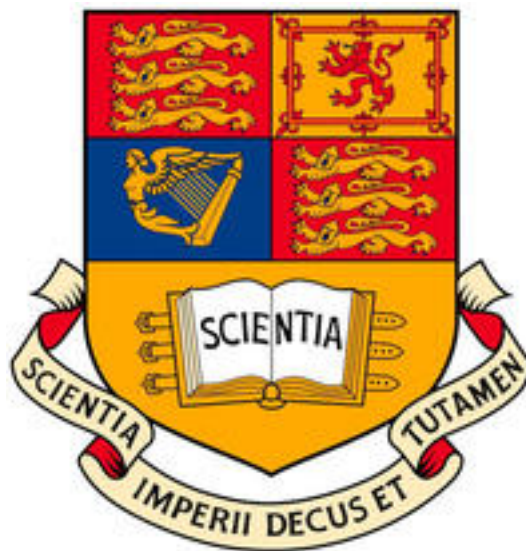# Model fitting and temperature effects - How biological traits response to changes in temperature

by

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1 Abstract

Global temperature increases as a result of climate change are occuring at an alarming rate, with future temperature predictions set to become worse. Whilst the effect of temperature on biological traits is well researched, the potential benefits of populations acclimatizing to different temperatures has been somewhat overlooked. The aim of this study was to investigate the effect of temperature on biological traits, and whether acclimatization temperatures dampened these effects. This study also looked at respiration response data to see whether mechanistic or phenomological models fit the data best. Linear plots of all response data were originally plotted; both cubic and Schoolfield functions were also fit to the respiration response data. Analysis of Covariance, conducted on respiration rate, feeding rate, and energetic efficiency, highlighted a significant effect of experimental temperature on all trait responses. Both respiration and feeding rate significantly increased, whilst energetic efficiency decreased. acclimatization temperature had a significant impact on energetic efficiency, but not on feeding rate. The model fitting results yielded the predicted outcome; the Schoolfield model produced a better fit to the data. Overall, the results obtained supported findings previously made in the field of thermal ecology, with further research into phenotypic plasticity and it's effects on thermal tolerance advised.

Keywords: Thermal Performance Curves, Schoolfield, Phenotypic plasticity, Climate change, Radix balthica.

Word count: 3097.

2   Introduction

Researching how individuals and populations respond to the changing climate is a global priority, due to the ever increasing knowledge of the changing climatic future of our planet and future temperature predictions. Current temperatures are increasing at an alarming rate; the Earth's average surface temperature has risen by about 0.8°C over the last century alone (IPCC 2014), with areas such as the Arctic experiencing surface air temperature (SAT) increases of up to 2°C (Przybylak 2007). Predictions of future temperatures are looking just as bleak, with the IPCC noting that if nothing changes in respect to emissions, then by 2100, average surface temperatures will further increase by 3°C (IPCC 2014).

Because of this, research into how both ecosystems and the individuals within them will cope with this increase in temperature is undeniably important. Research has already shown that certain populations are shifting their ranges towards higher latitudes whilst others are simply loosing lower latitude edges and failing to expand their poleward ranges (Chen et al. 2011; Sunday et al. 2014; Kerr et al. 2015). Despite the potential for certain populations to track climate change along a latitude, certain habitats restrict this movement (i.e. lakes, isolated patches of forest), resulting in either adaptation to a changing environment, or local extinction.

Fundamentally, temperature increases affect biological organisms by increasing enzymatic reactions; both metabolic rates (Gillooly et al. 2001) and photosynthesis are subsequently affected, which in turn can impact on whole ecosystem dynamics. The effect of temperature on metabolic rates is well researched (see: Brown et al. 2004; Price et al. 2010), and there is ever growing research into the effects that global warming may bring to species at such a fundamental, biological level (Clusella-Trullas et al. 2011; Manciocco, Calamandrei and Alleva 2014; Gandar et al. 2017).

Despite this potentially negative impact, certain species display some plasticity within their phenotypes (e.g. *Sitta* sp: Ghalambor and Martin 2002; common killifish, *Fundulus heteroclitus*: Schulte, Healy and Fangue 2011; wandering snail, *Radix balthica*: Ahlgren et al. 2013), which could be beneficial in coping with changes to the local environment. The term "Phenotypic flexibility", a sub-category of phenotypic plasticity first proposed by Piersma & Drent (2003), aims to describe adjustments of physiological traits in response to changes in environmental conditions, both in the laboratory or the field. Since this term was first proposed, several papers have looked into the effects of this, or similar phenomenons, on biological traits between populations (McKechnie 2008; Marshall and McQuaid 2011; Ahlgren et al. 2013).

