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RESEARCH ARTICLE

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Does the cost of development scale allometrically with offspring size?

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Abstract

1. Within many species, larger offspring have higher fitness. While the presence of an offspring size–fitness relationship is canonical in life-history theory, the mechanisms that determine why this relationship exists are unclear.
2. Linking metabolic theory to life-history theory could provide a general explanation for why larger offspring often perform better than smaller offspring. In many species, energy reserves at the completion of development drive differences in offspring fitness. Development is costly, so any factor that decreases energy expenditure during development should result in higher energy reserves and thus subsequently offspring fitness.
3. Metabolic theory predicts that larger offspring should have relatively lower metabolic rates and thus emerge with a higher level of energy reserves (assuming developmental times are constant). The increased efficiency of development in larger offspring may therefore be an underlying driver of the relationship between offspring size and offspring fitness, but this has not been tested within species.
4. To determine how the costs of development scale with offspring size, we measured energy expenditure throughout development in the model organism *Danio rerio* across a range of natural offspring sizes. We also measured how offspring size affects the length of the developmental period. We then examined how hatchling size and condition scale with offspring size.
5. We find that larger offspring have lower mass-specific metabolic rates during development, but develop at the same rate as smaller offspring. Larger offspring also hatch relatively heavier and in better condition than smaller offspring. That the relative costs of development decrease with offspring size may provide a widely applicable explanation for why larger offspring often perform better than smaller offspring.

KEYWORDS

allometry, development, embryo size, geometric biology, maternal effect

1 | INTRODUCTION

Offspring size is a fundamental, yet highly variable trait that reflects both a maternal and offspring phenotype (Bernardo, 1996). Offspring size (which we refer to as the per propagule structure and yolk provisioned by a mother) affects fitness—larger offspring generally have higher fitness than smaller conspecifics (Stearns, 1992). Increased maternal investment in each offspring can enhance their survival, reproductive output and growth, or may reduce their susceptibility to predation and starvation (Cipollini & Stiles, 1991; Hutchings, 1991; Janzen, Tucker, & Paukstis, 2000; Moran & Emlet, 2001; Uller & Olsson, 2010). The benefits of increased offspring size are pervasive in life-history theory; however, there are exceptions, and the size–fitness relationship is often context dependent (Mousseau & Fox, 1998; Reznick, Bryga, & Endler, 1990). Although an increase in offspring size often confers a fitness benefit for the offspring, mothers must trade-off per-offspring investment with fecundity (Lack, 1947; Smith & Fretwell, 1974). Thus, the strength and direction of the offspring size–fitness relationship, together with size-number trade-off should drive the evolution of offspring size. Although life-history theory has long considered offspring size–fitness relationships within a wide range of taxa, the proximate mechanisms driving this relationship remain less well explored.

Various approaches have been taken to explain why offspring size often affects fitness, but the effects of offspring size are idiosyncratic. Larger offspring can feed better, can pass through vulnerable life stages faster (or slower), and be more (or less) susceptible to predators (Fox & Mousseau, 1996; Kosman & Pernet, 2011; Marshall & Keough, 2008; Rivest, 1983). What is lacking is a general mechanistic explanation for why offspring size affects fitness at all. It is often implicit in life-history theory that larger offspring have more "energy" to dedicate to fitness-enhancing processes (Sinervo, 1990; Stearns, 1992; Wootton & Smith, 2014). That larger offspring have more energy is a reasonable and potentially general explanation, but this idea is incomplete because larger bodies are more costly to maintain. For larger offspring to have more energy to dedicate to fitness-enhancing processes, they need access to more energy reserves than smaller offspring, relative to their size (and therefore energy demands). Otherwise, any size-related increases in energy reserves will simply be offset by concomitant size-related increases in energy demands. Importantly, studies often find that the level of resources that an offspring has available once development is complete is a strong predictor of subsequent fitness. For example, experimental reductions of energy reserves at the end of development tend to reduce subsequent offspring fitness (Emlet & Hoegh-Guldberg, 1997; Marshall & Keough, 2006; Sinervo & McEdward, 1988), even when offspring size per se is held constant. Similarly, offspring with naturally higher energy reserves at the end of development tend to have greater fitness than offspring with lower energy reserves (Berkeley, Chapman, & Sogard, 2004). Thus, any factor that affects the level of energy reserves at the end of development is likely to affect subsequent offspring fitness.

Development is costly. If development becomes too costly during crucial developmental stages such as from the zygote to larvae, then this can lead to significant consequences for offspring survival or fitness in later life stages (Gagliano & McCormick, 2007; Goulden, Henry, & Berrigan, 1987). For species with complex life cycles that undergo complete reorganisation of tissue during development (e.g. fish, amphibians, insects and marine invertebrates), energy loss during development and metamorphosis accounts for *c.* 30%–60% of initial energy reserves (Merkey, Wong, Hoshizaki, & Gibbs, 2011; Seymour, Geiser, & Bradford, 1991; Wendt, 2000). Factors that exacerbate energy costs throughout this developmental period, such as extended larval periods or delayed metamorphosis, can be detrimental to survival and post-metamorphic fitness (Marshall, Pechenik, & Keough, 2003; Mitchell & Seymour, 2000). For species that do not undergo metamorphosis during development through embryogenesis to hatching (i.e. "direct" developers such as reptiles and birds), offspring can use around 25%–35% of their maternal derived energy reserves (Deeming & Birchard, 2007; Vleck & Hoyt, 1991). Although the use of endogenous energy reserves (such as the yolk) during development for non feeding direct developers have been widely measured, how these costs scale with offspring size throughout this critical period so far remains unresolved.

