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The Effect of Water Currents on the Survival and Distribution of Fish Larvae

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Introduction

Water currents are among the most important factors affecting the distribution of the pelagic larvae of fish. When hatched, the larvae have a large yolk-sac and cannot swim very well. Thus during their early stages the larvae may be passively carried by the water currents. The current not only affects the eggs and larval distribution by carrying them to different sea areas, but also indirectly affects their survival. Thus if the eggs or larvae drifted to unfavourable areas where food conditions are poor, high mortality of the brood takes place, and vice versa.

The influence of currents on the survival and distribution of eggs and larvae of sea fish was pointed out by numerous nvestigators (FULTON, 1897; PETERSEN, 1903 and 1924; OTTERSTRØM, 1906; SCHMIDT, 1909; DAMAS, 1909; HUNTSMAN, 1918; JOHANSEN, 1924, 1926, 1927, and 1929; KRAMP, 1924; RUNNSTRÖM, 1934; WALFORD, 1938; BONNET, 1939; DANNEVIG, 1940; KÄNDLER, 1950; JENSEN, 1952; and many others).

GRAHAM, CARRUTHERS, and GOODCHILD (1926) established a close correlation between the drift of cod eggs and larvae, and the known movements of water during 1924 in the North Sea. RUSSELL (1937), however, showed that the dispersal of eggs and larvae which begins as a passive movement in the direction of the current soon changes into a search for their normal habit by young fish, though he did not give any evidence for his statement. TESTER (1951) found that anchovy larvae were able to swim freely in later stages but were largely at the mercy of currents in the early stages of development. BONNET (1939) concluded that cod eggs and larvae when present in the wind-agitated surface layers drift before they take to the bottom; and that the mortality due to high temperature was not a normal factor limiting the distribution and development of such eggs.

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As the surface currents are mainly caused by wind and the former affects the distribution of fish larvae, workers tried to find a correlation between year broods and early stages of development and wind force and direction. Such work has been done by THOMPSON (1930), CARRUTHERS (1938, 1951), CARRUTHERS, LAWFORD, and VELEY (1951,1953), CARRUTHERS, *et al.* (1951), and VELEY (1952). These investigators emphasized the importance of studying the current as a factor in dispersing the spawning products and indirectly affecting their survival by taking them to unfavourable areas. They found a correlation between the yearly brood and the wind prevailing during the early stages of development.

GRAHAM (1952), SIMPSON (1952), and GULLAND (1953), however, did not agree with these conclusions especially in that the critical drift given by CARRUTHERS, LAWFORD, and VELEY (1951) did not agree with the work of HENSEN and APSTEIN (1897) and GRAHAM (1926). Moreover many of the good years occurred in spite of the assumption that the fry is carried to unfavourable places. CARRUTHERS, LAWFORD, and VELEY (1953) discussed these views.

While currents affect the survival and distribution of pelagic marine fish larvae either directly or indirectly, they affect freshwater fish larvae in other ways. Thus although many freshwater larvae are pelagic and are affected by currents in their distribution, many others are demersal, i. e., they pass their early stages on the bottom of streams or rivers. An example of such larvae is that of the salmonids. My observations showed that the newly hatched larvae are incapable of active swimming in mid water because of their large yolk-sac. Although the larvae can swim for a short distance, they pass most of their time in their redds under the gravel and stones. With further development the fish become more active. This activity is shown by their ascent in the water which is however not vertical but spiral, circular, or at an angle. Once the larvae arrive near the surface they allow themselves to fall to the bottom once more.

Apparatus and Technique

No apparatus has been described in the existing literature for the study of the reaction of pelagic fish *larvae* towards a current of known velocity although adult fish and other aquatic animals have been investigated (ALLEE, 1912; SHELFORD, 1929; LYON, 1904, and 1909; CHIDESTER, 1922; GRAY, 1937; ELSON, 1939; and MCHINNON and HOAR, 1953).

The construction of a current apparatus presents many difficulties. An apparatus in which a constant uniform current is maintained for long periods requires a large supply of water. Also when experimenting with pelagic marine fish larvae, the presence of obstructions, air bubbles, etc. must be avoided as these may affect the reaction of fish towards the current. In addition, a long distance is necessary: a fish may maintain itself against a certain current for a short time but then is weakened by the current and may drift with it if it lasts for long periods. Moreover, marine fish larvae are small and transparent and difficult to observe so that an apparatus in which they can be easily seen must be used.

