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RESEARCH PAPER

Population energy use scales positively with body size in natural aquatic microcosms

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ABSTRACT

Aim We test the 'energetic equivalence rule' (EER) – the idea that the amount of energy used by a population per unit area per unit time is independent of body mass – in meio-invertebrate communities from a series of natural, multitrophic aquatic 'rock pool' microcosms. Our study represents the first rigorous test of the EER at local scales of observation in a community of naturally coexisting species.

Location Discovery Bay, Jamaica.

Method We estimated population energy use (PEU) for every occurrence of every species of meio-invertebrate fauna found in each of 29 microcosms (233 observations of 31 species) using estimates of population density obtained in January 2005 in combination with published metabolism–mass relations for closely related taxa.

Results In the rock pool system as a whole, population density decreased (ANCOVA: $b = -0.38$ (–0.55 to –0.19), $r^2 = 0.19$, $P < 0.001$) and PEU increased with body mass (ANCOVA: $b = 0.55$ (0.36–0.73), $r^2 = 0.28$, $P < 0.001$).

Main conclusions The positive PEU–body mass relation found here suggests that larger organisms are energetically dominant and points to the importance of size-structured competition in these systems. Our results contrast those obtained in the few other previously published tests of the EER and challenge the idea that all species use similar amounts of energy regardless of their size.

Keywords
Allometry, energetic equivalence rule, Jamaica, metabolic theory of ecology, metabolism, microcosms, population density.

INTRODUCTION

The 'energetic equivalence rule' (EER), which postulates that the amount of energy used by a population per unit area per unit time is independent of body mass (Damuth, 1981, 1987), has been a source of great interest and debate in ecology for nearly 30 years. Some of this debate undoubtedly stems from the fact that the EER challenges our understanding of the relative importance of the processes that structure communities: despite the great diversity in organism physiology, life-history strategies and interspecific interactions that has long been the focus of community ecology, the EER suggests that all species are roughly equivalent in an energetic sense and hints that the relatively simple relation between metabolism and body mass may play a principal role in structuring communities. Whereas conventional community ecology would suggest that the details of species ecology should strongly influence the amount of energy that species are actually able to procure in community, the degree to which the EER should be expected to hold true in all communities at all times remains an area of emphatic debate.

The EER was originally formulated based on Damuth's (1981) empirical observation that population density (D_i) tends to scale as a function of organism mass (M_i) to the power of –0.75 in terrestrial mammals ($D_i \propto M_i^{-0.75}$) Since organism metabolic rate (B_i) scales as a function of M_i to the power of 0.75 ($B_i \propto M_i^{0.75}$) (Kleiber, 1932, but see Savage *et al.*, 2004b, and Glazier, 2005), Damuth (1981, 1987) reasoned that the amount of energy used by a population per unit area per unit time (population energy

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use, PEU) should, as a general trend, be invariant with body mass (PEU = $D_iB_i \propto M_i^{-0.75}M_i^{0.75} \propto M_i^0$). However, nearly 30 years of investigation into the relationship between population density and body mass have revealed inconsistent patterns across communities and at different scales of observation (White *et al.*, 2007).

Although the relation between population density and body mass does tend toward a scaling exponent of –0.75 on average, it can be highly variable, particularly at smaller scales of observation (White *et al.*, 2007). Over small geographical areas, within lower taxa, and across narrow ranges of body mass the D_i–M_i relation has been observed to be negative and linear with a slope close to –0.75 (Damuth, 1991), positive and linear (Damuth, 1991; Nee *et al.*, 1991; Patterson, 1992; Cotgreave & Harvey, 1994), negative and nonlinear (Silva *et al.*, 2001), and sometimes shows only a weakly detectable negative slope or no discernible trend at all (Griffiths, 1986; Brown & Maurer, 1987; Morse *et al.*, 1988; Damuth, 1991; Nee *et al.,* 1991; Cyr & Pace, 1993; Marquet *et al.*, 1995; Blackburn & Gaston, 1997; Navarrete & Menge, 1997; deBruyn *et al.*, 2002; Ackerman & Bellwood, 2003; Reuman *et al.*, 2008). Furthermore, there seem to be more generalizable exceptions to the –0.75 scaling rule for the D_i–M_i relation: (1) in higher-level trophic groups (e.g. terrestrial carnivores) the exponent of the D_i–M_i relation has been shown to be more strongly negative (Carbone & Gittleman, 2002; Long *et al.*, 2006); (2) in aquatic systems the exponent tends to be closer to –1 (Patterson, 1992; Cyr *et al.*, 1997; Marquet, 2000; Gaedke *et al.*, 2004). These inconsistencies in the relation between population density and body mass – which almost certainly result from the details of species ecology – are of critical importance in terms of the strength and utility of the EER: if population density generally fails to scale with body mass to the power of –0.75, the EER would generally prove false. In fact, the EER will prove false whenever the B_i–M_i and D_i–M_i scaling exponents do not match.

