

EMBRYONIC GROWTH IN THE VIVIPAROUS POECILIID, *HETERANDRIA FORMOSA*¹

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In *Heterandria formosa* the fertilized eggs are minute and the embryos secure their nourishment for development through a placental type of association with the mother. This paper presents an analysis of embryonic growth in this viviparous species and a comparison of this growth with that in oviparous fishes. In the discussion an attempt is made to evaluate the factors restricting growth in *Heterandria*. A similar study of embryonic growth in a number of ovoviviparous fishes is to follow.

Bailey (1933) and Turner (1937) have directed attention to the development of embryos in poeciliid fishes in relation to the mother. Turner (1940a, b, c, d) surveyed the various types of association between mother and embryo for the four viviparous Cyprinodont families (Poeciliidae, Anablepidae, Goodeidae, and Jenynsiidae).

For the oviparous fishes, the work of Gray (1926, 1928) on the development of the trout *Salmo fario* stands almost alone. However, Kronfeld and Scheminzki (1926) have also contributed data on the trout. This work on a fish species totally dependent upon yolk for its embryonic nourishment provides the basis for the comparison and interpretation of many of the observations described below.

MATERIAL

Heterandria formosa is remarkable in showing a high degree of superfetation. As many as eight broods of developing embryos occur within the ovary of a single female. Active sperm are retained in the ovary for many months following a single copulation. Thus it is impossible to determine the exact time of fertilization or the time it has taken any particular brood to reach the stage in which it is found.

Its embryonic development resembles in its general aspects that of *Fundulus* and other Cyprinodont fishes. In *Heterandria*, as in all poeciliid fishes, the embryos are retained until parturition within the follicles of the single median ovary. Following fertilization the ovum and the follicle become separated by the perivitelline space and fluid. The follicular membrane is henceforth generally referred to as the ovisac. Its diameter increases with the extension of the fluid filled spaces associated with the embryo and with the growth of the embryo itself.

Sections of the immature ova show little yolk, but numerous small oil globules are already present (Fig. 1). The latter increase in volume as the eggs grow, and their number is reduced by the coalescence of the small vacuoles (Fig. 2). The large oil globules fuse at the time of fertilization to form a single large spherical oil

¹ The author expresses appreciation to Dr. Leigh Hoadley for suggestions and encouragement in this work.

mass which occupies from 50 to 75 per cent of the volume of the ripe ovum (Fig. 3). When the blastodisc appears, it bears the same relation to the oil globule in *Heterandria* as it does to the yolk mass in the more typical teleost egg. Thus a central periblast is observed beneath the blastodisc and a thin syncytial periblast eventually surrounds the oil globule in precisely the same manner as it surrounds the yolk in *Fundulus*.

The chemical composition of the oil globule has not been determined, but it stains deeply with the fat dyes Sharlach R and Sudan III. The great reduction in the amount of the other yolk components present would suggest that the food of the embryo during the first part of its development might be derived from the oil. Figure 4 shows the relation between the diameter of the ovisac and the volume of

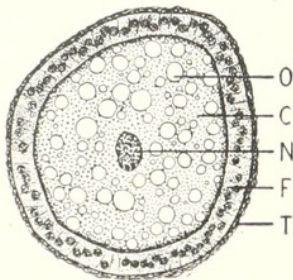


FIGURE 1

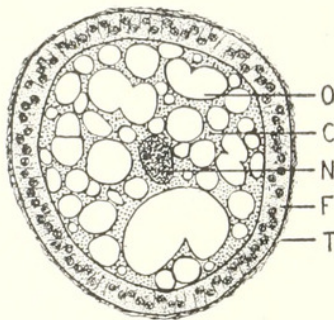


FIGURE 2

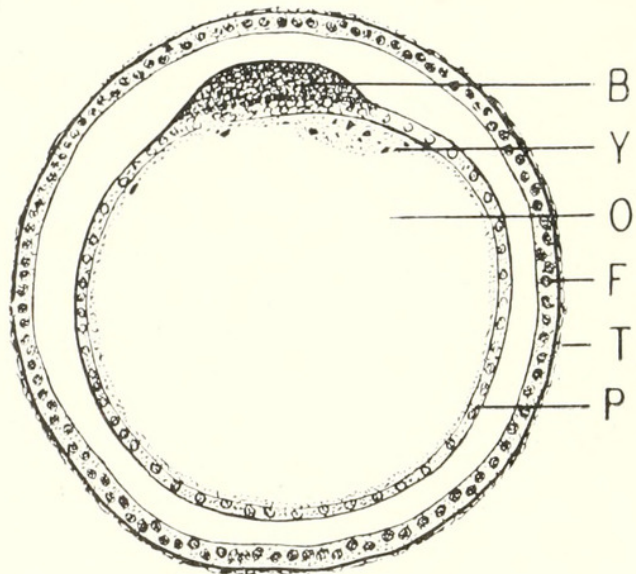


FIGURE 3

FIGURE 1. Early ovum of *Heterandria formosa*. O, oil; C, cytoplasm; N, nucleus; F, follicular epithelium; T, theca.

FIGURE 2. Late ovum of *Heterandria formosa*.

FIGURE 3. Early blastodisc of *Heterandria formosa*. B, blastodisc; Y, yolk periblast; Ch, chorion.

the oil globule. It indicates that the volume is decreased by less than 30 per cent up to the time that the pseudo-placenta is fully formed.

Fraser and Renton (1940) and Turner (1940a) have described the fetal adaptations associated with viviparity in *Heterandria*. These are unique and may be summarized as follows: The antero-ventral somatopleure of the embryo becomes enormously extended and encloses the head completely. This produces a large extraembryonic pericardial cavity extending into the head fold. The postero-ventral somatopleure is also somewhat expanded and contains the liver, gut and the much extended urinary bladder. An extensive capillary network develops on this expanded portion of the somatopleure so that its whole surface opposing the follicular epithelium is highly vascularized. Since the latter has likewise developed an extensive vascular system, an association between embryonic and maternal circulation comparable to a non-deciduate mammalian placenta is formed.

