



# Effects of cold and warm thermopeaking on drift and stranding of juvenile European grayling (*Thymallus thymallus*)

Stefan Auer  | Daniel S. Hayes  | Simon Führer | Bernhard Zeiringer | Stefan Schmutz

Department of Water, Atmosphere and Environment, Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Vienna, Austria

## Correspondence

Stefan Auer, Department of Water, Atmosphere and Environment, Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Vienna, Austria.  
Email: [stefan.auer@boku.ac.at](mailto:stefan.auer@boku.ac.at)

## Funding information

European Commission under Framework Program 7, Grant/Award Number: 603378

## Abstract

Intermittent water releases from hydropower plants, called hydropeaking, negatively affect river biota. The impacts mainly depend on hydrological alterations, but changes in physical habitat conditions are suspected to be co-responsible. For example, hydropeaking accompanied by a sudden change of water temperature in the downstream river—called thermopeaking—is also presumed to impair aquatic ecosystems. Still, knowledge about these thermopeaking impacts on aquatic species and life-stages is limited. We performed flume experiments under semi-natural conditions to fill this knowledge gap, simulating single hydropeaking events with a change in water temperature. As response parameters, we quantified the drift and stranding of early life-stages of European grayling (*Thymallus thymallus* L.), a key fish species of Alpine hydropeaking rivers. Hydropeaking events with a decrease in water temperature (“cold thermopeaking”) led to significantly higher downstream drift (mean = 51%) than events with increasing water temperature (“warm thermopeaking”, mean = 27%). Moreover, during cold thermopeaking, a comparably high fish drift was recorded up to 45 min after the start of peak flows. In contrast, drift rates quickly decreased after 15 min during warm thermopeaking. Remarkably, the spatial distribution of downstream drift along gravel bars during cold thermopeaking showed the opposite pattern compared to those triggered by warm thermopeaking events indicating different behavioral responses. Furthermore, the stranding rates of the cold thermopeaking trials were twice as high (mean = 31%) as those of the warm thermopeaking experiments (mean = 14%). The outcomes present vital information for improving mitigation measures and adapting environmental guidelines.

## KEYWORDS

downstream displacement, ecohydraulics, flow ramping, hydropower, impact mitigation

## 1 | INTRODUCTION

Intermittent releases from (pump-)storage power plants are of fundamental importance for present and future hydroelectric energy

production. However, this mode of operation, known as hydropeaking, alters the natural flow regime (Greimel et al., 2016), which may entail diverse consequences for riverine organisms (Bejarano, Jansson, & Nilsson, 2018; Bondar-Kunze, Maier, Schönauer, Bahl, &

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *River Research and Applications* published by John Wiley & Sons Ltd.

Hein, 2016; Greimel et al., 2018; Bruno, Siviglia, Carolli, & Maiolini, 2013; Hauer, Unfer, Holzapfel, Haimann, & Habersack, 2014; Schültling, Feld, & Graf, 2016; Young, Cech, & Thompson, 2011). Regarding fish, it has been well documented that hydropeaking entails stranding and downstream displacement of individual fish (Nagrodski, Raby, Hasler, Taylor, & Cooke, 2012; Young et al., 2011; Hunter, 1992; Saltveit et al., 2001; Halleraker et al., 2003; Auer, Zeiringer, Führer, Tonolla, & Schmutz, 2017; Führer et al., 2022), which, in turn, diminishes population vitality (Hayes et al., 2021; Schmutz et al., 2015).

Linked to artificial flow alteration, hydropeaking possibly also causes unnatural short-term water temperature fluctuations, referred to as “thermopeaking” (Hayes et al., 2022; Ward & Stanford, 1979; Zolezzi, Siviglia, Toffolon, & Maiolini, 2011). In detail, thermopeaking is caused by a seasonal pattern of water stratification in reservoirs (McCartney, 2009). When water is released from stratified reservoirs, this can lead to a decrease of water temperature in the receiving river in summer (cold thermopeaking) and an increase in winter (warm thermopeaking)—a pattern typical of many temperate hydropeaking rivers receiving hypolimnetic releases (Zolezzi et al., 2011). Indeed, thermopeaking patterns alter water temperature fluctuations of impacted rivers in terms of frequency, daily and seasonal timing, and amplitudes (Webb & Walling 1996; Steel & Lange, 2007; Zolezzi et al., 2011).

Water temperature is a fundamental driver of aquatic ecosystem processes and freshwater organisms (Webb et al., 2008) and may even be considered as an ecological resource similar to food (Magnuson, Crowder, & Medvick, 1979). Fish are ectothermic organisms, meaning that their body temperature and metabolism are directly linked to river water temperatures (Beitinger, Bennett, & McCauley, 2000; APEM, 2015; Bakken, King, & Alfresden, 2016; Heggenes et al., 2017). Subsequently, the ability to acclimate to daily or seasonal thermal changes is essential for bioenergetics (Crawshaw, 1977, Donaldson, Cooke, Patterson, & Macdonald, 2008), and thermal tolerance ranges depend on the developmental stage and fish species (e.g., Smythe & Sawyko, 2000). Acclimation responses require hours to days (Crawshaw, 1977) and include hormonal and cellular modifications, as well as physiological and behavioral responses, such as a change in microhabitat use to maintain homeostasis (reviewed in Donaldson et al. 2008). Exposure to a sudden temperature drop increases energy expenditure and may reduce a fish's swimming ability due to slower muscle contraction (Wardle, 1980). Juvenile fish are likely more affected by temperature fluctuations than adults. For example, swimming during a temperature drop at high velocities is more energy-intensive for Danube bleak (*Alburnus chalcoides*) larvae than for adult individuals, which use different muscle fibers (Rome, 1990; Wieser & Kaufmann, 1998). Similarly, smaller fish may exhibit less reactivity to predation as the frequency of tail sweeps may be reduced under such circumstances (Wardle, 1980).

Considering the effects of water temperature changes on fish, it would hardly be surprising if drift and stranding—two main impacts of hydropeaking—were affected by thermopeaking (Hayes et al., 2022). In this context, Zolezzi et al. (2011) emphasized the need to study ecological response mechanisms and patterns to thermopeaking. Although scientific research on the thermal behavior of flowing

waters gained increased attention within the last decades, research in thermopeaking is still rather scarce (Moreira et al., 2019) especially when it comes to impacts on fish populations (Reid et al., 2022). Here, we fill this knowledge gap by assessing how cold and warm thermopeaking affects juvenile European grayling (*Thymallus thymallus*, L.), a key species of Alpine hydropeaking rivers (Hayes et al., 2021). In detail, we quantified downstream drift, lateral distribution patterns of drifted organisms, and stranding as response parameters, hypothesizing that cold thermopeaking entails higher responses than warm thermopeaking for juvenile grayling and that smaller fish are more heavily impacted than larger specimens.

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental facility

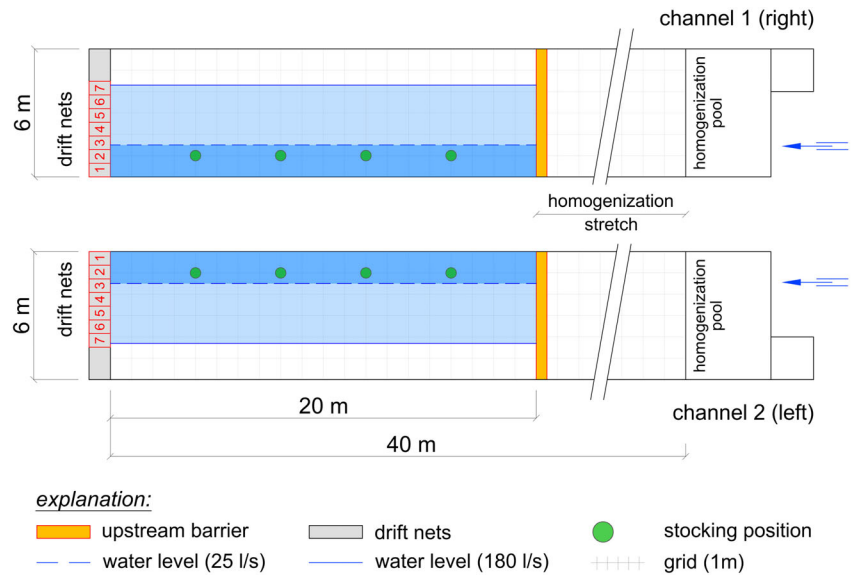
We performed thermopeaking experiments at an outdoor facility in Lunz/See, Austria, consisting of two nature-like channels (HyTEC: Hydromorphological and Temperature Experimental Channels). Each channel is 40 m long and 6 m wide and enables the simulation of different hydrological and water temperature scenarios. Water used for experiments is diverted from the nearby Lake Lunz; a surface and bottom outlet allow adjustments of channel water temperature. The reader is referred to Auer et al. (2017), Führer et al. (2022) and <https://hydropeaking.boku.ac.at/> for a more detailed description of the HyTEC facility.