A paper by Marshall & McQuaid (2011) looked into the benefits of increasing temperature on *Echinolittorina malaccana*, a species

of snail commonly found in "stressful" environments. They found that the Universal Temperature Dependence model (UTD) from the Metabolic Theory of Ecology (MTE) does not explain metabolic rates of organisms from stressful environments, who are constantly exposed to fluctuating or high temperatures; their results showed a lowering of metabolism when heated for 7-42 days (Marshall and McQuaid 2011). Certain populations of a species from a more "stressful" environment therefore may display unexpected outcomes in relation to the MTE; their population may have a higher degree of phenotypic flexibility, allowing them to cope with higher temperatures. Individuals displaying this flexibility would be greatly beneficial to the species as a whole, and could potentially alleviate the pressures of global warming on the entire ecosystem.

Several methods are currently being utilized to study individual and species specific responses to varying temperatures, ranging from field to lab based experiments (Schulte, Healy and Fangue 2011; Brusch, Taylor and Whitfield 2016). This paper will take advantage of a naturally occurring experiment; *Radix balthica*, a common species of freshwater snail, can be found in most streams of the Hengill geothermal valley, which displays streams varying in temperatures from 4-50°C(Friberg et al. 2009; O'Gorman et al. 2012). Stream 15 (Mean summer temperature, 50°C) was not included in this study due to *Radix balthica* not being present. These streams are very similar in their physical and chemical composition (O'Gorman et al. 2012), with temperature being the only strong ecologically meaningful difference among them (Friberg et al. 2009). This provides a rare opportunity to compare individual responses to both changing experimental temperatures and different initial stream (acclimatization) temperatures, to see if prior acclimatization to higher temperatures has an impact on biological traits.

This study was undertaken to examine the effects of temperature on *Radix balthica*, and aims to address five questions: Can different mathematical models reliably fit and predict the data (question 1)? Does increasing experimental temperature impact on respiration rates (question 2), feeding rates (question 3) and energetic efficiency (question 4), and finally, does the initial stream temperature (hereafter, acclimatization temperature) impact on these results (question 5)?

Based on the principles of the Metabolic Theory of Ecology and of species Thermal Performance Curves (TPCs), I predicted that the Schoolfield (mechanistic) model should produce better fit results in comparison to a cubic (phenomenological) model (hypothesis 1), due to the more biologically informative nature of the mechanistic model's parameters. Questions 2 and 3 look at the link between respiration/feeding rate and experimental temperature; enzymes begin denaturing past temperatures of approximately 30°C, due to exceed-

ing the Physiological Temperature Range (PTR; Savage et al. 2004; Pawar et al. 2016), therefore biological rates would be unlikely to continue to increase. Because of this, I predict that both respiration and feeding rates should increase up to a maximum of 30°C (maximum temperature 30°C, hypotheses 2 and 3: Gillooly et al. 2001). Energetic efficiency should decrease with increasing experimental temperature (maximum temperature 30°C, hypothesis 4: Savage et al. 2004); finally, I predicted that the acclimatization temperature should aid in dampening the effects of experimental temperature on the biological traits (hypothesis 5: Marshall and McQuaid 2011).

3   Materials & Methods

Data and composition

The data were collected from the Hengill valley, Southwest Iceland (64°03'N: 21°18'W) by Dr R. Kordas and Eléa Giraud from the Hengill valley between May 2015 to August 2017. These datasets consisted of a respiration set; respiration data (in micromoles per hour) on individuals from 7 different streams (5.5 - 19.3 °C), exposed to experimental temperatures ranging from 5-45 °C, and a feeding dataset; feeding data (in milligrams per m^2 per hour) on individuals from 3 different streams (9.6, 14.4 and 19.3 °C) exposed to experimental temperatures ranging from 5.2-27.5 °C. Included with both of these datasets were the mass of the individuals prior to experimentation; this was used to correct all measured biological traits by multiplying by $Mass^{-3/4}$ (Brown et al. 2004). The final datasets consisted of 529 respiration observations, and 89 feeding observations. Plots were then run to check for characteristic patterns in the data, such as skewed bell curve (observed in Figure 1), typical of thermal performance curves (TPCs); following this, several models were run on both datasets using Python 3.6.3 (Rossum and Drake 2001).
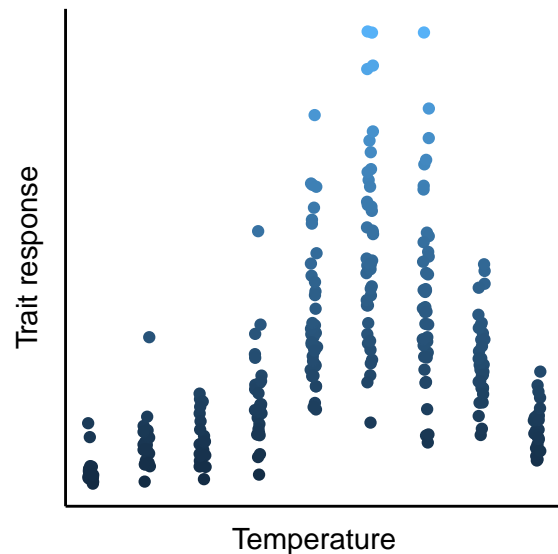
Data modelling

