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Increased Temperature and Discharge Influence Overwinter Growth and Survival of Juvenile Salmonids in a Hydropeaking River: Simulating Effects of Climate Change Using Individual-Based Modelling

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Abstract: Climate change causes warming of rivers and may increase discharge, particularly during winter. Downstream of hydropower plants, fluctuating water temperature and flow create dynamic overwintering conditions for juvenile salmonids. We used inSTREAM 7.2-SD to simulate the effects of increased temperature (+2 °C) and discharge (+10%) on the overwinter growth and mortality of one-summer- and two-summer-old Atlantic salmon and brown trout in a river with a hydropeaking flow regime in a 2 × 2 design with replicated simulations. Water temperature had a major positive relationship with growth for both species and year classes, whereas increased flow alone had no major general effect on overwinter growth. For one-summer-old trout experiencing the high temperature regime, however, increased flow resulted in reduced growth. There were no major effects from temperature and flow on the survival rate of the two-summer-old fishes. On the other hand, there were significant interaction effects for the one-summer-olds, indicating that the effect of flow depended on temperature. For one-summer-old salmon, high flow resulted in increased survival in the low temperature regime, whereas it resulted in reduced survival in high temperature. In contrast, for one-summer-old trout, high flow resulted in reduced survival in the low temperature regime and increased survival in the high temperature. Different hydropower operation alternatives may interact with warming, affecting the relative competitive abilities of stream salmonids. Ecological models that predict the effects of different environmental conditions, such as temperature and flow regimes, may offer insight into such effects when in situ experiments are not feasible.

Keywords: flow; global warming; habitat; IBM; inSTREAM; salmon; trout

Key Contribution: Using the individual-based model inSTREAM 7.2-SD, we predicted how altered temperature and discharge regimes in a future climate would influence the growth and survival of brown trout and Atlantic salmon in the Gullspång River, Sweden, from September to April. Increased temperature and flow, and their interaction, affected the two species and the different age classes differently.

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1. Introduction

Climate change causes warming of rivers and streams [1], and during winter it may increase discharge, resulting in less snow and ice on streams at high latitudes. In rivers that do not freeze during winter, elevated water temperature and winter spates affect the riverine biota [1–3]. Fish that are winter active, such as salmonids, must cope with these changing winter conditions by adjusting their behaviour and physiology [4–6].

Many salmonid populations inhabit regulated rivers, and the operation of hydroelectric power plants, which affects downstream flow and temperature, plays a key role in ensuring that there is enough suitable rearing and spawning habitat for salmonid populations to survive [5,7]. In regulated rivers with hydropower generation that must meet sub-daily fluctuations in electricity demand, hydropeaking flow may contribute further to dynamic winter conditions by causing a fluctuation in water temperature and flow, which in turn affects ice dynamics [8] and fish habitat [4,9,10]. These changing environmental winter conditions affect the risk of stranding [11] and displacement [12] and may increase energy expenditure [4–6] in juvenile salmonids.

Typically, it is not generally feasible to test in situ the effects of different hydropower operation alternatives on salmonid population dynamics. In lieu of such field studies, ecological models that predict the effects of different environmental conditions, such as temperature and flow regimes, may offer insight. In particular, bioenergetic individual-based models (IBMs) have given biologically meaningful and mechanistically understandable explanations for observed ecological phenomena [13–15].

Here, we used inSTREAM 7.2-SD (an IBM of salmonids in a stream environment with sub-daily flow fluctuations) [16] to simulate the effects of increased temperature and discharge on the overwinter mortality and growth of one-summer- and two-summer-old Atlantic salmon and brown trout in the Gullspång River, Sweden. These two salmonid populations have high cultural, economic and conservation value [7]. This river is subject to sub-daily flow fluctuations because the hydropower plant that regulates the river operates with hydropeaking power generation [17]. Our study built on the work by Hajiesmaeili et al. [17], in which the effects of different hydropeaking and non-hydropeaking flows were compared. Here, we used the same study system to assess how winter conditions, including temperature change, may affect the two species. Specifically, we compared mortality and growth under current flow and temperature conditions and compared these to the growth and mortality in an environment with a 2 °C higher temperature and 10% higher discharge.

