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ADVERTISEMENT.

THE Committee appointed by the *Royal Society* to direct the publication of the *Philosophical Transactions* take this opportunity to acquaint the public that it fully appears, as well from the Council-books and Journals of the Society as from repeated declarations which have been made in several former *Transactions*, that the printing of them was always, from time to time, the single act of the respective Secretaries till the Forty-seventh Volume; the Society, as a Body, never interesting themselves any further in their publication than by occasionally recommending the revival of them to some of their Secretaries, when, from the particular circumstances of their affairs, the *Transactions* had happened for any length of time to be intermitted. And this seems principally to have been done with a view to satisfy the public that their usual meetings were then continued, for the improvement of knowledge and benefit of mankind: the great ends of their first institution by the Royal Charters, and which they have ever since steadily pursued.

But the Society being of late years greatly enlarged, and their communications more numerous, it was thought advisable that a Committee of their members should be appointed to reconsider the papers read before them, and select out of them such as they should judge most proper for publication in the future *Transactions*; which was accordingly done upon the 26th of March, 1752. And the grounds of their choice are, and will continue to be, the importance and singularity of the subjects, or the advantageous manner of treating them: without pretending to answer for the certainty of the facts, or propriety of the reasonings contained in the several papers so published, which must still rest on the credit or judgment of their respective authors.

It is likewise necessary on this occasion to remark, that it is an established rule of the Society, to which they will always adhere, never to give their opinion, as a Body,

upon any subject, either of Nature or Art, that comes before them. And therefore the thanks, which are frequently proposed from the Chair, to be given to the authors of such papers as are read at their accustomed meetings, or to the persons through whose hands they received them, are to be considered in no other light than as a matter of civility, in return for the respect shown to the Society by those communications. The like also is to be said with regard to the several projects, inventions, and curiosities of various kinds, which are often exhibited to the Society; the authors whereof, or those who exhibit them, frequently take the liberty to report, and even to certify in the public newspapers, that they have met with the highest applause and approbation. And therefore it is hoped that no regard will hereafter be paid to such reports and public notices; which in some instances have been too lightly credited, to the dishonour of the Society.

IV.—*The Breeding Places of the Eel.*

By JOHS. SCHMIDT, *D.Sc.*, *Copenhagen.*

Communicated by C. T. REGAN, F.R.S.

(Received July 8, 1921—Read February 2, 1922.)

[PLATES 17 AND 18.]

The problem of the propagation and breeding places of the Common or Fresh-water Eel is one of great antiquity; from the days of Aristotle naturalists have occupied themselves therewith, and in certain regions of Europe it has exercised popular imagination to a remarkable degree. It is only during the last three decades, however, that any real results have been attained.

It has long been known that the full-grown eels move down in the autumn from their rivers and lakes to the sea; the most important eel fisheries, indeed, are based upon this seaward migration. The eels do not return again from the sea, but in early spring there appear on the coasts myriads of small young eels, eagerly seeking their way up to fresh-water. These eel fry are known in most countries of Europe, and occur in some parts in such quantities as to form the object of a particular industry; for instance, in the River Severn in England, where they are known as “elvers.” Until 1896, the elver stage was the earliest stage of development in which the eel was known on the shores of Europe, and it was generally supposed that the elvers arriving in the spring were the offspring of the eels which had migrated during the previous autumn. They are not, however, altogether minute, like the newly-hatched larva of a cod or herring; on the contrary, they are no less than 6–7 cm. in length.

We know, then, that the old eels vanish from our ken into the sea, and that the sea sends us in return innumerable hosts of elvers. But whither have they wandered, these old eels, and whence have the elvers come? And what are the still younger stages like, which precede the “elver” stage in the development of the eel? It is such problems as these that constitute the “Eel Question.”

The earliest possibility of attacking this ancient problem scientifically was afforded by the Italians GRASSI and CALANDRUCCIO, of whom the former published in 1896, in the ‘Proceedings of the Royal Society of London,’ a report of their investigations at Messina, entitled: “The Reproduction and Metamorphosis of the Common Eel (*Anguilla vulgaris*).”

GRASSI and CALANDRUCCIO found that the elver stage is preceded by a larval stage, inasmuch as they were able to show that the little fish from the Straits of

Messina, described by KAUP in 1856 as *Leptocephalus brevirostris*, is not an independent species, but the larva of the eel. The larva is leaf-shaped, transparent as glass, and about $7\frac{1}{2}$ cm. in length. By a process of metamorphosis it is transformed into the eel-shaped elver, a reduction in both height and length taking place.

This Italian discovery was of great importance; we had now learned to know a stage still younger than the elver, and it did not seem difficult from this to infer the remainder of the life-history of the eel. GRASSI was therefore justified in assuming that he had been able "to dispel, in the most important points, the great mystery which has hitherto surrounded the reproduction and the development of the Common Eel (*Anguilla vulgaris*)" (*loc. cit.*, p. 261). Even after the discovery of the larva, however, certain points still seemed vague; one might yet ask, for instance: (1) why were not the larvæ, like the elvers, found promiscuously about the shores of Europe, but only in the waters of Southern Italy, especially the Straits of Messina; and (2) why should we find in that water, not minute, newly-hatched larvæ, but only specimens already fully grown, or nearly so, of about 7 cm. in length?

Briefly, GRASSI conceived the circumstances to be as follows:—The breeding grounds of the eel lie in the great depths of the sea—in the abyssal region—which in the Mediterranean is not far from the shores. In these depths the ova, suspended in the water, are developed, and here the larvæ live, normally without rising to the upper water layers. The Straits of Messina, however, form an exception. There are some peculiar currents here, that "tear up the deep-sea bottom, which everywhere else is inaccessible"; hence, it is just in the Straits of Messina that these larvæ are brought to the surface and come under observation.

This, roughly speaking, was the state of the eel question at the commencement of the present century. In the year 1904 I was led by chance to touch upon it myself. My very first investigations confirmed in every respect the Italian discovery of the eel larva and its transformation into the elver. I have not been able, however, to confirm GRASSI's theory as to the origin, manner of life, and age, of the larvæ. Still, as I have said before, that theory might well appear justified from the state of things at the time it was first advanced.

The Danish eel investigations were commenced, as mentioned, in 1904. I was then on board the research steamer "Thor," engaged on fishery investigations in the Iceland and Faroe waters, according to the programme of the International Council for the Study of the Sea. In May, 1904, after towing a Petersen's young-fish trawl near the surface of the water, west of the Faroes, it was found, on examining the contents of the net, that in addition to various other forms of pelagic life, we had also captured a specimen of *Leptocephalus brevirostris*, $7\frac{1}{2}$ cm. long.

Thus the larva of the eel was for the first time found outside the Mediterranean. And the find, which was followed in the same year by another, made by Mr. FARRAN from the S.S. "Helga," off the West Coast of Ireland, afforded a starting point for future investigations. Owing to various circumstances it came about that Denmark,

a country where eel fishing is a specially important industry, was accorded the task of prosecuting the investigations farther, and it fell to my lot to take charge of the work.

I had little idea, at the time, of the extraordinary difficulties which the task was to present, both in regard to procuring the most necessary observations and in respect of their interpretation. Our work on these eel investigations has now extended some 16 or 17 years, with a lengthy interruption occasioned by the recent War. The task was found to grow in extent, year by year, to a degree we had never dreamed of; in fact, we have been obliged, in order to procure the necessary survey material, to make cruises of investigation ranging from America to Egypt, from Iceland to the Canary Islands. And this work has been handicapped throughout by lack of suitable vessels and equipment, and by shortage of funds; indeed, had it not been for the private support afforded from numerous different sources, we should have had to relinquish the task long since.

I propose now to give a brief survey of the results attained. They are based on dry figures, representing measurements and other observations; yet taken in conjunction, they give us at least the outline of a life-history which in point of interest is, I think, hardly surpassed by that of any other species in the Animal Kingdom.

In 1905, then, systematic investigations into the life-history of the eel were included in the Danish programme. The researches we have carried out since that date fall into two groups: (1) investigations at sea; and (2) investigations in the laboratory.

The aim of the former was to obtain a survey of the breeding grounds of the eel, similar to that I had made of the breeding places of the Gadoids in the Atlantic from Iceland to Spain,* and the starting point in this case was the find already mentioned, of a full-grown eel larva west of the Faroes in 1904. We hoped, by tracking down the larvæ in ever younger stages, to be able to chart the area or areas where the eel first enters on its existence, and, at the same time, to determine the rate of growth of the larvæ and thereby the age of the elvers which appear on the shores of Europe in the spring.

The second group of investigations was, in contrast to the first, carried out on land, in the laboratory. It consisted of a statistical examination of samples of eels from the greater part of the Atlantic area, where fresh-water eels occur. The samples contained as a rule some 200 specimens, and the number of various organs, such as vertebræ and fin-rays, was determined in all individuals. I have published detailed reports of the results of this statistical investigation, and to these I must

* "The Distribution of the Pelagic Fry and the Spawning Regions of the Gadoids in the North Atlantic from Iceland to Spain" ('Rapports et Procès-Verbaux du Conseil International pour l'Exploration de la Mer,' vol. 10, Copenhagen, 1909).

refer.* It must here suffice to lay down the fact that only two species of fresh-water eels could be shown to exist in the Atlantic area: a western, *Anguilla rostrata*, which is met with in the West Indies and northward of there in America, and an eastern, *Anguilla vulgaris*, which is distributed throughout Western Europe, the Mediterranean countries, and the islands of the Atlantic from Iceland to the Canaries. The eels found in the Azores are also *Anguilla vulgaris*, whereas the eels of Bermuda belong to *Anguilla rostrata*. In externals, the two species are hardly distinguishable one from another, but certain numerical characters afford a means. The number of vertebræ in particular is a valuable character, *Anguilla vulgaris* having on an average about seven and a half more vertebræ than the American eel (*ca.* 114·7 against *ca.* 107·2—*cf.* fig. 1). If we take the trouble of counting the vertebræ, it will be only a very few specimens per thousand which cannot be referred with certainty to the one or the other of the two species. This fact has proved of great importance in the investigations at sea, since it was found that the larvæ of the European and of the American eel are mingled together in certain areas of the ocean.

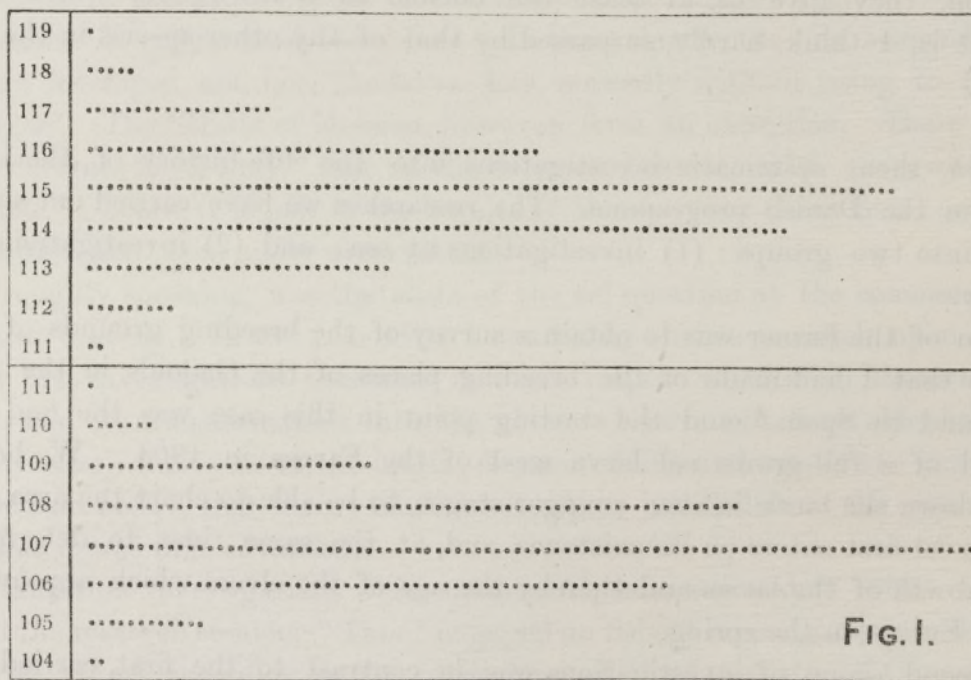


FIG. 1.—Number of Vertebræ in 266 eels from Denmark (*Anguilla vulgaris*, top graph), and in 266 eels from Mass., U.S.A. (*Anguilla rostrata*, lower graph).

