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Universal Maturity Scale for the Commercially-important Squids (Cephalopoda: Teuthoidea). The Results of Maturity Classification of the *Illex illecebrosus* (LeSueur, 1821) Populations for the Years 1973-1977

by

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A b s t r a c t

The paper gives a description of universal maturity scale for the commercially important species of squids. This six - grade scale was substantiated by maturity analysis of the following species of squid: Loligo pealei, L. vulgaris, Illex illecebrosus, I. argentinus, Todaropsis oblanae, Todarodes angolensis, T. filippovae, Ommastrephes bartrami, Sthenoteuthis pteropus, Martialia hyadesi, Lycoteuthis diadema and Abraliopsis gilchristi.

The results of the Illex illecebrosus maturity analysis and the fecundity of two females of this species are also presented. Results of the maturity analysis of other species mentioned will be published later, with results of histological findings.

The fecundity of females of Illex illecebrosus ranged from 31.1 to 83.1 thousand eggs, depending on the method used.

It was found that the period of sexual maturity of Illex considerably varies between stocks and/or years.

I n t r o d u c t i o n

The maturity analysis is the important factor in squid population research. The results of such an analysis may

have many different applications, as was shown by Fields /1965/, Summers /1968, 1971/, Mercer /1973, 1973a/, Mercer and Paulmier /1974/, Paulmier /1974/ and Holme /1974/.

The maturity scale /MS/ for the squids appeared considerably later than that for fishes. The first papers on this subject were published by Tinbergen and Verwey /1945/, Mangold-Wirz /1963/, Castellanos /1964/ and others. Most of these papers treated squid ecology very widely, the MS itself having been only a small part of the whole. Papers, concerned only with the MS appeared much later. It seems, however, that the use of the results of Hayashi /1970/, Vowk /1972/, Mercer /1973/ and Durward et al. /1978/ is restricted to particular species of squids. Filippova /1972/ and Burukovsky et al. /1977/ made the first attempts to work out a universal maturity scale for the squids.

It is believed that the MS presented here is useful for the commercially important species of squids. This category of squids was defined elsewhere /Lipiński, 1977/.

Material and Methods

The MS, described here, was worked out in the years 1972--1974 and tested in the field in the years 1973-1978 for the following species of squids /number of specimens analysed is given in parentheses/: Loligo pealei /1,845/, L. vulgaris /49/, Illex illecebrosus /9,889/, I. argentinus /267/, Todaropsis eblanae /13/, Todarodes angolensis and T. filippovae /156/, Ommastrephes bartrami /116/, Sthenoteuthis pteropus /207/, Martialia hyadesi /37/, Lycoteuthis diadema /214/ and Abraliopsis gilchristi /100/.

Descriptions of the reproductive systems of the Loligo opalescens, L. edulis, Sepioteuthis sepioidea, Doryteuthis singalensis and Sthenoteuthis oulaniensis were also considered /Fields, 1965; Zuev, 1971/.

The material was mostly analysed fresh, but also thawed and from 4% formalin or 70% ethyl alcohol.

Each squid was measured to the nearest mm /DML was used as a standard/ and weighed to the nearest gram. The nidamental glands of the females as well as the hectocotylus and both arms IV of the males were measured to the nearest mm. The measurements, counts, relative proportions /indexes/ of the various parts of the reproductive system were omitted, however, in the descriptions of the maturity stages. Instead, the developmental sequence was selected from each sample: this covered both growth and maturity of specimens. The "discrete" changes in each series was morphologically described. Changes which occurred in different species were taken into account for the description of maturity stages.

The gonads and other parts of the reproductive system of males and females of various species were preserved in 4% formalin, 70% ethyl alcohol or Bouin solution for histological studies. The results of these studies and the results of maturity classifications /other than for Illex illecebrosus/ will be published separately.

The methods used to estimate the fecundity of the Illex illecebrosus were mainly adopted from MacGregor/1957/. The volumetric method was also used for comparison. Routine maturity analyses usually contained more than 100 specimens, randomly selected from each catch.

T e r m i n o l o g y

1. The spermatophoric complex is the morphological unit which contains: the vas deferens, spermatophoric organ, spermatophoric duct, Needham's sac and "penis". The term itself was previously used by Roper /1966, p. 29/;
2. An oviduct meander is identical with the "internal membranous oviduct" as in the paper by Fields /1965/, but here the use of the term is restricted to immature squids /stages II - III/;
3. The testis structure is the morphological feature which could be seen on the surface of the testis of maturing and mature specimens /stages IV - V/.

Results

Introductory notes

1. The morphology and developmental pattern of the reproductive system differs greatly for different species of squids, as was shown during the testing procedure. It seems evident that the testing procedure for only 12 species of squid is insufficient to ensure the universal application of the MS described below.
2. It was found that the MS presented here applies mainly to fresh squid. The differences between stages III and IV of the squids preserved for a long time in formalin, and stages V - VI of all squids /except fresh/ in particular, were hardly noticeable.
3. After considerable field experience the use of a morphological "habitus" of a given stage instead of the numerical parameters was preferred. The latter differ greatly for the various species of squids, and the collection of these data is fairly time-consuming.

Description of the maturity stages

The maturity stages of squids are described in Table 2 and illustrated in Fig. 3. The key-words for identification of "discrete" changes in the developmental sequence are in Table 1.

Fecundity of Illex illecebrosus females

The fecundity of two Illex illecebrosus females was analysed. The results are shown in Table 3.

The results of volumetric analyses were completely different, i.e. 82,500 and 83,100, respectively. These results were considered as highly biased because of the differences in the sedimentation rate between large and small eggs /Crossland, 1977/.

The results of maturity classifications of Illex illecebrosus in the years 1973-1977.

The results of maturity classifications of Illex illecebrosus are shown in Tables 4-29.

Table 1. The key-words for identification of the maturity stages.

