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Why does offspring size affect performance? Integrating metabolic scaling with life-history theory

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Within species, larger offspring typically outperform smaller offspring. While the relationship between offspring size and performance is ubiquitous, the cause of this relationship remains elusive. By linking metabolic and life-history theory, we provide a general explanation for why larger offspring perform better than smaller offspring. Using high-throughput respirometry arrays, we link metabolic rate to offspring size in two species of marine bryozoan. We found that metabolism scales allometrically with offspring size in both species: while larger offspring use absolutely more energy than smaller offspring, larger offspring use proportionally less of their maternally derived energy throughout the dependent, non-feeding phase. The increased metabolic efficiency of larger offspring while dependent on maternal investment may explain offspring size effects—larger offspring reach nutritional independence (feed for themselves) with a higher proportion of energy relative to structure than smaller offspring. These findings offer a potentially universal explanation for why larger offspring tend to perform better than smaller offspring but studies on other taxa are needed.

1. Introduction

Offspring size is a key life-history trait that can affect all aspects of performance [1]. Within many taxa, larger offspring perform better than their smaller conspecifics; they survive, grow and reproduce more than smaller offspring [2–4]. Larger offspring can also be more resistant to predation and starvation and are often better competitors than smaller offspring [5–8]. Benefits of increased offspring size are not inevitable however, and they are not universal [3]. For example, in some instances, increased offspring size can confer a fitness disadvantage, where bigger offspring have higher mortality than smaller offspring [9]. Generally, offspring size effects manifest in early development, but they can persist throughout the life history affecting reproduction and even the performance of the subsequent generation [10]. Understanding the relationship between offspring size and performance is of fundamental importance to life-history theorists because this relationship should drive the evolution of offspring size and explain the massive variation in offspring size we observe among species [11]. While many studies have documented the offspring size–performance relationship, surprisingly few have identified why this relationship occurs.

There are several viable explanations for why larger offspring often perform better than smaller offspring. A general consensus is that bigger offspring tend to have more mass and so it is often inferred that larger offspring have more energy to devote to fitness-enhancing processes such as growth [12]. While it seems intuitive that larger offspring have more maternally derived energy in total, presumably the associated costs of maintaining a larger size must also be higher. It then follows that in order for larger offspring to have proportionally more energy, the ratio of energy to the combined costs of maintenance and construction must also be higher in larger offspring than in smaller offspring. So far, there is no evidence to support the hypothesis that larger offspring have proportionally more energy than small individuals. In fact, some studies suggest that

larger offspring have lower levels of mass relative to volume and should have relatively less surplus energy [13,14]. Another potential explanation for the offspring size–performance relationship is the scaling of offspring size with structural components, such as feeding structures, which may allow larger offspring to better assimilate resources [15,16]. Several studies have also shown that larger hatchling size reduces susceptibility to predation [6,9,17], however there are exceptions [18,19]. While these explanations are all plausible, they are unlikely to provide any common explanation for the effects of offspring size on performance across taxa; instead, their relevance will vary according to trophic mode and life history [20]. One explanation that has received little attention, although common to all organisms, is the interaction between offspring size and metabolic scaling.

Metabolic scaling with body size is one of the most ubiquitous and contentious relationships in biology. While there are many competing explanations for metabolic scaling with size and much controversy (see, for example, [21] for a recent review), there is a consensus that increases in mass rarely result in perfectly proportional increases in metabolism, rather the scaling exponent relating mass to metabolism is often less than 1 [22–24]. Because metabolic scaling with size is allometric, larger organisms have lower mass-specific metabolic rates than smaller organisms both within and among species [25]. The extent to which metabolic rate scales with size changes considerably among individuals and throughout ontogeny, and the causes for these changes are unclear [26]. To date, most intraspecific studies have examined ontogenetic scaling and measured how metabolic rate scales with size as animals grow, usually by comparing large and small individuals of different ages or by experimentally manipulating individuals to create size gradients [27–31]. Many of these types of studies have found isometric or near-isometric scaling in the early life history [32,33], especially for pelagic species and life stages [34] but they confound size for age and developmental stage. An alternative and preferable approach to ontogenetic scaling is the examination of static scaling (e.g. [35–37]), where the relationship between metabolic rate and body size is examined for animals at the same age and developmental stage, by comparing individual metabolic rates across a naturally varying size range [38,39]. The general implications of static allometry remain the same for life-history theory; smaller individuals should have greater energy expenditure for a given mass than larger individuals [23].

Despite the likely implications of metabolic scaling for offspring size evolution, we are aware of only one study that has explored the interaction between natural offspring size variation and static metabolic scaling. Kinoshita *et al.* [40] found an allometric relationship between body mass and metabolic rates of ephyra larvae where mass variation was obtained through measurements of one to multiple individuals per respiration container. Technological innovations now provide higher throughput arrays with more sensitive equipment such that much higher levels of replication using individual offspring as replicates is now possible, and should provide more precise estimates of the relationship between offspring size and metabolic rate. This is the first study to measure static metabolic scaling for individual offspring. Here, we determine the static metabolic scaling exponents across natural variation in offspring size for two marine invertebrates, *Bugula neritina* and *Watersipora subtorquata*, repeating this at multiple stages of development until individuals reach the stage of independence (where offspring commence feeding and no longer rely on maternally supplied energy provisioning). Offspring size effects in these species have been well studied; larger offspring produce colonies that have higher survival, growth rates and reproductive output [41,42]. We then estimate the total energy use of maternal energy provisioning for different sizes of offspring in order to determine how energy use to independence scales with offspring size.

2. Material and methods

(a) Experimental overview

To understand how metabolic theory can be used as a potential explanation for the offspring size–fitness relationships central to life-history theory, it is important to understand the extent to which metabolism scales with offspring size. In order to do this, we (i) used measurements of volume and density of individual larvae to obtain estimates of offspring mass (details in electronic supplementary material, M1), (ii) measured the rate of oxygen consumption ($\dot{V}_{O_2}$) as a proxy for metabolic rate for individual offspring within a naturally occurring size range. We then (iii) calculated the total energy use as a proportion of the supplied energy throughout the dependent phase in order to determine the magnitude to which offspring size dictates energy consumption. Non-feeding offspring, which rely completely on a mother's allocation of energy supplies (which we assume is proportional to offspring mass), offer us the best study organism to examine the scaling of maternally provisioned energy use in offspring, as sources of external energy supply do not need to be considered. Thus, depending on the environment post-release, non-feeding offspring often reach a stage of independence with significantly depleted energy. Energy use is therefore of key importance to the fitness of both offspring and mother.