In spite of the enormous area of the European eel, statistical investigations failed to demonstrate the existence of local races, as has been done with so many

* "First Report on Eel Investigations" and "Second Report on Eel Investigations" ('Rapports et Procès-Verbaux du Conseil International pour l'Exploration de la Mer,' vol. 18, 1913, and vol. 23, 1915); further, "On the Classification of the Fresh-Water Eels (*Anguilla*)," ('Meddelelser fra Kommissionen for Havundersøgelser, Serie Fiskeri,' vol. 4, No. 7, Copenhagen, 1914).

other species of fishes. All the samples, from Iceland to Madeira and from Cyprus to the Azores, yielded the same average values for the characters under consideration.

As will be seen from the following, this is entirely in agreement with the result of our work at sea.

The investigations made at sea fall naturally into two groups: (1) those carried out from the State-owned S.S. "Thor," which is equipped for marine research, during the years 1903–1910. These investigations, the general purpose of which was to study the reproduction and breeding-grounds of the principal food-fishes, were made in Danish waters, in the North Sea, and in the Norwegian Sea, in the Atlantic off the West Coast of Europe from Iceland to Morocco, and in the Mediterranean. (2) Investigations in the open Atlantic, carried out in 1911–1921, but with a lengthy interruption occasioned by the War. For these, we were unable to use the "Thor," her radius of action being too small. They were made from numerous Danish vessels on Transatlantic routes, with no equipment for marine research, and no experts to assist with the work, but furnished only with a net, and with instructions drawn up by myself. Though naturally of a very casual nature, restricted as they were to the course of the vessel in each particular case, these investigations have nevertheless yielded important results, and hearty thanks are due to the Danish seamen who contributed thereto. On some few occasions we were able to work more systematically and with the assistance of our own staff, as for instance in 1913, with the schooner "Margrethe" belonging to the Vendsyssel Packing Co., and in 1920 and 1921, with the schooner "Dana," owned by the East Asiatic Company. In both these cases, despite the fact that the vessels had not the special equipment of the "Thor," important results were obtained, and the owners, who generously placed them at our disposal for the work, have highly deserved the thanks of science.

I will now give an account of our investigations at sea, touching very lightly upon the earlier ones, which are dealt with in detail in the reports already published.

Following on cruises made in 1903–05 with the "Thor," I was able to show (1906)* that full-grown eel larvæ were found in quantities in the Atlantic west of Europe throughout the entire range from the Faroes to Brittany, west of the 1000 metre line. They were, however, not found east of this line; *i.e.*, not over the coastal banks, nor in the North Sea, the English Channel, the Baltic, etc. In June, 1905, the larvæ were full-grown, averaging 75 mm. in length (*cf.* fig. 2). They occurred pelagically in the upper water-layers, and were all unmetamorphosed. From these investigations I was able to conclude that *all the eels of Western Europe come from the Atlantic*, and that they come from the sea beyond the coastal banks. It was thus evident that the eel—as also, by way, the conger—occupies

* "Contributions to the Life-History of the Eel (*Anguilla vulgaris*)," ('Rapports et Procès-Verbaux du Conseil International pour l'Exploration de la Mer,' vol. 5, Copenhagen, 1906).

an exceptional position among food-fishes, inasmuch as I had been able to show that the minute larvæ of most of these species belonged to the coastal banks west of the shores of Europe, and were not met with farther out. Closer study of the great elver fisheries of Western Europe (Bristol Channel, west of France and north of Spain) supported to a high degree the conclusions I have formed as to the Atlantic origin of the eel, and I was able to point out that both the Bristol Channel and the Bay of Biscay served, practically speaking, as two enormous wing-nets or funnels, which, facing west, would be specially calculated to pick up the eel fry coming from the Atlantic.

In 1906, we made two cruises with the "Thor" in the Atlantic, one in the spring and another in the autumn. On both these cruises

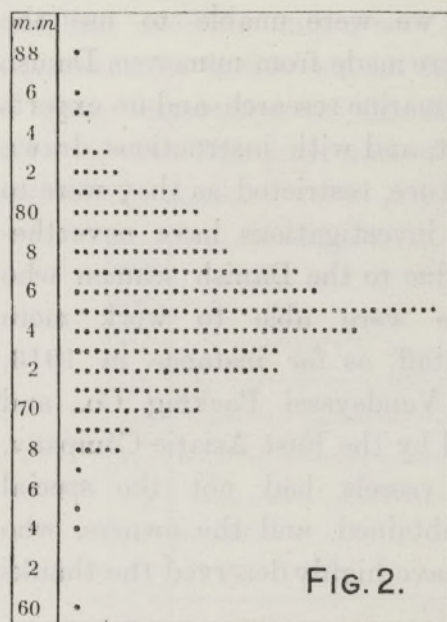


FIG. 2.

FIG. 2.—Sizes of Eel Larvæ (*Anguilla vulgaris*), II-group, at Stations S.W. of Ireland; "Thor," June, 1905. Lengths in millimetres.

full-grown larvæ were found in great numbers west of Europe, but in spring and early summer none of them had entered upon metamorphosis, whereas in August and September the majority were undergoing the process. It appears, then, that there is a certain periodicity in the occurrence of the larvæ; the full-grown larval stages are met with in spring and early summer, metamorphosis takes place in the autumn, and the elvers appear in winter and spring. With the abundance of material at my disposal, I found occasion to make a closer study of the metamorphosis, and was able, by means of numerous measurements, to ascertain that the larvæ, during the process of metamorphosis, are reduced in length about 1 cm., from about 75 mm. in June, 1905, to about 66 mm. in May, 1906) and in weight to less than a quarter of that before metamorphosis (fig. 10). The fully metamorphosed small eels, averaging about 6½ cm.

in length, which occur in Europe in early summer, must, therefore, be presumed to be about a year older than the larvæ found at the same time in the Atlantic west of Europe, which are on an average about 7½ cm. long.

Our investigations in 1906 to the west of France showed that the larvæ occurred even over the greatest depths, over 5000 metres; we found, moreover, that they were always distributed in a particular manner, the specimens which had not yet commenced metamorphosis being taken farther from the coastal banks than the older ones, which were undergoing the process. This led me to point out the probability that the breeding grounds of the eel were situated out in the ocean far from the coasts (1909),*

* "Remarks on the Metamorphosis and Distribution of the Larvæ of the Eel (*Anguilla vulgaris*)" ('Meddelelser fra Kommissionen for Havundersøgelser, Serie Fiskeri,' vol. III, No. 3, Copenhagen, 1909).

a supposition which was to be further supported, in the very next year after it had been advanced, by the appearance of new material of eel larvæ from the open Atlantic.

In a study published almost at the same time (1909)* on the 'Distribution of the Fresh-water Eels throughout the World,' I drew attention to the fact that the distribution of the eels in the Atlantic area distinctly coincides with the periphery of the great anti-cyclonic circulation of the water-masses in the North Atlantic.

The new material referred to—eel larvæ from the open Atlantic Ocean—was derived, partly from the cruise of the Norwegian S.S. "M. Sars" in the Atlantic, June–July, 1910, partly from some old collections of Leptocephali which had lain for many years unexamined at the Zoological Museum in Copenhagen. Before proceeding to this new material, I would call to mind that the eel larvæ—nearly 800 in all—which I had taken on board the "Thor" in 1905 and 1906 from the waters west of Europe, averaged about $7\frac{1}{2}$ cm. in length. The largest measured 88 mm. and the smallest 60 mm. (see graph, fig. 2, p. 184). As to determining the age of these larvæ there was nothing of any certainty to go upon.

A highly interesting and suggestive article on the eel larvæ from the cruise of the "M. Sars," by J. HJORT, appeared in "Nature," 1910 ("Eel Larvæ from the Central Atlantic").† From this it appeared that forty-four eel larvæ were taken during the cruise, twenty-three to the west of Europe (north of 40° N., east of 30° W.), and twenty-one south and west of the Azores. The former ranged from $6\frac{1}{2}$ to 8 cm. in length, and were thus of the same size as those I had taken on board the "Thor." The rest, however, were considerably smaller, viz., 4–6 cm. long (one was 41 mm., three were close on 5 cm., and the remainder between 5 and 6 cm.). The smaller larvæ were taken at five stations situated between lat. 31° and 40° N. and between long. 30° and 48° W. According to HJORT's interpretation, the twenty-one smaller larvæ represent the young of that year (the O-group), the larger ones those of the previous year (the I-group). This being so, the first-year larvæ should by June be $5-5\frac{1}{2}$ cm. long, and the full-grown larvæ of about $7\frac{1}{2}$ cm. length should be a year older. Without venturing to assert anything definite on the basis of so small a material, HJORT surmised that the breeding grounds of the eel might be in the Central Atlantic, between the Azores and Bermuda.

The eel larvæ which, as mentioned above, I found among some old collections of Leptocephali in the Zoological Museum, Copenhagen, had been procured by the Danish Captain A. ANDREA, a zealous collector of pelagic fauna, somewhere about 1865. There were only three specimens, of which one, taken near Florida Strait, proved to belong to the American species, the two others being larvæ of *Anguilla vulgaris*.

* 'On the Distribution of the Fresh-Water Eels (*Anguilla*) throughout the World' (*ibid.*, No. 7, 1909).

† The same material was later dealt with by E. LEA, in 'Murænoid Larvæ from the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910' (Bergen, 1913).

The smaller of these measured 41 mm. and was taken in the vicinity of Madeira (lat. $34^{\circ} 20' N.$, long. $18^{\circ} 30' W.$); the larger, 53 mm. in length, was found considerably farther west, lat. about $30^{\circ} N.$, long. about $32^{\circ} W.$

A comparison of these two stations with the five from the "M. Sars," did not make it easier to determine the origin of the larvæ; rather, indeed, the reverse. The two smallest extant specimens, both 41 mm. in length, were taken at long. $48^{\circ} W.$ (HJORT) and long. $18^{\circ} 30' W.$ (ANDREA) respectively; that is to say, at a distance of about 1500 miles one from another. If these two larvæ were in their first year, and had not moved any great distance from the spot where they came into the world, this would mean that the breeding-grounds of the eel embraced the entire eastern half of the Atlantic south of the Azores. Or did they, on the other hand, indicate that there were several distinct breeding-grounds, so that for instance the eels of the Azores had theirs in one place, and those of Madeira in another? If this were so, then where were the first-year larvæ of the enormous hosts of eels from the Continent of Europe? For it must be remembered that the Norwegian Expedition with its effective fishing apparatus had taken comparatively very few larvæ of the smaller group, while Captain ANDREA's large collection of Leptocephali contained but two specimens of the European eel. And finally, there was the natural question: how old were the smallest extant larvæ, with their length of just over 4 cm.? This question was obviously of great importance, since if the larvæ were some few months old, they might have been carried great distances during that time by the ocean currents, and in such case, it would be impossible to determine, for instance, whether the larvæ found south of the Azores had originally come from somewhere farther to the east or somewhere farther west.