Stage number	Males	Females
I	Spermatophoric complex as a whole unit, "spot". The rest invisible.	Nidamental glands as transparent strips. The rest invisible.
II	Parts of the spermatophoric complex.	Meander of oviduct. Isomorphic /homogenous/ ovary.
III	White streak. Vas deferens.	Meander extended. Immature ova.
IV	Vas deferens. White particles in the Needham's sac. Testis structure.	Nidamental glands large. Maturing ova.
V	Spermatophores	Mature ova. The secretion of nidamental glands.
VI	Degenerating spermatophores and sexual organs.	?

Table 2. The maturity stages of squids.

Number and name of the stage	Description of the stage	
	Male	Female
I JUVENILE	The sexual organs are very hard to find with the naked eye. Spermatophoric complex appears /if at all/ as transparent or translucent spot. The testis is transparent, membranous.	The sexual organs are very hard to find with the naked eye. The oviducts and nidamental glands appear /if at all/ as very fine transparent strips. The ovary is translucent, membranous.

Table 2. (cont'd)

Number and name of the stage	Description of the stage	
	Male	Female
II IMMATURE	The sexual organs translucent or whitish. The separate parts of the spermatophoric complex are clearly visible. The testis small; its structure invisible.	The sexual organs translucent or whitish. The oviducts and nidamental glands form clearly visible translucent or whitish strips. The oviduct meander visible /Fig. 1/. Nidamental glands small; all viscera behind them can be easily observed. The ovary clearly visible, in most cases without structures observable with the naked eye.
III PREPARATORY	The sexual organs are not translucent. The was deferens whitish or white, spermatophoric organ with white streak. The testis in most cases is white or pink; its structure is invisible.	The sexual organs are not translucent. Meander of the oviduct is extended. The nidamental glands enlarged, covering some internal organs. The structures inside the ovarium /immature ova/ clearly visible.
IV MATURING	The was deferens white, meandering, enlarged. Needham's sac long, with structureless whitish particles inside, but without formed spermatophores. The testis tight, crispy. The testis surface covered with structure /Fig. 2/.	The nidamental glands large, also cover kidneys and distal part of the liver; the external glandular oviducts are fleshy and swollen Plenty of eggs in the oviducts; the meanders hardly noticeable. The eggs not transparent /roughly 95%/ and are pressed together at least in the proximal part of the oviduct. There are may or may not be many different stages of eggs in the distal part of the oviduct.

Table 2. (cont'd)

Number and name of the stage	Description of the stage	
	Male	Female
V MATURE	As above, except that spermatophores are present in the Needham sac.	As above, but the eggs are translucent /more than 60%/ at least in the proximal part of the oviduct. Cut open, the nidamental glands secrete a viscous substance.
VI SPENT	There are no spermatophores in the Needham sac, or only "exploded", degenerating ones. Spermatophoric complex contains many membranous structures. The condition of the animal is very poor.	There are almost no eggs in the oviduct, or only degenerating ones. The nidamental glands are small, tissue slack and desintegrated. The condition of the animal is very poor. The hypothetical stage /see Fields, 1965/.

Table 3. Fecundity of *Illex illecebrosus*.

Date and position of capture	ML /mm/	Total weight /g/	Maturity stage	Total weight of ova /g/	Weight of subsample /g/	Number of eggs in the subsample	Total number of eggs
22.V. 1975 39°57'N 69°48'W	233	288	IV	31.750	5.315	6,600	39,400
30.V. 1975 40°01'N 70°06'W	220	231	IV	28.622	4.787	5 200	31,100

Discussion

The author considers that the Mizukovsky et al. /op. cit./ opinion that a maturity scale worked out for only one species can be applied for all squids is too optimistic. The different species have different developmental sequences and the scale presented here should be modified. It will probably take a long time to collect sufficient material from all existing families of squids.

The results of the fecundity analyses considerably differ from those of Durward et al./1976/. The total egg mass produced was approximately 11 and 12% of the total body weight of a given female instead of 25% obtained by the authors cited. The number of eggs also differed considerably: 39,400 and 31,100 instead of 420,000. It would appear that a more detailed study is urgently needed to confirm one ore the other result. It should be noted, however, that Durward et al. /op. cit./ calculated the total number of eggs starting from individual ovum weights and total weight of eggs; substantial variation between individual ovum weight could be a serious source of error in such analyses.

The results of maturity studies of Illex illecebrosus could only be discussed here very briefly. This is rather a source of material for further analysis than a detailed study of the life cycle of Illex. It was found that males reached sexual maturity between June and August in 1976 /Canyon Veatch/. The females remained immature. In 1977 the maturity process in males started at the end of July /Nova Scotia/ and in the middle of August there was only 2% of mature squids, while on western Georges Bank there was 45% of mature squids at the end of August, and 22% in the Mid Atlantic Bight at the same time. The number of mature males on western Georges B. increased to 60 - 63% in the first half of September. Mature males were also found on Georges Bank in September 1973 /13%/, the end of June - first half of July 1974 /generally about 1%/ and

in March 1975 /53%/; both males and females were immature in 1975 /with some exceptions - see part concerning fecundity of Illex/.

Mature females were found in September 1973 /Georges Bank, Mid-Atlantic Bight/ and in the second half of October-first half of November 1973 /Cape Hatteras/. In 1974 a mature female was found on Georges Bank in the second half of June, and two at the end of May 1975. A mature female was also found near the Veatch Canyon in the first half of July 1976.

The males always predominated in the all seasons of high abundance /i. e. during summer months/. It is interesting that this observation was contradictory to Sato /1974/ data concerning results of the jigging operations.

This very brief discussion /without growth changes problem/ suggests the following conclusions:

1. Structure within- and among populations of Illex from Subarea 4 to SA 6 is complicated and diverse depending on the year and region. The life cycle of this species probably differs in the different regions.
2. There may be at least three different populations /or subpopulations of one superpopulation/ from Cabot Strait to Cape Hatteras. These are the Nova Scotia population /from Cabot Strait to Browns Bank/, the Canyon Veatch population /from Corsair or Lydonia Canyon to Veatch Canyon/ and the Mid-Atlantic Bight population /from Hudson Canyon to Cape Hatteras/.

   The Newfoundland Illex probably form a separate population /Lipiński, unpubl. data/.

