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Article

Standard metabolic rate differs between rainbow trout (*Oncorhynchus mykiss*) growth forms

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Abstract

In variable environments, repeatable phenotypic differences between individuals provide the variation required for natural selection. The pace-of-life syndrome (POLS) provides a conceptual framework linking individual physiology and life histories to behaviour, where rapidly growing individuals demonstrate higher rates of resting or "standard" metabolic rate (SMR). If differences in SMR are consistent between fast- and slow-growing individuals, these differences may be important to capture in bioenergetic relationships used to describe their growth, energy acquisition, and allocation. We compared growth rates and SMR between a domesticated and wild strain of rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) using intermittent flow respirometry. Though mass-scaling exponents were similar between strains, mass-scaling coefficients of SMR for fast-growing rainbow trout were 1.25 times higher than those for slower growing fish. These observed differences in mass-scaling coefficients between fast- and slow-growing rainbow trout were consistent with data extracted from several other studies. Bioenergetic estimates of consumption for domestic strain fish increased as the difference in SMR and wild strain fish increased, and increased as activity level increased. Our results indicate patterns of SMR consistent with POLS, and suggest that strain-specific SMR equations may be important for applications to active populations (i.e., field observations).

Key words: Salmonidae, bioenergetics, resting metabolism, personality, metabolic allometry, *Oncorhynchus mykiss* (Walbaum, 1792)

Introduction

The importance of within-population individual genotypic and phenotypic variation in relation to behavioural and physiological processes is the material on which natural selection acts in the process of evolution. In some circumstances, the existence of variable selective processes can lead to the expression of distinct trait groups in populations, which are alternately favoured as selective gradients vary (Biro and Stamps 2010; Réale et al. 2010). For example, the observed pattern of countergradient growth, or the inherent differential patterns of growth of organisms under common conditions when sourced from different latitudes (Conover and Present 1990; Present and Conover 1992). These represent adaptations to a specific environment, where rapid growth is required to achieve maturation in colder regions with shorter growing seasons. However, repeatable individual variation in aggressiveness ("personality") has also been observed within populations that also vary in growth forms, which can be advantageous in cases where environmental conditions are variable, favouring one form over another depending on the selective pressures present (Biro et al. 2006, 2007).

Besides differential personalities within populations leading to differential growth and life history outcomes like investment in reproduction and survival (Biro and Stamps 2008), differences in more cryptic traits have also been observed, including immune responsiveness and metabolic rates (Previtali et al. 2012; Sandmeier and Tracy 2014; Eliason and Farrell 2016). These concepts are unified under the pace-of-life syndrome (POLS; Ricklefs and Wikelski 2002; Réale et al. 2010), which predicts that certain traits and outcomes will differ between bolder, more rapid-growing individuals and their slower growing counterparts.

The pace-of-life hypothesis predicts connections among behavioural, physiological, and life history phenotypes that are fundamentally linked (Ricklefs and Wikelski 2002; Réale et al. 2010). Specifically, that "fast"-paced individuals tend to have rapid growth, shorter lifespans, and increased levels of activity, metabolism, and aggressiveness. In contrast, "slow"-paced individuals generally have slower growth, longer lifespans, and lower levels of aggression, activity, and metabolism (Réale et al. 2010). Several investigations have demonstrated positive correlations between the metabolic rate of an organism, its activity level, and its dominance status in support of the pace-of-life hypothesis (but see Závorka et al. 2015; Laskowski et al. 2016). Further, these syndromes have been observed across a variety of taxa across the animal world (Wikelski et al. 2003; Biro and Stamps 2008, 2010; Careau et al. 2008; Metcalfe et al. 2016).

Understanding rates of basal metabolism (termed standard metabolic rate or SMR) for organisms provides critical information regarding the metabolic "machinery" available to support basic life functions of organisms. While metabolism itself reflects a net loss of energy to the organism, and is therefore a cost, those costs can be countered if they are directed to foraging activity or the costs associated with extracting nutrients from food (Biro and Stamps 2010; Metcalfe et al. 2016). Furthermore, SMR directly relates to the energy available for maximum performance (Cutts et al. 1998; Allen et al. 2016; Metcalfe et al. 2016). Both aspects are important in considering how SMR aligns with rapid growth and other predicted life history outcomes related to survival and timing of reproduction within the context of POLS theory (Réale et al. 2010).

Understanding how SMR scales with body size is also critical for understanding patterns of energy use in organisms. General descriptions of how metabolic costs (including SMR) vary with both temperature and body size have led to the development of bioenergetic models, which equate as a mass balance the energy consumed by fish with the energy lost to metabolic costs, wastes, reproduction, and somatic growth (Weatherley 1966; Kitchell et al. 1974, 1977; Deslauriers et al. 2017). Significant time and energy have been dedicated to generating parameter estimates for these models, such that bioenergetic model output may more accurately reflect growth and energy use in the species of interest; for several species, differential models describing different life stages exist (Deslauriers et al. 2017). However, despite evidence in the literature that SMR can vary consistently and predictably between growth forms, no attempts have been made to evaluate whether "form"-specific models might be justified. Observable and significant differences in mass-scaling exponents and (or) coefficients of SMR between growth forms may provide this justification.

