Reactions of Larval and Young Salmonids to Water of Low Oxygen Concentration

By

H. M. Bishai

Faculty of Science, Department of Zoology, Cairo University, El Giza, Egypt, U.A.R. and

Zoology Department, University of Khartoum, Sudan

Introduction

In nature fish may encounter waters of low oxygen concentration or waters where complete oxygen depletion is taking place. Various investigators have shown that fish are always present where the oxygen concentration is high enough to maintain their life and that fish tend to choose water of high oxygen concentration (JUDAY and WAGNER, 1909; BIRGE and JUDAY, 1911; ROULE, 1914, 1933; THOMPSON, 1925; CHEVEY, ROULE and VERRIER, 1927; ELLIS, 1937: ERIKSEN and TOWNSEND, 1940; HILE and JUDAY, 1941; ALLAN, HERBERT and ALABASTER, 1958; ALABASTER, 1959; and many others). To find out if fish are able to detect and avoid water containing different concentrations of dissolved gases, experimental studies were carried out by various investigators (SHELFORD and ALLEE, 1913, 1914; SHELFORD, 1917, 1918a and b; POWERS, 1921; COLLINS, 1952; and JONES, 1952). These studies were mainly carried out on young or adult fish. However, the study of the reactions and behaviour of the early larval and post-larval stages of fish was overlooked. These stages are very important in the life of fish because they may encounter unfavourable environmental conditions which they may be unable to detect or avoid, and thus die. High mortality at the early stages of life of fish may be among the factors leading to a poor brood.

The present investigation which is a part of a series of studies on larval and young fish (BISHAI, 1960a-d; 1961, a and b) to determine the direct effect of the different environmental conditions on these stages, and the response of the fish to them. Experiments were carried out on the alevins and fry of *Salmo salar* L. and *Salmo trutta* f. *fario* L. of the same brood and which were reared in the laboratory under controlled environmental conditions.

The aim of the present experiments was to find out: ---

(1) Are salmonids, at the early larval and young stages, able to detect and 4.

avoid water of low oxygen content? If so, to what concentrations do they respond?

(2) Is there any relation between the age of the fish and its ability to discriminate between waters of different oxygen concentrations?

(3) Are the oxygen concentrations which the fish are able to detect and avoid lethal to them, and do the fish always prefer water of high oxygen content when placed in a gradient?

(4) Is there any specific difference in the response and behaviour of the two related species (i.e. *Salmo salar* L. and *S. trutta* f. *fario* L.) to low oxygen concentrations?

Material

The fish used were the larval and fry stages (1 to 26 weeks after hatching) of salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* f. *fario* L.). The fish were reared at the Dove Marine Laboratory, Cullercoats, Northumberland, England. Artificial fertilization was carried out at Rothbury Fish Hatchery, England, through the courtesy of the Northumberland River Board, and at Welham Park Fish Hatchery, Melton, Yorkshire. Rearing took place in glass and earthenware tanks. The average lengths of the alevins used and the temperature at which they were reared were as follows: —

Species	Temperature (°C)	Length of alevins (mm)	Age (days)
Salmo salar L	5°–10·5°	18–24	1-42*
S. trutta f. fario L	5°– 9·2°	16–25	1-42*

*) Yolk-sac absorption took place 28-35 days after hatching.

The fry were reared at $12^{\circ}-16^{\circ}C$ and were fed with crab liver (*Carcinus maenas*) and live *Daphnia*. In the first month they were fed three times daily, after which they were fed twice a day.

Apparatus and Technique

Many methods were adopted to study the reactions of fish to different gradients (i.e. oxygen, carbon dioxide, alkalinity, toxins, temperature, salinity, currents, light, etc.). The gradient tank used by SHELFORD and ALLEE (1913, 1914), WELLS (1913, 1915a, b) and SHELFORD (1917, 1918a) is unsatisfactory because in addition to being exposed to the atmosphere, separate control and experimental tanks were used. In the controls the behaviour of the individual fish varied considerably. BULL (1938) and JONES (1947) discussed the defects of these gradient tanks. Other experimental tanks have been devised by CAHN (1927); DOUDOROFF (1938); FISHER and ELSON (1950); BRETT (1952); HÖGLUND (1952); and MCKINNON and HOAR (1953).

JONES (1947) designed an apparatus in which there was no gradient but contained two contrasted bodies of water which are very sharply differentiated in the middle of the experimental tube. A modification of the apparatus (JONES, 1948) was used to study the reaction of fish to toxic solutions (JONES, 1951) and to water of low oxygen concentrations (JONES, 1952). HODGSON (1951) used the same apparatus in his study of the reaction of aquatic beetles to salts and alcohols.

