RESPONSE OF FISH COMMUNITIES TO HYDROLOGICAL AND MORPHOLOGICAL ALTERATIONS IN HYDROPEAKING RIVERS OF AUSTRIA

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ABSTRACT

Climate change asks for the reduction in the consumption of fossil-based fuels and an increased share of non-regulated renewable energy sources, such as solar and wind power. In order to back up a larger share of these intermittent sources, ‘battery services’ are needed, currently provided only in large scale by hydropower, leading to more rapid and frequent changes in flows (hydropoeaking) in the downstream rivers. Increased knowledge about the ecosystem response to such operations and design of cost-effective measures is needed.

We analysed the response of fish communities to hydropoeaking (frequency, magnitude, ramping rate and timing) and the interaction with the habitat conditions in Austrian rivers. An index of biotic integrity (Fish Index Austria) was used to compare river sections with varying degrees of flow fluctuations under near-natural and channelized habitat conditions. The results showed that habitat conditions, peak frequency (number of peaks per year), ramping rate (water level variation) and interaction between habitat and ramping rate explained most of the variation of the Fish Index Austria. In addition, peaking during the night seems to harm fish more than peaking during the day. Fish communities in hyporhithral and epipotamal types of rivers are more affected by hydropoeaking than those in metarhithral type of rivers. The results support the findings of other studies that fish stranding caused by ramping rates >15 cm h⁻¹ are likely to be the main cause of fish community degradation when occurring more often than 20 times a year. While the ecological status degrades with increasing ramping rate in nature-like rivers, fish communities are heavily degraded in channelized rivers regardless of the ramping rate. The mitigation of hydropoeaking, therefore, requires an integrative approach considering the combined effects of hydrological and morphological alterations on fish. © 2014 The Authors. River Research and Applications published by John Wiley & Sons, Ltd.

KEY WORDS: flow fluctuation; habitat; ramping rate; flow ratio; fish zone; European grayling (Thymallus thymallus); brown trout (Salmo trutta); Fish Index Austria

INTRODUCTION

Climate change asks for the reduction in the consumption of fossil-based fuels and an increased share of renewable energy sources. Several countries have launched ambitious programmes to stimulate further development renewables, and European Union (EU) has agreed upon the Renewable Energy Sources Directive (EU RES Directive, 2009). Renewable sources such as solar and wind power will, however, provide non-regulated power, that is, only producing energy during favourable climatic conditions. An increased share of non-regulated renewables will hence lead to a larger need for intermittent power, a service that currently only hydropower can provide in large scale (IPCC, 2012). A possible outcome of such a shift in the energy production system might lead to more rapid and frequent changes in the operation of the hydropower plants causing larger fluctuations in flow in the downstream rivers (‘hydropoeaking’). In order to protect aquatic ecosystems in regulated rivers exposed to hydropoeaking, better understanding about the ecological responses to changes in hydrology is needed, as well as to design cost-effective mitigating measures that pose reasonable restrictions on the hydropower operation.

European rivers show declining trends in response to different types of pressures. While water quality is a major concern in most European ecoregions in Alpine regions, only the hydromorphological conditions continue to degrade (Schinegger et al., 2012). Among the hydromorphological pressures, hydropoeaking has been identified as one of the key threats for fish populations in Alpine rivers (Table I).

Fish in hydropoeaking rivers may be affected by stranding along the changing channel margins, downstream displacement of fishes and drift, redd (spawning habitat) dewatering, spawning interference, untimely or obstructed migration, loss of food and increased predation (Hunter, 1992; Young et al., 2011). Reds are exposed to scouring risk (at peak flow) and dewatering (at off-peak flow), which might impair egg development and recruitment success (McMichael et al., 2005).
The extent of stranding is dictated by the complex interaction of a variety of biotic and abiotic factors. With respect to the physical conditions, stranding depends on ramping rate, flow ratio (amplitude), substrate composition, channel morphology (potholes) and bank slope. In addition, critical minimum flow, frequency of flow fluctuations, timing (daytime and season) and duration of stranding influence stranding mortality rate. Juvenile fish are more vulnerable to stranding than adults (Young et al., 2011; Nagrodski et al., 2012; Harby and Noack, 2013).

