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Distribution and reproduction of the southern lantern shark from New Zealand

B. M. WETHERBEE

Department of Zoology, 2538 The Mall, University of Hawaii, Honolulu, HI 96822, U.S.A.

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Distribution, population structure and reproduction are described for the southern lantern shark *Etmopterus granulosus* at the Chatham Rise, New Zealand. Depth of capture for *E. granulosus* ranged from 744 to 1420 m, with highest catch rates between 800–1200 m. More than twice as many females as males were captured, and the majority of sharks caught were mature, indicating that there may be segregation according to sex and size class. Only 10 of 492 female sharks captured contained ova in uteri, and none contained embryos. The absence of pregnant females suggests that they move to another area or depth prior to pupping. Size of sharks captured ranged from 20·0 to 78·8 cm total length. Females began to mature at 62 cm total length, and males at 52 cm. There was no evidence of a seasonal reproductive cycle. Ovulation appeared to occur when ova reached a diameter of 40–45 mm. The average number of ova in mature females was 12·7. This information is crucial for assessing the impact of fisheries on *E. granulosus* populations.

Key words: distribution patterns; size at maturity; deep-sea fisheries.

INTRODUCTION

Sharks form a substantial part of the bycatch in commercial deep-sea fisheries, in some instances constituting as much as 50% of the catch (Deprez *et al.*, 1990). Sharks captured in these trawls are usually discarded, and very few individuals are alive when returned to the water. The fishery potential of some deep-sea sharks has been investigated because of the value of their liver oil for industrial, medical, cosmetic and other uses (Summers, 1987; Davenport & Deprez, 1989; Summers & Wong, 1992). In New Zealand, one of the most common sharks caught in deep-sea trawl fisheries is the southern lantern shark *Etmopterus granulosus* Günther 1880 (King & Clark, 1987).

This poorly known lantern shark was described as a new species, *E. baxteri*, by Garrick (1957), and has recently been synonymized with *E. granulosus* (Tachikawa *et al.*, 1989). These sharks have been recorded also in waters off South America, South Africa, Tasmania, and Sierra Leone (Bigelow *et al.*, 1953; Bigelow & Schroeder, 1957; Fricke & Koch, 1990; Golovan & Pakhorukov, 1986). In New Zealand, these sharks were rarely encountered before the establishment of extensive deep-sea fisheries, and studies of their biology have been limited largely to composition of their liver oil (Summers, 1987; Deprez *et al.*, 1990; Bakes & Nichols, 1995), and taxonomic comparisons with other species in the genus *Etmopterus* (Garrick, 1960*a*,*b*; Yamakawa *et al.*, 1986;

Tel.: (808) 956-8617; fax: (808) 956-9812; email: bwetherb@zoogate.zoo.hawaii.edu

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Fricke & Koch, 1990). The diet of *E. granulosus* from the south-west Chatham Rise in New Zealand was described by Clark *et al.* (1989), and from South Africa by Ebert *et al.* (1992). King & Clark (1987) provided limited information on the distribution and reproduction of this species in New Zealand.

Because sharks grow slowly, mature late, and have few offspring, they are vulnerable to overfishing, and shark fisheries generally have not been sustainable (Hoenig & Gruber, 1990; Manire & Gruber, 1993). Since *E. granulosus* forms a large component of the catch in deep-sea fisheries in New Zealand, and is a potential target of directed fisheries, the objective of this study is to provide basic biological information essential for assessing the impact that fishing pressure may exert on their populations.

MATERIALS AND METHODS

Sharks were obtained with bottom trawls from the Chatham Rise, off the east coast of New Zealand, during surveys by the New Zealand Ministry of Agriculture and Fisheries for orange roughy *Hoplostethus atlanticus* Collett and smooth oreo *Pseudocyttus maculatus* Gilchrist. Sampling for orange roughy was conducted during late June and throughout July 1990, on the north Chatham Rise (NCR) aboard the F.V. *Cordella*. Smooth oreo trawls were carried out primarily during October and the first week of November 1993 on the south Chatham Rise (SCR) aboard the R.V. *Tangaroa*. Fishing in both surveys was conducted throughout the day and night at depths ranging from 700 to 1500 m.