The degree of variability in the relationship between population density and body mass at different scales of observation and in different systems has led many to conclude that the EER is unlikely to hold in a sufficiently consistent manner to be of much use to ecology. However, few studies have actually tested the EER directly through the examination of the relation between population energy use and body mass. Of those studies that have tested the EER more directly, many have simply assumed that $B_i \propto M_i^{0.75}$ for all species and have completely disregarded differences in the value of the slope and intercept among taxa (Currie & Fritz, 1993; Silva & Downing, 1995; Russo *et al.*, 2003). The consequence of using such simplifications is that no species-specific differences have been accounted for in the calculation of B_i (and subsequently PEU) from M_i data: since there can be substantial variation among taxa in both the intercept and the slope of the B_i–M_i relation (Agutter & Wheatley, 2004; Bokma, 2004; Glazier, 2005), such tests of the EER are dubious. Of the three studies that have provided a more thorough examination of the EER, incorporating species-specific differences in the scaling of metabolism with mass, all have occurred at large scales of observation (Marquet *et al.*, 1995; Medel *et al.*, 1995; Ernest *et al.*, 2003). Since the relation between population density and body mass can take several forms and tends to be much more highly variable at smaller scales of observation (White *et al.*, 2007), whether the EER will generally hold at local scales of observation among communities of interacting species is an important question: indeed, there is good reason to believe that other factors related to species ecology (organism physiology, life-history strategy and interspecific interactions) will play a more important role in structuring population densities at local scales of observation.

Here we test whether the EER holds in natural aquatic microcosms using observed population density and body size data for meio-invertebrate communities in combination with published data on the scaling of metabolic rate with body mass for closely related taxa. Whereas earlier tests of the EER have either been carried out over large scales of observation using data compiled from a number of distinct systems or have failed to account for species-specific differences in the scaling of metabolic rate with body mass, this study represents the first explicit test of the EER in a community of naturally coexisting species.

METHOD

Study system

To test the EER, we examined the relation between PEU and body mass in meio-invertebrate communities from 29 natural, multi-trophic aquatic 'rock pool' microcosms in January 2005. Rock pools are small, predominantly rain-fed ponds that form in natural cavities eroded in limestone fossil reef. The 29 rock pools used in this study are a subset of more than 250 pools located within a *c.* 50 m radius at the Discovery Bay Marine Lab on the north coast of Jamaica, 49 of which have been studied intensively for nearly two decades (Romanuk & Kolasa, 2002). Rock pool biotic communities consist of microorganisms, periphyton and phytoplankton, and over 70 species of zooplankton and other small invertebrates (Romanuk & Kolasa, 2002). The 29 pools used in this study vary in size by nearly two orders of magnitude (0.9–72.3 L), with an average volume of 17.85 L. Pool morphometry, desiccation frequency, salinity and nutrient concentrations all vary substantially among pools (Kolasa *et al.*, 1998; Therriault & Kolasa, 1999; Therriault, 2002).

Population density

The densities (L^{-1}) of meio-invertebrates (zooplankton, benthic invertebrates and crab and insect larvae) were estimated for all 29 pools by counting the number of individuals retained on a 63-μm net after passing 500 mL of pool water through the net (see Kolasa *et al.*, 1998 for sampling details). Meio-invertebrate samples were preserved in 50% ethanol and enumerated in the laboratory using a dissecting microscope. System-wide average population density was calculated for each species as the average density of that species across all of the pools in which it was found, since the presence or absence of a particular species in an individual pool is often driven by abiotic tolerances alone (Therriault & Kolasa, 1999; Romanuk & Kolasa, 2002; Therriault, 2002).

Body size

Body size data were obtained for all of the individual meio-invertebrates retained on the 63-μm net that were present in 15 of the 29 pools using a dissecting microscope, a Media Cybernetics Evolution QEi monochrome camera and ImagePro software. Measuring the body size of meio-invertebrates in this manner takes considerable time (months). Consequently, detailed body size measurements were obtained for only 15 of the 29 pools. Body sizes were estimated as biovolumes using the geometric equations suggested in Wetzel and Likens (1991) (see Appendix S1 in Supporting Information). Length–, width– and depth–biovolume relations were established in TABLE CURVE 2D using morphospecies-specific versions of the general power equation $y = ax^b$ for a subset of individuals of a number of abundant species in order to speed biovolume estimations for the remaining individuals of that species (see Appendix S1). Biovolumes were converted into fresh weight assuming a density of 1.0 (Patterson, 1992). Fresh weight was converted into dry weight according to taxon-specific values established in the literature (see Appendix S2). Dry weight was converted into ash-free dry weight using a factor of 0.4 (Peters, 1983). Average mass (M_i) was calculated for each species using all of the individuals measured in the 15 pools.

