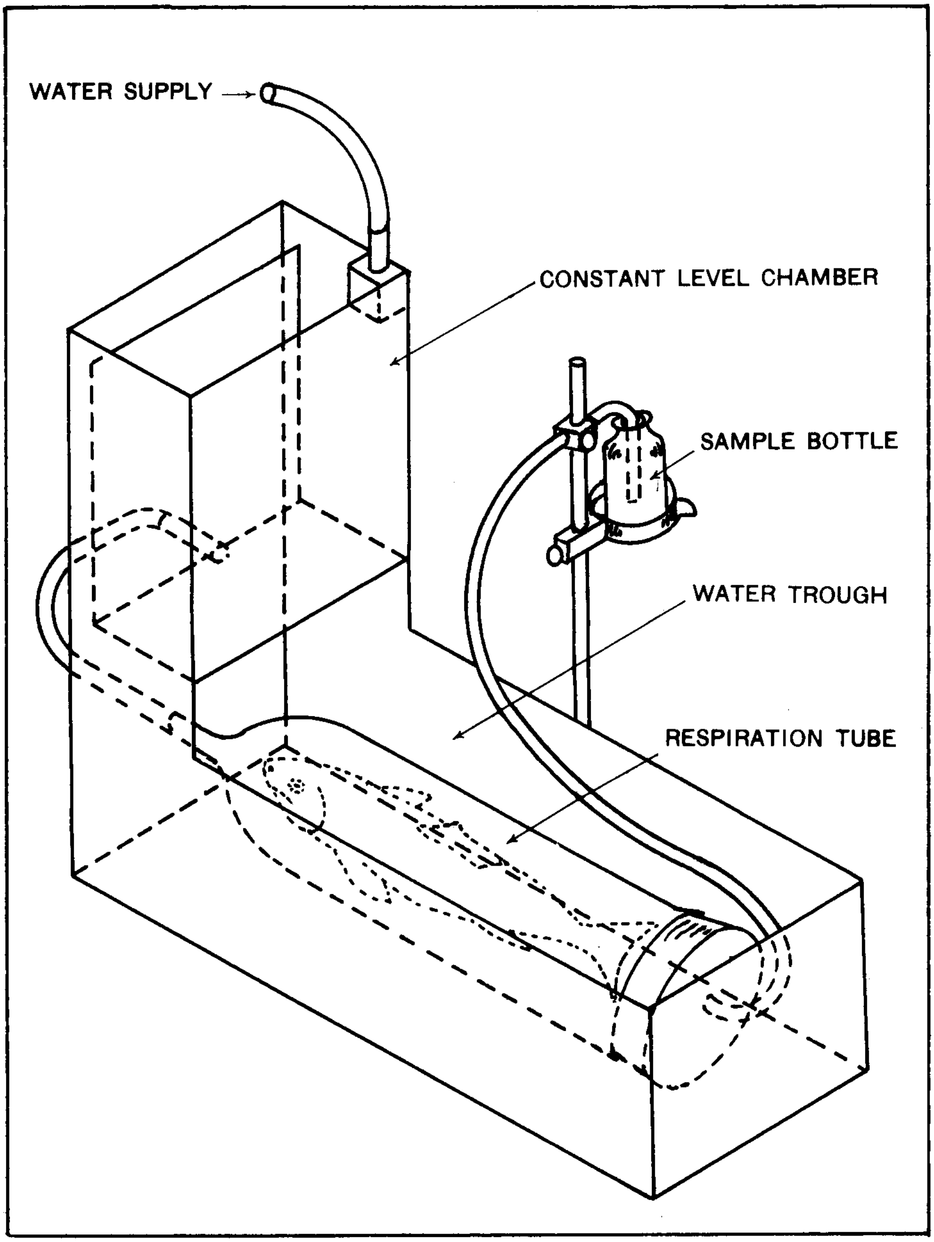

Fig. 1. Details of continuous-flow apparatus used for measuring the oxygen consumption of young salmon.