Our objective in the current study was therefore to (a) measure and compare growth rates in a domestic and "wild" strain of rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), (b) measure and compare SMR in these same groups of fishes using two different estimation methods, (c) compare our results with those in the literature to determine the biological significance of our findings, and (d) evaluate the importance of differences in SMR in bioenergetic modelling efforts when applied to rapidly growing strains of rainbow trout.

Materials and methods

Fish husbandry

Two genotypes of rainbow trout—a mixed-sex wild diploid strain from the Ganaraska River and a domesticated triploid strain—were obtained from the Dorion Fish Culture Station operated by the Ontario Ministry of Natural Resources and Forestry (OMNRF) (Dorion, Ontario, Canada). Fish were hatched during the spring of 2016. We secured 150 fish of each strain on 12 December 2016. Initial lengths (mm) and weights (g) were taken from a subsample of 20 individuals from both strains on 15 December 2016, which was marked as day 1 of the experiment. There are several naturalized strains of rainbow trout in Ontario lakes and rivers, but the OMNRF has exclusively used the Ganaraska strain for stocking since the early 1970s (Ontario Ministry of Natural Resources and Forestry 2015). The genetic and phenotypic differences between the Ganaraska strain and other wild strains are negligible so it is assumed the Ganaraska strain acquired is an accurate representation of wild rainbow trout (Kerr and Lasenby 2000).

Both strains were housed at the Biology Aquatics Facility (BAF) at Lakehead University. Fish were initially held in several 80 L tanks, to keep densities below 10 g of fish L^{-1}, with strains of fish kept separate from one another. All tanks were on the same circulation system. Once large enough, fish were moved to four larger 500 L circular tanks on a common flow-through system, again keeping strains separated in different tanks. All tanks were kept under constant conditions of 11.5 ± 1 °C. Fish were fed 1.5% of their estimated body weight with commercial fish food pellets daily.

The lab was on an automated day/night cycle of 16 and 8 h, with a 45 min gradual lighting/dimming period. Fish were housed in accordance with the Lakehead University standard operating procedure for Fish Husbandry in the BAF. Temperature, pH, and dissolved oxygen (DO) were monitored daily, and water quality was tested bi-weekly at a minimum, with 20% water changes conducted every 4–7 days as required. Fish handling and experimentation was conducted under Lakehead AUP # 1465505.

Experimental setup

Metabolic rates of rainbow trout (48 wild and 25 domestic) were estimated by measuring mass specific oxygen uptake rates ($\dot{M}O_2$: $mgO_2\,kg^{-1}\,h^{-1}$), determined from intermittent-flow respirometry software and equipment (Loligo Systems, Tjele, Denmark). The size of the respirometry chamber used was dependent on the size (volume) of the fish. Trout with a mass less than 20 g were placed in 45 mm diameter (224 mL in volume) chambers, whereas 62 and 100 mm diameter chambers (676 and 2360 mL, respectively) were used for trout between 21–130 and 131–280 g, respectively. On average, the volume ratio of experimental chambers to fish was 29 for 45 mm diameter chambers, 13 for 62 mm diameter chambers, and 11 for 100 mm diameter chambers. While these ratios are somewhat lower from our larger chambers than the recommended range of 20–50 (Svendsen et al. 2016), acceptable $\dot{M}O_2$ measurements were obtained with only a few exceptions (see description regarding filtering of $\dot{M}O_2$ measurements below). Chambers were submerged in an aerated water bath and maintained at a temperature of 11.5 ± 0.5 °C using a chiller unit. Submersible water pumps (Compact 300 or 600 pumps depending on chamber size, EHEIM, Germany) were automated via AutoResp control software (Loligo Systems, v.2.2.0), and chambers were refreshed with oxygenated water for 5 min over every 10 min cycle. A recirculation loop was also connected to each chamber, which consisted of a second submersible pump in the loop to ensure proper mixing of water through the respirometer, and an optical oxygen dip-

ping probe (PreSens, DP-PSt8), which was calibrated before the beginning of the experiment.

Respirometry trials had a maximum biological load of four individuals per tank and a minimum of two. Up to four fish were measured for the rate of oxygen uptake simultaneously. Rainbow trout were fasted for 24–36 h to ensure they were in a post-absorptive state. Blood chemistry of rainbow trout fed artificial pellets is observed to return to baseline conditions within 24 h (Brezas and Hardy 2020), suggesting this time period was adequate. Fish selected for respirometry were lightly anesthetized to be weighed and measured (fork length and total length) prior to entering the respirometry chamber. In forced swimming trials, the effects of anaesthetic were negligible by 6 h after exposure (Hayashida et al. 2013); given that we employed only light anaesthetic and ignored the first 12 h of data after fish were placed in respirometry chambers, it is unlikely that anaesthesia impacted our results. A 10 min $\dot{M}O_2$ measurement cycle began once fish were added and the chambers were sealed. The measurement cycle began with a 5 min flush phase, during which oxygenated water from the holding tank was circulated through the chamber. At the end of this period, water circulation with the holding tank was shut off and the closed measurement circuit was initiated. This was followed by a 30 s wait period to allow the water in the closed circuit to stabilize after flushing. The measurement phase was then initiated, during which oxygen concentrations were measured in the chamber continuously for 4.5 min. Each respirometry trial lasted for 36 h, where the first 12 h were not included as they were assumed to encompass acclimation. During the entire 36 h period, fish in their chambers were in a separate procedure room behind a closed door, where noise and activity was minimized. A curtain was in place, separating the computer from the holding tanks so that the experimenter could monitor the status of the experiment via the computer without disturbing the fish. Background respiration was measured for an hour at the beginning of seven different trials over the course of the experiment using empty chambers, and in each instance, was found to be negligible.

