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Atlantic *Anguilla*. A presentation of old and new data of total numbers of vertebrae with special reference to the occurrence of *Anguilla rostrata* in Europe

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Abstract

The author has placed together all published data known by him about total numbers of vertebrae in the two Atlantic species of *Anguilla*. To this has been added unpublished results from J. Schmidt and from other sources. Moreover selected material from Schmidt's left collections has been worked up for the purpose. The material is presented in a primary table with notes to individual samples.

The European material is considered for three geographical regions separately: a northern, a central and a southern. The areas correspond to the three main routes of elver invasion. It is stated, that in the northern region a relatively high degree of mixing between the two species (.1-.4 per cent *A. rostrata*) was present, while in the southern region specimens of *A. rostrata* were hardly present.

Material of *A. rostrata* from Europe comprises all developmental stages from 0-group elver to silver eel.

Northern samples from certain years showed relatively low numbers of total vertebrae in *A. anguilla*.

Contents

Preface

The total number of vertebrae was early pointed out by Johannes Schmidt as the best distinguishing character between the American and European species of *Anguilla*. Especially his classic documentations from 1913 and 1915 have been used up to present days as a base of reference.

From 1915 to his death, 1933, Schmidt and his collaborators continued their work on meristic characters in Atlantic *Anguilla*, especially counts of total numbers of vertebrae of eels from different geographical areas. These data, however, were never published. Thus at his death Schmidt left several notes and protocols and also a collection of preserved material of Atlantic elvers, which was not worked up at all.

About a decade ago Dr. E. Bertelsen, at that time the director of this institute, asked me to go through the material in question and decide if the rather scattered data could be arranged in such a form, that a publication was justified.

This paper is my answer to Bertelsen's question, and I have taken the opportunity to place together all data – published as well as unpublished – known by me about total numbers of vertebrae in Atlantic *Anguilla*.

Table 1. Sources and size of material.

Source	Number of eels	
	Europe	America
I. Previously published data		
Schmidt, 1909, 13 and 15	3041	882
Boëtius, 1976	6460	
Other	427	184
II. Data left by Schmidt	3496	141
III. New countings from Schmidt's left collection	1965	259
IV. Other unpublished data	465	143
Total	15854	1609

Sources of material

Vertebrae counts of a total of 72 samples are arranged geographically in the primary table pp 104-107 (currently cited as PT). Additional information about stage, season, locality and size is given for individual samples in the notes pp 108-110 (NPT). In NPT the sample no.s are followed by the symbols I-IV given in brackets. Symbols I-IV indicate the source of material and are explained as follows:

I. Previously published material. Proper references to authors are given in NPT. (As I have had the opportunity also to consult the primary data of Schmidt's *published* work, I have been able to give information in NPT, which was not given by Schmidt himself.)

II. Unpublished data left by Schmidt.

III. New data from Schmidt's left collection of preserved specimens worked up for the present purpose.

IV. Other unpublished data worked up from samples recently received or data placed at my disposal by colleagues.

Table 1 gives a survey of the proportions of sources I-IV. All counts in III and in the greater part of IV were made by Mr. Paul Juhlin of this institute. Dr. Jørgen Nielsen and Mr. G. Brovad, both of the Zoological Museum, Copenhagen, have kindly given their help in preparing the X-rays used for vertebrae counting. Dr. E.F. Harding, Statistical Laboratory, Cambridge University, has made the appendix.

The principle of counting was that of Schmidt's, 1913: The short atlas was counted as no. 1 and the last hour-glass shaped vertebra was taken as the next but last vertebra. It has been carefully checked that all samples listed in PT have been counted in accordance with this principle.

Table 2. European and American material. Total of all stages. Distribution of total numbers of vertebrae.

Total number of vertebrae	European material		American material	
	Number	% of total	Number	% of total
120	3	*.02*		
119	30	*.19*		
118	211	*1.33*		
117	1023	*6.45*		
116	2744	*17.31*		
115	4611	*29.08*		
114	4093	*25.82*		
113	2221	*14.01*		
112	692	*4.36*	1	*.06*
111	173	*1.09*	9	*.56*
110	27	*.17*	47	*2.92*
109	9	*.06*	170	*10.57*
108	7	*.04*	416	*25.85*
107	5	*.03*	491	*30.52*
106	3	*.02*	351	*21.81*
105	1	*.01*	97	*6.03*
104	1	*.01*	20	*1.24*
103			7	*.44*
N	15854		1609	
Mean	114.617		107.190	
S.E.	.011		.032	

American versus European vertebrae numbers

In table 2 and fig. 1 distributions are presented of vertebrae numbers of the total material of eels from both sides of the Atlantic.

Vertebrae numbers in the American material are seen to range 103-112, in the European material 104-120. The maximum overlapping taking place at 111 verte-

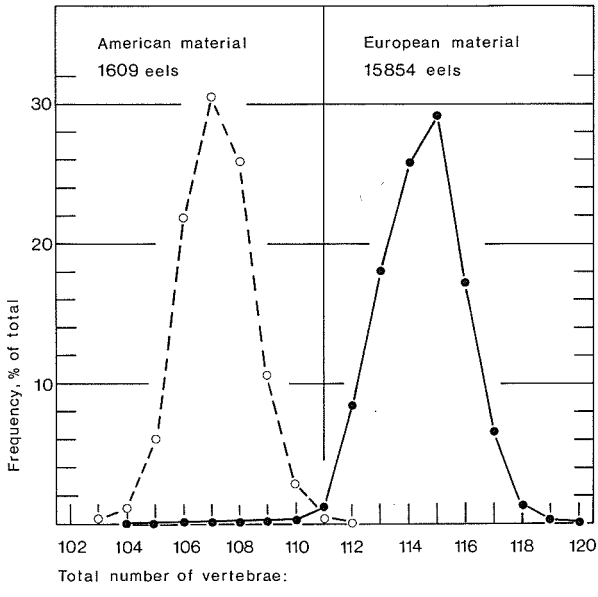

Fig. 1. Distribution of total numbers of vertebrae in total American and European material. Absolute figures are given in table 2.

brae: 1.1 % of the European and 0.6 % of the American material share this number of vertebrae.

Compared with Schmidt, 1913, and Ege, 1939, the present material represents an extension by a factor 5.7 of the European material and by a factor 1.7 of the American. In spite of this, the European mean value of vertebrae number has changed from 114.73 to 114.62, the American mean from 107.23 to 107.19 only.

