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Growth, Reproduction and Population Structure of a Marine Snake, *Enhydrina schistosa* (Hydrophiidae)

HAROLD K. VORIS AND BRUCE C. JAYNE

A population of the beaked sea snake, *Enhydrina schistosa* was sampled at Muar, Malaysia over a nine month period. Males and females have synchronous annual reproductive cycles. Gestation extends from November to February and March. The growth of young *E. schistosa* was rapid (about 0.12 cm per day) with no major seasonal decline. The rate of growth in snout-vent length slows after the first 18 months post-parturition. Males and females mature in about 18 months and females give birth to their first clutch of young at about 24 months. Clutch size increases with the size of the female and can reach thirty or more. Estimates of survival indicate that about 10 to 20% of the newborn snakes survive the first year of life and about 6% of the females survive to reproduce. Snakes four or more years old appear to make up a very tiny fraction of the population.

ALTHOUGH the systematics of the sea snakes (Hydrophiidae) have enjoyed considerable attention over the years (Wall, 1909; Smith, 1920, 1926; McDowell, 1972; Cogger, 1975; and Voris, 1977) their life histories have received little attention. The only major exception is the work of R. A. M. Bergman, who had marine snakes collected off the coast of Java, at Surabaia, between 1936 and 1942. Although most of these specimens were lost during World War II, Bergman published many of the data he had collected from the specimens including information on growth and reproduction (Bergman, 1943, 1962). Some very tentative data on the population structure of the pelagic sea snake, *Pelamis*, have been published (Kropach, 1975), and Saint Girons (1964) reported on a population of amphibious sea snakes (*Laticauda*).

The purpose of my study was to examine the growth, reproduction and age structure of a population of *Enhydrina schistosa*. Although individuals were not followed through time, the sampling procedures allowed a static view of the age structure for one year. It is very likely that variations in growth rates, reproductive cycles and the population structure occur between populations and from year to year within a population at one locality as has been demonstrated by Fox (1954) in *Thamnophis*. Thus

this study is clearly only a first approximation to certain life history phenomena which must be much more complex and variable than our present understanding of them.

The beaked sea snake, *E. schistosa*, has a wide geographic range including the Indian Ocean, northern Australian seas and the South China Sea. It is often abundant where it occurs and thus its anatomy (Bergman, 1956; Kasturirangan, 1951; Samuel, 1944), venom (Tamiya, 1975) and diet (Voris et al., 1978) have been studied in some detail.

MATERIALS AND METHODS

The snakes studied were collected at stake nets located in the mouth of the Muar River on the west coast of the Malay Peninsula in the state of Johore, Malaysia. Nets were operated only during the two strong tide periods of each month. Details on sampling procedures and the physical aspects of the habitat will be reported later.

During most sampling periods all snakes captured were preserved. These complete samples have been used to estimate the age distribution and growth rates of *E. schistosa*. Subsamples have been used for analysis of reproduction. In some additional sampling periods, collections of only the first year class were made to refine

TABLE 1. SAMPLE SIZES OF *E. schistosa* COLLECTED AT MUAR DURING DIFFERENT PERIODS. Specimens used in growth studies were not necessarily included in reproductive studies. See the text for an explanation of the year class designations.

Collection Dates (1975)	Growth Samples						Reproduction Samples	
	Young		Yearlings		Adults			
	♂	♀	♂	♀	♂	♀	♂	♀
Jan. 10–Feb. 4	—	—	41	26	18	26	20	53
Feb. 25–Mar. 13	98	95	61	42	45	23	10	23
Mar. 26–Apr. 3	50	41	—	—	—	—	—	—
May 10–14	43	35	14	15	10	8	10	27
June 13–24	11	20	—	—	—	—	—	—
July 17–25	18	14	—	—	—	—	—	—
Aug. 8–14	21	9	—	—	—	—	—	—
Sept. 5–8	14	15	8	4	7	5	25	24
Nov. 20–21 ^a	—	—	—	—	—	—	8	5

^a Collection made at Muar in 1971.

estimates of early growth rates. For analysis, specimens from two consecutive tidal periods were pooled to make up the first two sampling periods. The 1975 sampling periods and the sample sizes of *E. schistosa* collected are given in Table 1.

Within five hours of capture, snakes were brought to the laboratory on ice in styrofoam boxes. They were injected with sodium pentobarbital and maintained on ice. Within the next 12 hours, each relaxed snake was tagged and measured (snout-vent (s-v) length to nearest half cm and girth at the neck and mid-body to the nearest mm). Next, snakes were cut open ventrally to remove stomach contents and then injected with a 12% formalin solution. Snakes were coiled in trays and covered with 10% formalin to harden. After shipment to Chicago they were placed in 70% ethanol for permanent storage.

Both ovaries and oviducts were removed from each female snake. The eggs in each ovary were counted and grouped by their maximum diameter into the following size classes: ≤ 1.0 mm, 1.0–2.0 mm, 2.1–3.0 mm, etc., 7.1–8.0 mm, and 8.1–10.0 mm, 10.1–15.0 mm, 15.1–25.0 mm. The number and condition of corpora lutea were also noted. The number and maximum diameters of intact oviducal eggs were recorded, after which the embryos were removed from the eggs, sexed, and their snout-vent and tail lengths measured. The fat bodies were removed from the five largest females from each of the 1975 sample periods (except

September, when $n = 4$). Excess liquid was allowed to drain from the fat and then volume was determined to the nearest ml by measuring the fluid displacement of the fat in 70% ethanol.

