School of Doctoral Studies in Biological Sciences

University of South Bohemia in České Budějovice

Faculty of Science

Anthropogenic impact on early-life stages of rheophilic fish

Ph.D. Thesis

RNDr. Daniel Bartoň

Supervisor: RNDr. Marek Šmejkal Ph.D.,
Biology Centre of the Czech Academy of
Sciences, Institute of Hydrobiology

České Budějovice 2024

This thesis should be cited as:
Bartoň, D., 2024: Anthropogenic impact on early-life stages of rheophilic fish. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 113 pp.

Annotation

This study focuses on the problems faced by the early-life stages of fish living in a river influenced by reservoirs and suggests possible solutions to enhance recruitment. The model fish for the study is the asp (*Leuciscus aspius*), known for its significant and protected population in the Želivka Reservoir, from where it migrates for reproduction to the tributary of Želivka River. The asp migrates upstream in spring to spawn in shallow, fast-flowing waters. At a research site, the adult population of asp is monitored using passive telemetry. Fish are caught, tagged, and released back into the reservoir. The asp population faces threats due to hydropeaking and river fragmentation. Hydropeaking causes egg detachment from the pebbles and their sedimentation in the reservoir. The study suggests that water should not exceed a velocity of 0.7 $m \times s^{-1}$ at the spawning ground. Periodically increasing discharge also shifts spawning fish outside their preferred spawning site, causing disruption of spawning and potentially lowering recruitment. A flow-deflector was built to protect newly spawned eggs from hydropeaking. However, there are additional threats to the asp recruitment process such as egg consumption by non-indigenous fish like common bream (*Abramis brama*). Water flow conditions are crucial for the conservation of rheophilic fish, as these fish, aside from habitat loss and modification, also face newly interacting generalist fish species moving from lentic to lotic sections of the system. Fish communities can be affected by reservoir construction far upstream, and these anthropogenic habitat alterations have severe negative impacts on threatened rheophilic fish recruitment.

Declaration

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

Daniel Bartoň
České Budějovice
February 6, 2024

This thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Hydrobiology, Academy of Sciences of the Czech Republic, supporting doctoral studies in the Hydrobiology study programme.

Přírodovědecká
fakulta
Faculty
of Science

BIOLOGY
CENTRE
CAS

Financial support

The work was partially supported by the project “The enhancement of rheophilous fish reproduction in the artificial river environment” (No. TJ02000012); “Aquaculture of rheophilous fish” (No. QK1920326); and AV 21 strategy support program “Water for life”.

List of papers and author's contribution

The thesis is based on the following papers:

I. **Bartoň D**., Breton F., Blabolil P., Souza A.T., Vejřík L., Sajdlová Z., Kolařík T., Kubečka J. Šmejkal, M. (2021). Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species. Ecohydrology 14: e2280. (IF= 3.166)

DB participated in the field work, designed the study, contributed to the statical analysis, graphically presented data and wrote the first draft with the help of co-authors. His contribution was 60 %.

II. **Bartoň D**., Brabec M., Sajdlová Z., Souza A. T., Duras J., Kortan D., Blabolil P., Vejřík L., Kubečka J., Šmejkal M. (2022). Hydropeaking causes spatial shifts in a reproducing rheophilic fish. Science of The Total Environment 806: 150649. (IF= 9.8)

DB participated in the field work, designed the study, graphically presented data and wrote the first draft with the help of co-authors. His contribution was 65 %.

III. **Bartoň D**., Sajdlová Z., Kolařík T., Duras J., Kortan D., Kubečka J., Šmejkal M. (2023) Use of a flow deflector to protect rheophilic fish spawning grounds during hydropeaking. River Research and Applications 39(3). (IF = 2.2)

DB participated in the field work, designed the study, contributed to the statical analysis, graphically presented data and wrote the first draft with the help of co-authors. His contribution was 70 %.

IV. **Bartoň D**., Brabec M., Sajdlová Z., Souza A. T., Kubečka J., Šmejkal M. Anthropogenic hydromorphological alteration increases vulnerability of rheophilic fish eggs to predation by generalists. (Manuscript)

DB participated in the field work, designed the study, graphically presented data and wrote the first draft with the help of co-authors. His contribution was 70 %.

V. Šmejkal, M., **Bartoň D.**, Duras J., Horký P., Muška M., Kubečka J., Pfauserová N., Tesfaye M., Slavík O., 2023. Living on the edge: Reservoirs facilitate enhanced interactions among generalist and rheophilic fish species in tributaries. Frontiers in Environmental Science Frontiers 11: 1099030. (IF=4.6)

DB prepared a chapter in the original manuscript with the help of co-authors. His overall contribution was 10 %.

Co-author agreement

RNDr. Marek Šmejkal Ph.D., the supervisor of this Ph.D. thesis and co-author of papers I. – V., fully acknowledges the stated contribution of Daniel Bartoň to these manuscripts.

……………………………………………
RNDr. Marek Šmejkal, Ph.D.

Table of contents

Introduction 1

Aims of the Thesis 10

Conclusions and Future Perspectives 12

References 14

Acknowledgements 23

Papers 25

- Paper I 27
- Paper II 41
- Paper III 55
- Paper IV 67
- Paper V 93

Curriculum Vitae 112

Introduction

The impact of human activities on nature is increasing and has already become in both science and public eyes an object of concern for some decades (Buytaert et al., 2006; Cardinale et al., 2012; Halpern et al., 2008; Hannah et al., 1994). It is fundamental to understand the conflicting interests of humankind and the environment, inspect their consequences in detail and potentially find solutions which will compromise between human needs and environmental conservation (Cardinale et al., 2012; Caughley, 1994). While it is not possible to solve all these problems at once, an effort should be aimed at identifying the most urgent human collisions with natural ecosystem processes resulting in its modified functioning.

There are several ways in which areas worthy of conservation can be selected (Caughley, 1994; Nilsen et al., 2018). One method is site-based: For example, by selecting a biome with high biodiversity richness, we can protect many species in a relatively small area (Nilsen et al., 2018; Southworth et al., 2006; Sutherland et al., 2009). Another example is a biome that is very rare and always has been, or that used to be widespread but is now disappearing (Nilsen et al., 2018). Another method of conservation is based on species or ecological groups of species. The species or group of species is known to be threatened by various factors and is in decline (Ando et al., 1998; Nilsen et al., 2018). In choosing this more specific type of conservation, a deeper understanding of the biology of the species is required (Nóbrega and De Marco, 2011). For example, we need to determine the most endangered life stages and their habitat requirements. In practice, conservation methods need to be combined based on the current state of knowledge (Hodgson et al., 2011; Tryjanowski et al., 2011).

Freshwater ecosystems are both the most diverse and species-rich ecosystems and the most threatened by biodiversity loss (Dudgeon et al., 2006; Tickner et al., 2020). The threats can essentially be divided into five categories: overexploitation, water pollution, flow alteration, habitat destruction or degradation, and species invasion (Dudgeon et al., 2006). Rivers are key to large and small cycles (water, nutrients, sediments), and they shape the appearance of the planetary surface on which we all live

(Grabowski and Gurnell, 2016). Unfortunately, our actions are altering rivers and destroying ecosystems (Jansson et al., 2000; Mueller et al., 2011). Only 37 % of large rivers (1000 km and longer) remain free-flowing, i.e. they have no major man-made barriers (Grill et al., 2019). The remaining connectivity is impaired by dams, reservoirs, weirs, etc., and that directly impacts river biodiversity (Mueller et al., 2011; Pringle, 2003). This poses a significant threat to rivers and their native inhabitants, and organisms with high migratory requirements are at high risk of extinction (Zhang et al., 2020). There is therefore an urgent need to protect rivers and their inhabitants, including fish.

Rivers around the world face heavy modifications and discharge regulations, and these changes have strong impacts on riverine wildlife (Poff et al., 2007). Dams and reservoirs constructed around the world pose serious threats to rheophilic species (Cooper et al., 2017; Wang et al., 2021, 2011). In not-so-recent years many fish species that depended on running waters got extirpated or faced a major threat (Liu et al., 2019; Lyons et al., 1998; Zimmerli et al., 2007). The main emphasis of this thesis is on migratory fish, their habitat fragmentation loss and disruption of life cycle. Fragmented rivers pose a threat for both anadromous fish, migrating from freshwater where they hatch to the ocean and later returning to spawn, and catadromous with other way around. Threatened are also potamodromous fish which migrate within freshwater i.e. between the main river and tributary to proceed in their life cycle (Koster et al., 2021).

Rheophilic fish as an important and increasingly endangered ecological group

A rheophile is by definition an animal that prefers to live in fluvial waters and it is a very common strategy in fish (Lujan and Conway, 2015). Out of 35 400 species of fish listed in FishBase 9700 are described as river native (Froese and Pauly, 2023). Similar adaptations for life in flowing environments evolved in several different taxa (Lamouroux et al., 2002). Rheophilic strategy is present in more than 60 fish families. Adaptations to live in flowing waters formed the evolution of these fishes to face this challenging environment. Life in fast-running waters can offer ecological advantages such as predation avoidance or foraging efficiency (Lujan and Conway, 2015). On the other hand, fish must resist environmental challenges such as downstream displacement or shifting, crushing substrates (Lujan and Conway, 2015; Poff et al., 2001) and in the modern era also with humans changing the face of the planet including its rivers (Bain et al., 1988; Perkin et al., 2015; Poulet, 2007).

Fish are an ecologically very important group in river ecosystems (Allan and Castillo, 2007), as they occupy various positions in the food chain from herbivores to apex predators (Poff et al., 2001)). The ability of some species to migrate long distances has a larger impact on nutrition relocations in different parts of rivers or even between freshwater and marine environments (Hansen et al., 1993; Poff et al., 2001).

Effects of habitat modification in rivers on fish ecology

To conserve and protect migratory species, enabling them to successfully finish their reproduction cycles is needed (Fuller et al., 2015; Sutherland et al., 2009). The reproductive period often limits the life stage deciding whether the populations will grow, remain stable or gradually extinct due to lack of recruitment (Janney et al., 2008; Terwilliger et al., 2010) The majority of species are most vulnerable in the earliest life stages and this period may be negatively affected by anthropogenic changes in the environment (Nilsen et al., 2018; Terwilliger et al., 2010). Life strategies of fish are often more r-selected, meaning their fecundity is high with the production of an enormous number of offspring which can sustain large losses (Helfman et al., 2009). Yet fish recruitment and its early-life stages are the key to fish population dynamic and worth protection in fish stock management and conservation (Blabolil et al., 2019; Jůza et al., 2014; Pankhurst and Munday, 2011; Paradis et al., 1996; Šmejkal et al., 2021).

Riverine fishes evolved many different habitat utilizations according to their reproductive state (Allan and Castillo, 2007; Helfman et al., 2009; Poff et al., 2001). Fish can be divided into three groups based on their habitat and reproductive behaviour. The first group consists of fish that live and reproduce exclusively in flowing water. The second group includes fish that inhabit other water habitats, such as marine, slow-flowing or still water, but choose flowing water for reproduction. The third group comprises fish that live in flowing water but leave it for reproduction. Both the second and third groups need to migrate longer distances through streams and rivers at some point in their life, which is ecologically important for river ecology and biodiversity functioning (Poff et al., 2001). It also has high socio-economic value in many commercially important species (Tamario et al., 2019). These migrations are weakened or completely disabled by loss of river connectivity (Grill et al., 2019), or it may lead to migration into suboptimal (spawning) habitat (Fuller et al., 2015; Ovidio and Philippart, 2008; Taylor et al., 2008).

Many migratory species are facing threats to their survival, including human impact through exploitation, pollution, habitat destruction, overfishing, and climate change. These climate changes bring more variable and extreme hydrological conditions (Tamario et al., 2019). Areas with the highest river fragmentation are typically the most developed and populous (United States, Europe, South Africa, India and China) (Barbarossa et al., 2020; Grill et al., 2019). River habitat fragmentation is also often caused by alterations in flow regimes introducing another human-induced factor to river ecology by increasing or delaying natural discharge in rivers for human needs (Sawyer et al., 2009).

Many studies are alerting the issue of river habitat loss and fragmentation causing threats to all its natural inhabitants including fish (Barbarossa et al., 2020; Grill et al., 2019; Schmutz et al., 2015; Tamario et al., 2019). Measures for remedy are being introduced to many rivers already in the form of weir and dam removal (Garcia De Leaniz, 2008; Im et al., 2011; Magilligan et al., 2016). In commercially important fish species such as salmon, their decline due to reservoir impact may convince authorities to destroy several reservoirs such as in River Klamath, California (Gosnell and Kelly, 2010). Another example of measures mitigating the impact of habitat fragmentation is fish passages enabling fish migration through migratory barriers, which are being built on many rivers and their efficiency and ecological benefits are being discussed, tested and studied (Bunt et al., 2012; Noonan et al., 2012). Part of the European Green Deal is to restore at least 25 000 km of rivers into a free-flowing state (Biodiversity strategy for 2030).

Flow alteration as a major threat for rheophilic fish

Dams are built on most rivers worldwide for water storage, flood control, flow balancing, recreation, and hydroelectricity (Barbarossa et al., 2020; Nilsson et al., 2005). Despite the well-known ecological risks associated with river damming, new reservoirs are still being constructed to mitigate the impacts of global warming. The rising levels of evaporation are depleting current water reserves, thereby necessitating the creation of additional storage capacity. One of the primary objectives of dams is to generate electricity through hydropower plants, which are regarded as a renewable energy source that is generally considered environmentally friendly (Singh and Singal, 2017). The advantage of hydropower is its ability to store energy and transform water storage into electricity at the right time when the energy demands are high (Akinyele and Rayudu, 2014).

The rapid flow alterations (hydropeaking) harm many river organisms including fish (Alexandre et al., 2016; Bruno et al., 2013; Hauer et al., 2017; Kennedy et al., 2016). Impacts of the flow alteration effects on the fish community include thermal shift, water level and speed changes, exposure to a higher risk of diseases and predation (Casas-Mulet et al., 2016; Jones and Petreman, 2015; Moreira et al., 2019; Schmutz et al., 2015). Flow fluctuations as well as temperature variations commonly connected to hydropeaking are factors causing stress, interruptions of spawning, food deprivation, altered hatching and migration of juvenile fish – all causing potential reduction of fish recruitment (Schmutz et al., 2015).

Hydropeaking can impact vulnerable stages in fish early life history such as the eggs developing in spawning sites or freshly hatched larvae (Schmutz et al., 2015). Eggs can be exposed to dewatering when flow is artificially decreased and spawning grounds can dry up causing high mortality of the eggs (Grabowski and Isely, 2007; McMichael et al., 2005). The opposite effect on the fish's early life stages may be caused by the artificial increase of flow that triggers high drift downstream (Young et al., 2011).

Considering the negative effects of human alterations of river habitats on early fish stages, it can be assumed that certain reproductive fish guilds are more vulnerable to the effects of hydropeaking than others. If we focus on the group of rheophilic fish (spawning fish in flowing waters), we can assume that pelagophilic fish are less affected by hydropeaking, as their eggs are carried by the current until hatching (Balon, 1975; Stanley et al., 1978).The group of phytophiles seems to be more vulnerable when using macrophytes as spawning sites, although partial protection from the fast flow by macrophytes can be expected (Allan and Castillo, 2007). Therefore, lithophiles with their eggs attached to gravel and stones are probably the most vulnerable reproductive guild to hydropeaking, as their eggs are most likely to be washed away to suboptimal conditions for hatching by the increase in current velocity during hydropeaking.

River fragmentation and habitat alteration

Rivers are not only fragmented by dam construction as a direct migration barrier but also by both downstream and upstream habitat alteration. Reservoirs, as non-natural water bodies built on rivers, are usually inhabited by fish species originating from the river on which the reservoir is located; often with the addition of fish from lower, bigger and slower parts of the river (Fernando and Holčík, 1991; Pfauserová et al., 2019) (**Paper V**). Fish from lower parts of the river then often thrive in reservoirs, for example, cyprinid species such as roach (*Rutilus rutilus*) and bream (*Abramis brama*), and their number and biomass are higher towards a tributary (Jůza et al., 2015; Vašek et al., 2016).

The impact of the reservoir on upstream river fish is further enhanced during spring, when cyprinid fish are migrating upstream to find suitable places to spawn (Hladík and Kubečka, 2004, 2003). Migrating fish are then further concentrated in a tributary potentially increasing predation pressure on the early life stages of rheophilic fish. The number of migrating fish by far exceeds the number of fish that would reach the spawning ground of rheophilic fish if no reservoir was present downstream of their spawning ground. This is another example of the negative impact on rheophilic fish eggs, which enhance predation pressure in comparison with freely flowing rivers without such artificial barriers (Šmejkal et al., 2018, 2017a).

Model fish and study side

An example of rheophilic fish potentially affected by anthropogenic changes is asp, *Leuciscus aspius*, losing natural habitats and being considered locally threatened due to man-made river alterations and finding alternative habitats in many reservoirs (Freyhof and Kottelat, 2008; Vašek et al., 2016). This large predator originally inhabits lowland rivers of Central and Eastern Europe (Kottelat and Freyhof, 2007). Due to a lack of natural reproduction possibilities, stocking in the reservoirs is often needed (Blabolil et al., 2019; Šmejkal et al., 2021). Asp migrate to fast-flowing waters which they need to spawn in the early spring (Šmejkal et al., 2017b). Asp was chosen as a main model fish for the study of anthropogenic impact on its early life stages also because its reproduction biology has been studied for a decade by the Institute of Hydrobiology, Biology Centre CAS. The study site is a tributary of a large Czech drinking water reservoir, Želivka, and the local asp population is protected by Natura 2000 with other 545 sites in Europe including six in Czech Republic; parts of rivers Sázava, Berounka, Dyje, Ohře, Labe a Želivka (Natura 2000 Viewer).

The main tributary of Želivka Reservoir is an example of a highly fragmented river with many barriers disabling fish migration such as weirs and dams. Two smaller dams, located upstream of the study site, are the source of hydropeaking for the asp spawning ground. The second most important canoe slalom in Czechia is located on Trnava River, below Trnávka Reservoir. The change in the water flow on the site is very high and happens usually in the spawning season or egg development phase (April and early May). The high peak flow comes during the day while asp is spawning more in the nighttime (Šmejkal et al., 2018, 2017a). The flow increase is so high that it can detach the majority of asp eggs. Furthermore, just below the area where spawning takes place the reservoir starts with an unsuitable substrate for rheophilic fish egg development (**Paper I**).

Possible solutions and measures for protection of early-life stages of rheophilic fish

For their ecological and socio-economic importance river fish and their life cycles are to some extent protected for a long time. The traditional method or approach is the construction of fish ladders also known as fish passes or fishways, fish steps etc. It is a construction enabling fish to pass around the barrier into the waters above or below. It is tricky to construct a very effective fish ladder because of the needed water velocity to attract fish into it. Fish ladders started to be constructed at the beginning of the industrial age (18th century) and with the advance of river obstructions, they became more common (Larinier and Marmulla, 2004). There are now many types of fish ladders but their efficiency is rarely sufficient and they can be very selective and even become predation hot spots (Agostinho et al., 2012, 2007; Volpato et al., 2009). On the other hand, fish ladders (especially those most natural looking) and side channels in heavily modified rivers can provide suitable grounds for rheophilic fish spawn and even can serve as safe ground from hydropeaking in the main river channel (Knott et al., 2021).

There is great importance in structures providing shelter for the fish. Hydropeaking impact on fish is greatly dependent on river morphology and habitat diversity in it (Boavida et al., 2015; Hayes et al., 2024). Flow deflectors can provide refuges for fish during the hydropeaking (Costa et al., 2019) and on a larger scale can be used as protection of spawning ground (**Paper III**).

Spawning substrate quality plays also a great role in rheophilic fish spawning and respirations of spawning grounds can be useful tools to improve the spawning. Restorations of the spawning grounds of salmonids can enhance the spawning and development of eggs and increase recruitment (Zeh and Dönni, 1994). Similarly, substrate cleaning can provide great service for lithophilic cypriniforms and enhance egg infiltration and protection of larvae in the interstitial zones before emergence (Duerregger et al., 2018; Nagel et al., 2020).

The most effective methods of conservation are complex combining several protection measures. The protection of rheophilic species in modified rivers also includes the concept of environmental flows (Arthington, 2015). Environmental flow is an established flow in rivers during the year based on its hydrology, biology, water quality, connectivity and geomorphology to conserve the ecosystem and protect the life within. In modified rivers where habitat connectivity and quality are limited, the construction of compensatory measures in the form of flow deflectors, fish passes and discharge limits can increase reproduction and to some extent provide repopulation of native rheophilic fish (Santos et al., 2023).

Aims of the Thesis

This Ph.D. thesis focuses on the study of rheophilic fish and aims to describe issues related to this topic. Papers I to IV investigate a protected asp population in a modified river habitat. The research is mainly focused on the spawning and early life history. All papers aim to extend their focus to provide wider knowledge and applicability outside the model fish species and its study site. Paper V is a review that demonstrates the effects of habitat fragmentation on rheophilic fish communities, expanding on the issue described in Paper IV.

Paper I aims to provide identification of the preferred spawning habitat for the fish, investigate if spawned eggs are affected by hydropeaking at the study site, and provide surface detachment rates of spawned eggs under hydropeaking conditions in a laboratory setup based on water flow velocities, time exposure, and surface type.

Paper II aims to investigate if changes in flow and temperature during hydropeaking affect the position of the spawning fish in the stream and test the hypothesis that high flow conditions can force fish to enter spawning shifts downstream outside the chosen site for egg deposition.

Paper III aims to test possibilities of retaining a higher number of eggs from detachment during hydropeaking with channel modification that attracts more fish to protect, implementation of flow deflector reducing discharge in the protected area, and further reducing incoming discharge during hydropeaking by diverting the peak to a mill channel outside the spawning area.

Paper IV aims to provide proof of asp egg predation by common bream and describe flow conditions and limitations for common bream in reaching the rheophilic asp spawning site.

Paper V aims to address the topic of edge effects on the generalist fish community of the reservoir and the community of rheophilic fish, summarize current knowledge of the reservoir fish community, its proliferation, an upstream migration, and effects on rheophilic fish via competition and predation, and describe possible protection methods.

Conclusions and Future Perspectives

The research papers in this thesis examine the loss of recruitment success of rheophilic fish and identify its sources. The focus is primarily on the model fish asp, which lives in heavily modified river systems. These rheophilic fish face numerous anthropogenic factors that fragment and alter their habitats, making it difficult for them to maintain or expand their populations.

Hydropeaking is a concerning issue with the ability to disrupt the life cycle of rheophilic fish. Rapid discharge increase can detach eggs from the substrate, shift them downstream in the reservoir where conditions are not suitable for egg development. This is also probably even more significant in cultural landscapes with straightened rivers where eggs cannot enter interstitial spaces due to fine sediment pollution. Our study shows that eggs are relatively easy to detach from the substrate surface with increased flow velocity, especially on surfaces with biofilm.

Adult fish entering spawning and seeking suitable areas for egg deposition are affected by discharge increase during hydropeaking. This forces fish outside their chosen spots and shifts them downstream where substrate quality, depth and water flow conditions are suboptimal and probably not suitable for successful egg development.

The flow deflector is a simple yet effective method for protecting a portion of the attached eggs at the study site. While it can be used in other locations, its use is relatively specific and only serves to lessen the impact of hydropeaking rather than solving it entirely. Additionally, installing the deflector was crucial in diverting some of the peak discharge into other channels where fish rarely or never spawned. As a result, cleaning and restoring a portion of the river using an excavator was necessary to further attract fish to the protected area. In the future, restoring the spawning site will be necessary and could involve constructing a weir bypass where asp could spawn without being affected by hydropeaking and with a larger area suitable for egg deposition.

Predation of spawned eggs by generalist common bream can significantly impact asp recruitment, particularly in years with high water levels in reservoirs. However, in tributaries or streams with shallow, fast-flowing water favoured by asp, common bream are unable to access these areas. This valuable insight can be incorporated into the design and restoration of natural spawning sites for rheophilic fish, helping to mitigate the negative effects of common bream proliferation in reservoirs and their upstream migration into lotic habitats.

The process of damming a river results in the formation of secondary lentic habitats, such as reservoirs. However, the fish communities in these reservoirs are often comprised of non-native and generalist fish that compete with the native rheophilic community. As these fish migrate from the reservoirs into the tributaries, especially during spring for spawning, they further deplete the available resources and prey on the existing fish. This ultimately leads to the fragmentation of the remaining habitats for the rheophilic fish, making them even smaller and more difficult to sustain.

During my studies, I primarily focused on researching a particular fish species. However, my supervisor allowed me to participate in other projects related to fish conservation. One such project focused on the conservation of an endangered species of fish, the crucian carp (*Carassius carassius*). During this project, we observed the loss of habitats due to human activities that have had a significant impact on freshwater habitats. I find the loss of these habitats to be alarming, and it has motivated me to pursue research in the field of habitat restoration and fish conservation.

I am planning to collaborate with the Vltava River Authority to find solutions for the natural spawning area of asp. One possible solution is to build a weir bypass. However, I also want to focus on other species of fish that thrive in fast-flowing water. The river authorities are monitoring fish fry in streams, and evaluating this data can provide more insight into the functioning or disruption of these habitats.

References

Agostinho, A.A., Agostinho, C.S., Pelicice, F.M., Marques, E.E., 2012. Fish ladders: safe fish passage or hotspot for predation? Neotropical Ichthyology 10, 687–696.

Agostinho, C.S., Agostinho, A.A., Pelicice, F., Almeida, D.A. de, Marques, E.E., 2007. Selectivity of fish ladders: a bottleneck in Neotropical fish movement. Neotropical Ichthyology 5, 205–213.

Akinyele, D.O., Rayudu, R.K., 2014. Review of energy storage technologies for sustainable power networks. Sustainable Energy Technologies and Assessments 8, 74–91. https://doi.org/10.1016/j.seta.2014.07.004

Alexandre, C.M., Almeida, P.R., Neves, T., Mateus, C.S., Costa, J.L., Quintella, B.R., 2016. Effects of flow regulation on the movement patterns and habitat use of a potamodromous cyprinid species. Ecohydrology. https://doi.org/10.1002/eco.1638

Allan, J.D., Castillo, M.M., 2007. Stream ecology: Structure and function of running waters: Second edition, Stream Ecology: Structure and Function of Running Waters: Second Edition. https://doi.org/10.1007-978-1-4020-5583-6

Ando, A., Camm, J., Polasky, S., Solow, A., 1998. Species distributions, land values, and efficient conservation. Science (1979). https://doi.org/10.1126/science.279.5359.2126

Arthington, A.H., 2015. Environmental flows: a scientific resource and policy framework for river conservation and restoration. Aquatic Conservation: Marine and Freshwater Ecosystems.

Bain, M.B., Finn, J.T., Booke, H.E., 1988. Stream flow regulation and fish community structure. Ecology 69, 382–392.

Balon, E.K., 1975. The main reproductive guilds of fish. Journal of Fish Biology 32, 821–864. https://doi.org/S0967-5868(12)00647-9 [pii]\r10.1016/j.jocn.2012.09.026

Barbarossa, V., Schmitt, R.J.P., Huijbregts, M.A.J., Zarfl, C., King, H., Schipper, A.M., 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. Proceedings of the National Academy of Sciences of the United States of America 117, 3648–3655. https://doi.org/10.1073/pnas.1912776117

Biodiversity strategy for 2030 [WWW Document] 2024, https://environment.ec.europa.eu/strategy/biodiversity-strategy-2030_en

Blabolil, P., Bartoň, D., Halačka, K., Kočvara, L., Kolařík, T., Kubečka, J., Šmejkal, M., Peterka, J., 2019. The fate of 0+ asp (*Leuciscus aspius*) after being stocked in a reservoir. Biologia (Bratislava). https://doi.org/10.2478/s11756-019-00355-3

Boavida, I., Santos, J.M., Ferreira, T., Pinheiro, A., 2015. Barbel habitat alterations due to hydropeaking. Journal of Hydro-Environment Research. https://doi.org/10.1016/j.jher.2014.07.009

Bruno, M.C., Siviglia, A., Carolli, M., Maiolini, B., 2013. Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. Ecohydrology 6, 511–522. https://doi.org/10.1002/eco.1275

Bunt, C.M., Castro-Santos, T., Haro, A., 2012. Performance of fish passage structures at upstream barriers to migration. River Research and Applications. https://doi.org/10.1002/rra.1565

Buytaert, W., Célleri, R., De Bièvre, B., Cisneros, F., Wyseure, G., Deckers, J., Hofstede, R., 2006. Human impact on the hydrology of the Andean páramos. Earth-Science Reviews. https://doi.org/10.1016/j.earscirev.2006.06.002

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature. https://doi.org/10.1038/nature11148

Casas-Mulet, R., Saltveit, S.J., Alfredsen, K.T., 2016. Hydrological and thermal effects of hydropeaking on early life stages of salmonids: A modelling approach for implementing mitigation strategies. Science of the Total Environment 573, 1660–1672. https://doi.org/10.1016/j.scitotenv.2016.09.208

Caughley, G., 1994. Directions in Conservation Biology. Journal of Animal Ecology. https://doi.org/10.2307/5542

Cooper, A.R., Infante, D.M., Daniel, W.M., Wehrly, K.E., Wang, L., Brenden, T.O., 2017. Assessment of dam effects on streams and fish assemblages of the conterminous USA. Science of The Total Environment 586, 879–889. https://doi.org/10.1016/J.SCITOTENV.2017.02.067

Costa, M.J., Ferreira, M.T., Pinheiro, A.N., Boavida, I., 2019. The potential of lateral refuges for Iberian barbel under simulated hydropeaking conditions. Ecological Engineering 127, 567–578. https://doi.org/10.1016/j.ecoleng.2018.07.029

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81, 163–182. https://doi.org/10.1017/S1464793105006950

Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., Geist, J., 2018. The importance of stream interstitial conditions for the early-life-stage development of the European nase (*Chondrostoma nasus* L.). Ecology of Freshwater Fish 27, 920–932. https://doi.org/https://doi.org/10.1111/eff.12403

Fernando, C.H., Holčík, J., 1991. Fish in Reservoirs. Internationale Revue der gesamten Hydrobiologie und Hydrographie. https://doi.org/10.1002/iroh.19910760202

Freyhof, J., Kottelat, M., 2008. *Leuciscus aspius* (amended version of 2008 assessment). The IUCN Red List of Threatened Species 2018. e.T2178A136077402.

Froese, R., Pauly D., 2023. www.fishbase.org [WWW Document]. FishBase.

Fuller, M.R., Doyle, M.W., Strayer, D.L., 2015. Causes and consequences of habitat fragmentation in river networks. Annals of the New York Academy of Sciences 1355, 31–51. https://doi.org/10.1111/NYAS.12853

Garcia De Leaniz, C., 2008. Weir removal in salmonid streams: Implications, challenges and practicalities, in: Hydrobiologia. https://doi.org/10.1007/s10750-008-9397-x

Gosnell, H., Kelly, E.C., 2010. Peace on the river? Social-ecological restoration and large dam removal in the Klamath basin, USA. Water Alternatives.

Grabowski, R.C., Gurnell, A.M., 2016. Hydrogeomorphology-Ecology Interactions in River Systems. River Research and Applications. https://doi.org/10.1002/rra.2974

Grabowski, T.B., Isely, J.J., 2007. Effects of Flow Fluctuations on the Spawning Habitat of a Riverine Fish. Southeastern Naturalist 6, 471–478. https://doi.org/10.1656/1528-7092(2007)6[471:EOFFOT]2.0.CO;2

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world's free-flowing rivers. Nature 569, 215–221. https://doi.org/10.1038/s41586-019-1111-9

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science (1979). https://doi.org/10.1126/science.1149345

Hannah, L., Lohse, D., Hutchinson, C., Carr, J.L., Lankerani, A., 1994. A preliminary inventory of human disturbance of world ecosystems. Ambio. https://doi.org/10.1016/0006-3207(96)83209-5

Hansen, L.P., Jonsson, N., Jonsson, B., 1993. Oceanic migration in homing Atlantic salmon. Animal Behaviour. https://doi.org/10.1006/anbe.1993.1112

Hauer, C., Holzapfel, P., Leitner, P., Graf, W., 2017. Longitudinal assessment of hydropeaking impacts on various scales for an improved process understanding and the design of mitigation measures. Science of The Total Environment 575, 1503–1514. https://doi.org/https://doi.org/10.1016/j.scitotenv.2016.10.031

Hayes, D.S., Hauer, C., Unfer, G., 2024. Fish stranding in relation to river bar morphology and baseflow magnitude: Combining field surveys and hydrodynamic–numerical modelling. Ecohydrology n/a, e2616. https://doi.org/https://doi.org/10.1002/eco.2616

Helfman, G.S., Collette, B.B., Facey, D.E., Bowen, B.W., 2009. The diversity of fishes: biology, evolution, and ecology, Atlantic. https://doi.org/10.1007/978-1-4615-2664-3_1

Hladík, M., Kubečka, J., 2004. The effect of water level fluctuation on tributary spawning migration of reservoir fish. Ecohydrology and Hydrobiology 4, 449–457.

https://doi.org/Doi 10.1007/Bf02758690

Hladík, M., Kubečka, J., 2003. Fish migration between a temperate reservoir and its main tributary. Hydrobiologia 504, 251–266. https://doi.org/10.1023/B:HYDR.0000008525.46939.42

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011. Habitat area, quality and connectivity: Striking the balance for efficient conservation. Journal of Applied Ecology. https://doi.org/10.1111/j.1365-2664.2010.01919.x

Im, D., Kang, H., Kim, K.H., Choi, S.U., 2011. Changes of river morphology and physical fish habitat following weir removal. Ecological Engineering. https://doi.org/10.1016/j.ecoleng.2011.01.005

Janney, E.C., Shively, R.S., Hayes, B.S., Barry, P.M., Perkins, D., 2008. Demographic Analysis of Lost River Sucker and Shortnose Sucker Populations in Upper Klamath Lake, Oregon. Transactions of the American Fisheries Society. https://doi.org/10.1577/t06-235.1

Jansson, R., Nilsson, C., Dynesius, M., Andersson, E., 2000. Effects of river regulation on river-margin vegetation: A comparison of eight boreal rivers. Ecological Applications. https://doi.org/10.1890/1051-0761(2000)010[0203:EORROR]2.0.CO;2

Jones, N.E., Petreman, I.C., 2015. Environmental Influences on Fish Migration in a Hydropeaking River. River Research and Applications. https://doi.org/10.1002/rra.2810

Jůza, T., Ricard, D., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Muška, M., Peterka, J., Prchalová, M., Říha, M., Sajdlová, Z., Šmejkal, M., Tušer, M., Vašek, M., Vejřík, L., Kubečka, J., 2015. Species-specific gradients of juvenile fish density and size in pelagic areas of temperate reservoirs. Hydrobiologia. https://doi.org/10.1007/s10750-015-2346-6

Jůza, T., Vašek, M., Kratochvíl, M., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Muška, M., Peterka, J., Prchalová, M., Říha, M., Tušer, M., Kubečka, J., 2014. Chaos and stability of age-0 fish assemblages in a temperate deep reservoir: Unpredictable success and stable habitat use. Hydrobiologia. https://doi.org/10.1007/s10750-013-1735-y

Kennedy, T.A., Muehlbauer, J.D., Yackulic, C.B., Lytle, D.A., Miller, S.W., Dibble, K.L., Kortenhoeven, E.W., Metcalfe, A.N., Baxter, C. V., 2016. Flow management for hydropower extirpates aquatic insects, undermining river food webs. Bioscience 66, 561–575. https://doi.org/10.1093/biosci/biw059

Knott, J., Nagel, C., Geist, J., 2021. Wasted effort or promising approach – Does it make sense to build an engineered spawning ground for rheophilic fish in reservoir cascades? Ecological Engineering 173. https://doi.org/10.1016/j.ecoleng.2021.106434

Koster, W.M., Stuart, I., Tonkin, Z., Dawson, D., Fanson, B., 2021. Environmental influences on migration patterns and pathways of a threatened potamodromous fish in a regulated lowland river network. Ecohydrology 14, e2260. https://doi.org/https://doi.org/10.1002/eco.2260

Kottelat, M., Freyhof, J.J., 2007. Handbook of European freshwater fishes, Copeia. https://doi.org/10.1643/OT-08-098a.1

Lamouroux, N., Poff, N.L., Angermeier, P.L., 2002. Intercontinental Convergence of Stream Fish Community Traits along Geomorphic and Hydraulic Gradients. Ecology 83, 1792–1807. https://doi.org/10.2307/3071765

Larinier, M., Marmulla, G., 2004. Fish passes: types, principles and geographical distribution-an overview, in: Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries. RAP publication Bangkok, Thailand, pp. 183–206.

Liu, X., Qin, J., Xu, Y., Ouyang, S., Wu, X., 2019. Biodiversity decline of fish assemblages after the impoundment of the Three Gorges Dam in the Yangtze River Basin, China. Rev Fish Biol Fish 29, 177–195. https://doi.org/10.1007/s11160-019-09548-0

Lujan, N.K., Conway, K.W., 2015. Life in the Fast Lane: A Review of Rheophily in Freshwater Fishes, in: Riesch, R., Tobler, M., Plath, M. (Eds.), Extremophile Fishes: Ecology, Evolution, and Physiology of Teleosts in Extreme Environments. Springer International Publishing, Cham, pp. 107–136. https://doi.org/10.1007/978-3-319-13362-1_6

Lyons, J., González-Hernández, G., Soto-Galera, E., Guzmán-Arroyo, M., 1998. Decline of Freshwater Fishes and Fisheries in Selected Drainages of West-Central Mexico. Fisheries (Bethesda) 23, 10–18. https://doi.org/https://doi.org/10.1577/1548-8446(1998)023<0010:DOFFAF>2.0.CO;2

Magilligan, F.J., Nislow, K.H., Kynard, B.E., Hackman, A.M., 2016. Immediate changes in stream channel geomorphology, aquatic habitat, and fish assemblages following dam removal in a small upland catchment. Geomorphology. https://doi.org/10.1016/j.geomorph.2015.07.027

McMichael, G.A., Rakowski, C.L., James, B.B., Lukas, J.A., 2005. Estimated Fall Chinook Salmon Survival to Emergence in Dewatered Redds in a Shallow Side Channel of the Columbia River. North American Journal of Fisheries Management 25, 876–884. https://doi.org/10.1577/M04-168.1

Moreira, M., Hayes, D.S., Boavida, I., Schletterer, M., Schmutz, S., Pinheiro, A., 2019. Ecologically-based criteria for hydropeaking mitigation: A review. Science of the Total Environment. https://doi.org/10.1016/j.scitotenv.2018.12.107

Mueller, M., Pander, J., Geist, J., 2011. The effects of weirs on structural stream habitat and biological communities. Journal of Applied Ecology. https://doi.org/10.1111/j.1365-2664.2011.02035.x

Nagel, C., Mueller, M., Pander, J., Geist, J., 2020. Making up the bed: Gravel cleaning as a contribution to nase (*Chondrostoma nasus* L.) spawning and recruitment success.

Aquatic Conservation: Marine and Freshwater Ecosystems 30, 2269–2283. https://doi.org/https://doi.org/10.1002/aqc.3458

Natura 2000 Viewer, [WWW Page] 2024. https://natura2000.eea.europa.eu

Nilsen, E.B., Bowler, D., Linnell, J., 2018. Directions in Conservation Biology Revisited. https://doi.org/10.17011/conference/eccb2018/107830

Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science (1979) 308, 405–408. https://doi.org/10.1126/science.1107887

Nóbrega, C.C., De Marco, P., 2011. Unprotecting the rare species: A niche-based gap analysis for odonates in a core Cerrado area. Diversity and Distributions. https://doi.org/10.1111/j.1472-4642.2011.00749.x

Noonan, M.J., Grant, J.W.A., Jackson, C.D., 2012. A quantitative assessment of fish passage efficiency. Fish and Fisheries. https://doi.org/10.1111/j.1467-2979.2011.00445.x

Ovidio, M., Philippart, J.C., 2008. Movement patterns and spawning activity of individual nase Chondrostoma nasus (L.) in flow-regulated and weir-fragmented rivers. Journal of Applied Ichthyology 24, 256–262. https://doi.org/10.1111/j.1439-0426.2008.01050.x

Pankhurst, N.W., Munday, P.L., 2011. Effects of climate change on fish reproduction and early life history stages. Marine and Freshwater Research. https://doi.org/10.1071/MF10269

Paradis, A.R., Pepin, P., Brown, J.A., 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Canadian Journal of Fisheries and Aquatic Sciences 53, 1226–1235. https://doi.org/10.1139/f96-051

Perkin, J.S., Gido, K.B., Cooper, A.R., Turner, T.F., Osborne, M.J., Johnson, E.R., Mayes, K.B., Nilsson, C., 2015. Fragmentation and dewatering transform Great Plains stream fish communities. Ecological Monographs 85, 73–92. https://doi.org/10.1890/14-0121.1

Pfauserová, N., Slavík, O., Horký, P., Kolářjová, J., Randák, T., 2019. Migration of non-native predator Asp (*Leuciscus aspius*) from a reservoir poses a potential threat to native species in tributaries. Water (Switzerland). https://doi.org/10.3390/w11061306

Poff, N.LeRoy., Angermeier, P.L., Cooper, S.D., Lake, P.S., Fausch, K.D., Winemiller, K.O., Mertes, L.A.K., Oswood, M.W., Reynolds, J., Rahel, F.J., 2001. Fish Diversity in Streams and Rivers. https://doi.org/10.1007/978-1-4613-0157-8_14

Poff, N.L.R., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104, 5732–5737. https://doi.org/10.1073/pnas.0609812104

Poulet, N., 2007. Impact of weirs on fish communities in a Piedmont stream. River

Research and Applications. https://doi.org/10.1002/rra.1040

Pringle, C., 2003. What is hydrologic connectivity and why is it ecologically important? Hydrological Processes. https://doi.org/10.1002/hyp.5145

Santos, R.M.B., Boavida, I., Cortes, R.M. V, Pacheco, F.A.L., Sanches Fernandes, L.F., Monteiro, S.M., Jesus, J.B., 2023. Effect of river restoration on spawning activity of Iberian barbel (*Luciobarbus bocagei*). Journal for Nature Conservation 76, 126488. https://doi.org/https://doi.org/10.1016/j.jnc.2023.126488

Sawyer, A.H., Cardenas, M.B., Bomar, A., Mackey, M., 2009. Impact of dam operations on hyporheic exchange in the riparian zone of a regulated river. Hydrological Processes 23, 2129–2139. https://doi.org/10.1002/hyp.7324

Schmutz, S., Bakken, T.H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., Melcher, A., Unfer, G., Zeiringer, B., 2015. Response of Fish Communities to Hydrological and Morphological Alterations in Hydropeaking Rivers of Austria. River Research and Applications 31, 919–930. https://doi.org/10.1002/rra.2795

Singh, V.K., Singal, S.K., 2017. Operation of hydro power plants-a review. Renewable and Sustainable Energy Reviews 69, 610–619. https://doi.org/10.1016/j.rser.2016.11.169

Šmejkal, M., Baran, R., Blabolil, P., Vejřík, L., Prchalová, M., Bartoň, D., Mrkvička, T., Kubečka, J., 2017a. Early life-history predator-prey reversal in two cyprinid fishes. Scientific Reports 7, 6924. https://doi.org/10.1038/s41598-017-07339-w

Šmejkal, M., Bartoň, D., Blabolil, P., Podhorec, P., Souza, A.T., Stejskal, V., Stepanyshyna, Y., Tapkir, S., 2021. Does Fish Conditioning in Aquaculture Increase Survival Success in the Wild? A Case Study on a Cyprinid Fish. Sustainability. https://doi.org/10.3390/su132413936

Šmejkal, M., Ricard, D., Vejřík, L., Mrkvička, T., Vebrová, L., Baran, R., Blabolil, P., Sajdlová, Z., Vejříková, I., Prchalová, M., Kubečka, J., 2017b. Seasonal and daily protandry in a cyprinid fish. Scientific Reports 7, 4737. https://doi.org/10.1038/s41598-017-04827-x

Šmejkal, M., Souza, A.T., Blabolil, P., Bartoň, D., Sajdlová, Z., Vejřík, L., Kubečka, J., 2018. Nocturnal spawning as a way to avoid egg exposure to diurnal predators. Scientific Reports 8, 15377. https://doi.org/10.1038/s41598-018-33615-4

Southworth, J., Nagendra, H., Munroe, D.K., 2006. Introduction to the special issue: Are parks working? Exploring human-environment tradeoffs in protected area conservation. Applied Geography. https://doi.org/10.1016/j.apgeog.2005.11.001

Stanley, J., Miley, W., Sutton, D., 1978. Reproductive requirements and likelihood of naturalization of escaped grass carp in the United States. Transactions of the American Fisheries Society 1919. https://doi.org/10.1577/1548-8659(1978)107

Sutherland, W.J., Adams, W.M., Aronson, R.B., Aveling, R., Blackburn, T.M., Broad, S., Ceballos, G., CÔtÉ, I.M., Cowling, R.M., Da Fonseca, G.A.B., Dinerstein, E., Ferraro, P.J., Fleishman, E., Gascon, C., Hunter, M., Hutton, J., Kareiva, P., Kuria, A., MacDonald, D.W., MacKinnon, K., Madgwick, F.J., Mascia, M.B., McNeely, J., Milner-Gulland, E.J., Moon, S., Morley, C.G., Nelson, S., Osborn, D., Pai, M., Parsons, E.C.M., Peck, L.S., Possingham, H., Prior, S. V., Pullin, A.S., Rands, M.R.W., Ranganathan, J., Redford, K.H., Rodriguez, J.P., Seymour, F., Sobel, J., Sodhi, N.S., Stott, A., Vance-Borland, K., Watkinson, A.R., 2009. One hundred questions of importance to the conservation of global biological diversity. Conservation Biology. https://doi.org/10.1111/j.1523-1739.2009.01212.x

Tamario, C., Sunde, J., Petersson, E., Tibblin, P., Forsman, A., 2019. Ecological and Evolutionary Consequences of Environmental Change and Management Actions for Migrating Fish. Frontiers in Ecology and Evolution 7. https://doi.org/10.3389/fevo.2019.00271

Taylor, C.M., Millican, D.S., Roberts, M.E., Slack, W.T., 2008. Long-term change to fish assemblages and the flow regime in a southeastern U.S. river system after extensive aquatic ecosystem fragmentation. Ecography 31, 787–797. https://doi.org/10.1111/J.1600-0587.2008.05526.X

Terwilliger, M.R., Reece, T., Markle, D.F., 2010. Historic and recent age structure and growth of endangered Lost River and shortnose suckers in Upper Klamath Lake, Oregon. Environmental Biology of Fishes. https://doi.org/10.1007/s10641-010-9679-9

Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., Cooke, S.J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclère, D., Lynch, A.J., Leonard, P., McClain, M.E., Muruven, D., Olden, J.D., Ormerod, S.J., Robinson, J., Tharme, R.E., Thieme, M., Tockner, K., Wright, M., Young, L., 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. Bioscience 70, 330–342. https://doi.org/10.1093/BIOSCI/BIAA002

Tryjanowski, P., Hartel, T., Báldi, A., Szymański, P., Tobolka, M., Herzon, I., Goławski, A., Konvička, M., Hromada, M., Jerzak, L., Kujawa, K., Lenda, M., Orłowski, G., Panek, M., Skórka, P., Sparks, T.H., Tworek, S., & A.W., Żmihorski, M., 2011. Conservation of Farmland Birds Faces Different Challenges in Western and Central-Eastern Europe. Acta Ornithologica 46, 1–12. https://doi.org/10.3161/000164511X589857

Vašek, M., Prchalová, M., Říha, M., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Jůza, T., Kratochvíl, M., Muška, M., Peterka, J., Sajdlová, Z., Šmejkal, M., Tušer, M., Vejřík, L., Znachor, P., Mrkvička, T., Seŋa, J., Kubečka, J., 2016. Fish community response to the longitudinal environmental gradient in Czech deep-valley reservoirs: Implications for ecological monitoring and management. Ecological Indicators 63, 219–230. https://doi.org/10.1016/j.ecolind.2015.11.061

Volpato, G.L., Barreto, R.E., Marcondes, A.L., Andrade Moreira, P.S., de Barros Ferreira, M.F., 2009. Fish ladders select fish traits on migration–still a growing problem for natural fish populations. Marine and Freshwater Behaviour and Physiology. https://doi.org/10.1080/10236240903299177

Wang, J., Chen, L., Tang, W., Heino, J., Jiang, X., 2021. Effects of dam construction and fish invasion on the species, functional and phylogenetic diversity of fish assemblages in the Yellow River Basin. Journal of Environmental Management 293, 112863. https://doi.org/https://doi.org/10.1016/j.jenvman.2021.112863

Wang, L., Infante, D., Lyons, J., Stewart, J., Cooper, A., 2011. Effects of dams in river networks on fish assemblages in non-impoundment sections of rivers in Michigan and Wisconsin, USA. River Research and Applications 27, 473–487. https://doi.org/10.1002/RRA.1356

Young, P.S., Cech, J.J., Thompson, L.C., 2011. Hydropower-related pulsed-flow impacts on stream fishes: A brief review, conceptual model, knowledge gaps, and research needs. Rev Fish Biol Fish 21, 716–731. https://doi.org/10.1007/s11160-011-9211-0

Zeh, M., Dönni, W., 1994. Restoration of spawning grounds for trout and grayling in the river High-Rhine. Aquatic Sciences 56, 59–69. https://doi.org/10.1007/BF00877435

Zhang, H., Jarić, I., Roberts, D.L., He, Y., Du, H., Wu, J., Wang, C., Wei, Q., 2020. Extinction of one of the world's largest freshwater fishes: Lessons for conserving the endangered Yangtze fauna. Science of the Total Environment. https://doi.org/10.1016/j.scitotenv.2019.136242

Zimmerli, S., Bernet, D., Burkhardt-Holm, P., Schmidt-Posthaus, H., Vonlanthen, P., Wahli, T., Segner, H., 2007. Assessment of fish health status in four Swiss rivers showing a decline of brown trout catches. Aquatic Sciences 69, 11–25. https://doi.org/10.1007/s00027-006-0844-3

Acknowledgements

I would like to thank the Faculty of Science of the University of South Bohemia in České Budějovice and its Department of Ecosystem Biology, which offers the Limnology (Hydrobiology) doctoral program, and especially its guarantor and head of department prof. RNDr. Jaroslav Vrba CSc. for his professional and friendly approach. Thanks to this Ph.D. program, I was able to visit the Chair of Aquatic Systems Biology at the TUM School of Life Sciences at the Technical University of Munich in Freising, Germany. I spent a nice time in Bavaria to learn about their methods and my thanks go to prof. Dr. Jürgen Geist, the head of the chair, and Dr. rer. nat. Christoffer Nagel, who shares a similar scientific topic with me took care of me during my stay and provided me with an interesting and diverse program.