Figure 1: Example Thermal Performance Curve Plot of *R. balthica*

Figure 1 shows a typical temperature performance curve; a near exponential increase in trait response up to a point (usually referred to as an optimal or peak temperature) proceeded by a rapid decrease in trait response. Due to the na-

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Table 1: Model fit comparisons of *R. balthica* respiration rate Performance Curves

Stream Temperature	Cubic			Schoolfield		
	AIC	BIC	R^{2}	AIC	BIC	R^{2}
5.6	-574	-564	0.53	**-584**	**-576**	**0.57**
8.1	-305	-298	0.55	**-322**	**-316**	**0.66**
9.6	-784	-773	0.58	**-790**	**-782**	**0.59**
13.2	-415	-407	0.58	**-424**	**-418**	**0.62**
13.9	-421	-412	0.61	**-423**	**-417**	**0.61**
14.4	-587	-577	0.58	**-604**	**-597**	**0.64**
19.3	-475	-465	0.56	**-483**	**-476**	**0.59**

ture of these plots, various models have been designed using a range of mathematical equations in an attempt to describe the data, with most functions stemming from polynomial models.

Such models include simple phenomenological models (e.g. cubic models) and mechanistic models (e.g. Schoolfield model). Both of these methods of modelling match observed data with a reasonable amount of accuracy (Affinito 2017); the difference between these two types of models is the underlying theory behind them.

Phenomenological

Phenomenological models describe the empirical relationship between phenomena, but do not attempt to explain why the particular variables interact in the way that they do. The cubic model formulae was as such:

$$B = aT^3 + bT^2 + cT + d \qquad (1)$$

Where B is the trait of interest (respiration rate), T is the temperature (in °C) and a,b,c, and d are all mathematical scalars of the function. This function was fitted to the entire respiration data set, and also to each individual stream/acclimatization temperature.

Mechanistic

A mechanistic model's main assumptions are that complex systems can be understood by examining its individual parts, and the way in which these phenomena interact.

For this study, a simplified version of the Schoolfield function (Schoolfield, Sharpe and Magnuson 1981), following from the Metabolic Theory of Ecology, was used:

$$B = \frac{B_\theta e^{\frac{-E}{kT}}}{1 + e^{\frac{E_h}{k}(\frac{1}{T_{pk}} - \frac{1}{T})}} \qquad (2)$$

Where B is the trait (respiration rate) value, T is the experimental temperature (in Kelvin), B_θ is the normalization constant, E is the activation energy of the curve (measured in eV) , E_h is the high temperature deactivation energy of the curve, T_{pk} is the temperature (in K) where the model peaks and k is the Boltzmann constant $(8.617 \times 10^{-5} \text{ eV} \cdot K^{-1})$.

This equation attempts to explain the relationship between temperature, T, and trait, B, on a fundamental level. Temperature is responsible for driving enzyme chemical reactions,

which in turn impact on metabolism. B_θ is the value of the trait at a low temperature (10 °C), and controls the lower end of the TPC, whilst the Arrhenius equation, $(e^{-E/kt})$, models the temperature dependance of reaction rates during the "normal operating range" (between 10 - 35 °C) (Brown et al. 2004).Within the Arrhenius equation, E controls the enzyme activation energy and is normally within the range of 0.1 - 1eV, with most studies reporting values between 0.5 - 0.7, regardless of species or location. E_h controls the high-temperature deactivation energy of the enzymes, and along with T_{pk}, models the rapid descent of the curve.

The simplified Schoolfield model was used as low temperature measurements (<5 °C) were not made.

Linear

Linear models were plotted on all biological trait data using the following equation from the Metabolic Theory of Ecology (Gillooly et al. 2001; Savage et al. 2004):

$$B = B_\theta e^{E_t \frac{T_t - T_0}{kT_t T_0}} \tag{3}$$

Where B is the trait of interest, B_0 is the constant, E_t is the activation energy of the trait, T_t is the experimental temperature (5 - 30°C, within PTR), T_0 is the average of the experimental temperatures used (17.5°C) and k is the Boltzmann constant. The equation was subsequently logged to allow for linear models to be plotted.

Model comparison

In order to compare the fits of models to the respiration data, Akaikes Information Criteria (AIC), Bayesian Information Criteria (BIC) and R^2 values were calculated. Both IC's have their merits, and so both were calculated to ensure the best fitting models were correctly identified. Models with lower AICs/BICs were considered to be better predictors of the data.

R^2 values show how well the model fits the data; the higher the R^2 value the more the model explains the data.

Statistical analysis

All statistical analses were carried out in R version 3.2.3 (Team 2013). ANCOVAS (Analysis of Covariance) were used to explore relationships between the dependant variables (respiration rate, feeding rate or energetic efficiency) and Temperature, both acclimatization and experimental. The experimental temperature was run in the model as a continuous explanitory variable, while the acclimatization temperature was used as a categorical variable with the levels: cold, tepid and warm.

