Individuals exhibit consistent differences in their metabolic rates across changing thermal conditions

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ARTICLE INFO

ABSTRACT

Metabolic rate has been linked to growth, reproduction, and survival at the individual level and is thought to have far reaching consequences for the ecology and evolution of organisms. However, metabolic rates must be consistent (i.e. repeatable) over at least some portion of the lifetime in order to predict their longer-term effects on population dynamics and how they will respond to selection. Previous studies demonstrate that metabolic rates are repeatable under constant conditions but potentially less so in more variable environments. We measured the standard (= minimum) metabolic rate, maximum metabolic rate, and aerobic scope (= interval between standard and maximum rates) in juvenile brown trout (*Salmo trutta*) after 5 weeks acclimation to each of three consecutive test temperatures (10, 13, and then 16 °C) that simulated the warming conditions experienced throughout their first summer of growth. We found that metabolic rates are repeatable over a period of months under changing thermal conditions: individual trout exhibited consistent differences in all three metabolic traits across increasing temperatures. Initial among-individual differences in metabolism are thus likely to have significant consequences for fitness-related traits over key periods of their life history.

1. Introduction

Metabolic rates reflect the energetic cost of living (Hulbert and Else, 2000). At the very minimum (standard metabolic rate in ectotherms, basal metabolic rate in endotherms), an organism must expend energy on essential functions that maintain homeostasis. Above this baseline expenditure, energy can be allocated to other physiological functions but within the aerobic scope set by the upper limits of their maximum metabolic rate, the maximum rate at which substrates can be oxidized to generate ATP. As such, the rate of energy metabolism is considered one of the primary physiological traits underlying organismal performance (reviewed in Careau et al., 2008; Biro and Stamps, 2010; Burton et al., 2011; Mathot and Dingemanse, 2015).

Metabolic rates can vary considerably among individuals within a population, sometimes 2–3 fold even after accounting for the influence of size, age, and sex (Burton et al., 2011). This variation in metabolic rates has been linked to individual differences in behavior, growth, reproduction, and survival (Burton et al., 2011) and can play an important role in determining the demographic rates of populations (Kooijman, 2000; Metz and Diekmann, 2014) and the evolutionary trajectories of species (Koteja, 2004; Brown and Sibly, 2006). However, from both an ecological and evolutionary perspective, metabolic rates must be consistent (i.e. repeatable) over at least some portion of the

lifetime in order to predict their longer-term effects on population dynamics and how they will respond to selection.

Metabolic rates are generally repeatable over the short term (hours to days), but their repeatability can decline over longer time periods (White et al., 2013; Auer et al., 2016a). This decline may be due in part to random variation and/or measurement error (Chappell et al., 1995) but also to changes in physiological state. Even if nutritional state is maintained, processes such as growth, metamorphosis, and maturation are marked by substantial changes in the masses and activity of the organs that contribute to whole-organism metabolic rates (Oikawa et al., 1992; Hulbert and Else, 2000) and may erode between-individual differences in metabolic rate over time. The repeatability of metabolic rate may also be affected by the stability of environmental conditions (Auer et al., 2016a). Most organisms live in environments where conditions can fluctuate remarkably through time via predictable seasonal changes or more stochastic events. In addition, there is increasing evidence that metabolic rates can change in response to a variety of environmental factors including food availability (Auer et al., 2015a), diet quality (Naya et al., 2007), hypoxia (Hochachka et al., 1996), and water salinity (Allan et al., 2006).

Fluctuations in temperature, whether on a daily or seasonal basis, are a ubiquitous feature of most environments. Temperature is known to have a significant impact on ectotherms because of its effects on rates

