

Changes in Length during the Larval Life and Metamorphosis of the Freshwater Eel (*Anguilla vulgaris* Turt.).

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With 5 Figures in the Text.

INTRODUCTION.

IN other papers (Ford, 2 and 3) attention was directed to a study of the changes in length which occur during the transformation of the transparent eel-shaped larval clupeoid into the silvery and scaled adolescent fish. The change in position of the anus and fins relative to the vertebrae was considered in connection with the altering proportions of the different body intervals as development proceeds, and simple models were used to illustrate important features.

Now the freshwater eel has its transparent larval stage and metamorphosis. As in the clupeoid, length-proportions change during development, while anus and fins undergo marked migrations with respect to the myomeres. It was therefore thought to be of no little interest to analyse the length-changes during development in a manner similar to that adopted for the herring, sprat and pilchard. Professor Johannes Schmidt most kindly supplied me with material upon which to work, and I have made much use of data already published by him in reports on his great pioneer investigations. I have also drawn extensively from the data given by Dr. Leon Bertin in his paper on the migrations of the anus in the eels during ontogeny. I may be permitted to add that much which follows is suggestive in nature, rather than proven fact. Nevertheless, it should prove of interest in its direct bearing upon questions of fundamental biological importance.

Following the principle adopted by the Italian zoologist Massimo Sella in 1911, Schmidt (6, pages 9 and 10) determined the total length and the length of the tail (ano-caudal distance) for each of a representative series of larval *Anguilla vulgaris* Turt. and plotted in a graph the ratio $\left(\frac{\text{total length}}{\text{length of tail}} \right)$ for eight average values of the total length. Schmidt's

figure is reproduced here in Figure 1. It will be seen that for a total length of 15 mm. the above ratio has a value of 4.35, whereas at a total length of 85 mm. it has fallen to 3.20. That is to say, at a total length of 15 mm. the

ano-caudal distance is $\frac{15}{4.35} = 3.45$ mm., and at 85 mm. it is $\frac{85}{3.2} = 26.55$ mm.

In the accompanying Figure 2, the line AB measures 15 units of length, of which PB represents 3.45 units. CD is drawn parallel to AB and measures 85 units of length, of which QD represents 26.55 units. The straight line connecting point A with point C is at right-angles to AB

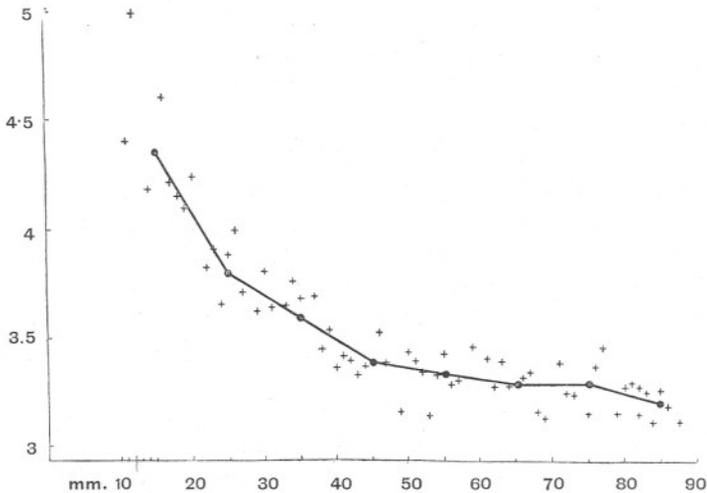


FIG. 1.—European Fresh-Water Eel (*Anguilla vulgaris* Turt.). Showing ratio between total length and length of tail during larval development. (After Schmidt, 6, page 10, figure 3.)

(or CD) and is of a length equal to the difference between the lengths of AB and CD, namely, $85 - 15 = 70$ units. Furthermore, AC is divided into equal intervals of 10 units at points *a* to *f*, and straight lines are drawn parallel to AB (or CD) from each of the points *a* to *f* to intersect PQ and BD.

