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The Oxygen Consumption of *Salvelinus fontinalis*

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THE OXYGEN CONSUMPTION OF SALVELINUS FONTINALIS

INTRODUCTION

THE INVESTIGATION presented in this paper was undertaken in order to study in the speckled trout the relation of size to the effects of the environmental factors of temperature and partial pressure of oxygen upon oxygen consumption. Although there have been many measurements of metabolism in relation to size, (Bertalanffy, 1949, 1951; Zeuthen, 1947, 1953; Kleiber, 1947; Edwards, 1946), there is no complete description for any one species of fish where oxygen consumption is related to size, temperature, and the environmental oxygen pressure. Beyond any virtue which may be attached to thoroughness, such a complete description of the rate of oxygen intake in relation to size has value in the following ways. Appropriate measures of the rate of oxygen uptake indicate the capacity of the organism to perform external work in relation to its size. Size also must be considered in relation to effects of oxygen concentration and temperature upon the uptake. Finally estimates of oxygen uptake in relation to size considered in conjunction with growth rate and the calorific equivalent of the metabolic rate permit estimates of the total energy requirement of the individual.

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MATERIALS AND METHODS

General

Source of materials. The fish were from both hatchery and wild stocks and ranged in size from about four grams to about one kilogram. As far as possible the same groups of fish were used repeatedly through all the series of experiments, sufficient time being allowed between experiments for them to recover from the effects of earlier treatment. They were held in large concrete tanks supplied with running water drawn from a well. The pH of the water was 7.3 to 7.5, with a total hardness of 181 and an alkalinity of 202 expressed as p.p.m. CaCO_3 . The details of the water analysis are given by Brett (1952). The temperature of the water in holding tanks fluctuated from 5°C . in the winter to about 10.5°C . in the summer.

Food. The fish were fed during the period from March 1951 until July 1953 with standard "Red-Gil" fish food supplied to the laboratory by Burns & Co. Ltd., Calgary, Alberta. This food is a preparation of liver, lungs, spleen, tripe, gelatin, meat meal, fish meal, bone meal, salt, yeast, wheat germ, carrot meal, alfalfa meal, wheat middlings, skim milk powder, and concentrated vitamin A, with the following analysis:

| | |
|--------------|------|
| Protein | 15% |
| Carbohydrate | 3.7% |
| Fat | 2.1% |

and a calorific value of 96 calories per 100 gm. wet weight.

Disease. While they were being held as reserve stock all the fish were subjected to routine measures to prevent disease, as recommended by Davis (1946). Healthy fish were selected from the reserve stocks and held in acclimation tanks without, as far as possible, further prophylactic treatment while a given series of experiments were in progress. In spite of

precautions disease attacked certain stocks. These were discarded as soon as the outbreak was noted.

Acclimation. It has been well established that organisms respond within certain limits to variations in the environment by changes in their physiological state. Such responses have been termed acclimatization or acclimation. In order to obtain a reproducible picture of the physiology of the speckled trout great care was therefore taken in acclimating them to the temperature at which the experiments were done. The times allowed for acclimation were those recommended by Brett (1941), Fry and Hart (1948), and Belding (1929) for the various temperatures. They were held at 5°C . and 10°C . for not less than a month, at 15°C . and 20°C . for about twenty days. The rise or fall of temperature of the acclimation tanks were regulated to steps no greater than 1°C . per day. Water for acclimation of the fishes to 5°C . and 10°C . was drawn from a refrigerated supply. For acclimation to 15°C . and 20°C . well water was run through pyrex tubes heated by electric coils. Since the supply had a constant temperature, the temperature in the acclimation tanks was constant to within plus or minus 0.2°C . at any desired level without further regulation once the flow was adjusted. A continuous record was kept of each temperature during the course of the work.

Temperature was the only factor controlled in the acclimation tanks. As far as possible the other factors were maintained constant. By vigorous aeration through air diffusers, each consisting of a 30 cm. length of 2.5 cm. carborundum tube, the oxygen pressure was maintained around 75 per cent air saturation. The pH in the holding tanks varied between 7.4 and 8.1. Free carbon dioxide was low, amounting at the most from 7 to 12 p.p.m.

Standard metabolism

Apparatus. The apparatus used here was that described by Fry and Hart (1948), modified to serve as a continuous flow apparatus. In essence this was the apparatus used by Keys (1930). It consisted of a large insulated rectangular tank with a capacity of about 100 litres in which the respiration chambers were immersed. Water was introduced continuously into the tank and passed into the respiration chambers, escaping through their outlets. Since the rate of flow through the respiration chambers had to be constant, the depth of water in the tank was maintained constant by a constant-level bottle. Enough water was introduced into the tank so that, in addition to that flushing the respiration chamber and escaping therefrom, there was always some excess which spilled over through the

constant-level bottle. The desired temperature in the insulated tank was maintained to within plus or minus 0.2°C . by adjusting the temperature of the water supply as was described for the acclimation baths. The water in the tank was aerated vigorously by air diffusers of the type mentioned earlier. Samples of water for oxygen concentration and temperature readings taken at different points in the tank indicated that these conditions were uniform throughout. The tank was covered during experiments by a lid.

The respiration chambers consisted of Erlenmeyer flasks with two-hole stoppers for the inlet and outlet, or of cylinders of glass or lucite which could be stoppered at both ends to form a chamber. The capacities of these chambers varied between 0.1 litre and about 5.0 litres. The water entered the chamber through a short narrow glass tube piercing the rubber stopper. The rate of flow of water into the chamber was controlled by a screw clamp on a short length of rubber tubing at the free end of the glass inlet tube. When Erlenmeyer flasks were used, the outlet from the chamber (flask) extended to about halfway into the flask, whereas the inlet was flush with the stopper. In the case of cylindrical chambers the inlet was at one end and the outlet at the other. The outlet of the respiration chamber was protected by a wire gauze screen so that any excreta dropped by the fish did not block the flow.

A series of perforations on the side of the tank near the bottom allowed the outlet tubes which conveyed the water from the chamber to pass to the bottom of the sampling bottles. These bottles were held in a fixed position by clamps brazed on to a horizontal bar, mounted alongside the tank to maintain a constant difference in head between the inlet of the chamber and its outlet. Provision was made for eight such samples to be collected simultaneously. Each sampling bottle had a capacity of approximately 60 cc. and was of the glass-stoppered type ordinarily used with the Winkler method of oxygen analysis.

Experimental procedure. The fish were starved for at least 12 hours prior to being placed in the respiration chambers, so that in almost all cases no excreta collected in the chambers while the experiment lasted. The transfer from the acclimation tanks to the respiration chambers was done with the least possible amount of disturbance to the fish.

Chambers of different sizes were used corresponding to the size of the fish. The assignment was made quite arbitrarily, without too much attention being paid to maintaining the exact relationship between the size of the fish and the volume of the water surrounding it. However, care was always taken to avoid too small a chamber for any one fish. The fish when enclosed could always move its fins with freedom but could not

easily execute any active swimming movement. The fish was usually placed with its head facing the inlet. If placed the opposite way, it tended to struggle to orientate itself in the former direction, and thus to remain excited for a long time.

The fish were not subjected to any form of anaesthesia during transfer from the acclimation tanks to the respiration chambers, since it was noted that individuals treated with ethyl carbamate (urethane) discharged abnormal quantities of mucous and that as they came out of the stupor they became excited, some even executing laboured respiratory movements. On the other hand, darkening the chamber caused the unanaesthetized fish to settle down in the chamber very readily. Therefore the chambers were darkened by covering them with the lid soon after the fish were enclosed.

In order to meet the initial high rate of oxygen consumption, the water was allowed to flush through the chambers as rapidly as possible for at least the first 3 hours. At the end of this initial period the flow was gradually reduced, without causing much disturbance to the fish, until the water leaving the chamber showed a concentration of the order of 50 per cent air saturation while the rate of oxygen consumption was falling but still high. Since the difference in the concentration of oxygen in the water entering and leaving the chamber was the basis for obtaining the rate of oxygen consumption, this margin was chosen so that when the fish did pass through the low rate of oxygen consumption later on there would still be a measurable difference in oxygen concentration between the inlet and outlet water while at the same time it also assured that oxygen pressure in the chamber did not fall so low as to restrict the standard respiration. The unmodified Winkler technique for the measurement of oxygen (Ellis *et al.*, 1946) was employed in this series of experiments.

A preliminary check on the carbon dioxide tension and the pH of the water entering and leaving the chambers under the experimental conditions described above showed no significant difference, so that it was taken that these could not have assumed the levels which have been stated by Graham (1949) and Needham (1938) to affect the standard respiration.

Each experiment lasted for 24 hours or a little more. Except for the few samples taken in order to adjust the rate of flow about 3 hours after enclosing the fish, the regular readings were begun 12 hours later towards late evening and were continued until well past noon the next day. Two hours were allowed to elapse between successive readings so that the fish could recover from the slight disturbance occasioned by the withdrawal of the samples (c.f. Wells, 1935a). The continuous-flow method used here cut down to a minimum the chances of the fish being disturbed in

the course of the experiments by extrinsic factors such as abrupt changes in the rate of flow or in the qualities of the water.

A respirometer was developed earlier in order to record standard metabolism automatically. But it was not used in obtaining the data presented in this paper except for one point (square) which is included in the graph showing standard consumption at 15°C. in Figure 2C. It was not necessary to use it because, by the time most of the technical rectifications it needed were accomplished, the data had been already collected by the method described.

At the end of each experiment the fish were weighed as accurately as possible and returned to their acclimation tanks for further use.

The calculation of the rate of oxygen consumption was based on the difference in the concentration of oxygen between the inflowing and outflowing water and on the rate of flow of water through the chamber. The lowest rate of oxygen consumption by the fish in any two-hour interval in this 24-hour cycle was taken as the standard rate.

Diel rhythm. The standard rate did not always occur at the same time of day in the manner of the diel rhythm recorded by Graham (1949). She noted that in the standard metabolism of the speckled trout there was a pronounced difference between the rate during the day and that at night, and that the low point in the cycle occurred sometime between midnight and the early hours of the morning. In the present investigation evidence of such a rhythm was sought and each measurement of the standard metabolic rate was carried through a 24-hour cycle. It was found that only in 60 per cent of the experiments did the low point occur during the period recorded by Graham. Such departures from the usual diel cycle of respiration have been observed by Keys (1930) and Wells (1932). Spencer (1939) and Spoor (1946) measured them as spontaneous activity. Spencer found that in some species such as the bluegill there was no diel rhythm. It seems therefore that the diel rhythm, while being a general characteristic, is however not a consistent one. As stated by Welsh (1938), it is perhaps a physiological characteristic which submits temporarily to environmental changes. Lawrie's experiments reported by Graham, were performed in chambers which were not darkened and in a place where light and other sources of disturbance were present during the day. The diel cycle obtained under these conditions was consequently more pronounced than that obtained in this investigation, done under conditions relatively free from such disturbances. The latter cycle may therefore represent an endogenous rhythm. Irrespective of the time of occurrence in the 24-hour period, the lowest rate measured was taken as the "standard" rate in the present investigation.

Group effect. In the standard respiration experiments single individuals were used in all cases except at 15°C., where groups of from two to six fish of the same size were used in seven cases. These groups were used in order to test the effect of such grouping on the rate of respiration. Because of the limitations in the apparatus, larger groups and groups of heavier fish could not be used.

The results obtained in these experiments showed that all but one point fell below the general mean. However, all six points lay within comparable low figures obtained for individual fish. In consequence it was concluded that, although isolating the fish may have caused a bias in the mean standard rate, such a bias was not a substantial one.