The present material contains samples of three categories: *1.* pure 0-group elvers, *2.* adult eels only, *3.* 'mixed' samples where both elvers and small yellow eels are present. In table 3 elvers and adults are treated separately and mixed samples not considered at all.

European adult eels have higher mean number of vertebrae than European elvers while American adults have lower mean than American elvers. A statistical treat-

Table 3. European and American material. Total numbers of vertebrae in elvers and adults excluding mixed samples with both elvers and adults.

	Europe		America	
	Elvers	Adults	Elvers	Adults
Mean	114.532	114.672	107.284	107.044
S.E.	.012	.040	.042	.055
Nb. of eels	11840*	1398**	896	595

* 17 specimens with vertebrae ≦ 109 excluded.
** 6 – – – ≦ 109 –

ment of the table 3 data indicate that the differences mentioned are significant in both species.

Boëtius, 1976, analysed a 'mixed' sample (here given as PT no. 25) and stated that vertebrae numbers of the I-group surpassed those of the 0-group elvers. The increase in vertebrae numbers was suggested to be related to growth. The data from table 3 are consistent with this suggestion.

European material, geographical variation

For the present considerations the European material is divided in three geographical units: the northern, the central and the southern area. The areas are given in fig. 2. They roughly correspond to three different migration routes of eel larvae invading the European continental shelf.

In the text to follow the symbol TNV has been introduced for 'total number of vertebrae'.

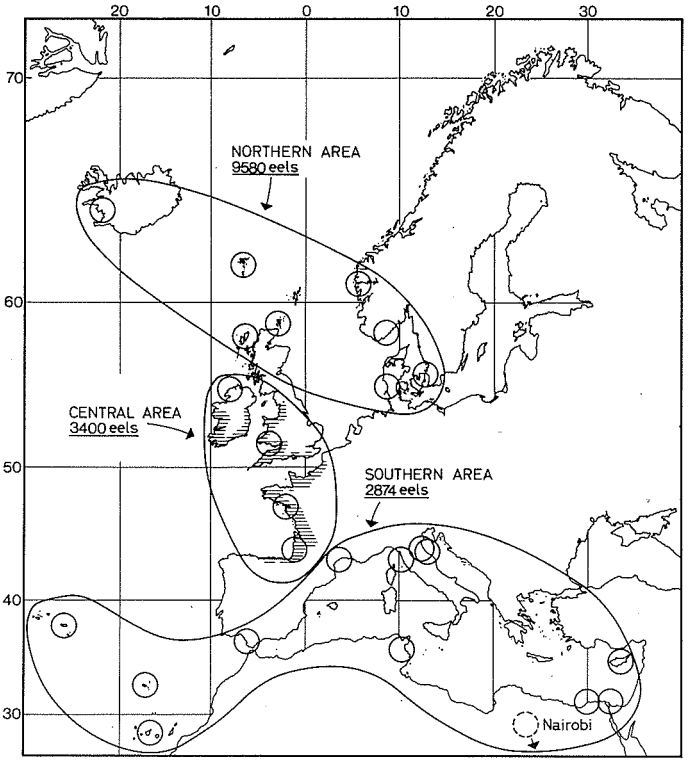

Fig. 2. Map presenting the three areas referred to in the text as northern, central and southern areas. Figures indicate numbers of eels from the area listed in primary table. Circles show sample localities. The hatched zone inside the central area indicates the so-called target area where elvers have been fished commercially.

Table 4. European material. Elvers. Total numbers of vertebrae in northern, central and southern areas.

Total number of vertebrae	Northern area		Central area		Southern area	
	Number	% of total	Number	% of total	Number	% of total
120					1	.04
119	4	.07	6	.18	5	.20
118	58	.96	36	1.10	27	1.07
117	287	4.74	177	5.39	163	6.48
116	939	15.50	517	15.75	472	18.77
115	1673	27.61	917	27.93	808	32.13
114	1684	27.79	901	27.44	642	25.53
113	988	16.31	517	15.75	300	11.93
112	323	5.30	163	4.96	82	3.26
111	75	1.24	45	1.37	14	.56
110	13	.21	2	.06	1	.04
109	4	.07	–	–		
108	3	.05	1	.03		
107	5	.08	–	–		
106	2	.03	–	–		
105	1	.02	–	–		
104			1	.03		
N	6059		3283		2515	
Mean	114.438		114.504		114.744	
S.E.	.018		.024		.026	

Elvers. In table 4 mean values of TNV are given for the total European material of 'pure' 0-group elver samples. On average the vertebrae number increases from the northern to the southern area by about one third of a vertebrae.

A more detailed information, however, is given in fig. 3 where frequencies of TNV means are given for the total European material. The elver material from table 4 is indicated by black circles. From fig. 3 is seen, that elver samples with low TNV means (i.e. $\leqq 114.0$) occur predominantly in the northern area and are not present at all in the southern.

In table 5 localities and dates are given for all samples with TNV means $\leqq 114.0$. Except for a single sample (France) they all origin from northwestern Europe. It is evident from the primary table, that the majority of samples from this region have quite 'normal' TNV means. The ascent of low TNV elvers thus seems to be an irregular phenomenon.

Let us consider the year 1906. Referring to table 5 low TNV elvers ascend in Iceland, Hebrides and Norway from January, 30th to July, 3rd. In the same year, however, 'normal' TNV elvers ascend at the Orkneys (spl. nos 16-18) June, 27th, i.e. 6 days before the Norwegian ascent. It seems reasonable to suggest that the low TNV elvers from 1906 belong to one and same wave of invasion. The 'normal' Orkney elvers could possibly belong to a later arriving invasion.

