

THE REPRODUCTION AND SPAWNING-PLACES OF THE FRESH-WATER EEL (*ANGUILLA VULGARIS*).

AMONG the apodal fishes of the British Museum described by Kaup in 1856 was a transparent, tape-like fish of about 8 cm. in length, similar to the uppermost specimen in Fig. 1 here

and Calandruccio that Kaup's *Lept. brevirostris* was no other than the larval form of the common eel living in the Mediterranean countries, a species supposed by some to be identical with the North European eel. These investigations were carried out at Messina, and left no doubt that the identification was correct. The mysterious problem of the reproduction of the eel was thus, about 1895, for the first time opened up to scientific investigation.

The Italian authors, however, did not stop at the facts observed; they put forward a number of suppositions regarding the reproduction of the eel, occurrence of the eggs, mode of life of the larvæ, etc. Egg "No. 10" of Raffaele, found in the Mediterranean, was supposed to belong to the common eel, the larvæ were imagined to be demersal, deep-water fishes, and Grassi's publication in the Proceedings of the Royal Society of London in 1896 led everyone to believe, as the one thing quite certain in the matter, that the spawning places of the eel are in the depths of the Mediterranean. Recent investigations have not altered the fact that *L. brevirostris* is the larval form of *Anguilla vulgaris*; but the biological conclusions have not proved to be correct.

In 1904 a new light was thrown upon the matter, when the *Thor* obtained a specimen of *Lept. brevirostris*, 7½ cm. in length, in the surface waters of the Atlantic west of the Faeroes. In the same year a second specimen was taken west of Ireland by the *Helga*. The year 1904 thus marked the beginning of the second stage in the solution of the eel problem; previously no *Lept. brevirostris* had been taken outside the Mediterranean. As Denmark is the country