FIELD MEASUREMENTS OF THE BASAL OXYGEN CONSUMPTION OF ATLANTIC SALMON PARR AND SMOLTS

G. Power*

THIS investigation was undertaken in order to study, under conditions as nearly natural as possible, the basal oxygen requirements of salmon parr and smolts living at the northern limit of their range in Ungava. The results are of interest for two reasons; (1) an indication is obtained of the way the salmon's metabolism responds to temperature changes in its environment; (2) a point of reference is provided which, when other suitable figures are available, may be used to detect possible adaptation to cold in the metabolism of northern races of salmon.

To date almost all measurements of the oxygen consumption of fish have been made in the laboratory, for the obvious reason that many of the variables inherent in the natural environment can be eliminated or controlled. From the results of such studies the behaviour of fish in nature can be predicted within limits. Caution must be exercised in doing this, since controlled laboratory conditions tend to be quite different from natural conditions where a fish is subjected to daily and seasonal fluctuations in temperature, oxygen concentration, light, food supply, and to other not so apparent changes. By carrying out measurements of oxygen consumption in the field these variations can be incorporated into the experiments, reducing to a minimum any disturbance of the fish. The physiological condition of an organism, influenced by the normal vicissitudes of its environment will be affected by changes from the normal, and results of field experiments are of value as an estimate of the natural behaviour of an organism no matter how difficult it is to interpret them. Temperature is undoubtedly the most important variable affecting the oxygen consumption of an organism in the natural environment and those inhabiting rivers are unable to avoid exposure to temperature fluctuations, which in Ungava often reach 3°C. daily, superimposed on a seasonal cycle with a range of approximately 15°C.

For studies of climatic adaptation, field experiments are indispensable. Lindroth (1942) gives figures for the oxygen consumption of young salmon, but his figures are so much greater than those obtained in the present study (40-gm. parr using approximately 0.080 ml. O_2/gm./hr. at 10°C. as against 0.061 ml. O_2/gm./hr. at 10°C. for an Ungava parr of equivalent weight) that comparison is not possible. The study of adaptation to cold of the

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basal metabolism in Ungava salmon must wait until more information is available from other regions.

Material and method

Source of material

Fish used in the experiments were taken from the George River at Helen Falls or from the Kaniapiskau tributary of the Koksoak River below Manitou Gorge. Generally a Fyke net was used to capture the fish and they were retained in the net for 24 hrs. before an experiment. Occasionally fish taken by hand net or by rod and line were used and then particular care was taken to see that the fish were not more than superficially injured at capture and they were retained in keep pools adjacent to the site of capture for a few days before being used in an experiment.

Method

Of the methods available for determining the oxygen consumption of poikilotherms (see Fry 1957) the continuous flow method has obvious advantages in the field. Water of known oxygen concentration is passed through a chamber containing the experimental organism and the overflow is collected to determine the amount of oxygen extracted and the rate of flow through the apparatus. By passing water taken directly from the river through the apparatus all changes in the river are immediately duplicated in the apparatus. Experiments can be continued over an indefinite period of time during the whole of which determinations of oxygen consumption can be made. In experiments with species of fish that usually inhabit running water the flow of fresh water over the animal possibly assists in keeping it tranquil by reproducing its ecological norm. In measuring basal metabolism it is particularly important that all activity be reduced to a minimum.

The apparatus itself is a simplification of that used by Keys (1930). Water is obtained upstream from the apparatus, and piped to the constant-level chamber (Fig. 1). The water that overflows from this chamber falls into the water trough, flows past the respiration tube and spills over the lower end of the trough. A small rubber tube carries water from the lower end of the constant-level chamber and delivers it to the respiration chamber in which the experimental fish is enclosed. Water flows through this chamber, past the fish and through the outflow tube into the sample bottle. The rate of flow through the respiration chamber can be regulated by altering the height of the sample bottle in relation to the level of the constant-level chamber. The overflow from the sample bottle is collected in a shallow tray and directed into a short spout. The rate of flow through the respiration chamber can be measured by collecting the overflow for a known period of time. In practice this was one minute during which between 50 and 90 ml. were delivered into a 100-ml. measuring cylinder.