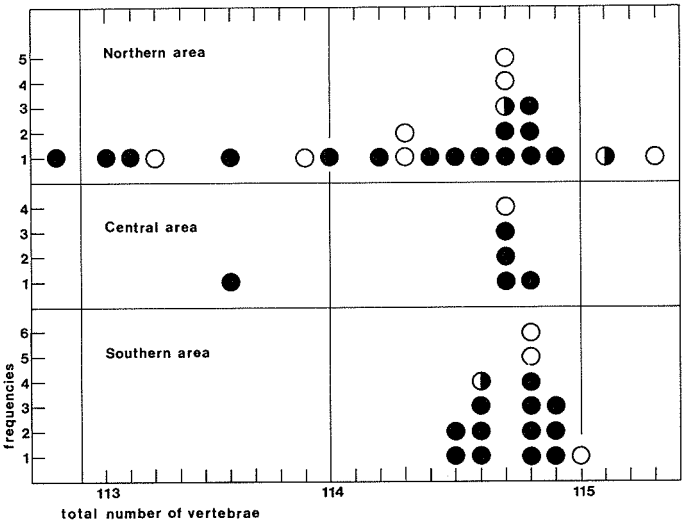

Fig. 3. European material. Frequencies of sample means of total numbers of vertebrae. *Signature*: elvers are indicated by black circles, adults by white circles and 'mixed' samples by black and white circles. (The figure comprises all European samples except nos 5, 15, 38, 39 and 52 where number of specimens in sample was below 10. Samples 3 and 4 were pooled.)

In table 5 the year 1912 is represented by two low TNV samples from the Faroes. Dates of collection were May, 12th and June, 4th. From the same year a sample (no. 13) with 'normal' TNV mean was collected August, 19th at the Faroes. As in 1906 elvers with low TNV seem to precede the 'normal'.

Adults. Two samples from Iceland, 1973 had mean TNV values below 114 (spl.s nos 6 and 7). Eels from these samples no doubt represent more than one year class. A sample of adult eels from Iceland, 1975, (no. 8) had 'normal' mean.

Concluding this section it can be stated, that in some years (or short sequences of years) elvers with low TNV means occur in Europe as the firstly arriving part of the ascent. Invasion seems predominantly to take place in northwestern Europe and apparently not at all in the Mediterranean.

Table 5. European material. Localities and dates of all samples with mean total number of vertebrae ≦ 114.0.

Stage	Total nb. of vertebrae. Mean	Locality	Date	PT no.
Elvers	112.9	Iceland	1906.01.30	1
–	113.1	Hebrides, Stornoway	1906.02.05	19
–	113.2	Norway, Bergen	1906.07.03	20
–	113.6	Faroes	1912.05.12	11
–	113.6	France, Loire	1932.03.?	32
–	114.0	Faroes, Thorshavn	1912.06.04	12
Adult	113.3	Iceland, Grindavik	1973, Autumn	6
–	113.9	Iceland, Hveragerdi	1973, Autumn	7

Anguilla rostrata in Europe

Schmidt has discussed the problem of a possible mixing of American and European stocks of adult eels in his papers 1912 (p. 337), 1915 (p. 5) and 1922 (p. 204). A small overlapping (.56 %) between distributions of vertebrae numbers was taken by him as an indication of a possible mixing.

In no case did Schmidt publish records of eels from European stocks with typical *A. rostrata* vertebrae numbers. His primary notes (see NPT nos 3 and 22), however, indicate that eels from Europe with vertebrae numbers 109 and 106 were present in his material published in 1913. In 1922 he states 'that the stock of eels in Europe is, *practically speaking*, pure, i.e., composed exclusively of Anguilla vulgaris'.

The first published evidence about an eel from Europe with TNV typical of *A. rostrata* was given by Bruun, 1937, who relates that a specimen (68 mm long, 108 vertebrae) was present in a Spanish sample sent to Schmidt from A. Gandolfi Hornyold. This sample is recorded here as no. 33.

Boëtius, 1976, found that *A. rostrata* was represented by small numbers (about .3 %) in elvers from two Danish localities. Eels with 110 vertebrae were considered 'most likely' *A. rostrata*, eels with TNV $\leqq 109$ as true *A. rostrata*. This assumption was supported by determinations of ano-dorsal distances. The material is recorded here as samples nos 25 and 27.

Inspecting the total European material presented here in table 2 it is seen that an expected mode of 107 vertebrae is not present at all. Judging from the table 2 data only, the European material could be considered as one (skew) distribution. Consequently the variation of TNV in *Anguilla anguilla* would cover the full range of the two species. The absence of a 107 mode, however, is not surprising according to the statistical considerations given in the appendix.

A clear 107 mode, however, is demonstrated for northern elvers in table 4. Actually all 5 specimens with 107 vertebrae from the total European material are elvers from the northern area. When placed together with eels from different areas and at different ages the 107 mode is covered as seen in table 2.

In table 6 eels with TNV $\leqq 110$ and $\leqq 109$ are listed for the total European material covered by the primary table. It is seen, that in each case the frequency decreases from the northern to the central area. In the southern area it cannot be

Table 6. European material. Frequencies of eels with total number of vertebrae $\leqq 110$ and $\leqq 109$.

Area	Number of eels counted	$\leqq 110$ vertebrae		$\leqq 109$ vertebrae	
		Number	%	Number	%
Northern	9580	47	.49	24	.25
Central	3400	4	.12	2	.06
Southern	2874	2	.07	0	.00
Total	15854	53	.37	26	.16

Table 7. Eels with ≦ 109 vertebrae from European material.

No.	Date	Locality	Tot. nb. of vertebrae	Total length, mm	Stage	PT no.
1	1905.10.10	Denmark, Kallebod Strand	106	–	silver ♀	22
2	1911, July	Iceland, Faxa Bay, Àlafoss	109	–	small yellow	3 + 4
3	1912.05.12	Faroes	106	68	elver	11
4	1912.06.04	Faroes, Thorshavn	107	62	elver	12
5	1930, Dec.	Spain, San Sebastian	108	68	elver	33
6	1932, March	France, Loire	104	73	elver	32
7	1969.07.04	Denmark, Esrom	109	86	I-group	25
8	– –	– –	108	90	I-group	25
9	1971.07.16	Denmark, Arresø	109	218	yellow	26
10	– –	– –	109	247	yellow	26
11-23*	1972, Apr.-June	Denmark, Højer	105-109	63-75	elvers	27
24	1973, autumn	Iceland, Hveragerdi	108	–	yellow	7
25	– –	– –	108	–	yellow	7
26	– –	– –	109	–	yellow	7

*For details, see Boëtius, 1976

stated with certainty if *A. rostrata* is present at all. Details of the 26 specimens with vertebrae ≦ 109 are listed in table 7. The specimens are seen to cover the full range of developmental stages.