Group effect appears to be a general manifestation in most cases. Schuert (1933) and Schlaifer (1939) who have performed interesting experiments to examine the effect of grouping the fish upon their respiration suggest that visual contacts and other sensory responses were partly responsible for the subsidence of respiratory rate. In the experiments recorded here, the fish used in groups arranged themselves in palisade fashion and not at random, even in the absence of light, showing that actual physical contact was conducive to their remaining less excited. Their quiescence therefore produced a corresponding reduction in their respiration. It was interesting to note that while a flashing light would disturb fish held individually, those in groups scarcely moved.

Variations in the respiratory rhythm among individual fish would naturally tend to be smoothed out in an experiment with grouped fish, and the actual rates measured may therefore represent also a mean of respiratory rhythms of all the fish. Thus, apart from the lowering of respiration due to corresponding subsidence in activity while the fish are held in groups, the results might also be more uniform as was indeed noted.

Active metabolism

Apparatus. The active or the maximum rate of oxygen consumption was measured in the apparatus of Fry and Hart (1948) but with some modifications. The apparatus consisted essentially of a double-walled drum. The outer wall was glass and the inner, metal. The bottom of the drum had a metal base which rested on a turntable. At the upper, open end of the drum a metal rim was mounted over the outer glass wall and was clamped firmly to the bottom plate by lucite brackets. The purpose of the metal rim was to provide an outer support for an inflatable rubber gasket that allowed complete closure of the top in place of the floating lid used formerly. The gasket was the inner tube of an aeroplane tire. The

metal rim had two openings in its upper face. On one was mounted a graduated cylinder with a long-handled screw valve, so that by operating the latter, a measured quantity of water could be allowed to enter the chamber. The other opening was plugged by a rubber stopper through which passed a thermometer.

Experimental procedure. The chamber was filled with water at the desired temperature and the fish introduced into it. The rubber gasket was then inflated rapidly, both the inlet (screw valve) and the outlet being kept open so that the pressure in the chamber could equalize with that of the atmosphere. If any excess pressure was created in the chamber, the fish reacted immediately and released gas from its swim bladder, thus creating a gas pocket. After enclosing the fish the gasket was squeezed all round where it was in contact with the walls of the chamber to release any air pockets that might have formed there.

After these preliminaries, the chamber was rotated rapidly for a minute in order to mix the water thoroughly. This was necessary because a certain amount of stratification might have taken place as a result of the fish using up part of the oxygen in the chamber while the preliminaries were attended to. The initial sample was taken immediately after the chamber had been rotated. Successive samples were taken at intervals of 20 minutes to 1 hour depending upon the rate of oxygen consumption by the fish.

Two sizes of chambers were used. The smaller chamber had an outer diameter of 30 cm. and an inner diameter of 15 cm. and a capacity of 10 litres. The larger chamber had an outer diameter of 50 cm., an inner diameter of 30 cm., and a capacity of 20 litres.

The chamber used in a given experiment was of such a size that the fish had freedom to swim. The fish were made to swim steadily, that is, to maintain a steady position in the chamber which was rotating at a speed above which even a slight increase would result in their falling back and being swept back by the current; no regular record of the maximum rate of swimming was kept. In several cases, the fish behaved erratically and would not swim steadily. In such cases the chamber was stopped and started abruptly, or its direction reversed frequently, to make the fish perform active swimming movements continuously except for brief intervals while the samples were being taken.

Activity and oxygen consumption. It was mentioned earlier that difficulty was experienced in keeping certain fish uniformly active. By plotting the rates of oxygen consumption of fish which did not swim regularly and comparing them with those of fish which did, it was found that in the former cases the rate of oxygen consumption fluctuated with the

activity of the animal as long as the pressure of oxygen was not limiting. Figure 1 illustrates how varied these patterns may be. It shows beyond

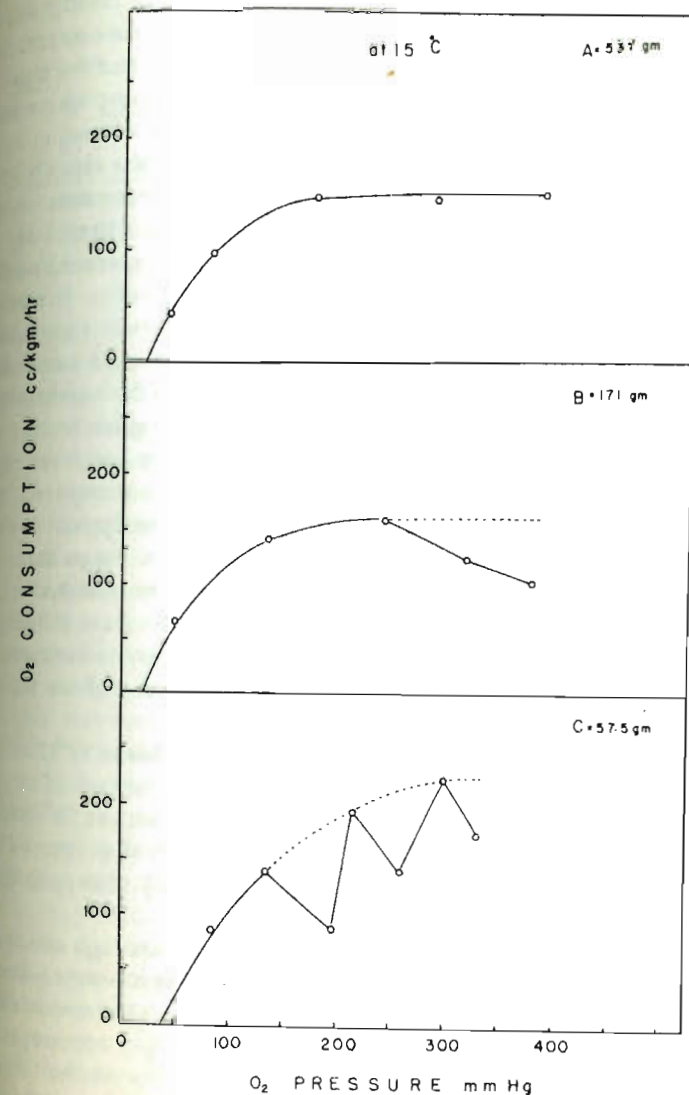


FIGURE 1. Data of active metabolism at 15°C. Panel A represents an ideal case. Panels B and C show instances where oxygen consumption varied and where the highest rate obtained was taken as the active metabolic rate.

doubt that mere handling of fish is not always enough to make them respire maximally, and that in order to obtain this value the fish have to be forced to swim and exert themselves in these experimental conditions. Panel A shows the ideal course of events. In the experiment represented here, there was a steady rate of oxygen consumption, termed the non-dependent phase, down to a point, termed the critical point, where oxygen pressure in the environment began to restrict the rate of oxygen uptake. This was followed by a dependent phase in which the rate dropped as a function of the partial pressure of oxygen in the environment. About 75 per cent of the experiments conformed to the above description at each level of temperature. The remaining experiments however showed divergences of the types displayed in Panels B and C. However it was generally observed that as the critical zone of respiration was approached, or in the critical zone itself, the fish apparently became more excited and showed a high rate of respiration which was equal to the maximum rate to be expected at higher levels of oxygen or at least close to it. Therefore, the highest rate of respiration obtained in such cases was taken to be the maximum rate when oxygen was not limiting consumption. On rare occasions when the result did not lend itself to this analysis, it was simply discarded. In all cases activity dropped rapidly as the partial pressure of oxygen in the medium was nearing levels known (Graham, 1949) to be lethal. At this stage, as was recorded by Van Dam (1938), the depth and frequency of breathing movements were very pronounced, and the rate of fall in oxygen consumption did not show any of the fluctuation noted in the non-dependent phase.

Use of oxygenated water. Experiments with larger fish at 10°C. showed that they were already dependent on the partial pressure of oxygen in the medium at air saturation. Therefore for experiments at 15° and 20°C. the water used was saturated up to partial pressure of oxygen of about 300 mm. Hg. in order to obtain a maximum steady of oxygen uptake.

Wiebe (1933) and Leiner (1938) have demonstrated that high concentration of oxygen in the medium tends to reduce the rate of oxygen consumption in fish. It will be noticed from Figure 1 that in the speckled trout high oxygen pressures did not affect the rate of oxygen consumption particularly when the fish were exerting maximally. However the characteristic variability in the respiratory pattern, such as those displayed in Panels B and C in the same figure, probably indicates that there was no uniformity in the effect of high concentrations of oxygen and much of the respiratory rate depended upon the degree of exertion on the part of the fish.

Group readings. As in the experiment on standard metabolism, fish in the series of active metabolism experiments were also used both singly and in groups, but the majority of experiments were with individual fish. One of the drawbacks to using them in groups is that all the fish could not be kept uniformly active, and there was therefore no uniformity in the respiratory rate as far as ability to consume their maximum was concerned.

Other precautions. Other precautions observed in these experiments were concerned with the duration of the experiment, and with changes in the quality of the water in the chamber. In order to lessen the effects of fatigue in complicating respiration, the duration of the experiment was limited to a maximum of four to five hours. This period was chosen arbitrarily and from experience. This limit to the maximum period was achieved by manipulating the volume of oxygen available for respiration by the degree of inflation of the gasket or by simply pushing the gasket deeper or raising it up further or by using glass marbles to displace water. That the duration so chosen was very satisfactory was seen in the fact that, in almost all cases, cessation of activity resulted primarily from lack of oxygen in the environment rather than from any other cause. In extended experiments, most fish swam very well until they turned over on their sides as a result of lack of oxygen. It is not suggested however that there was no effect of fatigue whatsoever.

As the volume of water drawn out for sampling was only 100 cc., no regular measurement of rise in the carbon dioxide concentration in the chamber was made. However, the hydrogen-ion measurements made regularly showed that at the end of each experiment there was a fall of only 0.5 of a pH unit on an average. The lowest pH reading recorded at the end of any experiment was 7.3, which corresponds to about 16-18 p.p.m. CO₂ at an alkalinity of 202 p.p.m. (as carbonate of lime) according to the table given by Theroux, Eldridge, and Mallmann (1943). The highest initial pH reading noted was 8.01.

Since the experiments on active metabolism were designed to study also the size-temperature relationship under falling oxygen pressures, they were continued until the partial pressure of oxygen approached the tolerance limits. At the conclusion of the experiments the fish were weighed and the volume of water in the chamber was measured. The rate of oxygen consumption was calculated from the rate of depletion of oxygen in the chamber per unit time, and expressed in the same way the standard rates were expressed. At each sampling the oxygen concentration of the water introduced was also measured so as to correct for the amount of oxygen thus added to the water in the chamber. The results

obtained in each experiment were plotted in the manner shown in Figure 1 and displayed also by Graham (1949) and described earlier by Hall (1929), Keys (1930), and Lindroth (1940).

Corrections to data. The efficiency of the gasket as a seal for the chamber was also determined. Experiments were run without fish but with the chamber filled with water very low in oxygen. It was found that in the larger chamber hardly any contamination was taking place through the gasket and no correction was applied to the final data from experiments carried out in it. In the smaller chamber, however, a measurable contamination took place when the partial pressure of oxygen in the chamber was below 35 mm. Hg. or above 380 mm. Hg. A correction figure of 0.2 cc./hour which was found by observation was therefore applied where necessary to the final data obtained from it.

Trial experiments were done with dye solutions to study the extent and nature of mixing taking place in the chambers at each sampling; i.e., whether the water drawn out represented an uncontaminated sample of water in the chamber alone or whether it contained in addition portions of water entering from the graduated cylinder at each sampling. It was found that, in the case of the smaller chamber which had its outlet located at the bottom, the sample was a true sample of the water in the chamber and did not contain any of the water coming into the chamber, from the graduated cylinder. In the case of the larger chamber, which unfortunately had its outlet halfway up the side of the outer wall, the sample did show traces of the water introduced during each sampling. The degree of contamination was accurately determined for a volume of 17 litres, which was the average amount of water in the chamber during an experiment; the error was insignificant and has been neglected.