The present apparatus was designed to provide a reasonable water current for any required length of time. Not all conditions were fulfilled in this apparatus, however. It is characterized by the following features:—

1. It can give a constant current flow.
2. The water flow can continue for any length of time required by the investigator.
3. The direction of water flow can be reversed when required.
4. Different constant flow rates can be obtained.
5. The flow rate of the water can be determined exactly.
6. The critical current velocity at which the larvae are just able to maintain themselves against the current can be found.

Principle

A constant-level water supply feeds a straight uniform tube with a constant water flow. Larvae are introduced into the experimental tube with the least possible disturbance.

Description of apparatus

This apparatus is shown in Figure 1. The tank is supplied with sea water through the inflow B. A constant level of water is maintained in it by the overflow C situated near the top. The outflow is taken from near the bottom of A by a tube D which fits through a rubber bung. Tube D is provided with a glass T-tube which in turn is connected by wide rubber tubing and T-pieces to both ends of the experimental tube E. One branch of each T-piece is thus attached to one side of the water supply (from tube D) whilst the other is connected to an overflow tube. The two overflow tubes G and H are provided with stop-cocks, 4 and 5. These can be opened and closed as desired. Introduction of the experimental animals into the experimental tube E is done through a cup-shaped vessel F connected to one end of the experimental tube by a T-piece as shown in the figure, the connexion of the vessel F to the T-piece consisting of rubber tubing provided with a screw clip. This is only opened when introducing the larvae from F into the experimental tube E.

All glass and rubber tubing used in this apparatus were more or less of the same internal diameter, namely 1 cm. The experimental tube was about 1·5 m long and about 1·2 cm in diameter. By opening and closing the appropriate stop-cocks a constant flow of water can be obtained in one direction, and can be reversed when wanted. Thus when opening stop-cocks 1, 2, and 5 the current direction is from left to right, and from right to left when 1, 3, and 4 are opened and 2 and 5 shut.

When introducing the larvae into the experimental tube they were transferred to vessel F previously half filled up with water. Then all the stop-cocks were closed (2, 3, 4, 5) and screw-clip 6 was opened. If the larvae were carried to the bottom of the cup-shaped vessel F, they were left till they reached the experimental tube, while if the larvae were swimming at the surface slight opening of stop-cocks 4 or 5 was necessary so that the larvae were carried down into the experimental tube. Before starting an experiment, the vessel F had to be full, with no air anywhere in the apparatus. This was ensured by closing all stop-cocks except one (either 2 or 3) on that side of the experimental tube where the larvae were not present, thus water was pushed into F and filled it. Screw-clip 6 was then closed and the apparatus was ready for the experiment. The cleanliness of the water supply is very important in water current experiments. As the sea water supply in the apparatus was not very clean, filtered sea

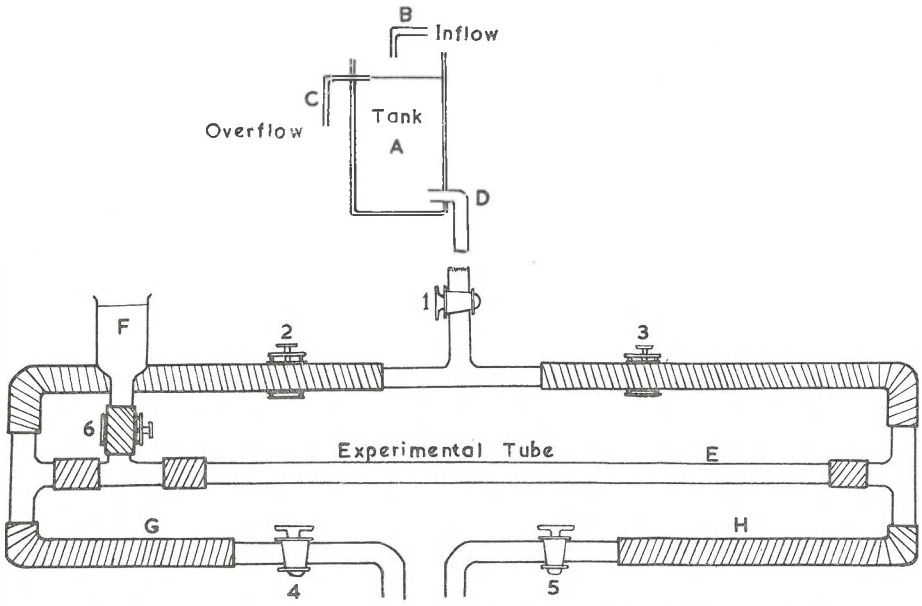

Figure 1. Apparatus used to test the reactions of fish larvae to water currents.

