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Evident but context-dependent mortality of fish passing hydroelectric turbines

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Article impact statement Downside of green hydroelectricity—detrimental impacts of hydropower on fish needs careful assessment, quantification, and mitigation.

Abstract

Globally, policies aiming for conservation of species, free-flowing rivers, and promotion of hydroelectricity as renewable energy and as a means to decarbonize energy systems generate trade-offs between protecting freshwater fauna and development of hydropower. Hydroelectric turbines put fish at risk of severe injury during passage. Therefore, comprehensive, reliable analyses of turbine-induced fish mortality are pivotal to support an informed debate on the sustainability of hydropower (i.e., how much a society is willing to pay in terms of costs incurred on rivers and their biota). We compiled and examined a comprehensive, global data set of turbine fish-mortality assessments involving >275,000 individual fish of 75 species to estimate mortality across turbine types and fish species. Average fish mortality from hydroelectric turbines was 22.3% (95% CI 17.5–26.7%) when accounting for common uncertainties related to empirical estimates (e.g., handling- or catch-related effects). Mortality estimates were highly variable among and within different turbine types, study methods, and taxa. Technical configurations of hydroelectric turbines that successfully reduce fish mortality and fish-protective hydropower operation as a global standard could balance the need for renewable energy with protection of fish biodiversity.

KEYWORDS
downstream passage, freshwater fish, hydropower, mortality, river

Mortalidad evidente, pero dependiente del contexto, de peces que pasan por turbinas hidroeléctricas

Resumen: Globalmente, las políticas que buscan la conservación de especies, el flujo libre de ríos y la promoción de la hidroeléctrica como una energía renovable y como un medio para reducir el carbono en sistemas de energía generan pros y contras entre la protección de la fauna de agua dulce y el desarrollo de la hidroeléctrica. Las turbinas hidroeléctricas ponen a los peces en riesgo de heridas severas al pasar por ellas. Por lo tanto, análisis integrales, confiables de la mortalidad de peces inducida por turbinas son esenciales para sustentar un debate informado de la sustentabilidad de la energía hidroeléctrica (i. e., que tan dispuesta esta una sociedad para pagar en términos de costos incurridos en los ríos y su biota). Compilamos y examinamos un conjunto de datos integrales, globales de evaluaciones de mortalidad de peces en turbinas involucrando >275,000 peces individuales de 75 especies para estimar la mortalidad en tipos de turbinas y especies de peces. La mortalidad promedio de peces en turbinas hidroeléctricas fue 22.3% (95% IC 17.5-26.7%) cuando se consideraron incertidumbres comunes relacionadas con las estimaciones empíricas (e. g., efectos relacionados con el manejo o captura). Las estimaciones de mortalidad fueron muy variables entre y dentro de los diferentes tipos de turbinas, métodos de estudio y taxones. Las configuraciones

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técnicas de las turbinas hidroeléctricas que exitosamente reduzcan la mortalidad de peces y proporcionen una operación protectora de peces como un estándar global podrían equilibrar la necesidad de energía renovable con la protección de la biodiversidad de peces.

PALABRAS CLAVE
Hidroeléctrica, mortalidad, paso río abajo, paso río abajo, peces de agua dulce, río

鱼类通过水电涡轮机时存在明显的但与环境相关的死亡现象

【摘要】在全球范围内, 旨在保护物种、促进河流自由流动, 以及促进水电作为可再生能源及作为能源系统碳减排方法的政策在保护淡水动物和开发水电之间存在着利弊权衡。鱼类在通过水电涡轮机时面临受到严重伤害的风险。因此, 对水电涡轮机引起的鱼类死亡情况进行全面、可靠的分析, 对于支持关于水电可持续性的基于知识的辩论(即社会愿意为河流及其生物群落付出多少成本)至关重要。我们整理并分析了一个全面的全球涡轮机导致鱼类死亡的评估数据集, 涉及75种鱼类超过275,000条个体, o以估计不同类型的涡轮机引起的不同鱼类物种的死亡率。我们将经验估计中常见的不确定性(如处理或捕鱼相关的影响)纳入考虑, 发现水电涡轮机导致的鱼类平均死亡率为22.3%(95%CI为17.5-26.7)。不同涡轮机类型、研究方法, 以及鱼类类群组内和组间的鱼类死亡率估计值都有很大差异。我们建议将成功降低鱼类死亡率并能为鱼类提供保护的水电装置作为全球水电涡轮机的标准技术配置, 以平衡对可再生能源的需求与对鱼类生物多样性的保护。**【翻译: 胡怡思;审校:聂永刚】**

关键词: 下游鱼道, 淡水鱼类, 水电, 死亡率, 河流

INTRODUCTION

To reduce dependency on fossil fuels, construction of hydropower plants (HPPs) has boomed (Hudek et al., 2020; Winemiller et al., 2016; Zarfl et al., 2015). As of 2019, about 16% of the global gross electricity production originated from hydropower (International Energy Agency, 2020), with countries like Norway, Austria, and Switzerland covering 93%, 60%, and 56% of their electricity production from hydropower, respectively (based on data from 2019) (International Energy Agency, 2021).

Manifold impacts of hydropower have been highlighted (Gibson et al., 2017; Reid et al., 2019; Winemiller et al., 2016) that relate to alterations of flow regimes (Young et al., 2011), sediment transport and river morphology (Hauer et al., 2018; Petts & Gurnell, 2005), alterations and loss of habitats to impoundments (Baxter, 1977; Birnie-Gauvin et al., 2017; Schmutz & Moog, 2018), greenhouse-gas emissions (Duchemin et al., 1995; Fearnside & Pueyo, 2012), up- and downstream migration barriers (Fuller et al., 2015; Noonan et al., 2012), and diverse socioeconomic impacts (Moran et al., 2018). The severe injury risks to fish in hydroelectric turbines have been a persistent focus in hydropower impacts research (Montén, 1985; Mueller et al., 2017; Von Raben, 1957).