The $\dot{M}O_2$ for each fish was estimated as the product of the measured slope of decline in oxygen concentration within the chamber during the closed measurement cycle and the volume of the chamber, corrected for the volume of fish within the chamber (with an assumed fish density of 1 kg L^{-1}). Values of $\dot{M}O_2$ with a coefficient of determination (R^2) less than 0.9 were not included in the SMR calculation to ensure high precision of the DO determinations over each closed measurement period. Over all trials, this excluded 172 of 11 853 $\dot{M}O_2$ measurements (excluding the acclimation period). For three trials from the wild strain, R^2 values for all $\dot{M}O_2$ measurements were below our cutoff and excluded from further analysis. To determine the sensitivity of SMR to the method of estimation (as each relies on different quantities of data for inclusion), SMR for each fish was determined by two ways: first, by taking the average of the 10 lowest recorded $\dot{M}O_2$ values after acclimation (low-10) and second, by estimating the 20% quantile of all measured $\dot{M}O_2$ values ($q_{0.2}$; Chabot et al. 2016). To facilitate data analysis, SMR was expressed in units of $mgO_2\ h^{-1}$.

Generally, SMR can be expressed as

$$\text{SMR} = \text{RA} * W^{\wedge \text{RB}} + F(T) \quad (1)$$

where RA is a mass-scaling coefficient, RB is a mass-scaling exponent, W is the mass of the fish (g), and $F(T)$ is a temperature dependence function. Our primary focus was to generate strain-specific estimates of RA and RB while holding temperature constant.

Respirometric measurements began on day 54, alternating between wild and domestic strains until day 129. After respirometric testing, fish were returned to their holding tanks. All fish were euthanized at the end of the experiment with an overdose of buffered tricane methanesulfonate followed by cervical transection.

Statistical analysis

Growth patterns (as length per unit time) for wild and domestic rainbow trout during the experiment were observed to be roughly linear during the course of the experiment (see results). As such, differences in growth rate between domestic and wild strains of rainbow trout were determined using a test for homogeneity of slopes. Growth in mass was also plotted for visual comparison, with exponential growth models fit to weight estimates over time.

To evaluate potential differences in the mass scaling of metabolic rates between domestic and wild strains of rainbow trout, a test for homogeneity of slopes (mass exponents) on log-transformed SMR and log-transformed fish mass was performed. Log transformation was required to linearize the relationship, given that SMR scales with body mass as a power function (eq. 1). With no significant interaction between strain and log-transformed fish mass (see results), an Analysis of covariance (ANCOVA) was conducted on the same log-transformed variables to determine differences in elevation (mass coefficients) between strains. We also applied tests of homogeneity of slopes and ANCOVA (where appropriate) to wild and domestic strains separately to determine whether the estimation method generated significantly different estimates of RB or RA. To confirm that these patterns were not influenced by a lack of overlap between strains at smaller body sizes, the analysis was repeated for fish greater than 70 g only to ensure that our conclusions did not change.

To help validate our metabolic estimates and ensure they were comparable to those reported for rainbow trout elsewhere, allometric mass-scaling exponents (RB) were compared to those published for other salmonids (Deslauriers et al. 2017) by visual comparison. We also summarized a (non-exhaustive) literature search of publications on salmonid respirometry from which mass-scaling exponents and coefficients could be derived for additional comparison to our estimates. Mass-specific RB in FB4 (and other sources as necessary) were converted to mass-relative RB (employed in the current study; see Appendix A).

Bioenergetic modelling

We applied SMR parameter estimates under a bioenergetic simulation to determine the impact of differences in SMR mass coefficients on consumption estimates of fast-growing