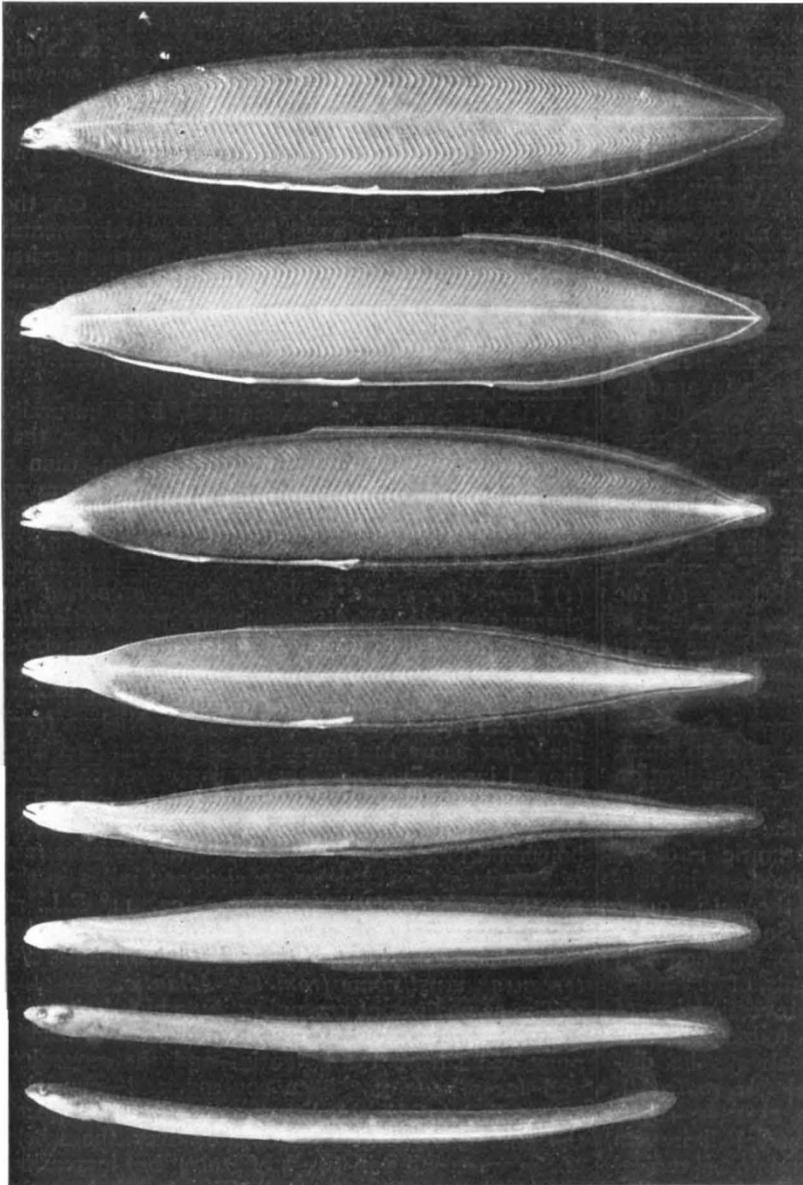


FIG. 1.—Larvæ of the eel (*Leptocephalus brevirostris*) and their metamorphosis to elvers. All figures slightly enlarged—Johs. Schmidt (1909).

reproduced. This received the name *Leptocephalus brevirostris*, and came from the Straits of Messina, practically the only place in Europe from which Leptocephali were known. Without knowing it, Kaup had given the first contribution to the question of the reproduction of the eel.

About forty years later we learnt from Grassi

in which the eel fisheries are of the greatest importance, it seemed fitting that the Danish Commission should carry the investigations further, and for this purpose we had the advantage, not only of a sea-going steamer, but also of the most modern apparatus—thanks to the experience and ability of the Director of the Danish Biological

Station, Dr. C. G. Joh. Petersen. How necessary both are can be judged from the sequel.

In 1905 we continued our work in the Atlantic between Iceland and Brittany. The larvæ of the eel were found in quantities, as many as seventy in a single haul, from the Hebrides southwards, but not to the north and not to the east of the 1000 m. line—thus not in the North Sea or Norwegian Sea. I drew the conclusion from this (1906), that *all the eels which occur in the North European countries must come from the Atlantic*. A comparison of all the available data for the time of appearance of the elvers in the rivers of West and North Europe confirmed me in this conclusion.

In 1906, May-June and August-September were devoted to an investigation of the waters between North Spain and South-West Ireland. No younger stages than those of 1905 were found, but it proved that the larvæ were not restricted to the belt between 1000 and 2000 m., where we had found them in 1905. They were taken out over 5000 m., the greatest depths investigated. More than 500 specimens were taken, and a curious thing was that the spring specimens were not yet metamorphosed, whilst those taken in autumn were for the most part in process of transformation. It proved, further, that the youngest specimens (not metamorphosed) occurred furthest out to sea, the oldest metamorphosing nearer the coasts (see Fig. 1).

It was thus perfectly clear that the larvæ of the eel are not demersal fishes, as Grassi and Calandruccio had supposed, but belong to the surface waters, even out over the greatest depths. Nevertheless, we had not yet found the early stages, and I was now (1909) inclined to the belief that the larvæ must be hatched out over great depths, far from the coasts and away from the bottom of the sea. This may be said to mark the end of the second stage in our investigation of the eel problem.

A study of the distribution of the adult eel in the countries bordering on the Atlantic afforded an instructive commentary on our deep-sea investigations. As is shown in Fig. 2, the eel is quite wanting along the coasts of the South Atlantic, and does not even reach down to the equator, whereas it occurs on all the islands of the temperate North Atlantic. From an investigation of a large number of specimens, I found that the European eel (*A. vulgaris*) could always be distinguished from the American eel (*A. rostrata*), from the fact that it has on an average seven more vertebræ than the latter. The eels living on the Azores, for example, were found to be typical *A. vulgaris*. The explanation of this peculiar occurrence seemed to lie in the distribution of temperatures and salinities in the deeper layers of the Atlantic. In the Northern, temperate Atlantic and in the Mediterranean, thus, where the larvæ occur, these have higher values than in the Southern Atlantic. On the supposition, therefore, that the eel requires a high temperature and salinity for spawning purposes, we can explain the absence of eels on the coasts of the South Atlantic; further, the direction of the currents

there is such that the larvæ cannot be carried to the South Atlantic coasts (Fig. 2).

The third stage in the solution of the eel problem began with our 1908 investigations in the Mediterranean and adjacent parts of the Atlantic. These investigations extended over both winter (1908-09) and summer (1910), so that all seasons of the year have been considered. The result has been a great surprise to me. Instead of finding here the youngest developmental stages of the eel—and Grassi's publication in the Royal Society's Proceedings of 1896 was certainly responsible for the general belief that the spawning places would be found there—I have been obliged to come to the conclusion that *the eel does not spawn in the Mediterranean at all*. The Mediterranean owes its stock of eels, like the North Sea and Baltic, to the Atlantic. On the other hand, I have found the early developmental stages (eggs or early larvæ) of fourteen other species of eels in the Mediterranean, which means that they must spawn there. This is in so far a distinct advance, for the eggs and early larvæ of these forms could not previously be identified with certainty in any single case.