Most fish-stranding studies have focused on salmon and trout, and little information is available for other species (Nagrodski et al., 2012). However, most rivers affected by hydropeaking in Austria are inhabited by European grayling (Thymallus thymallus). Interactions between hydropeaking, channel morphology and habitat conditions have been investigated in some field studies (Vehanen et al., 2000) but have received less attention than investigating stranding in experimental channels. Most Alpine rivers are channelized, resulting in degraded habitat conditions for fish. It is uncertain whether increased habitat complexity influences downstream displacement of fish and over what magnitudes of pulse that this complexity may reduce displacement. Channel morphology interacts with the effects of pulsed flows; however, it is still unknown whether there are hydromorphological thresholds, related to pulse duration or frequency, beyond which cumulative long-term effects on fish communities would be expected (Young et al., 2011). Without appropriate flow refugia, the hydropeaking-impacted flow regime becomes energetically costly for fish and affects their over-wintering survival (Scruton et al., 2008).

During the off-peak phase, sediment is deposited, which may result in bed clogging, whereas during the peak phase, the sediment is re-suspended, which causes higher erosion and water turbidity (Anselmetti et al., 2007; Wang et al., 2013). Although fish mortality as a result of stranding is well documented for some species, little is known about the sublethal and long-term consequences of stranding and how stranding risk for juvenile fish affect species abundance and persistence (Nagrodski et al., 2012), and only few studies focused on the fish community or system level (Smokorowski et al., 2011).

Most of the hydropeaking field studies investigated a single river (Young et al., 2011; Harby and Noack, 2013), making it difficult to transfer results to other systems and to identify general patterns. There have been no research programmes studying stranding in a hydropeaking context using multiple systems in a comparative framework (Nagrodski et al., 2012).

A greater knowledge of the consequences of hydropeaking would promote the development and refinement of mitigation strategies that are economically and ecologically sustainable. Without knowing the effects at the population and community levels, managers lack the impetus to design and implement mitigation strategies. Such knowledge is essential to inform decision makers about the choice of appropriate mitigation strategies that are likely to improve the ecological status of running waters as required for the implementation of the EU Water Framework Directive (WFD). In the case of granting new hydropower licences and revision of old, there is also a need to define the restrictions on hydropeaking operations more specific, and scientific knowledge on impacts and cost-efficient mitigating measures is needed in order to carry out knowledge-based management.

The objectives of this work are (i) to use multiple rivers in a comparative framework in order (ii) to analyse the effects of hydropeaking on fish using multiple hydrological

Table I. Main effects of hydropeaking on fish (based on Hunter, 1992; Anselmetti et al., 2007; Scruton et al., 2008; Young et al., 2011; Smokorowski et al., 2011; Nagrodski et al., 2012; Harby and Noack, 2013; Bruno et al., 2013)

| Hydropeaking operation | Implications | Consequences for fish |
|------------------------|--------------|-----------------------|
| Flow increase          | Flow velocity increase | Drift of small fish |
|                        | Drift of macroinvertebrates | Reduced food supply |
|                        | Scouring of redds | Reduced recruitment |
|                        | Scouring of algae | Reduced food supply |
|                        | River bed clogging | Reduced food supply |
| Down-ramping           | Dewatering of river banks | Stranding of small fish |
|                        | Dewatering of spawning sites | Reduced recruitment |
|                        | Dewatering of side channels and floodplains | Trapping and stranding of fish |
| Increased turbidity    | Reduced visibility | Decreased feeding |
|                        | Reduced algal production | Reduced food supply |
| Flow fluctuation       | Habitat maintenance or shifts | Physiological stress, reduced growth |
|                        | Spawning behaviour | Interrupted or ceased spawning |
|                        | Migration and hatching cues | Altered of ceased migration and hatching |
| Temperature variation  | Migration and hatching cues | Reduced recruitment |
|                        | Drift of macroinvertebrates | Reduced food supply |
characteristics, (iii) to analyse the effects of habitat conditions and the interactions with hydrology and (iv) to assess the resulting effects for fish at the population and community levels for different fish communities in Austria.

