TECHNISCHE UNIVERSITÄT MÜNCHEN

TUM SCHOOL OF LIFE SCIENCES

Integrative assessment of the effects of hydropower use and agricultural land use on stream ecosystems

Josef Michael Georg Knott

Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften

(Dr. rer. nat.)

genehmigten Dissertation.

Vorsitzende/-r:	Prof. Dr. Johannes Kollmann
Prüfende/-r der Dissertation:	1. Prof. Dr. Jürgen Geist
	2. Prof. Dr. Ralph Kühn
	3. Prof. Dr. Stefan Schmutz

Die Dissertation wurde am 10.11.2021 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 29.03.2022 angenommen.

Contents

List of Figures

List of Tables

Preface

This dissertation aims to assess the impacts of two main anthropogenic stressors, hydropower use and agricultural land use, on stream ecosystems using a holistic approach that considers longitudinal, lateral, vertical and temporal relationships. First, an overview of the different stressors and current main threats to freshwater biodiversity is given. Subsequently, frequently applied instream- and catchment-related measures are presented to counteract the proceeding decline in aquatic biodiversity, and potential shortcomings associated with the implementation of mitigation and restoration measures are identified. After a brief overview of the study sites and applied methods in Chapter 2, the results of four scientific case studies are presented in the following chapters.

In order to assess the effects of hydropower plants on aquatic biodiversity and fish health in lotic ecosystems, it is essential to provide precise knowledge of the fish species inventory occurring in the respective river stretch and its downstream movement behaviour. Therefore, in a first step, four rivers in the Danube and Main catchment areas were investigated to identify which fish species occur in the immediate headwaters of the respective hydropower plants and how they differ in their diurnal and seasonal downstream movement behaviour (Chapter 3).

Next, the acceptance of different opening sizes of a surface bypass at an innovative moveable hydropower plant as well as the injuries which fish experience during the passage were examined (Chapter 4). The results were then used to derive management recommendations for a more "fish-friendly" operation of the hydropower plants as well as to identify possibilities for improvements in order to guide fish safe and more efficiently into the tailrace via alternative bypasses.

Expanding the view from the stream to its catchment, Chapter 5 examined how the type of agricultural land use in the catchment area and various implemented erosion protection measures to reduce the fine sediment input into the main stream and its tributaries affect the biotic community composition of fishes, macroinvertebrates and periphyton as well as physical and chemical instream parameters.

Finally, the potential of restoration in heavily modified stream systems was investigated. The effectiveness of an engineered spawning ground in the tailrace of a hydropower plant was assessed, which was built to compensate for a spawning ground lost due to the construction of the power plant. Over a period of six weeks, it was investigated whether this engineered spawning ground was used by rheophilic target fish species for spawning and whether fish larvae developed successfully (Chapter 6).

The final general discussion in Chapter 7 highlights the importance of a comprehensive understanding of functional processes as a basis for selecting appropriate mitigation and restoration measures and discusses adequate measures to counteract the negative impacts of hydropower use and fine sediment pollution on stream ecosystems.

The thesis at hand presents a set of different methods that can be used to record and analyse the described effects of the aforementioned stressors on multiple dimensions in stream ecosystems in a standardized way. From the obtained results, mitigation and restoration strategies could be derived on how to reduce the fine sediment load through erosion protection measures in the catchment area, how to improve fish protection at hydropower plants and the downstream passage of fish, and how to maintain the functionality of engineered spawning grounds as key habitat for target fish species of conservation in the long term.

Summary

Lotic ecosystems are currently among the most threatened ecosystems in the world. A steadily growing population and its rising demand for water, food and energy are leading to an ever increasing pressure on rivers. In addition to anthropogenic instream interferences, such as dam and hydropower plant constructions, land use changes and intensification as well as advancing climate change are also leading to a rapidly proceeding decline in aquatic biodiversity. In order to counteract this development through appropriate mitigation and restoration measures, it is necessary to close existing knowledge gaps and gain a better understanding of the functional processes in stream ecosystems. The core objective of this thesis was to investigate the effects of the anthropogenic stressors hydropower use and agricultural land use on stream ecosystems. For this purpose, an integrative assessment approach was applied, which considered the dynamic and hierarchical structure of rivers at different spatial and temporal scales. These included longitudinal interactions in the aquatic community composition and of abiotic parameters, lateral interactions between river and catchment, vertical interactions between open water, river bed and interstitial zone as well as the temporal dimension on different scales (e.g. days, weeks, months, years).

The longitudinal downstream movement behaviour of wild fish caught with stow-nets during the passage of four hydropower plants was investigated and compared with the resident fish community caught in the power plants headwaters by electrofishing (Chapter 3). The recorded 15,825 individuals of 40 fish species provided new insights into species-specific seasonal and diurnal movement patterns of hitherto scarcely studied species as well as into the species and size composition of the resident and the downstream moving fish community. The finding that many species preferred to move downstream during night in autumn can be used to operate hydropower plants in the most “fish-friendly” way possible, for example by temporarily shutting down turbines during the main migration periods, opening additional alternative corridors and/or increasing the bypass discharge.

However, hydropower plants not only disrupt fish migrations, but can also cause serious injuries or death when fish are passing these facilities. Besides turbine passage, the passage of alternative corridors can also cause injuries. In Chapter 4, a surface bypass of a movable hydropower plant was used to investigate the passage efficiency of this corridor compared to the turbine corridor and whether fish suffer injuries during passage. It was found that although fish suffer only minor injuries during downstream passage, only a small proportion of fish used this alternative corridor. The construction of additional bypasses for near-bottom and mid-water moving fish species, as well as a larger dimensioning of the examined surface bypass, would presumably increase bypass efficiency and thus better protect fish from harmful turbine passage.

The lateral interactions between agricultural land use and fine sediment input, physical and chemical instream parameters and aquatic community composition were investigated in a small river system over a period of two years (Chapter 5). The results indicated that catchment erosion protection measures successfully reduced the immediate fine sediment input resulting in positive effects on interstitial habitat quality and aquatic community composition including fishes, macroinvertebrates and periphyton. Despite the observed improvements through the catchment measures, a combination with additional instream measures, such as natural flow regime restoration, is necessary to further improve the habitat quality for rheophilic species.

The construction and restoration of spawning grounds for target fish species is a commonly applied method to restore degraded or lost habitats. In Chapter 6, the effectiveness of an engineered spawning ground at the turbine outlet of a hydropower plant located in a reservoir was investigated for rheophilic target fish species of conservation concern. For this purpose, physicochemical water parameters were measured and approx. 4,000 fish larvae and 18,000 eggs were recorded using drift nets and surber-sampling over a period of six weeks and genetically identified. Although successful recruitment of rheophilic target fish species has been proven in this heavily modified water body, the long-term functionality of this measure is linked to an adapted reservoir management that takes into account the spawning habitat requirements of the target species with regard to water depth and current velocity at the spawning ground.

The integrative assessment approach applied in this thesis is a valuable tool to record and evaluate the effects of various anthropogenic stressors on stream ecosystems on different temporal and spatial scales. The results could be used to derive practical recommendations for mitigation and restoration measures, how to improve downstream passage and fish protection at hydropower facilities, how to reduce fine sediment input through erosion protection measures in the catchment, and how to maintain the functionality of an engineered spawning ground as key habitat for rheophilic target fish species in the long term. The systematic and reproducible study design can be easily applied to other rivers, thus addressing the frequently criticized lack of harmonization and comparability among scientific studies. A comprehensive understanding of functional processes in stream ecosystems, which takes into account different temporal and spatial scales as well as different biotic and abiotic indicators, is a fundamental prerequisite for choosing appropriate mitigation and restoration measures to protect and enhance aquatic biodiversity.

Zusammenfassung

Fließgewässer-Ökosysteme gehören zu den weltweit am stärksten bedrohten Ökosystemen. Eine stetig wachsende Bevölkerung und ihr steigender Bedarf an Wasser, Nahrung und Energie führen zu einer immer stärkeren Beanspruchung von Fließgewässern. Neben unmittelbaren anthropogenen Eingriffen in Fließgewässer-Ökosysteme, wie z.B. durch den Bau von Dämmen und Wasserkraftanlagen, führen auch die Änderung und Intensivierung der Landnutzung sowie der voranschreitende Klimawandel zu einem zunehmenden Rückgang der aquatischen Biodiversität. Um dieser Entwicklung durch geeignete vorbeugende Maßnahmen und Renaturierungsmaßnahmen entgegenzuwirken, ist es erforderlich, bestehende Wissenslücken zu schließen und ein besseres Verständnis über die funktionalen Prozesse in Fließgewässer-Ökosystemen zu erlangen.

Das Hauptziel der vorliegenden Dissertation war, die Auswirkungen der anthropogenen Stressoren Wasserkraftnutzung und landwirtschaftliche Nutzung auf Fließgewässer-Ökosysteme zu untersuchen. Dazu wurde ein integrativer Bewertungsansatz angewandt, welcher die dynamische und hierarchische Struktur von Fließgewässern auf verschiedenen räumlichen und zeitlichen Ebenen berücksichtigte. Diese Ebenen beinhalteten longitudinale Interaktionen in der Zusammensetzung der aquatischen Lebensgemeinschaft und der Ausprägung abiotischer Parameter, laterale Interaktionen zwischen Fluss und Einzugsgebiet, vertikale Interaktionen zwischen Freiwasser, Gewässerbett und Interstitial sowie die zeitliche Dimension auf verschiedenen Skalen (z.B. Tage, Wochen, Monate, Jahre).

In Kapitel 3 wurde das longitudinale, flussabwärts gerichtete Wanderverhalten von Wildfischen untersucht, die mit Hamennetzen bei der Passage von vier Wasserkraftanlagen gefangen wurden, und mit der ansässigen Fischartenzusammensetzung verglichen, die im Oberwasser der Kraftwerke mittels Elektrobefischung erfasst wurden. Die insgesamt gefangenen 15.825 Individuen von 40 verschiedenen Fischarten lieferten dabei neue Erkenntnisse zu artspezifischen jahres- und tageszeitlichen Verhaltensmustern bisher wenig untersuchter Arten sowie zur Arten- und Größenzusammensetzung der ansässigen und der wandernden Fischartengemeinschaft. Der Befund, dass viele Arten in den untersuchten Flüssen bevorzugt nachts im Herbst wanderten, kann dazu genutzt werden, Wasserkraftanlagen möglichst „fischschonend" zu betreiben, indem beispielsweise Turbinen während der Hauptwanderzeiten zeitweise abgeschaltet, zusätzliche alternative Korridore geöffnet und/oder Bypässe mit mehr Wasser beaufschlagt werden.

Wasserkraftanlagen unterbrechen jedoch nicht nur Fischwanderungen, sondern können auch zu schwerwiegenden Verletzungen oder zum Tod führen, wenn Fische diese Anlagen passieren. Aber nicht nur die Turbinenpassage, sondern auch der Abstieg über alternative Korridore kann Verletzungen verursachen. In Kapitel 4 wurde an einem Oberflächenbypass eines beweglichen Kraftwerks untersucht, wie hoch die Akzeptanz dieses Korridors im Vergleich zum Turbinenkorridor ist und ob Fische bei der Passage Verletzungen erleiden. Dabei wurde festgestellt, dass Fische bei der Passage zwar nur geringe Verletzungen erleiden, aber diesen alternativen Korridor im Vergleich zum Turbinenkorridor nur wenig nutzen. Der Bau zusätzlicher Bypässe für sohlnah und in der Wassermitte wandernde Fischarten sowie eine möglichst große Dimensionierung würde vermutlich die Akzeptanz dieses alternativen Abstiegskorridors deutlich erhöhen und dadurch die Fische besser vor einer schädlichen Turbinenpassage schützen.

In Kapitel 5 wurden in einem kleinen Fließgewässersystem über einen Zeitraum von zwei Jahren die lateralen Interaktionen zwischen landwirtschaftlicher Nutzung und Feinsedimenteintrag, physikalischer und chemischer Gewässerparameter und Artenzusammensetzung der aquatischen Lebensgemeinschaft untersucht. Dabei zeigte sich, dass Erosionsschutzmaßnahmen im Einzugsgebiet nicht nur den unmittelbaren Feinsedimenteintrag reduzierten, sondern sich auch positiv auf die Habitatqualität im Interstitial und die Zusammensetzung der aquatischen Lebensgemeinschaft aus Fischen, Makrozoobenthos und Periphyton auswirkten. Trotz der beobachteten Verbesserungen durch die Maßnahmen im Einzugsgebiet ist eine Kombination mit weiteren Maßnahmen im Fluss, wie die Wiederherstellung des natürlichen Abflussregimes, erforderlich, um die Habitatqualität für spezialisierte rheophile Arten weiter zu verbessern.

Der Bau und die Renaturierung von Laichplätzen für Zielfischarten ist eine häufig angewandte Maßnahme, um degradierte oder verloren gegangene Habitate wiederherzustellen. In Kapitel 6 wurde die Wirksamkeit eines künstlich angelegten Laichplatzes am Turbinenauslauf eines in einem Stausee gelegenen Kraftwerks für rheophile Zielfischarten untersucht. Dazu wurden über einen Zeitraum von sechs Wochen physikalisch-chemische Gewässerparameter gemessen sowie ca. 4.000 Fischlarven und 18.000 Eier mittels Driftnetzen und Surber-Sampling erfasst und genetisch identifiziert. Obwohl eine erfolgreiche Reproduktion von rheophilen Zielfischarten in diesem hochgradig veränderten Wasserkörper nachgewiesen wurde, ist die dauerhafte Funktionalität dieser Maßnahme jedoch an ein angepasstes Stausee-Management gekoppelt, welches die Ansprüche der Zielarten hinsichtlich Wassertiefe und Strömungsgeschwindigkeit auf dem Laichplatz berücksichtigt.

Der in dieser Dissertation angewandte integrative Bewertungsansatz ist ein nützliches Werkzeug, um die Einflüsse verschiedener anthropogener Stressoren auf Fließgewässer-Ökosysteme auf verschiedenen zeitlichen und räumlichen Ebenen zu erfassen und zu bewerten. Aus den Ergebnissen ließen sich konkrete Empfehlungen für vorbeugende Maßnahmen und Renaturierungsmaßnahmen ableiten, wie die flussabwärts gerichtete Passage und der Fischschutz an Wasserkraftanlagen verbessert werden kann, wie sich der Feinsedimenteintrag durch Erosionsschutzmaßnahmen im Einzugsgebiet reduzieren lässt und wie die Funktionalität eines künstlich angelegten Laichplatzes als Schlüsselhabitat für rheophile Zielfischarten langfristig erhalten werden kann. Das systematische und reproduzierbare Untersuchungsdesign kann dabei an weiteren Fließgewässern angewandt werden, wodurch dem häufig angemahnten Mangel an Harmonisierung und Vergleichbarkeit von wissenschaftlichen Studien begegnet werden kann. Dabei ist ein möglichst umfassendes Prozessverständnis, welches sowohl verschiedene zeitliche und räumliche Betrachtungsebenen berücksichtigt als auch verschiedene biotische und abiotische Indikatoren, eine Grundvoraussetzung, um geeignete vorbeugende Maßnahmen und Renaturierungsmaßnahmen zum Schutz und zur Förderung der aquatischen Biodiversität ergreifen zu können.

Acknowledgements

I would not have been able to finish my dissertation without the support of a large number of people and I am grateful to everyone for their individual ways of contributing.

First of all, I would like to express my deepest gratitude to my advisor, Prof. Dr. Jürgen Geist, who encouraged me to persue a PhD, provided always highly valuable scientific input and continuously supported me in every phase of my PhD and my entire time at the Aquatic Systems Biology Unit. His positivity, optimism and dedication to science were always inspiring and motivating, and his confidence in me gave me the support to successfully complete my PhD alongside many other tasks. I am also grateful to Prof. Dr. Ralph Kühn and Prof. Dr. Stefan Schmutz for examining this thesis and to Prof. Dr. Johannes Kollmann for chairing the examination committee.

Furthermore, I would like to express my sincere thanks to Dr. Joachim Pander and Dr. Melanie Müller, who already supervised me during my Master's thesis and have not only been nice colleagues throughout my time at the Aquatic Systems Biology Unit, but have also become good friends. Their manifold support from the beginning of my Master's thesis to the completion of this dissertation deserves special recognition.

During my time at this chair, I have not only met many nice colleagues, but also made good friends with whom I share unforgettable memories. Special thanks go to all my companions during my PhD: Dr. Melanie Müller, Dr. Joachim Pander, Dr. Leonhard Egg, Christoffer Nagel, Nico Geveke, Jörg Steinhilber, Philipp Roschmann, Fabian Gräfe, Florian Parsche, Julia Mayr, Giulia Villa, Carola Suttor, Isabelle Studer, Rebecca Höß, Nicole Smialek, Jason Hartmann, Heiko Höge, Romy Wild, Dr. Katharina Stöckl, Dr. Bernhard Stoeckle, Dr. Sebastian Beggel, Dr. Beate Bierschenk, Christine Seidel, Veronika Schuhmann, Claudia Steinmetz, Silvia Betz and the entire former and current team of the Chair of Aquatic Systems Biology.

Great thanks also go to all the students, interns, assistants and volunteers for their support during the extensive field samplings and laboratory work. Since the first investigations started in 2013, more than 200 people have been involved in the research projects listed below. Their commitment and good teamwork have contributed considerably to the success of this thesis, but naming all of them would go beyond the scope.

This thesis would not have been possible without the funding of the projects "Fischökologisches Monitoring an innovativen Wasserkraftanlagen" by the Bavarian State Ministry of the Environment and Consumer Protection (grant number OelB-0270-45821/2014), "Sedimentmanagement am Mertseebach" by the Water Authority Deggendorf and "Überprüfung der Wirksamkeit des neu angelegten Laichplatzes im Unterwasser der Wasserkraftanlage Eixendorf II" by the Bayerische Landeskraftwerke GmbH (grant number 581 0456).

The funding of these projects made it possible to carry out such extensive research over several years with a large number of involved staff and a high workload. I am very grateful to Birgit Lohmeyer, Dr. Christoph Mayr, Diana Genius, Piet Linde, Dr. Madlen Gerke, Dr. Heidi Kammerlander and Hannah Ingermann from the Bavarian Environment Agency as well as Jochen Zehender from the Bayerische Landeskraftwerke GmbH for the trusting and constructive cooperation. Furthermore, I would like to thank the involved Fisheries Authorities, fisheries rights owners, Rural District Offices, Water Authorities as well as all power plant operators for granting the necessary permits and their support on site.

Special thanks also go to my parents Notburga and Joseph Knott for their emotional and financial support throughout my entire academic career and beyond.

Last but not least, I would like to thank my gorgeous wife Daniela and my three adorable daughters Helena, Marlene and Antonia, the most important people in my life. Their tolerance for my numerous absences over several weeks, especially during field investigations at various hydropower plants, and the mental distraction during the times when I was at home, contributed substantially to being able to complete this thesis.

1 General Introduction

1.1 Stressors and main threats of aquatic biodiversity

Rivers and streams have been extensively used and modified by mankind for thousands of years (Allan & Flecker, 1993; Grill et al., 2019). In addition to sources of food and drinking water, lotic ecosystems are primarily used for energy production, irrigation of agricultural crops and transportation (Grill et al., 2019; Nilsson et al., 2005). This use was increasingly intensified with the beginning of industrialisation at the end of the 18th century, the beginning of the so-called Anthropocene (Crutzen, 2002). Under the pressure of an ever-growing population and its increasing demand for food, water, energy and improved living conditions, substantial land use changes occurred (Crutzen, 2006).

Large-scale deforestation or draining of wetlands converted intact terrestrial ecosystems into cropland and pasture. Consequently, the global share of cropland increased from 2% in AD 1700 to 11% in AD 2000, while the share of pasture land grew from 2% to 24% during this period (Klein Goldewijk et al., 2011). As a result of this development, 55% of the earth's ice-free surface had been converted into agricultural land and settled areas by AD 2000 (Ellis et al., 2010).

Due to the close interconnectedness of lotic ecosystems with their catchment area (Hynes, 1975), such land use changes have also had substantial impacts on the river integrity. For example, the increased susceptibility of agricultural land to erosion and the resulting increased inputs of fine sediment, nutrients and pollutants, as well as wastewater discharges from residential areas have contributed significantly to the increasing threat to stream ecosystems (Bierschenk et al., 2019; Davies et al., 2009; Walsh et al., 2005; Wood & Armitage, 1997).

According to Dudgeon et al. (2006) and Dudgeon (2019), the main threats to global freshwater biodiversity can be grouped into the following interacting categories: flow regulation, land use change, overexploitation, water pollution, invasive species and climate change. The resulting habitat degradation is a main reason for the species decline in freshwater ecosystems (Dudgeon et al., 2006). In order to counteract this ongoing process, the effects of the main threats need to be assessed according to a systematic and evidence-based approach (Geist, 2015; Geist & Hawkins, 2016). Flow regulation by damming, impoundments and hydropower use as well as agricultural land use are identified as main stressors (Bierschenk et al., 2019; Mueller et al., 2020a).

Flow regulation is often considered the most severe and persistent threat to the conservation of lotic ecosystems (Bunn & Arthington, 2002; Dynesius & Nilsson, 1994). The construction of dams, weirs and other transverse structures leads to the fragmentation of rivers, which fundamentally changes the hydromorphological conditions. According to Belletti et al. (2020), there are currently at least 1.2 million instream barriers in 36 European countries, 68% of which are less than two meters in height. Europe is thus the continent with the highest density of instream barriers (0.7 barriers per km). With approx. 2.2 barriers per km (224,658 in total), Germany was found to have the highest density of barriers in Europe after the Netherlands (19.4 barriers per km, 62,610 in total).

Damming increases the water depth in the headwaters and the current speed is significantly reduced or even lentic areas are created with no current at all. In addition to restrictions on the longitudinal transport of sediments, nutrients and organic carbon, this also has serious and long-lasting effects on riverine aquatic organisms (e.g. Dudgeon et al., 2006; Malmqvist & Rundle, 2002; Mueller et al., 2011).

Fish communities are particularly affected by the installation of transverse structures and the use of hydropower. Not only the longitudinal and lateral connectivity and thus the accessibility of different key habitats in the life cycle of fish (e.g. spawning grounds in the upper reaches of the main stream or in tributaries or juvenile habitats in the floodplain) is restricted by transverse structures, but also the availability and quality of these habitats is governed by the interruption of the serial continuity (Ward & Stanford, 1983). The best documented consequences are those for economically important migratory fish species such as salmon or eel. For example, the interruption of the migration routes of the anadromous fish species Chinook salmon and white sturgeon by the construction of four dams on the Lower Snake River, USA, has led to a dramatic population decline of these species (Malmqvist & Rundle, 2002). However, the migration of catadromous fish species, such as eel, can also be impeded and delayed by transverse structures. During downstream migrations, there is a high risk of being injured or killed when entering a turbine at a hydropower facility (Algera et al., 2020; Pracheil et al., 2016; Schilt, 2007). By disrupting migration routes, river fragmentation ultimately leads to a reduction in genetic exchange, suggesting that migration is important for the viability of lotic fish populations in fragmented rivers (Geist, 2011; Malmqvist & Rundle, 2002).

Moreover, the aquatic community composition changes fundamentally in fragmented rivers: The reduced current speed and the higher proportion of fine sediment in dammed sections upstream of transverse structures generally leads to a decline in rheophilic specialists and to the dominance of generalists. These changes in the aquatic community composition can be observed across all taxonomic groups, including fishes, macroinvertebrates and periphyton (Bunn & Arthington, 2002; Mueller et al., 2011).

However, the natural flow regime of rivers is also massively modified by other flow regulation measures such as course straightening, bank reinforcement and canalisation. The resulting restrictions on river dynamic processes often lead to the loss or degradation of habitats, since, for example, sediment relocation processes or natural dead wood dynamics can usually only take place to a very limited extent.

In an era of ongoing urbanisation and substantial land use changes and intensification, rivers as sinks of urban and agricultural land use effluents are particularly affected (Dudgeon et al., 2006; Walsh et al., 2005). The increasing input of fine sediment, nutrients and pollutants (e.g. pesticides, hormones, endocrine disruptors) poses a major threat to freshwater ecosystem health (Bernhardt & Palmer 2007; Bierschenk et al., 2019; Jones et al., 2012; Mueller et al., 2020a).

For instance, a high input of fine sediment can clog the gravel gap system of the stream bed, which impairs the oxygen exchange between the hyporheic interstitial zone and the free flowing water (Geist & Auerswald, 2007; Regh et al., 2005). This can lead to the degradation of spawning grounds and hinder or even prevent egg and larval development of gravel-spawning fish species (Duerregger et al., 2018; Sternecker et al., 2014). However, the hyporheic interstitial zone is also a key habitat for many riverine macroinvertebrates and provides substratum for benthic algae and biofilms (Boulton et al., 1998; Bretschko, 1995; Mueller et al., 2014a; Müllner & Schagerl, 2003). Since high fine sediment loads increase turbidity and thus reduce light penetration, primary productivity is presumably also reduced, which in turn affects the entire food chain in lotic ecosystems (e.g. Henley et al., 2000; Wood & Armitage, 1997).

If habitats have already been degraded by instream stressors, such as flow regulation, they can be further degraded by additional stressors from the catchment, such as high fine sediment input. Therefore, not only the sinks (e.g. hydropower use) but also the sources of the stressors (e.g. agricultural land use) need to be considered. Due to the global increase in these anthropogenic stressors, freshwater ecosystems, which are global hotspots of biodiversity, are now among the most endangered ecosystems throughout the globe (Dudgeon et al., 2006; Dudgeon, 2019). The decline in freshwater biodiversity is far greater than in the most affected terrestrial ecosystems such as tropical rainforests (Reid et al., 2019; Sala et al., 2000). While freshwater ecosystems contain only about 0.01% of the world's water and cover less than 1% of the Earth's surface, they contain about 10% of all known animal species and one-third of all vertebrates (Magurran, 2009; Stendera et al., 2012; Strayer & Dudgeon, 2010).

Meanwhile, more than 60% of freshwater habitats are classified as moderately or severely threatened by human activity (Vörösmarty et al., 2010), which is also reflected in the increasing number of aquatic organisms listed in the IUCN Red List of Threatened Species (IUCN, 2021). According to Su et al. (2021), particularly fish assemblages in temperate regions experienced the greatest biodiversity changes. In Europe, for example, 39% of freshwater fishes are threatened (as of 2011), which is one of the highest threat levels of any major taxonomic group assessed to date for Europe, along with freshwater molluscs (44% of all species are threatened) (Freyhof & Brooks, 2011). However, the number of endangered freshwater fish species in North America has also increased dramatically in recent decades: In 2008, for example, 39% of fish species were endangered, an increase of 92% compared to 1989 (Jelks et al., 2008).

1.2 Applied mitigation and restoration measures

In order to counteract the proceeding decline in aquatic biodiversity, a variety of mitigation and restoration measures have been applied worldwide since decades (Søndergaard & Jeppesen, 2007). These measures aim to improve hydrological, geomorphological and/or ecological processes in lotic ecosystems by applying instream measures as well as measures in the catchment area (Wohl et al., 2005).

Generally applied methods to improve the instream habitat conditions are, for example, additions of woody debris, placement of boulders, gravel introduction, substratum raking (e.g. Mueller et al., 2014a; Roni et al., 2002). These measures aim to increase the structural diversity in rivers and thus create suitable habitats for different groups of aquatic organisms and their different life stages. Also measures such as the removal of bank reinforcements or grade-control structures should enable the river to regain its natural dynamics and thus increase habitat diversity (e.g. Kail et al., 2015; Muhar et al., 2016; Sundermann et al., 2011).

In order to restore the longitudinal river continuity at transverse structures, different types of fish passes for upstream migrating fish have been constructed for decades (e.g. vertical slot fish pass, pool-type fish pass, nature-like fish pass). However, the need for functional bypasses that allow a safe and undelayed downstream passage has long been underestimated (Larinier & Travade, 2002). Downstream moving fish are exposed to a high risk of injury and mortality when passing hydropower turbines (Algera et al., 2020; Pracheil et al., 2016; Schilt, 2007). Various physical (mostly fish protection screens) or behavioural barriers (e.g. electrical, sound, light, bubble screens) are designed to prevent fish from passing through the turbines and to guide them to alternative bypasses (e.g. surface bypass, bottom bypass, spillway). Recently, new types of turbines have been developed that are supposed to be more "fish-friendly" than conventional turbines (Hogan et al., 2014). Generally, no physical or behavioural barriers are installed on these so-called innovative hydropower plants, as fish are supposed to get into the tailrace via the turbines (Anderson et al., 2015). However, in recent years, efforts are increasing to remove unused weirs or no longer profitable hydropower plants in order to restore unimpeded continuity not only for aquatic organisms but also for sediment, dead wood and nutrients (e.g. O'Connor et al., 2015; Foley et al., 2017).

Another important restoration measure is the reconnection of rivers with their floodplain (Auerswald et al., 2019; Opperman et al., 2009). By enabling natural flooding processes, a lateral exchange of nutrients, organic material, sediment and organisms between the river and its floodplain should take place again. However, it is often difficult to restore the connection between river and floodplain in heavily modified water bodies due to various restrictions. Targeted management measures such as artificially induced floodings, which are controlled by humans in terms of frequency, extent and duration, can partly mimic natural flooding processes (Arthington et al., 2006; Davies et al., 2014; Pander et al., 2019).

Yet, degraded rivers that suffer from stressors such as high fine sediment loads cannot be restored in the long term through instream measures alone. Therefore, it is important to understand the underlying processes in the catchment and to identify the source of the stressors (Geist, 2015). In order to reduce the input of fine sediment, nutrients and pollutants into lotic ecosystems from the surrounding landscape, there are a number of different erosion control measures that are applied in the catchment. In addition to establishing riparian buffer strips, measures such as terracing of agricultural land, ploughing and drilling across the slope, cultivation of catch crops, mulch tillage, no-till cultivation and agroforestry are often used (Pimentel et al., 1995; Rickson, 2014). The most effective measures are based on ensuring a protective plant cover for the longest possible period to protect the soil from erosion by reducing water runoff (Pimentel et al., 1995; Zuazo & Pleguezuelo, 2008).

1.3 Potential shortcomings of mitigation and restoration projects

A frequently identified problem in river restoration projects is that there is often no or only insufficient scientific monitoring (Jansson et al., 2007; Roni et al., 2002; Søndergaard & Jeppesen, 2007). For instance, Bernhardt et al. (2005) reported that only 10% of the recorded US river restoration projects were accompanied by a monitoring programme. Although more and more river restoration projects are now evaluated by monitoring, most projects are still unevaluated or the results are rarely published (Rubin et al., 2017).

In addition, the quality and quantity of pre- and post-project monitoring data is often low (Miller et al., 2010). This impedes systematic comparisons on the effectiveness of different measures (Mueller et al., 2014a) and the success of an implemented measure or reasons for its failure often cannot be determined (Bond & Lake, 2003; Lake, 2001).

For some time now, the scientific community has been calling for a systematic and evidence-based assessment approach, rather than the general practice of carrying out restoration based on common sense or personal experience (Geist & Hawkins, 2016; Sutherland et al., 2004). In addition to the definition of clear objectives, this comprises, amongst others, a thorough assessment of the pre- and post-restoration status, the publication of both positive and negative results as well as the inclusion of the gained knowledge in adaptive management (Geist, 2015; Palmer et al., 2014).

1.4 The four-dimensional nature of lotic ecosystems according to Ward (1989)

Natural rivers represent a continuum of biotic and abiotic variables as originally described in the “River Continuum Concept” by Vannote et al. (1980). Ward and Stanford (1983) developed this theoretical concept further in their "Serial Discontinuity Concept" by taking into account that only a few rivers are still free-flowing over their entire course. Many rivers are already regulated by dams, weirs and other obstacles, creating a series of lotic and lentic sections in a river. But rivers are not just a one-dimensional continuum, they are also interconnected with their environment in many ways. Ross (1963) and Hynes (1975) already reported that rivers and their aquatic inhabitants are significantly influenced by the surrounding landscape, their catchment area. Finally, Ward (1989) demands that a holistic view of stream ecosystems requires the identification of basic interactive pathways as well as their hierarchical structure. He proposes a concept according to which rivers can be understood as four-dimensional systems (cf. Figure 1.1):

1) The longitudinal dimension represents the upstream-downstream interactions within a river. This includes, for example, longitudinal fish migrations for spawning, foraging or dispersal, downstream drift and upstream compensatory migrations. The downstream transport of nutrients from the source to the mouth has a decisive influence on the aquatic community composition in lotic ecosystems (Newbold et al., 1982). River

regulation by dams, weirs and other transverse structures is a striking example of anthropogenic disruption of these upstream-downstream interactions (Ward, 1989).

2) The lateral dimension includes interactions between the river and its catchment area/floodplain. Examples include the input of nutrients and organic matter from the catchment after heavy storm water run-offs and flood events, as well as active and passive movements of organisms between the river and its floodplain water bodies.
3) The vertical dimension describes the exchange between the water body, the stream bed and the adjacent groundwater. These vertical interactions affect abiotic parameters as well as the aquatic community. For example, there is a permanent exchange of nutrients and organic matter between surface and groundwater. This transition zone, the hyporheic zone, is also a key habitat for macroinvertebrates and gravel spawning fish for egg and embryonic development.
4) The fourth dimension is the temporal scale. The appropriate temporal scale strongly depends on the study object of interest. For certain questions, such as the investigation of the diurnal hatching behaviour of fish larvae or diurnal patterns in the movement behaviour of fish, a period of a few days to weeks may be sufficient. Longer study periods of a few months to several years are usually necessary to record seasonal effects or to evaluate the success of restoration measures.

According to Ward (1989), this holistic approach can lead to a better understanding of the processes in natural and anthropogenically altered lotic ecosystems. The identification of natural drivers and stressors affecting aquatic biodiversity across different dimensions, scales and organism groups enables the development of adapted restoration concepts or mitigation measures. But also the identification of knowledge gaps in terms of ecosystem processes and biotic response can be used to intensify research in this field (Stendera et al., 2012).

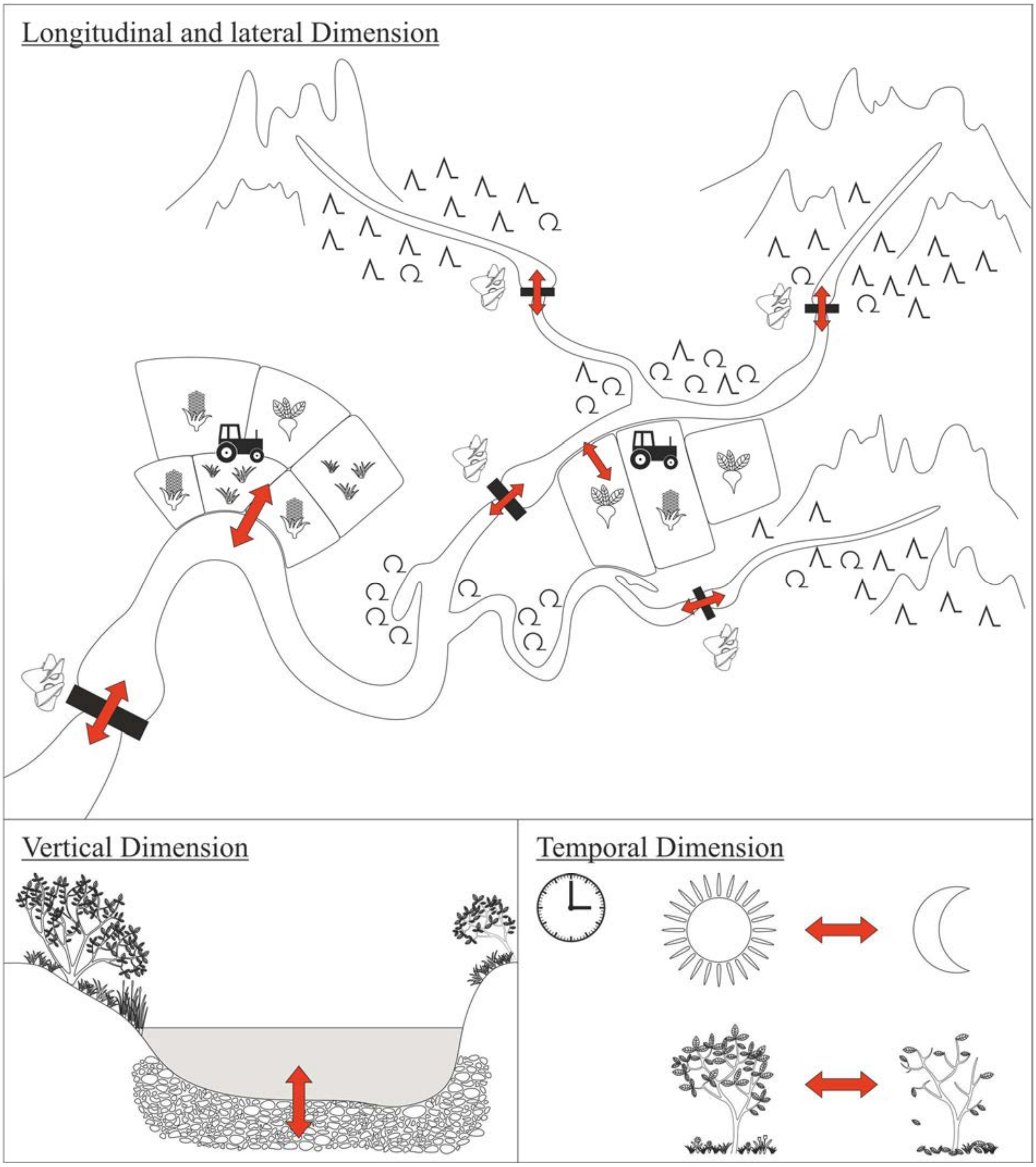


Figure 1.1 Schematic illustration of the different spatial and temporal dimensions investigated in this thesis: The longitudinal dimension represents the upstream-downstream interactions within a river, the lateral dimension includes the relationships between river and catchment (top), the vertical dimension includes interactions between open water, river bed and interstitial zone (bottom left), the temporal dimension includes diurnal and seasonal differences (bottom right). Interactions on the various dimensions are symbolized by red arrows.

1.5 Objectives

The core objective of this thesis was to investigate the influence of the anthropogenic stressors hydropower use and agricultural land use on stream ecosystems using a holistic, four-dimensional approach according to Ward (1989) (Figure 1.1).

The longitudinal dimension, which represents the upstream-downstream interactions in rivers, was investigated at several hydropower plants (Chapter 3) as well as in the course of a small river and its tributaries (Chapter 5). At the hydropower facilities, the downstream moving fish community was compared with the fish community composition in the headwaters directly upstream of the transverse structures. At another hydropower plant, the bypass efficiency and the injury risk during passage of a surface bypass was examined (Chapter 4).

Furthermore, different taxonomic groups (fishes, macroinvertebrates, periphyton) and their reactions to changing abiotic conditions were investigated along the course of a small river and its tributaries in a catchment area of about 32 km². At this study site, the lateral dimension was also taken into account, which includes the interactions between water bodies and their catchment area. In particular, the influence of various erosion-reducing measures in the catchment on the species composition of fish, macroinvertebrates, periphyton and the fine sediment load was investigated (Chapter 5).

With regard to the vertical dimension, the fine sediment deposition, the clogging of the stream bed, the exchange rate of the hyporheic interstitial zone with the open water as well as the reproductive success of gravel spawning fish species at an engineered spawning ground (Chapter 6) were investigated.

The fourth dimension, time, was considered on different scales: On the one hand, diurnal differences in spawning and hatching behaviour (Chapter 6) and in downstream movement patterns of different fish species were recorded, as well as seasonal changes (spring vs. autumn) in downstream movement patterns (Chapter 3) and in the community composition of fishes, macroinvertebrates and periphyton as well as abiotic water parameters (Chapter 5).

The results of the above-mentioned studies were used to derive management recommendations for the operation of hydropower plants, to propose structural improvements to hydropower plants and to make recommendations for instream and catchment restoration measures in order to improve fish protection at hydropower plants and to protect and enhance aquatic biodiversity.

2 Materials and Methods

In the present thesis, different methodological approaches were chosen to investigate the effects of the anthropogenic stressors hydropower use and agricultural land use on stream ecosystems across different dimensions, scales and taxonomic groups. The studies presented were carried out at six different sites in Bavaria, Germany (Figure 2.1).

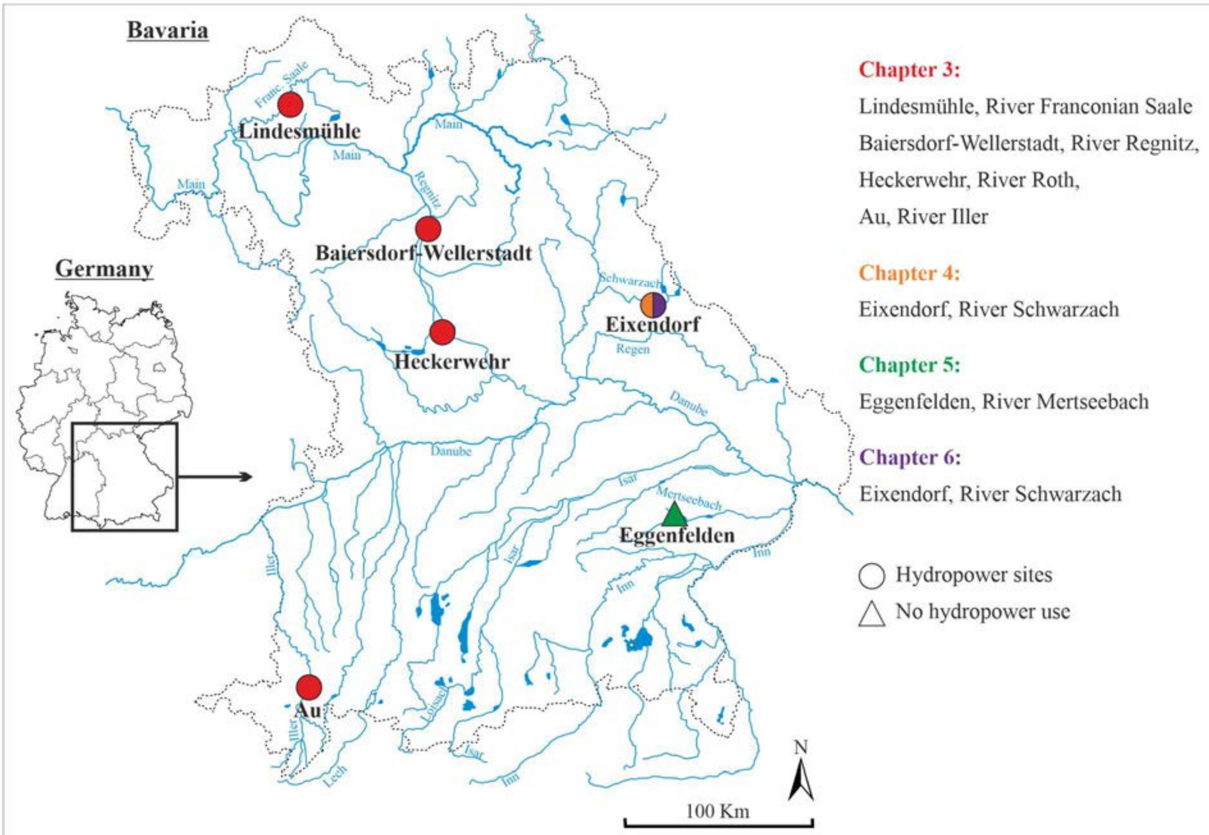


Figure 2.1 Map and location of the study sites in Bavaria, Germany. Different colors indicate which site was investigated in which chapter.

The seasonal and diurnal downstream movement behaviour of wild fish was studied using net-based catching techniques at four different hydropower plants (Table 2.1). For this purpose, stow-nets were installed at all possible corridors into the tailrace of the power plants, which were checked regularly at emptying intervals of 1–2 hours at day and night. At another power plant, stow-nets were installed to investigate the bypass efficiency and the injury risk for fish during the passage of a surface bypass. The study was carried out with hatchery-reared test fish of different species and sizes, which were examined for external injuries and kept for 96 hours to record potential delayed mortality (animal care permit ROB–55.2–2532.Vet_02–15–31).

To investigate the effects of agricultural land use and various erosion protection measures in the catchment on a small river system, the aquatic community composition including fishes, macroinvertebrates and periphyton was assessed and abiotic parameters were measured (Table 2.1). Juvenile and adult fishes were caught by electrofishing. To characterize the communities of macroinvertebrates and periphyton, samples were taken in the field, preserved and subsequently determined in the laboratory. Physical and chemical instream parameters were either measured directly on site or samples were taken and subsequently analysed in the laboratory.

To assess the effectiveness of a spawning ground restoration, the abiotic habitat characteristics of the spawning ground were evaluated and the spawning habitat use and recruitment success of target species for conservation were examined. For this purpose, fish eggs and larvae were caught by drift-netting and surber-sampling and identified to species level using DNA barcoding (Table 2.1).

Table 2.1 Overview of the study sites in the different chapters, the applied methods, the different dimensions according to Ward (1989) considered with the study design and the respective research objectives.

Chapter	Study sites	Methods	Dimensions	Research objectives
Chapter 3	- Baiersdorf/ River Regnitz - Lindesmühle/ River Franc. Saale - Au/ River Iller - Heckerwehr/ River Roth	- Net-based catching techniques - Electrofishing - Measurement of abiotic parameters	longitudinal temporal	Seasonal and diurnal fish movement patterns in relation to the fish community composition of resident fishes
Chapter 4	Eixendorf/ River Schwarzach	- Net-based catching techniques - Evaluation of external injuries - Determination of delayed mortality - Measurement of abiotic parameters	longitudinal	Surface bypass efficiency and injury risk during bypass passage
Chapter 5	Eggenfelden/ River Mertseebach	- Electrofishing - Kick-sampling of macroinvertebrates - Sampling of periphyton - Sediment sampling - Measurement of abiotic parameters	lateral longitudinal vertical temporal	Influence of catchment land use on aquatic community composition of fishes, macroinvertebrates and periphyton as well as abiotic parameters
Chapter 6	Eixendorf/ River Schwarzach	- Drift-netting & surber-sampling - Electrofishing - DNA barcoding - Sediment sampling - Measurement of abiotic parameters	vertical temporal	Spawning habitat use and recruitment of target species for conservation

2.1 Assessing fish at hydropower plants using net-based catching techniques

Depending on the size of the study river, catching fish at hydropower plants can involve considerable effort. In order to record and quantify the natural diurnal and seasonal movement behaviour as well as the plant-related mortality and injuries of all fish species and size classes, taking into account the available downstream migration corridors, it was necessary to take fish from the river for individual assessment. For this purpose, different types of catching nets were used, which, depending on the design, are called stow-nets or fyke-nets.

Stow-nets in combination with fyke-nets were used to catch fish at large turbine outlets, while different types of fyke-nets were used to investigate small bypasses such as fish passes (Table 2.2, Figure 2.2). The stow-nets consisted of a several meters long, tapering knotless nylon net with decreasing mesh size (from 30 mm to 10 mm), which was kept open by the current. The actual catching device was located at the end of the net and consisted of a catching net with one or more funnel-shaped throats (mesh size 8 mm) (Figure 2.2). The funnel-shaped throat should prevent the fish from escaping. Due to the small mesh size of the catching net, it was possible to catch small fish species as well as juvenile fish.

In order to cover 100% of the respective corridors discharge, the catching nets were attached to a railing welded to a metal frame and inserted into u-profiles. Depending on the water depth in the tailrace, the catching units at the hydropower plants were emptied either by wading or from a boat. After emptying the nets, the captured fish were examined for their injuries and subsequently transferred to fish tanks with fresh water and oxygen supply for 96 hours to determine potential delayed mortality.

Table 2.2 Number, type and dimensions of the different catching devices installed at the investigated hydropower plants.

