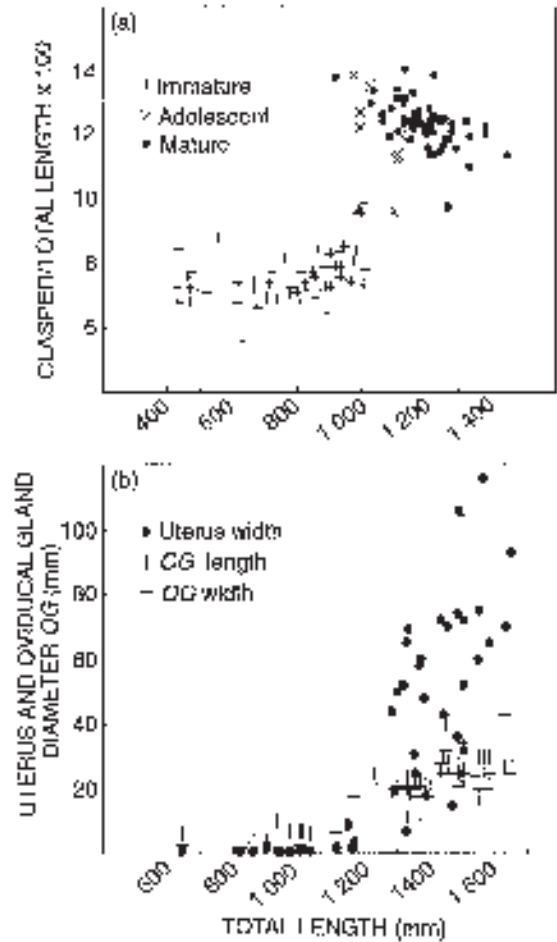
had taken place. This varied over several months, but the cycle appeared to be broadly seasonal (Fig. 6c). Adult female *M. mustelus* showed a seasonal variation in the proportion of pregnant individuals (Fig. 6d). No evidence of mating scars was observed, which is not unexpected, given the crushing dentition of the species.

Seasonality in the reproduction of *M. mustelus* was also apparent from the embryo length (Fig. 7a). Fertilized eggs with little or no embryo growth were found in the uteri between October and January, and embryo growth continued through winter, with term-
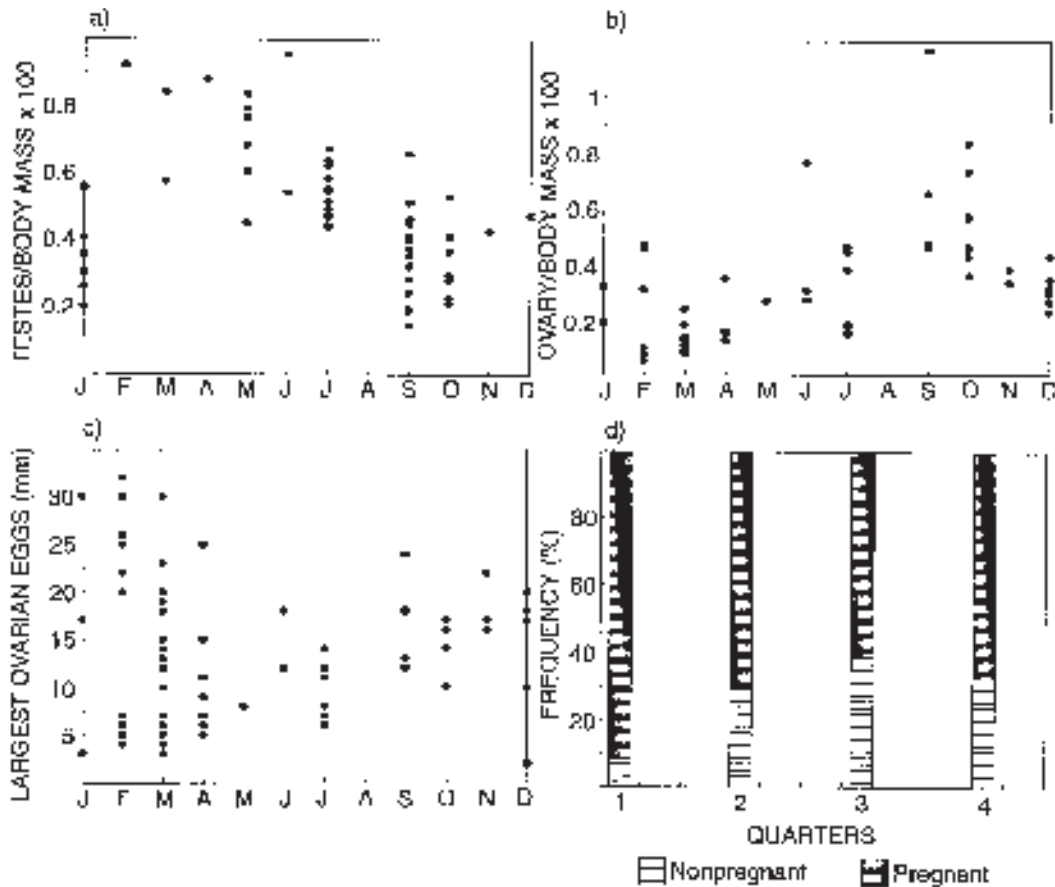
Fig. 6: Monthly gonadosomatic indices for (a) male and (b) female *M. mustelus*. Monthly measurements of the largest eggs in (c) the ovary and (d) the frequency of pregnant and non-pregnant mature females on a quarterly basis

young being recorded from about September, but mainly in October and November. This suggests that the gestation period is about 9–11 months. The largest embryos recorded were 425 and 422 mm for males and females respectively. The presence of a resting period after pregnancy is unclear, but non-pregnant mature females may consist of as much as 40% of quarterly samples (Fig. 6d), which suggests that there may be a resting period at least in some females. The ovarian eggs of females with term-embryos varied between about 12 and 17 mm. Therefore, it is considered that the reproductive cycle may take approximately one year in those females which do not have a resting year, but may be up to two years in some females.

The average litter size was 11.54 ($SD = 5.091$, $n = 93$), but it varied between 2 and 23. Although there was a significant trend for larger females to have larger litters ($p < 0.001$, $df = 93$, Fig. 7b), there may be a maximum litter size. However, this does not appear to be related to either the number of empty egg cases or to the number of unfertilized eggs and runts in the uteri, because these do not increase with increasing female size (Fig 7b).

EMBRYONIC DEVELOPMENT

After ovulation and the passage of the ova through the nidamental gland (presumably the site of fertilization), each egg was covered by a soft, flimsy egg case. In some females, intact egg cases were found without the egg. These egg cases had the same shape as normal egg cases and contained a small amount of clear fluid. In one individual, 10 empty egg cases
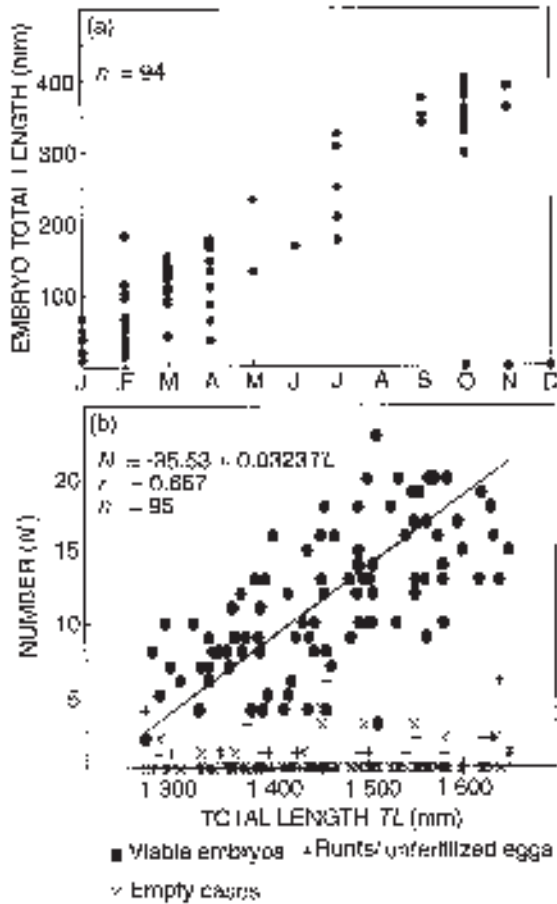
Fig. 7: Relationships between (a) mean embryo length (excluding runts and abnormal individuals) of litters of *M. mustelus* and month and (b) the number of viable embryos, runts and empty egg cases and female total length of *M. mustelus*

Fig. 8: Relationships between liver mass and total length for (a) male and (b) female *M. mustelus*

were found in the left uterus and 10 embryos (two of which were runts) and one empty egg case were found in the right uterus.

