Relationship between summated tissue respiration and body size in a marine teleost, the porgy *Pagrus major*

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**ABSTRACT:** Our hypothesis that the regular decrease in the mass-specific rate of metabolism with increasing body mass can be explained principally by a combination of a decrease in the rate of tissue respiration and an increase in the relative size of tissues of low metabolic activity with increasing body mass was examined with a marine teleost, the porgy *Pagrus major*. Summated oxygen consumption rate *in vitro* of an individual (*M*<sub>in vitro</sub>) was calculated from an allometric relationship of mass of an organ or part (*P*) to body mass (*W*) as *P* = *kW*<sub>s</sub>, and another allometric relationship of rate of tissue respiration *in vitro* (*QO*<sub>2</sub>) to body mass (*QO*<sub>2</sub> = *cW*<sup>d</sup>), determined with 28 organs and parts. The relationship between *M*<sub>in vitro</sub> (μmol O<sub>2</sub>/h) at 20°C and *W* (g) was expressed by the formula *M*<sub>in vitro</sub> = 5.30*W*<sup>0.816</sup> in fish weighing 0.01–1000 g. The mass exponent 0.816 was very close to that (0.821) in another formula (*M*<sub>vivo</sub> = 16.88*W*<sup>0.821</sup>) determined in our previous study at 20°C with intact porgy weighing 0.005–270 g. These results indicate that our hypothesis is quantitatively valid.

**KEY WORDS:** allometry, body size, fish, metabolism, O<sub>2</sub> consumption, oxygen, scaling.

**INTRODUCTION**

Mass-specific rate of basal, standard, resting or routine metabolism of animals generally decreases with increasing body mass. This phenomenon has been observed widely and discussed repeatedly in both vertebrates, including many species of fish, and invertebrates.1–11 However, its causal relationships have not been adequately interpreted yet.

The relationship between metabolism of an intact animal (*M*) and body mass (*W*) is expressed by an allometric formula:

\[ M = aW^b \]  

where *a* and *b* are constants. The value of *b* was inter- or intraspecifically determined in many animals and found to be smaller than unity. Because the mass-specific metabolic rate (*M/W*) decreases with increasing body mass, the mass-exponent *b* is smaller than unity, being expressed by a derived formula:

\[ M/W = aW^{b-1} \]  

where (*b* − 1) is a negative.

Various hypotheses have been proposed to explain the phenomenon of decrease in *M/W* with increasing body size.8,12–16 One of these hypotheses to interpret the phenomenon is based on a decrease in tissue respiration *in vitro* with increasing body size.13 However, the decrease in tissue respiration was not steep enough to explain the phenomenon.13–15,17–19 Then, we proposed a hypothesis that the regular decrease in the mass-specific rate of metabolism with increasing body mass can be explained principally by a combination of a decrease in the rate of tissue respiration and an increase in the relative size of tissues of low metabolic activity with increasing body mass.8 To verify this hypothesis, respiration *in vitro* of almost all tissues and organs composing the whole body of individuals over a wide range of body sizes needs to be summed.

However, only a few studies regarding the relationship between summated respiration *in vitro* of isolated tissues and *in vivo* respiration of intact animals have been performed. Summated tissue respiration of three species, namely the rat,20 mouse and dog,21 has been compared interspecifically with respiration *in vivo* of intact animals. Summated tissue respiration of a freshwater teleost, namely the carp *Cyprinus carpio* weighing 0.1–1000 g, has been
compared intraspecifically with respiration in vivo of intact fish. In the present paper, we show that our hypothesis is quantitatively valid using a marine teleost, the porgy Pagrus major.

MATERIALS AND METHODS

Relative growth and tissue respiration in vitro (QO2) of organs and parts

Relative growth

The mass of 36 different organs and parts was determined in 128 porgy ranging in weight from 0.0033 to 1234 g. The relationship between the mass of an organ or part (P; in g) and body mass (W; in g) was expressed by an allometric formula:

\[ P = k W^s \]  \[3\]

where k and s are constants.

QO2

Respiration rate in vitro of 26 different tissues and parts was determined volumetrically at 20°C in 236 porgy ranging in weight from 0.039 to 985 g. The relationship between the respiration rate of tissues (QO2; in \( \mu \text{mol O}_2/\text{h} \)) and body mass (W; in g) was expressed by another allometric formula:

\[ QO2 = c W^d \]  \[4\]

where c and d are constants.