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Table 4. Sexual maturity of Illex illecebrosus in the fall 1973. (Mean catch per hour in research fisheries less than 0.01 tons.)

Date	ICNAF Div.	ML range /cm/		$\overline{ML}$ /cm/		Number of squid in a given maturity stage			
		♂	♀	♂	♀	♂		♀	
5-9.IX.1973	6 AB	10.0-22.0	17.5-24.5	18.0	20.0	10.0 cm ML	1 /I/		15 /II/
							16 /II/	20.0 cm ML	1 /III/
						22.0 cm ML	1 /V/	22.5 cm ML	1 /V/
13-24.IX.1973	5Ze	16.5-24.0	14.0-29.0	20.0	22.0		27 /II/		51 /II/
						21 cm ML	1 /V/	24.5 cm ML	1 /III/
						21.5 cm ML	1 /V/	29.0 cm ML	1 /III/
						23.5 cm ML	2 /V/	24.0 cm ML	2 /IV/
21.X.-3.XI.1973	6 C	13.5-21.5	13.0-23.0	17.0	18.0		19 /II/		17 /II/
						20.5 cm ML	1 /IV/	22.5 cm ML	1 /III/
						21.0 cm ML	1 /V/	23.5 cm ML	1 /III/
						21.5 cm ML	1 /V/	24.0 cm ML	1 /III/
								25.5 cm ML	1 /IV/

Table 5. Sexual maturity of Illex illecebrosus in the summer 1974. (Mean catch per hour in commercial fisheries - 0.5 tons.)

Date	Position	ML range /cm/		ML /cm/		Number of squid in a given maturity stage	
22-23.VI.1974	40°49'N 66°41'W	13.0-21.0	13.0-23.0	17.3	17.5	639 /I-II/	404 /I-II/ 4 /III/ 18 cm ML 1 /IV/
26,28.VI.1974	40°40'N 67°05'W	5.0-20.0	6.0-23.0	17.5 16.7	18.5 16.8	216 /I-II/ 223 /I-III/ 1 /IV/ 18 cm ML 1 /V/	473 /I-II/
30.VI.1974	40°00'N 69°35'W	7.0-20.0	7.0-21.0	16.5	16.6	236 /I-II/ 7 /III/ 4 /IV/ 2 /V/	196 /I-II/ 2 /III/
5-9.VII.1974	40°39'N 67°06'W → 40°36'N 67°23'W	6.0-22.0	7.0-25.0	17.6	18.0	570 /I-II/ 699 /II/ 10 /III/ 5 /IV/ 6 /V/	426 /I-II/ 692 /II/ 18 cm ML 1 /III/

Table 6. Sexual maturity of Illex illecebrosus in the winter of 1975 (6, 13 and 22 March) at positions 39°15'N, 72°25'W; 39°55'N, 69°44'W; and 40°25'N, 68°16'W. (Mean catch per hour in research fisheries less than 0.01 tons.)

ML class /cm/	Stage number / ♂ /					Stage number / ♀/		
	I	II	III	IV	V	I	II	III
8.0						1		
8.5								
9.0								
9.5								
10.0								
10.5								
11.0		1				2		
11.5		1				1		
12.0		2						
12.5		1						
13.0	1	3				1	1	
13.5		-				1	2	
14.0		3	2		1	-	1	
14.5			2				2	
15.0				1			1	
15.5			1	4	2		2	
16.0			2	4			4	
16.5				2	7		7	
17.0				3	9		7	
17.5				1	11		4	
18.0				1	5		6	
18.5			1		5		6	
19.5					1		8	
20.0							5	
20.5							7	
21.0							4	1
21.5								
22.0					1			
22.5								
23.0					1		1	
23.5					1			1
24.0								
Total	1	11	8	16	45	6	74	2

Table 7. Sexual maturity of Illex illecebrosus in the spring of 1975 (2 May) at position 38°57'N, 72°52'W. (Catch per hour in commercial fisheries was 0.02 tons.)

ML class /cm/	Stage number / ♂♂ /								Σ♂♂	Stage number / ♀♀ /								Σ♀♀
	I	II	III	IV	V	VI	VII	VIII		I	II	III	IV	V	VI	VII	VIII	
10.0																		
10.5																		
11.0																		
11.5																		
12.0		3							3									
12.5		3							3		1							1
13.0		7							7		8							8
13.5		6							6		9							9
14.0		13							13		13							13
14.5		8							8		11							11
15.0		3							3		6							6
15.5		2							2		4							4
16.0											3							3
16.5																		
17.0																		
17.5																		
18.0																		
18.5																		
19.0																		
19.5																		
20.0																		
Total		45							45		55							55

Table 8. Sexual maturity of Illex illecebrosus in the spring of 1975 (8, 11 and 12 May) at position 40°00'N, 69°50'W. (Mean catch per hour in commercial fisheries was 0.6 tons.)

ML class /cm/	Stage number /♂♂/							Σ♂	Stage number /♀♀/							Σ♀
	I	II	III	IV	V	VI	VII		I	II	III	IV	V	VI	VII	
7.0									1							1
7.5	1							1	1							1
8.0	2							2	1							1
8.5																
9.0																
9.5																
10.0																
10.5																
11.0																
11.5																
12.0																
12.5										2						2
13.0		4						4		3						3
13.5		10						10		6						6
14.0		18						18		7						7
14.5		17						17		20						20
15.0		22						22		29						29
15.5		11						11		18						18
16.0		12						12		16						16
16.5		8						8		11						11
17.0		3						3		7						7
17.5		2						2		3						3
18.0										1						1
18.5										1						1
19.0										2						2
19.5																
20.0																
20.5																
21.0																
Total	3	107						110	3	126						129

Table 9. Sexual maturity of Illex illecebrosus in the spring of 1975 (19-22 May) at position 40°00'N, 39°53'W. (Mean catch per hour in commercial fisheries was 1.7 tons.)

