A re-examination of Johannes Schmidt's Atlantic eel investigations

Jan Boëtius
The Danish Institute for Fisheries and Marine Research,
Charlottenlund Castle, DK-2920 Charlottenlund, Denmark

E.F. Harding
Statistical Laboratory, Cambridge University,
16 Mill Lane, Cambridge CB2 1SB, U.K.

> '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 larvae 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 larvae in all parts of the sea, it would hardly be possible to form definite conclusions as to the origins of the eels of our European continent.'
>
> *(Johs. Schmidt, 1922, page 186)*

Contents

Summary and overview

Schmidt's account of the breeding of the two Atlantic *Anguilla* species is reviewed, using his own extensive data on larval captures published for the first time in this volume. The review traces Schmidt's own steps exactly, and where crucial decisions were made these are critically examined. Following the Introduction (Section

1) and overview of Materials (Section 2), Section 3 gives a purely descriptive historical outline of the series of investigations leading to the definitive 1922 paper, and refers to fundamental criticisms since 1959.

In order not to break the flow of the main critique, Section 4 discusses Schmidt's morphometric work on vertebra and myomere counts. The vertebra investigations were important at a relatively early stage in supporting a decision that the entire European eel spawning took place in the Atlantic; these are discussed under 4A (Vertebra investigations). The myomere investigations were chiefly crucial for species identification of larvae taken in the open Atlantic; they are discussed under 4B (Myomere investigations), and related to the work on vertebrae.
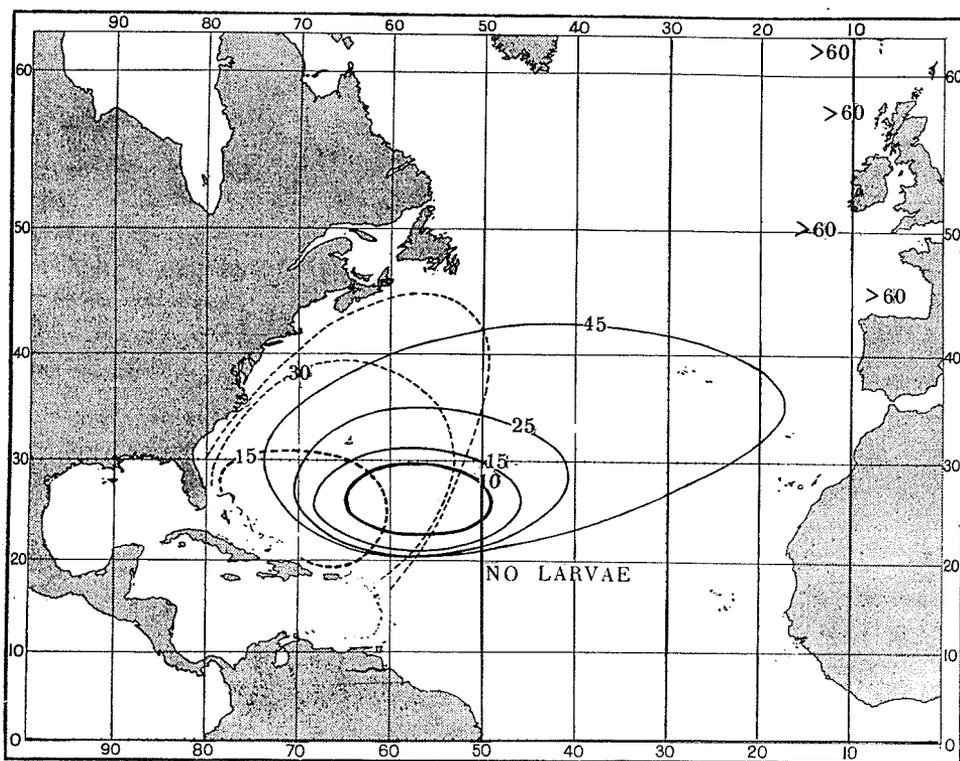

Fig. 1. Schmidt's chart showing the distribution of sizes of larvae captured in the Atlantic, based mainly on data to hand in 1920. 'The curves show limits of occurrence, i.e. specimens less than 25 mm in length have only been found inside the 25 mm curve, etc.' (Reproduced from fig. 4 of Schmidt (1922).)

Our main work begins at Section 5, which reviews the logic of Schmidt's investigations. First we go over the historical account, considering implications of the distributions of effort and of sizes of larvae caught. Schmidt's case rests on the chart of closed curves for captures of larvae of different sizes (reproduced here as Fig. 1), and in this section we prepare the ground for examining the validity of these as indicators of occurrence of larvae in the sea. At the end of the section are

considered the Mediterranean larval catches (chiefly relevant to an early stage in Schmidt's investigations), and we also raise the issue of Schmidt's solution (a kind of necessary afterthought to his main thesis) to the problem arising from the catch of both species together in the hypothesized spawning area.

The remaining sections are devoted to deeper analysis of the main issues raised in Section 5. First, Section 6 sets out the salient features of the distribution of effort in time and space.

Section 7 takes up the 'both-species' problem and Schmidt's solution in terms of hypothetical differential growth rates and durations of larval life. It is established that there is no basis for supposing that the two species differ in growth rate.

Section 8 is the first of two that investigate whether Schmidt's claim to have circumscribed the occurrence of the smallest larvae is well founded on adequate negative results. It is shown, in rather general terms, that effort outside the central area was largely inadequate and that the length curves of the published chart are such as might be expected from the distribution of effort alone. ·

Section 9 pursues the same question in more rigorous terms by formulating a precisely stated null hypothesis to the effect that the length curves are artefactual. This hypothesis is tested against relevant data (details in the Appendix), and it is shown that while the North-South boundary is apparently valid, no East-West boundary to the occurrence of the smallest larvae can be discerned.

Finally, Section 10 summarizes the main results and conclusions established in this paper.

1. Introduction

Motivated by the controversy begun by Tucker (1959) over the spawning of the European eel (*Anguilla anguilla*), and realising that such conflict between hypotheses can only be resolved by reference to data, we have collated the largely unpublished corpus of data collected by Johannes Schmidt during his 25 years of researches into the matter. The data are published in the present volume (see next section).

Our original and no doubt ambitious hope was that detailed examination of the Schmidt data, which were not available to Tucker, might suffice to resolve the controversy over whether the European eel indeed succeeds in spawning in the open ocean. It became clear that, of itself, it would not.

Even assuming that the European eel does so spawn, however, many problems remain with Schmidt's account of the process. According to Schmidt, the European population is homogenous and originates from a single spawning-ground in the South-West Sargasso Sea, to which European adults migrate. The American eel (*A. rostrata*) is a distinct species which also spawns in the same area. The larvae are supposed to drift coastwards on major North Atlantic surface currents, and the two species segregate geographically as a result of differing times of metamorphosis of larva into elver.

Difficulties have been found for all these points, countertheories have been raised against some, and other have been said to lack foundation. Chapter 5 of the

book by Harden Jones (1968) gives an excellent summary. No adult eels have ever been caught in the open Atlantic nor eggs definitely identified in the wild. Migration routes and spawning conditions for adults are unknown or conjectural, as are many details of the development, feeding and growth of larvae. Mechanisms for species separation during larval migration are speculative, and details of larval migration or drift are uncertain.

Even with access to Schmidt's data it became clear that many of the above problems remain, and will require further research. The best contribution we can make at present to defining the scope and purpose of such future research is, we believe, to re-examine Schmidt's published account of the spawning of the eel in the light of his own data. Our primary 'target' is his 1922 publication 'The Breeding Places of the Eel', because it is fairly clear to us, from Schmidt's own publications and from internal evidence in the now published Schmidt data, what observations had been taken into account for this publication. It is much less clear how much of the data that was in principle available at the various times was actually considered for later versions of the same story (Schmidt 1925, 1935); there are many indications that not all the data had been worked up, nor was it all used.

We stress that this study is not an attempt to revise the scientific status of the eel 'spawning question' in the light of all the information available in 1985, together with the newly available data from the Schmidt era. It is strictly an examination of the Schmidt thesis of 1922, and it could have been made at any time after 1922 if the available data had been published. That thesis was definitive for 40 years, is in its own terms complete, and has dominated almost all research ever since. If the 'spawning question' is to be objectively reconsidered as a whole, that is where we must begin.

Nonetheless, we have every intention of pursuing our studies into later periods in future work, taking subsequent data into account according to its availability at the time.

In this re-examination, we take account of what Schmidt had to say about both *Anguilla anguilla* and *A. rostrata*. However, our primary interest is the Schmidt theory of the breeding place of *A. anguilla*, and we are chiefly concerned with *A. rostrata* considerations only in so far as they influenced Schmidt's conclusions for *A. anguilla*.

We use mainly data up to 1922 because this was practically the whole basis for the theory thenceforth accepted. The essentials of the theory were never changed, and Schmidt himself did not much extend its empirical basis in later years.

We make very little reference to the data for catches near the coast of Europe, or in the Mediterranean, since they have little bearing on conclusions that may be drawn about the open Atlantic.

2. Materials

Our primary material is the collection of hitherto unpublished data which appears in this volume as 'List of Atlantic and Mediterranean *Anguilla* leptocephali: Danish material up to 1966' (hereafter called LAMA) (Boëtius & Harding 1985). Our

sources are described in the Introduction to LAMA. In addition, we naturally depend heavily on data and arguments given by Schmidt in his many publications (see References) and, in particular, on the published Lists of Stations (References I, (1)-(6)).

The material includes data regarding the lengths, and the places, times and circumstances of capture, of all leptocephali of *Anguilla anguilla* and *A. rostrata* in the Danish collections which we have been able to trace (some 19 800 in all). We have also included available data on total numbers of myomeres (TNM) for those specimens where a definite myomere count was noted in the Protocols (see the Introduction to LAMA), which in practice mean only for larvae at least 20 mm long. It appears that TNM counts were recorded for very few (84 in all) of the larvae caught East of 40°W.

Our primary purpose is to examine critically the basis for the announcement by Johannes Schmidt (1922) of his classical theory regarding the breeding places of the Atlantic *Anguilla* species. From the LAMA, which is in chronological order, it can be determined that this theory rests essentially on the material up to mid-1921 ('Dana I' Station 952, 1921.05.13). In subsequent publications, Schmidt modified his account only in minor details, and the later LAMA data do not much extend the coverage, in space or in time, of the earlier investigations.

3. Historical summary

We give a terse résumé of the investigations culminating in 'The Breeding Places of the Eel' (Schmidt 1922). They fall into a series of well-defined stages, and it is important to realise that to Schmidt these stages constituted a logical progression (see, for instance, Reference I(5), page 8). Crucial questions are discussed in subsequent sections.

(1) The empirical confirmation that *Leptocephalus brevirostris* is the larva of *A. anguilla* (Grassi & Calandruccio 1894, 1897; Grassi 1896), and the inference that eels from Mediterranean fresh-waters probably reproduced in the deep waters of that sea. This inference is accepted by Schmidt (1906, p. 184).

(2) Schmidt captures in 1904, South of Iceland ('Thor' Station 100(04), 1904.05.22), the first recognised *A. anguilla* larva in the Atlantic. In 1904-1905 he seeks and finds larvae along the edge of the North European continental shelf (Schmidt 1906). He concludes that eels from Atlantic fresh-waters spawn in the Atlantic, and 'far out from the coasts' (loc. cit. p. 188). The observation, that the 1000 metre depth contour is an apparent Eastern limit for the occurrence of leptocephali, is peculiar and significant.

(3) From 1906 to 1912, two parallel investigations are pursued. In one, morphological studies of eel samples from all over Europe, and from some places in the U.S., convince Schmidt that the European and American eels (*A. anguilla* and *A. rostrata*) are distinct species, and that, most importantly, the European eel does not display in the slightest degree the minor geographical differences that are normal between local races with different spawning grounds (Schmidt 1912, 1913).