In males, the right testes were removed. Because it was difficult to separate the epididymis from the testis, the epididymis was left attached. The testes were then blotted dry on a paper towel and their volumes determined using 70% ethanol in a burette graduated to 0.01 ml. After the volumetric measurements were completed, cross sections were made near the middle of the testes and prepared for microscopic examination using Van Gieson's stain for one preparation and a combination of hematoxylin and eosin for another.

RESULTS

Growth.—Thirty-one gravid females were collected between 10 Jan. and 3 March 1975. The average s-v lengths of the embryos ranged from 4.0 to 22.1 cm. The variation in size of embryos within a single sampling period was also great. The 18 gravid females collected between 24 Jan. and 4 Feb. contained clutches of embryos which had mean s-v lengths ranging from 6.0 to 17.1 cm, nearly a three-fold difference. However, comparison of the mean of the average s-v length for clutches collected between 24 Jan. and 4 Feb. ($n = 18$, $\bar{x} = 128.13$ mm, $s = 29.9$) with the mean for clutches collected between 25 Feb. and 3 March ($n = 6$, $\bar{x} =$

TABLE 2. SNOUT-VENT LENGTH DATA ON 31 CLUTCHES OF *E. schistosa* EMBRYOS FROM THE 31 GRAVID FEMALES COLLECTED BETWEEN 10 JAN. AND 3 MARCH 1975. Data are arranged according to increasing mean s-v lengths of embryos.

FMNH No.	Female		n	Embryo Snout-vent length (mm)			
	S-V length (cm)	Collection Date		Range	\bar{x}	s	cv
198587	92	12 Jan.	24	¹	40.0	—	—
198731	85	31 Jan.	11	55–64	59.9	2.8	4.80
198601	89	13 Jan.	17	48–78	70.3	7.8	11.32
198639	79	24 Jan.	8	70–87	78.5	5.9	7.76
198733	86	31 Jan.	7	86–98	91.3	4.5	5.15
198582	73	10 Jan.	1	—	92.0	—	—
198641	112	25 Jan.	33	89–103	96.3	3.8	3.97
198586	86	13 Jan.	12	90–102	98.3	3.2	3.29
198795	83	31 Jan.	10	115–124	119.2	3.3	2.80
198697	94	28 Jan.	19	112–129	119.8	5.1	4.30
198873	86	4 Feb.	6	110–129	122.0	7.1	6.04
198708	106	28 Jan.	23	115–132	125.4	4.8	3.89
199029	96	26 Feb.	21	116–142	129.4	5.9	4.60
198603	105	10 Jan.	31	120–140	131.1	5.4	4.13
198602	97	13 Jan.	29	122–146	134.2	5.2	3.88
198647	80	25 Jan.	3	134–138	135.7	2.1	1.66
198705	85	29 Jan.	14	127–146	136.7	5.9	4.39
198591	95	11 Jan.	12	132–151	140.6	5.7	4.11
198698	100	29 Jan.	13	130–152	140.6	6.0	4.21
198707	90	29 Jan.	11	115–153	145.3	11.0	7.73
198734	99	31 Jan.	23	140–156	149.0	4.2	2.81
198699	90	29 Jan.	21	119–162	150.4	8.9	5.97
198704	110	29 Jan.	20	135–162	151.8	10.1	6.72
198640	91	25 Jan.	19	146–172	156.2	7.3	4.70
198638	101	26 Jan.	27	146–169	157.0	5.1	3.27
198730	93	31 Jan.	15	165–181	171.3	5.0	2.94
199030	90	26 Feb.	24	177–197	186.0	4.8	2.58
199519	90	3 Mar.	16	188–207	198.7	5.3	2.72
199168	96	26 Feb.	28	190–216	203.6	7.9	3.92
199012	100	25 Feb.	25	143–233	206.8	23.7	11.55
199028	96	27 Feb.	20	213–232	221.8	5.6	2.57

¹ Due to the delicate condition of these embryos the average size was estimated.

191.05 mm, $s = 32.4$) suggests a growth of about 6 cm in the 30 days between 28 Jan. and 28 Feb. (the midpoint, of these two sampling periods) or a rate of about 0.20 cm per day.

The largest embryo observed (23.3 cm, s-v) was removed from a female collected on 23 Feb., and the largest mean s-v length for a single clutch was 22.1 cm. The shortest free-swimming snake was captured on 3 March, and measured 21.0 cm in s-v length. Thus, 23 cm appears to be a good estimate of the mean s-v length at birth. Data in Table 2 suggest that the s-v length at birth could be expected to range from about 21 to 24 cm.

Young *E. schistosa* were first caught on 24 Feb. at the beginning of a period of high tides. Nets had not been operated for two weeks prior to this date. Within the next three days, 34 juveniles were collected with s-v lengths ranging from 22.0 to 29.5 cm ($\bar{x} = 25.8$ cm, $s = 1.7$). Thus, births apparently started about the middle of February and extended into March.