2. Material and Methods

2.1. Model Description and Study Site

The inSTREAM models are fed the following input: (1) a shapefile of cell geometry and habitat features imported from a geographical information system (GIS), (2) 2D bathymetry-based hydraulic modelling output to predict water velocity and depth in the cells at different discharges, (3) time-series information of turbidity, discharge and temperature (Figure 1), (4) parameters specific for the simulated reach and the fish species investigated and (5) the initial fish population at the start of the simulation (Table 1). The models provide different outputs at the individual level, such as growth and survival, as well as the selected cell position and the proportion of individuals displaying different behaviour (drift feeding, cruise feeding and hiding) at each time step. All choices are based on maximizing individual short-term fitness. These data can be summarized into population responses, such as population growth or decline, and spatial and temporal distribution patterns.

Using the NetLogo modelling software platform, the 7th version of inSTREAM is the most recent update that uses multiple time steps per day related to the light (dawn, day, dusk and night) and enables the user to incorporate additional flow change-dependent time steps (inSTREAM 7-SD [16,18]), thereby making this version suitable for simulations of rivers that have a hydropeaking flow regime [17]. At every time step, each individual fish selects its habitat cell and activity (drift feeding, search feeding or hiding) and experiences growth or weight loss based on its net energy intake. In addition, survival for each individual at each time step is determined in relation to mortality risks: high temperature, stranding (associated with an extremely shallow habitat), poor condition (starvation), and predation by terrestrial animals and other fish. Habitat selection (and consequently growth and survival) is modelled using a hierarchy of fish length. Selecting where to feed or hide is executed from the largest to the smallest fish, and individuals can only use food and velocity shelters that had not been used by larger fish. Growth is modelled as proportional to the net rate of energy intake, which was the difference between the energy from feeding and the metabolic costs.

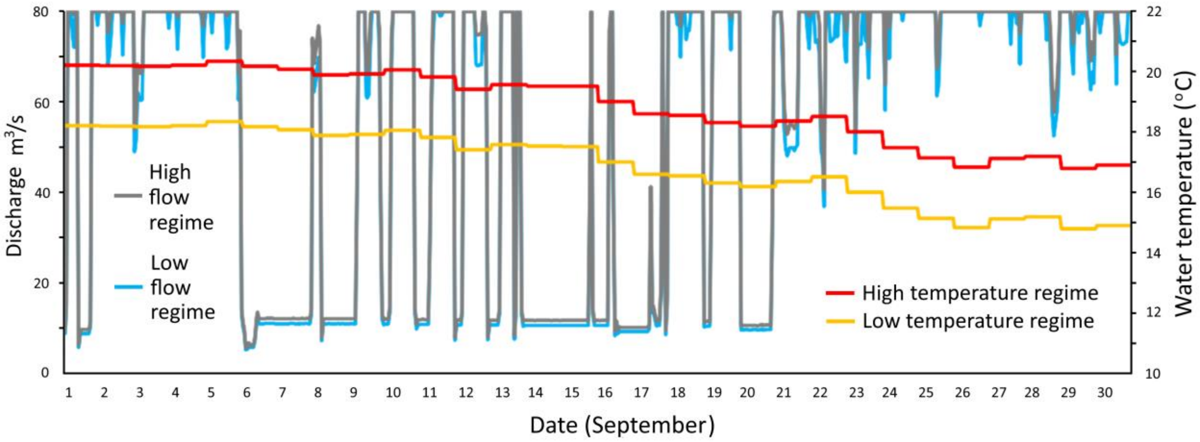

Figure 1. Effects of increased temperature and flow on growth and survival of Atlantic salmon and brown trout in a Swedish hydropeaking river was investigated by simulating population responses from 1 September to 30 April using the individual-based salmonid population model inSTREAM 7-SD. In the 2 × 2 design, each combination of low (baseline) and high temperature (+2 °C) and flow (+10%) regime was tested. As an example of how the treatments affect discharge and temperature, the figure shows the hydrograph and water temperature during the month of September.

