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On the orientation of migrating elvers (Anguilla vulgaris Turt.) in a tidal area

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swimming with the current as if retreating before unfavourable conditions. Similarly, CZELOTH (1931) demonstrated a positive anemotaxis in *Triton* when the air current carries a smell of garden mould and a negative anemotaxis when the air current is free from odour.

At higher current velocities positive rheotaxis made the elvers cling to the bottom or burrow in the sand, while on the other hand negative rheotaxis produced an upward movement to higher water levels.

In some respects, however, the mechanism is not so clear. When during the flood tide elvers rise to higher water levels they stay in the same water mass all the time. It is hard to see how under such conditions they can perceive the end of the flood tide. Nevertheless they return to the bottom at the turn of the tide.

Hitherto we have not discussed the roles of temperature and salinity. Field observations produced the impression that the inward migration of elvers is to some extent governed by these factors too. When it is very cold fresh water seems to be avoided and under extreme conditions (in 1958 for instance) even the passage of elvers through the Wadden Sea can be delayed. Internal factors (DEELDER, 1958) also appear to restrain them from immediately invading inland waters. This complex of questions has received scant attention so far.

In the present state of our knowledge we may assume that tidal streams constitute the sole directional factor for elvers migrating through a tidal area. Changes in the odour content of the water, though in fact nondirectional, determine the actual response (positive or negative) to the tidal streams.

A behaviour pattern as described presupposes a physiological condition which is likely to be influenced by the temperature (possibly in conjunction with changes in the duration of daylight). The migration will probably also be affected directly by the temperature, particularly in extreme conditions (possibly in conjunction with the salinity). Most probably, however, neither the temperature nor the salinity interfere in the orientation mechanism.

4. SUMMARY

A. FIELD OBSERVATIONS

Each spring large numbers of elvers enter the Dutch Wadden Sea through the Marsdiep tidal inlet and migrate to places where fresh water is discharged, such as the sluices in the Enclosing Dam at Kornwerderzand and at Den Oever.

Catches were made in the North Sea and in the Wadden Sea, at the surface and partly at a depth of 8 m, with a one m^2 ring trawl, and in front of the sluices in the Enclosing Dam near Den Oever with a dip net. The following conclusions could be drawn.

In the Wadden Sea (here considered as an estuarine area), especially in the Marsdiep and Texelstroom, a distinct inward migration takes place during the months of February, March and April. This migration alternately consists of a stage of inward transport in higher water levels by the flood stream and a stage during which the elvers dwell near the bottom while the tide runs out with the result that they are not washed back to the sea. This migratory behaviour persists both during the night and in the day time. By day, however, the elvers do not reach the surface.

It is supposed that the elvers will be transported by any water movement directed towards estuarine areas and that they will dwell near the bottom during any water movement away from them. Observations made in the coastal waters off Scheveningen suggest that elvers are transported in a south-westerly direction by the ebb stream, running towards the estuary of the river system of the Rhine, while they dwell near the bottom during the flood stream, coming from that area.

From observations made in the Wierbalg (further inward in the Dutch Wadden Sea) and in front of the sluices it was found that near fresh water outlets the migration is delayed approximately a fortnight. In the Wierbalg the elvers are transported to and fro in about the same amounts during both ebb and flood. Factors, such as salinity, temperature and physiological condition are believed to be responsible for this delay. Under extreme cold weather conditions (spring 1958) the migration appeared to have been delayed in the Texelstroom and Marsdiep as well.

Observations made from the lightvessels "Texel" and "North Hinder" did not lead to conclusions as to whether the open sea migration of elvers is controlled by a tidal mechanism. Because of the ellipsoid nature of the tidal streams in the open sea and the apparent accumulation of elvers in coastal waters the results are difficult to interpret. As an alternative conjecture, passive pelagic transport of elvers by residual currents is discussed. On the strength of observations in the open sea by several workers and of the author's own findings a tentative exposition is given of the seasonal advance of elvers in the North Sea and the British Channel. This advance proved to be of the same order of magnitude as the residual current velocities revealed by observations made from lightvessels (British Admiralty, 1946) and observations by TAIT (1937), CRAIG (1959), GLOVER (1955) and DIETRICH (1950).

B. EXPERIMENTS

Once it had been established that their migration is controlled by a tidal mechanism as described above, it was evident that elvers must be able to discriminate certain characteristics of ebb and flood. In accordance with the view put forward by VAN HEUSDEN (1943), salinity changes such as occur in the tidal streams were made the starting point for an experimental approach to the problem. A circular stream apparatus was constructed in which the ebb phase was imitated by a salinity decrease and the flood by a salinity increase. Mixtures of sea-water and tap water were used. However, no satisfactory results could be obtained with this device.

As a result of these experiments, in which the elvers failed to show an "inward migration", an attempt was made to reproduce the findings of VAN HEUSDEN (1943), and FONTAINE and CALLAMAND (1941), who showed a distinct preference of elvers for fresh water to sea-water. When tap water was used, however, no preference for fresh water was found. Natural water from inland sources, on the other hand, such as from the North Holland Canal or the IJssel Lake, proved very attractive. This feature appeared to be due to the occurrence of an attractive substance, removable by treatment with a charcoal filter, which is presumably an odour specific to inland water, and to which elvers show an innate response.

Further, it was demonstrated that inland water can lose its attractiveness in the course of time. This means, on the one hand, that the odour influence of fresh water outlets does not reach so far into the open sea as the salinity influence. On the other hand, the odour-gradient will be steeper and may thus guide the elvers more effectively to the source of newly discharged inland water.

After these findings the experiments with the circular stream apparatus were continued. But now the ebb stream was imitated by an increase in the odour content by admitting untreated water from the IJssel Lake and the flood stream was imitated by a decrease in the odour content by supplying odour-free sea-water filtered over charcoal. With low and moderate current velocities (10 and 22 cm/sec) a distinct increase of positive rheotaxis and a decrease of negative rheotaxis was indeed observed during the ebb phase, while the reverse took place during the flood. Of the phenomenon, observed in nature, that elvers are transported by the flood stream in higher water levels and dwell near the bottom during the ebb, no symptoms were found until higher current velocities (36 and 49 cm/sec) were applied. At these velocities, which more closely approximate those occurring in the Wadden Sea (100 cm/sec), a distinct upward movement to higher water levels was seen during the flood phase, while the elvers kept close to the bottom during the ebb.

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