NOTES ON EEL LARVAE (*ANGUILLA ANGUILLA* LINNAEUS, 1758) FROM THE CENTRAL AND EASTERN NORTH ATLANTIC AND ON GLASS EELS FROM THE EUROPEAN CONTINENTAL SHELF[1])

by

W. L. VAN UTRECHT & M. A. HOLLEBOOM

Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam, P.O. Box 20125, 1000 HC Amsterdam, The Netherlands

ABSTRACT

Eel larvae caught in the mid North Atlantic and along the continental slope off the Portuguese coast are studied together with samples of glass eels caught just before entering fresh water along the Dutch and French coasts.

During their migration from the mid Atlantic towards the continental slope the mean length of the larvae investigated increased from 56 to 66 mm, while the mean diameter of their otoliths increased from 0.17 to 0.23 mm. The animals from the mid Atlantic had three complete growth zones in their otoliths, while the majority of those from the continental slope had four complete growth zones.

The specimens from the mid Atlantic show typical larval aspects as e.g. position of the anus and reaction to preservation, this in contrast to most of the animals caught along the continental slope. In 70% of the latter the position of the anus is varying and they turned completely opaque after preservation in alcohol; the remaining animals showed all typical larval aspects.

In the glass eels the numbers of growth zones varied from two to six complete ones, about 40% of the animals having four or more growth zones in their otoliths.

The results indicate that the variation in age found in the glass eels most probably comes into existence along the continental slope, where a number of larvae lag behind in metamorphosis.

The growth zones in the otoliths seem to represent completed regular growth cycles which are supposed to be annual.

RÉSUMÉ

Sont étudiées des larves d'Anguille capturées dans la partie centrale de l'Atlantique Nord et le long du versant de la plate-forme continentale au large des côtes du Portugal, ainsi que des échantillons de civelles prélevés juste avant la pénétration dans les eaux douces, le long des côtes des Pays-Bas et de France.

Pendant la migration des larves à partir du centre de l'Atlantique vers la plate-forme continentale, leur longueur moyenne augmente de 56 à 66 mm, tandis que le diamètre moyen de leurs otolithes augmente de 0,17 à 0,23 mm. Dans les otolithes des exemplaires capturés au centre de l'Atlantique il y a trois zones complètes de croissance, tandis qu'il y en a quatre dans la plupart de ceux du bord de la plate-forme continentale.

Les exemplaires de l'Atlantique central présentent des aspects typiques pour les larves, par exemple la position de l'anus et la réaction à préservation en alcool, tandis que dans 70% des exemplaires capturés le long du versant de la plate-forme continentale la position de l'anus est variable et ils deviennent complètement opaques après préservation en alcool (les autres 30% montrant les aspects typiques pour les larves).

Chez les civelles, le nombre de zones complètes de croissance dans les otolithes varie de deux à six, approximativement 40% des exemplaires ayant quatre zones ou plus.

Les résultats obtenus montrent que les différences d'âge trouvées chez les civelles se manifestent à partir du séjour le long du bord de la plate-forme continentale, car c'est ici qu'il se produit un retard dans la métamorphose d'un certain nombre de larves.

Les zones de croissance des otolithes semblent correspondre à des cycles de croissance dont on suppose qu'ils sont annuels.

INTRODUCTION

In the past, two possible spawning areas have been nominated for the European eel. Grassi (1896) supposed that eels spawned in deep water near the coast, in the Atlantic as well as in the Mediterranean. Schmidt (1923) postulated that they spawned in the Sargasso Sea; this idea was mainly based on the areas in which very small larvae were caught. In more recent years new theories have been developed without, however, giving a final solution of this problem.

---

[1]) This paper is dedicated to Dr. C. L. Deelder on the occasion of his retirement.

Schmidt's opinion — based on the increase in length of the leptocephali and the distribution of length classes in the North Atlantic — was that they migrate towards the continental shelf in about three years. In his opinion their transport is passive by means of oceanic currents. Objections, however, can be put forward to this view, because it is known that objects can move from the western part of the North Atlantic towards the European continental shelf within one year. Moreover, leptocephali can swim vigorously, as observed when they are kept in tanks. Besides, new data and theories about oceanic currents and transport of water masses in the North Atlantic make it necessary to look again into the problem of the migration of eel larvae and glass eels towards the European continent.

One opinion is that the distribution of eel larvae in the North Atlantic is mainly determined by the Gulf Stream system. However, Worthington (1976) proposes two gyres in the West Atlantic, one forming the Sargasso Sea area (Gulf Stream) and one more to the north, between the Sargasso area and the Grand Banks. According to him there is no direct flow of water towards western Europe. The only northward flow he proposes is along the north-west African coast along Portugal into the Norwegian Sea. Both opinions do not correlate very well with the observed distribution of eel larvae, nor do they support the idea of passive transportation.

Tucker (1959) reviewed the problem and developed the theory that the European eel does not spawn in the Sargasso Sea. In his view the maturing eels could not reach this area because they do not feed anymore once maturation begins, and their energy reserves should be insufficient for swimming the considerable distance from western Europe to the area between about 50°W and 60°W, and 20°N and 30°N. They would die before reaching that area. He supported his view by the evidence that only a few maturing eels were caught beyond the continental shelf. This theory initiated considerable discussion (cf. Sinha & Jones, 1975).

Concerning the migration over the North Atlantic, Harden Jones (1970: 77-80) stated that knowledge of the age of leptocephali taken in various areas, e.g. around the Azores, along the continental shelf of Europe and in the Mediterranean, is important.

As far as could be ascertained, the only data about the age of leptocephali and glass eels of A. anguilla are those from an initial study by Ehrenbaum & Marukawa (1913), whereas Liew (1974) studied the otoliths of glass eels and elvers of A. rostrata (Lesueur).

The present paper deals with age determination of leptocephali (larvae) from the central North Atlantic and off the Portuguese coast, and of glass eels, caught along the Dutch and French coasts when they were about to enter fresh water.