In relatively advanced embryos the pericardial hood ruptures over the forepart of the head, leaving a strap of somatopleure over it. This strap gradually decreases in size and eventually disappears. As a result the area of the vascular association between embryo and ovisac has been considerably reduced by the time of parturition.

Special types of cells in connection with the maternal and embryonic components of the pseudo-placenta also appear. Turner (1940a) has stated that the outer layer of the extra-embryonic pericardial cavity, the ectoderm, is equipped with "conical cells, which are granular at the base and vacuolated apically . . . and sometimes gathered into low mounds." Their role has not been determined but it

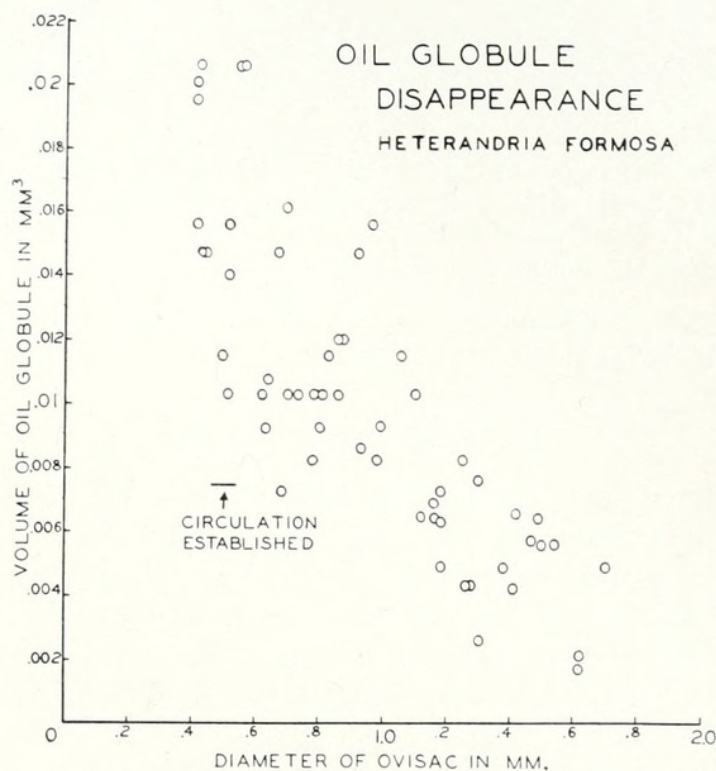


FIGURE 4. The volume in cubic millimeters of the oil globule in fertilized eggs and embryos of *Heterandria* is plotted as a function of the diameter of the ovisac in millimeters. Each point represents a single pair of readings.

is assumed that they aid in some way the nourishment of the embryo through the pseudo-placenta.

Another cell specialization has not been described previously but seems to become important about the time that the head breaks through the enveloping pericardial sac. It probably represents a supplementary nutritive mechanism which helps to compensate for the reduction in association surface. Sometime during the last quarter of development, the wall of the ovisac, which has appeared as a squamous epithelium since fertilization, hypertrophies. In a restricted region of the ovisac prominent secretory cells are developed. These seem to form an approximately one-third of the surface of the ovisac and parallel more or less closely the embryonic vascular surface. In Figure 5 these cells are seen opposite the blood vessels in the wall of the pericardium, but they may also occur opposite nonvascularized body epithelium. Histologically they appear to be active secretory cells

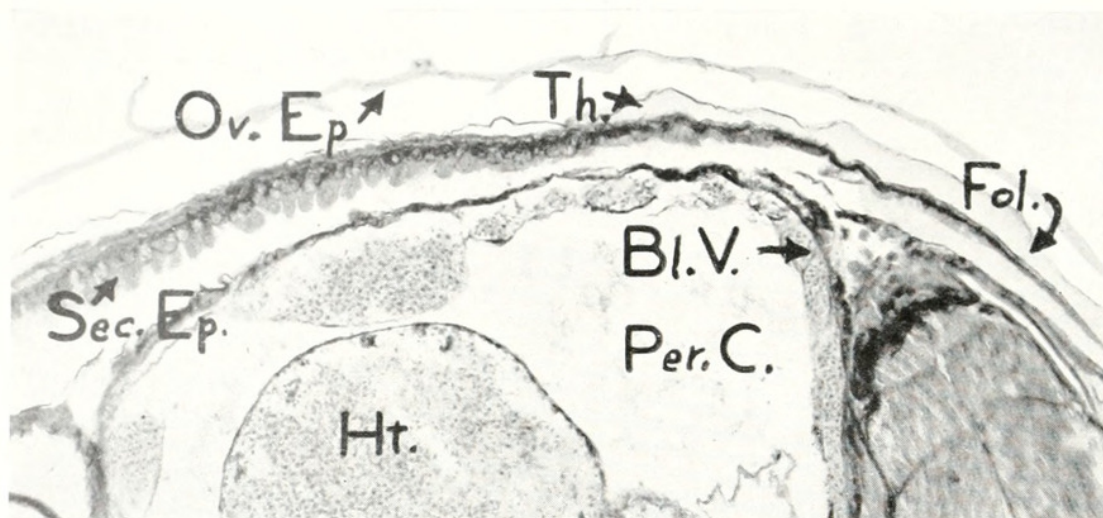


FIGURE 5. Photomicrograph of a section through the ovisac and pericardium of a later embryo of *Heterandria formosa* showing secretory cells of the ovisac epithelium. Ov. Ep., ovarian epithelium; Th., theca; Fol., follicular epithelium; Sec. Ep., secretory portion of follicular epithelium; Bl. V., blood vessel; Per. Cav., pericardial cavity; Ht., heart.

containing many secretion granules. Coagulum which may be from this source appears in sections through the cavity of the ovisac and also in the gut.

METHODS

Both wet and dry weights were determined for members of each brood of embryos taken from 16 females with varied previous histories. One hundred and fifty-one embryos were weighed either individually or in groups belonging to the same brood. The embryos were dissected from the ovary with the ovisac intact. The diameter² of the ovisac was measured with an ocular micrometer. The embryos were allowed to touch fine absorbent paper to remove surplus fluid and immediately placed on flamed platinum squares of known weight. These were weighed at once in a single rapid trial to determine the wet weight of the embryo in the intact ovisac. They were then dried over calcium chloride to constant weight.