**METHODS**

**Study area**

In Austria, most hydropower plants with peaking operation are located in the Alpine region. Mainly, rivers classified as hyporhithral and dominated by European grayling are affected, and also, the adjacent upper and lower parts of the rivers (metarhithral and epipotamal) are exposed to peak flows (BMLFUW, 2010).

Fish samples were retrieved both from the rivers affected by hydropeaking and from the so-called reference sites without impacts resulting from hydropower operation (impoundment, residual flow). All sites meet the water quality criteria for at least the ‘good chemical status’ (BMLFUW, 2010). We, therefore, can assume that water quality is not affecting the fish communities under study (Figure 2).

**Fish data**

Fish data were provided by the Austrian Ministry of Life sampled for the national monitoring programme performed in compliance with the EU WFD. We complemented the dataset with new field samples in order to cover different fish zones (sensu Huet, 1959) and a gradient from no-to-strong or low-to-strong peaking intensity. This was achieved by placing the sampling sites at different distances from the peak releases of the hydropower plants.

Fish sampling of all sites followed the Austrian standard for fish sampling developed for the implementation of the WFD (Haunschmid et al., 2006a, 2006b): electrofishing is employed during autumn at low-flow conditions. In small rivers (width ≤ 15 m, depth ≤ 0.7 m), the entire habitat of the selected river stretch is sampled at least two times (removal method). Fish are sampled by wading upstream using one anode per 5-m river width, and upstream block nets impede fish escapement. River length sampled equals at least 10 times the average river width. In larger rivers (width 15 m, depth > 0.7 m), habitats are proportionally sub-sampled using two electrofishing boats: one for instream and one for riparian habitats. The boats are equipped with a boom of anodes mounted in front of the boat, and the effective width of operation is about 6 m. A minimum of 25 subsamples with an average length of 175 m (50–300 m) is taken at each site. This equals a sampled river length of 4.4 km or a sampled area of 26250 m². Stunned fish are caught with dip nets. In case of high densities, visible fish not caught with the dip nets are counted and added to the total catch. The total length and weight of the fish are measured, and the fish are released back to the water after sampling is completed. Fish density and biomass are calculated as number and biomass per hectare based on the sampled area. Wading and boat fishing differ in methodology; however, it is assumed that higher sampling effort for boat fishing compensates for potential sampling bias in larger rivers. Nevertheless, for the Fish Index Austria (FIA), stock estimates are only used to distinguish among the three biomass levels, that is, <25, 25–50 and >50 kg ha⁻¹. Further details on boat sampling methodology are given by Schmutz et al. (2001).

For assessing the fish ecological status, we used the ‘FIA’, the official method for the WFD in Austria (Haunschmid et al., 2006a, 2006b). The FIA—as a multi-metric index—follows the methodology of the index of biotic integrity. Unlike single biological metrics, the index of biotic integrity integrates biological responses to human stressors across multiple levels of biological organization, that is, life stages, populations and communities, and, therefore, represents a robust and more holistic method for bioassessment (Karr, 1981). The FIA employs eight metrics, that is, number of dominating species, number of accompanying species, number of rare species, number of habitat guilds (rheophil, limnophil and indifferent), number of reproductive guilds (lithophil, phytophil and psammophil), fish zone index, biomass and population structure (length frequency distribution) of dominating and accompanying species. Reference values for metrics are pre-defined for all river types and fish zones in Austria and are included in an Excel® spreadsheet for the index calculation provided by the Ministry of Life (www.baw-igf.at). Biomass is used as a ‘knock-out’ or ‘k.o.’ criterion whereby sites with biomass less than 50 or 25 kg ha⁻¹ are assigned to ‘poor’ or ‘bad’ ecological status, for example, class 4 or 5, respectively, independent of the scores of the other metrics. Other metrics are scored by comparing observed with expected reference values, and finally, the index is calculated as a weighted mean of grouped metrics. The final index ranges from class one (high status) to five (bad status) according to the WFD. To test if the response of fish communities is different in the various fish zones (‘FIZO’), we used a simplified fish zone classification of the FIA assessment approach discriminating between metarhithral, hyporhithral and epipotamal river types.