As the embryo developed, the egg case became closely associated and apparently interdigitated with the wall of the uterus. This condition was noted in one individual with embryos 121–145 m long. As the embryo developed further and used up its yolk supply (at about 130–170 mm), the yolk sac became closely associated, interdigitated and adherent to the wall of the egg case and the highly vascularized uterus. This was recorded in embryos 200–252 mm long.

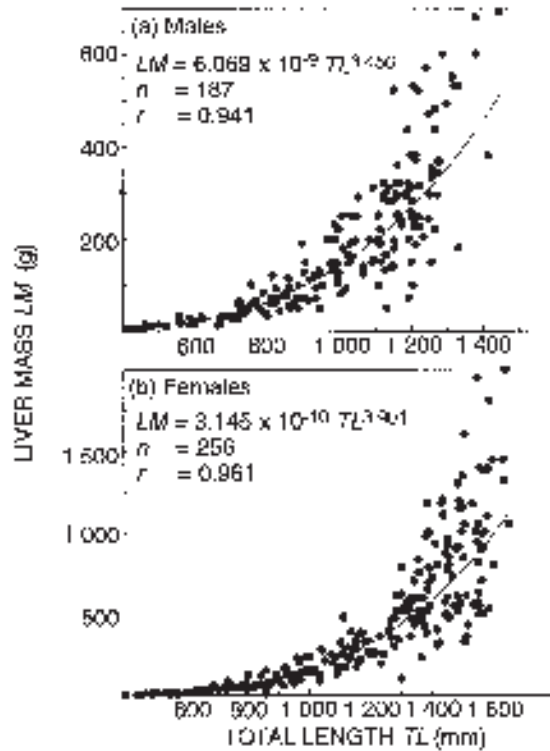The embryos generally lay with their heads pointing anteriorly. When the embryos were well developed, the "umbilical cord" was sometimes found twisted around the embryos, possibly as a result of embryonic contortions when the mother died and uterine dissolved oxygen levels declined.

By the time the embryos were about 200 mm long, the yolk sac placenta was strongly adherent to the wall of the uterus, although the embryos were still in their egg cases. The fins were bent over and lay against the embryo's body. Individuals apparently remained in the egg cases until birth, because term-embryos 368–410 mm long were found still encased in the membranous case in one female examined.

There was a notable variation in the size of individuals within a litter. Those lying anteriorly in the uterus could be 20% shorter and 47% lighter than the largest individuals found at the posterior end of the uterus. This difference probably reflects the sequence of ovulation and growth of the embryos, but other factors such as food supply and vascularization of the uterus could also play a role.

Embryos developed a colour pattern from about 100 mm long, when the tips of the dorsal fins became edged in black. The bodies of such embryos were sandy brown and the irises were olive to sandy brown.

Table I: Stomach contents per length-class of *M. mustelus* from the Cape south coast, expressed as percentage frequency of occurrence (%*F*), number (%*N*) and mass (%*M*). Totals are the number of predators, number of prey and total prey mass (g)

Prey	Value per fish length-class											
	< 600 mm			600–799 mm			800–1200 mm			> 1200 mm		
	%*F*	%*N*	%*M*	%*F*	%*N*	%*M*	%*F*	%*N*	%*M*	%*F*	%*N*	%*M*
Rhodophyta										0.85	0.43	0.02
Polychaeta	20.41	11.18	2.42	5.77	1.69	0.19	2.22	0.61	0.23	0.85	0.22	0.08
Echinodermata												
Ophiothrix sp.				1.92	3.93	0.13						
Crustacea	28.57	12.50	10.02	7.69	3.37	1.44	2.96	1.43	0.33	5.13	1.30	0.63
Cirripedia							0.74	0.20	0.15			
Decapoda				1.92	0.56	0.43						
Caridea	12.24	9.87	1.07									
Macrura				1.92	0.56	0.05						
Macropetasma africanum							0.74	0.41	0.05			
Penaeidae	2.04	0.66	0.89	3.85	1.12	0.70	0.74	0.20	0.05			
Jasus lalandii							0.74	0.20	1.91			
Palinurus gilchristi										5.13	1.30	1.20
Panulirus homarus							0.74	0.20	0.03	3.42	0.87	0.35
Scyllarides elisabethae							0.74	0.20	0.47	4.27	1.08	1.06
Pterygosquilla armata capensis	6.12	2.63	3.88	1.92	0.56	0.32	2.96	0.81	0.36	1.71	0.87	0.08
Anomura	18.37	7.89	1.91	1.92	6.74	0.65	1.48	0.41	0.06	1.71	0.87	0.20
Callianassa sp.				1.92	0.56	0.10						
Upogebia capensis				1.92	0.56	0.17				0.85	0.22	0.05
Brachyura	20.41	8.55	9.87	36.54	16.29	11.63	28.89	14.66	8.16	21.37	20.78	6.09
Brachyura limb							1.48	0.41	0.02	4.27	1.08	0.58
Diaroides sp.										1.71	2.38	1.28
Dromeidae	2.04	0.66	1.49							0.85	0.22	0.06
Goneplax angulata	26.53	12.50	28.36	26.92	14.04	17.55	20.74	14.66	8.60	15.38	11.69	5.51
Mursia cristimanus	6.12	3.29	5.96	13.46	5.62	8.33	18.52	11.41	5.78	13.68	7.14	3.25
Nautilocorystes ocellata	6.12	6.58	10.44	9.62	3.37	3.84	9.63	4.68	2.15	5.13	2.81	0.79
Ovalipes punctatus	2.04	0.66	2.09	26.92	11.24	30.04	22.96	11.41	13.97	17.95	8.44	7.22
Philyra punctata	10.20	7.89	6.47	9.62	8.43	3.40	6.67	5.30	1.02	4.27	1.08	0.13
Plagusia chabrus							2.22	1.02	1.02	6.84	2.60	4.59
Portunidae							0.74	0.20	0.10			
Varuna sp.										0.85	0.22	0.37
Mollusca							1.48	0.41	0.05			
Cephalopod juv.							0.74	0.20	0.00			
Loligo vulgaris reynaudii	6.12	2.63	1.22	9.62	11.80	10.75	35.56	16.09	35.89	27.35	13.42	19.93
Octopus magnificus										0.85	0.22	1.82
Octopus sp.							9.63	3.05	7.18	29.06	9.74	29.23
Octopus vulgaris										0.85	0.22	3.28
Sepia spp.							0.74	0.20	0.04	0.85	0.22	0.01
Perna perna							0.74	0.20	0.12			
Osteichthyes												
Sardine heads										0.85	0.22	0.02
Sardinops sagax				1.92	0.56	4.33	2.22	1.22	1.41	0.85	0.43	0.63
Etrumeus whiteheadi	2.04	0.66	0.98									
Engraulis capensis	8.16	5.26	7.31	5.77	1.69	1.30	3.70	1.02	0.46	2.56	1.52	0.18
Anchovy heads	6.12	3.29	3.43	7.69	4.49	2.33	3.70	2.85	0.44	0.85	0.87	0.07
Hake heads							0.74	0.41	1.28	0.85	0.22	0.15
Merluccius capensis							1.48	0.61	4.61	0.85	0.22	3.19
Sygnathus acus							0.74	0.20	0.10			
Helicolenus dactylopterus										0.85	0.22	0.65
Congipodus spinifer										0.85	0.22	1.37
Pomatomus saltatrix							0.74	0.20	0.45			
Pomadasys olivaceum										0.85	0.22	0.61
Sparidae							0.74	0.20	0.04			
Spicaria axilaris							0.74	0.20	0.96			
Argyrosomus sp.				1.92	0.56	0.02				2.56	0.65	0.21
Trachurus trachurus capensis				1.92	0.56	1.08	4.44	1.22	1.31	4.27	1.30	1.81
Cheilodactylus sp.										0.85	0.22	0.37
Mugillidae												
Liza richardsoni										0.85	0.22	0.56