Of special interest is the Danish silver eel with 106 vertebrae listed as no. 1 in table 7. The eel was caught together with 127 female silver *A. anguilla* leaving the Baltic on their autumnal migration. *A. rostrata* thus seems capable not only to share growth conditions with *A. anguilla* but also to turn silver and leave (for the Sargasso Sea?) together with true European silver eels.

The eel was caught in 1909. Future records of adult *A. rostrata* in European waters should be considered with a certain caution. During the last decades adult American eels have been imported live into several European countries on a commercial scale.

American material

The hitherto unpublished data on TNV of American eels given here do not add much to what was already known. New data from Greenland (no. 54) and Bermuda (nos 70 and 71) confirm earlier statements, that these two areas are populated by *A. rostrata* solely.

Mean TNV values of samples with more than 10 specimens all range between 107.0 and 107.5 except for sample no. 58. This sample (from Woods Hole, Mass.) was counted and published by Schmidt, 1909. Mean TNV of the 19 specimens was extremely high, 108.6, and one of the eels had 112 vertebrae.

Sample no. 66 (from Biloxi, Miss.) was originally counted and published by Petersen, 1905, and claimed to contain a specimen with 113 vertebrae. The sample was recounted by Schmidt and latest from X-rays by me. Both recountings gave

111 vertebrae as a maximum (see notes to no. 66).

Thus the only possible *A. anguilla* (out of 1609) from American coastal areas seems to be the 112-eel from sample no. 58. Being accompanied by eels with unusually high vertebrae numbers it should possibly be considered a hybrid.

Discussion

Position and extension of the spawning area of *A. anguilla* is a rather well established result of Schmidt's classic investigations. Corresponding information about *A. rostrata* is very poor. Vladykov, 1964, has proposed the spawning area of *A. rostrata* to be situated south of that of *A. anguilla* (not west of *A.a.* as did Schmidt). Spawning of the two Atlantic species are likely to overlap in space and possibly also in time.

Based on surface current studies, Harden Jones, 1968, has constructed the drifts of two patches of eel larvae, both hatched in March in each of the two supposed breeding areas. The main routes are re-drawn (from his fig. 21) in fig. 4 in the present paper. On both sides of the central *A. anguilla*-route marginal branches are added by dotted lines. The northern branch (N) indicates, that *A. anguilla* larvae emerging from the southern part of the breeding area end up in northern Europe.

As the northern branch has the closest relation to the *A. rostrata* route it is

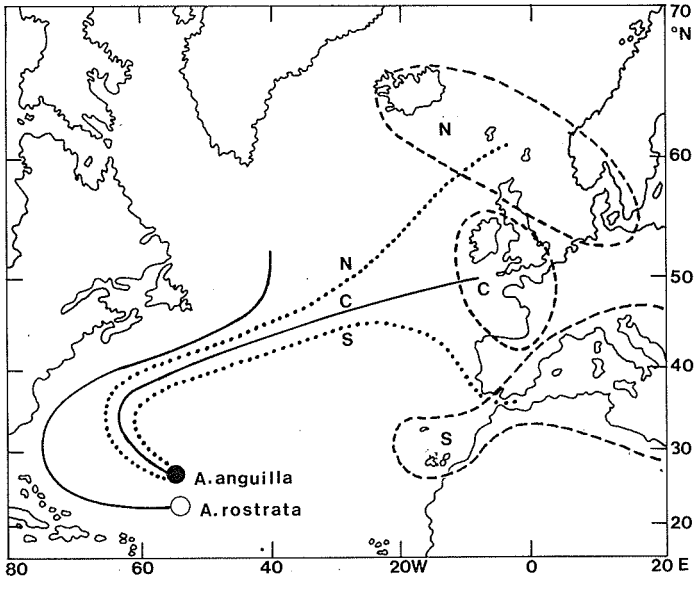

Fig. 4. Map and fully drawn routes of drifting Atlantic eel larvae re-drawn from Harden Jones, 1968. The dotted lines indicate the supposed routes of *A. anguilla* from southernly and northernly situated positions within the European breeding area. Larvae of southernly origin are seen to form the northern branch supplying area N with elvers while larvae hatched in the northern part of the breeding area end up in area S.

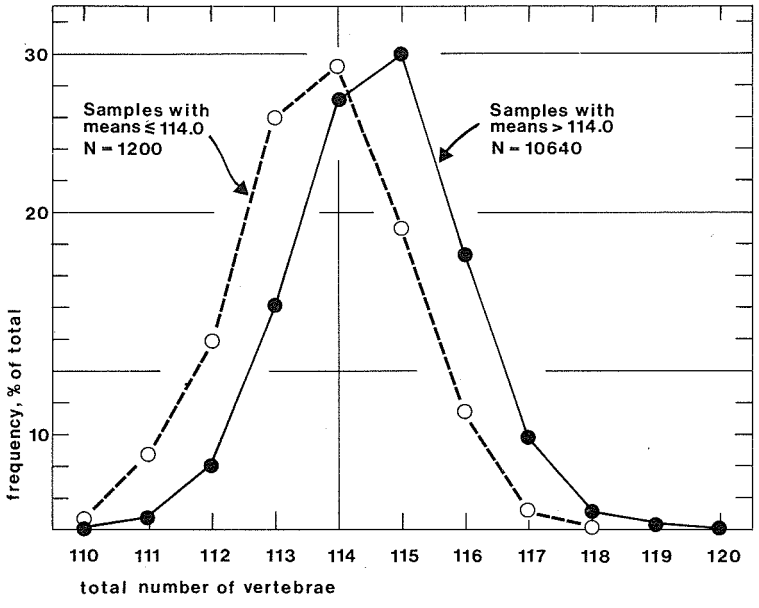

Fig. 5. European elvers. Distributions of total numbers of vertebrae of pooled samples with means ≦ 114.0 and > 114.0.

reasonable to expect a relatively high degree of mixing of the two species in northern Europe. This is actually what has been stated in the present paper.

Overlapping of the two breeding areas could possibly cause hybrydization. In this case also the hybrids would most likely end up in northern Europe. The presence of relatively high numbers of eels with 111 vertebrae in northern and central areas (table 4) might indicate a small amount of hybrids.

