The Effect of Pressure on the Survival and Distribution of Larval and Young Fish

By

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Introduction

This work is one of a series of studies carried out on the effect of the different environmental factors on the very early stages of some marine and freshwater fish (BISHAI, 1960a–d, 1961). The aim of this study is to find an explanation for the behaviour of the early larval stages of fishes under natural conditions. Such early stages — which are considered as being critical in the life of a fish — may react differently to the various factors as compared with older stages. Little work has been done on the early larval stages and therefore it was found necessary to carry out the present investigation. The results of this experimental study may throw light on our knowledge on the behaviour, distribution, and survival of the early larval stages of fish in their natural environment.

In the present investigation the effect of pressure (either higher or lower than one atmosphere) was studied in order to find out the behaviour and reaction of fish at different ages to compression and decompression. The results of this study are compared with the previous work.

The effect of pressure on the survival and distribution of larval and young fish was studied experimentally by A. DANNEVIG and G. DANNEVIG (1950), DANNEVIG and HANSEN (1952), and HENLY (1952). They found that cod larvae respond to changes in water pressure as soon as the yolk-sac was absorbed. In addition, cod larvae could not be reared in shallow aquaria as high mortality took place when they were 3–6 weeks old. A similar observation was mentioned by MCINTOSH and MASTERMAN (1897) who pointed out that cod larvae move into midwater and later to the bottom after the yolk-sac absorption.

The response of fish larvae to pressure seems to depend on the presence or absence of a swimbladder. Thus cod and other physoclistous (closed swimbladder) larvae are affected by pressure in a different way to either herring larvae (physostomous, open swimbladder) or plaice larvae (no swimbladder).

The importance of the study of the swimbladder in the early stages of development was emphasized by SCHACH (1939), A. DANNEVIG and G. DANNEVIG (1950), HENLY (1952), JONES and MARSHALL (1953), and JONES (1957). The latter authors gave a recent review on the swimbladder and its function and showed that the presence or absence of the swimbladder is one of the most important factors affecting fish distribution. Thus while those with a closed swimbladder are restricted in their vertical movements (MOREAU, 1876; JONES, 1951, 1952; SCHOLANDER, et al., 1951; and JONES and MARSHALL, 1953), those with an open swimbladder live mostly near the air water interface where they can swallow air bubbles from the air. Fish without a swimbladder can move freely in the water. JONES and MARSHALL (1953) pointed out that the presence of a swimbladder in the early stages of some fish may be very important in connection with the type of life they are living. CUNNINGHAM (1896) and KYLE (1913) showed that the larvae of flat fishes with well developed larval swimbladder have a fairly long pelagic life as compared with those larvae without a swimbladder. Thus there is a correlation between the development of the swimbladder and the duration of the pelagic phase.

The initial filling of the swimbladder with gas was studied by many investigators (VOGT, 1842; VON LEDEBUR, 1928; WUNDER, 1935; VON LEDEBUR and WUNDER, 1937; JACOBS, 1938, etc.), who found that the swimbladder is first filled with air bubbles swallowed by the fish and passing through the pneumatic duct. JACOBS (1938) believed that the swallowed air does not entirely fill the swimbladder but it stimulates the production of gas by the gas gland. McEWEN (1940), however, thought that the first filling of the swimbladder can take place even if some physoclists were not given the chance to reach the surface. JONES and MARSHALL (1953) emphasized the importance of the study of the way in which the swimbladder is first filled with gas, and its correlation with the development of the pneumatic duct and the ecology of the larvae. Since the gas regulation in the swimbladder is under nervous control (MOREAU, 1865, 1876; BOHR, 1894; KUIPER, 1915; JACOBS, 1932; FRANZ, 1937; and FÄNGE, 1953), the extent of development of such nerves in the early larval stages is relevant to their behaviour.

The effect of pressure on physostomes differs from that on physoclists, because in the former adjustment to pressure change can be made by swallowing or releasing gas bubbles through the pneumatic duct (MOREAU, 1876; GUYÉNOT, 1909; KUIPER, 1915; EVANS and DAMANT, 1929; JACOBS, 1934; FRANZ, 1937; and JONES and MARSHALL, 1953). Salmonidae are among the physostomes (VOGT, 1842; HOAR, 1937; and JONES and MARSHALL, 1953) which have a poorly developed retia mirabilia (CORNING, 1888; DE BEAFORT, 1909; RAUTHER, 1922; MAIER and SCHEURING, 1923; and JONES and MARSHALL, 1953). JACOBS (1938) noticed that salmonids were unable to replace gas lost from the bladder when prevented from reaching the surface.

The effect of *decompression* (pressure reduction) on fish may cause them to develop well marked symptoms which are often termed "gas disease" or "decompression sickness". These symptoms comprise the formation of gas bubbles in the heart and blood vessels, under the skin and over the fins, and the eyes bulge due to the accumulation of gas behind them. This gas disease is not only caused by changes in pressure (HOPPE-SEYLER, 1857; GORHAM, 1899 a & b; MARSH and GORHAM, 1905; DAMANT, 1920; VON LEDEBUR, 1936; WALLS, 1942; JONES and MARSHALL, 1953; and DOUDOROFF, 1957), but is also

due to supersaturation of water with gas (OSGOOD, 1904; MARSH and GORHAM, 1905; SHELFORD and ALLEE, 1913; SEMPER (in HENLY, 1952); PLEHN, 1922; ROTH, 1922; MR̆SIC, 1933; HAEMPEL, 1937; A. DANNEVIG and G. DANNEVIG, 1950; DANNEVIG and HANSEN, 1952; HENLY, 1952; and DOUDOROFF, 1957).

Many authors have observed that the occurrence of gas disease was related to the presence of swimbladder (GORHAM, 1899a; MARSH and GORHAM, 1905; DAMANT, 1920; VON LEDEBUR, 1936; and JONES and MARSHALL, 1953). The latter authors stated that "only fish with swimbladder are affected by decompression and the degree to which the symptoms develop varies from species to species and with the depth from which they were taken".

Many explanations were put forward to explain how decompression causes gas disease: —

1. Due to temperature change within the body, i.e. the venous circulation being warmer (MARSH and GORHAM, 1905). These authors pointed out that when a fish with swimbladder is brought up to the surface, it may not be able to get rid of the gas quickly through the gills and gas bubbles may be released in the blood due to temperature differences within the body.

2. Disengagement of gas from the tissues of the fish during decompression (VERRIER, 1931; RABAUD and VERRIER, 1931, 1932b & c, 1933a & b, 1934a–d; and DOUDOROFF, 1957).

3. JONES and MARSHALL (1953) did not agree with RABAUD and VERRIER's views. They suggested the following two explanations for the development of the symptoms of the gas disease but were not able to say which of the two was the more likely to be correct.

(a) Blood and tissues can be saturated with gas by resorption of the gas through the oval; once saturated any further reduction of pressure would lead to the formation of gas bubbles (in the body cavity, beneath the skin or behind the eyes, etc.).

(b) A reduction in pressure might rupture the swimbladder wall (JONES, 1949) and bubbles of gas might, therefore, enter into the broken blood vessels giving rise to symptoms of decompression sickness throughout the body of the fish.

