Personality in hatchery Atlantic salmon (*Salmo salar*) is associated with growth but not metabolic rate or performance

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Abstract

The pace of life hypothesis (POLS) predicts that personality traits, like activity and boldness, are positively correlated with growth and metabolism. Here, we assess whether personality could predict body mass, metabolic rate, and performance under stress for hatchery-raised Atlantic salmon (*Salmo salar*) 15 months post fertilization. Personality was evaluated for individual fish using a series of repeated trials alongside two stressful events (PIT tagging, simulated transport), to determine performance under stress. Standard metabolic rate (SMR) was then assessed via intermittent flow respirometry, and the relationships between personality, body mass, performance, and SMR were evaluated. Fish displayed repeatable behaviours, but not in accordance with POLS hypothesis. Smaller fish were more active and responsive to stimuli, while personality was not associated with SMR. Although smaller fish and fish with higher SMR both performed better under stress, body mass was unrelated to SMR. We discuss the utility of supporting the occurrence of a wider range of growth rates and body sizes in hatchery environments, as a means of promoting greater stress tolerance as well as faster growth.

Key words: hatchery-raised, pace of life, personality, *Salmo salar*, SMR, performance under stress

Résumé

L'hypothèse du rythme de vie prédit que des traits de personnalité, comme l'activité et la hardiesse, sont positivement corrélés à la croissance et au métabolisme. Nous tentons de déterminer si la personnalité peut permettre de prédire la masse du corps, le métabolisme et la performance en situation de stress pour des saumons atlantiques (*Salmo salar*) élevés en écloseries à 15 mois post-fécondation. La personnalité individuelle est évaluée en utilisant une série d'essais répétés jumelés à deux évènements stressants (pose d'une étiquette PIT, transport simulé) afin de déterminer la performance en situation de stress. Le taux métabolique standard (TMS) est ensuite évalué par respirométrie par débit intermittent, et les relations entre la personnalité, la masse corporelle, la performance et le TMS sont évaluées. Les poissons présentent des comportements pouvant être reproduits, mais pas de manière conforme à l'hypothèse du rythme de vie. Les poissons plus petits sont plus actifs et réagissent plus aux stimuli, alors que la personnalité n'est pas associée au TMS. Si les poissons plus petits et les poissons au TMS plus élevé performent mieux en situation de stress, la masse corporelle n'est pas reliée au TMS. Nous abordons l'utilité de soutenir la présence d'une plus grande fourchette de taux de croissance et de tailles du corps dans les écloseries comme approche pour favoriser une meilleure tolérance au stress ainsi qu'une croissance plus rapide. [Traduit par la Rédaction]

Mots-clés : élevé en écloserie, rythme de vie, personnalité, Salmo salar, TMS, performance en situation de stress

Introduction

The study of life history emerged from observations regarding age-specific patterns of survival and reproduction that exhibit a distribution of "fast" and "slow" traits when plotted along a single axis, the r/K-axis (MacArthur and Wilson 1967; Pianka 1970; Stearns 2000). Life history traits, such as large body size and a fast rate of development, and vice versa, often covary across diverse populations and species (i.e., Stearns 1984; Roff 1992; Ricklefs and Wikelski 2002), with populations of animals that suffer substantially higher mortality rates rapidly evolving faster life history traits (Reznick et al. 1990; Stearns et al. 2000). In general, fast and slow life histories represent a trade-off between current and future reproduction (Ricklefs and Wikelski 2002). Animals that prioritize current reproduction over survival tend to exhibit a faster life history, while those that prioritize future reproduction tend to exhibit a slower life history (Montiglio et al. 2018).

Currently, the covariation between physiological and behavioural traits representing fast and slow life histories are captured by the Pace of Life syndrome (POLS) hypothesis (Réale et al. 2010). POLS predicts that the relative success of an organism's life-history traits within a given environment is constrained by physiological limitations (e.g., metabolism; Ricklefs and Wikelski 2002). As well, the coevolution of life history, physiology and behavioural traits necessitates that an individual's behaviour be considered alongside its life history and physiology (see Réale et al. 2010). Indeed, empirical work shows that higher food consumption and reproductive success are often observed in more active, aggressive, and bold individuals, as predicted by POLS hypothesis (e.g., Biro and Stamps 2008; Le Galliard et al. 2013; Montiglio et al. 2018).

Moreover, higher standard metabolic rates (SMR) are often associated with competitive dominance (Metcalfe et al. 1995; Cutts et al. 1998; Yamamoto et al. 1998; McCarthy 2001). Such associations between metabolism and competition may arise in part due to physiological constraints (Careau et al. 2008), with higher metabolic activity physiologically incompatible with a slower life history (Wiersma et al. 2007). Furthermore, aggression and boldness are often associated with higher resource acquisition (Biro and Stamps 2008), a key component of faster growth and larger body size (Enberg et al. 2012). Due to trade-offs among life history characteristics that underly energetically expensive processes such as growth, faster life history is also associated with lower stress tolerance (Lochmiller and Deerenberg 2000; Palacios et al. 2012). According to POLS hypothesis, higher levels of activity, aggression, and boldness are therefore associated with a faster pace of life strategy, including higher metabolic rates, lower stress tolerance, and higher rates of mortality (Réale et al. 2010). However, the many variable associations between personality (i.e., repeatable behavioural difference among individuals; Réale et al. 2007) and life history described in published studies suggest that the costs and benefits of personality traits are determined by the particular features of a given environment (i.e., Adriaenssens and Johnsson 2009; Killen et al. 2013). As such, there appears to be no general rule, as associations between some personality traits (i.e., aggression, activity, boldness) and life history can be positive—as predicted by POLS (i.e., Careau et al. 2010; Dijkstra et al. 2013; Gangloff et al. 2017; Rádai et al. 2017; Cornwell et al. 2020), non-existent (Le Galliard et al. 2013; Debecker et al. 2016; White et al. 2016), or negative (Martins et al. 2011; Niemelä et al. 2013).

Knowledge of the relationships between behaviour, performance under stress and metabolism in captive-reared animals can help to identify stress-resistant individuals better able to tolerate the stressful environments experienced immediately prior to release. In Lake Ontario, reintroduction efforts are currently underway to re-establish a population of Atlantic salmon (*Salmo salar* L), however a self-sustaining population has yet to be established (MacCrimmon 1977; Stanfield and Jones 2003; Bowlby et al. 2007). Here, we explore whether a relationship exists between behaviour, metabolic rate, performance under stress and mortality in hatchery-raised Atlantic salmon parr, using the POLS framework. This study combines repeated personality assays and exposure to two stressors common to hatchery-reared fish (PIT tagging, simulated vehicle transport), followed by an assessment of standard metabolic rate via intermittent flow-through respirometry, while also calculating growth rate during this time (as a measure of performance). Specifically, we assess whether (*i*) repeatable personality traits (activity, exploration, neophobia) are coupled with physiological traits (body mass, SMR, performance under stress) in the manner predicted by POLS; (*ii*) metabolic rate is positively associated with body mass and negatively associated with performance under stress; (*iii*) performance under stress is positively associated with body mass; (*iv*) mortality is predicted by personality according to POLS, and (or) positively associated with body mass and metabolic rate; and (*v*) if a characteristic bimodal distribution representing "slow" and "fast" physiological and behavioural traits is detectable in the combined physiological and behavioural data, in support of POLS (summarized in Table 1).

Table 1. POLS predictions for slow and fast life histories, representing a bimodal distribution of "slow" and "fast" life history, physiology and behavioural traits, and whether they are associated with acquisition of resources or timing of reproduction.

Slower Life History	Faster Life History
Lower rate of acquisition	*Higher rate of acquisition*
Slower growth rate	Faster growth rate
Smaller body mass	*Larger body mass*
Slower SMR	*Faster SMR*
Lower activity	*Higher activity*
Later reproduction	*Earlier reproduction*
Longer lifespan	Shorter lifespan
Higher stress tolerance	Lower stress tolerance
Less weight loss under stress	*More weight loss under stress*
Lower mortality	*Higher mortality*
Shyer	Bolder
Higher anxiety	Lower anxiety
Spend more time in periphery	*Spend more time in centre*
More neophobic	Less neophobic
Respond less to stimuli	*Respond more to stimuli*

Note: Predictions assessed in this study are in italics.

Materials and methods

The care and use of experimental animals complied with the Canadian Council on Animal Care animal welfare laws, guidelines and policies as approved by the University of Windsor Animal Care Committee (AUPP #18-08).

Source population

The *S. salar* population used in this study originated from a landlocked population in Lake Sebago (ME, USA; 43.9° N, 70.6° W). Nine females and nine males were obtained from the Ontario Ministry of Natural Resources and Forestry (OM-NRF) Harwood Fish Culture Station (Harwood, ON, Canada).

This population has been maintained within the hatchery system of the Ontario Ministry of Natural Resources and Forestry since 2006 (Gradil et al. 2016; Houde et al. 2015), with approximately 3 or 4 generations spent in captivity (B.D. Neff, personal observation). Juvenile fish of this particular strain are currently stocked into numerous tributaries of Lake Ontario (LOASRP 2019). Fertilization occurred in blocks of 2 × 2 crosses, resulting in a total of 36 families (Gradil et al. 2016). Each family was reared in duplicate Heath tray sections until the eggs hatched. For the purposes of this study, 24 families were haphazardly selected to be used in the behavioural trials and respirometry. Based on the quantities of full and half-siblings, relatedness between two randomly selected individuals was approximately 21%.

