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The optimal combination of standard metabolic rate and aerobic scope for somatic growth depends on food availability

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Summary

1. Metabolic rates can vary as much as threefold among individuals of the same size and age in a population, but why such variation persists is unclear given that they determine the energetic cost of living. Relationships between standard metabolic rate (SMR), growth and survival can vary with environmental conditions, suggesting that the fitness consequences of a given metabolic phenotype may be context-dependent. Less attention has focused on the link between absolute aerobic scope (AS, the difference between standard and maximum metabolic rate) and fitness under different environmental conditions, despite the importance of aerobic scope to an organism's total energetic capacity.

2. We examined the links between individual variation in both SMR and AS and somatic growth rates of brown trout (*Salmo trutta*) under different levels of food availability.

3. Standard metabolic rate and AS were uncorrelated across individuals. However, SMR and AS not only had interactive effects on growth, but these interactions depended on food level: at *ad libitum* food levels, AS had a positive effect on growth whose magnitude depended on SMR; at intermediate food levels, AS and SMR had interactive effects on growth, but at the low food level, there was no effect of either AS or SMR on growth. As a result, there was no metabolic phenotype that performed best or worst across all food levels.

4. These results demonstrate the importance of aerobic scope in explaining somatic growth rates and support the hypothesis that links between individual variation in metabolism and fitness are context-dependent.

5. The larger metabolic phenotype and the environmental context in which performance is evaluated both need to be considered in order to better understand the link between metabolic rates and fitness and thereby the persistence of individual variation in metabolic rates.

Key-words: aerobic scope, energy metabolism, fitness, intraspecific variation, maximum metabolic rate, somatic growth, standard metabolic rate

Introduction

Metabolic rate determines the energetic cost of living and, as such, is a fundamental trait underlying organismal performance (Hulbert & Else 2000). At the very minimum, an animal must expend energy on the maintenance of tissues and homeostatic mechanisms needed to sustain life (Fry 1971). This is referred to as standard metabolic rate (SMR) in ectotherms and basal metabolic rate in endotherms. After meeting these baseline energy requirements, an individual can allocate excess energy to other functions such as growth and reproduction but within the upper bounds set by its maximum metabolic rate (MMR), the maximum rate at which oxygen can be supplied to tissues and ATP can be produced (Fry 1971). Both SMR and MMR are to some extent heritable (Nilsson, Åkesson & Nilsson 2009; Wone *et al.* 2009), and their relative values (i.e. rank order among individuals) are generally repeatable through time (Nespolo & Franco 2007). However, they also vary considerably among individuals within a

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population, some individuals having 2–3 times the metabolic rate of others, even after correcting for the effects of size, age and sex (Burton *et al*. 2011).

Metabolic rates are thought to have important impacts on fitness, but their expected consequences are unclear. On the one hand, a higher SMR may confer a fitness advantage if it maintains a larger 'metabolic machinery' that facilitates a higher MMR and thereby higher resource intake rates (Biro & Stamps 2010). Under this 'increased intake' hypothesis, SMR is expected to have a positive effect on fitness (Burton *et al*. 2011). On the other hand, SMR is energetically expensive, constituting up to 50% of an individual's daily expenditure (Nagy, Girard & Brown 1999), so a lower SMR may actually be more adaptive because a greater excess of resources can then be directed to other functions such as growth and reproduction (Wieser 1994). This latter hypothesis, referred to as the 'compensation' hypothesis, predicts that SMR will be negatively correlated with fitness (Burton *et al*. 2011).

Individual differences in SMR have been linked to several fitness measures, but results thus far are equivocal. In some cases, SMR is positively associated with growth (McCarthy 2000), reproduction (Sadowska, Gębczyński & Konarzewski 2013) and survival or life span (Jackson, Trayhurn & Speakman 2001; Niitepold & Hanski 2013) thereby supporting the 'increased intake' hypothesis. However, other studies report negative associations between SMR and growth (Norin & Malte 2011), reproduction (Blackmer *et al*. 2005) and survival (Artacho & Nespolo 2009) that support the 'compensation' hypothesis. The association between SMR and fitness is therefore not as straightforward as that postulated by either the 'increased intake' or 'compensation' hypotheses.