The young appeared as a discrete size class in the Feb.–March sample (Fig. 1c, d) and remained distinct through September (Fig. 1e–h). The pattern of size class distribution suggests that the Jan.–Feb. sample consists of a merger of the young of the previous year with the year-

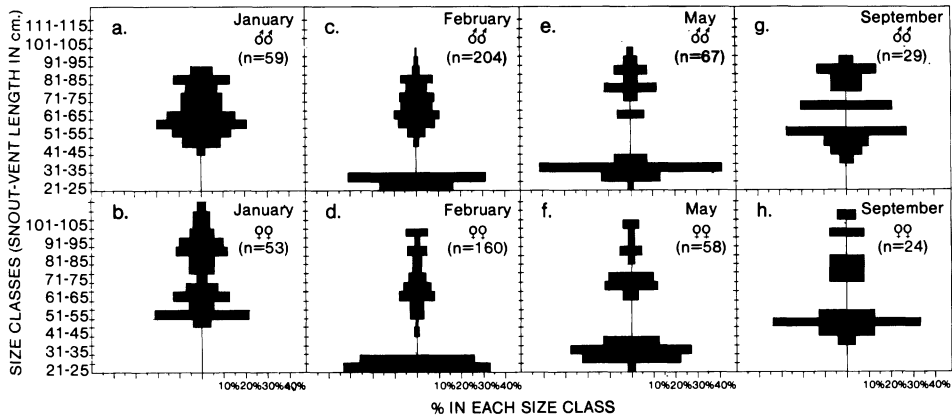


Fig. 1. The distribution of size classes of male and female *E. schistosa* collected during sampling periods in 1975 at Muar. The January snakes (a and b) were collected in January and early February and the February snakes were collected in late February and early March (Table 1).

lings and adults, thus making all individuals in the Jan.-Feb. sample older than 10 months. This assertion is supported by data which are given later which document annual synchronous reproductive cycles among adult male and female snakes at Muar. No discrete size classes can be observed in the Jan.-Feb. sample or in the non-young portions of the other periods (Fig. 1a-h). However using the bimodality in size classes suggested in Figure 1a-f, and the smallest gravid female, 73 cm long (s-v), the yearlings can be approximately delineated. The upper s-v length limit for yearlings would thus be 70 cm for the Jan.-Feb. sample (11 months old), 75 cm for the Feb.-March and May samples (12 months old) and 85 cm for the September sample (18 months old). Fig. 2 illustrates the size distribution of snakes within each of the three size classes thus formed, young, yearlings and adults, for each sampling period. Mean s-v lengths for males and females were not significantly different except in adults captured in Jan.-Feb. and Feb.-March (Student's *t*-test, $P < .001$).

Growth of the young is well documented for the first eight months post-parturition (Fig. 2). In the 185 days between the middle of the first sample period which included young (6 March, $\bar{x} = 25.7$ cm) to the last sample period (7 Sept., $\bar{x} = 48.6$ cm), the average s-v length increased to 22.9 cm to give an average growth rate of 0.12 cm per day. Growth rates between sample periods were not constant and reached a maximum of 0.33 cm per day between July and August.

To examine the first year growth it is necessary to compare cohorts, that is, the young and the yearling collected in Feb.-March. The mean s-v lengths for the two groups were 25.7 cm and 63.0 cm respectively (Fig. 2). Thus in their first year *E. schistosa* grow at a rate of approximately 0.10 cm per day and increase in s-v length by a factor of about 2.5.

Using the year class boundaries approximated above, female snakes have increased to an estimated average s-v length of approximately 85 cm by the end of their second year (Feb.-March females 76-90 cm s-v, $n = 13$, $\bar{x} = 84.7$ cm, $s = 4.74$, see section on population structure), while males have increased to an average length (s-v) of only about 78 cm (Feb.-March males 71-85 cm s-v, $n = 38$, $\bar{x} = 78.2$ cm, $s = 4.66$). Females ultimately become substantially larger than males. Only five males were collected with s-v lengths exceeding 90 cm; the longest male captured measured 97 cm. On the other hand, 30 females were collected which exceeded 90 cm in s-v length; of these, 15 were longer than 97 cm, and the longest was 112 cm.

Reproductive output (female).—The reproductive potential of female *E. schistosa* as measured by the number of ovarian eggs, increases dramatically with size (age) as it does in many other ophidians (Bauman and Metter, 1977; Bergman, 1954; Tinkle, 1957, 1962). The number of ovarian eggs increased from a mean of 12.5 for females less than 50 cm in s-v length, to 83.4 for females larger than 100 cm (Table 3).