### 2.2 | Experimental setup

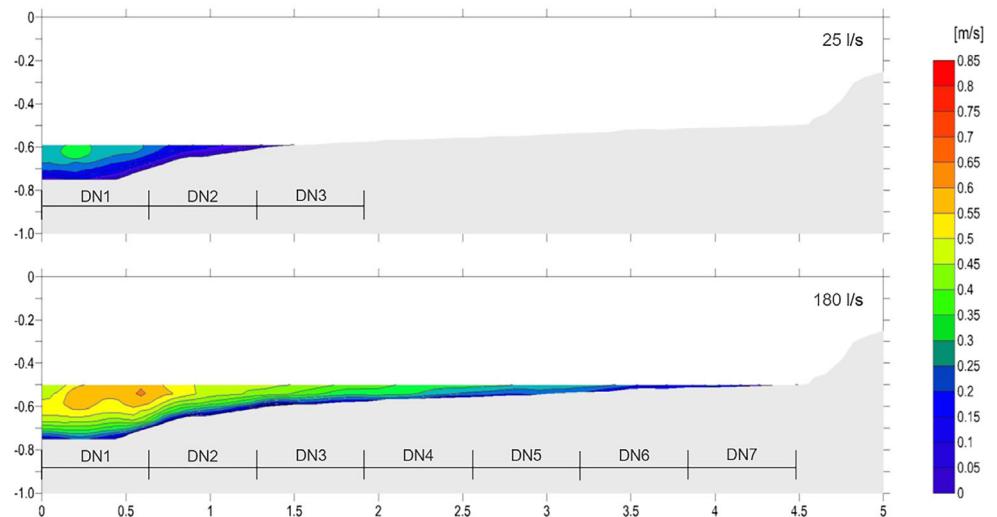
For our experiments, the upstream 20 m of the channel distributed water flowing from the pipes into the channels evenly. The experiments were conducted in the downstream 20 m stretches of each channel, which provided a longitudinal slope of 0.5% and a lateral slope of 3% (Figure 1). The channel substrate originated from a nearby pre-Alpine river, the Ybbs River, and was dominated by medium-sized gravel with proportions of fine and coarse particles ( $d_{10} = 0,8$  mm;  $d_{50} = 19$  mm;  $d_{90} = 27$  mm). A physical barrier at the upstream end of the experimental stretches hindered fish from escaping this way out of the experimental area. Water flowing out of the downstream end of each channel dropped into rectangular net frames ( $64 \times 75$  mm, mesh size 3 mm), which were arranged transversely to the flow direction to collect downstream drifting individuals (Figure 1). The fish used for the experiments were reared from wild fish caught in the nearby Ybbs River. The treatment of obtained eggs and larvae was identical to Auer et al. (2017). Individuals used for our experiments had mean total body lengths of 21–46 mm (mean = 29.0 mm  $\pm$  7.4 mm SD).

We conducted 31 single trials between June 9 and July 13, 2015. At each trial, fish were subjected to a single hydropeaking wave with different changes in water temperature. Half of the trials were subjected to a decrease in water temperature (cold thermopeaking “TPC,”  $n = 15$ ) and the other half to an increase in water temperature

**FIGURE 1** Overview of the two experimental channels with detailed information on the experimental stretch, including water level at base flow and peak flow, stocking positions and arrangement of drift nets [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jra.4077)]



**FIGURE 2** Cross-section view of the experimental channel showing prevailing flow velocities and water depths during base flow (top;  $25 \text{ L s}^{-1}$ ) and peak flow (bottom;  $180 \text{ L s}^{-1}$ ); the lateral positioning of drift nets at the downstream end is shown at the bottom (DN1 – DN7) [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jra.4077)]



(warm thermopeaking “TPW,”  $n = 16$ ). At each replicate, we stocked 100 fish in four groups of 25 fish, each separated by a distance of 4 m along the channel at a baseflow discharge of  $25 \text{ L s}^{-1}$ . Stocking in groups ensured better distribution of fish along the experimental stretch and less stress for the fish during counting, transferring, and stocking. Each trial consisted of three main phases: (a) acclimation during baseflow (AP), (b) peak flow (PP, divided into four consecutive subphases of 15 min each for sampling drifted individuals), and (c) down-ramping (DP). The acclimation phase lasted for 30 min, starting from stocking, and allowed fish to adjust to prevailing habitat conditions. To avoid any temperature-related influences, water temperature during this phase was identical to that of the fish holding tanks. The hydraulic setting (i.e., flow velocity, water depth, and substrate size) in the channels’ riverbanks was comparable to habitat conditions selected by juvenile grayling in Austrian rivers, thereby avoiding unintentional drift (Unfer, Leitner, Graf, & Auer, 2011; see Figure 2). At the beginning of the 60 min peak phase, we increased the discharge to  $180 \text{ L s}^{-1}$  with an average up-ramping rate (change

of vertical water level) of  $4.4 \text{ cm min}^{-1}$  for approximately 2 min. This increased maximum flow velocities in the mid-channel section from about  $0.25 \text{ m s}^{-1}$  to  $0.55 \text{ m s}^{-1}$  and increased water depth from 16 cm to 26 cm. The experiment ended with the down-ramping phase. In this phase, the discharge returned to the initial baseflow of  $25 \text{ L s}^{-1}$  over 3 min, resulting in a vertical water level drop of  $2.5 \text{ cm min}^{-1}$  and a dewatered width of 3 m in lateral extent, in which stranding could occur. After the down-ramping phase, we cleared the residing fish in the channel using hand nets and electrical devices.

We recorded the amount of drifted fish for each phase separately. For a better temporal resolution of the peak phase (PP), we sampled drifted fish every 15 min. Which defined the breakdown into the four subphases. We recorded the lateral distribution of drifted fish based on driftnets mounted next to each other; in total, seven driftnets spanned the entire channel width from the mid-channel section to the outermost shoreline. A visual tarpaulin vertically mounted upstream of the drift nets provided shielding for the staff to avoid interference during recording and removing drifted fish in the nets.

**TABLE 1** Calculation of drift and stranding rates for each experimental phase

Metric	Phase	Calculation	
Drift	AP (acclimation phase)	$D_{AP} (\%) = (d_{AP}/B) * 100$	(Equation 1)
Drift	PP (peak phase)	$D_{PP} (\%) = d_{PP}/(B-d_{AP}) * 100$	(Equation 2)
Drift	DP (Down-ramping phase)	$D_{DP} (\%) = d_{DP}/(B-d_{AP}-d_{PP}) * 100$	(Equation 3)
Stranding	DP	$Str (\%) = (B-d_{AP}-d_{PP}-d_{DP}-C)/(B-d_{AP}-d_{PP}) * 100$	(Equation 4)

Note: B, number of stocked fish;  $d_{AP}$ , number of drifted fish during the acclimation phase;  $d_{PP}$ , number of fish drifted during the peak phase;  $d_{DP}$ , number of drifted fish during the down-ramping phase; C, number of fish removed from the channel after the end of the down-ramping phase.