Considering these points, I perceived that if the problem were to be solved in anything like a satisfactory manner it would be necessary to ascertain, not only where the youngest larvæ were to be found, but also where they were not. Until a comprehensive survey had been obtained as to the distribution and respective density of the various sizes of larvæ in all parts of the sea, it would hardly be possible to form definite conclusions as to the origin of the eels of our European continent. The task was thus one of enormous dimensions, albeit with the consolation that the South Atlantic might be disregarded as being devoid of any representative of the genus *Anguilla*, a fact which I had been able to prove in my previously mentioned work on the distribution of this genus throughout the world (1909, *loc. cit.*).

In order to proceed further, then, it was evidently necessary to procure observations from the greatest possible area of the North Atlantic. As I have already stated, the "Thor" was useless for such work as this; I had, therefore, to endeavour to procure the requisite material by other means. In pursuance of the project, application was made from time to time to one and another of the Danish shipowning companies with vessels sailing regularly on Transatlantic routes, requesting that the ships might

occasionally be allowed to draw a pelagic net for half an hour, and send in the resulting captures for investigation. Our request was on the whole very courteously complied with, and during the years 1911–1915 hauls were made at about 550 “Stations” by twenty-three different vessels, steamers and sailing ships, of Danish nationality, one of them belonging to the Danish Royal Navy. A chart of the stations* shows that they are well distributed throughout the North Atlantic area. I may state at once, that the yield of larvæ of the European eel amounted in all to 120. This represents about one larva for every fourth or fifth station, a result which must be considered satisfactory in view of the highly primitive equipment, the short hauls, and the fact that a great number of the stations were in areas where eel larvæ do not occur.

During the first two years (1911–12) the collections of material made were chiefly from vessels sailing between the English Channel and the West Indies, but the yield was generally poor, three larvæ from one station being the highest. An encouraging feature, however, was the finding of a larva only 34 mm. in length at 25° N., 51° W., both from the fact that the previous minimum record (41 mm.) was thereby beaten, and also because the locality of the find suggested a place of origin even more to the south and west than we had hitherto been warranted in imagining. The material, however, was still too small and too sparsely distributed to give us the distinct indication we desired; indeed it is hardly too much to say that with each new observation a new problem arose, demanding a solution of itself, without otherwise contributing to the elucidation of the matter as a whole. Consequently, when, in 1912, I published my last report of the investigations at sea,† I was obliged to express myself with the greatest reserve on the question of the breeding grounds of the eel, despite the fact that the finds of larvæ in the open Atlantic Ocean had considerably increased in number as shown in the chart, Plate VI, *loc. cit.*, 1912. In a summary which appeared in ‘Nature’ for August 22, 1912, I summed up the position as follows:—“We cannot say as yet where exactly the spawning takes place, and but little more than that the spawning places must lie in the Atlantic beyond the Continental slope, and that they must lie in the northern Atlantic.” There was one point in particular which made the matter difficult. As already mentioned the “M. Sars” had in the month of June found a score of larvæ, 4 to 6 cm. in length, which were classed by HJORT as belonging to that year (the O-Group), his view being that they had come into the world the previous winter and spring. Our investigations, however, repeatedly gave us larvæ of the same size, but taken in winter and spring. Thus, for instance, we had three specimens taken early in December not far from the Azores (Station 397), measuring 43, 48,

* “Stations in the Atlantic, etc.,” with Two Charts and Introductory Remarks (‘Meddelelser fra Kommissionen for Havundersøgelser, Serie Fiskeri,’ vol. 5, No. 7, Copenhagen, 1919).

† “Danish Researches in the Atlantic and Mediterranean on the Life-History of the Fresh-water Eel (*Anguilla vulgaris*),” (‘Internat. Revue der gesamten Hydrobiologie und Hydrographie,’ Leipzig, 1912).

and 56 mm.; other samples taken in March and April contained specimens measuring 47, 49, 50, 57 and 59 mm. in length. It therefore seemed doubtful whether HJORT's interpretation of his specimens taken in summer as being first year larvæ could be correct, since if this were the case one would have expected to find much smaller specimens in winter. There was, however, the possibility that both HJORT's summer specimens and our winter specimens were in their first year, but if so, it had to be presumed that a regular production of ova and larvæ took place all the year round, so that not the season, but the locality, *i.e.*, the distance from the site of production, would be responsible for the size of the larvæ. There were, however, several facts which spoke against the theory of such uninterrupted production, as, for instance, the periodicity in the occurrence and metamorphosis of the larvæ which I had discovered on board the "Thor" in 1905-06.

The net result, then, of our investigations by the close of 1912 was that a great deal more research work would be needed, since the new data obtained had practically raised new difficulties in the way of an interpretation—as, indeed, often happens when an investigation has passed beyond the earliest stages, when the paucity of facts gives freer play to the imagination.

The year 1913 was marked by important progress. Not only did our fishing cargo vessels send us in richer material, but we succeeded in getting the little schooner "Margrethe," belonging to the Vendsyssel Packing Co., of Copenhagen, equipped and sent out on a cruising expedition over the Atlantic, with a supply of nets, etc., for pelagic work. The investigations were carried out during the months of August-December along the following three lines: (1) from the Faroes to south-west of the Azores (about 28° N., 40° W.); (2) thence to the Newfoundland Banks; and (3) from there to the West Indies. The yield was 714 larvæ of the European eel, besides a small number (24) of the American. We had now at last obtained a large amount of material from the open Atlantic Ocean, and the study of this yielded important results. It was very significant, in the first place, that the larvæ increased in numbers from east to west, the greatest quantities being taken west of long. 50° W. In this area the "Margrethe" succeeded in taking no less than 154 specimens at one station (Station 1040) with a net 2 m. in diameter at opening, and one of the sailing vessels fishing for us, the schooner "Agent Petersen," took 24 specimens in one haul with a small net only 1 m. in diameter (Station 765). By way of comparison, it may be mentioned that our greatest number of larvæ per haul in the eastern Atlantic, with the far more intensively working "Thor," was 70.

No less interesting was the size of the larvæ at the different stations. The following representative stations will serve to illustrate this:—

Sizes of Eel Larvæ (*Anguilla vulgaris*) at Stations from East to West, lat. 35° N.;
“Margrethe,” September, 1913.

Longitude.	29° W.	45° W.	56° W.
Station No. and date . .	1013, 24/8	1020, 11/9	1030, 1/10.
Length in mm.	65, 63, 59	55, 53, 50	40, 36, 35.

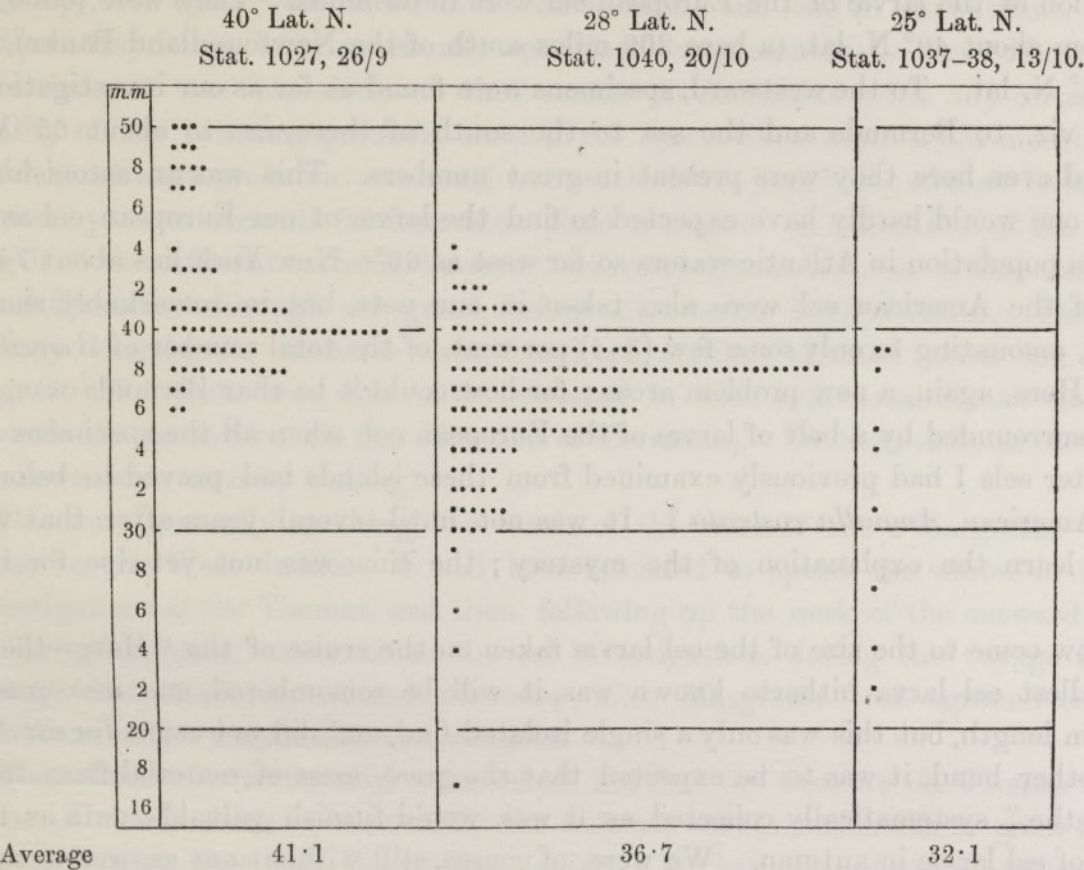


FIG. 3.—Sizes of Eel Larvæ (*Anguilla vulgaris*) at Stations from North to South, Western Atlantic between 50° and 60° long. W.; “Margrethe,” October, 1913.

It will be seen from the above measurements that the sizes of the larvæ decrease from east to west and from north to south. A good general idea may also be gained by marking off the “Margrethe’s” hauls on a chart of the North Atlantic, and drawing a line from Newfoundland in a south-easterly direction, towards Cape Verde. It will then be seen that, west of this line, no larvæ over 5 cm. in length were taken, whereas most of those taken east of this line were 5 cm. or more, and none less than 4 cm.

It had now been shown, by systematic investigation across the Atlantic Ocean, that the larvæ of the European eel increase in number, but decrease in size from east to west. This placed it beyond doubt that the stock of eels in Europe must have its origin in an area situated far to the west in the Atlantic Ocean.

The question now was, what further conclusions could be drawn from the wealth of material obtained from the "Margrethe's" seventy-three stations, comprising, as it did, apart from larvæ of the fresh-water eel, close on 10,000 larvæ of other eel-fishes.

In October and November, and the early part of December, 1913, the "Margrethe" was working in the western part of the Atlantic, between Newfoundland and the West Indies, in the course of which cruise the northern and southern limits of distribution of the larvæ of the European eel were determined. They were found to occur from about 40° N. lat. (a bare 200 miles south of the Newfoundland Banks), to about 24° N. lat. To the westward, specimens were found as far as our investigations reached, viz., to Bermuda and the sea to the south of there, i.e., to about 65° W. long., and even here they were present in great numbers. This was an astonishing fact, for one would hardly have expected to find the larvæ of our European eel as a numerous population in Atlantic waters so far west as 65°—New York lies about 74°! Larvæ of the American eel were also taken in our nets, but in remarkably small numbers, amounting to only some few (3-4) per cent. of the total number of *Anguilla* larvæ. Here, again, a new problem arose; for how could it be that Bermuda was, as it were, surrounded by a belt of larvæ of the European eel, when all the specimens of fresh-water eels I had previously examined from these islands had proved to belong to the American *Anguilla rostrata*? It was not until several years after that we were to learn the explanation of the mystery; the time was not yet ripe for its solution.