Fish might get injured due to abrupt pressure changes, cavitation, shear forces and turbulence, and, most obviously, mechanical contact with the turbine (e.g., blade strike) (Coutant & Whitney, 2000; Pracheil et al., 2016). Injuries involve scale loss, bruising, emboli, and amputation of body parts, and death may ensue (Mueller et al., 2017). The severity of injuries primarily depends on turbine type and technical characteristics in relation to fish. For example, the collision risk of fish of a given length is related to rotational speed and spacing between turbine blades (Deng et al., 2007). This is further complicated by varying turbine entrance points and swimming behavior, both introducing inherent stochasticity and uncertainties associated with mortality estimates. Mortality rates might be overestimated due to injuries that occurred before turbine entrance, detrimental sampling methods and fish handling, or other sources of injuries not related to turbine passage (Mueller et al., 2017; Pander et al., 2018). Mortality rates might also be underestimated due to less obvious (e.g., internal, Mueller et al., 2020) injuries that cause delayed mortality (Ferguson et al., 2006). In addition, in small samples, the effect of false positives or negatives (i.e., misclassification of fish into lethal vs. sublethal) on the mortality estimate is larger than it is in large samples. However, compared with physical models (Deng et al., 2007; Montén, 1985) or in situ experiments involving sensor devices (Carlson & Duncan, 2003; Deng et al., 2014), the empirical on-site assessment of mortality rates provides the most reasonable real-life estimates because it implicitly accounts for differences in (swimming) behavior (Pracheil et al., 2016), swimming performance, body size and shape, and resistance to injuries between species, life stages, and individuals. Because of the high variability of empirical estimates of fish mortality associated with turbines among and within species and turbine types, neither meaningful cross-site comparisons have been made nor straightforward general conclusions drawn. The latter is essential to support an informed choice on the sustainability of hydropower. That is, how much is a society willing to pay in terms of costs incurred on rivers and to improve hydropower operations to reduce impacts on the environment and fauna. This question is highly timely in light of the planned diversification of hydropower in all megadiverse, large river systems, such as the Amazon, Congo, and

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Mekong (Reid et al., 2019; Winemiller et al., 2016; Zarfl et al., 2015).

We conducted the first comprehensive analysis of a large, global data set on fish mortality due to hydroelectric turbines to synthesize observed mortality estimates across turbine types and fish species while accounting for associated uncertainties (e.g., related to handling or catch-related effects); identify species and turbine types that are less studied or are associated with inconsistent mortality rates; and stress challenges to the assessment and importance of hydropower-induced fish mortality and its larger-scale implications in light of sustainable hydropower operation.

METHODS

Data acquisition

Data on turbine-related mortality were retrieved from peer-reviewed and grey literature via literature searches in Web of Science and Google Scholar. The literature search was based on established methods used for structured reviews (e.g., Algera et al., 2020). Details on the search strings and keywords, the article screening process, and article eligibility criteria are in Appendix S1. Articles retrieved from bibliographic databases were complemented by assessment reports of turbine-related injuries at (mostly) German HPP locations that had been partly provided by the *Forum Fischschutz & Fischabstieg* (Forum Fish Protection and Downstream Fish Migration) (Appendix S1).

Assessments of turbine-related injuries and mortality are frequently commissioned by operators of HPPs, regional or federal angling and fishing associations, and public authorities. Along with the different objectives, the methods to evaluate turbine-related injuries under field conditions varied among studies. Assessments ranged from counting killed fish only to determining different categories of severity of injuries or describing specific injury types (Mueller et al., 2017). We included only studies in which fish mortality associated with turbines was assessed based on naturally downstream moving wild fish and on live test fish purposely introduced upstream from a turbine. Studies with anaesthetized or dead dummy or sensor fish and laboratory studies were excluded. For field assessments, fish were commonly sampled with stow nets or similar netting techniques (e.g., Janac et al., 2013; Mueller et al., 2017; Pander et al., 2018) in the tail water of the HPP. However, we also considered radio telemetry (e.g., Calles et al., 2010; Kärgenberg et al., 2020) and balloon tagging (e.g., Heisey et al., 2019; Tuononen et al., 2020) methods. The turbine-related mortality estimates used here generally referred to direct mortality; thus, specific indirect effects, such as predation after turbine passage, were usually not included. Some studies reported several assessments of the same HPP over multiple years or under varying flow rates. We generally treated these separately.

Mortality data typically consisted of reported lethal and sublethal injuries and death counts, often based on categories of severity (Mueller et al., 2017). Most studies used five severity classes: no obvious external injuries (class 1); scale losses or minimal dermal lesions or bruises (2); externally visible deformation of the spinal column, obvious wounds, and bruises (3); partial amputation or detachment of body parts (4); and complete transection of the body (5). We reclassified data into the two general categories *sublethal* and *lethal* because not all studies reported detailed injury categories or those reported were not always directly comparable. The category *sublethal* included all fish that were originally classified as alive and not injured or as alive and showing only minor injuries (e.g., punctual scale losses, minimal dermal abrasions, classes 1–2). The category *lethal* included reportedly dead and medium to severely injured fish (classes 3–5). Consequently, fish of the *lethal* category might have been alive after turbine passage; however, their severe injury was considered ultimately lethal. Fish with considerable internal injuries (e.g., identified via transillumination, X-ray, or surgery) that became obvious during postexposure monitoring were also assigned to the *lethal* category.

We calculated mortality rates based on the relationship between the number or percentage of lethally injured fish and the total number of investigated fish for a given case. We considered each species in each experiment a case (i.e., data point).

For each case, we retrieved mean, minimum, and maximum body length of the investigated fish. If the original study provided length–frequency relationships, the mean fish length per case was used as reported or calculated. If only a range was reported, the mean length was calculated as the average of minimum and maximum. Mean lengths were reported in 884 cases; length range was 1.5–102 cm (mean = 19.6 cm, median = 12 cm).

Besides biological data, we also obtained information on sampling method, geographical location, mean discharge of the river, and technical HPP parameters. The latter included the number and types of turbines (e.g., Kaplan or similar propeller-type turbines, Francis turbines, cross-flow turbines [e.g., Ossberger], water wheel, Archimedes' screw, or other type [e.g., hydrostatic pressure machine and Pelton turbines]), hydraulic head, turbine diameter, number of blades, rotational speed, and flow rate. Technical turbine data were retrieved from the original studies or additional sources (e.g., HPP operators) wherever possible. We distinguished among four categories of sampling methods: netting (e.g., stow nets and drift nets), balloon tagging (i.e., inflatable devices to recover fish), hydroacoustic telemetry, and other. The latter category applied to two experiments, one that applied electrofishing in the tailrace and another that applied a combination of methods (netting and diving) for which mortality estimates could not be assigned to a single method. We further considered the specific experiment at a given location because some studies repeatedly investigated mortality at the same HPP under different configurations (e.g., different flow rates). Finally, we retrieved information about the total generating capacity as an estimate of the overall scale of the HPP. In cases where generating capacity of an HPP was neither reported nor available from other sources, it was approximated from maximum turbine flow × hydraulic head × 8.5 (Gulliver & Arndt, 1991). Each HPP was categorized as large hydropower (LHP) (≥10 MW), small hydropower (SHP) (1 <10 MW), or very small hydropower (vSHP) (<1 MW).

