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DIFFERENCES IN DEVELOPMENT STAGE AND STOCK DENSITY OF LARVAL *ANGUILLA ANGUILLA* OFF THE WEST COAST OF EUROPE

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LARVES
RECRUTEMENT
ANGUILLA ANGUILLA
ATLANTIQUE NORD

RÉSUMÉ. — La présence de larves d'Anguille à différents stades de métamorphose le long du talus continental du Golfe de Gascogne et des régions septentrionales proches du détroit de Gibraltar, est suivie à l'aide de prélèvements effectués à l'IKMT, de nuit et à 25-100 m de profondeur environ. Des prélèvements au MOCNESS ont confirmé leur présence en grande quantité pendant la nuit à cette profondeur. La densité des larves d'Anguille pendant les mois de novembre-décembre 1982-1984, est toujours plus faible dans le Golfe de Gascogne que dans la région occidentale du détroit de Gibraltar. On remarque une chute considérable de la densité moyenne du stock de larves du Golfe de Gascogne pendant la période 1982-1985 comparée à celle de 1971-1977. Le pourcentage de larves en cours de métamorphose est plus faible à l'ouest du détroit de Gibraltar que dans le Golfe de Gascogne. Aussi la longueur des larves du secteur Gibraltar est significativement inférieure à celle des larves du Golfe de Gascogne, confirmant les résultats antérieurs. La discussion porte sur l'interprétation de ces résultats en accord avec l'hypothèse de migration passive des Anguilles.

FISH LARVAE
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NORTH ATLANTIC

ABSTRACT. — The occurrence of eel larvae and their stages of metamorphosis along the continental slope from the Bay of Biscay and adjacent northern areas to the entrance of the Mediterranean was investigated with IKMT night hauls at depths of about 25 to 100 m. This was, at night, the main depth of preference of the eel larvae as examined by using MOCNESS hauls. The density of eel larvae in the Bay of Biscay in November/December 1982-1984 was always lower than in the vicinity west of the Straits of Gibraltar. When the density of the larval stock in the Bay of Biscay 1982-1985 is compared with that of the average stock from 1971-1977, a considerable decrease has occurred. Examination of the development stage of the larvae in 1982 to 1984 showed that west of the Straits of Gibraltar the percentage of metamorphosing larvae was much smaller than in the Bay of Biscay. Also the length of the larvae near Gibraltar was significantly smaller than in the Bay of Biscay which is in agreement with earlier investigations. It is discussed how far these results are in agreement with the eel larval drift hypothesis.

INTRODUCTION

A study on the occurrence of fluctuations in the recruitment of eel during arrival of the larvae at the continental slope in the Bay of Biscay and of the glass eels at the coasts has been made for the years 1971 to 1977 (Tesch, 1980). This was repeated only in 1982 (Tesch, Deelder and Niermann, 1983). In the meantime, samples were taken occasionally during Sargasso Sea and other cruises (Kracht and Tesch, 1981; Tesch, 1982a, b; Kracht, 1982) mainly in different areas and seasons. In 1982 we found that the eel larval density in the Bay of Biscay was far below the level registered for the years 1971 to 1977 which corresponded with low glass eel catches at the coasts (Tesch, Deelder, Niermann, 1983). In 1983 and 1984 we continued sampling in the Bay of Biscay and farther south. The results are presented in this paper.

In the 1979 Sargasso Sea cruises, differences in sizes of the eel larvae in the Bay of Biscay and near the entrance of the Mediterranean were observed which threw some doubt on the hypothesis of the mainly passsive drift of the larvae from the Sargasso Sea spawning area to the European coasts (Kracht and Tesch, 1981; Kracht, 1982). We therefore present results on size and development stage of the larvae in the different sampling areas near the European continental slope.

In addition to the horizontal distribution of the larvae, the results of some hauls are given to describe their vertical distribution. This should confirm earlier results (Tesch, 1980; Kracht, 1982) and show that the towing depth used during the surveys met the main depth layer of occurrence.

MATERIALS AND METHODS

For the survey (Table I), an Isaacs Kidd Midwater Trawl (IKMT) with an opening of 6 m^2 and a mesh size of 1 800 µm was mainly used; this concerns especially the surveys from 1982 to 1984 in the Bay of Biscay and around the Iberian Peninsula. The sampling from 1979 to 1981 took place during cruises with only occasional hauls in or north of the Bay of Biscay, with partly other mesh sizes and net openings, or not during the standard season (autumn). At the standard areas and season the collections were carried out generally with three hauls at one position with horizontal towing depths of about 25, 70 and 100 m respectively during darkness.