Fish rearing and housing

Salmo salar were raised from the egg to parr stage at Western University, London, Ontario. Six blocks (24 families) of juvenile fish were transported from Western University to Central Animal Care Facilities at the University of Windsor, Windsor, Ontario, in separate 18 L plastic Sterilite® bins (l × w × h: 527 mm × 368 mm × 333 mm; N = 24), with aeration provided to each bin via an airstone during transport. Fish were housed at Central Animal Facilities prior to the experiments and during the individual behavioural assays.

Fish were held within six 420 L recirculating flow through tanks (2.30 m × 0.61 m × 0.30 m) on a 12:12 h light/dark schedule in temperatures ranging from 13 to 16 °C. Prior to the behavioural testing, families (7–15 fish; mean length ± SD: 80 mm ± 10 mm) were housed together within mesh baskets (370 mm × 370 mm × 570 mm) placed inside the tanks; following the first behavioural tests (when fish were individually tagged), fish from different families were randomly housed together at similar densities. The mesh baskets enabled water and waste products to flow through, while keeping the experimental groups separate. Each basket had gravel substrate and a shelter, comprised of a PVC pipe fitting (36 mm × 114 mm); fish did not exhibit any territorial behaviour and were often observed sharing the shelter (K.D.W. Church and L. Nguyen-Dang, personal observations). Although salmonids have been found to exhibit physiological consequences of dominance status (Gilmour et al. 2005), no detectable differences in social status were observed in fish housed together. Fish did not exhibit aggressive behaviour towards each other in their holding tanks during feeding or at any other time, with no evidence for dominance hierarchies (K.D.W. Church and L. Nguyen-Dang, personal observations). Consequently, no lingering winner or loser effects (i.e., Dugatkin and Druen 2004; Rhodes and Quinn 1998) are expected to affect fish behaviour during the individual behavioural assays. Fish were fed once a day to satiation using enhancement starter feed (EWOS® Commercial Feeds, Bergen, Norway), except when otherwise specified (e.g., 24 h prior to respirometry testing). Tanks were siphoned daily to remove waste, while individual baskets were checked for any mortalities or visibly unwell fish, which were removed and euthanized via clove oil. All fish were held for a minimum of 3 weeks following transport, before being used in the behavioural tests.

Fig. 1. Diagram of the overhead view of the experimental arenas used for the repeated individual behaviour assays of *Salmo salar* parr (0.53 m × 0.37 m × 0.33 m; N = 215 fish).
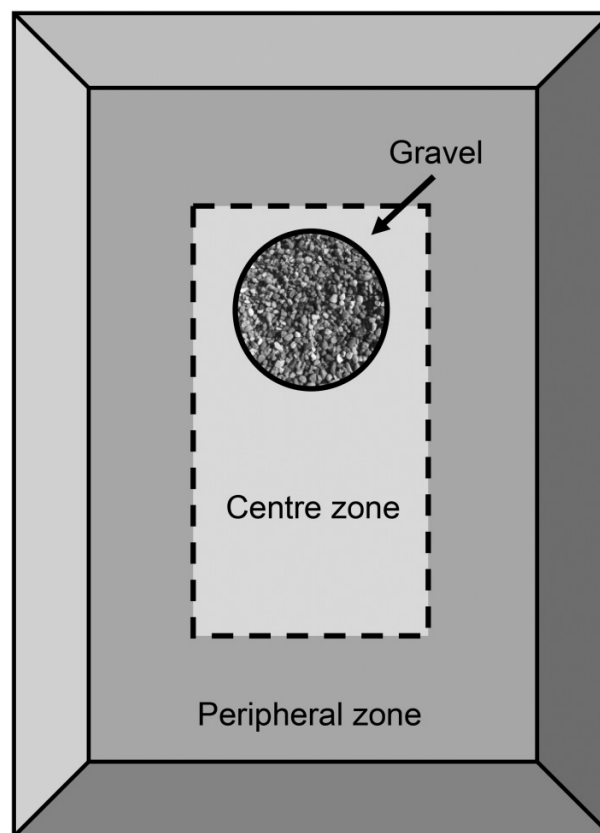
Individual behavioural assays

Pilot observations revealed that the *S. salar* strain used in our study typically acclimated to new holding tanks quickly and exhibited normal swimming behaviour in the arena within 10–15 min following transfer; consequently, we allowed fish to acclimate to the holding tanks for a period of 30 min, and excluded these first 30 min of each trial from the analysis. The experimental arenas used for the individual behavioural assays were the same plastic Sterilite® bins used for transport (described above). A maximum of 32 individuals (N = 7 groups, N = 215 fish) were tested on the same day, with a maximum of 8 fish tested at a time. To randomize any genetic effects, each of these groups contained fish from each sibling group. Fish were netted from their respective mesh bins, then placed individually into 1 L plastic water pitchers before being gently transferred into the testing arena for the duration of the behavioural trial. Experimental arenas were filled with 18 L of dechlorinated water, and were provided with a centrally located circular gravel bed (diameter: 110 mm, depth: 15 mm; Fig. 1).

Individual behaviour within each group of fish was assessed repeatedly over a 9-day period (Table 2A) to determine personality, or consistent individual behavioural differences that occur across time and (or) context (e.g., activity, exploration, neophobia; Réale et al. 2007). All fish underwent three behavioural assays (the same series of tests each time—see

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Table 2. (A) Schedule of individual behavioural tests and stressors experienced by groups of hatchery-raised *Salmo salar* parr, and (B) summary of three behaviour tests given sequentially to all individual fish ($N = 215$ fish) during the individual behavioural assays.*Note – 0-30 min was the acclimation period.*

(A)

Day	Experimental treatment
1	Behavioural assay 1
	PIT tag
5	Behavioural assay 2
	Simulated transport
7	Behavioural assay 3
9	Behavioural assay 4

(B)

Behavioural test	Cumulative Timing	Stimulus response	Observations
Open field (no disturbance)	30–40 min	N/A	Activity, space use observed for 10 min
Bead test (bead stimulus)	40–50 min	Activity immediately following bead	Activity, space use observed for 10 min
Bead test (food stimulus)	50–60 min	Activity immediately following food	Activity, space use observed for 10 min

Note: 0–30 min was the acclimation period.

below) and experienced two stressors during this period that would be relevant to stressors experienced during reintroduction (e.g., Barton 2000; Koehn et al. 2008; Chase et al. 2013; behavioural assay 1 and 2): (1) sedation using clove oil solution prior to injection with a 12 mm Full Duplex (FDX) Passive Integrated Transponder (PIT) identification tag (Biomark, Boise, Idaho); and (2) simulated car transport for a period of 1 h. Fish were exposed to both stressors immediately following the behavioural assays. A 12-gauge hypodermic needle equipped with a plunger was used to pierce the peritoneal cavity of the fish and inject the PIT tag, while all tags were inserted in the ventral region of the fish, just anterior to the pelvic fin (sensu Parker and Rankin 2003). For the simulated car transport, fish were netted and placed in one of two 18 L bins, with a density of 4–8 fish per bin. The bins were then placed on a wagon with their lids and taken on four 10 min rides around campus that included many sharp turns and inclines, followed by a 6 min rest. During the rest period, the bins were jostled by hand every three min. Aeration was provided to each bin through an airstone only during the rest periods.

Following anesthesia and PIT tagging, all fish recovered quickly and resumed normal swimming behaviour within an hour. Tag sites were observed to heal quickly over the subsequent tests (K.D.W. Church and L. Nguyen-Dang, personal observations); all tagged fish also retained their tags, with one exception (99.6% retention rate). Although mortality is rarely a direct result of PIT tagging (Dare 2003), tagging-related mortality tends to be higher for smaller fish (Navarro et al. 2006; Acolas et al. 2007). As we found no relationship between body mass and mortality rates in our study, it is likely that the mortalities in our study ($N = 34$) were not due to the effects of PIT tagging.

Behavioural trials (Table 2B) were captured using two monochrome GigE cameras with a 4.5–12.5 varifocal lens (Basler, Germany) connected to a laptop, and were recorded using Media Recorder (v. 4 Noldus Information Technology, Wageningen, Netherlands). The cameras were mounted on booms at a height of approximately 1.6 m above the experimental arenas, with each camera viewing four arenas simultaneously. Recording began immediately after all eight fish were placed into their respective arenas and continued for a period of 60 min. (assays 1–3). All behavioural assays included a 30 min acclimation period (0-30 min), followed by a 10 min observation of initial behaviour ("open field test"; 30–40 min), a 10 min post-disturbance observation following the introduction of a bead ("bead test"; 40-50 min), and a 10 min observation following the introduction of previously frozen mysis shrimp (family Mysidae; "food test"; 50–60 min).

Following the 30 min acclimation, fish were observed for 10 min for the open field test, then a small bead was tossed into the experimental arena from an approximate height of 20 cm above the water line, at a distance of approximately 15 cm from the edge of the bin, for the bead test. Beads used in subsequent behavioural trials differed in both colour and pattern, to maintain novelty throughout the repeated tests (sensu Church and Grant 2018). All beads were round in shape, with a width of 10 mm in diameter, and containing a central hole of 2 mm. The beads were white and light blue, dark blue, light purple, or dark purple, each with distinct patterns consisting of high-contrast zig zags, small circles, straight or wavy lines. A novel food, mysis shrimp (Omega Sea, Painesville, OH, USA), was then provided at 50 min. For both the bead and food tests, the behaviour of the focal fish immediately following the disturbance was categorized. Fish were ranked scored from a substantial decrease to an increase in movement for active fish, and from no movement to highly active for stationary fish (Table S1). These mysis shrimp were chosen due to their small body size ($\sim$10 mm) and similarity to the invertebrate drift consumed by juvenile salmon in stream habitats in the wild (Keeley and Grant 1995).