Study site	Corridor	Catching device	Material dimensions/properties
Baiersdorf/ River Regnitz	Turbine	4 Stow-nets with attached fyke-nets	Metal frame length: 3.2 m, height: 3.2 m, dimensions square tube: 80/120/5 mm, railing: Ø 33 mm, stow-net length: 16.0 m, fyke-net length: 6.8 m
	Vertical-slot fish pass	1 Stow-net with attached fyke-net	Metal frame length: 1.0 m, height: 2.0 m, dimensions square tube: 40/80/5 mm, railing: Ø 12 mm, stow-net length: 6.0 m, fyke-net length: 5.5 m
	Flushing channel	1 Fyke-net	Metal frame length: 1.2 m, height: 1.4 m, dimensions square tube: 40/60/4 mm, railing: Ø 18 mm, fyke-net length: 4.0 m
Lindesmühle/ River Franconian Saale	Turbine	1 Stow-net with attached fyke-net	Metal frame length: 5.0 m, height: 5.1 m, dimensions square tube: 120/120/5 mm, railing: Ø 33 mm, stow-net length: 26.0 m, fyke-net length: 7.5 m
	Nature-like fish pass	1 Fyke-net with 2 wings	Fyke-net length: 4.0 m wings length: 5.0 m, heigth: 1.0 m
	Flap gate	1 Fyke-net	Metal frame length: 1.4 m, height: 2.5 m, dimensions square tube: 40/60/4 mm, railing: Ø 18 mm, fyke-net length: 8.0 m
	Fish slide	1 Fyke-net	fyke-net length: 5.5 m
Au/ River Iller	Turbine	2 Stow-nets with attached fyke-nets	Metal frame length: 7.0 m, height: 4.5 m, dimensions square tube: 120/180/5 mm, railing: Ø 30 mm, stow-net length: 29.0 m, fyke-net length: 7.5 m
	Vertical-slot fish pass	1 Stow-net with attached fyke-net	Metal frame length: 2.1 m, height: 1.4 m, dimensions square tube: 40/80/5 mm, railing: Ø 12 mm, stow-net length: 3.0 m, fyke-net length: 5.5 m
Heckerwehr/ River Roth	Turbine	1 Stow-net with attached fyke-net	Metal frame length: 5.4 m, height: 0.9 m, dimensions square tube: 100/90/5 mm, railing: Ø 20 mm, stow-net length: 12.5 m, fyke-net length: 4.5 m
	Turbine	1 Stow-net with attached fyke-net	Metal frame length: 1.1 m, height: 1.1 m, dimensions square tube: 40/80/5 mm, railing: Ø 12 mm, stow-net length: 8.0 m, fyke-net length: 5.5 m
Eixendorf/ River Schwarzach	Turbine	1 Stow-net with attached fyke-net	Metal frame length: 2.8 m, height: 2.6 m, dimensions square tube: 100/40/3 mm, railing: Ø 18 mm, stow-net length: 5.0 m, fyke-net length: 4.0 m
	Crest cut-out (small)	1 Fyke-net	Metal frame length: 0.4 m, height: 0.4 m, dimensions angle profile: 40/40/5 mm, fyke-net length: 2.0 m
	Crest cut-out (large)	1 Fyke-net	Metal frame length: 0.7 m, height: 0.8 m, dimensions angle profile: 40/40/5 mm, fyke-net length: 4.0 m

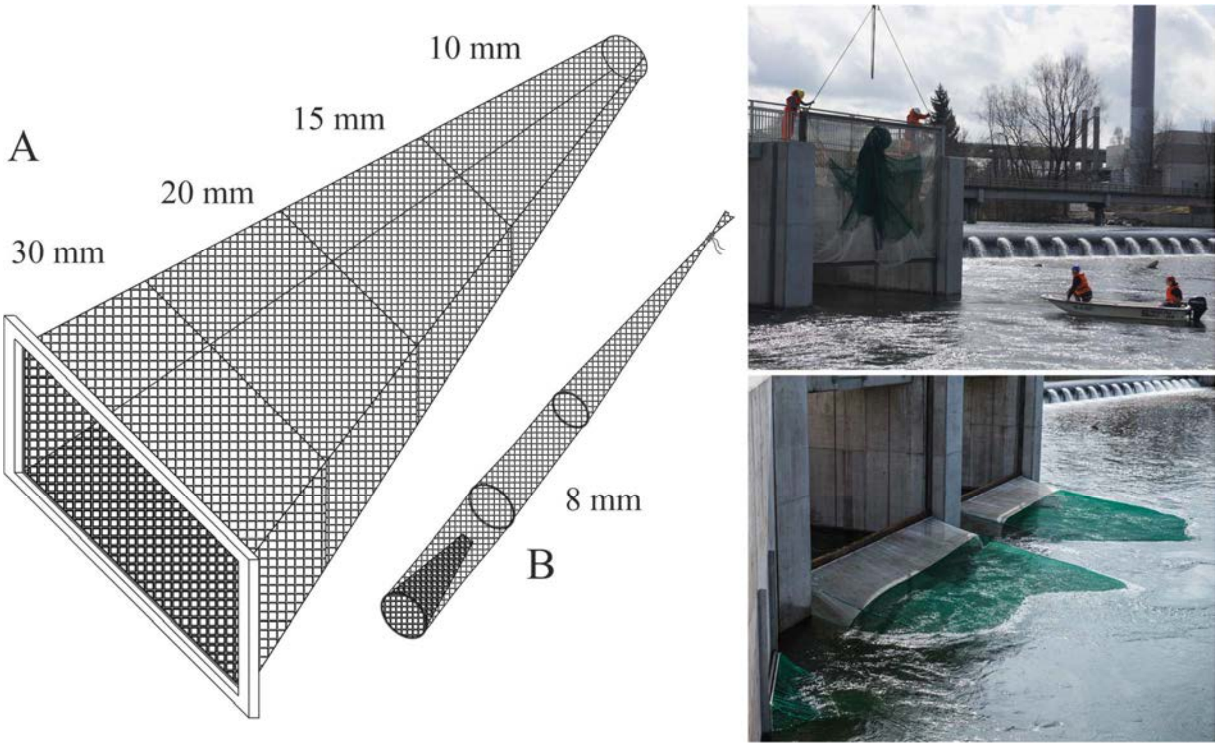


Figure 2.2 Schematic of a stow-net with decreasing mesh size (A) and a fyke-net (B), modified from Pander et al. (2018) (left) and installation of the nets at the turbine outlet to catch downstream moving fish (right).

2.2 Assessment of downstream moving wild fish

The assessment of the downstream moving wild fish at the investigated hydropower plants was carried out seasonally in spring and autumn at different times of day in order to investigate the diurnal and seasonal movement patterns of downstream migrating and drifting fish. Sampling was carried out in intervals of one to two hours each, evenly distributed over four time periods: The first half of the day (from sunrise to noon), the second half of the day (from noon to sunset), the first half of the night (from sunset to midnight) and the second half of the night (from midnight to sunrise). This allows conclusions to be drawn about the preferred times of day for downstream movement.

2.3 Standardized experiments with hatchery-reared fish

In order to investigate the injury risk of fish passing a surface bypass at a moveable hydropower plant, standardized fish experiments were conducted (Chapter 4). These were necessary because in the case of downstream moving wild fish, catch-related injuries cannot be clearly differentiated from plant-related injuries and the pre-damage of the fish, for example by upstream located hydropower plants or piscivorous fishes, birds or mammals, is not known. For this purpose, a defined number of fish from different species and known pre-damage were released upstream of the hydropower plant and caught in the tailrace using stow-nets as part of an approved animal experiment (animal care permit number ROB–55.2–2532.Vet_02–15–31). In addition, injuries that may result from catching and handling were also investigated.

The necessary number of test fish per treatment and fish species was determined using power analysis (Cohen, 1992) and applied for in the animal care permit. Eight fish species with different morphological characteristics were selected for the experiments (Figure 2.3). These were species with a spindle-shaped body form (brown trout, *Salmo trutta* L.; Danube salmon, *Hucho hucho* L.), with a spindle-shaped, laterally flattened body form (common nase, *Chondrostoma nasus* L.; European grayling, *Thymallus thymallus* L.), dorsoventrally flattened bottom-dwelling fish (barbel, *Barbus barbus* L.), rather high-backed fish (roach, *Rutilus rutilus* L.), fish with a serpentine, cross-sectionally rotund body (European eel, *Anguilla anguilla* L.), and fish with ctenoid scales and hard-spined fins (European perch, *Perca fluviatilis* L.). European perch is a physoclist species without a connection between swim bladder and esophagus and therefore reacts more sensitively to rapid pressure changes than physostomous species (Abernethy et al., 2001; Mueller et al., 2020b). To investigate correlations between total fish length and injury risk, the largest possible size range was used for each fish species.

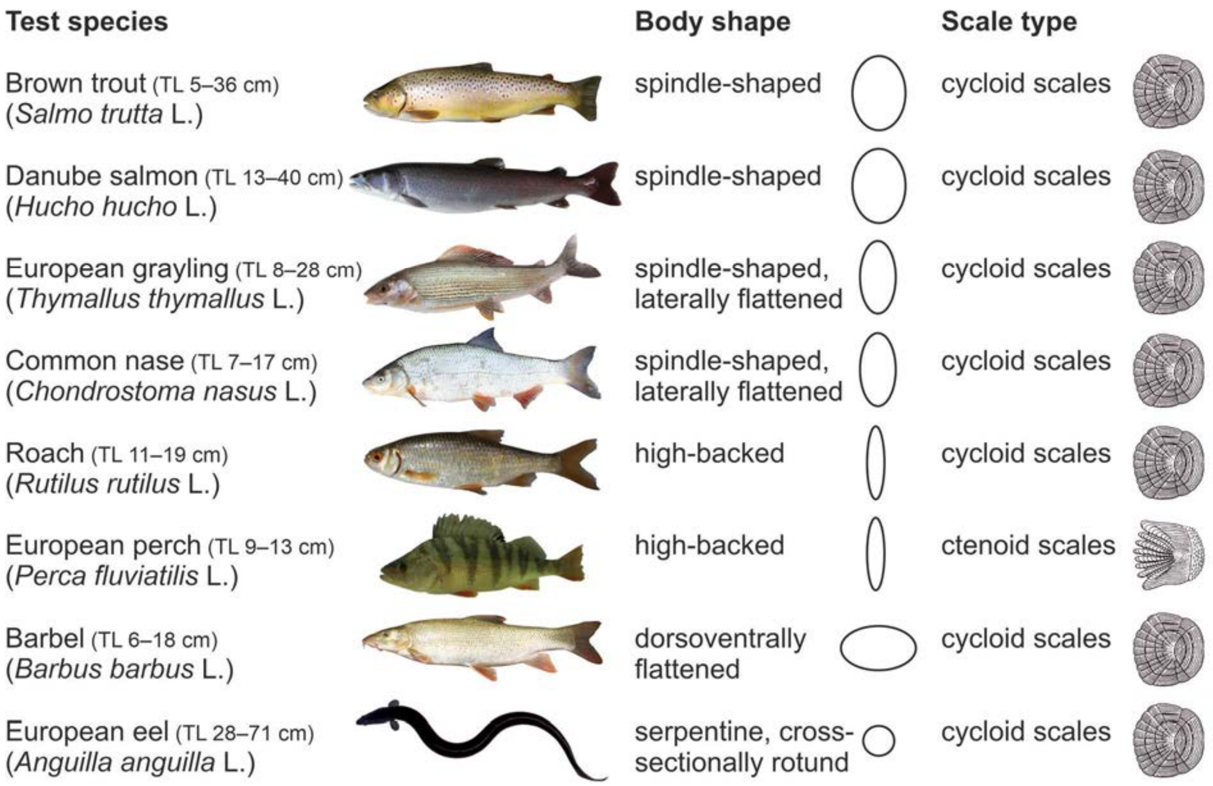


Figure 2.3 Species and size range of the hatchery-reared test fish and their morphological characteristics regarding body shape and scale type. TL = total length.

2.4 Evaluation of external injuries

Fish that were caught during the standardized experiments in Chapter 4 were examined for potential power plant-related injuries after being recovered from the catching nets. Externally visible injuries were recorded by visual inspection.

In contrast to an exclusive recording of mortality, a closer look at the various injuries, differentiated according to distinct anatomical sections, can establish correlations between injury patterns and specific components of hydropower plants. Since even minor injuries, for example at highly regenerative body parts such as the fins, can cause a loss of energy and lead to an increased infection risk for the fish, it is important to quantify all injuries and their intensity when assessing power plant-related effects.

To document the individual injuries, the fish body was subdivided into head, eyes, opercula, anterior (without head) and posterior body part, dorsal, ventral, dorsal fin, caudal fin, anal fin, pelvic fins and pectoral fins, if applicable differentiated into left and right half of the body. The following injury types were assessed: spine deflections, amputations, hemorrhages, bruises, emboli, dermal lesions, tears in fins, scale loss and pigment anomalies. The possible combinations of body parts and injuries are summarized in a table on the protocol sheet in which the intensity of the respective injuries on a certain body part can be entered in four categories: 0 = no damage, 1 = minor damage, 3 = medium damage, 5 = severe damage (Figure S 1). The assignment to the different intensity levels followed a detailed score sheet (cf. Mueller et al., 2017).

For each assessed fish, an individual barcode was stuck on the protocol sheet (Figure S 1). Since all evaluated fish were kept in compartments in water-filled tanks for 96 hours to record potential delayed mortality (cf. Chapter 2.5), another identical barcode was assigned to the compartment in which the fish was kept. Thereby, fish that died delayed could be clearly identified by their individual barcode and their specific injuries.

2.5 Determination of delayed mortality

In order to investigate delayed power plant-related effects, the delayed fish mortality was recorded during the standardized experiments in Chapter 4. For this purpose, the fish were kept in compartments (perforated plastic boxes, 60 × 40 × 44 cm; Allibert Logic Box; Allibert Home, Villepinte, France) in water-filled tanks (310 × 80 × 90 cm; Aquacultur Fischtechnik GmbH, Nienburg, Germany), separated by species and experimental groups (Figure 2.4). The tanks were continuously supplied with fresh river water and were shaded to minimise stress for the test fish due to permanent exposure to light. The fish were kept for 96 hours. Fish and dissolved oxygen, water temperature, pH value and electric conductivity of the water in the tanks were checked daily. Dead fish were removed, identified by their barcode on the injury protocol sheet and the time of death noted on the protocol sheet.

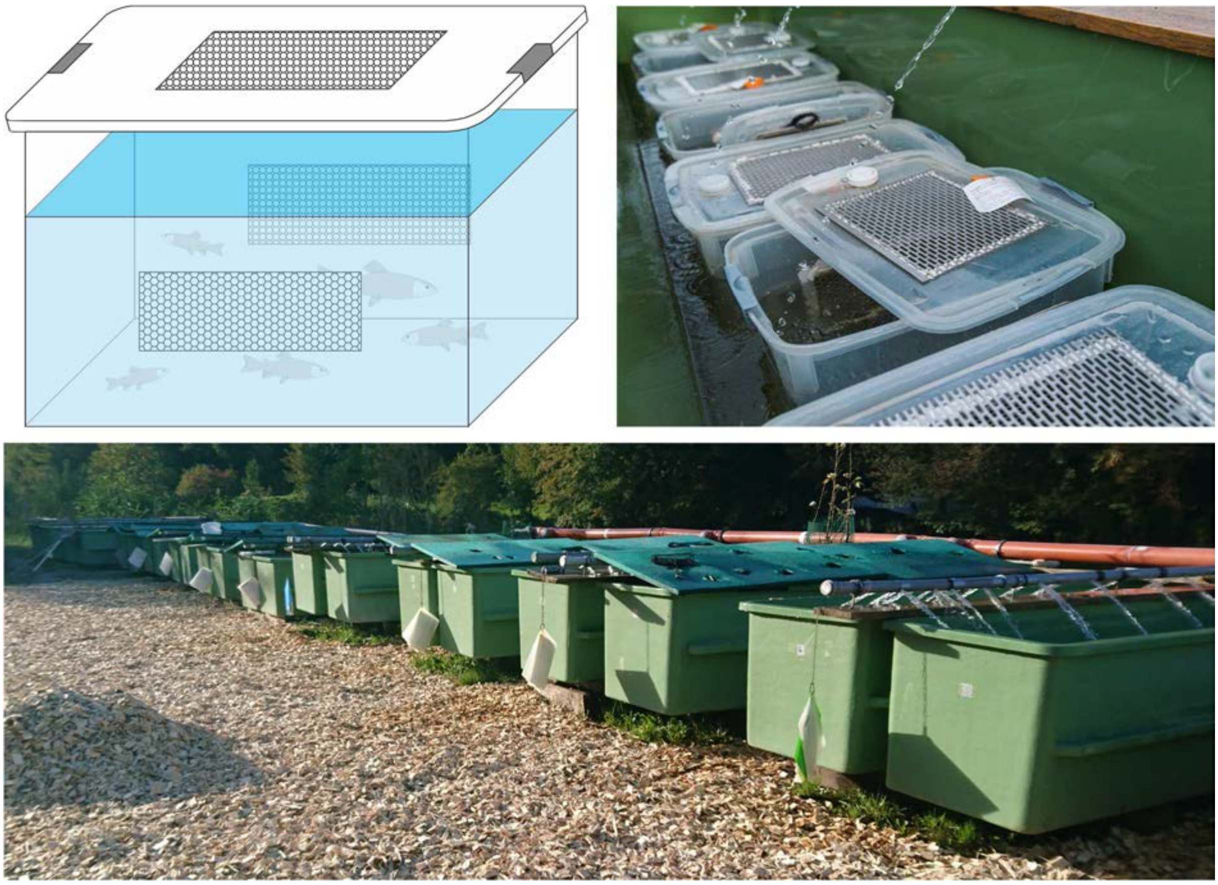


Figure 2.4 Schematic of a perforated plastic box (top left) and lined up plastic boxes in a fish tank to separate test fish per treatment and species (top right) as well as arrangement of the tanks with circulating fresh water supply and covers to shade the tanks (bottom).

2.6 Measurement of abiotic parameters

Abiotic habitat characteristics have a decisive influence on the functionality of the aquatic habitat (Jungwirth et al., 2003). They are subject to natural, seasonal and event-related fluctuations (e.g. floods, dry periods) and can be altered by anthropogenic interventions (Allan, 2004; Henley et al., 2000).

To characterize the abiotic habitat properties, physical and chemical parameters in the open and interstitial water, substratum composition and sediment deposition as well as river morphology were assessed.

Physical water parameters were characterized by measuring dissolved oxygen, water temperature, electric conductivity, pH-value (Multi 3430, WTW, Weilheim, Germany) and redox potential (pH 3110, WTW, Weilheim, Germany).

In Chapter 5, the chemical parameters total organic carbon (TOC), biochemical oxygen demand after five days (BOD_5), calcium, magnesium, sodium, sulphate, phosphorus, ammonium, nitrate and chloride were analysed both in the open water and in the interstitial water from 10 cm water depth. TOC analysis was carried out by catalytic oxidation at 680°C (Shimadzu TOC-5050A analyzer, Kyōto, Japan). The BOD_5 was determined according to DIN EN 1899-2 (1998) for undiluted samples. Cations and anions were analysed by ion chromatography (Dionex ICS-1100, Thermo Fisher Scientific, Braunschweig, Germany).

The particle size distribution of the autochthonous substratum is an important parameter with regard to the habitat quality of the stream bed and the living conditions in the interstitial zone. To characterize the grain size distribution, substratum samples were taken using a box sampler (29.5 cm × 17.0 cm × 17.0 cm) or the freeze-core method. In the laboratory, a fractionation of the substratum was carried out by wet-sieving (Retsch GmbH, Haan, Germany) using 20.0 mm, 6.3 mm, 2.0 mm and 0.85 mm sieves. The separated size classes were dried and weighed and the percentage of each particle size fraction was calculated.

Suspended sediment load is an important indicator of fine and ultrafine sediment input into rivers. Since the suspended sediment load and the actual sediment deposition on the river bed or the clogging of the interstitial zone are not necessarily correlated, both turbidity measurements (PhotoFlex Turb, WTW, Weilheim, Germany) and measurements of fine sediment deposition were carried out using sediment traps. To determine the sediment deposition, plastic boxes (190 mm × 160 mm × 90 mm, ROTHO clear boxes, ROTHO AG, Würenlingen, Switzerland) filled with gravel (grain size = 22–32 mm, mean filling weight = 3.2 kg) were buried in the river bed (Figure 2.5). These sediment traps integrate continuous sediment deposition over a given period of time (cf. Denic & Geist, 2015, Pander et al., 2015a). In the laboratory, the extracted substratum was fractionated with a wet-sieving tower (Retsch GmbH, Haan, Germany) of decreasing mesh sizes (2.0, 0.85, 0.63 and 0.20 mm).

Figure 2.5 Sediment trap filled with gravel in grain sizes of 22–32 mm (left) and sediment traps buried in the river bed at the end of the exposure period (right).

In order to characterize the river morphology, water depth and current speed measurements (HFA, Höntzsch, Waiblingen, Germany; MFpro, OTT Hydromet, Kempten, Germany) as well as measurements of the penetration resistance (EijkelkampAgrisearch Equipment, Giesbeek, the Netherlands) of the river bed were carried out.

2.7 Biotic community assessment

2.7.1 Sampling and determination of periphyton

Periphyton, defined as attached microcommunities comprising benthic algae and cyanobacteria, is a valuable biological indicator and plays an important role in assessing anthropogenic and/or environmental stressors on lotic ecosystems (Li et al., 2010; Mueller et al., 2011). Due to its relatively short generation times, periphyton can react quickly to short-term changes in environmental conditions, such as changes in water temperature, fine sediment load, nutrient level or current speed (Li et al., 2010; Lobo et al., 2016).

For periphyton sampling, benthic algae were scraped off suitable substratum (stones or dead wood) and preserved in Lugol's iodine solution (Mueller et al., 2011). In the laboratory, algae samples sedimented for at least 24 hours according to the sedimentation method of Utermöhl (1931). Using an inverted microscope, species were determined and cell numbers were counted at 400 × magnification (DIN EN 15204, 2006). The determination of diatoms to species level was based on the structures of the silica skeleton. After acid digestion, permanent preparations were made, which were embedded in Naphrax and then determined using a light microscope (Schaumburg et al., 2012).

2.7.2 Sampling and determination of macroinvertebrates

Macroinvertebrates are an important component of the food web of lotic ecosystems, as they are the main food source for many fish species and the main consumer of plant biomass (Wallace & Webster, 1996). Due to their lower mobility compared to fish, their relatively long life span and their partly high habitat requirements, site-specific ecological conditions and potential anthropogenic stressors can be inferred from the prevailing community composition.

Macroinvertebrates were sampled by "kick-sampling" following Hauer and Lamberti (2007) and DIN EN ISO 10870 (2012). Sampling was carried out at representative sites based on the multi-habitat sampling procedure according to the Water Framework Directive (Meier et al., 2006). Macroinvertebrates were collected using a sampling net (35 cm × 35 cm, mesh size 500 µm) and preserved in 50% ethanol. In the laboratory, the macroinvertebrates were pre-sorted to order level and then determined to species level, if not possible at least to family level using a binocular.

2.7.3 Fish community assessment

The fish community composition was assessed by electrofishing. For this purpose, study segments of 30 m length each were sampled by wading or from a boat, following the methodology described in Pander and Geist (2010) and DIN EN 14011 (2003). Caught fish were kept in plastic bins with oxygen supply. All individuals were determined to species level and the total length was measured. Afterwards, all fish were released. The individual fish weight was calculated using corpulence factors according to Pander and Geist (2010) and Mueller et al. (2011).

2.7.4 Sampling and identification of fish eggs and larvae

The drift of fish eggs and larvae was investigated using drift nets consisting of rectangular aluminium frames (external dimensions: 34 × 28 cm, mouth: 30 × 24 cm) attached to iron bars positioned in the stream bed (cf. Nagel et al., 2020b). A 3 m long net made of tear-resistant polyester with a density of 155 meshes per cm² (mesh size ~ 800 µm) was attached to the frame. The end of the net was removable for emptying via a zipper (catch bag length 0.5 m). The passive drift traps were exposed to the current and thus caught hatched fish larvae drifting with the current as well as drifting eggs. The drift traps covered the entire water column and thus filtered all water horizons from the stream bed to the surface (Figure 2.6).

In order to detect fish eggs and larvae in the interstitial zone, surber-sampling was carried out (Surber, 1930). The surber-sampler was placed on the stream bed against the current and the substratum in this defined area was dug up to a depth of approx. 10 cm (Figure 2.6). Loosened eggs and larvae were then transported with the current into a collecting container via a 500 µm net.

All samples were screened for fish larvae and eggs. Eggs and larvae were euthanised using a twentyfold overdose of MS 222 (Tricaine Methane Sulphonate) following Adam et al. (2013) and then preserved in 96% ethanol. After taxonomic identification to family level, the fish larvae were assigned to groups with similar phenotypic characteristics (cyprinids: Pinder, 2001; Spindler, 1988; percids: Ramler et al., 2014; Urho, 1996). The classification was based on the criteria of developmental stage, body shape, pigmentation, head and mouth shape and fin position (if developed). Due to a lack of identification features, the recorded eggs were classified according to their size.

Subsequently, samples of larvae from each identified group were randomly selected and used for DNA barcoding. If DNA barcoding confirmed the homogeneity of a pre-sorted group (i.e.

all analysed individuals belong to the same species), the detected species was transferred to all other individuals of this group for the following data analyses. For species identification, the obtained sequences of the genetic analysis were matched in a query search with a database (cf. Nagel et al., 2021).

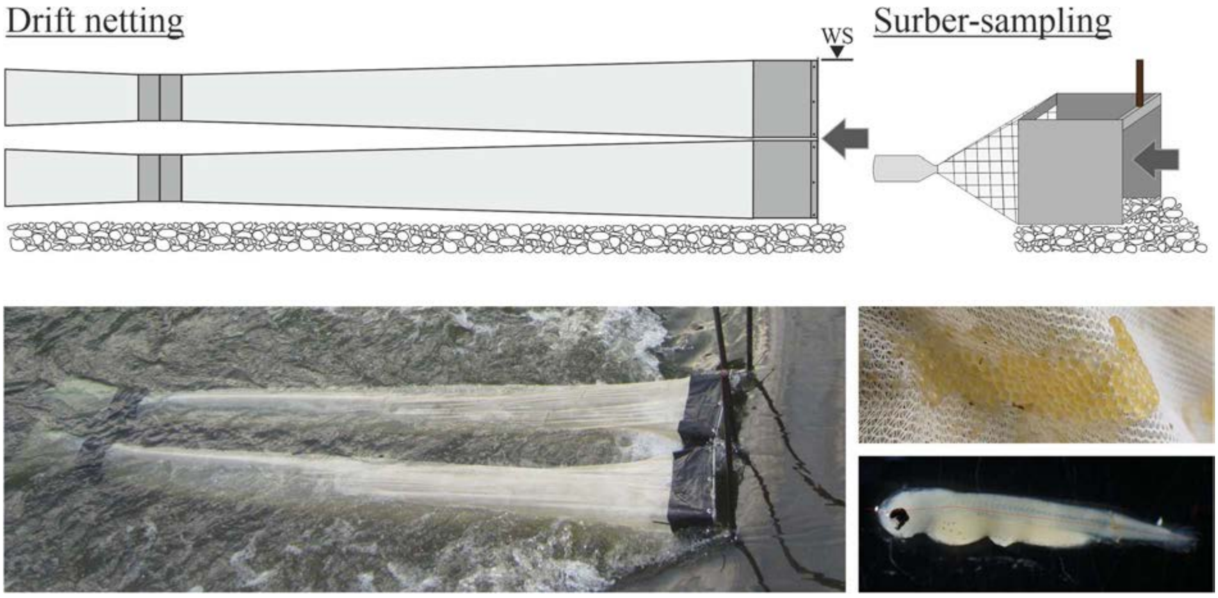


Figure 2.6 Top: schematics of two vertically stacked drift nets, modified from Nagel et al. (2021) and a surber-sampler to assess fish eggs and larvae; grey arrows indicate the flow direction, WS = water surface. Bottom: pictures of two drift nets installed at the turbine outlet of a hydropower plant, fish eggs sticking to a drift net and a fish larvae being measured under a stereomicroscope.

3 Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants

A similar version of this chapter was published: Knott, J., Mueller, M., Pander, J. & Geist, J. (2020). Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants. *Ecology of Freshwater Fish*, 29(1), 74–88.

Author contributions: Josef Knott (JK), Melanie Mueller (MM), Joachim Pander (JP) and Jürgen Geist (JG) jointly conceptualized and designed the study. The investigations at the various hydropower plants were mainly carried out by JK and MM. Statistical analysis, visualization and data interpretation was done by JK. The initial draft was prepared by JK and continuously improved, revised and edited by JK, MM, JP and JG.

3.1 Abstract

Hydropower structures hinder the movement and migration of fishes, impairing their life cycles. Additionally, downstream moving fish are often at risk of being injured during turbine passage. To improve hydropower production towards more fish-friendly techniques and management, knowledge on timing and extent of natural patterns of fish downstream movement is necessary. So far, migration behaviour of long-distance migrators such as eel or salmon has been well studied, but little is known about seasonal and diurnal movement patterns of non-migratory species or medium-distance migrators. In this study, movement patterns of 39 fish species captured by stow-nets while transiting hydropower facilities in four impounded rivers were assessed and compared with the fish community composition directly upstream of the hydropower plants assessed by electrofishing. Strong differences between the fish community composition inhabiting the upstream sides of the dams and the fish detected in downstream passage were evident. In each study river, the downstream moving fish community composition differed significantly between spring and autumn. On average, significantly more fish were caught during the night (2.9 fish/h) than during the day (1.3 fish/h). Topmouth gudgeon, European grayling and pike-perch mostly moved downstream during the night, whereas roach, spirlin and bleak were the most frequent downstream moving fish during daytime. Downstream fish movement was positively related with turbidity, water temperature and discharge. The strong differences in seasonal and diurnal fish movement patterns suggest that fish damage can be strongly reduced by adaptive turbine and corridor management, e.g. by shutting down turbines at peak movements.

3.2 Introduction

Freshwaters, in particular streams and rivers, are amongst the most threatened ecosystems, being prone to multiple stressors (e.g. Allan, 2004; Ormerod et al., 2010; Vörösmarty et al., 2010). For instance, the world's increasing energy needs currently result in further expansion of hydropower (Zarfl et al., 2015). The construction of dams and hydropower plants hinders the movement and migration of fishes, which is often an obligatory element in their life cycle (Lucas & Baras, 2001; Schilt, 2007). The passage of fish individuals through hydropower structures poses a threat to fish that can be harmed or even killed (Mueller et al., 2017; Williams et al., 2012). In order to mitigate possible negative effects of hydropower plants on fish populations, knowledge on species ecology, particularly on seasonal and diurnal fish activity patterns and downstream movement (i.e. active migration and passive displacement), is essential. Because it is thought that the scale and pattern of fish behaviour and downstream movement varies widely among species and habitats, it is important to consider such differences for species specific conservation and management. This necessity is even more obvious because existing studies in the context of fish downstream movement are mainly limited to a few economically important species such as eel and salmon (e.g. McCormick et al., 1998; Riley et al., 2002; Travade et al., 2010). For most other species (particularly potamodromous species) little is known at what time of day and season downstream movement occurs. Fish activity can potentially significantly differ during different seasons or times of day due to spawning migrations of adult fishes, drift of larvae, downstream movements of juvenile fishes, searching for feeding areas, winter habitats or due to predation or intraspecific competition (Brönmark et al., 2013; Lucas & Baras, 2001; Northcote, 1984). A better knowledge of diurnal and seasonal patterns of fish downstream movement can help to develop and improve facility design (e.g. spatial arrangement and dimension of fish guiding structures; Katopodis, 2005) or management strategies. For instance, adaptive management can include shutting down turbines at peak times of fish movement (Trancart et al., 2013), opening of additional corridors (e.g. undershot sluice gate opening; Egg et al., 2017), or providing seasonally higher discharges for a better functionality of fish bypass systems (Haro et al., 1998). Moreover, for the monitoring of the effects of hydropower plants on fish, it is important to know which day and night times should be taken into consideration for a representative sampling that comprehensively evaluates effects of the facility on the fish community, since a continuous sampling of the whole day and night is mostly not feasible.

In this study, four hydropower plants at four different study rivers in Central Europe were assessed regarding comparisons of their adjacent upstream fish community (UP) and the downstream moving fish community (DM) that passed the hydropower plants during spring/autumn and day/night. Specifically, we hypothesized that (i) the downstream moving fish community composition caught while moving through hydropower facilities reflects the fish population directly upstream of the dams in terms of species abundance and length-frequency distribution, that (ii) the number of individuals and the species composition of downstream moving fish varies between spring and autumn and day and night, and that (iii) there are species- and river-specific differences in seasonal and daytime downstream movements.

3.3 Materials and Methods

3.3.1 Study rivers

The study was carried out at four run-of-the-river hydropower plants in Bavaria, Germany (Table 3.1, Figure 3.1). One power plant is located at the river Regnitz in Baiersdorf (N 49.6706, E 11.0424). The power plant is placed in a headrace channel and is equipped with two identical horizontal Kaplan turbines with four turbine blades each (diameter = 2 m, drive = 150 rpm, power = 15–324 kW). The drop height between headrace and tailrace is 2.3 m. Upstream fish passage is enabled by a vertical-slot fishway. At this site, the Regnitz has a mean annual discharge of 34.8 m^3/s and a catchment area of 7,521 km^2. It belongs to the barbel fish ecoregion (Huet, 1949) with a potentially natural fish fauna of 33 species, which is based on historic records, recent data, stream morphology and expert knowledge (Schubert, 2007).

Table 3.1 Characterisation of the four study rivers regarding drainage system, stream zonation (Illies & Botosaneanu, 1963), fish region index (FRI; Dußling et al., 2005), physical and chemical parameters. Numbers in the cells are arithmetic mean values. Additionally, for discharge, turbidity, dissolved oxygen, temperature, pH-value and electric conductivity the standard deviation (±) and the minimum and maximum values (in parentheses) are presented. EP = epipotamal, Cyp-R = cyprinids dominated rhithral, SA-HR = salmonids dominated hyporhithral.

		Regnitz	Franconian Saale	Roth	Iller
Drainage system		Main/Rhine	Main/Rhine	Main/Rhine	Danube
Stream zonation		EP	Cyp-R	Cyp-R	SA-HR
FRI		6.2	5.6	5.8	5.3
River bed slope (%)		0.9	0.8	4.7	1.8
Mean width (m)		54.8	20.1	13.4	70.3
Depth (cm)		116 ± 59	123 ± 79	65 ± 30	117 ± 55
		(27–283)	(19–310)	(13–170)	(17–340)
Discharge (m^3/s)	Spring	28.8 ± 4.0	8.8 ± 0.6	1.4 ± 0.6	28.8 ± 12.7
		(24.1–36.7)	(7.8–10.0)	(0.8–2.7)	(19.1–62.1)
	Autumn	26.7 ± 1.2	3.0 ± 0.8	4.5 ± 0.4	29.4 ± 11.1
		(25.4–29.0)	(2.3–5.8)	(3.3–5.2)	(21.2–58.5)
Turbidity (NTU)	Spring	11.7 ± 3.7	4.5 ± 0.5	7.5 ± 6.6	3.5 ± 1.9
		(6.0–18.4)	(3.6–5.6)	(3.6–29.0)	(0.6–8.5)
	Autumn	3.9 ± 0.8	6.6 ± 1.0	3.2 ± 2.5	24.7 ± 51.9
		(2.7–5.3)	(5.6–10.5)	(1.5–11.8)	(4.2–227.8)
Dissolved oxygen (mg/L)	Spring	9.8 ± 0.3	9.7 ± 0.5	11.4 ± 0.4	11.9 ± 0.2
		(9.3–10.5)	(9.3–10.4)	(10.4–12.0)	(11.4–12.6)
	Autumn	10.0 ± 0.5	9.7 ± 0.4	9.2 ± 0.4	10.0 ± 0.3
		(9.1–10.8)	(8.9–10.3)	(8.4–9.7)	(9.3–10.6)
Temperature (°C)	Spring	12.8 ± 1.1	11.8 ± 0.6	9.4 ± 0.9	6.0 ± 1.2
		(11.7–14.4)	(11.0–12.5)	(7.7–11.1)	(4.3–8.6)
	Autumn	15.2 ± 1.4	12.7 ± 1.2	18.5 ± 1.5	13.6 ± 1.2
		(13.4–17.8)	(10.8–14.1)	(16.4–21.6)	(11.8–15.4)
pH–value	Spring	7.9 ± 0.1	8.0 ± 0.0	8.3 ± 0.1	8.5 ± 0.1
		(7.8–8.1)	(8.0–8.1)	(8.1–8.4)	(8.3–8.7)
	Autumn	8.6 ± 0.1	8.1 ± 0.1	8.1 ± 0.1	8.2 ± 0.0
		(8.4–8.7)	(8.0–8.2)	(7.8–8.2)	(8.0–8.3)
Electric conductivity (µS/cm)	Spring	637 ± 30	859 ± 10	512 ± 35	395 ± 54
		(591–695)	(845–877)	(417–572)	(280–443)
	Autumn	667 ± 10	1108 ± 87	552 ± 28	380 ± 20
		(641–688)	(889–1218)	(469–575)	(316–403)

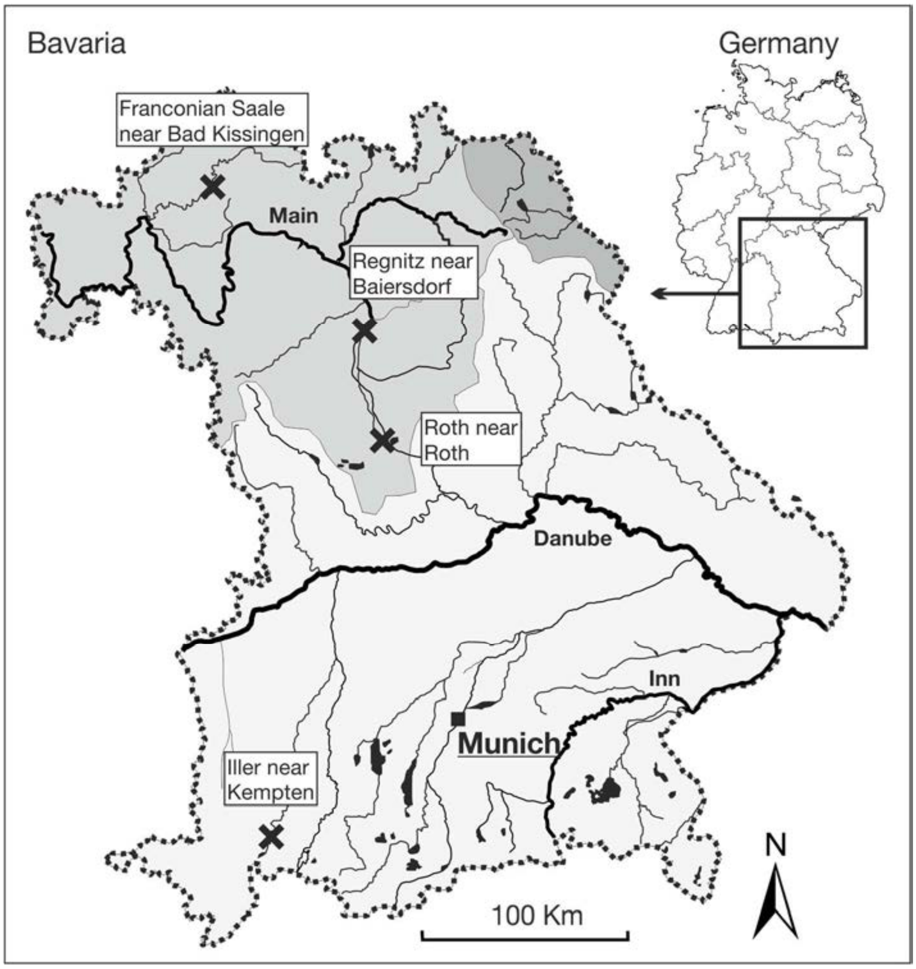


Figure 3.1 Map and location of the four study rivers in Bavaria, Germany. Different shades of grey symbolize the main drainage systems in Bavaria: = Elbe, = Main/Rhine, = Danube.

The second hydropower plant is located at the river Franconian Saale in Bad Kissingen (N 50.1879, E 10.0744) and is operated with a horizontal Kaplan turbine with three turbine blades. With a head of 2.81 m and a flow rate of 10.8 m^3/s, the maximum power of the turbine is 270 kW (diameter = 1.5 m, drive = 212 rpm). Upstream fish passage is enabled by a nature-like fishway. The mean annual discharge at the study site is 12.3 m^3/s (catchment area 2,766 km²). The Franconian Saale belongs to the grayling fish ecoregion with a potentially natural fish fauna of 30 species.

The third power plant contains an Archimedes screw turbine and is located at the river Roth near the city of Roth (N 49.2332, E 11.1230). The screw turbine has a 5.4 m long and 3.2 m diameter rotor set at an inclination of ~ 22°. The rotor consists of three helical blades welded to a central shaft. At a head of 2.6 m and a maximum flow rate of 5 m^3/s the screw turbine is capable of rotating at 3–26 rpm (depending on discharge). The energy yield of the turbine ranges from 10–71 kW. Upstream fish passage is enabled by a screw pump fish lift. At this site, the Roth has a mean annual discharge of 3.2 m^3/s and a catchment area of 173 km². It belongs to the grayling fish ecoregion with a potentially natural fish fauna of 24 species.

The fourth study site is located at the river Iller near the city of Kempten (N 47.6851, E 10.3203). The power plant is equipped with two very low head (VLH) turbines with 5 m diameter, variable speed (19.5–32.7 rpm) and eight adjustable runner blades. At a head between 1.55 m and 2.35 m and a design flow of 54 m^3/s a maximum performance of 900 kW can be achieved. Upstream fish passage is enabled by a vertical-slot fishway. The mean annual discharge of the Iller is 46.5 m^3/s (catchment area 2,147 km²). At the study site, the Iller belongs to the grayling fish ecoregion with a potentially natural fish fauna of 19 species.

3.3.2 Experimental design

Fish community composition in the directly adjacent upstream sides of the hydropower plants (< 1,000 m from the dams) was assessed using a boat-based electrofishing generator (11.0 kW, EFKO-GmbH, Leutkirch, Germany). A single anode and a dip net was used to collect stunned fish while the boat was operating from downstream to upstream direction according to DIN EN 14011 (2003) with minor modifications considering the length of the fished stretches as specified in Pander and Geist (2010) and Mueller et al. (2014a). The total investigation stretch equaled 500–1,000 m per site and was subdivided into 30 m segments as suggested by Grossman et al. (1987). According to Mueller et al. (2011), 15 (Franconian Saale, Roth) and 20 (Regnitz, Iller), respectively, sampling stretches at the upstream sides of the hydropower plants were assessed, depending on the mean width of the rivers (Table 3.1). All sampling stretches were consecutively sampled during stable weather and discharge conditions by the same crew throughout the entire study period in 2015 and 2016 both in spring and in autumn. Fishes from each replicate were held in separate plastic tanks with oxygen supply. Fishes were identified to species level and total length was measured (± 0.5 cm).

For the assessment of the naturally DM transiting the dams, all possible corridors into the tailrace of the hydropower plants were sampled with stow-nets. These corridors included the turbine outlets, fish passes and spillways (if existent). Downstream moving fish were caught with knotless stow-nets of decreasing mesh size and narrowing diameter (mesh sizes: 30 mm, 20 mm, 15 mm, 10 mm and 8 mm), applying 1–2 h emptying intervals during day and night to minimize the catch-related damage to fish (Pander et al., 2018a). This system is most commonly used to catch fish at hydropower turbine outlets (Dubois & Gloss, 1993) and considered best practice design (Ebel, 2013). The stow-nets had a rectangular opening, which was knotted with each mesh to a metal frame that allowed the fixation in u-profiles to cover 100% of the respective corridors discharge. Fyke-nets with a circular opening of 60 cm diameter were attached to the end of the stow-nets with strong zip ties. They had a funnel-shaped throat at the entrance, were 5.5 m long, had three metal rings to keep the net open throughout the length, and had a mesh size of 8 mm. The net consisted of a knotless polyamide material. The end of the fyke-net could be easily closed with a rope. To recover the fish, the fyke-net was lifted into a boat, the end of the net was opened and the content of the trap was emptied into a large water-filled bin with oxygen supply. All fishes were identified to species level and the total length was measured to the nearest 0.5 cm.

The assessment of the naturally downstream moving fish was carried out in 2015 and 2016 both in spring and in autumn, as recommended for the assessment of migratory fish communities in many European rivers (Lucas & Baras, 2001). During winter, many fish are not very active or fall into a state similar to hibernation (mainly cyprinids) because of reduced metabolic demands due to the low water temperatures (Cunjak, 1996). Summer is often inappropriate to assess fish communities, especially during hot weather conditions, because of the high risk for fish to die from oxygen deficiency during sampling (Pander et al., 2018a; Portt et al., 2006). Throughout all study rivers, a total of 2,143 hours of stow-net fishing over 140 days were carried out (Table 3.4). The individual emptying intervals (1–2 hours each) were carried out in different time segments according to day (sunrise until sunset) and night (sunset until sunrise) that were further subdivided into first or second half of the day and first or second half of the night.

3.3.3 Measurement of abiotic parameters

Water temperature (°C), dissolved oxygen (mg/L), electric conductivity (µS/cm at 25°C), pH-value and turbidity (NTU) were recorded at each study site three times a sampling day using a handheld measuring device (Multi 3430 Set G, Turb 355 T, WTW, Weilheim, Germany). In addition, the discharge (m^3/s) of each study river was also recorded three times a day at the nearest water gauge of the investigated hydropower plants (Table 3.1).

3.3.4 Statistical analyses

To test for potential gear bias of the methods used to assess UP (electrofishing) and DM (stow-net fishing), the minimum and maximum total lengths of the most frequent species of each river that were captured both in UP and DM were compared. It was assumed that capture probability was based on fish size regardless of the species. If the smallest or largest fish across all species were absent in UP or DM, this would indicate gear bias. If the minimum and maximum fish sizes were comparable, this would indicate the gear was capable of capturing fish across all sizes encountered. Even if no gear bias is detected, the two gear types may have different capture probabilities at certain fish sizes.

To compare the average fish lengths between UP and DM and the number of downstream moving fish between the study rivers, the season and the time of day, univariate statistics were used (software R 3.4.1; R Core Team, 2017). All data were tested for normality with the Shapiro-Wilk-test and for homogeneity of variances with the Levene-test. Since all data were not normally distributed and the variances were not homogenous, non-parametric Kruskal-Wallis-tests and Bonferroni-corrected post-hoc pairwise Mann-Whitney-U-tests were used for further testing. To test for links between different abiotic river parameters and the number of downstream moving fish, Spearman rank correlations were performed.

To test for differences between UP and DM, the season and the time of day, a multivariate approach was used. For the comparison of the UP and the DM relative frequencies of the species length-frequency data were calculated, in order to ensure an equal weighting of the two data sets collected by different methods (electrofishing and stow-net fishing). For all multivariate analyses, species abundance and species length-frequency data were transformed into a resemblance matrix containing similarity values for each comparison of samples (emptying intervals). As similarity measure, the Bray-Curtis coefficient was chosen (Bray & Curtis, 1957). If variables among samples happened to be entirely zero, a zero-adjusted Bray-Curtis coefficient, including a virtual dummy variable being one for all objects, was used as suggested by Clarke et al. (2006). Differences between UP and DM, study rivers, seasons and times of day were analysed using one-way analysis of similarities (ANOSIM) based on Bray-Curtis similarities calculated from species abundance and species length-frequency data (Clarke, 1993).

To identify the most common and steadily occurring species in the UP and the DM at different times of day or different seasons, a one-way Similarity-Percentage-Analysis (SIMPER; Clarke et al., 2014) was carried out to determine the average abundance of species and the contribution to the between group-dissimilarity in the respective season, time of day or between UP and DM.

The data set with relative frequencies of the UP and the DM was used for hierarchical clustering (Clarke et al., 2014) with group-average linking based on pairwise Bray-Curtis similarities between variables (river & method & season). A dendrogram was generated to identify any grouping of the different study rivers regarding UP and DM. Similarity profiles (SIMPROF; Clarke et al., 2014) were used to test for significant groupings. All multivariate analyses were carried out using the statistic software PRIMER v7 (Plymouth Marine Laboratory, Plymouth, UK). For all statistical analyses, significance was accepted at $p \leq 0.05$.

3.4 Results

3.4.1 Interrelation between upstream fish community and downstream moving fish

During the investigation period, a total of 36 fish species and 10,923 individuals were caught by electrofishing at the upstream sides of the dams of the four study rivers. A higher number of 39 fish species, but less individuals (4,902) were caught by stow-nets during downstream passage of the power plants (Table 3.2). The most frequently caught species were roach (*Rutilus rutilus*, L. 1758), round goby (*Neogobius melanostomus*, Pallas 1814), common dace (*Leuciscus leuciscus*, L. 1758), bleak (*Alburnus alburnus*, L. 1758) and chub (*Squalius cephalus*, L. 1758), summing up to 69% of the total catch of individuals.

Species and size composition of the UP in the four study rivers differed significantly from the DM (ANOSIM: Global $R = 0.96$; $p < 0.001$). Clustering (Figure 3.2, cophenetic correlation = 0.96; $p < 0.05$) identified two main clusters (SIMPROF-test: $\pi = 5.37$; $p < 0.001$), separating the UP of the four study rivers from the DM. The roach was detected by SIMPER analyses consistently throughout all study rivers both in the UP (except in the river Iller) and in the DM (Figure 3.3). Small-bodied species like bullhead (*Cottus gobio*, L. 1758), gudgeon (*Gobio gobio*, L. 1758), bleak, spirlin (*Alburnoides bipunctatus*, Bloch 1782), topmouth gudgeon (*Pseudorasbora parva*, Temminck & Schlegel 1846) and ruffe (*Gymnocephalus cernua*, L. 1758) were typically detected in the DM. In contrast, European grayling (*Thymallus thymallus*, L. 1758), chub, round goby and rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) were more frequently caught in the UP than in the DM.