After Tesch (1980), the depth preference of the "II group" eel larvae is probably within these limits although variations could occur depending on the lunar cycle (Kracht, 1982). We therefore checked the depth preference once more using a Multiple Opening and Closing Net and Environmental Sensing System (Mocness) with a theoretical opening of 1 m^2. This net is obviously rather small for the catch of the "II group" eel larva. In an area of comparably strong larvae concentration, west of the Straits of Gibraltar, 10 Mocness hauls, 8 nets each, were therefore necessary to catch a minimum quantity of larvae. The towing depth of the Ikmt was registered by a time depth recorder and occasionally controlled by a pressure sensing transmitter fixed at the IKMT. The towing time was generally one hour, the speed 2 kn which was controlled by rail log. Flow meter measurements in front of and above the net opening were found to be too variable. For comparison of the larval density in one-hour towing units, night hauls only were used since during the day the larvae occur at greater depths and over a greater depth range (Table II). Length measurements, taken, on freshly caught larvae, were used for evaluation. Measurements on larvae preserved in a 10 % formalin-seawater solution showed 1.5 % shrinkage after one month and negligible additional shrinking one year later. We differentiated between two stages of development, the younger larvae which correspond to development stage I-II (after Schmidt, 1906) and older larvae, corresponding to stages III-V.

Table I. — Type of ship, area and IKMT used for towing.

Date	Ship	Opening of IKMT (m^2)	Mesh size (µm)	Number of hauls	Area	
21.-22.04.79	Friedrich Heincke	2	850	6	Biscay 43°38'N 9°36'W to 56°23'N 7°16'W	1)
07.05.79	Anton Dohrn	6	500	2	Biscay 47°45'N 8°58'W 47°58'N 8°16'W	1)
02.12.79	Anton Dohrn	6	850	1	Biscay 48°23'N 11°50'W	
17.08.-23.08.80	Friedrich Heincke	6	1 000	27	West of Ireland 51°35'N 12°35'W to 56°09'N 9°29'W to 54°06'N 15°56'W	
18.02.-23.04.81	Friedrich Heincke	6	1 800	10	Biscay 45°06'N 8°14'W to 47°19'N 6°24'W	2)
28.10.-21.11.82	Friedrich Heincke	6	1 800	44	from Biscay to Gibraltar	3)
10.11.-11.12.83	Friedrich Heincke	6	1 800	74	from Biscay to Mediterranean to 2°49'W	
15.11.-13.12.84	Friedrich Heincke	6	1 800	29	from Biscay to Gibraltar	
11.11.-14.11.85	Friedrich Heincke	6	1 800	22	Bay of Biscay	

1) Kracht (1982), Tesch (1982a)
2) Tesch (1982b)
3) Tesch *et al.*, 1983)

Table II. — Vertical distribution of leptocephali and metamorphosis stages at about 36°00'N, 6°40'W (west of the Straits of Gibraltar) obtained by 10 MOCNESS hauls and 5 horizontal IKMT (6 m^2) daylight hauls (90 min each) at different depths.

MOCNESS hauls							IKMT hauls		
Depth (m)	Volume of water filtered ($10^4 m^3$) at night	Volume of water filtered ($10^4 m^3$) during daylight	Number of larvae caught (in brackets No./$10^4 m^2$) at night: *A. Anguilla*	at night: Other Anguilliformes	during daylight: *A. Anguilla*	during daylight: Other Anguilliformes	Depth (m)	Number of larvae caught: *A. anguilla*	Congridae
0- 50	2.78	1.05	7 (2.5)	4 (1.4)	0	0			
50-100	2.04	1.41	9 (4.4)	3 (1.5)	0	0			
100-150	1.85	1.04	1 (0.5)	3 (1.6)	0	0	100	0	2
150-200	1.11	0.74	0	3 (2.7)	0	1 (1.3)			
200-250	0.19	0.92	0	0	1 (1.1)	1 (1.1)	200	0	0
250-300	0.19	0.56	0	0	0	0			
300-350	0.37	0.93	0	0	0	0	350	0	1
350-460	0.56	1.11	0	0	1 (0.9)	0	425	16	0
450-560	—	1.11	—	—	1 (0.9)	0	425	5	0

RESULTS

1. Depth occurrence

Table II shows that the highest number of larvae at night occurred between 50 and 100 m with a stronger tendency toward 50 than to 100 m. Compared with the other Anguilliformes (mainly Congridae), they occurred in greater concentration and nearer the surface. The result during daylight is rather poor but confirms that they occur much deeper, as noted in earlier investigations. Horizontal hauls at the same place with the much more powerful IKMT showed that the migration during daylight goes downwards to at least 425 m, which also confirms the earlier results (Tesch, 1980).

