

# Size-density scaling in protists and the links between consumer–resource interaction parameters

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## Summary

**1.** Recent work indicates that the interaction between body-size-dependent demographic processes can generate macroecological patterns such as the scaling of population density with body size. In this study, we evaluate this possibility for grazing protists and also test whether demographic parameters in these models are correlated after controlling for body size.

**2.** We compiled data on the body-size dependence of consumer–resource interactions and population density for heterotrophic protists grazing algae in laboratory studies. We then used nested dynamic models to predict both the height and slope of the scaling relationship between population density and body size for these protists. We also controlled for consumer size and assessed links between model parameters. Finally, we used the models and the parameter estimates to assess the individual- and population-level dependence of resource use on body-size and prey-size selection.

**3.** The predicted size-density scaling for all models matched closely to the observed scaling, and the simplest model was sufficient to predict the pattern. Variation around the mean size-density scaling relationship may be generated by variation in prey productivity and area of capture, but residuals are relatively insensitive to variation in prey size selection. After controlling for body size, many consumer–resource interaction parameters were correlated, and a positive correlation between residual prey size selection and conversion efficiency neutralizes the apparent fitness advantage of taking large prey.

**4.** Our results indicate that widespread community-level patterns can be explained with simple population models that apply consistently across a range of sizes. They also indicate that the parameter space governing the dynamics and the steady states in these systems is structured such that some parts of the parameter space are unlikely to represent real systems. Finally, predator–prey size ratios represent a kind of conundrum, because they are widely observed but apparently have little influence on population size and fitness, at least at this level of organization.

**Key-words:** allometry, macroecology, optimal foraging, predator–prey dynamics, predator–prey size ratio

## Introduction

The scaling of population abundance with body size is one of the most widespread patterns in community ecology (White *et al.* 2007; Yvon-Durocher *et al.* 2011). Diverse taxa including plants (Belgrano *et al.* 2002), birds (Russo, Robinson & Terborgh 2003), plankton (Huete-Ortega *et al.* 2012) and insects (Meehan 2006) show a

pattern in which species drawn from a global or regional species pool show declining population density with increasing body size. This form of size-density scaling, called a global size-density scaling relationship in the study of White *et al.* (2007), usually takes the form of a power law,  $\bar{C} = c_0 M_c^\chi$ , where  $\bar{C}$  is the average long-term density of the consumer population (in this study, we will consider consumers but the concept applies to all trophic levels),  $M_c$  is the mass of the consumer,  $c_0$  is a pre-factor that gives the abundance for a consumer when  $M_c = 1$ , and  $\chi$  is a scaling exponent. Population abundance also

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may be related to body size within communities either at the species or at the individual level, but we will not focus on those patterns here (White *et al.* 2007; Reuman *et al.* 2008; Yvon-Durocher *et al.* 2011).

A common explanation for size-density scaling is that mean steady-state abundance ( $\hat{C}$ ) is set by the interaction of body-size-independent resource levels ( $R_{\text{tot}}$ ) and average *per capita* body-size-dependent resource requirements ( $\bar{R}_{\text{ind}}$ ). Invoking the energetic-equivalence rule (EER; Damuth 1981), it has been suggested that  $R_{\text{tot}}$  is independent of body size, while  $\bar{R}_{\text{ind}}$  reflects the scaling of metabolic rate, so  $\hat{C} = \frac{R_{\text{tot}}}{\bar{R}_{\text{ind}}} \propto \frac{M_c^0}{M_c^\theta} \propto M_c^{-\theta}$ , where  $\theta$  is the scaling exponent for metabolic rate with body size (Brown *et al.* 2004; Marquet, Labra & Maurer 2004). The exponents for size-density scalings tend to be close to the negative of metabolic scaling exponents and nearly always fall in the same general range of values as metabolic scaling exponents (−0.6 to −1), providing some support for the EER and its use as an explanation for size-density scaling patterns (Damuth 1981; Meehan 2006; White *et al.* 2007; Hechinger *et al.* 2011; Huete-Ortega *et al.* 2012). Furthermore, by expanding this approach to include variation in consumer behaviour, a variety of size-density scaling exponents can be obtained (Carbone *et al.* 2007).

