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ENERGY BUDGETS CAN EXPLAIN BODY SIZE RELATIONS

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Energy Budgets Can Explain Body Size Relations

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The size-dependence of some 20 physiological variables has been derived from a rather simple model for energy budgets. This nine parameter model is based on detailed observations on the growth and reproduction at varying food densities, and has the state variables size and storage. The size-dependence of some variables works out to be different for animals of the same species as opposed to animals of different species. The reproductive rate, for instance, tends to increase with size for animals of the same species, but to decrease with size for animals of different species. This is because the parameter values are constants within a species, but vary in a size dependent manner for animals of different species. Although growth at constant food density is assumed to be of the von Bertalanffy type, and routine metabolism to be proportional to size, respiration turns out to be about proportional to size to the power 3/4, both within and between species. The value of about 3/4 has frequently been found, but it has always been thought to be incompatible with von Bertalanffy growth.

1. Introduction

The aim of this paper is to show that, starting from assumptions on the quantitative aspects of energy budgets, we can derive in a systematic manner the way in which many physiological and ecological variables, such as ingestion, growth and reproduction, depend on body size. These types of relations have recently come to the forefront, (McMahon & Bonner, 1983; Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1984) and are used to predict, e.g., food chain efficiencies in ecology. Body size relations are invariably taken to be of the allometric type, i.e. $Y = aW^b$, where the parameters a and b are estimated by linear regression in a log-log plot of the dependent variable Y against body size W. The parameter b has become particularly popular, and will be called the scaling parameter. Apart from heat production, only relevant for endotherms, the most important body size relation concerns respiration, i.e. rate of oxygen consumption or carbon dioxide production, where the scaling parameter has the value 0·66 for unicellular organisms, 0·88 for ectotherms, and 0·69 for endotherms, (see Phillipson, 1981). The exact value of the scaling parameter differs among authors who take their data from the literature. The variations are due in part to differences in the species included and in the experimental conditions under which respiration rates were measured. For crustaceans Vidal & Whitledge (1982) quote values of 0·72 and 0·85, and Conover (1978) gives 0·74. If the regression covers a great many species, from bacteria up to elephants, the scaling parameter

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is found to be 0·75, an almost magic number in scaling relations. Since it is less than unity, it has often been concluded that large animals use energy more efficiently than small ones, even though this has not been substantiated for ectotherms. An implied assumption in this conclusion is, however, that respiration rate corresponds to routine metabolic rate, which includes energy investment in the reconstitution of enzymes and membranes and in routine movements, but not in growth, reproduction, digestion and differentiation. We shall see that this assumption does not hold in the following simple model for energy budgets. Together with routine metabolism energy investments in the other processes mentioned prove to contribute substantially to respiration rate. The model is formulated in terms of the state variables size and energy storage as functions of fluctuating food density. The relevance of the model has been checked for the water flea *Daphnia magna* (Kooijman & Metz, 1984), and Kooijman (1986*a*) on the basis of a wide variety of experimental data and for egg development in fish and birds (Kooijman, 1986*b*). Only a minor part of the data will be considered in this paper for illustrative purposes. We shall confine the discussion to ectotherms. For the extension of the model to endotherms, see Kooijman (1985). Here we shall first derive the model on the basis of a set of assumptions, and then consider scaling relations within and between species.

2. Energy Budgets

The energy budget model is based on the assumptions listed in Table 1. It regards an animal as an input-output system, as illustrated in Fig. 1, with state variables size, W, and storage, S. The basic idea is that:

—the tissue cells use energy, which is distributed by the blood at a rate that depends on the energy content of the blood.

—the blood circulates through the body at a rate that is high with respect to the change in the energy content of the blood.

—the mechanism that determines the energy content of the blood (which will be low, anyway) only depends on the energy content of the blood and on the amount of energy kept in storage in certain tissues (which may be considerable).

This process is summarized in assumption 1.

Two key assumptions are that food intake is proportional to surface area, so to $W^{2/3}$, and that growth is of the von Bertalanffy type (assumptions 7 and 12 in Table 1). The validity of the assumptions is illustrated in Figs 2 and 3 for *Daphnia magna*. These two results pose a fundamental problem for any detailed quantitative description of the energy budget. Observations on these daphnids reveal that individuals larger than 2·5 mm produce young at each moult, and that the amount of energy involved in this process is quite substantial (see Kooijman, 1986*a*). Since there is no significant reduction in growth (Fig. 3), nor any notable increase in food intake (Fig. 2) around 2·5 mm, we are faced with the problem of the destination of an energy flow in animals less than 2·5 mm, which corresponds to the energy spent on reproduction in larger animals. This is the basis of assumption 9, where this destination is called differentiation. It is a direct consequence of the assumption 3 that routine metabolic rate is proportional to size W. The basis of this assumption is two-fold. First we have the results of Smith (1957) and Vleck *et al.* (1980) that respiration in eggs of fish and birds is well described by a weighted sum of size and observed growth of the embryo (these results are more conclusive than results for

