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Relative Growth of Organs and Parts of a Marine Teleost, the Porgy, *Pagrus major*, with Special Reference to Metabolism-Size Relationships

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Abstract Organ-body mass relationships were examined for 36 different organs and parts in porgies, *Pagrus major*, ranging in body mass from 0.0033 to 1200 g. Organs with high metabolic activity, e.g. brain, intestine, pyloric caeca and heart showed negative allometry except during very early stages in the life history. On the other hand, the trunk, which comprised mainly musculature with low metabolic activity, showed positive allometry.

These results support our idea that the decline in mass-specific metabolic rate in animals with increasing body mass can be explained, partly at least, by tissues with low metabolic rates becoming heavier in proportion to the whole body with growth.

Mass-specific metabolic rate (metabolic rate per unit body mass) of animals usually decreases with increasing body mass. This phenomenon has been widely observed and repeatedly discussed for various animals, both homoiotherms and poikilotherms, including many species of fish (Rubner, 1883; Winberg, 1956; Schmidt-Nielsen, 1984; Itazawa and Oikawa, 1986; Oikawa et al., 1991). The relationship between the metabolic rate of an individual animal (M) and its body mass (W) is expressed by an allometric equation $M=aW^b$, where a and b are constants. Because the mass-specific metabolic rate (M/W) decreases with increasing body mass, the b-value is smaller than unity, that is, (b-1) in $M/W=aW^{b-1}$ is negative.

Much effort has been made to interpret the above phenomenon (Rubner, 1883; Krebs, 1950; von Bertalanffy and Pirozynski, 1953; Ultsch, 1976). We proposed a hypothesis that the decline in mass-specific metabolic rate with increasing body mass could be explained by a combination of an increase in the relative size of tissues of low metabolic activity and a decrease in the metabolic activity of tissues with increasing body mass, and demonstrated its validity, both qualitatively and quantitatively, for a freshwater teleost, the carp *Cyprinus carpio* (Itazawa and Oikawa, 1986). The present study examined the validity of the hypothesis for a marine teleost, the porgy *Pagrus major*. The relative growth of organs and tissues comprising the body, as well as tissue respiration of the organs or tissues at various body mass are needed for such examination.

The relative growth of organs or tissues have been reported for many species of fish, but most reports were limited to a single or limited number of organs for any one species, or to narrow ranges of body mass.

This paper presents data on the relative growth of 36 different organs and parts, comprising the major part of the body in the marine teleost, *Pagrus major*.

Materials and Methods

Measurements of the wet mass of 36 organs and parts were made on 86 porgies, *Pagrus major*, ranging from 0.0033 g (25 days old) to 1234 g (3+ years old). Fish up to 2 g were hatched and raised at the Saga Prefectural Sea Farming Center. Fish larger than 2 g were raised at a commercial fish farm from young fish spawned and raised at the Center. Four groups were sampled as follows: Group Su = 55 specimens sampled from June to Sept. 1987 (0.0033–54 g in wet body mass, 7.2–146 mm in total length); Group Au = 14 specimens sampled in Oct. and Nov. 1987 (160–1234 g, 214–434 mm); Group Wi = 5 specimens sampled in Dec. 1987 (16–95 g, 101–178 mm); Group Sp = 12 specimens sampled in Apr. 1989 (100–985 g, 184–380 mm). Fish were not fed for 12–

