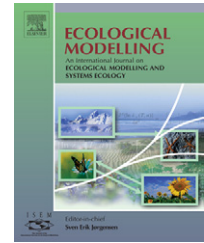




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The power of size: A meta-analysis reveals consistency of allometric regressions

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ABSTRACT

The recent revival of body size relationships in ecology has boosted our understanding of ecosystems. Here, a simple model, based on energy equivalency, integrates rate, age, density and area parameters that are important in ecological modelling. Allometric relationships for quantities as diverse as ingestion, mortality, age at maturity, maximum density, territory size of different species groups and trophic levels are derived from production and some ecological transfer efficiencies.

The theory is supported by a meta-analysis of 230 allometric regressions derived from over 100 publications. The relationships are shown to be mutually consistent and fit into the model. Rate constants generally decrease with organism mass at an exponent of $-1/4$. Age and density parameters increase in the same direction following a slope of $1/4$. Differences between plants, invertebrates, cold-blooded vertebrates and warm-blooded vertebrates are reflected in the intercepts and can be anticipated from temperature, trophic position and evolutionary history. Cold-blooded species have lower rate constants but reach higher ages and densities than equally sized warm-blooded organisms. Intercepts of body size distributions tend to decrease with trophic position, at a level that is predicted by ecological efficiencies.

Area parameters, such as the territory size and geographic range, tend to decrease with species size, but slopes and intercepts were often different from the expected value. Occasionally, outliers were also noted for rate, time or density parameters. With the model at hand, such deviations can be easily identified and subjected to more extensive empirical and theoretical research. With these restrictions, specific issues can now be addressed by a framework that complies with extensive information on related parameters.

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1. Introduction

For almost a century, biologists have been fascinated by the scaling of processes and patterns to body size (Kleiber, 1932;

Peters, 1983). Numerous plant and animal characteristics x have been correlated to organism mass m according to

$$x = \gamma m^{\pm\kappa} \Leftrightarrow \log(x) = \log(\gamma) \pm \kappa \log(m) \quad (1)$$

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In the last decade, various intriguing theories have been developed to explain why the slopes $\pm\kappa$ for rate, time, density and area parameters tend to be multiples of 1/4 or 1/3. A value of 1/3 is usually attributed to geometric area–volume ratios while 1/4 has been explained allometrically from metabolic restrictions imposed by transport of substances via branching networks (e.g., Heusner, 1982; West et al., 1997; Banavar et al., 1999; Jørgensen et al., 1999; Dodds et al., 2001; West et al., 2002; Enquist and Niklas, 2002; Savage et al., 2004). Although equally important for understanding and predicting biological phenomena, intercepts $\log(\gamma)$ and coefficients γ have received far less attention. Selecting the correct exponents and coefficients facilitates parameter setting of ecological models, especially for relatively unknown species. Allometric relationships provide body-size specific parameters instead of values that are arbitrary or taken from a well-known species.

Here, the variability of the slopes $\pm\kappa$ and, in particular, the coefficients γ for different parameters, taxons and conditions is explored by a meta-analysis on body size correlations. These separate relationships are brought together in a coherent framework to verify their consistency, needed to underpin assumed mechanisms and to identify exceptions. Regressions published in the last decades have been brought together in some reviews (Peters, 1983; Calder et al., 2000; Hendriks, 1999). In addition, some have studies have put a limited subset of these correlations into a general framework (e.g., Brown et al., 2004; Marquet et al., 2005). The present study combines both approaches to arrive at a general model with default parameter values for the intercepts. It is intended to help ecological and environmental modellers in selecting appropriate settings. Following good modelling practice, a distinction is made between calibration of principal constants, in particular transfer efficiencies and production rate constants, and independent validation of derived parameters.

2. Methods

Allometric regressions derived before 1983 were collected from an extensive review (Peters, 1983). Papers published afterwards were obtained in a literature search on ecological journals. Nearly all body size correlations were checked in the original papers (references for regressions given in Table S1 of the Supplementary Material). Collection and treatment of data by the authors was assumed to be adequate. Possible errors introduced by sampling and statistical techniques have been discussed extensively elsewhere (Dodds et al., 2001; Griffiths, 1998; Arneberg and Andersen, 2003). Some multi-modal relationships between density and body size were included as linear trends to allow comparison to other regressions.

Correlations with high coefficients of determination and high levels of significance were preferred but regressions with no or weaker statistics were taken into account if no alternatives were available. Occasionally, correlations were derived by myself from the original data. Where possible, deviating regressions were double-checked by consulting the authors of the papers. If there was no obvious artefact, outliers were included in the analysis to illustrate variability and possible other solutions found by nature. To allow for comparison, the

bewildering variety of units found was converted to wet weight kg (mass), km² (area) and days (time).

Quantities for body size correlations have been measured in various environments. Organisms kept for experimental, production and recreational purposes are supplied with substantial resources and protected against predators or pathogens. These artificial conditions allow estimation of minimum rate constants and maximum time and density parameters, reflecting endogenous or physiological restrictions. Average levels are obtained from field surveys that include exogenous or ecological limitations as well.

3. Theory

The flow and storage of energy, mass, nutrients and toxicants along food chains are characterized by various rate, age, density and area parameters (Table 1). Data on transfer efficiencies p and allometric regressions on rate constants k tend to be more abundant and consistent than those on time and density parameters. Consequently, efficiencies and rate constants are defined first. Plants obtain energy from available light with an interception efficiency $p_{n,1}$. Part of the plant production, called the ingestion efficiency $p_{n,2}$, is eaten alive by herbivores. Where needed, this fraction can be divided in sub-categories, such as foliovores, frugivores and granivores. The rest $1 - p_{n,2}$ dies and is consumed by detritivores and reducers. Likewise, carnivores and cadaverivores take in $p_{n,3}$ and $1 - p_{n,3}$ of the production by herbi-detritivores, respectively. The assimilation efficiency p_a is the fraction of the intercepted or ingested energy that is absorbed or digested by the organisms and spent on production and respiration. The amount directed to new biomass is represented by the production efficiency p_p . The production rate constant k_p (kg kg⁻¹ d⁻¹) is related to adult mass m as (Peters, 1983)

$$k_p = q_T \gamma_p m^{-\kappa} \quad (2)$$

where the coefficient γ_p represents the intercept standardized to 20 °C. The correction factor q_T depends on the actual temperature T and is derived from biochemical reaction kinetics as (Jørgensen et al., 1999; Gillooly et al., 2001).

$$q_T = e^{(E_a/1.4 \times 10^{-23})(T-20)/((T+273)(20+273))} \quad (3)$$

with 1.4×10^{-23} as the Boltzmann's constant and E_a as the activation energy.