In the present investigation the same apparatus devised by JONES (1948 and 1952, p. 404) was used and the reader is referred to his papers for its description. The water and solution under test are sharply differentiated thus presenting the fish with an opportunity to discriminate between ordinary water and a definite concentration of any substance under test. In addition, the properties of the water in both halves of the experimental tube remain constant and uniform. Furthermore, it is possible to conduct experiments on fish for any length of time on the same individuals and under the same conditions.

The precautions taken by JONES (1947) were also followed. Uniform background and illumination were used. The experimental water was clean and devoid of any objects or air bubbles to which the fish may react. The experimental tube was surrounded by a sheet of paper as the fish reacted to the presence of the observer. The reactions of the fish were observed and recorded from a hole at the side of this sheet. A fish may prefer one end of the tube rather than the other, but this preference was not consistent and the reason for it could not be known. A similar observation was recorded by SHELFORD and ALLEE (1914) and JONES (1947).

In the present investigation the apparatus was used to study the reactions of larval and young fish to differences in the oxygen content of water. Experiments on differences of hydrogen ion concentration were also carried and the results will be given in a separate paper (BISHAI, 1962).

Procedure

The fish were introduced into the experimental tube at one end. After removal of all the air bubbles, well aerated water was allowed to flow into the tube where the fish were left for an hour before starting the experiment. This precaution was carried out so that the fish recovers from handling and introduction into the apparatus and gets accustomed to the new environment. Most of the fish were active and swam to and fro along the length of the tube and then came to rest quietly on the bottom at one end. They usually showed a positive reaction to the current. However, in few cases the fish faced towards the centre of the tube.

The movements of the fish tend to cause mixing of the water but soon differentiation was restored. This has been previously observed by SHELFORD and ALLEE (1913, 1914), JONES (1947, 1948), and HÖGLUND (1951) who showed that there is no evidence that this mixing interfered with the main boundary.

In most experiments one fish was used at a time, but in some cases two or three fish were used simultaneously. In the latter case it was rather difficult to record accurately the movements of all the fish. Many experiments were carried out using two fish of different species (i.e. Salmo salar L. and S. trutta f. fario L.) or of different ages. The aim of these experiments was to find out whether the age and species had an effect on the sensitivity of the fish in detecting and avoiding the modified water.

At the beginning of each experiment the movements of fish were recorded in well aerated water for about 5 minutes, after which the modified water was allowed to pass into one half of the tube. If the fish was active and made exploratory movements at both ends of the experimental tube, the modified water was usually passed in from the end where the fish was for the moment absent. On the other hand, if the fish was inactive and spent most of the time at one end, the modified water was allowed to pass in that end, when reversal of the water flow was desired this was done either directly or indirectly by passing aerated water for 3 to 10 minutes before the modified water was passed to the other half.

Duration of the experiment

SHELFORD and ALLEE (1913) and WELLS (1915a, b) carried out experiments of short duration (20 minutes), JONES (1947, 1948, 1951) extended his observations on the reactions of fish to toxic solutions to 60 minutes. However, in the experiments with low oxygen concentrations the maximum duration in JONES' (1952) experiments was 20 minutes. In the present investigation experiments were carried out in most cases up to 60 minutes.

Preparation of water of low oxygen content

This can be done by boiling normal water followed by the addition of the required quantity of gas. Alternatively the water may be subjected to low pressure or a stream of nitrogen passed through it. JONES (1952) prepared water of low oxygen content by bringing the water to the boiling point then allowing it to boil at least for 15 minutes, using a filter pump.

In the present investigation nitrogen was used for deoxygenation. By bubbling nitrogen in water both oxygen and carbon dioxide contents are decreased and nitrogen is increased. Thus the pH of the deoxygenated water is changed. As the pH of the local tap water — used for rearing the fish and for all the experiments — was $7\cdot3-7\cdot5$, the change of the pH of the deoxygenated water was slight, i.e. $0\cdot1$. Furthermore, experiments carried out on the same fish to study their response to differences in the pH using carbon dioxide, showed that they only respond to water of a pH less than $6\cdot6$. The high nitrogen content of the modified water does not appear to affect the response of fish to low oxygen concentrations (SHELFORD and ALLEE, 1913).