Table 1. Initial size of one- and two-summers-old Atlantic salmon and brown trout population in a hydropeaking Swedish river used as input data for the individual-based salmonid population model inSTREAM 7-SD. Fish sizes were matched to electrofishing data.

Species	Starting Age	Number	Length (Min–Mode–Max; mm)
Atlantic salmon	one summer	810	6.2–9.0–14.3
	two summers	40	15.5–17.2–18.6
Brown trout	one summer	360	4.6–10.5–19.0
	two summers	20	19.7–22.5–23.5

Discharge affects water depth and velocity, which influences prey capture probability and energy expenditure, which in turn is affected by the availability of velocity shelters and fish size. The energy budget, in turn, affects growth rates and mortality risk. Various temperature effects are incorporated in the model, including metabolic rates and physical performance, which are represented through a bioenergetics approach. If the fish lose weight, they are vulnerable to poor condition (starvation) and predation because the decision of an individual fish on where and when to feed or hide depends on its own state. Predation risk from piscivores also increases with temperature due to increases in metabolic demands and feeding activity. Furthermore, temperature affects the maximum sustainable swimming speed, which influences the success of drift feeding. All the parameters in the model and detailed documentation of its formulation are described in the inSTREAM 7 user manual [16,18].

The 8 km-long Gullspång River, which connects Lakes Skagern and Vänern, serves a 5000 km^2 catchment area of mainly forested land and has a mean discharge at the mouth of 62 m^3 s^{-1}. The river harbours migratory populations of land-locked, large-bodied Atlantic salmon and brown trout, and because of their high cultural, conservation and economic value [7,19], river restoration projects have been initiated to help these populations to recover. However, the efficiency of these restorations has not been thoroughly assessed, in particular in face of further climate change. Spawning and rearing habitats are limited to three rapids, and this study used the Lilla Åråsforsen rapids, as the study site (59.012 °N, 14.098 °E). Hydropeaking in this river is allowed from 20 August to 19 April, with a minimum base flow of 9 m^3 s^{-1}. The maximum capacity of the hydropower plant is 230 m^3 s^{-1}, but not all of this high discharge reaches Lilla Åråsforsen because a diversion weir upstream reduces the maximum flow. In our simulations, we assumed that all water over 80 m^3 s^{-1} would be directed to the diversion channel and not reach Lilla Åråsforsen.

The model was calibrated using electrofishing data on growth for the different year classes and adjusting drift and benthic food availability in addition to aquatic and terrestrial predation risk because these parameters have been shown to affect model output the most [17,18,20]. A detailed description of the hydrodynamic modelling (using MIKE 21; DHI Sweden), Lilla Åråsforsen model application description, model calibration and a map of the area can be found in Hajiesmaeili et al. [17]. The model covered 24,000 m^2 (5500 cells) and was populated by 810 one-summer-old and 40 two-summer-old salmon and 360 one-summer-old and 20 two-summer-old trout with sizes according to those electrofished in the same reach [17].

2.2. Flow and Temperature Scenarios

We used two temperature and two discharge time series in a 2 × 2 full factorial design. For the temperature time series, which represented the current temperature, we used modelled data based on air temperature for 2013–2014 [21]. The temperature model was validated by empirical water temperature data from 2019 to 2021. We used the temperature time series from 2013–2014 in our simulations because these years were not unusually warm or cold. To create the time series that represented an increased temperature regime, we used the first temperature time series and added 2 °C to all data points (Figure 1). In arctic rivers with ice dynamics, climate change will likely have less effect on winter water temperatures because these rivers will stay frozen [1]. However, in the Gullspång River, an increase can be expected because it is rarely ice covered and typically has winter water temperatures > 0 °C (SMHI's Vattenwebb [22]), and it will likely be affected by a milder and wetter winter. The discharge time series that represented the current flow regime was based on data having a high temporal resolution (1 h^{-1}) provided by the hydropower operator, and originating from years that were not unusually dry or wet (2013–2014). For the time series 1 September to 30 April, which represented a future flow regime in a climate with wetter winters, we used the first discharge time series and added a 10% discharge to all data points (Figure 1). We could not reliably estimate when conditions similar to those in our scenarios may occur. Nevertheless, as a comparison, modelling results from the Norwegian River Mandalselva (at approximately the same latitude as the Gullspång River) predict a substantially larger increase than 2 °C and 10% more discharge within 100 years [23].

