Received: 15 November 2021 | Accepted: 24 May 2022
DOI: 10.1111/1365-2664.14236

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Experimental comparison of fish mortality and injuries at innovative and conventional small hydropower plants

Melanie Mueller | **Josef Knott** | **Joachim Pander** | **Juergen Geist**

Aquatic Systems Biology, Technical University of Munich, Freising, Germany

Correspondence
Juergen Geist
Email: geist@tum.de

Funding information
Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, Grant/Award Number: OelB-0270-45821/2014

Handling Editor: Paulo S. Pompeu

Abstract

1. Resolving the controversy about hydropower is only possible based on reliable data on its ecological effects, particularly fish welfare.
2. Herein, we propose a comprehensive assessment of conventional and innovative hydropower using a dataset of 52,250 fish.
3. The effects of hydropower on fish were most harmful at sites with Kaplan turbines, showing ≤83% mortality. Innovative hydropower, often termed 'fish-friendly', caused ≤64% mortality.
4. Our findings suggested that the runner peripheral speed, number of turbine blades and turbulence at turbine outlets were the most important factors.
5. *Synthesis and applications*. To reduce the impact of hydropower on fish, site-specific characteristics such as head drop, bypass options and river-specific species composition need to be more intensively considered in optimal turbine technologies and operation modes.

KEYWORDS
Archimedes screw turbine, fish damage, fish injury, fish mortality, fish welfare, innovative hydropower, Kaplan turbine, VLH turbine

1 | INTRODUCTION

Hydropower is usually promoted as a 'green' renewable energy source; however, some term it 'red' energy due to the resulting fish damage and its ecological consequences on freshwater habitats (Geist, 2021). More than 90% of the world's freshwater fish species depend on long- or medium-distance migration (Brönmark et al., 2014) to reach spawning grounds, juvenile habitats, feeding grounds or to disperse. Thus, hydropower turbines along their migration route are inescapable during their life cycles. The world-wide expansion of hydropower poses a great challenge to the future conservation of biodiversity (Zarfl et al., 2015), particularly concerning freshwater fish that can suffer from damage during the downstream passage.

Physical injuries that happen to fish during hydropower turbine passage are mainly related to blade strike, rapid pressure change and shear stress (Hogan et al., 2013). Currently, different hydropower technologies are in place which differ in their injury and mortality risk for fish due to differences in turbine characteristics, such as runner speed, number of turbine blades, turbine diameter or head drop. Kaplan turbines have been widely used world-wide since the early 19th century and are referred to as a conventional turbine type (Čada, 2001). It is a propeller-type turbine with adjustable blades and wicket gates (double-regulated, constant runner speed), allowing efficient power production at low-head sites (Ujwala et al., 2017). There are variations in Kaplan turbine construction, including vertical or horizontal orientation and the newly developed 'movable power plant' (Thorstad et al., 2017). Kaplan turbines are harmful to fish due to their high runner speeds, shear stress and rapid pressure changes (Hogan et al., 2013), but are known to be less damaging than Francis turbines (e.g. Algera et al., 2020; Fu et al., 2016; Vikström et al., 2020). Recent novel turbine technologies have been proposed to be more 'fish-friendly' than conventional hydropower turbines, particularly in improving fish downstream passage by reducing the risk of blade strike, shear stress or the risk of barotrauma injuries (Hogan et al., 2013). For instance, the innovative very low-head (VLH) turbines and Archimedes screw turbines have a lower runner speed and larger turbine diameter than most conventional Kaplan turbines and are expected to reduce the risk of blade strike and related fish injury such as amputations, bone fractures and bruises. The screw turbine has become popular during the last two decades as a so-called 'fish-friendly' hydropower technology due to its low runner speeds, pressure changes and shear stress (Lubitz et al., 2014; Nuernbergk & Rorres, 2013). The VLH turbine is a special type of Kaplan turbine with a relatively low runner speed, developed in the early 2000s to optimise the power production efficiency at low-head sites with a head drop of 1.5–4.5 m and to minimise the impact on fish (Wright & Rival, 2013). The low-head differentials of the sites where those turbine types are usually installed are expected to contribute to less rapid rates of pressure change during turbine passage and therefore cause less risk for barotrauma injuries such as swim bladder rupture, emboli and haemorrhages. Besides turbine and site characteristics, the operation mode of the turbine may also influence fish mortality and injuries. Particularly for Kaplan-type turbines, runner blades are set in a more narrow angle during low turbine load, reducing gap size for fish to pass and therefore bearing higher risk of blade strike compared to high load settings. In contrast, for turbines with variable runner speed, such as screw turbines or VLH turbines, operational modes of low or high turbine loads may result in different collision risk and injury patterns.

Knowledge of the injury and mortality risk of different turbine technologies is essential for the conservation of healthy aquatic ecosystems, particularly for the planned expansion of hydropower in the few remaining free-flowing river systems in Eastern Europe (Costea et al., 2021), Asia (Baumgartner et al., 2017), South America (Couto et al., 2021) and Africa (Zarfl et al., 2019). Most of the current assessments of hydropower effects on fish only cover conventional turbine types (e.g. Kaplan or Francis turbines), which have been in use for many decades; however, biological evaluation research at the field sites of innovative technologies is currently at an early stage. For future fish population management, knowledge of the ecological impact of conventional and innovative hydropower technologies under different site conditions will be essential in balancing the needs of hydropower development and fish conservation. A major drawback in the objective ecological comparison of hydropower technologies is the limited comparability of available studies, which currently primarily comprise single-case studies using different methodologies such as modelling, recovery nets, telemetry and immediate versus delayed mortality on different species (Geist, 2021).

The effects of conventional large-dam, high-head hydropower plants on fish are well known, especially for economically important species such as eel and salmonids (Fjeldstad et al., 2018). Conversely, the ecological consequences of smaller facilities at low-head sites (<10 m high) and other fish species such as cyprinids, which often comprise the largest proportion of river fish in Europe, are largely unknown. Small hydropower has recently increased in popularity (Balkhair & Rahman, 2017; Gibeau et al., 2017) since there is still great potential for expansion—only 36% of world potential is currently used (Markin et al., 2020). In contrast, most opportunities for economically profitable medium- to large-scale schemes have already been developed, particularly in Europe (Anderson et al., 2015), where >99% of all barriers are <10 m high (Belletti et al., 2020; Garcia de Leaniz et al., 2019). Therefore, low-head sites are the focus of innovative hydropower technologies.

Modelling approaches are often favoured over field evaluations to determine fish mortality since they can be easily applied to different types of hydropower sites (high- and low-head sites) and are less costly. However, current modelling approaches rely primarily on blade-strike models (Deng et al., 2011), which may well describe collision-related injuries, but do not account for multiple other effects on fish such as barotrauma or shear stress. The species-specific tolerance levels of stressors remain largely unconsidered yet essential in realistic effect assessment. Conversely, meta-analyses of field-study results using different sampling regimes are often limited by not considering pre-damage from other sources such as predation, upstream hydropower plants and handling effects (Mueller et al., 2017).

Reliable data on the hydropower effects on fish can only be provided if current knowledge from modelling approaches, laboratory experiments and single-case studies are extended and validated by comparative field studies covering different turbine types and fish species within one standardised, systematic experiment that accounts for handling effects.

Herein, we propose a standard for a comprehensive assessment of the effects of conventional and innovative hydropower on fish, which we validated by investigating the effects of three turbine types on eight fish species of known pre-condition at seven low-head hydropower sites (eight hydropower plants: six sites with one hydropower plant, one site with two different hydropower plants). Applying this comprehensive assessment, we specifically tested the following hypotheses: (a) The passage of low-head hydropower turbines causes significant mortality and injury to fish, (b) with innovative, so-called 'fish friendly' turbine types (i.e. screw turbines and VLH turbines) being less harmful compared to conventional Kaplan turbines. (c) The observed injuries can be explained by the main geometry features and operation modes of the turbines and hydropower plants, such as turbine diameter, number of blades or runner speed.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

The study was approved for appropriate animal care and use according to the European laws (European Parliament, 2010), national standards and guidelines (Adam et al., 2013) by the Bavarian Government (permit numbers ROB-55.2-2532.Vet_02-15-24 and ROB-55.2-2532.Vet_02-15-31). The application documents received ethical approval from the Technical University of Munich animal welfare officer and the Ethical Commission of the Bavarian Government prior to receiving permission. All field work was carried out under permission of the fisheries right owners and water management authorities.