**Hydromorphological data**

Flow data were retrieved from gauging stations maintained by the provincial governments and hosted in a national database by the Ministry of Life. A total of 80 gauging stations (62 affected by hydropeaking and 18 unaffected by hydropower) with a time resolution of 15 min were analysed.
Flow peaks were split into different types of events, that is, increase (IC), peak (PK) and decrease (DC), and analysed separately. The following hydrological variables were calculated: duration of flow—‘DUR’ (min), base; peak flow ratio—‘RAT’ average and maximum speed of flow alteration—‘dQ_mean’, ‘dQ_max’ (m³ s⁻¹ min⁻¹), amplitude of flow alteration—dQ_AMP (m³ s⁻¹), and amplitude of flow alteration in relation to mean flow—‘dQ_MQ’ (%) (Figure 1). The statistical characteristics of event frequencies were based on yearly averages. We selected the flow data out of a 5-year period ranging from 2004 to 2008 in order to match with flow conditions before and during fish sampling. The flow data of gauging stations close to the sampling sites, that is, less than 1-km distance if no significant tributaries entering in between the stations, were directly assigned to fish sampling sites; others were interpolated between the nearest two stations using catchment size.

Stranding of juvenile fish depends on the hydromorphological conditions during the peak decrease, that is, how fast gravel bars are dewatered, and is commonly defined as water level alteration per time unit, also called ramping rate (Hunter, 1992; Halleraker et al., 2003). In more detail, water level variation is linked to flow alteration and also depends on channel size and form and other hydraulic factors. To estimate water level variation, respectively, ramping rate—‘RARA’ (cm h⁻¹), at our sampling sites, we used a subsample of recently investigated rivers with known Q/dh relationships (Hauer et al., 2013) and developed a simplified regression model with upstream drainage area as independent variable and water level fluctuation (cm m⁻³ s⁻¹) as dependent variable to correct for stream size for sites with unknown Q/dh relationship.

In order to consider both yearly average and extreme events, we calculated the 50 percentile and 90 percentile of each metric (e.g. ‘RARA50’ and ‘RARA90’). As hydropeaking effects, particularly stranding, might depend on light conditions, we also discriminated between night and day events on the basis of sunset and sunrise data.

In order to consider the effect of habitat conditions, we estimated the quality of habitat conditions on the basis of the pressure and impact analyses for the Austrian river basin management plan (BMLFUW, 2010). Additionally, aerial photographs provided by the provincial governments were used to complement the data. We defined two groups of habitat quality: ‘nature like’ and ‘channelized’. Nature-like sites have retained most of the river-type-specific habitat features, that is, river pattern, substrate conditions, riparian vegetation and instream habitats, whereas channelized sites are characterized by straightened longitudinal profiles, uniform channel cross sections, lack of riparian vegetation and lack of instream habitats (gravel bars, pools, woody debris, etc.).

Substrate conditions are not directly measured at investigated sites but indirectly covered by river type (and fish zone) classification reflecting a gradient from coarse to fine substrates from metarhithral to epipotamal.

**Statistical analyses**

Before developing a model by regressing FIA against hydromorphological variables including fish zones, we eliminated redundant hydromorphological variables by using Spearman rank correlation (|r| > 0.9). We then developed a generalised linear model by testing all potential combinations of the remaining variables using the package ‘glmulti’ within R®. ‘glmulti’ is a model selection tool automatically generating all possible models (under constraints set by the user) with the specified response and explanatory variables, and finding the best models in terms of an information criterion, in our case, the Akaike information criterion. Non-normally distributed variables were log transformed (log x + 1) before being integrated into the model. In order to avoid overfitting, we limited the number of potential predictors for tested models to five predictors. In the last step, we included the habitat variable (‘HAB’) as an interactive term to test for interaction with the hydrological variables. Only significant interactions were retained in the final model. To test diurnal effects, model variants including either day or night events were developed.

Residuals of the model were checked visually for normality. The model was validated by 200-fold bootstrapping. The relative importance of predictors was calculated by partitioning $R^2$ using the method ‘averaging over orders’ as proposed by Lindeman et al. (1980), a tool that is implemented in the R® package ‘relaimpo’. To test the singular effect of predictors on the FIA, we excluded the predictor

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**Figure 1.** Schema of hydrological variables derived from flow curves. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

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of interest from the model and regressed the residuals of this new model against the predictor of interest.