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of biochemical and physiological reactions and hence metabolism (Tattersall et al., 2012). How ectothermic organisms deal with temperature fluctuations is therefore of wide interest, particularly given current climate change and predicted future scenarios (Somero, 2010; Hoffmann and Sgrò, 2011). In ectotherms, standard metabolic rate increases with temperature (Gräns et al., 2014; Norin et al., 2014), whereas maximum metabolic rate and aerobic scope can either increase (Gräns et al., 2014; Norin et al., 2014) or reach a peak and then decrease with temperature (Lee et al., 2003; Johansen and Jones, 2011) depending on the species. Below lethal conditions, food intake can also increase with temperature (Elliott, 1976; Houlihan et al., 2008) and may influence rates of metabolism to varying degrees (Auer et al., 2015a, 2016b). However, we know little about whether individuals exhibit consistent differences in their metabolism under changing temperature regimes, and even less so under more natural conditions where temperature, temperature-dependent food intake, and ontogenetic changes may all influence metabolism. Individuals have been shown to exhibit repeatable differences in standard metabolic rate, maximum metabolic rate, and aerobic scope across short-term fluctuations in temperature (Nespolo et al., 2003; Careau et al., 2014; Norin et al., 2016). However, there is evidence that the repeatability of standard metabolic rate may decline across more gradual seasonal temperature changes (Seppänen et al., 2010; but see Cutts et al., 2001). To our knowledge, the long-term repeatability of maximum metabolic rate and aerobic scope under changing temperatures has not previously been investigated.

We examined the repeatability of standard metabolic rate, maximum metabolic rate, and aerobic scope within individual juvenile brown trout (*Salmo trutta*) across increasing temperatures and associated rates of food intake in their first summer of life. Metabolic rates were evaluated at three consecutive test temperatures – 10, 13, and then 16 °C – that simulate the warming conditions trout would naturally experience at this life stage and to which they are presumably adapted (Webb and Walling, 1993; Langan et al., 2001). This experimental design allowed us to assess whether long-term relative performance can be predicted from single measurements of young animals living in seasonal environments where the temporal sequence of temperatures frequently coincides with changes in body size.

2. Materials and methods

2.1. Animal origin and care

Eggs of wild-origin brown trout parents (*n* = 7 pairs) from the River Tweed, Scotland were hatched overwinter (2013–2014) in the laboratory and kept in stock tanks at 8 °C during the egg stage and then 9 °C during the juvenile stage in an indoor facility at the University of Glasgow. In May 2014, juveniles (*n* = 40) were transferred to individual compartments in a stream tank system located in that same facility (see Auer et al., 2015b for details), water temperature was increased to 10 °C, and fish were given 3 weeks to acclimate before the experiment began. Fish were then kept for five weeks at each test temperature (10, 13, and then 16 °C) before their metabolic rates were measured and temperatures were increased to the next level.

Fish were fed commercial trout pellets (EWOS, West Lothian, UK) on a ration that corresponded to roughly 80% of their maximum intake at each test temperature. Specifically, daily caloric intake for each fish was computed as a function of its body mass (*W*, g) and temperature (*T*, °C) using equations from (Elliott, 1976); at 10 °C: $14W^{0.79}e^{0.17T}$, at 13 °C: $14W^{0.81}e^{0.17T}$, and at 16 °C: $26.433W^{0.75}e^{0.112T}$. As such, food levels increased across temperatures but were kept at a fixed percentage of their maximum (Supplementary File 1). Fish were measured every 2–3 weeks while under a mild anaesthetic (benzocaine 40 mg L^{-1}), and rations were then adjusted for changes in body size. Fish were fed twice daily, and faecal matter was siphoned from the system on a daily basis to maintain water quality.

2.2. Metabolic rate measurements

Standard metabolic rate was measured as the rate of oxygen consumption using continuous flow-through respirometry (see Auer et al., 2015b for details). The experimental setup consisted of 16 chambers submerged in water and arranged in parallel in a large central container. Water was pumped through a peristaltic pump via oxygen-impermeable tubing from an aerated upper bin, through each chamber, passed an oxygen sensing electrode and then into a lower bin before being recirculated back to the upper bin. The peristaltic pump ensured that flow rates were the same across all chambers. A chiller was used to keep the water at the desired test temperature, while a UV filter helped to minimize background respiration rates. Chambers were 0.120 L in volume for standard metabolic rate measurements at 10 and 13 °C but then replaced for measurements at 16 °C by larger 0.400 L chambers to accommodate fish growth.