**TABLE 2** Mean water temperatures and temperature changes during experiments (TPW, warm thermopeaking; TPC, cold thermopeaking)

Water temperature-measurement time/phase	TPW	TPC
	Mean (°C) ± SD	Mean (°C) ± SD
Acclimation phase: Start	13.2 ± 1.45	13.1 ± 1.38
Peak phase - subphase 1: Start	13.2 ± 1.48	13.0 ± 1.52
Peak phase - subphase 2: Start	17.3 ± 2.93	10.5 ± 0.73
Peak phase - subphase 3: Start	17.5 ± 3.20	9.9 ± 0.97
Peak phase - subphase 4: Start	17.6 ± 3.51	9.9 ± 1.01
Peak phase - subphase 4: End	17.6 ± 3.13	10.0 ± 1.17
Change during peak phase - subphase 1	4.2 ± 1.57	-2.4 ± 1.27
Change during peak phase - subphase 2	0.3 ± 0.32	-0.7 ± 0.44
Change during peak phase - subphase 3	0.1 ± 0.18	0.0 ± 0.68
Change during peak phase - subphase 4	0.0 ± 0.13	0.1 ± 0.34
Change during the entire peak phase	4.4 ± 1.84	-3.0 ± 1.55

Based on these data, we calculated the relative rates of drifted individuals per phase (Equations 1–3 in Table 1), as well as the stranding rates during the down-ramping phase (Equation 4 in Table 1). Regarding the latter, we determined the number of residing fish at the end of an experiment divided by the number of (non-drifted) fish residing still present at the beginning of down-ramping. To validate the calculated stranding rates, we conducted clearing experiments, in which fish were exposed to a constant low flow situation of  $25 \text{ L s}^{-1}$  during the entire experimental period. After removing residing fish ( $96.5\% \pm 2.5 \text{ SD}$ ), we could estimate the number of missing individuals, representing the systematic uncertainty of stranding calculation. This data shows that calculated stranding rates may be overestimated by 3.5%.

## 2.3 | Water temperature

Water temperature was measured by temperature probes (PT100) installed inside the pipes for each channel. We programmed the discharge and water temperature settings required for the experiments based on these values. To detect spatio-temporal retention effects in the channels, we additionally measured the water temperature with

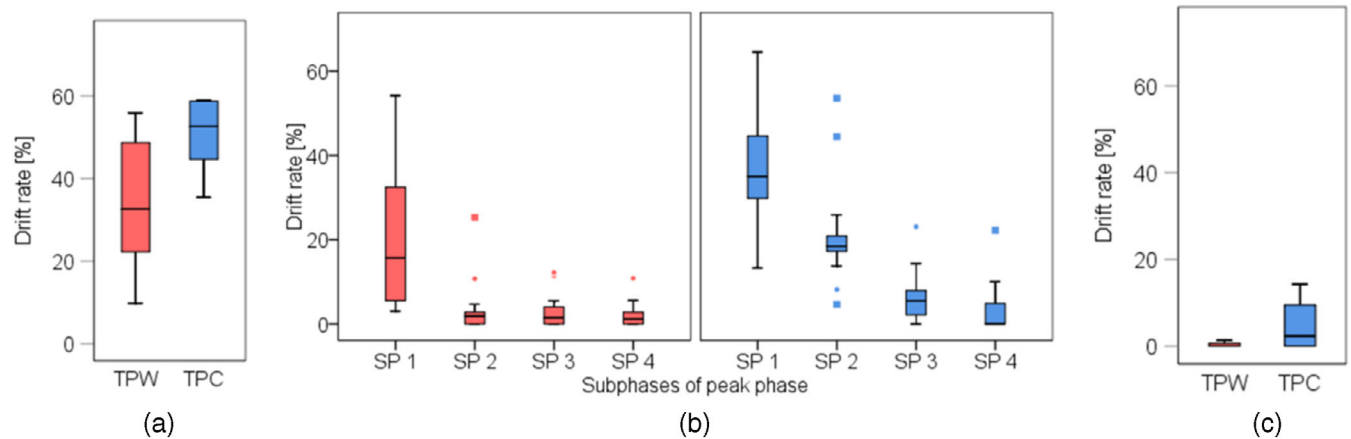
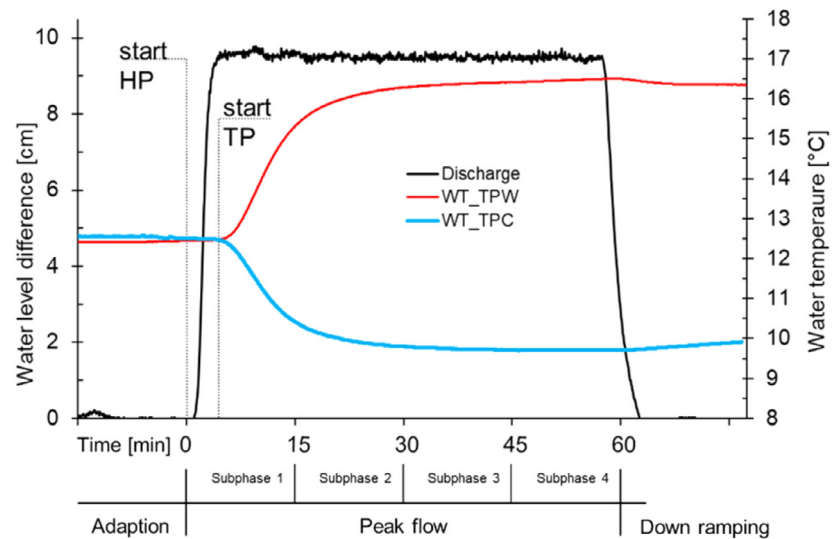
pressure probes (ATP00, Aquitronic) in the section upstream of the experimental stretch. For comparable analyses regarding drift and stranding, we used the absolute water temperature values from the beginning of the acclimation phase ( $WT_{AP}$ ), as well as the water temperature difference during each peak flow subphase and the peak phase as a whole (Table 2).

Water extracted from the lake's epilimnion increases temperatures in the experimental facility, whereas hypolimnetic extraction leads to a temperature drop. Seasonal and daily temperature fluctuations in the lake make it difficult to use the same temperature for all trials. Moreover, the exact water temperatures for the cold and warm thermopeaking trials were also subject to the temperature of the 500 m long pipes, which are impacted by underground temperatures. Besides, we observed temperature retention effects in the experimental channels (between the pipe's outlet and the experimental section), leading to a decoupling of the hydrodynamic and the temperature wave described by Toffolon, Siviglia, and Zolezzi (2010). These factors led to different temperature amplitudes and impacted the exact rate of change of temperature alterations during the experiments. The mean initial water temperature at the beginning of the acclimation phase was almost identical for both treatments (TPW:  $13.2^\circ\text{C} \pm 1.45 \text{ SD}$ ; TPC:  $13.1^\circ\text{C} \pm 1.38 \text{ SD}$ ). The change in water temperature occurred predominantly during subphase 1 of the peak phase. It remained almost constant after min 20–25 until the end of the down-ramping phase when discharge was lowered again (Figure 3).

