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VARIATION OF THE OCEANIC LARVAL MIGRATION OF *Anguilla anguilla* (L.) GLASS EELS FROM A TWO YEAR STUDY IN THE VILAINE ESTUARY (FRANCE)

Y. Désaunay[1], *D. Guérault*[1] *and R. Lecomte-Finiger*[2]

[1]IFREMER, Rue de l'Ile d'Yeu, Bp 1049 44037 Nantes cedex 01, France
[2]Université de Perpignan, Laboratoire de Biologie Marine, Faculté des Sciences, Avenue de Villeneuve, 66025 Perpignan, France

A B S T R A C T. Glass eels were sampled nearly monthly in 1990 and from September 1991 to December 1992 in the Vilaine estuary (Northern Bay of Biscay). Biometry and otolith examinations were carried out. In both years the immigration showed a continuous flow, with the same seasonal pattern. Length and weight showed similar trends, with some differences between seasonal mean values. The average total age of all the samples varied from 7 to 10 months. Although the leptocephalus phase appeared to be rather steady (160 to 210 days), the duration of transport of metamorphosing glass eels across the continental shelf varied from 50 to 70 days in 1990 and from 80 to 100 days in 1991-1992. In addition, the otolith structure was of various types as regards the end of the larval migration. This seasonal variation is supposed to affect the estuarine recruitment through the length of the starvation period.

Key words: GLASS EEL, LARVAL MIGRATION, RIVER ESTUARY, BIOMETRY, OTOLITH EXAMINATION

INTRODUCTION

Various hypotheses about the early life history of *Anguilla anguilla* (L.) have been assumed from morphological and biometric observations of oceanic larvae. Successive proposals led to a decrease in the estimated larval migration, from 2.5 or 3 years (Schmidt 1922) to 2 years (Tesch et al. 1986) and to 12 to 15 months (Wegner 1982). Conversely, the global pattern of distribution of the eel larval stages over the Atlantic Ocean is still commonly accepted, even if some assumptions related to the migration routes are questionable. After a widespread diffusion of pelagic leptocephali over 5 to 6000 km, eel larvae begin to transform into glass eels when arriving above the continental shelf edge. In the meantime they are likely to change to a demersal behaviour to reach the coastal regions after having crossed the continental shelf (about 50 to 500 km minimum width according to the latitude) without feeding.

In addition to biometric observations, the otolith examination recently provided new information on the duration of oceanic stages and the dynamics of growth and transport. Using the otoliths of immigrating glass eels, Lecomte and Yahyaoui (1989) showed that the oceanic larval migration needs less than one year. Then Guérault et al. (1991) applied this tool to successive samples of glass eels entering the Vilaine estuary, and noted a range of variation in migration phases according to the season. These preliminary data should be verified in a more complete sampling scheme. The present study comprised the former results and the results of an additional 16-month survey in the same estuary.

MATERIALS AND METHOD

This study deals with „transparent" glass eels, i.e. those identified as VB stage (Elie et al. 1982). The Vilaine estuary is located at 47°30′ N and 02°25′ W. It is an important glass eel fishery, with a concentration of up to 100 boats working downstream the estuarine dam (mid December to mid April). The short route to the shelf edge is 240 km across the Bay of Biscay.

SAMPLING CHRONOLOGY (TAB. 1)

17 samples were collected (4621 glass eels) from January to December 1990, and 25 samples (4497 individuals) were collected from September 1991 to December 1992, at monthly or fortnigthly intervals. The catching process was always the same, using two subsurface hoopnets hauled by an active boat at about 3 knots. Sampling dates and hours conformed to standardized conditions, around high tide at spring tide periods during night between 3 and 6 a. m.

BIOLOGICAL EXAMINATION

Pigmentation stages and biometry (length and weight) were observed on freshly killed individuals, after about five minutes, in water with a pinch of tobacco. Pigmentation was determined according to Elie et al. (1982) scale, with the help of Grellier et al. (1991) catalogue. About 150 VB glass eels per sample were measured and weighed, totalling 666 individuals for 6 samples in 1990 and 3804 individuals for 25 samples in 1992. They were then preserved in 70% alcohol. Two samples (May and December

TABLE 1

Sampling and observations chronology. VB: pigmentation stage according to Elie et al. (1982). 1990 samples are rearranged to build up a theoretical cohort.