Following each assay, fish were netted from the experimental arenas and weighed to the nearest 0.01 g and measured to the nearest mm before being returned to their housing along with the rest of the mixed-family experimental group.

A sedative, clove oil, was given only following the initial behavioural assay, to provide anesthesia (Anderson et al. 1997; Welch et al. 2007) and analgesia (i.e., Correia et al. 2017) for the PIT tagging procedure.

Behavioural analysis

To assess space use, a proxy for anxiety as anxious fish tend to avoid open spaces (i.e., Hope et al. 2019), the arenas were divided into peripheral and central "zones." The width of the peripheral zone was approximately equivalent to one body length of the test fish ($\sim$10 cm), while any fish either touching or within 5 cm of the gravel were classified as using the gravel. Following the trials, videotaped behaviours (i.e., movement and space use) were then coded with Ethovision XT13 (Noldus Information Technology, Netherlands), while changes in behaviour were evaluated manually and quantified (i.e., behavioural changes following stimuli; Table S1).

Overall activity and activity within the different zones were assessed for each fish via Ethovision using the total distance travelled, the total time spent active, and the activity in each zone, during the three observation periods. We included multiple measures of exploration (response to bead and food, activity in open field), activity (total time active, distance travelled), and space use (activity in different zones) to ensure our behavioural assays demonstrated convergent validity (Burns 2008; Beckmann and Biro 2013).

Respirometry chamber

Following the behavioural trials, a subset of fish were then placed individually within an intermittent flow respirometry chamber (QUBIT systems; Kingston, ON, Canada) to measure the rate of oxygen consumption, a proxy for metabolic activity due to its relationship with mitochondria activity (Nelson 2016). Standard metabolic rate (SMR), or the "minimal cost of living" (Frappell and Butler 2004), was assessed. Fish were not fed for 24 h before testing to ensure fish were not actively metabolizing food (Chabot et al. 2016), while only the latter 12 h of the 22–24 h testing period was used in the calculation of SMR to eliminate lingering behavioural effects of handling stress (Herrmann and Enders 2000; Chabot et al. 2016). For our trials, we used repeated cycles consisting of a 6 min measurement period, when oxygen depletion is measured, followed by a 4 min flush period, when oxygen depleted water is exchanged for freshly oxygenated water, and a 1 min wait period, to facilitate mixing within the chamber (sensu Svendsen et al. 2016; Yuan et al. 2018). To ensure accuracy of metabolic measurements, we accounted for background bacterial respiration by measuring the empty respirometry chamber for several hours after removing the fish from the chamber, then subtracted this value from the oxygen consumption measured with the test fish (Svendsen et al. 2016). To minimize background respiration, water was changed between trials, and all submerged equipment was flushed through with a bleach solution for 30 min every few trials to minimize bacterial growth (Svendsen et al. 2016). Additionally, all air bubbles were removed from the system prior to data collection, while any accumulated air bubbles were regularly removed from the chamber via the bubble release valve (Svendsen et al. 2016).

Oxygen consumption within the chamber was calculated using the formulas for absolute (eq. 1) and mass-specific (eq. 2) metabolic rates (Claireaux and Lagardère 1999):

(1) $\quad \mathrm{absMO_2} = \Delta\left[O_2\right]/\Delta t \times (V - D/m)$

(2) $\quad \mathrm{massMO_2} = \mathrm{absMO_2} \times m^{-1}$

where $\Delta[O_2]/\Delta t$ is the slope of the linear decline in oxygen during the measurement phase ("CO_2 unit"/L/h), m is the mass of the test animal (kg), V is the chamber volume (L), and D is the density of the test animal (default = 1000 kg/m^3).

Graphs of oxygen consumption were generated for each fish using the "Q-box Aqua" software (Qubit Systems) and visually inspected; graphs that failed to show a linear decline in oxygen during the measurement phase were excluded from analysis ($N_{\mathrm{excluded}} = 9$). Although Qubit software is able to control for background respiration and mass-specific metabolic rates (Morozov et al. 2019), we also used additional calculations (see below) to control for the influence of body mass on oxygen consumption, as larger fish use more oxygen, but less oxygen per unit mass (Chabot et al. 2016; Chrétien and Chapman 2016; Guzzo et al. 2019).

The raw metabolic rates obtained by eq. 2, and the mass of each fish (in kg), were used to calculate the slope (b) of the relationship between the log of the raw metabolic rates and the log of the mass (Rodnick et al. 2004; Chrétien and Chapman 2016). We then used the calculated value of b to obtain mass-adjusted values of metabolism, using the formula:

(3) $\quad \mathrm{MO_{2adj}} = \mathrm{absMO_2}^{b}$

where b is the slope of the log-log relationship between metabolic rate and body mass ($b_{\mathrm{SMR}} = 0.6778$ for this study), mass is in kilograms, and the observed MO_2 values were obtained by eq. 2 and expressed in milligrams per hour per kilogram (sensu Killen et al. 2013).

SMR was then calculated in either one of two ways, depending on the value of the coefficient of variation (CV) of the mass-independent oxygen uptake values classified into the mean lowest normal distribution (MLND). In cases when the CV was < 5.4, we used the MLND to determine SMR. Otherwise, when the CV was > 5.4, SMR was assessed via a 20% quantile ($q_{0.2}$), which assigns 20% of the oxygen uptake values below SMR (sensu Chabot et al. 2016). Additional information on the respirometry methods is available in Table S2 (sensu Killen et al. 2021).

Life history

Initial body mass served as a correlate of growth in the absence of stress, as all fish were the same age; while growth rate (Ω; Ostrovsky 1995) measured during the 9-day testing period, was used to measure performance under stress (i.e., stress tolerance). Fish require more energy (Davis 2006) and are also less efficient at converting food into energy as a result of stressful situations (Santos et al. 2010). This is due to trade-offs between energy allocated for growth and energy allocated for maintenance, including responses to stress

(Santos et al. 2010); consequently, reduced growth is an indicator of stress (i.e., Pankhurst and Van der Kraak 1997). Fish were not anticipated to grow as expected during this period due to the stress of PIT-tagging, simulated vehicle transport, and repeated handling. Fish were weighed and body mass was recorded following each of the four behavioural assays, while the standardized body size-specific growth rate ($\Omega\%$) was calculated as:

$$\Omega = 100^* \left(M^b_2 - M^b_1 \right) / (b^*t)$$

where M_2 is body mass at the end of the testing period, M_1 is body mass after the first test, t is the length of the growth period in days, and b is a mass exponent used to scale growth rates to a common body size ($b = 0.31$ for Atlantic salmon; Elliott and Hurley 1997; Ostrovsky 1995; Forseth et al. 2001). All fish exhibited a similar body shape regardless of body mass (i.e., Paez et al. 2008).

Mortalities were expected during the testing period due to the low survival previously shown by fry of this strain in captivity (i.e., 55.6% survival; Houde et al. 2015). To assess survival, the identity of each deceased fish was determined through their PIT tag numbers, while the dates of all mortalities were recorded to determine the length of the survival period (in days) from the initial personality test/date of PIT tagging (occurred concurrently).

Statistical analysis

All statistical analyses were conducted in R (R version 4.1.1; R Core Team, 2021). A PCA was initially used to explore the associations between variables, using the 'FactoMineR' package (Le et al. 2008), with p-values obtained via the 'InPosition' package (Beaton et al. 2014). However, the number of behavioural variables were not effectively reduced via PCA (see Table S3), and were considered individually. To determine the predictors of behaviour for all of the fish, the repeated behaviours observed during the behavioural assays (i.e., behaviour following stimuli, activity, use of zones) were used as the response variables in mixed models created with the 'lme4' package (Bates et al., 2014), with p-values attained using the 'lmerTest' package (Kuznetsova et al. 2017). Behaviour was first assessed using all tested fish ($N = 215$ fish), with initial body mass (continuous; range: 2.6–20.8 g), arena water temperature (continuous; range: 6.8–14.1 °C), performance under stress (i.e., growth rate during 9-day testing period); continuous; range: −2.70–2.15), type of test (categorical, 3 levels: open field, bead, food) and number of tests (categorical, 4 levels: 1–4) included as the fixed effects, while individual ID (to control for the repeated tests) and family ID were set as random effects. The personality assays were conducted across a change of seasons, from winter into spring, and fish housing was not fully insulated from the outside; consequently, the temperatures in the experimental arenas were lower during winter; temperature was used as a covariate in the models to control for this variation. To account for individual differences in acclimation speed to the repeated tests, random intercepts and slopes were modelled, with covariance between individual ID and the number of tests. As nesting of individuals within the trial and family groups occurs automatically with lmer models due to the data structure (i.e.,

providing unique identifiers per variable; Bates 2010), nesting of the random effects was not specified in the models. Variance inflation factors were checked for all predictor variables using the 'car' package (Fox and Weisberg 2019) and tended to be low (i.e., <2; Akinwande et al. 2015), while normality of residuals was again assessed via diagnostic q-q plots for each model to validate the use of linear mixed effects models (Pinheiro and Bates 2000). For behaviour observed throughout the four repeated personality tests, repeatability with bootstrapped confidence intervals were calculated using the 'rptR' package (Stoffel et al. 2017).

