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Maturation index and fecundity for female *Illex illecebrosus* (LeSueur, 1821)

by

R. D. Durward, T. Amaratunga* and R. K. O'Dor
Department of Biology, Dalhousie University
Halifax, Nova Scotia, Canada

and

*Fisheries and Marine Service
Resource Branch
P. O. Box 550
Halifax, Nova Scotia, Canada

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ABSTRACT

The sexual maturation continuum in female Illex illecebrosus has been divided into five discrete stages based on the development of the nidamental gland. Analysis of laboratory and field data show that the development of the nidamental gland is well correlated with ovarian development. Using a ratio of nidamental gland length to mantle length, the maturity stage is expressed quantitatively. The numerical values for each maturation stage (m) using this ratio are: Stage 1, $m \leq 0.09$; Stage 2, $0.09 < m \leq 0.125$; Stage 3, $0.125 < m \leq 0.2$; Stage 4, $0.2 < m \leq 0.35$, and Stage 5, $0.35 < m$. This index is convenient and accurate in determination of the female maturity conditions in both the field and laboratory.

Ovarian weight is shown to be dependent on the total weight of the individual female. The total egg mass produced is approximately 25% of its total body weight. Since the size of a mature egg is a fixed value, it is shown that the total number of eggs produced can be estimated for a given population.

INTRODUCTION

The life cycle of Illex illecebrosus is still largely a matter of conjecture (Mesnil, 1976; Squires, 1967) because these squid disappear from areas where they are normally fished when they reproduce. There is an adequate description of sexual development in males, since their onset of maturation is relatively early in the season (Amaratunga et al, 1978; Mercer, 1973); but information on female maturation is scant, as few mature females have been observed in the wild population (Amaratunga et al, 1978; Mesnil, 1976; Squires, 1957).

Advanced stages of maturity have been observed in captive female I. illecebrosus as a result of maintaining these squid in the Aquatron Laboratory at Dalhousie University, Halifax, Nova Scotia (Q'Dor et al, 1977). Precocious maturation occurred in most females held in the pool tank. Although the exact cause of this phenomenon is not certain, squid entering the pool were exposed to increased photoperiods. Utilizing the data obtained from these squid, along with those collected from the wild population throughout the summer and fall, the complete maturation process in female I. illecebrosus is examined in this report.

Examination and observation of maturing females not only provides required data on gonadal development and fecundity, but also a knowledge of female behavioral patterns during the maturation process. These may provide a key to ascertaining the time and location of spawning, information essential for proper management of the developing fisheries for this species of squid.

Several methods have been used in describing the maturation stages in cephalopods. In most cases, maturation is determined by (1) examination of the size (weight and length) and colouration of the gonad and accessory organs (Mercer, 1973; Vovk, 1972a; Hayaski, 1970; Tinbergen and Verwey, 1945), or (2) histological analysis of the ovary (Takahashi and Yahaya, 1973). Although histological analysis is perhaps the most reliable indicator of maturity condition, it is tedious and often impossible in field work.

In this report, simple measurements of nidamental gland length (an accessory sex organ) and mantle length are combined to produce a maturity index. The index, nidamental gland length to mantle length ratio, correlates well with ovarian development and is applicable to and practical in both field and laboratory work. Fecundity of I. illecebrosus was determined from females which were maintained in captivity.

MATERIALS AND METHODS

The majority of specimens used for this analysis were taken in a floating box trap in inshore waters of less than 20 meters, off Herring Cove, near the mouth of Halifax Harbour, Nova Scotia. Supplemental offshore samples of females were obtained from the Department of Fisheries, Halifax Laboratory.

Individual catches ranged from a few to several thousand, and over 90% of the inshore catch was female. A random sample of 25 females was examined in detail from each catch.

Over 150 squid have been maintained in captivity for periods up to 12 weeks, in a 15 m diameter pool tank in the Aquatron Laboratory at Dalhousie University. Animals remained in excellent condition and grew at rates comparable to the wild population. All females were approaching full maturity within 40-60 days after entry to the pool tank (O'Dor et al, 1977).

The following data were collected from all captive females and from approximately 400 wild population females: dorsal mantle length (ML), total body weight (BW), nidamental gland length (NGL), and ovary weight (OW). After the ovaries were weighed, they were fixed in Bouin's solution and routinely processed for light microscopy. The histological work is still in progress and only a few preliminary conclusions from it are reported in this paper.

