

Behavioural plasticity in circadian foraging patterns increases resistance of brown trout populations to environmental change

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Abstract

Stream-dwelling salmonids in the low-latitude and -altitude margins of their range are particularly threatened by climate change. However, they possess a variety of evolutionary, plastic, and behavioural mechanisms that provide resistance against rapid changes in their environment. Behavioural plasticity can be important under rapid environmental change because it is relatively fast and flexible. In particular, salmonids can exhibit flexible diel activity patterns in response to new environmental conditions, but the consequences of this capability for long-term population persistence in the face of climate change remain unclear. We used an individual-based model to simulate the trajectory of a brown trout population at the warmest edge of its range under three environmental-change scenarios of increasing warming and streamflow reduction. We assessed (1) how simulated trout responded behaviourally to climate change by modifying their circadian foraging patterns, and (2) how much this behavioural plasticity buffered the population-level consequences of environmental change. Our simulations showed that under current conditions trout of different age classes segregated foraging both temporally and spatially. The most consistent response to environmental change was more diurnal feeding in all age classes and under all scenarios, with the strength of this response increasing with the severity of change. In addition, total daily foraging activity increased in all age classes. A second experiment indicated that virtual populations of individuals capable of flexible circadian feeding were more resistant to environmental change than populations restricted to fixed feeding patterns. Thus, our computational experiment suggests that the ability of fish to adaptively select when as well as where to feed, well-documented at the individual level in the empirical literature, could potentially buffer the demographic impacts of long-term environmental change.

Key words: Activity selection, adaptive behaviour, climate change, diel activity, individual-based modelling, resource partitioning, salmonids



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Introduction

Freshwater fishes are one of the most endangered animal groups on Earth: for species with adequate information to assess their status, about 30% are threatened with extinction (Tickner et al. 2020; Moyle and Leidy 2023). Recent

studies estimate that the rate of endangerment will accelerate, to the point that 40–50% of all freshwater fish species might be extinct or close to it by the end of the century (Moyle and Leidy 2023). Cold-water specialists like salmonids are particularly endangered: nearly three quarters of assessed freshwater salmonids are threatened with extinction and their populations must cope with rapidly changing environments resulting from the interaction of climate change with other anthropogenic stressors, such as invasive species, habitat loss, pollution, and overfishing (Muhlfeld et al. 2019). Global meta-analyses predict a marked reduction in salmonid productivity at low latitudes and altitudes where stressful thermal regimes predominate, especially in regions where droughts are becoming more frequent during the hottest months (Gallagher et al. 2022). In fact, strong climate-driven declines in stream-dwelling salmonid populations occupying low-altitude habitats in low-latitude range margins have already been reported (e.g., Almodóvar et al. 2012; Ayllón et al. 2013a).

On the other hand, salmonid fishes are among the most adaptable, resistant and resilient to change of any freshwater fish group. Stream salmonids possess a variety of evolutionary, plastic, compensatory, and behavioural mechanisms that allow some degree of population stability under climate change (reviewed in Kovach et al. 2019; Rosenfeld et al. 2024). For example, there is large intraspecific variation in tolerance of warming due to heritable genetic variation (among individuals, either within or among populations of a species) and to phenotypic plasticity (variation within and among individuals, due to mechanisms including acclimation, and developmental and transgenerational plasticity), which might provide a buffering effect against the impacts of global warming (Jonsson and Jonsson 2019; McKenzie et al. 2021; Jonsson 2023). Indeed, plastic and evolutionary phenotypic changes in thermal tolerance and in fitness-related life-history traits as a response to climate change are widely documented (e.g., reviewed in Crozier and Hutchings 2014; Myers et al. 2017; Kovach et al. 2019; McKenzie et al. 2021; Jonsson 2023; Rosenfeld et al. 2024; synthesised in databases, Krabbenhoft et al. 2020). There is also evidence that density dependence, especially density-dependent growth, can create compensatory dynamics that partially buffer the demographic impacts of climate change (e.g., Bassar et al. 2016; Ayllón et al. 2019).

Behavioural plasticity can be also important under rapid environmental change because it is relatively fast, reversible and usually already present within populations (Van Buskirk 2012). In fact, stream salmonids actively respond to environmental changes through several kinds of behavioural plasticity. First, phenological responses, like earlier seaward migration or delayed spawn timing, associated with environmental change have been observed or predicted by models (Crozier and Hutchings 2014; Rosenfeld et al. 2024); these changes in phenological traits are most often plastic and not a genetic response (Crozier and Hutchings 2014), and they might involve a strong behavioural component.

Second, behavioural thermoregulation could be a key mechanism allowing thermally vulnerable salmonid populations to persist in warming rivers (Amat-Trigo et al. 2023). In a global meta-analysis, Amat-Trigo et al. (2023) showed that the deliberate movement of fish from warm to cool habitats within thermally heterogeneous rivers substantially reduced the temperature they experienced in summer (mean difference between habitats of 4.7 °C), and the warmer the original habitat, the greater the extent of temperature difference with the thermal refuge. Due to the asynchrony of temperature and prey abundance across the river

network, stream salmonids can track spatio-temporal variation in growth potential by moving up and down the network on a seasonal basis; i.e., shifting from cooler upstream habitats that support some growth potential in summer to warmer downstream habitats that provide much higher growth in spring and autumn, thus enhancing annual fish production (Armstrong et al. 2021; Rossi et al. 2024).

A third and less-explored form of behavioural plasticity involves adaptive changes in diel activity and habitat selection. Salmonids make selection contingent not only based on where, but also when, they feed or hide over the daily light cycle, while considering a state-dependent trade-off between growth and survival (Metcalf et al. 1998; Railsback et al. 2020; Naman et al. 2022). These decisions produce flexible circadian behavioural patterns presumably driven by the effects of light on both feeding success and predation risk, and also by competition and the internal state of individuals (Railsback et al. 2020). Generally, daytime foraging is more efficient but riskier, so daytime feeding is expected only for fish that cannot meet their metabolic demands by feeding during other phases of the cycle or for those that can secure daytime habitat that is safe as well as profitable. These behaviours favour not only spatial but also temporal resource partitioning as multiple fish can feed at the same habitat if they do so at different times of day (Railsback and Harvey 2011). Importantly, fish can change their diel activity patterns to adapt to new environmental conditions; for example, more diurnal and crepuscular (compared to nocturnal) feeding is expected to balance decreased food availability—or increased competition for it—at reduced flows, or higher metabolic costs at elevated temperatures (Railsback et al. 2020). Simulation studies suggest that the ability to adapt circadian foraging patterns over time provides trout populations with a higher capacity to resist short-term streamflow reductions compared to less complex feeding behaviours (Harvey et al. 2014).

Even though we know that diel habitat and activity selection are important mechanisms of adaptive behaviour, it is not clear how important these mechanisms—or behaviours, in general—are to long-term population persistence in the face of climate change. To shed light on this matter, we used an individual-based model to simulate the trajectory of a brown trout (*Salmo trutta* L.) population at the warmest edge of its range under three environmental-change scenarios of increasing severity in warming and streamflow reduction. We assessed (1) how simulated trout responded behaviourally to environmental change by modifying their circadian foraging patterns, and (2) whether this behavioural plasticity improved individual fitness, and thus buffered to some extent the population-level consequences of environmental change. We tested the latter by analysing whether a flexible circadian foraging pattern—in which individuals adapt their activity decisions over time—provided higher fitness than a fixed circadian foraging pattern in which individuals always feed during daytime and hide during the other phases of the daily cycle.