Respirometry

We used a subset of the fish for respirometry testing, while the remainder of the personality-tested fish were used in another experiment (unpubl). SMR was evaluated once for the tested fish SMR (sensu Behrens et al. 2020; Shen et al. 2021). The package 'mclust' was used to calculate SMR via the MLND, CV_{MLND}, and $q_{0.2}$ (Scrucca et al. 2016). Equation 3 was then applied to the calculated SMR values, and these mass-adjusted values of SMR were then used in all subsequent models. Specifically, using the behavioural variables as the response variable (similar to described above), these models were repeated with the subset of fish tested via respirometry ($N = 39$), with the mass-adjusted SMR (continuous; range: 14.71–53.64 MO_2) as an additional fixed effect. For these models, metabolic chamber (categorical, 4 levels: 1–4) was included as the random factors using the 'lme4' package in R. Variance inflation factors of the predictor variables were found to be low (i.e., <2; Akinwande et al. 2015), using the 'car' package (Fox and Weisberg 2019), while normally distributed residuals were observed for each model using diagnostic quantile–quantile (q–q) plots (Pinheiro and Bates 2000). Then, structural equation models (SEM) were constructed via the 'lavaan' package (Rosseel 2012) to determine the relationships between mass-adjusted SMR, initial body mass, and performance under stress. Seven models representing all possible relationships were constructed (Fig. 2) and compared via AIC, then estimates for the relationships between variables were extracted from the best model (i.e., Hennin et al. 2018; Steenweg et al. 2022).
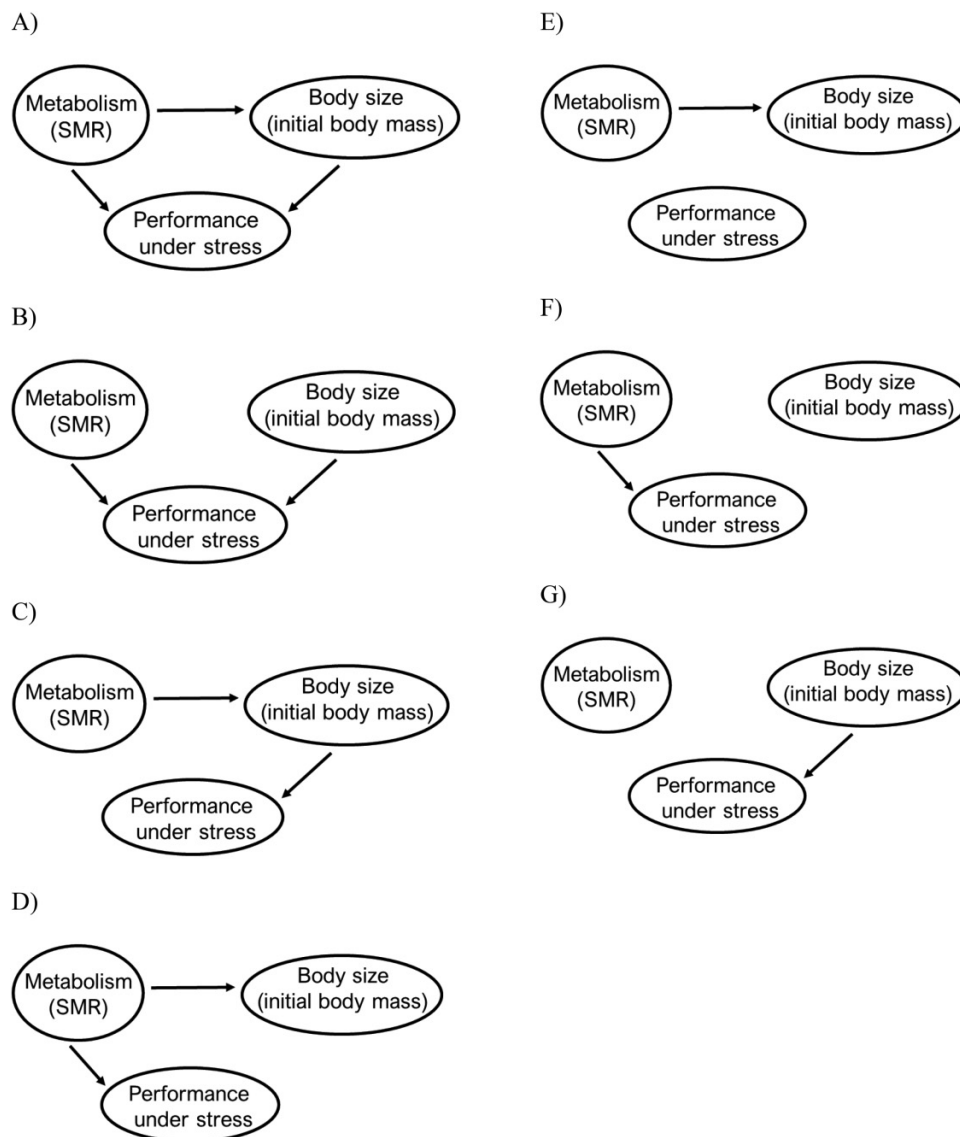
Mortality

Initial body mass and performance under stress of fish that died during the experiment were compared to fish that survived for the duration of the experiment via Welch's t-tests. Cox regression was then performed using the "survival" package (Therneau 2022) to assess the effects of these three variables on the survival period of the deceased fish, or the number of days past the first test the fish remained alive (continuous; range: 1–8).

Distribution of data

Finally, K-means clustering tools from the package 'cluster' (Maechler et al. 2021) were used to determine whether (i) the behavioural data per fish from all repeated trials and

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2011

Fig. 2. Potential models representing all possible relationships between mass-adjusted SMR, body size, and performance under stress, evaluated via structural equation modelling (SEM).

Results

Behavioural trials

As expected (i.e., Elias et al. 2018), fish became acclimated to both the food and the bead following repeated exposure, showing an increasingly dampened response to stimuli across the repeated tests (Table 3). This pattern was similar for both the bead and food, implying similar acclimation to both types of stimuli, with no significant interaction between stimuli type and the number of tests (LMM, $F_{3,1432} = 0.18$, $p = 0.91$; Fig. 3). Fish also showed acclimation to the arena over time by travelling shorter distances across the four repeated tests (Fig. 4A). Additionally, time spent moving in the gravel decreased across the repeated tests (Table 3).

Fish spent more time moving and travelled further during the open field test than during the bead and food tests (Fig. 4B). This increased activity was not restricted to a particular zone and was higher in all three zones (Table 3). In contrast, although activity was positively affected by temperature (mean $\pm$ SD: 9.46 °C $\pm$ 1.68 °C), with fish spending more time moving and travelling farther distances in warmer temperatures (Table 3), fish were more active only in the periphery and the gravel, but not in the centre of the arena, when temperatures were warmer (Table 3).

across all test types, and then (*ii*) the combined behavioural and physiological (i.e., performance under stress; initial body mass, and length) data for all fish, exhibited a bimodal distribution. First, the gap statistic method was run, with 50 initial configurations, to determine the optimal number of clusters; this is done by comparing the total intracluster variation with the expected values of a reference distribution with no obvious clustering, generated using Monte Carlo simulations (Tibshirani et al. 2001). If the optimal number of clusters was ≥ 2, we then ran a final analysis with the optimal number of clusters determined by the gap statistic to extract the final data, including the cluster means.

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Table 3. Predictive factors of behavioural changes for different response variables, and their estimates and calculated repeatability in hatchery-raised *Salmo salar* (N = 215 fish) parr during the individual behavioural assays. P-values were obtained from anova outputs, while variable estimates were obtained from model summaries of final mixed models.

Response variable	Significant factors	Estimate [LCI, UCI]	Behavioural changes	Repeatability [LCI, UCI]
Response to stimuli	Initial body mass (p = 0.0043)	−0.03 [−0.04, −0.009]	• Smaller fish respond more than larger fish	0.125
	Type of test (p = 0.00013)	0.15 [0.07, 0.22]	• Fish respond less after bead, more after food	[0.084, 0.182]
	Number of tests (p < 0.00001)	−0.09 [−0.12, −0.05]	• Fish respond less across repeated tests	—
	Temperature (p = 0.0011)	0.04 [0.02, 0.07]	• Fish respond more in warmer temperatures	—
Overall activity	Initial body mass (p = 0.00008)	−5.67 [−8.42, −2.91]	• Smaller fish more active than larger fish	0.224
	Type of test (p < 0.00001)	58.32 [48.65, 67.98]	• Fish more active in open field test	[0.156, 0.297]
	Number of tests (p = 0.01)	−8.17 [−14.35, −1.98]	• Fish less active across repeated tests	—
	Temperature (p < 0.00001)	9.17 [5.70, 12.64]	• Fish more active in warmer temperatures	—
Distance travelled	Type of test (p < 0.00001)	473.07 [318.80, 627.34]	• Fish travel farther in open field test	0.192
	Number of tests (p = 0.023)	−76.72 [−142.46, −10.98]	• Fish travel less across repeated tests	[0.147, 0.239]
	Temperature (p < 0.00001)	212.72 [164.27, 261.17]	• Fish travel farther in warmer temperatures	—
	Performance under stress (p = 0.066)	145.49 [−8.62, 299.60]	• *Fish that grow more travel farther[a]*	—
Activity in centre	Initial body mass (p = 0.000025)	−1.29 [−1.88, −0.70]	• Smaller fish more active than larger fish	0.205
	Type of test (p < 0.00001)	8.15 [5.74, 10.55]	• Fish more active in open field test	[0.163, 0.25]
Activity in periphery	Initial body mass (p = 0.0049)	−3.98 [−6.71, −1.24]	• Smaller fish more active than larger fish	0.208
	Type of test (p < 0.00001)	46.87 [36.63, 57.10]	• Fish more active in open field test	[0.153, 0.278]
	Number of tests (p = 0.003)	−9.68 [−15.99, −3.36]	• Fish less active over time	—
	Temperature (p < 0.00001)	13.16 [9.53, 16.79]	• Fish more active in warmer temperatures	—
Activity in gravel	Initial body mass (p = 0.012)	−0.15 [−0.27, −0.04]	• Smaller fish more active than larger fish	0.170
	Type of test (p < 0.00001)	1.75 [1.28, 2.21]	• Fish more active in open field test	[0.126, 0.213]
	Test number (p = 0.033)	−0.24 [−0.46, −0.02]	• Fish less active across repeated tests	—
	Temperature (p = 0.01)	0.20 [0.05, 0.34]	• Fish more active in warmer temperatures	—
	Performance under stress (p = 0.097)	0.38 [−0.07, 0.82]	• *Fish that grow more are more active*	—