Inconsistencies among previous results may occur because the association between SMR and fitness varies with environmental conditions. For example, laboratory experiments in juvenile Atlantic salmon (*Salmo salar*) demonstrate a positive association between SMR and growth, but only under conditions where food is offered *ad libitum or* is easy to locate and acquire because of lower population densities or simpler habitat structure (Reid, Armstrong & Metcalfe 2011, 2012). Similarly, larvae of a marine fish (*Ulvaria subbifurcata*) with higher estimated embryonic SMR had a relatively shorter life span, but only under low food levels (Bochdansky *et al*. 2005). The link between SMR and components of fitness is also known to vary with conditions in the wild. Correlations between SMR and growth and survival in juvenile salmonid fishes (*S. salar* and *S. trutta*) have been found to be positive, negative or nonsignificant depending on which stream they are measured in, even when the genetic make-up of individuals does not differ across streams (Álvarez & Nicieza 2005; Robertsen *et al*. 2014). These studies suggest that the fitness consequences of a given SMR are context-dependent.

Consideration of aerobic scope (AS), in addition to SMR, may also improve our understanding of the links between energy metabolism and fitness. Aerobic scope is bounded by an individual's MMR and SMR and determines the extent to which metabolic rate can be increased above baseline energy requirements to finance key functions such as digestion, locomotion, growth and reproduction (Guderley & Pörtner 2010). Hypotheses for how metabolic rates should impact fitness have focused on variation in SMR and have generally ignored MMR and AS despite their importance to an organism's total energetic capacity (Burton *et al*. 2011). Variation in AS among species and populations has been linked to differences in geographic distributions (Naya & Bozinovic 2012), ability to cope with environmental extremes (Pörtner & Knust 2007; Kassahn *et al*. 2009) and migratory effort (Tudorache, Blust & De Boeck 2007; Eliason *et al*. 2011), suggesting that it might be a trait of ecological relevance. Aerobic scope is also known to vary considerably among individuals. While the 'increased intake' hypothesis assumes a positive correlation between SMR and MMR (Biro & Stamps 2010), there is increasing evidence that the association between these two metabolic traits is not as strong as previously thought and that, even when they are positively related, there is still considerable individual variation in MMR and thus AS for a given SMR (Wone *et al*. 2009; Norin & Malte 2012; Huang *et al*. 2013). This individual variation in AS might be expected to have important consequences for fitness, but remains largely unexplored. Furthermore, SMR and AS may have interactive effects on organismal performance such that both traits need to be considered as part of a larger metabolic phenotype in order to fully understand the link between energy metabolism and fitness.

Here, we test how intraspecific variation in somatic growth rates of juvenile wild-origin brown trout (*S. trutta*) under different levels of food availability relates to variation in their SMR and/or AS to assess whether the performance of different metabolic phenotypes depends on environmental conditions. In juvenile salmonid fishes, larger body size often confers an advantage in competition over feeding sites (Johnsson, Nöbbelin & Bohlin 1999) and survival (Einum & Fleming 1999; Carlson, Olsen & Vøllestad 2008), so early growth rates may have important consequences for fitness. However, growth is highly dependent on food availability which can exhibit pronounced and unpredictable spatial and temporal variation in the freshwater streams they inhabit (Martin-Smith & Armstrong 2002). As such, we might expect the performance advantage of different metabolic phenotypes to differ across food levels. Individuals with higher SMR and higher AS might grow faster at high food levels since they can digest meals faster (Millidine, Armstrong & Metcalfe 2009), and their higher postprandial response might permit them to consume larger meal sizes (Carter & Brafield 1992), respectively. In contrast, fish with a low SMR and low AS might fare better under low food conditions where lower energy costs are advantageous (Killen, Marras & McKenzie 2011).

Materials and methods

FISH COLLECTION AND REARING

Young of the year brown trout (n = 120) were caught by electrofishing in a tributary to the River Endrick, Scotland in August 2013. Fish were transported to the University of Glasgow where they were held in a 400-litre tank and allowed to acclimate for one month in a temperature controlled room (11·5 ± 1 °C; mean ± actual range) with a 12L:12D cycle. In September 2013, 120 fish were transferred to individual compartments in two separate recirculating stream tank systems. Individual compartments (60 per stream system; 190 × 130 × 200 mm) within each stream were separated by a fine mesh net (1·5 mm^2) that stopped food from floating downstream from one compartment to the next. During this acclimatization phase, fish were placed on an intermediate food ration level of INICIO Plus trout pellets (BioMar Ltd, Grangemouth, UK) based on their body size and fed individually twice daily (see definition of intermediate ration and determination of food levels in Appendix S1, Supporting information). Fish were then measured every 2–3 weeks until the start of the experiment to adjust feeding rations to changes in their body size. Faecal matter and water were siphoned from each tank twice daily (5–10% water change) before each feeding session to maintain water quality.