We used a one-sided \( t \)-test to test the hypothesis that sites impacted by hydropower had higher FIA than reference sites. All analyses were completed using R\textsuperscript{®} version 3.0.2.

**RESULTS**

In total, we analysed 74 sites from 16 rivers including 18 ‘nature-like’ and 56 ‘channelized’ sites. Among these sites, 14 were classified as ‘reference’ site, and 60 as ‘hydropeaking’ site. Hydropowering takes place mainly in the western, more mountainous parts of Austria in rivers classified as hyporhithral. Species richness increases from metarhithral to epipotamal rivers, that is, 2 to 20 species per river (Figure 2, Tables II and III).

The field samples of the fish communities covered a wide range of fish ecological conditions (FIA 1.5–5.0). The FIA of hydropowering sites was higher (mean = 4.15, SD = 0.968) than the FIA of reference sites (mean = 2.06, SD = 0.383; \( t = 13.128, p < 0.001 \), Figure 3). While the FIA varies only within one ecological status class under reference conditions, the FIA ranges from 1.5 to 5 under hydropowering conditions (Figure 3).

After removing redundant variables, 10 variables were left for testing in the modelling approach. Out of the 10 variables, four variables and one interactive term were retained in the final model: fish zone (‘FIZO’), number of events with high flow ratios (‘RAT90’), habitat (‘HAB’), ramping rate (‘RARA90’) and the interaction between ‘HAB’ and ‘RARA90’ (Table IV). In our dataset, ‘RAT90’ varies between 0.8 and 170 events per year (mean = 47), and ‘RARA90’ varies between 4.8 and 42.2 cm h\(^{-1}\) (mean = 17.5), indicating that also ‘reference sites’ are exposed to flow fluctuations due to flood events. The model explains 66.5% of the variation of the FIA with a bootstrapping range of 46.3–84.3% (Figures 4 and 5).

The variable with the highest relative importance is ‘HAB’ indicating better fish ecological status (lower FIA values) in ‘nature-like’ habitat conditions. The second ranked variable is ‘RAT90’, followed by ‘FIZO’, ‘RARA90’ and the interactive term. The combined importance of predictors associated with ramping rate (‘RARA90’

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### Table II. Characteristics of sampled sites

| River type  | Fish zone  | River width [m] mean, range | Discharge \( [m^3 s^{-1}] \) mean, range | Catchment size \( [km^2] \) mean, range | Number of samples | Number of species sampled per site |
|-------------|------------|-----------------------------|------------------------------------------|----------------------------------------|-------------------|-----------------------------------|
| Metarhithral | Brown trout | 12 (7–24)                   | 7 (2–21)                                | 201 (84–517)                          | 9                 | 1–4                              |
| Hyporhithral | Grayling   | 44 (15–105)                 | 68 (8–166)                              | 2264 (320–4647)                      | 81                | 2–17                             |
| Epipotamal  | Barbel     | 86 (75–110)                 | 144 (10–239)                            | 3815 (769–8833)                      | 8                 | 9–12                             |

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### Table III. List of species occurring in investigated rivers and associated river types