From these primary parameters, many secondary quantities for rate, time and density can be conveniently derived. The production efficiency p_p equals $k_p/(k_r + k_p)$ by definition. This can be rewritten to arrive at an respiration rate constant k_r (kg kg⁻¹ d⁻¹) of

$$k_r = \left(\frac{1}{p_p} - 1\right) k_p = \left(\frac{1}{p_p} - 1\right) q_T \gamma_p m^{-\kappa} \quad (4)$$

where $1 - p_p$ is the fraction of the assimilation that is directed to respiration. The rate constants for interception of light by autotrophs and ingestion of food by heterotrophs k_n

(kg kg⁻¹ d⁻¹) are expected to be

$$k_n = \frac{k_p + k_r}{p_a} = \frac{k_p + ((1/p_p) - 1)k_p}{p_a} = \frac{k_p}{p_p p_a} = \frac{q_T \gamma_p}{p_p p_a} m^{-\kappa} \quad (5)$$

Rate constants for fluxes of air, water, nutrients, toxicants and other components can be obtained analogously (Hendriks, 1995; Hendriks and Heikens, 2001).

Time constants τ (d) are reciprocal to rate constants k (kg kg⁻¹ d⁻¹), and thus, expected to scale to mass m as $\tau \propto 1/k \propto 1/m^{-\kappa} = m^\kappa$. The age at maturity or first reproduction, τ_m is obtained from a sigmoid function for individual growth between egg mass m_e and final juvenile mass m_j as (West et al., 2001; Gillooly et al., 2002)

$$\tau_m = \frac{(1/2)^{1-\kappa} (1 - (1/2)^\kappa)}{k_p} \frac{1/\kappa}{(m_j/m)^\kappa} \ln \left(\frac{1 - (m_e/m)^\kappa}{1 - (m_j/m)^\kappa} \right) \\ \approx \frac{0.5 \dots 1.4}{q_T \gamma_p} m^\kappa \quad (\kappa = 1/4, \quad m_e/m < 0.1, \quad 0.5 < m_j/m < 0.9) \quad (6)$$

The factor $(1/2)^{1-\kappa} (1 - (1/2)^\kappa)$ reflects my assumption that the rate of individual growth at half of the final adult size m is equal to the average production k_p between the egg and adult stage.

The generation time or age at average reproduction τ_g is closely related to the juvenile period τ_m . By definition, age at first τ_m and average τ_g reproduction are equal for semelparous species that reproduce in a single clutch. In addition, maturation and generation time are nearly similar for expanding populations of iteroparous species that are dominated by initial reproduction. Under these conditions, the intrinsic rate of population increase $\max(r)$ (ind ind⁻¹ d⁻¹) can be estimated as (May, 1976)

$$\max(r) = \frac{\ln(\max(R_0))}{\tau_g} \approx 0.5 \dots 1.4 \ln(\max(R_0)) k_p \quad (7)$$

where $\max(R_0)$ represents the maximum lifetime fecundity (eggs ind⁻¹) under optimal conditions, that is, in the presence of sufficient food and absence of predators and pathogens.

The age at death τ_d can be obtained in two ways. In a stable population, mortality equals production and the residence time of an individual is

$$\tau_d = \frac{1}{k_p} = \frac{1}{q_T \gamma_p} m^\kappa \quad (8)$$

Alternatively, if each age class suffers from the same mortality k_p , the fraction surviving until cohort a equals $e^{-k_p a}$. The lifespan reached by half of the individuals yields the nearly identical value of (Hendriks, 1999)

$$\tau_d = \frac{-\ln(50\%)}{k_p} = \frac{0.69}{q_T \gamma_p} m^\kappa \quad (9)$$

The age of death τ_d and the corresponding rate of mortality k_p depend on physiological ageing and ecological interactions, such as starvation and predation. Unfortunately, field studies that cover both endogenous and exogenous causes are scarce. Instead, lifespan is often measured in artificial situations where organisms are fed and protected.

To allow testing to these data, one needs to derive an equation for the age at physiological death $\tau_{d,in}$ in the absence of ecological restrictions. One option is to assume that predation is the dominant exogenous cause in the field, so that the total death rate constant k_p can be sub-divided into exogenous $p_{n,i+1} k_p$ and endogenous $(1 - p_{n,i+1}) k_p$ mortality. The corresponding age at physiological death $\tau_{d,in}$ should now equal.

$$\tau_{d,in} = \frac{1}{(1 - p_{n,i+1}) k_p} = \frac{1}{(1 - p_{n,i+1}) q_T \gamma_p} m^\kappa \quad (10)$$

Eq. (10) implies that organisms die because of ageing after production of $\tau_{d,in} k_p = 1/(1 - p_{n,i+1})$ (kg kg⁻¹) tissue or respiration of $\tau_{d,in} k_r = 1/(1 - p_{n,i+1})(1/p_p - 1)$ biomass, independently of the species size and metabolic type. As an alternative, one may of course also use these invariant factors as a starting point.

If starvation rather than predation or ageing causes mortality, time to death is shortened to

$$\tau_s = \frac{1/2}{k_r} = \frac{1/2}{((1/p_p) - 1) q_T \gamma_r} m^\kappa \quad (11)$$

because, organisms die after they have lost about half of their body weight to respiration (Kleiber, 1961; Peters, 1983).

A flux through a trophic level can temporarily be stored in small organisms with a rapid turnover, short life span and low mass density (e.g., algae in oceans) as well as in large organisms with a slow turnover, long life span and high mass density (e.g., trees in forests). As an analogy, one may think of one river with a fixed discharge that flows through both small and large lakes with a short and long residence time, respectively. Just as the discharge is fixed, one may assume that the total energy flow in an area is invariant. This is known as the energy equivalency rule. To arrive at the same exploitation of resources, large species need to compensate lower rate constants $k \propto m^{-\kappa}$ by proportionally higher mass densities $N \propto m^\kappa$ (kg km⁻²). The total production F_i (kg km⁻² d⁻¹) at a trophic level i distributed over n_i species, each with a mass density N , can now be calculated from the input into the system F_0 and the fractions available for interception or ingestion $p_{n,i}$, assimilation $p_{a,i}$ and production $p_{p,i}$ as

$$F_i = F_0 \prod_{i=1}^i p_{n,i} p_{a,i} p_{p,i} \\ = \sum_{i=1}^{n_i} k_p N \\ = \sum_{i=1}^{n_i} q_T \gamma_p m^{-\kappa} \gamma_{N,i} m^\kappa \\ = n_i q_T \gamma_p \gamma_{N,i} \quad (12)$$

A reduction of the production at a level i due to smaller input F_0 or lower conversion efficiencies $p_{n,i}, p_{a,i}, p_{p,i}$ needs to be counterbalanced by a proportional diminution of the number of species n_i or the mass density coefficient $\gamma_{N,i}$. As will be shown later, regressions indicate that the production rate coefficient γ_p is invariant. Rewriting Eq. (12) yields the mass density for a species ($n_i > 1$) or trophic level ($n_i = 1$) as a function

of the (average) adult mass m .

$$N = \gamma_{N,i} m^\kappa = \frac{F_0 \prod_{i=1}^i p_{n,i} p_{a,i} p_{p,i}}{n_i q_T \gamma_p} m^\kappa \quad (13)$$

Area A is the inverse of density, and thus, expected to scale with $-\kappa$ if expressed per mass ($\text{km}^2 \text{kg}^{-1}$). The territory that one individual needs for its energy intake A_t ($\text{km}^2 \text{ind}^{-1}$) can now be derived as

$$A_t = \frac{m}{N} = \frac{1}{\gamma_N} m^{-\kappa+1} \quad (14)$$

A minimum territory $\min(A_t)$ is reached if all production from the previous trophic level is directed to one species ($p_{n,i} = 1$, $n_i = 1$). If the available energy is distributed over sub-categories, e.g. foliovores, frugivores and granivores or over competing species, the area needed to support an individual increases ($p_{n,i} \ll 1$, $n_i \gg 1$). The geographic range of a species A_r may be obtained by multiplying the individual territory A_t with the number of individuals needed for a viable population S as

$$A_r = A_t S = \frac{S}{N/m} \quad (15)$$

The theoretical model described-above will be compared to empirical data below. The values for the production rate coefficient γ_p , the efficiencies p and the temperature correction will be selected first (calibration). With these values at hand, all other rate, time and density parameters will be calculated

by the model and compared to measured values (validation) (Table 1).