In the other, owing to the limited cruising range of the 'Thor', Schmidt visits the Mediterranean in the winter of 1908-09 and the summer of 1910. On both occasions he fails to find small *Anguilla* larvae, and concludes that there is no spawning in the Mediterranean (Schmidt 1912, p. 321). In our opinion, this is a crucial conclusion on Schmidt's part. Henceforth he is convinced that the entire European eel population must spawn in the open Atlantic Ocean. He is still, however, of the opinion that the spawning area is likely to be very widely spread (Schmidt 1912, p. 336). By now (cruise of the 'Michael Sars', 1910, and catches by 'Ingolf', 1911), larvae much smaller than full size have been found far out in the Central North Atlantic (Hjort 1910; Schmidt 1912, pp. 323, 335; Lea 1913. See also the LAMA, 'Ingolf' Stations 257, 259).

(4) Starting in 1911, still limited by the range of the 'Thor', he enlists the help of Danish Commercial and Navy ships to make casual tows in the Atlantic and Mediterranean. This series continues until 1915. In 1913, he obtains the schooner 'Margrethe' and makes a transect across the Atlantic from N. Europe to the West Indies. Though the great majority of larvae exceed 35 mm length, a few stations find the eagerly sought smaller larvae:

AGENT PETERSEN	765	1913.06.25	30°N 65°W	(26 mm)
MARGRETHE	1037	1913.10.13	25°N 52°W	(24 mm)
	1038	1913.10.14	25°N 52°W	(22 mm)
	1039	1913.10.18	27°N 54°W	(25 mm)
	1040	1913.10.20	28°N 55°W	(17 mm)
SAMUI	788	1914.05.07	29°N 51°W	(16 mm)
	789	1914.05.08	26°N 55°W	(9-21 mm)
	793	1914.06.11	26°N 56°W	(13-26 mm)
	794	1914.06.12	28°N 53°W	(15-19 mm)
BINTANG	773	1914.05.12	28°N 53°W	(13 mm)
	813	1915.07.11	24°N 52°W	(9-36 mm)
TRANQUEBAR	818	1915.05.22	20°N 57°W	(21 mm)

At the same time, Schmidt has his first encounter with the unexpected difficulty that larvae of both *A. anguilla* and *A. rostrata* are taken at the same station (indeed in the same net):

MARGRETHE	1027	1913.09.26	40°N 52°W

In December 1913, on Anegada Island in the West Indies, the 'Margrethe' is, however, wrecked and from 1914 to 1918 the World War supervenes. No investigations at sea occur from 1915 to 1920.

(5) In 1920, research resumes in the 'Dana I', and effort is concentrated on the area where the smallest larvae have been found. very large numbers of larvae, many of them less than 10 mm in length, are taken (see especially 'Dana I' Station 855) in June and July 1920. These form the raw material for 'The Breeding Places of the Eel' (Schmidt 1922), which is received by the Royal Society of London on 8 July, 1921. Here first appears the celebrated chart of closed curves, embracing

catches of ever smaller larvae, which will become the definitive delineation of the spawning grounds of the European eel (reproduced here, Fig. 1). Also, in its final form, appears the hypothetical mechanism (different durations of the larval stage) which Schmidt used to explain the separation of the two species (Schmidt 1922, pp. 198-199 and 203-204).

(6) In 1921, the 'Dana' again investigates the same region in March and April. Qualitatively similar results are obtained, but these are not available for the 1922 paper (Schmidt 1922, pp. 193-194). Further investigations were made in the 'Dana I' and 'Dana II' (1921-24). However, the revision of the 1922 paper published by the Smithsonian Institute (Schmidt 1925, but ready in 1924) is still based essentially on the data to hand in 1920, though some further details have been added, based on later data (1920-1922) incompletely worked up (loc. cit. p. 279).

(7) In 1932 appears 'Danish Eel Investigations during 25 years' (Schmidt 1935, posth.). Here is the final version of the chart, very little different. The great circumnavigation in the 'Dana II' has been completed (1928-1930), and further data from the Atlantic have been obtained in 1931.

Clearly, then, Schmidt's account of the spawning was essentially in final form by 1922, and depended for its detail on the data available by 1920. The conclusions were extensively cited, and even generalised (see for instance Bertin, 1956), for nearly 40 years, apparently without a single attempt to judge their empirical basis. Even today, the outstanding exceptions are the famous challenge by Tucker (1959), and the very well-balanced fundamental critique by Harden Jones (1968, Chapter 5).

   Schmidt's practices in publication of primary data differed, before and after the Great War. Prior to 1916, most of his major publications contained extensive, sometimes complete, listings of the relevant data available at the time. The publications describing the 'breeding grounds' (1922 onwards), on the other hand, cite details only of selected samples for illustrative purposes; the fundamental assertions underlying the theory rest on very little published evidence.

4. Vertebra and myomere investigations

We discuss here Schmidt's investigations into Total Number of Vertebrae (TNV), reported chiefly in Schmidt (1912, 1913, 1915) and mainly concerning the homogeneity of the European eel population, and also the available data on Total Number of Myomeres (TNM), of which very little was ever published or discussed by Schmidt.

4A. *Vertebra investigations*

The TNV count was first used by Schmidt (1906, p. 239 ff) to confirm and make precise its value for distinguishing between the European (*A. anguilla*) and American (*A. rostrata*) species. From 1906 to 1912, extensive further European material was obtained and counted for TNV (Schmidt 1913), and used to study the geographical variation of this character over the whole European seaboard (Schmidt

1912, 1913). This work is discussed in detail in this volume by Harding (1985); the results are summarized below.

The first striking result (Schmidt 1912, p. 324) is that ca. 1000 'Mediterranean' eels had mean TNV of 114.736, 1700 'Atlantic' eels a mean TNV of 114.731; 'a more complete agreement could hardly have been imagined', says Schmidt, 'and we see, that there is absolutely nothing in the way of our conclusion, that the Mediterranean eels come from the Atlantic. At the same time, these results give the first evidence that only one species of *Anguilla* occurs in North and South Europe ...'. The later, definitive publication (Schmidt 1913) lists the 16 samples in detail and it appears that there is very little variability over the whole of Europe. The significance of this extreme agreement is discussed by Harding (1985).

Boëtius (1980) has studied original records of TNV counts made by Schmidt (some never published), and has counted vertebrae of hitherto uncounted specimens preserved in the Schmidt collections, amounting to several thousand specimens in all. He finds that there are present specimens (known to Schmidt for the counted samples) whose TNV (at 106, 107 or 108) was typical of the American eel, *A. rostrata*. (Schmidt (1912, p. 337) refers briefly to such specimens.) Similar specimens were found in later samples from Denmark and Iceland (Boëtius 1976, 1980). Mean TNV also varied somewhat according to developmental stage, and geographical location. It is concluded: (a) that the European eel is not homogenous for TNV to the extent claimed by Schmidt, Northern eels having slightly lower TNV than Southern; (b) that there is present in Europe a small but definite proportion (2 per 1000) that satisfy the criteria for *A. rostrata*, or are intermediate.

In addition, Harding (1985) has studied in detail some large samples from Højer in Denmark (Boëtius 1976), and finds evidence that two, possibly three, distinct groups are present. He also finds, from Boëtius (1980), that samples not counted or published by Schmidt were more variable than the published samples. Taking all the evidence together, Schmidt's claim of the extreme homogeneity of the European eel appears as an unjustified overstatement. We have no opinion as to whether the observed variability is consistent with a unique spawning area and a homogenous re-distribution of the offspring.

4B, *Myomere investigations*

Schmidt systematically made TNM (myomere) counts on larvae taken west of 40°W, for species identification. This counting is a notoriously tricky operation, especially with smaller larvae (where myomeres are incompletely differentiated) and there is evidence that different workers adopt different conventions and follow different practices in determining doubtful cases. In our work, we have considered only larvae where Schmidt has recorded a definite count (see above). The only statement we have found about a principle of counting presumably adopted by Schmidt is that given by Jespersen (1942, p. 9).

We have studied a possible relation between length and TNM. While we find a certain correlation in some samples, it is not clear or consistent.

A more valuable conclusion can be drawn by comparing histograms of TNM counts for both species with TNV counts for the adult eels. Allowing for a possible
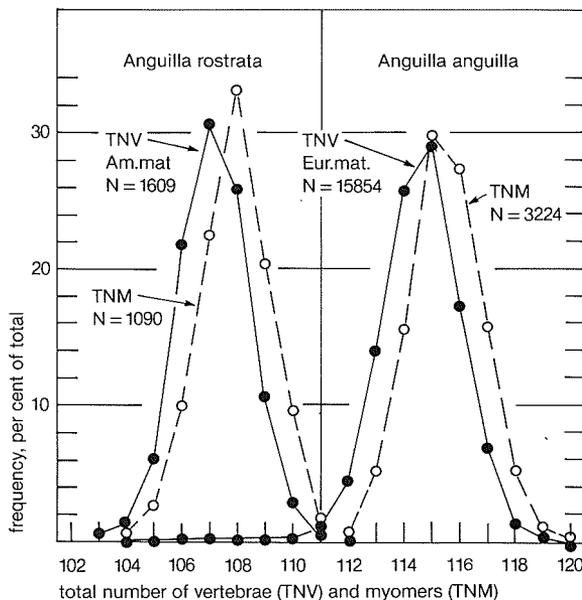
Fig. 2. Histograms showing distributions of total numbers of vertebrae (TNV, elvers and adults) and myomeres (TNM, leptocephali) in the two Atlantic *Anguilla* species. The TNV-data are from Boëtius (1980), the TNM-data are compiled from the LAMA-list in this volume. Leptocephali with TNM $\geqq 112$ are considered *A. anguilla*.

systematic difference between the two characters, estimated by Jespersen (1942, p. 10) at about 1 myomere more than the vertebrae, the close agreement between TNM and TNV histograms (Fig. 2) suggests that, on the assumption that the larvae represent two species, TNM is a good basis for identification (at any rate for larvae greater than a certain size). There is a danger, however, in this work that the known distributions for the easily-counted TNV of eels may become normative for the TNM of larvae, more liable to subjective interpretation.

5. The logic of Schmidt's investigations

We summarize the well-documented reasoning which underlies Schmidt's classical theory, that the breeding places of the European and American eels are in 'a certain area situated in the Western Atlantic, northeast and north of the West Indies' (Schmidt 1922, p. 206; 1925, p. 313). As we have explained, this theory, and its underlying logic, were essentially in final form by 1922 and as such were generally accepted until, at any rate, 1959. Since we are concerned to examine critically to what extent Schmidt, as the creator of the theory, was justified in reaching his conclusions at the time, we shall not at this stage refer in detail to later information from any source.

The earlier and simpler stages have been covered above from the historical point of view: (1) it is known from earlier Italian work that the eel spawns in the sea, and its larvae are the leptocephali; (2) from the 'Thor' 1904 leptocephalus discovery, some eels breed in the Atlantic; (3a) from the failure ('Thor' 1908-1910) to capture tiny larvae, probably no eels breed in the Mediterranean; (3b) from the vertebra studies (1906, 1912, 1913), all European eels probably breed in the same place; (3c) from the 'Michael Sars' cruise (1910), the breeding place is probably far to the west; (4) from the catches by commercial ships (1913-1915) and 'Margrethe' (Fig. 3), small larvae (ca. 10 mm) can be caught in the southern Sargasso Sea.

Thus by 1912 Schmidt was able to formulate his general strategy for future work. 'The road is now clear for future investigations, and the discovery of every step from the smallest known larvae, 35 mm in length to the still younger stages is now mostly a question of time and money.' Schmidt (1912, p.337).