Before the start of the experiment, nitrogen was passed through diffusers in one of the aspirators for a certain time — depending on the required oxygen concentration — after which the gas was switched to pass over the surface of water in order to prevent the diffusion of atmospheric gases into the already modified water. In addition, only three quarters of the modified water was used, a precaution taken to ensure the uniformity of the modified water allowed to pass into the experimental tube. During every experiment several water samples were collected at different intervals for the determination of the oxygen content. Analysis of these samples showed that the oxygen content remained fairly constant throughout the whole experiment which lasted up to an hour. The oxygen content of water was determined by WINKLER's method as given by SUTTON (1924). The results are given in mg O_2/l and percentage oxygen saturation.

Presentation of Results

The movements of fish were recorded on sheets of graph paper divided into two halves, each representing one half of the experimental tube, the time in minutes being plotted along the vertical axis. The modified water is shown as stippled areas and the movements of fish by horizontal lines. Vertical lines represent the time spent in a resting position. Recording the reactions of fish at intervals of time was done as accurately as possible using a stop watch. From the diagrams the number of turns performed in each half of the tube can be counted and the time passed in the modified and aerated water determined.

Experimental Results

Experiments on the early larval stages of salmonids (1 to 4 weeks after hatching, reared at 6°C) using water of low oxygen content (0·18–1·6 mg/l at 10°C) showed that these larvae lie on their sides at the bottom of the experimental tube without showing any preference to water of high oxygen concentration. When the partially deoxygenated water was passed into the half of the experimental tube where the alevins were present, they remained in the same half of the tube exhibiting increased respiratory movements but in no case attempted to pass to the other half containing well aerated water. Twenty experiments were carried out at this stage and it is concluded that at the early stages of development (until 4 weeks after hatching) salmonid alevins do not respond to changes of the oxygen content of the water. Long-term experiments using salmon and brown trout alevins (up to 4 weeks after hatching) showed that they can live for at least 48 hours at 0·4–1·3 mg O₂/l at 5°–6°C (2·8–9·9 % saturation). Even in water deprived of oxygen salmonid alevins can live at least for 20 hours at 5°C (BISHAI, 1960a).

Experiments on older stages (5–7 weeks after hatching) showed that they are more sensitive than younger ones. The fry showed a marked negative response towards an oxygen concentration up to 4.6 mg O_2/l at 13.5°C (40% saturation), while no significant response to water of higher oxygen concentrations (i.e. 5.8 mg O_2/l) was observed (Table 1). Thus while the fish passed most of the time in water containing 5.8 mg O_2/l , it stayed for 12 minutes in 5.1 mg O_2/l before it turned to the aerated water (Table 1). In the latter experiment the partially deoxygenated water was then passed into the region where the fish was present. After three minutes the fish swam quickly to the aerated water to which it showed a marked preference.

Experiments were carried out on older fry (9–16 weeks old) and in some cases two fish of the two different species (i.e. Salmo salar L. and S. trutta f. fario L.) were used simultaneously. Results showed that their behaviour was more or less the same and thus experiments carried out on one species or the other represent the behaviour of both species. Fifty experiments were carried out using modified water of the following oxygen concentrations: 0·35, 0·4, 0·7, 1·1, 1·4, 1·6, 2·4, 2·5, 4, 5, 6, and 7·2 mg O₂/l at 13·5° to 15°C. Several experiments were carried out on young brown trout (26 weeks old) using water containing 0·3, 2·6, and 3·5 mg O₂/l at 15°C. The results are given in Table 1 showing the percentage time passed in the modified and well aerated water, and in Figures 1–2 which are typical examples. The results show that the reac-

Table 1

Reactions of salmonid alevins and fry to water of low oxygen content as shown by percentage time passed in modified water

		-	Observation	Oxygen content of		% time passed in*	
	Age	Temp.	time	modifie		modified	aerated
Fish	(weeks)	(°C)	(min.)	mg/l	% sat.	water	water
Salmon	4	9 ∙2	20	0.5	4	90	10
Salmon	4	9.2	25	2.5	21	95	5
Salmon	6	9.2	20	2.5	21	5	95
Salmon	6	9.2	20	3.9	34	10	90
Salmon	6	9.2	20	5.1	44	60	40
Salmon	6	9.2	25	5.8	51.8	90	10
Salmon	7	10	20	4.6	40	15	85
Salmon	9	13.5	25	2.4	23	20	80
Salmon	11	13.5	25	1.4	14	8	92
Salmon	12	13.5	25	4.0	38	12	88
Salmon	13	13.5	20	1.6	16	20	80
Salmon	14	13.5	25	3.5	33	28	72
Brown trout	13	13.5	30	0∙4	3.3	7	93
Brown trout	15	13.5	30	6.9	68	97	3
Brown trout	16	13.5	30	1.6	16	23	77
Brown trout	16	13.5	25	4 ∙0	38	28	72
Brown trout	16	13.5	25	5∙0	47	24	76
Brown trout	17	13.5	30	6.0	56	47	53
Brown trout	26	15	35	0·4	3.3	14	86
Brown trout	26	15	30	2.6	26	33	67
Brown trout	26	15	30	3.4	34	93	7