RESULTS

Standard metabolism

Basic data. The data obtained from this series of experiments carried out at 5°, 10°, 15°, and 20°C. respectively are given in Figure 2. The data on which this figure is based, together with all other data pertinent to the investigation, are deposited in the Library of the University of Toronto as an appendix to a Ph.D. thesis (Job, 1954). In the figure the data are plotted on a double logarithmic grid. The lines of best fit were drawn according to the principle of least squares, assuming the respiratory rates only to be in error. Fiducial limits of 99 per cent were drawn to this figure according to the method described by Bliss (1952).

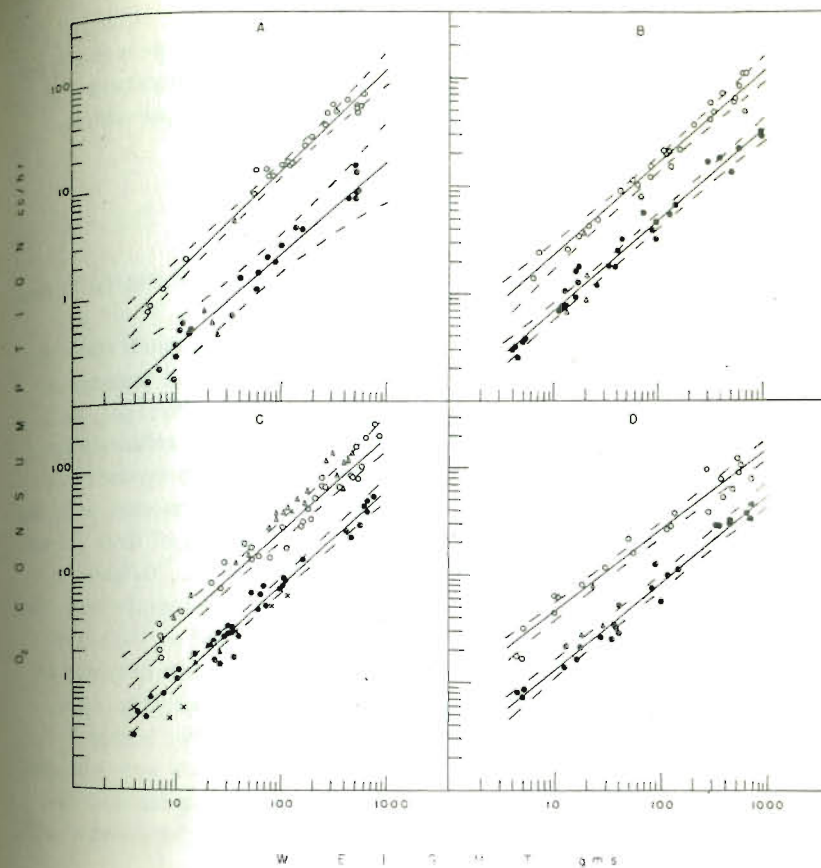


FIGURE 2. Data of standard and active metabolic rates measured at 5°, 10°, 15° and 20°C. (panels A - C respectively). Standard metabolism - closed circles, active - open circles. Lines of best fit were drawn according to the principle of least squares. Fiducial limits for the 99 per cent level are shown in broken lines. Each point represents an individual experiment. Graham's data are shown by closed and open triangles but were not included in calculating the lines of best fit. In panel C crosses represent determinations of standard metabolism made on groups.

Included in this figure are also data (triangles) obtained by Graham (1949) so that these may be discussed later.

It will be noted that the data in this transformation satisfactorily fit straight lines and that the rate of oxygen consumption per fish increases with increasing weight. The slopes obtained for these lines were 0.8562

at 5°C., 0.8489 at 10°C., 0.8469 at 15°C., and 0.8015 at 20°C. There was thus a fair degree of parallelism in the rate of gain in oxygen consumption with increasing weight at the different temperatures. However there was also a slight but progressive fall in the slopes with increasing temperature.

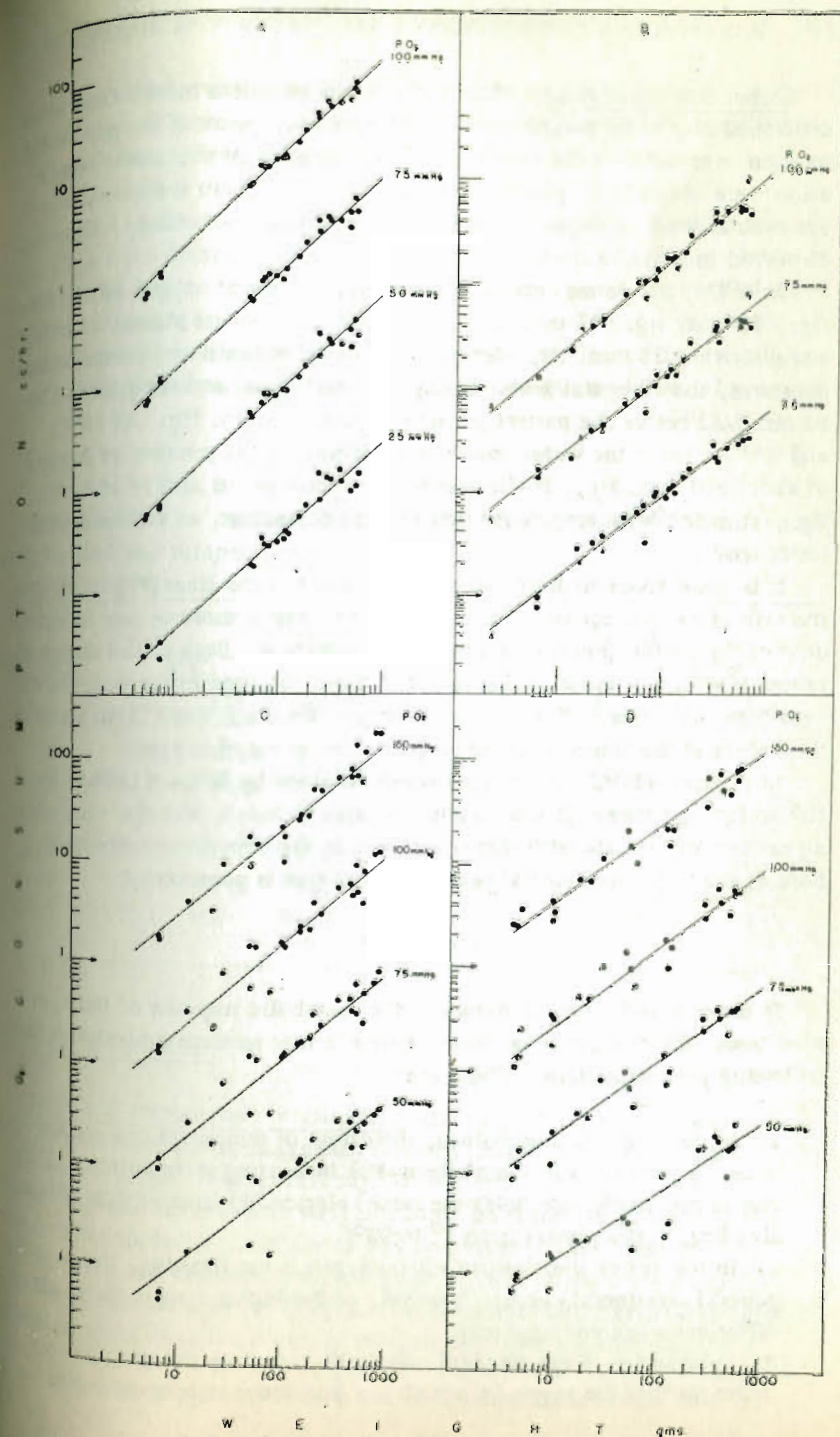
Active metabolism

The data obtained from this series of experiments are treated in two parts.

Non-dependent metabolism. These measurements, taken when the rate of oxygen consumption is not restricted by the partial pressure of oxygen in the water, are also plotted in Figure 2 (open circles). It is evident that more or less the same size and temperature relationships occur in these cases also. However, there is a greater progressive decrease in the slopes with increasing temperature in comparison with that suggested by the standard metabolism lines. The slopes of lines for active metabolism were 0.9425 at 5°C., 0.8625 at 10°C., 0.8509 at 15°C., and 0.7502 at 20°C., In Figure 2, the active metabolism data at 15°C. obtained by Graham (unpublished) are plotted on the respective line (triangles), and it will be noticed that the points obtained by her, especially for fish weighing over a 100 gm., are slightly higher than those obtained in this investigation. This is possibly because of the magnitude of correction applied to her results, which were obtained with a floating lid for the apparatus, prior to the development of the rubber gasket. In addition, her published data are also included at all temperatures.

Both wild and hatchery fish were used in the present experiments but, since no difference was seen between their performance, they are both designated by open circles. A similar observation was made by Kerr (1953) on salmon who also noted no difference between hatchery and wild fish.

FIGURE 3. Data of dependent active metabolism at various partial pressures of oxygen and measured at 5°C. (A), 10°C. (B), 15°C. (C), 20°C. (D). At the upper end of each line is indicated the corresponding partial pressure of oxygen. The lines of best fit were drawn according to the principle of least squares. The arrows along the ordinate indicate the logarithmic cycle corresponding to the respective lines. The triangles in panel B are points obtained by Shepard 1954.



Dependent metabolism. The experiments on active metabolism were continued also under conditions when the partial pressure of oxygen in the medium was limiting the rate of uptake. The data on dependent respiration were obtained by plotting the values obtained from individual curves such as those in Figure 1 and interpolating where necessary. They are displayed in Figure 3.

At 5°C., the points obtained at partial pressures of oxygen of 25 mm. Hg., 50 mm. Hg., 75 mm. Hg., and 100 mm. Hg. are shown. At 10°C. and above the 25 mm. Hg., level could not be shown since, at these temperatures, the asphyxial levels of oxygen were higher and the fish had to be removed before the partial pressure reached 25 mm. Hg. At 15°C. and 20°C., when the water used had an initial partial pressure of oxygen of about 300 mm. Hg., it was possible to obtain points also at 150 mm. Hg., at which level respiration was already dependent, as well as at the lower levels.

It is quite apparent from the parallel nature of the lines (Figure 3) that the rate of oxygen consumption in relation to size is more or less independent of the partial pressure at any one temperature. Each of the slopes obtained is within or close to the values of those obtained in the non-dependent maximal rates at the respective temperatures and there is no trend in the values of the slopes at different partial pressures of oxygen.

In Figure 3 (10°C.) points (triangles) obtained by Shepard (1954) for fish weighing between 2 and 25 gm. are also included, and the very close agreement of his data with slopes obtained in the experiment reported here at the respective partial pressures of oxygen is noteworthy.

DISCUSSION

In order to interpret the nature of the metabolic response of the speckled trout, the discussion has been treated in four sections embodying the following generalizations. These are:

1. In the standard metabolism, the effect of temperature is to produce a general rise in metabolism with increasing temperature. This rise in metabolic rate holds the same relationship irrespective of body size over temperatures from 5° to 20°C.
2. In the active metabolism when oxygen is not limiting, the same general relationship holds; however, at the higher temperatures size differences become apparent.
3. Subtraction of the standard metabolic rate from the active rate indicates that the scope for activity or performance of speckled trout

under various environmental conditions such as temperature is not the same for all sizes and that the smaller fish are better able to withstand the effects of higher temperature.