MATERIAL AND METHODS

The leptocephali from the mid North Atlantic are caught during cruises of the Amsterdam Mid North Atlantic Plankton Expedition with the R.V.H.M. "Tydeman"[2]) held in 1980-1983 (fig. 1). The samples were taken in 1980 (44 specimens) and 1981 (9 specimens) with a combined opening-closing Rectangular Midwater Trawl (RMT 1 + 8), developed by the Institute of Ocean Studies, between 55° and 28°N, along the 30°W meridian. The leptocephali caught off the Portuguese coast (fig. 1) were sampled during a cruise of the F.R.S. "Tridens" with a pelagic trawl in which a modified Isaacs Kidd net was mounted. In this case sampling took place just beyond the 1000 m depth line. For further details about the samples see table I; the samples taken with the R.V.H.M. "Tydeman" in 1980 are listed by Van Utrecht (1983: 230). In all cases the leptocephali were immediately preserved in 70% alcohol.

The glass eels studied were taken at random from a large series of samples caught in successive years at a number of localities along the Dutch coast, in a sampling program of the Eel Department of the Netherlands Institute for Fisheries Investigations (R.I.V.O.), IJmuiden (see Heermans & Van Willigen, 1982). These samples were taken with a 1 m² square net. In 1979 two more samples of glass eels, one taken near Nantes and one near Bordeaux, France, were added.

After measuring and weighing, the samples became available for further study. The deep-frozen samples were thawed in 70% alcohol. When this was completed, the animals were stored in fresh 70% alcohol. No formalin was used, in order to avoid etching or dissolution of the otoliths. From each sample of glass eels 100 animals were taken at random. After measuring total length and the dimension of the head, the sagittae were taken out and mounted on glass slides in Canada balsam. Microscopic examination was made with transmitted light at 450 × magnification. Morphometric and meristic data of leptocephali and glass eels caught in the mid- and eastern North Atlantic in 1981 and 1982 are listed in table II.
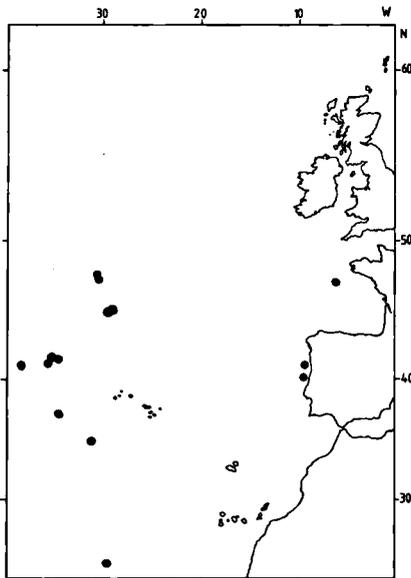
Fig. 1. Positions where larvae of *A. anguilla* were taken.

The diameter of the otoliths was measured, the number of growth zones counted, and the distance from the centre of the otolith to the first opaque ring was measured, that from the first opaque ring to the second, and so on.

The otoliths (sagittae) from leptocephali and glass eels are more or less . flattened round bodies that are transparent in transmitted light. In the centre is a dark round spot or kernel. At a short distance from this spot is a dark circular ring.

This part is considered to be formed in the period from hatching to the moment the yolk reserves have gone. At that time, the larva has also the true leptocephalus form. Then follows a zone with patterns of circular light (translucent) and dark (opaque) rings (fig. 2). At certain distances from the centre, groups of two or three evidently thicker and darker rings, grouped close together, are present (fig. 2; in this figure the centre of the otolith is not well-defined, because it was out of focus when trying to get

TABLE I

Larval and metamorphosing eels caught in the mid- and eastern North Atlantic in 1981 and 1982.

Samples of leptocephali of *A. anguilla* taken by the Amsterdam Mid North Atlantic Plankton Expedition during the period September 15 - October 6, 1981 (R.V.H.M. "Tydeman") (cf. fig. 1). (ZMA = Zoölogisch Museum Amsterdam coll. no.)

Station 39; haul 2; 5-X-'81; 05.29-06.29 h; 55-100 m; 47°56.3'N 30°38.3'W; (ZMA 119.158, 3 specimens).
Station 39; haul 10; 5-X-'81; 12.58-13.59 h; 405-500 m; 47°43.4'N 30°18.8'W; (ZMA 119.159, 1 specimen).
Station 42; haul 9; 30-IX-'81; 15.01-16.02 h; 110-200 m; 41°44.7'N 34°25.0'W; (ZMA 119.161, 1 specimen).
Station 43; haul 7; 29-IX-'81; 21.15-23.00 h; 0-421 m; 41°11.1'N 35°42.5'W; (ZMA 119.160, 1 specimen).
Station 45; haul 1; 27-IX-'81; 10.21-11.21 h; 80-195 m; 37°09.0'N 34°48.6'W; (ZMA 119.162, 1 specimen).
Station 47; haul 7; 24-IX-'81; 00.49-01.48 h; 95-190 m; 35°07.1'N 31°19.5'W; (ZMA 119.163, 1 specimen).
Station 52; haul 11; 18-IX-'81; 17.32-18.33 h; 100-205 m; 25°02.3'N 29°58.2'W; (ZMA 119.164, 1 specimen).

Samples of leptocephali and glass eels of *A. anguilla* taken during a fishing cruise of the F.R.S. "Tridens" from November 1 - November 6, 1982 (cf. fig. 1).

Station 1; haul 1; 1-XI-'82; 08.45-11.36 h; 340 m; 40°01'N 09°45'W; (ZMA 119.165, 1 specimen, in early stage of metamorphosis).
Station 1; haul 2; 1-XI-'82; 20.30-21.30 h; 50 m; 41°10'N 09°26'W; (ZMA 119.166, 14 specimens, of which 1 in early stage of metamorphosis).
Station 1; haul 3; 1-XI-'82; 22.05-23.30 h; 125 m; 41°14'N 09°26'W; (ZMA 119.167, 10 specimens, of which 2 in early stage of metamorphosis).
Station 3; haul 2; 2-XI-'82; 19.23-20.13 h; 50 m; 47°10'N 06°08'W; (ZMA 119.168, 2 specimens, glass eel stage).

the other growth features clearly defined). Such a group of thicker and darker rings is considered to mark as a border line the end of a growth cycle and the start of a next one, and is comparable to the "winter zone" as described by Liew (1974: fig. 4).

The zone of the otolith between two such border lines is optically less dense, by which the fine, very regularly interspaced, slightly darker lines in them become visible (fig. 2). These zones comprise the "summer zone" of Liew (Liew, 1974). In the translucent zones about 13 of these fine rings could be counted.