Now it is obvious that in taking the step of 10 units downwards from point A to point *a*, the length *ag* is greater than AB by an amount equal to one-seventh of the difference (CD-AB) which would be brought about by proceeding the whole distance of 70 units from A to C. Similarly, *pg* exceeds PB by an amount equal to one-seventh of the difference between QD and PB.

Let us assume that this figure is a diagrammatic representation of the manner in which a larval freshwater eel at Schmidt's 15 mm. stage

grows in length to the 85 mm. stage, PB and QD being the corresponding lengths of the tail (ano-caudal distances). The values of the total length and length of tail for successive steps of 10 units along AC in the direction of point C, and of the ratio $\left(\frac{\text{Total length}}{\text{Length of tail}}\right)$ are :—

TOTAL LENGTH.	LENGTH OF TAIL.	$\left(\frac{\text{TOTAL LENGTH}}{\text{LENGTH OF TAIL.}}\right)$
15	3.45	4.35
25	6.75	3.70
35	10.05	3.48
45	13.35	3.37
55	16.65	3.30
65	19.95	3.26
75	23.25	3.23
85	26.55	3.20

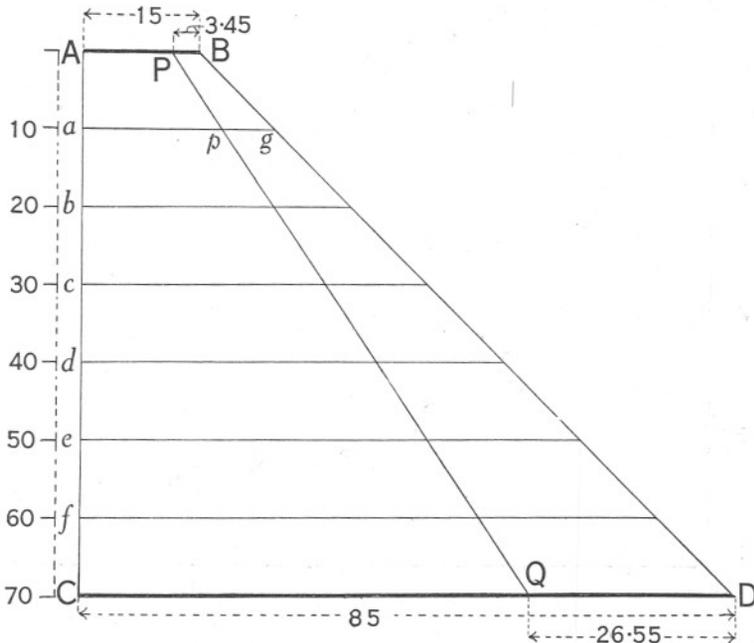


FIG. 2.—For explanation see text page 988.

In Figure 3 the values of the ratio $\left(\frac{\text{Total length}}{\text{Length of tail}}\right)$ have been superimposed on Schmidt's figures (see my Figure 1) and it will be seen that they are quite a fair approximation. In other words, there is evidence for the

assumption that *during growth as a larva, the length of the tail increases uniformly by 3.3 mm. for each increase of 10 mm. in the total length.*

This being so, it can be shown by simple calculation that *the pre-anal length increases uniformly by 6.7 mm. for each increase of 10 mm. in the total length.*

These two deductions may be expressed in the form of equations, thus :—

$$Y_m = 0.33 M - 1.50$$

$$Z_m = 0.67 M + 1.50$$

where Y_m = Ano-caudal distance at a total length of M millimetres

Z_m = Pre-caudal length " " "

Calculating the value of Y_m when M is 12,

$$Y_{12} = 0.33 (12) - 1.50$$

$$= 3.96 - 1.50$$

$$= 2.46$$

The value of the ratio $\left(\frac{\text{Total Length}}{Y_{12}}\right)$ is thus $\frac{12}{2.46} = 4.88$.