The right ovary produced significantly more

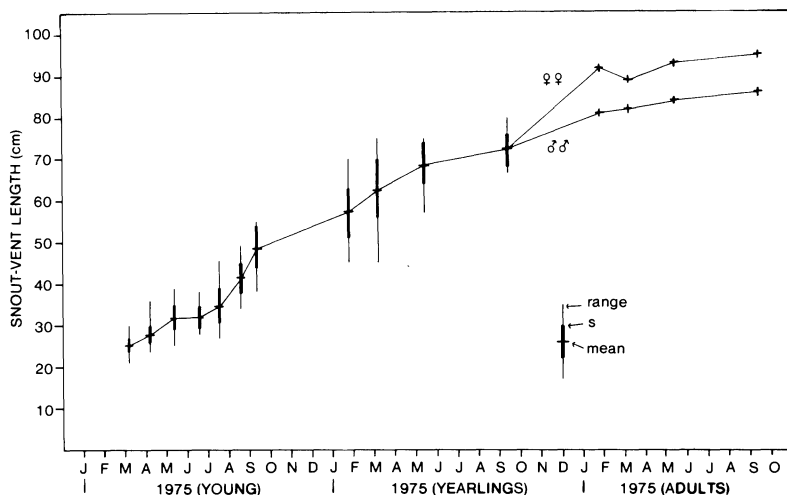


Fig. 2. The average s-v lengths of *E. schistosa* cohorts for each sampling period. All snakes were collected in 1975 at Muar, Malaysia. The young constituted a discrete size class throughout the sampling but the size distribution of the yearlings and adults overlapped and the separation was estimated from the bimodality observed in Fig. 1. The sample sizes for each size group are given in Table 1.

eggs than the left ovary in all yearling and adult females (Student's t-test, paired samples, $P < .001$). Of the 127 females in the yearling and adult classes, 103 had more right ovarian eggs than left, while the reverse was true in only 18 females; six females had equal numbers of eggs in each ovary.

Oviducal egg number also increased with female size (Table 3). Although the average number of eggs was greater in the right oviduct ($\bar{x} = 9.8$, $s = 4.64$) than in the left ($\bar{x} = 8.9$, $s = 4.56$), the difference in number of eggs was not statistically significant between right and left ovi-

ducts according to the paired t-test. Of the 27 females in which there was a difference between the number of right and left oviducal eggs, 19 had more eggs in the right oviduct than in the left, while only eight had more eggs in the left oviduct. This difference is significant at $P < .05$, according to the Sign test (Siegel, 1956:68).

The plot of the number of embryos (Y) vs. s-v length of the gravid females in Fig. 3 documents an increase in clutch size with the size of the females. The linear regression determined by least squares was $Y = 0.7529X -$

TABLE 3. THE AVERAGE NUMBER OF OVARIAN AND OVIDUCAL EGGS, AND THE TOTAL NUMBER OF OVIDUCAL EGGS AND FERTILIZATION RATES FOR FEMALE *E. schistosa* OF DIFFERENT SIZE CLASSES. For each female in which developing eggs were observed, fertility was calculated as the total number of developing embryos divided by the total number of oviducal eggs. The mean fertility rate was then calculated for size classes.

Size Class Snout-vent Length (cm)	♀♀ n	Number of Ovarian Eggs		♀♀ n	Oviducal eggs				Mean % Fertility
		\bar{x}	s		Number of eggs	\bar{x}	s	Number Fertile	
≤50	15	12.5	8.99	—	—	—	—	—	—
51–60	19	28.0	8.99	—	—	—	—	—	—
61–70	29	41.2	11.88	—	—	—	—	—	—
71–80	18	48.1	16.93	4	23	5.8	2.63	14	59.5
81–90	20	62.2	21.65	12	174	14.5	6.07	149	81.3
91–100	17	77.7	20.94	12	279	23.3	4.75	247	88.7
101–112	8	83.4	22.88	5	143	28.6	4.98	133	92.4

TABLE 4. THE PERCENT DISTRIBUTION OF OVARIAN EGGS INTO VARIOUS SIZE CLASSES FOR FEMALE *E. schistosa* CAUGHT DURING FOUR SAMPLING PERIODS AND DATA ON THE SIZE OF THE 10 LARGEST OVARIAN EGGS OF EACH MATURE FEMALE MORE THAN 80 CM IN S-V LENGTH.

Period	Number of Snakes	(cm) Size Range Snakes	Total No. of Eggs	Ovarian Egg Size Classes (mm)										Size of 10 largest ovarian eggs			
				≤1	1.1-2	2.1-3	3.1-4	4.1-5	5.1-6	6.1-7	7.1-8	8.1-10	10-15	15-25	n	\bar{x}	s
Jan-Feb	26	73-112	1619	23.5	36.1	27.5	11.8	1.1							24	3.2	.41
Feb-Mar	10	79-100	810	21.4	33.0	29.9	13.2	2.6							9	3.6	.41
May	12	77-105	863	26.5	29.9	26.4	13.0	3.9	0.2						10	3.5	.62
September	9	72-109	771	13.9	20.9	16.7	10.1	8.2	6.9	5.4	2.9	6.9	2.2	6.0	5	13.9	5.67

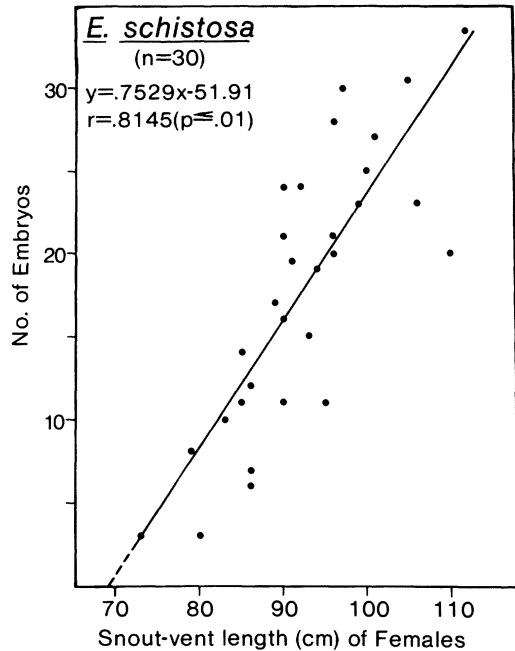


Fig. 3. The number of embryos observed in the oviducts of 30 female *E. schistosa* from Muar is plotted against the female's s-v length. The line represents the least squares linear regression for the 30 data points.