Apparatus and Technique

Previous methods were mainly concerned either with the study of the behaviour of fish under pressure or on the effect of decompression. PLATTNER (1941) studied the effect of decompression by using a flask filled with water placed in a chamber in which the pressure could be reduced. DIJKGRAAF (1942) in his study on the effect of pressure used a maximum pressure of 50 cm Hg. JONES (1952) used an apparatus in which a continuous water flow was maintained and the fish were subjected to a total pressure of 131 cm Hg. Reduction of pressure in this apparatus was achieved by releasing a flow control clip. For decompression JONES (1952) used a vacuum pump connected to his experimental tank.

In the present investigation two apparatus were used: one for pressure in which the fish can be subjected to a total pressure of 170 cm Hg (i.e., atmospheric pressure plus 94 cm Hg); the other apparatus is for decompression in which fish can be subjected to a pressure of 10 cm Hg.
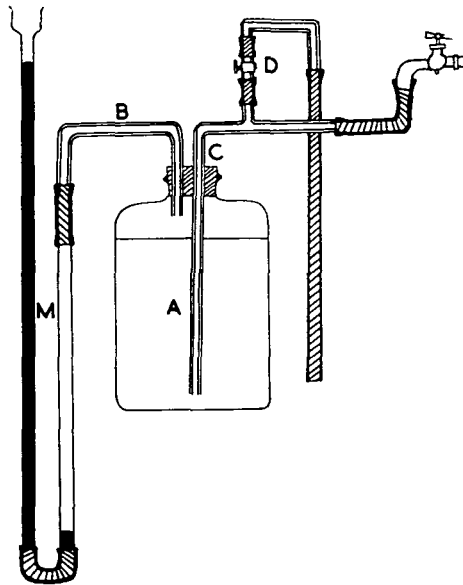
Figure 1. Apparatus for subjecting larval and young fish
to a total pressure of 170 cm Hg.

1. Apparatus for compression

In this apparatus the pressure of the tap water was used which once achieved in the experimental tank would remain when the tap was closed. However, there was no water circulation. In this apparatus air was left over the water so as to allow the fish to gulp air at the surface thus entering into hydrostatic equilibrium much more quickly than if they had to secrete the gas themselves. The difficulty in using this method is that the experimental water as well as the blood and tissues of the fish will be supersaturated with gas.

The apparatus consisted of a thick-walled glass experimental vessel of 6 litres capacity closed by a two-hole rubber bung. Through one of the holes passed a capillary tube B of 8 mm thickness and 2 mm inner diameter (see Fig. 1). The tube was attached to a mercury manometer M. In the other hole a tube C was placed which was also a capillary tube of the same dimensions as B. Tube C was T-shaped with one limb bent down so as to reach the bottom of the experimental vessel, and the other limb connected to the tap by rubber pressure tubing. To the third limb a stop-cock D was fixed controlling the outflow to waste. All connections consisted of pressure tubing.

For pressure higher than two atmospheres Dr. H. O. BULL's pressure tank (unpublished work) was used where fish can be subjected to pressure as high as 8 atmospheres.

2. Apparatus for decompression

This consisted of the same experimental vessel A of 6 litres capacity closed by a two-hole rubber bung through which passed a tube B connected to the
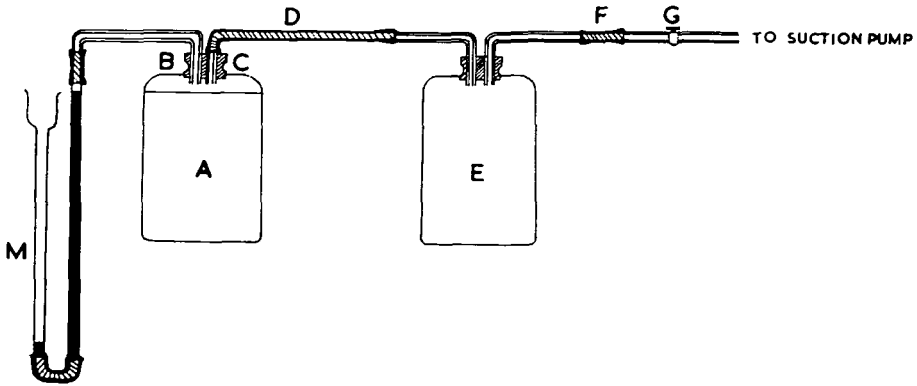
Figure 2. Apparatus for subjecting larval and young fish
to pressures below one atmosphere.

mercury manometer M and a tube C connected by the pressure tube D to a 6 litre reservoir E for pressure regulation. The latter was connected to a suction pump through pressure tubing F provided with a stop-cock G (see Fig. 2).

In neither apparatus was there any water renewal. This was found unnecessary as fishes used in the experiment (either early larval or post-larval stages or even young fish) could live in this apparatus for a period from a week to a fortnight (in some cases for 25 days) without any apparent ill-effects. In every case control experiments were carried out.

Procedure

1. Compression

The fish larvae or young fish were placed in the experimental bottle two-thirds full of well aerated water (fresh or sea water). The rubber bung was then fitted tightly into the neck of the bottle, made possible by pushing the glass tube B into position only after fitting the rubber bung. After connecting with the tap, stop-cock D was closed and the fish were left in the experimental bottle for two hours before starting the experiment. The tap was then opened slightly to cause a slow increase of pressure. The period of augmenting the pressure to the desired level was regulated by manipulating the tap. After the required pressure had been reached (measured by the mercury manometer) the tap was closed. The volume of water in the experimental bottle increased owing to the water introduced from the tap. But about a litre of air was left over the surface of water. The reactions of the fish associated with the increase of pressure could now be recorded. When using pressures of 160 cm Hg there was occasionally a slight loss of pressure (i.e., 1–2 cm Hg) but this was easily corrected. In experiments with marine fish larvae and young fish, some tap water entered the experimental vessel causing a decrease in salinity. It was found, using a pressure of 160 cm Hg, that the salinity changed from 33⁰/₀₀ to 29⁰/₀₀ which, however, was not harmful to the experimental fish as shown by experiments on the same fish using low salinities (BISHAI, 1961).

At the end of the experiment the pressure was released by opening stop-cock D, slowly or quickly according to the requirements of the observations on the reaction of the fish to decreasing pressures.

2. Decompression

After introduction of the fish into vessel A, the apparatus was prepared for the experiment by connecting it to the manometer, and to the suction pump and opening stop-cock G. Once the desired pressure level was reached stop-cock G was closed. To restore the former pressure stop-cock G was partly opened.

In all experiments the oxygen tension, hydrogen ion concentration, and salinity (in case of marine fish) remained within the limits of toleration of the fish. The only change was that of the pressure. In experiments on young fish, which lasted for long periods, food in the form of living animals was introduced into the experimental vessel. In all experiments the pressure is either given in atmospheres or cm Hg. The pressure under which the fish is subjected is the total pressure, i.e. 2 atmospheres means the atmospheric pressure plus 1 atmosphere increase in pressure.