We now come to the size of the eel larvæ taken on the cruise of the "Margrethe." The smallest eel larva hitherto known was, it will be remembered, one measuring 34 mm. in length, but this was only a single isolated find, and did not count for much. On the other hand, it was to be expected that the great mass of material from the "Margrethe," systematically collected as it was, would furnish valuable data as to the size of eel larvæ in autumn. We were, of course, still without any answer to the important question as to whether larvæ were produced uninterruptedly throughout the year, or if a particular season of the year could be defined as the breeding-season of the eel. Not until these points were settled should we have anything to go upon in judging the age of the older larvæ from the central and eastern Atlantic.

The graph, Stat. 1040, fig. 3 on p. 189, gives a good idea of the size of the larvæ in autumn in the western Atlantic. In the first place, it will be seen that the smallest specimen was 17 mm. long only—a marked lowering of the previous minimum record of 34 mm.—but, despite the intensive fishery, only a single specimen of this small size was taken throughout the whole cruise, and only a very few slightly larger, 2-3 cm., amounting to 1-2 per cent. of the total number. Furthermore, the graph shows that an overwhelming majority of the larvæ were of sizes varying between 3½ and 4½ cm. in length. (As mentioned above, no specimen over 5 cm. was taken by the "Margrethe" in the western area, west of the line referred to on p. 189.)

These facts, in my opinion, warranted the following conclusions:—The spawning of

of the eel cannot go on regularly throughout the whole year; there must, in autumn at any rate, be a cessation or decrease in the production, otherwise we must have found tiny larvæ in greater numbers at this season. Even though the time when the eels did spawn could not be determined with certainty, the size of the larvæ nevertheless rendered it likely that they had come into the world during the first half of the year 1913. We were dealing, that is to say, with larvæ in their first year (the O-group), and these were as we have seen about $3\frac{1}{2}$ cm. long in the autumn.

Since tiny larvæ were practically speaking unrepresented in the "Margrethe's" collections, it was impossible at that season to determine with any certainty the locality of the breeding-grounds, since if the larvæ were even a few months old—which must seem probable—we could not overlook the possibility of their having been carried by ocean currents far from their place of origin. A calculation of the average length at the different stations, however, was not without interest in this connection, the differences, although not great, being nevertheless beyond doubt. The lowest average lengths for instance were found at stations situated about lat. 26° N., long. 55° W.; from here, the larvæ increased in size both towards the north and towards the north-west (in the direction of Bermuda). To the south, as mentioned, the larvæ were entirely lacking.

This was, generally speaking, the result of the work of the "Margrethe" on her cruise to the West Indies. It had been intended to spend the winter in fisheries investigations at St. Thomas, and then, following up the work of the outward voyage of the "Margrethe," to continue the eel investigations during the voyage home in spring. Fate, however, ordered otherwise; the "Margrethe" ran aground on one of the West Indian islands and was wrecked.

The collections, fortunately, were saved, but here we were at St. Thomas with no ship. The only thing to be done for the moment was to endeavour to press forward the work being done from the trading vessels. We had now, of course, some definite facts to go upon. We knew that the tiny larvæ were to be sought during the first half of the year, and the record specimen of only 17 mm. length, already frequently referred to, would also be a good guide. I was now able to issue instructions far more precise in character than hitherto, both as regards time and place, and also the depth, to be chosen for fishing. Through the very generous co-operation of the East Asiatic Company of Copenhagen, a considerable number of hauls were taken in the spring and summer of 1914 by steamers of this line on the West Indies route, and these did not fail to produce their result. As early as June, the S.S. "Bintang" and S.S. "Samui" brought us plankton samples, taken in May and June about lat. 20° N., long. 55° W., all of which were found to contain larvæ of the European eel, for the most part tiny stages. At one of the stations for instance (Station 789, 8/5, 1914) seven specimens of the following lengths were taken: 9, 9, 11, 16, 16, 16, 21 mm., i.e., an average of 14 mm., and another (Station 793, 11/6, 1914) yielded eleven specimens averaging 18.1 mm. in length.

On returning from the West Indies we set about endeavouring to get another schooner to work in place of the "Margrethe," but then came the Great War, and all plans for further researches at sea had to be laid aside. The work of the trading vessels, however, was maintained during the first years of the War, and continued to yield valuable information. In 1915, for instance, we obtained confirmation of the fact that tiny larvæ occur in summer, and a sample taken at the end of September, 1915, contained eight specimens of about $3\frac{1}{2}$ cm. long, *i.e.*, of the same size as those taken by the "Margrethe" in the autumn of 1913. As the War increased in extent, however, our collecting work died out, and several of the vessels which had been assisting us were sunk by submarines. During the next five years, therefore, from 1915 to 1920, the investigations at sea were altogether at a standstill; I was able, however, on the basis of material from the western Atlantic, to work out a description of the development of the larvæ of the two *Anguilla* species and a series of other Atlantic murænoids (1916).^{*} The larvæ of the European eel were now known in all stages of development, from that of 9 mm. up to full-grown larvæ averaging $7\frac{1}{2}$ cm. in length, and in their metamorphotic stages. I was also able to describe the development and metamorphosis of the larvæ of the American eel, which proved to be considerably smaller—1 cm. at least—than that of the European, in a fully grown state.

The few metamorphotic stages of the American eel I had at my disposal I had found in a collection of murænoid larvæ from a cruise of the United States S. "Bache" sent me by the United States Commissioner of Fisheries, Dr. HUGH M. SMITH, of Washington. The work of the "Bache" was carried out in January, February and March, 1914, in connection with the programme of the International Council for the Study of the Sea, in the Gulf Stream area and along two sections between Bermuda and the United States coast. The collection consisted of several hundred murænoid larvæ, among which I found thirty-seven specimens belonging to the genus *Anguilla*, taken near Bermuda or in the waters between there and the United States. Closer examination showed that only six of these thirty-seven belonged to the American species, the remainder being larvæ of *Anguilla vulgaris*, 4–5 cm. in length. Thus the collections from the "Bache" furnished additional evidence of the mysterious fact that, as we had shown in 1913, the larvæ of the European eel may, even in the American waters of the Atlantic, predominate greatly over those of the species of eel which has its habitat in America. A remarkable feature of the case was that at more than one of the "Bache's" stations, as also of the "Margrethe's," larvæ of both species were brought up in the same net at the same time. I shall later, in dealing with the investigations undertaken by the schooner "Dana," return to this point, which I found altogether incomprehensible at the time.

The collections of material from trading vessels had, in the five years they covered,

^{*} "On the Early Larval Stages of the Fresh-water Eels (*Anguilla*) and some other North Atlantic Murænoids" ('Meddelelser fra Kommissionen for Havundersøgelser, Serie Fiskeri,' vol. V, No. 4, Copenhagen, 1916).

been of great assistance to us, first and foremost by showing in what parts of the Atlantic eel larvæ were to be found and where they were lacking. We were, however, indebted to them for more than this. During the last two years during which such collections were made, 1914 and 1915, the West Indies steamers had regularly brought us in larvæ so small in size that we were able with perfect certainty to conclude therefrom that the steamship route from the English Channel to St. Thomas must pass through the breeding-grounds of the eel. This was indeed a point of the highest importance in the task we had before us: to chart the spawning area of the eel. Ships bound to follow a certain particular route, however, could not, of course, assist us in ascertaining the boundaries of such an area. Altogether, matters were now so far advanced that we could hardly expect to gain any great further advantage from occasional hauls by trading vessels. For the work now to be done we needed a vessel specially equipped, which could be employed on that work all the time, and follow any course laid down, as might seem desirable from the results of expert examination of the material on board from one station to another.

Our endeavours were accordingly directed towards this end as soon as the War ceased, and it was possible once more to think of work at sea. The plans met with great difficulties, but, on the other hand, were strongly supported in various private quarters, both with financial help and in other ways. Particularly effective was the assistance here rendered by the East Asiatic Company of Copenhagen, which I have already had occasion to mention in a like connection, and whose Director, His Excellency H. N. ANDERSEN, placed at our disposal a vessel, fully ready for sea and actually at work, the four-masted motor schooner "Dana," of 550 tons, for the purpose of these investigations.

With the schooner "Dana" we have, during the years 1920 and 1921, made hauls at a great number of stations, partly in March and April (about seventy stations) and again in June and July (about sixty stations). Most of the stations were situated in the western Atlantic. A great quantity of material was obtained; this has not, however, yet been dealt with in detail, especially the yield of 1921.* The murænid eggs have not been identified as yet, and I have therefore been unable to take them into consideration.† For the purpose of mapping out the breeding-grounds of the eel I have employed—as previously when dealing with the Gadoids—the earliest larval stages, less than 10 mm. in length. These are so tiny that there can be no question of their having moved any considerable distance from the spot where the eggs were spawned.

* The "Dana's" yield of eel larvæ in 1920 amounted to about 6000 specimens of the European and about 1000 of the American eel, besides many thousand specimens of other murænid larvæ.

† Since it has been questioned whether the ripe eggs of the eel contain oil-globules, I may mention in this connection that the remnants of the yolk-sac found in larvæ about 5 mm. in length prove to contain a large, quite distinct oil-globule. This observation confirms the conclusion arrived at by T. WEMYSS FULTON in 1897 from the study of the ovarian eggs of the eel.

These tiny larvæ were found at a considerable number of stations, about twenty-five. On marking these off upon a chart (fig. 4), it will be seen that the breeding-grounds of the European eel form a continuous area situated in the western Atlantic between about 22° and 30° N. lat. and about 48° and 65° W. long. The central portion will be found to lie about lat. 26° N., or approximately equidistant from the Leeward Isles in the West Indies and from Bermuda.

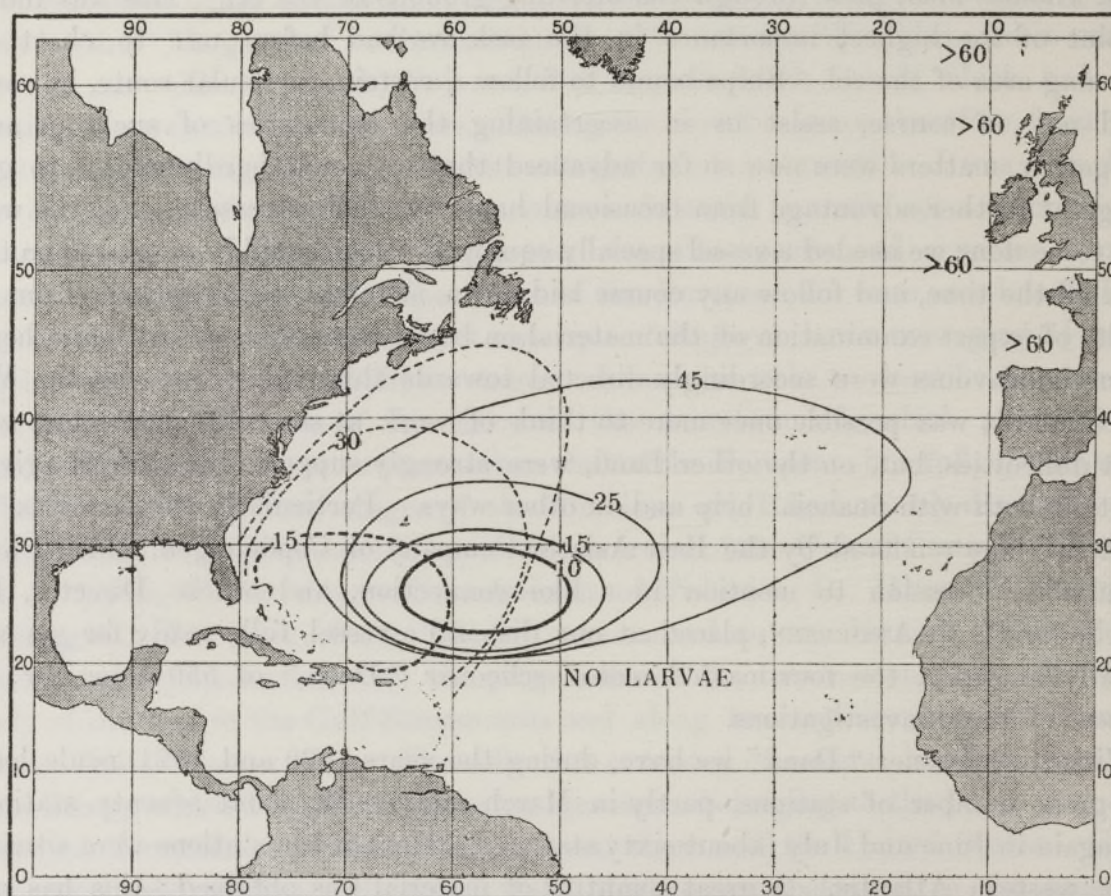


FIG. 4.—European Eel (*Anguilla vulgaris*) and American Eel (*Anguilla rostrata*); breeding areas and distribution of larvæ shown by curves (dotted for the American, continuous for the European species). The heavily-drawn innermost curves embrace the breeding areas of the two species. The curves show limits of occurrence, *i.e.*, specimens less than 25 mm. in length have only been found inside the 25 mm. curve, etc.