In order to illustrate these generalizations as clearly as possible the basic data have been treated by taking the mean metabolic rates - both standard and active - from the regression lines in Figure 2 for each of six weights, viz. 5, 15, 45, 135, 405, and 1000 gm. taken at logarithmic intervals except for the last group which was the maximum size investigated. The mean values for these type-sizes are given in Table I.

TABLE I

Mean values for standard and non-dependent active metabolism according to size and temperature.

| Wt. gm. | Oxygen consumption in cc./hr. at | | | | | | | |
|---------|----------------------------------|------|-------|------|-------|------|-------|------|
| | 5°C. | | 10°C. | | 15°C. | | 20°C. | |
| | Std. | Act. | Std. | Act. | Std. | Act. | Std. | Act. |
| 5 | 0.19 | 0.94 | 0.39 | 1.32 | 0.57 | 1.85 | 0.76 | 2.70 |
| 15 | 0.49 | 2.60 | 0.99 | 3.50 | 1.45 | 4.65 | 1.86 | 6.30 |
| 45 | 1.27 | 7.00 | 2.50 | 8.80 | 3.60 | 11.2 | 4.50 | 14.2 |
| 135 | 3.22 | 20.0 | 6.40 | 23.7 | 9.30 | 28.0 | 10.8 | 32.0 |
| 405 | 8.20 | 51.2 | 15.5 | 59.0 | 22.7 | 68.0 | 26.0 | 74.0 |
| 1000 | 17.5 | 126 | 34.8 | 134 | 48.0 | 145 | 54.1 | 150 |

Standard metabolism

Size and temperature relationship. It is an oft-repeated observation that the metabolism of an organism is accelerated when its temperature is elevated, e.g., Heilbrun (1943), Prosser *et al.* (1950). Various theories to explain this effect as well as various units for measuring this increment by applying principles of thermodynamics have been offered. Their merits and demerits from the point of view of the intact organism have been discussed by Fry (1947). But considerable differences in interpretation exist as to the effect of temperature upon the metabolism of animals of different sizes. One of the difficulties is the lack of adequate data. Further, the interpretation has been generalized on the basis of

absolute response rather than of proportionate response.

Figure 4 gives, in a semilogarithmic plot, the relationship of tempera-

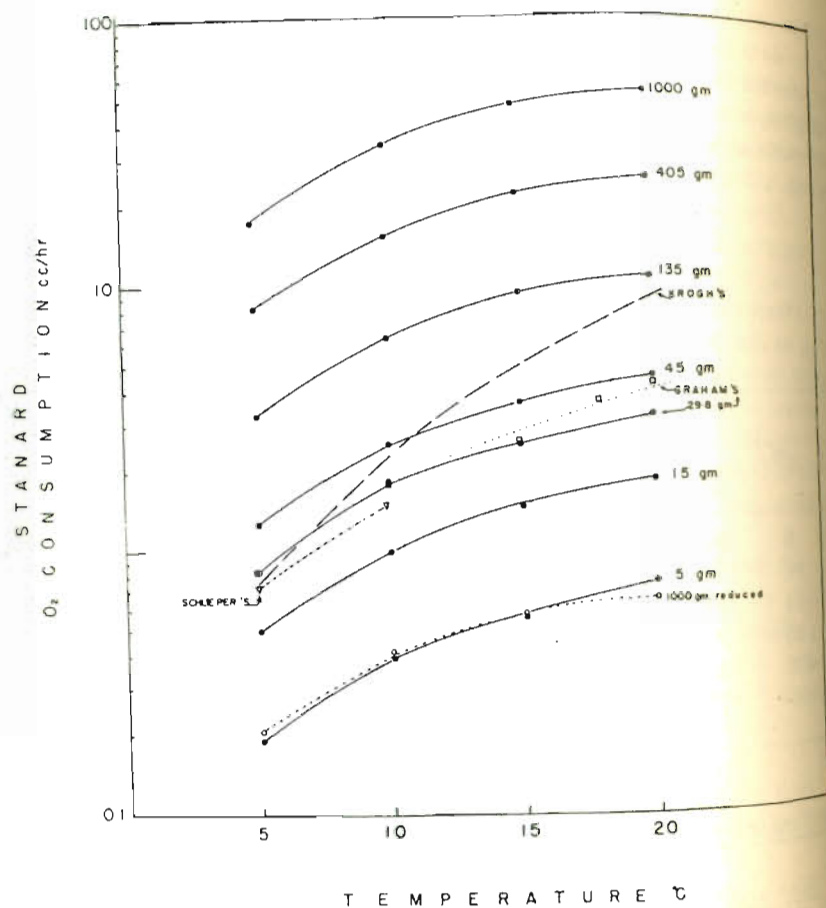


FIGURE 4. Size and temperature relationship in standard metabolism. The respective weight of the fish is given at the end of each curve. The broken line represents Krogh's standard curve for goldfish plotted to scale. Open circles represent the points for a 1000 gm. fish reduced by a factor in order to compare them with the points for the 5 gm. fish. Squares are Graham's data (1949) for fish of an average weight of 28.9 gm. Triangles are Schlieper's data for 5 gm. fish.

ture and standard metabolism according to the representative weight classes. The rate of oxygen consumption shows a continuous rise from 5° to 20°C. and the parallel nature of the curves in the figure shows that the proportional rate of gain in the oxygen consumption with increasing temperature is almost the same irrespective of the size of the fish.

There is, however, a slight reduction in relative response in the larger fish. For the sake of comparison, the curve for the 1000 gm. fish was reduced by multiplying the values by a constant of 0.015, which superimposed this curve over the curve for the 5 gm. fish. It will be noticed that the curve for the large fish is a little flatter, showing about 15 per cent less rise at 20°C. than does that for the small fish.

The similarity in proportionate response of the standard metabolic rate to temperature displayed by the speckled trout is probably a general phenomenon. For example, the data of Wells (1935b) apparently show the same type of response in *Fundulus parvipinnis*, although his technique somewhat confuses the interpretation. For a third species of fish, *Pungitius pungitius*, Scholander et al. (1953) show data which similarly indicate the same proportionate response in metabolic rate which increase in temperature, for individuals of different size. Yet another indication of the constancy of the proportionate response of standard metabolism to change in temperature in fish is given by the data for the goldfish by Ege and Krogh (1914), Fry and Hart (1948), Gardner, King and Powers (1922).

In the Phylum Arthropoda, the same response has been reported by two authors. Müller (1942a) demonstrated that the stick insect *Dixippus morosus* showed the same proportionate response in metabolic rate over the weight range of 60-100 mgm. at temperatures of 20° and 25°C. Edwards (1946) has provided a series of observations on three arthropods. His data are also in concordance with the other observations reported above, and appear the most extensive available for comparison with the data for the speckled trout.

For this reason and because Edwards did not himself treat them from this point of view, his data for *Melanotus communis*, the click beetle, for specimens weighing 40, 50, and 70 mgm., have been plotted for comparison on a semilogarithmic grid in Figure 5. The close parallelism of the lines is obvious, including a drop at 27°C. which one is inclined to regard as being probably an experimental incident. Prosser et al. (1950) have also used this figure of Edwards' in the unmodified form, but apparently have not recognized the significance of the proportionate response.

Specificity in response to temperature. Comparison of the effect of temperature on standard metabolism of various species on a semilogarith-

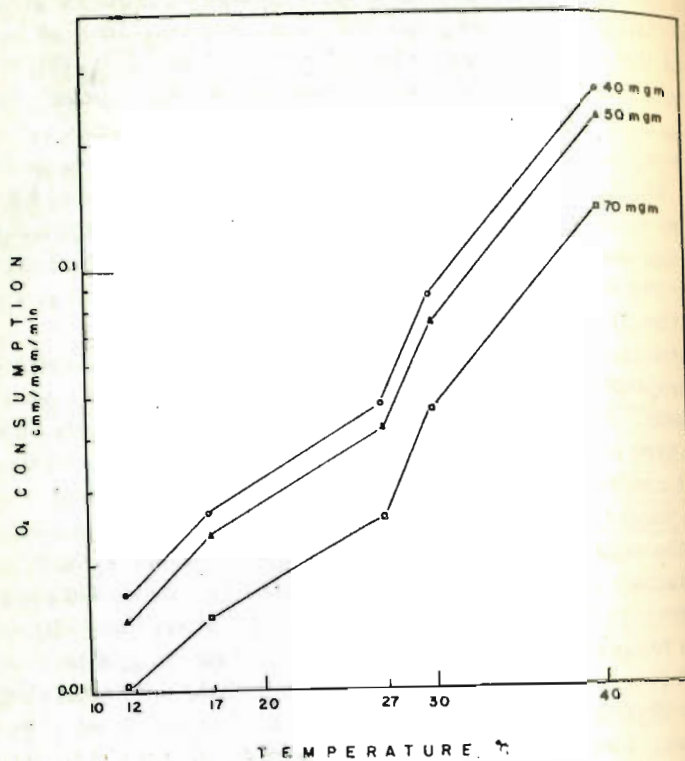


FIGURE 5. Size and temperature response of standard metabolism in *Melanotus communis* (click beetle). Data of Edwards (1946) replotted as the logarithm of oxygen consumption against temperature. At the upper end of the lines are given the respective weights of the specimens used. Note that oxygen consumption here is expressed in terms of unit weight.

mic basis suggests that probably species vary in their response to temperature in this respect.

It was mentioned above that stability of response of metabolism to temperature occurred in the goldfish, as was pointed out by Fry and Hart (1948). The data obtained from the speckled trout provide a second instance suggesting the stability of metabolic response in another species of fish. Two other workers, Graham (1949) and Schlieper (1951), offer data which are in general concordance with the author's as regards slope except that Graham's two upper points diverge from the author's; this agreement is displayed in Figure 4 where their points are also plotted.

On the other hand, while there is concordance in the metabolic response to temperature within the species, considerable difference exists between species as is indicated by the nature of the slopes of the curves for the goldfish and speckled trout. It will be seen in Figure 4 that Krogh's standard curve for goldfish (Ege and Krogh, 1914) does not fit any of the curves for speckled trout and it is obvious therefore that such standards cannot be universally applied to interspecific comparisons and that to this extent there is a specificity in the metabolic response to temperature.

Size and standard metabolism. Since the relation between temperature and metabolic rate showed only a minor variation in the response between individuals of different sizes, the relation of size to the standard metabolic rate can be discussed independent of temperature, as indeed it has often been in the past without actual experimental proof.

Bertalanffy (1941, 1951), on the basis of the magnitude of the metabolic rate in relation to body size, classified animals into three major groups of metabolic types. He uses the slope of a straight line fitted to data plotted as the logarithm of metabolic rate against the logarithm of body weight (cf. Huxley, 1932). The groups he considers are: (1) respiration surface proportional, the allometric line showing a slope of $2/3$ ($b = 0.67$); (2) respiration weight proportional ($b = 1$); and (3) an intermediate group with neither surface nor weight proportionality ($b > 0.67$ and < 1.0). According to this classification, the response of the speckled trout places it in the third group, since the slopes of the weight-metabolic rate lines, Figure 2, are between 0.8 and 0.9.

The response for the speckled trout is in disagreement with the classification given for another species of fish, the guppy *Lebistes reticulatus*, investigated by Bertalanffy and his pupil, Müller (1942b), which is placed in the surface proportional group. However observations by Scholander and his colleagues (1953) for both arctic and tropical fishes reduced to a standard rate at 0° and 30°C . followed a regression line in which $b = 0.85$, a value close to that obtained here for the speckled trout. Even though not strictly comparable, the data for *Chanos chanos*, obtained by Viswanathan and Tampi (1952), also fall close to this value. Zeuthen's (1947) data for various species of fish under a similar treatment gave a line in which $b = 0.78$. Well's (1935b) data, however, gave for *Fundulus parvipinnis* a slope of 0.59, which is much lower than those referred to above. Therefore it seems rather likely that the Pisces fall into at least two of Bertalanffy's metabolic types, some being of the first group, i.e., surface proportional and others of an intermediate type, neither surface nor weight proportional.

