





# Why hydropeaking frequency matters: effects of recurring stranding on fish

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## ABSTRACT

Research and management of hydropeaked rivers largely overlook the ecological impacts of recurring flow fluctuations, such as fish stranding, on ecosystem health. This article synthesizes scientific and grey literature, field studies, and experiments to assess the effects of frequent hydropeaking on fish. Findings show that hydropeaking frequency significantly affects the ecological integrity of alpine rivers, with an average of three daily down-ramping events. Despite some evidence of behavioral adaptation of fish to recurrent flow fluctuations, this adaptation appears insufficient to counter the cumulative effect of a series of single hydropeaking events. Larval and juvenile fish are particularly vulnerable, with stranding impacts extending to the population and community levels. Effective mitigation should prioritize reducing the cumulative impact of recurring hydropeaks while ensuring single-event ramping rates and flow amplitudes remain within ecological limits. To effectively safeguard sensitive habitats, targeted mitigation efforts informed by an understanding of habitat dynamics are critical. Furthermore, maintaining lateral connectivity within river systems is essential for supporting resilient fish populations, especially where hydropeaking mitigation possibilities are limited. Finally, this study identifies future research directions on hydropeaking frequency and its ecological effects.

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## 1. Introduction

Intermittent hydropower generation resulting in hydropeaking – artificial sub-daily flow fluctuations – is currently key to balancing volatile renewable energy production (i.e. wind and solar) in a carbon-neutral way. It is expected that this trend will increase hydropeaking frequency (Hayes et al. 2022; IEA 2022; Koolen et al. 2023). In this regard, the deregulation of energy markets has already led to an increase in hydropeaking frequency in some rivers (Wandurraga 2019), albeit likely with lower flow amplitudes than before. The literature on the ecological effects of hydropeaking, as well as hydropeaking mitigation guidelines, have largely focused on assessing the role of flow intensity parameters, such as peak magnitude, ramping rate, or

duration of single flow fluctuation events (Tonolla et al. 2017; Moreira et al. 2019; Hayes et al. 2024). However, hydropeaking flow regimes, driven by sub-daily fluctuations in power demand, are not only characterized by single artificial short-term flow fluctuations but also by recurring events — often multiple times per day (Greimel et al. 2016; Bätz et al. 2023). Nonetheless, the cumulative ecological effects of recurrent hydropeaking have rarely been studied to date despite it becoming increasingly relevant.

Rapid and frequent flow fluctuations are detrimental to river ecosystems (Cushman 1985; Hayes et al. 2022; Bipa et al. 2024), affecting many freshwater organism groups, including riparian vegetation (Bejarano et al. 2018; Baladrón et al. 2022), riparian beetles (Van Looy et al. 2007), macroinvertebrates (Salmaso et al. 2021),

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and fish (Young et al. 2011; Nagrodski et al. 2012). For fish, an indicator of hydro-morphological integrity, the increase in spatio-temporal habitat dynamics due to recurrent hydropeaking (Bätz et al. 2024) may affect their behavior, movement, activity, and metabolism (Taylor and Cooke 2012; Costa et al. 2017), with potential repercussions on the successful completion of key life stages necessary to maintain a resilient population and community (Schmutz et al. 2015; Hayes et al. 2019). However, it is unclear to what extent an increase in hydropeaking frequency is detrimental to fish.

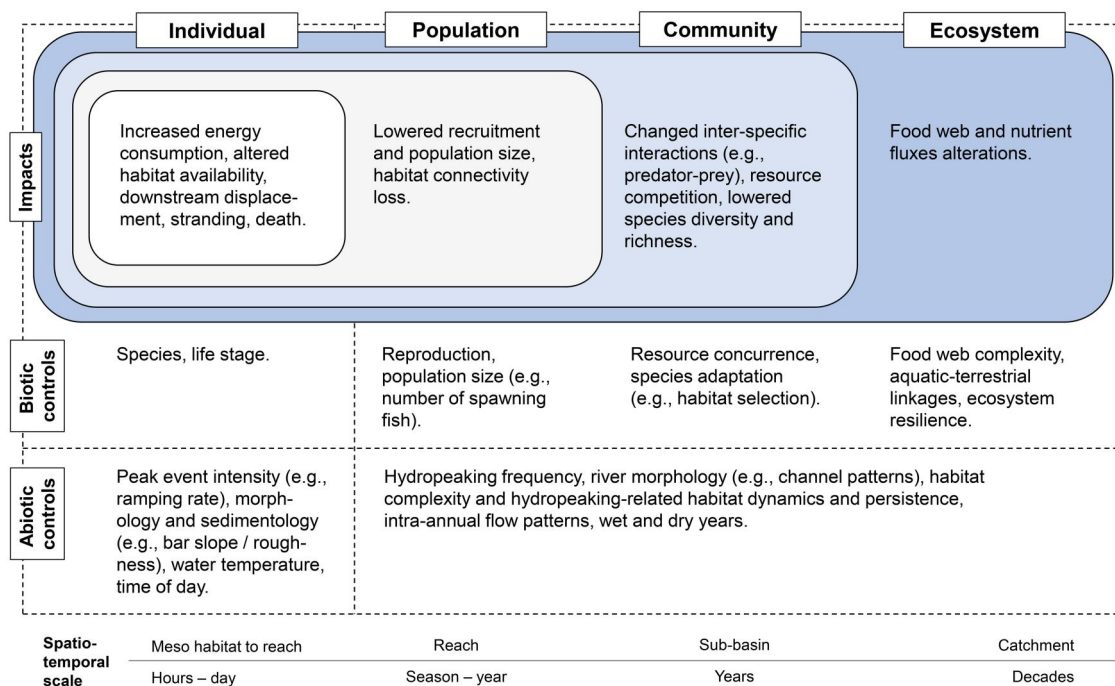
In hydropeaked rivers, stranding occurs during flow reductions (down-ramping) when organisms are left in habitats that dry up before they can relocate to permanently wetted habitats, often leading to their death through desiccation or predation (Nagrodski et al. 2012; Glowa et al. 2023; Reis-Filho and Leduc 2024). Similarly, organisms can be trapped in side channels or pools that become disconnected from the mainstem at low flow, increasing their susceptibility of becoming predated (Nagrodski et al. 2012; Insulaire et al. 2024). Stranding and trapping (henceforth called “stranding”) affects fish and other organism groups (Moog 1993), and an increase in hydropeaking frequency could be catastrophic. Stranding of larval and juvenile fish, which prefer shoreline habitats prone to dewatering (Young et al. 2011; Hayes et al. 2019, 2024; Führer et al. 2022, 2024), likely represents a bottleneck as feedbacks propagate to the population level and beyond (Puffer et al. 2017; Hedger et al. 2018), as the adverse effects of single down-ramping events can accumulate with increased hydropeaking frequency (Bauersfeld 1978). Therefore, it seems logical that a thorough assessment and discussion of

hydropeaking frequency is expedient (Bätz et al. 2023; Hayes et al. 2023b) to explore how frequency contributes to fish stranding and how these effects propagate from the individual fish to the population, community and ecosystem levels. Such multi-level effects also need to be placed in the context of biotic and abiotic controls (Figure 1), behavioral adaptations and the availability of refugial habitats in order to shed light on potential cumulative stranding effects and derive mitigation recommendations.

This article aims to stimulate the discussion about hydropeaking frequency by addressing the concept and hypothesizing its potential effects with a focus on fish stranding caused by flow down-ramping. We present a hydrological analysis of hydropeaking frequency in two alpine countries (Austria and Switzerland) and exemplify the cumulative effects of recurrent down-ramping events on fish stranding, synthesizing fish research from the field and the laboratory. We then discuss the effects of recurrent hydropeaks across different levels of the biological hierarchy (individual fish, population, community, ecosystem; Figure 1) by reviewing the relevant scientific and grey literature, also deducing first recommendations for more effective hydropeaking mitigation. Finally, we present an outlook on research needs by highlighting key topics for future studies on hydropeaking frequency.