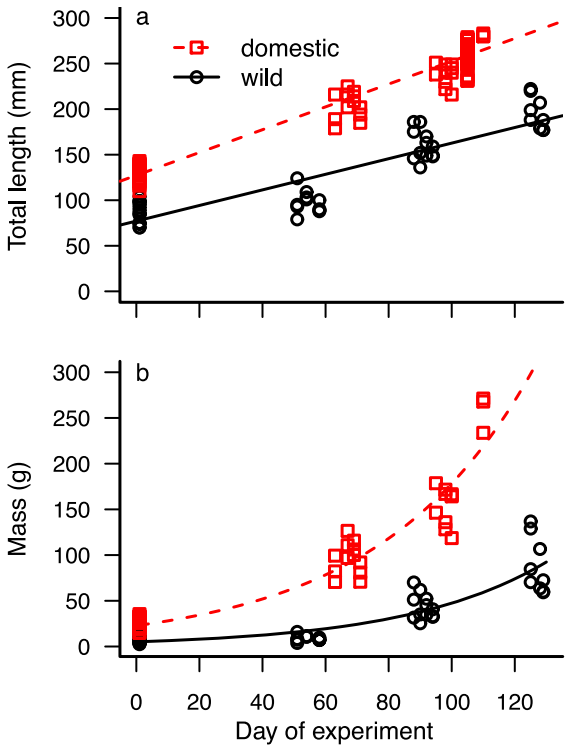
domestic rainbow trout, using initial and final mass estimates for this strain observed in our experiment (26 and 271 g, respectively) over a 110 day period of growth, at the water temperature fish experienced over this period (11.5 °C). For this simulation, we evaluated differences in our SMR estimates between wild and domestic strains, as well as differences between fast- and slow-growing strains in another study (Sloat and Reeves 2014). We used the SMR temperature dependence functions for juvenile rainbow trout reported in Tyler and Bolduc (2008). Parameters for maximum consumption listed in Tyler and Bolduc (2008) were too low to allow for growth rates observed in our study. Their method for determining maximum consumption in fishes is likely underestimated due to fish being under significant stress during feeding trials—fish were moved to 5 L buckets for 1 h to measure maximum consumption, with no period of acclimation provided prior to feeding trials (Tyler and Bolduc 2008). We therefore used the parameters for consumption from Railsback and Rose (1999), as implemented in van Poorten and Walters (2010). Consumer energy density was a function of mass, based on the equation provided for rainbow trout in Weatherley and Gill (1983). Prey energy density was set to 4500 J. All other parameters for specific dynamic action (SDA) and losses to egestion and excretion are common among all other models describing this species (Deslauriers et al. 2017). Using this set of parameters, we modelled consumption under varying levels of activity rates, where activity was modelled as a multiple of SMR. The percent difference in mass-specific consumption rates estimated between wild and elevated SMR was estimated and plotted for visual comparison.

Results

Growth rates of both strains (as length in mm day^{-1}) were generally linear over the course of the experiment (Fig. 1*a*). A test for homogeneity of slopes indicated that the approximately linear growth rate was significantly greater in the domestic strain than in the wild strain ($F_{[1,151]} = 42.2$, $P < 0.0001$). Domestic fish grew at a rate of 1.25 mm day^{-1}, compared to the wild strain that grew at a rate of 0.86 mm day^{-1} (Fig. 1*a*). Similarly, the rate of mass accumulation in both strains was explained well by an exponential growth model. The domestic fish strain accumulated mass at a rate nearly three times that of the wild strain over the course of the experiment (Fig. 2*b*).

When examining SMR calculated using the low-10 method, a test of homogeneity of slopes indicated no differences in slope (RB) of SMR with body mass (both log-transformed) among strains ($F_{[1,63]} = 1.09$, $P = 0.23$), and we proceeded with ANCOVA. The ANCOVA revealed significantly higher SMR across all sizes evaluated in domesticated rainbow trout compared with the wild strain ($F_{[1,64]} = 6.64$, $P = 0.012$, Fig. 2*a*). Converting intercepts (mass coefficients or RA) from the log–log relationships back to arithmetic values, the SMR intercept (RA) for domestic fish (0.117 mgO_2 h^{-1}; 0.00282 g O_2 day^{-1}) was 1.29 times greater than that of the wild strain (0.091 mgO_2 h^{-1}; 0.00219 g O_2 day^{-1}). The value of the common slope (mass exponent, RB) among wild and domestic rainbow trout was 0.9690 mgO_2 h^{-1}.