*) Figures representing mean of 5 observations.

tions of salmonid fry to low oxygen concentrations depend on the age of the fish. Thus while fry 6-16 weeks old showed a definite negative response to oxygen concentrations up to 4.6 mg O_2/l (Figs. 1 and 2), older stages (26 weekolds) did not show such response even to water containing 3.4 mg O_2/l (34% saturation at 15°C). However, they were sensitive to and showed a negative response to 0.35 and 2.6 mg O_2/l at 15°C (Fig. 2 and Table 1).

Observations on the Response of Salmonids to Differences in the Oxygen Content of Water

The behaviour of the fish in the experimental tube was studied before allowing the partially deoxygenated water to pass into one end of the tube. The fish followed one of three patterns: (1) staying at one end with its head opposing the incoming flow of water. In this case the fish is responding to the water current; (2) staying at one end but periodically swimming; or (3) active fish continuously swimming from one end to the other.

In the first case the water of low oxygen content was admitted at the end where the fish was present. As soon as this took place the fish developed dyspnoea and the amplitude and frequency of its respiratory movements increased. The fish showed discomfort by gulping, gasping, and yawning. After some time (which depended on the oxygen content of the water) the fish became suddenly active and swarm to lie in that half of the tube containing well aerated water. The fish did not swim to the aerated water unless their

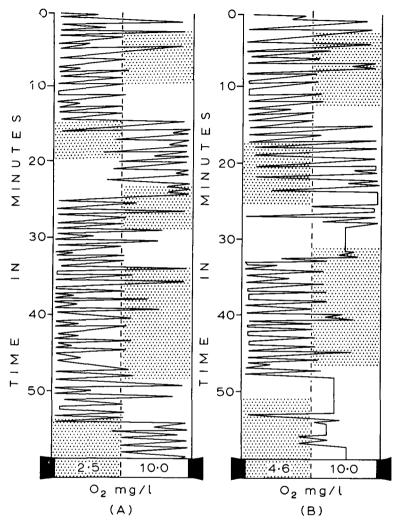
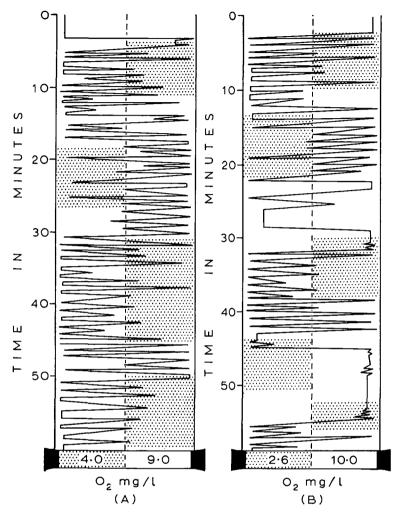
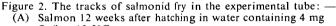


Figure 1. The tracks of salmon fry in the experimental tube: —
(A) 6 weeks after hatching in water containing 2.5 mg O₂/l at 9.2°C.

(B) 7 weeks after hatching in water containing 4.6 mg O_2/l at 13.5 °C.

respiratory movements were affected and then only after passing some time in the water of low oxygen content. A similar observation was made by JONES (1952) who concluded that the basis for avoidance of water of abnormally low oxygen content by the fish would appear to be the active, random swimming and struggling that appears to be incited by dyspnoea. However, this behaviour may be attributed to the strong positive response of the fish to water currents which could be masking their preference to well aerated water. A fish which spent a long time in water of low oxygen content was responding to the inflow current of water, and only swam to the other half of the experimental tube





- $O_2/l \text{ at } 13.5^{\circ}C.$
- (B) Brown trout 26 weeks after hatching in water containing 2.6 mg O₂/l at 15°C.

after the development of dyspnoea. This type of behaviour was noticed in only few cases during the present investigation. Other fish behaved as described above but towards the end of the experiment they became active and showed a true preference to aerated water.