All weighings were made with a Sartorius balance. The initial weights of the platinum squares and the final weights of the squares plus dried embryos were each determined by 10 to 20 readings (with zero correction before and after each reading). The standard deviation³ for a given series of readings was rarely over .05 mg. In several trial cases two weeks in the dessicator intervened between the first and second group of ten readings. The standard deviation was still below .05 mg.

The smaller embryos were weighed in groups. The average wet weight of 30 of the earliest embryos was 0.026 mg. After a consideration of all sources of error,

² The ovisac is spherical at first but becomes increasingly ellipsoidal as development progresses. In the late stages the average of several measurements made on the same ovisac proved to be a reasonably consistent measure of size and was recorded as if it were a true diameter.

$$^3 \sigma = \sqrt{\frac{\Sigma d^2}{n-1}}.$$

this value was estimated to be within at least 0.008 mg. of the true wet weight at the time of fertilization. The dry weight value of 0.017 mgs. was similarly estimated to be within at least 0.002 mgs. of the correct value for this stage. In all of the weight measurements except those on the very early stages the experimental error was small compared to the normal variation of the material.

Ash determinations are impractical for early stages because of the extremely small weights involved. Later stages were ashed in a small muffle furnace and an average ash content of 2 to 3 per cent of the dry weight found.

WEIGHT CHANGES OF THE DEVELOPING EMBRYO

Since the age of the embryos was not known, the diameter of the ovisac was selected as a convenient indication of the stage of development, and the weight determinations were correlated with this dimension. When this was done the great increase in weight of the embryo in the intact ovisac was apparent (Fig. 6). The relationship between dry weight and ovisac diameter is repeated on a larger scale for later comparisons (Fig. 7).

Before any appreciable gain in dry weight can be detected the wet weight can be seen to have increased markedly. In fact, the water content of the whole egg

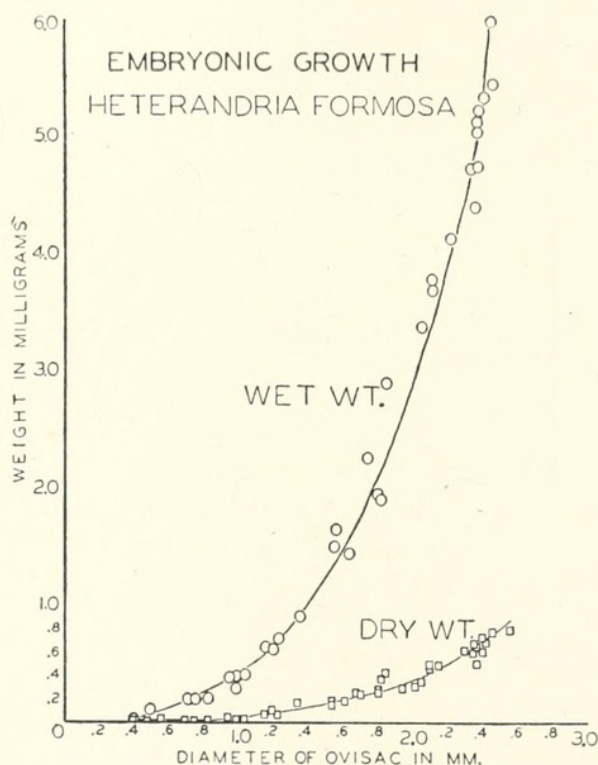


FIGURE 6. The curves show the increase in both wet and dry weights of developing embryos of *Heterandria formosa* plotted as a function of the diameter of the ovisac, a convenient measure of development.

plus ovisac increases from 34.6 per cent to 86.8 per cent in this period. There is considerable experimental error in the first figure because of the small weights involved, but a value of 35 per cent is consistent with the large amount of oil present.

After the dry weight has begun to increase, the relation between wet and dry weight stays remarkably constant. When the period was divided into two sub-

periods, the first including embryos with ovisac diameters between 1.00 and 2.00 and the second including embryos with ovisac diameters greater than 2.00, the differences in per cent dry weight were not significant. During the first sub-period the dry weight average 12.84 per cent of the wet weight (σ 1.8%) and during the second it was 13.49 per cent (σ 1.9%). The average was 13.2 per cent.

After parturition the embryo breaks out of the fluid-filled ovisac and the extra liquid in the expanded pericardial cavity disappears. Accordingly the percentage dry weight increases abruptly to a stable value for the young fish of 20.6 per cent (σ 1.7%). This information can be diagrammed to show the changes in composition from the egg at the time of fertilization to the larva at the time of parturition (Fig. 8).

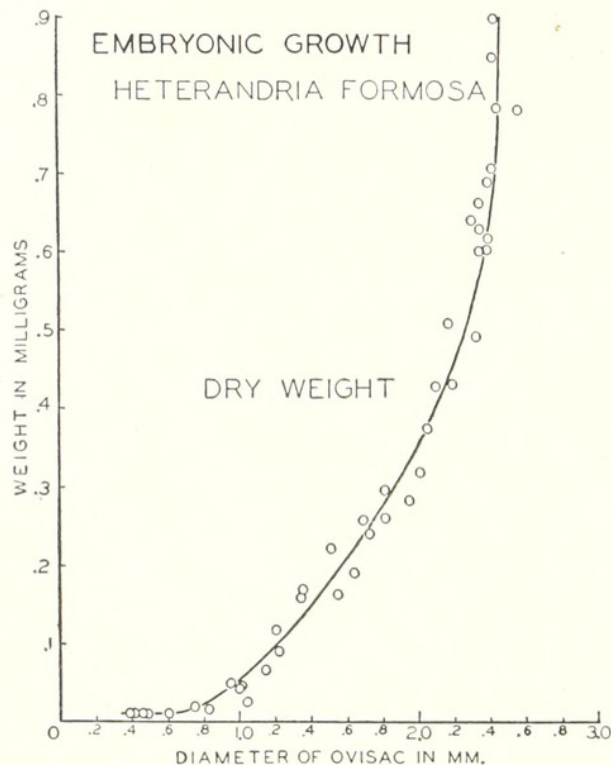


FIGURE 7. The curve shows the increase in the dry weight of embryos of *Heterandria formosa* plotted as a function of the diameter of the ovisac. This represents the same weight values shown in the dry weight curve of Figure 6, but the units of the weight ordinate are much expanded.