Applying metabolic scaling principles to offspring size may provide a general explanation for the offspring size–fitness relationship, when it is observed. Both within and among species, the scaling exponent relating mass to metabolic rate is typically <1 (Glazier, 2010). For species undergoing costly development, an allometric relationship between offspring mass and metabolic rate could provide a general explanation for the offspring size–fitness relationship, assuming that it outweighs any potential size-specific disadvantages (Pettersen, White, & Marshall, 2015). Because larger offspring are predicted to use relatively less energy per unit mass during development (assuming increases in offspring size do not extend the developmental period—an assumption that must be tested), larger offspring should reach the end of their developmental phase with a higher proportion of endogenous reserves. Importantly, this higher proportion of energy reserves may therefore allow larger offspring to perform better—they have relatively more energy available for fitness-enhancing functions. Indeed, a recent study in bryozoans showed that metamorphosis was less costly for larger offspring relative to smaller offspring (Pettersen et al., 2015). Similarly, Goulden et al. (1987) explored macroevolutionary patterns among species of daphniid Cladocera neonates, where developmental energy efficiency increased with offspring size throughout development—offspring hatching from larger eggs possessed more post-embryonic yolk than offspring from smaller eggs. They suggested that this may be because the rate of energy reserve loss scaled allometrically with body mass among species. Whether such benefits first proposed by Goulden et al. (1987) extend to the entire developmental period within species remains unclear.

If larger offspring use relatively less energy than smaller offspring throughout development, then we would predict that larger offspring hatch with a higher proportion of maternal energy investment remaining than smaller offspring. A corollary of this prediction would be that post-development mass scales hyperallometrically

with initial offspring size—that is, hatchlings from larger eggs should not only weigh more than hatchlings from smaller eggs, they should also lose *relatively* less mass. Hatchlings from larger eggs should also emerge in better condition because, relative to their size, they burn less resources throughout development than individuals hatched from smaller eggs. Here, using the model organism *Danio rerio*, we test first whether metabolic rate scales allometrically with offspring size (the per propagule combined structure and yolk provisioned by a mother) throughout development. Because some theory predicts that larger offspring should have longer developmental periods (Gillooly, Charnov, West, Savage, & Brown, 2002; but see Vance, 1973), thereby offsetting any metabolic efficiency of larger offspring, we also examined how offspring size affects the rate of development. We found strong evidence for allometric scaling of metabolism throughout development and no evidence for an effect of offspring size on the length of the development (see Section 3), so we then tested whether larger offspring hatch with a higher proportion of their initial mass and with relatively larger yolk reserves than smaller offspring. For larger offspring to be considered more energy "efficient," they should also reach the same developmental stage with a higher proportion of hatchling mass relative to energy expended; that is, the conversion of energy to tissue should scale hyperallometrically with offspring size. To determine if larger offspring are more efficient, we calculated the key ratio for estimating energy efficiency during development: the ratio of (1) the energy that is expended during development to (2) the amount of hatchling tissue created (energy use: hatchling size). This ratio should decrease with offspring size if hypoallometric scaling of metabolic rate is to adequately explain the offspring size–fitness relationship.

2 | MATERIALS AND METHODS

2.1 | Experimental overview, collection and measurement of embryo mass

To determine how the energy costs of development scale with offspring size, we: (1) measured developmental time from fertilisation until hatching; (2) measured rate of oxygen consumption ($\dot{V}O_2$, a proxy for metabolic rate) across three developmental stages; (3) estimated the relationship between offspring size and hatchling size; (4) estimated the relationship between offspring size and hatchling condition (hatchling yolk area relative to hatchling size) across a range of offspring sizes through development, and from this, (5) calculated energy efficiency with offspring size, that is, the scaling of offspring size with the ratio of total energy used to hatchling mass. As per Parichy, Elizondo, Mills, Gordon, and Engeszer (2009), we use the term "embryo" to include both the developing hatchling and the yolk that it uses through development. Furthermore, from a life-history perspective, total offspring size is the most relevant description of the total per offspring unit of investment by mothers.