In the second and third cases the fish seem to detect and avoid water of low oxygen concentrations. This is manifested by the fish which avoid water of low oxygen content after several initial trials (Figs. 1–2). The reaction towards the partially deoxygenated water does not show itself in a uniform gradual decrease in the time spent in that water. The response is rhythmic rather than cumulative. After a number of successive trials of the water of low oxygen content, either

the time spent in the latter or the number of turns is lessened (Figs. 1 and 2). This always results in the fish spending more time in the well aerated water where it restricts its movements. However, after spending some time in the aerated water there is a tendency to enter the water low in oxygen content (Figs. 1 and 2) but the fish soon returns to the end containing aerated water. In most of the experiments a rhythm in the response towards water of low oxygen content was observed.

In most cases, especially when the fish is actively swimming, the negative response to the water of low oxygen content is quick, taking place 5 to 10 seconds after entering the modified water and before the appearance of any respiratory difficulties. This response not only takes place at low oxygen concentrations which are lethal, but also at those concentrations which are well above the lethal limit. Long-term experiments carried out on fish of the same age and from the same stock, and in the same water and at the same temperatures under which response experiments were carried out, showed that the lower incipient limiting level of oxygen was 18-26% oxygen saturation at 9°-15.8°C corresponding to 2.2-2.5 mg O₂/l respectively (BISHAI, 1960a). It can be seen from Figures 1 and 2 and Table 1 that the fish showed, in every case, a definite avoiding reaction of the partially oxygenated water.

Many experiments suggest that some form of conditioning took place. In Figure 1 it can be seen that the fish reacted negatively to the aerated water in that half of the tube which formerly contained water of low oxygen content. This conditioning took place not only at water of low oxygen concentration but also at comparatively higher concentration (Fig. 1, 4.6 mg O_2/l). Conditioning took place in a short time, i.e. at 1.4 mg O_2/l it took 4 minutes. After admittance of the aerated water in that half of the tube formerly containing water of low oxygen content, the fish reacted to this half as if it was still low in oxygen content. This behaviour was repeated for 7–8 minutes. Then the fish began to make frequent visits to this end as soon as it became aware of the nature of the water, and spent as much time in this half of the tube as in the other half.

Two main features were observed in the response of salmonid fry to differences in the gas content of the water: —

1. If the fish is continuously and actively swimming when the partially oxygenated water is admitted in the experimental tube, the fish may enter and leave this modified water many times. Later the turnings away from the water of low oxygen content occurred more often and the fish only entered the partially deoxygenated water after passing some time in the aerated water. The time the fry passes in the partially deoxygenated water does not depend on the oxygen content of that water but is dependent on the age of the fish. Thus while fry up to 16 weeks old passed a short period in oxygen concentration up to $4.6 \text{ mg O}_2/\text{l}$ (Figs. 1 and 2), 26 week-old fry remained for longer periods in a concentration of $3.4 \text{ mg O}_2/\text{l}$ without showing any preference to the well aerated water.

2. In many cases the fish stopped suddenly at the centre of the tube before proceeding further into the water of the low oxygen content, backed quickly for a few millimetres and either moved on into the modified water to the end of the tube, or it returned to the latter at once. A similar observation was made by JONES (1952, Fig. 8) in his experiment on trout fry. This author showed that

H. M. BISHAI

at 20°C and an oxygen concentration of 0.56 mg O_2/l (5% saturation) the fish showed an immediate recognition and rejection of the poorly oxygenated water, for on swimming into it the trout would stagger, gulp violently, and retreat in less than 5 seconds. In addition, JONES (1952) found a good avoiding reaction at higher concentrations (i.e. $3.2 \text{ mg } O_2/l$ at 20°C).

Discussion

The present results show that salmon and brown trout fry (Salmo salar L. and S. trutta f. fario L.) 6-26 weeks old are able to detect and avoid water of low oxygen concentrations. The fry showed a rapid response to water of low oxygen content and their behaviour appeared to be an immediate recognition and rejection of the modified water. SHELFORD and ALLEE (1913, p. 261) pointed out that fishes react to oxygen gradients, though usually indefinitely. JONES (1952) stated that "fish do not have any instinctive ability to recognize immediately and avoid water of abnormally low oxygen content, that they swim into it with little or no hesitation when the oxygen concentration and temperature do not provoke immediate and acute respiratory distress, and if they eventually avoid it the basis of the reaction would appear to be the active, random swimming and struggling that appears to be incited by dyspnoea". In his experiments with trout fry (30-32 mm long) JONES (1952) showed that they respond to a concentration of 1.3 mg O_2/l (12.1% O_2 at 13°C) after developing a marked dyspnoea in the modified water. In the present investigation salmon and brown trout fry of nearly the same age and at nearly the same temperature as those in JONES' (1952) experiments were used. The results of the present experiments differ from those found by JONES (1952) and show that salmonid fry (6-26 weeks old) respond definitely and negatively to water of low oxygen concentrations (up to $4.6 \text{ mg O}_2/l$ at 13.5° C).