2. Density of the stock

Figure 1 shows the mean density of the eel larval stock, combined for three different areas. In all three years, the density was lowest in the Bay of Biscay. It seems to be highest west of the Straits of Gibraltar except for 1982 when the highest density was found west of Portugal. If the catches near the entrance, west of Gibraltar, are compared with those farther out to sea, nearer the southwest corner of Portugal, it is obvious that the density farther out is lower than near Gibraltar and not much different from the other two areas.

The density of the Bay of Biscay stock is compared with the numbers found during earlier investigations (Table III). Because the catch numbers of the years 1971 to 1977 were obtained by an IKMT with 3 times smaller opening these figures were adjusted by multiplying them with three. It is evident that in 1982 to 1985 the density was much smaller than in 1971 to 1977, and even the earlier years with

A

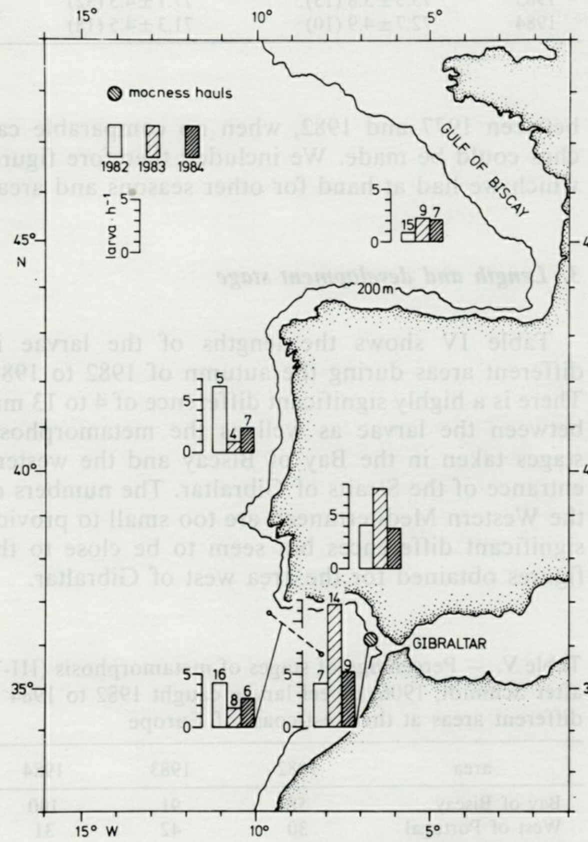

Fig. 1. — Density of eel larvae (n · h^{-1} of towing) in different areas of the European continental slope. West of the Straits of Gibraltar, the data are shown combined for the whole area south of 38°N in the upper arrangement of columns. Below, they are split between 6° and 7°W (right) and the more westerly positions (left, indicated by a stippled line). Number in the columns : number of hauls.

the poorest results (1972, 1974, 1976) yielded two to five times higher catches than the more recent years. It would be interesting to know what occurred

Table III. — Number of eel larvae ($n \cdot h^{-1}$ of towing) 1979-84 in the Bay of Biscay in comparison with results obtained during 1971 to 1977 (Tesch, 1980). The hauls of 1980 are combined data from the northern Bay of Biscay to the area west of Ireland.

year	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
spring	30,3	7,4													
autumn		43,5	5,7	42,0	5,1	21,9			5,3		0,9	2,2	2,1	2,7	
spring and autumn									4,2						
number of hauls									9	27	10	15	17	7	22

Table IV. — Length (mm) of eel larvae (L) and their metamorphosis stages (M) in different areas with standard deviation and number of individuals examined (in brackets).

	Biscay, north of 42 °N		West of Gibraltar		West-Mediterranean
	L	M	L	M	L
1982	75.1 ± 3.6 (11)	75.1 ± 5.1 (11)	62.0 ± 3.6 (75)	66.9 ± 4.0 (19)	—
1983	75.5 ± 3.8 (13)	77.1 ± 4.3 (32)	65.8 ± 5.9 (156)	69.7 ± 3.6 (50)	68.0 ± 5.7 (4)
1984	72.7 ± 4.9 (10)	71.3 ± 4.5 (18)	64.7 ± 5.6 (53)	64.5 ± 6.8 (12)	—

between 1977 and 1982, when no comparable catches could be made. We included therefore figures which we had at hand for other seasons and areas.

