

Allometric growth, life-history invariants and population energetics

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Abstract

Population and community level processes must be at least partially determined by variation in the body sizes of constituent individuals, implying quantitative scaling relations can be extended to account for variation in those processes. Here we integrate allometric growth and life-history invariant theories, and use this approach to develop theory describing the energetics of stationary populations. Our predictions approximate, with no free parameters, the scaling of production/biomass and assimilation/biomass ratios in mammalian populations and work partially for fish populations. This approach appears to be a promising direction and suggests the need for further development of the growth and life-history models, and extensions of those theories.

Keywords

Allometric growth, allometry, bioenergetics, efficiency, life-history invariants, metabolism, population energetics, production, scaling.

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INTRODUCTION

Most ecological systems are characterized by inherent complexity and variability. This has led to much discussion on whether there are any general 'laws' or 'principles' to be discovered (Lawton 1999; Simberloff 2004), an absence of which would resign us to descriptive studies and case-specific inference. A macroecological approach seeks to highlight pattern at multiple scales of observation and levels of biological organization (Brown 1995, Maurer 1999, Brown *et al.* 2003, 2004). These patterns are often (but not always) attributable to surprisingly simple and general principles. Macroecological studies regularly ignore important variation on finer scales and detail about specific organisms or systems. Indeed, in many cases, context dependent and historically contingent factors may obscure more simple explanations. Nevertheless, general principles provide a broader context for understanding these idiosyncrasies. If general principles and simple models explain even some portion of the overall variation, then they are worth exploring as a baseline for more detailed theoretical developments.

Here we explore the integration of metabolic scaling theory (Brown *et al.* 2004) and life-history invariant theory (Charnov 1993, 2002) as a synthetic theory of population energetics. Organismal physiology, growth, and life history ultimately govern the energy transformations of populations

and communities. Many of the qualitative and quantitative relationships between individual and population level process rates are well explored and understood (Allen 1971; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; van Straalen 1985; Kooijman 2000; Kerr & Dickie 2001; de Roos *et al.* 2003; Savage *et al.* 2004). What is lacking, however, is a framework which allows quantitative comparative study among populations, species, and higher taxonomic groups. Such a framework should standardize mathematical functions describing growth, metabolic rate, and life history, allowing direct comparison of biologically meaningful parameters. We argue that the generality of physiological allometries and life-history invariants provides a foundation for similarly general theories of higher level energetics. We first review pertinent aspects of physiological allometries and life-history theory, and then demonstrate an application to the description of population energetics.

Allometric metabolism and growth

Past and recent theoretical and empirical research (Calder 1984; Schmidt-Nielsen 1984; West *et al.* 1997; Banavar *et al.* 1999; West *et al.* 2001; Brown *et al.* 2004) suggest that general allometric patterns exist that link body masses and energetics of organisms. Most famous is the power law scaling of metabolic rate (B) with body size (M), which takes the form,

$$B = B_0 M^{3/4} \quad (1)$$

where B_0 is a normalization constant with dimensions of power·mass^{-3/4}. West *et al.* (2001) have developed a general growth model based on this relationship. Assuming gross biosynthesis rates scale as metabolic rate, they introduced the parameter a , which simply is B_0 converted from dimensions of power·mass^{-3/4} to mass^{1/4}·time⁻¹ with a constant reflecting the energetic content of biomass. The parameter a reflects developmental constraints that vary between major taxonomic groups (mammals, birds, etc.), but are highly conserved within them. Assuming rates of maintenance-related energy use are proportional to body mass during an ontogeny (m) by a rate constant b , the growth rate is described by,

$$\frac{dm}{dt} = am^{3/4} - bm \quad (2)$$

Integrated across ages (x), and setting ($m = 0$ at $x = 0$), this becomes

$$m(x) = \left(\frac{a}{b}\right)^4 \left(1 - e^{-\frac{bx}{4}}\right)^4 \quad (3)$$

This equation, similar to the von Bertalanffy growth equation (von Bertalanffy 1957), shows that organismal mass, m , follows a sigmoidal growth curve over ontogeny that asymptotically approaches a maximum mass, M , where $M = (a/b)^4$. The rate constant b reflects the (energetic) turnover rate (time⁻¹) of body tissues, which describes the energetic costs of maintaining live biomass (West *et al.* 2001). Across species, within a given major taxonomic group the value of b scales with maximum body mass as $b \propto M^{-1/4}$. Note that growth efficiency (net assimilation/gross assimilation = $(am^{3/4} - bm)/am^{3/4}$) is highest in the earliest part of the curve and declines monotonically as it asymptotes.