These changes can also be represented in the form of a generalized equation which shows the relation of .1 mg. of ovum to the final weight of the larva.

$$\begin{array}{ccccccc}
 0.1 \text{ mg.} & + & 2.6 \text{ mg.} & + & 15.8 \text{ mg.} & = & 18.5 \text{ mg.} \\
 \text{(wet weight of egg)} & & \text{(dry weight from mother)} & & \text{(wet weight from mother)} & & \text{(wet weight of young fish)}
 \end{array}$$

This equation expresses the overall changes. A similar expression has been developed for the trout by Gray (1926). His formula holds from the time the embryo is 50 per cent developed to the time it is 80 per cent formed during which time it has increased about 400 per cent in weight. During this period the trout embryo converts 1.0 grams of yolk (wet weight) plus 0.7 grams of water into 1.56 grams of fish,

Since the yolk makes up almost the entire egg, it can be estimated that one gram of trout egg makes only slightly more than 1.5 grams of trout embryo. In comparison one gram of *Heterandria* egg would result in 185 grams of embryo. This strikingly illustrates the importance of the maternal contribution of nourishment in this species.

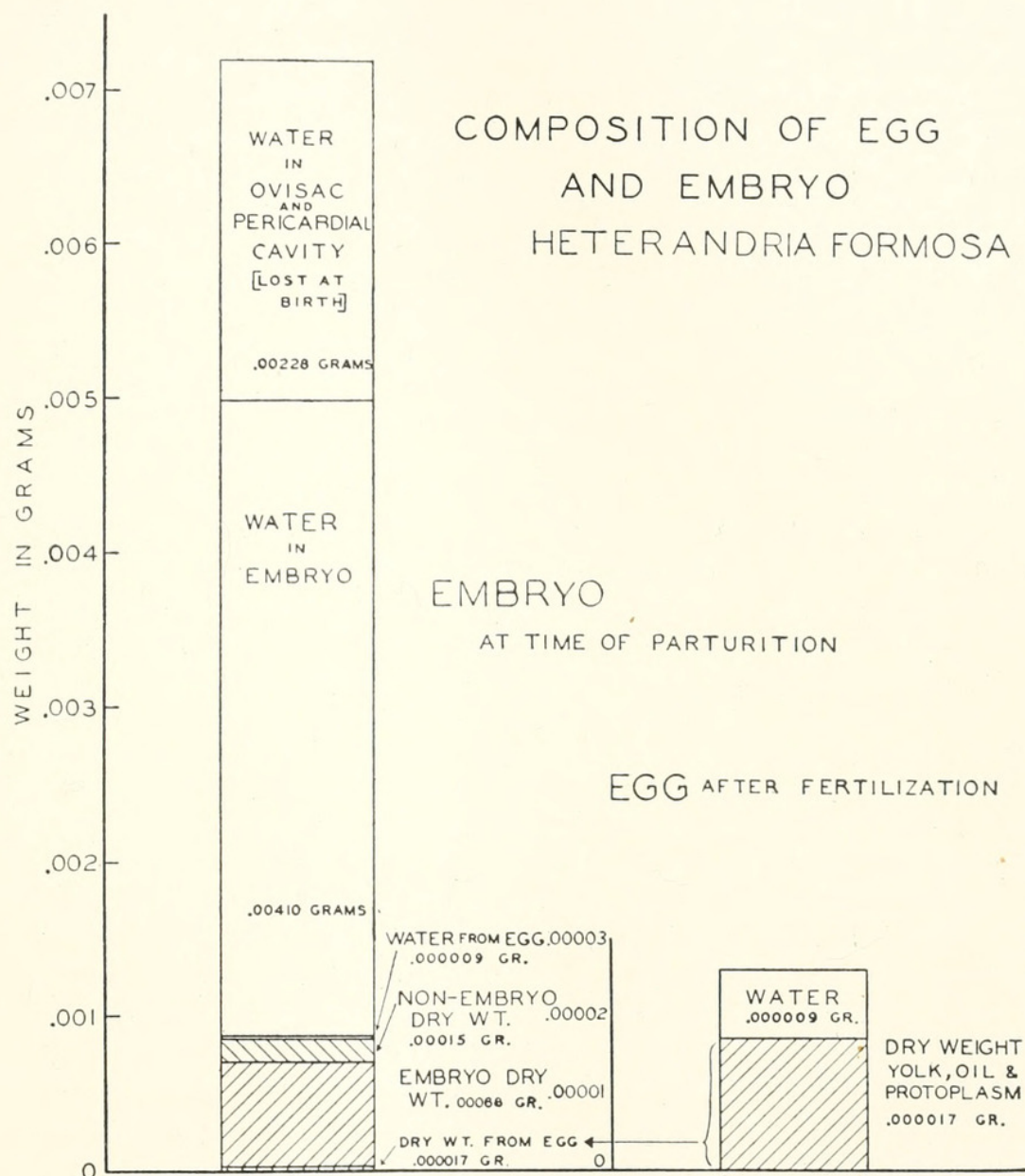


FIGURE 8. The composition of a typical embryo ready for parturition and of a recently fertilized egg is diagrammed. Wide variations from the actual figures cited were found but the proportions remained generally the same in the various larvae studied. As discussed in the text, the weight figures and the relative amounts of wet and dry material in the fertilized egg have been determined only approximately.