I am honoured that I was able to write my dissertation at the Institute of Hydrobiology of the Biology Centre of the Academy of Sciences of the Czech Republic under the great supervision of former and current directors prof. Jan Kubečka Ph.D. and RNDr. Jiří Peterka Ph.D.. I would like to thank all my colleagues at the Fish Ecology Unit of the Department of Fish and Zooplankton Ecology for their supportive and friendly cooperation during my studies. It was always a pleasure to work together on various field campaigns, including those important for this thesis.

I would like to express my sincere gratitude to all those who participated in the Želivka field campaign, which presented challenging conditions, including harsh and cold weather during early spring. I would like to specifically acknowledge the contributions of Mgr. Luboš Kočvara, Mgr. Zuzana Sajdlová Ph.D., Aneta Schreinerová, Ing. Ondřej Remeš, and Ing. Tomáš Kolařík, who helped set up and operate our field station on numerous occasions. Of course, there were many other individuals involved in this campaign, and I am truly grateful to all of them. I would also like to extend special thanks to Zdeněk Popelka and his mother. Although Zdeněk started as an observer, he quickly became a valuable local guide and an essential member of our team throughout the years.

I would like to take a moment to express my appreciation to the Vltava River Authority for their valuable cooperation. Specifically, I am grateful to

RNDr. Jindřich Duras Ph.D. for his inspiring dedication to water protection and Ing. David Kortan Ph.D. for his invaluable assistance with water flow measurements, as well as for the delicious sausages he provided.

I must also extend my heartfelt thanks to all my coauthors, whose contributions and suggestions helped to bring my thesis to completion. Additionally, I am deeply grateful for the funding provided by research projects that made this study possible, and we acknowledge this financial support in each paper included in the thesis.

I would like to express my gratitude towards my family and buccaneers. My parents, RNDr. Irena Králová and Ing. David Bartoň, have been a constant source of support throughout my life and academic career. I am also thankful to my siblings, particularly my sister RNDr. Alena Sucháčková Ph.D., who not only offered her support as an older sibling but also as an experienced scientist to look up to. I owe a special thanks to my wife, MDDr. Kateřina Bartoňová, for her emotional and financial support, and our two children, Oskar and Anna, who were both born during my Ph.D. study. I understand it must have been difficult for them since I spent countless days away in the field during those years, returning with fishy-smelling clothes.

Lastly, but most importantly, I would like to express my heartfelt gratitude to RNDr. Marek Šmejkal Ph.D, my supervisor, he played the most crucial and essential role in this thesis. This thesis would not have been possible without his guidance, support, and encouragement at every stage of the dissertation. I look forward to further cooperation in exciting and rewarding research.

Papers

Paper I

Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species

Received: 31 July 2020 | Revised: 13 November 2020 | Accepted: 9 January 2021
DOI: 10.1002/eco.2280

RESEARCH ARTICLE

WILEY

Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species

Daniel Bartoň[1,2] | Felipe Bretón[2,3] | Petr Blabolil[1,2] | Allan T. Souza[1] | Lukáš Vejřík[1] | Zuzana Sajdlová[1] | Tomáš Kolařík[1] | Jan Kubečka[1] | Marek Šmejkal[1]

[1]Biology Centre of the Czech Academy of Sciences, Institute of Hydrobiology, České Budějovice, Czech Republic

[2]Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

[3]Biology Centre of the Czech Academy of Sciences, SOWA, České Budějovice, Czech Republic

Correspondence
Marek Šmejkal, Biology Centre of the Czech Academy of Sciences, Institute of Hydrobiology, České Budějovice, Czech Republic, Na Sádkách 7, 370 05.
Email: marek.smejkal@hbu.cas.cz

Funding information
NAZV, Grant/Award Number: QK1920326; TACR, Grant/Award Number: TJ02000012

Abstract

Human-induced changes in the hydrological regimes of lotic waters such as hydropeaking have significant negative impacts on riverine life. However, the impacts of dynamic changes in water flow on adhesive fish eggs are not very well known. We focused on the effects of hydropeaking on the spawning ground of a rheophilic cyprinid fish, the asp (*Leuciscus aspius*). We tested whether a sudden increase in water velocity caused by hydropeaking may have negative effect on the adhesive eggs by the combination of field observations and laboratory experiments. The main objectives of the study were to (i) investigate abiotic characteristics of an asp spawning ground, (ii) monitor egg densities in relation to hydropeaking events and (iii) test detachment rates of the asp eggs in laboratory conditions in relation to water velocity. The asp spawning ground was associated with shallow water depths (0.2–0.4 m) and flowing water (0.1–0.4 m s^{-1}) during base flow. The water velocity that occurred on the spawning ground during the hydropeaking event was measured to be from 0.7–1.2 m s^{-1}. Asp eggs nearly disappeared from the spawning ground before their hatching time probably due to several hydropeaking events. The laboratory experiments showed the significant dependency of egg detachment rates on the water velocity and substrate type with a critical value of 0.7 m s^{-1}. Our data suggested that eggs may be negatively impacted by flow alterations. Avoiding hydropeaking or keeping water velocity below critical values is recommended for the management of rheophilous fish spawning grounds.

KEYWORDS
fish reproduction, habitat alternation, *Leuciscus aspius*, river ecology, wildlife conservation

1 | INTRODUCTION

Man-made reservoirs have been built on the majority of rivers around the world due to their social benefits (Nilsson, Reidy, Dynesius, & Revenga, 2005). Hydropower is an effective and widespread energy source, and as a renewable source, it is generally considered environmentally friendly (Singh & Singal, 2017). One of the advantages of reservoirs generating hydropower through turbines is the ability to use energy from running water as electricity by increasing the water flow at the time when needed (Akinyele & Rayudu, 2014). But with advantages come many disadvantages for both the nature and the mankind. Currently, many rivers are managed with flow regulation regimes, such as hydropeaking—pronounce periodic pulsing of water discharge, especially in the densely populated area all over the world (Grill et al., 2019). The hydropeaking occurrence in rivers is expected to increase in some parts of the world (Ashraf et al., 2018). This energy source and reservoirs in general have their downsides in terms of negatively impacting river ecosystems (Bain, Finn, & Booke, 1988;

https://doi.org/10.1002/eco.2280

Bejarano, Jansson, & Nilsson, 2018; Kennedy et al., 2016; Vanzo, Zolezzi, & Siviglia, 2016).

Various negative effects on riverine life caused by artificial altering of river flow have been described (Schmutz et al., 2015; Shen & Diplas, 2010). Hydropeaking can negatively affect biomass development of the stream periphyton (Bondar-Kunze, Maier, Schönauer, Bahl, & Hein, 2016) as well as macrophyte (Bejarano et al., 2018) and insect diversity (Kennedy et al., 2016). Moreover, hydropeaking also causes artificial drift and a potentially critical decrease in the biomass of river benthic invertebrates (Bruno, Siviglia, Carolli, & Maiolini, 2013). Therefore, the fishes preying on invertebrates might be locally deprived from food resources and hence forced to shift their feeding habits or forced to be bottom-up limited (Dodrill, Yackulic, Kennedy, & Hayes, 2016; Power, 1992).

In addition to this indirect effect on fish fauna, hydropeaking was found to influence fish ecology directly, impacting the vulnerable stages in fish early life history, such as egg development in spawning sites or freshly hatched larvae (Hayes et al., 2019). One issue can be the dewatering of the spawning grounds (redds) when the river is off peak, which can cause high mortality of the eggs (Grabowski & Isely, 2007; McMichael, Rakowski, James, & Lukas, 2005). The opposite effect on the early fish life stages may be caused by an artificial increase in flow that triggers high downstream drift (Young, Cech, & Thompson, 2011). Flow fluctuations as well as the temperature variations commonly connected to hydropeaking are the factors causing stress, interruptions in spawning, altered hatching and migration of juvenile fish, which all lead to a reduction in fish recruitment (Hayes et al., 2019; Moreira et al., 2019). In artificial channels with unstable flow and different substratum conditions, loss of dace (*Leuciscus leuciscus*) eggs has been previously recorded mostly in unsuitable substratum but adhered well to appropriate substrate size (Mills, 1981).

Considering the negative effect of hydropeaking, it may be expected that particular reproductive guilds of fishes will be more vulnerable than others (Balon, 1975). Among the guild of rheophilic fishes that seeks open substratum for reproduction, we can consider pelagophils less affected by hydropeaking, since their eggs have evolved to be taken by the current and drift until hatching (Balon, 1975; Stanley, Miley, & Sutton, 1978). Likely the most vulnerable reproductive guild to rapid hydropeaking are lithophiles (which have adhesive eggs that attach to gravel and stones), given that their eggs are at greatest risk of being washed away due to their exposed location in the riverbed.

As a lithophilic fish model for this study, we chose the asp (*Leuciscus aspius*), a large cyprinid predator originally inhabiting the lowland rivers of Central and Eastern Europe (Kottelat & Freyhof, 2007) and thriving in many European reservoirs (Vašek et al., 2016). Asps migrate to fast-flowing waters where they spawn on stony and gravel substratum in the early spring (Šmejkal, Baran, et al., 2017; Šmejkal, Ricard, et al., 2017). The majority of their eggs are laid at night (Šmejkal et al., 2018); hence, during the off-peak period since at the study site peaks come during the daytime, this could vary at other locations based on e.g. hydropower optimisation (Huuki, Karhinen, Ashraf, Torabi Haghighi, & Marttila, 2020). Asp releases eggs freely in the water column and eggs adhere to the substrate (Mills, 1981) due to their modified zona radiata, which creates sticky structures over the entire egg surface (Riehl & Patzner, 1998). Eggs are developing approximately within 20 days in average spring temperature around 10°C. Juvenile fish migrate to slow-flowing waters after hatching; after reaching adulthood between their fourth and sixth year of life, they return to the tributary to reproduce (Peterka, Vasek, Kubeka, Hladik, & Hohausova, 2004; Říha, Hladík, Mrkvička, Prchalová, & Čech, 2013; Šmejkal, Ricard, et al., 2017).

Several studies focused on off-peak effects of hydropeaking and impact of dewatering on river fish fauna (Bain et al., 1988; Casas-Mulet, Saltveit, & Alfredsen, 2015; Korman, Kaplinski, & Melis, 2011; McMichael et al., 2005; Schmutz et al., 2015), but the potential negative effect of peaking conditions on the adhesive eggs has not yet been properly studied. Studies dealing with hydropeaking are rarely focused on the fate of eggs and instead focus on juvenile and adult fishes (Auer, Zeiringer, Führer, Tonolla, & Schmutz, 2017; Hayes et al., 2019; Schmutz et al., 2015; Scruton et al., 2008; Young et al., 2011). In this study, we aim to (i) identify the water velocity and depth at which our model lithophilic asp preferentially lays its eggs; (ii) investigate whether the eggs were affected by hydropeaking on the spawning ground under field conditions; and (iii) identify the detachment rates of the eggs under peaking conditions in a laboratory setup based on water flow velocities, exposure time and type of surface.

2 | MATERIALS AND METHODS

2.1 | Study site

The study site is located in the Želivka River, the main tributary of the Želivka Reservoir (39 km long, 1602 ha), (49°578497′N, 15°251671′E) Czech Republic. The migration upstream of the spawning site is restricted by a concrete weir. The tributary hosts more than 2000 adult asps during the spawning season, which migrate from the reservoir to reproduce in the early spring (Šmejkal, Ricard, et al., 2017). This tributary appears to be the only suitable spawning site for asp in the reservoir.

Two hydroelectric power plants are located approximately 12 km upstream, one on the Želivka River and another on a tributary (Trnava River, Figure 1). The hydropower plant on the Trnava River has the ability to release water in the channel for canoe slalom trainings and races, which seriously affects the conditions on the spawning ground. The base flow conditions vary between 3 and 6 $m^3 s^{-1}$. Hydropeaking occurred six times with the amplitude of 12 $m^3 s^{-1}$ during the 1-month-long reproductive season and egg development in 2018. Spawning started at the end of March and ended in the middle of April, while the eggs developed according to temperature and laying date until early May according to day degrees estimated in the literature (Kujawa, Mamcarz, & Kucharczyk, 1997).

2.2 | Characterisation of spawning site

The water velocity was measured in 2018 using FlowTracker2® (SonTrek, San Diego, USA). In approximately 150 m of the river where

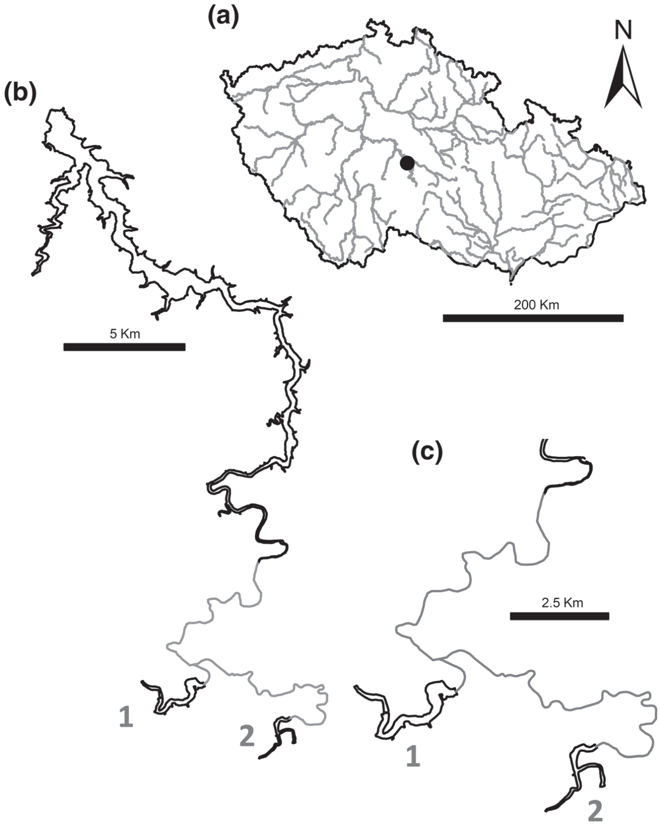


FIGURE 1 A map showing (a) position of the Želivka reservoir within Czech Republic and (b and c) position of the Trnávka (1) and Sedlice (2) Reservoir causing hydropeaking on the study site

asps aggregate for spawning (Šmejkal, Ricard, et al., 2017), 11 transects were defined that were perpendicular to the river flow direction, and on each transect, we measured the velocity of the flow 20 cm above the bottom. We took measurements for at least 10 points per transect (10–29) (every 1 or 2 m). Measurements of water depth were taken simultaneously. Where the river was not wadable, a boat fixed with the rope to the shore was used to measure the depth and velocity. The temperature during the monitoring campaign was measured from 31 March to 25 April by datalogger (HOBO Pendant Temperature/Light 64K Data Logger, Onset Computer Corporation, Bourne, Massachusetts, USA) placed in the tributary at 0.5-m depth. Substrate type was evaluated from the pictures taken during the egg densities estimation (see more bellow in the chapter Assessing effects of hydropeaking).

2.3 | Velocity during hydropeaking

For safety reasons, it was impossible to measure the water velocities in the main course of the river during hydropeaking (left channel under the weir in Figure 2). On 22 March 2019 before the spawning season, hydropeaking was simulated by the river authority (Povodí Vltavy s.p.) to assess the velocities that the eggs are exposed to during the hydropeaking. The water velocity 5 cm above the substrate (the get the closest value that the eggs are exposed to) was measured only in the right channel in the transect 4 with lower discharge. To obtain the order of magnitude of the expected mean velocities under peak flows in the main stream, we ran a simple hydraulic model using HEC-RAS 1D (USACE, 2010). It was a steady flow model based on 11 transects. This bathymetry included the heights of both the river bottom and water surface, and it was surveyed when river discharge was 6 $m^3\ s^{-1}$. Meanwhile, the water surface levels during hydropeaking were gauged at 18 $m^3 s^{-1}$. In the model, we assumed a constant 0.04 Manning roughness coefficient, and additional river cross sections were generated every metre by linear interpolation. First, we ran the model for the two abovementioned flow rates. In both cases, boundary conditions were known (measured) water depths at the extremes of the bathymetry (upstream and downstream). The resulting water levels were simulated in between the extremes of the model were compared with water surface measurements available for five cross sections, which differed by less than ±5 cm. This difference may be attributed to slight changes in the

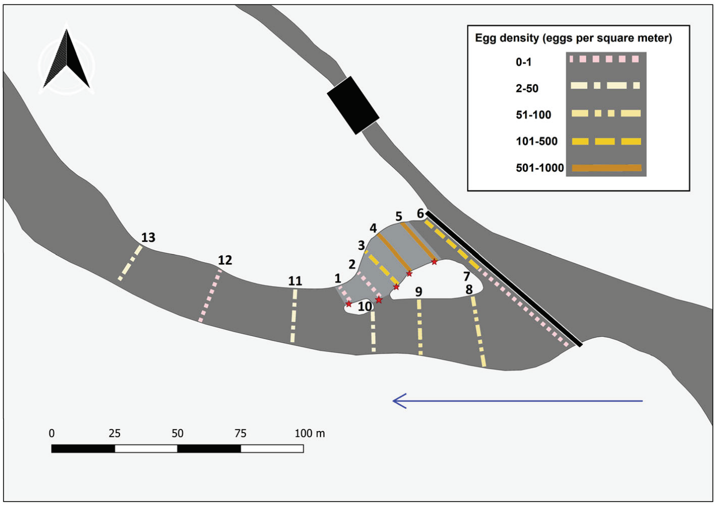


FIGURE 2 Schematic representation of average density distribution of asp eggs recorded on 9 April. Eggs were counted from bottom photos of 0.09 m2 and then average egg densities per m^2 of transect were counted and colour and line scaled to transects shown on the map. First five transects marked with red star were further used to investigate the fate of eggs during the season. The arrow shows the direction of the flow, main flow is going through measured area (in colour), the black rectangle in the top centre represents old watermill on millrace, where nearly no water runs through. Black line crossing the river above the study area represent a weir (a barrier for further fish migration)

actual bottom roughness coefficients along the river reach, which we considered irrelevant for this purpose (estimating an order of magnitude of peak flow velocities). Then, we simulated two flow conditions considered representative of the base and peak flows: 4 and 16 m^3 s^{-1}, respectively (Table 1). Since we did not have measurements for these representative flow rates, we set as boundary condition a downstream energy slope instead of a known water level. It was assumed that the energy slope for 4 and 16 m^3 s^{-1} has to be similar to when the river is carrying 6 and 18 m^3 s^{-1}, respectively (not necessarily water level). Therefore, we used the energy slopes that were computed in the first simulation.

2.4 | Assessing the effects of hydropeaking

We used the transects characterising spawning site to estimate the asp egg densities on 9 April 2018. The activity of the spawning fish was known to us because the adult fish movement is yearly tracked by passive telemetry (Šmejkal et al., 2018; Šmejkal, Ricard, et al., 2017). To map the egg density, we used underwater cameras (Epoque Edivecam, Epoque World Co., Ltd., Japan) to photograph 0.09 m^2 of the bottom surface every 0.5 or 1.0 m, with at least 10 points per transect (range 10–36). The minimum sampling depth was limited by the camera position, which was 25 cm above the river bottom. The presence of the eggs was verified by visual observation during wading and snorkelling. The egg densities were estimated from the transect survey with similar transects as used for velocity and depth measurements (2 more added) (Figure 2). Eggs were counted using the image processing software ImageJ 1.52i (ImageJ, 2018). Pale spots on the pictures of asp egg size were defined as eggs and counted. Number of stones covering 90% of the picture was counted in order to avoid categorising invisible parts among the stones. Photos covered with fine gravel were categorised as fine gravel. Photos covered with leaves or biofilm preventing counting the stones were omitted from the analysis. No other fish species were observed to spawn in the tributary during the monitoring period, and species such as common bream (*Abramis brama*), bleak (*Alburnus alburnus*) and roach (*Rutilus rutilus*) have higher temperature preferences for spawning in the tributary (Hladík & Kubečka, 2003).

The transect method was used to determine how the egg counts were affected by hydropeaking. The five transects with high abundance of eggs located between the right riverbank and the islets were examined multiple times (Figure 2). The egg density was investigated on 11, 16, 21 and 25 April 2018 between 9 AM and 11 AM (time schedule was chosen due to good light level and low river flow conditions).

TABLE 1 Sum up of flow condition measured and model during normal condition (base flow) and hydropeaking events (peak flow)

			Velocity (m s^{-1}) mean, range, SD	
Flow condition	Discharge (m^3 s^{1-})	Water elevation (m) mean, range, SD	Measured	Modelled
Base flow	4	376.48, 376.40–376.65, 0.09	0.3, 0.1–0.4, 0.1	0.5, 0.2–0.5, 0.1
Peak flow	16	376.78, 376.51–377.13, 0.22	1.0, 0.7–1.2, 0.2[a]	1.1, 0.3–1.4, 0.3

[a] Measured only in right channel.

2.5 | Experimental evaluation of critical velocity

Adult asps were caught on 8 April and transported to the laboratory at the Institute of Hydrobiology in České Budějovice to obtain eggs for the experiment. Asps were kept in the same temperature of water as that where they were caught (11°C). Females were stimulated for ovulation by Ovopel (Unic-trade, Budapest, Hungary). All females started ovulating after 12 hours. The eggs obtained were fertilised through the ‘dry’ method with milt from the batch sample obtained from three males (Kupren, Mamcarz, & Kucharczyk, 2011; Vostradovský & Váša, 1981). The water temperature was kept constant at 11°C in the whole system during fertilisation and the experiment.

To determine the influence of different abiotic variables (flow velocity, substrate type and exposure time) on the egg detachment rate, we performed an experiment in which a modified Brett-type tunnel (Brett 1962, Enders and Scruton 2006) with an adjustable flow rate up to 3.0 m s^{-1} was used for the experiment. The tunnel was made from PVC (120 × 8 × 8 cm, length–width–height; Figure 3). A flow straightener was installed at the beginning of the tunnel to homogenise the flow in the longitudinal direction while reducing the lateral and vertical velocity components. Ten eggs were laid on tiles (specification below), and a drop of water on each of them triggered the adhesion process. Tiles of 8 × 8 cm with three different roughnesses were used, and three replicates were conducted for each flow condition and each time of exposure separately (excluding the 2.5-m s^{-1} velocity, for which longer time of exposure was not conducted); in total, there were 18 replicates per flow condition including all substrate types and both time treatments. The following types of tiles were designed to test the effect of substrate roughness on the egg detachment probability: smooth concrete substrate with a flat surface, medium with gravel of 2–5 mm and coarse with 7- to 20-mm gravel. Five flow conditions with nominal velocities 0.3, 0.7, 1.0, 1.7 and 2.5 m s^{-1} were chosen according to the spawning site water velocities, which were 0.16–0.34 m s^{-1} under normal off-peak conditions with discharge between 3 and 6 m^3 s^{-1} (Šmejkal, Ricard, et al., 2017), and the discharge was three to six times higher during hydropeaking according to data obtained from the river authority (Povodí Vltavy s.p.). The water velocities in the laboratory experiments were measured using FlowProbe (Global Water, College Station, USA). The difference in detachment rates related to exposure time was tested in two time treatments—15 and 60 min.

Additionally, to test whether the effects of water velocity were not overstated in comparison with the natural conditions with biofilm occurrence, we repeated the experiment in 2019 to compare smooth tiles with and without biofilm. Smooth concrete tiles were left on the river bottom for 2 months (from 31 January). Eggs were attached using the same method in 0.3, 0.7, 1 and 1.7 m s^{-1} velocity and were tested on tiles with and without biofilm for 15-min exposures. These tests were repeated three times for each velocity and type of substrate.

2.6 | Statistical analysis

To investigate which abiotic factors influence asp egg density on the spawning ground, we used generalised linear models (GLMs) to test the explanatory abiotic variables of water velocity and water depth. The egg density counts used in this test were taken from measurements on 9 April, which were closest in time to the water velocity and depth measurements conducted on 3 April. The density of the eggs was very low at many points of measurement, so we used the Poisson family of error distribution. Analysis of variance (ANOVA) was used to compare the best GLM model with the null model. An interactive forward procedure based on the lowest possible Akaike information criterion (AIC) was used to select the best combination of variables (Hastie, 2017). To test if egg densities changed significantly over time, non-parametric Spearman's rank correlation analysis was used to investigate the correlation between the date and egg densities measured during the spawning season (Nian Shong Chok, 2010).

To understand which factors caused asp egg detachment in the laboratory, we used generalised linear models (GLMs) to test the influence of individual explanatory variables on the number of detached eggs. For the first tunnel experiment was best fitting Poisson family of error distribution but in the experiment with and

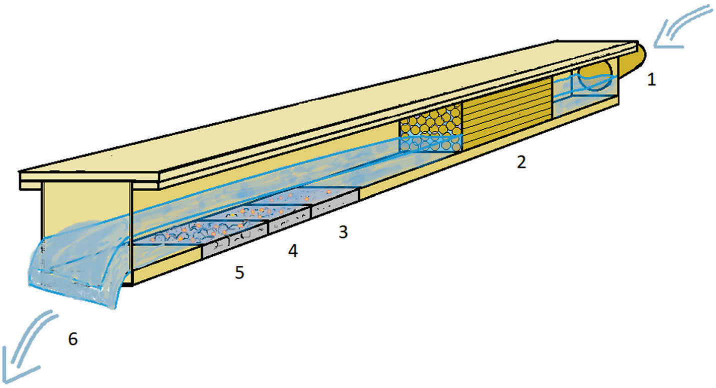


FIGURE 3 Graphical visualisation of flow tunnel with dimensions of 120 × 8 × 8 cm (length–width–height). Description: 1—water input from water pump with adjustable velocity, 2—flow straightener, 3—tile with smooth substrate, 4—tile with medium substrate, 5—tile with coarse substrate, 6—water output returning water to circulation

without biofilm many of the measurements resulted in either detachment or survival of all eggs, we used a quasibinomial family of error distributions. We used analysis of variance to compare (ANOVA) the models and an interactive forward procedure to select the best combination of variables based on the lowest possible AIC.

All statistical analyses were conducted in the computer software R version 3.5.1 (R Development Core Team, 2016). For visual presentation of the egg densities, depths and velocities on the spawning ground we used the programmes QGIS 3.4.2 (QGIS Development Team, 2018) and GIMP 2.10.8 (GIMP Develepment Team, 2018).

3 | RESULTS

3.1 | Characterisation of spawning site

The lowest average water velocity per transect was 0.08 m s^{-1}, and the highest was 0.38 m s^{-1} (Table 2). The average depth of water in the same transects ranged from 0.24 to 1.02 m (Table 2). The egg densities ranged from 0 to 1933 per m^2 (mean: 106, SD: 315), with the highest densities recorded below the weir between the right side of the bank and the upstream island (Figure 2). The water temperature during the monitoring season in 2018 increased from 4°C on 31 March to 14°C on 25 April (mean temperature 9.7°C). Eggs were attached to rocky substrate. Boulders were counted from 242 points representing pictures taken in the transects resulting in 8.6 boulders on average per 0.09-m^2 river bottom (range: 1–36, SD: 7,2). Only five points were with fine gravel and 37 points were uncountable due to high biofilm or foliage cover.

The egg densities measured at the study site were significantly dependent on the water depth and water velocity. The GLM with a single explanatory variable revealed that egg density was negatively influenced by the water depth and positively influenced by water velocity. The lowest AIC for a single explanatory variable was for the depth model. The strongest full model involved the depth and water velocity (Table 3). The full model showed importance in both variables. Estimated coefficient of depth for the model was negative −0.037 ($p < 0.001$) and positive for the velocity 0.196 ($p = 0.037$).

TABLE 2 Water velocity and depth measured on the study site

Transect number	Velocity (m s^{-1}) mean, range, SD	Depth (m) mean, range, SD
1–2	0.14, −0.03–0.31, 0.12	0.35, 0–0.46, 0.16
3–4	0.13, −0.07–0.36, 0.14	0.23, 0–0.34, 0.11
5	0.14, 0–0.22, 0.07	0.37, 0–0.50, 0.16
6	0.38, −0.05–0.89, 0.27	0.44, 0.35–0.6, 0.09
7	0.08, −0.13–0.50, 0.19	0.50, 0–0.80, 0.20
8	0.24, 0–0.39, 0.11	0.57, 0–0.76, 0.21
9	0.23, 0–0.31, 0.09	0.61, 0–0.78, 0.23
10	0.21, 0–0.29, 0.09	0.71, 0–0.9, 0.28
11	0.14, 0–0,26, 0.08	0.90, 0–1.15, 0.36
12	0.11, −0.01–0.24, 0.08	1.02, 0–1.3, 0.36
13	0.12, 0–0.19, 0.05	1.00, 0–1.35, 0.38

Note: Measurements were taken on 3 April 2018 during off-peak period. Velocity were measured 20 cm above the river bottom. Transect numbers are visualised in Figure 2.

3.2 | Velocity during hydropeaking

Measured velocities during peak flow ranged from 0.7 to 1.2 m s^{-1} at the transect 4. Modelling results show the average flow from 0.2 to 0.8 m s^{-1} under base flow and from 0.3 to 1.4 m s^{-1} under peak flow among the cross sections (Table 1). Our simulation computed maximum water depths in the area of highest egg density (transects 4 and 5 on the right-hand channel) of 24 and 56 cm for the base and hydropeaking flows, respectively.

3.3 | Assessing the effects of hydropeaking

We recorded a significant decrease in egg density during the spawning season. The average egg density measured in the five transects (total of 60–62 points) did not drop after the first hydropeaking occurrence; from a mean of 348 eggs per square metre on 9 April to 375 eggs per square metre on 11 April, but rapidly decreased after the next hydropeaking events. On 12 April, hydropeaking occurred, and egg density dropped sharply to 38 eggs per square metre on 16 April and did not recover in two following measurements (Table 4). The average egg density negatively correlated with the date of sampling (rho = −0.417, $p = 0.038$), demonstrating a decrease in egg density on the spawning ground.

3.4 | Experimental evaluation of critical velocity

Water velocity was the major significant abiotic variable causing egg detachment from the tiles in the laboratory tests and the substrate type and the time of exposure had a significant influence (Figure 4). The lowest AIC observed corresponded to the GLM with the velocity, substrate type and time of exposure (Table 5). The best univariate GLM was with the water velocity. There was no large difference in the AICs of the GLMs suggesting that there is one prevailing variable. The most influential abiotic variable of the best model is the water velocity ($p < 0.001$) with an estimated coefficient of 0.586. Time of exposure and substrate also showed significant p values (time: $p = 0.015$, substrate: $p = 0.040$) but with a very low estimated coefficient for the time of exposure (0.006) and the negative coefficient for substrate type (−0.266) which was not a quantitative variable and was treated as a factor.

The test of water flow on the eggs attached to tiles with and without biofilm showed a significant difference in egg detachment for both velocity and biofilm presence. Best overall GLM according to lowest AIC was egg detachment explained with both velocity and biofilm presence. Velocity in the model resulted with lower p value

TABLE 3 Generalised linear models of asp *Leuciscus aspius* egg density influenced by abiotic factors measured on the spawning ground (water velocity, depth)

Model	df	Resid. dev.	AIC
NULL (egg density ~ + 1)	272	106,855	106,857
Egg density ~ velocity	1.27	105,015	105,019
Egg density ~ depth	1.27	79,143	79,147
Egg density ~ depth + velocity	**1.27**	**77,556**	**77,562**

Note: The most significant single explanatory model of egg density is depth and strongest full model is with water velocity added (in bold).

TABLE 4 Average values of asp *Leuciscus aspius* egg density per square metre in measured from transects in the Figure 2

Date	Transect 1: mean, max, SD	Transect 2: mean, max, SD	Transect 3: mean, max, SD	Transect 4: mean, max, SD	Transect 5: mean, max, SD
9 April	0, 0, 0	1, 11, 2.87	556, 1,578, 457.94	748, 1933, 636.01	434, 2300, 678.73
11 April	69, 267, 94.91	29, 267, 71.56	339, 756, 217.70	625, 6444, 1604.52	812, 2300, 894.81
16 April	0, 0, 0	0, 0, 0	3, 33, 9.50	95, 422, 143.82	89, 367, 113.67
21 April	1, 11, 3.35	0, 0, 0	3, 33, 9.70	64, 200, 73.10	198, 967, 299.34
25 April	0, 0, 0	5, 56, 16.04	2, 22, 6.16	1, 11, 3.21	5, 33, 10.00

Note: Minimal measured value was always 0 in all transects within all days so only maximal value (max) is presented to see the range.

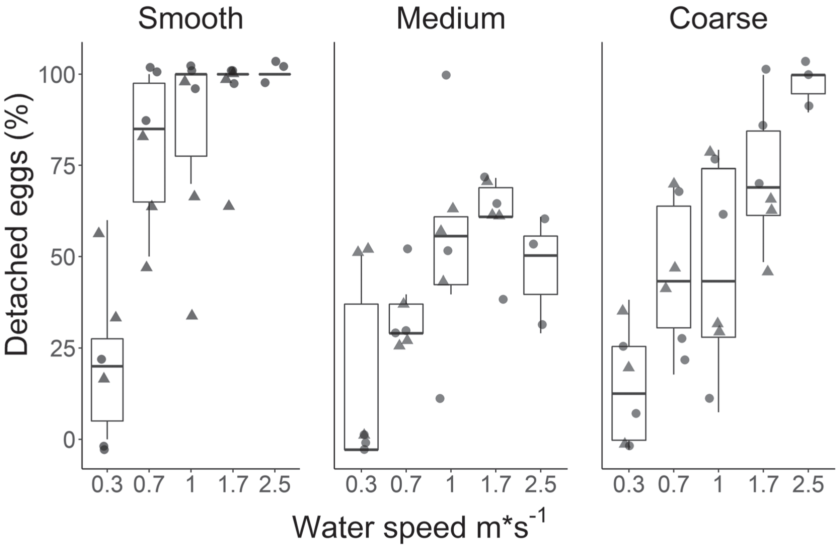


FIGURE 4 Boxplot plot of percentage of detached eggs in the experiment under influence of significant abiotic variables water velocity and substrate type. The boxes represent the boundaries of the upper and lower quartiles; the thick lines represent medians, the whiskers upper and lower adjacent value. Each roughness of substrate is plotted separately, showing distribution of observed detachments in different water velocities. Number of observations per treatment was 6 (3 in 2.5 m s^{-1}). Dots indicate exposition time 15 min and triangles 60 min

(p < 0.001) with an estimated coefficient of 6.70 but presence of biofilm also showed influence on egg detachment (p = 0.001) and an estimated coefficient of 2.95 (Table 6). The eggs detached more from tiles with biofilms (mean: 7.25, range: 0–10, SD: 3.85, sample size: 12) than from the tiles lacking natural river biofilms (mean 4.25, range 0–10, SD: 3.88, sample size: 12).

TABLE 5 Generalised linear models of asp *Leuciscus aspius* eggs detachment in flow tunnel related to explanatory variables (water velocity, substrate type and time of exposure)

Model	df	Resid. dev	AIC
NULL (detachment ~ + 1)	80	195.45	197.45
Detachment ~ velocity	1.79	128.56	132.56
Detachment ~ substrate	1.78	190.74	196.74
Detachment ~ time	1.79	195.45	199.45
Detachment ~ velocity+ substrate	2.77	123.85	131.85
Detachment ~ velocity + time	1.78	122.67	128.67
Detachment ~ velocity + substrate + time	**2.76**	**117.96**	**127.96**

Note: Strongest model with single explanatory is velocity and the strongest full model of egg detachment is explanation of water velocity, substrate type as factor (*substrate*) and time (in bold).

TABLE 6 Generalised linear models of asp *Leuciscus aspius* eggs detachment in flow tunnel related to explanatory variables (substrate type and presence of biofilm)

Model	Df	Resid. Dev.	AIC
NULL (detachment ~ + 1)	23	22.255	22.7333
Detachment ~ biofilm	1.22	20.007	20.9630
Detachment ~ velocity	1.22	8.566	9.5223
Detachment ~ biofilm + velocity	**1.21**	**3.892**	**5.3265**

Note: Strongest model with single explanatory is velocity and the strongest full model of egg detachment is explanation of water velocity and biofilm presence.

4 | DISCUSSION

Asps prefer stretches with hard bottoms and moderate flow for spawning (Šmejkal, Ricard, et al., 2017). Our study suggested that water depth between 0.2 and 0.4 m and velocity between 0.1 and 0.3 during baseflow conditions were the main factors in spawning ground selection. During the spawning season, several hydropeaking events occurred that exceeded the base discharge three to six times. Water velocity exceeding 1 m s^{-1} on the spawning ground may have a substantial impact on attached asp eggs (at this velocity, on average 61.7% of all eggs detached from all substrate types, with substantially higher detachment on the smooth substrate or biofilm). Detachment from substrate may cause higher predation pressure due to predation in the drifting stage (Šmejkal, Baran, et al., 2017).

The results from the hydraulic model applied here suggested a two-fold average increase in the water velocities with river discharge, which was a relative underestimation of the measured velocity under hydropeaking. Based on an attempt by the river authority to measure the velocity in 2019, the actual values reached 0.7 to 1.2 m s^{-1}, with a discharge in the river of 16 m^3 s^{-1}. Therefore, the velocities of 0.7 and 1.0 m s^{-1} in the laboratory settings were representative of the changes in hydrodynamics from the base to peak flows. These values were already quite critical for the number of detached eggs in the laboratory settings. Our results of high detachment of eggs were different from Mills (1981), his experiment did not show such a high detachment of eggs from related fish but the experiment water increase was only up to 0.65 m s^{-1}.

The simple 1D hydraulic model was applied with the purpose of having a rough estimation of the mean velocity magnitudes during hydropeaking. However, such a model has significant limitations that prevented us from further data analysis. Not only because it provides cross-sectional integrated results, but also because it does not consider lateral flow. Assessing the spatial and temporal distribution of two key hydraulic parameters for fish habitat (water depth and velocity) requires a more sophisticated numerical scheme. For instance, Kopecki, Schneider, and Tuhtan (2017) proposed a 2D depth-averaged model that includes a depth-dependent roughness characterisation. Such correction may prevent water depths underestimations in the shallowest margins of rivers, which was observed in our simulation.

Experimentally, our tests showed that a water velocity of 0.7 to 2.5 m s^{-1} detached more than 66% of eggs on average. Differences in the detachment rates among the three roughness types were also recorded, so we expect that the river substrate type of the spawning ground also plays a role in egg survival. It seems that eggs attached on the gravel substrate will have higher resistance to hydropeaking than eggs attached on smooth stony substrate. The data demonstrated that in the particular species under study, critical changes in the water velocity occurred already, shifting from 0.3 to 0.7 m s^{-1}, and higher velocities did not increase the detachment rates substantially, especially in the case of the smooth substrate. The higher complexity of other substrates provided some protection to part of the eggs and decreases the detachment rates. Due to erosion processes, smooth stones are common in the river environment (Allan & Castillo, 2007; Thomson, Taylor, Fryirs, & Brierley, 2001), although eggs ending in crevices may have relatively good protection. According to our evaluation of river substrate at the study site, eggs were attached to quite large stones commonly present at the area. This implies that the occurring velocities during the hydropeaking may have quite large impact on the eggs, especially those that adhered on the large and smooth stones.

The biofilm results indicated that the biotic conditions were important to consider and could influence egg detachment rates. Periphyton production increase with eutrophication (Mattila & Räisänen, 1998) and hydropeaking supports fast growing species (Bondar-Kunze et al., 2016). Dissolved organic matter in dammed river seams to also be increasing with global warming (Hejzlar, Dubrovský, Buchtele, & Růžička, 2003). This can indicate also a significant importance for substrate spawning rheophilic fish. Potentially artificially increased production of biofilm could be harmful for their reproduction success.

Every experimental design includes some degree of approximation. We are aware that the artificial flows generated in our experimental setup were not necessarily hydrodynamically similar with the flow regime expected at the study site. Therefore, as a first approximation, our main conclusions were based on a comparison of the two flow conditions studied separately in the lab and field and using the mean velocity as the closest scaling parameter. Moreover, the lab experiment was not as complex as a real hydropeaking event in a river for several reasons. The tiles used for the experiment were made with three different roughnesses, but the river bottom of the study site was much more diverse; therefore, the experiment simplified the factors affecting egg survival. River substrate consists of flat stones of various sizes, gravel, sand, woody debris, and some macrophytes. In the experimental tunnel, the eggs were exposed to a homogenised flow field of constant velocity with water running through a smooth PVC surface, but in the river, the flow is more turbulent due to eddy development and therefore had a variable velocity and direction as the water runs over stones and bumps. Additionally, the eggs in nature are spawned above the river bottom and then attach to the substrate at random places (e.g., the eggs can be attached to exposed surfaces or even behind stones where they could be protected from direct river flow; Mills, 1981; Šmejkal, Baran, et al., 2017). In the laboratory experiment, we only specifically considered a few factors: exposure time, substrate roughness, and water velocity. Medium substrate provided in the experiment the most protection for the eggs, likely due to the highest surface contact of the egg with substrate (eggs often attached among several grains of gravel). However, fine gravel may not be the best substrate in for the eggs in the river, since it may shift during the hydropeaking and potentially damage the eggs.

The changes in egg densities after hydropeaking events vary according to the date of observation. The density did not decrease considerably after the first hydropeaking event. The period approximately 10 April coincides with peak spawning based on daily observations (M. Šmejkal, personal communication), and it is likely that this hydropeaking detached many eggs, intensely spawning asp was able to compensate for the losses of eggs on the spawning ground. A fraction of the previously observed eggs may have been swept away and then replaced by new eggs produced by fresh spawners. On the other hand, hydropeaking that occurred on 13 of April washed out almost all eggs, which is also suggested by the experimental results especially on the smooth substrate or smooth substrate with biofilm. After this hydropeaking event, the abundance of the eggs was not recovered to the first measurements.

The visualisation of egg densities on the spawning ground relies on the precision of the monitoring camera. In some pictures, eggs could have been on top of each other in clutches or behind stones, which would have prevented them from being visible in the picture and underestimate overall density. The camera type was used in the past for monitoring of asp eggs during the drift with accurate results (Šmejkal, Baran, et al., 2017), but we did not run an experiment testing how precise is the method for egg counting, therefore the measurement may contain some bias. Since all transect monitoring was done with the same methodology, the result of egg disappearance over the time should be still valid (Krebs, 1999).

The observed disappearance of asp eggs during the spawning season could be described as a consequence of hydropeaking or explained by predation or a combination of both (Paradis, Pepin, & Brown, 1996; Šmejkal, Baran, et al., 2017; Vanzo et al., 2016) but could not be possibly explained by the hatching of eggs because incubation takes longer than our sampling frequency (Targońska, Żarski, & Kucharczyk, 2008). According to Kujawa et al. (1997), the shortest time of hatching is 7 days at water temperatures of 17°C. In our study site, the water temperatures increased gradually from 4°C to approximately 14°C during the spring observation period from March to April, which implies that hatching occurs after more than 20 days according to hatching experiments (Kujawa et al., 1997). The incubation period of the asp under current temperatures is not short and should be taken into account when sustainable water discharges for reproduction are considered. This could provide information for establishing ‘emergence window’ of stabilised flow for asp egg development as is already known for other fish species (Hayes et al., 2019).

Another important factor could be the high concentration of fish such as bream (*Abramis brama*) and roach (*Rutilus rutilus*) migrating from the reservoir to the tributary, which occurs during spring (Hladík & Kubečka, 2003, 2004; Šmejkal, Ricard, et al., 2017). Migrating fish are forced to stop by the weir, which is situated just above the spawning ground, and hence, the concentration of fish and eggs may have increased in this area. High concentrations of eggs may lead to enhanced predation pressure on asp eggs in comparison within freely flowing rivers without such artificial barriers (Šmejkal et al., 2018; Šmejkal, Baran, et al., 2017). The limited extent of suitable spawning grounds for rheophiles is common in many fragmented and regulated rivers. According to our observations, migrating fish are concentrating in the main channel and practically do not enter in the five transects where the decline of the eggs was observed (Šmejkal and Bartoň, personal observation in 2019). Therefore, we assume that observed egg disappearance in the monitored transects are caused primarily by hydropeaking effect on the eggs.

The population of asps in Želivka Reservoir has been strengthened by stocking artificially spawned juvenile asp for several decades (Vostradovský & Váša, 1981). During a two-season study that took place on Želivka Reservoir in 2017 and 2018, all stocked 0 + asp were marked with alizarine red (Halačka, Mareš, Vetešník, & Blabolil, 2019). In a controlled electrofishing effort, which was designed to estimate the proportion of stocked individuals in recruitment, almost none of the captured asp came from natural recruitment (Blabolil et al., 2019). This study therefore suggested very low success of natural spawning. Our results suggest that hydropeaking could be a crucial factor in the low natural reproductive success.

The problem of hydropeaking and its destructive effect on fish eggs can probably occur in many other riverine systems where water flow is artificially managed. Fish with shorter hatching times may be less vulnerable due to lower exposure to hydropeaking than fish that require longer periods of time to hatch (Gillooly et al., 2002; Targońska et al., 2008). The probability of egg loss is somewhat higher in species with long development times, since an extreme hydropeaking event can potentially destroy all population recruitment for the year (Hayes et al., 2019). The developmental time of our model species is not extremely long nor short, with an approximate development time of 20 days (Kujawa et al., 1997). Potential management restrictions on the water regime are easier to achieve for species with short development times if the spawning period is well defined.

Information on the spawning migration timing using passive or active telemetry monitoring along with egg development times can be used to determine the exact time when hydropeaking should be limited or at least decreased in its magnitude. The early life stages of many species of fish (smaller than 40 mm in total length) are unable to withstand a water flow velocity of 0.6–1 m.s^{-1} for more than a few seconds (Grift et al., 2003; Wolter & Arlinghaus, 2003), meaning that even hatched juvenile fish could be swept away by hydropeaking, possibly harming the newly hatched recruits (Lagarde et al., 2017; Peterka et al., 2004; Wolter, Arlinghaus, Sukhodolov, & Engelhardt, 2004). The water velocity could be decreased to suitable velocities for juvenile fish in some parts of rivers by creating sheltered areas (Wolter et al., 2004), and this approach (building sheltered zones in rivers) could possibly decrease the impacts of hydropeaking on the fish population.

Overall, carrying out the study included many challenges and it has its limitations in the terms of a possible future application. The spawning ground of rheophilic fish species has to be suitably located to enable researcher access with heavy equipment for monitoring. Water clarity must be good enough to enable egg densities assessment, which proves difficult especially after the hydropeaking event. Detailed water velocity measurements during hydropeaking may be impossible to take due to the short hydropeaking period and floating woody debris presenting a danger to the research crew.

