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Metabolic rate covaries with fitness and the pace of the life history in the field

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Metabolic rate reflects the 'pace of life' in every organism. Metabolic rate is related to an organism's capacity for essential maintenance, growth and reproduction—all of which interact to affect fitness. Although thousands of measurements of metabolic rate have been made, the microevolutionary forces that shape metabolic rate remain poorly resolved. The relationship between metabolic rate and components of fitness are often inconsistent, possibly because these fitness components incompletely map to actual fitness and often negatively covary with each other. Here we measure metabolic rate across ontogeny and monitor its effects on actual fitness (lifetime reproductive output) for a marine bryozoan in the field. We also measure key components of fitness throughout the entire life history including growth rate, longevity and age at the onset of reproduction. We found that correlational selection favours individuals with higher metabolic rates in one stage and lower metabolic rates in the other—individuals with similar metabolic rates in each developmental stage displayed the lowest fitness. Furthermore, individuals with the lowest metabolic rates lived for longer and reproduced more, but they also grew more slowly and took longer to reproduce initially. That metabolic rate is related to the pace of the life history in nature has long been suggested by macroevolutionary patterns but this study reveals the microevolutionary processes that probably generated these patterns.

1. Introduction

Metabolic rate is associated with the 'pace of life' and is a fundamental trait relevant to all organisms. The rate at which organisms use, transform and expend energy essential for all biological functioning varies both among and within species [1,2]. Intuitively, one expects there to be an association between this key trait and fitness—the rate at which individuals use and process energy should inevitably have consequences for function and performance. Early work examining the consequences of variation in metabolic rate for organismal performance focused on the 'rate-of-living' hypothesis, which proposes that an animal's pace of life (its metabolic rate) is inversely related to its lifespan [3]. The rate-of-living hypothesis remains controversial [4,5] and recent studies have expanded the search for the performance consequences of variation in metabolic rate to a wider range of fitness proxies and components.

The strength and direction of selection on metabolic rate is predicted to vary among fitness proxies or components. Lower resting, routine or maximal metabolic rates may allow for the reallocation of energy towards growth, reproduction and increased immune function, in what is known as the 'compensation hypothesis' (e.g. [6–8]). Alternatively, low metabolic rates may be unable to service essential physiological processes, and high metabolic rates may provide an increased capacity for functions that enhance fitness (the 'increased-intake' hypothesis; [9]). For the increased-intake hypothesis, high maximal metabolic rates might improve aerobic performance, the ability for thermogenesis, and enable faster energy consumption and mobility (e.g. [8,10,11]). Still other studies find no relationship between basal metabolic rate and rates of important physiological processes (e.g. [12,13]). One potential reason for the absence of any clear pattern of association between metabolic rate and fitness proxies is that attempts at estimating selection on metabolic rate have often relied on fitness components that are likely to show complex and idiosyncratic relationships with each other,

and more importantly, with actual fitness. An essential next step, therefore, is to estimate the relationship between metabolic rate and fitness using the appropriate evolutionary currency for actual fitness: lifetime reproductive output [14,15].

Estimating lifetime reproductive output in field populations of animals remains challenging and is often restricted to very large species that are easily tracked and where reproduction can be measured (e.g. [16]). Despite these challenges, field studies are likely to provide essential insights into selection on metabolic rate because selection is highly context-dependent: the strength and even direction of selection can change when comparing across laboratory and field populations. Recent studies have overcome these formidable challenges by measuring selection on fitness components under realistic field conditions [17,18]. Importantly, these studies have used the Lande & Arnold [19] approach to formally estimate selection on metabolic rate so that comparisons can be made across studies. Here, we extend these studies by applying this classic multiple regression framework to estimate selection on metabolic rate at two life stages, where we use lifetime reproductive output as our measure of fitness in the field. We take advantage of the sessile nature of the adult stage of the marine bryozoan *Bugula neritina* to measure lifetime reproductive output. We also measured additional fitness components (early-life-stage survival, growth, phenology and longevity) so as to understand the various correlations between metabolic rate and life-history traits that will ultimately affect fitness.