Nets used in each survey were six-panel bottom otter-trawls with cut-away lower wings. Cod-end mesh-sizes were 110 mm for the *Cordella* and 100 mm for the *Tangaroa*. The door spread for the *Cordella* trawls was 75 and 119 m for the *Tangaroa*. Towing speed for both vessels was 3·0 kn. Individual trawls were approximately 1 h in length.

Total weight of each species caught and depth of capture were recorded for each trawl. All *E. granulosus* from each trawl were examined, except when large numbers of sharks were caught and lack of time precluded examination of every shark. In these cases, approximately 50% of the sharks were selected randomly and examined. A total of 744 individuals was examined, and hence this number represents over 50% of the *E. granulosus* captured in all fishing during the two cruises.

Sharks were weighed, precaudal (L_P) and total length (L_T) were measured to the nearest 0·1 cm, and reproductive status was recorded. Length of sharks refers to L_T in the remainder of this paper. For females, the maximum width of the uterus and the width of the largest ovarian egg were recorded. The number of eggs and weight of ovaries were noted also. Females with thin, ribbon-like uteri and small ova (<2 mm) were considered immature, while all others were considered mature (Yano, 1995).

For males, claspers were measured from insertion to tip, and degree of calcification was noted. Seminal vesicles were examined for presence of semen, and the degree of convolution of the sperm ducts and weight of testes were recorded. Males were considered mature if they possessed calcified claspers with developed spurs, heavily convoluted sperm ducts, and if the seminal vesicles contained sperm (Yano, 1995).

RESULTS

Depth of capture for *E. granulosus* ranged from 744 to 1420 m. Catch rates were highest between 800–1200 m (where 91·5% of *E. granulosus*, on a weight basis, was captured), and declined sharply at depths >1250 m (Table I). Catch rates were higher on the SCR than the NCR except at depths of <900 m, and the overall catch rate on the SCR was over twice that of the NCR (Table I). At depths between 800–1200 m the catch rate on the SCR (29·1 kg trawl^{-1}) was

TABLE I. Total catch (kg) and catch rate (kg trawl^{-1}) of *Etmopterus granulosus* at 50-m depth intervals on the north and south Chatham Rise, New Zealand

Depth (m)	North Chatham Rise			South Chatham Rise		
	Trawls	kg	kg trawl^{-1}	Trawls	kg	kg trawl^{-1}
700–750	1	14·0	14·0	1	0·0	0·0
750–800	13	267·4	20·6	4	5·0	1·3
800–850	19	249·2	13·1	6	34·3	5·7
850–900	33	469·5	14·2	11	122·8	11·2
900–950	39	650·7	16·7	20	962·2	48·1
950–1000	36	374·5	10·4	20	711·8	35·6
1000–1050	26	546·9	21·0	19	625·8	32·9
1050–1100	18	196·1	10·9	12	178·3	14·9
1100–1150	13	71·9	5·5	5	105·9	21·2
1150–1200	21	126·5	6·0	2	18·9	9·5
1200–1250	12	61·5	5·1	3	91·9	30·6
1250–1300	14	20·5	1·5	2	13·3	6·7
1300–1350	7	22·0	3·1	1	5·4	5·4
1350–1400	15	0·0	0·0	2	3·0	1·5
1400–1450	8	1·1	0·1	1	2·8	2·8
1450–1500	5	0·0	0·0	0	0·0	0·0
1500–1550	1	0·0	0·0	0	0·0	0·0
Total	281	3071·8	10·9	109	2881·4	26·4

TABLE II. Depth of capture, number of female and male *Etmopterus granulosus* examined, sex ratio of females to males (F : M), χ^2 and *P* value for significance of difference in number of females and males

Depth (m)	Females	Males	F : M	χ^2	*P*
700–800	1	1	1·0 : 1		
800–900	48	15	3·2 : 1	20·3	0·0001
900–1000	247	83	3·0 : 1	110·9	0·0001
1000–1100	167	85	2·0 : 1	128·3	0·0001
1100–1200	46	21	2·2 : 1	33·4	0·0001
1200–1300	15	7	2·1 : 1	10·3	0·0014
1300–1400	5	1	5·0 : 1		
1400–1500	1	1	1·0 : 1		
Total	530	214	2·5 : 1		

nearly three times that of the NCR (13·1 kg trawl^{-1}). Females were more abundant than males during both sampling periods, with sex ratios ranging from 2·0 : 1 (F : M) at depths of 1000–1100 m to 5·0 : 1 of 1300–1400 m (Table II).