5 | CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Rheophilic fish are assumed to be well-adapted to fluvial conditions and increased discharges (Blake, 2004). On the other hand, correct choice of fluvial conditions in rivers can be the key and this ability may be impaired by unpredictable flow alternations. There are very few unregulated rivers left and rheophilic fish are forced to inhabit altered conditions and habitats (Birnie-Gauvin, Aarestrup, Riis, Jepsen, & Koed, 2017; Grill et al., 2019). This ecological group face severe population losses and insights in their ecology are the key for their conservation. Under both field and experimental conditions, we found that even relatively low increase in water velocity may have a significant effect on egg detachment. We recorded no differences between the two exposure time treatments, so this finding suggests that hydropeaking should be preferably done at a lower flow with longer hydropeaking period, when a certain amount of water needed to be discharged. The mean flow velocity at the spawning site should be kept ideally on the base flow and at least lower than 0.7 m s^{-1} to maintain natural recruitment of asp, although further research is required to validate the maximum safe velocity. The most of the established regulations for hydropeaking so far are aimed for minimal discharge to avoid stranding and dewatering of fish and their spawning ground (Moreira et al., 2019). Future research may aim to disentangle whether the structural complexity found in the natural conditions mitigates the impact of hydropeaking as it is known that some hydromorphological structures in the river can serve as refuge for fish in increased water flow (Costa, Boavida, Almeida, Cooke, & Pinheiro, 2018) as well as reduce risks for fish connected to decreased water flow (Moreira et al., 2019). We conclude that hydropeaking may have a considerable impact on asp egg detachment probability and should be better managed in rivers where rare rheophilic fish species with adhesive eggs are reproducing. Reduced populations of rheophilic fish can also harm possibilities for commercial and recreational fishermen and riverine ecosystem services.

ACKNOWLEDGEMENTS

We thank Luboš Kočvara and Zdeněk Popelka for their assistance during fieldwork. This research was supported by the project 'The enhancement of rheophilous fish reproduction in the artificial river environment' (No. TJ02000012) and by the project 'Aquaculture of rheophilous fish' (No. QK1920326). The work was supported by BC CAS (IHB & SoWa) and by the Vltava River Catchment Authority.

CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

DB, MŠ, ATS, PB, ZS, LV, TK, FB and JK participated in the field work. MŠ and DB designed the study. FB did the hydraulic model. DB, ATS and MŠ contributed to the statistical analysis. DB and MŠ graphically presented data. DB wrote the first draft.

DATA AVAILABILITY STATEMENT

Data will be made freely available on author's ResearchGate webpage upon manuscript acceptance.

ORCID

Marek Šmejkal https://orcid.org/0000-0002-7887-6411

REFERENCES

Akinyele, D. O., & Rayudu, R. K. (2014). Review of energy storage technologies for sustainable power networks. *Sustain. Energy Technol. Assessments*, *8*, 74–91. https://doi.org/10.1016/j.seta.2014.07.004

Allan, J. D., & Castillo, M. M. (2007). *Stream ecology: Structure and function of running waters* (Second ed.). https://doi.org/10.1007/978-1-4020-5583-6

Ashraf, F. B., Haghighi, A. T., Riml, J., Alfredsen, K., Koskela, J. J., Kløve, B., & Marttila, H. (2018). Changes in short term river flow regulation and hydropeaking in Nordic rivers. *Scientific Reports*, *8*, 17232. https://doi.org/10.1038/s41598-018-35406-3

Auer, S., Zeiringer, B., Führer, S., Tonolla, D., & Schmutz, S. (2017). Effects of river bank heterogeneity and time of day on drift and stranding of juvenile European grayling (*Thymallus thymallus* L.) caused by hydropeaking. *Sci. Total Environ.*. https://doi.org/10.1016/j.scitotenv.2016.10.029

Bain, M. B., Finn, J. T., & Booke, H. E. (1988). Streamflow regulation and fish community structure. *Ecology*, *69*, 382–392. https://doi.org/10.2307/1940436

Balon, E. K. (1975). The main reproductive guilds of fish. *J. Fish Biol.*, *32*, 821–864. https://doi.org/10.1139/f75-110

Bejarano, M. D., Jansson, R., & Nilsson, C. (2018). The effects of hydropeaking on riverine plants: A review. *Biological Reviews*, *93*, 658–673. https://doi.org/10.1111/brv.12362

Birnie-Gauvin, K., Aarestrup, K., Riis, T. M. O., Jepsen, N., & Koed, A. (2017). Shining a light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers, and its implications for management. *Aquat. Conserv. Mar. Freshw. Ecosyst.*, *27*, 1345–1349. https://doi.org/10.1002/aqc.2795

Blabolil, P., Bartoň, D., Halačka, K., Kočvara, L., Kolařík, T., Kubečka, J., … Peterka, J. (2019). The fate of 0+ asp (*Leuciscus aspius*) after being stocked in a reservoir. *Biologia (Bratisl).*, *75*, 989–996. https://doi.org/10.2478/s11756-019-00355-3

Blake, R. W. (2004). Fish functional design and swimming performance. *Journal of Fish Biology*, *65*, 1193–1222. https://doi.org/10.1111/j.0022-1112.2004.00568.x

Bondar-Kunze, E., Maier, S., Schönauer, D., Bahl, N., & Hein, T. (2016). Antagonistic and synergistic effects on a stream periphyton community under the influence of pulsed flow velocity increase and nutrient enrichment. *Sci. Total Environ.*, *573*, 594–602. https://doi.org/10.1016/j.scitotenv.2016.08.158

Bruno, M. C., Siviglia, A., Carolli, M., & Maiolini, B. (2013). Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology*, *6*, 511–522. https://doi.org/10.1002/eco.1275

Casas-Mulet, R., Saltveit, S. J., & Alfredsen, K. (2015). The survival of Atlantic Salmon (*Salmo salar*) eggs during dewatering in a river subjected to Hydropeaking. *River Research and Applications*, *31*, 433–446. https://doi.org/10.1002/rra.2827

Chok, N. S. (2010). Pearson's versus Spearman's and Kendall's correlation coefficients for continuous data. *Grad. Sch. Public Heal.*, *32*, 1365–1367. https://doi.org/10.1017/CBO9781107415324.004

Costa, M. J., Boavida, I., Almeida, V., Cooke, S. J., & Pinheiro, A. N. (2018). Do artificial velocity refuges mitigate the physiological and behavioural consequences of hydropeaking on a freshwater Iberian cyprinid? *Ecohydrology*, *11*. https://doi.org/10.1002/eco.1983

Develepment Team, G. I. M. P. (2018). GIMP. *GNU Image Manip. Progr.*, *18*, 564–575. https://doi.org/10.1080/15320380903085675

Development Core Team, R. (2016). R: A language and environment for statistical computing. *R Found. Stat. Comput.*. https://doi.org/10.1007/978-3-540-74686-7

Development Team, Q. G. I. S. (2018). QGIS geographic information system. *Open Source Geospatial Found. Proj.*, *7*, 130–141. https://doi.org/10.1038/nrg1769

Dodrill, M. J., Yackulic, C. B., Kennedy, T. A., & Hayes, J. W. (2016). Prey size and availability limits maximum size of rainbow trout in a large tailwater: Insights from a drift-foraging bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 759–772. https://doi.org/10.1139/cjfas-2015-0268

Gillooly, J. F., Charnov, E. L., West, G. B., Savage, V. M., & Brown, J. H. (2002). Effects of size and temperature on developmental time. *Nature*, *417*, 70–73. https://doi.org/10.1038/417070a

Grabowski, T. B., & Isely, J. J. (2007). Effects of flow fluctuations on the spawning habitat of a riverine fish. *Southeastern Naturalist*, *6*, 471–478. https://doi.org/10.1656/1528-7092(2007)6[471:EOFFOT]2.0.CO;2

Grift, R. E., Buijse, A. D., Van Densen, W. L. T., Machiels, M. A. M., Kranenbarg, J., Klein Breteler, J. G. P., & Backx, J. J. G. M. (2003). Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. *River Research and Applications*, *19*, 353–374. https://doi.org/10.1002/rra.711

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., … Zarfl, C. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*, 215–221. https://doi.org/10.1038/s41586-019-1111-9

Halačka, K., Mareš, J., Vetešník, L., & Blabolil, P. (2019). Application of the alizarin red S mass marking technique and its detection in stocked asp (*Leuciscus aspius*). *Biologia (Bratisl).*, *74*, 1359–1362. https://doi.org/10.2478/s11756-019-00247-6

Hastie, T. J. (2017). *Generalized additive models*. New York: Routledge. https://doi.org/10.1201/9780203738535

Hayes, D. S., Moreira, M., Boavida, I., Haslauer, M., Unfer, G., Zeiringer, B., … Schmutz, S. (2019). Life stage-specific hydropeaking flow rules. *Sustain.*, *11*. https://doi.org/10.3390/su11061547

Hejzlar, J., Dubrovský, M., Buchtele, J., & Růžička, M. (2003). The apparent and potential effects of climate change on the inferred concentration of dissolved organic matter in a temperate stream (the Malše River, South Bohemia). *Sci. Total Environ.*, *310*, 143–152. https://doi.org/10.1016/S0048-9697(02)00634-4

Hladík, M., & Kubečka, J. (2003). Fish migration between a temperate reservoir and its main tributary. *Hydrobiologia*, *504*, 251–266. https://doi.org/10.1023/B:HYDR.0000008525.46939.42

Hladík, M., & Kubečka, J. (2004). The effect of water level fluctuation on tributary spawning migration of reservoir fish. *Ecohydrology and Hydrobiology*, *4*, 449–457.

Huuki, H., Karhinen, S., Ashraf, F., Torabi Haghighi, A., & Marttila, H. (2020). The economic cost of hydropower environmental constraints under decreasing Price volatility. *SSRN Electronic Journal*. https://doi.org/10.2139/ssrn.3539491

ImageJ. (2018). ImageJ. *ImageJ Dev. Team.*, *9*, 676–682. https://doi.org/10.1038/nmeth.2019

Kennedy, T. A., Muehlbauer, J. D., Yackulic, C. B., Lytle, D. A., Miller, S. W., Dibble, K. L., … Baxter, C. V. (2016). Flow management for hydropower extirpates aquatic insects, undermining river food webs. *Bioscience*, *66*, 561–575. https://doi.org/10.1093/biosci/biw059

Kopecki, I., Schneider, M., & Tuhtan, J. A. (2017). Depth-dependent hydraulic roughness and its impact on the assessment of hydropeaking. *Sci. Total Environ.*, *575*, 1597–1605. https://doi.org/10.1016/j.scitotenv.2016.10.110

Korman, J., Kaplinski, M., & Melis, T. S. (2011). Effects of fluctuating flows and a controlled flood on incubation success and early survival rates and growth of age-0 rainbow trout in a large regulated river. *Transactions of the American Fisheries Society*, *140*, 487–505. https://doi.org/10.1080/00028487.2011.572015

Kottelat, M., & Freyhof, J. (2007). Handbook of European freshwater fishes. *Copeia. Berlin.*, *2008*, 725–727. https://doi.org/10.1643/OT-08-098a.1

Krebs, C. J. (1999). Ecological methodology 2nd edition. *Menlo Park, California: Benjamin/Cummings.*. https://doi.org/10.1109/NANO.2014.6968124

Kujawa, R., Mamcarz, A., & Kucharczyk, D. (1997). Effect of temperature on embryonic development of asp (*Aspius aspius* L). *Polish Archives of Hydrobiology*, *139–143*.

Kupren, K., Mamcarz, A., & Kucharczyk, D. (2011). Effect of variable and constant thermal conditions on embryonic and early larval development of fish from the genus *Leuciscus* (Cyprinidae, Teleostei). *Czech J. Anim. Sci.*, *56*, 70–80. https://doi.org/10.17221/312/2009-CJAS

Lagarde, R., Teichert, N., Faivre, L., Grondin, H., Magalon, H., Pirog, A., … Ponton, D. (2017). Artificial daily fluctuations of river discharge affect the larval drift and survival of a tropical amphidromous goby. *Ecology of Freshwater Fish*, *27*, 646–659. https://doi.org/10.1111/eff.12381

Mattila, J., & Räisänen, R. (1998). Periphyton growth as an indicator of eutrophication; an experimental approach. *Hydrobiologia*, *377*, 15–23. https://doi.org/10.1023/A:1003265208397

McMichael, G. A., Rakowski, C. L., James, B. B., & Lukas, J. A. (2005). Estimated fall Chinook Salmon survival to emergence in dewatered Redds in a shallow Side Channel of the Columbia River. *North am. J. Fish. Manag.*, *25*, 876–884. https://doi.org/10.1577/M04-168.1

Mills, C. A. (1981). The attachment of dace, *Leuciscus leuciscus* L., eggs to the spawning substratum and the influence of changes in water current on their survival. J. *Fish Biol.*, *19*, 129–134. https://doi.org/10.1111/j.1095-8649.1981.tb05817.x

Moreira, M., Hayes, D. S., Boavida, I., Schletterer, M., Schmutz, S., & Pinheiro, A. (2019). Ecologically-based criteria for hydropeaking mitigation: A review. *Sci. Total Environ.*, *657*, 1508–1522. https://doi.org/10.1016/j.scitotenv.2018.12.107

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science 308*(80), 405–408. https://doi.org/10.1126/science.1107887

Paradis, A. R., Pepin, P., & Brown, J. A. (1996). Vulnerability of fish eggs and larvae to predation: Review of the influence of the relative size of prey and predator. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 1226–1235. https://doi.org/10.1139/f96-051

Peterka, J., Vasek, M., Kubeka, J., Hladik, M., & Hohausova, E. (2004). Drift of juveniles after riverine spawning of fishes from the Rimov reservoir, Czech Republic. *Ecohydrology and Hydrobiology*, *4*, 459–468.

Power, M. E. (1992). Habitat heterogeneity and the functional Signifiance of fish in river food webs. *Ecology*, *73*, 1675–1688. https://doi.org/10.2307/1940019

Riehl, R., & Patzner, R. A. (1998). Minireview: The modes of egg attachment in teleost fishes. *The Italian Journal of Zoology*, *65*, 415–420. https://doi.org/10.1080/11250009809386857

Říha, M., Hladík, M., Mrkvička, T., Prchalová, M., & Čech, M. (2013). Post-spawning dispersal of tributary spawning fish species to a reservoir system. *Folia Zoologica*, *62*, 1–13. https://doi.org/10.25225/fozo.v62.i1.a1.2013

Schmutz, S., Bakken, T. H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., … Zeiringer, B. (2015). Response of fish communities to hydrological and morphological alterations in Hydropeaking Rivers of Austria. *River Research and Applications*, *31*, 919–930. https://doi.org/10.1002/rra.2795

Scruton, D. A., Pennell, C., Ollerhead, L. M. N., Alfredsen, K., Stickler, M., Harby, A., … LeDrew, L. J. (2008). A synopsis of "hydropeaking" studies on the response of juvenile Atlantic salmon to experimental flow alteration. *Hydrobiologia*, *609*, 263–275. https://doi.org/10.1007/s10750-008-9409-x

Shen, Y., Diplas, P., 2010. Modeling unsteady flow characteristics of Hydropeaking operations and their implications on fish habitat. *Journal of Hydraulic Engineering 136*, 1053–1066.DOI: https://doi.org/10.1061/(ASCE)HY.1943-7900.0000112

Singh, V. K., & Singal, S. K. (2017). Operation of hydro power plants—A review. *Renewable and Sustainable Energy Reviews*, *69*, 610–619. https://doi.org/10.1016/j.rser.2016.11.169

Šmejkal, M., Baran, R., Blabolil, P., Vejřík, L., Prchalová, M., Bartoň, D., … Kubečka, J. (2017). Early life-history predator-prey reversal in two cyprinid fishes. *Scientific Reports*, *7*, 6924. https://doi.org/10.1038/s41598-017-07339-w

Šmejkal, M., Ricard, D., Vejřík, L., Mrkvička, T., Vebrová, L., Baran, R., … Kubečka, J. (2017). Seasonal and daily protandry in a cyprinid fish. *Scientific Reports*, *7*, 4737. https://doi.org/10.1038/s41598-017-04827-x

Šmejkal, M., Souza, A. T., Blabolil, P., Bartoň, D., Sajdlová, Z., Vejřík, L., & Kubečka, J. (2018). Nocturnal spawning as a way to avoid egg exposure to diurnal predators. *Scientific Reports*, *8*, 15377. https://doi.org/10.1038/s41598-018-33615-4

Stanley, J., Miley, W., & Sutton, D. (1978). Reproductive requirements and likelihood of naturalization of escaped grass carp in the United States. *Transactions of the American Fisheries Society 1919*. https://doi.org/10.1577/1548-8659(1978)107

Targońska, K., Żarski, D., & Kucharczyk, D. (2008). A review of the artificial reproduction of asp, *Aspius aspius* (l.), and nase, *Chondrostoma nasus* (l.). arch. *Polish Fish.*, *16*, 341–354. https://doi.org/10.2478/s10086-008-0022-4

Thomson, J. R., Taylor, M. P., Fryirs, K. A., & Brierley, G. J. (2001). A geomorphological framework for river characterization and habitat assessment. *Aquat. Conserv. Mar. Freshw. Ecosyst.*, *15*, 373–389. https://doi.org/10.1002/aqc.467

Vanzo, D., Zolezzi, G., & Siviglia, A. (2016). Eco-hydraulic modelling of the interactions between hydropeaking and river morphology. *Ecohydrology*, *9*, 421–437. https://doi.org/10.1002/eco.1647

Vašek, M., Prchalová, M., Říha, M., Blabolil, P., Čech, M., Draštík, V., … Kubečka, J. (2016). Fish community response to the longitudinal environmental gradient in Czech deep-valley reservoirs: Implications for ecological monitoring and management. *Ecological Indicators*, *63*, 219–230. https://doi.org/10.1016/j.ecolind.2015.11.061

Vostradovský, J., & Váša, J. (1981). Asp (*Aspius aspius* L.) as a new fish species for rearing. Bull. *VURH Vodn.*, *17*, 10–13.

Wolter, C., & Arlinghaus, R. (2003). Navigation impacts on freshwater fish assemblages: The ecological relevance of swimming performance. *Reviews in Fish Biology and Fisheries*, *13*, 63–89. https://doi.org/10.1023/A:1026350223459

Wolter, C., Arlinghaus, R., Sukhodolov, A., & Engelhardt, C. (2004). A model of navigation-induced currents in inland waterways and implications for juvenile fish displacement. *Environmental Management*, *34*, 656–668. https://doi.org/10.1007/s00267-004-0201-z

Young, P. S., Cech, J. J., & Thompson, L. C. (2011). Hydropower-related pulsed-flow impacts on stream fishes: A brief review, conceptual model, knowledge gaps, and research needs. *Reviews in Fish Biology and Fisheries*, *21*, 716–731. https://doi.org/10.1007/s11160-011-9211-0

How to cite this article: Bartoň D, Bretón F, Blabolil P, et al. Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species. *Ecohydrology*. 2021;e2280. https://doi.org/10.1002/eco.2280

Paper II

Hydropeaking causes spatial shifts in a reproducing rheophilic fish

Science of the Total Environment 806 (2022) 150649

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Hydropeaking causes spatial shifts in a reproducing rheophilic fish

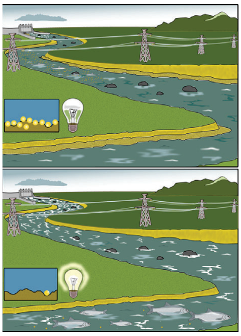
Daniel Bartoň [a,b], Marek Brabec [c], Zuzana Sajdlová [a], Allan T. Souza [a], Jindřich Duras [d,e], David Kortan [f], Petr Blabolil [a], Lukáš Vejřík [a], Jan Kubečka [a], Marek Šmejkal [a,*]

[a] Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic
[b] Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic
[c] Institute of Computer Science, Czech Academy of Sciences, Prague, Czech Republic
[d] University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Vodňany, Czech Republic
[e] Department of Water Management Planning, Vltava River Authority, State Enterprise, Plzeň, Czech Republic
[f] Department of Biology, State Enterprise Vltava River Authority, České Budějovice, Czech Republic

HIGHLIGHTS

- Hydropeaking affects fish movement ecology.
- Flow changes decrease the probability of fish reproduction.
- Hydropeaking likely causes spawning interruptions.
- We advise hydropeaking reduction during reproductive phase.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 4 June 2021
Received in revised form 20 September 2021
Accepted 24 September 2021
Available online 29 September 2021

Editor: Sergi Sabater

Keywords:
River research
Flow alteration
Fish reproduction
Passive telemetry
PIT-tag

ABSTRACT

The hydropeaking regime below hydropower facilities represents a serious threat to riverine fauna and may cause declines in populations living under its influence. However, the knowledge on direct fish responses to the threat of hydropeaking is limited. Here, we aimed to test whether the hydropeaking generated 12 km upstream may have a negative effect on the position of actively spawning rheophilic fish, asp, *Leuciscus aspius*. Two passive telemetry antenna arrays were used to record fish position on the spawning ground. We monitored the position of spawning fish (545, 764 and 852 individuals) in three one-month long spawning seasons in 2017–2019 and related the changes in detection probability on the two antenna arrays to flow conditions, temperature, time of a day and individual fish ID. The fish detection on the spawning ground was negatively affected by the flow change (both increase and decrease) in time. Moreover, the probability of fish detection was also influenced by water temperature, the time of the day and, as seen from the magnitude of individual random effect variability, the detection probability was rather individual-specific. Hydropeaking resulted in the change of spawning behaviour and likely caused interruption of spawning or shifting spawning outside the optimal area for egg development. We therefore advise to reduce the hydropeaking regime during the rheophilic fish spawning season under fisheries or conservation interests.

---

[*] Corresponding author.
E-mail address: marek.smejkal@hbu.cas.cz (M. Šmejkal).

https://doi.org/10.1016/j.scitotenv.2021.150649

1. Introduction

Majority of the world's large rivers are no longer free-flowing and their connectivity is lost due to man-made dams and weirs (Grill et al., 2019; Poff et al., 2007). Artificial barriers modify seasonal natural river flow and often alter daily discharge with substantial magnitude (Barbarossa et al., 2020; Casas-Mulet et al., 2015). Hydropeaking is a discontinuous water release from water retaining structures. It allows to run water turbines in the particular time, in order to cover uneven daily demands for electric power. In addition to electricity production, hydropeaking can serve transportation and recreational activities (e. g. log transportation, canoeing or water slalom). Hydropeaking is a very common phenomenon worldwide and its future expansion due to expected transformation of human society to renewable energy resources is predicted (Ashraf et al., 2018; Horowitz, 2016).

Flow alteration as a result of hydropeaking can have negative effects on various river biota – e.g. algae (Hall et al., 2015), macrophytes (Bejarano et al., 2018), benthic invertebrates (Kjærstad et al., 2018) and also fish (Boavida et al., 2013). Among fishes, the ecological group of rheophilic fish is considered among the most vulnerable to hydropeaking regime due to their frequent and direct exposure to hydropeaking effects (García et al., 2011; Moreira et al., 2019). This group of fish has been declining in abundances for last 50 years (Deinet et al., 2020), since rheophilic fish often depend on migration between different river gradients and due to massive river fragmentation, many of them are threatened worldwide (Branco et al., 2017; Ovidio and Philippart, 2008; Pfauserová et al., 2020).

All life stages of rheophilic fish can be negatively affected by hydropeaking: from the fragile stages of eggs (Bartoň et al., 2021) and larvae to juvenile fish and adults. Both high-flow and low-flow phases of hydropeaking are potentially threatening for rheophilic fish species. There is an evidence of habitat unsuitability for various fish species during low peaks causing fish stranding or egg dewatering (Nagrodski et al., 2012). Highly variable water flow can have direct impact on fish individuals by trapping them in dewatered river zones during lowered flow. On the other hand, high flow can force fish to relocate their stream positions and hide in shelters (Baladrón et al., 2021; Costa et al., 2019) and can severely increase egg detachment rates in fish with adhesive eggs (Bartoň et al., 2021). Besides the direct effects on the fish, there are also indirect effects in lowering food availability by reduction of benthic invertebrate's populations due to their vulnerability to hydropeaking-caused drift, especially combined with a temperature decrease following the high-flow (Bruno et al., 2013).

Reproductive period is crucial for species population dynamics and potentially limiting factor for species conservation efficiency, so factors threatening successful reproduction such as hydropeaking are important to be identified and investigated (Arthington et al., 2016; Helfman et al., 2009). Hydropeaking is affecting riverine fish by altering their individual habitat use in the stream (Capra et al., 2017; King et al., 1998), but direct impact on behaviour of spawning fish during artificial high peak conditions and its impact on fish reproduction success is poorly understood.

Hydropeaking not only changes river discharge but often also affects river temperature which even more contributes to discontinuity and reduction of habitats for rheophilic organisms (Bruno et al., 2013; Casas-Mulet et al., 2016). Flow alterations might not completely block upstream migration to spawning sites (Jones and Petreman, 2015), but during the high flow, the release of cold water can reduce the oxygen consumption rate and disrupt optimal swimming economy (Alexandre and Palstra, 2017). Release of cold water can further affect the ripeness and the willingness to migrate to the spawning ground and therefore can affect the overall reproductive success (King et al., 1998). On the other hand, increasing temperature up to species optima also positively affects fish swimming speed (Fuiman and Batty, 1997), although extremely high temperatures combined with hypoxia result in limitation of a fish swimming potential (Nudds et al., 2020).

Hydropeaking occurs usually on a scheduled time of a day; therefore, this can interplay with the timing preferences of fish spawning activity. Daily variability in reproductive migration and fish reproductive effort are often driven, apart from water temperature and seasonality, by the time of the day (Migaud et al., 2010; Rakowitz et al., 2008; Robertson, 1993). Species such as *Danio rerio* spawn in early morning hours in both natural and laboratory environment (Spence et al., 2007), barbel *Barbus barbus* spawns during day hours, in normal conditions (Baras, 1995) and asp *Leuciscus aspius* prefers nocturnal spawning (Šmejkal et al., 2018), although asp is less strict in the time choice than *Danio rerio*. Therefore, time of the day has to be incorporated in the model in order to evaluate the effects of hydropeaking on the spawning activity.

In this study, we focused on the influence of hydropeaking on the reproductive behaviour of asp - a large predatory cyprinid fish inhabiting lowland rivers and lakes of central and eastern Europe (Šmejkal et al., 2017b; Pfauserová et al. 2019; Kärgenberg et al., 2020). Asp is a rheophilic and lithophilic fish reproducing in shallow fast-flowing water (Bartoň et al., 2021). Asp migrate between lakes or slow-flowing lowland rivers to fast-flowing rivers and streams, where they seek for suitable water flow and depth in the early spring (Kärgenberg et al., 2020; Šmejkal et al., 2017b). Females are releasing their adhesive eggs into the water current which are being simultaneously fertilized by one or several males. Eggs are usually drifting for several meters before adhering to the stony bottom of the fast flowing river (Mills, 1981; Šmejkal et al., 2017a), where they develop for approximately 20 days in usual spring conditions before hatching.

Using a system of passive telemetry arrays, we aimed to investigate whether the changes in river flow due to hydropeaking conditions affect the position of the fish in the stream. We recorded behaviour of 545, 764 and 852 adult asp individuals in reproductive seasons 2017–2019, respectively, along with timestamp of a detection, flow and temperature with 10-min resolution. Specifically, we tested the hypothesis that high flow conditions have the potential to shift adult fish position downstream from their spawning ground, potentially affecting the choice of site for egg deposition or temporarily interrupting fish reproduction.

2. Materials and methods

2.1. Species description and study site

The study site was located on the entry of Želivka River into Želivka (Švihov) Reservoir, Czech Republic (Fig. 1). Želivka Reservoir is the largest drinking-water supply in the Czech Republic and the water level fluctuation is minimized to promote macrophyte development in the littoral zone. The maximum retention level is 380 m above sea level. Study site is subjected to long-term monitoring due to the occurrence of the largest asp population within the Czech Republic protected by European act NATURA 2000. Fish migratory timing on the spawning ground has been yearly tracked by passive telemetry since 2015 (Šmejkal et al., 2021). The migration upstream is restricted by a weir, which results in the spawning activity just below the weir in the most fluvial part of the river that is available (Bartoň et al., 2021). It is a broad-crested weir, 2 m high, 10 m wide and 70 m long. The weir was originally constructed to supply a water mill with water and alters the depth of the river above spawning ground. Location of spawning ground was determined in a previous study by the estimation of asp eggs density using underwater camera (Bartoň et al., 2021; Fig. 1). Adult asp migrate to fluvial spawning grounds with water flow around 0.3 m^*s^{-1} in the early spring and reproduce at temperatures between 5 and 14 °C (Bartoň et al., 2021). The whole spawning event lasts for approximately one-month long period each year. Individuals repeatedly migrate to the upper parts of the reservoir to regain energy and return to the spawning ground with males undergoing substantially more spawning ground visits than females (Šmejkal et al., 2017b, 2021).

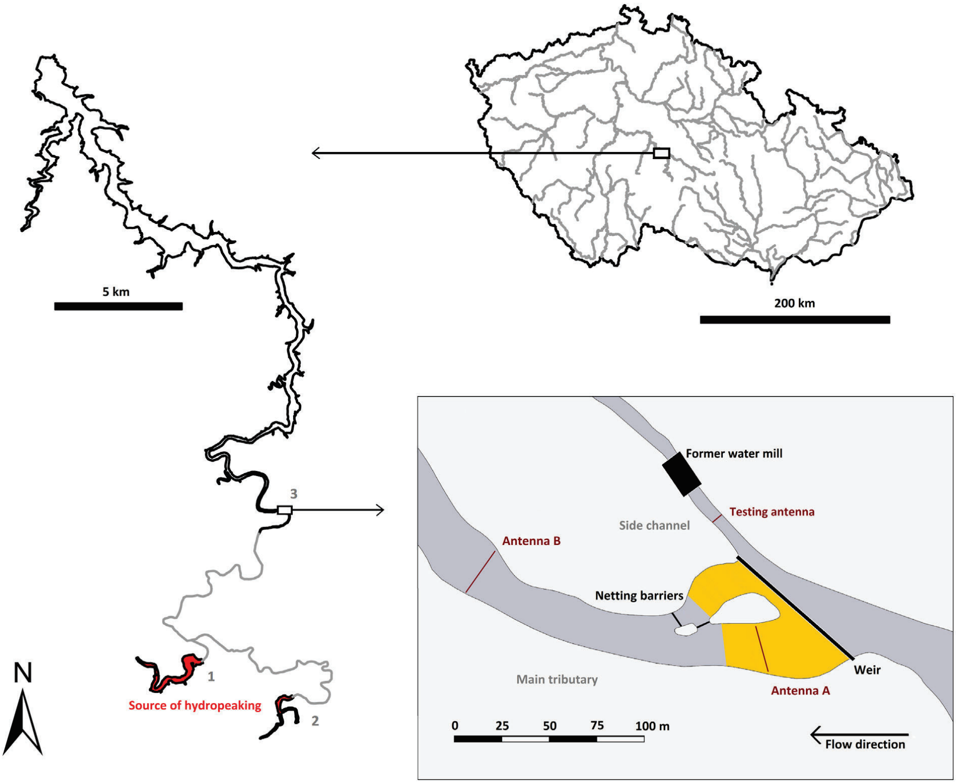


Fig. 1. Map representing Želivka Reservoir and its main tributary. The tributary is under conditions of hydropeaking coming mainly from Trnávka Reservoir (1) and Sedlice Reservoir (2). River inflow into the Želivka Reservoir and the spawning ground (3), the location of the study side with marked positions passive telemetry antennas on the main tributary. The side channel is closed with valves located in a former water mill marked as black rectangle and the main tributary is where the asp spawning takes places (yellow area) – the first 100 m below the weir (black long line). Black lines coming from the lower island are the netting barriers built to ensure fish are moving through antenna. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Two reservoirs with hydroelectric power plants are located approximately 12 km upstream. Sedlice Reservoir on the Želivka River with maximum retention level 489 m above sea level and Trnávka Reservoir on the Trnava River with maximum retention level 415 m above sea level (Fig. 1). Both hydroelectric power plants release in base conditions hypolimnetic water. Hydropower plant on the Trnava River releases water from epilimnetic layer from the Trnávka reservoir in a scheduled date in the channel for canoe slalom purposes, which seriously affects the conditions of the spawning ground, raising water flow three to six times (Bartoň et al., 2021). Hydropower plant on Želivka River produced longer hydropeaking events with less amplitude for electricity production only in 2017. Hydropeaking events occurred daily in 2017 and 7 times during 2018 spawning seasons (Fig. 2), while in 2019 only one substantial hydropeaking event occurred before the arrival of the main part of the asp population and the remaining hydropeaking was rather small scale (the base flow was increased usually by approximately 50%). Main hydropeaking events seriously affected river conditions on the spawning site (Bartoň et al., 2021).

2.2. Fish tagging procedure

Fish were obtained yearly outside of the spawning ground by an electrofishing boat (electrofisher EL 65 II GL DC, Hans Grassel, Schönau am Königsee, Germany, 13 kW, 300/600 V). A “booming” boat had approximately six meters wide electricity field, to which fish are attracted, paralyzed and retrieved into aerated vat (Miranda, 2005; Miranda and Kratochvíl, 2008). The individuals were anaesthetized with MS-222 and individually marked with passive integrated transponder tag (PIT tags, OregonRFID, half-duplex, length 32 mm, diameter 3.65 mm, weight 0.8 g, ISO 11784/11785) for subsequent passive telemetry. Tags were applied directly into the body cavity and no sutures were used to close the incision due to their potential adverse effects on fish health (Hulthén et al., 2014; Skov et al., 2005). The PIT tag loss is not so high using this method with approximately 2 and 15% probability in males and females, respectively (Šmejkal et al., 2019, 2020) and in the laboratory experiment, the mortality after tagging did not exceed 1% after two weeks from the tagging in juvenile asp (Šmejkal and Bartoň, unpublished data). The mean standard length and weight at the tagging were 470 ± 32 mm standard deviation (SD) and 1576 ± 361 g SD in males and 492 ± 43 mm SD and 1977 ± 590 g SD in females. The tagged individuals were released immediately after recovery from anaesthesia and their return into normal swimming position.

2.3. Fish passive telemetry and discharge and water temperature recording

Fish were tracked by passive telemetry antennas installed in the cross-sections of the spawning ground. Two antenna loops (A located on the spawning ground and B located below the spawning ground)

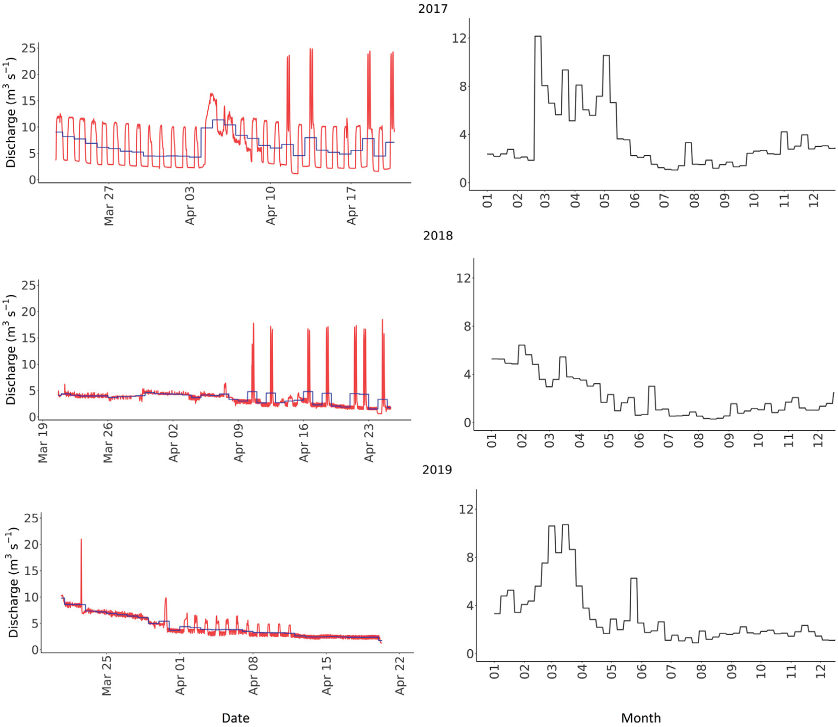


Fig. 2. Left panel: hydropeaking events during the asp spawning period in 2017-2019. The red line is the discharge measured in 10-min interval and the blue line is the average daily discharge. Right panel: average weekly discharge for whole years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were built having a width of 10 m and height of 60 cm with detection range of 80 cm (Fig. 1). Fish were led to pass through the antenna loop by the netting barriers (mesh size 5 cm) placed in the river sections where fish asp could avoid the antennas. The charging and recording frequency were set to 10 energize cycles s^{-1} with LF HDX RFID readers (OregonRFID, Portland, Oregon, USA). Fish's individual code was stored along with time of detection and number of reads per continuous detection every time fish passed the antenna loop along with timestamp information. Discharge data were obtained with a 10-min resolution from the Vltava River Authority. The temperature during the monitoring campaigns was measured by dataloggers (HOBO Pendant Temperature/Light 64 K Data Logger, Onset Computer Corporation, Bourne, Massachusetts, USA) placed in the spawning ground at 0.5-m depth.

Induced flow fluctuations occurred in 2017 daily due to hydropower operation with four times increase during high flow (~10 $m^{3}*s^{-1}$) compared to base flow (~2.5 $m^{3}*s^{-1}$), additionally, four larger hydropeaking events occurred reaching up to 10 times flow increase from the base flow (~25 $m^{3}*s^{-1}$, Fig. 2). In 2018, 7 hydropeaking events occurred with approximately 5 - 6 times flow increase from otherwise relatively stable base flow (~3 $m^{3}*s^{-1}$), and the discharges during high-peaked events reached on average to 16 $m^{3}*s^{-1}$ at a maximal flow. No hydropeaking events occurred during the monitored period of asp spawning in 2019 (only one before the start of spawning) with only small occasional fluctuations from the average base flow of ~3 $m^{3}*s^{-1}$ into ~5 $m^{3}*s^{-1}$ discharge in the first two weeks of April (Fig. 2).To compare flashiness of hydropeaking of the studied site we computed Richards-Baker index (R-B index) by dividing the sum of the absolute day to day changes in average daily flow by the sum of daily average flows in the studied period for each year (Baker et al., 2004). For 2017 the value of the R-B index is 0.21, for 2018 is 0.25, and 0.07 for 2019.

2.4. Antenna detection efficiency

To verify whether PIT tag detection efficiency is not lower during the high flow conditions than low flow conditions, we designed a waterproof tube of length 3 m where PIT tag travels with constant speed of 1 $m*s^{-1}$ forward and 0.75 $m*s^{-1}$ backwards using a simple modeler engine (PB model s.r.o., Dobrá Voda, Czech Republic). The testing was conducted on 25 April 2021. Antenna 2.5 m * 1.2 m was constructed in the side channel of the tributary (Fig. 1), where we could regulate the water velocity without disturbing the spawning ground and the development of the eggs. A PIT tag (half-duplex, length 32 mm, diameter 3.65 mm, weight 0.8 g, ISO 11784/11785) was driven through with 100 passages in each of the two different water flows set for testing: slow with 0.13 $m*s^{-1}$ and fast with 1.73 $m*s^{-1}$.

2.5. Data preparation and analysis

Detections of fish tagged in the same seasons as movement patterns were recorded were discarded due to potential adverse effects of tagging on their behaviour, therefore only fish tagged in previous seasons entered the analysis below. The number males and females that did not enter the analysis in the tagging year were 281, 166, 101, and 304, 205 and 88 in 2017-2019, respectively. Spawning activity of 317, 412, and 446 males, and 228, 352, and 406 females in 2017–2019, respectively, and tagged at least one season before behavioural recording, was recorded by the passive telemetry arrays and entered the analysis. Obtained timestamps of individual fish detections by each antenna array were rounded to 10-min interval to obtain matching timestamp with flow and temperature measured with 10-min resolution. To create a moving window for each fish ID, antenna (we have two antennas: A and B, where A is upstream, relative to B) and detected time for subsequent analyses, we modelled potential fish presence for two hours before and after individual detection on any antenna with 10-min resolution. Data were transformed into the binary form of presence indicators for a given timestamp, antenna and fish ID. Moreover, the total detections for each fish ID on the antenna during 10-min interval was computed as well. Explanatory variable of main interest is the river flow, but we adjusted for some obvious nuisance variables as well as for fish individuality and its immediate detection history. In order to see whether temperature and flow can enter the model as separate variables, we tested their correlation with Spearman's rank correlation coefficient. The results of the Spearman correlation indicated that there was a significant negative association between flow and temperature, (rs(3.5507*e^{-11}) = -0.37, $p < 0.001$), which may be due to generally higher base flow during early spring due to snow melting (Fig. 2). Data were processed using packages dplyr, data.table and lubridate within R software version 4.0.1 (Dowle, 2016; R Core Team, 2019; R Core Team, 2020; Spinu et al., 2017).

Our dynamic model for fish presence data on the antenna A is:

$$Y_{ijt}\tilde{Bin}(\pi_{Ait},1)$$

$$logit(\pi_{Ait}) \equiv log\left(\frac{\pi_{Ait}}{1-\pi_{Ait}}\right) = \beta_0 + b_i + \tag{1}$$

$$\beta_{A10}.I(fish\ i\ present\ on\ antenna\ A\ within\ the\ time\ interval\ (t-10,t-20])+$$

$$\beta_{B10}.I(fish\ i\ present\ on\ antenna\ B\ within\ the\ time\ interval\ (t-10,t-20])+$$

$$\beta_{A20}.I(fish\ i\ present\ on\ antenna\ A\ within\ the\ time\ interval\ (t-20,t-30])+$$

$$\beta_{B20}.I(fish\ i\ present\ on\ antenna\ B\ within\ the\ time\ interval\ (t-20,t-30])+$$

$$\beta_{TL}.TL_i + s_{TWD}(TWD_t) + s_T(T_t) + s_{TD}\left(TD_{i,t-10}\right) + s_F(F_t) + s_{FD}(F_t - F_{t-10})$$

where:

- Y_{ijt} is the 0/1 indicator variable (having the value of 0 or 1) for presence of the i-th fish on j-th antenna (A or B) during time interval *(t,t-10]* where t is measured in minutes from the beginning of the study
- $logit(x) \equiv log\left(\frac{x}{1-x}\right)$ is the standard (canonical) logit link for binomial distribution assumed for Y_{ijt}'s
- π_{Ait} is the probability that the i-th fish is present at the antenna A during (t,t-10]
- β_0 is the (unknown) intercept to be estimated from data
- $b_i \sim N(0,\sigma^2)$ is the fish-specific random effect
- $I(.)$ is the indicator function – it assumes value of 1 if its argument is true and value of 0 otherwise
- β_{A10} ,β_{B10} are the (unknown) coefficients describing the first order dependence on the past values
- β_{A20} ,β_{B20} are the (unknown) coefficients describing the second order dependence on the past values
- TL_i is the tagging length of the i-th fish
- β_{TL}. TL_i is the effect of tagging length (with unknown coefficient β_{TL} to be estimated from data), assumed to be linear on the logistic scale
- s_{TWD}, s_T, s_{TD}, s_F, s_{FD} are unknown "functional parameters" (to be estimated from data) describing relationship of the presence probability and various explanatory variables (potentially nonlinear even on the logistic scale). They are implemented as (roughness penalized) cubic splines
- TWD_t is time within day ($TWD_t = hour(t) + \frac{minute(t)}{60}$). Hence, the s_{TWD} (TWD_t) has a form of a seasonal component and has to be periodic. To this end, we implement it via penalized cyclic cubic spline (unlike the other smooth (s) components which are cubic splines).
- T_t is the water temperature at time t
- $TD_{i,\ t-10}$ is the total number of detections (sum of detections on antennas A and B) of the i-th fish during the interval $(t-10, t-20)]$
- F_t is the river flow velocity at time t
- FD_t is the river flow difference between t and t - 10

Taken overall, the model is a dynamic (discrete-time after aggregation) GAM (Hastie and Tibshirani, 1990; Wood, 2017) model with an individual-specific random effect. Conditionally on the random effect (individuality), we do have a nonhomogeneous Markov chain model (Gagniuc, 2017) of second order. Inhomogeneity is introduced by the effect of several explanatory variables. Of main interest in this paper is the effect of flow velocity (F) and its change or first difference (FD). To clean for potential nuisance effects, we include in the model corrections for tagging length, within-day seasonality (or periodicity), and the effect of water temperature.

The model was identified (i.e. its unknown parameters and "functional parameters' estimated) via maximization of the penalized likelihood (Wood, 2017) when roughness penalty coefficients were estimated via REML (Wood et al., 2016).

The model was stratified on sex (i.e. fitted separately for males and females) to see potential differences in the dynamic fish behaviour as well as different reactions to the flow velocity as the explanatory variable of main interest. Models for both antenna A and B had lower AIC when stratified on sex (A - 1,361,116 and B - 1,261,685) than model with sex as a main effect (1,368,165 and 1,267,288, respectively). The model for fish presence on the antenna B is analogous (obtained by just replacing symbol A by B and vice versa). Altogether, four models were constructed: males on the antenna A (MA), males on the antenna B (MB), females on the antenna A (FA) and females on the antenna B (FB; Tables 1–4).

The statistical analyses were performed using R software version 4.0.1 and package mgcv (R Core Team, 2020; Wood, 2001) and data were visualized using ggplot2 and mgcViz package (Fasiolo et al., 2020; Wickham, 2016).

3. Results

The temperatures during the spawning seasons varied between 3.3 and 16.6 °C also detections of male and female asp were different in years 2017 to 2019 (Table 5). The detection on one antenna indicated higher probability of being detected by the same antenna after 10 min or 20 min interval and lesser probability to be detected by the other antenna. The detections of males and females on both antennas were

Table 1
Parametric coefficients and approximate significance of smooth terms for model MA.

Parametric coefficients:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.838879	0.932030	-5.192	2.08e-07
binomial_detections_lag10_ant1	1.279727	0.009991	128.090	< 2e-16
binomial_detections_lag10_ant3	-1.475467	0.022967	-64.243	< 2e-16
binomial_detections_lag20_ant1	1.105225	0.006339	174.343	< 2e-16
binomial_detections_lag20_ant3	-0.574756	0.018906	-30.401	< 2e-16
tagging length	0.002205	0.001985	1.111	0.267
Approximate significance of smooth terms:	edf	Ref.df	Chi.sq.	*p*-value
s(Fish ID)	579.784	619.000	74,428	<2e-16
s(Time of a day)	7.899	8.000	85,082	<2e-16
s(Temperature)	8.962	8.999	10,931	<2e-16
s(Previous fish detection)	8.489	8.890	19,018	<2e-16
s(Flow)	8.902	8.996	1219	<2e-16
s(Flow difference in 10 min interval)	8.773	8.975	1435	<2e-16

Table 2
Parametric coefficients and approximate significance of smooth terms for model MB.

Parametric coefficients:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.1183717	0.4286980	-2.609	0.00909
binomial_detections_lag10_ant1	-1.5784321	0.0246656	-63.993	< 2e-16
binomial_detections_lag10_ant3	1.2561246	0.0109831	114.369	< 2e-16
binomial_detections_lag20_ant1	-0.8540842	0.0204962	-41.670	< 2e-16
binomial_detections_lag20_ant3	1.1525612	0.0071774	160.582	< 2e-16
tagging length	-0.0044565	0.0009139	-4.876	1.08e-06
Approximate significance of smooth terms:	edf	Ref.df	Chi.sq.	p-value
s(Fish ID)	586.124	619.000	62,460	<2e-16
s(Time of a day)	7.972	8.000	95,882	<2e-16
s(Temperature)	8.876	8.992	2337	<2e-16
s(Previous fish detection)	8.154	8.735	8487	<2e-16
s(Flow)	8.978	9.000	2542	<2e-16
s(Flow difference in 10 min interval)	8.942	8.998	1745	<2e-16

Table 4
Parametric coefficients and approximate significance of smooth terms for model FB.

Parametric coefficients:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.6292464	0.2729215	-9.634	<2e-16
binomial_detections_lag10_ant1	-0.9082859	0.0380474	-23.872	<2e-16
binomial_detections_lag10_ant3	0.9501798	0.0272964	34.810	<2e-16
binomial_detections_lag20_ant1	-0.6100517	0.0276202	-22.087	<2e-16
binomial_detections_lag20_ant3	0.6729108	0.0130507	51.561	<2e-16
tagging length	-0.0003434	0.0005544	-0.619	0.536
Approximate significance of smooth terms:	edf	Ref.df	Chi.sq.	p-value
s(Fish ID)	497.117	568.000	13,170.19	<2e-16
s(Time of a day)	7.837	8.000	14,738.33	<2e-16
s(Temperature)	8.859	8.992	683.43	<2e-16
s(Previous fish detection)	3.745	4.557	89.62	<2e-16
s(Flow)	8.959	8.999	1079.92	<2e-16
s(Flow difference in 10 min interval)	8.643	8.939	245.00	<2e-16

significantly dependent on fish ID, flow difference during 10-min interval, flow, previous fish detections, time of a day and temperature (Tables 1–4). The flow difference during 10-min interval was negatively affecting the probability of detection of females and had a slightly positive effect on males during the medium flow reduction on the antenna A, while it was negatively affecting the probability of detection of both males and females on antenna B (Figs. 3 and 4). The stable high flow conditions resulted in higher detection probability on the antenna A and reduction of detection probability on the antenna B, suggesting the tendency for upstream migration during the stable high flow conditions (Fig. 5). Both sexes used antenna A mostly during twilight and nocturnal period, while antenna B had higher probability of fish detection during daytime (Fig. 6). The probability of fish detection increased with temperature on the antenna A in both sexes, while the probability was relatively stable with increasing temperature for females on antenna B and slightly decreasing with temperature for males (Fig. 7). The effect of fish tagging length was not significant in all models. The model MA explained 49.1% of deviance with $R^2 = 50.5\%$, model MB explained 37.8% of deviance with $R^2 = 38\%$, model FA explained 20.5% of deviance with $R^2 = 15\%$ and model FB explained 14.4% of deviance with $R^2 = 9.37\%$.