51.91. As the s-v length of the female size class increased, the average fertility rate also increased from 59.5 to 92.4% (Table 3).

Reproductive cycle (female).—From January until May, the size distribution of ovarian eggs remained stable with none of the eggs exceeding 6.0 mm in length (Table 4). Between May and September some eggs began to increase in size, so that in the September sample of nine females ≥ 72.5 cm long (s-v), 23.4% of the ovarian eggs were over 6.0 mm in length, and 8.2% were over 10 mm long. The increase in egg size between May and September is also documented in Table 4, which presents the mean ovarian egg length for each collecting period, calculated from the average length of the 10 largest ovarian eggs from each female measuring ≥ 80 cm long (s-v). Because the clutch size for females ≥ 80 cm long (s-v) was generally greater than 10 (Fig. 3), the 10 largest ovarian eggs can be assumed to be among those destined to be ovulated next. In addition, one mature female collected in Nov. 1976 had just ovulated, and another still had 12 eggs measuring over 30

mm long in the ovaries. Thus based on the size of the ovarian eggs in the Sept. sample, and on two mature females collected in Nov. 1976, ovulation appears to take place in November.

All 26 females ≥ 73 cm long (s-v) collected in January were gravid. The Feb.–March sample contained both gravid and spent females, while the May sample lacked any gravid females. These observations and the data on the size and first appearance of young snakes indicate that births begin around mid-February and extend to mid-March.

Adult females ≥ 90 cm long (s-v) collected in Feb.–March had the least amount of fat storage (mean volumes of 27.0 and 30.4 ml, respectively). In May, fat bodies were larger ($\bar{x} = 49.0$ ml) and by September females had an average fat volume of 57.5 ml.

Reproductive cycle (male).—The volume of the right testis was determined for the 10 largest male snakes (>70 cm, s-v) from each of the four 1975 sampling periods and for 8 male snakes (61–92 cm, s-v) collected in November 1971. The mean volumes for the five sampling periods are shown in Fig. 4. A two-way analysis of variance indicated that there were no significant differences among the mean s-v lengths of the snakes collected in the four sampling periods of 1975 ($F = 1.35$, $P > .05$). Highly significant differences in mean testis volumes were found among the four sampling periods ($F = 126.8$, $P < .01$). The data clearly suggest that testis size varies seasonally with a maximum occurring about September. This type of cyclical change has been found in several temperate zone snakes (Cieslak, 1945; Fox, 1952, 1954; Volsøe, 1944) and is closely correlated with spermatogenesis.

The right testes of two of the largest males from each of the 1975 samples and from the November 1971 sample were sectioned. Although sperm were observed in all the sections, there was a pronounced variation in the number of sperm present. September males had the greatest concentration of mature sperm and spermatids in the seminiferous tubules. The average diameter of the seminiferous tubules of September males was also larger than it was in males from other sample periods.

Reproductive maturity (female).—The smallest gravid female was collected on 10 Jan. 1975 and was 73 cm in s-v length. The growth data suggest that this snake was approximately 22

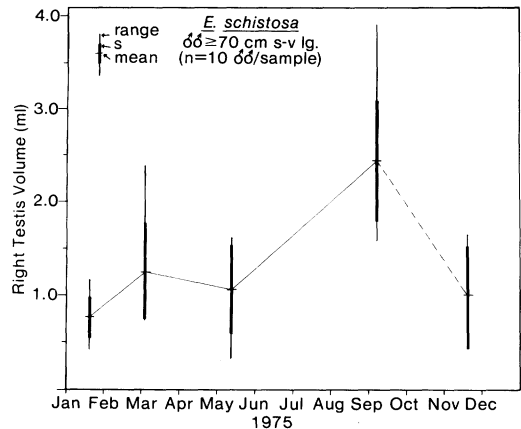


Fig. 4. The mean volume for the right testes of male *E. schistosa* ≥ 70 cm in s-v length is plotted for the four 1975 sampling periods ($n = 10$ in each case), and for one collection made in November, 1971 ($n = 8$). In the latter sample males were between 61–92 cm long. All snakes were collected at Muar.

months old and small for her age. All larger females in the January sample ($n = 26$) were gravid. Thus it appears that females become sexually mature at about 18 months and bear young at the end of their second year.