With regard to the common eel, it is naturally more difficult to prove a negative result, e.g. that it does not spawn in the Mediterranean, than a positive one, e.g. that *Muraena helena* spawns there. It has been necessary, therefore, to take a number of conditions into consideration, of which the following are the most important. (1) *Large quantities of eel larvæ are carried by currents into the Mediterranean from the Atlantic*. This has been proved by investigations on both sides of the Straits of Gibraltar, and I have been able to follow their drift further east. The hydrographical investigations of Dr. J. N. Nielsen from the *Thor* show that the surface waters, in which the eel larvæ live, are moving eastwards from the Straits of Gibraltar the whole year round. The current bottles I have had put out in the neighbourhood of the Straits further show that the rate of flow is at least twelve to eighteen miles in the twenty-four hours, as far east as ca. 11° E.L. at any rate. *These observations prove incontestably that a portion at least of the eel stock of the Mediterranean must come from the Atlantic*.

The same lines of reasoning, by which I showed, in 1906, that the eels of the North Sea and Baltic must come from the Atlantic—and the reasoning and facts have not been controverted—can also be applied to the Mediterranean. The larvæ of the eel were found by the *Thor* over the whole of the western basin (west of Italy), but increasing greatly in numbers towards Gibraltar, where the quantities were greatest. In the eastern basin (east of Italy) no larvæ of the eel were found—compare Italy with the 1000 m. line west of South Ireland. The eel larvæ taken nearest Gibraltar were on an average smaller than those found further east, both by the *Thor* and in the collections I have had made for me at Messina during fourteen months (see Table). Further, at Messina, most larvæ were taken in spring and summer, fewest in winter, and this agrees with the fact

that at Gibraltar most larvæ were taken in winter. With an average rapidity of twelve miles in the day, the currents will carry the larvæ from Gibraltar to Messina in the course of three months.

Larvæ of the Eel (Lept. brevirostris). Distribution compared with Age (from Investigations with the Thor and other Danish Vessels).

Region	Percentage of specimens smaller than 70 mm.
Atlantic S. of ca. 45° N. and W. of ca. 20° W. ...	100
„ N. of ca. 45° N. and E. of ca. 15° W. ...	ca. 5
Mediterranean W. of 3° W and Straits of Gibraltar	„ 60
„ E. of 3° W. ...	„ 5
Messina (collections between March 1911–May 1912)	„ 3

Atlantic eels all belong to the same species. Further, Cand. Strubberg has counted the vertebrae in 2000 specimens from the Atlantic and 1000 from the Mediterranean, and found as average number for the former 114'731, for the latter 114'736, thus complete agreement, and there is nothing to oppose the view that the Mediterranean eels come from the Atlantic. (4) The eel larvæ which I have taken in the Mediterranean measure 60–85 mm., those of Grassi were 60–77 mm. This good agreement, based on a large number of specimens taken throughout the year, shows that the Mediterranean larvæ are older, almost or quite full-grown specimens—a condition very different from what we

find far out in the Atlantic, where all the larvæ obtained are less than 60 mm. (see Table and Fig. 2).

This positive evidence that the eel larvæ are carried into the Mediterranean from the Atlantic may be supplemented by the negative. In spite of our excellent apparatus and numerous stations at all times of the year, we have never found larvæ or eggs of the eel in the Mediterranean. Nor have other investigators found them; the eggs and larvæ which Grassi (latest in 1910) referred with much doubt to the eel belong to other species, as I have been able to show in my detailed work which has just been published.

Altogether, the result is that *the stock of eels in the Mediterranean comes from the Atlantic*. Just as from the North Sea, Baltic, and northern Norway, the maturing eels must migrate out of the Mediterranean—even from its most eastern parts—to spawn in the Atlantic, and thereafter probably die. 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 be in the Northern Atlantic*.

