Abundance–body size relationships: the roles of metabolism and population dynamics

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Summary

1. Species’ abundance scales approximately as an inverse power of body mass. This property has been explained on the basis of metabolic rates of organisms of different sizes.
2. This paper considers the additional effect of population dynamics on the abundance–body size relationship, on the grounds that mass flow through food webs also depends on interactions between predators and their prey. To do this, an analysis of simple dynamical food-chain models was carried out, using rate parameters which scaled with body mass according to empirically based rules.
3. The analysis shows that a function for the abundance–body size relationship derived from metabolic theory is a good first approximation to a function derived for food chains at dynamic equilibrium, although the mechanistic interpretation of terms in the functions is not the same.
4. The results are sensitive to assumptions about the scaling of the self-limitation of basal species with respect to body size. Depending on the assumption made, the abundance–body size relationship may have a power parameter –1 at all trophic levels, or be described by different functions at different trophic levels.

Key-words: abundance-mass scaling, energetic equivalence rule, linear biomass hypothesis, metabolic theory.

Introduction

Many properties of species scale with body mass according to a power law relationship $Y = a m^\alpha$, where $Y$ is the trait value and $m$ is species body mass. Such properties include ingestion rate, metabolic rate, growth rate, birth rate, death rate and generation time (Peters 1983). One of the best documented ecological relationships is that between body mass and mass generation time (Peters 1983). One of the best documented metabolic theory provides an argument to explain the species' abundance scales approximately as an inverse power of body mass. This property has been explained on the basis of metabolic rates of organisms of different sizes.

This paper considers the additional effect of population dynamics on the abundance–body size relationship, on the grounds that mass flow through food webs also depends on interactions between predators and their prey. To do this, an analysis of simple dynamical food-chain models was carried out, using rate parameters which scaled with body mass according to empirically based rules.

The analysis shows that a function for the abundance–body size relationship derived from metabolic theory is a good first approximation to a function derived for food chains at dynamic equilibrium, although the mechanistic interpretation of terms in the functions is not the same.

The results are sensitive to assumptions about the scaling of the self-limitation of basal species with respect to body size. Depending on the assumption made, the abundance–body size relationship may have a power parameter –1 at all trophic levels, or be described by different functions at different trophic levels.

Key-words: abundance-mass scaling, energetic equivalence rule, linear biomass hypothesis, metabolic theory.

Here $\alpha$ is the ratio of total metabolic rate at adjacent trophic levels, $\beta$ is ratio of body sizes at adjacent trophic levels (the predator : prey size ratio), and $K$ is a constant. The values of $\alpha$ and $\beta$ are assumed to remain unchanged at all adjacent pairs of trophic levels. The reasoning behind the relationship starts from an observation that an individual’s metabolic rate scales approximately as $m^{3/4}$ (Kleiber 1932; Peters 1983; West, Brown & Enquist 1997), and hence the total metabolic rate $B_i$ at trophic level $i$ scales as $x_i m_i^{3/4}$. The argument assumes that, irrespective of trophic level, the ratio of $B_i$s at adjacent trophic levels all have the same value $\alpha$. So $B_i$ at trophic level $i$ is related to the total rate of metabolism of basal species, $B_t$, by $B_i/B_t = \alpha^{-i}$. In a similar way, the body size of an organism at trophic level $i$ is related to the body size $m_i$ of one at trophic level 1 as $m_i/m_1 = \beta^{-i}$. Taking logarithms, this means that $i - 1 = \log(m_i/m_1)/\log(\beta)$, and therefore that $B_i/B_t = \alpha^{-i} (m_i/m_1)^{\log(\beta)/\log(\beta)}$; using the laws of logarithms, this gives $B_i/B_t = (m_i/m_1)^{\log(\beta)/\log(\beta)}$. Algebraic manipulation of these relationships results in eqn 1. Taking values $\alpha = 0.1$ and $\beta = 10 000$, ...
the power parameter is \(-1\), corresponding to the approximate empirical relationship (Brown et al. 2004).