(Continued)

Table I *(continued)*

Prey	Value per fish length-class											
	< 600 mm			600–799 mm			800–1200 mm			> 1200 mm		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
Diodontidae							0.74	0.20	0.34	0.85	0.22	0.08
Cyclichthys sp.										0.85	0.22	0.34
Teleost remains	8.16	2.63	2.09	3.85	1.12	0.76	9.63	2.65	0.84	7.69	1.95	1.11
Unidentified material	2.04	0.66	0.09	1.92	0.56	0.43				2.56	0.65	0.61
Hook and line										0.85	0.22	0.04
Black skin							0.74	0.20	0.04			
Cartilage										0.85	0.22	0.12
Wood										0.85	0.22	0.01
Sand										0.74	0.20	0.01
Pebbles										0.85	0.43	0.07
Totals	49	152	335	52	178	924	135	491	7 316	117	462	12 301

Females attained larger liver masses than males (Fig. 8). A plot of hepatosomatic index of the mother against mean viable embryo length (Fig. 9) shows high variability, but the negative relationship was significant ($p = <0.001$).

BEHAVIOURAL OBSERVATIONS

Observations were made of at least 30 *M. mustelus* of both sexes over the size range of the species in a 900 m³ tank at the Port Elizabeth Museum during a five-year period. These revealed that individuals usually swam only about 50 mm off the sandy bottom of the tank, apparently in search of benthic prey. Occasionally, they rose well above the bottom and swam faster, usually around the edge of the tank.
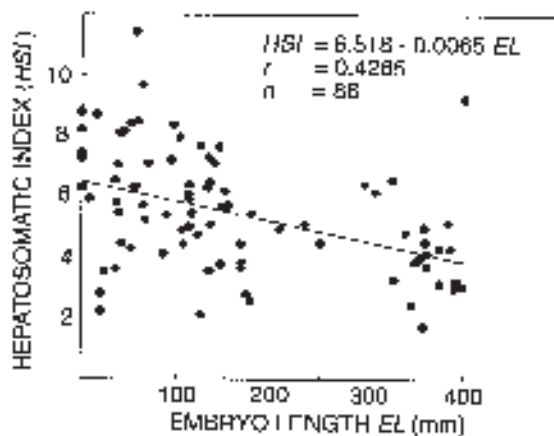
Trawl catches often revealed individuals of similar

Fig. 9: Relationship between the hepatosomatic index of the mother and embryo length in *M. mustelus*

size in the same net. These catches included either both sexes in the catch or one sex only. It is not possible to determine whether the species forms sexually segregated schools or aggregations, because the nets are trawled for more than a kilometre and may therefore encounter more than one school or group. Line-fishermen have often reported catching individuals of more or less the same size during a fishing trip. The sharks do not appear to be strongly aggregated most of the time, and catch rates are generally fairly sporadic. However, sporadic large catches of individuals of similar-sized by linefishermen from the same spot in a short-time span suggests some schooling, or at least aggregations, for at least some of the time.

FEEDING

Of the 402 stomachs of *M. mustelus* examined, 35 (8.7%) were empty. Feeding data collected from *M. mustelus* revealed a broadening of the diet with an increase in fish size (Table I). Small specimens (<600 mm) took a total of 19 prey types, whereas the larger groups (600–800, 800–1 200 and >2 000 mm) took 24, 39 and 44 taxa respectively. Changes in prey taken showed a shift in importance from crustaceans and polychaetes to cephalopods (especially octopods and the squid *Loligo vulgaris reynaudii*) with growth (Table II). It was noted that, whereas small Caridea and polychaetes were important components of the diet in small sharks, these were replaced by larger crustacea, such as spiny lobsters, with growth. There is a possibility that the teleost component of the diet was at least partly scavenged, especially for pelagic prey species. This was particularly noticeable in instances when only fish heads in very early stages of digestion were found in the stomachs.

There was a tendency for prey size to increase with fish size. Significant trends were found for regres-
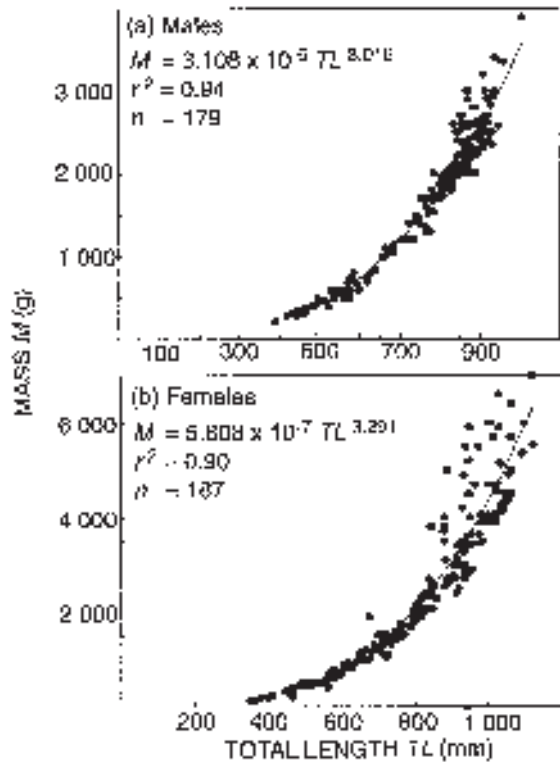
Fig. 10: Relationship between total length and mass for (a) male and (b) female *M. palumbes*

Table III: Stomach contents of *M. mustelus* from Lange-baan Lagoon (all sizes combined), expressed as percentage frequency of occurrence (%F), num-ber (%N) and mass (%M). Totals are the number of predators, number of prey and total prey mass (g)

Prey	%F	%N	%M
Crustacea	26.32	7.69	11.55
Callianassa sp.	10.53	15.38	4.20
Upogebia sp.	31.58	29.23	12.61
Jasus lalandii	5.26	1.54	1.05
Brachyura	26.32	7.69	23.11
Portunidae	5.26	1.54	2.10
Goneplax angulata	5.26	1.54	1.05
Plagusia chabrus	5.26	1.54	6.30
Mollusca	10.53	3.08	4.73
Loligo vulgaris reynaudii	5.26	1.54	4.20
Osteichthves			
Engraulis capensis	10.53	12.31	9.45
Sardinops sagax	5.26	1.54	3.15
Sardine heads	15.79	9.23	11.24
Mugilidae	10.53	4.62	1.05
Teleost remains	5.26	1.54	4.20
Totals	19	65	952.0

sions of predator total length against prey carapace width of *Goneplax angulata* ($r = 0.417$, $df = 39$, $p < 0.01$), *Ovalipes punctatus* ($r = 0.412$, $df = 43$, $p < 0.01$) and *Philira punctata* ($r = 0.413$, $df = 33$, $p < 0.01$), and against mantle length of *Octopus* spp. ($r = 0.54$, $df = 53$, $p < 0.001$). Not only were larger

octopods eaten by large smoothhounds, but they also appeared to avoid, or were unable to capture, smaller specimens. The relationship between *M. mustelus* size and prey size was not significant in the case of *Mursia cristimanus* ($r = 0.207$, $df = 32$, $p > 0.05$), *Nautilocorystes ocellata* ($r = 0.262$, $df = 16$, $p > 0.05$), or *Loligo vulgaris reynaudii* ($r = 0.092$, $df = 108$, $p > 0.05$).