Nonetheless, the EER does not always hold. In some cases, exponents for density and metabolic scaling relations differ, and in other cases, population-level resource supply rates are not independent of body size (Brown & Maurer 1986; Blackburn *et al.* 1993; Russo, Robinson & Terborgh 2003; DeLong 2011; Isaac, Storch & Carbone 2011; DeLong & Vasseur 2012). In addition, the use of the EER as an ‘explanation’ for size-density scaling is circular because the EER is identified by the correspondence of scaling exponents for population density and metabolic rates. An alternative explanation for size-density scaling may be found through the use of body-size-dependent consumer–resource models (Yodzis & Innes 1992; Weitz & Levin 2006; DeLong & Vasseur 2012). Solved for their steady states, consumer–resource models provide explicit predictions for size-density scaling, and the particular processes that generate the scaling can be identified when multiple consumer–resource models are compared. Furthermore, this approach provides a mechanistic link between size-dependent processes at the individual, population and community levels, providing a useful tool for understanding size-structuring in ecosystems (Yvon-Durocher *et al.* 2011). The approach has been used to successfully predict both the height and slope of the size-density scaling relationship for mammalian carnivores (DeLong & Vasseur 2012), but other groups have not been evaluated.

Here, we use the consumer–resource model approach to understand the size-density scaling for heterotrophic protists grazing algae, which show typical size-density scaling in both laboratory microcosms and natural environments (Finlay 2002; Petchey, Long & Morin 2007). Protists show different patterns of body-size-dependent energetics than carnivores (DeLong *et al.* 2010), and they occupy

three-dimensional soil and aquatic habitats rather than two-dimensional terrestrial habitats (Pawar *et al.* 2012). Thus, exploration of size-density scaling for protists may reveal important differences and similarities between them and carnivorous mammals.

In this study, we predicted the height and slope of the size-density scaling relationship for protists grazing algae in laboratory cultures from data on the body-mass dependence of consumer–resource interaction parameters in these organisms. The prediction closely matched an observed size-density scaling that was based on a new compilation of data from the literature. We also controlled for protist body size and looked for links between model parameters. These links shed light on how the selection of a relatively small or large prey influences steady-state consumer density and individual- and population-level energetics.

## Materials and methods

### MODELS

We used three standard consumer–resource models to describe the dynamics of a consumer organism ( $C$ ) and its prey (resource,  $R$ ). The first was the Lotka–Volterra (LV; Model 1) predator–prey model with simple birth and death terms (Lotka 1925; Tables 1,2). Greater realism and complexity may be added to the LV model by using alternative birth and death terms. Adding resource self-limitation to the model with a logistic growth term gives Model 2, and further adding predator satiation to the model with a type II functional response gives the MacArthur–Rosenzweig model (MR; Model 3; Rosenzweig & MacArthur 1963).

To use these models to understand size-density scaling, each model must be solved for its non-trivial steady-state consumer density,  $\hat{C}$ , and each parameter in that expression must be evaluated for the presence and form of body-size dependence. For example, with the LV model, the steady-state consumer density is  $\hat{C} = \frac{r}{a}$ , where  $r$  is the maximum population growth rate of the resource species and  $a$  is the area of capture of the predator, or the amount of area or volume cleared of prey per unit time per predator (Table 2). Substituting the body-size dependencies of  $r$

**Table 1.** Parameters and allometric relationships for those parameters used in the models. For simplicity, pre-factors in the allometric relationships are given as lower-case Arabic letters subscripted with 0, and all exponents are given by closest Greek counterparts

Parameter	Description	Scaling
$C$	Consumer density	$c_0 M_c^\zeta$
$r$	Maximum population growth rate of resource	$r_0 M_r^\rho$
$K$	Carrying capacity of resource	$k_0 M_r^\kappa$
$a$	Attack efficiency of consumer	$a_0 M_c^\alpha$
$e$	Conversion efficiency of consumer	$e_0 M_c^\epsilon$
$h$	Handling time for consumer	$h_0 M_c^\phi$
$m$	Mortality rate of consumer	$m_0 M_c^\mu$
$M_r$	Resource size	$s_0 M_c^\psi$

**Table 2.** Models used in this study and their steady states. For parameters and their estimated values

Equations	Isoclines	Predicted size-density scaling of consumers
<p>Model 1 – Lotka–Volterra (LV)</p> $\frac{dR}{dt} = rR - aRC$ $\frac{dC}{dt} = eaRC - mC$	$C = \frac{r}{a}$ $R = \frac{m}{ea}$	$\hat{C} = \frac{r_0 s_0^p}{a_0} M_c^{\psi\rho - \alpha}$
<p>Model 2 – LV model with logistic growth of prey</p> $\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - aRC$ $\frac{dC}{dt} = eaRC - mC$	$C = \frac{r}{a} \left(1 - \frac{R}{K}\right)$ $R = \frac{m}{ea}$	$\hat{C} = \frac{r_0 s_0^p}{a_0} M_c^{\psi\rho - \alpha} \left(1 - \frac{m_0}{e_0 a_0 k_0 s_0^k} M_c^{\mu - \varepsilon - \alpha - \psi\kappa}\right)$
<p>Model 3 – MacArthur–Rosenzweig</p> $\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{aRC}{1 + ahR}$ $\frac{dC}{dt} = \frac{eaRC}{1 + ahR} - mC$	$C = \frac{r}{a} \left(1 - \frac{R}{K}\right) (1 + ahR)$ $R = \frac{m}{a(e - hm)}$	$\hat{C} = \frac{r_0 s_0^p}{a_0} M_c^{\psi\rho - \alpha} \left(1 - \frac{m_0}{a_0 k_0 s_0^k (e_0 M_c^\varepsilon - h_0 m_0 M_c^{\phi + \mu})} M_c^{\mu - \alpha - \psi\kappa}\right) \times \left(1 + \frac{h_0 m_0 M_c^{\phi + \mu}}{e_0 M_c^\varepsilon - h_0 m_0 M_c^{\phi + \mu}}\right)$