Life-history invariants

Species life histories are highly variable and can be quite complicated. However, at least within higher taxa, several major life-history parameters exhibit body size allometries. Charnov has given us a new perspective on life-history variation, focusing on the prevalence of dimensionless numbers that are invariant with size (Charnov 1993, 2001, 2002; Charnov *et al.* 2001). These numbers reflect general life-history patterns among species of a major taxonomic group (e.g. mammals, fish, birds) after removing the dimensions of mass and time. They include αZ (age at maturity · mortality rate), C/Z (fraction of mass given to reproduction · mortality rate⁻¹), and b/Z (internal turnover rate · mortality⁻¹), and for some taxa I/m (mass at

birth · mass at maturity⁻¹). The invariance of αZ , C/Z , and (sometimes) I/m has been empirically documented (Charnov 2002), while b/Z is a theoretical result. We note that b/Z invariance is essentially a re-expression of the observation that lifespan scales such that lifetime mass specific energy fluxes are approximately constant despite interspecific variation in adult body size (Calder 1984).

These life-history invariants are usually taken to represent trade-off surfaces, and models have been proposed to show how they could represent outcomes of fitness optimization. These models generally assume some developmental constraint (often itself a dimensionless number) and show how the other invariants may have evolved in response to environmental variation (Charnov 1993, 2001, 2002; Charnov *et al.* 2001).

Parameters of general importance

The overall growth and life-history pattern that emerges is hierarchical. The universal form of the growth curve and consistency in allometric exponents most likely reflect very fundamental dimensional and biophysical constraints (West *et al.* 1997, 2001, West *et al.* 1999, Banavar *et al.* 1999; Ernest *et al.* 2003). Certain rates and relationships are highly conserved within major taxonomic groups (e.g. mammals, fish). These include the parameter a , describing gross biosynthesis rates. This parameter has been shown to have a fundamental relationship to body temperature (Gillooly *et al.* 2001, 2002). Body size differences within a group reflect variation in the parameter b , or physiological turnover rates (West *et al.* 2001). The values of the dimensionless invariants are also highly conserved within groups (but not among them), implying relationships between developmental and reproductive rates are more or less independent of physical and temporal scales.

In summary, the life-history invariants describe the general dimensionless features of a life history. The parameters a and b determine the actual scale of the life history in dimensions of mass and time. Note that b determines how fast the growth trajectory approaches the asymptotic size, but not necessarily the adult mass itself. The invariant b/Z , where Z is the mortality rate, constrains an organism's life cycle to a given region of the (dimensionless) growth curve. The parameter a determines the actual scale of the process on the body mass continuum (Fig. 1). As we shall see, this fact is important for a host of population level energetic rates. In general, this is because organisms which mature, reproduce, and die well before reaching their (energetic) asymptotic mass, M , will operate at a higher efficiency (i.e. they are able to devote a larger fraction of assimilated energy to growth) than those who spend large portions of their lives near their asymptotic size.

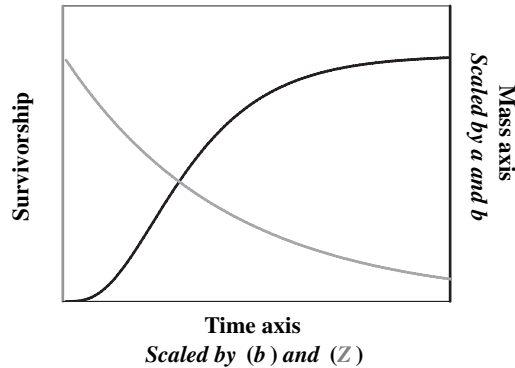


Figure 1 Growth (black, increasing) and survivorship (grey, decreasing) curves plotted as a function of time. The parameter a scales the mass axis among major taxonomic groups (e.g. mammals, fish), while b scales it within a taxon. Therefore the parameter b/Z is essentially how fast individuals die relative to how fast they approach their asymptotic size, and scales the two lines relative to each other. Ultimately the position of the survivorship curve relative to the growth curve determines population level energetic partitioning.