## 2.4 | Data analysis

We used the Median-test to assess differences in drift and stranding (target variables) during each experimental phase (i.e., acclimation, peak flow, down-ramping) between the two experimental treatments, namely cold and warm thermopeaking (effect sizes). Next, we tested whether the four peak subphases differed in each treatment with Friedman's two-way ANOVA. We then employed correlation analysis (Pearson) to determine if the absolute water temperature difference affected the target variable's variability in each treatment, hypothesizing that the larger the difference, the greater the drifting or stranding rate. The change in water temperature was calculated and tested for the total peak flow and each peak flow subphase. Finally, we present plots linking the variability of the effect sizes with the fish length for each treatment to understand the role of fish size in the outcomes of

**FIGURE 3** Characteristics of water level (black graph) and water temperature for a typical warm (TPW, red graph) and cold (TPC, blue graph) thermopeaking experiments; start HP, hydropeaking; start TP, thermopeaking [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 4** Box-plot of calculated drift rates for warm (TPW, red) and cold thermopeaking (TPC, blue) during the (a) peak flow phase, (b) the four subphases (SP1-SP4) of the peak flow phase, and (c) during the down-ramping phase; the boxplots with the associated bold lines and whiskers refer to median values and interquartile ranges [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the experiments. For all tests, we considered a significance level of  $\alpha = 0.05$ .

### 3 | RESULTS

#### 3.1 | Drift

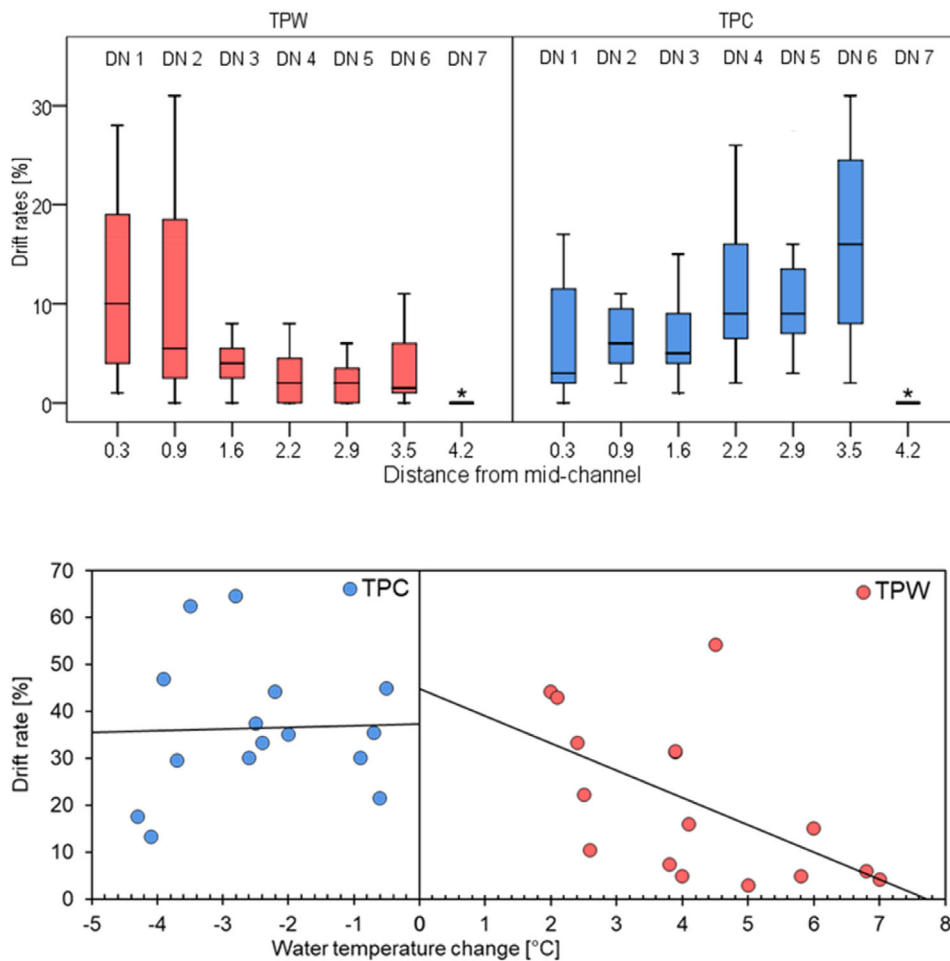
Drift rates during the acclimation phase were low, with a mean drift of 9.1% and 8.1% for TPW and TPC, respectively; this did not differ between the treatments (Median-test:  $\chi^2 = 0.03$ ,  $p = .861$ ).

During the peak phase, we identified a significant disparity between warm and cold thermopeaking (Median-test:  $\chi^2 = 5.45$ ,  $p = .020$ ). Mean drift rates were 26.9% for warm thermopeaking and 51.3% for cold thermopeaking (Figure 4a). A detailed analysis of the four peak subphases revealed significant differences in each of the two treatments (TPW: Friedman-test  $\chi^2 = 28.57$ ,  $p = .000$ ; TPC:  $\chi^2 = 37.73$ ,  $p = .000$ ). Drift was most pronounced during subphase

1 and decreased over time during warm and cold thermopeaking. Both treatments, however, exhibited different drift rates per subphase (Figure 4b). For TPW, drift during the first subphase ranged between 3.0–54.2% and was significantly higher than the other three following subphases, which did not differ from each other. In contrast, subphases 2 and 3 showed a significant difference in drift rates during TPC, meaning that the first two subphases were significantly higher than the last two (Friedman-test  $\chi^2 = 1.33$ ;  $p = .028$ ). The mean drift rate decreased by a factor of 1.7 from the first to the second subphase, but this trend was not significant (Friedman-test  $\chi^2 = 0.80$ ;  $p = .538$ ).

Fish drift rates during the down-ramping phase were low for both treatments (Figure 4c). However, there was minor evidence that fish drifted less during TPW (mean = 0.9%) than TPC (mean = 4.8%, Median-test:  $\chi^2 = 3.88$ ,  $p = .049$ ).

Regarding the lateral distribution of drifted fish during the peak flow phase, our data revealed that the warm scenario entailed the highest drift rates in drift net 1, situated in the mid-channel section with the highest flow velocities and water depths (Figure 2).



**FIGURE 5** Box-plots of drift rates of each driftnet of each driftnet during the peak flow phase for both treatments (red, warm thermo-peaking; blue, cold thermo-peaking). Driftnets (DN) are numbered in rising order, beginning at the mid-channel and going towards the riverbank (see Figure 2 for a cross-section view on the experimental channel); the boxplots with the associated bold lines and whiskers refer to median values and interquartile ranges [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**FIGURE 6** Calculated drift rates during the first 15 min of the peak flow phase (subphase 1) depending on the absolute water temperature change, separated by cold thermo-peaking (TPC: left) and warm thermo-peaking trials (TPW: right). Black line indicates the linear trend of each scenario [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

Other nets exhibited decreasing drift rates in the lateral direction towards the shoreline (Figure 5). In contrast, the mid-channel related nets 1–2 showed lower drift rates during cold than warm thermo-peaking. Also, rates of drifted fish during TPC increased from the mid-channel section towards the riverbank, revealing the highest drift rates in net 6. For both scenarios, the lowest number of drifted fish occurred in the outermost riverbank section at net 7 because the depth was not more than 2 cm, flow velocity was almost stagnant, and not the whole width was watered.