This paper considers the effect of population dynamics on the relationship between abundance and body mass at dynamic equilibrium. The motivation for this is that, in addition to basic matters of metabolism, the transfer of energy through ecological communities depends on the behaviour of predators and prey, and how this behaviour impacts on their population dynamics.

There are two different ways in which dynamics can be incorporated, depending on what is meant by body size. The first takes body size as being fixed for a species, and is used in the metabolic theory and much research on food webs (e.g. Cohen, Jonsson & Carpenter 2003; Brown et al. 2004; Woodward et al. 2005; Brose, Williams & Martinez 2006). The second allows body size of individuals to change as feeding takes place so a species (or some aggregation of species) is represented by a spectrum of sizes at different densities (Silvert & Platt 1978, 1980; Camacho & Solé 2001; Benoît & Rochet 2004; Maury et al. 2007a,b). We use the former approach here, as this is in keeping with the approach used in metabolic theory.

Although metabolic theory does recognize that dynamics could leave their mark on equilibrium population densities (Brown, Allen & Gillooly 2007), the quantitative effects of food-chain dynamics on eqn 1 have not previously been studied. There are also empirical matters left unresolved by the metabolic argument such as the large amount of unexplained variation around the predicted relationship (Peters & Raedlas 1984; Juanes 1986; Robinson & Redford 1986; Horn 2004; Long et al. 2006), and differences in the relationships at different trophic levels (Long et al. 2006; Blanchard unpublished). Loeuille & Loreau (2006) and Rossberg et al. (2008) give related analyses on the emergence of the energetic equivalence rule; these use more complex communities and are not amenable to a formal analysis of scaling.

The simple population-dynamic approach developed here is based on a chain of three species with Lotka–Volterra dynamics, but it extends to a larger class of dynamical systems at equilibrium. This makes the comparison with metabolic theory conservative: discrepancies between metabolic theory and population dynamics are likely to be greater when more details of predator–prey interactions are introduced. The analysis shows that population dynamics generate a relationship between abundance and body size close to that observed in nature, and that the metabolic model (eqn 1) (Brown & Gillooly 2003; Brown et al. 2004) emerges as a good approximation to this relationship. A feature of the results is that different forms of intraspecific competition in the basal species generate different scalings within trophic levels elsewhere in the food chain, and can offer an explanation for nonlinear relationships between log abundance and log mass sometimes observed in nature. Small differences in scaling of abundance with body size within trophic levels could, however, be hard to detect in practice. It is important to be aware that the reduction of interactions in food webs to a single ratio \(\beta\) of predator to prey mass used in metabolic theory and the corresponding analysis here greatly simplifies a complex ecological process.

### Materials and methods

#### Dynamics and equilibrium point

We investigated the role of population dynamics in determining abundance-mass scalings by considering a three-species food chain with simple population dynamics. The basal autotrophic species is labelled species 1; the primary consumer and the top consumer are labelled species 2 and species 3, respectively. Each species, \(i\), was considered to consist of individuals of a fixed body size \(m_i\). Consumer species were assumed to be \(\beta\) times larger than their resource species. Therefore, \(m_2 = \beta m_1\), and \(m_3 = \beta^2 m_1\), where \(\beta\) is fixed. To be explicit about flows of energy, the dynamics were given in terms of a transformed state variable, the biomass density \(y_i\); this is the population density multiplied by species body size, i.e. \(y_i = x_i m_i\). The dynamical system takes the form:

\[
\begin{align*}
\frac{dy_1}{dt} &= y_1 (\xi - c_1 y_1 - c_{12} y_2) \\
\frac{dy_2}{dt} &= y_2 (-\xi + c_1 y_1 - c_{23} y_3) \\
\frac{dy_3}{dt} &= y_3 (-\xi + c_2 y_2),
\end{align*}
\]

where the \(\xi\) are intrinsic rates, the \(c_i\) are interaction terms between species, and \(c_{ij}\) is a self-limitation term for the basal species. All parameters are positive. The equilibrium point at which all species have positive densities from eqns 2 is

\[
\begin{align*}
y^{eq}_{1*} &= \frac{c_{23} y^{eq}_{2*} - c_{12} y^{eq}_{1*}}{c_{12} y^{eq}_{1*}}, \\
y^{eq}_{3*} &= \frac{\xi}{c_{23}}, \\
y^{eq}_{2*} &= \frac{c_{31} y^{eq}_{3*} - c_{23} y^{eq}_{2*} - c_{12} y^{eq}_{1*}}{c_{12} y^{eq}_{1*} c_{31} y^{eq}_{3*}}.
\end{align*}
\]

If this equilibrium point exists (i.e. gives positive biomass densities for all species), it is globally stable (Hofbauer & Sigmund 1988, pp. 63–64).