Table 1

Species	Temperature °C	Length of larvae (mm)	Age (days)
Clupea harengus L.	13·1–14·8	6·5– 8	1– 9
Salmo salar L.	7·9–12·5	20 –25	1–42*)
Salmo trutta L.	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.

Material

The fish larvae and young used in these experiments were herring (*Clupea harengus* L.); salmon (*Salmo salar* L.); sea trout (*Salmo trutta* L.), and brown trout (*Salmo trutta* f. *fario* L.). These fish were reared at the Dove Marine Laboratory, Cullercoats, England. The artificial fertilization was carried out at sea or at fish hatcheries. Methods of rearing these fish larvae are given in a separate paper (BISHAI, in press). Young plaice (*Pleuronectes platessa* L.) ranging from 37–50 mm collected from near the Laboratory were also used.

The average lengths of the larvae used and the temperatures at which they were reared were as shown in Table 1.

Rearing of the salmonids was continued at an average temperature of 13·2° ± 2·5°C.

Experimental Results

I. Compression Experiments

A. Herring Larvae

1. Pressure from 1–2 atmospheres

Two experiments were carried out in the pressure apparatus using 50 newly hatched larvae together with their food (*Artemia salina* larvae and *Tigriopus fulvus*). Each experiment lasted for 12 days at an average temperature of 14·8°C. The pressure was raised from 1 atmosphere (75·7 cm Hg) to 2 atmospheres (151·5 cm Hg) in ten minutes. During compression the larvae behaved normally swimming most of the time near the surface. Mortality began on the 7th day but was the same as in the control experiments. However, larvae under pressure, although not feeding, lived longer than those under normal conditions. On the 12th day the pressure was released in ten minutes. During decompression the larvae behaved normally and continued to live for a few days. Gas bubbles were not released from the larvae. At this stage (newly hatched to 12 day-old) the swimbladder is not yet developed. Examination of the blood capillaries of the larvae after decompression was not carried out as the larvae continued to live normally as in the controls.

2. Pressure from 2–4 atmospheres

This experiment was carried out in Bull's pressure tank using two finger bowls each containing 12 newly hatched larvae. A third bowl containing larvae was left at room temperature as a control. On the first day the pressure was raised in 10 minutes to 2 atmospheres; 3 atmospheres on the second, 4 atmospheres on the third day. The experiment lasted for five days at an average temperature of 15·5°C. The larvae were behaving normally both during compression or when under pressure. On the 5th day the pressure, which had been dropping gradually since the 4th day, was released in 30 minutes. The larvae behaved normally and did not seem to be affected by decompression. Analysis of the water showed a high content of oxygen (120% saturation at NTP and a little change in the pH (from 8·00 to 7·85)). No gas disease was observed due to pressure reduction. In addition the formation of air bubbles in the supersaturated water did not take place.

B. Young Plaice
(3·7–5·0 cm long)

Seven experiments were carried out using two or three fish in each case, together with their food (*Artemia salina* larvae and *Tigriopus fulvus*). The experiments lasted for 2 days (2 experiments); 3 days (1 experiment); 6 days (1 experiment); and 8 days (3 experiments). All experiments were performed at 16·5 to 18·3°C and at a pressure of two atmospheres (from 154·2 to 159·5 cm Hg, i.e. atmospheric pressure plus 76·5 cm Hg). The rise of pressure took place quickly (from 5 to 10 minutes). During compression as well as during the experiment the fish lived normally without showing any ill-effects.

At the end of each experiment, although decompression took place quickly, (from 5 to 10 minutes), the fish did not seem to be affected. They behaved normally, passing most of the time near the bottom, but sometimes showing

an increase in their respiratory movements. No gas bubbles were seen either inside or outside the body of the fish and no gas bubbles were released. The oxygen content of the water at the end of the experiment ranged from 82 to 70% oxygen saturation. After decompression the fish continued to live normally without any mortality.

C. Salmon, Sea Trout, and Brown Trout

1. Pressure from 1–2 atmospheres

(i) Newly hatched larvae

(a) Ten newly hatched sea-trout larvae were subjected to a gradual rise in pressure from 1 to 2 atmospheres. The rise in pressure took 9 days after which the experiment was continued for three days at an average temperature of 16·1°C. During the experiment the larvae behaved normally without showing any sign of discomfort. On release of the pressure on the 12th day, the larvae became very active for a while, swimming vigorously upwards. They did not, however, show any ill-effects and lived normally without developing any gas disease.

(b) Five newly hatched larvae of each species were subjected to quick rise of pressure. The pressure was raised from 1 to 2 atmospheres (154 cm Hg) in twenty minutes. With increase of pressure the larvae showed unusual activity by swimming vigorously near the bottom. Such activity continued for one hour, after which the larvae were again behaving normally.

The experiment lasted for 25 days at the end of which the pressure was reduced to one atmosphere in 10 minutes. During decompression the larvae did not show any discomfort and they lived normally without showing any disease. One brown trout was seen swimming near the surface during decompression and continued to do so for the first 24 hours after the end of decompression. Then it spent most of its time near the bottom. The swimbladder, which developed in these larvae, can be easily seen through the body wall.

In these experiments food was not given to the larvae as they do not feed at this stage and the yolk-sac was absorbed 28–35 days after hatching.

(ii) 30 day-old larvae (yolk-sac nearly absorbed)

Five larvae of each species, together with their food (live *Daphnia*) were subjected to a quick rise of pressure. The pressure was raised from 1 to 2 atmospheres in 30 minutes. During the experiment, which lasted for 18 days at an average temperature of 13°C, all the fish behaved normally. On reduction of pressure (i.e., from 2 to 1 atmosphere) which took place in 20 minutes, all the fish showed increased activity but none died. Some of the larvae, especially those with the completely absorbed yolk-sac, were seen swimming near the surface after the end of decompression. Although the swimbladder is well developed at this stage, the release of gas bubbles was not observed. In addition gas bubbles were not formed on the walls of the experimental tank after decompression.

(iii) 56 day-old larvae

Five larvae of each species, together with live *Daphnia* were introduced into the pressure apparatus in which the pressure was raised to 2 atmospheres in

15 minutes. The experiment lasted for 8 days at an average temperature of 16·1°C. On the 8th day reduction of pressure took place in two hours. As soon as decompression started most of the fish were swimming or even floating on the surface. Gas bubbles began to appear on the walls of the experimental vessel. Ten minutes after the end of pressure reduction, two salmon and two sea trout showed distress by bending their bodies quickly and then floated on the surface. Examination of these fish showed the presence of air bubbles inside the mouth, behind the gills, and within the viscera. The rest of the fish had their swimbladder distended and some had gas bubbles attached to their bodies. In no case was the release of gas bubbles from the mouth of the fish observed. All fish were placed in a jar through which air was bubbled overnight. In the morning (after 16 hours) all the larvae were alive and healthy, their swimbladders were normal and no gas disease developed among them.