Testing the antenna array during the slow flow resulted in 353 lines of detections and 351 lines of detections in high flow, with mean number of reads per detection 1.65 and 1.8, respectively. The decrease in number of reads during the high flow conditions was not confirmed (Wilcoxon rank sum test W = 66,675, $p = 0.9735$).

4. Discussion

Our study suggested, among the other observed effects, the shift of fish positions during the change in the flow to downstream sections of the spawning area. Hydropeaking events on the study site occur during daytime (between 10:00 a.m. and 6:00 p.m. depending on the particular event) and approximately two thirds of the fish are spawning during the night (Šmejkal et al., 2018), therefore hydropeaking usually does not affect the majority of the fish spawning in the given day. Considering this fact, the dislocation of adult spawning asp from spawning ground might be not directly too harmful for the reproductive behaviour on the particular research site, while reported detachment of spawned adhesive eggs can be the bigger issue (Bartoň et al., 2021). On the other hand, other indirect negative factors might be connected with dislocation during high peaks such as fish exhaustion or additional fish stress especially in rivers with absence of natural shelters from the high flow conditions (Boavida et al., 2013). Observed fish dislocation may be potentially more important for streams where hydropeaking period lasts longer, or other parameters of hydropeaking are ecologically more challenging such as amplitude, rate of change, frequency, duration, and timing (Moreira et al., 2019).

Table 3
Parametric coefficients and approximate significance of smooth terms for model FA.

Parametric coefficients:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.346283	0.498381	-4.708	2.5e-06
binomial_detections_lag10_ant1	0.128352	0.046605	2.754	0.00589
binomial_detections_lag10_ant3	-2.071189	0.053597	-38.644	< 2e-16
binomial_detections_lag20_ant1	0.759106	0.011794	64.364	< 2e-16
binomial_detections_lag20_ant3	-0.339911	0.024790	-13.712	< 2e-16
tagging length	-0.001943	0.001013	-1.917	0.05519
Approximate significance of smooth terms:	edf	Ref.df	Chi.sq.	p-value
s(Fish ID)	498.241	568.000	13,433.2	<2e-16
s(Time of a day)	7.978	8.000	27,628.7	<2e-16
s(Temperature)	8.543	8.887	3641.7	<2e-16
s(Previous fish detection)	8.533	8.907	1862.2	<2e-16
s(Flow)	8.834	8.989	987.8	<2e-16
s(Flow difference in 10 min interval)	8.988	9.000	1968.9	<2e-16

Migration of fish is driven by various factors such as temperature, light, and water current. These environmental stimuli are key in timing of migration (Jones and Petreman, 2015; Northcote, 1984). In the altered system where natural regime is artificially changed, migration triggers can be also disturbed causing potential mismatch between food availability and hatching time (Asch et al., 2019; Rolls et al., 2013). This can lead to large influence on fish migration in much bigger scale than change in individual fish behaviour (King et al., 1998). Results of this study show a tendency to upstream movement or migration of spawning asp with slightly increasing flow, especially in males. Increased water flow or temperature change can be recognized as incoming flood which may trigger the fish upstream migration (Reynolds, 1983) as some rheophilic fish tend to prefer larger flow for upstream movement (Jones and Petreman, 2015). In conditions of our study (the temperate river during the early spring), the effects of lowering temperature can be also important for the reduction of fish metabolism and thus swimming performance decrease (Alexandre and Palstra, 2017), not allowing fish to reach maximum speed (Wardle, 1980), increase in time needed for gonad maturing and for egg incubation (Targońska et al., 2008). However, we believe that hydropeaking may affect the short-term individual decisions about when to migrate, while the spawning migration itself occurs on the research site even when hydropeaking was banned (authors unpublished observation).

The effects of tested variables on the fish were not uniform, but there was a significant effect of fish ID on the response to the variables. This suggests e.g., that while in general majority of fish can be negatively influenced by hydropeaking, some individuals with migratory tendencies may use high flow events as an opportunity to overcome weir restricting asp upstream movement (Jones and Petreman, 2015; Jonsson, 1991). Individuality in overcoming small barriers was previously shown in barbel movement in the stream (Branco et al., 2017). Previous studies on asp

Table 5
Water temperature on the study site and asp detections with standard deviation (SD) on antennas A and B.

Year	Temperature (°C)			Detections			
				Antenna A		Antenna B	
	Min.	Max.	Mean	Males	Females	Males	Females
2017	4.5	10.9	8.4	6071 ± 25,188 SD	253 ± 485 SD	2362 ± 11,714 SD	141 ± 170 SD
2018	3.3	16.0	10.4	1842 ± 9147 SD	111 ± 479 SD	898 ± 6905 SD	114 ± 194 SD
2019	4.9	10.3	7.7	85 ± 315 SD	110 ± 854 SD	104 ± 574 SD	43 ± 126 SD

also showed that this species has relatively high intra-population variability in their performance on the spawning ground between males and females (Šmejkal et al., 2017b), and male's individual reproductive performance during adult life improves with increasing age (Šmejkal et al., 2021).

Our model fish is a migratory species with different breeding and foraging habitats. Asp accumulates energy for spawning from late spring until next winter (typical “capital breeder”). This reproductive strategy is more common in areas with high seasonality (Mcbride et al., 2015) and the precise timing of spawning migration is of the essence to the reproductive success (Šmejkal et al., 2021). Capital breeders may be more threatened by artificial disruptions of reproduction since they aim to certain short time period in contrast to species with prolonged spawning season allocating energy to spawning directly (income breeders) (Stephens et al., 2009), and potentially, species with batch spawning strategy (multiple times per year) may be less vulnerable to irregular hydropeaking regimes.

Physiological reproductive timing is driven by the photoperiod and is sensitive to environmental disturbances (Migaud et al., 2010; Vinagre et al., 2009). The suboptimal conditions on the spawning ground can severely affect the ovulation processes of females and decrease the egg quality (Gaudemar and Beall, 1998). The ovulated eggs in females have to be spawned within given period of time to avoid their increased post-spawning mortality or egg hardening and resorption in females (Lahnsteiner, 2000; Samarin et al., 2015). The maximum time from ovulation to spawning is usually dependent on fish species and temperature since delayed spawning can substantially affect female fitness (Samarin et al., 2015). Therefore, it may be possible that disruption of spawning by the hydropeaking may be especially threatening for species with short optimal time from ovulation to spawning and for species that use only a fraction of the day period for reproductive activity (e.g. early morning; Spence et al., 2007), while species capable of spawning in any time of a day can probably compensate delay of spawning activity when the hydropeaking ceases. Furthermore, rheophilic nest-building species may be even more affected by the hydropeaking due to their dislocation from the nest site during the hydropeaking period.

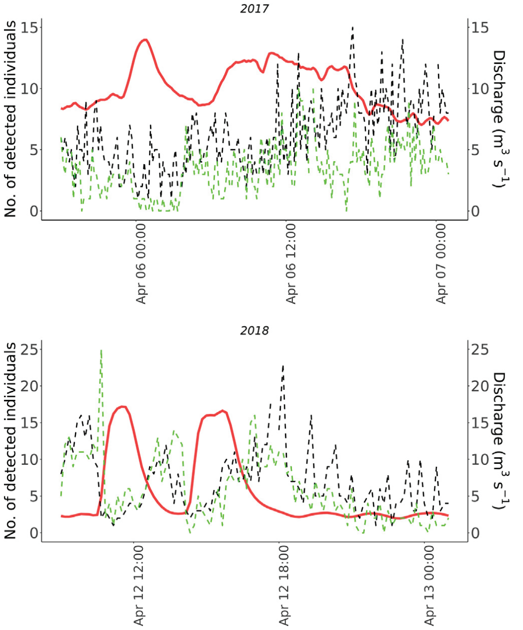


Fig. 3. Examples of reduction in fish detection in relation to hydropeaking events. Antenna A is visualized by green dashed line, antenna B by black dashed line and the discharge by red solid line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Migration and spawning success are very dependent on the fish's physical condition (Northcote, 1984). Females use the energy mainly to produce eggs while males allocate most of the energy to compete with males over the hierarchy status, find female and secure fertilization of the eggs (Morbey and Ydenberg, 2001; Šmejkal et al., 2017b). Hydropeaking during spawning season affects male by pushing them out of their territories and forcing them to use more energy in order to stay or to return to reproduction later, while females have increased energy usage for swimming, at the same time, their energy is allocated to eggs that can be devalued by releasing them in unsuitable conditions, where they cannot effectively develop during the low flow conditions. Another potential effect that was not addressed in this study is the increase of turbidity in the river caused by increased sediment transport (Hauer et al., 2017). Decreased water transparency may have some consequences to the mating activity of fish. Males usually maintain spacing (usually 1 m or more) among themself in the flow (Šmejkal et al., 2021), but the increase in turbidity may reduce the visual contact during and several hours after the hydropeaking event.

The three years of observation varied in the hydropeaking regime. While the majority of peaks in 2017 were run due to electricity production on a daily basis, the source of hydropeaking in 2018 was caused by canoe slalom. In 2019, the variation in flow on the spawning ground due to the hydropeaking was not that detrimental and this year can be seen as the closest to natural flow conditions. This is also shown in the R-B index which quantifies hydropeaking as it reflects rapidity and frequencies of flow fluctuations (Baker et al., 2004). Seasons 2017 and 2018 were according to R-B indexes almost the same with values of 0.21 and 0.25. This also corresponds with Fig. 2, where in 2018 the effect of hydropeaking on detection is more apparent than in 2017 example. The R-B index value for 2019 is much lower compared to the previous years at value of 0.07. Number of detections on the antennas also varies year to year and it was the lowest in 2019 where conditions were possibly closest to natural. This may correspond with repeated disruption of spawning in previous seasons (2017 and 2018) and thus more attempts to spawn or migrate upstream when the hydropeaking occurred. On the other hand, hydrological conditions also varied and higher average discharge in 2019 could prevent fish to stay longer in the antenna detection field and reduce the number of detections. Due to the nature of the data and the primary goal of the study (to study the effect of instant effect of flow and the flow change between a short period of time and not long-term effects), we decided not to

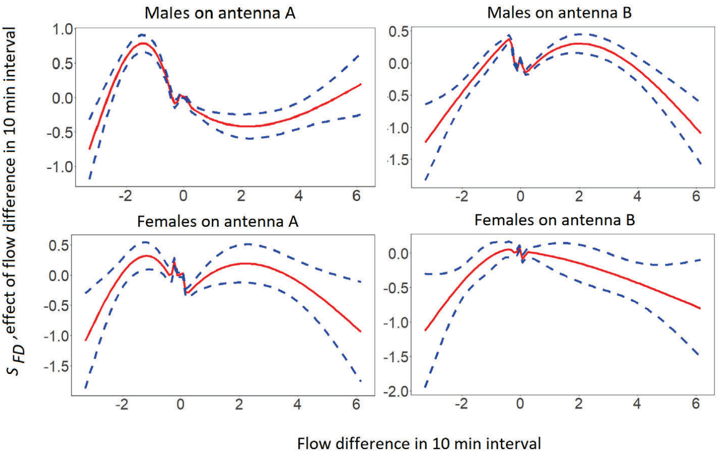


Fig. 4. GAM model outputs showing (on the logistic scale) the change of detection probability with change in discharge (i.e. estimated of the s_{FD},effect in model (1) together with the pointwise constructed 95% confidence intervals). Antenna array A was situated on the main spawning ground, while antenna array B was situated approximately 150 m downstream from spawning ground (depending on the year of monitoring). Red lines represent GAM trendlines and dashed lines confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

include year as a factor due to the huge complexity of such model (potentially limiting the model strength).

It is important for the fish population viability to protect a reproductive phase to secure recruitment (Erisman et al., 2017). Especially when the spawning season is short and happens once a year, it is a key to assure its success in order to protect the species. In artificially regulated and altered river ecosystems, located in the region with high seasonality, spawning sites are not only limited by time but also space. Space for spawning is often bounded by artificial barriers on rivers and only a limited amount of habitats with suitable conditions for spawning and egg development, having e.g. proper depth and water velocity, remains (Bartoň et al., 2021). Hydropeaking events increase water depth on the study site. Due to asp preferences of low water depth (0.5 m) and high water speed (0.3 m^*s^{-1}) (Bartoň et al., 2021), this change may reduce spawning options considerably and result in depositing adhesive eggs in river sections not suitable for egg development during the base flow. Those limitations make undisturbed course of spawning very important for asp conservation in the area. Since the spawning fish on the research site are affected by hydropeaking, we suggest reduction of flow fluctuations as much as possible in order to help asp population of Želivka Reservoir. To meet the needs for hydropeaking and the needs for asp protection, technical solutions should be also considered and developed, such as water bypasses during the high flow periods, or altering timing of hydropeaking outside asp spawning season and egg development.

The recent biodiversity crisis occurs in various levels of biota, from decline in invertebrate species to all classes of vertebrates (Deinet et al., 2020; Kleijn et al., 2011; Wagner et al., 2021; Whitfield et al., 2007; Woinarski et al., 2015). Recently published report of the World Fish Migration Foundation estimated the decline of rheophilic fish species by 76% worldwide and 93% in Europe from 1970 to 2016 (Deinet et al., 2020). As in other animal taxa, the decline is connected with

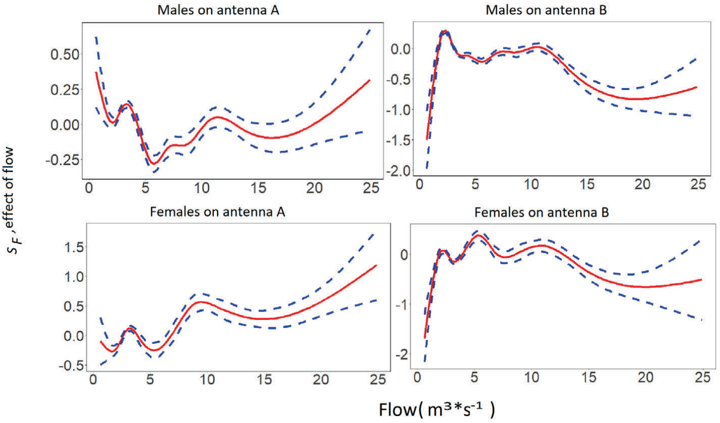


Fig. 5. GAM model outputs showing (on the logistic scale) the relationship of the detection probability to the discharge (i.e. estimated of the s_F,effect in model (1) together with the pointwise constructed 95% confidence intervals). Red lines represent GAM trendlines and dashed lines confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

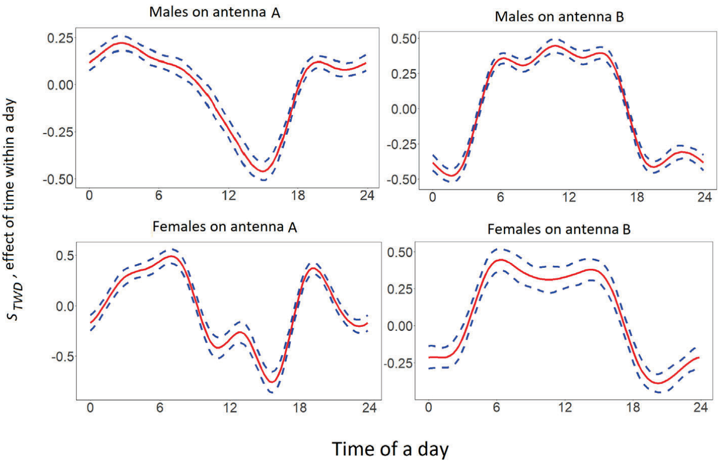


Fig. 6. GAM model outputs showing (on the logistic scale) the changes of detection probability within a day (i.e. estimated of the s_{TWD},effect in model (1) together with the pointwise constructed 95% confidence intervals). Red lines represent GAM trendlines and dashed lines confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

multiple cuts to populations (Wagner et al., 2021) occurring due to anthropogenic influence on the ecosystems such as habitat alteration and degradation, habitat loss, overexploitation, pollution, species invasions, spread of diseases and climate change. Hydropeaking likely represents one of the serious stressors for the aquatic taxa, yet many of its effects on various parts of biota are probably still waiting to be recognized.

CRediT authorship contribution statement

Conceptualization: MŠ, DB, JD, JK
Data curation: MB, MŠ, AS, DK
Data collection: all authors
Formal analysis: MB, MŠ
Funding acquisition: MŠ, JK, JD
Investigation: MŠ, DB, MB, AS
Methodology: DB, MŠ
Project administration: MŠ
Visualization: MŠ, MB, DB, ZS
Writing – original draft: DB, MŠ and MB
Writing – review and editing: all authors

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

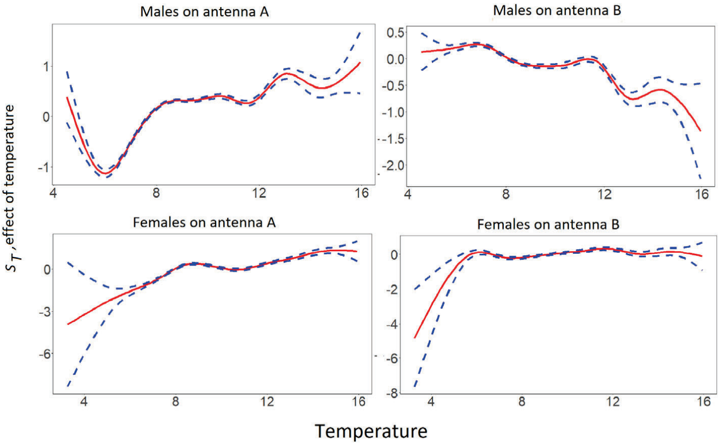


Fig. 7. GAM model outputs showing (on the logistic scale) the relationship of the detection probability to water temperature (i.e. estimated of the s_T,effect in model (1) together with the pointwise constructed 95% confidence intervals). Red lines represent GAM trendlines and dashed lines confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Acknowledgements

We thank Luboš Kočvara, Tomáš Kolařík and Zdeněk Popelka for their assistance during fieldwork and Vilém Děd and Tomáš Jáchym for asp database maintenance.

Funding

This research was supported by the project "The enhancement of rheophilous fish reproduction in the artificial river environment" (No. TJ02000012) and also partially supported by the long-term strategic development financing of the Institute of Computer Science (Czech Republic RVO 67985807).

Ethical approval

The field sampling methods and experimental protocols used in this study were performed in accordance with the guidelines and permission from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. CZ 01679) and approved by the Experimental Animal Welfare Commission of Biology Centre of the Czech Academy of Sciences.

References

Alexandre, C.M., Palstra, A.P., 2017. Effect of short-term regulated temperature variations on the swimming economy of Atlantic salmon smolts. Conserv. Physiol. 5. https://doi.org/10.1093/conphys/cox025.

Arthington, A.H., Dulvy, N.K., Gladstone, W., Winfield, I.J., 2016. Fish conservation in freshwater and marine realms: status, threats and management. Aquat. Conserv. Mar. Freshw. Ecosyst. https://doi.org/10.1002/aqc.2712.

Asch, R.G., Stock, C.A., Sarmiento, J.L., 2019. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Glob. Chang. Biol. 25, 2544–2559. https://doi.org/10.1111/gcb.14650.

Ashraf, F.Bin, Haghighi, A.T., Riml, J., Alfredsen, K., Koskela, J.J., Kløve, B., Marttila, H., 2018. Changes in short term river flow regulation and hydropeaking in Nordic rivers. Sci. Rep. https://doi.org/10.1038/s41598-018-35406-3.

Baker, D.B., Richards, R.P., Loftus, T.T., Kramer, J.W., 2004. A new flashiness index: characteristics and applications to Midwestern rivers and streams. J. Am. Water Resour. Assoc. 40, 503–522. https://doi.org/10.1111/j.1752-1688.2004.tb01046.x.

Baladrón, A., Costa, M.J., Bejarano, M.D., Pinheiro, A., Boavida, I., 2021. Can vegetation provide shelter to cyprinid species under hydropeaking? Sci. Total Environ. 769. https://doi.org/10.1016/j.scitotenv.2021.145339.

Baras, E., 1995. Thermal related variations of seasonal and daily spawning periodicity in Barbus barbus. J. Fish Biol. 46, 915–917. https://doi.org/10.1111/j.1095-8649.1995.tb01617.x.

Barbarossa, V., Schmitt, R.J.P., Huijbregts, M.A.J., Zarfl, C., King, H., Schipper, A.M., 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. Proc. Natl. Acad. Sci. U. S. A. https://doi.org/10.1073/pnas.1912776117.

Bartoň, D., Bretón, F., Blabolil, P., Souza, A.T., Vejřík, L., Sajdlová, Z., Kolařík, T., Kubečka, J., Šmejkal, M., 2021. Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species. Ecohydrology. https://doi.org/10.1002/eco.2280.

Bejarano, M.D., Jansson, R., Nilsson, C., 2018. The effects of hydropeaking on riverine plants: a review. Biol. Rev. 93, 658–673. https://doi.org/10.1111/brv.12362.

Boavida, I., Santos, J.M., Ferreira, M.T., Pinheiro, A., Zhaoyin, W., Lee, J.H.W., Jizhang, G., Shuyou, C., 2013. Fish habitat-response to hydropeaking. Proc. 35th Iahr World Congr. Vols I Ii.

Branco, P., Amaral, S.D., Ferreira, M.T., Santos, J.M., 2017. Do small barriers affect the movement of freshwater fish by increasing residency? Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2016.12.156.

Bruno, M.C., Siviglia, A., Carolli, M., Maiolini, B., 2013. Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. Ecohydrology 6, 511–522. https://doi.org/10.1002/eco.1275.

Capra, H., Plichard, L., Bergé, J., Pella, H., Ovidio, M., McNeil, E., Lamouroux, N., 2017. Fish habitat selection in a large hydropeaking river: strong individual and temporal variations revealed by telemetry. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2016.10.155.

Casas-Mulet, R., Alfredsen, K., Hamududu, B., Timalsina, N.P., 2015. The effects of hydropeaking on hyporheic interactions based on field experiments. Hydrol. Process. 29, 1370–1384. https://doi.org/10.1002/hyp.10264.

Casas-Mulet, R., Saltveit, S.J., Alfredsen, K.T., 2016. Hydrological and thermal effects of hydropeaking on early life stages of salmonids: a modelling approach for implementing mitigation strategies. Sci. Total Environ. 573, 1660–1672. https://doi.org/10.1016/j.scitotenv.2016.09.208.

Costa, M.J., Ferreira, M.T., Pinheiro, A.N., Boavida, I., 2019. The potential of lateral refuges for Iberian barbel under simulated hydropeaking conditions. Ecol. Eng. 127, 567–578. https://doi.org/10.1016/j.ecoleng.2018.07.029.

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W.M., Marconi, V., McRae, L., Baumgartner, L.J., Brink, K., Claussen, J.E., Cooke, S.J., Darwall, W., Eriksson, B.K., Garcia de Leaniz, C., Hogan, Z., Royte, J., Silva, L.G.M., Thieme, L.M., Tickner, D., Waldman, J., Wanningen, H., Weyl, O.L.F., Berkhuysen, A., 2020. The Living Planet Index (LPI) for Migratory Freshwater Fish - Technical Report.

Dowle, M., 2016. Package 'data.table.' Cran.

Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O., Nemeth, R.S., 2017. Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. Fish Fish. https://doi.org/10.1111/faf.12132.

Fasiolo, M., Nedellec, R., Goude, Y., Capezza, C., Wood, S.N., 2020. Package 'mgcViz'.

Fuiman, L.A., Batty, R.S., 1997. What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. J. Exp. Biol. 200, 1745–1755.

Gagniuc, P.A., 2017. Markov Chains: From Theory to Implementation and Experimentation. John Wiley & Sons, USA, NJ.

García, A., Jorde, K., Habit, E., Caamaño, D., Parra, O., 2011. Downstream environmental effects of dam operations: changes in habitat quality for native fish species. River Res. Appl. 27, 312–327. https://doi.org/10.1002/rra.1358.

Gaudemar, B., Beall, E., 1998. Effects of overripening on spawning behaviour and reproductive success of Atlantic salmon females spawning in a controlled flow channel. J. Fish Biol. 53, 434–446. https://doi.org/10.1111/j.1095-8649.1998.tb00991.x.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world's free-flowing rivers. Nature. https://doi.org/10.1038/s41586-019-1111-9.

Hall, R.O., Yackulic, C.B., Kennedy, T.A., Yard, M.D., Rosi-Marshall, E.J., Voichick, N., Behn, K.E., 2015. Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon. Limnol. Oceanogr. https://doi.org/10.1002/lno.10031.

Hastie, T., Tibshirani, R., 1990. Generalized Additive Models. Chapman Hall & CRC, Monographs on Statistics & Applied Probability. Chapman and Hall/CRC.

Hauer, C., Siviglia, A., Zolezzi, G., 2017. Hydropeaking in regulated rivers – from process understanding to design of mitigation measures. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2016.11.028.

Helfman, G.S., Collette, B.B., Facey, D.E., Bowen, B.W., 2009. The Diversity of Fishes, Biology of Fishes. https://doi.org/10.1007/s13398-014-0173-7.2.

Horowitz, C.A., 2016. Paris agreement. Int. Leg. Mater. 55, 740–755. https://doi.org/10.1017/s0020782900004253.

Hulthén, K., Chapman, B.B., Nilsson, P.A., Hansson, L.A., Skov, C., Baktoft, H., Brodersen, J., Brönmark, C., 2014. Sex identification and PIT-tagging: tools and prospects for studying intersexual differences in freshwater fishes. J. Fish Biol. 84, 503–512.

Jones, N.E., Petreman, I.C., 2015. Environmental influences on fish migration in a hydropeaking river. River Res. Appl. https://doi.org/10.1002/rra.2810.

Jonsson, N., 1991. Influence of water flow, water temperature and light on fish migrations in rivers. Nord. J. Freshw. Res. 66, 20–35.

Kärgenberg, E., Økland, F., Thalfeldt, M., Thorstad, E.B., Sandlund, O.T., Tambets, M., 2020. Migration patterns of a potamodromous piscivore, asp (Leuciscus aspius), in a river–lake system. J. Fish Biol. https://doi.org/10.1111/jfb.14454.

King, J., Cambray, J.A., Impson, N.D., 1998. Linked effects of dam-released floods and water temperature on spawning of the Clanwilliam yellowfish Barbus capensis. Hydrobiologia 384, 245–265. https://doi.org/10.1023/a:1003481524320.

Kjærstad, G., Arnekleiv, J.V., Speed, J.D.M., Herland, A.K., 2018. Effects of hydropeaking on benthic invertebrate community composition in two central Norwegian rivers. River Res. Appl. https://doi.org/10.1002/rra.3241.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tscharntke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2011.05.009.

Lahnsteiner, F., 2000. Morphological, physiological and biochemical parameters characterizing the over-ripening of rainbow trout eggs. Fish Physiol. Biochem. 23, 107–118. https://doi.org/10.1023/A:1007839023540.

Mcbride, R.S., Somarakis, S., Fitzhugh, G.R., Albert, A., Yaragina, N.A., Wuenschel, M.J., Alonso-Fernández, A., Basilone, G., 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish Fish. https://doi.org/10.1111/faf.12043.

Migaud, H., Davie, A., Taylor, J.F., 2010. Current knowledge on the photoneuroendocrine regulation of reproduction in temperate fish species. J. Fish Biol. 76 (1), 27–68. https://doi.org/10.1111/j.1095-8649.2009.02500.x.

Mills, C.A., 1981. The attachment of dace, Leuciscus leuciscus L., eggs to the spawning substratum and the influence of changes in water current on their survival. J. Fish Biol. 19, 129–134. https://doi.org/10.1111/j.1095-8649.1981.tb05817.x.

Miranda, L.E., 2005. Refining boat electrofishing equipment to improve consistency and reduce harm to fish. N. Am. J. Fish. Manag. 25, 609–618. https://doi.org/10.1577/m04-094.1.

Miranda, L.E., Kratochvíl, M., 2008. Boat electrofishing relative to anode arrangement. Trans. Am. Fish. Soc. 137, 1358–1362. https://doi.org/10.1577/t07-243.1.

Morbey, Y.E., Ydenberg, R.C., 2001. Protandrous arrival timing to breeding areas: a review. Ecol. Lett. https://doi.org/10.1046/j.1461-0248.2001.00265.x.

Moreira, M., Hayes, D.S., Boavida, I., Schletterer, M., Schmutz, S., Pinheiro, A., 2019. Ecologically-based criteria for hydropeaking mitigation: a review. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2018.12.107.

Nagrodski, A., Raby, G.D., Hasler, C.T., Taylor, M.K., Cooke, S.J., 2012. Fish stranding in freshwater systems: sources, consequences, and mitigation. J. Environ. Manag. 103, 133–141. https://doi.org/10.1016/j.jenvman.2012.03.007.

Northcote, T.G., 1984. Mechanisms of fish migration in rivers. Mechanisms of Migration in Fishes. https://doi.org/10.1007/978-1-4613-2763-9_20.

Nudds, R.L., Ozolina, K., Fenkes, M., Wearing, O.H., Shiels, H.A., 2020. Extreme temperature combined with hypoxia, affects swimming performance in brown trout (Salmo trutta). Conserv. Physiol. 8. https://doi.org/10.1093/conphys/coz108.

Ovidio, M., Philippart, J.C., 2008. Movement patterns and spawning activity of individual nase Chondrostoma nasus (L.) in flow-regulated and weir-fragmented rivers. J. Appl. Ichthyol. 24, 256–262. https://doi.org/10.1111/j.1439-0426.2008.01050.x.

Pfauserová, N., Slavík, O., Horký, P., Kolářová, J., Randák, T., 2019. Migration of Non-Native Predator Asp (Leuciscus aspius) from a Reservoir Poses a Potential Threat to Native Species in Tributaries. Water 11. https://doi.org/10.3390/w11061306.

Pfauserová, N., Slavík, O., Horký, P., Turek, J., Randák, T., 2020. Spatial distribution of native fish species in tributaries is altered by the dispersal of non-native species from reservoirs. Sci. Total Environ., 143108. https://doi.org/10.1016/j.scitotenv.2020.143108.

Poff, N.L.R., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proc. Natl. Acad. Sci. U. S. A. 104, 5732–5737. https://doi.org/10.1073/pnas.0609812104.

R Core Team, 2019. Package 'dplyr' - A Grammar of Data Manipulation. CRAN Repos.

R Core Team, 2020. R Development Core Team, R: A Language and Environment for Statistical Computing, R: A Language and Environmental for Estatistical Computing.

Rakowitz, G., Berger, B., Kubecka, J., Keckeis, H., 2008. Functional role of environmental stimuli for the spawning migration in Danube nase Chondrostoma nasus (L.). Ecol. Freshw. Fish 17, 502–514. https://doi.org/10.1111/j.1600-0633.2008.00302.x.

Reynolds, L.F., 1983. Migration patterns of five fish species in the Murray-Darling river system. Mar. Freshw. Res. 34, 857–871. https://doi.org/10.1071/MF9830857.

Robertson, D.R., 1993. In: Sale, P. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press LTD, pp. 356–386.

Rolls, R.J., Ellison, T., Faggotter, S., Roberts, D.T., 2013. Consequences of connectivity alteration on riverine fish assemblages: potential opportunities to overcome constraints in applying conventional monitoring designs. Aquat. Conserv. Mar. Freshw. Ecosyst. 23, 624–640. https://doi.org/10.1002/aqc.2330.

Samarin, A.M., Policar, T., Lahnsteiner, F., 2015. Fish oocyte ageing and its effect on egg quality. Rev. Fish. Sci. Aquac. 23, 302–314. https://doi.org/10.1080/23308249.2015.1053560.

Skov, C., Brodersen, J., Bronmark, C., Hansson, L.-A., Hertonsson, P., Nilsson, P.A., 2005. Evaluation of PIT-tagging in cyprinids. J. Fish Biol. 67, 1195–1201.

Šmejkal, M., Baran, R., Blabolil, P., Vejřík, L., Prchalová, M., Bartoň, D., Mrkvička, T., Kubečka, J., 2017a. Early life-history predator-prey reversal in two cyprinid fishes. Sci. Rep. 7, 6924. https://doi.org/10.1038/s41598-017-07339-w.

Šmejkal, M., Ricard, D., Vejřík, L., Mrkvička, T., Vebrová, L., Baran, R., Blabolil, P., Sajdlová, Z., Vejříková, I., Prchalová, M., Kubečka, J., 2017b. Seasonal and daily protandry in a cyprinid fish. Sci. Rep. 7, 4737. https://doi.org/10.1038/s41598-017-04827-x.

Šmejkal, M., Souza, A.T., Blabolil, P., Bartoň, D., Sajdlová, Z., Vejřík, L., Kubečka, J., 2018. Nocturnal spawning as a way to avoid egg exposure to diurnal predators. Sci. Rep. 8, 15377. https://doi.org/10.1038/s41598-018-33615-4.

Šmejkal, M., Blabolil, P., Bartoň, D., Duras, J., Vejřík, L., Sajdlová, Z., Kočvara, L., Kubečka, J., 2019. Sex-specific probability of PIT tag retention in a cyprinid fish. Fish. Res. 219. https://doi.org/10.1016/j.fishres.2019.105325.

Šmejkal, M., Bartoň, D., Děd, V., Souza, A.T., Blabolil, P., Vejřík, L., Sajdlová, Z., Říha, M., Kubečka, J., 2020. Negative feedback concept in tagging: ghost tags imperil the long-term monitoring of fishes. PLoS One 15, e0229350. https://doi.org/10.1371/journal.pone.0229350.

Šmejkal, M., Bartoň, D., Brabec, M., Sajdlová, Z., Souza, A.T., Moraes, K.R., Soukalová, K., Blabolil, P., Vejřík, L., Kubečka, J., 2021. Climbing up the ladder: male reproductive behaviour changes with age in a long-lived fish. Behav. Ecol. Sociobiol. 75, 1–13. https://doi.org/10.1007/s00265-020-02961-7.

Spence, R., Gerlach, G., Lawrence, C., Smith, C., 2007. The behaviour and ecology of the zebrafish, Danio rerio. Biol. Rev. 83, 13–34. https://doi.org/10.1111/j.1469-185X.2007.00030.x.

Spinu, V., Grolemund, G., Wickham, H., Lyttle, I., Constigan, I., Law, J., Mitarotonda, D., Larmarange, J., Boiser, J., Lee, C.H., 2017. R: Package 'lubridate' [WWW Document]. CRAN.

Stephens, P.A., Boyd, I.L., Mcnamara, J.M., Houston, A.I., 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90, 2057–2067. https://doi.org/10.1890/08-1369.1.

Targońska, K., Żarski, D., Kucharczyk, D., 2008. A review of the artificial reproduction of asp, Aspius aspius (l.), and nase, Chondrostoma nasus (l.). Arch. Pol. Fish. 16, 341–354. https://doi.org/10.2478/s10086-008-0022-4.

Vinagre, C., Ferreira, T., Matos, L., Costa, M.J., Cabral, H.N., 2009. Latitudinal gradients in growth and spawning of sea bass, Dicentrarchus labrax, and their relationship with temperature and photoperiod. Estuar. Coast. Shelf Sci. 81, 375–380. https://doi.org/10.1016/j.ecss.2008.11.015.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the Anthropocene: death by a thousand cuts. Proc. Natl. Acad. Sci. U. S. A. https://doi.org/10.1073/PNAS.2023989118.

Wardle, C.S., 1980. Effects of temperature on the maximum swimming speed of fishes. Environmental Physiology of Fishes, pp. 519–531. https://doi.org/10.1007/978-1-4899-3659-2_20.

Whitfield, S.M., Bell, K.E., Philippi, T., Sasa, M., Bolaños, F., Chaves, G., Savage, J.M., Donnelly, M.A., 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. Proc. Natl. Acad. Sci. U. S. A. 104, 8352–8356. https://doi.org/10.1073/pnas.0611256104.

Wickham, H., 2016. ggplot2 Elegant Graphics for Data Analysis. Springer.

Woinarski, J.C.Z., Burbidge, A.A., Harrison, P.L., 2015. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proc. Natl. Acad. Sci. U. S. A. https://doi.org/10.1073/pnas.1417301112.

Wood, S.N., 2001. mgcv: GAMs and Generalized Ridge Regression for R. R News.

Wood, S.N., 2017. Generalized Additive Models: An Introduction With R, Second Edition. Chapman & Hall. https://doi.org/10.1201/9781315370279.

Wood, S.N., Pya, N., Säfken, B., 2016. Smoothing parameter and model selection for general smooth models. J. Am. Stat. Assoc. 111, 1548–1563. https://doi.org/10.1080/01621459.2016.1180986.

Paper III

Use of a flow deflector to protect rheophilic fish spawning grounds during hydropeaking

Received: 26 November 2021 | Revised: 10 October 2022 | Accepted: 9 November 2022
DOI: 10.1002/rra.4084

RESEARCH ARTICLE

WILEY

Use of a flow deflector to protect rheophilic fish spawning grounds during hydropeaking

Daniel Bartoň[1,2] | Zuzana Sajdlová[1] | Tomáš Kolařík[1] | Jan Kubečka[1] |
Jindřich Duras[3,4] | David Kortan[5] | Marek Šmejkal[1]

[1]Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic
[2]Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic
[3]Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, University of South Bohemia in České Budějovice, Vodňany, Czech Republic
[4]Department of Water Management Planning, Vltava River Authority, State Enterprise, Plzeň, Czech Republic
[5]Department of Biology, State Enterprise Vltava River Authority, České Budějovice, Czech Republic

Correspondence
Marek Šmejkal, Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic.
Email: marek.smejkal@hbu.cas.cz

Abstract

Rheophilic fishes are one of the ecological groups of fishes declining most quickly in number due to various habitat modifications and discharge regulations. Artificial rapid increases and decreases in discharge (hydropeaking) can cause severe damage to the eggs of rheophilic fishes. We investigated whether the effects of a water increase in hydropeaking on a spawning ground may be mitigated by a deflector installed at the top of the weir that diverts flow to other sections. At the research site, rheophilic asp (*Leuciscus aspius*) spawn annually in early spring, and their success might be affected by hydropeaking, with base discharge ranging from 3 to 7 $m^3 \times s^{-1}$ and peak discharge ranging from 16 to 25 $m^3 \times s^{-1}$ occurring 4 to 7 times during the asp spawning season and egg development period. To protect the adhesive eggs from detachment during peak discharge, a flow deflector (a wooden wall at the selected part of the weir) was installed to regulate discharge on the protected spawning ground. This measure allowed normal discharge under base flow conditions. During peak flow, a significant portion of the additional water was directed to the part of the river channel where egg abundance was lower and to the mill channel, where asp spawning was not present. While the total discharge increased 4.1 times compared to the base flow, the water discharge in the protected spawning ground increased only 2.7 times. This resulted in more than half of the asp eggs being retained in the protected channel. Although the use of such a measure is limited to specific local conditions where eggs are located just downstream of the weir, it can be a valid solution in highly fragmented rivers with hydropeaking and can lead to higher recruitment of rheophilic fishes.

KEYWORDS
fish conservation, fish eggs, habitat degradation, hydropeaking mitigation, *Leuciscus aspius*, reproduction

1 | INTRODUCTION

Rivers around the world face heavy modifications and discharge regulations, and these changes have strong impacts on riverine wildlife (Deinet et al., 2020; Grill et al., 2019). Dams and reservoirs constructed around the world pose serious threats to rheophilic species (Barbarossa et al., 2020). Flow fluctuations and hydropeaking (periodic rapid change in discharge) represent one of the threats to rheophilic fishes in human-modified rivers (Grabowski & Isely, 2007; Schmutz et al., 2015). Hydropeaking is usually conducted on a daily basis to meet the uneven demand for electric energy during the day (Ashraf et al., 2018). Another example is the need for a sudden increase in discharge to enable water sports, such as white water slalom, which is usually not periodic but may nonetheless have an impact on riverine life (Bartoň et al., 2021; Tszydel & Kruk, 2015).

Hydropeaking is known to have serious negative impacts on river flora and fauna, including fish (Casas-Mulet, Saltveit, & Alfredsen, 2016; Schmutz et al., 2015; Young, Cech, & Thompson, 2011). Indirectly, fish can be negatively affected by decreased invertebrate densities, as hydropeaking also causes a decline in river benthos due to extensive drift during hydropeaking periods (Bruno, Siviglia, Carolli, & Maiolini, 2013; Kjærstad, Arnekleiv, Speed, & Herland, 2018). With respect to the influence of hydropeaking on rheophilic fishes, negative impacts may occur from the beginning of their life history, as their eggs can be dewatered when the river is off-peak (McMichael, McKinstry, Vucelick, & Lukas, 2005). During peak flow, adhesive eggs from egg depositors may be detached from the substrate in large quantities and be carried away by the current (Bartoň et al., 2021). Fish larvae can also be dislocated during the peak flow (Auer, Zeiringer, Führer, Tonolla, & Schmutz, 2017), as can adult spawning fish (Bartoň et al., 2022). In highly hydropeaking rivers, some fish are even unable to find shelter during the peak flow (Boavida, Santos, Ferreira, & Pinheiro, 2015; Costa, Ferreira, Pinheiro, & Boavida, 2019). Therefore, potential mitigation measures for hydropeaking may be important to preserve fish in the stretches of rivers influenced by hydropeaking.

Due to the severe decline of many fish species, it is essential to protect their spawning grounds to secure the long-term viability of the population (Arlinghaus, Matsumura, & Dieckmann, 2010; Erisman et al., 2017; Wang & Xia, 2009). Rheophilic fishes that deposit their eggs often migrate upstream to find suitable shallow, swift-flowing water, where they lay their adhesive eggs on the stone and gravel substrate (Baras, 1995; Rakowitz, Berger, Kubecka, & Keckeis, 2008; Šmejkal et al., 2021). These lithophilic species are a threatened ecological group due to habitat degradation, flow regulation, and hydropeaking (Aarts, Van Den Brink, & Nienhuis, 2004; Bartoň et al., 2022), and there is a need to reverse the trend of their global population decline.

The impact of hydropeaking on fish in general as well as specifically on rheophilic fishes can be mitigated in several ways (Bruder et al., 2016; Moreira et al., 2019). Mitigation measures fall into three categories (Charmasson & Zinke, 2011). The first and most practical category includes operational measures that aim to temporally maneuver peaks at their source. These include slowing down the ramping rate, limiting the minimum and maximum discharge during the critical time period, and limiting the magnitude of peaks (ratio of high runoff to low runoff) (Charmasson & Zinke, 2011; Hauer, Siviglia, & Zolezzi, 2017; Moreira et al., 2019). Ecologically based hydropeaking mitigation criteria have been established in some countries to mitigate the effects of hydropeaking on river organisms (Moreira et al., 2019). The second category of hydropeaking mitigation measures includes large hydraulic construction measures such as retention ponds, additional channels, multilevel outlet structures in dams, and so forth. (Charmasson & Zinke, 2011). These methods are quite demanding in terms of construction investment, data collection, analysis, funding, management, and authorization. For that reason, these two categories of methods are currently not possible to implement at our site. The third category, according to Charmasson and Zinke (2011), includes compensatory measures, for example, river widening, gravel, boulder, or sediment placement, planting of trees or grass patches, cover structures, weir restoration, placement of large woody debris, and so forth. The discharge regulating measures designed in this study belong to this category and target a small but crucial part of the river for rheophilic fish reproduction.

In this study, we designed and tested a flow deflector situated on a part of a weir. Together with the supporting measures described below, it was designed to reduce the negative impacts of discharge during peak flow on rheophilic fish spawning grounds. We focused on the spawning grounds of a rheophilic cyprinid species, the asp, *Leuciscus aspius*. The asp is a large predator that migrates to fluvial river sections in early spring to spawn (Kärgenberg et al., 2020; Šmejkal et al., 2017; Vašek et al., 2018). It lays its adhesive eggs on a stony and gravelly substrate at flow velocities usually between 20 and 50 cm × s^{-1}. We verified the effectiveness of the flow deflector by measuring flow reduction and egg densities in protected and unprotected areas below the weir before and after hydropeaking events. The aim of the study was to retain a higher proportion of adhesive eggs at the spawning ground than would be the case without mitigation measures through (i) channel modification that attracts more fish to the protected area of the spawning ground; (ii) installation of the flow deflector that reduces discharge to create the protected area of the spawning ground; and (iii) diverting a portion of the peak discharge to the mill channel where fish do not spawn.

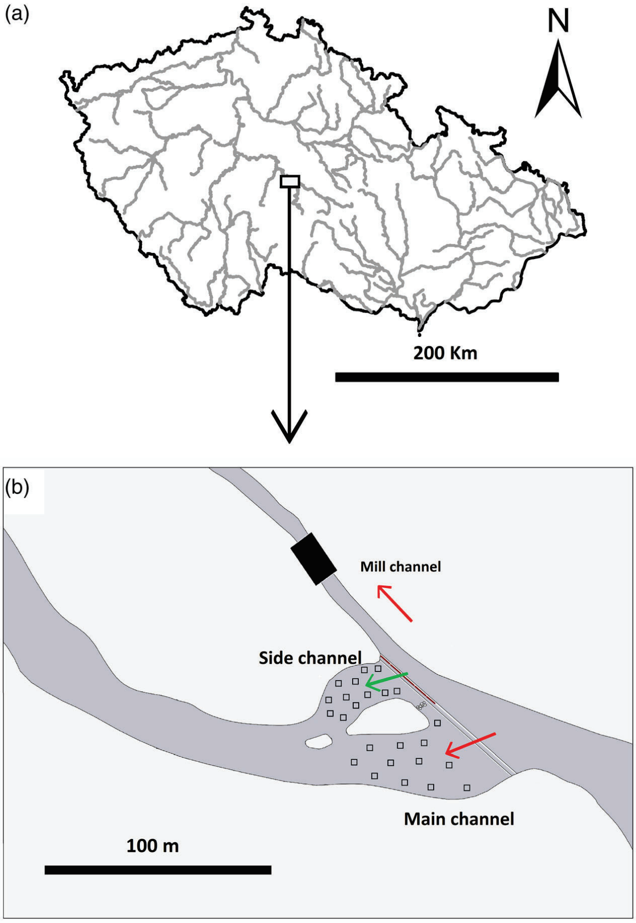
2 | MATERIALS AND METHODS

2.1 | Species description and study site

The asp is a species protected by NATURA 2000 at many European localities, including the study site—a tributary of Želivka Reservoir, Czech Republic (49.5782969N, 15.2539036E) (Lusk, Hanel, & Lusková, 2004). At the research site, adult fish aggregate in the tributary just below the first weir upstream of the reservoir (Figures 1 and 2), where they reproduce over a 1-month-long period from mid-March to mid-April. Asp eggs are adhesive and usually adhere to rocks and pebbles on the river bottom (Targoñska, Zarski, & Kucharczyk, 2008). The fish choose relatively shallow and fast flowing waters to spawn (Bartoň et al., 2021).

The research site is influenced by hydropeaking due to the canoe slalom course located 12 km upstream below the Trnávka Reservoir. Slalom operation occurs irregularly due to scheduled water canoe slalom competitions, qualifications, and training, but usually twice a day for 1 h (Figure 3). Water discharge usually increases from 3–6 $m^3 \times s^{-1}$ to 15–18 $m^3 \times s^{-1}$. During peak flow, more than 90% of eggs can be detached and drift in slower flowing sections of the river (Bartoň et al., 2021), which can result in high mortality due to egg sedimentation in the mud (Bartoň and Šmejkal, unpublished data).

FIGURE 1 Location of the study area in the Czech Republic (a). Weir at the tributary of the Želivka Reservoir—the study site (b), where the deflector was installed to prevent egg detachment in the asp spawning ground (green arrow), where the majority of the asp aggregate. Additional hydropeaking water was directed to the unprotected channel and the mill channel (red arrows). The dark gray bar upstream of the island marks an additional stone wall that diverts water into the unprotected channel. The positions of the frames where egg densities were monitored with the camera are indicated by the black outlined squares [Color figure can be viewed at wileyonlinelibrary.com]



2.2 | Spawning ground modification

The river below the weir is divided into two channels with an island in between (Figures 1 and 2). A small semipermeable stone barrier (an extension of the isle) was constructed with an excavator (Menzi Muck M3, STAVOPLAST KL, Stachy, Czech Republic) on February 28, 2020, to separate the channels below the weir during hydropeaking to prevent water from the main channel (hereafter unprotected) from entering the side channel (hereafter protected), increasing the velocity (Figure 1). The average flow velocity of the base flow measured in April 2018 was 0.14 m $\times$ s^{-1} in the protected channel with an average depth of 0.3 m and 0.23 m $\times$ s^{-1} and 0.6 m in the unprotected channel, and the base flow discharge of both channels combined ranged from 3 m^3 $\times$ s^{-1} to 6 m^3 $\times$ s^{-1}, being 4 m^3 $\times$ s^{-1} at the time of measurement (Bartoň et al., 2021). The substrate at the site is rocky with boulders (average of 95.6 boulders per m^2 counted) (Bartoň et al., 2021). The protected channel was cleaned by the river authority in February 2020 using an excavator (Menzi Muck M3, STAVOPLAST KL, Stachy, Czech Republic). The top layer of loose and fine sediments was excavated, the river bottom was sloped to increase the water velocity, and larger stones were arranged to add structures to further increase the heterogeneity and attractiveness of the spawning ground, with the objective of directing spawning fish mainly to the protected area. The average depth increased to 0.48 m, and the water speed doubled to 0.32 m $\times$ s^{-1} in the protected channel.