POPULATION ENERGETICS

Recently Cohen *et al.* (2003) proposed a 'trivariate' structure to the description of ecological communities with trophic position, abundance, and body size being the principle dimensions. From an energetic perspective, this framework is more complete than conventional food webs in that it explicitly describes community structure in terms of biomass and body size allometry and not just a static network topology. As those authors and Gillooly & Brown (2003) point out, the explicit flows, storages and transformations associated with metabolism are not directly incorporated into the trivariate framework. Cohen *et al.* suggest case-specific stage-structured population modelling while Gillooly and Brown suggest a more general (but less precise) approach based on allometry. While ultimately the ideal approach would depend on the availability of relevant data and the question one seeks to address, we follow Gillooly and Brown's conjecture and show how general taxon-specific population energetic parameters can be deduced from allometric and life-history theory. These parameters are potentially useful in understanding general patterns of taxonomic and body size distributions in communities.

Metabolism is the fundamental rate of individual energy flow and transformation, but its allometric dependence with body size is not in itself sufficient to describe the energetics of a population. The ecological literature relating a population's energetic rates, age and size distributions, and physiological growth curves is well developed. These studies have ranged from population-specific empirical analysis to

general, theoretical synthesis (Allen 1971; Banse & Mosher 1980; Humphreys 1981; van Straalen 1985; Odum 1994; Kooijman 2000; Kerr & Dickie 2001). This work has demonstrated the importance of metabolism, growth and life history to population energetics, but the qualitative and quantitative features of these models have remained phenomenological. We seek to formalize them in terms of the growth model and life-history invariants. The following theoretical development should be interpreted as a zeroth order model, in that we make many assumptions in order to demonstrate and evaluate the prospects of the approach. Part of the reason for this is ambiguity and uncertainty in the underlying models, and one of our main points is their need for further development. So in lieu of definitive answers we have favoured the simplest assumption wherever possible. Future work can relax our assumptions and explore more complicated and realistic situations.

Population energetics entails both the energetics of individuals and the structure and dynamics of the population. In the most general terms, energy is gained in a population through assimilation (A) stored in total population biomass (M_{tot}) and removed by respiration (R) and biomass mortality (L_Z). In a stationary population, biomass mortality (L_Z) is equal to production. At the population level, respiration consists of energy spent in the biosynthesis process, and biomass turnover because of physiological maintenance (L_b). These quantities and rates describe how much energy is needed to sustain a given stock of biomass, and how much of that energy is dissipated or remains biologically available in dead biomass. General relations for population energetic rates are presented as aggregates of individual rates in Table 1, along with a list of variables appearing in the text. The overbar denotes an average. Note that the mean of a quantity taken to a power is not necessarily the same as taking the mean of the quantity, then taking it to a power ($\overline{x^y} \neq \overline{x}^y$) (Pasztor *et al.* 2000; Savage 2004). Converting numbers to biomass, these can be aggregated into a mass balance equation similar to eqn 2, where $\overline{m_Z}$ is the average mass at death.

$$\frac{1}{M_{\text{tot}}} \cdot \frac{dM_{\text{tot}}}{dt} = \frac{A - L_b - L_Z}{M_{\text{tot}}} = a \cdot \frac{\overline{m^{3/4}}}{\overline{m}} - b - Z \cdot \frac{\overline{m_Z}}{\overline{m}} \quad (4)$$

For this exercise we assume steady-state energetics and stationary demographics and set the left side of eqn 4 to zero. Our goal is to re-express the phenomenological aspects of eqn 4 in terms of the growth parameters and life-history invariants. The quantities \overline{m} , $\overline{m_Z}$ and $\overline{m^{3/4}}$ can be determined from the stable size distribution $p(m)$. In a stationary population the probability density function of the age distribution equals the survivorship curve over its integral,