## 2. Peaking frequency: a hydrological assessment

In the last two decades, various hydrological methods have been established to characterize hydropeaking



**Figure 1.** Conceptual figure on the effects of hydropeaking frequency on fish by considering different levels of biological organization (individual, population, community, ecosystem), including biotic and abiotic controls and the spatio-temporal scale of the impacts.

flows (Carolli et al. 2015; Bejarano et al. 2020; Courret et al. 2021; Sauterleute & Charmasson, 2014). Methods range from wavelet-based approaches (Zolezzi et al. 2009; Wu et al. 2015), to graphical analyses (Alonso et al. 2017) and event-based algorithms (Greimel et al. 2016). In this study, we adopt the methodology proposed by Greimel et al. (2016) to explore sub-daily flow fluctuation frequency patterns. The algorithm detects increasing or decreasing flow events by calculating flow differences of consecutive time steps (here: 15 min), whereby continuous time steps with equal trends are defined as a single flow fluctuation event. This approach diverges from traditional methods that often require subjective manual definitions of flow fluctuation rate thresholds (Sauterleute and Charmasson 2014; Li and Pasternack 2021). Instead, this method identifies ecologically-relevant flow fluctuation events by considering the magnitude of natural sub-daily flow changes. Establishing a supra-regional benchmark based on the highest natural sub-daily flow fluctuation event observed annually in Austrian rivers allows for the comparison of sub-daily hydrological conditions across various rivers in Austria and similar alpine areas, eliminating the need for arbitrary or subjective criteria in counting flow fluctuation events (Greimel et al. 2016; Greimel 2022).

We assessed the frequency of flow reduction (i.e. down-ramping) events for a representative selection of Austrian and Swiss stream gauges influenced by (a) hydropeaking or (b) hydrofibrillation (i.e. low-intensity artificial flow fluctuations as defined by Greimel et al. 2016) and non-regulated rivers with a (c) glacial or (d) rainfall flow regime (Figure 2, Table S1). As expected, hydropeaked rivers exhibit the highest event frequency, with a mean of three down-ramping events per day. There is little seasonal change when considering median values. However, considering the lower (Q1) and upper quartiles (Q3), a higher frequency is detected in the summer months compared to winter (Figure 2a). The annual frequency distribution of both countries show that 25% of the values are below one (Q1) and 25% are over four down-ramping events per day (Q3).

The mean daily frequency in rivers affected by hydrofibrillation (0.35 daily down-ramping events) is almost nine times lower than in hydropeaked rivers, and the data are skewed towards the lower end, with quartiles at 0.00 (Q1) and 0.40 (Q3). In these rivers, Swiss gauges feature slightly higher frequencies than Austrian ones, particularly during the summer and fall (Figure 2b).

Glacier-fed rivers exhibit a strong seasonal pattern, with hardly any flow fluctuations in the winter and early spring (Nov.-April). Most flow fluctuations occur during late spring and summer,

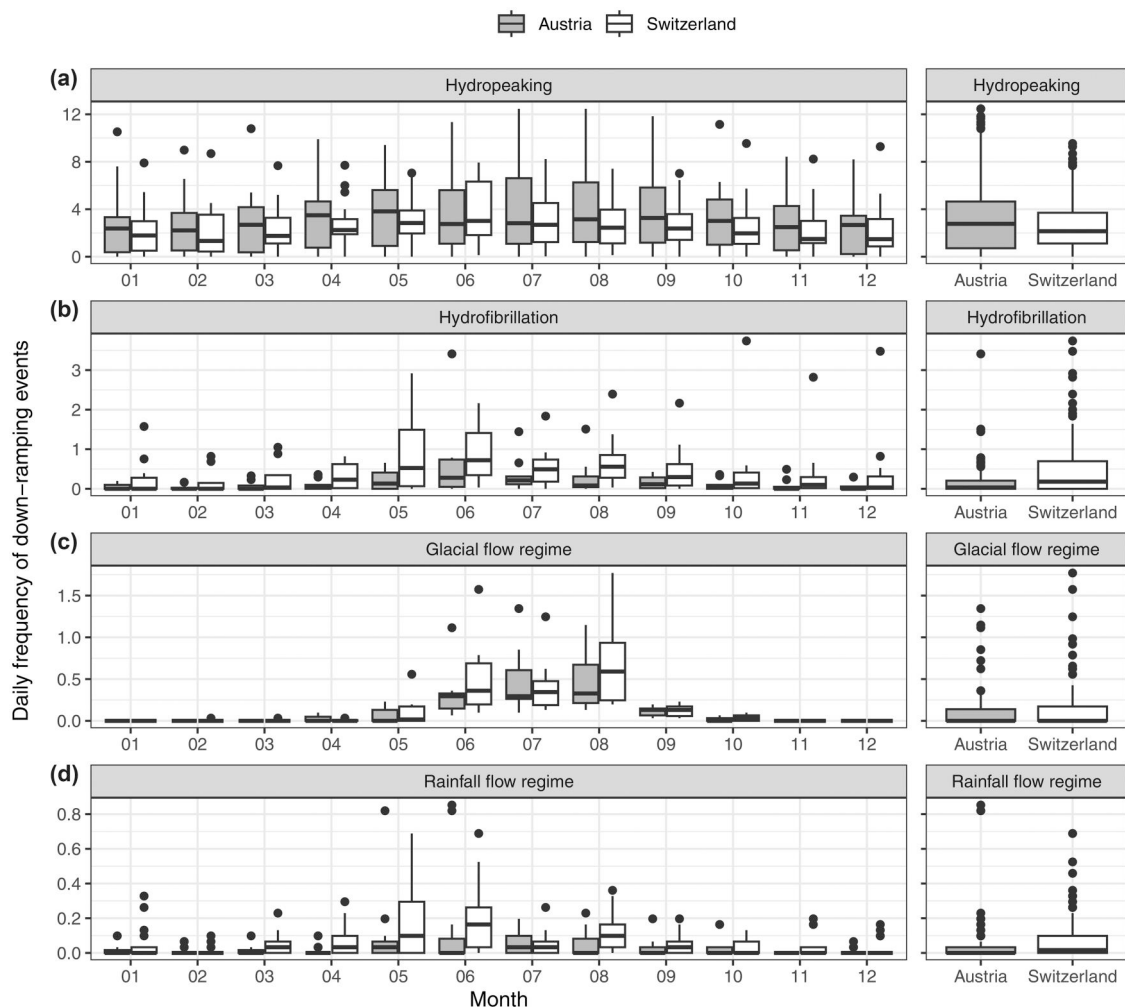
coinciding with the daily cycle of snow and glacier melt. During late spring and summer, the frequency is below that of hydropeaking and hydrofibrillation gauges (Figure 2c). For example, in May, a critical month for larvae development of salmonid fish in Europe, flow fluctuations at hydropeaking (mean = 3.50 daily down-ramping events) and hydrofibrillation gauges (mean = 0.60 daily down-ramping events) are around 36 and 6 times more frequent than those at glacial gauges (mean = 0.10 daily down-ramping events), respectively. In June, the mean daily count in glacier rivers is 0.44, which is around 12% of the frequency in hydropeaked rivers (mean = 3.76 daily down-ramping events) and 57% of the frequency in rivers affected by hydrofibrillation (mean = 0.78 daily down-ramping events).

Rivers with flow regimes driven by precipitation (rain and snow), feature the lowest flow fluctuation frequency with a mean of 0.05 daily down-ramping events and lower and upper quartiles at 0.00 and 0.04, respectively (Figure 2d). This example shows that monthly flow fluctuations in hydropeaked rivers exceed the natural flow variability, on average, 20-fold and 60-fold when compared to glacier-fed and rainfall rivers, with the highest difference observed from November to February and the lowest for June to August.