4. Results and discussion

4.1. Slopes

Regressions for rate and time constants have slopes κ that vary around $\pm 1/4$ and $\pm 1/3$ (Table 2). Exponents for heterotherms are generally close to $\pm 1/4$, whereas, slopes for homeotherms are steeper and tend to cover both $\pm 1/4$ and $\pm 1/3$ (Table 2). Exponents of $\pm 1/4$ can be explained from allometric restrictions on distribution in networks (West et al., 1997; Banavar et al., 1999). Comparison of these theoretical models to the empirical regressions collected here thus suggests that heterothermic rates are controlled by the distribution of substances along vessels. Slopes of $\pm 1/3$ on the other hand, can be understood from transport governed by geometric area–volume relationships (Kleiber, 1932). The steeper slopes observed for warm-blooded species, indicate that homeothermic rates are also influenced by transport of a more geometric nature. The most obviously explanation would be diffusive heat dispersion via the skin. Such an explanation would resolve the controversy between geometric explanations of $\pm 1/3$ that are underpinned by warm-blooded data and allometric justification of $\pm 1/4$ supported by cold-blooded or overall assessments. Yet, a re-analysis of mammalian data indicate that their slopes may be closer to $1/4$ than previously calculated (Savage et al., 2004).

Table 1 – Main factors used in the equations

Symbol	Description	Unit	Value
A_t, A_r	Individual territory, species geographic range	km^2	Eqs. (14) and (15)
F	Mass production	$\text{kg km}^{-2} \text{d}^{-1}$	Eq. (12)
γ_p	Scaling coefficient for production	$\text{kg}^\kappa \text{d}^{-1}$	7.5×10^{-4}
i	Trophic level	–	1–4
k_p, k_r, k_n, r	Rate constants for production, respiration, light interception or food ingestion and population increase	d^{-1}	Eqs. (2)–(5)
κ	Scaling exponent	–	1/4
N	Mass density	kg km^{-2}	Eq. (13)
m_e, m_j, m	Egg, juvenile and adult mass	kg	Variable
p_n	Interception/ingestion efficiency	/	^a 0.2, ^b 1, ^c 0.8
p_a	Assimilation efficiency	/	^{ab} 0.02, ^c 0.2, ^d 0.4, ^e 0.8
p_p	Production efficiency	/	^{ab} 0.5, ^f 0.25, ^g 0.1, ^h 0.02
$\max(R_0)$	Maximum lifetime fecundity	eggs ind^{-1}	^f $g e^4$, ^h $e^{1.5}$
q_T	Temperature quotient	/	Eq. (3)
S	Number of individuals in a viable population	ind	10^4
T	Temperature	$^\circ\text{C}$	Variable
$\tau_m, \tau_g, \tau_d, \tau_{d,in}, \tau_s$	Age at first reproduction, average reproduction and death, endogenous death and survival time after starvation	d	Eqs. (6)–(11)

^a Aquatic plants.

^b Terrestrial plants.

^c Detritivores.

^d Herbivores.

^e Carnivores.

^f Invertebrates.

^g Cold-blooded vertebrates.

^h Warm-blooded vertebrates.

Table 2 – Average and 95% confidence interval of exponents κ for rate, time, density and area for the regressions plotted in Figs. 1–3

Parameter	Heterotherms	Homeotherms
Population production (d^{-1})	–0.25 (–0.29––0.21)	–0.35 (–0.48––0.23)
Individual growth (d^{-1})	–0.24 (–0.43––0.05)	–0.35 (–0.47––0.23)
Respiration (d^{-1})	–0.23 (–0.25––0.20)	–0.28 (–0.30––0.25)
Consumption (d^{-1})	–0.25 (–0.32––0.18)	–0.33 (–0.41––0.26)
Age at first reproduction (d)	0.23 (0.16–0.31)	0.29 (0.26–0.32)
Age at endogenous death (d)	0.21 (0.12–0.29)	0.20 (0.18–0.22)
Aquatic density (kg km^{-2})	0.36 (0.28–0.44)	–
Terrestrial density (kg km^{-2})	0.37 (0.22–0.51)	0.27 (0.15–0.30) ^a , 0.05 (–0.13–0.22) ^b
Individual territory (km)	0.70 (0.17–1.23)	0.88 (0.73–1.04) ^a , 1.20 (1.01–1.39) ^b

^a Herbivores and invertebrates.
^b (Including) vertebrates.

Mass density N (kg km^{-2}) increases with organism size (Fig. 3a and b). Exponents tend to decrease with the width of the mass range covered by the regressions, as has already thoroughly been demonstrated (Blackburn and Gaston, 1997). Slopes for density of aquatic invertebrates are often substantially steeper than the expected value of 1/4. Terrestrial plants, heterotherms and herbivorous or invertebratevorous homeotherms scale with exponents at or above 1/4, whereas, those for warm-blooded predators that feed on vertebrates are equal to or less than 1/4 (Fig. 3a and b, Table 2). It indicates that the model requires taxon specific differentiation or that the regressions suffer from artefacts.

Vice versa, slopes for the area occupied by individual cold-blooded carnivores and warm-blooded herbivores vary around 3/4, as expected from Eq. (14). Territories of warm-blooded carnivores scale with an exponent of 1.20, which deviates significantly from 3/4 and from the value of $1 - 0.05 = 0.95$, derived from the density correlations (Fig. 3c, Table 2). Area slopes that are steeper than expected from the density regressions and the model indicate an increase of territory overlap with increasing organism size. This has been related to social hunting, habitat fragmentation and territory defence (Haskell et al., 2002; Jetz et al., 2004).

For the generic approach in the present paper, a universal exponent of $\pm 1/4$ is used because it is covered by most confidence intervals for both cold-blooded and warm-blooded species. Moreover, intercepts for warm-blooded species are largely independent of the slope because the median mass of the correlations is often close to 1 kg.