(b) Study species, collection and measurement of offspring size

Two marine bryozoans, the arborescent *B. neritina* and encrusting *W. subtorquata*, represent two subtidal species abundant in shallow temperate and tropical waters. Colonies brood larvae in either specialized chambers called ovicells (*B. neritina*) or on the body wall (*W. subtorquata*) for approximately one and two weeks, respectively [4,5]. The released, non-feeding larvae are competent to settle and begin metamorphosis immediately but in the field, settlement can be delayed for more than 24 h [43]. We define the dependent phase as commencing with release of larvae, up until the post-settlement period once metamorphosis is complete and the feeding structure (the lophophore) is fully developed. During the dependent phase, offspring are completely reliant on maternally provided energy, although it has been suggested that they may uptake dissolved organic matter (DOM; [44]). However, for *B. neritina* at least it has been shown that larvae do not use significant amounts of DOM and studies on the effect of extending the larval duration support this [45,46]. The duration of post-settlement metamorphosis is independent of larval size and lasts approximately 2–5 days, depending on temperature (A. K. Pettersen 2014, unpublished data).

Sexually mature colonies of *B. neritina* and *W. subtorquata* were collected at Royal Brighton Yacht Club in Victoria, Australia (37°54′18.9″ S, 144°58′48.3″ E) and Blairgowrie Yacht Squadron, Victoria, Australia (38°21′20.4″ S, 144°46′24.8″ E), respectively, during January to February 2014. Five colonies were then spawned using standard procedures [41]: following the maintenance of colonies in an aerated seawater system for 2–3 days at 17.5°C, colonies were exposed to bright light to stimulate larval release.

3

Upon release, larvae were haphazardly sampled for measurement of body area then either introduced directly into individual respiration vials or allowed to settle onto roughened acetate sheets that were cut out and placed into vials. However, for *W. subtorquata* settlers, body area of 24-h-old settlers was used as it has been shown to provide a good predictor of larval size [42]. Body areas of larvae were determined for both larval and settler experiments using standard techniques developed previously [41]. Larvae and settlers were photographed with a Moticam 5 digital camera (Motic, Hong Kong, China) mounted on a dissecting microscope and body area was estimated using image analysis software (IMAGEJ, 1.47v). Larvae were positioned such that the cillial groove was facing directly upwards, and length of the ciliated groove and the body area were measured to the nearest micrometre. Pilot studies of this method indicated that measurement error in larval size is small; measurement error accounted for 0.8% and 4.4% of all variation in offspring size in *B. neritina* and *W. subtorquata*, respectively, and this low error was also observed in the experimental measurements. In other words, the repeatability of our measures was 99.2% for *B. neritina* and 95.6% for *W. subtorquata*, reflecting an intraclass correlation coefficient of 0.995 and 0.977, respectively, and suggesting that measurement error accounted for very little variation in our estimates of body size. For a detailed account of how offspring mass and energy content were determined, see electronic supplementary material, M1.

(c) Metabolic scaling exponents: fluorescence-based oxygen measurements ($\dot{V}_{O_2}$) and conversion to metabolic rate (mJ h^{-1})

The rate of oxygen consumption ($\dot{V}_{O_2}$) was measured as a proxy for metabolic rate for larvae and two post-settlement stages of *B. neritina* and *W. subtorquata*. Oxygen consumption was measured using a 24-channel PreSens sensor dish reader (Sensor Dish Reader SDR2, PreSens), with 24-chamber glass micro plate (200 µl) (Loligo Systems Aps, Tjele, Denmark) according to standard techniques [47,48]. Individual larvae or settlers were placed in a glass vial containing 0.2 µm filtered seawater and a non-consumptive O_2 sensor spot and $\dot{V}_{O_2}$ was calculated from the rate of change of O_2 saturation (m_a; %h^{-1}) as $\dot{V}_{O_2} = -1 \, (m_a - m_b/100) \, V\beta_{O_2}$ (as per [26]), where m_b is the rate of change of O_2 saturation for blank vials containing no larvae or in the case of settlers, only acetate (%h^{-1}), β_{O_2} is the oxygen capacitance of air-saturated (AS) seawater at 17.5°C (5.8 ml l^{-1}; [49]) and V is water volume (chambers were 2.0×10^{-4} l, and water volume was calculated by subtracting the volume of acetate and animals). Four blank vials were recorded simultaneously to account for microbial oxygen consumption, and sensor spots were calibrated with AS seawater (100% AS) and water containing 2% sodium sulfite (0% AS). All $\dot{V}_{O_2}$ measurements were conducted in a dark, constant-temperature room at 17.5°C. For $\dot{V}_{O_2}$ measurements for larvae, oxygen concentration in the vials was recorded over 30 min (we used a short period to ensure no larvae began settlement while in the chambers). For settlers, oxygen concentration was recorded over 3 h at two different stages of development prior to completing metamorphosis and development of the lophophore (from here on, designated early and late). Pilot studies showed no systematic differences in the duration of metamorphosis associated with offspring size. Hence, $\dot{V}_{O_2}$ for all metamorphosing individuals was measured at two discrete times; 0 h and 24 h for *B. neritina* and *W. subtorquata* was measured at 0 h and 54 h post-settlement to represent the start and mid-point of the post-settlement-dependent phase. Each experimental run consisted of simultaneous $\dot{V}_{O_2}$ measurements for 20 individuals recorded at three development stages (larval, early and late stage). To determine the rate of energy expenditure by different sized offspring, $\dot{V}_{O_2}$ (µl h^{-1}) was converted to metabolic rate (mJ h^{-1}) using the calorific conversion factor of 20.08 J ml^{-1} O_2 [50].

All data were analysed in a log–log framework. Due to various logistical limitations (for a detailed description of the analytical approach, see electronic supplementary material, M2), scaling exponents and coefficients for larvae were analysed independently to those of the post-settlement stages (early and late) for both species. A repeated-measures ANCOVA approach was taken for measuring the same individual settlers throughout the early and late stages. As different individuals were measured for the larval stage, a linear mixed-effects ANCOVA was used to determine whether differences existed between larval and settler stage metabolic rates. All analyses included the random effect of Experimental Run and all possible interactions with stage and $\log_{10}$ mass. A standard ANCOVA framework rather than RMA approach was used as the error structure of our data was not suited to RMA (see the electronic supplementary material for details).

