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Thermal regime shapes metabolic effects on growth, survival, and migration in salmonid fish

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Author Contributions

Fieldwork and sample collection was conducted by Peter Betts, Eoin O'Gorman, Rasmus Lauridsen, and Colin Bull. Sample processing and analysis was conducted by Peter Betts. Peter Betts analysed the results with the input of Eoin O'Gorman, Anna Sturrock, Rasmus Lauridsen and Thomas Cameron. Peter Betts led the writing of the manuscript with support from all coauthors.

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Data and Code Availability

All data and code are provided with the submission and will be freely available within the Essex repository upon acceptance.

Competing Interests

The authors declare that they have no conflict of interest.

Abstract

Climate warming is reshaping freshwater ecosystems, yet how temperature modifies the ecological consequences of metabolic variation in wild populations remains poorly understood. Here, we quantified *in situ* routine metabolic rate, growth rate, migration timing, and survival in juvenile salmonids across a broad latitudinal gradient spanning rivers from Spain to Iceland. Metabolic rate increased consistently with temperature across populations, but its relationship with daily growth depended strongly on thermal regime. Individuals with elevated metabolic rates grew faster in warmer rivers but more slowly in colder rivers, indicating that the fitness consequences of metabolism reverse across thermal environments. Higher metabolic rates were also associated with reduced survival and earlier migration timing, suggesting a trade-off between rapid growth and long-term fitness. Daily summer growth rates were highest at both warm and cold range extremes, implying distinct mechanisms underpinning performance across latitudes. Together, these results demonstrate that thermal regime alters how metabolic phenotype translates into growth, survival, and migration timing in wild fish populations. Warming may therefore change selection pressures on fish populations, not only through direct thermal stress, but also by shifting the balance between energetic demand, resource acquisition, and seasonal energy limitation.

Introduction

Climate warming is restructuring ecosystems worldwide, but predicting biological responses requires understanding not only thermal limits, but how temperature alters the energetic mechanisms underpinning growth, survival, and life-history variation [1–3]. Freshwater ecosystems are particularly vulnerable to warming because of accompanying changes in hydrology, habitat connectivity and generally fewer opportunities for mobility and range shifts within and across river networks [4,5]. Migratory salmonids are especially sensitive to these changes owing to their complex life histories [6], with Atlantic salmon (*Salmo salar*) populations declining throughout much of their native range [7,8]. Meanwhile, brown trout (*Salmo trutta*) habitat suitability is predicted to decline by 40% in the southern portion of their range [9].

The ecological impacts of warming may emerge well before organisms approach upper thermal limits, because temperatures that maximise fitness are often considerably lower than those inducing acute physiological stress [10]. Understanding how warming reshapes the energetic basis of performance is therefore central to predicting future population dynamics. One of the primary ways temperature influences ectotherm performance is through metabolism, which governs organismal energy demand and allocation [11]. As temperatures rise, metabolic maintenance costs increase, elevating energetic demand even in the absence of growth or reproduction [12,13]. Higher metabolic costs can constrain performance and reduce survival likelihood if energy acquisition does not increase proportionally [14]. However, elevated metabolic rates may also confer ecological advantages due to increased activity, digestion and absorption rates, and thus greater resource acquisition [15–18]. Metabolic phenotype may therefore either

enhance or reduce fitness depending on the balance between energetic demand and energetic gain, but this is likely to vary across thermal environments. Whether this balance changes predictably remains largely unknown because metabolic thermal sensitivity is often assumed to be conserved within species, despite growing evidence for local adaptation [19,20]. Notwithstanding extensive work describing thermal effects on metabolism, far less is known about whether the ecological consequences of metabolic phenotype themselves change across climatic gradients.

In cold, strongly seasonal systems, elevated metabolic costs may be difficult to sustain because feeding opportunities and digestion rates are constrained by low temperatures and reduced prey abundance during long winters [18,21]. Conversely, in warmer and more productive environments, elevated metabolic rates may support greater activity, dominance, and resource acquisition, promoting faster growth and earlier life-history transitions such as migration to sea [22,23]. However, as temperatures approach thermal optima, maintenance demands may rise faster than energy intake, suppressing growth and survival [24,25]. Together, these dynamics predict that the growth consequences of elevated metabolic rate should be greatest at intermediate temperatures but diminish at both cold and warm extremes.

These energetic differences are expected to influence not only somatic growth but also key life-history transitions. Faster juvenile growth is often associated with earlier seaward migration and improved marine survival, and warming has also been linked to migration and maturation timing [26–28]. However, the growth-survival relationship documented in these studies reflects size-selective and condition-dependent marine mortality and does not necessarily extend to the physiological costs of sustaining an

elevated metabolic rate. Because high routine metabolic rate requires consistent, high-rate food intake, individuals with elevated metabolism face increased starvation or predation risk especially during periods of resource shortfall, independent of any growth benefit [16,29]. Faster juvenile growth also allows more fish to reach the smolt threshold after a single freshwater year, reducing cumulative freshwater mortality [30,31]. However, because older and larger smolts generally experience higher marine survival, the lifetime fitness consequences of accelerated freshwater growth remain uncertain [27]. Warming-associated declines in growth and distribution have also been documented in brown trout (*Salmo trutta*), particularly near southern range limits [32]. Metabolic phenotype may therefore shape not only somatic growth, but also migration timing and survival across contrasting environments [23].

Here, we tested whether thermal regime influences metabolic phenotypes and their ecological consequences in wild salmonid populations. We combined *in situ* measurements of routine metabolic rate with growth reconstruction from scale annuli and tagging-based estimates of migration timing and survival of Atlantic salmon and brown trout from six rivers across a broad latitudinal gradient from Spain to Iceland (Fig. 1). We used a series of mixed-effects models to test the following hypotheses: (H1) Metabolic rate exhibits different thermal sensitivity across the latitudinal gradient consistent with local adaptation or acclimation; (H2) Thermal regime modifies the growth consequences of metabolic phenotype, such that high metabolic rates confer a growth advantage at intermediate temperatures but become disadvantageous under both cold and warm thermal extremes; (H3) Elevated metabolic rates lead to earlier juvenile outmigration, but impose a survival cost irrespective of thermal regime, reflecting the inherent risk of a strategy requiring consistently high resource intake.