Methods

Model description

We used version 7 of the inSTREAM individual-based stream trout population model (Railsback et al. 2021a, 2021b). A complete description of the model following the ODD protocol (Overview, Design concepts, Details; Grimm et al. 2020), model parameterisation, sensitivity and uncertainty analyses, and model

validation are provided in the InSTREAM 7 User Manual (Railsback et al. 2023), which can be downloaded from [here](#). We provide in Suppl. material 1 a summary of inSTREAM evaluation and validation published studies performed to test the structural realism and validity of the model. We present below a summary of how the model works, where we indicate the sections of the User Manual where specific details about the submodels' implementations can be found.

InSTREAM 7 simulates the trout population of a stream reach by representing every fish as an individual, with variables for length, weight, body condition, age and sex. The reach is made up by cells that are characterised by their physical habitat—water depth and velocity, substrate, and availability of three cover types: velocity shelter for drift feeding, escape cover that reduces predation risk when feeding, and concealment cover that reduces predation risk when hiding—, and their production rate of drift and benthic food (Section 4.1). Each day is represented with four time steps representing the four phases of the circadian cycle: night, dawn, day and dusk. The length of each phase of the cycle varies realistically with date and latitude (Sect. 9.6). Every time step the environmental conditions (streamflow and water temperature) in the reach are updated from input files, and cell velocity and depth are calculated from input functions previously produced by a hydraulic model. Light intensity at the water surface is calculated from a model of mean sunlight irradiance, and light irradiance in the water decreases exponentially with depth. Finally, food availability in each cell is calculated from cell area, velocity and depth, and the reach's food parameters (Sects. 8.1 and 9.1–9.10). Once the habitat is updated, each fish:

- (1) Selects its habitat cell and activity, deciding whether and where to feed or hide (Sect. 9.13). The fish predicts the potential growth and survival probability it would experience in every habitat cell within a radius that increases with trout length, and considers the growth (or weight loss) and mortality risk experienced in the three preceding time steps. The trout then selects the combination of cell and activity that provides the best probability of surviving starvation (due to poor condition) and predation over a time horizon. The model assumes a size-based dominance hierarchy among individuals (Sect. 5) so that resources (food, shelter and concealment cover) used by larger individuals are depleted and cannot be used by smaller fish (Sect. 9.11).
- (2) Feeds and grows (or loses weight) as a consequence of its habitat and activity. The model represents two feeding types, drift feeding and active search for benthic food on the streambed, but in general, search feeding is profitable only for age-0 trout. Fish growth is modelled as the difference between energy intake and respiration costs using standard bioenergetic approaches (Sect. 9.21). The drift intake rate is calculated as the mass of prey passing through the capture area times the capture success: the amount of food drifting increases with water velocity, but a fish detects drift food only within a reactive distance that increases with body length and irradiance, while capture success decreases with water velocity (Sect. 9.22). Benthic food intake decreases linearly with water velocity but is independent of irradiance (Sect. 9.23). The energetic costs of metabolism and swimming include the resting metabolic rate that increases with fish size and water temperature, and an additional activity respiration that increases with swimming speed, which is the same as the cell's water velocity unless the fish is

using a velocity shelter (when drift feeding) or is hidden (Sect. 9.25). Daily growth is proportional to energy intake, so a fish can gain or lose weight in the time step. Length increases only when trout in healthy condition gain weight, while losing weight decreases body condition (Sect. 9.20).

- (3) Is subject to five sources of mortality (Sects. 9.15–9.19), the most important of which are poor condition, predation by terrestrial animals, and predation by fish (including piscivorous trout), because they have especially strong effects on habitat and activity selection, which then affects growth and survival. The model calculates the daily probability of the trout surviving each mortality source, which depends on characteristics of the fish and the cell's habitat (Sect. 9.14). The risk of both terrestrial and aquatic predation increases with increasing cell irradiance. Choosing the hiding activity only has benefits for survival if the fish has access to hiding cover.
- (4) Spawns if several criteria are all met (Sect. 9.27). Trout become sexually mature when they reach their maturity size threshold. During the spawning season (a range of dates), adult females determine each day whether they are ready to spawn, which depends on environmental conditions (temperature, and flow magnitude and steadiness) and on their own state (age, and body condition over a minimum threshold). If ready, female trout select and move to the available cell having the best spawning quality (Sect. 9.29) and create a redd with a number of eggs that is a power function of her length (Sect. 9.28). The eggs are fertilised by the largest available male spawner (Sect. 9.30). Spawners incur a weight loss to represent the energetic cost of spawning, so they lose body condition, which significantly affects their habitat selection and survival (Sect. 9.28).

InSTREAM also represents redd incubation and mortality. Extreme streamflows, extreme temperatures, or the superimposition of redds can cause egg mortality (Sects. 9.31–9.36). The development rate of surviving eggs is a non-linear function of temperature (Sect. 9.37). Once redds are fully developed, a new trout emerges from each surviving egg and its state variables are initialised (Sect. 9.38). These new trout are ready to swim and feed (swim-up fry).

Mechanisms driven by temperature, streamflow and light intensity in inSTREAM 7

InSTREAM 7 represents multiple effects of temperature, and many of them affect trout behaviour. (1) Energetic effects: increasing temperature increases metabolic rates and so decreases growth (Jonsson 2023; Rosenfeld et al. 2024). (2) Survival effects: reduced body mass results in higher mortality due to poor condition (Simpkins et al. 2003) and due to predation when trout feed more often, or in riskier habitats or times of the day, to regain body condition (Metcalf et al. 1998). The risk of predation by piscivorous fish also increases with temperature because of their increased metabolic rates and thus feeding activity. The risk of acute mortality by thermal stress increases sharply at temperatures above 24 °C (Jonsson 2023). (3) Effects on reproduction: temperature affects spawn timing, and eggs develop faster as temperature increases, which affects emergence timing (Jonsson and Jonsson 2011). As noted above, extreme temperatures increase egg mortality (Elliott and Elliott 2010).

InSTREAM 7 also represents multiple effects of streamflow reduction, with consequences for trout behaviour. (1) Effects on available space and food: depending on the reach's cross-sectional profile, reduced flow may result in strong reductions in wetted area. Reduced velocity and depth decrease available drift food within habitat cells. On the other hand, reduced velocity decreases the respiration costs of swimming (Gallaughier et al. 2001) and increases capture success (Hill and Grossman 1993). (2) Survival effects: flow reduction typically leads to reduced growth (Rosenfeld et al. 2024), with the same consequences for survival as increasing temperatures. Reduced velocity and depth increase predation risk by terrestrial animals (Harvey and White 2017), but reduced depth decreases risk of predation by large fish. (3) Effects on reproduction: reduced body condition may prevent some sexually mature trout from spawning (Jonsson and Jonsson 2011). Extreme low-flow events increase egg mortality due to dewatering (Rosenfeld et al. 2024).