Calculation of summated oxygen consumption

Metabolism (oxygen consumption) of an organ or a part (m; in \( \mu \text{mol O}_2/\text{h} \)) at a given body mass (W; in g) was calculated by a combined allometric formula from eqns 3 and 4 as follows:

\[ m = c \cdot k W^{d+s} \]  \[5\]

The summated value of oxygen consumption in vitro of a whole body (\( M_{\text{in vitro}} \) in \( \mu \text{mol O}_2/\text{h} \)) was calculated by the formula:

\[ M_{\text{in vitro}} = W \cdot (\sum m/\Sigma P) \]  \[6\]

where \( \Sigma m \) is the summation of m of all the organs and parts examined and \( \Sigma P \) is the summation of mass, in g, of the organs and parts examined.

Constants in eqns 3 and 4 used for calculation of \( M_{\text{in vitro}} \) are given in Table 1. Calculation of \( M_{\text{in vitro}} \) was conducted on the juvenile and adolescent stages (0.01–10 g) and the adolescent and later stages (1–1000 g), corresponding to those given in Table 1.

RESULTS

Adolescent and later stages (1–1000 g)

Preceding calculation of \( M_{\text{in vitro}} \) for these stages relative growth (eqn 3) and QO2 (eqn 4) of four parts (head, trunk, fins and viscera) were calculated. The formulae for relative growth (eqn 3) for head, trunk and fins are given in Table 1.

The QO2 of the head

The QO2 of the head was determined directly and its relationship to body mass was expressed as 

\[ QO2 = 5.63 W^{-0.233} \] in fish weighing 0.039–8.2 g (Table 1). However, this equation is not suitable to apply to fish in the range 1–1000 g because the brain and gill filaments have an inflection point at 56 and 5 g in their relative growth, respectively (Table 1). Then, the following procedure was followed. In fish weighing 0.016–6.3 g, the QO2 of the head, excluding the brain and gill filaments, was expressed by the equation 

\[ QO2 = 2.81 W^{-0.218} \] (Fig. 1). Applying this equation to weight range 1–1000 g, the QO2 of the head, including the brain and gill filaments, was expressed by the following equation (Fig. 2):

\[ QO2 \text{ of head} = 5.12 W^{-0.167} \]  \[7\]

The QO2 of the trunk

The QO2 of the trunk was calculated from the mass and QO2 of white muscle, dermis and scales with epithelium of the trunk region, assuming the component composing the trunk other than dermis and scales with epithelium to be white muscle. Therefore, the mass of white muscle was calculated by subtracting the mass of dermis and scales with epithelium from the mass of the trunk. The calculated QO2 of the trunk was expressed by the following equation (Fig. 2):

\[ QO2 \text{ of trunk} = 2.06 W^{-0.140} \]  \[8\]

This relationship is very close to that of the trunk obtained by direct determination in fish weighing 0.039–8.2 g (\( QO2 = 1.42 W^{-0.133} \); see Table 1).

The QO2 of fins

The QO2 of fins was calculated as the weighted mean of QO2 of pectoral fins, dorsal fin and caudal fin and expressed by the following equation (Fig. 2):

\[ QO2 \text{ of fins} = 17.89 W^{-0.184} \]  \[9\]
The QO$_2$ and mass of viscera

Viscera in the present study refers to the stomach, pyloric ceca, intestine, hepatopancreas, spleen, head kidney, body kidney, atrium, ventricle, arterial bulb and gonads. The QO$_2$ of viscera was expressed by the following equation (Fig. 2):

$$QO_2 \text{ of viscera} = 24.54 \ W^{-0.104}$$  \[10\]

The mass of the viscera was expressed by the following equation (Fig. 3):

$$P \text{ of viscera} = 0.058 \ W^{0.938}$$  \[11\]

Calculation of $M_{\text{in vitro}}$

Using eqns 7–11 and values of k and s in the equations for relative growth of head, trunk and fins given in Table 1, $M_{\text{in vitro}}$ was calculated and expressed by the following equation (Fig. 4A):