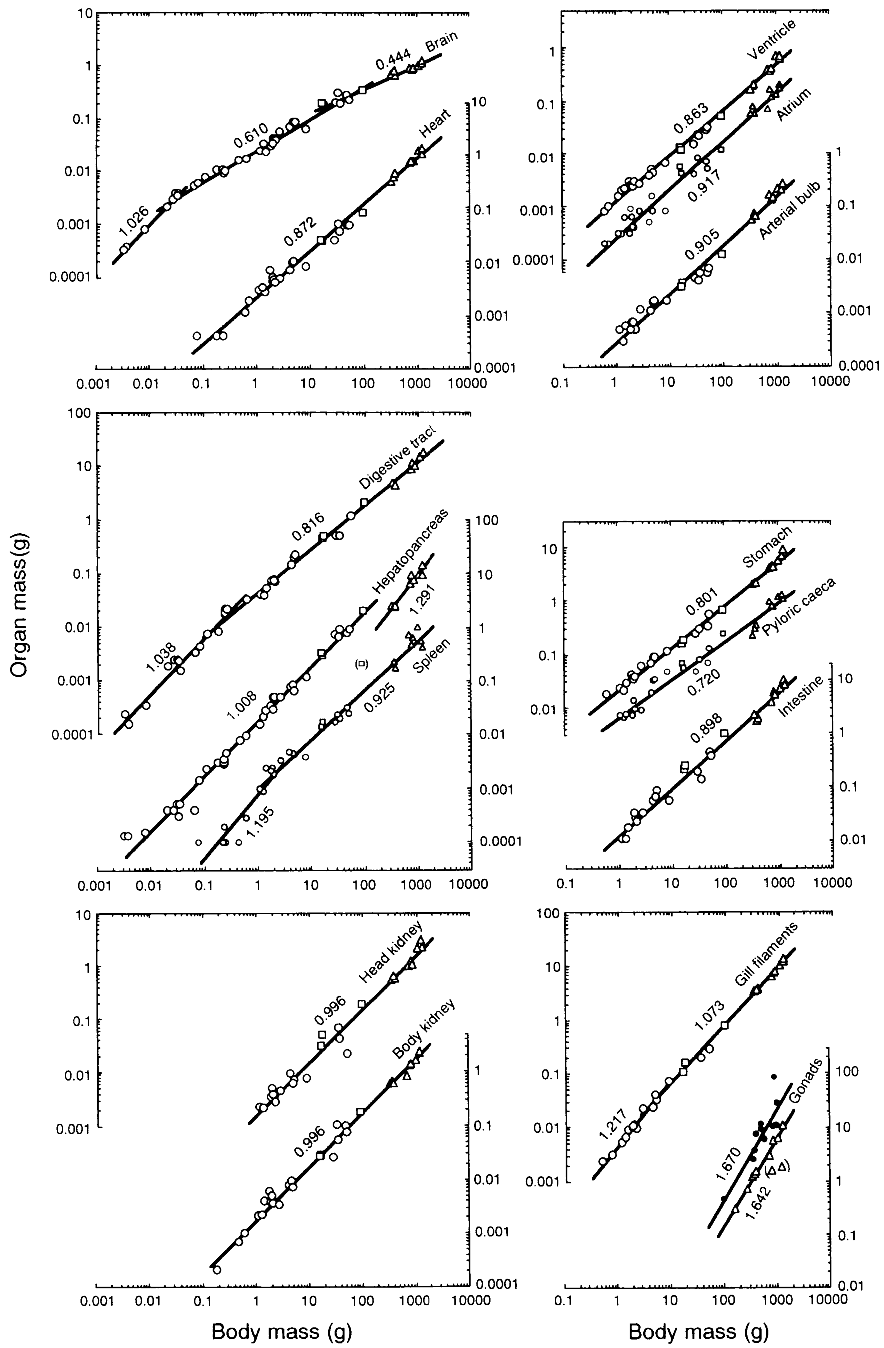

Fig. 1. Relative growth of 15 different organs in the porgy. Figures alongside the regression lines indicate the slope of the lines (the s-value in the equation $P = kW^s$). Symbols indicate different groups of porgies (see text): ○=Su, □=Au, △=Wi, and ●=Sp. For the spleen and gonads, values indicated by symbols in parentheses were omitted from the calculation of regression lines.

24 hr prior to experimentation.

A fish (several in the case of very small specimens) was anesthetized in ethyl *p*-aminobenzoate, 35–40 ppm, weighed, killed instantly by cutting the spinal cord just posterior to the head, and promptly dissected for excision of organs. The stomach, pyloric caeca, intestine, hepatopancreas, spleen, gall bladder, gonad, air bladder, head kidney, body kidney, atrium, ventricle and arterial bulb were excised. The excised organs were washed in chilled physiological saline for marine teleosts (Yamamoto, 1949) to remove blood and contaminants, and weighed to the nearest 0.0001 g, after blotting with a piece of moistened filter paper. After blood vessels, such as the celiaco-mesenteric artery, and the urinary duct and fat, had been removed from the abdominal cavity, and the residual body washed with physiological saline to remove blood and contaminants from the cavity, the head, trunk and fins were separated and weighed. In this paper, the "head" refers to that part anterior to a vertical plane through the dorsal half of the body at the posterior end of the operculum and a plane through the ventral half of the body at the posterior ends of the operculum and base of the pectoral fin, and the anterior end of the ventral fin. "Fins" refers to all fins. The "trunk" is the remaining part of the above-mentioned "residual body," after removal of the head and fins, i.e., musculature, skeleton and skin with scales. The brain (from the telencephalon to the vagal lobe), gill filaments (all filaments on the 1st to 4th gill arch on the left side), all gill arches and pseudobranchs on the left side were excised from the head, and weighed. Scales were removed from the trunk by forceps and weighed. Skin was also removed from the trunk and weighed. The mass of organs on the left side was doubled to obtain total organ values (left and right sides).