ML class /cm/	Stage number / ♂♂/						Σ ♂	Stage number / ♀♀/						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
12.0									1					1
12.5									-					-
13.0									-					-
13.5									1					1
14.0		2					2		3					3
14.5		5					5		3					3
15.0		6					6		2					2
15.5		10					10		7					7
16.0		18					18		9					9
16.5		14					14		11					11
17.0		14					14		12					12
17.5		8					8		10					10
18.0		4					4		10					10
18.5		1					1		11					11
19.0		-					-		7					7
19.5		-					-		2					2
20.0		1					1		1					1
20.5									-					-
21.0									2					2
21.5														
22.0														
22.5														
23.0														
24.0														
Total	-	83	-	-	-	-	83	-	92	-	-	-	-	92

Table 10. Sexual maturity of Illex illecebrosus in the spring of 1975 (24 May) at position 40°35'N, 68°10'W. (Mean catch per hour in commercial fisheries was 0.01 tons.)

ML class /cm/	Stage number /♂♂/						Σ ♂	Stage number / ♀♀ /						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
9.0									1					1
9.5									-					-
10.0	1						1		2					2
10.5	3						3		2					2
11.0	1						1		4					4
11.5	4						4		5					5
12.0	7						7		5					5
12.5	-						-		2					2
13.0	4						4		2					2
13.5	2						2		1					1
14.0	1						1		1					1
14.5	2						2		-					-
15.0									-					-
15.5									-					-
16.0									1					1
16.5									2					2
17.0														
17.5														
18.0														
18.5														
19.0														
19.5														
20.0														
Total	25						25		28					28

Table 11. Sexual maturity of Illex illecebrosus in the spring of 1975 (26-31 May) at position 39°58'N, 69°30'W. (Mean catch per hour in commercial fisheries was 1.4 tons.)

ML class /cm/	Stage number / ♂ ♂/						Σ ♂	Stage number / ♀ ♀/						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
10.0														
10.5		1					1							
11.0		-					-							
11.5		2					2		1					1
12.0		1					1		-					-
12.5		-					-		1					1
13.0		2					2		2					2
13.5		3					3		2					2
14.0		13					13		9					9
14.5		17					17		9					9
15.0		24					24		14					14
15.5		26					26		6					6
16.0		28	1				29		11					11
16.5		27					27		14					14
17.0		8					8		8					8
17.5		9					9		10					10
18.0		4					4		4					4
18.5		2					2		5					5
19.0									4					4
19.5									1					1
20.0									1					1
20.5									1					1
21.0									1					1
21.5									-					-
22.0									2					2
22.5														
Total	-	167	1	-	-	-	168	-	106	-	-	-	-	106

Table 12. Sexual maturity of Illex illecebrosus in the spring of 1975 (1-2 June) at position 40°04'N, 70°08'W. (Mean catch per hour in commercial fisheries was 4.4 tons.)

ML class /cm/	Stage number /♂ ♂/						Σ♂	Stage number /♀ ♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
12.0														
12.5														
13.0		2					2							
13.5		-					-							
14.0		3					3							
14.5		11					11		5					
15.0		20					20		13					13
15.5		16					16		13					13
16.0		18					18		15					15
16.5		3					3		6					6
17.0		3					3		10					10
17.5		3					3		2					2
18.0		1					1		4					4
18.5		1					1		6					6
19.0		2					2		7					7
19.5		3					3		8					8
20.0		3					3		9					9
20.5									6					6
21.0									8					8
21.5									5					5
22.0									8					8
22.5									3					3
23.0									1					1
23.5														
24.0														
Total	-	89	-	-	-	-	89	-	129	-	-	-	-	129

Table 13. Sexual maturity of Illex illecebrosus in the summer of 1976 (12 June) at position 40°26'N, 68°05'W. (Mean catch per hour in commercial fisheries was 0.7 tons.)

ML class /cm/	Stage number (♂♂)						Σ♂	Stage number (♀♀)						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
11.0														
11.5														
12.0														
12.5														
13.0														
13.5														
14.0														
14.5														
15.0														
15.5														
16.0														
16.5														
17.0														
17.5		1					1		1					1
18.0		1					1		1					1
18.5		5					5		1					1
19.0		5					5		4					4
19.5		3					3		4					4
20.0		5					5		2					2
20.5		4					4		2					2
21.0		2					2		-					-
21.5		1					1		3					3
22.0							-		1					1
22.5			1				1		4					4
23.0														-
23.5														-
24.0														-
24.5									1					1
25.0														-
25.5														-
26.0														-
26.5														-
27.0														-
27.5														-
28.0														-
Total	-	27	1				28		23					23

Table 14. Sexual maturity of Illex illecebrosus in the summer of 1976 (30 June) at position 40°30'N, 67°17'W. (Mean catch per hour in commercial fisheries was 1.0 tons.)

ML class /cm/	Stage number (♂♂)						Σ♂	Stage number (♀♀)						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
15.0														
15.5														
16.0														
16.5														
17.0														
17.5														
18.0														
18.5		3					3		3					3
19.0		4					4		1					1
19.5		6					6		1					1
20.0		4					4		3					3
20.5		8					8		2					2
21.0		5					5		4					4
21.5			1				1		-					-
22.0			1				1		2					2
22.5			2				2		-					-
23.0														
23.5														
24.0														
24.5														
25.0														
25.5									1					1
26.0														
26.5														
27.0														
27.5														
28.0														
28.5														
29.0														
29.5														
30.0														
Total		30	4				34		17					17

Table 15. Sexual maturity of Illex illecebrosus in the summer of 1976 (22, 23 and 28 August) at position 40°16'N, 68°57'W. (Mean catch per hour in commercial fisheries was 0.1 tons.)