TABLE 1

Assumptions of the energy budget model

1. Energy utilized for maintenance $\dot{M}$, for growth $\dot{W}$, and for reproduction or differentiation is at the expense of stored energy.
2. For given size, the size-specific storage and its dynamics do not depend on any partitioning rule for energy utilized.
3. Maintenance energy is proportional to size: $\dot{M} = \dot{\zeta} W$.
4. A unit increase in size consumes a fixed amount η of energy.
5. Assimilation $\dot{A}$ is proportional to ingestion $\dot{I}$: $\dot{A} = \dot{I}[\dot{A}_m]/\{\dot{I}_m\}$.
6. Ingestion starts at birth size W_b, so $\dot{I} = 0$ for $W < W_b$.
7. For $W > W_b$, ingestion is proportional to $W^{2/3}$: $\dot{I} = \{\dot{I}_m\} f W^{2/3}$, where f is a function of food density, defined on (0, 1).
8. The scaled functional response f depends hyperbolically on food density X: $f = X/(K + X)$, where K is a constant.
9. Differentiation stops and reproduction starts at size W_j.
10. Initially, size and storage are $(0, S_0)$, where the initial egg storage, S_0, is a number such that no assumption is violated.
11. The animal dies as soon as assumption 3 has to be violated.
12. At constant food density, growth $\dot{W}$ is of the von Bertalanffy type after birth, i.e. $\dot{W} = \dot{\rho} W^{2/3} - 3\dot{\gamma} W$, where $\dot{\rho}$ and $\dot{\gamma}$ are positive and constant.
13. At constant food density, the ultimate size, W_∞, is proportional to f^3.
14. At constant food density, $1/\dot{\gamma}$ is linear in f.
15. Energy expenses on growth are non-decreasing with increasing size-specific storage for an animal of a certain size.

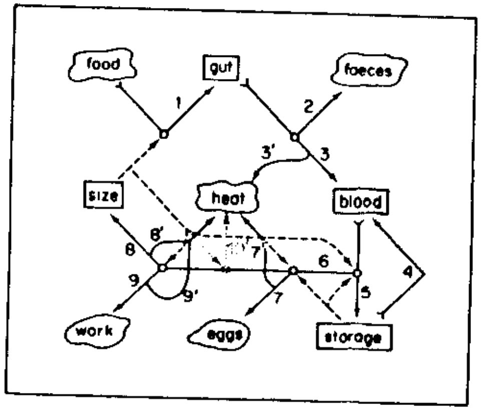

FIG. 1. Energy flow through an animal. Rates: 1. ingestion, 2. defecation, 3. assimilation, 4. mobilization, 5. demobilization, 6. utilization, 7. reproduction, 8. growth, 9. maintenance, 10. heating (only in endotherms). Symbols: → energy flow, ⇢ information flow, ○ decision valve, ′ heat loss rate, □ state variable, ⬭ source or sink.

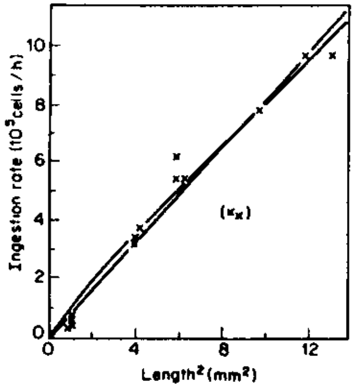

FIG. 2. Measured ingestion rate $\dot{I}$ of *Chlorella pyrenoisoda* cells as a function of body length L of *Daphnia magna* at 20°C and 10^5 cells per ml. The measurements are based on counts of resin particles (± 5 μm ϕ) in resuspended faeces of individual daphnids by means of laser optics. The concentration of resin particles is 4 to 7 times 10^3/ml. The function $\dot{I} = \dot{a}L^b$ has been fitted by least squares. The value obtained for $b = 1{\cdot}81$ (95% c.i.: 1·59, 2·03), not significantly different from 2. this leads to $\dot{I} = \dot{a}L^2$ with $\dot{a} = 0{\cdot}81$ (95% c.i.: 0·76, 0·85) cells/(h × mm²).

animals after birth, because the (relative) size increase is much larger before birth than after, and because the interpretation of respiration data before birth is not complicated by the process of feeding and reproduction). The second basis for the assumption that routine metabolic rate is proportional to size is that only if it is so, can the scaling parameter for the respiration rate be somewhere between 2/3 and 1. This will be clarified in the next section.

In the appendix, it is shown how the change in the state variables, size W and size-specific storage $[S]$, can be derived from the assumptions given in Table 1, the

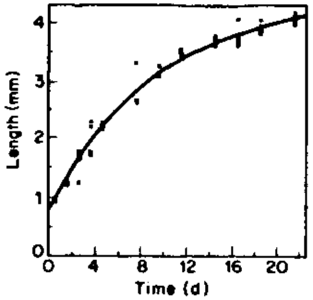

FIG. 3. The measured change in length L in individuals of *Daphnia magna* at 20°C, in 40 ml, supplied with 10^8 cells of *Scenedesmus subspicatus* a day. The curve is of the von Bertalanffy type: $L(t) = L_\infty - (L_\infty - L_0)\,e^{-\dot{\gamma}t}$, where L_0, L_∞ and $\dot{\gamma}$ are parameters and t the time.

result being

$$\dot{W} = \{(W^{2/3}[\dot{A}_m][S]/[S_m] - W\dot{\zeta}/\kappa)/([S] + \eta/\kappa)\}_+$$
$$[\dot{S}] = [\dot{A}_m]\,W^{-1/3}\{(W \geq W_b)X/(K + X) - [S]/[S_m]\}$$

where X is food density, the dots indicate rates or derivatives with respect to time and $(W \geq W_b)$ has a value of 1 or 0 if true or false. The parameters, which are assumed to be constants for a species in a constant environment (apart from, possibly, a fluctuating food density), are described in Table 2. The initial size is a model parameter, W_b and the size-specific storage at birth has to be equal to that of the mother at the moment of egg formation, if it is to be consistent.