The prey of *M. mustelus* varied with depth and location (Table II). Individuals taken inshore ate shallow-water prey such as *Ovalipes punctata* and *Plagusia chabrus*, as well as *L. vulgaris reynaudii*. In sharks taken between 50 and 100 m deep, crustaceans were more important, whereas in sharks caught deeper than 100 m, octopods were dominant (by mass, although crustaceans were numerically important).

Table II: Relative abundance of different prey taxa (expressed as a percentage of total mass of all prey in the stomachs) per length-class of *M. mustelus,* per depth of capture on the Cape south coast, and from individuals taken from Langebaan Lagoon

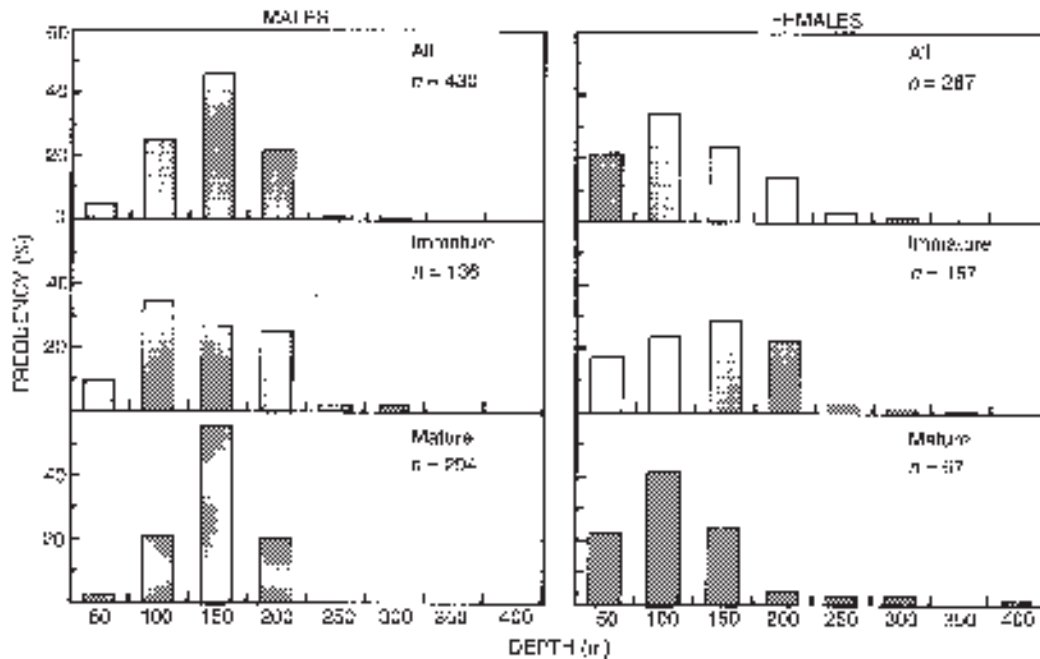| Prey taxon	Mass (%)							
	Fish length-class				Depth of capture			Langebaan Lagoon
	< 600 mm (n = 49)	600−799 mm (n = 52)	800−1 200 mm (n = 135)	> 1 200 mm (n = 117)	< 50 m (n = 213)	50−99 m (n = 65)	> 99 m (n = 9)	861−1 621 mm *TL* (n = 19)
Crustaceans	82.46	78.78	44.21	33.44	42.53	68.11	4.14	61.97
Cephalopods	1.22	10.76	43.24	54.28	50.53	19.14	75.89	8.93
Teleosts	13.81	9.83	12.23	11.35	6.94	12.75	4.14	29.10
Polychaetes	2.42	0.20	0.23	0.08	–	–	–	–
Others	0.09	0.43	0.05	0.85	–	–	–	–

Fig. 11: Depth distribution of different maturity stages of *M. palumbes* sampled in this study, where depth was known

Teleosts were found in the stomachs at all depths, and deeper-water teleosts dominated this component at greater depths.

In a sample taken at Langebaan Lagoon, the sharks had high proportions of the crustaceans *Callionassa* sp., *Upogebia* sp., *Jasus lalandii* and *Plagusia chabrus* in the stomachs (Table II). These prey types are essentially inshore species (Table III).

Mustelus palumbes

SIZE RANGE

The 821 free-swimming *M. palumbes* sampled ranged in length between 275 and 1 126 mm; males (*n* = 491) between 275 and 1 008 mm (78–3 900 g) and females (*n* = 330) between 285 and 1 126 mm (124–7 000 g).

MORPHOMETRICS

Females attained a larger length and mass than males (Fig. 10). Because the slopes of the lines of the relationship between total length and precaudal length (*PCL*) were not significantly different between sexes

(ANCOVA , p = 0.922, df = 234), the following relationship is given for both genders;

$$PCL = 0.817 \, TL - 7.624 \; (r^2 = 0.99, n = 236).$$

DISTRIBUTION

M. palumbes was distributed over a wide depth range, from the shallow subtidal to >300 m deep. Although both sexes were found over the same depth range, the majority of males were taken between 100 and 180 m deep, whereas females were taken more often at depths of between 60 and 140 m (Fig. 11).

SIZE AT MATURITY

Male *M. palumbes* began to mature from 750 mm and were all mature by 850 mm. Females matured from 800 mm and all were mature by 1 000 mm (Fig. 12a, b). The smallest pregnant female measured 836 mm.

There was a rapid increase in clasper length during adolescence in males of 600–800 mm (Fig. 13a). Calcification was usually from a size upwards of about 750 mm *TL* (Fig. 13a). Maturation of the reproductive organs of *M. palumbes* is similar to that of *M. mustelus*.
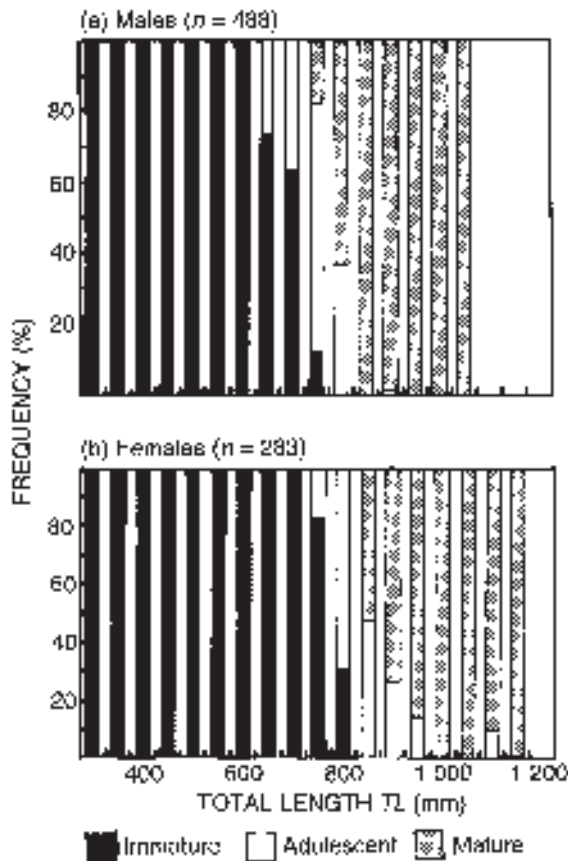
Maturation of female *M. palumbes* was from about

