Contributions from the Biological Laboratory of the U. S. Fish Commission, Woods Hole, Massachusetts.

THE EGG AND DEVELOPMENT OF THE CONGER EEL.

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On July 31, 1900, at 10 o'clock a. m., the U. S. Fish Commission schooner *Grampus*, while on the tile-fish grounds about 30 miles south of South Shoal, secured some pelagic fish eggs. These eggs were collected by Dr. Porter E. Sargent. Among them were many which he supposed to be the eggs of the tile-fish, which they resembled in many respects.[1] They were brought to the Woods Hole laboratory on August 1. It was soon seen that they were the eggs of some eel, and since no eel eggs had been observed in American waters, in fact, none outside a limited region in the Mediterranean, it seemed doubly desirable to follow their development.

When the eggs were secured, the gastrula was said to cover about half of the yolk. On August 1 the tail was well developed. During the night between August 2 and 3 many of them hatched. The last one died in the night between August 13 and 14. The eggs were divided into two lots on August 1. Some were left in running sea water, others placed in a shallow dish of standing water. Since, on August 2, many of those in the running water had died while none of those in standing water perished, they were all placed in standing water, which was occasionally changed.

Before describing these eggs more in detail, a brief review of the eel-development question may be given. The ancient history is given fully by Jacoby.[2] The modern history begins with the discovery of Raffaele,[3] who in 1888 described five species of pelagic fish eggs secured during August, September, October, and November, which, on account of the character of the larvæ they produced, he referred to species of eels. This is the first description of the developing eggs of any eel-like fishes. The common characters of the eggs described by Raffaele are: (1) Their large size; (2) the large perivitelline space; (3) the delicate membrane lacking pore canals and usually with iridescent reflections; (4) the vesicular yolk. They differed from each other in size and in the possession or absence of an oil-sphere.

The eggs and larvæ derived from the eggs secured by Raffaele were characterized as follows: No. 6 had a large perivitelline space, diameter of the eggs 2 to 2.5 mm., diameter of the vitellus 1.20 to 1.50 mm., 1 to 3 oil-spheres of 0.30 to 0.35 mm. The larva developing from this possessed 72 (or 73) abdominal segments. No. 7 had a

[1] Ripe eggs taken from a tile-fish and preserved in formalin measure as follows: The yellow oil-sphere 0.2 mm., the yolk 1.09 mm., from membrane to membrane 1.25 mm. The eggs are much smaller than those of the eel here described.

[2] Report U. S. Fish Commission, 1879.

[3] Le Uova Galleggianti e le Larve dei Teleostei nel Golfo di Napoli. Mittheilungen aus der Zool. Station zu Neapel, 8, pp. 1–84, tav. 1–5.

diameter of 3 mm., 6 to 12 oil-spheres which occupied the posterior (ventro-anterior in the figure) part of the vitellus when the embryo developed; 59 (60?) abdominal segments were developed. No. 8 had a diameter of 2 mm. and about 30 oil-spheres; the larva had 72 (73?) abdominal segments. No. 9 had a diameter of 2 mm., the yolk attached to the membrane by filaments; when the young developed, the oil-sphere occupied an anterior position and had the form of a club; 66 (67?) abdominal segments; larva much smaller than that of No. 6. No. 10 had a diameter of 2.7 mm., was without oil-sphere, and yielded a larva with 44 (45?) abdominal segments.

All of these were taken between August and November, being more abundant in September and October. The earlier stages had a well-formed blastodermic callote. The yolk becomes well constricted after the blastodermic rim has passed the equator. The larvæ had a number of characters in common, viz, an enormous fourth ventricle, a large œsophageal pouch, an elongate body with numerous abdominal segments, the position of the anus about halfway to the margin of the ventral fin fold, very large and striking teeth, and a series of pigment spots along the lower parts of the sides.