2.2 | Study sites

This study investigated three hydropower turbine technologies for fish injury and mortality, Kaplan, Archimedes screw and VLH turbines. Since the hydropower effects on fish are likely to vary among sites within one turbine technology due to site-specific characteristics such as river discharge and head drop, at least two sites per turbine type were investigated. Four sites were investigated for Kaplan turbines and two each for VLH and screw turbines. The hydropower test sites were located in Bavaria, Germany (Figure 1). See Table 1 for the hydropower plant characteristic details. The test sites are described in greater detail in Mueller et al. (2017), Knott et al. (2019) and Knott et al. (2020).

2.3 | Experimental design

Eight species of hatchery-reared fish were used in a standardised experiment to quantify hydropower-related fish injury and mortality. In contrast to wild fish, hatchery-reared fish allow accounting for pre-damage (e.g. from aquaculture, transportation or natural anomalies) and catch-related effects due to the ability to assess their condition upon delivery prior to turbine passage. The experimental design was based on a group comparison approach to distinguish treatment effects ('treatment fish') from the control ('sham fish') as described in detail in Mueller et al. (2017). Released fish were not forced to swim downstream to prevent the introduction of a potential behavioural bias. In brief, the 'treatment fish' were released upstream of the hydropower plants in front of the trash racks or fish protection screens at two different operation modes referred to as 'high' and 'low' turbine load. These two operation modes are not to be understood as discrete and exactly defined states, but were used to cover the site-specific range of typical operation conditions in the best possible way under the local conditions during the study period (Table 1).

Fish were recaptured at the turbine outlets during 1 hr emptying intervals, using stow nets as described in Pander et al. (2018). Stow nets had a rectangular opening, covering 100% of the turbine outlet and were reduced to a circular opening of 60 or 70 cm at the end. The nets had a decreasing mesh size from 30 to 20, 15 and 10 mm. The stow nets were connected to a fyke net as a fish trap at the end (Pander et al., 2018). The 'sham fish' were released at the opening of the stow net at the turbine outlets and caught with the same technique as the 'treatment fish' (Mueller et al., 2017). All experimental fish were marked with fin clips on different fins to distinguish 'treatment fish', 'sham fish' and wild fish. All turbine and hydropower plant characteristics that vary over time (e.g. power capacity, wicket gate opening, turbine discharge, head drop) were recorded hourly during the experiments.

Altogether 122,375 fish were released into the study streams, resulting in a dataset of 42,332 fish (low turbine load: 19,522 individuals in 1,108 net emptying intervals, high turbine load: 22,810 individuals in 683 net emptying intervals) recaptured after passage through eight investigated hydropower plants ('treatment fish') or after being exposed to the capturing facility ('sham fish'), examined for immediate and delayed mortality, and external and internal injuries (a subset of 7,940 fish was x-rayed). Nine thousand nine hundred eighteen additional fish were examined as controls to account for possible aquaculture and transportation effects, resulting in a total dataset of 52,250 specimens.

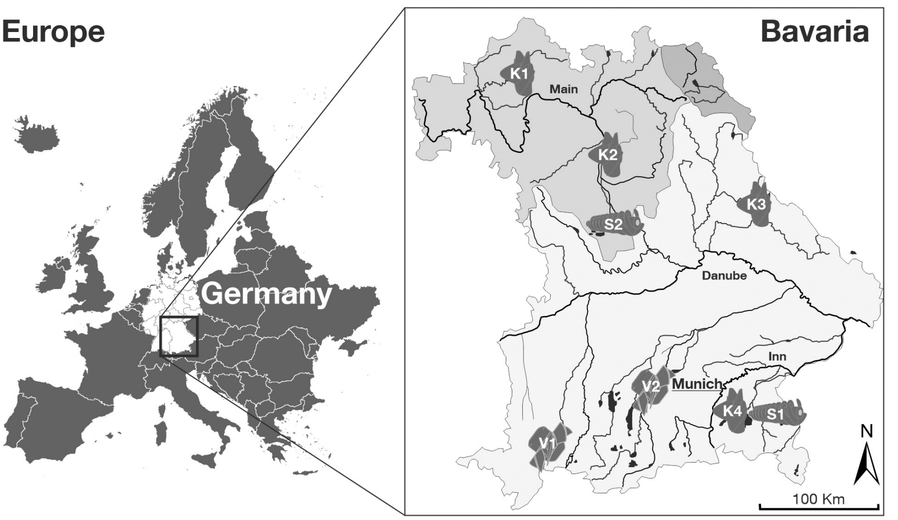


FIGURE 1 Map of the study locations in Bavaria, Germany including the type of investigated hydropower technologies (pictograms) and the main drainage systems in Bavaria (▇ = Elbe, ▇ = Main/Rhine, ☐ = Danube). K1–K4, Kaplan turbines; S1–S2, Archimedes screw turbines; V1–V2, Very low-head turbines.

2.4 | Fish injury and mortality assessment

External and internal fish injuries were assessed following the protocols in Mueller et al. (2017, 2020). The assessment comprised five general fish health criteria (vitality, respiratory movements, parasitic infestations, fungal infections and nutritional status), 86 combinations of body parts with external injury types and 36 combinations of body parts with internal injuries. Externally visible injuries were screened on-site following a systematic visual estimation and intensity scoring. After evaluation, the vital fish were returned to the fish tanks and kept in compartments per treatment and species for 96 hr to account for potential 'delayed mortality'. The dead and severely injured fish, after euthanasia, were frozen at −20°C for later evaluation of internal injuries. Additionally, a random reference sample from the treatment groups was euthanised and frozen immediately after external injury evaluation and the 96 hr holding period (Mueller et al., 2020). Contact radiography was used to assess internal injuries as described in Mueller et al. (2020). The resulting X-ray images were evaluated by systematic screening using a dimmable A4 light table and magnification glasses. The intensity of the external and internal injuries was differentiated into four categories as follows: no injury = 0, minor injury = 1, medium injury = 3 and severe injury = 5. Greater detail on the scoring of each injury type can be found in the score sheets in Mueller et al. (2017) and Mueller et al. (2020). Experienced experts trained the investigators on injury scoring and the protocols.

2.5 | Data analysis

2.5.1 | Calculation of mortality rates and injury prevalence

To calculate the mortality rates and injury prevalence, we followed the assumption of Dubois and Gloss (1993) that the majority of fish not recovered after turbine passage had escaped upstream before entering the hydropower plants. For fish that had not escaped upstream but were not recovered, it was assumed that dead, injured and unharmed fish had equal chances of not being recovered. To control the mortality rates for the catch- and handling-related mortality ('sham fish' mortality), we used a relative recovery rate estimator previously applied in the same type of experiment (Dubois & Gloss, 1993). The following basic formula was used:

$$M = 1 - \left[\left(T / R_t \right) / \left(S / R_s \right) \right],$$

with M = mortality rate, T = number of 'treatment fish' alive after recovery, R_t = number of 'treatment fish' recovered, S = number of 'sham fish' alive after recovery, R_s = number of 'sham fish' recovered.

The same formula for mortality was applied to calculate the injury prevalence by replacing the number of 'alive' fish with the number of unharmed 'treatment fish' and unharmed 'sham fish', respectively, for each injury type. To visualise the prevalence of different injury types after the passage of the investigated hydropower turbines, a clustered heatmap was calculated using the ComplexHeatmap package in R (Gu et al., 2016). Clustering was performed using default settings in ComplexHeatmap (hierarchical clustering with complete linkage method).