A total of 492 females and 208 males were examined internally. Females ranged from 22·6 to 78·8 cm, and males were between 20·0–69·7 cm (Fig. 1). The relation between PCL and TL is given by the equation: $L_T = -1{\cdot}872 + 0{\cdot}8271\ L_P$;

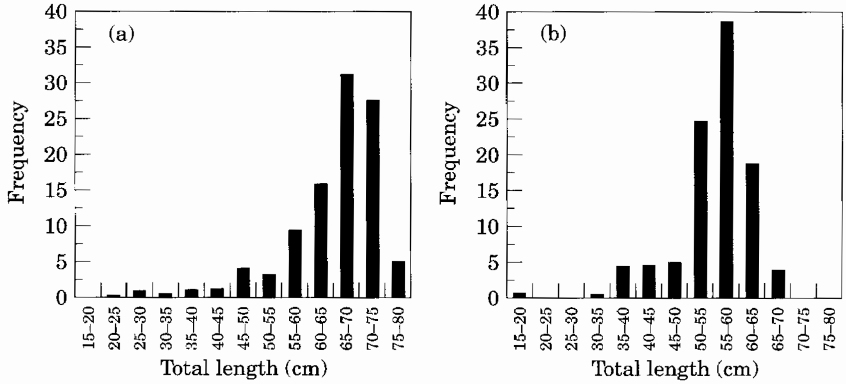

FIG. 1. Length frequency for 5-cm size classes of (a) female (n=492) and (b) male (n=208) *Etmopterus granulosus* caught in research trawls on the Chatham Rise, New Zealand.

r^2=0·994; n=699. Weight of females ranged from 52 to 3505 g, and males weighed between 35–1705 g (Fig. 2). Most sharks captured were large, mature individuals; 76% of females were >60 cm, and 85% of males were >50 cm. The smallest shark examined was a 20-cm male, which was apparently free-swimming, since its stomach contained squid remains.

The uteri were thin and ribbon-like in all females smaller than 56 cm, and started to increase in width as females reached 62 cm (Fig. 3). The maximum ova diameter showed a similar rapid increase in size as females attained a size of 62 cm (Fig. 4). The largest single egg found in an ovary was 45 mm, and only two females contained ova >40 mm.

All females <62 cm (n=112) and 97·1% of 140 females <64 cm had uteri <8 mm diameter and a maximum ova diameter <10 mm. For females of 64–69 cm (n=127), 65·3% had uteri >8 mm and a maximum ova diameter ⩾10 mm. Of 160 sharks >69 cm, 87·5% had uteri >8 mm in diameter and a maximum ova diameter ⩾10 mm. Thirty-six per cent of non-gravid females with expanded uteri (>8 mm) contained ripe ova (>30 mm), and 61% contained developing ova (10–30 mm).

There was also a rapid increase in ovary weight as females reached 62 cm (Fig. 5). Ovary weight ranged from 0·03 to 0·97% body weight (%BW) in females classified as immature (mean=0·29, S.D.=0·16, n=175), and from 0·21 to 17·3% in mature females (mean=3·62, S.D.=4·47, n=233). All sharks <62 cm had ovaries <1·0%BW (n=59), and 69·0% of 149 females >69 cm had ovaries >0·5%BW. There was no apparent difference in uterus diameter, maximum ova diameter or the relative size of ovaries between females collected in July and October.

Ovaries of females contained 7–30 eggs >10 mm in diameter (mean=14.9, S.D.=3·47, n=111). Of 492 females examined, none contained embryos. However, 10 females (65·6–76·1 cm) had ova in their uteri; two caught in July, and eight in October. The number of ova in uteri varied from nine to 15, with an average of 12·7 (S.D.=2·2). The total number of ova in right and left uteri was nearly equal: 37 and 39. The diameter of uterine eggs ranged from 40 to 55 mm. One shark was a hermaphrodite; it had partially developed claspers externally, as well as ovaries internally.