2. Material and methods

(a) Study species, site and larval mass measurements

Adult colonies of the aborescent bryozoan, *B. neritina* grow via asexual budding, by producing new pairs of zooids (individual subunits) at distal ends combined with regular bifurcations after approximately every four pairs of zooids to produce symmetrical branching [20,21]. Once sexually mature, *B. neritina* zooids brood single embryos in clearly visible, calcified structures called ovicells which act as a placenta-like system and supply the offspring with maternally derived nutrients [22]. Once embryogenesis is complete, the developed non-feeding larvae are released into the plankton where they are competent to settle almost immediately, yet remain dependent on maternally derived energy reserves from release as larvae through post-settlement until the end of metamorphosis. This 'dependent phase' (*sensu* [23]) lasts approximately 2 days before the development of the first zooid with feeding structure (lophophore) is complete, and offspring feed for themselves.

All *B. neritina* colony collections and outplanting were conducted at Royal Brighton Yacht Club in Port Phillip Bay, Victoria, Australia (−37.909, 144.986), from March to November 2014. Sexually mature colonies were transported to the laboratory and maintained in darkened, aerated tanks at 17.5°C—a similar temperature to that of the bay at the time of the study. After 2 days, approximately 10 colonies per experimental run were induced to spawn according to standard light-shock procedures: colonies were placed in beakers of filtered seawater and exposed to bright light [24]. The released larvae were then immediately photographed on a glass slide using a Moticam 5 digital camera (Motic, Hong Kong, China) mounted on a dissecting microscope as per standard techniques developed previously [24]. Measurements of larval body area and length of the ciliated groove were estimated to the nearest micrometres using ImageJ software (v. 1.47) and larvae mass estimates based on calculations obtained in a previous study [23]. Once photographed, larvae were then pipetted in a drop of seawater directly onto roughened acetate sheets to induce settlement. The range of larval mass measured in this study reflected the natural variation observed in larval size by this species [24].

(b) Metabolic rate measurements

Oxygen consumption rate ($\dot{V}O_2$; a commonly used proxy for metabolic rate) was measured for individual settlers of *B. neritina* at two developmental stages: 0 h and 24 h post-settlement (from here-on designated metabolic rate early (MR_E) and metabolic rate late (MR_L), respectively). Individual settlers were cut out on small sheets of acetate and placed into glass vials containing pasteurized, 0.2 µm filtered seawater and a non-consumptive O_2 sensor spot. For each experimental run, $\dot{V}O_2$ was measured for 36 individuals at the same time along with 12 controls (blank vials containing only seawater and acetate) using 24-channel PreSens sensor dish readers (Sensor Dish Reader SDR2, PreSens), with 24-chamber 200 µl glass micro plates (Loligo Systems Aps, Tjele, Denmark). $\dot{V}O_2$ was calculated from the rate of change of O_2 saturation over time (m_a; $\%h^{-1}$) as per White *et al.* [25]:

$$\dot{V}O_2 = -1\left(\frac{m_a - m_b}{100}\right) V \beta O_2,$$

where m_b is the rate of change of O_2 saturation for control vials (% per hour), βO_2 is the oxygen capacitance of air-saturated seawater at 17.5°C (5.8 ml l^{-1}; [26]) and V is water volume (the volume of acetate and the animals was subtracted from the total chamber volume of 2.0×10^{-4} l). Prior to $\dot{V}O_2$ measurements sensor spots were calibrated with air-saturated (AS) seawater (100% AS) and water containing 2% sodium sulfite (0% AS). In order to obtain proxies for standard metabolic rate, all $\dot{V}O_2$ measurements were recorded in a darkened, constant-temperature room at 17.5°C over 3 h, such that temperature in the vials became stable and individual settlers were not negatively affected by the procedure (i.e. all measurements were undertaken at O_2 saturation levels greater than the critical partial pressure of O_2 for aerobic metabolism, below which $\dot{V}O_2$ declines). Each set of two $\dot{V}O_2$ measurements on 36 individuals represented a single 'experimental run', which was repeated six times. To convert oxygen consumption, $\dot{V}O_2$ (microlitres per hour) to metabolic rate (milliJoules per hour) the calorific conversion factor of 20.08 J ml^{-1} O_2 was used [27]. Ideally, in addition to measuring $\dot{V}O_2$ during two early-life stages, we would also measure $\dot{V}O_2$ later in ontogeny. However, measuring metabolic rates of large numbers of larger individuals would have required the return of individuals to the laboratory for several days and our primary goal was to gain as realistic measures of fitness as possible by leaving individuals in the field throughout their post-metamorphic lives.