The part from one border line up to and including the next one is considered to represent a complete growth cycle or growth zone. There is no difference in shape and
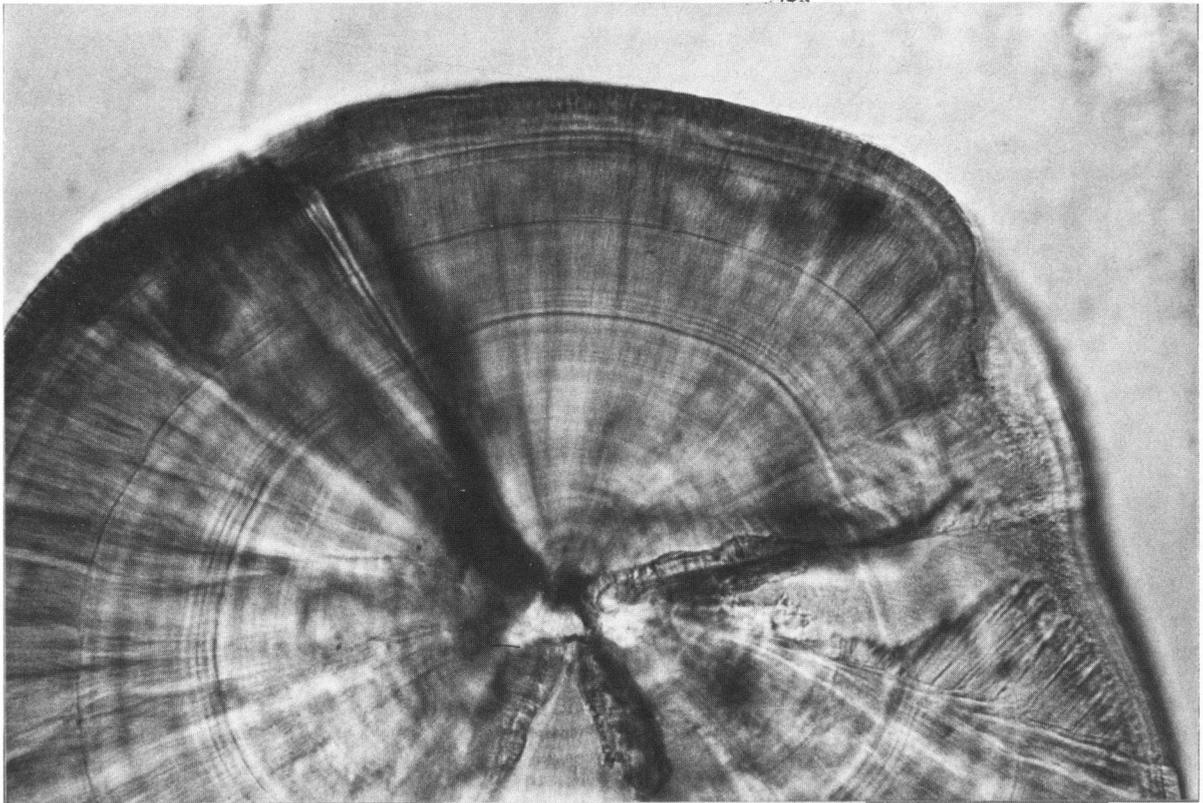
Fig. 2. Otolith of a glass eel showing two complete growth layers; diameter of the otolith 0.37 mm. (Photo L. A. van der Laan.)

aspects between the otoliths of leptocephali and glass eels, except in the diameter and numbers of growth rings. The otoliths of the glass eels have a far greater diameter and consist of more complete growth zones.

RESULTS

The eel larvae

For the present study 78 leptocephali were available, 53 (from which 9 are used for studying the otoliths) of them were caught in the mid North Atlantic and 25 along the continental slope off the Portuguese coast (see table I and Van Utrecht, 1983: 230).[3])

The results of the myomere counts are given in table III. From the figures it is clear that most of the leptocephali belong to *A. anguilla*.

Though the numbers of leptocephali caught in the mid Atlantic and along the continental slope are small, they show clear differences in mean length. Those caught in the mid North Atlantic had a mean length of 56 mm, they actually show a greater length than is generally supposed. Those caught along the continental slope had a mean length of 61.4 mm. The mean length of four animals in early stage of metamorphosis was 66.3 mm. From these figures it can be concluded that during their migration from the mid North Atlantic to the

[3]) From these 25 specimens from the continental slope off Portugal, 23 of two samples (ZMA coll. no. 119.166 and 119.167) were used for the calculations about mean width of the growth layers, standard deviation, etc. The other

specimens came from various localities in the mid North Atlantic and along the southern European continental slope. However, they all are incorporated in figs. 4 and 5 to demonstrate the continuity of the growth features in their otoliths.

TABLE II

Morphometric and meristic data of leptocephali and glass eels caught in the mid- and eastern North Atlantic in 1981 and 1982.

position	total length in mm	tip snout – anus in mm	length postanal part in % TL	N of myomeres			N of growth layers	remarks
				total	preanal	postanal		
47°56'N 30°38'W	54	36	34*	111	70	41	3 +	
do.	59	41	31*	111	68	43	3 +	
do.	60	42	30*	111	72	39	3 +	
47°43'N 30°19'W	63	42	34*	115	71	44	3 +	
41°45'N 34°25'W	63.5	42.5	33*	117	70	47	—	
41°11'N 35°42'W	61	43	30*	114	73	41	—	
37°09'N 34°49'W	52.2	36.3	31*	113	73	40	—	
35°07'N 31°19'W	52	36	31*	119	74	45	3 +	
25°02'N 29°58'W	52.8	32.6	38*	118	71	47	—	
40°01'N 09°45'W	58.5	24	58	118	36	82	3 +	beginning metamorphosis
41°10'N 09°26'W	58.5	26.3	55	118	46	72	4 +	
do.	64	31.9	50	112	48	64	4 +	
do.	59	40	32*	115	72	43	4 +	
do.	64	37.8	41	115	45	70	4 +	beginning metamorphosis
do.	59	40.4	32*	114	70	44	3 +	
do.	61	41	33*	118	76	42	4 +	
do.	62	43.4	30*	115	73	42	4 +	
do.	50.3	34.4	32*	115	75	40	—	
do.	57.5	27.0	53	113	46	67	4 +	
do.	65.4	27.7	58	115	40	75	5 +	
do.	58.7	27.4	53	118	48	70	3 +	
do.	61.7	27.7	55	118	43	75	4 +	
do.	62.8	24.5	61	115	38	77	4 +	
do.	56.9	38.9	32*	117	63	54	4 +	
41°14'N 09°26'W	57.8	31.8	45	118	54	64	5 +	
do.	63.2	43.8	31*	117	71	46	4 +	
do.	64.6	31.7	51	113	48	65	4 +	
do.	66.6	32.6	51	114	48	66	4 +	
do.	63.3	25	61	119	34	85	4 +	
do.	71	41	42	114	62	52	4 +	
do.	70	31.5	55	118	41	77	4 +	
do.	69.2	28.4	59	117	39	78	4 +	beginning metamorphosis
do.	73.6	28.9	61	115	40	75	4 +	beginning metamorphosis
do.	55.9	23.6	58	112	37	75	4 +	
47°10'N 06°08'W	74.5	29.2	61	glass eel			4 +	
do.	79.5	29.5	63	glass eel			4 +	