(d) Predicting proportional energy use from offspring size

In order to calculate the proportional energy use for offspring of different sizes, we parametrized the power relationship between mass (M) and metabolic rate (MR), where $MR = aM^b$. Using the coefficients (a) and scaling exponents (b) estimated by our experiments, combined with the approximate length of time spent in each stage, we were able to predict total energy consumption throughout the dependent or non-feeding stage of development.

To determine whether the energy difference between large and small offspring was substantial, such that it may affect settlement success or post-settlement survival, we compared the proportional energy use for offspring at the extremes of our observed size distribution. We calculated energy use by offspring across an approximately threefold difference in size (see electronic supplementary material, S1), which reflects the size range of offspring in natural populations of these species [41,42].

3. Results

(a) Metabolic scaling exponents

Allometric scaling relationships of metabolic rate were observed for both species and across all developmental stages (table 1), where the scaling exponents were significantly different from both 0 and 1 ($p < 0.05$). For offspring in both species, there was a significant development-stage effect where overall metabolic rate was highest during the larval phase in *B. neritina* and lowest in the early settler stage (tables 2 and 3). Conversely, metabolic rate overall increased through ontogeny in *W. subtorquata* (tables 2 and 3). For *W. subtorquata*, no interaction between stage and mass was detected; therefore, a single scaling exponent was obtained for all three stages. For *B. neritina*, the slopes among the early and late settler stages were found to be significantly different (table 2) and therefore separate scaling exponents were obtained for each stage. For each analysis, there were significant effects of experimental run for the pooled larvae and early-stage settlers of *B. neritina* (table 1) and for late-stage settlers of *B. neritina* (table 2). There was also a significant effect of experimental run for the pooled larvae, early-stage and late-stage settlers of *W. subtorquata* (table 3). We found no support for fitting a random-slopes model (i.e. no significant run × mass effect was detected), but there was significant among-run variation in the intercept of the relationship between size and metabolic rate (tables 2 and 3). This run-associated

Table 1. Summary of scaling exponents and coefficients ($\pm$ s.e.) for metabolic rate and mass of the development stages of *B. neritina* and *W. subtorquata*, using a log–log transformed linear relationship, where $\log_{10}$ metabolic rate = $b \times \log_{10}$ mass + a. Wald tests were used to determine whether the scaling exponent (b) was significantly different from both 0 and 1. Early stage = 0 h post-settlement. Late stage for *B. neritina* = 24 h post-settlement, for *W. subtorquata* = 54 h post-settlement.

species	*B. neritina*					*W. subtorquata*				
	coefficient (*a*)	scaling exponent (*b*)	*p*-value *b* > 0	*p*-value *b* < 1	R^2	coefficient (*a*)	scaling exponent (*b*)	*p*-value *b* > 0	*p*-value *b* < 1	R^2
developmental stage										
larvae	−1.15 (±0.14)	0.76 (±0.11)	<0.01	<0.05	0.75	−1.08 (±0.15)	0.66 (±0.11)	<0.01	<0.01	0.62
early	−1.66 (±0.13)	0.76 (±0.11)	<0.01	<0.01	0.75	−1.34 (±0.15)	0.66 (±0.11)	<0.01	<0.01	0.62
late	−0.77 (±0.11)	0.29 (±0.10)	<0.01	<0.01	0.29	−0.89 (±0.15)	0.66 (±0.11)	<0.01	<0.01	0.62

variation could stem from multiple sources (phenotypic and genetic differences among colonies, temporal effects). Crucially however, the relationship between mass and metabolic rate was constant among all runs, so our principle findings hold across colonies and times.

(b) Predicting proportional energy use from offspring size

The coefficient and scaling exponent values obtained from the linear model of $\log_{10}$ transformed data for each developmental stage were then used to predict metabolic rate according to the power function $MR = aM^b$ (figure 1). The predicted metabolic rate was then multiplied by the average amount of time spent at each developmental stage based on previous observations (*B. neritina*; larval stage 0.5 h, early stage 24 h, late stage 30 h, *W. subtorquata*; larval stage 0.5 h, 54 h, 52 h) to obtain total energy consumption from release as larvae until the completion of metamorphosis and development of the feeding structure. The predicted total energy use by the smallest observed *B. neritina* offspring of 6.7 µg was 11.2 mJ, while the largest offspring with a mass of 24.5 µg uses only 19.4 mJ. For *W. subtorquata*, the smallest offspring of 9.3 µg uses 39.9 mJ, and the largest offspring of 25.3 µg uses 77.2 mJ by the end of the dependent phase. Thus, where a large offspring is twice the mass of a small offspring, it consumes only 1.3 times the energy in *B. neritina* and 1.5 times the energy in *W. subtorquata* than that of a small offspring in reaching a stage of independence.

Using carbon content values reported by Wendt [45], the energy density for *B. neritina* was found to be 3.85×10^{-6} µg µm^{-3}. As a proportion of known energy content extrapolated from Wendt [45], we can compare proportional energy use for the natural size range we found in this species. The smallest observed *B. neritina* larvae (6.7 µg) will use 46.7% of maternal energy provisioning, while the largest observed offspring (24.5 µg) will use only 22.1% of its supplied energy to reach independence. For *W. subtorquata*, the oxygen consumption rate increased twofold through development and total energy use was over 3.5 times that of *B. neritina* such that energy density must be higher. Based on our estimate of offspring energy density of 7.78×10^{-6} µg µm^{-3}, as a proportion of total energy supply, the smallest offspring (9.3 µg) would use 60.6% total energy compared with 43.2% of total energy for the largest offspring (25.3 µg) to reach independence.

4. Discussion

(a) Allometric scaling of metabolism and the benefits of increased offspring size

We found that when offspring depend entirely on maternal resources to complete metamorphosis and burn around 30–50% of their total energy content, larger offspring have much lower relative metabolic rates than their smaller conspecifics. Both *B. neritina* and *W. subtorquata* show strong relationships between offspring size and post-metamorphic performance—bigger larvae survive better and reproduce more as colonies [41,42]. The allometric scaling of metabolic rate with offspring size may explain this relationship. We found that the metabolic dynamics of small and large offspring

4

Table 2. Repeated-Measures analysis for the longitudinal study between $\log_{10}$ metabolic rate and $\log_{10}$ offspring mass. Metabolic rate for the same individuals of *B. neritina* and *W. subtorquata* was measured at two distinct post-settlement development stages; early and late (d.f. presented as num d.f., den d.f.).