Metabolism

The metabolic rate of each individual was estimated based on published allometric equations describing the metabolic rates of closely related species (see Appendix S3). To enable system-wide interspecific comparisons, metabolic rates were temperature-corrected to 20 °C using the Boltzmann factor [$\exp(-E_i/kT)$], where E_i is the activation energy of metabolism [*c.* 1.04 J (0.65 eV); Gillooly *et al.*, 2001], k is the Boltzmann constant (1.381×10^{-23} J K^{-1}), and T is temperature in Kelvin. Average metabolic rate was calculated for each species using all of the individuals measured in the 15-pool subset.

Population energy use

PEU was calculated for every species in each pool as the density of its individuals in that pool multiplied by the average metabolic rate of that species. Average PEU (PEU_{avg}) was calculated for each species in the rock pool system as a whole as the average PEU of that species across all of the pools in which it was found.

Statistical analyses

We examined the effect of M_i on D_i and PEU in two principal ways. First, D_i and PEU were regressed against M_i in individual pools. Second, we examined the D_i–M_i and PEU–M_i relations in the rock pool system as a whole by performing three kinds of system-wide analyses:

1. We regressed all of the observations for every occurrence of every species in every pool together in a simple regression.

2. We regressed the system-wide average D_i and PEU for each species against M_i.

3. We used ANCOVA to determine the system-wide effect of M_i on D_i and PEU while taking differences among pools into consideration.

Curvilinear functions were fitted to already ln-transformed data in TABLE CURVE 2D. It has been argued that reduced major axis (RMA) regressions, which account for measurement error in the independent variable, provide better estimates of the slopes of allometric relations (Niklas, 2004). Since our most robust analyses and main conclusions stem from the use of ANCOVA, which relies on ordinary least squares (OLS) regression techniques, we present only OLS regression slopes here. However, RMA slopes may be calculated from OLS slopes as b_{OLS}/r, where r is the correlation coefficient of the OLS regression (Niklas, 2004). All analyses were carried out in STATISTICA (version 6.0, StatSoft, Tulsa, OK, USA).

RESULTS

When the relations between D_i and M_i and PEU and M_i were examined for each pool individually, none remained significant following the application of a Bonferroni correction to the significance level, suggesting that neither D_i nor PEU depend on mass in our system (Table 1). However, sample sizes are generally small within individual pools (3–15 species; Table 1) and the rock pool system as a whole is fairly open, with an environmentally mediated metacommunity-type structure (Romanuk & Kolasa, 2002; Therriault, 2002). Thus, in order to rigorously determine the effect of M_i on D_i and PEU in the rock system as a whole, we performed system-wide analyses by pooling the data from individuals pools together in three ways:

1. We regressed all of the observations for every occurrence of every species in every pool together in a simple regression (Fig. 1).

2. We regressed the system-wide average D_i and PEU for each species against M_i (Fig. 1).

3. Since rock pools differ along a number of abiotic gradients (Kolasa *et al.*, 1998; Therriault & Kolasa, 1999; Therriault, 2002), we used ANCOVA to determine the system-wide effect of M_i on D_i and PEU while taking differences among pools into consideration (Table 2).

Body size

Although species–body mass distributions differed from log-normality in three pools, the distribution of body masses in the system as a whole conformed to log-normality (Table 3).

Population density

When all of the data for every species occurrence in the 29 pool set were analysed together in a simple regression, D_i scaled as a function of M_i to the power of –0.32 (Fig. 1a). However, when D_i was averaged for each species across the 29 pools, D_i was unrelated to M_i in a simple regression (Fig. 1a). Controlling for the effect of pool characteristics (ANCOVA), D_i scaled as a function of M_i to the power of –0.38 (Table 2). Species–density distributions

Table 1 Bivariate regression statistics for the population density–body mass (D_i–M_i) and population energy use–body mass (PEU–M_i) relations in individual pools and across all pools. Bold type indicates significant results.