Fig. 12: Percentage of immature, adolescent and mature
M. palumbes for (a) males and (b) females from
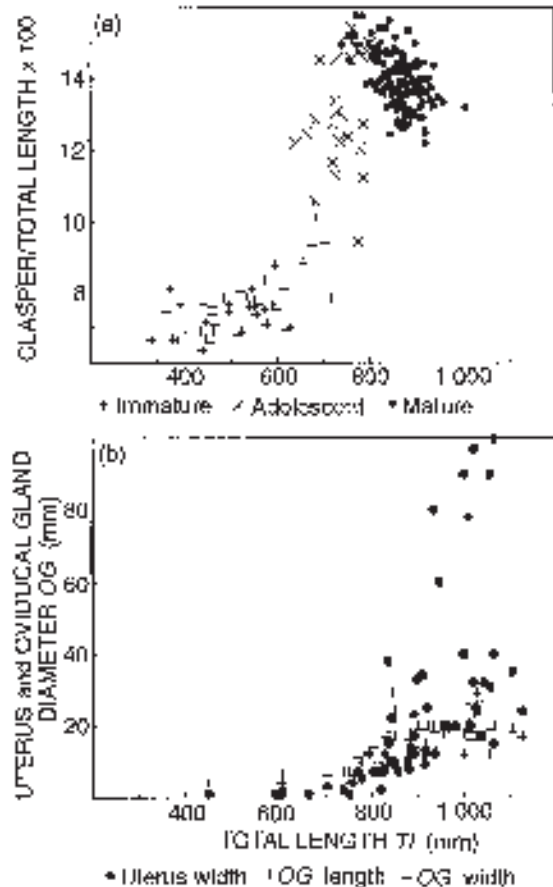Cape waters in 50-mm length-classes

Fig. 13: Relationship between (a) clasper length and total
length of *M. palumbes*, expressed as a percentage
of total length, and (b) uterus width, oviducal gland
length and width, and total length of *M. palumbes*

800 mm, when the oviducal glands and the uterus
began to enlarge. Although the uterus expands consider-
ably with reproductive activity (Fig. 13b), it widens
initially from the posterior end during maturation.

REPRODUCTION

The plot of gonadosomatic index against month
for mature male and female *M. palumbes* failed to
show a marked reproductive seasonality (Fig. 14 a, b),
and this was supported by the absence of seasonal
changes in the largest ovarian egg diameter (Fig. 14 c).
M. palumbes showed a less pronounced seasonality
in the proportion of pregnant females in the sample
(Fig. 14 d) than *M. mustelus*. No mating scars were
seen.

M. palumbes failed to show reproductive seasonality

when the size of embryos was plotted against months
(Fig. 15 a). Both early developing embryos and term-
young were present in most months when large samples
were available. The largest embryos recorded were
340 and 332 mm long for males and females respec-
tively. It is possible that, after parturition, there is a
delay or resting period before the next pregnancy,
because the ovarian eggs were often small when
term-foetuses were present (6–7 mm diameter), and
non-pregnant females may represent as much as 60%
of seasonal samples (Fig. 14 d).

The litter size varied between 3 and 15 young. The
average litter size was 6.9 (SD = 2.5, n = 27), and
there was a positive relationship between female size
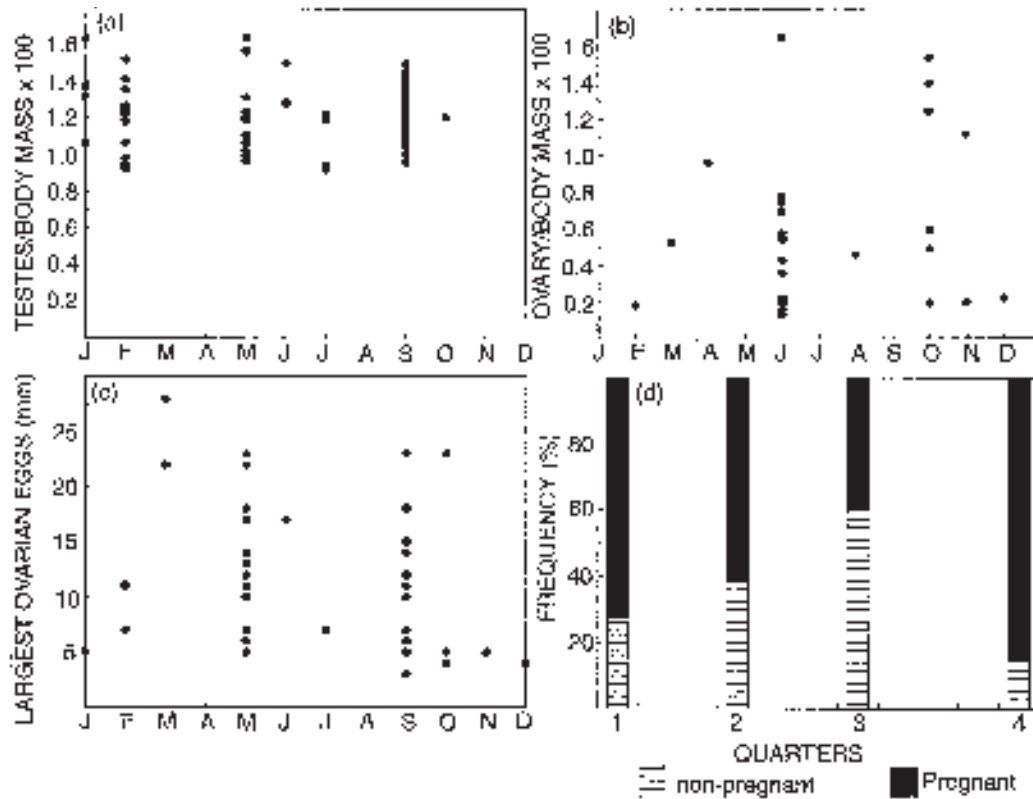and litter size ($p < 0.001$, df = 33, Fig 15 b).

Fig. 14: Monthly gonadosomatic indices for (a) male and (b) female *M. palumbes*. Monthly measurements of the largest eggs in (c) the ovary and (d) the frequency of pregnant and non-pregnant mature females on a quarterly basis

EMBRYONIC DEVELOPMENT

Passage of the egg through the nidamental gland resulted in it being covered with a membranous egg case, presumably after fertilization. The yolk measured about 44×25 mm and had a mass of 6.8 g ($SD = 0.24$, $n = 7$). Embryos developed inside their egg cases throughout their uterine development. The yolk supply was exhausted by the time the embryos attained about 185 mm (about 20 g wet mass), and the yolk sac decreased in size and was gradually absorbed into the embryo. At no time did the yolk sac adhere to the uterus wall. There is therefore no visible source of nutrition for the embryo until the time it is born, once the yolk sac is resorbed by the embryo. The size range of term-embryos was about 305–340 mm, which suggests that there may be an alternative source of nutrients, possibly in the uterine fluid, that contributes to embryonic growth after yolk depletion. Body

colouration was visible by the time the embryos attained 160 mm. At this stage they had pale grey bodies and black leading and trailing edges to the dorsal and caudal fins, and a black line in the inter-dorsal space and along the top of the caudal peduncle.

In term-embryos, the denticles and teeth had erupted and the external yolk sac was totally resorbed. Thereafter, the umbilical scar healed prior to birth. At this stage the embryos were grey dorsally and off-white ventrally. The leading edges of the dorsal fins and the trailing edge of the second dorsal were black, whereas the trailing edge of the first dorsal was white, with a narrow black mark on the distal tip. The other fins had white trailing edges, were grey dorsally and laterally, but white ventrally. Small white spots were usually visible on the sides of the body.

The relationship between liver mass and total length was variable (Fig. 16) and females had larger liver masses than males. A plot of hepatosomatic index of
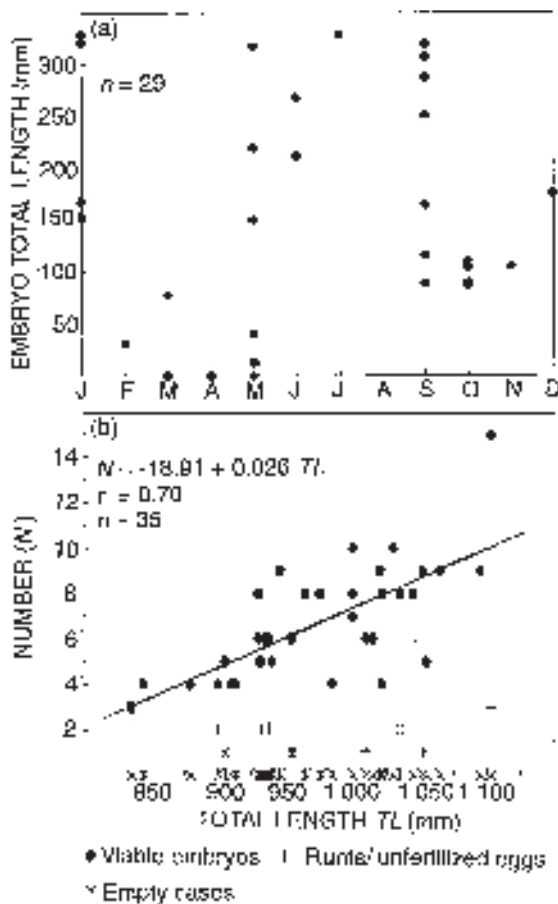
Fig. 15: Relationship between (a) mean embryo length (excluding runts and abnormal individuals) of litters of *M. palumbes* plotted by month and (b) the number of viable embryos, runts and empty egg cases plotted against female total length of *M. palumbes*

Fig. 16: Relationship between liver mass and total length for (a) male and (b) female *M. palumbes*

the mother against mean viable embryo length (Fig. 17) showed high variability, but the negative relationship was significant ($p < 0.001$).