Reproductive maturity (male).—Comparisons of testis volume and sperm content were initially made on three size classes of males collected in Sept. 1975, because sexual activity approached a peak around this time. Mean testis volumes for the Sept. sample of 10 large males (>70 cm, s-v), 5 medium males (66–70 cm, s-v), and 10 small males (45.8–55 cm, s-v) were 2.44, 1.54 and 0.20 ml respectively. In order to compare relative testis size among the three size groups of snakes a ratio of the testis volume to s-v length was calculated for each snake. The mean ratios of testis volume (ml) to s-v length (cm) were .0289, .0225 and .0038 for large, medium and small males respectively. The Mann-Whitney U test (Siegel, 1956) showed that highly significant differences existed between the ratios of large and small snakes ($P < .001$), between medium and small males ($P < .001$), but no significant differences existed between large and medium males. These results suggest that reproductive maturity, as indicated by attainment of a particular level of testis size relative to body length, occurs in snakes about 66–70 cm long (s-v). These males appear to be about 18 months old. Additional evidence for the at-

TABLE 5. AGE CLASS DISTRIBUTIONS FOR FEMALE *E. schistosa* COLLECTED IN JANUARY, FEBRUARY-MARCH AND MAY AT MUAR. Dashed lines delineate approximated age classes.

Size class	January			January-March			May		
	Snakes	%	Σ%	Snakes	%	Σ%	Snakes	%	Σ%
21-25				53	33.1	59.3%	1	1.7	60.3%
26-30				42	26.2		13	22.4	
31-35							16	27.6	
36-40							5	8.6	
41-45				2	1.2	26.2%			25.9%
46-50	2	3.8	51.0%	1	.6				
51-55	11	20.8		5	3.1				
56-60	3	5.7		5	3.1		2		
61-65	7	13.2	24.6%	13	8.1	8.1%	7	3.4	8.6%
66-70	4	7.5		10	6.2		6	12.1	
71-75	1	1.9		6	3.8			10.3	
76-80	3	5.7		3	1.9		1		
81-85	3	5.7	15.1%	3	1.9	6.3%	3	1.7	5.2%
86-90	6	11.3		7	4.4		1	5.2	
91-95	5	9.4		2	1.2		1	1.7	
96-100	3	5.7		8	5.0		1	1.7	
101-105	2	3.8	9.5%				2	3.4	
106-110	2	3.8							
111-115	1	1.9							

tainment of reproductive maturity by 66-70 cm males, comes from the sectioned testes of six 66.5-70 cm s-v length Sept. males and two 50-51.5 cm s-v length Sept. males. The 66.5-70 cm s-v length September males showed a high density of mature sperm, while no mature sperm were observed in the two smaller males.

A comparison was made of the ratios of testis volume (ml) to s-v length (cm) of 10 large males (80-89 cm s-v length) with those of 10 small males (45-57 cm s-v length) from the January sample and they differed at the $P < .001$ level according to the Mann-Whitney U test (means were 0.0091 and 0.0019 respectively). Further, no mature sperm were detected in sectioned testes of six Jan.-Feb. males from the 45-57 cm size class while two males of 89 cm s-v length had spermatozoa. These data indicate that the 45-57 cm Jan.-Feb. males (which were on the small side of the 10-month-old class, Fig. 1a), were not reproductively active during their first year.

Population structure.—In this study individual snakes were not monitored with respect to growth or movements. The age of individuals has been inferred from the size class distribution of sequential samples (Figs. 1, 2, and growth section). The largest collections of

snakes in which all age classes were represented were made in Feb.-March and May 1975 (Table 1), hence it is appropriate to use these samples to estimate the overall age structure of the population. The Feb.-March and May samples also contain the largest collections of females. Table 5 presents the size class distributions for the female snakes collected in January ($n = 53$), Feb.-March ($n = 160$) and May ($n = 58$) samples, in five cm increments of s-v length.

In the Feb.-March sample the young (21-30 cm s-v length) are a discrete size class and constitute about 60% of the female population in the sample.

Because the data presented earlier indicate that reproduction is synchronous and annual, the next larger snakes are presumed to be one year old. The lower size limit for this group is clearly the 41-45 cm size class (Table 5), however the upper limit must be approximated. On the basis of the shape of the size class distribution of Feb.-March females (Fig. 1d), and estimates of the growth rate of the young from February until September, the upper limit can be set at 75 cm. It is also possible to get an estimate of the upper size limit for one-year-old females in another way. The largest young at an age of six months are 51-55 cm long (s-v) (Fig. 1h). If these fast growers were to continue

at the same maximum rate for six more months, they would be approximately 81–85 cm long (s-v) at the end of one year. However this is probably not the usual case since growth rates are likely to vary for an individual throughout its first year, and furthermore snakes also clearly grow considerably in girth in the second half of their first year of life. Thus it seems more likely that very few individuals would exceed a s-v length of 80 or even 75 cm in one year. The bulk (23 snakes) of the females from 41–75 cm s-v lengths fall between 61 and 70 cm. This group of one-year-old females (41–75 cm s-v) constituted about 26% of the Feb.–March 1975 female population (Table 5).

The female snakes >75 cm long (s-v) are probably all at least 18 months old. Because all females ≥ 73 cm long (s-v) in the Jan.–Feb. sample were gravid, it is likely that growth in length declines in females 75–80 cm long (s-v) as fat accumulation and reproductive activities occur toward the end of the second year. Thus a s-v length of 90 cm seems to be a reasonable upper limit for two-year-old females. The size limits for this group are then 76–90 cm, and the average s-v length is 85.0 cm ($n = 13$, $s = 4.9$). From the regression line in Fig. 3, a clutch size of about 15 young would be predicted for females reaching the 90 cm size s-v length. The two-year-old females make up about 8% of the Feb.–March 1975 female population sample, and the remaining females (>90 cm), which are three or more years old, make up about 6% of the female population sample for Feb.–March.