		D_i–M_i				PEU–M_i			
Pool	*n*	*a*	*b*	r^2	*P*	*a*	*b*	r^2	*P*
1	12	4.55	0.04	0.00	0.922	0.42	0.90	0.43	0.022
2	9	3.04	–0.08	0.01	0.837	–1.33	0.85	0.46	0.046
3	12	3.17	0.27	0.03	0.572	–1.03	1.17	0.38	0.032
4	9	4.52	–0.50	0.22	0.203	0.56	0.30	0.09	0.445
7	9	3.98	–0.60	0.26	0.159	–0.17	0.41	0.14	0.319
8	11	3.51	–0.78	0.26	0.113	–0.74	0.14	0.01	0.794
9	10	3.11	0.18	0.03	0.649	–1.15	1.15	0.55	0.014
10	8	4.40	–0.56	0.37	0.113	0.08	0.34	0.21	0.250
11	6	2.09	–0.66	0.15	0.453	–2.34	0.61	0.15	0.452
13	6	6.73	–0.89	0.49	0.122	2.30	0.11	0.02	0.792
15*	3	8.74	–1.64	0.69	0.376	3.89	–0.65	0.27	0.654
20	6	4.90	–0.38	0.09	0.559	0.89	0.40	0.12	0.511
23*	4	8.91	–3.74	0.46	0.324	4.08	–1.97	0.27	0.484
26*	4	9.35	–5.23	0.58	0.239	4.29	–3.50	0.39	0.377
29	8	4.17	–0.46	0.16	0.321	–0.09	0.43	0.13	0.378
32	10	5.44	–0.51	0.17	0.242	1.21	0.31	0.07	0.456
35	15	5.47	–0.77	0.33	0.024	1.39	0.14	0.02	0.612
36	7	1.99	0.18	0.02	0.774	–2.42	1.45	0.67	0.024
38	11	4.19	–0.10	0.01	0.819	–0.39	0.97	0.37	0.046
39	10	5.15	–0.38	0.08	0.433	–1.39	0.48	0.11	0.351
41	10	4.19	–0.26	0.04	0.571	–0.26	0.77	0.27	0.125
42*	5	6.42	–0.93	0.38	0.268	2.51	–0.17	0.03	0.798
44*	5	7.36	–0.65	0.17	0.486	3.16	0.24	0.02	0.820
47	10	3.59	0.26	0.03	0.659	–0.44	0.95	0.24	0.150
178	7	5.85	–1.69	0.65	0.028	1.71	–0.69	0.17	0.355
188*	5	4.85	1.53	0.24	0.402	1.15	2.01	0.30	0.335
205	8	4.82	0.12	0.01	0.819	0.38	1.42	0.53	0.041
1520	8	4.10	0.17	0.02	0.734	–0.23	1.04	0.36	0.119
1620*	5	7.18	–0.24	0.00	0.946	2.90	0.74	0.01	0.857
All pools									
	233†	**4.52**	**–0.31**	**0.04**	**<0.001**	**0.28**	**0.60**	**0.15**	**<0.001**
All pools averages									
	31‡	4.59	–0.39	0.07	0.084	**0.55**	**0.55**	**0.16**	**<0.02**

*Due to small sample sizes ($n \leq 5$), results should be interpreted with caution (see the discussion of the effects of the species–M_i and species–D_i distribution on the D_i–M_i relation in the Discussion and Table 3).

†The total number of species occurrences in all pools.

‡The total number of species found in the 29 pools studied here.

differed from log-normality in two pools and when all species were considered simultaneously in the system as a whole (Table 3).

Population energy use

When all of the data for every species occurrence in the 29-pool set were analysed together in a simple regression, PEU scaled as a function of M_i to the power of 0.60 (Fig. 1b). A curvilinear fit ($y = -1.37 + 2.74x^{0.21}$) to the already ln-transformed data provides a slightly better fit ($r^2 = 0.20$). When PEU was averaged for each species across the 29 pools, PEU scaled as a function of M_i to the power of 0.55 in a simple regression (Fig. 1b). A curvilinear fit ($y = -1.73 + 3.47x^{0.16}$) to the already ln-transformed data provides a slightly better fit ($r^2 = 0.23$). Controlling for the effect of pool characteristics (ANCOVA), PEU scaled as a function of M_i to the power of 0.55 (Table 2).

DISCUSSION

Although both D_i and PEU were unrelated to M_i in individual pools (Table 1), D_i scaled negatively and PEU scaled positively with M_i in the rock pool system as a whole (Fig. 1, Tables 1 & 2). The positive relation between PEU and M_i found here indicates that larger species are able to procure a disproportionately large share of the total resources available in the rock pool system, pointing to the importance of size-structured competition in these systems (Brown & Maurer, 1986; Nee *et al.*, 1991; Marquet