	1990	Observations			1991 1992	Observations		
	Date	Pigmen-tation	Biomet-ry (VB)	Age (VB)	Date	Pigmen-tation	Biomet-ry (VB)	Age (VB)
September	21.09.90	214	95		25.09.91	104	92	13
October					10.10	170	160	10
	22.10	180			25.10	159	147	
November	6.11	201	64	14	8.11	150	145	17
					26.11	149	144	
December					10.12	184	179	11
	5.12	196	190	16	20.12	168	166	
January					10.01.92	167	159	14
	30.01	497			23.01	161	159	
February	12.02	166			7.02	150	147	13
	26.02	249			20.02	170	162	
March	13.03	497			10.03	179	168	12
	27.03	312	78	12	24.03	182	156	
April	12.04	166			7.04	185	168	
	25.04	264	138	16	17.04	173	149	
May	11.05	303			4.05	210	126	33
	24.05	308	101	16	18.05	253	157	
June	8.06	373			2.06	224	108	15
	22.06	265			16.06	230	180	
					30.06	222	143	21
July	24.07	247						
August	20.08	183			13.08	208	168	
September					10.09	185	169	17
October					13.10	187	157	
November					13.11	169	145	
December					15.12	158	150	
Total		4621	666	74		4497	3804	176

1990) were measured and weighed after preservation, a correction for shrinkage was adopted.

For every month one subsample of 20 to 30 preserved animals was taken for the otolith extraction. In 1990, 5 samples were studied giving 74 „readable" otoliths, whereas in 1992, 11 samples provided 176 otoliths. This was made according to Lecomte and Yahyaoui (1989) and different parts and microstructures of the otoliths were expressed according to Lecomte et al. (in print). 5 zones were identified as the reference pattern of the otolith (Fig. 1): Zone 1 is considered to cover the period from birth to the

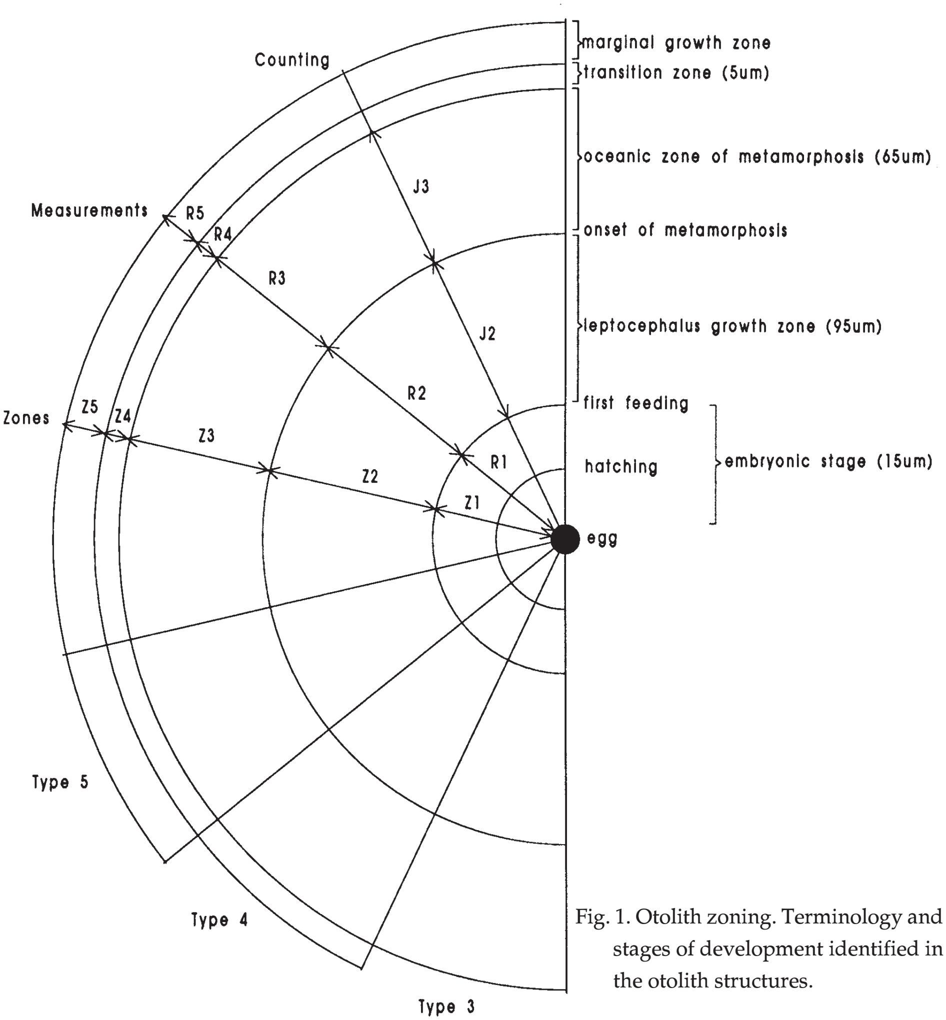

Fig. 1. Otolith zoning. Terminology and stages of development identified in the otolith structures.

first feeding; zone 2 represents the leptocephalus stage; zone 3 gives the begining of metamorphosis and the transport of glass eels across the shelf; zone 4 has been called „transition zone" by Castonguay (1987) and its validation is problematic (Lecomte et al. 1996); and zone 5 appears as an occasional structure, called the marginal growth zone. Counting daily increments on photographs from the scanning electron microscope was possible only for zones 2 and 3, which gives an estimate of the duration of the pelagic leptocephalus stage and of the glass eel migration above the shelf. Back-calculation of the larval events from the date of sampling is possible only on otoliths without zones 4/5. According to the position of the edge of the otolith, we call

„type 3" those which exhibit such structure, „type 4" is limited by the transition zone, and „type 5" presents an external homogeneous zone.