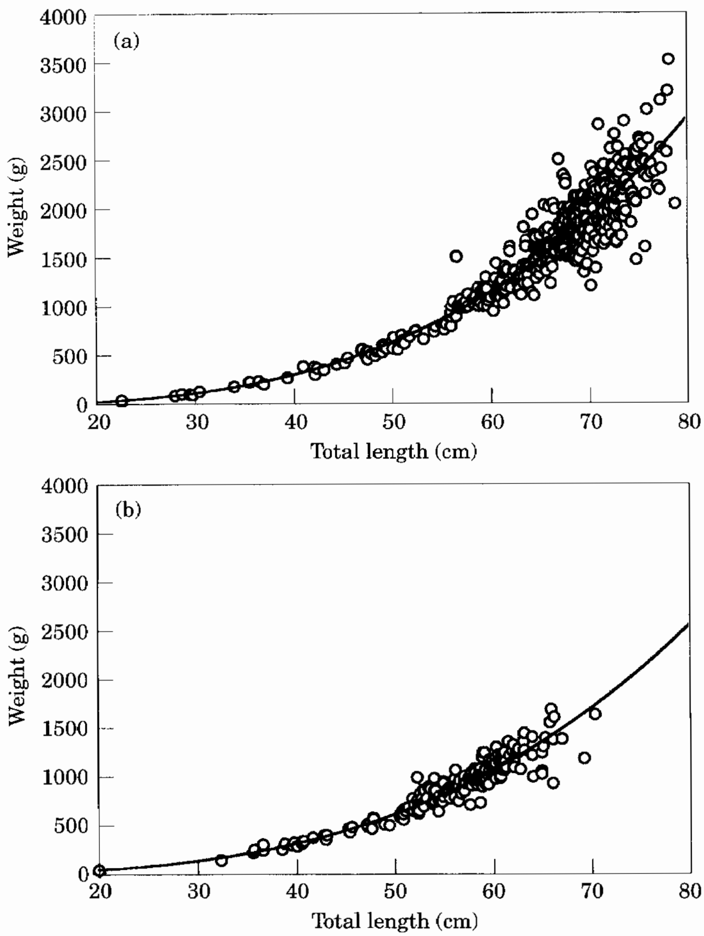

FIG. 2. Length–weight relationship for (a) female ($y=0{\cdot}004x^{3{\cdot}062}$; $r^2=0{\cdot}952$; $n=491$) and (b) male ($y=0{\cdot}002x^{3{\cdot}236}$; $r^2=0{\cdot}953$; $n=203$) *Etmopterus granulosus* caught in research trawls on the Chatham Rise, New Zealand.

Claspers increased rapidly in size and started to become calcified as males exceeded 52 cm L_T (Fig. 6). The smallest male with calcified claspers was 51·9 cm, and only five males <56 cm had calcified claspers. For males of 56–58 cm, 50% had calcified claspers ($n=24$). All males >65·3 cm, and 90·0% of those 58·7 cm ($n=73$) had calcified claspers. Testes weight as %BW ranged from 0·02 to 1·93% for males classified as immature (mean=0·33, S.D.=0·32, $n=103$), and from 0·14 to 3·03% for mature males (mean=1·51, S.D.=0·55, $n=78$) (Fig. 7). No male <55·5 cm, and all males >58·3 cm had coiled sperm ducts. No males <55·3 cm, and 96·3% of males >58·3 cm had semen in their seminal vesicles.

DISCUSSION

The capture of *E. granulosus* near the bottom, at depths of 744–1420 m, is consistent with depth of capture in other reports. Bass *et al.* (1986) reported a maximum depth of 1464 m for this species, and Garrick (1960*a*) noted capture of

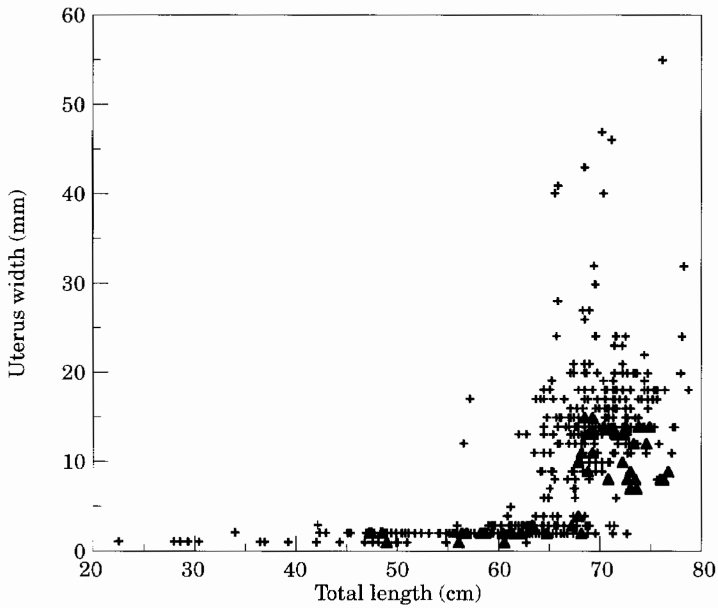

FIG. 3. Uterus width *v.* total length for female *Etmopterus granulosus* caught in research trawls on the north Chatham Rise (NCR: ▲ July; n=48) and south Chatham Rise (SCR: + October; n=387), New Zealand.