water was prepared for all current experiments by filtering through sand followed by glass fabric. This proved to be the most effective method although it does not free the water from very fine particles. As a strong continuous water supply was required, this was found to be the only practicable method.

Detection of water flow inside the experimental tube was done by using either a dye or milk, introduced at one end of the tube through the vessel F. The flow velocity in such a tube was found to be greatest in the middle, diminishing towards the wall.

The current apparatus described was mainly used for the study of the response of pelagic fish larvae towards different current velocities. In addition to experiments on the early stages of herring larvae, a series of experiments on lump-sucker larvae were also performed.

Calculation of the rate of water flow

The rate of the water flow can be calculated if the volume of the water passing through the experimental tube in a definite time is known. Time was measured with a stop-watch and the water collected (at either overflows G or H) in a graduated cylinder. Knowing the area of cross section of the tube, the different rates of water flow can be derived from volume measurements. In the experimental tube a flow rate of 1 mile/hour corresponds to 44·7 cm per second (area of cross section: 0·947 cm^2).

Method

Having determined the rate of flow, the fish larvae were introduced into the container F and left for some time before being introduced into the experimental

tube by the method described above. The larvae were then left in the tube for at least an hour so as to become accustomed to the new surroundings. The direction of the current flow was decided with reference to the end of the tube at which the larvae were present.

The behaviour and reactions of the larva were recorded at fixed intervals. In order to know exactly the points at which the fish reacted, the experimental tube was lined on the outside with a strip of paper divided into centimetres. When the larvae reached the other end of the tube relative to the beginning of the experiment, the flow was stopped and reversed. This was repeated at least 10 times, the larva having then travelled 50 feet. The same larva was used in 10 of such experiments (using the same flow rate), after which a new larva was introduced and the experiment repeated in the same way.

Occasionally more than one (e.g., 2–5) fish larvae were used. Individual differences within the small groups were observed but their overall reactions towards the currents were more or less uniform. A change in the rate of flow was produced by adjusting stop-cock 1, and the experiments were then repeated.

In order to determine the critical flow velocity stop-cock 1 was adjusted to produce a rate of flow at which the larvae could just maintain itself without being carried along for at least one hour.

In each experiment an attempt was made to maintain other factors such as temperature and light uniform throughout the duration of the experiment. The temperature of the water in the experimental tube was the same as that of the tanks in which the larvae were reared. It remained constant through the whole period of the experiment. In addition, the light conditions were the same as those in the rearing tanks. The experiments were peformed near the window, when dark a 100 watt bulb above the centre of the tube was used. Vibrations were avoided. The behaviour of the larvae was observed before the current flow started, and the response recorded was only that due to the current.

Material

The fish larvae used in these experiments were herring (*Clupea harengus* L.), lump-sucker (*Cyclopterus lumpus* L.), salmon (*Salmo salar* L.), sea trout (*Salmo trutta*), and brown trout (*Salmo trutta* f. *fario*). These fish larvae were reared at the Dove Marine Laboratory, Cullercoats, North Shields, England. Artificial fertilization was carried out at sea or at fish hatcheries. Experimental results in rearing of these larvae will be published later.

Rearing of the larvae took place either in glass or glazed earthenware tanks and all the experiments were carried out under the same conditions of light and temperature at which they were reared.

The average lengths of the larvae used and the temperatures at which they were reared were as follows:—

Species	Temperature °C	Length of larvae mm	Age (days)
Clupea harengus L.	13·1–14·8	6·5–8	1–9
Cyclopterus lumpus L.	10·1–13·2	6–9	1–28
Salmo salar L.	7·9–12·5	20–25	1–42*)
Salmo trutta	5–10·5	18–24	1–42*)
Salmo trutta f. *fario*	5– 9·2	16–25	1–42*)

*) Yolk-sac absorbed 28–35 days after hatching.