2.3. Data Analysis

For each of the four combinations of temperature and flow regimes in our 2 × 2 design, we carried out five replicated simulation runs using different random seeds each time for a total of 20 runs. We calculated the overwinter growth and survival for each species and year class based on the mean mass and number of individuals at the start of the simulation (1 September) and the end (30 April) (Table 1). Specifically, we calculated the mean instantaneous growth rate (g) as

$$g = (\ln(M_{end}) - \ln(M_{start}))/\Delta t$$

where M_{end} and M_{start} are the mean body masses at the end and the start of the simulation, and Δt is the duration of the simulation. Specific growth rate (SGR, % per day) was calculated per Crane et al. [24]:

$$\text{SGR} = 100 \times (e^{g} - 1)$$

Survival rates were calculated as the proportion of live fish at the end of the simulations. We arcsine square root- transformed the proportions to achieve normal distribution. Levene's test for equality of variances showed that variances were similar among the groups ($p > 0.05$). We argue that inferential statistical methods based on null hypothesis testing may be relevant when the model used for the simulations is complex; the prediction of the treatment effects is not trivial; and the results are presented as both statistical significance and effects size [25]. To analyse the effect of increased temperature and flow (and their interaction term) on the overwinter growth and survival of juvenile salmon and trout in the Gullspång River, we used two-way ANOVAs and analyzed the data using SPSS Statistics 28 (IBM, Armonk, NY, USA).

3. Results

3.1. Specific Growth Rates

Both the salmon and trout grew during the simulated period 1 September to 30 April the following year. The mean lengths of the salmon at the start of the simulations were 9.8 and 17.1 cm for the one-summer-olds and two-summer-olds, respectively, and 14.1 and 27.9 cm, respectively, at the end. The corresponding values for trout were 11.4 and 22.0 cm at the start and 17.3 and 29.7 cm at the end. The mean body mass growth (SGR) across all treatment combinations was 0.52% day^{-1} for the one-summer-olds and 0.60% day^{-1} for two-summers-olds. One-summer-old trout had higher growth (0.62% day^{-1}), whereas two-summer-old trout had lower growth (0.39% day^{-1}).

Increased flow had no major effect on overwinter growth (Table 2; Figure 2). Only for one-summer-old trout experiencing a high temperature regime did the increased flow result in reduced SGR (Figure 2), as indicated by a significant interaction term in the ANOVA (Table 2). For one-summer-old trout in high temperature, mean SGR decreased from 0.68% day^{-1} for the low flow regime to 0.65% day^{-1} for high flow. Water temperature had a major positive relationship with growth for both species and year classes (Figure 1; Table 2).

Table 2. Results from two-way ANOVAs, presenting the effects of temperature and flow regimes on specific growth and survival rates of one-summer-old and two-summer-old Atlantic salmon and brown trout. Growth and survival rates were extracted from simulations (n = 5) of salmonid populations in a Swedish hydropeaking river in low (baseline) and high (+2 °C increase from baseline) temperature regimes and low (baseline) high (+10% from baseline) flow regimes in a 2 × 2 design. The individual-based salmonid population model inSTREAM SD-7 was used for the simulations. The *p* values in boldface indicate significant effects (α = 0.05).