BEHAVIOURAL OBSERVATIONS

There were few observations of the five captive *M. palumbes*. They displayed similar swimming patterns to those of *M. mustelus*, spending most of their time close to the sandy substratum.

Trawl catches often revealed individuals of similar-size of one or both sexes in the same net. Aggregations of individuals were observed, which suggests schooling behaviour.
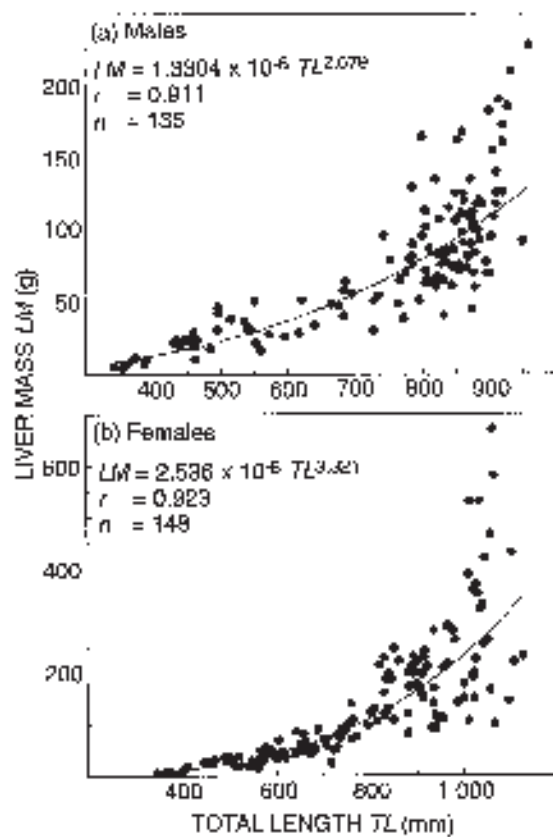
FEEDING

Of the 265 stomachs of *M. palumbes* examined, only two (0.8%) were empty. South Coast samples revealed that small sharks fed mainly on Caridea, unidentified crustaceans, *Mursia cristimanus* and large mysids (Table IV). With growth, small prey became less important and the crabs *Mursia cristimanus*, *Goneplax angulata* and *Nautilocorystes ocellata* became more dominant. *Pterygosquilla armata capensis* and unidentified stomatopods were taken by all size-classes. Cephalopods, polychaetes, and fish were minor prey items. Fish may have been commonly scavenged, because they were usually recovered as heads and vertebral columns only, often showing little evidence of digestion. Crustaceans dominated the diet of all size-classes sampled, although the species composition changed with

Table IV: Stomach contents per length-class of *M. palumbes* from the Cape south coast according to size, expressed as percentage frequency of occurrence (%*F*), number (%*N*) and mass (%*M*). Totals are the number of predators, number of prey and total prey mass (g)

Prey	Value per fish length-class								
	< 600 mm			600–799 mm			800–1200 mm		
	%*F*	%*N*	%*M*	%*F*	%*N*	%*M*	%*F*	%*N*	%*M*
Polychaeta				2.22	0.60	0.10	1.79	0.29	0.03
Crustacea									
Amphipoda	6.25	0.74	0.07	4.44	12.08	0.22	0.89	0.44	0.00
Crustacea	50.00	5.93	22.37	40.00	6.95	14.39	29.46	5.75	9.96
Tanaidacea	6.25	2.22	0.07						
Pterygosquilla armata capensis	25.00	3.70	11.01	4.44	0.60	0.79	28.57	10.77	10.49
Stomatopoda	6.25	2.22	4.97	13.33	7.25	17.50	15.18	7.37	7.37
Isopoda				4.44	0.60	1.97			
Mysidacea	31.25	19.26	4.47	2.22	0.30	0.01			
Decapoda				2.22	1.51	1.92	1.79	0.44	0.32
Caridea	62.50	50.37	16.90	20.00	14.80	1.53	11.61	3.24	1.23
Funchalia sp.				2.22	0.30	0.14	0.89	0.15	0.07
Parapagurus sp.	12.50	1.48	1.78	15.56	6.04	2.46	8.93	1.92	1.20
Upogebia capensis				8.89	2.72	2.45	8.04	5.75	2.9
Calapidae							0.89	0.15	0.30
Crab limb				2.22	0.30	0.10	2.68	0.44	0.45
Crab remains	12.50	1.48	4.26	28.89	7.25	10.69	32.14	9.44	13.35
Dromeidae				2.22	0.30	0.58	3.57	0.59	0.46
Eriphia sp.				2.22	0.30	0.19			
Goneplax angulata	18.75	4.44	6.04	44.44	18.73	25.90	43.75	26.99	29.49
Megalopae	6.25	0.74	0.14				0.89	0.15	0.01
Mursia cristimanus	37.50	4.44	16.55	53.33	14.80	14.34	41.96	16.81	13.50
Nautilocorystes ocellata	12.50	1.48	9.59	4.44	0.60	0.86	6.25	3.83	4.30
Philyra punctata							1.79	0.74	0.27
Plagusia chabrus							3.57	0.59	1.77
Mollusca							0.89	0.15	0.02
Cephalopoda									
Loligo vulgaris reynaudii							7.14	1.47	0.47
Ommastrephidae	6.25	0.74	0.36						
Octopus sp.							0.89	0.44	0.09
Osteichthyes									
Sardinops sagax							0.89	0.15	0.90
Sardine heads							0.89	0.15	0.05
Etrumeus whiteheadi							0.89	0.15	0.08
Anchovy heads				11.11	1.81	0.72	2.68	0.44	0.1
Engraulis capensis				6.67	0.91	0.72	0.89	0.15	0.07
Gonorynchus gonorynchus							0.89	0.15	0.05
Macrouridae				2.22	0.30	0.05			
Scomberesox saurus scomberoides (heads)							0.89	0.15	0.18
Trachurus trachurus capensis							1.79	0.29	0.07
Teleost remains				4.44	0.60	2.11	0.89	0.15	0.21
Unidentified material	6.25	0.74	1.42	2.22	0.30	0.29	1.79	0.29	0.18
Totals	16	135	140.8	45	331	1 042.6	112	678	4 337.9

increasing predator size (Table IV). Significant, positive trends between predator total length and carapace width were observed for *Goneplax angulata* ($r = 0.306$, $df = 106$, $p < 0.01$) and *Mursia cristimanus* ($r = 0.285$, $df = 79$, $p < 0.01$). The relationship between *M. palumbes* length and prey size was not significant for *Nautilocorystes ocellata* ($r = 0.309$, $df = 29$, $p > 0.05$) or *Ovalipes punctatus* ($r = 0.401$, $df = 14$, $p > 0.05$).