Table 1 Allometric relationships used for the calculation of summated tissue respiration of the porgy between mass of an organ or part ($P_i$; in g) and body mass ($W$; in g) and between tissue respiration ($QO_2_i$; in $\mu$mol/g per h) and body mass ($W$; in g)

<table>
<thead>
<tr>
<th>Organ or part</th>
<th>Size range examined (g)</th>
<th>$P = kW^s$</th>
<th>Size range examined (g)</th>
<th>$QO_2 = cW^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$k$</td>
<td>$s$</td>
<td>$c$</td>
<td>$d$</td>
</tr>
<tr>
<td>Juvenile and adolescent stages (data from Oikawa and Itazawa$^{23}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>0.039–8.2</td>
<td>0.354</td>
<td>0.932</td>
<td>0.039–8.2</td>
</tr>
<tr>
<td>Trunk</td>
<td>0.039–8.2</td>
<td>0.443</td>
<td>1.118</td>
<td>0.039–8.2</td>
</tr>
<tr>
<td>Fins</td>
<td>0.039–8.2</td>
<td>0.0258</td>
<td>0.947</td>
<td>0.039–8.2</td>
</tr>
<tr>
<td>Viscera$^1$</td>
<td>0.039–8.2</td>
<td>0.0929</td>
<td>0.971</td>
<td>0.039–8.2</td>
</tr>
<tr>
<td>Adolescent and later stages (data from Oikawa et al.$^{22}$ and Oikawa and Itazawa$^{19}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>0.021–1234</td>
<td>0.355</td>
<td>0.963</td>
<td>0.074–970</td>
</tr>
<tr>
<td>Brain</td>
<td>0.0033–0.027$^*$</td>
<td>0.113$^b$</td>
<td>1.026$^b$</td>
<td>0.074–970</td>
</tr>
<tr>
<td>Brain</td>
<td>0.027$^<em>$–55.6$^</em>$</td>
<td>0.0251</td>
<td>0.610</td>
<td>0.074–970</td>
</tr>
<tr>
<td>Brain</td>
<td>55.6$^*$–1234</td>
<td>0.0489</td>
<td>0.444</td>
<td>0.074–970</td>
</tr>
<tr>
<td>Gill filaments</td>
<td>0.48–5.02$^*$</td>
<td>0.00486</td>
<td>1.217</td>
<td>0.26–911</td>
</tr>
<tr>
<td>Gill filaments</td>
<td>5.02$^*$–1234</td>
<td>0.00613</td>
<td>1.073</td>
<td>0.26–911</td>
</tr>
<tr>
<td>Trunk</td>
<td>0.068–1.84$^*$</td>
<td>0.492</td>
<td>1.148</td>
<td>0.26–911</td>
</tr>
<tr>
<td>Trunk</td>
<td>1.84$^*$–1234</td>
<td>0.533</td>
<td>1.017</td>
<td>0.26–911</td>
</tr>
<tr>
<td>White muscle</td>
<td>0.097–985</td>
<td>0.80</td>
<td>0.935</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Scales$^9$ of trunk</td>
<td>1.2–1080</td>
<td>0.0704</td>
<td>0.895</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Skin of trunk</td>
<td>20–1080</td>
<td>0.0477</td>
<td>0.947</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Stomach</td>
<td>0.64–1234</td>
<td>0.0202</td>
<td>0.801</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Pyloric ceca</td>
<td>1.1–1234</td>
<td>0.00626</td>
<td>0.72</td>
<td>0.13–911</td>
</tr>
<tr>
<td>Intestine</td>
<td>1.1–1234</td>
<td>0.0124</td>
<td>0.898</td>
<td>0.13–911</td>
</tr>
<tr>
<td>Hepatopancreas</td>
<td>0.0033–95</td>
<td>0.0170$^b$</td>
<td>1.008$^b$</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Spleen</td>
<td>0.082–2.54$^*$</td>
<td>0.00778</td>
<td>1.195</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Spleen</td>
<td>2.54$^*$–1234</td>
<td>0.00100</td>
<td>0.925</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Head kidney</td>
<td>1.1–1234</td>
<td>0.00120</td>
<td>0.863</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Body kidney</td>
<td>1.1–1234</td>
<td>0.00246</td>
<td>0.917</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Artrium</td>
<td>0.64–1234</td>
<td>0.00246</td>
<td>0.917</td>
<td>0.348$^b$</td>
</tr>
<tr>
<td>Ventricle</td>
<td>0.64–1234</td>
<td>0.00120</td>
<td>0.863</td>
<td>0.325$^b$</td>
</tr>
<tr>
<td>Arterial bulb</td>
<td>1.1–1234</td>
<td>0.00294</td>
<td>0.905</td>
<td>0.310$^b$</td>
</tr>
<tr>
<td>Gonads</td>
<td>156–1234</td>
<td>0.00080$^b$</td>
<td>1.642$^b$</td>
<td>0.338$^b$</td>
</tr>
<tr>
<td>Fins</td>
<td>0.066–1234</td>
<td>0.0243</td>
<td>0.939</td>
<td>0.097–985</td>
</tr>
<tr>
<td>Pectoral fins</td>
<td>1.1–1234</td>
<td>0.00100</td>
<td>0.947</td>
<td>0.45–488</td>
</tr>
<tr>
<td>Ventral fins</td>
<td>1.1–1234</td>
<td>0.00269</td>
<td>1.009</td>
<td>0.45–488</td>
</tr>
<tr>
<td>Dorsal fin</td>
<td>1.1–1234</td>
<td>0.00265</td>
<td>0.903</td>
<td>0.45–488</td>
</tr>
<tr>
<td>Anal fin</td>
<td>1.1–1234</td>
<td>0.00258</td>
<td>0.906</td>
<td>0.45–488</td>
</tr>
<tr>
<td>Caudal fin</td>
<td>1.1–1234</td>
<td>0.00353</td>
<td>1.032</td>
<td>0.45–488</td>
</tr>
</tbody>
</table>