In the above figures for the trout the discrepancy of .14 grams between the 1.7 grams of yolk and water and the resulting 1.56 gram weight of the larva represents the dry weight used for maintenance metabolism. The dry weight used for maintenance in *Heterandria* could not be measured directly. However, it can be as-

sumed that approximately one-third of the total food available is used for the maintenance of the embryo in *Heterandria* as well as in the trout.⁴ The maintenance dry weight calculated in this way can be introduced into an equation expressing the actual dry weight drain on the mother per embryo.

$$\begin{array}{ccccccc} \text{water} & + & 6.8 \text{ mg.} & + & 2.2 \text{ mg.} & = & 9.0 \text{ mg.} & + & \text{water} \\ & & \text{(dry weight} & & \text{(maintenance} & & \text{(total dry} & & \\ & & \text{of embryo)} & & \text{dry weight)} & & \text{weight from} & & \\ & & & & & & \text{mother)} & & \end{array}$$

GROWTH RATE OF THE DEVELOPING EMBRYO

Thus far the magnitude of the embryonic weight increase has been described, but no indication of the rate has been obtained. Observations of living gravid females suggested a method whereby a time axis might be obtained. The young of females kept under constant conditions showed a tendency to be born at regular intervals.⁵ Accordingly, the weights of all the broods of a single female kept under relatively constant conditions were plotted as if the time intervals between them were the same. This treatment yielded consistent and apparently significant growth curves.

The female whose embryos are presented in Figure 9 has the unusually large number of eight broods. The growth relationships believed to be general for *Heterandria* are therefore well shown. The initial portion of the curve is a straight line which appears to be parallel to the time axis. This line represents the early developmental period when no post-fertilization contribution of nourishment from the mother can be detected. The second part of the curve is a steeply ascending straight line. It extends throughout the greater part of the embryonic period and represents an approximately constant growth increment in dry weight contributed by the mother. Obviously, there must be a transitional period, which the data cannot show, during which the pseudo-placental associations are being established. This has been indicated by the dotted lines in Figure 9 and also in Figure 10 which represents the similar treatment of embryo weights obtained in the study of other females. All of the females which had been kept under relatively constant conditions showed this relationship. Unfortunately, the concept cannot be tested for females with fewer than five broods as can be seen from the number of points required to establish the two straight lines in Figures 9 and 10.

In order to extend the study to more females, records of ovaries dissected over a three year period were re-examined. These records gave the number of broods per female together with their average ovisac diameters for fish kept under a variety of experimental conditions. The average weight of the broods in these females

⁴ The ratio between the dry weight of the embryo and the dry weight of nutriment required to produce this quantity of embryo is the efficiency coefficient of development. Gray reports a value of .65 for the trout and points out that this figure has been found to be approximately the same for a wide variety of organisms (cf. Murray, 1926, chick; Hayes, 1930, Atlantic salmon; etc.).

⁵ Unpublished data. It is difficult to obtain precise records because the young are frequently eaten by the parent and are so small as to be easily missed. Rather constant optimal conditions and mature females in good health are required to demonstrate this. Small females will not show it clearly. On the whole it is remarkable that this tendency toward even spacing of the broods is as frequent and demonstrable as the data suggest it to be.

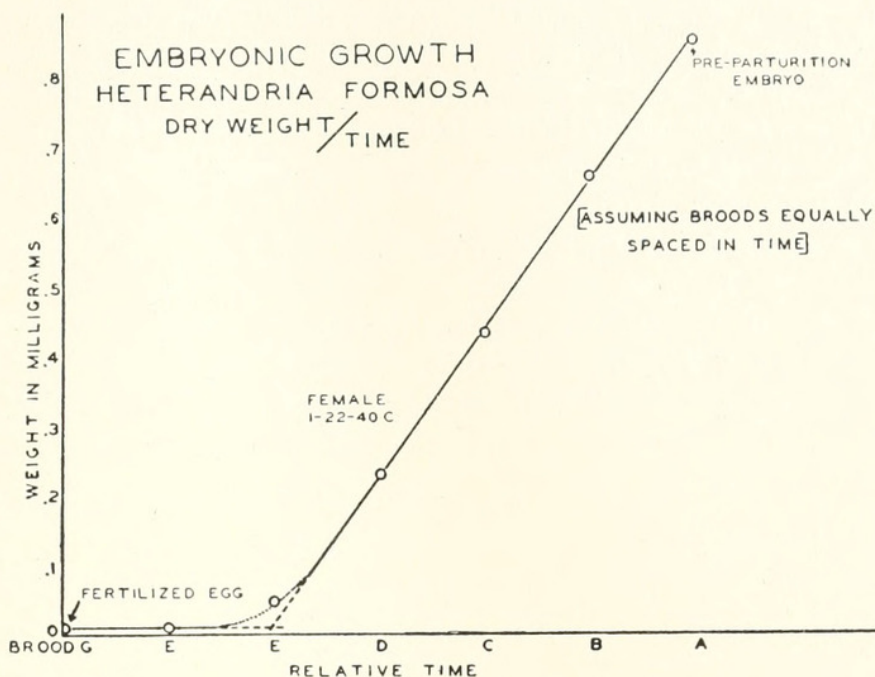


FIGURE 9. The average dry weight of the embryos in each brood of a female with eight fertilized broods is plotted as a function of time. Since the actual age of the embryos cannot be determined, no specific time units can be employed. However, in any large, mature female of *Heterandria* kept under reasonably constant conditions the broods of embryos seem to be born at approximately equal intervals. Therefore, the broods of embryos still in the ovary can be equally spaced on a time axis without the necessity of specifying the actual number of days or hours between them. Since the time relations between the various broods contained in the ovary are thus represented without using known time units, a relative time scale is actually employed. This concept of relative time is also used in Figures 10-12 and throughout the text. The female has been kept under constant illumination in a room with only slight variations in temperature.