4   Results

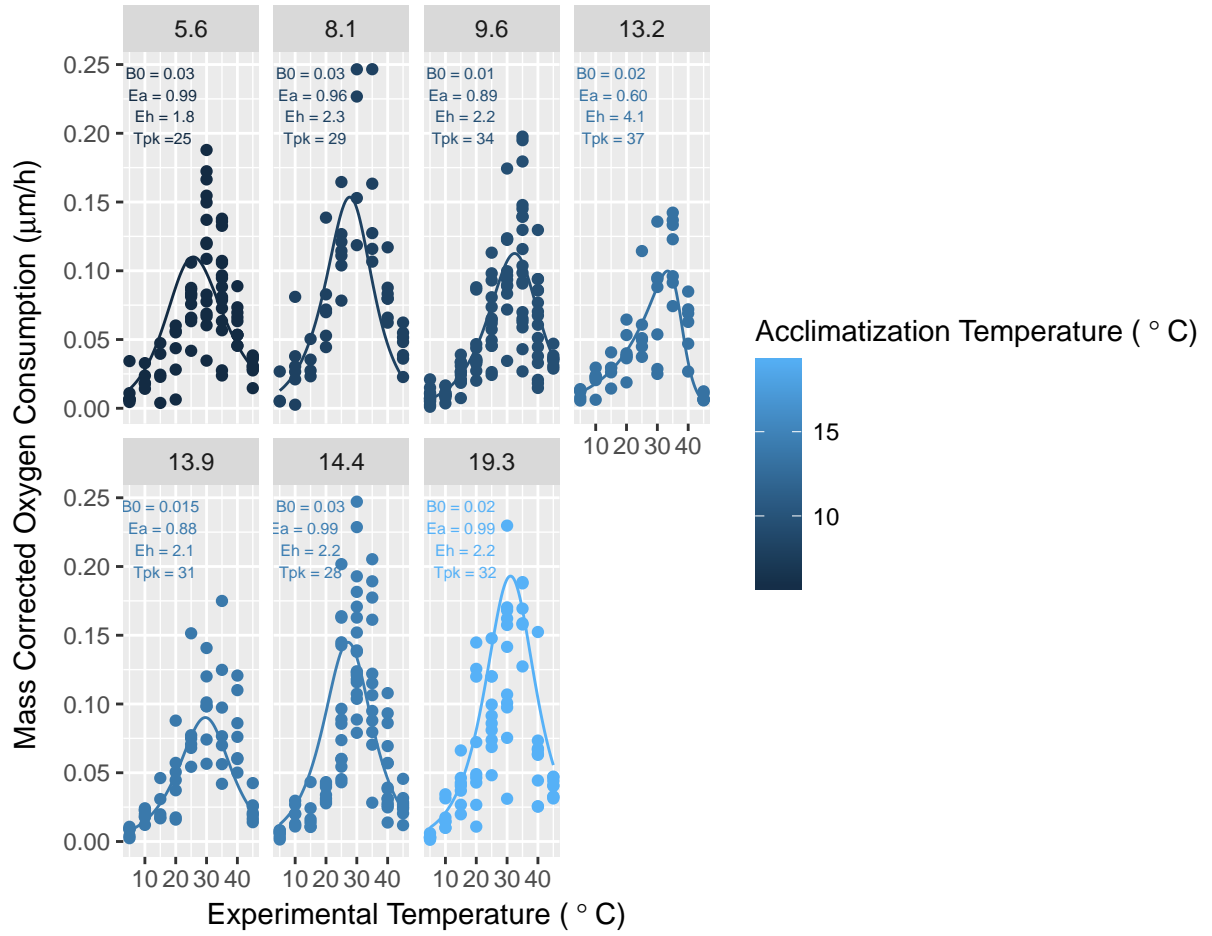Models were originally plotted on both the entire datasets and individual streams; this was done

Figure 2: Schoolfield Temperature performance curves of *R. balthica* plotted for increasing acclimatization temperatures. Parameters of the function are displayed in each unique plot

so as to gauge whether acclimatization temperature significantly affected the overall results. Preliminary results showed that there was a significant difference between streams in regards to the model parameter values used, and so subsequent models were plotted on individual streams only.

Respiration rate

A linear model was plotted on the respiration data first in order to estimate a value for E and B_0, and to calculate significance. The linear model was plotted over the temperatures 5-30°C; the parameter outcomes where then used as the starter parameters for subsequent models. Repiration rate significantly increased with increasing experimental temperature (ANCOVA: $F_{1,322} = 1027.27$, p <0.000001).