Oxygen determinations, using the unmodified Winkler method, were carried out on water collected in the sample bottle, which was replaced hourly during an experiment, and simultaneously on a sample of water taken from the tube supplying the constant-level chamber. The unmodified Winkler method of oxygen determination is generally adopted for work of this nature and gives entirely satisfactory results in the waters of lakes and streams that do not contain high concentrations of iron, nitrates or organic matter.

Certain precautions were taken to prevent disturbing the fish during an experiment. The apparatus, which was constructed of plexiglass, was covered with a dark cloth that restricted the vision of the fish. The bottom of the water trough was covered with clean river gravel so that conditions in the respiration tube resembled as closely as possible the environment of a fish lying quietly under a rock on the river bed. The hose supplying water to the apparatus was immersed in the river for its whole length to prevent warming of the water in the hose on a hot day and the apparatus itself was partly submerged in the river and located in the shade to prevent warming by the sun.

In a typical experiment the fish was placed in the apparatus in the evening and given the following night to settle down and become accustomed to confinement in the respiration chamber. The size of the chamber was chosen to allow the fish room for restricted movement. If the chamber is too small the fish is unable to move sufficiently to maintain normal equilibrium and often falls over on one side and remains in an excited condition. Sampling was begun the next morning, usually 2 hours after sunrise and continued at hourly intervals until about noon. Six samples were considered desirable in each experiment.

At least 6 hours should elapse between placing the fish in the respiration chamber and beginning to measure the basal oxygen consumption. Handling the fish is sufficient to cause it to respire at a maximal rate for some time, after which the rate gradually falls to a minimum (Keys 1930, Wells 1932). This was confirmed in a number of experiments in which the oxygen consumption was determined at intervals beginning immediately after the fish was introduced into the apparatus. Fig. 2 shows the results of one such experiment carried out on a salmon parr and typical of the pattern found: a high initial rate that falls rapidly during the first 2 hours until a basal level is reached, usually after 3 to 4 hours. Sometimes fish never settled down, or became disturbed during the course of an experiment. The commonest causes of excitement were either loss of equilibrium or the passing of faeces. Faeces caused a certain amount of trouble in that they occasionally obstructed the flow of water through the apparatus. One further cause of trouble was supersaturation of the water. This happened at only one locality in Manitou Gorge, where bubbles of gas came out of solution in the apparatus and often blocked the smaller tubes. Experiments in which disturbances occurred were abandoned and disregarded.

Results and discussion

The juvenile salmon were divided into two groups, parr and smolts, and an attempt was made to keep these groups quite distinct and fairly uniform in size. Experiments were conducted on 11 parr and 20 smolts, from both the George and Koksoak rivers. For complete details of each experiment see Power (1959). The mean weight of the parr was 42.5 gms., standard deviation 11.2, and that of the smolts was 80.0 gms., standard deviation 9.9. Experiments were conducted at temperatures from 4°C. to 16°C.