When the larva is five or six days old it is slender and elongated, with a greatly compressed body, very transparent, and with little pigment. The vitellus is very elongated and diminishes from in front backwards. The intestine ends in the ventral fin fold a short distance from the body in a small accumulation of cells. The notochord is formed of a single series of segments. The mouth opens during the second day after hatching. The teeth develop rapidly. Three pairs are developed in the upper jaw. This dentition is absolutely exceptional among fishes. Contemporaneously with the development of the mouth the choroidal pigment and five or six black pigmented spots form along the body. No noteworthy changes take place between the fourth and fifth days after hatching. Beyond this time Raffaele was unable to rear the eggs. He supposed these eggs to be those of eels, without more closely identifying them. Grassi, in his epoch-making researches in eel development,[1] identified Raffaele's egg No. 10, without oil-spheres and with a diameter of 2.7 mm., as that of the common European eel, *Anguilla vulgaris.* While unable to keep eggs like those described by Raffaele—which he secured at Naples—alive for many days, he showed that the newly hatched larvæ described by Raffaele have essentially the character of *Leptocephali.* He states that females of eels can only mature in very profound depths, i. e., at least a depth of 500 meters. The male can mature in shallow water:

Fertilization takes place at great depths; the eggs float in the water; nevertheless they remain at a great depth in the sea, and only exceptionally, for unknown reasons, some of them mount to the surface. From the egg issue rapidly a præ-larva, which becomes a larva (*Leptocephalus*) with the anus and urinary opening near the tip of the tail. The larva then becomes a hemi-larva, the two apertures just named moving their position toward the anterior part of the body, which becomes thickened and nearly round. By further change the hemi-larva assumes the definitive or adult form. The larva, as well as the hemi-larva, shows a length of body much greater than that exhibited by the young Murænoid of adult form into which they are transformed. By keeping specimens in an aquarium I was able to establish a diminution of more than 4 cm. during the metamorphosis. With regard to the greatest

[1] Grassi, B. The Reproduction and Metamorphosis of the Common Eel (*Anguilla vulgaris*), Q. J. M. S., vol. 39, page 371.
Grassi, B., and Calandruccio, S.

a. Ulteriori ricerche sulle metamorfosi dei Murenoidi. Rend. Acc. Lincei, VI, p. 43.

b. Descrizione d' un Leptocephalus brevirostris in via di trasformarsi in Anguilla vulgaris. L. C. pp. 239, 240. (Translation in Nature, LVI, p. 85).

c. Reproduzione e metamorfosi della Anguille. Giorn. Ital. Pesca e Acqui., 1887, Nos. 7, 8. (Abstract in Monit. Zool. Ital., VIII, pp. 233 and 234.)

length which the larva can attain in a given species, and the amount of diminution which accompanies metamorphosis, there are great individual variations.

Grassi assumes that three vertebræ develop to correspond to the first four protovertebræ and one for each following protovertebra. He "ascertained in an absolute manner that during the metamorphosis of the Murænoids the number neither of the myomeres, nor of the vertebral arches, nor of the spinal ganglia, is subjected to any change." He referred the following Leptocephali to their respective species:

Leptocephalus brevirostris	Anguilla vulgaris.
Leptocephalus stenops (in part), morrisii, punctatus	Conger vulgaris.
Leptocephalus hæckeli, yarreli, bibroni, gegenbauri, köllikeri, stenops (in part)	Congromuræna mystax.
Leptocephalus tænia, inomatus, diaphanus	Congromuræna balearica.
Leptocephalus kefersteini	Numerous species of Ophichthys.
Leptocephalus longirostris and Hyoprorus messanensis	Nettastoma melanuruni.
Leptocephalus oxyrhynchus	Saurenchelys cancrivora.

The eggs described by Raffaele have all the characteristics of pelagic eggs, and the one to be described here, which is very closely related to No. 6 of Raffaele, is certainly a typical pelagic egg. Grassi also secured the eggs of eels on the surface at Naples. Why, under the circumstances, he concludes that "they remain at great depths in the sea, and only exceptionally, for unknown reasons, some of them mount to the surface" is not apparent. Being lighter than sea water, having oil-spheres, and being in all respects typical pelagic eggs found on the surface, we must conclude that "if fertilization takes place at great depths" it must be "only exceptionally, for unknown reasons," that they remain at the great depths. The fact that Raffaele never secured eggs younger than when the gastrula was well formed would favor the supposition that they were fertilized at a great depth and rose slowly in the water.