Model fitting - Phenomenological vs Mechanistic

The cubic and Schoolfield models applied to stream specific data fit with a reasonable amount of accuracy; the worst performing model
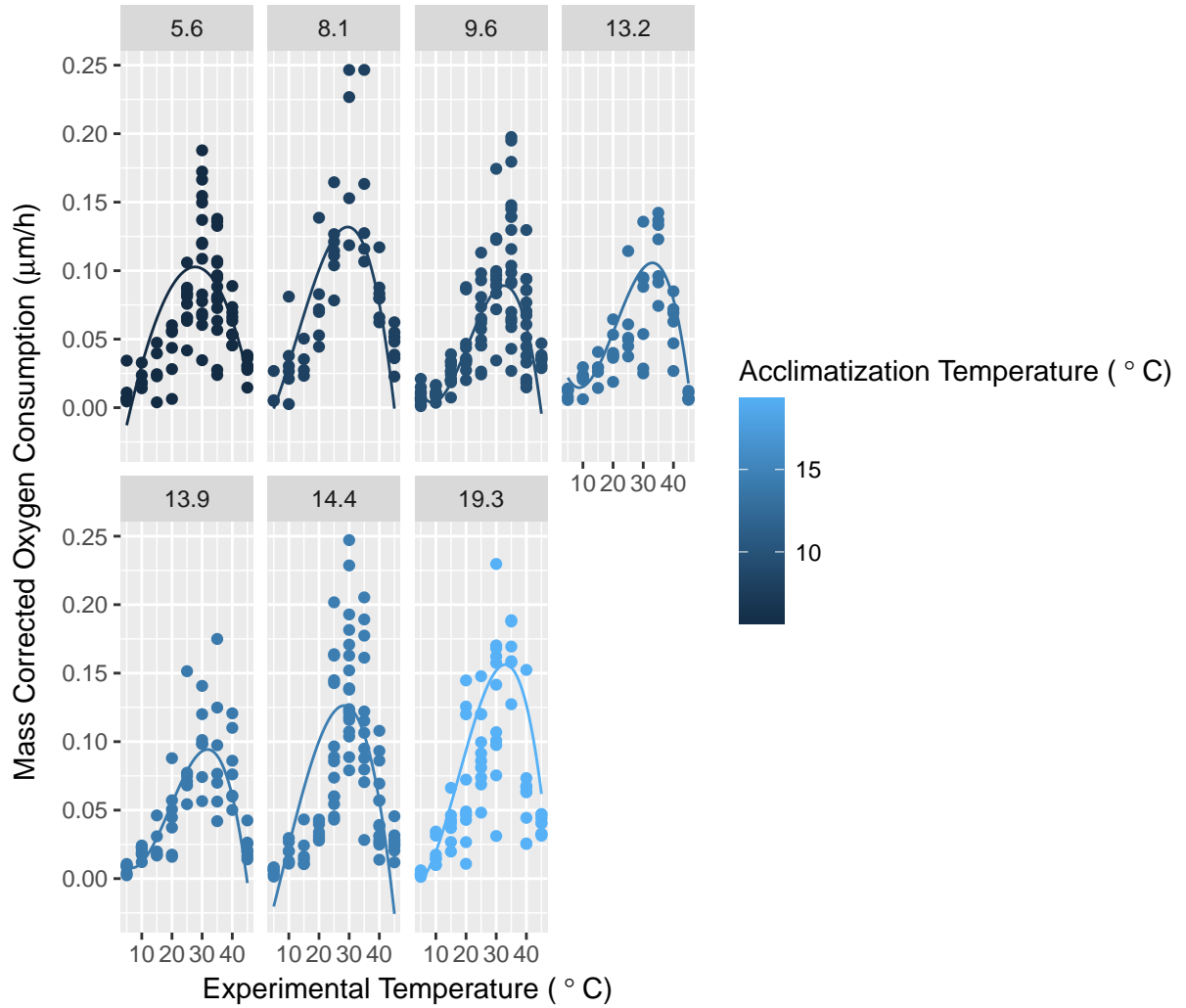
Figure 3: Cubic Temperature performance curves of *R. balthica* plotted for increasing acclimatization temperatures. Parameters of the function are displayed in each unique plot

(cubic, fit to stream 5.6) still achieved an R^2 value of 0.53.

An overarching theme produced by the model fitting was that the Schoolfield model consistently produced a better fit than the cubic model (Table 1, Figures 1-2). Despite this statement, both models produced results with R^2 values of above 50%, and AICs/BICs below -290, indicating either model could be used without risking excessive data loss. Both mod-els produced the expected pattern of a TPC for streams 9.6, 13.2, 13.9 and 19.3 °C, but whilst the Schoolfield also showed the pattern for streams 5.6, 8.1 and 14.4 °C, the cubic model poorly represented these datasets despite reasonable model fit results. Even when comparing the remaining streams, the Schoolfield model still produces a better fit due to a steeper decrease after the temperature peak.