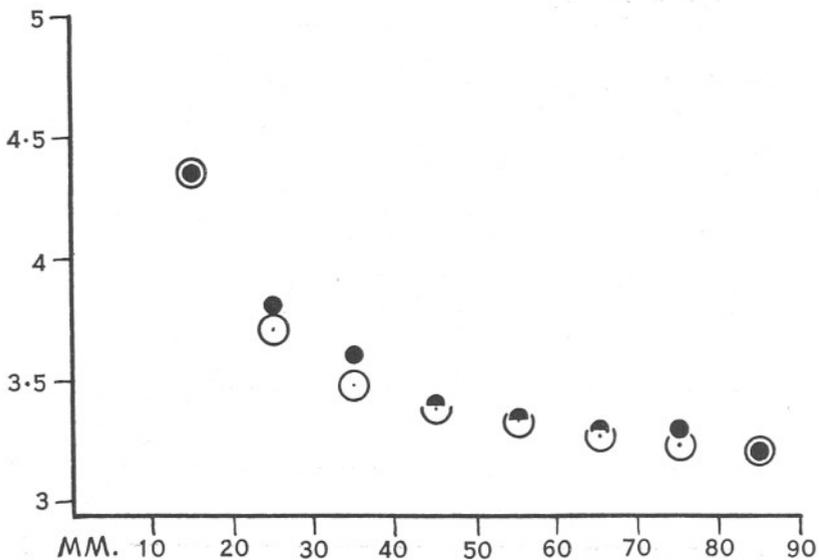


FIG. 3.—Ratio between total length and length of tail during development. Solid black dots are Schmidt's averages (see Fig. 1). Dots within circles are values calculated as explained in text in page 989.

Consulting Schmidt's graph once more (*vide* my Figure 1) it is seen that the solitary record for the ratio at a total length of 12 mm. is about 4.98, a value not greatly different from the above one of 4.88.

The increase in the proportionate length of the tail from the smallest

to the largest larva results in a relative movement of the anus along the ventral surface of the body in the direction of the head. It is important to note, however, that the anus appears not to change its position with respect to the myomere under which it lies. Writing on this point, Bertin (1, page 329) summarises the observations by Lea, Grassi and Schmidt on the position of the anus in leptocephaline stages of *Anguilla vulgaris* varying from 8.5 mm. to 83 mm. in length—observations which clearly demonstrate that the anus remains under practically the same myomere throughout. It can be stated, therefore, that growth in length along the vertebral column must agree with that along the ventral surface of the body in being relatively greater post-anally than pre-anally. Otherwise the anus would alter its position with respect to myomeres as growth proceeded. Nor is there any evidence that growth in length along the dorsal surface of the body is of a different nature, since the dorsal fin possesses its full complement of rays at an early leptocephaline stage and its anterior end appears to remain in a constant position relative to the anus throughout leptocephaline life. Thus it may be concluded that *the leptocephalus as a whole increases in length differentially, growth in length being greater post-anally than pre-anally. Neither anus nor dorsal fin alter their position relative to the myomeres.*

LENGTH-CHANGES DURING METAMORPHOSIS.

As an introduction to the study of the changes in length which occur during the transformation of the flattened leptocephalus into the rounded elver, I draw attention to a footnote to one of Schmidt's earlier papers (Schmidt, 4, page 167) on the metamorphosis:—

“It is very interesting to note the gradual change in the nerves which pass to the rays and interspinous rays in the dorsal and anal fins. Though all or at any rate the majority of the rays are present even in the 1st stage, yet both the dorsal and the anal fin are much shorter than in the following stages. In the 1st stage we see how the nerves emerge from the column *far in front of even the beginning of the fins* and are therefore *closely packed together* opposite the fins themselves. In the following stages, when the front part of the fins grows much forwards the nerves become *shortened* and more *separated*, and at the same time their direction relative to the longitudinal axis is quite changed (from being almost parallel or forming a very acute angle at the most with this they become almost perpendicular to it).”