RESPIROMETRY

Standard metabolic rate

Standard (SMR) and maximum (MMR) metabolic rates were measured in December 2013. Specific dynamic action, that is the energetic costs of digestion, leads to an elevation in metabolic rate (Secor 2009), so fish were not fed for 48 h prior to measurements. This time frame has been shown to be long enough for salmonid fish on intermediate food levels to evacuate their guts at the test temperature (Higgins & Talbot 1985).

Standard metabolic rates were measured using continuous flow-through respirometry (see Appendix S2, Supporting information for full details). Fish were placed in the respirometry chambers in the afternoon, and their oxygen consumption was measured continuously over the next 20 h (from roughly 1400–1000 h). Flow rate was set at 2.1 L h^{-1} for the first 3 h while the fish settled down but was then reduced to 1.47 L h^{-1} for the remainder of the measurement period. These flow rates allowed us to detect oxygen consumption rates of the fish but ensured that oxygen levels in the chambers always remained above 80% saturation. This method of measuring SMR was found to be repeatable over a one-month time period (Spearman's rho = 0·71, n = 37 fish, $P < 0{\cdot}01$).

The system permitted the simultaneous continuous measurement of oxygen consumption rates of 15 fish each day (a total of 8 batches over 9 days), with a fish-free chamber serving as a control measure of background respiration. Standard metabolic rate (mg O_2 h^{-1}) was measured as

$$M_{O2} = V_w \times (C_{wO_2}\text{control} - C_{wO_2}\text{fish})$$

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, after adjusting for temperature and barometric pressure (Clark, Sandblom & Jutfelt 2013). SMR 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, that is those measurements below two standard deviations from this mean (Clark, Sandblom & Jutfelt 2013).

Maximum metabolic rate and aerobic scope

Maximum metabolic rate (MMR) was elicited by exhaustive exercise, and excess post-exercise oxygen consumption was measured immediately afterwards using intermittent flow-through respirometry since this is more sensitive to rapid changes in oxygen consumption. More specifically, each fish was placed in a 42-cm-diameter circular bucket after measurement of its SMR, and it was chased in circles to exhaustion (usually <2 min) against a circular current (600 L h^{-1}) created by a short length of curved tubing attached to a pump in the centre of the bucket (Norin & Malte 2012). Water temperature in the chase bucket was maintained at 11·5 °C by a chiller. Fish were determined to be exhausted when they could no longer swim and did not resist being picked up by hand, that is they were unresponsive. After exhaustion, fish were transferred within 15 s to a 400-mL glass respirometry chamber submerged in a water bath maintained at 11·5 °C by a chiller. Water in this system flowed at a rate of 12 L h^{-1} through the respirometry chamber, oxygen-impermeable Tygon tubing, and then past an oxygen sensor sealed in a small glass chamber before being recirculated via additional lengths of tubing back to the respirometry chamber by a peristaltic pump. Each fish was left in the respirometry chamber for 6 min, and its oxygen consumption measured (see Appendix S2 for details of software and oxygen sensors). The fish was then removed from the chamber, anaesthetized in a mild solution of benzocaine (40 mg L^{-1}), and its body mass (±1 mg) and fork length (±0·1 mm) were measured before it was returned to its stream tank. The respirometry chamber was emptied of deoxygenated water, refilled, and a flush pump connected via tubing to one end of the respirometry chamber was then turned on to flush the whole system of deoxygenated water before measuring MMR in the next fish.

Maximum metabolic rate (mg O_2 h^{-1}) was calculated for each fish using the equation:

$$M_{O2} = (V_r - V_f) \times \Delta C_{wO_2}/\Delta t$$

where V_r is the volume of the respirometry system (chamber and tubing = 0·41 L) and V_f is the volume of the fish (L) assuming 1 g of fish is equivalent to 1 ml of water. $\Delta C_{wO2}/\Delta t$ is the rate at which the oxygen concentration decreased over the 5-min time period (mg O_2 L^{-1} h^{-1}), after adjusting for changes in temperature and barometric pressure. Slopes for the decline in oxygen concentration were derived for each fish from linear regressions of oxygen concentration against time over a 5-min period starting after the ~30 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. This method of eliciting maximum metabolic rate was found to be repeatable over a one-month time period (Spearman's rho = 0·33, n = 37 fish, P = 0·04). Absolute aerobic scope for each fish was calculated as the difference (mg O_2 h^{-1}) between its maximum and standard metabolic rate (AS = MMR-SMR).