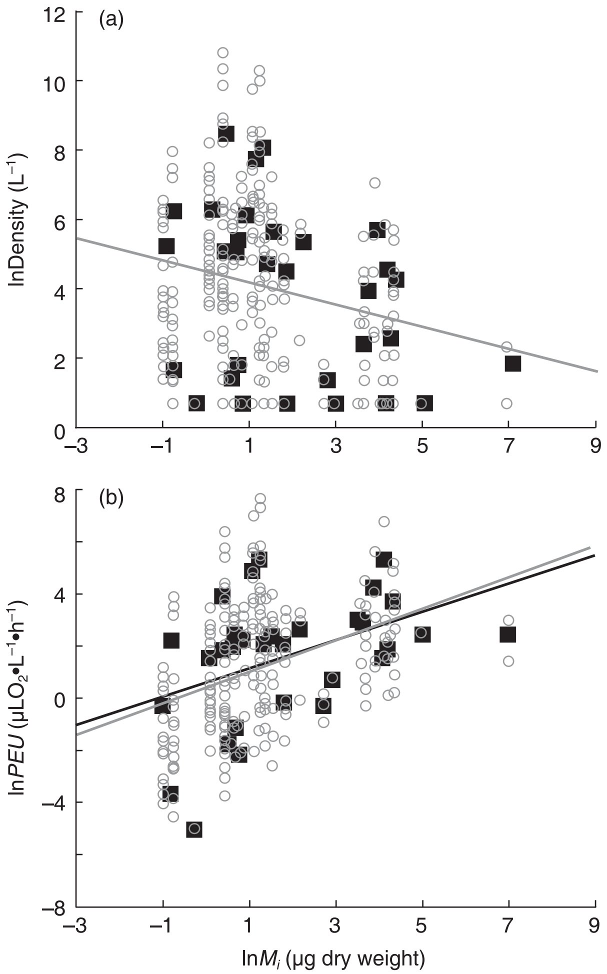

Figure 1 (a) Population density (D_i) and (b) population energy use (PEU) as a function of body mass (M_i) in the rock pool system as a whole. For both (a) and (b) open grey circles represent the occurrence of a species in a pool and solid black squares represent system-wide species averages which were calculated based only on pools in which the species was present. (a) The relation between D_i and M_i: The solid grey line represents a significant correlation between D_i and M_i when every occurrence of every species in every pool was included in the analysis [$a = 4.52$ (4.15–4.90), $b = -0.32$ (–0.50 to –0.13), $r^2 = 0.04$, $P < 0.001$]. There is no significant correlation between D_i and M_i when system-wide species averages are used for the analysis [$a = 4.59$ (3.37–5.80), $b = -0.39$ (–0.84 to 0.06), $r^2 = 0.07$, $P = 0.084$]. (b) The relation between PEU and M_i: The solid grey line represents a significant correlation between PEU and M_i when every occurrence of every species in every pool is included in the analysis [$a = 0.28$ (–0.10 to 0.66), $b = 0.60$ (0.42–0.79), $r^2 = 0.15$, $P < 0.0001$]. The solid black line represents a significant correlation between PEU and M_i when system-wide species averages are used for the analysis [$a = 0.55$ (–0.63 to 1.72), $b = 0.55$ (0.11–0.98), $r^2 = 0.16$, $P < 0.02$].

et al., 1995). Interestingly, the PEU data presented in Fig. 1(b) show a saturating curvilinear relation: It therefore seems that whatever competitive advantage the larger species in the system garner on account of their size decreases as size increases and that size-related metabolic constraints become an increasingly important determinant of community structure as the difference in size among the constituent organisms increases. Alternatively, the apparent saturating relation between PEU and M_i may reflect the fact that the total amount of energy available to organisms in successively higher trophic positions is expected to decrease, relative to the total amount of energy available to basal species, as a consequence of losses associated with inefficiencies in trophic transfers (Brown & Gillooly, 2003; Jennings & Mackinson, 2003; Long *et al.*, 2006, Arim *et al.*, 2007; Reuman *et al.*, 2008). Since trophic position is generally thought to scale positively with body size (Fry & Quinones, 1994; Cohen *et al.*, 2003), the saturating nature of the PEU–M_i relation observed here may reflect increases in trophic position with body size in our system. Whether the slope of the PEU–M_i relation may have decreased as far as zero, resulting in the emergence of the EER, had the range of body mass included in the study been increased is an interesting and open question.