* Specimen remaining transparent after preservation in alcohol.

continental slope they increase in length. The mean diameter of their otoliths increased from about 0.17 mm to 0.23 mm.

A difference between the two samples of leptocephali appeared after preservation in 70% alcohol. In both cases the freshly caught animals were completely transparent. The animals from the mid North Atlantic remained more or less transparent so that the blood vessels and other internal structures remained visible. However, those caught along the continental slope turned completely white (opaque)

TABLE III

Summary of the results of the myomere counts in
74 leptocephali.

N of myomeres	N of specimens	% of total number
120	—	—
119	3	4.1
118	8	10.8
117	5	5.8
116	3	4.1
115	12	15.2
114	17	23.0
113	13	17.6
112	8	10.8
111	3	4.1
110	2	2.7
109	—	—

Moreover, from table II it becomes clear that all specimens caught in the mid North Atlantic varied in length between 50 mm and about 65 mm. Those caught along the continental slope showed a much greater variation between 55 mm and about 75 mm (see also fig. 3).
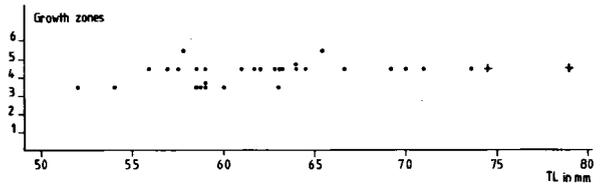
Fig. 3. Relation between the length of the eel larvae and the numbers of growth zones in their otoliths. The two animals marked + are true glass eels.

after preservation, so that no internal structures could be seen and counting of the myomeres had to be done with incident light. This was not the case with the marked animals in the lower part of table II, which also remained more or less transparent after preservation.

Ford (1931) examined leptocephali and glass eels of *A. anguilla* with respect to the change in position of the anus during metamorphosis. He found that in the leptocephalus the anus lies beyond the 71th myomere and in the glass eel beyond the 35th, while the postanal distance is more than 60% after metamorphosis.

Vladikov & March (1975) mentioned that in the leptocephalus of *A. anguilla* there are 67-75 preanal myomeres and 38-48 postanal ones. Schoth (1982) found about the same figures.

From table II it is clear that the leptocephali in the samples from the mid North Atlantic all have a high preanal count and a postanal distance much shorter than 60% of the total length. In the samples taken along the continental slope this is quite different. Seven (marked *) out of 24 animals have a high number of preanal myomeres, and a low percentage of the postanal distance. In the other animals the number of preanal myomeres varied between 41 and 63. Here the postanal distance varied between 41% and 61% of the total length.

Likewise the counting of the otolith growth rings showed a clear difference between the animals from the mid North Atlantic and those from the continental slope. All animals caught in the mid North Atlantic had three complete growth rings, while far the greatest majority of those caught along the continental slope had four complete growth rings (table II).

The results of some calculations on the measurements of the width of the successive growth layers present in the otoliths of 23 eel larvae are given in table IV. From these data

TABLE IV

Width of the successive growth layers (mm) in the otoliths of eel larvae.

growth layer no.	N	mean	variance	S.D.	S.E.
1	23	0.017	0.00009	0.010	0.002
2	23	0.034	0.0001	0.010	0.002
3	23	0.034	0.0001	0.007	0.001
4	23	0.030	0.0001	0.009	0.002
5	21	0.034	0.0002	0.016	0.003

and from fig. 4 it can be concluded that the mean width of the growth layers is fairly constant. The data for the fifth growth zone show a greater variation, because in most animals this zone is still incomplete.
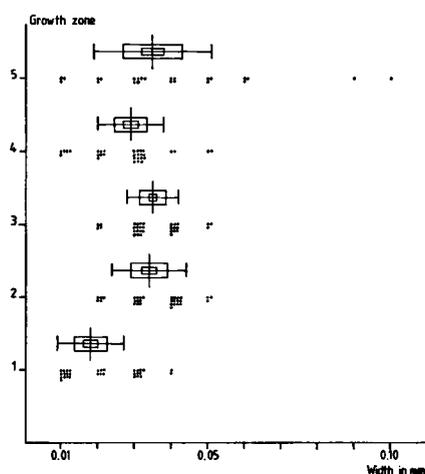
Fig. 4. Width of the successive growth zones in 32 eel lar-
vae otoliths. The vertical line represents the arithmetic
mean, the horizontal line the range. The outer box
represents the standard deviation, the inner box the
standard error.

Fig. 5. Distance of the successive opaque border lines from
the centre of the otolith in 32 eel larvae. For further ex-
planation see fig. 4.

The actual width of the growth layers varies
between 0.01 mm and 0.05 mm, though in
most animals the width is about 0.035 mm. It
may be concluded that the growth of the otolith
in the eel larvae is fairly constant in spite of in-
dividual variation. The same is found when the
data are cumulated. Here the distances from
the centre of the otolith to the consecutive
(opaque) dark lines were measured. These data
are plotted in fig. 5 and show a regular increase
in diameter of the otolith of about 0.035 mm
per growth cycle.

The glass eels

The mean lengths of the glass eels and the mean
diameters of their otoliths are given in table V.
It is clear that the length of the animals varies
considerably as is expressed in the high values
of the variance and standard deviation. In fact,
in all samples the lengths of the glass eels vary
between 63 and 82 mm. This great variation in
length is certainly caused by the reduction in
length and weight during the migration of the
glass eels over the continental shelf (Gilson,
1908; Strubberg, 1913; Tesch, 1980). During
this period they do not feed. This decrease in

length continues when they have entered fresh
water and still do not feed (Deelder, 1970).
From the same table it is also evident that the
otoliths vary only slightly in diameter; their
otoliths have a mean diameter of 0.33 mm to
0.35 mm. The values for the standard deviation
and variance are small.