It was demonstrated earlier in this paper that samples from certain years showed low TNV values. In fig. 5 TNV distributions of the total material of European pure elver samples are given for samples with means ≦ 114 and > 114 respectively. Tests for skewness have proved that both distributions are highly symmetrical. There is hardly reason to believe, that the low vertebrae numbers in the ≦ 114 group are due to mixing with hybrid specimens.

Concludingly it is proposed, that in some years the process of differentiation of vertebrae number seems to stop a little earlier than usual.

Little is known about the larval TNV during growth. Jespersen, 1942, gave myomer counts of larvae (of total lengths > 40 mm) from the Danish expeditions 1913 and 1920-21. He concluded that for both species the number of myomers would exceed that of the final vertebrae number by about one. Vladykov & March, 1975, however, have myomer counts which at an average were 3-4 myomers lower than those of Jespersen's. This difference Vladykov & March attribute to several causes: 'counting technique, different numbers of specimens, variation in size of specimens, and difference in collecting localities.'

Primary table

Total number of vertebrae	European material, Northern Area								
	Iceland								Faroes
	*no. 1**	*no. 2*	*no. 3*	*no. 4*	*no. 5*	*no. 6*	*no. 7*	*no. 8*	*no. 9*
120									
119			1					1	
118			2	3				1	
117			10	11	1		7	5	
116		2	30	27	2	4	20	19	3
115	8	7	62	50	3	3	23	18	10
114	9	2	47	42		3	19	18	8
113	14	2	19	23		7	10	26	1
112	8	2	8	4		5	10	10	1
111	7		–	–		4	10	1	1
110	2		–	2			5		
109			1				1		
108							2		
107									
106									
105									
104									
103									
N:	48	15	180	162	6	26	107	99	24
Mean:	112.9	114.3	114.69	114.68	115.7	113.3	113.89	114.31	114.4

Total number of vertebrae	Northern Area, cont.								
	Faroes, cont.						Orkneys		
	no. 10	*no. 11*	*no. 12*	*no. 13*	*no. 14*	*no. 15*	*no. 16*	*no. 17*	*no. 18*
120									
119									
118	3			1			1	1	
117	22		7	2	3		6	2	
116	55	8	40	7	18	1	15	5	9
115	75	25	88	11	28	1	25	9	13
114	80	48	98	13	24	3	20	8	19
113	42	39	76	5	4	1	7	5	13
112	3	16	29	2	5		–	1	4
111		7	8		1		1		
110		1	3						
109		–	–						
108		–	–						
107		–	1						
106		1							
105									
104									
103									
N:	280	145	350	41	83	6	75	31	58
Mean:	114.77	113.57	114.03	114.6	114.68	114.3	114.89	114.7	114.17

*No. of sample refers to notes pp 108-110

Total number of vertebrae	Northern Area, cont.								
	Hebrides	Norway		Denmark					
	no. 19	*no. 20*	*no. 21*	*no. 22*	*no. 23*	*no. 24*	*no. 25*	*no. 26*	*no. 27*
120							2		
119			1		1		11		3
118			6	2	5	6	63	7	41
117			26	9	19	22	253	32	204
116	2		69	22	46	56	475	58	675
115	6	1	119	43	82	84	679	69	1208
114	10	5	96	26	71	81	441	42	1190
113	15	3	74	17	31	34	169	13	699
112	6	4	22	5	9	8	41	1	227
111	3		2	3	2	2	14	–	43
110			3	–			–	–	7
109				–			1	2	4
108				–			1		3
107				–					4
106				1					1
105									1
104									
103									
N:	42	13	418	128	266	293	2150	224	4310
Mean:	113.4	113.2	114.55	114.61	114.76	114.78	115.12	115.27	114.45

Total number of vertebrae	Central Area						Southern Area		
	Ireland	England		France		Spain	Acores		Madeira
	no. 28	*no. 29*	*no. 30*	*no. 31*	*no. 32*	*no. 33*	*no. 34*	*no. 35*	*no. 36*
120									
119		1	4			1			1
118	2	7	11	3	2	13			3
117	9	26	51	15	7	78	2	6	16
116	20	87	144	43	39	204	3	18	32
115	36	154	236	65	100	362	12	32	57
114	31	133	203	58	180	327	7	27	31
113	14	60	98	33	165	161	5	13	24
112	3	13	23	11	79	37	1	4	8
111	2	4	2		31	8		1	1
110			1		1	–			
109					–	–			
108					–	1			
107					–				
106					–				
105					–				
104					1				
103									
N:	117	485	773	228	605	1192	30	101	173
Mean:	114.73	114.70	114.76	114.67	113.63	114.67	114.6	114.61	114.83

Total number of vertebrae	Southern Area, cont.								
	Madeira, cont.		Canary Isl.	Spain	France	Tunisia	Italy		
	no. 37	*no. 38*	*no. 39*	*no. 40*	*no. 41*	*no. 42*	*no. 43*	*no. 44*	*no. 45*
120									
119							1		
118				1	2		1	5	3
117	4		1	5	12	6	14	24	15
116	21		1	2	37	21	29	61	33
115	46			4	43	29	33	130	70
114	50	2		6	36	27	33	122	42
113	16	–		4	18	11	14	49	28
112	4	–			4	6	7	15	5
111	2	1				1	1	3	1
110									
109									
108									
107									
106									
105									
104									
103									
N:	143	3	2	22	152	101	133	409	197
Mean:	114.49	113	116.5	115.0	114.89	114.62	114.83	114.63	114.77

Total number of vertebrae	Southern Area, cont.							American material	
	Italy, cont.		Egypt			Cyprus	E. Africa	Greenland	
	no. 46	*no. 47*	*no. 48*	*no. 49*	*no. 50*	*no. 51*	*no. 52*	*no. 53*	*no. 54*
120				1					
119	1		1	2					
118	2	3	3	3	3	2			
117	24	9	12	21	18	6	1		
116	65	40	44	45	70	15	2		
115	106	75	54	89	97	28	3		
114	66	66	44	69	82	26	2		
113	27	42	17	28	35	9	1		
112	10	9	6	5	9	2			
111	2	1		2	1	–			
110				1		1			1
109									2
108									5
107								3	7
106								1	6
105								2	–
104									2
103									
N:	303	245	181	266	315	89	9	6	23
Mean:	114.88	114.53	114.92	114.83	114.78	114.75	115.0	106.2	107.0