TABLE 2

Parameters of the energy budget model

Symbol	Dimension	Interpretation	Symbol	Dimension	Interpretation
W_b	length³	Birth size	κ		Proportion of utilized energy channelled to growth and routine metabolism
K	biomass · length⁻³	Food density resulting in half the max. input	$\dot{\zeta}$	energy · length⁻³ · time⁻¹	Size specific routine metabolic rate
$[\dot{I}_m]$	biomass · length⁻² · time⁻¹	Surface area specific maximum ingestion rate	η	energy · length⁻³ ·	Energy requirement for a unit increase in size
$[\dot{A}_m]$	energy · length⁻² · time⁻¹	Surface area specific maximum assimilation	$[S_m]$	energy · length⁻³	Size specific maximum storage

In Kooijman (1986*a*), the energy content of an egg has been derived on basis of the assumptions given in Table 2. This is necessary for the calculation of the reproduction rate, i.e. the energy channelled into reproduction ($(\kappa - 1)$ times the utilization rate in situations of growth), divided by the energy investment per egg.

The energy content of the gut has not been modelled as a state variable, because its relaxation time is assumed to be small with respect to that of the storage. This seems to be reasonable for animals like daphnids, in which the gut residence time at 20°C can be as short as 20 min. For animals with a large stomach, this assumption may not be appropriate, but the model would still apply in comparing different but constant food inputs.

The state variable energy content of blood only appears implicitly in assumption 1 because of its low energy capacity and small relaxation time. For the purpose in hand, we only have to deal with the utilization rate, and not with the mobilization and demobilization rates indicated in Fig. 1. Substitution of the equations for the assimilation rate and the storage change rate from the appendix, shows that the utilization rate in situations of growth equals

$$\dot{C} = \{([S]/[S]+\eta/\kappa)\}\{W^{2/3}(\eta/\kappa)[\dot{A}_m]/[S_m]+W\dot{\zeta}/\kappa\}.$$

This equation will be used in the next section.

The different types of energy losses in the form of heat indicated in Fig. 1 are supposed to be fixed fractions of the energy flows involved. (This is in contrast to endotherms, where there is also another type energy drain to heat production for the purpose of heating the body. This flow rate is an order of magnitude larger (see Kooijman, 1986*a*).) Therefore there is no need to model them explicitly. They only show up in the values of the parameters. The parameter η, for instance, will be larger than the energy released in the decomposition of a unit of body tissue, partly because of its entropy or "information content", and partly because of the heat loss involved in growth.

Energy losses in movements have not been modelled explicitly here. In fact they are considered to be negligible as compared with the other energy flows. If they do not happen to be negligible, it may be that average energy losses in movements can be written as a weighted sum of size and surface area. In that case, the formulas do not change, but only the parameter values of $\dot{\zeta}$ and $[\dot{A}_m]$, which increase and decrease, respectively.

The present paper does not deal with the estimation of parameter values from experiments (this is dealt with in Kooijman, 1986*a*), but some remarks on the von Bertalanffy growth curve might be appropriate here. There is a lot of literature showing that von Bertalanffy growth curves fit experimental data on a wide variety of species very well. This is in itself remarkable because most of them concern data on animals in field situations, where food density is usually not constant nor abundant. Computer simulation studies which will be reported elsewhere show the energy storage, as introduced here, flattens out rather wild fluctuations in food density. This (partially) explains the fit.

First, we will consider how a number of variables depend on size within a species, and, secondly, how they do so between species.

3. Body Size Relations in Animals of the Same Species

Energy is normally stored in the form of carbohydrates, proteins and, especially, lipids. The utilization of the energy involves oxygen consumption and a carbon dioxide production. In animals with empty guts, ($\dot{A} = 0$), the respiration rate therefore corresponds to the utilization rate in previous section. As shown in Table 3, at constant food density, it can be written as a weighted sum of $W^{2/3}$ and W, which can appear almost linear in a log-log plot with a slope somewhere between 2/3 and 1 (Fig. 4). Although we have assumed that routine metabolic rate increases linearly with size, the increase in respiration rate with size is less steep, owing to the decreasing amount of energy invested in growth and reproduction. In the case of ectotherms, there is no reason to believe that these flows are negligible in short term measurements of respiration rates. Although the actual size increase during this measurement may be negligible, the energy invested in (the overhead of) this increase may not. In endotherms, routine metabolism, including heat production, dominate. (An endotherm eats ten times as much as an ectotherm of comparable size (Farlow, 1976).) It follows that large endotherms are more efficient than small ones, because they lose relatively less energy in cooling. The routine metabolic rate being proportional to size, the fact that the scaling parameter of the respiration is less than one does not necessarily imply that large ectotherms are more efficient users of energy than small ones, and we should seriously consider the possibility that they are not.