VARIATION OF ABUNDANCE IN THE ESTUARY

To give a rough figure of the amount of arriving glass eels in the year, two indices of abundance were calculated: i) the catches of one fisherman for the fishing period in kg per fortnight and ii) the number of VB glass eels per hour in the samples.

RESULTS

Because the first sample series in 1990 covered two successive cohorts (the end of 1989 year class and the begining of 1990 class), a logical figure was rebuilt and given in the sequence: November, December, then March, April and May.

VARIATION OF ABUNDANCE (TAB. 2)

Experimental catches showed that minimum yields occured during summer, with the lowest values in September (46 individuals per hour). Maximum catches (51519 ind./h.) observed in April occured immediately after the closure of the fishing season. This may explain sudden increase of the catch. Yields from December to April showed maximum mean catches between the end of January and the end of March which is quite usual (Guérault et al. 1986).

VARIATION OF PIGMENTATION (FIG. 2)

The VB stage was always dominating, with lower frequency in summer, when a temporary increase of more pigmented individuals was observed. Therefore, stage VB characterizes the immigrating glass eels. Only slight differences appeared between the two series: i) the presence of apparent „waves" of entering glass eels in spring 1990 was not so obvious in 1992; ii) a higher percentage of VB fishes in 1992, even in summer.

It was assumed from the variations of pigmentation and abundance that a new year class of eels was immigrating from September in the Vilaine estuary.

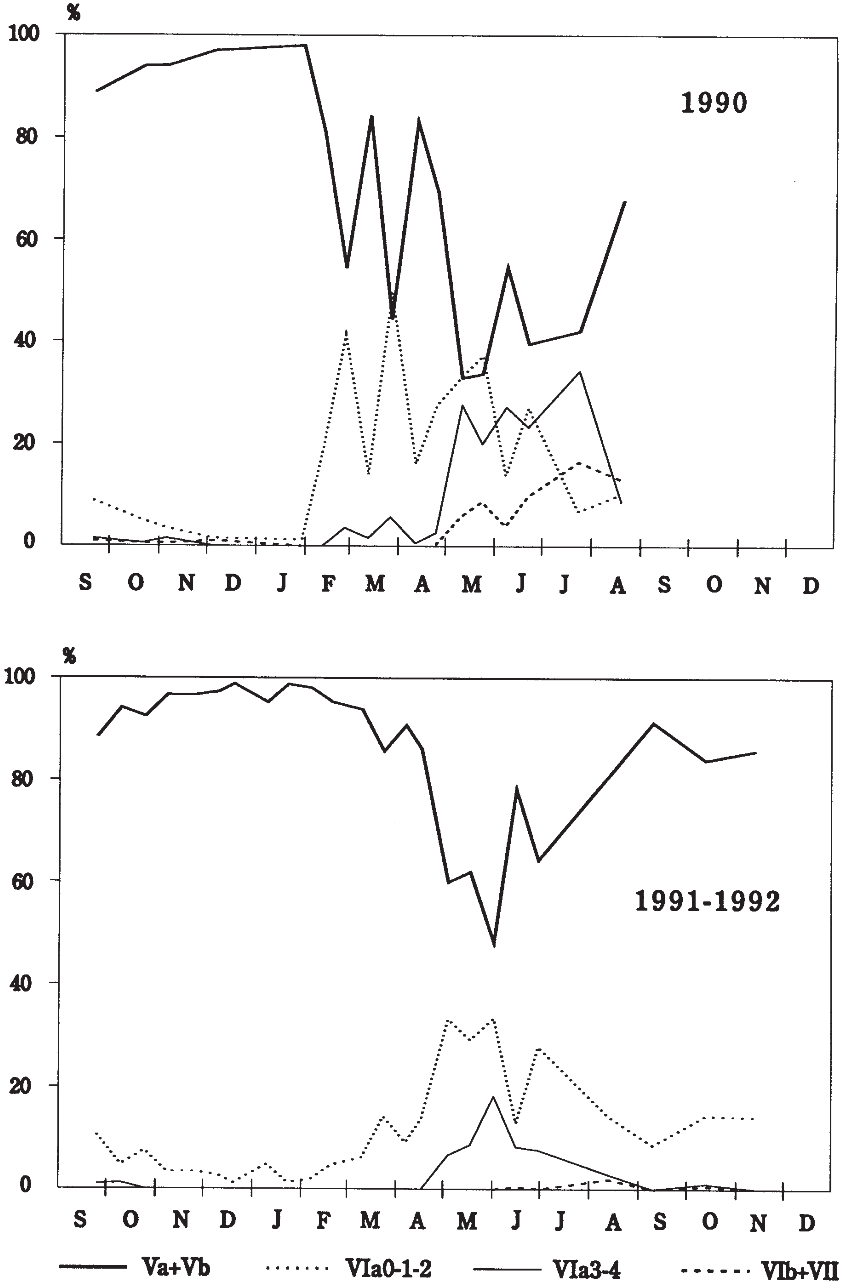

Fig. 2. Relative frequency of pigmentation stages in the glass eel samples from both series 1990 and 1991-1992.