Cunningham's interesting observations on the conger eel, if they are generally true for eels, would account for the fact that ripe females are rarely taken, and those of Schmidtlein and Hermes point against the supposition of Grassi that the females of eels in general ripen only at depths of at least 500 meters.

Schmidtlein [1] and Hermes [2] both noted that female conger eels sometimes died in confinement, the result of excessive development of ovaries which were not emptied.

In 1888 Cunningham [3] wrote:

> No one has yet, I believe, seen the fertilized egg of either the eel or the conger, although the ovaries and testes have been recognized and described.

He had not at that time found a male conger. In a later paper [4] he gives a general résumé of the work done on the conger. He himself found a perfectly ripe male 45 cm. long on December 13. Its eyes were strikingly prominent and its mouth short and broad. On December 19, among 9 congers caught, one 48 cm. and one

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[1] Schmidtlein, R.
Beobachtungen über Trächtigkeits- und Eiablage-Perioden verschiedner Seethiere. Mitth. aus der zool. Station zu Neapel. I, p. 135, 1879. (Young conger eels scarcely 3 cm. long are captured in the middle of April.)
Beobachtungen über die Lebensweise einiger Seethiere innerhalb der Aquarien der zoologischen Station. Mitth. aus der zool. Station zu Neapel. I, p. 492. (Ripe female conger eels sometimes come to the surface and die from the presence of excessive numbers of ripe eggs, which for unknown reasons are not expelled.)

[2] Hermes, Otto.
Zoologischer Anzeiger, vol. IV, 1881.
The Propagation of the Eel. Rept. United States Fish Commission, 1879, pp. 457–463, 1882. Translated from circular No. 6, November 25, 1880, of the Deutscher Fischerei-Verein.
The Migration of Eels. Rept. United States Fish Commission, 1884, p. 1123, 1888.

[3] The Breeding of the Conger. Journ. M. B. A., old series, No. 2, p. 245, 1888.

[4] On the Reproduction and Development of the Conger. Journ. M. B. A., new series, II, p. 16, 1891.

66 cm. were males. The sexes can be detected by the following constant secondary sexual characters: The head in the female from above appears triangular, in the male the snout is distinctly blunter. In the female the snout is rounded in transection, in the male the surfaces of the snout are flat.[1] During December, January, and February Cunningham collected 8 male congers. The largest female conger ceased to feed in March. On July 24 a few eggs were obtained by squeezing. These contained no oil-spheres and sank in water with a density of 1.027. The diameter of one after the formation of the perivitelline space was 1.6 mm. This female died on September 10. Her ovaries weighed 7 pounds 5 ounces. The "ovaries increase very much in size and weight during the fasting period at the expense of the rest of the body, while in the total weight of the fish a great reduction takes place. Each conger eel breeds only once in a lifetime." He calculated the eggs in another female to be 7,925,280. Out of a total number of 34 congers 11 were males and 23 were females. That no ripe congers are caught is because they do not feed for weeks before becoming ripe.

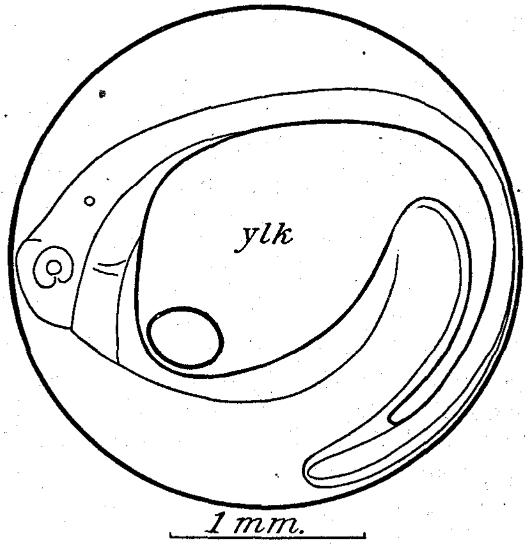


FIG. 1.—Outline of embryo, showing position in membrane and shape of the yolk. August 1.