Ovaries from six mature (Stage 5) females were used to estimate fecundity. Fecundity was defined as the total number of mature ova present in a female immediately prior to spawning. All mature ova in a 250 mg subsample from each ovary were counted. The total number of ova in the ovary was estimated from the equation $F = nG/g$; where F = fecundity, G = total weight of ovary, g = weight of the subsample, and n = number of ova in the subsample.

In order to divide what is essentially a continuum into five discrete development stages, three assumptions about ovarian development were considered: (1) The total weight of mature ova produced by an individual is a fixed proportion of total body weight. (2) The size of a fully developed ovum does not vary with body weight and, therefore, it is the number of ova which varies with body weight. (3) The weight of the ovary in a female at any stage of ovarian development will be equal to the product of the weight of one ovarian follicle at that stage and the number of finished ova predicted for a female of that weight. An examination of the data of Vovk (1972b) on Loligo pealei and of Fields (1965) on L. opalescens indicate that assumptions 1 and 2 are approximately correct for these species. Thus, the number of finished ova an animal will produce can be predicted from body weight.

The developmental stage of a follicle was determined through histological examination, and was defined on the basis of the stages of oogenesis proposed by Selman and Arnold (1977) in L. pealei. A sample of 30 of the largest follicles in each stage were measured in order to determine the follicular diameters.

RESULTS

The nidamental glands increase in both length and weight during sexual maturation (Rowe and Mangold, 1975). The relationship between nidamental gland length (NGL) and ovary weight (OW) for squid from the wild and precociously maturing captive squid is demonstrated in Figure 1, showing that NGL increased consistantly with an increase in OW ($\hat{y} = 27.12\ x^{.34}$, $r^2 = 0.89$). This implies that the growth of the accessory sex organ, the nidamental gland, is related to maturation of the ovary, since OW increases with maturation. OW was also tested against another linear measurement, mantle length. The observed relationship between NGL and OW is not characteristic of overall growth, as correlation between ML and a wide range of OW's is low in maturing females ($\hat{y} = 231.54\ x^{.04}$, $r^2 = 0.25$) (Figure 1).

The fully mature females (average total weight 440 g) contained an average of 100 g of mature ova, each weighing approximately 240 µg. Thus, the total number of ova in females of this weight class was estimated to be 420,000. In *I. illecebrosus*, as well as other squid (Vovk, 1972a; Fields, 1965), it appears that the number of mature eggs ultimately formed depends on the size of the female (see Materials and Methods). Since the OW/BW ratio is a fixed value at full maturity, the same relationship should apply to all stages of maturation.

We would predict, based on this relationship, that females averaging 440 g would have ovaries weighing about 1.2 g if all the follicles were in Stage 1 (no proliferation of follicle cells), and the OW/BW ratio would be 0.00275. This ratio is roughly equivalent to that observed in *O. vulgaris* prior to activation of the optic glands (Wells and Wells, 1959). With all the follicles in Stage 2 (proliferation of follicle cells), the OW/BW ratio would be 0.005, and the OW would be 2.45 g. The calculated OW/BW ratio would be 0.015, 0.10, and 0.25 for females with ova in Stage 3 (proliferation of follicles completed), Stage 4 (vitellogenesis), and Stage 5 (mature ova), respectively (Table 1).

In Figure 2, all animals were classified on the basis of their OW/BW ratio and graphed to compare NGL and ML. The OW/BW classes were selected using the estimated maximum OW/BW ratio assuming that all follicles were in a given stage of development. Much of the scatter in Figure 1 is eliminated when length or weight-based indices are used, since NGL is related to ML, and OW to BW, in addition to their mutual relationship to maturity stage. The upper limit of the NGL/ML ratio defining each maturation stage is based on the largest value in a given OW/BW class. The mean and range of the OW and NGL in each stage of maturation as defined by the NGL/ML ratio in Figure 2 are shown in Figure 1, illustrating that the NGL/ML ratios are a good indicator of ovarian development. This applies not only to ovarian weight, but also to oocyte development. Preliminary histological examination of ovaries within the various OW/BW classes confirms this.

Table 1 summarizes the NGL/ML index values corresponding to distinguishable stages of ova development and relates them to other measurable or grossly apparent parameters. Representative females from Stages 1, 2, 3, and 5 are shown in Figure 3.

