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Sexual maturity and sex ratios of the ommastrephid squid, Illex illecebrosus (LeSueur), at Newfoundland (Subarea 3)

by

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Introduction

The squid Illex illecebrosus is a seasonal migrant to Newfoundland inshore waters. Immature juveniles arrive inshore in late June or July and depart generally in November by which time many of the males are mature although females remain in the immature state (Squires, 1957, 1967; Mercer, 1965, 1969). Spawning areas and times are unknown but Squires (1957) has suggested winter spawning offshore at an age of one year; the species is presumed to be monotelic and to die after spawning (Mercer, 1965; Squires, 1967).

The following preliminary account proposes a simple unambiguous series of maturity stages for males and describes seasonal, year to year and areal variation in maturities and sex ratios. As female squid remain in the immature state during their sojourn in Newfoundland inshore waters, female maturities will not be discussed in this paper.

Materials and Methods

Specimens examined

All specimens were taken by handline and jigger in inshore waters of less than 20 metres depth (Fig. 1). Conception Bay samples were taken at various localities in 1965 and all were obtained at Holyrood in succeeding years. Hermitage Bay samples were taken at various localities in 1966 and at Rencontre West only in 1965 and 1967.

Dorsal mantle lengths were measured to the nearest centimetre from the antero-dorsal protuberance to the apex of the tail fin. Maturities were classified according to the scale defined below and testis weights recorded to the nearest 0.1 g.

Maturity stages

Stages of maturity for males were determined by gross visual inspection of the vas deferens and the spermatophoric organ and sac (Fig. 2) as follows:

Immature: Spermatophoric organ thin and transparent to translucent. Vas deferens thin and transparent. Spermatophoric sac empty.

Maturing Stage I: Spermatophoric organ with a thin white mid-lateral streak. Vas deferens thin and transparent or with a slight white streak. Spermatophoric sac empty.

Maturing Stage II: Spermatophoric organ with a white mid-lateral streak. Vas deferens thick and creamy white. Spermatophoric sac empty or containing a few whitish particles (no complete spermatophores).

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Mature: As for previous stage except that the spermatophoric sac contains spermatophores.

The stages represent sequential changes in the appearance of only part of the genitalia during the course of spermatophore formation but these stages are unambiguous and have been found not to offer problems of reproducibility between workers. The definitions purposefully exclude reference to attendant changes in size, appearance or histology of the testis.

Data analysis

Maturities. The technique applied to analysis of the maturity data was that developed for comparison of dosage-mortality data (Bliss, 1935a,b). The technique is widely applied in bioassay (see Finney, 1952) and has previously been used in analyzing maturity data (see Fleming, 1960). As adapted here, maximum likelihood estimates of a and b for the probit equation $Y = a + bx$ were obtained by an iterative scheme; the program was modified from Subroutine PROBT of the IBM System 360 Scientific Subroutine Package. The procedure assumes normality in the distribution of critical values.

Numbers at each length in each maturity stage were summed by month for each year and area. The samples were "dosed" with mantle length, the resultant Mat_{50} values obtained being the mantle length (cm) at which 50 percent of the specimens leave or enter the given maturity stage. While size frequency distributions of the immature and mature stage animals present sigmoids the intervening maturing I and maturing II stages fall in normal distributions. To render these into sigmoids the maturing classes were summed with the adjacent immature or mature classes and Mat_{50} values were then obtained for immature, immature + maturing I, maturing II + mature, and mature specimens.

Between year comparisons of size at 50 percent maturity in a given month and area were made employing a one-sided t test, the one-sided test being applicable as the ordering of the Mat_{50} values was by prior hypothesis. The t test application to the probit equations of slightly differing slope is here considered equivalent to its application to comparison of skewed and thus slightly non-normal distributions; the robustness of the test indicates its applicability in this circumstance. Sample sizes of specimens cannot be used in the analysis as numbers examined at the ends of the range outside the zone where the change in maturity class is occurring are irrelevant and their inclusion would bias the analysis. Probit weighting factors were employed instead of the sample sizes. For purposes of this paper time precluded the covariance analysis which is the most suitable test.

Length-gonad weight equations were computed using the equation $W = cL^b$ in which W = testis weight, L = mantle length and c and b are constants which were estimated from a least squares regression of the logarithmic transformation $Y = a + bx$ in which $Y = \log_{10}W$, $a = \log_{10}c$ and $x = \log_{10}L$.

Sex ratios. Each sample was examined for deviation from numerical equality of the sexes. The χ^2 test was applied (1 df) and all probability values are tabulated, a 10 percent probability of inequality being considered "significant" enough to merit discussion in the results.