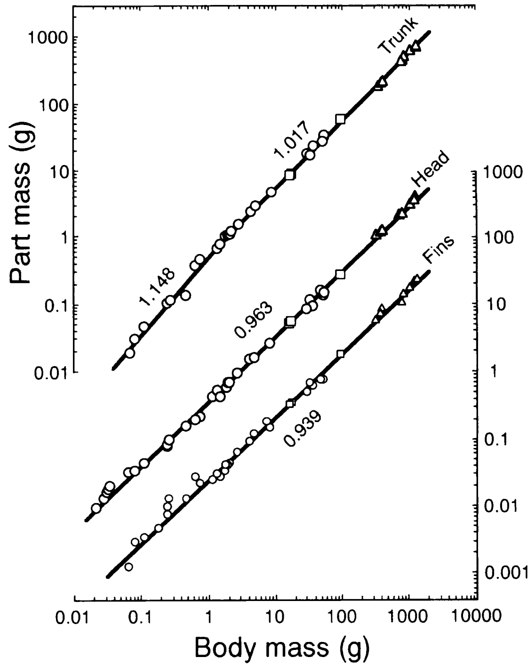

Fig. 2. Relative growth of 3 parts in the porgy. Figures alongside the regression lines indicate the slope of the lines (the s-value in the equation $P = kW^s$). Symbols indicate different groups of porgies (see text): ○=Su, □=Au, and △=Wi.

Results

A log-log plot of the mass of an organ or part (P in g) against body mass (W in g) showed a linear relationship, expressed by the allometric equation $P = kW^s$. Relative growth of an organ or part was classified as negative allometry ($s < 1$) or positive allometry ($s > 1$), where s differed significantly ($P < 0.05$) from unity. Allometry with an s-value not differing significantly from unity was classified as isometry ($s \doteqdot 1$).

Results for the main organs and parts are shown in Figs. 1 and 2, the regression analyses being summarized in Table 1. Many organs and parts showed diphasic or triphasic allometry, wherein the slopes decreased in the later stages. The brain, heart, atrium, ventricle, arterial bulb, digestive tract, stomach, pyloric caeca, intestine, spleen, head, fins, scales of the trunk, air bladder, eye balls, and eye lenses showed negative allometry against body mass, except in the case of very small fish, in which the brain and digestive tract were isometric. On the other hand, the trunk, gill filaments and gonads showed positive allometry at all developmental stages examied. The trunk of a specimen of body mass 840 g comprised white muscle 84.7%, scales 5.9%, skin 5.4% and bones 4.0%. The hepatopancreas, gall bladder, head kidney, body kidney and ventral fin showed isometry.

The mass of the hepatopancreas and gonads was different between both groups and seasons (Table 1, Fig. 1). Fish sampled in April showed gonad weight values about 3 times larger than in October and November.

Table 1. Regression analyses based on the equation, $\log P = \log k + s \cdot \log W$, where P is the mass of an organ or a part in grams and W the mass of the fish in grams