and  $a$  ( $r = r_0 M_r^p$  and  $a = a_0 M_c^\alpha$ ; Table 1) gives  $\hat{C} = \frac{r_0 M_r^p}{a_0 M_c^\alpha}$ , and including a scaling relationship for prey size selection ( $M_r = s_0 M_c^\psi$ ; Table 1) allows one to express  $\hat{C}$  in terms of consumer mass:

$$\hat{C} = \frac{r_0 s_0^p}{a_0} M_c^{\psi\rho - \alpha} \tag{eqn 1}$$

This model produces an empirical prediction for the size-density scaling parameters with  $c_0 = \frac{r_0 s_0^p}{a_0}$  and  $\chi = \psi\rho - \alpha$  (DeLong & Vasseur 2012). Using independent data to estimate the component parameters, a prediction for the overall size-density scaling can be generated without reference to specific species. For example, estimates of  $a_0$  and  $\alpha$  are obtained from a data set on the body-size dependence of the functional response, and these estimates are then used in conjunction with the other parameters to generate predictions for  $c_0$  and  $\chi$  (see below for handling of error in parameter estimates). Importantly, none of the parameters in eqn 1 are estimated from density data, so predictions for the size-density scaling parameters using this approach will be completely independent of the density observations.

Each model also can be solved for steady-state foraging and biomass intake rates at both the individual and population levels (DeLong 2011; DeLong & Vasseur 2012). These values give a prediction for the ecologically relevant resource fluxes occurring at both individual and population levels of organisation, allowing us to test additional predictions and assumptions. In particular, we can use the models to determine whether the body-mass-dependent resource fluxes of individuals are parallel to metabolic scaling (which is expected because resource use drives metabolism) and whether the population-level resource use conforms to the EER. The steady-state average *per capita* foraging rate,  $\hat{f}_{\text{ind}}$ , with the LV model is  $\hat{f}_{\text{ind}} = \frac{m}{e}$ , where  $m$  is the consumer natural mortality rate and  $e$  is the number of new consumer individuals produced per consumed resource individual (Table 1; DeLong 2011). This foraging rate, multiplied by the body mass of the prey species, gives an estimate of the biomass intake rate at the individual level:

$$\hat{B}_{\text{ind}} = \frac{m}{e} M_r. \tag{eqn 2}$$

The biomass intake rate at the population level is simply eqn 2 times the steady-state consumer density:

$$\hat{B}_{\text{pop}} = \frac{r m}{a e} M_r. \tag{eqn 3}$$

DATA

We acquired data from the literature to determine the body-size dependence of all parameters as well as the size-density scaling for protists. We collected data on a wide variety of heterotrophic protists grazing a wide range of phytoplankton; bacterivorous or carnivorous protists were not included because data on these trophic interactions are far less abundant. We searched Google Scholar for terms including combinations of ‘grazing’, ‘growth’, ‘protist’, as well as many individual species names and authors who had previously published work that contained the appropriate data. We also used the studies of Rose & Caron (2007) and Fenton, Spencer & Montagnes (2010) for their compilations of appropriate literature and followed linked citations between sources. Existing data sets for phytoplankton growth rate (Tang 1995), phytoplankton average population density (Agusti & Kalf 1989) and protist mortality rate (Jackson & Berger 1984) were obtained and reanalysed.

We searched for raw time-series data to determine the steady-state density of grazing protists in laboratory microcosm cultures with respect to body size. Field estimates of abundance were not included. Data for 15 species were included, and sources used in this compilation were (Gast & Horstmann 1983; Caron *et al.* 1985; Gao & Li 1986; Capriulo, Schreiner & Dexter 1988; Goldman & Dennett 1990; Nakamura, Yamazaki & Hiromi 1992; Jacobson & Anderson 1993; Jeong & Latz 1994; Simek *et al.* 1997; Strom & Morello 1998; John & Davidson 2001; Lin *et al.* 2004; Menden-Deuer *et al.* 2005; Gismervik 2006). This data set is available in Appendix S1.