TABLE 2

Variation of yields from experimental catches (nb. VB glass eels/hour) and professional catches (kg/fortnight) in the Vilaine estuary

		1990	1991–1992		
Month	Fortnight	Professional catch	Date	Professional catch	Experimental catch
September	2		25.09.91		46
October	1		10.10.91		473
	2		25.10.91		1133
November	1		8.11.91		5725
	2		26.11.91		399
December	1		10.12.91		307
	2	19.3	20.12.91	11.5	653
January	1	29.1	10.01.92	37.3	2935
	2	143.8	23.01.92	26.6	1635
February	1	68.5	7.02.92	99.4	7216
	2	54.5	20.02.92	101.7	10942
March	1	47.4	10.03.92	91.4	7631
	2	20.1	24.03.92	62.5	4368
April	1	16.8	7.04.92	49.1	5983
	2		17.04.92		51519
May	1		4.05.92		22176
	2		18.05.92		7246
June	1		2.06.92		832
	2		10.06.92		487
July	1				
	2		30.06.92		521
September	1		13.09.92		84
October	1		13.10.92		145
November	1		13.11.92		202

BIOMETRY (FIG. 3)

Length and weight of 1991-1992 sample series, which covered a whole cohort, are presented together with those from the 1990 series, which covered two parts of different cohorts. Both series showed similar trends with the highest values of length at the end of the year, and the lowest values in May - June. Similarly, mean weights showed a peak around December - January and a drop in May - June. The range of variation through the year reached respectively 7% and 8% for length, 40% and 42% for weight