To date, there have been only three rigorous tests of the EER (tests that have accounted for species-specific differences in the relation between metabolism and mass). The results of these three tests are, on the whole, somewhat inconclusive. First, in an examination of eutherian mammals, Medel *et al.* (1995) found an overall PEU–M_i slope of –0.18, with some variation in the slope according to feeding guild: Most intraguild relations exhibited slightly negative slopes (ranging from –0.04 to –0.29); only granivores exhibited a positive slope (0.15). However, the results of Medel *et al.* (1995) differ from those of the two other more rigorous tests of the EER, both of which analysed data from Damuth (1987). Using a subset of Damuth's data, Marquet *et al.* (1995) found an overall PEU–M_i slope of 0, but a positive slope for omnivores and a negative slope for insectivores when trophic group was included as a covariate. Examining an impressive 365 plant and 547 mammal species, Ernest *et al.* (2003) found a PEU–M_i slope of 0. However, although Ernest *et al.* (2003) used taxon-specific intercept information, they assumed a B_i–M_i slope of 0.75 for all species. Our results, which represent a fourth rigorous test of the EER, show a reasonably strong, positive relation between PEU and M_i (Fig. 1, Table 2) and contrast with those of Medel *et al.* (1995), Marquet *et al.* (1995) and Ernest *et al.* (2003). Notably, our study is the only one to have examined the EER in a community of naturally coexisting species at local scales of observation.

Since there tends to be large variation in the scaling of population density with body mass at small scales of observation, the results obtained in our study may not be particularly surprising. In agreement with the vast majority of studies that have examined the relation between D_i and M_i at smaller scales of observation (e.g. Griffiths, 1986; Brown & Maurer, 1987; Morse *et al.*, 1988; Damuth, 1991; Nee *et al.*, 1991; Cyr & Pace, 1993; Marquet *et al.*, 1995; Blackburn & Gaston, 1997; Navarrete & Menge, 1997; deBruyn *et al.*, 2002; Ackerman & Bellwood, 2003; Reuman *et al.*, 2008; but see Marquet *et al.*, 1990; Schmid *et al.*, 2000), we find that the relation between D_i and M_i (–0.38) is shallower than expected. As a number of other authors have previously assumed (e.g. Currie & Fritz, 1993; Taper & Marquet,

Table 2 Results for homogeneity of slopes and ANCOVA analyses. For both population density (D_i) and population energy use (PEU) analyses, homogeneity of slopes analysis found no interaction effect between pool and body mass (M_i) on either D_i or PEU, indicating that ANCOVA is a more appropriate method of statistical analysis here.

	Effect	*P*	*b* (95% CL)	Whole model
Homogeneity of slopes				
D_i–M_i, by pool	Pool	<0.001	–0.63	$r^2 = 0.20$, $P < 0.001$
	M_i	<0.001	(–0.99 to –0.27)	
	Pool*M_i	>0.36		
PEU–M_i, by pool	Pool	<0.001	0.36	$r^2 = 0.28$, $P < 0.001$
	M_i	>0.05	(–0.01 to 0.72)	
	Pool*M_i	>0.41		
ANCOVA				
D_i–M_i, by pool	Pool	<0.001	–0.38	$r^2 = 0.19$, $P < 0.001$
	M_i	<0.001	(–0.55 to –0.19)	
PEU–M_i, by pool	Pool	<0.001	0.55	$r^2 = 0.28$, $P < 0.001$
	M_i	<0.001	(0.36–0.73)	

CL, confidence limit.

Table 3 Number of species present (*n*), mean, standard deviation (SD), skewness (Skew.), kurtosis (Kurt.), and significance level for a Shapiro–Wilks test for normality (*P*) for the species–body mass (species–M_i) and species–density (species–D_i) frequency distributions. Bold type indicates significant results.