[a]0.05 ≤ p < 0.1 for factors with italic font.

Smaller fish spent more time active than larger fish across all tests (Fig. 5). As well, smaller fish did not restrict their activity to a particular zone, and were more active in all three zones. Distance travelled was not affected by initial body mass (LMM, $F_{1,2148} = 0.31$, $p = 0.58$; Table 3).

All behaviours observed during the individual assays were significantly repeatable for individual fish across the four tests (Table 3). Performance under stress did not predict the response to stimuli for either the bead or food (LMM, $F_{1,1492} = 0.02$, $p = 0.88$), although fish that performed better (i.e., grew more during the experimental time period) tended to travel farther and spent more time moving in the gravel (Table 3).

Performance under stress

Smaller fish exhibited higher performance under stress (i.e., growth rate) during the 9-day personality testing period than larger fish (LMM, $F_{1,190} = 15.06$, $p = 0.00016$; Fig. 6). As

Fig. 3. Mean ± SE of behaviour immediately following exposure to a novel object (a bead), and food (previously frozen mysis shrimp) for hatchery-raised *Salmo salar* parr during the bead and food tests ($N = 215$). Positive numbers indicate increased movement, while negative numbers indicate decreased movement. Note that beads were distinct in appearance across the repeated tests, to maintain novelty. Different letters indicate statistically significant differences.
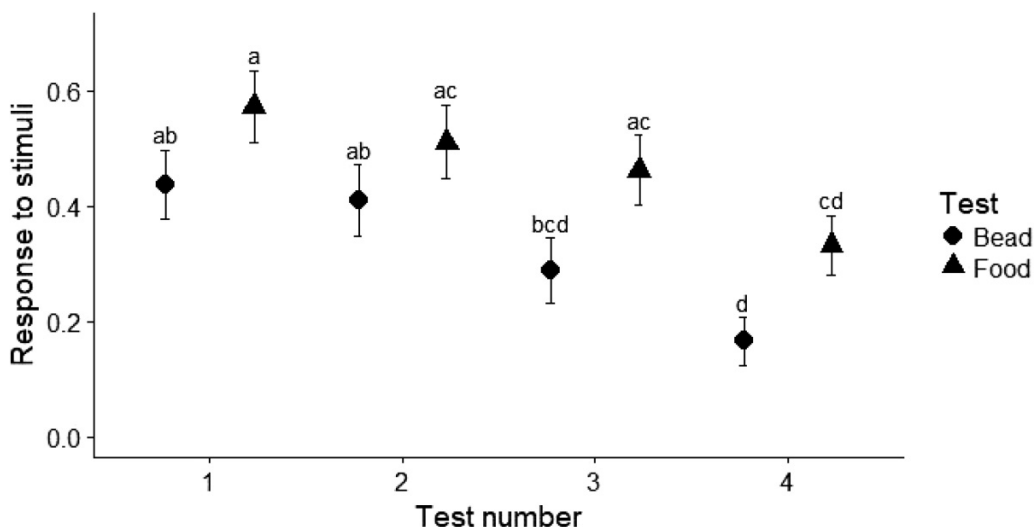

Table 4. Comparison of models linking performance under stress (i.e., growth rate during the testing period), mass-adjusted SMR, and initial body mass, using structural equation models (SEM) in hatchery-raised *Salmo salar* ($N = 39$ fish) parr.

Model	AIC	ΔAIC	Likelihood	RMSEA
B	1196.746	0	−595.373	0
G	1236.051	39.305	−616.025	0
F	1256.438	59.692	−626.219	0
E	1282.414	85.668	−639.207	0
D	2479.160	1282.414	−1234.580	0
A	2479.160	1282.414	−1234.580	0
C	2518.465	1321.719	−1255.233	0.293

well, initial body mass and performance under stress were similarly related in the subset of fish tested via respirometry ($N = 39$), as smaller fish had higher performance than larger fish (LMM, $F_{1,39} = 7.79$, $p = 0.0085$).

Respirometry

No relationships were found between mass-adjusted SMR and behaviour, including distance travelled, responses to stimuli, overall time spent moving, or time spent moving in the different zones (LMM's, all p's > 0.13). Mass-adjusted SMR (mean ± SD: 28.79 ± 9.976) was not found to be related to initial body mass (LMM, $F_{1,39} = 2.38$, $p = 0.13$; Fig. 7). In contrast, fish with higher mass-adjusted SMR lost less weight under stress, exhibiting higher performance under stress during the 9-day personality testing period than fish with lower SMR (LMM, $F_{1,39} = 6.24$, $p = 0.017$; Fig. 8).

The best structural equation model included relationships between performance under stress and SMR, and between performance under stress and initial body mass, but not between SMR and initial body mass (Fig. 2; Table 4). Within this model, higher SMR was associated with higher performance under stress, or increased growth during the trials (SEM,

estimate = 0.277, $z = 6.57$, $p < 0.00001$), while lower initial body mass was associated with higher performance under stress (SEM, estimate = −0.342, $z = −8.12$, $p < 0.00001$).

Mortality

Out of the 215 fish that underwent the repeated personality tests, 181 survived throughout the testing period, while 34 fish died before the completion of the four personality tests (Fig. 9). No deceased fish were observed with visible signs of injury, and mortality rates were similar before, during and after the testing period (K.D.W. Church and L. Nguyen-Dang, personal observations). Of the fish that died, 25 fish were only tested once, 6 were tested twice, and 3 were tested three times. Fish that died during testing did not differ in their behaviour following exposure to the bead or to food, or in their time spent moving or space use, relative to fish that survived the testing period (LMMs, all p's > 0.25). Relative to the fish that survived for the entire testing period, the 34 fish that died showed no statistically detectable differences in mean initial body mass (Welch's t-test, $t_{50} = 0.75$, $p = 0.45$; mean ± SD: survived, 7.525 g ± 2.867 g; died, 7.163 g ± 2.512 g). The 9 fish that were tested at

Fig. 4. Mean ± SE of (A) distance travelled, and (B) time spent moving, during the open field, bead, and food tests for hatchery-raised *Salmo salar* parr (*N* = 215 fish), across all repeated testing periods combined. Different letters indicate statistically significant differences.
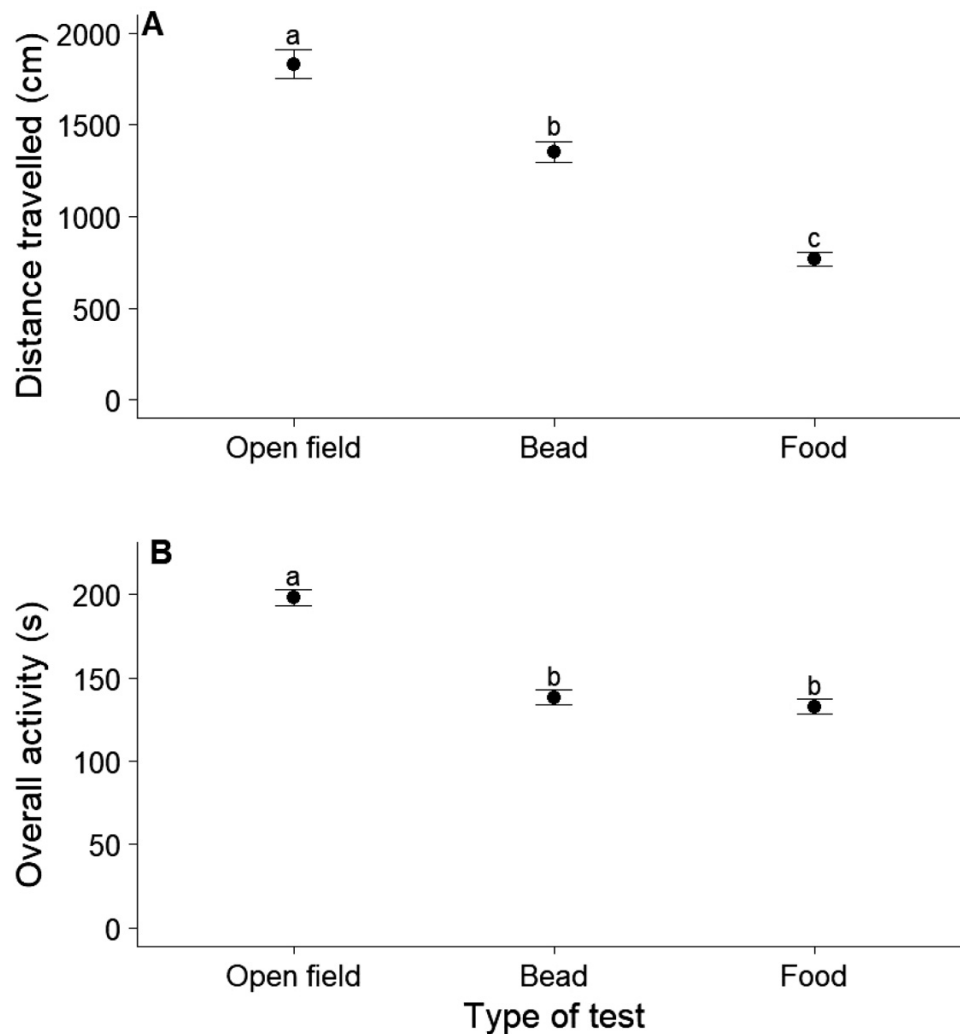
least twice before dying did not differ in their performance under stress relative to fish that did not suffer mortality (Welch's *t*-test, $t_8 = -0.79$, $p = 0.45$; mean ± SD: survived, −0.803 g ± 0.774 g; died, −0.489 g ± 1.173 g). The length of the survival period for the fish that died (mean ± SD: 3.41 days ± 1.79 days) was not related to initial body mass (Cox regression, $z = 0.96$, $p = 0.34$). For the 9 fish that were tested at least twice, fish that survived longer tended to have lower performance under stress (Cox regression, $z = 1.71$, $p = 0.087$).