Organ or Part	Group of fish	Size range (g)	*N*	k	s ($\bar{X} \pm SEM$)	*r*
Brain	Su	0.0033–0.035	8	0.113	1.026±0.026	0.998
Brain	Su & Wi	0.021–95	36	0.0251	0.610±0.013***	0.993
Brain	Su, Au & Wi	16–1234	17	0.0489	0.444±0.022***	0.983
Digestive tract§1	Su	0.0033–0.64	17	0.0677	1.038±0.046	0.985
Digestive tract§1	Su, Au & Wi	0.11–1234	31	0.0442	0.816±0.013***	0.996
Stomach	Su, Au & Wi	0.64–1234	29	0.0202	0.801±0.071***	0.997
Pyloric caeca	Su, Au & Wi	1.1–1234	27	0.00626	0.720±0.025***	0.985
Intestine	Su, Au & Wi	1.1–1234	27	0.0124	0.898±0.025***	0.990
Hepatopancreas	Su & Wi	0.0033–95¶	38	0.0170	1.008±0.019	0.993
Hepatopancreas	Au	330–1234¶	9	0.00131	1.291±0.125	0.969
Spleen	Su	0.082–2.1	13	0.000778	1.195±0.154	0.920
Spleen	Su, Au & Wi	1.1–1234	27	0.00100	0.925±0.026**	0.991
Gall bladder	Su, Au & Wi	0.24–1234	31	0.000643	1.062±0.045	0.975
Air bladder	Su, Au & Wi	0.48–1234	24	0.00256	0.917±0.021***	0.994
Head kidney	Su, Au & Wi	1.1–1234	27	0.00165	0.996±0.030	0.989
Body kidney	Su, Au & Wi	0.18–1234	31	0.00173	0.996±0.019	0.995
Heart§2	Su, Au & Wi	0.082–1234	35	0.00211	0.872±0.016***	0.994
Atrium	Su, Au & Wi	0.64–1234	31	0.000246	0.917±0.026**	0.988
Ventricle	Su, Au & Wi	0.64–1234	32	0.00120	0.863±0.013***	0.997
Arterial bulb	Su, Au & Wi	1.1–1234	30	0.000294	0.905±0.023***	0.991
Gill filaments	Su	0.48–8.5	15	0.00486	1.217±0.053**	0.988
Gill filaments	Su, Au & Wi	2.8–1234	19	0.00613	1.073±0.017***	0.998
Gill filaments (1st)	Su	0.48–8.5	14	0.00165	1.227±0.084*	0.973
Gill filaments (2nd)	Su	0.48–8.5	14	0.00161	1.118±0.089	0.964
Gill filaments (3rd)	Su	0.48–8.5	14	0.00109	1.199±0.083*	0.973
Gill filaments (4th)	Su	0.48–8.5	14	0.000540	1.384±0.126*	0.954
Gill filaments (1st)	Su, Au & Wi	2.8–1234	19	0.00232	1.039±0.020	0.997
Gill filaments (2nd)	Su, Au & Wi	2.8–1234	19	0.00166	1.075±0.022**	0.996
Gill filaments (3rd)	Su, Au & Wi	2.8–1234	19	0.00127	1.086±0.018***	0.998
Gill filaments (4th)	Su, Au & Wi	2.8–1234	19	0.000847	1.128±0.019***	0.998
Pseudobranchs	Su & Wi	2.0–17	6	0.000373	1.358±0.183	0.966
Pseudobranchs	Su, Au & Wi	5.0–1234	11	0.00136	0.822±0.033***	0.993
Gill arches	Su	0.48–8.5	15	0.00440	1.169±0.075*	0.975
Gill arches	Su, Au & Wi	2.8–1234	19	0.00616	0.992±0.013	0.999
Eye balls	Su & Wi	0.068–37	24	0.0414	0.880±0.021***	0.994
Eye balls	Su, Au & Wi	16–1234	17	0.0704	0.726±0.029***	0.988
Eye lenses	Su & Wi	0.068–54	25	0.00357	0.956±0.039	0.981
Eye lenses	Su, Au & Wi	16–1234	17	0.00981	0.670±0.033***	0.982
Gonads	Au	156–1234¶	9	0.000080	1.642±0.070***	0.994
Gonads	Sp	100–985¶	12	0.000181	1.698±0.302*	0.871
Fat§3	Su, Au & Wi	30–1234	12	0.0178	0.929±0.123	0.922
Head	Su, Au & Wi	0.021–1234	42	0.355	0.963±0.006***	0.999
Trunk	Su	0.068–2.1	15	0.492	1.148±0.036**	0.994
Trunk	Su, Au & Wi	1.5–1234	27	0.533	1.017±0.004***	0.9998
Scales of trunk	Su, Au & Wi	1.2–1080	12	0.0704	0.895±0.028**	0.995
Skin of trunk	Su, Au & Wi	20–1080	6	0.0477	0.947±0.045	0.996
Fins	Su, Au & Wi	0.068–1234	39	0.0243	0.939±0.012***	0.997
Pectoral fins	Su, Au & Wi	1.1–1234	29	0.00401	0.947±0.018**	0.995
Ventral fins	Su, Au & Wi	1.1–1234	29	0.00269	1.009±0.018	0.996
Dorsal fin	Su, Au & Wi	1.1–1234	29	0.00625	0.903±0.008***	0.999
Anal fin	Su, Au & Wi	1.1–1234	29	0.00258	0.906±0.015***	0.996
Caudal fin	Su, Au & Wi	1.1–1234	29	0.00553	1.032±0.012*	0.998