Confirmation of this conclusion has been obtained from two different sides. On a cruise over the Atlantic in 1910 with the *Michael Sars*, Dr. Hjort has taken twenty-one eel larvæ south of the Azores, the majority of which were 1, a few even 2 cm. smaller than the smallest I had found west of Europe in 1905–6. This was a most important discovery. Further, surface collections made by Danish vessels crossing the Atlantic, both fifty years ago and recently, have yielded a large material of these young larvæ. Our captures are shown on the chart, Fig. 2, from which it will be seen that *larvæ of the genus Anguilla occur across the*

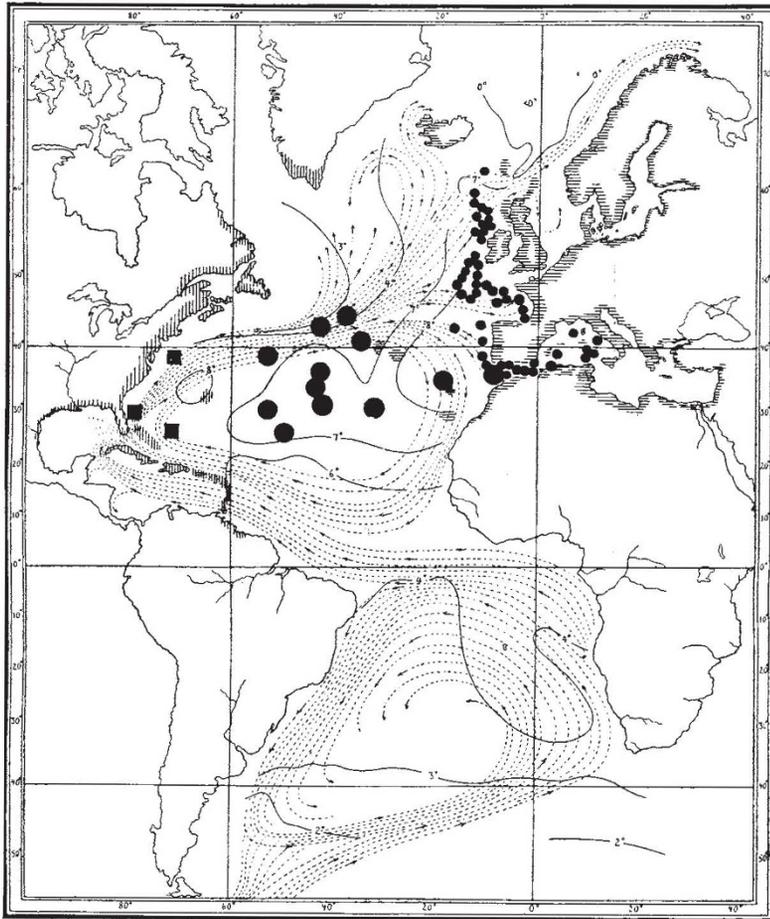


FIG. 2.—Distribution of the freshwater eels (*Anguilla*) and of their larvæ in the Atlantic regions, according to Danish investigations. Occurrence of *Anguilla vulgaris* shown by horizontal, of *Anguilla rostrata* by vertical, shading of the coasts. ● Younger (3½–6 cm.) and ● older (>6 cm.) larvæ of *Anguilla vulgaris*, ■ larvæ of *Anguilla rostrata* recorded. The unbroken lines indicate the temperature at 1000 m. depth.—Johs. Schmidt (1909 and 1912).

(2) The elver fishing, such as we know in the rivers of West Europe, is in the Mediterranean only carried on in the western basin (West Italy), not further to the east. Just as in North Europe this indicates that the elvers decrease in quantity from west to east, and in the same way we may compare the scarcity or absence of eels in the Black Sea region with the similar condition in the inner Baltic or northernmost Norway. (3) A very extensive investigation has given the result that the North European, South European, and

whole of the North Atlantic between ca. 25° and ca. 45° N.L. Of these the specimens from west of ca. 20° W. were the smallest in size, namely, $3\frac{1}{2}$ –6 cm.

To make quite certain of the forms we were dealing with, it has been necessary to examine thousands of eels, not only from the continents, but also from all the Atlantic islands where the eel occurs (Iceland, Faeroes, Madeira, Canaries, Azores, Bermudas, and the West Indies). The result is also shown on Fig. 2. There are only two species of eel in the North Atlantic region, an eastern (*A. vulgaris*), which has its western limit at the Azores, and a western (*A. rostrata*). A further result has been that the stocks are practically unmixed, each being restricted to its own region. On counting the vertebræ (myomeres) in our larvæ from the Atlantic, we were now able to prove that only the larvæ taken west of the Bermudas belonged to *A. rostrata*, whilst larvæ of *A. vulgaris* were found in large quantities as far west as 53° W.L.—though, as mentioned, the western limit of the adult is at the Azores, ca. 30° W. The larvæ may even occur further west.