(iv) 98 day-old brown trout

Two experiments were carried out in which two fish were subjected to a quick rise of pressure (i.e., from 1 to 2 atmospheres in 5 minutes). At the beginning of compression the fish remained motionless at the bottom. The fish never swam near the surface. After half an hour the respiratory movements increased. The fish showed discomfort, occasionally gulping, and bended their bodies. After 6 hours of compression the fish were showing regular but sudden gulping movements. Then they died 16–22 hours after compression. Analysis of the experimental water before and after the experiment showed no significant change either in the oxygen content or pH value. The swimbladder at this stage is well developed.

Two control experiments were carried out; one using the same volume of water but in another jar, and the other using the same water in which the fish died. In both experiments the fish lived for a week without being fed.

(v) 102 day-old brown trout

A fish was subjected to a slow rise of pressure, i.e. from 75·5 cm to 103·5 cm Hg (+ 28 cm Hg or 0·36 atmosphere) in 5 hours. After 17 hours at the highest pressure the fish died.

(vi) 105 day-old brown trout

Two fish were subjected to a gradual increase of pressure, i.e. from 75·9 cm to 116·4 cm Hg (+ 40·5 cm Hg or 0·53 atmosphere in 30 minutes). Two hours after raising the pressure the fish died.

(vii) 133 day-old brown trout

Three experiments were carried out subjecting the fish to a quick rise of pressure, 37 cm Hg (0·48 atmosphere in 5 minutes) and 15 cm Hg (0·19 atmosphere, 2 experiments). In the first experiment the fish died after 13 hours. In the 2nd and 3rd experiments (i.e., 15 cm Hg increase of pressure) the fish, although living for 17 hours, were more or less moribund, staying at the bottom and laying on its side. On releasing the pressure air bubbles were seen coming out from the mouth of the fish, but they were still alive.

(viii) 178 day-old salmon

Two experiments were carried out, as in No. vii, placing a salmon with the brown trout and subjecting them to 37 and 15 cm Hg increase in pressure. While the salmon lived in the first experiment for 12 hours (duration of experiment) it died in the second after 5 hours of restoring the new pressure (i.e., 1 atmosphere plus 15 cm Hg).

(ix) 272 day-old brown trout

Two fish together with their food (live *Daphnia*) were subjected to a quick increase in pressure, i.e. from 1 to 2 atmospheres in 10 minutes. During compression the fish were very active, occasionally visiting the water surface and gulping air. After going up to the surface, the fish usually went to the bottom where they showed rapid spasmodic respiratory movements. 15 minutes after reaching the experimental pressure of 2 atmospheres the fish rested at the bottom where they remained quiet. The experiment lasted for 7 days at an average temperature of 16·5°C. At the end of the 7th day reduction of pressure was carried out slowly taking 80 minutes (i.e., from 157 cm Hg to 74·4 cm Hg). During decompression emission of small gas bubbles either from the mouth or from behind the gill covers was observed (11 bubbles from the mouth and 5 from behind the gill covers). The fish, which were resting at the bottom, no longer took up a horizontal position. The body was inclined to the bottom with the tail well above the head. The fish were trying to keep themselves at the bottom by pushing their nose at the bottom, but they poised a few centimetres off the bottom. After 33 minutes of the beginning of decompression (atmospheric pressure plus 30 cm Hg) the fish appeared to be disturbed and excited, swam upwards and made occasional visits to the bottom. Sixteen minutes after the end of decompression the fish were floating at the surface upside down. Then their respiratory movements stopped suddenly and they died. Their bodies were intact and no gas bubbles were seen inside the fins, blood vessels or heart. However, tiny bubbles of gas appeared on the body of the fish. These bubbles which were formed due to separation of gas from the water caused by decompression, were seen attached to any particle inside the experimental bottle.

(x) 220 day-old salmon

A fish together with its food (live *Daphnia*) were placed in water in which oxygen was bubbled for 15 minutes. The aim of this experiment was to find out the effect of water supersaturated with oxygen (after compression) on young fish. Compression from 1 to 2 atmospheres took place in 35 minutes during which the fish was very active, swimming frequently near the surface. The fish was seen swallowing air bubbles by pushing its head above the surface of water. The fish which was very active and excited for 15 minutes — after the end of compression — went to the bottom and remained quietly till the end of the experiment which lasted for 7 days at an average temperature of 14·85°C.

On the 7th day decompression was carried out slowly taking 145 minutes (from 2 to 1 atmospheres). During decompression the escape of gas bubbles from mainly behind the gill covers was observed (15 bubbles from behind the

gill cover and 1 from the mouth). The fish, which was resting most of the time near the bottom, showed quick respiratory movements. After 120 minutes from the beginning of decompression the fish which was disturbed and restless began to swim near the surface. Then it went to the bottom. At the end of decompression (i.e., atmospheric pressure) the fish was still alive, but 15 minutes later it swam suddenly, jumped and showed signs of distress. The fish then floated on the surface upside down and died. The dead salmon sank to the bottom at an increase of pressure of 11·5 cm Hg (i.e., 1 atmosphere plus 11·5 cm Hg). Gas bubbles began to accumulate on the body of the dead fish. Examination of the fish showed the presence of a large gas bubble inside the mouth, and two elongated gas bubbles inside the caudal fin. No gas bubbles were seen either inside the gills, the skin, or viscera.

2. Pressure from 3–5 atmospheres

(i) 17 day-old larvae

Ten larvae of each species (salmon, sea trout, and brown trout) were introduced into the pressure tank. The larvae were placed in rectangular dishes 10″ long, 6″ wide, and 2″ high. The experiment lasted for 12 days at an average temperature of 15·2°C during which the fish were subjected to the following pressures: —

Duration of pressure (days)	Total pressure to which larvae were subjected (atmospheres)
1	3
3	4
1	3
3	4
2	5
1	4
1	3

The increase in pressure took one hour for every atmosphere. During compression and throughout the experiment the fish behaved normally without showing any sign of discomfort. On the 13th day, reduction of pressure took place from 3 to 1 atmospheres in 30 minutes. All larvae showed signs of discomfort by increased activity. However, none of the larvae died either due to compression up to 5 atmospheres, or due to decompression. Neither was the release of gas bubbles from the larvae observed. Towards the end of the experiment the swimbladder was well developed. During the experiment food was not given to the larvae as the yolk-sac was not completely absorbed and the larvae did not take food during this stage. After decompression all the larvae continued to live normally.

(ii) 195–220 day-old salmon and brown trout

Two fish, one of each species, were placed in the pressure tank together with their food (live *Daphnia*). Compression took place gradually, i.e. it took 3 days to raise the pressure from 1 to 4 atmospheres. The increase in pressure for every atmosphere took one hour. The pressure under which the fish were subjected was as follows: —

Duration of pressure (days)	Total pressure to which fish were subjected (atmospheres)
1	2
1	3
2	4
1	3
1	2
1	1

The fish which were behaving normally before any rise of pressure, became excited and active when compression began and were seen coming to the surface of water apparently gulping air. After the 3rd day the salmon was eaten alive by the trout. On the 4th day decompression was allowed to set in slowly and it took 24 hours for each atmosphere reduction. On the 7th day the young trout floated on the surface upside down with the ventral wall ruptured and the stomach bulging out. Examination of the fish showed the presence of gas inside the stomach. The swimbladder, although distended with gas, did not rupture. No gas bubbles were seen inside the fins or blood vessels.