Table 3.2 Upstream fish community (UP) and downstream moving fish community (DM) at the four study rivers Regnitz, Franconian Saale, Roth, Iller and overall study rivers (Overall). Absolute catch numbers are given to indicate the size of the data set.

Scientific name	Common name	Regnitz		Franconian Saale		Roth		Iller		Overall	
		UP	DM	UP	DM	UP	DM	UP	DM	UP	DM
Abramis brama	Common bream	14	14		1	17	2		17	31	34
Alburnoides bipunctatus	Spirlin	149	372	19	30				1	168	403
Alburnus alburnus	Bleak	186	467		1	8				194	468
Ameiurus melas	Black bullhead		2								2
Anguilla anguilla	European eel	11	15	74	15	53	5		2	138	37
Barbatula barbatula	Stoneloach	1	6			3			37	4	43
Barbus barbus	Barbel	2	5	7	9		8		13	9	35
Blicca bjoerkna	White bream	16	3						57	16	60
Carassius auratus	Goldfish								1		1
Carassius gibelio	Prussian carp	14	9		6	29	11			43	26
Chondrostoma nasus	Common nase	3	105	345	20	3	1		1	351	127
Cottus gobio	Bullhead			35	28			3	157	38	185
Cyprinus carpio	Common carp	18	9	1	5	27				46	14
Esox lucius	Northern pike	6		12	2	58		1	10	77	12
Gasterosteus aculeatus	Three-spined stickleback		15	2			3		12	2	30
Gobio gobio	Gudgeon	4	29	217	118	8	20			229	167
Gymnocephalus cernua	Ruffe	1	5	42	72		13			43	90
Hucho hucho	Danube salmon								2		2
Lampetra planeri	European brook lamprey		10								10
Lepomis gibbosus	Pumpkinseed	11	4							11	4
Leucaspius delineatus	Sunbleak	1								1	
Leuciscus idus	Ide		2	2	1					2	3
Leuciscus leuciscus	Common dace	132	196	275	80	2	1		1	409	278
Lota lota	Burbot				1	2	3	2	5	4	9
Neogobius melanostomus	Round goby	999	103			188	31			1,187	134
Oncorhynchus mykiss	Rainbow trout							51	5	51	5
Perca fluviatilis	European perch	51	51	67	80	57	11	20	98	195	240
Phoxinus phoxinus	Eurasian minnow			26	21				1	26	22
Ponticola kessleri	Bighead goby	21	8			9	7			30	15
Proterorhinus semilunaris	Tubenose goby	49	62			32	8			81	70
Pseudorasbora parva	Topmouth gudgeon	11	302	3	2	3	60		1	17	365
Rhodeus amarus	European bitterling	4	7	1						5	7
Rutilus rutilus	Roach	537	255	1,840	397	4,155	250		193	6,532	1,095
Salmo trutta	Brown trout	5	241		19		12	1	6	6	278
Sander lucioperca	Pike-perch	4	151			5	33		1	9	185
Scardinius erythrophthalmus	Rudd	1	16	215	20	127	53		3	343	92
Silurus glanis	European catfish	3	2	4	4		7		4	7	17
Squalius cephalus	Chub	344	8	181	29			20	37	545	74
Thymallus thymallus	European grayling		2		2			40	201	40	205
Tinca tinca	Tench	9	15		2	24	40		1	33	58
Number of species		**29**	**32**	**20**	**25**	**20**	**21**	**8**	**26**	**36**	**39**
Number of individuals		**2,607**	**2,491**	**3,368**	**965**	**4,810**	**579**	**138**	**867**	**10,923**	**4,902**

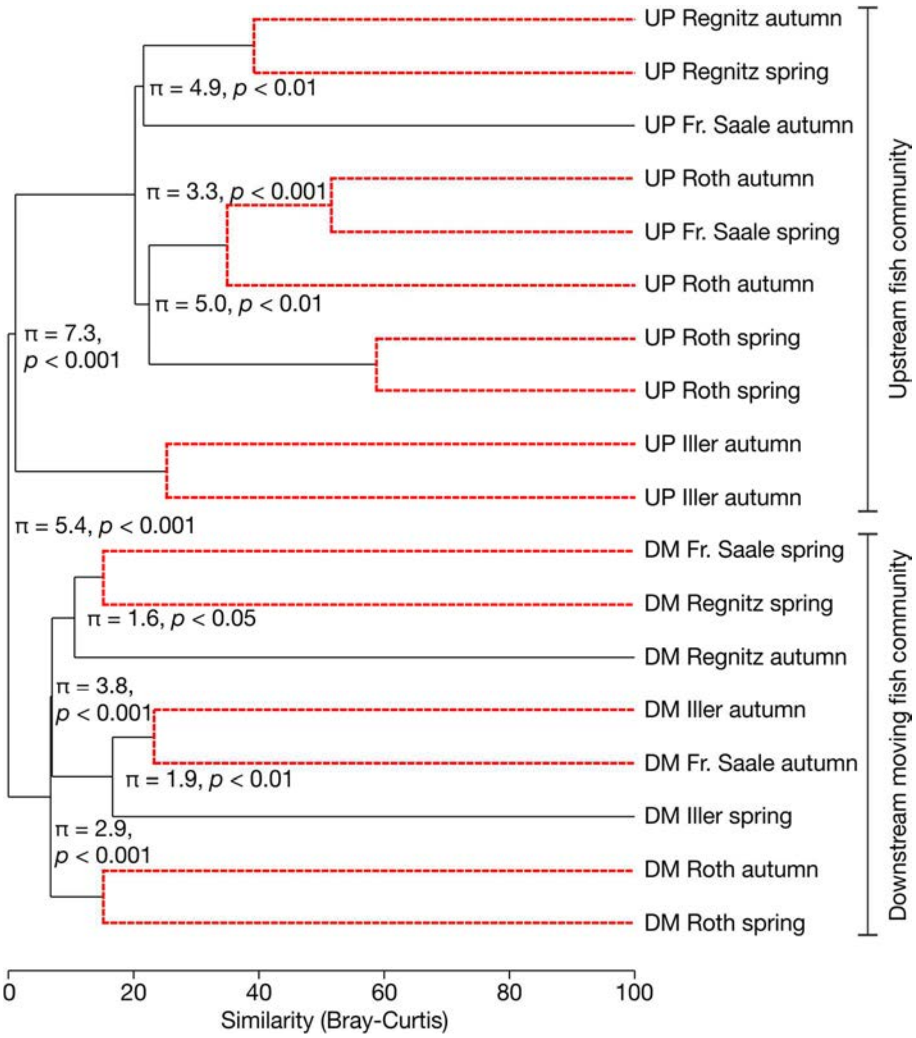


Figure 3.2 Dendrogram for hierarchical clustering (using group-average linking) of the upstream fish community (UP) and the downstream moving fish community (DM) in the four study rivers at two seasons, spring and autumn, based on Bray-Curtis similarities (cophenetic correlation = 0.96, $p \leq 0.05$). Continuous black lines indicate significant tree structure, which is supported by SIMPROF tests, red dashed lines indicate no further significant tree structure. For every significant sub-structure the test statistic (π) and the significance value (p) is presented at each branch.

The average fish length of the five most abundant species of each study river, which were present both in the UP and in the DM, was significantly larger in the DM than in the UP at the study rivers Regnitz, Franconian Saale and Roth (Regnitz: Mann-Whitney U-test: $W = 774550$; $p < 0.001$; Franconian Saale: Mann-Whitney U-test: $W = 386390$; $p < 0.001$; Roth: Mann-Whitney U-test: $W = 592850$; $p < 0.001$). However, the largest individuals in these rivers were caught in the UP. Only at the Iller, the average fish length of the five most abundant species was significantly larger in the UP than in the DM (Mann-Whitney U-test: $W = 37202$; $p < 0.001$), while the largest individuals were caught in the DM (Table 3.3).

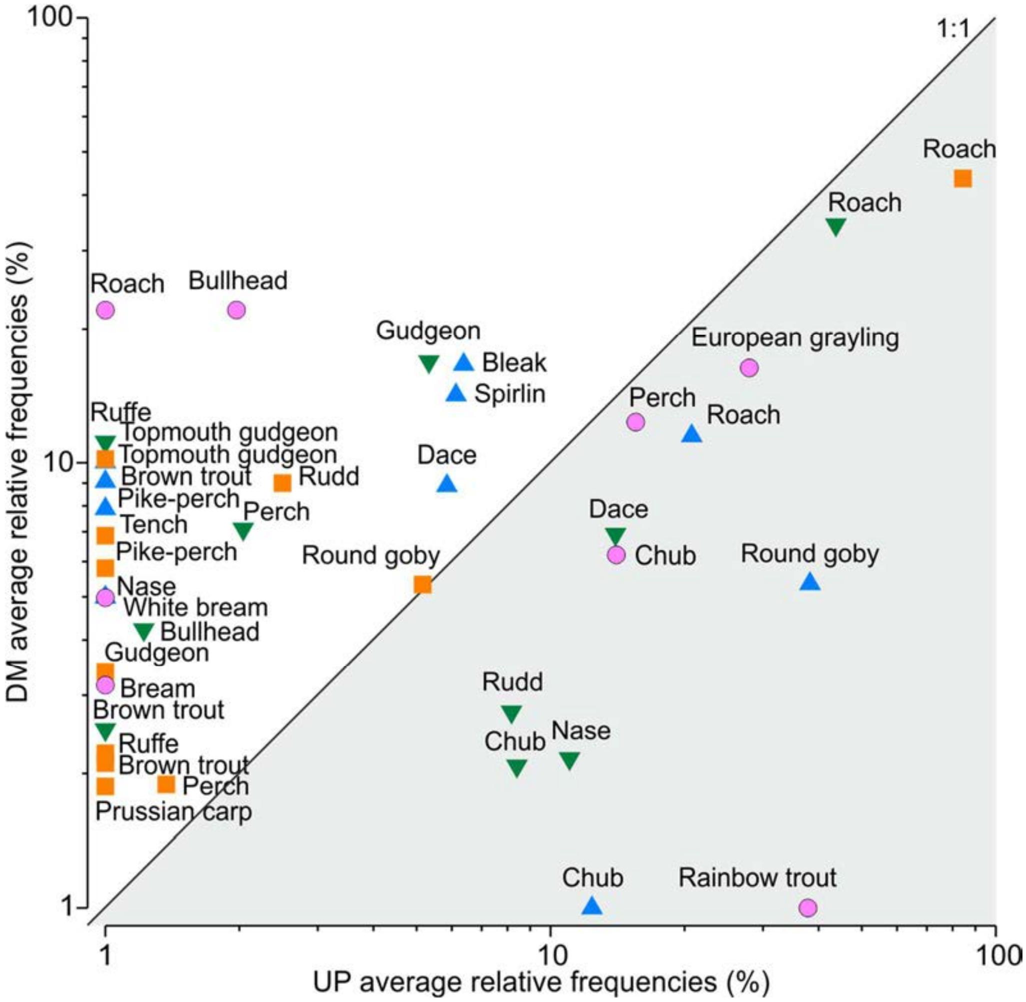


Figure 3.3 Scatterplot of the average abundance (based on relative frequencies (%)) of upstream resident and downstream moving fishes, which contributed most to the dissimilarity between the upstream fish community (UP) and the downstream moving fish community (DM) according to SIMPER (cut-off value 90%). Different colored symbols indicate species from different study rivers: ▲ = Regnitz, ▼ = Franconian Saale, ■ = Roth, ● = Iller.

In 10 out of 20 comparisons of the median total fish length of the five most abundant species in each study river, there was a significant difference between UP and DM (Figure 3.4). However, only marginal differences in minimum and maximum fish lengths for species caught both in UP and DM were found (Figure 3.4), suggesting that no gear-related exclusion effect on species and sizes prevails. This is also supported by the finding that even species that were exclusively caught in the DM (total length from 1.8 to 80.0 cm) were of a body size that was frequently detected at upstream sides of the dams (total length from 1.0 to 91.0 cm; Table 3.3).

Table 3.3 Average total fish length (cm) of all species of the upstream fish community (UP) and the downstream moving fish community (DM) and average total fish length (cm) of species, which were exclusively present in the upstream fish community (UP exclusively) and exclusively present in the downstream moving fish community (DM exclusively) recorded at each study river and overall study rivers (Overall). Within the cells of the table the arithmetic mean, the standard deviation (±) and the minimum and maximum values (in parentheses) are presented.

	Regnitz	Franconian Saale	Roth	Iller	Overall
HW	10 ± 8 (2-91)	6 ± 7 (2-85)	9 ± 8 (1-78)	26 ± 16 (1-56)	8 ± 8 (1-91)
HW exclusively	38 ± 23 (6-66)	4 ± 0.5 (3-4)	29 ± 19 (5-65)	NA	28 ± 20 (3-66)
DM	11 ± 5 (2-75)	9 ± 7 (2-82)	10 ± 5 (2-45)	9 ± 7 (2-80)	10 ± 6 (2-82)
DM exclusively	11 ± 6 (3-24)	14 ± 6 (4-24)	15 ± 9 (4-41)	6 ± 7 (2-80)	8 ± 8 (2-80)

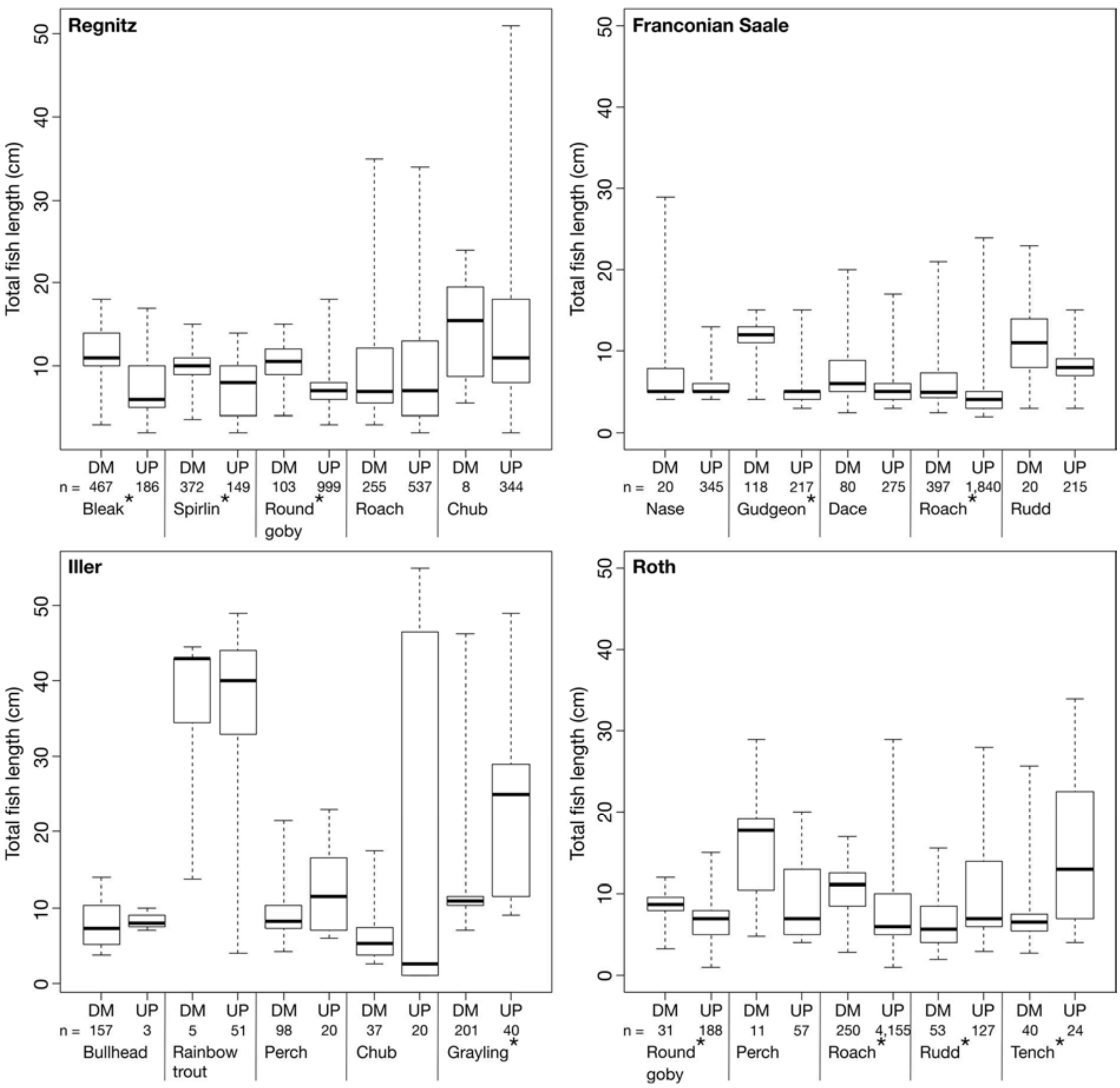


Figure 3.4 Total fish length (cm) of the five most frequent species of each study river that were present both in the upstream fish community (UP) and in the downstream moving fish community (DC). Box: 25% quantile, median, 75% quantile; whisker: minimum, maximum values. Superscript stars indicate significant differences ($p \leq 0.05$) in the total length of the respective species between UP and DM; n = number of individuals.

3.4.2 Downstream fish movement

During the entire study period, an average of two individuals per hour moved downstream (Table 3.4). The highest absolute movement rate was detected at the river Regnitz with six fish per hour. However, considering the different levels of discharge of the investigated rivers, more fish per m^3 of water volume were caught in the small rivers than in the large ones. Based on 1,000 m^3 of discharge, in the river Roth 0.15 individuals moved downstream, followed by the Franconian Saale with 0.10 individuals, the Regnitz with 0.07 individuals and the Iller with 0.03 individuals (Table 3.4).

There was a significant positive relation of the turbidity (Spearman rank correlation, *rho* = 0.38; $p < 0.001$), the water temperature (Spearman rank correlation, *rho* = 0.43; $p < 0.001$) and the discharge (Spearman rank correlation, *rho* = 0.41; $p < 0.001$) of the four investigated study rivers, within the ranges of variables given in Table 3.1, with the number of downstream moving fish.

Table 3.4 Number of sampling days and total sampling time during the assessment of the downstream moving fish community at the different study rivers in spring and in autumn as well as number of fish caught per hour. Arithmetic mean, standard deviation (±) and minimum and maximum values (in parentheses) are presented. Additionally the mean number of downstream moving fish during the whole study period per 1,000 m^3 of discharge (Overall fish/1,000 m^3) was calculated and shown at the bottom of the table.

		Regnitz	Franconian Saale	Roth	Iller	Overall
Sampling period	Spring: days (hours)	11 (174)	12 (246)	20 (285)	24 (494)	66 (1,197)
	Autumn: days (hours)	14 (138)	22 (363)	21 (263)	17 (192)	74 (956)
Fish caught per hour	Daytime	3 ± 4 (0–18)	2 ± 8 (0–72)	1 ± 2 (0–12)	1 ± 3 (0–35)	1 ± 4 (0–72)
	Nighttime	9 ± 6 (0–28)	1 ± 1 (0–5)	1 ± 2 (0–10)	4 ± 6 (0–33)	3 ± 5 (0–33)
	First half of the day	2 ± 2 (0–10)	3 ± 12 (0–72)	1 ± 1 (0–6)	0 ± 1 (0–7)	1 ± 5 (0–72)
	Second half of the day	3 ± 3 (0–12)	1 ± 2 (0–13)	1 ± 2 (0–12)	1 ± 4 (0–35)	1 ± 3 (0–35)
	First half of the night	11 ± 5 (4–21)	2 ± 1 (0–5)	2 ± 2 (0–10)	6 ± 8 (0–33)	4 ± 5 (0–33)
	Second half of the night	8 ± 7 (0–28)	1 ± 1 (0–4)	1 ± 1 (0–3)	3 ± 4 (0–14)	3 ± 5 (0–28)
	Spring	7 ± 5 (1–18)	1 ± 1 (0–5)	1 ± 2 (0–12)	0 ± 1 (0–8)	1 ± 3 (0–18)
	Autumn	5 ± 6 (0–28)	2 ± 7 (0–72)	1 ± 2 (0–11)	4 ± 7 (0–35)	3 ± 6 (0–72)
	Overall	6 ± 6 (0–28)	2 ± 6 (0–72)	1 ± 2 (0–12)	2 ± 5 (0–35)	2 ± 5 (0–72)
	Overall fish/1,000 m^3	0.07	0.10	0.15	0.03	0.09

3.4.3 Seasonal variation of movement patterns

Considering all study rivers, twice as many downstream moving fish per hour were caught in autumn (2.5 fish/h) than in spring (1.2 fish/h; Mann-Whitney U-test: $W = 61436$; $p < 0.001$). The Regnitz was the only study river where more fish per hour moved downstream in spring (Av. 7 fish/h, SD 5 fish/h) than in autumn (Av. 5 fish/h, SD 6 fish/h; Table 3.4).

In each study river fish community composition differed significantly between spring and autumn (Table 3.5). Throughout all study rivers roach, common dace, European perch (*Perca fluviatilis*, L. 1758), nase (*Chondrostoma nasus*, L. 1758), European grayling and pike-perch

(*Sander lucioperca*, L. 1758) were consistently detected by SIMPER analyses in higher abundances in autumn than in spring (Figure 3.5). In contrast, topmouth gudgeon, bleak, spirlin, gudgeon, ruffe and rudd (*Scardinius erythrophthalmus*, L. 1758) more frequently moved downstream in spring. In addition to topmouth gudgeon, the average abundance of spirlin and bleak was more than twice as high in spring than in autumn at the river Regnitz. Gudgeon and ruffe were typical species that moved downstream predominantly in spring at the river Franconian Saale. At the river Iller, only a few fish species (e.g. stone loach (*Barbatula barbatula*, L. 1758), brown trout (*Salmo trutta*, L. 1758), chub) moved downstream in spring in a higher average abundance than in autumn, but with a very low contribution to the dissimilarity between the seasons. European grayling was the most frequently downstream moving species at the river Iller in autumn followed by roach and bullhead. At the rivers Regnitz, Franconian Saale and Roth fish downstream movement in autumn was dominated by roach. Furthermore, at these rivers pike-perch, brown trout and common dace were typical species, which were mainly detected in autumn (Figure 3.5).

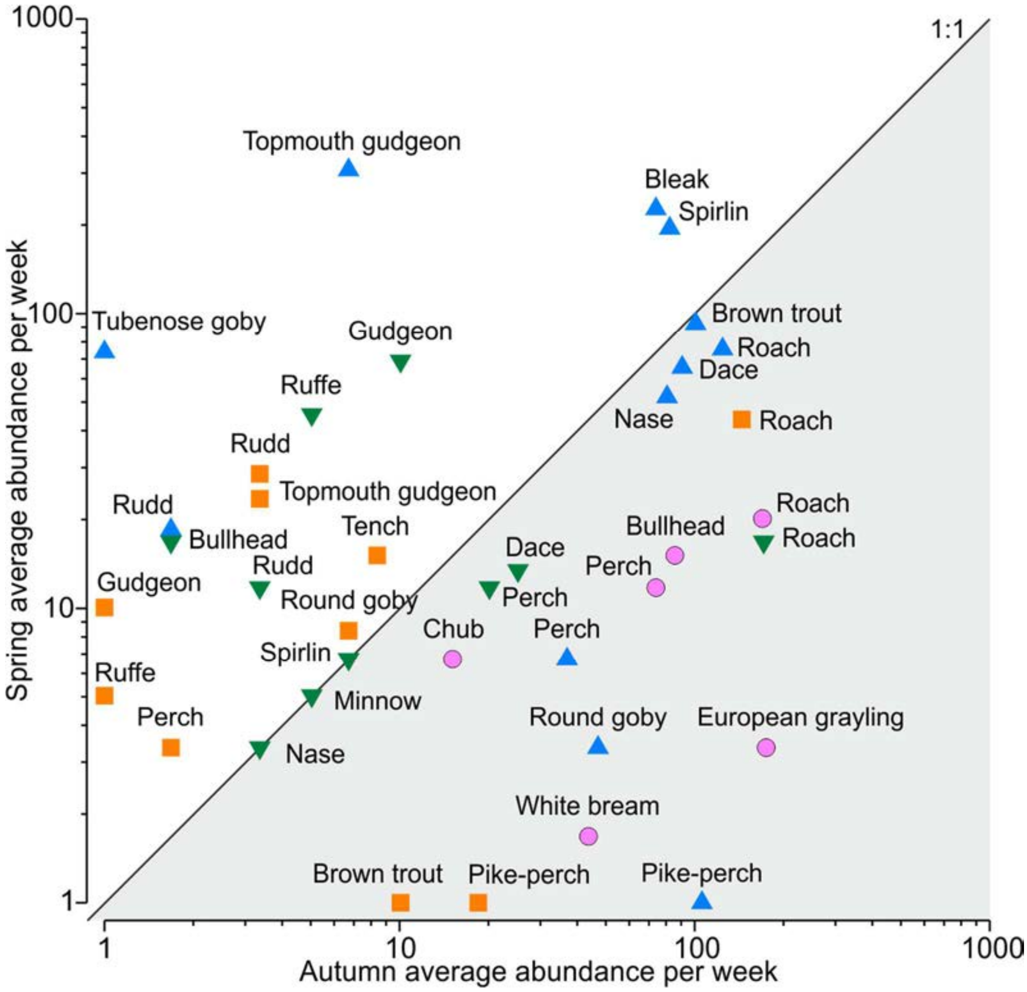


Figure 3.5 Scatterplot of the average abundance of downstream moving fishes per week, which contributed most to the dissimilarity between spring and autumn according to SIMPER (cut-off value 90%). Different colored symbols indicate species from different study rivers: ▲ = Regnitz, ▼ = Franconian Saale, ■ = Roth, ● = Iller.

3.4.4 Diurnal variation of movement patterns

On average, significantly more fish per hour moved downstream during the night (2.9 fish/h) than during the day (1.3 fish/h) (Mann-Whitney U-test: $W = 103090$; $p < 0.001$). Moreover, there was a significant difference in the DM between day and night, both in spring and in autumn, in each of the study rivers and over all study rivers (Table 3.5). There was no significant difference in the DM and the number of fish caught during the first and the second half of the day and the first and the second half of the night. Considering the diurnal variation in different seasons, the same trend was observed for the comparison of the different halves of day except for the pairwise comparison of the first and the second half of the day in spring at the Iller (ANOSIM: Global $R = 0.02$; $p < 0.05$) and of the first and the second half of the night in autumn at the Roth (ANOSIM: Global $R = 0.12$; $p < 0.001$).

Table 3.5 Global *R* values from the analysis of similarities (ANOSIM) pairwise comparisons of the downstream moving fish community in the four study rivers and overall study rivers (Overall) for the investigated seasons and different times of day. Superscript stars indicate significant differences of the pairwise comparisons, with the significance levels * = significance ($p < 0.05$), ** = high significance ($p < 0.01$) and *** = highest significance ($p < 0.001$).

Pairwise-tests		Regnitz	Franconian Saale	Roth	Iller	Overall
Spring	Autumn	**0.29*** **	**0.16***	**0.04****	**0.28*****	0.01
Day	Night	**0.27*****	**0.05****	**0.08*****	**0.39*****	**0.14*****
Spring daytime	Spring nighttime	**0.27*****	**0.30*****	**0.22*****	**0.51*****	**0.31*****
Autumn daytime	Autumn nighttime	**0.40*****	**0.03***	**0.05****	**0.24*****	**0.06*****
First half of day	Second half of day	0.02	-0.01	-0.01	0.00	0.00
First half of night	Second half of night	0.07	-0.04	0.01	-0.03	0.00
Spring first half of day	Spring second half of day	-0.14	-0.24	0.02	**0.02***	0.00
Spring first half of night	Spring second half of night	0.01	0.00	-0.06	-0.12	-0.03
Autumn first half of day	Autumn second half of day	0.06	0.00	0.00	0.03	0.01
Autumn first half of night	Autumn second half of night	-0.05	-0.02	**0.12*****	-0.02	0.03

According to SIMPER analyses, topmouth gudgeon, European grayling, pike-perch, bullhead, common dace and brown trout preferentially migrated during the night. The most frequently caught species roach moved downstream in higher abundances during the nighttime at the rivers Regnitz and Iller, while it moved downstream more consistently during the daytime at the rivers Franconian Saale and Roth. Spirlin, bleak (mainly at the river Regnitz) and rudd (mainly at the river Roth) were species that moved downstream mostly during the day (Figure 3.6).

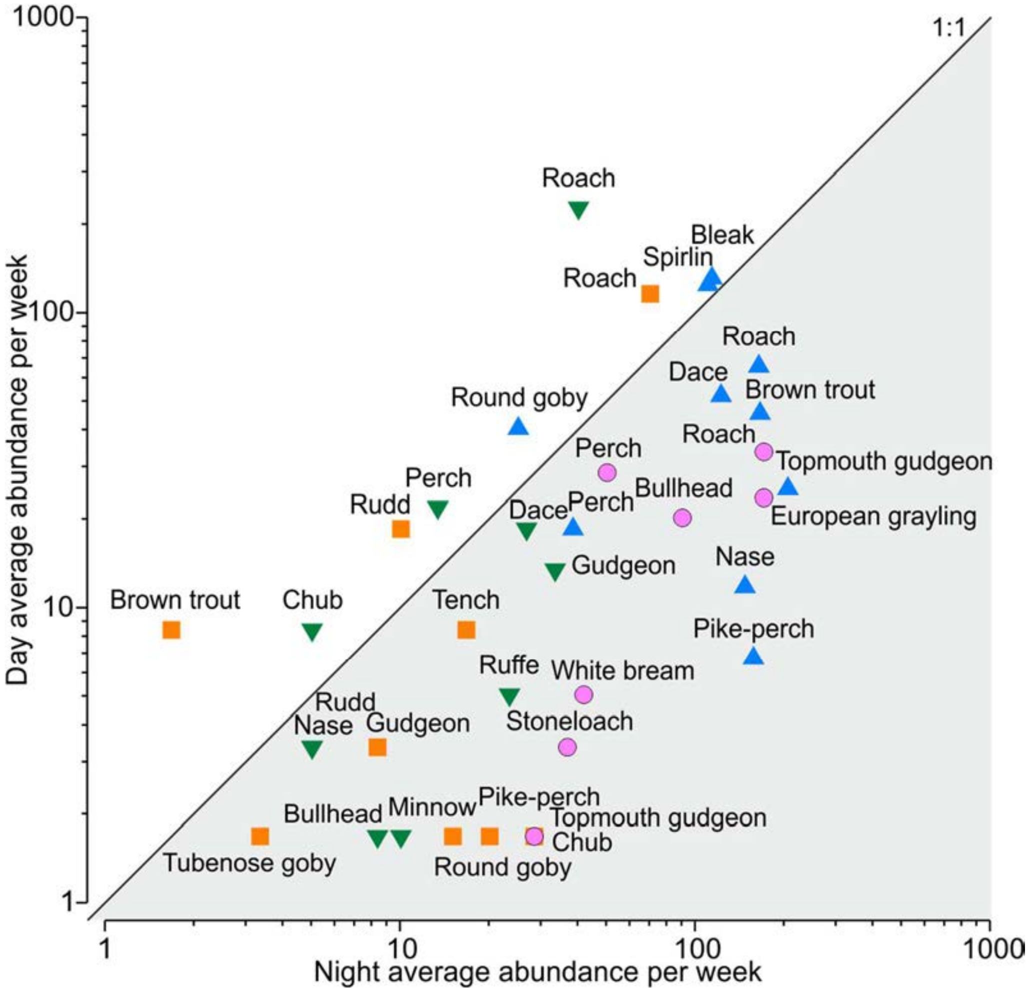


Figure 3.6 Scatterplot of the average abundance (based on relative frequencies (%)) of upstream resident and downstream moving fishes, which contributed most to the dissimilarity between the upstream fish community (UP) and the downstream moving fish community (DM) according to SIMPER (cut-off value 90%). Different colored symbols indicate species from different study rivers: ▲ = Regnitz, ▼ = Franconian Saale, ■ = Roth, ● = Iller.

3.5 Discussion

Although there is a wide body of literature dealing with the movement behaviour of individual fish species, there are few studies that consider the entire fish community, particularly potamodromous species. This is surprising since knowledge on seasonal and diurnal fish downstream movement is a key component for the assessment of possible negative effects of hydropower plants on fish populations and needs to be integrated more efficiently into the operational management of hydropower plants for both ecological and animal welfare reasons. The novelty of this study is that it examined seasonal and diurnal downstream movement patterns of the entire fish community in relation to the detected species assemblage directly upstream of small-scale hydropower plants.

3.5.1 Seasonal and diurnal variation of movement patterns

Fish downstream movement occurred mostly during the nighttime and in autumn. Many authors have already stated that downstream movement predominantly takes place during darkness (Jonsson, 1991). Downstream movement at night is probably an adaption to minimize predation risk from visual predators and therefore increase survival rates (Jonsson, 1991; Lucas & Baras, 2001). Not only the number of downstream moving fish, but also the species composition varied between day and night. This is due to the fact that the daily cycle of sunrise and sunset decisively influences the behaviour and activity of fishes. Fish differ in their behaviour due to feeding, spawning or resting at different times of the day, which forces them to move between different habitats (Helfman, 1986). The DM during daytime was dominated by small species of the cyprinids family like roach, spirlin, bleak and rudd. In contrast, the DM during nighttime was much more diverse, mainly consisting of nocturnal predators (e.g. pike-perch), salmonids (e.g. European grayling, brown trout), bottom- (bullhead) and surface-oriented (topmouth gudgeon) fish. Only a few species revealed an exclusive preference for a specific time of day to move downstream (e.g. pike-perch at nighttime). Most species showed a bimodality in downstream movement with single detections during the day and an increased downstream movement during night. Since no pronounced differences in movement rates of the DM between the first and the second half of the day and the first and the second half of the night could be detected, it is likely that the main trigger for the behavioural change is the availability of daylight.

Differences in downstream movement rates between spring and autumn predominantly result from species-specific seasonal movements and behaviour which include remigration after spawning, food availability, drift of larvae, competition or colonization (Larinier & Travade, 2002; Lucas & Baras, 2001). In this study, rudd, topmouth gudgeon and gudgeon were the most frequent downstream moving species in spring, while the DM in autumn was dominated by roach, pike-perch and European grayling. The observed movement patterns of the fish community differed significantly between the study rivers, even for the very same fish species. This indicates that findings on the downstream movement of fish in a specific river can hardly be transferred to other rivers, because biotic (e.g. species inventory) and abiotic (e.g. water chemistry, size, discharge, geographical location) river characteristics may decisively influence downstream movement patterns. Beside the different mean discharge of the study rivers, also the change in discharge and other abiotic river characteristics could have a significant effect on the number of migrating fishes (Jonsson, 1991; Pavlov et al., 2008), which was also supported by the results of this study. In general, many fish migrate downstream in autumn after spawning to reach their deeper and less current-exposed foraging and winter habitats (Lucas & Batley, 1996). The seasonal pattern of passive displacement of fish larvae and juvenile fish is mainly dependent on spawning times and hydrological conditions (Sonny et al., 2006). In addition to foraging and passive drifting, downstream spawning migrations may also play a role in spring, as reported for chub, roach and dace (Champion & Swain, 1974; Fredrich et al., 2003). In this study, we could not detect any peak downstream movements of single species during their main spawning season.

3.5.2 Interrelation between upstream fish community and downstream moving fish

In this study, the resident UP did not match the complete set of species and sizes of the DM, suggesting a bias if only one of them is being considered (as done in most studies). There were both species- and size-specific differences between the UP and the DM that are unlikely to be attributed to a potential gear bias, because with both methods the smallest as well as the largest fish sizes could be detected. The greater species richness of the DM compared to the UP could be explained by the fact that species from upstream tributaries or backwaters only temporarily migrate into the main stream to move downstream and pass the hydropower plant. The upstream sides of low head hydropower plants usually provides deeper habitats with less flow current speed compared to the downstream sites. Such habitats are mainly dominated by ubiquitous species with no specific current preference (Mueller et al., 2011; Slawski et al., 2008). Large individuals of short-distance migrators like northern pike (*Esox lucius*, L. 1758), common carp (*Cyprinus carpio*, L. 1758), bream (*Abramis brama*, L. 1758) and European catfish (*Silurus glanis*, L. 1758), rarely moved downstream during the study period. The likelihood that large fish could have escaped from the stow-nets due to their strong swimming speed is assumed to be low due to the construction of the net and the applied short emptying intervals (Pander et al., 2018a). For large individuals of these species downstream sites at dams are probably less suited as habitat, because of the shallower water level and the faster current speed compared to the upstream sides of the dams. Additionally, large individuals may be prevented from downstream movement by fish protection screens installed at the turbine inlets if bypass efficiency is low (Larinier & Travade, 2002; Noonan et al., 2012).

Moreover, the tenfold higher proportion of detected juvenile fish ≤ 3 cm in the UP compared to the DM, mainly of medium-sized species such as roach, chub and rudd, was responsible for the significant difference in the length-frequency distribution between UP and DM. The upstream sides of the dams are probably suitable as spawning habitat for these ubiquitous species and therefore a high number of juvenile fish could be detected there. On the other hand, it is possible that some of the downstream drifting juvenile fish could not be detected by the stow-nets used (mesh size fish trap 8 mm), since very small fish can potentially escape from the net. Based on the highly similar minimum and maximum sizes of all species in the UP and DM as well as the more frequent (topmouth gudgeon, three-spined stickleback (*Gasterosteus aculeatus*, L. 1758), stone loach, bullhead) or exclusive (brook lamprey (*Lampetra planeri*, Bloch 1784)) detection of several small-bodied species (total length from 2.0 to 19.5 cm) in the net-based catch of the DM compared to the electrofishing-based catch of the UP (Table 3.2) all suggest a minor importance of a gear-based bias at least.

3.5.3 Conclusions and adaptive management implications

The results of this study indicate that fish protection at hydropower plants and other river infrastructure (e.g. pumping stations) in general is most crucial during night in autumn. They also suggest that there is sufficient variation in seasonal and diurnal movement patterns to substantiate consideration of these findings in the adaptive management of such facilities. Knowledge on the main movement activity times can be used to operate them in the most fish-friendly way with a wide range of options that can be applied. The most promising management option is the complete shut-down of the turbines at peak movement times, particularly if the main movement happens within short periods of time. Alternative options include opening of additional corridors such as undershot sluice gates which has been demonstrated to be successful in mitigating silver eel downstream migration (Egg et al., 2017), and/or increasing water discharge to bypass channels (Pander et al., 2013). In addition, operational adjustments such as running one turbine at maximum capacity instead of running two turbines at lower capacity can be an adaptive management tool for certain species and turbine types (Ebel, 2013). Since movement patterns were also highly species- and river-specific, management needs to be adapted to the river-specific fish community. To achieve this, a preliminary monitoring of downstream movement is necessary, since single samplings of the UP using electrofishing turned out not to be a sufficient proxy for the DM. Monitoring of downstream moving fish should consider different seasons and different times of day. Sampling should include several replicate intervals both during day and during night as well as measurements of abiotic parameters to link catch data with abiotic stream characteristics, and use changes in these variables to predict fish movement and guide hydro turbine management decisions.

4 Fish passage and injury risk at a surface bypass of a small-scale hydropower plant

A similar version of this chapter was published: Knott, J., Mueller, M., Pander, J. & Geist, J. (2019). Fish Passage and Injury Risk at a Surface Bypass of a Small-Scale Hydropower Plant. *Sustainability*, 11, 6037.

Author contributions: The concept and methodology of this study were designed by JK, MM, JP and JG. The standardized fish experiments at the movable hydropower plant were mainly performed by JK and MM. Data verification, statistical analysis, data interpretation and presentation was done by JK. The original draft was prepared and finalized by JK. Amendment, revision and editing of the article was jointly done by JK, MM, JP and JG.

4.1 Abstract

In contrast to the efforts made to develop functioning fishways for upstream migrants, the need for effective downstream migration facilities has long been underestimated. The challenge of developing well-performing bypasses for downstream migrants involves attracting the fish to the entrance and transporting them quickly and unharmed into the tailrace. In this study, the acceptance of different opening sizes of a surface bypass as well as the injuries which fish experience during the passage were examined. Overall bypass acceptance was low compared to the turbine passage. There was no significant difference in the number of downstream moving fish between the small and the large bypass openings. Across all fish species, no immediate mortality was detected. Severe injuries such as amputations or bruises were only rarely detected and at low intensity. Scale losses, tears and hemorrhages in the fins and dermal lesions at the body were the most common injuries, and significant species-specific differences were detected. To increase bypass efficiency, it would likely be useful to offer an alternative bottom bypass in addition to the existing surface bypass. The bypass injury potential could be further reduced by structural improvements at the bypass, such as covering protruding components.

4.2 Introduction

In order to meet the rising global energy demand and to increase the percentage of renewable energies, there is a huge global effort to push ahead the expansion of hydropower (Prado et al., 2016; Zarfl et al., 2015). The construction of dams and hydropower plants can result in reduced serial continuity and habitat changes in streams, mainly from the fragmentation and the change in the hydrological conditions of the affected river systems (Grill et al., 2015; Mueller et al., 2011; Nilsson et al., 2005). As a result, upstream and downstream fish migrations are often impaired or even impossible (Larinier, 2000; Lucas & Baras, 2001), which can lead to population declines or extinctions, particularly in migratory fish populations (Noonan et al., 2012; Northcote, 1998).

In contrast to the efforts made to develop functioning fishways for upstream migrants, the need for effective facilities for downstream migration has long been underestimated (Calles & Greenberg, 2009; Larinier, 2008). During their downstream migration, fish usually tend to follow the main current (Williams et al., 2012) and are therefore often directed to the turbine inlet at many hydropower plants. Since the turbine passage is generally considered the route that most likely harms fish, it is important to develop strategies to bypass or protect fish at power plants to minimize turbine entrainment and associated fish mortality (Čada, 2001; Haro et al., 1998; Schilt, 2007). One option would be to use less harmful turbine types, which reduce the injury potential and increase the survival rate (Čada, 2001; Hogan et al., 2014). Alternatively, physical (e.g. vertical/horizontal bar screens) or behavioural barriers (e.g. louvers, sound/light/electrical screens) are often installed upstream of the turbine inlet to prevent fish from swimming through the turbine and guiding them via alternative corridors into the tailrace (Egg et al., 2019; Larinier & Travade, 2002). Such alternative corridors include spillways, undershot sluice gates, surface and bottom bypasses and nature-like fishways (Egg et al., 2017; Gosset et al., 2005; Lucas & Baras, 2001). The challenge of developing functioning bypasses for downstream migrants involves attracting the fish to the entrance and transporting them quickly and unharmed into the tailrace (Schilt, 2007). Critical points that need to be considered for a successful downstream passage include adequate dimensioning of the bypass, the location of the bypass (top, middle, bottom), proper hydraulic conditions at the entrance and a low fish injury risk of the bypass itself (Katopodis, 2005; Larinier & Travade, 2002; Williams et al., 2012). However, even state-of-the-art downstream migration corridors can cause unexpected problems such as poor fish attraction, inappropriate location of entrances or an increased risk of injury (Calles et al., 2012; Scruton et al., 2002). Therefore, it is important to provide alternative corridors and to examine these in light of their functionality with a properly designed monitoring (Roscoe & Hinch, 2010), analogous to evidence-based concepts in stream restoration (e.g. Geist & Hawkins, 2016). There are already several studies dealing with the acceptance of various downstream migration corridors (e.g. Johnson et al., 2005; Scruton et al., 2007), but studies that also investigate the injury potential of such alternative corridors in a standardized way with a broad range of fish species are rare.

In this study, the acceptance of differently sized openings of a surface bypass, installed in the flap gate of a movable power-plant as well as the injury potential to which fish are exposed during the passage of this route were examined. Specifically, we hypothesized that (i) fish can find the surface bypass and especially large fish that do not fit through the fish protection screen of the turbine are successfully guided to the tailrace, (ii) the percentage of inflow used for surface bypass attraction is proportional to the percentage of downstream moving fish and (iii) fish do not get injured while passing the surface bypass and sliding down to the tailrace.

4.3 Materials and Methods

The animal experiments in this study were carried out following national animal care laws and regulations, and all procedures were approved for appropriate animal care by the ethics commission of the Bavarian government (permit number ROB–55.2–2532.Vet_02–15–31). Discomfort or pain of the fish was minimized according to European standards (European Parliament, 2010) and national guidelines for the use of aquatic animals in scientific experiments (Adam et al., 2013).

4.3.1 Study site

The study was carried out at an innovative movable run-of-the-river hydropower plant in Bavaria, Germany. The power plant is located at the dam of an artificial reservoir (approx. 100 ha) at the river Schwarzach near the city of Rötz (N 49.3396, E 12.4799). The 4.8 m high dam separates the site into a main reservoir and a pre-storage basin. The moveable power plant was installed in winter 2016/2017. It is equipped with a four-bladed Kaplan turbine with 190 kW of installed power at a head of 5.0 m and a maximum flow of 4.5 m³/s (diameter = 1.0 m, drive = 333 rpm). The Kaplan turbine, which is housed in a swiveling steel casing, can be lifted by a hydraulic device, in order to allow sediment transport and downstream movement of aquatic organisms during high flow conditions. As a fish protection device, a round screen with a bar spacing of 20 mm, is installed in front of the 2.64 m wide turbine inlet. To pass the power plant downstream, surface-orientated fish can swim through a permanently opened crest cut-out (CC) in the middle of the flap gate and slide on top of the steel casing into the tailrace (fish slide; Figure 4.1).

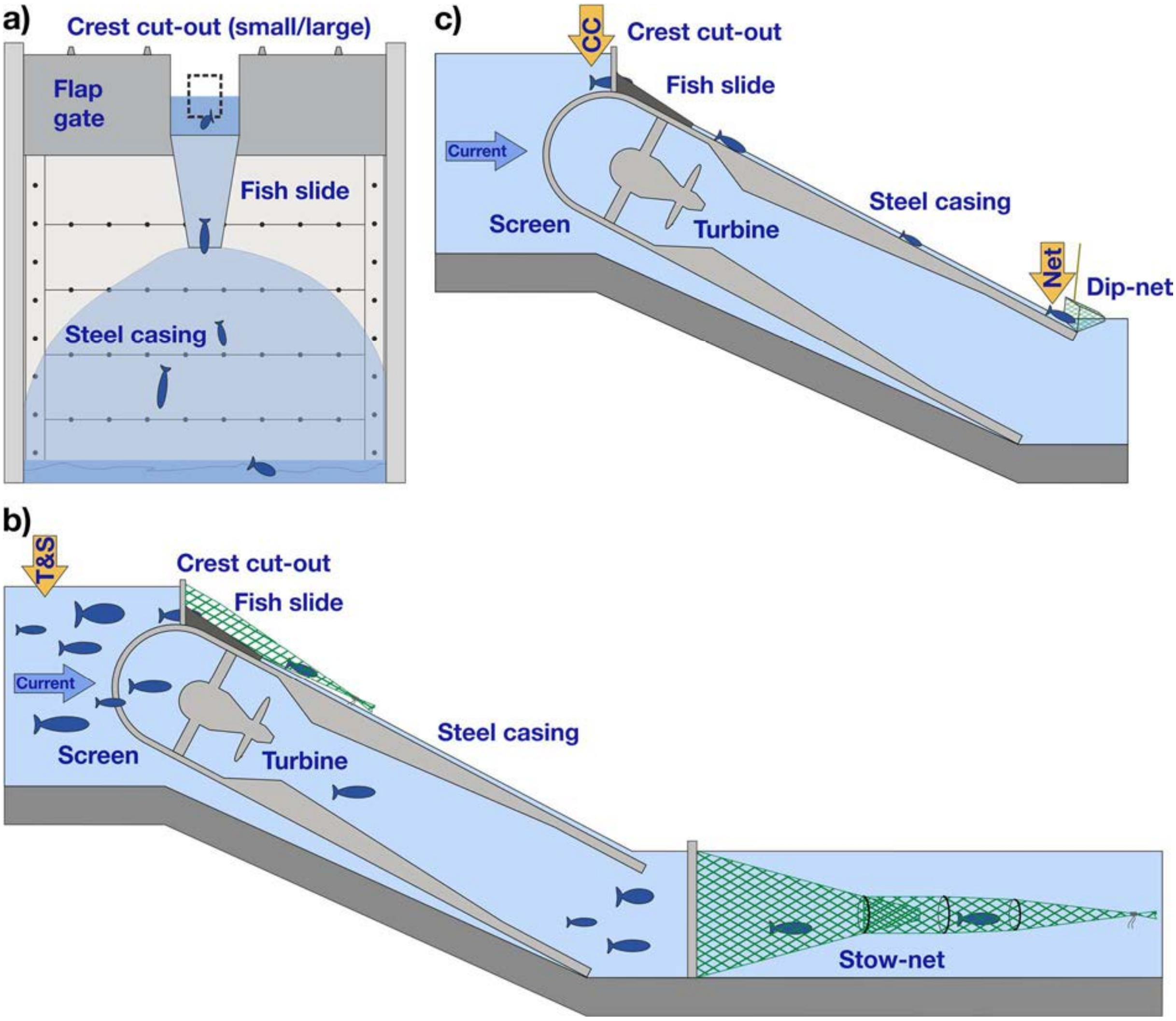


Figure 4.1 Schematic of the hydropower plant and experimental design. Orange arrows = release point of hatchery-reared fish; blue arrows = flow direction; T&S = upstream of the fish protection screen, CC = crest cut-out, Net = entrance of the dip-net. (**a**) View of the hydropower plant from the tailrace. The dotted rectangle symbolizes the small CC. (**b**) Schematic cross-section of the movable power plant. To assess the acceptance of different sized CCs, fish were caught with stow-nets at the fish slide and at the turbine outlet. (**c**) For the assessment of potential injuries, fish of the treatments CC and Net were caught with a dip-net at the bottom of the steel casing.

