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Weight-specific oxygen consumption of intact bluegill sunfish was estimated in relation to body weight and temperature by the sealed jar method. The relationship between body weight and weight-specific oxygen consumption was represented by the equation: $Y = aX^{b-1}$ in which Y is the weight-specific oxygen consumption, expressed as cc/kg/hr, X the body weight, and a and b-1 are constants indicating the intercept and slope, respectively, of the curve of log metabolism versus log body weight. The mean slope of the regressions was found to be -0.3800 at ten degrees C. and -0.4285 at 20 degrees C.

Tissue QO_2's for gill, liver and muscle in relation to body weight were determined at ten and 20 degrees C. The regression coefficients for gill, liver and muscle at ten degrees were -0.0852, -0.1505 and -0.3116, and at 20 degrees -0.0799, -0.2070 and 0.1247. Muscle tissue at 20 degrees C. thus showed an increase in QO_2 with

increasing body size. At ten degrees muscle showed metabolic over-compensation. Metabolic compensation to low temperature was not seen in gill, liver, or the intact animal.

THE RELATIONSHIP BETWEEN BODY SIZE AND METABOLISM IN *LEPOMIS MACROCHIRUS* RAFINESQUE

by

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THE RELATIONSHIP BETWEEN BODY SIZE AND METABOLISM IN LEPOMIS MACROCHIRUS RAFINESQUE

INTRODUCTION

The effect of body size upon oxygen uptake in animals has long been a subject of intensive study and a well documented literature on the subject exists. The general result obtained is a decline in the weight-specific oxygen consumption (i.e., oxygen consumption per unit weight per unit time) with increase in body mass. Among the most extensive reviews on this topic are the works of Zeuthen (1947) and Hemmingsen (1960) in which the authors consider the relation of body size to metabolism in a large variety of organisms. Zeuthen and Hemmingsen plotted the total oxygen uptake of the organism (cc O_2 per hour) against body size on a double logarithmic grid and observed a linear relationship with a slope of about 0.75 for both homeotherms and poikilotherms. Zeuthen (1953) plotted the metabolism of numerous species of animals against their body weights on a logarithmic grid and arrived at the following relation:

$$Y = a X^b,$$

where Y is the metabolic rate, expressed as the total oxygen uptake in cc O_2/hour, X the body weight, and a and b are constants indicating the intercept and slope respectively of the curve of log

metabolism versus log weight.

A consideration of whether the metabolic rate of an animal is dependent upon the total area of body surface or some other function of body mass was discussed in detail by von Bertalanffy and Krywienczyk (1953). These workers examined a variety of crustaceans and reviewed the literature on a number of other animals, and arrived at a concept of "metabolic types" as determined by the slope of the log oxygen uptake-log size relationship. Three metabolic types were found, in which oxygen consumption fell into one of the following categories:

(1) proportional to body surface (b=0.67).

(2) proportional to body weight (b=1.0),

(3) intermediate in proportion to surface and weight (b intermediate between 0.67 and 1.0).

The first record of an observation that the oxygen uptake per unit weight decreases with an increase in body weight in fish was made in 1807 by Humboldt and Provencal (cited by Gardner and Leetham, 1914). The slope of the curve of a log of total oxygen uptake (cc/hr) versus log body weight in fish ranges from 0.6 to 1.0. Zeuthen (1947, op. cit.) gives a value of 0.78 for various species of fish. Job (1955) gives a value of 0.85 for the speckled trout (Salvelinus fontinalis). In contrast, Wells (1935) gives a slope of 0.5 to 0.6 for the Pacific Killifish (Fundulus parvipinnis). However,

Zeuthen's, Job's and Wells' slope values were obtained through work on a relatively small size range of fish. Pritchard, Florey, and Martin (1958), working on fish which weighed up to 20 kg, report a slope value of 0. 74 for dogfish (Squalus suckleyi) and 0. 78 for lingcod (Ophiodon elongatus). Beamish (1964a) has investigated several species of fresh-water fishes and reports some of the highest slope values in the literature: 0. 877 for Salmo trutta, 1. 052 for Salvelinus fontinalis, 0. 864 for Catostomus commersonii, 0. 925 for Ictalurus nebulosus and 0. 894 for Cyprinus carpio. In summary, then, most slope values for fish seem to fall between 0. 75 and 0. 90.

At least one group of investigators have failed to observe a relation between body size and weight-specific oxygen consumption in fish. Moss and Scott (1961), working on three species of warm-water fish, Bluegill Sunfish (Lepomis macrochirus), Largemouth Black Bass (Micropterus salmonoides), and Channel Catfish (Ictalurus punctatus), find that in the Largemouth Bass and the Bluegill Sunfish the weight-specific oxygen uptake decreases with increasing size up to weights between ten and 15 grams, but that beyond this size there is no measurable drop in weight-specific oxygen uptake over the size range tested. The size range for the Bluegill was about three to 45 grams, and for the Largemouth Bass about four to 75 grams. Furthermore, Moss and Scott state that there was no detectable difference in weight-specific oxygen consumption in catfish over the

size range (20 to 105 grams) studied. Beamish (1964a, op. cit), however, finds a relationship between body size and weight-specific oxygen uptake in Ictalurus nebulosus, a species related to the one studied by Moss and Scott (1961, op. cit).

It is well known that an increase in temperature results in an increase in the metabolic rate of a poikilothermic animal, and many studies have been carried out to determine whether or not temperature alters the relationship between body size and oxygen uptake. Wells (1935, op. cit.), working with Fundulus, notes that with a rise in the environmental temperature, the increase in metabolic rate is more pronounced in small fish than in large ones. Rao and Bullock (1954), working on a number of crustaceans, and reviewing the information on various other poikilotherms, observe that for a given rise in temperature, the smaller individuals of a species increase their oxygen uptake more markedly than do the larger ones. This was also observed by Morris (1962) in the cichlid (Aequidens portalegrensis). Beamish and Mookherjii (1964), on the other hand, report that in the goldfish (Carassius auratus) the proportionate change in oxygen consumption for a given shift in temperature appears to be independent of body size.

In their efforts to explain the mechanism responsible for the decline in weight-specific oxygen uptake of the intact animal, various workers have investigated the respiration of individual tissues.