(c) Field deployment and measures of fitness traits

Following the final $\dot{V}O_2$ measurement, each piece of acetate containing a single settler was glued onto labelled PVC plates (55 × 55 × 3 mm) and maintained in tanks overnight with unfiltered seawater at 17.5°C before being outplanted into the field the following morning. For each experimental run ($n = 6$), 36 plates were randomly assigned onto a single PVC backing panel (570 × 570 × 6 mm) such that a total of 216 settlers were deployed into the field. The backing panels were then suspended 1.5 m below the water surface with the settlement plates face down (for a detailed description of the field deployment, see Marshall & Keough [28]). Several trait measurements were recorded for every individual over the entire life history, until all individuals had died (March–November 2014) to provide various components of fitness [29]. Measures of early-stage survival (at eight weeks post outplant) and growth (number of bifurcations as an indication of colony size, see Keough & Chernoff [20] for details) were recorded

Table 1. Selection coefficients (±s.e.m.) for larval mass (micrograms), metabolic rate early (MR_E; milliJoules per hour), metabolic rate late (MR_L; milliJoules per hour) with total lifetime reproductive output (cumulative number of offspring produced) for *B. neritina* colonies. (β and γ represent linear and nonlinear selection gradients, respectively. *$p < 0.05$.)

		γ		
	β	mass	MR_E	MR_L
larval mass	−0.094 (0.070)	−0.067 (0.054)	−0.022 (0.064)	−0.092 (0.085)
MR_E	0.070 (0.070)		−0.037 (0.040)	*−0.194** (0.083)
MR_L	−0.040 (0.072)			0.046 (0.060)

weekly. Mortality was noted for individual colonies when the individual was either absent from the plate or less than 10% of feeding zooids remained. Colonies were regularly checked for development of ovicells which were visible under a field microscope (×10). Age (number of days) at onset of reproduction was noted and occurred approximately six weeks post-settlement. Reproductive output was measured as a count of the number of ovicells from thereon every two weeks to provide a total cumulative value for lifetime reproductive output. Longevity was recorded as the number of days from outplant of individuals up until mortality.

(d) Statistical analyses

We used two statistical approaches to analyse the data. First, we used a classic multiple regression approach to formally estimate the direction and strength of selection on our three traits of interest (larval mass, and the metabolic rate of two post-settlement stages) for the fitness measure of lifetime reproductive output [19]. Second, we modelled the remaining life-history traits of early-stage survival, growth and at onset of reproduction as a function of larval mass and metabolic rate. Data were analysed using multivariate linear mixed models, fitted with maximum likelihood for longevity, logistic regression for age at onset of reproduction and for size over time (growth), repeated measures within a general linear model framework. This approach allowed us to determine the relationship between metabolic rate and key life-history traits, and to determine whether trade-offs among fitness components may help to explain why we see mixed results in the literature. Metabolic rates at each stage were found to be significantly correlated (where mass was included as a covariate; $\chi^2_1 = 22.434$, $p < 0.001$). However, this relationship was relatively weak ($r^2 = 0.19$)—all variance inflation factors were less than 5, and no evidence for multicollinearity was found. Larval mass, MR_E and MR_L were, therefore, treated as independent variables (see the electronic supplementary material, figure S1).

(e) Estimating selection gradients

Standardized estimates of linear (β) and nonlinear (γ) gradients of selection for total reproductive output were generated using a multiple regression approach [19,30]. The form of selection was tested with likelihood ratio tests and the strength of selection gradients for total reproductive output (coefficient estimates) were calculated using linear regression.

(f) Covariance between larval mass, metabolic rate and life-history traits

The relationship between continuous predictor variables of larval mass, MR_E and MR_L with key life-history response variables of growth, longevity and age at onset of reproduction were analysed separately. Biplots were produced to check for autocorrelation among response variables and to ensure variation in one response variable was not explained by another measured response variable. Longevity and growth over 20 weeks were found to be significantly positively correlated ($\chi^2_1 = 26.794$, $p \leq 0.001$). However, as the relationship between longevity and growth was not strong ($r^2 = 0.48$), the variables were analysed separately. No significant relationships between age at onset of reproduction and longevity ($\chi^2_1 = 1.452$, $p = 0.228$) or growth ($\chi^2_1 = 0.242$, $p = 0.623$) were found (see the electronic supplementary material, figure S2). For each model, experimental run was included as a random categorical factor—where run or its interactions were found to be non-significant, they were first removed from the model. Longevity was tested using a linear mixed model (maximum likelihood), using stepwise removal of non-significant terms. Age at onset of reproduction was treated as a binary response variable and tested with logistic regression. As development of ovicells on individual colonies occurred either much earlier or much later than 60 days post outplant, individuals that reproduced earlier than 60 days were assigned a value of 1 and individuals with late onset of reproduction (greater than or equal to 60 days) with a value of 0. The relationship between larval mass, metabolic rates and growth over the first 20 weeks of development (number of bifurcations over time) was tested using repeated measures analysis.