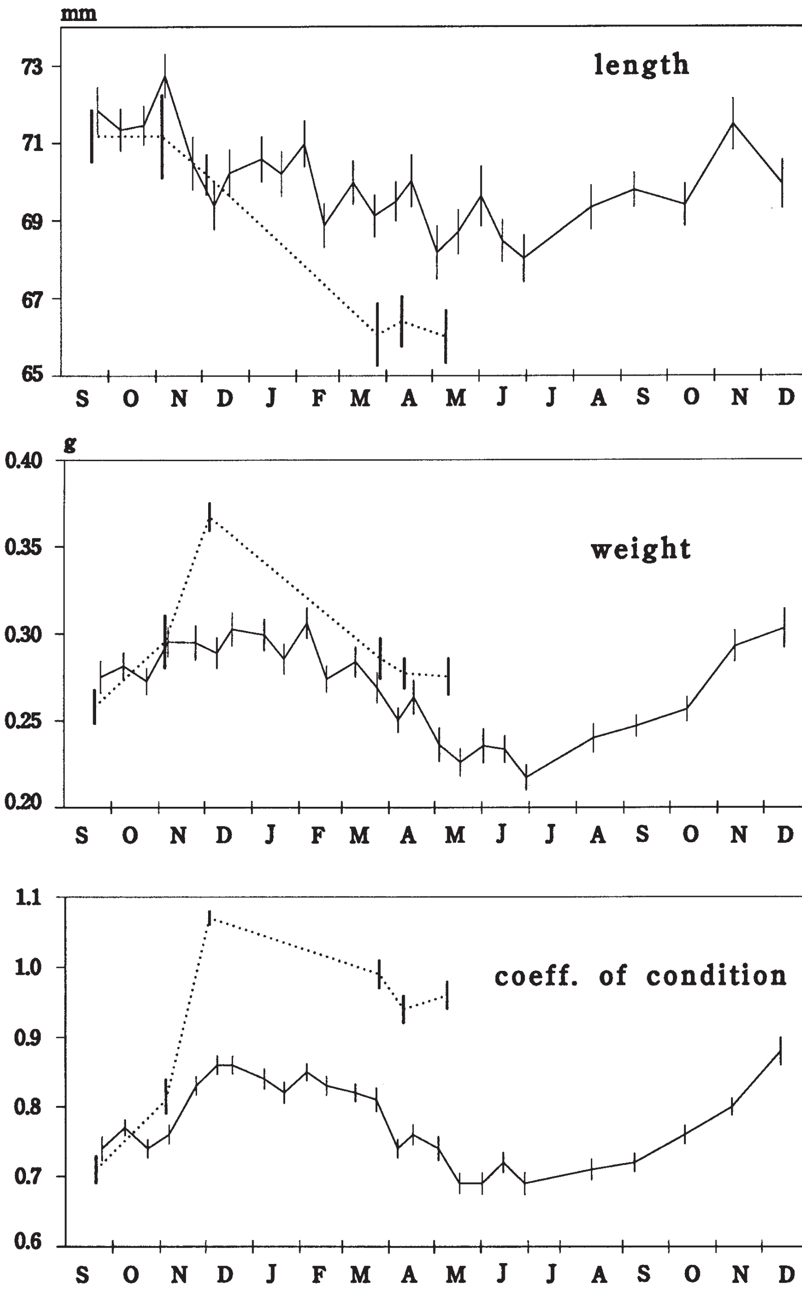

Fig. 3. Mean length, weight and coefficient of condition of stage Vb glass eels sampled in 1990 (dotted line) and in 1991-1992 (solid line)

in 1990 and 1992, so that coefficient of condition oscillated within a range of 51% (1990) and 25% (1992), with the highest values from November to March. The general trend of recruitment through a year followed the sequence:

- in autumn, the first arriving glass eels were generally longer, moderately heavy, and thin;
- in winter, the peak of immigration consisted of heavier and thicker glass eels;
- the last entering glass eels in spring and summer were shorter and lighter but they might have had a variable index of condition.

Nevertheless, noticeable discrepancies occured between the years in the average values for the given period. Particularly, samples from March, April and May were significantly different between the two years, with shorter and heavier, hence, „thicker" glass eels in 1990 than in 1992.

OTOLITH STRUCTURE AND LARVAL PHASES DURATION (TAB. 3, FIG. 4)

In 1992 only 26% of the examined otoliths belonged to the type 3, without external zones 4 (transition zone) and 5 (marginal growth zone), whereas in the previous series 89% of the otoliths were of type 3. This different appearance of the otoliths in 1992 reduced the number of „readable" otoliths, since no daily ring could be detected in zones 4 and 5. Consequently, the age was determined on 66 individuals from the first series (1990) and only 46 out of 176 from the 1992 sampling. The mean duration of each larval phase for montly samples can be summarized from the data in tab. 4:

Both series differ as to the structure of the otoliths and the duration of the metamorphosis phase which increased by about 40% in spring 1992. Low numbers of interpreted otoliths in each sample makes impossible any comparison on a monthly scale.

EARLY LIFE EVENTS (FIG. 5)

Results of back calculation for 1991-1992 samples are quite comparable to those given for the first 1990 series by Guérault et al. (1991). The first feeding date covers all the year long. If we consider only the individuals of the same year class (samples from October 1991 to July 1992), the main period of hatching would begin in late December 1990 and would end in November 1991. The overall period of the begining of metamorphosis was less extended in time than the spawning period and lasted only 9 months, from July 1991 to April 1992. If only the peak of immigration was taken into

TABLE 3

Otolith typing from microstructure examination

Sampling date	Nb. Otoliths	Type 3	Type 4	Type 5
6.11.90	14	11 (79%)	1 (7%)	2 (14%)
5.12.90	16	16 (100%)	0 (0%)	0 (0%)
27.03.90	12	11 (92%)	1 (8%)	0 (0%)
25.04.90	16	13 (81%)	0 (0%)	3 (19%)
11.05.90	16	15 (94%)	1 (6%)	0 (0%)
Total	74	66 (89%)	3 (4%)	5 (7%)
25.09.91	13	0 (0%)	6 (46%)	7 (54%)
10.10.91	10	2 (20%)	3 (30%)	5 (50%)
8.11.91	17	2 (12%)	5 (29%)	10 (59%)
10.12.91	11	5 (45%)	5 (45%)	1 (9%)
10.01.92	14	11 (79%)	2 (14%)	1 (7%)
7.02.92	13	9 (69%)	2 (15%)	2 (15%)
10.03.92	12	4 (33%)	5 (42%)	3 (25%)
4.05.92	33	1 (3%)	10 (30%)	22 (67%)
2.06.92	15	5 (33%)	4 (27%)	6 (40%)
30.06.92	21	3 (14%)	2 (10%)	16 (76%)
10.09.92	17	4 (24%)	3 (18%)	10 (59%)
Total	176	46 (26%)	47 (27%)	83 (47%)

account, the main spawning period would cover February to July and the peak of the onset of metamorphosis would cover September to December.

Therefore, May and June would be the time when leptocephali were likely to be scarce, while October was probably the best period to catch leptocephali above the continental shelf.

DISCUSSION

Guérault et al. (1991) stated that more information were needed to modelize the early life history of *Anguilla anguilla*. Indeed, the addition of a regular sampling scheme during a whole period of immigration in 1991-1992 brought new data which, however, were still limited in sample size and showed a number of similarities but also discrepancies between the two series.