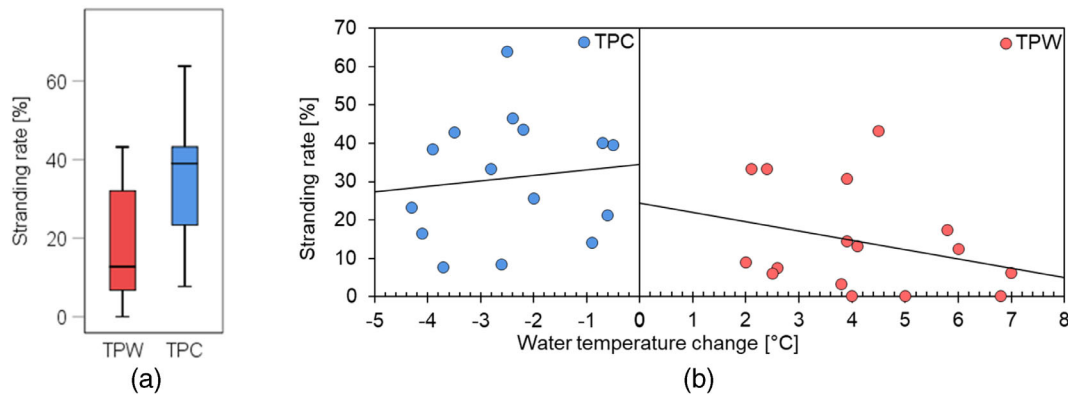
When pooling both experiments, we found that the relative drift rates during the first 15 min of peak flow (subphase 1) were negatively correlated with the absolute change in water temperature (Pearson- $r = -0.541$ ;  $p = .002$ ). In detail, this correlation was solely based on warm thermo-peaking trials ( $r = -0.571$ ;  $p = .021$ ), as higher water temperature changes led to decreasing drift rates (Figure 6). In contrast, despite the significantly higher drift during TPC trials, those were not related to the absolute change in water temperature ( $r = 0.034$ ;  $p = .905$ ). During subphase 2, the effect principle for the two treatments was the same as for subphase 1, but the correlations were not significant neither for warm thermo-peaking ( $r = 0.418$ ;  $p = .107$ ) nor for cold thermo-peaking ( $r = -0.103$ ;  $p = .714$ ). We detected no trend for subphases 3 and 4, which generally exhibited low drift rates and constant water temperatures (Figure 4; Table 2).

### 3.2 | Stranding

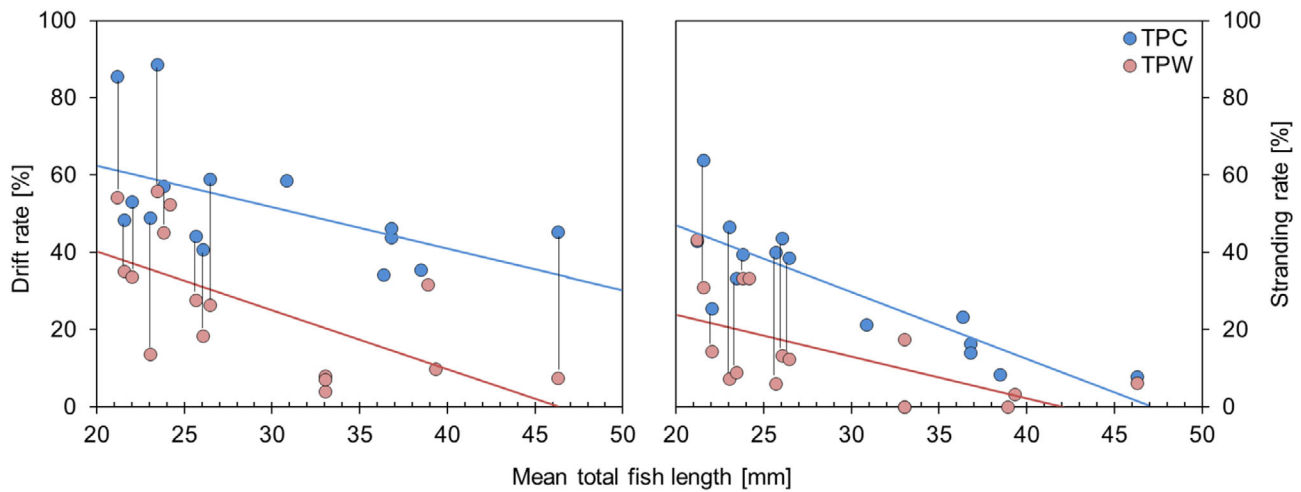
Similar to drift, stranding rates depended on the direction of the water temperature change (positive or negative) during the peak phase: cold thermo-peaking led to stranding rates more than twice as high (mean = 31.0%) as those during warm thermo-peaking (mean = 14.3%), and this was statistically significant (Median-test:  $\chi^2 = 5.44$ ;  $p = .020$ , Figure 7a). Even though the stranding rate showed a slight trend regarding absolute water temperature change during the peak flow phase for TPW trials (Figure 7b), this was not significant ( $R = -0.301$ ;  $p = .257$ ). Also, we could not find evidence for a strong correlation between stranding rates and the intensity of the temperature change during subphase 1 (Table 2), nor with the initial or final water temperature during the peak flow phase for both scenarios.

### 3.3 | The effect of body length on drift and stranding

Considering that fish grew in length during the experimental season, we could also assess the effect of body length on ecological responses. The comparison of paired trials, where fish of the same body length were subjected to TPW and TPC on a given day



**FIGURE 7** (a) Box-plot of stranding rates of both setups (TPW, warm thermopeak; TPC, cold thermopeak) and (b) stranding rate during the down-ramping phase depending on the absolute water temperature change during the peak phase, sep. *Black line indicates the linear trend of each scenario* [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jra.4077)]



**FIGURE 8** Calculated drift (left) and stranding rates (right) of both setups (TPW, warm thermopeak; TPC, cold thermopeak) depending on fish length. Values from trials using fish with the same mean total length are paired with vertical lines ( $n = 10$  each). The lines of two pairs of stranding rates are not visible due to too similar values (21 mm and 46 mm total length) [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jra.4077)]

( $n = 10$  each), showed that drift and stranding during cold thermopeak are always higher than in warm thermopeak, except for stranding rate in one instance (Figure 8). On average, drift and stranding are 1.5 and 1.7 times higher during TPC than TPW, respectively. Nevertheless, the data shows that a fish's risk of being displaced downstream or strand decreases as it grows in size. This trend is more pronounced for stranding (8) than for drift, the latter exhibiting comparably high drift rates for TPC at all fish lengths (Figure 8).

## 4 | DISCUSSION

Recent works pinpointed the need to assess the effects of thermopeak on fish (Hayes et al., 2019; Schmutz et al., 2015). Hence, this study tested the effects of water temperature fluctuations due to intermittent water releases from storage hydropower plants on drift

rates and stranding rates on early life-cycle stages of grayling. We did this by conducting single-peak thermopeak experiments in nature-like channels, allowing us, for the first time, to quantify the consequences of hydropeak coupled with a decrease or increase in water temperature on fish.

### 4.1 | Drift

As expected, drift rates during the acclimation phase were similarly low for both experimental setups, considering the thermal and hydrological constancy in that phase. Previous experiments demonstrated that 30 min is sufficient time for juvenile grayling to acclimate to the new habitat conditions and offset drift caused by stocking (Auer et al., 2017). Indeed, drift rates even decreased over time during the acclimation phase; all of these drifted fish were considered excluded from the experiments.

Cold thermopeakings triggered significantly higher drift rates than warm thermopeakings during the peak flow phase, the first setup being on average almost twice as high as the latter. In detail, analyses of the four 15 min long subphases of the peak flow phase revealed that most fish drifted during subphase 1, irrespective of the experimental setup. Rapid changes in hydraulic conditions likely cause this pattern due to up-ramping (Valentin, Sempeski, Souchon, & Gaudin, 1994; Parasiewicz et al., 1998) and following water temperature changes (Toffolon et al., 2010; Figure 3). Comparing both setups shows that cold thermopeakings displaced significantly more fish downstream during subphase 1 than warm thermopeakings. Moreover, during warm thermopeakings trials, drift dropped to rates below 10% in each of the three successive subphases; this was not the case for cold thermopeakings trials, which still showed comparably high drift rates in subphases 2 and 3 (Figure 4), suggesting that fish exhibit a reduced capability to withstand increased flow velocities if water temperature rapidly decreases at the same time (Graham, Thorpe, & Metcalfe, 1996). Since fish generally comprise a higher tolerance and better adaptation to heating than cold-water shocks (Beitinger et al., 2000), it is no surprise that warm thermopeakings consistently exhibited lower drift rates than cold thermopeakings. This pattern was still visible during the down-ramping phase when hydraulic stress, such as higher water velocities due to peak flows, was reduced (Figure 4).