3. Results

(a) Selection gradients

No significant linear selection on larval mass or metabolic rate was detected ($\chi^2_3 = 2.35$, $p = 0.50$). We found significant nonlinear selection on metabolic rate ($\chi^2_6 = 12.67$, $p = 0.04$). When we explored the two forms of nonlinear selection, we found no support for significant quadratic selection but we did find support for significant correlational selection (table 1). Significant negative correlational selection showed that individuals which had higher metabolic rates in both stages or lower metabolic rates in both stages had the lowest fitness, whereas individuals that had higher metabolic rates in one stage but lower metabolic in the other stage had the highest fitness (figure 1). The relatively strong correlational selection gradient of −0.194 indicated that correlational selection is acting to decrease the positive covariance between MR_E and MR_L [31].

(b) Covariance among traits

(i) Growth

Over the first 20 weeks post-settlement, individuals that developed from settlers with higher MR_E and lower MR_L grew larger

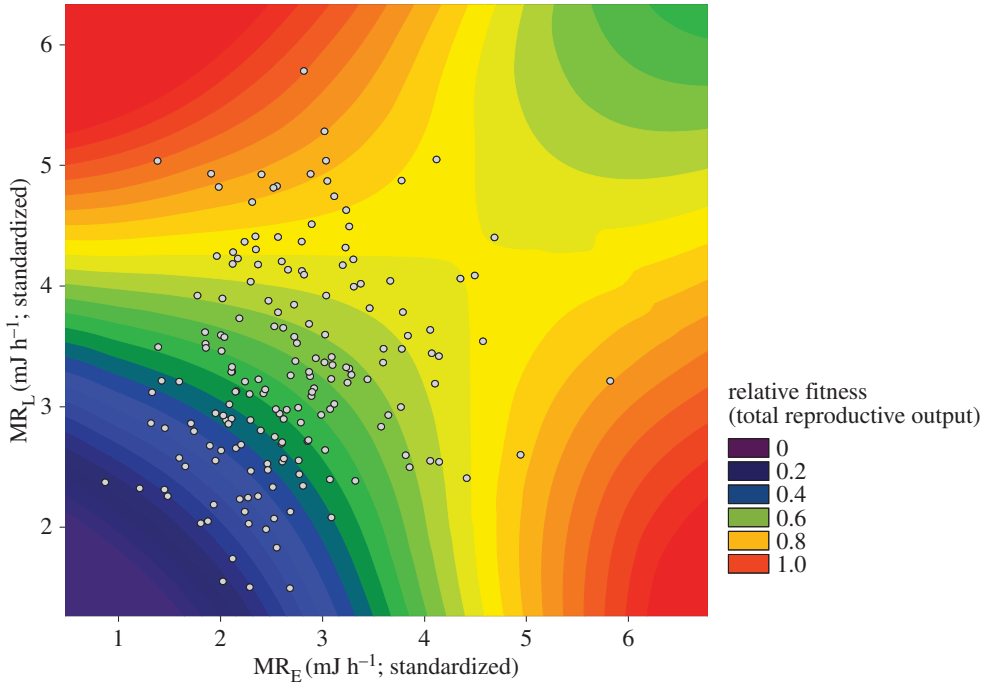

Figure 1. Predicted relative fitness (total reproductive output) plotted against metabolic rate early (MR_E; milliJoules per hour) and metabolic rate late (MR_L; milliJoules per hour) for *B. neritina* settlers. White dots represent raw data points between MR_E and MR_L ($n = 179$). Relative fitness of individuals is highest (red area) with either lower values of MR_E and higher values of MR_L, or higher values of MR_E and lower values of MR_L.