Experimental Results

A. Herring Larvae

Experiments were carried out on the early stages of herring larvae in which the yolk-sac was not completely absorbed (1 day to 5 days old). Older stages (up to 9 days old), however, were used, but experiments with these stages were not reliable as the yolk-sac was nearly absorbed and the larvae needed food. Most of the older larvae used in these experiments were not feeding and were weak.

In addition, herring larvae were very delicate to handle. As soon as they were transferred from the rearing tanks to the experimental tube many of them died. However, in all the experiments only the healthy larvae which behaved normally in the experimental tube were used.

1. Behaviour of larvae without current

Newly hatched herring larvae swim at random. Their swimming activity is at irregular intervals. When not swimming about they either maintain themselves near the surface or in mid water (in the rearing tanks). Swimming is by darting to and fro while moving their body (wriggling). When the larvae become older (3–7 days) they are more active and swim for longer periods, although they become weaker unless they are fed.

2. Behaviour of larvae to currents

In every case the fish orientated itself — if not at first, then in a few seconds — to face into the current whether drifting or actively swimming. Velocities investigated were 0·58 cm/sec. (0·013 mile/hour); 1·03 cm/sec. (0·023 mile/hour); 1·16 cm/sec. (0·026 mile/hour); 1·70 cm/sec. (0·038 mile/hour); 2·10 cm/sec. (0·047 mile/hour); 3·00 cm/sec. (0·067 mile/hour); 3·49 cm/sec. (0·078 mile/hour); 3·89 cm/sec. (0·087 mile/hour); 4·47 cm/sec. (0·10 mile/hour); 7·60 cm/sec. (0·17 mile/hour).

In most cases when the larvae were maintaining themselves or swimming against the current, their bodies were inclined downwards at 45° to the horizontal. In order to see if the orientation of the larvae was due to their shape, dead larvae were used in each experiment as controls. Experiments with these dead larvae showed that they drifted either head with or opposing the current and in most cases rolling, whilst the rate of drifting was in most cases higher than that of live specimens.

Movements of surrounding objects seem to have no effect on the response of herring larvae to currents. No reaction took place when passing a striped paper back and forth beneath and at the sides of the tube where the larvae were enclosed.

(i) *Response of larvae to a 0·58 cm/sec. water current*

Two newly hatched larvae were used in this experiments. The swimming larvae orientated themselves to face the current as soon as it started. The larvae remained in the middle of the tube where the current was strongest. They wriggled and maintained themselves against the current. Occasionally when the larvae ceased moving their bodies, they drifted downstream, but they neither