It is on the 1920 investigations in particular that the chart is based. As to how far the area may vary in extent from one year to another I am unable to say. This much, however, is certain, that tiny larvæ, less than 10 mm. in length, have now been found within this area in no fewer than four different years, *viz.*, 1914, 1915, 1920, and 1921.

The position of the area will be seen from the chart, fig. 4, where it is indicated by the heavily drawn curve, which I have termed the 10-mm. line, as marking the limits of occurrence of larvæ less than 10 mm. in length. Similar lines have been drawn

for the 15, 25, and 45 mm. limits, taking all our finds of eel larvæ into consideration. I shall revert later on to these curves and the conclusions which they warrant in regard to the trans-oceanic migrations of the larvæ. First of all, I propose to deal with their occurrence on the breeding-grounds in the western Atlantic.

In the latter half of April, the average length is about 12 mm.; in May, June and July, it is increased, but in each of these months specimens less than 10 mm. are found. From this we may conclude that the spawning season of the eel commences in late winter or early spring and lasts to well on in summer. In autumn and early winter tiny larvæ were not found, as mentioned when dealing with the "Margrethe's" investigations in 1913.

The "Dana" stations from June, 1920, within the breeding area yielded large hauls, which gave us an extremely lucid picture of the larvæ of that year (the O-Group) which in June averaged about 25 mm. in length. By way of example we may take a haul of two hours' duration at about 50 m. depth, Station 871 (lat. $27^{\circ} 15' N.$, long. $61^{\circ} 35' W.$) on June 27, 1920. The contents of the net when drawn on board presented a remarkable sight: of the pelagic forms it contained the great majority were larvæ of our European eel. A count showed close upon 800 specimens (reproduced here in the photograph, Plate 17, fig. 3, measurements in the graph, fig. 5). This one haul alone gave us a greater number of specimens of eel larvæ than had hitherto been obtained in the whole course of any expedition. It affords us, in conjunction with many other hauls from the "Dana" stations, a clear idea of the enormous quantities in which the young larvæ of the European eel are present here in the western Atlantic.

As mentioned, the average length in June was about 25 mm., and the great majority of larvæ of this size were found to occur near the surface—from a depth

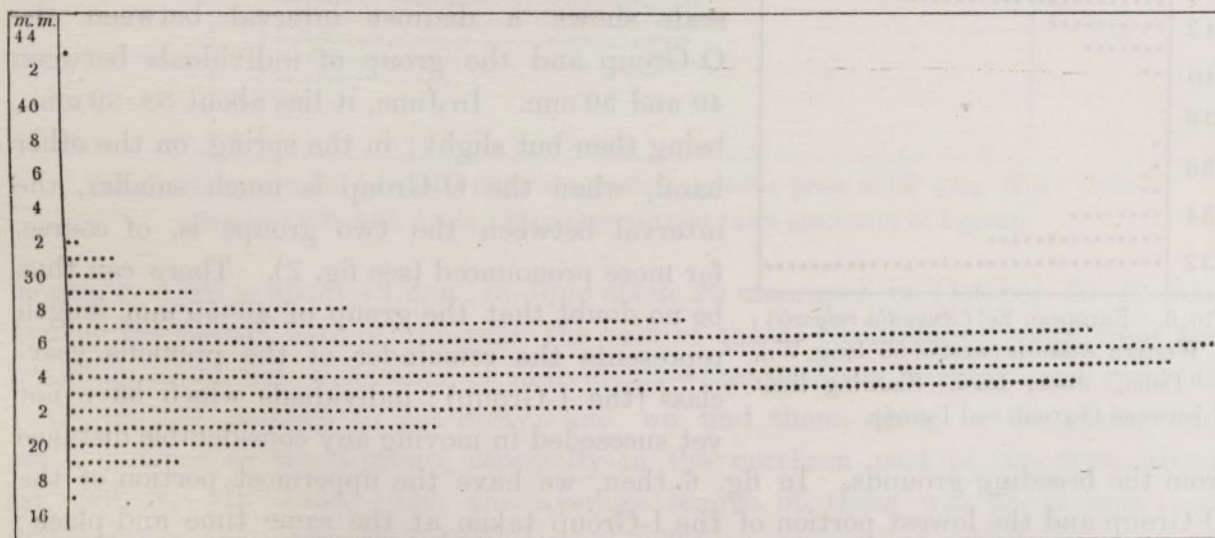


FIG. 5.—Sizes of Eel Larvæ (*Anguilla vulgaris*) caught in a single haul of two hours' duration at "Dana" Station 871 (lat. $27^{\circ} 15' N.$, long. $61^{\circ} 35' W.$) in the western Atlantic, June 27, 1920; depth about 50 m. The largest specimen shown belongs to the I-group, the remainder to the O-group.

of about 50 m. to the surface itself. The younger larvæ (7–15 mm. long) were taken somewhat deeper, at depths ranging from about 200 to about 75 m.; but it must be borne in mind that the depth of the ocean here is over 6000 m. We may, therefore, assert that the larvæ of the eel, even at these early stages of development, are true pelagic organisms, pertaining to the upper water layers, as the 1905 investigations had shown was the case with the full-grown larvæ.

A closer investigation of the sizes of the larvæ from the "Dana" stations in the western Atlantic is of interest. The figures provide a far sounder basis for determining the age of the larvæ than we had before. Fig. 7 shows the sizes of the youngest year-class (the O-Group) in April, 1921, and fig. 5 the O-Group in June, 1920. The measurements from June are from specimens taken in a single haul. If we include the entire material from the "Dana" stations in June, 1920, we find that the O-Group varies from 7 to 37 mm., with an average length of about 25 mm. We have a very large quantity of material from the month of June, between four and five thousand specimens, so that the average length of the group for this month is determined with a high degree of accuracy.

Now it has been noticed for several years, that in spring a few eel larvæ, between 43 and 50 mm. long, appear in or near the spawning area in the western Atlantic. In June, 1920, also, some of these larvæ—78 in all—were taken by the "Dana," more especially in the northern part of the area.

The measurements will be seen from fig. 5, showing one, and fig. 7, showing three of these larvæ among the O-Group. The graph, fig. 6, also indicates the lengths

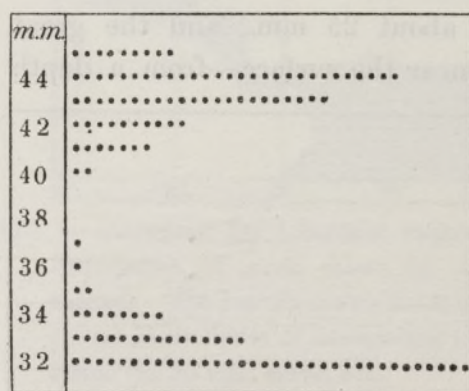


FIG. 6.—European Eel (*Anguilla vulgaris*); Western Atlantic (west of 50° long. W.), "Dana," June, 1920. Showing limit between O-group and I-group.

of the largest specimens of the O-Group, which, as mentioned, varied at this season from 7 to 37 mm. It will be noticed that the millimetre scale shows a distinct interval between the O-Group and the group of individuals between 40 and 50 mm. In June, it lies about 38–39 mm., being then but slight; in the spring, on the other hand, when the O-Group is much smaller, the interval between the two groups is, of course, far more pronounced (see fig. 7). There can thus be no doubt that the group of 40–50 mm. length represents the remainder of the previous year-class (the I-Group); individuals which have not yet succeeded in moving any considerable distance

from the breeding-grounds. In fig. 6 then, we have the uppermost portion of the O-Group and the lowest portion of the I-Group taken at the same time and place; the figure thus serves very satisfactorily to show the limit between the two year-classes in the month of June. The "Dana" stations in July, 1920, also, in the outer parts of the breeding area, show a distinct interval between the

O- and I-Groups; here, however, it is found a little higher up the scale, on account of the growth which has taken place. Even in September there is a trace of what is probably the same at the "Margrethe" Station 1027, south of the Newfoundland Banks, the interval in this month lying at about 45–47 mm. length (fig. 3, p. 189).

We are now enlightened as to the sizes of the larvæ in the western Atlantic at the different seasons. The larvæ found here, *i.e.*, west of long. 50° W., are almost without exception under 50 mm. in length. They belong to the two youngest year-classes, the O-Group being by far predominant in point of numbers. Its average

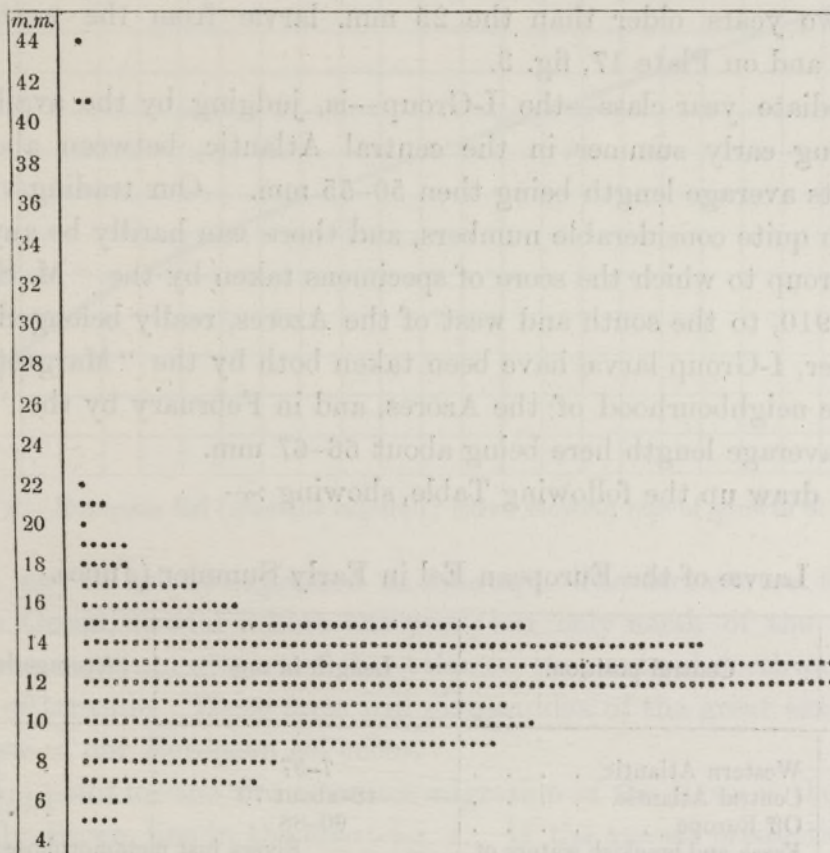


FIG. 7.—European Eel (*Anguilla vulgaris*); western Atlantic (west of 50° long. W.), "Dana" Stations 935–948, April, 1921; O-group and three specimens of I-group.

length in April is about 12 mm., in June about 25 mm., and in October 30–40 mm. During the second half of the year, the bulk of the O-Group move away from the breeding area, but a number of individuals—the numbers varying from year to year—do not manage to get away, and we find them, then, in the spring and early summer as the I-group, especially in the northern part of the area, about lat. 30° N. In June, 1920, the average length of these was 43–44 mm.; in other years they may be a little larger. They represent the last or youngest portion of the I-Group, the great majority of which have already moved away from the area.