The numbers of growth zones were counted
in each of 973 otoliths from the samples men-
tioned in table V from animals caught along the
Dutch coast. In table VI the numbers of com-
plete growth zones are given, while the + sign
indicates that the next zone is under formation.
In one individual from the present series of
samples only one complete growth zone was
present, with a second zone partly formed.
These data and fig. 6 show that about 60% of
the animals had been through three complete
growth cycles or less, and about 40% had four
complete zones or more, before entering fresh
water.

The relation of the age of the glass eels, ex-
pressed in growth zones, and their lengths, is
plotted in fig. 7 for two samples, of which the
sample "IJmuiden, 17-V-'79" is chosen for
further analysis, together with two more
samples, one taken near Nantes and the other

TABLE V

Morphometric data of glass eels.

		length in mm				diameter left otolith			
		N	mean	variance	S.D.	N	mean	variance	S.D.
IJmuiden	31-V-'78	100	68.2	9.09	3.01	97	0.35	0.0009	0.03
IJmuiden	22-III-'79	100	74.1	16.57	4.07	100	0.33	0.0004	0.02
Stellendam	10-V-'79	100	71.7	6.20	2.49	99	0.33	0.0006	0.03
IJmuiden	30-IV-'79	100	71.5	15.71	3.96	100	0.34	0.0005	0.02
Lauwersmeer	28-V-'79	100	70.3	14.85	3.85	99	0.34	0.0004	0.02
Stellendam	17-IV-'79	100	73.4	17.22	4.13	100	0.34	0.0006	0.02
IJmuiden	10-IV-'79	81	74.2	14.62	3.82	81	0.35	0.0004	0.02
IJmuiden	17-V-'79	100	71.7	12.14	3.48	100	0.35	0.0005	0.02
Stellendam	28-III-'78	100	69.0	10.24	3.20	100	0.34	0.0004	0.02
Stellendam	21-IV-'78	100	68.2	9.52	3.09	100	0.34	0.0004	0.02
Katwijk	17-III-'78	100	69.1	11.38	3.37	100	0.35	0.0004	0.02
Katwijk	12-IV-'78	100	67.5	7.48	2.73	100	0.34	0.0004	0.02
Bordeaux	10-III-'79	100	72.9	20.83	4.54	95	0.34	0.0005	0.02
Nantes	20-III-'79	65	74.0	17.25	4.12	44	0.34	0.0009	0.03

near Bordeaux. The plots of the other samples are practically identical to each other. It is evident that no relation exists between the length of the glass eels and their age in growth zones. Nearly all length classes are present in each age group, and each length class comprises generally three or more age groups.

When looking through the series of otoliths, the width of the growth zones seems to be fairly constant. To verify this, the width of the layers of one sample of glass eels, "IJmuiden, 17-V-'79" was measured. Although the otoliths from 100 individuals were available, accurate measurements could be taken from 83 otoliths.

The results have been plotted in fig. 8. The figures for the mean, variance, standard deviation and standard error are given in table VII.
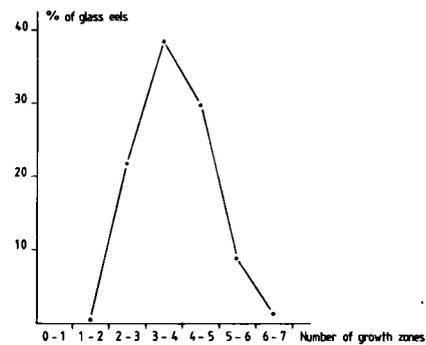
Fig. 6. Percentages of the total numbers of glass eels caught along the Dutch coast arranged according to the numbers of growth zones in their otoliths.

From these data and from fig. 8 one can conclude that the mean width of the growth zones is fairly constant, though the actual width varies between 0.01 mm and 0.1 mm. However, most layers are 0.03 mm to 0.07 mm wide. So the growth of the otolith is fairly regular notwithstanding the individual variation. The same is found when the data are cumulated. The distances from the centre of the otolith to

TABLE VI

Numbers of growth zones in 973 left otoliths from samples of glass eels caught along the Dutch coast.

N of growth zones	N of animals	% of total number
1 +	1	0.1
2 +	210	21.7
3 +	371	38.1
4 +	291	29.9
5 +	87	8.9
6 +	13	1.3
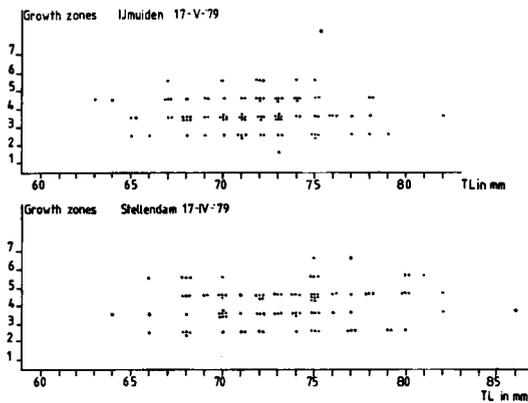
Fig. 7. The age-length relation plotted for two samples of glass eels from The Netherlands.

In table VIII the results of the counting of growth zones in these two samples are given. These figures are plotted in fig. 10 and compared with the data from the sample of IJmuiden. The graphs for the sample from IJmuiden and Bordeaux are nearly identical. In both cases 60% or more animals went through

TABLE VII

Width of the successive growth layers (mm) in the otoliths of 83 glass eels from IJmuiden, caught 17-V-'79.

growth layer no.	N	mean	variance	S.D.	S.E.
1	83	0.054	0.0004	0.019	0.002
2	83	0.042	0.0002	0.014	0.002
3	82	0.044	0.0004	0.021	0.002
4	75	0.054	0.0009	0.029	0.003
5	30	0.044	0.0009	0.031	0.006

the consecutive (opaque) dark lines were measured. These data are plotted in fig. 9 and illustrate the regular increase in diameter of the otolith.