4.3.2 Experimental design

To assess the acceptance and the fish injury risk of the downstream migration corridor CC, eight hatchery-reared fish species were used, which were transported from the fish hatcheries to the hydropower plant one day before the experiments started. Fish were transferred into rectangular tanks (300 cm × 70 cm × 70 cm, Aquacultur Fischtechnik GmbH, Nienburg, Germany) after being adapted to reservoir temperature and water chemistry. Fresh water from the tailrace was permanently supplied to the tanks by a submersible motor pump (Easy-Mix-U20, Aquacultur Fischtechnik GmbH, Nienburg, Germany).

4.3.2.1 Acceptance of different sized crest cut-outs

In April 2018, two different opening sizes of the CC installed in the middle of the flap gate were comparatively examined for their acceptance as a downstream migration corridor. The mean flow rate through the small CC (27.6 cm × 36.0 cm) is approx. 26 L/s (0.6% of the turbine flow) at a water depth of 9.0 cm in the CC and a maximum turbine flow rate of 4.5 m³/s. About 160 L/s (3.6% of the turbine flow) flow through the large CC (59.0 cm × 71.0 cm) at a water depth of 18.5 cm in the CC and a maximum turbine flow rate of 4.5 m³/s. The different opening sizes were the two construction options provided by the power plant operator. The small opening was designed according to the operator's ideal conception (low loss of turbine discharge) and the larger opening complies with the minimum requirements according to Ebel (2013). There were almost no variations in physical and chemical water parameters, which were measured three times a day during the investigation period of the small and the large CC (Table 4.1).

Table 4.1 Arithmetic mean, standard deviation (±), minimum and maximum values (in parentheses) for the measured physical and chemical parameters during the investigation period of the small and the large crest cut-out. Discharge = total discharge through turbine and crest cut-out. Current speed was measured in the headrace channel.

	small crest cut-out	large crest cut-out
Turbidity (NTU)	3.4 ± 0.7 (2.4–4.1)	3.1 ± 0.5 (2.3–3.9)
Dissolved oxygen (mg/L)	9.9 ± 0.4 (9.3–10.6)	10.1 ± 0.5 (9.5–10.7)
Temperature (°C)	12.1 ± 0.2 (11.9–12.3)	11.1 ± 0.2 (10.9–11.5)
pH-value	7.7 ± 0.1 (7.6–7.8)	7.5 ± 0.1 (7.3–7.7)
Electric conductivity (µS/cm)	179 ± 4 (175–184)	174 ± 4 (170–178)
Discharge (m³/s)	3.2 ± 0.1 (3.0–3.3)	3.0 ± 0.2 (2.8–3.3)
Current speed (m³/s)	0.38 ± 0.02 (0.36–0.40)	0.40 ± 0.02 (0.38–0.43)

In order to determine the downstream movement rate through the turbine corridor and the two different sized CCs, a total of 6,888 individuals of the fish species grayling (*Thymallus thymallus*, L.), brown trout (*Salmo trutta*, L.) and barbel (*Barbus barbus*, L.; Table 4.2) were released directly into the headrace channel of the hydropower plant. Fish were transferred into a 40 L bucket and carefully stocked about 5 m upstream of the power plant over a period of four consecutive days, while both the small and the large CC were installed at the same position in the flap gate on two days each. Fish passing through the turbine and the CC were caught with knotless stow-nets of decreasing mesh size and narrowing diameter, applying 1 h emptying intervals (8 am–6 pm) to minimize the catch-related damage to fish (Pander et al., 2018a). The rectangular opening of the stow-nets was knotted to a metal frame with each mesh, allowing the fixation in u-profiles and covering 100% of the flow-through. To recover the fish, the cod-end was opened, the trapped fish were transferred into a large water-filled bin and supplied with oxygen. Each individual was identified to species level and total length was measured.

Table 4.2 Total number of test fish (N_{total}), number of caught fish in the crest cut-out (N_{caught} CC) and in the turbine (N_{caught} TU), arithmetic mean (AM), standard deviation (SD), minimum (MIN) and maximum (MAX) of the total fish length (TL) in cm as well as ratio of the percentage of captured fish to the percentage of inflow for the crest cut-out (N_{CC} (%)/inflow $_{CC}$ (%)) and the turbine (N_{TU} (%)/inflow $_{TU}$ (%)) during the investigation period of the small and the large crest cut-out.

	Grayling		Brown trout		Barbel		Overall	
	small	large	small	large	small	large	small	large
N_{total}	754	721	1,509	1,442	1,226	1,236	3,489	3,399
N_{caught} CC	22 (5.7%)	27 (8.0%)	61 (25.6%)	76 (32.6%)	4 (0.7%)	0 (0.0%)	87 (7.4%)	103 (9.7%)
N_{caught} TU	364 (94.3%)	312 (92.0%)	177 (74.4%)	157 (67.4%)	549 (99.3%)	487 (100.0%)	1,090 (92.6%)	956 (90.3%)
$TL_{AM \pm SD}$ (cm)	10.9 ± 1.8	10.6 ± 1.6	14.6 ± 8.2	13.1 ± 8.1	8.9 ± 1.5	8.9 ± 1.4	10.7 ± 4.5	10.4 ± 4.4
$TL_{MIN–MAX}$ (cm)	6.9–19.6	7.1–16.0	3.9–38.5	3.6–39.1	6.3–18.2	6.9–17.1	3.9–38.5	3.6–39.1
N_{CC} (%)/ inflow $_{CC}$ (%)	9.9	2.2	44.4	9.2	1.3	0.0	12.8	2.7
N_{TU} (%)/ inflow $_{TU}$ (%)	0.9	1.0	0.7	0.7	1.0	1.0	0.9	0.9

4.3.2.2 Fish injury risk of the downstream migration corridor crest cut-out

For the assessment of potential injuries that fish may experience during the passage of the CC, 660 individuals of eight hatchery-reared fish species (grayling, brown trout, barbel, eel (*Anguilla anguilla*, L.), perch (*Perca fluviatilis*, L.), Danube salmon (*Hucho hucho*, L.), nase (*Chondrostoma nasus*, L.), roach (*Rutilus rutilus*, L.); Table 4.3) were tested in a standardized experiment in which individuals were introduced at specific parts of the power plant. The eight fish species tested were chosen according to their ecological relevance in Bavarian streams and covered different morphological types (Mueller et al., 2017; Pander et al., 2018a).

Table 4.3 List of species and number (N) of fish used to assess the fish injury risk of the downstream migration corridor crest cut-out as well as arithmetic mean (AM), minimum (MIN) and maximum (MAX) of the total length (TL) in cm.

Scientific name	Common name	$N_{\text{Crest cut-out}}$	N_{Net}	TL_{Am}	TL_{Min}	TL_{Max}
Anguilla anguilla	Eel	40	40	44.2	28.0	71.4
Thymallus thymallus	Grayling	40	40	16.5	7.8	28.3
Salmo trutta	Brown trout	43	40	19.3	5.1	35.8
Barbus barbus	Barbel	41	40	10.8	5.8	17.8
Perca fluviatilis	Perch	40	40	11.1	8.5	13.2
Hucho hucho	Danube salmon	41	40	28.8	12.9	39.8
Chondrostoma nasus	Nase	40	40	10.8	7.2	16.5
Rutilus rutilus	Roach	55	40	14.1	11.0	19.4

To quantify fish damage caused by the passage of the CC (fish pass through the opening of the bypass and subsequently slide on top of the steel casing into the tailrace), hatchery-reared fish were used. To account for injuries related to aquaculture, transportation, handling and catching them with the net, two different treatments were applied (CC, Net; Figure 4.1). For the treatment CC, each individual was investigated for its pre-damage first (injuries related to aquaculture, transportation and other handling such as touching and taking them out of the fish tanks) and then introduced directly in front of the entrance of the CC. After passing the CC and the fish slide, every fish was caught individually with a large dip-net at the bottom part of the Kaplan turbine steel casing and then re-evaluated for its injuries by the same person. For the treatment Net, the pre-damage was also evaluated as described above and afterwards every fish was released individually directly into the dip-net and then immediately re-evaluated for its injuries by the same person. Fish injury assessment was carried out as described in Mueller et al. (2017) using a detailed protocol comprising 86 combinations of injury types at different body parts as well as five general fish health criteria. The intensity of a single injury type can vary between 0 (not injured) and 5 (severely injured). The number of injuries per individual fish can reach a maximum of 86, and the injury intensity a maximum of 430 (meaning each injury can be found at each body part with the highest intensity level 5). Staff was intensively trained on the use of the protocol and the scoring system. The same evaluation procedure was followed for all species and treatments. After evaluation, fish were kept in fish tanks with fresh water and oxygen supply for 96 hours to account for potential delayed mortality.

4.3.3 Statistical analyses

To examine the acceptance of the two different sized bypass openings, recapture rates, downstream movement rates per hour and the ratio of the percentage of captured fish passing the surface bypass to the percentage of inflow used for surface bypass attraction were calculated.

For the injury risk assessment of the surface bypass, the number of injuries and the injury intensity of every individual fish were calculated (cf. Mueller et al., 2017). To compare the number of injuries and the injury intensity between treatments and the total lengths of fish passing the turbine or the different sized CCs, univariate statistics were used (software R 3.4.1; R Core Team, 2017). Normality was tested using the Shapiro-Wilk-test and homogeneity of variances was checked using Levene's-test. Exclusively non-parametric tests were used since normality and homogeneity of variances did not apply to any of the data (Mann-Whitney-U-tests for comparison of two groups, Kruskal-Wallis-tests and Bonferroni-corrected post-hoc pairwise Mann-Whitney-U-tests for comparison of more than two groups).

To test for relations between the total lengths of specimens from the tested fish species with the number and intensity of the injuries, mixed effects models were applied using the function "lmer" in R (R Core Team, 2017) package "lme4" (Bates et al., 2014). Response variables were number of injuries and injury intensity. Total length and fish species were set as fixed effects with treatment as a random effect. For model selection, the Akaike Information Criterion (AIC) based on the restricted maximum likelihood (REML) was chosen. The lower the AIC value, the better the fit of the model (Zuur et al., 2009). A similar amount of deviation of the residuals from the predicted values indicates homoscedasticity. Wald chi-square tests were performed to obtain p-values for predictor variables of the best fitting model.

To analyse differences in fish injury patterns between treatments and between species, a multivariate approach was used. For all multivariate analyses, raw data on fish injury intensity were transformed into a resemblance matrix containing similarity values for each comparison of samples (fish individuals). As similarity measure, the Bray-Curtis coefficient was used (Bray & Curtis, 1957). If variables among samples happened to be entirely zero, a zero-adjusted Bray-Curtis coefficient, including a virtual dummy variable being one for all objects, was used as suggested by Clarke et al. (2006).

Differences between multivariate injury patterns of different treatments were analysed using one-way analysis of similarities (ANOSIM) based on Bray-Curtis similarities (Clarke, 1993).

To identify the most common and steadily occurring injury patterns in the different treatments, a one-way similarity percentage analysis (SIMPER; Clarke et al., 2014) was carried out to determine the average intensity of injuries and the contribution to the between group-dissimilarity between treatments. All multivariate analyses were carried out using the statistic software PRIMER v7 (PRIMER-e, Massey University, Auckland, NZ). For all statistical analyses, significance was accepted at $p \leq 0.05$.

4.4 Results

4.4.1 Acceptance of different sized crest cut-outs

Out of a total of 6,888 fish from three species that were released directly upstream of the hydropower plant, 2,236 (32%) individuals were recaptured. Most of the non-recaptured fish presumably remained in the headrace, swam upstream or moved downstream after completion of the investigation. The recapture rate was highest for the grayling with 49%, followed by the barbel with 42% and the brown trout with 16%. During the investigation period of the small CC, a total of 92.6% of the recaptured individuals passed the 20 mm screen and the turbine to reach the tailrace, and 7.4% of the fish moved downstream via the surface bypass (Table 4.2). The percentage of fish using the small CC as downstream migration corridor was highest for brown trout at 25.6%. Only 0.7% of the barbels and 5.7% of the graylings moved downstream via the small CC. During the investigation period of the large CC, 90.3% of the recaptured individuals used the turbine corridor for downstream movement and 9.7% the surface bypass. More brown trout (32.6%) and graylings (8.0%) used the large CC than the small CC as downstream migration corridor. However, no barbels moved downstream via the large CC (Table 4.2). There was no significant difference in the number of downstream moving fish per hour between the small CC and the large CC (Mann-Whitney-U-test: $W = 85$; $p > 0.05$). The ratio of the percentage of captured fish passing the surface bypass to the percentage of inflow used for surface bypass attraction was almost five times higher for the small CC than for the large CC (Table 4.2).

The entire range of fish sizes of the examined grayling (maximum total length 19.6 cm) and barbel (maximum total length 18.2 cm) was able to swim through the vertical round screen of the turbine inlet with a bar spacing of 20 mm. Regarding the brown trout, only individuals up to a total length of 29.4 cm passed the screen and moved downstream through the turbine. According to Ebel (2013) the examined species have a relative body width (= width/total length) of about 0.1 and only individuals with a total length of less than 20 cm should be able to pass the 20 mm vertical screen. Larger brown trout were exclusively detected in the surface bypass (Figure 4.2).

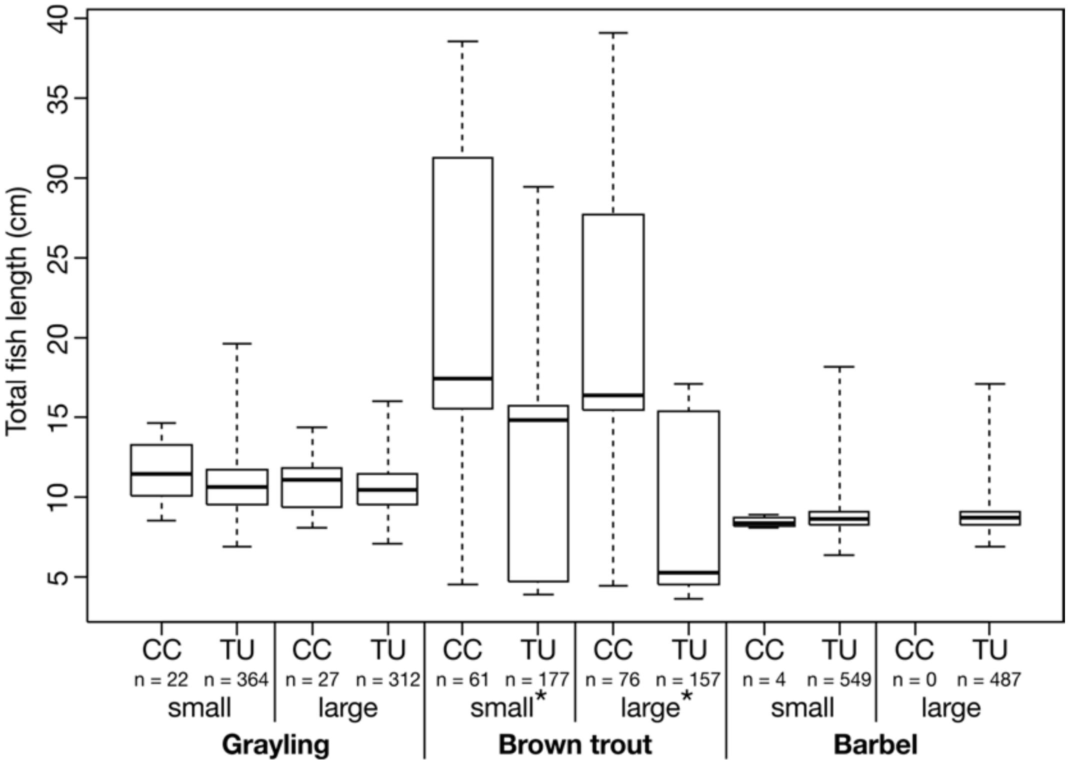


Figure 4.2 Total fish length (cm) of the three test species after the passage of the crest cut-out (CC) and the turbine (TU) during the investigation period of the small and the large CC. Box: 25% quantile, median, 75% quantile; whisker: minimum, maximum values. Asterisks indicate significant differences ($p \leq 0.05$) in the total length between CC and TU; n = number of individuals.

4.4.2 Fish injury risk of the downstream migration corridor crest cut-out

Across all fish species, no immediate mortality was detected in the treatments CC and Net. After an observation period of 96 hours, two individuals of roach from the treatment CC and one brown trout from the treatment Net died. Scale losses, tears and hemorrhages in the fins and dermal lesions at the body were the most common injuries of all fish species studied. Severe injuries such as amputations or bruises were only rarely detected and at low intensity. There was no significant difference in the injury patterns between the pre-damage conditions and the treatments Net and CC (ANOSIM: Global $R = 0.01$, $p > 0.05$) across all fish species. However, injuries like scale loss, tears in the fins, hemorrhages in the head and fins as well as dermal lesions on the head and body occurred at a higher intensity in the treatment CC than in the pre-damage conditions. These injuries were also detected more frequently in the treatment Net than in the associated pre-damage conditions. Both the number (Kruskal-Wallis-test: $X^2 = 76.8$, df = 2, $p < 0.001$) and the intensity (Kruskal-Wallis-test: $X^2 = 64.2$, df = 2, $p < 0.001$) of all recorded injuries were significantly higher in the treatments CC (post-hoc Mann-Whitney-U-test; number of injuries: $p < 0.001$; injury intensity: $p < 0.001$) and Net (post-hoc Mann-Whitney-U-test; number of injuries: $p < 0.001$; injury intensity: $p < 0.001$) than in the pre-damage conditions. There was no significant difference in the number and intensity of the injuries between the treatments CC and Net (Figure 4.3). In addition to the effects of the different treatments, the number of injuries and the injury intensity were significantly affected by the total fish length and the species tested (Table 4.4). Larger fish usually had more injuries with a slightly higher injury intensity than smaller fish.

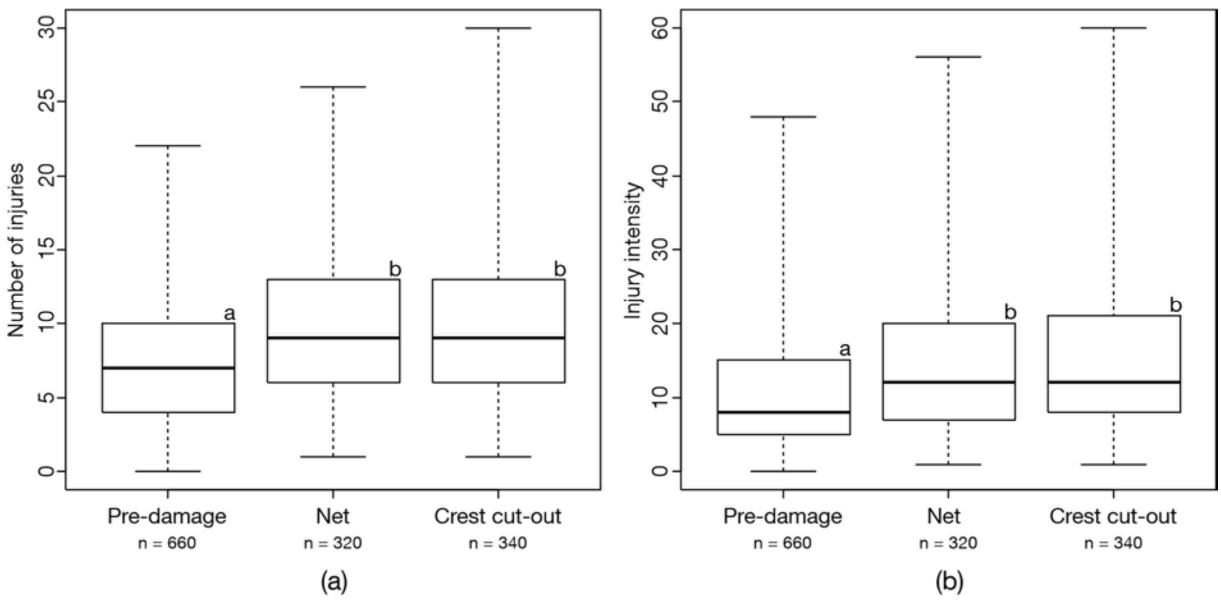


Figure 4.3 (**a**) Number of injuries and (**b**) injury intensity in the different treatments to assess the fish injury risk of the downstream migration corridor crest cut-out. Different lowercase letters indicate significant differences ($p \leq 0.05$) according to Bonferroni-corrected post-hoc pairwise Mann-Whitney-U-tests. Box: 25% quantile, median, 75% quantile; whisker: minimum, maximum values; n = number of individuals.

Table 4.4 Test statistics of the best fitting mixed effects models with number of injuries and injury intensity as response variables and treatment as random effect. AIC = Akaike Information Criterion, Residuals = Deviations of the observed values from the predicted values, χ^2 = chi-square value, SD = standard deviation, asterisks indicate significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Number of injuries	Injury intensity
AIC	6,962.5	8,687.5
Residuals:		
Minimum	−2.72	−2.50
First quartile	−0.61	−0.61
Median	−0.06	−0.09
Third quartile	0.58	0.47
Maximum	6.51	6.72
Fixed effects:		
Total length	χ^2 = 49.69***	χ^2 = 42.35***
Species	χ^2 = 884.5***	χ^2 = 867.1***
Random effects:		
Treatment	SD = 1.44	SD = 2.45
Residual	SD = 3.49	SD = 6.82

The species-specific consideration of the injury patterns, which were caused by the passage of the CC, revealed significant species-specific differences (Figure 4.4). Eels had on average a higher intensity of dermal lesions on head and body in the treatment CC than in the treatment Net, in which more pigment anomalies and dermal lesions on the opercula were detected. The species nase had on average more tears in the fins in the treatment CC than in the treatment Net, in which scale losses, dermal lesions on the head and hemorrhages of the head occurred more frequently. For brown trout, especially pigment anomalies and dermal lesions on the head were more frequent in the treatment CC than in the treatment Net. For perch, in particular tears in the fins and emboli in the eyes were detected more frequently in the treatment Net than in the treatment CC, in which primarily the intensity of scale losses was higher. In the treatment CC, barbels had mainly more intense hemorrhages in the head and tears in the fins. However, scale losses were more frequently detected in the treatment Net. For the roach, the differences in the injury patterns between the treatment CC and Net were most pronounced. In particular, hemorrhages of the head and body, dermal lesions on the head, tears in the fins and scale losses were more common after the passage of the CC than in the treatment Net. Typical injuries of the grayling, which were found at a higher intensity after the passage of the CC than in the treatment Net, were tears and hemorrhages of the fins. Danube salmon had on average more scale losses and dermal lesions on the head in the treatment CC than in the treatment Net, in which tears and hemorrhages of the fins occurred more frequently (Figure 4.4).

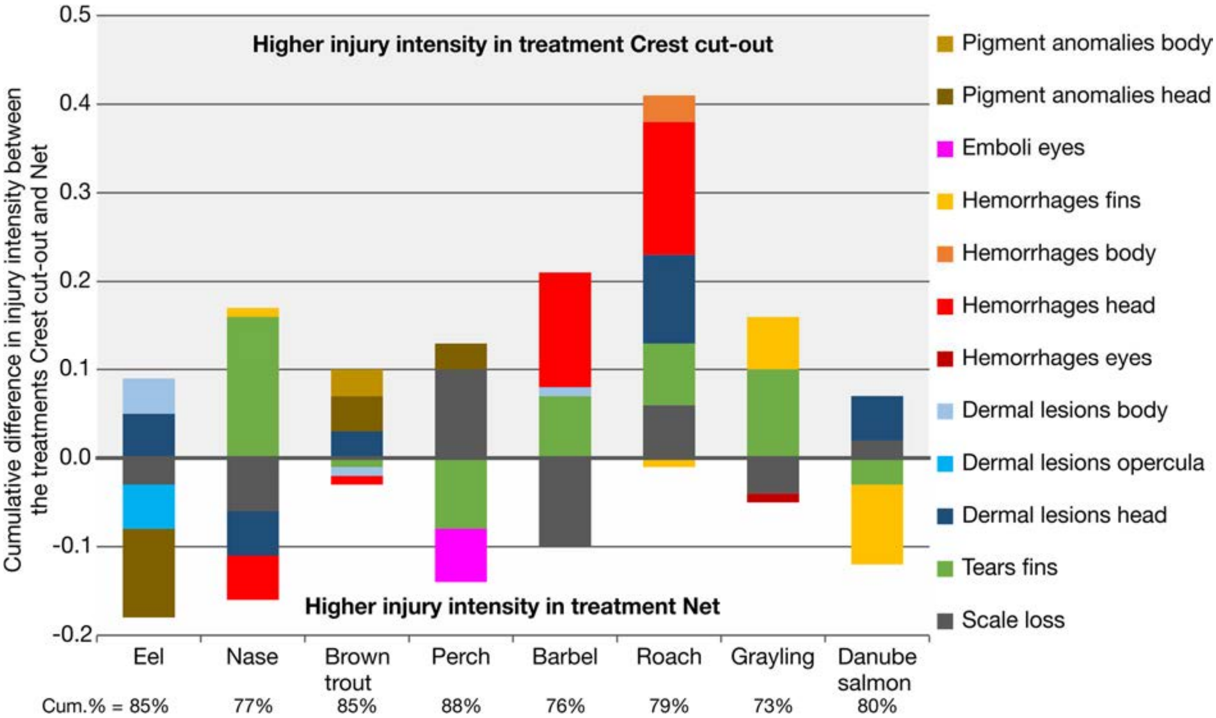


Figure 4.4 Absolute differences in the injury intensity for each test species between the treatments Crest cut-out and Net for injuries with a contribution to between-group dissimilarity (Crest cut-out vs. Net) larger than 5% according to similarity percentage analyses (SIMPER). The size of the bar components indicates the delta in intensity values for the respective injury type. Positive values indicate injuries with a larger intensity in the treatment Crest cut-out, negative values indicate injuries with a larger intensity in the treatment Net. Cum.% = cumulative contribution to between-group dissimilarity according to SIMPER. Contribution to between-group dissimilarity of single injury types ranged between 5% and 47%. For the number of replicates within each species and treatment see Table 4.3.

4.5 Discussion

There are many studies, in particular for salmon smolts and eels, in which the efficiency of surface bypasses as well as the behaviour and migrations in the forebay have been investigated by hydroacoustics and radio-telemetry (e.g. Gosset et al., 2005; Johnson et al., 2005; Scruton et al., 2007). However, effects of downstream passage via bypasses on fish health are often only modeled or roughly estimated (e.g. Bickford & Skalski, 2000; Muir et al., 2001). The novelty of the present study is that both the acceptance of two differently sized openings of a surface bypass and detailed injury patterns of different fish species passing that surface bypass were evaluated for eight fish species using a detailed fish injury assessment protocol. The findings suggest that the CC can principally provide a safe downstream passage if carefully constructed (e.g. avoiding open screw heads on the fish slide), but it still needs to be improved concerning dimensioning and position to contribute to a more sustainable hydropower development.

In this study, hatchery-reared fish were used. The advantage is that both the number of test fish and the extent of pre-damage are well known, allowing a clear link between observed post-passage injury patterns against pre-treatment conditions and a reference that accounts for catch-related damage. The assessment of the injury risk of a downstream migration corridor for naturally migrating fish is only possible to a limited extent, if the health condition of the fish before the downstream passage is not well known. We are aware that hatchery-reared fish may not fully represent the natural migratory behaviour of fish. Therefore, quantitative studies of bypass efficiency or downstream migration corridor selection should be conducted also using naturally migrating fish. Furthermore, naturally migrating fish can provide important information on seasonal and diurnal variations of downstream fish movement (Knott et al., 2020; Lucas & Baras, 2001; Pander et al., 2013) as well as on fish behaviour in front of hydropower plants (Egg et al., 2017; Travade et al., 2010).

4.5.1 Acceptance of different sized crest cut-outs

The percentage of fish that moved downstream via the large CC was only slightly higher than via the small CC. However, the ratio of the percentage of captured fish to the percentage of inflow was significantly larger in the small CC than in the large CC (Table 4.2). It is possible that even the large CC is still too small and fish are prevented from the downstream passage by the dimensions (width and water depth) of the bypass. Larinier and Travade (2002), for example, recommended a minimum width and depth of 40 cm for a surface bypass for salmon smolts. Although the bypass discharge of 3.6% in the large CC should be sufficient, the effectiveness of the bypass depends not only on the discharge carried but also on the hydraulic conditions at the entrance (Haro et al., 1998; Larinier & Travade, 2002). Particularly, when the current is very turbulent and fast-changing, fish can be scared away (Williams et al., 2012).

The different recapture rates of the test species in the downstream migration corridors turbine and CC can be attributed to species-specific behaviour. The percentage of brown trout using the CC was considerably higher than for grayling and barbel. This is not surprising since brown trout are known to migrate near the surface (Arnekleiv et al., 2007) and thus have a higher chance of finding the CC. The CC was rarely used by the barbel, which can be explained by their bottom-oriented way of life (Kottelat & Freyhof, 2007) and their migration behaviour near the river bed (Ebel, 2013). Due to its position above the turbine inlet, the CC is probably also hard to locate for other bottom-oriented fish species and therefore less efficient. To increase bypass efficiency, it would likely be useful to offer an alternative bottom bypass in addition to the existing surface bypass.

The majority of the test fish used the turbine corridor to get into the tailrace. This route carries a high risk of being injured or killed by a fast-moving Kaplan turbine (333 rpm). The 20 mm fish protection screen in front of the turbine inlet was only an effective barrier for brown trout > 30 cm. For many small and medium-sized fish, such a physical barrier is not very effective as a large part of the population can pass through. These fish species would benefit from the use of less harmful turbine techniques that reduce the mortality and injury risk when passing hydropower plants (Čada, 2001). Reducing the bar spacing of the screen could also contribute to a higher acceptance of the CC, but would reduce turbine performance and impede the screen cleaning process.

For naturally migratory fish, the effectiveness of the CC may be higher, as they may be searching longer for an alternative corridor than hatchery-reared fish if they cannot pass the fish protection screen in front of the turbine inlet. Nonetheless, most of the naturally downstream migrating fish presumably follow the main current and pass through the turbine to reach the tailrace, if they fit through the fish protection screen.

4.5.2 Fish injury risk of the downstream migration corridor crest cut-out

Several authors have already stated that not only the turbine passage but also the passage of alternative downstream migration corridors can cause injuries (Deng et al., 2005; Ferguson et al., 2007; Pflugrath et al., 2019). Injuries at surface bypasses can be caused either by a large head or by structural details of the bypass (Larinier & Travade, 2002). The greatest potential for injuries at the investigated CC results from protruding screws and connections of the steel casing that could injure fish while sliding on top of the steel casing into the tailrace.

However, the injury risk of the assessed surface bypass can be classified as low. Fish that passed through the CC did not experience immediate mortality or serious injuries such as amputations or bruises on the body. On the other hand, injuries such as scale loss, tears, hemorrhages and dermal lesions were more common. However, these injuries were also often caused by the catching technique and the handling procedure.

The species-specific differences in injury patterns are mainly due to a different degree of pre-damage and the specific morphological characteristics and sensitivity of the tested species. Considering the individual species, the roach was most sensitive to the passage of the CC. In contrast, almost no effects were detected for rheophilic brown trout and Danube salmon. These species are probably evolutionarily more adapted to live in harsh environments of alpine rivers, where it can be necessary to cross large natural barriers during their migrations.

In general, the injuries caused by the passage of the surface bypass were not severe, as evident from the small difference to the catch-related injuries. However, even less severe injuries such as scale loss or dermal lesions may increase the risk of fungal and bacterial infections (Dastjerdi & Barthelat, 2015). Under unfavorable circumstances, resulting diseases can reduce the vitality and ultimately lead to death (Mueller et al., 2017). The risk of sublethal and lethal injuries is particularly high for long (e.g. eel) and medium (e.g. barbel, nase) distance migrating fish species. These species are increasingly exposed to cumulative effects of hydropower plants, as they encounter many bypasses and turbines on their downstream migration route. Fish with delayed mortality had no serious external injuries in this study, so they died probably due to stress or unrecognized internal injuries.

4.6 Conclusions

In this study, the acceptance of the surface bypass was only marginally improved by increasing the flow area by a factor of four, and the mean flow rate by a factor of six (at maximum turbine flow) compared to the original conditions. Overall bypass efficiency was low and ranged between 7.4% (small CC) and 9.7% (large CC). For the bottom-oriented fish species barbel the surface bypass was highly ineffective. Besides a presumably still insufficient dimensioning, the greatest deficit seems to be the position of the bypass itself. To increase bypass acceptance, especially for bottom-oriented fish species, it would likely be useful to offer alternative bypasses near the bottom and in the middle of the water column in addition to the existing surface bypass. The surface bypass and the fish slide at the investigated movable power plant (head 5.0 m) seem to be suitable for passing downstream moving fish into the tailrace without severe injuries. However, the injury potential could probably be further reduced by covering protruding components, such as screw heads and flanges on the power plant steel casing. In addition to the evaluation of the pre-damage, it was crucial for this study also to record the catch-related injuries in order to separate the different effects of handling, catching and passing the CC and to avoid an overestimation of the effects of the downstream migration corridor. For future research, it would also be valuable to examine different positions of the downstream migration bypass in the water column (e.g. middle, bottom), other sizes (> 3.6% of turbine flow) as well as alternative shapes (e.g. round-shaped) to determine the best bypass configuration.

5 Effectiveness of catchment erosion protection measures and scale-dependent response of stream biota

A similar version of this chapter was published: Knott, J., Mueller, M., Pander, J. & Geist, J. (2019). Effectiveness of catchment erosion protection measures and scale-dependent response of stream biota. *Hydrobiologia*, 830(1), 77–92.

Author contributions: The study concept and the sampling design was conceived by JK, MM, JP and JG. The monitoring of abiotic and biotic parameters as well as the laboratory work was planned and carried out by JK. JK digitalized all data, carried out the statistical analyses, interpreted and visualized the results. The initial draft was prepared by JK and continuously improved, revised and edited by JK, MM, JP and JG.

5.1 Abstract

Many rivers in Central Europe are heavily affected by increased sedimentation due to erosion from agricultural land. High fine sediment loads can clog the interstitial system, increase turbidity, limit light penetration and potentially reduce primary productivity with negative impacts on stream biota such as reduced abundance and diversity. In this study, the effects of different erosion protection measures on instream sedimentation and the communities of fishes, macroinvertebrates and periphyton were evaluated. The erosion protection measures in the catchment successfully reduced the fine-sediment and nutrient input into the river system resulting in positive effects on interstitial habitat quality and the species assemblage of the assessed biota. The single taxonomic groups differed in their response both to catchment-related and instream-related variables. Fish community composition was best explained by catchment scale variables, while periphyton and macroinvertebrate assemblage structure was significantly governed by instream-scale variables. For increasing restoration success, a combination of measures in the catchment area with structure-enhancing measures within the stream is necessary. The results also suggest that an integrative assessment of abiotic and biotic variables in monitoring increases the detectability of effects on the instream scale.

5.2 Introduction

Many rivers in Central Europe are heavily affected by increased sedimentation due to erosion from land use (Davies et al., 2009; Kemp et al., 2011; Wood & Armitage, 1997), damming and flow regime changes (Poff et al., 2007), with manifold consequences for the biota in them (e.g. Acornley & Sear, 1999; Bunn & Arthington, 2002). The pathways of terrestrial eroded material into surface water bodies are not always easy to localize and occur as a result of point and diffuse sources. The fine sediment inputs to surface water bodies are also associated with nutrient input (Lemly, 1982), which increases autotrophic biomass and primary production, potentially reducing water quality and resulting in the loss of sensitive stream species (Weijters et al., 2009). Furthermore fine sediment input determines the quality of important key habitats for lithophilic fish, such as spawning grounds (e.g. Sternecker et al., 2013a), habitats for juveniles (Kemp et al., 2011) or hyporheic interstitial habitats (Denic & Geist, 2015; Walser & Bart, 1999).

In addition to its habitat function for lithophilic fish, which prefer coarse substrate for spawning, the sediment surface and the boundary zone to the hyporheic interstitial is a key habitat for macroinvertebrates and provides substratum for benthic algae and biofilms (Boulton et al., 1998; Bretschko, 1995; Mueller et al., 2014a; Müllner & Schagerl, 2003). As a result of high fine sediment loads, the interstitial system in the gravel bed can become colmated (Kondolf, 2000; Soulsby et al., 2001), reducing the exchange between free flowing water and hyporheic water (Davies et al., 2009; Geist & Auerswald, 2007; Mueller et al., 2013; Regh et al., 2005). Suspended and deposited fine sediments also increase turbidity, limit light penetration and potentially reduce primary productivity with resultant impacts on the entire food chain (Davies-Colley et al., 1992; Henley et al., 2000; Van Nieuwenhuyse & LaPerriere, 1986; Wood & Armitage, 1997). For instance, macroinvertebrates are affected by a reduced habitat space and lower density of prey items (Peckarsky, 1985), a reduced food value of periphyton (Cline et al., 1982; Graham, 1990) and increasing drift due to sediment deposition or substrate instability (Culp et al., 1986; Rosenberg & Wiens, 1978). Similar to the macroinvertebrates, high fine sediment loads reduce the food supply for fish (Bruton, 1985; Doeg & Koehn, 1994; Gray & Ward, 1982), the suitability of spawning habitats and hinder the development of fish eggs, larvae and juveniles (Chapman, 1988; Duerregger et al., 2018; Moring, 1982; Sternecker et al., 2014).

Due to these negative effects of sedimentation, many aquatic organisms are highly threatened (Geist, 2011), making the establishment of functional stream beds a key component of effective stream restoration. Since instream restoration measures alone cannot be successful in the long run if fine-sediment loads continue to be high (Mueller et al., 2014a; Pander et al., 2015a), catchment effects have been increasingly considered in restoration projects (Bernhardt & Palmer, 2011; Wood & Armitage, 1997).

In practice, there are several erosion protection measures (EPM) and land management strategies to reduce the fine sediment input to rivers. Methods, such as mulch tillage or catch crops, reduce erosion rates by maintaining a protective vegetative cover over the soil, often accompanied by a reduction in the frequency of plowing (Pimentel et al., 1995). Other methods, such as vegetation strips located at downslope ends of fields, along the thalweg and as buffers along streams, are intended to trap sediments and reduce sediment loads entering rivers.

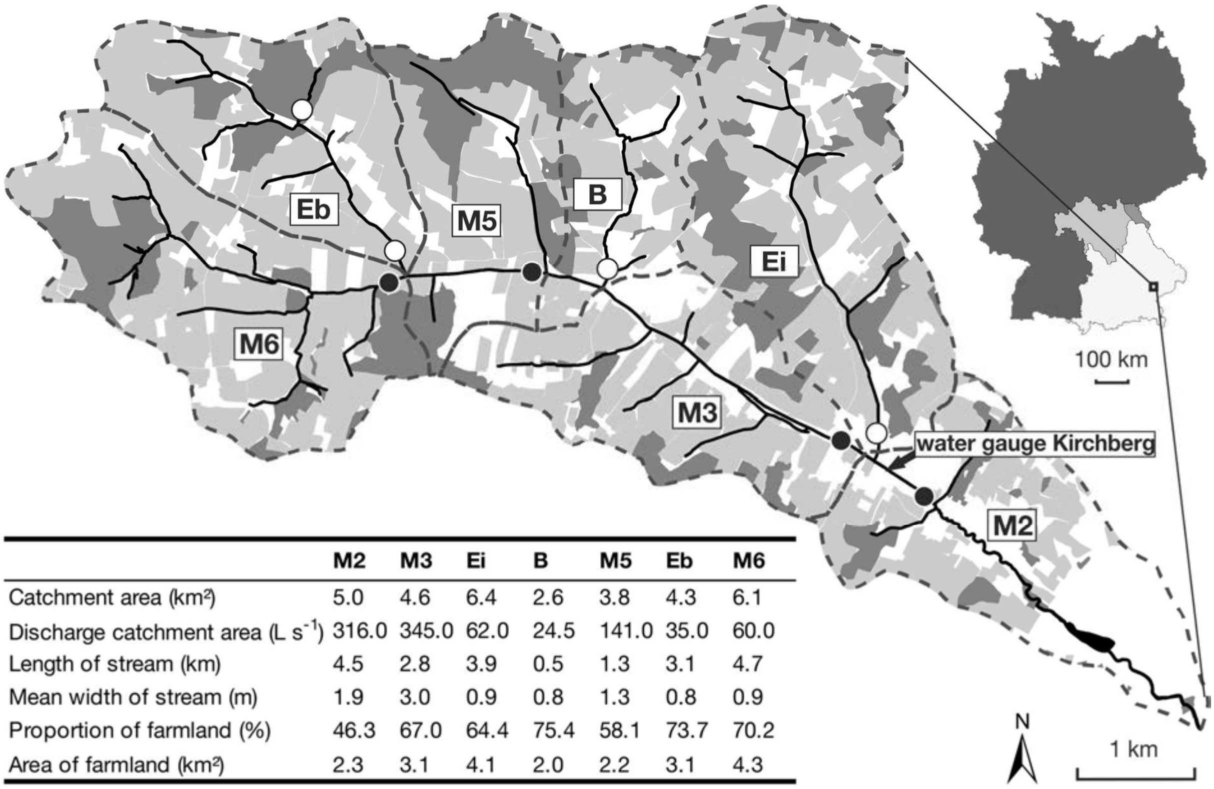
In this study we tested the effects of different EPM in the catchment, including mulch tillage, catch crops and buffer strips, on instream sedimentation and the communities of fishes, macroinvertebrates and periphyton in a small river system. Specifically, we hypothesized that (i) the fine sediment content in the stream bed and the instream habitat characteristics (i.e. interstitial habitat quality and water chemistry) are correlated with catchment scale variables (i.e. area of EPM), and that (ii) scale-dependence (instream versus catchment factors) determines differences in the response of taxonomic groups and traits, with e.g. periphyton community composition being more strongly governed by microhabitat factors and fishes being more strongly influenced by catchment variables.

5.3 Materials and Methods

5.3.1 Study area and study design

This study was carried out in the Mertseebach catchment (area of 32.31 km², mean annual discharge at water gauge Kirchberg, N 48.4208, E 12.7285: 0.218 m^3/s) in the district of Rottal-Inn, Germany (Figure 5.1). This area has the highest soil erosion rates in Bavaria (up to 10–12 t/ha/y; Auerswald et al., 2009; Cerdan et al., 2010), resulting in adverse effects on stream biota. To ameliorate the negative effects of soil input into the streams, three different EPM (buffer strips, mulch tillage, catch crops) have been implemented in the Mertseebach catchment area since 2009: Buffer strips are intended to reduce direct sediment input of adjacent erosion-prone farmland into the river by their surface roughness and the perennial rooting of the soil. For mulch tillage the main crop is sown in the harvest residues of the previous crop by plough-less soil tillage using seedbed or rotary harrows. The soil coverage with harvest residues is at least 30% in order to protect the soil effectively from wind- and rain-induced soil erosion. The catch crop cultivation is intended to avoid nutrient leaching and soil erosion.

Eight sampling sites (each comprising three sampling stretches of 30 m) within the Mertseebach and its tributaries were defined, with at least one sampling site per sub-catchment (Figure 5.1). Field sampling was carried out between September 2013 and May 2015, i.e. four to six years after the first implementation of the EPM. To account for seasonal fluctuation of aquatic communities and abiotic habitat characteristics, sampling was conducted at four time points seasonally, twice in spring (May 2014 and 2015) and twice in autumn (September 2013 and 2014).



	M2	M3	Ei	B	M5	Eb	M6
Catchment area (km²)	5.0	4.6	6.4	2.6	3.8	4.3	6.1
Discharge catchment area (L s^{-1})	316.0	345.0	62.0	24.5	141.0	35.0	60.0
Length of stream (km)	4.5	2.8	3.9	0.5	1.3	3.1	4.7
Mean width of stream (m)	1.9	3.0	0.9	0.8	1.3	0.8	0.9
Proportion of farmland (%)	46.3	67.0	64.4	75.4	58.1	73.7	70.2
Area of farmland (km²)	2.3	3.1	4.1	2.0	2.2	3.1	4.3

Figure 5.1 Map and location of the study area (top right; main drainage systems in Bavaria: ▬ = Elbe, ▬ = Rhine, ▭ = Danube), as well as map of the Mertseebach catchment area (main map) with location of the sampling sites and land use characteristics of the seven sub-catchment areas (M2, M3, Ei, B, M5, Eb, M6). ● = sampling sites within the Mertseebach, ○ = sampling sites within the tributaries, ▬ = stream course, ▪▪▪ = sub-catchment boarders. Different shades of grey symbolize the main land use in the catchment area: ▭ = farmland, ▬ = forest use, ▭ = other, i.e. non-agricultural or non-forest land use (e.g. urban area).

5.3.2 Physical and chemical instream effects

To assess the effects of the EPM on physicochemical instream properties, three groups of variables were assessed: effects on the open water (e.g. turbidity, nutrients), on the stream bed (fine sediment deposition, stream bed texture and compaction), as well as on exchange between open and interstitial water (calculated as difference between values from open water samples and interstitial water), which has previously been determined as an important variable for biological communities (Geist & Auerswald, 2007).

To assess water chemical effects, total organic carbon (TOC), biochemical oxygen demand after five days (BOD_5), calcium, magnesium, sodium, sulphate, phosphorus, ammonium, nitrate and chloride were determined using a Shimadzu TOC-5050A analyzer by catalytic oxidation at 680°C and ion chromatography (Dionex ICS-1100, Thermo Fisher Scientific, Braunschweig, DE). The determination of BOD_5 was carried out according to the DIN EN 1899-2 (1998) for undiluted samples. These analyses were analogously executed for samples from open water (100 mL) sampled in wide-mouth bottles (Carl Roth GmbH, Karlsruhe, DE) as well as from interstitial water samples that were collected from 10 cm stream bed depth according to the methodology described in Pander et al. (2015a) and Geist and Auerswald (2007) with three replicates at each sampling site. Water samples were filtered with an untreated nitrocellulose membrane filter (0.45 µm, Carl Roth GmbH, Karlsruhe, DE).

Physical water parameters were characterized by analysing dissolved oxygen (O_2, mg/L), temperature (T, °C), electric conductivity (EC, µS/cm, based on 25°C), pH-value (pH) and redox potential (EH, mV), all of which were measured in the free flowing water (FW) and in the interstitial water (INT) with three replicates at each sampling site (Multi340i device, pH 3110, WTW, Weilheim, DE).

Since the suspension load and the actual sedimentation on the river bed or the clogging of the interstitial zone are not necessarily correlated, both turbidity measurements (for three 20 mL subsamples per site using PhotoFlex Turb, WTW, Weilheim, DE) as well as measurements of fine sediment deposition into sediment traps were conducted following the methodology described in Denic et al. (2014), Denic and Geist (2015) and Pander et al. (2015a). Specifically, three sediment traps were installed at the left, middle and right side of the river at each cross-section per sampling site. Plastic boxes (190 mm × 160 mm × 90 mm, ROTHO clear boxes, ROTHO AG, Würenlingen, CH) were filled with a defined substrate (grain size = 22–32 mm, mean filling weight = 3.2 kg), and buried in the river bed (Pander et al., 2015a). After one month of exposure in the river bed, the sediment traps were closed and the deposited sediment was collected as described in Denic et al. (2014). The sediment suspension was fractioned with a wet-sieving tower (Retsch GmbH, Haan, DE) of decreasing mesh sizes (2.0, 0.85, 0.63 and 0.20 mm), dried and weighed.

To characterize the particle size distribution of the autochthonous substrate, three substratum samples per sampling site were collected from the uppermost 10 cm of the substratum layer using a box sampler with a rectangular opening of 16.0 cm × 12.2 cm and a length of 29.3 cm (Pander et al., 2015a). In the laboratory, a fractionation of the substratum was carried out with a wet-sieving tower (Retsch GmbH, Haan, DE) using the mesh sizes 20.0 mm, 6.3 mm, 2.0 mm and 0.85 mm.