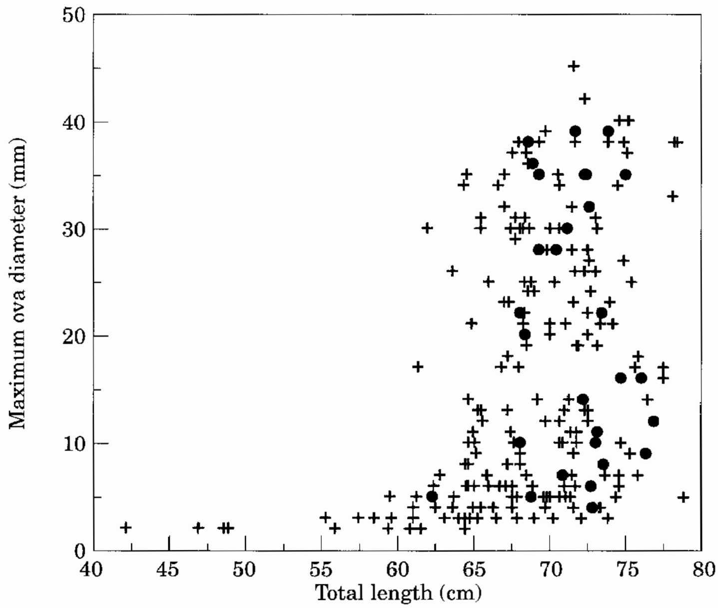

FIG. 4. Diameter of largest ovarian egg *v.* total length for female *Etmopterus granulosus* caught in research trawls on the north Chatham Rise (NCR: ● July; n=30) and south Chatham Rise (SCR: + October; n=187), New Zealand.

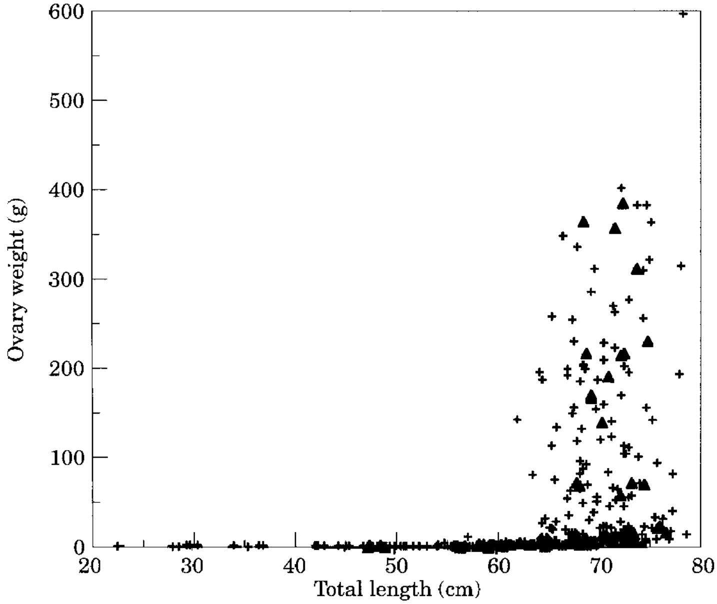

FIG. 5. Ovary weight *v.* total length for female *Etmopterus granulosus* caught in research trawls on the north Chatham Rise (NCR: ▲ July; $n=52$) and south Chatham Rise (SCR: + October; $n=362$), New Zealand.