We searched for functional and numerical response data to produce a data set on consumer–resource interaction parameters. Data were found for 44 different protist–algae combinations,

and sources used in the compilation on consumer–resource interactions were (Hansen 1992; Jacobson & Anderson 1993; Buskey, Coulter & Brown 1994; Jeong & Latz 1994; Jakobsen & Hansen 1997; Kamiyama 1997; Jeong *et al.* 1999, 2001a,b, 2002, 2003, 2007, 2011; Muller & Schlegel 1999; John & Davidson 2001; Weisse *et al.* 2001; Tillmann & Reckermann 2002; Kim & Jeong 2004; Lin *et al.* 2004; Weisse 2004; Gismervik 2005; Kamiyama *et al.* 2005; Kimmance, Atkinson & Montagnes 2006; Frangópulos, Spyarakos & Guisande 2011). This data set is available in Appendix S1.

## ANALYSIS

Protists frequently display a classic sigmoidal growth curve (Gause 1934). Population density data that were presented in a time series and for which an approximate steady state was achieved after a sigmoidal growth phase, for at least two time steps (mostly more than three time steps), were digitized. The average of the densities during the steady state was determined in cells per mL. Time series of growing populations that did not reach a steady state or for populations that peaked and crashed without showing a period of stable densities were not used. Steady-state densities were averaged for species with multiple usable time series.

Functional response parameters (area of capture,  $a$  and handling time,  $h$ ) were either used as reported or recalculated, depending on the units and reporting details. To recalculate, we digitized data, converted data to standardized units and fit a standard Holling type II functional response,  $f = \frac{aR}{1+ahR}$ , to the data using ordinary least-squares nonlinear fitting in Matlab © R2009b. Prey size selection was estimated only from these functional response observations, with the size of the protist and the phytoplankton prey typically given in the same source, but in some cases, cell sizes were taken from other sources.

Numerical response parameters (maximum growth rate  $\mu_{\max}$  and half-saturation constant  $K_{\mu}$ ) were taken as reported or digitized, again depending on the units and reporting details. To recalculate, we digitized data and fit it using ordinary least-squares nonlinear fitting to a standard Michaelis–Menten model,  $\mu = \frac{\mu_{\max}R}{K_{\mu}+R}$ . Conversion efficiency,  $e$ , is the number of new cells produced for each prey cell consumed and was calculated for steady-state conditions following the model of Fenton, Spencer & Montagnes (2010),  $e = \frac{\mu_{\max}(K_I+R')}{I_{\max}(K_{II}-R')}$ . In this model,  $I_{\max}$  is the maximum ingestion rate of the consumer at saturating prey conditions, given as  $1/h$ , and  $K_I$  is the half-saturation constant for ingestion (following a Michaelis–Menten model instead of a Holling model in this case).  $R'$  is the threshold resource level for positive growth in the numerical response.

The body-size dependence of each parameter was determined using both ordinary least-squares (OLS) and reduced major axis (RMA) regression to fit a line to log-transformed data. This approach is justified given that allometric data usually have a multiplicative error structure (Xiao *et al.* 2011). We averaged the parameters from the OLS and RMA regressions to approximate the likely error distribution between the  $x$ -axis and  $y$ -axis variables in these data sets [see DeLong & Vasseur (2012) for a discussion of this approach]. Phylogenetic independent contrasts cannot be used in this group because the evolutionary relationships are not clearly known.

To determine 95% confidence intervals for the average scaling parameters, we used a bootstrapping approach. Each data set was sampled with replacement, and OLS and RMA fits were

calculated for each sample, producing a distribution of average scaling slopes and pre-factors. Confidence intervals were taken as the 2.5 and 97.5 percentiles of these distributions. To produce 95% prediction intervals from the models, we took into account the error distribution of each contributing parameter using a Monte Carlo approach (a full uncertainty analysis). We took 10 000 random samples (with replacement) from each observed scaling distribution, and made predictions for the exponent and pre-factor with all parameter distributions. The upper and lower prediction intervals were then taken from these prediction distributions using the 2.5 and 97.5 percentiles.

Finally, we analysed links between the consumer–resource interaction parameters in two ways. First, we controlled for the size dependence of all parameters by comparing residual area of capture, prey size selection, handling time and conversion efficiency using pairwise correlations. Residuals were calculated using logged data and the mean scaling fit, and relationships were tested with Pearson's correlations. This approach has been advocated as suitable when an *a priori* primary explanatory variable is known and when multicollinearity would be present in a multiple-regression framework (in this case, all model parameters are correlated with consumer volume) (Graham 2003). Second, we conducted multiple regressions to assess the relationship between the same interaction parameters, here controlling for consumer volume by including it as a predictor variable. The multiple-predictor approach is advocated over residual analysis because residual analysis may have low power and produce type II errors (Darlington & Smulders 2001), but because in our case all predictor variables are correlated, the multiple-predictor approach also may produce type II errors as well as yield unreliable parameter estimates (Graham 2003). We conducted both analyses to balance the pros and cons of each, but we use parameter estimates from the residual analysis because it allows for our use of averaged OLS and RMA parameters.