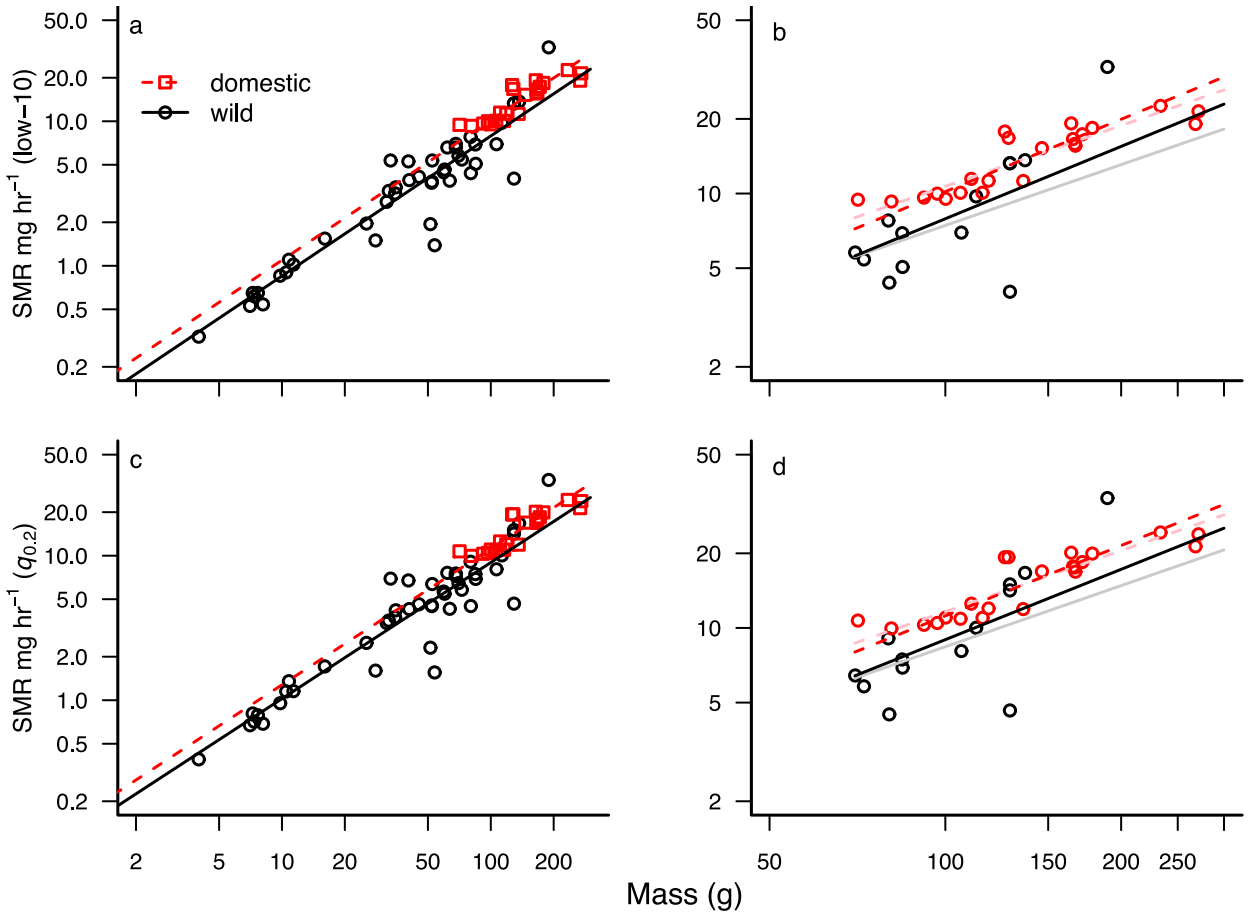
Fig. 1. Size of domestic (red squares, dashed line) and wild strains (black circles, solid line) of rainbow trout (*Oncorynchus mykiss* (Walbaum, 1792)) during the course of the experiment. Panel a, growth as total length (mm); Panel b, growth as mass (g).



The 20% quantile approach ($q_{0.2}$) method to estimating SMR yielded nearly identical patterns as the low-10 approach, but with slightly different parameter estimates. A test for homogeneity of slopes again revealed no differences in slope (RB) between strains ($F_{[1,63]} = 1.11$, $P = 0.3$), so an ANCOVA was conducted. As with the low-10 method, The ANCOVA of $q_{0.2}$-derived SMR was significantly higher in domestic rainbow trout compared with the wild strain ($F_{[1,64]} = 4.95$, $P = 0.0297$, Fig. 2*c*). Again converting intercepts (RA) from the log–log relationships back to arithmetic values, the SMR intercept for domestic fish (0.146 mgO_2 h^{-1}; 0.0035 g O_2 day^{-1}) was 1.25 times greater than that of the wild strain (0.117 mgO_2 h^{-1}; 0.00281 g O_2 day^{-1}). The value of the common slope (mass exponent, RB) among wild and domestic rainbow trout was 0.9422 mgO_2 h^{-1}.

These patterns of significant offset in RA between fast- and slow-growing rainbow trout strains persisted when we limited data to only size ranges of fish where there was significant overlap (i.e., fish greater than 70 g; Figs. 2*b* and 2*d*). When limiting data to only the largest fish in the dataset, one outlier for the wild strain with high leverage in the truncated dataset (mass = 190 g) was excluded. Once doing so, we found that under either estimation scenario, slopes between strains were equal, though shallower than when considering the entire dataset (0.815 and 0.819 for the low-10 and $q_{0.2}$ methods, respectively), and that the offset between strains was significant (low-10, $F_{[1,31]} = 14.3$, $P = 0.0006$; $q_{0.2}$, $F_{[1,31]} = 11.3$, $P = 0.002$)

Fig. 2. Standard metabolic rate (SMR) of domestic and wild strains of rainbow trout (*Oncorynchus mykiss* (Walbaum, 1792)) over the range of sizes evaluated during the experiment. Note log-scale on both axes. Panels a and b show estimates based on low-10 method of calculation, panels c and d show $q_{0.2}$ method (see text). Symbols as in Fig. 1. Red dashed and black lines are relationships over all fish sizes. Panels b and d show separation between strains for fish over 70 g only. Pink and grey lines in panels b and d show relationships for fish over 70 g only (excluding single wild outlier at 190 g with large leverage).



and consistent in direction with the analysis from the entire dataset; RA for the domestic strain was greater than for the wild strain, though differences between strains were greater than in the whole dataset (2.3 and 2.1 times greater in domestic than in wild for the low-10 and $q_{0.2}$ methods, respectively).