Table 1 Various parameters or variables appearing in the text

Parameter or variable	Description	Dimensions
a	Biomass assimilation parameter from growth model (West <i>et al.</i> 2001)	$\text{time}^{-1} \cdot \text{mass}^{1/4}$
b	Time constant reflecting physiological turnover rates of biomass, or energy dissipated for maintenance (West <i>et al.</i> 2001)	time^{-1}
M	Asymptotic organismal mass for a given species, equal to $(a/b)^4$	mass
m	Organismal mass	mass
M_{tot}	Total population biomass	mass
\bar{m}	Mean organismal mass in population	mass
$\bar{m}^{3/4}$	Mean 3/4 power of organismal mass	$\text{mass}^{3/4}$
\bar{m}_Z	Average mass at death	mass
N	Number of individuals	–
A	Assimilation Rate, $= N \cdot a \cdot \bar{m}^{3/4}$	$\text{mass} \cdot \text{time}^{-1}$
L_b	Population level physiological turnover rate, $= b \cdot \bar{m} \cdot N$	$\text{mass} \cdot \text{time}^{-1}$
L_Z	Population biomass loss rate due to mortality, $= Z \cdot \bar{m}_Z \cdot N$, at steady-state this is equivalent to population production	$\text{mass} \cdot \text{time}^{-1}$
ϵ	Biochemical efficiency of assimilation	–
R	Respiration rate $= L_b + (1/\epsilon - 1) \cdot A$	$\text{mass} \cdot \text{time}^{-1}$
E	Net growth efficiency $= \epsilon \cdot L_Z \cdot A^{-1}$	–
α	Age at maturity	time
m_α	Mass at maturity	mass
Z	Mortality rate	time^{-1}

$$p(x) = \frac{l(x)}{\int_0^\infty l(x) dx}$$

We can convert this to a size distribution by substituting in the inverse of the growth function and its derivative,

$$p(m) = \frac{l[x(m)]}{\int_0^\infty l(x) dx} \cdot x'(m) \tag{5}$$

where

$$x(m) = \frac{-4}{b} \cdot \ln\left(1 - \frac{bm^{1/4}}{a}\right)$$

and

$$x'(m) = (am^{3/4} - bm)^{-1}$$

Given a survivorship curve $l(x)$, one can integrate $p(m) \cdot m$ and $p(m) \cdot m^{3/4}$ to find \bar{m} and $\bar{m}^{3/4}$ respectively. We can now make use of the life-history invariants to further constrain eqn 4. In the life-history models, the mortality rate Z is assumed to be constant at all but the early juvenile stages. For simplicity, we ignore the early juvenile stages and assume mortality rate is constant through all age classes. Later we discuss this assumption further and how deviations from the assumption may affect our results. Under this simplifying assumption, we can return to eqn 4

and reduce it further. If Z is constant in all age classes, $\bar{m}_Z = \bar{m}^{3/4}$, leaving the second and third terms of eqn 4, $-b$ and $-Z$. We can then use eqn 3 to solve for b and Z in terms of the species-specific mass at maturity (m_α) and the taxon specific life-history invariants b/Z and αZ and growth. Setting ($x = \alpha$), eqn 3 becomes

$$m(\alpha) = \left(\frac{a}{b}\right)^4 \left(1 - e^{-\frac{b\alpha}{4}}\right)^4$$

We can then solve the equation for b and Z , as b/Z is invariant yielding biomass-specific predictions for the population-level rate of physiological turnover (L_b) and biomass production (L_Z), both expressed per unit standing biomass (M_{tot}).

$$\frac{L_b}{M_{\text{tot}}} = b = (a) \cdot \left(1 - e^{-\frac{b\alpha}{4}}\right) \cdot m_\alpha^{-1/4} \tag{6}$$

$$\frac{L_Z}{M_{\text{tot}}} = Z = \left(\frac{a}{b/Z}\right) \cdot \left(1 - e^{-\frac{b\alpha}{4}}\right) \cdot m_\alpha^{-1/4} \tag{7}$$

The key point here is that within a taxon, the coefficients of $m_\alpha^{-1/4}$ in eqns 6 and 7 are constants, as a , b/Z , and $b\alpha = b/Z \cdot \alpha Z$ are all invariant. With our assumption of demographic and energetic stationarity, we can indirectly find the population level assimilation rate (again per unit standing biomass, A/M_{tot}) as the sum of L_b and L_Z .

$$\frac{A}{M_{\text{tot}}} = a \cdot \frac{\overline{m^{3/4}}}{\overline{m}} = (a) \cdot \left(\frac{Z}{b} + 1\right) \cdot \left(1 - e^{-\frac{bZ}{4}}\right) \cdot m_{\alpha}^{-1/4} \quad (8)$$

Table 2 summarizes several of the population level rates from Table 1 in terms of the growth parameters and life-history invariants. The idea that population energetic rates should exhibit a negative 1/4 power scaling with body size has been put forward based on simpler arguments (Brown *et al.* 2004; Savage *et al.* 2004), but partitioning population energy budgets and making more specific quantitative predictions requires the further development explored here.