		Species–M_i distribution					Species–D_i distribution				
Pool	*n*	Mean	SD	Skew.	Kurt.	*P*	Mean	SD	Skew.	Kurt.	*P*
1	12	1.22	1.57	0.73	0.42	0.392	4.59	1.76	0.42	0.23	0.695
2	9	1.38	1.69	0.75	0.07	0.405	2.93	1.73	1.43	3.13	0.158
3	12	0.85	1.46	1.05	2.10	0.173	3.40	2.19	0.78	–0.02	0.197
4	9	1.45	1.75	0.67	–0.90	0.303	3.79	1.88	–0.64	–0.83	0.261
7	9	1.33	1.61	0.86	–0.09	0.238	3.19	1.88	–0.20	–1.22	0.340
8	11	1.03	1.30	0.85	0.48	0.559	2.70	2.02	0.89	–0.02	0.156
9	10	0.83	1.47	1.49	3.69	0.070	3.25	1.61	–0.47	–1.64	0.105
10	**8**	**1.50**	**2.01**	**0.59**	**–1.34**	**0.000**	**3.55**	**1.87**	**–0.22**	**–1.01**	**0.000**
11	6	0.15	0.89	–0.04	–1.19	0.761	**2.00**	**1.51**	**0.79**	**–1.85**	**0.042**
13	6	0.88	1.57	1.20	2.24	0.468	5.95	1.99	–0.01	0.43	0.969
15	3	1.63	2.37	1.69		0.133	6.07	4.68	–0.01		0.995
20	**6**	**0.87**	**1.78**	**2.00**	**4.60**	**0.020**	4.57	2.23	–0.92	–1.64	0.131
23	4	0.64	0.54	0.93	1.18	0.761	6.52	2.96	0.20	–4.35	0.399
26	4	0.67	0.51	0.12	–1.92	0.908	5.85	3.53	0.62	–2.52	0.271
29	**8**	**0.55**	**1.73**	**1.73**	**3.45**	**0.045**	3.91	1.97	–0.53	–1.12	0.511
32	10	2.49	2.10	1.04	1.12	0.291	4.16	2.65	0.45	–1.08	0.510
35	15	2.53	1.91	0.94	0.60	0.272	3.52	2.54	0.21	–1.33	0.069
36	7	0.42	0.72	–1.20	2.03	0.069	2.07	0.96	0.24	–0.46	0.926
38	11	1.50	1.52	0.48	0.10	0.643	4.04	1.85	–0.61	–0.54	0.528
39	10	0.87	1.50	1.33	2.87	0.181	4.82	2.06	–0.57	–1.50	0.979
41	10	1.76	1.87	0.40	–1.08	0.143	3.73	2.42	0.58	0.01	0.139
42	5	1.43	1.90	0.84	1.22	0.812	5.09	2.88	0.41	–2.18	0.475
43	5	2.08	1.79	0.36	–2.47	0.365	6.01	2.78	0.57	–0.90	0.825
47	10	1.09	1.24	1.11	2.68	0.388	3.88	2.00	0.15	–1.70	0.195
178	7	0.23	0.85	–0.32	–1.19	0.501	5.46	1.78	0.47	–2.12	0.124
188	5	0.81	0.90	–1.85	3.70	0.076	6.09	2.83	0.20	–1.94	0.701
205	8	1.48	1.66	0.51	–0.11	0.499	5.00	2.04	0.31	–0.43	0.740
1520	8	1.64	1.78	0.34	–0.37	0.623	4.38	2.15	–0.40	–1.66	0.219
1620	5	1.33	0.37	0.35	–0.80	0.955	6.85	2.12	1.27	1.59	0.454
All pools											
	233	n/a*					**4.12**	**2.33**	**0.42**	**–0.36**	**0.000**
All pools averages											
	31	1.92	1.94	0.65	–0.08	0.099	**3.83**	**2.42**	**0.11**	**–1.17**	**0.017**

*Since system-wide average body masses were used for each observation of each species, it is nonsensical to evaluate the species–body mass distribution for every observation of each species in the system as a whole: the same body mass would be repeated for each occurrence of each species.

1996), this in itself suggests that PEU should scale positively with M_i, since it implies that the D_i–M_i and B_i–M_i exponents do not cancel one another out to produce mass invariance according to $\mathrm{PEU} = D_i B_i \propto M_i^{-0.75} M_i^{0.75} \propto M_i^{0}$. Interestingly, however, in our study the PEU–M_i relation does not seem to strictly reflect the deviation of the D_i–M_i relation from broader expectations in our system: the observed PEU–M_i exponent (0.55) is statistically distinguishable from the exponent that would be expected if we derived such an expectation using the observed D_i–M_i exponent (–0.38) and the average observed B_i–M_i exponent (0.58), weighted by the number of individuals of each species, for the species in our system alone (i.e. $\mathrm{PEU} \propto D_i B_i \propto M_i^{-0.38} M_i^{0.59} \propto M_i^{0.22}$) (Table 2). This discrepancy between the expectations for the PEU–M_i slope derived from the D_i–M_i and B_i–M_i relations and the observed slope of the PEU–M_i relation in our system probably stems from Jensen's inequality and 'the fallacy of averages' – a more general problem that arises from using two allometric relations to extrapolate a third (Savage, 2004). However, the discrepancy between the observed and expected slopes also highlights the fact that caution should be exercised when attempting to draw conclusions about the scaling of PEU with body mass based on the scaling of population density with body mass alone (as is largely done in the literature concerning the EER).

In contrast to the results presented here, it is generally accepted that smaller species tend to be energetically dominant in aquatic food webs, where D_i–M_i slopes tend toward –1 (Patterson, 1992; Marquet *et al.*, 1995; Cyr *et al.*, 1997; Marquet, 2000; Gaedke *et al.*, 2004). Instead, the positive relation between PEU and M_i found here indicates that larger species are energetically dominant in the rock pool system (Brown & Maurer, 1986; Nee *et al.*, 1991; Marquet *et al.*, 1995). While the dominance of larger over smaller meio-invertebrate species observed here also opposes the long-held belief that respiration is controlled by smaller organisms in oligotrophic aquatic systems (del Giorgio & Peters, 1994), our results should be interpreted with some caution, since the meio-invertebrates examined here do not represent the full spectrum of organism body size in these ecosystems.