The analysis of the lateral distribution of drifted fish led to an interesting finding, revealing an inverse pattern between cold and warm thermopeakings trials (Figure 5). Fish tended to drift more closely to the riverbanks during experiments with decreasing water temperature; in contrast, fish drift predominantly occurred in the mid-channel section when the temperature rose. This observed pattern may be explained by the organism's thermoregulation as fish shift laterally towards more favorable thermal habitats supporting homeostasis (Casas-Mulet, Alfredsen, Hamududu, & Timalina, 2015; Donaldson et al. 2008; Reynolds & Casterlin, 1980). In this regard, fish may seek near-shore habitats during cold thermopeakings. These areas feature higher water temperatures than the mid-stream section through atmospheric warming or a delayed temperature decrease during thermopeakings (Korman, & Campana, 2009). We observed that water temperature changes can be offset with flow alterations (Figure 3). Moreover, detailed temperature measurements of subsequent experiments (unpubl. data) confirmed that riverbank areas can serve as warm temperature refugia during cold-water releases, defying temperature decreases for extended periods, particularly during sunny summer days.

## 4.2 | Stranding

Similar to fish drift, stranding rates were significantly higher during cold thermopeakings than during warm thermopeakings (Figure 7a). In light of the lateral distribution patterns mentioned above, this result is no surprise. The fish' preference for flat and shallow riverbanks encourages them to seek habitats during peak flow that will be

dewatered during down-ramping. Considering that fish may also exhibit a delayed reaction time due to temperature decreases their stranding probability on already risky habitats in the ramping zone becomes exacerbated. The related ecological effects of stranding, such as death through desiccation or predation, are detailed in Young et al. (2011) and Nagrodski et al. (2012).

As juvenile grayling are about twice as likely to strand during cold than during warm thermopeakings, the former can lead to even quicker population depletion than the latter (Hayes et al., 2021). This can be particularly fatal in regions such as the European Alps, where cold thermopeakings tends to occur in spring and summer with temperature drops of up to 6°C (Toffolon et al., 2010; Zolezzi et al., 2011) during the early life cycle stages of salmonids (Hayes et al., 2019).

## 4.3 | Fish length

It is already well known that particularly early life cycle stages are sensitive to flow fluctuations, playing a major role in ecological processes such as drift and stranding (Moreira et al., 2019). This understanding has recently led to the development of the "emergence window" concept, which calls for the enforcement of strict hydropeaking restrictions during the time starting from the highly sensitive alevin phase up to 2–4 weeks after fish have emerged from the gravel bed (Hayes et al., 2019). Similarly, data from our experiments also show a reduction in drift and stranding rates over time. As grayling grew in size, they were less susceptible to being flushed downstream or becoming stranded. This pattern was observed for both cold and warm thermopeakings trials. However, even though larger fish were less impacted by hydropeaking than smaller ones, both treatments still showed distinct drift and stranding rates (Figure 8).

In detail, our data indicate that fish <25 mm are particularly sensitive to thermopeakings, exhibiting mean drift rates of 52% and stranding rates of 33%. In this length group, warm thermopeakings led to a mean drift of 64% and stranding of 42%, compared to a mean drift of 41% and stranding of 24% during warm thermopeakings trials.

Fish >45 mm exposed to warm thermopeakings are at low risk of being involuntarily displaced downstream (mean = 16%) or becoming stranded (mean = 7%). In these cases, fish have likely already outgrown the critical life stage. However, during cold thermopeakings, this risk of displacement and stranding (40 and 19%, respectively) is still higher for the same length cohort compared to warm thermopeakings. This is particularly true regarding drift, and more studies are needed to establish when grayling can better deal with peaking-induced water temperature decreases without being displaced downstream.

## 4.4 | Mitigation

This study shows that changes in water temperature during a single hydropeaking event influence the intensity and lateral distribution of drift as well as stranding frequencies of juvenile fish. These effects were especially pronounced during water temperature decreases.



These findings directly affect river management, considering that cold thermopeaking occurs in alpine hydropeaked rivers during early juvenile development (Hayes et al., 2019; Toffolon et al., 2010; Zolezzi et al., 2011).

Thermopeaking is a direct consequence of water stratification in the (high-altitude) reservoir, leading to temperature changes in the receiving river – depending on the season and depth of the water intake structure (Hayes et al., 2022; Vanzo, Siviglia, Carolli, & Zolezzi, 2016; Zolezzi et al., 2011). In this regard, a recent study highlighted the feasibility of dynamic reservoir intakes as an emerging good-practice measure to mitigate adverse thermopeaking effects (Halleraker et al., 2022). Indeed, newer hydropower facilities are increasingly upgraded with selective intake structures to meet downstream temperature requirements (Feng et al., 2018). Suppose the water release depth can be controlled. In that case, the release temperature can be manipulated to prevent thermopeaking by mimicking more natural water temperatures in the downstream river, including natural diurnal temperature fluctuations. These and further benefits of multi-level draw-offs are described in greater detail by Olden and Naiman (2010). Moreover, with regard to climate change predictions and associated run-off reductions of alpine European rivers during summer (LIT), a continuous cool water supply from reservoirs between peak energy production may benefit residual flow stretches (hydropeaking baseflows), which would otherwise exhibit increasing temperatures. Such water releases would lower thermal and hydrological amplitudes due to cold thermopeaking.

Morphological river restoration measures may reduce adverse thermopeaking effects. Studies have shown that morphologically complex water bodies, such as braided rivers or floodplain systems, exhibit a high thermic variability, including high lateral temperature gradients (Arscott, Tockner, & Ward, 2001; Tockner, Malard, & Ward, 2000; Tonolla, Acuna, Uehlinger, Frank, & Tockner, 2010). Therefore, morphologically diverse rivers with a high variability of water depths, flow velocities, and varying lateral connectivity gradients may offer suitable thermal refugia for aquatic organisms impacted by thermopeaking, especially regarding hydrological-related drift incidents. The risk of stranding in morphologically intact river stretches may even increase due to higher variability of temporal habitats with lower gradients with increased wetted areas compared to simplified or channelized morphological river stretches with steeper or artificial river banks (Vanzo, Zolezzi, & Siviglia, 2016). However, even if stranding or trapping risk is reduced in these channelized stretches, they do not provide suitable habitats for early life stage fish and, in the best case, only serve as downstream-oriented corridors linking suitable habitats for larvae or juveniles. In any case, morphologically intact rivers exhibit better hydrological retention than channelized ones, thereby dampening the hydrological effects of hydropeaking.

Worldwide, the river's water temperatures are expected to increase (Langan et al., 2001), and linking future change trajectories to current mitigation needs may pose additional management challenges. However, hypolimnetic releases may actually be used to lower consequences of water temperature increase during summer caused by climate warming (Null, Ligare, & Viers, 2013; Feng et al., 2018), favoring

cold-water stenotherm fish species, such as salmonids (Feng et al., 2018). Despite the emerging solutions described above, the need remains to better integrate thermopeaking into hydropeaking mitigation frameworks (Hayes et al., 2019).

## 5 | CONCLUSIONS

For the first time, this study tested how juvenile grayling respond to cold and warm thermopeaks. The results show that water temperature decreases during hydropeaking led to higher drift and stranding rates than temperature increases. Considering also the effects of absolute temperature changes and fish length, it becomes clear that particularly cold thermopeaking during the earliest life cycle stages must be avoided to prevent adverse ecological responses for salmonids in alpine rivers. Therefore, the effects of thermopeaking must be better integrated into hydropeaking mitigation frameworks, including, for example, dynamic reservoir intakes as a mitigation measure.

## ACKNOWLEDGMENTS

The authors want to thank Larissa Kaiser, Anna Jeworrek, and Lennet Leuchter for their countless hours working at the HyTEC facility, as well as Erwin Lautsch and Patrick Leitner for their assistance with data analysis. Furthermore, we would like to thank two anonymous reviewers for their critical comments and suggestions to improve the quality of the presented paper. This study was part of the MARS project (Managing Aquatic ecosystems and water Resources under multiple Stress) funded by the European Commission under Framework Program 7, contract no. 603378.