4.2. Efficiencies and temperature

For an approximate check of the consistency between different parameters, we need generic values for the transfer efficiencies p and temperature correction q_T . Sun irradiation enters the atmosphere at the solar constant of $1.2 \times 10^{11} \text{ kJ km}^{-2} \text{ d}^{-1}$ but the visible light useful to primary producers F_0 is about $7.6 \times 10^9 \text{ kJ km}^{-2} \text{ d}^{-1}$ at the earth surface (Whittaker, 1975). Dense plant communities on land absorb all incoming light, viz. the interception efficiency $p_{n,1}$ equals 100%. Aquatic producers intercept only $p_{n,1} = 20\%$ because of various factors including loss to extinction and adaptation in (turbid) waters

(Duarte and Kalff, 1987; Sand-Jensen and Krause-Jensen, 1997). About $p_{a,1} = 2\%$ of the light energy intercepted by plants is converted to gross production (Whittaker, 1975). The fraction of the primary production removed alive by herbivores $p_{n,2}$ does not depend on the plant productivity and is about 50% for aquatic communities and 10% for terrestrial systems (Whittaker, 1975; McNaughton et al., 1989; Cyr and Pace, 1993). The remaining $1 - p_{n,2}$ is directed towards detritivores and reducers. The dominant cause of death for herbi-detritivores themselves is reported to be predation (Strayer, 1991; Prins and Olff, 1998). In the absence of a quantitative review, the ingestion efficiency for carnivores $p_{n,3}$ is tentatively set on 80%. Assimilation efficiencies p_a for animals are independent of the metabolic type but vary in relation to food composition (Calow, 1977; Schroeder, 1981). Detritivores, herbivores and carnivores digest about 20, 40 and 80% of the ingested food, respectively (Hendriks, 1999).

Production efficiencies p_p of autotrophs and heterotrophs have a theoretical maximum around 70% (Penning de Vries et al., 1974; Calow, 1977). In laboratory experiments, values for cold-blooded and warm-blooded animals vary around 50 and 25%, respectively. Field surveys suggest that the production efficiency p_p decreases in a phylogenetic order. It ranges from 50% for plants, 25% for invertebrates, 10% for fish to 2% for birds and mammals, with an exceptional value of 40% for insects (Humphreys, 1979; Sand-Jensen and Krause-Jensen, 1997). Production efficiencies are independent of temperature (Angilletta and Dunham, 2003).

Variability due to temperature can be accounted for by Eq. (3). For respiration, the activation energy E_a is in the range of 0.41–0.74 eV or $0.41\text{--}0.74 \times 1.6 \times 10^{-19} \text{ J}$. The average value of 0.58 eV corresponds to a factor of 2.2 difference between rates at 15 and 25 °C. The ratio in any 10 °C interval (Q_{10}) is in the range of 1.4–4.2 for respiration, 1.3–2.7 for production and 2–2.9 for consumption (ranges obtained from publications cited in Table S1 of the Supplementary Material). Values refer to laboratory experiments with the same species at different temperatures and to field observations on different species in different climates. Temperature differences of rates can thus roughly be accounted for by an average activation energy E_a of $0.58 \times 1.6 \times 10^{-19} \text{ J}$ or a temperature quotient Q_{10} of 2.2 in the 15–25 °C range.

4.3. Rate intercepts

Coefficients γ_p for the production rate constant are remarkably similar for species groups and different growth parameters, even without temperature correction (Fig. 1a–d, regressions are referred to by panel and number). This holds especially for population production, measured as the production to biomass ratio (Fig. 1a). Regressions that are partly below the average for cold-blooded species apply to studies where temperature was reported to be variable or in the 5–20 °C range (Fig. 1a: 10, 12, 13,

and 15). Production by heterotherms differs less than a factor of 5 from that of homeotherms (Fig. 1a: 30–33). According to the model, this ratio can be attributed to the body temperature difference between heterotherms and homeotherms ($q_T = 3.5$ for 20–37 °C). The intercept for birds is probably underestimated because biomass is measured in the favourable season only (Fig. 1a: 30; Farlow, 1976).

Intercepts for individual growth between 10 and 90% of the final size tend to be equal to or larger than the average production used in the model (Fig. 1b). Growth of immature fish

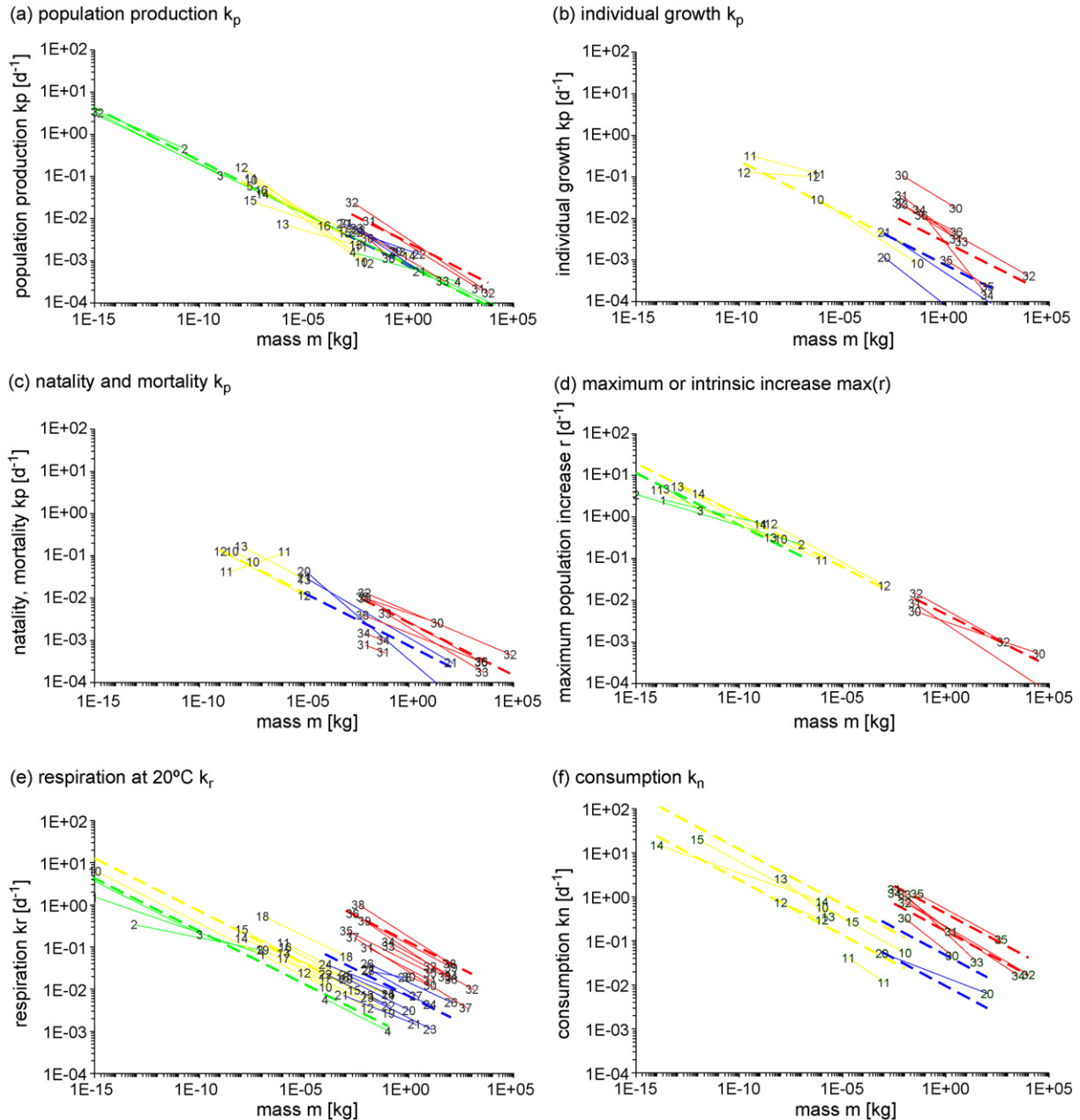


Fig. 1 – Rate constants k ($\text{kg kg}^{-1} \text{d}^{-1}$) vs. organism mass m (kg) for several species groups. Model estimations (dashed lines) and measurements (solid lines) on bacteria and plants (green), invertebrates (yellow), cold-blooded vertebrates (blue) and warm-blooded vertebrates (red). Ambient temperature for cold-blooded species at 13–25 °C or not reported in panels a–d and f, and at 20 °C in panel e with exception of field respiration by reptiles. Model range represents average and maximum in panel f. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