In addition, the gates of a former mill channel were modified to allow a portion of the peak discharge to flow sideways from the research site (2.6 m^3 $\times$ s^{-1}, open only during peak discharge; Table 1).

2.3 | Deflector specification

On the right side of the weir, steel sockets were screwed to the top of the weir every 2 m to hold wooden planks (2 $\times$ 0.5 $\times$ 0.05 m;

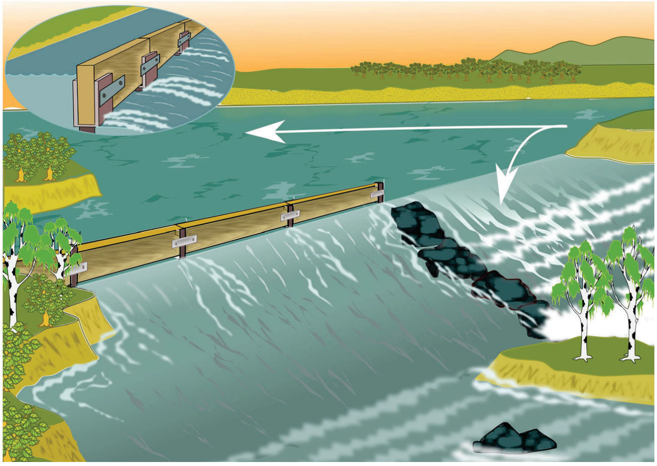


FIGURE 2 Illustration of the deflector installed on top of the weir to mitigate hydropeaking impact on the rheophilic fish spawning ground and to protect at least a portion of the adhesive eggs [Color figure can be viewed at wileyonlinelibrary.com]

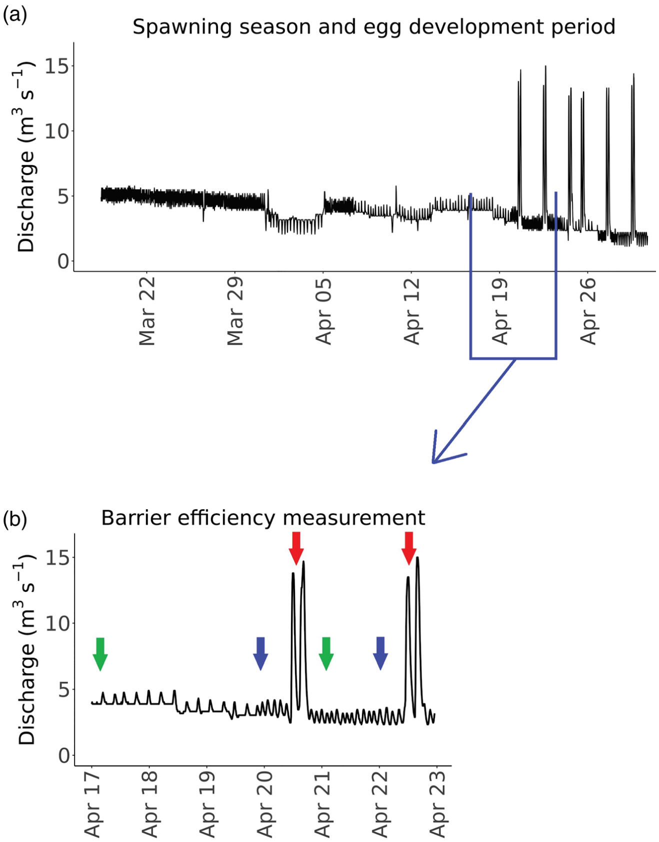


FIGURE 3 Hydrograph of the Želivka River—the tributary of the Želivka Reservoir in spring 2021 with apparent hydropeaking events (a). The lower hydrograph (b) shows the days when measurements took place. The arrows show the measurements of the egg density (green), the discharge measurements during the base discharge (blue) and the peak discharge (red) [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Measured discharge at the study side during hydropeaking—peak and base discharge conditions

	Peak discharge ($m^3 \times s^{-1}$)				Base discharge ($m^3 \times s^{-1}$)		
	Mean	Range	Prop. increase	*SD*	Mean	Range	*SD*
Protected channel	4.55	4.35–4.77	2.66	0.17	1.71	1.26–2.27	0.5
Unprotected channel	9.75	9.16–10.69	4.62	0.70	2.11	1.65–2.47	0.42
Mill channel	2.61	2.43–2.8	8.70	0.20	0.30	0.05–0.6	0.24
Total	16.91	16.05–18.27	4.09	1.03	4.13	3.02–5.32	1.14

Note: A total of 24 measurements were taken in 2021 (eight times in each channel—four times during peak discharge and four times during base discharge). Prop. increase, peak discharge/base discharge.

Figure 2). The planks were placed 0.07 m above the top of the weir (just above the water level at base flow) to allow regular water flow.

When discharge and water level increased during hydropeaking, the gates leading to the mill channel were opened manually (taking 2.6 m × s^{-1} on average), and additional water also went through the unprotected channel of the river and to a lesser extent through the opening below the deflector (Table 1, Figures 1 and 2). The flow deflector was installed prior to the first hydropeaking event on April 19, 2021 and April 15, 2022, and removed on May 10, 2021 and May 3, 2022, respectively, to cover the spawning season and egg development period. The wooden debris was cleaned periodically to maintain the base flow conditions.

2.4 | Water discharge and egg abundance measurements

Before and during hydropeaking, water discharge was measured using a SonTek FlowTracker2 handheld acoustic Doppler velocimeter (ADV), Yellow Springs Instruments, OH. Measurements of discharge to the protected and unprotected channels were performed on top of the weir. Measurements were taken from April 20 to April 22, 2021, four times during the peak discharge and four times during the base discharge (from 10 a.m. to 7 p.m.). To verify that the deflector reduced the flow in the protected channel, an additional measurement during hydropeaking was performed without the deflector installed on May 7, 2022 (from 13 a.m. to 8 p.m.), when the spawning and egg development phases had ended.

Egg density was quantified from images taken with an underwater camera (Hero 8, GoPro, CA) on a metal stand. The camera stand was moved to a specific location in the river marked with frames. Metal frames (0.3 × 0.3 m) were permanently installed in the river bottom of protected and unprotected channels before the spawning period. Twelve and 20 metal frames were placed in each channel in 2021 and 2022, respectively. The camera´s metal stand fit precisely on the metal frames to ensure that the exact same sampling location was recorded each time. Continuous video was recorded with the camera, and clearly focused snapshots were taken at all sampling locations. Images were taken before and after the hydropeaking event (17 April, 2021, April 21, 2021, and April 16, 2022). More detailed monitoring was not conducted in 2021 due to the negative effects of wading on protected spawning grounds. The number of eggs at each site was counted from video recordings. Due to the modified nature of the river, the sediment between boulders tends to be rather fine and composed of clay and sand, so we assumed that surface eggs were important for recruitment size in the system.

In addition, the temporal trends in egg densities were monitored using the method described above. In 2021 and 2022, egg density was estimated at 5-day intervals of seven and eight times during the spawning season, respectively. The data were compared to the temporal trend in 2018 with no protective measures applied (Bartoň et al., 2021).

2.5 | Data analysis

The percentage of eggs remaining in each frame after hydropeaking was computed. If the egg count was higher after the hydropeaking event due to the last spawners at the end of the spawning season, the value was standardized to 100%. Normality and homoscedasticity assumptions were tested using Shapiro–Wilk and Levene tests. To test whether the protected channel hosted a higher density of eggs than the unprotected channel, a two-sample *t* test was performed. The same test was used to compare protected and unprotected channels for a relative decrease in egg abundance after the hydropeaking event. Egg density among years was evaluated using a generalized linear mixed model fitted with a maximum likelihood model with a Poisson distribution in the lme4 package (Bates, Maechler, Bolker, & Walker, 2014). The egg density was related to year and random intercept of day in season. Analyses were performed using the program R version 4.1.1 (R Core Team, 2021).

3 | RESULTS

The total discharge at peak discharge increased 4.1 times compared to the base flow (Table 1). The discharge in the protected channel was on average 2.66 times higher at peak discharge compared to base flow, accounting for 26.9% of the discharge; the increase in the unprotected channel was on average 4.61 times higher at peak discharge compared to base discharge, and it received 57.7%. The mill channel received 15.4% of the peak discharge (Table 1). When the mill

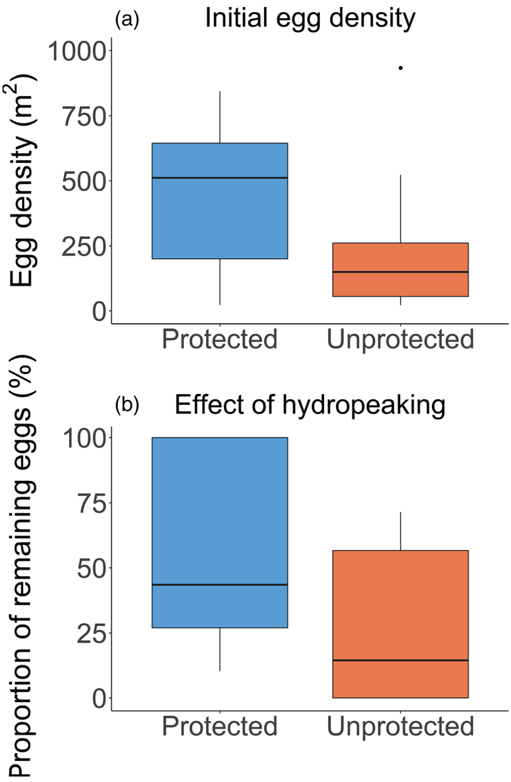


FIGURE 4 Comparison of initial egg densities before hydropeaking (a) and percent of remaining eggs in protected and unprotected channels (b) in 2021. The lower plots show the percentage of eggs remaining after hydropeaking (at 12 measurement points in each channel). The boxes represent the upper and lower quartiles, thick lines represent the medians, and whiskers represent 1.5 times the interquartile range [Color figure can be viewed at wileyonlinelibrary.com]

channel was closed and the deflector was removed, the discharge was distributed between the protected and unprotected channels at 40.8% and 59.2%, respectively, suggesting that the measures did not increase the portion of water leading to the unprotected channel.

In 2021, the initial egg count in the protected channel (mean (M) = 96.3, standard deviation (SD) = 110.9) was significantly higher than that in the unprotected channel (M = 20.5, SD = 23.8; $t(12) = 2.32$, $p < .05$; Figure 4), suggesting that protection measures were targeted to the more important part of the spawning ground. The percentage of eggs that resisted detachment was significantly higher in the channel protected by the deflector (M = 57.5%, SD = 39.03%) than in the unprotected channel (M = 27.1%, SD = 28.57%; $t(12) = 2.17$, $p < .05$; Figure 4).

In 2022, almost no eggs were deposited in the unprotected channel (M = 0.5, SD = 1.3), suggesting a strong preference for the protected channel (M = 118.4, SD = 90.5; $t(20) = 2.68$, $p < .05$). Therefore, it was not possible to compare egg detachment between the two channels. After the hydropeaking event, 54.8% of the eggs (M = 64.8, SD = 46.0) remained in the protected channel. In both 2021 and 2022, egg density was higher and more stable than without any measure in 2018 (general linear mixed effect Model $Z = 118.8$, $p < .001$ and $Z = 177.1$, $p < .001$, respectively; Figure 5).

4 | DISCUSSION

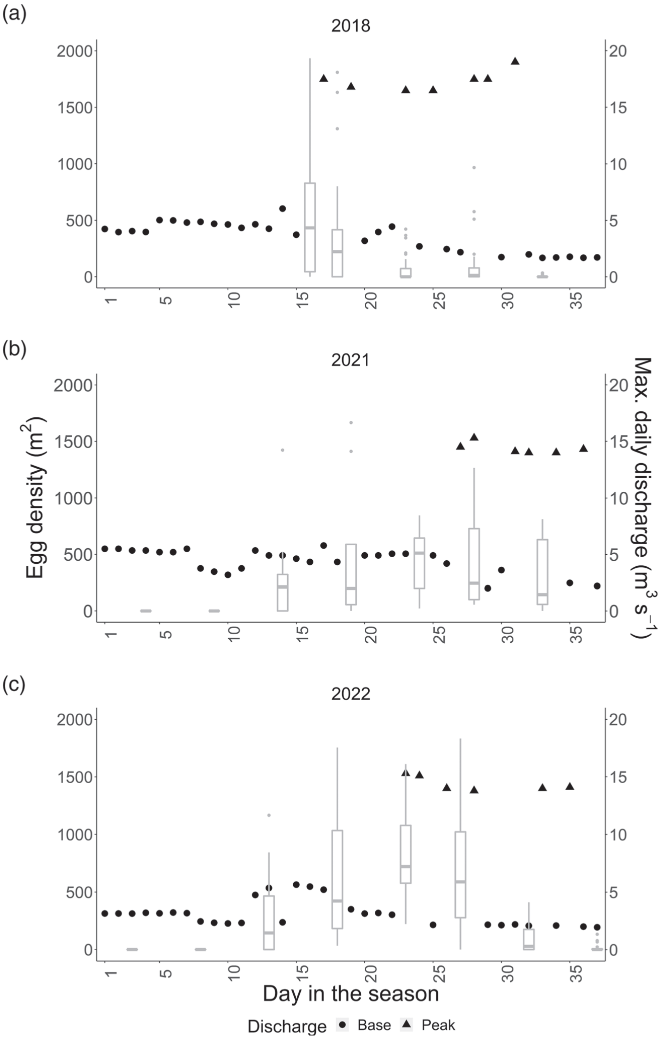
In this study, we demonstrated that the impact of hydropeaking on adhesive eggs could be reduced by installing a deflector and diverting much of the discharge away from the main spawning ground. However, the barrier was not able to protect all of the eggs due to a more than double increase in the discharge in the protected channel. If such a measure were implemented in the future, the barrier could be designed to facilitate the manipulation and reduction of space between the deflector and the weir once hydropeaking begins. Such a measure could potentially ensure that the discharge at the protected channel is very similar during base and peak discharge. This should lead to a lower number of detached eggs, since the proportion of detached adhesive eggs positively correlates with water speed during hydropeaking (Bartoň et al., 2021). However, in the case of the installed deflector, manipulation was difficult with its height above the weir crest and impossible during peak discharge due to its fixed position.

To monitor the eggs, we counted only the surface layer visible on the camera images. We can assume that part of the eggs were below the surface, but the importance of the interstitial spaces for recruitment depends on substrate quality (Duerregger et al., 2018; Nagel, Pander, Mueller, & Geist, 2020). At our research site, the removal of the loose sediment did not last until the spawning and interstitial spaces were clogged with fine sediment, so the substrate quality for the reproduction of rheophilic fishes was low. For this reason, we only monitored the top layer of the substrate for eggs. Other measures may include cleaning the substrate, which can be very effective but not very long lasting (Nagel, Mueller, Pander, & Geist, 2020).

The effectiveness of the method presented is limited to specific conditions, and the prerequisite is that the position of the spawning ground is determined in advance. The position of the monitored spawning ground is known due to long-term monitoring efforts (Šmejkal et al., 2018; Šmejkal et al., 2021). Furthermore, the modification of the river channel can be used to guide fish to the optimal position for egg protection under the discharge deflector. It should be verified that the unprotected channel does not host a significant proportion of egg abundance, and therefore, a potential additional increase in discharge is not as important as no action. This condition was met, especially in 2022, when fish spawning effort was concentrated almost exclusively in the protected channel.

We assume that the total loss of eggs at the spawning ground would have been significantly higher in both years if no protection had been implemented, since spawning was concentrated in the

FIGURE 5 Comparison of temporal trends in egg density development in the protected area of the spawning ground before (a) and after (b, c) the installation of the deflector and accompanying measures. The black dots indicate base discharge, and triangles indicate peak discharge. See Figure 4 for a boxplot description. Data from 2018 according to Bartoň et al. (2021)



protected channel thanks to additional measures. In the 2018 spawning season, without protective measures, nearly all attached eggs were removed early in the season by hydropeaking (Bartoň et al., 2021), and natural recruitment for the young of the year was not detectable by electrofishing (Blabolil et al., 2020). Therefore, mitigating the effects of hydropeaking on the spawning ground is important for the conservation of the species population protected by the act NATURA 2000 (Lusk et al., 2004).

A limitation represents the counting method of the remaining eggs in 2021, as some eggs could have been freshly spawned the night after hydropeaking. The 2022 data, measured immediately before and after hydropeaking on the same day, are very similar to the 2021 data, suggesting that the deflector is an improvement.

5 | CONCLUSIONS

The reported decline in rheophilic fish populations in recent decades undeniably has many causes (Tamario, Degerman, Polic, Tibblin, & Forsman, 2021). Constraints on recruitment size due to anthropogenic changes in rivers are among the most severe (Aarts et al., 2004; Rolls, Ellison, Faggotter, & Roberts, 2013), so any improvement in reproductive success that can help maintain or improve their population numbers is needed. The most affected parts of the world are developed and intensively used for human needs (Deinet et al., 2020). In highly regulated rivers, the reported decline in migratory rheophilic fishes is so severe that any mitigation of the reproductive bottleneck is very important.

Although this study attempts to improve the spawning success of rheophilic asp under strong anthropogenic impacts (hydropeaking and sedimented interstitial spaces due to fragmentation and dam construction) and is therefore far from natural river conditions, its results may help to manage better natural recruitment under similar scenarios in fragmented rivers (Belletti et al., 2020). Compared to large-scale restoration programs, the implemented flow deflector represents a low-cost solution that may help under similar conditions with a limited restoration budget. Although egg detachment did not reach the values previously reported from this site, it remains to be investigated whether such enhancement can actually lead to stronger cohorts compared to no protection measures.

ETHICS STATEMENT

The field sampling methods and experimental protocols used in this study were performed in accordance with the guidelines and permission from the Ministry of Environment of the Czech Republic (OZPZ 201/2019 Vac/3).

AUTHOR CONTRIBUTIONS

Marek Šmejkal, Daniel Bartoň, Tomáš Kolařík, Jindřich Duras, Zuzana Sajdlová and David Kortan participated in the field work. Marek Šmejkal, Daniel Bartoň and Jan Kubečka designed the study. Daniel Bartoň prepared the data for the analysis. Daniel Bartoň and Marek Šmejkal conducted the statistical analysis. Daniel Bartoň and Marek Šmejkal wrote the first draft. All authors contributed substantial feedback during manuscript preparation.

FUNDING INFORMATION

This research was supported by the Technology Agency of the Czech Republic (project “The enhancement of rheophilous fish reproduction in the artificial river environment,” No. TJ02000012).

CONFLICT OF INTEREST

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

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

ORCID

Marek Šmejkal https://orcid.org/0000-0002-7887-6411

REFERENCES

Aarts, B. G. W., Van Den Brink, F. W. B., & Nienhuis, P. H. (2004). Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: The transversal floodplain gradient. *River Research and Applications*, *20*, 3–23. https://doi.org/10.1002/RRA.720

Arlinghaus, R., Matsumura, S., & Dieckmann, U. (2010). The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing. *Biological Conservation*, *143*, 1444–1459. https://doi.org/10.1016/j.biocon.2010.03.020

Ashraf, F. B., Haghighi, A. T., Riml, J., Alfredsen, K., Koskela, J. J., Kløve, B., & Marttila, H. (2018). Changes in short term river flow regulation and hydropeaking in Nordic rivers. *Scientific Report*, *8*, 17232. https://doi.org/10.1038/s41598-018-35406-3

Auer, S., Zeiringer, B., Führer, S., Tonolla, D., & Schmutz, S. (2017). Effects of river bank heterogeneity and time of day on drift and stranding of juvenile European grayling (*Thymallus thymallus* L.) caused by hydropeaking. *Science of the Total Environment*, *575*, 1515–1521. https://doi.org/10.1016/j.scitotenv.2016.10.029

Baras, E. (1995). Thermal related variations of seasonal and daily spawning periodicity in *Barbus barbus*. *Journal of Fish Biology*, *46*, 915–917. https://doi.org/10.1111/j.1095-8649.1995.tb01617.x

Barbarossa, V., Schmitt, R. J. P., Huijbregts, M. A. J., Zarfl, C., King, H., & Schipper, A. M. (2020). Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 3648–3655. https://doi.org/10.1073/pnas.1912776117

Bartoň, D., Blabolil, P., Sajdlová, Z., Vejřík, L., Souza, A. T., Kubečka, J., & Šmejkal, M. (2021). Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species. *Ecohydrology*, *14*, e2280. https://doi.org/10.1002/eco.2280

Bartoň, D., Brabec, M., Sajdlová, Z., Souza, A. T., Duras, J., Kortan, D., … Šmejkal, M. (2022). Hydropeaking causes spatial shifts in a reproducing rheophilic fish. *Science of the Total Environment*, *806*, 150649. https://doi.org/10.1016/J.SCITOTENV.2021.150649

Bates, D., Maechler, M., Bolker, B., & Walker, S. 2014. lme4: linear mixed-effects models using S4 classes. R package version 1.1-6. R. Retrieved from http://CRAN.R-project.org/package=lme4

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., … Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*(7838), 436–441. https://doi.org/10.1038/s41586-020-3005-2

Blabolil, P., Bartoň, D., Halačka, K., Kočvara, L., Kolařík, T., Kubečka, J., … Peterka, J. (2020). The fate of 0+ asp (*Leuciscus aspius*) after being stocked in a reservoir. *Biologia (Bratisl)*, *75*, 989–996. https://doi.org/10.2478/s11756-019-00355-3

Boavida, I., Santos, J. M., Ferreira, T., & Pinheiro, A. (2015). Barbel habitat alterations due to hydropeaking. *Journal of Hydro-Environment Research*, *9*, 237–247. https://doi.org/10.1016/j.jher.2014.07.009

Bruder, A., Tonolla, D., Schweizer, S. P., Vollenweider, S., Langhans, S. D., & Wüest, A. (2016). A conceptual framework for hydropeaking mitigation. *Science of the Total Environment*, *568*, 1204–1212. https://doi.org/10.1016/j.scitotenv.2016.05.032

Bruno, M. C., Siviglia, A., Carolli, M., & Maiolini, B. (2013). Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology*, *6*, 511–522. https://doi.org/10.1002/eco.1275

Casas-Mulet, R., Saltveit, S. J., & Alfredsen, K. T. (2016). Hydrological and thermal effects of hydropeaking on early life stages of salmonids: A modelling approach for implementing mitigation strategies. *Science of the Total Environment*, *573*, 1660–1672. https://doi.org/10.1016/j.scitotenv.2016.09.208

Charmasson, J., & Zinke, P. (2011). Mitigation measures against hydropeaking effects. *SINTEF Energy Research*, *1*, 51.

Costa, M. J., Ferreira, M. T., Pinheiro, A. N., & Boavida, I. (2019). The potential of lateral refuges for Iberian barbel under simulated hydropeaking conditions. *Ecological Engineering*, *127*, 567–578. https://doi.org/10.1016/j.ecoleng.2018.07.029

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson, B.K., Garcia de Leaniz, C., Hogan, Z., Royte, J., Silva, L. G. M., Thieme, L. M., Tickner, D., Waldman, J., Wanningen, H., Weyl, O. L. F., & Berkhuysen, A. (2020). The Living Planet Index (LPI) for migratory freshwater fish—Technical Report.

Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., & Geist, J. (2018). The importance of stream interstitial conditions for the early-life-stage development of the European nase (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, *27*, 920–932. https://doi.org/10.1111/EFF.12403

Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O., & Nemeth, R. S. (2017). Fish spawning aggregations: Where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries*, *18*, 128–144. https://doi.org/10.1111/faf.12132

Grabowski, T. B., & Isely, J. J. (2007). Effects of flow fluctuations on the spawning habitat of a riverine fish. *Southeastern Naturalist*, *6*, 471–478. https://doi.org/10.1656/1528-7092(2007)6[471:EOFFOT]2.0.CO;2

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., … Zarfl, C. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*, 215–221. https://doi.org/10.1038/s41586-019-1111-9

Hauer, C., Siviglia, A., & Zolezzi, G. (2017). Hydropeaking in regulated rivers – From process understanding to design of mitigation measures. *Science of the Total Environment*, *579*, 22–26. https://doi.org/10.1016/j.scitotenv.2016.11.028

Kärgenberg, E., Økland, F., Thalfeldt, M., Thorstad, E. B., Sandlund, O. T., & Tambets, M. (2020). Migration patterns of a potamodromous piscivore, asp (*Leuciscus aspius*), in a river–lake system. *Journal of Fish Biology*, *97*, 996–1008. https://doi.org/10.1111/jfb.14454

Kjærstad, G., Arnekleiv, J. V., Speed, J. D. M., & Herland, A. K. (2018). Effects of hydropeaking on benthic invertebrate community composition in two central Norwegian rivers. *River Research and Applications*, *34*, 218–231. https://doi.org/10.1002/rra.3241

Lusk, S., Hanel, L., & Lusková, V. (2004). Red list of the ichthyofauna of The Czech Republic: Development and present status. *Folia Zoologica*, *53*, 215–226.

McMichael, G. A., McKinstry, C. A., Vucelick, J. A., & Lukas, J. A. (2005). Fall Chinook Salmon spawning activity versus daylight and flow in the tailrace of a large hydroelectric dam. *North American Journal of Fisheries Management*, *25*, 573–580. https://doi.org/10.1577/m04-044.1

Moreira, M., Hayes, D. S., Boavida, I., Schletterer, M., Schmutz, S., & Pinheiro, A. (2019). Ecologically-based criteria for hydropeaking mitigation: A review. *Science of the Total Environment*, *657*, 1508–1522. https://doi.org/10.1016/j.scitotenv.2018.12.107

Nagel, C., Mueller, M., Pander, J., & Geist, J. (2020). Making up the bed: Gravel cleaning as a contribution to nase (*Chondrostoma nasus* L.) spawning and recruitment success. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *30*, 2269–2283. https://doi.org/10.1002/AQC.3458

Nagel, C., Pander, J., Mueller, M., & Geist, J. (2020). Substrate composition determines emergence success and development of European nase larvae (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, *29*, 121–131. https://doi.org/10.1111/EFF.12500

R Core Team, 2021. R A Lang. Environ. Stat. Comput. R Found. Stat. Comput. Vienna, Austria. Retrieved from http://www.R-project.org/; ISBN 3-900051-07-0.

Rakowitz, G., Berger, B., Kubecka, J., & Keckeis, H. (2008). Functional role of environmental stimuli for the spawning migration in Danube nase *Chondrostoma nasus* (L.). *Ecology of Freshwater Fish*, *17*, 502–514. https://doi.org/10.1111/j.1600-0633.2008.00302.x

Rolls, R. J., Ellison, T., Faggotter, S., & Roberts, D. T. (2013). Consequences of connectivity alteration on riverine fish assemblages: Potential opportunities to overcome constraints in applying conventional monitoring designs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *23*, 624–640. https://doi.org/10.1002/aqc.2330

Schmutz, S., Bakken, T. H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., … Zeiringer, B. (2015). Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. *River Research and Applications*, *31*, 919–930. https://doi.org/10.1002/rra.2795

Šmejkal, M., Bartoň, D., Brabec, M., Sajdlová, Z., Souza, A. T., Moraes, K. R., … Kubečka, J. (2021). Climbing up the ladder: Male reproductive behaviour changes with age in a long-lived fish. *Behavioral Ecology and Sociobiology*, *75*, 1–13. https://doi.org/10.1007/s00265-020-02961-7

Šmejkal, M., Ricard, D., Vejřík, L., Mrkvička, T., Vebrová, L., Baran, R., … Kubečka, J. (2017). Seasonal and daily protandry in a cyprinid fish. *Scientific Reports*, *7*, 1–9. https://doi.org/10.1038/s41598-017-04827-x

Šmejkal, M., Souza, A. T., Blabolil, P., Bartoň, D., Sajdlová, Z., Vejřík, L., & Kubečka, J. (2018). Nocturnal spawning as a way to avoid egg exposure to diurnal predators. *Scientific Reports*, *8*, 15377. https://doi.org/10.1038/s41598-018-33615-4

Tamario, C., Degerman, E., Polic, D., Tibblin, P., & Forsman, A. (2021). Size, connectivity and edge effects of stream habitats explain spatio-temporal variation in brown trout (*Salmo trutta*) density. *Proceedings of the Royal Society B*, *288*, 20211255. https://doi.org/10.1098/RSPB.2021.1255

Targońska, K., Zarski, D., & Kucharczyk, D. (2008). A review of the artificial reproduction of asp, *Aspius aspius* (L.), and nase, *Chondrostoma nasus* (L.). *Archives of Polish Fisheries*, *16*, 341–354.

Tszydel, M., & Kruk, A. (2015). Tailwater habitat stability after dam removal and return to a natural hydrological regime. *Oceanological and Hydrobiological Studies*, *44*, 410–425. https://doi.org/10.1515/ohs-2015-0038

Vašek, M., Eloranta, A. P., Vejříková, I., Blabolil, P., Říha, M., Jůza, T., … Peterka, J. (2018). Stable isotopes and gut contents indicate differential resource use by coexisting asp (*Leuciscus aspius*) and pikeperch (*Sander lucioperca*). *Ecology of Freshwater Fish*, *27*, 1054–1065. https://doi.org/10.1111/EFF.12414

Wang, Y., & Xia, Z. (2009). Assessing spawning ground hydraulic suitability for Chinese sturgeon (*Acipenser sinensis*) from horizontal mean vorticity in Yangtze River. *Ecological Modelling*, *220*, 1443–1448. https://doi.org/10.1016/j.ecolmodel.2009.03.003

Young, P. S., Cech, J. J., & Thompson, L. C. (2011). Hydropower-related pulsed-flow impacts on stream fishes: A brief review, conceptual model, knowledge gaps, and research needs. *Reviews in Fish Biology and Fisheries*, *21*, 716–731. https://doi.org/10.1007/s11160-011-9211-0

How to cite this article: Bartoň, D., Sajdlová, Z., Kolařík, T., Kubečka, J., Duras, J., Kortan, D., & Šmejkal, M. (2022). Use of a flow deflector to protect rheophilic fish spawning grounds during hydropeaking. *River Research and Applications*, 1–9. https://doi.org/10.1002/rra.4084

Paper IV

Anthropogenic hydromorphological alteration increases vulnerability of rheophilic fish eggs to predation by generalists

(Manuscript)

Anthropogenic hydromorphological alteration increases the vulnerability of rheophilic fish eggs to predation by generalists

Daniel Bartoň[a,b], Marek Brabec[c], Zuzana Sajdlová[a], Allan T. Souza[a], Jan Kubečka[a], Marek Šmejkal[a]

[a] Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic
[b] Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic
[c] Institute of Computer Science, Czech Academy of Sciences, Prague, Czech Republic

Running title: Habitat modification enhances fish interaction.

Abstract

Rheophilic fish face a severe decline in their abundance due to human modification of riverine ecosystems. The damming of rivers favours generalist fish species, which may further negatively influence the remaining populations of rheophilic fish. Here, we focused on the interaction of two fish species, rheophilic asp (*Leuciscus aspius*) and generalist common bream (*Abramis brama*), where the latter poses a threat to asp eggs. Specifically, we addressed the hypothesis that the accessibility of asp spawning ground is directly related to the degree of habitat modification caused by the slow-down of water speed due to water level manipulation in a reservoir. We monitored the asp egg abundance in the fluvial spawning ground from 2018 to 2020. The common bream presence on the spawning ground was monitored by passive telemetry arrays. The predation of eggs of asp was confirmed by a gut content analysis in common bream on the site. High water levels in 2018 and 2019 facilitated easier access of common bream to the spawning ground due to slower water flow. In 2020 the water level was significantly below the usual value, which increased the flow rate on the spawning ground two to three times, limiting the accessibility of the spawning ground by common bream. Based on the results of statistical modelling, we suggest that river habitat modification may enforce interspecific interactions among fish species that usually do not interrelate strongly in the natural river environment. We suggest that these inconspicuous changes in trophic interactions of the anthropogenic riverine landscape may constitute one of the causes of rheophilic fish decline.

Keywords: habitat modification; connectivity interruption; reservoir management; fish conservation; *Abramis brama*; water discharge; water level fluctuation; fish telemetry

Introduction

The natural species composition of freshwater fish fauna is exposed to challenging conditions made by human modifications of the riverine landscape. The majority of rivers are no longer free-flowing, and the migration of many fish species is reduced or prevented by barriers in the form of dams and weirs (Grill et al., 2019; Nilsson et al., 2005). Even small barriers can affect fish movement, fragment their habitats and thus force fish populations to adjust their life-history strategy (Branco et al., 2017). Fish migrating upstream are being stopped at choke points downstream of the barriers (Tamario et al., 2019; Volpato et al., 2009).

Damming of the river not only provides physical challenges for native rheophilic fish in the form of barriers and habitat loss, but it also enables the establishment of lowland riverine fauna by promoting their population growth in reservoirs and slowed-down section of the rivers (Cooper et al., 2016; Šmejkal et al., 2023b). Before man-induced changes in the stream connectivity, these generalist fish species (that may be even locally non-native in their current distribution range) constituted zero to very low percentage of the fish composition, but the habitat modification along with fisheries stocking practices enabled their establishment (Loures and Pompeu, 2019; Říha et al., 2009). As a consequence of their spread, fish from artificial river sections can then threaten native rheophilic fish populations in their remaining habitat (Pfauserová et al., 2019; Šmejkal et al., 2023b). However, the implications of enhanced interactions between proliferating generalist species in altered riverine habitats and their native riverine fauna are not very well explored in the literature (Šmejkal et al., 2023b).

Introductions of non-native fish might lead to diversity loss and homogenization of fish populations in favour of generalist species (Olden and Rooney, 2006; Poff et al., 2007; Rahel, 2000). Non-native fishes from the reservoir migrating upstream outnumber pristine river species with various impacts (Hladík et al., 2008). The presence of introduced fish in spawning areas can lead to threatening native fish by egg predation (Schaeffer and Margraf, 1987; Šmejkal et al., 2017a), and thus substantially reduce the population's yearly recruitment (Silbernagel and Sorensen, 2013). Upstream migration of cyprinid fishes peaks during the spring season when a great portion of fish from deeper sections of the dammed river heads towards shallow flowing water to spawn (Hladík and Kubečka, 2003), this can lead to enormous use of the tributaries and river sections under the weirs (Prchalová et al., 2008; Říha et al., 2009).

In this study, we focused on two cyprinid species migrating towards tributaries during the spring. Asp (*Leuciscus aspius*) is a rheophilic fish species spawning in fast-flowing water. Its adhesive eggs remain on the gravel substrate for approximately 20 days (depending on the temperature) before hatching (Targoñska et al., 2008). Common bream (*Abramis brama*) aggregates in the tributaries in the spring (Hladík and Kubečka, 2003) and its migration to asp spawning ground may pose a potential predation threat for asp eggs in the modified river ecosystem. By using passive telemetry arrays on the spawning ground, we tested the availability of rheophilic species spawning ground for a possible generalist egg predator under different flow and water level conditions. We tested whether the accessibility of the spawning ground is a function of the water speed and that common bream access to the spawning ground is facilitated by the reduction of the water current due to an unnaturally high level of retained water in the reservoir.

Materials and methods

Study site

The study site is located in the tributary of the Želivka Reservoir, Czech Republic (Figure 1). The reservoir is positioned on Želivka River with former species composition of rheophilic fish species such as barb (*Barbus barbus*), dace (*Leuciscus leuciscus*) and asp (*Leuciscus aspius*). After dam construction and filling from 1965 to 1975, the species composition evolved in recent typical lowland community with dominant species common bream (*Abramis brama*), bleak (*Alburnus alburnus*), roach (*Rutilus rutilus*), European perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernua*), Northern pike (*Esox lucius*), pikeperch (*Sander lucioperca*) and European catfish (*Silurus glanis*) (Matěna et al., 2015). From the rheophilic fish that formerly inhabited the river section, only asp remained in the studied area in substantial numbers (Matěna et al., 2015). It uses the lacustrine part of the reservoir for most of the year and migrates to the tributary for spawning in early spring. Around 2000 individuals migrate each year to the spawning ground and reproduce in the spatially restricted area (Šmejkal et al., 2023a, 2021). Since this population is the largest isolated population in the Czech Republic, it became protected by the European Act NATURA 2000 (Lusk et al., 2004).

Species description

Asp (family Leuciscidae) is a large predator inhabiting large rivers in Europe and part of Asia (Kottelat and Freyhof, 2007). Spawning takes place during early spring for which individuals migrate upstream seeking fast-flowing waters (Bartoň et al., 2021; Šmejkal et al., 2017b). Common bream (family Leuciscidae) is an opportunistic benthivorous species with a similar distribution range as asp (Kottelat and Freyhof, 2007) and commonly has the highest biomass in temperate eutrophic reservoirs in central Europe (Šmejkal et al., 2015). In conditions of low abundance of zoobenthos, it is an effective planktivorous filter-feeder (Jarolím et al., 2010; Van Den Berg et al., 1994) and in some extreme conditions exhibits opportunistic feeding on small fish (Vejřík et al., 2016). This implies that its ability to find and utilize large-scale food sources is as great as its movement potential to find it (Brodersen et al., 2019; Muška et al., 2013).

Fish capture and tagging procedure

Common bream were captured for tagging within 0.5-3 km from the asp spawning ground using an electrofishing boat (electrofisher EL 65 II GL DC, Hans Grassel, Schönau am Königsee, Germany, 13 kW, 300/600 V). Captured common bream were anesthetized with MS-222. Three to four scales were removed above the pelvic fin and the fish were individually tagged with passive integrated transponder tags (PIT tag, Oregon RFID, half-duplex, length 32 mm, diameter 3.65 mm, weight 0.8 g, ISO 11784/11785 compatible). No sutures were used due to the potential negative impact on an individual´s health in cyprinids (Skov et al., 2005). Despite the open scar wound, the majority of tagging is successful with this approach in cyprinids (Skov et al., 2005; Šmejkal et al., 2019). Standard length (SL) and identification code were recorded. In the spawning seasons 2017 – 2020, we tagged 60, 138, 177 and 247 common bream with mean standard lengths 321 ± 25 mm standard deviation SD, 326 ± 25 mm SD, 325 ± 29 mm SD and 310 ± 29 mm SD, respectively.

Fish passive telemetry

Fish were tracked by passive telemetry antennas installed in the cross-sections of the spawning ground. Three antenna loops were built with a width of 10 m and height of 60 cm with a detection range of 80 cm in 2018 and 2019 and 5 antenna loops were built in 2020 due to the low water level in the reservoir and therefore longer riverine section suitable for asp spawning as a consequence (Figure 1). The charging and recording frequency were set to 10 energize cycles s^{-1} with LF HDX RFID readers (OregonRFID, Portland, Oregon, USA). The fish´s individual code was stored along with the time of detection every time the fish passed the antenna loop along with timestamp information.

Common bream gut inspection

Due to the nocturnal trend of the common bream presence on the spawning ground, we conducted night electrofishing to reveal whether common bream consumes asp eggs. At 11 pm 10 April 2021, 28 individuals of common bream were caught using an electrofishing boat (electrofisher EL 65 II GL DC, Hans Grassel, Schönau am Königsee, Germany, 13 kW, 300/600 V) at the tributary right under antenna 2 (Figure 1). Gut content was washed out by filtered water injection inserted into the pharynx (Faina, 1983)and fish were released back to the river after recovery from electrofishing. Gut content was investigated on the spot. The fullness was estimated on the scale of 0 – 5 (0 – no food content, 5 – full guts, linear scale) as well as the category of gut content found in the guts: benthos, algae, sand and fish eggs with a volumetric estimation of the percentage of each content.

Asp egg monitoring

Eggs densities were monitored by underwater cameras (Hero 8, GoPro, California, U. S.). Clear pictures of river substrate were chosen from video recording and analysed to estimate the abundance of asp eggs. Pale spots representing attached eggs were counted from the video records (Bartoň et al., 2021).

Water flow monitoring and temperature monitoring

Discharge and water level data were obtained with a 10-minute resolution from the Vltava River Authority. The temperature during the monitoring campaigns was measured by dataloggers (HOBO Pendant Temperature/Light 64K Data Logger, Onset Computer Corporation, Bourne, Massachusetts, USA) placed in the tributary at 0.5-m depth. The approximate water speed at each antenna site was computed from discharge data and the measured surface of the river cross-section.

Data preparation and analysis

Timestamps of individual fish detections by each antenna array were rounded to 10-minute intervals to obtain matching timestamps with flow and temperature measured with 10-minute resolution. From there, we got a time series of presence/absence indicators (0/1 binary data) in 10 minutes resolution. For each individual, we analysed only the time interval between the time of its first detection on any antenna array and the time of its last detection on any antenna array in a given year. Hence, fish not detected in a given year did not yield any data for that year (but it might for other years). The probability of presence was modelled by a binomial GAM (Generalized Additive Model) (Wood, 2017) allowing for parametric terms and both smooth and random effects. We used canonical link (logit) and implemented the smooth terms as splines (de Boor, 1978) with roughness penalization (Wood, 2017). The model was fitted via penalized likelihood with automatic selection of penalty coefficients (de Boor, 1978; Wood et al., 2016). Explanatory variables of main interest were: water flow, fish SL, time of day (nested within a year), antenna position (nested within a year) and temperature. Dependence among the data of the same individual was modelled via the random fish ID effect. Our GAM model is:$Y_{it} \sim Bernoulli(\pi_{it})$

$$\begin{aligned} logit(\,\pi_{it}) = \sum_{y}\sum_{a} \beta_{ya}.\,I(\text{time } t \text{ is in year } y\,) + b_i + s_{diurnal}(diurnal_t) \\ + s_{temperature}(temperature_t) + \beta_{length}.\,length_i \\ + s_{flow}(flow_t) \\ + \sum_{y} s_{seasonal,y}(day\_within\_a\_year_t)\,.\,I(\text{time } t \text{ is in year } y) \end{aligned}$$

Where:

- Y_{it} is the random variable describing presence of i-th fish at time *t* (1 if the i-th fish was present at time *t* and 0 otherwise)
- $logit(x) = log\left(\frac{x}{1-x}\right)$ for $0 < x < 1$ is the canonical link for the binomial distribution (and hence for Bernoulli as the special case)
- $I(.)$ is the indicator function (assumes value of 1 if the statement in its argument is true and value of 0 otherwise)
- b_i is the random fish effect (assuming $b_i \sim N(0, \sigma^2\,)$)
- $s_{diurnal}$ is the smooth effect of time within a day. Since this term is necessarily periodic, it is implemented as a cyclic cubic spline
- $s_{temperature}$ is the smooth effect of water temperature (implemented

via cubic spline)

- β_{ya} is effect of a-th antenna in y-th year (precise positions of the antennas differed from year to year, but the ordering is kept over the years)
- β_{length} is the effect of fish length (measured at the time of tagging) – assumed linear on the logit scale
- s_{flow} is the smooth effect (implemented via cubic spline) of flow
- $s_{seasonal,y}$ is the smooth seasonal effect (nested within a year to account for different positioning of asp spawning season in different years)

Data were processed using packages dplyr, data.table, mcgv, mgcViz and lubridate within R software version 4.0.1 (Dowle and Srinivasan, 2021; Fasiolo et al., 2020; Grolemund and Wickham, 2011; R Core Team, 2020; Wickham et al., 2023; Wood, 2017).

Results

We detected 123, 131 and 233 tagged common bream by the installed antenna arrays in the monitored area of the spawning ground from 2018 to 2020, respectively.

The detections of common bream on the antennas were significantly dependent on fish ID, flow, time of day, year and temperature (Table 1). The effect of tagging fish length was not significant in the model. The model explained 17.3 % of deviance with R^2 = 1.03 %. Relative detections of common bream were higher in the afternoon and during the night with a drop of detection probability between 6 and 12 am and another drop of detection probability around 9 pm (Figure 2). Detection probability increased from temperature from 3 °C to approximately 7 °C and then became relatively stable (Figure 2). During low discharge around 3 $m^{3}*s^{-1,}$ the detection probability of common bream was the highest and then declined with increasing discharge with a tendency to increase again in the highest discharge recorded (Figure 2). Relative detections in dependency on date had a similar course in both 2018 and 2019 but with higher fluctuations in 2020. With a later date in the asp spawning season, relative detections of common bream tend to increase every year (Figure 2).

The majority of common bream captured for gut analysis had egg content (27 out of 28). Average fullness was 2,7 (on a scale from 1 to 5). The eggs represented 31.4 % of gut volume content and the rest (68.6 %) consisted of algae, sand and benthic invertebrates.

The velocity of water flow on the antennas was much higher in 2020 compared to previous years (Figure 3). The water level in 2018 was the highest and remained high the whole asp spawning season. In 2019 the water level gradually increased to the maximum level. The season of 2020 had the lowest water level of the reservoir due to drought, in comparison with previous seasons around 1.5 m lower (Figure 4). In 2020 common bream were almost not able to reach antenna 3 or more upstream located antennas, while in 2018 and 2019 only antenna 1 (the most upstream located) had much lower common bream detections than the others (Figure 5).

The relative abundance of asp eggs was in 2018 and 2019 highest in the first half of April and that rapidly decreased. In 2020 the highest relative abundance of eggs measured was on 22 April and the eggs were present for the whole asp spawning season (Figure 6).

Discussion

Upon monitoring the asp egg density on the spawning ground in 2018 – 2020, we verified that common bream presence on the spawning ground is accompanied by egg predation by gut content analysis. Our study can contribute to knowledge of threats that are induced by dam and weir construction on rivers which already represent one of the greatest threats to freshwater fish diversity (García et al., 2011; Grill et al., 2019; Nilsson et al., 2005; Power, 1992). In the case of our study, the lacustrine environment of the Želivka Reservoir is enabling the expansion of generalist fish, common bream. During the fish spring migration, the weir built on the tributary prevents asp from finding more remote spawning sites with faster flow conditions for its reproduction (Hladík and Kubečka, 2003), which has repercussions on fish interaction on the spawning ground.

Results of the study suggest that with decreasing water level in the reservoir, asp may be able to find better spawning conditions in longer stretches of fast-flowing water further from the lacustrine impounded part. Such conditions would partially eliminate the presence of generalists such as common bream, and therefore also reduce the predation effects of the asp eggs. Asp is the only rheophilic species surviving in the reservoir (Matěna et al., 2015). However, even the reproduction of asp is complicated by many significant constraints. The natural reproduction of asp is frequently disturbed by hydropeaking in the tributary river, where the increased water velocity is causing an eggs detachment and transport to less favourable habitats (Bartoň et al., 2021). Asp egg density is severely reduced by bleak predation of drifting eggs (Šmejkal et al., 2018, 2017a). When the distance from the impounded lacustrine part is low, the generalists like common bream prey on asp eggs. Utilizing asp eggs during the spring period may be valuable for their subsequent spawning effort since the fish eggs have a high nutritional value and are often utilized with both fish and non-fish predators (Karjalainen et al., 2015; Lutz et al., 2020; Paradis et al., 1996; Schaeffer and Margraf, 1987). Consequently, the reproduction success of asp seems to be very uncertain (Blabolil et al., 2020), and the majority of asp recruitment in the reservoir is coming from restocking (artificial reproduction of local population and stocking at the size of 7 – 10 cm SL) and not from the natural reproduction to support asp role as a predator for biomanipulation of water quality (Blabolil et al., 2020; Vašek et al., 2013)

Asp has the role of one of the top predators in the system. Reduction of its successful recruitment can lead to population decrease or collapse and cause the decrease of top-down control for some omnivorous species, especially bleak (*Alburnus alburnus*), asp main fish prey item (Šmejkal et al., 2017a; Vašek et al., 2018). Since the reservoir's main purpose is to supply of drinking water, predator fish including asp are supported by artificial spawning and subsequent release of 0+ fish in autumn to increase water quality (Blabolil et al., 2020; Vašek et al., 2013). The natural reproduction of asp is frequently disturbed by hydropeaking in the tributary river, where the increased water velocity causes an egg detachment (Bartoň et al., 2021) and egg density is severely reduced by bleak predation of drifting eggs (Šmejkal et al., 2018, 2017a). Therefore, the majority of asp recruitment is likely coming from stocking (artificial reproduction of the local population and stocking at a size of 7 – 10 cm SL) and not natural reproduction (Blabolil et al., 2020).

Common bream is a generalist fish species with a high range of food sources it can utilize. It can be very effective as a benthivore but is also able to filter-feed on zooplankton (Jarolím et al., 2010). Utilizing asp eggs during the spring period may be valuable for their subsequent spawning effort since the fish eggs have a high nutritional value and are often utilized with both fish and non-fish predators (Karjalainen et al., 2015; Lutz et al., 2020; Paradis et al., 1996; Schaeffer and Margraf, 1987).