FEEDING REGIME AND GROWTH MEASUREMENTS

After measurement of metabolic rates, each fish was returned to its compartment in the stream tank and assigned to one of three rations of trout pellets – low, intermediate and *ad libitum* – for the next two weeks. The three ration levels were determined using equations from Elliott (1976) that describe the growth of brown trout as a function of caloric intake, temperature and initial body size and calculated individually for each fish based on its weight (see Appendix S1 for details).

Individual fish in each batch of 15 were randomly assigned to a food level but under the condition that fish differing in

body length and mass-independent SMR and AS (see derivation in data analyses section below) were evenly distributed across the three food levels and that an equal number of fish from each batch was assigned to each food level. Fish were then fed twice daily, once in the early morning and once in the late afternoon to mimic twice-daily pulses in food observed in the wild (Elliott 1970; Martin-Smith & Armstrong 2002). They were then allowed 1 h to consume each meal before leftover food and faecal matter were siphoned from their tanks. The fork length and body mass of each fish were measured again after one week, and rations were adjusted to account for increases in body size. Additionally, consumption rates of fish on the *ad libitum* food level were monitored on a daily basis, and their rations adjusted upwards whenever fewer than 5 pellets remained in their tanks one hour after a meal. These adjustments kept their rations at *ad libitum* levels for the duration of the experiment. Fork length was measured at the end of the second week, and specific daily growth rate over the two-week growth period was calculated as $100 \times [\log_e (\text{final fork length}) - \log_e (\text{initial fork length})]/14$ days.

DATA ANALYSES

We first examined the relationships between body mass and SMR, MMR and AS using regression analyses. Body mass and metabolic rates were $\log_{10}$-transformed prior to analyses to normalize and linearize the data. Residuals (rSMR, rMMR and rAS) generated from each of these analyses differentiated those individuals with higher than expected SMR, MMR and AS for their body size, that is those with positive residuals, from those who had metabolic rates that were lower than expected, that is those with negative residuals. Since body mass can influence both metabolism and growth rates, these estimates of mass-independent metabolic rates were used in subsequent analyses.

We then used correlation analysis to test whether rMMR and rAS were correlated with rSMR. Finally, we examined the links between metabolic traits and growth rates at different food levels using a mixed model approach. The model included specific growth rate as the dependent variable, food level as a categorical effect, and rSMR and rAS as continuous predictors. Log_e-transformed initial fork length was centred on the mean (4·5 mm) and included as a continuous covariate to control for effects of body size on growth rate. Stream system and batch number ($n = 15$ fish per group) nested within stream system were included as random effects to control for spatial position in the aquarium room and the timing in which fish entered the experiment, respectively. Error variances differed among the three food treatments ($\chi^2 = 16{\cdot}21$, d.f. = 3, $P < 0{\cdot}01$), so their errors were modelled separately. Output from the model revealed complex 3-way interactions between the three predictors (food × rSMR × rAS), so the effects of SMR and AS were further evaluated at each food level by testing whether their individual and interactive effects at each food level differed from zero. To ease interpretability, results are presented graphically as the mean growth rates of individuals categorized as being one of four metabolic phenotypes (high SMR/low AS, high SMR/high AS, low SMR/low AS and low SMR/high AS) based on whether their rSMR and rAS lay below or above zero.

The regression, correlation and mixed model analyses above were conducted using the REG, CORR and MIXED procedures in SAS version 9.3 (SAS Institute, Cary, NC, USA), respectively. It should be noted that while our experiment assessed only correlations and not causal links between metabolic traits and growth, we refer to metabolic traits (SMR and AS) as 'effects' because they were included as predictors of growth in our statistical model. Differences among treatment groups and effects of metabolic rates were considered significant when $P < 0{\cdot}05$. All means given are ±1 SE.