| River type       | Grossache | Großarler Ache | Isel | Zederhausbach | Drau | Enns | Il | Möll | Mur | Rhein | Saalach | Ziller | Bregenzerach | Inn | Salzach | Kainach |
|------------------|-----------|----------------|------|---------------|------|------|---|------|-----|-------|---------|-------|---------------|-----|---------|---------|
| Metarhithral     | x         | x              | x    | x             | x    |      |   |      |     |       |         |       |               |     |         |         |
| Hyporhithral     | x         | x              | x    | x             | x    | x    |   | x    |     |       |         |       |               |     |         |         |
| Epipotamal       |           |                |      |               |      |      |   | x    | x   |       |         |       |               |     |         |         |
| Native species   |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Alburnoides bipunctatus |         |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Alburnus alburnus |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Anguilla anguilla |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Barbatula barbatula |         |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Barbus barbus     |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Carassius gibelio |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Chondrostoma nasus |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Coregonus sp.     |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Cottus gobio     |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Cyprinus carpio  |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Esox lucius      |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Eudonotymyzon mariae |         |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Gobio gobio      |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Hucho hucho      |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Leuciscus leuciscus |         |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Lota lota        |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Perca fluviatilis|           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Phoxinus phoxinus |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Rutillus rutillus|           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Salmo trutta fario|           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Salmo trutta lacustris |       |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Squalius cephalus |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Telestes souffia |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Thymallus thymallus |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Zingel streber   |           |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Non-native species |         |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Oncorhynchus mykiss |         |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Salvelinus fontinalis |       |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Gasterosteus aculeatus |       |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Pseudorasbora parva |       |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Ctenopharyngodon idella |       |                |      |               |      |      |   |      |     |       |         |       |               |     |         |         |
| Total            | 3         | 2              | 2    | 2             | 15   | 11   | 3 | 3    | 15  | 12    | 3      | 5     | 13           | 8   | 15     | 11     |

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and interactive term) amounts to 10% compared with 17% associated with peak frequency (‘RAT90’). Replacing night by day events (‘RAT90’) demonstrates that night peaks seem to affect fish communities more than day peaks. In terms of fish zones, the fish response to hydropoeaking is more pronounced in the hyporhithral and epipotamal than in the metarhithral (Figures 6 and 7). The interactive term indicates different reactions of fish communities to altered ramping rates in nature-like compared with channelized rivers. Predictions show that, when eliminating the effects of the other variables, reduced ramping rates may improve the fish ecological status by two classes in nature-like rivers, while no effect is expected in channelized rivers (Figure 8).

**DISCUSSION**

Although the effects of pulsed flows on fish communities have been studied for over 35 years, many questions are still open. Researchers and managers still do not know with certainty how large a pulsed flow, relative to the natural seasonal flow, is likely to harm fish. For most stream fish species, we lack adequate relationships to determine the effects of different magnitudes, ramping rates and timing (season and photophase) of pulsed flows on the fish community level (Young et al., 2011).

On the basis of an extensive field dataset including both fish community and a number of different types of hydrological and morphological data, we were able to demonstrate that fish communities are strongly affected by hydropoeaking in Alpine rivers of Austria. Rivers with heavy peaking tend to fall in the ‘poor’ (class 4) and ‘bad’ (class 5) classes following the WFD classification scheme. The main reason for that is that the FIA is set to class 4 and class 5 when the fish biomass is below 50 to 25 kg ha\(^{-1}\), respectively (Figure 4). Median biomass of sites not affected by hydropoeaking was 140 kg ha\(^{-1}\) whereas median biomass of

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**Table IV. Results of the generalized linear model comparing Fish Index Austria with hydromorphological pressures**

| Variable            | Coefficient | Std. error | t-value | Pr(>|t|) |
|---------------------|-------------|------------|---------|----------|
| Intercept           | 0.7414      | 0.6012     | 1.2331  | 0.2218   |
| FIZO_HR             | -9.265      | 0.2793     | -3.3168 | 0.0015   |
| FIZO_MR             | -1.9555     | 0.4493     | -4.3521 | 0.0000   |
| RAT90               | 0.3307      | 0.0828     | 3.9966  | 0.0002   |
| HAB_channelized     | 3.0113      | 0.6075     | 4.9566  | 0.0000   |
| RARA90              | 7.6833      | 2.4107     | 3.1871  | 0.0022   |
| HAB_channelized * RARA90 | -6.9690 | 2.4812     | -2.8088 | 0.0065   |

FIZO_HR = fish zone hyporhithral, FIZO_MR = fish zone metarhithral, RAT90 = number of peaks with high flow ratio (90 percentile), HAB_channelized = habitat channelized, RARA90 = ramping rate (90 percentile), AIC = Akaike information criterion.
hydropeaking sites was only 26 kg ha\(^{-1}\). The low biomass indicates that the fish community capacity falls below critical levels and is not able to cope with the conditions in hydropowering river stretches. Very low biomasses of 0–12.4 kg ha\(^{-1}\) were already demonstrated in earlier studies, for example, in the Bregenzerach (Parasiewicz et al., 1998), an Austrian river with high ramping rates, which is also included in our dataset.