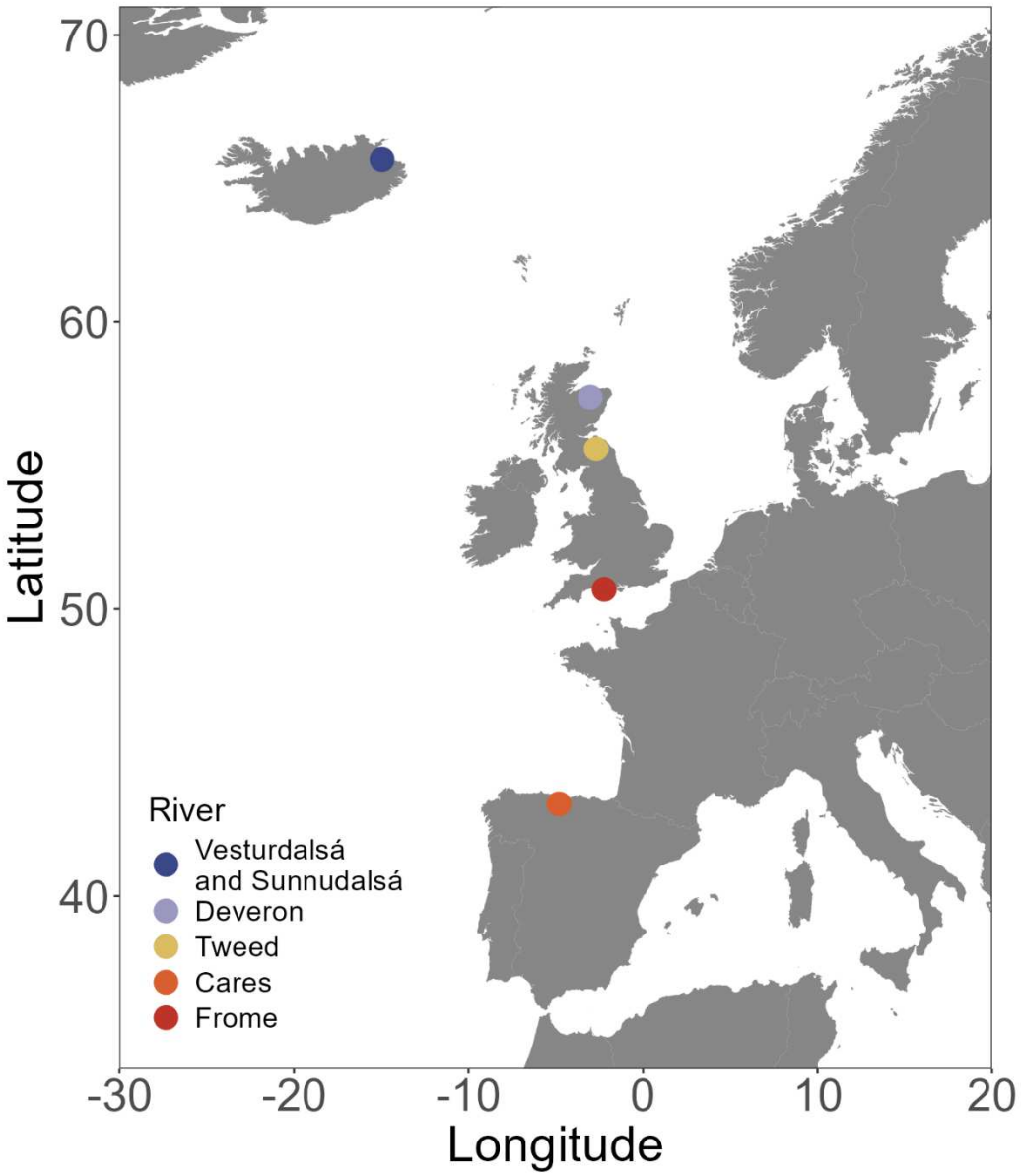


Figure 1 – Map of all sampled rivers coloured by temperature following a gradient of blue (coldest) to red (warmest).

Methods

Sites

Six river systems were selected along the latitudinal range of Atlantic salmon and brown trout, from the Iberian Peninsula to Iceland (Fig. 1). The selected rivers included: the Cares, Frome, Tweed, Deveron, Vesturdalsá, and Sunnudalsá (Table S5). The rivers contained fixed Passive Integrated Transponder (PIT) antenna to allow tracking of both downstream and returning migrations with the exception of the Cares and Sunnudalsá. Sampling for all rivers occurred in late summer of 2023 or 2024, whereby each river was sampled over a week with up to 4 experimental runs per day comprising 21 - 41 fish per run (see Table S5 for full sampling details).

The River Frome is an English lowland chalk stream which flows through highly braided channels and is equipped with nine PIT antenna sites distributed between 50.7167, -2.3539 and 50.6814, -2.2082. The River Cares is a steep, high-gradient mountain river in northern Spain that rises in the Picos de Europa and flows through a deeply incised limestone gorge with confined channels, coarse cobble-boulder substrate, and highly variable discharge regimes. While this river is the most southerly, it exhibits a lower productivity and temperature than the Frome as it is montane. The River Tweed is a gravel-bed river that rises in the Southern Uplands on the border between Scotland and England and flows east through a broad alluvial valley to the North Sea, equipped with two PIT antenna sites deployed during April and May at 55.6212, -2.8159. The River Deveron is a spate-driven upland river that rises in the Grampian foothills in Scotland, with a PIT antenna site at 57.5081, -2.7814. The Vesturdalsá is a short, high-gradient subarctic river in Iceland flowing through confined bedrock and coarse cobble–boulder

channels with step-pool morphology, equipped with three PIT antenna sites between 65.6834, -15.0543 and 65.7390, -14.9248. Finally, the Sunnudalsá is a small subarctic river in northeast Iceland characterised by cold, snow melt inputs through summer with confined channels, and coarse cobble–boulder substrate with alternating riffle–run habitat.