TABLE 3

Some quantities Y expressed as a function of size W and the best fitting scaling parameter b in the allometric equation $\ln Y = a + b \ln W$. *Where this relation is not strictly linear, the maximum range for b is indicated*

Quantity	Equation	Scaling parameter within species	 between species
Max ingestion rate	$\dot{I}_m = [\dot{I}_m]W^{2/3}$	2/3	1
Max filtering rate	$\dot{F}_m = [\dot{I}_m]W^{2/3}/K$	2/3	2/3
Saturation constant	$K = \dot{I}_m/\dot{F}_m$	0	1/3
Max assimilation rate	$[\dot{A}_m]W^{2/3}$	2/3	1
Routine metabolic rate	$\dot{\zeta}W$	1	1
Threshold food density	$KW^{1/3}/([\dot{A}_m]/\dot{\zeta}-W^{1/3})$	≥1/3	1/3
Thresh. ingestion rate	$W\dot{\zeta}[\dot{I}_m]/[\dot{A}_m]$	1	1
Max size	$W_m = (\kappa[\dot{A}_m]/\dot{\zeta})^3$	0	1
Max storage	$[S_m]W$	1	4/3
Threshold storage	$W^{4/3}\dot{\zeta}[S_m]/[\dot{A}_m]$	4/3	4/3
Max starvation time	$W^{1/3}([S_m]/[\dot{A}_m]) \ln\{[\dot{A}_m]/(\dot{\zeta}W^{1/3})\}$	−1/3 to 1/3	1/3
Abundance	(max/threshold ingestion)$^{-1}$	−1 to −2/3	−1
Max growth rate	$(4/27)W_m(\dot{\zeta}/\kappa)/([S_m]+\eta/\kappa)$	0	2/3
Max respiration rate	$\dot{C}_m = (W^{2/3}W_m^{1/3}\eta/\kappa + W[S_m])\dot{\zeta}/(\eta+\kappa[S_m])$	2/3 to 1	2/3 to 1
Birth, adult size	$W_b,\ W_j$	0	1
Min pre-reprod. period	$J = (3/\dot{\zeta})(\eta+\kappa[S_m]) \ln \dfrac{W_m^{1/3}-W_b^{1/3}}{W_m^{1/3}-W_b^{1/3}}$	0	1/3
Max egg storage	$S_0 \cong W_b[S_m]\{1-1/4(W_b/W_m)^{1/3}\}^{-3}$	0	4/3
Min water loss in eggs	$S_0 - W_b[S_m]$	0	4/3
Min incubation time	$\dfrac{3\kappa}{2\dot{\zeta}}[S_m]^{3/4}\left(\dfrac{S_0}{W_m}\right)^{1/4} \times \left(\dfrac{1}{2}\ln\dfrac{\upsilon^2+\upsilon\sqrt{2+1}}{\upsilon^2-\upsilon\sqrt{2+1}} + \arctan\dfrac{\upsilon\sqrt{2}}{1-\upsilon^2}\right)$ where $\upsilon = \{4(W_m/W_b)^{1/3}-1\}^{-1/4}$	0	1/3
Max reproductive rate	$\dot{R}_m = (1-\kappa)\dot{C}_m/S_0$	2/3 to 1	−2/3 to −1/3
Max pop. growth rate	$\dot{R}_m/(1+\dot{R}_mJ)$	—	−2/3 to −1/3

In the literature, it has been observed several times that there exists a negative correlation between the von Bertalanffy growth parameter $\dot{\gamma}$ and the ultimate size; see e.g. Duineveld & Jenness (1984). This observation has been used by Knight (1968), to assault the von Bertalanffy model as a reasonable model for growth. In order to remove this correlation, Gallucci & Quin (1979) suggested the transformation $3\dot{\gamma} = kW_\infty^{1/3}$. In the appendix, the ultimate size at constant food density is found

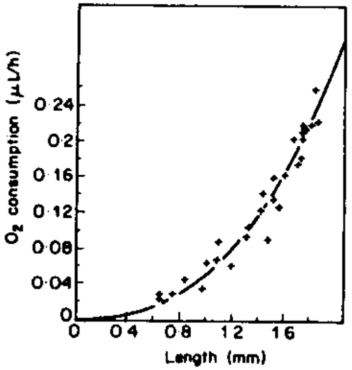

FIG. 4. Respiration rate of *Daphnia pulex* with few eggs at 20°C as a function of length. Data are from Richman (1958, Table 5). The fitted curve is $0{\cdot}0336L^2+0{\cdot}01845L^3$, and is indistinguishable from the curve $0{\cdot}0516L^{2{\cdot}437}$.

to be $W_\infty=(f\kappa[\dot{A}_m]/\dot{\zeta})^3$. Substitution in the expression found for $\dot{\gamma}$ gives $(3\dot{\gamma})^{-1}=\eta/\dot{\zeta}+W_\infty^{1/3}[S_m]/[\dot{A}_m]$. Apart from $\eta/\dot{\zeta}$, which has a small numerical value (Kooijman, 1986*b*), the proposed transformation indeed renders $\dot{\gamma}$ independent of $W_\infty^{1/3}$. Based on the present model, this dependence is caused by the dynamics of stored energy, and it by no means detracts from the von Bertalanffy model as a model for growth at a constant food density. (The parameter $\dot{\zeta}/\eta$ can be shown to the so-called maintenance rate constant, which appears only in the microbial literature, but which deserves wider attention (see Kooijman, 1986*b*). There are indications that the maintenance rate constant increases in the sequence bacteria, daphnids, fish and birds, and decreases in the sequence bacteria and algae, suggesting lines of evolutionary development.)