Results

Maturity

Maturation was found to be related to the correlated variables squid size and season and between year and areal variation was observed (Table 1, Fig. 3). Goodness of fit to the probit equation varied considerably. For instance in September 1967 at Rencontre West where only 4 of 950 specimens examined were mature $\chi^2 = 2.09$ and $P = .98$ whereas at Holyrood where 252 of 795 specimens were mature $\chi^2 = 32.98$ and $P = .00052$.

Seasonal variation. At the time of their arrival inshore in late June or early July all squid were found to be immature and, except for one 21 cm maturing I squid taken at Holyrood on July 12, 1971, all squid sampled in July were classified as immature. In August 1966 at Holyrood immature males ranged to 25 cm mantle length but in subsequent months the largest were 23 cm. Size at which 50 percent of the samples left the immature stage dropped from 22.6 to 21.8 cm from August to September 1966 and more slowly thereafter. Whereas in August only 14.3 percent of 14 specimens 24 cm or larger were in stage maturing II, in September 57.5 percent of 137 specimens of this size were maturing II or mature. The trend is consistent for all years and areas studied, size at which 50 percent of the specimens leave the immature and both immature and maturing I stages and enter the maturing II and mature stages decreases over the season. The only anomalies occurred in November (1966 Fortune Bay and Holyrood immature class, and 1967 Holyrood mature class) involving small sample sizes and/or poor fits to the probit equation.

Areal variation. Various comparative data are available for Conception Bay (Holyrood), Fortune Bay and Hermitage Bay in 1966-67. Sizes at 50 percent exit from immature-maturing I in September 1966 were 24.03, 23.91 and 23.37 cm respectively in the three areas, the paired comparisons by one-sided t test being highly significant ($P << .0005$). Other comparisons of immature and immature-maturing I animals result in a similar ordering of Mat_{50} values. Mat_{50} values for mature animals on the south coast are higher than at Holyrood (Conception Bay) and few mature animals were taken in south coast samples. However, maturing II stage animals bulked larger in south coast samples (Fig. 4).

Between year variation. Comparative data are available for three years from Holyrood only. Most increasing Mat_{50} values fall in order of years 1967, 1971, 1966 (Table 1) which is the order of decreasing water temperatures. Based on the hypothesis that more rapid maturation occurs under warmer temperature conditions (see Richard, 1966) one-sided t tests were used to compare differences observed at Holyrood in September of each of the three years (Table 2). Three of four comparisons indicated highly significant differences (which would also be highly significant in a two-sided test). Anomalies from this trend are seen in comparisons of Mat_{50} values for immature squid at Holyrood for August 1966 and 1971 and for November 1967 and 1971 immature-maturing I and mature squid.

Testis weights. Testis weight increases as a function of mantle length and with advancing maturity (Fig. 5 and 6). Calculations from the fitted regressions (Fig. 6) indicate testis weights of 0.8, 2.2, 4.0 and 5.7 g for 23 cm immature, maturing I, maturing II and mature squid respectively.

Sex ratios

Data for the years 1966, 1967 and 1971 are given in Fig. 7. Males predominated significantly ($P < .05$) in only 1 of 32 south coast samples in 1965-67, this being taken early in the season (Sept. 13, 1966). Females predominated significantly in most of the other samples ($P < .05$ for 19 samples and $P < .1$ for 1 sample), this preponderance being most striking late in the 1966 season.

At Holyrood the pattern is somewhat different. In considering samples collected July 6 to the end of September males predominated significantly in 5 of 12 samples ($P < .05$ in 3 and $P < .1$ in 2) in 1966, in 5 of 10 samples ($P < .05$ in 3 and $P < .1$ in 2) in 1967, but in only 1 of 10 samples ($P < .02$) in 1971 and 0 of 4 in 1965. In only one early season sample taken 1966-71 (July 19, 1971) were females preponderant ($P < .01$), but in 1965 females comprised a significant majority in 3 of 4 samples ($P < .05$ in 1 and $P < .1$ in 2). Late in the season the pattern changed. Females were significantly more abundant in 6 of 13 samples ($P < .05$ in 4 and $P < .1$ in 1) and males in only 2 ($P < .001$ in 1 and $P < .1$ in 1), both of these latter being in 1967.

Females were more abundant in all 5 samples taken at Englee Aug. 11-Sept. 14, 1965 but in only the last was the difference significant ($P < .1$).

In a Trinity Bay sample taken July 27, 1965 males were preponderant ($P < .01$) but females comprised a majority in the 4 remaining samples taken Aug. 18-Sept. 9 ($P < .05$ in 2).