Active metabolism

Size and temperature relationship. There is a continuous rise in the active metabolic rate with increasing temperature from 5° to 20°C. However, unlike the case in the response of standard metabolism, a noticeable difference with respect to size exists in the proportionate rate of increase in active metabolism in relation to increase in temperature. The active metabolic rate of large fish does not increase with increasing temperature to the same relative extent as does that of small fish. In Figure 6 the effect of temperature upon the active metabolism of the speckled trout is shown according to the six size groups adopted above, on a semilogarithmic grid. The difference in the proportionate gain in metabolic rate with increasing temperature is seen especially when the line for the 5 gm. fish is compared with that of the 1000 gm. fish. The active metabolic rate in the 5 gm. fish increases from 0.94 to 2.7 cc./hr. or 2.8 times, whereas the 1000 gm. fish shows only an increase from 120 to 160 cc./hr. or 1.3 times. Fish of intermediate size show an intermediate response between the extremes cited above. The data obtained by Graham (1949) for fish of an average weight of 29.8 gm. are included in the figure and show general agreement with the author's data except that they are somewhat higher.

Size and active metabolism. Although there is in the weight-active metabolic rate relationship a greater progressive change with increasing temperature, general characteristics of the slope may be discussed independent of temperature. The slopes obtained for active metabolism were: 0.94 at 5°C., 0.86 at 10°C., 0.85 at 15°C., and 0.75 at 20°C. Thus even at the highest temperature in the series, the slope for active metabolism is greater than 0.67, the slope required by the surface law, which confirms what was noted with reference to standard metabolism.

Non-conformity to the surface rule occurs in fish also in the growth and capacity of such organs as the gills and heart, which are most intimately involved in the support of the performance of muscular activity. Price (1931), who studied the growth and gill development of the small-mouth black bass, obtained a body weight - gill surface correlation with a slope of 0.79. Hart (1945), in a similar treatment on the stroke output of the heart of various species of freshwater fishes, obtained slopes which though slightly different from each other, were yet of the same order. The slope he obtained for largemouth bass and chubsucker was 0.83 and for eel 0.84.

Size and dependent metabolism. In the study of active metabolism the observations on temperature and size relationships were extended to

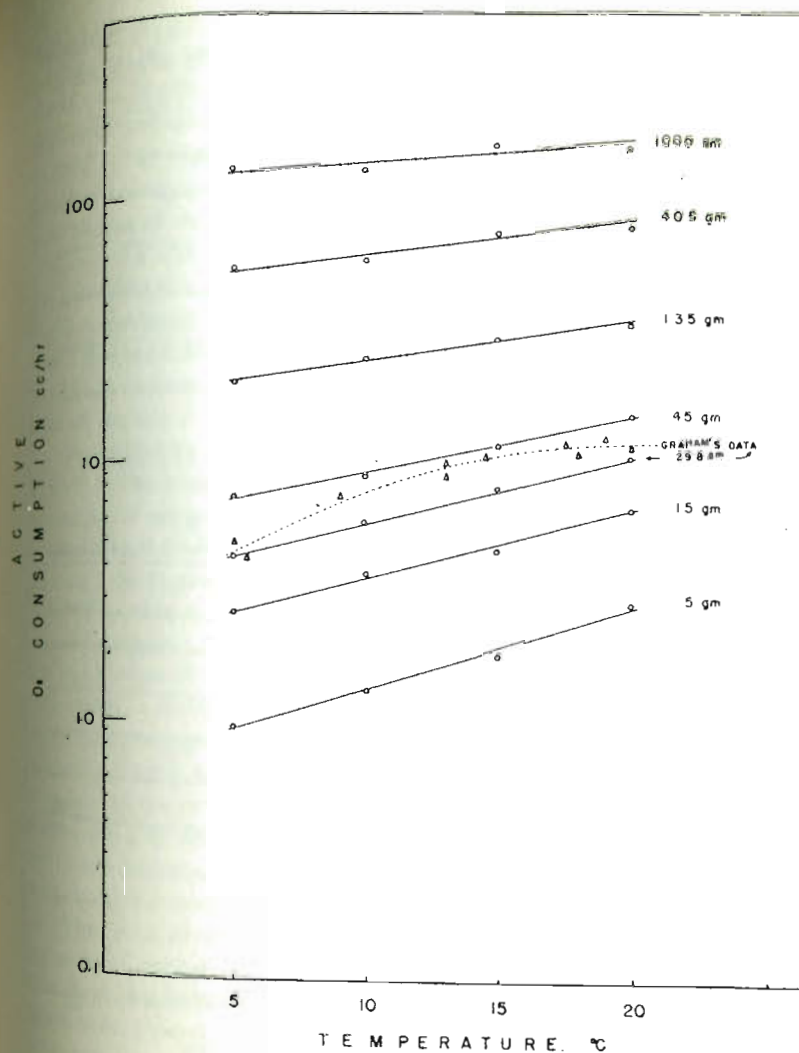


FIGURE 6. Illustration of size and temperature relationship in active metabolism when oxygen is not limiting. The respective weight of fish is given at the upper end of each line. Triangles are data obtained by Graham (1949) for fish of an average weight of 29.8 gm.

conditions where the partial pressure of oxygen in the environment limits the rate of oxygen consumption. It has already been shown (Figure 3) that the slopes obtained at the different temperatures and various partial

pressures maintained the same order of relationship to the slopes obtained at the corresponding temperatures when the partial pressure of oxygen in

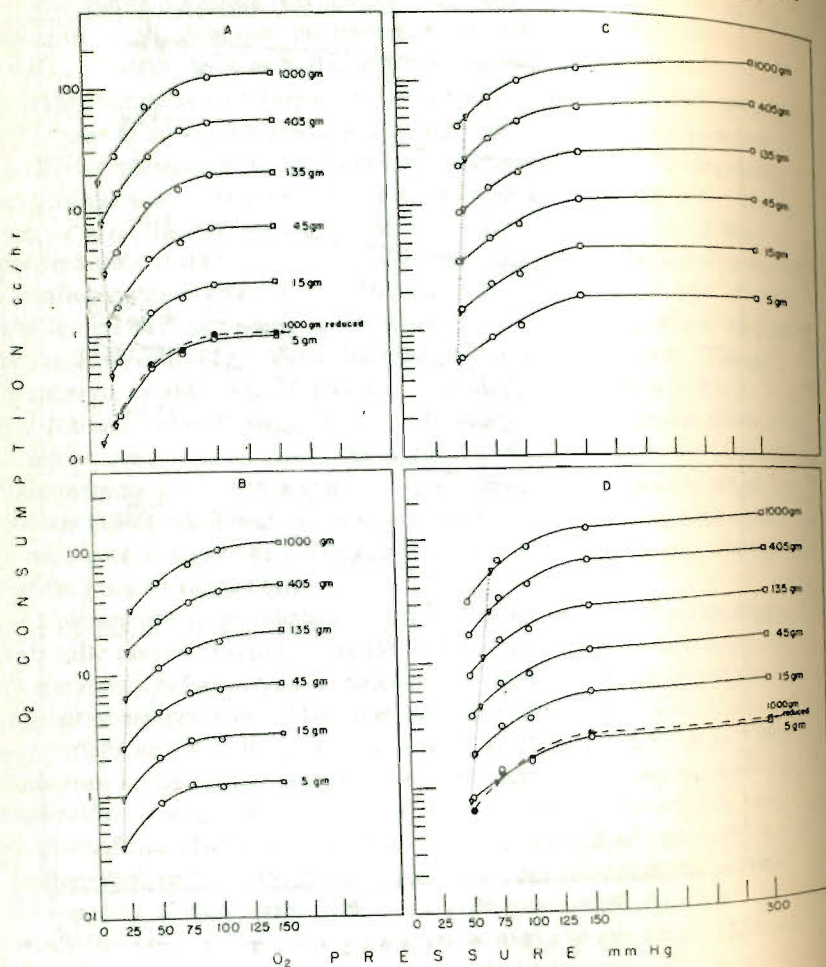


FIGURE 7. Illustration of size and dependent respiration at various partial pressures of oxygen at 5°C (A), 10°C (B), 15°C (C) and 20°C. (D). The weight of fish is given at the upper end of each curve. The broken lines in Panels A and D indicate the curve for the 1000 gm. fish reduced by a factor for comparison with the curve for the 5 gm. fish. Squares indicate the maximum non-dependent rates. Triangles indicate the standard rates. The dotted line connecting the triangles in each panel represents the tolerance level for low oxygen at the respective temperatures.

the water did not restrict its consumption by the fish. To make this comparison on the basis of the six groups set up for consideration in earlier sections, the logarithms of the respective rates are plotted against the oxygen pressures in Figure 7 the data being taken from the regression lines in Figure 3. In Figure 7, the respective non-dependent maximum rates of oxygen consumption (squares) as well as the standard rates (triangles) are also shown at the two extremities of each of the curves. In Panels A (for 5°C.) and D (for 20°C.), at the two extremes of temperature, the curves for the 1000 gm. fish, reduced by multiplying by factors of 0.007 and 0.02 respectively, are drawn over the curves of the 5 gm. fish. This further illustrates that the relative rate of oxygen consumption with reference to size is essentially the same for all sizes irrespective of the partial pressure of oxygen.

Temperature and dependent metabolism. Since the proportionate rate of fall in the respiratory rates at any one temperature under various partial pressures of oxygen is more or less the same for all sizes (cf. Figure 7, Panels A and D), the effect of temperature can be discussed independent of size. In Figure 8 are displayed the data for speckled trout weighing 45 gm. The rate of oxygen consumption is plotted against the partial pressure of oxygen. Below a partial pressure of oxygen of about 100 mm. Hg. all the curves for the various temperatures show the same general trend. The general trend recorded by Graham (1949) over this region of the curve (closed triangles) is shown for comparison; the agreement with the author's data is limited to this extent, since there was no consistent relationship of the remaining part of the curves with the corresponding curves above the 100 mm. Hg. zone of partial pressure of oxygen obtained by her. A consistent relationship as displayed by Graham for the speckled trout has been recorded for the goldfish by Fry and Hart (1948).

The general effect of temperature on the level at which the partial pressure of oxygen restricts the respiratory rate can be verified from Figure 7 without particular attention to size. In Panel A (5°C.) it will be noticed that dependency of the respiratory rate does not commence until 100 mm. Hg. partial pressure of oxygen is reached. However, in the other three panels dependency is noticeable even at partial pressures of 150 mm. Hg. and is observed up to 300 mm. Hg. at the two higher temperatures.