It is a point of great significance that in the fully-grown leptocephalus the rays of the fins are innervated, *not* from the myomeres immediately above or beneath which they lie, but from myomeres some considerable distance in front. Using a binocular microscope, it is possible to trace in

a formalin-preserved leptocephalus the path of an individual nerve from its ending in the fin, forward to the myomere from which it emerges. In a leptocephalus 68 mm. long, having a total of 115 myomeres, I determined that the nerve supplying the first ray of the dorsal fin emerged from the 25th myomere (counted from the head). In contrast with this, the fin ray itself lay immediately above the 65th myomere, that is, forty myomeres farther back towards the tail. Similarly, the first anal ray, lying beneath the 71st myomere, was innervated from the 35th myomere. The observed particulars of this leptocephalus may be summarised thus:—

Length (Snout to end of body)	. . .	68 mm.
Total number of myomeres	. . .	115
Snout to 25th myomere	. . .	18 mm.
Snout to 35th myomere	. . .	25.5 mm.
Snout to 40th myomere	. . .	29 mm.
Snout to 46th myomere	. . .	33 mm.
Snout to 65th myomere	. . .	46 mm.
Snout to 71st myomere	. . .	49.5 mm.

In Figure 4A I have given a diagrammatic representation of the leptocephalus, incorporating the above data together with an indication of the paths of the nerves emerging from selected myomeres. I next draw attention to Figure 4B which lies immediately below Figure 4A. Instead of using the outline of a leptocephalus, that of an elver has been employed, the total length being the same. No change has been made in the position of the myomeres, but the nerves emerging from them have been made to pass out at right-angles to the vertebral column, instead of running far back as in Figure 4A. By so doing, however, the position of the dorsal and anal fins with respect to the myomeres, and the proportions of the several body intervals have been greatly altered. The first dorsal ray has come forward forty myomeres to lie over the 25th myomere, while the distance from the snout to the first dorsal ray has become shortened from 46 mm. to 18 mm. The distance from the first dorsal ray to the posterior end of the body, on the other hand, has increased from 22 mm. to 50 mm. Similarly, the anus has advanced thirty-six myomeres and now lies under the 35th myomere, while the distance from the snout to the anus has been reduced from 49.5 mm. to 25.5 mm. The ano-caudal distance has increased from 18.5 mm. to 42.5 mm.

Comparison with the measurements of actual specimens reveals the fact that Figure 4B is a good representation of the proportions of an elver at a length of 68 mm. The significance of this lies in the fact that a close approximation to the elver has been reached by a simple readjustment of the characters of the leptocephalus so that fins and anus are made to lie