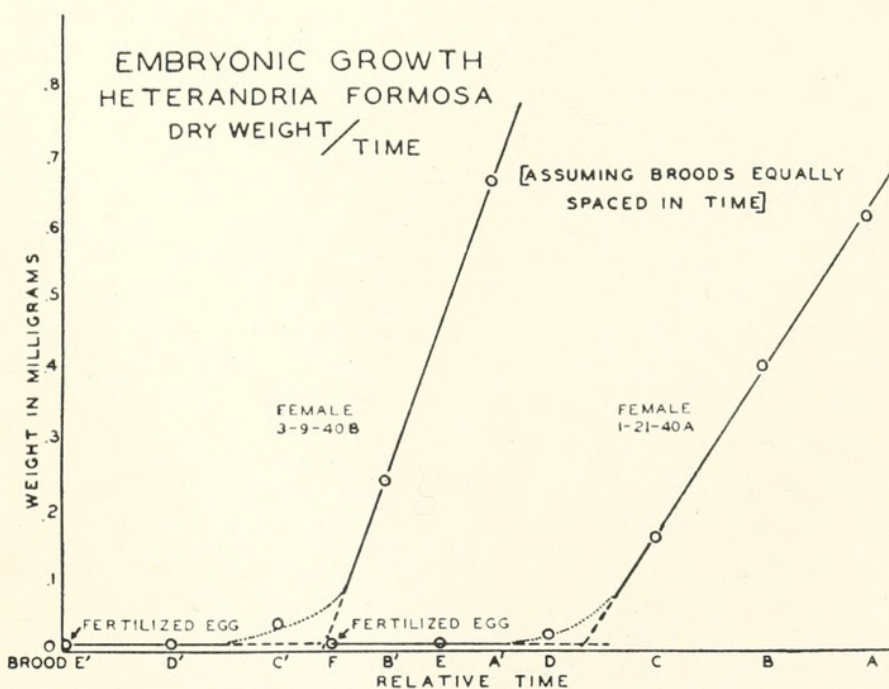


FIGURE 10. The average dry weight of the embryos in each brood of two different females, one with five and the other with nine broods, is plotted as a function of relative time. The treatment is the same as in Figure 9.

could be estimated by comparison of the ovisac diameters with the average weight of the embryos as shown in Figure 7. The results were plotted exactly as in the above cases where the weights were obtained directly. Despite the wide variety of ages and conditions represented, the majority showed the generally linear nature of growth in the two periods. Data from three such females are presented in Figure 11.

This even spacing can also be demonstrated by the superposition of growth curves from different females. Numerous females were examined by this method and their intermediate broods were found to fall on the growth curves of other females. For example, Figure 9 shows the growth curve for the embryos of a female with eight broods. Broods B and E of this female (second and fifth broods respectively) were found to correspond in weight to the first and third broods of

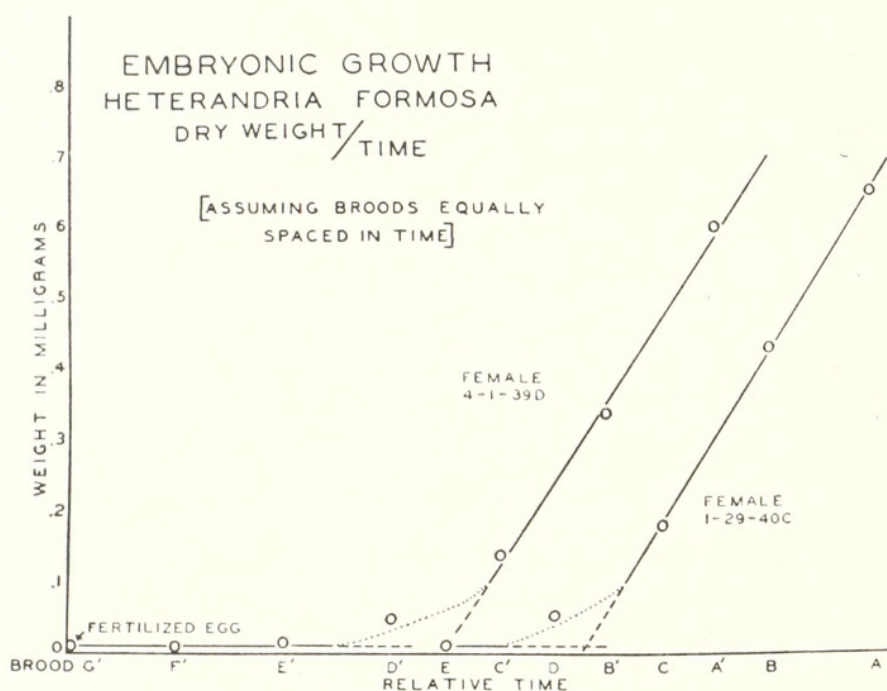


FIGURE 11. The average dry weight of the embryos in each brood of two different females, one with seven and the other with five broods, is plotted as a function of relative time. The dry weight values have been obtained by use of the ovisac diameter and the dry weight curve of Figure 7. The broods are assumed to be evenly spaced in time.

a four-brooded female. When the second brood of the four-brooded female was arbitrarily placed midway between broods B and E on the time axis, it was found to have a weight value which placed it on the growth curve representing the embryos of the eight-brooded fish.

The diameter of the ovisac for each brood of an eight-brooded female can itself be plotted as a function of relative time (Fig. 12). The resulting curve is smooth and sigmoid, showing a slower diameter increase during the early and late periods. In the female represented in Figure 12 the earliest brood was observed to represent recently fertilized ova, and the latest brood was found to represent embryos ready for parturition. Hence a point midway on the relative time axis should indicate the ovisac diameter of an embryo roughly half way through development. It is possible in this fashion to determine the percentage of development represented by other ovisac diameters.

In the course of these studies on Heterandria the specific stage of development corresponding to various ovisac diameters has been noted. It is now possible to assign the percentages of development determined for certain ovisac diameters to developmental stages in Heterandria. These can then be compared with similar stages described in closely related fish in which a more direct measure of time can be obtained. Bailey (1933) faced with similar difficulties in determining the exact time of development in the poeciliid *Xiphophorus helleri*, staged 50 ova and embryos and selected the tenth, twentieth, thirtieth, etc. as representing corresponding percentages of development. *Fundulus heteroclitus* was studied at the Marine Biological Laboratory, Woods Hole, in July 1939 and together with *Xiphophorus* was compared with Heterandria. The relative times between common stages were