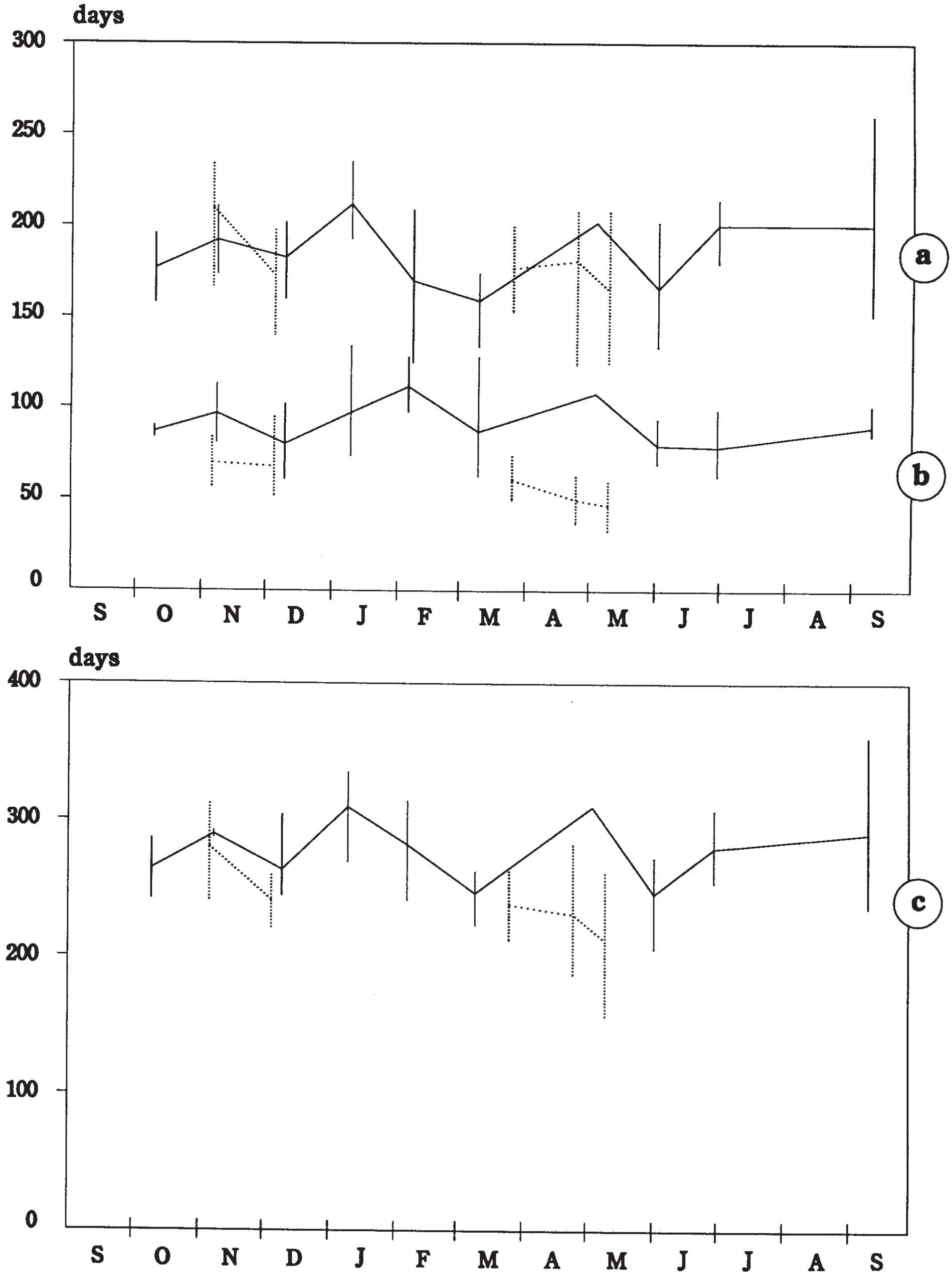

Fig. 4. Mean duration of larval phases for every monthly sample: a - leptocephalus stage, b - metamorphosis stage, c - total marine larval life. 1990 (dotted line), 1991-1992 (solid line) and mini-maxi