Kleiber (1941) measured the in vitro rate of oxygen consumption of liver slices from rabbit, sheep, horse, and cow. Comparing the rate of tissue oxygen uptake interspecifically, he found that the oxygen uptake of liver decreases significantly with an increase in body size. It thus seemed that the factors which determine the metabolic rate of the intact animal might be present in the tissues respiring in vitro. Weymouth, Field, and Kleiber (1942) pursued this problem with the same homeotherms as Kleiber (1941, op. cit.), but on several tissues (liver, muscle, kidney), and concluded that the control of oxygen consumption on the tissue level is not systemic; i.e., the relationship of oxygen consumption of the whole animal to body weight is the same as that of tissue slices in vitro in relation to body weight. However, these authors were making interspecific comparisons and were not comparing tissue QO_2's of a large range of individuals from the same species. Weymouth et al. (1944) found a similar interspecific relationship in tissue QO_2's in a comparison of crustaceans and mammals. The latter workers hypothesize that the mechanism of metabolic regulation is probably that regulating the development of intra-cellular enzymes, "the concentrations of which, as of other chemical constituents of the organism, appear to maintain during the growth of the cell a power relation to the total weight of the cell".

Several workers have observed the relationship of body size

to tissue oxygen consumption in intraspecific studies. Dehnel and McCaughran (1964) state that in two species of shorecrab, Hemigrapsus nudus and H. oregonensis, gill tissue respiration is dependent upon the size of the animal. The mean regression slope for the weight-specific oxygen consumption-whole body weight plot has a value of -0.169 for both species. In their work on the respiration rates of the excretory and gill tissues of the cutthroat trout (Salmo clarkii clarkii), Holmes and Stott (1960)found a decline in the weight-specific oxygen consumption with an increase in the body weight of the fish for both tissues, observing a mean regression slope of -0.148 for kidney and -0.139 for gill.

Several workers have observed a relationship between weight-specific oxygen uptake in some tissues but have failed to see it in other tissues of the same animal. Crandall and Smith (1952) have found a relationship between body size and the weight-specific oxygen consumption of liver slices of growing birds, whereas kidney tissue has essentially the same oxygen uptake for all sizes of birds. von Bertalanffy and Estwick (1953) report a relationship between the oxygen uptake of mammalian diaphragm musculature and body size, whereas the relationship is absent in the rate of oxygen consumption of skeletal muscle. Krebs (1950) further documents this inconsistency from tissue to tissue in the relationship between body size and weight-specific oxygen consumption in the same animal. He reports a relationship between body size and weight-specific oxygen consumption for liver, but does not observe such a

relationship in the oxygen uptake in brain, kidney, spleen or lung tissue of mammals. Krebs emphasizes discrepancies in experimental procedure as perhaps partially explaining the lack of agreement with respect to the relationship between tissue QO_2 and body weight. Thus, some workers slice their tissues, others mince them, and yet others employ a homogenate. At any rate, there does not appear to be a consistent pattern in the relationship of tissue QO_2 to body size, as there is in the intact animal.

The relationship between body size and weight-specific oxygen consumption in fishes is rather firmly established. However, the report of an observation that the relationship between body size and weight-specific oxygen consumption is seen only in small Lepomis macrochirus (Moss and Scott, 1961 op. cit.), which contrasts strongly with the findings in the literature, warrants further investigation. The inconsistencies in the literature with respect to the relationship between tissue QO_2 and body size, and a rather incomplete knowledge of how temperature affects the relationship between body size and weight-specific oxygen consumption in both the tissues and intact animal, are additional reasons for extended study. The following experiments were designed to determine the effect of body size upon the weight-specific oxygen consumption of Lepomis macrochirus Rafinesque and its tissues, and to determine the influence of temperature upon this relationship.

METHODS AND MATERIALS

Bluegill Sunfish (Lepomis macrochirus Rafinesque) were collected by hook and line from Triangle Lake near Corvallis, Oregon, and from the hatchery ponds at the Game Commission warm-water fish rearing farm in St. Louis, Oregon.

The fish were kept in 30 gallon fiberglass tanks in the laboratory where they were provided with a constant supply of fresh well-aerated water. Chlorine was removed by means of a charcoal filter (Pritchard, Kerley and Heath, 1960). Temperatures in the tanks were approximately ten degrees Centigrade in the winter and 20 degrees in the summer. The fish, upon arrival in the laboratory, were treated with Terramycin (Pfizer) in tablet form to halt the growth of fungus infections and to ward off gill diseases. The fish were fed a diet of chopped earthworms and dried fish-food pellets. In all cases the fish were kept in the laboratory for more than two weeks before being used in any of the experiments. All the experiments were carried out at the two acclimation temperatures: ten degrees in the winter and 20 degrees in the summer.

Before commencement of any of the experiments, the fish were not fed for 24 hours.

All the experiments on oxygen consumption of the whole animal were carried out during the same time of day in order to avoid any

discrepancies due to circadian rhythms in the animals. Although none have been demonstrated in the Bluegill Sunfish, rhythms have been observed in a number of other fishes (Clausen, 1936; Spencer, 1939; Higginbotham, 1949).

The sealed jar method was used for the determination of the oxygen consumption of the whole animal. Fish were placed into Erlenmeyer flasks of varying volume, dictated by the size of the fish. The containers were completely covered by black polyethylene to prevent undue disturbance of the fish during the experiments. The stopper for the respirometer was provided with three tubes; one for incoming water, one for outgoing water, and one for sampling. After the fish had been placed into the container, it was left for at least 12 hours without further disturbance. While the fish was acclimating, the sample line was closed and the inlet and outlet lines open, providing a continuous flow of well-aerated water through the container.

After the fish had been in its container for 12 hours or more, determinations of the oxygen consumption were begun. First, the outlet line was closed and the sample line opened, so that there was still a continuous flow through the respirometer. An initial sample of 125 ml was drawn off, and all three openings were closed immediately following. The fish was allowed to respire for one-half hour, following which the sample and outlet lines were opened and a final

sample taken. The water samples were analyzed for dissolved oxygen content by the unmodified Winkler Method (American Public Health Association, 1955).

Immediately upon removal of the final water sample, the sample line was again closed and the inlet and outlet opened to replace the water that had been removed, and to provide a circulation of fresh water. The water was kept circulating for 30 minutes, at the end of which time the above procedure was repeated. In this manner measurements of the dissolved oxygen content in the water were taken every 30 minutes for five hours.