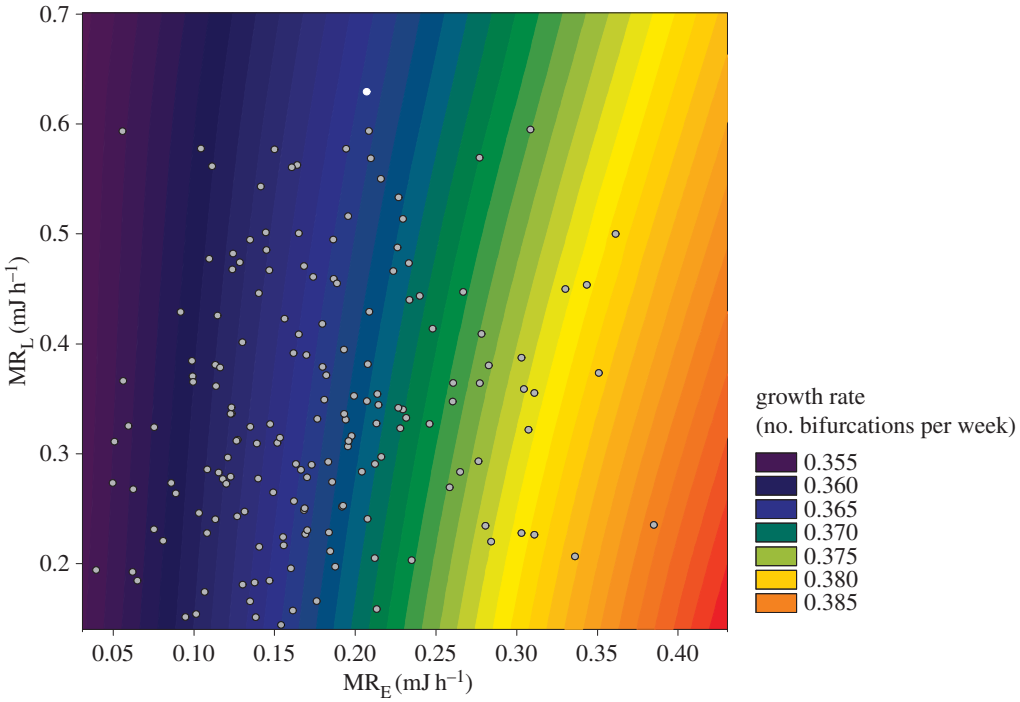

Figure 2. Predicted growth rate (number bifurcations per week for first 20 weeks of development) plotted against metabolic rate early (MR_E; milliJoules per hour) and metabolic rate late (MR_L; milliJoules per hour) for *B. neritina* settlers. Data points show raw data for measures of MR_E and MR_L ($n = 179$). Growth rate is highest for values of higher MR_E and lower MR_L.)

than individuals from settlers with lower MR_E and higher MR_L (figure 2). While MR_E was positively correlated with individual colony size (coefficient = 1.97, $F_{1,111} = 6.283$, $p = 0.014$), MR_L showed a negative relationship with individual colony size over the first 20 weeks of development (coefficient = −0.9, $F_{1,111} = 4.415$, $p = 0.038$). Repeated measures analysis showed that the effects of larval mass, MR_E and MR_L did not change over time (no significant time × larval mass × MR_E × MR_L interaction was detected; $F_{6,648} = 0.252$, $p = 0.227$).

(ii) Longevity

Individuals originating from smaller larvae and with lower MR_L lived for longer than individuals that had originated as