Finally, inSTREAM 7 includes many mechanisms that drive the time of day when fish feed: predation risk is lower at night and twilight (dawn and dusk) (Metcalf et al. 1999; Harvey and Nakamoto 2013), but drift feeding is most efficient during daytime, as light increases reaction distance (Hansen et al. 2013). Indeed, drift feeding at night is profitable only in relatively low velocities (see fig. 31 in Railsback et al. 2023), so habitat area providing profitable drift feeding positions is limited. That is, drift feeding during daytime is more profitable but riskier, while doing it at night is safer but less efficient, and feeding during twilight provides near-daytime growth and somewhat-reduced risk. Thus, fish feed during day and twilight only as needed to meet their metabolic demands (Metcalf et al. 1998). Consequently, declines in food availability (at reduced flows), increased metabolic demands (at elevated temperatures) or increased competition for safe and efficient feeding habitat at night, all should increase drift feeding during day and twilight. Habitat and activity selection patterns of larger individuals affect the behaviour of smaller fish (age 0 and 1), such that temporal partitioning of feeding by size might occur.

Study site and input

We parameterised the model using topographic, environmental, habitat and population data from a resident brown trout population in the River Eska (altitude 655 m.a.s.l.), a Mediterranean mountain river in northern Spain, tributary of the River Aragón in the River Ebro basin. The simulated reach is approximately 250 m long with an area of 5625 m² at an average flow of 4.28 m³ s⁻¹ (mean summer flow 0.71 m³ s⁻¹, minimum flow 0.39 m³ s⁻¹). Annual maximum temperatures in the simulated reach (mean 18.1 °C, range between 16.1–20.3 °C) can exceed values at which substantial reductions in growth have been observed for brown trout (e.g., 19.5 °C according to Elliott and Elliott 2010).

Simulation scenarios

We simulated the trajectory of the modelled population between 1996 and 2100 under four environmental scenarios representing increasing severity of environmental changes. Each scenario was replicated six times. We modelled a baseline scenario that projects the historical temperature and flow regimes

into the future without environmental change, while the other three scenarios simulated concurrent water warming and flow reduction, differing in the rates of change over time in the environmental variables. We used data collected by the closest meteorological (Urzainqui, AEMET) and stream gauging (Roncal, Navarra Government) stations to generate the water temperature and flow time series for the 1996–2011 period. Time series for years 2012–2100 were projected following the methods described in Ayllón et al. (2016) (Fig. 1).

We used three future climate projections corresponding to the Representative Concentration Pathways RCP4.5, RCP6.0 and RCP8.5 (Taylor et al. 2012) to generate the air temperature time series. As in Ayllón et al. (2019), we used the inter-model median of regional daily air temperature projections for the Urzainqui meteorological station developed by AEMET through statistical downscaling techniques based on data from six global climate models associated with the 5th Coupled Model Intercomparison Project: (1) BCC-CSM1-1 (Beijing Climate Center, China), (2) CanESM2 (Canadian Centre for Climate Modelling and Analysis, Canada), (3) GFDL-CM3 (Geophysical Fluid Dynamics Laboratory, USA), (4) MIROC-ESM-CHEM (Japan Agency for Marine-Earth Science and Technology, Japan), (5) MPI-ESM-LR (Max-Planck Institute, Germany), and (6) MRI-CGCM3 (Meteorological Research Institute, Japan). Air temperature time series were converted into water time series using the regression model described in Ayllón et al. (2016) (Fig. 1).

Scenarios of hydrological change relied on streamflow projections performed by López-Moreno et al. (2014) for the River Aragón basin for 2021–2050 under the A1B scenario of greenhouse gas emissions used in the AR4 assessment report. Temperature predictions under the A1B scenario fall between those of the RCPs 6.0 and 8.5. López-Moreno and collaborators predicted a continuous decrease in runoff from late winter to the end of autumn, with reductions in streamflows exceeding 30–40% relative to the historical baseline, especially in summer, when temperatures are highest. Thus, we employed the flow time series generated for the baseline scenario, and then modified daily values for the 2012–2050 period at a rate calculated to equal changes projected by López-Moreno et al. (2014). Therefore, the flow time series for the 1996–2050 period was the same for the three environmental-change scenarios, but the flow decrease rate for 2051–2100 differed among them (Fig. 1).

To summarise, the four simulated scenarios were:

No environmental change (Baseline): This scenario mimicked observed variability in water temperature and flow, without any imposed climatic trends.

Moderate environmental-change scenario (RCP 4.5 + Moderate flow change):

This scenario combines the temperature projection corresponding to the RCP 4.5 with a hydrological-change scenario in which the flow decrease rate for 2051–2100 is set to half the rate assumed for 2012–2050. Under the RCP 4.5 projection, greenhouse gas emissions peak in 2040 and then decline, so total radiative forcing stabilises shortly after 2100, resulting in moderate warming.

Intermediate environmental-change scenario (RCP 6.0 + Intermediate flow change): This scenario combines the temperature projection corresponding to the RCP 6.0 with a hydrological-change scenario in which the flow decrease rate for 2051–2100 is the average between the rates simulated for

the moderate and extreme scenarios. The RCP 6.0 is an intermediate stabilisation pathway where total radiative forcing stabilises after 2100, resulting in substantial, but not extreme, warming.

Extreme environmental-change scenario (RCP 8.5 + Strong flow change): This scenario combines the temperature projection corresponding to the RCP 8.5 with a hydrological-change scenario in which daily flows for 2051–2100 continue to decrease at the same rate as for 2012–2050. The RCP 8.5 is characterised by increasing greenhouse gas emissions over time, leading to high greenhouse gas concentration levels and thus to very strong warming.