Variable	Population	Source of Variation	F	df	p	η_p^2
Specific growth rate	Atlantic salmon, one summer	Temperature	112.65	1, 16	**<0.001**	0.876
		Flow	<0.01	1, 16	1.000	<0.001
		Temperature × Flow	0.67	1, 16	0.426	0.040
	Brown trout, one summer	Temperature	136.97	1, 16	**<0.001**	0.895
		Flow	2.80	1, 16	0.114	0.149
		Temperature × Flow	4.98	1, 16	**0.040**	0.237
	Atlantic salmon, two summers	Temperature	13.13	1, 16	**0.002**	0.451
		Flow	0.04	1, 16	0.851	0.002
		Temperature × Flow	1.78	1, 16	0.201	0.100
	Brown trout, two summers	Temperature	8.08	1, 16	**0.012**	0.336
		Flow	1.29	1, 16	0.272	0.075
		Temperature × Flow	<0.01	1, 16	1.000	<0.001
Survival rate	Atlantic salmon, one summer	Temperature	158.24	1, 16	**<0.001**	0.908
		Flow	0.20	1, 16	0.661	0.012
		Temperature × Flow	11.84	1, 16	**0.030**	0.425
	Brown trout, one summer	Temperature	7.26	1, 16	0.160	0.312
		Flow	0.10	1, 16	0.752	0.006
		Temperature × Flow	5.29	1, 16	**0.035**	0.248

Table 2. *Cont.*

Variable	Population	Source of Variation	*F*	df	*p*	η_p^2
	Atlantic salmon, two summers	Temperature	0.90	1, 16	0.358	0.053
		Flow	0.07	1, 16	0.800	0.004
		Temperature × Flow	0.36	1, 16	0.555	0.022
	Brown trout, two summers	Temperature	0.18	1, 16	0.679	0.011
		Flow	0.18	1, 16	0.679	0.011
		Temperature × Flow	1.60	1, 16	0.224	0.091