In 1920, therefore, it is easy to suppose that Schmidt could conclude that 'the' breeding area must be near where the small larvae had been caught, and had only to be searched for. Compare 'There seems but little reason to suppose, that all specimens of this fish ... are spawned within a single, very limited district inside the places where the small larvae have been taken; on the contrary, the vast extent of this area seems to indicate the reverse' (Schmidt 1912, p.336), with 'In the Sargasso Sea the newly hatched larvae of our eel were found, and with the aid of numerous fishing experiments we had been able to determine their distribution and settle conclusively that they are found in an area to the north-east of St Thomas and south-east of the Bermudas and nowhere else'. ('og *udelukkende* dér') (Schmidt 1935, p.5, and Schmidt 1932, p.232). Already, as the citation at the start of this section shows, the latter conclusion was essentially finalised by 1921.

After a delay of six years, then, Schmidt took the 'Dana I' to the Sargasso Sea and, in June 1920, sailed in a complicated course around the spot (ca. 26°N, 55°W) where the 'Margrethe' had found small larvae in 1913 (Figs 4, 5, 6), as had other ships (see the list above). Apart from two typically well-grown larvae taken near Gibraltar (Stns 823, 825), none was caught on the whole transect (at about 25°N) until longitude 48°W was reached (Stn 840) – 15 stations, 47 hauls, all null.

General Caption to Figs 3-8. Catches of *Anguilla anguilla* larvae by Danish research vessels 1913-1922 in the region of the 'breeding grounds' (25°N60°W). The plotted points on the ships' tracks indicate all stations at which gear adequate for eel larvae has been used.

White circles: no larvae.

Black-and-white circles: 1 to 10 larvae.

Black circles: more than 10 larvae.

The histrograms linked to positive stations show the numbers of larvae caught per unit effort of positive hauls per station, by length, as follows:

Ordinate: Total length of larvae, mm, in size classes of 2 mm. The scale of the ordinate is one-half natural size, so that 1 mm along the ordinate represents 2 mm of larva.

Abscissa: each 10 mm (measured directly on the Fig.) parallel to the abscissa denotes 2 larvae caught at the station per unit of effort aggregated over positive hauls (negative hauls not counted). The unit of effort corresponds to a 1-metre ring net towed for 1 hour under standard conditions.
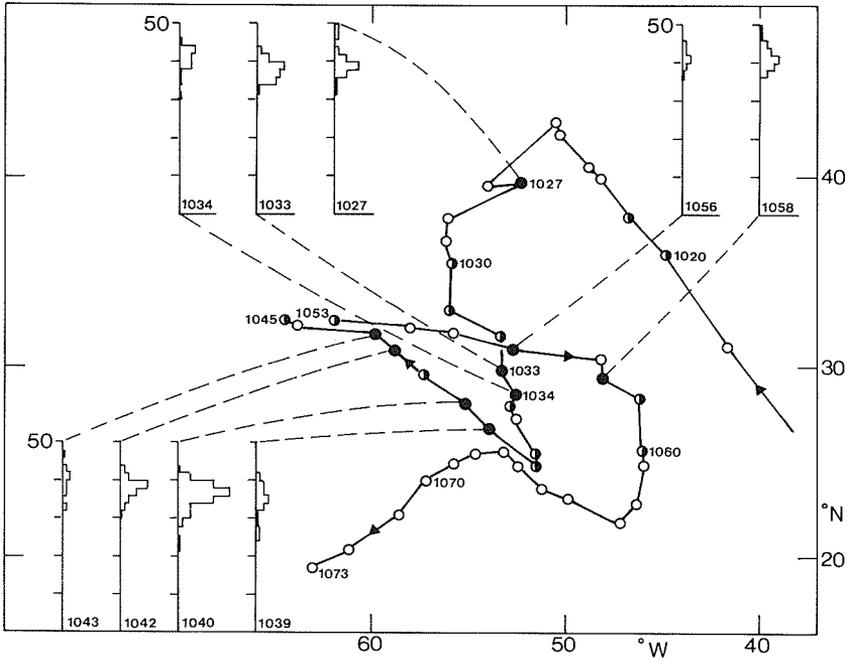
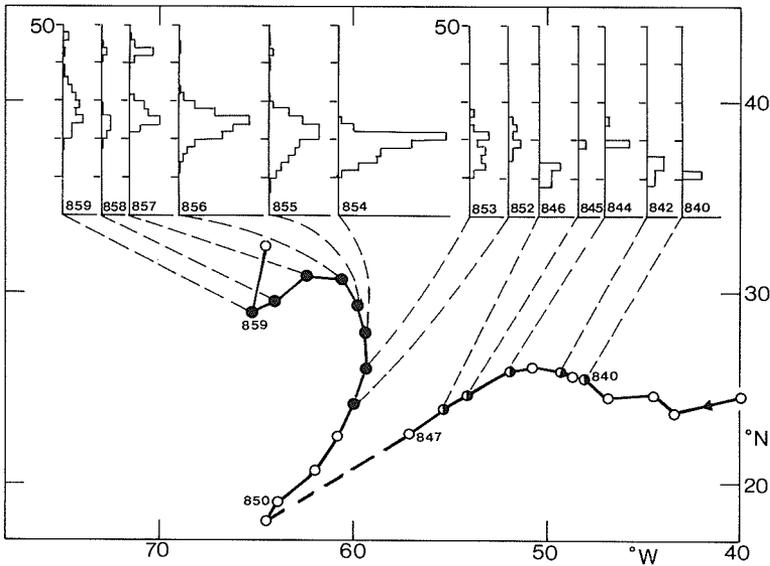Fig. 3. 'Margrethe' 1913, Stns 1019-1073, 8 Sept. to 20 Dec.

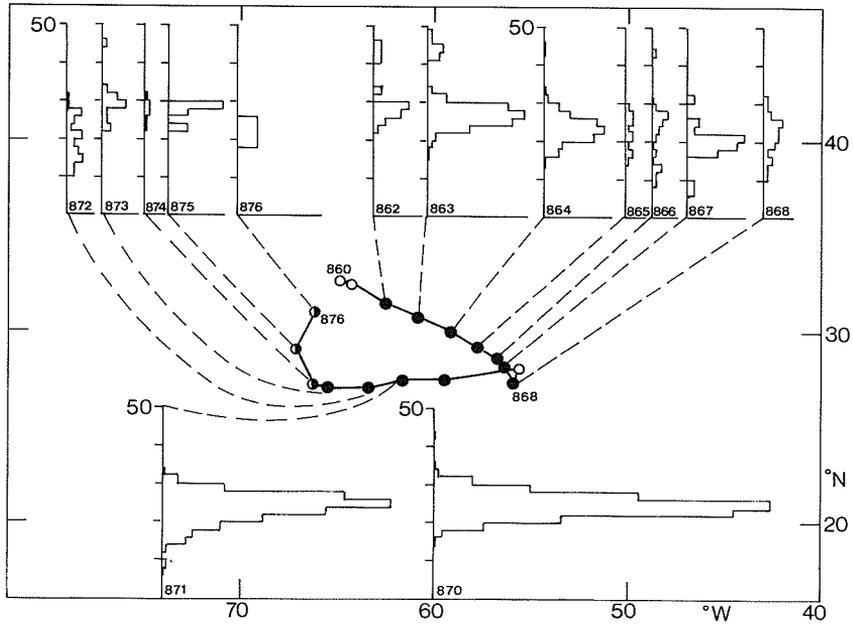Fig. 4. 'Dana I' 1920, Stns 836-860, 22 Apr.-16 June.

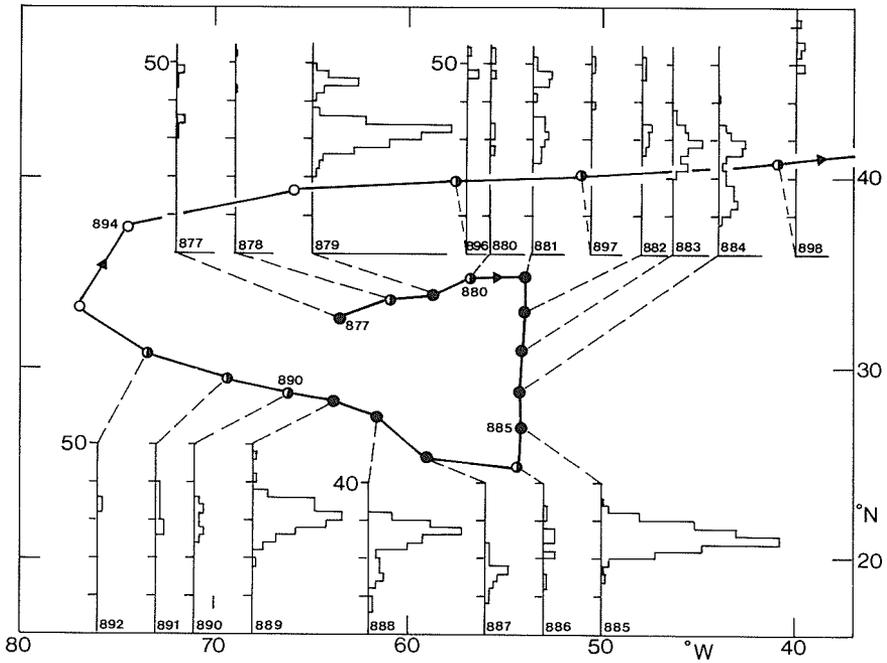Fig. 5. 'Dana I' 1920, Stns 860-876, 16 June-2 July.

Fig. 6. 'Dana I' 1920, Stns 877-898, 8 July-21 Aug.
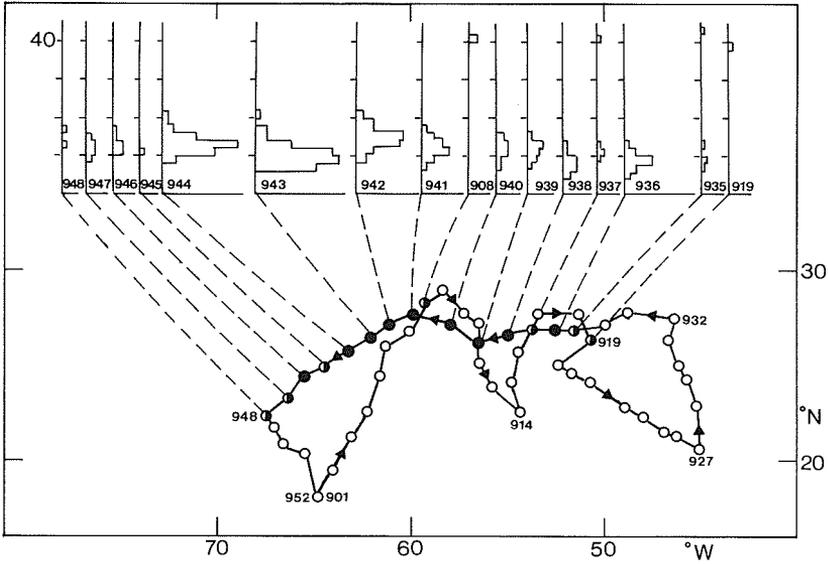
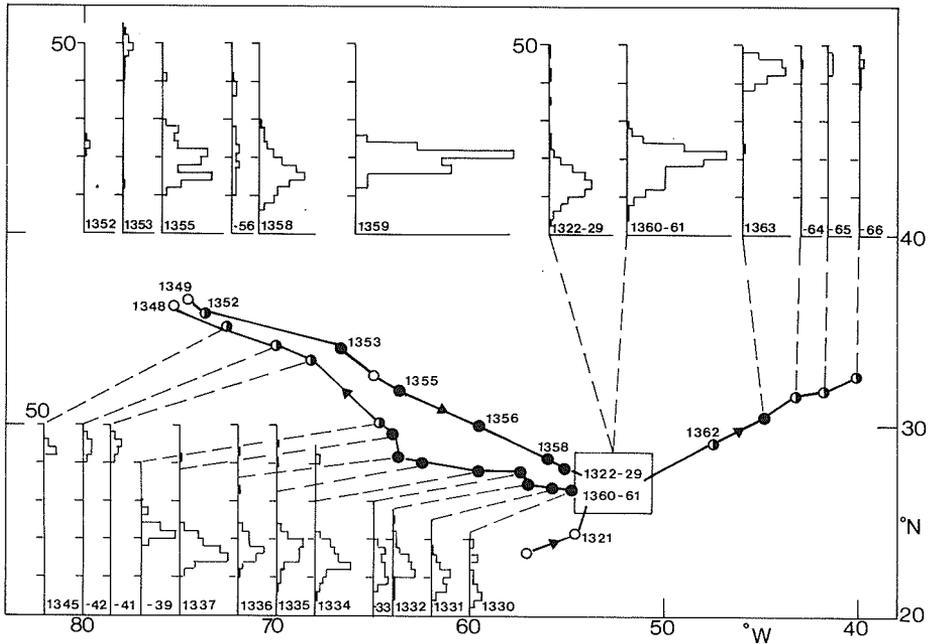Fig. 7. 'Dana I' 1921, Stns 901-952, 22 Feb.-13 May.