3. Length and development stage

Table IV shows the lengths of the larvae in different areas during the autumn of 1982 to 1984. There is a highly significant difference of 4 to 13 mm between the larvae as well as the metamorphosis stages taken in the Bay of Biscay and the western entrance of the Straits of Gibraltar. The numbers of the Western Mediterranean are too small to provide significant differences but seem to be close to the figures obtained for the area west of Gibraltar.

Table V. — Percentage of stages of metamorphosis (III-V, after Schmidt, 1906) of eel larvae caught 1982 to 1984 in different areas at the west-coast of Europe

area	1982	1983	1984
Bay of Biscay	58	91	100
West of Portugal	30	42	31
West of the Straits of Gibraltar	18	22	19

The percentage of leptocephalus stages I-II are compared with the more developed metamorphosing stages of three different areas from north to south (Table V). In the Bay of Biscay in all three years the percentage of metamorphosis stages was highest, nearly 100 % in 1983 and 1984, west of Gibraltar about 20 % only, in the area between north and south intermediate.

It seems likely that the density from 1979 to 1981 was average or at least close to the values found for the poorer years from 1971 to 1977.

DISCUSSION

The reliability of our IKMT catch data can be examined when they are compared with the MOCNESS data west of Gibraltar near 6°40'W. 14 IKMT hauls in 1983 at this place yielded 10.9 larvae per one hour of towing. When we assume a 100 % filtration rate, this would correspond to 4.9 larvae/10^4 m^3. The MOCNESS catch yielded 4.4 larvae/10^4 m^3 in the main layer of occurrence (Table II) which is rather similar. In 1982 our catches in addition could be compared with catches obtained by a different ship towing with quite a different net. The results were similar (Tesch, Niermann and Deelder, 1983).

Most striking is the low stock density observed first in 1982 (Tesch, Deelder and Niermann, 1983), and the fact that this low level of larval abundance continued during the following two years. This is in contrast to the rich abundance during the years 1971 to 1977 even though a considerable annual fluctuation also took place here. The poorest year of the earlier period (1976) seems to have more than twice as high a density than the richest from 1982 to 1985 (1983). The average density from 1971 to 1977 (22.4 larvae per one hour of towing of a 6 m^2 IKMT) dropped to an eleventh during 1982 to 1985 (2,0 larvae). The catch was low (4.2 larvae) as in spring/autumn 1979 (Fig. 1; Kracht, 1982) and was probably on a similar level during the following two years; no recovery to peak values, as known from the four years between 1971 to 1977, occurred during the 6 years period after 1978. The question arises, therefore, whether some conditions important for the recruitment have developed negatively. These conditions might not only be connected with the environment in the spawning area in the Sargasso Sea or with the migration from and to the continent but also with the number of individuals or the physiological conditions of the spawners starting for or arriving at the spawning area. A long-term fluctuation caused by natural conditions is also possible, but this possibility should not divert attention from the question of whether damages of anthropogenic origin have occurred.

The higher density of the larvae in the southern areas compared with that in the Bay of Biscay is probably due to a certain stowing or bottleneck effect in the funnel between Europe and Africa which leads to the Straits of Gibraltar. If the density farther outside is considered, there is little or no difference in comparison with that of the Bay of Biscay. Similarly, Kracht (1982) found that the density in the open Atlantic, e.g. west of 15°W was in 1979 much lower than near Gibraltar.

This leads to the question of how the larvae succeed in passing this bottleneck and how they move at all when crossing the Atlantic. If drift is supposed to be the transportation mechanism into the Mediterranean, how might this function ? The current regime in the Straits of Gibraltar is comparatively well known (e.g. Lacombe and Richez, 1982). In the west in front of the sill, a comparatively weak surface current flows to the east (Fig. 2) and a fast deep undercurrent to the west. The vertical distribution samples of the eel larvae shown in Table I are made at 6°40'W, on the left hand side of Figure 2. Beginning at this position, after low speed eastward drifting during the night at the surface they are exposed to a high speed current westward when diving to a depth of 400 m and more. As a result the larvae would have a net westward drift. Compensation would require a swimming speed of at least 20 cm · s^{-1}. This struggle against the current is probably an additional factor which produced the accumulation of larvae at the entrance of the Straits.

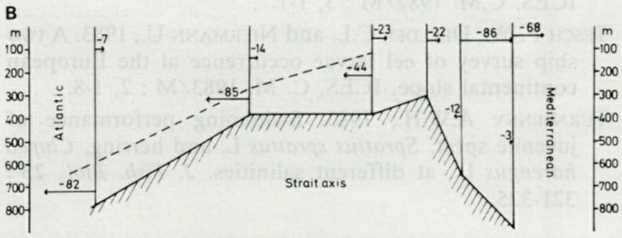

Fig. 2. — Longitudinal section through the Straits of Gibraltar with mean currents (numbers in cm · sec^{-1}) in the upper and the lower layer from 6°40'W to the meridian of Gibraltar (after Lacombe and Richez, 1982, modified).