From our investigations with the "Thor" in 1905-06 it will be remembered that the full-grown larvæ occur in early summer outside the coastal banks to the west of Europe. They vary in length from 60 to 88 mm.; in June, 1905, the average was about 75 mm. (fig. 2). In the same month, the great bulk of the O-Group, averaging 25 mm. in length, are still on or near the breeding-grounds. During the journey, then, from here to the shores of Europe, these larvæ grow on an average 50 mm. Plotting the lengths for the different months in a graph, we find that the larvæ take on an average two years to grow so much (fig. 8). The full-grown larvæ in fig. 2 from June, 1905, thus represent the II-Group, and are on an average, two years older than the 25 mm. larvæ from the western Atlantic shown in fig. 5 and on Plate 17, fig. 3.

The intermediate year-class—the I-Group—is, judging by the available data, to be found during early summer in the central Atlantic, between about 50° and 20° W. long., its average length being then 50-55 mm. Our trading vessels caught them in May in quite considerable numbers, and there can hardly be any doubt that it was this I-Group to which the score of specimens taken by the "M. Sars" expedition in June, 1910, to the south and west of the Azores, really belonged (see p. 185). Later in summer, I-Group larvæ have been taken both by the "Margrethe" and the "Dana" in the neighbourhood of the Azores, and in February by the "Thor" near Gibraltar, the average length here being about 66-67 mm.

We can now draw up the following Table, showing :—

Larvæ of the European Eel in Early Summer (June).

Year-class.	Central position.	Length in mm.	Average length in mm.
O-Group . .	Western Atlantic	7-37	25
I-Group . .	Central Atlantic	40-about 70	52
II-Group . .	Off Europe	60-88	75
(III-Group . .	Fresh and brackish waters of Europe.	Elvers just metamorphosed.)	

The eels, then, spawn in spring, their larvæ take on an average about 2 years to attain full larval size, and nearly 3 years elapse before the metamorphosis is completed. The elvers which make their appearance on our shores in spring will accordingly be, on an average, about 3 years old.

The illustration, Plate 17, fig. 2, shows the same as the Table above.

Reverting now to the distribution of the various larval stages in the Atlantic, let us glance once more at the chart (fig. 4). I may supplement the indications there given by noting here our northernmost, southernmost, westernmost, and easternmost finds of larvæ of the European eel :—

Larvæ of the European Eel (*Anguilla vulgaris*).

Northernmost find: lat. 61° 21' N., long. 10° 59' W. ("Thor").

Southernmost „ : „ 20 14 N., „ 57 03 W. (S.S. "Tranquebar").

Westernmost „ : long. 73 30 W. lat. 30 49 N. ("Dana").

Easternmost „ : „ 15 35 E. „ 38 07 N. ("Thor").

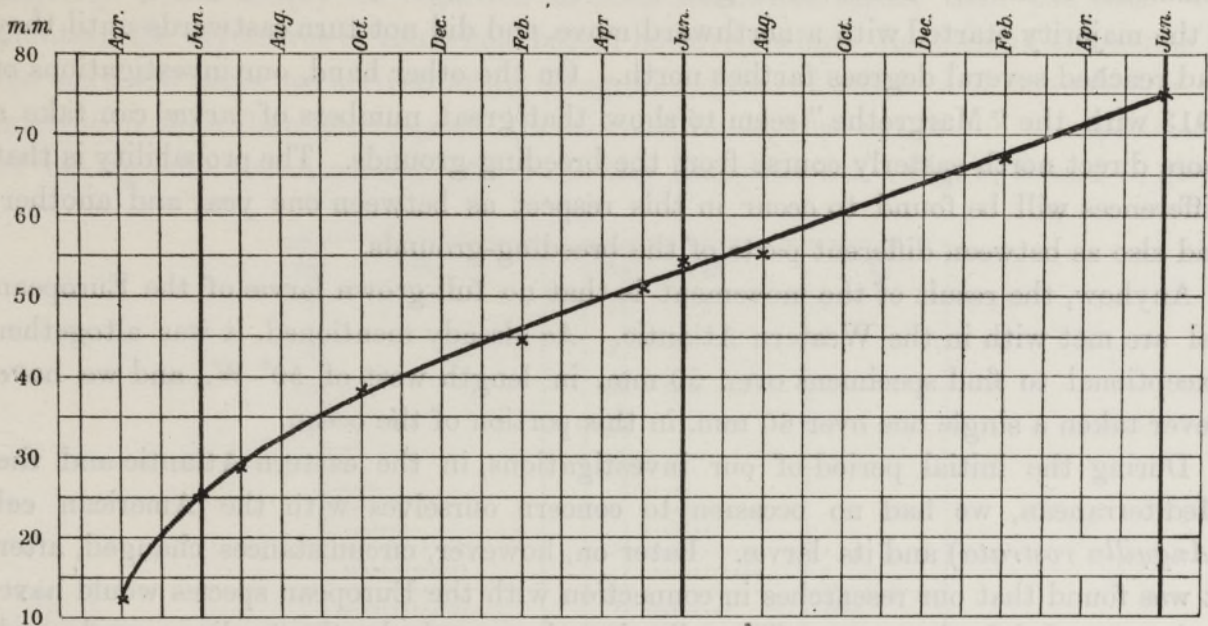


FIG. 8.—European Eel (*Anguilla vulgaris*); curve showing rate of growth of Larvæ.

The result may be briefly expressed as follows :—The larvæ were found all across the Atlantic Ocean, coastal waters excepted, but only north of the 20th degree of lat. N. In the easternmost part of the Atlantic, they extend northwards beyond the 60th degree of latitude. These facts will give an idea of the great extent of the area in which larvæ of our European eel occur.

The starting-point for the trans-oceanic migration of the larvæ is the area encircled by the heavily-drawn line in the chart fig. 4. If the annual production of eel larvæ only occupied a very brief period, say 1 month, and provided that all individuals came from the same spot and made equal progress, alike in their growth and in their movement eastwards, then it would be an easy matter to indicate the position of each particular stage of development in the ocean by curves representing the average lengths of the specimens. As it is, neither of these conditions is fulfilled, and it is difficult, therefore, to draw up a clear and simple chart of the material. After various experiments in this direction, I have adopted the method of noting on a large chart the minimum length of the specimens found at each station, these values being then used in constructing the curves shown in fig. 4. These curves are to be understood as limits of occurrence, *i.e.*, specimens less than 25 mm. have only been found within the area embraced by the 25 mm. line, and so on.

The chart gives the main sum of the conclusions to be drawn from the material.

collected in the course of years. The position of the curves clearly shows that the principal resultant of the movement of the eel larvæ from the breeding-grounds is directed towards N.E., that is to say, towards Europe. It will be noticed that there is also a certain movement towards the north and north-west. From the data available, it is not easy to determine in what direction the main body of the larvæ commence to move. From investigations with the "Dana," in 1920, it might seem as if the majority started with a northward move, and did not turn eastwards until they had reached several degrees farther north. On the other hand, our investigations of 1913 with the "Margrethe" seem to show that great numbers of larvæ can take a more direct north-easterly course from the breeding-grounds. The probability is that differences will be found to occur in this respect as between one year and another, and also as between different parts of the breeding-grounds.

Anyhow, the result of the movement is that no full-grown larvæ of the European eel are met with in the Western Atlantic. As already mentioned, it was altogether exceptional to find specimens over 50 mm. in length west of 50° W., and we have never taken a single one over 60 mm. in this portion of the ocean.

During the initial period of our investigations, in the eastern Atlantic and the Mediterranean, we had no occasion to concern ourselves with the American eel (*Anguilla rostrata*) and its larvæ. Later on, however, circumstances changed, after it was found that our researches in connection with the European species would have to be extended farther west. The collections here made by the trading vessels, and by the "Margrethe" in 1913, brought us already certain specimens which, though outwardly indistinguishable from *Leptocephalus brevirostris*, proved, on being tested for number of muscle-segments (myomeres), to belong to the American eel. These larvæ were taken in the same area as those of the European species, even, indeed, at one or two of the "Margrethe's" stations, in the same haul. It was with mingled feelings that we noted this fact, since it involved a further complication of the eel question, which at this point seemed more intricate than ever. Technically, also, it increased the difficulty of our investigations, since the only means whereby the larvæ of the two species can be distinguished one from the other is by counting, under the microscope, the 104-120 myomeres in each individual specimen—a very lengthy and laborious business, especially on board a small vessel at sea.

After the cruise of the "Dana," in 1920, I look upon the matter in quite a different way. True, the technical difficulties have not diminished—I have in mind the counting of myomeres in the 7000 specimens obtained on the cruise—but the comparison of the life-history of the two species which our investigations have enabled us to make is, to my thinking, one of the most interesting chapters in the history of the eel. Indeed, it is hardly too much to say that the life-history of the European eel can only be properly understood at all by comparison with that of the American. This will be seen from what now follows.

At the "Dana" Station 827, S.E. of Bermuda (30° 47' N., 62° 27' W.), we made a

haul on June 13, 1920, at about 25 metres depth, bringing up 150 *Anguilla* larvæ. These were measured, as usual, as soon as possible after preservation, giving the result shown in fig. 9, A. Believing that we had here solely to deal with *Leptocephalus brevirostris*, we naturally regarded the haul as practically representative of the youngest year-class (the O-group), and a few specimens of greater length than the majority would simply be regarded as born somewhat earlier than the rest. On counting the myomeres of the whole batch, however, which was done in the course of the next few days, we arrived at an altogether different result, and one which is of interest in more than one respect. It was now found that out of the 150 specimens, 94 belonged to the American and 56 to the European eel. Fig. 9, B and C, gives

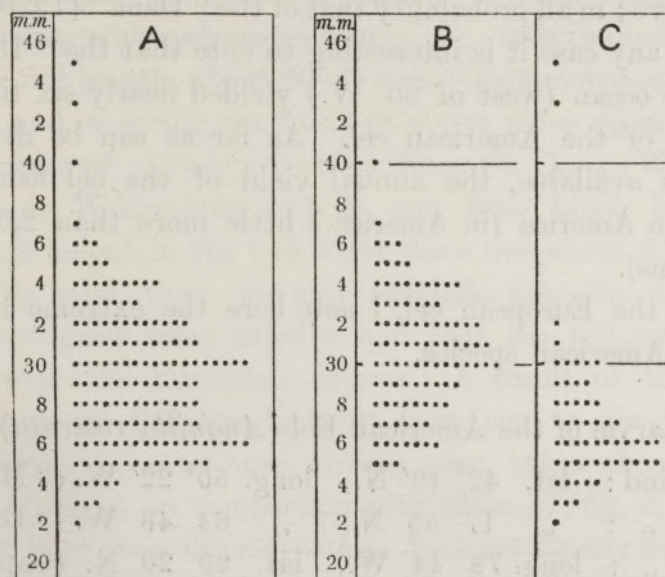


FIG. 9.—European Eel (*Anguilla vulgaris*) and American Eel (*Anguilla rostrata*); sizes of Larvæ from one haul at "Dana" Station 857, 30° 47' N., 62° 27' W., depth about 25 metres, June 13, 1920.