Testing the predictions

In order to test the predictions for a given taxon, values for a , αZ , b/Z are required. Here we focus on the population energetics of mammals and fish, which have the most complete sets of parameter estimates and data available to confront the predictions. The growth and life-history parameters a , αZ , and b/Z have been estimated to be $0.25 \text{ g}^{1/4}/\text{day}$, 0.7 , and 14 for mammals and $0.02 \text{ g}^{1/4}/\text{day}$, 2 , and 0.13 for fish respectively (Charnov *et al.* 2001; Charnov 2001; West *et al.* 2001). Biosynthesis efficiency (ϵ) is generally high and has been estimated to be *c.* 80% (Morowitz 1968). The values of a and αZ are empirical measurements while that of b/Z is the outcome of life-history models in both cases. It should be noted that these parameters are variable, reflecting interspecific differences in physiology and life history. However, we have chosen not to transfer that variation into our predictions because it is nearly impossible to separate measurement error from real biological variation. Table 2 gives predictions for the scaling and normalization for: (i) the mass specific rate of dead biomass production L_Z/M_{tot} , which under stationarity is equivalent to the traditional production/biomass ratio (P/B in traditional notation) and (ii) the ratio of assimilation to biomass A/M_{tot} . Plugging the values for the growth and life-history parameters for mammals yields the predictions: $L_Z/M_{\text{tot}} = 0.0164 m_{\alpha}^{-0.25}$, and $A/M_{\text{tot}} = 0.3059 m_{\alpha}^{-0.25}$.

Table 2 Population level energetic rates re-expressed as a function of growth and life-history parameters. In descending order, the scaling laws reflect mass specific assimilation, mass specific physiological turnover, mass specific population biomass production, and net growth efficiency

Population energetic parameter	Derived scaling law
$\frac{A}{M_{\text{tot}}}$	$\frac{a}{\epsilon} \cdot \left(\frac{Z}{b} + 1\right) \cdot \left(1 - e^{-\frac{bZ}{4}}\right) \cdot m_{\alpha}^{-1/4}$
$\frac{L_Z}{M_{\text{tot}}}$	$a \cdot \left(1 - e^{-\frac{bZ}{4}}\right) \cdot m_{\alpha}^{-1/4}$
$\frac{L_Z}{M_{\text{tot}}}$	$\left(\frac{a}{b/Z}\right) \cdot \left(1 - e^{-\frac{bZ}{4}}\right) \cdot m_{\alpha}^{-1/4}$
E	$\frac{1}{b/Z+1} \cdot \epsilon$

Likewise for fish, the predictions are $L_Z/M_{\text{tot}} = 0.0097 m_{\alpha}^{-0.25}$, and $A/M_{\text{tot}} = 0.0137 m_{\alpha}^{-0.25}$. Note that in addition to the exponent of the scaling relations, we are independently predicting the intercepts as derived from the growth and life-history parameters, eliminating any free parameters.

Data were taken from Banse & Mosher (1980) and Humphreys (1981) and body mass allometries were calculated for both fish and mammals. As mammals are deterministic growers, mass at maturity, average adult mass, and maximum mass are likely to be quite similar (West *et al.* 2001), it is reasonable to combine data that is reported using these variables. Banse and Mosher report mammal production/biomass as a function of average adult mass and Humphreys' report assimilation/biomass and production/biomass as a function of maximum mass. For fish, mass at maturity and maximum mass are likely to be quite different, so we only include Banse and Mosher's production/biomass data reported as a function of mass at maturity. We can, however, use Humphreys' (1979) calculation of efficiency (which he found to be size independent) to indirectly evaluate our assimilation/biomass prediction.