### 3. Why frequency matters: extrapolating stranding rates

The hydrological analysis presented above shows that the frequency of sub-daily flow fluctuations in regulated rivers far exceeds those in rivers with a natural flow regime. Considering that each down-ramping event may put fish at risk of becoming stranded (Nagrodski et al. 2012), we hypothesize that hydropeaking frequency is a key factor affecting the population size of fish, particularly if the recurring events exceed ecological thresholds, e.g. fast down-ramping rates that cause fish to strand (Moreira et al. 2019).

To consider the potential cumulative effects of recurrent hydropeaks on fish stranding and, subsequently, mortality, we modeled the density of European grayling (*Thymallus thymallus*) larvae, brown trout (*Salmo trutta*) larvae, and grayling juveniles over 100 down-ramping events (Figure 3). We defined scenarios based on mean stranding rates at certain vertical down-ramping rates (0.2, 0.3, 0.5, and 2.9/3.0 cm/min) derived from outdoor flume studies during the day (Table S2). This example takes a reductionist approach by assuming a closed population, that all fish are located in the dewatered area and respond identically to each down-ramping event, and that stranded fish die while disregarding



**Figure 2.** Daily frequency of down-ramping events at gauging stations classified as (a) hydropeaking, (b) hydrofibrillation sensu Greimel et al. (2016), (c) glacial flow regime, or (d) rainfall flow regime, for Austria and Switzerland, respectively (see Table S1 for details). The assessment is based on flow data from the period 2015–2020. Note the difference in the y-axis scaling (see Figure S1 for a log-transformed version of this plot). The boxplots show the median, the bottom and top of the boxes the lower (Q1) and the upper quartile (Q3), the lengths of the whiskers represent the data within 1.5 of the interquartile range, and points are considered outliers.

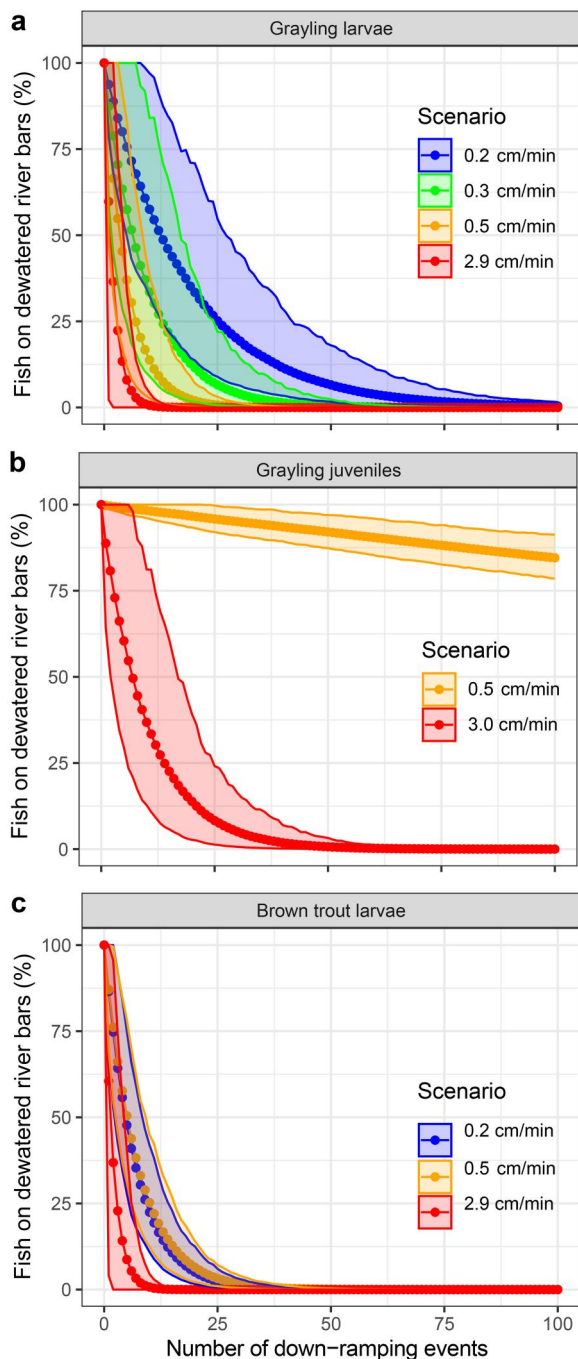
natural mortality. In detail, the magnitude of a fish stranding event depends on various biotic and abiotic controls (Figure 1), including fish species and life stages, season, light conditions, water temperature, substrate characteristics, bank structures, and river bar slope (Nagrodski et al. 2012; Larrieu et al. 2021; Führer et al. 2024).

The modeled scenarios illustrate that different down-ramping rates quickly reduce the stock of grayling (Figure 3a) and brown trout larvae (Figure 3c). Faster ramping rates have drastic negative effects if they recur often. However, even slower down-ramping events, such as 0.1 or 0.2 cm/min, can potentially reduce the grayling larvae stock by 66% or 88% within 20 events (Figure 3a). When considering the same scenarios, brown trout larvae are even more sensitive than grayling; after about 25 down-ramping events, all scenarios show an almost complete depletion of the larvae stock (Figure 3c).

Regarding juvenile fish, a down-ramping rate of 3.0 cm/min leads to an 86% decline in the grayling cohort after 20 down-ramping events, and this number approaches zero after 50 events. In contrast, a lower down-ramping rate of 0.5 cm/min reduces the grayling abundance by an average of 3% over 20 events. Even after 100 events, mean fish density remains at 85% (Figure 3b). These model results indicate that the impact of stranding on fish stocks depends not only on the down-ramping rate or the dewatered area but also on the down-ramping frequency.

#### 4. First insights regarding hydropeaking frequency and fish

The section above showcases that hydropeaking frequency is likely a key factor affecting fish in regulated rivers. Following, we provide first insights from field and experimental studies as a basis for



**Figure 3.** The modeled decline of European grayling (*Thymallus thymallus*) (a) larvae and (b) juveniles, and (c) brown trout (*Salmo trutta*) larvae based on mean stranding rates from outdoor flume studies at semi-natural river bars during the day (Auer et al. 2014, 2017), assuming a closed population, that all fish are located in the dewatered area and respond identically to each down-ramping event, and that stranded fish die while disregarding natural mortality. The scenarios are defined by vertical down-ramping rate (Table S1). The curves represent the mean reduction in fish abundance per down-ramping event; the shaded area shows the 95% confidence interval based on 1000 simulations to adequately capture the variability and uncertainty inherent in the population dynamics. Each of the 1000 simulations represents a potential realization of how the population density might evolve over the 100 events, subject to the specific mean reduction rates and variability (standard deviation) defined for each scenario.