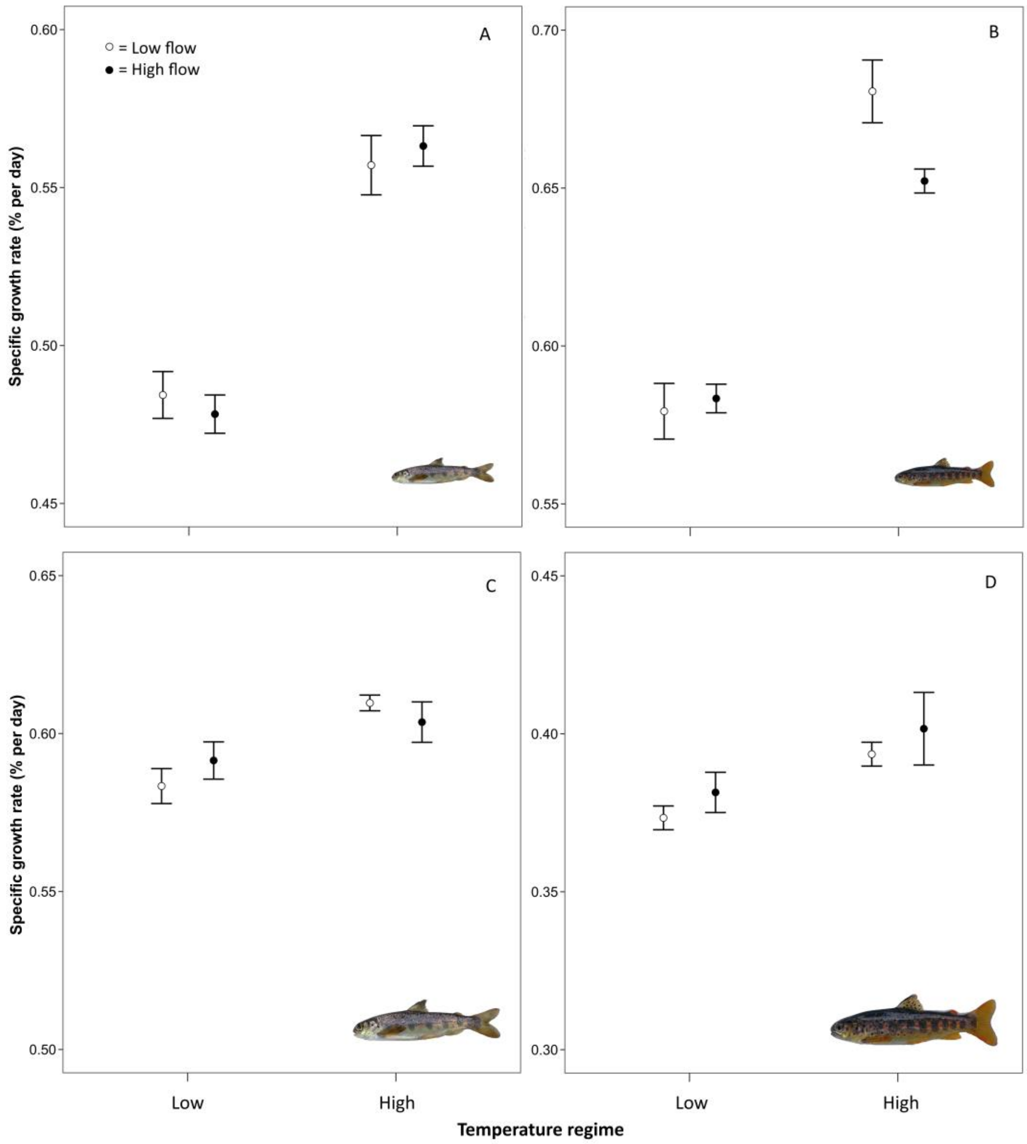

Figure 2. Mean specific growth rate (1 September–30 April) of (**A**) one-summer-old Atlantic salmon and (**B**) brown trout and (**C**) two-summer-old Atlantic salmon and (**D**) brown trout estimated from simulations (n = 5) of a Swedish hydropeaking river in low (baseline) and high (+2 °C increase from baseline) temperature regimes. Open circles represent a low (baseline), and filled circles a high (+10% from baseline) flow regime. The individual-based salmonid population model inSTREAM SD-7 was used for the simulations. Error bars indicate ± 1 SE.

3.2. Survival

One-summer-olds had lower mean survival rates (salmon: 40%; trout: 50%) than did the two-summers-olds (salmon: 84%; trout: 92%). Temperature and flow regimes did not affect the survival rates of the two-summer-olds (Figure 3; Table 2). For the analysis of survival rates for one-summer-old fish of both species, there was significant interaction between the temperature and flow regime (Figure 3; Table 2), indicating that the effect of the flow depended on the temperature. For one-summer-old salmon, high flow resulted in increased survival in low temperatures, whereas it resulted in reduced survival in high temperatures. For one-summer-old trout, the pattern was the reverse; high flow resulted in reduced survival in the low-temperature and increased survival in the high-temperature regimes (Figure 3).