Distribution of data

The clustering approach was used to determine whether a two-cluster model, as predicted by POLS hypothesis and prior demonstrations of animal personality, fit the data better than a single continuous distribution. The gap statistic for the behavioural data, for all fish from all repeated trials and across all test types, only revealed that the data were best distributed into two clusters (within cluster sum

of squares = 21.5%). K-means clustering showed that the first cluster represented lower overall activity and lower responsiveness to stimuli, while the second cluster represented higher overall activity and higher responsiveness to stimuli. Activity differed during all three tests and in all zones of the arena. Similarly, two clusters were also revealed when both the behavioural and physiological data were considered together (within cluster sum of squares = 18.6%), with lower performance under stress and larger initial body mass and length associated with lower overall activity.

Discussion

In this study, we tested the POLS hypothesis in hatchery-reared Atlantic salmon parr. We found that standard metabolic rate (SMR) was not associated with personality, in contrast to POLS. Also contrary to POLS, fish with smaller body size, a correlate of slower growth (as fish were the same age), were more active overall than larger fish, and increased

Fig. 5. Mean ± SE of (A) behaviour immediately following exposure to stimuli during both the bead and food tests, and (B) time spent moving, during all three observation periods (open field test, bead test, food test), for hatchery-raised *Salmo salar* parr (N = 215 fish) across all repeated testing periods combined. Positive numbers indicate increased activity, while negative numbers indicate a decrease in activity, as summarized in Table 3. All fish were the same age.
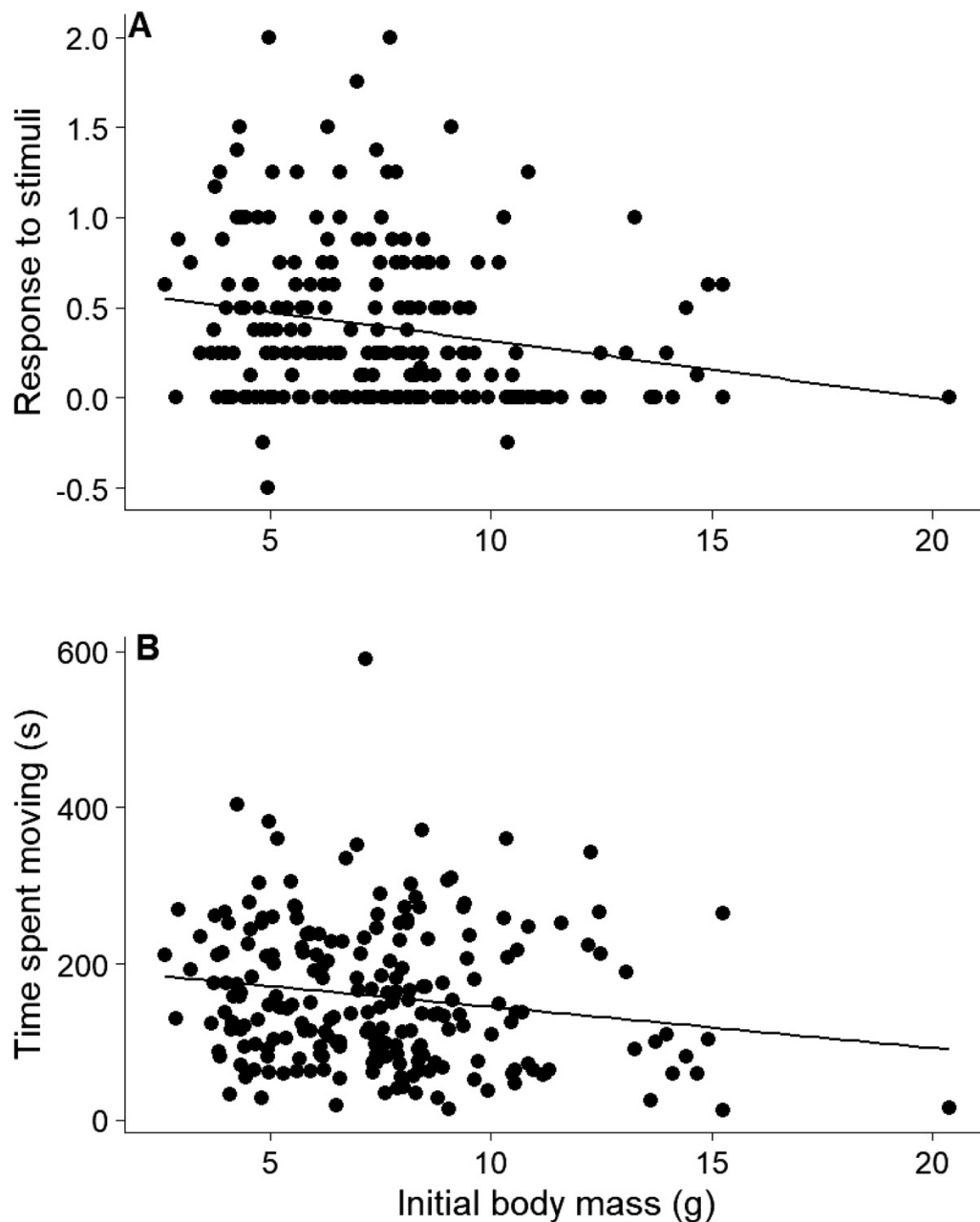
their activity more than larger fish following exposure to a stimulus. Performance under stress during the personality testing period, a correlate of stress tolerance, was also not associated with personality; as well, mortality rates during this period were unrelated to personality, body size, and performance under stress. Although smaller fish did perform better under stress than larger fish, as predicted by POLS, this was not due to lower metabolic costs, as no relationship was detected between SMR and body size for the sample size and body mass range in the present study. Additionally, fish

with higher SMR also lost less weight under stress, exhibiting higher performance under stress than fish with lower SMR, contrary to POLS. Finally, a bimodal distribution with two distinct clusters of "fast" and "slow" activity were detected within the behavioural data, similar to what has been seen in wild brown trout (Näslund and Johnsson 2016). However, when physiological variables were also included, high activity was associated with smaller fish and better performance under stress, while low activity was associated with larger fish and lower performance under stress, suggesting