In some cases, high control-mortality resulted in negative values for both mortality and injuries (e.g. due to unfavourable conditions in the recovery net or the small effect size of the turbine or both). Negative values were interpreted as the observed injuries or mortality not being related to turbine passage.

To estimate the overall mortality rate for each hydropower plant site, different calculation scenarios were applied to account for species- and operation mode-specific effects. First, the mortality rates were calculated separately for each species as well as for high and low turbine load, since different turbine loads and species can yield different mortality probabilities. Subsequently, the arithmetic mean values were calculated across the operation modes and species. Second, data were pooled across all species and operation modes to calculate the overall mortality rate, resulting in values weighted by the recapture rates for different species and operation modes. This scenario was calculated to consider the assumption that less fish are harmed if a low number of fish pass the turbines. In both calculation scenarios, the negative mortality rates from single species or operation modes were either excluded or set to zero. The calculation scenarios resulted in up to four different values for the overall site-specific mortality. Since there is no widely accepted standard for calculating overall mortality, we decided to present the range of resultant values from all possible calculations rather than single values from one preferred calculation method.

2.5.2 | Multivariate hierarchical generalised linear mixed modelling

Multivariate hierarchical generalised linear mixed modelling from the R package Hmsc was used to explore the effects of turbine- and site-specific characteristics (turbine discharge, head drop, runner speed, runner peripheral speed, number of turbine blades and turbine diameter), fish characteristics (total length, body mass and condition = vitality of 'sham fish' after 96 hr) and sampling conditions (biomass and debris in the recovery net) on fish injuries (Tikhonov et al., 2020). The Hierarchical Modelling of Species Communities (HMSC), a joint species distribution model (Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017), was used to analyse how fish injuries (instead of species) respond to physical characteristics during hydropower plant passage. Turbine parameters, site-specific characteristics, fish characteristics and sampling conditions were included as fixed effects. While our primary interest was in the effect of turbine- and site-specific characteristics, we controlled for fish characteristics and sampling conditions owing to their known influence on fish injuries (Mueller et al., 2017; Pander et al., 2018). The fish species and hydropower plant sites were included as random effects. Fish injury data were averaged per species and emptying interval and the respective

TABLE 1 Number of experimental fish and species, recapture rates of fish and dummies (to check the catching effectiveness of the recovery nets), and characteristics of the hydropower plants and operating conditions

Hydropower sites	K1	K2	K3	K4	S1	S2	V1	V2
Number of species	4	4	8	8	8	7	8	8
Number of fish	461	2,852	5,108	5,041	6,403	6,206	9,406	6,855
Recapture rate fish (%)	4	61	23	40	32	36	49	31
Recapture rate dummies (%)	2	91	88	94	90	96	96	94
Turbine type	Kaplan turbine	Kaplan turbine	Kaplan turbine	Kaplan turbine	Archimedes screw turbine	Archimedes screw turbine	VLH turbine	VLH turbine
Number of turbines	1	2	1	1	2	1	2	1
Number of turbine blades	3	4	4	4	5	4	8	8
Turbine diameter (m)	1.5	2.0	1.0	2.5	4.3	3.2	5.0	3.6
Runner speed variation min–max (RPM)	212	150	333	100	6–19	3–26	22–33	39–56
Runner peripheral speed min–max (m/s)	16.7	15.7	17.4	13.1	1.4–4.3	0.5–4.4	5.8–8.6	7.2–10.4
Nominal installed capacity per turbine (kW)	270	324	190	265	153	80	450	450
Power capacity variation min–max (kW)	16–62	233–253	33–174	227–326	56–160	11–62	76–342	70–327
Wicket gate opening (%)	20–45	76–85	35–73	61–95	n.a.	n.a.	32–96	n.a.
Turbine discharge variation min–max (m^3/s)	2.0–3.3	12.1–13.6	1.9–4.5	10.5–17.1	2.5–8.5	1.0–4.8	8.0–24.1	5.0–12.1
Head drop variation min–max (m)	2.7–2.8	2.4–2.5	4.6–4.8	1.9–2.4	1.8–2.4	1.6–2.3	1.1–2.3	3.5–4.0

recordings of explanatory variables were assigned to the intervals by their time mark (continuous data). Consequently, each emptying interval can be interpreted as one replicate in the model. The models were fitted assuming the default prior distributions and sampling the posterior distribution with four Markov chain Monte Carlo (MCMC) chains, each run for 3,750,000 iterations, of which the first 125,000 were removed as burn-in. The chains were thinned by 1,000 to yield 250 posterior samples per chain, therefore 1,000 posterior samples in total. We examined the MCMC convergence by examining the potential scale reduction factors (Gelman & Rubin, 1992) of the model parameters. The explained variation was partitioned among the fixed and random effects included in the model (positive or negative response with at least 95% posterior probability) to quantify the injury-pattern drivers.

3 | RESULTS

3.1 | Mortality

For all investigated hydropower sites, the standardised experiment resulted in significant mortality of 'treatment fish' compared to 'sham fish' for the total catch from all species, independent of turbine type, conventional or innovative design (Figure 2). Results were highly variable among hydropower sites and within the same turbine technology, with mortality rates ranging between 0% and 83% for specific species and operation modes (Figure 2; Table S1). The maximum mortality rates were ≤83% for conventional Kaplan turbines and ≤64% for innovative turbines (Figure 2; Table S1). The lowest average mortality rates with mean values ranging from 2% to 6% across all tested species and operation modes were observed in the VLH turbines at VLH site 1, followed by the screw turbines at Screw site 1 with 3%–6% and the conventional Kaplan turbine at Kaplan site 4 with 5%–8% (Figure 2). The highest average mortality of 35%–43% was observed at Kaplan site 1. However, it should be noted that the recapture rates at Kaplan site 1 were much lower than at the other hydropower plants due to the specific conditions at this site. The second-highest average mortality of 22%–25% was observed at Kaplan site 3, followed by Kaplan site 2 with 13%–21% mortality (Figure 2). At sites with the highest maximum and average mortality rates (Kaplan sites 1–3 and VLH site 2), most lethally injured fish died immediately after turbine passage (64%–94% of all dead fish). In contrast, at sites with the lowest observed mortality rates (Kaplan site 4, VLH site 1 and the screw turbine sites), 36%–71% of all dead fish were not immediately dead, but died within the 96 hr observation period.

The species-specific mortality rates (Figure 3; Table S1) indicated that the European eel *Anguilla anguilla* showed particularly low mortality at all innovative turbine sites (0%–2% at VLH sites 1 and 2, and Screw sites 1 and 2) compared to 4%–58% at the Kaplan sites. Another notable finding was that currently minimally considered cyprinid species, such as the common nase *Chondrostoma nasus* and