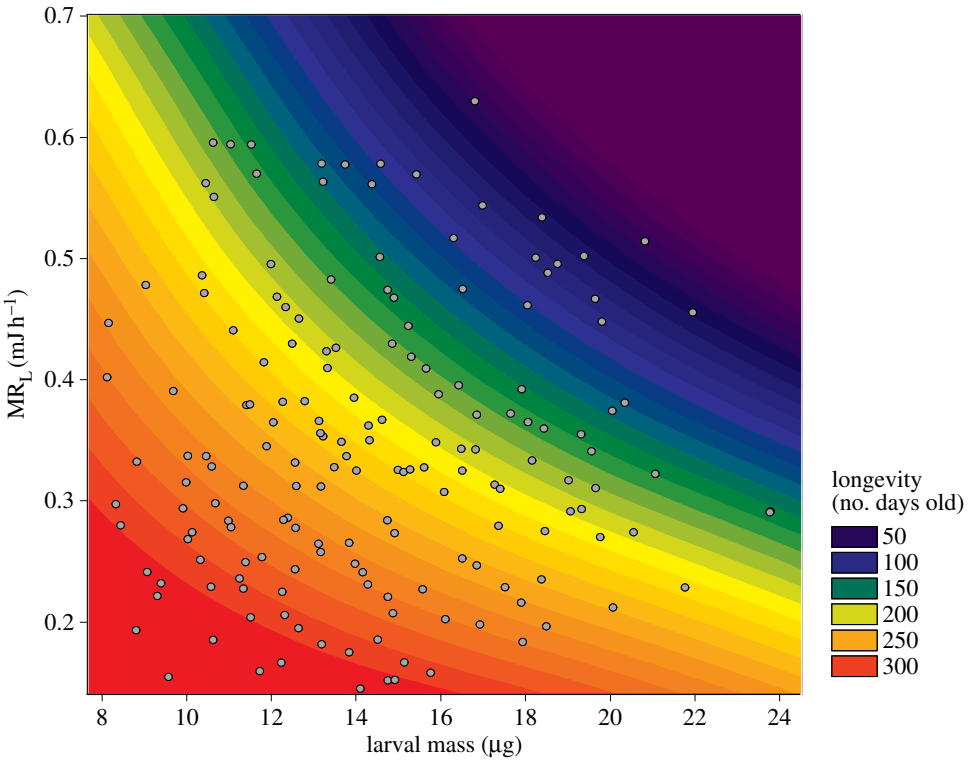

Figure 3. Predicted longevity (number of days until less than 10% colony alive) plotted against larval mass (micrograms) and metabolic rate late (MR_L; milliJoules per hour) for *B. neritina* settlers. Data points show raw data for measures of larval mass and MR_L ($n = 179$). Longevity of a colony is highest for individuals from smaller larvae with lower MR_L.

larger larvae with a higher MR_L (figure 3). The final model showed a significant interaction between offspring mass and MR_L ($\chi^2_1 = 4.24$, $p = 0.039$) where the two traits were negatively correlated with longevity of the settlers (table 2).

(c) Age at onset of reproduction

Individuals with higher MR_E reproduced sooner than individuals with lower MR_E (figure 4). When fitting the model, MR_E, larval mass, MR_L, larval mass × MR_E and MR_E × MR_L all showed marginally significant effects and were, therefore, retained in the final model [32]. However, log-likelihood tests revealed MR_E ($\chi^2_1 = 5.064$, $p = 0.002$) was the only trait to have significant effects on age at onset of reproduction (table 3).

4. Discussion

(a) Correlational selection for decreased covariance between metabolic rates

We found selection for decreased covariance between metabolic rates at each stage—individuals with high metabolic rates in one stage and low metabolic rates in another stage had higher lifetime reproductive output than individuals with either both high or both low metabolic rates in each stage. Assuming that our estimates of selection are persistent, and that metabolic rate is heritable, we would expect to see decreased covariance between metabolic rates at different developmental stages—leading to individuals with metabolic rates that are either high or low in both stages, being purged from the population. Until now, findings of correlational selection on metabolic rates had yet to be demonstrated—most other studies find benefits to either a higher or lower metabolic rate overall. By contrast, we found a benefit to having metabolic rates that are dissimilar to each other across developmental stages.

While we observed a slight, positive correlation for metabolic rate among developmental stages, selection favoured a negative correlation between these traits. That the strength and direction of selection on key life-history traits fluctuates across development has been previously demonstrated [33,34]. However, that selection should act to reduce covariance between two correlated traits appears to be counterintuitive. A lower metabolic rate early in development may need to be offset by a higher metabolic rate later in development in order to meet energy requirements for essential biological processes. Conversely, high energy expenditure early in development may be unsustainable, and a shift to a low metabolic rate in later development may be required to maintain energy reserves. If this is the case, then why consistently intermediate metabolic rates were not selected for throughout development remains unclear. We do not know what drives the negative correlational selection on two metabolic rates separated by only 24 h, but that the selection exists suggests that more studies should estimate selection on multiple metabolic rates across ontogeny.