There are several ways to investigate fish egg predation; one of them being DNA gut analysis which can identify the exact species on which eggs are introduced species feeding (Lutz et al., 2020). In our study at a given time, only asp is actively spawning in the given river section and therefore the recognition of the fish eggs in the gut content was sufficient for the study. For this reason, passive telemetry was chosen as a suitable method for quantifying the migratory tendencies of common bream with the potential to tag a large number of individuals (Bond et al., 2018; Gibbons and Andrews, 2004). In order not to disturb the recording of fish movement between antennas, gut content was examined on only 28 common bream specimens during one night when asp spawning was intense and large numbers of common bream were visually observed. Since almost every examined individual had eggs in their gut content, we found it not necessary to repeat the examination and risk a disturbance of asp spawning and common bream movements.

Common bream is often important dominant of late succession state of mesotrophic and eutrophic European reservoirs and lakes, where it can contribute half of the biomass to total fish stock (Říha et al., 2009; Šmejkal et al., 2015). This state is also characterized by quite high turbidity and a generally low proportion of predators in the community (Říha et al., 2009). This study suggests a potential link between the common bream's high abundance and the reduction of asp predatory stock through egg consumption facilitated by riverine habitat modification.

Common bream tend to migrate when water temperatures increase while seeking refuge from flowing water during periods of low temperatures

(Gardner et al., 2013). Since water temperatures are still low (5-6 deg. C) when asp start to spawn in flowing water, the eggs are relatively safe early in the season. However, due to their long development time of approximately 20 days (Targońska et al., 2008), they may face a strong migration of egg-eating fish in the later stages of their development. Results of this study suggest that the velocity of water flow in the river is a limiting factor for common bream during the asp spawning period.

With this knowledge, we suggest providing as natural river-like conditions in tributary as possible during the spawning season to protect asp reproduction. Asp should be able to get in rivers with shallow fast-flowing rifles with relatively stable discharge.(Bartoň et al., 2021) Common bream appears to have limited ability to access asp eggs in these rapids. On our research site and other reservoirs tributaries have barriers asp spawning success can be improved by lowering the water level to create better spawning conditions in entering the river. Even more effective can be the destruction of upstream barriers to fully restore fluvial habitat, but the final decision needs thorough study and planning, since such a decision may have negative effects on current upstream biota.

Acknowledgements

We thank Luboš Kočvara, Tomáš Kolařík and Zdeněk Popelka for their assistance during fieldwork.

Funding

This research was supported by the project “The enhancement of rheophilous fish reproduction in the artificial river environment” (No. TJ02000012), AV 21 strategy support program “Water for Life” and also partially supported by the long-term strategic development financing of the Institute of Computer Science (Czech Republic RVO 67985807).

Conflict of interest

The authors declare no competing financial interests.

Ethical approval

The field sampling methods and experimental protocols used in this study were performed following the guidelines and permission from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. CZ 01679) and approved by the Experimental Animal Welfare Commission of Biology Centre of the Czech Academy of Sciences.

Authors' contributions

DB, MŠ, ATS, ZS and JK participated in the field work and writing the manuscript. MŠ and DB designed the study. MB, ATS and MŠ contributed to the statistical analysis. MŠ, MB and DB graphically presented data. DB wrote the first draft.

References

Bartoň, D., Bretón, F., Blabolil, P., Souza, A.T., Vejřík, L., Sajdlová, Z., Kolařík, T., Kubečka, J., Šmejkal, M., 2021. Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species. Ecohydrology. https://doi.org/10.1002/eco.2280

Blabolil, P., Bartoň, D., Halačka, K., Kočvara, L., Kolařík, T., Kubečka, J., Šmejkal, M., Peterka, J., 2020. The fate of 0+ asp *(Leuciscus aspius*) after being stocked in a reservoir. Biologia (Bratisl) 75. https://doi.org/10.2478/s11756-019-00355-3

Bond, R.M., Nicol, C.L., Kiernan, J.D., Spence, B.C., 2018. Occurrence, fate, and confounding influence of ghost PIT tags in an intensively monitored watershed. Canadian Journal of Fisheries and Aquatic Sciences. https://doi.org/10.1139/cjfas-2017-0409

Branco, P., Amaral, S.D., Ferreira, M.T., Santos, J.M., 2017. Do small barriers affect the movement of freshwater fish by increasing residency? Science of the Total Environment. https://doi.org/10.1016/j.scitotenv.2016.12.156

Brodersen, J., Hansen, J.H., Skov, C., 2019. Partial nomadism in large-bodied bream (*Abramis brama*). Ecol Freshw Fish 28, 650–660. https://doi.org/10.1111/eff.12483

Cooper, A.R., Infante, D.M., Wehrly, K.E., Wang, L., Brenden, T.O., 2016. Identifying indicators and quantifying large-scale effects of dams on fishes. Ecol Indic. https://doi.org/10.1016/j.ecolind.2015.10.016

de Boor, C., 1978. A Practical Guide to Spline, Applied Mathematical Sciences, New York: Springer, 1978. https://doi.org/10.2307/2006241

Dowle, M., Srinivasan, A., 2021. data.table: Extension of `data.frame`. R package version 1.14.2.

Faina, R., 1983. Využívání přirozené potravy kaprem v rybnících, metodika (in Czech), Use of natural food by carp in ponds, methodology.

Fasiolo, M., Nedellec, R., Goude, Y., Wood, S.N., 2020. Scalable Visualization Methods for Modern Generalized Additive Models. Journal of Computational and Graphical Statistics 29, 78–86. https://doi.org/10.1080/10618600.2019.1629942

García, A., Jorde, K., Habit, E., Caamaño, D., Parra, O., 2011. Downstream environmental effects of dam operations: Changes in habitat quality for native fish species. River Res Appl 27, 312–327. https://doi.org/10.1002/rra.1358

Gardner, C.J., Deeming, D.C., Eady, P.E., 2013. Seasonal movements with shifts in lateral and longitudinal habitat use by common bream, *Abramis brama*, in a heavily modified lowland river. Fish Management Ecology 20, 315–325. https://doi.org/10.1111/fme.12014

Gibbons, J.W., Andrews, K.M., 2004. PIT Tagging: simple technology at its best. Bioscience 54, 447–454. https://doi.org/10.1641/0006-3568(2004)054[0447:PTSTAI]2.0.CO;2

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world's free-flowing rivers. Nature. https://doi.org/10.1038/s41586-019-1111-9

Grolemund, G., Wickham, H., 2011. Dates and Times Made Easy with lubridate. Journal of Statistical Software 40, 1–25. https://doi.org/10.18637/jss.v040.i03

Hladík, M., Kubečka, J., 2003. Fish migration between a temperate reservoir and its main tributary. Hydrobiologia 504, 251–266. https://doi.org/10.1023/B:HYDR.0000008525.46939.42

Hladík, M., Kubečka, J., Mrkvička, T., Čech, M., Draštík, V., Frouzová, J., Hohausová, E., Matěna, J., Matěnová, V., Kratochvíl, M., Peterka, J., Prchalová, M., Vašek, M., 2008. Effects of the construction of a reservoir on the fish assemblage in an inflow river. Czech Journal of Animal Science. https://doi.org/10.17221/370-cjas

Jarolím, O., Kubečka, J., Čech, M., Vašek, M., Peterka, J., Matěna, J., 2010. Sinusoidal swimming in fishes: The role of season, density of large zooplankton, fish length, time of the day, weather condition and solar radiation. Hydrobiologia 654, 253–265. https://doi.org/10.1007/s10750-010-0398-1

Karjalainen, J., Ruokonen, T.J., Marjomäki, T.J., Martikainen, A., Pursiainen, M., Sarvala, J., Tarvainen, M., Ventelä, A.M., 2015. Predation by signal crayfish *Pacifastacus leniusculus* on fish eggs and its consequences for coregonid recruitment. J Fish Biol 86, 651–667. https://doi.org/10.1111/jfb.12588

Kottelat, M., Freyhof, J.J., 2007. Handbook of European freshwater fishes, Copeia. https://doi.org/10.1643/OT-08-098a.1

Loures, R.C., Pompeu, P.S., 2019. Temporal changes in fish diversity in lotic and lentic environments along a reservoir cascade. Freshw Biol 64, 1806–1820. https://doi.org/10.1111/fwb.13372

Lusk, S., Hanel, L., Lusková, V., 2004. Red List of the ichthyofauna of the Czech Republic: Development and present status. Folia Zool Brno 53, 215–226.

Lutz, E., Hirsch, P.E., Bussmann, K., Wiegleb, J., Jermann, H.P., Muller, R., Burkhardt-Holm, P., Adrian-Kalchhauser, I., 2020. Predation on native fish eggs by invasive round goby revealed by species-specific gut content DNA analyses. Aquat Conserv. https://doi.org/10.1002/aqc.3409

Matěna, J., Říha, M., Soukalová, K., Kočvara, L., Kubečka, J., 2015. Complex ichtyological assessment of Želivka Reservoir in 2014 (in Czech).

Muška, M., Tušer, M., Frouzová, J., Draštík, V., Čech, M., Jůza, T., Kratochvíl, M., Mrkvička, T., Peterka, J., Prchalová, M., Říha, M., Vašek, M., Kubečka, J., 2013. To migrate, or not to migrate: Partial diel horizontal migration of fish in a temperate freshwater reservoir. Hydrobiologia. https://doi.org/10.1007/s10750-012-1401-9

Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science (1979) 308, 405–408. https://doi.org/10.1126/science.1107887

Olden, J.D., Rooney, T.P., 2006. On defining and quantifying biotic homogenization. Global Ecology and Biogeography 15, 113–120. https://doi.org/10.1111/J.1466-822X.2006.00214.X

Paradis, A.R., Pepin, P., Brown, J.A., 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Canadian Journal of Fisheries and Aquatic Sciences 53, 1226–1235. https://doi.org/10.1139/f96-051

Pfauserová, N., Slavík, O., Horký, P., Kolářjová, J., Randák, T., 2019. Migration of non-native predator Asp (*Leuciscus aspius*) from a reservoir poses a potential threat to native species in tributaries. Water (Switzerland). https://doi.org/10.3390/w11061306

Poff, N.L.R., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proc Natl Acad Sci U S A 104, 5732–5737. https://doi.org/10.1073/pnas.0609812104

Power, M.E., 1992. Habitat Heterogeneity and The Functional Signifiance of Fish in River Food Webs. Ecology 73, 1675–1688. https://doi.org/10.2307/1940019

Prchalová, M., Kubečka, J., Vašek, M., Peterka, J., Sed'a, J., Jůza, T., Říha, M., Jarolím, O., Tušer, M., Kratochvíl, M., Čech, M., Draštík, V., Frouzová, J., Hohausová, E., 2008. Distribution patterns of fishes in a canyon-shaped reservoir. Journal of Fish Biology, https://doi.org/10.1111/j.1095-8649.2008.01906.x

R Core Team, R.D., 2020. R Development Core Team, R: a language and environment for statistical computing, R: A Language and Environmental for Estatistical Computing.

Rahel, F.J., 2000. Homogenization of Fish Faunas Across the United States. Science (1979) 288, 854–856. https://doi.org/10.1126/science.288.5467.854

Říha, M., Kubečka, J., Vašek, M., Seďa, J., Mrkvička, T., Prchalová, M., Matena, J., Hladík, M., Čech, M., Draštík, V., Frouzová, J., Hohausová, E., Jarolím, O., Jůza, T., Kratochvíl, M., Peterka, J., Tušer, M., 2009. Long-term development of fish populations in the Římov Reservoir. Fish Management Ecology. https://doi.org/10.1111/j.1365-2400.2008.00650.x

Schaeffer, J.S., Margraf, F.J., 1987. Predation on fish eggs by white perch, *Morone americana*, in western Lake Erie. Environmental Biology of Fishes. https://doi.org/10.1007/BF00002331

Silbernagel, J.J., Sorensen, P.W., 2013. Direct field and laboratory evidence that a combination of egg and larval predation controls recruitment of invasive common carp in many lakes of the upper Mississippi River basin. Transactions of the American Fisheries Society 142, 1134–1140.

Skov, C., Brodersen, J., Bronmark, C., Hansson, L.-A., Hertonsson, P., Nilsson, P.A., 2005. Evaluation of PIT-tagging in cyprinids. Journal of Fish Biology 67, 1195–1201.

Šmejkal, M., Baran, R., Blabolil, P., Vejřík, L., Prchalová, M., Bartoň, D., Mrkvička, T., Kubečka, J., 2017a. Early life-history predator-prey reversal in two cyprinid fishes. Scientific Reports 7, 6924. https://doi.org/10.1038/s41598-017-07339-w

Šmejkal, M., Bartoň, D., Blabolil, P., Kolařík, T., Kubečka, J., Sajdlová, Z., Souza, A.T., Brabec, M., 2023a. Diverse environmental cues drive the size of reproductive aggregation in a rheophilic fish. Movement Ecology 11. https://doi.org/10.1186/s40462-023-00379-0

Šmejkal, M., Bartoň, D., Brabec, M., Sajdlová, Z., Souza, A.T., Moraes, K.R., Soukalová, K., Blabolil, P., Vejřík, L., Kubečka, J., 2021. Climbing up the ladder: male reproductive behaviour changes with age in a long-lived fish. Behavioral Ecology and Sociobiology 75, 1–13. https://doi.org/10.1007/s00265-020-02961-7

Šmejkal, M., Bartoň, D., Duras, J., Horký, P., Muška, M., Kubečka, J., Pfauserová, N., Tesfaye, M., Slavík, O., 2023b. Living on the edge: Reservoirs facilitate enhanced interactions among generalist and rheophilic fish species in tributaries. Frontiers of Environmental Science 11, 1099030. https://doi.org/10.3389/FENVS.2023.1099030

Šmejkal, M., Blabolil, P., Bartoň, D., Duras, J., Vejřík, L., Sajdlová, Z., Kočvara, L., Kubečka, J., 2019. Sex-specific probability of PIT-tag retention in a cyprinid fish. Fisheries Research 219, 105325.

Šmejkal, M., Ricard, D., Prchalová, M., Říha, M., Muška, M., Blabolil, P., Čech, M., Vašek, M., Jůza, T., Herreras, A.M., Encina, L., Peterka, J., Kubečka, J., 2015. Biomass and abundance biases in European standard gillnet sampling. PLoS One. https://doi.org/10.1371/journal.pone.0122437

Šmejkal, M., Ricard, D., Vejřík, L., Mrkvička, T., Vebrová, L., Baran, R., Blabolil, P., Sajdlová, Z., Vejříková, I., Prchalová, M., Kubečka, J., 2017b. Seasonal and daily protandry in a cyprinid fish. Scientific Reports 7, 4737. https://doi.org/10.1038/s41598-017-04827-x

Šmejkal, M., Souza, A.T., Blabolil, P., Bartoň, D., Sajdlová, Z., Vejřík, L., Kubečka, J., 2018. Nocturnal spawning as a way to avoid egg exposure to diurnal predators. Scientific Reports 8, 15377. https://doi.org/10.1038/s41598-018-33615-4

Tamario, C., Sunde, J., Petersson, E., Tibblin, P., Forsman, A., 2019. Ecological and Evolutionary Consequences of Environmental Change and Management Actions for Migrating Fish. Frontiers in Ecology and Evolution. https://doi.org/10.3389/fevo.2019.00271

Targoñska, K., Zarski, D., Kucharczyk, D., 2008. A review of the artificial reproduction of asp, *Aspius aspius* (L.), and nase, *Chondrostoma nasus* (L.). Archives of Polish Fisheries 16, 341–354. https://doi.org/10.2478/s10086-008-0022-4

Van Den Berg, C., Van Snik, G.J.M., Van Den Boogaart, J.G.M., Sibbing, F.A., Osse, J.W.M., 1994. Comparative microanatomy of the branchial sieve in three sympatric cyprinid species, related to filter-feeding mechanisms. Journal of Morphology. https://doi.org/10.1002/jmor.1052190109

Vašek, M., Eloranta, A.P., Vejříková, I., Blabolil, P., Říha, M., Jůza, T., Šmejkal, M., Matěna, J., Kubečka, J., Peterka, J., 2018. Stable isotopes and gut contents indicate differential resource use by coexisting asp (*Leuciscus aspius*) and pikeperch (*Sander lucioperca*). Ecology of Freshwater Fish 27, 1054–1065. https://doi.org/10.1111/eff.12414

Vašek, M., Prchalová, M., Peterka, J., Ketelaars, H.A.M., Wagenvoort, A.J., Čech, M., Draštík, V., Říha, M., Jůza, T., Kratochvíl, M., Mrkvička, T., Blabolil, P., Boukal, D.S., Duras, J., Kubečka, J., 2013. The utility of predatory fish in biomanipulation of deep reservoirs. Ecological Engineering 52, 104–111. https://doi.org/10.1016/j.ecoleng.2012.12.100

Vejřík, L., Matějíčková, I., Sed'a, J., Blabolil, P., Jůza, T., Vašek, M., Ricard, D., Matěna, J., Frouzová, J., Kubečka, J., Říha, M., Čech, M., 2016. Who is who: An anomalous predator-prey role exchange between cyprinids and perch. PLoS One. https://doi.org/10.1371/journal.pone.0156430

Volpato, G.L., Barreto, R.E., Marcondes, A.L., Andrade Moreira, P.S., de Barros Ferreira, M.F., 2009. Fish ladders select fish traits on migration–still a growing problem for natural fish populations. Marine and Freshwater Behaviour and Physiology. https://doi.org/10.1080/10236240903299177

Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D., 2023. dplyr: A Grammar of Data Manipulation. R package version 1.1.4.

Wood, S.N., 2017. Generalized additive models: An introduction with R, second edition, Generalized Additive Models: An Introduction with R, Second Edition. Chapman & Hall. https://doi.org/10.1201/9781315370279

Wood, S.N., Pya, N., Säfken, B., 2016. Smoothing Parameter and Model Selection for General Smooth Models. Journal of the American Statistical Association 111, 1548–1563. https://doi.org/10.1080/01621459.2016.1180986

Tables

Table 1: Approximate significance of smooth terms for the GAM model of common bream presence probability. The model explained 17.3 % of deviance with $R^2 = 1.03$ %.

Smooth effect	edf	p-value
random fish effect	299.084	<0.0001
diurnal effect, $s_{diurnal}$	7.867	<0.0001
temperature effect, $s_{temperature}$	7.368	<0.0001
flow effect, s_{flow}	5.634	<0.0001
$s_{seasonal,2018}$	6.805	<0.0001
$s_{seasonal,2019}$	3.778	<0.0001
$s_{seasonal,2020}$	8.495	<0.0001

Figures

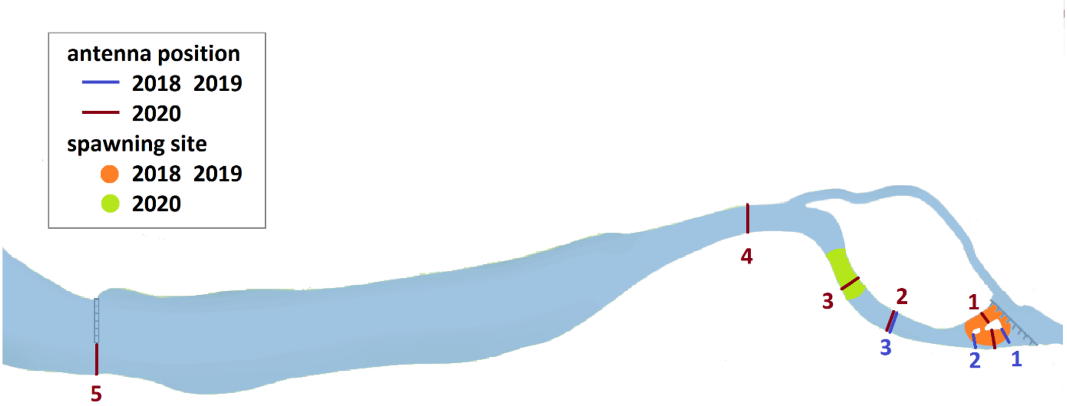


Figure 1: The study site at Želivka Reservoir main tributary – Želivka River - with marked antenna array positions. Spawning area of asp is indicated by highlighted areas with highest egg densities.

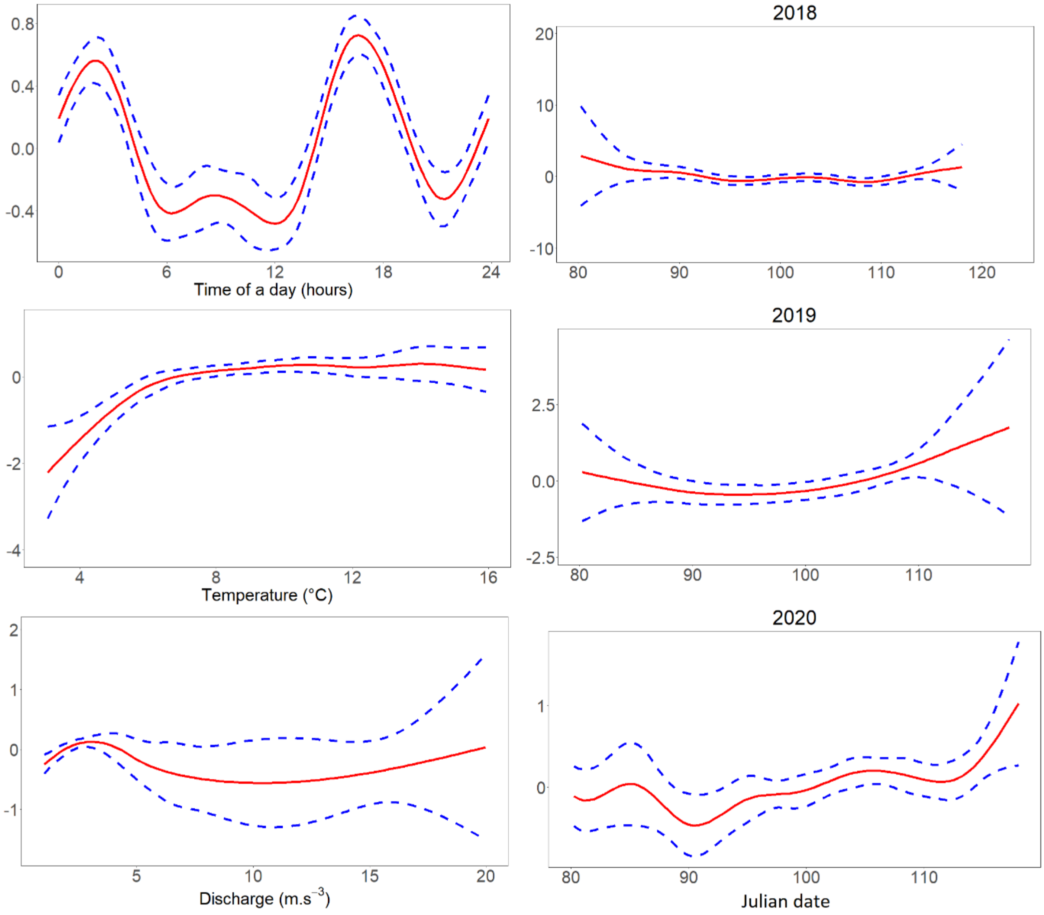


Figure 2: Smooth effects of various covariates on logit-transformed probability of common bream detection on antennas estimated by GAM model. Red lines represent GAM estimates and dashed lines asymptotic (pointwise constructed) confidence intervals.

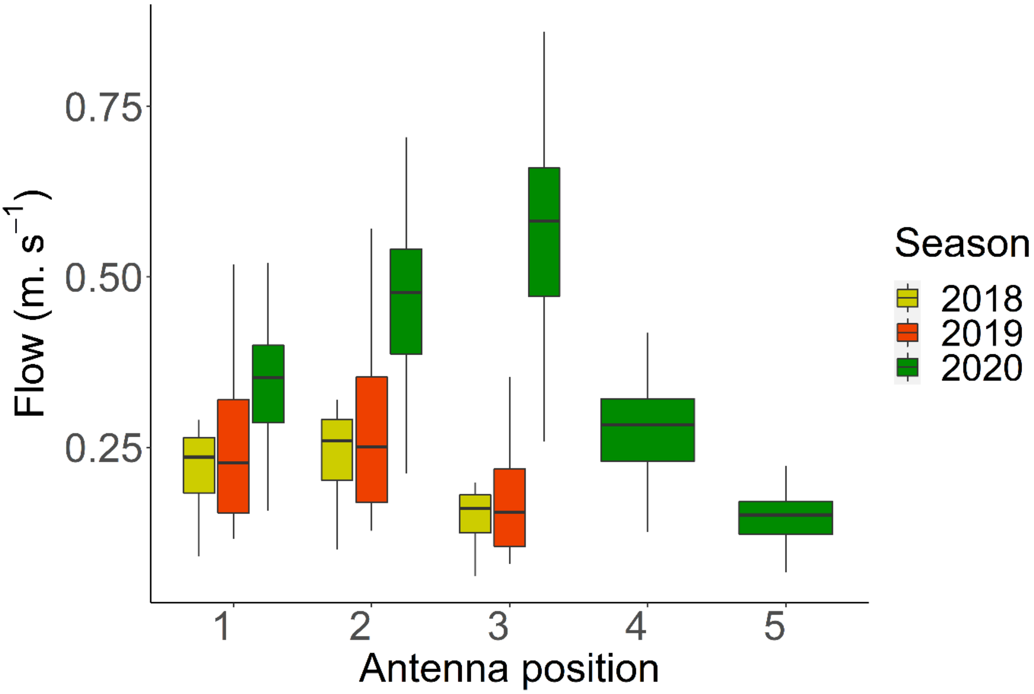


Figure 3: Water flow on antennas located in the Želivka Reservoir tributary in 2018 to 2020. Positions of antenna is marked in Figure 1. The boxes represent the boundaries of the upper and lower quartiles; the thick lines represent medians, the whiskers upper and lower adjacent value.

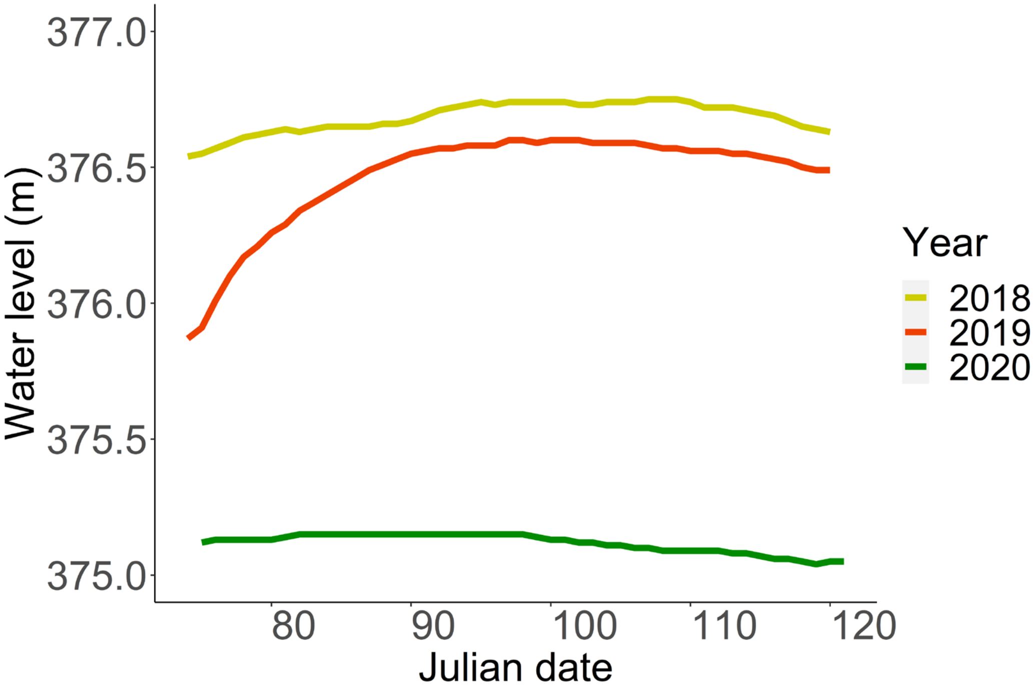


Figure 4: Water level (m a.s.l.) in the Želivka reservoir during early spring season in years from 2018 to 2020.

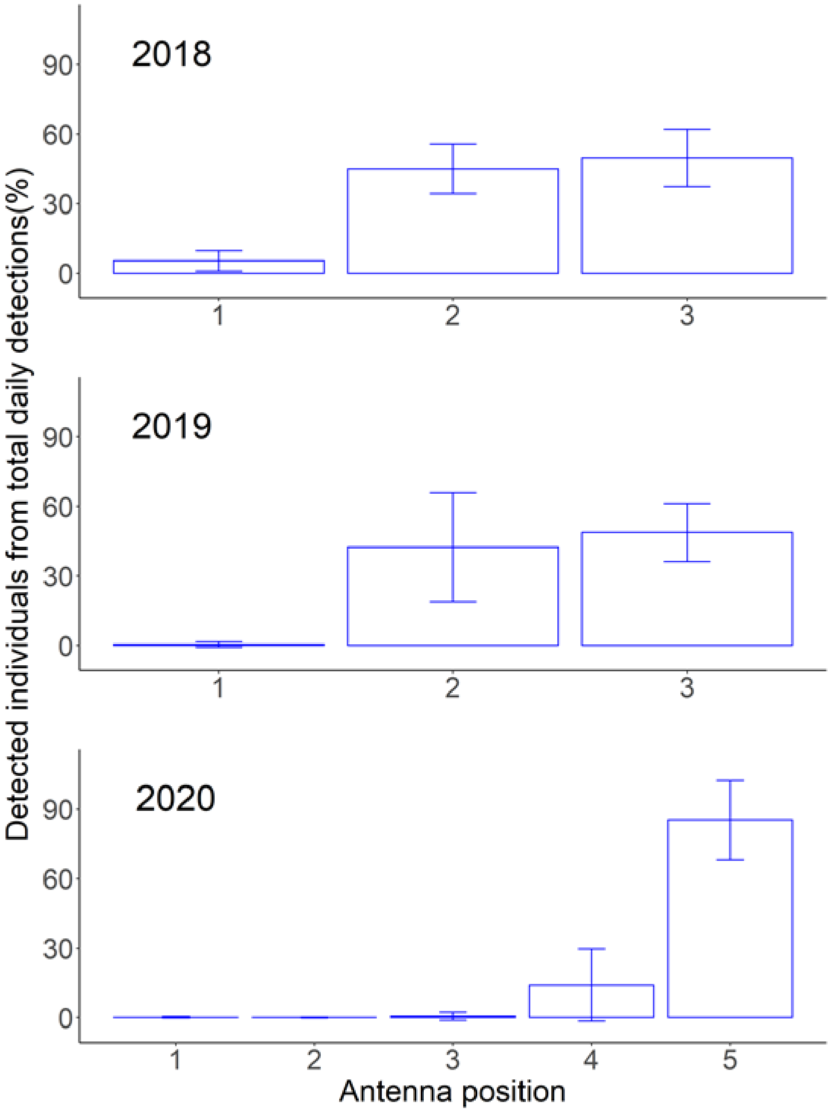


Figure 5: Daily detected individuals of common bream on antenna loops located in the tributary where asp spawning takes place. Higher number of antennas is located further downstream. The whiskers represent upper and lower quartile. A subset of days where at least five common bream individuals was chosen for the plotting.

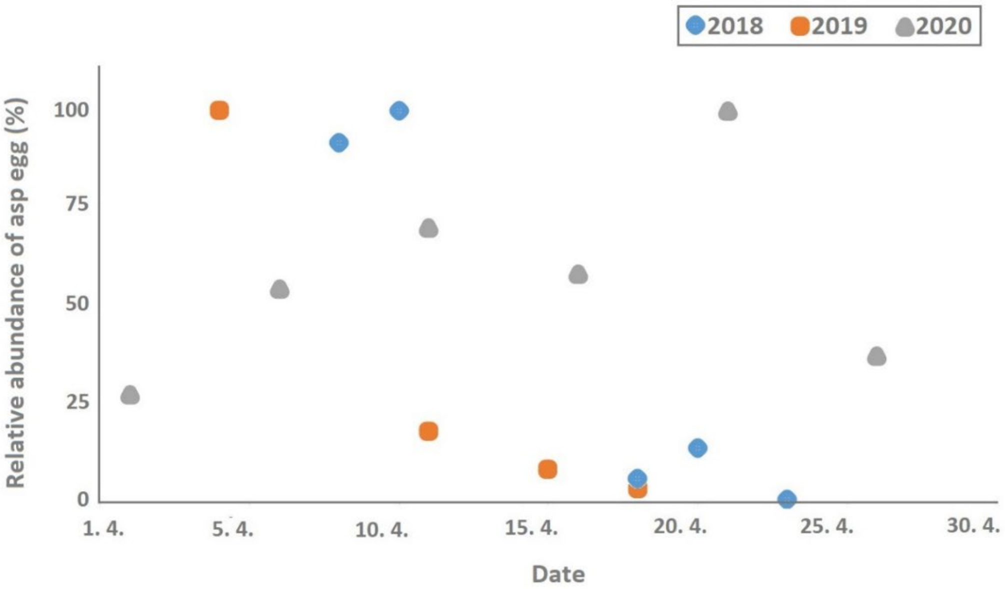


Figure 6: Relative abundance of asp eggs on the study site during four seasons from 2018 to 2020. The drop of egg abundance in 2018 was mainly caused by hydropeaking (Bartoň et al., 2021), while seasons 2019 and 2020 were both characterized by no major hydropeaking effects with the major difference in the flow conditions and accessibility of the spawning ground by common bream.

Paper V

Living on the edge: Reservoirs facilitate enhanced interactions among generalist and rheophilic fish species in tributaries

frontiers | Frontiers in Environmental Science

TYPE Review
PUBLISHED 19 January 2023
DOI 10.3389/fenvs.2023.1099030

OPEN ACCESS

EDITED BY
Stefano Basso,
Norwegian Institute for Water Research (NIVA), Norway

REVIEWED BY
Jason Deboer,
Illinois Natural History Survey, United States
Luca Carraro,
Swiss Federal Institute of Aquatic Science and Technology, Switzerland

*CORRESPONDENCE
Marek Šmejkal,
✉ marek.smejkal@hbu.cas.cz

SPECIALTY SECTION
This article was submitted to Freshwater Science, a section of the journal Frontiers in Environmental Science

RECEIVED 15 November 2022
ACCEPTED 09 January 2023
PUBLISHED 19 January 2023

CITATION
Šmejkal M, Bartoň D, Duras J, Horký P, Muška M, Kubečka J, Pfauserová N, Tesfaye M and Slavík O (2023), Living on the edge: Reservoirs facilitate enhanced interactions among generalist and rheophilic fish species in tributaries. *Front. Environ. Sci.* 11:1099030. doi: 10.3389/fenvs.2023.1099030

Living on the edge: Reservoirs facilitate enhanced interactions among generalist and rheophilic fish species in tributaries

Marek Šmejkal[1]*, Daniel Bartoň[1,2], Jindřich Duras[3,4], Pavel Horký[5], Milan Muška[1,6], Jan Kubečka[1], Nikola Pfauserová[5], Million Tesfaye[1,4] and Ondřej Slavík[5]

[1]Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czechia, [2]Faculty of Science, University of South Bohemia, České Budějovice, Czechia, [3]Department of Water Management Planning, Vltava River Authority, State Enterprise, Plzeň, Czechia, [4]Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Vodňany, Czechia, [5]Department of Zoology and Fisheries, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences, Prague, Czech Republic, [6]Nature Conservation Agency of the Czech Republic, Prague, Czech Republic

Most lotic ecosystems have been heavily modified in recent centuries to serve human needs, for example, by building dams to form reservoirs. However, reservoirs have major impacts on freshwater ecosystem functions and severely affect rheophilic fishes. The aim of this review is to gather evidence that aside from direct habitat size reductions due to reservoir construction, competition for food and space and predation from generalist fishes affect rheophilic community compositions in tributaries (river/stream not directly affected by water retention). River fragmentation by reservoirs enables the establishment of generalist species in altered river sections. The settlement of generalist species, which proliferate in reservoirs and replace most of the native fish species formerly present in pristine river, may cause further diversity loss in tributaries. Generalist migrations in tributaries, spanning from tens of metres to kilometres, affect fish communities that have not been directly impacted by reservoir construction. This causes "edge effects" where two distinct fish communities meet. Such interactions temporarily or permanently reduce the effective sizes of available habitats for many native specialized rheophilic fish species. We identified gaps that need to be considered to understand the mechanistic functioning of distinct fauna at habitat edges. We call for detailed temporal telemetry and trophic interaction studies to clarify the mechanisms that drive community changes upstream of reservoirs. Finally, we demonstrate how such knowledge may be used in conservation to protect the remnants of rheophilic fish populations.

KEYWORDS

edge effects, habitat fragmentation, non-native species, biodiversity loss, biotic homogenization, freshwater fauna, potamodromous fish, fish migration

1 Introduction

Riverine ecosystems host much of the world's biodiversity (Dudgeon et al., 2006; Reid et al., 2019), yet they have been so significantly modified to meet human needs that few free-flowing rivers remain (Grill et al., 2019; Belletti et al., 2020). Rivers have always been considered as essential sources of human wellbeing, which provide food and water for domestic and agricultural use, colonization pathways and transportation corridors, as well as being recognized as sources of energy generation, which range from simple water wheels to sophisticated hydropower plants

(Grill et al., 2019). With the increasing demands of growing human populations, rivers are being regulated, impounded, and harnessed to meet electricity, irrigation, water supply, and flood management needs (Nilsson et al., 2005; Lehner et al., 2011; Reid et al., 2019). In addition to their primary purposes, artificial structures such as flumes, sluices, weirs and dams interfere with the natural processes of entire ecosystems. Such impoundments cause river fragmentation, flow regime modifications, sediment deposition, nutrient cycle alterations, and temperature changes, which lead to rapid declines in biodiversity (Belmar et al., 2010; Lehner et al., 2011; Feng et al., 2018; Grill et al., 2019; Jumani et al., 2019). Due to the overall complexity of the impacts of fragmentation on aquatic biodiversity that are caused by damming, the long-term scale of these impacts, and the time lags between causes and consequences, the changes in river functioning are likely underestimated (Fuller et al., 2015; Belletti et al., 2020; Arboleya et al., 2021).

Habitat fragmentation is a paramount topic in biodiversity conservation. One of the most important concepts is called “edge effects”, which in a broad context can be described as the changes in resource availability, physical and biological conditions at ecosystem boundaries or within adjacent ecosystems (Fischer and Lindenmayer, 2007). Its biotic component, on which we focus in this review, includes interactions among generalists occupying human-altered environments and specialized species present in the remaining pristine fragments (Andren and Angelstam, 1988). This primarily terrestrial concept has the potential to be more widely used in fish conservation due to similarities in the interactions among generalist and rheophilic fish fauna living side by side (Tamario et al., 2021). In particular, we review here evidence that reservoir construction may induce similar biotic edge effects between generalists and rheophilic fishes in interconnected rivers and streams (Figure 1), ranging from tens of meters to kilometers depending on the particular system and species.

Fish communities along river continua have evolved and are maintained by a series of biotic and continuous longitudinal gradients of abiotic variables through processes known as environmental filtering (Jackson et al., 2001; Kraft et al., 2015), which are reflected by the zonation patterns of fish communities (Aarts and Nienhuis, 2003; Buisson et al., 2008; Troia and Gido, 2014). Increasing riverbed steepness and water discharges and decreasing trophic status, conductivity, and temperature constitute natural barriers to dispersal for generalists and their proliferation in upstream lotic environments inhabited by potamodromous rheophilic species (Vannote et al., 1980; Johnson et al., 1995; Troia and Gido, 2014). These natural processes are seriously damaged by reservoir construction, and the impacts of reservoirs have been monitored with special attention paid to altered habitats below reservoir and newly established fish communities within reservoirs (Bain et al., 1988; Kubečka, 1993; Říha et al., 2009; Ganassin et al., 2021) and to river function alterations downstream and between reservoirs (Preece and Jones, 2002; Perkin et al., 2015; Bartoň et al., 2022). A significant scientific effort has been aimed to discover the effects of limited gene flow due to migration constraints between isolated sites and the way how construction of fish ladders could avert these effects (Roscoe and Hinch, 2010; Kemp, 2016; Tamario et al., 2019; Sun et al., 2022). However, the contact of two distinct fauna that occupy lentic reservoirs and their fluvial tributaries is to the authors' best knowledge not well covered.

Although edge effects are a critical issue in the global declines of native rheophilic fish species populations in fragmented rivers (Limburg and Waldman, 2009; Deinet et al., 2020), the effect of

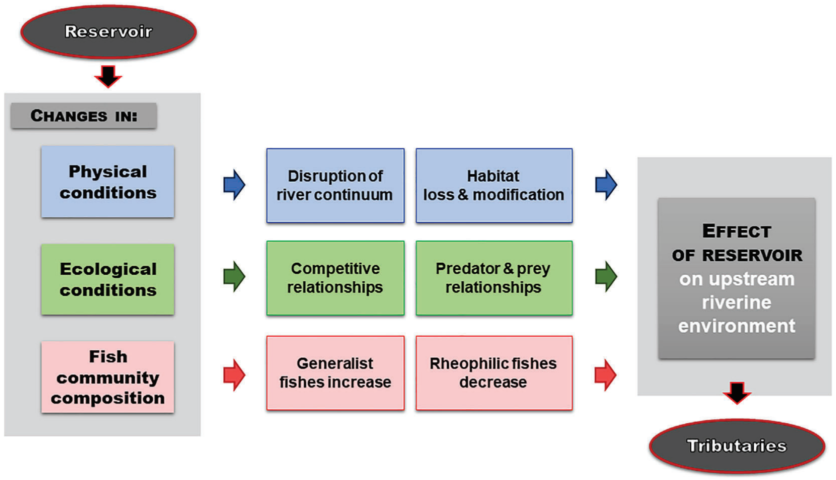


FIGURE 1
Conceptual scheme of synergistic negative effects of reservoir construction on rheophilic fishes in tributaries (river/stream not directly affected by the water retention function of a reservoir). While rheophilic fishes face a range of stressors varying from change in physical conditions to community change, this review focuses on biotic interactions that are modified by reservoir construction (green and pink color). Due to the proliferation of generalists in impounded sections of reservoirs, competitive interactions (e.g., food availability, spawning habitat, spatial niche) and predator-prey relationships (increased mortality of rheophilic fish in various life stages) are compromised, leading to community change in tributaries and negatively impacting rheophilic fishes. Please see main text for details and examples of interactions.

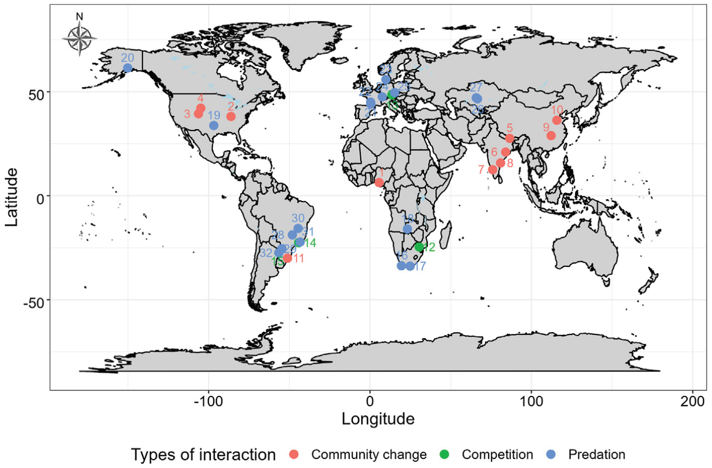


FIGURE 2
Map of evidence for interactions between rheophilic fishes and generalist fishes compiled by the study. The numbers in the map correspond to numerical order of case studies and their supporting references in Table 1.

reservoir fish fauna (which often predominantly consist of locally non-native species) on rheophilic fish has received relatively little attention. To date, most studies have evaluated biodiversity and trait-based metrics in relation to reservoir occurrences and overall river fragmentation and have provided useful insights into the biodiversity declines and functional changes in impounded rivers (Degerman et al., 2007; Wang et al., 2011; Esselman et al., 2013; Van Looy et al., 2014; Cooper et al., 2017; Turgeon et al., 2019). To much less extent were studied generalist fish migrations from reservoirs to riverine sections on habitat edges, which can further degrade river status (Andren and Angelstam, 1988; Tamario et al., 2021). While some fish community changes in rivers can be attributed to abiotic changes in ecosystems, others are likely related to biotic interactions among unnaturally close lentic and lotic fish fauna (Pringle et al., 2000; Jackson et al., 2001).

The aim of this review is to address the topic of edge effects of lentic fish fauna that are composed of generalists in reservoirs and their competitive and predation effects on rheophilic fish communities. We summarize the current state of knowledge, from reservoir settlement of generalist fish species, which is often driven by intentional or unintentional fish transport, to dynamic migrations of generalists into reservoir tributaries. Most importantly, we suggest that predation and the competitive interactions among lotic and lentic fauna are among the causes of the declining biotic integrity of reservoir tributaries. Finally, we show that it is possible to protect riverine communities by intentional fragmentation, where the conservation benefits of such measures exceed their negative impacts. We focus our attention on the impacts of generalist fishes that may come from three sources: 1) local fish species that proliferate after reservoir construction in impounded sections, 2) locally non-native species (species native in the region that were not formerly present in local communities) and 3) regionally non-native species (species not native to the focal region). We mainly focused our attention on the impacts on potamodromous rheophilic fish species, but when we did not find a good example of biotic interactions due to edge effects, we used examples of anadromous rheophilic fish species, which are better studied due to their commercial importance. We have reviewed literature and identified examples of such interactions ranging from temperate to tropical climates (Figure 2). We aim to draw attention to this topic, which is not yet explored in full, since it may help in conservation efforts aimed to preserve declining rheophilic fish species located upstream of reservoirs.

2 Proliferation of generalists in reservoirs

Dams create lentic or slow-flowing environments that are generally much deeper than the original river channels (Figure 3). Rheophilic fish are able to survive in such environments until they are occupied by other species (Irz et al., 2002; Lenhardt et al., 2009; Knott et al., 2021). However, on a longer time scale, the proportions of rheophilic fish in impounded environments generally become low, and they are replaced by quickly proliferating generalists (Figures 3, 4; Gido et al., 2009; Clavero and Hermoso 2010).

The community change has been described e.g. in mainland Europe: a typical reservoir fish community is dominated by bream (*Abramis brama*), roach (*Rutilus rutilus*), and bleak (*Alburnus alburnus*) in the final stage of community succession, although many reservoirs were constructed in rheophile-dominated community zones (Kubečka, 1993; Říha et al., 2009). Two rheophilic fish groups have been classified in Europe: More specialized rheophiles A (e.g., *Barbus barbus, Chondrostoma nasus, Leuciscus leuciscus, Squalius cephalus, Alburnoides bipunctaus, and Vimba vimba*), which require river conditions at all stages of their life histories, and less specialized rheophiles

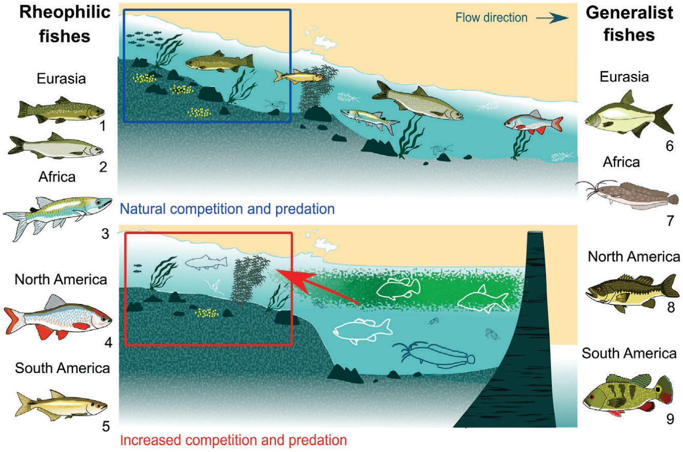


FIGURE 3
Schematic representation of the community changes before (blue rectangle) and after reservoir construction (red rectangle) and the biotic interactions among two distinct faunas of generalist fishes and rheophilic fishes in the tributary at the habitat edge. Rectangle indicates river section that is not directly influenced by increase of water level, yet the community changes due to reservoir construction. The green dots in lower panel indicate shift from littoral primary production to pelagic production and examples of invertebrates indicate the change in the major prey items for omnivorous fish within reservoir driving settlement of generalist fishes. Red arrow indicates enhanced interaction between generalist fishes in reservoir and rheophilic fishes in the tributary. Only subset of fish species reviewed is depicted to maintain clarity—rheophilic fish examples: 1—*Salmo trutta*, Salmonidae; 2—*Leuciscus aspius*, Leuciscidae; 3—*Hepsetus odoe*, Characidae; 4—*Cyprinella lutrensis*, Leuciscidae; 5—*Oligosarcus hepsetus*, Characidae; typical generalists: 6—*Abramis brama*, Cyprinidae; 7—*Clarias* sp. Clariidae; 8—*Micropterus salmoides*, Centrarchidae; 9—*Cichla ocellaris*, Cichlidae. Drawn by Zuzana Sajdlová.