Danio rerio (Hamilton 1822; henceforth *Danio*) is a tropical freshwater teleost used extensively as a model organism. *Danio* embryos undergo rapid development—the zygote consists largely of yolk that is absorbed throughout development and hatching until construction of feeding structures at *c.* 72 hr post-fertilisation, with the larva retaining some residual yolk (Jardine & Litvak, 2003). All experiments were conducted during November 2015–April 2016, using wild-type strains maintained under standard operating procedures approved by the Monash Animal Services Animal Ethics Committee. *Danio* are oviparous and reproduce by external fertilisation, spawning gametes in response to a combination of light, visual and olfactory cues (see Westerfield, 2000 for details). Hence, all embryo collections were carried out in the morning with eight 1 L tanks containing single male and female pairs separated by a plastic barrier to prepare individuals for gamete production. Once the barrier was removed, naturally released pheromones stimulated ovulation and oviposition in females and spawning by males (Vandenhurk & Lambert, 1983). The 1 L tanks contained slits in the base of the tank that separated adults from the embryos, and thereby prevented cannibalism by adults. Each experimental run ("Experiment") consisted of fertilised embryos from parental pairs ("Parent ID") collected on different days. Embryos from parent pairs with highest fertilisation success were collected within 1 hr of barrier removal, transferred onto a mesh strainer and washed to remove debris. Embryos were then transferred into a Petri dish and placed in an incubator at 28.5°C as per standard rearing techniques. After 4 hr, embryos were pipetted into individual plate wells with 1 ml filtered freshwater and photographed at the "sphere" stage (Olympus 1X73; ×40). Embryonic developmental stages were identified based on Kimmel, Ballard, Kimmel, Ullmann, and Schilling (1995) where the equatorial diameter during the period directly preceding the gastrula stage (the "sphere stage") has shown to provide a good indication of embryo size (Bownds, Wilson, & Marshall, 2010). All measurements of equatorial diameter were taken using Olympus cellSens Dimension software. Embryo area (μm^2) was calculated from embryo radius (μm) and embryo volume (μl) was calculated as $(\frac{4}{3} \cdot \pi \cdot \text{embryo radius} \cdot 10^{-3})$. In order to allow for direct comparison of our scaling relationships with other studies, we used embryo mass as our measure of offspring size. Importantly, because the relationship between volume and mass was best fit by a linear function, using either measure of offspring size gave equivalent the scaling relationships with metabolic rate (see Data S1 for details). Due to the destructive nature of embryo mass sampling, double sampling was required in order to obtain estimates for projected embryo mass (here on referred to as "embryo mass"). We therefore weighed a separate sample of "sphere" stage embryos and calculated the relationship between embryo volume and mass (see Data S1 for details).

2.1.1 | Scaling of developmental time and embryo mass

To determine whether embryo mass affects developmental time, 144 embryos were measured following the above methods and pipetted into a 24-well plate with 2 ml of pasteurised "egg water" (60 μg/ml stock salts in 1 L distilled water, as per Westerfield, 2000) and placed in a controlled temperature room at 28°C until hatching (where fertilisation until hatching was used to represent the "dependent phase").

Embryos were then photographed every 0.5 hr until hatching using time-lapse software (Olympus 1X73; ×10, Olympus cellSens Dimension software). We ran a GLM to test for an effect of embryo mass on developmental time (v3.2.5; R Development Core Team, 2016) and significance tested using maximum likelihood using the package lme4. We then ran a power analysis (G*Power 3.1.9.2) and calculated to a 95% confidence level what extent development time would need to scale with embryo mass in order to offset the efficiency of larger offspring through allometric scaling.

2.1.2 | Scaling of metabolic rate and embryo mass

We measured the rate of oxygen consumption ($\dot{V}O_2$) as a proxy for metabolic rate, across three developmental stages of *Danio* in November 2015–January 2016. $\dot{V}O_2$ was measured for 20 individuals of known size in individual vials simultaneously using a 24-channel PreSens sensor dish reader (Sensor Dish Reader SDR2, PreSens), with a 24-chamber glass microplate (vial volume: 750 µl) (Loligo Systems Aps, Tjele, Denmark) at 28°C ± 1°C as per standard techniques (Pettersen et al., 2015). Prior to the experimental runs, the non-consumptive O_2 sensor spots were calibrated using air-saturated (100% AS) egg water and egg water containing 2% sodium sulphite (0% AS). For each individual embryo within each experimental run, oxygen consumption was recorded at three stages over a 3-hr period to signify the beginning (gastrula stage), middle (prim-5 stage) and end (high-pec stage) of the dependent phase: 6, 24 and 44 hr post-fertilisation (Kimmel et al., 1995). At each development stage, the same 20 embryos were placed individually into glass vials containing pasteurised egg water while the remaining four vials were used as controls, containing only pasteurised egg water. Air saturation for each individual embryo was recorded every 2 min and $\dot{V}O_2$ was calculated from the rate of change of O_2 saturation (m_a; % per hr) as $\dot{V}O_2 = -1\ (m_a - m_b/100)\ V\beta O_2$ (as per White, Kearney, Matthews, Kooijman, & Marshall, 2011) where m_b is the rate of change of O_2 saturation for blank vials containing no embryos (% per hr), βO_2 is the oxygen capacitance of air-saturated egg water at 28°C (5.48 ppt; Cameron, 1986), and V is water volume in the vial (volume of individual embryos were subtracted from volume of 7.5×10^{-4} L chambers). To convert $\dot{V}O_2$ (µl/hr) to metabolic rate (mJ/hr), the calorific conversion factor of 20.08 J/ml O_2 was used (Crisp, 1971). This procedure consisting of three $\dot{V}O_2$ measures for 20 individuals was repeated five times so we accumulated measures for a total of 100 individuals across three developmental stages.