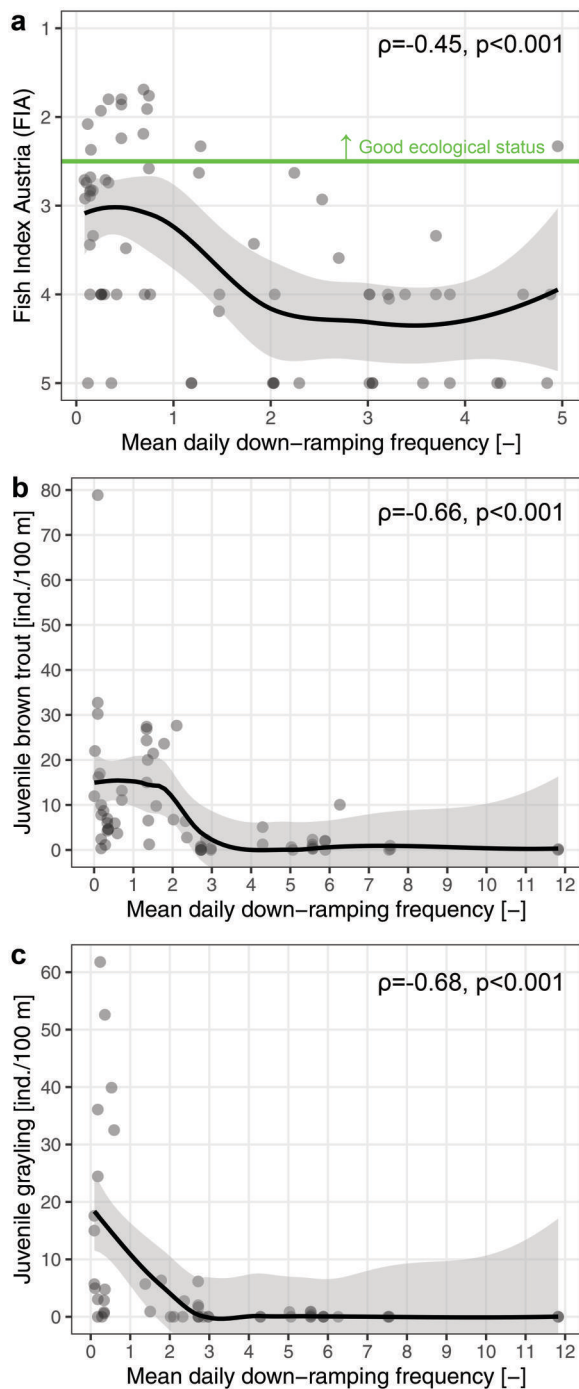
further discussions on the topic of hydropeaking frequency and fish stranding.

#### 4.1. First insights from the field

As illustrated in the previous chapter, recurring hydropeaking events are expected to amplify the impacts of fish stranding caused by single down-ramping events at the population and community level (Bauersfeld 1978), particularly through the reduction of juvenile recruitment (Cowx and Gould 1989; Almodóvar and Nicola 1999; Liebig et al. 1999; Saltveit et al. 2020).

To understand the effect of hydropeaking frequency on fish communities, we analyzed fish sampling sites from Austrian mountain rivers (Hayes et al. 2021) by comparing mean multi-annual hydropeaking frequency (Greimel et al. 2016) with an index of biological integrity, the “Fish Index Austria” (Haunschmid et al. 2019). This fish ecological index, officially adopted in Austria according to the EU Water Framework Directive, assesses impacts on fish population structure and community due to anthropogenic pressures, with a scale ranging from 1 (best) to 5 (severely degraded). The data presented in Figure 4a show a significant decrease in fish ecological integrity with an increase in daily down-ramping frequency ( $\rho = -0.45$ ,  $p < .001$ ). Sites with  $<1$  event per day have a mean status of  $2.98 \pm 0.93$  SD. In contrast, sites with  $>1$  daily event exhibit a mean status of  $4.16 \pm 0.86$  SD, which is, on average, one class worse than for the former group. In this dataset, sites with  $>1$  down-ramping event per day do not attain the good ecological status, as hydropeaking appears to be the main limiting factor. Some sites with  $<1$  down-ramping event per day reach the good ecological status (Figure 4a), which likely depends on the interaction with other stressors (Schmutz et al. 2015; Hayes et al. 2021).

Field studies conducted in hydropeaked rivers in France (Liebig et al. 1999; Hurel 2010) and Austria (Merl et al. in prep.) have demonstrated that flow fluctuations during and after the emergence period influence juvenile fish abundance in the summer due to stranding effects, among other reasons. In terms of hydropeaking frequency, the Austrian field study linked the abundance of juvenile brown trout and grayling to the number of daily down-ramping events six months prior to the sampling date, capturing the life cycle stages of fish emergence and post-emergence rearing (Merl et al. in prep.). First assessments show that juvenile fish abundances significantly decrease as frequency increases (brown trout:  $\rho = -0.66$ ,  $p < .001$ ; grayling:  $\rho = -0.68$ ,



**Figure 4.** Relationship between mean daily down-ramping frequency and (a) the “Fish Index Austria” (FIA), a fish-based measure of ecological integrity according to the requirements of the EU Water Framework Directive (1 being best, 5 worst), in Austrian hyporhithral Rivers (flow data averaged from 5 years before sampling; Hayes et al. 2021), as well as the abundance of juvenile (b) brown trout (*Salmo trutta*) and (c) European grayling (*Thymallus thymallus*) from field surveys in Austrian hydropeaked and unregulated rivers (flow data averaged from six months before sampling; data source: Merl et al. in prep.). The smoothing line (LOESS curve) highlights the trend in data, with Spearman’s correlation coefficient and  $p$ -value indicating the strength and significance of the relationship. A horizontal reference line (green) is drawn in panel (a) at FIA = 2.5, representing the threshold value for the good ecological status according to the EU Water Framework Directive.

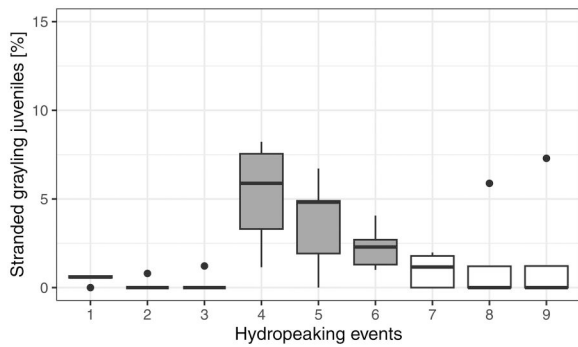
$p < .001$ ) (Figure 4b,c). Higher abundances almost exclusively occur at sites with low down-ramping frequency. Sampling sites in river reaches with a frequency of  $< 1$  down-ramping event per day exhibit mean fish densities of 14 brown trout and 18 grayling per 100 m river length. This is, on average, 2.3 and 18 times higher than at sites with  $> 1$  daily down-ramping events (brown trout: mean = 6 ind./100 m; grayling: mean = 1 ind./100 m). It should be noted, however, that the event count of these sampling sites also include events of relatively low intensity, and other factors which could impact fish.

The above examples focus solely on the frequency of down-ramping events (Figure 4), disregarding the intensity of flow fluctuations, such as ramping rate or flow amplitude. When connecting hydropeaking frequency with ramping rate, it has been noted that ramping rates  $> 0.25$  cm/min can degrade fish communities when occurring more than 20 times a year (Schmutz et al. 2015). These findings underscore the impact of hydropeaking frequency on fish ecological integrity, warranting a closer exploration of the cumulative effects related to recurring fish stranding events.

#### 4.2. First insights from flume experiments

Experimental approaches are paramount to understanding the effects of recurrent hydropeaks on ecological processes. To this aim, Auer et al. (2014) tested how nine recurring hydropeaking events over 24 h affect the stranding of juvenile grayling. Each hydropeak consisted of three flow phases (up-ramping, peak flow, down-ramping), followed by base-flows between single events. Almost no stranding happened during the first three daytime hydropeaks (Figure 5), most likely as fish, having a length of 60–75 mm, had outgrown the most critical early life cycle stage (Hayes et al. 2019). During the night, however, stranding increased. The first nighttime event exhibited highest stranding rates. Stranding slightly decreased from the first to the second night peak and from the second to the third one. The last three daytime events exhibited a lower stranding rate than the ones at night but were consistently higher than during the first three daytime hydropeaks (Figure 5).