Feeding rate

Feeding rate was found to significantly increase with increasing experimental temperature(ANCOVA: $F_{1,83} = 21.93$, p <0.0001), but there was no significant effect with acclimatization temperature (ANCOVA: $F_{2,83} = 1.37$, p = 0.261). acclimatization temperature also did not modify the relationship between feeding rate and experimental temperature (ANCOVA: $F_{2,83} = 2.01$, p = 0.141).

Energetic efficiency

Energetic efficiency significantly decreased with increasing experimental temperature (ANCOVA: $F_{1,83} = 14.61$, p <0.0005), and there was a significant effect of acclimatization temperature on energetic efficiency (ANCOVA: $F_{2,83} = 5.67$, p <0.005, Figure 6). There was no significant effect of acclimatization on the temperature effect on energetic efficiency (ANCOVA: $F_{2,83} = 0.78$, p = 0.46).
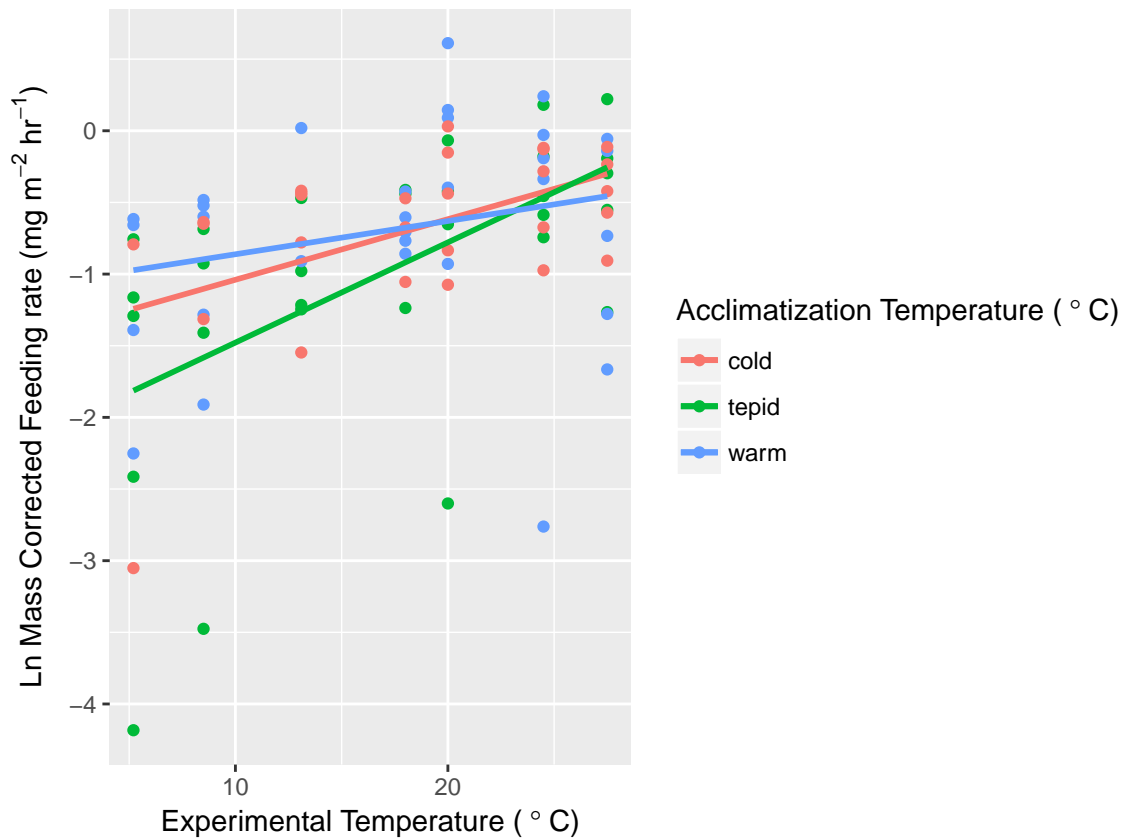

Figure 4: Feeding rate response of *R. balthica* to experimental temperature, with acclimatization temperature included as a factor.

362 The results support 4 out of 5 of the proposed
363 hypotheses; hypothesis 5 (acclimatization damp-
364 ening the effects of experimental temperature)
365 was not supported, most likely due to the lack
366 of replicates, although this result could also
367 support research into rejecting the Beneficial
368 Acclimation Hypothesis (BAH; Leroi, Bennett
369 and Lenski 1994). These findings are neces-
370 sary to the current growing research body into
371 global warming effects on species; further re-
372 search could provide an insight into the coping
373 strategies of species to warming pressures.