B (e.g., *L. aspius, L. idus, Pelecus cultratus, Gobio gobio, Lota lota, and Cobitis taenia*), which are well adapted to lentic conditions during part of the ontogeny (Schiemer and Waidbacher, 1992). This classification appears to be valid in most systems outside Europe, and the rheophiles A formerly abundant before dam construction move upstream from lentic parts of reservoir (Agostinho et al., 1999). Adult rheophiles B can inhabit suitable reservoir habitats but usually become less abundant when reservoirs are occupied by other species. All rheophilic species require flowing water for reproduction, and their early stages have higher dissolved oxygen requirements than generalist and limnophilic species (Balon, 1975). The need for specific water flows and the risk of being displaced from suitable habitats by flow fluctuations (Bartoň et al., 2021; Bartoň et al., 2022) represent a clear disadvantage of rheophilic fishes compared to generalists, which are extremely flexible in their spawning substrate choices and do not rely on narrow ranges of optimal conditions to provide spawning sites (Hladík and Kubečka, 2004).

One of the main factors favoring the replacement of rheophilic fish by generalists in reservoirs is changes in food resources. While the main autochthonous primary production in rivers comes from benthic systems, primary production in reservoirs is mostly pelagic (Ward and Stanford, 1995). Littoral habitats with benthic food chains may be the most productive per unit area, but due to large pelagic spatial proportions of reservoirs, most production occurs in pelagic areas (Fernando, 1994; Moraes et al., 2021). The bulk of production in reservoirs goes from phytoplankton to zooplankton. For rheophilic species, benthic macroinvertebrates and algae are the main autochthonous food sources (Vannote et al., 1980; Aarts and Nienhuis, 2003; Bešta et al., 2015). These resources are generally limited in reservoirs (Agostinho et al., 1999; Moraes et al., 2021) because productive benthic habitats are limited and the benthos are also heavily used by omnivores (Agostinho et al., 1999; Schleuter and Eckmann, 2008). Another important food source for rheophilic fishes is terrestrial insects, which are generally rarely available in reservoirs and are also preyed upon by generalists (Mehner et al., 2005; Vašek et al., 2008). Although specialized, truly planktivorous fishes are often found in small numbers in reservoirs (Fernando and Holčík, 1991), while omnivorous generalists such as cyprinids, characids, percids, and centrarchids are well equipped to prey on zooplankton, which leads to zooplankton size reduction (Seďa and Kubečka, 1997; Hülsmann et al., 1999; Quintana et al., 2015). The main adaptations of omnivorous generalists for zooplankton feeding are dense branchial sieves (Van Den Berg et al., 1994) and sinusoidal swimming to detect dense aggregations of zooplankton (Jarolím et al., 2010). Rheophilic species have no such adaptations and thus cannot compete efficiently for the main food sources in reservoirs. Although rheophiles B may survive as predators or specialized benthivores, rheophiles A slowly disappear from these sites: when the barbel (*B. barbus*) was locked in the large newly filled Orava Reservoir (Slovakia), its growth rate decreased significantly despite a trophic upsurge in the newly flooded reservoir (Havlena, 1964). Additionally, study conducted in the Medjuvrsje Reservoir (Serbia) shows that the decline of rheophilic fishes gradually increases with reservoir aging (Lenhardt et al., 2009), and the increasing domination of generalists may have further negative impact on the tributaries.

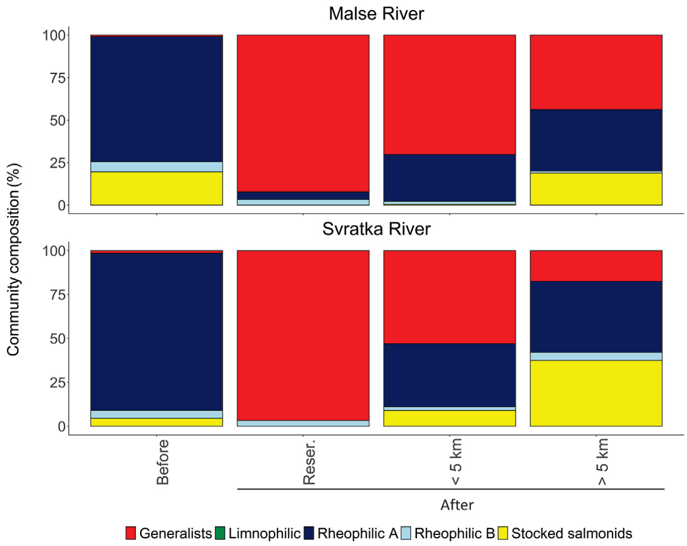


FIGURE 4
Changes in fish guild compositions after the construction of reservoirs in two rivers in the Czech Republic. Four fish faunas are considered: Former river community (Before), reservoir (Reser.), river locations less than 5 km upstream of the reservoirs (<5 km) and more than 5 km upstream of the reservoirs (>5 km). Stocked salmonids refer to brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) that are artificially supported by fisheries (according to (Peňáz et al., 1968; Hladík et al., 2008)).

3 Human-driven translocation of lowland species to upstream man-made habitats

Reservoirs often serve as stepping stones for non-native generalists, which facilitates generalists dispersal across the landscape (Havel et al., 2005; Johnson et al., 2008; Liew et al., 2016; Silva-Sene et al., 2022) and thus reservoir communities have usually high similarity with each other, despite their presence in relatively distant watersheds with distinct riverine fish communities. Therefore, reservoirs are one of the sources of biotic homogenization in river ecosystems, which is characterized by a loss of biological uniqueness (Olden and Rooney, 2006; Poff et al., 2007; Clavero and Hermoso, 2010). An example of such homogenization is introduction of *Cichla spp.* Into reservoirs of Upper Paraná river basin and other Brazilian regions resulting in the biotic homogenizations of native fish assemblages (Franco et al., 2021). This genus has been widely introduced within and outside the Neotropical region and its introduction are mostly occurring in presence of reservoirs (Franco et al., 2022a; Franco et al., 2022b).

In upper-river drainage areas, the colonization mechanisms of newly established reservoirs by non-native generalists act more slowly in the absence of fish transport (Olden et al., 2004). Considering non-human driven reservoir colonization, opportunities would often be limited to external or internal transport of fish eggs by birds, which is a process whose frequency is still unknown in the context of fish dispersal mechanisms (Hirsch et al., 2018; Silva et al., 2019; Lovas-Kiss et al., 2020) and extreme flood events (Taylor and Cooke, 2012). Therefore, the organized breeding and translocation of angler-preferred generalists into novel environments poses a serious threat to native fish communities (Copp et al., 2009; Volta et al., 2013; Early et al., 2016). In addition, many small-sized generalists are introduced accidentally with economically important stocking materials (Lusk et al., 2010) and through the release of ornamental organisms (Patoka et al., 2017) or live baitfish (Drake and Mandrak, 2014). Since these impacts are directly driven by human activities, areas with higher human population densities are more vulnerable to introductions of non-native species (Dawson et al., 2017).

4 Timing of fish migrations from reservoirs to tributaries

Animal migrations, including those of fish, are characterized as regular movements between environments (Northcote, 1984), which are influenced by individual characteristics (Chapman et al., 2011; Skov et al., 2011; Harrison et al., 2015) and can be decomposed into one-way migration events (Lucas and Baras, 2001). In general, fish migrations between lentic and lotic habitats, e.g., between lakes and their tributaries, are species-specific and depend on the food availability in lakes and their tributaries, as well as trade-offs such as predation risk or reproduction (Brönmark et al., 2008; Brodersen et al., 2014; Šmejkal et al., 2018). Some of the generalists that thrive in impounded habitats actively migrate over long distances into tributaries, such as European bream (Hladík and Kubečka, 2003; Pfauserová et al., 2021) or bleak (Šmejkal et al., 2017; Šmejkal et al., 2018) and interacting strongly with rheophilic brown trout

(*Salmo trutta*) and asp (*Leuciscus aspius*), respectively. Thus, fauna that interact at the edges of habitats can affect fish communities located hundreds of meters to more than one hundred kilometers upstream of impounded reaches (Perkin and Gido, 2011; Pfauserová et al., 2021; Tamario et al., 2021).

Reproductive migrations appear to be the main reason that cause fish to temporarily return from reservoirs to tributaries. In many species, spawning areas and spawning grounds are well defined and persist for many decades (Arnold et al., 2019), For example, lithophils that spawn on gravel and phytophils that spawn on macrophytes or flooded vegetation (Balon, 1975) migrate to tributaries when these substrates are limited in reservoirs (Hladík and Kubečka, 2003). In the case of European fish, spring migrations of rheophilic fish from reservoirs into tributaries are regularly recorded, with lithophilous asp and chub (*Squalius cephalus*) searching for gravel substrata (Benitez, et al., 2015; Pfauserová et al., 2019; Pfauserová et al., 2021; Šmejkal et al., 2021). Tributaries may also be used by reproducing generalists such as bream that are not strictly dependent on a single spawning substrate and use a wide range of available substrates (Hladík and Kubečka, 2004; Říha et al., 2013) and by phytophilous pike (*Esox lucius*) searching for submerged vegetation (Sandlund et al., 2016).

Reservoirs contain relatively high abundances of fish, with many generalist species, such as bream and roach, which are food-limited and fail to reach their maximum size due to intra- and interspecific competition and a lack of optimal food sources (benthos) (Šmejkal et al., 2015; Žák et al., 2020). As tributary temperatures drop, food resources become scarcer in the tributary, while predation risks increase (Harvey and Nakamoto, 2013). For this reason, most generalist species occupy tributaries in productive period of the year and return to reservoirs for overwintering (Pfauserová et al., 2021; Pfauserová et al., 2022). Although the mechanisms driving fish migrations from reservoirs to tributaries are not completely understood, it appears that the motivations may be similar to fish migrations from lakes to tributaries, where reproduction plays an important role (Kristiansen and Dølving, 1996; Baril and Magnan, 2002), as well as the predator-prey relationships (Skov et al., 2011).

The migratory activities between shallow lakes and their tributaries and the high species abundances in shallow lake tributaries in winter differ significantly from the dynamics of cyprinid migration between deeper canyon-shaped reservoirs and tributaries, where generalist fishes in tributaries peak in spring and summer and return to reservoirs in winter (Hladík et al., 2008; Pfauserová et al., 2021). For example, common bream, silver bream (*Blicca bjoerkna*) and roach migrate to small tributaries for overwintering to evade predation when the food availability in lakes is low and predation risks in lakes are relatively higher compared to tributaries (Skov et al., 2008; Skov et al., 2011). Whether the available depths in reservoirs are essential for fish decisions regarding where to overwinter (and thus affecting interactions with rheophilic fish) remains to be investigated.

5 Predation of rheophilic species by generalists in tributaries

One of the key factors that affects fish community structures in freshwater ecosystems is predation (Persson, 1997; Jackson et al., 2001; Temming et al., 2007). Generalist predators that thrive in the human-made lentic parts of river systems interfere with lotic waters, although the magnitude of the edge effects is unknown. In altered ecosystems, adjacent lotic river fauna may be heavily preyed upon (Table 1; Jepsen et al., 2000; Tamario et al., 2021). Introduction of predatory fish can lead to extinction of local species, destruction of unique communities, and severe loss of diversity (Chapleau et al., 1997; Hermoso et al., 2011; Pelicice et al., 2015). For example, the preys for introduced pike consist of native juvenile salmonids or other native rheophilic species where salmonids are less abundant (Sepulveda et al., 2013). Another effect observed in North America is the difference between unfragmented and fragmented streams, where in unfragmented streams more rheophilic specialists persist, and fragmented streams are significantly more dominated by generalist predatory species (Guenther and Spacie, 2006). Reservoir construction on the Laramie River, Wyoming, also caused higher abundances of non-native generalist predatory fish and led to extirpation and population reductions of selected rheophilic fishes (Quist et al., 2005). The authors of this study did not determine the specific mechanisms for the changes in the fish communities upstream of the reservoir, but they expected that non-native predators were the principal cause of community change (Quist et al., 2005). The introduction of peacock bass (*Cichla ocellaris*) in South America caused considerable negative impacts on fish assemblage composition of upper stream riverine native small-sized fish through predation (Franco et al., 2021). Another example of the influence of generalists on fish species occupying reservoir tributaries is the disappearance of red shiner (*Cyprinella lutrensis*) from streams directly connected to Lake Texoma, United States, with predation by centrarchids as a likely contributing mechanism (Matthews and Marsh-Matthews, 2011). Similarly, generalist predators threatened native rheophilic fish fauna after the construction of the Kenney Reservoir, USA (Martinez et al., 1994), although a detailed investigation of the modified interactions between species is missing in this study.

A notable example in this regard is the largest European freshwater fish, the European catfish (*Silurus glanis*), which is now regionally non-native in portions of European freshwaters (Copp et al., 2009). Catfish are typically introduced to reservoirs and spread into higher-order rivers (Gago et al., 2016); in some instances, they change fish communities during invasion (Guillerault et al., 2015). Catfish cause high mortality in the critically endangered allis shad (*Alosa alosa*) during spawning in one of Europe's most important spawning areas (e.g., Garonne River, Southwest France) (Boulêtreau et al., 2021) but also in the endangered sea lamprey (*Petromyzon marinus*) (Boulêtreau et al., 2020), Atlantic salmon (*Salmo salar*) (Boulêtreau et al., 2018) or vimba bream (*Vimba vimba*), European nase (*Chondrostoma nasus*) and barbel (*Barbus barbus*) (Lyach, 2021). Predation on native fishes by African catfish (*Clarias gariepinus*) caused a drastic reduction in the abundance of endemic and endangered *Pseudobarbus asper* and *Sandelia bainsii in* South Africa impoundments (Weyl et al., 2016).

Migratory success or mortality at early life stages can strongly influence population sizes (Larsson, 1985). Most rheophilic fish species must migrate downstream or upstream once or regularly during their lives (Lucas and Baras, 2001). As a result, they inevitably pass through altered sections of rivers with lentic waters where the risk of predation is high (Jepsen et al., 1998; Olsson et al., 2001). An example of how environmental alterations can increase mortality is the massive predation of Atlantic salmon smolts by striped bass (*Morone saxatilis*) as they pass through reservoirs (Table 1;

TABLE 1 Examples of field-based evidence of the biotic interactions among generalist fish fauna of reservoir species and rheophilic fish with negative impacts on the remaining rheophilic fish populations based in reservoir tributaries. Number (No) indicates the geographical position of the study in the map (Figure 2).

No	Continents	Country	Latitude	Longitude	Generalist species	Rheophilic/riverine species	Eco-region	Type of interaction	Season	References
1	Africa	Nigeria	6.350006	5.650000	*Unspecified*	*Unspecified*	Ikpoba River	Community change	Spring, Summer	Victor and Tetteh (1988)
2	North America	United States	38.099791	−86.158582	*M. salmoides, Morone chrysops*	*Micropterus dolomieu, Esox americanus*	Central Indiana and Central Till Plain.	Community change	Spring	Guenther and Spacie (2006)
3	North America	United States	39.424294	−106.30112	*Unspecified*	*Unspecified*	White River	Community change	Spring	Martinez et al. (1994)
4	North America	United States	42.104124	−104.877552	*Unspecified*	*Unspecified*	Great Plains river	Community change	Spring, Summer	Quist et al. (2005)
5	Asia	India	27.590000	86.560000	*Unspecified*	*Schizothorax richardsonii, Labeo dero, Labeo dyocheilus*	Himalayas	Community change	Spring	Sugunan, (1995)
6	Asia	India	21.012094	84.040789	*Unspecified*	*Puntius sarana, Tor mahanadtcus, Tor mosal*	Mahanadi	Community change	Spring, Summer	Sugunan (1995)
7	Asia	India	12.528591	75.993629	*Unspecified*	*P. dobsoni, P. dubius, P. carnaticus*	Cauvery	Community change	Spring, Summer	Sugunan (1995)
						C. drrhosa and Labeo kontius				
8	Asia	India	15.754239	80.89727	*Unspecified*	*P. kolus, P. dubius, P. sarana*	Krishna River	Community change	Spring	Sugunan (1995)
						P. porcellus, L.fimbrtatus, L. calbasu, L. pangusia and Tor kudree				
9	Asia	China	28.900000	112.228777	*Unspecified*	*Unspecified*	Southeast Asia	Community change	Spring, Summer, fall	Li et al. (2021)
10	Asia	China	36.308176	115.783497	*Unspecified*	*Unspecified*	Huang He Plain	Community change	NA	Zhang et al. (2018)
11	South America	Brazil	−30.005117	−51.123734	*Unspecified*	*Unspecified*	Paraná	Community change	NA	Li et al. (2013)
12	Africa	South Africa	−24.58456	30.44019	*Oncorhynchus mykiss*	*Enteromius treurensis*	Zambezi	Competition	NA	Maimela et al. (2022)
13	Europe	Czech Republic	48.51219	13.55126	*Abramis brama*	*Salmo trutta*	Central and Western Europe	Competition	NA	Pfauserová et al. (2021)
14	South America	Brazil	−22.51000	−44.21000	*Cichla ocellaris*	*Rhamdia quelen, Hoplias malabaricus*	Paraná	Competition	NA	Franco et al. (2022a)
15	South America	Brazil	−27.396172	−56.516809	*Pterygoplichthys ambrosettii*	*Unspecified*	Upper Paraná	Competition	NA	Nobile et al. (2018)
16	Africa	South Africa	−33.652437	19.453672	*Oncorhynchus mykiss*	*Pseudobarbus, Burchelli, Sandelia capensis, Galaxias zebratus*	Zambezi	Predation	NA	Shelton et al. (2015)
17	Africa	South Africa	−33.820655	24.845112	*Clarias gariepinus*	*Pseudobarbus asper, Sandelia bainsii*	Zambezi	Predation	NA	Weyl et al. (2016)

(Continued on following page)

TABLE 1 (*Continued*) Examples of field-based evidence of the biotic interactions among generalist fish fauna of reservoir species and rheophilic fish with negative impacts on the remaining rheophilic fish populations based in reservoir tributaries. Number (No) indicates the geographical position of the study in the map (Figure 2).

No	Continents	Country	Latitude	Longitude	Generalist species	Rheophilic/riverine species	Eco-region	Type of interaction	Season	References
18	Africa	Zambia	−15.961329	23.14447	*Hydrocynus forskahlii*	*Hepsetus odoe*, Cyprinodontidae,Characidae	Upper Zambezi	Predation	NA	Winemiller and Kelso-Winemiller (1994)
19	North America	United States	33.7705278	−96.8194926	*Micropterus* sp., *Lepomis* sp.	*Cyprinella lutrensis*	US Southern Plains	Predation	NA	Matthews and Marsh-Matthews (2011)
20	North America	United States	61.41340	−150.18230	*Esox lucius*	*Oncorhynchus tshawytscha, O. kisutch, Lethenteron camtschaticum, Cottus cognatus*	Alaska and Canada Pacific Coastal	Predation	NA	Sepulveda et al. (2013)
21	Europe	France	44.06376	0.55333	*Silurus glanis*	*Salmo salar*	Cantrabic Coast - Languedoc	Predation	NA	Boulêtreau et al. (2018)
22	Europe	France	45.02458	0.364156	*Silurus glanis*	*Petromyzon marinus*	Cantrabic Coast - Languedoc	Predation	NA	Boulêtreau et al. (2020)
23	Europe	Denmark	55.87037	9.813089	*Esox lucius, Stizostedion lucioperca*	*Salmo trutta*	Central and Western Europe	Predation	NA	Jepsen et al. (2000)
24	Europe	Switzerland	47.5595986	7.5885761	*Neogobius melanostomus*	*Chondrostoma nasus*	Central and Western Europe	Predation	NA	Lutz et al. (2020)
25	Europe	Czech Republic	49.578497	15.251671	*Alburnus*	*Leuciscus aspius*	Central and Western Europe	Predation	NA	Šmejkal et al. (2017)
26	North America	Canada	46.600481	66.632079	*Morone saxatilis*	*Salmo salar*	Northeast US and Southeast Canada Atlantic Drainages	Predation	NA	Daniels et al. (2018)
27	North America	Canada	47.094277	65.837024	*Morone saxatilis*	*Salmo salar*	Northeast US and Southeast Canada Atlantic Drainages	Predation	NA	Blackwell and Juanes (1998)
28	South America	Brazil	−18.78962	−48.14334	*Cichla ocellaris*	*Gymnotus carapo, Psalinodon fasciatus*	Paraná	Predation	NA	Franco et al. (2022a)
29	South America	Brazil	−25.405789	−54.5862	*Cichla ocellaris*	*Gymnotus carapo, Psalinodon fasciatus*	Paraná	Predation	NA	Franco et al. (2022a)
30	South America	Brazil	−15.72000	−44.60000	*Cichla ocellaris*	*Gymnotus carapo, Psalinodon fasciatus*	Paraná	Predation	NA	Franco et al. (2022a)
31	South America	Brazil	−22.21000	−43.31000	*Cichla ocellaris*	*Astyanax bimaculatus, Oligosarcus hepsetus*	Paraíba do Sul river basin	Predation	NA	Franco et al. (2022a)
32	South America	Brazil	−27.396172	−56.516809	*Pterygoplichthys ambrosettii*	*Unspecified*	Upper Paraná	Predation	NA	Franco et al. (2022a)

Blackwell and Juanes, 1998; Daniels et al., 2018). Predation of eggs by non-native species can also be problematic for the recruitment of native fish (Table 1; Schaeffer and Margraf 1987; Silbernagel and Sorensen 2013; Karjalainen et al., 2015). Because of the spawning migrations of generalists in the spring into tributaries (Hladík and Kubečka, 2003), predation on eggs and juveniles may be an important issue. Another example of edge effects is predation of eggs by generalist bleaks, which reduced the reproductive success of rheophilic asp in a tributary of a reservoir (Šmejkal et al., 2017; Šmejkal et al., 2018).

Some rheophilic fish migrate to slower river sections and pools for overwintering (Näslund et al., 1998) and remain nearly inactive during the winter. However, if they use artificial impoundments as overwintering habitats, they may be at higher risk of mortality because many predators are still active when temperatures drop (Brönmark et al., 2008). Although little studied, this may be a very important hidden interaction in altered freshwater ecosystems (Jackson et al., 2001; Hurst, 2007).

6 Temporal habitat displacement of rheophilic species by generalists in tributaries: Competition for food and space

Competitive interactions among fish species may lead to habitat niche displacement or even extirpation of native species (Pfauserová et al., 2021; Tapkir et al., 2022). Strong seasonal migration patterns in generalists such as roach and bleak have been described for fragmented habitats (Slavík et al., 2009; Lothian et al., 2019; Mader et al., 2020). These result in community structure changes with seasonal patterns in tributaries: The ecological quality of fish stocks in the Vltava River, as classified by the European Fish Index (Breine et al. 2005), varied seasonally from good conditions in spring to moderate conditions in autumn, which reflected seasonal colonization by generalist species from the Lipno Reservoir (Pfauserová et al., 2021). Some populations of non-native species, including generalist bream, use this reservoir for overwintering during harsh conditions and tributaries for feeding and/or spawning during the rest of the year (Pfauserová et al., 2021). Such competition for food sources or habitats often results in displacement of native species from tributaries (Hoxmeier and Dieterman, 2016). Accordingly, the presence of non-native fish in tributaries forced native brown trout to relocate to small brook tributaries (Pfauserová et al., 2021). Spatial segregation is a known response of brown trout to increasing competition (Vehanen et al., 1999); however, it might have broader ecological consequences. For example, the critically endangered freshwater pearl mussel (*Margaritifera margaritifera*) utilizes brown trout as the primary host for its glochidia larvae (Bauer et al., 1991). Forced declines in the usage of the main river by brown trout during the summer when glochidia are released could be considered a threat to reproduction of this mussel, which is considered key to its conservation (Modesto et al., 2018). Seasonal colonization of tributaries by generalist species can thus alter habitats and available resources for native fishes but also affects interactions with other species.

Similar to the evidence from Europe, a study conducted in a reservoir located on the White River, United States showed increased competition of rheophilic fishes with non-native generalists. Generalist species proliferated in the reservoir and comprised up to 90% of the fish community, which also affected the remaining original fish community in the tributary (Martinez et al., 1994). The negative effects of competition with reservoir generalists may also be visible in the significant positive associations of certain species with increasing distances from reservoirs (Falke and Gido, 2006). Another example is the construction of the Three Gorges Reservoir, China, which led to a reduction in rheophilic fishes in the tributaries and increased competition with 18 non-native generalists that proliferated in the modified reservoir environment (Liao et al., 2018; Lin et al., 2018; Liu et al., 2019). Maimela et al. (2022) revealed that adverse impacts on community structure and function were observed due to competition for food and space between *O. mykiss* and indigenous species in the upper Blyde River Catchment, South Africa. *Psedudobarbus verloenii*, a tropical rheophilic species, is reported to decline in South Africa due to reservoir construction. This species spawns in clear water, moderate to fast flow throughout the year and rocky substratum. It was widespread throughout the Verlorenvlei and Langvlei River system, South Africa in the past, but the population declined during the last century due to competition with banded Mozambique tilapia (*Oreochromis mossambicus*), tilapia (*Tilapia sparrmanii*), and common carp (*Cyprinus carpio*) (Chakona et al., 2014; Shelton et al., 2015).

Competition for food and space in tributaries is not limited to adult fish. During spring spawning, reservoir generalists can outnumber native rheophilic species and deposit enormous numbers of eggs in tributaries (Hladík and Kubečka, 2004). This deposition of generalist offspring may affect the rheophilic species recruitment as they compete for very similar food sources as juveniles (Specziár and Rezsu, 2009); thus, there is the potential to investigate how rheophilic recruitment is affected by habitat edges with adjacent reservoir fauna. We are not aware of any studies that have quantified this effect.

7 Intentional fragmentation as a tool for reducing the spread of generalist species

Since generalist species usually occupy artificial, degraded habitats (Corbacho and Sánchez, 2001; MacDougall and Turkington, 2005), the simplest strategy to exclude them from uninvaded sites is to protect natural habitats or restore degraded environments and allow them to act as natural barriers against invasions of undesirable species (Rahel, 2007). This restoration measure has been used, e.g., by the removal of the Woolen Mills Dam, United States, and subsequent habitat improvement work, which reduced the dominance of non-native common carp (*Cyprinus carpio*) in favor of smallmouth bass (*Micropterus dolomieu*) (Kanehl et al., 1997). Although dam removal (reviewed in e.g. Bednarek, 2001; Tonitto and Riha, 2016; Ding et al., 2019) is optimal solution of strong interaction between generalist fishes and rheophilic fishes, the global trend is to increase proportions of rivers that will be affected by damming (Grill et al., 2015; Zarfl et al., 2015; Winemiller et al., 2016; Cutler et al., 2020). In cases where restoration of degraded environments are not possible, there is a possibility to disrupt the connection between the remaining unoccupied tributary to isolate the habitats that are already occupied by generalist species (Rahel, 2013). This approach, known as intentional fragmentation or isolation management, has been used worldwide and increasingly since the 1950's (Jones et al., 2021). This management measure significantly increases the eradication success of

TABLE 2 Examples of different types of barriers used to reduce the spread of generalists that were selected by using the criterion of estimated effectiveness.

Barrier type	Target species	Advantages	Disadvantages	Effectivity	Relevant citations
Mechanical—culvert	brook trout (*Salvelinus fontinalis*)	Easy construction	Association with road crossing	100%	
Gabions		Easy to build	Free interstitial spaces pervious	80%–100%	Thompson and Rahel (1998)
Electricall—small	Mediterranean trout (*Salmo cettii*) common carp (*Cyprinus carpio*)	Maintain hydrologic connectivity, flexible deployment	Size selectivity, chance of equipment or power outage	100%	Sabatini et al. (2018)
Large				>99%	Sparks et al. (2010)
Chemosensory alarm cue	Sea lamprey (*Petromyzon marinus*)	Maintain hydrologic connectivity, cheap, environmentally benign, potential species selectivity	High effort to produce sufficient bulk of cue, danger of habituation	97%[a]	Di Rocco et al. (2016); Imre et al. (2016)
Carbon dioxide	silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys* nobilis)	Maintain hydrologic connectivity, environmentally benign	Large investments in facility, danger of habituation	50%–66%	Schneider et al. (2018)
Light (600 FPS)	brown trout (*Salmo trutta*)	Less infrastructure, low costs	Species, life-history, ambient conditions dependent	88% (day); 67% (night) **	Jesus et al. (2019b)
Sound (sweep up mode)	brown trout (*Salmo trutta*)	Effective across wide range of environments	Variable effectiveness, species specific	16%	Jesus et al. (2019a)
	Douro nase (*Pseudochondrostoma duriense*)			91%	Jesus et al. (2019a)
	Iberian barbel (*Luciobarbus bocagei*)			96%	Jesus et al. (2019a)
Bubble curtain	common carp	Low cost	Low effectivity under certain conditions	74% (upstream); 28 (downstream)	Zielinski and Sorensen (2015)
	silver carp			80% **	Zielinski and Sorensen (2016)
	bigheaded carp			83% **	Zielinski and Sorensen (2016)
Hydraulic	Round goby (*Neogobius melanostomus*)	Selectively excludes nuisance species	Major modification to channel; few sites meet criteria	100% **	Wiegleb et al. (2021)

[a]The calculated effectiveness represents the proportion of directed individuals outside the treated stream; however, there was the possibility of migrating into the control (untreated) stream.** laboratory conditions.

targeted species in riverine sections, which has otherwise rarely been successful (Simberloff, 2013).

There are several ways to create intentional fragmentation in aquatic systems, and we present the most-often used methods. They consist of mechanical, electrical, chemical or other non-mechanical methods (Table 2). Most commonly, exclusion barriers are used to prevent upstream migration of undesirable species (Rahel 2013). Examples of mechanical barriers include constructing low head dams, gabion barriers, or culvert barriers to restrict common carp and other reservoir generalists from entering the upstream tributaries of the Roaring River, United States (Bulow et al., 1988), limit sea lamprey access to the spawning grounds in the Laurentian Great Lakes basin (McLaughlin et al., 2007; Miehls et al., 2020) and protect native salmonids in western North America (Novinger and Rahel, 2003; Kirk et al., 2018). Although creating new barriers increases fragmentation and can to some extent create new lentic habitats, this impact is exceeded by the benefits of preventing intrusion of unwanted taxa. Moreover, isolation management has been shown for a long time to support native trout populations in headwater streams, when strategically placed barriers isolate catchments that are large enough to allow seasonal movements and maintain metapopulation structures (Harig and Fausch, 2002) and the isolated population is large enough to avoid extinction due to loss of genetic variability or stochastic demographic or environmental events (Cook et al., 2010).

Isolation management using electric barriers has been successfully used to block non-native trout and protect reintroduced populations of native Mediterranean brown trout (*Salmo cetti*) (Sabatini et al., 2018) and a similar device is used seasonally to block the migration of sea lamprey (*Petromyzon marinus*) and limit its reproduction in the Black Mallard River, Michigan (Johnson et al., 2021). Electric barriers meet the conflicting demands of managers to disrupt biological connectivity while maintaining hydrologic connectivity. Despite this advantage, there is a possibility of power or equipment failure (Clarkson, 2004); these barriers could be overcome by jumping fish, or their effectiveness may decrease during the navigation of metal-hulled barges through these barriers (Parker et al., 2015). The world's largest and well-known electric barrier system was activated in the Chicago Sanitary and Ship Canal in 2002. Two additional barriers were added in 2009 and still function as the primary barrier to the spread of bigheaded carps (i.e., silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*) between the Mississippi River and the Great Lakes basin (Parker et al., 2016).

Various types of chemical barriers have been used worldwide, but their use is much less widespread compared to mechanical and electric barriers. Application of taxon-specific piscicides can be quite effective in preventing the invasion of non-native species in target areas (Araújo et al., 2018). Although their effects can be effectively neutralized by other substances (Weyl et al., 2014), they are potentially dangerous due to their possible negative effects on entire ecosystems (Birceanu et al., 2014). The use of chemosensory alarm cues (i.e., facilitating early warning for prey fish) could be a cheaper and safer alternative (Frisch, 1938; Ferrari et al., 2010; Imre et al., 2010). The effect of chemical alarm cues was demonstrated primarily under laboratory conditions (Wagner et al., 2011) and showed a significant reduction in the occurrence of non-native species in the field (Di Rocco et al., 2016); however, this effect is not absolute, and combinations with other measures are needed. Carbon dioxide and ozone are other options that can be used to block fish migration and prevent the further spread of non-native species, and they are relatively environmentally benign compared to other chemicals in aquatic systems (Buley et al., 2017; Suski, 2020). While the knowledge of fish behavior with respect to these substances is relatively well known, there are still many data gaps regarding the use of CO_2 and O_3 in the field, including determining how freshwater river systems will respond to the use of O_3 barriers.

Other types of non-mechanical devices that provide barriers to migrations of fish species, which are based on the behavioral responses of fish to physical stimuli (e.g., light, sound, and air bubbles; Bullen and Carlson 2003), are also being used more frequently. Some species are attracted to light (Stamplecoskie et al., 2012), while others are repelled (Hadderingh, 1982), but strobe lights repel most target species and are most effective at pulse rates greater than 300 flashes per minute (Kim and Mandrak, 2017). Experiments showed that acoustic signals influence fish behavior (Vetter et al., 2015), but the observed response was not sufficient to produce a strong deterrent effect in the field (Deleau et al., 2020) and is affected by strong species-specific variability that is likely caused by species differences in auditory sensitivity (Bullen and Carlson, 2003). The efficiency of this type of barrier could be increased in the future by using a sweep or modulated sound (Jesus et al., 2019a) or in combination with air-bubbles (ensonified bubble curtain), which helps to focus and enhance sound fields while often causing its bubbles to resonate (Dennis et al., 2019). The air-bubble curtains that are emitted from air diffusers located along the water bottom achieved over 80% efficiency in reducing passage for bigheaded and common carps (*Cyprinus carpio*) under laboratory conditions (Zielinski et al., 2014). Although the efficiency was lower in field experiments when fish were more motivated to migrate (Zielinski and Sorensen, 2016), the combination with sound (ensonified bubble curtain) increased its efficiency to 95% or more for bigheaded carps (Taylor et al., 2005). On the other hand, combination of ensonified bubble curtain with strobe light has been show unlikely to block upstream sea lamprey migration in laboratory (Miehls et al., 2017). A new approach to protect pristine upstream areas from invasion by non-native fish consists of hydraulic or velocity barriers (Wiegleb et al., 2021) and these have been tested under laboratory conditions. Based on knowledge of the differences in swimming performance under artificially elevated water flows (Kemp, 2016), environments can be created to prevent passage of the tested non-native species (e.g., round goby *Neogobius melanostomus*) and allow passage of desired species (e.g., gudgeon *Gobio gobio* and bullhead *Cottus gobio*). However, the performance of such barriers has yet to be tested in the field.

In summary, mechanical barriers, when properly operated and maintained, can achieve 100% fish exclusion. Other barrier types are either not 100% effective, are prone to fail in extreme or unexpected events or have not yet been properly tested under field conditions (Table 2). However, the resulting disruption of natural flows by mechanical barriers and blockage of non-target species pose significant challenges. The effectiveness of all behavioral and chemical barriers may continue to decrease over time due to the habituation process of target species (Imre et al., 2016). Nevertheless, they may significantly decrease the number of generalist fishes and potentially reduce the impacts on rheophilic species when combined with other management measures. A systematic review on barrier types and efficiencies along with proper identification of knowledge gaps may be beneficial in this field to achieve progress in the conservation of reservoir tributaries.

8 Conclusion and future directions

Here, we reviewed the impacts on generalists due to damming (which also applies to smaller impoundments) on rheophilic fish fauna based in tributaries and the potential solutions to mitigate their impacts through intentional fragmentation. We suggest that the observed changes in fish diversity and fish functional traits in reservoir tributaries following reservoir construction can be partly attributed to changes in the intensities of interactions among generalists and rheophilic species. We emphasize that the management of edge effects may be critical to maintaining viable populations of rheophilic fishes in lotic ecosystems that are modified to meet human needs. Although many studies have examined the effects of reservoirs on fish diversity (e.g. Esselman et al., 2013; Van Looy et al., 2014; Cooper et al., 2017), detailed data on the intensified interactions among generalists and rheophilic fish and ontogenetic bottlenecks due to competition or predation are generally lacking (Tamario et al., 2021). In particular, we call for detailed temporal telemetry, reproductive migration, and trophic interaction studies to move from descriptive and correlative science to a better understanding of the mechanisms behind the community changes that are caused by artificially enhanced fish fauna interactions. This knowledge may not only provide novel insights into the observed trends but also may lead to novel solutions for rheophilic species conservation efforts, which may be targeted to specific bottlenecks that emerge due to habitat degradation. An example of such conservation measures can consist of blocking the migration of generalists to enable year-round utilization of river channels by brown trout (Pfauserová et al., 2021).

One of the targets of future studies could be determining the habitat proportions that need to be maintained to sustain potamodromous rheophilic fish populations, e.g., (Fausch et al., 2002; Isaak et al., 2007; Perkin et al., 2015). In particular, an important issue is the magnitude of edge effects for protected rheophilic fish species that would prevent their long-term population stability in the face of competition and predation by generalists (e.g. Tamario et al., 2021). Since these patterns will often be species- and site-specific to some extent, considerable conservation efforts will need to be made to minimize local extinctions of rheophilic fishes in fragmented rivers. In case a barrier is important to human needs more than to protecting targeted species, what measures can be implemented to minimize the predation and competition pressures from generalists? Antimigration barriers that prevent generalists and other non-native species from entering tributaries can help preserve the remaining free-flowing segments, and much has been done in recent decades to make progress in this area. However, efficiency evaluations of particular barrier types need more research under comparable field conditions. Migrations of generalists from reservoirs to tributaries provide an opportunity to apply temporarily installed barriers and mitigate edge effects for conservation needs.

Author contributions

MŠ initiated a topical workshop on the manuscript concept and manuscript outline. All authors contributed by drafting manuscript chapters. All authors provided substantial feedback to the first and subsequent drafts.

Funding

MŠ, DB, and JK were supported by the project "The enhancement of rheophilous fish reproduction in the artificial river environment" (No. TJ02000012) and AV 21 strategy support program "Water for Life". OS, PH, and NP were supported by the European Regional Development Fund Project (No. CZ.02.1.01/0.0/0.0/16_019/0000845). MM was supported by project TAČR "Water systems and water management in the Czech Republic in conditions of climate change" (No. SS02030027).

Acknowledgments

We would like to express thanks to Zuzana Sajdlová for drawing Figure 3.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Aarts, B. G. W., and Nienhuis, P. H. (2003). Fish zonations and guilds as the basis for assessment of ecological [2pt] integrity of large rivers. *Hydrobiologia* 500, 157–178. doi:10.1023/A:1024638726162

Agostinho, A. A., Miranda, L. E., Bini, L. M., Gomes, L. C., Thomaz, S. M., and Suzuki, H. I. (1999). "Patterns of colonization in neotropical reservoirs, and prognoses on aging," in *Theoretical reservoir ecology and its applications*. Editors J. G. Tundisi and M. Straskraba (Leiden: Blackhuys Publisher), 585.

Andren, H., and Angelstam, P. (1988). Elevated predation rates as an edge effect in habitat islands: Experimental evidence. *Ecology* 69, 544–547. doi:10.2307/1940455

Araújo, C. V. M., Silva, D. C. V. R., Gomes, L. E. T., Acayaba, R. D., Montagner, C. C., Moreira-Santos, M., et al. (2018). Habitat fragmentation caused by contaminants: Atrazine as a chemical barrier isolating fish populations. *Chemosphere* 193, 24–31. doi:10.1016/J.CHEMOSPHERE.2017.11.014

Arboleya, E., Fernández, S., Clusa, L., Dopico, E., and Garcia-Vazquez, E. (2021). River connectivity is crucial for safeguarding biodiversity but may be socially overlooked. Insights from Spanish University students. *Front. Environ. Sci.* 9, 231. doi:10.3389/fenvs.2021.643820

Arnold, G. P., Shipley, O. N., and Siskey, M. R. (2019). Fish migration, horizontal. *Encycl. Ocean. Sci.*, 205–216. doi:10.1016/B978-0-12-409548-9.11339-9

Bain, M. B., Finn, J. T., and Booke, H. E. (1988). Streamflow regulation and fish community structure. *Ecology* 69, 382–392. doi:10.2307/1940436

Balon, E. K. (1975). Reproductive guilds of fishes: A proposal and definition. *J. Fish. Res. Board Can.* 32, 821–864. doi:10.1139/f75-110

Baril, M., and Magnan, P. (2002). Seasonal timing and diel activity of lacustrine brook charr, *Salvelinus fontinalis*, spawning in a lake outlet. *Environ. Biol. Fishes* 64, 175–181. doi:10.1023/A:1016097704008

Bartoň, D., Blabolil, P., Sajdlová, Z., Vejřík, L., Souza, A. T., Kubečka, J., et al. (2021). Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species. *Ecohydrology* 14, e2280. doi:10.1002/eco.2280

Bartoň, D., Brabec, M., Sajdlová, Z., Souza, A. T., Duras, J., Kortan, D., et al. (2022). Hydropeaking causes spatial shifts in a reproducing rheophilic fish. *Sci. Total Environ.* 806, 150649. doi:10.1016/J.SCITOTENV.2021.150649

Bauer, G., Hochwald, S., and Silkenat, W. (1991). Spatial distribution of freshwater mussels: The role of host fish and metabolic rate. *Freshw. Biol.* 26, 377–386. doi:10.1111/J.1365-2427.1991.TB01405.X

Bednarek, A. T. (2001). Undamming rivers: A review of the ecological impacts of dam removal. *Environ. Manage.* 27, 803–814. doi:10.1007/s002670010189

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., et al. (2020). More than one million barriers fragment Europe's rivers. *Nat* 588, 436–441. doi:10.1038/s41586-020-3005-2

Belmar, O., Velasco, J. V., Martínez-Capel, F., and Marín, A. A. (2010). Natural flow regime, degree of alteration and environmental flows in the Mula stream (Segura River basin, SE Spain). *Limnetica* 29, 353–368. doi:10.23818/limn.29.29

Benitez, J.-P., Matondo, B. N., Dierckx, A., and Ovidio, M. (2015). An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. *Aquat. Ecol.* 49, 481–497. doi:10.1007/s10452-015-9541-4

Bešta, T., Muška, M., Juggins, S., and Těšitel, J. (2015). Comparison of diatom community structure from epilithon and fish guts: Implications for inferring past changes in water quality. *Hydrobiologia* 742, 233–248. doi:10.1007/s10750-014-1987-1

Birceanu, O., Sorensen, L. A., Henry, M., McClelland, G. B., Wang, Y. S., and Wilkie, M. P. (2014). The effects of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) on fuel stores and ion balance in a non-target fish, the rainbow trout (*Oncorhynchus mykiss*). *Comp. Biochem. Physiol. C. Toxicol. Pharmacol.* 160, 30–41. doi:10.1016/J.CBPC.2013.10.002

Blackwell, B. F., and Juanes, F. (1998). Predation on atlantic salmon smolts by striped bass after dam passage. *North Am. J. Fish. Manag.* 18, 936–939. doi:10.1577/1548-8675(1998)018<0936:poassb>2.0.co;2

Boulêtreau, S., Carry, L., Meyer, E., Filloux, D., Menchi, O., Mataix, V., et al. (2020). High predation of native sea lamprey during spawning migration. *Sci. Rep.* 10, 6122–6129. doi:10.1038/s41598-020-62916-w

Boulêtreau, S., Fauvel, T., Laventure, M., Delacour, R., Bouyssonnié, W., Azémar, F., et al. (2021). The giants' feast": Predation of the large introduced European catfish on spawning migrating allis shads. *Aquat. Ecol.* 55, 75–83. doi:10.1007/s10452-020-09811-8

Boulêtreau, S., Gaillagot, A., Carry, L., Tétard, S., De Oliveira, E., and Santoul, F. (2018). Adult Atlantic salmon have a new freshwater predator. *PLoS One* 13, e0196046. doi:10.1371/JOURNAL.PONE.0196046

Breine, J., Simoens, I., Haidvogl, G., Melcher, A., Pont, D., and Schmutz, S. (2005). Manual for application of the european fish index - EFI: A fish-based method to assess the ecological status of European rivers in support of the water framework directive. *FAME*, 81.

Brodersen, J., Chapman, B. B., Nilsson, P. A., Skov, C., Hansson, L.-A., and Brönmark, C. (2014). Fixed and flexible: Coexistence of obligate and facultative migratory strategies in a freshwater fish. *PLoS One* 9, e90294. doi:10.1371/JOURNAL.PONE.0090294

Brönmark, C., Skov, C., Brodersen, J., Nilsson, P. A., and Hansson, L.-A. (2008). Seasonal migration determined by a trade-off between predator avoidance and growth. *PLoS One* 3, e1957. doi:10.1371/journal.pone.0001957

Buisson, L., Blanc, L., and Grenouillet, G. (2008). Modelling stream fish species distribution in a river network: The relative effects of temperature versus physical factors. *Ecol. Freshw. Fish.* 17, 244–257. doi:10.1111/J.1600-0633.2007.00276.X

Buley, R. P., Hasler, C. T., Tix, J. A., Suski, C. D., and Hubert, T. D. (2017). Can ozone be used to control the spread of freshwater aquatic invasive species? *Manag. Biol. Invasions* 8, 13–24. doi:10.3391/MBI.2017.8.1.02

Bullen, C. R., and Carlson, T. J. (2003). Non-physical fish barrier systems: Their development and potential applications to marine ranching. *Rev. Fish. Biol. Fish.* 13, 201–212. doi:10.1023/B:RFBF.0000019481.10670.94

Bulow, F., Webb, M., Crumby, W., and Quisenberry, S. (1988). Management briefs: Effectiveness of a fish barrier dam in limiting movement of rough fishes from a reservoir into a tributary stream. *North Am. J. Fish. Manag.* 8, 273–275. doi:10.1577/1548-8675(1988)008<0273:mbeoaf>2.3.co;2

Chakona, A., Swartz, E. R., and Skelton, P. H. (2014). A new species of redfin (teleostei, Cyprinidae, Pseudobarbus) from the Verlorenvlei River system, South Africa. *Zookeys* 121, 121–137. doi:10.3897/ZOOKEYS.453.8072

Chapleau, F., Findlay, S. C., and Szenasy, E. (1997). Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Québec. *Écoscience* 4, 259–268. doi:10.1080/11956860.1997.11682404

Chapman, B. B., Hulthén, K., Blomqvist, D. R., Hansson, L.-A., Nilsson, J.-Å., Brodersen, J., et al. (2011). To boldly go: Individual differences in boldness influence migratory tendency. *Ecol. Lett.* 14, 871–876. doi:10.1111/j.1461-0248.2011.01648.x

Clarkson, R. W. (2004). Effectiveness of electrical fish barriers associated with the Central Arizona project. *North Am. J. Fish. Manag.* 24, 94–105. doi:10.1577/M02-146

Clavero, M., and Hermoso, V. (2010). Reservoirs promote the taxonomic homogenization of fish communities within river basins. *Biodivers. Conserv.* 20, 41–57. doi:10.1007/S10531-010-9945-3

Cook, N., Rahel, F. J., and Hubert, W. A. (2010). Persistence of Colorado River cutthroat trout populations in isolated headwater streams of Wyoming. *Trans. Am. Fish. Soc.* 139, 1500–1510. doi:10.1577/T09-133.1

Cooper, A. R., Infante, D. M., Daniel, W. M., Wehrly, K. E., Wang, L., and Brenden, T. O. (2017). Assessment of dam effects on streams and fish assemblages of the conterminous USA. *Sci. Total Environ.* 586, 879–889. doi:10.1016/J.SCITOTENV.2017.02.067

Copp, G. H., Robert Britton, J., Cucherousset, J., García-Berthou, E., Kirk, R., Peeler, E., et al. (2009). Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish. Fish.* 10, 252–282. doi:10.1111/j.1467-2979.2008.00321.x

Corbacho, C., and Sánchez, J. M. (2001). Patterns of species richness and introduced species in native freshwater fish faunas of a mediterranean-type basin: The guadiana river (southwest iberian peninsula). *Regul. Rivers Res. Manag.* 17, 699–707. doi:10.1002/RRR.631

Cutler, J. S., Olivos, J. A., Sidlauskas, B., and Arismendi, I. (2020). Habitat loss due to dam development may affect the distribution of marine-associated fishes in Gabon, Africa. *Ecosphere* 11. doi:10.1002/ecs2.3024

Daniels, J., Chaput, G., and Carr, J. (2018). Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic telemetry. *Can. J. Fish. Aquat. Sci.* 75, 1811–1822. doi:10.1139/cjfas-2017-0373

Dawson, W., Moser, D., Van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., et al. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nat. Ecol. Evol.* 17 (1), 0186–0187. doi:10.1038/s41559-017-0186

Degerman, E., Beier, U., Breine, J., Melcher, A., Quataert, P., Rogers, C., et al. (2007). Classification and assessment of degradation in European running waters. *Fish. Manag. Ecol.* 14, 417–426. doi:10.1111/J.1365-2400.2007.00578.X

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., et al. (2020). The living planet index (LPI) for migratory freshwater fish - technical report.