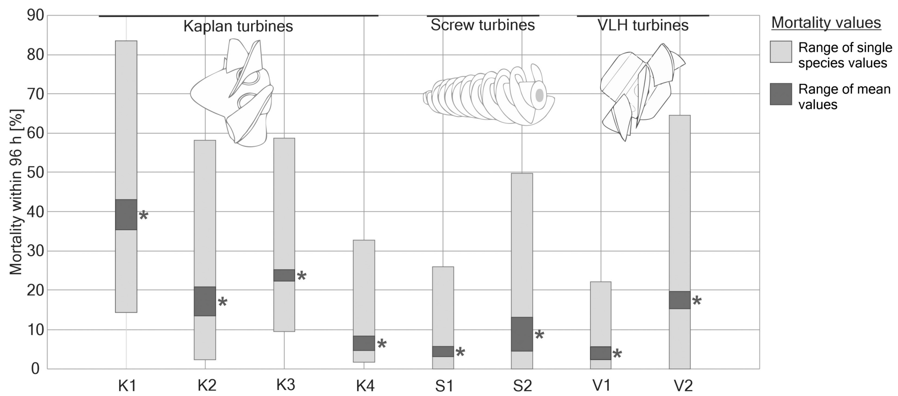
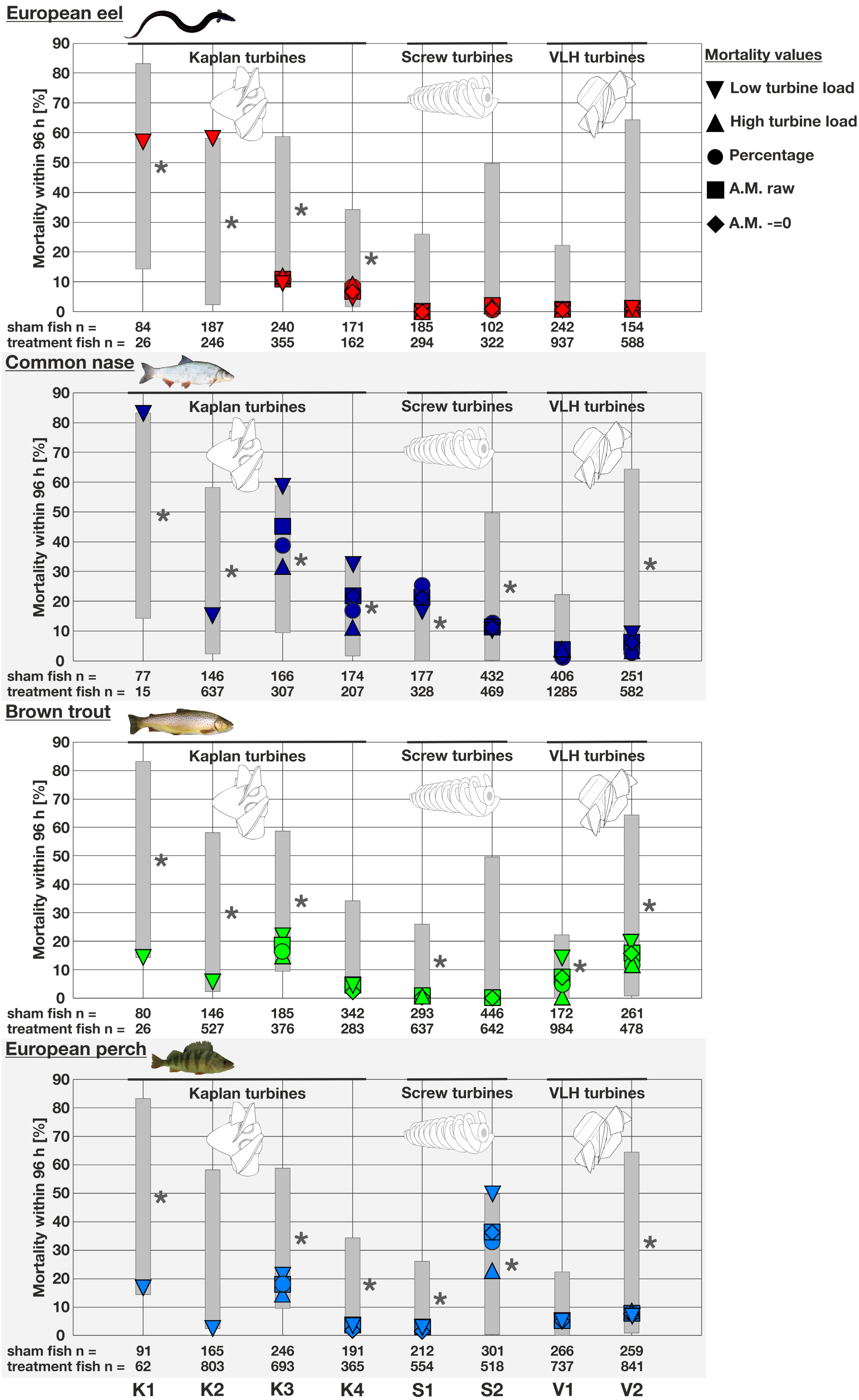


FIGURE 2 Comparison of fish mortality for Kaplan (K1–K4), screw (S1–S2) and very low-head (VLH, V1–V2) turbines. The mortality rates are corrected for species- and site-specific handling effects. Light grey bars show the range of species- and operation mode-specific mortality rates, dark grey bars indicate the range of mean values over the tested species and operation modes (see Section 2 for further details). Significant mortality compared to control fish was determined using proportion tests indicated by asterisks at the mean value bars. Numbers of fish and species- and site-specific characteristics are presented in Table 1. Underlying mortality values of single species and operation modes are presented in Table S1.

FIGURE 3 Comparison of species-specific mortality of four example species for Kaplan (K1–K4), screw (S1–S2) and very low-head (VLH, V1–V2) turbines. The mortality rates are corrected for species- and site-specific handling effects. Light grey bars show the range of species- and operation mode-specific mortality rates over all species, see Figure 2. Significant mortality compared to control fish was determined using proportion tests indicated by asterisks at the mean value bars. Underlying mortality values of single species and operation modes are presented in Table S1. Low/high turbine load = low/high operation mode of the hydropower plant, percentage = proportion of dead fish in the total catch across operation modes, A.M. = arithmetic mean across operation modes, raw = negative mortality rates were excluded, − = 0 = negative mortality rates were set to 0, n = number of assessed fish.


European eel
Common nase
Brown trout
European perch
Kaplan turbines
Screw turbines
VLH turbines
Mortality within 96 h [%]
Mortality values
Low turbine load
High turbine load
Percentage
A.M. raw
A.M. -=0
sham fish n = 84 187 240 171 185 102 242 154
treatment fish n = 26 246 355 162 294 322 937 588
sham fish n = 77 146 166 174 177 432 406 251
treatment fish n = 15 637 307 207 328 469 1285 582
sham fish n = 80 146 185 342 293 446 172 261
treatment fish n = 26 527 376 283 637 642 984 478
sham fish n = 91 165 246 191 212 301 266 259
treatment fish n = 62 803 693 365 554 518 737 841
K1 K2 K3 K4 S1 S2 V1 V2

roach *Rutilus rutilus* (Table S1), were highly sensitive to turbine passage, showing up to 83% mortality in common nase at Kaplan site 1 and 64% in roach at VLH site 2.

Regarding operational conditions, pronounced effects of the operation mode were detected. Low power seemed most harmful in Kaplan and for some species in VLH turbines (Table S1), particularly to larger fish, due to the narrow positioning of the turbine blades, resulting in increased risk of blade strike.

3.2 | Injuries

After passage through the investigated hydropower turbines, internal and external injuries to fish were classified into four clusters based on their prevalence after correction for handling effects (Figure 4). The first cluster comprised fin tears and scale loss, two comparatively low-severity injury types that frequently occurred across all treatment groups, including the control fish, but increased in intensity after hydropower plant passage in all investigated turbine types (Figure 4). Both injury types increased at the VLH sites, while their occurrence was more site specific at the screw and Kaplan turbines (Figure 4). The second cluster comprised mainly medium to high severity injuries, such as skeleton deformations, bruises or eye amputation. These injuries infrequently occurred also in 'sham fish', but in some cases, increased slightly in 'treatment fish' after turbine passage. For instance, the prevalence of vertebrae compressions (Kaplan site 3), internally visible skull injuries, fractures and deformations (Kaplan sites 1–3), and internal radiopaque materials (Kaplan site 2) were higher at Kaplan turbines compared to the other turbine types. The third cluster comprised injuries of low (e.g. pigmentations) or medium (e.g. deformations and rib, pterygiophore and spine fractures) severity with enhanced prevalence after turbine passage, particularly at Kaplan sites 1–3 and VLH site 2. Kaplan site 2 caused particularly high prevalence of internal rib, pterygiophore and spine deformations. The passage through both VLH hydropower plants increased pigmentations. Cluster 4 comprised severe injuries, almost exclusively occurring in 'treatment fish', including vertebrae fractures, amputation of body parts or severe swim bladder anomalies that may lead to death (Figure 4). These injuries were highest at Kaplan sites 1–3 (mean prevalence in dead fish 20%), medium at VLH site 2 and Kaplan site 4 (mean prevalence in dead fish 6%), and lowest at VLH site 1 and Screw sites 1–2 (mean prevalence in dead fish 3%, Figure 4). Swim bladder anomalies also increased at Screw site 2 and VLH sites 1–2, despite pressure-related injuries being expected to be low in these turbine types according to physical measurements (Boys et al., 2018).