Combination of standard and active metabolism

The level of no excess activity. A feature of the dependent stages of respiration is the point at which the maximum rate of uptake corresponds

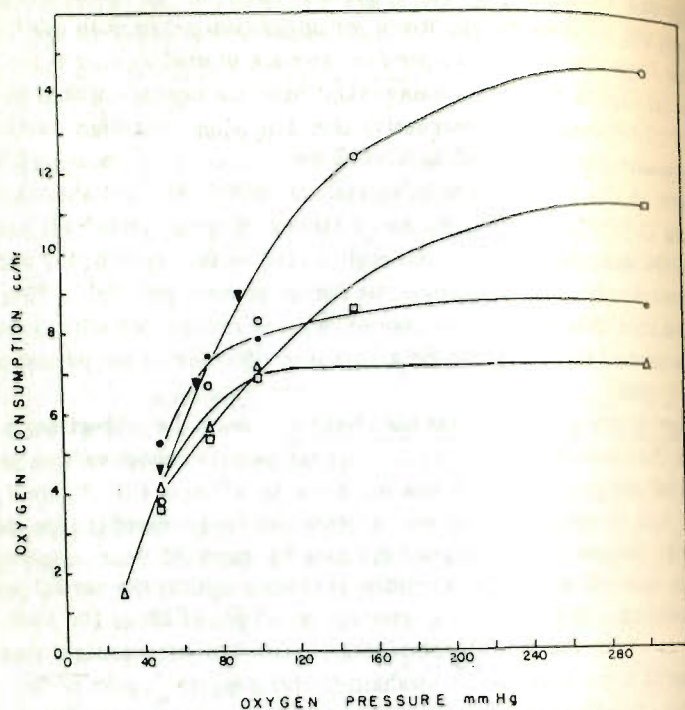


FIGURE 8. Illustration of the effect of temperature upon dependent active metabolism. The oxygen consumption of a 45 gm. fish is plotted against the partial pressure of oxygen. Open triangles are points obtained at 5°C., closed circles 10°C., squares at 15°C., open circles 20°C. Closed triangles are mean values from Graham (1949) for maximum rates of uptake at partial pressures of oxygen below 100 mm. Hg. at various temperatures.

to the standard oxygen consumption. This level of partial pressure of oxygen is elsewhere termed the level of no excess activity, Lindroth (1940), Fry (1947), and Graham (1949). It marks the minimum oxygen requirement of the fish in order to maintain all the ancillary activities which are essential for the sustenance of normal life. It is a basic minimum. Any other form of activity involving expenditure of energy will therefore have to depend, within limits, upon how much extra energy is available over and above this basic requirement. In other words the performance of external work is not possible below this level, termed, therefore, the level of no excess activity.

The levels of no excess activity for the six sizes of speckled trout at the four temperatures can be derived from Figure 7. There the standard rates of oxygen consumption corresponding to each of the six sizes are plotted as triangles and connected by a dotted line. It will be noticed that the points where the dotted line intersects the curves fall against partial pressures of oxygen which show an over-all shift of the level of no excess activity with increasing temperature from about 14 to 22 mm. Hg. partial pressure of oxygen at 5°C. to about 45 to 70 mm. Hg. at 20°C. This is largely due to the increase in the standard metabolic rate with increasing temperature.

The points of intersection of the dotted line when examined groupwise show a definite effect of size in the respective partial pressures of oxygen against which they fall as well as a reversal in the order of tolerance at the two extremes of the temperature range in this investigation. At 5°C. the 5 gm. fish reaches the level of no excess activity at a partial pressure of oxygen of 20 mm. Hg. whereas a 1000 gm. fish reaches it at 14 mm. Hg. At 20°C., however, this relationship reverses, the 5 gm. fish reaching it at 47 mm. Hg. and a 1000 gm. fish reaching it at 70 mm. Hg.

Comparison of the level of no excess activity and the lethal level of oxygen. The level of no excess activity was defined earlier as the basic minimum partial pressure of oxygen required in the environment; any drop below this level would be lethal. In actual experiments there is a lag between the two levels which theoretically are one. Therefore in order to make a general comparison of the relationship of the level of no excess activity to the lethal level of oxygen for this species, Graham's (1949) data have been incorporated into this discussion in Figure 9, since no experiments on lethal level of oxygen were actually done in the present study. In Figure 9, the open circles indicate her determinations of levels of no excess activity and the closed circles the lethal levels of oxygen. The triangles show levels of no excess activity taken from Figure 7 for the type sizes.

The levels of no excess activity obtained in the present investigation fall within the general region of Graham's two types of determinations. However at the two lower temperatures the present determinations of the level of no excess activity approximate her lethal determinations. The difference does not appear to be too significant, and could possibly have happened if there were some variations between the two methods of experimentation such as differences in the degree to which the fish were held quiescent in the measurement of standard metabolism - such a difference was indeed referred to earlier (p. 6).

Scope for activity. There is yet another important correlation which

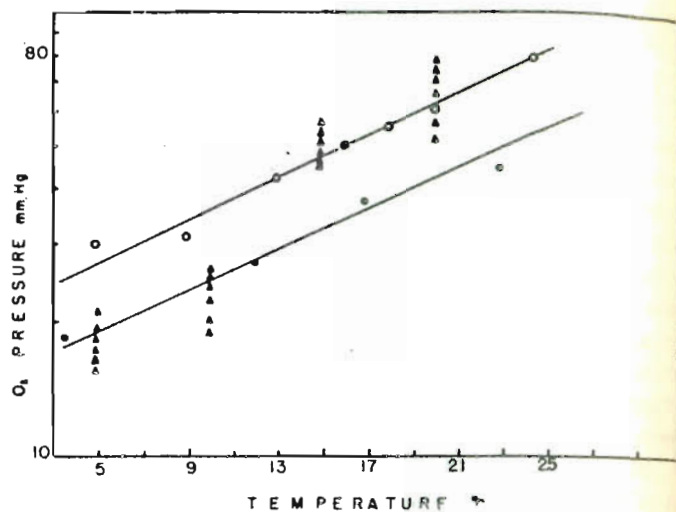


FIGURE 9. Comparison of the levels of no excess activity with those of Graham (1949) at various temperatures. Open circles are levels of no excess activity and closed circles are lethal levels of oxygen according to Graham. Triangles are the levels of no excess activity for various sizes obtained in the present investigation.

may be derived by comparing the active and standard metabolic rates. This correlation has been termed by Fry (1947) the scope for activity. As a corollary to the definition of the level of no excess activity, it can be stated that the maximum rate of oxygen consumption represents the sum total of the cost of maintaining ancillary activities as well as the amount of energy required to perform other activities. If then the actual amount of energy required to perform this extra work is to be measured or given expression, it could be obtained by subtracting the level of no excess activity i. e., the standard rate of oxygen consumption, from the maximum rate. This difference is therefore the scope for activity.

From the basic data displayed in Figures 2, 3 and 7, the scope when the partial pressure of oxygen in the environment is not limiting and when it is limiting activity can be described.

In Figure 10 is given the size-temperature relationship of the scope for activity when the partial pressure of oxygen is not limiting together with the scope at air saturation. It is very clearly seen on this semilogarithmic grid, that the tendency for the scope to increase with rising temperature becomes progressively reduced with increasing weight. In fact

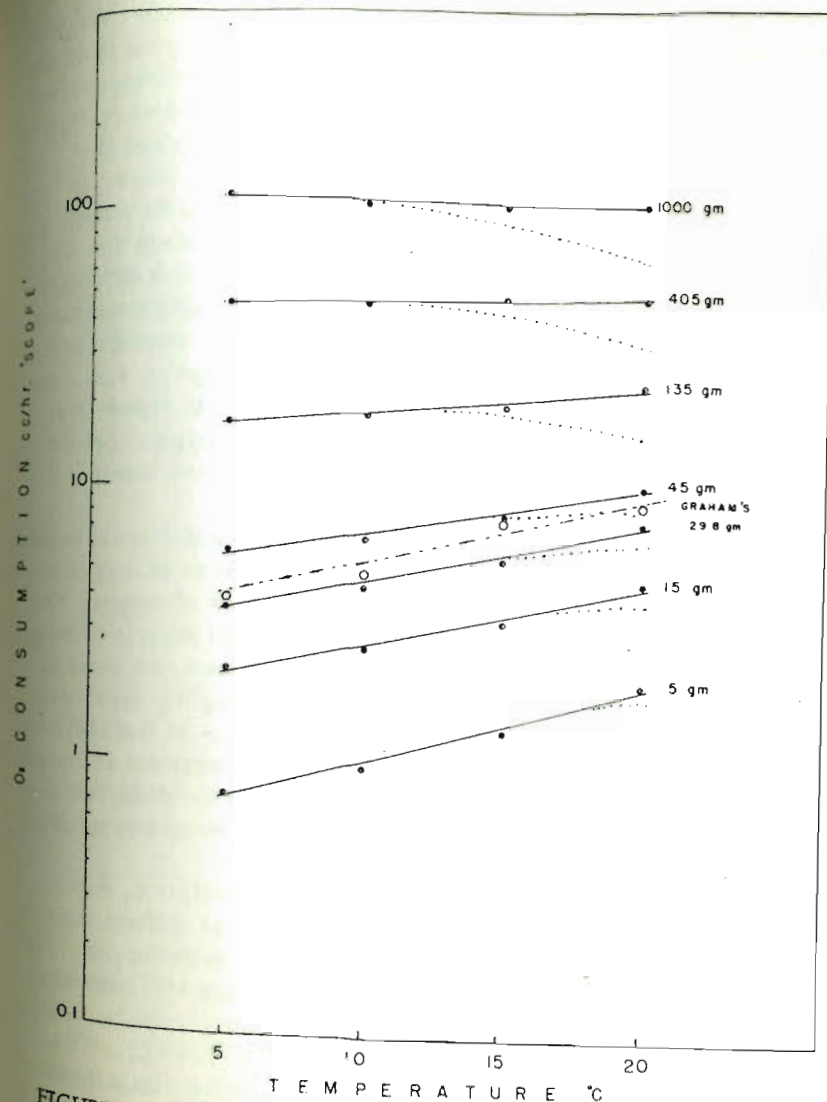


FIGURE 10. Illustration of the size-temperature relationship of the "scope for activity" when the partial pressure of oxygen is not limiting. The logarithm of oxygen consumption is shown against temperature. The weight of fish is given at one end of each line. Graham's (1949) data for fish of an average weight of 29.8 gm. are plotted as open circles for comparison. The dotted lines indicate the extent of loss in the scope when the partial pressure of oxygen is 150 mm. Hg. (near air saturation).

in the last two groups hardly any increase is noticeable and the 1000 gm. fish show a decline with rising temperature even at partial pressure of oxygen of 300 mm. Hg. At 150 mm. Hg. partial pressure of oxygen (approximately air saturation), as indicated by the dotted lines, there is a marked loss of scope in larger fish at 15° and 20°C. Data obtained by Graham (1949) are included in Figure 10 for comparison. There is a general agreement between her data and those obtained in the present investigation, if her points are fitted to a straight line, except that her values are a little higher especially at 15° and 20°C., which difference could easily be due to the different technique employed in the two cases.

In Figure 11 are shown data for the scope for activity when the partial pressure of oxygen is limiting the rate of oxygen consumption, i. e., the scope in the zone of respiratory dependence. Each line in Figure 11 represents the scope at one particular partial pressure of oxygen. For the sake of comparison, the scope lines from Figure 10 are also shown as a heavy line for the respective temperatures.

It will be noticed that at 5°C. (Panel A) there is no difference between the heavy line showing the scope when the partial pressure of oxygen is not limiting and the scope at 100 mm. Hg. partial pressure of oxygen. This indicates that at that temperature 100 mm. Hg. partial pressure of oxygen does not restrict the scope. However at 10°C. and above, the scope becomes restricted even at 100 mm. Hg. to an extent which is seen by the degree to which the heavy line becomes separated from the rest in Panels B, C and D. The levels at which the scope becomes restricted at the various temperatures follow, of course, the same order in which the levels of dependency of respiration upon the partial pressure of oxygen commence, (cf. Figure 8).