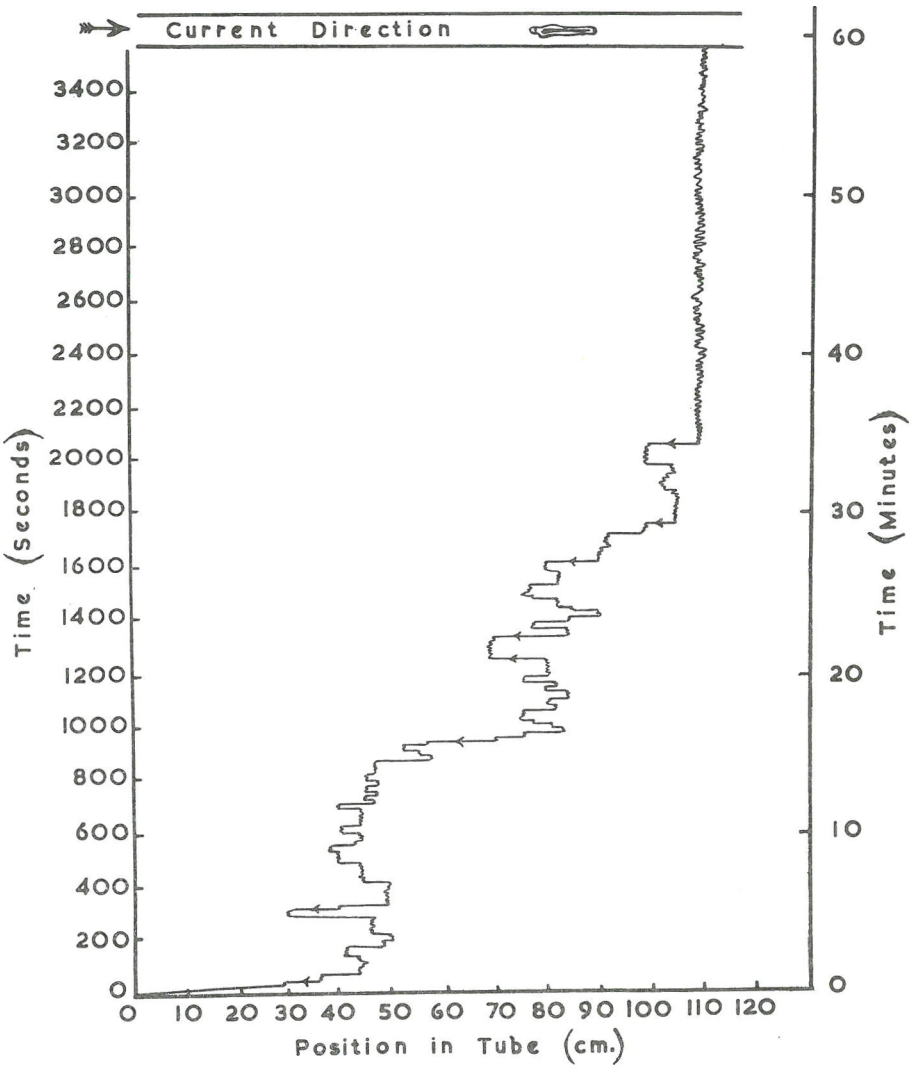

Figure 2. Response of a herring larva to a water current velocity of 2·10 cm/sec. (0·047 mile/hr).

rolled nor changed the direction of their heads. Immediately after drifting for a few centimetres they swam once more against the current and would move forward a few centimetres. In rare cases the larvae swam in the direction of the current, but soon turned to face into it and then swam against it. The larvae were not seen touching the sides of the tube.

After maintaining themselves for 14 minutes at the same spot, the larvae swam upstream and succeeded in moving a distance of 20 cm. The larvae maintained themselves against the current for at least 45 minutes without drifting from their position.

Table 1

Response of herring larvae to water currents and the relation between current velocity and drifting rate

Length of larvae: 6·5–8 mm.

Current velocity Mile/hour	cm/sec. (A)	Average drifting rate (B) cm/sec.	$\frac{B}{A}$	Age of larvae (days)
0·013	0·58	0	0	1
0·023	1·03	0·43	0·42	1
0·026	1·16	0·62	0·53	5
0·047	2·10	0·49	0·23	6
0·067	3·00	1·48	0·49	8
0·078	3·49	1·47	0·42	1
0·087	3·89	2·6	0·66	4
0·094	4·20	3·23	0·77	8
0·10	4·47	3·15	0·70	6
0·17	7·60	4·2	0·55	1

(ii) *Response of larvae to a 2·10 cm/sec. water current*

Thirty-five experiments were carried out with different individuals at this speed and they all showed more or less the same reaction. One of the experiments is represented in Figure 2 where the abscissa represents the location of the fish (i. e., the tube divided into centimetres) while the ordinates represent the time in seconds and minutes. The diagram shows clearly *where* the larva maintained itself.

The experiment showed that the larva orientated itself throughout the experiment and attempted to swim against the current. It often succeeded in maintaining itself against the current for some time. In many cases the fish swam upstream by one dart or jump. To maintain itself at the same position the body of the fish was moving all the time. The fish remained in the middle of the tube throughout.

(iii) *Response of larvae to water current velocities higher than 2·10 cm/sec.*

More than 200 experiments were carried out with higher current velocities (i. e., 3·00, 3·49; 3·89, 4·2, 4·47, 6·25, and 7·60 cm/sec.). Table 1 shows the relationship between current velocity (cm/sec.) and drifting rate (cm/sec.). The drifting rate is defined as the distance in centimetres which the larva drifts in a second at a given current velocity. It is calculated by dividing the distance (in cm) drifted by the larva by the time in seconds. From the experiments it is possible to find out the "critical current velocity" which is the velocity at which a larva can maintain itself without being passively drifted with the current for at least one hour.