Discussion

Squires (1957) reported no mature males prior to September but in September to November he reported "early" or "late" spermatophores in 75 percent of specimens examined. (Terms were not defined.) Squires noted an increase in testis weight for squid at a given length throughout the season but he supplied no supporting data. The maturation of males at progressively smaller sizes later in the season is consistent with available information on maturation in cephalopods. Wells and Wells (1969) described, in an octopod, a negative feedback system involving the optic glands and testes (or testicular ducts) which is a functional analogue of the pituitary system in mammals. This system explains the prolonged maturity of males, compared with females, where there is apparently no ovarian hormone. Richard (1968) found that photoperiod affected maturation of female cuttlefish (*Sepia officinalis*) and it is likely that the same situation obtains in males. The pattern observed was a quickening of maturation with decreasing day length and our data on maturation of male *Illex illecebrosus* are consistent with the same situation obtaining for this species.

In controlled rearings of female cuttlefish, Richard (1966) demonstrated the accelerating effect on maturation of elevated temperatures. Observations reported here indicate that year to year and regional differences in maturation of male *Illex illecebrosus* in the Newfoundland region may also relate to temperature differences with more rapid maturation occurring under warmer temperature conditions.

The dearth of mature specimens and higher Mat_{50} values for the mature class in south coast samples may reflect reduced catchability of mature squids possibly related to offshore migration (Mercer, 1969). The lower proportion of males in the catch late in the season (Fig. 7) supports this conjecture.

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Table 1. Comparison of probit analyses of _Illex illecebrosus_ maturities by month, year and area. Mat_{50} indicates mantle length (cm) at which 50 percent of the specimens leave (immature and immature-maturing I) or enter (maturing II-mature and mature) the given stage of maturity. Slope and intercept only are given for maturing II-mature as other data are redundant with those given for immature-maturing I.

Time	IMMATURE						No. Imm	IMMATURE-MATURING I						No. Imm-Mat I
	Mat_{50}	$SE(Mat_{50})$	Slope	Intercept	Fit of line			Mat_{50}	$SE(Mat_{50})$	Slope	Intercept	Fit of line		
					x^2	Prob.						x^2	Prob.	
Holyrood														
1966 Aug.	22.6326	0.1063	-1.1361	30.7126	144.6193	0.00000	581	25.3504	0.7127	-1.2437	36.5199	1.8521	0.9993	667
Sept.	21.7687	0.0762	-1.3370	34.1050	1.7931	0.98568	322	24.0325	0.0939	-0.8690	25.8845	10.0598	0.2615	579
Oct.	21.7666	0.1198	-1.2301	31.7749	4.8486	0.77478	78	24.0579	0.0961	-1.0749	30.8593	426.3835	0.0000	244
Nov.	21.9115	0.1538	-1.1074	29.2657	1.1918	0.97581	83	23.9349	0.2936	-0.8818	26.1051	1.8681	0.9307	121
1967 Aug.	22.0469	0.0499	-0.5040	16.1126	42.5676	0.00004	660	24.8209	0.2348	-0.6757	21.7703	324.1064	0.0000	988
Sept.	21.4258	0.0869	-0.8444	23.0923	0.6908	0.99984	155	23.0869	0.0557	-0.8382	24.3517	8.3293	0.5978	375
Oct.	no imm						0	22.0058	0.2682	-0.8543	23.7988	31.7954	0.0001	19
Nov.	21.1267	0.5391	-1.4149	34.8930	0.6637	0.99915	4	21.6622	0.3581	-1.0412	27.5550	4.1913	0.8399	10
1971 Aug.	22.6929	0.0713	-0.8627	24.5759	42.1450	0.00005	976	25.2902	0.3556	-0.6905	22.4640	1.4790	0.99846	1172
Sept.	21.7719	0.1197	-0.8837	24.2394	0.8990	0.92321	64	23.6854	0.1746	-0.7482	22.7215	0.6681	0.95274	154
Nov.	no imm						0	21.3339	0.3630	-0.8986	24.1706	1.5987	0.81085	9
Hermitage Bay														
1966 Sept.								23.3663	0.2569	-0.8676	25.2737	2.1928	0.9938	730
1967 Aug.	21.7624	0.2853	-0.5548	17.0730	11.2218	0.12999	859							886
Sept.	19.9428	0.0466	-0.5118	15.2071	5.8673	0.66380	429	22.4737	0.0889	-0.8373	23.8164	9.6583	0.2904	819
Oct.	19.3971	0.0800	-0.6411	17.4355	3.3407	0.94867	144	22.0117	0.0719	-0.8249	23.1581	5.2676	0.8109	358
Fortune Bay														
1966 Sept.								23.9147	0.1107	-1.0105	29.1658	16.0578	0.0667	420
Oct.								22.4956	0.0842	-0.8450	24.0096	12.5094	0.1875	521
Nov.	20.2012	0.3040	-1.4866	35.0315	1.4084	0.96407	24	21.6943	0.2743	-0.9764	26.1829	1.5268	0.9566	36

. . . Cont'd.