To characterise the water temperatures experienced by the subject animals, we used continuous water temperature records over their lifetime where available (Frome, Tweed, Vesturdalsá, Sunnudalsá), from 2016-2021 for the Deveron, and from August 2014 to August 2015 for the Cares. In all cases, water temperature loggers were located within 5 km of the sample sites. We then calculated mean annual water temperature using all available complete years of data for all rivers (Table S5), which is referred to as mean river temperature hereafter.

An index of productivity was calculated for each sampling site using Normalized Difference Vegetation Index (NDVI), with higher values indicating healthier, denser vegetation. NDVI was obtained from the MODIS MOD13Q1 product (250 m resolution, 16-day composites) using the MODISTools R package [62]. Specifically, for each site, NDVI values were extracted from the MODIS pixel or pixels within 250m of each site and averaged across the 12 months preceding the sampling month (following an established method) [63]. The climate of each system was broadly characterised using local air temperature from all monthly averages of surface temperature (°C) for 1981-2010 from the CRU TS (v. 4.06) dataset (see Table S5). Photoperiod was calculated from site latitude and day of year using astronomical equations implemented in the R package

geosphere [64]. Minimum, maximum, and annual range in daylength were extracted for each site to quantify photoperiod seasonality (see Table S5).

Sampling Regime

For each experimental run, fish were caught by single pass electrofishing until enough fish for an experimental run were captured. A total of 1,043 fish were sampled (Table S5), excluding fish >50 g and >4 years old to keep size and age consistent among rivers. Fish were individually transferred into a 7.2 L closed respirometer, which was filled with river water filtered through a 250 µm sieve to remove any detritus. Each chamber also contained a probe (miniDOT, Precision Measurements Engineering "PME", accurate to 0.01mg/L ± 5%) to measure dissolved oxygen concentrations and experimental temperature every minute, and an underwater motor (Underwater motor: 7350, Playmobil) to circulate the water. Chambers were sealed and checked for air bubbles before being submerged in the river to a depth of 1-20 cm from the lid. Each chamber was then left for 90-120 minutes over which the oxygen consumption rate was measured. Each run also contained a "control" chamber without a fish to measure background respiration. Thus, the oxygen consumption rate and a short-term "experimental temperature" of each fish was measured for each run within each day.

After metabolic measurements, fish were individually transferred into either clove oil or 2-phenoxyethanol anaesthetic. Once fish were under anaesthesia, they were identified to species level, and fork length and wet weight were measured. An 11 x 1.5 mm PIT tag was then surgically implanted in the coelomic cavity, after which a scale sample was taken from each fish's dorsal flank and transferred to a dry scale packet. Fish were then transferred to a recovery holding chamber and released back into the river when they

had fully recovered. Animal handling and processing procedures were approved by the GWCT Animal Welfare and Ethical Review Body and the University of Essex (ETH2324-192) and were carried out by licensed personnel under a UK Home Office ASPA licence (PPL PP9506723).

Metabolic Rate

To calculate routine metabolic rate in the field (RMR_F), a 30-minute habituation period was excluded from all experiments, then 20-minute rolling linear regressions of dissolved oxygen concentration against time were performed across all remaining data. The mean of the lowest 20% of these slopes with $R^2 > 0.8$ was used in the calculation of RMR_F (following a modified version of an established approach and no metabolic rate was calculated if there were no slopes with an R^2 exceeding this threshold (as occurred in 2 % of cases) [65]. The oxygen consumption rate of the organism (mg O_2 h^{-1}) was calculated by multiplying each of the accepted slope values by the volume of the water (i.e. the volume of the chamber minus the volumes of the miniDOT, motor, and fish) and subtracting background respiration, which was modelled linearly over the duration of the experiment in the control chamber.

Growth Estimates

3-5 scales from each individual were gently cleaned in water and mounted on glass slides before being photographed and the scale in the best condition was used to estimate the age of the fish by counting winter checks, see Table S3 [66]. Fish can grow replacement scales if they are lost through damage or injury, but these scales will grow at a different rate and not contain winter checks from previous years [66,67]. Thus, if all imaged scales were replacement scales, then that individual was excluded from further

analysis. Size (fork length) at their first winter check was estimated using the Fraser-Lee method of linear back-calculation based on size-at-capture, and length of scale at winter check, assuming a size at first scale formation of 30 mm [68–70]. This size at first winter check was then converted into growth in mm per day over the growing period (spring – late autumn) by dividing by the estimated number of growing days between emergence and the formation of each fish's first winter check. This required us to estimate an average spawn and first feeding for each river, and to estimate the end of the growing season. Spawning was assumed to be 1st November in the Icelandic rivers [49], 14th November in the Scottish rivers (J. Hunt, personal communication, March 18, 2026), 1st December in the Cares [71], and 1st January on the Frome [72]. Brown trout are known to generally spawn earlier than salmon and so where we did not have a specific spawn date for trout they were assumed to spawn 15 days earlier than the salmon [73]. Note that these estimates followed the established temperature gradient of spawning, i.e. lower temperatures result in earlier spawning [6,74,75].

Average daily river temperature data were used to calculate the most likely fry emergence date for each river. Fry emergence was estimated using a temperature-dependent developmental model in which daily river temperatures were converted to relative developmental units (τ_s), following an established method [76]. These units were cumulatively summed from the spawning date, and emergence was defined as the date at which embryos reached ~450 τ_s, corresponding to emergence from the gravel and first exogenous feeding. River temperature for the year of emergence was used where possible (Frome, Vesturdalsá, Sunnudalsá, and Tweed), or else the average daily temperature from the available data (Deveron and Cares). Finally, the winter check was estimated to form when growth potential for salmonids reached zero, which was

assumed to be approximately 5.2 °C (a temperature experienced by all rivers) [6,77,78]. Thus, average daily growth over the year was calculated and is henceforth referred to as growth rate. Size at first winter was used to minimise ontogenetic effects and maximise our sample size, as many fish were sampled at <2 years old.