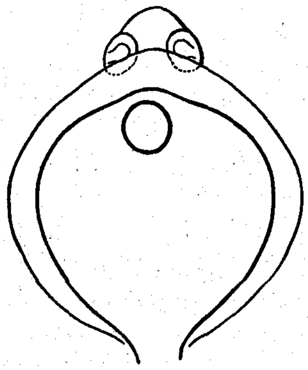


FIG. 2.—Outline of enlarged part of the yolk and yolk-sac of an embryo of the same age as fig. 1, from below.

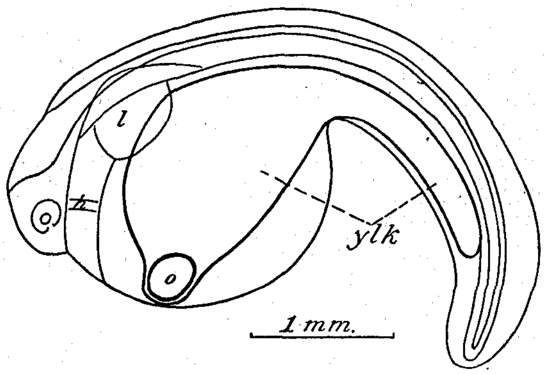


FIG. 3.—Embryo freed from its membrane, showing beginning of the constriction of yolk at its anterior end. August 1.

The eggs secured by Dr. Sargent measure 2.4 to 2.75 mm. from membrane to membrane.[2] The yolk, as in the eggs described by Raffaele, is made up of trans-

[1] In Nineteenth Report of the Commission of Fisheries of New York, page 280, Bean describes 5 male eels. It is very probable from Grassi's observations that these were the males of the common eel in their nuptial dress.

[2] Among other eggs collected by Dr. Sargent and preserved in formalin were six with many of the characters of eel eggs. They were large, with a very large perivitelline space, the yolk in spheres and with one large and a number of smaller oil-spheres. These eggs were notably larger than those brought home alive. They measure 3 mm. from membrane to membrane; the yolk measures 1.75 mm. or a little more. It is possible that these are identical with those to be described. The germ lies at one side of the egg, the oil-sphere at the other.

parent spheres not unlike those of the eggs of certain clupeoids. There are present, from one to six light-yellow oil-spheres of variable size. If more than one are present, then one is always much larger than any of the others. The yolk measures 1.75 to 2 mm. Some of the young were found to be hatched on the morning of August 3.

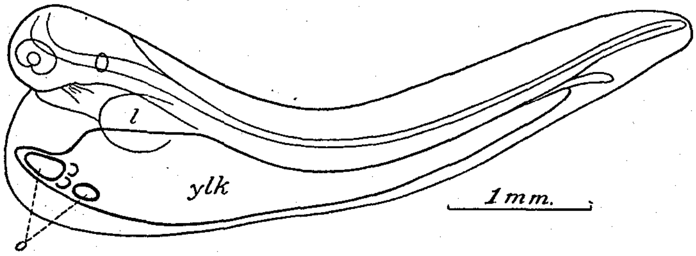


FIG. 4.—Embryo freed from its membrane, showing continued constriction of anterior end of yolk and general diminution of the enlarged anterior portion of yolk with the corresponding increase of caudal portion of yolk. August 2, 7.30 a. m.

Since many of these developed gaping jaws and some others, which did not hatch till several days later, developed normally, it is possible that the early hatching was not normal. Raffaele's eggs hatched in five or six days. He was able to keep them four or five days after hatching. For some time after hatching the larvæ floated with their heads upward—the probable result of the location of the oil-spheres. On August 6 they had assumed a normal horizontal position and the characteristic eel-like progression, but the pectorals were not yet used in swimming. Later they were seen eeling their way through the water, not infrequently nosing about the bottom and voraciously seizing anything that came in their way.