Within each temperature, over the size range investigated, except for the heaviest fish at 20°C. the response appears to be uniform and to be described by parallel straight lines on a double logarithmic plot. The slopes of these lines however, become progressively less with increasing temperature. The slopes found between scope and weight for the lines in Figure 11 are approximately as follows. 5°C. - 0.94, 10°C. - 0.94, 15°C. - 0.78, 20°C. - 0.68. At 20°C. (Panel D) when the partial pressure of oxygen is 75 mm. Hg. the linear relation for the heavier fish and breaks down and these suffer a marked loss of scope.

Routine metabolism. In measurements of respiratory metabolism the term standard metabolism has in general been used rather loosely. This is so because often in such measurements no strict attention has been paid to obtaining the lowest rate of oxygen consumption when the animal is maintained quiescent for a time sufficient to enable the investigator

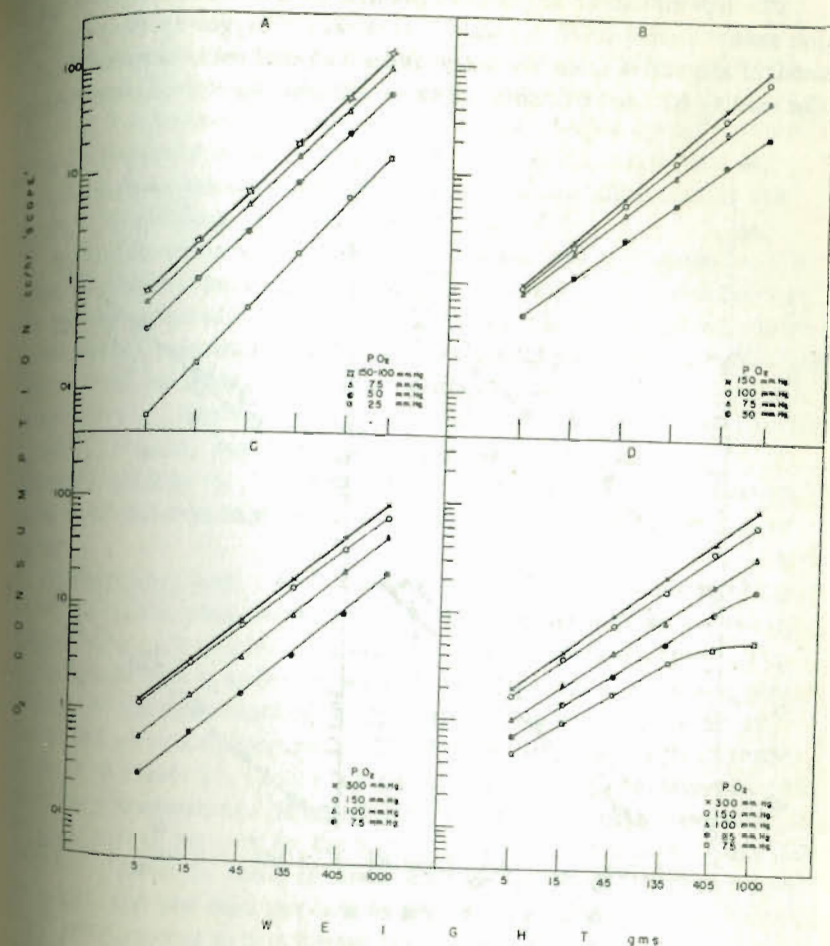


FIGURE 11. Illustration of the scope for activity at various temperatures in relation to size when the pressure of oxygen is limiting. The heavy line indicates the scope when the partial pressure of oxygen is not limiting and is included in order to illustrate the degree to which the scope is limited by the partial pressure of oxygen. The legends for the various lines are given in the bottom right-hand corner of each of the panels. Panel A for 5°C., B for 10°C., C for 15°C., D for 20°C.

to obtain it over a general metabolic rhythm that the animal may pass through. In other words such measurements have often been the record of the metabolism which the animals do as a routine.

The experiments on standard metabolism undertaken in this investigation enable a comparison of such a routine rate of oxygen uptake with the standard and active rates in order to assess the relationship between them. The reading for each individual in an experiment was plotted with the rate

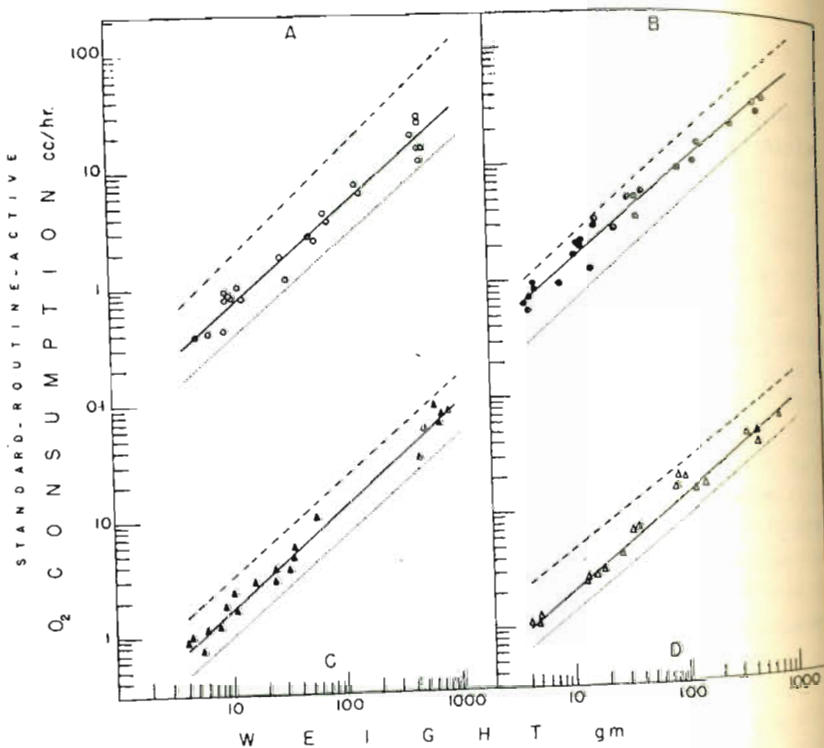


FIGURE 12. Illustration of routine (resting) metabolism at 5°C. (A), 10°C. (B), 15°C. (C), and 20°C. (D). The logarithms of standard (dotted line), routine (unbroken line), and active (broken line) rates of oxygen consumption are shown against the logarithm of weight. The routine consumption line was drawn for the points (average rate per hour) by eye.

of oxygen consumption on the ordinate and the time in hours on the abscissa. Then by counting the squares under the graph so obtained the total routine oxygen consumption was obtained. This was not an absolute estimate since the readings included in the calculation were taken from about six hours after the fish were enclosed in the respiration chamber to

the end of the 24-hour period and the fish were not in any uniform state of activity or excitement. Therefore the lines obtained for routine consumption were drawn by eye and not derived from elaborate analytical treatment. The values obtained have been plotted in Figure 12. Two features that become clear from this figure are that the routine consumption as measured is nearly 50 per cent of the active metabolism and that the slope when drawn by eye is the same as that of the active and standard metabolism at the various temperatures.

Since the slopes of the active, the standard, and the routine metabolism follow the same trend, comparative studies on metabolism, such as the general metabolic type in Bertalanffy's (1951) classification, can be made without too strict an adherence to standard procedures for obtaining nearly basal metabolic rates, as is exemplified in this work on speckled trout. Further, because of the latitude that exists for comparison between standard, routine, and active metabolism without erring too much, a treatment such as that by Zeuthen (1947, 1953) is also possible where a number of different data obtained under different conditions are compared.

Maintenance costs. An interesting observation is also available to which no significance can be attached at present for want of any comparable data. The title of this aspect is therefore only tentative. The maintenance cost is arrived at when the standard rate is taken as a percentage of the active rate of oxygen consumption for the various sizes and at the various temperatures. The data are illustrated against temperature in Figure 13. There is a general rise in the percentage rate with increasing temperature. However, it is interesting to note that at 5°C. the rate is 20.2 per cent for the 5 gm. fish and 13.9 per cent for the 1000 gm. fish. At 20°C. the order is reversed and becomes 28.1 per cent for the 5 gm. fish and 38.2 per cent for the 1000 gm. fish.

It is interesting to note further that all the lines have a definite point of intersection when the rate is approximately 32 per cent, which falls at 14°C. approximately. It has been pointed out already that the proportionate response of the standard metabolism of the various sizes of speckled trout to different temperatures is constant. Therefore any size differences noted in the above consideration are chiefly due to corresponding differences in the active metabolic rate and what proportion of extra energy is available for activity above the energy expended as standard metabolism. While not attaching too great an importance to this, it may be stated that the above further illustrates the differential size effects in the scope or maintenance of activity, and that the smaller fish are better off at 15°C. and 20°C. than at 5°C. and 10°C. whereas for the

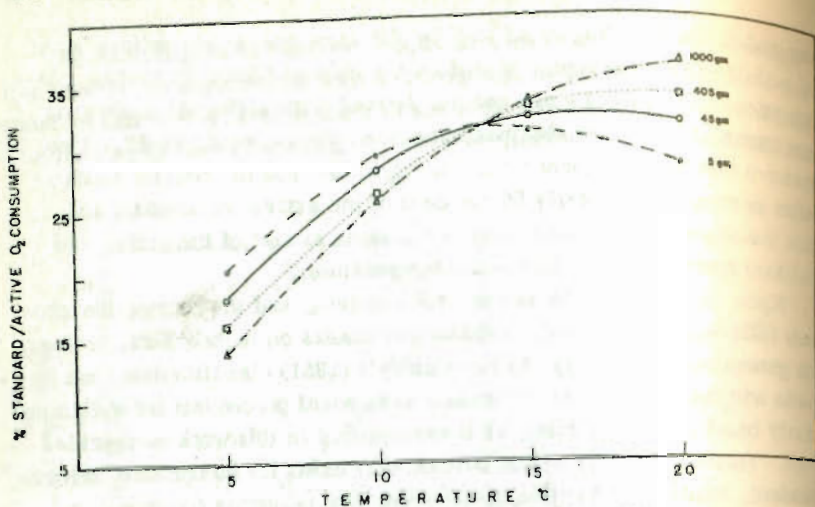


FIGURE 13. Maintenance costs - an illustration of the size-temperature relationship when the standard metabolic rate is expressed as a percentage of the active rate. The percentage rate is indicated along the ordinate and the temperature along the abscissa. The weights of the fish are given at the top end of each line.

larger fish the opposite is true.

SUMMARY

1. The oxygen consumption of the speckled trout, both wild and hatchery stocks, ranging in size from 4 gm. to 1000 gm. was measured after appropriate acclimation at 5°, 10°, 15°, and 20°C. Two measurements, viz., of a standard rate which was the minimum observed under conditions of rest and an active rate observed under conditions of steady exercise, were made. These two levels are taken to approximate respectively minimum and maximum rates of oxygen intake. The standard rate was measured with air saturation partial pressures of oxygen and the active both under high oxygen and when the oxygen partial pressure was gradually falling to near lethal levels. The active metabolic rate when the partial pressure of oxygen is not limiting uptake is termed the non-dependent phase and that when the partial pressure of oxygen is limiting uptake is termed the dependent phase.

2. The rate of oxygen consumption in relation to size was expressed by means of the equation $Y = b x^k$, where Y is the log rate of oxygen consumption, x the log of weight, b the slope of the line, and k a con-

stant. See pages 13 and 14.

3. The proportionate response of standard metabolism for a given change in temperature was essentially independent of size, over the temperature ranges investigated.

4. Within certain limits a specificity of relative response of standard metabolism to temperature exists, as is suggested by a comparison of the responses of the goldfish and the speckled trout.

5. The proportionate response of non-dependent active metabolism for a given change of temperature, showed perceptible differences with size. The gain in metabolic rate for a 5 gm. fish showed an increase of 2.3 times and a 1000 gm. fish showed an increase of only 1.3 times in the rates between 5° and 20°C. Intermediate sizes show intermediate trends.