It is concluded that salmonid fry are not only able to detect and avoid water of low oxygen concentrations which are lethal to them, but also those concentrations which are well above the lower incipient level of oxygen. In nature, ERIKSEN and TOWNSEND (1940) showed that trout and salmon selected water having a dissolved oxygen content of 4 ppm or more, below this figure these fish found it impossible to establish an appreciable population.

Experimental results showed that salmonid fry are able to detect and avoid low oxygen concentrations which they never encountered during their life. The fry used in the present investigation were incubated and reared in well aerated running water. SHELFORD and ALLEE (1914), however, pointed out that stimuli which give rise to modifications very quickly are those commonly encountered by fish in nature.

Although the response of salmonid alevins and fry to low oxygen is not dependent on the species used yet it differs with the age of the fish. Thus while alevins (1-4 weeks after hatching) show no response to abnormally low oxygen concentrations, the fry (5-16 weeks old) show a definite negative response to oxygen concentrations up to $4.6 \text{ mg } O_2/l$ at 13.5° C. Older stages (26 weeks), however, are less sensitive and behave indifferently to the same oxygen concentration and even to lower ones (i.e. $3.4 \text{ mg } O_2/l$). Nevertheless they are able to detect and avoid low oxygen concentrations which are less than $3.0 \text{ mg } O_2/l$ at 15° C.

The present results suggest that salmonid fry (6-26 weeks old) obviously

avoid the partially oxygenated water by trial or choice and not by random swimming after developing respiratory distress as shown by JONES (1952). In JONES' experiments the fish seem to have a greater positive response to the current of the inflowing water than to the well aerated water, thus masking their preference to water of high oxygen content. WELLS (1913, 1915a) and HÖGLUND (1951) pointed out that salmon fry have a strong positive response to water currents. CHIDESTER (1924) pointed out that SHELFORD's (1917) idea of intoxication by chemicals was not tenable and that occasionally the fish in SHELFORD's experimental tank moved towards toxic substances because they were attracted by the force of entering water. It is concluded that the response of salmonid fry to water currents increases as they get older. Hence their negative reaction to low oxygen concentrations decreases at older stages. This conclusion is supported by experimental results which show that the sensitivity of the fry to low oxygen decreases as they get older, as mentioned above.

The fish apparently become better at avoiding the modified water with the passage of time so learning or conditioning must have taken place. In many experiments conditioning to low oxygen concentration was recorded. Such conditioning took place in a short period (4–8 min.) and at comparatively high oxygen concentrations (4 to 4.5 mg O_2/l at 13.5°C). The fish reacted negatively to that half of the experimental tube containing aerated water which was formerly occupied by water of low oxygen content. Conditioning took place after 12 to 30 trials of the poorly oxygenated water. BULL (1957) pointed out that conditioned responses in fish are built after a variable number of presentations, rarely less than 10 or more than 80 and, more generally, about 30.

It is not obvious that the low oxygen is the specific factor affecting the behaviour of salmonid fry. Fish learned to avoid water which was low in oxygen but not low enough to produce signs of dyspnoea. If low oxygen content had some unpleasant effect on the fish (before signs of dyspnoea develop) the fish would equally associate this with any other factor in the modified water as with a "memory" of oxygen content particularly as with CO_2 and nitrogen contents had changed. Thus associative memory appears to play an important role in the response of fish to changes in the oxygen content of water. It is concluded that low oxygen was the conditioned factor but not necessarily the sensory clue for the detection of the water.

The results of this experimental study may contribute to our knowledge on the reactions of larval and young salmonids to different oxygen concentrations. Although the conclusions drawn are exclusively from experimental data, they may throw light on what is taking place in nature. Salmonid alevins which live at the bottom of streams, before the absorption of the yolk-sac, will be seriously affected if they encounter low oxygen concentrations which are lethal and prevail for long periods. This is attributed to their inability to select the favourable conditions for their life. The fry stage, however, is more sensitive and is able to avoid and detect water of low oxygen concentrations which are not lethal to them.

Acknowledgements

This work was carried out at the Dove Marine Laboratory, Cullercoats, Northumberland, England. I am greatly indebted to Dr. H. O. BULL, Deputy Director, for his invaluable advice and help throughout this investigation. My thanks are due to the Northumberland and Tyneside River Board and to Mr. G. L. TETHAM of Welham Park Fish Hatchery, Melton, Yorkshire, England, for supplying me with running fish used for the artificial fertilization.