It has been argued that negative D_i–M_i relations may arise as a consequence of a community's underlying species–body mass and species–density distributions rather than as a consequence of size-mediated energetic limitation *per se* (Blackburn *et al.*, 1990, 1993; Silva *et al.*, 2001). In fact, models of D_i–M_i scaling based on the concatenation of the underlying species–body mass and species–density distributions predict that D_i should scale with M_i with slopes less than –0.49 (Blackburn *et al.*, 1993), a range that includes the confidence intervals surrounding the slope of the system-wide D_i–M_i relation observed here (Table 2). Such non-metabolic explanations of the D_i–M_i relation require that both the species–body mass and species–density distributions conform to lognormality (Blackburn *et al.*, 1993). Although the system-wide species–body size distribution observed here does not differ significantly from a lognormal distribution, suggesting that the system-wide D_i–M_i and PEU–M_i relations may result from sampling artefacts rather than energetic constraints, the system-wide species–density distribution is better described as bimodal and differs significantly from lognormality (Table 3).[1] Consequently, a non-metabolic explanation of D_i–M_i scaling, based on the concatenation of the underlying species–body mass and species–density distributions, is unlikely to satisfactorily account for the system-wide D_i–M_i and PEU–M_i relations observed here (though many of the underlying species–body mass and species–density distributions in individual pools do not differ significantly from lognormality; Table 3). The system-wide D_i–M_i relation observed here is also unlikely to result from differences in the total area over which small- and large-bodied species were censused (Blackburn & Gaston, 1998; Silva *et al.*, 2001), since every species was censused over the same total area in our study. Note, however, that we do not have sufficient sample sizes to conduct the robust sorts of analyses carried out by Blackburn *et al.* (1990) to definitively rule out the possibility that the system-wide D_i–M_i relation observed here results from non-energetic factors.

Implications for metabolic theory

The EER links organism physiology with ecological processes to produce generalized predictions about how communities are structured. This aspect of the EER has proven particularly interesting to ecologists attempting to link ecological pattern to the mass- and temperature-dependence of organism metabolism ('the metabolic theory of ecology'; Brown *et al.*, 2004). In fact, the EER is a central tenet in the derivation of predictions for patterns in structure and function at higher levels of biological organization (see Enquist *et al.*, 1998, 2003). While the metabolic approach to ecology has proven fruitful for predicting and deciphering population-level patterns (Enquist *et al.*, 1998; Ernest *et al.*, 2003; Savage *et al.*, 2004a) and has yielded some qualified success in predicting patterns in ecosystem energy use (Enquist *et al.*, 2003; George-Nascimento *et al.*, 2004; Allen *et al.*, 2005; Kerkhoff & Enquist, 2006), many of the derivations for higher-level patterns hinge on the legitimacy of the EER. The failure of the EER demonstrated here suggests that it may not be possible to consistently derive accurate predictions about patterns at higher levels of biological organization from the mass- and temperature-dependence of the metabolism of the constituent organisms alone at smaller scales of observation.

CONCLUSIONS

In the first rigorous test of the EER at local scales of observation, we show that PEU scales as a positive function of M_i, suggesting that larger species are energetically dominant and pointing to the importance of size-structured competition as a determinant of

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[1] The bimodal species–density distribution may result from the tolerances of species to salinity or disturbance regime in our system (Romanuk & Kolasa, 2002): the peak at lower densities may reflect species that specialize in a particular set of environmental conditions (either high or low salinity or high disturbance frequencies) and consequently have relatively low densities across the system as a whole. Conversely, the peak in higher densities may reflect species with broad tolerances to salinity or disturbance regime (i.e. generalist species), which could achieve higher densities across the system as a whole.

community structure in these systems. Broadly speaking, the failure of the energetic equivalence rule demonstrated here suggests that species ecology plays an important role in determining patterns of energy use in naturally occurring communities. Consequently, at smaller scales of observation, it may not be possible to consistently derive accurate predictions about structural and functional patterns at higher levels of biological organization from the mass- and temperature-dependence of the metabolism of the constituent organisms alone.

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SUPPORTING INFORMATION

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

Appendix S1 Biovolume equations.

Appendix S2 Fresh weight to dry weight conversion factors.

Appendix S3 Metabolism–mass equations.

BIOSKETCHES

April Hayward is a post-doctoral fellow at Dalhousie University whose research ultimately focuses on understanding how life emerged from a pre-biotic soup. Current efforts toward this end centre on understanding the flow and retention of matter and energy through different levels of biological organization.

Maaheen Khalid has recently completed her undergraduate degree in biology and is now pursuing a career in dentistry at the Schulich School of Medicine and Dentistry.

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