Embryo mass and metabolic rates were log-transformed and analysed in a linear framework in order to reduce increased variation with the mean and thereby satisfy the assumption of homoscedasticity (Niklas & Hammond, 2014). Repeated measures ANCOVA (using the package lme4) was used to test for significance of the random effects of parent pair ("Parent ID") nested within experimental run ("Experiment"), and its interactions with $\log_{10}$ mass ("$\log_{10}$ Embryo mass") across the repeated measure factor of time, i.e. developmental stage ("Stage"). While there was a significant effect of Parent (nested within Experiment) and Stage × Experiment on $\log_{10}$ Metabolic Rate, we found no support for fitting a random-slopes model (no significant Stage × $\log_{10}$ Embryo mass effect was found), therefore Parent within Experiment, Stage and $\log_{10}$ Embryo mass were retained in the final model. A formal test of Stage × $\log_{10}$ Embryo mass interaction provides an estimate of whether the scaling exponent differs significantly across stages—for *Danio* embryos this interaction was found to be non-significant, therefore a single scaling exponent was used for all three stages using aggregated data (Table 1).

TABLE 1 Repeated measures analysis for the longitudinal study between $\log_{10}$ Metabolic rate and $\log_{10}$ Embryo mass and scaling exponents and coefficients (±CI) for metabolic rate and mass across developmental stages of *Danio rerio* throughout the dependent phase until hatching using a log-log transformed linear relationship, where $\log_{10}$ Metabolic rate = $b \times \log_{10}$ Embryo mass + a

Parameter	*df*	*F*-ratio	*p*-Value	Developmental stage	Coefficient (*a*)	Scaling exponent (*b*)	*p*-Value *b* > 0	*p*-Value *b* < 1
Between subjects								
$\log_{10}$ Embryo mass	1,72	4.76	<.05	1	−0.52 (±0.30)	0.32 (±0.16)	<.05	<.001
Experiment	4,72	1.52	.21	2	−0.14 (±0.30)	0.32 (±0.16)	<.05	<.001
Parent ID (Experiment)	5,72	0.57	.73	3	−.05 (±0.27)	0.32 (±0.16)	<.05	<.001
$\log_{10}$ Embryo mass × Experiment	4,68	0.50	.73					
Within subjects								
Stage	2,144	3.37	<.05					
Stage × $\log_{10}$ Embryo mass	8,144	1.93	.15					
Stage × Experiment	8,144	5.25	<.01					
Stage × Parent ID (Experiment)	10,144	1.31	.23					
Stage × Experiment × $\log_{10}$ Embryo mass	8,136	0.09	1.00					

Developmental stage 1 = gastrula stage (6 hr p.f.), stage 2 = prim-5 stage (24 hr p.f.) and stage 3 = high-pec stage (44 hr p.f.) (*df* presented as num *df*, den *df*).

2.1.3 | Scaling of developmental time and hatchling mass with embryo mass

In order to determine how initial offspring size affected the amount of mass lost during development through to hatching, we weighed individuals of known initial embryo size (measured as per methods Section 2.1.1) upon hatching. Larvae were photographed at the long-pec stage within 1 hr of hatching, using methods described earlier for embryos, and transferred into pre-weighed tin foil cartridges in 100 μl of distilled water. Samples were dried at 60°C for 48 hr, and weighed with a microbalance (Mettler Toledo XP2U) to the nearest 0.1 μg as per Hachicho et al. (2015). As there was no effect of embryo size on developmental time (see Section 3), we sampled hatchlings for mass measurements over 48–60 hr post-fertilisation (any individuals that hatched after this time were excluded from the study). Hatchling masses increased over the experimental period, so Parent ID (timing of experimental run), was treated as a continuous factor. To test for an interaction between $\log_{10}$ Embryo mass and Parent ID on $\log_{10}$ Hatchling mass, a GLM was used, and significance tested using maximum likelihood. No interaction between $\log_{10}$ Hatchling mass × Parent ID was found (regardless of whether Parent ID was treated as a continuous or categorical variable), so it was excluded. Parent ID was retained in the model as a covariate. In order to fit untransformed data in a power function, we then used nonlinear multiple regression to directly estimate parameters of interest. Parameter estimates were tested as significantly different from 0 and 1 using Wald tests.

2.1.4 | Scaling of the ratio between hatchling yolk area and hatchling area with embryo area

To quantify the relative yolk consumption among embryos of different initial size throughout development, we measured the size of the yolk sac area retained at the end of the dependent phase (as per Jardine & Litvak, 2003). "Embryo area" (μm^2) and "Hatchling area" (μm^2) were estimated as above. Photographs from the same hatched individuals taken from a lateral view were used to measure "Yolk Area" in μm^2. We then ran a linear model to test how offspring size affected the ratio between hatchling yolk area and hatchling area. Due to a lack of overlap among parent pairs for embryo area, we could not include "Parent ID" in the models (Quinn & Keough, 2002). Furthermore, because we found that embryo metabolism scaled allometrically with size, we were interested in whether this was driven by larger embryos possessing relatively higher amounts metabolically inert yolk relative to smaller embryos. We therefore measured a subsample of embryos photographed at the sphere stage and measured and calculated the relationship between embryo yolk area and total embryo area (see Data S1 for details).

