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ON THE MIGRATION OF THE ELVER (*ANGUILLA VULGARIS* TURT.) AT SEA

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On the Migration of the Elver (*Anguilla vulgaris* Turt.) at Sea.

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Introduction.

After the enclosure of the Zuyder Zee in 1932, it soon appeared that in the newly formed freshwater Lake Yssel the eel population developed very well, and big catches were made. Nevertheless, in view of the great economic importance of the eel, it is obviously desirable to try to raise the yield still further. This may be done, for instance, by legal measures to regulate the catch, or by increasing the rate at which the population is recruited. This latter method is only possible, however, by increasing the number of elvers migrating from the North Sea into the lake, and our efforts to bring this about are the subject of the present paper.

As has already been mentioned, Lake Yssel is the former Zuyder Zee, and is separated from the Dutch Wadden Zee (part of the North Sea) by a large dike, a so-called "Afsluitdijk" (i.e., "enclosing dike"). The fresh water flowing into the lake is discharged into the Wadden Zee at both ends of the dike, near Den Oever and near Kornwerderzand. At the former place there are three sets of 5 sluices, and at the latter, there are two such sets. There are also 3 locks for ships, one at Den Oever, two at Kornwerderzand. A peculiarity of the sluices is that each gate has two hatches, one behind the other, several metres apart, each of which can be moved up or down. In this way the sluice can be opened or closed.

Now the only passages by which elvers could migrate into Lake Yssel are the sluices and locks through the dike. At first the elvers were allowed to pass by simply opening all the sluices, when the water levels were the same. The disadvantage of this method was that very much salt water entered the lake, and as the aim was to get the lake as fresh as possible, the method had to be abandoned.

The late biologist J. J. ter Pelkwijk then developed a method which consisted of the alternate opening of the sluice hatches several times a night, and this method is still in use. First the outer hatches are opened, the elvers swim into the sluices and assemble in front of the inner hatches. Then after two hours the outer hatches are closed and the inner hatches opened for about a quarter of an hour, to allow the elvers in the sluices to enter the lake. After this, the inner hatches are closed and the outer hatches are opened again for two hours. By this method the elvers are passed in the same way as locks are used for a ship. This method is working very well, as is proved by the still large catches of eels in the lake, about 4,000,000 kg. a year.

An attempt to learn more about the factors influencing the inward migration of elvers was made by van Heusden (1943), who studied the reactions of elvers in laboratory tests. The desirability of further investigations nevertheless remained, and I was charged with their execution.

It must be emphasized that the purpose of my studies was purely practical, viz., to develop a method of attracting a larger number of elvers out of the North Sea into the Wadden Zee and subsequently into Lake Yssel. It was therefore necessary to discover the factors which influenced the migrations of the elvers *at sea*. Accordingly the migration from the sea to fresh water and in fresh water will not be dealt with in this paper.

During my investigations I received much help from several persons, to whom I wish to express my gratitude:— Ir. H. A. M. van Erp, Inspector of Fisheries; Mr. Ch. Gilis, Expert of the Belgian Government Institute of Fisheries; Dr. P. Groen, Oceanographer of the Royal Dutch Meteorological Institute; Dr. B. Havinga, Director of the Government Institute for Fishery Investigations; J. H. Jones, M.I.C.E., M.I.M.E., Chief Engineer of the Ministry of Finance, Works and Public Buildings of Northern Ireland; F. T. K. Pentelow, Chief Inspector of Salmon Fisheries in England; H. Postma, Oceanographer of the Zoological Station at Den Helder; Dr. J. Verwey, Director of the Zoological Station at Den Helder, and A. Volker, Chief Engineer of the Government Board of Zuyder Zee Works.

I should also like to thank the following gentlemen for their assistance in fishing elvers on many days and nights:— Messrs. P. van Gorkom, J. Mennema, J. Pijl, J. F. de Veen, M. Weenink, A. J. van Tooren. Mr. de Veen also gave me much help in both observing and calculating.

Finally, I should like to express my thanks to Prof. Dr. G. P. Baerends and Dr. B. Havinga for having read and corrected my manuscript.

Records and methods.

The data studied came from two sources. The first is the statistical records from the Afsluitdijk, the River Bann, and the River Severn, and the second is my own observations.

Despite much effort, we were unable to obtain data on elver migration from other parts of Europe.

1) Afsluitdijk. As has already been mentioned, the Afsluitdijk sluices are used as elver locks during the migration season from March to May, by passing the elvers every two hours from the sea into the lake. To estimate the numbers migrating, hauls with a dip-net of 1 m^2. were made from the bottom to the water surface in the westernmost sluice of the middle set. It was situated 20·5 m. from the inner hatch, and 1·5 m. from nearest side of the sluice.

A haul was made on each occasion just before the elvers were passed through the sluices, so that the hauls were at two-hour intervals. The elvers caught were counted and the number recorded. It is assumed that a fresh group of elvers was always caught each time, because after each dip the elvers were passed through the sluices. This procedure was carried out at Den Oever from 1938 to the present time, the only break occurring in 1945, when no hauls could be made owing to the war.

A dip-net like that at Den Oever was installed at Kornwerderzand in 1948. This was located in the westernmost sluice of the eastern set, at a distance of 19·5 m. from the inner hatch and 1·5 m. from the nearest side. At Kornwerderzand great quantities of elvers are caught every year in the adjacent locks by the Fisheries Inspectorate, for transportation to inland waters, and these catches may be compared with those of the dip-net.

It was very soon evident that no constant relation existed between dip-net catches and Fisheries Inspectorate catches. The catches for short periods in a season do not tally, and the total catches for the season also differ very much. This discrepancy is only explicable on the assumption that the intensity of migration is not connected with one—or both—of the catch series. This matter is now being studied but no definite reason has so far been found. However, the dip-net data have the great advantage that the catches were made regularly, while the commercial catches were not only very irregular, but were made with different fishing intensities, and are thus likely to be less useful. We shall therefore prefer the dip-net data for our attempts to correlate different factors or combinations of factors and the migrations of the elvers at sea.

2) River Bann. In this river, which flows through Northern Ireland towards the Atlantic Ocean, elvers have been trapped and transported to inland waters from 1932 to April 1948, as has been described by Menzies (1936) and Frost (1950).

Thanks to the assistance of Mr. J. H. Jones, I have received the records of elver transportation covering the years 1936 to 1948. The records for the years 1932 to 1935 are not entirely reliable.

We must assume that the majority of the elvers reaching the Bann weir were trapped. However, it is fairly certain in my opinion that some elvers managed to pass through the lock, and in this way escaped recording. This would explain the statement by Frost (1950) that she observed elvers swimming in the river when transportations were being made.

In addition to the elver records I also received records of the daily water discharge of the River Bann in cubic feet per minute.

3) River Severn. This well known river flows into the Bristol Channel. Elvers migrating upstream were caught for a long time near Epney, a village in the vicinity of Gloucester. They were stored there and afterwards distributed, mainly to Germany, but also to other European countries. During the second world-war the English Fisheries Inspectorate took over the storage installation.

The elvers were caught with scoops of linen mesh, placed in the river with the opening facing downstream. The elvers assemble in the scoops and can then easily be landed. It is obvious that the quantities caught do not represent the total quantity of elvers migrating upstream, but are heavily influenced by several factors, e.g., the price paid for the elvers.

Catch records have been published by Röhler (1939); those for more recent years were communicated to me by Mr. F. T. K. Pentelow.

Own observations.

To obtain information about the factors influencing the migration of elvers in the sea, I decided it would be best to begin by studying their behaviour in nature. This might yield clues which would suggest more detailed laboratory work, if wanted.