The difference of s-value from unity was determined by t-test.
*$0.01 < P < 0.05$, **$0.001 < P < 0.01$, ***$P < 0.001$.
¶ The slopes were not significantly different, but the organ masses were significantly different ($P < 0.05$), between the groups.
§1 Composed of stomach, pyloric caeca and intestine.
§2 Composed of atrium, ventricle and arterial bulb.
§3 Within abdominal cavity.

Among the gill filaments on the 1st to 4th gill arches, the mass of those on the 4th gill arches was the smallest (Table 1).

The trunk comprised the largest part of the whole body, its proportion increasing from 35% to 60% in fish of 0.1 g to 1000 g, respectively. On the other hand, the proportion comprising viscera decreased with growth (Fig. 3).

Discussion

The mass-specific rate of routine metabolism (M/W in $\mu l \cdot g^{-1} \cdot min^{-1}$) of intact porgies, ranging from 0.0044 to 270 g, at 20°C, has been reported to decrease with increasing body mass (W in g), following the equation $M/W = 6.3W^{-0.179}$ (Oikawa et al., 1991).

The mass of the trunk relative to the whole body mass increased with increasing body mass, while that of the viscera decreased (Fig. 3). The trunk was composed mainly of white muscle, which has very low metabolic activity ($0.26 \mu l \cdot g^{-1} \cdot min^{-1}$ in tissue respiration, Qo_2, at 20°C, in a porgy of 100 g in body mass), whereas the brain, intestine and other visceral organs have high metabolic activities (e.g. pyloric caeca: 10.1, brain: 9.3, intestine: $9.1 \mu l \cdot g^{-1} \cdot min^{-1}$ in Qo_2 at 20°C, in a porgy of 100 g, Oikawa and Itazawa, in press). This is considered to support the hypothesis that the decline in mass-specific metabolic rate with increasing body mass can be explained, partly at least, if tissues with low metabolic activity increase in mass relative to the whole body with growth (Itazawa and Oikawa, 1986).

Among the visceral organs with high metabolic activity, only the gill filaments contradicted the general tendency for a decline in mass-specific metabolic rate with increasing body mass showing positive allometry (Fig. 1). However, this apparent contradiction is balanced by a decrease in Qo_2 of the gill filaments with increasing body mass (Oikawa and Itazawa, in press). In the respiratory organ, dimension of the surface area rather than the organ mass is functionally significant. Mass-specific surface area of an organ theoretically decreases by $-1/3$ power of the organ mass as the latter increases. The positive allometry shown by the gill filaments is suggested to be a compensation for the loss of mass-specific area of the organ with growth.

In many fish species, relative growth has been studied for various organs, including the brain (Sasaki, 1926; Matsui, 1942; von Geiger, 1956; Smirnov and Brusynina, 1972; Packard and Wainwright, 1974; Bauchot et al., 1977), heart (Wilber et al., 1961; Poupa et al., 1981; Feller, et al., 1983; Weatherley and Gill, 1983), liver (Yamamura and Kondo, 1949; Noguchi and Bito, 1953; Delahunty and de Vlaming, 1980; Weatherley and Gill, 1983), Spleen (Weatherley and Gill, 1983), ovary (Hanaoka, 1977; Delahunty and de Vlaming, 1980; Erickson et al., 1985), and skeleton (Reynolds and Karlotski, 1977). These works, however, were limited to a single or few organs for each species. Krumholz (1956) studied the relative growth of various organs and tissues of several freshwater teleosts, but his specimens were limited to a narrow range of body mass.