In field samples taken inshore in October, 1977, majority of the females were in maturity Stage 2. Analysis of a random sample of offshore animals in Subareas 4 and 5 in November, 1977, using the proposed maturation index showed that most females were in Stage 3, with some entering Stage 4 (Amaratunga et al, 1978). This suggests that the time course of proliferation of the follicle cells is very short, and the rate of maturation in the wild population appears to parallel that observed in the females maintained in captivity. Further data on late season females are required to verify this.

DISCUSSION

Mantle length is a standard field measurement and the nidamental gland, the most obvious structure of the female reproductive system, is presently used for sexing the animals and qualitatively as an indicator of maturity (Vovk, 1972a). Even in the field, accurate measurement of NGL takes only a few seconds more, and when used in the NGL/ML ratio, it provides a quantitative maturation index well correlated with ovarian development.

The need for a complete maturation index for female *I. illecebrosus* is increasing. Although relatively few mature females have been observed to date in the wild population (Amaratunga et al, 1978; Squires, 1957; Mesnil, 1976), the expanding fisheries will allow for extensive collecting later in the year, from which more specimens in advanced stages of maturation will be collected.

When maintained in captivity, females reached full maturity within 40-60 days after entry into the pool tank in September (O'Dor et al, 1977). In the past year, we have been able to induce precocious maturation in squid (Stage 1) caught as early as July, using increased photoperiod. Two conclusions have been derived from this work: (1) photoperiod is one of the environmental cues responsible for "triggering" the hormonal system which drives the maturation (see Wells and Wells, 1959 for description of hormonal system). Photoperiod has been shown to be a cue in other cephalopods (Richard, 1967). (2) the rate of maturation, or maturity state in females, is not dependent on the size of the individual, as all females (ML from 200 mm to 280 mm) surviving over 40 days in captivity reached advanced stages of maturity. We have also noted that when females reach the advanced stages of maturation, they no longer feed. This behavior is also common in other cephalopods (see Wodinsky, 1977).

As estimate of egg production would provide an upper limit on the size of a new year class. Since feeding and growth are reduced in the later stages of maturation, and the number of eggs produced is related to maximum body weight (see results), egg production should be predictable from data on the number and size of females in late November, when the females are beginning to mature. For example, if the total biomass at this time were 10,000 MT and the sex ratio 50:50, the estimated egg mass would be 1,250 MT (25%) or about 5×10^{12} eggs. Clearly, allowances must be made for mating success and embryo and larval survivorship in predicting stock recruitment. Although no data are available at present, further studies on captive populations could provide valuable insights on this critical phase of the life cycle.

The proposed maturation index is based on data collected under artificial conditions; however, field data conflicts in no way with the observations on captive animals. We suggest that this index can be effectively used to analyze the female life cycle and that correlations between the cycles of the two sexes will provide insights into the reproductive patterns of the species leading to improved predictions of stock recruitment.

SUMMARY

1. The development of the nidamental gland during the maturation process is well correlated with ovarian development.

2. Using the relationship between the nidamental gland and ovary, the ratio of nidamental gland to mantle length can be used to express the female maturity condition quantitatively.
3. A maturity index for female I. illecebrosus is described based on a study of the complete maturation process.
4. The number of eggs produced by an individual female is proportional to body weight.
5. The number of eggs produced by a population can be predicted from the number and size of females in the population late in the autumn.

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Table 1. Characteristics of the Maturation Stages in Female *Illex illecebrosus*

MATURATION STAGE	NGL/ML RANGE§	NG (mm) RANGE	OW/BW RANGE§	OW (g) RANGE	FOLLICLE STAGE∂	FOLLICLE SIZE δ (mm)* (µg)†	DISTINQUISHING MORPHOLOGICAL FEATURE
1	$M \leq 0.09$	11 - 25	$M \leq 0.00275$	.14 - .9	1	.20 X .14 2.9 µg	NG thin and transparent
2	$0.09 < M \leq 0.125$	20 - 35	$0.00275 < M \leq 0.005$	.68 - 1.6	2	.26 X .16 5.66 µg	NG transparent to translucent ovary - granular
3	$0.125 < M \leq 0.2$	25 - 60	$0.005 < M \leq 0.015$	1.1 - 5.42	3	.35 X .25 16.04 µg	NG translucent to opaque
4	$0.2 < M \leq 0.35$	55 - 90	$0.015 < M \leq 0.10$	6.0 - 30.0	4	between stages 3 & 5	NG white oviducts forming
5	$0.35 < M$	110 - 120	$0.10 < M$	50.0 - 104.0	5	.9 X .625 240.0 µg	eggs in the oviducts