Fig. 8. 'Dana II' 1922, Stns 1320-1366, 22 Apr.-9 June.

Here the one specimen taken was gratifyingly small (12 mm). The next few stations (841-854) were mostly positive, and always with small larvae (9-23 mm). Then came the great Station 855 (29°N, 60°W), with 28 hauls and 1302 larvae of *A. anguilla*, many of them small and a good few from 7 to 10 mm in length. Subsequent stations (856-872, 884-888) hereabouts confirmed the presence of small larvae, though nothing like the same abundance was observed. Finally the 'Dana' moved rapidly away, taking a few stations at around 40°N before heading for home.

Here then, in a 'square' (ca. 25°-35°N, 55°-65°W) had been found good numbers of larvae which were probably only a few days old, and abundant larvae only slightly larger. The 'square', however, was delimited not by the occurrence of small larvae but by the cruise track of the 'Dana' (Figs 4, 5, 6).

The following year, from February to May 1921, the 'Dana' followed a narrow closed track centred on 27°N, 59°W (Stns 901-952) (Fig. 7). Once larvae began to be caught (Stn 935) every station was positive, sometimes abundantly (Stn 944), for very small larvae, often less than 10 mm and even down to 5 mm (Stns 936, 938). It is remarkable that a good part of the outward leg (Stns 906-919, 1921.03.02-20) and of the inward leg (Stns 934-943, 1921.04.11-22) were almost coincident, yet the former were negative and the latter positive; it is tempting to suppose that the inward leg passed through a concentration of larvae that had hatched during the intervening 3 weeks. What we now believe about their rate of growth is consistent with this hypothesis, and if it is true then, on the outward leg, Schmidt must have missed the hatching by a few days at most, possibly by hours only.

As Schmidt himself states (1922, p.193), the announcement of the 'breeding area' is founded mainly on the data from 1920 (even that not completely worked up) and earlier. The displayed evidence that it is within a definite closed curve (the '10-mm. line'), covering ca. 22°-30°N by 50°-65°W, is the diagram of contours of length (Fig. 1). He argues that only within this curve were the tiniest larvae (less than 10 mm long) found, and only within surrounding curves are larvae less than 15, 25 or 45 mm long found (loc. cit. pp.194, 199). These curves were drawn by noting on a chart the minimum length of specimens taken at each station and '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' (loc. cit. p.199). It is now but a short step to asserting that 'Here lie the breeding grounds of the eel' (pp.199, 206).

It is clear from the above descriptions that this curve also encloses the greatest concentration of effort made by Schmidt in the open Atlantic, viz. the compact region worked intensively by each expedition, to which he returned time after time (Fig. 9 and Table 1).

A diagram of this form will inevitably be obtained, as a necessary consequence of its method of construction alone and regardless of the true distribution of the small larvae, provided very small larvae are caught at one place at least. The reason is that by definition the curves corresponding to greater lengths must enclose curves corresponding to shorter lengths. It does not follow, for instance, that 45 mm larvae will be found right out to the boundary of the 45 mm curve in all
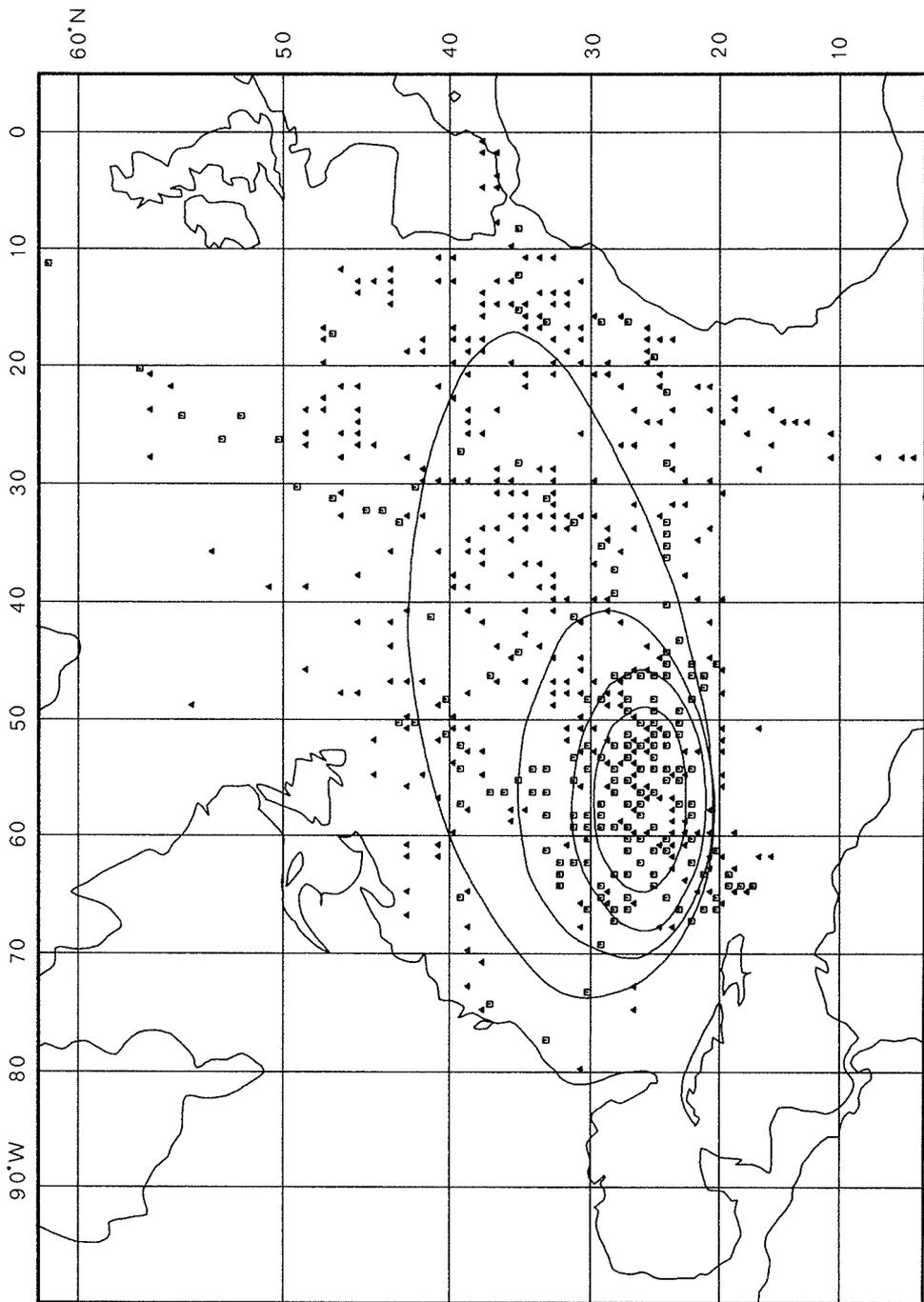
Fig. 9. Chart showing the distribution of stations taken by Danish ships west of the Greenwich meridian, 1911-May 1921 ('Dana I' Stn 952). A small triangle denotes effort by commercial ships. A square symbol denotes effort by research vessels ('Margrethe', and 'Dana I' Stns 823-952). Each symbol is nominally at the centre of a one-degree map square within which effort of the corresponding kind was made. However, for clarity, each square symbol has been displaced a quarter of a degree to the south and to the east, and each triangle a quarter of a degree to the north and to the west.

Table 1. Statistics of distribution of effort by research vessels 'Margrethe' and 'Dana I' (to station 952, 13 May 1921). Percentages of total effort distributed over the regions defined by the length curves of Fig. 1:

    I = as percentage of all effort
    II = as percentage of effort inside '45 mm' curve,

(a) at any time of year; (b) between the dates (Days 100-205) when larvae less than 10 mm are likely to be found. The unit of effort is a 100-cm ring net towed for 1 hour under standard conditions. All hauls with *Anguilla* adequate gear are counted.

	(a) At any time		(b) Days 100-205	
	I	II	I	II
Inside '10 mm'	37%	44%	50%	64%
'10-15 mm'	13%	16%	8%	10%
'15-25 mm'	16%	20%	16%	21%
'25-45 mm'	17%	20%	4%	5%
Outside '45 mm'	17%	–	22%	–

directions; in fact (see below) the 40-46 mm larvae occur well to the North (6°) of the Southern boundary and barely overlap with the occurrence of larvae of 10 mm or less. The position and size of the innermost curve will be to some extent a matter of luck — the chance of catching the tiny larvae here rather than there, given that they are present — and partly a result of the distribution of effort.

We conclude that from Schmidt's observations up to mid-1921, it can be proved only that if appropriate effort is made around 25°N, 60°W in mid-April to May, very tiny larvae of *A. anguilla* will be taken. Schmidt's subsequent expeditions, and many of those later made by others, have mainly verified that this is so.

Schmidt's observations are consistent with the breeding grounds of the European eel being as he has stated. In order to establish the hypothesis, it was at least necessary that his later investigations should have been capable of disproving it — by, say, equally intensive investigation of other areas at the appropriate time of year. This was not the case, to more than a very limited extent. Schmidt's own words from 1922, quoted above our Introduction, can hardly be bettered as commentary.

Leptocephali from the Mediterranean

In this section we give a brief survey of the data available to Schmidt from the Mediterranean, with particular reference to the thesis that spawning does not occur in that Sea.

The 1908-1910 series taken by the 'Thor' are listed in Reference I(1) as 9(08/09)-61(08/09) (1908.12.14-1909.02.21) and 98(10)-167(10) (1910.06.23-1910.08.05) followed by 179(10)-228(10) (1910.08.13-1910.09.07) (omitting a series at and East of the Dardanelles). Of these 173 stations, according to the LAMA only 21

were positive for larvae, and only 45 larvae were taken in all (of which 13 were in some stage of metamorphosis, taken in the months of December, January, February, June, July and September). The smallest non-metamorphosing larva listed is 60 mm (the same as found by Grassi (1896)). The smallest of the metamorphosing larvae was 61 mm long. This is the total known to us of Mediterranean larvae taken by Schmidt by 1912. Only stations 9(08/09) and 189-193(10) were in or at all near the Straits of Messina and no larvae were taken at any of these.

This is a very small material on which to base the 1912 conclusion that tiny larvae simply cannot be taken in the Mediterranean, and the discussion leading to this conclusion in Schmidt (1912, pp. 320-321) is worth re-reading in the light of these figures, not previously published. (We discount, for obvious reasons, the many larvae taken in non-standard circumstances by Hansen, Trombetta and Sella in 1911-13 at the Straits of Messina – see the LAMA.)