Stream morphology was characterized by measurements of water depth (cm), current speed 5 cm above ground and 5 cm below surface (m/s; HFA, Höntzsch, Waiblingen, DE) and penetration resistance (kg m^{-2}; EijkelkampAgrisearch Equipment, Giesbeek, NL) in three successive cross sections with three replicates per cross section as described in Geist and Auerswald (2007) and Pander et al. (2015a).

5.3.3 Biological community effects

Biological community effects were assessed for the groups of periphyton, macroinvertebrates, and fishes (Table 5.1). Three replicate periphyton samples (each ~ 1 cm²) per sampling site were scraped off the substratum surfaces (stones or dead wood) and preserved with 20 ml of acidified Lugol's iodine solution per Mueller et al. (2011). For diatoms, permanent preparations in Naphrax were made (Crawford, 1975). All algae in a transect from 200 × 100 µm² squares were determined to species level and counted using an inverted microscope at 400 × magnification (DIN EN 15204, 2006).

Macroinvertebrates were collected using a modified kick-sampling method (Hauer & Lamberti, 2007; DIN EN ISO 10870 (2012); sampler opening 35 cm × 35 cm, mesh size 500 µm). At all sampling sites three samples were collected, each comprising an area of approximately 0.7 m² (length two meters, width 35 cm), representatively covering all present habitat structures as required for the monitoring according to the European Water Framework Directive (Meier et al., 2006). Macroinvertebrates were preserved in 50% ethanol in the field and classified to the finest taxonomic resolution possible as described in Mueller et al. (2014a).

Fish community was assessed using an electrofishing generator (1.7 kW, FEG 1700, EFKO GmbH, Leutkirch, DE) with a single anode, working from downstream to upstream direction according to DIN EN 14011 (2003). The investigated length of the study segments was standardized to 30 m as suggested by Grossman et al. (1987). All sampling stretches were consecutively sampled during stable weather and discharge conditions by the same crew throughout the entire study period (Sep 2013–May 2015). Fishes from each replicate were identified to species level and measured (total length ± 0.5 cm).

Table 5.1 Number of individuals, taxa and families as well as percentage of rheophilic species respectively non-mobile diatoms of the taxonomic groups assessed in the study area.

	Individuals	Taxa	Families	Rheophilic species/non-mobile diatoms
Periphyton	N/A	369	58	14%
Macroinvertebrates	42,921	163	67	41%
Fishes	3,059	14	5	30%

5.3.4 Data analyses

A geographical information system (ArcGIS 10, ESRI 2010) was used to determine the composition of the land use (total area of farmland, maize cultivation area, winter crops on farmland) and surficial geology characteristics (soil loss, slope) for each sub-catchment within the Mertseebach catchment area. Additionally, the percentage of EPM (buffer strips, mulch tillage, catch crops) on different types of land use (i.e. buffer strips on maize cultivation area) was determined from ArcGIS shapefiles for each of the sub-catchments to link this information with the physical, chemical and biological instream variables of each sampling site.

The catchment-related variables contained information on the agricultural land use, erosion hotspots (visual mapping), EPM and geology. The instream-related variables were classified according to hydraulic conditions, sediment deposition, penetration resistance, water chemistry, exchange rate, nutrients, turbidity and BOD_5.

Shannon diversity index (Shannon & Weaver, 1949) was calculated for the combined data of fishes, macroinvertebrates and periphyton. To test if traits of the investigated taxonomic groups differ in their response to instream versus catchment-related factors, fishes (Zauner & Eberstaller, 1999) and macroinvertebrates (Meier et al., 2006) were classified regarding their flow current preference. Current preferring (= rheophilic) fishes and macroinvertebrates indicate good substratum quality, because they depend on clean gravel and sufficient oxygen in the interstitial zone for spawning, egg development and feeding (Balon, 1975; Henley et al., 2000; Wood & Armitage, 1997). Since high occurrence of non-mobile diatoms can be used as an indicator of low fine sediment loads (Dickman et al., 2005), the diatoms were classified regarding their mobility according to Spaulding et al. (2010) and Jones et al. (2014).

To test for relations between instream- and catchment-related variables with the aquatic community composition, mixed effects models for designs with crossed random effects were applied as suggested by Bates et al. (2014) using the function "lmer" in R (R Core Team, 2017) package "lme4". Response variables were Shannon diversity, number of rheophilic/non-mobile species, sediment deposition, substratum composition, EC, TOC, O_2 and EH. Physical and chemical instream properties, land use and EPM were set as fixed effects, and sampling season and sub-catchment as random effects to account for seasonal and catchment variability. Model selection followed the top-down strategy (Diggle et al., 2002) as described in Zuur et al. (2009). The Akaike Information Criteria (AIC) based on the restricted maximum likelihood (REML) was chosen as model selection tool. To test for potential multi-collinearity among predictor variables, variance inflation factors (VIF) were calculated (Fox & Weisberg, 2011). If VIF exceeded a cut-off value of 10, predictor variables were identified as non-independent (Belsley et al., 2005; O'brien, 2007) and were dropped during model selection. P-values for predictor variables of the best fitting model were obtained by Wald chi-square tests. For the visualization of monotonic trends scatter plots were presented and smooth curves, which are locally weighted regression (loess; Cleveland & Devlin, 1988) fits to the data, were displayed on the plots.

For the summarized multivariate analysis of all taxonomic groups, the data of the species composition of periphyton, macroinvertebrates and fishes was normalized prior to the combination of data matrices to ensure that each taxonomic group had the same weighting in the subsequent analyses without losing quantitative information (Mueller et al., 2014b). In order to test if the scale-dependence (instream versus catchment factors) determines differences in the response of the taxonomic groups, Biota-Environmental matching (BIOENV) analyses (Anderson et al., 2008; Clarke & Gorley, 2006) based on Bray-Curtis-similarities (Bray & Curtis, 1957) were carried out, using species catch data as response variables and environmental variables as predictors. Subsequently, multivariate mixed modeling was performed using the PERMANOVA routine (Anderson et al., 2008). The best matching variables of the BIOENV analyses were set as fixed effects and season and catchment as random effects in the PERMANOVA design. For all statistical analyses, significance was accepted at $p \leq 0.05$.

5.4 Results

5.4.1 Effects on the open water and on the exchange between open and interstitial water

Short and long term oxygen supply in the interstitial zone and sum parameters such as TOC and EC revealed a significant relation with land use patterns in the catchment area. Land use variables, EPM, BOD_5, temperature and turbidity significantly influenced the short and long term oxygen supply in the interstitial zone (Table 5.2). The content of TOC both in the open water and in the interstitial zone increased significantly with increasing area of maize cultivation (Figure 5.2). The TOC content in the open water was also significantly affected by the EPM mulch tillage on maize and mulch tillage on winter crops (Table 5.2). EC, which is a sum parameter for ions dissolved in the water, was significantly influenced by the content of sodium, sulphate, magnesium and nitrate in the open water and in the interstitial zone. The land use and EPM in the catchment area were also significant predictors of EC (Table 5.2). No significant relations between BOD_5 as well as single nutrients like nitrate, sulphate and chloride and the area of EPM could be detected.

5.4.2 Effects on the sediment composition of the stream bed

Analogously to the effects of catchment land use on open water and exchange between open and interstitial water, there was also a significant positive relation of the amount of fine sediment in the stream bed and in the sediment traps with the maize cultivation area (Table 5.3, Figure 5.3). Moreover, turbidity, hydraulic conditions, land use and the EPM “mulch tillage on maize” were significant predictors of the sediment deposition and the substratum composition of the stream bed (Table 5.3).

5.4.3 Effects on the community composition of fishes, macroinvertebrates and periphyton

The observed effects of the EPM on water chemistry, interstitial habitat quality and instream sedimentation were also mirrored in the community response of fishes, macroinvertebrates and periphyton. Shannon diversity was significantly affected by water temperature, TOC, discharge and land use in the catchment area (Table 5.3). Not only the species diversity, but also the numbers of rheophilic fish and macroinvertebrate taxa as well as of non-mobile diatoms were significantly influenced by the land use in the catchment area (Figure 5.3). Additionally, significant predictors of the numbers of rheophilic species were temperature and the EPM “mulch tillage on maize” (Table 5.3).

Table 5.2 Test statistics for the fixed effects of the applied mixed effects models with O_2 INT, EH INT, EC FW, EC INT, TOC FW and TOC INT as response variables and sampling season and sub-catchment as random effects. t = estimate divided by standard error, χ^2 = chi-square value, superscript stars indicate significant differences: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. AIC values, residuals and standard deviation (SD) of random effects of the best fitting model are presented at the bottom of the table.

	O_2 INT		EH INT		EC FW		EC INT		TOC FW		TOC INT	
	t	χ^2	t	χ^2	t	χ^2	t	χ^2	t	χ^2	t	χ^2
BOD_5	3.09	9.55**										
Calcium							-1.81	3.29				
Sodium					-4.34	18.82***						
Sulphate					9.05	81.83***						
Magnesium					3.94	15.52***	2.37	5.59*				
Nitrate							3.81	14.54***				
Temperature	-3.05	9.28**										
Turbidity	-4.41	19.45***										
Area of farmland			1.99	3.97*			2.83	7.98**				
Maize cultivation area									1.99	3.96*	3.54	12.55***
Area winter crops on farmland	3.28	10.78**	-4.09	16.69***	-1.92	3.67*	-2.01	4.04*				
Area mulch tillage on farmland	3.54	12.50***										
Area mulch tillage on maize			3.70	13.68***	2.88	8.29**	1.78	3.18	2.02	4.09*		
Area mulch tillage on winter crops					-2.55	6.51*	1.35	1.83	-2.17	4.71*		
AIC	512.08		1109.0		1051.1		1314.7		607.83		683.17	
Residuals												
Minimum	-1.74		-2.77		-2.59		-1.47		-1.34		-1.38	
First quartile	-0.79		-0.58		-0.52		-0.51		-0.53		-0.68	
Median	-0.20		-0.01		0.09		-0.17		-0.18		-0.20	
Third quartile	0.68		0.58		0.59		0.27		0.23		0.44	
Maximum	2.39		2.28		1.95		4.41		7.06		5.41	
Random effects												
Season SD	0.00		24.42		33.85		73.48		2.42		0.00	
Residual SD	2.46		49.52		37.34		145.86		4.05		6.27	

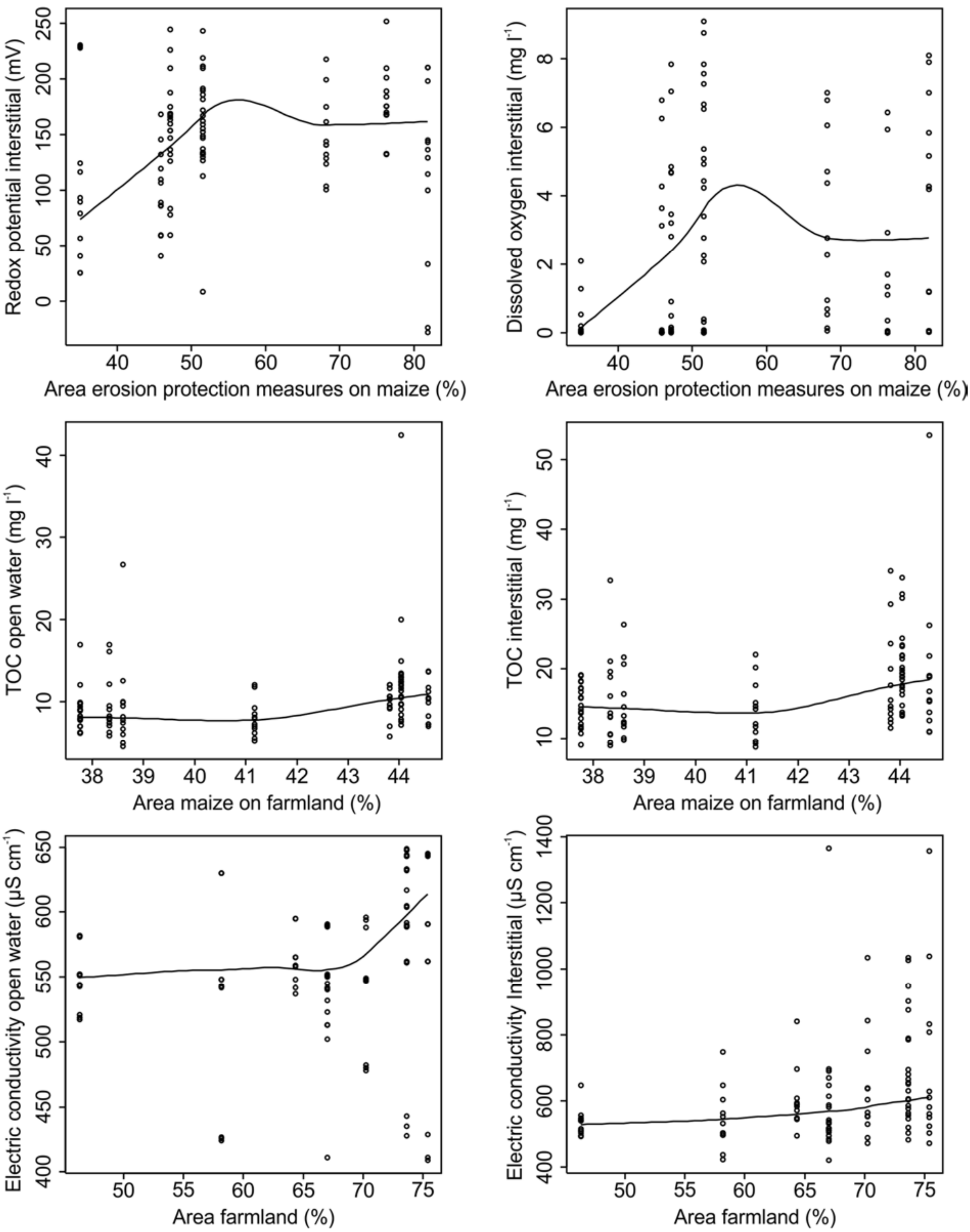


Figure 5.2 Scatter plots of redox potential, dissolved oxygen, TOC and electric conductivity as a function of the area of EPM on maize, the area of maize on farmland and the area of farmland. The smooth curves are locally weighted regression (loess; Cleveland & Devlin, 1988) fits to the data of the plots.

Table 5.3 Test statistics for the fixed effects of the applied mixed effects models with sediment deposition, substratum composition, Shannon diversity index and number of rheophilic species as response variables and sampling season and sub-catchment as random effects. t = estimate divided by standard error, χ^2 = chi-square value, superscript stars indicate significant differences: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. AIC values, residuals and standard deviation (SD) of random effects of the best fitting model are presented at the bottom of the table.

	Sediment deposition		Substratum composition		Shannon diversity		Rheophilic species	
	t	χ^2	t	χ^2	t	χ^2	t	χ^2
Temperature INT					2.54	6.46*	2.92	8.53**
TOC INT					2.49	6.18*		
Turbidity			2.63	6.90**				
Current speed	-3.55	12.57***						
Discharge			-2.01	4.06*	3.61	13.02***		
Area of farmland	3.19	10.17**			-5.10	26.00***		
Maize cultivation area	6.33	40.04***	3.51	12.30***	3.18	10.11**	2.50	6.27*
Area winter crops on farmland			-4.58	20.96***	4.82	23.27***		
Area mulch tillage on maize	-4.29	18.42***					2.93	8.57**
AIC	832.35		944.11		137.47		398.46	
Residuals								
Minimum	-3.17		-1.85		-2.32		-3.28	
First quartile	-0.65		-0.63		-0.55		-0.53	
Median	-0.07		-0.15		0.03		-0.02	
Third quartile	0.61		0.68		0.64		0.52	
Maximum	2.90		2.30		2.04		3.10	
Random effects								
Season SD	2.07		3.40		0.36		0.00	
Residual SD	13.08		21.46		0.38		2.75	

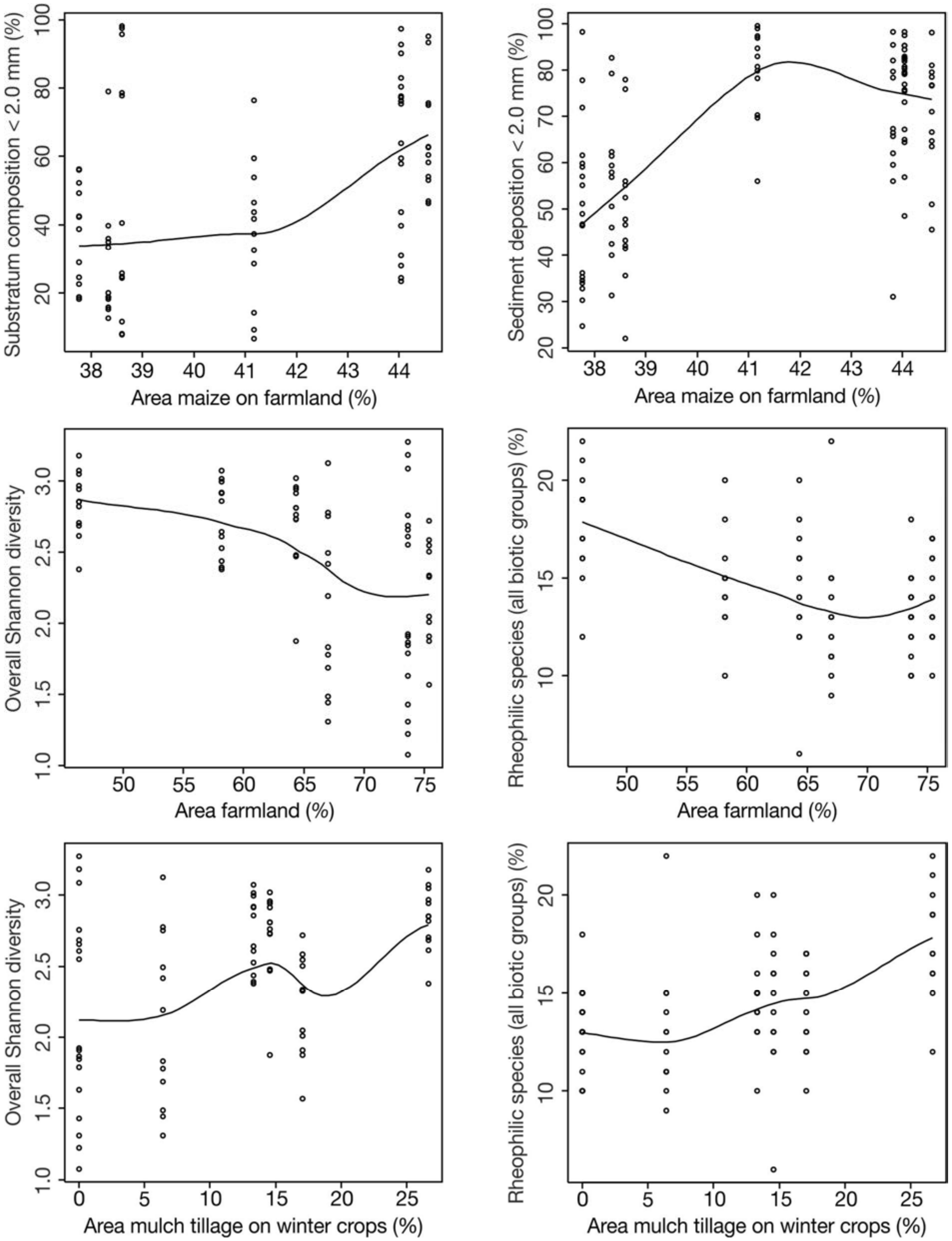


Figure 5.3 Scatter plots of the sediment deposition rate, the amount of fine sediment in the stream bed, the Shannon diversity and the number of rheophilic species as a function of the area of maize on farmland, the area of farmland and the area of mulch tillage on winter crops. The smooth curves are locally weighted regression (loess; Cleveland & Devlin, 1988) fits to the data of the plots.

5.4.4 Community response on catchment versus instream scale

A different set of variables correlating with the community composition for each of the three taxonomic groups at the instream and the catchment scale was detected. The correlation of the species assemblage structure with catchment-related variables significantly increased with increasing trophic level.

At the instream scale, the assemblage structure of the overall aquatic community (including periphyton, macroinvertebrates and fishes) was best explained by BOD_5, turbidity, hydraulic conditions (i.e. flow and discharge), penetration resistance and the exchange rate of redox potential and oxygen between the open water and the interstitial water (Table 5.4). At the catchment scale, the variability in the assemblage structure of the overall aquatic community was significantly affected by the land use in the catchment (e.g. area of farmland). There were also significant effects of the random factor catchment and significant interactions of the random factors season and catchment on the variability of the overall aquatic community assemblage both at the instream and at the catchment scale (Table 5.4).

Periphyton community composition in the study area was significantly influenced by BOD_5 and the random factors season and catchment and interactions between both at the instream scale. At the catchment scale, no significant correlation of the periphyton assemblage structure with catchment-related variables was found (Table 5.4).

The assemblage structure of macroinvertebrates at the instream scale was best explained by BOD_5, hydraulic conditions (i.e. flow and discharge), penetration resistance and the exchange rate of redox potential and oxygen between the open water and the interstitial water. There were also significant effects of the random factor catchment and significant interactions of the random factors season and catchment on the variability of the macroinvertebrates assemblage structure. At the catchment scale significantly influencing variables comprised the agricultural land use and the area of EPM in the catchment as well as interactions of the random factors season and catchment (Table 5.4).

The fish assemblage structure at the catchment scale was significantly influenced by the agricultural use in the study area and interactions of the random factors season and catchment. At the instream scale, the fish assemblage structure was best explained by turbidity, hydraulic conditions (i.e. flow and discharge), penetration resistance, deposition of fine sediment on the stream bed and the random factor catchment and interactions of season and catchment (Table 5.4).

Table 5.4 Results of BIOENV and PERMANOVA analyses for the community composition of the taxonomic groups periphyton, macroinvertebrates, fishes and for all taxonomic groups correlated with the instream- and catchment-related environmental variables. Distance-based pseudo-*F* ratios (Pseudo-*F*), based on the expectations of mean squares and estimates of the components of variation (Estimate) for fixed and random factors of the best fitting multivariate mixed model are presented. Superscript stars indicate significant fixed and random factors: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

		Periphyton	Pseudo-*F*	Estimate	Macroinvertebrates	Pseudo-*F*	Estimate	Fishes	Pseudo-*F*	Estimate	All taxonomic groups	Pseudo-*F*	Estimate
Instream	Fixed	BOD_5	12.07***	319.33	BOD_5	5.66***	123.37	Turbidity	3.77**	87.20	BOD_5	5.31***	183.67
					Hydraulic conditions	3.57***	192.04	Hydraulic conditions	4.45***	426.77	Turbidity	4.31***	131.63
					Penetration resistance	2.22*	78.78	Penetration resistance	1.85	84.42	Hydraulic conditions	3.01***	237.29
					Exchange rate redox	2.37*	49.31	Sediment deposition	1.51	31.35	Penetration resistance	1.63	66.86
											Exchange rate redox	2.52**	74.61
	Random	Season	3.48*	220.49	Season	2.07	116.47	Season	1.84	75.46	Season	1.74	91.39
		Catchment	1.58*	164.27	Catchment	1.75**	289.14	Catchment	3.10**	591.48	Catchment	2.17***	489.51
		Season×Catchment	1.43**	171.41	Season×Catchment	2.17***	362.34	Season×Catchment	2.49***	286.57	Season×Catchment	2.44***	408.77
		Residual		2870.1	Residual		2180.70	Residual		1133.20	Residual		1629.30
Catchment	Fixed	EPM on hotspots	1.10	7.82	Agricultural use	3.05*	143.68	Agricultural use	5.45**	443.33	Agricultural use	3.07**	237.07
					EPM on hotspots	1.20	23.30						
	Random	Season	3.81*	228.76	Season	2.22	122.19	Season	1.48	35.63	Season	1.70	79.99
		Catchment	1.53	163.11	Catchment	1.52	178.19	Catchment	2.74	376.51	Catchment	2.03*	347.82
		Season×Catchment	1.16	71.21	Season×Catchment	1.89***	300.38	Season×Catchment	2.32**	242.57	Season×Catchment	2.14***	351.53
		Residual		3277.40	Residual		2478.30	Residual		1159.7	Residual		1951.80
Instream & Catchment	Fixed	BOD_5	12.07***	319.33	BOD_5	5.59***	123.03	Penetration resistance	5.00**	305.13	Turbidity	3.87***	104.51
					Hydraulic conditions	3.36**	187.26	Sediment deposition	0.72	-12.47	Hydraulic conditions	2.53*	214.84
					Penetration resistance	2.12*	75.68	Agricultural use	3.87**	358.53	Penetration resistance	1.50	47.71
					Exchange rate redox	1.89*	41.62				Agricultural use	3.20**	247.94
					EPM on hotspots	0.67	-42.80				EPM on hotspots	1.18	35.45
	Random	Season	3.48*	220.49	Season	2.07	116.34	Season	1.66	55.90	Season	1.71	85.59
		Catchment	1.58*	164.27	Catchment	1.86**	333.68	Catchment	2.43	353.83	Catchment	1.69	270.89
		Season×Catchment	1.43**	171.41	Season×Catchment	2.17***	362.34	Season×Catchment	2.49***	238.38	Season×Catchment	2.35***	402.29
		Residual		2870.1	Residual		2180.70	Residual		1148.4	Residual		1769.20

5.5 Discussion

In this study, the linkage between agricultural land use, in particular of EPM, and instream properties like substratum composition, water chemistry and biological community composition was integratively evaluated. The impact of catchment parameters on streams has long been suspected to be an essential determinant for their ecological functionality and the effectiveness of structural restoration measures (Allan, 2004; Roth et al., 1996; Townsend et al., 1997), yet few studies have systematically quantified such impacts.

It is well known that agricultural land use has a strong influence on water chemistry, instream sedimentation and the biotic components (Ometo et al., 2000). In particular, streams in areas with a high proportion of arable crops highly susceptible to erosion are most affected, especially in conjunction with row crop farming (e.g. maize). In addition, crops such as maize are often heavily fertilized resulting in a conjunction of increased fine sediment and nutrient input into streams from such land use. Due to the low soil coverage of maize, fine sediments and nutrients are washed into the streams during heavy rainfall events. As a result of high fine sediment loads, the interstitial system in the gravel bed can become colmated (Kondolf, 2000; Soulsby et al., 2001), reducing the oxygen content in the hyporheic zone (Geist & Auerswald, 2007). Whilst in the present study these effects were not detectable for single variables (e.g. nitrate and phosphorus), they were well expressed by sum parameters such as TOC and EC, for which such links have been postulated (Wilson & Xenopoulos, 2009). Increased ion concentration through nutrient input is a common effect in intensively used agricultural areas and can be detected by increased electric conductivity (Cooper et al., 2013). Additionally agricultural streams receive maize detritus following heavy rainfall events or storms, which is a relevant carbon source (Griffiths et al., 2009) and thus can be detected by an increasing TOC content in the open water and in the interstitial zone. Alternatively, an increased input of nutrients from maize crops in the catchment may result in increased instream productivity and thus increased TOC.

5.5.1 Effectiveness of erosion protection measures

The EPM applied in the Mertseebach catchment area successfully reduced the fine-sediment and the nutrient input into the river system resulting in positive effects on interstitial habitat quality and the species assemblage of rheophilic fishes and macroinvertebrates as well as non-mobile periphyton taxa. However, the implemented measures have not yet been sufficient to reach a good ecological condition class according to the European Water Framework Directive (2006/60/EC). The overall classification of the study area calculated for fishes, macroinvertebrates and periphyton revealed the ecological condition class “poor” (data not shown in the manuscript). Various mechanisms can be responsible for this. On the one hand, the temporal dimension can play a major role – the measures may not yet be in place long enough to result in the maximum effects. Restoration of stream beds can indeed involve long lag-times (Lake, 2000; Lorenz et al., 2009) between reducing erosion and improving conditions in the river bed. Since many organisms comprise relatively long generation times and therefore require several years for a resettlement and establishment of a complete population structure, a longer period of observation may be necessary (Pander et al., 2015b).

Furthermore, it is possible that the spatial extent of the erosion protection measures in the study area was too small to achieve stronger effects. Davies et al. (2009) found that small-scale measures such as buffer strips can only be used to achieve a minor improvement in stream conditions, and that agricultural structural measures such as the relocation of agricultural land to areas distant from the stream could significantly contribute to the protection of aquatic biodiversity. This can likely be explained by the fact that fine sediment input in rivers often occurs via point sources such as drainage systems rather than 2-dimensional runoffs that can be filtered through buffer strips.

In addition to the high fine sediments loads, there are other strong structural deficits in the Mertseebach catchment area (straightening of the stream, weirs, bank and stream bed reinforcement) which can have significant negative effects on the living conditions of the various groups of organisms. Such deficits cannot be compensated by the erosion reduction measures in the catchment area. A recent study has demonstrated that erosion reduction measures alone typically cannot solve the problem of fine sedimentation since generally only a small percentage of the introduced material gets deposited on the stream bed (Auerswald & Geist, 2018). In addition, the stream bed naturally is prone to clogging, which arises from erosion and sedimentation processes during low to medium flow conditions. High flow conditions relocate the gravel of the stream bed and ensure that fines are washed out regularly. Gravel-dependent species are evolutionarily adapted to periods of these sediment dynamics (Kemp et al., 2011; Kottelat & Freyhof, 2007). If increased fine sediment loads from the catchment in combination with reduced flow dynamics degrade sediment conditions more quickly and more strongly, favourable conditions within the hyporheic zone may not persist long enough for a successful reproduction of most species (Pander et al., 2015a; Mueller et al., 2014a). In order to restore disrupted natural sediment and flow dynamics, it is necessary to reconnect the stream with its floodplain and to remove channel and bank reinforcement. Moreover fishes, macroinvertebrates and periphyton would probably benefit from restoring the biological continuity and further instream habitat restoration measures like stream bed substratum restoration or dead wood introduction (Angermeier & Karr, 1984; Pander et al., 2015a; Sternecker et al., 2013a).

5.5.2 Community response on catchment versus instream scale

The single taxonomic groups differed in their response both to catchment-related and instream-related variables, which may be explained by differences in their mobilities and trophic levels. Periphyton, which reacts sensitively and directly to chemical, physical and biological changes (Biggs, 2000; Smol & Stoermer, 2010) was influenced in this study mainly by the instream-related variable BOD. Differences in the BOD are caused by differently strong organic and nutrient pollution from the catchment and can thereby cause changes in the nutrient availability and water-chemical properties which are both directly relevant drivers for primary producers. These changes can have a strong impact on the periphyton communities (Yamada & Nakamura, 2002).

Compared to the periphyton, a considerably stronger influence of the agricultural land use and of EPM was observed in the macroinvertebrate data set. However, instream scale variables like the hydraulic conditions and the oxygen content in the interstitial zone, which have been identified as factors that affect community composition (Bonada et al., 2007; Rempel et al., 2000), had a stronger impact on the species assemblage of the macroinvertebrates than the variables at the catchment scale.

Fishes are highly mobile organisms that occupy the highest trophic levels within aquatic food webs. Thus, effects on the lower trophic levels of the food chain, particularly on macroinvertebrates that comprise a major food source for most fish, can have strong effects on the fish community. The fish community composition in the study area was strongly correlated with area-specific land use patterns. This means in the present study that the more sediment retention measures in the catchment area were implemented or the less land was used for agriculture, the more rheophilic fishes could be found. In the concrete case of the study area, the spatial patterns of land use, EPM and sampling sites (Figure 5.1) excludes that this effect is merely an artefact due to land use gradients along the course of the river.

5.5.3 Management recommendations

For the best possible restoration success, a combination of measures in the catchment area with structure-enhancing measures within the stream is necessary (Mueller et al., 2014a; Pander et al., 2015a). The measures implemented in the Mertseebach catchment, such as mulch tillage, catch crops and buffer strips, can be successfully used to reduce fine sediment input in river systems. In addition, there are a number of further reliable and well-established soil conservation technologies such as no-till cultivation, crop rotations, agroforestry and terracing (Pimentel et al., 1995), which could ideally be combined with the measures implemented herein to further improve effectiveness. For the improvement of the instream conditions in the Mertseebach, it is crucial to additionally identify habitat-forming processes, such as sediment and dead wood dynamics, that have been degraded and that need to be restored (Roni et al., 2002).

Monitoring would underestimate the effect strength if only single variables (e.g. water chemistry) were taken into account. Therefore, an integrative assessment of abiotic and biotic groups appears essential. Since different groups of organisms (e.g. periphyton, macroinvertebrates and fishes) were shown to strongly differ in their responses to both disturbance and restoration at instream and catchment scale, an assessment of effects must consider taxonomic representativeness for each spatial scale.

6 Wasted effort or promising approach – Does it make sense to build an engineered spawning ground for rheophilic fish in reservoir cascades?

A similar version of this chapter was published: 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, 106434.

Author contributions: This study is an equal-authorship publication of JK and Christoffer Nagel (CN). JK and CN developed the study design and methodology with constant advice from JG. Sampling of fish larvae and eggs as well as measurement of abiotic parameters were carried out equally by JK and CN. Statistical data analysis, data interpretation and visualization were also performed equally by JK and CN. The original draft was prepared and finalized by JK and CN. Amendment, revision and editing of the article were jointly done by JK, CN and JG.

6.1 Abstract

Anthropogenic alterations such as the construction of dams and reservoirs led to a loss of quantity, quality and connectivity of habitats for riverine fish species. The resulting decline of freshwater fishes has prompted many restoration efforts addressing bottlenecks in their life cycles such as improving spawning habitat quality. Whilst there is a wealth of studies addressing the benefits and challenges of spawning ground restoration for rheophilic fishes in lotic ecosystems, there is a paucity of information on the usefulness of such measures in almost lentic systems. In this study, an engineered spawning ground with areas of different grain sizes, built as a mitigation measure for a hydropower plant construction in a near-stagnant reservoir cascade, was assessed including physical and chemical characterisation, spawning habitat use and recruitment of target species for conservation. During the six-week investigation period, about 4,000 larvae and 18,000 eggs of mainly ubiquitous species such as roach (*Rutilus rutilus*, L.) and European perch (*Perca fluviatilis*, L.) were detected by drift netting and sampling of the gravel bed. The engineered spawning ground was successfully used for recruitment by the rheophilic gravel spawning cyprinids asp (*Leuciscus aspius*, L.) and ide (*Leuciscus idus*, L.). For all species, the highest density of eggs and larvae was found in the area with the highest current velocity directly at the turbine outlet. The findings of this study illustrate the potential of engineered spawning grounds for fish conservation even in heavily modified water bodies such as reservoir cascades. However, evidence of successful reproduction of rheophilic species

on the spawning ground alone does not allow any predictions on further population development, since crucial prerequisites in the further ontogeny may pose additional bottlenecks.

6.2 Introduction

Due to centuries of anthropogenic alteration, rivers are considered one of the most heavily modified ecosystems (Gleick, 2003; Poff et al., 2007). Anthropogenic alterations include river channelisation (Brooker, 1985), construction of dams (Dynesius & Nilsson, 1994) as well as land use change (Bierschenk et al., 2019), often associated with climate change impacts (Bussi et al., 2016; Scheurer et al., 2009). Ultimately, this resulted in a loss of quantity, quality and connectivity of habitats for the different life stages of riverine fish species, which is considered as one of the main reasons for the decline of the fish fauna in European rivers (Aarts et al., 2004; Mueller et al., 2020).

Effects of anthropogenic alterations in rivers are particularly evident when reservoirs are constructed, thereby changing streams to large stagnant water bodies. In general, damming of rivers is known to cause distinct differences in abiotic habitat conditions of upstream and downstream areas, specifically related to water depth, current velocity, substratum composition and hyporheic exchange rates (Mueller et al., 2011). This in turn deteriorates the spawning habitat quality for many rheophilic (= current preferring) fish species, which depend on shallow gravel banks with medium to rapid current for egg deposition and development (Gönczi, 1989; Horký & Slavík, 2017; Melcher & Schmutz, 2010). As findings from 84 reservoirs in Central and Eastern Europe demonstrate, reservoir construction leads to profound changes of the fish community evolving from rheophilic specialists to ubiquitous species (Kubečka, 1993). As a result, not only diadromous species such as European eel (*Anguilla anguilla*, L.), but also potamodromous species such as common nase (*Chondrostoma nasus*, L.), barbel (*Barbus barbus*, L.) and asp (*Leuciscus aspius*, L.) faced strong population declines in their distribution area (e.g. Peňáz, 1996; Swatdipong et al., 2010), and especially in Bavaria, Germany (Mueller et al., 2018).

Susceptibilities to environmental disturbances are strongly pronounced in the egg and larval stages of most fish species, owing from the particular sensitivity of these life-stages (Schiemer et al., 2002). At the same time, data availability on specific traits in the embryonic development of gravel spawning species is still insufficient (Smialek et al., 2019). Yet, the body of knowledge on habitat requirements and threats in the early-life stages has grown significantly in the last decades, particularly for salmonids (e.g. Greig et al., 2005; Hamor & Garside, 1976;

Kondolf, 2000; Smialek et al., 2021; Sternecker & Geist, 2010; Sternecker et al., 2013a), but also for rheophilic cyprinids like common nase (Duerregger et al. 2018; Nagel et al., 2020a) and barbel (Bašić et al., 2019; Vilizzi & Copp, 2013). Surprisingly, knowledge on spawning habitat preferences and embryonic development is distinctly underrepresented for the rheophilic cyprinids asp and ide (*Leuciscus idus*, L.), despite their economic importance for recreational fisheries (Rohtla et al., 2020; Targońska et al., 2010). In addition, the asp is of particular conservation value, as evident from its listing in Annexes II and V of the European Habitats Directive (European Commission, 1992), requiring member states to manage core areas of its distribution range in accordance with its ecological needs (Annex II) and to protect it from uncontrolled removal (Annex V).

To mitigate negative consequences of anthropogenic alterations to rivers, a wide variety of restoration measures can be applied. While barrier removal and the reconnection of rivers with their floodplain are the most efficient approaches to restore the longitudinal and lateral connectivity in rivers (cf. Magilligan et al., 2016; Pander et al., 2015b), these measures are often hardly feasible due to various restrictions (e.g. flood protection, usage and property rights of different stakeholders). Frequently applied restoration and mitigation measures are, for instance, re-stocking of extinct or threatened fish species (Aprahamian et al., 2003), fish protection facilities at hydropower plants (Larinier & Travade, 2002; Schilt, 2007), restoration of longitudinal and lateral connectivity by the construction of bypass systems (Jungwirth, 1996) and the reconnection of floodplain areas (Bond et al., 2009; Pander et al., 2015b). Among the most widely applied measures are instream habitat improvements, particular the construction or restoration of spawning grounds (Nagel et al., 2020b; Sternecker et al., 2013b; Taylor et al., 2019). While a variety of studies demonstrate the benefits as well as possible pitfalls of spawning ground restoration in lotic ecosystems (e.g. Pander et al., 2015a; Taylor et al., 2019), there is less evidence of how these measures might work in almost lentic systems. In these systems, areas of some current velocity are typically limited to the areas directly downstream the dams. In the context of evidence-based aquatic conservation and restoration, a critical evaluation of such restoration measures is necessary to increase their effectiveness (Geist, 2015; Geist & Hawkins, 2016). In particular, fisheries management and aquatic biodiversity conservation can greatly benefit from realising restoration options at hydropower sites (Geist, 2021).

Between 1972 and 1987, the Eixendorf reservoir cascade (Bavaria, Germany) was constructed by damming the River Schwarzach. As a result, the fish fauna shifted from rheophilic specialists towards ubiquitous species dominance (cf. Kubečka, 1993). However, rheophilic species such as common nase, barbel, asp and ide are still present in relict populations. In 2016/17, the construction of a hydropower plant in an existing weir that separates the pre-storage basin from the main reservoir (cf. Knott et al., 2019) resulted in a loss of potential spawning habitats for the occurring target species of conservation, downstream of the formerly overflown weir crest. This raised concern that these species could become extinct without the implementation of habitat-improving measures. To mitigate the loss of potential habitats for rheophilic target species, the hydropower company had to construct an artificial spawning ground in the main reservoir near the turbine outlet, comprising two areas of differently grained substratum. This study site was chosen to assess the functionality of spawning habitat construction in a near-stagnant reservoir cascade considering physical and chemical variables, spawning habitat use and recruitment of target species for conservation.

Specifically, we hypothesised that (i) the abiotic habitat characteristics of the spawning ground provide suitable conditions for rheophilic gravel spawning species by meeting their spawning habitat requirements. Consequently, (ii) spawning activity of these species occurs there, as measured by the numbers of laid eggs, and (iii) embryonic development conditions are sufficient for successful development and hatching of larvae.

6.3 Materials and Methods

6.3.1 Study site

The study was carried out in an artificial reservoir (approx. 100 ha) of the River Schwarzach near the city of Rötz, Bavaria, Germany (N 49.3394, E 12.4794). In the study area, the River Schwarzach is assigned to the transition region between the grayling and barbel fish ecoregion (Huet, 1949). The potential natural fish fauna (based on historic records, recent data, stream morphology and expert knowledge; Schubert, 2007) consists of 19 species, being dominated by chub (*Squalius cephalus*, L.) and the rheophilic species gudgeon (*Gobio gobio*, L.), common dace (*Leuciscus leuciscus*, L.), common nase and barbel (Table 6.1). A 4.8 m high dam separates the reservoir into a main basin and a pre-storage basin. In 2016/2017, a movable run-of-the-river hydropower plant was installed on the orographic left side of the dam (cf. Knott et al., 2019). As a compensatory measure, a gravel spawning ground for rheophilic fish was built directly at the turbine outlet. The engineered spawning ground consists of two areas with differently grained substratum: In the area close to the turbine (approx. 530 m²), gravel with grain sizes between 60–120 mm was used (coarse gravel area, CGA). In the area further downstream (approx. 890 m²), the bed substratum consists predominantly of fine gravel with grain sizes between 2–8 mm (fine gravel area, FGA; Figure 6.1).

Table 6.1 List of fish species of the potential natural fish fauna (= PNFF; Schubert, 2007) of the River Schwarzach at the study site and of fish species detected by electrofishing in the main basin (< 500 m from the engineered spawning ground) of the Eixendorf reservoir cascade in 2018 (= EF 2018). For each species, the flow current preference (adapted from Schiemer & Waidbacher, 1992) and the relative abundance (%) are given.

Scientific name	Common name	Current preference	PNFF (%)	EF 2018 (%)
Abramis brama (L.)	Common bream	indifferent		0.22
Alburnoides bipunctatus (Bloch)	Spirlin	rheophilic	1.00	0.05
Alburnus alburnus (L.)	Bleak	indifferent	2.00	13.46
Anguilla anguilla (L.)	European eel	indifferent		0.02
Barbatula barbatula (L.)	Stone loach	rheophilic	10.00	
Barbus barbus (L.)	Barbel	rheophilic	5.00	0.08
Blicca bjoerkna (L.)	White bream	indifferent		0.02
Chondrostoma nasus (L.)	Common nase	rheophilic	5.00	0.26
Cottus gobio (L.)	Bullhead	rheophilic	2.00	
Cyprinus carpio (L.)	Common carp	indifferent		0.02
Esox lucius (L.)	Northern pike	indifferent	0.80	0.42
Gobio gobio (L.)	Gudgeon	rheophilic	19.00	0.02
Gymnocephalus cernua (L.)	Ruffe	indifferent		0.86
Lampetra planeri (Bloch)	European brook lamprey	rheophilic	0.90	
Leuciscus aspius (L.)	Asp	rheophilic		0.12
Leuciscus idus (L.)	Ide	rheophilic	2.00	0.04
Leuciscus leuciscus (L.)	Common dace	rheophilic	19.00	0.69
Lota lota (L.)	Burbot	rheophilic	0.90	0.12
Perca fluviatilis (L.)	European perch	indifferent	2.00	75.50
Phoxinus phoxinus (L.)	European minnow	rheophilic	4.90	
Rhodeus amarus (Bloch)	European bitterling	stagnophilic		0.16
Rutilus rutilus (L.)	Roach	indifferent	0.50	2.36
Salmo trutta (L.)	Brown trout	rheophilic	2.00	
Sander lucioperca (L.)	Pike-perch	indifferent		1.03
Scardinius erythropthalmus (L.)	Rudd	stagnophilic		0.02
Silurus glanis (L.)	European catfish	indifferent		0.02
Squalius cephalus (L.)	Chub	indifferent	19.00	4.35
Thymallus thymallus (L.)	European grayling	rheophilic	2.00	
Vimba vimba (L.)	Vimba bream	rheophilic	2.00	

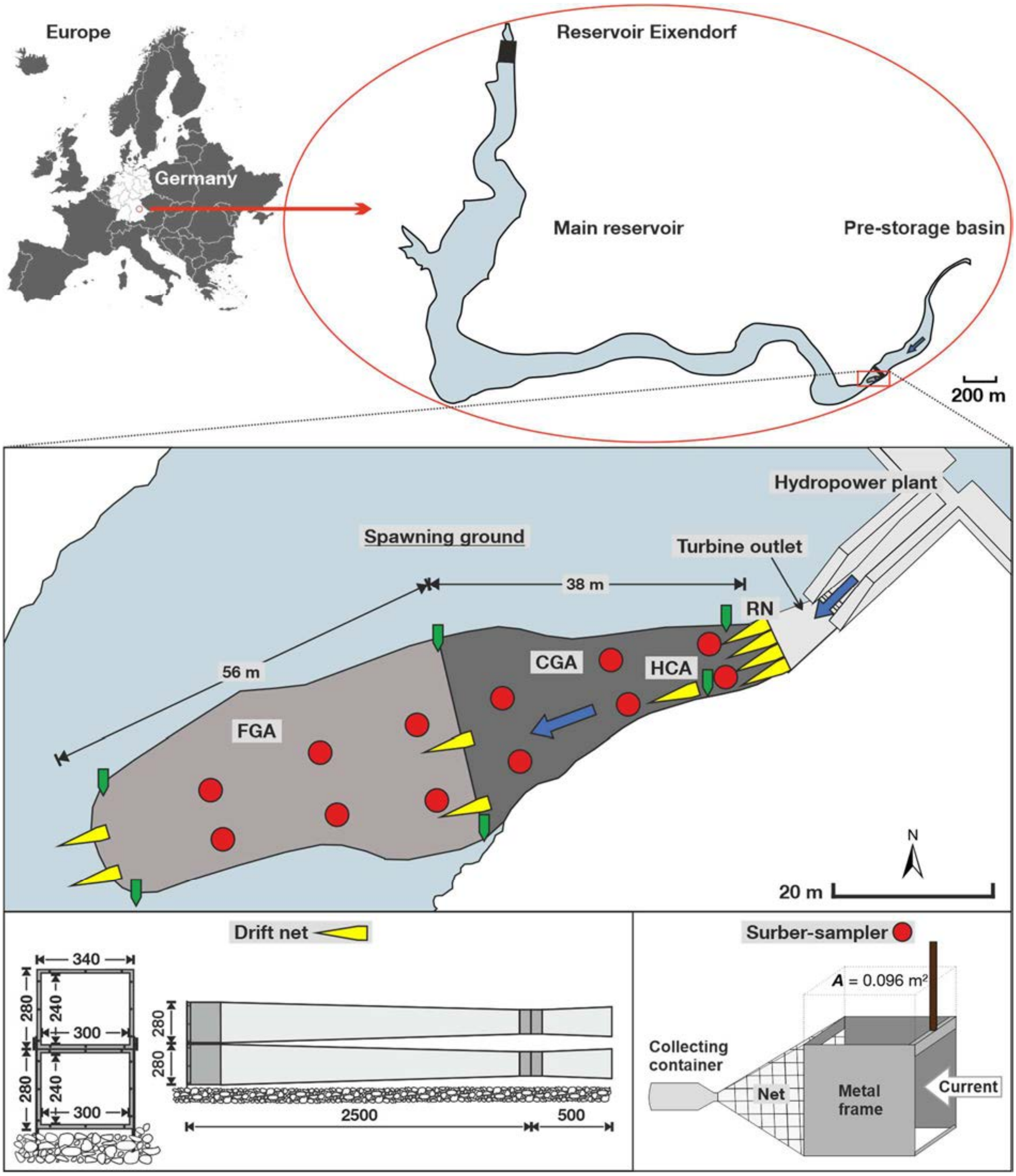


Figure 6.1 Location of the study site in the Eixendorf reservoir cascade of the River Schwarzach, Bavaria, Germany (upper part of the figure), schematic study design (mid part) and schematics of the sampling devices used to detect fish eggs and larvae (lower part). Different coloured symbols indicate the areas for the measurement of abiotic parameters and the locations for drift- and surber-sampling: = drift net setup, = surber-sampling, abiotic measurements, = temperature logger, = flow direction. FGA = fine gravel area, CGA = coarse gravel area, HCA = sampling site with the highest current velocity, RN = reference nets installed at the turbine outlet. The dimensions of the drift nets are given in mm.