PIT Tagging

In total, 786 fish were tagged across the four rivers with PIT tag antenna (Table 1). Detections of tagged fish from each river were processed and the species, size, timing, frequency, and direction of detection were all used to determine smolt periods. Migration date was estimated as the last detection of each fish meeting these criteria, following a modified approach [46]. A total of 85 fish were detected out-migrating from freshwater (11% of the total tagged), which is in line with observed annual juvenile survival rates of 7 - 18% [79]. All outmigration events were for Atlantic salmon, so trout were excluded from all analyses of movement and survival. Detections were monitored until November 2025, at which point salmon that were not detected out-migrating were assumed to have died. This assumption likely holds true for the warmer low latitude rivers where fish migrate within 1-2 years, but may be weaker for the Icelandic rivers where fish typically remain for one to five years [80].

Table 1 – Number of fish by species that were sampled and PIT tagged in each river. The fraction of salmon that were detected out-migrating is also shown.

River	N Total	N Tagged	N Trout	N Salmon	N Salmon detected out-migrating
Cares	171	0	171	0	-
Frome	184	183	88	96	8 (8%)
Tweed	176	165	28	148	9 (6%)
Deveron	188	186	6	182	46 (25%)
Vesturdalsá	252	252	0	252	22 (9%)
Sunnudalsá	72	0	0	72	-
Total	1043	786	293	750	85 (11%)

Statistical analysis

Before all analyses, RMR_F was first mass-corrected by modelling ln metabolism against ln mass for every fish, including an effect of experimental Arrhenius temperature and a random effect of run nested within sampling day nested within system. The slope of this relationship was then used to allometrically correct for body mass following equation 1:[10]

$$I_M = \frac{I}{M^b} \quad (1)$$

Where I_M is mass-corrected metabolism, I is whole organism metabolic rate, M is mass of the organism, and b is the allometric scaling exponent (0.86 in this study).

To determine how metabolism varied *in situ* with temperature across the dataset, ln mass-corrected metabolism was modelled as a function of all main and two-way interactive combinations of experimental temperature, river, age, and species, including a random effect of sampling run nested within sampling day using the '*lmer*' function in the '*lme4*' package and a Type II ANOVA to test significance [81]. Three-way interactions were excluded for parsimony and to aid interpretation as 3-way interactions may lack ecological meaning and this approach was taken for all subsequent modelling. We then applied stepwise model simplification removing non-significant terms until the most parsimonious remained.

I_M was then temperature-corrected to 12°C as follows for all subsequent analyses: [10]

$$I_{MT} = \frac{I_M}{e^{E_A \frac{T-T_0}{kTT_0}}} \quad (2)$$

Where E_A is the activation energy in electron volts (eV) (i.e. slope of the relationship between metabolic rate and Arrhenius temperature, which was 0.36 across all fish), T is temperature in kelvin, T_0 is the mean temperature of all chambers in the study over the measurement period, and k is the Boltzmann constant ($8.617 \times 10^{-5} eVK^{-1}$). This mass- and temperature-corrected metabolism is referred to simply as metabolism within this study.

Growth was then modelled as a function of all possible two-way interactions of ln metabolism, mean river temperature, and species, including a random effect for experimental run nested within sampling day nested within river and a random effect of age class nested within river. Mass was excluded due to expected covariation with age and mass at the end of the first year, i.e. growth. We then undertook backward stepwise

model selection removing non-significant terms until the most parsimonious model remained. The main model included a random effect for age class nested within river as different age classes will have undergone different conditions in their first year of growth. This was also repeated with the same model containing a second order polynomial for temperature to test for a nonlinear unimodal relationship with temperature. The linear and polynomial models were compared using AIC, with the optimal model determined as the lowest value with a difference >2 AIC units [82].

To ensure results from this model were not due to 0+ fish (born that calendar year) exhibiting higher daily growth or biases in rivers exhibiting more 0+ fish, the model was also run excluding all 0+ individuals. These were then visualised by calculating the partial residuals (i.e. the model residuals with the addition of all main effects), thereby correcting for the random effects of sampling run nested within sampling day nested within river and age class nested within river.

To illustrate growth rate differences between rivers, growth was corrected using a random effect from the same model of age class not nested within rivers. Age-class-corrected growth between rivers was then compared with a linear model and these were then visualised using the partial residuals, as above.

To determine whether metabolism is associated with survival probability in tagged salmon, a binomial GLMM was modelled using the '*glmer'* function in the '*lme4*' package [81]. The full model included all independent terms deemed to influence survival including the main effects of age, ln mass, mean river temperature, and ln metabolism with a random effect for river. All possible two-way combinations of these factors were examined before applying backward stepwise model selection, removing non-

significant terms until the most parsimonious model remained. Given that fish may defer migration in the high latitude streams and therefore not migrate but still survive within our measurement window, this model was also rerun excluding all high latitude (Icelandic) fish.

Finally, a relationship between metabolism and migration timing in surviving salmon was explored using the 'coxme' function in the 'coxme' package [83]. Migration timing was normalised, so each river had the same start day, while age was normalised within river and mass was normalised within river and age class. The full model included ln metabolism, mean river temperature, normalised ln mass, and normalised age, alongside a random effect for river. All possible two-way combinations of these factors were examined before applying backward stepwise model selection removing non-significant terms until the most parsimonious model remained. Hazard ratios output by the model were then used to infer if the factor resulted in earlier or later migration. Hazard ratios qualify how the event rate changes with a predictor, whereby values >1 signify the event occurring sooner than average and values <1 signify later than average. A hazard ratio of 1.5 represents an increase in migration probability per day of 50% compared to an average value.

Results

Metabolism and temperature

The most parsimonious model determining the factors influencing mass-corrected metabolism included only the significant main effects of experimental temperature (X^2 = 7.21, p = 0.007, conditional R^2 = 0.65; Table S1, Fig. 2) and river (X^2 = 175.89, p <0.001). This indicated a consistent slope for the relationship between temperature and metabolism across sites, contrary to H1. River intercepts were generally similar, except for the Deveron which exhibited approximately 30% lower metabolism than all other sites (p < 0.001). Interestingly, neither species nor age were included in the final model.