$^\dagger$ Viscera in this table means the stomach, pyloric ceca, intestine, hepatopancreas, spleen and gall-bladder.

$^\ddagger$ With epithelium.

$^*\text{Body mass at the inflection point.}$

$^\S\text{Includes the larval stage.}$

$^\#\text{Gonad mass in autumn.}$

$^\text{Mean body mass and QO}_2.$
The ratio of $\Sigma P$ to $W$ was 0.95–0.93 in fish weighing 1–1000 g.

**Juvenile and adolescent stages (0.01–10 g)**

The $M_{\text{in vitro}}$ in juvenile and adolescent stages was calculated from relative growth and $QO_2$ of four parts. It was expressed by the following equation (Fig. 4B):

$$M_{\text{in vitro}} = 5.28 \ W^{0.810} \quad [13]$$

The ratio of $\Sigma P$ to $W$ was 0.88–0.99 in fish weighing 0.01–10 g.

**Juvenile and later stages (0.01–1000 g)**

There was no substantial difference between eqns 12 and 13 (Fig. 4). Therefore, these two equations were combined into one equation that could be used during the juvenile and later stages (0.01–1000 g), as follows (see Fig. 5):

$$M_{\text{in vitro}} = 5.30 \ W^{0.816} \quad [14]$$
**Change of relative contribution of metabolism of organs and parts to the whole metabolism**

Relative contribution ($R_m$; in %) of metabolism of a part, an organ or an organ system to metabolism of the whole body ($M_{in~vitro}$; eqn 13) was calculated in fish weighing 1–1000 g.

### The $R_m$ of parts and organs

The $R_m$ decreased in the head, whereas it increased in the trunk, with increasing body mass (Table 2). The $R_m$ was almost constant in the viscera, in the digestive organs (stomach, pyloric ceca, intestine and hepatopancreas) and in the kidneys (body kidney and head kidney) independent of body mass, but decreased markedly in the brain and increased in the gill filaments with increasing body mass (Table 2).

### Cutaneous respiration

To estimate the $R_m$ of cutaneous respiration to whole metabolism, the area-specific rate of cutaneous respiration was calculated for the dermis, for the scales with epithelium and for fins. Body surface area ($S_b$) and bilateral fin area ($S_f$) were applied to the calculation, in which

$$S_b = 7.62W^{0.657}$$

and

$$S_f = 3.41W^{0.642}.$$  

The area-specific rate of cutaneous respiration ($R_c$, in $\mu$mol O$_2$/h per cm$^2$) was calculated in the dermis and in the scales with epithelium based on the formula