Summarv

1. The study of the reactions of larval and young salmon (Salmo salar L.) and brown trout (S. trutta f. fario L.) to water of low oxygen content was carried out using the apparatus designed by JONES (1948, 1952).

2. There is no specific difference in the behaviour of both salmon and brown trout fry to water of low oxygen concentration.

3. The response of salmonids to poorly oxygenated water depends on their age. While alevins, up to the absorption of the yolk-sac, are unable to detect and avoid water of low oxygen content, the fry showed a marked definite negative reaction. The sensitivity of the fry decreases as it gets older. Thus while 6-16 weeks old fry showed a marked negative response to oxygen concentrations up to 4 mg O_2/l at 13.5°C, 26 weeks old fry showed this response to concentrations less than $3 \text{ mg O}_2/1$ at 15° C.

4. Salmonid fry are able to detect and avoid low oxygen concentrations which are well above the lower incipient limiting level and which they never encountered during their life. Such response takes place by trial or choice and not by random swimming.

5. The fish seem to become better at avoiding the modified water with the passage of time suggesting that learning or conditioning must have taken place. Conditioning took place after 12-30 trials.

6. It is concluded that low oxygen was the conditioned factor and not necessarily the sensory clue for the detection of the water. In addition, associative memory may participate in the response of fish to water of low oxygen content.

References

- ALABASTER, J. S., 1959. "The effect of a sewage effluent on the distribution of dissolved oxygen and fish in a stream". J. Anim. Ecol., 28: 283–91. ALLAN, J. R. H., HERBERT, D. W. M., & ALABASTER, J. S., 1958. "A field and laboratory
- investigation of fish in a sewage effluent". Fish. Invest. Lond., 1 (6), 76 pp.
- BIRGE, E. A., & JUDAY, C., 1911. "The inland lakes of Wisconsin. The dissolved gases of the water and their biological significance". Wisconsin Geol. Nat. Hist. Sur., Bull. No. 22, Sci. Ser. 7.
- BISHAI, H. M., 1960a. "The effect of gas content of water on larval and young fish". Z. wiss. Zool., 163: 37-64.
- BISHAI, H. M., 1960b. "The effect of hydrogen ion concentration on the survival and distribution of larval and young fish". Z. wiss. Zool., 164: 107-18.

BISHAI, H. M., 1960c. "Upper lethal temperatures for larval salmonids". J. Cons. int. Explor. Mer, 25: 129-33.

- BISHAI, H. M., 1960d. "The effect of water currents on the survival and distribution of fish larvae". J. Cons. int. Explor. Mer, 25: 134-46.
- BISHAI, H. M., 1961 a. "The effect of salinity on the survival and distribution of larval and young fish". J. Cons. int. Explor. Mer, 26: 166-79.
- BISHAI, H. M., 1961 b. "The effect of pressure on the survival and distribution of larval and young fish". J. Cons. int. Explor. Mer, 26: 293-311.
- BISHAI, H. M., 1962. "The reactions of larval and young salmonids to different hydrogen ion concentrations." J. Cons. int. Explor. Mer, 27: 181-91.
- BRETT, J. R., 1952. "Temperature tolerance in young pacific salmon genus Oncorhyncus". J. Fish. Res. Bd Can., 9: 265-323.