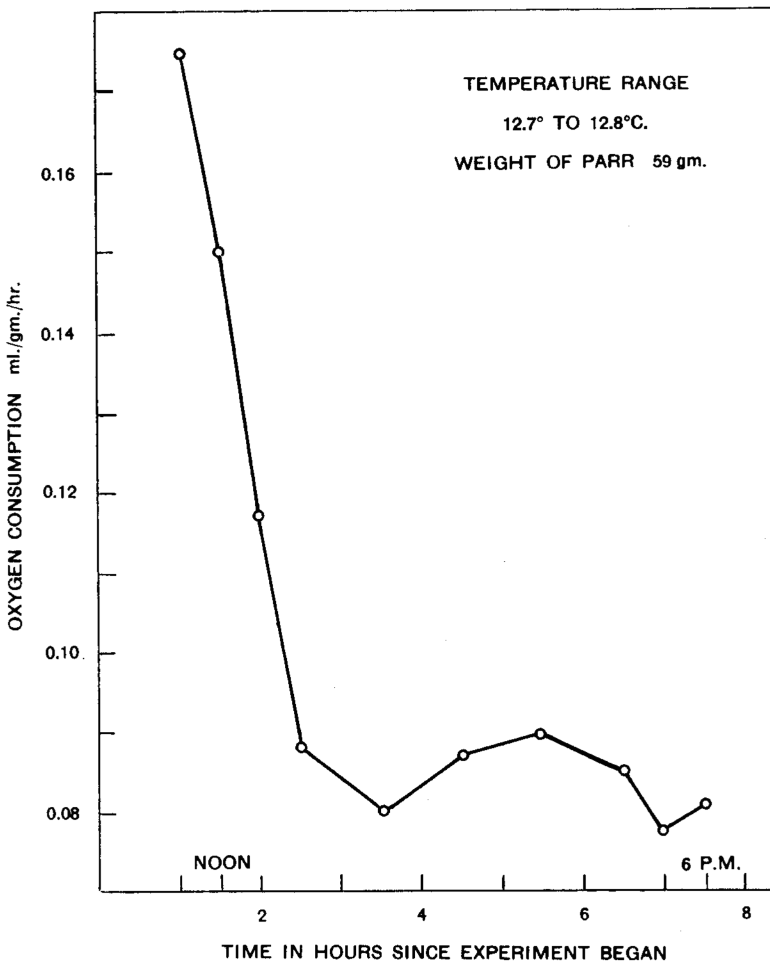

Fig. 2. The rate at which the oxygen consumption of salmon parr falls to the basal level after handling the fish.

Diurnal rhythm

Diurnal rhythms in the oxygen consumption of fish have been described by a number of workers, for example, Clausen (1936), Graham (1949), and Job (1954). Possibly related to these rhythms are variations in motor activity during a 24-hour period demonstrated by Spoor (1946) and variations in feeding activity shown by Hoar (1942). In measuring the basal metabolism of fish attention should be paid to the presence of any endogenous metabolic cycle and, ideally, basal oxygen consumption is measured when the cycle is at its minimum. In his work on the speckled trout Job (1954) found that the position of this minimum point varied, but in 60 per cent of his experiments it was in the night. In calculating the basal oxygen consumption he considered the lowest value obtained during a 24-hour experiment to be the basal value. For practical reasons it was not possible to adopt a comparable procedure in the field as experiments during the night were impracticable. In an attempt to find whether an endogenous cycle of oxygen consumption exists in salmon, experiments with three smolts were continued over a 26.5-hour period. The results are presented graphically in Fig. 3. The curves of oxygen consumption are smoothed by plotting in groups of three. The curves denoting temperature and oxygen content of the water are plotted directly. The most striking feature of the results is the similarity of the curves for the three fish. All show maximum oxygen consumption at midnight and midday and minima during early morning and late afternoon. Hoar (1942) found a somewhat similar cycle in the feeding activity of young salmon. They fed actively in the evening usually not ceasing until dark. Feeding recommenced at daybreak, increased in intensity during the morning, and was often followed by a slight cessation around midday.

General temperature response

The smolt data were analysed taking into account the differences between fish and the differences between rivers and it was found that a single slope adequately described the relationship between the logarithms of the oxygen consumption and the temperature. The results of other experiments on fish carried out under laboratory conditions (see Fry 1957) indicate that such a relationship could be expected over an environmental temperature range of 12°C. Although a significant difference in oxygen consumption between fish was found to exist, the F ratio being 19.3 with 18 and 97 degrees of freedom, no explanation for this is offered. It is apparently not correlated with weight, age or sex of the individual.

The regression equation describing the smolt data is

$$\log y = 0.06123x + \bar{2}.1087$$

where y = oxygen consumption in ml./gm./hr.
x = temperature °C.