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Statistical analyses and accounting for uncertainties

We used alluvial diagrams (R package flipPlots, version 1.2.0) (Displayr, 2020) to visually describe observed relationships between taxonomic order, hydropower scale, and turbine types and lethal versus sublethal effects on fish. Alluvial diagrams are flow diagrams used to visualize connections between groups as bands. The widths of bands were proportional to the number of fish. We used the bias-corrected Cramér's V (R package rcompanion, version 2.3.25) (Mangiafico, 2020) and analyses of contingency tables with a bootstrap correction for multiple testing (ACT) (García-Pérez et al., 2015) to investigate two-way association patterns between turbine type, hydropower scale, and taxonomic family (excluding families with <5 experiments). Cramér's V measures the association between two discrete variables and varies from 0 to 1; 1 indicates complete association (Mangiafico, 2016). We used the ACT for subsequent cell-wise adjusted residual analysis (50,000 bootstrap replicates) to determine taxonomic families that were over- versus understudied at a particular turbine type.

Triangular distributions, described by a lower limit a, an upper limit b, and the mode c, with $a<b$ and $a\leq c\leq b$ (Forbes et al., 2011), were used to account for uncertainty. This simple probability distribution is commonly used in simulation studies to account for uncertainty around a most likely value (Johnson, 1997). For each case, the originally reported mortality rate was used to define parameter c of the respective distribution. Depending on the data, sampling procedure, and sample size in the original study, we arbitrarily set the limits a and b at 0%, 12.5%, or 25% lower or higher than the mode c (Appendix S2). Highest uncertainty (lower and upper limits ±25%; corresponding to approximately 1 sample SD across all cases) was assigned to the least reliable cases with a very low sample size (n<10 individuals), those lacking postexposure monitoring in tanks and assessment of internal injuries and not accounting for handling and sampling-related mortality. The assigned lower and upper uncertainty levels were rather conservative estimates within the range of previously reported effects of handling and catch-related mortality (Mueller et al., 2017; Pander et al., 2018) or delayed mortality (Ferguson et al., 2006; Mueller et al., 2020).

Bootstrap samples were obtained by resampling entire cases from our original data set with replacement and with respect to hierarchical clusters (cases or species nested within experiments) (Leeden et al., 2008), a procedure adapted from the R package lmeresampler (Loy & Steele, 2020). For each bootstrap sample and each case, the mortality rate was randomly selected from the respective triangular distribution. We calculated the 95% CI (percentile method) of the mean mortality rate over all individuals (i.e., abundance-weighted mean) based on 10,000 bootstrap replicates (Carpenter & Bithell, 2000). Analogously, we calculated mean mortality rates and corresponding 95% CI for single generating capacity classes, turbine types, taxonomic orders, families, and species. Mean mortality and its 95% CI were also calculated separately for the single classes of uncertainty to reveal mean mortalities of studies that corrected for handling effects. Furthermore, we created violin plots (adapted from the R package vioplot) (Adler & Kelly, 2019) of the original data and 100 bootstrap samples to visualize the variability of observed mortality rates among the most frequently studied orders and species.

We applied generalized linear mixed models (GLMM) (Bolker et al., 2009) to explore relationships between mortality rates (binomial model, logit link) and turbine type, fish length, sampling method, and HPP generating capacity class as fixed effects in the R package lme4 (version 1.1-27.1) (Bates et al., 2015). Models were fitted with nested random effects (intercepts) for experiment within location (1 | location/experiment) and species within family (1 | family/species). An observation-level random effect (1 | case) was included to account for overdispersion (Harrison, 2014). For the most inclusive models, we specified interaction terms between turbine type × fish length. The GLMMs were calculated using complete cases of the original data set with available length estimates for the six most studied turbine types Kaplan, Francis, Cross-flow, VLH, Archimedes' screw, and water wheel. Two experiments with sampling methods other than netting, balloon tags and telemetry, were not considered in the GLMMs. In all GLMMs, the response (i.e., mortality rate) was specified as a two-column matrix giving the number of lethal and sublethal individuals per case. Fish length was scaled by dividing it by the overall mean. Fitted models were compared with a likelihood ratio test (R function anova). The selected model was then repeatedly (n = 10,000) recalculated applying the outlined nonparametric bootstrapping to obtain parameter estimates while accounting for within and between case variability and uncertainty. In addition to a random selection of the mortality rate from the triangular distributions, the fish length estimate was resampled from a triangular distribution (a and b = minimum and maximum reported length, c = mean reported length) for each bootstrap sample and case. From the 10,000 bootstrap GLMM replicates, we calculated the 95% CI (percentile method) of the parameter estimates (Carpenter & Bithell, 2000). This allowed inferring the effects of turbine type and fish length on turbine-induced mortality under uncertainty. Finally, we used the bootstrap-framework to obtain the 95% CI band around model predictions of mean mortality rates for different turbine types and generic fish body lengths from 1 to 105 cm.

All statistical analyses were performed in the software R, version 4.1.1 (R Core Team, 2021). All data sets and computer code we used are publicly available from Zenodo/Github at https://doi.org/10.5281/zenodo.5749725.