is lower, possibly due to low temperatures (Fig. 1b: 20). Juveniles of altricial birds grow much faster (Fig. 1b: 30). Natality and mortality also vary around the average production level (Fig. 1c). High intercepts apply to correlations where birth was expressed as eggs per breeding adult, whereas, low levels refer to the amount of new-borns in relation to the number of juveniles and adults present (Fig. 1c: 31, 33 versus 30, 32). Death rates for fish in aquaculture are 1 to 6 times lower than in nature (Fig. 1c: 20 < 21). This corresponds well to the difference calculated by the model. At an ingestion efficiency $p_{n,3}$ of 80%, intercepts for endogenous death rates are expected to be a factor of $1/(1 - p_{n,3}) = 1/(1 - 0.8) = 5$ less than total mortality. Mortality and natality of small tropical birds is exceptionally low (Fig. 1c: 31, 34).

The intercepts for maximum or intrinsic rates of increase r of heterotherms and homeotherms are similar and about 4 to 1.5 times above those for average production, respectively (Fig. 1d). According to Eq. (7), the corresponding maximum lifetime fecundity $\max(R_0)$ is expected to be about $e^4 = 55$ and $e^{1.5} = 4.5$. There are no allometric correlations to verify this outcome directly. However, the number of eggs in ovaries or clutches generally varies between 10 and 10^4 for cold-blooded species. For warm-blooded species, the number of eggs in a clutch and neonates in a litter varies around 2.5 for mammals and 4 for birds, independent of organism size. The lifetime fecundity $\max(R_0)$ for algae equals 2 by definition, yielding measured and predicted slopes that are slightly lower (Fig. 1d: 1–3).

Intercepts for respiration differ substantially, even after correction for ambient temperature (Fig. 1e). Metabolic coefficients γ_r generally increase in the sequence of plants, invertebrates, cold-blooded vertebrates and warm-blooded vertebrates (Fig. 1e: 1–4 < 10–19 < 20–28 < 30–39). The model follows this pattern using the subsequent values for the production efficiency p_p in Eq. (4). With a few exceptions, intercepts for invertebrates increase in the sequence of protozoans, molluscs, oligochaetes, crustaceans to insects (Fig. 1e: 10 < 11–12 < 13 < 14–15 < 16–18). The higher end of this range coincides with that noted for minimum metabolism of cold-blooded vertebrates (Fig. 1e: 20–25). Levels for more active organisms, in particular reptiles in deserts, are higher (Fig. 1e: 26–28). Within mammals, standard metabolism increases gradually from monotremates to primates (30–34). For both lab and field respiration, intercepts of regressions on birds are higher than on mammals (Fig. 1e: 36 > 37, 38 > 39). These trends are mirrored in several morphological, physiological and ecological properties that change in the same direction. The relative size of inactive components such as water and skeletons generally decrease in the sequence of plants, invertebrates and vertebrates. Concentrations of components and fractions of organs involved in metabolism scale to species size with a slope of $-1/4$ while the intercepts reflect above-mentioned differences between species groups (Peters, 1983). For instance, brains in homeotherms are about 20 times larger than in equally sized heterotherms (Martin, 1981). This corresponds exactly to the difference noted for respiration. Plants are generally sessile and transport substances often passively, whereas, animals are often mobile and distribute metabolic compounds actively (Ernest et al., 2003). Intercepts are small for animals with a “sit and wait” rather than a “hit and run”

strategy (Persson and Lohm, 1977; Greenstone and Bennett, 1980; Seibel et al., 1997; Lovegrove, 2000). Cold-blooded species such as insects and reptiles can increase their body temperature by flying, running and sun-bathing (Peters, 1983). The metabolic trend in warm-blooded animals can be anticipated by Eq. (3) of the model from the average body temperature of monotremates (30 °C), marsupials (35 °C), eutherian mammals (37 °C) and birds (40 °C). The distinction between cold-blooded and warm-blooded animals can partly be ascribed to the difference between body temperatures of 20 °C and 37 °C ($q_T = 3.5$, Eq. (3)). The remaining variability apparently reflects the energy required to maintain a homeothermic metabolism. As temperature both requires and enhances activity, intercepts for metabolism have increased during evolution and can be used as a criterion for taxon classification (Zotin and Konoplev, 1978).

Ingestion rate constants for cold-blooded animals are about 10 times lower than those for warm-blooded animals (Fig. 1f: 10–20 < 30–35). Experimental values are within or near the average-maximum interval calculated by the model on the basis of production and respiration needs for herbivorous invertebrates and carnivores vertebrates (Eq. (5)). High intercepts apply to studies that explicitly described food conditions to be near saturation, in particular for short-term intake by mammals (Fig. 1f: 14–15, 35). Ingestion as well as respiration by terrestrial detritivores is substantially slower (Fig. 1f: 11; Reichle, 1967). Ingestion by birds is consistently different from intake by mammals. Levels for warm-blooded herbivores are up to 2 times higher than those for homeothermic carnivores as can be understood from their lower assimilation efficiency p_a (Fig. 1f: 31 > 33, 32 > 34). The similarity between measured and predicted slopes for warm-blooded animals can be improved by using an exponent of $1/3$ instead of the universal $1/4$ in the model.

4.4. Time intercepts

The regression for different age parameters follow the patterns expected from the rate constants (Fig. 2). Intercepts for cold-blooded species are about 3.5 times higher than those for warm-blooded animals, as calculated by the model too. Intercepts for the age of first reproduction τ_m for unicellular organisms are clearly below the level for multicellular heterotherms. According to the model, this can be attributed to the “egg”-adult weight ratio m_e/m defined to be 0.5 for the binary division of single cells. For multicellular organisms, an average of 0.01 was used. Since no allometric relationships on the age of average reproduction τ_g were found in literature, I developed a regression from generation times measured in controls of toxicity experiments (Fig. 2a: 11). For the species and conditions used in these studies, age at average reproduction τ_g appears indeed similar to the juvenile period τ_m .