The results obtained from this study support hy- 375
pothesis 2, that respiration rate increases with 376
temperature. This result also goes towards sup- 377
porting current research into the effects of global 378
warming on species metabolism (Grigaltchik, 379
Ward and Seebacher 2012; Sentis, Hemptinne 380
and Brodeur 2012). The underlying mechanism 381
behind this increase in respiration is already well 382
known, (Arrhenius equation; $e^{E/kT}$), but this 383
equation only fits the data over a normal biolog- 384
ical operating range (5-30 °C). Due to this, most 385
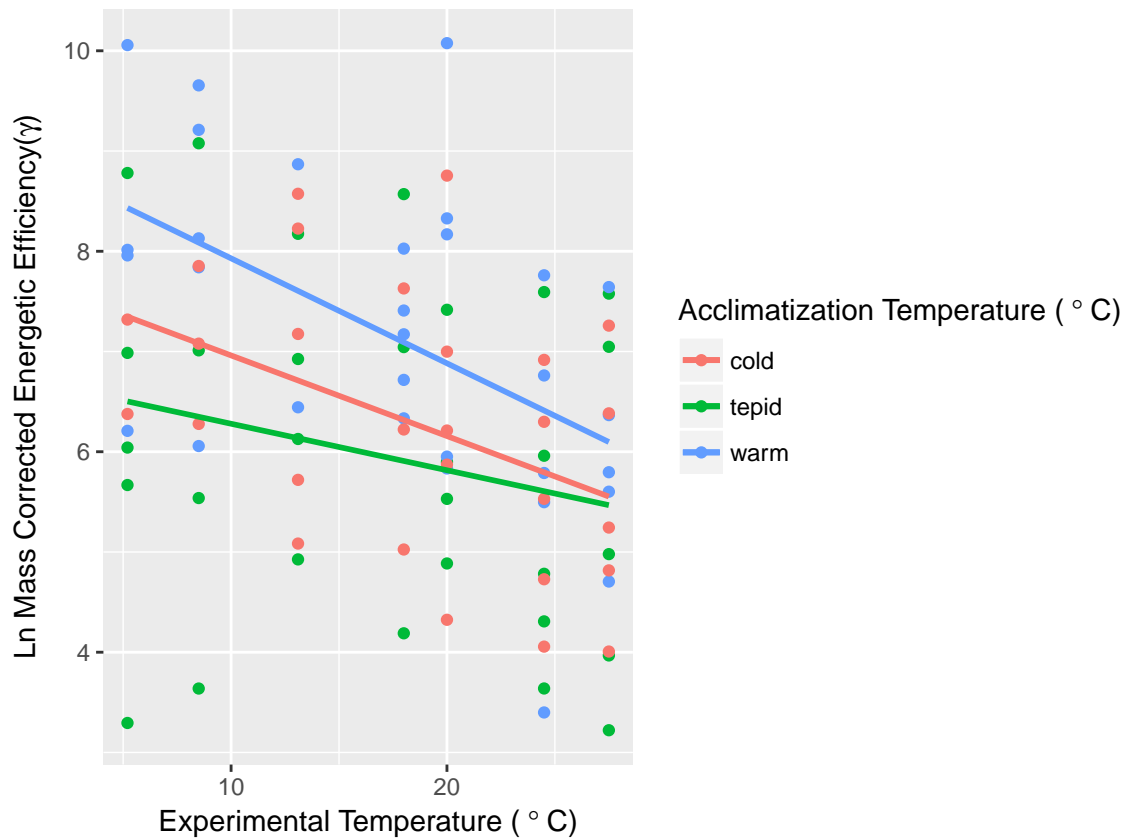thermal ecological data is also plotted against 386

Figure 5: Energetic efficiency response of *R. balthica* to experimental temperature, with acclimatization temperature included as a factor.
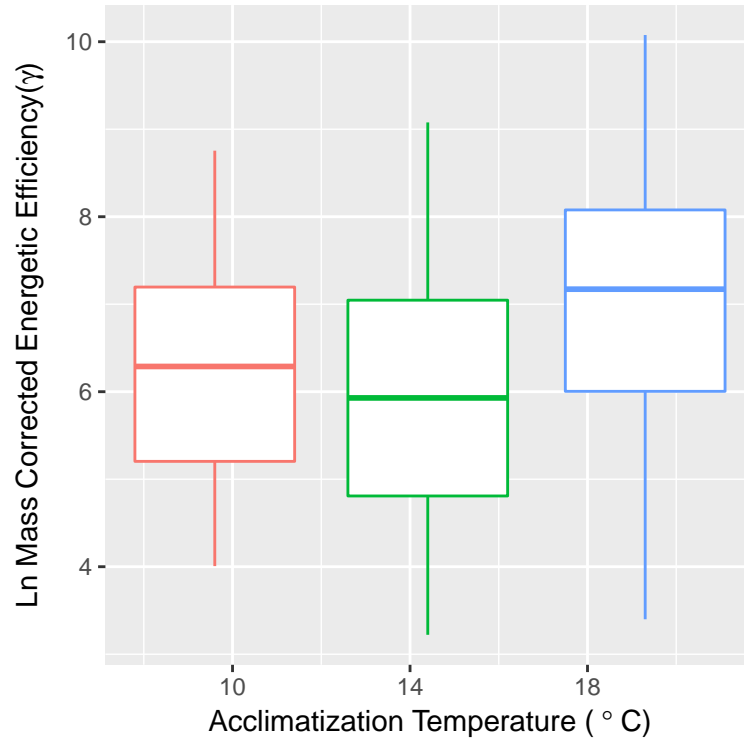
Figure 6: Energetic efficiency of *R. balthica* plotted against acclimatization temperature. Tepid (14.3°C) and warm (19.3°C) acclimatization differed significantly (p <0.01), whilst cold (9.6°C)/warm and cold/tepid returned non-significant results (p >0.08).

polynomial models.