2.1.5 | Estimating efficiency

To determine whether the scaling of yolk sac area upon hatching was due to a more efficient conversion to tissue and not simply an artefact of larger offspring possessing larger yolk mass relative to embryo size, we calculated the size-dependent energy expenditure relative to the mass of new tissue synthesised throughout development (i.e. proportion of embryo mass converted to hatchling mass not including leftover yolk). Size-dependent total energy use was calculated from the scaling exponents and coefficients obtained above, multiplied by the average developmental time of 54 hr (since development time is unrelated to embryo mass, an average time was taken, see Section 3). To convert our measures of hatchling length to hatchling mass independent of remaining yolk, we compiled estimates for the within-species relationship between length and weight of larval fish using FishBase (www.fishbase.org). Within species, available data suggested that the length–weight relationship is higher for larval fish than for post-larval fish (Le Cren, 1951; Osse, 1990; Vilizzi, 1998). For the 12,139 length–weight relationships in FishBase, the scaling exponent (d, where weight is proportional to length^d) was never <1.5 and 95% of the scaling exponents were between 2.44 and 3.54 (range = 1.51–4.5, median = 3.01); however, in order to provide conservative estimates of energy efficiencies, we present both the minimum (1.5) and median (3) scaling exponents of hatchling mass to hatchling length.

3 | RESULTS

3.1 | Scaling of developmental time and embryo mass

We found no effect of embryo mass on developmental time in *D. rerio* reared under standard laboratory conditions ($F_{1,102} = 0.054$, $p > .05$; Figure S1). We calculated that for the advantages of allometric scaling with embryo mass to be offset, the slope of the relationship between developmental time and embryo mass would need to be 0.64 or greater (where developmental time = 0.64 × embryo mass + constant). Our power to detect such a relationship, were one to exist, exceeds 0.95, such that we can reasonably rule out the possibility that larger eggs take longer to develop and therefore can also rule out that the mass-specific metabolic benefits of increased offspring size are offset by a lengthened developmental period.

3.2 | Scaling of metabolic rate and embryo mass

The relationship between $\log_{10}$ Embryo mass and $\log_{10}$ Metabolic rate was found to be allometric throughout development (Figure 1), where the scaling exponent was found to be significantly different from both 0 and 1 (estimate ± CI: 0.32 ± 0.16, $p < .05$; Table 1) and significantly lower than common theoretical slopes of 0.66 ($p = .02$) and 0.75 (<.001). We found a strong developmental stage effect on energy use—metabolic rate was lowest early in development during the gastrula period and increased over the 3 days until hatching as larvae (Table 1).

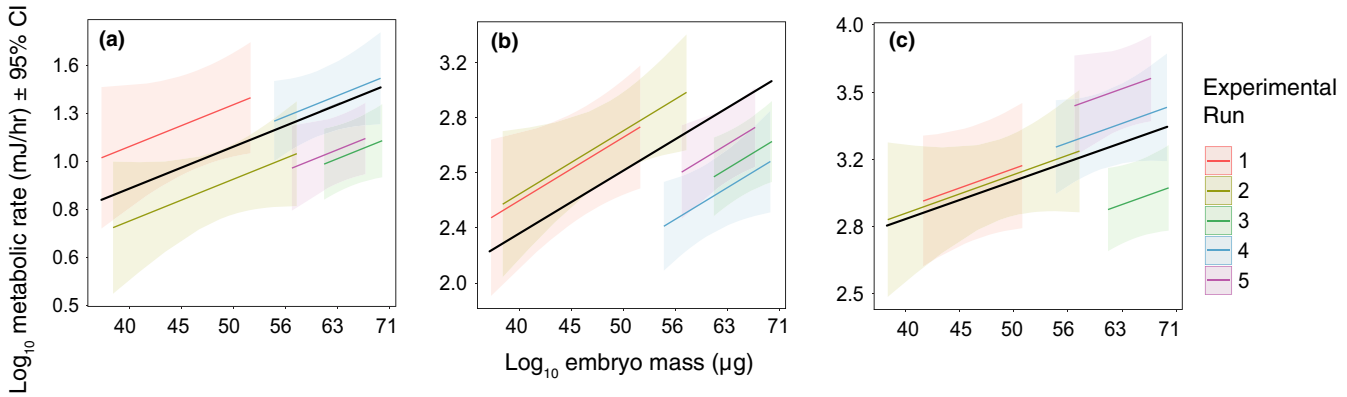

FIGURE 1 Mixed-effects model (±95% CI) for the relationship between $\log_{10}$ Metabolic rate (mJ/h) and projected embryo mass ($\log_{10}$ Embryo mass; µg) during *Danio rerio* developmental stages; (a) Stage 1; 6 hr p.f., (b) Stage 2; 24 hr p.f., (c) Stage 3; 44 hr p.f. Each coloured line represents an experimental run with a common slope and its own intercept per developmental stage. Bold line represents overall line of best fit. Shaded areas represent 95% CIs for each experimental run. All axes labels log-untransformed

3.3 | Scaling of developmental time and hatchling mass with embryo mass

Heavier embryos hatched as proportionally heavier larvae ($F_{1,200}$ = 273.54, p < .001; Figure 2). The scaling exponent for the relationship between Embryo mass and Hatchling mass was found to be significantly >1 (p < .05; Table 2). We found no significant interaction between Parent ID and $\log_{10}$ Embryo mass ($F_{1,199}$ = 2.02, p > .05); however, Parent ID showed a significant effect on $\log_{10}$ Hatchling mass ($F_{1,200}$ = 74.77, p < .001) and was therefore retained in the final model. Possible sources of variation among Parent ID may include temporal differences across experimental run, or genetic differences between parent pairs. The relationship between Hatchling mass and Embryo mass was described by the following nonlinear power function