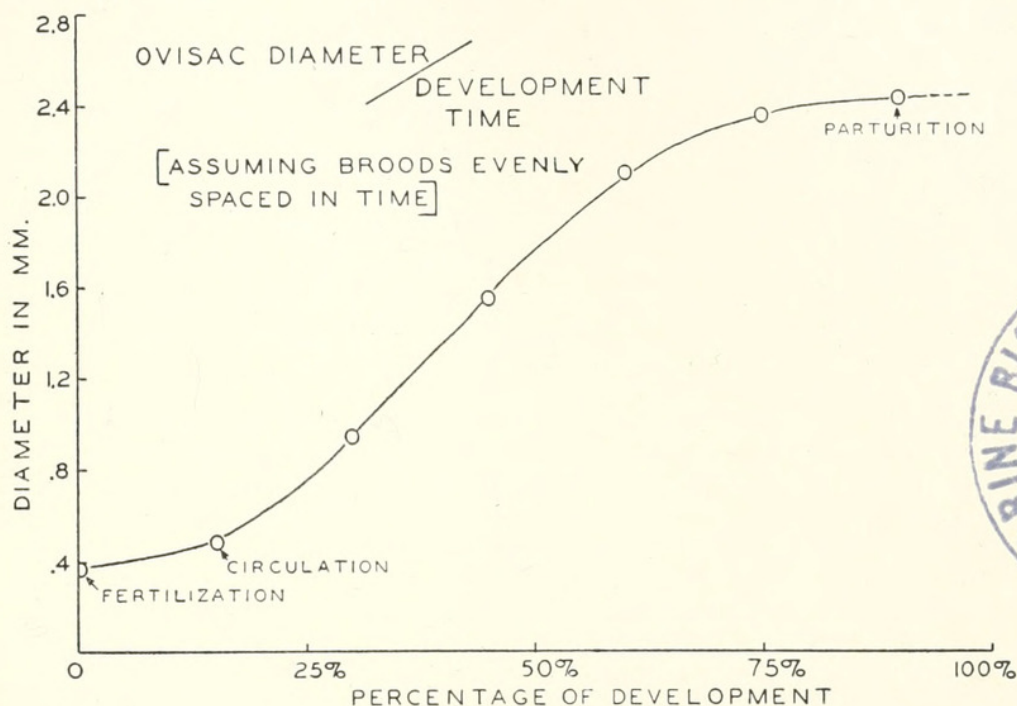
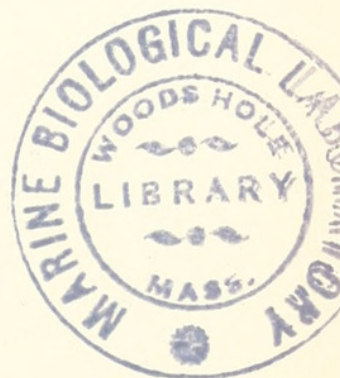


FIGURE 12. The average ovisac diameter of each brood in a female with eight broods is plotted as a function of percentage of development. This is the same female shown in Figure 6 and the time units are obtained in the same manner. However, since the entire range from the fertilized egg to the embryo ready for parturition is represented, these extremes are indicated as 0 per cent and 100 per cent of development and the relative time axis is subdivided accordingly.

clearly similar in the three species. Although the comparison could be only approximate,⁶ it reduced the likelihood of a serious error in the time relations assigned to Heterandria.

If these time relationships are used to determine the increments of growth per unit of time during the later embryonic period, it will be seen that the increments remain constant. When the percentage of maximum increment of dry weight is plotted as function of time in Heterandria (Fig. 13), the result is a straight line parallel to the time axis throughout most of the embryonic period. Gray, treating

⁶ In addition to the difficulties of comparing stages described for different species, the relative time between embryonic stages may be changed by exposure to different temperatures. At the same temperature the relative time between similar stages in two different species may be different (Moore, 1939; Worley, 1933).



his growth rate data for the trout in this manner, demonstrated an asymmetrical rise and fall (Fig. 13). This represented a deviation from Robertson's formula (1923) in which the percentage of maximum increment plotted as a function of the size of the embryo shows a symmetrical rise and fall. This difference Gray was

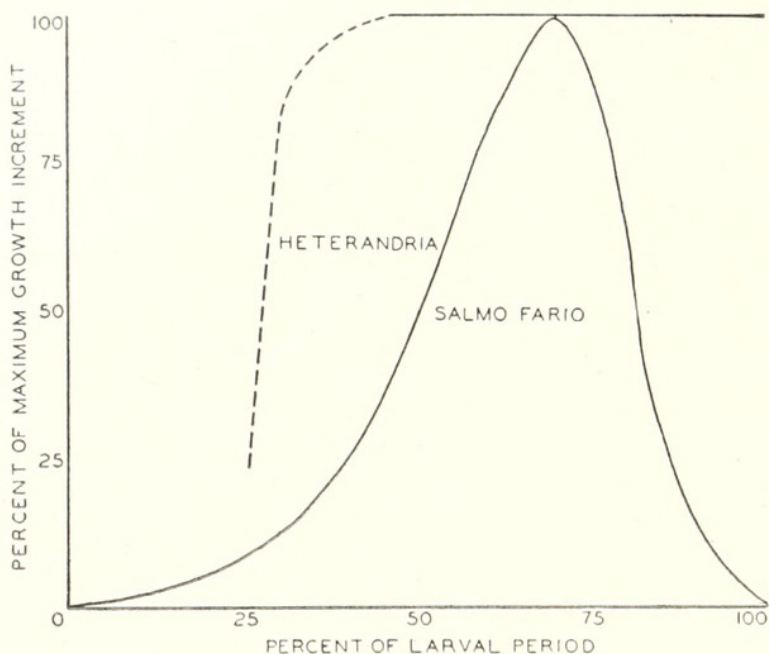


FIGURE 13. The percentage of maximum increment of embryonic growth is plotted as a function of the per cent of the larval period for both *Heterandria formosa* and *Salmo fario*. No measurements are available for the early stages of *Heterandria* and the growth increments are necessarily inferred. The curve for *Salmo* also represents the product of the dry weight of the embryo times the dry weight of the remaining yolk plotted as a function of the per cent of larval development.

able to explain by demonstrating that the growth rate is also a function of the yolk remaining in the yolk sac.

DISCUSSION

The fact that *Heterandria formosa* represents the development of a true viviparity in which nearly all of the nourishment for embryonic development comes from the mother is of interest in itself. When the assumption of equal spacing of broods is made and the data treated accordingly, it also appears that the nourishment for the growth process is being used by the embryo at a constant rate. If this is true, it suggests that some specific extrinsic factor or factors is limiting embryonic growth in this species. Restricted food supply and limited oxygen availability were considered likely to affect the growth rate in this manner. The discussion which follows is an attempt to evaluate these two factors.