A.—Sizes of total catch. B and C.—Same individuals as in A after their identification by means of counting the myomeres. B.—*Anguilla rostrata*, all of the O-Group. C.—*Anguilla vulgaris*, two of the I-Group, the remainder of the O-Group.

the respective values separately shown. They are now seen to have an entirely different meaning. The specimens of both species are of the current year-class (the O-group), but those of the American eel are, on an average, larger than those of the European. From this we may conclude that the former species must spawn earlier or grow more rapidly than the latter. Furthermore, we notice that the two specimens of the European eel of 43 and 45 mm. are so much larger than the bulk of the specimens belonging to this species, that they must be supposed to be left-overs from the previous year (the I-group). These conclusions were frequently confirmed as the cruise went on. Plate 18 shows, in the form of an illustration, the contents of a similar haul. Both serve well to show how delicate an analysis is needed in the classification of material before it can be used as a basis for conclusions. The

following figures show the numerical proportion between the larvæ of the two species in our collections :—

	<i>Anguilla rostrata.</i>	<i>Anguilla vulgaris.</i>
Captain ANDREA (about 1865) . . .	1	2
Trading vessels, 1911–1915 . . .	3	120
“Margrethe,” 1913	24	714
U.S. S. “Bache,” 1914	6	31
“Dana,” 1920	Ca. 1000	Ca. 6000

In all the collections the European eel predominates, even in the western Atlantic. This is presumably the case also in reality. The collections can hardly be taken as properly representative; in all probability that of the “Dana” (1920) is nearest the true state of things. In any case it is interesting to note that the “Dana’s” hauls in the western parts of the ocean (west of 50° W.) yielded nearly six times as many larvæ of the European as of the American eel. As far as can be determined from the incomplete statistics available, the annual yield of the eel fisheries in Europe is several times that in America (in America a little more than 2,000 tons, in Europe more than 10,000 tons).

As in the case of the European eel, I note here the extreme limits for our finds of the larvæ of the American species.

Larvæ of the American Eel (*Anguilla rostrata*).

Northernmost find: lat. $42^{\circ} 19' N.$, long. $50^{\circ} 22' W.$ (“Margrethe”).

Southernmost „ : „ $17^{\circ} 55' N.$, „ $64^{\circ} 48' W.$ (“Dana”).

Westernmost „ : long. $78^{\circ} 44' W.$, lat. $29^{\circ} 20' N.$ (Capt. A. ANDREA, 1862).

Easternmost „ : „ $50^{\circ} 22' W.$, „ $42^{\circ} 19' N.$ (“Margrethe”).

I would also refer to fig. 4, where the occurrence of the larvæ of the American eel is indicated by curves. The result may be briefly stated as follows: We found the larvæ throughout the greater part of the western Atlantic between the West Indies and the Newfoundland Banks, where they occur together with the larvæ of the European eel. East of 50° long. W. we have not met with larvæ of the American eel, which have thus a far more limited area of occurrence than those of the European species.

Most of the “Dana” stations in June–July, 1920, west of 50° W., gave larvæ of both species, but *Anguilla vulgaris* was, as a rule, the more numerous. The larvæ of the two species were by no means evenly distributed throughout the area; west of about 62° W. long., and south of about 24° N. lat., *Anguilla rostrata* predominated over *Anguilla vulgaris*, and in this part of the area we took as many as 219 larvæ of the American eel at one haul (Station 891, lat. $29^{\circ} 28' N.$, long. $69^{\circ} 25' W.$, July 24, 1920).

The dotted lines on the chart (fig. 4) show the distribution of the larvæ of the American eel. The outermost curve marks the limit of occurrence, the next is that for 30 mm., and the innermost for 15 mm., to be understood as in the case of the European eel.

From the position of the curves we can conclude that the breeding area of the American eel lies along the entire range north of the West Indian islands. Its central portion lies west and south of the central breeding-grounds of the European eel; the areas embraced by the two species, however, are apparently not separated, but seem to overlap.

The early tiny larvæ, 7–8 mm. long, of *Anguilla rostrata* were taken in February.* In April the average length was about 20–25 mm., in June about 30–35 mm., in July about 40 mm., and in September about 50–55 mm. Towards the end of the year the larvæ have attained their full length, about 60–65 mm.; metamorphosis takes place during the winter months, and in spring the hosts of elvers move up into fresh water. We have examined samples of pigmented elvers from St. Croix (West Indies) (March), from the Potomac at Washington (April), and from Little River, Massachusetts (May). The average length in the two latter cases was about 57 mm.

From the data to hand, then, we may conclude that the American eel spawns earlier, that its larvæ grow more rapidly, and that the full-grown larva is smaller than is the case with the European species. A result of this is that *Anguilla rostrata* can complete its full development from egg to elver in about one year, whereas *Anguilla vulgaris*, as we have already seen, takes about three years. The photograph, Plate 17, fig. 1, in comparison with Plate 17, fig. 2, illustrates this, and shows that the I-group of *Anguilla rostrata* in June are already metamorphosed elvers, while this stage of development is in the case of *Anguilla vulgaris* only attained by the III-group. Despite the fact that the two species are outwardly so alike as to be hardly distinguishable, they differ to such an extent that the one takes about three times as long as the other to pass through the same cycle of development.

The recognition of this difference between *Anguilla rostrata* and *Anguilla vulgaris* is of decisive importance to the comprehension of the life-history of the two species, and the fact provides a natural explanation of several points that seemed mysterious before.

As already mentioned, an investigation of samples of eels from Bermuda showed that they all belonged to the American species (*Anguilla rostrata*). This in itself

* It is not easy to distinguish the two *Anguilla* species in their early larval stages, when the hind-most myomeres cannot yet be counted with certainty. On an average, however, *Anguilla vulgaris* has a few preanal myomeres more than *A. rostrata*. In both species, there are a couple of black chromatophores on the embryonic fin near the tip of the tail. As a rule, these are more pronounced, and remain longer in *A. rostrata* than in *A. vulgaris*. In the latter they are often difficult to discern, and seem always to disappear before the larva reaches a length of 20 mm.; in *A. rostrata* they are sometimes discernible at a length of 30–35 mm.

was not surprising. But in the winter of 1913-14, both the "Margrethe" and "Bache" found the waters round Bermuda populated chiefly by larvæ of the European eel. I called attention to this point when dealing with the collections from the two vessels (*cf.*, p. 192), but was obliged to confess that it was beyond my comprehension. Viewed in the light of our subsequent investigations, however, the explanation is perfectly simple. The larvæ of the European eel which are found at Bermuda and in the western Atlantic generally are, owing to the vicinity of the breeding-grounds, all young, belonging to the O- and I-groups, and consequently as yet far from that stage of development at which they seek the shores. It is only larvæ of the American eel which are found so far west in the full-grown and metamorphotic stages, at which they are drawn to the coasts. Consequently, *Anguilla rostrata* is the only one of the two species which "lands" at Bermuda, the hosts of larvæ of *Anguilla vulgaris* which surround these islands being only passers-by on their way to a far more distant goal.

As we have learned, the breeding-grounds both of the European and of the American eel lie west of long. 50° W. Although the larvæ of *Anguilla rostrata* become far more numerous in proportion from east to west, it is nevertheless a fact that there are extensive areas where the larvæ of the two species are greatly intermingled. The "Dana" stations provide many examples of such intermingling, as shown in the photograph (Plate 18) and the graph fig. 9.

It is very natural then to ask: If the larvæ of the two species are found greatly intermingled in certain areas of the ocean, how is it that the stock of eels in Europe is, practically speaking, pure, *i.e.*, composed exclusively of *Anguilla vulgaris*, and that in America of *Anguilla rostrata*? The question may also be formulated as follows:—How do the masses of larvæ in the western Atlantic sort themselves out, so that those individuals which belong to *Anguilla vulgaris* ultimately find themselves in Europe, while those of *Anguilla rostrata* "land" on the shores of America and the West Indies?

In the main, the question is no longer difficult to answer. In the case of the American eel, the pelagic larval stage is terminated in about one year; consequently the larvæ have not time to make the journey to Europe, the distance being more than they can cover in that period. It is otherwise with the European eel, which takes nearly three times as long over its larval development, as a result of which practically all of them are far away from the western (American) portion of the Atlantic when the time comes for them, as elvers, to seek the coasts.

We can thus indicate both a geographical and an ethological cause for the distribution of the two species of fresh-water eels. The former lies in the fact that *Anguilla rostrata* has its centre of production somewhat farther west and south than *Anguilla vulgaris*. The latter is the different duration of the pelagic migratory stage. These two facts, in conjunction with the ocean currents as an aid to transport, and later—once the earliest stages of development are past—the active movements of the larvæ themselves, must be regarded as the causes which lead the two Atlantic species of

eels to find each its own side of the ocean, despite the close proximity of their breeding-grounds.

That fish should undertake migrations of considerable extent while in the pelagic larval stage is nothing unusual. I need only call to mind the young of the Gadoids, and their migrations round Iceland, which I had an opportunity of studying in 1903–1905 (*loc. cit.*, 1909). The point which makes our eel an exception among fishes, and among all other animals, is the enormous extent of its journeyings in the larval stage. This is indeed a migratory stage *par excellence*, the unusual duration of which must be regarded as an adaptation—effected by selection—to the distances of many thousand miles to be traversed. So great are these distances, that the class of one year cannot reach its goal, the fresh-waters of Europe, until a second and a third have started on their way. As a matter of fact, we have in early summer three year-classes of larvæ on their journey; the youngest in the western, the next in the central, and the oldest in the eastern waters of the Atlantic, off the coastal banks of Europe (*cf.*, Plate 17, fig. 2). There can be no doubt that a great wastage of individuals takes place in the course of these years of migration, but it is in all probability insignificant in view of the enormous production of larvæ, of which the “Dana” stations in the western Atlantic give evidence.

The *Anguilla* species, in contrast to other murænoids, are usually termed fresh-water eels, and are reckoned among the fresh-water fishes of Europe and North America. From what we have now learned this is far from literally strict. Both from their history and their actual manner of life, these “fresh-water eels” are true oceanic fishes, and the remarkable point in their life-history is not so much the fact of their migrating out into the sea to spawn, as in their leaving it in order to pass their period of growth in an environment so unusual for murænoid fishes as fresh-water.

I have in the foregoing pages described the course of our investigations, and set forth their results. In conclusion, I will endeavour very briefly to give an outline of the life-history of our eel, as indicated by the facts now ascertained.

During the autumn months, the silvery eels leave the lakes and rivers and move out into the sea. Once beyond fresh-water limits, the eels are, in most parts of Europe, outside our range of observation. Exceptions are, however, found as in the case of the Danish sounds and belts, and adjacent waters, which are passed by great quantities of eels on their way to the Atlantic, and form the site of important fisheries about October. In the western part of the English Channel, trawlers may, towards the end of the year, occasionally bring up a few big specimens in their nets, but after this, the last trace of the eel on European ground is lost. No longer subject to pursuit by man, hosts of eels from the most distant corners of our continent can now shape their course south-west across the ocean, as their ancestors for unnumbered generations have done before them. How long the journey lasts

we cannot say, but we know now the destination sought: a certain area situate in the western Atlantic, N.E. and N. of the West Indies. Here lie the breeding-grounds of the eel (fig. 4).