The age at first reproduction τ_m is three to four times higher than the age at death for organisms in natural conditions τ_d (Fig. 2a and b). If exogenous factors are absent, lifespan increases about five-fold (Fig. 2b and c). The model generally predicts the age at death $\tau_{d,in}$ in artificial conditions well. However, the high intercept for the lifespan of trees cannot be explained from the factor of $1/(1 - p_n)$ in Eq. (10). This indicates

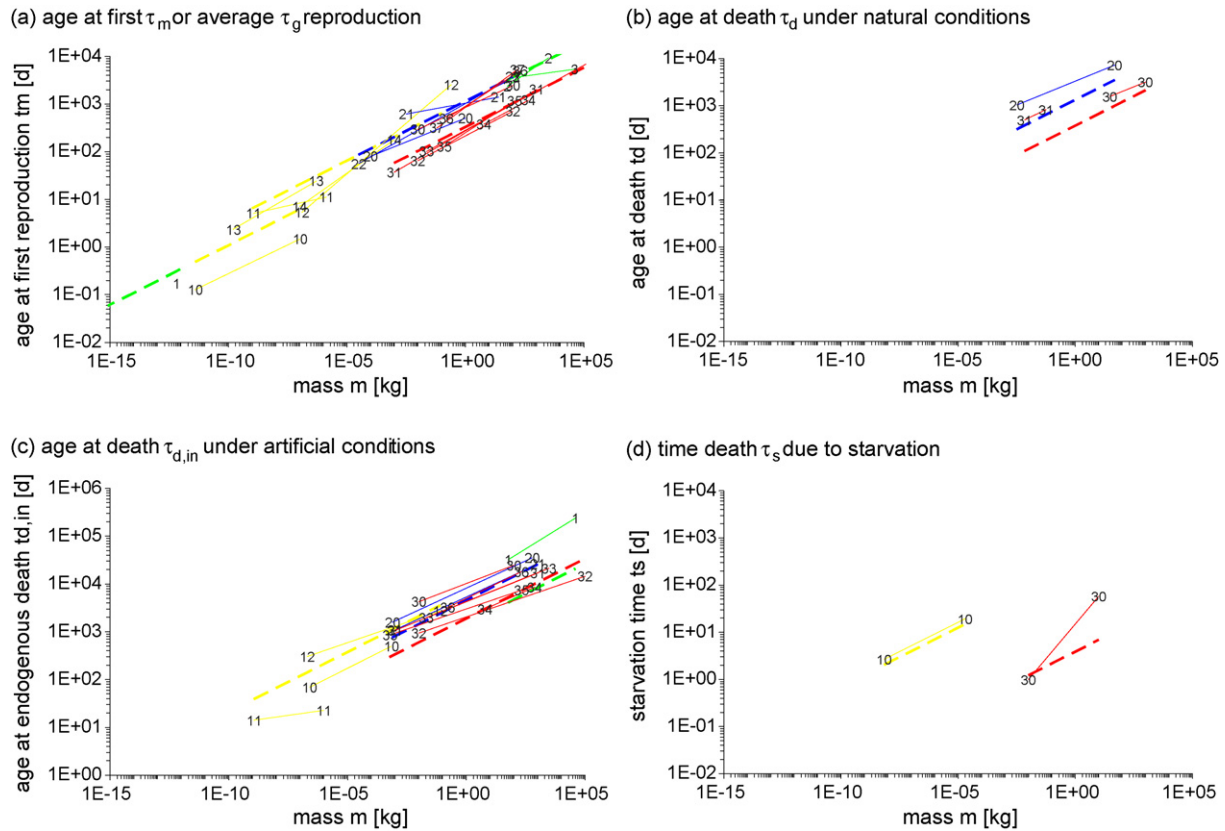


Fig. 2 – Time constants (d) vs. organism mass m (kg) for several species groups. Model estimations (dashed lines) and measurements (solid lines) on plants (green), invertebrates (yellow), cold-blooded vertebrates (blue) and warm-blooded vertebrates (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

that our assumptions need a correction for organisms, such as deciduous trees, that continuously shed a substantial part of their production, before the individual dies. As the intercepts for plants and heterothermic animals are similar, the alternative concept of a lifetime production $\tau_{d,in}k_p$ of about 5 kg kg^{-1} that is independent of size and metabolic group seems even better. In contrast, the traditional hypothesis that organisms die after they have respired an invariant amount of biomass is less attractive. The intercepts for respiration vary within a factor of 170, whereas, those for age at death differ only a factor of 3.5 or less. The total energy expenditure per lifespan $\tau_{d,in}k_r$ of 200 kcal/g, as known since 1883 (Azbel, 1994), thus, applies to warm-blooded animals only. It corresponds well to the value of $1/(1 - p_{n+1})(1/p_p - 1) = 1/0.2 \cdot (1/0.02 - 1) = 245 \text{ kg kg}^{-1}$ derived here. While respiration cannot explain the lifespan differences in the presence of food, metabolism nicely predicts the time to death due to starvation τ_s (Fig. 2d).

The time parameters for invertebrates are sometimes lower than predicted, perhaps due to a somewhat higher juvenile growth (Fig. 1b: 10–12). Age at maturity or death for birds and primates are higher than for mammals in general (Fig. 2a: 30,36–37, Fig. 2c: 30+36). This corresponds to a slow rate of individual growth for primates but not for birds (Fig. 1b: $34-36 < 30-31$). It suggests that birds put more effort in somatic versus gonadic growth in comparison to mammals.

4.5. Density and area intercepts

Allometric regressions for mass density (kg km^{-2}) are generally more variable than those for rate constants, probably because methods are less well standardized (Fig. 3a and b). Maximum levels may refer to the total standing stock of all species in relation to the average weight or to the upper range of abundance noted for populations with densities that fluctuate in time. Correlations for average density N (kg km^{-2}) are expressed per \log_{10} size class or per species. Size class distributions may be unimodal or multimodal rather than linear, partly due to undersampling of certain taxa. Regressions on species density may or may not include rare species. In addition, intercepts depend on the productivity of the ecosystems and menu of the guilds sampled. With these uncertainties in mind, a detailed analysis with contemporary diversity theory is beyond the purpose of the present paper. An indication of the order of magnitude of intercepts however, is within reach if the number species n is tentatively set at some typical value. Ecosystems may carry hundreds of species of producers and herbi-detritivores, dozens of primary carnivores and several top predators (Chase et al., 2000). On average, lakes contain about 100 species of phytoplankton, 20 species of zooplankton and 17 species of fish that make up more than 1% of the biomass (Cyr, 2000). Terrestrial systems may contain thou-