Fish were deprived of food for 48 h prior to their metabolic rate measurements so as to eliminate metabolic costs of digestion that can otherwise increase estimates of standard metabolic rate (Higgins and Talbot, 1985; Secor, 2009; Rosenfeld et al., 2015). Fish were then placed in individual respirometry chambers and their oxygen consumption was measured over a 22-hour period (from roughly 12.00 h to 10.00 h the following day). Flow rates were set at 0.25, 0.81, and 1.89 L h^{-1} at test temperatures 10, 13, and 16 °C, respectively, to allow detection of oxygen consumption rates but not permit oxygen levels to drop below 80% saturation. Oxygen concentrations in the water flowing out of the chambers were recorded every 2-sec using multi-channel oxygen meters (FireStingO2, PyroScience GmbH, Aachen, Germany) and attached sensors and associated FireSting software version 3.0 (PyroScience). The system permitted the continuous simultaneous measurement of oxygen consumption in 15 fish with a 16th fish-free chamber serving as a control measure of background respiration rates. Metabolic rate (mg O$_2$ h^{-1}) was calculated for each fish using the equation: $M_{O2} = V_w \times (C_{wO2control} - C_{wO2fish})$ where V_w is the flow rate of water through the respirometry chamber (L h^{-1}), and $C_{wO2control}$ and $C_{wO2fish}$ are the concentrations of oxygen (mg L^{-1}) in the outflow of the chambers lacking and containing fish, respectively (Clark et al., 2013). Standard metabolic rate for each fish was calculated by taking the mean of the lowest 10th percentile of oxygen consumption measurements over the 20 h measurement period, and then excluding outliers, i.e. those measurements below 2 standard deviations from this mean (Clark et al., 2013).

Maximum metabolic rate was then determined using an exhaustive chase protocol followed immediately by measurement of oxygen consumption during the recovery period using closed-system respirometry (see Auer et al., 2015b for details). Each fish was chased to exhaustion (< 2 min) in a bucket and against a circular current (600 L h^{-1}). Fish were considered exhausted when they could no longer swim and were unresponsive when picked up by hand. They were then transferred immediately (< 10 s) to a glass respirometry chamber submerged in a water bath. A peristaltic pump moved water (7.35 L h^{-1}) through the chamber and past an oxygen sensing electrode via a circuit of oxygen-impermeable tubing before being returned to the chamber. The water volume of the closed system, including the chamber and tubing, was 0.070 L for tests at 10 and 13 °C and 0.120 L for tests at 16 °C since a larger chamber was needed to accommodate the fish by the time of this test temperature. The decline in water oxygen levels was measured every 2 s while the fish was in the respirometry chamber using the same type of oxygen meter, sensor, and software as described above. The respirometry chamber was emptied and the system refilled with oxygenated water before measurement of the next fish commenced.

Maximum metabolic rate (mg O$_2$ h^{-1}) was calculated for each fish using the equation:

$M_{O2} = (V_r - V_f) \times \Delta C_{wO2}/\Delta t$ where V_r is the volume of the respirometry system (L), V_f is the volume of the fish (L) assuming 1 g of fish is equivalent to 1 mL of water, and $C_{wO2}/\Delta t$ is the rate at which the

oxygen concentration decreased over time ($mg\ O_2\ L^{-1}\ h^{-1}$). Slopes for the decline in oxygen concentration were derived for each fish from linear regressions of oxygen concentration against time over a 1-min period (Norin and Malte, 2011), starting after the ~5 s lag between the time the fish was placed in the respirometry chamber and the initial decline in oxygen concentration was detected by the oxygen sensor. After their metabolic rate measurements, fish were weighed ($\pm 1\ mg$) under a mild anaesthetic (Benzocaine $40\ mg\ L^{-1}$) and returned to their stream compartments. Aerobic scope was defined as the difference between the maximum and standard metabolic rates.

2.3. Statistical analyses

We used mixed model analyses to examine how each of the three measures of metabolism – standard metabolic rate, maximum metabolic rate and aerobic scope – changed with temperature and whether differences among individuals in their relative rates of metabolism remained consistent over the time that temperatures increased. For each metabolic trait, we first tested for its general repeatability across all three test temperatures and then across paired temperatures to assess whether repeatabilities differed between temperatures and thus over variable time scales (13 vs 10 °C, 16 vs 13 °C, and then 16 vs 10 °C). Each model included temperature as a categorical fixed effect, body mass as a continuous fixed effect, and individual identity as a random effect. Repeatability (R) was calculated as the ratio of the among-individual variance (V_I) to the sum of V_I and the residual within-individual variance V_e. This measure of repeatability, also known as the intraclass correlation coefficient, was used to determine the repeatability of each metabolic trait after taking effects of both body mass and temperature into account (Singer and Willett, 2003; Careau et al., 2014; Biro and Stamps, 2015). Likelihood ratio tests (LRT), using the χ^2 statistic, were then used to assess the statistical significance of R for each metabolic trait by comparing the log-likelihood of a full model that included V_I versus a reduced model that excluded it (Singer and Willett, 2003; Careau et al., 2014). P-values for each χ^2 test were halved since we were testing whether $V_I > 0$; this is because when the variance is restricted to be nonnegative, the χ^2 statistic is distributed as a 50/50 mixture of a χ^2 with 0 and 1 degrees of freedom (LaHuis and Ferguson, 2009; Snijders and Bosker, 2012).