6.3.2 Experimental design

Abiotic conditions, presence of eggs and hatching of larvae at the different parts of the spawning ground were examined weekly between April 22nd and May 28th, 2020. This period covers the main reproduction period of the rheophilc target species of conservation concern (e.g. asp, ide, common nase and barbel; Kottelat & Freyhof, 2007) occurring in the investigated reservoir cascade (own electrofishing data from 2018; Table 6.1). The assessment of a potential functionality of the engineered spawning ground was carried out on the basis of relevant water chemical parameters (e.g. dissolved oxygen, redox potential), which were measured in both the free flowing water and the interstitial zone of the spawning ground. Spawning activity (= presence of eggs) and success (= hatching of larvae) were assessed with two methods: Firstly, fine-meshed nets were used to catch eggs and larvae drifting from the spawning ground and secondly, standardized areas of the spawning substratum were directly checked for the presence of eggs and larvae. To assess the juvenile and adult fish community in the adjacent area of the spawning ground, electrofishing of mainly shallow areas in the littoral zone was carried out three months after the completion of the spawning ground examination in August 2020.

6.3.2.1 Measurement of water chemical and hydromorphological parameters

At each sampling date, the water chemical properties of the free flowing water, the current velocity and the water depth were measured at 12 sampling points, representatively distributed over both substratum areas of the spawning ground (Figure 6.1). Dissolved oxygen (mg/L), water temperature (°C), electric conductivity (µS/cm; based on 25°C) and pH-value were determined using a hand-held multimeter probe (Multi 3430; WTW, Weilheim, Germany). Turbidity (NTU) was determined using a hand-held PhotoFlex Turb 3430 (WTW, Weilheim, Germany).

The redox potential (mV), as an indicator for long-term oxygen supply, was measured at every second sampling date (three times in total) in both the free flowing water and in-situ in the interstitial zone in 10 cm substratum depth according to Geist and Auerswald (2007). Analogously, dissolved oxygen, temperature, electric conductivity and pH were measured in the interstitial zone. Interstitial water was taken from 10 cm substratum depth using a perforated metal tip with attached silicone tubing and a 100 mL plastic syringe.

Current velocity (m/s) 10 cm above ground and 10 cm below water surface as well as water depth (cm) were measured at each sampling location (MFpro, OTT Hydromet, Kempten, Germany). In addition, the water temperature (°C) was recorded hourly throughout the entire investigation period with temperature loggers (EL-USB-1, Lascar Electronics Ltd., www.lascarelectronics.com), installed close to the reservoir bed at the downstream end of the FGA, the CGA and the turbine outlet (Figure 6.1).

In order to characterize the substratum composition at the spawning ground, six freeze-core samples each were taken in the FGA and the CGA (Figure 6.1) on May 27th, 2020. In the laboratory, grain size fractionation was carried out by wet sieving (Retsch GmbH, Haan, Germany) using 20 mm, 6.3 mm, 2.0 mm, and 0.85 mm sieves. For each grain size fraction, the dry mass was determined and the percentage of the total weight of the sample was calculated.

6.3.2.2 Drift sampling of eggs and larvae

To assess spawning activity and success at the engineered spawning ground, drift nets were installed at the downstream end of each bed substratum area to catch fish eggs and larvae drifting off the spawning ground. Another drift net setup was positioned in the area with the highest current velocity at the spawning ground (HCA; cf. Figure 6.1), which was expected to be most frequently used by rheophilic spawners. To quantify the input of ichthyoplankton from the headwater (pre-storage basin) of the dam, four additional drift nets (reference nets = RN) were installed directly at the turbine outlet (Figure 6.1). At each sampling site, the entire water column was covered by drift nets.

The drift nets consisted of a rectangular aluminium frame (mouth 30 × 24 cm), connected to a tear-resistant polyester net with a density of 155 meshes per cm² (mesh size ~ 800 µm, total length 3 m). The end of the net can be removed via a zipper for emptying (catch bag length 0.5 m, cf. Nagel et al., 2020b). Collected eggs and larvae were euthanised using a twentyfold overdose of MS 222 (Tricaine Methane Sulphonate) following Adam et al. (2013) and subsequently preserved in 96% ethanol.

Drift sampling of eggs and larvae was carried out at each sampling date in a two-hour interval covering both dusk (about 20:00–22:00) and dawn (about 6:00–8:00). These periods were chosen because the emergence of many fish larvae is higher during the night than during the day (negative phototactic) and many fish species spawn during the night (Copp et al., 2002; Zitek et al., 2004), resulting in higher proportions of drifting eggs during this time.

To determine the drift density (individuals per m³ of filtered water), the current velocity was measured before each sampling interval in the inflow area of the respective drift net (MFpro, OTT Hydromet, Kempten, Germany).

6.3.2.3 Sampling of eggs and larvae in the gravel bed

Since fish eggs and larvae of rheophilic cyprinids often develop in the interstitial zone (Gutmann Roberts & Britton, 2020) and eggs do not drift far and settle quickly at low current velocities (Mills, 1981), the substratum was also sampled. To detect fish eggs and larvae in the gravel bed of the spawning ground, surber-sampling (Surber, 1930) was carried out at each sampling date at six sampling sites each in the CGA and the FGA (Figure 6.1). For this purpose, the cube-shaped metal frame of the surber-sampler was positioned five times per sampling site (5×0.096 m² = 0.48 m²) against the current and the substratum in this area was dug up to a depth of 10 cm for two minutes using a garden fork. The loosened eggs and larvae drifted into a collecting container via a net (mesh size 500 µm). Collected ichthyoplankton was euthanised as described in 6.3.2.2.

6.3.2.4 Species identification of fish eggs and larvae using DNA barcoding

In the laboratory, all larvae were determined to family level and then divided into groups according to similar phenotypic characteristics (cyprinids: Pinder, 2001; Spindler, 1988; percids: Ramler et al., 2014; Urho, 1996). The classification was based on the following criteria: stage of development, body shape, pigmentation, head and mouth shape and fin position (if developed). For each sampling day, individual total lengths of a randomised subsample of max. 30 larvae per group were measured with a stereomicroscope (Olympus SZX10, Olympus Deutschland GmbH) with an accuracy of 0.1 mm (cellSens software, Olympus Europe) and photographed. Only morphologically intact larvae were selected. Non-intact larvae were categorised as indeterminable and a subsample (21 larvae) of them was genetically identified. Due to the absence of characteristic classification criteria, the recorded eggs were divided into groups according to their size for each sampling date.

For species identification, subsamples of larvae were randomly selected from each group and used for DNA barcoding following the approach by Nagel et al. (2021). DNA barcoding was based on a fragment of the gene of the cytochrome c oxidase subunit I (COI), which is widely used in the identification of fish species (Bingpeng et al., 2018). NucleoSpin® tissue kits (Macherey-Nagel, Düren, Germany) were used for DNA extraction from fish eggs and larvae according to the manufacturer's protocol. The amplification of the COI fragment (~ 600 base pairs) was performed according to the fish barcode protocol using the primer C_FishF1t1 and C_FishR1t1 (Ivanova et al., 2007). Subsequently the PCR products were purified (NucleoSpin®Gel and PCR clean-up kit, Macherey-Nagel) and sequenced (Genewiz, Leipzig, Germany). For species identification, the obtained sequences were matched in a query search with BLAST (Basic Local Alignment Search Tool, Genbank, www.ncbi.nlm.nih.gov/blast).

Using this protocol, a total of 131 larvae and 21 eggs were successfully analysed to species level. If DNA barcoding confirmed the homogeneity of a group (i.e. all analysed individuals belong to the same species), the result was transferred to all other individuals in that group for subsequent data analysis. In case DNA barcoding revealed several species in a pre-sorted group, a further differentiation with regard to morphological characteristics was conducted, followed by the genetic validation of another subsample. If this did not provide homogeneous species evidence either, larvae were classified as indeterminable and not used for further species-specific analyses.

In the case of eggs, due to the high variability of detected species and the small sample size in relation to the total amount of recorded eggs, it was not possible to transfer the results to the entire group. Therefore, these results were only used qualitatively.

6.3.2.5 Fish community assessment by electrofishing

To document the young-of-the-year (YOY) fish fauna in the immediate vicinity of the spawning ground (max. distance 100 m), electrofishing was conducted after the reproduction period in late summer (August 2020). At 12 representative sections, a stretch of approx. 30 m length each was assessed, following the methodology described in Pander and Geist (2010) and DIN EN 14011 (2003). The investigated sections mainly included shallow bank areas, which are known to be potential habitats for juvenile fish (Copp, 1992; Pander et al., 2017). Each section was fished from a boat with a mobile electrofishing generator (11 kW, EFKO-GmbH, Leutkirch, Germany), a single anode and a dip net to collect stunned fish. All individuals were measured (total length ± 0.5 cm) and identified to species level. Following Kottelat and Freyhof (2007) and Pinder (2001), all fish were classified into the categories "YOY fish" and "fish older than one year" (≥ 1+) based on their total length.

6.3.3 Statistical analyses

Prior to further analysis, drift densities (Ind/1,000 m³) for each drift net at each sampling interval were calculated from the number of detected larvae or eggs (Ind) and the flow rate (m³; covered area (m²) × current velocity (m/s) × duration of exposure (s)). Hyporheic exchange rates were calculated for the water chemical parameters by subtracting the interstitial values from the corresponding open water values.

Abiotic water parameters and drift densities of the recorded larvae and eggs were compared between different areas of the spawning ground and between dawn and dusk (only drift density of larvae and eggs) using univariate statistics.

Data were tested for normal distribution with the Shapiro-Wilk-test and for homogeneity of variances with the Levene-test. To test for statistical differences, the t-test was used for normally distributed data and homogeneous variances. If there was no normal distribution of the data, Wilcoxon-test (comparison of two groups) or non-parametric Kruskal-Wallis-test and Bonferroni corrected post hoc pairwise Mann-Whitney U-test (comparison of more than two groups) were used.

To analyse the increase in larval total length over the study period, linear regression analyses were performed, with "sampling time" as predictor variable and "larval total length" as dependent variable. The species-specific length distribution over time was presented in scatter plots using the "geom_jitter" function from the "ggplot2" package (Wickham, 2016) in R (R Core Team, 2020). Linear regression lines were displayed using the function "geom_smooth" from the package "ggplot2" (Wickham, 2016). All univariate analyses were performed with the statistics software R Studio (version 4.0.2; R Core Team, 2020). Statistical test results were classified as significant with an error probability of $p < 0.05$.

6.4 Results

6.4.1 Abiotic characterisation of the spawning ground

The current velocities at the spawning ground varied between 0.0 m/s and 0.5 m/s (Table 6.2). The current velocity in the CGA (av. 0.17 m/s) close to the turbines was significantly higher than in the FGA (av. 0.06 m/s; Wilcoxon-test: $W = 1146.5$, $p < 0.001$). The water depth, however, was significantly higher in the FGA of the spawning ground with an average of 85 cm than in the CGA near the turbine with an average of 72 cm (Welch t-test: $t = 5.9$, df = 70, $p < 0.001$).

As expected, the results of the substratum sampling using the freeze-core method showed a markedly different grain size composition between the FGA and the CGA of the spawning ground (Figure 6.2). On average, about 86% (m/m) of the bottom substratum in the CGA was > 20 mm. In the FGA, the proportion of the two grain size fractions "> 2.0–6.3 mm" and "> 6.3–20 mm" was highest with an average of 88% of the total weight. The proportion of fine sediment (< 0.85 mm) was slightly higher in the CGA (av. 5.0%) than in the FGA (av. 3.8%).

Table 6.2 Mean values ± standard deviation of physical, chemical and hydromorphological habitat parameters in the free flowing water and in the interstitial zone of the fine gravel (FGA) and coarse gravel areas (CGA) of the investigated spawning ground in the Eixendorf reservoir cascade. Minimum and maximum values are presented in parentheses. Different lower case letters on the mean values symbolise significant differences ($p < 0.05$) according to Wilcoxon- or t-test between FGA and CGA.

	FGA		CGA	
	Free flowing water	Interstitial zone	Free flowing water	Interstitial zone
Temperature [°C]	$14.6^{a} \pm 2.4$ [11.9–19.1]	14.1 ± 1.9 [11.7–17.6]	$14.0^{b} \pm 1.8$ [11.9–17.3]	13.7 ± 1.7 [11.2–15.9]
Dissolved oxygen [mg/L]	$11.0^{a} \pm 1.8$ [9.5–17.3]	$3.9^{a} \pm 1.1$ [2.3–6.4]	$10.1^{b} \pm 1.0$ [8.5–13.1]	$8.2^{b} \pm 2.4$ [1.6–10.2]
Electric conductivity [µS/cm]	186 ± 5 [179–193]	201 ± 14 [187–243]	187 ± 6 [179–194]	196 ± 12 [184–234]
ph-value	$8.0^{a} \pm 0.9$ [7.3–10.4]	7.0 ± 0.3 [6.7–7.9]	$7.6^{b} \pm 0.6$ [6.7–9.2]	7.1 ± 0.3 [6.5–7.6]
Redox potential [mV]	480.7 ± 55.8 [394.3–542.0]	400.2 ± 74.9 [186.3–498.0]	498.5 ± 49.1 [399.8–543.9]	347.6 ± 111.0 [189.4–500.7]
Turbidity [NTU]	19.6 ± 37.7 [3.2–167.1]		10.1 ± 12.4 [4.3–65.5]	
Water depth [cm]	$85^{a} \pm 8$ [65–101]		$72^{b} \pm 10$ [47–92]	
Current velocity surface [m/s]	$0.08^{a} \pm 0.08$ [0.00–0.32]		$0.20^{b} \pm 0.14$ [0.01–0.50]	
Current velocity bottom [m/s]	$0.05^{a} \pm 0.04$ [0.00–0.20]		$0.13^{b} \pm 0.11$ [0.01–0.40]	
Substratum > 20 mm [%]	3.0 ± 6.8 [0–18.3]		86.1 ± 9.9 [69.4–97.8]	
Substratum 6.3–20 mm [%]	43.8 ± 5.1 [35.5–50.1]		3.6 ± 3.2 [0.3–9.0]	
Substratum 2.0–6.3 mm [%]	44.2 ± 3.2 [38.5–49.2]		3.7 ± 3.6 [0.2–9.8]	
Substratum 0.85–2.0 mm [%]	5.2 ± 0.9 [3.7–6.5]		1.7 ± 1.5 [0.1–4.5]	
Substratum < 0.85 mm [%]	3.8 ± 2.4 [2.0–9.0]		5.0 ± 3.0 [1.5–9.4]	

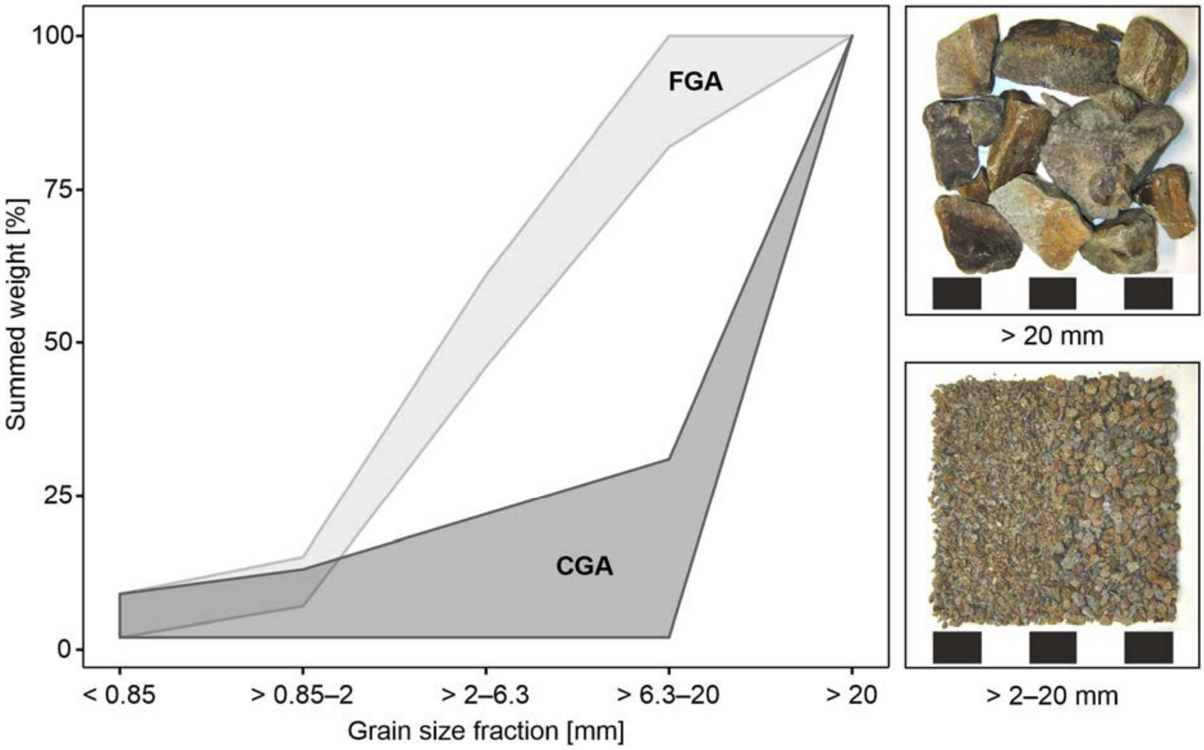


Figure 6.2 Summed weight (%) of the grain size fractions (mm) determined by freeze-core sampling for the fine gravel area (FGA) and the coarse gravel area (CGA) of the investigated spawning ground in the Eixendorf reservoir cascade. The grey-shaded areas cover the respective range of values. In the right part of the figure, the main grain size fractions of the two spawning ground areas are shown: above – grain size fraction > 20 mm, below – grain size fractions > 2–6.3 mm and > 6.3–20 mm, a section of the black and white scale corresponds to 50 mm.

Dissolved oxygen in the interstitial zone varied between 1.6 mg/L and 10.2 mg/L (Table 6.2). In the FGA (av. 3.9 mg/L) of the spawning ground, the dissolved oxygen in the interstitial zone was significantly lower than in the CGA (av. 8.2 mg/L; Wilcoxon-test: $W = 29.5$, $p < 0.001$). No significant differences between the FGA and the CGA were detected in the interstitial zone for pH (Wilcoxon-test: $W = 136$, $p = 0.42$), temperature (Wilcoxon-test: $W = 191.5$, $p = 0.36$), electric conductivity (Wilcoxon-test: $W = 202$, $p = 0.21$) and redox potential (Wilcoxon-test: $W = 197$, $p = 0.28$). The temperature in the free flowing water was on average 12.7°C at the beginning of the survey (April 22nd/23rd) and increased to an average of 15.9°C on the last sampling day (May 28th). In the meantime, particularly from May 11th to 15th, the temperature dropped by approx. 4°C (from 16°C to 12°C) and then increased again by approx. 5°C to an average of 17°C on May 20th.

6.4.2 Drift sampling of eggs and larvae

During the six-week investigation period, a total of 3,900 larvae and 18,037 eggs were detected in the drift nets. The genetic analysis identified 131 larvae (3.4% of the captured larvae) and 21 eggs (0.1% of the captured eggs) to species level, thereby proving the occurrence of

12 species from the families Cyprinidae and Percidae (Table 6.3). By transferring the results to the different morphological groups, a total of 1,777 of the 3,900 detected larvae could be identified to species level with high probability.

The two most abundant species were European perch (*Perca fluviatilis*, L.) and roach (*Rutilus rutilus*, L.) with 69% and 23% of larvae identified to species level respectively, followed by asp (5%), ide (2%) and pike-perch (*Sander lucioperca*, L.) (1%). Covering the whole study period, the mean drift density of larvae was at 140 individuals per 1,000 m³ of filtered water (Ind/1,000 m³), in contrast to a sevenfold higher mean drift density observed for eggs (1,053 Ind/1,000 m³). The mean drift density was by far the highest for European perch at 46 Ind/1,000 m^3 and more than twice as high as for roach at 19 Ind/1,000 m³. For asp, ide and pike-perch, the mean drift density was below 3 Ind/1,000 m³.

6.4.3 Sampling of eggs and larvae in the gravel bed

By surber-sampling, a total of 65 larvae and 661 eggs were detected in the substratum of the spawning ground. 10 larvae (15% proportion of the total) and 12 eggs (2%) could be identified to species level. This approach identified seven species, from which roach and ruffe (*Gymnocephalus cernua*, L.) were most abundant. Larval density in the gravel was on average 1,881 individuals per 1,000 m² spawning ground (Ind/1,000 m²), in contrast to a tenfold higher density observed for eggs (19,126 Ind/1,000 m²).

6.4.4 Fish community assessment by electrofishing

During electrofishing in August 2020, a total of 19 species and 546 individuals were caught. The most frequently caught species were European perch (44% of the total catch), bream (*Abramis brama*, L.; 15%) and roach (11%), which were caught predominantly as YOY fish. All species that were recorded in the drift and substratum investigation on the spawning ground in spring, were also detected as YOY fish in late summer by electrofishing, except gudgeon, ide and asp (Table 6.3).

Table 6.3 List of fish species detected by drift-netting, surber-sampling and electrofishing in the Eixendorf reservoir cascade of the River Schwarzach. For each species, the current preference (adapted from Schiemer and Waidbacher, 1992), the spawning guild (Balon, 1975) and the density of recorded individuals are given. FGA = fine gravel area, CGA = coarse gravel area, HCA = sampling site with the highest current velocity, RN = reference nets installed at the turbine outlet, YOY = young-of-the-year fish, ≥ 1+ = fish older than one year, E = detection of eggs, L = detection of larvae. Superscript letters indicate the conservation status according to the European Habitats Directive (European Commission, 1992): AII = Annex II species, AV = Annex V species.

Scientific name	Common name	Spawning guild	Drift-netting (Ind/1,000 m³)				Surber-sampling (Ind/1,000 m²)		Electrofishing (Ind/1,000 m²)	
			FGA	CGA	HCA	RN	FGA	CGA	YOY	≥ 1+
Abramis brama (L.)	Common bream	phyto-/lithophilic		0.3	0.2	0.03			5.8	14.2
Alburnoides bipunctatus (Bloch)	Spirlin	lithophilic							1.4	0.3
Alburnus alburnus (L.)	Bleak	phyto-/lithophilic			0.5 (E)		(E)	(E)	0.6	0.3
Blicca bjoerkna (L.)	White bream	phyto-/lithophilic	(E)	(E)					2.8	2.2
Chondrostoma nasus (L.)	Common nase	lithophilic				0.04				0.6
Cyprinus carpio (L.)	Common carp	phytophilic								0.3
Esox lucius (L.)	Northern pike	phytophilic							3.6	0.8
Gobio gobio (L.)	Gudgeon	psammophilic	(E)		(E)					0.8
Gymnocephalus cernua (L.)	Ruffe	phyto-/lithophilic	0.2 (E)		0.7	(E)	(E)	(E)	1.1	0.3
Leuciscus aspius[AII, AV] (L.)	Asp	lithophilic		1.8	18.9		(E)	(E)		
Leuciscus idus (L.)	Ide	lithophilic	0.2		6.4			(E)		0.8
Leuciscus leuciscus (L.)	Common dace	phyto-/lithophilic							0.3	
Perca fluviatilis (L.)	European perch	phyto-/lithophilic	14.9	61.9	160.9	12.6 (E)		(L)	52.8	13.3
Rhodeus amarus[AII] (Bloch)	European bitterling	ostracophilic							0.3	
Rutilus rutilus (L.)	Roach	phyto-/lithophilic	11.9 (E)	19.2 (E)	69.5 (E)	1.5	(L, E)	(L)	11.1	5.3
Sander lucioperca (L.)	Pike-perch	phytophilic	0.5	0.6	0.7	0.3	(L)	(L)	3.1	4.7
Scardinius erythropthalmus (L.)	Rudd	phytophilic							1.1	11.7
Silurus glanis (L.)	European catfish	phytophilic								0.6
Squalius cephalus (L.)	Chub	lithophilic			0.5	0.04			1.1	5.0
Tinca tinca (L.)	Tench	phytophilic							1.9	4.2
Total density of fish			35.1	137.9	703.8	18.2	347.2	3,414.4	86.4	65.3
Total density of eggs			38.9	2,353.1	2,299.3	0.4	12,615.7	25,636.6		

6.4.5 Variation in larval and egg drift over time

The mean drift density of the larvae and eggs varied strongly between the sampling dates (Figure 6.3). With an average of 481 Ind/1,000 m³, the highest drift density of the larvae was detected on April 29th/30th. Except for the sampling on April 29th/30th and on May 19th/20th, the average drift density of larvae was slightly higher than the drift density of eggs (Figure 6.3). It is noticeable that the peaks in the drift of eggs and larvae (April 29th/30th and May 19th/20th) were associated with an increase of the water temperature compared to the previous sampling. The dropping water temperature led to an obvious decrease in the drift density of larvae and eggs (Figure 6.3).

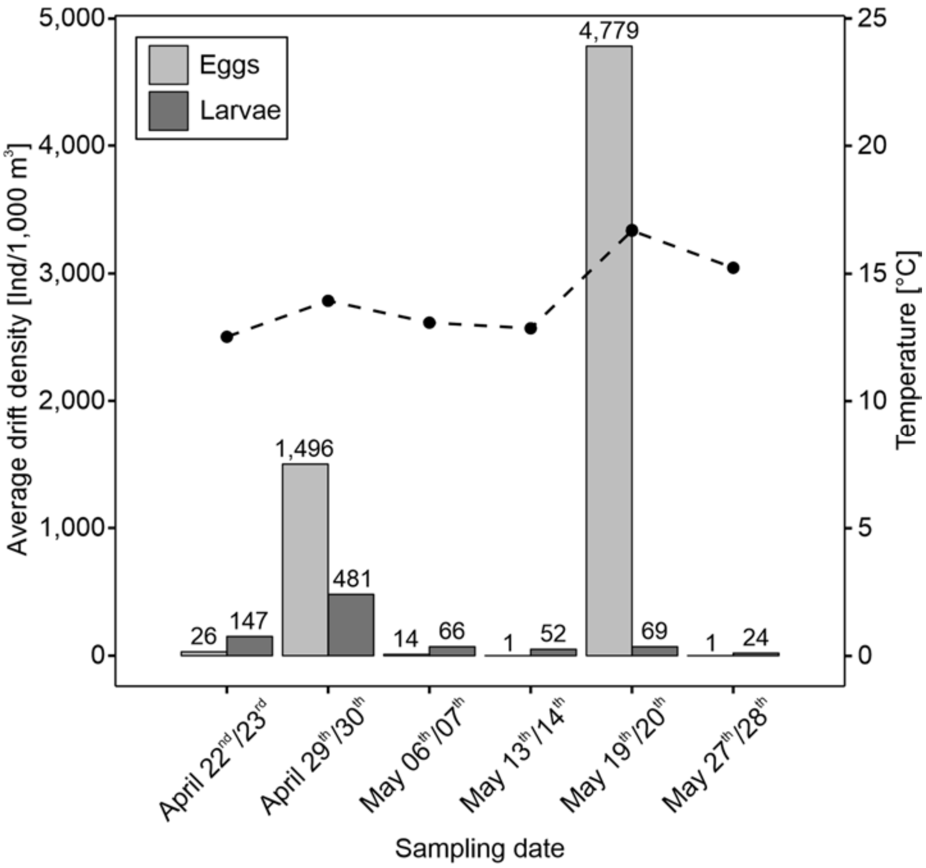


Figure 6.3 Average drift density (Ind/1,000 m³; y-axis left) of all sampled eggs and larvae in relation to the temperature profile (°C; y-axis right) at the individual sampling dates in April and May 2020 on the investigated spawning ground in the Eixendorf reservoir cascade.

The drift density of the larvae was on average twice as high during dusk (190 ± 594 Ind/1,000 m³) than during dawn (89 ± 263 Ind/1,000 m³; Wilcoxon-test: $W = 7103$, $p < 0.01$). In contrast, the egg drift density was on average higher during dawn (1,996 ± 14,819 Ind/1,000 m³) than during dusk (110 ± 713 Ind/1,000 m³). However, this difference was not significant ($p = 0.09$).

Clear differences in the seasonal drift pattern of the five most abundant species were identified over the entire study period. European perch was the only species that was detected at all sampling dates. 45% of all European perch larvae were already recorded during the first sampling. The total larval length ranged between 5–6 mm during the first two sampling dates and increased to a maximum of 29 mm at the last sampling date (linear regression: $R^2 = 0.79$, $p < 0.001$). However, European perch larvae smaller than 10 mm were regularly detected until to the penultimate sampling on May 19th/20th (Figure 6.4).

Most of the roach larvae were detected between the third (May 06th/07th) and the fifth (May 19th/20th) sampling. Roach eggs were also detected regularly over a period of five weeks from April 22nd/23rd to May 19th/20th, except on May 13th/14th. The total length of most roach larvae was in a very narrow range (approx. 6–7 mm; Figure 6.4) between April 29th/30th and May 19th/20th. A clear increase in the total length (up to 18 mm) was only observed at the last sampling on May 27th/28th (linear regression: $R^2 = 0.55$, $p < 0.001$).

Asp larvae and eggs were only detected between April 22nd/23rd and May 06th/07th. 70% of all asp larvae were recorded on April 29th/30th. Asp eggs were only detected during the first sampling. The total length of the asp larvae ranged between 8–9 mm (Figure 6.4).

90% of all ide larvae were already detected at the first sampling on April 22nd/23rd. Eggs were only detected during the first sampling date. From May 6th onwards, no more ide larvae and eggs were detected. The larval total lengths ranged between 6–7 mm (Figure 6.4).

28% of all pike-perch larvae were detected on April 29th/30th and May 06th/07th and 72% during the last sampling on May 27th/28th. No pike-perch eggs were recorded over the entire study period. What is striking is the clear difference in the larval lengths over time: on April 29th/30th and May 06th/07th, the total length of the larvae ranged between 5–7 mm, at the last sampling on May 27th/28th between 30–35 mm (linear regression: $R^2 = 0.96$, $p < 0.001$; Figure 6.4).

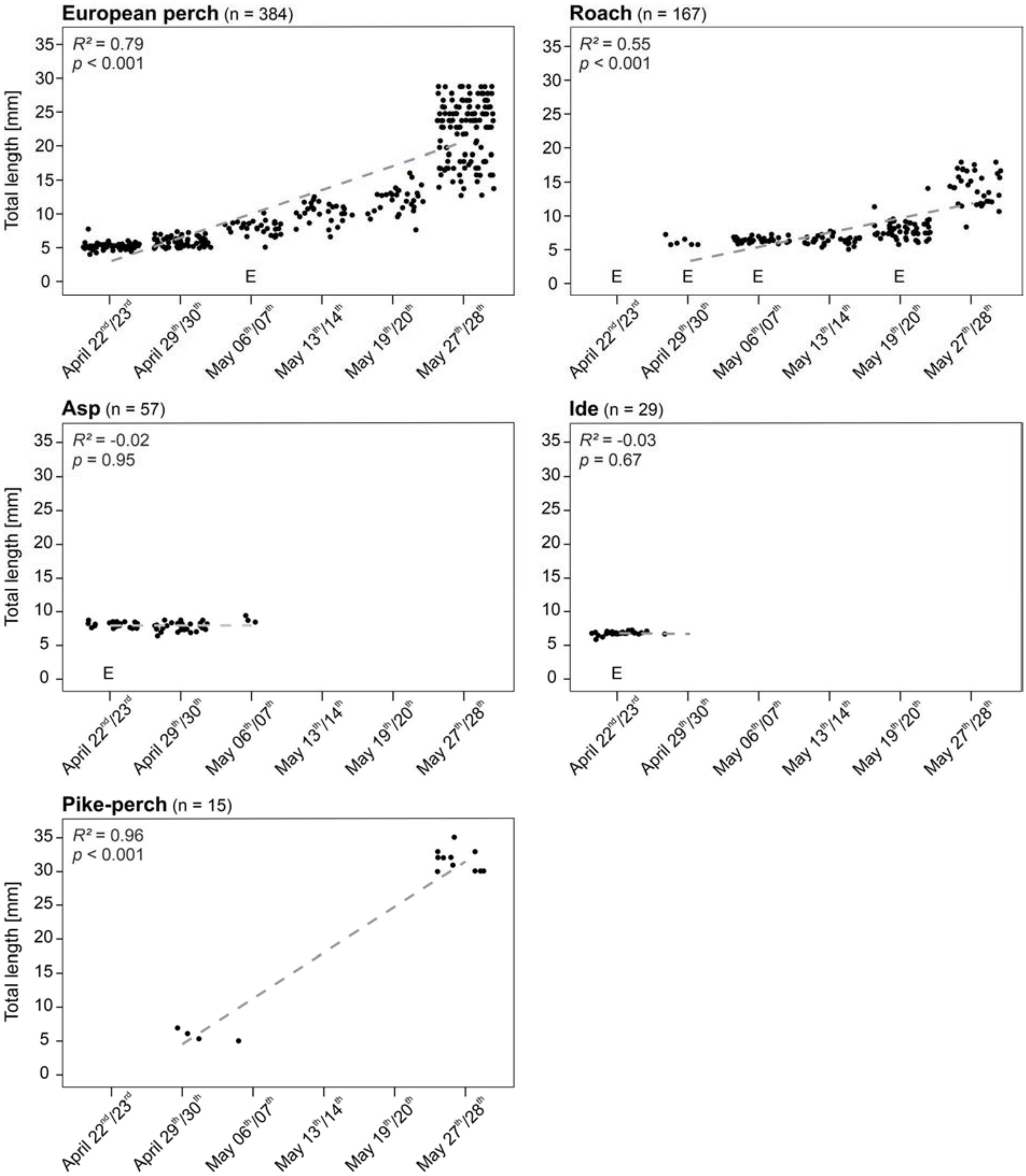


Figure 6.4 Increase in larval total length (mm) over time of the five most abundant species European perch, roach, asp, ide and pike-perch detected at the investigated spawning ground in the Eixendorf reservoir cascade; n = number of measured individuals. For each species, the adjusted coefficient of determination (R^2) and the significance level (p) of the linear regression are presented. E = detection of eggs.

6.4.6 Spatial differences in the number of detected larvae and eggs

Large spatial differences in the drift densities for larvae and eggs at the spawning ground were evident over the entire study period (Table 6.3; Figure 6.5). The drift densities for both larvae and eggs were significantly higher at the sampling site with the highest current velocity on the spawning ground (HCA; cf. Figure 6.1) than at all other sampling sites (Figure 6.5; Kruskal-Wallis-test larvae: $\chi^2 = 39.1$, df = 3, $p < 0.001$; eggs: $\chi^2 = 45.0$, df = 3, $p < 0.001$). The drift density of the larvae in the CGA (279 Ind/1,000 m^3) of the spawning ground was on average eight times higher than in the FGA (35 Ind/1,000 m^3). At the sampling site with the highest current velocity (HCA; cf. Figure 6.1), the difference in the average drift density of the larvae was even more pronounced (704 Ind/1,000 m^3 = twentyfold increased drift density in comparison to the FGA).

The average drift density of eggs was around 60 times higher in the CGA than in the FGA. The lowest average drift densities of larvae (18 Ind/1,000 m^3) and eggs (0.4 Ind/1,000 m^3, a total of eleven eggs from European perch and ruffe) were detected in the reference nets at the turbine outlet.

The drift densities of the five most abundant species (European perch, roach, asp, ide, pike-perch) were higher in the CGA close to the turbine than in the FGA (Figure 6.5). Asp and ide were only detected downstream of the reference nets on the spawning ground, and asp exclusively in the CGA. European perch, roach and pike-perch were also detected in the reference nets at the turbine outlet. Consequently, there was a drift of these species from the pre-storage basin to the main basin via the turbine. In addition, the species chub, bream and common nase were detected in the reference nets. Except for common nase, these species have also been identified as larvae or eggs on the spawning ground. Neither eggs nor larvae from rheophilic barbel were caught during the study period.

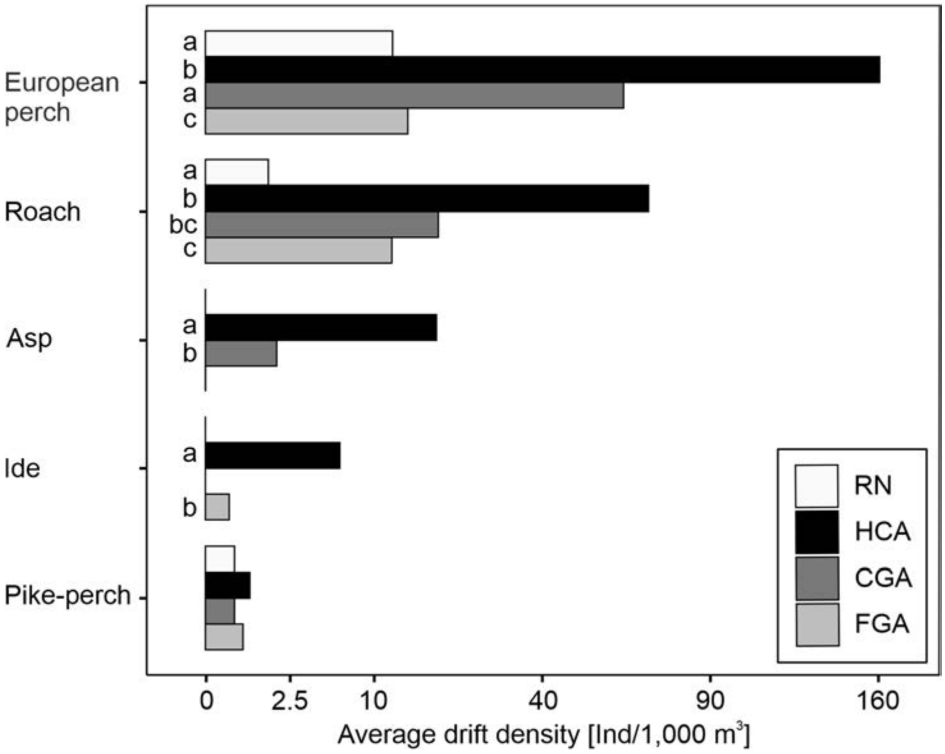


Figure 6.5 Average larval drift densities (Ind/1,000 m³; x-axis is x²-scaled) of the five most abundant species European perch, roach, asp, ide and pike-perch over the entire study period, differentiated according to the different areas of the investigated spawning ground in the Eixendorf reservoir cascade. RN = reference nets installed at the turbine outlet, HCA = sampling site with the highest current velocity, CGA = coarse gravel area, FGA = fine gravel area. Different lowercase letters on the bars indicate significant differences in drift density within a species between the different areas of the spawning ground (pairwise Mann-Whitney U-test or Wilcoxon-test).

6.5 Discussion

The construction and restoration of spawning grounds for target fish species of conservation is a commonly used method to support recruitment success in riverine ecosystems that can mitigate anthropogenic alterations caused by damming and hydropower use (Sternecker et al., 2013b; Taylor et al., 2019). Since the construction of reservoirs converted many streams into almost stagnant water bodies, thereby often degrading or destroying key habitats of specialised species, there is a great need to implement habitat-improving measures there as well. The results of this study demonstrate that an engineered spawning ground in a reservoir cascade can be successfully used as spawning and larval habitat by a variety of fish species. In accordance with the fish community inhabiting the reservoir cascade, mainly eggs and larvae of ubiquitous species were detected on the spawning ground. However, the unambiguous proof of spawning and recruitment of asp and ide highlights the importance of spawning habitat construction as a valuable tool to support the survival of rheophilic species in such heavily modified water bodies.

6.5.1 Functionality of the spawning ground based on abiotic parameters

Spawning ground quality for rheophilic gravel spawning species is governed by a variety of abiotic parameters, from which water depth, current velocity and substratum composition are among the most important ones. Therefore, spawning ground construction needs to consider these aspects in connection with the preferences of the specific target species for conservation. While spawning habitat preferences of the lithophilic (= gravelly spawning substratum preferring) cyprinids common nase and barbel is well understood (Britton & Pegg, 2011; Duerregger et al., 2018; Melcher & Schmutz, 2010; Nagel et al., 2020b), the results of this study reveal novel insights in the spawning habitat preferences of the rather poorly studied asp and ide. Rheophilic fish species that are assigned to the lithophilic spawning guild (Balon, 1975) usually require shallow, but in any case moderately to fast flowing and gravelly areas for egg deposition.

The average water depths at the examined spawning ground (av. 72–85 cm) were at the upper end of the preferred water depths for spawning which range from 10–90 cm for common nase and barbel (Melcher & Schmutz, 2010) and up to 1 m for asp and ide respectively (Rohtla et al., 2020; Šmejkal et al., 2017a). In this study, spawning mainly took place in the area with the highest current velocity close to the turbine outlet, which indicates a high importance of this spatially small area. Common nase and barbel prefer current velocities between 0.2 m/s and > 1 m/s for spawning (Gutmann Roberts & Britton, 2020; Melcher & Schmutz, 2010). Comparable to these species, the ide spawns at current velocities of up to 0.6 m/s (Rohtla et al., 2020), while Šmejkal et al. (2017a) showed that asp preferentially spawned in areas with current velocities > 0.3 m/s. This corresponds to the results of our study, where eggs and larvae of asp and ide were mainly detected in the area with current velocities of 0.15–0.5 m/s.

Recent studies revealed that, analogously to salmonids, the substratum composition on spawning grounds is a key parameter governing the success and timing of the embryonic development of common nase and barbel (Bašić et al., 2019; Duerregger et al. 2018; Nagel et al., 2020a; Vilizzi & Copp, 2013). Since egg properties and duration of embryonic development of asp and ide (Riehl et al., 2002) are similar to these species, it is likely that findings from studies on common nase and barbel are also transferable to asp and ide. This may apply to the depths of egg and larval development in the interstitial zone up to 20–30 cm (Bašić et al., 2019; Nagel et al., 2020b; Pinder et al., 2009) as well as to susceptibilities to fine sediment infiltration (e.g. Duerregger et al., 2018). Therefore, the substratum composition – in particular the fine sediment content (here grain sizes < 0.85 mm) – is of high importance for the functionality of a spawning ground for these species. Due to the artificial construction and the limited hydromorphological dynamics in the reservoir cascade, substratum composition was very homogeneous in both the FGA and the CGA, even almost four years after construction. In both the FGA and the CGA, fine sediment content was distinctly below 10% and thus below the threshold that has a negative impact on the hatching success of eggs of riverine fish species such as common nase and brown trout (*Salmo trutta*, L.) (Nagel et al., 2020a; Pulg et al., 2013). Yet, it seems unlikely that this situation will persist. Owing from the limited sediment transport and the resulting accumulation of particular fine grain sizes, reservoirs throughout the globe constantly loose useable storage capacity (Kondolf et al., 2014). Sediment flushing has therefore become a common solution to solve this issue (Lai & Shen, 1996). Consequently, huge amounts of fines are transported to downstream areas, where they can severely affect the functionality of the hyporheic zone by clogging the interstices of the stream bed (Kondolf et al., 2014). Sediment composition and compaction is directly linked to hyporheic exchange rates (Packman & Salehin, 2003), which in turn affects development conditions for biota in the interstitial zone (Geist & Auerswald, 2007). This is especially true for the early life stages of lithophilic fish species, as a constant oxygen supply is known to be a key parameter for successful egg development (Sear et al., 2017). The dissolved oxygen in the interstitial zone of the spawning area differed significantly between the FGA and the CGA. The small difference in dissolved oxygen between free flowing water and interstitial zone in the CGA shows a significantly higher exchange rate between free flowing water and interstitial zone than in the FGA, where successful egg development might be impaired.

However, even if all the above-mentioned abiotic parameters are present in the required quality, the functionality of a spawning ground downstream of a reservoir outlet can be severely impaired by thermal pollution. This holds true for both cold and warm water pollution caused by hypolimnetic or epilimnetic water withdrawal from the reservoir (e.g. Olden & Naiman, 2010; Preece & Jones, 2002; Sherman et al., 2007). Consequently, reservoir management in terms of thermal interference of downstream sections is of crucial importance, as water temperature and related oxygen supply decisively influence the duration of the embryonic period, embryonic mortality as well as growth and condition of newly hatched larvae (Schiemer et al., 2002).

6.5.2 Detected fish eggs and fish larvae on the spawning ground

During the six-week investigation of the spawning ground, mainly ubiquitous species such as roach and European perch were detected, which are characterized by a high level of adaptability to different environmental conditions. This corresponds to the type four transient fish fauna in European reservoirs according to the classification of Kubečka (1993), which is dominated by European perch (20–50%) and ubiquitous cyprinids such as roach, bream or white bream (*Blicca bjoerkna*, L.). The potential natural fish fauna of the River Schwarzach, which is the tributary of the Eixendorf reservoir cascade, lists mainly rheophilic species such as gudgeon, common dace, common nase and barbel (Schubert, 2007). Yet, these species were only caught in very low numbers during recent electrofishing surveys. Remarkably, successful recruitment of rheophilic asp and ide was detected during the spawning ground survey by a proof of eggs and larvae.

A spatial comparison of the drift densities showed that asp larvae were exclusively caught in drift nets that covered the CGA and particularly the area with the strongest current. No asp larvae were caught in the reference nets at the turbine outlet recording larval drift from the headwater, which strongly indicates spawning of this species must have occurred at the CGA of the spawning ground. The detection of asp eggs on the first day of sampling via the surber-sampling method confirms this finding. Together, both results can be seen as clear evidence of successful spawning of this rheophilic species on the engineered spawning ground, since the detection of drifting larvae indicates a successful reproduction in nearby upstream areas (Lechner et al., 2016). In addition, the spatial comparison of species-specific drift densities is an established method for the precise localisation of spawning activity (Meulenbroek et al., 2018; Nagel et al., 2020b). A similar result was found for the rheophilic ide, as all larvae of this species were also caught in drift nets at the spawning ground, but none in the upstream located reference nets. In addition, ide eggs were also detected at the first day of the investigation and exclusively in the CGA. As evident from these results, the abiotic conditions in this coarse gravel and comparatively strong flowing area immediately downstream of the turbine outlet seem to be suitable for successful spawning and egg development of these rheophilic cyprinids. The lack of evidence of eggs and larvae of the rheophilic cyprinids common nase and barbel and the low number of individuals caught during electrofishing support previous observations that there are only relict populations of these species left in the investigated section of the reservoir cascade. Yet, it cannot be excluded that these species used the spawning ground prior or after the investigated period, that the spawning ground was not effective for common nase and barbel or that these species were outcompeted on the spawning ground by more frequently occurring species such as European perch and roach. Thus, the chance for a conservation of rheophilic common nase and barbel in reservoirs in the long run by only constructing spawning grounds seems doubtful, as these species require a variety of habitats (Pander et al., 2017, Schiemer et al., 2002) and food sources (Reckendorfer et al., 2001) in subsequent life-stages. In contrast, studies on the migratory behavior of asp revealed habitat usage of stagnant waters during a large time of the year, e.g. for feeding in summer (Kärgenberg et al., 2020) or overwintering (Fredrich, 2003). They also describe spawning migrations during early spring in lotic systems, e.g. to the main channel of a large stream (Fredrich, 2003), as well as to tributaries of lakes and reservoirs (Hladík & Kubečka, 2003; Kärgenberg et al., 2020). These findings, in conjunction with the results of our study, suggest that even in almost stagnant reservoirs, the creation of an engineered gravel spawning ground in areas with low current velocities could provide a valuable restoration tool to sustain populations of less specialised rheophilic cyprinids, such as asp and ide. However, since the investigated reservoir cascade is predominantly populated by ubiquitous species and suitable habitat conditions for rheophilic species prevail only in a small area downstream of the turbine outlet, it is not to be expected that the fish community composition will shift towards a higher proportion of rheophilic species despite the proven functionality of the engineered spawning ground for asp and ide.

In general, structural properties with special regard to substratum composition, as well as reservoir operations schemes governing water depths, current velocities and water temperature in the time of spawning and egg incubation, need to be adapted to the spawning habitat requirements of these species. Furthermore, for the conservation of a (relict) population of a rheophilic species in a heavily modified water body, such as a reservoir, the simultaneous presence and connectivity of other necessary key habitats (e.g. juvenile, foraging and winter habitats) in the further life cycle is crucial (Pander & Geist, 2016).

In contrast to asp and ide, the other frequently recorded species roach, European perch and pike-perch were also caught in the reference nets installed at the turbine outlet, albeit in very low densities. These findings suggest that these species also reproduce in the headwater of the power plant. However, the drift densities of roach, European perch and pike-perch were highest in the nets positioned in the area with the strongest current at the spawning ground, which indicates that these species have also successfully reproduced there.