However, the study of elvers in nature has one great disadvantage, namely, that data obtained are mainly indirect: it is practically impossible to study the movements of the elvers in the sea by direct visual observation. The only available method is to draw conclusions from the catches made. Despite this drawback, it was decided to collect data on catches so that an attempt could be made to discover at least the most important factors. In the first two seasons a ship belonging to the Fisheries Inspectorate was used; it was in great demand, however, for inspection work, so that no regular observations could be made. During the last three seasons the "Max Weber," owned by the Zoological Station at Den Helder, was kindly put at our disposal, and in 1950 the fishery research vessel "Antoni van Leeuwenhoek" was also employed.

Our material was obtained by fishing funnel-shaped nets—a kind of plankton net—in the tidal streams from an anchored ship. The elvers caught must have been borne by the flow into the nets. Two nets were used simultaneously—except in 1946, when only one net was used—one at the bottom, and one near the water surface. The wire warp used for the surface net was attached to a spar projecting horizontally from the stem of the ship; the warp for the bottom net was secured to the anchor. The mouth of the net was 1 m^2. in area, circular in the surface net, rectangular in the bottom net, with sides of 141 and 71 cm. The nets first used were of woven hemp, and later on of woven flax, with a mesh surface of about $2^1/_4$ mm^2.

The length of the nets varied somewhat. At first hemp nets of 3 m. length were used; in the fourth season the flax nets were 6 m. long and in the last season about $12^1/_2$ m. long. I am convinced that the nets were long enough in relation to the speed of the streams to ensure proper filtration. The hemp was smoother than the flax, so that at first short nets were sufficient. However, the possibility existed of the nets becoming dirty and impermeable, so that I finally decided to change over to nets of about $12^1/_2$ m. length. A flap prevented the elvers from swimming out of the net once they had entered it.

Observations and tests showed that elvers did not try to escape while they were in plenty of water; they passed through the meshes only when the nets were hauled and the cod-end was out of the water, and when there were many jelly-fish (*Pleurobrachia*) present.

The "Max Weber" was not equipped to withstand much bad weather and we were accordingly obliged to anchor only at such places from which we could easily return to harbour. As a result we could fish at only a few places in the Wadden Zee. This was not a great disadvantage, however, for I decided it would be better to get a series of data from one position than to get data from several places, which might be difficult to interpret. It would certainly have been best to get simultaneous data from several places, but no ships were available, so that this was beyond our resources.

During the cruises water samples were taken regularly for temperature and salinity determination.

The question of using stationary gear was considered, but the idea was abandoned, on account of the fact that bad weather would have made it impossible to approach these nets at the desired time. Moreover, it is probable that heavy seas would have destroyed the nets.

Migration intensity.

The best idea of the variation in strength of the elver migration from year to year is furnished by the Bann data (Table 1b). It can be seen that the catches decreased regularly over the period considered, as was also the case at Den Oever and in the Severn (Tables 1a and 1c).

To show this decline more clearly and to minimize the influence of local factors, 3-year running means were calculated for each of the three series (Table 1). These figures indicate that the decline is fairly regular. The average catch for 1945, '46, and '47 in the Bann is 31 % less than that for 1936, '37, and '38, which is a very considerable difference.

We do not know the cause of the decline. It is possible that size of the eel population alternately rises and falls as is the case with many other animal populations. This would agree with a paper by Schnakenbeck (1950), in which he stated that the number of small eels in the Elbe estuary (which is of course dependent on the number of elvers reaching the estuary) changes very much. In 1929 small eels were very numerous. From 1929 to 1932 the number

Table 1. Yearly catches of elvers in three different localities.

a. Den Oever.

Year	Catch in numbers of fish	3-year running mean
1938	7806	—
1939	26028	12902
1940	4873	12134
1941	5502	5269
1942	5433	5770
1943	6375	9716
1944	16340	8717
1945	—	—
1946	2436	6780
1947	1564	1832
1948	1495	1702
1949	2046	1929
1950	2247	—

b. River Bann.

Year	Catch in lb.	3-year running mean
1936	16215	—
1937	19890	17915
1938	17640	17235
1939	14175	16923
1940	18955	18243
1941	21600	18633
1942	15345	17010
1943	14085	13605
1944	11385	12406
1945	11748	12665
1946	14861	12423
1947	10668	—

c. River Severn.

Year	Catch in 1/2 kg.	3-year running mean
1908	344	—
1909	1633	—
1910	3396	—
1911	3765	3212
1912	2476	3375
1913	3885	3319
1914	3596	—
1924	678	—
1925	933	—
1926	1531	—
1927	2400	—
1928	4092	3287
1929	3369	3786
1930	3897	3840
1931	4254	4093

Year	Catch in 1/2 kg.	3-year running mean
1932	4128	3718
1933	2773	3239
1934	2815	3098
1935	3707	3411
1936	3711	3765
1937	3876	4033
1938	4512	4800
1939	6012	—
1943	1042	—
1944	999	1227
1945	1639	1383
1946	1510	1296
1947	740	841
1948	274	349
1949	32	—

1 lb. = 0·454 kg. = about 1400 elvers.

decreased, but afterwards increased till 1935, after which they steadily decreased again; no further increase was mentioned.

A second possible cause is the steady increase in the eel fishery in all countries in which this species occurs. There is no doubt that as a consequence of this the number of eels reaching their breeding places must also diminish, so that egg production will decrease too.

Comprehensive and reliable data on the catch of eels in all the European countries concerned are lacking. Even in Holland the quantity of eels caught in inland waters is unknown, except for Lake Yssel. For this reason it cannot be proved that eel catches increased generally, but from various remarks in fishing journals about increased

Table 2. The dates on which elvers were first noticed at Den Oever, and the temperature of the water in Marsdiep on the six preceding days.

	1938			1939			1940			1941	
	Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.
6·III.	—	5·1	22·II.	—	4·1	29·III.	—	4·4	14·III.	—	3·9
	—	5·5		—	4·1		—	4·8		—	3·9
	—	5·6		—	4·5		—	4·6		—	4·0
	—	5·8		—	4·5		—	5·4		—	4·2
	—	6·1		—	4·6		—	5·8		—	4·1
	—	6·2		—	4·6		—	5·6		—	4·2
12·III.	23	6·0	28·II.	43	4·4	4·IV.	83	5·8	20·III.	5	4·7
	1942			1943			1944			1946	
6·IV.	—	4·7	27·II.	—	5·1	15·III.	—	4·1	5·II.	—	4·2
	—	5·4		—	5·2		—	4·3		—	4·3
	—	5·3		—	5·5		—	4·6		—	4·5
	—	5·5		—	5·7		—	4·7		—	4·8
	—	5·1		—	5·9		—	4·8		—	4·7
	—	5·4		—	5·0		—	4·7		—	4·3
12·IV.	2	6·0	5·III.	11	5·4	21·III.	3	4·7	11·II.	3	4·7
	1947			1948			1949			1950	
5·IV.	—	4·6	11·III.	—	4·5	11·II.	—	4·1	3·III.	—	4·7
	—	4·4		—	4·8		—	4·4		—	5·1
	—	4·4		—	5·0		—	4·3		—	5·3
	—	3·7		—	5·1		—	4·7		—	5·3
	—	4·4		—	5·3		—	4·9		—	5·0
	—	4·2		—	4·3		—	4·9		—	5·3
11·IV.	5	4·8	17·III.	3	5·5	17·II.	6	4·7	9·III.	16	5·6

fishing intensity and improvement of methods, we may assume with fair certainty that this is so.

Influence of wind and temperature.

Our investigations provide no evidence that wind exerts any influence upon migration at sea.

In the vicinity of sluices or other freshwater outlets there seems to be a relation between the wind and the dispersion of the elvers. This matter is being investigated and will not be discussed at present.

With regard to temperature, we may assume that this is a factor starting or delaying migration. This may be studied by considering the temperatures on the days on which the elvers were noticed for the first time.