II. Decompression Experiment

Pressure below one atmosphere

In addition to those experiments in which the fish were subjected to pressure reductions down to one atmosphere, one experiment was carried out to find out the effect of pressures below one atmosphere. For this experiment a 103 day-old brown trout was used. The young fish was placed in the decompression apparatus and the pressure was reduced slowly, i.e. from 75·8 cm Hg to 25·8 cm Hg in 260 minutes. During decompression gas bubbles were released either from the mouth or from behind the gill covers. 180 minutes after the beginning of decompression, gas bubbles began to appear on the body of the fish. To get rid of these bubbles the fish swam in the water. The formation of gas bubbles was also seen on the walls of the experimental vessel as well as on any particle present in the water. Although the fish made occasional visits to the surface it mainly remained at the bottom.

At the end of decompression the normal pressure was restored (i.e., atmospheric pressure) during which the fish seemed restless and swam near the surface. The next morning (after 16 hours) it had recovered.

A summary of the experimental results is given in Table 2.

Discussion

My results show that newly hatched herring larvae (6·5–8 mm long) and salmonid alevins (until the yolk-sac is nearly absorbed) can live at pressures as high as 5 atmospheres (corresponding to a depth of 40 m) and that they are apparently not affected by compression either quick or slow. However, young salmon and brown trout (98–178 day-old) die within 24 hours when subjected to an increase of pressure of more than 15 cm Hg (0·19 atmosphere). This is difficult to explain as at this stage the young fish have a well developed open swimbladder. Moreover, if they are subjected to an increase of pressure

Table 2

The effect of pressure on larval and young fish
Summary of the experiments described in the text

Experiment	Species	Age or size	Swimbladder	Experimental treatment (Pressure in atmospheres)	Results Compression	Decompression
A-1	Herring	Newly hatched (6·5–8 mm)	Not developed	+ 2	Lived	Lived
A-2	Herring	Newly hatched (6·5–8 mm)	Not developed	+ 4	Lived	Lived
B	Plaice	37–50 mm	Absent	+ 2	Lived	Lived
C-1 (i)	Salmon, sea trout, and brown trout	Newly hatched (16·20 mm)	Not well developed	+ 2	Lived	Lived
C-1 (ii)	Salmon, sea trout, and brown trout	30 day-old	Well developed	+ 2	Lived	Lived
C-1 (iii)	Salmon, sea trout, and brown trout	56 day-old	Well developed	+ 2	Lived	Lived
C-1 (iv)	Brown trout	98 day-old	Well developed	+ 2	Died	—
C-1 (v)	Brown trout	102 day-old	Well developed	+ 0·36	Died	—
C-1 (vi)	Brown trout	105 day-old	Well developed	+ 0·53	Died	—
C-1 (vii)	Brown trout	133 day-old	Well developed	+ 0·48	Died	—
C-1 (vii)	Brown trout	133 day-old	Well developed	+ 0·19	Lived for 17 hours	Lived
C-1 (viii)	Salmon	178 day-old	Well developed	+ 0·19	Died	—
C-1 (viii)	Salmon	178 day-old	Well developed	+ 0·48	Lived for 12 hours	Lived
C-1 (ix)	Brown trout	272 day-old	Well developed	+ 2	Lived	Died
C-1 (x)	Salmon	220 day-old	Well developed	+ 2	Lived	Died
C-2 (i)	Salmon, sea trout, and brown trout	17 day-old	Not well developed	+ 5	Lived	Lived
C-2 (ii)	Salmon	195 day-old	Well developed	+ 4	Lived	—
C-2 (ii)	Brown trout	220 day-old	Well developed	+ 4	Lived	Died
Section II	Brown trout	103 day-old	Well developed	− 0·66	—	Lived

following decompression to less than one atmosphere (i.e., from 25·7 to 75·7 cm Hg) they seem to be less affected. Several experiments were carried out (experiments Nos. C-1 (iv) to C-1 (viii)) at this stage — subjecting the fish to an increase of pressure of more than one atmosphere — and in all cases the fish died. The death of the young fish could not be due to supersaturation of the experimental water as analysis showed no significant change in its oxygen content or the

pH. Later stages of salmonids (older than 178 days) are not affected under the same conditions by the increase of pressure. It is concluded that the reaction of young salmonids towards the increase of pressure depends on the age of the fish. Thus, while the alevins are not affected until the absorption of the yolk-sac, young fish from 98–178 days old are affected, while older stages are not affected.

Young plaice (3·7–5 cm long) tolerate pressures at least as high as two atmospheres (higher pressures were not investigated). Plaice do not have a swimbladder and thus they are not affected by the increase of pressure. It is concluded that the distribution of plaice at this stage is not affected by pressure.

It is clear that the effect of decompression on fish differs according to the species and age. In addition, the presence or absence of a swimbladder seems important. In the present investigation newly hatched herring larvae, salmonid alevins as well as young plaice were studied. In newly hatched herring larvae the swimbladder is absent and not yet developed. FULTON (1906) pointed out that there is no trace of the swimbladder in newly hatched herring larvae. Later MAIER and SCHEURING (1923) found that the swimbladder bud first appears in herring larvae at 9–10 mm stage. In salmonids, the swimbladder is not well developed in the early larval stages (3 weeks after hatching), but it is well developed in older stages (4 weeks after hatching). The swimbladder of salmonids is of the open type.

The results showed that newly hatched herring larvae (6·5–8 mm long) are not affected by decompression, either quick or slow, although they were subjected to a reduction of pressure of 3 atmospheres. After decompression the larvae continued to live normally. Thus pressure is unlikely to affect the distribution of newly hatched herring larvae and goes to confirm field observations which show that herring larvae undertake a diurnal vertical migration (JOHANSEN, 1925, 1927; and BURD and LEE, 1951). During decompression gas bubbles were not seen on the larvae or inside them. Neither was there a release of gas bubbles from the larvae.

Until the pre-feeding stage, salmonid alevins are not affected by quick or slow decompression. Although the alevins were subjected to a pressure reduction of 3 atmospheres, they continued to live normally after decompression. In some cases gas bubbles were seen attached to the fish but these bubbles came from the water which was supersaturated with gas. Such gas bubbles attach themselves to the walls as well as any solid object inside the experimental tank. One fish that died a day before decompression, was seen to be covered all over with tiny gas bubbles when decompression took place, which caused it to float. The bubbles covering the body of the dead fish could not be due to diffusion of gas from inside the tissues as RABAUD and VERRIER (1932b & c, 1933a & b, and 1934a–d) claimed. My observations confirm the earlier findings of many authors (MEIERHANS, 1935a–c; GUYÉNOT and PLATTNER, 1938, 1939; PLATTNER, 1937, 1938a & b, 1941; and JONES and MARSHALL, 1953).