Model fitting

Our model fitting analysis supported the general trend in thermal ecology models; respiration rate in response to temperature changes show a strong fit to polynomial models.

Both the cubic (Figure 3) and the simplified Schoolfield (Figure 2) models fit with reasonable accuracy; as hypothesised (hypothesis 1), the simplied Schoolfield produced better fit results.

This result is most likely due to the nature of the model, with it having a biologically relevant parameters, as opposed to the cubic, phenomenological model. Despite the cubic model still fitting approximately 55% of the data, due to the lack of biological meaning, it increases the risk of over-fitting on the data. Future experiments should aim at collecting data from a broader range of experimental temperatures to test whether the Schoolfield model still produces the best fit.

As well as the model comparisons, the models also produced unique parameters. The parameters of particular interest are E_h and T_{pk}, which varied significantly between streams. As temperature increased from 5.6°C to 13.2°C, T_{pk} gradually increased from 25 - 37°C, with E_h also increasing from 1.8 - 4.1. As temperature

then increased from 13.2 - 19.3°C, T_{pk} and E_h decreased to 32°C and 2.2 respectively. These results could be explained as a trait showing phenotypic plasticity or "flexibility", whereby the individual responds to the changing environment by altering it's behaviour. Due to the peak of both E_h and T_{pk} at 13.2, this could further imply that there is a cost to this behaviour; past a certain temperature, this heat tolerance becomes more costly then beneficial.

Our species of interest, *R balthica*, is already known to display flexibility in it's phenotypes (Ahlgren et al. 2013). Our results support the potential for this species to also display flexibility in its respiration/ metabolic rate, with the added potential for a trade off to explain the midrange peak.

Future experiments to test whether all populations of *R balthica* display this potential flexibility could yield exciting and beneficial results, which also have the potential to aid in mitigation of global warming pressures.

Feeding rate

Like both Rall *et al* 2012, and Sentis *et al* 2012, we found feeding rate to increase with increasing experimental temperature, thus supporting hypothesis 2 (Figure 4). This finding is likely due to the impact of temperature on metabolism; increasing metabolic rate will in turn lead to a higher demand for food, and subsequently a higher feeding rate.

Despite the results supporting hypothesis 3, hypothesis 5 (acclimatization damping the effects of experimental temperature), was not supported by feeding results. This may be explained by a lack of replicates, but it is also possible that this result could support the rejection of the Benefical Acclimation Hypothesis (BAH; Leroi, Bennett and Lenski 1994).

Future experiments should focus on testing these hypotheses over a wider range of both experimental and acclimatization temperatures. These results should aid research into how species will cope with global warming, and the potential domino effect it may have on ecosystems.

Energetic efficiency

Hypothesis 4 (Energetic efficiency decreasing with temperature) was supported by the results (Figure 5). Previous studies have shown decreases both gut passage rate (McConnachie and Alexander 2004) and ingestion efficiency (Rall et al. 2010); a decrease in energetic efficiency could be caused by inefficient and slow digestion, and therefore potentially result in starvation if energetic efficiency continues to decline (Rall et al. 2010; Sentis, Hemptinne and Brodeur 2012).

acclimatization temperature had a significant impact on overall energetic efficiency; warm acclimatization (19.3°C) was significantly higher than the tepid (14.3°C) acclimatization (Figure 6). This result goes towards supporting the notion of "phenotypic flexibility" (Piersma and Drent 2003; Ahlgren et al. 2013); the individuals

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acclimated to warmer temperatures may have been able to withstand higher experimental temperatures due to their prior, long term exposure.

Despite both experimental and acclimatization temperature significantly impacting on energetic efficiency, the effect of experimental and acclimatization temperature together on energetic efficiency returned a non-significant result, causing a rejection of hypothesis 5.

6   Conclusion

Overall the results obtained from this study support findings previously made in the field of thermal ecology; this study highlights the impact of temperature on several vital biological processes, and the potential impact of acclimatization on these traits. With the global temperature set to increase, it is vital to understand the implications that this will have on our ecosystems and the species within them.

Further research into phenotypic flexibility and it's potential impacts on both heat tolerance and biological traits, could yield insightful and valuable results into how species will cope with the ever changing temperatures.

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