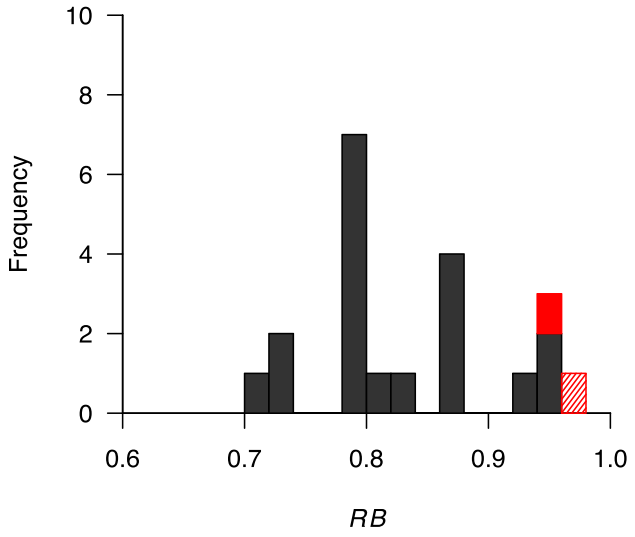
Despite apparent differences in RA and RB estimates between SMR estimation methods, they were not statistically significantly different. For the wild strain, there was no significant difference in slopes (RB) between the low-10 and $q_{0.2}$ methods (test of homogeneity of slopes, $F_{[1,86]} = 0.3$, $P = 0.6$), nor were there differences between methods in intercept (RA) assuming a common slope ($F_{[1,87]} = 1.2$, $P = 0.3$). For the domestic strain, no significant difference in slopes between SMR calculation was observed (test of homogeneity of slopes, $F_{[1,40]} = 0.3$, $P = 0.6$) nor were differences in intercept assuming a common slope, but only marginally ($F_{[1,41]} = 3.7$, $P = 0.06$).

The allometric mass exponents (RB) derived from the two SMR calculation methods were compared to those published from other salmonids in the Fish Bioenergetics 4.0 (FB4) "parameters official" file, which provides a summary of all published bioenergetic models for aquatic organisms (Deslauriers et al. 2017). A histogram was generated from all salmoniformes from the 2021 version of FB4 (Deslauriers et al. 2017). While both methods (low-10 and $q_{0.2}$) generated similar values on the higher end of estimates reported in the literature, the estimate using the $q_{0.2}$ method was more similar to that of other salmonids than the low-10 method (Fig. 3). Further, the mass exponent from the $q_{0.2}$ method was very similar to that reported for juvenile rainbow trout (0.9422; Tyler and Bolduc 2008).

Our allometric mass exponents (derived from both the low-10 and $q_{0.2}$ methods of estimation) were also comparable to RB values from other published allometric mass exponents for salmonids that are not also included in FB4; published literature values ranged from 0.757 to 1.107, with a mean value of 0.898 (Table 1).

Observed differences between wild and domestic strain RA values from this study (1.2 and 2 times greater) as well as a value of 1.5 derived from Sloat and Reeves (2014) were used to parameterize bioenergetic simulations. Higher RA values provided higher estimates of consumption for rapidly growing rainbow trout (Fig. 4). This effect was most pronounced under a high-offset scenario (RA values 1.5–2 times

Fig. 3. Histogram of published salmonid standard metabolic rate (SMR) mass-scaling exponents (RB, as units of oxygen consumption per day; $n = 19$). Data from Deslauriers et al. (2017). Mass-scaling exponent estimated from the $q_{0.2}$ method (this study) is shown in solid red and exponent from the low-10 method is shown in hashed red.



greater than for slow-growing strains) and at higher activity rates.

Discussion

As predicted by POLS, the faster growing individual rainbow trout from the domestic strain had higher resting metabolisms (due to higher metabolic coefficients) than the wild strain, regardless of the method of SMR calculation applied. Biro and Stamps (2010) reviewed the existing literature at the time and proposed a conceptual model demonstrating how higher metabolic costs can result in greater individual production (i.e., growth rate); as tissue elaboration is costly, a more energetic "idling cost" can better facilitate the physiological framework to support rapid growth. Similarly, Reale et al. (2010) argued that more metabolically active organs are associated with "proactive" behaviours, which is in turn often associated with more rapid growth rates (Biro et al. 2005; Biro and Stamps 2008; Huntingford et al. 2010). As in our study, Sloat and Reeves (2014) reported higher SMR (metabolic coefficient) in dominant (territorial) rainbow trout individuals compared to subordinate (disperser) individuals, with a common metabolic exponent between types. Recent work on rainbow trout also supports the positive correlation between resting metabolism and growth rates (Kindschi et al. 1991; Allen et al. 2016), but also suggests that increased resting metabolism may limit aerobic scope (Allen et al. 2016). More broadly, studies on salmonids have reported positive correlations between dominance/bold personality traits with higher SMR (Metcalfe et al. 1995; Cutts et al. 1998). A relatively recent review of metabolism of the *Oncorhynchus* genus recognized that SMR is positively correlated with behavioural traits that would fall under the "bold" characteristics of POLS in salmonids, generally including dominance, aggression, and territoriality, all positively associated with growth rate (Eliason and Farrell 2016).