From Table 1, it can be seen that between a current velocity of 0·58 cm/sec. and 1·03 cm/sec. lies the "critical current velocity".

B. Lump-Sucker Larvae

Lump-sucker larvae have the ventral fin modified to form a sucker-like structure by which they can stick to solid objects.

About 450 experiments were carried out on early larval stages. The following current velocities were used: 7·60 cm/sec. (0·17 mile/hour); 11·18 cm/sec.

Table 2

Response of lump-sucker larvae to water current and the relation between current velocity and drifting rate

Current velocity mile/hour	Current velocity cm/sec. (A)	Average drifting rate cm/sec. (B)	Drifting rate / Current velocity B/A
0·17	7·60	6·6	0·87
0·25	11·18	13	1·16
0·50	22·35	27	1·20
0·75	33·53	38	1·13
1·00	44·70	57·7	1·29

(0·25 mile/hour); 22·35 cm/sec. (0·50 mile/hour); 33·53 cm/sec. (0·75 mile/hour); and 44·70 cm/sec. (1 mile/hour).

It was not easy to find the critical current velocity for these larvae as once the larvae were stuck to the tube by their sucker, they could withstand current velocities as high as one mile/hour. The resistance of the larvae when stuck showed that at 7·60 cm/sec. the larvae remained firm for 92 minutes and at 44·7 cm/sec. about 22 minutes.

Table 2 gives the relation between current velocity and average drifting rate.

Behaviour of the larvae to current flow

The larvae swam randomly up and down the experimental tube. Occasionally they swam the whole length of the tube at a time and then rested at the bottom. As soon as the current began the larvae either simultaneously orientated their heads to face the current or they drifted for a few seconds with their heads directed downstream, but soon turned round and opposed the current. In most cases the head remained opposing the current the whole time until the fish was carried by the current out of the experimental tube. On many occasions the larvae were seen inclined with their heads towards the bottom and their tail upwards (i.e., larvae inclined downwards at 45°). Many of the larvae attempted to stick themselves to the wall of the tube; if successful they resisted the current. When this happened the larvae usually swam upstream, then stuck fast for sometime, then again swam upstream and fastened themselves on again. In some cases when a larva was stuck fast with its head facing downstream, it orientated itself so that its head opposed the current as soon as this began to flow. In other cases, when the fish had drifted for some time with the current, it soon orientated itself to oppose it.

Experiments with recently dead larvae showed that their shape had no effect on the orientation of the larvae to current. In many cases the dead larvae drifted more slowly than the living ones due to the latter remaining mostly in the middle of the tube in the strongest current whilst the dead larvae stayed at the bottom with the least current.

Exceptionally, larvae were observed rolling with the current and just leaving themselves to its mercy without making any efforts to orientate themselves against it. The larvae did not react to any moving object outside the tube in which they are enclosed.

C. Salmon, Sea Trout, and Brown Trout Larvae

No detailed experiments were carried out on the salmonids due to technical reasons but observations in the rearing tanks showed that these larvae in the

early stages (when the yolk-sac is present up to 28 days old and rearing at 5·6°C) do not seem to respond to the current. All the time they lay on their side at the bottom of the tank darting about occasionally. Sometimes they swam for a few centimetres but they soon passed into a period of rest.

Sometimes in the pre-feeding stage when the yolk-sac is nearly absorbed, and the fish are about 35 days old, they began to react to the current and orientated themselves against it.

Using a 1·5 m length of 25 mm diameter glass tubing, a current velocity of 11·18 cm/sec. (0·25 mile/hour) caused the 35 days old alevins to orientate themselves against the current and in many cases to swim upstream. This behaviour continued till the alevins were drifted back to the other end of the tube. As soon as the current stopped they swam quickly upstream.

In the early stages (up to 21 days old) the alevins showed no reaction to any moving object outside the tube in which they were enclosed, but in later stages (pre-feeding stages) they showed a slight reaction.