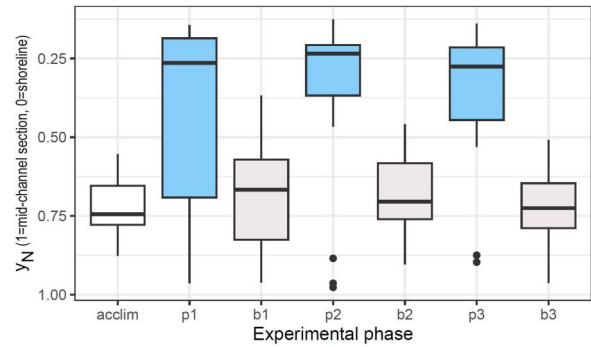
Extending this research, Auer et al. (in press) tested the stranding susceptibility of juvenile nase (*Chondrostoma nasus*) to three recurrent single hydropeaking events, conducted separately for day and night to assess time of day effects. The results show a decrease in stranding during the three hydropeaks in both day and night experiments. Comparing daytimes, mean stranding was four



**Figure 5.** Boxplot of juvenile grayling stranding during nine recurrent hydropeaking events consisting of up-ramping, peak flow, and down-ramping ( $n = 5$ ). Daytime events 1-3 and 7-9 are colored white, and nighttime events 4-6 are grey.  $Q_{base} = 25$  L/s,  $q_{peak} = 400$  L/s, up-ramping rate = 3.7 cm/min, down-ramping rate = 3.0 cm/min. The boxplots show the median, the bottom and top of the boxes the lower (Q1) and the upper quartile (Q3), the lengths of the whiskers represent the data within 1.5 of the interquartile range, and points are considered outliers. Data source: Auer et al. (2014).

times higher during the first night peak than the first day peak. In the following events, diurnal differences in stranding diminished, with stranding rates of about 5% during the third day and night peak, respectively (Auer et al. [in press](#)).

Although our understanding of the direct impacts of hydropeaking on aquatic biota has increased (Hayes et al. 2022; Smokorowski 2022), we still lack fundamental knowledge of how individual behavior, such as movement, habitat perception, and habitat memory, responds to changes in flow (Bätz et al. 2024). To shed light on these behavioral responses, Naudascher et al. (2024) exposed hatchery-sourced brown trout parr to three recurrent hydropeaks. By merging a semi-transparent gravel bed with state-of-the-art fish tracking (Walter and Couzin 2021) in a hydraulic flume, individual fish trajectories could be derived during transient flow conditions. Trout parr repeatedly relocated laterally during hydropeaking to seek areas of low water depth and low flow velocities during the up-ramping phase (Figure 6). On average, the lateral relocation response was enhanced at the second and third hydropeaking events, possibly indicating a faster response to seek shelter areas behind cobblestones. This response suggests that over short time scales of minutes, trout can reduce or delay drift during recurring flow fluctuations and memorize where to find low flow velocities (Naudascher et al. 2024). During down-ramping, the lateral relocation of fish into deeper flume areas was delayed compared to up-ramping. Fish parr followed the receding water line during down-ramping. No stranding was observed during the experiments, likely due to the flume's boundary conditions (i.e. a steep lateral bed slope of 14% and a narrow dewatered width) (Naudascher et al. 2024).



**Figure 6.** The normalized mean lateral phase position  $y_N$  of individually tested ( $n = 20$ ) hatchery-reared brown trout (*Salmo trutta*) parr during multi-peaking experiments. Each run consisted of 20 min of acclimation (acclim; white box), followed by three hydropeaks (each consisting of 6 min of peak- (blue boxes) and baseflow (grey boxes): p1, b1, p2, b2, p3, b3). Ramping rate: 2.0 cm/min. The boxplots show the median, the bottom and top of the boxes the lower (Q1) and the upper quartile (Q3), the lengths of the whiskers represent the data within 1.5 of the interquartile range, and points are considered outliers. Data source: Naudascher et al. (2024).

Nevertheless, the findings shed light on behavioral responses preceding potential fish stranding. For a given ramping rate, the delayed response of fish during down-ramping could be a critical factor contributing to an increased risk of stranding, especially on river bars with low lateral slopes and large dewatering areas (Bätz et al. 2024; Vanzo et al. 2016; Hayes et al. 2024). In essence, when the rate of habitat dewatering exceeds the fish's ability to relocate in time, the likelihood of stranding may significantly increase.

## 5. Fish stranding over space and time

Recurring fish stranding resulting from frequent hydropeaking can affect fish over different spatio-temporal scales (Figure 1). Adverse effects can propagate from an individual fish to the level of the population, the community, and the ecosystem, or vice versa. The following chapter synthesizes the current state of knowledge on the primary impacts and control mechanisms across the four levels, with a focus on salmonids.

### 5.1. Individual fish

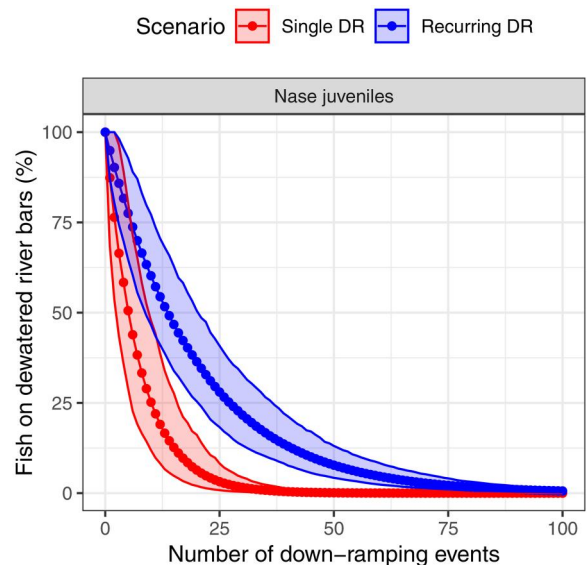
The ability of fish to withstand recurrent hydropeaking events is closely linked to their specific life cycle stages (Hayes et al. 2019). Fish appear to be consistently tolerant to both single and daily dewatering events during the intra-gravel stages, such as cleavage eggs and embryos (Becker et al. 1982, 1983). In these life stages, recurrent hydropeaking might not endanger their survival too much if they remain wet, above freezing temperatures, and attached to the substrate (Casas-Mulet et al., 2015).

In contrast, the tolerance to dewatering changes in eleutheroembryos and pre-emergent alevins as they become more sensitive to single and recurring dewatering (Becker et al. 1982, 1983). When salmonid fish larvae leave the gravel, then they are particularly vulnerable to down-ramping as their risk of stranding significantly increases (Young et al. 2011; Nagrodski et al. 2012; Hayes et al. 2019; Moreira et al. 2019). The stranding simulations in Figure 3 suggest that even a small number of down-ramping events already lead to significant fish stock declines, particularly for the larvae life stages. In-situ experiments suggest that the stranding risk for wild fish (Berger et al. 2022) is slightly lower than for hatchery-reared ones (Auer et al. 2014, 2017). However, even for wild fish, relatively low down-ramping rates can result in a considerable proportion of fish to become stranded (Berger et al. 2022; Tonolla 2023). These effects are species-specific (Moreira et al. 2019; Reis-Filho and Leduc 2024) and may be even more severe in the presence of coarse substrate sizes (Hauer et al. 2014), low-angled (Bradford et al. 1995; Führer et al. 2022) and structured river bars (Auer et al. 2017; Larrieu and Pasternack 2021; Hayes et al. 2023a), or during cold thermopeaking (Auer et al. 2023).