Table 1. Cont'd.

Time	MATURING II-MATURE		No.	MATURE						No.	d.f.	Total
	Slope	Intercept	Mat II-Mature	Mat_{50}	$SE(Mat_{50})$	Slope	Intercept	Fit of line		Mature		examined
								χ^2	Prob.			
Holyrood												
1966 Aug.	not fitted		2	no mature						0	12	669
Sept.	0.8693	-15.8904	108	25.4037	0.1982	0.7179	-13.2373	11.6898	0.16654	37	8	687
Oct.	1.0748	-20.8582	115	24.7617	0.1181	1.0103	-20.0165	27.5394	0.00090	71	8	359
Nov.	0.8816	-16.1007	12	24.6949	0.5537	1.6905	-36.7461	0.0956	0.99979	3	6	133
1967 Aug.	0.6758	-11.7727	32	27.7266	0.5956	0.3944	- 5.9363	51.4359	0.00001	11	10	1020
Sept.	0.8384	-14.3550	420	24.1452	0.0590	0.7344	-12.7334	32.9789	0.00052	252	10	795
Oct.	0.8539	-13.7910	467	22.6950	0.1677	0.7739	-12.5639	5.8734	0.56102	438	6	486
Nov.	1.0414	-17.5582	584	22.8736	0.1740	1.0929	-19.9984	21.4749	0.00661	553	8	594
1971 Aug.	0.4628	- 7.7496	16	no fit to probit						7	10	1188
Sept.	0.7482	-12.7219	42	25.3328	0.5744	0.7916	-15.0545	2.4683	0.65383	6	4	196
Nov.	0.8992	-14.1840	160	21.9719	0.2316	0.6834	-10.0152	2.1482	0.71192	145	4	169
Hermitage Bay												
1966 Sept.	0.8677	-15.2748	15							3	10	745
1967 Aug.			0	no mature						0	7	886
Sept.	0.8375	-13.8225	131	24.7149	0.6937	1.0181	-20.1622	2.0915	0.97714	4	8	950
Oct.	0.8252	-13.1649	215	24.5401	0.1537	0.5880	- 9.4300	9.8973	0.3597	55	9	573
Fortune Bay												
1966 Sept.	1.0106	-19.1690	88								9	508
Oct.	0.8454	-14.0164	150	25.2748*	0.2038	0.7090	-12.9211	2276.9921	0.00000	25	9	671
Nov.	0.9768	-16.1920	14	no mature						0	6	50

*Deleting a single precocious male recorded as mature at 19 cm
Mat_{50} = 24.9136, χ^2 = .1942, P = .9999

Table 2. Between year comparisons (one-sided t test) of size at which 50 percent of squid a) pass beyond stages immature and maturing I and b) enter the mature stage at Holyrood in September. Air temperatures given are the means of daily high and low air temperatures for the period July 1-Sept. 30 at Torbay. Water temperatures are means of daily high and low surface temperatures at Holyrood July 5-Sept. 24.

Sept.	Mean Temp. (C)		Immature-maturing I				Mature			
	Water	Air	Mat_{50}	t	df	P	Mat_{50}	t	df	P
1967	11.4	16.5	23.09				24.15			
				52.92	416	<< .0005		36.06	361	<< .0005
1971	8.8	14.7	23.69				25.33			
				20.75	256	<< .0005		1.02	122	.15<P<.20
1966	-	14.4	24.03				25.40			

Table 3. Numbers of testis weights used in computing the regressions in Fig. 6.