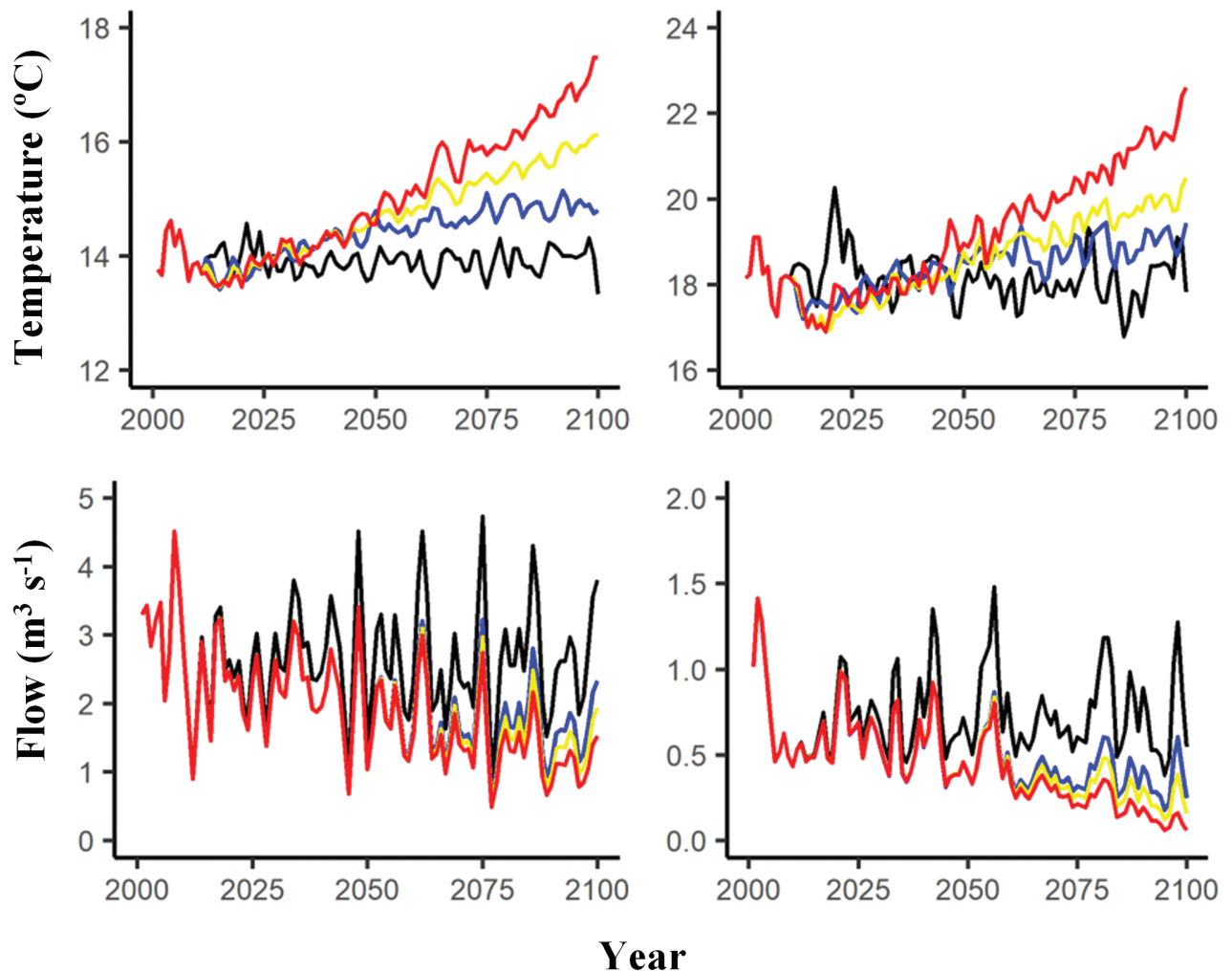


Figure 1. Time series of environmental variables under the baseline and environmental-change scenarios. Two-year moving average values of: mean daily temperature (top-left), seven-day maximum daily temperature (top-right), mean daily flow (bottom-left) and seven-day minimum daily flow (bottom-right) during spring-summer (April to September) under the baseline (black), moderate (RCP 4.5 + moderate flow change; blue), intermediate (RCP 6.0 + intermediate flow change; yellow) and extreme (RCP 8.5 + strong flow change; red) environmental-change scenarios.

Model versions

To determine whether behavioural changes in diel activity patterns could significantly contribute to buffer the demographic impacts of environmental changes on the simulated population, we ran the six replicates of each environmental scenario with two different versions of inSTREAM 7 and contrasted

their results. The two model versions differed only in their treatment of the circadian light cycle, following the approach of Railsback et al. (2021b):

- (1) The circadian-feeding version is the standard version of inSTREAM 7, which explicitly simulates the circadian cycle as four phases: night, dawn, day and dusk.
- (2) The diurnal-feeding version assumes that trout always feed during day-time and hide during other phases. It ignores the twilight phases by making them very short and skipping all trout actions. Growth is determined by food intake and metabolic costs during the day plus resting metabolism during the night. Trout remain subject to mortality risks at night. Therefore, trout select their habitat cell to feed at the start of each day phase and then select the best cell for hiding at night.

Because the model versions make different assumptions about when trout can feed, they were calibrated independently to reasonably reproduce the mean and range of variation of values of nine time series of abundance, biomass and length-at-age of three age classes (age-1, 2 and 3+) under the baseline conditions. We specifically calibrated the values of six parameters: three controlling food availability (density of drift food, regeneration distance of drift food and production of benthic food), two controlling the intensity of terrestrial and aquatic predation, and one parameter controlling the probability of surviving low condition.

Model outputs

In each replicate, both the circadian-feeding and the diurnal-feeding versions of the model recorded the biomass of four age classes (0, 1, 2, and 3+) on September 1st of every simulated year. The age structure of the population was measured as the adult (trout age > 1) to juvenile (ages 0 and 1) biomass ratio. We also recorded at the end of each reproductive season the total number of eggs produced by female spawners as a measure of total population fecundity. To characterise feeding behaviour, the circadian-feeding model version recorded the percentage of trout feeding and the mean length of the trout that were (a) feeding and (b) hiding (broken down by age classes) during the four daily phases of each August 1st, 8th, 15th, 22nd and 29th, which we then averaged. Because they differed very little, the model results from the dawn and dusk phases were combined into one category (“twilight phase”).

Output analysis

First, we used the rank-based non-parametric Mann-Kendall test to detect significant upward or downward trends over time in all model outputs recorded with the circadian-feeding model version. The analysis was performed using a modified version of the Yue Pilon’s method to account for temporal autocorrelation recently implemented in the *zyp* v0.11-1 R package (Bronaugh et al. 2023). We computed in each analysis the Sen’s slope to quantify the trend per unit time, as well as the Kendall’s tau statistic and its P value to test for significance. Second, we performed ANOVAs to detect significant differences between model version results for demographic outputs (biomass of age-0, 1, 2

and 3+ trout, total biomass, adult to juvenile biomass ratio, and total fecundity) over the last 15 simulated years (2086–2100). Because we contrasted outputs from separately calibrated models, for the ANOVA analyses we used the ratio of model outputs under the environmental change scenarios to those under the baseline scenario with no environmental change. All statistical analyses were performed with R software v. 4.2.2 (R Core Team 2023).

Results

Circadian foraging patterns under the baseline scenario

Because even baseline summer temperatures are stressfully high (Fig. 1), in the baseline simulations most individuals had to feed during at least two phases of the daily cycle to meet their metabolic demands (Table 1).

Under baseline conditions, most age-0 trout fed during all phases, the percentage of individuals feeding ranging from 78% at day to 95% at night, mainly on drift (Table 1). However, some relatively small individuals (ratio of length of fish feeding to length of fish hiding: $L_{\text{feed}}/L_{\text{hide}} < 0.96$) fed on the benthos. Almost all age-1 trout fed at night (Table 1), except the smallest individuals ($L_{\text{feed}}/L_{\text{hide}} = 1.12$). However, nocturnal feeding was not enough to meet their metabolic demands, so a large fraction of the largest age-1 individuals had to feed also during day ($L_{\text{feed}}/L_{\text{hide}} = 1.03$), while smaller age-1 fish fed only during twilight ($L_{\text{feed}}/L_{\text{hide}} = 0.97$). At least half the age-2 trout fed during each phase, with the percentage of individuals feeding being highest at night and lowest at day (Table 1). The largest age-2 trout fed during day ($L_{\text{feed}}/L_{\text{hide}} = 1.04$) while smaller individuals fed mostly during other phases. Likewise, at least half the age-3+ trout fed during each phase, but the percentage of individuals feeding was highest at day and night, decreasing at twilight (Table 1). The largest age-3+ trout also fed during day ($L_{\text{feed}}/L_{\text{hide}} = 1.12$). On the whole, these patterns provide evidence for temporal partitioning of food acquisition across age 1, 2 and 3+ individuals.