ML class /cm/	Stage number (♂♂)						Σ♂	Stage number (♀♀)						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
15.0														
15.5														
16.0														
16.5														
17.0														
17.5														
18.0														
18.5														
19.0														
19.5														
20.0														
20.5														
21.0														
21.5			1			1	2							
22.0			1	2			2							
22.5			1	2	5		8		1					1
23.0		3	3	3	9		18		2					2
23.5			1	8	4	1	14		1					1
24.0			1	4	6	2	13		1					1
24.5		1		2	6	1	10		3					3
25.0					4		4		3					3
25.5					1		1		2					2
26.0					1		1		7					7
26.5									2					2
27.0									2					2
27.5									3					3
28.0									1					1
28.5									2					2
29.0									1					1
Total		4	7	21	36	5	73		29					29

Table 16. Sexual maturity of Illex illecebrosus in the summer of 1976 (10, 13 and 14 June) at position 39°57'N, 69°44'W. (Mean catch per hour in commercial fisheires was 1.3 tons)

ML class /cm/	Stage number (♂♂)						Σ ♂	Stage number (♀♀)						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
11.0														
11.5														
12.0														
12.5	1						1							1
13.0							-	1						
13.5	1						1	2						2
14.0	2						2	-	2					2
14.5	2	1					3	2	1					3
15.0	1	3					4	1	4					5
15.5	-	3					3	1	3					4
16.0	1	5					5		8					8
16.5		2					3		2					2
17.0		7			1		8		7					7
17.5		7					7		7					7
18.0		17					17		2					2
18.5		7					7		17					17
19.0		4					4		4					4
19.5		4					4		2					2
20.0		1					1		1					1
20.5		1					1		3					3
21.0		1					1		-					-
21.5									4					4
22.0									2					2
22.5									1					1
23.0									-					-
23.5									1					1
24.0									-					-
24.5									1					1
25.0														
25.5														
26.0														
26.5														
27.0														
27.5														
28.0														
Total	8	63			1		72	7	75					82

Table 17. Sexual maturity of Illex illecebrosus in the summer of 1976 (19, 21) 24 and 28 June) at position 39°57'N, 69°51'W. (Mean catch per hour in commercial fisheries was 2.4 tons.)

ML class /cm/	Stage number / ♂♂ /						Σ♂	Stage number / ♀♀ /						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
11,0														
11,5														
12,0														
12,5														
13,0														
13,5														
14,0														
14,5														
15,0														
15,5		1					1		1					1
16,0									1					1
16,5		1					1		1					1
17,0		3					3							
17,5		16					16		6					6
18,0		12					12		3					3
18,5		30					30		14					14
19,0		26	1				27		13					13
19,5		18					18		8					8
20,0		3					3		10					10
20,5		2	1				3		9					9
21,0		3	1	1			5		9					9
21,5		1		1			2		6					6
22,0			1				1		3					3
22,5				1			1		3					3
23,0		1					1		4					4
23,5			1				1		5					5
24,0									3					3
24,5									2					2
25,0									-					-
25,5									1					1
26,0														
26,5														
27,7														
28,0														
Total		117	5	3	-	-	125	-	102	-	-	-	-	102

Table 18. Sexual maturity of Illex illecebrosus in the summer of 1976 (2, 6, 10 and 12 July) at position 39°56'N, 69°40'W. (Mean catch per hour in commercial fisheries was 1.8 tons.)

ML class /cm/	Stage number /♂♂/						Σ♂	Stage number /♀♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
11,0														
11,5														
12,0														
12,5														
13,0														
13,5														
14,0														
14,5														
15,0														
15,5														
16,0														
16,5														
17,0														
17,5					1		1							
18,0									1					1
18,5		1					1							
19,0		7	1				8		1	1				12
19,5		8					8		1					1
20,0		18	1				19		4					4
20,5		21	7	1			29		5					5
21,0		13	11	3			27		10		1			11
21,5		10	12	3			25		11					11
22,0		3	12	5	1		21		7	1				8
22,5		5	4	2			11		6					6
23,0				1			1		3					3
23,5			1		1		2		4					4
24,0									2					2
24,5					1		1		1					1
25,0									1					1
25,5									2					2
26,0														
26,5									2					2
27,0														
27,5									1					1
28,0														
Total		86	49	15	4		154		62	2	1			65

Table 19. Sexual maturity of Illex illecebrosus in the summer of 1976 (17, 19, 26 and 30 July) at position 39°57'N, 69°33'W. (Mean catch per hour in commercial fisheries was 1.9 tons.)

ML class /cm/	Stage number /♂♂/						Σ♂	Stage number /♀♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
18,0														
18,5														
19,0														
19,5			2				2							
20,0		2		1			3		2					2
20,5		7	1		1		9		2					2
21,0		10	10	4		1	25		2					2
21,5		10	9	3	2		24		5					5
22,0		4	12	15			31		12					12
22,5		5	3	3	3	1	15		3					3
23,0				5	2		7		11					11
23,5		2		4	2		8		7					7
24,0					2		2		4					4
24,5					1		1		3					3
25,0									3					3
25,5									3					3
26,0									3					3
26,5									5					5
27,0														
27,5														
28,0														
28,5														
29,0														
29,5														
30,0														
30,5									1					1
31,0														
31,5														
32,0														
32,5														
33,0														
33,5														
34,0														
34,5														
35,0														
Total		40	37	35	13	2	127		66					66

Table 20. Sexual maturity of Illex illecebrosus in the summer of 1976 (14, 16, 18 and 19 August) at position 39°56'N, 69°41'W. (Mean catch per hour in commercial fisheries was 1.5 tons.)

ML class /cm/	Stage number /♂♂/						Σ♂	Stage number /♀♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
15,0														
15,5														
16,0														
16,5														
17,0														
17,5														
18,0									1					1
18,5														
19,0														
19,5					1		1							
20,0														
20,5		6	2				8		1					1
21,0		6	3	9	6		24		1					1
21,5			6	12	8		26		3					3
22,0		1	4	13	14		32		11					11
22,5				2	3	1	6		7					7
23,0			1	5	5		11		8					8
23,5		1			5		6		3					3
24,0					5		5		3					3
24,5					4		4		2					2
25,0														
25,5									2					2
26,0									1					1
26,5									4					4
27,0									5					5
27,5									1					1
28,0														
28,5									1					1
29,0									1					1
29,5														
30,0														
30,5									1					1
31,0														
31,5														
32,0														
Total		14	16	41	51	1	123		56					56

Table 21. Sexual maturity of Illex illecebrosus in the summer of 1977 (27-29 July) at position 42°50'N, 62°57'W. (Mean catch per hour in commercial fisheries was 4.1 tons.)