Length / No. examined	Immature	Maturing I	Maturing II	Mature
15	1			
16	5			
17	9			
18	24			
19	33			
20	52	1		
21	59	8		2
22	52	40	4	1
23	14	60	15	14
24	3	29	23	59
25	1	4	10	88
26			1	56
27				3
28				1
Totals	253	142	53	224

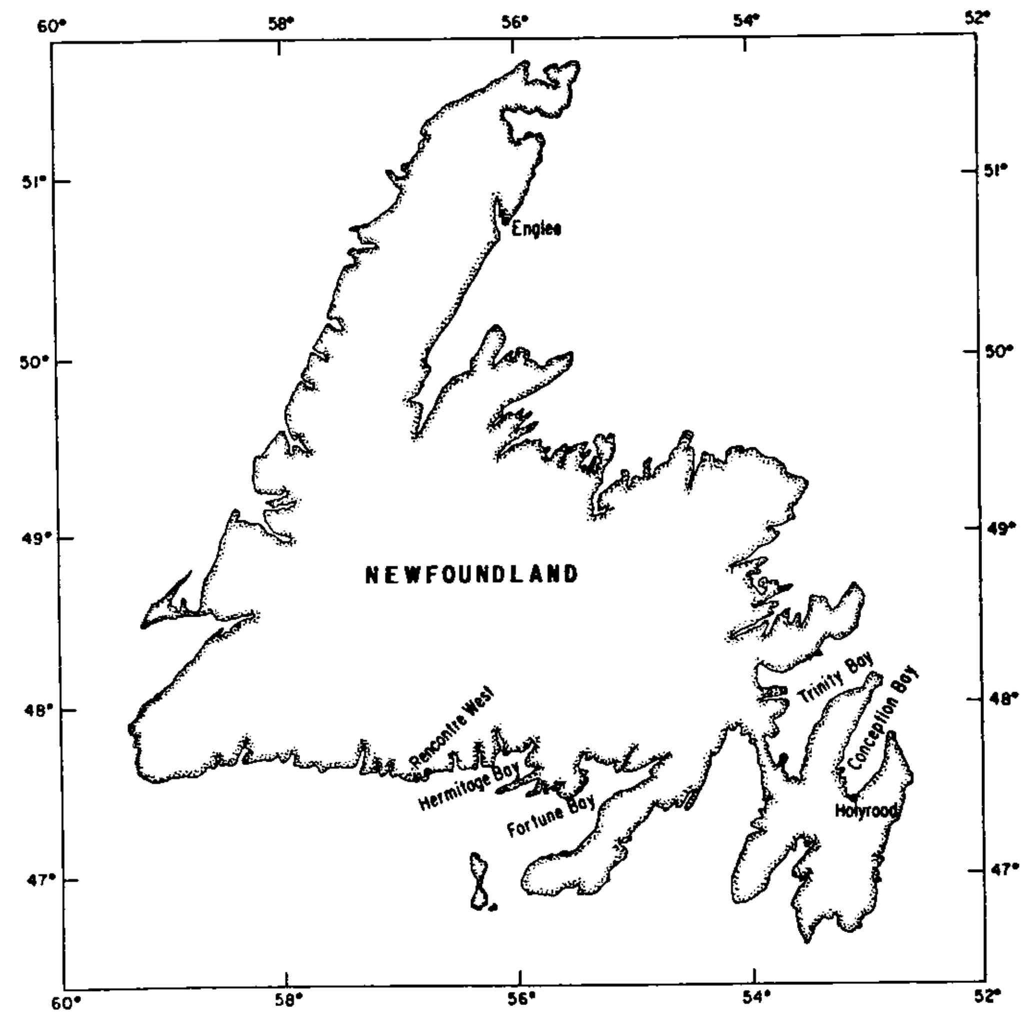

Fig. 1. Map of Newfoundland showing place names mentioned in the text.

Fig. 2. Lateral views of the spermatophoric organ and sac and vas deferens of Illex illecebrosus from Newfoundland. Top to bottom: maturing stage I, maturing stage II, mature. See text for descriptions.