3.3 | What causes injuries and mortality?

Multivariate generalised mixed modelling of the effects of turbine type, site and fish characteristics on injury patterns revealed that the runner peripheral speed had a greater influence on fish injuries than the other turbine parameters included in the models (Figure 5). This phenomenon was particularly evident in typical collision-related injuries such as vertebrae fractures, followed by skull fractures and deformations,

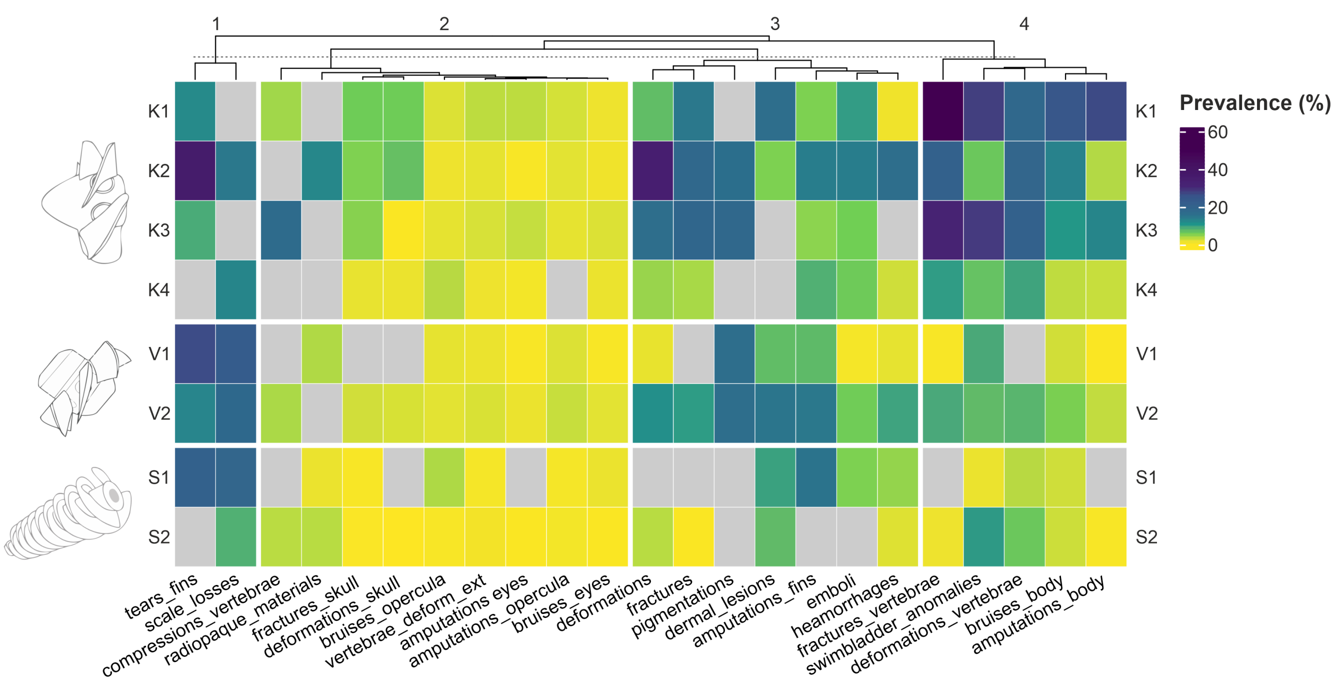


FIGURE 4 Prevalence of injuries in fish (overall species) that died immediately or within 96 hr after passaging through Kaplan (K1–K4), very low-head (V1–V2) or screw turbines (S1–S2). The prevalence values were corrected for site-specific handling effects using the mortality formula (see Section 2 for further details). Grey fields indicate that correction for handling effects resulted in negative values (i.e. the observed injuries could not be related to turbine passage).

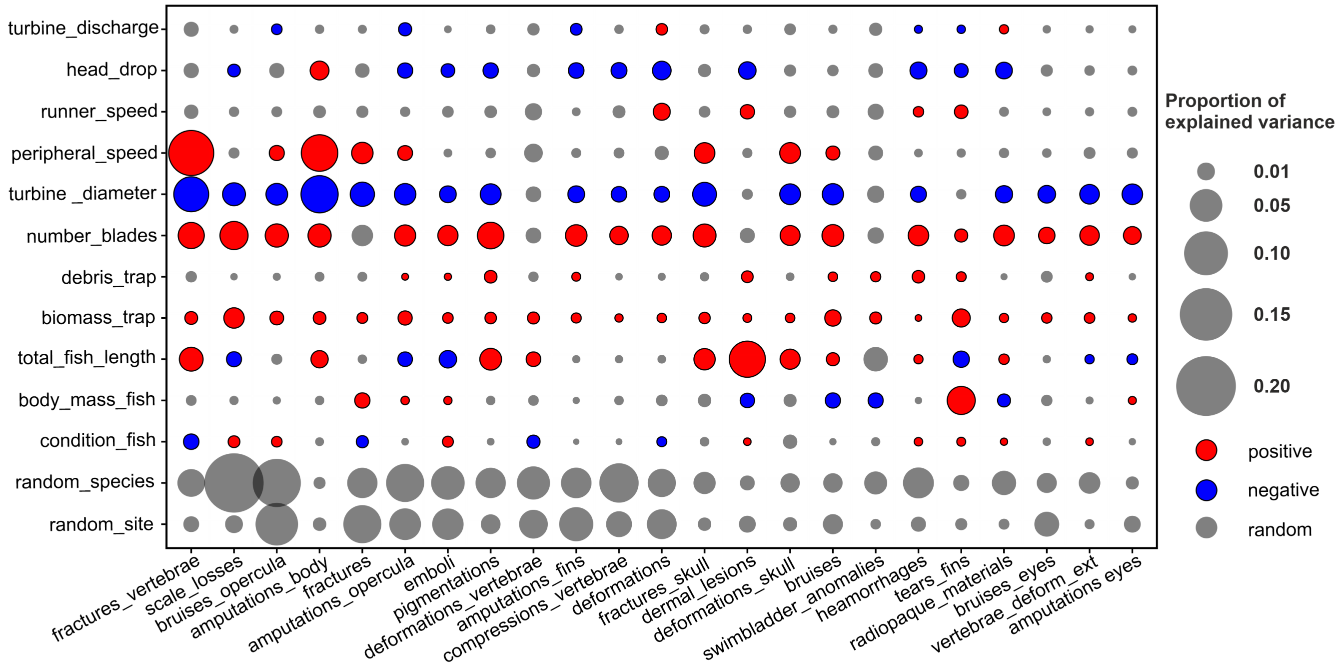


FIGURE 5 Results of multivariate hierarchical generalised linear mixed models of fish injury presence–absence, fixed effects (turbine/hydropower plant and fish characteristics) and random effects (site and fish species). The size of the bubbles indicates the proportion of explained variance by each explanatory variable in each injury type. Red bubbles indicate a positive, and blue bubbles a negative correlation. Grey bubbles indicate a random relationship. Peripheral speed = runner peripheral speed.

other bone fractures and body part amputations. According to the site-specific injury types described in the previous paragraph, blade strike was the main factor contributing to mortality in the investigated Kaplan turbines. This was also the case for VLH turbines; however, their passage primarily resulted in collision-related injuries that were either only internally visible or of lower severity, such as internally visible vertebrae fractures or deformations and other bone fractures (Figure 5). In addition, number of turbine blades, head drop and total fish length had a notable influence on some injury types. For instance, scale loss, internal fractures, pigmentations and fin amputations increased with the number of turbine blades. This was most applicable to VLH turbines with the highest number of turbine blades (eight) but a comparatively low runner speed, resulting in a high probability for low-intensity collisions, fitting well with the increased scale loss and pigmentations observed at VLH sites. Additionally, body part amputations increased with increasing head drop, and increased total fish length and runner peripheral speed increased vertebrae fractures, consistent with the result that European eel, the longest fish in this study, showed the highest mortality in Kaplan turbines (Table S1).