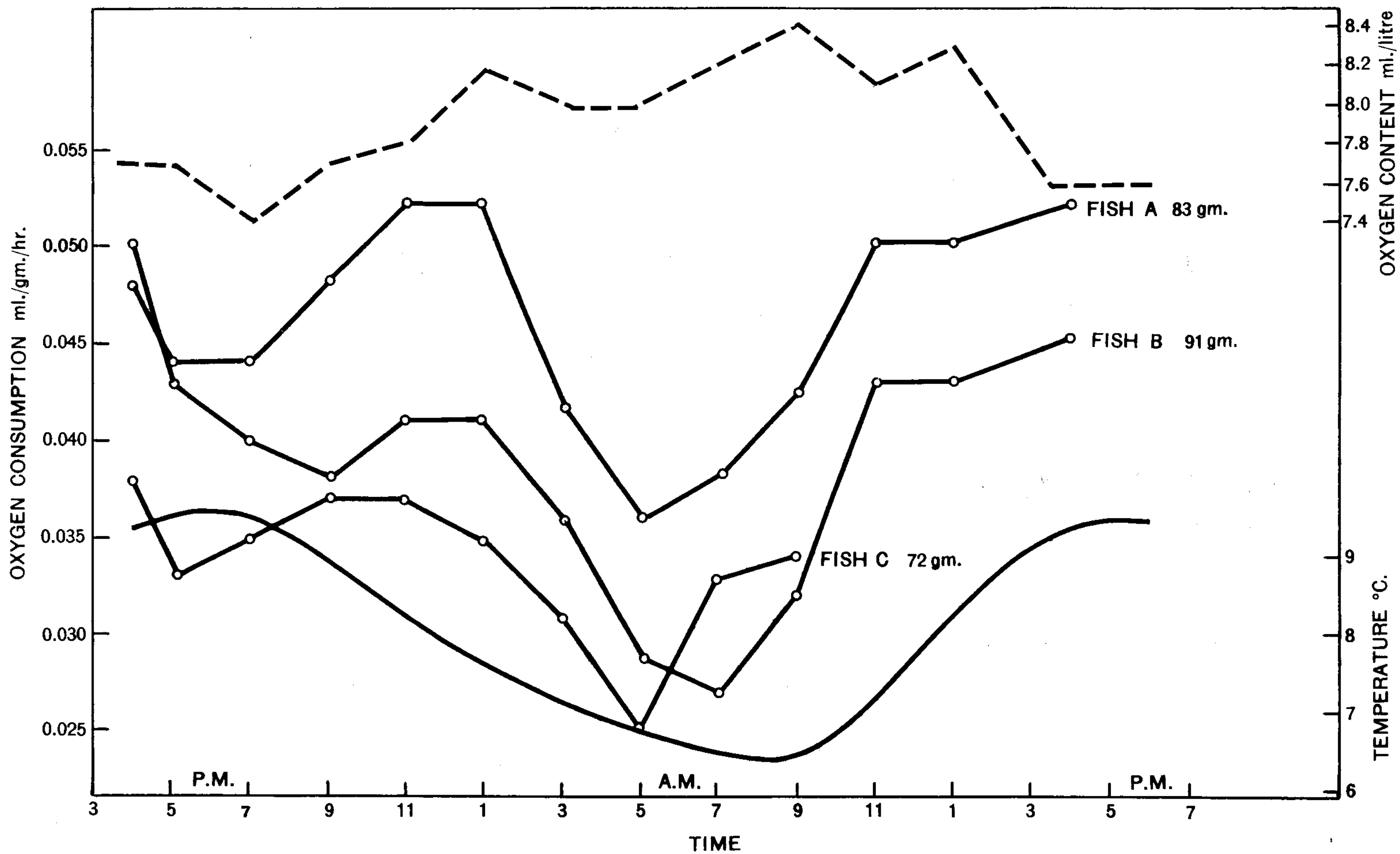

Fig. 3. The diurnal rhythm of oxygen consumption of three salmon smolts under natural environmental conditions.