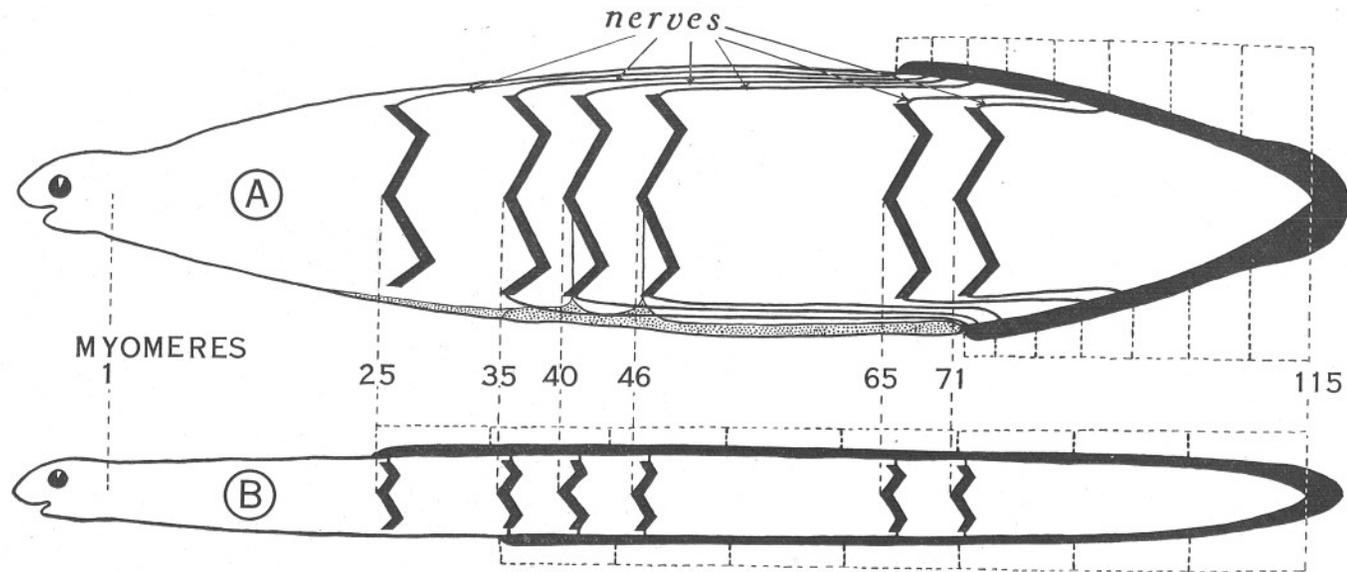


FIG. 4A.—Diagrammatic representation of leptocephalus described in text in page 992. Six myomeres and the dorsal and anal fins are shown in solid black. The nerves from the myomeres to the fins run almost parallel to the spinal column for the great part of their length.

FIG. 4B.—Hypothetical elver deduced from the leptocephalus represented in Fig. 4A. The myomeres remain in the same position as in the leptocephalus, but the nerves are now placed at right-angles to the spinal column. The new positions of the dorsal and anal fins are indicated in solid black.

immediately opposite the myomeres from which they are innervated, instead of being held remote from them.

It is at once realised that the length-changes of the intervals along the dorsal and ventral surfaces of the body during metamorphosis are very different from those which take place while the fish is growing as a leptocephalus. Before metamorphosis, every interval steadily increases in length, growth as a whole being such that the first dorsal ray and anus come gradually to occupy a position relatively nearer the head, although neither changes its orientation with respect to the myomeres. But while the fish is actually undergoing metamorphosis, some intervals increase rapidly in length at the direct expense of others, so that the resultant forward movements of the first dorsal ray and anus are not relative but real. Moreover, in the process of moving, the first dorsal ray and the anus entirely change their position with respect to the myomeres.

BIOLOGICAL SIGNIFICANCE OF RESULTS.

If Figures 4A and 4B really depict the principle underlying the transformation of the leptocephalus into the elver, save only that no account is taken of the undoubted shrinkage in total length, then there remain many interesting morphological problems to be solved. How do the nerves shorten? How does the dorsal fin grow forward at the expense of the predorsal portion of the upper surface? How does the anus come to lie so much further forward? Some further information concerning the forward movement of the fins and anus can alone be offered here. The examination of the fins of the leptocephalus shows that the fin rays are closely packed anteriorly, but become progressively wider and wider apart towards the posterior end (see Fig. 4A). It may well be, therefore, that the first ray moves forward as the result of the rapid growth of tissues between the fin-rays, causing the fin to "open out" (rather as a collapsible bellows lengthens as it is opened out), until ultimately the rays are uniformly wide apart over a longer length (as suggested in Fig. 4B). Concerning the movement of the anus, Bertin (1, page 332) speaks of the autonomous shortening of the digestive tube, and the descriptions given by Schmidt show that the rectal portion of the larval gut gradually shortens during metamorphosis.

It cannot have escaped attention that Figures 4A and 4B raise an interesting question in phylogeny. Which is the more primitive position of the anus—posterior as in the leptocephalus, or anterior as in the elver? In the leptocephalus, the anus lies a considerable distance behind the myomere from which it is apparently innervated, but moves forward to lie beneath this myomere in the elver. Thus, in effect, Figures 4A and 4B may be interpreted to imply that *the leptocephalus is a specialised form of*

larva in which the anus is temporarily held in a posterior position, moving forward to its true position during metamorphosis.

In this connection, it is instructive to refer to a Table given by Bertin (1, page 333, Table VI) in which the French investigator has summarised data concerning the number of pre-anal myomeres and total myomeres in the leptocephaline and adult stages of 15 species of eel. Bertin calculates for each species what he calls "l'amplitude des déplacements anaux," as a convenient measure of the anal displacement during metamorphosis.