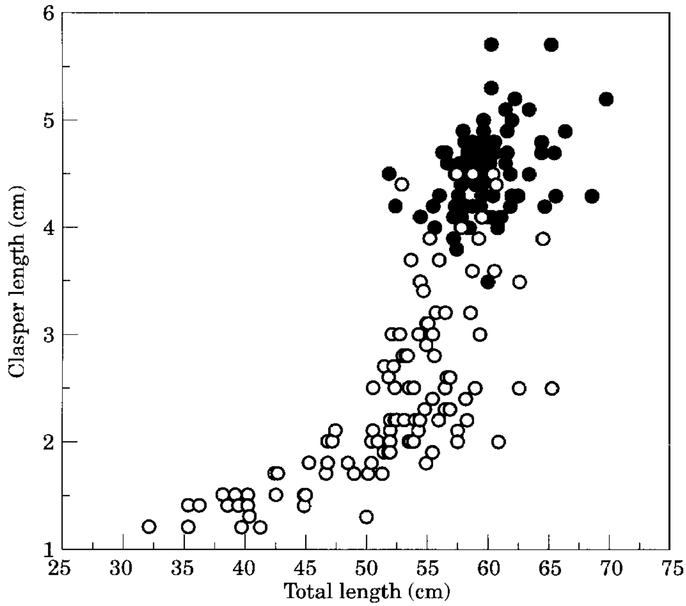

FIG. 6. Length of calcified (●; $n=89$) and uncalcified (○; $n=110$) claspers *v.* total length for male *Etmopterus granulosus* caught in research trawls on the Chatham Rise, New Zealand.

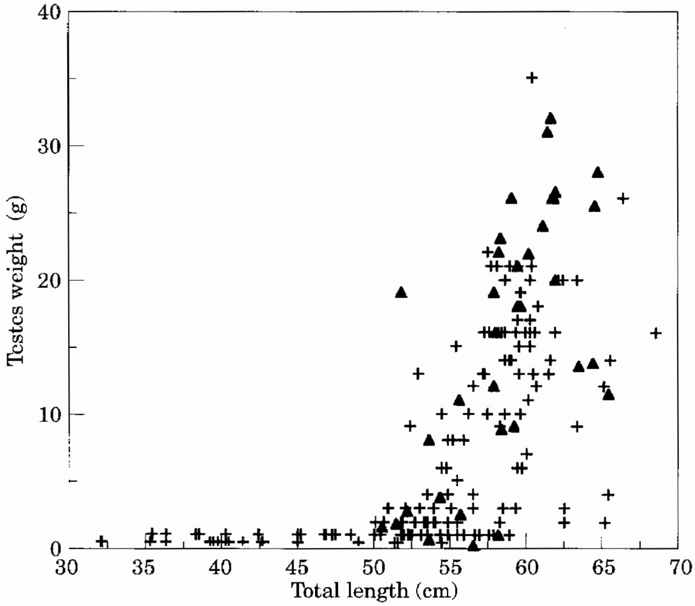

FIG. 7. Testes weight *v.* total length for male *Etmopterus granulosus* caught in research trawls on the north Chatham Rise (NCR: ▲ July; n=35) and south Chatham Rise (SCR: + October; n=148), New Zealand.

a specimen at 1426 m in New Zealand. In the present study, several sharks were captured at 744 m, near the minimum depths fished, suggesting that this species occurs at shallower depths as well. Bass *et al.* (1986) described the capture of *E. granulosus* as shallow as 220 m in South America. High catch rates between 800–1200 m are in agreement with other studies, where highest catch rates were observed between 800–1000 m (King & Clark, 1987; Compagno *et al.*, 1991).

Differences between catch rates on the SCR in comparison to the NCR indicate that there may be geographical or temporal differences in abundance of these sharks. Higher catch rates at depths <900 m on the NCR suggest that these sharks may be more abundant at shallower depths on the NCR than on the SCR. It is possible that higher catch rates on the SCR are due to use of a trawl with a greater door spread in SCR fishing than for the NCR. However, on the basis of kg of sharks captured, *E. granulosus* accounted for only 14·9% of all species of sharks caught on the NCR (3071·8 kg of 20 642·6 kg total sharks), in comparison to 40·1% of all sharks caught on the SCR (2881·4 kg of 7191·1 kg total sharks). Although *E. granulosus* was the most abundant shark at 600–1200 m off east central New Zealand (King & Clark, 1987), they were uncommon in deep-water trawls off the North Island of New Zealand (Clark & King, 1989).