$$R_c = m_t/(S_fP_t/(P_{h+t})),$$

where $m_t$ is the oxygen consumption of the dermis or the scales with epithelium of the trunk, $S_t$ is the body surface area, $P_t$ is the trunk mass and $P_{h+t}$ is the summated mass of the head and trunk. In this formula, ($S_f/P_t/(P_{h+t})$ means body surface area of the trunk and ($P_{h+t}$) is approximately equal to 0.887 $W$. The $R_c$ of the dermis increased with increasing body mass as follows:

$$R_c = 0.0370W^{0.264} [15]$$

The $R_c$ of the scales with epithelium was almost constant, independent of body mass, as follows:

$$R_c = 0.147W^{-0.027} [16]$$

The area-specific rate of fin respiration was calculated based on the formula

$$R_c = m_f/S_f,$$

where $m_f$ is oxygen consumption of all fins and $S_f$ is the bilateral fin area. The $R_c$ of the fins increased with increasing body mass as follows:

$$R_c = 0.127W^{0.113} [17]$$

Using equations for $S_b$ and $S_f$ and eqns 15–17, the $R_m$ of cutaneous respiration was calculated. The $R_m$ of cutaneous respiration increased with increasing body mass in the dermis other than the fins and

### Table 2  Change in relative contribution of metabolism of a part, an organ or an organ system to whole metabolism ($M_{in~vitro}$) with increasing body mass

<table>
<thead>
<tr>
<th>Part or organ</th>
<th>Relative metabolism (%) at body mass of:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 g</td>
</tr>
<tr>
<td><strong>Parts</strong></td>
<td></td>
</tr>
<tr>
<td>Head, including brain and gill</td>
<td>37</td>
</tr>
<tr>
<td>Trunk</td>
<td>20</td>
</tr>
<tr>
<td>Fins</td>
<td>9</td>
</tr>
<tr>
<td>Viscera*</td>
<td>29</td>
</tr>
<tr>
<td><strong>Organs</strong></td>
<td></td>
</tr>
<tr>
<td>Brain</td>
<td>16</td>
</tr>
<tr>
<td>Gill filaments</td>
<td>5</td>
</tr>
<tr>
<td>Digestive organs**</td>
<td>25</td>
</tr>
<tr>
<td>Head kidney and body kidney</td>
<td>4</td>
</tr>
<tr>
<td><strong>Cutaneous parts</strong></td>
<td></td>
</tr>
<tr>
<td>Dermis other than fins</td>
<td>6</td>
</tr>
<tr>
<td>Scales with epithelium</td>
<td>23</td>
</tr>
<tr>
<td>Fins</td>
<td>9</td>
</tr>
</tbody>
</table>

* Stomach, pyloric ceca, intestine, hepatopancreas, spleen, head kidney, body kidney, atrium, ventricle, arterial bulb and gonads.
** Stomach, pyloric ceca, intestine and hepatopancreas.
decreased in the scales with epithelium and the fins (Table 2).

DISCUSSION

The $QO_2$ values of the head, trunk, fins and viscera decreased with increasing body mass. The trunk showed the lowest $QO_2$ and its relative growth was positive allometry. Other parts showed higher $QO_2$ than the trunk and the relative growth of the parts was negative allometry. These relationships qualitatively support our abovementioned idea. The lower decreasing part mass. For example, in the head, in tissues of high metabolic activity decreases with increasing part mass. For example, in the head, in the relative size of tissues of low metabolic activity and a decrease in the metabolic activity of tissues ($QO_2$) with increasing body mass.

Summated oxygen consumption, $M_{in vitro}$ of porgy (the present study) was almost parallel to $M_{in vitro}$ of intact porgy, although $M_{in vitro}$ was always lower than $M_{in vivo}$. These relationships quantitatively support our abovementioned idea. The lower values in $M_{in vitro}$ are considered to have been caused by lack of energy expenditure for locomotion, movement of opercula and fins, heart beat, peristalsis of the digestive tract and other physiological activities in excised tissues. That is, the difference between $M_{in vitro}$ and $M_{in vitro}$ is considered to be due to metabolism associated with locomotor activity and physiological activity.