$$\text{Hatchling mass} = 0.230 \times \text{Embryo mass}^{1.296} + 0.573$$

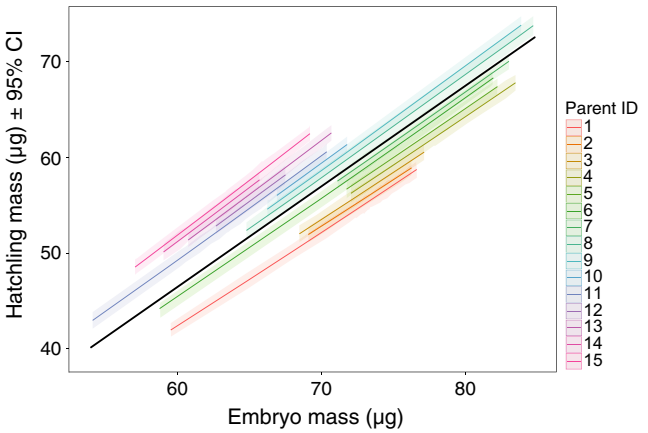

FIGURE 2 Multiple nonlinear regression (±95% CI) for the relationship between hatchling mass (µg) and projected embryo mass (embryo mass; µg) in *Danio rerio*. Each coloured line represents Parent ID with a common slope and its own intercept. Bold line represents overall line of best fit (slope estimate: 1.23 ± 0.10). Shaded areas represent 95% CIs for each parent ID. Note: original data analyses were performed on $\log_{10}$ transformed data for hatchling mass and embryo mass; however, to aid with interpretation, this relationship was plotted on arithmetic axes

3.4 | Scaling of the ratio between hatchling yolk area and hatchling area with embryo area

Hatchlings from larger eggs hatched as larvae with a relatively larger yolk area for their size (Figure 3). Embryo area had a significant effect on yolk area relative to Hatchling Area ($F_{1,59}$ = 25.89, p < .001) where the slope of the linear relationship was found to be significantly >0 (p < .05; Table 3). We found an isometric relationship between initial embryo area and yolk area (Data S1); hence our finding that larger embryos hatch with relatively higher amounts of residual yolk are likely to be due to our findings of allometric scaling, rather than due to larger embryos possessing a higher proportion of initial yolk relative to smaller embryos.

3.5 | Estimating efficiency

By combining our estimates of energy use and hatchling length with embryo mass, we calculated that the ratio of energy expenditure relative to hatchling mass (independent of residual yolk mass) decreases with embryo mass (Figure 4). The direction of this relationship holds regardless of whether hatchling mass scales as a cubic function of hatchling length or even a more conservative estimate of mass α hatchling length$^{1.5}$. Total energy used throughout development was measured as the rate of energy use (mJ/hr) multiplied by developmental time (h).

4 | DISCUSSION

We found an allometric relationship between metabolic rate during development and offspring size in *Danio*, a relationship that is likely to be widespread in other taxa. We found strong evidence larger

TABLE 2 General linear model for hatchling mass in relation to embryo mass and scaling exponents and coefficients (±CI) for the nonlinear relationship, where hatchling mass = a × embryo mass^b + c × Parent ID (*df* presented as num *df*, den *df*)

Parameter	*df*	*F*-ratio	*p*-Value	Parameter	Estimate	*p*-Value $b > 1$
$\log_{10}$ Embryo mass	1,200	273.54	<.001	*a*	0.23 (±0.10)	
Parent ID	1,200	74.77	<.001	*b*	1.30 (±0.10)	<.001
Parent ID × $\log_{10}$ Embryo mass	1,199	2.02	.16	*c*	0.76 (±0.10)	

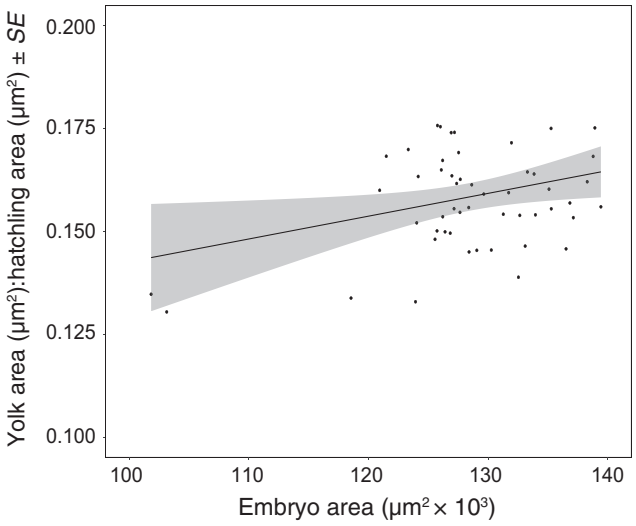

FIGURE 3 General linear model (±*SE*) for the relationship between yolk area (µm^2):hatchling area (µm^2) relative to embryo area (µm^2) in *Danio rerio* (slope estimate: 0.73 ± 0.21, R^2 adj. = .29). Dots represent raw data points. Shaded area represents *SE*