All three measures of metabolic rate (standard metabolic rate, maximum metabolic rate, aerobic scope) and body mass were log_{10}-transformed to linearise the data. Interactions between body mass and temperature were found to be nonsignificant in initial analyses, i.e. slopes were homogeneous, so were excluded from final models. Analyses were conducted using the MIXED procedures in SAS version 9.3 (SAS Institute, Cary, North Carolina, USA). Differences among models and the parameters estimates for fixed effects were considered significant when $p < 0.05$. All means given are ± 1 SE.

3. Results

Metabolic rates changed as a function of temperature, but the direction of change differed among traits (Fig. 1). At each temperature, standard metabolic rate ($F_{1,77} = 52.1$, $p < 0.001$), maximum metabolic rate ($F_{1,77} = 146.8$, $p < 0.001$), and aerobic scope ($F_{1,77} = 95.6$, $p < 0.001$) were all positively related to body mass as expected. After correcting for individual variation in body mass, standard metabolic rate increased with temperature ($F_{2,77} = 5.6$, $p < 0.01$), while both maximum metabolic rate ($F_{2,77} = 4.5$, $p = 0.014$) and aerobic scope ($F_{2,77} = 8.6$, $p < 0.01$) decreased with temperature.

At each temperature, individuals exhibited up to 2-fold differences in each of the three metabolic traits after taking body mass into account (Figs. 1, 2). These individual differences were repeatable across temperatures (Fig. 2), so that, when considering the complete dataset, individuals differed significantly and consistently from one another in their overall standard metabolic rate ($R = 0.32$, $\chi^2 = 10.54$,
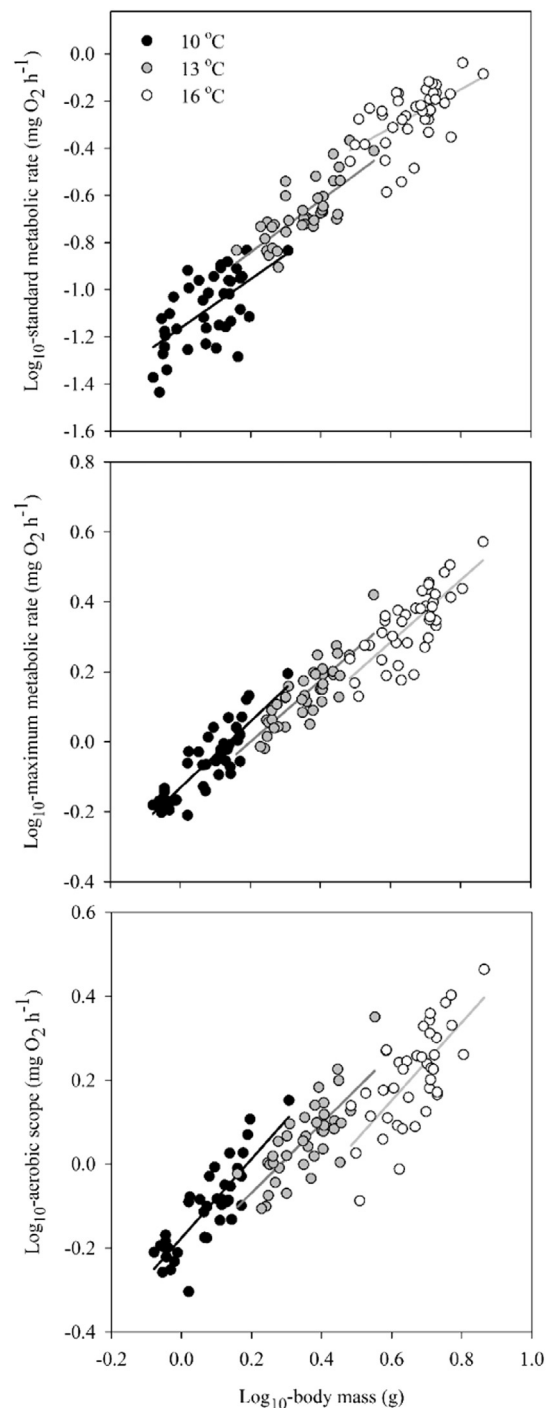