Menzies (1936) states that low air temperatures in the Bann check elver movement into the trap. It is possible, however, that this is due to local effects and it does not follow that this applies to elver migration in the sea too.

Table 3. Number of elvers caught at Den Oever and the water temperature at Marsdiep, 1949.

	Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.		Elvers	Temp. °C.
17·II.	6	4·7	27·II.	—	5·4	8·III.	0	2·0	17·III.	1	4·1
	9	4·3		—	5·0		0	2·1		8	4·3
	5	5·0	1·III.	—	4·5	10·III.	0	2·3		3	4·2
20·II.	8	4·6		4	4·2		2	3·1	20·III	6	4·1
	4	5·2		2	3·8		0	3·2		13	4·5
	11	5·0		0	3·8		0	4·4		19	4·2
	5	5·5		10	2·4		3	4·3		31	4·9
	2	5·4		6	2·2		10	4·3		8	5·1
	7	5·5	7·III.	1	2·5	16·III.	12	4·4	25·III.	53	5·3
26·II.	5	5·4									

Table 2 enables the dates on which elvers were first caught at Den Oever to be compared with the corresponding water temperatures near Den Helder (the nearest place for which temperature data were available). We must recognize, however, that fishing with the dip-net did not begin until there were elvers present, and until there were no objections from the Board of Zuyder Zee Works, e.g., with regard to the water discharge. That is to say, fishing never began early, but only either late or in time. Bearing this in mind, we can perceive in the table a fairly close relation between water temperature and the date of arrival of the elvers. Below a temperature of about 4·5°C. elvers do not usually arrive. We are inclined to believe that the elvers require this temperature at least, before they begin migrating at sea. This is demonstrated nicely by the following instance. In 1949, the elver migration began early. Later on the onset of very cold weather caused the water temperature to fall suddenly, immediately after which the elver migration ceased entirely. Although elvers were observed in the sluice when the temperature was 2·2°C., the migration itself was interrupted. An uninterrupted elver migration did not begin again until the temperature rose to about 4·5°C.

Van Heusden (1943) was also aware of this. He stated that no elvers appeared at a water temperature of 3°C., and that, in his opinion, the main migration occurred at temperatures between 6° and 11°C. He assumed that this was a direct effect, i.e., that elvers wanted to migrate only when the temperature was between these two limits and that the migration urge disappeared when the temperature was lower than 6° or higher than 11°C.

A similar relation can be found, of course, for every animal which migrates in a certain season, but this does not imply that the effect is direct. It is much more probable that it is indirect. If we compare, for instance, temperature and catch for the River Bann (Table 4), we see that the main elver migration takes place between 7° and 10°C.; that is, between temperature limits other than those operating at Den Oever. These temperature data were collected at a position 54°57′N., 5°28′W.,

Table 4. 5-day averages of elver catches in the River Bann during the period 1936-1946, and 5-day averages of sea water temperature in the North Channel.

Elvers lb.	Temp. °C.	Elvers lb.	Temp. °C.	Elvers lb.	Temp. °C.	Elvers lb.	Temp. °C.
0	6·9	247	7·5	324	8·2	93	9·3
67	6·9	373	7·6	204	8·6	91	9·6
80	6·9	319	7·7	246	8·9	142	9·8
209	7·0	321	8·1	204	9·0	82	9·9
186	7·1						

about 100 km. from the Bann estuary. According to the monthly synoptic charts published by the Fisheries Laboratory at Lowestoft, in a distance of this order the temperature change in the sea water is considerably less than 1°C., so that we may correlate these temperatures with the Bann catches.

It is logical to assume that once the migration has begun it will continue, so long as the temperature is above the minimum value. In that case the quantities of elvers arriving will be determined primarily by the number of elvers in the sea. The coincidence of greatest intensity of migration with certain water temperatures may be due to accident, and cannot be regarded as significant. Moreover, we must suppose that the end of the migration will be determined by the absence of elvers in the sea and not by water temperature.

This view is supported by the fact that in late summer every year (in July and even August) some migrating elvers can still be observed in the locks and sluices of the Afsluitdijk, and this migration is not apparently checked by high temperatures.

The data collected during our work at sea also support this view; no correlation between migration and water temperature can be found from them.

Another possibility is that it is temperature differences which act as guiding factors. It is sometimes thought that temperature differences are responsible for the elver migration from the North Sea into the Dutch Wadden Zee; the warmer water of the Wadden Zee should "attract" the elvers away from the cold North Sea. That this opinion cannot be true is evidenced by figures published by Postma and Verwey (1950) for the water temperature at a certain point in the North Sea, at the entrance to the Wadden Zee, and at a point in the Wadden Zee. They show that at exactly the time when migration is most intense (March—April) the average temperatures are the same at all those places, so that there can be no attraction by warmer water in the Wadden Zee.

Influence of light.

It is commonly known that light exerts a great influence upon the conduct of migrating elvers. An interesting proof that in the dark elvers prefer to swim near the surface has been given by van Heusden

Table 5. Elver catches expressed as percentages of the nightly total catch at different times of the night at Den Oever. (Amsterdam mean time).

1938		1939				1940	
hrs.	%	hrs.	%	hrs.	%	hrs.	%
1910	4·8	1900	5·1	1800	3·3	1900	5·4
2110	13·5	2100	14·6	2000	11·0	2100	14·3
2330	22·5	2300	17·8	2200	23·0	2300	22·5
0150	28·0	0100	24·3	2400	25·1	0100	24·7
0410	26·3	0300	23·4	0200	31·3	0300	23·3
0610	10·3	0500	14·7	0400	3·3	0500	10·3

	1941	1942	1943				1944	
hrs.	%	%	hrs.	%	hrs.	%	hrs.	%
1820	5·1	1·6	1920	4·3	1820	1·6	1920	8·4
2020	8·3	10·4	2120	13·0	2020	11·7	2120	20·6
2220	16·9	26·8	2320	24·2	2220	25·8	2320	21·7
0020	25·4	31·2	0120	22·0	0020	27·4	0120	20·0
0220	25·5	19·7	0320	24·6	0220	20·3	0320	18·5
0420	16·2	10·2	0520	12·6	0420	12·6	0520	11·1

1944			1946	1947	1948	1949
hrs.	%	hrs.	%	%	%	%
1820	1·6	1920	7·6	2·5	9·1	2·9
2020	9·3	2120	17·4	10·3	16·8	12·8
2220	18·8	2320	28·4	24·6	23·4	22·0
0020	24·9	0120	25·2	24·0	26·0	29·7
0220	24·0	0320	18·5	27·4	17·6	28·3
0420	21·4	0520	10·5	6·8	8·6	4·1

(1943), who kept elvers in an aquarium in a room that was completely blacked out. Van Heusden turned the light on and off an hour earlier each day, so that at last a situation was reached at which the room was light at night, and dark by day. In these conditions the elvers swam only in the dark hours, that is, during the day, and kept themselves dug in the sand during the night when the lights were burning; they thus behaved in complete contrast with their congeners not kept in this room.

A good opportunity to study the relation between light intensity and migration urge is provided by the numerous dip-net data for Den Oever from 1938 to 1950. For this purpose these are used for comparison with each other and not for quantitative studies, and in this respect they may be regarded as fully trustworthy.

For this comparison those nights were selected on which at least 20 elvers were caught. The catch of each seperate haul is expressed as a percentage of the total catch (of 6 hauls at 2-hour intervals) for each night.