The difference in the oxygen content, in cc/l, between the initial and final sample was multiplied by the volume of the body of water in which the fish was kept, corrected for the displacement of the fish, divided by the weight of the fish, and multiplied by two to arrive at the oxygen uptake per kilogram of animal per hour.

For the determination of tissue oxygen consumption the manometric technique as set forth by Umbreit, Burris, and Stauffer (1964) was employed. The medium used in the flasks was trout saline prepared to the specifications of Holmes and Stott (1960, op. cit.). The composition of the saline is given in the table below:

Substance	Concentration (mM)	Parts
NaCl	19.35	103
KCl	1.19	4
KH_2PO_4	2.19	1
$MgSO_4 \cdot 7H_2O$	3.97	1
$NaHCO_3$	1.35	3
PO_4 buffer		18
Na_2HPO_4	1.47	4
NaH_2PO_4	1.43	1

pH 7.2

The tissues used were gill, liver, and epaxial muscle, the latter from just below the anterior end of the dorsal fin.

The fish were removed from the acclimation tanks, killed by a blow on the head, and immediately weighed. The tissues were then removed and prepared as described below, and placed into chilled Warburg flasks. The gills were removed from the fish and placed on a chilled porcelain plate. The filaments were cut away from the gill bars with fine scissors and placed into the flasks. In the case of the liver, it was decided to use slices, assuming that fewer cells would be damaged than in the other methods of preparation (Krebs, 1950, op. cit.). The liver was sliced on a template, a small plastic plate with several small holes cut into it. The tissue was pushed through these holes, and cut by a stainless steel razor into slices approximately one mm thick. In the case of the muscle, which lends itself poorly to slicing, another method had to be used. A slab of epaxial muscle was removed from the right side of the fish,

just below the anterior end of the dorsal fin. The tissue was placed on the chilled porcelain plate and teased apart with glass needles.

The flasks were placed into the water bath of a Warburg apparatus which was set to shaking at the rate of 100 times per minute. The temperature in the water bath was the same as the acclimation temperature of the fish: ten degrees in the winter, and 20 degrees in the summer. The flasks were equilibrated with an open manometer for 20 minutes. At the end of this time the manometer was closed and readings commenced. Readings were continued for two hours, since it was determined in preliminary work that after two hours the tissues begin to deteriorate rapidly, and subsequent readings become more and more inconsistent. The readings were fairly uniform up to two hours. After the experiment the tissues were removed from the flasks, dried at 60 degrees Centigrade for three days and reweighed.

The oxygen consumption of the tissues was calculated as microliters of oxygen per gram of tissue (dry weight) per hour. The regression of weight-specific oxygen consumption of the tissues and intact animal with body size was determined using the least squares method as outlined by Simpson, Roe, and Lewontin (1960), and the data plotted on a double logarithmic grid.

RESULTS

In most studies concerning the effects of body size on metabolism, the relationship has been expressed by the equation: $Y = aX^b$, where Y is the total oxygen uptake in cc/hr, X the body weight, and a and b are constants indicating the intersect and slope of the curve of log total oxygen uptake versus log body weight. The relationship between weight-specific oxygen consumption (oxygen consumed per unit weight per unit time) and body size may be derived by dividing both sides of the above equation by the weight of the animal. Thus:

$$Y/X = aX^b/X$$
$$= aX^{b-1}.$$

The regression coefficient for the relationship between the logarithm of weight-specific oxygen consumption and logarithm of body weight is now b-1. In the present study, regression coefficients for both whole animal and tissue metabolic rates were computed from the latter equation. The regression equations and weight ranges used, for both temperatures, are given in Table 1. Also included in Table 1 are metabolic rate values calculated for a "standard" 50 gram fish (about the middle of the size range tested) from the regression equation.

The relationship between log weight-specific oxygen consumption

of whole animals and log body weight at ten and 20 degrees C. is shown graphically in Figure 1. At ten degrees C. the regression coefficient for the curve is -0.3800, and at 20 degrees it is -0.4285. These figures correspond to values of 0.6200 and 0.5715, respectively, for the regression coefficients of the relationship of log total oxygen uptake versus log body weight. The relationship between log tissue QO_2 (μl/gm dry wt./hr) and log body weight is shown, for each of the tissues studied, in Figures 2, 3, and 4. Figure 2 shows the relationship between log QO_2 of gill tissue and log body weight at the two test temperatures. At ten degrees the regression coefficient is -0.0852, while at 20 degrees it is -0.0799. The QO_2 of liver tissue slices shows a more noticeable size dependence (Figure 3). The regression coefficients for ten and 20 degrees are -0.1505 and -0.2070, respectively, indicating a definite decrease in liver QO_2 with increasing body weight. Figure 4 shows the relationship between log QO_2 of muscle tissue and log body weight. At ten degrees the regression coefficient is -0.3116; there is thus a definite decrease in QO_2 of muscle tissue with an increase in body weight. However, at 20 degrees in the summer, the relationship appears to be reversed, so that there is an increase in muscle QO_2 with an increase in body size. The regression coefficient for the curve is 0.1247.

Table 1. Metabolic rate of bluegill in relation to body size. Regression equations represent the relationship of weight-specific oxygen consumption (Y) against body weight (X), as described in text. Whole animal metabolic rate values for a "standard" 50 gram fish given in cc/kg/hr; tissue metabolic rate values given in μl/gm dry wt. /hr (QO_2).

