A quantitative interpretation of the metabolism-size relationship in animals

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Summary. Experimental studies with carp supported our hypothesis, that the regular decrease in the mass-specific rate of resting metabolism with increasing body mass may be explained principally by a combination of a decrease in the mass-specific rate of tissue metabolism, and an increase in the relative size of organs and parts of low metabolic activity with increasing body mass.
Key words. Metabolism-size relation; carp.

The regular decrease in the resting metabolic rate per unit body mass of an animal with increasing body mass is a well-known phenomenon, important in nutrition and pharmacology as well as physiology and ecology. Much effort has been directed towards interpreting this phenomenon, but its causal relationships seem not to have been explained quantitatively[1-3]. This paper presents, using carp, a quantitative interpretation of the phenomenon based on our hypothesis, which has already been proposed in part[4], that the phenomenon may be explained, intraspecifically and interspecifically, principally by a combination of a decrease in the mass-specific rate of tissue metabolism and an increase in the relative size of organs and parts of low metabolic activity with increasing body mass. The summated rate of oxygen consumption in vitro of the whole body of carp was calculated, based on the rate of oxygen consumption per unit mass of tissue of various organs (Q_{O_2}) and the relative size of the organs (parts in some regions), for individuals with various body masses, over a wide range. The summated rate of oxygen consumption showed a slope, 0.871, which is very close to the slope for the resting rate of oxygen consumption in vivo of intact carp, 0.832, when plotted against body mass in a log-log plot. This fact is considered to support our idea.

The decrease in the mass-specific rate of metabolism of an animal with increasing body mass was first interpreted by the 'surface rule' in terms of homoiothermy[5]. But this interpretation was proved incorrect when the mass exponent b in the allometric formula, $M = aW^b$, where M is metabolic rate and W body mass, was found to be not ⅔ which is the mass exponent of body surface, but ¾ in mammals and birds[6], and was decisively denied when very similar relationships between metabolic rate and body mass were found in many poikilothermal animals[7]. Interpretation by a theory of decrease in the mass-specific rate of tissue respiration with increasing body mass was then tried. But the slopes of the Q_{O_2}-body mass relationship in most tissues were found not to be steep enough to explain the phenomenon[8-10]. Interpretation by 'regulative factors lying in the organism as a whole' was then proposed[9], but quantitative data to support this argument have not been presented. On the other hand, it has been argued that the rate of oxygen consumption is closely correlated with the amount of respiratory surface area[11-14]. But we found in carp weighing 0.0016–2250 g that both the gill area and the body surface area, except the former in the third phase of its triphasic change in mass-specific value, showed slopes very different from the slope for metabolic rate of intact carp, when plotted against body mass in a log-log plot[15]. The respiratory surface area is, therefore, not considered to be the principal factor regulating the resting rate of oxygen consumption of the animal, in the early stage at least.

We tested our hypothesis qualitatively and quantitatively by examination of Q_{O_2} values and relative size of organs and parts in carp of various body masses over a wide range. The Q_{O_2} values of 11 main tissues, which were prepared mostly by, chilling and chopping to form a paste[16], were manometrically determined at 20 °C with 212 carp of 0.5–1100 g. These values conformed to an allometric formula, $Q_{O_2} = cW^d$, where mass-specific Q_{O_2} is oxygen consumption of a tissue in $\mu l \cdot min^{-1} \cdot g^{-1}$, c and d are con-