Spawning commences in early spring, lasting to well on in summer. The tiny larvæ, 7–15 mm. long, float in water-layers about 200–300 metres from the surface, in a temperature of about 20° C. The larvæ grow rapidly during their first months, and in their first summer average about 25 mm. in length (fig. 8). They now move up into the uppermost water-layers, the great majority being found between

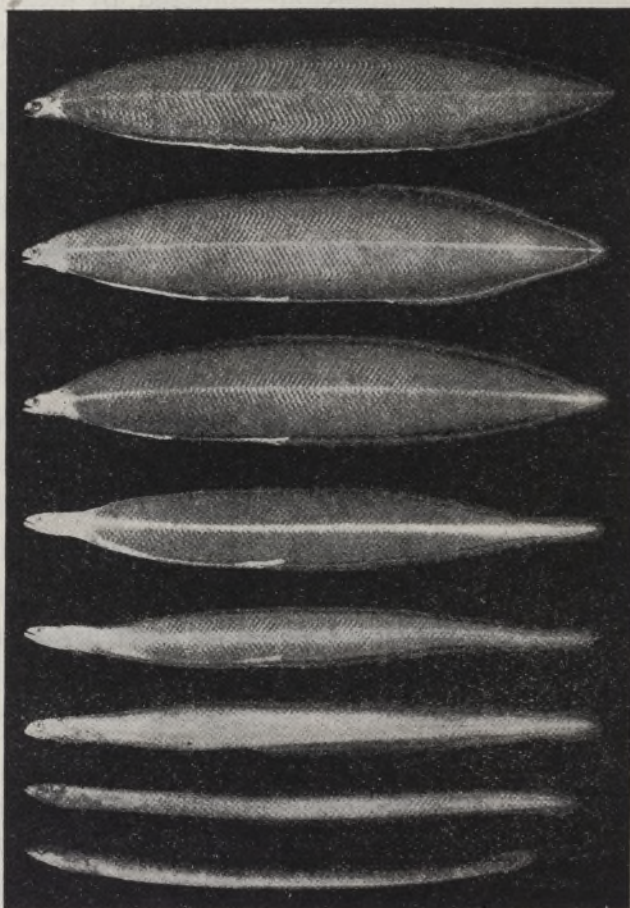


FIG. 10.—Metamorphosis of eel larvæ (*Anguilla vulgaris*). The top specimen is a full-grown larva before metamorphosis, the two lower ones are elvers. Atlantic W. of British Isles, "Thor," 1906; the elvers from Danish waters. Natural size.

50 and 25 metres, or at times even at the surface itself. Then they commence their journey towards the shores of Europe, aided by the eastward movement of the surface-water itself. During their first summer, they are to be found in the western Atlantic (west of 50° long. W.). By their second summer they have attained an average length of 50–55 mm., and the bulk are now in the central Atlantic. By the third summer, they have arrived off the coastal banks of Europe, and are now full-grown, averaging about 75 mm. in length, but still retaining the compressed,

leaf-shaped larval form. In the course of the autumn and winter, they undergo the retrograde metamorphosis which gives them their shape as eels and brings them to the elver stage, in which they move in to the shores and make their way up rivers and watercourses everywhere (fig. 10). The average age of the elvers in spring is about three years. Many individuals, especially males, keep to the brackish water in lagoons or estuaries; others, especially females, move far up the streams they have entered, and may in the course of their wanderings penetrate far into the interior of the continent. In Switzerland, for instance, considerable quantities of eels occur, and specimens have been taken there in waters at an altitude of 3000 feet above the level of the sea. The eels utilise their sojourn in fresh water to feed and grow big, but the duration of their stay here varies greatly, according to sex, climate and quantity of food, ranging from about 5 to about 20 years or more. All the large eels are females; the males seldom exceed 45 cm. in length. During its period of growth, the eel is of a yellowish or greenish colour, with no metallic lustre; these growing eels are generally termed "yellow eels." When they have reached the stage where the migratory instinct begins to assert itself, the desire for food, otherwise voracious, is lessened, the body takes on a metallic sheen, and the pectorals become black and pointed. In this guise, the eels are termed "silver eels," their flesh is very firm and rich in fat, and they are thus well equipped for entering upon their second and last great journey, this time back to the breeding-grounds across the ocean.

Before concluding this survey of the Danish Eel investigations, it is my pleasurable duty to thank all those who have contributed to the progress of the same. I have already mentioned how decisively important was the aid afforded us from outside. Special thanks are here due to Admiral H.R.H. Prince VALDEMAR of Denmark, and to His Excellency H. N. ANDERSEN, Director of the East Asiatic Company of Copenhagen. But in our Commission for Investigation of the Sea, also, much and most valuable work has been done to further these investigations, first and foremost by the Chairman, Commodore C. F. DRECHSEL, Danish R.N.

Last, but not least, I thank my assistants who helped to carry out the actual work at sea and on land. These, during the first years, A. STRUBBERG, M.Sc., later P. JESPERSEN, M.Sc., and Å. V. TÅNING, M.Sc., have each taken a great share of the work with much skill and enthusiasm. Further, the Captain of our research vessel, Captain G. HANSEN, has, in addition to the other duties falling to his share, on more than one occasion carried out work on board which called for training in marine biological research.

EXPLANATION OF PLATES.

PLATE 17.

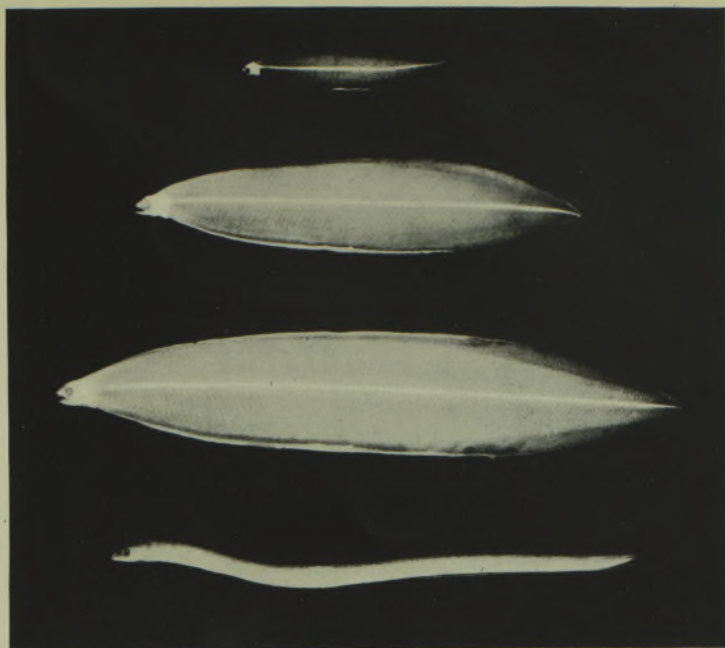
- Fig. 1.—American Eel (*Anguilla rostrata*); showing the size of the two youngest year-classes in June; about natural size.
- Fig. 2.—European Eel (*Anguilla vulgaris*); showing the size of the four youngest year-classes in June; about natural size.
- Fig. 3.—European Eel (*Anguilla vulgaris*); same haul as that represented in the graph, fig. 5. Below, a II-Group specimen, length 74 mm., from the eastern Atlantic, is shown for comparison. Reduced about half size (cf. the centimetre-scale below).

PLATE 18.

European Eel (*Anguilla vulgaris*) and American Eel (*Anguilla rostrata*).
 Larvæ from one haul at "Dana" Station 855, 29° 15' N., 59° 45' W., depth about 50 m., June 8, 1920. Similar haul to that shown in fig. 9. The group of specimens on the left are *Anguilla rostrata* (all of O-group), that on the right *Anguilla vulgaris* (three of I-group, the remainder of O-group). Slightly reduced.



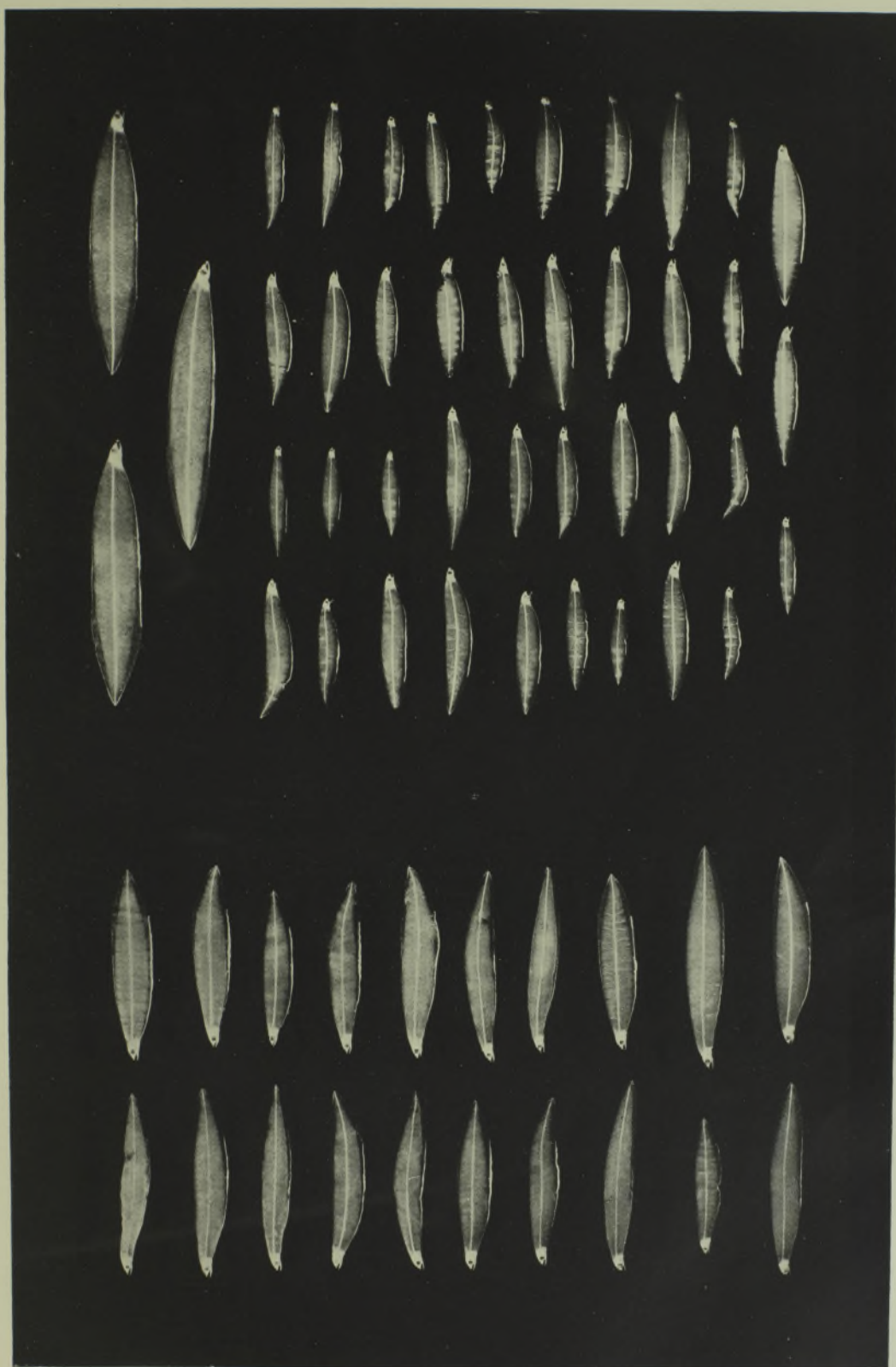
1.



2.



3.



Anguilla vulgaris.

Anguilla rostrata.