#### Scaling of model parameters \(\xi\) and \(c_{ij}\)

Intrinsic rates \(\xi\) were assumed to scale as \(m_i^{14}\), in keeping with the available data (Blueweiss et al. 1978; Brown et al. 2004).

Self-limitation of the basal species \(c_{11}\) was assumed to scale as \(m_i^{14}\). This was motivated by the linear biomass hypothesis (Sheldon, Prakash & Sutcliffe 1972; Sheldon, Sutcliffe & Paranjape 1977), which states that, across a wide range of body sizes, biomass density is approximately independent of body mass. With logistic growth, the equilibrium biomass density in the basal species \(y^{eq}_{1*}\) in the absence of other species, is \(y^{eq}_{1*} = \xi/c_{11}\). As the rate parameter of species 1 has the scaling \(\xi = p_1 m_1^{14}\), biomass density is independent of body mass if \(c_{11} = D_1 p_1 m_1^{14}\), where \(p_1\) and \(D_1\) are mass-independent constants.

The per unit mass effect of the biomass of species \(j\) on consumer species \(i\), \(c_{ij} (i < j)\), was assumed to scale as \(m_j^{14}\). We show later that this assumption, together with the assumptions about scaling in the \(\xi\) and \(c_{11}\) above, has the consequence that the per unit mass consumption rates, \(c_{ij}^{eq}\), are proportional to \(m_j^{14}\). This is equivalent to a per-capita feeding rate of the consumer which scales with...
consumer body mass as $m^{3/4}$, a result that has been observed in empirical studies (Peters 1983).

The per unit mass effect of the biomass of species $i$ on consumer species $j$, $e_{ij}$, is smaller than $e_{ii}$, related through a conversion efficiency, $\lambda$, with which prey biomass is converted into predator biomass. In general, this efficiency is equivalent neither to Lindeman’s progressive efficiency (Lindeman 1942) nor to the efficiency used by Brown et al. (2004).

Rate parameters were partitioned into terms dependent on mass, and constants $p_i$ and $D_{ij}$ independent of mass: $\gamma_i = p_i m_i^{-3/4}$, $c_{ij} = D_{ij} m_i^{-3/4}$ ($i < j$), and $c_{jj} = D_{jj} m_j^{-3/4}$ ($i = j$). Analytical work kept this general form for $c_{ij}$ but simulations were explicitly modelled as $c_{ij} = \lambda c_{ij} = \lambda D_{ij} m_j^{-3/4}$ ($i < j$), where $\lambda$ is the conversion efficiency.  

SCALING OF ABUNDANCE WITH MASS

Relationships between equilibrium biomass density and body mass for species within trophic levels in a three-species chain were found by incorporating the mass scalings of the parameters into the equilibrium values (eqns 3). Population densities were obtained from biomass densities using the relationship $x_i = y_i/m_i$. This method generalizes to a food chain of arbitrary length (Appendix S1). Within-trophic-level scaling gives the relationship that would be observed if data from distinct food chains were grouped together in a meta-analysis as is often the case in empirical studies.

The more general scaling of abundance with mass across trophic levels is less tractable than the scaling within trophic levels. To describe the multitrophic pattern, analytical expressions were derived for the line through log abundance and log mass at each trophic level (see Appendix S1 for the extension to an arbitrary number of trophic levels). In log space, this relationship becomes

$$\Delta = \frac{1}{2} \log \lambda \left( \sum_{m} \log m \gamma_i - 2 \sum_{m} \log y_i \gamma_i \right) - 1,$$

(eqn 4)

(see Appendix S2 for derivation). Note that, although $\Delta$ is expressed as a function of $\gamma_i$ here, it is still the power parameter for the mass scaling of $x^*$ used in metabolic theory (eqn 1).