(b) Metabolic rate and the pace of life history

Metabolic rate was associated with other important life-history traits, and together these life-history traits drive the pace of the life history. We found no directional selection for higher or lower metabolic rates, but we did find strong evidence that certain metabolic rates may be associated with the timing of key life-history events. Overall, individuals with lower metabolic rates lived for longer, had slower growth rates and reproduced later in life than individuals with higher metabolic rate; while higher metabolic rates were generally correlated with higher growth rate, lower longevity and an earlier onset of

Table 2. Linear mixed model for the relationship between individual colony longevity (number of days until less than 10% colony alive) with larval mass (micrograms), metabolic rate early (MR_E; milliJoules per hour) and metabolic rate late (MR_L; milliJoules per hour). (Model reduced using maximum log-likelihood to remove non-significant interactions ($p > 0.05$). All d.f. = 1. *$p < 0.05$.)

trait	estimate	χ^2	*p*-value
fixed effects			
larval mass		0.386	0.534
MR_E		0.000	1
MR_L		0.343	0.558
larval mass × MR_E		0.080	0.777
larval mass × MR_L	*−126.375*	*4.244*	*0.039**
MR_E × MR_L		0.058	0.810
larval mass × MR_E × MR_L		2.967	0.085
random effects			
experimental run		0.001	0.975
experimental run × mass		0.000	1
experimental run × MR_E		0.000	1
experimental run × MR_L		0.620	0.431
experimental run × mass × MR_E		0.272	0.602
experimental run × mass × MR_L		0.272	0.602
experimental run × MR_E × MR_L		0.000	1
experimental run × mass × MR_E × MR_L		0.000	1

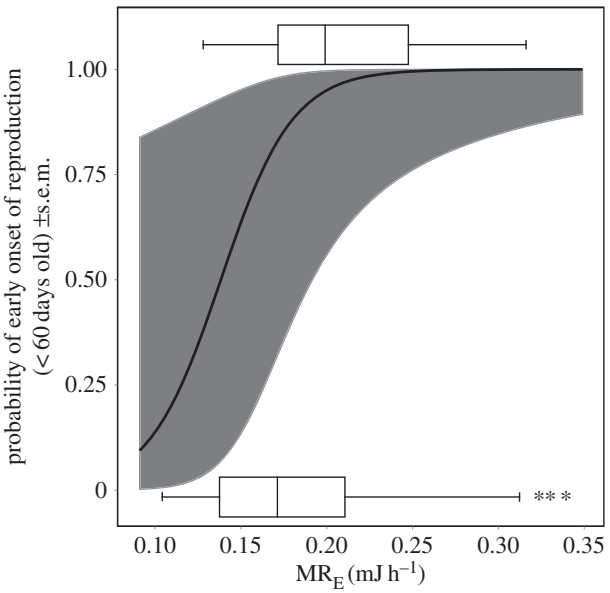

Figure 4. Predicted logistic regression between metabolic rate early (MR_E; milliJoules per hour) and probability of early onset of reproduction using logistic regression ± standard error. Early onset of reproduction (colony less than 60 days old) is assigned a value of 1 while late onset of reproduction (greater than or equal to 60 days old) is assigned a value of 0. Onset of reproduction occurs earliest for higher values of MR_E.

Table 3. Final logistic regression model for age at onset of reproduction (number of days) in relation to larval mass (micrograms), metabolic rate early (MR_E; milliJoules per hour) and metabolic rate late (MR_L; milliJoules per hour) for *B. neritina* where age at onset of reproduction (development of reproductive structures) was assigned either early = 0 (less than 60 days old) or late = 1 (greater than or equal to 60 days old). (Model reduced after testing for non-significant interactions ($p > 0.05$). All d.f. = 1. *$p < 0.05$.)

trait	estimate	χ^2	*p*-value
fixed effects			
larval mass		1.596	0.207
MR_E	*−47.822*	*5.064*	*0.024**
MR_L		1.526	0.217
MR_E × MR_L		2.604	0.107
larval mass × MR_E		2.714	0.099
larval mass × MR_L		0.029	0.865
larval mass × MR_E × MR_L		0.008	0.929

reproduction. Across taxa, studies have shown that slow growth, late onset of reproduction and greater longevity that is often associated with low metabolic rate, can serve as an advantageous strategy in low stress environments, for instance, when competition and predation pressure are low and resources are abundant [35–39]. Conversely, a faster pace of life is likely to be advantageous in stressful environments, such as when food levels are low or predation is high, and thus higher metabolic rates are likely to be beneficial [40–44]. Contrary to this, in environments where reduced energetic requirements are advantageous such as during periods of starvation or temperature stress, then lower metabolic rates may be selected for [45,46].