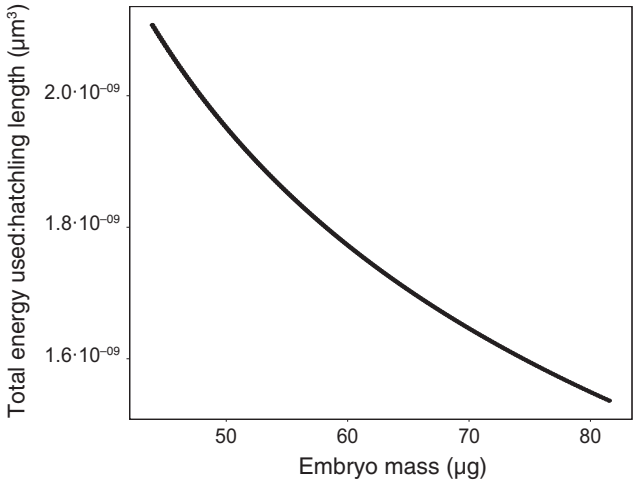

FIGURE 4 Predicted relationship between projected embryo mass (embryo mass; µg) and energy efficiency, calculated as the ratio of total energy used relative to hatchling mass (calculated as hatchling length; µm^3) in *Danio rerio*

TABLE 3 General linear model for hatchling yolk area:hatchling area in relation to total embryo area and estimate of the slope (b) where embryo area = b × hatchling yolk area:hatchling area + c

Parameter	*df*	*F*-ratio	*p*-Value	Estimate	*p*-Value $b > 0$
Embryo area	1,59	12.31	<.005	0.73 (±0.21)	<.005

Wald tests were used to determine whether slopes were significantly different from both 0 and 1 (*df* presented as num *df*, den *df*).

offspring use their endogenous reserves more efficiently, and hatch with a higher proportion of their initial energy reserves than smaller offspring. Allometric scaling between metabolic rate and mass is one of the most fundamental relationships studied in metabolic theory—static allometric scaling (within developmental stages) has been well documented in adults across a range of taxa (Damme, Pirchner, Willeke, & Eichinger, 1987; Greenlee & Harrison, 2004; Labocha, Sadowska, Baliga, Semer, & Koteja, 2004). We now show that the same scaling relationship occurs across a range of offspring sizes for *Danio*. The presence of allometric scaling during development implies that larger offspring should hatch with proportionally more energy than smaller offspring upon reaching the independent phase. We now find support for this prediction—relative to their size, larger embryos retained a higher proportion of their initial yolk reserves than smaller embryos, and hatched relatively heavier than their smaller conspecifics. Our findings show that the relative costs of development decrease with offspring size and that larger offspring end their developmental phase with a higher proportion of energy reserves—this greater proportion of energy reserves may provide a general explanation for why larger offspring perform often better than smaller offspring.

Across a range of taxa, condition at the end of development is a good predictor of subsequent survival and growth (e.g. Baker & Fowler, 1992; Janzen, 1993; Jarrett & Pechenik, 1997; Naef-Daenzer, Widmer, & Nuber, 2001). In fish, various proxies of hatchling condition (including yolk area, and oil globule size and hatchling size), correlate with key fitness traits such as survival, starvation resistance and dispersal potential (Busch, 1996; Probst, Kraus, Rideout, & Trippel, 2006; Semmens & Swearer, 2011). The emergence of hatchlings with relatively more mass and larger yolk reserves will influence subsequent survival and fitness throughout the life history (Houde, 2002). For species that undergo organogenesis (i.e. animals), the transition from embryo to actively feeding larvae is regarded as the most critical event during early life (Hjort, 1914). For early life stage development in *Danio*, we calculated that for a standard 54-hr developmental period at 28°C, the largest embryos size (73.5 µg) would use 18.7% of total reserves, while the smallest embryo (37.4 µg) would use 29.7% of its total energy reserves. The costs of development are not equivalent

to embryo size—despite a twofold decrease in size, the smallest measured embryo uses *c.* 1.6 times its energy reserves relative to that of the largest measured embryo. These estimates are similar to those showing that the costs of metamorphosis in bryozoans decrease relative to offspring size (Pettersen et al., 2015). Our expectation is that allometric scaling renders the development of larger offspring more efficient within a range of taxa but this requires further testing.

In addition to our discovery of allometric scaling with offspring size in *Danio*, we found that larger embryos also hatch relatively heavier and in better condition than offspring hatched from smaller embryos. That larger offspring use relatively less energy throughout development and hatch with a higher proportion of their initial energy provides further evidence to support allometric scaling as a potentially universal mechanism for the offspring size–fitness relationship. Our findings reflect broader interspecific patterns of hatchling quality with offspring size. Among daphniid Cladocera, neonates of larger species metabolise proportionally less post-embryonic yolk, and are born with a larger relative amount of yolk than species with smaller neonates (Goulden et al., 1987). In a review of endogenous feeding in fish, Kamler (2008) showed that yolk absorption was related to egg size, but the rate of yolk absorption relative to total endogenous energy reserves was considerably lower in species with the largest eggs (chum salmon; 1.4% per day) and highest in that with the smallest eggs (bluegill sunfish; 50.2% per day). Through direct measurement of the condition of hatchlings across a range of embryo sizes, our study also confirms predictions made in Pettersen et al. (2015) that larger offspring should hatch with a higher proportion of their initial maternal provisioning. Importantly, our findings may explain a long-standing puzzle in bird life histories. Williams (1994) found that in a range of species, "… chicks from larger eggs are heavier at hatching rather than structurally larger, i.e. that they hatch with more nutrient (yolk) reserves." These are exactly the effects we would expect if development is more metabolically efficient for larger eggs. Given that metabolic rate also scales allometrically with mass in some birds, our explanation for why egg size affects hatching mass and reserves is likely to apply (Williams & Ricklefs, 1984).