Table 1. Behaviour under the baseline scenario. Mean value of behavioural responses over the 1996–2100 time period under the baseline scenario. Behavioural outputs were (1) the proportion of fish drift feeding at each phase of the daily light cycle, broken out by age classes, plus the proportion of age-0 trout benthic feeding, and (2) the ratio of mean length of fish feeding to mean length of fish hiding, broken out by age classes and phase.

Variables \ Phase	Day	Twilight	Night
Proportion of fish feeding			
Age-0 (benthic feeding)	0.33	0.21	0.27
Age-0 (drift feeding)	0.45	0.69	0.68
Age-1	0.35	0.91	0.98
Age-2	0.51	0.65	0.80
Age-3+	0.75	0.56	0.76
Ratio of length of fish feeding / length of fish hiding			
Age-0 (benthic feeding)	0.96	0.90	0.93
Age-0 (drift feeding)	1.05	1.02	1.02
Age-1	1.03	0.97	1.12
Age-2	1.04	0.96	0.94
Age-3+	1.12	1.00	0.99

Individual-level behavioural responses to environmental changes

The most consistent pattern in behavioural response to environmental change was that the proportion of fish drift feeding during day significantly increased over time in all age classes and scenarios, and generally the rate of change in daytime feeding increased with the severity of the scenario (Table 2, Fig. 2). A second relevant pattern was that the proportion of age-2 and 3+ trout drift feeding also showed a significant upward trend in the other two phases (Table 2, Fig. 2). That is, more age-2 and 3+ trout fed during the whole daily cycle. Third, while the proportion of age-1 trout drift feeding increased over time during day, it also significantly decreased during twilight and night (Table 2), although to a much lesser extent (Fig. 2). The fourth clear pattern was that a large fraction of age-0 trout shifted from benthic feeding to drift feeding in all phases (Table 2). Also, age-0 trout did more diurnal feeding, while the proportion of fish feeding (drift plus benthic feeding) remained stable in the other two phases.

Table 2. Trends in behavioural responses under environmental change. Trends in proportion of fish drift feeding and in the ratio of mean length of fish feeding to mean length of fish hiding of four age classes over the 1996–2100 time period for the moderate (RCP 4.5 + moderate flow change), intermediate (RCP 6.0 + intermediate flow change) and extreme (RCP 8.5 + strong flow change) environmental-change scenarios. Trends were analysed using the Mann-Kendall test and P values were corrected for serial correlation. Trends are represented as the Sen's slope in %/decade. All trends were highly significant ($P < 0.001$) except when indicated otherwise (ns non-significant, * $P < 0.05$, ** $P < 0.01$).

Variable:	Proportion of fish feeding			Ratio of length of fish feeding/hiding		
Scenario:	Moderate	Intermediate	Extreme	Moderate	Intermediate	Extreme
Day						
Age-0 (benthic)	-4.30	-4.69	-7.63			
Age-0 (drift)	3.57	4.09	5.92	-0.65 *	-0.45 *	-0.40 ns
Age-1	7.40	11.05	12.10	0.59 ns	0.05 ns	-0.20 ns
Age-2	3.57	5.08	5.13	0.08 ns	0.25 ns	-0.05 ns
Age-3+	1.70	1.81	1.06	-0.66 **	-1.32	-1.67
Twilight						
Age-0 (benthic)	-3.11	-2.47 **	-1.05 ns			
Age-0 (drift)	0.36 ns	0.54 ns	0.13 ns	-0.55 **	-1.02	-1.56
Age-1	-1.40	-2.46	-2.57	1.81	1.51	1.25 **
Age-2	2.43	2.39	1.93	-0.09 ns	0.05 ns	0.35 **
Age-3+	1.18 ns	2.74 *	3.47	0.58 ns	0.46 ns	0.23 ns
Night						
Age-0 (benthic)	-3.31 **	-2.49 *	-1.65 ns			
Age-0 (drift)	0.85 **	0.88 **	0.51 ns	-0.82 **	-1.64	-2.01
Age-1	-0.39	-0.77	-0.68	0.77 ns	0.36 ns	0.18 ns
Age-2	1.27 **	1.29 **	1.42	-0.18 ns	0.06 ns	0.39 **
Age-3+	0.41 ns	1.05 *	1.64	0.59 ns	0.49 ns	0.37 ns

Trends in the ratio of mean length of fish drift feeding to mean length of fish hiding ($L_{\text{feed}}/L_{\text{hide}}$) were complex and differed across age classes. The $L_{\text{feed}}/L_{\text{hide}}$ for age-0 trout markedly decreased over time in all phases (Table 2), which indicates that a large fraction of the small individuals that were benthic feeding or hiding under baseline conditions switched to drift feeding. The $L_{\text{feed}}/L_{\text{hide}}$ for age-1 trout increased over time, more strongly