Young herring of about 50 mm TL and young sprat (38 mm TL) sustained a critical swimming speed of 10-12 body length · s^{-1} (Turnpenny, 1983). Applied to the eel larvae with a body length of 65 mm this would produce a swimming speed of about 72 cm · s^{-1}. Probably the leptocephalus is not such a fast swimmer. But 20 cm · s^{-1} would require a swimming speed of 3 body lengths only, which seems quite possible.

The problem of orientation remains. This is possible on the basis of a compass course orientation as proposed for the adult eels which have the same problem when migrating in the opposite direction Sargasso Sea (e.g. Tesch, 1978). Also young chum salmon have been found to be oriented by the earth's magnetic field (Quinn and Groot, 1983).

Our results also give rise to doubts on the hypothesis that the eel larvae are mainly drifting when migrating to the continent. We found that the eel larvae as well as the metamorphosing stages near Gibraltar are 4 to 13 mm smaller than in the Bay of Biscay. This confirms earlier results (Kracht and Tesch, 1981; Kracht, 1982) and means that similar differences occurred during all the four years of study. In addition, the larvae in the Bay of Biscay exhibited considerably more stages of advanced development than in the south which could indicate that they are not only longer but also older.

Lower length and earlier development stages in the south than in the north suggest that the larvae are younger in the south. It is therefore unlikely that they are conducted or transported by Gulf Stream and North Atlantic current. This is not the direction to the Mediterranean. In this case, they should be older than the larvae in the Bay of Biscay. That the larvae are mainly transported by the Gulf Stream system is also unlikely considering that the younger larvae are distributed all over the area outside the Gulf Stream and to at least four degrees south of the Azores (Kracht, 1982). This wide distribution is also known from the data of J. Schmidt (Boëtius and Harding, 1985).

A critical light can also be thrown on the drift hypothesis when our density data of the larvae stock near the European continent are compared with those of recent studies obtained further to the west (e.g. Schoth, 1981; Schoth and Tesch, 1982; Kracht, 1982), and a similar comparison is made with the Gulf Stream watermasses reaching Europe. As the density numbers found 1979 to 1981 at the European continental slope are very similar from year to year it does not matter if it is always the same year class which is traced from the Sargasso Sea to Europe. This is also difficult because the conventional year-class classification (0-11) is doubtful (Boetius and Harding, 1985). Night catch data only are used for the small larvae (0-group) in the Sargasso Sea. In 1979 they had a mean TL of 12 mm and a density of 33 per 1 h of towing (= 100 %); between 50°W and Azores, the larvae of a mean TL of 47 mm decreased to 21 per 1 h of towing (= 64 %) and in front of the European continental slope (lengths see Table IV) to about 5 per 1 h of towing (= 15 %). Although these are not the figures of mortality, they are in accordance with the comparatively low mortality calculated for the oceanic stage until the beginning of the glass eel stage (Tesch, 1980). For the percentage of the water masses of the Gulf Stream reaching the European continent the calculation of Dietrich *et al.* (1979) shows that North Atlantic and Portugal Current may be the main contributors to the transport of the larvae. Out of the initial Gulf Stream, south of Newfoundland these two currents carry 17 % of the original water mass. Our calculation showed that the density of the larval stock in the Sargasso Sea decreased to 15 % upon arrival at the European continent which is nearly congruent with the loss of the Gulf Stream. But there is nothing left for the loss of larval stock density by mortality which seems unlikely and speaks for an additional mechanism moving the larvae across the Atlantic.

It is therefore suggested that transportation by currents is a factor which can modify the migratory route, e.g. arrival farther north or south and earlier or with delay. It may be imagined that some larvae are indeed taken by the Gulf Stream and not diverted by one of the various branchings. They could arrive much earlier and then are characterized by an essentially smaller size than the average. The length frequency distribution (Tesch, 1980) observed in the Bay of Biscay in 1975 showed five larvae of a length of 55 to 58 mm only; the average was about 70 mm. The essential factor which moves the larvae across the Atlantic is therefore suggested to be more active swimming. To overcome the direct distance from the central Sargasso Sea spawning area to the coasts of Europe and Africa, a two-year swimming effort of 50 mm long larvae at a speed of two fish lengths $\cdot$ s^{-1} is sufficient. From the east end (50°W) of the spawning area (Schoth and Tesch, 1982) to Gibraltar, the speed could be even lower or the arrival earlier.

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