Results

Fork length ranged from 78·5 to 103·1 mm (mean: 91·1 ± 0·5 mm) across individuals at the start of the experiment but did not differ between fish subsequently assigned to the three food treatment groups ($F_{2,117} = 0{\cdot}099$, $P = 0{\cdot}91$). The same was true for starting body mass (range: 5·37–12·67 g; mean: 8·45 ± 0·13 g; comparison of food treatment groups: $F_{2,117} = 0{\cdot}020$, $P = 0{\cdot}98$). Log_{10}-transformed SMR, MMR and AS all increased with $\log_{10}$-transformed body mass (Table 1) and differed up to twofold among individuals of the same body mass (Fig. 1). After correcting for body mass, SMR ($F_{2,117} = 0{\cdot}13$, $P = 0{\cdot}88$) and AS ($F_{2,117} = 0{\cdot}53$, $P = 0{\cdot}59$) did not differ between fish subsequently assigned to the 3 food treatments. A fish's rMMR and rSMR were positively correlated (Fig. 2; $r = 0{\cdot}26$, $n = 120$, $P = 0{\cdot}01$). In contrast, there was no relationship between a fish's rSMR and its rAS (Fig. 3; $r = 0{\cdot}07$, $n = 120$, $P = 0{\cdot}43$).

Table 1. Parameters (±1 SE) from regression analyses of $\log_{10}$-transformed metabolic rates (mg O_2 h^{-1}) as a function of $\log_{10}$-transformed body mass (M, g), $\log M_{O2} = \log a + b \log M$

	log*a*	*b*	r^2	*P*
Standard metabolic rate	−0·85 ± 0·07	0·85 ± 0·08	0·512	<0·001
Maximum metabolic rate	−0·02 ± 0·06	0·82 ± 0·06	0·600	<0·001
Aerobic scope	−0·09 ± 0·07	0·81 ± 0·07	0·526	<0·001

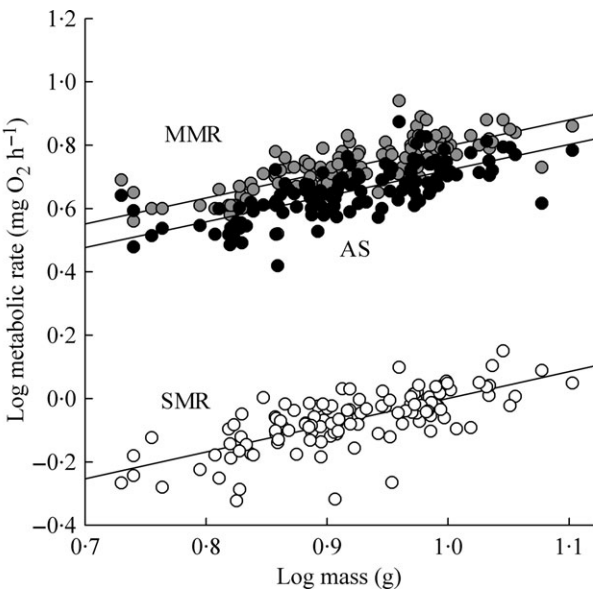

Fig. 1. Relationships between $\log_{10}$-transformed standard metabolic rate (SMR), maximum metabolic rate (MMR), aerobic scope (AS) and body mass (g) of juvenile brown trout. See Table 1 for regression equations.

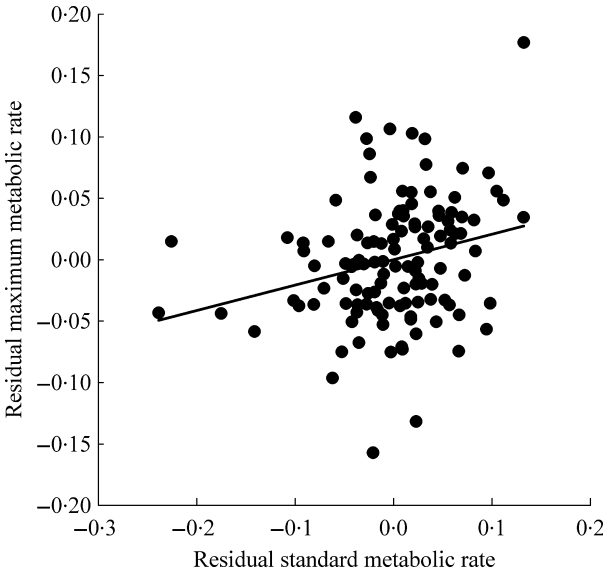

Fig. 2. Relationship between residual maximum metabolic rate (MMR, mg O_2 h^{-1}) and residual standard metabolic rate (SMR, mg O_2 h^{-1}) in juvenile brown trout. Residuals were generated from linear regressions of $\log_{10}$-transformed MMR and $\log_{10}$-transformed SMR on $\log_{10}$-transformed body mass (g).