Furthermore, hydropeaking alters the quantity and quality of fish habitats, leading also to increased energy consumption (Puffer et al. 2015) and downstream displacement (Auer et al. 2017). An increase in flow fluctuation events can markedly increase habitat patch dynamics and reduce their persistency (Bätz et al. 2024). This raises the question of how individual fish cope with such an increase in patch dynamics and frequent dewatering of their habitats. There are indications that fish can memorize habitats and environmental cues; therefore, they could avoid being stranded in recurring hydropeaking events. The intertidal goby *Bathygobius soporator*, for example, is able to map the habitat topography during high flows and use this knowledge to jump from tide pool to tide pool to escape predators during low flows (Aronson 1971, 1951). In the hydropeaking context, data from Halleraker et al. (2003) indicates that fish learn to avoid stranding as juvenile trout exhibit higher stranding rates during the first dewatering event than subsequent ones. A telemetry study at the Rhône River, France, suggests that adult fish can memorize past environmental changes for up to two weeks, avoiding previously dewatered areas (Capra et al. 2017). For juvenile fish, this duration of memory retention to avoid stranding may be shorter than 24 h, as indicated by a selection experiment in a nature-like flume (Auer et al. 2014).

To explore the potential learning mechanisms to mitigate the impact of event frequency on fish stranding, we analyzed the effect of recurrent hydropeaks on the density of juvenile nase by comparing mean stranding rates of a single down-ramping event to those of recurrent events (i.e. the third event in a row) (Chapter 4.2; Auer et al. in press). The findings reveal differences when comparing the stranding rates of both scenarios for the first events. Nonetheless, after around 50 down-ramping incidences, there is a notable reduction in the abundance across both scenarios (Figure 7). This suggests that despite potential adaptive responses (Flodmark et al. 2002; Odling-Smee and Braithwaite 2003; Patton and Braithwaite 2015), such behaviors are unlikely to counterbalance the extensive environmental consequences of recurring hydropeaking.

Furthermore, stranding rates may be influenced by fatigue or energy depletion resulting from repeated habitat shifts (Bätz et al. 2024). Even though some studies indicate that behavior, energy, and stress in 1+ fish may not be affected by recurrent hydropeaking (Flodmark et al. 2006, 2002), this may not be the case for all juvenile fish. We assume that constant stress could override any learning adaptations if the frequency of daily hydropeaking events (e.g. a mean of three events per day, as illustrated in Figure 2a) exceeds a certain threshold (e.g.



**Figure 7.** The modeled decline of juvenile nase (*Chondostroma nasus*) based on mean stranding rates of single and recurring (i.e. the third event in a row) down-ramping (DR) events in an outdoor flume at semi-natural rivers bars during the day (Auer et al. in press), assuming a closed population, that all fish are located in the dewatered area and respond identically to each down-ramping event, and that stranded fish die, while disregarding natural mortality. The curves represent the mean reduction in fish abundance per down-ramping event, and the shaded area shows the 95% confidence interval based on 1000 simulations (see the caption of Figure 3 for details).

Figure 4) as the physical toll and stress induced by frequent shifts in habitat conditions may limit the effectiveness of behavioral adaptations in mitigating stranding occurrences. In a field enclosure study, Saltveit et al. (2001) exposed the same group of 1+ fish to three recurrent hydropeaks within three days. No stranded fish were found after the first dewatering event as they returned to the deepest section. At the second and third events, however, around 27% and 24% of all fish became stranded (Saltveit et al. 2001), pointing to fatigue or energy loss as a stranding mechanism (Auer et al. 2014) in the absence of flow velocity shelter areas (e.g. Figure 6).

## 5.2. Fish population

The field data exemplified in Figure 4 underline the effects of down-ramping frequency on fish density at the river reach scale. Fish stranding through hydropeaking down-ramping is known to lower recruitment rates and, subsequently, population size (Sauterleute et al. 2016; Hedger et al. 2018; Hayes et al. 2021). Although stranding does not always end fatal for the individual (Glowa et al. 2023), the potential cumulative effects of recurring hydropeaks are striking (Figures 3 and 7). In this regard, the literature largely considers early juvenile life cycle stages as a population bottleneck in hydropeaked rivers, although spawning and egg development may also be affected (Hayes et al. 2019; Pander et al. 2023).

Given the substantial natural mortality observed in early salmonid life stages (Elliott 1994), it is critical to consider the impact of hydropeaking frequency on fish mortality within this natural context. Density-independent abiotic processes, particularly high flow events during the interstitial and larval phases, play a dominant role in determining juvenile fish densities in alpine rivers (Unfer et al. 2011). Juveniles that survive until after emergence seek out and colonize suitable nursery habitats, and their survival strategies vary. For example, brown trout defend territories (Elliott 1994), while grayling and cyprinids form small groups or larger schools (Sempeksi and Gaudin 1995; Baras and Nindaba 1999). The availability of adequate food and hydraulically favorable habitats shortly after hatching also directly affects survival rates. Hydropeaking impacts likely interact with density-dependent regulation processes, for example, by leading to juvenile fish stranding in prime rearing habitats (Nagrodski et al. 2012), highlighting its role as an anthropogenic factor that amplifies naturally occurring density-dependent mortality. Still, the extent of this amplification remains largely unexplored. However, significantly lower fish populations in rivers affected

by recurring down-ramping events compared to unaffected ones (e.g. Figure 4) suggest that hydropeaking elevates mortality beyond natural levels. A population dynamics study of Atlantic salmon (*Salmo salar*) in a river subjected to five hypothetical hydropeaks per week showed long-term impacts of stranding (Hedger et al. 2018). This particular study noted a decline in population abundance and density due to stranding mortality, whereby juvenile stranding mortality significantly influenced the survival rates in later life stages and subsequently reducing density-dependent mortality (Hedger et al. 2018).

## 5.3. Fish community

Hydropeaking can alter the fish community structure (Schmutz et al. 2015; Judes et al. 2021) by affecting some species and life stages more than others, leading to a reduction in fish diversity and richness (Figure 1). Even though community-level effects of stranding events are generally difficult to assess (Welcomme 1985), it is known that some fish species, such as those preferring habitats along the river bar, are more vulnerable to down-ramping than species which remain in midstream sections (Glowa et al. 2023; Judes et al. 2023; Reis-Filho and Leduc 2024). Similarly, juveniles and small-bodied species are more susceptible to becoming stranded than larger fish (Eppehimer et al. 2021; Glowa et al. 2023), and stranding risk generally reduces as fish grow in size (Führer et al. 2022; Auer et al. 2023).

Recurrent stranding of certain fish species or life cycle stages can, therefore, likely alter intra- or interspecific competition, for example, by lowering density-dependent mortality (Welcomme 1985). If stranding only affects a part of the community, this may enable the coexistence of subordinate species (Power et al. 1996). For instance, if stranding largely affects piscivorous species, prey fish enjoy a decreased predation pressure. Recurrent hydropeaking can also lead to higher resource competition as flow fluctuations cause increased habitat dynamics (Bätz et al. 2023). The way in which hydropeaking affects fish community structure will ultimately depend on the characteristics of the species present, their life-cycle histories, including the use of connected flow refuge habitats (see Chapter 5.5).

## 5.4. Ecosystem effects

Recurring hydropeaks likely affect the ecosystem through alterations of food webs and nutrient fluxes (Figure 1). However, food web effects of stranding of fish (and other aquatic organisms) due to recurring hydropeaking have hardly been investigated

(Smokorowski 2022), potentially due to the general difficulty in detecting and quantifying stranded organisms in the field and tracking their fate (Nagrodski et al. 2012; Hayes et al. 2024). Nevertheless, two mechanistic pathways can be assumed from studies on fish stranding resulting from different types of stressors in other environmental settings (e.g. drying of ephemeral pools in seasonally flooded wetland habitats). First, the stranding of fish can lead to important amounts of aquatic energy being transferred to higher trophic levels at land (Yurek et al. 2013), thereby having potentially cascading effects on community composition and food web dynamics (Nagrodski et al. 2012). Fish that suffocate from beaching or that are trapped in isolated pools can offer prey for (wading) birds, small mammals and scavenging organisms. Predation risk is particularly high if stranded fish are not equally distributed across the shoreline but locally concentrated, allowing predators to capture them with little energy expenditure (Yurek et al. 2013; Glowa et al. 2023). Secondly, fish themselves, particularly benthic feeders, may face nutritional implications when their prey – macroinvertebrates – undergo reductions in densities due to massive stranding or drift (Lagarrigue et al. 2002). In this regard, recurring hydropeaking can cause a depletion of fatty acids in periphyton (Cashman et al. 2017), likely reducing a river's nutritional quality and biomass on other trophic levels.