§ M = maturation stage
∂ as defined by Selman and Arnold (1977)
δ measurements on fixed follicles
† calculated using the formula $4/3\ \pi\ a^2b$, where a is the major axis and b the minor axis
* similar to *I. coindetii*, Boletzky et *al*, 1973

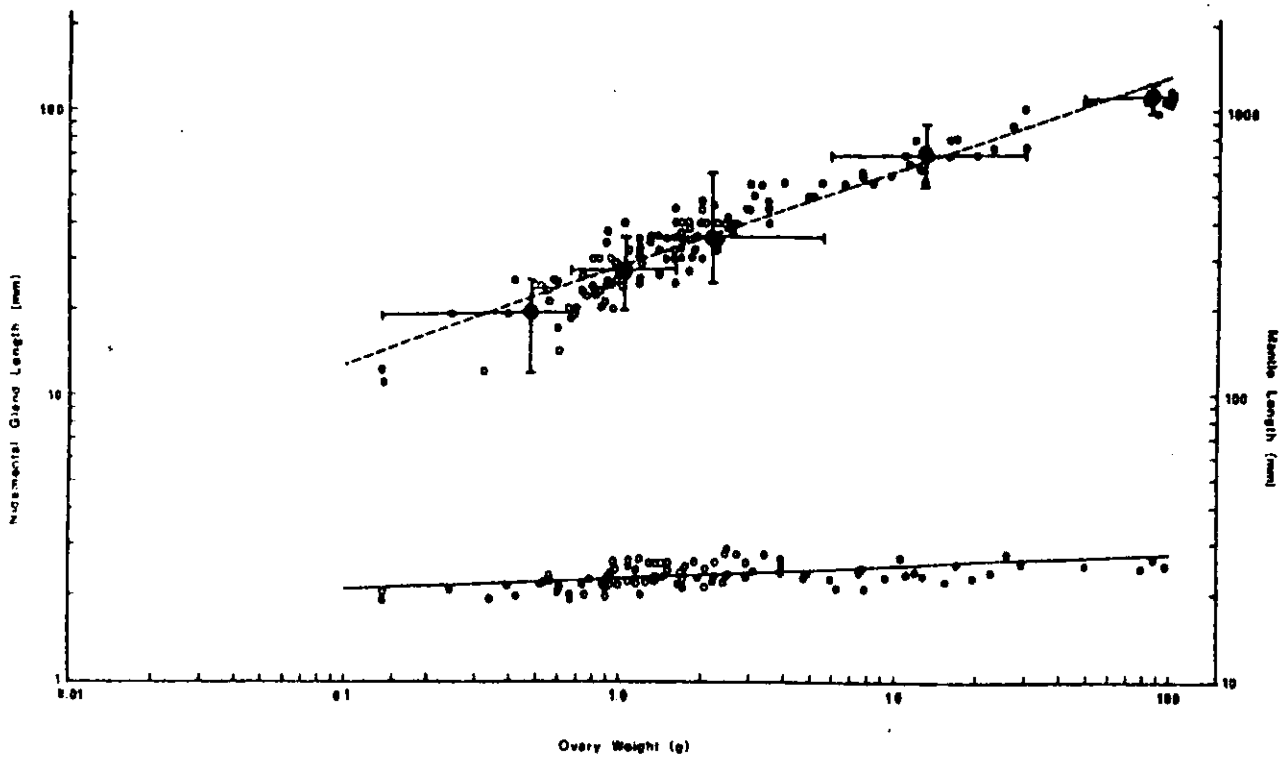

FIGURE 1. Nidamental gland length, mantle length, and ovary weight of squid analyzed during the 1976 and 1977 seasons. Open circles represent females taken from the wild population and solid circles represent females kept in the pool tank. The solid line is the regression ($\hat{y}=27.12\ X^{.34}$, $r^2=0.89$) for NGL verses OW, and the broken line is the regression ($\hat{y}=231.54\ X^{.04}$, $r^2=0.25$) for ML verses OW. The large solid circles and bars indicate the mean and range of NGL and OW for the stages defined in Figure 2.