The hauls were made at the same hour each night. By summing the respective percentages, we have computed the average percentage

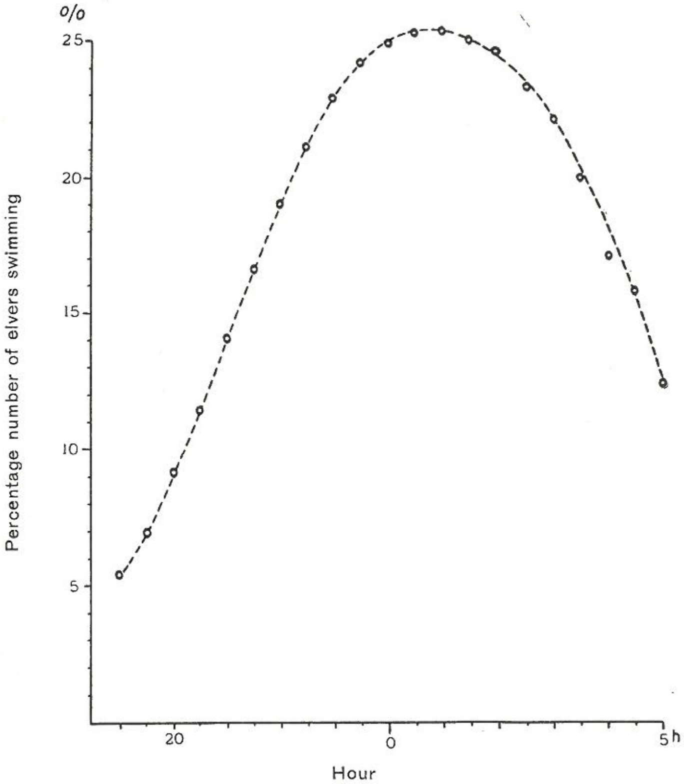

Figure 1. Average course of the nightly activity of the elvers at Den Oever, 1938—1949.

catches for various times, and so shown the average course followed by the elver activity during the night (Table 5). A graph was drawn for each season, and the values read off at the intersections of the curves with the ordinates at half-hour intervals.

The averages so obtained for each set of these values is shown by the curve in Figure 1. This graph represents the average nightly swimming activity of the elvers. Similar graphs have been drawn for 1938 by ter Pelkwijk and for 1942 by van Heusden (1943).

Figure 1 demonstrates that swimming activity is greatest during the night. Furthermore, it may be seen that activity does not immediately become maximal at the beginning of the night but increases gradually, i.e., more and more elvers swim as the night advances. This may be explained by assuming that the migration urge also increases gradually during darkness, and that the elvers begin swimming after the urge has reached a certain strength. As this intensity will be attained at different times in different individuals—just as with many other species—it is obvious that the number of elvers swimming will gradually increase during the course of time.

During the day almost no elvers are recorded, as our graph indicates. It must be concluded that the elvers are not then entirely absent from the vicinity of the sluices, but are dug into the sand on the bottom, as described by van Heusden (1943), or remain stationary in deeper water, as was found in the following way. At a distance of about 150 m. from the sluices there is a deep pit in the sea bottom. When dip-netting here at about noon on 6. April 1951 at a depth of 5 m., we caught 1, 1, 1, 2, and 0 elvers. Repeating the hauls at a depth of 20 m. immediately afterwards, we caught 40, 30, 59, 54, and 43 elvers. There was no difference in temperature, and a difference of 1 $^0/_{00}$ in chlorinity between the two depths. For the most part they do not migrate, at this time, in contrast with their behaviour in the open sea, which will be discussed later on.

A question which may be put is whether the curve (Figure 1) retains the same shape throughout the migration season. This has been investigated by drawing four similar graphs for four subsequent fortnights (Figure 2). Not enough data were available for a fifth period.

We again observe the fact that elvers begin swimming about sunset, i.e., the migration urge accumulates during the day and activates the elvers when it is getting dark. Extrapolation suggests that elvers begin to swim about $1^1/_2$ hours before sunset. The number of elvers swimming gradually increases up to a certain point, after which it decreases. We cannot help thinking that the number at this point is determined by the beginning of astronomical dusk, i.e., when the sun is 18° below the horizon.

The peaks of the earlier curves are distinctly flatter than the later ones. This can be explained by the fact that with the first curves the nights are longer. There will therefore be more time for swimming —when the greatest intensity of migration is attained—than later on in the season. A peculiar phenomenon is that in later periods maximal elver activity is reached at an earlier hour than in the beginning of the season. This may be understood by considering that in the later period water temperature is higher than in the earlier. As we may suppose that temperature influences the sensibility to light, as is the case with other animals, this would mean that in the later periods elvers would be more sensible than in the earlier, and would thus react more quickly.

As regards the effect of moonlight on elver migration, it may be that moonlight exerts no influence at all, or that it completely stops the elvers from swimming. A third possibility is that the effect of moonlight is delayed, so that the migration urge accumulates until the elvers eventually swim.

To investigate this, the average catches on days of full and new moon were calculated from the Bann data (Table 6). From these figures we cannot conclude that elvers migrate less actively at full than at new moon, whence it would seem that our second supposition does not hold good. Whether the first and third suppositions are true I cannot decide.

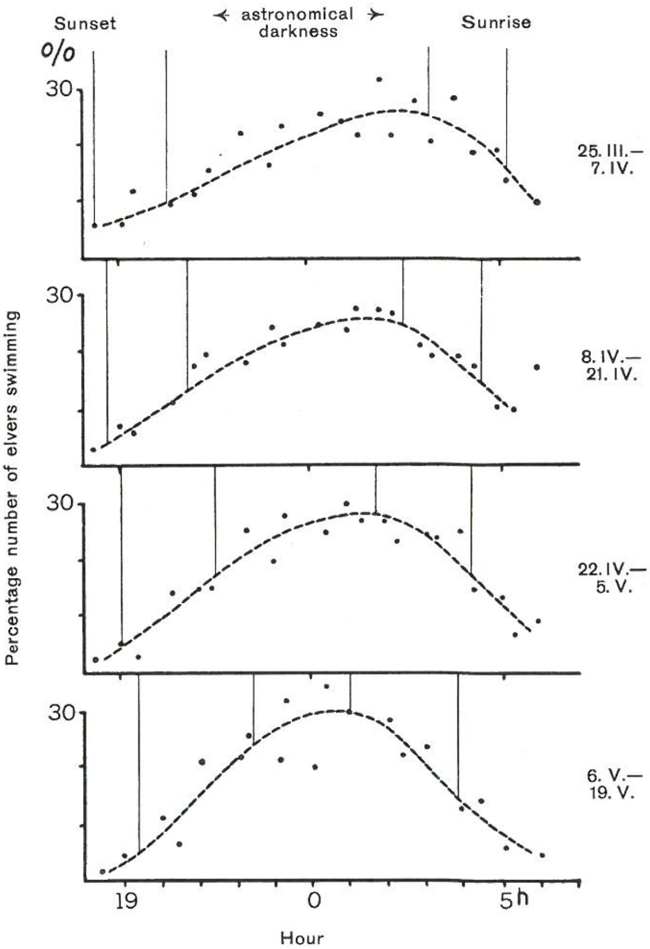

Figure 2. The average course of the nightly activity of the elvers at Den Oever in four successive fortnights, 1938—1949.

Table 6. Average daily catch of elvers (lb.) in the River Bann at full and new moon.

Phase of the moon: Full	Phase of the moon: New	Daily catch made at:
319	268	two days before
349	329	one day before
316	300	the day itself
320	251	one day after
316	225	two days after
Total		
1620	1373	

It is often alleged that an artificial light attracts migrating elvers, and elver fishermen make use of this idea to improve their catches. However, Eichelbaum (1923—'30) could not confirm that this is the case.

Preliminary observations have given the impression that elvers are attracted by light within a certain intensity range and are repelled when the intensity is beyond this range. Presumably also other factors, operating in the past or present, may effect the reactions of elvers to various intensities and quantities of light.

The influence of the saltness of the water.

Verwey (1949) supposed that elvers find their way from the sea into fresh water by indulging an innate preference for certain conditions of milieu, and it is commonly supposed (see van Heusden, 1943) that the most important of them is the proportion of fresh water present, as indicated by the salinity.