species	*B. neritina*				*W. subtorquata*			
	d.f.	mean squares	*F*-ratio	*p*-value	d.f.	mean squares	*F*-ratio	*p*-value
between subjects								
$\log_{10}$ mass	1184	1.04	37.38	<0.01	1,50	0.35	21.31	<0.01
experimental run	11 184	0.08	2.76	<0.01	3,50	0.20	12.02	<0.01
$\log_{10}$ mass × experimental run	11 173	0.03	0.94	0.50	3,47	0.01	0.28	0.84
within subjects								
stage	1184	0.49	31.19	<0.01	1,47	0.09	4.78	0.03
stage × $\log_{10}$ mass	1184	0.17	11.05	<0.01	1,47	0.02	1.21	0.28
stage × experimental run	11 184	0.01	0.70	0.73	3,47	0.01	0.66	0.58
stage × $\log_{10}$ mass × experimental run	11 173	0.01	0.81	0.63	3,47	0.01	0.54	0.66

Table 3. Linear mixed-effects model for cross-sectional study between $\log_{10}$ metabolic rate and $\log_{10}$ offspring mass. Metabolic rate was measured for different individuals of *B. neritina* and *W. subtorquata* at two development stages; larval and early post-settlement stage.

species	*B. neritina* (larval and early stages)			*B. neritina* (late stage)			*W. subtorquata* (larval, early and late stages)		
	d.f.	χ^2	*p*-value	d.f.	χ^2	*p*-value	d.f.	χ^2	*p*-value
$\log_{10}$ mass	1	39.21	<0.01	1	6.57	<0.01	1	24.50	<0.01
experimental run	1	19.41	<0.01	1	27.25	<0.01	1	22.65	<0.01
stage	1	37.07	<0.01				1	11.93	<0.01
$\log_{10}$ mass × experimental run	1	0.21	0.65	1	0.05	0.83	1	0	1
$\log_{10}$ mass × stage	1	0.21	0.65				1	0	1
stage × experimental run	1	0	1				1	0	1
$\log_{10}$ mass × stage × experimental run	1	0	1				1	0	1

are very different: on an absolute scale, larger offspring use more energy sourced from the mother than smaller offspring; however, on a relative scale (i.e. per unit of body mass), larger offspring use less energy than smaller offspring. In effect, larger offspring are more metabolically efficient during the key phase of dependence on maternal energy, whereas smaller offspring could be regarded as more wasteful. Hence, larger offspring not only reach nutritional independence with absolutely more energy, but also with relatively more energy because, relative to structural components of size, they use fewer resources during the phase in which they depend on maternal resources. Note that this increased efficiency of larger offspring will occur regardless of the initial composition of smaller and larger larvae. For example, different sized larvae could have different proportions of lipid (although this is unlikely given larval sizes were all of similar density in each species), which would affect the final energy content of different sized offspring, but would not alter our finding that larger larvae burn proportionally less of their reserves.

In a previous study, Sinervo [12] alluded to a potential metabolic mechanism for the observed relationship between offspring size and performance in lizards, where 'juvenile size and growth rate are functionally related because some underlying determinants of growth rate (e.g. metabolism) are allometrically related to size'. Despite this prescient suggestion, there has been little evidence for static (within developmental stage) allometric scaling relationships between naturally occurring offspring size variation and metabolism until now. In contrast, static allometric scaling of metabolic rate has been observed in adult insects (e.g. [35–37]), mammals (e.g. [51,52]) and chickens [53], but the static scaling exponent of metabolic rate is almost isometric in adult pied flycatchers *Ficedula hypoleuca* [54], and metabolic rate and body mass are independent in some (e.g. [55]), but not all (e.g. [56]), studies of adult *Drosophila melanogaster*. Thus, although static allometric scaling of metabolic rate is not ubiquitous, it may be widespread within life stages throughout development (e.g. [57,58]), such that it may provide a general explanation for the often-observed positive relationship between offspring size and performance across a wide range of taxa. We believe the metabolic benefits of producing larger offspring offer several exciting new lines of inquiry for understanding variation in offspring size.
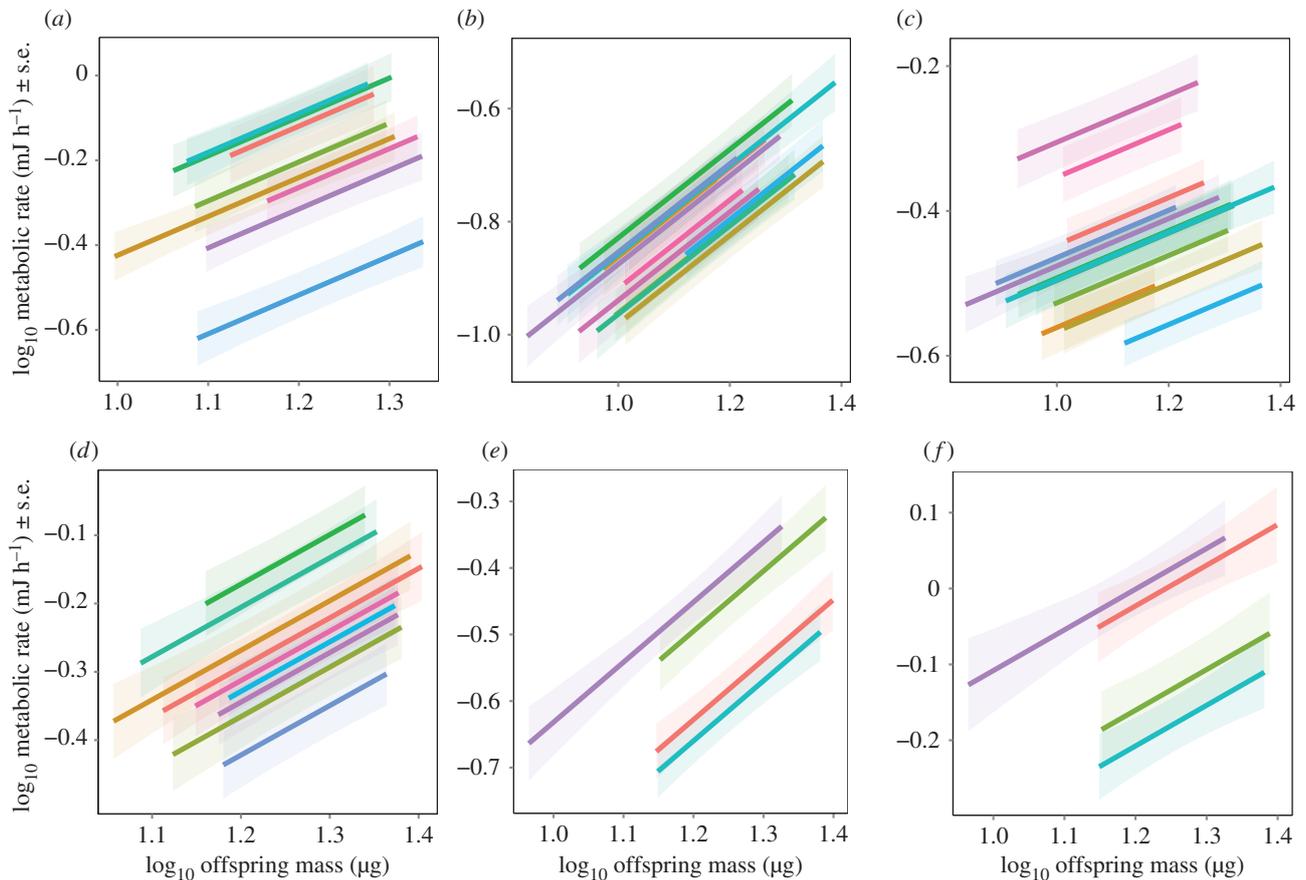
6