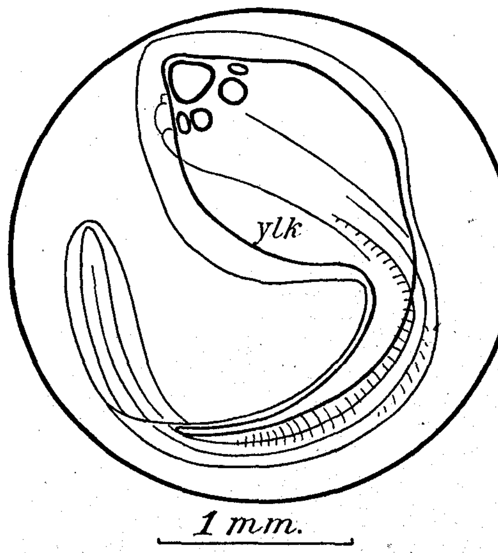


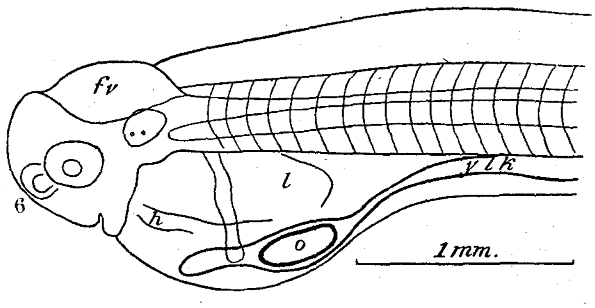
FIG. 5.—An embryo, of the same stage as Fig. 4, in its membrane, from below.

The characteristic feature of the eggs at the time I began to observe them, August 1, was the shape of the yolk. The bulk of this occupied the usual position, but a narrow stalk extended back below the alimentary canal. The oil-sphere or spheres occupied the extreme anterior part of the yolk[1] (figs. 1 and 2). The further history of the yolk in this species is unique among fishes and not sufficiently emphasized by Raffaele. In fig. 3 it is seen that the yolk is no longer rounded anteriorly, but that it ends in a marked protuberance and that the oil-sphere lies in this. The general mass of the yolk still retains the original shape and distribution. The anterior protuberance now becomes longer and at the same time narrower, so that the oil-sphere loses its rotundity and becomes elongate (fig. 4). At the same time the general mass of the

[1] All drawings were made from living specimens, or such as had just been killed by formalin. In the drawings, *al*, alimentary canal; *fv*, fourth ventricle; *ylk*, yolk; *l*, liver; *h*, heart; *o*, oil-spheres.

yolk diminishes rapidly in the yolk-sac, while in the elongated pouch along the ventral side of the alimentary canal no diminution is evident. On the contrary, there is an apparent increase; the entire yolk-sac becomes notably longer with the increase in the length of the body. Very soon (figs. 6 and 7) the oil-spheres, much elongated, with a small surrounding mass, are all that remains as a spindle-shaped figure (fig. 6) in the yolk-sac.

The yolk-sac does not at once lose its shape and bulk, but serves as an unusually large pericardial chamber which is equaled only in the practically yolkless *Cymatogaster*. On August 5 the yolk along the alimentary canal had suffered little diminution, and its outlines were quite regular (figs. 8 and 9). On August 6 this part of the yolk had become constricted in places, the outlines being less regular (fig. 10). The yolk had become yellowish in color and more fluid than vesicular. On the following day the constriction had deepened, and on August 11 the remains of the yolk were located in a series of minute globule more or less widely separated from each other. Long before this condition was reached, about August 8, the larvæ were taking food.



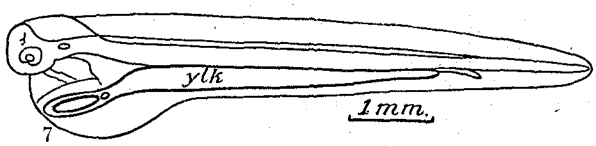
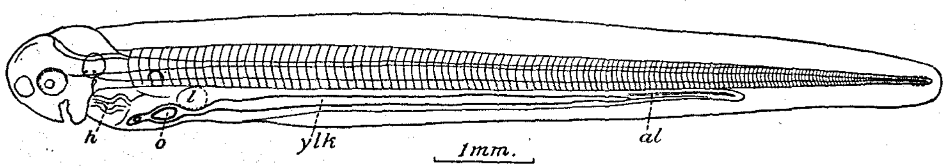


FIG. 6.—Head and anterior part of body, showing the continued reduction of the yolk and the very large fourth ventricle. August 3.
FIG. 7.—Outline of a larva somewhat older than that of fig. 6.