Fig. 6. Initial body mass (i.e., mass at the time of PIT tagging) and performance under stress (i.e., growth rate) during the testing period of hatchery-raised *Salmo salar* parr (N = 190 fish, p = 0.00016). Fish were the same age and underwent repeated behavioural assays and exposure to two stressors (PIT tagging, simulated facility move) during the testing period.
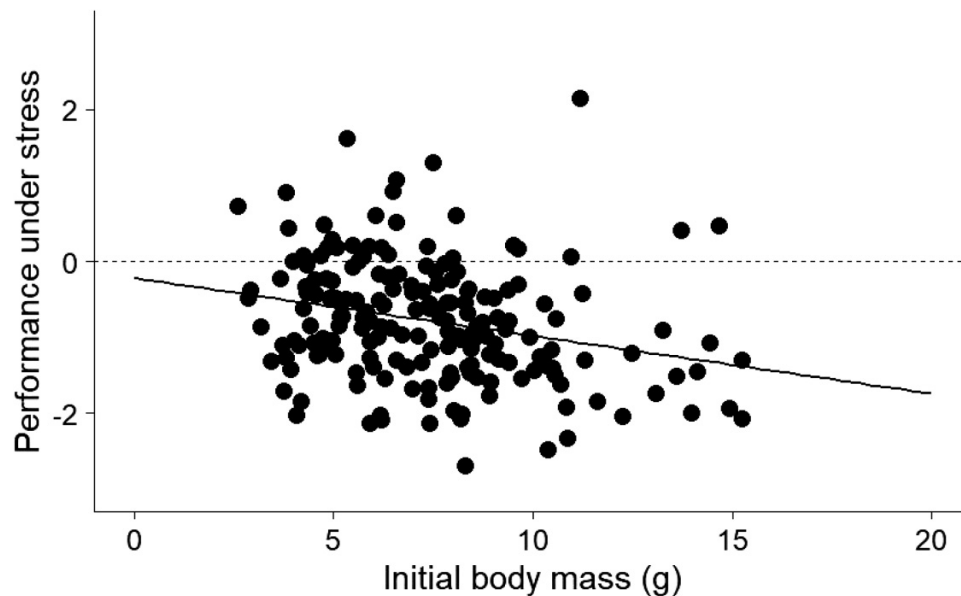
Fig. 7. Mass adjusted metabolic rate (SMR), tested via intermittent flow respirometry, in relation to the initial body mass of *Salmo salar* parr (N = 39 fish) at the beginning of the 9-day personality testing period. As fish were all the same age, initial body mass is a correlate of growth rate prior to the start of the experiment.
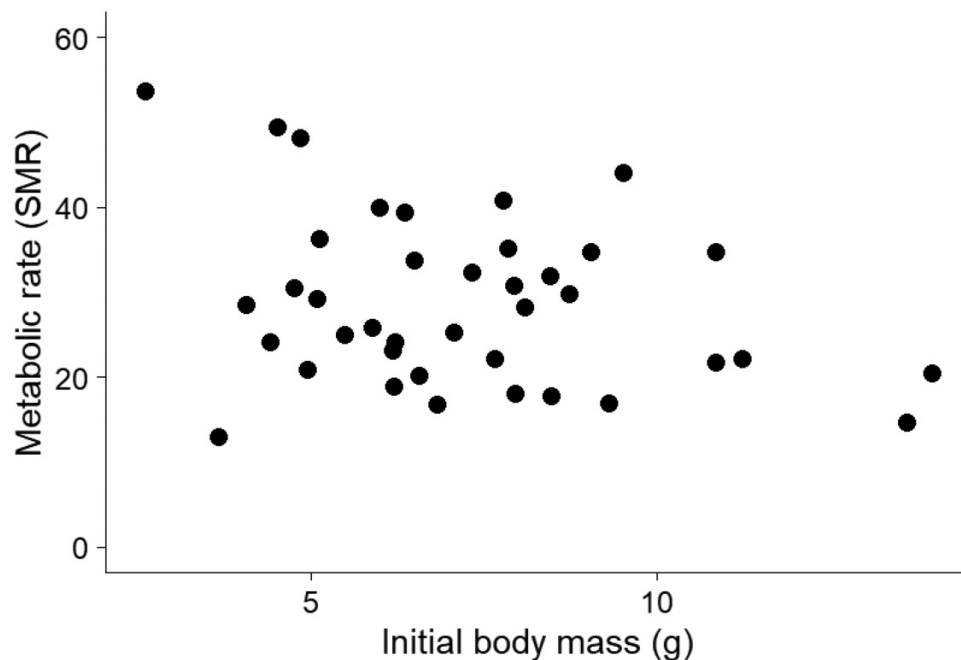
that POLS is not supported in this population of hatchery-raised *S. salar*.

Personality

Personality is often inferred from repeatable behaviours that differ among individuals. Our results for personality show low but significant repeatability for activity, space use, and behavioural changes following stimuli that ranged from

0.125 to 0.224. Although these repeatability estimates are low relative to the overall mean of 0.37 observed for behavioural traits across a broad range of taxa, they fall within the mode (i.e., repeatabilities between 0.1 and 0.2; Bell et al. 2009). Comparable repeatabilities of 0.287 and 0.206 were found for avoidance and site attachment behaviours, respectively, in a semi natural field experiment with juvenile Atlantic salmon (Church and Grant 2018). However, repeatability estimates

Fig. 8. Performance under stress (i.e., growth rate) during the 9-day personality testing period, of hatchery-raised *Salmo salar* parr (N = 39 fish) in relation to mass adjusted standard metabolic rate (SMR), tested via intermittent flow through respirometry. Fish were not expected to show natural growth during the testing period, due to exposure to two stressors: anesthetization, followed by injection of a PIT tag, and simulated vehicle transport.
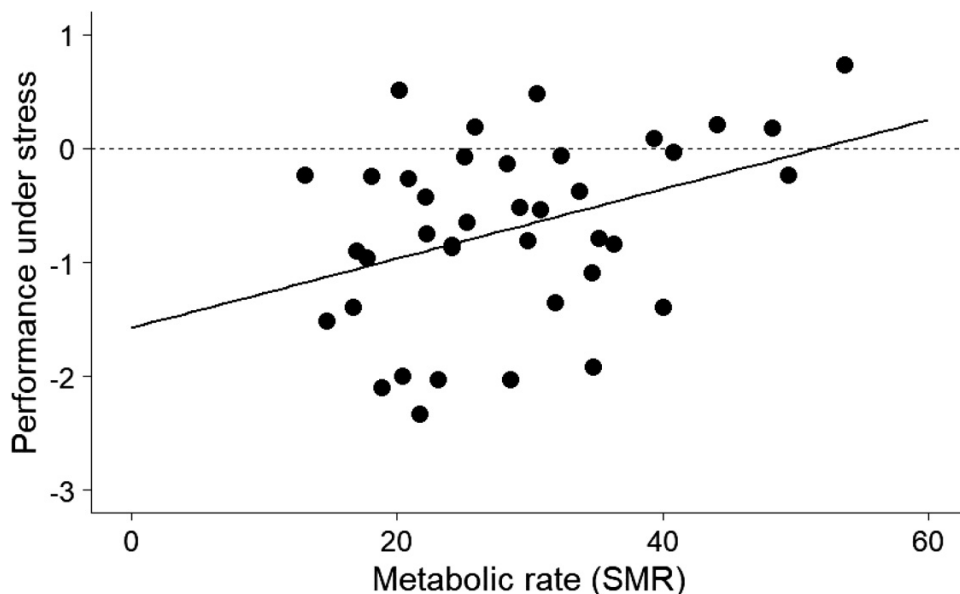
Fig. 9. Histogram of survival period following tagging, for hatchery-raised *Salmo salar* parr that died during the 9-day testing period (N = 34).
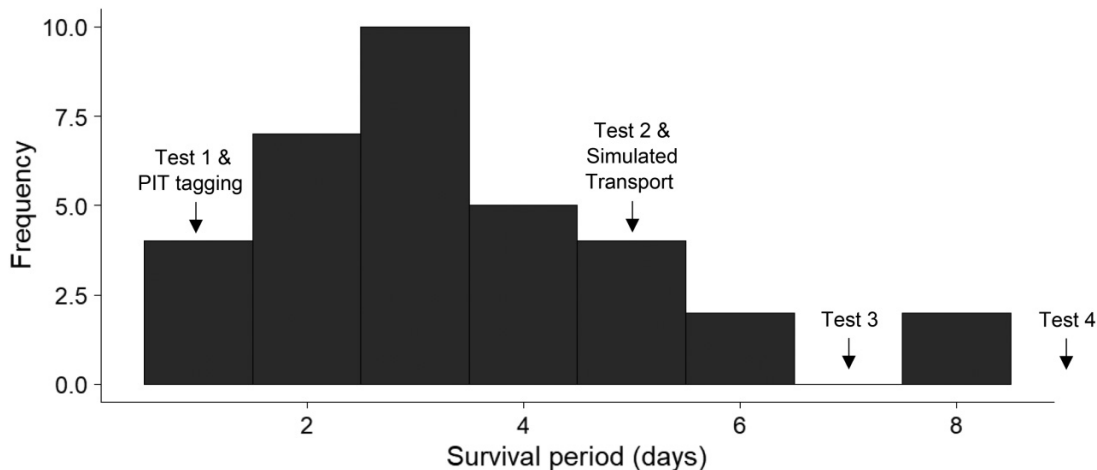
can be highly variable across studies (Bell et al. 2009), and substantially higher repeatabilities of 0.45 to 0.51 were found in a series of laboratory open field tests with juvenile arctic charr (*Salvelinus alpinus*; Philip et al. 2022), while repeatabilities of 0.503 to 0.753 were found in a field study on migratory behaviour in sea trout (*Salmo trutta*; Birnie-Gauvin et al. 2021). Likewise, mass-adjusted SMR values were low relative to other salmonids, including Atlantic salmon smolts (123 mg O^2 kg^{-1} h^{-1}, Hvas and Oppedal 2019) and post-smolts (84 mg O^2 kg^{-1} h^{-1}, 65 mg O^2 kg^{-1} h^{-1}, Hvas et al. 2020), juvenile rainbow trout (*O. mykiss*; 57 mg O^2 kg^{-1} h^{-1}, 114 mg O^2 kg^{-1} h^{-1}, Rao 1968; ~120 mg O^2 kg^{-1} h^{-1}, Darcy et al. 2019) and lake trout (*Salvelinus namaycush*; 47 mg O^2 kg^{-1} h^{-1}, Gibson and Fry 1954; 108 mg O^2 kg^{-1} h^1,