ML class /cm/	Stage number /♂♂/						Σ♂	Stage number /♀♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
16,0														
16,5														
17,0									1					1
17,5		1					1		1					1
18,0														
18,5		3					3		2					2
19,0		13					13		6					6
19,5		36					36		7					7
20,0		41					41		30					30
20,5		44					44		21					21
21,0		51					51		20					20
21,5		25	1				26		14					14
22,0		16					16		15					15
22,5		8		1	1		10		11					11
23,0		1	1				2		12					12
23,5		2		1			3		7					7
24,0									5					5
24,5									4					4
25,0									2					2
25,5									1					1
26,0									3					3
26,5									2					2
27,0									6					6
27,5									6					6
28,0									1					1
28,5														
29,0														
29,5														
30,0														
Total		241	2	2	1		246		177					177

Table 22. Sexual maturity of Illex illecebrosus in the summer of 1977 (30 July) at position 43°23'N, 60°45'W. (Mean catch per hour in commercial fisheries was 18.5 tons.)

ML class /cm/	Stage number /♂♂/						Σ ♂	Stage number /♀♀/						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
11,0														
11,5									1					1
12,0														
12,5														
13,0														
13,5														
14,0														
14,5														
15,0														
15,5									1					1
16,0														
16,5														
17,0														
17,5														
18,0														
18,5		1					1							
19,0		1					1		2					2
19,5		7					7		3					3
20,0		20					20		4					4
20,5		20					20		4					4
21,0		22	1				23		12					12
21,5		20	1				21		11					11
22,0		17					17		13					13
22,5		2					2		11					11
23,0		1	1				2		10					10
23,5		2	1				3		4					4
24,0									9					9
24,5									1					1
25,0									1					1
25,5														
26,0														
26,5									1					1
27,0														
27,5														
28,0														
Total		113	4				117		88					88

Table 23. Sexual maturity of Illex illecebrosus in the summer of 1977 (1, 3-5 August) at position 43°19'N, 60°59'W. (Mean catch per haul in commercial fisheries was 6.2 tons.)

ML class /cm/	Stage number (♂♂)						Σ♂	Stage number (♀♀)						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
12.5														
13.0														
13.5														
14.0														
14.5														
15.0														
15.5														
16.0														
16.5														
17.0		1					1		3					3
17.8		3					3							
18.0		1					1		1					1
18.5		4					4		1					1
19.0		9					9		4					4
19.5		22					22		8					8
20.0		52					52		10					10
20.5		61	1				62		24					24
21.0		49	-				49		34					34
21.5		41	1	1			43		24					24
22.0		20	4	-			24		42					42
22.5		9	1	1			11		28					28
23.0		3		1			4		15					15
23.5		2		1	1	1	4		11					11
24.0		1					1		7					7
24.5									4					4
25.0														-
25.5									1					1
26.0														
26.5														
27.0														
27.5														
28.0									1					1
28.5														
29.0														
29.5		1												
Total		278	7	4	1	1	290		218					218

Table 24. Sexual maturity of Illex illecebrosus in the summer of 1977 (5 August) at position 43°26'N, 60°29'W. (Mean catch per haul in commercial fisheries was 10.0 tons.)

Ml class /cm/	Stage numer / ♂♂ /						Σ ♂	Stage number / ♀♀ /						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
16,0														
16,5														
17,0		1					1							
17,5		1					1							
18,0		1					1							
18,5		-					-		1					1
19,0		-					-		1					1
19,5		5					5		1					1
20,0		10					10		5					5
20,5		22					22		6					6
21,0		20	1				21		6					6
21,5		27	3				30		15					15
22,0		16	2	2			20		11					11
22,5		4	2	4			10		8					8
23,0		3	1	1			5		9					9
23,5			1		1		2		5					5
24,0				-			-		4					4
24,5				-			-		2					2
25,0				1	1		2							
25,5														
26,0														
26,5														
27,0														
27,5														
Total	-	110	10	8	2		130	-	74	-	-	-	-	74

Table 25. Sexual maturity of Illex illecebrosus in the summer of 1977 (8-9 August) at position 43°37'N, 59°36'W. (Mean catch per haul in commercial fisheries was 10.2 tons.)

ML class /cm/	/Stage number/ ♂♂/						Σ ♂	Stage number/ ♀♀/						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
18,0		1					1							
18,5		2					2							
19,0		7					7		2					2
19,5		29					29		6					6
20,0		40					40		17					17
20,5		31					31		16					16
21,0		21					21		10					10
21,5		6	1				7		14					14
22,0		5	1				6		18					18
22,5		7	1	1			9		6					6
23,0		1		3			4		9					9
23,5		1		4	1		6		11					11
24,0		-					-		6					6
24,5		1		2			3		9					9
25,0		2					2		3					3
25,5									4					4
26,0									1					1
26,5														-
27,0									1					1
27,5									1					1
28,0		1					1		1					1
28,5														
29,0														
29,5														
30,0														
Total		155	3	10	1		169		135					135

Table 26. Sexual maturity of Illex illecebrosus in the summer of 1977 (11-14 August) at position 43°35'N, 59°50'W. (Mean catch per hour in commercial fisheries was 8.1 tons.)

ML class /cm/	Stage number / ♂♂ /						Σ ♂	Stage number / ♀♀ /						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
18,0														
18,5														
19,0		4					4		1					1
19,5		21					21		5					5
20,0		46					46		11					11
20,5		49	2				51		15					15
21,0		45	3				58		20					20
21,5		24	1				25		29					29
22,0		10	3	1			14		18					18
22,5		6	5	5			11		26					26
23,0		4		2	1		7		15					15
23,5				1	1		2		14					14
24,0				1	1		2		7					7
24,5					1		1		2					2
25,0									1					1
25,5									2					2
26,0									2					2
26,5									1					1
27,0					1		1							
27,5														
28,0									1					1
28,5														
29,0														
29,5														
30,0														
Total		209	14	10	5		238		170					170

Table 27. Sexual maturity of Illex illecebrosus in the summer of 1977 (25 August) at position 41°20'N, 68°53'W. (Mean catch per hour in research fishery was 0.1 tons.)