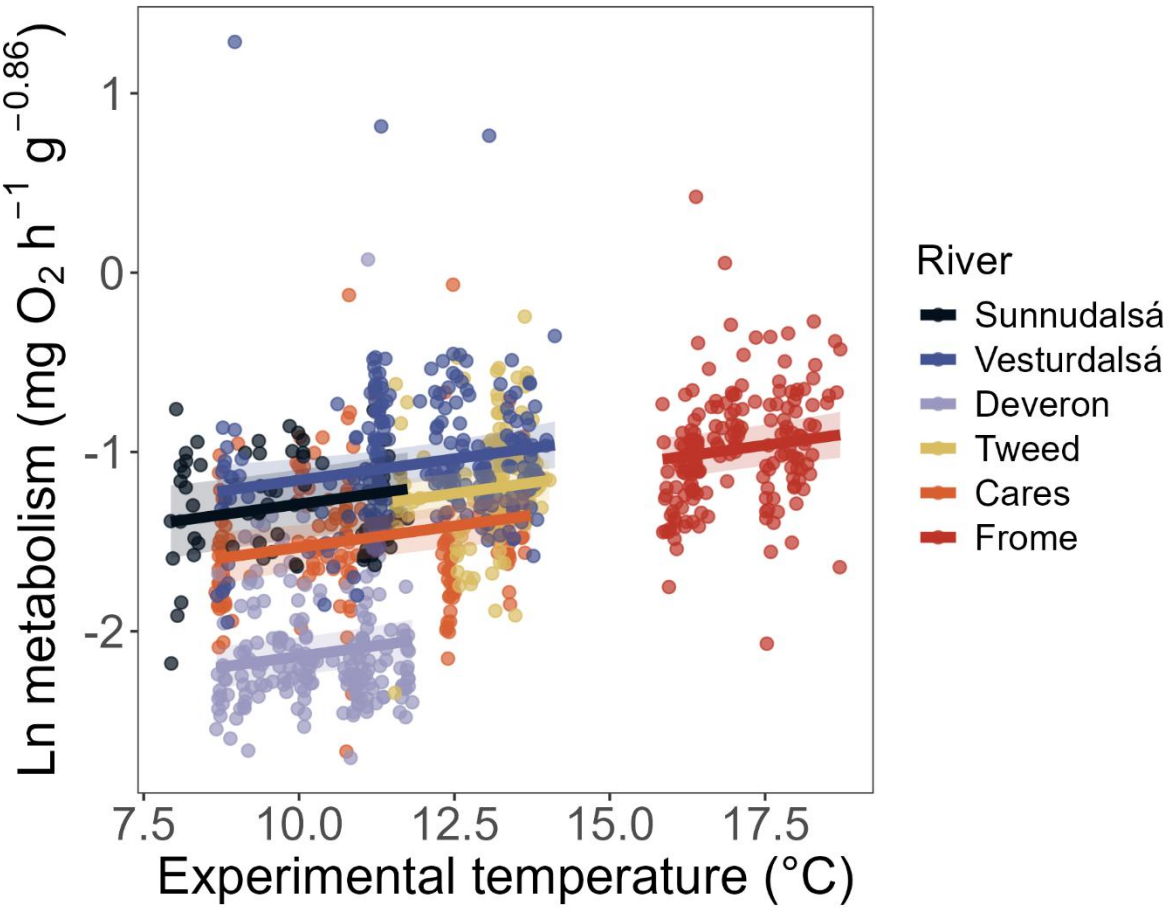


Figure 2 – The relationship between ln mass-corrected metabolism and experimental temperature within each river. Lines show the predictions for each river based on the

fixed and random effects (see Table S1) with 95% confidence intervals for the model predictions around each line. Note that metabolism is mass corrected with an allometric exponent of 0.86 (see Methods).

Metabolism and growth

The most parsimonious model determining the factors influencing growth in the first year included no polynomial effects, in contrast to H2. But main effects of mean river temperature, metabolism, and species, as well as interactions between metabolism and both mean river temperature and species (conditional R^2 = 0.77; Fig. 3, Table S2). Temperature had a marginally non-significant positive effect on growth (t = 1.98, p = 0.062), whilst metabolism had a negative effect on growth (t = -3.09, p = 0.002). However, temperature and metabolism interacted such that fish with higher metabolic rates grew faster under warmer conditions, whereas individuals with lower metabolic rates grew better in cooler environments (t = 3.47, p <0.001; Fig. 3a). Brown trout exhibited a more negative relationship between metabolism and growth than Atlantic salmon, with a lower growth rate in higher metabolic rate fish (t = -3.36, p <0.001; Fig. S1). Indeed, high metabolic rate was only associated with increased growth rates in trout inhabiting the warmest waters (Fig. S1b). Fish that hatched in the year of sampling (0+ fish, occurring in all non-Icelandic rivers, Table S3) had not yet completed a year of growth and so may show different daily growth rates when averaged over their life so far, however, we observed the same directionality and significance of terms after excluding all 0+ fish (Fig. S2). There was a significant effect of river on age-class-corrected growth (F = 78.4, p <0.001; Fig. 3b), with growth rates significantly higher at the range extremes

(Sunnudalsá = 0.327, Vesturdalsá = 0.229, Frome = 0.228 mm day^{-1}) than at intermediate temperatures (Tweed = 0.206, Cares = 0.212, Deveron = 0.198 mm day^{-1}; $p < 0.03$).