If a modest amount of growth is allowed for, proportions of the size classes in the May sample are very similar to those observed in the Feb.–March sample.

An estimate of the female mortality during the first year, 45.8%, was obtained by subtracting the percentage of one-year-old females in the Feb.–March sample (26.2%) from the percentage of newborn females (59.3%) and dividing by the percentage of newborn females (Table 5). Using a similar calculation, it can be estimated that 68.5% of the females alive at the end of their first year are lost from the population during their second year of life. Accordingly, the total female mortality by the end of the second year as a percentage of young females is 86.1%. Other estimates of mortality are presented in the Discussion.

The comparable age class data for males collected in January ($n = 59$), Feb.–March ($n = 204$) and May ($n = 67$) are illustrated in Fig. 1.

For Feb.–March males the upper limits for the first- and second-year classes were set at 66–70 cm and 81–85 cm respectively. These values are lower than those set for females but they reflect the earlier tentative conclusion that growth of males begins to slow relative to that of females sometime during the second year of life (Fig. 2). Also, the smallest gravid female was 73 cm (s-v) while the testes of Sept. males measuring 66.5 to 70 cm (s-v) contained high densities of mature sperm and are presumed to be 18 months of age. The demarcation of the upper limit of two-year-olds follows the pattern used for females and is at best a rough approximation due to the fact that males attain less total length and thus “bunching” of age classes occurs at shorter s-v lengths.

Calculation of mortality rates for males in a manner analogous to that for females gives remarkably similar mortality rates for first- and second-year males, 37.5 and 36.7% respectively.

DISCUSSION AND CONCLUSIONS

Growth and reproduction.—Our 1975 data indicate that juvenile *E. schistosa* grow at a rate of about 1 mm per day at Muar. Growth proceeds under rather constant temperature conditions (approximately 28 to 29 C) at Muar throughout the year. The young snakes feed avidly, specializing on abundant estuarine catfish (Tachysuridae and Plotosidae), and their digestive rates are rapid (Voriss et al., 1978).

Females apparently begin to accumulate fat in about May and continue to do so through September. Ovarian eggs begin to enlarge very gradually in May, and by September those ovarian eggs which are destined to produce the next young are clearly distinguishable. Eggs enlarge rapidly in September and October and are ovulated in November, at a size of about 30 mm. Gestation extends until the latter part of February. In 1975, all 18-month-old females produced large eggs for ovulation. Two- and three-year-old females appear to dominate the reproductive effort and there is an increase in fecundity with increasing s-v length. The reproductive cycle among female *E. schistosa* collected in 1975 from the mouth of the Muar River was synchronous. An analysis of the reproductive condition of the females and the presence or absence of particular size classes of young in small collections taken at Muar in November 1971, December 1976 and February 1977 support the hypothesis that the cycle is

not only synchronous but also annual. The distribution of these samples over the seven year period from 1971 to 1977 eliminates the possibility that a biannual cycle might be occurring. The maximum testicular activity from September to November coincides with what would be expected on the basis of the synchronous, annual reproductive cycle of the females. Ovulation occurs in November, and peak mating activities likely occur in September and October.

Bergman (1956) reported a growth rate for *E. schistosa* of 0.19 cm/day over a two month period. Bergman's data suggest that 25 cm s-v length snakes, i.e., newborns, should appear in the Surabaia population about late November or early December, which agrees with what Bergman postulated. It is thus very likely that interpopulation variability in the time of births exists between the Surabaia and Muar populations of *E. schistosa*. Based on a sample of two specimens, Bergman (1956) suggested that the minimum adult length was reached one year after birth. This is in contrast to the conclusions of this study. Twelve females ranging in size from 68.5 to 93.8 cm were gravid but showed a weak correlation ($r = .60$, $P \geq .02$) between their s-v lengths and clutch size. The basis of this difference between the Muar and Surabaia females is unknown.

Wall (1921) reported that *E. schistosa* newborn from Indian waters measured 25.4 to 27.9 cm. Wall indicated that the young doubled in length in their first year of life, resulting in lengths of 51 to 61 cm. He also stated that snakes would likely be about 76 cm at the end of their second year. Wall noted that snakes appeared in various stages of pregnancy in December, January and February and he speculated that births occurred in February through May. In a sample of "many gravid females," he found that clutch size ranged from 4 to 9, with the smallest gravid female measuring 96.5 cm.

Smith (1920) gave the clutch size for four female *E. schistosa* from Malaysian seas as 2, 7, 7 and 18. Volsøe (1939) reported on one female *E. schistosa* from the Gulf of Iran with nine oviducal eggs and estimated the month of birth as April.

In general, data in the literature on the growth and reproduction of *E. schistosa* are consistent with the Muar observations, although they also suggest possible interpopulation variations.