Results

SCALING OF POPULATION DENSITY WITH MASS: WITHIN TROPHIC LEVELS

The scaling of population density with mass, within each trophic level, is the same at all trophic levels (Fig. 1a). This is because all rate terms $\gamma_i$, $c_{ij}$, and $e_{ij}$ ($i \neq j$) are proportional to $m_i^{-3/4}$. From the structure of the equilibrium biomass densities (eqns 3), the effects of body size then cancel out and the $y^*_i$ are independent of body size, scaling with $m_i^0$. This in turn implies that the equilibrium population density within trophic levels scales like $m_i^{-3/4}$, that is, $x^*_i = k_i m_i^{-3/4}$ irrespective of trophic level (see Appendix S1 for the extension to an $n$-species food chain). In log space, this relationship becomes

$$\log x^*_i = -\log m_i + \log k_i.$$  

Thus the relationship between log abundance and log mass at each trophic level is a straight line with slope $-1$, with an intercept dependent on the constant of proportionality, $k_i$, determined by the $p$, and $D_{ij}$ parameters. In other words, the gradient is independent of trophic level, whereas the intercept depends on trophic level.

A consequence of the independence of equilibrium biomass densities from body size is that the feeding rate $c_{ij} y^*_i$ of a consumer $j$ (per unit biomass of $j$) carries only the scaling $m_i^{-3/4}$ from $y^*_i$. Equivalently, the feeding rate of $j$ (per capita of $j$) scales as $m_i^{-3/4}$. This corresponds to approximate empirical patterns (Peters 1983), and is consistent with consumers that feed to meet their basic metabolic requirements (Kleiber 1932; Peters 1983; West et al. 1997).

This match of the model and data only applies if all parameters scale as $m_i^{-3/4}$ with body size. We illustrate this
using a different scaling $m_i^{1/2}$ for the self-limitation of the basal species $c_{i1}$. This scaling is motivated by the energetic equivalence rule (Damuth 1981; Nee et al. 1991; Loeuille & Loreau 2006), which states that the amount of energy a population uses is independent of body size (Damuth 1981). The scalings in eqns 3 become: $y_i^* = k_i^{*} m_i^{\alpha_i}$, $y_i^* = k_i^{*} m_i^{\alpha_i}$, and do not in general give a feeding rate $c_{i1} y_i^*$ scaling as $m_i^{\alpha_i}$. (The $k_i^{*}$'s are mass-independent constants with $k_i^{*} > 0$, $k_i^{*} < 0$.) Equivalently $x_i^* = k_i^{*} m_i^{\alpha_i}$, $x_i^* = k_i^{*} m_i^{\alpha_i}$, so the relationships between abundance and log body mass are different at different trophic levels and at the top level it is nonlinear (Fig. 1b).

**Scaling of population density with mass: between trophic levels**

Substituting the equilibrium biomass densities from eqns 3 into eqn 4, together with the relationships $m_i = \beta m_i$ and $m_i = \beta^{1/2} m_i$, gives a between-trophic-level scaling relationship for log abundance with log mass:

$$\Delta = \frac{1}{2 \log \beta} \left[ \frac{\log \beta + \log \left( \frac{D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij}}{D_{ij} (D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij} - D_{ij})} \right)}{\log \beta} \right]$$

Eqn 5

across trophic levels in food chains of length three. This is independent of mass. It has the property that $\Delta$ approaches $-7/8$ as $\log \beta$ gets large, and that $\Delta$ approaches $-\infty$, as $\log \beta$ approaches 0. Figure 2 shows the dependence of $\Delta$ on $\log \beta$ for comparison with results from metabolic theory. The figure shows that $\Delta$ is in the region of $-1$ over the range of $\beta$ of biological interest, in keeping with the observed patterns of abundance and body size in nature. Moreover, the results from population dynamics and from the energetic argument (Brown & Gillooly 2003; Brown et al. 2004) are in approximate agreement when a conversion efficiency of $\lambda = 0.1$ is used in the dynamical eqn 5, and $\alpha = 0.1$ in the metabolic eqn 1.