The reasoning set forth in the previous section has many additional consequences. We shall briefly consider starvation processes, because these are ecologically interesting. Suppose that an animal experiences a period of starvation after a period of constant food supply. From the storage balance equation for the dynamics of the size-specific storage, together with growth being zero, we see that the storage decreases exponentially until the utilization rate equals the routine metabolic rate. Any further decrease in storage would cause death by starvation. When the animal is about to die, we can calculate the minimum storage, the time to death by starvation and the threshold food density (see Table 3), i.e. the food density at which the animal is just able to survive for a long period, (or $\dot{A}=\dot{C}=\dot{M}$, growth and reproduction being zero), as functions of the parameters and the size of the animal. The threshold food density is a hyperbolic function in $W^{1/3}$. Therefore, small animals can survive at food densities at which large ones cannot. Since size tends to increase with age, (which trivially holds at constant food density), the average age of the population decreases in periods at the beginning of starvation. The effect of a temporary drop in food density reflected in the time until death by starvation depends on the parameter values. In the order of the values for *Daphnia magna*, the large ones tend to die a little earlier than the small ones, but the differences are slight. This has been verified experimentally (Kooijman, 1986*a*). As we shall see, this behaviour constrasts with that of animals of different species.

From the energy preservation law it follows that the energy spent on reproduction equals $\dot{C}-\dot{M}-\eta\dot{W}$. Substitution of the energy investment in growth shows that the reproductive rate is simply related to the utilization rate, viz. $(W\geq W_j)(1-\kappa)\dot{C}/S_0$ in the growth region of the state space and $(W\geq W_j)(\dot{C}-\dot{M})/S_0$ in the no-growth region, $(W\geq W_j)$ taking the values 1 or 0 if true or false, and S_0 being the initial storage, i.e. the energy investment per young. The expression for S_0, given in Table 3 is derived in Kooijman (1986*b*). As storage at birth is in assumption 12 laid down to be $S_b=[S_m]fW_b$ for a mother feeding at (constant) input level *f*, the energy consumed during the egg stage, $W<W_b$, equals S_0-S_b. In animals like birds, this use of energy corresponds to the loss of water in eggs, because the metabolic degradation of yolk, releases water that would drown the chicken if it did not evaporate. This water includes water arising from the metabolism of energy-rich chemicals, as well as water deriving from the watery matrix in which these chemicals, are embedded for the purpose of degradation and transport. The observation that loss of water from bird eggs corresponds to the use of energy, and so with S_0-S_b will be used in the next section. The derivation of the incubation time is given in Kooijman (1986*b*). In the growth region of the state space, the reproduction rate is thus proportional to the utilization (or respiration) rate. So their size dependences are similar. See Kooijman (1984) for a test against experimental data.

The pre-reproductive period at constant food density is obtained from the inverse function of size as a function of age, which is a rather simple function due to the von Bertalanffy growth from size W_b (see Kooijman, 1986*a*).

4. Body Size Relations in Animals of Different Species

Within a species, the nine parameters listed in Table 2 are assumed to be constant in a constant environment (apart from, possibly, a fluctuating food density). This is because the energy budget model is basically a model for growth. Any change in the parameter values would immediately result in a violation of one of the assumptions (in particular of assumption 12). The maximum size W_m an individual can reach (at a high age and with an abundance of food), can be written as a function of three parameters (see Table 3). Species that differ in this maximum size therefore have to differ in one or more of these three parameters. Consistent with the basic model formulation, we shall assume that the size specific routine metabolic rate and the fraction of the utilization rate channelled into differentiation or reproduction do not depend on the (maximum) size. This implies that the parameter for the assimilation, $[\dot{A}_m]$, scales with $W_m^{1/3}$. The maximum assimilation rate itself, which is given by $[\dot{A}_m]W^{2/3}$ (see Table 3) therefore scales with W_m, so the scaling parameter is 1.

Since the ingestion rate is assumed to be proportional to the assimilation rate, the ingestion rate also scales with W_m. Farlow (1976) gives a scaling parameter of 0·88 for the ingestion rate, but I also fits the data well. The maximum ingestion rate as well as the threshold value scales with W_m, so we may expect the abundance of species of body size W_m to scale with W_m^{-1}, very nearly what was found by Peters (1983). For filter feeders, where filtering rate $\dot{F}$ is ingestion rate $\dot{I}$ divided by food density so that $F=[\dot{I}_m]W^{2/3}/(K+X)$, the shape parameter K of the Holling functional response can be interpreted as the quotient of maximum ingestion rate and maximum filtering rate, i.e. in absence of food so that $K=\dot{I}_m/\dot{F}_m$. If the filtering rate is dependent on the surface area of the filtering apparatus, it scales with $W_m^{2/3}$ (see Brendelberger & Geller, 1985), so the shape parameter scales with $W_m^{1/3}$ and the threshold food density with $W_m^{2/3}$. This means that a constant environment tends to select for small species, because they are able to outcompete the large ones. Fluctuating environments, on the other hand, tend to select for large species because the time until death by starvation scales with $W_m^{1/3}$. (Threlkeld (1976) found a scaling parameter of 1/4, but 1/3 also fits the data well.) In contrast to what has been found in the previous section for animals of the same species a large specimen of a large species is thus better equipped to survive a period of food shortage than a small specimen of a small species. Brook & Dodson (1965) observed that in the absence of predators, the larger species of zooplankton dominate. On basis of the present theory, the explanation does not lie in the size dependence of the threshold food density as they suggested (because this would operate the other way round), but in the length of periods during which no animal can find sufficient food. This has been confirmed experimentally by Goulden & Hornig (1980).