Figure 1. Predicted lines of best fit per experimental run from linear mixed-effects model ($\pm$ s.e.) for the relationship between $\log_{10}$ offspring mass (μg) and $\log_{10}$ metabolic rate (mJ h^{-1}) for *B. neritina*: (*a*) larval stage, (*b*) early post-settlement stage, (*c*) late post-settlement stage and *W. subtorquata*: (*d*) larval stage, (*e*) early post-settlement stage, (*f*) late post-settlement stage. Each line represents an experimental run with a common slope and its own unique intercept per development stage.

(b) Hidden metabolic costs of smaller offspring

Life-history theory has long assumed that the fitness benefits of producing smaller offspring come from smaller offspring being 'cheaper' to make, allowing mothers to make many more offspring. While smaller offspring almost certainly require fewer maternal resources to make, our findings show that they use these resources much less efficiently than larger offspring. Per unit of body mass, metamorphosis costs more for smaller offspring than larger offspring. Interestingly, the size–fecundity relationship exacerbates these metabolic costs of producing smaller offspring. To illustrate this, we compare two mothers with equal reproductive investment, but which produce offspring of very different mean size. As shown in figure 2, mothers producing smaller offspring will lose 11 mJ per offspring investment to the metabolic costs of offspring development, while a mother producing larger offspring will lose 19 mJ (figure 2*a*). Because fecundity is inversely proportional to offspring size, mothers producing smaller offspring will lose 47% of their total investment to metabolic costs of development while mothers producing larger offspring will lose only 22% (figure 2*b*). While smaller offspring are much cheaper to make initially, they are much more expensive to provision through to nutritional independence—a finding that current life-history theory fails to consider explicitly. For species with post-release care (e.g. mammals and birds), this suggests that any decrease in initial offspring size via egg size or birth weight must be overcompensated for via parentally supplied resources. A simple trade-off between pre- and post-release investment will not yield identical outcomes due to the reduced

efficiency of smaller offspring during development. Instead, a small decrease in offspring size must be accompanied by a larger increase in post-release parental investment. For species with no post-release care, the increased inefficiencies of smaller offspring size will simply exacerbate the costs of smaller initial parental investment, extending the phase that smaller offspring need to feed simply to attain equivalent sizes to larger offspring. These subtle costs of producing smaller offspring should be included in future models of offspring size.

(c) Modifiers of the offspring size–energy consumption relationship

Factors that increase the length of the dependent phase should increase the benefits of larger offspring sizes (and also increase the costs of smaller offspring sizes). For example, our results may explain the well-known relationship between temperature and offspring size, whereby mothers often produce larger offspring in cooler temperatures [59]. If temperature affects developmental rates more than metabolic rates, then mothers may make smaller offspring at higher temperatures because the relative costs of development are offset by faster development under those conditions. Conversely, in cooler temperatures where development time is increased to a higher extent than metabolic rate is decreased, offspring will require larger energy stores to reach independence [60]. In species with extended periods of time that offspring depend on maternal resources (e.g. altricial species of birds), we would expect the benefits of increased egg size to be enhanced,
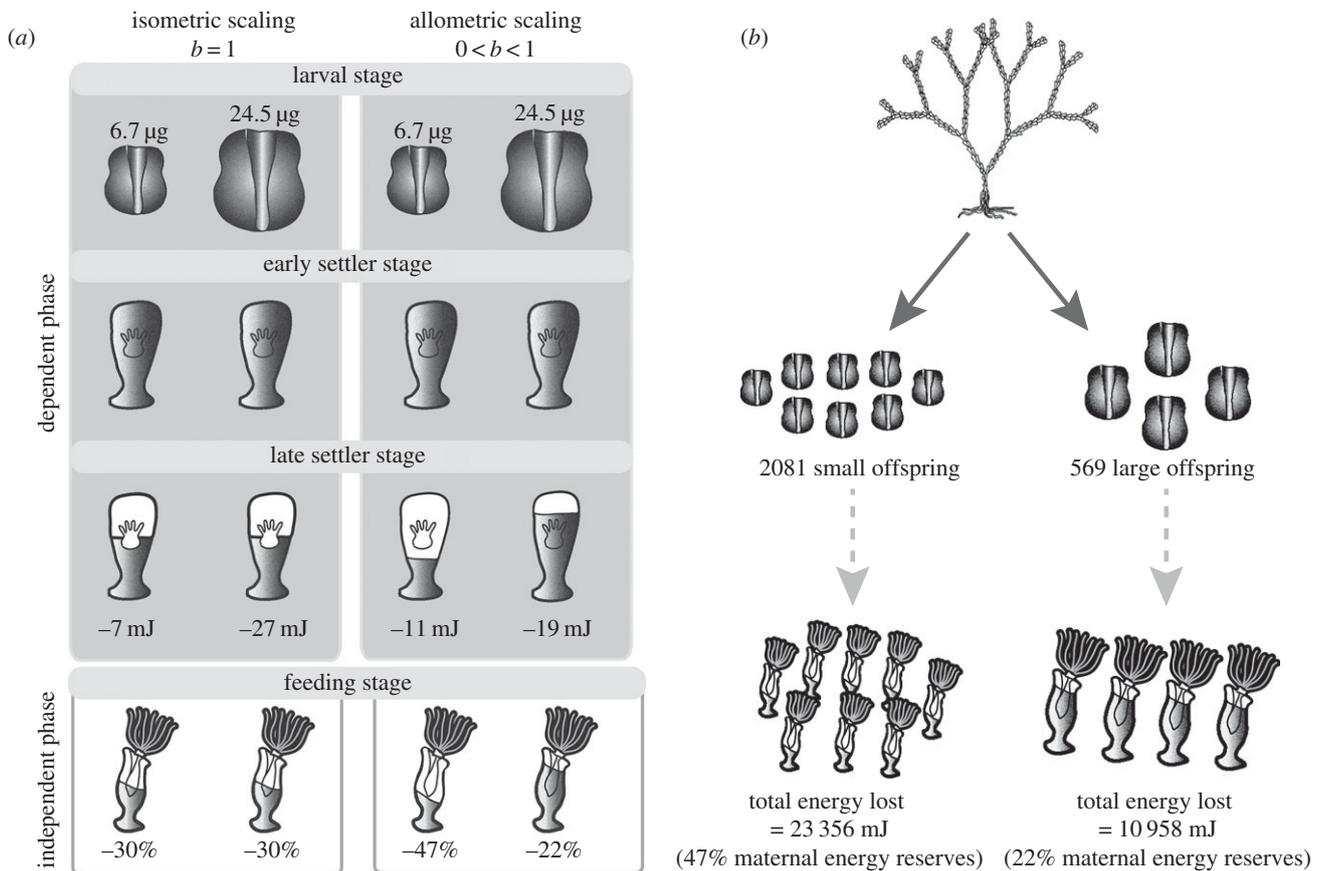
Figure 2. Schematic showing proportion of energy used by the smallest (6.7 μg) and largest (24.5 μg) *B. neritina* larvae observed in our study. (*a*) Hypothetical isometric relationship (scaling exponent, *b* = 1; as assumed by life-history theory) versus an allometric relationship between size and metabolic rate up until the independent phase based on scaling exponents obtained from our results (larval stage; *b* = 0.76, early stage; *b* = 0.76, late stage; *b* = 0.29). According to the power function, MR = aM^b, energy use is directly proportional to body mass in an isometric relationship (where *b* = 1), while in an allometric relationship, smaller offspring use relatively more energy per unit body mass than larger offspring (*b* < 1). (*b*) The relative amount of energy that is consumed in the dependent phase for mothers with identical total reproductive investments (fecundities based on field observations at our field site) but where one mother produces the largest observed offspring and the other produces the smallest observed offspring. As a proportion of total supplied energy, the fewer, larger offspring in total will use less than half of the maternally supplied energy relative to the many smaller offspring (i.e. mother producing larger offspring: total energy (50 000 mJ)/per offspring energy (87.9 mJ) = offspring number (569) × individual energy burned (19.3) = total metabolic cost (10 958 mJ)).