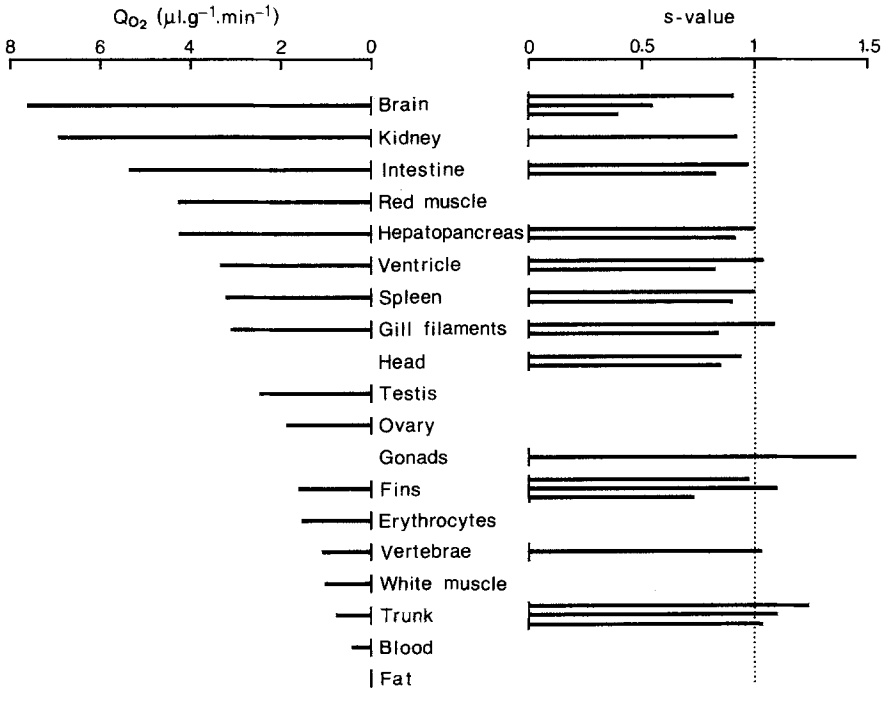

Figure 1. Levels of mass-specific rate of tissue respiration determined by a manometric method[16] at 20 °C in carp of approximately 200 g (left) and s-values of an allometric formula for relative size of organs and parts, $P = kW^s$, where P is mass of organs and parts in g and W body mass in g, in carp of 0.07–1900 g (right), constructed on the basis of our studies[4,10,17]. Two or three different s-values for a single organ or part show s-values of different phases in its diphasic or triphasic change. A single s-value for an organ means that the relative growth of the organ is monophasic. The k-values are not given in this figure and were quoted from our study[17] when m-values were calculated. 'Trunk' is the residual part of body after removal of head, fins and viscera, and it is composed of white muscle (81 %), skin (7 %), scales (7 %), bones (3 %) and red muscle (2 %)[4]. The Q_{O_2} value of the trunk was calculated from Q_{O_2} values[4,10] and mass proportion[4] of the five main components of the trunk, and was converted to the value in vivo based on Q_{O_2} value of the white muscle determined at the estimated P_{O_2} in carp muscle[16].

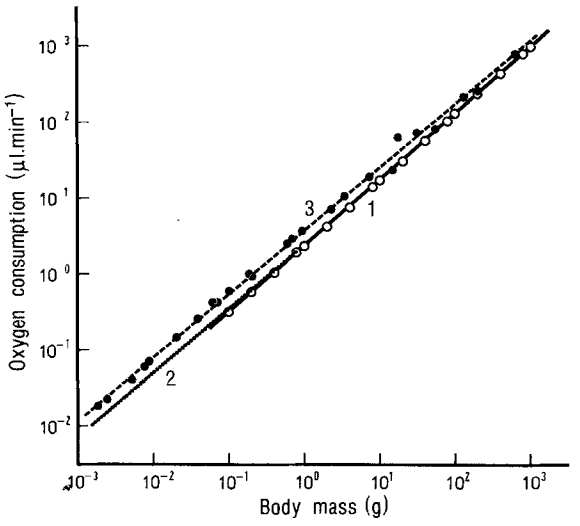

Figure 2. Oxygen consumption of carp in vitro, manometrically determined at 20 °C (line 1: summated for a whole body, present study; line 2: of a chopped whole body prepared by the same method as for tissues, constructed based on our study[10]), and oxygen consumption in vivo of intact carp determined at 20 °C by a constant flow method except for the two smallest size-groups to which a closed method was applied (line 3, present study).