Deleau, M. J. C., White, P. R., Peirson, G., Leighton, T. G., and Kemp, P. S. (2020). The response of anguilliform fish to underwater sound under an experimental setting. *River Res. Appl.* 36, 441–451. doi:10.1002/RRA.3583

Dennis, C. E., Zielinski, D., and Sorensen, P. W. (2019). A complex sound coupled with an air curtain blocks invasive carp passage without habituation in a laboratory flume. *Biol. Invasions* 21, 2837–2855. doi:10.1007/s10530-019-02017-6

Di Rocco, R. T., Johnson, N. S., Brege, L., Imre, I., and Brown, G. E. (2016). Sea lamprey avoid areas scented with conspecific tissue extract in Michigan streams. *Fish. Manag. Ecol.* 23, 548–560. doi:10.1111/FME.12198

Ding, L., Chen, L., Ding, C., and Tao, J. (2019). Global trends in dam removal and related research: A systematic review based on associated datasets and bibliometric analysis. *Chin. Geogr. Sci.* 29, 1–12. doi:10.1007/s11769-018-1009-8

Drake, D. A. R., and Mandrak, N. E. (2014). Ecological risk of live bait fisheries: A new angle on selective fishing. *Fisheries* 39, 201–211. doi:10.1080/03632415.2014.903835

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., et al. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182. doi:10.1017/S1464793105006950

Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., et al. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat. Commun.* 7, 12485. doi:10.1038/ncomms12485

Esselman, P. C., Infante, D. M., Wang, L., Cooper, A. R., Wieferich, D., Tsang, Y. P., et al. (2013). Regional fish community indicators of landscape disturbance to catchments of the conterminous United States. *Ecol. Indic.* 26, 163–173. doi:10.1016/J.ECOLIND.2012.10.028

Falke, J. A., and Gido, K. B. (2006). Spatial effects of reservoirs on fish assemblages in Great Plains streams in Kansas, USA. *River Res. Appl.* 22, 55–68. doi:10.1002/RRA.889

Fausch, K. D., Torgesen, C. E., Baxter, C. V., and Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience* 52, 483–498. doi:10.1641/0006-3568(2002)052[0483:ltrbtg]2.0.co;2

Feng, M., Zolezzi, G., and Pusch, M. (2018). Effects of thermopeaking on the thermal response of alpine river systems to heatwaves. *Sci. Total Environ.* 612, 1266–1275. doi:10.1016/J.SCITOTENV.2017.09.042

Fernando, C. H. (1994). Zooplankton, fish and fisheries in tropical freshwaters. *Hydrobiol* 272, 105–123. doi:10.1007/BF00006516

Fernando, C. H., and Holčík, J. (1991). Fish in reservoirs. *Int. Rev. gesamten Hydrobiol. Hydrogr.* 76, 149–167. doi:10.1002/iroh.19910760202

Ferrari, M. C. O., Wisenden, B. D., and Chivers, D. P. (2010). Chemical ecology of predator–prey interactions in aquatic ecosystems: A review and prospectusThe present review is one in the special series of reviews on animal–plant interactions. *Can. J. Zool.* 88, 698–724. doi:10.1139/z10-029

Fischer, J., and Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: A synthesis. *Glob. Ecol. Biogeogr.* 16, 265–280. doi:10.1111/J.1466-8238.2007.00287.X

Franco, A. C. S., García-Berthou, E., and Santosdos, L. N. (2021). Ecological impacts of an invasive top predator fish across South America. *Sci. Total Environ.* 761, 143296. doi:10.1016/J.SCITOTENV.2020.143296

Franco, A. C. S., Petry, A. C., García-Berthou, E., and dos Santos, L. N. (2022a). Invasive peacock basses (*Cichla* spp.) and decreased abundance of small native fish in Brazilian reservoirs. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 32, 1852–1866. doi:10.1002/AQC.3874

Franco, A. C. S., Petry, A. C., Tavares, M. R., de Fátima Ramos Guimarães, T., and dos Santos, L. N. (2022b). Global distribution of the South American peacock basses *Cichla* spp. follows human interference. *Fish. Fish.* 23, 407–421. doi:10.1111/FAF.12624

Frisch, K. R. von (1938). Zur psychologie des fisch-schwarmes. *Naturwissenschaften* 26, 601–606. doi:10.1007/bf01590598

Fuller, M. R., Doyle, M. W., and Strayer, D. L. (2015). Causes and consequences of habitat fragmentation in river networks. *Ann. N. Y. Acad. Sci.* 1355, 31–51. doi:10.1111/NYAS.12853

Gago, J., Anastácio, P., Gkenas, C., Banha, F., and Ribeiro, F. (2016). Spatial distribution patterns of the non-native European catfish, *Silurus glanis*, from multiple online sources – A case study for the river tagus (iberian peninsula). *Fish. Manag. Ecol.* 23, 503–509. doi:10.1111/FME.12189

Ganassin, M. J. M., Muñoz-Mas, R., de Oliveira, F. J. M., Muniz, C. M., dos Santos, N. C. L., García-Berthou, E., et al. (2021). Effects of reservoir cascades on diversity, distribution, and abundance of fish assemblages in three Neotropical basins. *Sci. Total Environ.* 778, 146246. doi:10.1016/J.SCITOTENV.2021.146246

Gido, K. B., Schaeffer, J. F., and Falke, J. A. (2009). Convergence of fish communities from the littoral zone of reservoirs. *Freshw. Biol.* 54, 1163–1177. doi:10.1111/J.1365-2427.2008.02162.X

Grill, G., Lehner, B., Lumsdon, A. E., Macdonald, G. K., Zarfl, C., and Reidy Liermann, C. (2015). An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environ. Res. Lett.* 10, 015001. doi:10.1088/1748-9326/10/1/015001

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., et al. (2019). Mapping the world's free-flowing rivers. *Nature* 569, 215–221. doi:10.1038/s41586-019-1111-9

Guenther, C. B., and Spacie, A. (2006). Changes in fish assemblage structure upstream of impoundments within the Upper Wabash River basin, Indiana. *Trans. Am. Fish. Soc.* 135, 570–583. doi:10.1577/T05-031.1

Guillerault, N., Delmotte, S., Boulêtreau, S., Lauzeral, C., Poulet, N., and Santoul, F. (2015). Does the non-native European catfish *Silurus glanis* threaten French river fish populations? *Freshw. Biol.* 60, 922–928. doi:10.1111/FWB.12545

Hadderingh, R. (1982). Experimental reduction of fish impingement by artificial illumination at Bergum power station. *Int. Rev. gesamten Hydrobiol.* 67, 887–900.

Harig, A. L., and Fausch, K. D. (2002). Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecol. Appl.* 12, 535–551. doi:10.1890/1051-0761(2002)012[0535:mhrfet]2.0.co;2

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J., and Power, M. (2015). Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behav. Ecol.* 26, 483–492. doi:10.1093/BEHECO/ARU216

Harvey, B. C., and Nakamoto, R. J. (2013). Seasonal and among-stream variation in predator encounter rates for fish prey. *Trans. Am. Fish. Soc.* 142, 621–627. doi:10.1080/00028487.2012.760485

Havel, J. E., Lee, C. E., and Zanden, M. J. Vander (2005). Do reservoirs facilitate invasions into landscapes? *Bioscience* 55, 518–526. doi:10.1641/0006-3568(2005)055[0518:drfiil]2.0.co;2

Havlena, F. (1964). Contribution to the study on age and growth in the barb, *Barbus barbus* (L.) in the drainage area of the Orava River dam basin. *Folia Zool.* 13, 321–326.

Hermoso, V., Clavero, M., Blanco-Garrido, F., and Prenda, J. (2011). Invasive species and habitat degradation in Iberian streams: An analysis of their role in freshwater fish diversity loss. *Ecol. Appl.* 21, 175–188. doi:10.1890/09-2011.1

Hirsch, P. E., N'Guyen, A., Muller, R., Adrian-Kalchhauser, I., and Burkhardt-Holm, P. (2018). Colonizing islands of water on dry land—On the passive dispersal of fish eggs by birds. *Fish. Fish.* 19, 502–510. doi:10.1111/FAF.12270

Hladík, M., and Kubečka, J. (2003). Fish migration between a temperate reservoir and its main tributary. *Hydrobiologia* 504, 251–266. doi:10.1023/b:hydr.0000008525.46939.42

Hladík, M., Kubečka, J., Mrkvička, T., Čech, M., Draštík, V., Frouzová, J., et al. (2008). Effects of the construction of a reservoir on the fish assemblage in an inflow river. *Czech J. Anim. Sci.* 53, 537–547. doi:10.17221/370-cjas

Hladík, M., and Kubečka, J. (2004). The effect of water level fluctuation on tributary spawning migration of reservoir fish. *Ecohydrol. Hydrobiol.* 4, 449–457.

Hoxmeier, R. J. H., and Dieterman, D. J. (2016). Long-term population demographics of native brook trout following manipulative reduction of an invader. *Biol. Invasions* 18, 2911–2922. doi:10.1007/s10530-016-1182-6

Hülsmann, S., Mehner, T., Worischka, S., and Plewa, M. (1999). Is the difference in population dynamics of *Daphnia galeata* in littoral and pelagic areas of a long-term biomanipulated reservoir affected by age-0 fish predation? *Hydrobiologia* 408–409, 57–63. doi:10.1007/978-94-017-2986-4_6

Hurst, T. P. (2007). Causes and consequences of winter mortality in fishes. *J. Fish. Biol.* 71, 315–345. doi:10.1111/j.1095-8649.2007.01596.x

Imre, I., Brown, G. E., Bergstedt, R. A., and McDonald, R. (2010). Use of chemosensory cues as repellents for sea lamprey: Potential directions for population management. *J. Gt. Lakes. Res.* 36, 790–793. doi:10.1016/J.JGLR.2010.07.004

Imre, I., Di Rocco, R. T., Brown, G. E., and Johnson, N. S. (2016). Habituation of adult sea lamprey repeatedly exposed to damage-released alarm and predator cues. *Environ. Biol. Fishes* 99, 613–620. doi:10.1007/S10641-016-0503-Z

Irz, P., Laurent, A., Messad, S., Pronier, O., and Argillier, C. (2002). Influence of site characteristics on fish community patterns in French reservoirs. *Ecol. Freshw. Fish.* 11, 123–136. doi:10.1034/J.1600-0633.2002.00004.X

Isaak, D. J., Thurow, R. F., Rieman, B. E., and Dunham, J. B. (2007). Chinook salmon use of spawning patches: Relative roles of habitat quality, size, and connectivity. *Ecol. Appl.* 17, 352–364. doi:10.1890/05-1949

Jackson, D. A., Peres-Neto, P. R., and Olden, J. D. (2001). What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* 58, 157–170. doi:10.1139/CJFAS-58-1-157

Jarolím, O., Kubečka, J., Čech, M., Vašek, M., Peterka, J., and Matěna, J. (2010). Sinusoidal swimming in fishes: The role of season, density of large zooplankton, fish length, time of the day, weather condition and solar radiation. *Hydrobiologia* 654, 253–265. doi:10.1007/s10750-010-0398-1

Jepsen, N., Aarestrup, K., Økland, F., and Rasmussen, G. (1998). Survival of radiotagged atlantic salmon (*Salmo salar* L.) – And trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia* 371–372, 347–353. doi:10.1023/A:1017047527478

Jepsen, N., Pedersen, S., and Thorstad, E. (2000). Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. *River Res. Appl.* 16, 189–198. doi:10.1002/(sici)1099-1646(200003/04)16:2<189:aid-rrr570>3.0.co;2-n

Jesus, J., Amorim, M. C. P., Fonseca, P. J., Teixeira, A., Natário, S., Carrola, J., et al. (2019a). Acoustic barriers as an acoustic deterrent for native potamodromous migratory fish species. *J. Fish. Biol.* 95, 247–255. doi:10.1111/JFB.13769

Jesus, J., Teixeira, A., Natário, S., and Cortes, R. (2019b). Repulsive effect of stroboscopic light barriers on native salmonid (*Salmo trutta*) and cyprinid (*Pseudochondrostoma duriense* and *Luciobarbus bocagei*) species of Iberia. *Sustain* 11, 1332. doi:10.3390/SU11051332

Johnson, B. L., Richardson, W. B., and Naimo, T. J. (1995). Past, present, and future concepts in large river ecology. *Bioscience* 45, 134–141. doi:10.2307/1312552

Johnson, N. S., Snow, B., Bruning, T., and Jubar, A. (2021). A seasonal electric barrier blocks invasive adult sea lamprey (*Petromyzon marinus*) and reduces production of larvae. *J. Gt. Lakes. Res.* 47, S310–S319. doi:10.1016/J.JGLR.2021.09.008

Johnson, P. T. J., Olden, J. D., and Vander Zanden, M. J. (2008). Dam invaders: Impoundments facilitate biological invasions into freshwaters. *Front. Ecol. Environ.* 6, 357–363. doi:10.1890/070156

Jones, P. E., Tummers, J. S., Galib, S. M., Woodford, D. J., Hume, J. B., Silva, L. G. M., et al. (2021). The use of barriers to limit the spread of aquatic invasive animal species: A global review. *Front. Ecol. Evol.* 9, 43. doi:10.3389/fevo.2021.611631

Jumani, S., Deitch, M. J., Kaplan, D., Anderson, E. P., Krishnaswamy, J., Lecours, V., et al. (2019). river fragmentation and flow alteration metrics: A review of methods and directions for future research. *Environ. Res. Lett.* 15, 123009. doi:10.1088/1748-9326/ABCB37

Kanehl, P., Lyons, J., and Nelson, J. (1997). Changes in the habitat and fish community of the milwaukee river, Wisconsin following removal of the woolen Mills dam. *North Am. J. Fish. Manag.* 17, 387–400. doi:10.1577/1548-8675(1997)017<0387:cithaf>2.3.co;2

Karjalainen, J., Ruokonen, T. J., Marjomäki, T. J., Martikainen, A., Pursiainen, M., Sarvala, J., et al. (2015). Predation by signal crayfish *Pacifastacus leniusculus* on fish eggs and its consequences for coregonid recruitment. *J. Fish. Biol.* 86, 651–667. doi:10.1111/jfb.12588

Kemp, P. S. (2016). Meta-analyses, metrics and motivation: Mixed messages in the fish passage debate. *River Res. Appl.* 32, 2116–2124. doi:10.1002/RRA.3082

Kim, J., and Mandrak, N. E. (2017). Effects of strobe lights on the behaviour of freshwater fishes. *Enviromental Biol. Fishes* 100, 1427–1434. doi:10.1007/S10641-017-0653-7

Kirk, M. A., Rosswog, A. N., Ressel, K. N., and Wissinger, S. A. (2018). Evaluating the trade-offs between invasion and isolation for native brook trout and nonnative Brown trout in Pennsylvania streams. *Trans. Am. Fish. Soc.* 147, 806–817. doi:10.1002/TAFS.10078

Knott, J., Nagel, C., and Geist, J. (2021). Wasted effort or promising approach – does it make sense to build an engineered spawning ground for rheophilic fish in reservoir cascades? *Ecol. Eng.* 173, 106434. doi:10.1016/j.ecoleng.2021.106434

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., and Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592–599. doi:10.1111/1365-2435.12345

Kristiansen, H., and Dølving, K. B. (1996). The migration of spawning stocks of grayling *Thymallus thymallus*, in Lake Mjøsa, Norway. *Environ. Biol. Fishes* 47, 43–50. doi:10.1007/BF00002378

Kubečka, J. (1993). Succession of fish communities in reservoirs of central and eastern Europe. *Comp. Reserv. Limnol. water Qual. Manag.* 77, 153–168. doi:10.1007/978-94-017-1096-1_11

Larsson, P. -O. (1985). Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar* L., populations. *J. Fish. Biol.* 26, 391–397. doi:10.1111/j.1095-8649.1985.tb04279.x

Lehner, B., Liermann, C. R., Revenga, C., Vörömsmarty, C., Fekete, B., Crouzet, P., et al. (2011). High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Front. Ecol. Environ.* 9, 494–502. doi:10.1890/100125

Lenhardt, M., Markovic, G., and Gacic, Z. (2009). Decline in the index of biotic integrity of the fish assemblage as a response to reservoir aging. *Water Resour. Manag.* 23, 1713–1723. doi:10.1007/S11269-008-9348-3

Li, B., Wang, Y., Tan, W., Saintilan, N., Lei, G., and Wen, L. (2021). Land cover alteration shifts ecological assembly processes in floodplain lakes: Consequences for fish community dynamics. *Sci. Total Environ.* 782, 146724. doi:10.1016/J.SCITOTENV.2021.146724

Li, J., Dong, S., Peng, M., Yang, Z., Liu, S., Li, X., et al. (2013). Effects of damming on the biological integrity of fish assemblages in the middle Lancang-Mekong River basin. *Ecol. Indic.* 34, 94–102. doi:10.1016/J.ECOLIND.2013.04.016

Liao, C., Chen, S., De Silva, S. S., Correa, S. B., Yuan, J., Zhang, T., et al. (2018). Spatial changes of fish assemblages in relation to filling stages of the Three Gorges Reservoir, China. *J. Appl. Ichthyol.* 34, 1293–1303. doi:10.1111/JAI.13798

Liew, J. H., Tan, H. H., and Yeo, D. C. J. (2016). Dammed rivers: Impoundments facilitate fish invasions. *Freshw. Biol.* 61, 1421–1429. doi:10.1111/FWB.12781

Limburg, K. E., and Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *Bioscience* 59, 955–965. doi:10.1525/BIO.2009.59.11.7

Lin, P., Xin, G., Liu, F., Li, M., and Liu, H. (2018). Long-term monitoring revealed fish assemblage zonation in the Three Gorges Reservoir. *J. Oceanol. Limnol.* 37, 1258–1267. doi:10.1007/S00343-019-8165-2

Liu, X., Qin, J., Xu, Y., Ouyang, S., and Wu, X. (2019). Biodiversity decline of fish assemblages after the impoundment of the three Gorges dam in the yangtze river basin, China. *Rev. Fish. Biol. Fish.* 29, 177–195. doi:10.1007/s11160-019-09548-0

Lothian, A. J., Gardner, C. J., Hull, T., Griffiths, D., Dickinson, E. R., and Lucas, M. C. (2019). Passage performance and behaviour of wild and stocked cyprinid fish at a sloping weir with a Low Cost Baffle fishway. *Ecol. Eng.* 130, 67–79. doi:10.1016/J.ECOLENG.2019.02.006

Lovas-Kiss, A., Vincze, O., Löki, V., Paller-Kapusi, F., Halasi-Kovács, B., Kovács, G., et al. (2020). Experimental evidence of dispersal of invasive cyprinid eggs inside migratory waterfowl. *Proc. Natl. Acad. Sci. U. S. A.* 117, 15397–15399. doi:10.1073/pnas.2004805117

Lucas, M. C., and Baras, E. (2001). *Migration of freshwater fishes*. Editors M. C. Lucas, E. Baras, T. J. Thom, A. Duncan, and O. Slavk (Oxford, UK). doi:10.1002/9780470999653

Lusk, S., Lusková, V., and Hanel, L. (2010). Alien fish species in the Czech Republic and their impact on the native fish fauna. *Folia Zool.* 59, 57–72. doi:10.25225/fozo.v59.i1.a9.2010

Lutz, E., Hirsch, P. E., Bussmann, K., Wiegleb, J., Jermann, H. P., Muller, R., et al. (2020). Predation on native fish eggs by invasive round goby revealed by species-specific gut content DNA analyses. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 30, 1566–1577. doi:10.1002/aqc.3409

Lyach, R. (2021). Harvest rates of rheophilic fish *Vimba vimba, Chondrostoma nasus*, and *Barbus barbus* have a strong relationship with restocking rates and harvest rates of their predator *Silurus glanis* in lowland mesotrophic rivers in Central Eu. *Sustainability* 13, 11379. doi:10.3390/SU132011379

MacDougall, A. S., and Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86, 42–55. doi:10.1890/04-0669

Mader, H., Brandl, A., and Käfer, S. (2020). Design and function monitoring of an Enature® vertical slot fish pass in a large potamal river in carinthia/Austria. *Water* 12, 551. doi:10.3390/W12020551

Maimela, L. T., Chimimba, C. T., and Zengeya, T. A. (2022). Niche expansion by indigenous fish species following the introduction of rainbow trout (*Oncorhynchus mykiss*) in a subtropical river system, upper Blyde River, South Africa. *Front. Environ. Sci.* 0, 1667. doi:10.3389/FENVS.2022.949353

Martinez, P. J., Chart, T. E., Trammell, M. A., Wullschleger, J. G., and Bergersen, E. P. (1994). Fish species composition before and after construction of a main stem reservoir on the White River, Colorado. *Environ. Biol. Fishes* 40, 227–239. doi:10.1007/BF00002509

Matthews, W. J., and Marsh-Matthews, E. (2011). Extirpation of red shiner in direct tributaries of Lake Texoma (Oklahoma-Texas): A cautionary case history from a fragmented river-reservoir system. *Trans. Am. Fish. Soc.* 136, 1041–1062. doi:10.1577/T06-059.1

McLaughlin, R. L., Hallett, A., Pratt, T. C., O'Connor, L. M., and Gordon McDonald, D. (2007). Research to guide use of barriers, traps, and fishways to control sea lamprey. *J. Gt. Lakes. Res.* 33, 7–19. doi:10.3394/0380-1330(2007)33[7:rtguob]2.0.co;2

Mehner, T., Ihlau, J., Dörner, H., and Hölker, F. (2005). Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes? *Limnol. Oceanogr.* 50, 2022–2031. doi:10.4319/LO.2005.50.6.2022

Miehls, S. M., Johnson, N. S., and Hrodey, P. J. (2017). Test of a nonphysical barrier consisting of light, sound, and bubble screen to block upstream movement of sea lampreys in an experimental raceway. *North Am. J. Fish. Manag.* 37, 660–666. doi:10.1080/02755947.2017.1308892

Miehls, S., Sullivan, P., Twohey, M., Barber, J., and McDonald, R. (2020). The future of barriers and trapping methods in the sea lamprey (*Petromyzon marinus*) control program in the Laurentian Great Lakes. *Rev. Fish. Biol. Fish.* 30, 1–24. doi:10.1007/s11160-019-09587-7

Modesto, V., Ilarri, M., Souza, A. T., Lopes-Lima, M., Douda, K., Clavero, M., et al. (2018). Fish and mussels: Importance of fish for freshwater mussel conservation. *Fish. Fish.* 19, 244–259. doi:10.1111/FAF.12252

Moraes, K., Souza, A. T., Vašek, M., Bartoň, D., Blabolil, P., Čech, M., et al. (2021). Openness of fish habitat matters: Lake pelagic fish community starts very close to the shore. *Water* 13, 3291. doi:10.3390/W13223291

Näslund, I., Degerman, E., and Nordwall, F. (1998). Brown trout (*Salmo trutta*) habitat use and life history in Swedish streams: Possible effects of biotic interactions. *Can. J. Fish. Aquat. Sci.* 55, 1034–1042. doi:10.1139/F97-313

Nilsson, C., Reidy, C. A., Dynesius, M., and Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science* 308, 405–408. doi:10.1126/science.1107887

Nobile, A. B., Lima, F. P., Freitas-Souza, D., Queiroz, J., Garcia, D. A. Z., Orsi, M. L., et al. (2018). Distribution of non-native suckermouth armoured catfish Pterygoplichthys ambrosettii in the upper Paraná River basin, Brazil. *J. Fish. Biol.* 92, 1198–1206. doi:10.1111/jfb.13561

Northcote, T. G. (1984). "Mechanisms of fish migration in rivers," in *Mechanisms of migration in fishes*. Editors J. McCleave, J. Dodson, and W. Neill (New York, NY, USA: Plenum), 317–355. doi:10.1007/978-1-4613-2763-9_20

Novinger, D. C., and Rahel, F. J. (2003). Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conserv. Biol.* 17, 772–781. doi:10.1046/J.1523-1739.2003.00472.X

Olden, J. D., Poff, N. L. R., Douglas, M. R., Douglas, M. E., and Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19, 18–24. doi:10.1016/j.tree.2003.09.010

Olden, J. D., and Rooney, T. P. (2006). On defining and quantifying biotic homogenization. *Glob. Ecol. Biogeogr.* 15, 113–120. doi:10.1111/J.1466-822X.2006.00214.X

Olsson, I. C., Greenberg, L. A., and Eklöv, A. G. (2001). Effect of an artificial pond on migrating Brown trout smolts. *North Am. J. Fish. Manag.* 21, 498–506. doi:10.1577/1548-8675(2001)021<0498:eoaapo>2.0.co;2

Parker, A. D., Glover, D. C., Finney, S. T., Rogers, P. B., Stewart, J. G., and Simmonds, R. L. (2015). Direct observations of fish incapacitation rates at a large electrical fish barrier in the Chicago Sanitary and Ship Canal. *J. Gt. Lakes. Res.* 41, 396–404. doi:10.1016/J.JGLR.2015.03.004

Parker, A. D., Glover, D. C., Finney, S. T., Rogers, P. B., Stewart, J. G., and Simmonds, R. L. (2016). Fish distribution, abundance, and behavioral interactions within a large electric dispersal barrier designed to prevent Asian carp movement. *Can. J. Fish. Aquat. Sci.* 73, 1060–1071. doi:10.1139/CJFAS-2015-0309/SUPPL_FILE/CJFAS-2015-0309SUPPL.DOCX

Patoka, J., Bláha, M., Kalous, L., and Kouba, A. (2017). Irresponsible vendors: Non-native, invasive and threatened animals offered for garden pond stocking. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 27, 692–697. doi:10.1002/AQC.2719

Pelicice, F. M., Latini, J. D., and Agostinho, A. A. (2015). Fish fauna disassembly after the introduction of a voracious predator: Main drivers and the role of the invader's demography. *Hydrobiologia* 746, 271–283. doi:10.1007/s10750-014-1911-8

Peňáz, M., Kubícek, F., Marvan, P., and Zelinka, M. (1968). Influence of the Vir river valley reservoir on the hydrobiological and ichthyological conditions in the river Svratka. *Acta Sci. Nat. Acad. Bohemoslov.* 2, 1–60.

Perkin, J. S., Gido, K. B., Cooper, A. R., Turner, T. F., Osborne, M. J., Johnson, E. R., et al. (2015). Fragmentation and dewatering transform Great Plains stream fish communities. *Ecol. Monogr.* 85, 73–92. doi:10.1890/14-0121.1

Perkin, J. S., and Gido, K. B. (2011). Stream fragmentation thresholds for a reproductive guild of Great Plains fishes. *Fisheries* 36, 371–383. doi:10.1080/03632415.2011.597666

Persson, L. (1997). Competition, predation and environmental factors as structuring forces in freshwater fish communities: Sumari (1971) revisited. *Can. J. Fish. Aquat. Sci.* 54, 85–88. doi:10.1139/f96-250

Pfauserová, N., Brabec, M., Slavík, O., Horký, P., Žlábek, V., and Hladík, M. (2022). Effects of physical parameters on fish migration between a reservoir and its tributaries. *Sci. Rep.* 12, 8612. doi:10.1038/s41598-022-12231-3

Pfauserová, N., Slavík, O., Horký, P., Kolářová, J., and Randák, T. (2019). Migration of non-native predator asp (*Leuciscus aspius*) from a reservoir poses a potential threat to native species in tributaries. *Water* 11, 1306. doi:10.3390/w11061306

Pfauserová, N., Slavík, O., Horký, P., Turek, J., and Randák, T. (2021). Spatial distribution of native fish species in tributaries is altered by the dispersal of non-native species from reservoirs. *Sci. Total Environ.* 755, 143108. doi:10.1016/j.scitotenv.2020.143108

Poff, N. L. R., Olden, J. D., Merritt, D. M., and Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proc. Natl. Acad. Sci. U. S. A.* 104, 5732–5737. doi:10.1073/pnas.0609812104

Preece, R. M., and Jones, H. A. (2002). The effect of keepit dam on the temperature regime of the namoi river, Australia. *River Res. Appl.* 18, 397–414. doi:10.1002/RRA.686

Pringle, C. M., Freeman, M. C., and Freeman, B. J. (2000). Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical-temperate comparisons. *Bioscience* 50, 807–823. doi:10.1641/0006-3568(2000)050[0807:reohao]2.0.co;2

Quintana, X. D., Arim, M., Badosa, A., María Blanco, J., Boix, D., Brucet, S., et al. (2015). Predation and competition effects on the size diversity of aquatic communities. *Aquat. Sci.* 77, 45–57. doi:10.1007/s00027-014-0368-1

Quist, M. C., Hubert, A. H., and Rahel, F. J. (2005). Fish assemblage structure following impoundment of a Great plains river | request PDF. *West. North Am. Nat.* 65, 53–63. Available at: https://www.researchgate.net/publication/286959005_Fish_assemblage_structure_following_Impoundment_of_a_Great_Plains_river (Accessed June 9, 2022).

Rahel, F. J. (2007). Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshw. Biol.* 52, 696–710. doi:10.1111/J.1365-2427.2006.01708.X

Rahel, F. J. (2013). Intentional fragmentation as a management strategy in aquatic systems. *Bioscience* 63, 362–372. doi:10.1525/BIO.2013.63.5.9

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., et al. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* 94, 849–873. doi:10.1111/brv.12480

Říha, M., Hladík, M., Mrkvička, T., Prchalová, M., Čech, M., Drastik, V., et al. (2013). Post-spawning dispersal of tributary spawning fish species to a reservoir system. *Folia Zool.* 62, 1–13. doi:10.25225/fozo.v62.i1.a1.2013

Říha, M., Kubečka, J., Vašek, M., Seďa, J., Mrkvička, T., Prchalová, M., et al. (2009). Long-term development of fish populations in the Římov Reservoir. *Fish. Manag. Ecol.* 16, 121–129. doi:10.1111/j.1365-2400.2008.00650.x

Roscoe, D. W., and Hinch, S. G. (2010). Effectiveness monitoring of fish passage facilities: Historical trends, geographic patterns and future directions. *Fish. Fish.* 11, 12–33. doi:10.1111/j.1467-2979.2009.00333.x

Sabatini, A., Podda, C., Frau, G., Cani, M. V., Musu, A., Serra, M., et al. (2018). Restoration of native Mediterranean Brown trout *Salmo cettii* Rafinesque, 1810 (Actinopterygii: Salmonidae) populations using an electric barrier as a mitigation tool. *Eur. Zool. J.* 85, 137–149. doi:10.1080/24750263.2018.1453554

Sandlund, O. T., Museth, J., and Øistad, S. (2016). Migration, growth patterns, and diet of pike (*Esox lucius*) in a river reservoir and its inflowing river. *Fish. Res.* 173, 53–60. doi:10.1016/J.FISHRES.2015.08.010

Schaeffer, J. S., and Margraf, F. J. (1987). Predation on fish eggs by white perch, *Morone americana*, in Western Lake Erie. *Environ. Biol. Fishes* 18, 77–80. doi:10.1007/bf00002331

Schiemer, F., and Waidbacher, H. (1992). "Strategies for conservation of a Danubian fish fauna," in *River conservation and management*. Editors P. J. Boon, P. Calow, and G. J. Petts (New York: John Wiley and Sons), 363–382.

Schleuter, D., and Eckmann, R. (2008). Generalist versus specialist: The performances of perch and ruffe in a lake of low productivity. *Ecol. Freshw. Fish.* 17, 86–99. doi:10.1111/J.1600-0633.2007.00262.X

Schneider, E. V. C., Hasler, C. T., and Suski, C. D. (2018). Fish behavior in elevated co2: Implications for a movement barrier in flowing water. *Biol. Invasions* 20, 1899–1911. doi:10.1007/s10530-018-1669-4

Seďa, J., and Kubečka, J. (1997). Long-term biomanipulation of rímov reservoir (Czech republic). *Hydrobiologia* 345, 95–108. doi:10.1023/A:1002911103252

Sepulveda, A. J., Rutz, D. S., Ivey, S. S., Dunker, K. J., and Gross, J. A. (2013). Introduced northern pike predation on salmonids in southcentral Alaska. *Ecol. Freshw. Fish.* 22, 268–279. doi:10.1111/eff.12024

Shelton, J. M., Samways, M. J., and Day, J. A. (2015). Predatory impact of non-native rainbow trout on endemic fish populations in headwater streams in the Cape Floristic Region of South Africa. *Biol. Invasions* 17, 365–379. doi:10.1007/s10530-014-0735-9

Silbernagel, J. J., and Sorensen, P. W. (2013). Direct field and laboratory evidence that a combination of egg and larval predation controls recruitment of invasive common carp in many lakes of the upper Mississippi River basin. *Trans. Am. Fish. Soc.* 142, 1134–1140. doi:10.1080/00028487.2013.788889

Silva, G. G., Weber, V., Green, A. J., Hoffmann, P., Silva, V. S., Volcan, M. V., et al. (2019). Killifish eggs can disperse via gut passage through waterfowl. *Ecology* 100, e02774. doi:10.1002/ECY.2774

Silva-Sene, A. M., Loures, R. C., de Andrade Neto, F. R., and Pompeu, P. S. (2022). Fish assemblage distribution along free-flowing rivers entering a reservoir cascade. *Environ. Biol. Fishes* 105, 1535–1547. doi:10.1007/s10641-022-01345-2

Simberloff, D. (2013). *Invasive species: What everyone needs to know*. 1st ed. New York: Oxford University Press.

Skov, C., Baktoft, H., Brodersen, J., Brönmark, C., Chapman, B. B., Hansson, L.-A., et al. (2011). Sizing up your enemy: Individual predation vulnerability predicts migratory probability. *Proc. Biol. Sci.* 278, 1414–1418. doi:10.1098/rspb.2010.2035

Skov, C., Brodersen, J., Nilsson, P. A., Hansson, L. A., and Brönmark, C. (2008). Inter- and size-specific patterns of fish seasonal migration between a shallow lake and its streams. *Ecol. Freshw. Fish.* 17, 406–415. doi:10.1111/j.1600-0633.2008.00291.x

Slavík, O., Horký, P., and Bartoš, L. (2009). Occurrence of cyprinids in fish ladders in relation to flow. *Biol. Bratisl.* 64, 999–1004. doi:10.2478/s11756-009-0157-9

Šmejkal, M., Baran, R., Blabolil, P., Vejřík, L., Prchalová, M., Bartoň, D., et al. (2017). Early life-history predator-prey reversal in two cyprinid fishes. *Sci. Rep.* 7, 6924. doi:10.1038/s41598-017-07339-w

Šmejkal, M., Bartoň, D., Brabec, M., Sajdlová, Z., Souza, A. T., Moraes, K. R., et al. (2021). Climbing up the ladder: Male reproductive behaviour changes with age in a long-lived fish. *Behav. Ecol. Sociobiol.* 75, 22–13. doi:10.1007/s00265-020-02961-7

Šmejkal, M., Ricard, D., Prchalová, M., Říha, M., Muška, M., Blabolil, P., et al. (2015). Biomass and abundance biases in European standard gillnet sampling. *PLoS One* 10, e0122437. doi:10.1371/journal.pone.0122437

Šmejkal, M., Souza, A. T., Blabolil, P., Bartoň, D., Sajdlová, Z., Vejřík, L., et al. (2018). Nocturnal spawning as a way to avoid egg exposure to diurnal predators. *Sci. Rep.* 8, 15377. doi:10.1038/s41598-018-33615-4

Sparks, R. E., Barkley, T. L., Creque, S. M., Dettmers, J. M., and Stainbrook, K. M. (2010). Evaluation of an electric fish dispersal barrier in the Chicago Sanitary and ship canal. *Am. Fish. Soc. Symp.* 74, 139–161.

Specziár, A., and Rezsu, E. T. (2009). Feeding guilds and food resource partitioning in a lake fish assemblage: An ontogenetic approach. *J. Fish. Biol.* 75, 247–267. doi:10.1111/j.1095-8649.2009.02283.x

Stamplecoskie, K. M., Thomas, R. B., Lower, N., Cottenie, K., Mc Laughlin, R. L., and Mc Donald, D. G. (2012). Response of migratory sea lampreys to artificial lighting in portable traps. *North Am. J. Fish. Manag.* 32, 563–572. doi:10.1080/02755947.2012.675963

Sugunan, V. V. (1995). *Reservoir fisheries of India*. Rome: FAO, 423. FAO Fisheries Technical Paper. No. 345.

Sun, J., Tummers, J. S., Galib, S. M., and Lucas, M. C. (2022). Fish community and abundance response to improved connectivity and more natural hydromorphology in a post-industrial subcatchment. *Sci. Total Environ.* 802, 149720. doi:10.1016/J.SCITOTENV.2021.149720

Suski, C. D. (2020). Development of carbon dioxide barriers to deter invasive fishes: Insights and lessons learned from bigheaded carp. *Fishes* 5, 25. doi:10.3390/FISHES5030025

Tamario, C., Degerman, E., Polic, D., Tibblin, P., and Forsman, A. (2021). Size, connectivity and edge effects of stream habitats explain spatio-temporal variation in Brown trout (*Salmo trutta*) density. *Proc. R. Soc. B* 288, 20211255. doi:10.1098/RSPB.2021.1255

Tamario, C., Sunde, J., Petersson, E., Tibblin, P., and Forsman, A. (2019). Ecological and evolutionary consequences of environmental change and management actions for migrating fish. *Front. Ecol. Evol.* 7. doi:10.3389/fevo.2019.00271

Tapkir, S., Boukal, D., Kalous, L., Bartoň, D., Souza, A. T., Kolar, V., et al. (2022). Invasive gibel carp (*Carassius gibelio*) outperforms threatened native crucian carp (*Carassius carassius*) in growth rate and effectiveness of resource use: Field and experimental evidence. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 32, 1901–1912. doi:10.1002/aqc.3894

Taylor, M. K., and Cooke, S. J. (2012). Meta-analyses of the effects of river flow on fish movement and activity. *Environ. Rev.* 20, 211–219. doi:10.1139/A2012-009/SUPPL_FILE/A2012-009SUPPL.DOCX

Taylor, R. M., Pegg, M. A., and Chick, J. H. (2005). Response of bighead carp to a bioacoustic behavioural fish guidance system. *Fish. Manag. Ecol.* 12, 283–286. doi:10.1111/j.1365-2400.2005.00446.x

Temming, A., Floeter, J., and Ehrich, S. (2007). Predation hot spots: Large scale impact of local aggregations. *Ecosystems* 10, 865–876. doi:10.1007/s10021-007-9066-3

Thompson, P. D., and Rahel, F. J. (1998). Evaluation of artificial barriers in Small Rocky Mountain streams for preventing the upstream movement of brook trout. *North Am. J. Fish. Manag.* 18, 206–210. doi:10.1577/1548-8675(1998)018<0206:EOABIS>2.0.CO;2

Tonitto, C., and Riha, S. J. (2016). Planning and implementing small dam removals: Lessons learned from dam removals across the eastern United States. *Sustain. Water Resour. Manag.* 2, 489–507. doi:10.1007/s40899-016-0062-7

Troia, M. J., and Gido, K. B. (2014). Towards a mechanistic understanding of fish species niche divergence along a river continuum. *Ecosphere* 5, art41–18. doi:10.1890/ES13-00399.1

Turgeon, K., Turpin, C., and Gregory-Eaves, I. (2019). Dams have varying impacts on fish communities across latitudes: A quantitative synthesis. *Ecol. Lett.* 22, 1501–1516. doi:10.1111/ELE.13283

Van Den Berg, C., Van Snik, G. J. M., Van Den Boogaart, J. G. M., Sibbing, F. A., and Osse, J. W. M. (1994). Comparative microanatomy of the branchial sieve in three sympatric cyprinid species, related to filter-feeding mechanisms. *J. Morphol.* 219, 73–87. doi:10.1002/JMOR.1052190109

Van Looy, K., Tormos, T., and Souchon, Y. (2014). Disentangling dam impacts in river networks. *Ecol. Indic.* 37, 10–20. doi:10.1016/J.ECOLIND.2013.10.006

Vannote, R. L., Wayne Minshall, G., Cummins, K. W., Seddel, J. R., and Cushing, C. E. (1980). The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37, 130–137. doi:10.1139/f80-017

Vašek, M., Jarolím, O., Čech, M., Kubečka, J., Peterka, J., and Prchalová, M. (2008). The use of pelagic habitat by cyprinids in a deep riverine impoundment: Římov Reservoir, Czech Republic. *Folia Zool.* 57, 324–336.

Vehanen, T., Mäki-Petäys, A., Aspi, J., and Muotka, T. (1999). Intercohort competition causes spatial segregation in Brown trout in artificial streams. *J. Fish. Biol.* 55, 35–46. doi:10.1111/j.1095-8649.1999.tb00654.x

Vetter, B. J., Cupp, A. R., Fredricks, K. T., Gaikowski, M. P., and Mensinger, A. F. (2015). Acoustical deterrence of silver carp (*Hypophthalmichthys molitrix*). *Biol. Invasions* 17, 3383–3392. doi:10.1007/s10530-015-0964-6

Victor, R., and Tetteh, J. O. (1988). Fish communities of a perturbed stream in Southern Nigeria. *J. Trop. Ecol.* 4, 49–59. doi:10.1017/S0266467400002492

Volta, P., Jeppesen, E., Leoni, B., Campi, B., Sala, P., Garibaldi, L., et al. (2013). Recent invasion by a non-native cyprinid (common bream *Abramis brama*) is followed by major changes in the ecological quality of a shallow lake in southern Europe. *Biol. Invasions* 15, 2065–2079. doi:10.1007/s10530-013-0433-z

Wagner, C. M., Stroud, E. M., and Meckley, T. D. (2011). A deathly odor suggests a new sustainable tool for controlling a costly invasive species. *Can. J. Fish. Aquat. Sci.* 68, 1157–1160. doi:10.1139/F2011-072/ASSET/IMAGES/LARGE/F2011-072F2.JPEG

Wang, L., Infante, D., Lyons, J., Stewart, J., and Cooper, A. (2011). Effects of dams in river networks on fish assemblages in non-impoundment sections of rivers in Michigan and Wisconsin, USA. *River Res. Appl.* 27, 473–487. doi:10.1002/RRA.1356

Ward, J. V., and Stanford, J. A. (1995). Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regul. Rivers Res. Manag.* 11, 105–119. doi:10.1002/rrr.3450110109

Weyl, O. L. F., Daga, V. S., Ellender, B. R., and Vitule, J. R. S. (2016). A review of *Clarias gariepinus* invasions in Brazil and South Africa. *J. Fish. Biol.* 89, 386–402. doi:10.1111/JFB.12958

Weyl, O. L. F., Finlayson, B., Impson, N. D., Woodford, D. J., and Steinkjer, J. (2014). Threatened endemic fishes in SouthSouth Africa's cape floristic region: A new beginning for the rondegat river. *Fisheries* 39, 270–279. doi:10.1080/03632415.2014.914924

Wiegleb, J., Hirsch, P. E., Seidel, F., Rauter, G., and Burkhardt-Holm, P. (2021). Flow, force, behaviour: Assessment of a prototype hydraulic barrier for invasive fish. *Hydrobiologia* 849, 1001–1019. doi:10.1007/s10750-021-04762-z

Winemiller, K. O., and Kelso-Winemiller, L. C. (1994). Comparative ecology of the African pike, Hepsetus odoe, and tigerfish, Hydrocynus forskahlii, in the Zambezi River floodplain. *J. Fish. Biol.* 45, 211–225. doi:10.1111/J.1095-8649.1994.TB01301.X

Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., et al. (2016). Balancing hydropower and biodiversity in the amazon, Congo, and mekong. *Science* 351, 128–129. doi:10.1126/SCIENCE.AAC7082/SUPPL_FILE/WINMEILLER-SM.PDF

Žák, J., Prchalová, M., Šmejkal, M., Blabolil, P., Vašek, M., Matěna, J., et al. (2020). Sexual segregation in European cyprinids: Consequence of response to predation risk influenced by sexual size dimorphism. *Hydrobiologia* 847, 1439–1451. doi:10.1007/s10750-020-04198-x

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., and Tockner, K. (2015). A global boom in hydropower dam construction. *Aquat. Sci.* 77, 161–170. doi:10.1007/s00027-014-0377-0

Zhang, C., Ding, L., Ding, C., Chen, L., Sun, J., and Jiang, X. (2018). Responses of species and phylogenetic diversity of fish communities in the Lancang River to hydropower development and exotic invasions. *Ecol. Indic.* 90, 261–279. doi:10.1016/J.ECOLIND.2018.03.004

Zielinski, D. P., Hondzo, M., and Voller, V. R. (2014). Mathematical evaluation of behavioral deterrent systems to disrupt fish movement. *Ecol. Modell.* 272, 150–159. doi:10.1016/J.ECOLMODEL.2013.10.009

Zielinski, D. P., and Sorensen, P. W. (2016). Bubble curtain deflection screen diverts the movement of both Asian and common carp. *North Am. J. Fish. Manag.* 36, 267–276. doi:10.1080/02755947.2015.1120834

Zielinski, D. P., and Sorensen, P. W. (2015). Field test of a bubble curtain deterrent system for common carp. *Fish. Manag. Ecol.* 22, 181–184. doi:10.1111/FME.12108

Glossary

Anadromous species fish species spending part of their life cycles in marine environments and reproducing in freshwater

Edge effects interactions among modified and natural environments on their neighboring edges through changes in biotic and abiotic conditions

Generalist species species that can utilize a wide range of ecological conditions and various food sources

Lentic environment a body of standing water

Lotic environment fluvial freshwater environments such as streams and rivers

Potamodromous species fish species spending their whole life cycle in freshwater and typically undergoing only short-distance migration

Rheophilic species fish species that are specialized to live in fast flowing streams and rivers at least for some of their life cycles

River continuum concept continuously integrating series of abiotic and biotic parameters from river spring to its estuary

Curriculum Vitae

Daniel Bartoň

Date and place of birth: 29. 4. 1992, Dačice, Czechoslovakia
Adress: V Oblouku 2215/12, 37004, České Budějovice 3
tel.: +420 775 856 730
E-mail: daniel.barton@hbu.cas.cz
Author identification: WOS - AAD-2407-2021, ORCID - 0000-0001-8042-4564, researchgate.net/profile/Daniel-Barton-2
H-Index: 9, Sum of Times Cited WOS: 159

Education
2018-2024 Ph.D. study, University of South Bohemia, Faculty of Science, České Budějovice - Hydrobiology
2015-2018 MSc. study, University of South Bohemia, Faculty of Science, České Budějovice – Zoology of vertebrate animals
2011-2015 BSc. study, University of South Bohemia, Faculty of Science, České Budějovice - Biology

Working experience
Since 2018 – part-time job as a student assistant worker at the Institute of Hydrobiology, Academy of Sciences of the Czech Republic, České Budějovice

Participation on projects
The enhancement of rheophilous fish reproduction in the artificial river environment (No. TJ02000012)
Aquaculture of rheophilous fish” (No. QK1920326)

Study stay
2022 – Chair of Aquatic Systems Biology, TUM School of Life Sciences, Technical University of Munich in Freising, Germany

Research papers not included in the dissertation:

Šmejkal, M., **Bartoň, D**. et al. Diverse environmental cues drive the size of reproductive aggregation in a rheophilic fish. Movement Ecology 11, 16 (2023). https://doi.org/10.1186/s40462-023-00379-0
Tapkir, S., **Bartoň, D**. et al. (2022). Invasive gibel carp (*Carassius gibelio*) outperforms threatened native crucian carp (*Carassius carassius*) in growth rate and effectiveness of resource use: Field and experimental evidence. Aquatic Conservation: Marine and Freshwater Ecosystems, 32(12), 1901–1912. https://doi.org/10.1002/aqc.3894
Šmejkal M., **Bartoň D**. et al. (2021). Climbing up the ladder: male reproductive behaviour changes with age in a long-lived fish. Behavioral Ecology and Sociobiology 75: 22. DOI: 10.1007/s00265-020-02961-7
Šmejkal M., **Bartoň D**. et al. (2020). Negative feedback concept in tagging: ghost tags imperil the long-term monitoring of fishes. PlosONE 15(3): e0229350. DOI: 10.1371/journal.pone.0229350
Blabolil P., **Bartoň D**. et al. (2020) The fate of 0+ asp (*Leuciscus aspius*) after being stocked in a reservoir. Biologia 75 : 989-996. DOI: doi.org/10.2478/s11756-019-00355-3
Šmejkal M., **Bartoň D**. et al. (2019) Sex-specific probability of PIT tag retention in a cyprinid fish. Fisheries Research 219: 105325. DOI: 10.1016/j.fishres.2019.105325
Vejřík L., **Bartoň D**. et al. (2019) The pros and cons of the invasive freshwater apex predator, European catfish *Silurus glanis*, and powerful angling technique for its population control. Journal of Environmental Management 241 : 374-382. DOI: 10.1016/j.jenvman.2019.04.005
Weber L., **Bartoň D**. et al. (2019) Testing the applicability of tagging the Great crested newt (*Triturus cristatus*) using passive integrated transponders. PLoS ONE 14 (7) : e0219069. DOI: 10.1371/journal.pone.0219069
Šmejkal M., **Bartoň D**. et al. (2017) Early life-history predator-prey reversal in two cyprinid fishes. Scientific Reports 7: 6924. DOI: 10.1038/s41598-017-07339-w

and 13 more research papers published in academic journals.