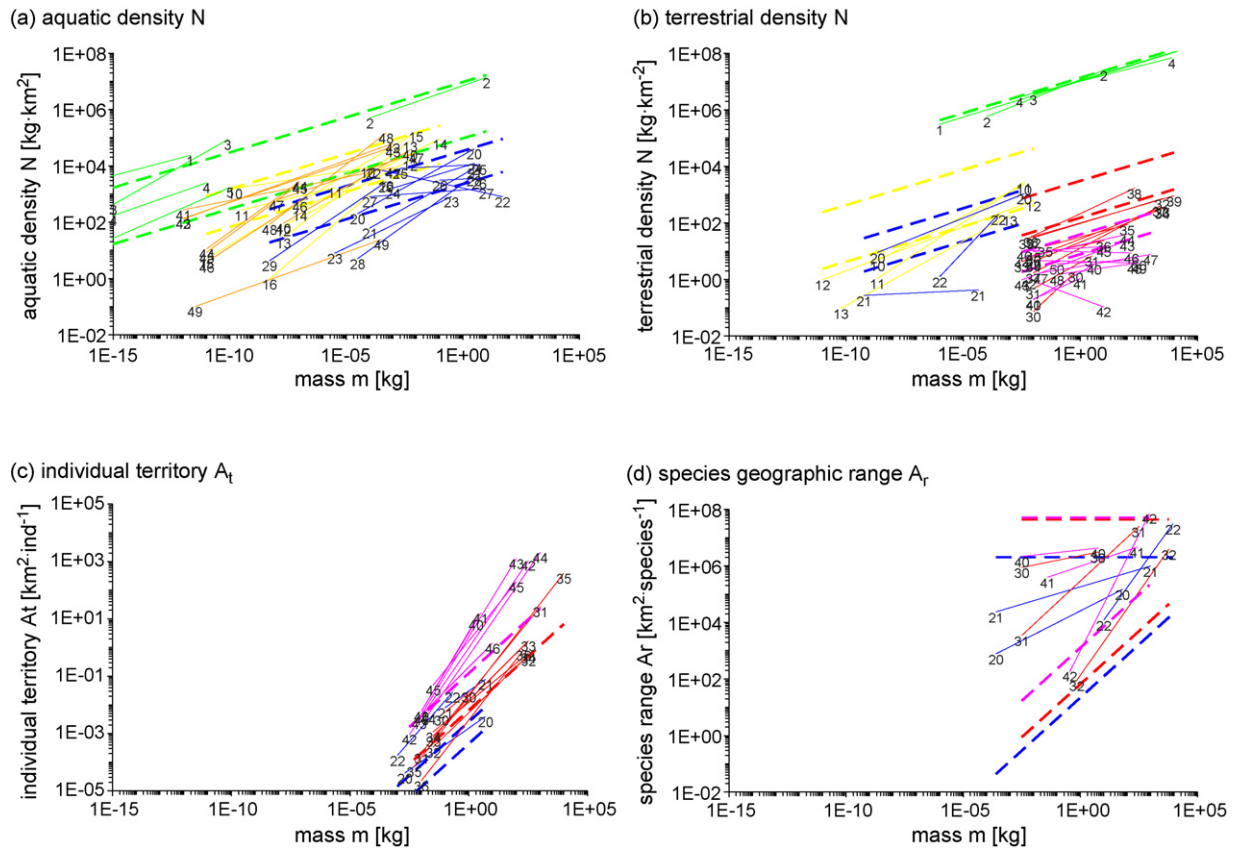


Fig. 3 – Mass density N (kg km^{-2}) and area (km^2) vs. organism mass m (kg) for different trophic levels. Measurements (solid lines) and model range (dashed lines) for plants (green), invertebrate herbivores (yellow in a), invertebrate detritivores (orange in a), invertebrate detritivores invertebrates (yellow in b), cold-blooded carnivores (blue), warm-blooded herbivores (red) and warm-blooded carnivores (pink). (a) Density in aquatic systems, model range for 1–100 (plants), 1–22 (invertebrate herbivores), 1–15 (fish) species. (b) Density in terrestrial systems, model range for 1 (plants), 1–100 (invertebrate herbivores), 1–15 (invertebrate carnivores), 1–20 (warm-blooded herbivores), 1–5 (warm-blooded carnivores). (c) Individual territory, model range for 15 (cold-blooded carnivores, lower represent fish, upper represent reptiles), 20 (warm-blooded herbivores), 5 (warm-blooded carnivores) species. (d) Species geographic range, model range represents maximum set by North American continent or world freshwater area and minimum with number of species as in c. Regressions 3,4,10–13, 21–23, 40–46 of panel a and 10–11, 20 of panel b are \log_{10} size class distributions, the others represent species densities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

sands of invertebrate species but the number of warm-blooded herbivores is limited to 10–35 (Anderson, 1975; Prins and Olff, 1998; Siemann et al., 1996). Following these general patterns, the model was set at a maximum density with $n=1$ species and at an average density with $n>1$ species (Fig. 3). Since the production rate coefficient γ_p was shown to be the same for all species (Fig. 1), the subsequent reduction $p_n p_a p_p$ of energy available at each trophic level is thus counterbalanced in the model by a diminution of both the density $\gamma_{N,i}$ (less biomass) and the number of species n_i (less partitioning) along food chains (Eq. (13)).

The density intercept $\log(\gamma_N)$ observed in the field decreases from plants to herbi-detritivores and carnivores as well as from cold-blooded to warm-blooded animals, as anticipated by the model (Fig. 3a and b). Maximum coefficients γ_N for aquatic and terrestrial producers are similar on a wet weight basis. According to the model, plant densities in water and on land are also expected to be approximately equal. The reduc-

tion of dry weight production and biomass by $p_{i,1}=20\%$ due to turbidity and extinction in water is balanced by a dry matter fraction p_s of 10% in aquatic plants, compared with 20–40% in terrestrial producers. Animal density does not exceed the maximum expected from the model at $n=1$.

Average density of phytoplankton in size classes is between 1 and 10 times lower than the maximum level and 10–20 times lower than that of dominant species (Fig. 3a: $1>3-4>5$). Thus, the 4 to 6 \log_{10} size classes of the first trophic level may together contain about $n_1=4 \dots 6 \times 10 \dots 20=40 \dots 120$ algae species. This empirical range encompasses the value of 100 assumed in the model.

Density of invertebrate detritivores and herbivores in aquatic systems, ranging from rivers to oceans, are largely within the interval used in the model. Size class densities for aquatic invertebrates vary around the level of average density for (dominant) species, suggesting that each \log_{10} size class includes no more than a few dominant species (Fig. 3a:

10–13 \approx 14–15, 40–46 \approx 14–15). The total species richness n_2 over all 4–9 size classes will not be far from the value of 20 dominant species set by the model. A clear deviation was noted for herbivores in rivers, obviously due to low primary production in lotic systems (Fig. 3a: 16). Another outlier applies to regressions on detritivores in streams that included over 200 species, including rare ones, instead of the $n_2 = 20$ used here (Fig. 3a: 49). Densities for cold-blooded carnivores also vary around the level calculated by the model at $n_3 = 10$. Intercepts for fish decrease from benthic to pelagic systems, both within size class and species regressions (Fig. 3a: 21 > 23, 24–25 > 26–28). Data on algae, invertebrates and fish obtained in the same study show that there is roughly one order of magnitude difference between each trophic level (Fig. 3a: 4–11–24, 5–15–27, 3–10–22).

The few regressions on density of *terrestrial* invertebrates per area are close to each other. Average density of herbivorous species is near that expected by the model for 100 herbivorous invertebrate species and at the level noted for \log_{10} size classes of arthropods in a tropical forest (Fig. 3b: 12–13 and 10–11). Levels for carnivorous invertebrates sampled in the same area are at or below those for herbivorous species (Fig. 3b: 20–21). Abundance of warm-blooded species has been investigated more extensively. Density of plant eating mammals is between 0.1 and 1 times the average expected from the model. Intercepts for birds are about one order of magnitude lower than for mammals, whether they feed on fruit, seeds, invertebrates or vertebrates (Fig. 3b: 30–31, 40–42 versus rest). Within birds or mammals, densities of granivores, frugivores and true herbivores are similar (Fig. 3b: 34–36). Intercepts for temperate mammals are about one order of magnitude larger than those of their tropical equivalents (Fig. 3b: 38 > 37). Levels for mammalian predators vary around the anticipated level. The intercepts of the regressions depend on the type of prey included: highest for invertebrates, lowest for vertebrates and intermediate value for compilations that include both (Fig. 3b: 43–44 > 45–47 > 48–50).