stants, different in different tissues, and W is body mass in g[10]. The relative size of 10 organs, 4 parts and 8 bones were examined in 225 carp of 0.07–1900 g and found to be expressed by another allometric formula, $P = kW^s$, where P is the mass of each organ or part in g, and k and s are constants different in different phases of their change in growth[17]. The values of Q_{O_2} at approximately 200 g in body mass and s-values for various organs and parts of carp of 0.07–1900 g are summarized in figure 1. Organs of high metabolic activity, e.g. brain and kidney, got smaller in mass in proportion to the whole body with growth ($s < 1$, negative allometric growth), while organs and parts of low metabolic activity, e.g. trunk, composed mainly of white muscle (81%), got larger ($s > 1$, positive allometric growth). These results qualitatively support our idea concerning the metabolism-size relationship.

The oxygen consumption in vitro of an organ or a part in $\mu l \cdot min^{-1}$, m, at a given body mass in g, W, was calculated by a combined allometric formula, $m = c \cdot kW^{d+s}$, and the summated oxygen consumption in vitro of a whole body, $M_{in\ vitro}$, in $\mu l \cdot min^{-1}$ at a given body mass was calculated by a formula, $M_{in\ vitro} = W \cdot \Sigma m / \Sigma P$, where Σm is the summation of m of all organs and parts examined and ΣP the summation of mass in g of the organs and parts. The values of c, d, k and s obtained by our studies[10,17] were applied to this calculation. The ratio of ΣP to W was 78–86% in fish of 0.1–1 g and 90% in fish of 2–1000 g. The residual part was head kidney, bulbus arteriosus, atrium, gas bladder, urinary duct, some blood and fat. The relationship between $M_{in\ vitro}$ and W was found to be expressed by an allometric formula, $M_{in\ vitro} = 2.32W^{0.871}$ (line 1 in fig. 2; N = 17, the correlation coefficient, r, between log $M_{in\ vitro}$ and log W was 0.999. This formula is very similar to that for Q_{O_2} of the whole body prepared by the same chopping method as for tissues, $M'_{in\ vitro} = 2.47\ W^{0.847}$ (line 2 in fig. 2; N = 14, r = 0.969), obtained at 20 °C with 600 carp of 0.0016–0.79 g[10]. We found, on the other hand, that the resting rate of oxygen consumption in vivo of an intact carp in $\mu l \cdot min^{-1}$, $M_{in\ vivo}$, determined by a constant flow method at 20 °C with 254 carp of 0.0019–620 g showed a relationship to body mass expressed by another allometric formula, $M_{in\ vivo} = 3.70\ W^{0.832}$ (line 3 in fig. 2; N = 25, r = 0.999). The metabolic rates in vitro (lines 1 and 2) were a little lower than the metabolic rate in vivo (line 3), probably because of a lack of energy expenditure for movement of opercula, heart beat, peristalsis of digestive tract and other physiological and biochemical activities. However, the slopes for the metabolic rate in vitro, 0.871 (summated for a whole body) and 0.847 (of a chopped whole body), were close to the slopes for the metabolic rate in vivo of intact carp at the same temperature, 0.832 (present study), 0.836[18], 0.909[19], and the average slope in many fish species, 0.86[20]. These results are considered to support quantitatively our idea concerning the metabolism-size relationship.

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Marked elevation of HDL-cholesterol in cold-adapted golden hamsters

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Summary. Golden hamsters with spontaneous hypercholesterolemia at 22 °C developed a further increase in plasma cholesterol when they were maintained at 6 °C. This hypercholesterolemia was associated with a redistribution of plasma cholesterol between VLDL and HDL. Plasma cholesterol transported in the VLDL decreased while cholesterol in the HDL increased by 45%. The LDL profile was not significantly modified.
Key words. Cold-acclimatation; lipoprotein profile; HDL-cholesterol; hypercholesterolemia; hamster.