It is unfortunate that the Bann data are of little help in studying this matter, for the following reason. The Bann weir is divided into three parts, the southern part with the sluice gates, the middle part with the fish cribs, and the northern part with a single weir (see Menzies, 1936). Normally, water is discharged through the middle part, so that the fresh water is discharged directly towards the estuary. As the river rises, first the northern part and then the southern part begin to discharge too. Moreover, the situation is further complicated, because the gates of the sluices can be drawn. The fresh water passing the northern and southern parts flows in a direction oblique to the estuary. It is certain, so a Chief Engineer of Rijkswaterstaat assured me, that these oblique movements drive great quantities of fast flowing water into the banks of the estuary in front of the weir. This does no harm because

Table 7. Average catch of elvers and quantity of water discharged at the first weir in the River Bann.
Elver catches in pounds/day; water discharge in 10^3foot^3/min./day.

1942	Elvers	Discharge	1945	Elvers	Discharge
2.—6. April	36	124	30. May—3. June	7	132
7.—11. „	36	338	4.—8. June	40	266
12.—16. „	0	460	9.—13. „	0	345
17.—21. „	441	121	14.—18. „	0	189
22.—26. „	405	47	19.—23. „	77	61
1943			1947		
30. Apr.—4. May	144	73	18.—22. April	132	40
5.—9. May	144	39	23.—27. „	28	281
9.—14. „	0	402	28. Apr.—2. May	0	308
15.—19. „	162	101	3.—7. May	0	279
20.—24. „	297	54	8.—12. „	171	139
			13.—17. „	627	96

Table 8. Chlorinity of the water at surface and bottom at various places on days during a certain period on which no water was discharged at Den Oever.

A. At Visjagersgaatje, 17. April to 8. May 1948.

Date April 1948	Time	Chlorinity (Cl ⁰/₀₀) Surface	Bottom	Date April 1948	Time	Chlorinity (Cl ⁰/₀₀) Surface	Bottom
18.	0000	14·56	14·54	19.	1300	15·20	15·20
	0100	14·71	14·71		1400	15·06	15·09
	0200	14·77	14·77		1500	15·15	15·14
	0300	14·21	14·72		1600	15·06	15·21
	0400	14·11	14·66		1700	15·19	15·45
	0500	14·11	14·58		1800	15·06	15·18
	0600	14·60	14·76		1900	15·30	15·30
	0700	14·79	14·91		2010	15·56	15·55
	0800	15·18	15·24		2100	15·57	15·57
	0900	15·07	15·31		2200	15·65	15·60
	1000	15·20	15·24		2300	15·64	15·65
	1100	14·56	14·57		2400	15·60	15·60
	1200	14·55	14·58	20.	0100	15·66	15·65
	1300	14·67	14·95		0200	15·52	15·48
	1400	14·76	15·26		0300	15·26	15·26
	1500	14·68	15·30		0400	15·28	15·31
	1600	14·57	15·16		0500	15·25	15·30
	1700	14·63	14·77		0600	15·25	15·25
	1800	14·76	14·77		0710	15·36	15·46
	1900	15·17	15·13		0800	15·55	15·56
	2000	15·47	15·46		0900	15·55	15·57
	2100	15·56	15·52		1000	15·65	15·60
	2200	15·56	15·56		1100	15·65	15·65
	2325	15·47	15·57		1200	15·65	15·56
19.	0025	15·34	15·36		1300	15·64	15·58
	0100	14·95	14·97		1400	15·56	15·56
	1200	15·54	15·56		1500	15·46	15·39

the banks of the Bann estuary are rocky, but this would not be the case in Holland, for instance; such violent oblique currents would destroy the river banks. It is therefore clear that even close to the banks of the Bann the flow of water is sometimes so strong that the tiny elvers can find no shelter there and are very much hindered or completely prevented from migrating upstream. Hence it can be understood why with high rates of discharge (Table 7) few or no elvers were recorded. This is not because no elvers were present at the moment, but because they were unable to pass certain particularly turbulent parts of the river. It seems to me improbable that the elvers would wait indefinitely for a suitable moment to pass; they may have done so for a while, but under the influence of their steadily accumulating migration urge, they would probably try again and again until they became exhausted and were smashed against the rocks and killed. We may also expect that this happened to some extent with lower rates of discharge, with for

Table 8, contd. **B. At Visjagersgaatje, 24. March to 21. April 1949.**

Date March 1949	Time	Chlorinity (Cl $^0/_{00}$) Surface	Bottom	Date April 1949	Time	Chlorinity (Cl $^0/_{00}$) Surface	Bottom
31.	0020	15·23		20.	0045	17·26	
	0120	15·27			0310	17·20	
	0220	15·33			0420	17·20	
	0320	15·31			0800	17·27	
	0400	15·22			0925	17·26	
	0450	15·25	15·26^5		1030	17·26	
	0550	15·22			1310	17·41	
	0635	15·22			1350		17·35
	0735	15·22			1505	17·23	
	0840	15·28	15·27		1610	17·25	
	0940	15·23			1740	17·28	
	1040	15·26			1910	17·36	
	1140	15·34			2030	17·38	
	1240	15·34			2135		17·36^5
	1340	15·34			2140	17·36	
	1440	15·32			2245	17·33	
	1540	15·26			2345	17·24	
	1650	?	15·26^5	21.	0210	17·41	17·33^5
	1735	15·35					
	1845	15·30					
	1950	15·31					
	2040	15·34	15·36^5				
	2235	15·39					
	2335	15·34					

instance only the weir working. It would seem unjust to correlate the quantity of water discharged with the numbers of elvers recorded at the Bann weir, because each state of water discharge is associated with its peculiar hydrographical conditions below the weir system, depending on the tides and wind direction.

As regards the Den Oever data, we have to reckon with the fact that we do not know the relation between the dip-net catches and the total number of elvers migrating. Hence no direct comparison between catches and water discharge can be made, but the problem can be approached in another way.

It is commonly assumed that elvers arrive at Den Oever when fresh water is discharged. When, however, this does not occur, the salinity differences in the sea water rapidly disappear. According to our observations, it takes only a few days for the water to become homogeneous over great stretches, under the influence of the wind, the differences in velocity in the tidal streams through the gullies and over the flats, etc. This effect is clearly shown by the data in Tables 8A, B, and C. Our ship being stationary, the tidal streams transported great masses of water past the ship. Accordingly a series of identical salinities indicates a large homogeneous water mass. The situation may then be such that as we go from Den Helder to Den Oever, the salinity remains

Table 11. Dip-net catches at Den Oever in 1942, and quantity of fresh water discharged.

Date April	Number of elvers caught	Quantity of water discharged 10^6 m.^{3}	Date May	Number of elvers caught	Quantity of water discharged 10^6 m.^{3}	Date May	Number of elvers caught	Quantity of water discharged 10^6 m.^{3}
11.	0	24	1.	162	0	21.	24	0
12.	2[1])	0	2.	124	0	22.	14	0
13.	1	120	3.	366	0	23.	44	0
14.	16	106	4.	374	0	24.	9	0
15.	33	80	5.	181	0	25.	17	0
16.	20	34	6.	311	0	26.	17	0
17.	217	0	7.	142	0	27.	20	30
18.	98	0	8.	149	0	28.	11	28
19.	93	0	9.	136	0	29.	24	30
20.	258	0	10.	59	0	30.	31	24
21.	134	0	11.	85	0	31.	23	0
22.	107	0	12.	93	0			
23.	337	0	13.	157	0	June		
24.	143	0	14.	110	0	1.	28	34
25.	179	0	15.	130	0	2.	9	34
26.	135	0	16.	139	0	3.	5	33
27.	172	0	17.	9	0	4.	11	0
28.	44	0	18.	85	0	5.	12	0
29.	68	0	19.	77	0	6.	5[2])	0
30.	127	0	20.	56	0	7.	0	0

[1]) Beginning of the season.
[2]) End of the season.