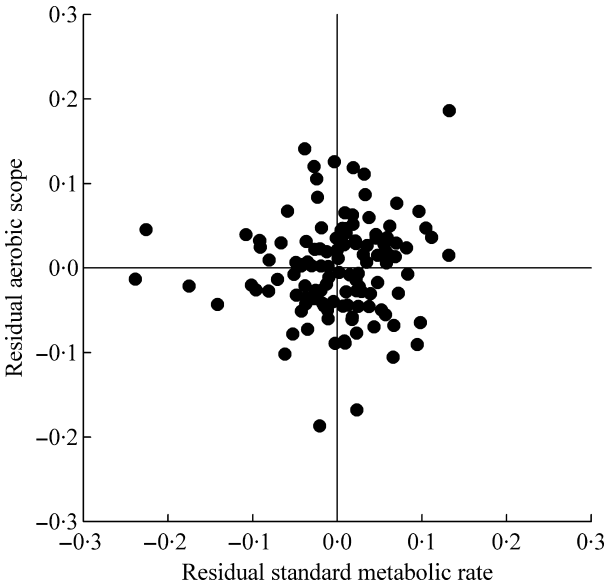

Fig. 3. Relationship between residual aerobic scope (mg O_2 h^{-1}) and residual standard metabolic rate (mg O_2 h^{-1}) in juvenile brown trout. Residuals were generated from linear regressions of $\log_{10}$-transformed aerobic scope (AS) and $\log_{10}$-transformed standard metabolic rate (SMR) on $\log_{10}$-transformed body mass (g). A positive residual value indicates that an individual had an AS or SMR higher than expected for its body mass, while those individuals with negative residual values were those that had a lower AS or SMR for their body mass. Together, residuals for AS and SMR distinguished individuals as having one of four different metabolic phenotypes (high SMR/low AS, high SMR/high AS, low SMR/low AS and low SMR/high AS).

Not surprisingly, food level had a positive effect on growth over the two-week growth period ($F_{2,107} = 161{\cdot}4$, $P < 0{\cdot}001$), but growth varied up to fivefold among individuals from the same food treatment (low food levels: 0·05–0·26 mm day^{-1}; intermediate: 0·15–0·49 mm day^{-1}; *ad libitum*: 0·15–0·61 mm day^{-1}). Standard metabolic rate and aerobic scope both influenced growth (SMR: $F_{1,107} = 5{\cdot}28$, $P = 0{\cdot}02$; AS: $F_{1,107} = 4{\cdot}46$, $P = 0{\cdot}03$), but they also had interactive effects that depended on food level (Fig. 4; SMR x AS: $F_{1,107} = 0{\cdot}59$, $P = 0{\cdot}44$; SMR x food: $F_{2,107} = 1{\cdot}19$, $P = 0{\cdot}31$; AS × food: $F_{2,107} = 6{\cdot}54$, $P < 0{\cdot}01$; SMR × AS × food: $F_{2,107} = 6{\cdot}81$, $P < 0{\cdot}01$) after controlling for the positive effects of initial fork length ($F_{1,107} = 4{\cdot}27$, $P = 0{\cdot}04$). At the low food level, there was no effect of SMR or AS on growth (Table 2, Fig. 4). However, at the intermediate food level, there was an interactive effect of SMR and AS such that growth was greatest in individuals with a low SMR and low AS, followed by those with a high SMR and high AS, and lowest in the remaining two categories (Table 2, Fig. 4). At the *ad libitum* food level, SMR and AS also had interactive effects on growth whereby individuals with a higher AS grew faster than individuals with a low AS, but among individuals with a low AS, those with a low SMR grew particularly slowly relative to those with a high SMR (Table 2, Fig. 4).