To quantitatively assess the effects of linked parameters on foraging rates, we translated residual correlations to absolute deviations as follows. Residuals were calculated as the difference between the log of the observed value and the log of the expected value (as given by the size scaling of that parameter). We were particularly interested in the link between prey size selection and conversion efficiency, so we developed an approach to link the absolute deviations of these parameters. First, we can portray the correlation of the residuals with the following equation:  $\log\left(\frac{e'_{\text{obs}}}{e'_{\text{exp}}}\right) = z \log\left(\frac{M_{r\text{obs}}}{M_{r\text{exp}}}\right)$ , where  $z$  is the slope of the relationship between the residuals. We estimated  $z$  as the mean of the RMA and OLS estimates. Defining the effect of a specific prey size deviation on efficiency as  $e' = e_{\text{obs}} - e_{\text{exp}}$ , we can rearrange and substitute to get an expression in terms of the prey size:

$$e' = e_{\text{exp}} \left( \exp \left( z \log \left( \frac{M_{r\text{obs}}}{M_{r\text{exp}}} \right) \right) - 1 \right). \quad \text{eqn 4}$$

Thus, when a predator picks a prey of a specific size,  $M_{r\text{obs}}$ , there is a change in the efficiency of magnitude  $e'$ . We used this formulation to quantitatively address the consequences of varying prey size selection on resource intake rates.

## Results

All parameters, including steady-state consumer density, were significantly related to consumer or resource size

(Table 3). With these parameters, all models produced nearly identical predictions for the size-density scaling of grazing protists (Fig. 1). Because the models are nested and the simplest model is sufficient to account for this pattern, predator satiation and self-limitation in the prey can be ruled out as contributing to the size-density scaling pattern. Therefore, the primary factors generating size-density scaling in this group are those represented in the LV model: area of capture, prey size selection and prey productivity.

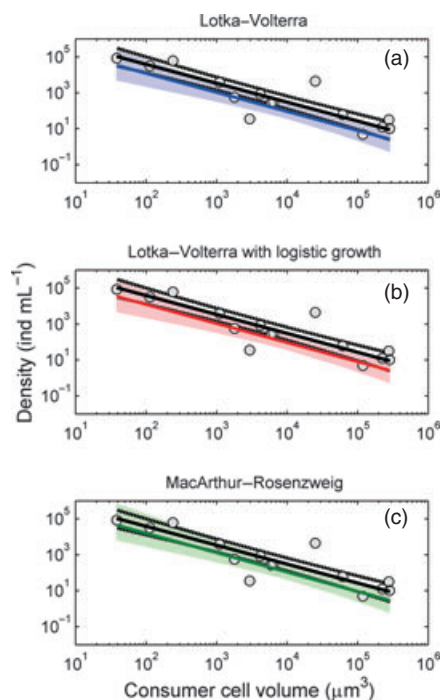
From the parameters that define the scaling of  $m$  and  $e$ , *per capita* resource intake rate is related to consumer size

by a scaling exponent of 0.94, (95% CIs: 0.56 to 1.62), which is very close to the observed metabolic scaling for protists of  $\sim 1$  (DeLong *et al.* 2010). Including all parameters in eqn 3, the estimated scaling of population-level resource intake rate is  $-0.12$  (95% CIs:  $-0.64$  to  $0.58$ ), which indicates that the EER hypothesis cannot be rejected in this group.

The four parameters for which we had concurrent data across multiple consumer species were prey size, efficiency, handling time and area of capture. Residuals of these parameters were significantly correlated for most pairwise

**Table 3.** Summary of scaling parameters and data sources. All scalings are defined as pre-factor\*consumer mass<sup>exponent</sup>. For simplicity, pre-factors are given as lower-case Arabic letters subscripted with 0, and all exponents are given by closest Greek counterparts. OLS is ordinary least-squares regression; RMA is reduced major axis regression; AVG is a bootstrapped-model average of 10 000 random samples (with replacement) from each data set. Mean and 95% confidence intervals for the average parameter estimates are given as the 2.5, 50 and 97.5 percentiles of the bootstrapped distributions. Sources are listed above in Methods and Data