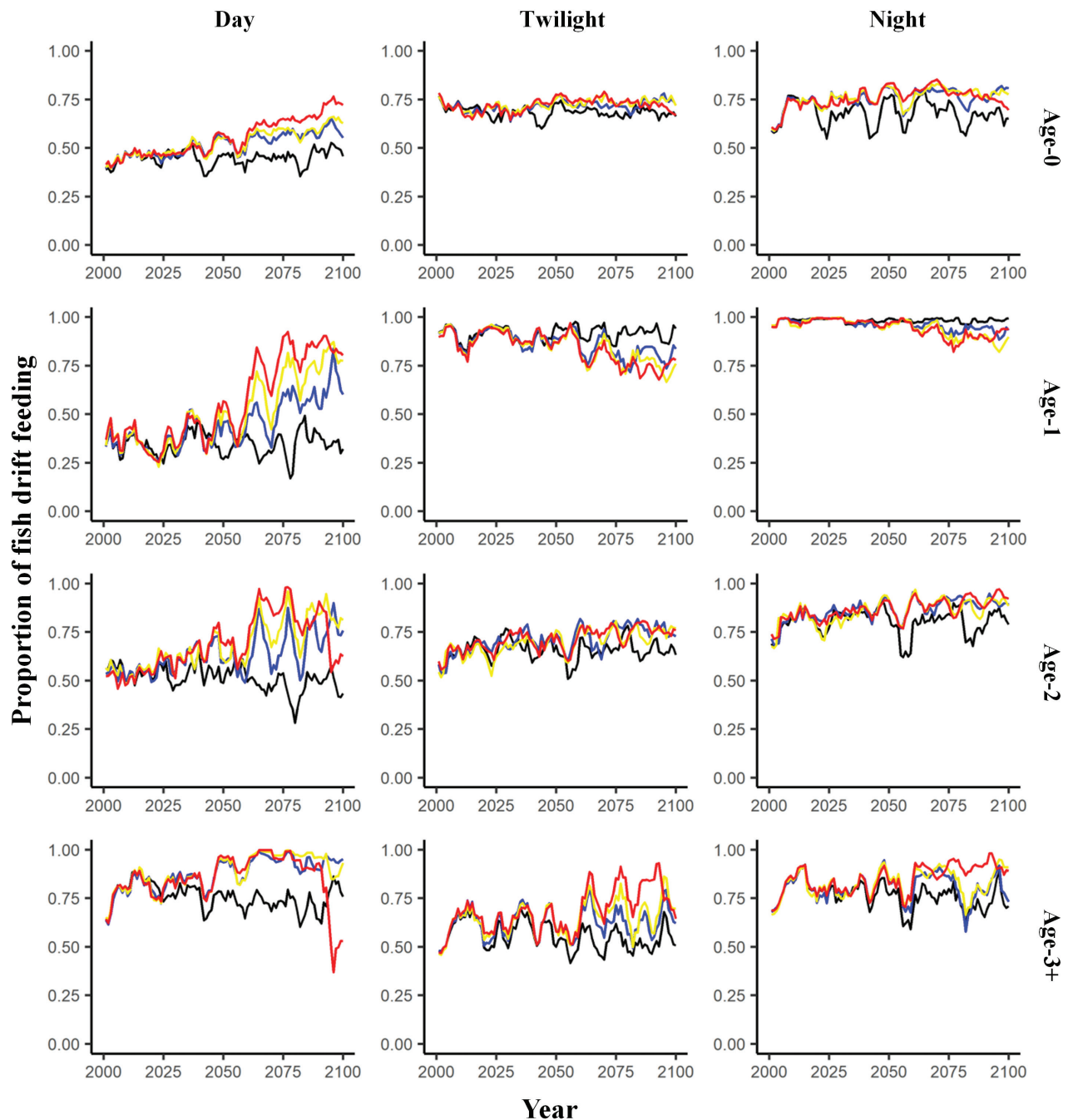


Figure 2. Change over time in feeding behaviour. Summer feeding behaviour (proportion of fish drift feeding) of age-0, 1, 2, and 3+ trout in each phase (day, twilight and night) over the 2000–2100 time period for the baseline (black line), moderate (RCP 4.5 + moderate flow change; blue), intermediate (RCP 6.0 + intermediate flow change; yellow) and extreme (RCP 8.5 + strong flow change; red) environmental-change scenarios. Values are means over five sampling dates in August (see Methods). Lines represent the 5-year moving average for visualisation.

during twilight (Table 2). Fish feeding were smaller than fish hiding in the twilight phase under the baseline conditions (Table 1), so the trend suggests that a fraction of small fish feeding during twilight switched to diurnal feeding, while fish of all sizes switched from nocturnal to diurnal feeding. The $L_{\text{feed/hide}}$ for age-2 trout increased in the twilight and night phases under the extreme scenario (Table 2). Fish feeding were smaller than fish hiding in these phases under the baseline conditions (Table 1), so the upward trends

suggest that under extreme conditions the largest age-2 fish must also feed in other phases of the cycle. The Lfeed/hide for age-3+ trout decreased over time, more markedly during day (Table 2). Only the smallest age-3+ individuals were hidden during day in the baseline scenario (Table 1), so this trend just indicates that a larger fraction of age-3+ fish had to feed in this phase as environmental conditions became more challenging.

Population-level impacts of environmental changes

The biomass of age-2 and 3+ trout showed a marked downward trend over the simulated time period, with steeper declines as the severity of environmental change increased (Table 3, Fig. 3). In contrast, in all scenarios the biomass of age-1 trout decreased during the first half of the simulated period but then stabilised (Fig. 3), so no significant trend was detected for the whole time series (Table 3). The biomass of age-0 trout displayed the same pattern under the moderate scenario, but showed a consistent downward trend under the intermediate and extreme scenarios (Table 3, Fig. 3). Because of the decline in adult trout biomass, total biomass, ratio of adult to juvenile biomass and total fecundity all decreased over time under all climate change scenarios, with the severity of decline increasing with the severity of environmental change (Table 3, Fig. 3).

Table 3. Trends in demographic outputs under environmental change. Trends in demographic outputs from the circadian-feeding model version over the 1996–2100 time period for the moderate (RCP 4.5 + moderate flow change), intermediate (RCP 6.0 + intermediate flow change) and extreme (RCP 8.5 + strong flow change) environmental-change scenarios. Trends were analysed using the Mann-Kendall test and P values were corrected for serial correlation. Trends are represented as the Sen's slope in %/decade. All trends were highly significant ($P < 0.001$) except when indicated otherwise (ns non-significant, * $P < 0.05$, ** $P < 0.01$).

Variables \ Scenarios	Moderate	Intermediate	Extreme
Biomass age-0	-2.17 ns	-3.69 *	-7.31
Biomass age-1	-2.06 ns	-1.67 ns	-2.08 ns
Biomass age-2	-4.03 *	-4.93 **	-10.24
Biomass age-3+	-9.49	-14.41	-18.55
Total biomass	-8.52	-11.75	-15.79
Ratio adults/juveniles	-3.72 *	-6.07	-8.46
Total fecundity	-8.31	-11.98	-16.71

Comparison of the circadian and diurnal-feeding model versions

Population-level results did not detectably differ between model versions under the moderate environmental-change scenario, but the biomass of age-1 and 2 trout and the ratio of adult to juvenile biomass predicted by the circadian-feeding model version were significantly higher than those predicted by the diurnal version under the intermediate and extreme scenarios (Table 4). The circadian-feeding model version also predicted a detectably higher total fecundity under the intermediate and extreme scenarios (Table 4).