Salmonid fry are affected by decompression in a different way than that shown by the younger stages. In experiment No. C-1 (iii) where 56 day-old alevins were used, the gas bubbles which were seen inside the mouth and behind the gill covers were separated from the water, due to decompression, and were swallowed by the fish which could not get rid of them. The fish died from asphyxia. It was also noticed that all fish had distended swimbladders and at no time the release of gas bubbles from the mouth or from behind the gill

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covers was observed. This suggests that the sphincter mechanism which controls the release of gas bubbles from the pneumatic duct was not fully developed at this stage. The fish with distended swimbladders recovered when left for 16 hours. Such experimental conditions are not met by the fish in nature as the alevins live in shallow water streams and come only to the surface for filling their swimbladders.

Older stages of brown trout (i.e., 103 day-old) do not seem to be affected by pressure reductions of less than one atmosphere. Gas bubbles are released from the mouth and from behind the gill covers. However at older stages (i.e., 220–272 day-old, experiments Nos. C-1 (ix) and C-1 (x)) the young fish are affected by pressure reduction of more than one atmosphere. Fish living at a pressure of two atmospheres usually die either immediately or soon after decompression when the pressure is reduced to one atmosphere (i.e., atmospheric pressure). The fish show signs of distress by jumping and gulping, after which they float upside down. Although the fish have an open swimbladder they die after quick or slow decompression. This may be attributed to the speed of decompression mechanically blocking the sphincter. Thus all the gas cannot escape from the swimbladder and the fish floats helpless on the surface of water. On decompression the release of gas bubbles from the mouth or from behind the gill covers was noticed. However, the gas escaped from the bladder was not sufficient to keep the fish in hydrostatic equilibrium under the new pressure. Gas was also noticed inside the gut. This gas was swallowed by the fish during compression. Similar observation was recorded by FRISCH and STETTER (1932) and GUYÉNOT and PLATTNER (1938) who found that air was retained in the intestine of the fish.

The formation of gas bubbles inside the caudal fin of young salmon (experiment No. C-1 (x)) after decompression may be attributed to: (a) The rupture of the swimbladder causing the entrance of gas bubbles into the broken blood vessels (JONES, 1949 and JONES and MARSHALL, 1953). This is not the case in the present investigation as the swimbladder was found intact. (b) Gas coming out of the fishes' blood and tissues. Under experimental conditions both water and blood and tissues of the fish become supersaturated with gas. On decompression gas bubbles not only separate from the water but also inside the tissues and blood capillaries of the fish. Thus the death of the fish is due to the decompression sickness. Nitrogen may not be the only gas which causes the gas disease as MARSH and GORHAM (1905) claimed, as carbon dioxide is an important factor in the initiation of the formation of gas bubbles in the early stages which are later maintained by nitrogen (HARRIS, et al., 1945). However, bubbling oxygen in the experimental water, to expel the oxygen, (experiment No. C-1 (x)) did not diminish the development of the gas disease. HARRIS, et al. (1945) found that the use of pre-oxygenated water before decompression reduces the incidence of bubble formation in decompressed bullfrogs.

Young plaice (3·7–5 cm long) were not affected by decompression. Contrary to RABAUD and VERRIER (1932b and 1934d) finding, although young plaice were subjected to quick decompression, gas bubbles were neither observed to escape from the mouth nor to cover the body. The fish continued to live normally after decompression, which indicated that bubbles were not formed in the blood capillaries although the water in which the fish were living was supersaturated with gas. DANNEVIG and HANSEN (1952) found that fine gas bubbles which accumulated in the veins of young plaice (some cm long) were

fatal to them. My observations support the work of former investigators (MEIERHANS, 1935a–c; GUYÉNOT and PLATTNER, 1938; PLATTNER, 1941; and JONES and MARSHALL, 1953) who showed that gas bubbles covering the body of the fish were no more than the extraction of the gas dissolved in the water. JONES and MARSHALL (1953) gave a critical discussion of RABAUD and VERRIER's work.

The formation of gas bubbles inside the tissues of young salmonids, due to decompression, and not in newly hatched herring larvae, young plaice, and salmonid alevins can be attributed to the presence of a swimbladder. While the swimbladder is absent in both newly hatched herring larvae and plaice, it is not completely developed in salmonid alevins, but is well developed in young salmonids. Another explanation that I put forward to account for the non-formation of gas bubbles inside the body of newly hatched herring larvae and salmonid alevins is that the gas can diffuse easily from the blood to the surrounding water through the skin covering the body. Moreover, a relatively larger area is exposed to the water, while young fish are covered with a thick skin so the diffusion of gas outside the body must be impossible or is very much slower. HARRIS, et al. (1945) pointed out that large frogs suffer from decompression while small ones do not. This they explained as due to the quicker rate of diffusion of carbon dioxide — which initiates the bubble formation — through the muscles of the small frogs.

It is concluded that the effect of pressure on the survival and distribution of larval and young fish depends on the species, the age of the fish, and the presence or absence of a swimbladder.

Acknowledgements

Summary

1. A review of the effect of pressure on larval and young fish is given. Apparatus and methods are described to study the effects of pressure changes on young fish.

2. Newly hatched herring larvae (*Clupea harengus* L.) could live at a pressure of 4 atmospheres. They are neither affected by compression nor by decompression. Thus newly hatched herring larvae can move from deep to shallow water without any ill-effects due to pressure changes even if the water in which they live is supersaturated with gas.

3. Young plaice (*Pleuronectes platessa* L.) are not affected by compression or decompression of at least 2 atmospheres. On decompression the release of gas bubbles was neither observed from the mouth nor from behind the gill

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covers, nor did gas bubbles form on the body of the fish although the water in which they were living was supersaturated.

4. The effect of pressure and decompression on salmonids (*Salmo salar* L., *Salmo trutta* L., and *Salmo trutta* f. *fario*) depends on the age of the fish. Until the absorption of the yolk-sac alevins can live under pressures as high as 5 atmospheres. They are neither affected by compression nor by decompression. The release of gas bubbles from the mouth or the appearance of gas bubbles on the body was not observed during decompression although the water in which the fish were living was supersaturated. The swimbladder at this stage is not completely developed.

At an age of 56 days, while the fish can stand pressures of two atmospheres (or perhaps more), they are affected by decompression even at a slow rate. Although the swimbladder is well developed, the release of gas bubbles did not take place on decompression and the swimbladder became distended with gas. This was attributed to the incomplete development of the sphincter mechanism which controls the release of gas bubbles from the pneumatic duct.

Salmon and brown trout 98–178 days old die within 24 hours when subjected to any increase of pressure of more than 15 cm Hg. Older fish (272 days), can live under such pressure as well as at higher pressures (4 atmospheres).

5. The death of young salmonids due to decompression is attributed to the supersaturation of the experimental water with gas. On decompression gas bubbles are separated from the water and attach themselves to the fish. In addition the fish may swallow gas bubbles which block their mouths and the fish die from asphyxia. Death of fish may be due to decompression sickness where gas bubbles are separated from the blood and tissues of the young fish on decompression. The ability of the blood to be supersaturated with gas under pressure may be a character of young fish with swimbladder.

References

BEAFORT, L. F. DE, 1909. "Die Schwimmblase der Malacoptergii". Morph. Jb., **39**: 526–44.

BISHAI, H. M., 1960 a. "The effect of gas content of water on larval and young fish". Z. wiss. Zool., **163**: 37–64.