The question is, now, whether we can prove that the smaller larvæ ($3\frac{1}{2}$ –6 cm.) from the central part of the Atlantic are the product of the main stock of *A. vulgaris*, which lives on the European continent. It might be thought, for example, that the larvæ found near the Azores come from the stock living on those islands; but, fortunately, we have now obtained from the Gulf Stream south of Newfoundland, 53° W., such a large number of half-grown larvæ that the quantity alone seems to exclude the possibility that they can spring from the inconsiderable stocks on the Azores or other Atlantic islands. The distance from Europe of the place in the Gulf Stream where they were found, is ca. 2000 miles, but there can be no doubt that they traverse this distance with the currents, for we have found the intermediate stages on the way, and another species, *Synphobranchus pinnatus*, whose full-grown larvæ are found in quantities west of Europe in company with those of the eel, has the same distribution.

We see from the Chart and Table how the larvæ of *A. vulgaris* are distributed in a very characteristic manner according to age or size, over the whole of an enormous area, by comparison with which the distances in the Mediterranean seem small. We have not yet attained to the full solution of the exceedingly difficult eel problem, but the steady progress of the last twenty years is full of promise for the future. We cannot say exactly where the eel spawns, though the Sargasso Sea is perhaps a principal spawning region, but continued collections and investigation of the currents will assuredly lead to the discovery of the eggs and earliest larvæ, perhaps not in deep water, as Grassi imagined, but nearer to the surface. There is even perhaps reason to believe that the eel spawns in the intermediate layers and not on the bottom. Altogether, the whole story of the eel and its spawning has come to read almost like a romance, wherein reality has far exceeded the dreams of phantasy.

JOHS. SCHMIDT.

THE FIFTH INTERNATIONAL CONGRESS OF MATHEMATICIANS.

THE International Congress of Mathematicians, which meets in Cambridge on August 22, is the fifth of a series inaugurated at Zürich in 1897 and continued in Paris, 1900, Heidelberg, 1904, and Rome, 1908. The inviting body is the Cambridge Philosophical Society, and the project of receiving the fifth Congress at Cambridge has been well supported, not only by Cambridge men, resident and non-resident, but also by others, in Oxford and in the country generally, who are interested in the progress of mathematics.

The congress is organised in four sections, devoted respectively to analysis, geometry, applied mathematics, and philosophical, historical, and didactical questions. The Section of Applied Mathematics is divided into two departments, one dealing with mathematical physics and astronomy, and the other with economics and statistics. Each section appoints its own chairman from day to day, the chairman for the first day being chosen by an international committee from among those persons who, in the preparation for the congress, have been charged with the duty of collecting papers for the sections. The sections also appoint their own secretaries. The work of preparation has been in the hands of an organising committee, presided over by Sir George Darwin, and having as treasurer Sir Joseph Larmor, and as secretaries Prof. E. W. Hobson, of Cambridge, and Prof. A. E. H. Love, of Oxford.

Owing to the great interest which is now taken in the study of improved methods of teaching, the department dealing with didactical questions has attracted to the congress many adherents interested in questions concerning the teaching of mathematics. Associated with this department is an international commission appointed at Rome four years ago to collect information in regard to the methods pursued in various countries, and to study the directions and effects of recent changes. In Great Britain the work of collecting this information has been done by an advisory committee of the Board of Education, and the information has been incorporated in a series of reports issued by the Board and now collected in two large volumes. These are intended for presentation to the congress, and similar reports have been compiled with the same view in Germany and the other countries.

In addition to the sectional meetings of the congress, there will be plenary sessions, at which lectures will be delivered, as follows:—"Boundary problems in one dimension," by Prof. M. Bôcher, of Harvard; "Définition et domaine d'existence des fonctions monogènes uniformes," by Prof. E. Borel, of Paris; "Periodicity in the solar system," by Prof. E. W. Brown, of Yale; "Il significato della critica dei principii nello sviluppo delle matematiche," by Prof. F. Enriques, of Bologna; "The principles of instrumental seismology," by Prince B. Galitzin, of St. Petersburg; "Gelöste und ungelöste Probleme aus der Theorie der Primzahlverteilung und der Riemannschen Zeta-