The environment is likely to influence the strength and direction of selection acting on metabolic rate [47]. In our study, individuals were insulated from interspecific competition by our experimental design (though they were exposed to predation). Under environmental conditions where mortality rates are higher or size-dependent (e.g. faster growing individuals reach a size refuge sooner; [48,49]), individuals with consistently higher metabolic rates may be favoured. In our species at least, it seems that metabolic rate is associated with key life-history traits that determine either a 'fast' (faster growth, earlier reproduction, shorter lifespan) or 'slow' (slower growth, later reproduction, longer lifespan) life history. For lifetime reproductive output under our experimental conditions, the environment favoured neither high nor low metabolic rates, rather individuals that had negatively correlated metabolic rates between developmental stages were favoured over those individuals with positively correlated metabolic rates.

(c) Metabolic rate and its effects on performance change throughout development

Studies of selection on metabolic rate have been largely based on measures of metabolic rate at single time points in the life

history (e.g. [50,51]). Our results suggest that metabolic rates at different stages throughout the life history can have different and interactive effects on performance. Metabolic rate can fluctuate throughout ontogeny, therefore, repeatability is often low and it is unlikely that individuals will express a single metabolic phenotype throughout the life history [52,53]. In our study, MR_E and MR_L were not strongly correlated, rather their effects on fitness were contingent upon each other and the effects of each measure differed across life-history traits. For example, while individuals with lower MR_L were longer lived, no significant correlation with longevity and MR_E was detected. Conversely, MR_E showed a stronger effect on growth rate than MR_L—when individuals had lower MR_E, then the effects of MR_L were much less important for growth rate than when individuals had higher MR_E. Our findings showed that fitness was dependent on the interaction between MR_E and MR_L, and therefore, raise the possibility that single measures of metabolic rate may not fully capture selection—rather, estimating multiple metabolic rates may increase inferential power. It seems that the fitness consequences of different metabolic rates are integrated across the life history. No single metabolic rate affects performance, rather multiple metabolic rates interact to affect performance. Ideally, we would have taken additional measures of metabolic rate in later life stages, as our findings reflect broader arguments that including more traits is likely to yield a more complete view of selection [29,54].

(d) Limitations and future directions

We detected a significant, though slight, positive correlation between metabolic rate at each developmental stage, yet we found strong negative correlational selection on metabolic rates such that the positive covariance should be reduced and ultimately made negative over time (assuming persistent selection across generations). If our estimate of correlational selection accurately reflects a persistent selection regime then the positive relationship between metabolic rates is unlikely to represent an adaptive response to selection. We suspect that genetic constraints maintain the positive relationship between metabolic rates, despite selection against this relationship. If metabolic rate in each stage is positively genetically correlated, then there is little genetic variation in the dimension in which selection acts and responses to correlation selection will be constrained. Estimates of the heritability of metabolic rate remain rare (see White & Kearney [1], table 5) and as far as we are aware, no study has examined genetic covariance between metabolic rates at different life stages. Thus, estimating the genetic covariance between metabolic traits measured at different stages is an important next step in the examination of the evolution of metabolic rate.

While we measured lifetime reproductive output, we insulated individuals from selection at two critical life stages: the larval and metamorphic phase. A necessary logistical constraint was to measure larvae and metamorphosing individuals in the laboratory. Individuals that expressed consistently high or low metabolic rate phenotypes across both developmental stages had poorest performance during the adult stage (in terms of reproductive output), however, it is possible that these phenotypic combinations may yield highest performance in the larval stage. For example, larvae with a higher metabolic rate may be better able to locate suitable settlement sites. Alternatively, individuals with lower metabolic rates may take longer to metamorphose and, therefore, suffer higher mortality during this key phase of the life history. Nevertheless, the benefits for those individuals with consistently high or low metabolic rates during the larval stage would have to be considerable in order to offset the fitness costs that are associated with consistent metabolic rates throughout the life history.

Data accessibility. Dryad data reference: doi:10.5061/dryad.13jv6.

Authors' contributions. A.K.P. carried out the experimental and fieldwork, data analysis, participated in the design of the study and drafted the manuscript; D.J.M. and C.R.W. conceived design of the study and helped with data analysis and drafting of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

Competing interests. The authors have no competing interests.

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