Fig. 1. Log_{10}-transformed standard metabolic rate, maximum metabolic rate, and aerobic scope as function of log_{10}-transformed body mass in juvenile brown trout (*Salmo trutta*) at three consecutive test temperatures. For fish of a given body mass, standard metabolic rate increased across the test temperatures whereas maximum metabolic rate and aerobic scope showed a decrease.

$p = 0.001$), maximum metabolic rate ($R = 0.43$, $\chi^2 = 19.16$, $p < 0.001$), and aerobic scope ($R = 0.42$, $\chi^2 = 18.33$, $p < 0.001$). In addition, all metabolic traits were repeatable between consecutive temperatures with the exception of aerobic scope that was not repeatable between 10 and 16 °C (Fig. 3). However, the repeatability of all metabolic traits was generally lower over longer periods of time as temperatures increased (Fig. 3).
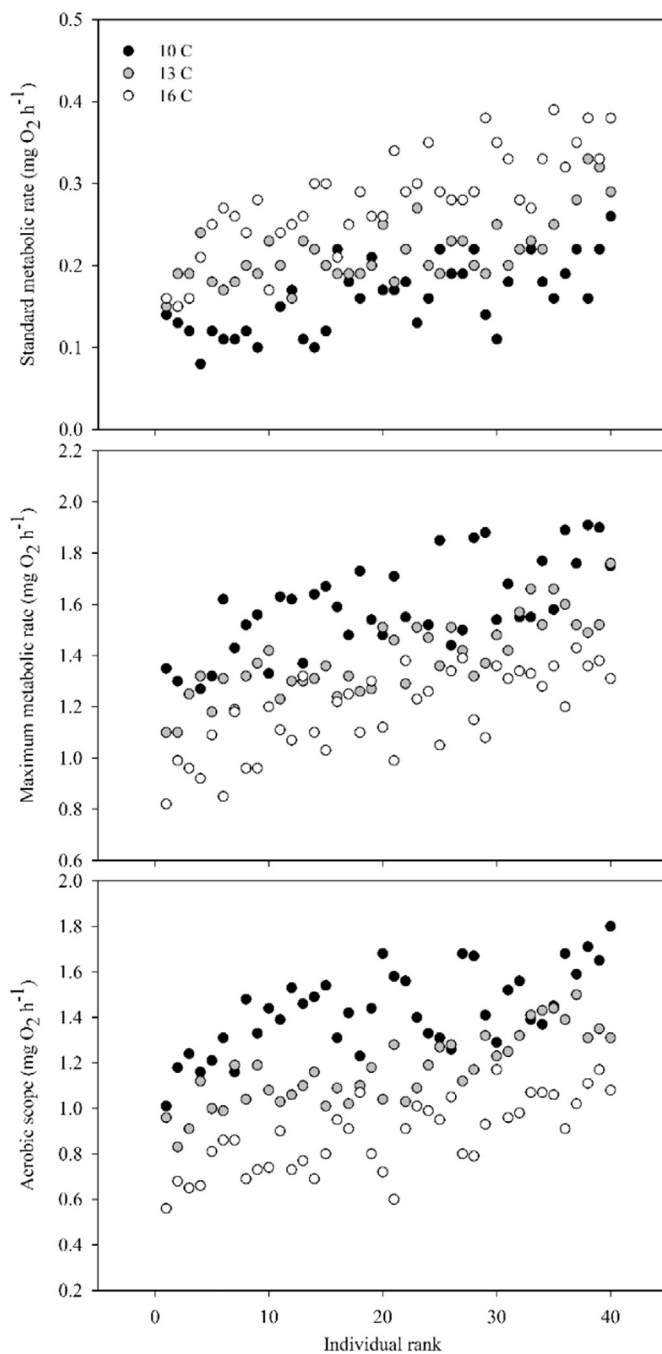
Fig. 2. Individual variation and thermal repeatability in standard metabolic rate, maximum metabolic rate, and aerobic scope of juvenile brown trout (*Salmo trutta*) across three consecutive test temperatures. Individuals are ordered along the x-axis according to their ranked mean value for each metabolic trait across the three temperatures. For each metabolic trait, the data points for the three temperatures increase from left to right in parallel, indicating repeatable differences among individuals. Note that individuals were ranked separately for each trait. Plotted are back-transformed partial residuals standardized for the mean body mass of 2.29 g.