The paucity of positive stations contrasts with the abundance of larvae claimed by Grassi (1897): '... in the month of March, in the year 1895, we captured several thousand of them in one day ...' (in the Straits of Messina). It must therefore be doubted whether Schmidt's effort at the time had a significant chance of capturing smaller larvae even if they were there; his conclusion of 1912 must appear hasty, in the light of the data available at the time.

In 1921 Schmidt had a further occasion to take Mediterranean larvae: 'Dana II' stations 1117-1138 (1921.09.21-1921.10.10), and no further stations were made in the Mediterranean before the circumnavigation of 1928-30. Of these 22 stations (148 hauls), 15 were positive (78 positive hauls) and some 1100 larvae were caught (an average of 14 per positive haul, 7.4 per haul), some as short as 54 mm. No metamorphosing larvae are listed. None of these stations is near the Straits of Messina, and all are late in the year.

The 'Dana II' stations from 1928-30 in the Mediterranean are 3520-3530 (1928.07.16-1928. 07.22) and 4025-4140 (1930.04.09-1930.06.08). Of the first series (11 stations, 29 hauls) 6 were positive (7 positive hauls), yielding a mere 9 larvae in all (1.3 per positive haul), and of the second (116 stations, 683 hauls) 34 were positive (206 positive hauls). Some 770 larvae were taken (1.1 per haul, 3.7 per positive haul) in the second series. The smallest were 65 mm for the first series and 56 mm for the second (none listed as metamorphosing in either case). Stations of the latter series taken in or near the Straits of Messina are 4053-4061 (1930.05.05-1930.05.12) and 4077-4078 (1930.05.23-1930.05.24); it can only be said that there is nothing exceptional about the captures made at any of these. The low yield is notable. Only the very last series (1930) can be considered to have great bearing on whether eels spawn in the Mediterranean.

The question of Anguilla rostrata

In considering the quest for the spawning grounds of the European eel, we have ignored data on American eel larvae. We could for critical purposes proceed as if the 'eel question' were posed in its purest and simplest form. Schmidt himself would have wished that this were so. However, as we have noted above, at the very place where the smallest European larvae were taken, so too were American larvae,

sometimes also extremely small; the two were found to be well mingled over much of the 'spawning area' (see discussion of 'double stations' below) at sizes from the smallest up to ca. 45 mm (see for instance 'Dana II' Stns 859, 947). This discovery posed the problem: how is it, when the two kinds of larvae are so mingled, that in Europe there are (almost) no American eels, and in America (almost) no European? Schmidt was obliged to suggest a mechanism which would cause the two species to separate when it came to populating the fresh waters. The result was the well known proposal that the American eel larvae grow more rapidly and are ready to metamorphose much earlier, while still off the American coasts (some 12 months after hatching), while for the European eel this process takes much longer and metamorphosis cannot take place until they are near or at Europe, some three years after hatching. We have studied this question carefully in the Schmidt data, and we have concluded that this hypothesis is at best only partially consistent with the data, while in important respects it is in conflict. Even if Schmidt were partially correct, this aspect of the matter is much less simple than he appeared to believe; a section is devoted to it below. The discussion of this question by Harden Jones (1968, Ch. 5), from another point of view, is valuable.

6. The distribution of effort in time and space

The following is a review of the Schmidt expeditions yielding data which can be considered 'scientific', i.e. obtained under normal oceanographic research conditions. Except as indicated, only the region of main interest is considered, namely the North Atlantic west of 20°W.

As to the casual investigations undertaken by commercial vessels, we take the attitude that the occasional catch of small larvae is good fortune, and shows that they may be found; while failure to observe small larvae may count for very little.

The pre-war 'Margrethe' cruise left the Faroes in July 1913, arrived at the Azores in August, during August and September travelled to the Sargasso area, and investigated the south-western Sargasso (around 25°N, 50°W) during October-December ('Margrethe' Stns 1001-1073, 303 hauls; Fig. 3).

The first post-war cruise was that of the 'Dana I', leaving Gibraltar in April 1920, reaching the Caribbean in May, investigating in the south-western Sargasso area (around 30°N, 60°W) in May-June, and crossing back from New York to Europe during July and August ('Dana I' Stns 823-900, 299 hauls; Figs 4, 5, 6). Next, 'Dana I' was in the Caribbean (around 20°N, 60°W), during February-early May 1921 ('Dana I' Stns 901-952, 320 hauls; Fig. 7).

The results of the above cruises are almost the entire scientific evidence about Atlantic *Anguilla* larvae available to Schmidt for 'The Breeding Places of the Eel' (1922, written in 1921).

In October 1921, the 'Dana II' left Gibraltar, passed near the Guianas, reached the West Indies in December, then spent December and January 1922 in the Gulf of Mexico and Panama. From February to March the region from Florida through the Bahamas to the Antilles was explored. Then during April-May the ship set out to the 'centre' at 25°N, 55°W, struck out to Cape Hatteras and back to the 'centre',

and finally in June headed directly back to Europe ('Dana II' Stns 1100-1388). A very large number of hauls was made with gear adequate for eel larvae – 1310 in all (Fig. 8).

By mid-1921 the region within 20°-35°N latitude and 40°-70°W longitude had been visited in all the months of the year save January, July and August, with a special concentration of effort within 20°-30°N and 55°-65°W in the months of April, May and June.

Other parts of the North Atlantic had received only partial coverage by mid-1921:

(a) East of 40°W –
    (i) North of 30°N in July (twice) and August (twice);
    (ii) South of 30°N in April (once).
(b) West of 70°W –
    (i) North of 30°N in June (once);
    (ii) South of 20°N not at all.*
(c) From 40°W to 70°W –
    (i) North of 30°N in July and September;
    (ii) South of 20°N not at all.*
(* discounting short legs to and from port at 19°N.)

The 1921-22 cruise of 'Dana II' added the following to the above: (a)(i) in June; (a)(ii) in November; (b)(i) in May; (b)(ii) in December and January; (c)(ii) in November. In addition the 'central square' (20°-30°N, 50°-70°W) was visited yet again in May and June.

The great circumnavigation by 'Dana II' visited (a)(ii), (b)(ii) and (c)(ii) in August 1928 ('Dana II' Stns 3532-3547, 80 hauls), and added very little to the effort in the open Atlantic, though considerable effort was expended in the Mediterranean.

Finally in 1931 the 'Dana II' made a series of stations around and North of the Azores and Madeira (32°-56°N, 12°-32°W) in may and June ('Dana II' Stns 4168-4208, 321 hauls).

7. Apparent growth régime of the leptocephali

We present apparent growth information as follows. In Figs 10 & 11 we show, for the leptocephali of each species separately, distributions of sizes caught at different times of year. Sizes are grouped by 2 mm intervals, and time of year by half-month. The sizes of the circles are proportional to numbers caught. Figs 10 & 11 refer only to leptocephali caught west of 40°W (A. rostrata larvae have not been taken east of this limit). In Fig. 12 we present data for larvae of A. anguilla caught anywhere. All three Figures cover only catches made up to the end of 1922.

When the size distributions of larvae are plotted against time of capture, certain trends leap to the eye. It is plausible, but not conclusive, that these trends approximate to the true growth curve. No means was available to Schmidt for determining
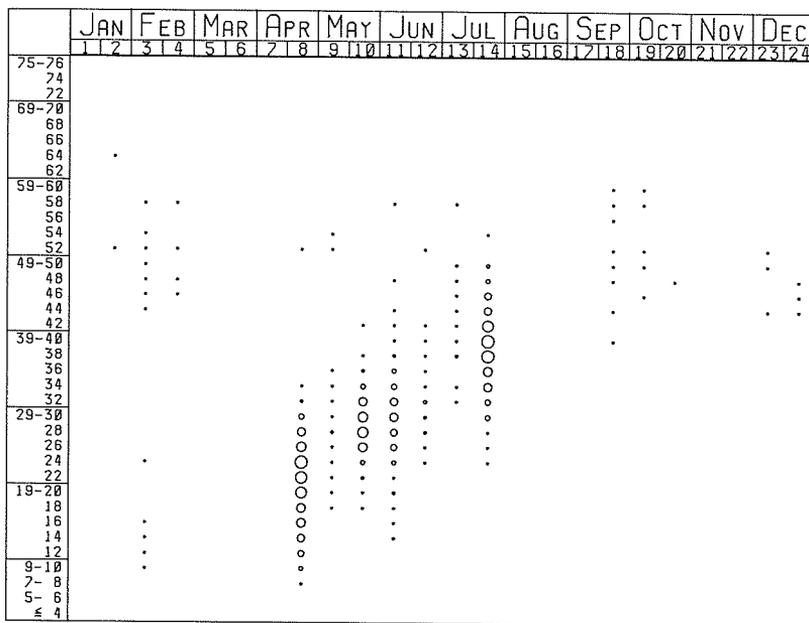
Fig. 10. *Anguilla rostrata*: length versus time of year, all Danish material up to the end of 1922 (including catches made by the U.S. research vessel 'Bache').

Ordinate: larval size in 2 mm intervals.

Abscissa: time of year in half-months (1-24).

The areas of circles are proportional to total numbers of larvae taken (largest circle corresponds to 140 larvae).

the age of a leptocephalus, and even today it has not definitely been achieved. We note the objection explicitly, since it is a fundamental one in principle and raises the usual difficulties about inferring 'longitudinal' conclusions from 'cross-sectional' data. Nonetheless, it will be seen that for the purposes of our argument the objection has little force.

For the leptocephali of *A. anguilla*, Schmidt has obtained a curve by 'plotting the lengths for the different months in a graph' (1922, p.198-199, Fig. 8; 1925, p.302-303, fig. 11). A similar curve for *A. rostrata* was never published by Schmidt, though Harden Jones (1968, p.75, fig. 20) has inferred one from such data as may be gleaned from Schmidt's publications. On comparison of the two curves it would indeed appear that 'the larvae of the American eel grow faster, and metamorphose at an earlier age and smaller size than those of the European eel.' (loc. cit.).