	Temperature °C	No. fish	Weight Range	Mean Weight grams	Regression equation	Value for 50 g fish	Q_{10}
Whole animal	10	32	1.0-75.2	12.2	logY = 1.9212 - 0.3800 logX	18.86	
							2.45
	20	35	0.6-84.0	17.3	logY = 2.3773 - 0.4285 logX	44.60	
gill	10	25	9.3-83.8	31.1	logY = 2.7376 - 0.0852 logX	391.6	
							1.81
	20	38	15.5-97.4	41.5	logY = 2.9864 - 0.0799 logX	708.9	
liver	10	22	9.8-83.8	32.6	logY= 2.8587 - 0.1505 logX	400.9	
							1.55
	20	39	15.5-97.4	43.8	logY = 3.1460 - 0.2070 logX	621.4	
muscle	10	24	11.5-83.8	34.2	logY = 3.1221 - 0.3116 logX	400.6	
							0.81
	20	41	15.5-97.4	41.8	logY = 2.2975 + 0.1247 logX	323.1	

DISCUSSION

"Standard metabolism" refers to oxygen consumption measured with minimal motor activity (Fry, 1947, 1957). Standard metabolic rate may best be determined by measuring the oxygen consumption at various levels of activity and extrapolating to a hypothetical level of minimum activity (Beamish, 1964a, op. cit.). An effort was made in the present study to control as many as possible of the factors known to influence metabolic rate in fish. Thus, the flasks were darkened, the fish were not fed within 24 hours of an experiment, and were allowed to remain in the respirometer flasks for 12 to 14 hours before metabolic rate measurements were begun. Since an activity meter was not used, the metabolic rate values in the present study may thus be more accurately considered as "routine" rather than "standard" values. It is of interest, however, to compare oxygen consumption rates found in the present investigation with those obtained by Beamish (1964a, op. cit.) using a specially designed activity meter to estimate standard metabolism in two warm-water fish, carp and brown bullhead. Beamish's values at 20 degrees C., corrected to a 50 gram fish using his regression equations, and converted to cc/kg/hr, give standard oxygen consumption rates of 35.95 and 49.65 cc/kg/hr for carp and bullhead, respectively. These values are quite close to the figure of 44.60

cc/kg/hr given in Table 1 for a 50 gram bluegill at 20 degrees C. This latter value is also in good agreement with the standard oxygen consumption rate of 31.5 cc/kg/hr at 20 degrees C. for a 45 gram pumpkinseed (Lepomis gibbosus), a species very closely related to bluegill sunfish (Brett and Sutherland, 1965).

The regression coefficients of -0.3800 and -0.4285 for the log-log plots of whole animal weight against weight-specific oxygen uptake at ten and 20 degrees C., correspond to slope values of 0.6200 and 0.5715 for a log-log plot of total oxygen uptake against body weight. These figures are lower than most of those previously reported for fish; for example, 0.875 for Salvelinus fontinalis (Job 1955, op. cit.), 0.877 for Salmo trutta, 0.864 for Catostomus commersonii (Beamish 1964a, op. cit.), 0.740 for Squalus suckleyi, and 0.750 for Ophiodon elongatus (Pritchard, Florey and Martin 1958, op. cit.). However, Wells (1935, op. cit.) gives a slope value of 0.5 to 0.6 for the Pacific killifish, a value similar to those obtained in the present experiments.

At ten degrees the slope of the log-log relation for the whole animal is slightly less than at 20 degrees; i.e., at ten degrees metabolic rate shows somewhat less size dependence than at 20 degrees. Beamish (1964a, op. cit.) also reports a very slight increase in size dependence with an increase in temperature in the following species: brown trout, brook trout, white sucker, brown bullhead and carp. It is worth noting that the 20 degree fish include a group of large bluegills with unusually high metabolic rate values (● symbols in Figure 1). These fish were all sexually mature males whose endocrine state may have influenced their level of standard metabolism.

Although all the tissues studied, with the exception of skeletal

Figure 1. Oxygen consumption (cc/kg/hr) versus body weight for intact fish. Regression coefficients are -0.3800 at ten degrees and -0.4285 at 20 degrees Centigrade. Open circles represent fish at ten degrees, closed circles fish at 20 degrees. Half-open circles denote male fish at 20 degrees.