It has been shown that morphogenesis in the oviparous fish adjusts itself to the amount of nourishment available, i.e. that the size of the larva is dependent on the amount of yolk available (Morgan, 1896) and not on the total amount of cytoplasm (Sumner, 1900; Hoadley, 1928). That the rate of growth of the oviparous fish embryo is dependent not only on the mass of the embryo but also on the actual amount of yolk remaining has been shown by Gray (1926; 1928a, b) (cf. Fig. 12).

It is conceivable that the pseudo-placental barrier itself may increase in effectiveness only enough to allow for the steadily increasing demands of the maintenance metabolism. Such a relationship seems rather remarkable under the circumstances and might be expected to break down with the complications of retraction of the pericardial sac and development of special secretory cells in the follicle wall. No alteration in growth rate can be detected when these changes in the pseudo-placental barrier occur.

Instead of the limitation lying in this barrier, it may be that certain of the raw materials for growth are present in the maternal blood stream in limited amounts. How such a limitation could affect all of the broods in a similar manner is not clear. There is, however, some indirect evidence that the growth of the individual embryo is responsive to changes in the total maternal supply of nourishment available to all the embryos.

This evidence involves the young of fish not heavily burdened with embryos. Since the straight line nature of the growth curve cannot be tested unless more than four broods are present, all of the data used to develop the idea of a constant increment of growth have been obtained from females with many broods. In these the food requirements of the embryo must constitute a great drain on the mother. The physiological drain would not be as great in females which are recovering from unfavorable conditions, because they contain fewer broods than they are capable of supporting. In these females more nourishment per embryo should be available than in females which have been kept under relatively constant conditions. If more nourishment is available, the embryos should be larger at the end of the larval period (cf. Gray, 1928a). The actual results in Heterandria are that the first young born of a female recovering from unfavorable conditions are large.⁷ This constitutes the best available evidence that the food supply of the embryos in a many brooded female is restricted in some manner, and supports the hypothesis that during the main growth period food may be the determining factor in the development of Heterandria at normal temperatures.

There is considerable evidence that at higher temperatures the oxygen supply to the embryo may be a factor limiting growth. According to Gray, all of the oxygen used by the trout embryo is for maintenance metabolism, the amount used for growth being almost negligible. He also found that a large drop in the growth rate of the trout caused no corresponding drop in oxygen consumption. Nevertheless, Jacques Loeb showed (1894) in *Fundulus* that development is directly retarded by lack of oxygen. The Heterandria females may under certain conditions at 25° temperature give birth to young regularly every four days. A rise in temperature of two or three degrees during the daytime for even two or three days may delay the next brood.⁸ It seems likely that the decreased oxygen supply may account for

⁷ The following figures will not be discussed in detail but are presented in support of the statements made above. A female recovering from unfavorable conditions was observed to give birth to young on Dec. 13 and 14 after a lapse of several months. These young were very much larger than those born four and ten days later. The actual dry weights were found to be:

Dec. 13 and 14, 1940

.88 mg.

.95 mg.

.89 mg.

Dec. 18 and 26, 1940

.63 mg.

.64 mg.

.61 mg.

⁸ Scrimshaw—unpublished data.

this. At the higher temperatures both the mother and the embryos require more oxygen per unit time, but less oxygen is dissolved in the water. It also seems likely (cf. Irving, 1941) that the oxygen dissociation curve of the hemoglobin in the blood would be shifted to the right and flattened, and as a result the oxygen carrying power of the blood would be reduced by the increased temperature.

It can also be observed that a female kept at a constant temperature of 25° C. will have a number of its embryos dying within several hours when the temperature is raised to 28° C.⁹ Such a temperature is not in itself supra-maximal, for the temperature tolerance of the mother runs well above 34° C. The young after birth grow well at this high temperature. The embryos at all stages of development seem to tolerate this temperature satisfactorily when isolated from the mother if the water is well aerated. For example, their heart rate shows no irregularity in μ value on an Arrhenius plot until the temperature reaches 34.6° C. The death of the embryos in the above case can be explained on the basis of limited oxygen supply to them.

Oxygen supply is not likely to be the limiting factor at ordinary temperatures. When exposed only to natural daylight, a female kept at a constant temperature and under approximately uniform feeding conditions will contain a certain number of embryos and these will show the constant growth increment described. When such a female, other conditions remaining the same, is exposed to continuous artificial light for about a month, the number of embryos markedly increases.¹⁰ There is no reason to believe that the total availability of oxygen has significantly increased.

It seems reasonable to believe that the oxygen is the principal limiting factor at higher temperatures, and food supply at the moderate ones. This would mean an intermediate range in which the two factors are complementary in a regular fashion. The data do not serve to distinguish between different degrees of limitation. Furthermore, *Heterandria* kept at temperatures high enough to limit the oxygen supply do not have enough broods to enable the growth rate to be determined. The possibility of other factors such as endocrine balance influencing the growth rate has not been excluded.

SUMMARY

The fertilized egg of the viviparous poeciliid *Heterandria formosa* is minute and is made up almost entirely of a single large oil globule. At least 70 per cent of the original volume of the oil globule is still present when maternal contribution of nourishment begins. Secretory cells develop in the ovisac wall late in the embryonic period. These together with adaptations previously described permit the mother to contribute nearly all of the raw materials for growth and development of the embryo after the egg has been fertilized.

The increase in wet and dry weight of the embryos at the expense of the mother has been determined by obtaining both wet and dry weights at various stages of development. The dry weight of the embryo increases from 0.017 milligrams at the time of fertilization to 6.8 milligrams at the time of parturition. The percent-

⁹ Scrimshaw—unpublished data.

¹⁰ Scrimshaw—unpublished data.

age dry weight remains constant at 13.2 per cent after the pseudo-placental association is established.

Observations of living females suggested that under constant optimal conditions the broods of a single female tend to be evenly spaced in time. Upon this assumption the dry weights of the embryos in each brood of suitable females were plotted against relative age. The resulting curves suggested that the rate of growth after the maternal contribution of nourishment can be detected is approximately constant. Food supply and oxygen supply are discussed as factors which might limit this growth. Embryonic growth in Heterandria is compared with that in oviparous fishes.

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