In order to couple the maximum storage capacity to the maximum energy intake, we assume that the size-specific maximum storage, $[S_m]$ scales with the parameter $[\dot{A}_m]$, i.e. with $W_m^{1/3}$ and that the birth size as well as the size at the end of the pre-reproductive period scales with W_m. These two assumptions complete the scaling relations for the parameters of the energy budget model collected in Table 2. We can now derive expressions for a variety of observable quantities such as maximum growth and minimum pre-reproductive period, write them as functions of the parameters and size and judge how they would behave in a log-log plot against size. In making this judgement, we must remember that the parameters are constants within a species, but allometric functions of size between species. Some of the expressions for the quantities collected in Table 3 then result in proper allometric functions, and so they are linear in a log-log plot against size. Some of the other expressions are not quite linear, but only approximately so (see legend to Fig. 4). In that case the maximum possible range of the scaling parameter is indicated in Table 3, if one nevertheless wishes to fit a linear relationship (in deference to tradition in biological literature). When comparing the results with data from the literature, we should bear in mind that, if the energy budget model really holds, the reported values for the scaling parameter should fall somewhere in this range, depending on the species included. From an analysis of the equations given in Table 3, it follows that the respiration rate scales with about $W_m^{3/4}$, as we also found within a species, a result that has frequently been found (see introduction). It also follows that maximum growth scales with $W_m^{2/3}$, which fits Calow & Townsend's data (1981) very well, that the minimum pre-reproductive period scales with $W_m^{1/3}$, which very well fits Bonner's data (1965) as given in Pianka (1978); that the energy investment per young, which correspond to egg size, scales with $W_m^{4/3}$ in ectotherms; that the water loss from bird eggs scales with $W_m^{4/3}$, i.e. with (egg size)^1; as found by Rahn *et al.* (1979), that incubation time scales with $W_m^{1/3}$, i.e. with (egg size)$^{1/4}$; as found by Rahn *et al.* (1974) and by Kooijman (1986*b*); and that maximum reproductive rate scales with $W_m^{-1/3}$, the exponent being close to the value of $-1/4$ given in e.g. Peters (1983), (in view of the data). It is interesting to note that, the maximum reproductive rate $\dot{R}_m$ decreases with increasing species size, not, as many authors have suggested, because size-specific routine metabolic rate, but size-specific storage depends on size. The same holds for the duration of the pre-reproductive period, which increases with species size. Since only the age of the mother when she gives birth for the first few times is relevant in the population growth rate and the duration of the pre-reproductive period J is small, and reproduction once started, soon reaches its maximum rate, the population growth rate can be approximated by $\dot{R}_m/(1+\dot{R}_m J)$, and consequently scales with $W_m^{-1/3}$. Considering the proliferation in microbial populations, we can assume that division occurs at given cell size (see Kooijman, 1986*a*). The division interval then corresponds to the expression given for the pre-reproductive period. Since the population growth rate is inversely proportional to the duration of this interval, it scales with $W_m^{-1/3}$. This fits the protozoa data of Fenchel (1974) well, who gave a scaling parameter of $-1/4$. Basic feature of this scaling is that ingestion rate is proportional to the surface area $W_m^{2/3}$. This appears to be particularly relevant for ciliates feeding by phagocytosis, but perhaps less so for bacilli, which change their shape during growth, because the rod diameter remains constant. In the latter case, the population growth rate is independent of cell size and ingestion rate scales with size. This relates to the findings of Banse (1976, 1982) who found a scaling parameter of $-1/4$ and 0, respectively.

Conclusions

Central to the reasoning outlined above are the Holling functional response, the diagram of Fig. 1, and the von Bertalanffy growth equation (von Bertalanffy, 1934). Though popular several decades ago, this growth equation has lost a great deal of its appeal, primarily owing to the observed scaling of respiration rate with body size. This argument does not appear to be a valid one; the scaling parameter of the respiration rate is smaller than that of the routine metabolic rate owing to less and less energy being invested in growth and reproduction with increasing size. The reason lies in the assimilation rate scaling with surface area for animals of the same species. In the considerations given above, I have not attempted to predict the value of the scaling parameter in body size relations correctly to two decimal places. Such an attempt at accuracy is bound to fail, because of the many biological exceptions to general tendencies in body size relations, and because body size relations are not necessarily of the allometric type. With reference to the aim of this paper, the gist of the reasoning is, in fact, that many of the relations between physiological variables and body size can be predicted simultaneously from an elementary knowledge of energy budgets. I have not devised my energy budget model to explain body size relations correctly, but to describe detailed observations of the feeding, growth and reproduction behaviour of daphnids. In explaining body size relations, storage considerations have proved to be more essential than has been recognized. These relations work out to be different for animals of the same species than for animals of different species. The most striking divergence is in the reproductive rate and in the starvation time. The energy budget model suggests that the environment selects for body size as a compromise between, on one hand, small, because small animals can better survive low food densities and, on the other, large, because large animals can better survive periods of starvation. If starvation periods last too long, however, the population numbers will follow the fluctuations in food density more closely. In that case, the environment will select for small species because of their large population growth rate. Conversely, the model indicates that there is an optimum relation of body size to the time scale in which fluctuations in food density take place.