## DATA AVAILABILITY STATEMENT

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

## ORCID

Stefan Auer  <https://orcid.org/0000-0002-2008-9108>

Daniel S. Hayes  <https://orcid.org/0000-0003-3709-8630>

## REFERENCES

- APEM. (2015). Literature review of the influence of large impoundments on downstream temperature, water quality and ecology, with reference to the Water Framework Directive. APEM Scientific Report 413570. Scottish Environment Protection Agency. pp 84.
- Arscott, D. B., Tockner, K., & Ward, J. V. (2001). Thermal heterogeneity along a braided floodplain river (Tagliamento River, northeastern Italy). *Canadian Journal of Fisheries and Aquatic Sciences*, 58(12), 2359–2373. <https://doi.org/10.1139/f01-183>
- Auer, S., Zeiringer, B., Führer, S., Tonolla, D., & Schmutz, S. (2017). Effects of river bank heterogeneity and time of day on drift and stranding of juvenile European grayling (*Thymallus thymallus* L.) caused by hydropeaking. *Science of the Total Environment*, 575, 1515–1521. <https://doi.org/10.1016/j.scitotenv.2016.10.029>
- Bakken, T. H., King, T., & Alfredsen, K. (2016). Simulation of river water temperatures during various hydro-peaking regimes. *Journal of Applied Water Engineering and Research*, 4(1), 31–43. <https://doi.org/10.1080/23249676.2016.1181578>

- Beitinger, T. L., Bennett, W. A., & McCauley, R. W. (2000). Temperature tolerances of north American freshwater fishes exposed to dynamic changes in temperature. *Environmental Biology of Fishes*, 58(3), 237–275. <https://doi.org/10.1023/A:1007676325825>
- Bejarano, M. D., Jansson, R., & Nilsson, C. (2018). The effects of hydropeaking on riverine plants: A review. *Biological Reviews*, 93(1), 658–673. <https://doi.org/10.1111/brv.12362>
- Bondar-Kunze, E., Maier, S., Schönauer, D., Bahl, N., & Hein, T. (2016). Antagonistic and synergistic effects on a stream periphyton community under the influence of pulsed flow velocity increase and nutrient enrichment. *Science of the Total Environment*, 573, 594–602. <https://doi.org/10.1016/j.scitotenv.2016.08.158>
- Bruno, M. C., Siviglia, A., Carolli, M., & Maiolini, B. (2013). Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology*, 6(4), 511–522. <https://doi.org/10.1002/eco.1275>
- Casas-Mulet, R., Alfredsen, K., Hamududu, B., & Timalsina, N. P. (2015). The effects of hydropeaking on hyporheic interactions based on field experiments. *Hydrological Processes*, 29(6), 1370–1384. <https://doi.org/10.1002/hyp.10264>
- Crawshaw, L. I. (1977). Physiological and behavioral reactions of fishes to temperature change. *Journal of the Fisheries Board of Canada*, 34(5), 730–734. <https://doi.org/10.1139/f77-113>
- Donaldson, M. R., Cooke, S. J., Patterson, D. A., & Macdonald, J. S. (2008). Cold shock and fish. *Journal of Fish Biology*, 73(7), 1491–1530. <https://doi.org/10.1111/j.1095-8649.2008.02061.x>
- Feng, M., Zolezzi, G., & Pusch, M. (2018). Effects of thermopeaking on the thermal response of alpine river systems to heatwaves. *Science of The Total Environment*, 612, 1266–1275. <https://doi.org/10.1016/j.scitotenv.2017.09.042>
- Führer, S., Hayes, D. S., Hasler, T., Graf, D., Fauchery, E., Mameri, D., Schmutz, S., & Auer, S. (2022). Stranding of larval nase (*Chondrostoma nasus* L.) depending on bank slope, down-ramping rate and daytime. *Frontiers in environmental science*, 1275. <https://doi.org/10.3389/fenvs.2022.966418>
- Graham, W. D., Thorpe, J. E., & Metcalfe, N. B. (1996). Seasonal current holding performance of juvenile Atlantic salmon in relation to temperature and smolting. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(1), 80–86. <https://doi.org/10.1139/f95-167>
- Greimel, F., Schülting, L., Graf, W., Bondar-Kunze, E., Auer, S., Zeiringer, B., & Hauer, C. (2018). Hydropeaking impacts and mitigation. *Riverine Ecosystem Management: Science for Governing towards a Sustainable Future*, 91–110. <https://doi.org/10.1007/978-3-319-73250-3>
- Greimel, F., Zeiringer, B., Höller, N., Grün, B., Godina, R., & Schmutz, S. (2016). A method to detect and characterize sub-daily flow fluctuations. *Hydrological Processes*, 30(13), 2063–2078. Portico. <https://doi.org/10.1002/hyp.10773>
- Halleraker, J., Kenawi, M. S. R., L'Abée-Lund, J. H., Bakken, T. H., & Alfredsen, K. (2022). Assessment of Flow Ramping in Water Bodies Impacted by Hydropower Operation in Norway – are Hydropower with Environmental Restrictions More Sustainable? *SSRN Electronic Journal*. <https://doi.org/10.2139/ssrn.4004060>
- Halleraker, J. H., Saltveit, S. J., Harby, A., Arnekleiv, J. V., Fjeldstad, H. P., & Kohler, B. (2003). Factors influencing stranding of wild juvenile brown trout (*Salmo trutta*) during rapid and frequent flow decreases in an artificial stream. *River Research and Applications*, 19(5–6), 589–603. <https://doi.org/10.1002/rra.752>
- Hauer, C., Unfer, G., Holzapfel, P., Haimann, M., & Habersack, H. (2014). Impact of channel bar form and grain size variability on estimated stranding risk of juvenile brown trout during hydropeaking. *Earth Surface Processes and Landforms*, 39(12), 1622–1641. <https://doi.org/10.1002/esp.3552>
- Hayes, D. S., Moreira, M., Boavida, I., Haslauer, M., Unfer, G., Zeiringer, B., ... Schmutz, S. (2019). Life stage-specific hydropeaking flow rules. *Sustainability*, 11(6), 1547. <https://doi.org/10.3390/su11061547>
- Hayes, D. S., Lautsch, E., Unfer, G., Greimel, F., Zeiringer, B., Höller, N., & Schmutz, S. (2021). Response of European grayling, *Thymallus thymallus*, to multiple stressors in hydropeaking rivers. *Journal of Environmental Management*, 292, 112737. <https://doi.org/10.1016/j.jenvman.2021.112737>
- Hayes, D. S., Schülting, L., Carolli, M., Greimel, F., Batalla, R. J., & Casas-Mulet, R. (2022). Hydropeaking: Processes, effects, and mitigation. In K. Tockner & T. Mehner (Eds.), *Encyclopedia of inland waters* (2nd ed.). Elsevier Inc..
- Heggnes, J., Alfredsen, K., Brittain, J. E., Adeva Bustos, A., Huusko, A., & Stickler, M. (2017). *Stay cool: Temperature changes and biological responses in hydropower-regulated northern stream systems* (p. 95). Bø i Telemark: University College of Southeast Norway, Publication series No 21 11250/2477901.
- Hunter, M. A. (1992). *Hydropower flow fluctuations and salmonids: A review of the biological effects, mechanical causes, and options for mitigation*. Technical Report No. 119. Department of Fisheries, State of Washington.
- Korman, J., & Campana, S. E. (2009). Effects of Hydropeaking on Near-shore Habitat Use and Growth of Age-0 Rainbow Trout in a Large Regulated River. *Transactions of the American Fisheries Society*, 138(1), 76–87. Portico. <https://doi.org/10.1577/t08-026.1>
- Langan, S. J., Johnston, L., Donaghy, M. J., Youngson, A. F., Hay, D. W., & Soulsby, C. (2001). Variation in river water temperatures in an upland stream over a 30-year period. *Science of the Total Environment*, 265(1–3), 195–207. [https://doi.org/10.1016/S0048-9697\(00\)00659-8](https://doi.org/10.1016/S0048-9697(00)00659-8)
- Magnuson, J. J., Crowder, L. B., & Medvick, P. A. (1979). Temperature as an ecological resource. *American Zoologist*, 19(1), 331–343. <https://doi.org/10.1093/icb/19.1.331>
- McCartney, M. (2009). Living with dams: Managing the environmental impacts. *Water Policy*, 11(S1), 121–139. <https://doi.org/10.2166/wp.2009.108>
- Moreira, M., Hayes, D. S., Boavida, I., Schletterer, M., Schmutz, S., & Pinheiro, A. (2019). Ecologically-based criteria for hydropeaking mitigation: A review. *Science of the Total Environment*, 657, 1508–1522. <https://doi.org/10.1016/j.scitotenv.2018.12.107>
- Nagrodski, A., Raby, G. D., Hasler, C. T., Taylor, M. K., & Cooke, S. J. (2012). Fish stranding in freshwater systems: Sources, consequences, and mitigation. *Journal of Environmental Management*, 103, 133–141. <https://doi.org/10.1016/j.jenvman.2012.03.007>
- Null, S. E., Ligare, S. T., & Viers, J. H. (2013). A method to consider whether dams mitigate climate change effects on stream temperatures. *JAWRA Journal of the American Water Resources Association*, 49(6), 1456–1472. <https://doi.org/10.1111/jawr.12102>
- Olden, J. D., & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, 55(1), 86–107. <https://doi.org/10.1111/j.1365-2427.2009.02179.x>
- Reid, C. H., Patrick, P. H., Rytwinski, T., Taylor, J. J., Willmore, W. G., Reesor, B., & Cooke, S. J. (2022). An updated review of cold shock and cold stress in fish. *Journal of Fish Biology*, 100, 1102–1137. <https://doi.org/10.1111/jfb.15037>
- Reynolds, W. W., & Casterlin, M. E. (1980). The role of temperature in the environmental physiology of fishes. In *Environmental physiology of fishes* (pp. 497–518). Boston, MA: Springer. [https://doi.org/10.1007/978-1-4899-3659-2\\_19](https://doi.org/10.1007/978-1-4899-3659-2_19)
- Rome, L. C. (1990). Influence of temperature on muscle recruitment and muscle function in vivo. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 259(2), R210–R222. <https://doi.org/10.1152/ajpregu.1990.259.2.R210>
- Schmutz, S., Bakken, T. H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., ... Zeiringer, B. (2015). Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. *River Research and Applications*, 31(8), 919–930. <https://doi.org/10.1002/rra.2795>