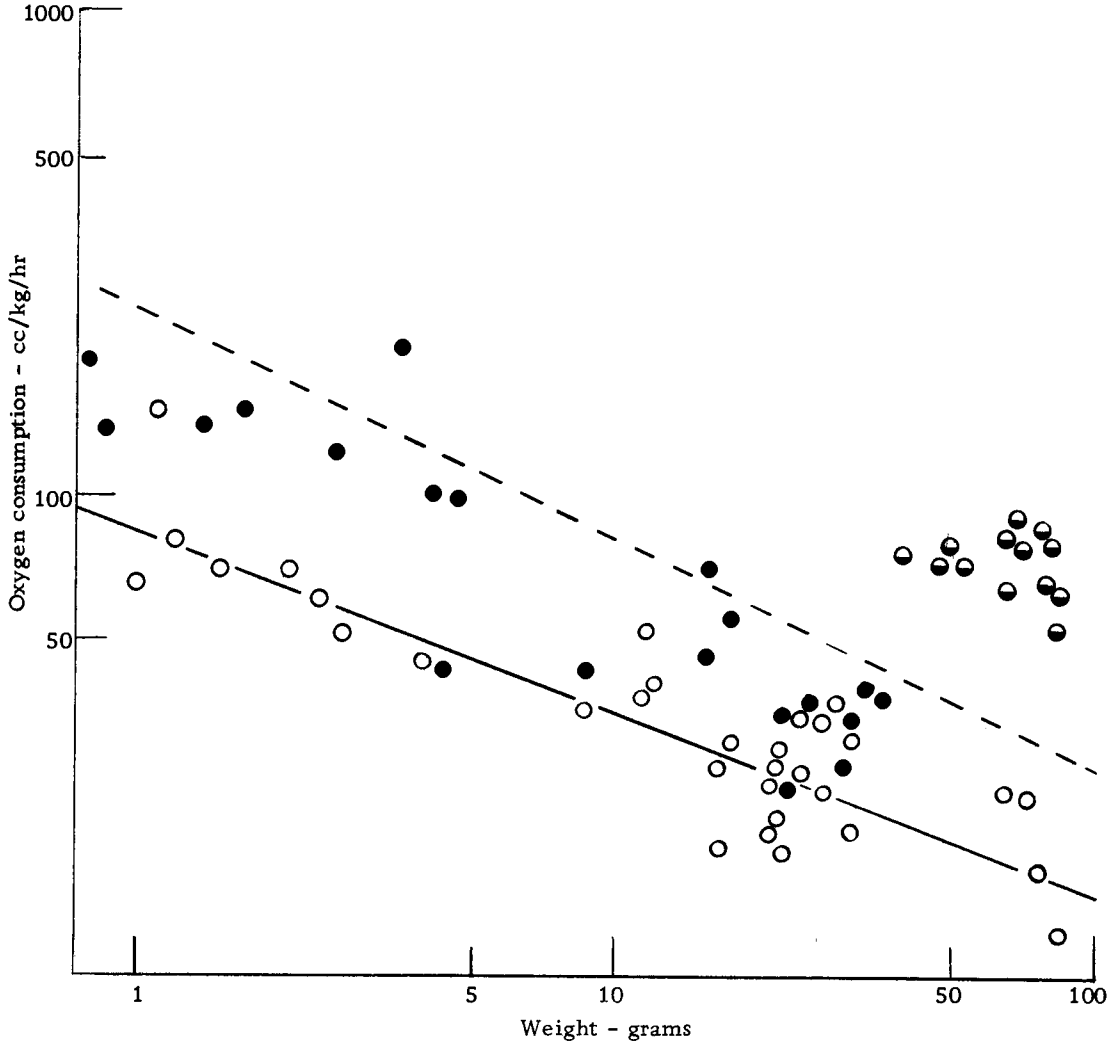

Figure 1. Oxygen consumption (cc/kg/hr) versus body weight for intact fish.

muscle from the summer fish, exhibit some decrease in QO_2 with increasing body weight, this decrease is never so great as that displayed by the whole animal. Part of the discrepancy may be due to increases in amounts of metabolically inert fat and bone minerals and decreases in relative weights of metabolically active tissues such as heart and kidney with increasing age, as has been shown in rats (Krebs, 1950, op. cit.; von Bertalanffy and Pirozynski, 1953; Conrad and Miller, 1956). Although conclusive demonstrations are lacking, considerable interest centers on the possibility that nervous and/or hormonal mechanisms are responsible for the size dependence of metabolic rate (Kleiber, 1941, op. cit.; von Bertalanffy and Pirozynski, 1953, op. cit.).

Gill tissue shows the smallest decrease in QO_2 with increasing body weight (Figure 2). The regression coefficients, -0.0852 at ten degrees C. and -0.0799 at 20 degrees C., are somewhat lower than the value reported by Dehnel and McCaughran (1964, op. cit.) who observed a regression coefficient of -0.169 for gill tissue of two species of shore crab, Hemigrapsus nudus and H. oregonensis, at both summer and winter temperatures.

Liver (Figure 3) shows a greater decrease in QO_2 with an increase in body weight. The regression coefficients -0.1505 and -0.2070 at ten and 20 degrees, respectively, agree reasonably well with the slope value of -0.1448 for slices of toadfish (Opsanus tau)

Figure 2. Oxygen consumption (μl/gm dry wt. /hr) versus body weight for gill tissue. Regression coefficients are -0.0852 at ten degrees and -0.0799 at 20 degrees Centigrade. Open circles are gill tissue at ten degrees and closed circles gill at 20 degrees.

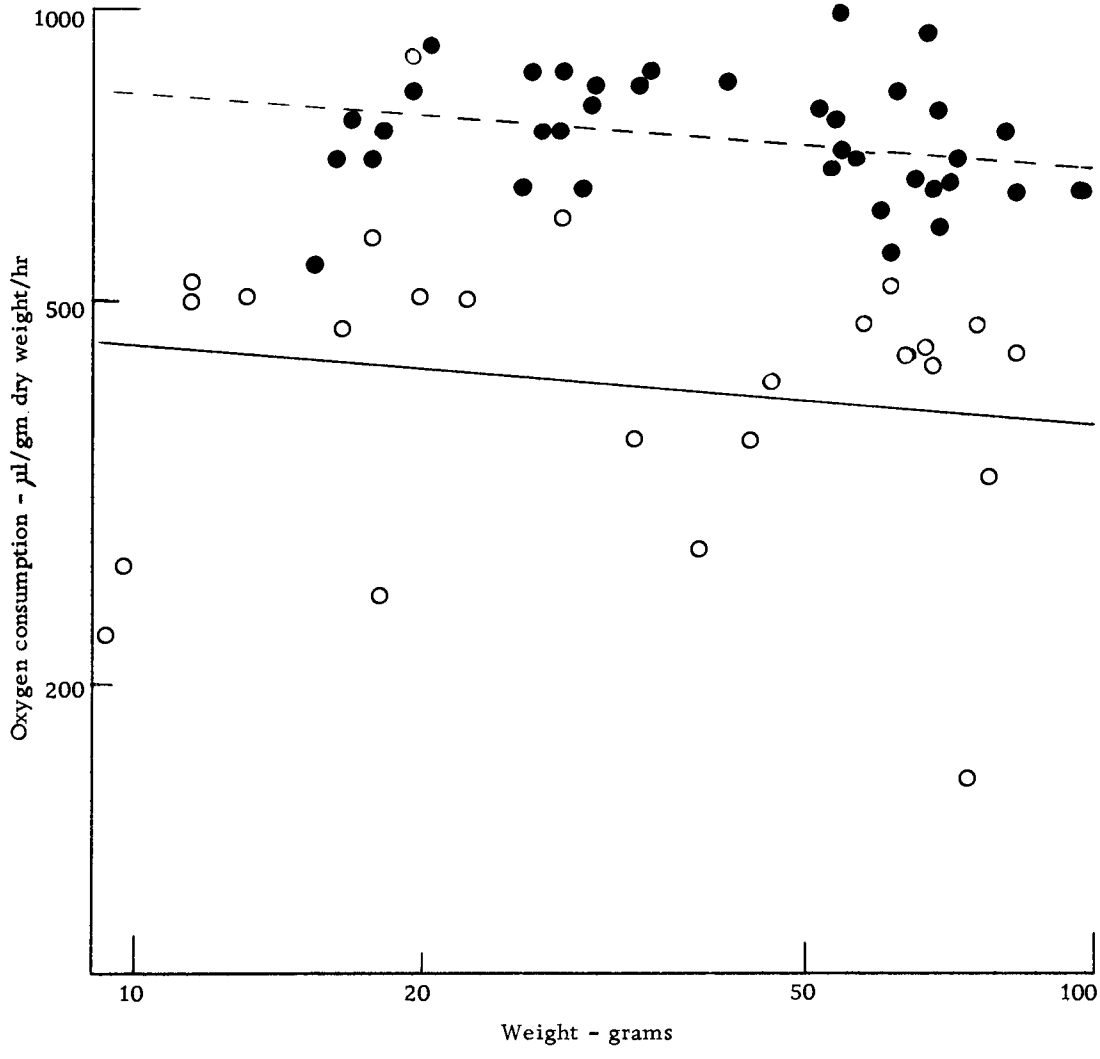

Figure 2. Oxygen consumption (µl/gm dry wt./hr) versus body weight for gill tissue.