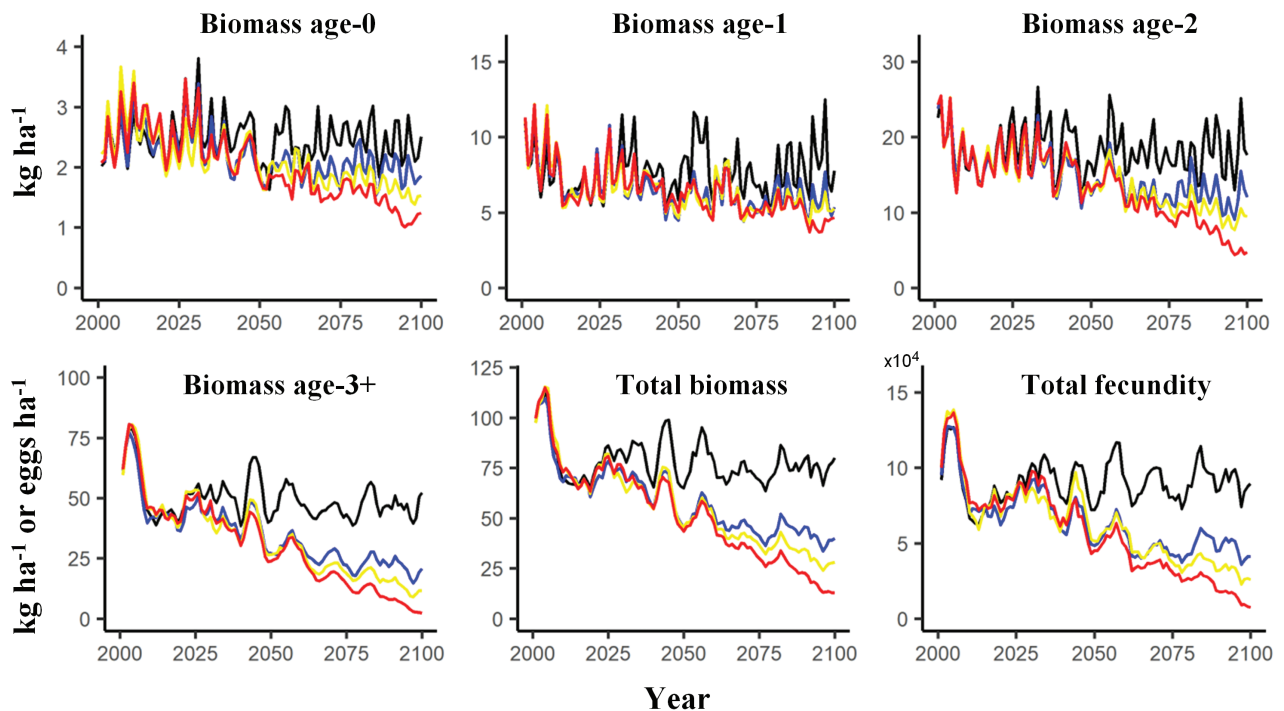


Figure 3. Change over time in demographic outputs. Demographic outputs from the circadian-feeding model version over the 2000–2100 time period for the baseline (black line), moderate (RCP 4.5 + moderate flow change; blue), intermediate (RCP 6.0 + intermediate flow change; yellow) and extreme (RCP 8.5 + strong flow change; red) environmental-change scenarios. Lines represent the 5-year moving average for visualisation.

Discussion

Temporal partitioning of foraging habitats under baseline conditions

Our simulations show that under baseline conditions, with trout already experiencing summer temperatures limiting growth, most simulated individuals must feed at multiple times of day to meet their metabolic requirements. Our results provide evidence that in this context fish of different age classes segregate temporally in addition to spatially: most simulated individuals fed at night, when foraging is safest but least efficient, so they had to achieve a higher intake than was possible by solely nocturnal feeding; but while the largest adults fed at day to complete their daily energetic demands, as they are capable of monopolising the most profitable and safe daytime habitats (e.g., pool heads where velocities and depths are sufficient to supply drift food and reduce predation risk), age-1 and smaller adults (with lower metabolic requirements) fed at twilight. Such patterns in circadian foraging based on the individuals' physiological state have been convincingly shown in real salmonid populations (e.g., Metcalfe et al. 1998).

Behavioural responses under environmental change

Our *in silico* experiments produced complex behavioural responses of individuals to continuous and directional long-term changes in their environment, responses that differed across age classes and whose intensity depended on the severity of the environmental changes. The tested scenarios led to increasingly harsh riverscapes, where elevated temperatures increased metabolic costs for fish, and flow reductions modified stream hydraulics, decreased drift and benthic

Table 4. Statistical contrasts between outputs from the circadian and diurnal feeding versions. Mean value over the last 15 simulated years (2086–2100) of demographic outputs from simulations run with the circadian-feeding and diurnal-feeding model versions under the moderate (RCP 4.5 + moderate flow change), intermediate (RCP 6.0 + intermediate flow change) and extreme (RCP 8.5 + strong flow change) environmental-change scenarios. Demographic outputs are expressed as the ratio between the tested and the baseline scenario (mean value of tested scenario/mean value of baseline scenario). Significance of differences in demographic outputs between model versions (ANOVA test) is reported in the last column ($F_{1,28}$ values are shown). Differences were not significant except when indicated otherwise (• $P < 0.1$, marginally sig.; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Variables	Circadian-feeding version	Diurnal-feeding version	ANOVA test
Moderate scenario			
Biomass age-0	0.75 ± 0.35	0.50 ± 0.33	3.97•
Biomass age-1	0.71 ± 0.49	0.45 ± 0.36	2.63
Biomass age-2	0.68 ± 0.41	0.54 ± 0.35	0.90
Biomass age-3+	0.43 ± 0.13	0.47 ± 0.18	0.68
Total biomass	0.52 ± 0.11	0.49 ± 0.15	0.50
Ratio adults/juveniles	0.35 ± 0.25	0.29 ± 0.26	0.45
Total fecundity	0.51 ± 0.15	0.44 ± 0.18	1.28
Intermediate scenario			
Biomass age-0	0.62 ± 0.18	0.51 ± 0.32	1.38
Biomass age-1	0.67 ± 0.29	0.38 ± 0.18	11.31**
Biomass age-2	0.53 ± 0.23	0.37 ± 0.14	5.4*
Biomass age-3+	0.26 ± 0.09	0.29 ± 0.11	0.65
Total biomass	0.38 ± 0.10	0.33 ± 0.11	1.58
Ratio adults/juveniles	0.20 ± 0.09	0.13 ± 0.05	7.29*
Total fecundity	0.34 ± 0.12	0.27 ± 0.10	3.40•
Extreme scenario			
Biomass age-0	0.48 ± 0.14	0.60 ± 0.43	0.91
Biomass age-1	0.59 ± 0.22	0.27 ± 0.15	21.71***
Biomass age-2	0.32 ± 0.15	0.18 ± 0.10	9.90**
Biomass age-3+	0.10 ± 0.06	0.10 ± 0.06	0.06
Total biomass	0.21 ± 0.08	0.16 ± 0.09	3.21•
Ratio adults/juveniles	0.11 ± 0.05	0.06 ± 0.02	12.62**
Total fecundity	0.15 ± 0.08	0.09 ± 0.06	5.73*

food availability, and increased competition for space by shrinking wetted area (see table 2 in Ayllón et al. 2019). Thus, behavioural responses emerged from state-dependent decisions of individuals facing continuous but heterogeneous changes in the availability of habitats providing safe and efficient foraging positions at different times of the day. Consequently, while we cannot be totally confident in the exact individual responses, observed patterns let us analyse the overall importance of adaptive ability in coping with climate change.

The most consistent response we observed was more diurnal feeding in all age classes and under all scenarios, with the strength of this response increasing in line with increasing severity of the simulated environmental changes. This pattern is consistent with patterns described in short-term observational field studies and laboratory experiments with salmonids: more diurnal feeding is expected when: food availability or fish condition is low (Metcalf et al. 1998,

1999; Orpwood et al. 2006), temperature increases (Fraser et al. 1993, 1995; Breau et al. 2007), streamflow—and thus food production and area providing efficient feeding—is reduced (Bradford and Higgins 2001), or competition for hiding places increases (Larranaga and Steingrímsson 2015).