Key pulsed flow characteristics include frequency, magnitude, timing and duration. Peak flows occur in natural and hydrologically altered rivers. However, while natural floods are limited to a few occurrences annually, peaks resulting from hydropower management generally act on a daily basis. When comparing the number of peaking events and the fish response in our dataset, a threshold of about 20 night peak events per year can be detected. Above this threshold, the FIA indicates degradation of the fish community, and below this threshold, a good ecological status is possible (Figure 7). The cumulative effects of single peaks over time can be inferred and may be acute or chronic (Young et al., 2011). Small losses from fry stranding and entrapment can accumulate to a substantial cumulative loss under conditions of repeated flow fluctuation. Baurersfeld (1978) estimated a 1.5% fry loss per drawdown with a total loss of 59% of the salmon fry population for one season. Likewise, stranding rate was significantly reduced in pink, chum and Chinook salmon fry when the annual number of down-ramping events was reduced in the upper Skagit River, Washington, USA (Connor and Ploug, 2004). Therefore, as shown also by Bain (2007), the cumulative impacts of multiple peaks may ultimately cause changes in fish abundance and community composition.

Stranding of juvenile fish <6 cm is considered to be the most important effect of hydropoeaking on fish (Young et al., 2011). In our dataset, ramping rates above 30 cm h\(^{-1}\) were associated with poor and bad ecological status. Ramping rates below 15 cm h\(^{-1}\) increased the probability of better ecological status (Figure 7). Halleraker et al. (2003) found a significant decrease in stranding of trout fry by reducing the dewatering speed from 60 to less than 10 cm h\(^{-1}\). On the Sultan River (Washington, USA), down-ramping rates ranging from 2.5 cm h\(^{-1}\) in the summer to 15 cm h\(^{-1}\) in spring and winter were required to protect steelhead and salmon fry (Olson, 1990).

As expected, we found that the ecological status is much better in nature-like than in channelized river sections. Nature-like rivers provide the essential habitats for different species and life stages, whereas in channelized rivers, fish species diversity and biomass are reduced (Jungwirth et al., 1995; Oscoz et al., 2005). Gravel bars and shallow habitats along the shoreline are favoured habitats of juvenile life stages. However, those habitats are high-risk areas with respect to stranding as the water level drops. The rate and intensity of stranding impacts depend on the slope of gravel bars, availability of potholes, substrate size and, in general, connectivity between refuge and main channel habitats. In the Cowlitz River (California, USA), most of the Chinook salmon (Oncorhynchus tshawytscha) fry stranding occurred on gravel bars of 2% slope (Baurersfeld, 1978). Monk (1989) reported that in an experimental channel, more Chinook salmon fry stranded on 1.8% slopes than on 5.1% slopes. Higher fish-stranding rates occur in larger cobbles where water drains through rather than flowing off (Hunter, 1992). Beck and Associates (1989) reported increased fish stranding with coarse (7.6 cm) substrates than in finer substrates. By applying a consistent methodology to different fish zones, we were able to assess different responses in the metarhithral, hyporhithral and epipotamal types of Alpine rivers. The results show that fish communities dominated by grayling and riverine cyprinids react more
sensitive to hydropeaking than communities dominated by brown trout (*Salmo trutta*). However, according to substrate gradients along the river continuum, one would expect higher stranding rates in metarhithral than in hyporhithral and epipotamal rivers.

It seems to be a contradiction that juvenile fish require nature-like riparian habitats, at the same time providing areas that have a high risk of stranding. However, these habitats are mandatory, and therefore, it is logical that despite hydropeaking, higher survival rates of juveniles should be expected in nature-like than in channelized rivers. This is also confirmed by our findings: indeed, when excluding the other effects in the model, the fish ecological status degrades with increasing ramping rate in nature-like rivers; however, it is heavily degraded in channelized rivers regardless of the ramping rate (Figure 8). River managers should therefore not fall into the trap of avoiding habitat restorations in channelized hydropeaking rivers.