RESULTS

Mammals (Fig. 2a) exhibit scalings of $L_Z/M_{\text{tot}} = 0.0235 m^{-0.30}$ (coefficient 95% CI: ± 0.00762 , exponent 95% CI: ± 0.06) and $A/M_{\text{tot}} = 1.063 m^{-0.34}$ (coefficient 95% CI: ± 0.226 , exponent 95% CI: ± 0.047). Figure 2 plots these predicted and observed scalings as a function of mass. On the log-log plot, the intercept corresponds to the normalization constant, and the slope of the line to the exponent. The intercepts are not strictly comparable with the predictions without fixing a common exponent, and small differences in the fitted slope can have a very large effect on the intercept. As there is reason to expect a quarter power scaling, we fix the exponent at -0.25 in order to better evaluate our predictions for the normalizations. They then become $L_Z/M_{\text{tot}} = 0.0236 m^{-0.25}$ (coefficient 95% CI: ± 0.0043) and $A/M_{\text{tot}} = 0.834 m^{-0.25}$ (coefficient CI: ± 0.111).

From the fish data (Fig. 2b), $L_Z/M_{\text{tot}} = 0.0065 m_{\alpha}^{-0.27}$ (coefficient 95% CI: 0.0019 , exponent 95% CI: ± 0.16). Fixing a slope of -0.25 , $L_Z/M_{\text{tot}} = 0.0053 m^{-0.25}$ (coefficient 95% CI: ± 0.0012). Net growth efficiency for both fish and mammals, being simply $(\epsilon \cdot L_Z/A)$ does not vary with body size within a taxon (i.e. it scales as M^0) in these data as predicted because of the similar body mass allometries of L_Z and A . In accordance with this prediction, Humphreys (1979) found that efficiency is size-independent in fish and calculated it to be approximately 9.8%. However, our model predicts fish efficiency to be much higher (*c.* 70%). Although we do not have direct measurements of A/M_{tot}

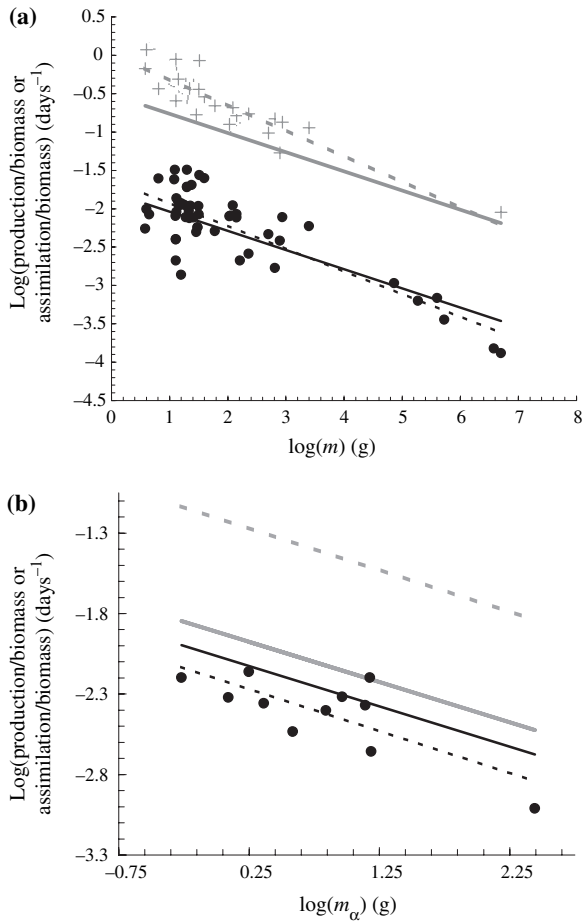


Figure 2 Logarithmic plot of L_z/M_{tot} (black) and A/M_{tot} (grey) vs. body mass for (a) mammals, (b) fish. For the mammal data and fish L_z/M_{tot} data, the dashed line represents a least squares regression of the data (Banse & Moshier 1980) and solid line represents the predicted scaling law. The dashed A/M_{tot} (grey) line for fish is an estimated assimilation/biomass scaling (see text) using the Banse and Moshier L_z/M_{tot} data and Humphreys' (1979) calculation of efficiency, and the solid grey line reflects our theoretical prediction.

as a function of mass at maturity, this efficiency estimate can be combined with the empirical L_z/M_{tot} data to indirectly provide an empirical estimate of A/M_{tot} . As our theoretical prediction approximates the empirical scaling of L_z/M_{tot} , the estimated A/M_{tot} scaling will reflect the efficiency estimate in being dramatically different.