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

BISHAI, H. M., 1960 c. "The effect of water currents on the survival and distribution of fish larvae". J. Cons. int. Explor. Mer, **25**: 134–46.

BISHAI, H. M., 1960 d. "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., 1961. "The effect of salinity on the survival and distribution of larval and young fish." J. Cons. int. Explor. Mer, **26**: 166–79.

BOHR, C., 1894. "The influence of section of the vagus nerve on the disengagement of gases in the airbladder of fishes". J. Physiol., **15**: 494–500.

BURD, A. C., & LEE, A. J., 1951. "The sonic scattering layer in the sea". Nature, Lond., **167**: 624–26.

CORNING, H. K., 1888. "Beiträge zur Kenntnis der Wundernetzbildungen in den Schwimmblase der Teleostier". Morph. Jahrb., **14**: 1–53.

CUNNINGHAM, J. T., 1896. "The natural history of the marketable marine fishes of the British Islands". pp. xvi + 368, Lond. Macmillan.

DAMANT, G. C. C., 1920. "A diver's note on submarine phenomena". Nature, Lond., **106**: 242.

DANNEVIG, A., & DANNEVIG, G., 1950. "Factors affecting the survival of fish larvae". J. Cons. int. Explor. Mer, **16**: 211–15.

DANNEVIG, A., & HANSEN, S., 1952. "Faktorer av betydning for fiskeeggenes og fiske-yngelens oppvekst". ("Factors involved in hatching and rearing fish eggs and larvae".) Fiskeridir. Skr., **10** (1): 1–36.

DIJKGRAAF, S., 1933. "Untersuchungen über die Funktion der Seitenorgane an Fischen". Z. vergl. Physiol., **20**: 162–218.

DIJKGRAAF, S., 1942. "Über Druckwahrnehmung bei Fischen". Z. vergl. Physiol., **30**: 39–66.

DOUDOROFF, P., 1957. "Water quality requirements of fishes and effects of toxic substan-ces". Chapter ix in "The physiology of fishes". Edited by M. E. BROWN, **2**: 403–30. Academic Press Inc., New York.

EVANS, H. M., & DAMANT, G. C. C., 1929. "Observations on the physiology of the swim-bladder in cyprinoid fishes". J. exp. Biol., **6**: 42–55.

FÄNGE, R., 1953. "The mechanisms of gas transport in the Euphysoclist swimbladder". Acta physiol. Scand., **30**, Suppl. 110: 1–133.

FRANZ, G., 1937. "Über den Reflex des Gasspuckens bei Fischen und die Funktion des Weberschen Apparates". Z. vergl. Physiol., **25**: 193–238.

FRISCH, K. VON, & STETTER, H., 1932. "Untersuchungen über den Sitz des Gehörsinnes bei der Elritze". Z. vergl. Physiol., **17**: 687–801.

FULTON, T. W., 1906. "On the growth and age of herring (*Clupea harengus*)". Rep. Fish. Bd. Scot., **24**: 293–338.

GORHAM, F. P., 1899 a. "The gas bubble disease in fishes and its cause". Bull. U. S. Fish. Comm., **19**: 33–37.

GORHAM, F. P., 1899 b. "Some physiological effects of reduced pressure on fish." J. Boston Soc. med. Sci., **3**: 250–56.

GUYÉNOT, E., 1909. "Les fonctions de la vessie natatoire des poissons Téléostéens". Bull. sci. Fr. Belg., **42**: 203–95.

GUYÉNOT, E., & PLATTNER, W., 1938. "Recherches sur la vessie natatoire des poissons. I. Ligature du canal pneumatique et cystectomie des poissons physostomes". Rev. suisse Zool., **45**: 469–86.

GUYÉNOT, E., & PLATTNER, W., 1939. "Recherches sur la vessie natatoire des poissons. II. Réponse à des critiques et valeur des documents radiographiques". Rev. suisse Zool., **46**: 325–62.

HAEMPEL, O., 1928. "Über die Wirkung höherer Sauerstoffkonzentration auf Fische nebst Untersuchungen über eingleiteten O_2". Z. vergl. Physiol., **7**: 553–70.

HAEMPEL, O., 1937. In E. HENLY, 1952.

HARRIS, M., BERG, W. E., WHITAKER, D. M., TWITTY, V. C., & BLINKS, L. R., 1945. "Carbon dioxide as a facilitating agent in the initiation and growth of bubbles in animals decompressed to stimulated altitudes". J. gen. Physiol., **28**: 225–40.

HENLY, E., 1952. "The influence of the gas content of sea-water on fish and fish larvae". Rapp. Cons. Explor. Mer, **131** (3): 24–27.

HOAR, W. S., 1937. "The development of the swimbladder of the Atlantic salmon". J. Morph., **61**: 309–20.

HOPPE-SEYLER, 1857. Müllers Arch. f. Anat. Phys. u. Wissenschaft. Med. p. 63 (in HILL, L. & GREENWOOD, M., 1910. "On the formation of bubbles in the vessels of animals submitted to partial vacuum". J. Physiol., **39**, Proc. Physiol. Soc., p. xxiii).

JACOBS, W., 1932. "Untersuchungen zur Physiologie der Schwimmblase der Fische. II. Die Volumregulation in der Schwimmblase des Flussbarsches". Z. vergl. Physiol., **18**: 125–56.

JACOBS, W., 1934. "Untersuchungen zur Physiologie der Schwimmblase der Fische. III. Luftschlucken und Gassekretion bei Physostome". Z. vergl. Physiol., **20**: 674–99.

JACOBS, W., 1938. "Untersuchungen zur Physiologie der Schwimmblase der Fische. IV. Die erste Gasfüllung der Schwimmblase bei jungen Seepferdchen." Z. vergl. Physiol., **25**: 379–88.

JOHANSEN, A. C., 1925. "On the diurnal vertical movement of young of some fishes in Danish waters". Medd. Komm. Havunders., Ser. Fisk., **8** (2): 1–28.

JOHANSEN, A. C., 1927. "On the migration of herring". J. Cons. int. Explor. Mer, **2**: 3–27.

JONES, F. R. H., 1949. "The teleostean swimbladder and vertical migration". Nature, Lond., **164**: 847.

JONES, F. R. H., 1951. "The swimbladder and the vertical movements of teleostean fishes. I. Physical factors". J. exp. Biol., **28**: 553–66.

JONES, F. R. H., 1952. "The swimbladder and the vertical movements of teleostean fishes. II. The restriction to rapid and slow movements". J. exp. Biol., **29**: 94–109.

JONES, F. R. H., 1957. "The swimbladder". Chapter IV from "The physiology of fishes". Vol. II edited by M. E. BROWN, Academic Press Inc., New York.

JONES, F. R. H., & MARSHALL, N. B., 1953. "The structure and functions of the teleostean swimbladder". Biol. Rev., **28**: 16–83.

KUIPER, K., 1915. "The physiology of the airbladder of fishes". Proc. K. Akad. Wet. Amst., **17**: 1088–95.