The above description of the method is clearly naive. Schmidt has in fact plotted length against 0-group month, or I-group month 12 months later, or II-group month 24 months later, as the case may be; and he has made the 0- or I- or II-group decision according to length, even within the same haul. In so doing he has, in our view, fallen into a subtle trap. Schmidt gives his reasons for the year-group distinctions at length in Schmidt 1922 (pp.196-198, see especially fig. 6). Observ-
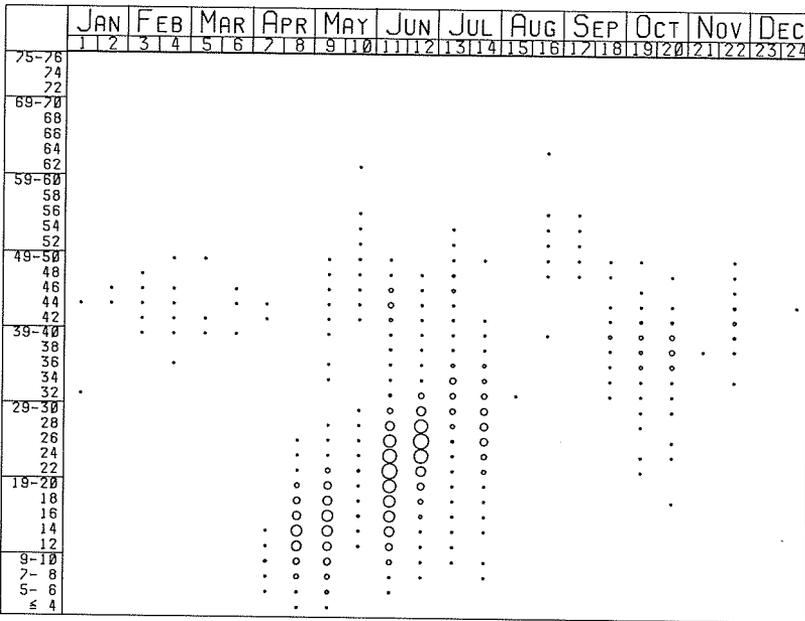
Fig. 11. *Anguilla anguilla*: length versus time of year, all Danish material up to the end of 1922 and west of 40°W. Details as for Fig. 10 (largest circle corresponds to 600 larvae).
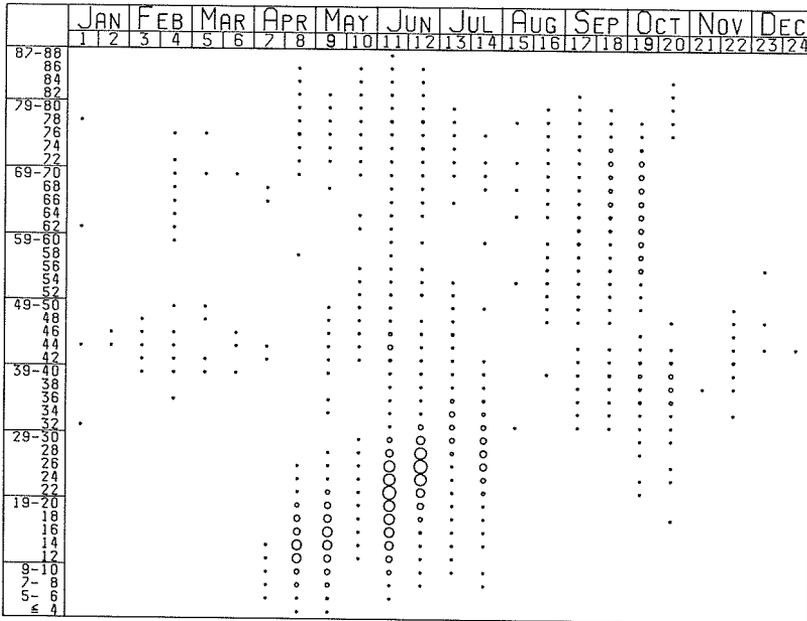

Fig. 12. *Anguilla anguilla*: length versus time of year, all Danish material up to the end of 1922, including east of 40°W and Mediterranean catches. Details as for Fig. 10 (largest circle corresponds to 600 larvae).
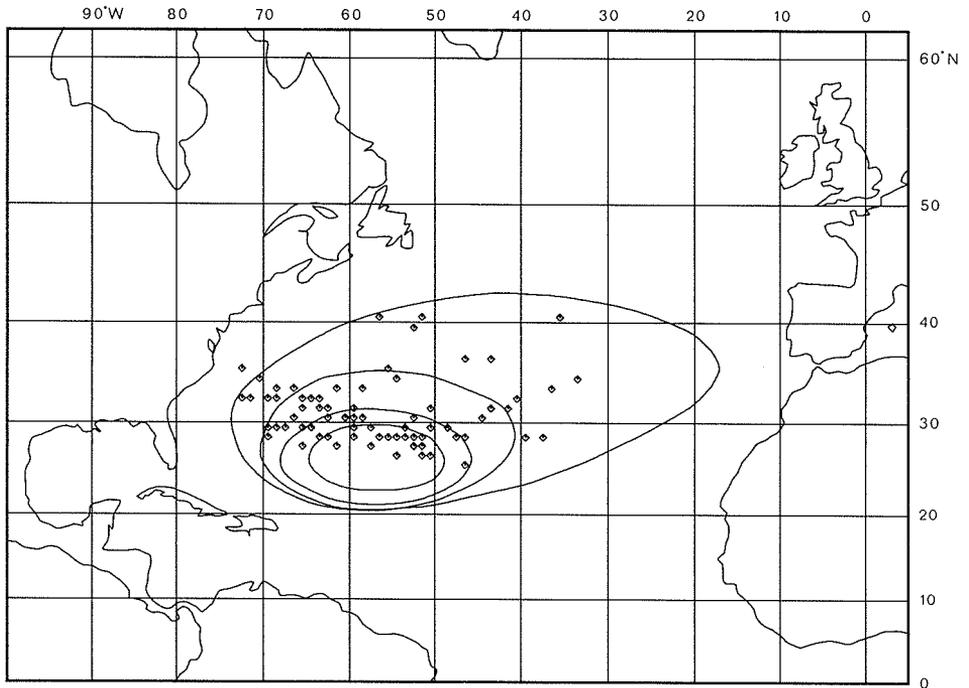
Fig. 13. Chart showing positions at which *Anguilla anguilla* larvae of length 40-46 mm were taken during Danish researches up to the end of 1922. Catches made by the U.S. research vessel 'Bache' are included. Each symbol is at the centre of a 1 degree square within which such larvae were taken.

ing that there is a distinct gap between the lengths of the '0-group' (7-37 mm) and the 'I-group' (40-50 mm), he concludes that the latter are the remainder of the previous year's 0-group 'which have not succeeded in moving any considerable distance from the breeding-grounds'.

We have plotted available data against month (simply) (Figs 10, 11, 12), and it is quite clear that Schmidt's so-called 'I-group' has a special status (see Fig. 11). These specimens, 40-50 mm long and slightly shorter at the beginning of the year than later, can clearly be found at any time of year. They are also found distributed over the North Atlantic from ca. 25-40°N and 30°-75°W (Fig. 13). For reasons associated with their distribution, we have named such larvae 'tramps'. Note that the larvae referred to above, taken by the 'Michael Sars' and the 'Ingolf', are of this size-group.

It is also clear (Fig. 12) that there is a continuum across this band of special individuals from those less than 40 mm to those greater than 50 mm. We conclude that it seems possible for the leptocephali of *A. anguilla* to grow continuously from 10 mm to 60 mm or more within a single year, and to reach a length of 80 mm within perhaps 15 months. *It is important to note that this special group, typically 40-45 mm in length, which can be found at any time and at any place within the Sargasso Sea, cannot, by the very description of their occurrence, participate in the larval growth curve according to Schmidt.*

It is worth observing that Schmidt himself (1912, pp. 335-336; 1922, pp. 187-188) has noted their presence, but without drawing the same conclusion. Their special status means that the 1910-11 captures (by 'Michael Sars' and 'Ingolf'), considered by Schmidt to be an important pointer to a possible spawning area, may have been misleading.

Accepting a nominal division of larval size distribution into '0-group' (less than 35 mm), 'I-group' (40-55 mm) and 'II-group' (over 60 mm) for May-July, without interpreting these as age-classes, we find abundant stations where '0-groups' and 'I-group' occur together. On the other hand there are very few where 'I-group' and 'II-group' occur together (and this most often in the Mediterranean, where a size-range of 55-70 mm was not uncommon).

We have made an analogous plot for the leptocephali of *A. rostrata* (Fig. 10), and we observe a similar though less clear-cut pattern.

It would appear that 'tramps' are a group of larvae which have reached a static stage of growth, and one can rather easily invent hypotheses to account for them. (a) larvae may grow in the Sargasso Sea until they reach 40-45 mm; then only larvae quitting the Sargasso area for water of a different quality may grow. (b) the main stream of larvae follow a régime of continual growth, and only those somehow trapped in special conditions remain as 'tramps'. Such hypotheses are interesting, but lack observational backing.

In considering possible growth curves, the 'tramp' phenomenon means that it is soundest to restrict attention to the larvae less than 40 mm in length. The length distributions at any time are somewhat widely spread and tend to be multimodal, so that a naive regression calculation would probably be misleading. By concentrating on the apparent modes of the size distributions we have determined that, over the range 0-40 mm, the size distribution of *A. rostrata* larvae increases at ca. 5.6 mm per month, and for *A. anguilla* larvae at ca. 5.3 mm per month.

In Fig. 14 we compare lengths of leptocephali of both species when caught in the same net ('double hauls'), again up to 1922. It is apparent from the LAMA that larvae of the same species, but different size distributions, can be caught in different nets on the same tow (no doubt because of the depth factor), so we have confined direct length comparisons to the double hauls. For *A. anguilla* larvae less than 40 mm in length it is clear that there is (to within statistical scatter) a constant difference between the two species (the hypothesis that the slope is unity not rejected – P = ca. 0.25), and the larvae of *A. rostrata* are on average 5.5 mm longer (0.3 mm S.D.). (At ca. 45 mm length, of course, the 'tramp' phenomenon causes almost complete dissociation of the length relationship.) It is not impossible that this observed constant difference for larvae caught in the same net may reflect different depth preferences of the two species.

In comparing the growth of larvae of the two species over the range 0-40 mm, we see from the above that the two apparent growth régimes are essentially parallel, the *A. rostrata* larvae having approximately a month lead. While it is more risky to continue the 'growth curves' across the 'tramps', if this is done it appears that the two species remain on parallel courses up to about 60 mm in length (Figs 10 & 11). However, it does appear that in order to grow to 70-80 mm (typical
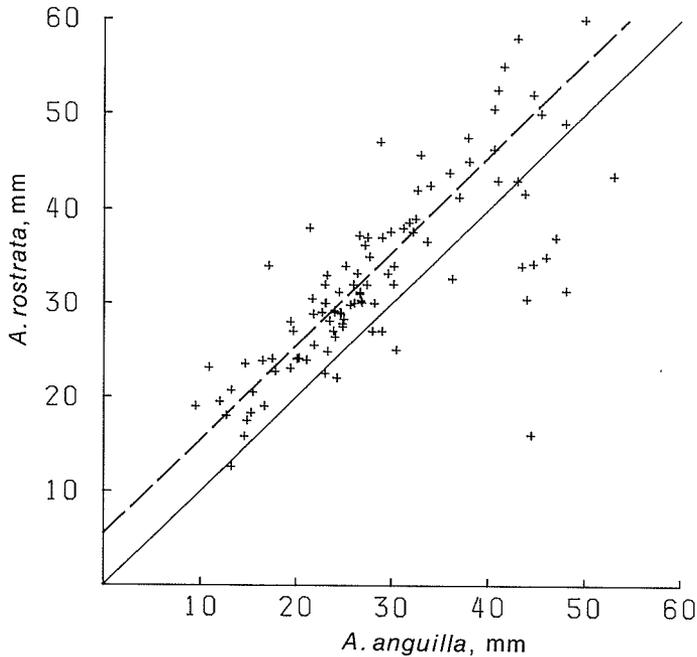
Fig. 14. Relation between lengths of *Anguilla rostrata* and *Anguilla anguilla* larvae in 'double hauls' (in which larvae of both species were taken in the same net). *Ordinate*: mean length of *A. rostrata* larvae in a haul (mm). *Abscissa*: mean length of *A. anguilla* larvae in the same haul (mm). The continuous line is the line of equal lengths; the broken line is the regression of *A. rostrata* on *A. anguilla* assuming that the slope is unity (see text).

lengths for *A. anguilla* larvae arriving at the North European continental shelf), rather more than a year may be necessary (Fig. 12).

We therefore conclude that Schmidt's proposed species separation mechanism is not implied by his own data, and even appears to conflict with it. This conclusion restores the original problem in full.

The LAMA presents data for 65 'double stations' in all (at which larvae of both species were captured). Fig. 15 shows data for the 53 taken by the end of 1922. The majority are within Schmidt's 15 mm curve and about one third are within the 10 mm curve. The greatest concentration is at the western end of the 10 mm curve. The extent of mingling can be seen by considering the four stations ('Dana I' 857, 859, 889 and 942) at which substantial numbers of larvae were taken, and the proportion of *A. rostrata* larvae is between 30 and 50 per cent. These four stations are all within, or just outside, the 10 mm curve. Over 5700 larvae are accounted for by these 'double stations', of which some 1900 are *A. rostrata*.