4. Discussion

Mass-independent standard metabolic rate increased while maximum metabolic rate and aerobic scope decreased with increasing temperature, as reported for other salmonids during the summer when they are within the upper range of their thermal tolerance zone (Lee et al., 2003; Eliason et al., 2011). In addition, all three metabolic traits were repeatable overall as well as between consecutive temperatures; individuals with a high metabolic rate at one temperature tended to have a high metabolic rate at the other temperatures. These results demonstrate that when juvenile fish experience increasing temperatures over the growing season, their metabolic rates are generally repeatable over both short and longer time intervals.

While the repeatability of metabolic rate has generally been assayed under constant temperature conditions (White et al., 2013; Auer et al., 2016a), there are a few published estimates of thermal repeatability with which to compare our results. Estimates of overall repeatability found over 10-day intervals of changing temperature in a salamander species (Careau et al., 2014) are similar to those found here (Fig. 3) for standard metabolic rate ($R = 0.34$) but lower for maximum metabolic rate ($R = 0.34$) and aerobic scope ($R = 0.34$). Seppänen et al. (2010) also reported that the standard metabolic rate of juvenile Atlantic salmon was repeatable across an 8 month interval during which temperature decreased from 13.9 to 10 °C, but not during an earlier 6 month interval when temperatures increased from 2.7 to 13.9 °C. The repeatability of metabolic rate generally declines with time under laboratory and more variable field conditions (White et al., 2013; Auer et al., 2016a). As such, the repeatabilities that we report may have been substantially lower had we measured metabolic rates at longer intervals and/or greater changes in temperature.

Repeatability estimates for maximum metabolic rate and aerobic scope were generally higher than for standard metabolic rate. These differences could arise due to dissimilar errors associated with their respective measurements. Alternatively, repeatabilities may vary among metabolic traits because they reflect different underlying processes, as has been found for various measures of locomotor performance (Austin and Shaffer, 1992). While measures of maximum metabolic rate necessarily incorporate energy utilization characterizing an organism's standard metabolic rate, the two traits are not necessarily functionally linked to one another: individual variation in standard and maximum metabolic rate are generally (Auer et al., 2017) but not always correlated (Gomes et al., 2004). Standard metabolic rate has been found to vary more with daily energy expenditure than maximum metabolic rate (Auer et al., 2017) and the two traits may not exhibit parallel responses to selection (Książek et al., 2004; Gębczyński and Konarzewski, 2009; Auer et al., 2017). Individuals may therefore differ in how their maximum metabolic rate and aerobic scope change over time and with increasing temperature without showing correlated changes in their standard metabolic rate.