The same procedure is followed for the samples of glass eels from Nantes and Bordeaux. The mean lengths are given in table V together with the mean diameter of the otoliths. These figures are within the range of the samples from the Dutch coast. The mean diameter of the otoliths is 0.34 mm and is the same as for the animals caught along the Dutch coast.

three complete growth zones or less before entering fresh water. In the sample from Nantes the curve has shifted to four complete growth cycles before entering fresh water. The reason of this shift is not clear. However, the sample of glass eels from Nantes consisted of less than half the number of that in the two other samples.
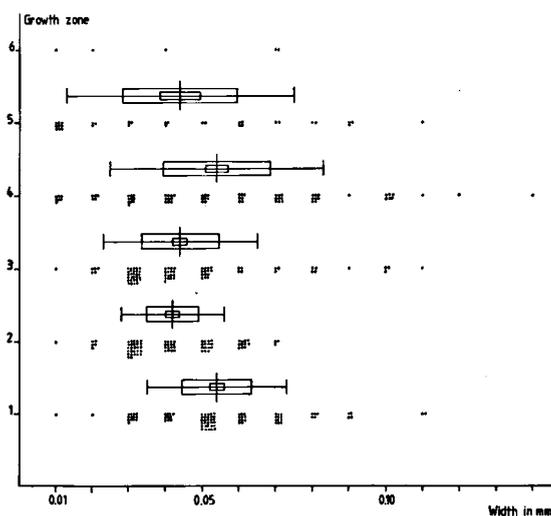
Fig. 8. Width of the successive growth zones in 83 glass eel otoliths from IJmuiden, caught 17-V-'79. For further explanation see fig. 4.
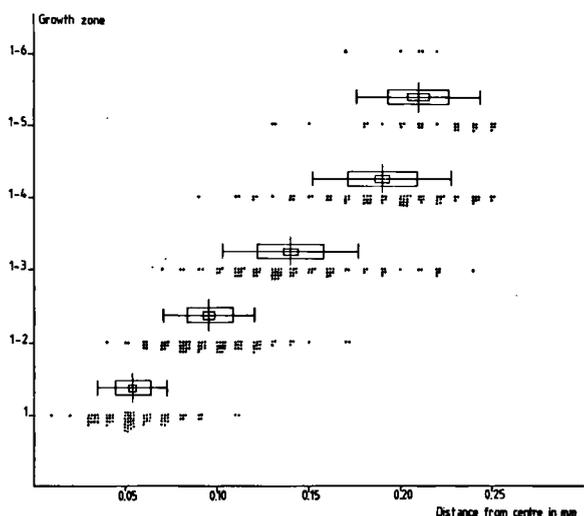
Fig. 9. Distance of the successive opaque border lines from the centre of the otoliths of 83 glass eels from IJmuiden, caught 17-V-'79. For further explanation see fig. 4.

TABLE VIII

Numbers of growth zones in otoliths from samples of glass eels from Nantes and Bordeaux.

N of growth zones	N of animals	% of total number
Bordeaux (N = 95)		
2 +	4	4.2
3 +	58	61.0
4 +	31	32.6
5 +	2	2.1
6 +	—	—
Nantes (N = 46)		
2 +	1	2.2
. 3 +	15	32.6
4 +	25	54.3
5 +	4	8.7
6 +	1	2.2

TABLE IX

Width of the successive growth layers (mm) in the otoliths of glass eels from Bordeaux and Nantes.

growth layer no.	N	mean	variance	S.D.	S.E.
Bordeaux 10-III-'79					
1	95	0.045	0.0003	0.017	0.002
2	95	0.044	0.0001	0.012	0.001
3	95	0.045	0.0004	0.020	0.002
4	89	0.068	0.0007	0.026	0.003
5	29	0.053	0.0008	0.028	0.005
Nantes 20-III-'79					
1	46	0.048	0.0003	0.016	0.002
2	46	0.038	0.0001	0.009	0.001
3	46	0.035	0.0002	0.014	0.002
4	45	0.055	0.0007	0.026	0.004
5	29	0.055	0.0008	0.027	0.005

Fig. 10. Percentages of the total numbers of glass eels arranged according to the numbers of growth zones in their otoliths. The samples are taken near Nantes (o), Bordeaux (x) and IJmuiden (+).

from 46 caught near Nantes the width of the successive growth layers could be measured. The results are given in table IX and plotted in figs. 12-13 and 15-16, respectively.

In fact there is no clear difference between the results from the samples from IJmuiden and those from Nantes and Bordeaux.

The relation between the numbers of growth layers and the length of the glass eels from Nantes and Bordeaux are given in figs. 11 and 14, respectively. These plots are likewise nearly identical to those given for animals caught at various sites along the Dutch coast (fig. 7). Here too, no relation exists between the length of the glass eels and their age.

From 95 animals caught near Bordeaux and

Fig. 11. The age-length relation plotted for the sample from Bordeaux.
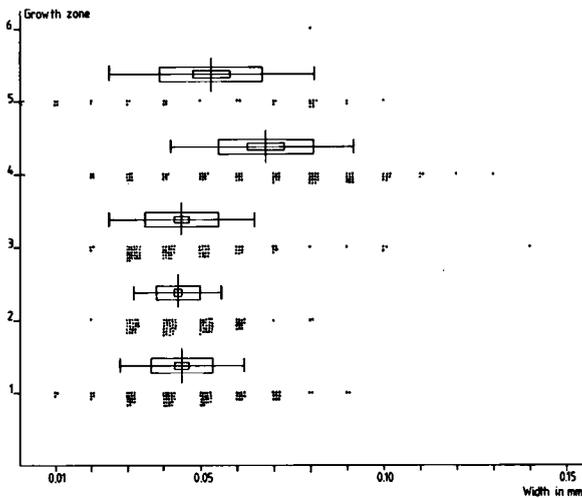
Fig. 12. Width of the successive growth zones in the otoliths of 95 glass eels from Bordeaux. For further explanation see fig. 4.
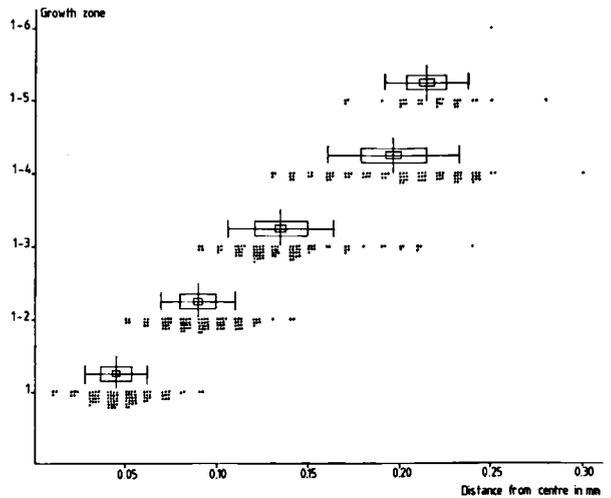
Fig. 13. Distance of the successive opaque border lines from the centre of the otoliths of 95 glass eels from Bordeaux. For further explanation see fig. 4.