5. The slopes obtained for the dependent phase of active metabolism in relation to size at various partial pressures of oxygen were the same as those found for the non-dependent phase at the respective temperatures. Thus the efficiency of oxygen uptake held the same relationship to weight under all partial pressures of oxygen at any one temperature.

7. The critical partial pressure of oxygen when the active oxygen uptake becomes dependent on the oxygen level lies above air saturation values at all temperatures above 5°C. for the speckled trout.

8. The difference between the active and standard rates of oxygen consumption, which is an expression of the scope for activity, varied markedly with size under various temperatures. In the non-dependent phase of active metabolism as related to standard rate, fish of 5 gm. showed a continuous rise in the scope with increasing temperature, whereas fish of 1000 gm. registered a slight but steady decline from 5° to 20°C. Intermediate groups showed intermediate scopes. In the dependent phase of active respiration the same size relationship was noted in a more pronounced manner.

9. The partial pressure of oxygen at which the rate of active oxygen consumption equals the standard rate marks the tolerance limit and is called the level of no excess activity. The speckled trout showed a very marked size and temperature relationship in the level of no excess activity. Apart from a general shift in the level with rising temperature, there was a reversal in the size relationship at the two extremities of the temperature range. At 5°C. a 5 gm. fish reached this level when the partial pressure of oxygen was 22 mm. Hg. and a 1000 gm. fish when it was 14 mm. Hg. At 20°C. the level for a 5 gm. fish was 45 mm. Hg. partial pressure of oxygen and for the 1000 gm. fish it was 70 mm. Hg.

10. Another correlation which showed a reversal in the sequences according to size and with increasing temperature was in the rate of standard metabolism when the latter was expressed as a percentage of the active. Apart from a general rise in the rate with increasing temperature, at 5°C. a 5 gm. fish had 20.2 per cent and a 1000 gm. fish 13.9 per cent rate, these rates became 28.1 per cent and 36.2 per cent respectively at 20°C. The curves for all sizes intersected at approximately 14°C. when the rate was 32 per cent.

REFERENCES

- Belding, D. V. 1929. The respiratory movements of a fish as an indicator of a toxic environment. *Trans. Am. Fish. Soc.* 59: 238-245.
- Bertalanffy, L. von. 1941. Stoffwechseltypen und Wachstumstypen: Untersuchungen über die Gesetzmäßigkeit des Wachstums. VII. *Biologische Zentralblatt* 61: 510-532.
- _____. 1949. Problems of organic growth. *Nature* 163: 156
- _____. 1951. Metabolic types and growth types. *Am. Nat.* 85: 111-117.
- Black, E. C., F. E. J. Fry, and W. J. Scott. 1939. Maximum rates of oxygen transport for certain fresh water fishes. *Anat. Rec.* 75, Supp. 80.
- Bliss, C. I. 1952. The statistics of bioassay - with special reference to the vitamins. New York: Academic Press Inc.: 445-628.
- Brett, J. R. 1941. Tempering versus acclimation in the planting of speckled trout. *Trans. Am. Fish. Soc.* 70: 397-403.
- _____. 1952. Temperature tolerance in young Pacific salmon, genus *Onchorhynchus*. *J. Fish. Res. Bd. Can.* 9 (6): 265-323.
- Davis, H. S. 1946. Care and diseases of trout. U.S. Dept. Int., Fish & Wildlife Service, Res. Rep. 12: 1-92.
- Edwards, G. A. 1946. The influence of temperature upon the oxygen consumption of several arthropods. *J. Cell. & Comp. Physiol.* 27: 53-64.
- Ege, R., and A. Krogh. 1915. On the relation between the temperature and the respiratory exchange in fishes. *International Rev. Hydrobiol. & Hydrograph.* 7: 48-55.
- Ellis, M. M., B. A. Westfall, and M. D. Ellis. 1946. Determination of water quality. U.S. Dept. Int., Fish & Wildlife Service, Res. Rep. 9: 1-122.
- Fry, F. E. J. 1947. Effects of the environment on animal activity. *Univ. Toronto, Biol. Series no. 55; Pub. Ont. Fish. Res. Lab. no. 68: 1-62.*
- _____. 1951. Some environmental relations of the speckled trout (*Salvelinus fontinalis*). Rept. Pro. N.E. Atlantic Fish. Conference.
- Fry, F. E. J., and J. S. Hart. 1948. The relation of temperature to oxygen consumption in the goldfish. *Biol. Bull.* 94: 66-77.
- Gardner, J. A., G. King, and E. B. Powers. 1922. The respiratory exchange in freshwater fish. III. Goldfish. *Biochem. J.* 16: 523-529.
- Geng, H. 1925. Der Futterwert der natürlichen Fischnahrung. *Zeit. f. Fischerei und deren Hilfswissenschaften* 23: 137-165.
- Graham, J. M. 1949. Some effects of temperature and oxygen pressure on the metabolism and activity of the speckled trout, *Salvelinus fontinalis*. *Can. J. Res. (D)* 27: 270-288.
- Hall, F. G. 1929. The influence of varying oxygen tensions upon the rate of oxygen consumption in marine fishes. *Am. J. Physiol.* 88: 212-218.
- Hart, J. S. 1945. The circulation and respiratory tolerance of some Florida freshwater fishes. *Pro. Florida Acad. Sci.* 7 (4): 221-246.
- Heilbrunn, L. V. 1947. An outline of general physiology. 2nd ed., Philadelphia: W. B. Saunders Co. 748 pp.
- Hodgman, C. D. 1945. Handbook of chemistry and physics. 29th ed., Cleveland: Chemical Rubber Publishing Co.
- Huxley, J. S. 1932. Problems of relative growth. London: Methuen & Co. Ltd. 276 pp.
- Job, S. V. 1954. The oxygen consumption of the speckled trout (*Salvelinus fontinalis*). Ph.D. Thesis, Univ. of T., Dept. of Zool.
- Ken, J. E. 1953. Studies on fish preservation at the Contra Costa steam plant of the Pacific Gas and Electric Co. Calif. Dept. Fish and Game. *Fish. Bull.* 92: 66 pp.
- Keys, A. B. 1930. The measurement of respiratory exchange of aquatic animals. *Biol. Bull.* 59: 187-198.
- Kleiber, M. 1947. Body size and metabolic rate. *Physiol. Rev.* 27 (4): 511-541.
- Kleiner, I. S. 1948. Human biochemistry. 2nd ed., St. Louis: C. V. Mosby Co.
- Leiner, M. 1938. Die Physiologie der Fischatmung. Leipzig: Akademische Verlagsgesellschaft M. B. H. 11: 1-134.
- Lindroth, A. 1940. Sauerstoffverbrauch der Fische bei verschiedenem Sauerstoffdruck und verschiedenem Sauerstoffbedarf. *Zeit. vergleich. Physiol.* 28: 142-152.
- Lindstedt, Ph. 1914. Untersuchungen über Respiration und Stoffwechsel von Kaltblutern. *Zeit. f. Fischerei* 14.

- Müller, I. 1942a. Untersuchungen zur Gesetzmäßigkeit des Wachstums. IX. Die Abhängigkeit der Atmung von der Körpergröße bei Dixippus morosus und ihre Beziehung zum Wachstum. Zeit. vergleich. Physiol. 30: 139-144.
- _____ 1942b. Untersuchungen über die Gesetzmäßigkeit des Wachstums von Bertalanffy. VIII. Die Abhängigkeit des Stoffwechsels von der Körpergröße und der Zusammenhang von Stoffwechselformen und Wachstumstypen. Rivista di Biologia 33: 48-95.
- Needham, P. R. 1938. Trout streams. New York: Comstock Publishing House Co. 233 pp.
- Price, J. W. 1931. Growth and gill development in the small-mouthed black bass, Micropterus dolomieu, Lacépède. Stone Lab., Put-in-Bay, Ohio, Contrib. no. 4: 1-46.
- Prosser, C. L., et al. 1950. Comparative animal physiology. Philadelphia: W. B. Saunders Co. 888 pp.
- Rubner, M. 1902. Die Gesetze des Energieverbrauches bei der Ernährung. Berlin.
- Schlaifer, A. 1939. An analysis of the effect of numbers upon the oxygen consumption of Carassius auratus. Physiol. Zool. 12 (4): 381-392.
- Schlieper, C. von. 1951. Versuch einer physiologischen Analyse der besonderen Eigenschaften einiger eurythermer Wassertiere. Biol. Zbl., 71: 449-461.
- Schmidt, P. J. 1950. Analyses of freshwater fishes from Canadian interior provinces. J. Fish. Res. Bd. Can., Pac. Fish. Exp. Stn., Industrial memo., no. 13: 1-8.
- Scholander, P. F. et al. 1953. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool. 26 (1): 67-92.
- Schuett, F. 1933. Studies in mass physiology: The effect of numbers upon the oxygen consumption of fishes. Ecology 14 (2): 106-122.
- Shepard, M. P. 1954. Resistance and tolerance of young speckled trout, (Salvelinus fontinalis Mitchill) to low oxygen. Ph. D. Thesis, Univ. of Toronto, Dept. of Zool.
- Smith, H. W. 1929. The excretion of ammonia and urea by the gills of fish. J. Biol. Chem. 81: 727-742.
- Spencer, W. P. 1939. Diurnal activity rhythm in freshwater fishes. Ohio J. Sci. 39 (3): 119-132.
- Spoor, W. A. 1946. A quantitative study of the relationship between the activity and oxygen consumption of the goldfish, and its application to the measurements of respiratory metabolism in fishes. Biol. Bull. 91 (3): 312-325.
- Theroux, F. R., E. F. Eldridge, and W. L. Mallman. 1943. Laboratory

- manual for chemical and bacterial analysis of water and sewage. 3rd ed., New York: McGraw Hill.
- Van Dam, L. 1938. On the utilization of oxygen and regulation of breathing in some aquatic animals. Diss. Groningen. 13: 138 pp.
- Viswanathan, R., and P. R. S. Tampi. 1952. Oxygen consumption and viability of Chanos chanos, Forskal, in relation to size. Proc. Indian Acad. Sci. 6 (B) 4: 148-157.
- Wells, N. A. 1932. The importance of the time element in the determination of the respiratory metabolism of fishes. Proc. Nat. Acad. Sci. 18: 580-585.
- _____ 1935a. The influence of temperature upon the respiratory metabolism of the Pacific killifish, Fundulus parvipinnis. Physiol. Zool. 8: 196-227.
- _____ 1935b. Variations in the respiratory metabolism of the Pacific killifish Fundulus parvipinnis due to size, season, and continued constant temperature. Physiol. Zool. 8: 318-336.
- Welsh, J. H. 1938. Diurnal rhythms. Quart. Rev. Biol. 13 (2): 123-139.
- Wiebe, A. H. 1933. The effect of high concentrations of dissolved oxygen on several species of pond fishes. Ohio J. Sci. 33 (2): 110-126.
- Wundsch, H. H. 1934. Nahrung, Verdauung und Stoffwechsel der Fische; in Mongole, E., Handbuch der Ernährung und des Stoffwechsels der landwirtschaftlich Nutztiere. 3rd ed., Berlin.
- Zeuthen, E. 1947. Body size and metabolic rate in the animal kingdom. Compt.-rend. Lab. Carlsberg, Ser. chim. 26 (3): 15-165.
- _____ 1953. Oxygen uptake as related to body size in organisms. Quart. Rev. Biol. 28 (1): 1-12.
- Zuntz, N. 1914. Respiration und Stoffwechsel der Fische. Deutsche med. Wochenschr. 40 (15): 777.