Prey diversity was lower on the Cape west coast than elsewhere, and the two dominant prey items were *P. armata capensis* and hermit crabs *Parapagurus* spp. (Table V). Hermit crabs were usually ingested whole, but without the "borrowed" gastropod shells, but there was no indication of the method that the sharks used to remove them from their shells. The crabs may have been sucked or squeezed out, because the intact shells occupied by West Coast hermit crabs
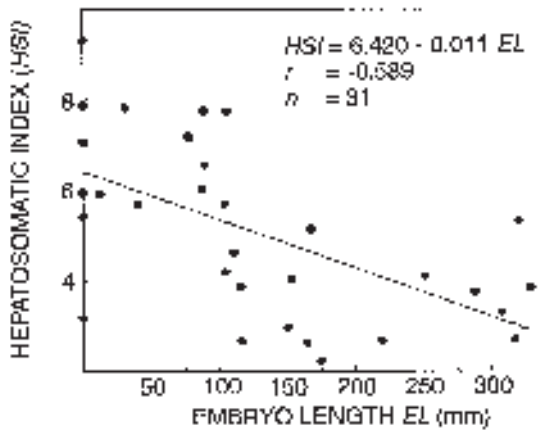
Fig. 17: Relationship between the hepatosomatic index of the mother and embryo length in *M. palumbes*

are generally decalcified and spongy, though they retain their original form. While the importance of these two crustaceans changed with predator size, crustacea dominated the prey of all size-classes (Table V).

DISCUSSION

Although differences in sampling method and effort allocation were not quantified, *M. mustelus* appear to be more abundant in shallow water than *M. palumbes*. This preference for shallow water was particularly noticeable off the West Coast, and *M. mustelus* was a common catch in Langebaan Lagoon, but were not trawled deeper than 38 m by F. R. S. *Africana*. Although it is possible that larger *M. mustelus* may be under-represented in trawls, because of net avoidance (Springer and Lowe 1963), sampling was not species-specific so that either species could be collected from the material taken by line or trawl. Interestingly, offshore linefishing at depths >50 m produced immature or male *M. mustelus* on the South-East Coast. The analysis of South Coast trawl data collected from F. R. S. *Africana* revealed that *M. mustelus* was associated with inshore species, whereas *M. palumbes* was classified with species more typical of the mid-shelf (Smale *et al.* 1993).

With the exception of one sample taken off Gans Bay in 38 m of water (Cruise 075), *M. mustelus* was generally not collected during F. R. S. *Africana* West Coast surveys (Compagno *et al*. 1991), which extended eastwards to 20°E. That one sample was not included in the present analyses. This absence of *M. mustelus* from the West Coast may have been partly a result of the depth range trawled there, as most stations were 70 m or deeper. The nature of the trawling grounds along most of the West Coast generally prevents trawling in water shallower than 70 m. *M. mustelus* is commonly recorded inshore on the West Coast, with records from St Helena Bay and False Bay (Compagno *et al.* 1991), and samples were collected during this study from Langebaan Lagoon. Cooler water and other oceanographic conditions on the West Coast may cause the species to be distributed closer inshore than on the South Coast, where it is found on the mid- to outer shelf in water >100 m deep.

Mature females of both species were observed to make more frequent use of shallower water, although the actual depth range of each was somewhat different. Whether this pattern is related to the distribution of food or physical factors, such as water temperature, is unclear at present. The factors involved in micro-habitat selection are subtle and much more work on this subject is needed to elucidate them.

There is a clear difference in the size at sexual maturity and the maximum size attained by *M. mustelus* and *M. palumbes.* In addition to the other features of use in identifying these sharks, such as colour pattern and labial folds (Heemstra 1973, Compagno 1984, Bass *et al.* 1986, Compagno *et al*. 1989), size may be useful in differentiating adults, especially when they are not fresh or when they have lost their colour pattern. Other differences between the two species include ovoviviparity (= aplacental viviparity) and smaller term embryos (c. 305–340 mm) in *M. palumbes*, and the presence of placental viviparity and greater size of term-embryos (c. 368–425 mm) in *M. mustelus*.

Capapé (1974) reported on seven pregnant female *M. mustelus* from Tunisia (Mediterranean Sea). These individuals ranged in size from 121 to 142 cm *TL*, which agrees with the range of adult females in this study. The smallest free-living specimen examined by Capapé (1974) was 39 cm, which also agrees with the present observations.

Both species lack mating or fighting scars, probably because the teeth are unable to penetrate the skin, unlike many other sharks. It is also possible (but unlikely given their morphology and size) that mating scars are absent, because these smoothhounds don't use their teeth in courtship or copulation.

Francis and Mace (1980) and Massey and Francis (1989) reported empty egg cases in the uteri of the New Zealand smoothhound *Mustelus lenticulatus*, as was found in some pregnant *M. mustelus* and *M. palumbes* in this study.

The presence of embryos within egg cases in the uterus was observed by Parker (1882) for the Australian

Table V: Stomach contents per length-class of *M. palumbes* taken from the Cape west coast, according to size expressed as percentage frequency of occurrence (%*F*), number (%*N*) and mass (%*M*). Totals are the number of predators, number of prey and total prey mass (g)

Prey	Value per fish length-class								
	< 600 mm			600–799 mm			800–1 200 mm		
	%*F*	%*N*	%*M*	%*F*	%*N*	%*M*	%*F*	%*N*	%*M*
Polychaeta	4.55	2.11	0.22						
Crustacea	11.36	6.32	4.07				16.67	9.55	7.25
Pterygosquilla armata capensis	77.27	53.68	67.26	85.71	46.43	63.66	66.67	17.98	22.76
Euphausiacea	2.27	1.05	0.02						
Caridea	2.27	4.21	0.02						
Funchalia sp.	4.55	2.11	0.93	28.57	7.14	8.51	33.33	11.80	9.57
Parapagurus sp.	27.27	25.26	19.89	42.86	46.43	27.84	87.50	51.69	48.61
Crab remains							4.17	0.56	0.31
Osteichthyes									
Exodromidia sp.	2.27	1.05	1.48				4.17	0.56	1.62
Goneplax angulata							4.17	0.56	0.54
Moroteuthis robsoni							4.17	0.56	0.31
Sardinops sagax							4.17	0.56	1.39
Etrumeus whiteheadi							8.33	1.12	3.86
Engraulis capensis	6.82	3.16	5.92				8.33	1.12	0.46
Gonorynchus gonorynchus							4.17	0.56	0.08
Maurolicus muelleri							4.17	0.56	0.15
Lampanyctodes sp.							4.17	0.56	0.31
Trachurus trachurus capensis							4.17	0.56	0.31
Teleost remains	2.27	1.05	0.19				12.50	1.69	2.47
Totals	44	95	540.4	7	28	194.0	24	178	1 296.0

smoothhound *M. antarcticus*. This species is similar to *M. palumbes* in appearance and reproductive biology (Lenanton *et al.* 1990), but it attains a larger size. Parker (1882) believed that the "chambers" in which the embryos were found were in-growths of the uterine wall. Judging by the developmental sequence of *M. mustelus*, this interpretation appears to need clarification, because the chambers Parker described were probably partly made up by the egg cases described previously. Lenanton *et al.* (1990) suggested that the compartments are formed by the fusion of egg-case tissue to ridges on the uterine wall. Francis and Mace (1980) indicated that embryos of *M. lenticulatus* were separated by "enveloping vascular uterine membranes". Daniel (1928) notes that, in higher vertebrates, the partitions between embryos are normally created by the embryo and not the maternal tissue, as suggested by Parker (1882). In both *M. mustelus* and *M. palumbes* the egg-case tissues form the partitions between embryos, and this material is derived from the female shell gland. Teshima *et al.* (1971) noted that *M. manazo* from Japan, which is similar to *M. palumbes* in appearance and reproductive biology, but smaller in size, lacks uterine partitions, but that each embryo is enveloped in embryonic membranes that are apparently egg-case tissue. Observations made on both species in this study suggest that the inner layer of

the uterus surrounds and adheres to the membranous egg case during the latter part of embryonic development only. These temporary partitions are absent from the uterus, except during that part of embryonic development. Details of the process are currently uncertain, but they may function to enhance gas, nutritional and/or waste exchange between the mother and embryo.