and indeed, altricial species do tend to produce larger eggs than precocial species [61]. Similarly, those species with longer incubation periods also have larger egg sizes [62]. In our system, larval period and temperature are key modifiers of the length of the dependent phase. For our study species, the larval phase varies in nature between a few minutes and up to 24 h [43]. A relatively long larval period of 12 h (and the same size-specific metabolic rate) would therefore yield an almost twofold increase in the differential of efficiency between big and small larvae in *B. neritina* and *W. subtorquata* (1.8 and 1.6 times, respectively). Our results may provide an explanation for the finding that larger larvae cope better with prolonged swimming periods in *B. neritina*. Burgess *et al.* [46] found that extending the larval period reduces post-metamorphic performance, but that smaller larvae showed the greatest reductions in performance relative to larger larvae. Furthermore, larger larvae in both *B. neritina* and *W. subtorquata* tend to reject low-quality settlement sites for longer than smaller larvae, thereby increasing their chances of colonizing higher quality environments [46]. Our results suggest that larger larvae can afford to be more selective of their settlement environment for longer, because the costs of extending the larval period are less for larger larvae relative to smaller larvae. Our results may therefore explain the well-known but poorly understood

relationship between offspring size and larval duration in marine invertebrates with non-feeding larvae [63]. If the patterns found here also apply to feeding larvae, the effects of egg size on metabolic efficiency could be even more profound. In such species, whose larval periods can extend for weeks to months depending on food and habitat availability (as reviewed in Strathmann [64]), even slight differences in relative metabolic rates will be magnified over such extended periods of time. An important next step will be to repeat our study in species with feeding larvae.

It is important to note that our results are subject to a number of caveats. First, we assume that carbon content scales isometrically and with the same intercepts across our offspring size range for all of our experimental runs. Any divergence from these assumptions may explain the run effects observed in both species. If carbon content is affected by variables other than offspring size, then this may alter our estimates of energy use. However, our main finding that larger larvae use relatively less energy is unaffected by whether carbon content is consistent across runs. Second, we found allometric relationships between offspring size and metabolic rate for two very different species from the same phylum; however, it is too soon to generalize as to whether our findings hold more broadly. Instead, our proposed mechanism remains an

attractive, but speculative, hypothesis as to why larger offspring perform better than smaller offspring, and more tests of static allometry in metabolic rate across offspring sizes in other taxa are needed.

5. Conclusion

We found that the scaling exponent of metabolic rate was less than 1 throughout the dependent phase in two marine bryozoans, *B. neritina* and *W. subtorquata*. We propose that the allometric scaling of metabolic rate during early development has important life-history consequences but, at this stage, must restrict our conclusions to the two species tested. Larger offspring are provisioned with more energy than smaller offspring but, because metabolic rate scales allometrically with offspring size, larger offspring use energy at a relatively lower rate than smaller individuals. Therefore, all else being equal, larger offspring should reach independence with a higher proportion of maternal investment than smaller offspring. Our results may provide a general explanation for why larger offspring do perform better than smaller offspring, given that most animals show allometry with respect to metabolism and that we expect the increased relative efficiencies of larger offspring to be widespread. However, this hypothesis requires further testing. Furthermore, our results show that there are

intrinsic benefits to producing larger offspring (i.e. they are more efficient users of maternal resources). Hence, for these species at least, conditions that favour the production of smaller offspring must overcome the intrinsic metabolic benefits of increased size. Despite the extensive theoretical treatment of offspring size, we are unaware of extant theory that explicitly considers the metabolic benefits of increased offspring size. Development of such theory is an important next step.