### 5.5. The role of habitat at various scales

Habitat plays a key role in the potential ecological effects of recurring hydropeaks, including aspects such as habitat dynamics and persistency (Bätz et al. 2023) as well as instream connectivity at the sub-catchment scale (Bond and Jones 2015; Milner et al. 2019).

The hydrological assessment presented in Chapter 2 provides a first overview of hydropeaking frequency in rivers with anthropogenic and natural flow regimes (Figure 2). Bätz et al. (2024) expand on this hydrological view by introducing a flow shift approach. This approach relates every flow condition to a corresponding unique composition of habitats in a river reach (i.e. habitat mosaic), therefore considering the specific river morphology. The recurrent, rapid changes in flow caused by hydropeaking make the habitat mosaic highly dynamic, in contrast to the more persistent habitat conditions under natural flow regimes. This dynamic nature of habitats in hydropeaked rivers poses challenges to the survival of organisms, particularly affecting those with limited mobility, such as fish in their early life stages. These individuals may be forced to relocate in search of their preferred conditions or to escape areas prone to drying (Bätz et al.

2024; Judes et al. 2023). Adult brown trout, for example, doubled their home range under a hydropeaking regime when compared to near-natural flow conditions (Rocaspana et al. 2019). Consequently, as movement distances increase, the probability of finding a suitable habitat may decrease, thereby raising their susceptibility to becoming stranded (Jelovica et al. 2023).

Recognizing that distinct flow conditions correspond to a unique habitat mosaic in a river reach, it follows that not every hydrological hydropeaking event, as counted in Figure 2, results in the same ecological impact (Meile et al. 2023). This is due to the complex interplay of factors such as river morphology, flow amplitude, and baseflow magnitude, which together affect the extent of river bar dewatering and, consequently, the stranding risk (Tuhtan et al. 2012; Harby and Noack 2013; Führer et al. 2022; Bätz et al. 2024; Hayes et al. 2024, 2023a). Therefore, hydropeaks that cause only a small dewatering area may pose a lower risk for stranding than those with a large dewatering area, particularly if the down-ramping rate is fast (Meile et al. 2023; Hayes et al. 2024). Moreover, hydropeaking events may also lead to changes in water temperature (i.e. thermopeaking) or supersaturation of dissolved gases (i.e. saturopeaking) affecting aquatic organisms (Pulg et al. 2016, 2024; Auer et al. 2023; Mameri et al. 2023; Meile et al. 2023).

Accounting for lateral and longitudinal gradients in regulated rivers is key when interpreting river integrity and productivity (Bond and Jones 2015; Greimel et al. 2023). A study on European grayling found that a minimum instream corridor length of several tens of kilometers is needed to support fish stocks in Austrian hydropeaked rivers, assuming that all key habitats to complete their life cycle are available (Hayes et al. 2021). This also necessitates the presence of refugial habitats from hydropeaking conditions to prevent stranding (Hauer et al. 2014). Various small-scale natural and engineered structural-morphological measures, such as dead wood accumulations, groynes, gravel bars, block stones, bays, or side channels, have the potential to reduce adverse hydropeaking effects on aquatic biota and have been discussed as complementary measures for hydropeaking mitigation (Friese et al. 2022). However, it needs to be clarified to what extent such local measures can support a resilient ecosystem while not contributing to fish stranding.

Recent studies highlighted the role of tributaries with a natural hydrological and sediment regime in hydropeaked river systems (Hauer et al. 2016, 2017; Vericat et al. 2020; Friese et al. 2022). Unregulated tributaries can serve as flow refugial habitats for aquatic organisms, possibly also creating sheltered

habitat patches in the confluence section. These tributary habitats may also serve as stable spawning habitats and recruitment areas without stranding risk (Hauer et al. 2016). Therefore, growing juveniles that migrate downstream can provide fresh fish contribution to hydropeaked sections. A recent study confirmed this notion, showing that in a Swiss hydropeaked river, most brown trout spawning grounds are located in the unregulated tributaries (Wagner 2024). This finding underlines the hypothesis that the preservation of viable and interconnected upstream communities within unregulated tributaries is crucial for maintaining fundamental demographic processes, particularly as a source population for downstream sink hydropeaking habitats (Bruno et al. 2016; Kennedy et al. 2016; Milner et al. 2019). Understanding that unregulated tributaries are crucial for connecting different parts of river networks highlights their role in overall strategies to reduce recurring hydropeaking impacts across the entire river basin (Milner et al. 2019).

### 5.6. First considerations for management

The above sections described how the cumulative effects of recurring down-ramping events on stranding may affect fish at various levels (Figure 1). However, restrictions on the number of hydropeaks within a specified period could substantially affect hydropower operations, especially their flexibility in rapidly responding to grid demand. This necessitates a detailed assessment, where not only operational and system-relevant factors at various scales are considered but also ecological thresholds essential for maintaining a resilient river ecosystem (Anindito et al. 2019; Haas et al. 2019; Dalcin et al. 2024), and, in the end, a political choice. Establishing these thresholds is crucial to ensure that the ecological integrity of river systems is preserved while optimizing energy production.

Recent fish-based research has included the number of annual hydropeaking events in a multi-indicator matrix for environmental assessments (e.g. Halleraker et al. 2022; Bakken et al. 2023; Godinho et al. 2023). Due to the difficulty in distinguishing the impacts of hydropeaking frequency from those of other stressors and environmental variability, this matrix could serve as a useful starting point for hydropeaking assessments. However, more studies are needed to establish thresholds on hydropeaking frequency, considering down-ramping rate and flow amplitude, as well as morphological parameters, with regard to fish life stage requirements.

Various countries are currently trying to lower hydropeaking impacts on river ecosystems (Moreira et al. 2019), with some, such as Austria and

Switzerland, having already developed hydropeaking mitigation guidelines (Tonolla et al. 2017; Tonolla 2023; Ofenböck 2024). Nonetheless, to the best of our knowledge, there are no legal frameworks to date that include thresholds for hydropeaking frequency. A common practice in several countries focuses on ecologically relevant intensity parameters, such as down-ramping rate and flow amplitude (Moreira et al. 2019), assuming that if critical flow rates are not exceeded, the hydropeaking frequency is irrelevant. The modeling results from Figure 3 suggest that ramping rates of 0.2 cm/min, which are considered safe for grayling larvae stranding, may still have cumulative impacts of stranding if combined with an average of three down-ramping events per day (Figure 2a).

The recently published Swiss report on hydropeaking mitigation (Tonolla 2023) summarizes experiences and findings from the application of the 2017 guideline (Tonolla et al. 2017) and from new applied research projects. The report highlights the importance of considering the hydropeaking frequency and provides useful recommendations for its consideration in hydropeaking mitigation projects. In this regard, Figure 3 shows that the cumulative effects of recurrent stranding events are likely similar during rare (i.e. low frequency) events with a high ramping rate or frequent events with a low ramping rate.

Moreover, Figure 3 suggests that seasonal restrictions regarding ramping rate and hydropeaking frequency are key to safeguarding the most sensitive post-emergence life cycle stages from becoming stranded (Hayes et al. 2019). Typical thresholds for down-ramping rates aiming at protecting juveniles are roughly an order of magnitude higher than the ones aiming at protecting larvae, underlining the idea of establishing seasonal restrictions to protect newly emerged fry (Greimel et al. 2017b; Hayes et al. 2019; Wagner 2024). By targeting frequency and intensity reductions at key life stages for the individual fish, positive outcomes for the other levels can be expected in the long term, too (Figure 1).

