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Reproductive Biology and Scale of Maturity Stages of the Reproductive System of Male Squid (*Illex illecebrosus*)

by

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Abstract

The reproductive biology of males is one of the least studied aspects of squid biology, both on the organism and population levels (review: Arnold, Williams, 1977). This has naturally been reflected in the insufficient groundfullness and completeness of maturity stage scales so far suggested for male squid reproductive system (review: Juanico, 1983). The maturity scales available, even in respect of one of the most studied *Illex* squids (Squires, 1957; Mangold, 1963; Castellanos, 1964; Nigmatullin and Vovk, 1972; Mercer, 1973; Amaratunga and Durward, 1978; Schuldt, 1979; Lipinski, 1979) are too general to study population cycles, especially of their later stages.

The purpose of this paper is to describe the maturity stage scale for male *Illex illecebrosus* as based on studies of the formation of reproductive system and spermatophores in ontogenesis, and the main features of male life history. The material used was sample collections of *Illex illecebrosus* made in 1966-1983 between Florida and Grand Bank. Also data was used on mature, mating and spent males of *I. argentinus*, and general ideas of the process of spermatophore formation, and of the periods of development of the reproductive system in oceanic species of Ommastrephidae (Zalygalin, Zuev and Nigmatullin, 1977; Zalygalin, Nigmatullin and Sabirov, 1983).

The reproductive system structure of male *Illex illecebrosus* is generally characteristic for representatives of the family Ommastrephidae, except for the fourth section of the spermatophore gland which is relatively small (9-10% ML, while in the other species it is 1.5-2 times larger).

During the ontogenesis, the allometric growth of various sections in the spermatophore complex of the organs (SCO) is uneven. Within the morphogenesis of SCO, and to a lesser extent during maturation (maturity stages I-IV) the growth of its parts is marked by the positive allometry. Only the third section grows isometrically. Conversely, during the formation and accumulation of spermatophores (stages V_1 and V_3) less prounced negative allometry is observed. In other genera of Ommastrephidae this period is marked by maximum values of the positive allometric growth.

As the study of the morphology of spermatophores of *I. illecebrosus*, and of other species of the genus, indicated the shape of the front of the cement body (suggested by Roper, Lu and Mangold, 1963 as a highly specific characteristic) is highly variable. Characteristic features of different species can be found among the spermatophores of even the same male. The variability of the cement body front structure is mostly determined by the difference in the extent of pressure on the outer parts of spermatophores during the later stages of their formation in the fourth section of the spermatphoric gland.

The males analysed had spermatophores 18-27 mm long (mean 10-11% of the length of the ML). There is no apparent growth in the absolute and relative size of spermatophores with the increase in male size. During the formation of spermatophores in ontogenesis their size increases very slowly. The

modal values of spermatophores out of the portions formed at various times usually coincide, or are similar. All this is the result of the pattern of allometric growth of the spermatophore gland, especially of its fourth section where the outer covers of spermatophores are formed. At the same time, the production of spermatophores in the ontogenesis without apparent increases in their overall size is accompanied by a considerable increase in the sperm reservoirs at the expense of the hind empty part.

The fecundity of male *I. illecebrosus* is within 600 to 1,000 spermatophores, their number being greater in larger individuals. The average capacity of the sperm reservoir of spermatophores is 0.45 mm^3, the total capacity of all spermatophores at the fecundity level close to maximum is 0.3 to 0.45 cm^3. Once the data on spermatozoa concentration in sperm reservoirs becomes available the effective production of sperm during the male ontogenesis may be estimated. The data on the allometric growth (SCO), and on the process of formation of spermatophores in *I. illecebrosus* differ greatly from those received from oceanic species Ommastrephidae (Zalygalin, Nigmatullin and Sabirov, 1983; Magaras, Nigmatullin and Sabirov, 1983).