Since the species bleak (*Alburnus alburnus*, L.), white bream, ruffe and rheophilic gudgeon were identified by the genetic analysis of fish eggs sampled at the spawning ground, it can be assumed that these species also used the spawning ground for reproduction. Fish eggs have different drift characteristics: It is known that the eggs of rheophilc cyprinids can drift a few meters, but then settle (Nagel et al., 2020b; Šmejkal et al., 2017b). It is therefore unlikely that a substantial proportion of eggs have drifted from the headwater to the spawning ground. This is also evident from the very low proportion (< 0.001%) of eggs caught in the reference nets relative to the total number.

Roach eggs were detected in both substratum samples and drift nets on almost every sampling day over a period of four weeks. This multiple detection is not only an indication of a reproduction at the spawning ground, but also shows multiple spawning events, which can be proven by the very small increase in total length of the roach larvae over this long period. In general, the increase in fish larvae size after hatching follows a linear growth (Schludermann et al., 2009). Only slightly varying total lengths of small larvae over a longer period of time therefore suggest that new larvae are hatching steadily (Ramler et al., 2016). The measured asp larvae also show a homogeneous size structure over time, which indicates several spawning events. This finding is confirmed by the simultaneous detection of already hatched larvae and freshly laid eggs on the first sampling day.

Besides being suitable for rheophilic species, an engineered spawning ground can apparently also be beneficial for other species that do not necessarily require current and gravel substratum for reproduction. It is specifically surprising that European perch and pike-perch reproduced on the gravel spawning ground, as according to literature, these species predominantly prefer submerged vegetation, fallen branches or roots for spawning (Čech et al., 2009; Schlumberger & Proteau, 1996; Snickars et al., 2010) instead of coarse gravel. The current at the turbine outlet and the resulting permanent oxygen input is presumably a decisive abiotic factor for the spawning ground choice even by ubiquitous species, which primarily have different spawning habitat requirements than rheophilic species.

6.6 Conclusions

The investigated engineered spawning ground was successfully used for recruitment by several fish species suggesting the applicability of this restoration measure in reservoir cascades. Early life stages of rheophilic asp and ide were exclusively detected at the spawning ground, which is a clear evidence of successful spawning in this area. However, since there is no investigation prior to the construction of the spawning ground, it cannot be evaluated whether the engineered spawning ground has led to an improvement in the spawning success of rheophilic species compared to the situation prior to the construction of the hydropower plant. Further investigations several years after implementation are needed to validate the long-term functionality of this measure.

The results further indicate a successful reproduction for ubiquitous species such as roach, European perch and pike-perch at the spawning ground. For all species, the highest density of eggs and larvae was found in the area with the highest current velocity, which underlines the importance of this parameter for the functionality of an engineered spawning ground in such a heavily modified water body.

Particularly during the main spawning season of the rheophilic target species, reservoir operation should therefore consider hydromorphological and physical conditions on the spawning ground, especially with regard to water depth, current velocity and water temperature. For instance, raising the water level in the main basin of the reservoir cascade would increase the water depth and further reduce the current velocity near the bottom. In contrast, current velocity at the spawning ground could be additionally increased by directing the entire turbine discharge towards the spawning ground. Furthermore, during the main spawning season, there should be no thermal interference of the spawning ground through excessive hypolimnetic or epilimnetic water withdrawal from the pre-storage basin, as water temperature and related oxygen supply are crucial for hatching and successful larval development.

This study also revealed that a comprehensive assessment of spawning ground functionality benefits from a combined evaluation of both abiotic habitat parameters and spawning success. When identification to species level is required and several species are expected to spawn simultaneously, as in this study, genotypic validation of morphometric pre-identified fish larvae is essential to obtain robust results in species determination.

Although applying measures such as the construction of an engineered spawning ground in such heavily modified water bodies cannot be expected to be sufficient to restore the historically natural fish community composition of the formerly free flowing river, this measure can help to prevent the local extinction of a relict population of threatened species and thus preserve biodiversity.

7 General Discussion

By applying an integrative, multidimensional assessment approach in this thesis (Figure 7.1), effects of the anthropogenic stressors hydropower use and agricultural land use on different taxonomic groups (fishes, macroinvertebrates, periphyton), different life stages of fishes and abiotic parameters could be recorded and evaluated in different dimensions of stream ecosystems. The investigated stressors hydropower use and agricultural land use are currently among the main threats to freshwater aquatic biodiversity (Hering et al., 2015; Reid et al., 2019). However, these stressors do not act independently of each other, but often occur simultaneously in many rivers due to the globally advancing expansion of hydropower (Zarfl et al., 2015), the intensification of agriculture (Kehoe et al., 2017) and climate change (Markovic et al., 2017), which means that their negative impacts can add up (i.e. additive effect) or even intensify (i.e. synergistic interaction). High fine sediment loads from the catchment area and damming caused by hydropower use result in profound habitat degradation, which has serious negative effects on aquatic community composition (e.g. Jones et al., 2012; Mueller et al., 2011; Wood & Armitage, 1997). Damming of rivers in combination with hydropower use not only disrupts longitudinal connectivity and thus, for example, fish migratory behaviour and genetic exchange (e.g. Geist, 2011; Malmqvist & Rundle, 2002), but fish are also exposed to an immediate injury and mortality risk when passing these facilities (e.g. Algera et al., 2020; Mueller et al., 2017).

The investigation of the longitudinal downstream movement behaviour of wild fish provided important insights into species-specific seasonal and diurnal movement behaviour patterns as well as into the species and size composition of the resident and downstream moving fish community (Chapter 3). The finding that many species preferred to migrate during night in autumn can be used to operate hydropower plants in the most "fish-friendly" way possible during the main movement periods, for example by temporarily shutting down turbines (Knott et al., 2020) or opening additional alternative corridors (e.g. Egg et al., 2017).

However, the disruption of the longitudinal continuity by hydropower plants not only hampers fish downstream movements (Lucas & Baras, 2001; Schilt, 2007), but also the passage of such facilities can lead to serious injuries or death (Amaral et al., 2018; Baumgartner et al., 2017). Whilst the results of an experiment with standardized test fish released in front of a surface bypass at a movable power plant revealed that fish suffer only minor injuries during downstream passage, the bypass efficiency was low compared to the use of the turbine corridor despite an installed fish protection screen (Chapter 4). In order to increase bypass efficiency at this site and to better protect fish from harmful turbine passage, the dimensioning of the surface bypass should be increased and additional bypasses for near-bottom and mid-water moving fish species should be installed (Knott et al., 2019b).

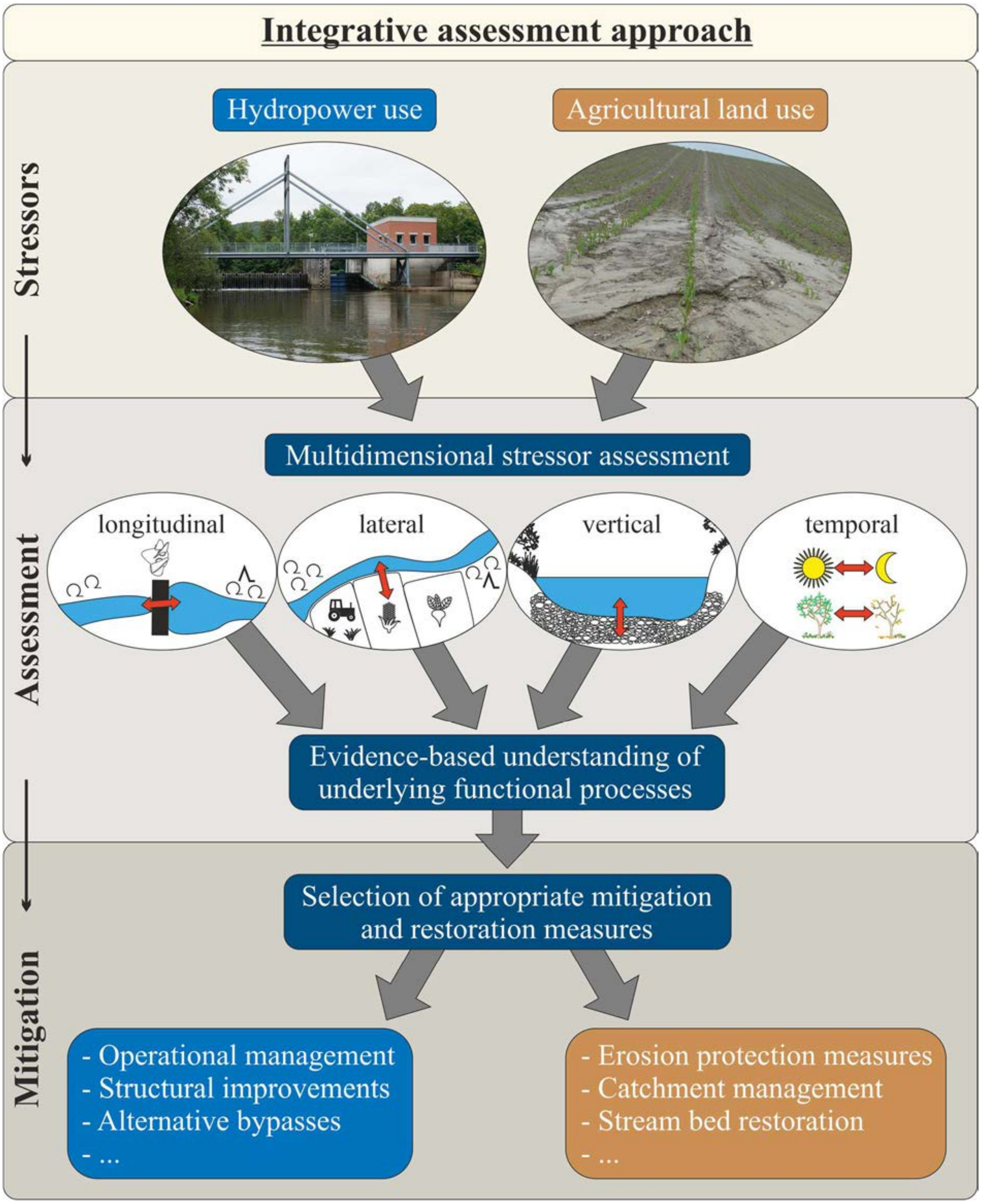


Figure 7.1 Flow chart of the integrative assessment approach applied in this thesis.

The results in Chapter 5 impressively demonstrate the linkage of the lateral dimension of a river in the form of the catchment area with the longitudinal, vertical and temporal dimensions. Erosion protection measures in the catchment area successfully reduced the fine sediment input resulting in positive effects on the aquatic community composition including fishes, macroinvertebrates and periphyton in the longitudinal course of a small river and its tributaries. Besides the effects on the longitudinal dimension, effects on the vertical dimension were also observed. The reduced fine sediment pollution from agricultural land and the associated reduced nutrient input led to an improved oxygen exchange rate between open water and interstitial water and thus enhanced interstitial habitat quality. Despite the observed improvements due to the measures in the catchment, additional instream measures, such as the restoration of the natural flow regime, are necessary to further improve the stream bed quality as a key habitat for many lithophilic species and to ultimately achieve an overall good ecological status (Knott et al., 2019a).

In addition to the impairments and hazards for fish during downstream movement described in Chapters 3 and 4, the alteration of the natural flow regime by damming and hydropower use leads to the degradation or loss of important key habitats, for example through siltation (Verdonschot & van der Lee, 2020; Zarfl et al., 2019). The construction and restoration of spawning grounds for target fish species of conservation is a frequently applied mitigation measure in this context (Nagel et al., 2020b; Sternecker et al., 2013a; Taylor et al., 2019). The assessed engineered spawning ground at the turbine outlet of a hydropower plant located in a reservoir has proven to be suitable for spawning and recruitment of rheophilic target fish species (Chapter 6). However, the long term functionality of this measure is only given if the spawning habitat requirements of the target species are considered in the operational management of the reservoir, as spawning success, for example, strongly depends on appropriate water depth and current velocity at the spawning ground (Knott et al., 2021).

Since different stressors can have different effects on the various dimensions in rivers, the basic prerequisite for successful restoration planning is a comprehensive understanding of the underlying processes that takes into account the dynamic and hierarchical structure of lotic ecosystems (cf. Ward, 1989). For instance, the stressor hydropower use does not only interrupt the longitudinal river continuity, but also changes instream habitat quality and the river-catchment relationships due to an altered flow regime (Geist, 2021; Poff et al., 2007). Consequently, not only effects on upstream-downstream interactions need to be considered, but also vertical (e.g. increased siltation due to damming degrades interstitial habitat quality) and lateral effects (e.g. high fine sediment input from the catchment further degrades habitats) at different temporal scales (e.g. weeks, months, years) depending on the study object. It is also important to include not only abiotic parameters in monitoring, but all relevant biotic groups, as the biological response should be the ultimate benchmark of restoration success (Roni et al., 2002).

Despite advances in the conceptual understanding of ecosystem processes, many studies still focus exclusively on a single stressor and its effect on a single biotic or abiotic response variable (Altshuler et al., 2011; Mueller & Geist, 2016; Spears et al., 2021). As a result, studies examining multiple stressors have long been sparse in international peer-reviewed literature (Ormerod et al., 2010). Meanwhile, the simultaneous consideration of multiple stressors and their interactions is increasingly being used in restoration ecology (Birk et al., 2020). However, since many studies are performed exclusively under controlled laboratory conditions, it often remains unclear how the findings from the laboratory can be transferred to realistic field conditions (Birk et al., 2020). This stresses the importance of integrative, multidimensional assessment approaches to collect and combine standardized monitoring data and to conduct controlled experiments under realistic field conditions in order to derive multiple stressor management strategies from the gained results (Altshuler et al., 2011; Spears et al., 2021).

7.1 Understanding of functional processes as a basis for the selection of appropriate mitigation and restoration measures

Regardless of the different objectives of mitigation and restoration measures, planning, implementation and evaluation should follow a systematic approach (Geist, 2015; Linke et al., 2011). Before implementing the measures, it is essential to understand the underlying functional processes. Ideally, the entire process chain should be considered, from the identification of the stressor to the ecological effects on the various biotic and abiotic levels. This requires a systematic and evidence-based assessment approach to select appropriate mitigation and restoration measures based on the gained knowledge (Figure 7.1).

7.1.1 Stressor hydropower

The impact of hydropower use on the river specific fish community can only be comprehensively assessed if the respective species inventory and the seasonal and diurnal movement patterns of the different fish species are known. Based on this knowledge, effective measures for fish protection at hydropower plants can be derived. Although there are many studies that have investigated the migration behaviour of economically relevant fish species such as salmon or eel in particular (e.g. McCormick et al., 1998; Riley et al., 2002; Travade et al., 2010), there are few studies that include the entire fish community.

The results in Chapter 3 show that the majority of fish at the four examined hydropower plants moved downstream during night in autumn. However, the observed downstream movement patterns of the fish community differed significantly between the study rivers, even for the very same fish species. This suggests that results on the downstream movement behaviour in one specific river cannot be transferred to others, as differences in species inventory or abiotic parameters (e.g. water chemistry, size, discharge, geographical location) can have a decisive influence on movement patterns.

It was remarkable that the downstream moving fish community differed significantly in both species and size composition from the resident fish community in the immediate headwaters of the hydropower plants. From this finding it can be concluded that single samplings, for example by means of electrofishing, which is usually carried out during the day, cannot be used to draw conclusions about downstream movement behaviour, since many species migrate during night (e.g. Jonsson, 1991) and fish from upstream tributaries or backwaters presumably only swim temporarily into the main stream in order to actively migrate or drift downstream.

Concerning the total length of the downstream moving fish, the results at all study sites were in a similar range (mean values ranging from 9–11 cm). This indicates that especially small fish species and fish sizes have to be included in concepts for fish passage and fish protection at hydropower facilities and not only economically important (e.g. salmon, eel) or from a recreational fisheries perspective desired species (e.g. rainbow trout, northern pike, pike-perch).

However, the downstream moving wild fish are not suitable for assessing mortality and injuries caused by hydropower facilities, as potential pre-damage, for example by upstream located hydropower plants or piscivorous fishes, birds or mammals, can only be insufficiently recorded and catch- and handling-related effects cannot be differentiated (Mueller et al., 2017). Therefore, in order to assess hydropower-related effects, it is essential to carry out experiments under realistic field conditions with fish of standardized size and quality, whose pre-damage is precisely known.

Field studies are absolutely necessary in order to verify the knowledge gained in laboratory experiments or modelling approaches under realistic environmental conditions (Côté et al., 2016; Spears et al., 2021). This should not be limited to one flagship species, but should include the entire river-specific fish community, or at least representative surrogates of the occurring species. Since the various fish species sometimes differ considerably in terms of morphology, anatomy, behaviour and size, the effects of hydropower plants on fish are also highly species-specific (Mueller et al., 2017; Mueller et al., 2020b).

In this context, the effects of hydropower facilities on fish are not only species-specific, but also site-specific. Site-specific parameters such as drop height, rotation speed, turbine diameter or number of turbine blades can have a decisive influence on mortality and the injury patterns of fish. Thus, the same turbine technology installed at different sites can sometimes cause considerable differences in fish injuries and mortality (Mueller et al., 2021). However, alternative corridors intended to enable downstream fish passage such as flap gates, flushing channels or crest cut-outs can also harm fish (Algera et al., 2020; Klopries et al., 2018). Therefore, not only the injuries occurring during turbine passage should be investigated in a standardized way, but of all possible corridors for downstream migration. Test fish obtained from fish hatcheries are best suited for this purpose, as their pre-damage is known and thus the effects of catching and handling can be investigated in a standardized manner (cf. Pander et al., 2018a).

The results from Chapter 4 showed that the passage of a surface bypass at a movable power plant with a drop height of approx. 5 m did not cause severe fish injuries. However, less severe injuries such as scale loss or tears in the fins were observed, which could presumably be further reduced if structural modifications, such as covering protruding components on the power plant steel casing, were made.

In order to record these small effect sizes in this study, it was imperative to conduct the experiment with standardized test fish. Only because the pre-damage of the fish was known precisely and the influence of catching and handling was differentiated, the actual effects caused by the passage of the bypass could be reliably quantified.

The injury assessment of downstream moving wild fish at hydropower plants is not suitable for the evaluation of power plant-related effects on fish health for the reasons already mentioned above. Hence, studies that have assessed the effects of hydropower plants exclusively with wild fish must be critically questioned, as an over- or underestimation of the effects cannot be ruled out.

In order to reduce the negative impacts of hydropower use on fish, the injuries during passage should be as low as possible and the bypasses should be optimally positioned and dimensioned to ensure the highest possible bypass efficiency for a wide range of fish species. However, at the hydropower plant studied in Chapter 4, more than 90% of the fish passed the turbine even after the dimensions of the bypass were enlarged. Despite a fish protection screen with 20 mm bar spacing, fish up to approx. 30 cm total length were able to pass through. Previous assumptions that fish screens with bar spacing between 15–25 mm cannot be passed by the majority of fish must therefore be questioned and verified. Since a large part of the downstream moving fish consists of small species or small individuals (cf. Chapter 3), these fish sizes must be given greater consideration in fish protection concepts at hydropower stations.

7.1.2 Stressor fine sediment

If the fine sediment load in a river system is to be investigated, it is not sufficient to quantify the input alone. Moreover, it is necessary to understand what the sources of the pollution are (Geist, 2015; Poeppl et al., 2019). These can be, for instance, agricultural areas in the catchment that are particularly susceptible to erosion, or point sources such as drainage ditches or field roads (Fiener et al., 2011). In this context, it is also important that the study period is chosen long enough to cover seasonal (e.g. due to changing land cover) and event-related fluctuations (e.g. due to heavy rainfall events). In order to be able to better classify the gained results, it is necessary to include control sites, ideally without adjacent agricultural use (e.g. woodland) or alternatively with exclusively extensive use (e.g. extensive grassland).

However, the amount of deposited fine sediment alone does not allow conclusions to be drawn about the effects on the aquatic community composition and other abiotic water parameters. Therefore, if possible, several representative taxonomic groups as well as physical and chemical parameters should be included in monitoring in order to obtain robust results (e.g. Wood & Armitage, 1997).

The selected study design in Chapter 5 showed that the erosion protection measures applied in the catchment successfully reduced the fine sediment and nutrient input into the river system resulting in positive effects on the interstitial habitat quality and aquatic community composition. For example, the proportion of rheophilic fishes and macroinvertebrates as well as non-mobile periphyton taxa was higher in the sub-catchments where the area of erosion protection measures was also higher.

Yet, the implementation of the erosion protection measures alone did not lead to a good ecological condition class according to the European Water Framework Directive (2006/60/EC). As there are further strong structural deficits such as straightening of the stream, weirs, bank and stream bed reinforcement in the study area, a combination of measures in the catchment area with structure-enhancing measures within the river is necessary for a successful restoration of disrupted natural sediment and flow dynamics (e.g. Auerswald & Geist, 2018; Denic & Geist, 2015).

However, in order to prioritize and select the most promising measures, other factors such as geology and topography of the catchment must be taken into account. Geist and Auerswald (2018), for example, found in their study on a river that flows mainly within a fen area that only about 1% of the deposited fine sediment originates from erosion in the catchment area and that siltation is predominantly governed by instream processes. Organic matter from the degraded peatland made a considerable contribution to the fine sediment composition (on average 16%).

In contrast, the study area in Chapter 5 was located in the most erosion-prone area of the Tertiary Hills in Bavaria (soil erosion rates up to 10–12 t/ha/y; Auerswald et al., 2009; Cerdan et al., 2010), which explains the high average gross fine sediment deposition rates of > 15 kg/m²/month compared to studies in other geological areas (cf. Denic & Geist, 2015; Pander et al., 2015a). The evident higher fine sediment deposition in months without protective plant cover on agricultural land and in areas with a low share of erosion protection measures further supports the finding that erosion protection measures in the catchment can contribute substantially to reduce fine sediment pollution in this particular study area.

Furthermore, the individual taxonomic groups were found to be influenced differently by both catchment-related and instream-related variables, which can be explained by differences in their mobility and trophic level. Since different taxonomic groups respond differently to both disturbance and restoration, appropriate monitoring should consider taxonomic representativeness for each spatial scale.

7.2 Which mitigation and restoration measures are suitable to protect and enhance aquatic biodiversity?

7.2.1 Technical solutions and adaptive management recommendations to reduce negative impacts of hydropower facilities on fish health

The advancing global expansion of hydropower (Zarfl et al., 2015) is not only accompanied by fundamental habitat changes in lotic ecosystems, but also poses a direct mortality and injury risk for downstream moving fish. The passage through the turbine is the most dangerous corridor. As downstream moving fish predominantly follow actively the main current or are passively displaced with it (Williams et al., 2012), and as the majority of the discharge usually flows through the turbines, a large proportion of fish will inevitably follow this route.

In order to reduce fish mortality and injuries at hydropower facilities, various approaches are being pursued: Fish should either be prevented from swimming into the turbines by different types of physical or behavioural barriers at the turbine inlet and guided to suitable bypasses, or the probability of turbine-related injuries should be significantly reduced by developing innovative turbine types compared to conventional systems.

To prevent fish from swimming into the turbine chamber, fish protection screens with bar spacings between 10–25 mm are often installed upstream of the turbine inlet. Due to the arrangement of the bars (horizontal vs. vertical) or different inclinations to the stream bed or to the flow direction, these fish protection screens are also intended to provide a behavioural barrier and to guide the fish to suitable bypasses. In addition to these physical barriers, other behavioural barriers are used that should prevent fish from passing through the turbine by means of electricity, sound, bubbles or light (e.g. Egg et al., 2019; Kammerlander et al., 2020; Schilt, 2007).

Initially, efforts to make hydropower plants passable for fish by means of functional bypasses were mainly limited to upstream migrating fish. Only in recent decades the focus has increasingly turned to problems and challenges that occur during the downstream migration of fish at hydropower plants. As a result, fish passage technology for upstream migrating fish is generally more advanced than bypass technology for downstream migration, partly because it is more difficult and complex to develop effective bypasses for downstream migration (Larinier & Travade, 2002).

However, there are now a number of bypass designs that have been developed exclusively for downstream migrating fish. Examples include surface bypasses (Klopries et al., 2018; Knott et al., 2019b; Tomanova et al., 2021), deep bypass systems with entrances located near the river bed (Baker et al., 2019) or the zig-zag eel bypass system with bottom and surface entries (Egg et al., 2017; Hassinger & Hübner, 2009). These bypasses are usually located in close proximity to fish protection and guidance facilities.

In addition to these bypasses specifically designed for downstream passage, there are other hydropower plant components that were not designed as bypasses but can still function as downstream migration corridors. For example, Egg et al. (2017) showed that an undershot sluice gate for the diversion of flotsam to the tailrace was successfully used by eels during their downstream migration. Furthermore, flushing channels, often installed at the upper end of the screen at the turbine inlet, spillways or flap gates can successfully guide fish into the tailrace (e.g. Gosset et al., 2005; Larinier & Travade, 2002; Økland et al., 2019). However, bypasses such as nature-like fish passes, vertical-slot fish passes or rock ramps, which were actually built to restore upstream continuity, are also used by downstream moving fish (Pander et al., 2013; Sanz-Ronda et al., 2021).

With all of the above-mentioned options to reduce hydropower plant-related effects on fish, it is important to ensure that both fish protection facilities and bypasses are designed in such a way that fish do not suffer any harm when getting into contact with these structures. Accurate construction should avoid injuries caused by protruding components, sharp edges or areas where fish can be crushed as far as possible. Moreover, there is a high injury risk when fish are pressed against components or even get pinched by high current speeds (e.g. at the fish protection screen). According to Ebel (2013), the critical current speed at the screen should not exceed 0.5 m/s. Furthermore, when entering the tailrace via a free overflow, the water depth in the plunge pool should always be large enough (> 70% of the water level differential; Pflugrath et al., 2019) to avoid collisions with concrete and metal parts.

In recent years, various types of so-called innovative turbine types have been developed which, according to manufacturers, are more “fish-friendly” than conventional Kaplan or Francis turbines, for example. Thus, these turbine types are usually operated without fish protection devices. Examples are VLH turbines or Archimedes screw turbines. Due to lower rotation speeds, larger turbine diameters and their use at low heads (usually less than 5 m), collisions are to be reduced and injuries due to large pressure-related differences are to be avoided.

In addition to the aforementioned technical options for fish protection at hydropower plants, the negative impacts of hydropower use on fish welfare can be reduced through adaptive management measures. Knowledge on the diurnal and seasonal fish movement behaviour can be used, for example, to completely shut down the turbines during the main migration periods or to operate them in a power state that is less harmful to fish (e.g. high or low power state, depending on turbine type and target fish species; cf. Mueller et al., 2021). The periodically opening of additional corridors, such as undershot sluice gates, can be a promising measure to enable successful downstream migration (cf. Egg et al., 2017). Such measures do not require structural changes to the facilities and can usually be implemented at low financial cost.

Besides adaptive management measures to protect fish during hydropower plant passage, the operational management of such facilities should also consider the requirements of the aquatic community occurring in the adjacent upstream and downstream sides. For instance, rapid and frequent changes in turbine discharge (= hydropeaking), which is also applied at run-of-the-river hydropower plants, can cause unnatural changes in water level and current velocity (Greimel et al., 2016; Moreira et al., 2019). This can lead to immediate negative impacts on aquatic organisms through downstream displacement and stranding and to the degradation or destruction of key habitats such as spawning grounds and juvenile habitats (Hayes et al., 2021; Person et al., 2014; Schmutz et al., 2015). Hence, effective mitigation measures must be based on the requirements of key species of conservation concern and take into account the hydromorphological processes that determine habitat conditions (Moreira et al., 2019; Schmutz et al., 2015).

7.2.2 Measures to reduce the fine sediment load in rivers

Increasing fine sediment input into rivers has become a growing stressor for aquatic biodiversity throughout the globe. In particular, expanding agricultural intensification in combination with climatically induced events such as the increase in heavy rainfall events or periods of drought contribute to exacerbating the problem. Currently, a number of instream measures and measures in the catchment area are being applied to counteract this development.

In order to reduce the deposition of fine sediment in rivers, functional processes such as the natural flow regime should be restored in a first step (Geist, 2015). This would allow natural sediment relocation processes to take place again, which, for example, could restore the functionality of the degraded interstitial zone, clogged by fine sediment, as habitat for fishes, macroinvertebrates, periphyton and microbial biofilms. But measures such as stabilizing river banks by planting trees or shrubs or installing guide groynes can also contribute to reduce instream erosion. However, several studies have already critically questioned that the problem of fine sediment pollution in rivers cannot be solved by instream measures alone (Mueller et al., 2014a; Pander et al., 2015a; Sternecker et al., 2013a).

Consequently, in addition to the implementation of instream measures, it is crucial to tackle the problem at its roots and to reduce erosion in the catchment area and to prevent fine sediment input as far as possible. Frequently applied erosion protection measures on agricultural land include no-till cultivation, mulch tillage, catch crops, crop rotations, strip cropping and terracing. Most measures have in common that soil erosion is to be reduced by maintaining a protective plant cover, often accompanied by a reduced frequency of ploughing (Pimentel et al., 1995). Moreover, reducing field size and thereby increasing patchiness can help to reduce surface runoff and associated soil erosion (Fiener et al., 2011).

In addition to erosion protection measures on agricultural land, the influence of linear structures must also be taken into account. For example, field roads or ditches along field borders can increase the input of fine sediment into rivers. However, surface runoff via these structures can be reduced if the hydraulic roughness (e.g. through grass cover) and the transverse profile (flat-bottomed better than slightly incised) of these structures are optimized (Fiener & Auerswald, 2005) or if these structures are terraced, thereby increasing the flow length (Fiener et al., 2011). This slows down surface runoff and facilitates infiltration. Combining the above mentioned measures with sediment retention ponds at the downslope end of fields or drainage ditches can also trap eroded soil after heavy rainfall events (Fiener et al., 2005; Hoess & Geist, 2021), thereby reducing fine sediment and nutrient loads entering rivers. Another proven measure is the implementation of grass filter strips at the downslope end of fields or along the drainage pathway. This slows down and filters surface runoff, which in turn reduces fine sediment and nutrient input to rivers.

The challenge of successfully reducing the increasing fine sediment input into lotic ecosystems in the long term can probably only be solved through an integrative approach by combining instream measures and erosion control measures in the catchment area (Knott et al., 2019a; Lummer et al., 2016). This emphasizes the importance of a holistic, multidimensional approach in aquatic conservation and restoration, which simultaneously considers catchment- and instream-related impacts at different temporal and spatial scales and their effects on abiotic parameters and the aquatic community (Mueller et al., 2020a).

7.2.3 Restoration of degraded or lost habitats due to hydropower use

It is well known that damming in rivers caused by hydropower generation results in profound changes in abiotic habitat conditions (cf. Mueller et al., 2011). These changes in current speed, water depth, substratum composition and hyporheic exchange rates often lead to the degradation or loss of important key habitats for aquatic species. This in turn affects the aquatic community composition, as typical rheophilic species are often replaced by ubiquitous species.

To counteract the negative consequences of these habitat changes, there are a number of applied restoration measures that often focus on the restoration of key habitats for endangered species. The construction or restoration of spawning grounds is one of the most frequently applied measures (Nagel et al., 2020b; Sternecker et al., 2013a; Taylor et al., 2019). The results in Chapter 6 illustrate that even an engineered spawning ground in a reservoir cascade was used by rheophilic species for spawning and that successful development of fish larvae was possible there. This impressively demonstrates that spawning ground restoration can be a valuable tool to enhance the survival of endangered rheophilic species even in highly modified water bodies. Other frequently applied habitat improvement measures are the restoration of shallow bank habitats for juvenile fish (Pander et al., 2017), reconnection of the main stream with its floodplain (Pander et al., 2018b) or the introduction of dead wood (Pander et al., 2016).

The success of such restoration measures in highly modified water bodies such as reservoir cascades is also linked to the operational management of these systems. The functionality of the studied spawning ground in Chapter 6 is strongly dependent on the prevailing hydromorphological conditions. For instance, if the water level is too high, the current speed and the water depth at the spawning ground no longer meet the requirements of the target fish species and thus the spawning ground is no longer used (Knott et al., 2021).

Consequently, successful mitigation and restoration measures require not only careful planning, implementation and evaluation of the measures, but also the involvement of local actors and stakeholders in management to ensure lasting functionality. In order to find the optimal solution for the prevailing local conditions, an individually customized solution is required for each site, as the applicability and thus the functionality of the available mitigation and restoration tools is very site-specific.

7.3 Outlook

In order to make progress in combating the threats to aquatic biodiversity, it is essential in a first step, as presented in this thesis, to investigate all underlying processes holistically according to a multidimensional approach that takes into account different temporal and spatial scales as well as different biotic and abiotic indicators. Only a fundamental understanding of functional processes enables the selection of appropriate mitigation and restoration measures to protect and enhance biodiversity (Geist, 2015; Søndergaard & Jeppesen, 2007).

The integrative assessment approach presented in this thesis is therefore a good tool for recording and evaluating the effects of various anthropogenic stressors on aquatic biodiversity at different temporal and spatial scales, following "the four-dimensional nature of lotic ecosystems" concept by Ward (1989). The standardized study design can be easily applied to other rivers that are impaired by hydropower use or fine sediment pollution. The frequently criticized lack of harmonization and comparability among scientific studies can only be countered if a systematic, reproducible study design is used and both positive and negative results are reported in detail.

The results from Chapters 3 and 4 provide important insights into the downstream movement behaviour of potamodromous fish species and the fish passage efficiency and injury risk at a surface bypass of a small-scale hydropower plant. The derived management recommendations for fish protection at hydropower facilities are not site-specific and can be transferred to low head hydropower plants worldwide. However, since different rivers often differ significantly in their fish community composition and little is still known about the movement behaviour of many potamodromous species, there is a considerable need for further scientific research to close this knowledge gap.

The applied study design in Chapter 4 is very well suited to investigate the mortality and injury risk for fish at other types of bypasses. Although there is a growing body of literature on hydropower-related effects on fish, the majority of available studies were conducted at North American high head facilities and are predominantly on economically valuable species such as salmonids (Algera et al., 2020). Research on fish species with little or no perceived economic value is severely underrepresented in the peer-reviewed and grey literature not only in North America, but worldwide. To address this knowledge gap, further studies on the impact of hydropower facilities on non-salmonid or non-sportfish target species are needed that not only focus on the functionality of fish protection facilities, but also assess possible passage-related injuries in detail (Algera et al., 2020; Mueller et al., 2021).

Based on the findings in Chapter 5 that erosion protection measures in an erosion-prone catchment successfully reduce fine sediment input and thus have positive effects on the aquatic community composition, these measures can presumably also be successfully applied in other catchments with intensive agricultural use. Soil erosion protection measures in the catchment can be an important component for the long term restoration of rivers with highly endangered target species such as the freshwater pearl mussel, as only short-term instream measures to reduce fine sediment loads often do not result in the desired success (Denic & Geist, 2015; Geist & Auerswald, 2007).

As climate change is expected to exacerbate the ongoing threat to aquatic biodiversity (Markovic et al., 2017), the results of this thesis should be linked to further studies on the impacts of climate change on freshwater ecosystems. Further research questions in this context are, for example, how the fine sediment load changes after pronounced periods of heavy rainfall events or drought, how this affects the aquatic community and abiotic parameters, and what measures can be taken to counteract this. There are also many unanswered questions about how climate change affects the migratory behaviour of freshwater fish species and to what extent management of fish passage infrastructure at hydropower facilities will need to take into account climate change effects such as long periods of low flow to maintain functionality (Lennox et al., 2019).

Finally, a basic understanding of functional processes not only serves to counteract the advancing threat to stream ecosystems through appropriate mitigation and restoration measures, but can also increase the (intrinsic) value and services of these systems for human beings. Stream ecosystems not only provide essential ecosystem services such as drinking water and food supply, but also contribute to human well-being through cultural services such as recreation, ecotourism, aesthetic and spiritual values.

8 Publication List

8.1 Publications related to this thesis

Knott, J., Mueller, M., Pander, J. & Geist, J. (2019). Effectiveness of catchment erosion protection measures and scale-dependent response of stream biota. *Hydrobiologia*, 830, 77–92.

Knott, J., Mueller, M., Pander, J. & Geist, J. (2019). Fish Passage and Injury Risk at a Surface Bypass of a Small-Scale Hydropower Plant. *Sustainability*, 11, 6037.

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

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, 106434.

8.2 Further publications not included in this thesis

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

Geist, J., **Knott, J.**, Mueller, M., Ingermann, H., Gerke, M., Mayr, C., Lohmeyer, B. & Pander, J. (2021). Fish Ecological Monitoring at Innovative and Conventional Hydropower Stations in Bavaria, Germany. *Danube News*, 43, 10–13.

Mueller, M., Pander, J., **Knott, J.** & Geist, J. (2017). Comparison of nine different methods to assess fish communities in lentic flood-plain habitats. *Journal of Fish Biology*, 91, 144–174.

Pander, J., Mueller, M., **Knott, J.**, Egg, L. & Geist, J. (2017). Is it worth the money? The functionality of engineered shallow stream banks as habitat for juvenile fishes in heavily modified water bodies. *River Research and Applications*, 33, 63–72.

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

Pander, J., **Knott, J.**, Mueller, M. & Geist, J. (2019). Effects of environmental flows in a restored floodplain system on the community composition of fish, macroinvertebrates and macrophytes. *Ecological Engineering*, 132, 75–86.

8.3 Oral presentation

Knott, J., Mueller, M., Pander, J. & Geist, J. (2018). Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants. Fish Passage 2018 – International Conference on River Connectivity, Albury, New South Wales, Australia, December 2018.

8.4 Poster presentation

Knott, J., Egg, L., Mueller, M., Pander, J. & Geist, J. (2015). Assessment of fish damage and habitat quality at new innovative hydropower plants. Fish Passage 2015 – International Conference on River Connectivity, Groningen, the Netherlands, June 2015.

9 Author contributions to the chapters

Chapter 3: Seasonal and diurnal variation of downstream fish movement at four small-scale hydropower plants

Conceptualization, JK, MM, JP and JG; methodology, JK, MM, JP and JG; validation, MM, JP and JG; formal analysis, JK; investigation, JK and MM; resources, JG; writing—original draft preparation, JK; writing—review and editing, JK, MM, JP and JG

Chapter 4: Fish Passage and Injury Risk at a Surface Bypass of a Small-Scale Hydropower Plant

Conceptualization, JK, MM, JP and JG; methodology, JK, MM, JP and JG; validation, MM, JP and JG; formal analysis, JK; investigation, JK and MM; resources, JG; writing—original draft preparation, JK; writing—review and editing, JK, MM, JP and JG

Chapter 5: Effectiveness of catchment erosion protection measures and scale-dependent response of stream biota

Conceptualization, JK, MM, JP and JG; methodology, JK, MM, JP and JG; validation, MM, JP and JG; formal analysis, JK; investigation, JK; resources, JG; writing—original draft preparation, JK; writing—review and editing, JK, MM, JP and JG

Chapter 6: Wasted effort or promising approach – Does it make sense to build an engineered spawning ground for rheophilic fish in reservoir cascades?

Conceptualization, JK, CN and JG; methodology, JK, CN and JG; validation, JG; formal analysis, JK and CN; investigation, JK and CN; resources, JG; writing—original draft preparation, JK and CN; writing—review and editing, JK, CN and JG

10 References

Aarts, B. G. W., Van den Brink, F. W. B. & Nienhius, 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.

Abernethy, C. S., Amidan, B. G. & Cada, G. F. (2001). *Laboratory studies of the effects of pressure and dissolved gas supersaturation on turbine-passed fish*. Pacific Northwest National Laboratory, Richland, WA, USA, pp. 61.

Acornley, R. M. & Sear, D. A. (1999). Sediment transport and siltation of brown trout (*Salmo trutta* L.) spawning gravels in chalk streams. *Hydrological Processes*, 13, 447–458.

Adam, B., Schürmann, M. & Schwevers, U. (2013). *Zum Umgang mit aquatischen Organismen – Versuchstierkundliche Grundlagen*. Springer Spektrum: Wiesbaden, Germany, pp. 188.

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

Allan, J. D. & Flecker, A. S. (1993). Biodiversity conservation in running waters. *BioScience*, 43, 32–43.

Allan, J. D. (2004). Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 35, 257–284.

Altshuler, I., Demiri, B., Xu, S., Constantin, A., Yan, N. D. & Cristescu, M. E. (2011). An integrated multi-disciplinary approach for studying multiple stressors in freshwater ecosystems: Daphnia as a model organism. *Integrative and Comparative Biology*, 51, 623–633.

Amaral, S. V., Coleman, B. S., Rackovan, J. L., Withers, K. & Mater, B. (2018). Survival of fish passing downstream at a small hydropower facility. *Marine and Freshwater Research*, 69, 1870–1881.

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

Anderson, M. J., Gorley, R. N. & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. 1st ed., PRIMER-E Ltd.: Plymouth, UK.

Angermeier, P. L. & Karr, J. R. (1984). Relationships between woody debris and fish habitat in a small warmwater stream. *Transactions of the American Fisheries Society*, 113, 716–726.

Aprahamian, M. W., Smith, K. M., McGinnity, P., McKelvey, S. & Taylor, J. (2003). Restocking of salmonids – opportunities and limitations. *Fisheries Research*, 62, 211–227.

Arnekleiv, J. V., Kraabøl, M. & Museth, J. (2007). Efforts to aid downstream migrating brown trout (*Salmo trutta* L.) kelts and smolts passing a hydroelectric dam and a spillway. In *Developments in Fish Telemetry*; Almeida, P. R., Quintella, B. R., Costa, M. J., Moore, A., Eds.; Springer: Dordrecht, Germany, Volume 195, pp. 5–15.

Arthington, A. H., Bunn, S. E., Poff, N. L. & Naiman, R. J. (2006). The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, 16, 1311–1318.

Auerswald, K., Fiener, P. & Dikau, R. (2009). Rates of sheet and rill erosion in Germany – A meta-analysis. *Geomorphology*, 111, 182–193.

Auerswald, K. & Geist, J. (2018). Extent and causes of siltation in a headwater stream bed: catchment soil erosion is less important than internal stream processes. *Land Degradation and Development*, 29, 737–748.

Auerswald, K., Moyle, P., Seibert, S. P. & Geist, J. (2019). HESS Opinions: Socio-economic and ecological trade-offs of flood management – benefits of a transdisciplinary approach. *Hydrology and Earth System Sciences*, 23, 1035–1044.

Baker, N., Haro, A., Watten, B., Noreika, J. & Bolland, J. D. (2019). Comparison of attraction, entrance and passage of downstream migrant American eels (*Anguilla rostrata*) through airlift and siphon deep entrance bypass systems. *Ecological Engineering*, 126, 74–82.

Balon, E. K. (1975). Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Board of Canada*, 32, 821–864.

Bašić, T., Britton, J. R., Rice, S. P. & Pledger, A. G. (2019). Does sand content in spawning substrate result in early larval emergence? Evidence from a lithophilic cyprinid fish. *Ecology of Freshwater Fish*, 28, 110–122.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

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

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, 436–441.

Belsley, D. A., Kuh, E. & Welsch, R. E. (2005). *Regression diagnostics: Identifying influential data and sources of collinearity*. Vol. 571. John Wiley & Sons.

Bernhardt, E. S., Palmer, M. A., Allan, J. D., Alexander, G., Barnas, K., Brooks, S., ... & Sudduth, E. (2005). Synthesizing U.S. river restoration efforts. *Science*, 308, 636–637.

Bernhardt, E. S. & Palmer, M. A. (2007). Restoring streams in an urbanizing world. *Freshwater Biology*, 52, 738–751.

Bernhardt, E. S. & Palmer, M. A. (2011). River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecological Applications*, 21, 1926–1931.

Bickford, S. A. & Skalski, J. R. (2000). Reanalysis and interpretation of 25 years of Snake–Columbia River juvenile salmonid survival studies. *North American Journal of Fisheries Management*, 20, 53–68.

Bierschenk, A. M., Mueller, M., Pander, J. & Geist, J. (2019). Impact of catchment land use on fish community composition in the headwater areas of Elbe, Danube and Main. *Science of the Total Environment*, 652, 66–74.

Biggs, B. J. F. (2000). *New Zealand periphyton guideline. Detecting, Monitoring and Managing Enrichment of Streams*. NIWA, Christchurch.

Bingpeng, X., Heshan, L., Zhilan, Z., Chunguang, W., Yanguo, W. & Jianjun, W. (2018). DNA barcoding for identification of fish species in the Taiwan Strait. *PLoS One*, 13, e0198109.

Birk, S., Chapman, D., Carvalho, L., Spears, B. M., Andersen, H. E., Argillier, C., ... & Hering, D. (2020). Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology & Evolution*, 4, 1060–1068.

Bonada, N., Rieradevall, M. & Prat, N. (2007). Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia*, 589, 91–106.

Bond, N. R. & Lake, P. S. (2003). Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. *Ecological Management & Restoration*, 4, 193–198.

Bond, M. H., Nodine, T. G., Beechie, T. J. & Zabel, R. W. (2019). Estimating the benefits of widespread floodplain reconnection for Columbia River Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 1212–1226.

Boulton, A. J., Findlay, S., Marmonier, P., Stanley, E. H. & Valett, H. M. (1998). The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics*, 29, 59–81.

Bray, J. R. & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27, 325–349.

Bretschko, G. (1995). The ecological importance of streambed sediments, regardless of whether or not they are inundated. *Folia Facultatis Scientarium Naturalium Universitatis Masarykianae Brunensis, Biologia*, 91, 5–17.

Britton, J. R. & Pegg, J. (2011). Ecology of European barbel *Barbus barbus*: implications for river, fishery, and conservation management. *Reviews in Fisheries Science*, 19, 321–330.

Brooker, M. P. (1985). The ecological effects of channelization. *The Geographical Journal*, 151, 63–69.

Brönmark, C., Hulthén, K., Nilsson, P. A., Skov, C., Hansson, L. A., Brodersen, J. & Chapman, B. B. (2013). There and back again: migration in freshwater fishes. *Canadian Journal of Zoology*, 92, 467–479.

Bruton, M. N. (1985). The effects of suspensoids on fish. *Hydrobiologia*, 125, 221–241.

Bunn, S. E. & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30, 492–507.

Bussi, G., Dadson, S. J., Prudhomme, C. & Whitehead, P. G. (2016). Modelling the future impacts of climate and land-use change on suspended sediment transport in the River Thames (UK). *Journal of Hydrology*, 542, 357–372.

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

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

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

Čech, M., Peterka, J., Říha, M., Jůza, T. & Kubečka, J. (2009). Distribution of egg strands of perch (*Perca fluviatilis* L.) with respect to depth and spawning substrate. *Hydrobiologia*, 630, 105–114.

Cerdan, O., Govers, G., Le Bissonnais, Y., Van Oost, K., Poesen, J., Saby, N., ... & Dostal, T. (2010). Rates and spatial variations of soil erosion in Europe: a study based on erosion plot data. *Geomorphology*, 122, 167–177.

Champion, A. S. & Swain, A. (1974). A note on the movements of coarse fish passing through the Ministry's trapping installation on the River Axe, Devon. *Aquaculture Research*, 5, 89–92.

Chapman, D. W. (1988). Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society*, 117, 1–21.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117–143.

Clarke, K. R. & Gorley, R. N. (2006). *PRIMER v6: User Manual/Tutorial*. 2nd ed., PRIMER-E Ltd.: Plymouth, UK.

Clarke, K. R., Somerfield, P. J. & Chapman, M. G. (2006). On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330, 55–80.

Clarke, K. R., Gorley, R. N., Somerfield, P. J. & Warwick, R. M. (2014). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. 3rd ed., PRIMER-E Ltd.: Plymouth, UK, 256 pp.

Cleveland, W. S. & Devlin, S. J. (1988). Locally weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association*, 83, 596–610.

Cline, L. D., Short, R. A. & Ward, J. V. (1982). The influence of highway construction on the macroinvertebrates and epilithic algae of a high mountain stream. *Hydrobiologia*, 96, 149–159.

Cohen, J. (1992). Statistical power analysis. *Current Directions in Psychological Science*, 1, 98–101.

Cooper, S. D., Lake, P. S., Sabater, S., Melack, J. M. & Sabo, J. L. (2013). The effects of land use changes on streams and rivers in mediterranean climates. *Hydrobiologia*, 719, 383–425.

Copp, G. H. (1992). Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. In *Environmental biology of European cyprinids. Developments in environmental biology of fishes*; Wieser, W., Schiemer, F., Goldschmidt, A., Kotrschal, K., Eds.; Springer: Dordrecht, Germany, Volume 13, pp. 181–193.

Côté, I. M., Darling, E. S. & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152592.

Crawford, R. M. (1975). The taxonomy and classification of the diatom genus Melosira C.Ag. I. The type species M. nummuloides C.Ag. *British Phycological Journal*, 10, 323–338.

Crutzen, P. J. (2002). Geology of mankind. *Nature*, 415, 23.

Crutzen, P. J. (2006). The "Anthropocene". In *Earth System Science in the Anthropocene*; Ehlers, E., Krafft, T., Eds.; Springer: Berlin, Heidelberg, Germany, pp. 13–18.

Culp, J. M., Wrona, F. J. & Davies, R. W. (1986). Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology*, 64, 1345–1351.