ML class /cm/	Stage number /♂♂/						Σ♂	Stage number /♀♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
17,0														
17,5														
18,0														
18,5														
19,0														
19,5														
20,0														
20,5														
21,0		1					1		1					1
21,5		1					1							
22,0		3	1	5	1		10		2					2
22,5		4	-	-	2		6		-					
23,0		-	1	6	6		13		7					7
23,5				3	5	2	10		4					4
24,0				2	4		6		9					9
24,5					2		2		5					5
25,0					3		3		4					4
25,5					1		1		7					7
26,0									3					3
26,5									3					3
27,0									-					
27,5									-					
28,0									1					
28,5									1					1
29,0									1					1
30,0									1					1
30,5														
31,0														
Total	-	9	2	16	24	2	53		49					49

Table 28. Sexual maturity of Illex illecebrosus in the summer of 1977 (28 August) at position 38°51'N, 72°56'W. (Mean catch per hour in research fishery was 0.05 tons.)

ML class /cm/	Stage number /♂♂/						Σ♂	Stage number /♀♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
18.0		1					1							
18.5		1					1							
19.0		5					5		1					1
19.5		15	1				16		1					1
20.0		5	2				7		6					6
20.5		3	-		1		4		6					6
21.0		2	2	1			5		6					6
21.5		2	3	1	1		7		2					2
22.0			-	4	5		9		4					4
22.5			1	-	3		4		3					3
23.0				1	4		5		3					3
23.5									-					-
24.0									1					1
24.5									1					1
25.0									1					1
25.5														
26.0														
26.5									1					1
27.0														
27.5														
28.0														
28.5														
Total		34	9	7	14		64		36					36

Table 29. Sexual maturity of Illex illecebrosus in the summer of 1977 (2, 5, 8 and 9 September) at position 41°55'N, 68°46'W. (Mean catch per hour in commercial fishery was less than 0.01 tons.)

ML class /cm/	Stage number /♂♂/						Σ♂	Stage number /♀♀/						Σ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
20.0														
20.5				1	1		2							
21.0		2		-	3		5		1					1
21.5		1		3	8		12							-
22.0		1		1	9		11		2					2
22.5			1	3	12		16		4					4
23.0				8	9		17		7					7
23.5				5	5		10		6					6
24.0			1	1	4		6		5					5
24.5				1	1		2		11					11
25.0		1					1		6					6
25.5									12					12
26.0									8					8
26.5									9					9
27.0									10					10
27.5									10					10
28.0									6					6
28.5									3					3
29.0									-					-
29.5									2					2
30.0									1					1
Total		5	2	23	52		82		103					103

Table 30. Sexual maturity of Illex illecebrosus in the summer of 1977 (12, 16 and 19 September) at position 41°24'N, 68°57'W. (Mean catch per hour in research fishery was less than 0.01 tons.)

ML class /cm/	Stage number (♂♂)						Σ♂	Stage number (♀♀)						Σ ♀
	I	II	III	IV	V	VI		I	II	III	IV	V	VI	
12.5	1						1							
13.0														
13.5														
14.0	1						1	1						1
14.5	2						2	1						1
15.0	1						1	-						-
15.5	2						2							
16.0								1						1
16.5														
17.0														
17.5														
18.0														
18.5														
19.0														
19.5														
20.0														
20.5									1					1
21.0			1				1		1					1
21.5		1	1	1			3							
22.0		3	4	3	4		14		4					4
22.5		2	2	7	7		18		2					2
23.0		1	1	6	19		27		3					3
23.5		1	1	5	9		16		7					7
24.0					11		11		4					4
24.5					8		8		11					11
25.0					9		9		6					6
25.5					1		1		8					8
26.0					1		1		3					3
26.5									8					8
27.0					1		1		11					11
27.5									12					12
28.0									7					7
28.5									5					5
29.0									10					10
29.5									7					7
30.0									3					3
31.0		1							1					1
31.5														
32.5									1					1
33.0									2					2
Total	7	8	10	22	70		117	3	117					120

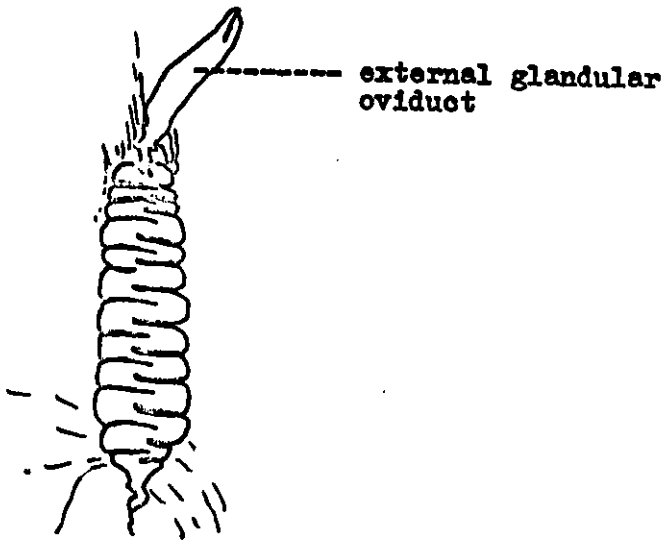

Fig. 1. The oviduct meander. Todarodes angolensis, ML = 32 cm.
Stage II. Scale 1:5.