Figure 3. Oxygen consumption (μl/gm dry wt. /hr) versus body weight for liver tissue. Regression coefficients are -0.1505 at ten degrees and -0.2070 at 20 degrees Centigrade. Open circles represent liver tissue at ten degrees and closed circles liver at 20 degrees.

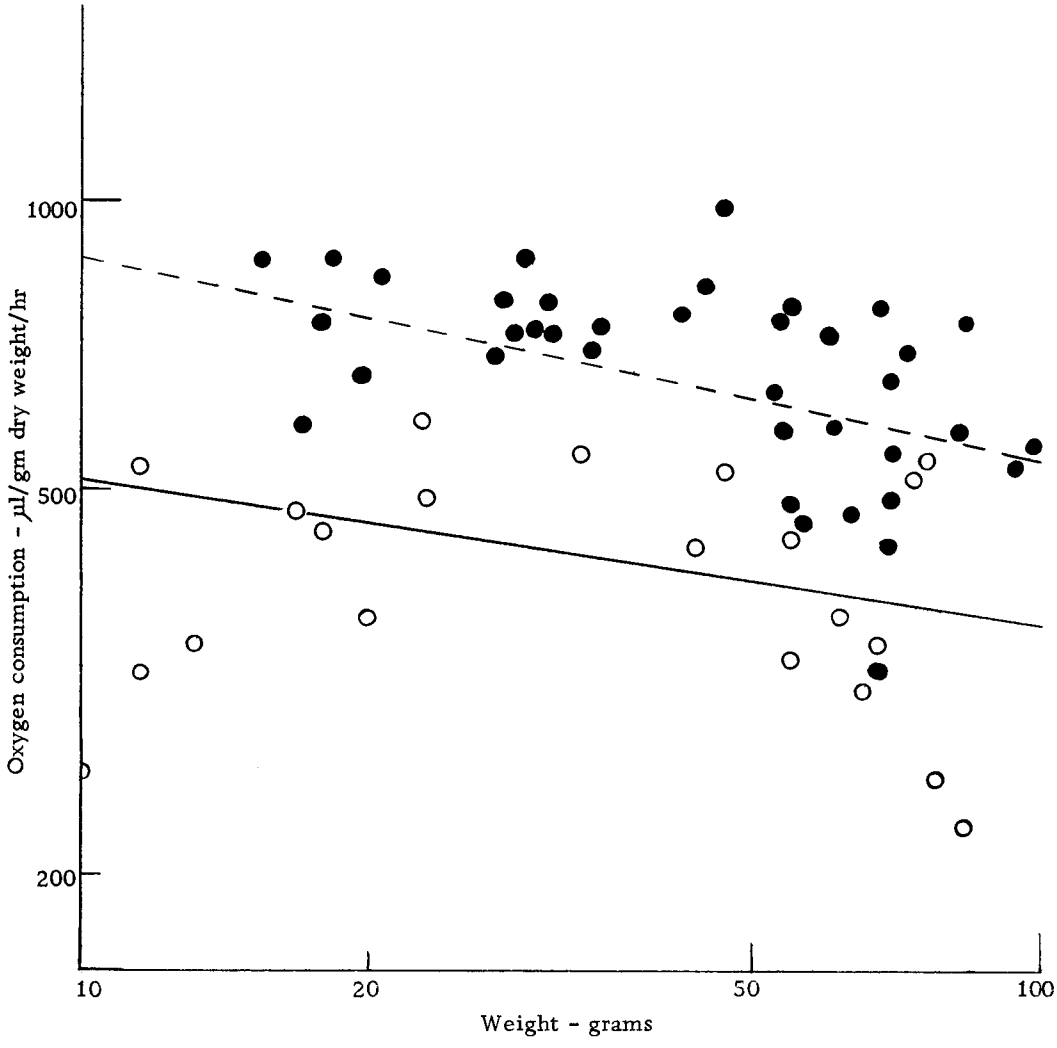

Figure 3. Oxygen consumption (µl/gm dry wt./hr) versus body weight for liver tissue.

liver at 30 degrees C. reported by Vernberg (1954), although the great difference in temperature in the two studies makes the comparison less valid.

Epaxial muscle at ten degrees C. shows a marked decline in QO_2 with increasing body weight, the regression coefficient for the plot of log QO_2 against log body weight being -0.3116 (Figure 4). The relationship is reversed in the summer, however, when the QO_2 of the muscle tissue rises with increasing body weight, resulting in a slope value of 0.1247. Vernberg (1954, op. cit.) also reports a positive slope of 0.1182 for muscle of toadfish at 30 degrees C. during the summer, as well as for brain tissue of toadfish and scup (regression coefficients of 0.2020 and 0.1504, respectively). Both Vernberg's animals and the larger summer bluegill in the present study were presumably in breeding condition. It is possible that hormonal changes associated with breeding affect the metabolic rates of the various tissues.

Gill, liver and muscle tissue give quite similar QO_2 values (corrected to a standard 50 gram fish) during the winter, whereas during the summer gill and liver respire much more rapidly than muscle, with gill having the highest rate (Table 1). The rise in temperature from ten to 20 degrees C. gives Q_{10} values of 1.81, 1.55, and 0.81, respectively, for gill, liver, and muscle QO_2 (Table 1). Bluegill muscle thus shows metabolic over-compensation

Figure 4. Oxygen consumption (μl/gm dry wt. /hr) versus body weight for muscle tissue. Regression coefficients are -0.3116 at ten degrees and 0.1247 at 20 degrees Centigrade. Open circles represent muscle tissue at ten degrees and closed circles muscle at 20 degrees.