RESULTS

Data set of assessments of turbine-induced fish mortality

Our data set contained 1058 turbine-related mortality assessments (i.e., cases) (experiments × species) obtained from 249 experiments reported in 91 studies. Mortality assessments were

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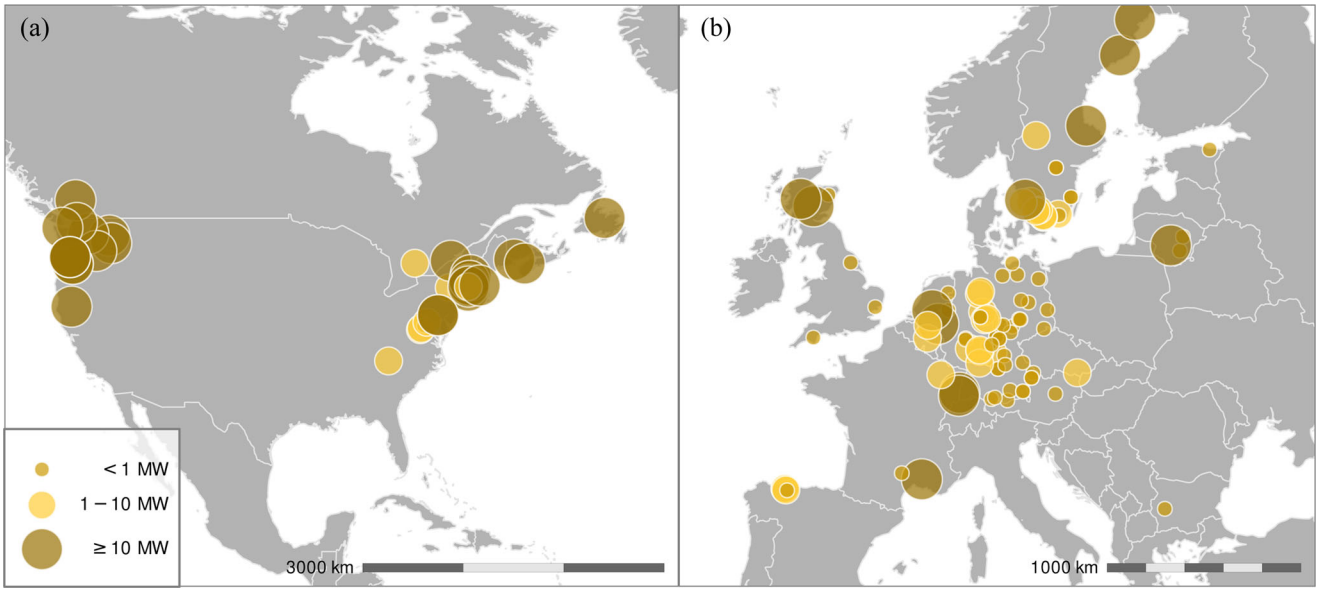

FIGURE 1 Distribution of analyzed studies on fish mortality induced by hydroelectric turbines across (a) North America (n = 93 locations) and (b) Europe (n = 155) and Oceania (n = 1) (small hydropower plant in New Zealand not displayed) differentiated according to total generating capacity installed

conducted at 122 locations in 15 countries worldwide (vSHP, n = 83 experiments; SHP, n = 53; and LHP, n = 113) (Figure 1). Turbine types included Kaplan (n = 119 experiments), Francis (n = 72), very low head turbines (VLH) (n = 15), Archimedes' screws (n = 22), water wheels (n = 11), cross-flow turbines (n = 5), and other turbine types (e.g., hydrostatic pressure machine and Pelton turbine) (n = 5). The most frequently applied sampling method was netting (predominately stow nets) (n = 179 experiments), followed by balloon tags (n = 38), telemetry (n = 30), and other sampling methods (n = 2). The data provided 276,890 individuals of 75 species in 27 families and 15 orders that were assessed for turbine-related injuries and mortality (Figure 2 & Appendix S3).

Among all studies, species, and settings, on average 22.3% (n = 61,797 individuals) of all fish passing through turbines got killed or showed severe, potentially lethal injuries. The remaining 77.7% (n = 215,093 individuals) were assessed as unharmed or sublethally injured in the original studies (Figure 2).

Context dependency of fish mortality due to turbines and uncertainties

Field-based mortality rates were considered uncertain estimates that might deviate from the true (unknown) mortality rates resulting from turbines at a given location (Appendix S2). For example, mortality estimates were explicitly corrected for handling- and catch-related effects with control groups in 21% of all 1058 cases. Forty-seven percent applied methods to minimize potential handling and sampling effects, but did not explicitly correct data. In about 42% of the cases, postexposure monitoring of delayed effects took place or an assessment of internal injuries was conducted, whereas 31% assessed only visible or obvious injuries without postexposure monitoring. Consequently, we described mortality rates as triangular probability distributions (Johnson, 1997) to explicitly account for uncertainties associated with data, method, and sample size of the original study (Appendix S2). We applied bootstrapping to resample a mortality rate for each case from the respective triangular distribution to account for bias and variance of the original data.

Reported on-site mortality rates were highly variable among and within taxonomic orders and species and ranged from 0 fish lethally harmed to 100% mortality (Figures 3 & 4). Based on bootstrapping, the 95% CI of the mean mortality rate (22.3%) over all individuals was estimated at 17.5–26.7%. When considering only data associated with low uncertainty (i.e., studies accounting for handling and catch-related mortality and conducting comprehensive postexposure monitoring [Appendix S2]), mean mortality rate was 20.2% (95% CI 12.4–30.4%) (Appendix S4). Largest and lowest species-specific mean mortalities (across studies and for species investigated in more than 10 experiments) occurred with common bream (*Abramis brama*) (53%, 95% CI 18–65%) and stone loach (*Barbatula barbatula*) (2%, 95% CI 0–14%), respectively (Figure 4 & Appendix S4).

The GLMM, including fish length and turbine type and their interaction, as well as sampling method and capacity class performed better than alternative models (likelihood ratio test, $\chi^2(2) = 7.79$, $p = 0.02$) (Appendix S5). Differences in mean mortality at vSHP (20%, 95% CI 11–32%), SHP (22%, 95% CI 15–29%), and LHP (24%, 95% CI 19–29%) were rather small. However, at LHP, odds for lethal effects were marginally but statistically significantly higher when accounting for turbine type, fish length, and sampling method compared with other HPP-generating capacity classes. Compared with net-based sampling methods, balloon-tag studies showed lower