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REFERENCES

Banse, K. (1976). *J. Phycol.* 12, 135.
Banse, K. (1982). *Limnol. Oceanogr.* 27, 1059.
von Bertalanffy, L. (1934). *Arch. f. Entwicklungsmech.* 131, 613.
Bonner, J. T. (1965). *Size and Cycle: an essay on the structure of biology.* New York: Princeton University Press.
Brendelberger, H. & Geller, W. (1985). *J. Plankton Res.* 7, 473.
Brooks, J. L. & Dodson, S. I. (1965). *Science* 150, 28.
Calder, W. A. (1984). *Size, Function and Life History.* Cambridge, Mass: Harvard University Press.
Calow, P. & Townsend, C. R. (1981). In: *Physiological Ecology.* (Townsend, C. R. & Calow, P. eds). Oxford: Blackwell Scientific.
Conover, R. J. (1978). In: *Marine Ecology, vol. 4 Dynamics.* (Kinne, O. ed.). pp. 221–499. New York: Wiley.
Duineveld, G. C. A. & Jenness, M. I. (1984). *Mar. Ecol. Prog. Ser.* 19, 65.
Farlow, J. O. (1976). *Ecology* 57, 841.
Fenchel, T. (1974). *Oecologia* 14, 317.
Galluccia, V. F. & Quinn, T. J. II (1979). *Trans. Am. Fish. Soc.* 108, 14.
Goulden, C. E. & Hornig, L. L. (1980). *Proc. natn. Acad. Sci. U.S.A.* 77, 1716.
Holling, C. J. (1959). *Can. Entomol.* 91, 385.
Knight, W. (1968). *J. Fish. Res. Bd. Canada* 25, 1303.
Kooijman, S. A. L. M. (1986*a*). In *The dynamics of physiologically structured populations.* (Metz, J. A. J. & Diekmann, O. eds). Springer Lecture Notes in Biomathematics. Berlin: Springer Verlag.
Kooijman, S. A. L. M. (1986*b*). *J. math. Biol.* 23, 163.
Kooijman, S. A. L. M. & Metz, J. A. J. (1984). *Ecotoxicology and Environmental Safety* 8, 254.
McMahon, T. A. & Bonner, J. T. (1983). *On size and life.* New York: Scientific American Books.
Peters, R. H. (1983). *The ecological implications of body size.* Cambridge: Cambridge University Press.
Phillipson, J. (1981). In: *Physiological Ecology.* (Townsend, C. R. & Calow, P. eds). pp. 20–45. Oxford: Blackwell Scientific.
Pianka, E. R. (1978). *Evolutionary Ecology.* New York: Harper & Row.
Richman, S. (1958). *Ecol. Monogr.* 28, 273.
Schmidt-Nielsen, K. (1984). *Scaling; Why is animal size so important?* Cambridge: Cambridge University Press.
Smith, S. (1957). In: *The physiology of fishes, vol. I.* (Brown, M. E. ed.). p. 323. New York: Academic Press.
Threlkeld, S. T. (1976). *Freshwater Biol.* 6, 489.
Vidal, J. & Whitledge, T. E. (1982). *J. Plankton Res.* 4, 77.
Vleck, C. M., Vleck, D. & Hoyt, D. F. (1980). *Amer. Zool.* 20, 405.

APPENDIX

Derivation of the Energy Budget Model

The change of the state variables, size and W and size-specific storage $[S]$ can be derived from the assumption listed in Table 1 as follows.

The energy channelled into differentiation or reproduction (cf. assumption 9) can (always) be written as a fraction $1-\kappa(W,S)$ of the utilization rate $\dot{C}$. This fraction may be a complicated function of the state variables. So the fraction channelled into maintenance plus growth equals $\kappa(W,S)\dot{C}=\dot{M}+\eta\dot{W}$, where the maintenance, $\dot{M}$, is given by $\dot{M}=\dot{\zeta}W$, and $\dot{W}$ stands for growth, i.e. the change in size, W. Assumption 1 states that the utilization rate, $\dot{C}$, equals $\dot{C}=\dot{A}-\dot{S}$, where $\dot{S}$ is the change in storage, S, and the assimilation rate, $\dot{A}$, is proportional to the ingestion rate, $\dot{I}$ (assumption 5), which is given by assumptions 6, 7, and 8. So we have $\dot{A}=[\dot{A}_m]fW^{2/3}$. On the basis of assumption 8, this type of ingestion rate is known as the Holling functional response (see Holling, 1959).