Cunjak, R. A. (1996). Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 267–282.

Dastjerdi, A. K. & Barthelat, F. (2015). Teleost fish scales amongst the toughest collagenous materials. *Journal of the Mechanical Behavior of Biomedical Materials*, 52, 95–107.

Davies, B., Biggs, J., Williams, P. & Thompson, S. (2009). Making agricultural landscapes more sustainable for freshwater biodiversity: a case study from southern England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19, 439–447.

Davies, P. M., Naiman, R. J., Warfe, D. M., Pettit, N. E., Arthington, A. H. & Bunn, S. E. (2014). Flow–ecology relationships: closing the loop on effective environmental flows. *Marine and Freshwater Research*, 65, 133–141.

Davies-Colley, R. J., Hickey, C. W., Quinn, J. M. & Ryan, P. A. (1992). Effects of clay discharges on streams. *Hydrobiologia*, 248, 215–234.

Deng, Z., Guensch, G. R., McKinstry, C. A., Mueller, R. P., Dauble, D. D. & Richmond, M. C. (2005). Evaluation of fish-injury mechanisms during exposure to turbulent shear flow. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 1513–1522.

Denic, M., Stoeckl, K., Gum, B. & Geist, J. (2014). Physicochemical assessment of *Unio crassus* habitat quality in a small upland stream and implications for conservation. *Hydrobiologia*, 735, 111–122.

Denic, M. & Geist, J. (2015). Linking stream sediment deposition and aquatic habitat quality in pearl mussel streams: implications for conservation. *River Research and Applications*, 31, 943–952.

Dickman, M. D., Peart, M. R. & Wai-Shu Yim, W. (2005). Benthic diatoms as indicators of stream sediment concentration in Hong Kong. *International Review of Hydrobiology*, 90, 412–421.

Diggle, P. J., Heagerty, P. J., Liang, K. Y. & Zeger, S. L. (2002). *Analysis of Longitudinal Data*. Second Edition. Oxford University Press, Oxford, England.

DIN EN 1899-2 (1998). *Water quality – Determination of biochemical oxygen demand after n days (BODn) – Part 2: Method for undiluted samples*. Beuth Verlag, Germany.

DIN EN 14011 (2003). *Water quality – Sampling of fish with electricity*. Beuth Verlag, Germany.

DIN EN 15204 (2006). *Water quality – Guidance standard on the enumeration of phytoplankton using inverted microscopy (Utermöhl technique)*. Beuth Verlag, Germany.

DIN EN ISO 10870 (2012). *Water quality – Guidelines for the selection of sampling methods and devices for benthic macroinvertebrates in fresh waters*. Beuth Verlag, Germany.

Doeg, T. J. & Koehn, J. D. (1994). Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. *River Research and Applications*, 9, 263–277.

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

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., ... & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182.

Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology*, 29, R960–R967.

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.

Dußling, U., Bischoff, A., Haberbosch, R., Hoffmann, A., Klinger, H., Wolter, C., ... & Berg, R. (2005). The Index of Fish Regions (FRI) – a tool for river assessment according to the EC water framework directive. *Wasserwirtschaft*, 7–8, 19–24.

Dynesius, M. & Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, 266, 753–762.

Ebel, G. (2013). *Fischschutz und Fischabstieg an Wasserkraftanlagen – Handbuch Rechen- und Bypasssysteme. Ingenieurbiologische Grundlagen, Modellierung und Prognose, Bemessung und Gestaltung*. Büro für Gewässerökologie und Fischereibiologie Dr. Ebel, 1. Auflage, Halle (Saale), Germany, pp. 483.

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

Egg, L., Pander, J., Mueller, M. & Geist, J. (2019). Effectiveness of the electric fish fence as a behavioural barrier at a pumping station. *Marine and Freshwater Research*, 70, 1459–1464.

Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, 19, 589–606.

European Commission (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Union*, 206, 7–50.

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

Ferguson, J. W., Sandford, B. P., Reagan, R. E., Gilbreath, L. G., Meyer, E. B., Ledgerwood, R. D. & Adams, N. S. (2007). Bypass system modification at Bonneville Dam on the Columbia River improved the survival of juvenile salmon. *Transactions of the American Fisheries Society*, 136, 1487–1510.

Fiener, P. & Auerswald, K. (2005). Measurement and modeling of concentrated runoff in grassed waterways. *Journal of Hydrology*, 301, 198–215.

Fiener, P., Auerswald, K. & Weigand, S. (2005). Managing erosion and water quality in agricultural watersheds by small detention ponds. *Agriculture, Ecosystems and Environment*, 110, 132–142.

Fiener, P., Auerswald, K. & Van Oost, K. (2011). Spatio-temporal patterns in land use and management affecting surface runoff response of agricultural catchments—A review. *Earth-Science Reviews*, 106, 92–104.

Foley, M. M., Bellmore, J. R., O'Connor, J. E., Duda, J. J., East, A. E., Grant, G. E., ... & Wilcox, A. C. (2017). Dam removal: Listening in. *Water Resources Research*, 53, 5229–5246.

Fox J. & Weisberg, S. (2011). *An {R} Companion to Applied Regression.* Second Edition. Thousand Oaks CA, Sage.

Fredrich, F. (2003). Long-term investigations of migratory behaviour of asp (*Aspius aspius* L.) in the middle part of the Elbe River, Germany. *Journal of Applied Ichthyology*, 19, 294–302.

Fredrich, F., Ohmann, S., Curio, B. & Kirschbaum, F. (2003). Spawning migrations of the chub in the River Spree, Germany. *Journal of Fish Biology*, 63, 710–723.

Freyhof, J. & Brooks, E. (2011). *European Red List of Freshwater Fishes*. Luxembourg: Publications Office of the European Union.

Geist, J. & Auerswald, K. (2007). Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). *Freshwater Biology*, 52, 2299–2316.

Geist, J. (2011). Integrative freshwater ecology and biodiversity conservation. *Ecological Indicators*, 11, 1507–1516.

Geist, J. (2015). Seven steps towards improving freshwater conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 25, 447–453.

Geist, J. & Hawkins, S. J. (2016). Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26, 942–962.

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

Gleick, P. H. (2003). Global freshwater resources: soft-path solutions for the 21st century. *Science*, 302, 1524–1528.

Gosset, C., Travade, F., Durif, C., Rives, J. & Elie, P. (2005). Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. *River Research and Applications*, 21, 1095–1105.

Gönczi, A. P. (1989). A study of physical parameters at the spawning sites of the European grayling (*Thymallus thymallus* L.). *Regulated Rivers: Research & Management*, 3, 221–224.

Graham, A. A. (1990). Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentrations in suspension. *Hydrobiologia*, 199, 107–115.

Gray, L. J. & Ward, J. V. (1982). Effects of sediment releases from a reservoir on stream macroinvertebrates. *Hydrobiologia*, 96, 177–184.

Greig, S. M., Sear, D. A. & Carling, P. A. (2005). The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. *Science of the Total Environment*, 344, 241–258.

Greimel, F., Zeiringer, B., Höller, N., Grün, B., Godina, R. & Schmutz, S. (2016). A method to detect and characterize sub-daily flow fluctuations. *Hydrological Processes*, 30, 2063–2078.

Griffiths, N. A., Tank, J. L., Royer, T. V., Rosi-Marshall, E. J., Whiles, M. R., Chambers, C. P., ... & Evans-White, M. A. (2009). Rapid decomposition of maize detritus in agricultural headwater streams. *Ecological Applications*, 19, 133–142.

Grill, G., Lehner, B., Lumsdon, A. E., MacDonald, G. K., Zarfl, C. & Liermann, C. R. (2015). An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. *Environmental Research Letters*, 10, 015001.

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.

Grossman, G. D., Sostoa, A. D., Freeman, M. C. & Lobón-Cerviá, J. (1987). Microhabitat use in a mediterranean riverine fish assemblage. *Oecologia*, 73, 501–512.

Gutmann Roberts, C. & Britton, J. R. (2020). Spawning strategies in cypriniform fishes in a lowland river invaded by non-indigenous European barbel *Barbus barbus*. *Hydrobiologia*, 847, 4031–4047.

Hamor, T. & Garside, E. T. (1976). Developmental rates of embryos of Atlantic salmon, *Salmo salar* L., in response to various levels of temperature, dissolved oxygen, and water exchange. *Canadian Journal of Zoology*, 54, 1912–1917.

Haro, A., Odeh, M., Noreika, J. & Castro-Santos, T. (1998). Effect of water acceleration on downstream migratory behavior and passage of Atlantic salmon smolts and juvenile American shad at surface bypasses. *Transactions of the American Fisheries Society*, 127, 118–127.

Hassinger, R. & Hübner, D. (2009). Entwicklung eines neuartigen Aal-Abstiegssystems mit Hilfe von Laborversuchen. *KW Korrespondenz Wasserwirtschaft*, 2, 276–281.

Hauer, F. R. & Lamberti, G. A. (2007). *Methods in Stream Ecology* (2nd ed.). Oxford: Elsevier.

Hayes, D. S., Lautsch, E., Unfer, G., Greimel, F., Zeiringer, B., Höller, N. & Schmutz, S. (2021). Response of European grayling, *Thymallus thymallus*, to multiple stressors in hydropeaking rivers. *Journal of Environmental Management*, 292, 112737.

Helfman, G. S. (1986). Fish behaviour by day, night and twilight. In *The behaviour of teleost fishes* (pp. 366–387). Springer, Boston, MA.

Henley, W. F., Patterson, M. A., Neves, R. J. & Lemly, A. D. (2000). Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. *Reviews in Fisheries Science*, 8, 125–139.

Hering, D., Carvalho, L., Argillier, C., Beklioglu, M., Borja, A., Cardoso, A. C., ... & Birk, S. (2015). Managing aquatic ecosystems and water resources under multiple stress – An introduction to the MARS project. *Science of the Total Environment*, 503, 10–21.

Hladík, M. & Kubečka, J. (2003). Fish migration between a temperate reservoir and its main tributary. *Hydrobiologia*, 504, 251–266.

Hoess, R. & Geist, J. (2021). Effect of fish pond drainage on turbidity, suspended solids, fine sediment deposition and nutrient concentration in receiving pearl mussel streams. *Environmental Pollution*, 274, 116520.

Hogan, T. W., Cada, G. F. & Amaral, S. V. (2014). The status of environmentally enhanced hydropower turbines. *Fisheries*, 39, 164–172.

Horký, P. & Slavík, O. (2017). Diel and seasonal rhythms of asp *Leuciscus aspius* (L.) in a riverine environment. *Ethology Ecology & Evolution*, 29, 449–459.

Huet, M. (1949). Aperçu des relations entre la pente et les populations piscicoles des eaux courantes. *Schweizerische Zeitschrift für Hydrologie*, 11, 332–351.

Hynes, H. B. N. (1975). The stream and its valley. *Proceedings of the International Association of Theoretical and Applied Limnology*, 19, 1–15.

Illies, J. & Botosaneanu, L. (1963). Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes, considerées surtout du point de vue faunistique: Avec 18 figures dans le texte et en supplément. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen*, 12, 1–57.

IUCN (2021). *The IUCN Red List of Threatened Species. Version 2021-1.* Available online: https://www.iucnredlist.org (accessed on 2 June 2021).

Ivanova, N. V., Zemlak, T. S., Hanner, R. H. & Hebert, P. D. (2007). Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Notes*, 7, 544–548.

Jansson, R., Nilsson, C. & Malmqvist, B. (2007). Restoring freshwater ecosystems in riverine landscapes: the roles of connectivity and recovery processes. *Freshwater Biology*, 52, 589–596.

Jelks, H. L., Walsh, S. J., Burkhead, N. M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D. A., ... & Warren Jr, M. L. (2008). Conservation Status of Imperiled North American Freshwater and Diadromous Fishes. *Fisheries*, 33, 372–407.

Johnson, G. E., Anglea, S. M., Adams, N. S. & Wik, T. O. (2005). Evaluation of a prototype surface flow bypass for juvenile salmon and steelhead at the powerhouse of Lower Granite Dam, Snake River, Washington, 1996–2000. *North American Journal of Fisheries Management*, 25, 138–151.

Jones, J. I., Murphy, J. F., Collins, A. L., Sear, D. A., Naden, P. S. & Armitage, P. D. (2012). The impact of fine sediment on macro-invertebrates. *River Research and Applications*, 28, 1055–1071.

Jones, J. I., Duerdoth, C. P., Collins, A. L., Naden, P. S. & Sear, D. A. (2014). Interactions between diatoms and fine sediment. *Hydrological Processes*, 28, 1226–1237.

Jonsson, N. (1991). Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*, 66, 20–35.

Jungwirth, M. (1996). Bypass channels at weirs as appropriate aids for fish migration in rhithral rivers. *Regulated Rivers: Research & Management*, 12, 483-–492.

Jungwirth, M., Haidvogl, G., Moog, O., Muhar, S. & Schmutz, S. (2003). *Angewandte Fischökologie an Fließgewässern*. Facultas Universitätsverlag, Vienna, Austria, pp. 547.

Kail, J., Brabec, K., Poppe, M. & Januschke, K. (2015). The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: A meta-analysis. *Ecological Indicators*, 58, 311–321.

Kammerlander, H., Schlosser, L., Zeiringer, B., Unfer, G., Zeileis, A. & Aufleger, M. (2020). Downstream passage behavior of potamodromous fishes at the fish protection and guidance system “Flexible Fish Fence”. *Ecological Engineering*, 143, 105698.

Katopodis, C. (2005). Developing a toolkit for fish passage, ecological flow management and fish habitat works. *Journal of Hydraulic Research*, 43, 451–467.

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.

Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H. & Kuemmerle, T. (2017). Biodiversity at risk under future cropland expansion and intensification. *Nature Ecology & Evolution*, 1, 1129–1135.

Kemp, P., Sear, D., Collins, A., Naden, P. & Jones, I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes*, 25, 1800–1821.

Klein Goldewijk, K., Beusen, A., Van Drecht, G. & De Vos, M. (2011). The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, 20, 73–86.

Klopries, E. M., Deng, Z. D., Lachmann, T. U., Schüttrumpf, H. & Trumbo, B. A. (2018). Surface bypass as a means of protecting downstream-migrating fish: lack of standardised evaluation criteria complicates evaluation of efficacy. *Marine and Freshwater Research*, 69, 1882–1893.

Knott, J., Mueller, M., Pander, J. & Geist, J. (2019a). Effectiveness of catchment erosion protection measures and scale-dependent response of stream biota. *Hydrobiologia*, 830, 77–92.

Knott, J., Mueller, M., Pander, J. & Geist, J. (2019b). Fish Passage and Injury Risk at a Surface Bypass of a Small-Scale Hydropower Plant. *Sustainability*, 11, 6037.

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

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, 106434.

Kondolf, G. M. (2000). Assessing salmonid spawning gravel quality. *Transactions of the American Fisheries Society*, 129, 262–281.

Kondolf, G. M., Gao, Y., Annandale, G. W., Morris, G. L., Jiang, E., Zhang, J., ... & Yang, C. T. (2014). Sustainable sediment management in reservoirs and regulated rivers: Experiences from five continents. *Earth's Future*, 2, 256–280.

Kottelat, M. & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Publications Kottelat, Cornol and Freyhof: Berlin, Germany, pp. 646.

Kubečka, J. (1993). Succession of fish communities in reservoirs of Central and Eastern Europe. In *Comparative Reservoir Limnology and Water Quality Management. Developments in Hydrobiology*; Straškraba, M., Tundisi, J. G., Duncan, A., Eds.; Springer: Dordrecht, Germany, Volume 77, pp. 153–168.

Lai, J. S. & Shen, H. W. (1996). Flushing sediment through reservoirs. *Journal of Hydraulic Research*, 34, 237–255.

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, 19, 573–592.

Lake, P. S. (2001). On the maturing of restoration: linking ecological research and restoration. *Ecological Management & Restoration*, 2, 110–115.

Larinier, M. (2000). Dams and fish migration. In *Dams, Ecosystem Functions and Environmental Restoration. Thematic Review II.1 prepared as an input to the World Commission on Dams*; Berkamp, G., McCartney, M., Dugan, P., McNeely, J., Acreman, M., Eds.; World Commission on Dams: Cape Town, South Africa, pp. 1–30.

Larinier, M. & Travade, F. (2002). Downstream migration: problems and facilities. *Bulletin Français de la Pêche et de la Pisciculture*, 364, 181–207.

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

Lechner, A., Keckeis, H. & Humphries, P. (2016). Patterns and processes in the drift of early developmental stages of fish in rivers: a review. *Reviews in Fish Biology and Fisheries*, 26, 471–489.

Lemly, A. D. (1982). Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia*, 87, 229–245.

Lennox, R. J., Paukert, C. P., Aarestrup, K., Auger-Méthé, M., Baumgartner, L., Birnie-Gauvin, K., ... & Cooke, S. J. (2019). One hundred pressing questions on the future of global fish migration science, conservation, and policy. *Frontiers in Ecology and Evolution*, 7, 286.

Li, L., Zheng, B. & Liu, L. (2010). Biomonitoring and bioindicators used for river ecosystems: definitions, approaches and trends. *Procedia Environmental Sciences*, 2, 1510–1524.

Linke, S., Turak, E. & Nel, J. (2011). Freshwater conservation planning: the case for systematic approaches. *Freshwater Biology*, 56, 6–20.

Lobo, E. A., Heinrich, C. G., Schuch, M., Wetzel, C. E. & Ector, L. (2016). Diatoms as Bioindicators in Rivers. In *River Algae*; Necchi Jr, O., Ed.; Springer, Cham, pp. 245–271.

Lorenz, A. W., Jähnig, S. C. & Hering, D. (2009). Re-meandering German lowland streams: qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. *Environmental Management*, 44, 745–754.

Lucas, M. C. & Batley, E. (1996). Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: implications for river management. *Journal of Applied Ecology*, 33, 1345–1358.

Lucas, M. C. & Baras, E. (2001). *Migration of freshwater fishes*. 47th ed.: Blackwell Science, Oxford, UK, pp. 420.

Lummer, E. M., Auerswald, K. & Geist, J. (2016). Fine sediment as environmental stressor affecting freshwater mussel behavior and ecosystem services. *Science of the Total Environment*, 571, 1340–1348.

Magilligan, F. J., Graber, B. E., Nislow, K. H., Chipman, J. W., Sneddon, C. S., Fox, C. A., ... & Olden, J. D. (2016). River restoration by dam removal: Enhancing connectivity at watershed scales. *Elementa: Science of the Anthropocene*, 4, 000108.

Magurran, A. E. (2009). Threats to Freshwater Fish. *Science*, 325, 1215–1216.

Malmqvist, B. & Rundle, S. (2002). Threats to the running water ecosystems of the world. *Environmental Conservation*, 29, 134–153.

Markovic, D., Carrizo, S. F., Kärcher, O., Walz, A. & David, J. N. (2017). Vulnerability of European freshwater catchments to climate change. *Global Change Biology*, 23, 3567–3580.

McCormick, S. D., Hansen, L. P., Quinn, T. P. & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 77–92.

Meier, C., Haase, P., Rolauffs, P., Schindehütte, K., Schöll, F., Sundermann, A. & Hering, D. (2006). *Methodisches Handbuch Fließgewässerbewertung. Handbuch zur Untersuchung und Bewertung von Fließgewässern auf der Basis des Makrozoobenthos vor dem Hintergrund der EG-Wasserrahmenrichtlinie*.

Melcher, A. H. & Schmutz, S. (2010). The importance of structural features for spawning habitat of nase *Chondrostoma nasus* (L.) and barbel *Barbus barbus* (L.) in a pre-Alpine river. *River Systems*, 19, 33–42.

Meulenbroek, P., Drexler, S., Nagel, C., Geistler, M. & Waidbacher, H. (2018). The importance of a constructed near-nature-like Danube fish by-pass as a lifecycle fish habitat for spawning, nurseries, growing and feeding: a long-term view with remarks on management. *Marine and Freshwater Research*, 69, 1857–1869.

Miller, S. W., Budy, P. & Schmidt, J. C. (2010). Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. *Restoration Ecology*, 18, 8–19.

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. *Journal of Fish Biology*, 19, 129–134.

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.

Moring, J. R. (1982). Decrease in stream gravel permeability after clear-cut logging: an indication of intragravel conditions for developing salmonid eggs and alevins. *Hydrobiologia*, 88, 295–298.

Mueller, M., Pander, J. & Geist, J. (2011). The effects of weirs on structural stream habitat and biological communities. *Journal of Applied Ecology*, 48, 1450–1461.

Mueller, M., Pander, J., Wild, R., Lueders, T. & Geist, J. (2013). The effects of stream substratum texture on interstitial conditions and bacterial biofilms: Methodological strategies. *Limnologica*, 43, 106–113.

Mueller, M., Pander, J. & Geist, J. (2014a). The ecological value of stream restoration measures: an evaluation on ecosystem and target species scale. *Ecological Engineering*, 62, 129–139.

Mueller, M., Pander, J. & Geist, J. (2014b). A new tool for assessment and monitoring of community and ecosystem change based on multivariate abundance data integration from different taxonomic groups. *Environmental Systems Research*, 3, 12.

Mueller, M. & Geist, J. (2016). Conceptual guidelines for the implementation of the ecosystem approach in biodiversity monitoring. *Ecosphere*, 7, e01305.

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

Mueller, M., Pander, J. & Geist, J. (2018). Comprehensive analysis of > 30 years of data on stream fish population trends and conservation status in Bavaria, Germany. *Biological Conservation*, 226, 311–320.

Mueller, M., Bierschenk, A. M., Bierschenk, B. M., Pander, J. & Geist, J. (2020a). Effects of multiple stressors on the distribution of fish communities in 203 headwater streams of Rhine, Elbe and Danube. *Science of the Total Environment*, 703, 134523.

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

Mueller, M., Knott, J., Pander, J. & Geist, J. (2021). How fish-friendly is small hydropower?. *Manuscript submitted for publication.*

Muhar, S., Januschke, K., Kail, J., Poppe, M., Schmutz, S., Hering, D. & Buijse, A. D. (2016). Evaluating good-practice cases for river restoration across Europe: context, methodological framework, selected results and recommendations. *Hydrobiologia*, 769, 3–19.

Muir, W. D., Smith, S. G., Williams, J. G. & Sandford, B. P. (2001). Survival of juvenile salmonids passing through bypass systems, turbines, and spillways with and without flow deflectors at Snake River dams. *North American Journal of Fisheries Management*, 21, 135–146.

Müllner, A. N. & Schagerl, M. (2003). Abundance and vertical distribution of the phytobenthic community within a pool and riffle sequence of an Alpine gravel stream. *International Review of Hydrobiology*, 88, 243–254.

Nagel, C., Pander, J., Mueller, M. & Geist, J. (2020a). Substrate composition determines emergence success and development of European nase larvae (*Chondrostoma nasus* L.). *Ecology of Freshwater Fish*, 29, 121–131.

Nagel, C., Mueller, M., Pander, J. & Geist, J. (2020b). 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.

Nagel, C., Mueller, M., Pander, J., Stoeckle, B. C., Kuehn, R. & Geist, J. (2021). Going with the flow: Spatio-temporal drift patterns of larval fish in a large alpine river. *Freshwater Biology*, 66, 1765–1781.

Newbold, J. D., O'Neill, R. V., Elwood, J. W. & Van Winkle, W. (1982). Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. *The American Naturalist*, 120, 628–652.

Nilsson, C., Reidy, C. A., Dynesius, M. & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, 308, 405–408.

Noonan, M. J., Grant, J. W. & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, 13, 450–464.

Northcote, T. G. (1984). Mechanisms of fish migration in rivers. In *Mechanisms of migration in fishes* (pp. 317–355). Springer, Boston, MA.

Northcote, T. (1998). Migratory behaviour of fish and its significance to movement through riverine fish passage facilities. In *Migration and Fish Bypasses*; Jungwirth, M., Schmutz, S., Weiss, S., Eds.; Fishing News Books: Oxford, UK, pp. 3–18.

O'brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity*, 41, 673–690.

O'Connor, J. E., Duda, J. J. & Grant, G. E. (2015). 1000 dams down and counting. *Science*, 348, 496–497.

Økland, F., Havn, T. B., Thorstad, E. B., Heermann, L., Saether, S. A., Tambets, M., ... & Borcherding, J. (2019). Mortality of downstream migrating European eel at power stations can be low when turbine mortality is eliminated by protection measures and safe bypass routes are available. *International Review of Hydrobiology*, 104, 68–79.

Olden, J. D. & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, 55, 86–107.

Ometo, J. P. H., Martinelli, L. A., Ballester, M. V., Gessner, A., Krusche, A. V., Victoria, R. L. & Williams, M. (2000). Effects of land use on water chemistry and macroinvertebrates in two streams of the Piracicaba river basin, south-east Brazil. *Freshwater Biology*, 44, 327–337.

Opperman, J. J., Galloway, G. E., Fargione, J., Mount, J. F., Richter, B. D. & Secchi, S. (2009). Sustainable floodplains through large-scale reconnection to rivers. *Science*, 326, 1487–1488.

Ormerod, S. J., Dobson, M., Hildrew, A. G. & Townsend, C. (2010). Multiple stressors in freshwater ecosystems. *Freshwater Biology*, 55, 1–4.

Packman, A. I. & Salehin, M. (2003). Relative roles of stream flow and sedimentary conditions in controlling hyporheic exchange. *Hydrobiologia*, 494, 291–297.

Palmer, M. A., Filoso, S. & Fanelli, R. M. (2014). From ecosystems to ecosystem services: Stream restoration as ecological engineering. *Ecological Engineering*, 65, 62–70.

Pander, J. & Geist, J. (2010). Seasonal and spatial bank habitat use by fish in highly altered rivers – a comparison of four different restoration measures. *Ecology of Freshwater Fish*, 19, 127–138.

Pander, J., Mueller, M. & Geist, J. (2013). Ecological functions of fish bypass channels in streams: migration corridor and habitat for rheophilic species. *River Research and Applications*, 29, 441–450.

Pander, J., Mueller, M. & Geist, J. (2015a). A comparison of four stream substratum restoration techniques concerning interstitial conditions and downstream effects. *River Research and Applications*, 31, 239–255.

Pander, J., Mueller, M. & Geist, J. (2015b). Succession of fish diversity after reconnecting a large floodplain to the upper Danube River. *Ecological Engineering*, 75, 41–50.

Pander, J. & Geist, J. (2016). Can fish habitat restoration for rheophilic species in highly modified rivers be sustainable in the long run?. *Ecological Engineering*, 88, 28–38.

Pander, J., Mueller, M., Knott, J., Egg, L. & Geist, J. (2017). Is it worth the money? The functionality of engineered shallow stream banks as habitat for juvenile fishes in heavily modified water bodies. *River Research and Applications*, 33, 63–72.

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

Pander, J., Mueller, M. & Geist, J. (2018b). Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation*, 217, 1–10.

Pander, J., Knott, J., Mueller, M. & Geist, J. (2019). Effects of environmental flows in a restored floodplain system on the community composition of fish, macroinvertebrates and macrophytes. *Ecological Engineering*, 132, 75–86.

Pavlov, D. S., Mikheev, V. N., Lupandin, A. I. & Skorobogatov, M. A. (2008). Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. *Hydrobiologia*, 609, 125–138.

Peckarsky, B. L. (1985). Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Canadian Journal of Zoology*, 63, 1519–1530.

Peňáz, M. (1996). *Chondrostoma nasus* – its reproduction strategy and possible reasons for a widely observed population decline – a review. In *Conservation of Endangered Freshwater Fish in Europe. ALS Advances in Life Sciences*; Kirchhofer, A., Hefti, D., Eds.; Birkhäuser: Basel, Switzerland, pp. 279–285.

Person, E., Bieri, M., Peter, A. & Schleiss, A. J. (2014). Mitigation measures for fish habitat improvement in Alpine rivers affected by hydropower operations. *Ecohydrology*, 7, 580–599.

Pflugrath, B. D., Boys, C. A., Cathers, B. & Deng, Z. D. (2019). Over or under? Autonomous sensor fish reveals why overshot weirs may be safer than undershot weirs for fish passage. *Ecological Engineering*, 132, 41–48.

Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., ... & Blair, R. (1995). Environmental and economic costs of soil erosion and conservation benefits. *Science*, 267, 1117–1123.

Pinder, A. C. (2001). *Keys to larval and juvenile stages of coarse fishes from freshwaters in the British Isles*. Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Cumbria, UK, Scientific Publication No. 60.

Pinder, A. C., Clough, S., Morris, K. & Fletcher, R. (2009). *An investigation into the spawning and recruitment success of barbel in the River Wensum.* APEM 410776, Environment Agency, 1–20.

Poeppl, R. E., Dilly, L. A., Haselberger, S., Renschler, C. S. & Baartman, J. E. (2019). Combining soil erosion modeling with connectivity analyses to assess lateral fine sediment input into agricultural streams. *Water*, 11, 1793.

Poff, N. L., 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*, 104, 5732–5737.

Portt, C. B., Coker, G. A., Ming, D. L. & Randall, R. G. (2006). *A review of fish sampling methods commonly used in Canadian freshwater habitats*. Canadian Technical Report of Fisheries and Aquatic Sciences, Ontario, 2604 pp.

Pracheil, B. M., DeRolph, C. R., Schramm, M. P. & Bevelhimer, M. S. (2016). A fish-eye view of riverine hydropower systems: the current understanding of the biological response to turbine passage. *Reviews in Fish Biology and Fisheries*, 26, 153–167.

Prado Jr, F. A., Athayde, S., Mossa, J., Bohlman, S., Leite, F. & Oliver-Smith, A. (2016). How much is enough? An integrated examination of energy security, economic growth and climate change related to hydropower expansion in Brazil. *Renewable and Sustainable Energy Reviews*, 53, 1132–1136.

Preece, R. M. & Jones, H. A. (2002). The effect of Keepit Dam on the temperature regime of the Namoi River, Australia. *River Research and Applications*, 18, 397–414.

Pulg, U., Barlaup, B. T., Sternecker, K., Trepl, L. & Unfer, G. (2013). Restoration of spawning habitats of brown trout (*Salmo trutta*) in a regulated chalk stream. *River Research and Applications*, 29, 172-–182.

R Core Team (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available online: https://www.R-project.org/.

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available online: https://www.R-project.org/.

Ramler, D., Keckeis, H. & Ahnelt, H. (2014). Gattungsbestimmung bei Embryonal-, Larval- und Juvenilstadien der Barsche (Percidae) und Meergrundeln (Gobiidae) Österreichs. *Österreichs Fischerei*, 67, 299–307.

Ramler, D., Ahnelt, H., Nemeschkal, H. L. & Keckeis, H. (2016). The drift of early life stages of Percidae and Gobiidae (Pisces: Teleostei) in a free-flowing section of the Austrian Danube. *Hydrobiologia*, 781, 199–216.

Reckendorfer, W., Keckeis, H., Tiitu, V., Winkler, G. & Zornig, H. (2001). Diet shifts in 0+ nase, *Chondrostoma nasus*: size-specific differences and the effect of food. *Archiv für Hydrobiologie Supplement*, 135, 425–440.

Regh, K. J., Packman, A. I. & Ren, J. (2005). Effects of suspended sediment characteristics and bed sediment transport on streambed clogging. *Hydrological Processes*, 19, 413–427.

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., ... & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94, 849–873.

Rempel, L. L., Richardson, J. S. & Healey, M. C. (2000). Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology*, 45, 57–73.

Rickson, R. J. (2014). Can control of soil erosion mitigate water pollution by sediments?. *Science of the Total Environment*, 468, 1187–1197.

Riehl, R., Patzner, R. A. & Zanger, K. (2002). Die Eier heimischer Fische, 14. Rapfen oder Schied – *Aspius aspius* (Linnaeus, 1758) (Cyprinidae). *Österreichs Fischerei*, 55, 275–281.

Riley, W. D., Eagle, M. O. & Ives, S. J. (2002). The onset of downstream movement of juvenile Atlantic salmon, *Salmo salar* L., in a chalk stream. *Fisheries Management and Ecology*, 9, 87–94.

Rohtla, M., Vilizzi, L., Kováč, V., Almeida, D., Brewster, B., Britton, J. R., ... & Copp, G. H. (2020). Review and Meta-Analysis of the Environmental Biology and Potential Invasiveness of a Poorly-Studied Cyprinid, the Ide *Leuciscus idus*. *Reviews in Fisheries Science & Aquaculture*, 1–37.

Roni, P., Beechie, T. J., Bilby, R. E., Leonetti, F. E., Pollock, M. M. & Pess, G. R. (2002). A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. *North American Journal of Fisheries Management*, 22, 1–20.

Roscoe, D. W. & Hinch, S. G. (2010). Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish and Fisheries*, 11, 12–33.

Rosenberg, D. M. & Wiens, A. P. (1978). Effects of sediment addition on macrobenthic invertebrates in a northern Canadian river. *Water Research*, 12, 753–763.

Ross, H. H. (1963). Stream communities and terrestrial biomes. *Archiv für Hydrobiologie*, 59, 235–242.

Roth, N. E., Allan, J. D. & Erickson, D. L. (1996). Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology*, 11, 141–156.

Rubin, Z., Kondolf, G. M. & Rios-Touma, B. (2017). Evaluating stream restoration projects: what do we learn from monitoring?. *Water*, 9, 174.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... & Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, 287, 1770–1774.

Sanz-Ronda, F. J., Fuentes-Pérez, J. F., García-Vega, A. & Bravo-Córdoba, F. J. (2021). Fishways as Downstream Routes in Small Hydropower Plants: Experiences with a Potamodromous Cyprinid. *Water*, 13, 1041.

Schaumburg, J., Schranz, C., Stelzer, D., Vogel, A. & Gutowski, A. (2012). *Verfahrensanleitung für die ökologische Bewertung von Fließgewässern zur Umsetzung der EG-Wasserrahmenrichtlinie: Makrophyten und Phytobenthos – Phylib*. Bayerisches Landesamt für Umwelt, Augsburg, 191 S.

Scheurer, K., Alewell, C., Bänninger, D. & Burkhardt-Holm, P. (2009). Climate and land-use changes affecting river sediment and brown trout in alpine countries—a review. *Environmental Science and Pollution Research*, 16, 232–242.

Schiemer, F. & Waidbacher, H. (1992). Strategies for conservation of a Danubian fish fauna. In *River Conservation and Management*; Boon, P. J., Calow, P., Petts, G. E., Eds.; Wiley: Chichester, UK, pp. 363–382.

Schiemer, F., Keckeis, H. & Kamler, E. (2002). The early life history stages of riverine fish: ecophysiological and environmental bottlenecks. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 133, 439–449.

Schilt, C. R. (2007). Developing fish passage and protection at hydropower dams. *Applied Animal Behaviour Science*, 104, 295–325.

Schludermann, E., Keckeis, H. & Nemeschkal, H. L. (2009). Effect of initial size on daily growth and survival in freshwater *Chondrostoma nasus* larvae: a field survey. *Journal of Fish Biology*, 74, 939–955.

Schlumberger, O. & Proteau, J. P. (1996). Reproduction of pike-perch (*Stizostedion lucioperca*) in captivity. *Journal of Applied Ichthyology*, 12, 149–152.

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.

Schubert, M. (2007). *Umsetzung der Europäischen Wasserrahmenrichtlinie (EU-WRRL) aus fischereilicher Sicht – Fischereibezogenes Monitoring nach Maßgabe der Europäischen Wasserrahmenrichtlinie*. VDSF Schriftenreihe 9/2007.

Scruton, D. A., McKinley, R. S., Kouwen, N., Eddy, W. & Booth, R. K. (2002). Use of telemetry and hydraulic modeling to evaluate and improve fish guidance efficiency at a louver and bypass system for downstream-migrating Atlantic salmon (*Salmo salar*) smolts and kelts. *Hydrobiologia*, 483, 83–94.

Scruton, D. A., Pennell, C. J., Bourgeois, C. E., Goosney, R. F., Porter, T. R. & Clarke, K. D. (2007). Assessment of a retrofitted downstream fish bypass system for wild Atlantic salmon (*Salmo salar*) smolts and kelts at a hydroelectric facility on the Exploits River, Newfoundland, Canada. *Hydrobiologia*, 582, 155–169.

Sear, D. A., Pattison, I., Collins, A. L., Smallman, D. J., Jones, J. I. & Naden, P. S. (2017). The magnitude and significance of sediment oxygen demand in gravel spawning beds for the incubation of salmonid embryos. *River Research and Applications*, 33, 1642–1654.

Shannon C. E. & Weaver, W. (1949). *The mathematical theory of communication.* Urbana: University of Illinois Press.

Sherman, B., Todd, C. R., Koehn, J. D. & Ryan, T. (2007). Modelling the impact and potential mitigation of cold water pollution on Murray cod populations downstream of Hume Dam, Australia. *River Research and Applications*, 23, 377–389.

Slawski, T. M., Veraldi, F. M., Pescitelli, S. M. & Pauers, M. J. (2008). Effects of tributary spatial position, urbanization, and multiple low-head dams on warmwater fish community structure in a Midwestern stream. *North American Journal of Fisheries Management*, 28, 1020–1035.

Šmejkal, M., Ricard, D., Vejřík, L., Mrkvička, T., Vebrová, L., Baran, R., ... & Kubečka, J. (2017a). Seasonal and daily protandry in a cyprinid fish. *Scientific Reports*, 7, 4737.

Šmejkal, M., Baran, R., Blabolil, P., Vejřík, L., Prchalová, M., Bartoň, D., ... & Kubečka, J. (2017b). Early life-history predator-prey reversal in two cyprinid fishes. *Scientific Reports*, 7, 6924.

Smialek, N., Pander, J., Mueller, M., Van Treeck, R., Wolter, C. & Geist, J. (2019). Do We Know Enough to Save European Riverine Fish? – A Systematic Review on Autecological Requirements During Critical Life Stages of 10 Rheophilic Species at Risk. *Sustainability*, 11, 5011.

Smialek, N., Pander, J. & Geist, J. (2021). Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. *Fisheries Management and Ecology*, 28, 437–467.

Smol, J. P. & Stoermer, E. F. (2010). *The diatoms. Applications for the environmental and earth sciences*. 2nd ed., Cambridge, New York: Cambridge University Press.

Snickars, M., Sundblad, G., Sandström, A., Ljunggren, L., Bergström, U., Johansson, G. & Mattila, J. (2010). Habitat selectivity of substrate-spawning fish: modelling requirements for the Eurasian perch *Perca fluviatilis*. *Marine Ecology Progress Series*, 398, 235–243.

Sonny, D., Jorry, S., Wattiez, X. & Philippart, J. (2006). Inter-annual and diel patterns of the drift of cyprinid fishes in a small tributary of the Meuse River, Belgium. *Folia Zoologica*, 55, 75–85.

Soulsby, C., Youngson, A., Moir, H. & Malcolm, I. (2001). Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: a preliminary assessment. *Science of the Total Environment*, 265, 295–307.

Søndergaard, M. & Jeppesen, E. (2007). Anthropogenic impacts on lake and stream ecosystems, and approaches to restoration. *Journal of Applied Ecology*, 44, 1089–1094.

Spaulding, S. A., Lubinski, D. J. & Potapova, M. (2010). *Diatoms of the United States*. Available online: http://westerndiatoms.colorado.edu (accessed on 9 December 2016).

Spears, B. M., Chapman, D. S., Carvalho, L., Feld, C. K., Gessner, M. O., Piggott, J. J., ... & Birk, S. (2021). Making Waves. Bridging theory and practice towards multiple stressor management in freshwater ecosystems. *Water Research*, 116981.

Spindler, T. (1988). Bestimmung der mitteleuropäischen Cyprinidenlarven. *Österreichs Fischerei*, 41, 75–79.

Stendera, S., Adrian, R., Bonada, N., Cañedo-Argüelles, M., Hugueny, B., Januschke, K., ... & Hering, D. (2012). Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. *Hydrobiologia*, 696, 1–28.

Sternecker, K. & Geist, J. (2010). The effects of stream substratum composition on the emergence of salmonid fry. *Ecology of Freshwater Fish*, 19, 537–544.

Sternecker, K., Wild, R. & Geist, J. (2013a). Effects of substratum restoration on salmonid habitat quality in a subalpine stream. *Environmental Biology of Fishes*, 96, 1341–1351.

Sternecker, K., Cowley, D. E. & Geist, J. (2013b). Factors influencing the success of salmonid egg development in river substratum. *Ecology of Freshwater Fish*, 22, 322–333.

Sternecker, K., Denic, M. & Geist, J. (2014). Timing matters: species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. *Ecology and Evolution*, 4, 2749–2758.

Strayer, D. L. & Dudgeon, D. (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, 29, 344–358.

Su, G., Logez, M., Xu, J., Tao, S., Villéger, S. & Brosse, S. (2021). Human impacts on global freshwater fish biodiversity. *Science*, 371, 835–838.

Sundermann, A., Antons, C., Cron, N., Lorenz, A. W., Hering, D. & Haase, P. (2011). Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. *Freshwater Biology*, 56, 1689–1702.

Surber, E. W. (1930). A quantitative method of studying the food of small fishes. *Transactions of the American Fisheries Society*, 60, 158–163.

Sutherland, W. J., Pullin, A. S., Dolman, P. M. & Knight, T. M. (2004). The need for evidence-based conservation. *Trends in Ecology & Evolution*, 19, 305–308.

Swatdipong, A., Primmer, C. R. & Vasemägi, A. (2010). Historical and recent genetic bottlenecks in European grayling, *Thymallus thymallus*. *Conservation Genetics*, 11, 279–292.

Targońska, K., Kucharczyk, D., Kujawa, R., Mamcarz, A. & Żarski, D. (2010). Controlled reproduction of asp, *Aspius aspius* (L.) using luteinizing hormone releasing hormone (LHRH) analogues with dopamine inhibitors. *Aquaculture*, 306, 407–410.

Taylor, J. J., Rytwinski, T., Bennett, J. R., Smokorowski, K. E., Lapointe, N. W., Janusz, R., ... & Cooke, S. J. (2019). The effectiveness of spawning habitat creation or enhancement for substrate-spawning temperate fish: a systematic review. *Environmental Evidence*, 8, 19.

Tomanova, S., Courret, D., Richard, S., Tedesco, P. A., Mataix, V., Frey, A., ... & Tétard, S. (2021). Protecting the downstream migration of salmon smolts from hydroelectric power plants with inclined racks and optimized bypass water discharge. *Journal of Environmental Management*, 284, 112012.

Townsend, C. R., Arbuckle, C., Crowl, T. & Scarsbrook, M. (1997). The relationship between land use and physicochemistry, food resources and macroinvertebrate communities in tributaries of the Taieri River, New Zealand: a hierarchically scaled approach. *Freshwater Biology*, 37, 177–191.

Trancart, T., Acou, A., De Oliveira, E. & Feunteun, E. (2013). Forecasting animal migration using SARIMAX: an efficient means of reducing silver eel mortality caused by turbines. *Endangered Species Research*, 21, 181–190.

Travade, F., Larinier, M., Subra, S., Gomes, P. & De-Oliveira, E. (2010). Behaviour and passage of European silver eels (*Anguilla anguilla*) at a small hydropower plant during their downstream migration. *Knowledge and Management of Aquatic Ecosystems*, 398, 1–19.

Urho, L. (1996). Identification of perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and ruffe (*Gymnocephalus cernuus*) larvae. *Annales Zoologici Fennici*, 33, 659–667.

Utermöhl, H. (1931). Neue Wege in der quantitativen Erfassung des Planktons (mit besonderer Berücksichtigung des Ultraplanktons). *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie*, 5, 567–596.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130–137.

Van Nieuwenhuyse, E. E. & LaPerriere, J. D. (1986). Effects of placer gold mining on primary production in subarctic streams of Alaska. *Water Resources Bulletin*, 22, 91–99.

Verdonschot, P. F. & van der Lee, G. H. (2020). Perspectives on the functional assessment of multi-stressed stream ecosystems. *Freshwater Science*, 39, 605–620.

Vilizzi, L. & Copp, G. H. (2013). Interstitial movement and emergence of barbel *Barbus barbus* free embryos and larvae. *Journal of Fish Biology*, 82, 1057–1063.

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., ... & Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, 467, 555–561.

Wallace, J. B. & Webster, J. R. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, 41, 115–139.

Walser, C. A. & Bart, H. L. (1999). Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River System. *Ecology of Freshwater Fish*, 8, 237–246.

Walsh, C. J., Roy, A. H., Feminella, J. W., Cottingham, P. D., Groffman, P. M. & Morgan, R. P. (2005). The urban stream syndrome: current knowledge and the search for a cure. *Journal of the North American Benthological Society*, 24, 706–723.

Ward, J. V. & Stanford, J. A. (1983). The serial discontinuity concept of lotic ecosystems. In *Dynamics of Lotic Ecosystems*; Fontaine, T. D. & Bartell, S. M., Eds.; Ann Arbor Science Publishers, Ann Arbor, MI, pp. 347–356.

Ward, J. V. (1989). The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, 8, 2–8.

Weijters, M. J., Janse, J. H., Alkemade, R. & Verhoeven, J. T. A. (2009). Quantifying the effect of catchment land use and water nutrient concentrations on freshwater river and stream biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19, 104–112.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag: New York, USA.

Williams, J. G., Armstrong, G., Katopodis, C., Larinier, M. & Travade, F. (2012). Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. *River Research and Applications*, 28, 407–417.

Wilson, H. F. & Xenopoulos, M. A. (2009). Effects of agricultural land use on the composition of fluvial dissolved organic matter. *Nature Geoscience*, 2, 37–41.

Wohl, E., Angermeier, P. L., Bledsoe, B., Kondolf, G. M., MacDonnell, L., Merritt, D. M., ... & Tarboton, D. (2005). River restoration. *Water Resources Research*, 41, W10301.

Wood, P. J. & Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management*, 21, 203–217.

Yamada, H. & Nakamura, F. (2002). Effect of fine sediment deposition and channel works on periphyton biomass in the Makomanai River, Northern Japan. *River Research and Applications*, 18, 481–493.

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

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

Zauner, G. & Eberstaller, J. (1999). Klassifizierungsschema der österreichischen Flußfischfauna in Bezug auf deren Lebensraumansprüche. *Österreichs Fischerei*, 52, 198–205.

Zitek, A., Schmutz, S. & Ploner, A. (2004). Fish drift in a Danube sidearm-system: II. Seasonal and diurnal patterns. *Journal of Fish Biology*, 65, 1339–1357.

Zuazo, V. H. D. & Pleguezuelo, C. R. R. (2008). Soil-erosion and runoff prevention by plant covers. A review. *Agronomy for Sustainable Development*, 28, 65–86.

Zuur, A. F., Ineo, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science and Business Media: New York, USA, pp. 574.

11 Supplementary Material

A novel field based evaluation of hydropower-induced external fish injury
(animal care permit number: ROB–55.2–2532.Vet_02–15–31)

Lehrstuhl für Aquatische Systembiologie

Fish injury protocol

Site: _________ Date of catch: __________ Time: _________ Repetition: _________

Treatment: ☐ Turbine & Screen ☐ Turbine ☐ Net ☐ Predamage

Emptying interval: __ Trap Nr. ___ Species: _______________ Total length: (cm): ____

General criteria

Vitality:	☐ 4	☐ 3	☐ 2	☐ 1	☐ 0
Respiratory movements:	☐ 4	☐ 3	☐ 2	☐ 1	☐ 0
Nutritional status:	☐ 4	☐ 3	☐ 2	☐ 1	☐ 0
Fungal infection:	☐ 0	☐ 1	☐ 2	☐ 3	☐ 4
Parasitic infection:	☐ 0	☐ 1	☐ 2	☐ 3	☐ 4

Injuries:

	Spine deflections	Ampu-tations	Hemorr hages	Bruises	Emboli	Dermal lesions	Tears in fins	Scale loss	Pigment anomalies
Head	X		X	X	X	X	X		
Eye right	X		X	X	X	X	X	X	X
Eye left	X		X	X	X	X	X	X	X
Operculum left	X		X	X	X	X	X		
Operculum right	X		X	X	X	X	X		
Body left anterior		X	X	X	X	X	X		
Body right anterior		X	X	X	X	X	X		
Body left posterior		X	X	X	X	X	X		
Body right posterior		X	X	X	X	X	X		
Body dorsal	X	X	X	X	X	X	X	X	X
Body ventral	X	X	X	X	X	X	X		
Pectoral fin right	X								
Pectoral fin left	X								
Ventral fin right	X								
Ventral fin left	X								
Dorsal fin	X								
Anal fin	X								
Caudal fin	X								

Injury intensities: **0 = no, 1 = minor, 3 = medium, 5 = severe**.

☐ Cryo-preservation ☐ Photograph

Fish tank: ________ Fish ID: *Stick barcode here*

Injury evaluation by: __________ Protocol by: _______________

Chief investigator: Prof. Dr. J. Geist Assistant investigator: Dr. S. Beggel Designated veterinarian: Dr. H. Kliem

Figure S 1 Fish injury protocol to document the individual injuries of each test fish, cf. Mueller et al. (2017).