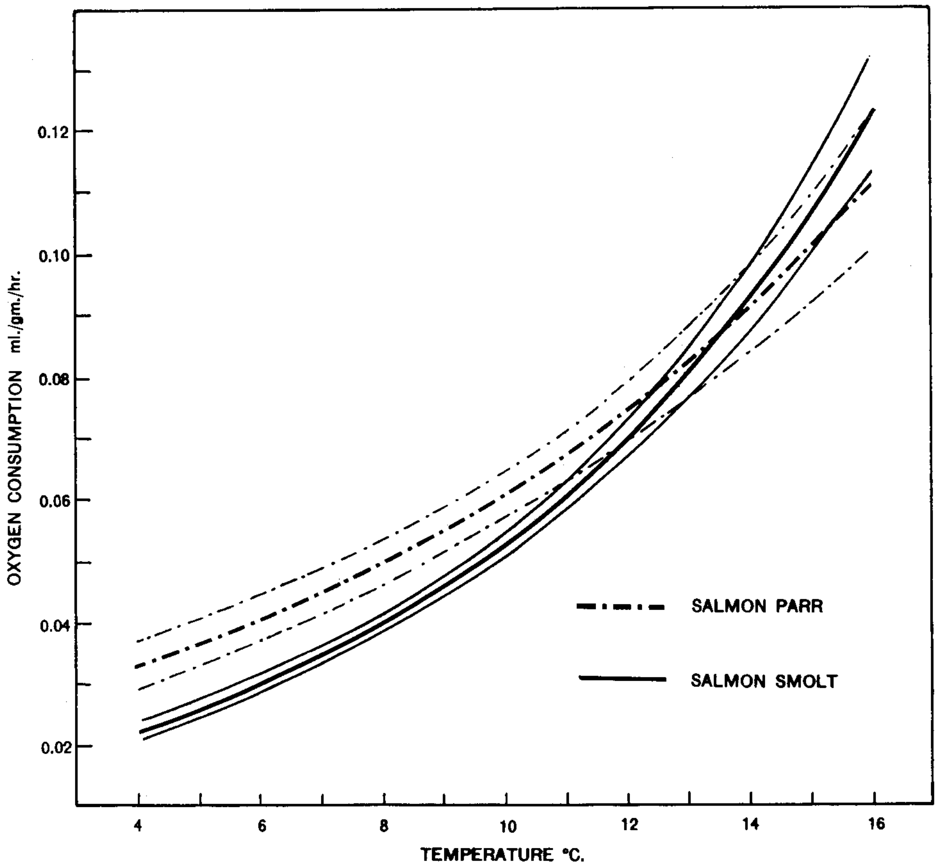

Fig. 4. The oxygen consumption of salmon parr and smolts from Ungava at temperatures between 4° and 16°C.

Fiducial limits to this line at the 95 per cent level of probability are given by

$$y^\circ = y^\circ \pm 1.98 \times 0.00784 \left[\frac{1}{137} + \frac{(x^\circ - 9.5044)^2}{1308.39} \right]$$

where $\tilde{y}^\circ$ is the calculated value of log y at a given temperature x°, and y° sets the limits for log y at that temperature.

The data obtained for the parr can be described by the regression equation

$$\log y = 0.04360x + \bar{2}.3497$$

and fiducial limits at the 95 per cent level of probability are given by

$$y^\circ = \tilde{y}^\circ \pm 2.0 \times 0.1215 \left[\frac{1}{68} + \frac{(x^\circ - 10.820)^2}{1022.12} \right]$$

In Fig. 4 the relationship between the oxygen consumption of salmon parr and smolts and the temperature is portrayed graphically and a number of deductions are made apparent. The oxygen consumption per unit weight of smolts is lower than that of parr below 13.5°C. but above that temperature it is higher. This is because the rate of increase of oxygen consumption with temperature is greater for smolts than for parr, (comparing regression coefficients $P < 0.001$) indicating that metabolically smolts are more responsive to temperature change. This may be of importance in the life of the salmon if temperature is one of the environmental factors important in initiating smolt migration. The physiological mechanism underlying this difference between smolts and parr may be related to changes in endocrine secretions that are associated with smolt development in salmon, notably increase in thyroid secretion. This is known to bring about an increase in metabolic rate in higher vertebrates although evidence from teleosts is conflicting (Hoar 1957).

Acknowledgements

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