Parameter (units)	Pre-factor	95% CI's	Exponent	95% CI's
Density, $C$ (ind mL <sup>-1</sup> )				
	$c_0$		$\chi$	
OLS	$2.69 \times 10^6$	( $1.44 \times 10^6$ , $5.2 \times 10^7$ )	-0.99	(-1.31, -0.67)
RMA	$8.91 \times 10^6$	( $2.31 \times 10^6$ , $8.88 \times 10^7$ )	-1.12	(-1.37, -0.98)
AVG	$4.91 \times 10^6$	( $8.64 \times 10^5$ , $2.60 \times 10^7$ )	-1.05	(-1.24, -0.89)
Resource maximum population growth rate, $r$ (day <sup>-1</sup> )				
	$r_0$		$\rho$	
OLS	4.15	(2.99, 5.66)	-0.16	(-0.20, -0.13)
RMA	8.74	(6.05, 12.83)	-0.26	(-0.31, -0.21)
AVG	6.02	(4.57, 8.51)	-0.21	(-0.26, -0.17)
Resource carrying capacity, $K$ (ind mL <sup>-1</sup> )				
	$k_0$		$\kappa$	
OLS	$5.43 \times 10^8$	( $3.04 \times 10^8$ , $9.68 \times 10^8$ )	-0.80	(-0.87, -0.73)
RMA	$6.33 \times 10^8$	( $4.07 \times 10^8$ , $1.25 \times 10^9$ )	-0.82	(-0.89, -0.75)
AVG	$5.81 \times 10^8$	( $3.88 \times 10^8$ , $1.06 \times 10^9$ )	-0.81	(-0.88, -0.74)
Area of capture, $a$ (mL day <sup>-1</sup> ind <sup>-1</sup> )				
	$a_0$		$\alpha$	
OLS	$9.48 \times 10^{-6}$	( $4.34 \times 10^{-7}$ , $2.08 \times 10^{-4}$ )	0.81	(0.49, 1.12)
RMA	$6.12 \times 10^{-7}$	( $7.67 \times 10^{-9}$ , $1.53 \times 10^{-5}$ )	1.09	(0.79, 1.51)
AVG	$2.31 \times 10^{-6}$	( $7.85 \times 10^{-8}$ , $4.52 \times 10^{-5}$ )	0.95	(0.68, 1.31)
Handling time, $h$ (day)				
	$h_0$		$\phi$	
OLS	0.51	(0.03, 8.69)	-0.32	(-0.61, -0.03)
RMA	30.6	( $2.16 \times 10^{-5}$ , $3.65 \times 10^2$ )	-0.76	(-0.72, -1.08)
AVG	3.91	(1.04, 19.1)	-0.54	(-0.37, -0.74)
Mortality rate, $m$ (day <sup>-1</sup> )				
	$m_0$		$\mu$	
OLS	1.17	(0.06, 24.3)	-0.18	(-0.41, -0.05)
RMA	11.21	(0.0001, 244)	-0.35	(-0.56, 0.53)
AVG	3.81	(0.003, 39.5)	-0.27	(-0.44, -0.33)
Prey size, $M_r$ (no units)				
	$s_0$		$\psi$	
OLS	31.41	(3.78, 261.8)	0.39	(0.18, 0.61)
RMA	2.91	(0.04, 17.73)	0.64	(0.43, 0.86)
AVG	9.01	(1.46, 34.4)	0.52	(0.36, 0.74)
Conversion efficiency, $e$ (no units)				
	$e_0$		$\varepsilon$	
OLS	3.43	(0.074, 150)	-0.42	(-0.82, -0.006)
RMA	486	(10.38, $8.89 \times 10^3$ )	-0.97	(-0.59, -1.38)
AVG	41.2	(4.18, 991)	-0.69	(-0.43, -1.08)

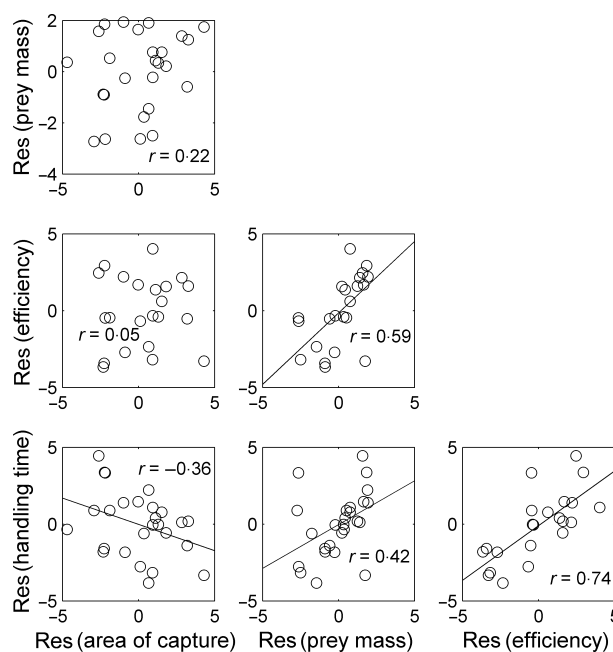


**Fig. 1.** Observed and predicted size-density scalings for protists. All panels show the same observed scaling relationship, with mean fit as solid black line and 95% confidence intervals with black dashed lines. The predicted relationship is shown in colour, with bold colour line showing mean prediction and the shaded colour region showing the 95% prediction interval.