With due regard to the functional characteristics of the development of the male reproductive system for *I. illecebrosus* in the ontogenesis, the scale of maturity stages was worked out (Table 1), and ecological periods of ontogenesis were established based on the importance of different periods of ontogenesis for preparation of males for participation in reproduction, as follows:

1. <u>The formation of reproductive system, and intensive somatic growth during the feeding period.</u> Two substages may be identified: (a) pelagic plankton-nekton (Stage I of maturity; ML 20-130 mm, mainly up to 110 mm; the duration is 3 to 5 months; pelagic waters over the continental slope and adjacent areas of the high seas); (b) bottom-pelagic, nekton (Stage II; ML 100-220 mm, mainly up to 180 mm; 2-3, <5 months; shelf and slope waters). The total duration of the stage is 6-7 months.
2. <u>Maturation</u> (increase in the share of generative growth). There occurs maturation, activie functioning of testis. Spermatophores begin to form (Stages III and IV; 130-250 mm; 1-1, 5 months mainly at the expense of the longer Stage III; shelf and slope waters).
3. <u>Formation of spermatophores and their accumulation in the spermatophoric sac</u>. The share of generative exchange dominates while little somatic growth still exists (Stages V_1 and V_2, ML 150-260 mm; 2-3 months; the end of the feeding period on the shelf - migration to the spawning areas.
4. <u>Mating</u>. Function of testis and SCO slows down up to full stop. Each male mates with different females for several times (promiscuity) (Stages V_3 and VI, 180-260 mm; 0.3-0.5 month; spawning areas over continental slope at the U.S. coast).
5. <u>Spent</u>. Most exhausted males at Stage VII; soon they die in the pelagic layer over the continental slope.

In terms of reproductive biology, male *I. illecebrosus* are marked by producing a great number of relatively small spermatophores whose size does not vary considerably with the increase of mantle length. Historically, this is probably a result of getting out of contradiction between the need to augment fecundity for multiple matings and a relatively stable speed of producing sperm and forming spermatophores. The mating occurs with 1 to 3 males before each portion of eggs is spawned.

The actual mating of a female with several males within spawning of each cohort provides for an increased recombination of the genetic material, and for a stronger tendency towards panmixis. This mechanism may be regarded to be the elementary level in implementing the stabilizing form of selection which makes good for withholding the specific population within the same population system, and to be operative within the same spawning season. The next and major level is the recombination of the composition of spawning cohorts in the interannual aspect (see Froerman and Dubinina, 1984; Froerman, 1984).

Table 1. Scale of maturity stages for the reproductive system of male *Illex illecebrosus*.

Maturity stage	Main functional characteristics of the stage	Status of testis TW/BW (%)	Status of SCO SCOW/BW (%)	Mean coefficient of maturity RSW/BW (%)
I	Formation and development of testis	Transparent, semi-transparent or grey narrow band (≤0.02-0.1)	Poorly visible as homogeneous formation (≤0.02-0.1)	0.1
II	Maturation of the testis	White-grey, oblong oval, flat (0.05-0.9)	Grey, well visible; some parts are not clearly separated; spermoduct is empty (0.05-0.3)	0.5
III	Beginning of sperm production	Size increases greatly; dense, milk-white (0.2-2.5)	Some parts are well pronounced; white sperm mass appears in the spermoduct, first as a thin band. By the end of the stage, it fully fills the tube and can easily be seen (0.12-0.54)	1.3
IV	SCO begins to function	Testis occupies the entire rear of ML cavity; milk-white, dense, homogeneous (0.8-3.5)	Forming spermatophores appear in the front section and in the appendage of the SCO (0.22-1.6)	2.2
V_1	Testis and SCO function actively.	Same as IV above (1.1-3.9)	First spermatophores appear in the sac. They fill its volume by no more than 10% (0.31-2.28)	2.9
V_2	Same as V_1, first mating probably occurs at the end of the stage	As in IV and V_1 (1.1-4.5)	The sac is 75-100% full with spermatophores (0.6-4.7)	3.9
V_3	Mating. Testis and SCO gradually cease to function	Becomes smaller by 0.3-3.0 times against V_1 and first half of V_2. Not solid (0.7-3.5)	The sac is 40-50% full of spermatophores (1.0-3.6)	3.4
VI	Mating. Testis and SCO cease to function	Destruction. Dirt-grey, heterogeneous, usually as a narrow band	The sac is 20-80% full of spermatophores	2.5
VII	Fully spent. ML, liver, gills diminish 3-4 times. They soon die.	Full destruction. Only individual "islets" of testis tissue remain	The sac is empty. In some cases several residual spermatophores may be formed	<2.0

(Full text of this paper will be available in about 2 months)