We cannot avoid raising the question: if no mechanism for species separation has been established, then may we assume that leptocephali – from that part of the ocean where both species are commonly caught together – will reach the coasts at all?
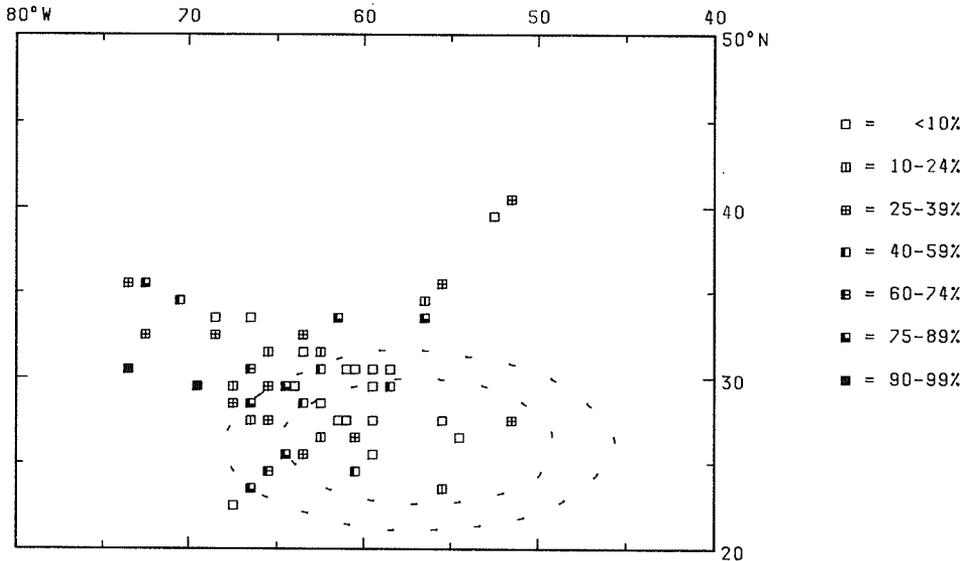
Fig. 15. Chart showing data for 'double stations' at which both *Anguilla anguilla* and *Anguilla rostrata* larvae were taken. Symbols correspond to percentages of *A. rostrata* larvae at the station. The 10 and 15 mm curves from the Schmidt chart (Fig. 1) are indicated.

8. The boundaries of the breeding grounds

The true boundaries of the breeding grounds will separate where the smallest larvae actually are from where they actually are not (provided there is little drift of eggs between spawning and hatching). Places are known where they may be found, and this is beyond doubt. We now consider what can be said about where they may not be found.

Our work above has laid an extensive foundation for this, and we can present our conclusions briefly. The question has two aspects:

(a) over an extended area, larvae of various sizes have been caught; where the smallest larvae are absent from the catches, can we conclude that they are not present in the sea?

(b) Schmidt has asserted that in some areas there are no larvae at all. Is this well founded? We refer especially to the earlier publications (Schmidt 1922, fig. 4; 1925, fig. 5) where in the charts of the 'breeding areas' we see 'NO LARVAE' at approximately 20°N, 30°-50°W (however, this is absent from the re-drawn chart which is fig. 1 of Schmidt 1935).

With regard to (a), it is clear from our discussion of the distribution of effort that Schmidt's *chance* of catching very small larvae, if present, was very much higher in the region that Schmidt has delineated as the 'breeding area', than it was anywhere else, and this can be said without regard to time of year. When time of year is taken into account, with the likely season over which small larvae might be

found, and catches by commercial ships are for the moment ignored, then it is clear that Schmidt's research cruises had very little chance of catching very small larvae outside the 'central area', with one exception. This is the segment of the 'Dana I' cruise from North Africa to the West Indies (1920.04.05-26, 'Dana I' Stns 826-839), ca. 25°N, 15°-47°W, during which in fact no leptocephali were obtained.

It is different with the stations made by commercial ships. Their catch effort, though of very low intensity, is widely dispersed in time and space (Fig. 9). They certainly caught a number of larvae, some small ones and even a few very small. (We find, for *A. anguilla*, 115 west of 20°W and 4 east of 20°W (Schmidt, 1922 p. 187, claims 120 in all), and 3 *A. rostrata* west of 40°W). We have, however, stated our opinion above about commercial stations. Nevertheless, the only 'commercial' stations to take larvae smaller than 25 mm are situated within the 15 mm curve; it follows that the situation of the 25 mm curve is determined almost entirely by the results of the scientific expeditions, and we have seen that the distribution of effort by research ships outside the central area is extremely sparse. Therefore the situation of the '25 mm' area – assuming it to be real – is only poorly determined. For this reason, in our detailed consideration, given below, of whether the apparent 'breeding area' is an artefact or not, we confine attention to the '10 mm' curve.

Our answer to question (a), therefore, is that it is very dubious to conclude from Schmidt's data that the smallest larvae are not present outside the area where they were caught; and this answer can be reached by simple considerations of a rather general kind. However, the question is so fundamental that we shall return to it below from another point of view, adopting the rather stringent procedures of a statistical test of a null hypothesis.

As to question (b), our answer can be short. The only visits to the area where the words 'NO LARVAE' appear on the chart are:

INGOLF   Stns 407- 409 (1911.11.07-09)
                 430- 438 (1911.11.09-17)
                 650- 654 (1912.10.28-11.05)
DANA II   Stns 1158-1182 (1921.10.28-11.23)

at none of which were larvae caught. Possibly, then, larvae are absent from this area in November.

9. Testing a null hypothesis

Schmidt's hypothesis of 1922 is that breeding takes place, and therefore the tiniest larvae are present, exclusively within the area delimited by the 10 mm curve. It explains the spatial distribution of larval sizes observed in catches, and could predict this for areas or times where investigations were sparse or absent.

We have criticised the spatial aspect of Schmidt's hypothesis on the grounds that, by restricting his distribution of effort mainly to the 'central area' in and around the 10 mm curve, he did not give himself adequate opportunity to disprove the hypothesis, nor to confirm it by showing that its predictions were observable,

and reproducible, on a scale that would allay all reasonable doubt. May we venture the further opinion that, once the 1922 paper had appeared, it was rather late for such investigations? We grant, however, that a prime motive for repeated return to the 'central area' was the quest for eggs and breeding adults.

Harden Jones (1968) has already confronted the Schmidt hypothesis with some awkward facts which it can ill predict. We have here argued that when Schmidt's own data are viewed sceptically, support for the hypothesis loses much of its apparent force. Now we approach the question from the opposite side – we shall formulate a hypothesis of our own. This is an artificial hypothesis, not claimed to represent any real truth, whose sole purpose is to provide predictions which we can compare with the data. It is in effect a Null Hypothesis, in a precise statistical sense, to the effect that Schmidt's delineated 'breeding place' is an artefact of his distribution of effort.

We shall, then, take as given:

(a) the distribution of effort by 'Margrethe', by 'Dana I' up to mid-1921, and by 'Dana II' in 1921, in terms of numbers of stations and numbers of hauls and their positions and dates.

(b) the distribution of larval sizes obtained by Schmidt in the intensively investigated 'central area', taking account of the time of year.

The Null Hypothesis to be tested is that conditions (b) obtain, not as Schmidt describes it, but uniformly over the whole area enclosed within Schmidt's 45 mm curve.

This amounts to supposing that spawning takes place, and therefore the smallest larvae are present, over the whole of this area uniformly, at the season inferred by Schmidt; and that as the year advances the growing larvae will likewise be present over the whole area uniformly.

In order to test this hypothesis against Schmidt's real data, its predictions will be evaluated by supposing that any station (or haul) within the 45 mm curve, taken at a time of year at which larvae 10 mm long or less might be taken, is as likely as any other to yield such larvae. This uniform likelihood will be expressed by a formal probability-model according to which the number of stations (or hauls) observed to be positive for such larvae is taken as constant, and any *random* selection of this number of stations (or hauls) from those eligible is (according to the Null Hypothesis) a possible observation which has the same probability as the observation actually made by Schmidt. The details of the procedure are given in the Appendix.

As is stated in the Appendix, we conclude that:

(i) the Null Hypothesis *is* rejected when applied to the north-south dimension. That is, there is effectively conclusive evidence for a northern limit on the occurrence of larvae 10 mm long or less, within the 45 mm curve. It has been determined (see the Appendix) that if attention is restricted to stations taken south of 30°N, the Null Hypothesis is just not rejected at 5% significance level, and we conclude that latitude 29°30'N is a 95% confidence limit for the northernmost occurrence of such larvae, based on the data available up to mid-1921 (and this is the most southerly position possible for such a limit). This northern limit is approximately the latitude of the northern side of Schmidt's '10 mm' curve.

(ii) there is no evidence in the data available by mid-1921 to indicate any east-west limit on the occurrence of larvae 10 mm long or less, when attention is restricted to stations falling within the 95 % confidence range for latitude given in (i) above. That is, the Null Hypothesis is not rejected when it is applied to longitudinal range of occurrence. Such a conclusion is not contradicted by results of later expeditions (see for instance Schoth & Tesch (1982)), though no expedition has a yet attempted to greatly broaden the geographical range of intense effort and thereby entirely circumscribe a region where the youngest larvae are found with a region where, beyond all doubt, they are not.

10. Conclusions

Schmidt's Atlantic eel investigations have been examined in the light of his own data. We have followed exactly in his footsteps, and at each crucial stage we have assessed his decisions by reference to the data available at the time. The main results are as follows.

(1) The conclusion that eels do not spawn in the Mediterranean was founded on a very sparse base of captured larvae. Data obtained much later (1930) do tend to support the conclusion, however.

(2) The homogeneity of the European eel population is dubious. Schmidt overstated his case, claiming a precision of uniformity not justified by the data.

(3) Schmidt's hypothetical species separation mechanism lacks foundation, and his argument for it is unsound. We grant the ambiguities of inferring a growth curve from data on captures, but the indication rather is that both *Anguilla anguilla* and *Anguilla rostrata* larvae grow at the same rate. *A. anguilla* can possibly reach the stage of metamorphosis within 12-15 months. If this is indeed the case, and if the main spawning area is where Schmidt has claimed, then the mechanism of larval transport to the European coast is an open problem.

(4) The larvae of ca. 45 mm length are ubiquitous in the Sargasso area, and occur at all times of year. They cannot fit as a whole onto a growth régime consistent with Schmidt's claims of a very localised spawning confined to a few months of the year.

(5) The close mingling of the two species almost at the very heart of Schmidt's main 'spawning area', and the lack of clear support for a species separation mechanism, raise the possibility that larvae from this area may not reach the coasts at all.

(6) There is no doubt that Schmidt's closed contours for lengths are to some extent an artefact of his distribution of effort. Whereas there are clear indications of a north-south limit on the occurrence of the smallest larvae in the Sargasso area, there is no evidence in Schmidt's data for an east-west limit.

Acknowledgments

References

I. Sources of Primary Data

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Appendix

A1. Here are given the details of the 'test of a null hypothesis' referred to in Section 9 of the main text. Ideally, a complete computer simulation would be made, of 'catches' made by imaginary expeditions whose distributions of effort in time and space were the same as those of Schmidt. This however would depend on assuming conditions which it has proved impracticable to estimate adequately from the original data, in particular the variation with time of year in abundance of larvae and in catch per unit effort. In the event, we have found it possible to work merely with the stations, designated as positive or not for larvae of 10 mm or less, in relation to a null hypothesis that the latter might be randomly chosen from those available at the appropriate time of year. In what follows, stations outside the 45 mm contour are not considered.

A2. Dates between which larvae 10 mm long or less are likely to be caught were estimated from *A. anguilla* data for all stations from 'Margrethe' and 'Dana I' up to number 950 (1921.04.29) lying within the 45 mm contour. Such larvae may occur from Day 100 (April 10) to Day 225 (July 14), where the upper limit is an extrapolation. We therefore restrict attention to those stations falling within this range of dates. There are 46 such stations from 'Dana I' in 1920 (numbers 836-883 except 848 and 849), 16 in 1921 (933-948), and none from 'Margrethe'.