The quantity of debris and fish biomass in the trap and the fish biomass and condition explained only a small proportion of variance in fish injuries because the methodology was optimised to achieve minimal catch-related effects in a pre-study (Pander et al., 2018). This confirms that hourly net emptying and carefully selecting healthy fish are key factors in successfully monitoring turbine-related effects on fish.

In addition to the fixed effects, the random effects included in the models explained a similar or even higher proportion of variance (Figure 5). Particularly, strong species-specific random effects were found. Scale loss, opercula injuries (bruises and amputations), pigmentations and vertebrae compressions were the most variable injury types among species. Species-specific random effects can indicate that one species is more prone to suffer from a certain stressor during passage or is more susceptible to specific injury types than others. For example, cyprinid species lose scales easily, while scales are more deep-seated in percids. Such differences were also observed for changes in pigmentation which were more frequently observed in salmonids, European perch *Perca fluviatilis* and European eel than in other species. In some injuries, there was a combined random effect of site and species (Figure 5), indicating that the injury type was characteristic of the fish delivered to a specific site. For instance, opercula bruises were present as pre-damage in European grayling *Thymallus thymallus* delivered to two sites. Similarly, internal skeleton deformation occurred in brown trout *Salmo trutta* or European perch delivered from specific hatcheries.

Despite the various fixed and random effects on fish injuries that the models could explain, there was still a high proportion of unexplained variance in the fish injury patterns, consistent with the observation that many fish that died during or after turbine passage, particularly the cyprinid species common nase and roach, did not show any explicit external or internal signs of lethal injury.

4 | DISCUSSION

Based on one of the largest datasets of its kind, this study provides novel insights into mortalities and injuries during downstream passage of a suite of fish species at innovative and conventional hydropower plants. Overall, the effects of hydropower on fish were most harmful at sites with conventional Kaplan turbines. However, mortality and injuries observed at different conventional and innovative hydropower plants in this study also indicated that innovative turbine technologies do not necessarily lead to less severe effects on fish, challenging the argument of their 'fish-friendliness'. Species-specific mortalities of up to 58% for European eel, 42% for Danube salmon *Hucho hucho* or 83% for common nase were unexpectedly high and suggest that they can be population threatening, especially considering cumulative effects of multiple consecutive hydropower stations (Larinier, 2008).

European eel mortality at the Kaplan turbines in our study was similar to previously published single-case studies (Calles et al., 2010: 30%; Calles et al., 2012: 67%), but higher than in other peer-reviewed screw turbine studies (Buysse et al., 2015: 14%–19%; Pauwels et al., 2020: 3%). Brown trout mortality at the Kaplan turbines studied herein, ranging from 2% to 30% was either lower or higher compared to previous studies (e.g. Calles & Greenberg, 2009: 11%). For screw turbines, the observed mortalities in our assessment were similar or lower compared to previous studies (Pauwels et al., 2020: screw turbine, 19% mortality of roach and 3% mortality of European eel; Havn et al., 2017: screw turbine, <10% mortality of salmon smolts). However, it has to be noted that our study sites had a lower head compared to, for example, Pauwels et al. (2020) who investigated a screw turbine with 10 m head. Although there are few single-case studies on fish mortality at VLH turbines on species other than eel and salmon smolts, our results indicated a significantly higher mortality risk from this turbine type for some species than is currently known (Lagarrigue, 2013: <4% mortality; Tuononen et al., 2022: <2% mortality).

Generally, strong site- and species-specific effects were observed within the same turbine technology, suggesting that local conditions must be better considered in assessments of hydropower installations. For instance, the conventional hydropower plant at Kaplan site 4, with a comparatively low runner speed of 100 revolutions per minute (RPM) and a 2 m head, caused less mortality than the innovative hydropower plant with a VLH turbine at VLH site 2 with a 3.5–4.0 m head and 39–56 RPM. Previous autonomous sensor measurements to characterise the hydraulic forces during turbine passage, the 'Sensor Fish' (Boys et al., 2018), revealed a higher frequency but lower intensity of collisions at a VLH turbine than at a Kaplan turbine, consistent with our result that the runner peripheral speed and turbine diameter best explained collision-related injuries such as vertebrae fractures. In VLH turbines with variable runner speed, conditions minimising the impact on fish can vary among species. Depending on the species-specific susceptibilities to different physical forces, low runner speed at low-power mostly resulted in fewer injuries, and narrower blade placement often had worse effects, as in Kaplan turbines. In screw turbines, high-power conditions resulted in higher mortality than low-power for most species. This indicates that the development of less harmful hydropower technology should minimise the runner peripheral speed, number of turbine blades and gap size between the turbine and its mounting as well as improve the shape of the turbine blades to reduce blade strike-related injuries. We would have expected pressure-related injuries such as swim bladder anomalies, emboli and haemorrhages to be partly explained by the head drop of the assessed sites. However, none of the explanatory variables investigated in the models herein explained a noteworthy proportion of variance in these injuries. Importantly, pressure-related injuries frequently occurred in physostomous species which are expected to have a low susceptibility (Boys et al., 2016a, 2016b; Brown et al., 2012, 2016), and at hydropower technologies designed to avoid pressure-related injuries (i.e. VLH and screw turbines). Possibly, not all aspects of pressure change are well explained by the variable head drop included in our model. Besides the ratio of pressure change, the rate of pressure change, that is, the quickness of pressure change, can be very challenging for fish (Silva et al., 2018). In addition, the tolerance levels of some Eurasian species may be much lower than expected from laboratory experiments on North American, Australian and Brazilian species (Beirão et al., 2018; Boys et al., 2016a; Brown et al., 2013; Pflugrath et al., 2018, 2019). Furthermore, potential factors other than rapid pressure changes can also lead to injuries as observed in our study, such as gas supersaturation (Cao et al., 2019; Lutz, 1995). Particularly the death of fish without any signs of severe injuries may also have been stress related (Beirão et al., 2018; Brown et al., 2014) and could therefore not be easily explained by any measured parameters. Site-specific characteristics such as head drop, discharge, bypass options and the river-specific species composition should be more intensively considered in planning and approving new and existing hydropower sites. Furthermore, an optimal turbine operation mode should be established by integrating site- and species-specific requirements and knowledge from hydropower-monitoring programmes (Knott et al., 2020), including avoiding low-power operation in Kaplan turbines during peak European eel-migration periods and providing suitable alternative migration corridors, such as undershot sluice gates (Egg et al., 2017).

In conclusion, the findings of this study suggest that the assumption of minimal ecological effects of 'fish-friendly' hydropower does not hold true, particularly considering the comparatively high mortality rates even in innovative technologies. They also suggest that a more critical consideration of adverse effects on fish populations and aquatic ecosystems is needed given the planned expansion of hydropower world-wide. Comparative assessments of fish mortality and injury, as conducted in this study, are the basis for determining animal welfare aspects as well as for a further assessment on population level effects. As a logical next step, the results from this study need to be incorporated in assessments of population level effects of entire fish communities and the habitat (Geist, 2021). A holistic assessment ultimately requires long-term monitoring of cumulative effects of hydropower in relation to other stressors, such as climate change and habitat degradation, in order to reach sustainable conservation targets of aquatic biodiversity.