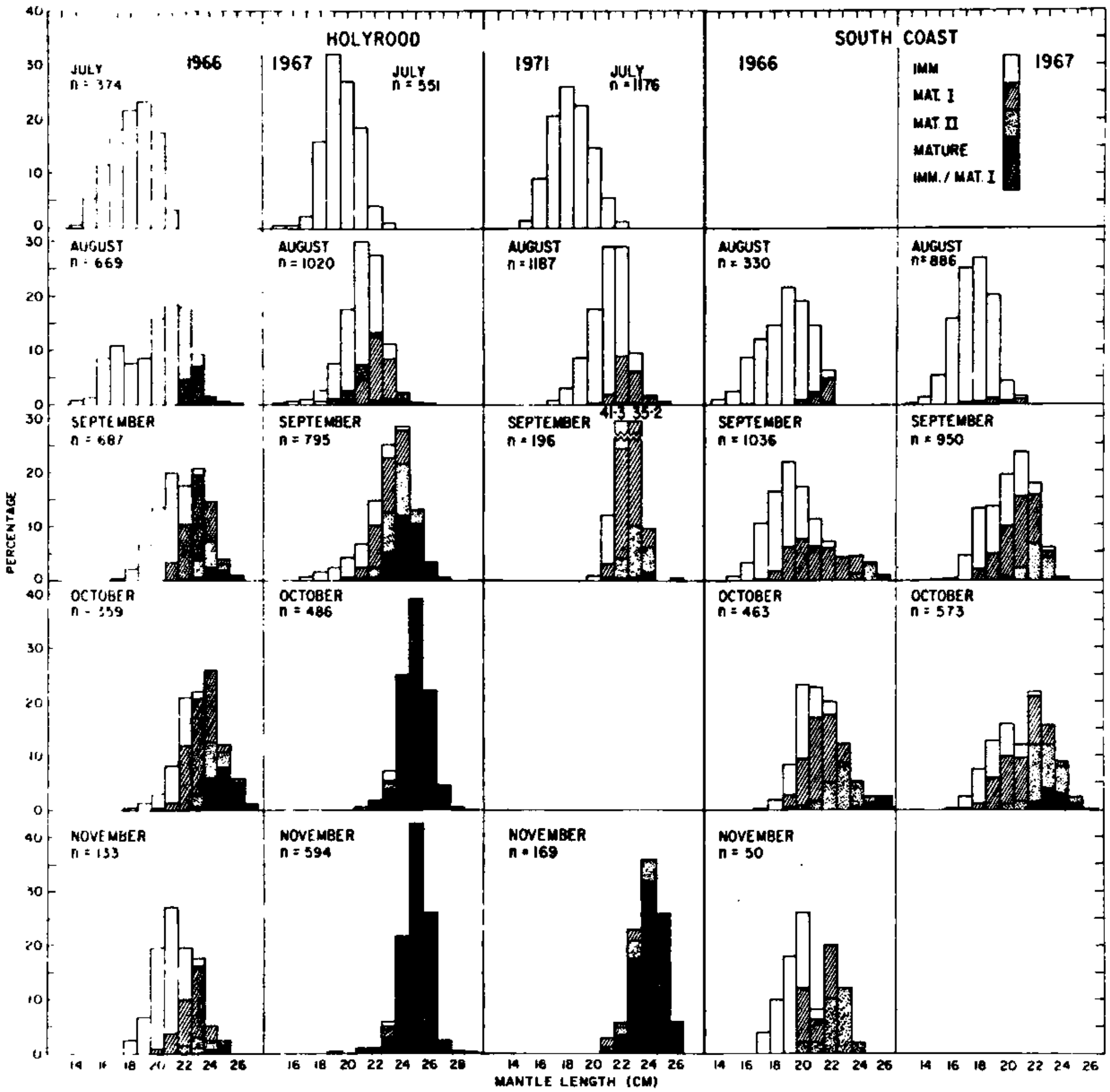

Fig. 3. Sexual maturities of male Illex illecebrosus from samples obtained at Newfoundland in 1966, 1967 and 1971. Numbers indicate sample sizes.