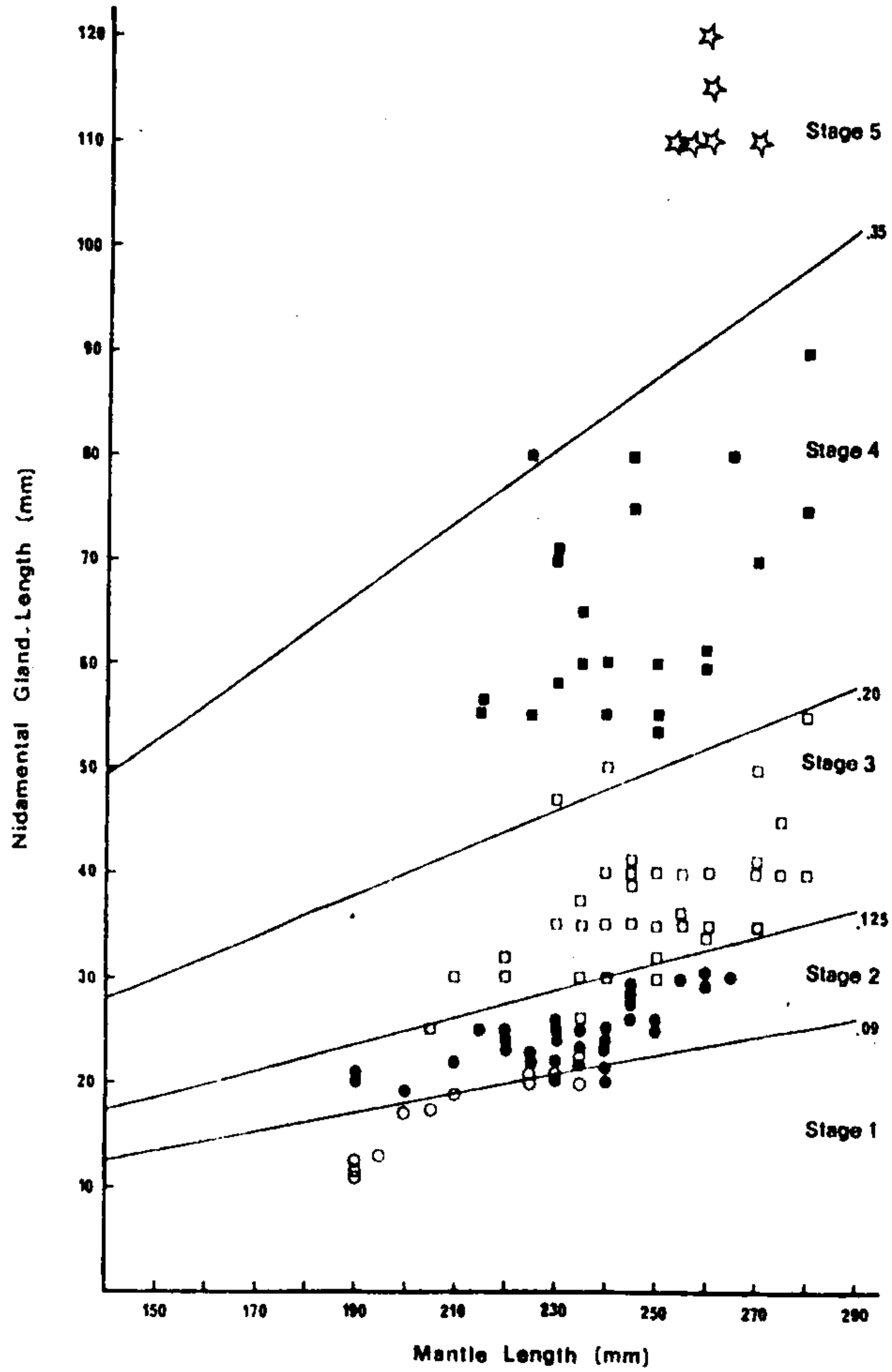

Figure 2. Relationship between nidamental gland length and mantle length for squid classified by ovary weight to body weight ratios. Symbols are: open circles OW/BW < 0.00275; closed circles 0.00275 < OW/BW < 0.005; open squares 0.005 < OW/BW < 0.015; closed squares 0.015 < OW/BW < 0.10; stars 0.10 < OW/BW. The solid lines represent the upper NGL/ML ratio for the OW/BW classes, and define the maturity stages proposed.