- BULL, H. O., 1938. "Studies on conditioned responses in fishes. Part VIII. Discrimination of salinity changes by marine teleosts". Rep. Dove Mar. Lab., Ser. 3, 5: 37-40.
- BULL, H. O., 1957. "Behaviour: Conditioned responses". In "The physiology of fishes". Acad. Press Inc., New York. Ed. by M. E. BROWN, 2: 211–24. CAHN, A. R., 1927. "An ecological study of southern Wisconsin fishes". Illinois biol.
- Monogr., 11: 1-150.
- CHEVEY, P., ROULE, L., & VERRIER, M., 1927. "Sur l'interruption de la montée des saumons par la diminution de la teneur du cour d'eau en oxygène dissous". C. R. Soc. Biol. Paris, 185: 1527-28.
- CHIDESTER, F. E., 1924. "A critical examination of the evidence for the physical and chemical influences on fish migration". J. exp. Biol., 2: 79-118.
- COLLINS, B. G., 1952. "Factors influencing the orientation of migrating anadromous fishes". Fish. Bull. U.S. Wildlife Serv., 52: 375-96.
- DOUDOROFF, P., 1938. "Reactions of marine fishes to temperature gradients". Biol. Bull. Woods Hole, 75: 494-509.
- ELLIS, M. M., 1937. "Detection and measurements of stream pollution". Bull. U. S. Fish. Comm., 22: 365-437.
- ERIKSEN, A., & TOWNSEND, L. D., 1950. "The occurrence and cause of pollution in Grays Harbour". State Pollution Commission. State of Washington. Pollution series, Bull. No. 2, Seattle, Washington.
- FISHER, K. C., & ELSON, P. F., 1950. "The selected temperature of Atlantic salmon and speckled trout and the effect of temperature on the response to an electric stimulus". Physiol. Zool., 23: 27-34.
- HILE, R., & JUDAY, C., 1941. "Bathymetric distribution of fish in lakes of north eastern highlands Wisconsin". Trans. Wis. Acad. Sci. Arts Lett., 33: 147-87.
- HODGSON, E. S., 1951. "Reaction thresholds of an aquatic beetle, Lacophilus maculosus Germ., to salts and alcohols". Physiol. Zool., 24: 131-40. Höglund, L. B., 1951. "A new method of studying the reactions of fishes in stable gradients
- of chemical and other agents". Oikos, 3: 247-67.
- JONES, J. R. E., 1947. "The reactions of Pygasteus pungitius L. to toxic solutions". J. exp. Biol., 24: 110-22.
- JONES, J. R. E., 1948. "A further study of the reaction of fish to toxic solutions". J. exp. Biol., 25: 22-34.
- JONES, J. R. E., 1951. "The reactions of the minnow, Phoxinus phoxinus L. to solutions of phenol, ortho-cresol and para-cresol". J. exp. Biol., 28: 261-70.
- JONES, J. R. E., 1952. "The reactions of fish to water of low oxygen concentration". J. exp. Biol., 29: 403–15.
- JUDAY, C., & WAGNER, G., 1909. "Dissolved oxygen as a factor in the distribution of fishes". Trans. Wis. Acad. Sci. Arts Lett., 16: 17-22.
- MCKINNON, D., & HOAR, W. S., 1953. "Responses of coho and chum salmon fry to cur-'. J. Fish. Res. Bd Can., 10: 523-38. rent'
- POWERS, E. P., 1921. "Experiments and observations on the behaviour of marine fishes towards the hydrogen ion concentration of the sea water in relation to their migratory movements and habitat". Publ. Puget Sd. Mar. (biol.) Sta., 3: 1-22.
- ROULE, L., 1914. "Sur l'influence excercée sur la migration de montée du saumon (Salmo salar L.) par la proportion d'oxygène dissous dans l'eau des fleuves". C. R. Acad. Sci. Paris, 158: 1364-66.
- ROULE, L., 1933. "Fishes. Their journey and migrations." Translated by C. ELPHINSON. W. W. Norton & Co., Inc., New York.
- SHELFORD, V. E., 1917. "An experimental study of the effects of gas waste upon fishes with special reference to stream pollution". Bull. Ill. Nat. Hist. Surv., 11: 381-412.
- SHELFORD, V. E., 1918a. "Ways and means of measuring the dangers of pollution to fisheries" . Bull. Ill. Nat. Hist. Surv., 13: 25-42.
- SHELFORD, V. E., 1918b. "The relation of marine fishes to acids with particular reference to the Miles Acid Process of sewage treatment". Publ. Puget Sd. Mar. (biol.) Sta., 2: 97-111.
- SHELFORD, V. E., & ALLEE, W. C., 1913. "The reactions of fishes to gradients of dissolved atmospheric gases". J. exp. Zool., 14: 207-66.
- SHELFORD, V. E., & ALLEE, W. C., 1914. "Rapid modification of the behavior of fishes by contact with modified water". J. Anim. Behav., 4: 1-31.
- SUTTON, F., 1924. "A systematic handbook of volumetric analysis". 11th Edit. J. and A. Churchill, London.

H. M. BISHAI

 THOMPSON, D. H., 1925. "Some observations on the oxygen requirements of fishes in Illinois River". Bull. Nat. Hist. Surv., Chicago, 15: 423-37.
 WELLS, M. M., 1913. "The resistance of fishes to different concentrations and combinations

WELLS, M. M., 1913. "The resistance of fishes to different concentrations and combinations of oxygen and carbon dioxide". Biol. Bull. Woods Hole, 25: 323–47.

WELLS, M. M., 1915a. "The reactions and resistance of fishes in their natural environment to salts". J. exp. Zool., 19: 213-83.

 WELLS, M. M., 1915 b. "Reactions and resistance of fishes in their natural environment to acidity, alkalinity and neutrality". Biol. Bull. Woods Hole, 29: 221-57.