DISCUSSION

The translucent growth zone and the opaque border lines in the otoliths of *A. anguilla* show the same features as those shown by the otoliths of *A. rostrata*, described and depicted by Liew (1974). They also fit the descriptions given by Brothers et al. (1976). Each growth zone, including a wide translucent zone and one or a few narrow opaque rings, is by these authors considered to represent a complete growth cycle. This is supported by the fact that the successive zones in an otolith and also in a series of otoliths, are identical. They are not caused by e.g. changes in water temperature met with during migration through various water bodies, because these are far more irregular.

The measurements show that the growth zones vary in width mainly between 0.03 and 0.07 mm. This also means that the increase of the otolith diameter is fairly regular and — in a graph — is along a line which forms an angle of about 45° with the horizontal axis. In most cases, in the translucent part of any growth zone 13 very regular interspaced fine rings are present. When taking Liew's (1974) results into account, it seems most likely that the growth zones are annual increments, implying that the

glass eels arriving along the Dutch and French coasts vary between about two to about six years in age.

If, otherwise, it is supposed that the growth zones are e.g. monthly increments, the duration of the migration of the leptocephali and
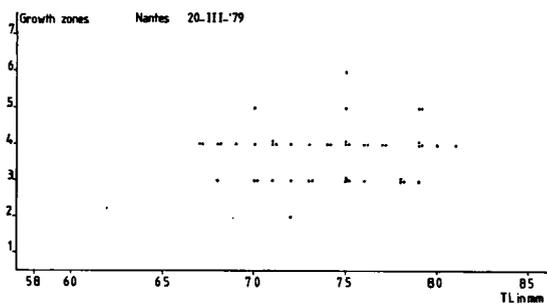
Fig. 14. The age-length relation plotted for the sample from Nantes.

glass eels should be unreasonably short. The migration from the Sargasso Sea towards the European continent should then take about two to seven months, which seems impossible.

Whatever the growth zones may indicate, annual increments or otherwise, they surely demonstrate that the animals have gone through different growth- and life-histories when they enter fresh water.
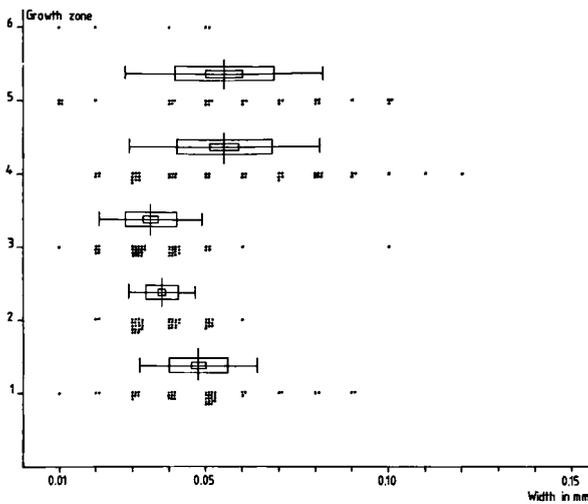
Fig. 15. Width of the successive growth zones in the otoliths of 46 glass eels from Nantes. For further explanation see fig. 4.
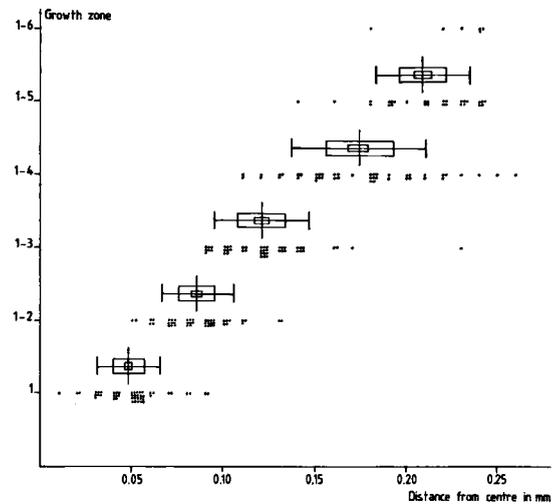
Fig. 16. Distance of the successive opaque border lines from the centre of the otoliths of 46 glass eels from Nantes. For further explanation see fig. 4.

Oceanographic evidence demonstrates that floating objects need at least ten months to drift from the Florida Strait to Great Britain, whereas turtles can cross the Atlantic in about one year (Brongersma, 1967). The distribution of eel larvae in the North Atlantic does not match with Worthington's (1976) opinion about the circulation system. It fits better with the current ideas about the circulation in the North Atlantic, although a number of points are then questionable as well.

In our opinion it seems more likely that the eel larvae use the currents as directional vectors rather than as means of transportation. Their movements in the North Atlantic towards the European continent seems to be far from passive. This is supported by the fact that they can swim vigorously and that in larvae from the central North Atlantic their senses for orientation, viz. smell, vision and inner ear, are very well developed.

The fact that about 60% of the glass eels examined had two or three growth zones in their otoliths is not surprising. It is, however, the remaining 40% with four or more growth zones, that puts question marks to the current ideas about the migration of leptocephali and glass eels in the North Atlantic. These results are not in agreement with Schmidt's (1922; 1923) idea that the migration of leptocephali of A. anguilla from the Sargasso Sea towards the European continental shelf lasts about three years. His views were mainly based on the distribution of length classes of leptocephali over the North Atlantic. Meanwhile, the age-length relation is questionable.

The eel larvae caught in the mid North Atlantic and studied by us had all three complete growth zones in their otoliths. They also had a high number of preanal myomeres and a short postanal distance. These animals were uniform, also with respect to their transparency, though one sample was caught in April 1980 and the other in October 1981.