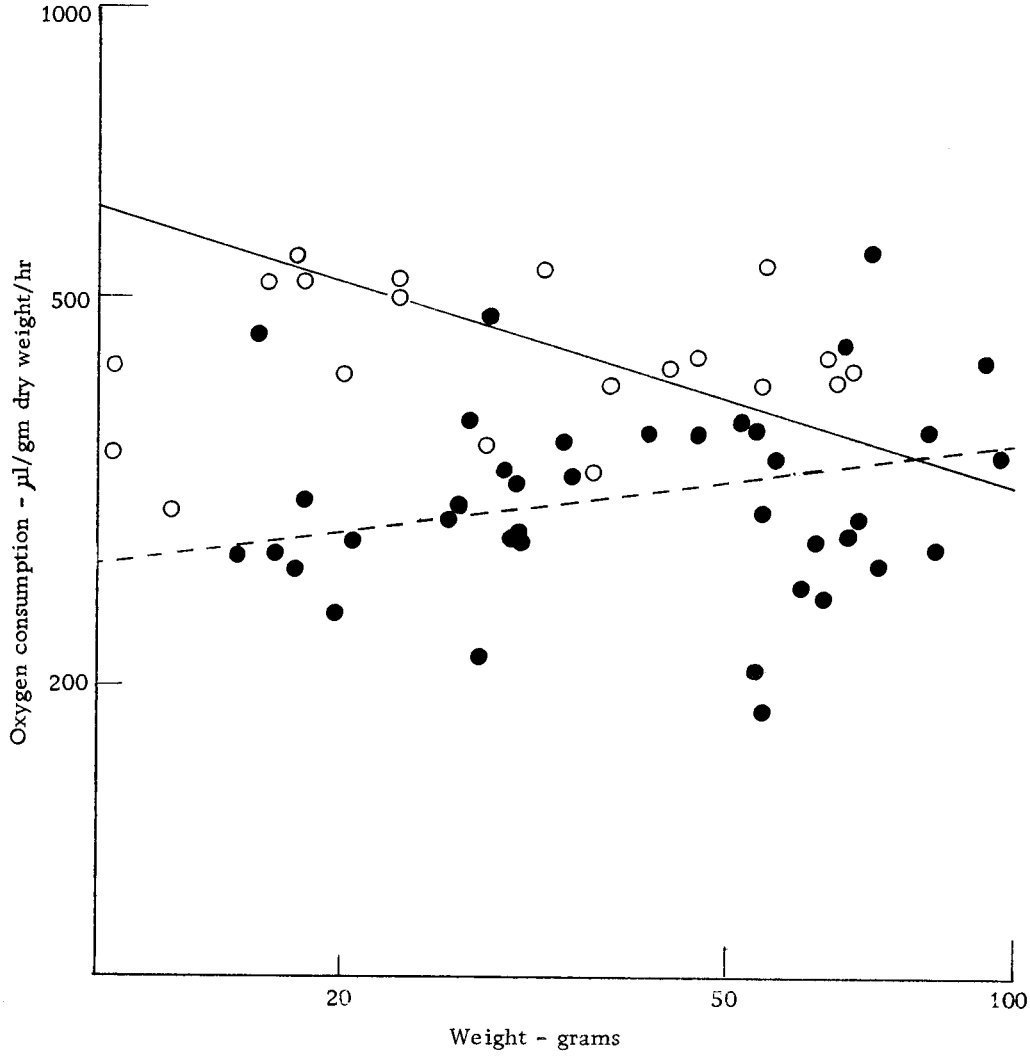

Figure 4. Oxygen consumption (µl/gm dry wt./hr) versus body weight for muscle tissue.

to lowered temperature; i.e., the rate of oxygen uptake is higher at ten than at 20 degrees, the higher values being much more pronounced in the smaller fish. Metabolic over-compensation in muscle QO_2 with acclimation to low temperature has also been reported for the common eel (Anguilla vulgaris) by Schultze (1965), and rainbow trout by Evans, Purdie and Hickman (1962), but is reported to be absent in goldfish muscle (Freeman, 1950). Evans, Purdie and Hickman, (1962, op. cit.) report that brain tissue of rainbow trout shows complete metabolic compensation with acclimation to lower temperature; i.e., the QO_2 at the lower temperatures is equal to the QO_2 at higher temperatures, whereas Freeman (1950, op. cit.) finds that goldfish brain tissue over-compensates with acclimation to cold. Over-compensation of QO_2 has been reported in cold-adapted gill tissue of goldfish (Ekberg, 1958), but was not observed in the present study.

The increase in rate of oxygen uptake in the muscle upon acclimation to cold may result from changes in the levels of activity of some of the enzymes involved in the intermediary metabolism of the tissue. For example, Kanungo and Prosser (1959b) report a shift from the glycolytic pathway to the hexose monophosphate shunt (H. M. S.) upon cold-acclimation. Ekberg (1962) found that cold-adaptation in goldfish gill tissues does not alter the activity of the enzyme glucose-6-phosphate dehydrogenase of the shunt, but greatly increases the activity of 6-phosphogluconic dehydrogenase, which

is also implicated in the H. M. S. Further support that the shunt becomes a primary oxidative pathway upon cold-adaptation is given by Hochachka and Hayes (1963) and Precht (1955). These authors report that iodoacetate, which blocks triose phosphate dehydrogenase of glycolysis in the mitochondria, does not inhibit the oxygen consumption of homogenates of cold-adapted trout muscle and cold-adapted goldfish gill tissue, which are respiring at a higher rate, implying that the main source of energy metabolism is the H. M. S. in the cytoplasm. Such an increase in H. M. S. activity suggests a correlation between protein synthesis and the shunt (Precht, 1955, op. cit). Hochachka and Hayes (1963, op. cit.) also report that there is a higher rate of synthesis of fat in cold-adapted trout. An activation of the H. M. S. could accommodate the higher rates of protein and fat synthesis in cold-adapted fish tissues showing over-compensation, which would thereby presumably increase the need for oxygen. Other enzymes which exhibit a rise in activity levels with acclimation to cold are catalase (Ekberg, 1962, op. cit.) which causes the release of oxygen from peroxide, and cytochrome oxidase of goldfish muscle (Freed, 1965), which is involved in the terminal step of biological oxidation. Metabolic adaptation of fish muscle, then, occurs at the cellular level through quantitative changes in the activities of several enzyme systems. There is some evidence that adaptive changes of the tissue are under hormonal control

(Precht, 1951; Schultze, 1965, op. cit.). Precht (1965) found that blood serum from cold-adapted carp, when administered to a muscle preparation from a warm-adapted fish, causes the rate of oxygen consumption of the warm-adapted tissue to increase.