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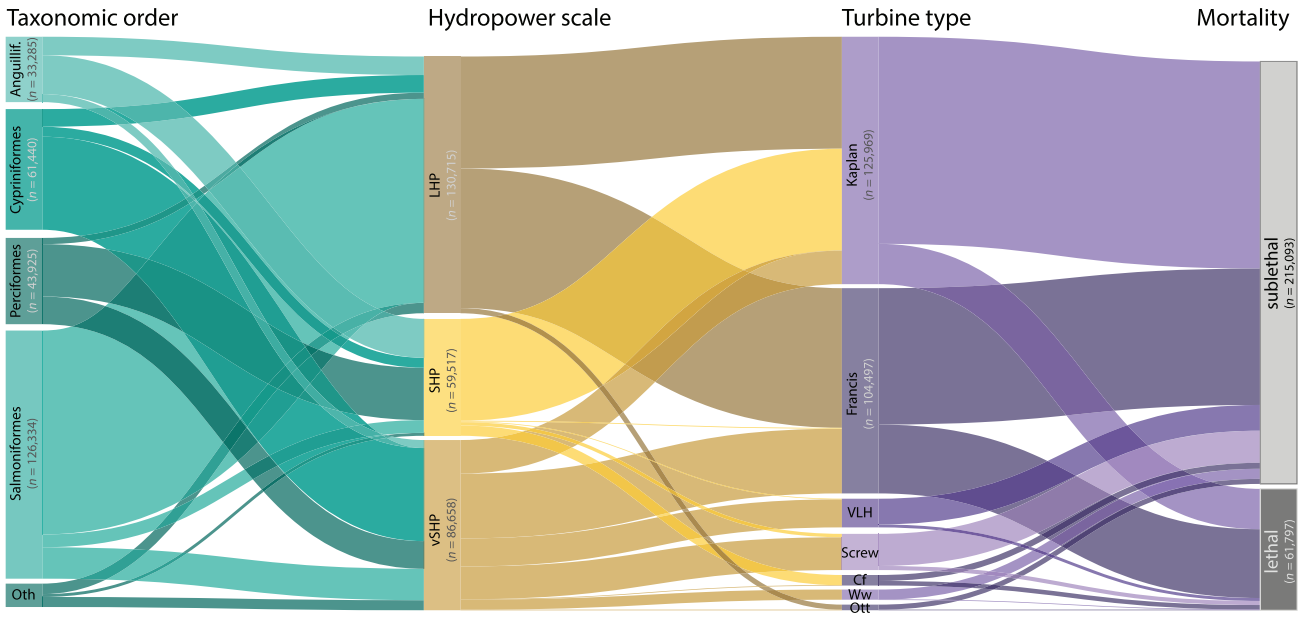

FIGURE 2 Relations among taxonomic order, hydropower scale, turbine type, and mortality in assessments of fish mortality in hydroelectric turbines (Oth, other fish orders $n = 11{,}906$; VLH, very low head turbine $n = 14{,}598$; screw, Archimedes' screw $n = 18{,}427$; Ww, water wheel $n = 5178$; Cf, cross-flow turbine $n = 5359$; Ott, other turbine type $n = 2862$). Widths of bands are proportional to the number of individuals. Hydropower scale refers to the generating capacity of a hydropower plant (vSHP, very small hydropower of < 1 MW; SHP, small hydropower of 1 < 10 MW; and LHP, large hydropower of ≥10 MW). Numbers of fish are provided only for groups of >20,000 individuals

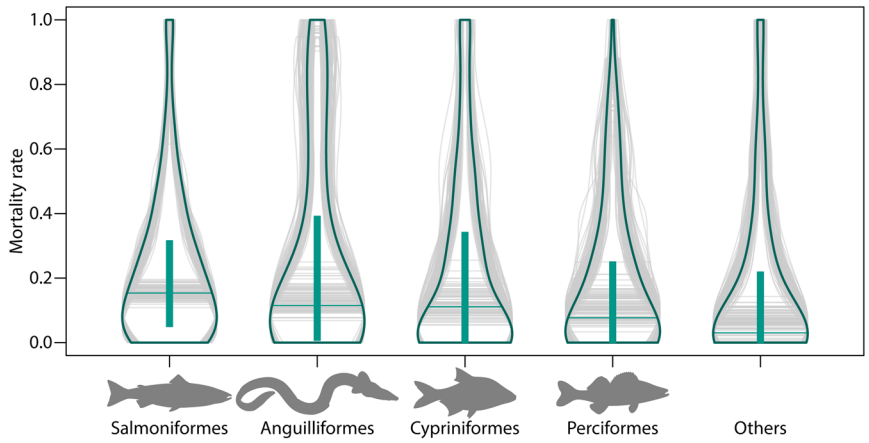

FIGURE 3 Observed fish mortality rates at hydroelectric turbines across orders of fishes in 249 experiments reported in 91 studies (vertical lines, interquartile range between first and third quartiles; horizontal lines, median; violins, distributions of the data as originally reported; shading, taxon-specific distributions of 100 bootstrap replicates of the data set with uncertainties associated with mortality data)

mortality rates (Appendix S5). While considering between- and within-case uncertainties, significant effects were found for fish length and turbine type water wheel (Appendix S5). The odds for lethal effects generally increased with fish length. The odds for lethal effects at water wheels were clearly lower compared with those in Kaplan turbines. For Kaplan turbines, a 10-cm increase in fish length (rescaled to 0.51) yielded a 43% (exp[0.70*0.51] = 1.43) and 56% increase (exp[0.87*0.51] = 1.56) in the odds of lethal turbine effects estimated from the models excluding versus including effects of generating capacity class and sampling method, respectively (Appendix S5). The interaction of fish length × turbine type was negative for Archimedes' screw and VLH turbines (Appendix S5). A 10-cm increase in fish length yielded about a 50% decrease (exp[{0.70–1.93}*0.51] = 0.53) in the odds of lethal passage at an Archimedes' screw. For a 25-cm-long fish, the 95% CIs of mean mortality were as follows: Kaplan turbines, 11–22%; Francis turbines, 10–27%; VLH turbines, 1–6%; Archimedes' screws, 2–8%; cross-flow turbines, 49–99%; and water wheels, 0–5% (Figure 5) when excluding effects of HPP generating capacity class and sampling method. The interactive effects of turbine type and fish length on mean mortality rates and their bootstrapped confidence bands are illustrated in Figure 5.