Total number of vertebrae	American material, cont.								
	Canada			U.S.A. Mass.				Wash. D.C.	
	no. 55	*no. 56*	*no. 57*	*no. 58*	*no. 59*	*no. 60*	*no. 61*	*no. 62*	*no. 63*
120									
119									
118									
117									
116									
115									
114									
113									
112				1					
111		1		–		3		1	
110	1	2		3	1	19	2	4	3
109	11	12	1	6	7	61	9	15	24
108	18	21	1	6	23	131	24	36	59
107	24	24	2	2	34	162	35	31	76
106	23	30	1	1	16	107	19	27	61
105	8	4			11	16	9	3	19
104	1	3			1	3	1	1	1
103		3			1			1	1
N:	86	100	5	19	94	502	99	119	244
Mean:	107.01	106.96	107.4	108.6	106.95	107.35	107.08	107.35	107.04

Total number of vertebrae	American material, cont.								
	N.C.	Georgia	Miss.	Virgin Isl.		Bermuda			Trinidad
	no. 64	*no. 65*	*no. 66*	*no. 67*	*no. 68*	*no. 69*	*no. 70*	*no. 71*	*no. 72*
120									
119									
118									
117									
116									
115									
114									
113									
112									
111			1			3			
110	7		–	3		1			
109	6	1	–	11		3	1		
108	20	4	–	29	8	23	3	3	2
107	24	5	1	30	4	21	4	2	
106	18	1	2	20	1	15	2		
105	3	1	2	7		10	2		
104	2	1	1	1		2			
103						1			
N:	80	13	7	101	13	79	12	5	2
Mean:	107.29	107.0	106.3	107.23	107.5	106.99	106.9	107.6	108

Notes to primary table

Symbols I-IV given in brackets after sample no.s stand for:

I: data cited from literature.
II: unpublished data left by Schmidt and co-workers.
III: data worked up by the author from preserved material left by Schmidt.
IV: data from recent material worked up by the author and others.

Other symbols:

E: elvers. Y: yellow eels. S: silver eels.

Measurements given in mm indicate mean total length. Ranges are given in brackets.

No. 1 (III) E. 1906.01.30. 'Iceland' – no locality given. 70.3 mm (65-75).
No. 2 (II) Adult eels. 1906.12.?. Reykjavik.
No. 3 (I) Schmidt, 1913. tab. IV, col. 1. E + small Y. 1911.07.9-19. Àlafoss, Faxa Bay. At least two year classes the youngest of which average 76 mm (61-86). In the present table is added a specimen with 109 vertebrae which according to Schmidt's primary notes has been excluded without comments.
No. 4 (III) Date and locality as in no. 3. Youngest year class average 77 mm (64-92), the remaining part (about 20 %) range from 95 to 135 mm.
No. 5 (IV) Y. 1972.05.10. Kollafirdir near Reykjavik. 302 mm (215-366). Received from Dr. Th. Gudjónsson.
No. 6 (IV) Y. 1973, autumn. Grindavik, the harbour.
No. 7 (IV) Y. 1973, autumn. Freshwater near Hveragerdi. (about 100-400). Prof. C.G. Williams, State Univ. New York at Stony Brook, has kindly allowed me to cite his countings of samples no.s 6 and 7 and to check the principle of counting from his X-rays.
No. 8 (IV) Y. 1975.08. Lóni Hornafjord, SE-Iceland. 330 mm (240-420). Received from Skúli Pálsson. Reykjavik.
No. 9 (III) E. 1909.08.06. Thorshavn. 66.7 mm (60-73).
No. 10 (I) Schmidt, 1913, tab. IV, col. 2. E. 1911.05.?. Thorshavn. 67.8 mm (58-79).
No. 11 (III) E. 1912.05.12. 'Faroes'. 66.6 mm (59-75).
No. 12 (III) E. 1912.06.04. Sandegærde near Thorshavn. 68.3 mm (61-81).
No. 13 (III) E. 1912.08.19. Small river to Kalbaksfjord. 66.1 mm (60-73).
No. 14 (III) E. 1913.08.14. Kalbaksfjord. 66.1 mm (60-73).
No. 15 (III) Small Y. 1925. Trangisvaag. 113 mm (92-135).
No. 16 (I) Schmidt, 1913, tab. IV, col. 3. E. 1906.06.27. Stromness.
No. 17 (II) E. Date and locality as in no. 16.
No. 18 (III) E. Date and locality as in no. 16. 68.0 mm (62-73).
No. 19 (III) E. 1906.02.05. Stornoway. 67.2 mm (60-75).
No. 20 (III) E. 1906.07.03. Bergen. 68.7 mm (65-74) + 1 spec. 113 mm.
No. 21 (I) Sivertsen, 1938, pp 10-11. Y + S. 1931-32. Pooled data of 3 samples from the Arendal district. About 550 (about 250-900).
No. 22 (I) Schmidt, 1913, tab. IV, col. 8. S (♀♀). 1905.10.10. The Sound near Copenhagen. In the present table is added a specimen with 106 vertebrae which according to Schmidt's primary notes has been excluded without comments.
No. 23 (I) Schmidt, 1915, tab. II, col. 1. E. 1911. Nykøbing, Sealand. 70.2 mm (59-81).
No. 24 (II) E. 1927.05.05. Højer Sluse (North Sea). 70.4 mm (62-80).
No. 25 (I) Boëtius, 1976. E and small Y. 1969.07.04. Esrom, Sealand. About 84 mm (62-119).
No. 26 (IV) Y. 1971.07.16. Lake Arresø, Sealand. 225 mm (170-310).
No. 27 (I) Boëtius, 1976. E. 1972. Pooled data from 3 samples: 1972.04.24, 72.05.14 and 72.06.09. Højer Sluse (North Sea). 72 mm (60-83).
No. 28 (I) Schmidt, 1913, tab. IV, col. 4. S (♀♀). 1905.10.30. Toomebridge.
No. 29 (I) Schmidt, 1913, tab. IV, col. 5, 6 and 7. E. 1908, 1909 and 1911. Bristol Channel.
No. 30 (II) E. 1932.03.25. Epney, Severn. 72.1 mm (59-83).
No. 31 (I) Schmidt, 1913, tab. IV, col. 9. E. 1906. Bayonne.
No. 32 (III) E. 1932.03.?. Loire. 77.1 mm (66-87).