Intercepts for *area* ($\text{km}^2 \text{ind}^{-1}$) generally mirror those for density, as noted for slopes before (Fig. 3). While density is between 1 and 10 times lower than expected from the model, area is usually within an order of magnitude above the calculated level. Fish *home ranges* in rivers are 20 times higher than those in lakes, whereas their densities differ only a factor of 3 (Fig. 3c: 20–21, Minns, 1995). Intercepts of warm-blooded herbivores tend to decrease in the sequence of birds, mammals and primates (Fig. 3c: 30 > 31–35 > 36). Regressions for warm-blooded predators are at the same level (Fig. 3c: 40–46).

Geographic ranges of species also increase with body size (Fig. 3d). Average trends for different species groups have gentle slopes. Levels increase from fish, to mammals and birds, and from herbivores to carnivores (Fig. 3d: 20–21 < 31–41 < 30–40). Regressions that apply to the size of islands and continents as a function of the largest animal present, reflects the minimum area needed to sustain that species, as smaller regions cannot carry it. Their intercepts rise from warm-blooded herbivores to cold-blooded and warm-blooded carnivores (Fig. 3d: 32 < 22 < 42). Both types of correlations largely fall within a “triangular envelope” with a maximum set by the total available area and a minimum imposed by energy requirements (Brown and Maurer, 1989).

Here, the upper limit is fixed by the size of the continent or biome concerned and the lower restriction was calculated by Eq. (15). In the absence of other information, the minimum viable metapopulation needed to sustain a species S is set at an indicative value of 10^4 individuals, needed to prevent extinction of local populations (Reed et al., 2002). With one exception, intercepts for individual and species area thus increase from cold-blooded to warm-blooded, from herbivores to carnivores and from mammals to birds as expected from the availability and exploitation of energy.

5. Conclusions

In this meta-analysis, 230 allometric regressions on ecological rate, time, density and area parameters were collected. Despite differences in sampling techniques, test conditions, study areas, species selection and statistical analyses, observations roughly fit into a simple model.

The meta-analysis shows that rate and time constants of cold-blooded organisms scale to $\pm 1/4$ as expected from allometric distribution of substances in networks (West et al., 1997 and subsequent papers by same authors). Exponents for warm-blooded species are in the range of $\pm 1/4 \dots 1/3$, suggesting that geometric phenomena are important too (Dodds et al., 2001). Possibly, metabolism of homeotherms is governed not only by advective transport of substances, but also by diffusive dispersal of heat. A recent re-analysis of mammalian data however, indicates that $1/4$ may apply to warm-blooded species too (Savage et al., 2004).

Empirical slopes for density and area are more variable than those for rate and age parameters. The present review shows that mass density N (kg km^{-2}) within a trophic level tends to increase with body size. The intercepts of these regressions generally decrease with the position in the food chain. As a result, exponents of correlations that include all species and trophic levels tend to be lower. This corresponds well to the observation that slopes of abundance versus body size relationships decrease with the width of the size interval covered (Blackburn and Gaston, 1997). Density exponents for plants and herbivorous or invertebrate herbivores are often close to $1/4$ (see e.g., Enquist et al., 1998; Belgrano et al., 2002; Enquist and Niklas, 2002; Niklas et al., 2003). However, slopes for heterothermic animals tend to be more variable and steeper (Table 2, Fig. 3). Density of warm-blooded predators that prey on vertebrates is independent of body size, as confirmed by regressions for individual area. It suggests that the model requires differentiation or that the regressions suffer from artefacts discussed above.

The slopes obtained for 230 allometric regression on rate, time, density and area parameters thus allow the universal scaling factor of $1/4$ recently proposed (West et al., 1997). However, deviations are noted in some cases, in particular for warm-blooded species as well as for density and area parameters. In these cases, more empirical evidence is needed to judge whether the variability reflects sampling biased in terms of species and conditions covered. If such artefacts can be excluded, more detailed models that explain deviations in both directions can be developed. In addition, alternative mod-

els based on thermodynamical concepts as well as non-living equivalents, may be explored (e.g., McMahon and Bonner, 1983; Jørgensen et al., 1999; Straškraba et al., 1999; Martin et al., 2005).

Regressions for rate constants of production, including individual and population growth, natality and mortality, are remarkably similar (Fig. 1). Intercepts for production can be extrapolated to those for other parameters, including respiration, ingestion, physiological or ecological mortality, age at maturity or death, maximum and average density, territory size. The predicted coefficients are usually within an order of magnitude difference of the measured values. The basic assumptions in the model, in particular the energy equivalence rule, and the setting of the parameters, in particular the typical values for transfer efficiencies, thus appear to be valid. For most of these parameters, there is a consistent difference between the intercepts for cold-blooded and warm-blooded species that is anticipated well by the model, following biochemical reaction kinetics with a constant value for the activation energy (Gillooly et al., 2001). Temperature correction can also explain some but not all of the differences observed between respiration of heterotherms. In addition to temperature, density and area regressions for different trophic levels can be understood well from the transfer efficiencies in aquatic and terrestrial foodchains. As such, the evidence collected on the intercepts supports the existence of a general framework based on a universal value for the slopes (as proposed by West et al., 1997). Yet, the number of regressions collected is too small to allow a detailed interpretation of differences between closely related species groups. Comparing avian and mammalian regressions for instance, rapid metabolism and juvenile growth in birds corresponds well to their low density and large area but not to their high age and slow turnover (population production, mortality, and natality). This suggests that trade-offs occur at more detailed mechanisms than incorporated in our model. Alternatively, the few regressions available per species group reflect specific conditions that are not representative for a comparison of closely related taxons. In any case, the benefits of the present meta-analysis and model are that such inconsistencies can now be identified. Vice versa, specific relationships, e.g. allometric regressions on dosing of pharmaceuticals or minimum viable population density, are more reliable if they comply with models and data sets that include other processes and patterns too (Mordenti, 1986; Thomas, 1990). More fundamental issues on evolution, e.g. of cold-blooded and warm-blooded species can also be underpinned by the present framework (Burness et al., 2001; Yoshida, 2006). The regressions collected in the meta-analysis and the framework derived in the model study facilitate selection of appropriate coefficients that are mutually consistent, covering different taxa. This is especially useful if conclusions of modelling are to be extrapolated beyond arbitrary, species-specific or single-regression parameter values, as, e.g. in size-class independent analyses (e.g., in Van Nes et al., 2002; Ramos-Jiliberto et al., 2006; Stahl and Oli, 2006; Baird and Suthers, 2007). Instead, size class, more in general, a macro(ecological) perspective contributes to our understanding by setting the rules that allows us to see the exceptions, at the level of species as well as taxons.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2007.02.029](https://doi.org/10.1016/j.ecolmodel.2007.02.029).

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