Understanding how metabolic rates change in response to variable environments is critical to our ability to predict the long-term performance of individuals. However, the link between metabolic rate and different components of fitness often depends on environmental conditions (Burton et al., 2011; Mathot and Dingemanse, 2015). For example, the relative standard metabolic rate of young Atlantic salmon is indicative of the age at which they will undertake their seaward migration if held under constant conditions (McCarthy, 2000), but not under variable temperatures (Seppänen et al., 2010). It is therefore important that we understand not just the repeatability of metabolic rates in one specific environment but also whether among-individual differences in metabolic rates are consistent across different environmental conditions. Additionally, more work is needed to examine how these differences impact individual performance both within and across seasons. This is especially relevant and timely given current global climate change and the role that energy metabolism is thought to play in determining an organism's capacity to cope with increasing temperatures and rapid environmental change (Somero, 2010; Hoffmann and Sgrò, 2011).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cbpa.2017.11.021.
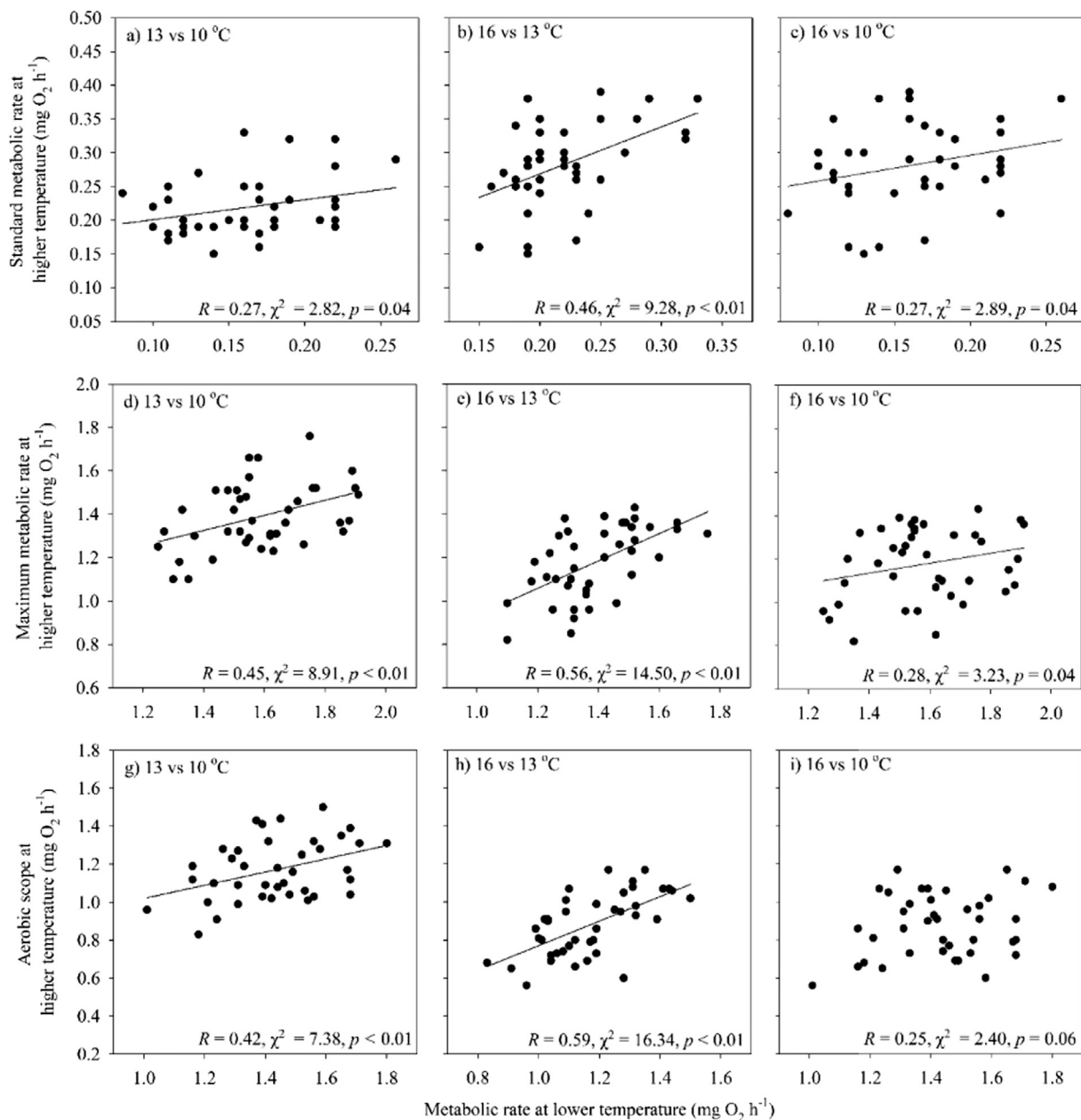
Fig. 3. Repeatability (R) of (a–c) standard metabolic rate, (d–f) maximum metabolic rate, and (g–i) aerobic scope of juvenile brown trout (*Salmo trutta*) across three consecutive test temperatures. *P*-values for each χ^2 test were halved since models were testing whether the between-individual variance > 0 (see text for details). Plotted are back-transformed partial residuals standardized for the mean body mass of 2.29 g.

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