This amplitude is in the form of a percentage $\left(\frac{a_2 - a_1}{t}\right) 100$, where a_1 and a_2 are the numbers of pre-anal myomeres in the leptocephaline and adult stages respectively, while t is the total number of myomeres for the species in question. It will be easily understood that if the value of this percentage-amplitude is small for a given species, the anus has migrated over a small number of myomeres, compared with the total number of myomeres in the fish. Conversely, a high value of the percentage-amplitude indicates that the anus has moved over a high proportion of the total number of myomeres. It is evident from Bertin's calculations that species differ greatly in the magnitude of the anal displacement during metamorphosis, for the values of his percentage-amplitude range from 0% to 49% in the 15 species for which data are given.

It is, however, important to observe that the value of the percentage-amplitude appears to be dependent upon the position the anus occupies in the leptocephalus. If the anus is far back towards the tail of the leptocephalus in relation to the myomeres, the percentage-amplitude is comparatively high, whereas if the anus is already well forward in the leptocephalus, the percentage-amplitude is small. It is as if in all species there were an attempt during metamorphosis to bring the anus forward to a fixed position in the adult, so that the number of pre-anal myomeres shall be about one-third of the total number. Hence, if in a leptocephalus the anus lies far back, there is a relatively large forward movement of the anus during metamorphosis; conversely, if in the leptocephalus the anus is well forward, little movement is necessary during metamorphosis to bring the anus to its adult position.

As an example, we may use the data on which Figures 4A and 4B are based. In the leptocephalus of the freshwater eel (Fig. 4A) the anus lies beneath the 71st myomere, but in the elver (Fig. 4B) it is under the 35th. The total number of myomeres is 115. Thus, in the elver the ratio $\left(\frac{\text{number of pre-anal myomeres}}{\text{total number of myomeres}}\right)$ is $\frac{35}{115}$, which is approximately $\frac{1}{3}$. During metamorphosis, the anus has moved from the 71st to the 35th myomere, so that the percentage-amplitude is $\left(\frac{71-35}{115}\right) 100$, or 31%.

Actually, the ratio $\left(\frac{\text{number of pre-anal myomeres}}{\text{total number of myomeres}}\right)$ in the adult is not invariably the same, but differs from species to species. Nevertheless, the values of this ratio tend to group themselves about an average of $\frac{1}{3}$, whereas in the leptocephalus, the corresponding values are widely separated and show no such tendency to group. That this is so is seen in the following Table which summarises Bertin's data for all the species dealt with by him, except *Sphagebranchus caecus* which he regards as a "mélange probable de deux races":—

Number of Species having the following values of ratio

	$\left(\frac{\text{Number of pre-anal myomeres}}{\text{Total number of myomeres}}\right)$:—							
	·2-·29	·3-·39	·4-·49	·5-·59	·6-·69	·7-·79	·8-·89	·9-·99
Adult	4	6	4	—	—	—	—	—
Leptocephalus	1	2	4	1	2	2	1	1

Thus, with regard to the position of the anus in relation to the myomeres, the eel species considered by Bertin agree more closely the one with the other in the adult stage than in the leptocephalus—a fact which is of some significance when considering the question of the morphology of the ancestral larva of the eel. It certainly lends support to the view that in the latter the anus lay beneath the myotome from which it was innervated, and was situated in the fore part of the body. Those present-day leptocephalid larvæ which have the anus far back beneath a posterior myotome, although the corresponding spinal nerves arise from an anterior point, must, in this event, be regarded as specialised forms. The degree of specialisation in a given leptocephalus may be estimated by calculating the value of Bertin's "percentage-amplitude" of the anal displacement during metamorphosis. If the value is large, the specialisation is great. To judge from Bertin's data, it would seem that the leptocephaline stages of the species of *Synaphobranchus*, *Congermuræna*, *Conger*, and *Anguilla* must be considered highly specialised, whereas those of *Sphagebranchus*, *Saurenhelys*, *Nettastoma*, and *Muræna* are the least so.