We calculated the hydrological variables separately for day and night events and found that night events contributed...
more to the model than day events (Figure 6). In the Nidelva River (Norway), Atlantic salmon (*Salmo salar*) and brown trout fry were less likely to be stranded at night than during the day because they were more active at night. When temperatures were $>9{\degree}C$, higher stranding rates were observed at night for both species (Heggenes *et al.*, 1993; Saltveit *et al.*, 2001; Halleraker *et al.*, 2003). Grayling larvae and juveniles use shallow marginal habitats and shift to even more shallow habitats at night, making them more exposed to stranding. At night, evidence for drift is also more pronounced than that during the day (Bardonnet and Persat, 1991; Sempeski and Gaudin, 1995). Relatively little information is available for cyprinid species in this context. However, because of the small sizes of their juvenile stages and related behavioural mechanisms, for example, nocturnal drift (Zitek *et al.*, 2004), increased nocturnal stranding and drift could be responsible for the effects we observed in our rivers.

Besides stranding, many other pressures are associated with hydropoeaking (Young *et al.*, 2011; Person, 2013). Temperature and discharge, both affected by peak operations, are key factors influencing spawning migration behaviour (Lucas and Baras, 2001). Dewatering of redds may lead to increased egg mortality (McMichael *et al.*, 2005). In addition, fine sediment accumulations resulting from peaking operation might impair dissolved oxygen consumption of eggs and impact salmonid embryos and alevins survival (Jensen *et al.*, 2009). Jensen and Johnsen (1999) showed that emerged brown trout are very sensitive, have limited swimming capabilities and are very vulnerable to high discharge and sediment transport during the first period after emergence. Discharge peaks resulting from hydropower operations are more detrimental for larval fish as they occur more often than natural floods and may result in multiple larval drift and displacement events. Concluding, several life stages of fish can be affected by hydropoeaking resulting in reduced recruitment and decreased population density or biomass, which also should be reflected by fish indices, such as FIA, when applied to hydropoeaking river sections.

Hydropoeaking may also be associated with thermopeaking. Zolezzi *et al.* (2010) reported for the Noce River, Italy, water temperature alterations of up to 6{\degree}C due to heavy hydropoeaking. Flume experiments demonstrated increased macroinvertebrate drift as a response to thermopeaking (Bruno *et al.*, 2013). Less is known about the reaction of fish to thermopeaking. Potential effects of temperature associated with hydropoeaking have not been investigated in our study or any other study in Austria so far. Preliminary analyses (unpublished data) show that water temperature may increase or decrease depending on season, type of water release (hypolimnion or epilimnion) and relation of base to peak flows. However, as far as known in most cases, the water temperature alteration during peak events does not exceed 2{\degree}C. Therefore, we assume that water temperature might have less effect than stranding in Austrian rivers. Nevertheless, further analyses have to be performed to answer this question in detail.

There is still no clear vision which mitigation measures are the most suitable for fish and most effective in terms of costs. Simulations for two case studies in Switzerland showed that operational measures such as limiting maximum turbine discharge, increasing residual flow and limiting drawdown range incur high costs in relation to their ecological effectiveness. Compensation basins and powerhouse outflow deviation
achieved the best cost–benefit ratio (Person et al., 2013). However, further studies are required to test the full set of potential mitigation measures under varying conditions.

CONCLUSIONS

Hydromorphological conditions of fish habitats are a consequence of the interplay between hydrological and morphological processes. Our results demonstrate that fish react to a combination of peak frequency, ramping rate and habitat conditions. Ramping rate and peak frequency amount to 23% relative importance in our model compared with 26% relative importance of the habitat conditions. This indicates equal importance of habitat and flow criteria for fish. In addition, the significant interaction term between habitat conditions and ramping rate in the model underlines the importance of the combined effects of hydrology and morphology on fish.

Summarizing, the results pinpoint that more attention should be dedicated in future fish ecological work to the combined effects of hydrological and morphological characteristics, that is, peak frequency, ramping rate and habitat conditions including diurnal aspects. Effective mitigation measures have to take into account the complexity of hydromorphological processes determining habitat conditions.

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