Tidebewegung zwangsläufig in diese Aalreuse (Bristol Channel) hineingetragen", and also, "Von diesen Frühjahrsspringfluten werden nun die . . . Glasaale erfasst und in den Severn hineingedrückt".

Röhler (1939) also considers that this applies to the elver migration in the River Severn, and Menzies (1936) states that in the River Bann the elvers migrate upstream on the spring flood.

The extensive data from the Bann permit us to investigate the validity of this concept. This has been done by computing the average catches on the days before, during, and after spring tides and of the days before, during, and after neap tides. If there is in fact a relation, we may expect the average catches of the first group at least to exceed those of the last. However, from the figures given in Table 12, it appears that the differences do not support such a view. As Table 12 is based on large numbers of data, we must draw the contrary conclusion that spring tides exert no special influence upon the elvers.

The reason why opposite opinions are held by some fisheries experts may be explained perhaps as follows:— These opinions are most strongly expressed in relation to the elver migration near Epney on the

Table 12. Average daily catch of elvers (lb.) in the River Bann during spring and neap tides.

Spring tide	Neap tide	Daily catch made at:
292	203	three days before
339	258	two days before
307[1])	280[2])	one day before
284	300	the day itself
268	320	one day after
204	331	two days after
204	304	three days after
Total		
1898	1996	

[1]) Full or new moon.
[2]) First or last quarter.

Severn. Here an up-river stream occurs only during spring tide; this flows for an hour and is followed by an out-going stream of nearly 11 hours. As the differences in water level at sea are greatest during springs, it is obvious that the speed of the out-going streams at springs will be greater than at neaps.

During my investigations I observed that when migrating into fresh water elvers are very sensitive to adverse currents. They do not allow themselves to be carried back by the flow, but immediately swim to the side where the current is less strong. In my opinion the method of fishing on the Severn is also based upon this feature; the elvers having discovered the lee afforded by the linen scoops, swim into them and remain there steadily stemming the weaker flow. Since the down-river flow is fastest at springs, it is reasonable to assume that at that time the elvers will tend to swim near the banks, and moreover are more inclined to seek the lee side of the scoops, and the catches will consequently be higher. This might be ascribed to a greater intensity of migration, which need not necessarily be the case.

Besides those at springs, the tidal streams at intermediate stages are also believed to carry elvers (Eichelbaum, 1923—'30). Van Heusden (1943) further assumed that at sea elvers make use of the flood stream for transport by swimming in the upper water layers while the stream is flowing, and keeping close to the ground or digging themselves in during the ebb stream. We may consider the validity of these opinions. During the years 1908—1914 and in 1924 and 1926 Mr. Ch. Gilis studied herring larvae; he fished both by day and by night with a fine-mesh net off the Belgian coast and in the English Channel. At the same time he also recorded the elvers caught and this information was kindly set at my disposal. If these data are arranged according to ebb and flood, 26 hauls at the surface on the flood, lasting 2240 minutes, yielded 171 elvers, i.e., 2·3 elvers per 30 minutes. For the ebb 41 hauls totalling 2275 minutes fishing gave a catch of 298 elvers, i.e., 3·9 elvers per 30 minutes. This finding is not in agreement with the opinion mentioned above.

The same conclusion can be derived from the Bann catches. Table 12 compares the average catches at springs with those at neaps. The data are used in a graph (Figure 3) showing the average catches during a whole tidal period. It may be noted that there is a slight error in the graph. The interval between two consecutive spring tides has been taken as 14 days, whereas it should be half a lunar month, i.e., 14·3 days (see Sverdrup, 1946).

According to the Dutch Admiralty, the "mean high water lunitidal interval" (the interval between the moon's meridian passage and the next high water) is 6 hours. This enables us to calculate the time of high water expressed in mean time on a certain day according to the moon's phase.

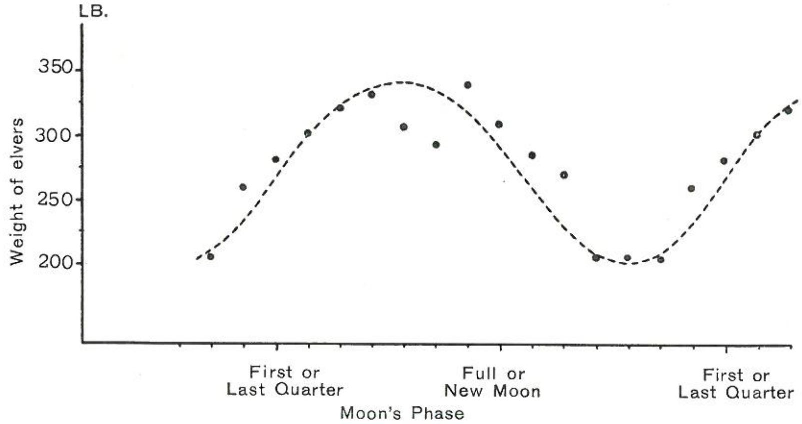

Figure 3. Showing the average daily catch of elvers in the River Bann at different phases of the moon.

Figure 3 indicates that relatively few elvers are caught in the period of about 3 days before first or last quarter, while in the period of about 3 days before full or new moon catches are relatively high. Now we may reckon that in the first period the time of high water is about 22.00 hrs. and about 16.00 hrs. in the second period. This means that in the first period the tide starts to fall early in the night, but in the second period it begins to rise at this time. Moreover, we must recognize that the falling and rising tides coincide with out-going and in-going currents in the estuary.

Let us suppose that a mass of elvers is moving towards the Bann weir. It is obvious that during a certain period (in this case the night) when the current is contrary (out-going flow) relatively fewer elvers will arrive than with a following current (in-going flow). We have already seen (page 197) that near freshwater outlets most elvers begin to swim after sunset. At that time the tide starts to rise in the period of 3 days before full and new moon, in complete contrast to the periods a week earlier or later when the tide starts falling at that time. This provides a plausible explanation of the alternately large and small

The only conclusion we may draw is that the correlation between elver catches and tides at the sluices of the Afsluitdijk is incidental, and caused by the coincidence of local hydrographical circumstances with the tidal movement. Possibly the streams occurring below the sluices during the ebb or the flood tide are such as to transport the bulk of the elvers towards or away from a certain set of sluices, thus biasing the catches. But in this case it would not be right to draw conclusions about the elver migration.

It may be asked why there is so much difference in the fishing at the Bann weir and at the Afsluitdijk.

The elver traps in the Bann river are situated at the head of an estuary. So the tidal streams are directed towards or away from the traps. At Den Oever and Kornwerderzand the situation is completely different. Here the tidal streams move along the freshwater outlets, i.e., the streams run perpendicularly to the axes of the sluices, while in the Bann they are in the same line. Hence it is obvious that the effects of the streams will differ in the two different sets of conditions.

Our own observations made in the Wadden Zee were collected as simultaneously as possible at the surface and the bottom of the water, as earlier described (page 190). Owing to the difference in velocity of the streams at surface and bottom these observations are not strictly comparable. As the difference is unknown, the catches do not provide a safe estimate of the relative amounts of elvers in the two water-layers. Unfortunately I did not manage to obtain accurate flow-meters for the nets.

On the other hand, although the difference in velocities is unknown their relation at a given place is practically constant, according to the experts. The bottom velocity depends on the surface velocity and the depth. We may therefore expect the relation between the quantities of elvers to be fairly constant also, provided that the elvers behave similarly in these two levels.

The complete data are not printed here, to save expense. Anyone interested may have them on application to the author.