comparisons, except that area of capture was not correlated with prey size or efficiency (Fig. 2). The correlation between area of capture and handling time was negative; all other significant correlations were positive. Handling time was correlated with efficiency in the residual analysis but not in the multiple-regression analysis (although both slopes were negative), and the significance and sign of all other relationships were consistent across statistical approaches (Table 4). Most importantly, the link between prey size and efficiency cancelled the potential benefit of taking larger prey on intake rates suggested by eqn 2, indicating that for protists of any given size, biomass intake rates are independent of prey size (Fig. 3).

## Discussion

We analysed body-size-dependent consumer–resource models that were fully parameterised for grazing protists grown in laboratory microcosms and successfully predicted both the height (intercept) and slope (exponent) of the size-density scaling relationship for this group. These predictions are completely independent of the size-density scaling relationship itself, as there are no fitted parameters that allowed tuning of the models to the data. And using nested models, we were able to reduce the range of potentially contributing processes to the few that were sufficient to explain the pattern. The size-density scaling



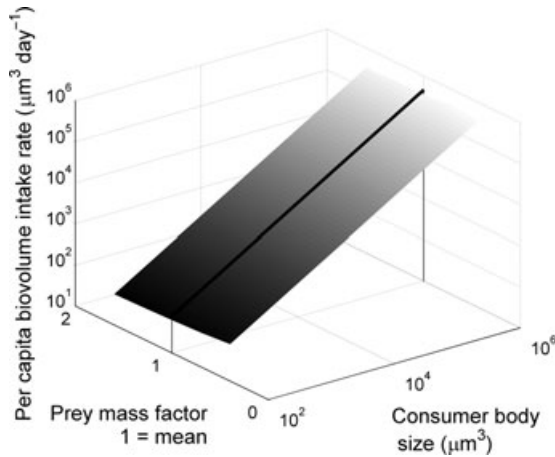
**Fig. 2.** Relationships between consumer–resource interaction parameters after controlling for consumer size. Significant correlations ( $P < 0.04$ ) are indicated by the presence of a least-squares line fitted to data. Pearson's correlation coefficients,  $r$ , are shown. Residuals are calculated from logged data.

**Table 4.** Results from multiple-regression analysis using consumer volume as a predictor variable plus prey volume, area of capture, conversion efficiency and handling time to examine for relationships between these parameters after controlling for consumer size. Each regression used predator volume and one of the above four parameters to predict the other four parameters to produce a correlation matrix. The results are similar to those produced in the residual analysis except that the multiple-predictor approach did not detect the negative relationship between handling time and area of capture detected by the residual analysis (Fig. 2). Such a difference may be due to multicollinearity in the multiple-regression models (Graham 2003)

Dependent variable	Independent variable	$t$	$P$
Prey volume	Area of capture	0.89	0.38
Efficiency	Area of capture	0.49	0.63
Efficiency	Prey volume	3.49	0.002
Handling time	Area of capture	-1.64	0.12
Handling time	Prey volume	3.02	0.006
Handling time	Efficiency	4.39	<0.001

of grazing protists is produced by the interaction of prey productivity, prey size selection and area of capture.

Taken together with our previous work on mammalian carnivores (DeLong & Vasseur 2012), our results provide strong evidence that global size-density scaling relationships arise from general processes described in the Lotka–Volterra predator–prey model that work across a broad size range of consumers. The protists in this study and the mammals in our previous work are very different, the former being single-celled grazers and the latter multicellular vertebrate carnivores. In addition, the mammals



**Fig. 3.** Empirical solution to individual biomass intake rates relative to the residual prey-size selection, using observed parameter estimates in eqn 4. Prey mass factor of one is when the prey size is equal to the expected from the allometric relationship.

occurred in the wild, while the protists were cultured in microcosms. Yet, the same model was able to quantitatively predict the pattern for both groups, given group-specific parameters, which suggests some level of generality for the explanation. Nonetheless, additional trophic interactions, such as body-size-dependent predation upon protists, may cause the laboratory patterns of the protists to differ from those in natural settings. When protists do not occupy the top trophic level of a food chain, a more complex model may be required to predict their size-density scaling.