References

1. Stearns SC. 1992 *The evolution of life histories*. New York, NY: Oxford University Press.

2. Fox CW, Czesak ME. 2000 Evolutionary ecology of progeny size in arthropods. *Annu. Rev. Entomol.* **45**, 341–369. (doi:10.1146/annurev.ento.45.1.341)

3. Krist M. 2011 Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.* **86**, 692–716. (doi:10.1111/j.1469-185X.2010.00166.x)

4. Marshall DJ, Keough MJ. 2008 The relationship between offspring size and performance in the sea. *Am. Nat.* **171**, 214–224. (doi:10.1086/524954)

5. Allen RM, Buckley YM, Marshall DJ. 2008 Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am. Nat.* **171**, 225–237. (doi:10.1086/524952)

6. Janzen FJ, Tucker JF, Paukstis GL. 2000 Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *J. Evol. Biol.* **13**, 947–954. (doi:10.1046/j.1420-9101.2000.00234.x)

7. Chen BJW, During HJ, Vermeulen PJ, Anten NR. 2014 The presence of a below-ground neighbour alters within-plant seed size distribution in *Phaseolus vulgaris*. *Ann. Bot.* **114**, 937–943.

8. Hutchings JA. 1991 Fitness consequences of variation in egg size and food abundance in brook trout *Salelinus fontinalis*. *Evolution* **45**, 1162–1168. (doi:10.2307/2409723)

9. Kaplan RH. 1992 Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. *Ecology* **73**, 280–288. (doi:10.2307/1938739)

10. Plaistow SJ, Lapsley CT, Benton TG. 2006 Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. *Am. Nat.* **167**, 206–215. (doi:10.1086/499380)

11. Smith CC, Fretwell SD. 1974 Optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506. (doi:10.1086/282929)

12. Sinervo B. 1990 Experimental and comparative analyses of egg size in lizards: constraints on the adaptive evolution of maternal investment per offspring. In *The unity of evolutionary biology* (ed. EC Dudley), pp. 725–734. Portland, OR: Dioscordies Press.

13. Chambers RC, Leggett WC, Brown JA. 1989 Egg size, female effects, and the correlations between early life-history traits of capelin, *Mallotis villosus*: an appraisal at the individual level. *Fish. Bull.* **87**, 515–523.

14. McEdward LA, Coulter LK. 1987 Egg volume and energetic content are not correlated among sibling offspring of starfish: implications for life-history theory. *Evolution* **41**, 914–917. (doi:10.2307/2408900)

15. Aubret F. 2012 Body-size evolution on islands: are adult size variations in tiger snakes a nonadaptive consequence of selection on birth size? *Am. Nat.* **179**, 756–767. (doi:10.1086/665653)

16. Hart MW. 1995 What are the costs of small egg size for a marine invertebrate with feeding planktonic larvae. *Am. Nat.* **146**, 415–426. (doi:10.1086/285807)

17. Rivest BR. 1983 Development and the influence of nurse egg allotment on hatching size in *Searlesia*

dira (Reeve, 1846) (Prosobranchia, Buccinidae). *J. Exp. Mar. Biol. Ecol.* **69**, 217–241. (doi:10.1016/0022-0981(83)90071-0)

18. Reznick DN, Butler MJ, Rodd FH, Ross P. 1996 Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* **50**, 1651–1660. (doi:10.2307/2410901)

19. Roff DA. 1992 *The evolution of life histories: theory and analysis*. New York, NY: Chapman and Hall.

20. Litvak MK, Leggett WC. 1992 Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Mar. Ecol. Prog. Ser.* **81**, 13–24. (doi:10.3354/meps081013)

21. White CR, Kearney MR. 2014 Metabolic scaling in animals: methods, empirical results, and theoretical explanations. *Compr. Physiol.* **4**, 231–256. (doi:10.1002/cphy.c110049)

22. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789. (doi:10.1890/03-9000)

23. Glazier DS. 2005 Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. *Biol. Rev.* **80**, 611–662. (doi:10.1017/s1464793105006834)

24. Kooijman SALM. 2010 *Dynamic energy budget theory for metabolic organisation*. Cambridge, UK: Cambridge University Press.

25. Glazier DS. 2010 A unifying explanation for diverse metabolic scaling in animals and plants. *Biol. Rev.* **85**, 111–138. (doi:10.1111/j.1469-185X.2009.00095.x)

26. White CR, Kearney MR, Matthews PGD, Kooijman SALM, Marshall DJ. 2011 A manipulative test of

competing theories for metabolic scaling. *Am. Nat.* **178**, 746–754. (doi:10.1086/662666)

27. Svetlichny LS, Abolmasova G, Hubareva ES, Finenko GA, Bat L, Kideys AE. 2004 Respiration rates of *Beroe ovata* in the Black Sea. *Mar. Biol.* **145**, 585–593. (doi:10.1007/s00227-004-1336-4)

28. Post JR, Lee JA. 1996 Metabolic ontogeny of teleost fishes. *Can. J. Fish. Aquat. Sci.* **53**, 910–923. (doi:10.1139/cjfas-53-4-910)

29. Giguere LA, Cote B, Stpierre JF. 1988 Metabolic rates scale isometrically in larval fishes. *Mar. Ecol. Prog. Ser.* **50**, 13–19. (doi:10.3354/meps050013)

30. Moran AL, Allen JD. 2007 How does metabolic rate scale with egg size? An experimental test with sea urchin embryos. *Biol. Bull.* **212**, 143–150. (doi:10.2307/25066591)

31. Hoegh-Guldberg O, Manahan DT. 1995 Coulometric measurement of oxygen consumption during development of marine invertebrate embryos and larvae. *J. Exp. Biol.* **198**, 19–30.

32. Zeuthen E. 1953 Oxygen uptake as related to body size in organisms. *Q. Rev. Biol.* **28**, 1–12. (doi:10.1086/399308)

33. Riisgard HU. 1998 No foundation of a '3/4 power scaling law' for respiration in biology. *Ecol. Lett.* **1**, 71–73. (doi:10.1046/j.1461-0248.1998.00020.x)

34. Glazier DS. 2006 The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience* **56**, 325–332. (doi:10.1641/0006-3568(2006)56[325:TPLINU]2.0.CO;2)

35. Vogt JT, Appel AG. 1999 Standard metabolic rate of the fire ant, *Solenopsis invicta* Buren: effects of temperature, mass, and caste. *J. Insect Physiol.* **45**, 655–666. (doi:10.1016/s0022-1910(99)00036-0)

36. Rogowitz GL, Chappell MA. 2000 Energy metabolism of eucalyptus-boring beetles at rest and during locomotion: gender makes a difference. *J. Exp. Biol.* **203**, 1131–1139.