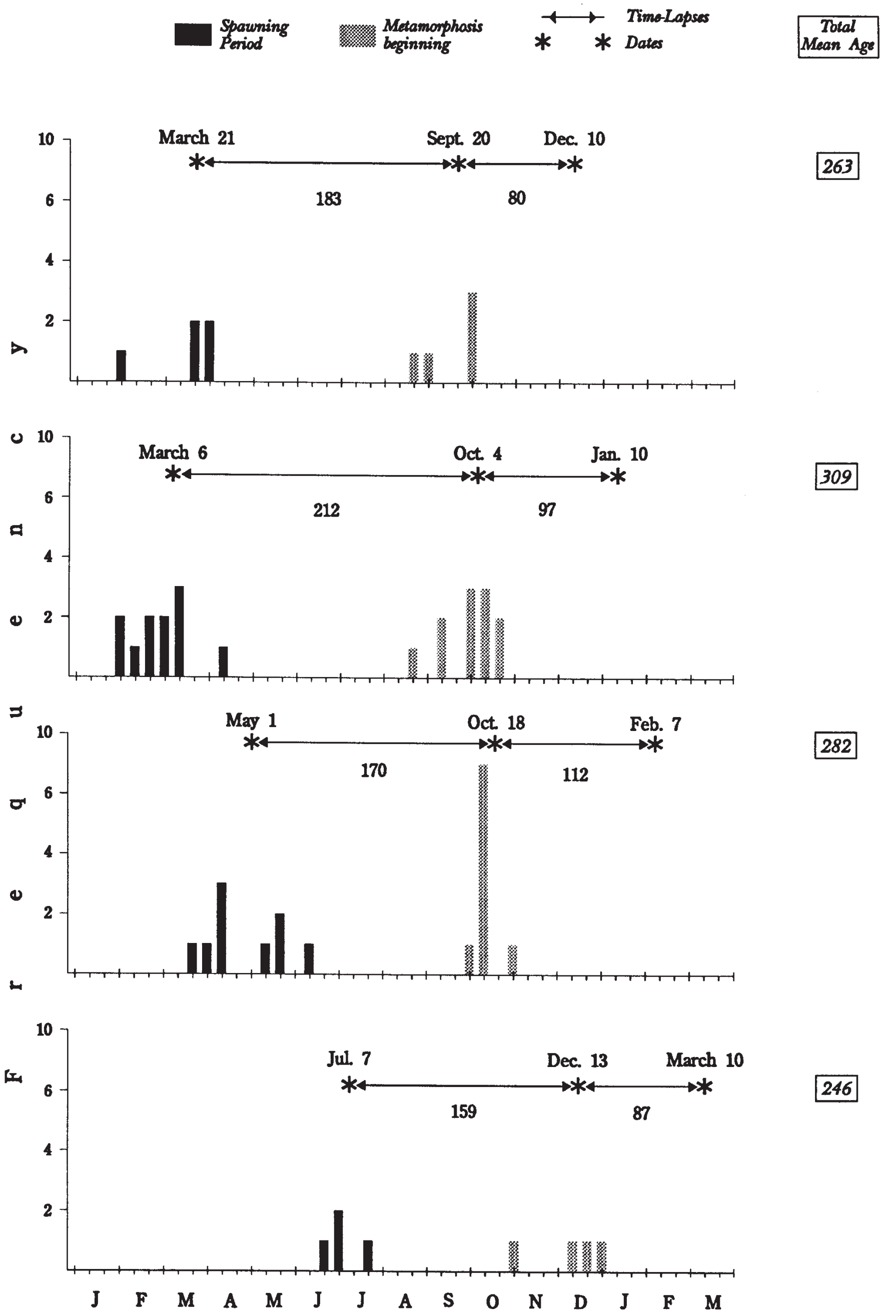

Fig. 5. Spawning period, begining of metamorphosis and duration (days from hatching to the sampling date) of the two larval phases of successive samples from December to March, resulting from back-cal-

TABLE 4

Estimated duration (in days) of larval phases for 1990 samples (a) and 1991–1992 samples (b) from „type 3” otoliths

a)	Month	S	O		N		D		J		F		M		A		M		J		J		A		S		Total
	Fortnight	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	
Leptocephalus stage	Mini				167		140							153		124	125									124
	Maxi				234		198							200		208	208									234
	Mean				210		173							177		181	165									180
	SD				21		17							14		25	30									27
Metamorphosis stage	Mini				57		52							50		37	33									33
	Maxi				84		95							74		63	60									95
	Mean				70		68							61		50	47									59
	SD				8		10							8		8	9									13
Marine larval life	Mini				241		221							212		187	157									157
	Maxi				312		259							265		282	261									312
	Mean				280		241							238		231	212									239
	SD				24		13							17		25	30									31
Nb. individuals					11		16							11		13	15									66

b)	Month	S	O		N		D		J		F		M		A		M		J		J		A		S	Total
	Fortnight	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	
Leptocephalus stage	Mini		158		174		160		193		125		134				202		134		180				151	125
	Maxi		196		211		202		235		209		174				202		202		214				260	260
	Mean		177		193		183		212		170		159				202		166		201				200	187
	SD		19		19		15		14		25		15						14		15				39	29
Metamorphosis stage	Mini		84		81		61		74		98		63				108		70		63				85	61
	Maxi		90		113		102		134		128		128				108		94		99				101	134
	Mean		87		97		80		97		112		87				108		80		79				90	93
	SD		3		16		17		16		8		24						9		15				7	18
Marine larval life	Mini		242		287		244		269		241		223				310		206		254				236	206
	Maxi		286		292		304		335		314		262				310		272		307				361	361
	Mean		264		290		263		310		282		246				310		246		279				290	280
	SD		22		3		22		18		24		14						25		22				45	33
Nb. individuals			2		2		5		11		9		4				1		5		3				4	46