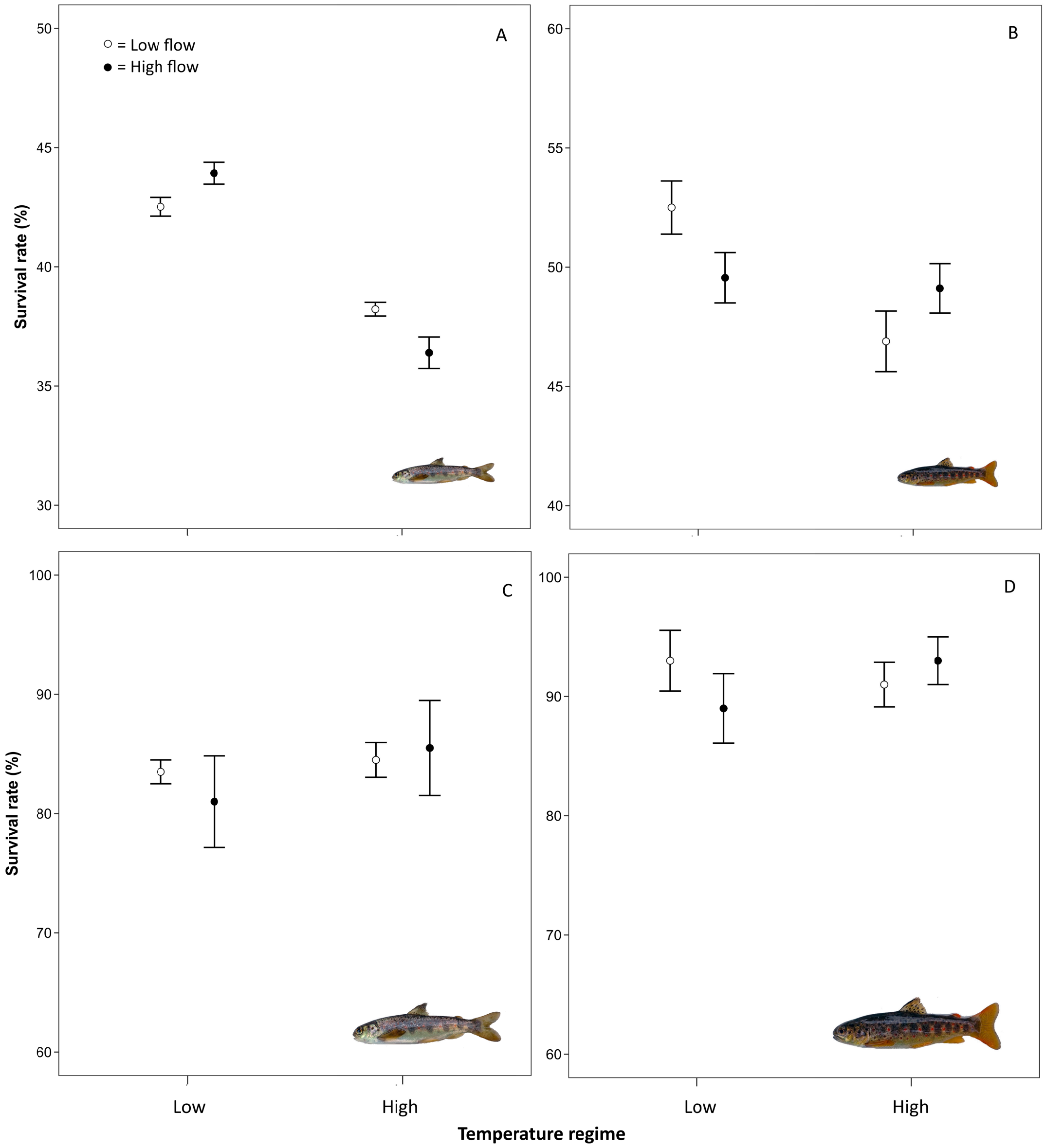

Figure 3. Mean survival rate (1 September–30 April) of (**A**) one-summer-old Atlantic salmon and (**B**) brown trout and (**C**) two-summer-old Atlantic salmon and (**D**) brown trout estimated from simulations (n = 5) of a Swedish hydropeaking river in low (baseline) and high (+2 °C increase from baseline) temperature regimes. Open circles represent a low (baseline) and filled circles a high (+ 10% from baseline) flow regime. The individual-based salmonid population model inSTREAM SD-7 was used for the simulations. Error bars indicate ± 1 SE.

4. Discussion

We used the salmonid population IBM inSTREAM 7.2-SD to simulate the effects of an increase in temperature and flow on overwintering juvenile Atlantic salmon and brown trout in a Swedish hydropeaking river. The results indicated the potential effects of climate change on two threatened salmonid populations in the Gullspång River and highlighted that the youngest size class (one-summer old) was the life stage most vulnerable to warming.

Increased winter temperature due to climate warming resulted in faster growth. Salmonid growth typically ceases at 1–3 °C [26], and with an increase of 2 °C in the Gullspång River, the period with little-to-no potential growth (water temperatures ≤ 3 °C) was considerably shorter by approximately 70% during the winter of 2013–2014). On the other hand, high winter temperatures resulting in increased metabolic rates required access to food resources and foraging opportunities to avoid starvation, and this feeding activity may have increased predation risk [4,6]. Although increased winter temperatures resulted in higher prey capture success for drift-feeding salmonids [27], foraging positions with a low predation risk may be lacking. Therefore, our result that the one-summer-old Atlantic salmon suffered from increased mortality in the high temperature regime was expected because small fish are typically more vulnerable to both predation and starvation compared to large fish [4,28].