A3. Defining a Unit of Effort (UE) to be a ring-net of 100 cm diameter towed for 1 hour under standard conditions, the variation in catch per unit effort by haul was studied. For hauls which were positive, this was extremely variable with time of

year, being less than 1/UE before Day 100 and rising to over 20/UE and even nearly 100/UE in certain hauls between Days 150 and 220, with a general level of less than 5/UE for much of the year. The extreme variability of this factor over the critical period (Days 100-225) meant that it was impossible to formulate a satisfactory and reliable model of it for simulation purposes (see above).

The association between Effort per Station, Date of Station and whether the Station was positive was studied. While Effort varied considerable with Date, as did proportion of positive stations, there was no strong association between Effort and proportion positive at a given Date. This result was unexpected, but convenient. Therefore the following will assume that the chance of an eligible station being positive is independent of effort, but in such a way that the resulting error will be on the safe side (i.e. so as to tend to favour Schmidt's theory).

A4. We now test a null hypothesis that the stations which were positive for larvae of 10 mm or less are a random selection of the stations within the 45 mm contour taken at such times of year as correspond to the possible presence of larvae so small.

Such a test in fact favours Schmidt, since there was greater effort per station within the 10 mm curve than outside it, and this factor is not taken into account in the test. Therefore the null hypothesis being tested predicts a greater chance of a station outside the 10 mm curve being positive for larvae of 10 mm or less than would be predicted if the effort factor could be adequately allowed for. It follows that if the null hypothesis is not rejected by this test, it would not be rejected by a test which allowed for variation of effort.

A5. *Eligible stations* are those which fall within the 45 mm curve and are taken between Days 100 & 225 of the year.

Hereafter, larvae of length 10 mm or less will be called *'10 mm' larvae*.

In the 1920 series there are 46 eligible stations of which 20 fall within the 10 mm contour and 7 are positive for '10 mm' larvae.

For the 1921 series, there are 14 eligible stations of which 12 fall within the 10 mm contour and 11 are positive for '10 mm' larvae.

There is now a question of what test statistic to use. We cannot proceed as if the 10 mm contour were given a priori, and calculate the probability that, given the number of eligible stations inside it, these should include by chance all those positive for larvae of 10 mm or less. The reason is that the contour was drawn in the first place to include all the observed ones, and such a test would necessarily be biased and give an apparent significance level more extreme than it should be.

A6. The approach adopted is to compare the north-south range, and independently the east-west range, for the stations positive for '10 mm' larvae, with the likely distribution of these ranges predicted from a Null Hypothesis that the stations positive for '10 mm' larvae are a randomly chosen subset of the eligible stations, all subsets of the same size being equally likely, and the total number of '10 mm'-positive stations being held fixed.

A7. The following mathematical results will be required. Consider the set $\{1,2,...,N\}$, and choose a subset of size m from it without replacement, and randomly so

that all subsets of size m are equally likely. Let U be the least of the numbers so chosen, and V the greatest; we seek the distribution of $(V - U + 1)$, the number of consecutive positions between the least and the greatest inclusive (i.e. the *range* of the subset). Denote the range $(V - U + 1)$ by R. Then a given value of R has probability

$$P(R) = (N - R + 1)\binom{R-2}{m-2}\Big/\binom{N}{m} \tag{A1}$$

for $R = m, m+1, ..., N$.

It is then straightforward to calculate that the expectation of $(R-1)$ is

$$E(R-1) = (N+1)(m-1)/(m+1) \tag{A2}$$

and the expectation of $R(R-1)$ is

$$E[R(R-1)] = (N+1)(N+2)m(m-1)/\{(m+1)(m+2)\} \tag{A3}$$

from which the mean and variance of R can easily be derived, as $E(R-1) + 1$ and $E[R(R-1)] + E(R) - \{E(R)\}^2$ respectively.

For a selection with given range R, there are $N - R + 1$ possible positions for it, viz. $(1, R), (2, R+1), ..., (N - R + 1, N)$, and these are all equally likely (so that no one possibility is to be preferred a priori).

A8. We shall apply the preceding results to the eligible stations in the following way. Given N eligible stations, these will be considered in terms of their latitudes from south to north in order, and again in terms of their longitudes from east to west in order. Let there be m stations that were positive for '10 mm' larvae; these will have a least latitude which will be for station number U_{lat} in the series ordered by latitude, and a greatest latitude which will be for station number V_{lat}. The latitude range (north-south range) will then be $R_{lat} = (V_{lat} - U_{lat} + 1)$. Similarly there will be least and greatest longitudes for stations numbered U_{long} and V_{long} in the series ordered by longitude, and a longitude range (east-west range) $R_{long} = (V_{long} - U_{long} + 1)$.

On the null hypothesis that '10 mm' larvae are present uniformly over the entire area, and taking as given that some m out of all N are positive for these larvae, the null distribution of R_{lat} and the null distribution of R_{long} can be calculated as in Section A7 above (the two distributions are identical). The values of R_{lat} and R_{long} observed in the data can then be compared with these distributions and appropriate conclusions drawn. Note that this test procedure has a 'non-parametric' character, in that the actual values of latitude and longitude (in degrees) are not used; the procedure in fact uses only the ranks of the latitudes, and the ranks of the longitudes, of the stations positive for '10 mm' larvae.

If the observed values of R_{lat} and R_{long} are significantly *small* in terms of the null distribution, then we have statistical evidence that the null hypothesis is false, and that the '10 mm' larvae are present in the sea over a smaller geographical range than is predicted by the null hypothesis.

A9. Confidence intervals for the latitude and longitude range of occurrence of '10 mm' larvae can be obtained in a similar way. When N, the total number of eligible stations, is as given (in the data), the probability of so small a range R as was

observed can be calculated (say it is $P = 0.001$). By considering hypothetical smaller values of N, the corresponding probabilities for the observed R can be found; as N decreases, m being held constant, the P-values increase. The value $\hat{N}$ of N at which the P-value just passes a threshold of acceptability (say 0.05) is a value of N for which the null hypothesis would just not be rejected at significance level 0.05, and so would be a 95% upper confidence limit for N. A set of $\hat{N}$ stations, consecutive in say latitude, which embraces the m stations positive for '10 mm' larvae, then covers a range of latitude which can be considered as a 95% confidence interval in latitude for the occurrence of such larvae. This is true in the sense that if we apply to this range of latitude the null hypothesis that at all eligible stations in this latitude range such larvae are equally likely to be present in the sea, then the null hypothesis will not be rejected at the 5% significance level. Similar considerations apply to longitude.

There are two major considerations for such a conclusion. The first follows from the remark at the end of Section A7 above. The set of $\hat{N}$ consecutive stations only has to embrace the m positive ones. In general $\hat{N} > m$, so there will be $(\hat{N} - m + 1)$ possible positions for them. There are no a priori grounds for preferring one possibility to another. One possibility might have the shortest range in degrees of latitude (or longitude), thus covering the smallest geographical area; another might have all stations as far north as possible, and so on. Such differences correspond to strengthening or weakening the test in terms of its power against various kinds of alternative hypothesis.

The second consideration is the obvious one, that only latitude (or longitude) values within the ranges of real stations actually taken can occur in the confidence interval. If the westernmost eligible station is in the confidence interval, for instance, then we have no basis whatever for setting a western limit to the occurrence of larvae in the sea (and similarly for the eastern limit).

A10. For the 1920 series, 7 stations out of 46 eligible were positive for '10 mm' larvae. For 7 randomly chosen from 46, the expected range is 36.25 and the variance is 38.19 (S.D. 6.2).

The southernmost positive station (846) is the 4th or 5th (tie) from the south, the northernmost (866) is the 27th. Hence the latitude range is $R_{lat} = 23$ or 24. The easternmost (842) is at position 7 and the westernmost (855) at position 27, giving a longitude range $R_{long} = 21$. Therefore R_{lat} is 2 S.D.s less than expectation ($P =$ ca. 0.03) and R_{long} is 2.5 S.D.s less than expectation ($P =$ ca. 0.006). These results are significant.

If there had been only 40 eligible stations, the expectation and S.D. of R_{lat} would be 31.75 and 5.31, and $R_{lat} = 23$ would just correspond to $P = 0.05$, barely significant at the 5% level. Hence any set of $\hat{N} = 40$ consecutive latitudes embracing the 7 stations positive for '10 mm' larvae would be a 95% confidence interval for the latitude range over which such larvae may be in the sea.

Similarly, any set of 37 consecutive longitudes embracing the 7 stations would be a 95% confidence interval for the longitude range of occurrence of '10 mm' larvae.

A11. For the 1921 series, 11 stations out of 14 eligible are positive for '10 mm' larvae, giving an expected range of 13.5 with variance 0.48 (S.D. = 0.69).

The southernmost (947) is number 2, the northernmost (941) is number 15, so $R_{lat} = 14$, which is within one S.D. of expectation (and greater). Hence there is no indication that larvae occur in the sea over a smaller range of latitude than the eligible stations of the 1921 series.

The easternmost (935) is number 3, the westernmost (947) is number 15, $R_{long} = 13$, again within one S.D. of expectation. Hence there is no indication that larvae occur in the sea over a smaller range of longitude than the eligible stations of the 1921 series.

A12. Combining the 1920 and 1921 data, we have $N = 62$ eligible stations of which $m = 18$ were positive for '10 mm' larvae. The range has expectations 57.3 and variance 13.05 (S.D. = 3.61).

The southernmost positive station (947) is number 5, and the northernmost (866) is number 43, so $R_{lat} = 39$. This is more than 5 S.D.s less than expectation, so there is clear evidence that the north-south range of larval occurrence is more restricted than would be implied by Null Hypothesis.

The easternmost positive station (842) is number 8, and the westermost (942) is number 60, so $R_{long} = 53$. This is 1.2 S.D.s less than expectation, so there is no evidence from the 1920-21 combined series that the east-west range of larval occurrence is more restricted than would be implied by the Null Hypothesis.

An interpretation of the difference between this last result and the result for longitude derived in Section A10 for the 1920 series alone will be discussed next.

A13. There are in the 1920 series of 46 eligible stations, 12 '10 mm'-negative in the quadrant north-west of 29°N, 60°W, which are common to the northernmost and to the westernmost '10 mm'-negative stations. All tests above agree that the Null Hypothesis is to be rejected for north-south range. A 95% confidence limit for the range was found to be $\hat{N} = 40$. If the northernmost 6 are removed from the series, leaving the southernmost 40, and the east-west test is repeated for these, we have $N = 40$ and $m = 7$, so that R_{long} has expectation 31.75 and variance 28.19 (S.D. = 5.3), whereas R_{long} is observed to be 27, which is only 0.9 S.D. below expectation.

Therefore this reduced series, with 6 northernmost stations removed, no longer provides any indication from 1920 data that the east-west range of larval occurrence is more restricted than is implied by the Null Hypothesis. The northernmost remaining station is at latitude 32°30'N, and all stations from the 1921 eligible series are south of this (being between 22°14'N and 27°40'N), so no conclusions from the 1921 data are altered.

If we combine the reduced 1920 series with the 1921 series, and repeat the tests, we finally obtain the conclusions:

(i) There is no evidence in the data available by mid-1921 to indicate any east-west limit on the occurrence of '10 mm' larvae in the sea.
(ii) A 95% confidence interval for north-south range would include $\hat{N} = 46$ stations arranged consecutively in latitude. If 46 such stations are taken in the most southerly possible positions (which is the case most favorable to Schmidt's view), the 95% northern confidence limit for occurrence of '10 mm' larvae in the sea is at approximately 29°30'N.