AUTHORS' CONTRIBUTIONS

M.M., J.P., J.K. and J.G. conceived the ideas and designed methodology; M.M., J.K. and J.P. collected the data; M.M. and J.K. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We are grateful to all staff, students and volunteers who took part in the field experiments and without whose help and endurance such a huge study would not have been possible. Moreover, we thank H. Kliem and S. Kisling for their great support in preparing the application documents for the animal use and care permit, particularly by reviewing the protocols from a veterinary perspective. We also appreciated the careful and thoughtful evaluation of the experimental design by the animal ethics committee of the Bavarian State Government. We further thank Prof. S. Milz and Dr. K. Sternecker for providing their X-ray laboratory and supporting the interpretation of internal injuries. The Bavarian Environmental Agency, the hydropower plant owners, the fisheries rights owners and the fisheries authorities are acknowledged for their great support. This work was supported by the Bavarian State Ministry of the Environment and Consumer Protection [grant number OelB-0270-45821/2014]. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.qv9s4mwhh (Mueller et al., 2022).

ORCID

Melanie Mueller https://orcid.org/0000-0003-2008-6027
Josef Knott https://orcid.org/0000-0003-3472-0228
Joachim Pander https://orcid.org/0000-0002-8322-9374
Juergen Geist https://orcid.org/0000-0001-7698-3443

REFERENCES

Adam, B., Schürmann, M., & Schwevers, U. (2013). *Zum Umgang mit aquatischen Organismen – Versuchstierkundliche Grundlagen*. Springer Spektrum.

Algera, D. A., Rytwinski, T., Taylor, J. J., Bennett, J. R., Smokorowski, K. E., Harrison, P. M., Clarke, K. D., Enders, E. C., Power, M., Bevelhimer, M. S., & Cooke, S. J. (2020). What are the relative risks of mortality and injury for fish during downstream passage at hydroelectric dams in temperate regions? A systematic review. *Environmental Evidence*, *9*, 3.

Anderson, D., Moggridge, H., Warren, P., & Shucksmith, J. (2015). The impacts of 'run-of-river' hydropower on the physical and ecological condition of rivers. *Water Environment Journal*, *29*, 268–276.

Balkhair, K. S., & Rahman, K. U. (2017). Sustainable and economical small-scale and low-head hydropower generation: A promising alternative potential solution for energy generation at local and regional scale. *Applied Energy*, *188*, 378–391.

Baumgartner, L. J., Thorncraft, G., Phonekhampheng, O., Boys, C., Navarro, A., Robinson, W., & Deng, Z. D. (2017). High fluid shear strain causes injury in silver shark: Preliminary implications for Mekong hydropower turbine design. *Fisheries Management and Ecology*, *24*, 193–198.

Beirão, B. V., Silva, L. G. M., Brown, R. S., & Walker, R. W. (2018). Determining barotrauma on the Amazonian catfish, *Pimelodus pictus*, experimentally exposed to simulated rapid decompression occurred in hydropower turbines. *Marine and Freshwater Research*, *69*, 1913–1921.

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., … Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*, 436–441.

Boys, C. A., Pflugrath, B. D., Mueller, M., Pander, J., Deng, Z. D., & Geist, J. (2018). Physical and hydraulic forces experienced by fish passing through three different low-head hydropower turbines. *Marine and Freshwater Research*, *69*, 1934–1944.

Boys, C. A., Robinson, W., Miller, B., Pflugrath, B., Baumgartner, L. J., Navarro, A., Brown, R., & Deng, Z. (2016a). A piecewise regression approach for determining biologically relevant hydraulic thresholds for the protection of fishes at river infrastructure. *Journal of Fish Biology*, *88*, 1677–1692.

Boys, C. A., Robinson, W., Miller, B., Pflugrath, B., Baumgartner, L. J., Navarro, A., Brown, R., & Deng, Z. (2016b). How low can they go when going with the flow? Tolerance of egg and larval fishes to rapid decompression. *Biology Open*, *5*, 786–793.

Brönmark, C., Hulthén, K., Nilsson, P. A., Skov, C., Hansson, L. A., Brodersen, J., & Chapman, B. B. (2014). There and back again: Migration in freshwater fishes. *Canadian Journal of Zoology*, *92*, 467–479.

Brown, R. S., Colotelo, A. H., Pflugrath, B. D., Boys, C. A., Baumgartner, L. J., Deng, Z. D., Silva, L. G. M., Brauner, C. J., Mallen-Cooper, M., Phonekhampeng, O., Thorncraft, G., & Singhanouvong, D. (2014). Understanding barotrauma in fish passing hydro structures: A global strategy for sustainable development of water resources. *Fisheries*, *39*, 108–122.

Brown, R. S., Cook, K. V., Pflugrath, B. D., Rozeboom, L. L., Johnson, R. C., McLellan, J. G., Linley, T. J., Gao, Y., Baumgartner, L. J., Dowell, F. E., Miller, E. A., & White, T. A. (2013). Vulnerability of larval and juvenile white sturgeon to barotrauma: Can they handle the pressure? *Conservation Physiology*, *1*, cot019.

Brown, R. S., Pflugrath, B. D., Colotelo, A. H., Brauner, C. J., Carlson, T. J., Deng, Z. D., & Seaburg, A. G. (2012). Pathways of barotrauma in juvenile salmonids exposed to simulated hydroturbine passage: Boyle's law vs. Henry's law. *Fisheries Research*, *121–122*, 43–50.

Brown, R. S., Walker, R. W., & Stephenson, J. R. (2016). *A preliminary assessment of barotrauma injuries and acclimation studies for three fish species*. Technical Report PNNL-24720, Pacific Northwest National Laboratory.

Buysse, D., Mouton, A. M., Baeyens, R., & Coeck, J. (2015). Evaluation of downstream migration mitigation actions for eel at an Archimedes screw pump pumping station. *Fisheries Management and Ecology*, *22*, 286–294.

Čada, G. F. (2001). The development of advanced hydroelectric turbines to improve fish passage survival. *Fisheries*, *26*, 14–23.

Calles, O., & Greenberg, L. (2009). Connectivity is a two-way street—The need for a holistic approach to fish passage problems in regulated rivers. *River Research and Applications*, *25*, 1268–1286.

Calles, O., Karlsson, S., Hebrand, M., & Comoglio, C. (2012). Evaluating technical improvements for downstream migrating diadromous fish at a hydroelectric plant. *Ecological Engineering*, *48*, 30–37.

Calles, O., Olsson, I. C., Comoglio, C., Kemp, P. S., Blunden, L., Schmitz, M., & Greenberg, L. A. (2010). Size-dependent mortality of migratory silver eels at a hydropower plant, and implications for escapement to the sea. *Freshwater Biology*, *55*, 2167–2180.

Cao, L., Li, Y., An, R., Wang, Y., Li, K., & Buchmann, K. (2019). Effects of water depth on GBD associated with total dissolved gas supersaturation in Chinese sucker (*Myxocyprinus asiaticus*) in upper Yangtze River. *Scientific Reports*, *9*, 6828.

Costea, G., Pusch, M. T., Bănăduc, D., Cosmoiu, D., & Curtean-Bănăduc, A. (2021). A review of hydropower plants in Romania: Distribution, current knowledge, and their effects on fish in headwater streams. *Renewable and Sustainable Energy Reviews*, *145*, 111003.

Couto, T. B., Messager, M. L., & Olden, J. D. (2021). Safeguarding migratory fish via strategic planning of future small hydropower in Brazil. *Nature Sustainability*, *4*, 409–416.

Deng, Z., Carlson, T. J., Dauble, D. D., & Ploskey, G. R. (2011). Fish passage assessment of an advanced hydropower turbine and conventional turbine using blade-strike modeling. *Energies*, *4*, 57–67.

Dubois, R. B., & Gloss, S. P. (1993). Mortality of juvenile American shad and striped bass passed through Ossberger crossflow turbines at a small-scale hydroelectric site. *North American Journal of Fisheries Management*, *13*, 178–185.

Egg, L., Mueller, M., Pander, J., Knott, J., & Geist, J. (2017). Improving European silver eel (*Anguilla Anguilla*) downstream migration by undershot sluice gate management at a small-scale hydropower plant. *Ecological Engineering*, *106*, 349–357.