Eqn 5 has a rather intricate dependence on the mass-independent constants of the population dynamics. The limiting behaviour of $\Delta$ as $\log \beta$ gets either large or small suggests a general form for the function

$$\Delta = \frac{C}{\log \beta} - \frac{7}{8}$$

Eqn 6

in which the term $C$ depends on the efficiency $\lambda$. To investigate this, we estimated $C$ from simulations of eqn 5 for seven values of $\lambda$ in the range 0–1, and 32 values of $\log \beta$ in the range 0–2.5–8, using randomized food chains. A function of the form

$$\Delta = \frac{a \log \lambda - b}{\log \beta} - \frac{7}{8}$$

Eqn 7

where $a$ and $b$ are parameters, gave a close fit to the average $\Delta$s as shown in Fig. 3. The general form of this function is similar to eqn 1 from metabolic theory (Brown et al. 2004), although the estimated parameter values depend on the mass-independent constants of the population dynamics and would change if different assumptions were made.

**Discussion**

**Comparison of metabolic and population-dynamic arguments**

The metabolic function given in eqn 1 (Brown & Gillooly 2003; Brown et al. 2004) is a good approximation in the
presence of simple population dynamics. For $\beta$ in the range $10^5$–$10^6$, a reasonable range in real world systems (Jennings & Mackinson 2003; Brown et al. 2004), the predictions of the metabolic argument with $\alpha = 0.1$ are similar to those of the population dynamics approach with $\lambda = 0.1$ in three-species food chains. All predict a power parameter in the approximate range $-1$ to $-1$, a range that covers many empirically observed values for between-trophic-level scalings (Damuth 1981; Boudreau & Dickie 1992; Jennings & Mackinson 2003; Long et al. 2006).

Some similarity between the results of metabolic theory and those of equilibrium population dynamics is expected if organisms simply feed to satisfy a fixed basal metabolic rate that scales with body mass. Although no direct assumption was made about metabolic rates in the population dynamics, a basic empirical feature, that per capita feeding rates scale as $m^{-3/4}$, does emerge from the equilibrium analysis as long as all rate terms scale as $m^{-3/4}$. It is important to note that the population dynamics contain a large amount of extra information in addition to metabolic rates. This is evident in eqn 5, which shows an intricate dependence on the mass-independent terms of the population dynamics, and these equations therefore carry information about predator–prey interactions absent in the metabolic function (eqn 1).

Although the functions from population dynamics (eqn 7) and metabolic theory (eqn 1) have similar structures, they have different mechanistic foundations. First, the term $-3/4$ in the metabolic function comes from the scaling of individual metabolic rate with body size and is independent of food-chain length. However, the corresponding term $-7/8$ in eqn 7 applies only to a food chain of length three and in fact varies from $-3/4$ when $n = 2$ to $-15/16$ as $n$ gets large (Appendix S3). Second, the ratio of total metabolic rates, $\log \alpha$, in eqn 1 is replaced by a function of mass-independent constants of the ecological rate terms in eqn 5. These rate constants carry details about predator–prey interactions that cannot be incorporated into $\log \alpha$. With the parameter values used in this study, the effect of such details was to make the power parameter $\alpha$ less negative than that of the metabolic function in the region of conversion efficiencies commonly observed (Fig. 2).

An important distinction between the metabolic and dynamical approaches is that the dynamical approach does not assume a constant ratio $\alpha$ of total metabolic rates at successive trophic levels. This assumption is needed in the metabolic argument to derive eqn 1 (Brown & Gillooly 2003; Brown et al. 2004), but is unlikely to hold in general, because factors other than an organism’s metabolic rate leave a footprint on equilibrium population densities. For instance, if there is an inherently high risk of mortality at the top trophic level, there is a corresponding reduction in the equilibrium density at this level that would not be evident in the metabolic argument. As in the case of the ecological efficiency (Slobodkin 1972), the ratio of total metabolic rates is better thought of as emerging from the underlying population dynamics, rather than as a fundamental ecosystem constant in its own right.