Because the scaling exponents of prey productivity and prey size selection diminish each other (eqn 1), the slope of the size-density scaling exponent depends most on the scaling of area of capture. In addition to predicting the mean scaling pattern, however, the consumer–resource model approach suggests that residual variation in population density is likely to be primarily a function of variation in prey productivity and area of capture. Consumers that focus on highly productive prey will have higher population densities, as shown previously for mammalian carnivores (Carbone & Gittleman 2002). Consumers that acquire more resources for their size than expected will have lower densities because they have, in essence, higher *per capita* requirements. The effect of variation in prey size selection is diminished relative to these parameters because the exponent  $\rho$ , which is negative, reduces its impact, allowing a range of prey sizes to be taken with relatively small population density consequences.

Our results also provide an explanation for the emergence of the energetic-equivalence rule (EER). The total biomass flux through these protist populations at steady state is independent of average individual body size as a result of the interacting effects of prey size and productivity and predator mortality, area of capture, and conversion efficiency (eqn 3). Thus, a suite of allometric processes combine to yield the EER, depending on the

specific scaling patterns of both the consumer and resource. In the case of protists, the EER emerged, but in the case of mammalian carnivores (DeLong & Vasseur 2012), population-level energy use declined with body size. The consumer–resource model approach therefore provides a useful way of understanding both the EER and size-density scaling in terms of the underlying ecological processes, rather than assuming the EER to explain size-density scaling, or using size-density scaling to demonstrate the existence of the EER. Here, we have shown that they both emerge from the same process but depend on different sets of parameters.

Of the several parameters important to generating the scaling of density and energetics at both the individual and population levels, the scaling of prey size selection appears to be the most dependent on behaviour. Other parameters such as area of capture, mortality rate and efficiency should be linked to the metabolic scaling of the predator (Yodzis & Innes 1992; Brown *et al.* 2004), and prey productivity is linked to the metabolic scaling of the prey (Fenchel 1974). It is curious that there is a scaling of prey size selection at all when eqn 2 suggests that consumers that take large prey for their size would have higher biomass intake rates and therefore higher population growth rates (fitness). According to eqn 2, there should be continued natural selection for consumers that take larger and larger prey, but clearly this is not the case.

To understand this problem, we evaluated the links between parameters after controlling for consumer size (Fig. 2, Table 4) to determine whether such links could counter the apparent advantage of taking larger prey. In most cases, parameters were linked, regardless of statistical method used (residual or multiple-predictor analysis). The positive correlation between residual prey size and efficiency creates a mechanism to counteract the prey size–fitness link, and indeed, quantitatively assessing the change in resource intake rate with variation in prey size (using eqn 4) indicates that prey size is effectively neutral with respect to fitness at this level (Fig. 3). As with the buffering effect of prey productivity on the impact of prey size selection on population density, this link enables broad variation in prey size selection among consumers with minimal fitness consequences. Although the correlation itself makes sense, as larger prey can be turned into more offspring, these results highlight gaps in our understanding of prey size selection. Prey size selection may be driven to intermediate levels owing to inefficiencies associated with capturing large or small prey (Brose *et al.* 2008), but how this translates to specific scaling patterns is unknown. Finally, prey size selection has no obvious link with the metabolic scaling for the prey or the predator.

There were other links between parameters as well (Fig. 2). Handling time was the only interaction parameter whose residuals were correlated with all other parameter residuals, although residual and multiple-predictor analyses differed on the case of handling time

and area of capture. If a consumer had a larger-than-expected handling time, it was dealing with a larger-than-expected prey and therefore also experienced a larger-than-expected conversion efficiency. In contrast, larger-than-expected handling times were negatively associated with area of capture. These correlations indicate that the parameter space of these consumer–resource models for protists is structured by linkages across the parameters. It is not necessarily realistic, then, to examine the effect of one parameter on a model's output while holding others constant because of these linkages. This result has strong implications for the way in which consumer–resource models are used to simulate dynamic processes.

Our results further the idea that global size-density scaling relationships can be quantitatively predicted by dynamic consumer–resource models using independent parameters. This has now been attempted for mammalian carnivores and grazing protists, but there likely are sufficient data with which to test this approach for other groups, notably cladocerans and other small aquatic invertebrates (Hansen, Bjornsen & Hansen 1997). Global size-density scaling relationships appear to have a very simple genesis, reflecting only a few processes operating similarly across a wide body-size range and for taxonomically very different groups. Our findings not only indicate that size-density scalings conform to the size-specific metabolic demands of consumers, as expected by the metabolic theory of ecology (Brown *et al.* 2004), but also lead to the EER as an outcome rather than an input. Finally, our work can be integrated into more complex community models to potentially predict other forms of scaling patterns.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** (a) Species, cell sizes, and average population densities for a range of taxa grown in laboratory cultures. (b) Sources, predator and prey taxa, and consumer–resource interaction parameters.

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