Discussion

In the early stages of development fish eggs or larvae or both are carried passively by water currents prevailing during these periods, from the spawning grounds to other places. The study of the surface currents and recently the study of the wind, its velocity, direction, and duration has been carried out by many investigators. In all the studies of the effect of current on fish larvae it is supposed that these larvae are carried passively and helplessly with the current. The experimental study of the response of pelagic marine fish larvae to current, however, remains very important and may give some indications whether pelagic larvae stages are carrried entirely passively or not. Its application to natural conditions will remain uncertain until observations in nature can be carried out.

Experiments in this investigation using herring and lump-sucker larvae inside a 12 mm diameter glass tube, show that these larvae respond to currents up to 44·70 cm/sec. (higher velocities were not investigated) by orientating themselves against the current and trying to swim upstream. Herring larvae at a current velocity between 0·58 and 1·03 cm/sec. maintain themselves against the current and swim upstream, thus not drifting passively with the current. It is assumed that the critical current velocity lies between 0·58 and 1·03 cm/sec. for the early stages of herring larvae (6·5–7·5 mm long). Even at higher current velocities the rate of drifting is less than the current velocity as can be seen from Table 1, a fact explicable by the struggle of the larvae against the current and thus not being passively carried by it. It may be argued that under experimental conditions the larvae tend to choose the places with the least current velocity (near the bottom). This was not usually so, herring larvae remained in the middle of the experimental tube orientating themselves against the current and attempting to swim upstream. Only unhealthy larvae stayed at the bottom and their average drifting rate was actually higher than the average current velocity.

Whether herring larvae respond to water currents in the open sea was not studied during this investigation. Mielck (1929) showed that herring larvae were not transported by water currents from either the Dogger area or Southern Bight. Very few observations have been made in nature on the response of

pelagic fish larvae to currents. This is presumably due to difficulties involved in such observations. CAHN (1927), however, noted that *Labidesthes sicculus* larvae showed in every case an indication of orientation with a tendency on the part of the larvae to head into the waves when the surface is agitated by wind.

Demersal fish larvae, especially those living in fresh water, are affected differently from pelagic larvae. Salmon, sea trout, and brown trout alevins do not respond to current before the pre-feeding stage when they respond to currents of different velocities. STUART (1953) made a similar observation on loch trout (*Salmo trutta*). WHITE (1915) concluded that newly hatched brook trout are positively rheotactic. In many of her experiments, however, a number of larvae were indifferent and some even lay still on the bottom although being drifted backwards. If these larvae had been positively rheotactic they would have reacted to the current. In the present investigation it was noticed that during the pre-feeding stage salmonid larvae (salmon, sea trout, and brown trout) could perceive currents of certain velocities. In the rearing tanks most of the fish were seen near the inflow, orientating themselves against the current. Experiments on the response of salmon fry (*Oncorhynchus* sp.), were recently made by HOAR (1951, 1954) and MCKINNON and HOAR (1953) who concluded that salmon fry respond positively to current and that a maximum response is shown at a particular current velocity. Specific differences were also observed.

Both marine fish larvae and salmonid fry exhibit an increased activity following an abrupt change from still water to currents or the reverse. These fish show a tendency to swim upstream as soon as the current begins. When the current ceases the fish usually continue to swim vigorously upstream. It thus seems that a change in conditions stimulates the fish to swim whilst orientation caused by current effects is responsible for the direction of their movements. A similar observation was made by ELSON (1939) on young speckled trout (4–6 cm long).

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Summary

1. A review of the effect of currents on the survival and distribution of larval fish is given.

2. An experimental study on the response of fish larvae (*Clupea harengus* L., *Cyclopterus lumpus* L., *Salmo salar*, *Salmo trutta*, and *Salmo trutta f. fario*) to current, was carried out. For this purpose an apparatus was designed.

3. Experiments showed that herring and lump-sucker larvae when subjectde to current in a glass tube of 12 mm diameter, are not carried passively, but

they respond positively to the current, orientate themselves against it, and try to resist it by swimming upstream.

4. For herring larvae a critical current velocity between 0·58 and 1·03 cm/sec. is found at which the larvae can maintain themselves (at least for an hour) against the current. At higher velocities the larvae are drifted with the current but the rate of drifting is less than the current velocity.

5. Salmonid larvae in the yolk-sac stage do not respond to currents. But in later stages when the yolk-sac is nearly absorbed they respond to current, orientate themselves against it and swim upstream.

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