SCALING OF ABUNDANCE WITH BODY MASS WITHIN TROPHIC LEVELS

If all rate parameters scale in the same way with mass, then abundance scales with $m^{-3/4}$, within trophic levels irrespective of the level. This holds for food chains of any length. Metabolic theory (eqn 1) also leads to a fixed scaling with mass within trophic levels irrespective of level, although in this case the power parameter is $-3/4$ (Brown et al. 2004). Empirical support exists for both scalings (e.g. Damuth 1981; Peters & Wassenberg 1983; Peters & Raelson 1984; Robinson & Redford 1986; Schmid et al. 2000; Cermeño et al. 2006; Long et al. 2006).

In practice, such simple scaling within trophic levels is not usually observed simultaneously at all trophic levels (e.g. Peters & Wassenberg 1983; Peters & Raelson 1984; Juanes 1986; Robinson & Redford 1986; Long et al. 2006). Empirical studies often, though not invariably, show more negative scaling at higher trophic levels (Peters & Wassenberg 1983; Peters & Raelson 1984; Juanes 1986; Long et al. 2006), and dome-shaped relationships have also been observed (Brown & Maurer 1986; Morse, Stork & Lawton 1988; Boudreau & Dickie 1992; Marquet et al. 1995, 2005). In the model the simple scaling within trophic levels also disappears if rate parameters scale in different ways with body size, as in the case of the energetic equivalence rule (Fig. 1b). In this case there can be nonlinear dependence of log abundance on log body mass, including a dome-shaped relationship between log abundance and log mass, which can be observed under certain parameterizations. However, these analytical results come with the warning that the resulting per capita feeding rates would not, in general, scale as $m^{-3/4}$ as the approximate results from field studies suggest (Peters 1983).

CAVEATS AND EXTENSIONS

It is important to be aware that the results from population dynamics are based on food chains, as opposed to more complex webs, so that relationships within trophic levels aggregate species from different communities. Many empirical studies are also based on aggregated data of this kind (e.g. Damuth 1981; Peters & Wassenberg 1983; Peters & Raelson 1984), although this is not always the case (e.g. Schmid et al. 2000; Cohen et al. 2003; Mulder et al. 2005). The Lotka–Volterra dynamics used here are a very simple formalization of food-chain dynamics. They are, however, sufficient to demonstrate the importance of dynamics in the relationship between abundance and body size because effects of dynamics are unlikely to become less important as more complicated dynamical systems are investigated. However, the analysis generalizes to the equilibrium biomass densities on an arbitrary food web (not just a chain) with Lotka–Volterra dynamics. This is because the equilibrium densities still have the form of intrinsic rate parameters $r_i$ divided by a $c_i$ and multiplied by a product of ratios of $c_{ij}$. Thus the scaling of abundance with body mass remains the same in food webs of general topology. The approach should also extend to other kinds of dynamics with
more realistic functional responses. The general feature about such extensions is that they introduce new ecological parameters that may also scale with body mass, thereby increasing the richness of effects of dynamics on the abundance–body mass relationship still further.

Conclusions

Metabolic theory sets constraints within which food web dynamics can operate. However, organisms in food webs obviously do more than balance their metabolic energy loss through feeding on other organisms: (1) they live in environments with different extrinsic risks of mortality; (2) they differ in their rates of reproduction; (3) they have different behaviours in their search for food, and so on. To learn about the effects of such processes on the abundance–body mass relationship, abundance needs to be determined by a dynamic coupling of population densities across trophic levels, within the constraints set by energetics. The challenge for ecologists is to understand the rich variation in the relationship between abundance and body size that remains unexplained by metabolic theory once this dynamic coupling is in place.

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References


Supplementary material

The following supplementary material is available for this article.

Appendix S1. Derivation of within-trophic-level scalings for $n$-species food chains.

Appendix S2. Derivation of between-trophic-level scaling using matrix linear regression.

Appendix S3. Derivation of asymptotic behaviour as $\log(\beta) \to \infty$.

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