Beamish et al. 1989; 108 mg O^2 kg^{-1} h^{-1}, Darcy et al. 2019), but comparable to mass-adjusted SMR measures for similarly sedentary, benthic species (i.e., ~28 mg O^2 kg^{-1} h^{-1} for family Cottidae; Steffensen et al. 1994). As aggressive behaviour is generally associated with dominance in salmonids (i.e., Metcalfe et al. 1995; Cutts et al. 1998; Reid et al. 2011; but see Sloman et al. 2000), more research is needed to determine whether the low SMR values in our study may be associated with the atypically low aggression these fish exhibited in their holding tanks. Surprisingly, we found no relationships between personality and SMR in hatchery-raised *S. salar*. Analogous to our findings, relationships between personality and metabolic rate were also not detected in wild and hatchery-reared brown trout (*Salmo trutta* L; Prokkola et al. 2021),

captive-raised guppies (*Poecilia reticulata* W. Peters, 1859; White et al. 2016), or in wild-caught pike (*Esox lucius* L.; Laskowski et al. 2016). On the other hand, contrary to our findings, positive relationships between personality traits and metabolism have been found in both hatchery-raised and wild species. For example, bolder and more competitive captive-bred common carp (*Cyprinus carpio* L.) showed higher SMR and lower levels of stress metabolites (Huntingford et al. 2010), while bolder wild juvenile bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819) demonstrated greater metabolic scope and higher maximum metabolic rates, but no differences in SMR, relative to shyer individuals (Binder et al. 2016). As well, a study on POLS in captive-raised guinea pigs (*Cavia aperea*) found only partial integration of personality with life-history, suggesting that a lack of consideration of complex interactions between ecological and biological factors and behavioural or physiological traits may limit the generalizability of POLS (Guenther 2018).

Metabolism

The relationships between metabolism and body size, and between metabolism and stress tolerance, are not always straightforward due to the complexities of energy consumption and allocation. Similar to our findings, Cutts et al. (1998) also found no relationship between SMR and growth for juvenile hatchery-raised *S. salar*; likewise, no relationship between SMR and growth was found for wild tadpoles (*Rana temporaria*; Lindgren and Laurila 2009). Álvarez and Nicieza (2005) also found growth rates to be unrelated to SMR for two out of four populations of wild brown trout (*S. trutta*), although growth was negatively related to SMR in the remaining two populations, in contrast to our results. As well, growth rates were also negatively related to SMR in wild juvenile snapping turtles (*Chelydra serpentina*; Steyermark 2002). In terms of SMR and performance under stress, Pottinger and Carrick (2001) also found that fish with higher SMR performed better under stress, as dominant hatchery rainbow trout (*Oncorhynchus mykiss* [Walbaum, 1792]), which often show higher SMR (i.e., McCarthy 2001), exhibited less stress following staged pairwise fights than subordinates of the same size (Pottinger and Carrick 2001). Likewise, subordinate hatchery rainbow trout also showed higher stress overall, relative to dominants (Gilmour et al. 2005). Higher SMR may enable better responses to external stressors due to lower internal stress, as wild *S. trutta* with higher SMR have been found to suffer lower rates of oxidative stress, an inevitable by-product of metabolism (Sopinka et al. 2016), relative to fish with lower SMR (Salin et al. 2015). Metabolic scope, or the difference between SMR and the maximum aerobic metabolic rate (AMR) obtained during sustained locomotion (Fry 1947), as well as routine metabolic rate (RMR), the metabolic rate during normal activity (Fry 1957), are additional measures of metabolism that we did not account for in this study, that may be related to growth rate or be more predictive of an individual's performance under stress. Further study will help to elucidate the effects of different components of metabolism on growth and stress tolerance.

Stress tolerance

Large body size for a given age is generally facilitated by faster metabolic activity and faster growth, and can be energetically costly to maintain. In our study, we found no relationship between growth rate (i.e., initial body mass) and SMR, contrary to expectations. Also contrary to predictions, the increased stress tolerance of fish with slower growth rates (i.e., smaller fish) was not due to lower energy maintenance costs (SMR). Instead, fish with higher SMR, found to be independent of body mass, a correlate of growth rate in our study, performed better under stress, characterized by better performance during the testing period. Similar to our findings, smaller hatchery-reared *O. mykiss* were less vulnerable to handling and transportation stress relative to larger individuals (Dabrowski and Ciereszko 1993). There is also evidence that smaller fish may take less time to recover from stress than larger fish. In a study of hatchery-raised European sea bass (*Dicentrarchus labrax* L.), smaller individuals recovered more quickly than larger fish after exposure to various stressors (Fatira et al. 2014), with a similar result found in hatchery *O. mykiss* (Goolish 1989). Similarly, wild smaller-sized largemouth bass (*Micropterus salmoides* [Lacepède, 1802]) required less time to recover following intense exercise due to lower concentrations of plasma glucose and sodium (Gingerich and Suski 2012). However, this does not seem to be a general rule, as smaller captive-raised zebrafish (*Danio rerio* [Hamilton, 1822]; Ramsay et al. 2006) and wild sharks (*Sphyrna mokarran* [Rüppell, 1837], *Carcharhinus leucas* [Valenciennes, 1839], *Carcharhinus limbatus* [Valenciennes, 1839], *Negaprion brevirostris* [Poey, 1868], *Galeocerdo cuvier* [Péron & Lesueur, 1822]; Gallagher et al. 2014) showed higher stress than larger fish. It appears that the relationship between growth rate and performance under stress may be species-, population-, or environmental-dependent, and warrants further exploration.

Mortality

Previously extirpated populations of Atlantic salmon in the Great Lakes have yet to be re-established despite decades of stocking efforts. Indeed, when released into Lake Ontario, hatchery-raised Atlantic salmon experience estimated mortality rates of 99.8% (Stewart and Johnson 2014). Although mortality occurred during this study, 15.8% mortality of parr was considerably lower than the 44.4% mortality observed for fry of the same strain in a previous study (Houde et al. 2015). Mortality rates of hatchery-raised *S. salar* during the personality testing period were unrelated to personality, performance under stress, and body size. Similar to our findings, mortality rates were also not associated with stress in wild-caught captive reared sablefish (*Anoplopoma fimbria* [Pallas, 1814]; Davis et al. 2001), while mortality of wild-caught *S. trutta* was unrelated to activity observed in the lab (Závorka et al. 2015). Although mortality rates of *O. mykiss* were higher for faster growing fish in the wild, this only occurred in the presence of predators (Biro et al. 2006). As an evolutionary hypothesis, POLS correlations arise from both genetics and adaptive responses to the environment, and thus may not be expected in an artificial predator-free hatchery

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environment. Indeed, the existence of POLS depends on particular selective pressures that may differ between populations (Réale et al. 2010). For example, support for POLS was only found in the captive-raised descendants of one of two populations of Eastern mosquitofish (*Gambusia holbrooki* Girard, 1859) facing different ecological conditions, which suggests POLS is able to evolve independently within different populations (Polverino et al. 2018). Additionally, the expected trade-offs between risk and reward that underlay POLS may not always apply to salmonids due to their territoriality, as fish compete for territories that offer both access to food and protection from predators (Näslund et al. 2017). Although POLS may exist in other domestic *S. salar* populations (i.e., Damsgård et al. 2019), we found no evidence that it exists in our hatchery-raised one.

Conclusion

A key objective of restoration effects is to promote a more natural distribution of behavioural and physiological traits among hatchery-raised fish. Hatchery-raised fish often exhibit differences in behaviour and physiology, especially growth rates, relative to wild fish. According to POLS, we identified two separate groups of less and more active fish; however, contrary to POLS, less active fish were also larger and performed worse under stress, while the opposite was found for more active fish. This lack of accordance with POLS may be due to the preferential selection for faster growth common in hatchery environments (i.e., Vainikka et al. 2010; Saikkonen et al. 2011); another factor is the decoupling of behaviour, metabolism, and growth that sometimes occurs in captive environments, which can lead to non-adaptive deviations from POLS (Killen et al. 2013). As well, hatcheries are generally expected to select against stress sensitivity in fish, as highly stress-sensitive phenotypes are less productive and tend to suffer more negative consequences in captivity (i.e., Ashley 2007; Solberg et al. 2013). However, selection may be limited for rare strains or those that lack genetic variability. Although POLS was not supported in our study, we did identify a negative relationship between body size and performance under stress. This finding suggests that promotion of larger body sizes and faster growth rates in hatchery-raised Atlantic may also promote poor performance under stress.

As restoration efforts benefit from a more balanced release of life history traits into natural environments, including a mix of both faster and slower growing individuals, fish released from hatcheries may not be appropriate for the restoration or supplementation of wild populations (i.e., Härkönen et al. 2014; Buoro et al. 2016). To remedy this, the identification (and indeed, promotion) of robust relationships that reintegrate these different traits within hatchery populations should be capitalized upon, as these individuals are likely better suited for release into the wild. Our findings indicate that to maximize production as well as viability under stress, hatcheries are likely to benefit from prioritizing a wider range of growth rates and body sizes, rather than exclusively promoting larger, faster-growing fish.

Article information

History dates

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Data availability
The data that support the findings of this study are available from the corresponding author, KDWC, upon reasonable request.

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Author contributions
CADS and BDN conceived and designed the experiment; KDWC and LN-D conducted the behavioral tests on the *S. salar*; KDWC analyzed the data and wrote the article; and KDWC, BDN, and CADS interpreted the data. All authors revised and commented on drafts of the article.

Competing interests
The authors declare there are no competing interests.

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