DISCUSSION

These simple equations make use of growth parameters and life-history invariants to approximate the energetic scaling of mammal populations with no free parameters. It is important to note that our theory not only predicts the

scaling exponents governing population energetics, as has been performed before (Brown *et al.* 2004; Savage *et al.* 2004), but also the normalizations or 'height' of the scaling function. Although the empirical confidence intervals do not include our predicted values for the intercepts, they are within a factor of 2–3, which is very close given the lack of free parameters and simplicity of the models. We attribute the match between our predictions and the empirical data to the powerful constraints imposed by the taxon-specific life-history invariants and growth parameters. For fish, observed L_z/M_{tot} scaling is close to the prediction but there is a marked difference between the predicted and observed efficiency, and by extension our prediction of A/M_{tot} .

The assumptions of our model warrant further discussion. First of all, we have attributed all the energetic investment in reproduction to the growth of the next generation by assuming that $m = 0$ at $x = 0$ and not penalizing adult metabolism. The underlying life-history models for fish (Charnov *et al.* 2001) and mammals (Charnov 2001) differ on whether energy shunted to reproduction is indeed taken from the normal energy budget or whether total intake is increased. For simplicity we have not distinguished these two models. The assumption that is most likely to be violated is the assumption of constant mortality rate with organismal size. Mortality rates in fish are usually extremely high in the earliest age classes compared with adult stages. This, however, is not sufficient to explain the deviations from the model here. Attributing higher portions of biomass to the early life stages will raise predicted A/M_{tot} , but would also raise L_z/M_{tot} because efficiency would still be very high. This is because individuals at the earliest stages of the growth curve operate at a higher energetic efficiency than larger individuals. We point out that if the life-history invariant and growth parameter estimates for fish are indeed correct, an individual becomes reproductively mature at very small fraction of its asymptotic size. This seems inconsistent with observations that fish mass at maturity is a large fraction of asymptotic size, from the original Beverton–Holt invariants (Beverton & Holt 1959; Beverton 1992; Charnov 1993).

The assumption of constant mortality within age classes of a species, while simplistic, works here because of a general feature of life-history allometry. That is, whatever form $l(x)$ takes for any given species, it is likely to be quite variable; body size constrains the scale on which it manifests. Although real survivorship curves are complex for fish, and even if the parameterized model here fails to predict all the patterns, there is a simple scaling of fish population energetics with body size. This strongly suggests, if not demands, that there is a simple growth/life-history model underlying this major axis of variation.

Finally, we know populations are not stationary, they exhibit complicated dynamics in response to environmental

fluctuations and biotic interactions. The potential utility of general allometric and life-history models is to pull out the major axes of variation and constrain the well-explored theoretical space of ecological dynamics to the much smaller biologically meaningful space. This idea has been explored in elegant work based on allometry (Yodzis & Innes 1992). We take the point further, and propose that such models can be linked to parameters of growth models and dimensionless life-history parameters.

We have proposed a general approach that integrates the metabolic theory of allometric growth and life-history theory. We have shown how together these theories are attractive building blocks of higher order, yielding predictive models with no free parameters. However, it is clear that the growth and life-history invariant models are still very much a work in progress. The general form of the growth model appears to be robust among taxa, but certainly deserves more exhaustive investigation and quantification. The dimensionless approach to life histories, while innovative and powerful, has in many ways given us more questions than answers. The parameters highlighted here may ultimately be replaced by those from qualitatively different models, and it is our intention to engender further criticism and modification while preserving the generality of the theory. As a framework continues to develop, empiricists will have the context to make meaningful measurements that can be used for comparative study.

Most problems in ecology are confounded with the effects of body size (Peters 1983; Brown *et al.* 2004) and scale (Levin 1992). The generality of energetic allometries and life-history invariants does us an enormous favour; we can often remove much of the apparent variation among systems by appropriately scaling the dimensions of mass and time (West *et al.* 2001; Charnov 2002; Brown *et al.* 2004). The remaining variation is not only complex and interesting, it is also arguably more ecologically and evolutionarily relevant.

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