The differences in magnitude observed in this study between fast- and slow-growing strains are also quantitatively consistent with other studies comparing SMRs between fast- and slow-growing groups of individuals. While not the main focus of their study, Allen et al. (2016) examined SMR for slow- and fast-growing strains of rainbow trout and found that fast-growing strains had SMR estimates that were 1.15 times greater than slower growing strains (based on model parameter coefficients describing differences among strains provided in their paper). Using the $q_{0.2}$ method, this agrees very closely with our study (domestic = 1.25 times wild SMR). The Allen et al. (2016) study observed these trends among fish that were smaller in size compared to those for which we report SMR in the current study. Yet, we observe this close agreement between both independent studies, examining different fast- and slow-growing strains under different experimental conditions, despite having experienced two different ambient temperatures (11.5 °C in the current study, 16.5 °C in Allen et al. 2016) and being conducted across different size ranges of fish. Other studies comparing high and low SMR strains appear to show differences of similar magnitude, if not slightly greater (Sloat and Reeves 2014); a reanalysis of the data presented in Sloat and Reeves (2014; their fig. 4) suggests that territorial individuals had SMR rates 1.5 times higher than those of dispersing individuals in streams (where territoriality in anadromous strains is thought to have an advantage by achieving larger size prior to smelting).

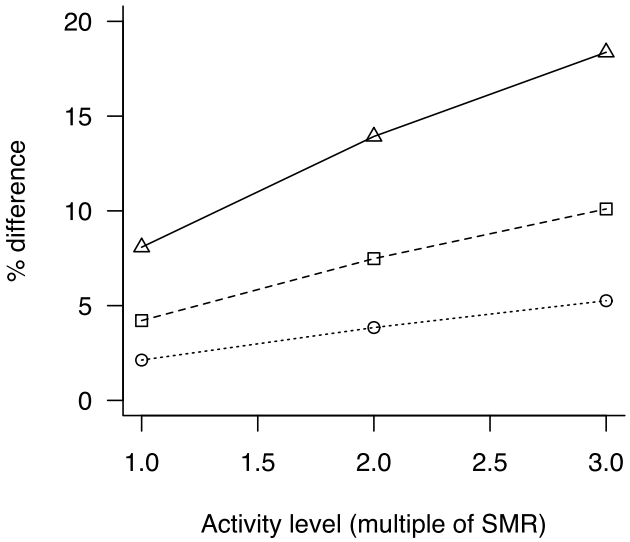
When applied to rapidly growing domestic strain fish, bioenergetic models employing higher RA values (larger differences in RA values compared to wild strain fish) resulted in a greater percent difference consumption estimates between strains. This was especially true in cases where RA for fast-growing fish was twice as high as slow-growing fish, and at higher activity levels. When estimated directly, field-based activity estimates frequently match or exceed three times basal metabolism (Boisclair and Leggett 1989; Rowan and Rasmussen 1996; Rennie et al. 2005, 2012*b*). As such, more accurate RA estimates may be an important consideration for researchers modelling rapidly growing rainbow trout strains experiencing field conditions. Early work in bioenergetics described RA as one of the more sensitive terms in these models (Kitchell et al. 1977), further emphasizing the potential importance of more accurately describing this parameter for fish with elevated SMR.

Metabolic scaling exponents were not significantly different between methods for either strain. However, the exponent derived by the $q_{0.2}$ method of estimation provided estimates that were more comparable to those reported in the literature for other salmonids than to those derived by the low-10 method. This observation, as well as the fact that the $q_{0.2}$ method likely provides a more robust estimate of SMR being based on a larger number of MO_2 estimates compared to the low-10 method, leads us to favour the results provided by the $q_{0.2}$ method. Previous comparisons of quan-

Table 1. Published mass-scaling exponents of standard metabolic rate (SMR) (WB) for Salmonidae that are not otherwise included in the Fish Bioenergetics 4.0 official parameter table.

Source	Species	Temperature (°C)	WB
Beamish (1964)	*Salmo trutta* Linnaeus, 1758	10	0.877
	Salvelinus fontinalis (Mitchill, 1814)	10	1.107
		15	1.014
		20	1.036
Job (1955)	*Salvelinus fontinalis* (Mitchill, 1814)	10	0.849
		15	0.847
		20	0.802
Beauregard et al. (2013)	*Salmo salar* Linnaeus, 1758	Various	1.020
Rao (1968)	*Oncorhynchus mykiss* (Walbaum, 1792)	5	0.784
		15	0.783
Allen et al. (2016)	*Oncorhynchus mykiss* (Walbaum, 1792)	16.5	0.757
Mean			**0.898**