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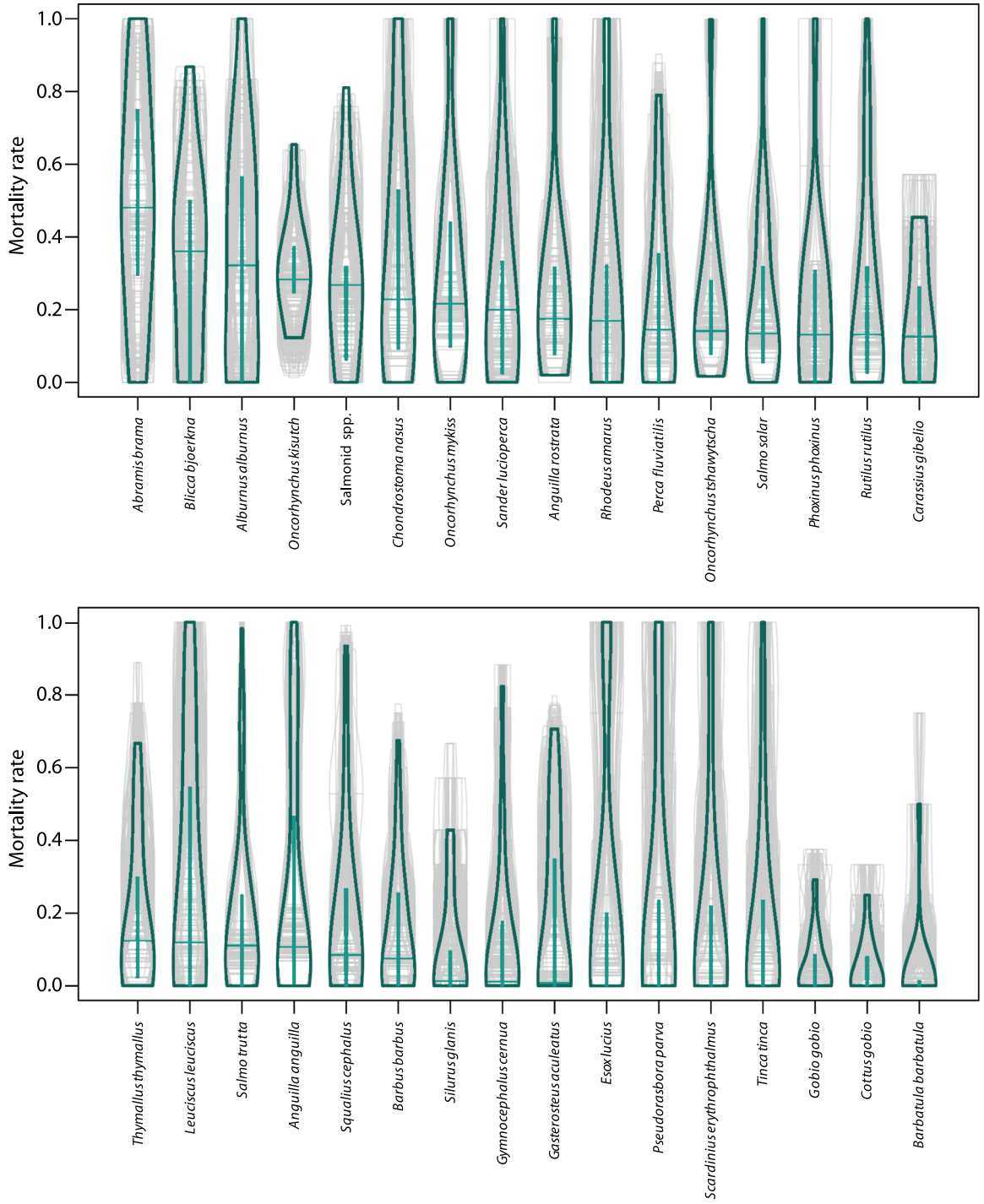

FIGURE 4 Observed fish mortality rates at hydroelectric turbines across fish species in 249 experiments reported in 91 studies (vertical lines, interquartile range between the first and third quartiles; horizontal lines, median; violins, distributions of the data as originally reported; shading species-specific distributions of 100 bootstrap replicates of the data set with uncertainties associated with mortality data). Only species with >10 assessments are shown

DISCUSSION

Significance of turbine-associated fish mortality and persisting knowledge gaps

Based on the assessment of >275,000 individual fish of 75 species, we evidentially demonstrated the deadly impacts of various hydroelectric turbines on passing fish. On average among all studies, species, and settings and under explicit consideration of uncertainties, from 17.5% to 26.7% (CI) of all fish were killed or showed severe, potentially lethal injuries. It is essential to view this rate in context of the large and increasing number of HPPs to comprehend its significance and to recognize the full extent of turbine impacts on fish. Considering the >21,000

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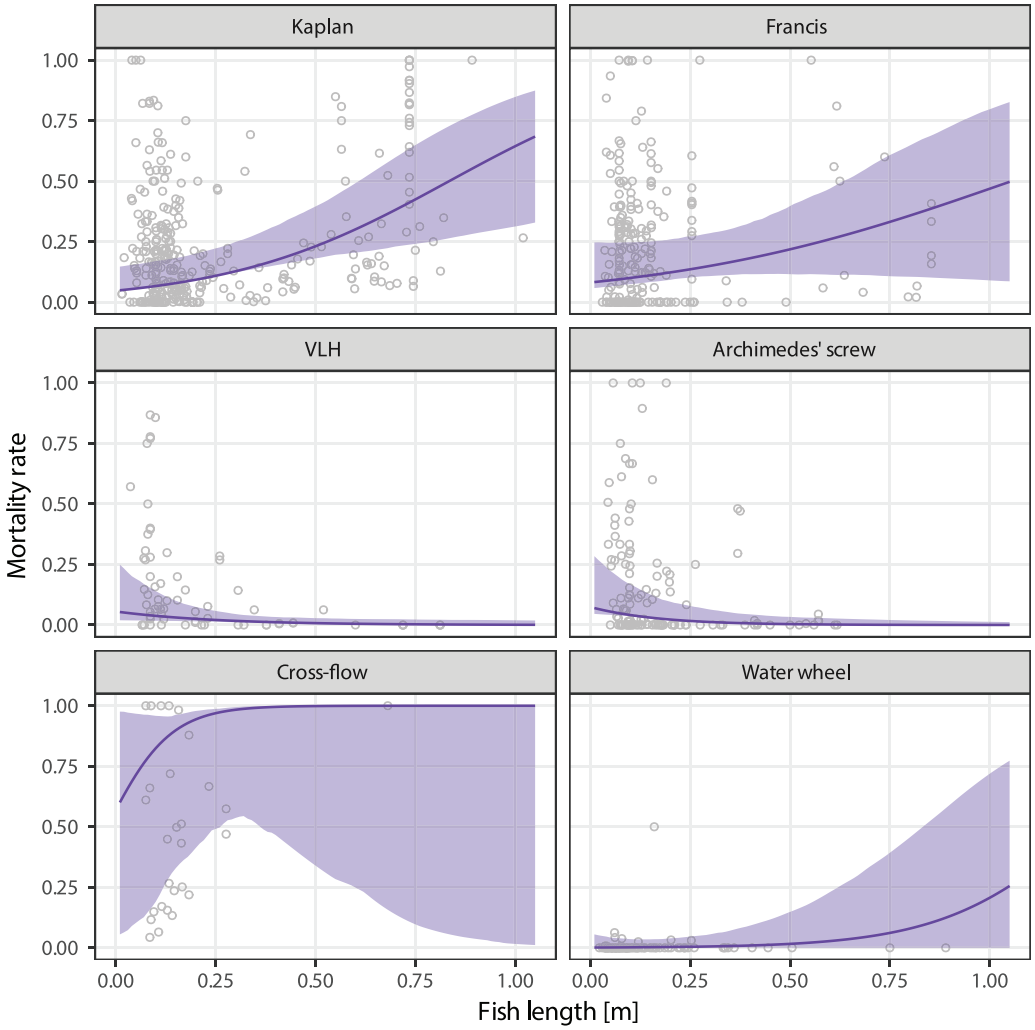