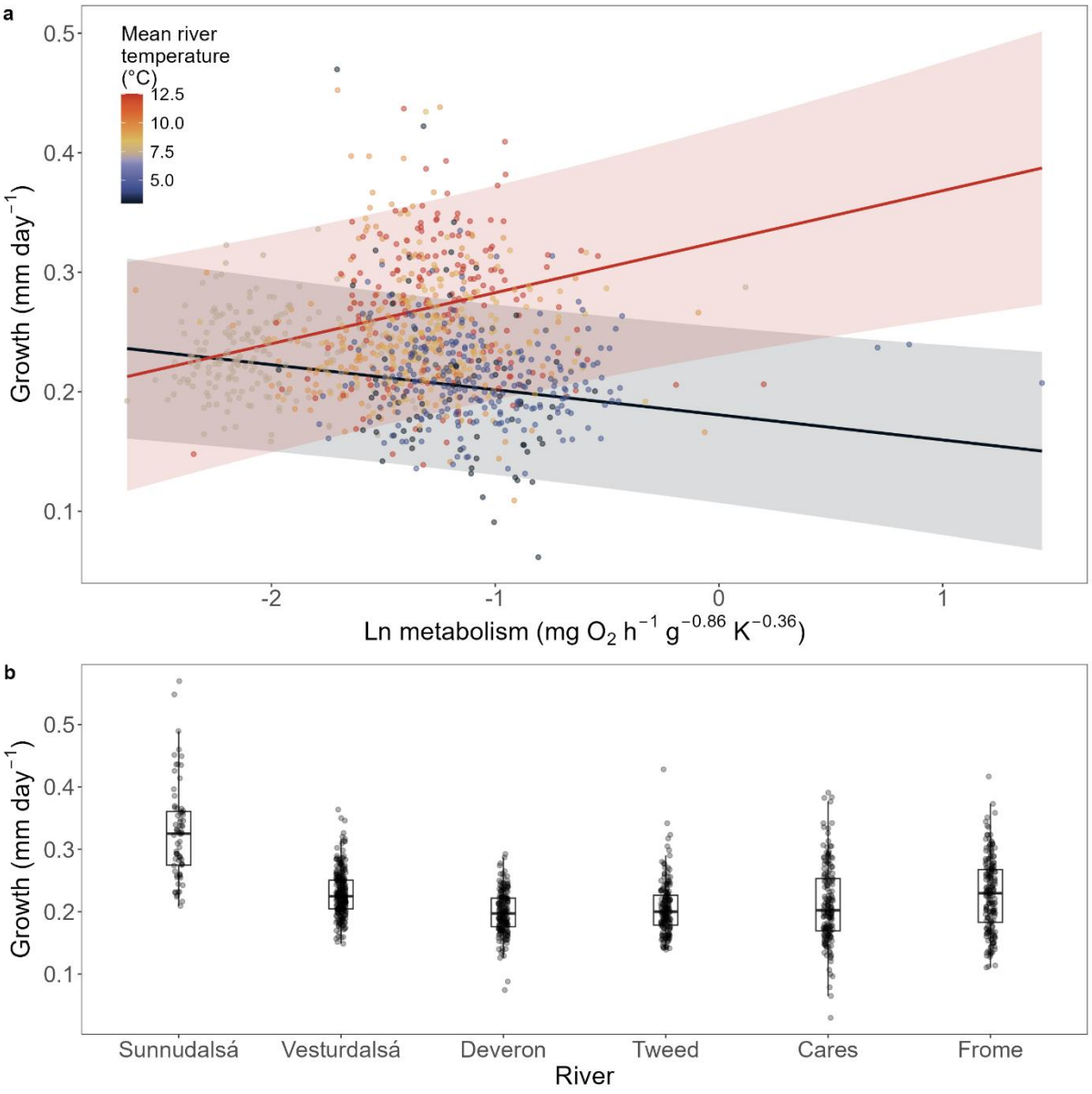


Figure 3 – Variation in growth due to metabolism, mean river temperature, fish species, and river systems. (a) Growth in the first year against mass- and temperature-corrected metabolism (with an allometric exponent of 0.86 and an activation energy of 0.36, see Methods) with model predictions (lines) and 95% confidence intervals given for

minimum (3.0 °C) and maximum (12.5 °C) mean river temperature (see Fig. S3 for raw growth data). (b) Differences in age-class-corrected growth rate between the rivers, ordered by mean river temperature.

Salmon survival and migration

The most parsimonious GLMM for determining the factors influencing salmon survival included the main effects of mean river temperature, metabolism, body mass, and an interaction between temperature and body mass (marginal R^2=0.239; Fig. 4a-d). Survival probability was negatively related to metabolic rate in support of H3 (z = –2.69, p = 0.007; Fig. 4a), but positively related to temperature (z = 3.70, p <0.001; Fig. 4b) and body mass (z = 4.494, p <0.001; Fig. 4c). However, there was a significant interactive effect of temperature and body mass, whereby large individuals at high temperatures exhibited reduced survival, whereas larger size increased survival at lower temperatures (z = -4.274, p <0.001, Fig. 4d). This results in the negative relationship observed in Fig. 4b at mean mass values, though at low masses could lead to a positive relationship with survival. Finally, the most parsimonious mixed-effects Cox model determining the factors influencing migration timing included positive main effects of mean river temperature, metabolism, and body mass. This model indicated a significant positive effect of temperature (z = 3.09, p = 0.002), metabolism (z = 2.15, p = 0.032), and body mass (z = 3.06, p = 0.002), with high values resulting in earlier migration, in support of H3 (Fig. 4e).