No. 33 (II) E. 1930.12.?. San Sebastian. 74.6 mm (65-83).
No. 34 (I) Schmidt, 1913, tab. IV, col. 11. E. 1909.
No. 35 (I) Schmidt, 1913, tab. IV, col. 11. E and small Y. 1912.01.04. 88 E: 61.8 mm (51-73), 13 Y: (78-102).
No. 36 (I) Schmidt, 1913, tab. IV, col. 10. E. 1911.08.?. Funchal. 66.9 mm (53-75).
No. 37 (III) E. 1921.05.02. 65.3 mm (57-74).
No. 38 (IV) Y. 1973.10.10. Funchal. Museum specimens (MMF 23019) borrowed for X-raying from Dr. G.E. Maul. 40, 41 and 56 cm.
No. 39 (II) Adult eels. 1911. St. Cruz de Tenerife.
No. 40 (II) Adult eels. 1911. Cadiz.
No. 41 (I) Schmidt, 1913, tab. IV, col. 12. E. 1911.01.26. Cette. 69.4 mm (58-80).
No. 42 (II) E. 1930.01.25. Salammbo. 69.4 mm (62-77).
No. 43 (I) Schmidt, 1913, tab. IV, col. 14. Y. 1906. Ravenna.
No. 44 (I) Schmidt, 1913, tab. IV, col. 13. E. 1911.01.27. Livorno. 67.7 mm (58-78).
No. 45 (I) Schmidt, 1913, tab. IV, col. 15. E. 1911.02.23. Comacchio. 67.5 mm (58-73).
No. 46 (II) E. 1922.12.?. Livorno. 70.6 mm (58-82).
No. 47 (III) E. 1931.05.16. Comacchio. 61.0 mm (55-69).
No. 48 (II) E. 1920.02.?. Port Said.
No. 49 (II) E. 1920.12.18. Mex, Alexandria.
No. 50 (II) E. 1922.01.01. Mex, Alexandria. 299 E: 59.3 mm (54-65) and 16 small Y: (67-96).
No. 51 (I) Schmidt, 1913, tab. IV, col. 16. S. 1911.05.13.
No. 52 (I) Schmidt, 1925, p. 335 and Ege, 1939, p. 128: Red Sea, Massaua. 1870. 228 mm. 115 vertebrae. Ege, 1939, p. 91, 129 and 149: Nairobi. 1931.12.03. 277, 290 and 298 mm. Vertebrae: 116, 117 and 115. 'East Africa'. 471-600 mm. Vertebrae: 113-116. 6 specimens in sample, vertebrae counted in 5 sp. only.
Comment. Tesch, 1973, p. 88 considers the two East African records doubtful. With reference to Jubb, 1961, p. 25 he remarks that confusion with *A. mossambica* is possible. Vertebrae numbers of this species, however, range between 100 and 106. I have consulted Ege's primary notes on the East African eels and also examined the 3 Nairobi specimens (ZMUC P31263-265). I can only confirm Ege's statements.
No. 53 (I) Jensen, 1937. Adult eels. 1841-1920. (Eels from Greenland mentioned by Schmidt, 1909, 1912 and 1913 are identical with eels no. 4 and 5 in Jensen's list).
No. 54 (IV) 1 specimen: Adult. 1965.08.28. Ilua Tunngdliarfik (ZMUC P31196). 22 specimens: Y + S. The fjord Kangerdluarssoruseq. 452 mm (345-667). Received from Mr. Bjarne Pedersen, Færingehavn.
No. 55 (I) Schmidt, 1913, tab. V, col. 1. Y. 1905. St. Lawrence. (550-750).
No. 56 (IV) Y. 1961, May-August. New Foundland. (400-800). Vertebrae counted by Dr. Gordon R. Williamson who kindly has placed his data at my disposal.
No. 57 (IV) E. 1967.08.14. Topsail. New Foundland. 74.6 mm (69-79). Received from Gordon R. Williamson.
No. 58 (I) Schmidt, 1909, p. 10. E. 1872.03.01. Woods Hole. 57.4 mm (52-63).
No. 59 (I) Schmidt, 1913, tab. VI, col. 2. Y. 1906. Tisbury. (400-700).
No. 60 (I) Schmidt, 1915, tab. I, col. 1. E. 1913.05.07. W. Gloucester, Little River. 57.1 mm (48-66).
No. 61 (I) Ege, 1939, tab. 135. Y. 1935. Mass. (250-500).
No. 62 (II) E. 1921.04.18. Potomac River, Chain Bridge. 54.7 mm (48-61).
No. 63 (III) Date and locality as in no. 62. 55.8 mm (50-64).
No. 64 (I) Schmidt, 1913, tab. VI, col. 3. Small Y. 1905.05.?. Weldon.
No. 65 (IV) Y. 1971. August-October. Sapelo Island. (310-510). Received from Dr. E. Rasmussen.
No. 66 (III) E. 1854. Biloxi. (45-53). 9 specimens, ZMUC 164-172. Vertebrae were counted and published by Petersen, 1905, as follows: 103, 104, 106, 106, 109, 109 and 113 (!). Later (unpublished) counts by Schmidt gave: 102, 104, 105, 105, 108, 108, 108, 108 and 111. The sample was re-counted by me from X-rays in 1970. 7 specimens were easily counted, 2 were discarded, possibly the same specimens discarded by Petersen. The figures given in the present table are those from 1970.

No. 67 (I) Schmidt, 1913, tab. VI, col. 4. St. Croix. 3 specimens: E. 1896.01.16. 6 specimens: E. 1906.02.14. (49-73). 92 specimens: small Y. 1911, June, July.
No. 68 (III) Y. 1913-15. St. Croix and St. Thomas. (95-540).
No. 69 (I) Boëtius & Boëtius, 1967. Y. 1966. (180-580).
No. 70 (II) E. + small Y. 58.8 mm (53-74). Received 1912 from U.S. Nat. Mus.
No. 71 (II) E. + small Y. Mud of a Mangrove swamp, Hungry Bay near Hamilton. 56.8 mm (54-60). received from Prof. Mark, 1915.
No. 72 (IV) Y. 1974. Shark River. 35 and 43 cm. Borrowed for X-raying from Dr. Gordon R. Williamson, U.K.