Now Schmidt (5, page 340) has already suggested the division of the Eel-fishes into two biological groups: (1) those which spawn far from the coasts over great depths, and (2) those which spawn in comparatively shallow water inside or near the 200 m. line. In his first group Schmidt places *Conger vulgaris*, *Conger* (= *Congermuræna*) *mystax*, and *Anguilla vulgaris*. These are species which, as indicated above, have highly specialised larvæ. To his second group Schmidt refers *Ophichthys* (= *Sphagebranchus*) *imberbis*, and *Muræna helena*—and these are species in which the leptocephalus is least specialised.

The conception of a specialised larva is thus brought into direct association with that of an adult habit. Eels which spawn far from the coast

have a specialised leptocephalus, while those which spawn in coastal waters have not. Furthermore, from our discussion of the structure of the ancestral larval eel, we see the possibility that both it and the primitive parent were inhabitants of inshore waters.

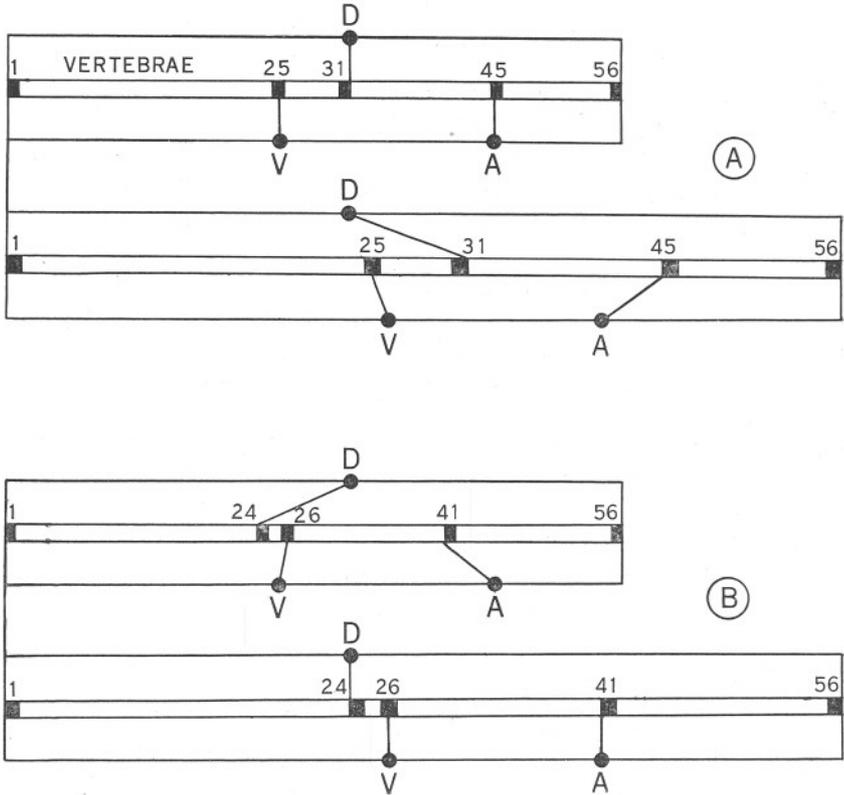
ANGUILLA AND CLUPEA.

In the growth-changes during early life, the eel, herring, sprat, and pilchard agree in some respects but differ in others. In each instance, the early larva is transparent with the anus situated beneath a posterior myomere. This larva grows and ultimately becomes transformed into an adolescent bearing the familiar characters of the adult. In doing so, the anus is brought forward in relation to the myomeres, and fins undergo a marked change in position. Furthermore, it has been shown in the preceding pages of this paper and elsewhere (Ford, 2 and 3) that such changes in length-relations can be expressed in terms of the varying rates at which the different body-intervals alter in length as development proceeds.