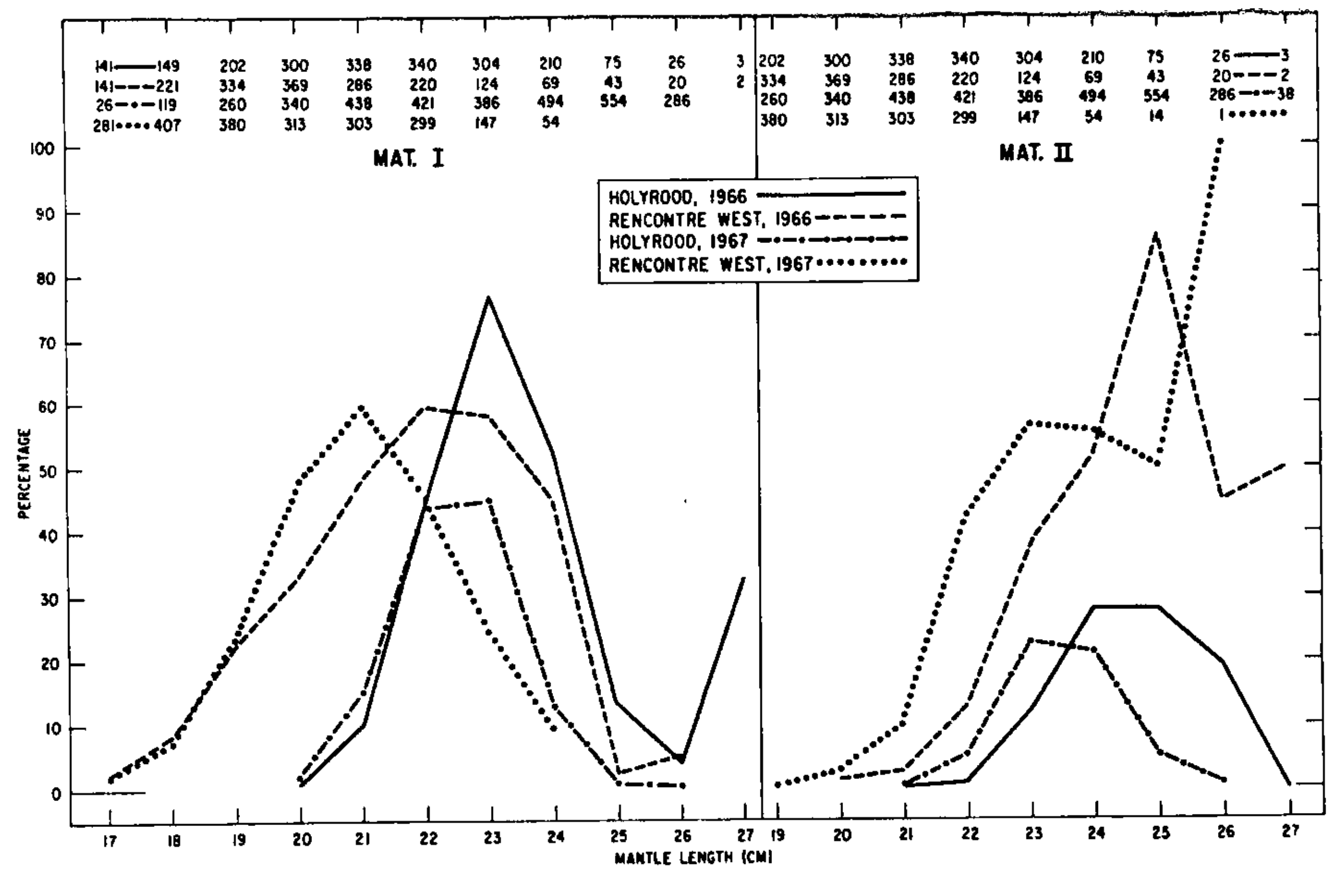

Fig. 4. Size distributions of male Illex illecebrosus in the maturing classes from samples obtained at Newfoundland in 1966 and 1967.

Fig. 5. Testes of Illex illecebrosus of mantle length 23 cm collected at Holyrood October 3, 1967. From left to right: mature, testis weight 7.6 g; maturing stage II, testis weight 6.0 g; maturing stage I, testis weight 4.5 g.