There is also evidence of segregation by sex and size class in the present study. The majority of both males and females were mature, and approximately two-thirds were females. Although it is unclear if adult males, pregnant females and immature sharks of both sexes are abundant in other locations, segregation according to sex and size has been observed in several other species of deep-sea squaloid sharks (Baba *et al.*, 1987; Yano & Tanaka, 1984, 1988). Several workers have demonstrated also that pregnant or mature female squaloid sharks inhabited different depths than the rest of the population (Yano, 1991; Yano & Tanaka, 1988). Movement of pregnant females away from the rest of the population may explain the absence of females with embryos, and the capture of only 10 out of 492 with ova in uteri. It is possible that directed fisheries for *E. granulosus* would reduce dramatically the reproductive potential of populations if the fishery targeted aggregations of mature or pregnant females. Distributional patterns should be considered in designing effective management plans for *E. granulosus* and species with similar population characteristics.

The largest shark observed in this study was a 78·8 cm female, which is close to the largest *E. granulosus* (79·0 cm) reported from New Zealand (King & Clark, 1987). Ebert *et al.* (1992) noted sharks to 85·5 cm in southern Africa. However, Compagno *et al.* (1991) indicated that there were two distinct species of *E. granulosus*-type sharks in South Africa, one of which exceeded 80 cm. The largest male captured in this study was 69·7 cm, although males as large as 73·0 cm have been reported from New Zealand (King & Clark, 1987).

Although no embryos were examined, size at birth is estimated to be slightly <20 cm. The smallest free-swimming shark in this study was 20·0 cm. Free-swimming *E. granulosus* from 17·2 to 20·0 cm have been captured in waters off Australia and southern Africa (Pavlov & Andrianov, 1986; Ebert *et al.*, 1992). Tachikawa *et al.* (1989) examined embryos from New Zealand that were between 17·8–20·0 cm, and King & Clark (1987) suggested that size at birth was between 17–20 cm in New Zealand.

Based on the rapid development of uteri, ovaries and ova in females >62 cm, most female *E. granulosus* appeared to mature between 64–69 cm. The sudden development of claspers, sperm ducts and testes as males reached 55 cm indicates that males matured between 55–58 cm. Size at maturity for sharks examined in this study confirms previous estimates of 64–65 cm for females and 55–56 cm for males (King & Clark, 1987; Yano, unpublished).

The average number of large ovarian eggs of *E. granulosus* in this study (14·9) was similar to results of King & Clark (1987), who found an average of 15 ova. The number of large ovarian eggs provides an approximation of litter size since there is a close relationship between the number of large ovarian eggs and embryos in other species of squaloid sharks (Yano, 1991; Yano & Tanaka, 1988). Yano (unpublished) found that litter size in *E. granulosus* ranged from six to 15, which corresponds well with the range of uterine eggs in the present study (nine to 15). Since the largest ovarian eggs were 45 mm in diameter, and the smallest ova in uteri were 40 mm, ovulation appeared to occur when ova were between 40–45 mm in diameter. The discovery of a hermaphroditic shark is not unusual. Hermaphrodites were observed in several other species of sharks captured in the trawls, and Yano & Tanaka (1989) reported a high incidence of hermaphrodism in *E. unicolor*.

Since sharks were sampled at only two times of the year, it is not possible to make conclusions about the seasonal cycle of reproduction. However, comparison of the reproductive status of sharks examined in July and October revealed no noticeable differences. Females with large ovarian eggs, and with ova in uteri were collected during both sampling periods. In addition, nearly all male sharks >58 cm, collected during both periods had semen-filled seminal vesicles. Lack of reproductive seasonality has been reported for other species of deep-sea squaloid sharks (Yano & Tanaka, 1988) and may be a function of the relative constancy of the environment in which they live. Additional sampling is necessary to examine this aspect of deep-sea shark biology in more detail.

Deep-water squaloid sharks are likely to have slow rates of growth, late maturity, prolonged gestation and few young in comparison to many species of shallow water sharks, making them particularly vulnerable to overfishing. Therefore, fisheries that directly target, or have large bycatches of deep-sea squaloid sharks, may have a substantial impact on shark populations. Although information on population structure, reproductive biology, and age and growth is essential for proper management of populations, this information is lacking for nearly every species of deep-sea shark. Large numbers of *E. granulosus* continue to be captured in deep-water fisheries, but there is virtually nothing known about the impact of these fisheries on the shark populations. The present study provides the first comprehensive examination of distribution patterns, size at maturity, size at birth, litter size and reproductive cycle of *E. granulosus*. This information is essential for management practices aimed at avoiding overexploitation of deep-sea sharks.

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