The number of segments developed in front of the anus differs slightly, ranging from 65 to 71. The number beyond this point could not be determined exactly. The



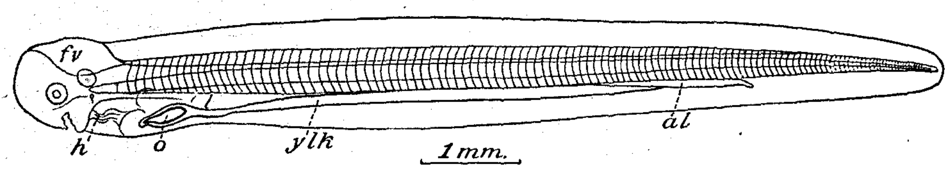


FIG. 8.—A larva on August 4. FIG. 9.—A larva on August 5.

notochord consists in its anterior fourth of single segments (fig. 11). In its middle region the segments do not extend through its entire thickness, but in the tail it is again formed of single segments. The lines separating these are so much more conspicuous than the lines separating successive myotomes that it is impossible to make out the latter in the thin transparent tail of living specimens. The segments represented in the last half of the tail in fig. 10 are therefore not at all reliable.

Color is late in making its appearance. It is first evident at the end of the tail. At 6 p. m. on August 5 some of the larvæ had the following six spots above the alimentary canal and along lower margin of the myotomes of the tail: (1) About

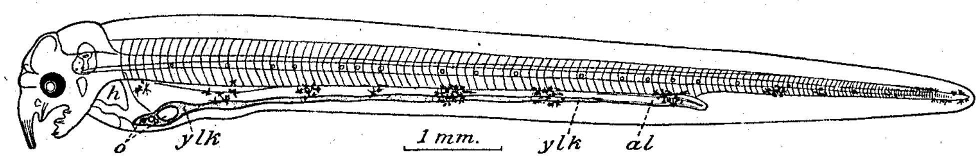


FIG. 10.—A larva on August 6; the mouth probably slightly abnormal.

middle of yolk; (2) halfway between this and end of yolk; (3) at end of yolk; (4) in front of anus; (5) some distance behind anus; (6) about the tip of the tail. The location of the spots coincides roughly with the moniliform enlargements of the abdominal yolk. Other spots are added between these already formed. The relative and actual size of the spots differ greatly, but the number is the same in different specimens of the same age. In the oldest larvæ the spots represented in fig. 14 were developed. Aside from those along the lower part of the sides there were a few cells on the upper jaw, and the scattered cells seen near the tip of the lower jaw as early as August 7 (fig. 12) have developed into a well-marked spot. The character of the pigment about the tail is also noteworthy. In the last stage figured the processes of the cells show a tendency to lie parallel to the embryonic fin rays. Pigment is formed in the eye with its earliest appearance on the body. No color, aside from the black pigment spots and the yellowish yolk, is seen anywhere about the larva during the time the larvæ were under observation.

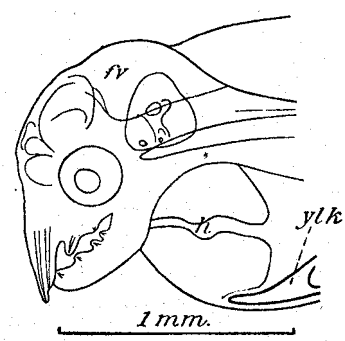


FIG. 11.—Head of larva of the same age as that of fig. 10, the mouth normal.

The fin fold is well developed, reaching from the nape around the tail to the yolk-sac. It is much wider along the back and in the region of the vent than about the tip of the tail or the ventral line of anterior abdomen. No rays had appeared in the oldest larvæ observed except about the tail, where there appears a distinct radiation.