Most of the larvae caught off the Portuguese coast had four complete growth zones in their otoliths, a low number of preanal myomeres and a varying postanal length of more than 40% of the total length. This, together with the disappeared transparency indicates that here the process of metamorphosis was developing, though most animals still had the typical larval shape. Moreover, about 30% of these animals appeared to lag behind in their development. These still had a high number of preanal myomeres, a short postanal distance and they

showed the same transparency as those caught in the mid North Atlantic, when preserved in 70% alcohol. In three cases the shape of the animals had changed in such a way that behind the head and in the tail the animals were somewhat constricted.

It is clear that the Portuguese larvae are in different stages of metamorphosis, contrary to what is seen in the samples taken in the mid North Atlantic, meaning that some larvae stay longer in the ocean than others do.

The present data indicate that the age composition and developmental stage of the larvae in the mid North Atlantic is homogenous and that the differences in age of the larvae come into existence along the continental shelf. Hence, the great diversity in age of the glass eels has developed along the continental shelf, where, as we know now, some larvae are soon ready to go into metamorphosis, while others take a longer time to reach this stage. Consequently, a certain number of eel larvae has a prolonged stay in the ocean.

At this moment there are no data available about the ages of eel larvae caught further to the north, e.g. along the continental slope northwest, west and southwest of Ireland. Here the situation is completely different from that off the Portuguese coast, which is also due to the very wide continental shelf. So, it is still difficult to explain fully the existing variation in age of the glass eels.

Marshall (1979: 449, 451) states: "In eels, after the yolk has gone, the larvae grow into leptocephali and become planktonic — in the European freshwater eel (*Anguilla anguilla*) for about 2½ to 3 years — before metamorphosis. Their growth and survival for long periods is puzzling, for food is never found in the gut. After close study of leptocephali of the bandtooth conger eel, *Ariosoma balearicum*, Hulet (1978) suggested that before metamorphosis leptocephali derive their nutrition from dissolved and minute particulate material in the sea, and there is preliminary evidence (from tracer work) of their uptake of solutes (Hulet, in litt.). The buccal lining of the leptocephalus of *Ariosoma*, like that over the tentacles of beardworms, bears myriads of microvillae."

REFERENCES

BRONGERSMA, L. D., 1967. Guide for the identification of stranded turtles on British coasts. Publs. Br. Mus. nat. Hist., **659**: 1-23 (Trustees British Museum (Natural History), London).

BROTHERS, E. B., C. F. MATHEWS & R. LASKER, 1976. Daily growth increments in otoliths from larval and adult fishes. Fishery Bull., **74** (1): 1-8.

DEELDER, C. L., 1970. Synopsis of biological data on the eel Anguilla anguilla (Linnaeus, 1758). EIFAC/FAO Fish. Synopsis, **80**: [i-iv], i-iii, 1-8, 1, 1-41, 1, 1-5, 1, 1, 1-10.

EHRENBAUM, E. & H. MARUKAWA, 1913. Über Altersbestimmung und Wachstum beim Aal. Z. Fisch., **14**: 89-127, Taf. IV-V.

FORD, E., 1931. Changes in length during the larval life and metamorphosis of the freshwater eel (Anguilla vulgaris Turt.). J. mar. biol. Ass. U.K., **17**: 987-1000.

GILSON, G., 1908. L'Anguille, sa reproduction, ses migrations et son intérêt économique en Belgique. Annls. Soc. r. zool. malacol. Belg., **43**: 7-58.

GRASSI, G. B., 1896. The reproduction and metamorphosis of the common eel (Anguilla vulgaris). Q. J. microsc. Sci., **39**: 371-385.

HARDEN JONES, F. R., 1970. Fish migration: i-viii, 1-325 (chapter The eel: 69-85) (Edward Arnold Ltd., London).

HEERMANS, W. & J. A. VAN WILLIGEN, 1982. Onderzoek naar de lengtesamenstelling, het gewicht en het voorkomen van naar de Nederlandse binnenwateren trekkende glasaal, Anguilla anguilla L. R.I.V.O. Rapport, ZA 82-01: 1-25.

HULET, W. H., 1978. Structure and functional development of the eel leptocephalus Ariosoma balearicum (De la Roche, 1890). Phil. Trans. R. Soc. Lond., (B) **282** (987): 107-138.

LIEW, P. K. L., 1974. Age determination of American eels based on the structure of their otoliths. In: T. B. BAGENAL ed., The proceedings of an international symposium on the ageing of fish: 124-136 (Unwin Brothers Ltd., The Gresham Press, Old Woking, Surrey).

MARSHALL, N. B., 1979. Developments in deep-sea biology: i-x, 1-566 (Blandford Press, Poole, Dorset).

SCHMIDT, J., 1922. The breeding places of the eel. Phil. Trans. R. Soc. Lond., (B) 211: 179-208.

——, 1923. Die Laichplätze des Flussaales. Int. Revue ges. Hydrobiol. Hydrogr., 11: 1-40, Taf. I-IV.

SCHOTH, M., 1982. Taxonomic studies on the 0-group eel larvae (Anguilla sp.) caught in the Sargasso Sea in 1979. Helgoländer Meeresunters., 35: 279-287.

SINHA, V. R. P. & J. W. JONES, 1975. The European freshwater eel. With a chapter on eel fisheries by R. S. PRITCHETT: i-xv, 1-146 (Liverpool University Press, Liverpool).

STRUBBERG, A., 1913. The metamorphosis of elvers as influenced by outward conditions. Some experiments. Meddr. Kommn. Havunders. (Fisk), 4 (3): 1-11.

TESCH, F. W., 1980. Occurrence of eel Anguilla anguilla larvae west of the European continental shelf, 1971-1977. Envir. Biol. Fishes, 5 (3): 185-190.

TUCKER, D. W., 1959. A new solution to the eel problem. Nature, Lond., 183: 495-501.

UTRECHT, W. L. VAN, 1983. Saurenchelys halimyon, a new species of nettastomid eel, with comments on Saurenchelys cancrivora Peters, 1864, and a preliminary list of larval and metamorphosed Anguilliformes caught in the mid North Atlantic. Bijdr. Dierk., 53 (2): 227-232.

VLADIKOV, V. D. & H. MARCH, 1975. Distribution of leptocephali of the two species of Anguilla in the western North Atlantic, based on collections made between 1933 and 1968. Syllogeus, 6: 1-38.

WORTHINGTON, L. V., 1976. On the North Atlantic circulation. Johns Hopkins Oceanogr. Stud., 6: 1-110.