The metabolic compensation taking place in the muscle of the bluegill sunfish, and in brain tissue of other fish (Freeman, 1950, op. cit.; Evans, Purdie and Hickman, 1962, op. cit.), would seem to be of adaptive value to the animal. Metabolic compensation to cold temperatures in nervous and muscular tissue would maintain nervous and motor coordination at optimal levels. This would permit a large degree of temperature independence of locomotor activity, thereby affecting the seasonal, ecologic, and geographic status of the fish.

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APPENDIX

Appendix Table 1. Metabolic rate of intact bluegill sunfish in relation to body weight. Metabolic rate given as cc/kg/hr. The group of large summer fish were the only ones for which sex could be determined.

Weight grams	Weight-specific O_2 consumption cc/kg/hr	Temperature °C range	Weight grams	Weight-specific O_2 consumption cc/kg/hr	Temperature °C range
1.0	63.890	8.5-10.5	0.6	273.41	18.0-21.0
1.1	94.448		0.8	185.65	
1.2	78.476		0.9	136.00	
1.5	69.620		1.4	140.00	
2.1	68.917		1.7	148.45	
2.4	60.328		2.6	119.88	
2.7	51.269		3.6	200.07	
4.0	44.677		4.2	99.79	
8.6	35.546		4.3	43.82	
11.2	37.787		4.7	97.49	
11.4	50.798		8.6	43.04	
11.8	39.917		15.1	67.72	
16.4	26.739		15.6	44.42	
16.5	18.630		17.3	54.74	
17.3	30.467		22.6	25.14	
21.2	20.221		23.7	34.33	
21.5	20.739		24.4	36.08	
21.9	25.537		29.2	26.93	
22.0	26.634		30.6	33.39	
22.0	25.727		33.2	39.04	
22.1	29.371		35.7	37.16	
22.1	18.199		38.9 m.	73.97	
23.8	26.143		48.2 m.	73.10	
24.0	34.829		48.7 m.	76.18	
26.8	33.428		52.1 m.	70.43	
26.9	24.006		66.2 m.	81.53	
28.9	36.471		66.3 m.	63.14	
31.1	19.727		68.4 m.	86.77	
31.2	31.345		70.1 m.	62.18	
65.8	24.071		76.4 m.	82.57	
72.1	23.308		77.5 m.	77.87	
75.2	16.100		77.5 m.	82.72	
			81.3 m.	61.91	
			84.0 m.	50.92	

Appendix Table 2. Metabolic rates of tissues in relation to body weight. QO_2 values given as μl/gm dry wt. /hr. Temperature = 10 degrees C.

Weight	Sex	Gill QO_2	Liver QO_2	Muscle QO_2
9.3	m.	221.655	-	-
9.8	f.	259.975	424.309	-
11.5	f.	510.996	522.510	431.100
11.6	m.	513.037	323.269	347.308
13.2	f.	467.237	347.308	305.308
16.7	m.	471.614	480.236	521.053
17.7	f.	580.451	461.348	544.759
18.2	f.	246.376	1060.104	530.256
19.8	m.	893.073	-	-
19.9	f.	502.886	373.392	417.710
22.7	f.	503.508	485.584	500.658
22.9	f.	-	598.947	582.831
28.3	m.	603.060	-	354.404
32.8	f.	357.589	544.201	537.911
35.9	f.	-	-	330.680
38.5	f.	275.343	-	410.769
43.3	m.	355.692	438.985	-
44.1	m.	-	-	430.997
46.8	f.	406.772	531.470	431.586
54.5	f.	-	443.168	540.426
55.5	m.	-	336.053	407.251
57.1	m.	463.686	-	-
61.1	m.	512.022	376.117	-
64.1	f.	436.898	-	440.864
66.0	f.	435.757	314.111	413.340
67.3	m.	423.733	350.301	423.693
73.6	m.	158.810	516.900	443.800
76.0	m.	467.320	535.743	502.553
76.9	m.	323.622	250.601	429.733
83.8	m.	439.399	229.304	444.187

Appendix Table 3. Metabolic rates of tissues in relation to body weight. QO_2 values given as μl/gm dry wt./hr. Temperature = 20 degrees C.

Weight	Sex	Gill QO_2	Liver QO_2	Muscle QO_2
15.5	m.	539.32	863.05	264.48
16.2	f.	692.49	-	457.80
17.1	f.	752.35	596.45	277.89
17.7	f.	687.17	599.73	262.74
18.2	f.	745.80	881.79	306.42
19.4	f.	806.61	659.97	235.46
20.6	f.	910.97	848.51	284.71
25.8	f.	662.48	-	289.23
26.5	f.	849.79	543.48	302.57
27.1	f.	739.33	695.64	302.57
27.4	f.	744.86	798.60	215.87
28.1	f.	853.49	732.03	481.83
29.5	f.	652.54	877.25	330.00
30.1	f.	847.52	720.82	325.82
30.4	f.	794.48	734.48	275.64
30.4	f.	151.92	-	280.72
34.2	f.	838.26	700.56	355.14
34.4	f.	853.04	739.73	325.15
41.5	m.	830.88	599.17	360.16
44.9	f.	-	821.25	-
46.9	m.	-	989.02	360.48
52.4	m.	772.17	634.63	373.92
53.1	m.	758.79	753.45	360.18
54.3	m.	671.30	570.97	203.86
55.5	m.	984.15	772.13	186.61
56.5	m.	687.01	463.64	336.19
60.5	m.	618.74	732.84	249.89
61.4	m.	546.07	595.46	283.03
62.7	m.	813.66	466.81	244.21
65.4	m.	638.69	324.65	449.18
67.5	m.	928.40	780.46	290.67
68.5	m.	593.48	494.54	292.70
68.7	m.	652.58	654.48	514.55
68.9	m.	-	437.88	289.96
69.1	m.	772.36	554.79	333.44
71.1	m.	644.94	407.35	563.38
73.2	m.	686.96	693.84	264.08
81.3	m.	734.23	577.05	365.72
84.0	m.	644.78	740.96	274.10
93.0	m.	413.63	534.33	425.17
97.4	m.	647.23	555.24	346.70