When studying our catch data, we must remember that the records do not account for the whole quantity of elvers present at the particular moment; doubtless many elvers remained buried in the sand, or were so close to the bottom that they were not carried along by the flow and could not therefore be caught. The elvers recorded were only those swimming or floating in the water, near either surface or bottom.

The fact that our nets caught elvers certainly indicates that elvers are transported horizontally by the flow of water. We shall later see that there are also vertical movements of elvers. As these cannot be caused by the flow, they must be determined by the elvers themselves.

Before considering the question of tidal influence, we must eliminate the effects of the day-night rhythm. These can be twofold and concern (a) the total number of elvers swimming and (b) their vertical movements.

a) Our data show that the total day-time catches are smaller than the night catches. By day we caught on an average 30 elvers a tide, but by night 116, i.e., 4 times as many. Hence we may conclude either that at sea elvers prefer to swim at night or that if they swim by day, they keep very close to the bottom, where they cannot be caught.
b) The vertical movements may be studied by comparing the catches of the bottom and surface nets. To facilitate this, surface catches have been expressed in percentages of the total catch per tide, without regard to the inequality between surface and bottom flow (Table 14). It is true that the surface percentages are weighted by this procedure relative to the bottom percentages, but as we compare surface percentages with each other only, our conclusions are not affected.

Table 14. The average catch of elvers (numbers) at the surface expressed as a percentage of the surface and bottom catches in the Wadden Zee.

The bracketed figures are the numbers of observations from which the average percentages have been derived.

	Night	Night to Day	Day	Day to Night
Flood	88 (22)	71 (7)	36 (12)	60 (6)
Ebb	74 (20)	48 (4)	7 (15)	0 (1)

The figures show that by night the majority of the elvers tend to stay near the surface, while by day they keep to the bottom. However, the vertical movement caused by the day-night rhythm is difficult to separate completely from tidal effects, for which reason both influences will be discussed together.

Comparing the catches at different stages of the tide we find that by night there is not much difference in the conduct of the elvers on the flood and ebb tides. It is true that the average percentage catches at the surface on the flood tide are somewhat higher than on the ebb, but they are both of much the same order of magnitude. This is not so for the day-time catches; by day, 36 % of the elvers at the surface were caught on the flood, while the corresponding number for the ebb is only 7 %. This difference may be explained in the following way. According to Mr. H. Postma (see also Canter Cremers, 1921) the turbulence in the water is on an average much greater on the flood than on the ebb tide. Hence bottom deposits are spread much more extensively through the water layers on the flood than on the ebb, and the water at the surface is rendered more turbid. Accordingly more elvers are attracted to the surface than when the water is relatively clear. Moreover, we must also reckon on the elvers being carried upwards more actively, and then staying there by their own powers of swimming. It is thus understandable that relatively more elvers are caught at the surface on the flood than on the ebb tide.

This conclusion, based upon the activity-light relation, is also supported in other ways by our observations. For instance, the surface catches made during twilight are intermediate between the respective day and night catches. Again, it will be noticed that the average catches in Table 14 reflect a gradually changing degree of light intensity in the water; the greatest contrast is shown by flood tide by night and ebb by day, while the remaining values lie between them. The difference between these two averages is statistically significant. Hence our observations indicate that on the average elvers swim at a relatively higher level on the flood tide than on the ebb, and that the most likely cause of this is the changing intensity of light in the water.

The phenomena discussed so far are mainly the indirect results of tidal movements. We may also consider the question of direct effect; for instance, do more elvers tend to be transported by the flood stream than by the ebb, as several authors suppose? Our observations are not well suited to a discussion of this matter, for we do not know exactly the number of elvers present at the time our observations were made. If on a particular ebb tide no elvers are present, it follows that our nets cannot catch any. Similarly if many are present on a particular flood many elvers will be caught, but it does not follow that elvers are transported by the flood and not by the ebb.

To investigate this matter, we must examine a series of observations made on subsequent days (so that we may suppose we fished the same stock of elvers) as, for instance, those of 20.—24. March 1950. The observations made in full daylight are omitted, for many elvers were probably not recorded then. There thus remain observations made during the night and at sunset and sunrise. The total quantities caught are 2697 elvers in 1900 minutes (142 elvers per 100 minutes) on the flood tide by twilight, and 2391 elvers in 2090 minutes (114 elvers per 100 minutes) on the ebb by night.

To interpret these figures we require to know the ratio of the flows at the different states of the tide. According to Mr. H. Postma both tides transport practically the same amount of water. Because the average duration of the flood in the Wierbalg—where the observations were made—is less than the duration of the ebb, the flood stream must be stronger than the ebb stream.

Over 8 flood tides we were able to fish for 1900 minutes with both nets, so an average "fishable" flood tide at that time lasted 119 minutes. In the same way we see that an average "fishable" ebb tide lasted 249 minutes, that is, 2·1 times longer than the flood. This implies that the average flood flow must have been 2·1 times stronger than the average ebb flow during our observations. Assuming that our nets filtered the same amount of water we thus get the following relation:—

$$\text{flood transport} : \text{ebb transport} = \frac{142}{2 \cdot 1} : 114 = 1 : 1{\cdot}7.$$

It may be recalled that the flood tide observations were made at twilight and it is probable that for this reason some elvers were not "catchable", despite the greater turbidity of the water, and the relation is probably weighted in favour of the ebb tide. Hence it appears that there is no reason to suppose that elvers choose the flood tide on which to be transported to their destination; it is more likely that rather the same number of elvers are swimming about on both flood and ebb tide. This is additional support for our view that tides exert practically no internal influence—if any—upon the behaviour of elvers.

The migration of the elver.

Our investigations suggested that the path followed by migrating elvers might be divided into two parts, that in the sea, and that near freshwater outlets. Although something of the characteristic behaviour of elvers near freshwater outlets has been discovered, we still know little about the orientation of elvers in such surroundings, so we shall not deal with it at present.

With regard to orientation and migration at sea, although we are better informed now, this subject requires more thorough discussion before it can be fully grasped. I believe I have formulated an explanatory hypothesis, which leads to a better understanding of the distribution of elvers, and which is in agreement with the numerous observations made.

Let us consider first the elver migration in the English Channel and North Sea. According to Schmidt (1906) elvers generally reach Brittany and Lands End in southern England in February. We know also that on an average elvers arrive at the Afsluitdijk in the last half of March. This indicates that a distance of some 900 km. is covered in about 45 days, giving an average daily speed of about 20 km. in the most favourable situation. At this speed elvers should first reach Denmark in the middle of April, which agrees with Schmidt's 1906 findings.

What we want to know is, How do elvers manage to travel at this speed? It can be attained in three ways, namely, passive transport by the water flow, swimming, or a combination of both.

Let us first consider the flow. In the region considered the tidal streams are the important features of the water movement. The conditions which elvers can encounter are as follows:—

	a)	b)	c)
night	1 flood tide	1 ebb tide	exceptionally 1 flood and ebb tide
intermediate period (sunrise or sunset occurs during a tide)	2 ebb tides	2 flood tides	—
day	1 flood tide	1 ebb tide	1 ebb and flood tide

To interpret these conditions we must remember that on the flood tide elvers usually swim at a higher level than on the ebb. In the Wadden Zee this is caused by the greater turbidity during the flood tide, as a consequence of the increased turbulence stirring up the bottom deposits. According to Mr. H. Postma this will also happen in the North Sea and English Channel, although the bottom deposits will probably not be brought right up to the surface. But near the bottom, the water will be more turbid during the flood than during the ebb.

For our calculations we need to know the average speeds of the flood and ebb streams between the mouth of the English Channel and Holland. These figures have been computed by van Heusden (1943) from the "Atlas der Gezeiten der deutschen Seewarte" (1926). He used the positions numbered 4, 5, 67, 86, 94, 101, 111, 113, 117, 161, 162, 182, 183, 186, 187, and 189 in this atlas, and these positions probably lie on the migration route of the elver. According to van Heusden the average surface flood flow is 28 m./min., while that of ebb is 29 m./min. Flood lasts 401 minutes and ebb 370 minutes. Hence we get an average transport of 11·2 km. for the flood, and 10·7 km. for the ebb.