A second relevant response was that overall daily activity of fish increased in all age classes. This pattern agrees with the literature describing increased daily activity linked to rising temperatures (Breau et al. 2007; Roy et al. 2013; Fingerle et al. 2016) or increased competition (Fingerle et al. 2016) in real salmonid populations. However, we observed differences across age classes in the distribution of daily activity: while the proportion of age-2 and 3+ trout feeding increased in all phases (i.e., adult trout had to feed more often), activity of age-0 fish did not change at twilight and night (although a fraction of the smallest fish switched from benthic to drift feeding), and activity actually decreased in age-1 trout in those phases. That is, a fraction of age-1 fish switched from crepuscular or nocturnal to diurnal feeding. Overall, while temporal resource partitioning decreased over time (and thus spatial habitat selection became more important), our simulated fish of different age classes kept segregating temporally to a certain extent.

Adaptive activity selection increases resistance to long-term environmental changes

Our simulations predicted strong demographic impacts on our virtual population, the magnitude of which increased with the severity of the environmental-change scenario. The largest, oldest age classes experienced the strongest declines, causing a severe reduction in total population fecundity and thus in recruitment. As a result, concurrent warming and flow reduction led to smaller and more unstable populations dominated by young individuals.

These responses differed between the model versions with and without adaptive selection of feeding time. Under the intermediate and extreme scenarios, the circadian-feeding version predicted higher age-1 and 2 trout biomass, higher total population biomass and egg production, and a more balanced age and size structure, than the diurnal-feeding version. That is, in our simulations, virtual trout populations of individuals capable of flexible circadian feeding were more resistant to long-term changes in their environment than populations exhibiting fixed feeding patterns. Thus, our computational experiment suggests that the ability of fish to adaptively select when as well as where to feed has the potential to buffer the impacts of long-term environmental changes in some degree.

Flexible diel activity and habitat selection not only allows temporal resource partitioning (Railsback and Harvey 2011), but also allows individuals to fine-tune, based on their current physiological state, the trade-off between growth and predator avoidance, which tracks temporal fluctuations in food availability, foraging efficiency and predation risk in habitat patches (Metcalf et al. 1998, 1999). However, this behavioural flexibility could not mitigate the negative effects of environmental change on the youngest (age 0) and oldest (age 3+) individuals. Under continuous warming—leading to strong increases in trout metabolic costs—and flow reduction—leading to lower wetted area and reduced water depth and velocity, and thus decreased food availability and increased predation risk—safe habitat patches providing enough energy to sustain large adult trout were extremely limited (but they still existed). In this context, flexible diel activity and

habitat selection do not provide any benefit to the large trout that do not hold such scarce safe-and-profitable positions because they must feed more often in riskier habitats. Selecting habitat that prevents starvation inevitably comes at the cost of higher predation risk, so overall mortality is not reduced in the long term. Age 1 and 2 trout benefited from the almost extinction of the largest individuals. It is worth noting that, apart from triggering such behavioural responses, the pressure to survive both starvation and terrestrial predation can elicit evolutionary responses, like selection for smaller size at emergence and sexual maturity, because larger trout have higher metabolic requirements and are more vulnerable to terrestrial predation, and because smaller size at emergence (and thus egg size) comes with a higher number of eggs for the same gonad mass (see Ayllón et al. 2019).

For age-0 trout, the scope for responding to higher metabolic demands was constrained by the fact that they were already feeding around the clock under baseline conditions, and by the changes in feeding patterns of larger fish. Indeed, observational studies indicate that elevated crowdedness of older cohorts restricts the range of habitats used by age-0 trout because of inter-cohort competition (Ayllón et al. 2013b). Under environmental change, age-1 individuals would increasingly feed during the day in habitat otherwise productive for younger trout, forcing the latter to use riskier habitats. In the same way, a fraction of the smallest age-0 trout had to switch from benthic to more productive drift feeding to meet their increased metabolic demands, moving to deeper habitats and thus assuming higher risk of aquatic predation. Consequently, more flexible behaviour does not translate into higher age-0 fish survival in the long term.

Behavioural plasticity as a mechanism to cope with environmental change

There is growing evidence that behavioural plasticity can be a key mechanism of coping with environmental changes like climate change. Compared to micro-evolutionary adaptation (or even phenotypic plasticity), behavioural plasticity is fast, reversible and often predictable, so its relevance should not be minimised.

We found that individual activity and habitat selection behaviour increases the resistance of a population to climate change even when temperature varied over time but not space. At larger scales, other behaviours can provide additional coping ability. A river network can be seen as a dynamic mosaic of thermally heterogeneous linked habitats where mobile freshwater fishes experience a changing mosaic of food abundance and accessibility, and physiological growth potential, which together provide a wide range of foraging and growth opportunities across the riverscape (Rossi et al. 2024). Behavioural thermoregulation provides an adaptive physiological response to such environmental heterogeneity, enabling mobile fish to rapidly and reversibly adjust their physiology to match ambient foraging conditions (Armstrong et al. 2013). In fact, behavioural thermoregulatory movements across the network by individuals seeking optimal or less-stressful temperatures seem ubiquitous in cold-water fish species, especially at low latitudes (Amat-Trigo et al. 2023). Interestingly, thermoregulatory movements can take place at different temporal scales: observational studies have shown that individuals that exploit thermal heterogeneity between foraging and resting habitats through diel long-distance movements grow at substantially faster rates than fish that assume other foraging behaviours (Armstrong

et al. 2013); fish can also profit from thermal heterogeneity by tracking peaks in growth potential across the network on a seasonal basis, residing in cold-water refuges in summer and making use of warmer and more productive habitats only in cooler seasons (Armstrong et al. 2021; Hahlbeck et al. 2022).

Behavioural exploitation of thermal heterogeneity can also occur at much smaller spatial scales, and so the availability of thermal refuges at the reach scale is important to the survival of cold-adapted taxa (e.g., salmonids and their invertebrate prey) under thermally stressful conditions (Morgan and O'Sullivan 2022; Nadeau et al. 2022; Railsback and Harvey 2023); still, the value of a thermal refuge depends not only on its size and temperature but also on other habitat characteristics that affect food availability, energy costs and predation risk (Railsback and Harvey 2023). Our study suggests that, even in the absence of thermoregulation, behavioural plasticity in diel activity and habitat selection patterns could be adaptive and thus important for buffering to some extent the demographic impacts associated with climate change.

However, in many cases the magnitude of the behavioural response to changes in the environment is not enough to keep pace with climate change (Van Buskirk 2012). Therefore, behavioural plasticity must complement and act in concert with rapid evolutionary adaptation, and intra- and trans-generational phenotypic plasticity, if vulnerable stream-dwelling salmonid populations are to persist in warming and drying rivers.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

DA: Conceptualization, methodology, field investigation, software programming, formal analysis, visualization, writing – original draft. SFR and BCH: Software programming, writing – review & editing. GGN, BE and AA: Funding acquisition, field investigation, writing – review & editing.

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Data availability

Model codes, input files and output data are available via this Figshare repository (https://figshare.com/articles/dataset/Behavioural_plasticity_in_circadian_foraging_patterns_increases_resistance_of_brown_trout_populations_to_environmental_change/28054238) (Ayllón et al. 2024).

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Supplementary material 1

Validation of inSTREAM

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Data type: pdf

Explanation note: Summary of inSTREAM evaluation and validation published studies performed to test its structural realism and validity.

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