SIMILAR FEATURES

A continuous flow of immigration was noticed during the whole study, since glass eels could be sampled at every occasion. This continuity in the Vilaine estuary had not been observed by Elie (1984) for 1982, as this author got zero catches during August and September. The lowest values of monthly yields suggest a new year class recruits in the Vilaine estuary from September to next July or August

Higher frequency of VB transparent glass eels was observed in both series. This confirms the previous statement. More pigmented individuals were caught in spring and summer; this could result from an increase of water temperature. We must however, remember that the fishing process is adapted to catch subsurface swimming fish, and that young eels may be distributed in deeper water or close to the bottom.

In spite of the differences in the absolute values, the seasonal evolution of mean length and weight showed comparable trends: transparent glass eels decreased in length and weight in the first half of the year. This is to be related to the continuing variation of successive larvae from a unique cohort rather than to possible discontinuing sub-cohorts of leptocephali, as advocated by Schmidt (1909), Bertin (1951) and Elie (1979).

As far as can be concluded from a too reduced sampling size, the global duration of the larval life for different cohorts varied between 7 and 9 months in 1990 samples, whereas in the 1992 series it varied between 8 and 10 months. This conforms to the range of the larval life from 7 to 11 months, as proposed by Lecomte and Yahyaoui (1989). As a whole, the two larval phases vary within a range of about 6 months for the pelagic leptocephalus and about 2 to 3 months for the newly glass eel. This is a striking figure in terms of migration speed, if we take into account hudge difference in the distances to cover (about 6000 km for leptocephali and about 250 km for glass eels to reach the Vilaine estuary).

DISCREPANCIES

As reavealed by professional catches, the peak of immigration in the estuary varied within one month in both years (from January to February). Such a delay was probably related to local environmental conditions (combination of tide coefficient and water discharge).

A major difference appeared between the years regarding the main structures of the otoliths: higher frequency of „type 4" and „type 5" otoliths during 1992 opened a new question on the ecological meaning of these structures. Moreover, it reduces the use of pigmentation stages to give even a relative age of the glass eels. It can be assumed that the pigmentation process was not dependent on the absolute age, but more likely on the estuarine hydrological conditions.

Seasonal differences in biometric parameters were noticeable during the period March, April and May, and there might be considerable differences in the larvae stage metamorphosis (zone 3). To sum up these results, arriving glass eels during 1990 spring appeared to have crossed the continental shelf faster (in about 2 months instead of 3) and they were shorter, heavier, with a better coefficient of condition. As a consequence, two questions are of a particular interest: i) to identify possible relationship between local and oceanic climatic conditions during winter and transport processes of glass eels on the continental shelf; ii) to characterize the suitability of glass eels to transform into „good" young yellow eels according to their condition index, the time of arrival, and the estuarine environment.

CONCLUSION

This additional study in the Vilaine estuary confirmed previous hypotheses on seasonal biometric variations, and the duration of the larval period. Several new information should still be confirmed, mainly on the abiotic factors affecting the dynamics of the offshore and the estuarine transport of larvae. To reach this goal, it is necessary i) to increase the numbers of the examined otoliths and ii) to collect data on the oceanic and coastal climate. Finally, the observed interannual variation of the eel recruitment processes suggests that great care is needed when comparing the results from different years and countries, or when setting an international glass eel sampling.

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STRESZCZENIE

ZMIENNOŚC OCEANICZNYCH WĘDRÓWEK LARWALNYCH SZKLISTEGO WĘGORZYKA (*ANGUILLA ANGUILLA* L.) NA PODSTAWIE DWULETNICH BADAŃ W UJŚCIU RZEKI VILAINE (FRANCJA)

Próby węgorzyka szklistego pobierano co miesiąc w roku 1990 i od września 1991 do grudnia 1992 r w obszarze ujściowym rzeki Vilaine (północna cześć Zatoki Biskajskiej). Przeprowadzono badania biometryczne i struktury otolitów. W obu latach dopływ i wedrówka węgorzyka szklistego miały podobny przebieg. Również długość i masa ryb układały się zgodnie z tym samym trendem, a różnice sezonowe były niewielkie. Średni wiek całkowity ryb w próbach wahał się od 7 do 10 miesięcy. Mimo, że stadium leptocefalusa okazało się mało zmienne (160-210 dni) czas trwania wędrówki węgorzyka po szelfie kontynentalnym wynosił od 50 do 70 dni w 1990 roku i od 80 do 100 dni w 1991/92. Stwierdzono ponadto różnice w strukturze otolitów w odniesieniu do momentu zakończenia wędrówki. Stwierdzona sezonowa zmienność może wpływać na wielkość dopływu węgorzyka szklistego głównie poprzez długość trwania okresu głodówki.