A decrease in $QO_2$ of the head, trunk, viscera and fins can be also explained by our idea. As given in Table 1, the extent of decrease in $QO_2$ of tissues composing these parts is smaller than the $QO_2$ of the whole parts. This implies that the relative mass of tissues of high metabolic activity decreases with increasing part mass. For example, in the head, in which $QO_2$ decreased with a mass exponent –0.167, the relative mass of the eyeballs in the head decreased from 14.1% at 0.1 g body mass to 3.9% at 1000 g, and that of the brain decreased from 15.9% at 0.1 g to 0.4% at 1000 g (calculated on the basis of the allometric equations of Oikawa et al.).

The $QO_2$ of the head, trunk and fins, which are covered by skin, decreased more sharply than that of the viscera. This is considered to be caused by a decrease in the relative mass of epithelia of high metabolic activity with increasing body mass. Area-specific oxygen consumption of scales with epithelium was almost constant, independent of body mass in fish weighing 1–1000 g (eqn 16). This implies that the thickness of the epithelium does not change much with increasing body mass within this size range because the scales themselves are considered to be inactive. Therefore, the relative mass of the epithelium of the skin is expected to decrease markedly with increasing body mass according to the surface–volume relationship. The $QO_2$ of the trunk would be expressed by the equation $QO_2 = 1.10 W^{-0.048}$ if scales would have no epithelium.

The $M_{in vitro}$ excepting scales together with epithelium ($M'_{in vitro}$) is calculated on the basis of eqn 14, subtracting the respiration of scales with epithelium (eqn 16 multiplied by total body surface area) from $M_{in vitro}$ (eqn 14), to be $M'_{in vitro} = 3.83 W^{0.855}$ (Fig. 6). The mass exponent b in the formula $M_{in vitro} = a W^b$ is 0.816 according to eqn 14. Therefore, the difference of 0.039 between 0.855 for $M'_{in vitro}$ and 0.816 for $M_{in vitro}$ is attributable to the cutaneous respiration of scales with epithelium. Similarly, another $M'_{in vitro}$ is calculated based on eqn 12 to be $M'_{in vitro} = 3.50 W^{0.876}$. By comparing the mass exponent in $M'_{in vitro}$ to that in eqn 12, we obtain the difference of 0.044 between 0.876 and 0.832. Thus, 0.039 or 0.044 of the absolute value of (b – 1) in the formula $M_{in vitro} / W = a W^{b-1}$ is attributable to cutaneous respiration.

The relationship between $M_{in vitro}$ and $M_{in vivo}$ of porgy in the present study is very similar to that of carp in our previous report, in which summated oxygen consumption at 20°C was expressed by the equation $M_{in vitro} = 6.21 W^{0.871}$ and resting routine oxygen consumption at 20°C of intact fish was expressed by the equation $M_{in vitro} = 9.91 W^{0.832}$. However, the mass exponent in vitro (0.871) is a
little larger than that in vivo (0.832) in the carp. This is considered to be because cutaneous respiration was not involved in calculation of $M_{\text{in vitro}}$ in the carp. In calculations for carp, the $d$ value in $QO_2 = cW^d$ of trunk and head (without brain and gill filaments) was assumed to be $-0.0748$, which was the $d$ value of white muscle (for details see Oikawa). If cutaneous respiration was involved in the calculation, the mass exponent in $M_{\text{in vitro}}$ of carp would have been 0.039 or 0.044 smaller than 0.871, namely 0.832 or 0.827, which is very close to the 0.832 in intact carp.

The results of the present study are considered to support our idea. Tissues that are the most essential to animal life (e.g. those of the brain and visceral organs) have a higher metabolic rate and tissues less essential to life (e.g. those of white muscle and fat) have a lower metabolic rate. Fat was not examined in the present study, but the $QO_2$ of fat was negligibly low in the carp. The relative size of tissues that are the most essential to life is larger at earlier stages and then decreases with growth, whereas the relative size of tissues that are less essential to life is smaller at earlier stages and then enlarges with growth.

From this, the regular decrease in the rate of metabolism per unit body mass of a whole animal with increasing body mass is considered to be principally explained by an increase in the relative size of tissues of low metabolic activity accompanied by a decrease in the rate of tissue metabolism. These results are considered to prove our hypothesis. We consider that our hypothesis can be applied widely to fish, mammals and probably invertebrates to explain the regular decrease in the mass-specific metabolic rate with increasing body size, although the hypothesis has not been tested with animals other than the carp and the porgy (the present study).

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