Let us now consider cases a) and b) together.

By night elvers will swim usually in the upper water layers, where the respective flows will transport them favourably at the rate of 0·5 km. in 2 days. According to our observations (Table 14) only a few elvers swim at the surface during the flood and in the bottom layers during the ebb. In this case they will also gain by the differences in stream speed at surface and bottom, if they act in this way persistently. By night the bottom of the sea will be dark; so elvers will not therefore swim close to it, and will be carried along by the flow, as our observations show. Their extra gain per 2 days will thus be small.

In the intermediate period, at this season the bottom of the English Channel and southern North Sea may be expected to be dark (Russell, 1931). Hence we may assume that elvers swim a little off the bottom during the ebb, and perhaps at a somewhat higher level during the flood. Thus their gain will be very slight, say 2×0·5 km./2 days.

By day. We do not know whether elvers swim by day, but let us suppose that they do. On the ebb tide elvers will swim close to the bottom; in the most favourable case they will not be transported backwards. On the flood they swim higher in the water and are transported forward, let us say, the maximum distance of 11·2 km. Their maximal gain is then 11·2 km./2 days. We thus get a total of 0·5+2×0·5+11·2 km./2 days = 6·4 km./day. This may be slightly more, if the elvers behave by night in the manner described above.

Case c) is exceptional, but may be considered here for the sake of completeness.

By night. Reckoning as above, we get a gain of 0·5 km./day, perhaps somewhat more.

By day. For part of the day during the ebb tide the bottom is dark (Russell, 1931), and the elvers accordingly swim at a distance from the bottom and are carried some 3—4 km. backward. Maximal gain on the flood is 11·2 km., giving a total day-time gain of 7·7 km. The total daily gain is at most 8·2 km., which agrees well with the value we found for cases a) and b).

A tidal transport of about 6·5 km./day, or somewhat more, we can understand, but this falls far short of the 20 km./day needed. Hence we are forced to assume that elvers cover a certain distance by active swimming, and they must do this both by day and by night. According to observations made by ter Pelkwijk (1938) and myself, the average speed at which elvers swim about is 15 cm./sec. or 13 km./day. This value added to that of 6·5, which we found, gives a transport of about 19·5 km./day, which fits very well with our earlier estimate, derived from the dates of arrival on various European coasts.

It must be remarked, however, that to reach the daily "mileage" the elvers need to swim in one direction, which is in the same line as the tidal streams. This might imply that elvers are able to recognize ebb and flood; on the ebb they swim against the stream, and on the flood they swim with it. One might expect them to be able to make this distinction when they are on the bottom, but how do they manage to keep their direction in the upper water layers, where they apparently lack any means of orientation? Deelder (1949a), however, proved the existence of an innate "sense of direction" in silver eels migrating to their spawning places. If silver eels possess such a sense, it is reasonable to assume that elvers also possess this sense. If this is so, elvers, whether swimming near the bottom or the surface, are able to follow a chosen direction. It is possible that the difference in turbulence enables elvers to distinguish between ebb and flood flows when they are on the bottom (although we obtained no support for this idea in the preceding section) and that they are able to "recollect" these directions when in the upper water layers.

Another possibility is that elvers keep to a direction with the help of the electric currents generated by the movements of sea water. The horizontal component of the current is perpendicular to the flow of the sea water. If elvers are able to perceive very small currents, they can align themselves with the water flow by taking up a position in which no electrical current runs from snout to tail or the reverse. Dr. P. Groen has estimated that in elvers this current would be almost 1×10^{-10} amp./mm^2. for a water speed of 1 m./sec., provided that the electrical resistance of elvers is the same as that of sea water. We do not know what current elvers can perceive, but Uzuha (1934) found that a catfish could perceive a current of 1×10^{-7} amp., which is 1000 times greater than the value mentioned above.

What are the consequences of these orientation hypotheses? Firstly, elvers travel in the same line as the tidal streams where these are present. This explains the arrival of many elvers on the coasts of Ireland, of western and southern England, of France, Spain, etc. ("Atlas der Gezeiten", 1926). Secondly, elvers evidently reach the southern North Sea through the Straits of Dover and migrate northwards, as the flood stream is north-going. Elvers reach the North Sea by the route north of England too (see Schmidt, 1906) and will migrate southward with the south-going flood stream, reaching the east coast of England sometimes in considerable numbers (Pentelow, private communication).

There is, however, a third explanation of these phenomena, which, I believe is the more plausible. We may recall that it is a very common characteristic in migrating birds (see Deelder, 1949b) that they migrate in a certain direction with the exercise of an innate sense of direction. When these birds (land or sea birds) reach a distinct boundary, e.g., a coastline, they exchange this innate orientation for a visual method, i.e., they fly along the coastline in the direction which deviates least from the chosen direction. If the coastline disappears the birds revert to their innate orientation and proceed in their original direction.

With regard to elvers, let us suppose with Verwey (1949) that they have an eastward sense of direction. Elvers swimming in this direction after metamorphosis will sooner or later reach a coastline. Now it has been proved (see also Dieselhorst 1938) that eels can hear. On an oceanic coast such as the Atlantic coast of Europe, there will be surf, the beat of which we may assume elvers can hear, the more so because water transmits sound much better than air. Just as a man can move along the shore with his eyes closed, orientating himself with his ears towards the breakers, so may elvers be able to do it. In this connexion Westenberg (1952) states that certain Indonesian fish are able to swim parallel to a coast; they are even able to keep along a certain depth contour. Westenberg explains this feature not as due to the surf, but to the ruffled water surface sending sound vibrations downward which are reflected from the bottom. This will set up resonance with an average wave-length of four times the depth, so that a particular resonance frequency will correspond to a certain depth.

In correspondence with what is known of birds, would it not be reasonable to assume that elvers, when in the vicinity of land, discard their innate sense of direction and travel along the coast in that direction which deviates least from their original one, orientating themselves acoustically? It is to be remarked that the elvers would then be travelling in the same line as the tidal streams, generally with the flood and against the ebb stream. In this case, however, the elvers need not be able to distinguish between these streams, which greatly simplifies the hypothesis and is also in agreement with the conclusions reached in the preceding section.

This hypothesis is based upon proven facts; it is the combination of them which must be proved. This is a very difficult task, however, perhaps impossible at present, for the technical facilities for making the necessary observations are not yet available.

Summary.

Investigations have been carried out on the factors influencing the migration of elvers at sea. These investigations have comprised the

collection and study of statistical data as well as the making of observations at sea. The main results are as follows:—

The intensity of the elver migration shows some decline in the period studied, namely, 1936—1950; the decline cannot be explained.

The minimum value of the range of sea water temperature in which elvers migrate is about 4·5°C. Temperature and intensity of migration are not correlated.

A relation exists between light intensity and elver activity, but there is no correlation between moon phase and migration intensity.

The rate of water discharge and the consequent fall in salinity some distance away from freshwater outlets do not affect the migration of elvers in the sea.

Spring and neap tides have no differential effect on elver migration, nor can a direct effect be traced directly to the direction of the tidal streams. Apparent connexions between tidal streams and elver migration near freshwater outlets must be ascribed to local factors.

It appears that elvers travel both by day and by night at sea; at night they swim at a much higher level in the water than by day, which must be ascribed to the differences in light intensity. As turbidity is higher with the flood than with the ebb in our waters, elvers travel at a higher level on the flood than on the ebb. Consequently over a large part of their migration, transport is effected by the tidal streams.

A hypothetical explanation of the migration of the elvers at sea is offered.

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