- Schülting, L., Feld, C. K., & Graf, W. (2016). Effects of hydro- and thermo-peaking on benthic macroinvertebrate drift. *Science of the Total Environment*, 573, 1472–1480. <https://doi.org/10.1016/j.scitotenv.2016.08.022>
- Smythe, A. G., & Sawyko, P. M. (2000). Field and laboratory evaluations of the effects of “cold shock” on fish resident in and around a thermal discharge: An overview. *Environmental Science & Policy*, 3, 225–232. [https://doi.org/10.1016/S1462-9011\(00\)00060-5](https://doi.org/10.1016/S1462-9011(00)00060-5)
- Steel, E. A., & Lange, I. A. (2007). Using wavelet analysis to detect changes in water temperature regimes at multiple scales: Effects of multi-purpose dams in the Willamette River basin. *River Research and Applications*, 23(4), 351–359. <https://doi.org/10.1002/rra.985>
- Tockner, K., Malard, F., & Ward, J. V. (2000). An extension of the flood pulse concept. *Hydrological Processes*, 14(16–17), 2861–2883. [https://doi.org/10.1002/1099-1085\(200011/12\)14:16/17<2861::AID-HYP124>3.CO;2-F](https://doi.org/10.1002/1099-1085(200011/12)14:16/17<2861::AID-HYP124>3.CO;2-F)
- Toffolon, M., Siviglia, A., & Zolezzi, G. (2010). Thermal wave dynamics in rivers affected by hydropeaking. *Water Resources Research*, 46(8), W08536. <https://doi.org/10.1029/2009WR008234>
- Tonolla, D., Acuna, V., Uehlinger, U., Frank, T., & Tockner, K. (2010). Thermal heterogeneity in river floodplains. *Ecosystems*, 13(5), 727–740. <https://doi.org/10.1007/s10021-010-9350-5>
- Unfer, G., Leitner, P., Graf, W., & Auer, S. A. (2011). Der Einfluss von Schwallbetrieb auf den Fischbestand der oberen Drau. *Im Auftrag der Verbund-Austrian Hydro Power AG*, pp 250.
- Valentin, S., Sempeski, P., Souchon, Y., & Gaudin, P. (1994). Short-term habitat use by young grayling, *Thymallus thymallus* L., under variable flow conditions in an experimental stream. *Fisheries Management and Ecology*, 1(1), 57–65. <https://doi.org/10.1111/j.1365-2400.1970.tb00006.x>
- Vanzo, D., Siviglia, A., Carolli, M., & Zolezzi, G. (2016). Characterization of sub-daily thermal regime in alpine rivers: Quantification of alterations induced by hydropeaking. *Hydrological Processes*, 30(7), 1052–1070. <https://doi.org/10.1002/hyp.10682>
- Vanzo, D., Zolezzi, G., & Siviglia, A. (2016). Eco-hydraulic modelling of the interactions between hydropeaking and river morphology. *Ecohydrology*, 9(3), 421–437. <https://doi.org/10.1002/eco.1647>
- Ward, J. V., & Stanford, J. A. (1979). Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In *The ecology of regulated streams* (pp. 35–55). Boston, MA: Springer. [https://doi.org/10.1007/978-1-4684-8613-1\\_4](https://doi.org/10.1007/978-1-4684-8613-1_4)
- Wardle, C. S. (1980). Effects of temperature on the maximum swimming speed of fishes. In *Environmental physiology of fishes* (pp. 519–531). Boston, MA: Springer. [https://doi.org/10.1007/978-1-4899-3659-2\\_20](https://doi.org/10.1007/978-1-4899-3659-2_20)
- Webb, B. W., & Walling, D. E. (1996). Long-term variability in the thermal impact of river impoundment and regulation. *Applied Geography*, 16(3), 211–223. [https://doi.org/10.1016/0143-6228\(96\)00007-0](https://doi.org/10.1016/0143-6228(96)00007-0)
- Webb, B. W., Hannah, D. M., Moore, R. D., Brown, L. E., & Nobilis, F. (2008). Recent advances in stream and river temperature research. *Hydrological Processes: An International Journal*, 22(7), 902–918.
- Wieser, W., & Kaufmann, R. (1998). A note on interactions between temperature, viscosity, body size and swimming energetics in fish larvae. *The Journal of Experimental Biology*, 201(9), 1369–1372. <https://doi.org/10.1242/jeb.201.9.1369>
- Young, P. S., Cech, J. J., & Thompson, L. C. (2011). Hydropower-related pulsed-flow impacts on stream fishes: A brief review, conceptual model, knowledge gaps, and research needs. *Reviews in Fish Biology and Fisheries*, 21(4), 713–731. <https://doi.org/10.1007/s11160-011-9211-0>
- Zolezzi, G., Siviglia, A., Toffolon, M., & Maiolini, B. (2011). Thermo-peaking in alpine streams: Event characterization and time scales. *Ecohydrology*, 4(4), 564–576. <https://doi.org/10.1002/eco.132>

**How to cite this article:** Auer, S., Hayes, D. S., Führer, S., Zeiringer, B., & Schmutz, S. (2022). Effects of cold and warm thermo-peaking on drift and stranding of juvenile European grayling (*Thymallus thymallus*). *River Research and Applications*, 1–11. <https://doi.org/10.1002/rra.4077>