KYLE, H. M., 1913. "Flat fishes (Heterosomata)". Rep. Danish oceanogr. Exped. Medit., **2** (1): 1–150.

LEDEBUR, J. VON, 1928. "Beiträge zur Physiologie der Schwimmblase der Fische". Z. vergl. Physiol., **8**: 445–60.

LEDEBUR, J. VON, 1936. "Beiträge zur Physiologie der Schwimmblase der Fische. III. Über Veränderungen der Gasdrüse bei trommelsüchtigen Fischen". Z. vergl. Physiol., **23**: 34–45.

LEDEBUR, J. VON, & WUNDER, W., 1937. "Beiträge zur Physiologie der Schwimmblase. IV. Beobachtungen an Stichlingen, die ihre Schwimmblase nicht mit Gas füllen konnten". Z. vergl. Physiol., **25**: 149–55.

MAIER, H. N., & SCHEURING, L., 1923. "Entwicklung der Schwimmblase und ihr Beziehungen zum statischen Organ und der Kloake bei Clupeiden". Wiss. Meeresunters. Helgoland, **15**: 1–22.

McEWEN, R. S., 1940. "The early development of the swimbladder and certain adjacent parts in *Hemichromis bimaculata*". J. Morph., **67**: 1–58.

McINTOSH, W. C., & MASTERMAN, A. T., 1897. "The life histories of the British marine food fishes". Cambridge University Press.

MARSH, M. C., & GORHAM, F. P., 1905. "The gas disease in fishes". Rep. U. S. Fish Comm. for 1904: 343–76.

MEIERHANS, J., 1935 a. "Le canal pneumatique et la vessie natatoire des poissons physostomes". C. R. Acad. Sci., Paris, **200**: 582–84.

MEIERHANS, J., 1935 b. "Comportement des poissons physostomes ayant subi l'extirpation de la vessie natatoire". C. R. Acad. Sci., Paris, **200**: 859–62.

MEIERHANS, J., 1935 c. "Vessie natatoire et canal pneumatique chez les poissons Cyprinidés". C. R. Soc. Phys. Hist. nat., Genéve, **52**: 62–64.

MOREAU, F. A., 1865. "De l'influence de la section du grand sympathique sur la composition de l'air de la vessie natatoire". C. R. Acad. Sci., Paris, **60**: 405–C8 & C. R. Soc. Biol., Paris, **2**: 21–24.

MOREAU, F. A., 1876. "Recherches experimentals sur les fonctions de la vessie natatoire". Ann. Sci. nat., (Zool.), Sér. 6, **4**: 85 pp.

MŘSIC, 1933. In E. HENLY, 1952.

OSGOOD, W. H., 1904. Notice of M. C. MARSH's paper on "The gas disease in fishes". Science, N. S., **19**: 70i.

PLATTNER, W., 1937. "Vessie natatoire et canal pneumatique". C. R. Soc. Biol., Paris, **126**: 1072–74.

PLATTNER, W., 1938 a. "Vessie natatoire et rejet de bulles gazeuses chez les poissons physostomes". C. R. Soc. Biol., Paris, **127**: 7–9.

PLATTNER, W., 1938 b. "Vessie natatoire et variations de volume de poissons physostomes en fonction de la décompression". C. R. Soc. Biol., Paris, **127**: 278–81.

PLATTNER, W., 1941. "Études sur la fonction hydrostatique de la vessie natatoire des poissons". Rev. suisse Zool., **48**: 201–38.

PLEHN, M., 1922. In E. HENLY, 1952.

RABAUD, E., & VERRIER, M. L., 1931. "Contribution à l'étude de la vessie natatoire chez les poissons physoclistes". Bull. Soc. sci., Arcachon, **29**: 1.

RABAUD, E., & VERRIER, M. L., 1932 a. "Effets de faibles décompressions sur la vessie natatoire". C. R. Soc. Biol., Paris, **109**: 1094–1196.

RABAUD, E., & VERRIER, M. L., 1932 b. "Effets de la décompression sur les poissons normalement sans vessie natatoire". C. R. Soc. Biol., Paris, **109**: 1277–78.

RABAUD, E., & VERRIER, M. L., 1932 c. "L'évacuation des gaz de la vessie natatoire et le fonctionnement du canal pneumatique". C. R. Acad. Sci., Paris, **195**: 906–08.

RABAUD, E., & VERRIER, M. L., 1932 d. "La projection des viscères abdominaux chez les poissons soumis à des décompressions". Bull. Soc. Zool. Fr., **57**: 297–302.

RABAUD, E., & VERRIER, M. L., 1933 a. "Système vasculaire et glande gazeuse de la vessie natatoire et comportement". Bull. Soc. sci., Arcachon, **30**: 167–78.

RABAUD, E., & VERRIER, M. L., 1933 b. "Morphologie comparée de la vessie natatoire". C. R. Soc. Biol., Paris, **112**: 22–24.

RABAUD, E., & VERRIER, M. L., 1934 a. "La vessie natatoire de la Loche (*Cobitis barbulata* L.)". C. R. Acad. Sci., Paris, **198**: 1073–75.

RABAUD, E., & VERRIER, M. L., 1934 b. "Vessie natatoire et variations des volumes des poissons". C. R. Acad. Sci., Paris, **199**: 888–90.

RABAUD, E., & VERRIER, M. L., 1934 c. "Vessie natatoire, densité, et plan d'équilibre des poissons". C. R. Acad. Sci., Paris, **199**: 1247–49.

RABAUD, E., & VERRIER, M. L., 1934 d. "Recherches sur la vessie natatoire". Bull. biol., **68**: 188–231.

RAUTHER, M., 1922. "Zur vergleichenden Anatomie der Schwimmblase der Fische". Ergebn. Zool., **5**: 1–66.

ROTH, 1922. In E. HENLY, 1952.

SEMPER, In E. HENLY, 1952.

SCHACH, V. H., 1939. "Die künstliche Aufzucht von *Clupea harengus* L.". Wiss. Meeresunters., Helgoland, **1** (3): 359–72.

SCHOLANDER, P. F., CLAFF, C. L., TENG, C. T., & WALTERS, V., 1951. "Nitrogen tension in the swimbladder of marine fishes in relation to depth". Biol. Bull., Woods Hole, **101**: 178–93.

SHELFORD, V. E., & ALLEE, W. C., 1913. "The reactions of fishes to gradients of dissolved atmospheric gases". J. exp. Zool., **14**: 207–66.

VOGT, C., 1842. "Embryologie des Salmonés". In: AGASSIZ, L. (1839–42): "Histoire naturelle des poissons d'eau douce de l'Europe centrale". 2 vols. Neuchâtel.

VERRIER, M. L., 1931. "Sur la suppression de la chaine des osselets de Weber et de la vessie natatoire chez les téléostéens". C. R. Soc. Biol., Paris, **107**: 1485–87.

WALLS, G. L., 1942. "The vertebrate eye". pp. xiv + 785, Cranbrook.

WUNDER, W., 1935. "Das Verhalten von Knochenfische beim Ausschlüpfen aus dem Ei und in den ersten Lebenstagen". Verh. deutsch. zool. Ges., **37**: 60–63.