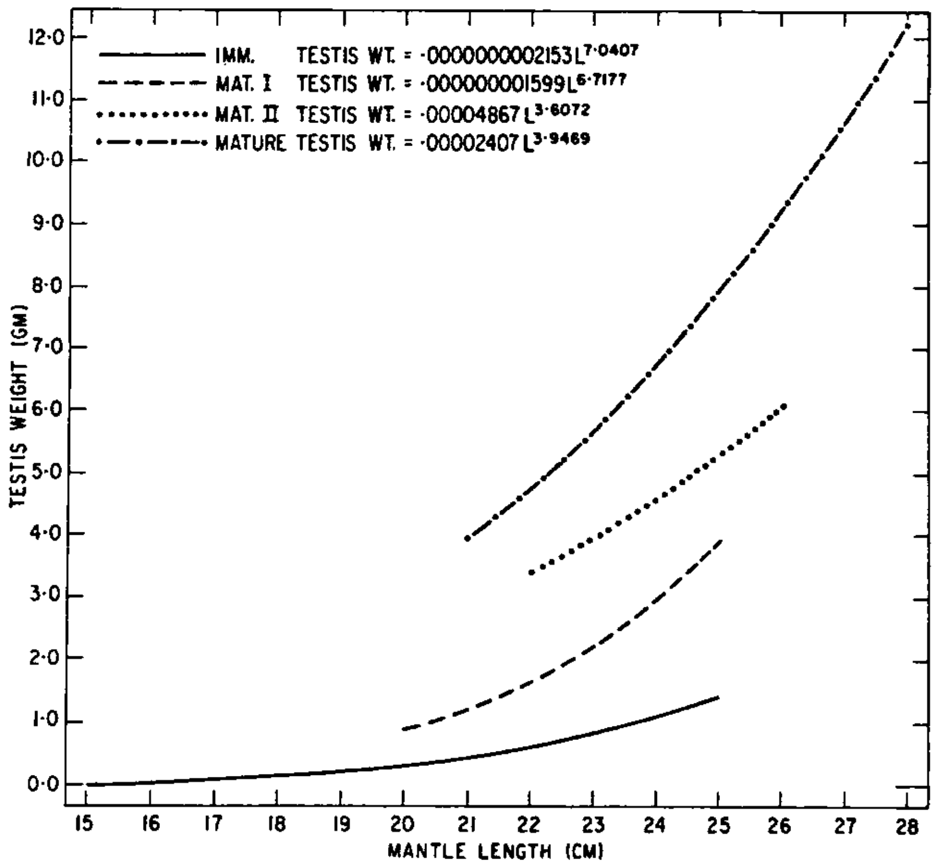

Fig. 6. Length-testis weight regressions for male Illex illecebrosus. Numbers of specimens used in computing the curves are given in Table 3.

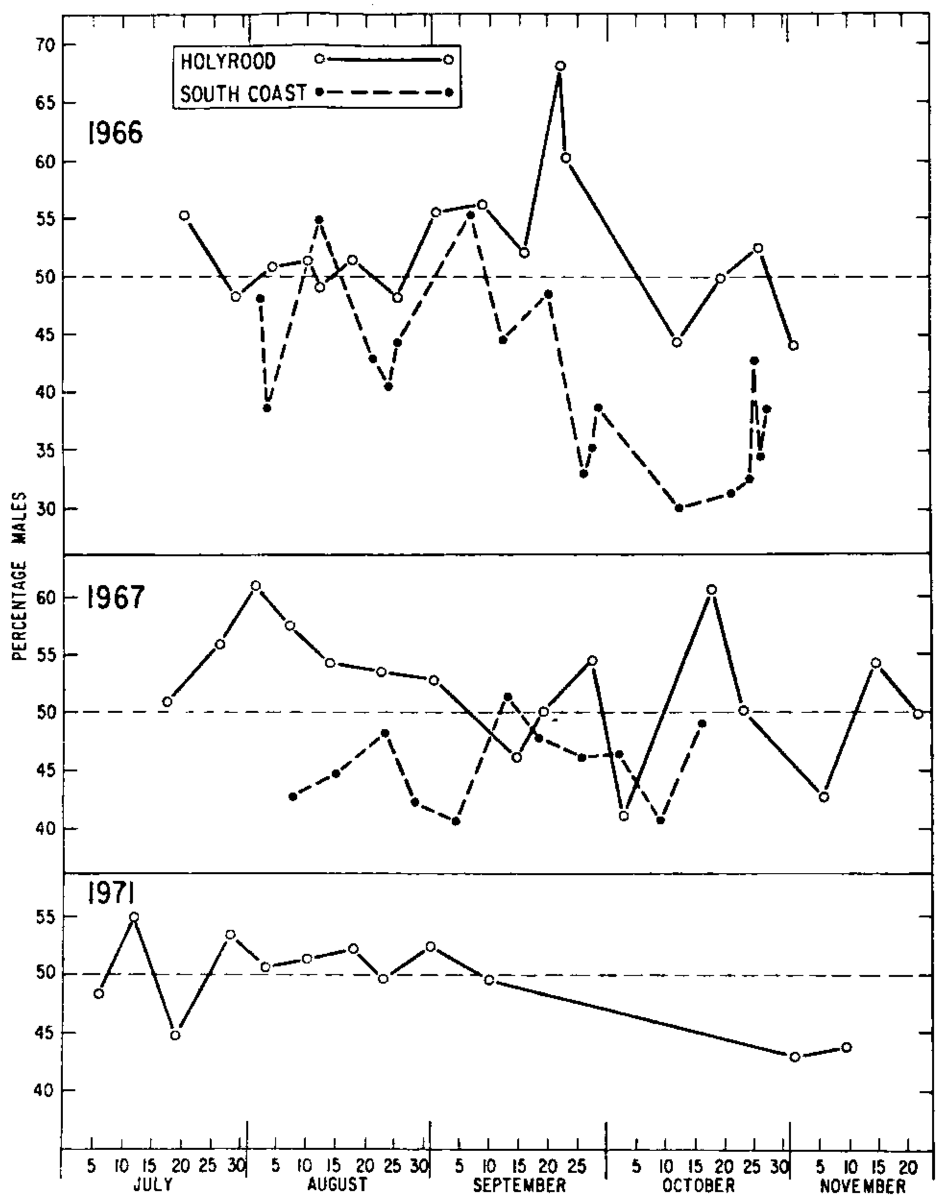

Fig. 7. Sex composition of samples of Illex illecebrosus obtained at Newfoundland in 1966, 1967 and 1971. Data points are joined for ease of interpretation of the figure.