FIGURE 5 Relationship between fish length and mean mortality rate across the six main turbine types (lines, predicted mean effects based on a generalized linear mixed model with an interaction term of turbine type × fish length; shading, 95% confidence bands of the mean based on 10,000 bootstrap replicates [i.e., confidence level of the mean]; points, specific mortality rates for a given fish length and turbine type [may be outside the confidence bands of the mean])

HPPs operational in Europe (additional >8500 are planned), of which many are small-scale (Schwarz, 2019) and negligibly contribute to renewable electricity production (ARCADIS & Ingenieurbüro Floecksmühle, 2011), an average 22% mortality will unquestionably affect fish stocks. This is particularly critical for diadromous fish, for which entire cohorts of juveniles or spawners need to migrate downstream. In addition, large portions of populations of potamodromous fish may need to pass HPPs given their long migrations (some over hundreds of kilometers). For facultatively migrating river fish, the share of the population that might pass an HPP is difficult to estimate. However, with regard to species conservation, the precautionary approach should be widely applied. In addition, rivers are often fragmented by sequences of HPPs. Thus, the cumulative impact of consecutive HPPs on the same fish population is substantially larger (Bracken & Lucas, 2013; Coutant & Whitney, 2000; Fraser et al., 2015).

Although not deliberately being geographically restricted, our literature search retrieved turbine assessments only from the temperate region of the Global North (Europe and North America), a feature shared with many biological monitoring programs (Radinger et al., 2019). Despite this, our findings and conclusions are of broad applicability because turbine types investigated and scales of large, small, and very small HPPs covered are comparable with those in other regions and our consideration of entire fish assemblages provides a more representative picture for a broader variety of taxa. However, we note that accessing on-site reports of fish mortality induced by turbines is difficult. Given that probably more HPPs have been investigated than reports are publicly available, their mortality estimates may be even higher. The general mechanisms causing injuries during turbine passage might be similar across species; however, specific responses usually differ between species (Coutant & Whitney, 2000). This needs to be considered when applying our results to other, for example, tropical, regions with fish with distinct ecological life histories. Nevertheless, we acknowledge that our results on context dependency reflect the interaction between macroecological relationships that govern

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fish distributions and the relationship between HPP type, head, and flow rate. For example, river fish distributions are particularly related to discharge (Oberdorff et al., 1995); likewise, the amount of power that can be generated depends on the type of turbine installed, the hydraulic head, and the available flow rate.

Our findings reinforce the importance of recognizing that mortality of fish from hydroelectric turbines is the consequence of deterministic and stochastic components. In our results, lethal impacts were more pronounced for Kaplan, Francis, and cross-flow turbines compared with Archimedes' screws, VLH turbines, and especially water wheels. However, we also acknowledge the large variability within a turbine type, ranging, for example, from 0% to 100% mortality in the common Kaplan and Francis turbines. Deterministic components include technical turbine parameters, such as rotational speed and blade spacing, in relation to fish characteristics (Čada et al., 1997). Our results agree with previous studies of blade-strike models (Čada et al., 1997; Deng et al., 2007; Ferguson et al., 2008; Montén, 1985); that is, collision probability increases with body length. Specifically, elongated fish, such as eels and other larger-bodied species (e.g., sturgeons and salmons) that are often associated with migratory behavior (Lucas & Baras, 2001), are particularly affected because they have higher encounter probabilities with HPPs and elevated collision risks. The on-site mortality studies used here mostly aggregated data over periods of different flows and operation modes. Different operation modes (i.e., full load vs. partial load) have been associated with variable fish mortality from turbines (Davies, 1988). However, other aspects related to such mortality, such as swim path and reactive behavior in a turbine (Coutant & Whitney, 2000), appear less predictable. Consequently, without acknowledging its uncertainty and any indication of confidence, a mean mortality estimate might be of limited meaningfulness.

Moreover, we focused on direct mortality due to turbine physical forces, such as blade strike, shear forces, and pressure changes. However, shear and turbulence, but also simple disorientation, might further result in indirect mortality by predation, which adds to the overall mortality ascribed to hydropower (Økland et al., 2017).

The diverging coverage of species in assessments of turbine-associated fish mortality was driven by the overrepresentation of studies on eels at SHP mostly equipped with Kaplan turbines and salmonids (frequently North American salmon species) at LHPs. Eels and salmons are the focus of studies of turbine-associated fish mortality because of their commercial importance in fisheries, cultural value, and extreme vulnerability due to their complex diadromous life cycles (Lucas & Baras, 2001). For example, in response to the continuously declining European eel (*Anguilla anguilla*) stock, which has been partly related to barriers and turbine-associated fish mortality at HPPs (Dekker, 2018), the European Union adopted the "eel regulation" (Council of the European Union, 2007), a plan for the recovery of European eel stocks to ensure migration to the sea of at least 40% of historic silver eel biomass (Dekker, 2016). This, in turn, requires sound monitoring and reliable rates of turbine-associated fish mortality at critical water ways.