Retention basins are effective in mitigating the impacts of hydropeaking impacts throughout the year, including ecologically sensitive periods, while still allowing for flexible hydropower production (Greimel et al. 2017a; Anindito et al. 2019). The effectiveness of these basins in dampening hydropeaking impacts increases with their volume. This effectiveness is further enhanced when they are equipped with a controllable outlet, which allows for the optimization of water discharge into rivers (Quaranta et al. 2023). Moreover, precise identification and analysis of specific areas prone to dewatering at various flows can enable targeted interventions, ensuring that

**Table 1.** Questions to be addressed by future research to improve our understanding of hydropeaking frequency and ecological effects.

1.	How is sub-daily flow variability related to intensity parameters (e.g. down-ramping rate, flow amplitude) at a monthly scale in natural and regulated rivers?
2.	How do the ecological effects of very frequent, low-intensity flow fluctuations [...] differ from those of regular but less frequent high-intensity hydropeaking? (Hayes et al. 2023b)
3.	To what extent do single high-flow events differ from recurring hydropeaks in determining habitat dynamics and biotic community composition? (Hayes et al. 2023b)
4.	To what extent do the effects of irregular (seasonal) hydropeaking differ from regularly (year-round) occurring hydropeaking in structuring habitat dynamics and biotic communities? (Hayes et al. 2023b)
5.	To what extent do tolerance, acclimation, or habituation allow aquatic species to live in regularly occurring hydropeaking conditions? (Hayes et al. 2023b)
6.	What is the contribution of regular fish stranding to aquatic and terrestrial food webs (i.e., shoreline predators and scavengers)?
7.	Can stranding modify selection pressures in particular systems?
8.	What is the added value of a mitigation measure that can also reduce the frequency of hydropeaking events (e.g. a diversion hydropower plant or a retention basin with a large reservoir)? (Meile et al. 2023)
9.	Which role do instream flow refugia and sheltered habitats play in mitigating the effects of increased habitat dynamics in hydropeaked rivers to sustain viable populations of aquatic organisms? (Bätz et al. 2024)
10.	What are ecological thresholds regarding hydropeaking frequency (in particular seasons) for selected key species and their life cycle stages?
11.	Which role do tributaries play in sustaining aquatic communities in hydropeaked rivers, and how can tributary connectivity and protection be integrated into hydropeaking mitigation strategies?

mitigation efforts are effective in preserving sensitive habitats. Also, the presence of well-connected habitats is particularly pivotal in sustaining aquatic populations in catchments with river reaches affected by hydropeaking when frequency and residual stranding mortalities cannot be sufficiently reduced.

Overall, fish stranding is determined by various aspects, including fish life cycle stage, learning and behavioral adaptations. In this context, we wish to stress the importance of adaptive management in light of hydropeaking mitigation needs despite limited knowledge regarding the fish ecological effects of hydropeaking frequency. Implementing adaptive management, which combines cutting-edge experimental methodologies and monitoring techniques, is essential to identify cost-effective mitigation strategies for minimizing the ecological impacts of hydropeaking frequency over the long term. This approach necessitates collaborative efforts among the energy sector, authorities, river managers, and scientists. Hydropower licensing can serve as a critical framework for adaptive management. Regular updates of licenses are essential to incorporate the latest technological advancements and ecological understanding, while also aligning with evolving energy production needs. Periodic reviews ensure a dynamic balance between ecological preservation and efficient energy production, accommodating changes in both environmental conditions and energy demands.

### 5.7. Research opportunities and needs

Undoubtedly, more research is needed to understand better how recurring fish stranding due to hydropeaking affects individual fish, populations, communities and how that propagates even to overall river ecosystem functioning (Hayes et al. 2023b). Even though this research need was highlighted over a decade ago (Zimmerman et al. 2010), few

studies have been performed on this topic (Halleraker et al. 2003; Burman et al. 2021). Based on the literature and the preceding sections, we, therefore, identified a list of open questions related to hydropeaking frequency (Table 1). Although this list is non-exhaustive, we believe that these questions can expedite research efforts to improve our understanding of hydropeaking frequency and ecological effects, ultimately leading to better management outcomes.

Hydrological studies are needed to assess sub-daily flow variability in relation to intensity parameters (e.g. flow amplitude and magnitude, down-ramping rate) at a monthly level. Such an assessment, characterizing natural and anthropogenic sub-daily flow regimes, may be pivotal in informing management decisions. However, it is imperative to recognize that the impact of hydropeaking on organisms is mediated through river hydraulics and associated habitats (Bätz et al. 2024). The alteration of the spatio-temporal distribution of habitats dictates the organisms' responses, including fish movement and potential stranding. A thorough understanding of such behavioral biota-habitat interactions is a prerequisite for developing critical indicators that include hydropeaking frequency and establishing effective ecological thresholds for hydropeaking mitigation (Halleraker et al. 2022; Bakken et al. 2023; Godinho et al. 2023). We advocate for the development of decision support tools that bridge knowledge gaps and facilitate the implementation of an adaptive management strategy, integrating hydrological, hydraulic, and ecological dimensions in its approach.

A meta-ecosystem perspective may provide a more holistic view towards river restoration. More research is needed to understand the role of tributaries in sustaining fish populations and communities in hydropeaked rivers. Based on such studies, seasonal mitigation frameworks (Hayes et al. 2019)

could be improved, for example, by incorporating the timing of fish emergence in the tributaries and downstream drift into the hydropeaked river section (Wagner 2024).

## 6. Conclusions

This article aims to advance the scientific discourse on the frequency of hydropeaking events and their impact on fish stranding by leveraging the latest data from recent studies. Our analysis and review highlight the vulnerability of fish populations — particularly larvae and juvenile life stages — to significant mortality caused by recurring hydropeaking, as commonly observed in alpine rivers. This places early life stages at heightened risk, with effects that may extend beyond individual fish to impact entire populations, communities, and the broader ecosystem.

Supporting evidence from various field studies corroborates these findings, indicating a direct correlation between increased hydropeaking frequency and larger ecological impacts on fish populations. Experimental research indicates that fish may display some behavioral adjustments in response to recurring flow fluctuations, which ostensibly diminish the hazards posed by hydropeaking events. Nonetheless, these adaptive behaviors are likely insufficient to counterbalance the extensive environmental impacts of hydropeaking. Furthermore, when considering larvae or juvenile stages, any potential learning or adaptive behavior is probably limited to short times—rendering it effectively inadequate for coping with the rapid and recurring flow changes associated with hydropeaking.

Therefore, frequency emerges as a critical factor in alpine rivers subjected to hydropeaking, which, on average, experience three hydropeaking events per day. Despite the implementation of moderate ramping rates, high fish mortality is expected due to the cumulative effect of stranding. Therefore, mitigation approaches should prioritize measures that can reduce the impacts associated with the cumulative effects caused by recurring hydropeaks while guaranteeing critical flow rates of single hydropeaks (e.g. ramping rate, flow amplitude) based on ecological thresholds. Moreover, targeted mitigation efforts informed by an understanding of habitat dynamics are critical to safeguard sensitive habitats. Additionally, the maintenance of healthy, well-connected lateral flows, such as between tributaries and the main river system, is vital for the support of aquatic populations. The significance of lateral connectivity underscores its potential to bolster aquatic ecosystems under the strain of hydropeaking impacts.

Finally, this study establishes a robust foundation for subsequent research on hydropeaking frequency, its role in fish stranding, and its effects on fish populations by highlighting key topics for future studies. Addressing these open questions on the effects of hydropeaking frequency on fish will contribute to more effective management strategies for regulated rivers.

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