Fig. 4. Application of a larger metabolic scaling coefficient (RA) to percent difference in mass-specific consumption estimates (domestics compared to wild fish) obtained from a bioenergetic model applied to rapidly growing domestic strain rainbow trout (*Oncorynchus mykiss* (Walbaum, 1792)) and at varying fish activity levels (expressed as a multiple of standard metabolic rate or SMR). Dotted line and circles show RA values 1.25 times those of wild RA (this study; Allen et al. 2016); dashed line and squares show RA values 1.5 times those of slower growing fish (Sloat and Reeves 2014); and solid line and triangles show RA values two times those of wild RA (this study; based on comparison of only fish larger than 70 g in the dataset).



tile versus low-10 methods have generally reported lower values from low-10 (Chabot et al. 2016), as was observed in the current study. Chabot et al. (2016) recommend the use of quantile methods over low-10 methods with the former being more robust against variable outliers, and not relying on any particular distribution for its interpretation. However, it is worth re-emphasizing that differences in parameter estimates between methods in this particular case were minor.

It is important to recognize that as food becomes limiting, either due to quantitative per capita limitation of prey per consumer, or through lack of predictability or accessibility due to habitat complexity, that relationships between SMR and growth may dissolve. Several studies have revealed that when food supplies become limiting, or in non-ideal situations in the field, positive correlations between SMR and growth may break down or become negative (Álvarez and Nicieza 2005; Reid et al. 2012). Other examinations in the field have also reported trade-offs between metabolic costs and fish growth (Trudel et al. 2001; Rennie et al. 2005, 2012*b*). However, in many cases, the selective advantage of rapid growth has been shown to be context dependent, and in cases of limiting food, high predation, or harvest, the high SMR phenotype may no longer be advantageous (Biro et al. 2006; Biro and Post 2008; Reid et al. 2012).

We believe our results demonstrating differences between strains are robust, despite what might be interpreted as potential shortcomings in our experiment. Though our study was conducted only at a single temperature, several other studies have shown that the slopes of metabolic rates with body size are generally consistent across temperature regimes (Beamish 1964; Rao 1968; Beauregard et al. 2013). Additionally, while we lacked SMR measurements on fast-growing domestic fish at the smaller size range of our distribution, the general agreement of both the direction and magnitude of the offset in SMR between our study (1.25 times greater in fast-growing fish, 5–200 g) is consistent with those considering only fish >70 g in our study (two times greater than slow-growing fish), as well as with independent studies for the same species at much smaller sizes (1.15 times greater in fast-growing fish, 3–18 g; Allen et al. 2016), and another study on fish of similar size (approx. 1.5 times greater in territorial fish, 20–100 g; Sloat and Reeves 2014) suggests that our results are broadly consistent across a large range of sizes for this species.

In summary, we found significant differences in SMR between fast-growing domestic and slow-growing wild strains of rainbow trout in a laboratory setting. Further, the consistency of our results (in terms of magnitude of differences between fast- and slow-growing individuals) with that of two independent studies on the same species (Sloat and Reeves 2014; Allen et al. 2016) suggests serious consideration for whether strain-specific bioenergetic models might be required for comparative bioenergetic investigations among strains, particularly in field settings (Biro et al. 2003, 2006; Biro and Post 2008). This becomes more evident as the world of animal tracking (and particularly fish tracking) enters a new era, and we find increasing evidence of differential growth forms associated with differences in metabolism (in particular, activities associated with migration or longer-range movements; Rennie et al. 2012*a*; Hayden et al. 2014; Kennedy et al. 2018; McKee et al. 2022). Future bioenergetic investigations of populations such as these, which differ in migration abilities associated with growth rates, may wish to also examine differences in basal metabolism, and consider the degree to which fundamental physiological differences might exist between these groups, or at least consider the potential biases of not doing so when applying bioenergetic models that do not take potential group-wise differences into account (e.g., Rennie et al. 2008).

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Data are available from the corresponding author on request.

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Competing interests

The authors declare there are no competing interests.

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Appendix A: unit conversions for allometric mass exponents (RB) and coefficients (RA)

Mass exponents provided in the FB4 bioenergetics model are expressed as slopes of mass-specific rates (i.e., change in units of O_2 day^{-1}) as opposed to the mass-relative rates reported here (i.e., change in units of O_2 day^{-1} $g_{fish}{}^{-1}$). Based on the law of exponents, the conversion of mass-relative to mass-specific rate is equivalent to adding a value of 1 to the reported RB exponent estimates from FB4, as demonstrated below, where W is the fish mass and RB_m is the mass-specific slope estimate,

$$W^{RB_m} \times \frac{W^1}{W^1} = \frac{W^{RB_m+1}}{W^1} = \frac{W^{RB_m+1}}{W}$$

To convert RA estimates from units reported here (mgO_2 h^{-1}) to those reported in the fish bioenergetics model FB4 (units of g O_2 day^{-1}; hereafter RA_m to be consistent with nomenclature above), the following equation is applied (converting mg O_2 to g O_2, and units of time to days from hours):

$$RA_m = \left(\frac{RA}{1000\,mg/g}\right) \times \frac{24\,h}{1\,day}$$