Table 2. Parameter estimates from linear mixed model of the effects of standard metabolic rate (SMR, mg O_2 h^{-1}) and aerobic scope (AS, mg O_2 h^{-1}) on specific growth rate (% day^{-1}) of brown trout at three different food levels

Food level	Estimate ± 1SE	*t*	*P*
Low			
Intercept	0·17 ± 0·02	11·27	<0·001
SMR	0·23 ± 0·14	1·59	0·11
AS	−0·07 ± 0·12	−0·55	0·58
SMR × AS	−2·11 ± 1·87	−1·13	0·26
Intermediate			
Intercept	0·35 ± 0·02	18·18	<0·001
SMR	0·06 ± 0·21	0·30	0·76
AS	−0·15 ± 0·25	−0·61	0·54
SMR × AS	13·00 ± 5·5	2·35	0·02
Ad libitum			
Intercept	0·45 ± 0·02	22·20	<0·001
SMR	0·60 ± 0·28	2·15	0·03
AS	1·13 ± 0·32	3·53	<0·001
SMR × AS	−17·37 ± 6·11	−2·84	<0·01

Discussion

Studies to date on the relationship between metabolic rate and different fitness components such as growth and survival have tended to focus on SMR, but the importance of AS and its interactions with SMR has received less attention. Here, we show that SMR and AS are not correlated. Additionally, not only did they have complex links with growth rates, but the magnitude and direction of their interactions also depended on food level.

Aerobic scope had important effects on growth rate. AS had a positive effect at *ad libitum* food levels that

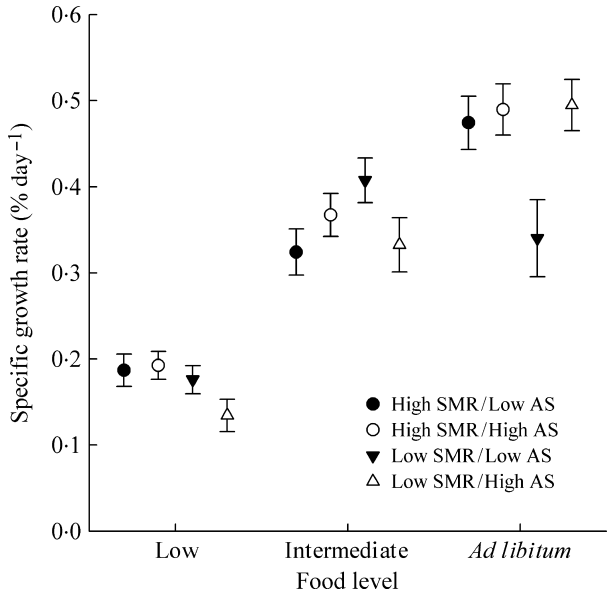

Fig. 4. Mean specific growth rates of four metabolic phenotypes (see Fig. 3) of juvenile brown trout at three different food levels. Shown are partial residuals after accounting for variation in fish fork length (mm). Data plotted as mean ± 1 SE (n = 5–12 fish per phenotype per food level). See text for statistical analyses.

also depended on SMR, interactive effects with SMR at intermediate food levels and no effect at low food levels. These positive effects at *ad libitum* food levels may arise because of links between MMR, digestive and assimilative capacity, and growth rates. Specific dynamic action (SDA) – the cumulative energy expenditure needed for the ingestion, digestion, absorption and assimilation of a meal (Secor 2009) – is positively correlated with meal size (Millidine, Armstrong & Metcalfe 2009) and can account for increases in metabolic rate of up to 60–80% of MMR in salmonids (Alsop & Wood 1997). SDA is often positively correlated with growth rate (Claireaux & Lefrançois 2007), likely because protein synthesis and deposition required for growth can constitute up to 40% of the SDA response (Lyndon, Houlihan & Hall 1992; Carter & Houlihan 2001). However, there is evidence in salmonids that the MMR elicited by exercise sets the upper limits of oxygen consumption for all processes including the SDA response and can lead to trade-offs between SDA and other functions such as swimming (Alsop & Wood 1997; Thorarensen & Farrell 2006). Food was offered for only one hour during each feeding session in our experiment, so only fish with a large AS may have been able to take full advantage of the *ad libitum* food rations. This can only be hypothesized at present since we did not explicitly measure SDA or the quantity of food consumed by each fish, but warrants further attention.

SMR also had complex links with growth rate. The 'increased intake' and 'compensation' hypotheses predict that SMR will be positively and negatively correlated with fitness, respectively, while the 'context-dependent' hypothesis predicts that the fitness consequences of a given SMR will vary between environments (Burton *et al.* 2011). This latter hypothesis would suggest that a high SMR would be advantageous at higher food levels, while individuals with a lower SMR might fare better at lower food levels since by definition they have lower maintenance costs (Burton *et al.* 2011). We did not find direct support for any of these hypotheses relating SMR to growth. Rather, we found that SMR and AS had interactive effects on growth at intermediate and *ad libitum* food levels, but were not linked to growth at the low food level.