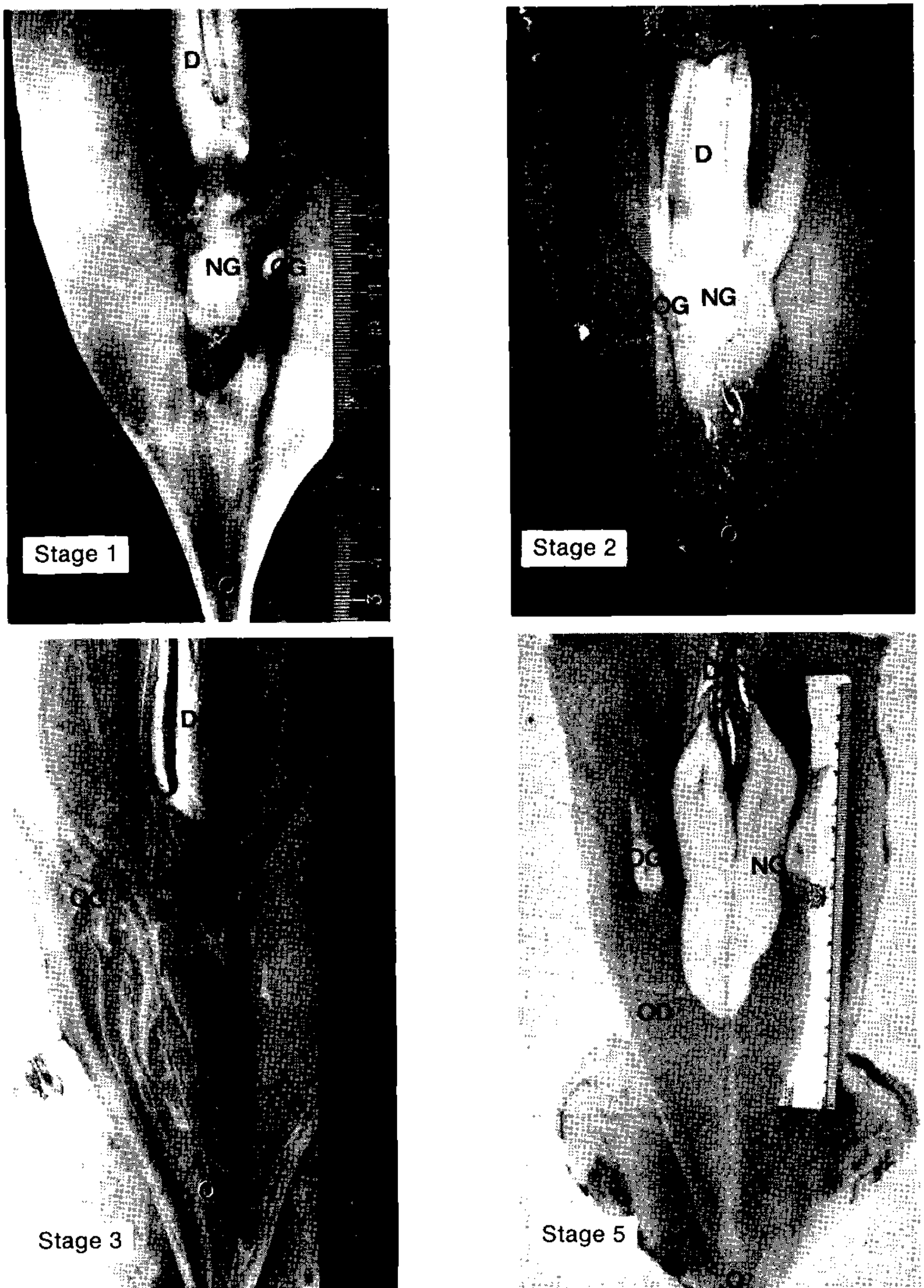

Fig. 3. Typical specimens of female *Illex illecebrosus* in late spring (stage 1), summer (stage 2), late autumn (stage 3), and the most advanced condition (stage 5). Reproductive organs represent one-third of the total body weight. (D = digestive gland, NG = nidamental gland, OG = oviducal gland, OD = oviduct, and O = ovary.)