References

Boëtius. I. & J. Boëtius, 1967: Eels, *Anguilla rostrata*, LeSueur, in Bermuda. – Vidensk. Meddr Dansk Naturh. Foren. *130*: 63-84.

Boëtius, J., 1976: Elvers, *Anguilla anguilla* and *Anguilla rostrata* from two Danish localities. Size, body weight, developmental stage and number of vertebrae related to time of ascent. – Meddr Danm. Fisk.- og Havuders. N.S. *7*: 199-220.

Bruun, A.F., 1937: Contributions to the life histories of the deep sea eels: *Synaphobranchidae*. – Dana-Report No. 9.

Ege, V., 1939: A revision of the genus *Anguilla* Shaw. A systematic, phylogenetic and geographical study. – Dana-Report No. 16.

Jensen, A.S., 1937: Remarks on the Greenland eel, its occurrence and reference to *Anguilla rostrata*. – Medd. om Grønland. *118*(9).

Jespersen, P., 1942: Indo-Pacific leptocephalids of the genus *Anguilla*. Systematic and biological studies. – Dana-Report No. 22.

Jones, F.R.H., 1968: Fish migration. – London, Edw. Arnold. 325 pp.

Jubb, R.A., 1961: The freshwater eels (*Anguilla* spp.) of Southern Africa. An introduction to their identification and biology. – Ann. of the Cape Provincial Museums. *1*: 15-48.

Petersen, C.G.J., 1905: Larval eels (*Leptocephalus brevirostris*) of the Atlantic coasts of Europe. – Medd. Komm. Havunders. Ser. Fiskeri. *1*(5).

Schmidt, J., 1909: On the distribution of fresh-water eels (*Anguilla*) throughout the world. I. Atlantic Ocean and adjacent regions. – Medd. Komm. Havunders. Ser. Fiskeri. *3*(7).

Schmidt, J., 1912: Danish researches in the Atlantic and Mediterranean on the life-history of the freshwater-eel (*Anguilla vulgaris*). – Int. revue d. ges. Hydrobiol. u. Hydrographie. *5*: 317-342.

Schmidt, J., 1913: First report on eel investigations. – Rapp. et Proc.-verb. Cons. Int. Expl. Mer. *18*: 1-30.

Schmidt, J., 1915: Second report on eel investigations. – Rapp. et Proc.-verb. Cons. Int. Expl. Mer. *23*: 1-24.

Schmidt, J., 1925: On the distribution of the Fresh-water Eels (*Anguilla*) throughout the world. II. Indo-Pacific region. – D. Kgl. Danske Vid. Selsk. Skr., Naturvidensk. og Mathem. Afd., 8. Række, *10*(4): 327-382.

Sivertsen, E., 1938: Undersøkelser over forholdet mellem spiss- og bredhodet ål og deres næring. – Fiskeridirektoratets Skrifter, Serie Havundersøkelser. (Report on Norwegian Fishery and Marine Investigations *5*(8))

Tesch, F.-W., 1973: Der Aal. Biologie und Fischerei. – Hamburg u. Berlin, Paul Parey. 306 pp.

Vladykov, V.D., 1964: Quest for the true breeding area of American Eel (*Anguilla rostrata* LeSueur). – J. Fish. Res. Bd. Can. *21*: 1523-1530.

Vladykov, 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 No. 6. National Museum of Natural Sciences. National Museums of Canada. Ottawa.

Appendix *by E.F. Harding*

Estimation of numbers of A. rostrata in European material.

It is assumed that

(i) any specimen with TNV less than 109 is certainly *A. rostrata.*

(ii) the TNV numbers of genuine *rostrata* in Europe follow (proportionally) the same frequencies as in America.

Of the American material in table 2, 86 % have TNV less than 109. Working from the material in the Primary Table, and ignoring mixed samples, the corresponding proportion for elvers is 84 %, and for adults 88 %.

Of the European material in table 2, 17 specimens have TNV less than 109. By the above assumptions we may estimate these as being 86 % of the total number of *rostrata* present (or at least between 84 % – the elver figure – and 88 %, the adult figure). The total number may thus be estimated as 17/.86 = 19.8 (or at least between 17/.88 = 19.3 and 17/.84 = 20.2). Taking 20 as a round figure, we have .13 % of European material (15854 specimens) as *rostrata.*

The expected distribution of these 20 by TNV, compared with that observed, is as follows:

TNV	*rostrata* observed	*rostrata* expected
112	?	.01
111	?	.11
110	?	.58
109	?	2.11
108	7	5.17
107	5	6.10
106	3	4.36
105	1	1.21
104	1	.25
103	0	.09

The absence of an 'expected mode' at TNV = 107 in the total European material of table 2 is not surprising, the observed frequencies at 108, 107, 106 (7,5,3) being well within acceptable statistical variation from the ideal frequencies (5.17, 6.10, 4.36).

Confidence limits for the expected number of *rostrata* per 1000 European specimens have been calculated, on the basis of assumptions (i) and (ii) above, as confidence limits for the mean of a Poisson distribution (see Biometrika Tables for Statisticians, E.S. Pearson & H.O. Hartley (eds), vol. I, Cambridge University Press 1966, p. 227). The central estimate is 20/15854.

Numbers of *A. rostrata* per 1000 European specimens: Central estimate and confidence limits (99 %, 95 %, 90 %).

Confidence Level	Lower Limit	Upper Limit	Central Estimate
99 %	.6	2.3	1.3
95 %	.7	2.0	
90 %	.8	1.9	

The residual doubt, about whether to take 84 %, 86 % or 88 % as the proportion of *rostrata* with TNV less than 109, has only a negligible influence on the estimates. A greater, but unassessable, uncertainty attaches to the use of assumption (ii) – but there is no better substitute. Thus the above confidence limits should be regarded as over-precise: they should certainly be somewhat widened, but by an unknown amount.

Corresponding calculations for samples with elvers only give:

(a) 13 in 11857 (N + C + S), Central Estimate 1.28/1000.
.68, 2.18 as 95 % Confidence Interval for numbers per 1000.

(b) 11 in 6059 (Northern), Central Estimate 2.11/1000.
1.05, 3.78 as 95 % Confidence Interval for numbers per 1000.

Similarly for samples with adults only (Northern area) we get

(c) 3 in 1029, Central Estimate 3.39/1000.
.38, 12.41 as 95 % Confidence Interval for numbers per 1000.