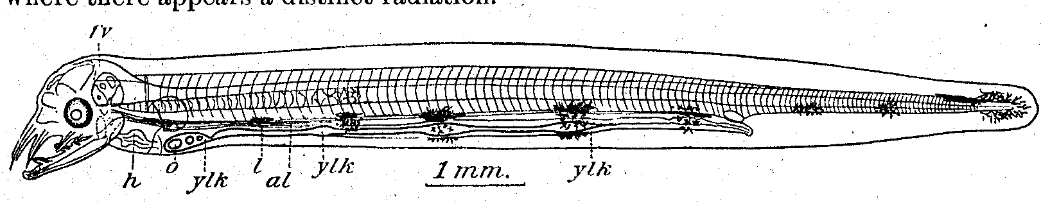


FIG. 12.—A larva on August 7.

The enormous development of the posterior half of the fourth ventricle is similar to the condition figured by Raffaele. In all but the last stage figured this part of the fourth ventricle is a large thin-roofed vesicle, separated from the fin fold in the earlier stages by a distinct notch (figs. 6, 7, 8, 9, 10, 11). The auditory capsules are conspicuous, and, viewed from above, are seen to protrude from sides of head (fig. 13).

The alimentary canal is marked (1) by large fang-like teeth, (2) the early vesicular development of the liver, (3) the position of the anus near the body and remote from the margin of the ventral fin fold. As soon as the mouth is open, about the fourth or fifth day from the beginning of development, the margins of the jaws are seen to be marked by small protuberances. These are the swellings within which the teeth are developing. In the upper jaw four pairs of teeth are developed, graded from in front back, the anterior ones being comparatively enormous fangs. In the lower jaw four pairs are also developed. These are more uniform in size, but with the second one larger than the rest. In the oldest individual there were five pairs of teeth in the lower jaw. I am unable to say whether this was a normal condition. The teeth of the upper jaw close over those of the lower jaw.

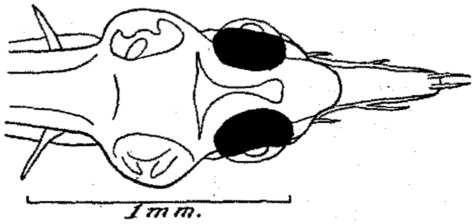


FIG. 13.—The head of a larva of August 7, from above.

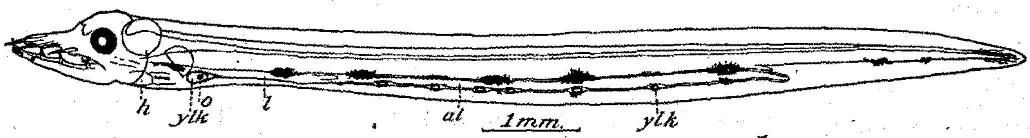


FIG. 14.—A larva of August 4. The fin fold of this larva is probably represented as too low.

The œsophageal pouch of Raffaele has been mentioned. Even before hatching, it is a conspicuous pouch behind the heart. Later, when the anterior yolk has been largely consumed and is separated from the posterior yolk by a constriction, the vesicular structure becomes converted into a lobulated organ about this constriction.

The evidence that the eggs here described are those of *Leptocephalus conger* is circumstantial rather than positive. There are two eels found in this region—the conger and the common eel. The common eel egg has been identified as one without an oil-sphere. This would leave the conger as the only possible parent of the present species. The conger was abundantly taken on the trawl at the bottom over which these eggs were secured. On the other hand, the ripe conger egg has not been described, in spite of the fact that Hermes and Schmidtlein have both seen it. The egg of the conger described by Cunningham was obviously not ripe. The present eggs may provisionally be identified as those of the conger.

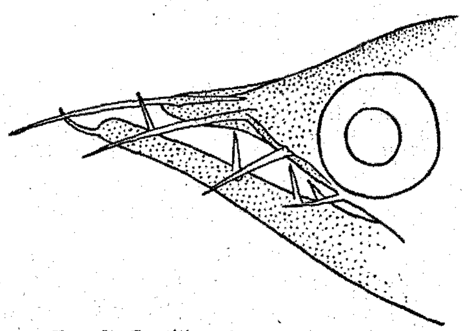


FIG. 15.—Dentition of a larva of August 14.