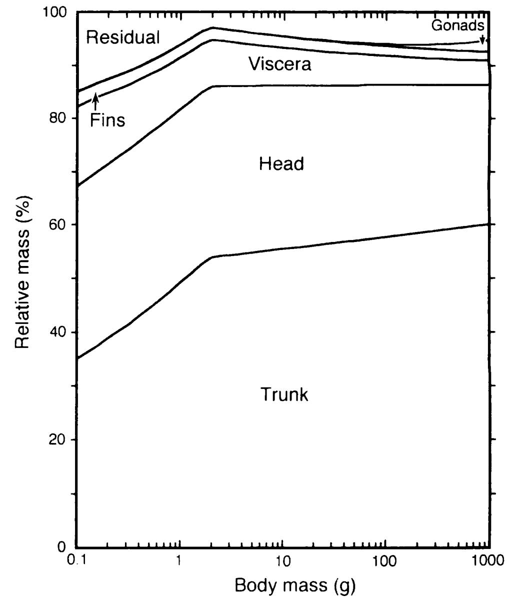

Fig. 3. Changes in relative mass of various parts of the porgy. "Viscera" comprised brain, gill filaments, pseudobranchs, heart, head kidney, body kidney, digestive tract, hepatopancreas and spleen. "Trunk" refers to musculature, skeleton, skin, and scales of body posterior to head. "Head" does not include brain, gill filaments, pseudobranchs, head kidney and heart. "Residual" includes air bladder, gall bladder, fat, blood vessels, urinary duct, blood and traces of other tissues. Relative mass of gonads was calculated from data from group Sp (see text).

Relative growth of organs and parts composing the most part of the body of a single species has been studied only in the smooth dogfish, *Mustelus canis* (Kellicott, 1908; Kearney, 1914) and the carp

(Oikawa and Itazawa, 1984), covering wide ranges of body mass. Patterns of relative growth of organs and parts in the porgy were similar to those in the carp. Distinct differences in organ size between the two species occurred in the body kidney and gill filaments, the relative mass of these organs in a fish of 100 g being 1.7% and 0.86% for the gill filaments, and 0.31–0.76% and 0.17% for the body kidney, in the carp and porgy, respectively.

The difference in gill filament mass between these two species is considered to be due, not to differences in filament length and gill area, but to structural differences such as in the degree of development of the interbranchial septum and the central venous sinus of the gill filaments, because the total filament length and total secondary lamellar area are not much different between the carp (Oikawa and Itazawa, 1985) and the porgy (Oikawa, unpublished data). The difference in body kidney mass between the two species is considered to reflect their different habitats, freshwater and seawater.

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マダイの諸器官の相対成長からみた代謝量—体重関係

及川　信・竹森美樹子・板沢靖男

動物の単位体重当り酸素消費量 (M/W) は，体重 (W) の増大に伴って低下し，魚類では一般に $W^{-0.15}$ に比例して低下する．この現象は過去 150 年以上に亘って論議されてきた生物学上の古典的話題であるが，その理由については未だに明らかでない．

我々は，体の大きさの増大に伴い，代謝活性の高い組織の体重に占める重量比が低下し，反対に代謝活性の低い組織の体重に占める重量比が上昇して，その結果この現象を生ずるのではないかと考えた．そしてこの仮説が定性的にも定量的にも妥当することを，淡水真骨魚のコイについて実証した．さらに海水真骨魚のマダイについても検証中であり，本研究ではその一環として，0.0033–1200 g のマダイ *Pagrus major* における 36 通りの器官ないし部分の重量 (P, g) と体重 (W, g) の関係を，相対成長式 $P=kW^s$ に基づいてしらべた．

脳，消化管，心臓など代謝活性の高い器官の相対成長は，生活史の初期を除き negative allometry ($s<1$) で，これらの器官の体重に占める割合は成長に伴って低下した．例えば脳の体重比は体重 0.01 g 前後では約 10%であったものが，それ以降体重の増大に伴って低下し，1000 g では 0.1%であった．これに対し，主として代謝活性の著しく低い筋肉から構成されている躯幹部は，positive allometry ($s>1$) で，体重に占める割合は成長に伴って 35%（体重 0.1 g）から 60%（体重 1000 g）まで増大した．これらの結果は，上述の我々の仮説を，定性的に支持するものである．

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