37. Schimpf NG, Matthews PGD, White CR. 2013 Discontinuous gas exchange exhibition is a heritable trait in speckled cockroaches *Nauphoeta cinerea*. *J. Evol. Biol.* **26**, 1588–1597. (doi:10.1111/jeb.12093)

38. Cheverud JM. 1982 Relationships among ontogenetic, static, and evolutionary allometry. *Am. J. Phys. Anthropol.* **59**, 139–149. (doi:10.1002/ajpa.1330590204)

39. Pelabon C, Bolstad GH, Egset CK, Cheverud JM, Pavlicev M, Rosenqvist G. 2013 On the relationship between ontogenetic and static allometry. *Am. Nat.* **181**, 195–212. (doi:10.1086/668820)

40. Kinoshita J, Hiromi J, Kadota S. 1997 Do respiratory metabolic rates of the scyphomedusa *Aurelia aurita* scale isometrically throughout ontogeny in a sexual generation? *Hydrobiologia* **347**, 51–55. (doi:10.1023/a:1002942806113)

41. Marshall DJ, Bolton TF, Keough MJ. 2003 Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. *Ecology* **84**, 3131–3137. (doi:10.1890/02-0311)

42. Marshall DJ, Monro K. 2013 Interspecific competition alters nonlinear selection on offspring size in the field. *Evolution* **67**, 328–337. (doi:10.1111/j.1558-5646.2012.01749.x)

43. Burgess SC, Marshall DJ. 2011 Field estimates of planktonic larval duration in a marine invertebrate. *Mar. Ecol. Prog. Ser.* **440**, 151–161. (doi:10.3354/meps09374)

44. Jaeckle WB, Manahan DT. 1989 Feeding by 'non-feeding' larva: uptake of dissolved amino-acids from seawater by lecithotrophic larvae of the gastropod *Haliotis rufescens*. *Mar. Biol.* **103**, 87–94. (doi:10.1007/bf00391067)

45. Wendt DE. 2000 Energetics of larval swimming and metamorphosis in four species of *Bugula* (Bryozoa). *Biol. Bull.* **198**, 346–356. (doi:10.2307/1542690)

46. Burgess SC, Bode M, Marshall DJ. 2013 Costs of dispersal alter optimal offspring size in patchy habitats: combining theory and data for a marine invertebrate. *Funct. Ecol.* **27**, 757–765. (doi:10.1111/1365-2435.12080)

47. Alton LA, White CR, Wilson RS, Franklin CE. 2012 The energetic cost of exposure to UV radiation for tadpoles is greater when they live with predators. *Funct. Ecol.* **26**, 94–103. (doi:10.1111/j.1365-2435.2011.01900.x)

48. Köster M, Krause C, Paffenhofer GA. 2008 Time-series measurements of oxygen consumption of copepod nauplii. *Mar. Ecol. Prog. Ser.* **353**, 157–164. (doi:10.3354/meps07185)

49. Cameron JN. 1986 The solubility of carbon dioxide as a function of temperature and salinity (Appendix table). In *Principles of physiological measurement* (ed. JN Cameron), pp. 254–259. London, UK: Academic Press.

50. Crisp DJ. 1971 Energy flow measurements. In *Methods for the study of marine benthos* (eds NA Holme, AD McIntyre), pp. 197–279. Oxford, UK: Blackwell Sci. Pub.

51. Heymsfield SB, Gallagher D, Kotler DP, Wang ZM, Allison DB, Heshka S. 2002 Body-size dependence of resting energy expenditure can be attributed to nonenergetic homogeneity of fat-free mass. *Am. J. Physiol. Endocrinol. Metab.* **282**, E132–E138.

52. Labocha MK, Sadowska ET, Baliga K, Semer AK, Koteja P. 2004 Individual variation and repeatability of basal metabolism in the bank vole, *Clethrionomys glareolus*. *Proc. R. Soc. Lond. B* **271**, 367–372. (doi:10.1098/rspb.2003.2612)

53. Damme K, Pirchner F, Willeke H, Eichinger H. 1987 Fasting metabolic rate in hens: 1. Effects of body weight, feather loss, and activity. *Poult. Sci.* **66**, 881–890. (doi:10.3382/ps.0660881)

54. Bushuev AV, Husby A, Sternberg H, Grinkov VG. 2012 Quantitative genetics of basal metabolic rate and body mass in free-living pied flycatchers. *J. Zool.* **288**, 245–251. (doi:10.1111/j.1469-7998.2012.00947.x)

55. Van Voorhies WA, Khazaeli AA, Curtsinger JW. 2004 Lack of correlation between body mass and metabolic rate in *Drosophila melanogaster*. *J. Insect Physiol.* **50**, 445–453. (doi:10.1016/j.jinsphys.2004.03.002)

56. Arnold PA, Johnson KN, White CR. 2013 Physiological and metabolic consequences of viral infection in *Drosophila melanogaster*. *J. Exp. Biol.* **216**, 3350–3357. (doi:10.1242/jeb.088138)

57. Greenlee KJ, Harrison JF. 2004 Development of respiratory function in the American locust *Schistocerca americana*. II. Within-instar effects. *J. Exp. Biol.* **207**, 509–517. (doi:10.1242/jeb.00766)

58. Snelling EP, Seymour RS, Matthews PGD, Runciman S, White CR. 2011 Scaling of resting and maximum hopping metabolic rate throughout the life cycle of the locust *Locusta migratoria*. *J. Exp. Biol.* **214**, 3218–3224. (doi:10.1242/jeb.058420)

59. Van Voorhies WA. 1996 Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution* **50**, 1259–1264. (doi:10.2307/2410666)

60. Niklas KJ, Hammond ST. 2014 Assessing scaling relationships: uses, abuses, and alternatives. *Int. J. Plant Sci.* **175**, 754–763. (doi:10.1086/677238)

61. Dyke GJ, Kaiser GW. 2010 Cracking a developmental constraint: egg size and bird evolution. *Rec. Aust. Mus.* **62**, 207–216. (doi:10.3853/j.0067-1975.62.2010.1547)

62. Clutton-Brock TH. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.

63. Marshall DJ, Keough MJ. 2008 The evolutionary ecology of offspring size in marine invertebrates. *Adv. Mar. Biol.* **53**, 1–60.

64. Strathmann RR. 1985 Feeding and non-feeding larval development and life history evolution in marine invertebrates. *Annu. Rev. Ecol. Syst.* **16**, 339–361. (doi:10.1146/annurev.es.16.110185.002011)