At constant food density X, the storage after birth can be written as a function, S^*, of size, W, and the scaled input $f=X/(K+X)$ (see assumption 8), so $\dot{S}^*=\dot{W}\,\partial S^*/\partial W$. Substituting this and the von Bertalanffy growth, $\dot{W}=\dot{\rho}W^{2/3}-3\dot{\gamma}W$ given in assumption 12, in the equation obtained above, $\kappa(W,S)(\dot{A}-\dot{S})=\dot{\zeta}W+\eta\dot{W}$, we can solve $\partial S^*/\partial W$, obtaining

$$\partial S^*/\partial W=(f_1+g_1W^{1/3})/(f_2+g_2W^{1/3}),\ \text{with}\ f_1=[\dot{A}_m]f-\dot{\rho}(f)\eta/\kappa;\ f_2=\dot{\rho}(f);$$
$$g_1=-\dot{\zeta}/\kappa+3\dot{\gamma}(f)\eta/\kappa \quad\text{and}\quad g_2=-3\dot{\gamma}(f).$$

From assumption 2 we have that the size-specific storage, $[S]=S/W$, is independent of the partitioning rule κ, so $\partial^2S^*/(\partial\kappa\,\partial W)=0$ for all values of W. For primes denoting derivation with respect to κ considered as a function of time we have that

$$\frac{\partial^2S^*}{\partial W\,\partial\kappa}=\frac{f_1'f_2-f_1f_2'+(f_1'g_2+f_2g_1'-f_1g_2'-f_2'g_1)W^{1/3}+(g_1'g_2-g_1g_2')W^{2/3}}{(f_2+g_2W^{1/3})^2}$$

has to vanish for all values of W, from which it follows that $(f_1/f_2)'=0$ and $(g_1/g_2)'=0$. This gives

$$\dot{\rho}'(f)=\dot{\rho}(f)^2\eta/(f[\dot{A}_m]\kappa^2) \quad\text{and}\quad (3\dot{\gamma}(f))'=(3\dot{\gamma}(f))^2\eta/(\kappa\dot{\zeta})-3\dot{\gamma}(f)/\kappa.$$

Solution of these differential equations gives $\dot{\rho}(f)=[\dot{A}_m]f/(\eta/\kappa+\partial S^*/\partial W)$ and $3\dot{\gamma}(f)=(\dot{\zeta}/\kappa)/(\eta/\kappa+\partial S^*/\partial W)$. Since $\dot{\rho}$ and $\dot{\gamma}$ are independent of size W, and so the ultimate size W_∞, which from $\dot{W}=0$ is given by $W_\infty^{1/3}=\dot{\rho}/(3\dot{\gamma})=[\dot{A}_m]f\kappa/\dot{\zeta}$, we have that κ is independent of size. From assumption 13 we also have that κ is independent of f, so κ is the same for different constant food densities. Since $\dot{\rho}$ and $\dot{\gamma}$ are independent of size, we also have that $\partial S^*/\partial W$ is independent of size, W, so S^* has the form $S^*=h(f)+g(f)W$. Assumption 1 states that growth utilizes stored energy, not directly assimilation energy. Therefore $\partial S^*/\partial W$, which is equal to $g(f)$, in $\dot{\rho}$ and $\dot{\gamma}$ has to be replaced by $S^*/W-h(f)/W$, which is only independent of f and W for $h(f)=0$. So we have $S^*=g(f)W$ or $[S^*]=g(f)$ for $[S^*]=S^*/W$. In accordance with assumption 1 f in $\dot{\rho}$ has to be written as a function of S, so f is replaced by $g^{-1}([S^*])$, where g^{-1} is the inverse function of g, i.e. $g^{-1}(g(f))=f$. We now obtain

$$\dot{W}=\dot{\rho}W^{2/3}-3\dot{\gamma}W=\{W^{2/3}[\dot{A}_m]g^{-1}([S^*])-W\dot{\zeta}/\kappa\}/(\eta/\kappa+[S^*]).$$

Growth depends on stored energy, S^*, as the only variable that is changing (it changes even when food density is constant), and it does so on its momentary value and not on earlier ones. We can therefore drop the asterisk and apply the equation for growth in situations of fluctuating food density. If however, the food density is fluctuating, the state variables can attain values they cannot attain at constant food density. These values correspond to growth becoming negative in the equation above. Assumption 15 in fact means that, in those situations, priority is given to differentiation or reproduction over growth, which ceases. The dynamics of the size-specific storage, $[\dot{S}]=\dot{S}W-S\dot{W}/W^2$, is now found from the balance equation, $\dot{S}=\dot{A}-\dot{C}$, to be $[\dot{S}]=[\dot{A}_m]W^{-1/3}\{f-g^{-1}([S])\}$.

Assumption 14 states that $1/\dot{\gamma}$ is linear in f, so g is proportional to f, say $g(f)=[S_m]f$, which implies that g^{-1} is proportional to $[S]$ and vice versa. In other words: the size-specific storage obeys a simple first-order process if and only if $1/\dot{\gamma}$ is linear in f. To summarize the final result, we have that the change of the state variables is given by

$$\dot{W}=\{(W^{2/3}[\dot{A}_m][S]/[S_m]-W\dot{\zeta}/\kappa)/([S]+\eta/\kappa)\}_+$$

$$[\dot{S}]=[\dot{A}_m]W^{-1/3}\{(W\geq W_b)X/(K+X)-[S]/[S_m]\}$$

where $(W\geq W_b)$ has value 1 or 0 if true or false, in accordance with assumptions 6 and 5. The model would be much simpler to derive if we assumed that κ is constant, in which case we can drop assumption 12 that growth at constant food density is of the von Bertalanffy type. The reason for not doing this lies in the experimental testing of the assumptions. It is very difficult to measure the different energy flows to growth, maintenance and reproduction directly. Among other things, we have to disentangle the heat losses involved in these processes and measure other forms of overheads (see text).