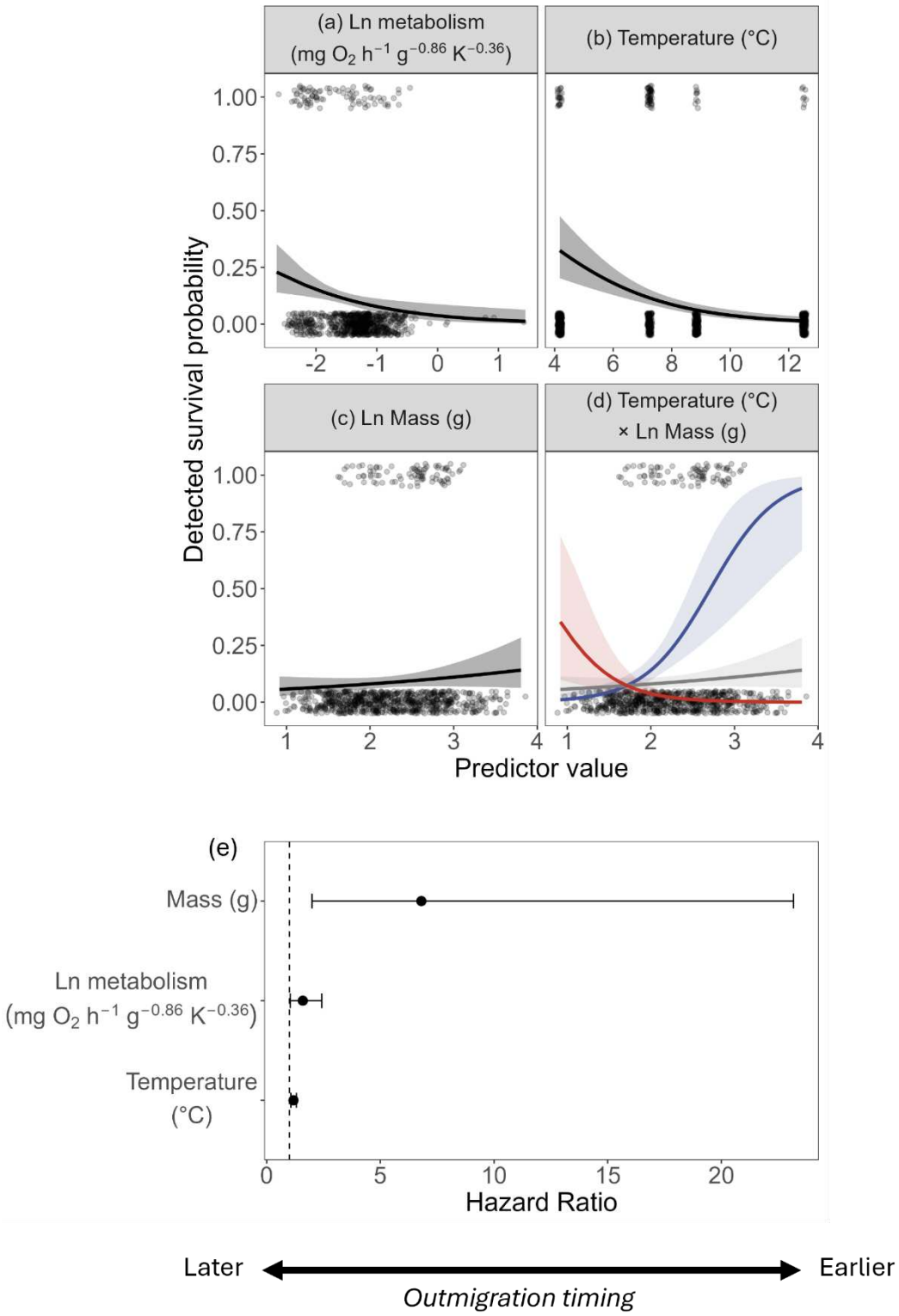


Figure 4 – Model-predicted survival probability and migration timing. Survival probability curves are shown for (a) ln mass- and temperature-corrected metabolism (with an allometric exponent of 0.86 and an activation energy of 0.36, see Methods), (b) mean

river temperature, (c) ln body mass, and (d) the interactions between mass and temperature with blue representing the minimum temperature (4.2°C) and red representing the maximum (12.5°C), with raw binomial data plotted. For a-c, all other model factors are held at mean levels, whilst survival probability is visualised at minimum, mean, and maximum temperatures in d. (e) Predicted hazard ratios with 95% confidence intervals of the significant factors affecting migration timing. Hazard ratios >1 signify earlier outmigration as that variable increases while those below one signify later outmigration.

Discussion

Across a broad latitudinal gradient, we show that the ecological consequences of metabolic phenotype are strongly dependent on thermal environment. Elevated metabolic rates promoted growth in warmer rivers but constrained growth in colder systems, demonstrating that metabolism does not exert universally positive or negative fitness effects. Instead, the balance between energetic demand and energy acquisition shifts across thermal regimes, providing a framework for understanding how warming may restructure populations across their geographic range.

Higher metabolic phenotypes are often associated with increased activity, dominance, and resource acquisition under controlled conditions [22,33]. Our findings suggest that these advantages translate into enhanced growth only where energetic demands can be subsidised by sufficient resource availability. In contrast to our expectations (H2), higher metabolism was not disadvantageous for growth at both thermal extremes. In warmer and more productive rivers, elevated metabolic rates may support higher feeding rates and sustained growth across longer growing seasons. In contrast, in

colder and more seasonal systems, the energetic costs associated with elevated metabolism appear to outweigh these benefits. Low temperatures may constrain feeding opportunity and digestive processing, while prolonged winters likely increase the importance of maximising energetic efficiency and overwinter persistence [18,34]. Under such conditions, lower metabolic phenotypes may be favoured because reduced maintenance lowers cumulative energetic costs across the annual cycle.

These findings align with laboratory evidence showing that relationships between metabolism and growth vary across thermal environments [35], but extend these patterns into wild populations spanning a large natural climatic gradient. Interestingly a previous laboratory study found the same relationship between maximum metabolic rate, growth, and temperature as we do, but the opposite in standard metabolic rate, suggesting activity and behaviour may be driving our observation more than basal rates [29]. Our results indicate that growth optimisation depends not simply on temperature or metabolism, but on the interaction between metabolic demand, seasonal energy budgets, and environmental productivity. The fitness consequences of metabolism should therefore be interpreted within broader seasonal or annual energy contexts rather than instantaneous thermal conditions alone.

Daily growth rates were highest at both warm and cold extremes of the latitudinal gradient, suggesting that distinct ecological mechanisms may support rapid growth in different environments. Higher temperatures and productivity in southern rivers may permit sustained growth throughout extended growing seasons, whereas rapid growth in Icelandic systems may reflect compensation for short growing seasons through extremely long summer photoperiods, which can extend feeding opportunities [36,37]. This

may allow for very high daily growth, though still resulting in smaller overall size at the end of the year (given the short growing season). These contrasting pathways highlight that similar growth outcomes may emerge through different energetic strategies across latitudes.