Linkages between SMR and AS and growth may depend on how these two metabolic traits change in response to different environmental conditions. While individuals tend to maintain their *relative* rates of standard and maximum metabolism, and thereby AS, over time (Nespolo & Franco 2007), the *absolute* rates of metabolism in ectotherms are also flexible and can change dramatically as a function of abiotic factors such as temperature and hypoxia (Pörtner & Knust 2007; Clark, Sandblom & Jutfelt 2013). SMR but not MMR has been shown to increase in response to food availability in salmonids (Van Leeuwen, Rosenfeld & Richards 2011, 2012), and individuals are known to differ in the degree to which their SMR changes as a function of food level (O'Connor, Taylor & Metcalfe 2000; Fu, Xie & Cao 2005). Variation among individuals in their metabolic responses to the different food levels might therefore explain why some metabolic phenotypes grew better than others at different food levels, but further research is needed to assess individual variation in metabolic flexibility and how it impacts growth under different food conditions.

There was a positive correlation between SMR and MMR after controlling for the effects of body mass, but this relationship was weak; individuals exhibited large differences in rMMR even for the same rSMR. A positive correlation is assumed under the 'increased intake' hypothesis because SMR is thought to reflect the idling costs of the metabolic machinery needed to fuel physiological and behavioural processes above the minimum required to sustain life (Biro & Stamps 2010). There is some support for this mechanistic link in fish (Norin & Malte 2012; Huang *et al.* 2013) and other animals (Rezende *et al.* 2009; Wone *et al.* 2009). However, there is also evidence that correlations between these two traits can depend on both evolutionary history and current environmental conditions. For example, negative, nonsignificant and positive relationships between intraspecific variation in SMR and MMR reported for closely related anuran species can be explained by species' differences in their ecology and behaviour (Gomes *et al.* 2004). In addition, other studies show that positive correlations, albeit between resting metabolic rate and daily energy expenditure, can arise simply because both metabolic traits are independently influenced by common environmental or individual factors such as food availability or reproductive status (Speakman *et al.* 2003; Careau *et al.* 2013). In our study of juvenile trout, where individual and environmental differences were mini-

mized by standardized conditions, we still observed a positive relationship between SMR and MMR. Since fish were collected from the wild though, we cannot rule out that individual histories, such as early conditions, played a role in influencing both SMR and MMR in similar ways. Clearly, more research is needed to ascertain the links between these different, yet equally important, aspects of energy metabolism.

Similar to patterns reported in other studies (Nespolo, Lardies & Bozinovic 2003; Steyermark *et al*. 2005; Norin & Malte 2012), we found a considerable degree of variation in SMR, MMR and AS among the group of brown trout we studied. Previous studies have demonstrated that the fitness advantages of a given SMR can depend on habitat structure, population density and the predictability of food (Reid, Armstrong & Metcalfe 2011, 2012). Here, we show that the growth performance of individuals under different food levels is linked not just to SMR but its interactive effects with AS. As a result, different phenotypes performed better at different food levels, and there was no phenotype that performed best or worst across all food levels. These laboratory experiments, together with field studies showing spatial variation in the correlation between SMR and fitness measures (Álvarez & Nicieza 2005; Robertsen *et al*. 2014), support the hypothesis that variation in these metabolic traits may be maintained by environmental variation that favours different phenotypes in different habitats or at different times within and across years (Burton *et al*. 2011).

Organisms in the wild must cope with simultaneous changes in a diversity of environmental factors, so the main and interactive effects of AS and SMR under different conditions such as temperature or hypoxia warrant further attention. Additionally, more work is needed to better understand the mechanisms underlying these interactions. Overall, the larger metabolic phenotype and the environmental context in which performance is evaluated both need to be considered in order to better understand the link between metabolic rates and components of fitness and thereby the persistence of different metabolic phenotypes.

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Data accessibility

Data is available in Appendix S3 in the online supporting information.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Equations used to calculate rations for each of the three food levels

Appendix S2. Description of respirometry system used to measure standard metabolic rates

Appendix S3. Data used in analyses of metabolic rates and growth