European Parliament. (2010). Directive 2010/63/EU of the European Parliament and of the council of 22 September 2010 on the protection of animals used for scientific purposes. *Official Journal of the European Union*, *276*, 33–77.

Fjeldstad, H. P., Pulg, U., & Forseth, T. (2018). Safe two-way migration for salmonids and eel past hydropower structures in Europe: A review and recommendations for best-practice solutions. *Marine and Freshwater Research*, *69*, 1834–1847.

Fu, T., Deng, Z. D., Duncan, J. P., Zhou, D., Carlson, T. J., Johnson, G. E., & Hou, H. (2016). Assessing hydraulic conditions through Francis turbines using an autonomous sensor device. *Renewable Energy*, *99*, 1244–1252.

Garcia de Leaniz, C., Berkhuysen, A., & Belletti, B. (2019). Beware small dams as well as large. *Nature*, *570*, 164.

Geist, J. (2021). Green or red: Challenges for fish and freshwater biodiversity conservation related to hydropower. *Aquatic Conservation*, *31*, 1551–1558.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*, 457–472.

Gibeau, P., Connors, B. M., & Palen, W. J. (2017). Run-of-river hydropower and salmonids: Potential effects and perspective on future research. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 1135–1149.

Gu, Z., Eils, R., & Schlesner, M. (2016). Complex heatmaps reveal patterns and correlations in multidimensional genomic data. *Bioinformatics*, *32*, 2847–2849.

Havn, T. B., Sæther, S. A., Thorstad, E. B., Teichert, M. A. K., Heermann, L., Diserud, O. H., Borcherding, J., Tambets, M., & Økland, F. (2017). Downstream migration of Atlantic salmon smolts past a low head hydropower station equipped with Archimedes screw and Francis turbines. *Ecological Engineering*, *105*, 262–275.

Hogan, T. W., Cada, G. F., & Amaral, S. V. (2013). The status of environmentally enhanced hydropower turbines. *Fisheries*, *39*, 164–172.

Knott, J., Mueller, M., Pander, J., & Geist, J. (2019). Fish passage and injury risk at a surface bypass of a small-scale hydropower plant. *Sustainability*, *11*, 6037.

Knott, J., Mueller, M., Pander, J., & Geist, J. (2020). Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants. *Ecology of Freshwater Fish*, *29*, 74–88.

Lagarrigue, T. (2013). Tests for evaluating damage to fish species migrating downstream during their transit through the VLH hydraulic turbine installed on the Tarn River in Millau – Report on tests run in May and June 2013. Prepared by Etudes et Conseils en Gestion de l'Environnement Aquatique (ECOGEA), Pins-Justaret, France.

Larinier, M. (2008). Fish passage experience at small-scale hydro-electric power plants in France. *Hydrobiologia*, *609*, 97–108.

Lubitz, W. D., Lyons, M., & Simmons, S. (2014). Performance model of Archimedes screw hydro turbines with variable fill level. *Journal of Hydraulic Engineering*, *140*, 04014050.

Lutz, D. S. (1995). Gas supersaturation and gas bubble trauma in fish downstream from a midwestern reservoir. *Transactions of the American Fisheries Society*, *124*, 423–436.

Markin, V. V., Kiselev, N. P., & Kmotrikov, N. I. (2020). Mini, micro, and small hydropower plants are returning to the market. *Power Technology and Engineering*, *54*, 494–499.

Mueller, M., Knott, J., Pander, J., & Geist, J. (2022). Data from: Experimental comparison of fish mortality and injuries at innovative and conventional small hydropower plants. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.qv9s4mwhh

Mueller, M., Pander, J., & Geist, J. (2017). Evaluation of external fish injury caused by hydropower plants based on a novel field-based protocol. *Fisheries Management and Ecology*, *24*, 240–255.

Mueller, M., Sternecker, K., Milz, S., & Geist, J. (2020). Assessing turbine passage effects on internal fish injury and delayed mortality using X-ray imaging. *PeerJ*, *8*, e9977.

Nuernbergk, D. M., & Rorres, C. (2013). Analytical model for water inflow of an Archimedes screw used in hydropower generation. *Journal of Hydraulic Engineering*, *139*, 213–220.

Ovaskainen, O., & Abrego, N. (2020). *Joint species distribution modelling: With applications in R*. Ecology, Biodiversity and Conservation, Cambridge University Press.

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*, 561–576.

Pander, J., Mueller, M., Knott, J., & Geist, J. (2018). Catch-related fish injury and catch efficiency of stow-net-based fish recovery installations for fish-monitoring at hydropower plants. *Fisheries Management and Ecology*, *25*, 31–43.

Pauwels, I. S., Baeyens, R., Toming, G., Schneider, M., Buysse, D., Coeck, J., & Tuhtan, J. A. (2020). Multi-species assessment of injury, mortality, and physical conditions during downstream passage through a large Archimedes hydrodynamic screw (Albert Canal, Belgium). *Sustainability*, *12*, 8722.

Pflugrath, B. D., Boys, C. A., & Cathers, B. (2018). Predicting hydraulic structure-induced barotrauma in Australian fish species. *Marine and Freshwater Research*, *69*, 1954–1961.

Pflugrath, B. D., Harnish, R., Rhode, B., Beirão, B., Engbrecht, K., Stephenson, J. R., & Colotelo, A. H. (2019). American eel state of buoyancy and barotrauma susceptibility associated with hydroturbine passage. *Knowledge and Management of Aquatic Ecosystems*, *420*, 20.

Silva, L. G., Beirão, B. V., Falcão, R. C., De Castro, A. L., & Dias, E. W. (2018). It's a catfish! Novel approaches are needed to study the effects of rapid decompression on benthic species. *Marine and Freshwater Research*, *69*, 1922–1933.

Thorstad, E. B., Havn, T. B., Sæther, S. A., Heermann, L., Teichert, M. A. K., Diserud, O. H., Tambets, M., Borcherding, J., & Økland, F. (2017). Survival and behaviour of Atlantic salmon smolts passing a run-of-river hydropower facility with a movable bulb turbine. *Fisheries Management and Ecology*, *24*, 199–207.

Tikhonov, G., Duan, L., Abrego, N., Newell, G., White, M., Dunson, D., & Ovaskainen, O. (2020). Computationally efficient joint species distribution modeling of big spatial data. *Ecology*, *101*, e02929.

Tuononen, E. I., Cooke, S. J., Timusk, E. R., & Smokorowski, K. E. (2022). Extent of injury and mortality arising from entrainment of fish through a very low head hydropower turbine in Central Ontario, Canada. *Hydrobiologia*, *849*, 407–420.

Ujwala, M., Chowdary, C. K., & Srinivas Naik, L. (2017). Design and analysis of low head, light weight Kaplan turbine blade. *International Refereed Journal of Engineering and Science*, *6*, 17–25.

Vikström, L., Leonardsson, K., Leander, J., Shry, S., Calles, O., & Hellström, G. (2020). Validation of Francis–Kaplan turbine blade strike models for adult and juvenile Atlantic salmon (*Salmo salar*, L.) and anadromous brown trout (*Salmo trutta*, L.) passing high head turbines. *Sustainability*, *12*, 6384.

Wright, M. K., & Rival, D. E. (2013). An experimental investigation of the approach flow conditions for a non-rotating, very low head water-turbine model. *Experimental Thermal and Fluid Science*, *49*, 105–113.

Zarfl, C., Berlekamp, J., He, F., Jähnig, S. C., Darwall, W., & Tockner, K. (2019). Future large hydropower dams impact global freshwater megafauna. *Scientific Reports*, *9*, 18531.

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, *77*, 161–170.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Mueller, M., Knott, J., Pander, J., & Geist, J. (2022). Experimental comparison of fish mortality and injuries at innovative and conventional small hydropower plants. *Journal of Applied Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2664.14236