Flow had only minor effects on growth and survival; however, in interaction with temperature it did affect one-summer-old Atlantic salmon survival. The combination of high flow and low temperature resulted in the highest survival rates, whereas high flow with high temperature resulted in the lowest. This may be worrisome because both temperature and flow will likely continue to increase. Here, we added 10% to the baseline scenario (empirical flow data from 2013–2014) as a constant addition. However, the potentially added discharge in northern rivers during winter will unlikely be released evenly over the year. Further simulations to investigate how an increased yearly discharge may be released over the year, i.e., different scenarios of hydropower generation schemes, may be worthwhile to find measures to minimize Atlantic salmon parr mortality in the Gullspång River. For one-summer-old brown trout, the pattern was the reverse: the highest survival was achieved under the low-flow and low-temperature regimes, whereas low flow and high temperature resulted in the lowest survival rates but the highest growth. Therefore, it is possible that by adjusting the flow under different warming scenarios, the relative competitive abilities of salmonid species will change [29,30].

In a previous study employing the same inSTREAM model, Hajiesmaeili et al. [17] tested the effects of hydropeaking scenarios with different baseflows. They found that increased flow generally had a negative effect on the survival of both species over the course of a whole year due to the increased aquatic predation facilitated by increased water depth. However, increasing the minimum base flow within hydropeaking flow scenarios had positive effects on the predicted growth of both species [17]. In the present study, focusing on the winter season, we demonstrated that these flow effects can be mediated by temperature at least for the one-summer-old fish.

The modelled species-specific differences in response to flow and temperature was likely driven by the size differences between species, a pattern reflecting observed life history variation [17]. In the Gullspång River, brown trout spawn in the fall earlier than Atlantic salmon, and their eggs hatch and emerge earlier in the spring. This difference in hatching date results in brown trout being larger than Atlantic salmon at the alevin, fry and parr life stages. Key inSTREAM factors, such as drift-feeding performance, predation risk, metabolic rate and habitat selection depend on the body size in the model [20]. Therefore, specific differences in these factors may relate to the different intra- (one- vs. two-summer-old) and interspecies (Atlantic salmon vs. brown trout) effects of flow and temperature regimes. The contrasting interaction effects of temperature and flow on one-summer-old Atlantic salmon and brown trout may be partly caused by brown trout outcompeting Atlantic salmon for the best feeding positions.

The inSTREAM modelling framework has the potential to develop hypothesis-driven research that may help to answer questions relating to complex ecological processes such as how sympatric species may respond to interacting factors like climate change and hydropeaking. This study, for example, highlighted the need for developing species-specific ecophysiological parameters for salmon and trout in the Gullspång River. Although conducting such ecophysiological studies would be a nontrivial task [31], further developed model capabilities may yield even more detailed and realistic results for these two populations. The alternative, replicated field studies under varying streamflow and temperature regimes, would clearly be impractical and require considerable resources. Thus, ecological modelling approaches will likely remain a key element of any research efforts that aim to assess the complex realities of river management, especially under future climate change scenarios.

5. Conclusions

In the Gullspång River, potential winter conditions with increased water temperatures and altered flows will likely influence the relative competitive abilities of Atlantic salmon and brown trout. In a warmer future, juvenile brown trout may dominate the most favourable feeding positions because of its competitive advantage of being larger at any given time and being a relatively more aggressive species [32] than the Atlantic salmon. On the other hand, the thermal preference of brown trout is lower than that of Atlantic salmon [26], but this physiological difference was not considered in the model we used due to a lack of standardized tests across species, size, temperature and water velocity [33]. Further modelling studies to investigate the potential non-linear effects and tipping points (using more than two levels of each treatment) should prove to be useful, together with species-specific physiological parameters, to assess the combined effects of different climate-change scenarios. We demonstrated potential trends in growth and survival of sympatric salmonid populations in hydropeaking rivers [34] caused by a future environment with warmer and wetter winters in temperate areas, which may influence the relative competitive abilities of juvenile salmonid species [30,32].

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Conflicts of Interest: The authors declare no conflict of interest.

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