By contrast, that our data were biased toward several smaller-bodied species, such as stone loaches and sticklebacks (Gasterosteidae) at water wheels and centrarchids at VLH turbines, was more surprising. The latter was specifically caused by the comparably small number of experiments at VLH turbines, which included one study of a centrarchid-dominated fish fauna at a Canadian VLH location. Furthermore, while we cannot fully deny that a certain bias regarding smaller-bodied species reflects some limitation of our data set insufficiently capturing the full body of mortality assessments, a general bias in studies of turbine-induced mortality might be causative. This might be related to life-history traits of certain fish that make them variously vulnerable to turbine entrainment and thus causing differences in representation in the samples. Moreover, sampling smaller-bodied ground-dwelling fishes in the tailrace proves difficult at large turbine flows. Also, the usefulness of telemetry may be limited in smaller-bodied species. In addition, these species are often commercially or socially less valued; hence, they might be less targeted (Miqueleiz et al., 2020). We argue that for any meaningful and inclusive conservation of freshwater biodiversity, an improved understanding of the fate of smaller-bodied and commercially less valued fishes during turbine passage is strongly required.

Each approach to measure fish mortality caused by turbines has its own limitations that might contribute to the variability in our study. For example, studies that did not acclimate fish to the natural depth prior to turbine passage might underestimate pressure-related injuries, which potentially dominate at many traditional Kaplan and Francis turbines. Moreover, fish handling, tagging, or detrimental sampling techniques might cause injuries that have to be considered for estimates to be reliable. Therefore, it was surprising that only 21% of all studies analyzed had corrected their mortality estimates for handling-related effects. However, this low share of less uncertain studies did not affect the overall results. Overall mean mortalities and their 95% CI estimated from all studies with statistical treatment of unreported uncertainties corresponded well with the results obtained from the 21% most certain studies.

Moreover, at a specific site, the comprehensive assessment of hydropower-related mortality may require using different complementary sampling methods. For example, acoustic telemetry, which is being increasingly used, provides valuable information on, for example, individual movement and partitioning of downstream migrants over different pathways or passage attempt rates and passage rates through turbines. But it is typically limited in sample size, identifying lethally injured and dead fish as well as exact site and time of death (Havn et al., 2017) and might be affected by the tag or tagging, which can lead to biased results (Deng et al., 2017). In this context, recent attempts to standardize ways to assess mortality at HPPs (Mueller et al., 2017) are beneficial. In fact, the large methodological variation among studies observed and the surprisingly low number of studies correcting for handling effects clearly shows that studies of fish mortality in hydroelectric turbines urgently need methodological standardization.

Assessments of hydropower impacts on fish mortality in turbines must not be viewed in isolation. It is equally important

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to consider the entrainment risk of fish, which is the probability of passing the turbines versus taking alternative pathways, such as spillways or fish bypass or migration facilities (Harrison et al., 2019; Schilt, 2007). Similar to the specific stressor (e.g., blade strike, shear, and rapid decompression), the probability of fish turbine entrainment depends on fish size, species, life stage, and life-history traits (Coutant & Whitney, 2000). If and how fish use alternative pathways depends on the complex interaction of water flow patterns and the ecohydraulic behavior of fish (e.g., Goodwin et al., 2014). Nevertheless, spillway passage and bypass systems might be fatal (e.g., Muir et al., 2001). Spillways are associated with particularly high injury risks, whereas bypasses are often the safest type of fish passage (Algera et al., 2020). Thus, successfully preventing fish from entering the turbines (e.g., via screens) and guiding them downstream in bypass systems is most important for sustainable HPP passage (Ebel, 2013; USFWS, 2017). It is essential to contextualize the rate of mortality to a realized rate on a per fish or per species basis to draw larger population-level conclusions, particularly for nonmigratory fishes that do not necessarily need to pass through HPPs to complete life cycles. While being beyond the scope of our analysis, the ecological and long-term population consequences are species specific and depend on a species' life-history traits (Harrison et al., 2019; van Treeck et al., 2020). Here, we refer to van Treeck et al. (2021), who recently provided a tool for screening hazards of HPPs to fish populations that explicitly considers species' life-history traits.

Future of hydropower in a field of conflicting interests

Any advantages of hydropower as clean and renewable energy must be debated in conjunction with fish injuries and other impacts it exerts. We argue that within such conflicting interests, agreeing on tolerable mortality rates is difficult and that stakeholders must consider aspects of animal welfare, population ecology, and biodiversity conservation, but also the economics of hydropower, environmental policy, and societal acceptance. Given the comprehensiveness of our data set and analyses, which also accounted for usually neglected uncertainties, our results support an informed choice and holistic debate on hydropower sustainability and the importance of elucidating the ecological costs incurred on rivers. For very small and small HPPs, there is a large burden of justification due to an overall mortality rate of 22.3% and their large numbers globally despite their negligible share of renewable hydroelectricity production (ARCADIS & Ingenieurbüro Floecksmühle, 2011; Schwarz, 2019).

The range of empirically observed mortalities indicated there were HPPs with common turbine types, technical and operational configurations, and fish protection measures implemented that successfully reduce mortality, in several cases even to 0. Such exemplary HPPs pave the way to more sustainable hydropower. In contrast, detrimental configurations that cause high mortality should be disclosed and shut down or at least substantially refurbished. Slower rotating turbines, such as Archimedes' screws, VLH turbines, and water wheels, are less harmful to fish compared with most conventional turbine types (Bracken & Lucas, 2013). Nevertheless, we emphasize the importance of further research into the development of generally more fish-protective turbines and adjustments of common turbines (Čada, 2001; Hogan et al., 2014). The functioning and protective effects of such turbines on fish must be evaluated with standardized, controlled methods under realistic field conditions. Fish-protective turbines accompanied with functioning up- and downstream fish-migration facilities must become the gold standard. Given the ongoing hydropower boom in megadiverse, large river systems (Anderson et al., 2018; Winemiller et al., 2016), globally adopting such a standard is even more important to balance the needs for renewable energy with those of biodiversity protection and environmental enhancement of riverine ecosystems.

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