Our data do not provide a mechanistic explanation for the low (b = 0.32) scaling exponent for the relationship between metabolic rate and total embryo mass. While scaling exponents between metabolic rate and adult body mass often fall between 0.66 and 0.75, values more extreme than this are not uncommon, and b can deviate as a result of metabolic characteristics associated with particular life-history stages (as discussed in Glazier, 2014). A number of previous studies have also identified shallow scaling exponents between metabolic rate and offspring size (<0.5; Bishop & Torres, 1999; Pettersen et al., 2015; Wieser & Oberhauser, 1984). This shallow scaling may arise for a multitude of reasons, including a relative lack of resource transport networks in developing embryos, differential allocation of energy to biological functions, or shifts in rates of cell proliferation and expansion, compared with adults (Gaitan-Espitia, Bruning, Mondaca, & Nespolo, 2013; Glazier, 2005; Kozlowski, Konarzewski, & Gawelczyk, 2003). Another possible mechanism for our observation is that mothers provision larger offspring with a higher proportion of yolk relative to total offspring (embryo and yolk) size. If we assume that embryo tissue is more metabolically active than yolk (which seems reasonable Kooijman, 2009), and if larger eggs have a greater proportion of yolk relative to embryo size, then offspring from larger eggs should have lower metabolic rates during development. That the relative amount of yolk increases with egg size seems likely based on the geometry of the developing egg (the embryo grows essentially as a two-dimensional sheet on the top portion of the egg so embryo size will scale with egg size at a lower power than yolk). Alternatively, if initial embryo size is directly proportional to total offspring size, then metabolic rate should be isometric with offspring size and this mechanism therefore does not hold. Testing whether a hyperallometric relationship between yolk and egg size exists is beyond the scope of this study; however, we advocate this as an important next step in identifying the underlying mechanism driving the allometric scaling of metabolic rate with offspring size.

Relative to smaller embryos, we found larger embryos use energy at a lower rate and hatch with a higher mass and in better condition; hence, we expect the consequences of allometric scaling to alter the size-number trade-off. Despite this intuition, mothers often produce small to intermediate offspring sizes, and the most energy efficient, largest possible offspring sizes are rarely observed (Bernardo, 1996). What then, are the benefits of producing smaller offspring and why do we continue to observe small offspring size? The benefits of increased fecundity may outweigh the costs of producing smaller, less fit, and less efficient offspring; if so theory predicts that mothers should produce many, small offspring. Producing smaller, more numerous offspring might be particularly advantageous when resources are abundant, such that larger offspring have little fitness advantage over smaller offspring and relative efficiencies of development are less important (Goulden et al., 1987; Monro, Sinclair-Taylor, & Marshall, 2010). Likewise, in extremely stressful environments, or when resources are patchy, and the offspring size–fitness relationship is absent, life-history theory predicts that there is no benefit to producing larger offspring at the expense of fecundity (Allen, Buckley, & Marshall, 2008; Einum & Fleming, 2000; Venable & Brown, 1988). Rather, increased fecundity which in turn enhances the opportunity for dispersal of offspring away from the stressful maternal environment is likely to be selected upon (Winemiller & Rose, 1993).

The offspring size–fitness relationship is often context dependent. The relative benefits of increased offspring size, such as enhanced metabolic efficiency may be widespread; however, if other factors reduce or even override the benefits of allometric scaling for larger offspring, then these effects may be masked. For example, in low oxygen conditions, larger offspring may be less able to acquire oxygen via diffusion, leading to a constraint on offspring size (Einum, Hendry, & Fleming, 2002). Similarly, larger offspring may be exposed to higher size-selective predation, or experience increased mortality when settlement is delayed, relative to smaller offspring (Reznick et al., 1990; Svanfeldt, Monro, & Marshall, 2016). The metabolic theory of ecology predicts that developmental time should scale to one-quarter power of mass (Gillooly et al., 2002), and this is supported by some interspecific comparisons (Clarke, 2006; Pauly & Pullin, 1988). If this is the case, then the benefits of allometric scaling for larger

offspring may be offset by extended developmental time, such that the costs of development become independent, or increase with offspring size. Within species, this trend is less well resolved with studies indicating positive (Marshall & Bolton, 2007), negative (Hinegardner, 1975; Sinervo & McEdward, 1988); and absent (Hoegh-Guldberg & Pearse, 1995) relationships between offspring size and development rate. While we did not detect any effect of embryo size on developmental time, further tests are needed to elucidate whether interspecific patterns are reflected on a microevolutionary scale, and how these patterns may change across the life history. If the benefits of allometric scaling can overcome the disadvantages of offspring size-dependent factors, such as extended developmental time, then the costs of development should decrease with offspring size.

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AUTHORS' CONTRIBUTIONS

A.K.P., D.J.M. and R.J.R.B. conceived the ideas and designed methodology; A.K.P. collected the data; A.K.P., D.J.M. and C.R.W. analysed the data; A.K.P. led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.p570g (Pettersen, White, Bryson-Richardson, & Marshall, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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