Some data are also available on other sea snake species. Bergman (1949) reported on 550

Lapemis hardwickii, from which a growth rate of 0.03 cm/day can be calculated for the first year. This is only about one-third the estimated growth rate of *E. schistosa*, however it is not surprising. Although *E. schistosa* and *L. hardwickii* have similar lengths at birth, *L. hardwickii* is a much stouter snake and reaches sexual maturity at about 45 cm (s-v) rather than 70 cm as does *E. schistosa*. Calculation of a growth rate for 539 *Thalassophis anomalus* reported on by Bergman (1954) also gives a rate of 0.03 cm/day. Female *T. anomalus* reach sexual maturity at between 45 and 50 cm (s-v) but are not stocky. Data on 347 *Hydrophis fasciatus* (Bergman, 1956) indicate a growth rate of about 0.05 cm/day. Female *H. fasciatus* become sexually mature at about 63 cm (s-v). The species is microcephalic, i.e., the head and anterior one-third of the body have a much reduced girth.

Population structure.—The age distribution data presented in the Results section were given a literal interpretation. Implicit in the previous analysis of the population data was the assumption that all size classes of snakes have an equal probability of capture. Once snakes reach the mouth of the net this is probably a good assumption, based on observations of the mesh size and mode of operation of the nets. However, if there are any differences in habitat preferences among snakes of different size classes or reproductive conditions, this assumption is no longer valid since the nets were fixed in place. Indeed, there are some significant variations in the data for which alternative interpretations need to be explored.

First, according to the Binomial test (Siegel, 1956), the distribution of adult specimens differs significantly ($P < .01$) from a 1:1 sex ratio in the February–March sample, but not in any of the others. In the February–March sample there are nearly twice as many males as females. Also, although the 193 newborn snakes make up 53% of the sample (364 snakes), all but one of the 23 adult females were still gravid. One interpretation of this is that about half the females were temporarily unavailable for capture, and it was those females which either had given birth or were about to do so.

A second peculiarity of the data is the relationship between the numbers of young and reproductive females. From the data in Fig. 3 fecundities can be estimated. Females between 72 and 90 cm s-v length (two-year-olds) have an average of 10.4 young ($n = 16$, range = 12–30,

$s = 6.8$); females between 90 and 100 cm (three-year-olds) have an average of 21.5 young ($n = 11$, range = 12–30, $s = 5.3$); and females greater than 100 cm s-v length (four or more years old) have an average of 24.5 offspring ($n = 6$, range = 13–33, $s = 7.4$). Multiplication of these fecundity estimates by the number of females in each size class and summing the results yields an estimate of the total number of young expected from those adult females. When this is done for the January sample (Table 5, e.g., 13 two-year-old females multiplied by 10.4 young per two-year-old female equals 135 young, etc.) an estimate of 430 young (including both males and females) is obtained. For February–March and May the estimates of young are 350 and 117 respectively. These estimates of expected captures exceed the observed numbers of young for February–March (191) and May (78) by 83 and 50% respectively.

These data suggest that either the young are unavailable for capture as they would be if their habitat preferences were different from those of the adults, or that there is high mortality among the young immediately after birth. If the latter is true, the number of young captured in February–March already reflects considerable mortality and an estimate of mortality during the first year which uses the number of young captured in February–March as a base, will be an underestimate.

There are two other independent ways of estimating mortality. If it is assumed that population size is relatively stable and that approximately the same number of young are born each year, one way of estimating mortality is to consider the difference between the number of unborn young and 11-month-old snakes in the January sample (430 and 67 respectively) as representative of the survival rate of young snakes during their first eleven months of life. Thus, since the 67 eleven-month-old snakes represent 16% of the 430 unborn young, the survival rate would be 16% (and mortality 84%) during the first eleven months of life.

Another approach is to compare the ratio of young to adults in different sampling periods. For example, in the January sample there are 12.7 unborn young per adult. If adult mortality is assumed to be small compared to the mortality of young, the expected number of young in September can be estimated by multiplying 12.7 young per adult by the number of adults in September, which was 12. This results in a figure of 151.8 expected young, however only

29 were captured. This represents an 81% loss (19% survival) in the 7.3 months between sampling periods.

The latter mortality estimate becomes completely independent of the January sample, if it is calculated in an analogous fashion between the May and September samples, a period of about 3.5 months (Table 1). Such a computation results in an estimate of 56% survival for the 3.5-month period between May and September samples.

Upon further investigation it may be seen that those two independent estimates of survival (16% for the 11-month period and 56% for the 3.5-month period) are remarkably similar. That is, if a half-life is calculated according to the method of Feynman et al. (1963), for the 3.5-month period, using the 56% survival rate, the result is 4.18 months. Then if the 4.18 months half-life figure is used in the same formula to calculate the expected survival rate after 11 months, the result is 16%, which is identical to the previous determination which was arrived at independently.

Such a high degree of agreement is in fact unusual. It is most likely related to a curve of survival for the first year. Since the 3.5-month interval used to estimate the half-life was taken from May to September, which is in the middle of the eleven month period from January unborn to January yearlings, it probably estimates an average survival for the first eleven months. Thus it would be expected to be similar to the estimate which is actually based on the entire eleven month period.

The two methods of estimating survival yield similar results and this suggests that the mortality in the first year is probably much closer to 80 to 90% than to the 36 to 45% estimated directly from the February–March sample data of newborn young and yearling males and females respectively in the Results section.

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