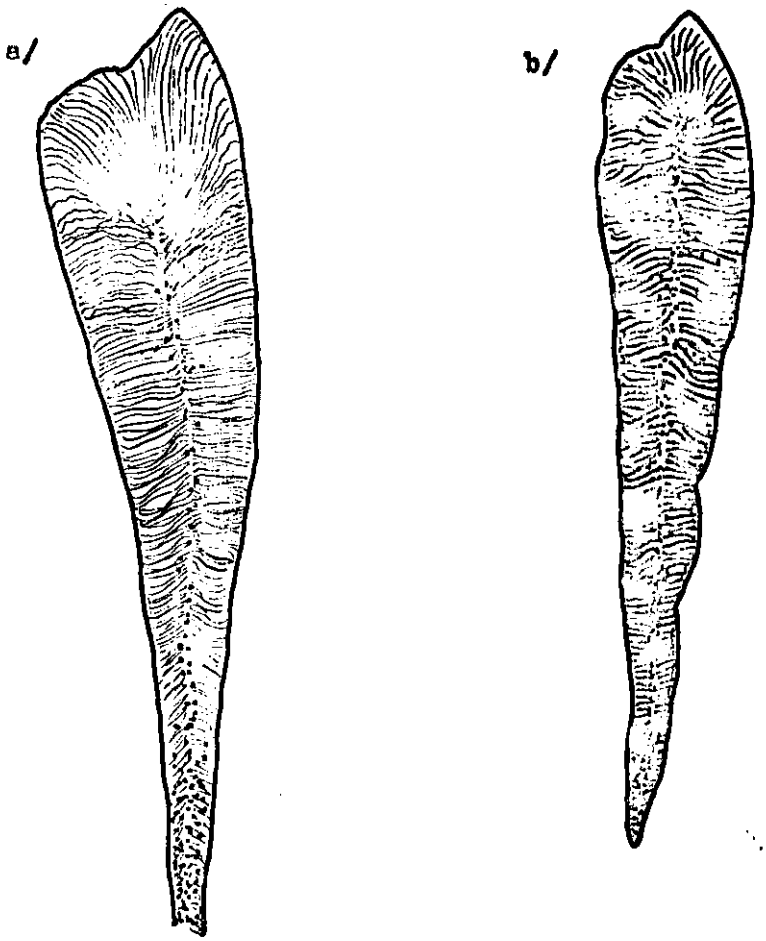

Fig. 2. The testis structure. Todarodes angolensis, ML = 25 cm.
Stage IV. Scale: a/ 1:1.5; b/ 1:1.

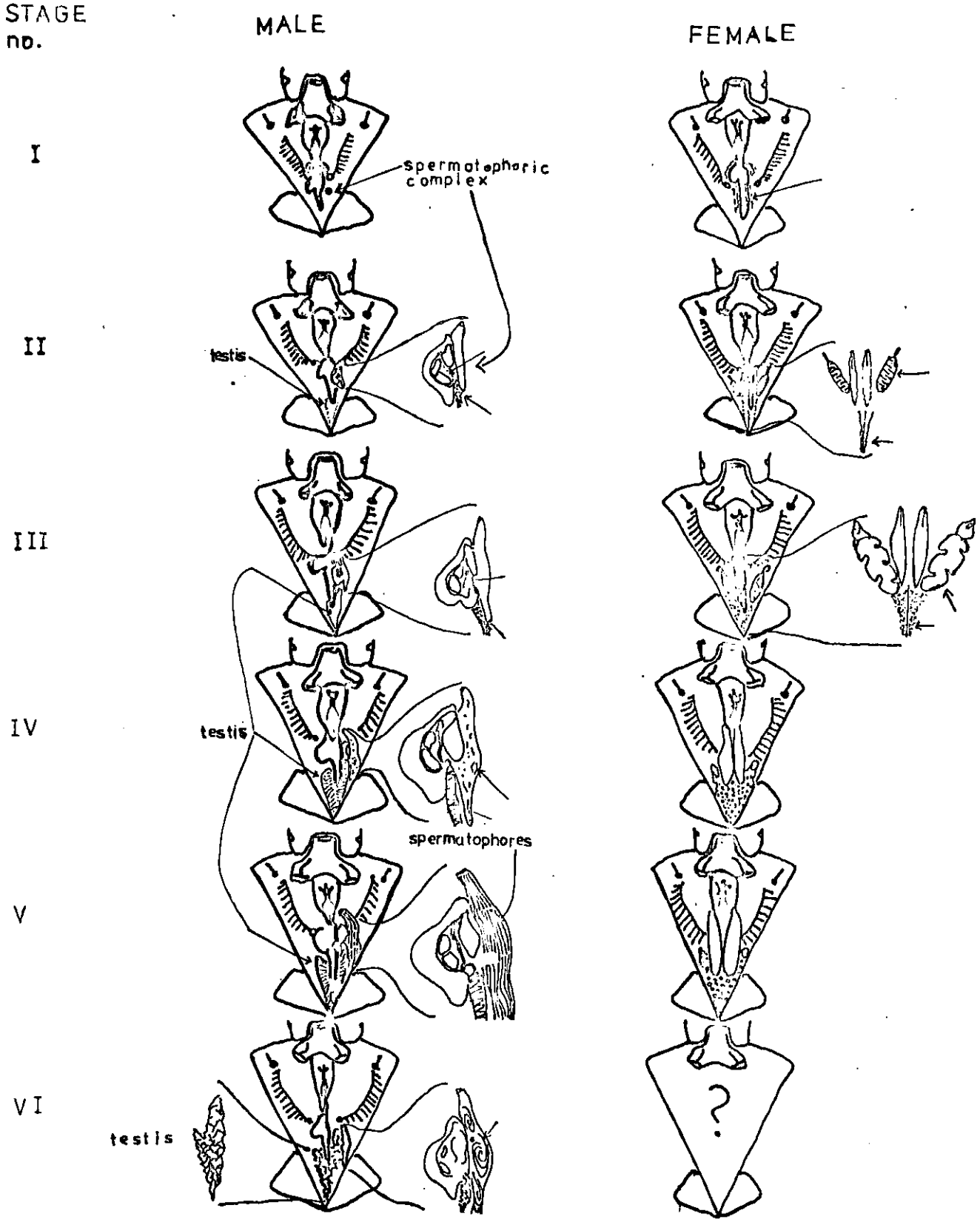

Fig. 3. Maturity stages of the squids. Arrows indicate key structures, separating consecutive stages.