We also found that brown trout exhibited a more negative relationship between metabolism and growth than salmon, however higher metabolic rates were associated with increased growth rates, but only in the warmest rivers. This contrasting pattern among species may reflect interspecific differences in life history, physiology, and thermal niche breadth, as brown trout generally occupy and tolerate warmer environments than Atlantic salmon [38,39]. Consequently, trout may be better able to offset the elevated energetic costs associated with higher metabolic rates under warmer conditions.

Although the relationship between metabolism and growth was strongly context dependent, elevated metabolic rate was consistently associated with reduced survival. This suggests that the energetic costs of maintaining higher metabolism may impose a persistent burden across environments, potentially increasing vulnerability during periods of reduced food availability or seasonal energetic stress [16,40]. Alternatively, these more dominant fish may be bolder increasing the risk of predation [15]. Temperature was also negatively associated with survival at most observed mass values, consistent with broader evidence that warming can reduce salmonid persistence across freshwater systems [41]. Though smaller fish did show a positive relationship between higher temperatures and survival. Taken together, our findings suggest that elevated metabolism may promote rapid growth under favourable conditions while

simultaneously increasing long-term energetic risk, reflecting a trade-off between resource acquisition and survival.

Body size positively influenced survival, consistent with previous work linking larger juvenile size to reduced predation risk and improved marine performance [42,43]. However, temperature and body size interacted to favour larger fish in cold conditions and smaller fish in warm conditions, following the established temperature size rule and expectation of reduced body size as temperatures rise [44–46].

Our survival estimates should be interpreted with some caution because non-detection at PIT arrays may reflect imperfect or differential detection rates or delayed migration rather than mortality [47,48]. This uncertainty is particularly relevant in northern systems where individuals may defer migration to older ages and thus survival at low temperatures may be higher than indicated by our data [49]. Nevertheless, the same directionality in model terms was observed when all northern (Icelandic) fish were excluded from the analysis (Table S4), suggesting confidence in our results.

Metabolic phenotype also influenced migration timing, with higher metabolic rates associated with earlier migration. One explanation is that individuals with elevated energetic demands transition earlier to marine habitats where feeding opportunities and growth potential are greater [50]. Another possibility is that higher metabolic rates accelerate development, leading to earlier smolting, although this mechanism has not, to our knowledge, been directly tested. Larger fish also migrated earlier, consistent with previous studies linking body size to smolt readiness and marine survival [51,52]. Finally, warmer rivers generally had more fish migrate earlier within their observed migration window, consistent with studies showing earlier migration in warmer years [53,54].

Metabolic rates and their relationship with temperature were broadly similar among rivers despite the large geographic range encompassed by the study, suggesting relatively conserved thermal sensitivity across populations. The exception was the Deveron, which exhibited consistently lower metabolic values and may reflect population-specific energetic strategies. The thermal sensitivity of routine metabolic rate was much lower (0.36 eV) than that generally expected of basal rates (0.65 eV), albeit measured over a narrow temperature range, suggesting that the thermal sensitivity of fish in their natural habitats may be much lower than expected [13,55]. Interestingly, some of the highest metabolic rates occurred in the coldest rivers, consistent with hypotheses predicting compensatory metabolic elevation in cold-adapted populations [56]. However, inference regarding adaptive divergence remains limited because temperature ranges within individual rivers only partially overlapped.

Projected climate warming is expected to elevate temperatures throughout much of the salmonid range [57], increasing metabolic demand across populations. However, increases in energetic expenditure are unlikely to be matched universally by equivalent increases in resource availability or growing-season opportunity. This mismatch may be particularly important in highly seasonal northern systems where photoperiod remains fixed despite warmer winters [58]. Under these conditions, elevated maintenance costs could increase cumulative energetic deficits, reduce survival, and weaken the advantage of high metabolic phenotypes despite potentially faster summer growth, although earlier springs may increase growth [59]. In contrast, warmer southern systems may increasingly approach physiological optima where aerobic capacity and feeding performance decline while maintenance demands continue to rise [25]. Our results suggest that warming may therefore simultaneously alter growth, survival, and

migration strategies by shifting the balance between energetic demand and resource acquisition across environments. Elevated metabolic phenotypes may initially gain growth advantages and migrate earlier under warmer conditions, but this could lead to mismatch with marine prey [60,61]. Furthermore, these benefits may be offset by reduced survival if energetic costs cannot be sustained across the annual cycle. Climate warming may consequently restructure salmonid populations not only through direct thermal stress, but by altering the energetic trade-offs linking metabolism, growth, survival, and life-history timing across latitudes.

Future work should directly evaluate the mechanisms inferred here by quantifying seasonal energy balance and its ecological drivers. Continuous measurement of overwinter metabolic expenditure, coupled with estimates of food availability and predator pressure, would allow explicit tests of whether maintenance demand versus energy acquisition governs growth and survival across thermal regimes. Refining survival inference will also be critical; integrating multi-array detection frameworks, independent estimates of detection probability, and complementary mark–recapture approaches would reduce uncertainty associated with non-detection and delayed migration. A priority is to partition metabolic phenotype in the field into its constituent components. Independent estimation of standard metabolic rate, maximum metabolic rate, and field or routine metabolic rate in wild individuals would allow mechanistic linkage between energetic capacity, maintenance demand, and realised performance. This is particularly relevant where our routine metabolic rate measurement integrates behaviour and physiological components [12]. Coupling these measurements with longitudinal growth trajectories and habitat-specific resource measurements would

clarify how different components of the energy budget translate into life-history variation.

Collectively, our findings demonstrate that the fitness consequences of metabolic phenotype emerge from interactions between temperature, seasonality, and energetic opportunity. Elevated metabolism promoted growth under warmer conditions but constrained performance in colder systems, while simultaneously imposing an apparent survival cost across environments. These results suggest that climate warming may restructure salmonid populations not only through direct thermal stress, but by altering the energetic trade-offs linking metabolism, growth, survival, and migration. Where warming increases metabolic demand without proportional increases in resource availability, populations may experience reduced survival and shifts in the distribution of favourable metabolic phenotypes. Such processes may contribute to ongoing declines in salmonids across both warm and highly seasonal regions.

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