Embryonic *M. palumbes* resorb their yolk sacs at a size much smaller than term-embryos, which suggests that there is some form of non-placental maternal nutrition. This is similar to two other white-spotted aplacental smoothhounds, *M. manazo* and *M. lenticulatus* (Teshima *et al.* 1971, Francis and Mace 1980).

Although *M. mustelus* exhibits seasonality in embryo development and parturition, and presumably mating, there was no obvious seasonal trend in reproduction of *M. palumbes*. This contrasts with *M. lenticulatus*, which is similar to *M. palumbes* in appearance, size, habitat and reproductive biology, but has strong seasonality and gives birth from September to December (Francis and Mace 1980, Massey and Francis 1989).

Fecundity increases with female size in both *M. mustelus* and *M. palumbes*, as reported for *M. lenticulatus* (Francis and Mace 1980, Massey and Francis 1989) and *M. antarcticus* (Lenanton *et al.* 1990). There is considerable variation in the relationship

between liver mass and animal size in both sexes of *M. mustelus* and *M. palumbes*. The livers of chondrichthyans are known to assist with buoyancy and to act as an energy reserve (Bone and Roberts 1969, Craik 1978). Rossouw (1987) showed that the liver lipids are correlated with reproductive condition in female *Rhinobatos annulatus*. In the two smooth-hounds under study, the females exhibited a significant, negative trend between embryo length and hepatosomatic index, the lowest values being noted at the end of the gestation period. Similar changes in liver condition were noted by King (1984) for pregnant female *Mustelus lenticulatus*. Therefore, liver stores appear to be used when food is scarce or during periods of physiological stress.

The prey-seeking behaviour of *M. mustelus* and *M. palumbes* observed here in captivity conforms with behaviour reported in experimental work on this genus in the wild (Kalmijn 1978), as well as with observations on other smoothhound species in captivity (Compagno 1984).

The diet of both species of *Mustelus* under study broadly conform to observations reported for other species, and for *M. mustelus* in the northern hemisphere. Smoothhounds of the genus *Mustelus* ate mainly crustaceans (Springer and Lowe 1963, Russo 1975, Talent 1976, Taniuchi *et al.* 1983, Compagno 1984), and the anatomy, dentition and behaviour is well adapted for this mode of feeding. Capapé (1975) noted that, of 27 specimens of *M. mustelus* from Tunisia with identifiable stomach contents, 16 (59%) contained crustaceans, 11 (41%) contained small, bottom-dwelling teleosts and six (22%) contained cephalopods (cuttlefish and squid). In *M. schmitti* from Argentina, polychaetes formed the second largest component (31–38%) of the diet (Menni 1985), followed by crustaceans (34–45%). Polychaetes were minor prey items in *M. mustelus* and *M. palumbes*, and also in some other species of *Mustelus* (Compagno 1984).

The trend for larger prey organisms to be eaten by larger sharks is partly related to the type and strength of the exoskeleton in crustaceans. Smaller sharks may be unable to handle and crush larger crustaceans. There was a poor correlation between cephalopod prey size and predator size, possibly because squid are easily manipulated in the mouth. On the other hand, *Octopus* species are able to hold onto the substratum and are therefore more formidable prey for smaller predators. In many cases, a large octopod could overcome and feed on small sharks, because they are powerful predators themselves (Smale and Buchan 1981).

The teleost component of the diet appeared to be partly scavenged either from fisheries offal, or the kills

of other predators. The extent to which *M. palumbes* and *M. mustelus* are able to chase and feed on active pelagic fish such as anchovy *Engraulis capensis* and sardine *Sardinops sagax* is unknown. Other smooth-hound species, such as *M. henlei* and *M. canis,* feed readily on fish (Compagno 1984), including some pelagic species, but mostly bottom-dwelling forms. A variety of small bottom fish, including flatfish, gobies, dragonets, gurnards, and cepolids, have been eaten by *M. mustelus* in Tunisia (Capapé 1975).

In both the southern African species, heads of anchovy and sardine were recorded. These were probably taken on the bottom and were likely to have been the discards of cephalopod feeding. From direct observation, *Loligo vulgaris reynaudii* is particularly well known for discarding heads and vertebral columns of fish (Lipiński 1987, C. J. Augustyn, Sea Fisheries Research Institute, pers. comm., MJS unpublished data). Given the large biomass of *L. v. reynaudii* in the study area and the dietary importance of pelagic fish to that species (Augustyn 1989, 1990, Sauer and Lipiński, 1991, Smale 1996b), the incidence of fish heads in shark stomachs is not surprising. Fisheries operations are another source of fish heads (especially from larger species such as the Cape hakes *Merluccius capensis* and *M. paradoxus*), because fish are frequently beheaded and cleaned at sea. *M. mustelus* and *M. palumbes,* unlike some other sharks, are not equipped for cutting and dismembering prey, and consequently, they tend to swallow prey items whole. It is unlikely, therefore, that they are regularly beheading pelagic fish and swallowing their heads only. Although Macpherson (1983) interpreted similar findings in kingklip *Genypterus capensis* as being attributable to a specialized feeding behaviour, the fact that the scavenging of fish heads often occurs in other demersal fish (Meyer and Smale 1991, Smale and Cowley 1992) suggests that Macpherson's interpretation is incorrect and that kingklip probably also scavenge fish offal (Smale 1996b).

Although there was an overlap in the diet of both species, there were considerable differences in the proportion of different prey species for the same size-classes of shark. For example, small individuals of both species consumed the crab *Goneplax angulata*, but that prey type was dominant in the diet of small *M. mustelus* and medium-sized *M. palumbes*. The greatest difference in the diets was the greater variety of food items taken by *M. mustelus*, and the higher proportion of non-crustacean prey, especially cephalopods. In both species, larger prey were taken by larger individuals. A broadening of the food resource base with increasing size may be attributable to larger prey size selection and the availability to them of bigger

prey species (such as spiny lobsters and octopods).

The data collected in this study show that diet varies considerably between localities. For example, hermit crabs dominated the diet of *M. palumbes* on the South Coast, but were replaced by stomatopods on the Cape west coast. Hermit crabs and stomatopods were commonly taken in the trawls and *Pterygosquilla armata capensis* is abundant on the West Coast (Griffiths and Blaine 1988). Similarly, for *M. mustelus,* the diet was dominated by anomurans and spiny lobsters *Jasus lalandii* in Langebaan Lagoon, but on the South Coast it contained more varied prey, including a strong cephalopod component. In inshore areas, the portunid crab *Ovalipes punctatus* was important in the diet of *M. mustelus*, but it was eaten less commonly by *M. palumbes*. This reflects the distribution of both the crab (Du Preez and McLachlan 1984) and also the smoothhounds. Differences in the prey taken by female and male *M. lenticulatus* reflect sexual segregation and seasonal differences in habitat between the sexes (King and Clark 1984). Observations on changes in the proportion of prey eaten with depth could also be related to changes in the abundance of prey. For example, *M. mustelus* consumed *L.v. reynaudii* primarily in shallow water, where these squid aggregate to spawn and where they are the dominant prey of several predators (Sauer and Smale 1991). Although it would appear that prey choice is strongly influenced by availability, the diet is mainly confined to benthic animals, so these sharks should be considered as relatively stenophagous.

Potential intraspecific competition between *M. mustelus* and *M. palumbes* is apparently reduced by changes in prey species and size with predator growth. Habitat choice is also an important factor in reducing both intraspecific and interspecific competition. It appears that depth, water temperature, oxygen and such factors as bottom type are the principal components that affect habitat choice in demersal species (Smale *et al.* 1993). The results presented here appear to fit the pattern Ross (1986) frequently found in marine coastal ecosystems, i.e. that spatial and trophic dimensions are approximately equal in importance in resource separation. The importance of other factors, such as microhabitat choice and temporal differences, and their impact on segregation is not known, although distribution patterns are thought to be dynamic and are likely to be related in part to oceanographic parameters (Smale *et al.* 1993). Given the similarity of body form and dentition in *M. mustelus* and *M. palumbes*, it seems likely that the mechanism of resource partitioning is habitat choice, and that within that habitat the prey taken is largely governed by availability.

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