This generalised agreement between the eel and the clupeoids has its interest, but there are equally important differences. We have seen that the leptocephalus grows in length while still retaining its typical leptocephaline form. Although growth in length is differential, being greatest at the tail-end, the anus and fins do not alter their position relative to the myomeres during this growth as a leptocephalus. The marked readjustment of body proportions whereby the anus and fins assume their adult position takes place as a distinct process of metamorphosis from leptocephalus to elver. In the larval clupeoids, however, differential growth in length is such that the anus and fins steadily change their position relative to the myotomes as the larva increases in length. This amounts to a process of gradual transformation into an adolescent of larger size, as opposed to one in which a larva first grows as a larva, and then changes to an adolescent by a distinct act of metamorphosis. The end result may be the same in the two cases, in that the anus is brought forward to its adult position, but the "timing" of the developmental events leading to the end result is different. In the clupeoid, growth in total length and anal migration proceed simultaneously; in the eel, growth in total length takes place while the fish is yet a leptocephalus, and the anal migration is postponed until later.

We know that the larval life of the eel is very lengthy compared with that of the clupeoid, and we have discussed the probability that the leptocephalus is a specialised larval form, organised in a manner suited to the conditions imposed by the oceanic spawning of the eel. We have suggested that the position of the anus in the after part of the body of the

leptocephalus is one of the special modifications, and have referred to the manner in which the spinal nerves have become drawn-out so that they end at a point much farther back than their origin in the spinal cord. What is the situation in the young of the clupeoid? What can we learn



FIGS. 5A and 5B.—*Clupea harengus*. Possible alternatives in innervation of young stages. (See text in page 999.)

D = First ray of dorsal fin. V = Pelvic fins. A = Anus.

- 5A. Upper. Length 88 units.
Nerves assumed to leave vertebral column at right-angles.
- 5A. Lower. Length 119.5 units.
Nerves originate and end at points identical with those shown in Fig. 5A. Upper.
- 5B. Lower. Length 119.5 units.
Nerves assumed to leave vertebral column at right-angles.
- 5B. Upper. Length 88 units.
Nerves originate and end at points identical with those shown in Fig. 5B. Lower.

from a study of the nerves in successive stages of development? Unfortunately, it is not possible by simple gross examination as with the leptocephalus to trace the spinal nerves of the clupeoid larva from source to end point, nor have I, as yet, found opportunity to conduct the necessary

micro-examination which would provide an answer to this question. But there are two alternatives which are well worth considering here. The spinal nerves of the clupeoid larva either pass out at right angles to the spinal cord so that they innervate parts of the body immediately opposite to their origin, or, failing this, they run out obliquely to innervate parts of the body which are not immediately above or below their origin.

Consider these alternatives as applied to the herring. Given the following data concerning a post-larva and an adolescent (from Ford, 2) :—

BODY INTERVAL.	POST- LARVA.	ADOLESCENT.
	(Units of Length.)	
Body Length	88.0	119.5
Head to 1st ray of Dorsal Fin	49.0	49.0
Head to Pelvics	39.0	54.9
Pelvics to Anus	30.5	30.5

In Figure 5A, upper, constructed in accordance with the above data for the post-larva, the nerves supplying certain points have been represented by lines drawn at right angles from the vertebræ. Figure 5A, lower, is constructed on the data for the adolescent, and lines have been drawn linking the same origin and end-point of nerves shown in Figure 5A, upper. It is seen that in the adolescent the path of each nerve is now oblique to the vertebral column, whereas in the post-larva it was at right-angles to it. In this case the adolescent is, so to speak, a distortion of the post-larva.

The other alternative is illustrated in Figures 5B, upper, and 5B, lower. It is here simpler first to construct a representation of the adolescent, as in Figure 5B, lower, inserting nerves at right-angles to the vertebral column. The figure for the post-larva (Fig. 5B, upper) is next drawn with the nerve origins and endings as in Figure 5B, lower. It is seen that it is now the post-larva and not the adolescent in which the nerves take an oblique course. In other words, the post-larva is now a distortion of the adolescent.

Which of these two is to be regarded as approaching the true state of affairs is a matter which can be settled by dissection, and is worth investigation, since it is of direct interest in the study of the evolutionary history of the fishes concerned. It is hoped that further investigation on this question will be made in the near future.

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